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A Study of the Skull of a Dicynodon by means of Serial Sections

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VI. *A Study of the Skull of a Dicynodon by means of Serial Sections.*

By Igerna B. J. Sollas, *B.Sc., Fellow of Newnham College, Cambridge, and* W. J. Sollas, *F.R.S., Professor of Geology and Palæontology in the University of Oxford.*

(Received June 9,—Read June 26, 1913.)

[Plates 17 and 18.]

In this communication we propose to give an account of the first results we have obtained with a new apparatus purchased by a grant from the Government Fund administered by the Royal Society.

Our previous work was accomplished by means of a grinding machine already described,* but this, though admirably adapted to the examination of small specimens (up to 20 mm. square), is inadequate for larger and more important objects, such as the skulls of fossil reptiles or mammals.

With increase in dimensions, unexpected mechanical difficulties arise, the friction, for instance, over a large surface becomes so great that it is impossible to grind with the face of a wheel, and recourse must be had to its edge. A machine to meet this and other requirements has been constructed for us by Mr. Carson, of Birmingham (text-fig. 1), and now answers its purpose admirably. The grinding wheel, which is driven by an electric motor, is mounted on a fixed horizontal axis supported by two bearings a considerable distance apart on an arm at the summit of a massive cylindrical iron column (CC); its edge is flat and $\frac{3}{8}$ inch in width. The substance of the wheel is carborundum; emery, which was used in our preliminary trials, proved powerless to grind such hard material as cherty limestone, and it was not till we had tried various devices to supplement its action, none of which proved successful, that we learnt of the existence of carborundum wheels. On substituting one of these for the emery wheel the change was truly astonishing: chert was as cleanly ground away as limestone and almost as speedily. The success of the new apparatus was assured, and we now use a carborundum disc instead of glass and emery in our smaller apparatus, with great saving in time and labour.

The specimen to be ground, mounted in a manner to be described later, is clamped on a horizontal bench which may be made to slide up and down on the vertical column CC. This movement is given to it by turning the handle H, which acts through a bevelled wheel on the vertical screw S. The screw works through a collar fixed on the side of the bench and carries at its upper end a disc graduated to tenths of a millimetre, by which the extent of the vertical movement is indicated. The bench is complex, its upper part consists of two tables, each of which slides in

* 'Phil. Trans.,' 1903, B, vol. 196, p. 259.

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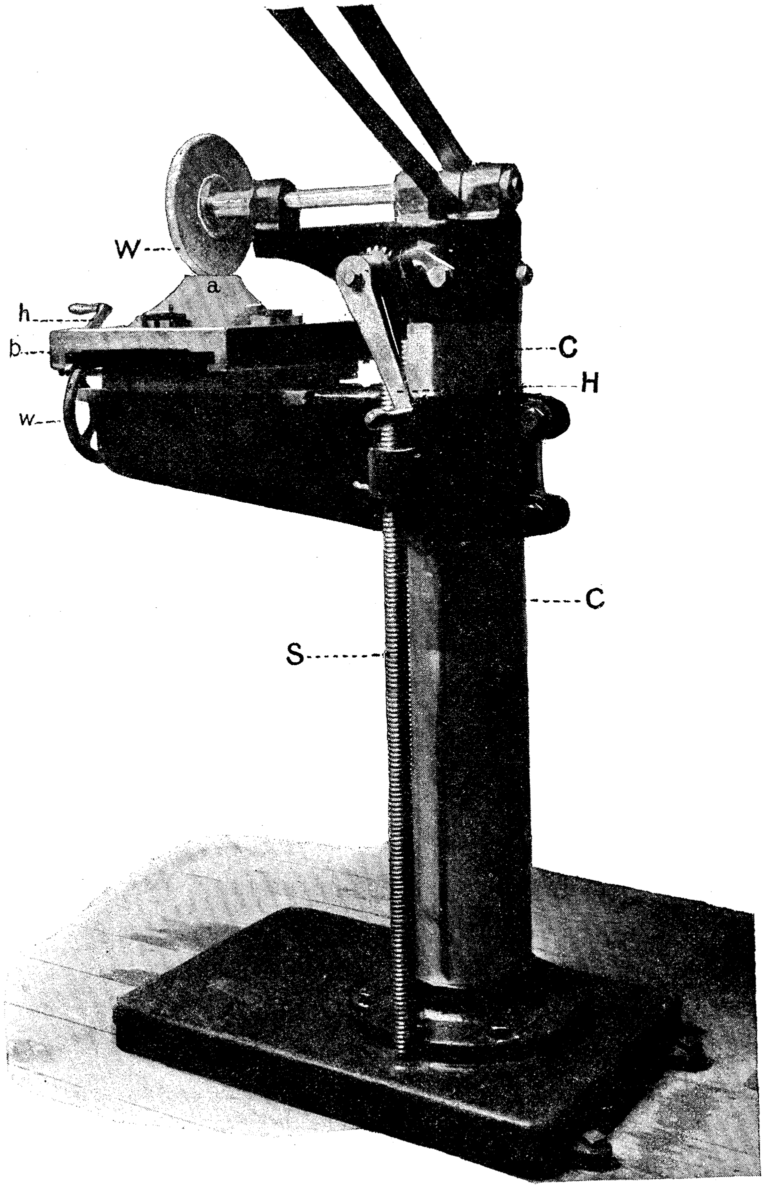
a horizontal plane: one of them in a direction parallel to the plane of the grinding wheel, the other at right angles to this. The latter is moved by the wheel *w*, the former by the handle *h*.



TEXT-FIG. 1.—Machine for Grinding-down large Fossils in order to obtain Serial Sections.

W, grinding wheel; CC, cylindrical column, which supports the bearings for the wheel W and carries the movable bench *b*; H, handle to turn the screw S, which determines the amount of the vertical movement of the bench *b*; *h*, handle which moves the bench horizontally and laterally; *w*, wheel which moves the bench to and fro horizontally; *a*, the object to be ground. ($\times \frac{1}{10}$.)

The operation of grinding is performed as follows:—The object, after being fixed on the bench, is brought just in contact with the edge of the grinding wheel and then

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raised, by turning the handle H through an interval equal to the thickness it is desired to grind away. On starting the motor the rotating wheel will, of course, do nothing more than grind out a concave pit (say 0·1 mm. deep) so long as the object is stationary, but on turning the handle *h* it is carried along under the wheel and the pit is extended into a long trough. If, now, we turn the wheel *w* so as to shift the object a little less than the thickness of the grinding wheel and again turn the handle *h*, a second trough similar to the first and overlapping it on one side will be produced; by repeating these movements trough is added to trough, till by the time the whole object has passed under the wheel their additive effect is a plane surface, 0·1 mm. below that with which we started.

The nature of the machine renders it impossible to flood the object with water while it is being ground: it must be fed dry, and to get rid of the vast amount of fine dust which is poured into the air as an inevitable result, the machine is mounted between two widely open windows.

A screen of wire netting, not shown in the figure, is mounted between the workman and the machine to protect him against accidents, such as the bursting of the grinding wheel.

Fossils are prepared for treatment in the following manner:—After being boiled in water they are painted with a thick coat of plaster of Paris and then placed, properly orientated, in a stout wooden box, made by a cabinet maker with the sides as true as possible to 90° and bound together by brass screws. Plaster is run in till the box is full; as soon as it has set, the sides of the box are unscrewed, the rectangular block of plaster is removed and placed in a similar but larger box, so as to leave a space about ½ inch wide surrounding it on all sides. This is filled by pouring in plaster which has been coloured black by indian ink; it adheres firmly to the white plaster, and the junction between the two is a sharply marked rectangle which affords a convenient means of registration when we arrive at that stage of the process in which the successive sections are superposed in the work of reconstruction.

The surface obtained by grinding is very smooth, but not sufficiently so to bring out all the minute details of structure: to obtain this effect it is evenly smeared with copal varnish, and it is then ready for photographing. It is better to photograph immediately after applying the varnish and not to wait till it has dried.

The photographing apparatus is set up in such a manner as to ensure that each section is presented to the camera in the same position as the rest. A special bench is assigned to the work and, after making the requisite adjustments for the first photograph, all the moving parts of the apparatus are rigidly fixed by screwing up. After each successive grinding, the face of the specimen is brought up against a stop immovably mounted on the bench; this ensures that it is always in focus.

The work of grinding-down and photographing requires no special skill, nothing beyond care and patience, and it may be safely entrusted to an intelligent laboratory

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boy. When the loss of a section or two in a long series is no great matter, a considerable saving of time and labour may be effected by dividing the object to be studied into two or more portions with a lapidary's cutting wheel and embedding these side by side in the same block of plaster for simultaneous treatment.

In the work of reconstruction we have found it convenient to trace the outlines of the sections from the printed photographs on to glass. The manufacturers of sensitised plates will supply gelatine-covered plates which are cut sufficiently true for this purpose. The method of building-up a reconstruction in plaster from these outlines has already been described by us,* but we may mention in passing that the substitution of glass plates for paper in tracing has this advantage, that when plates with their outlines are piled up in proper order, they afford a tridimensional figure of the object which may prove useful for reference if any difficulty should arise over the registration of the wax sheets.

We have been able to include the sutures in our reconstructions, with an inevitable exaggeration of their thickness it is true, by the following device. In cutting out those parts of the wax sheets which represent the bones, the scalpel is made to follow the sutures at a little distance on each side, so that when the "bone" is removed the "suture" is left behind as a narrow partition. Plaster is cast in the cavities as usual, and after it has set and been planed down the partitions are removed and their place filled with fresh plaster, but this time coloured by the addition of some pigment. This involves a second planing down. The process answers its purpose very well, but it doubles the labour of reconstruction.

When all the wax stencils of the fossil have been filled and superposed in the work of building-up, the result is a rectangular block of wax, within which the plaster reconstruction lies concealed. It is allowed to rest in a warm room for a considerable time, the longer the better, so that the plaster may become as dry as possible. It is then placed in a rectangular metal tank provided with a false bottom, and this in turn is placed in a water-bath, the temperature of which is raised to 90° C.; the wax as it melts penetrates the plaster while setting it free, and gives it additional strength on consolidation. As soon as the wax is all melted the false bottom is withdrawn, carrying the reconstruction with it.

Reconstructions have been made of two skulls of Dicynodon: one of these, presented to us by our friend Dr. ROGERS, Director of the Geological Survey of Cape Colony, had suffered less by distortion than the other, which we owe to the generosity of the Trustees of the British Museum; but, on the other hand, its sutures were very imperfectly preserved and its roof had almost disappeared. Our description is taken, therefore, from the second of these skulls, which is numbered R. 857 in the British Museum Catalogue and described by Mr. R. LYDEKKER, under the name of *Dicynodon leoniceps*, Owen, as an ". . . . imperfect skull from the Karoo System of

* 'Phil. Trans.,' 1912, B, vol. 202, p. 231.

