III. *The Skull of Ichthyosaurus, Studied in Serial Sections.*

By W. J. Sollas, *F.R.S., Professor of Geology in the University of Oxford.*

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[Plate 1.]

Over two centuries have elapsed since the remains of this strange Mesozoic analogue of the Dolphin first began to attract attention* and at least a century since they became the subject of serious scientific investigation, yet many points in the anatomy of the fossil still remain obscure, especially in the region of the head; and it was to elucidate these, that the present study, based on serial sections, was undertaken.

A remarkably well-preserved skull in our University Collection provided excellent material (text-fig. 1). It bore the label *Ichthyosaurus communis* (but does not, I think, belong to that species†) and was obtained from the Lower Lias of Lyme Regis. At some time or other it had been broken by clean fractures into four pieces, which had afterwards been cleverly cemented together so as to form an almost complete skull, the only parts missing being the supratemporal and articular bones, and two fragments of each of the lower jaws.

The length of the skull was 520 mm. and it was ground down by means of the apparatus described in a previous communication so as to furnish transverse sections at intervals of 1 mm. To reduce the labour of preparation it was separated into its four pieces by removing the cement; these were then mounted side by side in the same block of plaster and all ground down together. In this way 520 sections were obtained by 258 grindings; the amount of labour thus saved at this stage and in the subsequent processes of photographing the sections, tracing their outlines on glass plates, cutting out the wax stencils and building up the reconstruction in plaster was very great; yet even with all this economy the work took more than one year to complete. The grinding down was begun by Sir Archibald Geikie, who prepared the first section; the rest of the grinding, the photographing, and cutting out of stencils was done by my assistant, Corporal Hambidge; the tracing of outlines and the actual work of reconstruction by my wife and myself. For the accompanying illustrations I am indebted to the Museum Assistant, Mr. C. J. Bayzand.

The results obtained are, I think, commensurate with this expenditure of time and labour; nearly all the doubtful points in the cranial anatomy are now cleared up, important features hitherto unsuspected stand revealed, and the skull is presented to us as a whole, in a state of perfection scarcely surpassed by the recent preparations

* J. J. Baier, 'Oryctographia Norica,' 1708.

† It is, however, closely allied, so that I propose to refer to it as *I. communis*, var. *a*.

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exhibited in our Museums. There is, indeed, an incidental advantage which this skull possesses over those preparations, for its structure is revealed in detail by serial sections recorded on photographic plates, and from these a surer knowledge can be obtained than from a mere inspection of a recent skull.

It is an æsthetic pleasure to handle the skull unobscured by adventitious material and set free as pure form. It is form alone that engages the attention of the morphologist: the original material is of no account and the fact that it is lost in the process of grinding down, blown in dust out of the window, need not give rise to any regrets.

Those palæontologists who have acquired skill with the chisel have sometimes been betrayed by their zeal for established procedure into contemptuous allusions to the new method and have compared it with the "shooting of a sitting hen," yet, rightly regarded, this is to proclaim its true merit, for science aims at assured results and is anxious above all to eliminate sporting chances.

That which is fundamental in the new method is the process for obtaining serial sections at any desired intervals; the reconstruction in plaster is only one of the consequent results; and here I would take occasion to mention that the reconstruction of objects in wax from serial sections was first accomplished by BORN,* but many improvements in technique, rendering the reconstructions more permanent and exact, have been introduced in the course of these investigations.

History.—Sir EVERARD HOME,† to whom the honour is due of first making known the genus Ichthyosaurus, did not enter into any detailed description of the skull. For our first knowledge of this we are indebted to DE LA BECHE and CONYBEARE,‡ who analysed it with remarkable skill, correctly determining most of its constituent bones. They were least successful with the palate and the nomenclature of the bones of the lower jaw.

Subsequently CUVIER§ in a masterly essay confirmed and amplified the work of these authors; recognised additional elements, including the pterygoid, and redescribed the lower jaw. Our knowledge of the interior of the skull even then remained incomplete, so that when OWEN,‖ with a wealth of material at his command far exceeding that of any of his predecessors, approached the subject he was able to make important contributions to it, especially in the region of the occiput and palate.

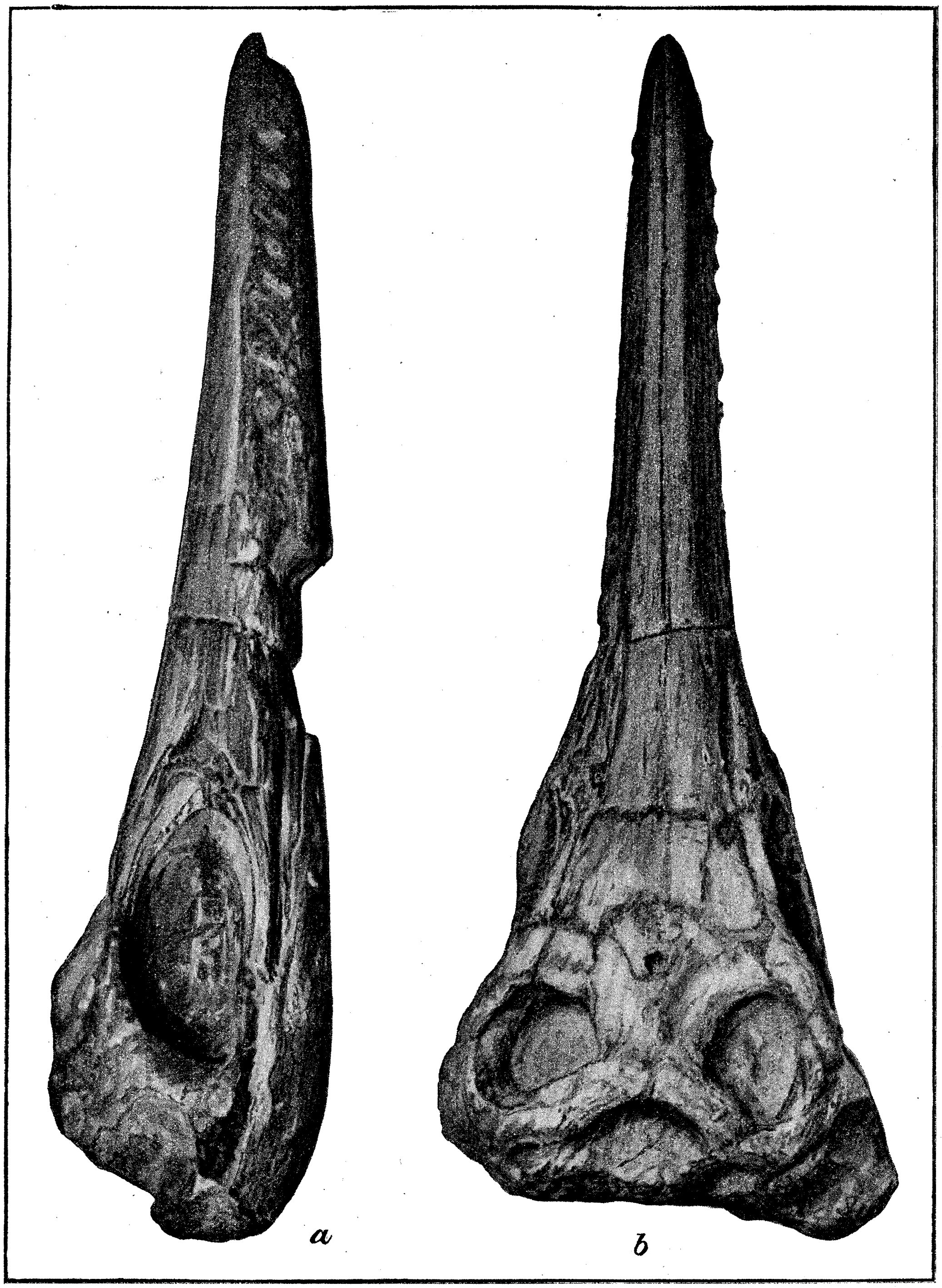
* G. BORN, "Über die Nasenhöhlen und den Tränennasengang der Amphibien," 'Morph. Jahrb.,' vol. 2, p. 577 (1876); see also KARL PETER, 'Die Methoden der Rekonstruktion,' Jena, 1906.

† 'Phil. Trans.,' 1814, 1816, 1818, 1819, 1820.

‡ H. T. DE LA BECHE and W. D. CONYBEARE, "Notice of a Discovery of a New Fossil Animal (Plesiosaurus), forming a Link between the Ichthyosaurus and Crocodile," 'Trans. Geol. Soc.,' vol. 5, p. 558 (1821); W. D. CONYBEARE, "Additional Notices on the Fossil Genera Ichthyosaurus and Plesiosaurus," *op. cit.*, Ser. 2, vol. 1, p. 103 (1822).

§ G. CUVIER, 'Recherches sur les Ossemens Fossiles,' Paris, vol. 5, Part II, p. 445, 4to (1824).

‖ R. OWEN, "Report on British Fossil Reptiles," 'Brit. Assoc.,' 1839, p. 86; and 'A Monograph of the Fossil Reptilia of the Liassic Formations,' Palæontographical Society, 1865, Part III, p. 83, 1865–1881.



TEXT-FIG. 1.—Lateral (*a*) and dorsal (*b*) view of the skull of *I. communis*, var. *a*, from which the transverse serial sections were obtained. (× $\frac{1}{3}$.)

On the other hand, the more brilliant COPE,* misled by an imperfectly preserved skull, confused the squamosal with the parietal: whence followed a series of remarkable errors; yet at the same time COPE made several valuable additions to our knowledge; he seems to have observed the columella cranii, and recognised the stapes, as well as the opisthotic or paroccipital of OWEN.

As morphological data accumulated, a clearer perception of taxonomic affinities was obtained. The first suspicion that the Ichthyosaurus might be a fish or an amphibian was soon dissipated, its reptilian nature was admitted and, though a place was at first sought for it near the crocodiles, it was not long before it was recognised as making a closer approach to the lizards. Then our knowledge of recent reptiles was enlarged by that closer acquaintance with the existing Hatteria (Sphenodon), which was afforded by GÜNTHER'S valuable memoir.†

Twenty years, however, elapsed before it was first pointed out by BAUR‡ that of all living reptiles Sphenodon is that which makes the nearest approach to the Ichthyosaur. BAUR indeed went so far as to speak of Ichthyosaurus as a specialised Sphenodon; an exaggeration, no doubt, but excusable when we consider how many and how close are the resemblances between the two forms.

It was the recognition of this fundamental similarity which later led LYDEKKER,§ whose work was mainly taxonomic, to correctly identify the palatine bones of Ichthyosaurus, which OWEN had wrongly interpreted as ectopterygoids; an identification afterwards welcomed and confirmed by BAUR.||

FRAAS,¶ however, with LYDEKKER'S work before him, repeated the old error and added others of his own.

The disposition of the otic bones has long offered a difficulty to observers, and the latest attempt to include them in a restoration of the back of the skull, which we owe to BAUER,** can scarcely be regarded as successful.

With the discovery of Ichthyosaurian remains in the Trias of California hopes were awakened of fresh light on the ancestry of the family; these, however, were disappointed, the type was already fully expressed at this period†† and the differences in detail as described by MERRIAM‡‡ are merely generic.

The marine Jurassic beds of Wyoming have furnished a nearly toothless Ichthyosaurus

* E. D. COPE, "On the Homologies of Some of the Cranial Bones of the Reptilia," 'Proc. Am. Assoc.,' vol. 19, p. 194 (1870).

† R. GÜNTHER, "Contribution to the Anatomy of Hatteria," 'Phil. Trans.,' vol. 157, p. 595 (1867).

‡ G. BAUR, "On the Morphology and Origin of the Ichthyopterygia," 'Am. Nat.,' 1887, p. 837.

§ R. LYDEKKER, 'Catalogue of Fossil Reptiles in the British Museum,' Part II, p. 5, 1889.

|| G. BAUR, "Die Palatingegend der Ichthyosaurier," 'Anat. Anz.,' vol. 10, p. 456 (1895).

¶ E. FRAAS, 'Die Ichthyosaurier der Süddeutschen Trias- und Jura-Ablagerungen,' Tubingen, 1891, 4to.

** F. BAUER, "Osteologische Notizen über Ichthyosaurier," 'Anat. Anz.,' vol. 18, p. 586 (1900).

†† "Primitive Characters of Triassic Ichthyosaurs," 'Bull. Geol. Soc. Am.,' vol. 14, p. 536 (1903).

‡‡ J. C. MERRIAM, "New Ichthyosauria from the Upper Trias of California," 'University of California Publications, Bull. Dept. Geol.,' vol. 3, p. 249 (1903–4), and vol. 5 (1910).

(Baptanodon) which has been admirably described and illustrated by GILMORE. The palate shows the vomers in their natural relations and the structure of the back of the head is more completely preserved and displayed than in any other specimen yet figured.*

By far the most important investigation since the time of CONYBEARE is that of ANDREWS† on Ophthalmosaurus, with which Baptanodon is closely allied, if not identical. This was based on separate but associated bones carefully extracted from the Oxford Clay of Peterborough. They are said to be almost as perfect as if they had just come from the macerating tub, and have been described with the same care as the bones of human anatomy. Our own results are in general accordance with those of Dr. ANDREWS, but the form of the bones in our restoration is often even better preserved than in his specimens, and their relative position has for the most part suffered little change.

Descriptive.—In the following account we shall base our descriptions on the bones of the right side of the head as this is rather better preserved than the left.

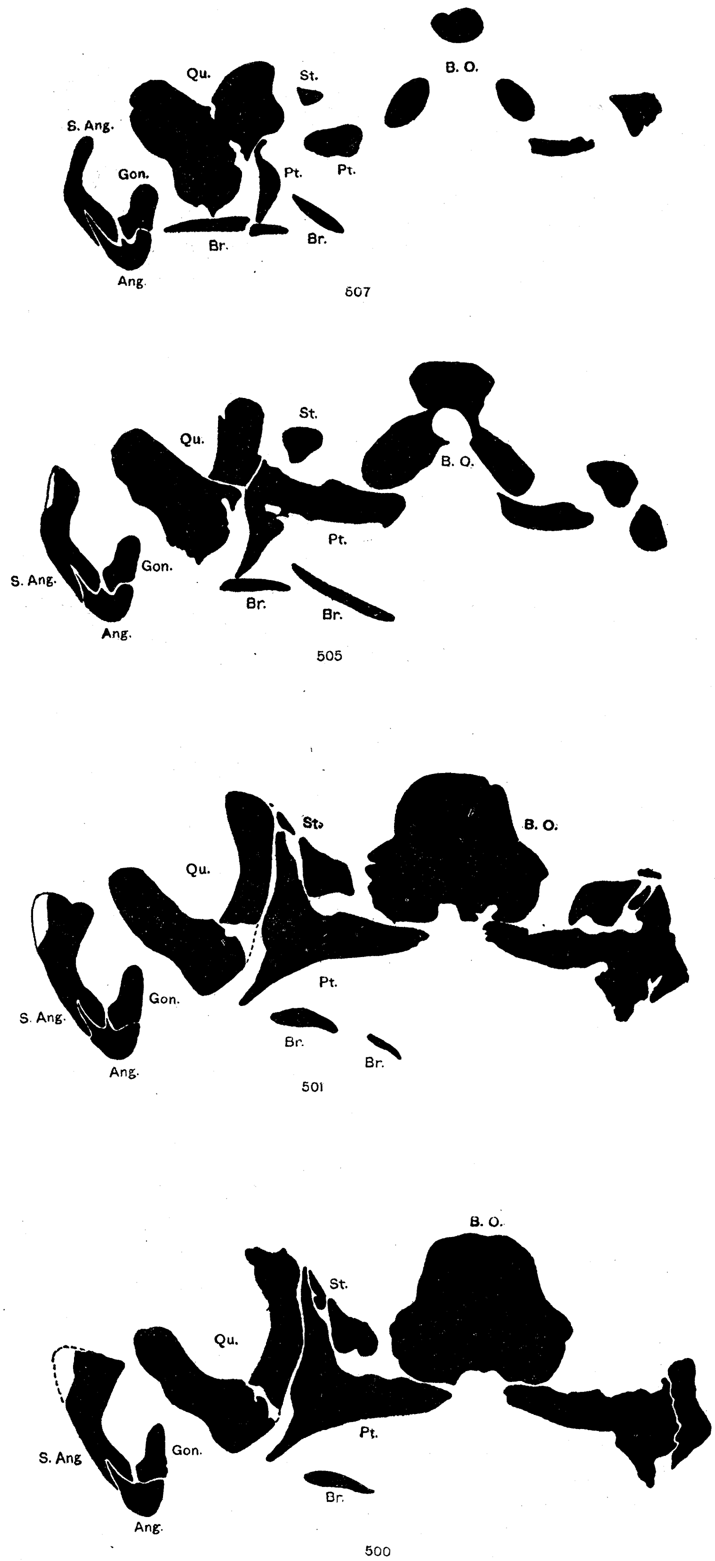
The Occipital Segment.—The occipital bones were almost certainly united by synchondrosis and set free by decomposition, so that when the skull was filled by a flow of mud into it, before petrifaction had begun, the supra-occipital and both the exoccipitals were carried forwards into the cranial cavity. The supra-occipital was carried farthest to the front, and now lies over the parasphenoid in the hinder part of the orbital region; the left exoccipital lies behind it, over the basisphenoid and between the columellæ cranii; and the right exoccipital, which has been least displaced, lies over the basisphenoid behind the right columella.

The Basi-Occipital (Plate 1, text-fig. 2, Secs. 476–507, and text-figs. 3 and 4).—This bone very nearly retains its original position, but it has been displaced to a slight extent by the action of pressure which has dislodged the adjacent opisthotic of the right side and driven it in under the posterior horn of the parietal. The chief effect on the basi-occipital has been to rotate its upper end through a small angle forwards.

The basi-occipital is a massive bone with a rather square outline, as seen from in front or behind (Plate 1, fig. 5*c*). Its posterior face presents two regions—an upper, which is rounded to form the broad gently convex occipital condyle, and a lower, which extends outwards and downwards on each side to form a pair of flanges which are swollen into large low oval prominences. There are thus three prominences separated by wide shallow grooves on the posterior aspect—a single median condyle above and a pair of lateral bosses below. As the flanges, of which the lateral bosses are the posterior termination, now rest on the pterygoids, we may distinguish them as the pterygoid flanges of the basi-occipital.

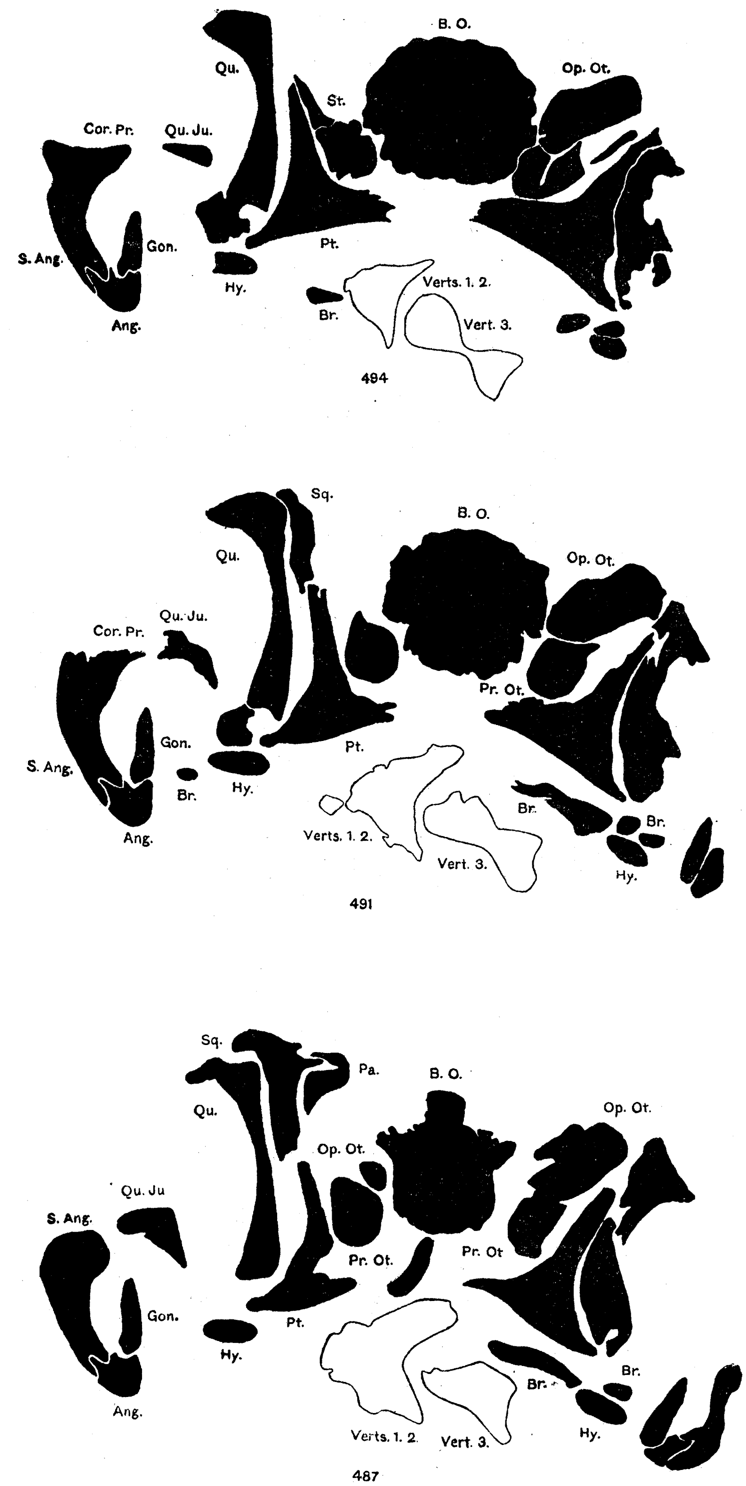
* C. W. GILMORE, "Osteology of Baptanodon," 'Mem. Carnegie Museum,' vol. 2, No. II, p. 77 (1904–6).

† C. W. ANDREWS, 'A Descriptive Catalogue of the Marine Reptiles of the Oxford Clay,' British Museum, Nat. Hist., 1910, Part I, p. 1.



TEXT-FIG. 2.—A selected series of the transverse sections. ($\times \frac{1}{2}$.)