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the Gouph district, near Beaufort West, south of the Nieuwveld range. Presented by T. Bain, Esq., 1880."*

Of course it was impossible for the authorities charged with the care of a collection to abandon to our destructive method any but a duplicate specimen, and, as Mr. LYDEKKER remarks, ours was imperfect—in precisely what particulars is revealed by the reconstructions—but, on the other hand, the sutures were in a perfect state of preservation and sharply defined, as will be seen from photographs of some of our sections (Plate 17). The distortion brought about by slowly accumulating pressure acting on the rock in which the fossil was embedded has resulted in an unequal compression of the skull, so that in a series of 105 sections intended to be sagittal the median section through the palate is separated by 8 sections (4 mm.) from that passing through the roof. The base of the skull has been broken across and its posterior part thrust upwards and forwards into the cranial cavity, carrying with it the occipital plate. The quadrate and quadrato-jugal of one side has been driven into the temporal fossa; those of the other side are lost. The posterior processes of the pterygoids have almost wholly disappeared, the stapes are absent, and the columellæ cranii are broken off. The lower jaw is intact, but one ramus is bent slightly out of shape.

These defects, however, are inconsiderable when compared with what remains, and the structure of this has been revealed by the new method with a completeness which could not have been greater had we been dealing with a recent skull. The original fossil is destroyed, blown in dust out of the window, but its structure—the form and relationship of its parts, all that is really essential—is preserved and open to the study of naturalists† as it could never have been in the days of the chisel, which leaves much that is important in obscurity and often mangles when it does not destroy.

The Structure of the Skull of Dicynodon; Historical Summary.

The Dicynodont skull has been studied and described ever since OWEN first named it in 1845,‡ and, though our knowledge of its structure has been gradually approaching completeness, there still remain many doubtful points to be determined. It is owing entirely to improvement in the method of study § that we are able to add anything to the patient and learned researches, which we will now briefly summarise.

In 1845 OWEN described two species of some skulls of Dicynodon brought from South Africa by T. BAIN. He was naturally impressed with their remarkable

* 'Catalogue of Fossil Reptiles and Amphibia in the British Museum, Nat. Hist.,' R. LYDEKKER, 1890, Part IV, p. 20.

† The original photographs of our sections (on glass) are preserved in the University Museum, Oxford; an album of platinum prints has been presented to the British Museum (Nat. Hist.), South Kensington.

‡ "Report on the Reptilian Fossils of South Africa.—Part I," 'Geol. Soc. Trans.,' 1845, p. 59.

§ SOLLAS, W. J., "A Method for the Investigation of Fossils by Serial Sections," 'Phil. Trans.,' 1903, B, vol. 196, p. 259.

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dentition, which, in conjunction with the great expanse of bone in the temporal region for the insertion of muscles, gives the skull so strong a resemblance to that of certain mammals, and he chose the name accordingly.

In this first paper OWEN gave an account of the general form of the skull in the species *D. lacerticeps* and *D. testudiceps*, identified some of the more obvious bones, and entered into a long discussion of the affinities of the new genus based upon necessarily slender knowledge. He was unable to determine the position of the posterior nares, and, as he could not find them in the position which they occupy in lizards, he says, "so I am disposed to conclude that the resemblance to the Chelonian type of cranium, so strikingly exemplified in the edentulous lower jaw and inter-maxillary border, may have been extended to the composition of the bony palate."

From the first he suspected the existence of a median unpaired vomer, and in 1876* he figured it quite correctly in the palate of *D. pardiceps*,† but he remained in doubt as to the position of the posterior nares, wondering whether they were interpterygoid "as in Crocodiles," or whether the palatines contributed to their boundary "as in lizards."‡ He maintained that the ectopterygoid (transverse or transpalatine) was absent and quoted this as "another mammalian character." But he made his comparisons somewhat lightly, thus, speaking of *D. lacerticeps*,‡ he says: "Crocodilian affinity is indicated by the well ossified occiput and fixed tympanic; lacertian by the divided nostrils and parietal foramen; the edentulous trenchant border of the lower jaw is a chelonian character, but the large downwardly prolonged pair of canine tusks seem borrowed as it were from the mammalian walrus (*Trichechus rosmarinus*). The proportion of breadth to length and the relative size of the temporal fossæ are rather mammalian than crocodilian or lacertian."

HUXLEY, in 1859,§ discovered the median internasal and interorbital septum by means of four sections which he cut across the snout of *Ptychognathus Murrayi*. These sections enabled him to show that the craniofacial axis of Dicynodonts is more completely ossified than that of any other reptile. But his interpretation of the parts of the septum was erroneous, chiefly because he failed to recognise that the anterior portion of the septum was contributed by an outgrowth of the premaxilla. He noticed that the interorbital septum was formed partly by a vertical plate-like expansion of the sphenoid bone of the base of the skull, which he calls presphenoid. In front of this he speaks of the septum as ethmovomerine and as expanding above into a mass of bone which appears on the face. His view of the nature of the median septum and of the palate led him to see bird-like characters in the skull. He speaks of the dentary as very chelonian and noted that the splenial meets its fellow at the symphysis.

* OWEN, R., 'Cat. Fossil Reptiles in Brit. Mus., 1876, from S. Africa.'

† *Ibid.*, Plate 39.

‡ *Ibid.*, p. 31.

§ "On *Dicynodon Murrayi*," 'Quart. Journ. Geol. Soc.,' 1859, vol. 15, p. 654.

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In 1865,* HUXLEY described for the first time the peculiar little bone now known as preparietal.

In 1870,† COPE described a skull of *Lystrosaurus frontosus* and made considerable additions to our knowledge of the Anomodont skull. His paper appears to have passed almost unnoticed, possibly because others felt, as SEELEY did, that it should have been more fully illustrated. However, his figures are clear and his text succinct, and many of his statements have now been justified. He was the first to notice the columella cranii and the descending plates of the parietal; he saw and figured two bones, the post-orbital and post-frontal, behind the orbit, and described and figured correctly the transpalatine bone.

COPE regarded the Anomodontia as "the most generalised order of Reptilia of which we have any knowledge" and he added that as they occupy almost the first place in geological time among Reptilia, they illustrate the fact that the older forms of any group are the more generalised.

SEELEY‡ (in 1889) was the first to attempt to determine the form of the cranial cavity. His paper is also the fullest and most complete description of the Dicynodont skull of its date. The vagueness of some of his figures gives a good idea of the difficulties he had to contend with in the determination of sutures: we may refer for example to his Plate 13, which represents a skull specially prized for the clearness of these lines. In a second paper SEELEY§ attempted to determine the constituent bones of HUXLEY's median vertical plate, and described some new points of detail, but his additions to the existing knowledge are not really very considerable. Modern zoologists will hardly be interested in his theories of the homologies of parts of the skull with parts of a neural arch.

The next important advance in our knowledge of these skulls was made by NEWTON,‖ in a remarkably successful study of fossils from the Elgin sandstones, in which the bones are represented only by cavities in the rock. Gutta-percha casts of these cavities were made, and it was often necessary to make separate casts of the various parts and piece them together. NEWTON was the first to show convincingly the existence of a rudimentary secondary palate; he was not able to speak with great definiteness of the bones which enter into it, owing to the lack of sutures (pp. 440 and 447).

Let us not overlook the fact, however, that LYDEKKER,¶ in 1890, had already

* 'Palæont. Indica,' 1865–1885, ser. 4, vol. 1.

† "On *Lystrosaurus frontosus*, Cope," 'Amer. Assoc. Proc.,' 1870, p. 194, and 'Amer. Phil. Soc. Proc.,' 1870, vol. 11 (II), p. 419.

‡ "On the Anomodont Reptilia and their Allies," 'Phil. Trans.,' 1889, B, vol. 180, pp. 215–296.

§ "On the Skull of *Mochlorhinus platyceps*, from Bethulie, Orange Free State," 'Ann. Mag. Nat. Hist.,' 1898, ser. 7, vol. 1, p. 164.

‖ 'Phil. Trans.,' 1893, B, vol. 184, p. 438.

¶ 'Cat. Fossil Reptiles in Brit. Mus.,' 1890.

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included the possession of a secondary palate among the diagnostic characters of the Dicynodontia.

Broom has contributed more than any one previous author, since Owen, to the knowledge of the Dicynodont skull. His main contributions have been an elucidation of the nature of the median septum,* a description of the palate which approximates more nearly to the truth than any previously published,† a description of the labyrinth of the ear and a correct identification‡ of the bone called by Seeley "malleus," and by himself in earlier papers "tympanic," as the columella auris. Those discoveries which concern the ear were made by dissolving the bone and studying the remaining cast.

Our own researches, based on serial sections, have had interesting results, which we will briefly summarise :—

(1) The vomer is grooved dorsally (text-fig. 5), the groove receiving at its posterior end the anterior rod-like termination of the cranial axis, which also is similarly grooved on its dorsal surface and receives the ethmoid. The anterior end of the groove of the vomer probably received the ethmoid directly. This arrangement is *sui generis* and at the same time a foreshadowing of the mammalian condition.

(2) A well-marked floccular recess exists.

(3) The existence of a transpalatine bone, which has so often been denied, is established beyond doubt (Plate 17, fig. 1, *Trans.*).

(4) The cavity which Broom has called the maxillary antrum proves to be an inter- and not a intra-osseal space, several bones contributing to the formation of its wall (Plate 17, fig. 2).

(5) Septo-maxillary bones are present (Plate 17, fig. 1, *smx*).

Besides these chief new facts, the method has enabled us to study more exactly the forms of the bones and cavities and their relation to each other, and to make all our statements with the confidence of certainty. Seeing that the skull has been studied since 1845, and that Broom has spoken of it as one of the most completely known fossil skulls, we think that the results of our investigation justify the expenditure of time necessitated by the method employed, an expenditure which, after all, is a saving in the end.

We now proceed to a description of the specimen we have investigated, but before doing so we insert here, for the assistance of the reader, a diagram of the roof (text-fig. 2) and the palatal surface (text-fig. 3) of the Dicynodon skull, in which we have embodied our own results with those of other observers.

* "On some Points in the Anatomy of the Anomodont Skull," 'Rec. Albany Mus.,' 1904, p. 75.

† "On the Anomodont Palate," 'S. African Phil. Soc. Trans.,' 1901, vol. 11, p. 169.

‡ "On the Structure of the Internal Ear, and the Relations of the Basicranial Nerves in *Dicynodon*, and on the Homology of the Mammalian Auditory Ossicles," 'Zool. Soc. Proc.,' 1912, p. 419.

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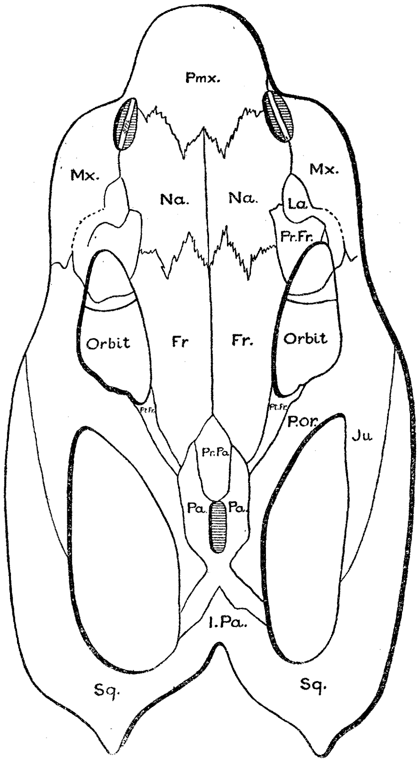
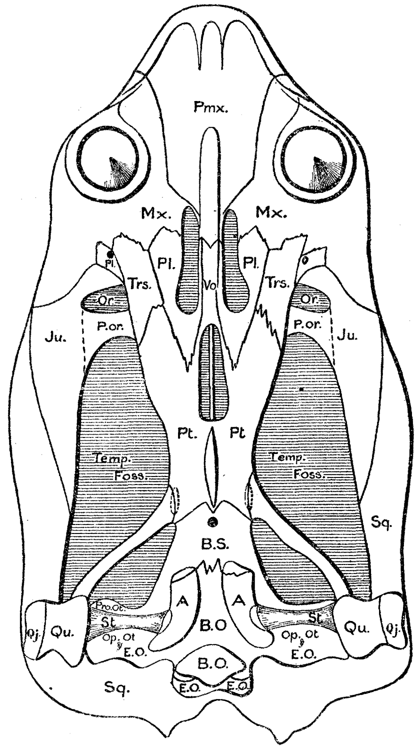


TEXT-FIG. 2.



TEXT-FIG. 3.

TEXT-FIG. 2.—Diagram of the Roof of the Skull of Dicynodon.

Pmx., premaxilla; *Na.*, nasal; *Mx.*, maxilla; *La.*, lachrymal; *Pr. Fr.*, prefrontal; *Fr.*, frontal; *Pt. Fr.*, postfrontal; *P. Or.*, postorbital; *Pr. Pa.*, preparietal; *Pa.*, parietal; *I. Pa.*, interparietal; *Ju.*, jugal *Sq.*, squamosal. The septo-maxillary bones are seen within the nostrils.

TEXT-FIG. 3.—Diagram of the Palatal Surface of the Skull of Dicynodon.

Pl., palatine; *Vo.*, vomer; *Trs.*, transverse or transpalatine; *Pt.*, pterygoid; *B. S.*, basi-sphenoid; *B. O.*, basi-occipital; *A*, part of auditory mass: *Pro. Ot.*, pro-otic; *Op. Ot.*, opisthotic; *St.*, stapes; *E. O.*, exoccipital; *Qu.*, quadrate; *Q. j.*, quadrato-jugal. The dotted areas immediately over the sutures of the pterygoids, with their "posterior processes," represent the columella cranii, which rise on the other side; the central spot behind the anterior suture of the basi-sphenoid represents the foramen for the internal carotid artery.

Base of the Skull and Median Septum.

A transverse fracture divides the craniofacial axis into two portions. This fracture runs obliquely across our vertical sections; it must have been coincident with the suture of the pterygoids against the basi-sphenoid, dividing the cranial axis from the palate, for neither of the portions shows any trace of the pterygoid-basisphenoid suture.

There are two very distinct sutures traversing the cranial axis (text-figs. 4 and 5, and Plate 17, fig. 1), and at first sight it would, perhaps, be natural to suppose that these sutures divide the basioccipital from the basisphenoid and the basisphenoid

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from the presphenoid, but on examining the relations of the bones more closely it becomes clear that the more posterior suture lies between the basioccipital in front and below, and the exoccipital behind and above, and that, in fact, the two exoccipital bones meet each other in the middle line, and form the dorsal and larger part of the condyle, while the basioccipital forms the lower part. The meeting of the exoccipitals across the middle line is cited by GREGORY* as occurring in Cynodonts, and as one of their primitive reptilian characters.

The more anterior suture lies between the basioccipital and the basisphenoid in the neighbourhood of the sagittal plane (text-fig. 4, Section 77); in the more lateral sections, where the pro-otic rests on the basioccipital, the suture lies between the basisphenoid on the one side and the basioccipital, *plus* the pro-otic, on the other (text-fig. 4, Sections 85 to 93). The course of the suture as seen in a vertical section is oblique. The basioccipital is deeply grooved on the ventral surface, or to express the same fact otherwise, its ventral surface is produced downwards on each side to form a pair of prominences (the hypapophyses of OWEN and others) which constitute the wall of the lower and inner part of the bony capsule surrounding the enormous vestibule of the ear, recently described by BROOM.† The basisphenoid contributes to the anterior wall of this prominence, but it does not extend on to the parotic processes, as BROOM seems to suppose when he says: "The basisphenoid sends two large plates backwards to clasp the large paroccipital processes."

The dorsal surface of the basioccipital at its anterior end is overlaid, except for a very narrow band in the median line, by the pro-otic, and this is raised in front into a pair of pointed ascending processes to which the basisphenoid also contributes.

The basisphenoid is also grooved ventrally for a short distance in its posterior region, a pair of lateral ridges on its ventral surface being the portions just mentioned which are applied to the ventral ridges of the basioccipital.

A canal (Plate 17, fig. 1, immediately below the letters B.S.) traverses the basisphenoid in the middle line vertically: it is apparently the internal carotid canal‡ which SEELEY described as forked. The skull in which he discovered the canal was fractured through this feature, and the forking branches he speaks of are not very clearly seen in his figure. In the "undescribed Dicynodont skull" which he figures on Plate 9, fig. 1, he finds apparently a single carotid canal (p. 225). Possibly the character is a variable one.

In front of this grooved basilar part follows the region of suture with the pterygoids, and in front of that again the basisphenoid is continued forwards as a very narrow median vertical plate of peculiar form (text-fig. 5, and Plate 18, fig. 2).

* "The Orders of Mammals," 'Amer. Mus. Nat. Hist. Bull.,' 1910, vol. 27, p. 118.

† "On the Structure of the Internal Ear, and the Relations of the Basicranial Nerves in *Dicynodon*, and on the Homology of the Mammalian Auditory Ossicles," 'Zool. Soc. Proc.,' 1912, p. 419.

‡ SEELEY, H. G., "On the Anomodont Reptilia and their Allies," 'Phil. Trans.,' 1889, B, vol. 180 p. 228, Plate 2.

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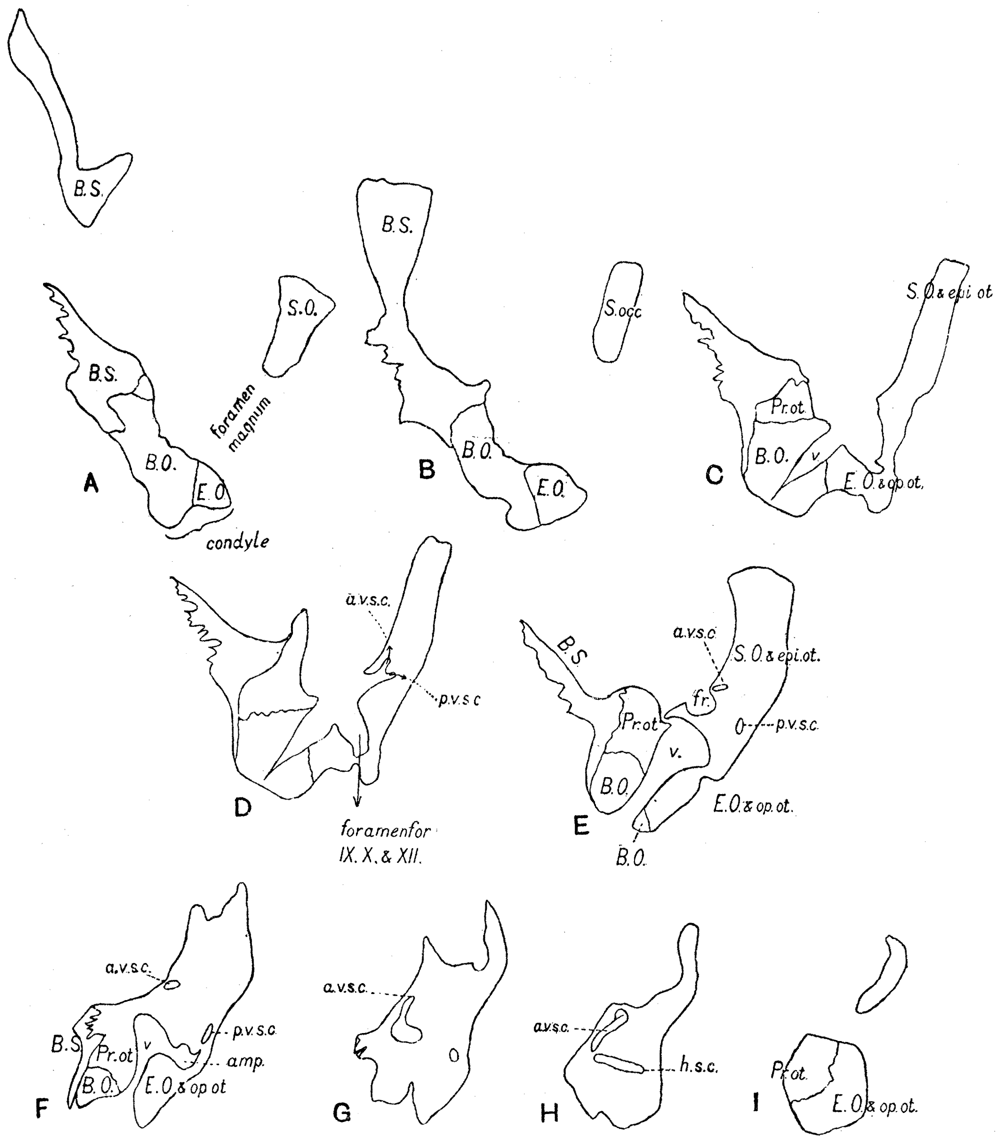
It is a laterally compressed curved rod, equal in length to the whole of the basicranial axis behind it, bearing on its posterior half a vertical expansion, which attains its greatest height at its anterior end and is wedge shaped. The anterior half of the rod