(*Continued on* pp. 70–76.)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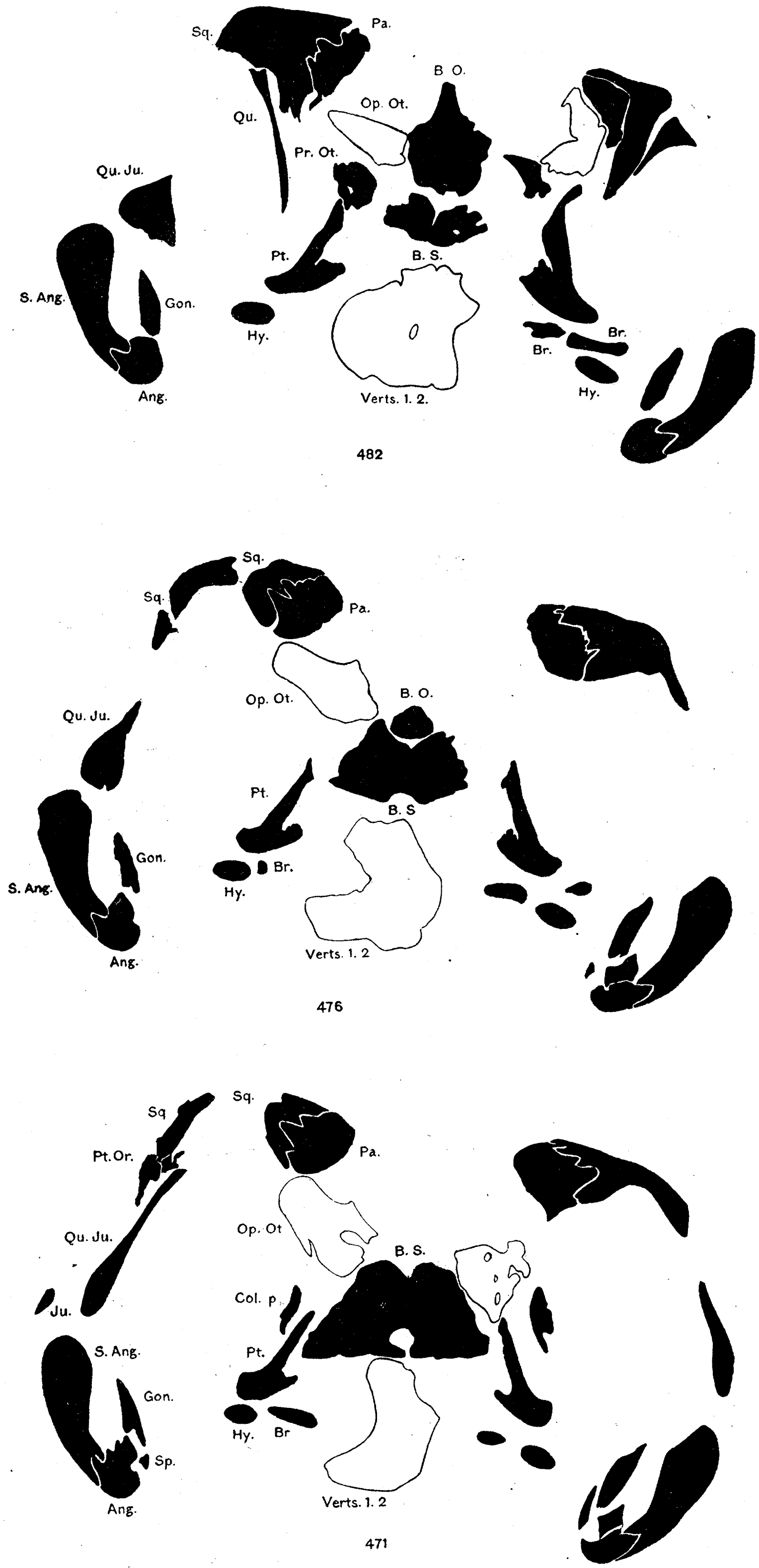
TEXT-FIG. 2 (2).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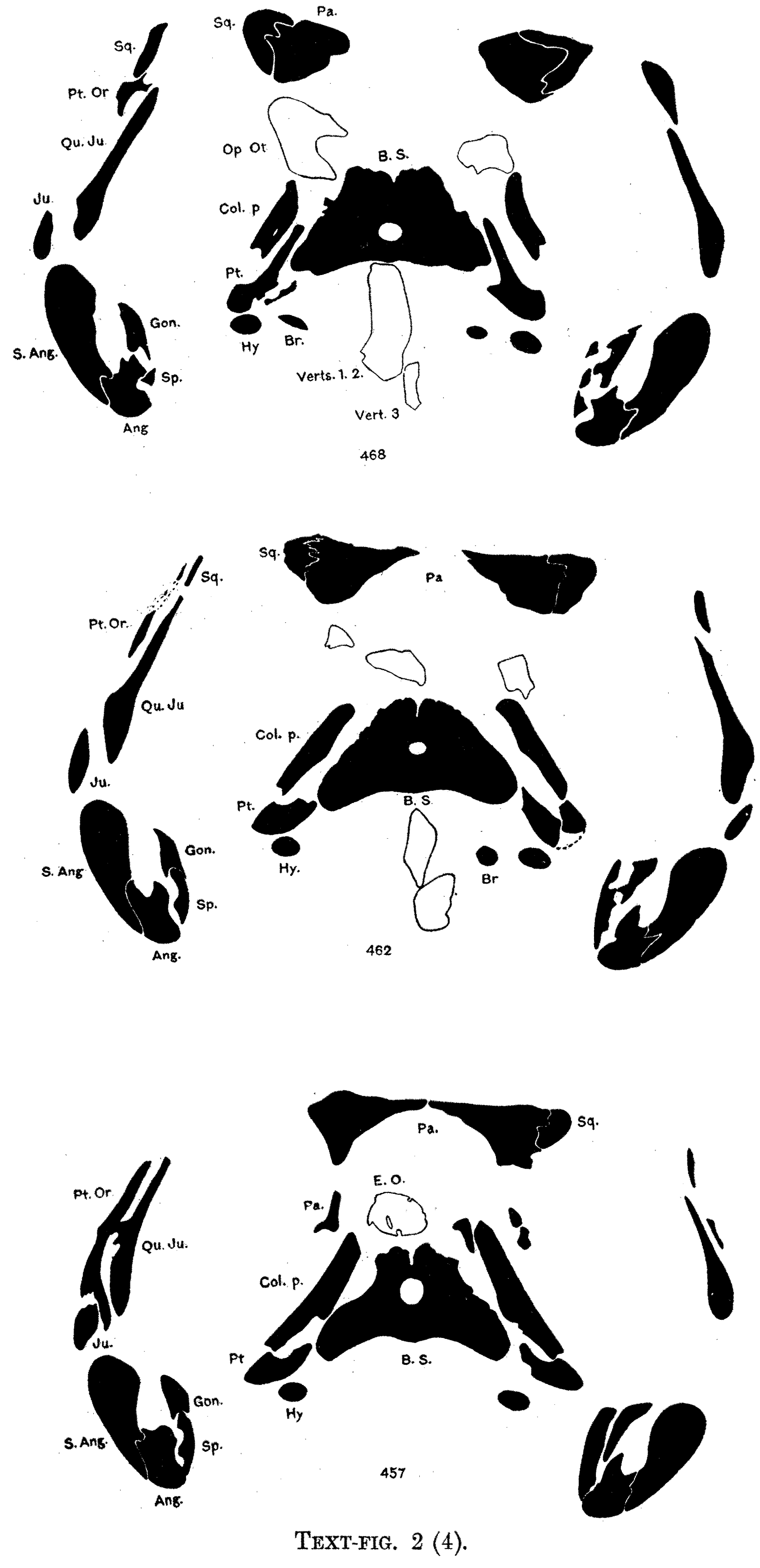
TEXT-FIG. 2 (3).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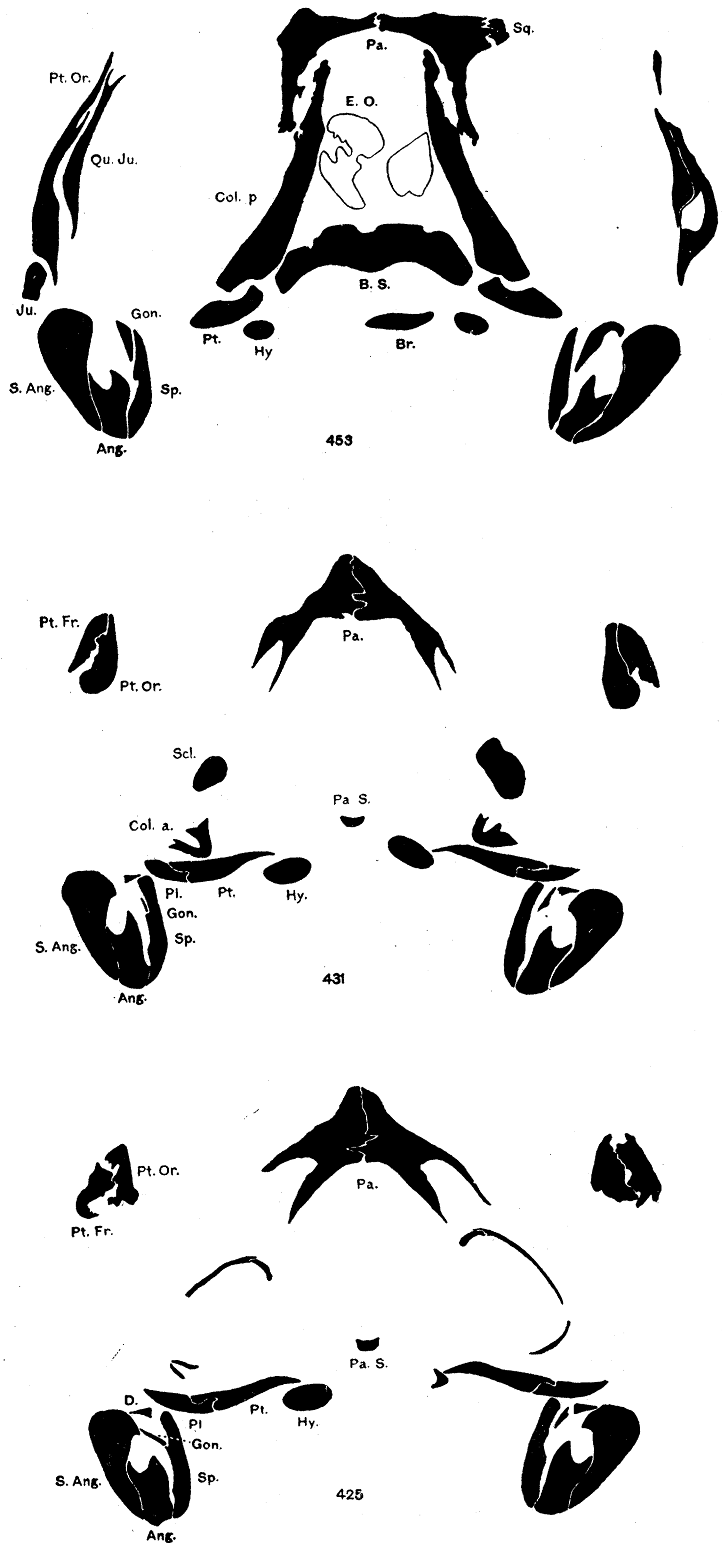
TEXT-FIG. 2 (4).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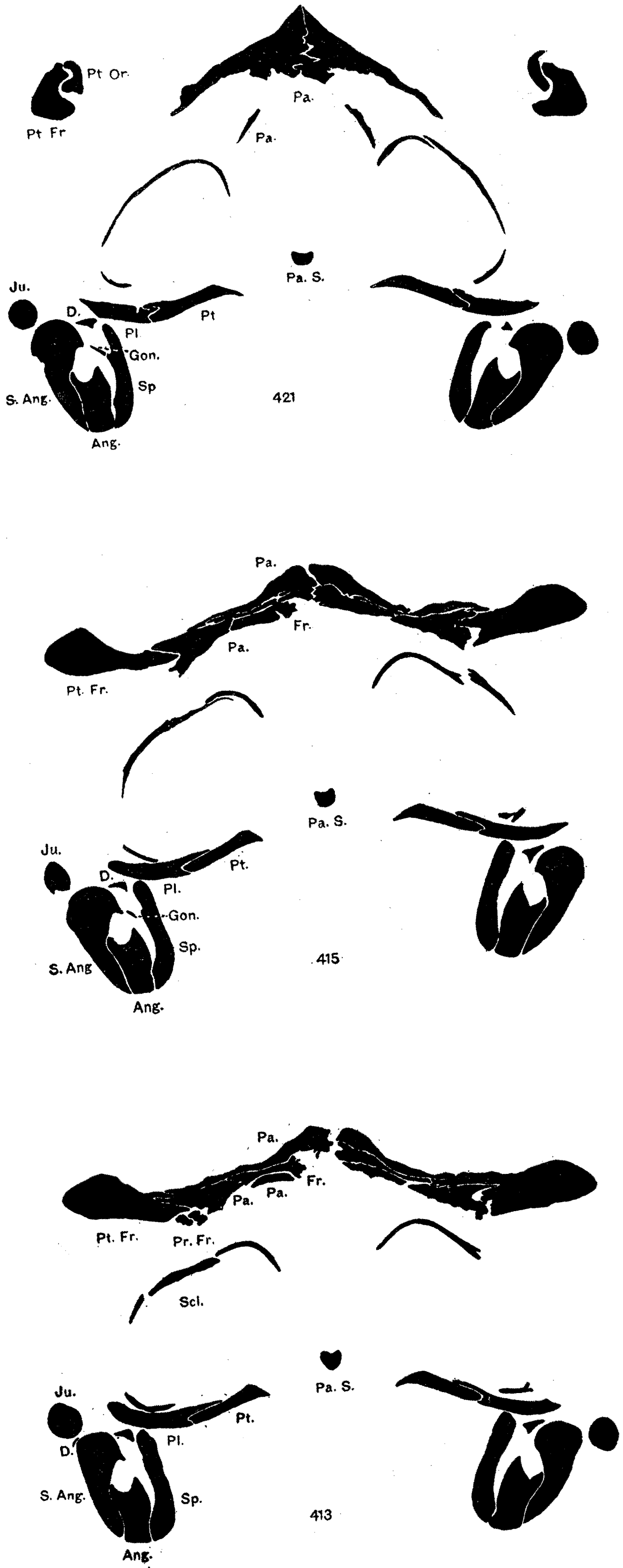
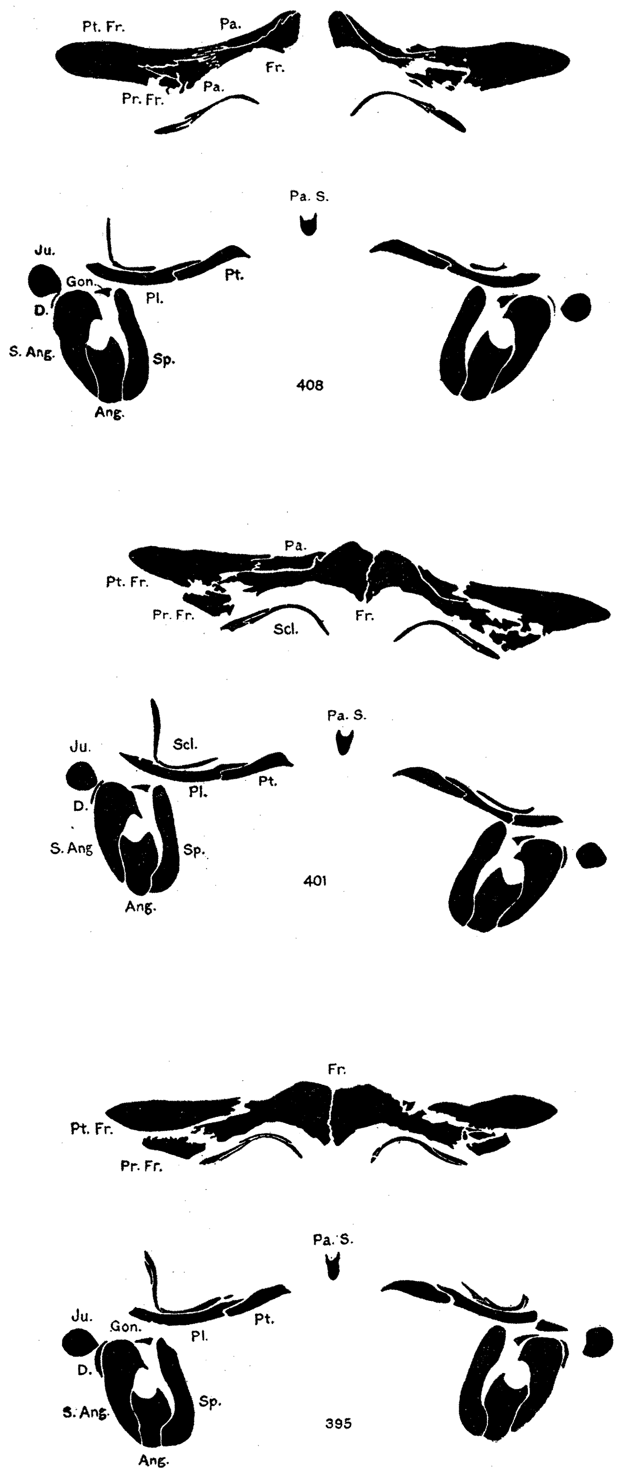
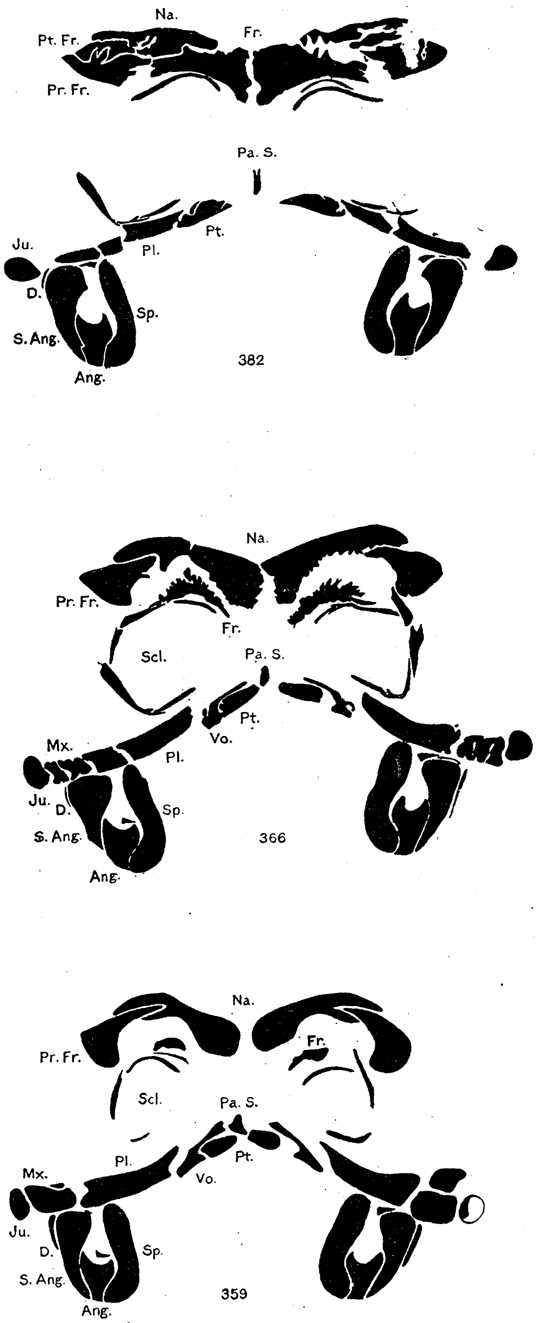
TEXT-FIG. 2 (5).



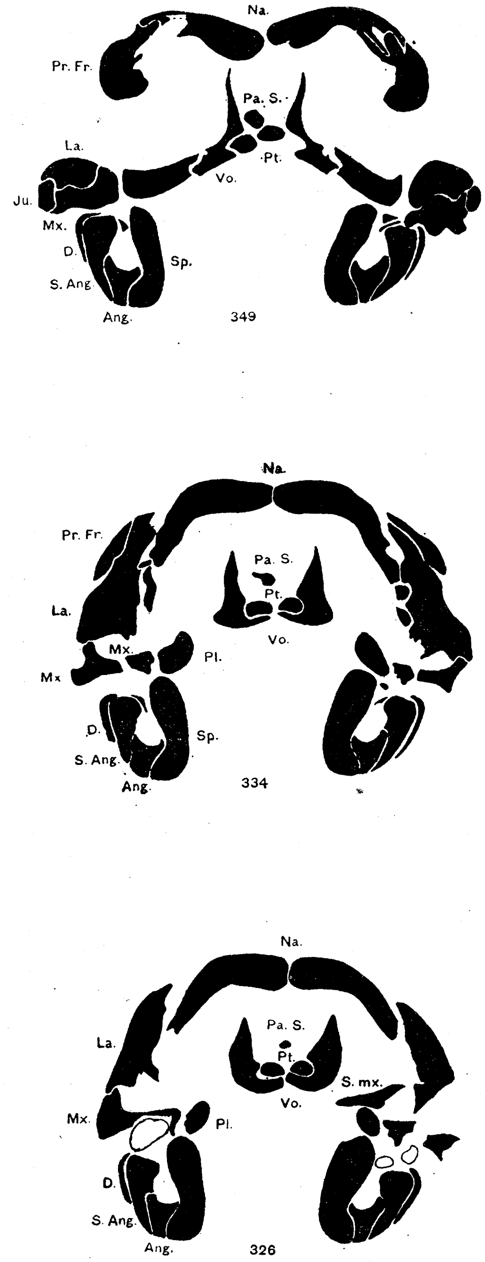
Text-fig. 2 (6).



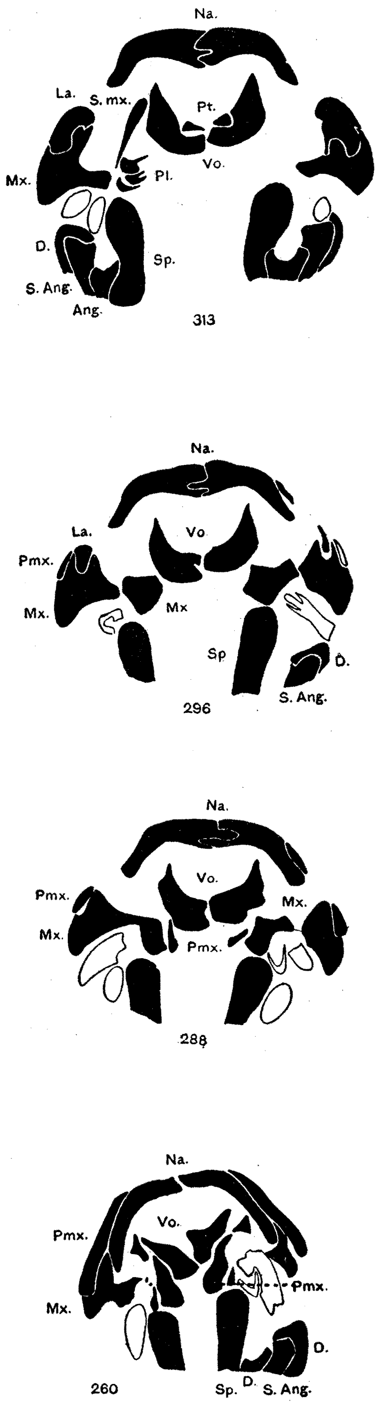
Text-fig. 2 (7).



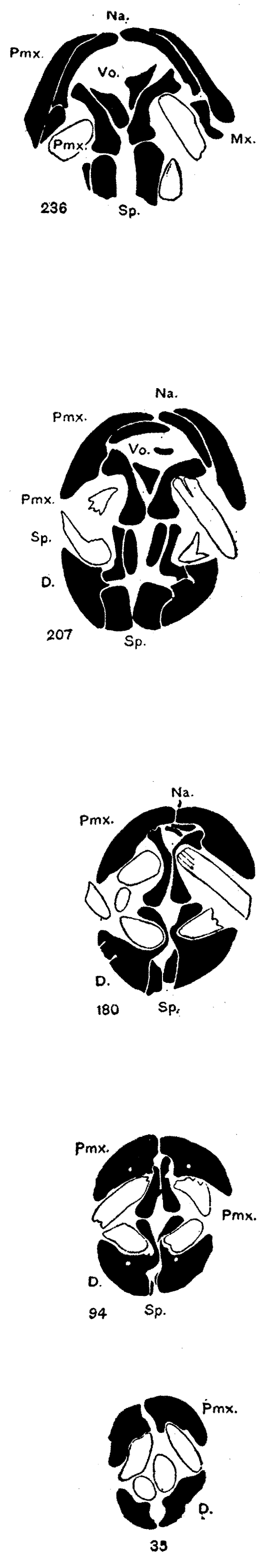
Text-fig. 2 (8).



Text-fig. 2 (9).



TEXT-FIG. 2 (10).



TEXT-FIG. 2 (11).

Seen from in front (Plate 1, fig. 5*c*), the bone rises in the middle in a large protuberant mass, almost escutcheon-shaped in outline, which culminates a little below the centre in a blunt conical or peg-like projection. This, since it fits into a corresponding groove at the back of the basisphenoid, may be termed the sphenoidal peg, or odontoid, of the basi-occipital. The central protuberance forms about one-half the thickness (antero-posterior length) of the bone, which expands all round its base to form the remaining part. Above, the central protuberance is produced into a strong steep-sided median ridge, and each of its upper lateral angles is also produced into a ridge, but less strongly marked and with more gently sloping sides; in the depressions between these ridges were seated the exoccipital bones.

Immediately below the exoccipital pits, and separated from them by the supralateral ridges, are two other depressions which may have lodged the postero-inner face of the pro-otics, the opisthotics articulating by their postero-inner end with the extremities of the supralateral ridges.

In a lateral view of the basi-occipital a rather irregular rounded ridge is seen running from the upper lateral ridges in front obliquely downwards and backwards towards the lower posterior bosses (Plate 1, fig. 5*d*); the lower lateral angles of the central protuberance are continued towards the same points and conjoin with the preceding to form the pterygoid flanges. These flanges are not truncated, as they are in some species of Ichthyosaurus, by the stapedial facet.

The Exoccipital (Text-fig. 7).—This resembles one side of an arch; it presents two regions—a lower and an upper; the lower, which is much the larger, was seated by a rounded roughened base in the upper concavity of the basi-occipital. From the posterior half of this lower part rises the smaller curved upper part, which articulates with the supra-occipital.

The concave inner face of the entire bone forms or contributes to form the outer wall of the foramen magnum.

The anterior face is excavated at the junction of the upper and lower regions by a deep notch which extends from side to side, and is continued on to the outer face; it doubtless corresponds, as suggested by ANDREWS* in the case of Ophthalmosaurus, with the jugular incisure of SIEBENROCK,† which in Sphenodon is converted into a complete foramen by a similar indentation in the basi-occipital and paroccipital, and gives passage to the vagus and glossopharyngeal nerves.‡

On the inner and outer surfaces, also situated at the junction of the upper and lower regions, are two other foramina, the openings of canals, which traverse the bone from

* C. W. ANDREWS, *op. cit.*, p. 6.

† F. SIEBENROCK, "Zür Osteologie des Hatteria Kopfes," 'S.B. d. K. Ak. d. Wiss. Wien.,' Math.-Naturw. Cl., 1893, vol. 102, p. 256.

‡ *Ibid.*, and G. OSAWA, "Beiträge z. Anatomie d. *Hatteria punctata*," 'Archiv f. Mikr. Anatomie,' vol. 51, p. 494 (1898).

side to side, and give exit, on the analogy of Sphenodon, to two branches of the hypoglossal nerve.

An isolated occipital bone in the Museum collection, obtained from the Lower Lias of Lyme Regis, resembles ours in all essential characters, presenting the same incisure and foramens, but it is more columnar in form, and the slope of its supra-occipital articular surface runs oblique to the long axis of the base. Its most interesting peculiarity, however, is the presence of two vertical channels crossing the anterior edge; one of them leads up to the smaller of the hypoglossal foramina, the other lies immediately below the larger of these foramina.

The Supra-Occipital (Text-fig. 8).—The supra-occipital, unfortunately not perfectly preserved, is a roughly triangular bone, strongly curved from side to side. In the middle of its base is an acute-angled incision, which, if it completed the foramen magnum above, would give to that opening the form of an ogee arch. On each side of the incision the ventral margin is much thickened and slightly excavated for articulation with the head of the exoccipital bone. Above this thickening on the posterior surface is a furrow ending in a notch on the lateral margin; this corresponds in position with the large foramen of unknown function described by ANDREWS in Ophthalmosaurus, and, as ANDREWS remarks, the furrow seems to mark off the epiotic from the occipital region of the bone.

The marginal face of the thickening is excavated from the anterior and posterior vertical semi-circular canals for the ear, as described by ANDREWS in Ophthalmosaurus.

The upper part of the lateral margins of the bone are furrowed by a deep groove which was applied to the posterior edge of the parietal. This, however, is only shown on the left side of our specimen, the right side having been damaged by decay.

The Opisthotic (Text-fig. 2, Secs. 471–494, and text-fig. 7).—The upper and outer end of this bone is a smooth-rounded oval process forming a sort of handle which we may call the quadrate head of the opisthotic; about the middle of the bone this rather rapidly thickens above and below, and at the same time is produced on each side, fore and aft, into a wing-like expansion; the more complicated mass thus formed is the larger part of the bone, and may be distinguished as the "body."

The anterior half of the body—the auricular moiety—is excavated above by a deep and wide recess which branches into two divergent furrows; these lodged part of the horizontal and the posterior vertical canals of the ear, as ANDREWS has shown in Ophthalmosaurus.

The posterior half is a solid process which articulated with the stapes and also probably with the basi-occipital; it may be named the stapedial process.

The upper surface of the bone is convex at the free end of the quadrate head, then concave from side to side as it passes into the body, which is traversed by a ridge running obliquely forwards and outwards. Where this ridge terminates in front is the projecting part of the auricular moiety which lodged a part of the posterior vertical semi-circular canal; the outer side of this projection meets the face of the head at a right angle, so that the anterior outer edge of the bone is cut away by a rectangular incision which appears to have fitted on to the edge of the posterior horn of the parietal bone; it may therefore be termed the parietal incision.

Both the opisthotic bones have been displaced from their original position, but that of the left side only slightly, so that it affords us important information in determining the relative position of the otic bones. The quadrate head of the opisthotic rests by its lower surface against the otic process of the quadrate and the ascending process of the pterygoid, thus recalling the position of the opisthotic in Sphenodon. By its anterior face it meets the squamosal and parietal bones, the incisura parietalis corresponding with the inner edge of the parietal. The body of the opisthotic rests by the medial extremity of its upper surface against the basi-occipital just above the pterygoid flange, and its stapedial process now overlies the medial end of the stapes.

The lower and inner or medial end of the body is opposed to a face of the pro-otic.

The general lie of the bone corresponds with that observed in other examples of Ichthyosauridæ, but among these there is great difference in detail, associated in some cases with other marked differences in the structure of the posterior region of the skull. Thus in the genus Ophthalmosaurus the otic process of the quadrate does not ascend so far as the superior angle of the squamosal, and consequently there is no contact between the quadrate and opisthotic bones. In this genus the parietal also seems to have been excluded from contact with the opisthotic. This is true also for Baptonodon.

When we come to accounts of the otic region in the genus Ichthyosaurus itself the differences become still greater. Thus both Cope and Fraas represent the opisthotic as articulating with the basi-occipital and exoccipital at the base, but as projecting freely, out of contact with any other bones, at the distal extremity. F. Bauer, in what appears to be a very artificial reconstruction, represents the opisthotic as extending horizontally from the side of the exoccipital to the top of the otic process of the quadrate, while Owen assigns to the bone called by him "paroccipital" a position which is usually occupied by the stapes.

The Pro-otic (Text-fig. 2, Secs. 487–494, and text-fig. 7).—This is a small rounded nodule of bone which in our specimen retains no recognisable traces of the semi-circular canals of the ear, such as Andrews has described in Ophthalmosaurus.

Very little is known about the position of this bone in the skull, and consequently there is much difference of opinion. Andrews leaves the question undecided; F. Bauer perches the pro-otic on the top of the opisthotic, leaning against the supra-occipital.