TEXT-FIG. 4.—A Series of Vertical Longitudinal Sections through the Base of the Skull.

v., vestibule of the ear; *a. v. s. c.*, anterior vertical semicircular canal; *p. v. s. c.*, posterior vertical semicircular canal; *h. s. c.*, horizontal semicircular canal; *fr.*, floccular recess. The other symbols as before. The position of each section in the series is as follows:—A, No. 77; B, No. 80; C, No. 85; D, No. 86; E, No. 91; F, No. 93; G, No. 96; H, No. 99; I, No. 107. The sections were taken at intervals of 0·5 mm. (Nat. size.)

is grooved dorsally except at the extreme tip, and the groove is continued posteriorly up the anterior border of the wedge-shaped expansion (text-fig. 5). This groove is a continuation of a similar groove on the dorsal edge or surface of the vomer, the

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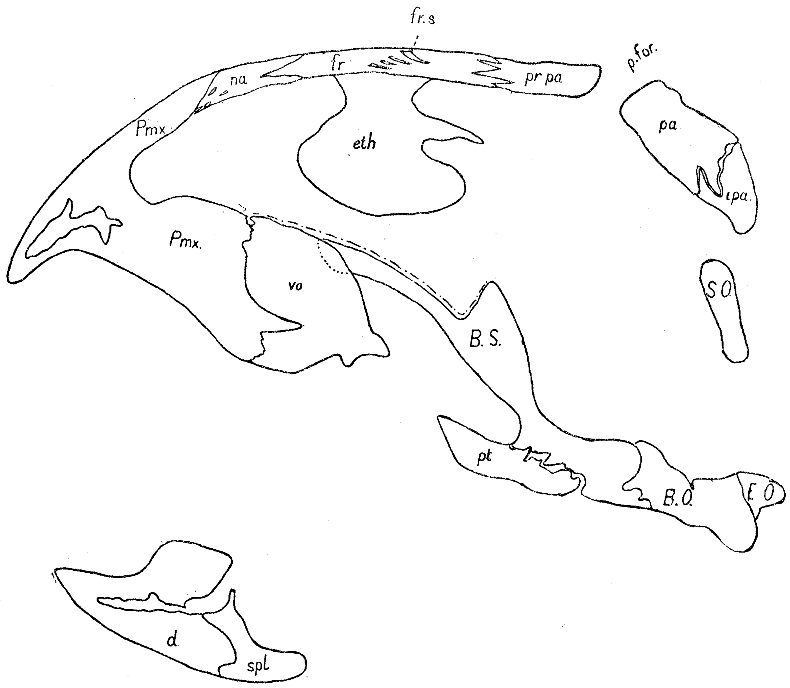
ungrooved tip of the basisphenoid lying in the groove of the vomer and the two together forming a curve which, roughly speaking, follows at a little distance the curved ventral border of the dorsal element of the interorbital septum. There can be very little doubt that a cartilaginous border of the dorsal element must have been received by this composite groove.



TEXT-FIG. 5.—Sagittal Section through the Skull of *Dicynodon leoniceps*.
eth., ethmoid; *p.for.*, pineal foramen; *d.*, dentary; *spl.*, splenial. The broken line over the B.S. and *vo* indicates the dorsal groove. (Nat. size.)

Dorsal Element of the Median Septum.

The bone which SEELEY called orbitosphenoid* and BROOM ethmoid† proves to be a very interesting structure lying beneath the frontal bones (text-figs. 5, *eth.*, and 6; Plate 18, fig. 4). It is an exceedingly thin median plate ventrally, but in the neighbourhood of its suture with the frontals it has considerable thickness throughout the anterior half of its length. This thicker region is perforated on each side of the middle line by a canal which presumably served for the passage of olfactory nerves (text-fig. 6). In the posterior half of its length the plate also possesses a lateral outgrowth (in this case at a little distance from the roof of the skull), which, bending up at its lateral edges, meets the frontal and forms the floor and sides of a cavity which no doubt lodged the olfactory lobes of the brain. Here, then, we seem to have a structure which might well be the first stage in the evolution of

* "On the Skull of *Mochlorhinus platyceps*, from Bethulie, Orange Free State," 'Ann. Mag. Nat. Hist.,' 1898, ser. 7. vol. 1, p. 164.

† "On some Points in the Anatomy of the Anomodont Skull," 'Rec. Albany Mus.,' 1904, p. 75.

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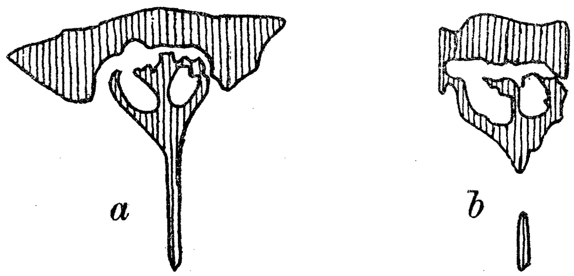
a cribriform plate. The thinner ventral region of the plate is deeply notched, possibly for the passage of optic nerves, its lateral anterior expansions lie between a pair of ridges which project downwards from the frontals.

The grooving of the upper edge of the vomer gives an even more mammalian



TEXT-FIG. 6.—Transverse Section through the Mesethmoid and Frontal.
a, through the middle; *b*, a little behind *a*. ($\times \frac{3}{2}$.)

character to this region of the skull than has hitherto been attributed to it, while at the same time the partly ossified interorbital septum to which the ethmoid contributes recalls in a general way the arrangement in birds; but while in Dicynodon it is the vomer and apparently the basisphenoid which receive the ventral edge of the septum in a groove, in birds it is the parasphenoid (rostrum).

There cannot be much doubt that BROOM is right in his identification of the dorsal element of the interorbital septum as the ethmoid. The only alternative we can see is to regard it as orbitosphenoid and ethmoid conjoined in one, but the extent to which it enters into the cranial wall does not justify such explanation, while it does find a parallel in the cribriform plate of mammals. SEELEY calls the bone in question orbitosphenoid, because it lies "between the orbits, below the front of the brain case and below the frontal," but the orbitosphenoid is essentially an ossification in the cranial wall, while this bone extends far forwards, its continuation into the nasal region by a cartilaginous border being rendered practically certain by the existence of the groove on the dorsal surface of the vomer. Further, it transmits the olfactory nerves and has relations with the cranial axis and vomer similar to those of the mesethmoid of mammals, in so far as its ventral edge lies over their junction, but the clasping of the ethmoid by the basisphenoid is, as far as we know, a feature peculiar to Dicynodon.

It is true that this bone is situated farther back than the ethmoid is in mammals, just as it is true that the interorbital septum does not exist in mammals, but these two characters—the presence of an interorbital septum and a more posterior position of the ethmoid—are what we might naturally expect to find in a lowly ancestral form, such as we imagine Dicynodon to be.

The development of a cribriform plate out of the primitive ethmoid would naturally accompany an increase in the size of the brain with its olfactory lobe and a multiplication of the olfactory nerves.

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It may be worth while to digress here for a moment to notice that the existence in Dicynodon of a grooved basi- (or pre-) sphenoid clasping the ventral edge of the ethmoid should warn us to be cautious in accepting such an interpretation as BROOM* offers of the bones of the cranial base in Diademodon.

BROOM has maintained since 1902 that the mammalian vomer had its homologue in the reptilian parasphenoid.

GAUPP† has drawn attention to the fact that the vomer in Echidna has a double origin, and that the same is true in the mouse also, and some other mammals; facts which he maintains militate against BROOM's view. He might have further pointed out that the vomer is a paired structure in the adult guinea-pig, a fact easy to verify and already mentioned by PARKER and BETTANY as long ago as 1877.

Now that we know that a median-grooved bone clasping the ethmoid is not necessarily the vomer, is it not possible to regard BROOM's vomer in Diademodon as part of the cranial axis and his prevomers in the same animal as possible homologues of the mammalian vomer ?‡

The Parotic Processes and Occipital Plate.

No sutures are distinguishable in the occipital plate, and this appears to be a common condition in skulls of Dicynodon, as well as of Ptychognathus and Gordonia. In the young skull figured by SEELEY§ and LYDEKKER,‖ a pair of lines mark off a superior median element, but while SEELEY regarded these lines as sutures, LYDEKKER denies the existence of any visible sutures in this occiput except those between the basi- and ex-occipitals. Hence the assumption that the median element represents a supra-occipital bone is based chiefly on comparison with allied forms in which sutures are visible.

COPE, in his account of *Lystrosaurus frontosus*, first described the ex-occipitals as meeting dorsal to the foramen magnum,¶ and the supra-occipital (*i.e.* interparietal of other writers) as a separate element above them. BROOM now speaks** of the median bone as "either supra-occipital or interparietal, probably the former," and SMITH WOODWARD figures it as supra-occipital in Ptychognathus.††

* "On the Structure of the Skull in Cynodont Reptiles," 'Zool. Soc. Proc.,' 1911, p. 920, Plate 46, fig. 9.

† In 'Semon, Zool. Forschungsreise,' 1908, and 'Anat. Anz.,' vol. 27, p. 273.

‡ As already stated in 'Nature' (vol. 92, p. 61), we have found in the skull of an unnamed Dicynodont suggestive evidence that the vomer of Dicynodon had a paired origin. We hope shortly to publish a description of this skull. (Note added in the press.)

§ "On the Anomodont Reptilia and their Allies," 'Phil. Trans.,' 1889, B, vol. 180, Plate 10, fig. 1.

‖ 'Cat. Fossil Reptiles in Brit. Mus.,' 1890.

¶ "On *Lystrosaurus frontosus*, Cope," 'Amer. Assoc. Proc.,' 1870, p. 194, and 'Amer. Phil. Soc. Proc.,' 1870, vol. 11 (II), p. 419.

** "Comparison of Permian Reptiles of N. America with those of S. Africa," 'Amer. Mus. Bull.,' 1910, vol. 28, p. 212.

†† 'Outlines of Vertebrate Palæontology,' fig. 100, p. 157.

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The exoccipital is perforated close to the condyle by the foramen which OWEN regarded as jugular, and which BROOM* has identified as giving passage to the 9th, 10th, 11th, and 12th nerves.