Frass has given two figures of a specimen of *Ichthyosaurus quadriscissus* in which the pro-otics lie below and slightly in front of the opisthotic; a position which other investigators do not seem to have considered probable. It is all the more interesting therefore to find these bones occupying a very similar position in our specimen. On the right side of the basi-occipital the right pro-otic now occupies the inferior lateral excavation of the front face, and on the left side the left pro-otic lies parallel with the fellow excavation of that side only a short distance away from it. In both cases the pro-otic lies below the opisthotic, and in one, that of the left side, the pro-otic is in close contact with the inferior inner end of the opisthotic, so that in reconstructions they adhere together.

The Stapes (Text-fig. 2, Secs. 494–507, and text-fig. 7).—This is a solid columnar bone expanded at each extremity, and extended horizontally from the base of the otic process of the quadrate on the one hand to the pterygoid flange of the basi-occipital on the other.

The stapes of the right side seems to be produced upwards in a long slender process which extends above the ascending process of the pterygoid to rest against the otic process of the quadrate.

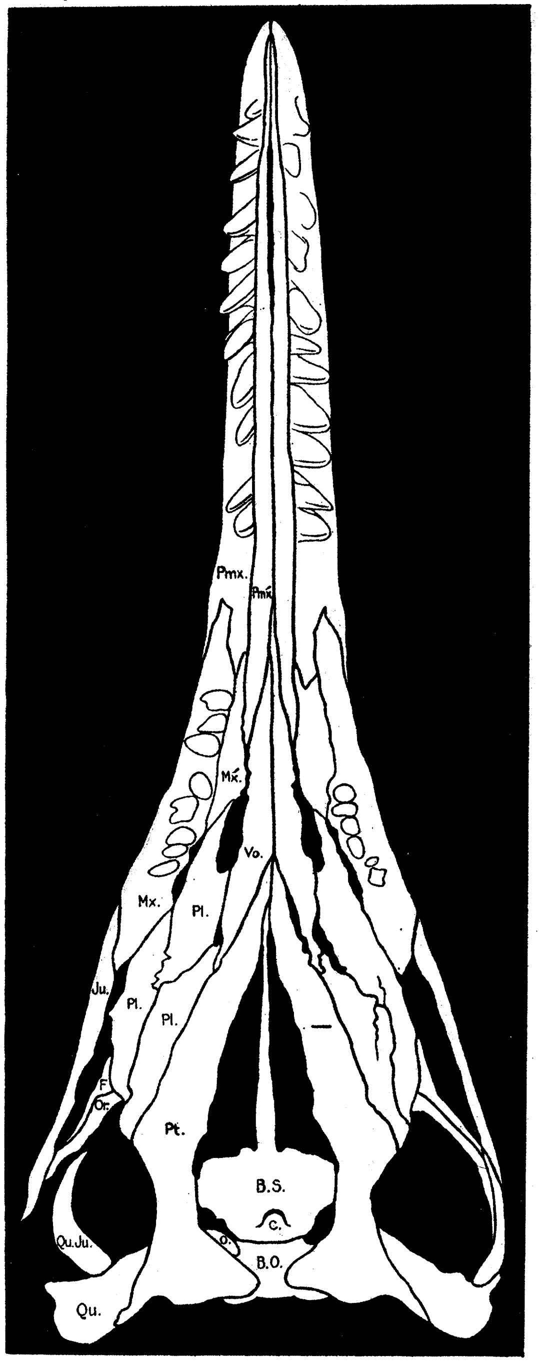
The Basisphenoid (Plate 1, figs. 5*a*, 5*b*, and 5*d*, and Text-fig. 2, Secs. 453–482).—The breadth of this massive bone exceeds both its length and height. Behind and above it swells into two prominent bosses or tuberosities (Plate 1, fig. 5*a*): the posterior moieties of these bound a broad and deep valley-like depression—the posterior fossa—within which is lodged the odontoid process of the basi-occipital: the anterior moieties are separated by a deep narrow cleft descending in the middle line to a depth of 6 mm. As it passes forwards this cleft becomes shallower and widens out at its termination between the posterior clinoid processes. Each of these processes forms the anterior termination of a well-marked ridge which runs backwards and downwards along the side of the bone as far as the posterior margin of the basipterygoid processes. This may be distinguished as the transverse crest of the basisphenoid.

The face of the basisphenoid descends vertically with a gentle backward inflection from the posterior clinoid processes, and ends in a transversely elongated median elliptical mass which rises on each side into a crescentic projection; these paired projections are the lower cylindrical processes of SIEBENROCK, as identified by ANDREWS in Ophthalmosaurus. Above them, in the centre of the anterior face, is the single* opening of the great carotid canal,† which passes obliquely through the bone to open on its lower face at a point removed from its posterior margin by about one-quarter of its total length. The posterior opening is thus situated considerably farther back than in Ophthalmosaurus. A median ridge rises behind the posterior opening, dividing the sulcus into which the opening is produced into two, an indication that the internal carotid arteries converged forwards to enter the canal side by side. The pituitary fossa is not sharply marked off from the anterior opening of the carotid canal.

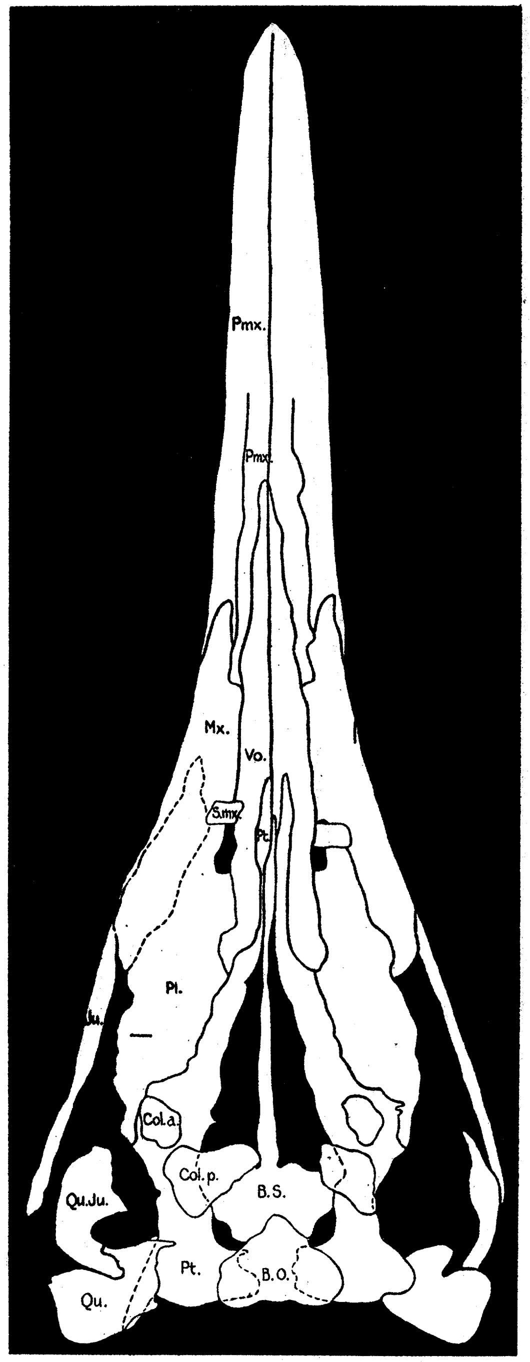
Midway between the lower cylindrical processes the lower edge of the bone is produced into the parasphenoid, the continuation of which backwards on the lower

* The carotid canal in the basi-sphenoid of Dicynodon is also single, SOLLAS and SOLLAS, 'Phil. Trans.,' B, vol. 204, p. 210 (1913).

† Mistaken by OWEN for the Eustachian canal; R. OWEN, 'Brit. Assoc. Rep.,' 1839, p. 87.



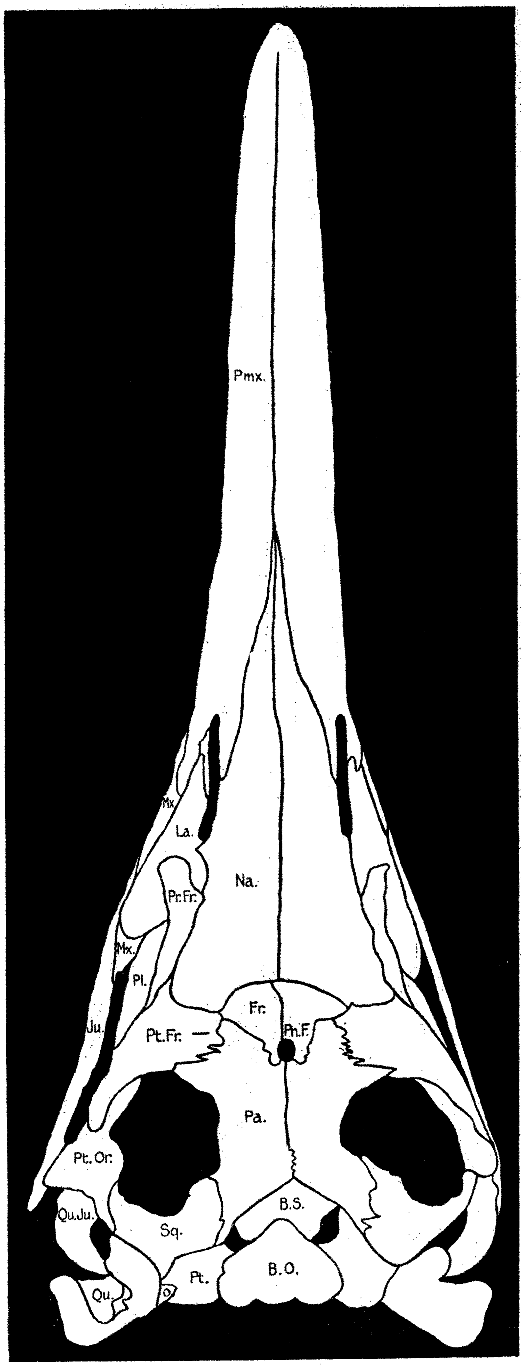
TEXT-FIG. 3.



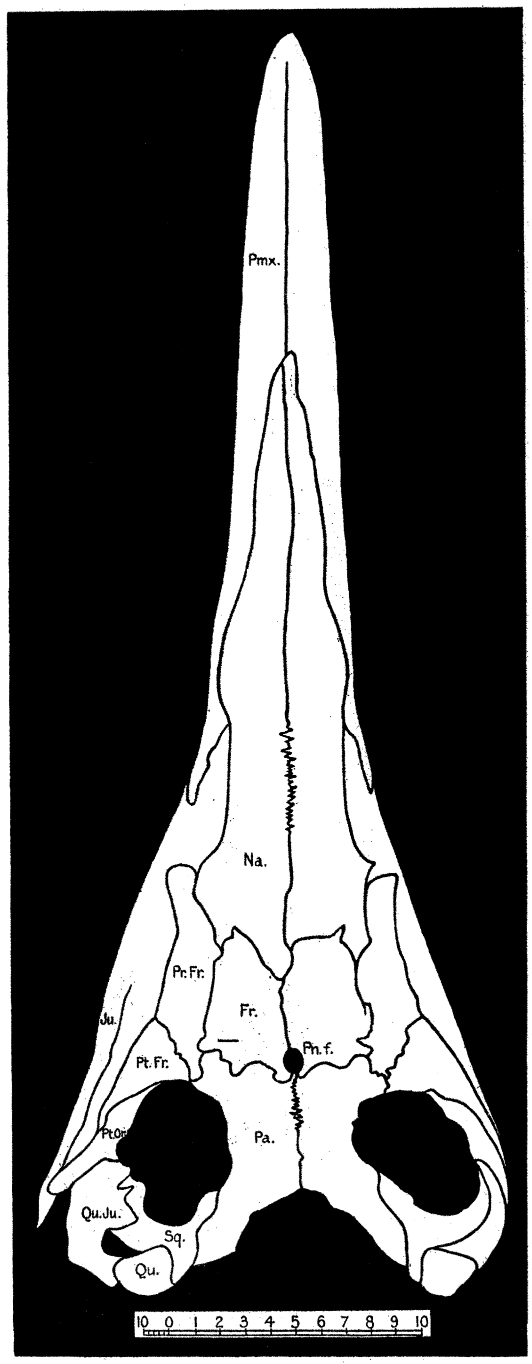
TEXT-FIG. 4.

TEXT-FIG. 3.—The floor of the skull (reconstructed from the sections) seen from below. (*F.* is used here for *Pt.Fr.*, *Or.* for *Pt.or.*, and the figure is reversed for comparison with the next, so that the right side represents the left side of the skull.)

TEXT-FIG. 4.—The same seen from above.



TEXT-FIG. 5.



TEXT-FIG. 6.

TEXT-FIG. 5.—Roof of the skull with some of the other bones seen from above. (This figure is reversed for comparison with the next.)

TEXT-FIG. 6.—The same seen from below. (The internal nares are omitted.) In figs. 3 to 6 the scale is the same (× $\frac{3}{10}$), and the right side of the figures has been slightly restored.

face of the basisphenoid seems to be indicated by a gently convex median ridge. None of the sections in this region show, however, any line of separation or other mark of distinction between the two bones.

The body of the basisphenoid, for the anterior two-thirds of its length, is produced below, outwards and downwards into two thick curved flanges, the basipterygoid processes (Plate 1, fig 5*a*, *pt.f*), which fit into the re-entrant angle of the pterygoids. Their upper surface is smooth, as if facetted. The anterior extremities of these processes are separated from the lower cylindrical processes by a well-marked notch.

Here it may be recalled that in the embryonic Sphenodon (stage R–S, HOWES and SWINNERTON) the basipterygoid process is similarly embraced by the pterygoid, and in precisely the same region, *i.e.*, below the columella. Further the articulation in this case is a true synovial joint with an independent cartilage—the *meniscus pterygoideus.** It may also be noted that above this articulation runs the VIth nerve (abducens) and the first branch of the Vth which farther forward divides into the nasal and frontal nerves.

Relative Position of the Occipital, Sphenoidal, and Otic Bones.—Owing to the displacement which has affected these bones the task of determining their original relation to one another is by no means an easy one. In order to obtain further information the bones in question were separately reconstructed, and an endeavour was then made to restore them to their original positions.

The pterygoid flanges of the basisphenoid were found to fit neatly into the re-entrant angles of the pterygoid,† and the basi-occipital fits into the posterior sphenoidal fossa by its odontoid peg. The anterior margin of the horizontal process of the right pterygoid‡ is now seen to underlie the posterior margin of the basisphenoid, its posterior margin being covered by the anterior half of the pterygoid flange of the basi-occipital.

This arrangement has a very natural appearance; the downward and forward slope which it gives to the basi-occipital throws the occipital condyle into its right attitude and confers on the exoccipitals just that forward inclination which they must have possessed in order to afford room for the supra-occipital in the posterior parietal angle. No other arrangement indeed seems to be possible, yet it leaves the opposed surfaces of the basisphenoid and the basi-occipital separated by a considerable interval. These surfaces, however, are roughened, as if for cartilage, and it seems natural to conclude that the intervening space was originally occupied by this substance.

Returning to our model, it will be seen that the horizontal process of the pterygoid forms the floor of a space bounded by the posterior region of the basisphenoid, the

* G. B. HOWES and H. H. SWINNERTON, "On the Development of the Skeleton of the Tuatara," 'Trans. Zool. Soc.,' vol. 16, p. 1 *et seq.* (1903).

† See p. 88.

‡ The left pterygoid was not reconstructed.

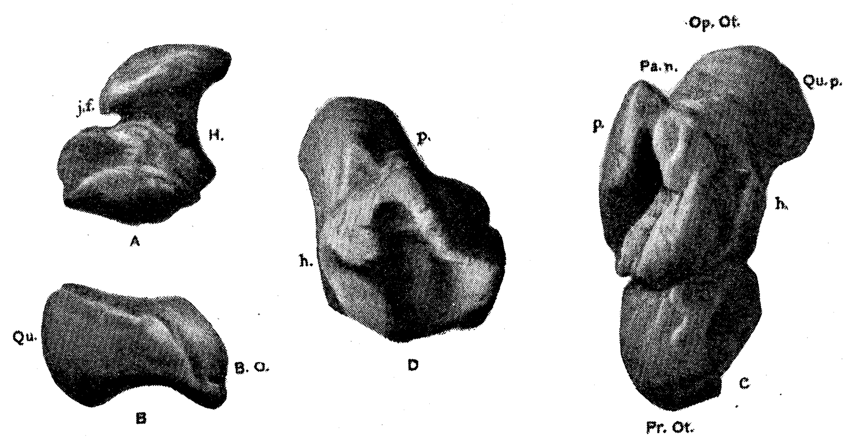
anterior region of the basi-occipital and the ascending process of the pterygoid. The surface of the pterygoids is smooth, except at the medial extremity of the horizontal process, which is frayed out. But the surfaces of the basisphenoid and basi-occipital bounding this cavity are roughened for cartilage, which here probably formed part of the otic capsule.

Further, on introducing the pro-otic into the cavity it falls neatly into place between the basi-occipital and basisphenoid, resting behind in the depression on one side of the odontoid escutcheon and in front against a depression between the oblique crest and posterior surface of the basisphenoid; very much in the same position as we have previously assigned to it. The opisthotic, articulated with a little flange-like process close to the outer end of the ridge bounding the articular depression for the exoccipital, stands above and behind the pro-otic. Finally, on superposing the supra-occipital upon the exoccipital its otic process (epiotic) is seen to lie above and in front of the excavation for a part of the posterior vertical semi-circular canal in the opisthotic bone.

The cavity with which we started is thus partly filled up, partly bounded by the otic bones; in front and on the outer side, where it now remains widely open, it was originally, no doubt, bounded by a cartilaginous wall, and the central space thus surrounded was large enough to have contained a sacculus proportionate in size to the other elements of the aural apparatus.

The stapes extends from the pterygoid flange of the basi-occipital to the quadrate, overlies the horizontal process of the pterygoid, and is overlaid by the posterior end of the opisthotic, which for the greater part lies in front of it.

This interpretation is in general harmony with that already given by ANDREWS for Ophthalmosaurus, which it thus completes and confirms. That there is room for



TEXT-FIG. 7.—A. Right exoccipital seen from the front; *j.f.*, jugular notch; H, on a line with the foramina for the twelfth nerve. B. Left stapes seen from behind; *Qu.* articular surface for quadrate, *B.O.* for basi-occipital. C. Right opisthotic and pro-otic; *p.* posterior and *h.* horizontal semicircular canal (the latter concealed); *Pa.n.*, parietal incisure; *Qu.p.*, quadrate head. D. Left opisthotic: in this the horizontal semicircular canal (*h*) is visible. ($\times \frac{1}{2}$.)

considerable differences in detail connected with the difference in genera will appear from the next section.

Isolated Basi-Occipital and Basiphenoid Bones (Plate 1, figs. 1–4).—After studying the reconstructed skull, fresh light was thrown on the relations of the basi-occipital and basiphenoid by some isolated examples of these bones collected at Lyme Regis and preserved in the University Museum.

Of the basi-occipital there are fifteen specimens differing in age and species. They range from minute and no doubt young forms, 2 cm. in breadth, up to large mature forms, nearly 9 cm. in breadth, and though differing considerably in detail they agree in general character.

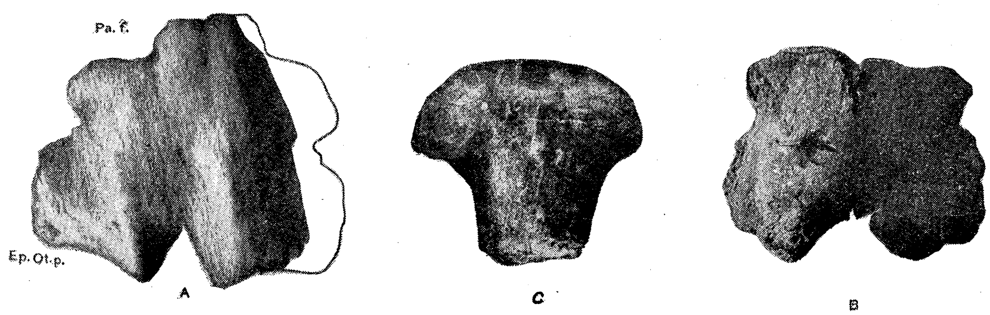
The youngest (Plate 1, fig. 1) is a little bone of which the features are indicated rather than expressed. The anterior and posterior surfaces meet in a sharp edge; the sessile condyle and neural ridge are but feebly marked; the articular depressions for the exoccipital and pro-otal bones are the merest dimples, and there is no discernible facet for the stapes. On the other hand, the odontoid process is well developed and terminates in a sharp point.

In contrast to this we may select one of the most completely differentiated forms (Plate 1, fig. 4), which is considerably larger (6·2 cm. in breadth) than that of our reconstruction. The condyle is seated on a massive pedicel, and bears a central ligamentous pit; the exoccipital articular depressions are well marked and bounded by a sharply-defined ridge; below them, close to the margin of the bone on each side, is a smooth facet—opisthotic facet; anterior to these is a depressed surface roughened for cartilage—pro-otic region—and on the margin, truncating the antero-lateral angles, are large vertical cup-shaped or conical facets for the stapes. In the middle line the neural gutter is closed in front by the escutcheon, from which the strongly-developed odontoid process projects, and in the middle line below this, surrounding its root, is a rather deep concentric furrow. The differences between this specimen and ours are marked, the most obvious being the truncation of the antero-lateral angles by the stapedial facets; another almost equally striking is the difference in inclination from the vertical of the posterior surface; in our specimen this does not exceed 45°, in the one under discussion it is nearly 90°, so that, excluding the condyle, the posterior has become the inferior surface. It is in this important feature that the different examples in our collection show the widest variation.

The isolated basisphenoids, which are only four in number, also agree in essential features but differ in detail.

The oblique crest delimits an anterior face formed of compact bone with a smooth lustrous surface, from a posterior region which for the most part is irregularly pitted for cartilage. The carotid canal opens slightly obliquely on the anterior face, and the sides of the opening are rounded—pillar-like; at the base of these pillars, truncating them where we should expect to find the lower cylindrical processes, are two oval, sharply-marked depressions (*d.*, Plate 1, fig. 3); the origin of the parasphenoid lies between them, below their point of contact.

The pterygoid flanges are produced a little beyond the anterior margin at the



TEXT-FIG. 8.—A. Supra-occipital bone of the reconstruction. *Pa.f.*, articular surface for the parietal; *Ep.ot.p.*, epiotic process, with impressions of posterior semicircular canals. B. Supra-occipital bone of an Ichthyosaurus from Lyme Regis for comparison. C. Cast taken from the inner surface of B, showing the posterior part of the lobes of the cerebellum. ($\times \frac{1}{2}$.)

base of the bone, and bear a facet on their outer face for articulation with the pterygoid.

The smallest (and youngest) of the basiphenoid bones is nowhere pitted for cartilage, presents no oval impressions nor lower cylindrical processes, and does not bear a smooth facet on the side of the pterygoid flanges. A marked ridge corresponding with the oblique crest and a V-shaped fossa are already developed as essential characters.

If now we select our basi-occipital and basiphenoid bones in pairs—*i.e.*, of corresponding size—and approach the posterior surface of the basisphenoid to the anterior surface of the basi-occipital, we shall find that in all cases they fit together with remarkable exactitude, the odontoid surface of the one corresponding with the V-shaped fossa of the other; and that this represents the natural relationship of the two bones is confirmed by one specimen in our collection which presents them still united together in this manner.* In this specimen the anterior margin of the base of the basi-occipital is very nearly conterminous with the posterior margin of the base of the basisphenoid, and the lower surfaces of the two bones flow together in an almost continuous curve, so that they have evidently not suffered from displacement, but retain their original relations.

With this fact established, the position we have assigned to the otic bones becomes confirmed, and it is of great interest to observe how closely the whole structure of this region of the skull corresponds with that in the Stegocephalian, *Lyriocephalus*

* It is interesting to find a similar character already in existence among the Stegocephalia. Thus, in describing Loxomma—which, however, possesses only one occipital condyle—WATSON states that "the back of the basi-sphenoid is recessed for the anterior end of the basi-occipital." (D. M. S. WATSON, "The Larger Coal Measure Amphibia," 'Mem. Manchester Lit. and Phil. Soc.,' vol. 57, p. 1 (1912)).

euri, as described by WIMAN.* There we find an epipterygoid, lamellar near the base, rod-like higher up, rising from the pterygoid just in front of the ascending process, and approaching the parietal; behind the epipterygoid, just under the ascending process of the pterygoid, lies the pro-otic, and behind the pro-otic is the stapes. All this is remarkably like what we find in Ichthyosaurus, and the opisthotic, although united with the exoccipital, harmonises in position.

The Parasphenoid.—This is a long slender rod-like bone which runs forwards from the basisphenoid in the middle line of the base of the skull for a distance of 127 mm. (Text-fig. 2, Secs. 326–431, and text-figs. 3 and 4.) For the greater part of its course it lies between the orbits, commencing on a line with the posterior margin of the orbit, and terminating 20 mm. in front of the anterior margin.

In its progress it undergoes frequent changes of form, as revealed in cross-sections. The most posterior sections are elliptic in section, the major axis being horizontal; passing forwards, the dorsal convexity disappears, and is replaced by a widely open groove; this deepens, and the major axis becomes vertical; then the bone is still more compressed, so that it acquires the form of a lath standing on its edge; the groove disappears (Sec. 377), and the section, diminished in size, again becomes an ellipse with a vertical major axis; later it grows larger again, then diminishes, and finally dwindles away at Sec. 322.

It is in the middle of its course, between the orbits, that the bone bears the groove on its dorsal edge (Secs. 432–378), and this interorbital groove no doubt received the lower edge of an interorbital cartilaginous septum.

In the anterior part of its course the parasphenoid approaches the rod-like termination of the pterygoid bones, lying just above them in the middle line, but it does not present any definite pterygoid facets such as are seen on the parasphenoid of Ophthalmosaurus. The parasphenoid in our specimen of Ichthyosaurus is a much slenderer bone than that of Ophthalmosaurus, but there is a close resemblance in general form.

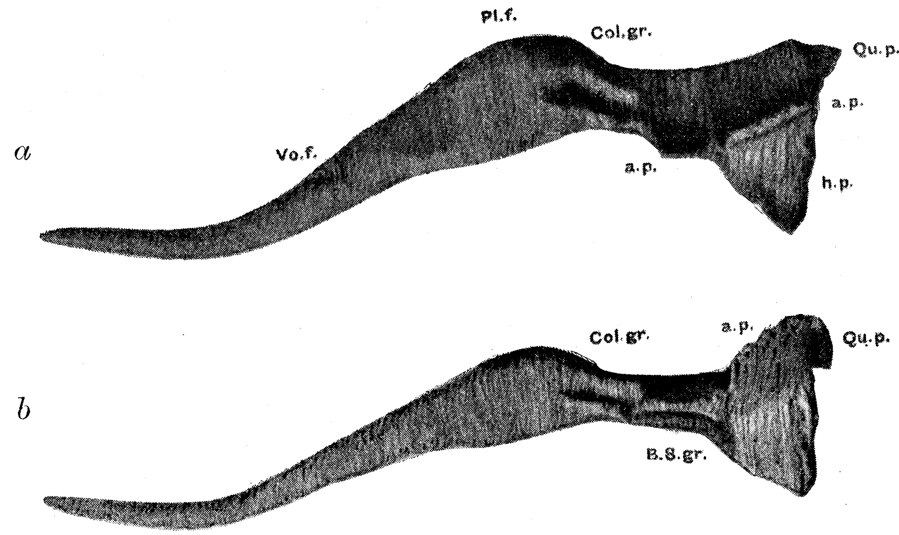
The Pterygoid (Text-fig. 2, Secs. 313–507; and text-figs 3, 4, and 9).—The pterygoid bones extend from the quadrate as far forwards as the mid-region of the internal nares, attaining a length of 220 mm., or 0·4 of the length of the skull.

For the greater part of the middle of their course they are almost flat, rather thin, plate-like bones, lying almost horizontally, but with a slight tilt upwards towards the middle line and towards the snout. They are thickest at the outer margin, where they articulate with the palatines and thin off towards the inner margin, which is a rather sharp edge.

In front of the broad basisphenoid, where they are widely separated by the great pterygoid flanges of that bone, they slowly converge till they meet in the middle line; at the same time they diminish in breadth, and are finally reduced to mere rounded

* C. WIMAN, "Ueber die Stegocephalen aus der Trias Spitzbergens," 'Bull. Soc. Geol.,' Upsala, vol. 13, p. 12 (separate copy) (1912).

rods, each of which lies in a trough-like recess excavated in the apposed vomers. These rods are at first almost fully exposed on the lower surface of the palate (text-



TEXT-FIG. 9.—Right pterygoid; *a*, dorsal; *b*, interior lateral view. ($\times \frac{1}{2}$.)

fig. 3), but later they become increasingly concealed by the lower limb of the vomers, and cease to be visible soon after entering the region of the internal nares, though they still continue their course above the vomers (text-fig. 4) for some distance farther, terminating finally in blunt points.

The pterygoids attain their greatest breadth (30 mm.) where they form, together with the posterior extremities of the palatines, the most posterior portion of the floor of the orbit; traced backwards from this, just in front of the basisphenoid, they become narrower and thicker, supporting the large plate-like bones of the columella cranii, which stand in a groove excavated on their upper surface (text-fig. 2, Secs. 457–468). The columella cranii, to be described directly, form the inner wall of the skull, and where they terminate behind a stout plate-like process rises upwards from the middle line of the pterygoid (text-fig. 2, Secs. 468-494), and, continuing in the same direction as the columella, but overlapped by it on the outside, takes on its function. We will call this the ascending process of the pterygoid.

The ascending process rises at first only as far as the top of the posterior wing of the columella cranii, but soon after passing this it increases suddenly in height to meet the descending process of the squamosal, which is inserted between it and the plate-like pterygoid process of the quadrate. Except where the process of the squamosal intervenes the pterygoid process of the quadrate is applied to the outer face of the ascending process of the pterygoid.

With the sudden increase in height of the ascending process other changes are associated. At first this process enters the body of the bone by a sweeping curve on the outer side, but on the inner side abruptly, forming with it an acute re-entrant angle in which is lodged the pterygoid flange of the basisphenoid. Almost as soon, however, as the process has attained its full height the re-entrant angle disappears, and is replaced by a flowing curve like that on the outer side, but with a smaller radius.

At the same time the whole bone increases in size, and the inner margin of the thickened body is produced into a massive horizontal plate which extends increasingly towards the middle line, below the basi-occipital, as it continues backwards.

In the present state of the skull the basi-occipital rests by its pterygoid flanges upon the horizontal processes of the two pterygoids, and the interval between the ends of these processes is bridged over by the medial concavity excavated in the base of the basi-occipital between its flanges.

The pterygoid is continued by its outer marginal region still farther backwards, and at the same time outwards and downwards, ending at last in a curved, almost vertical, plate which is closely applied to the inner face of the articular head of the quadrate. This may be termed the descending process of the pterygoid. Its lower margin is continuous with the outer margin of the more anterior part of the quadrate.

In the angle between the ascending and horizontal processes of the pterygoid at their posterior termination is a well-marked groove which seems to stand in some relation to the pro-otic and stapes.

The Columellæ Cranii (Text-fig. 2, Secs. 431–471, and text-figs. 4 and 11).—The columellæ are stout plate-like, rather rudder-shaped bones. The base is convex from side to side and rests in a corresponding concavity of the pterygoid. In front the columellæ rise on each side of the basisphenoid like props (the stem of the rudder) 65 mm. high, towards the roof of the skull and pass inside the descending walls of the parietal by which they are overlapped for a considerable distance. Originally the overlap was probably accompanied by suture, but the bones are now separate and slightly displaced. They were not fused together as COPE supposed. The lower half of the anterior stem is continued backwards as a stout lamellar wing which fails to reach the parietal, but overlaps the ascending process of the pterygoid. The length of the columella, fore and aft measurement, is 26 mm.

The presence of a columella cranii in Ichthyosaurus was first pointed out by COPE,* subsequently a good example was described and figured by Dr. A. SMITH WOODWARD,† and it was this which led BAUR to assert that the columella of Ichthyosaurus has the same form and connections as that of Sphenodon. The resemblance is certainly very close, especially if we restrict our attention to Dr. SMITH WOODWARD'S example, but there are marked differences, *e.g.*, in Sphenodon the expanded base of the columella is not connected solely with the pterygoid; for even more than one-half of its course it is suturally united with the pterygoid expansion of the quadrate, while in Ichthyosaurus the columella is separated from the quadrate by a considerable interval. This difference may be attributed, however, to the excessive growth forwards of the

* E. D. COPE, 'Proc. Am. Assoc.,' vol. 19, p. 233 (1870).

† A. SMITH WOODWARD, 'Proc. Zool. Soc.,' 1886, p. 405, Plate 3.

pterygoid expansion in Sphenodon. In our specimen the upper end of the columella shows no such posterior expansion as occurs in Sphenodon but, on the contrary, tends to taper away.

Where the columella terminates in front, another bone, now separate from it, makes its appearance. If it were connected with the columella it would be regarded as an anterior prolongation of the base of that bone. The existing separation may be due to *post-mortem* decay, but provisionally we may distinguish this bone as the anterior columella. If the posterior columella is to be homologised with the alisphenoid, then the anterior columella might represent the orbitosphenoid.

The anterior columella (text-fig. 2, Sec. 431) has the form of an angle plate or the rounded corner of a hollow cube; running along the end of each limb is a longitudinal groove. It is seated by its lower limb conformably on the flat surface of the pterygoid, and ends immediately behind the sclerotic skeleton of the eye.

The anterior columella contributes so little to the side wall of the skull that we are tempted to regard it as serving for the attachment of a muscle, possibly the retractor muscle of the eye. This is the most important of the ocular muscles in Sphenodon and in that reptile it rises in the posterior angle of the orbit from the base of the columella.*

It would seem that in Plesiosaurus the columella cranii presents an interesting resemblance to that of Ichthyosaurus. ANDREWS† describes it as rising from the upper surface of the pterygoid opposite the junction of this bone with the basisphenoid, and states that the base of attachment is very long from before backwards and extends for a considerable distance along the upper edge of the quadrate process of the pterygoid.

The Palatine (Text-fig. 2, Secs. 313–431, and text-figs. 3 and 4).—OWEN's mistaken identification of this bone with the ectopterygoid seems to have passed unchallenged by succeeding authors until LYDEKKER, recognising the essential similarity in structure of the palate in Ichthyosaurus and Sphenodon, indicated its true nature.‡ BAUR confirmed LYDEKKER's view, which, as it is the only one consistent with the disposition of the bones about the internal nares, is now generally accepted.§

The palatine arises posteriorly at the outer margin of the pterygoid on a line with the back of the orbit, the face of the basisphenoid and the anterior end of the great columella (Sec. 447); it thus extends much farther back than in Sphenodon. In Sphenodon, it is true, the palatine ends about on a level with the back of the orbit, but this is far in advance of the basisphenoid and the columella. For the greater part of its course it is a plate-like bone united with the pterygoid by a more or less

* G. OSAWA, 'Archiv f. Mikros. Anat.,' vol. 51, p. 536 (1898).

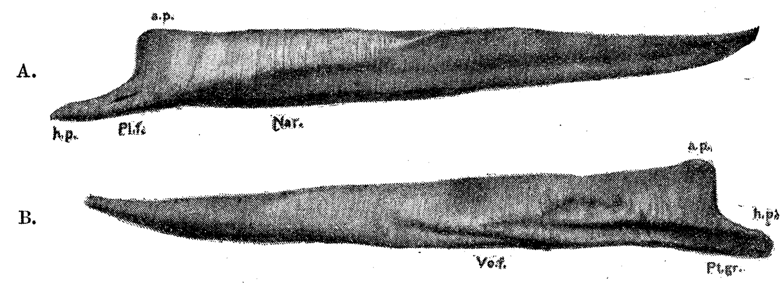
† C. W. ANDREWS, "On the Structure of the Plesiosaurian Skull," 'Quart. Journ. Geol. Soc.,' vol. 52, p. 246 (1896).

‡ R. LYDEKKER, 'Catalogue of Fossil Reptiles,' British Museum, Part II, p. 5.

§ G. BAUR, "Die Palatingegend der Ichthyosauria," 'Anat. Anz.,' vol. 10, p. 456 (1895).

complicated suture. At first very minute, it grows broader as it proceeds, until the vomer is introduced between it and the pterygoid (Sec. 380). At this point the single complex palatal plate formed by the pterygoid, palatine, vomer, and maxilla, with, in this region, the jugal as well, attains its greatest breadth. The palatine bone then narrows away, at first slowly, but after bounding the posterior end of the internal nares more rapidly, until it terminates almost in a point at Section 312. From here onwards its direction is continued by the palatal plate of the maxilla, which completes the outer boundary of the nares. The plate-like form of the palatine is lost in that part of its course where it forms the outer boundary of the internal nares; there it becomes a rounded rod, running parallel with the palatal plate of the maxilla, but separated from it by a distinct interval, which forms a slit-like vacuity running outside and parallel with the internal nares. A similar vacuity appears between the biting ridges of the palatine and maxilla in Sphenodon, but situated in that case completely behind the internal nares and not alongside them.

The length of the palatine bone is 135 mm.



TEXT-FIG. 10.—Right vomer; A, outer lateral; B, inner lateral view. *a.p.*, ascending process; *h.p.*, horizontal process; *Pl.f.*, palatine articulation; *Nar.*, margin of internal maris; *Pt.gr.*, pterygoid grooves; *Vo.f.*, articulation with left vomer. (× $\frac{1}{2}$.)

The Vomer (Text-fig. 2, Secs. 207–366, and text-figs. 3, 4, and 10).—The vomers are paired bones which arise posteriorly a little in front of the middle of the orbit (Sec. 376). Each begins as a narrow plate intercalated between the palatine and the pterygoid, with both of which it is united by suture. This plate is produced upwards into a thin lamella which curves over the pterygoid—here reduced to a rod-like form—and partly conceals its dorsal surface. Passing forwards, the palatal plate-like body broadens out; the overlapping lamella grows thicker, especially at its upper end (Sec. 357), and then becomes produced upwards into a vertically ascending lamella (Sec. 349) which rises till it is not far from reaching the nasal bones above. The pterygoid now lies in a groove, the lower lip of which is furnished by the body of the vomer and the upper lip by the base of the ascending lamella of that bone: it is more concealed above than below. Still farther forwards the lower lip of the groove grows thicker and extends towards the middle line till it meets its fellow a little in front of the posterior boundary of the internal nares. Up to this point the pterygoids are exposed to a greater or lesser extent on the lower face of the palate;

beyond it they are concealed. At the same time the upper lip of the groove becomes smaller, and finally disappears, leaving the pterygoids completely exposed on the upper surface of the palate.

With these changes others are associated, the whole bone becomes more massive, and the outer angular end of its palatal portion becomes rounded off to form the inner boundary of the internal nares (Secs. 334–313).

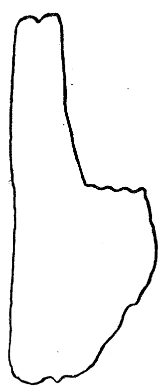
The apposed vomers now form a rounded trough; the parasphenoid lies above them in the middle line, but terminates about halfway between the anterior and posterior boundaries of the internal nares; the pterygoids, which lie on each side of the parasphenoid, but below it, continue a short distance farther, but terminate before reaching the anterior boundary of the nares.

The rounded trough formed by the apposed vomers and the arch formed by the apposed nasals are then the only bones bounding the inner cavity of the skull or snout.

Farther on the vomers become less regular in form, and terminate as rather triangular rods which no longer lie side by side, but one over the other (Sec. 207). They are visible on the under surface of the palate for a considerable distance beyond the region of the internal nares, but are at length concealed by the palatal plates of the premaxillæ, which approach one another below till they meet in the middle line.

As we have seen, the vomers first appear in Sec. 376; they disappear in Sec. 182, and are thus 195 mm. in length, or 0·375 of the total length of the skull. They evidently play a much more important part here than in Sphenodon, and they are not only in contact with the extremity of the pterygoids, but overlap these bones (Secs. 376–306) for 70 mm., or more than one-third of their length.

In Sphenodon the vomers do not extend backwards beyond the nares; in Ichthyosaurus they approach the middle region of the orbit. In Sphenodon the pterygoids do not reach so far forwards as the internal nares; in Ichthyosaurus they pass beyond the posterior boundary of these apertures.



TEXT-FIG. 11.—Outline of the left posterior columella cranii seen from the side. (× $\frac{3}{4}$.)

It is in their backward extension, however, that the vomers of Ichthyosaurus differ most from those of Sphenodon, and it is interesting to observe that it is a similar backward extension which in birds, such as the Emu and the Rhea, has brought the vomers to meet the pterygoids, which have undergone no forward extension, but remain confined within the region of the orbits.

Transverse Bone.—After numerous efforts to discover some definite region in the palatal plate which might correspond with this bone, I am led to conclude that it is not represented as a separate element, and probably not at all.

On each side of the floor of the orbits a part of the palatal plate lying next to the maxilla is separated from the remainder for a considerable distance, but does not reach the pterygoid (text-fig. 3). It was tempting to regard this as the missing bone; but the line of separation, which should in that case be a line of suture, lies on both sides immediately above, and in contact with, the edge of the splenial bone of the lower jaw, and follows its course. It would seem that pressure acting through this bone has broken the palatal plate across along the line of separation, which is therefore a fracture and no suture. This conclusion is confirmed by the fact that the lines of separation on the two sides do not correspond with each other as closely as might be expected were they true sutures.

The absence of a transverse bone is possibly a primitive character, and recalls the prevalent structure of the Stegocephalian palate.

The Parietal (Text-fig. 2, Secs. 401–487, and text-figs. 5 and 6).—Looked at from above the parietal bones form together a St. Andrew's cross raised to an elongated peak in the middle. The posterior arms of the cross unite by a complicated suture with the squamosals, which form the upper and outer angle of the skull; the anterior arms will be described later. The posterior angle of the cross, now vacant, was originally occupied by the supra-occipital; the anterior angle provides the posterior boundary of the pineal foramen and is filled by the frontals; the lateral angles form part of the supra-temporal fossa.

On examination of the interior of the skull the posterior moiety of the united parietals is seen to form a simple arch, the roof of the cranial cavity, the sides of which are completed by the columellæ cranii. The parietals are not grooved for the reception of the upper ends of the columellæ as ANDREWS suggests in the case of Ophthalmosaurus, nor are the columellæ situated so far forwards as ANDREWS' figure would suggest.*

The anterior moiety presents some features of remarkable interest. A great thickening of the bones on each side of the sagittal suture gives rise to the median ridge or crest. The sides of the arch are no longer simple, but split, as it were, by a longitudinal fissure which rises and widens in its forward course so as to divide the bone on each side into two wings, an upper outer and a lower inner wing, which become more widely divergent from each other as they proceed forwards. (Text-fig. 2, Secs. 421-431.)

The inner wings, which end freely below, continue the cranial arch of the posterior moiety, though with continually decreasing span and diminishing height, so that if the greater part of the wings were broken away their basal part would present some resemblance to a shelf, and it is this, I think, which ANDREWS† has described as a sort of tentorium.

The outer wings, freely terminating at first, splay outwards and upwards to unite by suture first with the postfrontals and later with yet other bones.

* C. W. ANDREWS, *op. cit.*, fig. 14, p. 25.

† C. W. ANDREWS, *op. cit.*, p. 26.

In this way a part of the skull becomes provided with a double roof precisely of the same character as that met with in the corresponding region of the skull of the Chelonia. If the free wings were to grow downwards they would meet the anterior columellæ and the resemblance would be complete.

There are some sutures in the anterior angle of the parietal cross, *i.e.*, in the posterior wall of the parietal foramen, which appear to indicate the presence of a pair of minute bones. These, if they exist, would be the last traces of a preparietal element such as exists in Dicynodon, though in that genus they lie in front of instead of behind the pineal foramen.

The Frontal (Text-fig. 2, Secs. 415–359, and text-figs. 5, 6, and 13).—The pineal foramen is bounded on all sides except behind by the frontals, which are exposed at the surface over a comparatively small lozenge-shaped area bounded by the parietals, postfrontals, and nasals. A considerable part of the frontals is concealed, however, by the surrounding bones. Posteriorly they are concealed by the parietals in a very remarkable manner, for the parietals not only overlap the frontals but receive these bones into their substance. The outer wing of each parietal is split into two plates, a thinner one below and a thicker above, and sandwiched in between these plates lie the frontals.

Each upper plate of the parietals as it proceeds forwards retreats by its inner margin from the middle line, descending down the sides of the great frontal ridges, so as to expose more and more of the frontal bones; it finally disappears, before reaching the nasals, at Sec. 396. For the most part the upper plate is simply apposed by its lower surface to the upper surface of the frontal, but here and there, especially on the sides of the frontal ridges, feeble sutures are present.

The outer margin of the upper plate is united with the postfrontal by deeply interdigitating sutures.

Each of the lower plates of the parietals may be distinguished into an inner and outer portion; the thinner inner portion is closely applied to the under surface of the frontal; the outer portion increases in thickness for some distance forwards and separates from the inner portion so as to present the appearance of a distinct bone (text-fig. 2, Sec. 413), it articulates on the inner side by an interdigitating suture with the outer edge of the frontal and on the outer side with the postfrontal.

At their posterior end the frontals are extremely thin lamellæ which make their appearance within the parietal 6 mm. behind the pineal foramen. Traced forwards they rapidly grow thicker, especially towards the middle line, swelling into a thick mass which is convex above, concave below. On the upper surface the convex margins form together a pair of ridges with a medial depression between; immediately in front of the pineal foramen these are well marked and steep-sided, but farther forwards, although the bones themselves become thicker, they broaden out and disappear. On the lower surface the sharp edges of the concave or arched bones meet to form a single cusp which is traversed by the sagittal suture (text-fig. 2, Secs. 395 and 401). The arched surface forms in part the roof of the great orbits. Still farther forward, where the frontals are overlapped by the nasals, they diminish in thickness, and failing to reach the middle line terminate in thin lamellæ.

The marginal limb of the frontal is concealed by the postfrontal which overlaps it, and is suturally united with it. Below the postfrontal in this region, and thus concealed by it, lies the prefrontal, which unites by suture with the outer margin of the frontal.

The Nasals (Text-fig. 2, Secs. 180–382, and text-figs. 5 and 6).—The nasal bones meet in the middle line, and are partly united by suture for nearly the whole of their length; it is only at their extreme posterior ends, where they overlie the postfrontals, that they become divergent (Secs. 379–390).

Posteriorly they are depressed towards the middle line, probably as a result of pressure, but on approaching the external nostrils they form a rather flat arch which continues up to their disappearance beneath the premaxillæ at about Sec. 210. They continue concealed below the summit of the more rounded arch formed by these bones, as far as Sec. 130, where they terminate in pointed extremities, so that they are exposed for 180 mm. and concealed for 80 mm. of their length. Their total length is 260 mm.—*i.e.*, no less than half the length of the whole skull. This marks the first step in that remarkable elongation which has affected the whole of that region of the skull which lies in front of the orbits.

Here, in the interest of students, attention should be called to an illustration which has found its way into ZITTEL's 'Handbuch der Palæontologie' (p. 458, fig. 427), and is reproduced in the English translation.* In this apparently faithful drawing of a part of the snout the nasals are represented in a region beyond that in which they terminate, and as overlying, instead of underlying, the premaxillæ. This amazing blunder was due in the first place to QUENSTEDT. The nasals, when they first make their appearance, cover out of sight all but the outer margin of the postfrontals in that region, but they encroach only to a slight extent upon the frontals; as they advance, however, they rapidly increase in breadth, especially towards the middle line, which they reach by the time the postfrontals have approached their anterior termination. From here onwards they completely cover the frontals up to the termination of the latter at Sec. 355.

The frontals, where they underlie the nasals, are suturally united to them, the upper surface of the frontals interlocking with the lower surface of the nasals by a coarse serration.

The frontals, as we have seen, begin behind at Sec. 417; they emerge from the parietals at Sec. 410, are exposed as far as Sec. 379, where they plunge below the nasals, and terminate below these bones at Sec. 355. Thus, out of a total length of 62 mm., only 31 mm., or just one-half, is exposed at the surface. Their union with the parietals extends over only 7 mm., but it is extremely close, so that in spite of

* 'Text-Book of Palæontology,' vol. 2, p. 168, fig. 266 (1902).

the action of subsequent pressure it has remained undisturbed. The strong sutural union of the parietals and frontals with the prefrontals and postfrontals has no doubt contributed to this effect. The nasals are united with the frontals for a length of 24 mm., but the connection was less firm, and these bones in consequence have been torn apart.

Most posteriorly the nasals overlie the postfrontals; passing forwards, they articulate at the margin first with the prefrontals, and then with the lacrymal; on reaching the nostrils their lower margin becomes free and rounded off to form the upper boundary of these apertures. Near the anterior end of the nostrils the upper facial branch of the premaxillæ is plastered over the flank of the nasals, and beyond the nostrils the upper and lower facial branches of the premaxillæ unite to form a single bone which ascends up the sides of the nasals till it completely conceals them. Over a considerable part of their course the nasals are not sutured together on the middle line (Secs. 324–364), but simply meet by their inner margins, which are rounded off.

The Quadrate (Text-fig. 2, Secs. 482–507, and text-figs. 3–6).—In this large bone we may distinguish two regions—the massive articular head and an ascending plate-like limb. Subsequent pressure has produced a fracture which roughly defines these two regions, and has slightly displaced the head by an upward rotation.

That side of the articular head which looks towards the median line is embraced, as previously mentioned, by the inferior and posterior process of the pterygoid. Traced forward the head loses its massive character, and becomes a thick curved plate.

The plate-like limb or pterygoid process of the quadrate passes forwards a considerable distance beyond the head, and at the same time diminishes in thickness; it expands both upwards and downwards, and curves outwards at its upper end.

In the lower half of its course the plate runs outside and almost parallel with the ascending process of the pterygoid; in the upper half it runs parallel with the descending process of the squamosal, its upper end fitting into the angle formed by the descending and the outer processes of that bone.

These relations recall those in Sphenodon, though in that form the pterygoid process of the quadrate extends much farther forwards, and is closely sutured with the ascending process of the pterygoid, so that the two apparently form one bone. There is no such close union of the two processes in Ichthyosaurus.

On the posterior inner side of the pterygoid process there is a little curved recess which receives the expanded end of the stapes.

The Squamosal (Text-fig. 2, Secs. 462–491, and text-figs. 5 and 6).—This is a triradiate, rather nail-like bone. The head is divided into two processes: one, on the inner side, larger and stouter, which is rigidly united with the posterior horn of the parietal by a deeply interlocking suture; the other, longer but slenderer, on the outer side, which overrides the curved end of the pterygoid process of the quadrate and runs forward as a thin vertical lamella which is applied by its lower edge to the upper edge of the postorbital bone.

The stout, peg-like, descending process is driven in between the pterygoid process of the quadrate on the one hand, and the posterior horn of the parietal together with the upper end of the ascending process of the pterygoid on the other. In their account of Sphenodon, HOWES and SWINNERTON* describe "a process of the squamosal, hitherto unrecognised, which extends downwards and forwards between the quadrate and pterygoid, and, together with a process arising from the posterior border of the squamosal, embraces the otic head of the quadrate." This description would apply equally well to Ichthyosaurus and to Dicynodon.

The inner side of the descending process of the squamosal is also in contact, near its origin, with the upper end of the opisthotic.

The Supratemporal.—This bone, as is so commonly the case with Ichthyosaurus skulls, is missing. When present its relation to the adjacent bones is precisely that of the outer bone in the Lizards which is called squamosal by HUXLEY, PARKER, and others. The subject has lately been treated by WATSON,† who argues that it is the inner bone, called supratemporal by HUXLEY and PARKER, which is in fact the squamosal; and the evidence for this seems to me overwhelming. But when WATSON proceeds to identify the outer bone with the quadrato-jugal, I think he is on less certain ground. The reason alleged is that "no other bone ever lies outside the squamosal," with the remark in a footnote, "except perhaps in Ichthyosaurus." The exception, however, is not doubtful. The supratemporal of this reptile is indeed overlapped by the process of the squamosal, which goes to meet the postfrontal; but this process is absent from the Lizards, and it is the inner process of the squamosal which joins the parietal that must be brought into comparison, and there can be no question about this. The supratemporal lies a long way outside it. I think therefore that HUXLEY and PARKER have simply inverted the names appropriate to these two bones.

The Quadrato-Jugal (Text-fig. 2, Secs. 453–494, and text-figs. 3, 4, 5, 6, and 12). —The greater part of the quadrato-jugal is concealed by the postorbital bone; when this is removed it presents itself as a large oblong lamina, with its longer side slightly curved, steeply sloping upwards. Anteriorly it is continued farther forwards above than below; posteriorly it is produced at its lower corner into a stout bar, which articulates with the quadrate, or did so originally, before it became dislocated by pressure.

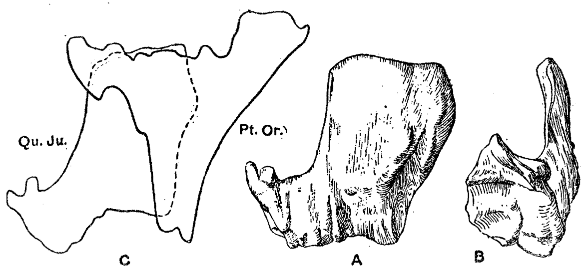
It thickens out from above downwards, becoming rather tear-shaped in section except in front, where it is cut away on the outer face for articulation with the jugal,

* G. B. HOWES and H. H. SWINNERTON, "On the Development of the Tuatara," 'Trans. Zool. Soc., London,' vol. 16, p. 53, Plate 4, fig. 11 (1903).

† D. M. S. WATSON, "On Pleurosaurus and the Homologies of the Bones of the Temporal Region of the Lizard's Skull," 'Ann. and Mag. Nat. Hist.,' Ser. 8, vol. 14, p. 84 *et seq.* (1914).

and behind, where it is continued into the quadrate process, which changes its shape, as shown by the sections in text-fig. 2, to form the articular surface with the quadrate.

The lamina is applied by its outer face to the inner face of the postorbital, and some of our sections suggest the presence of one or two bony trabeculæ connecting the two bones; but these may be deceptive appearances due to mineralisation.



TEXT-FIG. 12.—Right quadrato-jugal and postorbital bones. A. The quadrato-jugal seen from the outer side. B. End on from behind. C. The two bones in their natural position, showing the overlap of the quadrato-jugal by the postorbital. ($\times \frac{1}{2}$.)