The parotic processes are divided vertically by a very distinct suture. The anterior element thus marked off is continuous with the bone which we have already identified as pro-otic, and which is separated by clear sutures from the basi-occipital and basi-sphenoid (text-fig. 4).

Bones of the Palate.

The premaxilla, as is well known, possesses a facial and a palatal portion. From the dorsal surface of the latter, as BROOM has shown, there rises a median vertical internasal plate. The ventral surface of the premaxilla is concave, terminating in front in the sharp biting edge; on its downwardly curved anterior portion this surface is raised into two low longitudinal ridges, bounding a median shallow groove. Posteriorly this groove is succeeded by a median ridge, which becomes higher as it passes backwards and terminates between the posterior nares, where the premaxilla meets the vomer.

The premaxilla and maxilla interlock with one another in a remarkably elaborate manner, so that at its lateral margins the palatal plate of the premaxilla is enclosed on both surfaces by laminæ of the maxilla, and the maxilla is also penetrated to some distance by processes of the premaxilla (Plate 17, fig. 2). The premaxilla is traversed on each side, not far from the middle line, by a canal, which runs very obliquely and connects the mouth cavity with the narial passage. The existence of a naso-palatine canal would naturally suggest the presence of Jacobson's organ, though the canals are somewhat far back, but as a similar pair of canals opens on the surface of the premaxilla a short distance in front of the pair just mentioned, and, continuing their direction, plunges into the spacious vascular sinuses of the premaxilla, it seems clear that these naso-palatine canals served for the passage of blood-vessels.

The palatal plates of the maxilla which overlie the palatal plates of the premaxilla (Plate 18, fig. 1) are of much greater extent than those which lie beneath it on its palatal surface. They reach close up to the internasal plate of the premaxilla. This median internasal plate of the premaxilla is an outgrowth from the dorsal surface of its palatal branch arising along the greater part of its extent (text-fig. 5). Its posterior margin articulates by an interdigitating suture with the vomer, and does not show the arrangement described by BROOM† in Ptychosiagum, of which he says that "superiorly the vomer divides into two branches, between which the premaxilla passes."

That part of the maxilla on the palatal surface which is not overlapped and

* "On the Structure of the Internal Ear, and the Relations of the Basicranial Nerves in *Dicynodon*, and on the Homology of the Mammalian Auditory Ossicles," 'Zool. Soc. Proc.,' 1912, p. 419.

† "On the Anomodont Palate," 'S. African Phil. Soc. Trans.,' 1901, vol. 11, p. 169.

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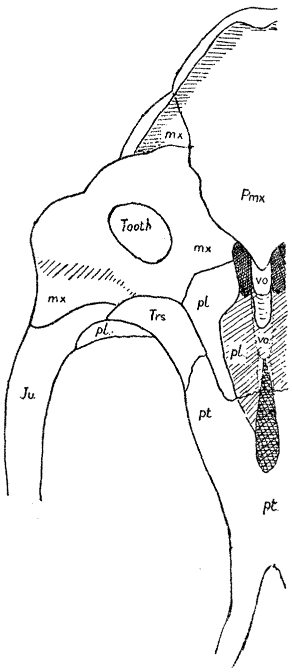
concealed by the premaxilla is bounded in front by the line of overlap of the premaxilla (text-fig. 7), on the inside by the anterior end of the internal nostril, behind, (1) by one of its sutures with the palatine, (2) by a second transverse suture rather farther back than (1), with a very distinct moderate-sized bone which passes from the junction of the palatine and pterygoid to the junction of the jugal and maxilla, and which is certainly no other than the transpalatine —a bone the existence of which in Dicynodonts has been disputed. COPE described and figured it in 1870 in *Lystrosaurus frontosus*, and SEELEY stated in 1889* that two skulls in the British Museum suggested doubt whether the bone was absent, as OWEN has considered, or whether it might not be hidden by the pterygoid, but SEELEY omits any mention of a transpalatine in giving his summary and plan of the skull. BROOM† says he has found no trace of a transverse bone in any Dicynodont. JAEKEL‡ describes what he believes to be a distinct transpalatine in Dicynodon, but BROOM,§ though he now admits that in at least some specimens belonging to this genus a transpalatine really exists, was unable to find any trace of it in *Oudenodon Kolbei*. As seen by us, it runs alongside the palatine and occupies a position corresponding in some respects to BROOM'S anterior spur of the pterygoid. It intervenes between the outer part of the anterior border of the pterygoid and the maxilla, and it lies against the outer border of the maxilla. Finally, this part of the maxilla is bounded by (3) a suture with the jugal which continues the last two sutures outwards.



TEXT-FIG. 7.—Freehand Drawing of Palatal Surface as seen in the Reconstruction.

The palatines extend close up to the middle line and overlap the vomer, as shown in the next figure (text-fig. 8).

Chamber surrounding the Root of the Tusk. (Dental Chamber.)

BROOM speaks of the maxilla of Udenodon as resembling that of man in having a large maxillary antrum. The antrum which surrounds the base of the tusk differs, however, from the maxillary antrum of man, since it is a cavity surrounded by a number of bones and not by the maxilla alone. This cavity may be described as having an inner and an outer wall. The inner wall is formed of that thin lamina of the maxilla which invests the root of the tusk. The outer wall is complex, the

* "On the Anomodont Reptilia and their Allies," 'Phil. Trans.,' 1889, B, vol. 180, pp. 215–296.

† "On the Anomodont Palate," 'S. African Phil. Soc. Trans.,' 1901, vol. 11, p. 169.

‡ 'Die Wirbelthiere,' 1911.

§ "On some Points in the Structure of the Dicynodont Skull," 'Ann. S. African Mus.,' July 12, 1912, vol. 7, pp. 337–351.

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lachrymal, the palatine, transpalatine, jugal, and maxilla all contributing to its formation (Plate 17, figs. 2 and 3).

The maxilla is a very massive bone forming the greater part of the face in front of the orbit and lodging the tusk. It joins suturally a large number of other bones. Thus, besides the sutures already mentioned in describing the palate, viz., that with the palatine part of the premaxilla, the palatine, and the transpalatine, the maxilla is also bounded above by suture with the facial part of the premaxilla and with the outer and anterior extremity of the nasal; the posterior limit of its facial aspect is marked by sutures with the lachrymal and jugal, while its ventral non-palatine portion is bounded by the jugal behind; then, passing forwards for a short distance, by an outward extension of the palatine, and lastly by the transverse. The share taken by the maxilla in the formation of the wall of the chamber can only be seen in sections. Besides forming, as we have said, the whole of the inner wall, it also contributes to the outer wall, but the portion which does so is concealed, in an external view of the skull, by the transverse bone, which is deeply embedded in the maxilla, as seen in the section shown in Plate 17, fig. 2. The outward extension of the palatine joins this concealed part of the maxilla suturally, and continues the outer wall of the chamber. In a section somewhat nearer the middle line than the preceding, the palatine extends over the inner surface of the maxilla, reaching right up to the base of the inner wall of the chamber which invests the tusk. The anterior edge of the outward extension of the palatine meets a large inwardly directed vaulted lamina of the jugal in a deeply dovetailed suture. This lamina of the jugal articulates in front with the lachrymal, which also has a large vaulted portion, its contribution being larger than that of any other single bone to this wall of the chamber. The other extremity of this vaulted part of the lachrymal meets the maxilla on the anterior side of the tusk.

The lachrymal has a very complicated form; if we examine from the inside a skull bisected along the sagittal plane (Plate 17, fig. 1) we shall readily observe the vaulted lamina of this bone which we have just described; this is produced into a thin wall which rises from its convex surface and meets the downward process of the prefrontal; passing outwards this wall acquires great thickness, extends forwards to the nostril and is largely concealed externally by the nasal. Passing still further outwards we find from sections that this thickened region is penetrated by the lachrymal duct. A deep lachrymal foramen is conspicuous, situated well within the orbit; a rod passed down it may be seen to enter the nasal cavity; the lachrymal bone forms a warty prominence on its outer side. Above and anterior to this prominence the lachrymal extends on to the face where it is bounded by the prefrontal, nasal, and maxilla.

A foramen (text-fig. 3) presumably for the entrance of the fifth nerve and for blood-vessels exists in the lower part of the outer wall of the chamber, between the palatine, transverse, and jugal bones.

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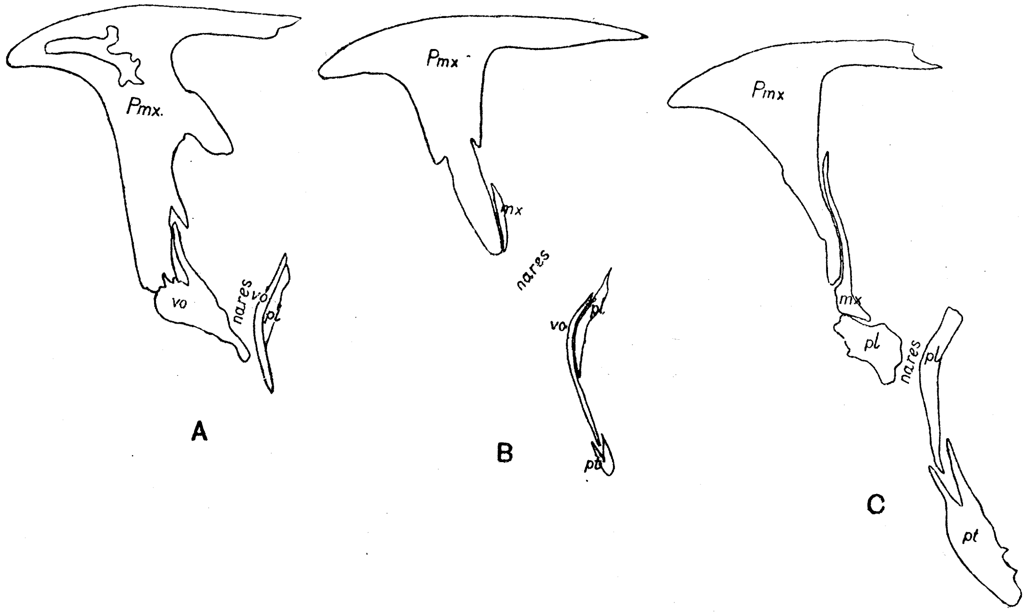
On its inner side the wall of the chamber is incomplete, leaving the cavity in free communication with the surrounding space; possibly it was completed in the living animal by cartilage.

The *vomer* (Plate 18, fig. 4, and text-figs. 5, 7, and 8) is a vertically placed three-sided lamina which could be described as triangular, with the apex of the triangle directed backwards, but for the fact that its sides are curved; along one side, that is its anterior edge, it is suturally united with the inter-nasal plate of the pre-maxilla; along its upper side it is grooved, the groove receiving the free edge of the ethmoid and the tip of the basisphenoid. Its third or ventral side is thickened and forms a bar separating the internal nares. The posterior region of the grooved upper edge is expanded into two thin flanges which contribute to the posterior wall of the nasal



TEXT-FIG. 8.—Sections showing the Relations of the Bones bounding the Posterior Nares. Of these sections A is nearest to the sagittal plane, and C most remote from it. (About natural size.)

passages and are overlapped by the palatines and so concealed from view for the greater part of their extent. At their anterior ends, however, the overlap of the palatines ceases and they are exposed to view on the dorsal and posterior aspect of the nasal passages. These two flanges are continued backwards, forming the bifid posterior extremity of the vomer, and each meets the pterygoid of its side.

The *palatines* form the upper and outer walls of the nasal passages, as well as part of the wall of the chamber which surrounds the root of the tusk (see p. 217). Each consists of a vertical and two alar portions; the inner of the two alar portions is simple and forms the vaulted roof of the posterior nares; the outer is of a more complicated form and contributes to the wall of the dental chamber and thus to the floor of the orbit; its contribution to the wall of the dental chamber is larger than

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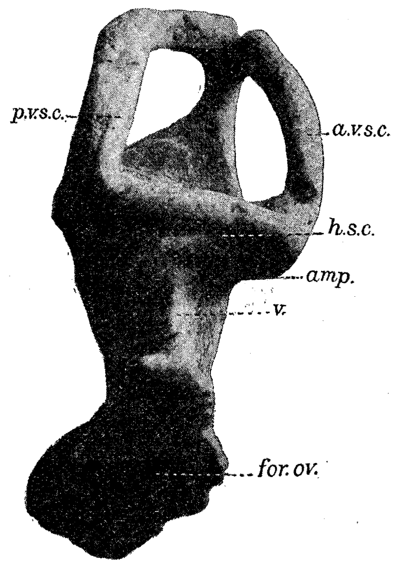
would be inferred from that part of it which is visible on the exterior (Plate 17, fig. 1, and Plate 18, figs. 2 and 4).

The *pterygoids* have a considerable vertical extent at their anterior ends, where they meet the transverse bone on the outside, the palatine and vomer on the inside. They pass up between the transverse and the palatine, and viewed laterally they are seen to grip the transverse bone (Plate 17, fig. 1, and Plate 18, fig. 3) as COPE has described,* one process passing above and another below it. The pterygoids meet each other in the middle line beneath the basisphenoid and become intimately united with each other; from this place of junction a knife-like process of bone projects downwards. Behind the junction they again diverge and proceed outwards to the quadrate, but the posterior rami are missing in this skull, except for a small portion near the origin on one side. Mr. GOODRICH having reminded us of certain facts which suggest that the posterior rami may be separate elements, we examined our photographs in search of a suture in this region and found to our satisfaction that it really exists, being situated precisely at the point where the ramus branches off from the main body.

BROOM has recently succeeded† in showing the form of the labyrinth of the ear, by dissolving away the surrounding bone; he has drawn attention to the extraordinarily large size of the vestibule, and identified the foramen ovale as the aperture at the extremity of OWEN's hypapophysis, and the columella auris as SEELEY's malleus and the tympanic of his own previous papers.

The question of sutures between the bones enclosing the labyrinth has hitherto remained rather vague.



TEXT-FIG. 9.—The Labyrinth of the Ear. (× about 3.)

amp., ampulla; *a. v. s. c.*, anterior vertical semicircular canal; *for. ov.*, foramen ovale; *h. s. c.*, horizontal semicircular canal; *p. v. s. c.*, posterior vertical semicircular canal; *v*, vestibule.

All the canals of the labyrinth are perfectly preserved in our specimen (text-fig. 4) and are shown in the photographs, from which the reconstruction (text-fig. 9) has been prepared. The anterior and posterior vertical semicircular canals proceed from the vestibule by a common trunk of origin, and at their place of re-entrance into the vestibule each enlarges into an ampulla, which it shares with the horizontal canal.

* "On *Lystrosaurus frontosus*," 'Amer. Assoc. Proc.,' 1870, p. 194, and 'Amer. Phil. Soc. Proc.,' 1870, vol. 11 (II), p. 419.

† "On the Structure of the Internal Ear, and the Relations of the Basicranial Nerves in *Dicynodon*, and on the Homology of the Mammalian Auditory Ossicles," 'Zool. Soc. Proc.,' 1912, p. 419.

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The photographs also show the only suture which exists between the otic bones, this clearly marks off the pro-otic, except in the middle of the periotic mass where all sutures are entirely lost.

A very conspicuous depression (text-fig. 4, section E) on the inner surface of the periotic mass lies in the concavity of the anterior semicircular canal, *i.e.*, precisely in the position of the floccular recess of mammals and birds. A similar recess was found by NEWTON* in the Pterodactyl *Scaphognathus purdoni;* this is as far as we know the only other case of a floccular recess having been observed in a reptile.

Roofing Bones (text-figs. 2 and 5, and Plate 17, fig. 1, and Plate 18).—The biting ridge of the upper jaw, which was ensheathed by the beak, is continued from the premaxilla on to the maxilla at some distance behind the alveolar border of the tusk. The facial part of the premaxilla narrows backwards to a blunt point which divides the nasals from each other in front; behind, these bones meet in a rather short median suture. The frontals are paired, the parietals fused indistinguishably into a median bone. Behind the parietal foramen, which occurs at about the middle of its length, the parietal is greatly thickened; in front of the foramen is a preparietal element defined by well-marked sutures. It is a long, narrow bone, half the length of the parietal and only about the breadth of the pineal foramen, wedged into the parietal, which forks about it to meet the frontal on each side of it. This bone, which has been seen by BROOM† commonly, as well as by NEWTON,‡ in other Anomodonts, appears to be a new element arising in this group; in Dicynodon it has not been definitely recognised before, except by HUXLEY, who described it in *D. lacerticeps* as well as in other Dicynodont genera.§ In his latest work BROOM‖ describes and figures the preparietal as completely surrounding the pineal foramen in *Oudenodon Kolbei*; it does not do so in our specimen of *D. leoniceps*, nor in that of Lystrosaurus described by VAN HOEFEN.¶ Possibly the difference is merely specific. On each side, at the limits of its thickened median region, the parietal sends down a process which no doubt marks the position of the side wall of the brain case. It shows how narrow was the cavity for the brain, and it shows also that the parietal roofed over an extra cranial part of the skull. Posteriorly the parietals extend farther back at the sides than in the middle line, and the V-shaped space between their posterior processes is filled up by a bone which has been identified as interparietal.

SEELEY was the first to show that the bone which he calls post-frontal** overlaps

* 'Phil. Trans.,' 1888, B, vol. 179, p. 519.

† BROOM, "On some Points in the Anatomy of the Anomodont Skull," 'Rec. Alb. Mus.,' 1904.

‡ 'Phil. Trans.,' 1893, B, vol. 184, p. 438.

§ 'Palæont. Indica,' 1865–85, ser. 4, vol. 1.

‖ 'Ann. S. African Mus.,' 1912, vol. 7, p. 345, and fig. 1, p. 338.

¶ "Bijdragen tot de Kennis der Reptielen van de Karroo-formatie," 'Ann. Transvaal Mus.,' 1913, vol. 4, pp. 1–46, 4 Plates.

** "On the Skull of *Mochlorhinus platyceps*, from Bethulie, Orange Free State," 'Ann. Mag. Nat. Hist.,' 1898, ser. 7, vol. 1, p. 164; BROOM has apparently not seen this paper, since he nowhere alludes to it.

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the parietal and forms the border of the temporal vacuity. These relations are clearly shown in our reconstructions. SEELEY was also the first to discover the existence of a second bone behind the orbit, which he calls post-orbital, but his discovery does not seem to have gained recognition. The bone, however, is clearly marked off by sutures in our reconstructions. But SEELEY's nomenclature is not that which is now accepted, for when two bones occur in this position it is the anterior which is commonly regarded as the post-frontal, the posterior as the post-orbital. BROOM writes in 1910:* "In Dicynodon post-frontals are usually absent but occasionally small ones are present in other Anomodonts." The discovery of the existence of a post-frontal bone removes what BROOM† spoke of as the only feature distinguishing the temporal region of Dicynodonts from that of Plesiosaurs. As seen on the dorsal surface of the skull the post-frontal has the form of a very long T, the stem of the T running between the frontal and post-orbital, the crossbar, which is obliquely set on the stem, forming part of the margin of the orbit, and one of its branches running for a short distance down the post-orbital bar (text-fig. 2). As seen on the ventral surface of the roof of the skull, this bone is shorter and broader than on the dorsal surface, and is, roughly speaking, triangular in form. The sections of the skull reveal a considerable amount of overlap of the frontal over the post-frontal, as well as the extensive interdigitation of the latter with the post-orbital bone. This last-named bone forms practically the whole of the post-orbital bar; the jugal contributes a low, upwardly directed process to its lower end, and the post-frontal, as we have just said, contributes slightly to its upper end (Plate 18, figs. 1 and 3).

The external nares lie in front of the nasal bones. Within each of these apertures, almost in contact with their anterior and posterior margins, but separated by a comparatively wide interval from their upper and lower margins, is a small bone convex inwardly, and not suturally united with any of its neighbours (Plate 17, fig. 1). This little bone suggests at first sight the existence of a valvular arrangement in the nostril, but apparently it has another significance. SEELEY‡ evidently refers to the same bone when he speaks of the "subnarial" which he has seen in *D. tigriceps.* He regards it as having a homologue in a bone which, according to him,§ appears on the face in Pareiasaurus, and he thinks it may be the germ of the turbinal bones of mammals. He recognised that his "subnarial" is the same bone as the "septomaxilla" of KITCHEN PARKER.‖ COPE¶ represents a well-defined bone

* "Comparison of Permian Reptiles of N. America with those of S. Africa," 'Bull. Amer. Mus.,' 1910, vol. 28, p. 212.

† "On the Structures and Affinities of Udenodon," 'Zool. Soc. Proc.,' 1901, vol. 2, p. 162.

‡ "On the Anomodont Reptilia and their Allies," 'Phil. Trans.,' 1889, B, vol. 180, p. 215.

§ *Ibid.*, p. 237.

‖ 'Phil. Trans.,' 1871, vol. 161, p. 137; 1876, vol. 166, p. 621; 1877, vol. 167, p. 529.