The Postorbital (Text-fig. 2, Secs. 421–471, and text-figs. 3, 5, 6, 12).—This also is in great part a lamellar bone produced at one corner, in this case the antero-superior, into a stout bar, which we may call the anterior process of the postorbital.

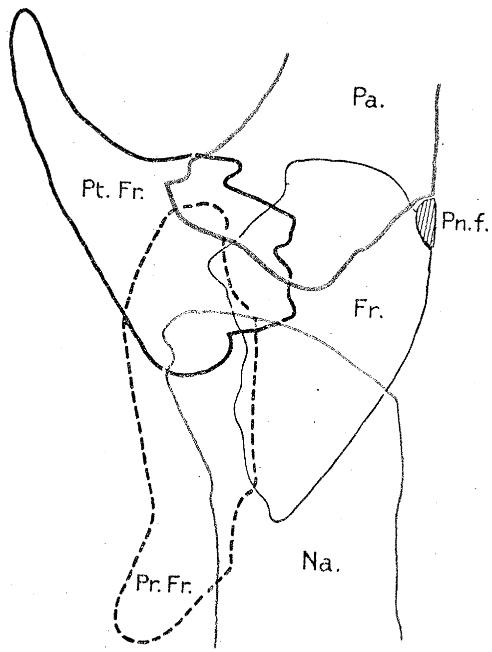
The bar is elongated vertically, thickened and rounded below, where it contributes to form part of the boundary of the orbit, and closely united with the postfrontal (Secs. 156-176), which lies outside it. From its almost pointed extremity in front it increases in thickness and elongates downwards as it extends backwards, the postfrontal correspondingly diminishing. Its cross-section on the disappearance of the postfrontal resembles an elongated ellipse flattened on the inner face. It continues to grow downwards till it acquires its full length, forming a fairly thick plate gently arched upwards, which articulates with the jugal below and with the quadrato-jugal by its inner face. It diminishes in thickness as the latter increases, and as soon as it is excluded from articulation with the jugal (Sec. 197), it disappears from below upwards, and thus terminates in a thin supero-posterior wing. The upper edge of this wing articulates with the lower edge of the antero-lateral process of the squamosal.

The Postfrontal (Text-fig. 2, Secs. 359–431, and text-figs. 5, 6, 13).—The posterior extremity of this bone is a lath-like process standing edgewise which extends backwards from the orbit outside the postorbital towards the squamosal. Traced forwards, it thickens into a stout, rather triangular bar with curved sides, and receives the anterior end of the postorbital in a recess on its inner side. On reaching the front of the temporal fossa this bar extends on the inner side into a horizontal plate which meets first the parietal and then the frontal towards the middle line and the nasal in front, covering a considerable area on the upper surface of the skull.

On meeting the nasal this expanded portion is continued below that bone, but the outer margin remains visible for a short distance farther as a wedge-like insertion between the nasal on the one side and the prefrontal on the other.

On the under side of the cranial roof the postfrontal is concealed over a considerable area by the frontal and prefrontal bones.

A closer knowledge of its relations to the surrounding bones can only be obtained by the aid of sections. When, advancing forwards, it first meets the parietal, the frontal has already made its appearance, but the postfrontal articulates with the parietal only, the two bones being united by a strong interdigitating suture; as the frontal increases in thickness the postfrontal articulates both with it and the parietal, and later, when the parietal has disappeared, with the frontal and prefrontal, its inner edge being sutured to the steep side of the recess excavated on the upper part of the frontal, its lower surface with the upper surface of the outer wing, the edge of this wing of the frontal being sutured with the prefrontal.



TEXT-FIG. 13.—Structure of the roof of the skull just in front of the right supratemporal fossa, as described in the text. (× 3/4.)

When the postfrontal reaches the nasal it is excluded from contact with the frontal by that bone, and becomes completely enclosed by the nasal above and the prefrontal below, a process of the nasal curling round its medial edge. It then diminishes in size and ends in a rounded process which lies in a hollow of the nasal close to its outer edge.

In the region just in front of the supratemporal fossa the relations of the postfrontal and adjoining bones are so complicated that a plan is introduced here (text-fig. 11) to represent them.

The Prefrontal (Text-fig. 2, Secs. 334–413, and text-figs. 5, 6, 13).—This makes its appearance on the lower surface of the cranial roof, just in front of the supratemporal fossa below the junction of the postfrontal and the lower tabula of the parietal, to both of which it is united by suture. It extends forwards as a bar of irregular outline, increasing in size as it proceeds, and on the disappearance of the parietal it lies below the union of the frontal and postfrontal, articulating with both of these bones, with the postfrontal by its upper surface, with the frontal by its inner edge.

On reaching the posterior termination of the nasal the prefrontal is exposed on the margin of the orbit, which it bounds above for the remainder of its course. As a curved plate with a sharp orbital edge it now articulates by its upper surface with the nasal, and at its inner edge with the concealed frontal. Previously thicker on the medial, it now becomes thicker on the orbital side, and as the frontal diminishes articulates solely with the nasal, the cleft margin of the nasal embracing the wedge-like margin of the prefrontal for a considerable distance; later this simple interlock becomes more complicated. The prefrontal at the same time curves downwards, and exchanges its previously almost horizontal disposition for one more nearly vertical. It continues to increase in size till, on meeting the ascending lacrymal, it divides into branches which embrace that bone, one being applied to its outer and the other to its inner face; these rather rapidly diminish and disappear.

The Jugal (Text-fig. 2, Secs. 359–471, and text-figs. 3, 4, 5, 6).—For the greater part of its course the jugal is a fairly straight, rounded rod which forms the exterior margin of the orbit below. Near the anterior boundary of the orbit it is concealed above by the lacrymal, but still remains exposed on the outside of the face. At the same time it is closely applied to the outer side of the maxilla, which is excavated by a groove to receive it. It terminates anteriorly just below the posterior end of the external nares, at Sec. 330.

Traced backwards it sweeps upwards in a gently rising curve as it passes beyond the orbit (Sec. 430); at the same time it widens vertically so as to present a vertically elongated ellipse in cross-section, and is received by the lower edge of the postorbital, which is grooved for the purpose. Farther back the outer lip of this groove disappears while the inner lip becomes more pronounced. The margin of the postorbital now rises upwards, and recedes from the jugal, which then adapts itself to the outside of the thickened lower end of the quadrato-jugal, or originally did so, the two bones being now separated by subsequent displacement. In its present state the jugal tapers away to its termination at Sec. 481; its total length is thus 151 mm.

The jugal of our specimen is on the whole a straighter bone than that of *I. communis*, as figured by OWEN, and in particular its upward curvature behind the post-orbital bone is slight, so that it makes no approach to parallelism with the posterior border of the orbit. It is also distinguished by its greater forward extension, for it does not terminate till it reaches a point below the posterior margin of the external nostril, while in *I. communis* it proceeds no farther than the anterior margin of the orbit.

The relative length and degree of curvature of the jugal differ considerably in different species of Ichthyosaurus; in some, as for instance *I. intermedius*, the bone is not so much curved as angulated.

In making a comparison with the jugal of Sphenodon it may first be pointed out that OSAWA has given an imperfect account of this bone owing to his having overlooked the prolongation of its horizontal limb beneath the orbit. This curious oversight is doubtless due to the fact that this prolongation cannot be seen on the face, where it is completely concealed by the maxilla, but is plainly visible on the floor of the orbit, and is well defined by sutures. HOWES and SWINNERTON have figured it correctly. The anterior (unlike the posterior) moiety of the horizontal limb is not compressed from side to side, but from above downwards, so that it forms a rather curved lamella, which is united with the postorbital, transverse, palatine and maxilla.

The most marked difference which distinguishes the jugal of Sphenodon is the presence of an ascending process at the junction of the anterior and posterior horizontal limbs, which is closely applied to the back of a descending process of the postorbital. This is absent in Ichthyosaurus or only faintly suggested by the slight widening upwards which it exhibits in the same region. If the posterior horizontal limb were to disappear from the jugal of Sphenodon then the remaining part would approach in form the jugal of many lizards. In Ichthyosaurus the upward curvature of the jugal behind the orbit in some species produces the same effect, giving to this bone a very Lacertilian aspect. The relation of the jugal to the surrounding bones is on the whole similar to that which obtains in Ichthyosaurus, though there are some differences in detail; thus in Sphenodon the posterior extremity of this bone meets a downward descending process of the squamosal, which is absent in Ichthyosaurus. The position of its anterior horizontal limb as a flooring bone of the orbit, median to the maxilla, is a feature peculiar to Sphenodon.

The Maxilla (Text-fig. 2, Secs. 236–366, and text-figs. 3, 4, 5).—Posteriorly the maxilla ends (Sec. 375) in a narrow plate-like process forming one of the series of plate-like bones which may be regarded in this region either as the floor of the orbit or the roof of the palate. Traced forwards it slowly broadens out and afterwards (Sec. 344) begins to thicken on the outer edge, so that a more massive facial region may be distinguished from the more plate-like palatal one. The facial region increases in thickness and height, attaining its greatest dimensions below the outer nostril (Secs. 309–312 about); it then slowly diminishes till it disappears at Sec. 222.

The palatal portion undergoes little change until the palatine bone has been passed (Sec. 311), but beyond this point its inner moiety rapidly thickens to form a stout polygonal bar, which remains connected with the facial portion by a narrow neck only, now often broken across by subsequent deformation,* so that the two portions, facial and palatal, are defined from each other above by a sharply marked channel, while below they bound together the broad alveolar groove.

In its further progress the palatal bar becomes separated from the facial part of the maxilla as a narrow vertical plate, which is applied to the outer face of the palatal process of the premaxilla, and, gradually diminishing, terminates in a point at Sec. 258, the facial part of the maxilla continuing its course, as already mentioned, to Sec. 222. The total length of the bone is thus 153 mm., or about 0·3 of the length of the skull.

* In some sections these two parts have the appearance of independent bones, and it is difficult to convince oneself that they are not so. This will be referred to again at the close of this section.

For the greater part of its course the maxilla is partly concealed by adjacent bones; on the face by the jugal behind and the premaxilla in front, and above by the lacrymal. Most posteriorly (Secs. 375–351) the jugal completely excludes the maxilla from the face, but beyond Sec. 351, where the jugal lies in a recess excavated chiefly in the maxilla but partly in the lacrymal, the lower lip of this recess is visible as a very narrow band. The maxilla bears its most posterior tooth in this region (Sec. 340).

The overlap of the premaxilla which commences below the nostril (Sec. 300) increases forwards so that the maxilla becomes increasingly concealed in this direction, but its lower margin continues to be visible as a narrow selvage as far as Sec. 228.

The lacrymal, which throughout its whole course is seated on the upper surface of the maxilla, is socketed into it by a tongue-like joint below the nostril (between Secs. 310–290).

As already pointed out, the palatal bar of the maxilla, which makes its appearance where the palatine bone comes to an end, has very much the appearance of an independent bone. This apparent independence is partly due to fracture and partly to the presence of an elongated foramen running lengthwise. The alveolar groove below and a deep sulcus above reduce the connection of the bar with the rest of the maxilla to a narrow neck, which under slight pressure, such as would be conveyed by the immediately underlying lower jaw, would be readily broken across.

That the bar is really a palatal process of the maxilla is strongly suggested by the fact that it bounds on one side the alveolar groove with its teeth.

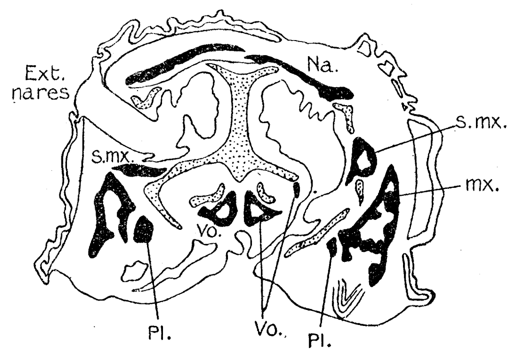
Mistrusting my own judgment I consulted Mr. GOODRICH on this question; he was kind enough to examine photographs of the serial sections as well as the reconstruction of this region, and came to the conclusion that the interpretation just given is correct. This is extremely satisfactory, for if the bar were an independent bone it would be difficult to find a place for it in a rational scheme of the skull.

On the upper side of the palate, just where the palatal bar of the maxilla terminates behind, the rounded angle by which the facial and palatal limbs of the maxilla pass into each other becomes more deeply excavated so as to form a recess on the side of the nasal chamber. This, as it is continued outwards and backwards, becomes roofed over by the descending edge of the base of the lacrymal bone, and is finally converted into a canal, which ends blindly against the maxilla and lacrymal at their common suture; the recess, however, farther forward opens on the face by a perforation which lies on the same suture. Can this feature be the lacrymal groove? My friend, Mr. GOODRICH, seems to think so.

Septomaxillary (Text-fig. 2, Secs. 313 and 326, and text-fig. 4).—These little splint-like bones are rather irregular four-sided plates, thick and rounded at one end and thinning away to a sharp-edged lamina at the other; they measure 22 mm. in length, 8 to 9 mm. in breadth, and 4·5 mm. in thickness where thickest. They lie free within the nasal chamber, that of the right side (Secs. 310–318) a little in front of that on the left (Secs. 319–328).

The right septomaxilla rests with its lower edge on the inner margin of the palatal process of the maxilla, and, leaning over the front border of the internal naris, is propped up by the vomer, with which its thicker upper end is in contact. The left septomaxilla lies horizontally, its thicker end pointing towards the maxilla and the other thinner end projecting freely into the internal naris: it rests on the rod-like terminal part of the palatine bone.

HOWES and SWINNERTON remark that the septo-maxilla in Sphenodon is "still more superficial and free from the nasal septum than this," *i.e.*, than the position assigned it by GAUPP in the Lacertilia. That it was free from the nasal septum in Ichthyosaurus is evident from its present position on the outside of the vomer. It may be of interest to compare our section across the skull of Ichthyosaurus in this region with that given by HOWES and SWINNERTON of the embryo Sphenodon in their Stage R.S. (text-fig. 14). The chief difference is the absence of the pterygoids in the section of Sphenodon, but in Ichthyosaurus these bones are already approaching their termination in the neighbourhood of the septomaxillæ.



TEXT-FIG. 14.—Transverse section across the embryonic skull (Stage R and S) of Sphenodon, after HOWES and SWINNERTON, for comparison with sections 326 and 313.

The Premaxillæ (Text-fig. 2, Secs. 35–296, and text-figs. 3-6).—The premaxillæ, which extend from the nostrils to the end of the snout, are still longer bones than the nasals, *i.e.*, 301 mm. as against 260 mm. They are more complicated than they at first appear; in front and for about 30 mm. backwards they form together a semi-cylindrical mass, but with the appearance of the alveolar groove a differentiation soon sets in, so that each bone, when traced backwards, presents an outer facial and an inner palatal part. The facial pair form together the arch of the snout; they meet along the middle line without any interlock, as far as Sec. 208; from there on they stop short of it by an increasing distance, thus revealing more and more of the nasals. On reaching the nostrils they subdivide into an upper and lower limb. The upper limb extends backwards, overlying the nasal for 10 mm.; the lower overlies the maxilla, which is excavated to receive it, for 26 to 30 mm., and terminates in contact with the much-diminished end of the lacrymal.

The palatal processes of the premaxillæ for a great part of their course are separated from the facial part, and have in consequence been mistaken for independent bones; they seem to have been mistaken by SEELEY for the vomers.

Posteriorly these processes first present themselves as very small vertical plates situated below the anterior region of the nostrils between the vomer and the palatal bar of the maxilla (Sec. 289); traced forwards, they increase in size as the maxillæ diminish and assume the form of a pair of curved vertical plates expanded at their extremities. At first their upper ends approach the under surface of the nasals and even abut against it (Secs. 263–160); later they touch both the nasals and the facial part of the premaxillæ, and at Sec. 154 they are in contact with the latter exclusively. So far, *i.e.*, for 135 mm. from their posterior termination, there is nothing to show that they are not separate elements. Farther onwards they seem to pass into the body of the premaxillæ; suggestions of a suture are to be seen in some sections, but the evidence as a whole is certainly in favour of their continuity with the rest of the bone.

The facial parts of the premaxillæ meet above at the middle line in rounded ends, leaving a cuspidate space between them below; the palatal parts with their outwardly diverging curved ends leave a similar space above; these two spaces form together a canal, lozenge-shaped in transverse section, which is a direct continuation of the cranial cavity and can be traced along the snout as far as its structure is preserved, *i.e.*, nearly to the end. The upper end of the palatal plate is sometimes deeply grooved, evidently for the passage of a blood vessel; vascular canals also occur in the body of the bone.

When the palate is viewed from below, the lower ends of the palatal processes are seen to be closely approximated in the middle of their course, forming two flat bands, one on each side of the middle line; thence they diverge as they proceed backwards and forwards, exposing the vomers behind and forming a deep sulcus in front which is closed above by the approximation of the limbs of the processes. The vomers are visible, or one of them, as far as Sec. 231.

The Lower Jaw (Text-fig. 2, Secs. 35–507).—The first attempt at a detailed description of the lower jaw was made almost a century ago by DE LA BECHE* and CONYBEARE (*loc. cit.*), who illustrated their account with numerous transverse sections. They noticed the absence of a vacuity, but in their identification of the constituent bones they mistook the surangulare for the coronoid, which they do not seem to have observed. In a subsequent paper CONYBEARE (*loc. cit.*) gives better figures of transverse sections, but does not correct his original mistake; he introduces, however, a new element which he styles the "crescent-shaped bone." This is, in fact, the true coronoid or rather goniale, and is faithfully represented in its relation to the splenial and other bones in his figures; indeed the lateral view which he gives of this region is even more correct than that of his successor, the great CUVIER himself.

CUVIER'S* description, illustrated by figures of the outer and inner side of the jaw, is of course excellent, all the bones are represented and correctly named, but the coronoid (goniale) is made to terminate behind just in front of the coronoid process and thus assumes a misleading resemblance to a true coronoid. This error may have

* G. CUVIER, *op. cit.*, p. 464, Plate 29, figs. 15 and 16.

been due to an accidental fracture which seems in the figure to form a natural boundary to the bone.

Owen,* although he suspected the presence of the coronoid, was unable to convince himself of its existence.

Fraas,† who like his predecessors studied the structure in cross-sections, made some curious errors in identification; thus he applies the synonymous terms splenial and operculum to different bones in the same section. That which he terms splenial is in fact the surangulare.

The admirable account given by Andrews of the lower jaw of Ophthalmosaurus leaves little to be desired, but it is evident that some differences in detail distinguish this jaw from that of Ichthyosaurus. In Ophthalmosaurus, for instance, the surangulare is represented as bearing a facet for the coronoid (goniale), while in Ichthyosaurus the coronoid (goniale) does not come into contact with the surangulare.

In our specimen the lower jaw is not quite complete at its posterior end and the articulare is missing. The right ramus, which is the better preserved, has lost the tip of its posterior end and a part of the lower edge in the middle, between Secs. 220 and 320.

The Angulare.—This, which, next to the dentary, is the most persistent bone in the jaw, can be traced from Sec. 515 to Sec. 303, where the jaw becomes imperfect, but it was evidently continued for some distance farther forward.

In the first complete section across the ramus it presents a crescentic outline with one long outer horn penetrating the surangulare like a wedge, and a short inner horn which articulates by its rounded end with the goniale. A little forward of this a short sharp ridge rises from the middle of the concavity of the crescent and is inserted between the goniale and surangulare, thus increasing the articular surface (text-fig. 2, Secs. 501–507).

The exterior horn, or the plate-like bone it indicates, grows shorter and thicker as it is continued forward, and at the same time passes towards the inner face of the surangulare, till at length it no longer penetrates that bone, but lies against the inner face (text-fig. 2, Sec. 453). At the same time it increases in size and changes its general form, increasing in height to form a thick plate excavated by a rounded trough at its summit. From here onwards to its termination it is embraced on the one hand by the surangulare and on the other by the splenial. But with further advance forward it changes its form; at first its basal half grows narrower, and later it diminishes as a whole to a thin lamina which gradually dwindles away.

The Goniale.—The presence of this element in the Vertebrate jaw was first recognised by Baur in 1905. It has since received several names, but Gaupp‡ has

* R. Owen, *op. cit.*, p. 97, Plate 26, figs. 2–6.

† E. Fraas, *op. cit.*, p. 16, Plate 6, figs. 8 and 9.

‡ E. Gaupp, "Beiträge zur Kenntnis des Unterkiefers der Wirbeltiere," 'Anat Anz., vol. 39, p. 433 (1911).

so clearly worked out its history and relations that the name "goniale" given by him seems to have received very general recognition. The "pre-articulare" of WILLISTON has, however, priority. The goniale is the thickest and best developed near its posterior end (text-fig. 2, Secs. 482–494), growing thinner and smaller as it passes forwards. It at first articulates with the angulare and surangulare, but soon leaves the latter bone, and a little later, after the appearance of the splenial, the angulare also, becoming supported wholly by the splenial. At first (text-fig. 2, Secs. 457, 462) it rides by a forked end on the upper margin of the splenial, but with the disappearance of the outer side of the fork and the upward growth of the splenial it becomes applied to the side of that bone, which is excavated by a recess to receive it (text-fig. 3, Secs. 415–421). It gradually diminishes in size, and disappears at Sec. 410. Its posterior extremity is broken off, but it appears in Sec. 519, and it is thus a little over 109 mm. in length.

ANDREWS has identified the bone in Ophthalmosaurus which corresponds with our goniale as the coronoid, though evidently not without some misgiving, but its position in the jaw and its relation to the surrounding bones harmonise best with our interpretation.

The presence of a goniale so well developed as that of Ichthyosaurus and Ophthalmosaurus is of considerable interest, for it is an admittedly primitive character.

The Surangulare (Text-fig. 2, Secs. 326–507).—At its posterior end this is a thick curved plate forming the outer wall of the jaw and firmly sutured by a mortise-and-tenon joint with the angulare below. Not far from its extremity its upper end is thickened and extended inward as a horizontal process above the cavity of the jaw (text-fig. 2, Secs. 491–500). This is the coronoid process; it can be traced forwards for 14 mm. (Secs. 486–500); after its disappearance the surangulare continues its course as a plate which thins off below and thickens into a rounded swollen margin above.

The curvature of the rounded margin is more convex than that of the outer flank below, and the change of curvature where they meet, just visible in Sec. 447 behind the orbit, grows more pronounced forward, and from Secs. 434–423—*i.e.*, in the region of the anterior end of the supratemporal fossa or the posterior third of the orbit—it becomes abrupt; beyond this it begins to diminish, and is scarcely perceptible in Sec. 402; but where it dies away the dentary spreading downwards over the outer side of the surangulare preserves this feature of that bone as a feature of the lower jaw which can be traced as far as Sec. 310, where the jaw becomes imperfect.

The cavity of the jaw, included by the surangulare, angulare, and splenial, becomes completely enclosed by these bones, and so converted into a closed canal (Meckelian canal) with a more or less circular lumen, and in adaptation to this the inner side of the upper end of the surangulare is excavated by a rounded furrow (text-fig. 2, Secs. 408–413).

As the dentary increases in importance the surangulare diminishes and narrows away to a lamellar plate, retaining, however, the same relations to the cavity of the jaw, the splenial, and angulare to the last.

There is a curious absence of vascular channels in the posterior bones of the lower jaw ; the only one I can perceive runs in the surangulare, close to the outer side of the marginal swelling, from Secs. 432–437, where it opens on the outside, as far as Sec. 461, where a notch on the inner side seems to indicate that it has crossed over the bone to open into the cavity of the jaw.

The Splenial (Text-fig. 2, Secs. 94–471).—This begins posteriorly as a narrow plate, as shown in sections ; in Sec. 473 its pointed extremity is seen lying in a recess on the exterior of the angulare (text-fig. 2, Sec. 468) ; anteriorly it rapidly increases in height, carrying with it the diminishing goniale, and forms for a great distance, as far as Sec. 224, the whole inner wall of the jaw ; it then, just before the anterior termination of the angulare and surangulare, divides into an upper and lower branch (text-fig. 2, Sec. 207) ; the latter, being the largest and longest, can be traced as far as Sec. 93 (text-fig. 2, Sec. 94), while the upper comes to an end at Sec. 178.

The total length of the splenial is 380 mm., or three-quarters of the length of the head, it runs for 249 mm. before it forks, and its lower branch enters into the symphysis of the jaw for a distance of 135 mm. The splenial symphysis is thus much longer than the dentary, which measures 92 mm. only.

The Dentary (Text-fig. 2, Secs. 35–207 and 260–413).—The proximal end of the dentary makes its appearance (Sec. 427) just before the anterior termination of the goniale as a blade-like lamina which is applied by one face to the inner side of the head of the surangulare (text-fig. 2, Sec. 425). Traced forwards it first extends over the head and creeps down the outer side of this bone, but acquires no great importance until it becomes dentigerous when it descends over the inner side of the head of the surangulare and crosses over the cavity of the jaw to apply itself to the face of the splenial on the other side, forming in this way a deep trough, the alveolar groove (text-fig. 2, Secs. 94–207). It now increases rapidly in thickness ; that part which ensheathed the exterior of the surangulare swells out to form the massive body of the bone, and the lamina applied to the face of the splenial thickens into a curved plate which is related to the body as the palatal plates of the premaxilla are to the body of that bone. With the increasing development of the dentary the other bones disappear, first the angulare, then the surangulare, and last the splenial. At this stage, when the dentary alone forms the lower jaw, it closely resembles the premaxilla in the same region, so that it is difficult to decide on first examining a cross-section of the snout which is premaxilla, and which dentary. Just as the cranial cavity is continued as a canal, formed by the upper angle between the palatal plates and the body of the premaxilla, so the cavity of the lower jaw is continued by the lower angle between the plates of the dentary and its body.

The dentary is 427 mm. in length, and is thus the longest bone in the head. There is nothing primitive in this, it is a mere adaptive character due to the excessive elongation forwards of the whole anterior region of the head. Posteriorly the dentary does not extend as far as the back of the orbit.

An excellent account of the vascular canals in this bone and their external openings was given long ago by CONYBEARE.*

The Teeth.—The teeth make their first appearance behind in the maxilla (Sec. 345) near the anterior angle of the orbit, behind the internal nares; but, so far as can be made out, they do not occur in the lower jaw till some distance in front of this (Sec. 303). There are 22 in the lower jaw on each side, and 29 in the upper jaw, 10 of these being maxillary, and of much smaller size than the others.

The teeth are subject to many irregularities both in disposition and form. In general they are seated on a long base, much compressed from side to side, especially near the base, where in one instance the antero-posterior diameter measures 13 mm. and the lateral only 7 mm. They gradually diminish in size from below upwards, to terminate in a blunt point, but are not edged as in *I. platyodon*. The anterior face of the upper teeth slopes backwards at a much sharper angle than the posterior; in the lower teeth this slope is reversed, or, in other words, the teeth appear to be directed backwards or recurved in the upper jaw and forwards in the lower jaw, the general plane of the base being oblique to the axis of the tooth. There are exceptions, however, to this rule, some due to irregularities in the dentition; but in the more posterior teeth there is a general tendency to assume a vertical position, the points of the teeth then biting well within the margin of the jaw.

The object of the oblique direction of the anterior teeth is evidently to ensure the capture of prey; the diminished size and vertical position of the posterior teeth to facilitate deglutition.

The Hyoid and Branchial Arches (Text-fig. 2, Secs. 425–507, and text-fig. 15).—The only part of the hyoidean skeleton so far known would appear to be the pair of stout rods which so commonly underlie the base of the skull, running between the rami of the lower jaw and parallel to them. They are commonly regarded as the cerato-hyals, and we will speak of them as the hyoid rods. As might readily be suspected, and as our sections clearly prove, these bones were only parts of a more complicated apparatus.

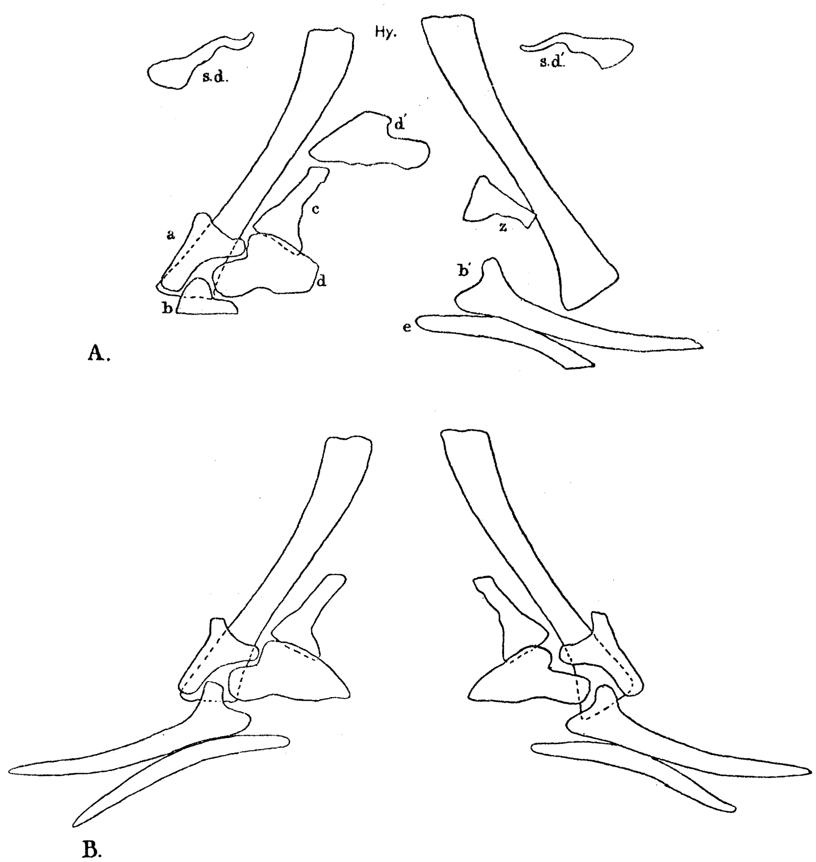
The hyoid rods are present in our specimen (*Hy*, text-fig. 15 A), and exhibit their usual characters. For the greater part of their length they are circular in transverse section, but flatten and broaden out posteriorly, so that their section becomes a transversely elongated ellipse.

On the left side of the skull lie four additional bones, which to all appearance still retain their original relations to one another.

The most external of these is a comparatively short, small, rounded rod expanded

* CONYBEARE, W. D., "Additional Notices, etc.," 'Trans. Geol. Soc.,' Ser. 2, vol. 1, p. 103.

for a short distance on the inner side near the front end into a plate-like process. It runs above, outside of and parallel to the posterior end of the hyoid rod, which it covers and conceals by its lateral plate-like process (*a*, text-fig. 15 A).



TEXT-FIG. 15.—A. Bones of the hyo-branchial apparatus shown in plan. *Hy.*, hyoid; *a* to *d*, bones of the left side in place; *b'*, *d'*, *e*, *z*, displaced bones of the right side; *s.d.*, transverse vertical section of *d* for comparison with *s.d'.*, a similar section of *d'*. B. Suggested restoration of the hyo-branchial skeleton. ($\times \frac{1}{2}$.)

If this bone is not merely the dorsal member of another element, we may fairly regard it as representing the first branchial arch.

Behind this, and overlying the posterior end of the hyoid rod, is another bone resembling the front half of the preceding—*i.e.*, it is rod-like, with a lateral plate-like process, but the rod-like portion does not continue behind the lateral plate (*b*, text-fig. 15 A). Possibly, however, it is incomplete; some of the other bones of the skull show clear evidence of decay after death.

In any case we may provisionally assign this bone to the second branchial arch.

The two remaining bones probably form parts of a single arch, which will be the third branchial. They follow one another in the same line on the inside of the hyoid rod.

The anterior begins as a more or less rounded rod in front, but flattens and widens out towards its posterior end, where it becomes rod-like again (*c*, text-fig. 15 A).

The posterior bone is a short broad plate (*d*, text-fig. 15 A), with a concave margin behind; in front is a rectangular excision on its outer side to receive the plate-like process of the bone which we assigned to the first branchial arch; the remaining much diminished anterior part overlaps the anterior bone just described, while the expanded posterior part fits into the angle formed by the rod and plate-like parts on the inner side of the bone of the second branchial arch.

These four bones seem to be parts of a connected whole, so exactly are they fitted together, but it is singular that all but the most anterior of them lie dorsal to the hyoid rods. They may have suffered some displacement.

On the right side there are also four bones associated with the hyoid rod, but only three of them can be correlated with those of the left side, and these have been greatly displaced.

Lying farthest in front is a bone (*d′*) which corresponds with the posterior member (*d*) of our third branchial arch; the anterior member (*c*) which occurs on the left side is either represented by the bone *z* or missing on the right.

Behind follows a bone which probably corresponds with and completes the bone *b* of our second branchial arch; it is prolonged behind into a rather long rod which runs more outwards than backwards, crossing the direction of the hyoid rod on the right side.

The fourth bone (*e*) is not represented on the left side. It is a long, slender, slightly curved rod which is situated above and behind the one just mentioned, runs almost at right angles to the middle line, and instead of lying in an almost horizontal plane, like the bones associated with it, descends from the exterior inwards at a fairly steep angle. It just touches the rod of the second branchial arch in the middle of its course, but with what arch it was originally connected there is nothing to show.

No trace of a "body" or "copula" has been preserved. It can scarcely be doubted that some parts of the apparatus were represented by cartilage and have disappeared with the dissolution of the soft tissues.

No existing reptile, so far as I know, possesses a hyobranchial skeleton resembling that of Ichthyosaurus. Sphenodon, to which we naturally first turn for comparison, affords nothing similar; the Chelonia make a nearer approach, but still remain remote, and it is not till we reach the Amphibia that we meet with structures at all reminding us of Ichthyosaurus. The general disposition of the parts in this group is suggestively similar in such forms as Cryptobranchus, Menobranchus, Amphiuma, and Menopoma, and the last named presents many points of resemblance. It would thus seem probable that the hyobranchial apparatus of Ichthyosaurus has retained some of the primitive characters of the Amphibia, no doubt as an inheritance from the Stegocephalia, through some ancestral reptile even more primitive than Sphenodon.

Openings in the Skull.—The orbits are greatly elongated, measuring 106 mm. in length and only 55 mm. in height. OWEN has noticed the elliptic form of the orbit in other species of Ichthyosaurus, but in the present instance the original ellipticity has been exaggerated by the subsequent action of pressure. This is shown by the deformation of the bony sclerotic ring. We may fairly assume that this was originally circular; it is now elliptical, measuring 79 mm. in length and 55 mm. in height. If we increase its height by 12 mm. and correspondingly diminish its length, we shall obtain an approximation to its original form. The roof of the skull has evidently been depressed in the region of the orbit, and, judging from general indications, to the extent of 12 mm. at least. If we allow for a deformation to this extent, then the length of the orbit may perhaps be reduced to 94 mm. and the height increased to 67 mm. This, however, is still a remarkable elongation.

The nostrils are bounded by straight, approximately horizontal margins above and below, the nasal bones forming the upper margin, the lacrymal and premaxilla the lower margin. The maxillæ are just excluded from it on the face but are visible on the inner side of the lower border. The length of the opening is 48 mm., the height 6 mm.

The internal nares, 27 mm. in length, are situated only a little behind the nostrils; their posterior end is 13 mm. behind the posterior end of the nostrils, and their anterior end 36 mm. behind the anterior end of the nostrils. They are bounded by the vomers on the inner side, by the palatines behind and on the outer side, and by the maxillæ in front. A slit-like aperture between the vomers and the maxillæ continues their direction for some distance forward.

The supratemporal fossa is bounded behind by the inner and outer processes of the squamosal, in front by the postfrontal and parietal, on the outside by the post-orbital and quadrato-jugal, and on the inner side by the parietal.

The post-temporal fossa is not defined.

The inner pterygoid vacuities are bounded by the pterygoids on each side in front of the basisphenoid, which closes them behind; in front they are closed by the approximation in the middle line of the pterygoids and parasphenoid.

The outer pterygoid vacuities are bounded, first by the pterygoids and then by the palatines on the inner side, by the postorbital, quadrato-jugal and jugal on the outside, by the quadrate behind and by the maxilla in front.

Apart from the pineal foramen and the maxillary fissure which runs between the palatal bar and the facial limb of the maxilla there are no other openings visible in the skull.

Vertebræ.—Immediately below the basioccipital and basi-sphenoid lie three bones, which are evidently the conjoined axis and atlas, the third cervical vertebra, and the first vertebral intercentrum.

The bone formed by the fusion of the axis and atlas vertebræ has twice the thickness of the succeeding simple vertebra. Viewed from in front or behind, its outline is escutcheon-like, but in front the lower or median corner of the escutcheon is cut away downwards and backwards to afford a facet for the first intercentrum. In front it is slightly larger than behind. On both faces it is deeply excavated by a conical cup-like hollow, but the anterior cup is bordered by a rounded margin while the posterior is bounded by a sharp edge.

The upper surface is almost flat, but traversed by a pair of low parallel ridges which mark the boundary of the neural canal; on each side of them is the surface of articulation for the neural arch.

A lateral view suggests the presence of two conjoined vertebræ. In front a rounded ridge runs down the margin, swelling into a diapophysis above and in the middle into a well-marked parapophysis; so, too, near the middle line, *i.e.* the front of the second vertebra, is a similar ridge, also thickened near the middle into a parapophysis, and above and behind into an anapophysis. Of the third cervical vertebra, unfortunately, only the upper half is preserved.

The vertebral intercentrum is a small oval nodule, on one face gently convex from side to side, and much more convex from above downwards; on the other more nearly flat but slightly convex from above downwards and gently concave from side to side. It is not quite symmetrical, and may have suffered from distortion.

This bone must have extended below the occipital condyle and the body of the first two vertebræ, and thus occupied a good part of the interval between the paired pterygoid tubercles of the basi-occipital.

Myology.—Speculations on the muscular anatomy of the head, founded on analogy with the Crocodile, naturally suggested themselves at an early date, and interesting remarks are to be found on this subject in CONYBEARE'S suggestive paper. It is certain, however, that we possess no data by which individual muscles can be determined, and we can only discuss the question in general terms.

The most important muscles were those of the temporal region, which served to open and close the jaws; they were, no doubt, of great size, and nearly filled the roomy temporal fossa.

Although the garfish, the gavial and the dolphin possess a very similar kind of jaw, it is not to them but rather to Sphenodon that we should turn for hints as to the musculature. In this reptile the most important muscle of the lower jaw is the *capiti-mandibularis*, which occupies the greater part of the temporal fossa; it arises from the parietal, squamosal, quadrate, the inner face of the postorbital, and the fascia temporalis, and passing down inside the jugal is attached to the coronary as well as both sides of the posterior third of the lower jaw.

In Ichthyosaurus the whole surface of the parietal facing the temporal fossa evidently served for the attachment of levator muscles, which possibly corresponded with the *capiti-mandibularis* of Sphenodon, and the crest of the parietal, together with the ridge continuing from it to the squamosal, marks the margin of this area of attachment, which doubtless extended still farther, over the quadrate, the quadrato-jugal, and postorbital.

On looking downwards through the temporal fossa it will be seen at once that the cavity of the lower jaw is open above throughout its whole extent where it lies beneath this opening, *i.e.* from the surangular (coronoid) process, which lies immediately in front of the articulare, as far as Sec. 430, *i.e.* for a distance of 82 mm. There as well as on the sides of the jaw the levator muscles were inserted. It is possible also that they were partly attached to Meckel's cartilage,* which no doubt extended through the greater part of the mandibular canal.

In Sphenodon there are two other powerful levators of the lower jaw, the external and internal pterygoid muscles, which proceed from the parietal, postfrontal, post-orbital, columella, and outer face of the pterygoid, and are inserted in the middle of the ventral edge of the posterior one-fifth of the lower jaw.

It was necessary that the temporal muscles of Ichthyosaurus should be very powerful, such as the temporal fossa could accommodate, because the lower jaw acts as a lever of the third order and thus at a great sacrifice of power.

If, for simplicity, we suppose the pull of the levator muscles to be concentrated at a single point, the centre of the open channel of the lower jaw, *i.e.* at Sec. 470, the fulcrum to be a point in the middle of the articular surface, *i.e.* at Sec. 520, and the resistance to be concentrated at a point midway between the extremities of the dental alveolus, *i.e.* at Sec. 170, where as it happens are situated the most powerful teeth, then the power at this last point is only one-sixth of that applied by the muscles. In the gavial we find a similar ratio.

But this loss of power means a gain in speed, since any movement at the point of application of the power will produce a movement six times greater at the point of resistance. The jaw is, therefore, admirably adapted for snapping and the Ichthyosaurus from all that we know of it must have obtained its food by seizing fish "upon the wing."

Some depressor muscle must have existed to disengage the teeth of their prey, and this may have corresponded with the parieto-mandibularis of Sphenodon, an important muscle which arises from the hinder edge of the parietal, part of the squamosal, and the ligamentum nuchæ, and curves round for insertion at the hinder end of the mandible.

In conclusion we may now turn, with our increased knowledge of the structure of the skull, to a consideration of the affinities of the Ichthyosauria.

In the first place, however, abstraction must be made of those characters which are obviously adaptive, such, for, instance, as the elongation of the head, which has especially affected all that part lying in front of the orbit as a result of specialisation in the method of seizing food. The squamous sutures, with their excessive overlap, are another. They stand related to a marine habit, and find a parallel in the Cetacea. The density of the medium imposes no narrow limit on the use of heavy material in

* In describing the musculature of the crocodile's jaw, LUBOSCH states that a branch of the temporal muscle is inserted in part into Meckel's cartilage (W. LUBOSCH, 'Jenaische Zeits. für Naturwiss.,' vol. 51, p. 697 (1914)).

the construction of the skeleton, and the excess of bony tissue involved in these sutures is in striking contrast to the economy we find in birds, which being compelled by the rarity of the medium to combine lightness with strength, have substituted fusion for suture—a mode of union which stands at the opposite pole to squamous overlap. The enormous size of the eye is possibly another adaptive character, connected perhaps with a habit of diving to great depths, where the light is crepuscular, as suggested by DOLLO*, though even of this it may be remarked that a large orbit is a recognised character of the primitive Stegocephalia.

The resemblance to Sphenodon, pointed out and insisted on by BAUR, is obvious enough. The general structure of the skull is remarkably similar in both; in the palate of Sphenodon, which afforded LYDEKKER the key to that of Ichthyosaurus, we see the palatines pushed aside and the vomers meeting the pterygoids behind; in both the internal nares are similarly bounded, and there is a bony floor to the orbit; in both the pterygoid meets the basisphenoid in a facet, and expands, behind a plate-like columella, into an ascending lamellar process which is applied to the inner side of the quadrate; and in both the squamosal sends down a process on the inner side of the same bone, and articulates with the parietal and postfrontal.

Other points of resemblance might be cited, but we may now pass on to the differences, which are both numerous and important. In Sphenodon there is a transpalatine bone which forms with the pterygoid an important process; the pterygoid does not extend so far back as in Ichthyosaurus, and does not send down a process over the articular head of the quadrate; on the other hand, the quadrate extends so far forwards that it reaches and underlies the columella, to which it is united by suture; the jugal is a more complicated bone,† and takes a larger share in the formation of the bony floor to the orbit; the opisthotic is not free, and the stapes has acquired an exclusively auditory function; the lateral temporal fossa is open, and there is no supratemporal bone; there is a lacrymal foramen, but no lacrymal bone; there is no separate goniale (prearticulare), and no splenial bone, while the coronoid, absent in Ichthyosaurus, is present in Sphenodon.

Finally, the hyobranchial apparatus is comparatively simple, and resembles that of birds, while in Ichthyosaurus it is more complex, and recalls the Amphibia.

The resemblances between the two forms are a common inheritance from more primitive ancestors; of the differences, some are almost certainly due to subsequent specialisation, while others stamping the Ichthyosaurus as the more primitive seem to point to a remote divergence in genealogical history.

The presence of a transverse bone in Sphenodon, and its apparent absence in Ichthyosaurus, may well be due to subsequent specialisation. In Ichthyosaurus the work done by the muscles of the jaw and the application of muscular power are so distributed

* L. DOLLO, 'Bull. Soc. Belge Géol.,' vol. 21, p. 157 (1907).

† In Ichthyosaurus the function of ascending process of the Sphenodon jugal is performed by the post-orbital and quadrato-jugal plates.

that the bony floor of the skull, almost continuous from the back of the orbits to the front of the nostrils, is sufficiently strong to meet all demands upon it, and the presence of a transverse bone would be superfluous; if, therefore, originally present —and such a bone occurs in some of the Stegocephalia—it might easily disappear. In Sphenodon, however, the maxillary and palatine teeth which apply most of the work of the muscles are situated directly below the orbits, in front of the large pyriform vacuity, where the presence of a strut, such as the transpalatine supplies, is of such importance that if this bone were to be lost it would have to be replaced by some other bony growth. Again, it is necessary for the proper action of the scissor-like jaws of Sphenodon that they should bite true—that is, without any lateral play; and this is ensured by the stop or guide which the transpalatine pterygoid process supplies.

The few isolated characters possessed in common by the Chelonia and Ichthyosaurus seem to be of doubtful significance. One of the most remarkable is the separate state of the opisthotic, for this is not met with in any other group of reptiles, not even in the ancestral Cotylosaurs and Stegocephalia, where the opisthotic is represented by the paroccipital. To discover a free opisthotic we must descend as far as the fishes. Perhaps in the higher forms this character may have arisen as a special adaptation to an aquatic habit, though as against this it may be urged that the habit of some Chelonia is not aquatic, but terrestrial.

The splitting of the parietal bone into two wings is another of these common characters, but in the Chelonia the inner wing is continued downwards to articulate with the columella, though this again in both groups is lamellar.

The existing Lacertilia are less closely related than Sphenodon to the Ichthyosaurs; but, if the Aræoscelis of WILLISTON* be, as he supposes, a true lizard, their Permian ancestors made a nearer approach. The differences which distinguished Aræoscelis are numerous, thus the maxilla in its upward growth has carried the anterior end of the jugal with it, bringing this bone into contact with the prefrontal, the lacrymal being absent, and again the postfrontal, in conjunction with the jugal, excludes the postorbital from the orbit. On the other hand, the resemblances are striking, especially in the temporal region, which presents a single vacuity—the supratemporal; and they would be more so if it were possible to regard the bone which WILLISTON† names "squamosal" as the quadrato-jugal, and that which he names "tabulare" as the squamosal. This emendation, it may be remarked in passing, would lend support to WATSON's interpretation of the outer bone in the squamosal region of the lizards.

Before proceeding further it should be at once remarked that Ichthyosaurus is a true reptile,† derived in all probability from terrestrial ancestors which were equally

* S. W. WILLISTON, "Osteology of Some American Permian Vertebrates," 'Journ. Geol.,' vol. 22, p. 391 (1914). WILLISTON now places Aræoscleris in the order Protorosauria, which are distinguished by the possession of a fixed quadrate, but he thinks that further knowledge of this order may lead to its inclusion with the Lacertilia; *v.* 'Water Reptiles of the Past and Present,' Chicago, no date, p. 135.

† The characters of the vertebræ are sufficient proof of this.

reptiles. As a family the Ichthyosaurus had already attained complete expression in the Trias, and the search for its terrestrial ancestors must go further back, at least into Permian times.

The Stegocephalous Amphibia, which are the source of this and all other reptiles, were in full development during the Carboniferous, and at that time in possession of a skull which requires but few modifications to pass into that of an Ichthyosaur. We may cite the well-known Loxomma, admirably described by EMBLETON and ATTHEY,* and again recently by WATSON.† The upper surface of its skull presents us with all the corresponding bones of the Ichthyosaur, arranged in precisely the same relations to each other, and a few additional ones which need not now concern us; but, as in all Stegocephalia, the temporal region is imperforate.

The palate, so completely made known by WATSON, presents the same general resemblance—general but precise. The basi-occipital articulates with the basi-sphenoid by an anterior process, which is received in a recess; there is a long parasphenoid, but not yet reduced in height; the palatines are pushed aside; the pterygoids extend forwards to meet the vomers, backwards to overlap the quadrate, and they articulate by a facet with a basipterygoid process. Further, the composition of the lower jaw is the same as that of Ichthyosaurus.

On the other hand, the floor formed by the palatine, pterygoid, and transpalatine bones is continuous and not interrupted by interpterygoid vacuities.

Loxomma is an amphibian, but in the Permo-carboniferous rocks we encounter a group of lowly but genuine reptiles which retain a precisely similar cranial structure. These are the Cotylosauria; reptiles with no neck or next to none, short legs and in many cases a long body; just the kind of material out of which we might imagine the Ichthyosaurs to arise.‡ They have acquired interpterygoid vacuities,§ but are still without a supratemporal fossa, and to discover temporal vacuities at all we must now ascend a step higher, into the so-called Theromorpha, a motley assemblage of forms which do indeed possess these openings, but none of them homologous with that of Ichthyosaurus.

It would seem reasonable therefore to conclude that the Ichthyosauria are directly descended from a Cotylosaurian ancestor in which the supratemporal fossa arose as an independent development. The Protorosauria may well be a collateral stem, and

* D. EMBLETON and T. ATTHEY, "On the Skull and some other Bones of *Loxomma Allmanni*," 'Ann. and Mag. Nat. Hist.,' vol. 14, p. 38 *et seq.* (1874).

† D. M. S. WATSON, "The Larger Coal Measure Amphibia," 'Mem. Manchester Lit. and Phil. Soc.,' vol. 57, p. 1 *et seq.* (1912–13).

‡ The neck in any case would probably be reduced in adaptation to a fish-like habit.

§ CASE argues that these could not have arisen in a Cotylosaurian ancestor, because the Cotylosaurs do not possess more than two bones below the parietal, but unless Seymouria be excluded from the Cotylosaurs this objection will not hold. E. C. CASE, "Paleozoic Reptilia and Amphibia," 'Bull. Geol. Soc. Am.,' vol. 23, p. 200 (1912).

perhaps, as VON HUENE* urges, the Proganosauria (Mesosaurus) also, but until the structure of the temporal region in this order is better known its claims must remain in abeyance.

The formation of temporal vacuities might have occurred independently in several groups of Cotylosaurus; thus regarded it was not a single event but a general process arising probably from a demand for greater efficiency in the biting apparatus. This would be brought about in the first place by a greater development of the muscles in the temporal region, and this again would lead to various modifications in the bony skull.† To give increased length to these muscles the roof in the posterior region might be raised farther from the floor. The increased strain thrown upon the plate-like bones could be met by a thickening along lines of greatest stress, and a system of ties and struts might thus be developed which would render unnecessary lamellar expansions. These would then disappear, and an open framework would replace the continuous sides of a box. In Ichthyosaurus the process is still incomplete, in Sphenodon it has advanced as far as the formation of two great temporal windows, but the bones which form the frame still retain lamellar flanges as a reminiscence of an earlier stage; though these flanges are still functionally active, giving rigidity on the principle of the angle-iron. It may be noticed by the way that in Sphenodon this "angle-iron" form is most pronounced in the ascending process of the jugal, just behind the orbit, where great strength is required to resist the pressure of the chief biting-teeth and great rigidity to prevent any lateral movement of the upper jaw.

Apart from mere speculation we cannot fail to recognise in the Ichthyosaurian skull many vestiges of a primitive state, which recalls in a striking manner the ancient Cotylosaurs. On this point there seems to be a general agreement; REPOSSI‡ has even argued in favour of a direct descent from the Stegocephalia; with certain reservations WILLISTON is prepared to accept this view, though on the whole he inclines more towards the Protorosauria or Proganosauria, and VON HUENE is decidedly of opinion that the Ichthyosauria and Proganosauria (Mesosaurus) are descended from a common Cotylosaurian ancestor. Long ago BAUR§ and BROOM‖ arrived at similar conclusions, BAUR pointed to the Proganosauria as the immediate ancestors of the Ichthyosauria, and BROOM stated that "the Ichthyosauria appear to have sprung directly from the primitive group (Cotylosauria) or to have branched off early from the Palæohatteria."

Intermediate links may reward future exploration, meanwhile it is satisfactory

* F. VON HUENE, "Die Cotylosaurier der Trias," 'Palæontographica,' vol. 59, p. 100. See also S. W. WILLISTON, 'Journ. Morph.,' vol. 23, p. 640 (1912).

† W. K. GREGORY and L. A. ADAMS, "On the Temporal Fossæ of Vertebrates in Relation to the Jaw Muscles," 'Science, N.S.,' vol. 41, p. 763 (1915).

‡ REPOSSI, 'Atti d. Soc. Ital. di Sci. Nat.,' vol. 41, p. 361 (1902).

§ G. BAUR, 'Zool. Anz.,' No. 240, 1886.

‖ R. BROOM, 'Proc. Zool. Soc.,' vol. 2, pp. 162–190, in particular p. 187 (1901).

to find that the oldest known Ichthyosaurs of the Trias, although they do not present any fundamental departure from the type, yet at least afford us indications of an approach towards a less specialised form.*

In conclusion, I should like to express my thanks to those kind friends who have assisted me in this investigation. In the first place to my wife for many industrious hours spent in building up the reconstruction, and next to Mr. GOODRICH, who has given me freely from his stores of knowledge, and helped me by discussion. To my indefatigable assistant, Mr. BAYZAND, I am indebted for the work of illustration and for help in many other ways.