¶ "On *Lystrosaurus frontosus*, Cope," 'Amer. Assoc. Proc.,' 1870, p. 194; and 'Amer. Phil. Soc. Proc.,' 1870, vol. 11 (II), p. 419.

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in front of the prefrontal and lachrymal and behind and bordering on the nostril which may well be a septomaxilla, and he remarks that OWEN had figured the same bone in *Ptychognathus latifrons*, but he gives no reference.

There can hardly be any doubt that this bone in Dicynodon is the same as that which BROOM* describes as the septomaxillary in the mammal-like and other reptiles. In the primitive forms, Pareiasaurus, Pariotichus, and Procolophon, he says: "it is mainly within the nostrils and probably fulfils its main function as a roof to Jacobson's organ." Among the mammal-like forms it is still within the nostril, in Pelycosaurs, Dinocephalians, Dromasaurians, and Therocephalians it comes on to the face. "In the Anomodonts it is absent, probably because they had lost their organ of Jacobson, as would appear from the loss of the prevomer."

GAUPP's researches have lent interest to the bone by showing that it is present in Monotremes, being fused in the adult with the premaxilla. GAUPP takes a somewhat different view from BROOM. He regards the position on the side of the face as primitive, and the condition in Sphenodon, lizards, and snakes—where the greater part of the bone lies within the nostril, in the floor of the nasal chamber extending to the septum nasi—as a roof to Jacobson's organ (hence the name septomaxilla), as a lateral development. GAUPP bases this view on the belief that in Rana and other Batrachia the septomaxilla already exists and is situated on the side of the face; and, in addition, he also points out that, in Lacerta, that part of the bone which lies on the face is situated in a precisely similar position to the septomaxilla of Echidna. If GAUPP'S view is correct, the condition in Dicynodon would appear to be a stage later than that found in Sphenodon, since of any facial portion of the bone it retains no trace.

On each side of the mesethmoid and close to the outer margin of its lateral expansions the ventral surface of the frontal is produced downwards into a thin ridge which runs forwards and is continued by extensions of the prefrontal and lachrymal. Each ridge forms part of the roof of an orbit and divides the orbit from the cavity of the snout. The groove which lies between this ridge and the bones from which it springs widens as it passes forwards and leads to a concavity on the inner side of the lachrymal bone and beyond this to the nasal chamber. A similar feature, but usually continued farther backwards, is developed to a various extent in other reptiles, and attains a great development in lizards.

Lying loose in the temporal fossa of one side of the skull was a piece of bone which proves to consist of the quadrate and quadrato-jugal. The existence of the latter element in Dicynodonts was discovered by BROOM,† who describes it as

* BROOM, in his latest paper ("On the Structure of the Internal Ear, and the Relations of the Basicranial Nerves in *Dicynodon*, and on the Homology of the Mammalian Auditory Ossicles," 'Zool. Soc. Proc.,' 1912, p. 419), received since this was written, states that a septomaxilla occurs in Dicynodon, and WATSON ('Rec. Albany Mus.,' 1912, vol. 2, pp. 287–295, 2 Plates) has seen it in Lystrosaurus.

† "On some Points in the Structure of the Dicynodont Skull," 'Ann. S. African Mus.,' July 12, 1912, vol. 7, p. 337.

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consisting of an articular end and a large plate-like expansion. Our specimen shows that, as he had surmised, there is a passage or aperture between the quadrate and the quadrato-squamosal.

The quadrate is a short, massive bone. The articular surface for the lower jaw, the inner two-thirds of which is formed by the quadrate and the outer one-third by the quadrato-jugal, is a groove bounded on each side by a ridge. The lower jaw bears a strong median ridge which plays in this groove and forms the main articular connection—a very mammalian character. The inner of the two ridges on the quadrate plays in a groove on the condyle of the jaw—thus recalling the Reptilia. Thus in the whole arrangement there is a mixture of characters, but the mammalian preponderates.

Another point of interest is the great length of the articular surface presented by the lower jaw as compared with that on the quadrate. This renders possible a great range of vertical movement or a wide gape, comparable with that of the sabre-toothed tiger, and necessitated, as in that animal, by the existence of long tusks. That the tusks were not used as digging organs is suggested, as OWEN pointed out, by the fact that they show no signs of wear; they were probably defensive organs, possessed by the male, but not by the female (Oudenodon).

Lower Jaw.—BROOM'S description of the lower jaw, written in 1904,* is a very great improvement on that of 1901.†

The dentary is by far the largest and most massive bone in the jaw and is more than half its length. Its upper surface presents two high and narrow ridges running practically parallel to each other along the symphysis and diverging behind it. Between them on the upper surface of the symphysis is a median prominence.

This arrangement of ridges and prominence is similar to that described by HUXLEY in (Dicynodon) *Ptychognathus Murrayi* in 1859.‡ On the outer side of the paired ridges the upper surface of the dentary extends outwards horizontally. From the edge of this platform there extends backwards along the lateral surface of the dentary an outwardly projecting ridge described by OWEN and later authors.

The posterior limit of the median prominence mentioned above is also, at this point, the limit between the dentary and splenial which, as was first pointed out by HUXLEY in 1859, meets its fellow in the middle line. It is a somewhat massive bone, having very little backward extension. A channel, which evidently lodged a large blood-vessel, runs between it and the dentary. Posteriorly this channel is very large and is protected behind by the dentary, articular and splenial. A downwardly projecting ridge of the dentary meets the upper edge of the anterior extremity of the articular, the lower edge of which meets the splenial. Below this channel and at its posterior termination the anterior end of the angular (Plate 17, fig. 1) is inserted

* "On some Points in the Anatomy of the Anomodont Skull," 'Rec. Albany Mus.,' 1904, p. 75.

† "On the Structures and Affinities of Udenodon," 'Zool. Soc. Proc.,' 1901, vol. 2, p. 162.

‡ "On *Dicynodon Murrayi*," 'Quart. Journ. Geol. Soc.,' 1859, vol. 15, p. 654.

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for a very short distance between the splenial and dentary and for a longer distance it is applied to the inner surface of the lower of the two processes into which the dentary divides as it passes backwards. The upper and stronger of these two processes is bifurcate at its extremity and receives, in the notch of the fork, the pointed anterior end of the surangular. Between the angular, surangular, and the upper and lower backwardly projecting branches of the dentary, is the well-known oval vacuity which has been described by so many authors.

The angular possesses, as BROOM has described, a complicated form. Its exact relations to the other bones are difficult to determine without the help of sections. These reveal the fact that the surangular is a bifurcate bone, one limb, the lower, being applied to the upper surface of a ventral and anterior process of the articular, and the prominence thus formed is clasped by the bifurcate posterior end of the angular. The angular extends upwards, reaching the ventral surface of the surangular for a considerable distance in front of this interlock.

Turning now to the dorsal surface of the ramus, the surangular is seen to have considerable thickness and to meet the articular in a suture which is directly transverse for some distance on the outer side and then runs obliquely inwards and forwards against a short dorsal anterior process of the articular. The ventral anterior process of the articular is at first narrow, but expands as it passes forwards. It is separated by a considerable interval from the angular which lies on the outer side of it. Looking at the ventral surface of the ramus, it is seen that a long, obliquely running suture divides the angular on the outside from the lower anterior process of the articular on the inside.

The articular forms the whole of the articulation, as BROOM has stated, and thus with its two processes is a bone of some size. We have already alluded to the mammalian character of the articular surface; BROOM speaks of a downward and inwardly directed plate of the angular, recalling the inflected angle of the marsupial jaw,* but in our specimens we can find no signs of such a feature.

Since writing this an excellent account of the lower jaw has been given by WATSON;† in addition to the elements we have described he figures the coronary, of which we find no trace. He also alludes to the characteristic articulation and speaks of it as "unique, but characteristic of the Anomodonts" generally.

* "On some Points in the Anatomy of the Anomodont Skull," 'Rec. Albany Mus.,' 1904, p. 75.

† "On some Reptilian Lower Jaws," 'Ann. Mag. Nat. Hist.,' 1912, vol. 10, pp. 575–8.