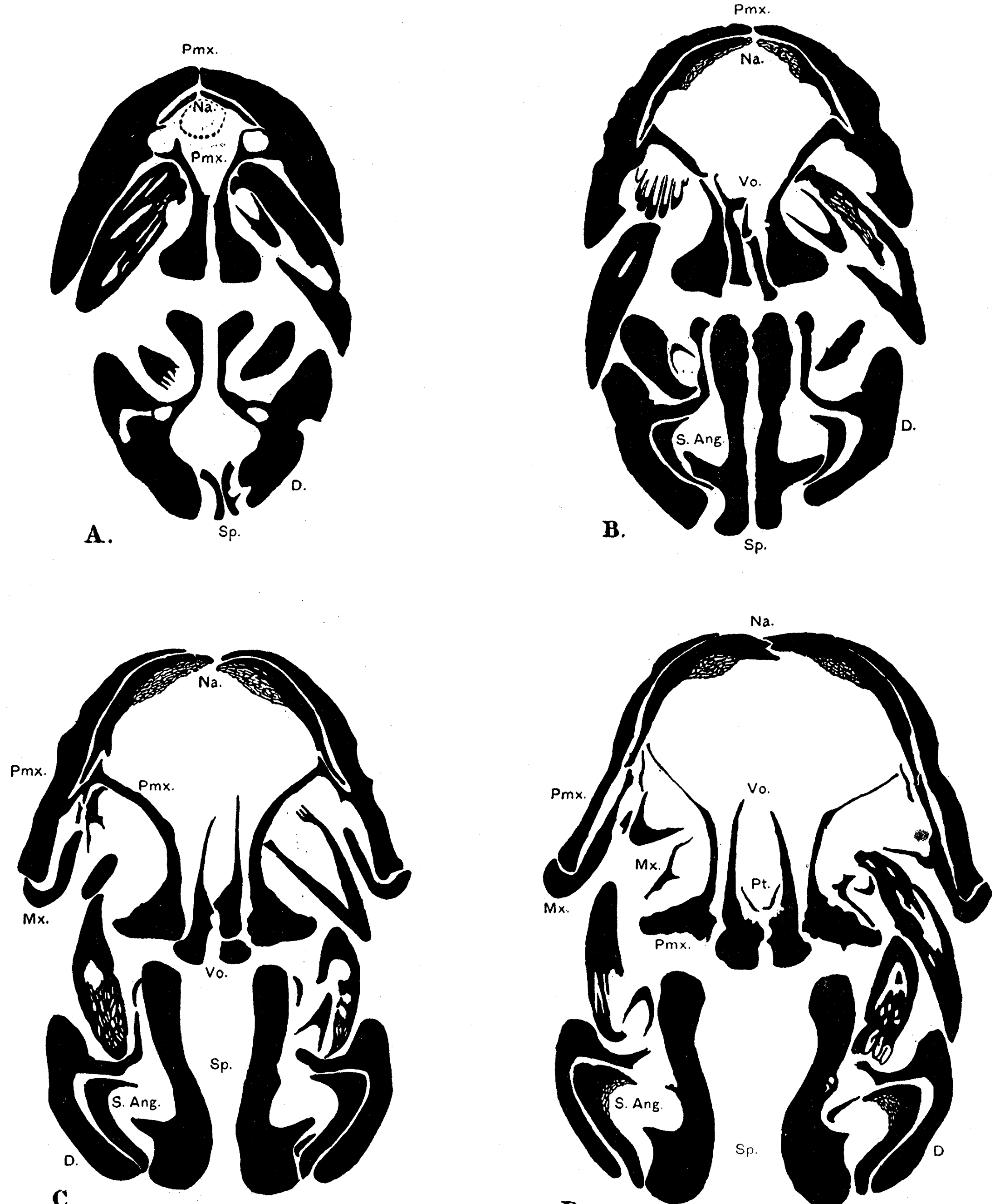
Postscript (March 15, 1916).—Most of the attempts at interpretation of chance sections through the skull of Ichthyosaurus have so far proved only partially successful, nor, considering how vague was our knowledge of its internal structure, could the result have well been otherwise. Now, however, that we possess a series of sections complete from end to end the way is made plainer, and I have therefore ventured upon a study of some isolated slices, chiefly those preserved in the Natural History Collection of the British Museum, for access to which I am indebted to the kindness of Dr. SMITH WOODWARD and Dr. C. W. ANDREWS.

One of the most instructive specimens is a beak from the Lower Lias of Lyme Regis. Its structure, admirably preserved and undistorted by pressure, has been displayed by a number of transverse sections in which the bones by their jet-black colour are sharply defined from the light grey matrix. These sections afford a welcome confirmation to our previous observations, and throw some additional light on a region which is less perfectly preserved in our specimen of *I. communis*, var. *a*; but as will be seen from the illustrations (text-fig. 16) the constituent elements have a very different character from that species, being distinguished by a much slenderer and more graceful form, which confers great lightness and elegance on the whole structure. Unfortunately, the species is undetermined.

The first section (text-fig. 16 A) shows the premaxillæ with their alveolar processes, which are perforated near the base by a canal for a nutrient vessel, and the nasal bones, on the point of disappearing, which terminate below in the acute angle made by the base of the alveolar processes with the premaxillæ from which they spring. In the middle line, below the nasals, is a clear circular area of matrix, which in an adjacent section is seen to be surrounded by a thin layer of bone: it seems to mark the course of a median vessel. The large teeth are in process of being superseded by their successors, which induce absorption on one side near the base, as was pointed out long ago by the earlier observers. In the lower jaw a vascular canal is present at the root of the alveolar process of the dentary bone, and on one side (the left) this is seen to be continued into a lateral branch which opens into an

* J. C. MERRIAM, "Primitive Characters of the Triassic Ichthyosaurs," 'Bull. Geol. Soc. Am.,' vol. 14, p. 536 (1903).

external longitudinal vessel, occupying a groove such as is seen on the side of the right dentary. The splenials are represented by the extremities of their lower branch.



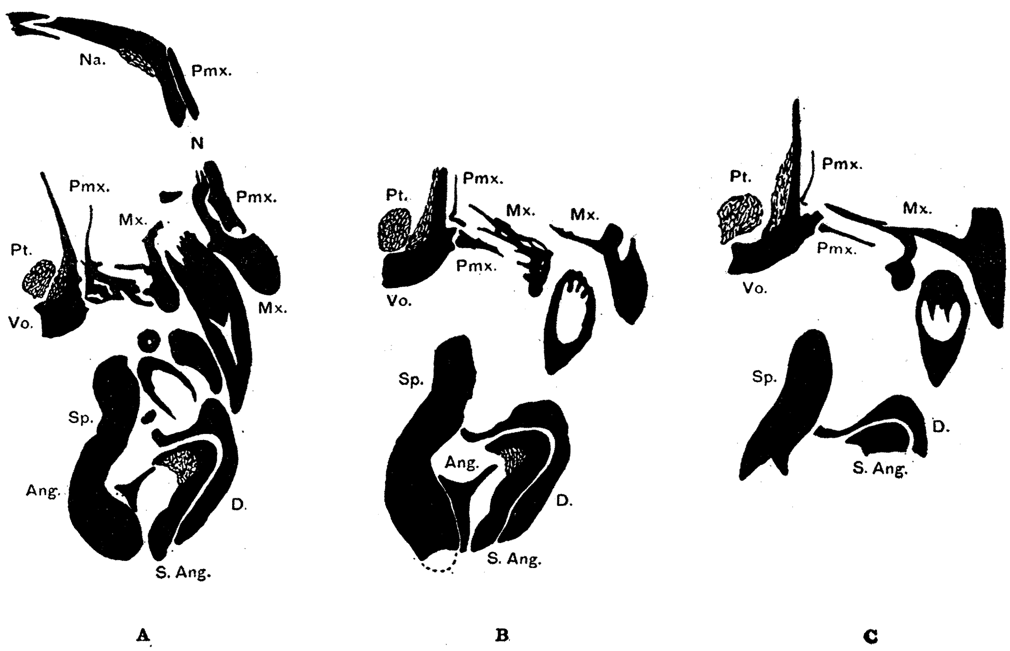
TEXT-FIG. 16.—Transverse sections of the anterior part of the skull of an undetermined species of Ichthyosaurus from the Lower Lias of Lyme Regis, preserved in the British Museum. (Nat. size.)

In the next section (text-fig. 16 B), taken a little farther backwards, the vomers make their appearance as thin vertical plates, very unlike the swollen rod-like vomers of this region in *I. communis*, var. *a*. The nasal bones, larger, but still completely concealed by the premaxillæ, articulate with the sharp inflection near the base of the alveolar processes of those bones; the upper part of their ventral side presents an open spongy structure, which in other specimens, but not in this, disappears, leaving behind a well-defined sinus.

In the lower jaw the splenial is shown, just posterior to its point of bifurcation, as an undivided plate produced into a lateral extension near the base—a feature I have not observed in other specimens, and probably specific. With the upward development of the splenials the alveolar processes of the dentary bones have become much reduced in thickness. The surangulare is also now visible.

In the third section (text-fig. 16 C) the maxillæ make their appearance as curved plates, embracing the edge of the premaxillæ. The articulation of the nasal bones with the alveolar process of the premaxillæ has become more pronounced, and the vomers are more clearly differentiated into a thicker part below and a thinner part above. In the lower jaw the alveolar process of the dentary is still further reduced, and the splenial correspondingly enlarged.

In the fourth section (text-fig. 16 D) the premaxillæ no longer completely conceal the nasals which emerge from beneath them; the alveolar processes are separated from their origin, and terminate in thin lamellæ against the nasals; the maxillæ still bend round the edge of the premaxillæ, but extend upwards on the inner side of these bones to articulate with the descending extremities of the nasals, giving off at the same time a lateral process towards the interior, which bends round to form the boundary of the alveolar groove, from which the premaxillæ are now excluded; the pterygoid bones, cut across near their anterior termination, are visible between



TEXT-FIG. 17.—Transverse sections of the anterior part of the skull of an undetermined species of Ichthyosaurus from the Lower Lias of Lyme Regis, preserved in the British Museum. (Nat. size.)

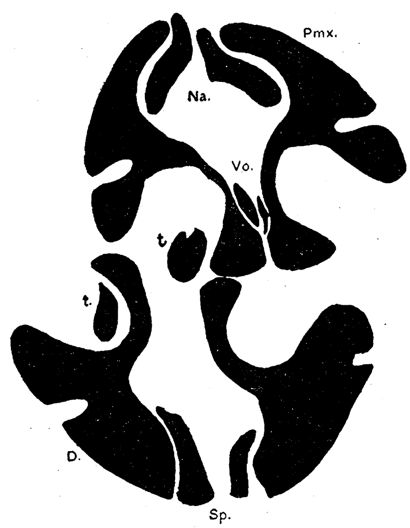
the vomers; they have here the form of thin vertical lamellæ, thus differing, like the vomers, from the corresponding bones in *I. communis*, var. *a*; they also extend farther forward than in that form. In the lower jaw the alveolar process of the dentary no longer extends up to the summit of the splenial, and the concavity of the surangulare presents the same spongy texture as was noted in the nasal bones, and as is not uncommon in similar portions in the vomer elsewhere.

Just beyond this section we enter the region of the external nares, and here, where the structure would be most interesting, it becomes incomplete. It will be seen (text-fig. 17, A–C) that the maxillæ have changed their form considerably, the outer moiety has grown more massive, and the palatal plate, much enlarged, extends beyond the alveolus towards the vomers. The bottom of the alveolar groove is perforated by a foramen (text-fig. 15 B), as it is also in the same region in our specimen. The base of the vomers is expanded into a plate-like process on each side, and a little beyond the section shown in text-fig. 17 C the outer process enters into articulation with the palatal plate of the maxilla. This lateral expansion of the vomers occurs in front of the internal nares, and we may presume will disappear when these apertures are reached, to be resumed as soon as they are passed.

The sections under description recall Secs. 276–289 of our series and may be compared with Sec. 288 of text-fig. 2. The most obvious differences, which are probably specific, are the further extension forwards of the pterygoids, the basal expansion of the vomers, and the continuation of the maxillæ towards the middle line beyond the alveolar groove.

In the lower jaw the angulare makes its first appearance.

There is an interesting section (text-fig. 18) in the British Museum Collection taken across the rostrum of a specimen assigned to that sword-fish of the Reptilia, *Ichthyosaurus longirostris.* It is not altogether dissimilar from the first figured section (text-fig. 16 A) just described, but the form of the premaxilla is different, the lateral nutrient canals are more deeply sunk into the substance of this bone, and the alveolar processes not only originate at a lower level but are continued downwards far beyond the inferior margin of the body of the premaxilla. The absence of nutrient canals at the base of these processes is accidental.



TEXT-FIG. 18.—Section across the rostrum of *I. longirostris* (?), from a specimen in the British Museum (Nat. size.)

The nasal bones have assumed a rather unusual attitude, which is not, I think, due to displacement; it is almost repeated by the nasals of the sections to be next described, and these are certainly in their natural position.

In contrast with the preceding specimen the teeth are small, as they are in recognised examples of *I. longirostris*.

The University Museum, Oxford, possesses a well-preserved example of that part of the snout of *I. longirostris* which in this species projects beyond the lower jaw like the rostrum of the sword-fish. It is 22 inches in length and posteriorly resembles a policeman's baton, but in front it diminishes to a pointed extremity. A section through this reveals the structure shown in text-fig. 19. This is not altogether unlike the section through the upper jaw just mentioned (text-fig. 18) but the alveolar processes are distinguished by their greatly expanded base, enlarged nutrient canals, and extremely spongy structure. The teeth are very small and lie scattered in the alveolar groove.

A polished slab from Lyme Regis bearing the number R. 1759, 44027 in the British Museum Collection, presents sections across the skull (text-fig. 20), which, though doubtfully attributed by LYDEKKER to *I. communis*, closely resemble those given by FRAAS of *I. quadriscissus*, which LYDEKKER assigns in part to *I. acutirostris*. They differ in several important details from any we have yet described.

The body of the premaxilla is short and thick and flanged outwards below the deeply incised channel for a lateral longitudinal vessel. The nasal bones differ considerably from any we have yet encountered. We may distinguish in them an upper from a lower limb, which pass into each other by a fairly sharp angle. The lower, which is concealed by the premaxilla, is of unusual thickness and several times thicker than the upper limb*; its squared lower end fits into the angle made by the alveolar process with the body of the premaxilla. The massive structure thus produced is in striking contrast with that shown in text-fig. 16.

The vomers appear to be approaching their termination in front. The bone marked x is probably a displaced fragment.

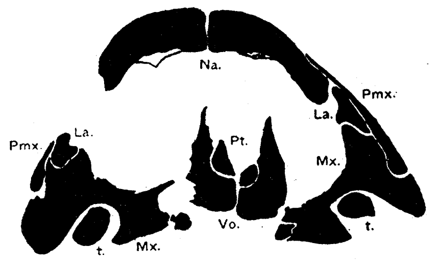
In a region where the nasal bones are so largely displayed at the surface we should expect the maxillæ to be fairly well developed, but in Sec. B they are already on the point of disappearance, and in Sec. A they have vanished. In the lower jaw the angulare is still well represented.

The last specimen to which we shall refer is of particular interest in this study, since it is a recognised example of *I. communis* and thus affords an opportunity for comparison. Unfortunately it is much distorted and the sutures are in many cases ill-preserved. Text-fig. 21 represents a section taken rather obliquely across the skull, passing on the right side just in front of the external naris and on the left through that aperture. In general character the structure much resembles our variety in the same region but differs in several details. The right side may be compared with our Sec. 273, in which the premaxillæ, closing the nostrils in front, extend, there as here, continuously from the maxillæ to the nasal bones; but in

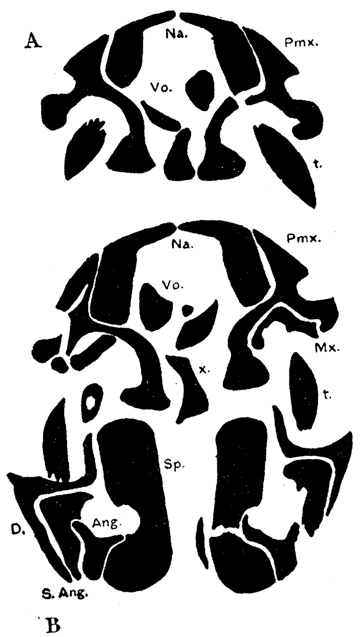
* Thus just the reverse of what we find in *I. communis* and *I. communis*, var. *a.*, in both of which the descending limb of the nasal is narrower than the roofing limb.

Sec. 273 the lacrymal is not present beneath the premaxilla as it is in text-fig. 21, nor in our series does it make its appearance till we reach Sec. 295. The left side may be compared with our Sec. 295 (*cf.* text-fig. 2, Sec. 296). On both sides the pterygoid bones extend farther forward than in our specimen, they are evidently

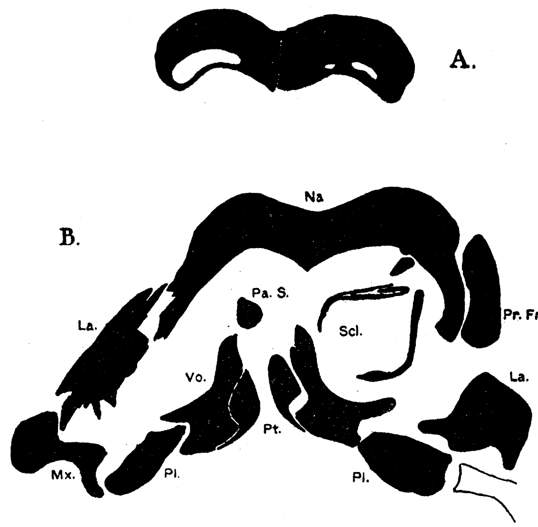
TEXT-FIG. 19.



TEXT-FIG. 21.



TEXT-FIG. 20.



TEXT-FIG. 22.

TEXT-FIG. 19.—Transverse section across the premaxilla of *I. longirostris*, from a specimen in the University Museum, Oxford. (Nat. size.)

TEXT-FIG. 20.—Sections across the rostrum of *I. quadriscissus* (?), Lyme Regis, from a specimen in the British Museum. ($\times \frac{1}{2}$.)

TEXT-FIG. 21.—Section across the skull of *I. communis*, Lyme Regis, from a specimen in the British Museum. ($\times \frac{1}{2}$.)

TEXT-FIG. 22.—The same, but from a region slightly farther back. A. The nasal bones, showing sinuses. B. Complete section. ($\times \frac{1}{2}$.)

present in a region which corresponds with our Sec. 273, while in our series we must go backward as far as Sec. 300 before we encounter their extreme anterior ends.

As a point of detail attention may be called to the sinuses which are beginning to appear on the ventral side of the nasal bones; in a section taken a little behind the preceding they have become larger and better defined (text-fig. 22 A).

The next section (text-fig. 22 B) crosses the skull obliquely behind the nostrils on on each side, and on the right enters the front of the orbit. The left side may be compared with our Sec. 326 (text-fig. 2), but it shows no trace of the internal naris, which is still present in Sec. 326, and even so far back as Sec. 338.

The pterygoids also present a characteristic difference, for they are produced downwards and outwards, closely overlapping the base of the vomers instead of being overlapped by these bones as they are in Sec. 326.

The right side corresponds with Secs. 343–346 (*cf.* Sec. 349, text-fig. 2). The base of the lacrymal is excavated above the maxilla (indicated by a thin line) producing a cavity like that already alluded to (p. 88), and doubtfully interpreted as the lacrymal duct.

The resemblances in these sections outweigh the differences, and we may fairly conclude that the specimen on which our reconstruction is based is nearly allied to *I. communis*, though not identical with it.

Conversion of Bone into Coal.—In conclusion a brief reference may be made to the colour of the bones of Ichthyosaurus. My friend Prof. DOLLO has offered the interesting suggestion that in some cases the colour of fossil bones may be due to the deposition of pigment within them during life, but, apart from the general question, I do not think this can have been the case with Ichthyosaurus, the bones of which pass from jet black at one end of a series, through various shades of brown, to light grey at the other. It has been shown conclusively that the bones of Coccosteus from the Old Red Sandstone have in some cases been converted into a true coal and have thus acquired a black colour,* and a similar change may well have occurred in other cases. To investigate this question a small fragment of an Ichthyosaurus bone was reduced to powder, treated with strong hydrochloric acid, and after washing with water and alcohol placed in a diffusion column. The powder floated in a zone ranging from 1·47 to 1·60 in density, thus within the limits of the density of true coal. A small quantity of the powder was then ignited on platinum foil ; it first gave off an empyreumatic odour, and then burnt like glowing charcoal, without flame, but with a strong smell of burning sulphur, leaving behind a considerable residue of reddish ash. The presence of iron and sulphur thus indicated was due to the presence in the bone of iron pyrites, which indeed was visible under a lens. The density observed is thus in excess of the true density of the carbonaceous matter.

A dark-brown bone similarly treated afforded a residue with a density of 1·37 ; it burnt without flame and left a greyish white ash. Heated in a closed tube it gave off a quantity of evil-smelling tar and a combustible gas.

Some household coal was subjected to similar treatment, it had a density of 1·33 and behaved on ignition in precisely the same way.

* SOLLAS and SOLLAS, "An Account of the Devonian Fish, *Palæospondylus Gunni*," 'Phil. Trans.,' vol. 196, B, p. 271 (1904).

Notwithstanding these resemblances, the substance which gives colour to the Ichthyosaur bones is not identical with Carboniferous coal, for on treatment with alcohol a part of it dissolves, yielding a yellow or brownish-yellow solution, and this, on evaporation, leaves a yellow or reddish-yellow structureless resin-like residue, which is soluble in caustic alkali, and is precipitated from its alkaline solution by hydrochloric acid, thus indicating the presence of a humic acid.

But these are precisely the characters by which brown coal is distinguished from Carboniferous coal; and thus, just as the Palæozoic bone coal (furnished by Coccosteus) agrees with the Palæozoic plant coal, so does the Neozoic bone coal (furnished by Ichthyosaurus) agree with the Neozoic plant coal.

It would thus appear that in Ichthyosaurus, as in Coccosteus, the original elasticin or ossein of the bone has not infrequently been transformed into some kind of coal —"stone" coal in the one case, brown coal in the other; sometimes the ossein has almost completely decomposed before mineralisation has set in; the fossil is then almost devoid of colour, and leaves scarcely any organic residue on treatment with acid; sometimes it has passed into a "brown" coal (which varies in shade from brown to black), and on the presence of this the colour of the fossil bones depends.

EXPLANATION OF ABBREVIATIONS.

Ang.	Angulare.
B.O.	Basi-occipital.
B.S.	Basisphenoid.
Br.	Branchial arch.
Col.a.	Anterior columella.
Col.p.	Posterior columella.
D.	Dentary.
E.O.	Ex-occipital.
Fr.	Frontal.
Gon.	Goniale.
Hy.	Hyoid.
Ju.	Jugal.
La.	Lacrymal.
Mx.	Maxilla.
Mx'.	Alveolar or palatal process of maxilla.
Na.	Nasal.
Op.Ot.	Opisthotic.
Pa.	Parietal.
Pa.S.	Parasphenoid.
Pl.	Palatine.
Pmx.	Premaxilla.
Pmx'.	Alveolar or palatal process of premaxilla.
Pn.f.	Pineal foramen.
Pr.Fr.	Prefrontal.
Pr.Ot.	Pro-otic.
Pt.	Pterygoid.
Pt.Fr.	Postfrontal.
Pt.Or.	Postorbital.
Qu.	Quadrate.
Qu.Ju.	Quadrato-jugal.
S.Ang.	Surangulare.
S.mx.	Septomaxilla.
Scl.	Sclerotic plate.
Sq.	Squamosal.
St.	Styloid.
Verts. 1 *and* 2	First and second vertebræ.

DESCRIPTION OF PLATE.

PLATE 1.

Fig. 1.—Basi-occipital of a young Ichthyosaurus from Lyme Regis. 1*a*, dorsal; 1*b*, lateral; 1*c*, ventral view.

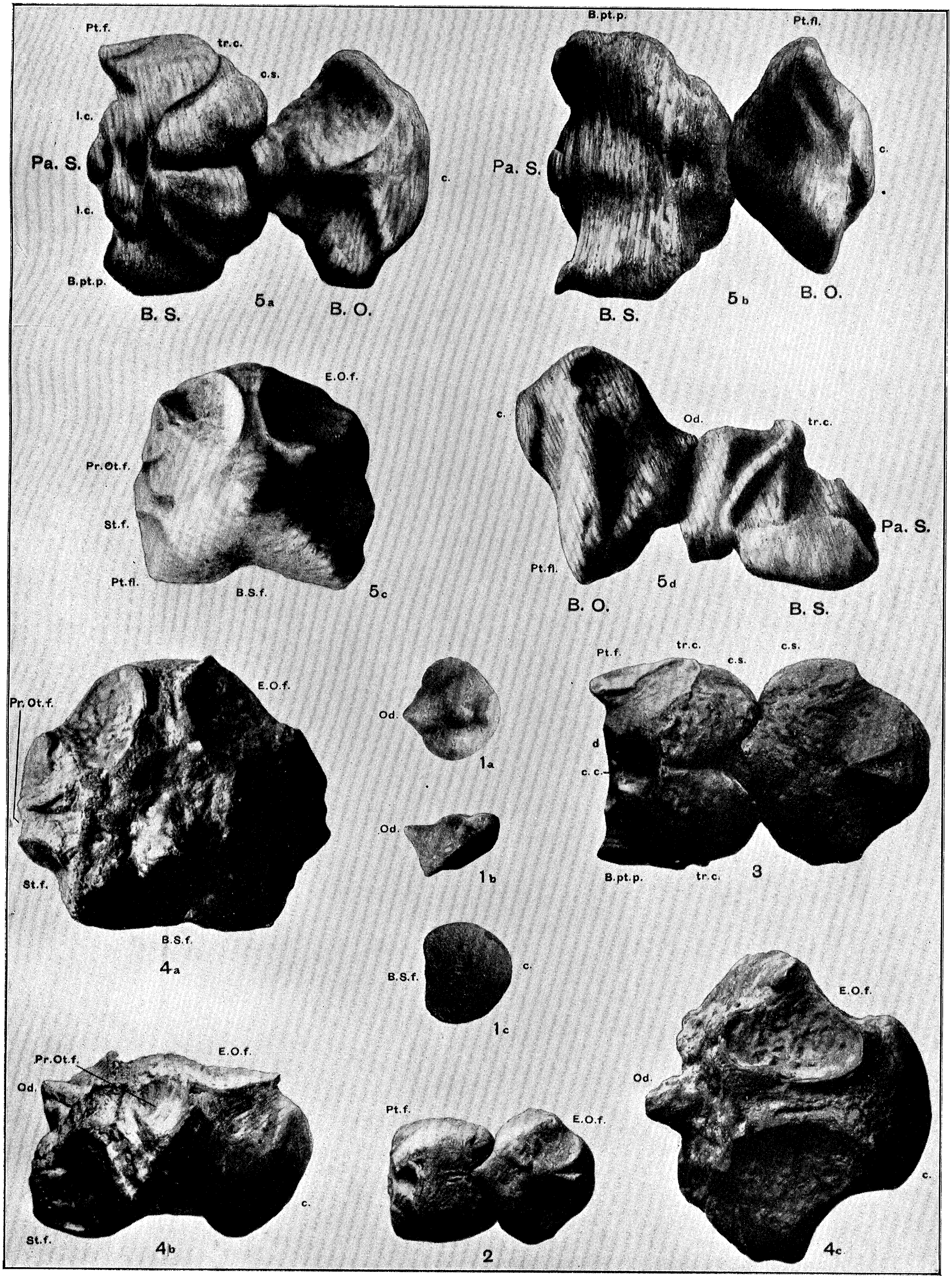
Fig. 2.—Basi-occipital and basisphenoid of a young Ichthyosaurus from Lyme Regis, shown in articulation with each other.

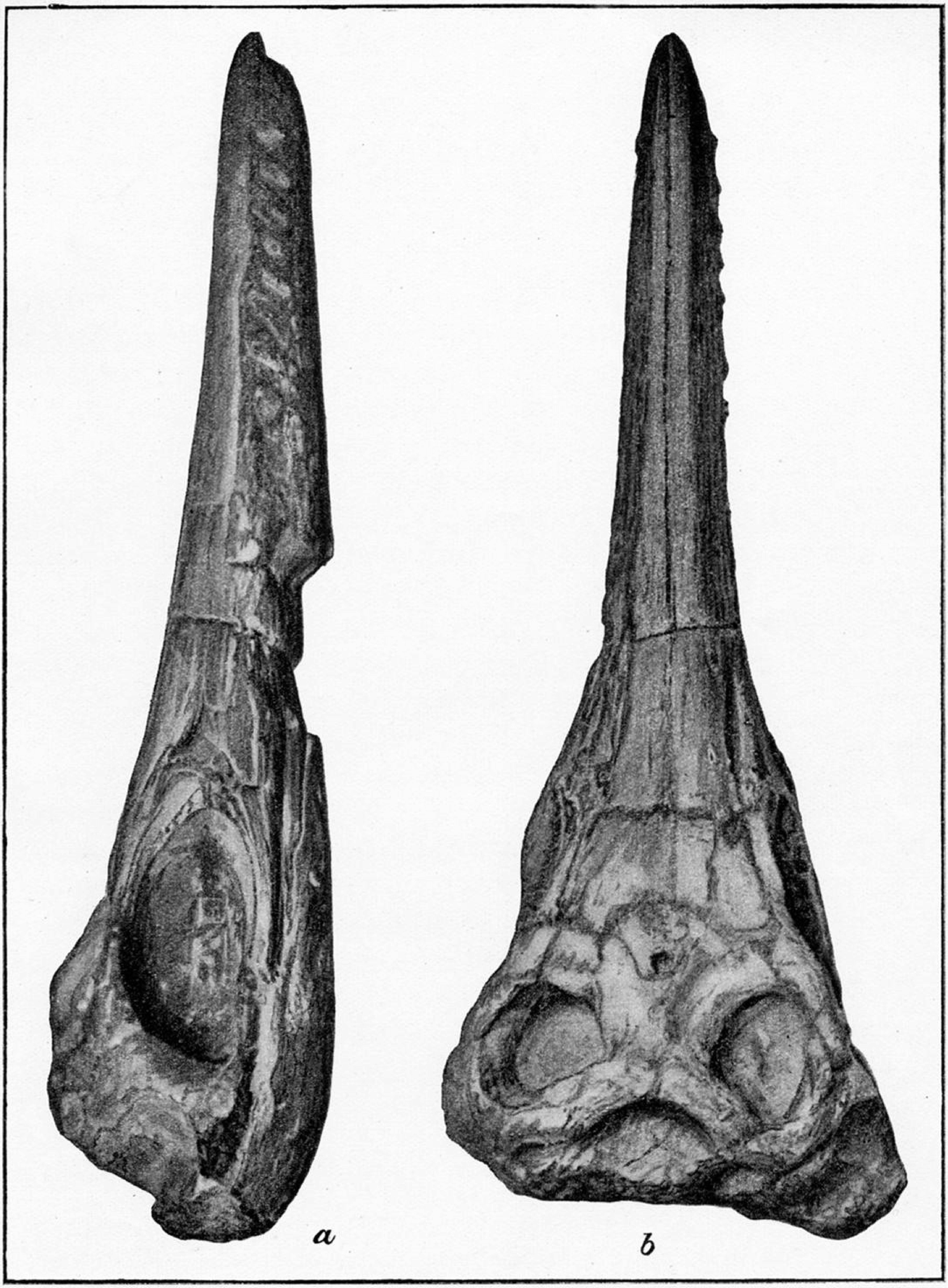
Fig. 3.—Basi-occipital and basisphenoid of an older specimen, also articulated together, and displaying roughened surface for cartilage. Lyme Regis.

Fig. 4.—Basi-occipital of a different species of Ichthyosaurus from Lyme Regis. 4*a*, anterior; 4*b*, lateral; 4*c*, dorsal view.

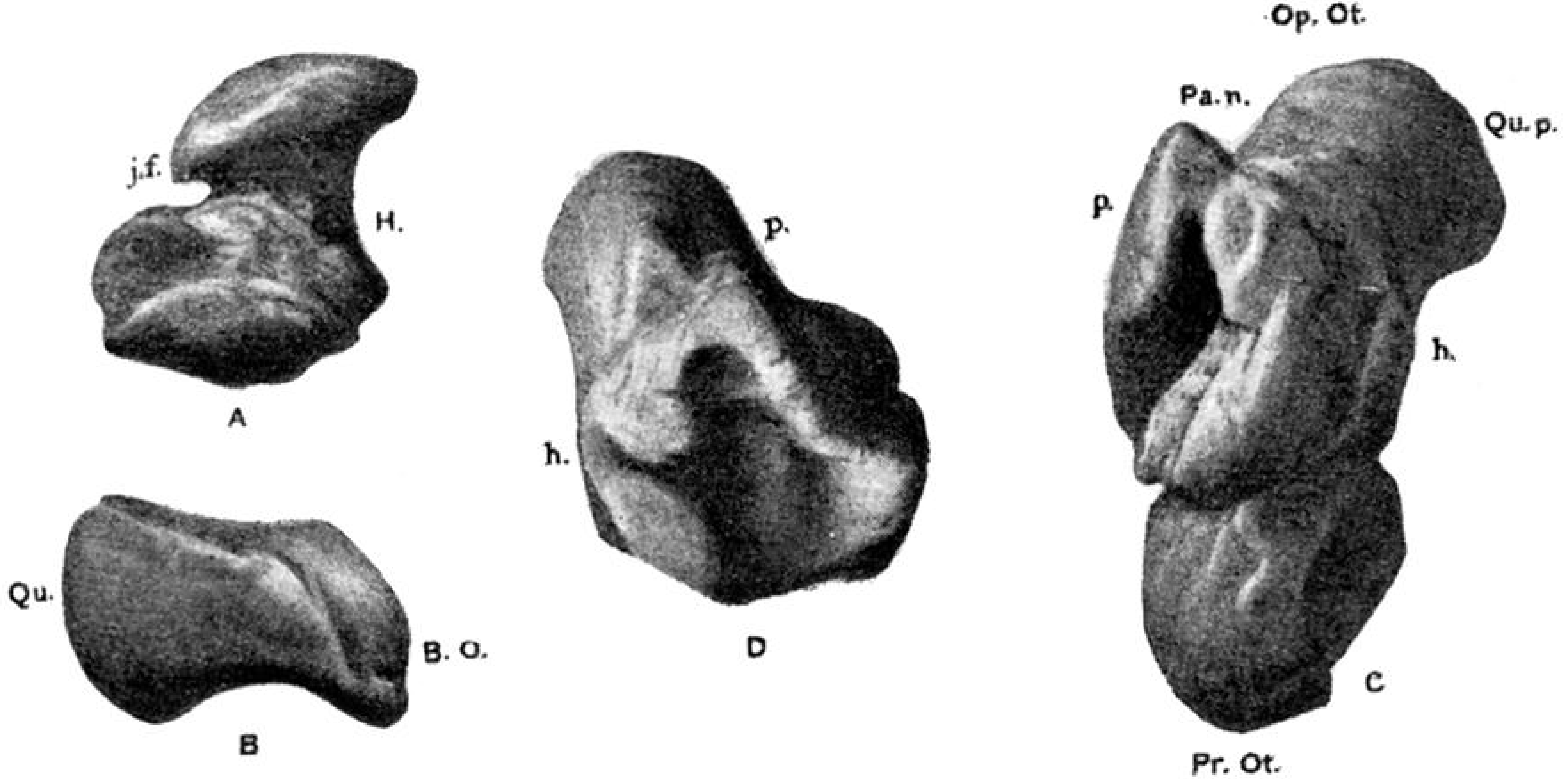
Fig. 5.—Basi-occipital and basisphenoid from the reconstructed skull. 5*a*, the bones in articulation seen from above; 5*b*, from below; 5*c*, basi-occipital seen from in front; 5*d*, the bones in articulation seen from the side.

EXPLANATION OF ABBREVIATIONS:—*B.pt.p.*, basipterygoid process; *B.s.f.*, articular surface for basisphenoid; *c.*, occipital condyle; *c.c.*, carotid canal; *c.s.*, surface for cartilage; *d.*, oval depressions in place of the lower cylindrical processes; *E.o.f.*, articular surface for exoccipital; *l.c.*, lower cylindrical process; *Od.*, odontoid peg of basi-occipital; *Pt.f.*, pterygoid facet; *Pt.fl.*, pterygoid flange; *Pr.ot.f.*, surface of articulation for pro-otic; *St.f.*, articular surface for stapes; *tr.c.*, transverse crest. (All the figures $\times \frac{8}{9}$.)

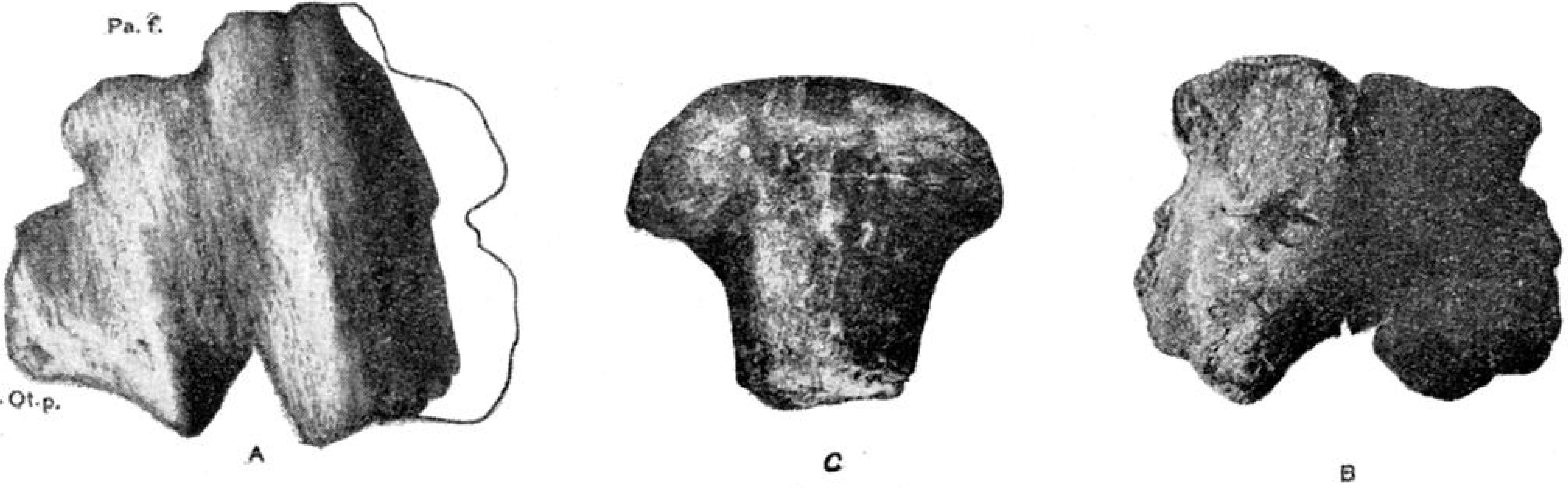

Pt.f.
tr.c.
c.s.
l.c.
Pa. S.
l.c.
B.pt.p.
B. S.
5a
B. O.
c.
B.pt.p.
Pt.fl.
Pa. S.
c.
B. S.
5b
B. O.
E.O.f.
Pr.Ot.f.
St.f.
Pt.fl.
B.S.f.
5c
c.
Od.
tr.c.
Pa. S.
Pt.fl.
B. O.
5d
B. S.
Pr. Ot.f.
E.O.f.
St.f.
B.S.f.
4a
Od.
1a
Od.
1b
B.S.f.
c.
1c
Pt.f.
tr.c.
c.s.
c.s.
d
c. c.
B.pt.p.
tr.c.
3
Pr.Ot.f.
E.O.f.
Od.
St.f.
c.
4b
Pt.f.
E.O.f.
2
E.O.f.
Od.
c.
4c



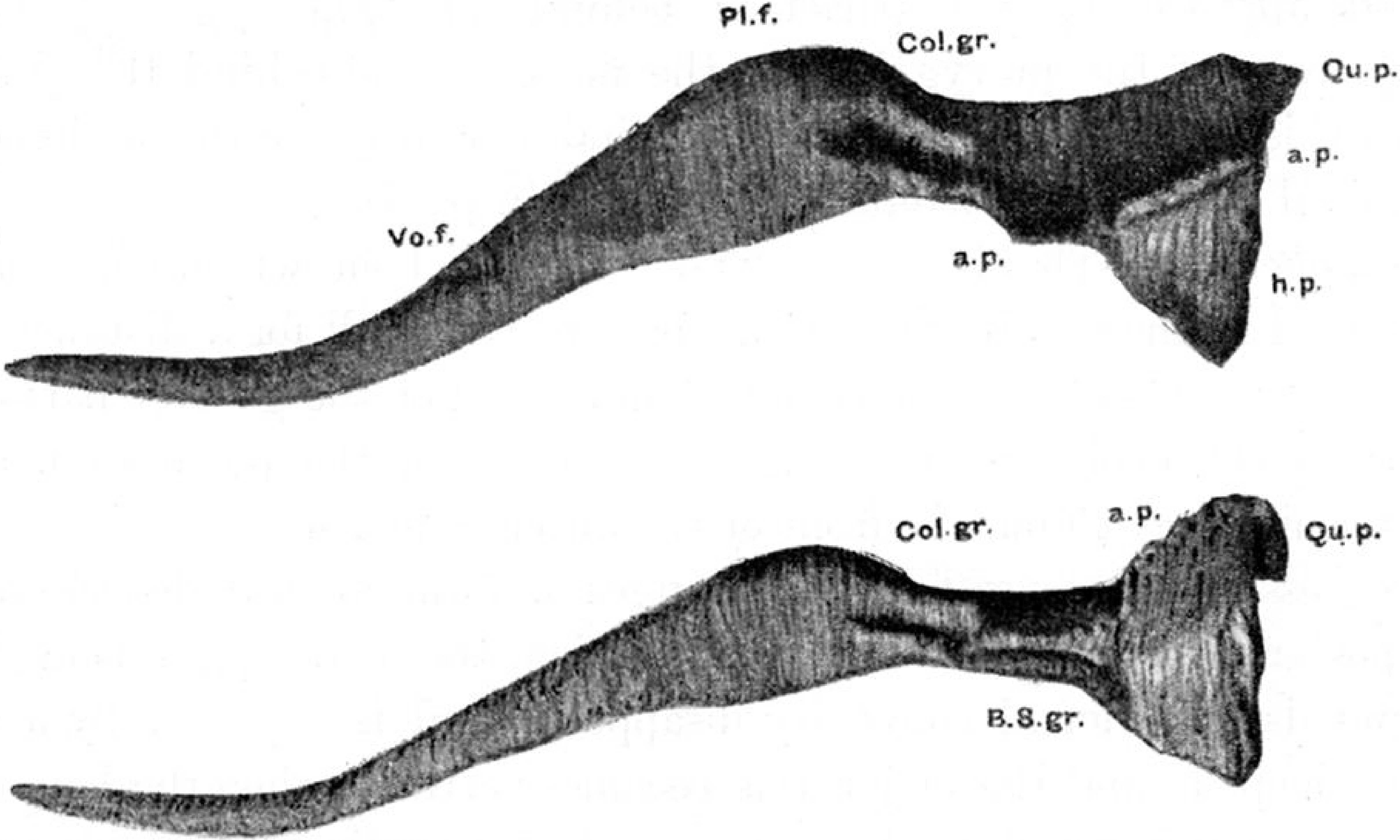
TEXT-FIG. 1.—Lateral (*a*) and dorsal (*b*) view of the skull of *I. communis*, var. *a*, from which the transverse serial sections were obtained. ($\times \frac{1}{3}$.)



TEXT-FIG. 7.—A. Right exoccipital seen from the front; *j.f.*, jugular notch; H, on a line with the foramina for the twelfth nerve. B. Left stapes seen from behind; *Qu.* articular surface for quadrate, *B.O.* for basi-occipital. C. Right opisthotic and pro-otic; *p.* posterior and *h.* horizontal semicircular canal (the latter concealed); *Pa.n.*, parietal incisure; *Qu.p.*, quadrate head. D. Left opisthotic: in this the horizontal semicircular canal (*h*) is visible. (× $\frac{1}{2}$.)



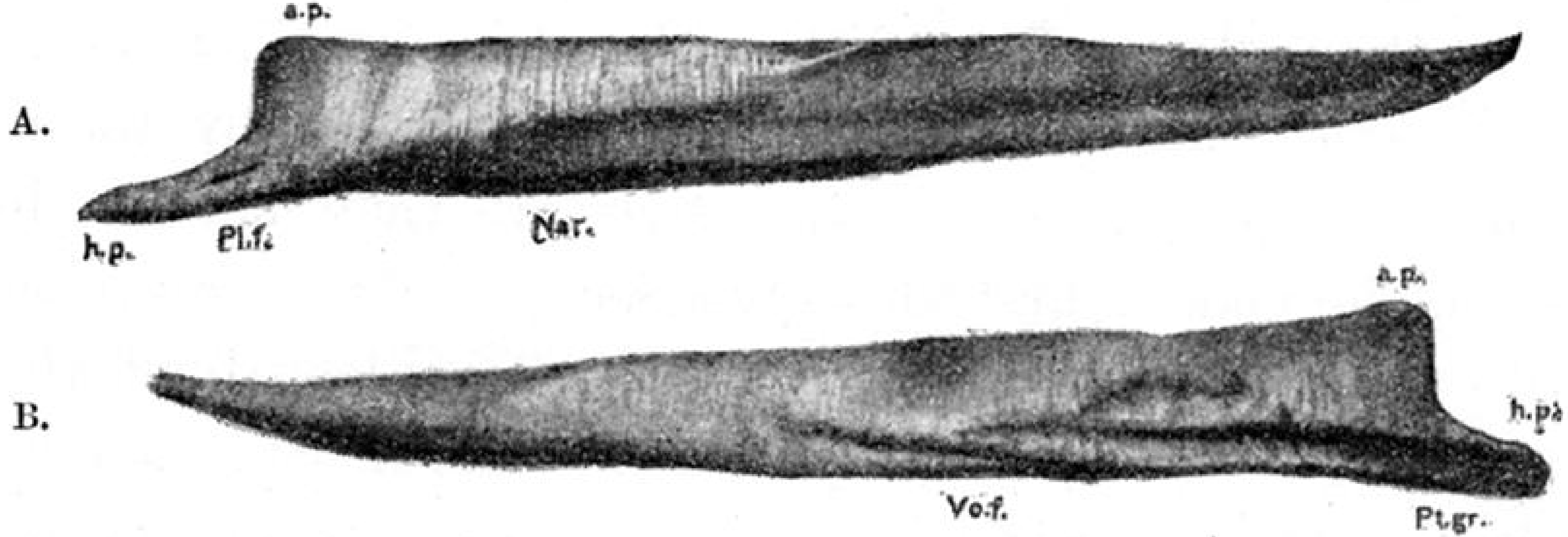
TEXT-FIG. 8.—A. Supra-occipital bone of the reconstruction. *Pa.f.*, articular surface for the parietal; *Ep.ot.p.*, epiotic process, with impressions of posterior semicircular canals. B. Supra-occipital bone of an Ichthyosaurus from Lyme Regis for comparison. C. Cast taken from the inner surface of B, showing the posterior part of the lobes of the cerebellum. ($\times \frac{1}{2}$.)



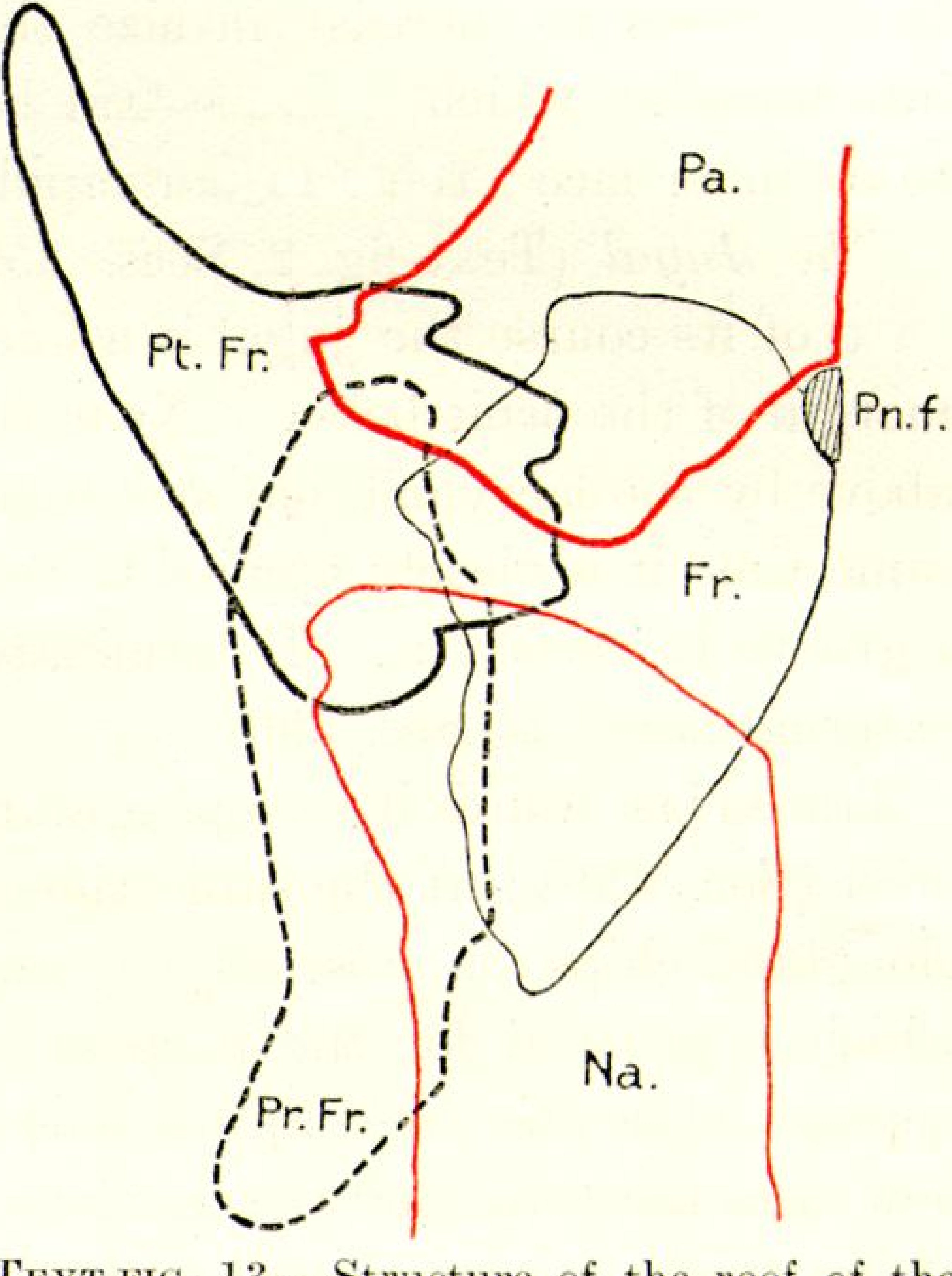
a

b

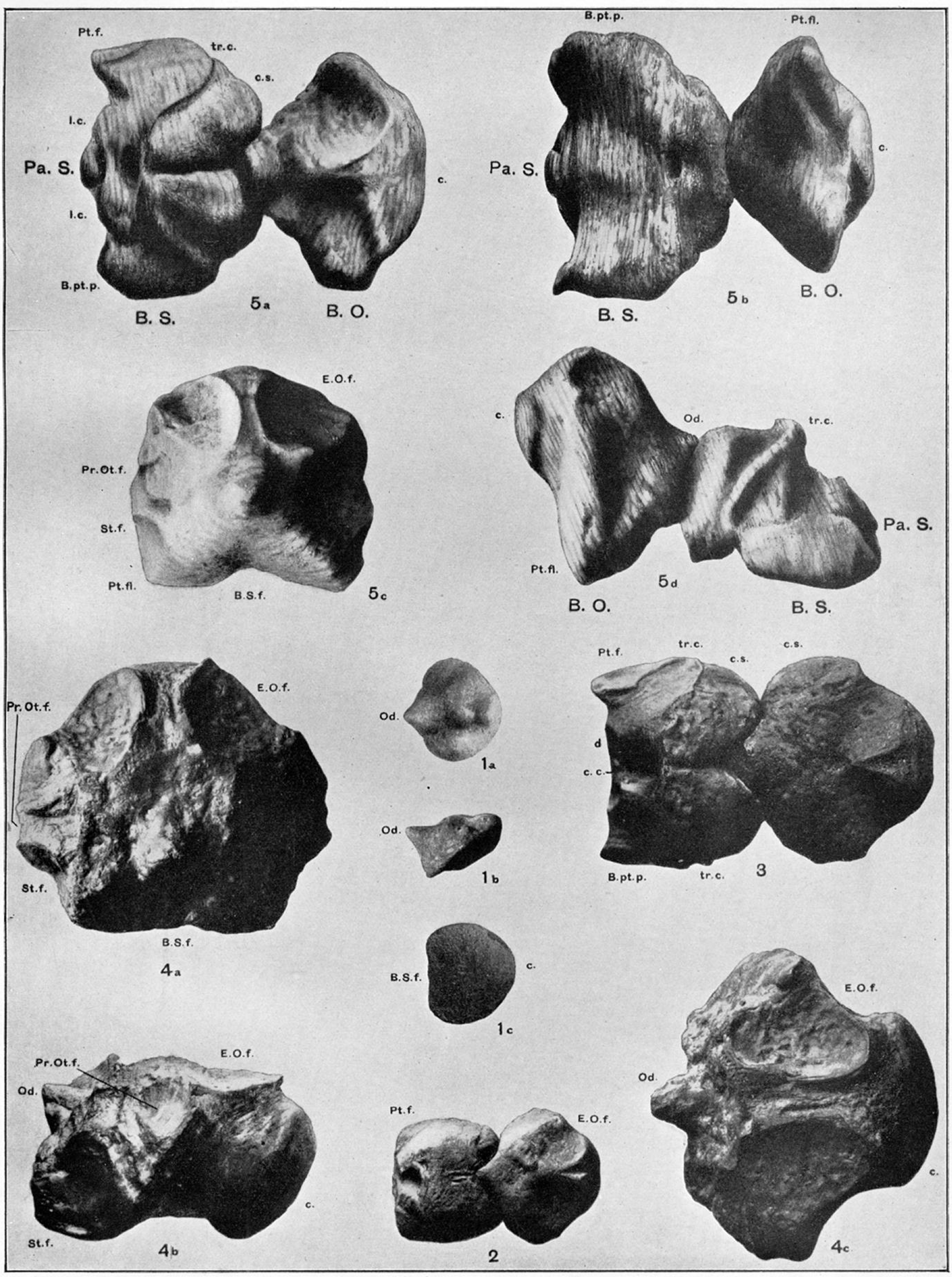
TEXT-FIG. 9.—Right pterygoid; *a*, dorsal; *b*, interior lateral view. (× ½.)



TEXT-FIG. 10.—Right vomer; A, outer lateral; B, inner lateral view. *a.p.*, ascending process; *h.p.*, horizontal process; *Pl.f.*, palatine articulation; *Nar.*, margin of internal maris; *Pt.gr.*, pterygoid grooves; *Vo.f.*, articulation with left vomer. ($\times \frac{1}{2}$.)



TEXT-FIG. 13.—Structure of the roof of the skull just in front of the right supra-temporal fossa, as described in the text. ($\times \frac{3}{4}$.)



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