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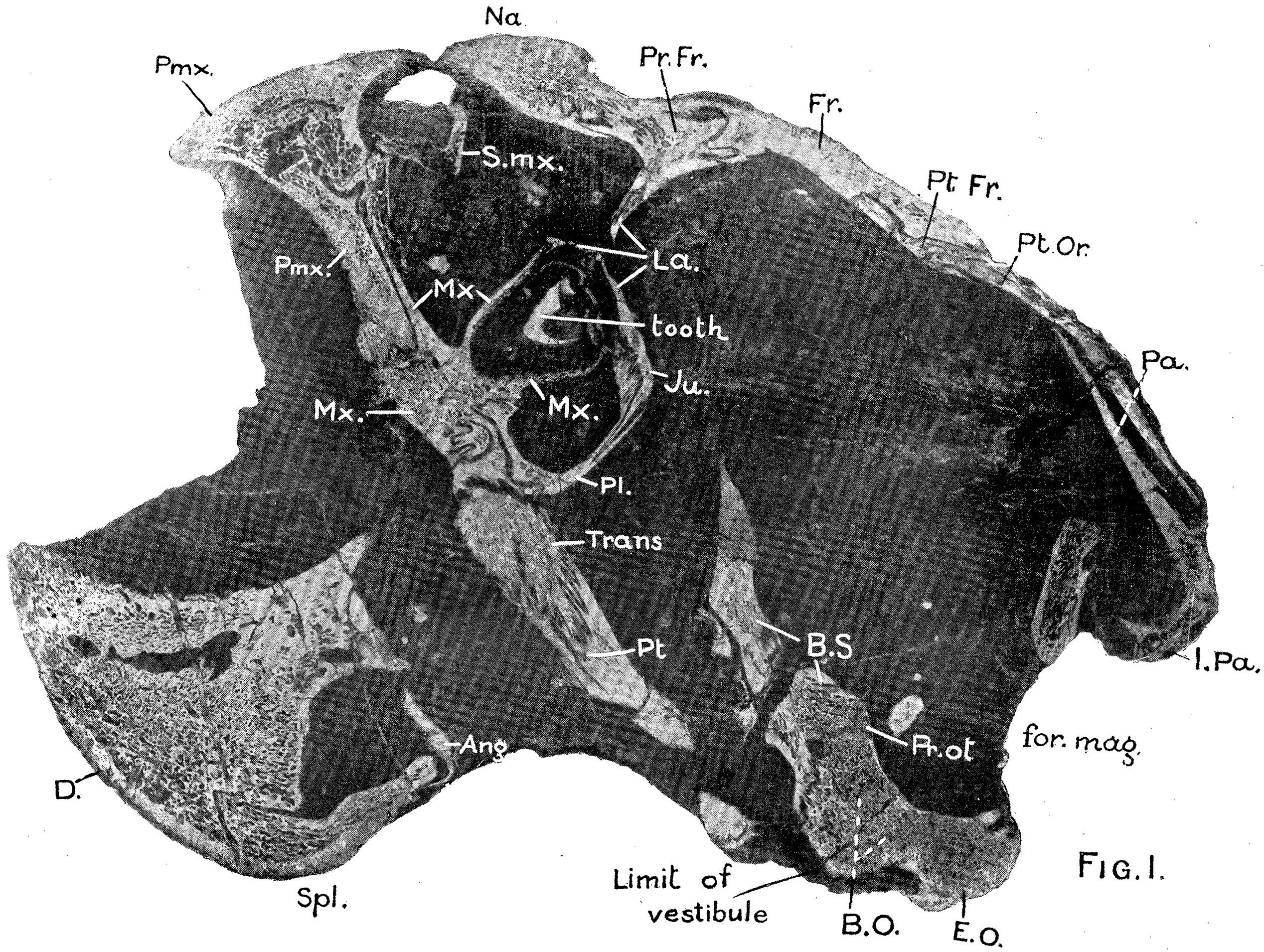
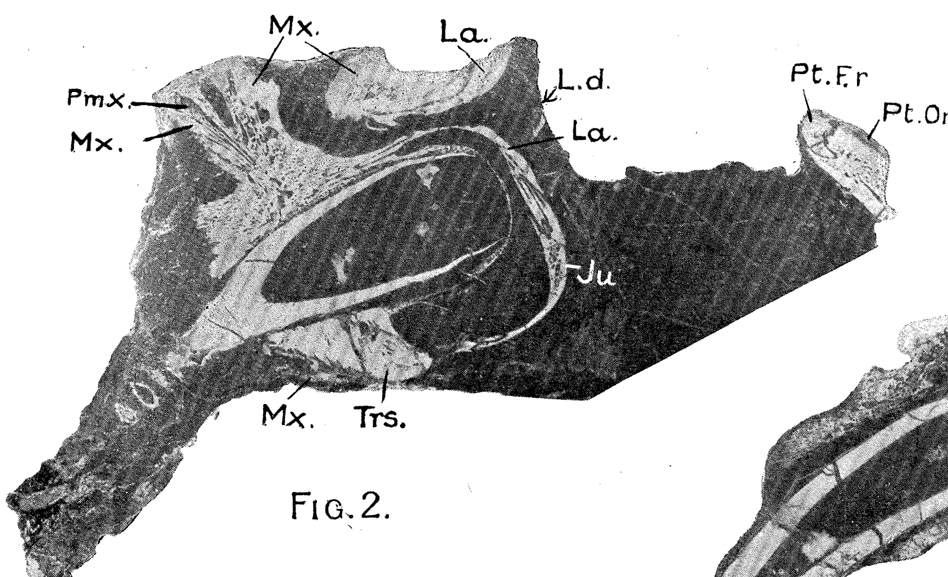


Fig. 1.



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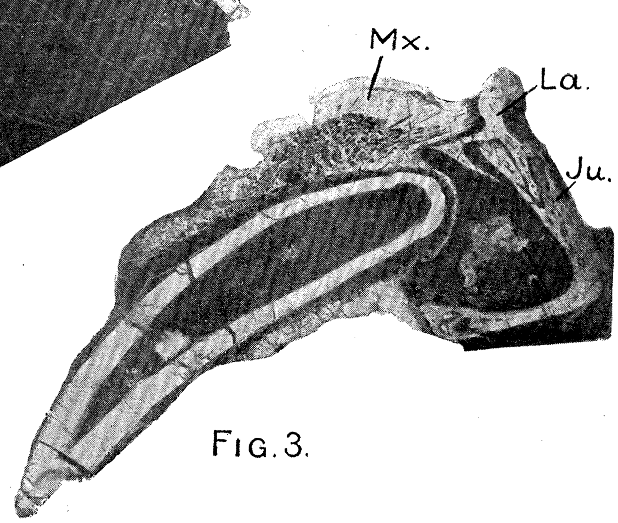

Fig. 3.

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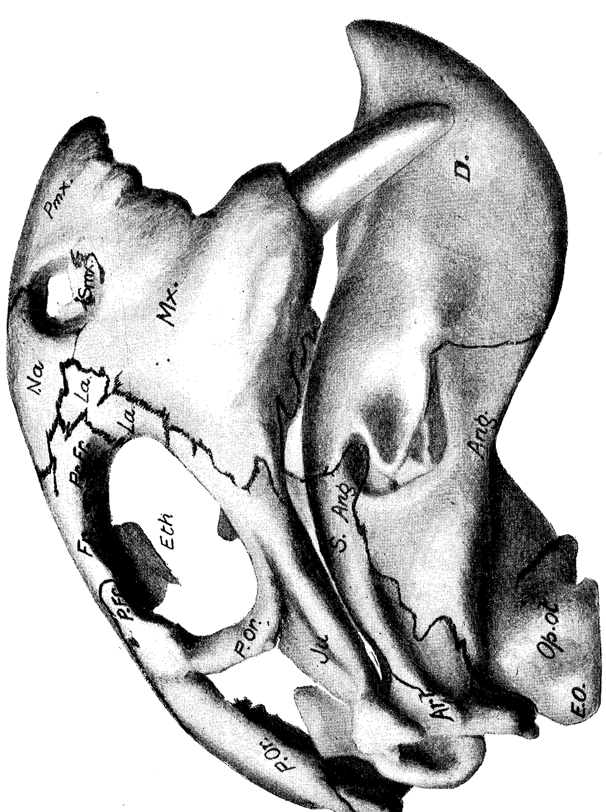

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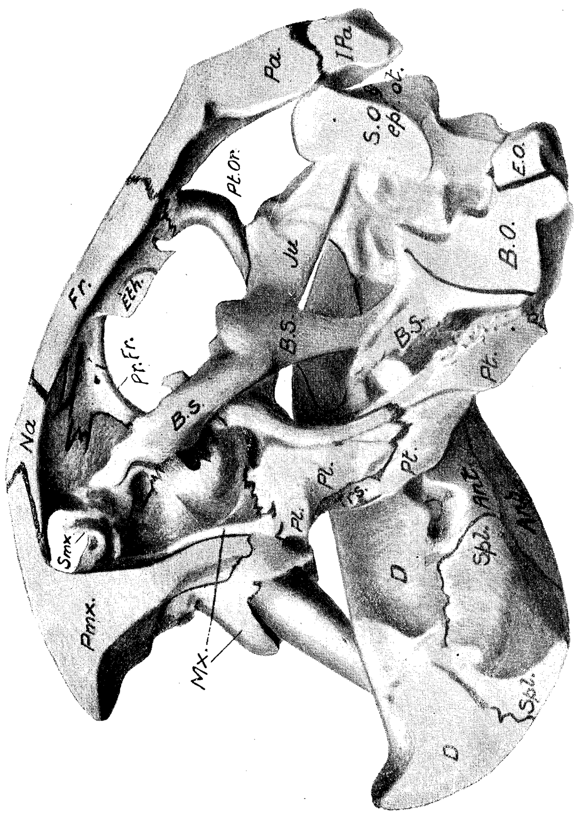

FIG. 2.

FIG. 3.

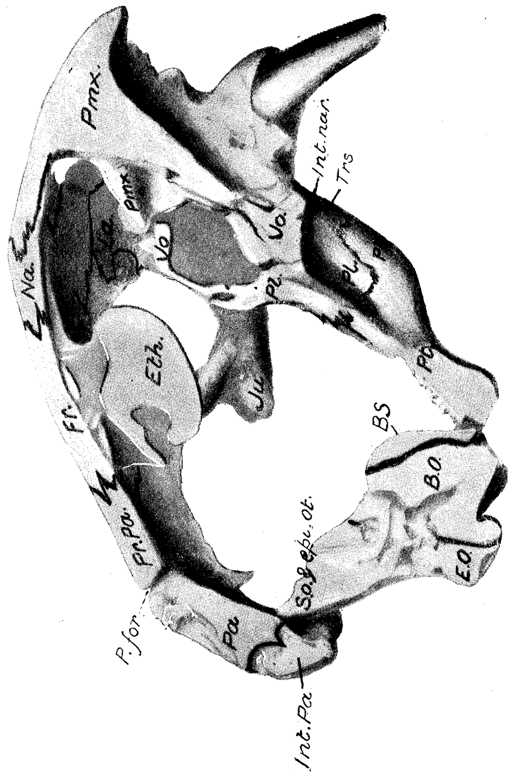

FIG. 4.

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DESCRIPTION OF PLATES.

Abbreviations used.

Ang. . . .	Angular.	P. fr. or Pt. Fr.	Post-frontal.
Art.	Articular.	P. for. . . .	Pineal foramen.
B. O. . . .	Basi-occipital.	Pl.	Palatine.
B. S. . . .	Basi-sphenoid.	Pmx.	Premaxilla.
D.	Dentary.	Pr. Fr. . . .	Prefrontal.
E. O. . . .	Exoccipital.	Pr. pa. . . .	Preparietal.
Epi. ot. . . .	Epiotic.	Pt.	Pterygoid.
Eth.	Ethmoid.	Pt. Or. . . .	Post-orbital.
For. mag. . .	Foramen magnum.	Qu.	Quadrate.
Fr.	Frontal.	Qu.-j. . . .	Quadrato-jugal.
Int. pa. . . .	Interparietal.	S. ang. . . .	Surangular.
Ju.	Jugal.	Smx.	Septomaxilla.
La.	Lachrymal.	Spl.	Splenial.
L. d.	Lachrymal duct.	St.	Stapes.
Mx.	Maxilla.	Trs. or Trans. .	Transverse.
Op. ot. . . .	Opisthotic.	Vo.	Vomer.
Pa.	Parietal.		

Plate 17.

Fig. 1.—Vertical longitudinal section through the skull of *Dicynodon leoniceps*, Owen, a little on one side of the median line. The section is the 82nd in our series. ($\times \frac{3}{2}$.)

Figs. 2 and 3.—Vertical longitudinal sections (numbered 92 and 100) through the "maxillary antrum." *L. d.* points to lachrymal duct. ($\times \frac{3}{2}$.)

The symbols are the same as those in the text-figures 2 and 3, except *Pt. Fr.* for *P. Fr.* and *Pt. Or.* for *P. Or.*

Plate 18.

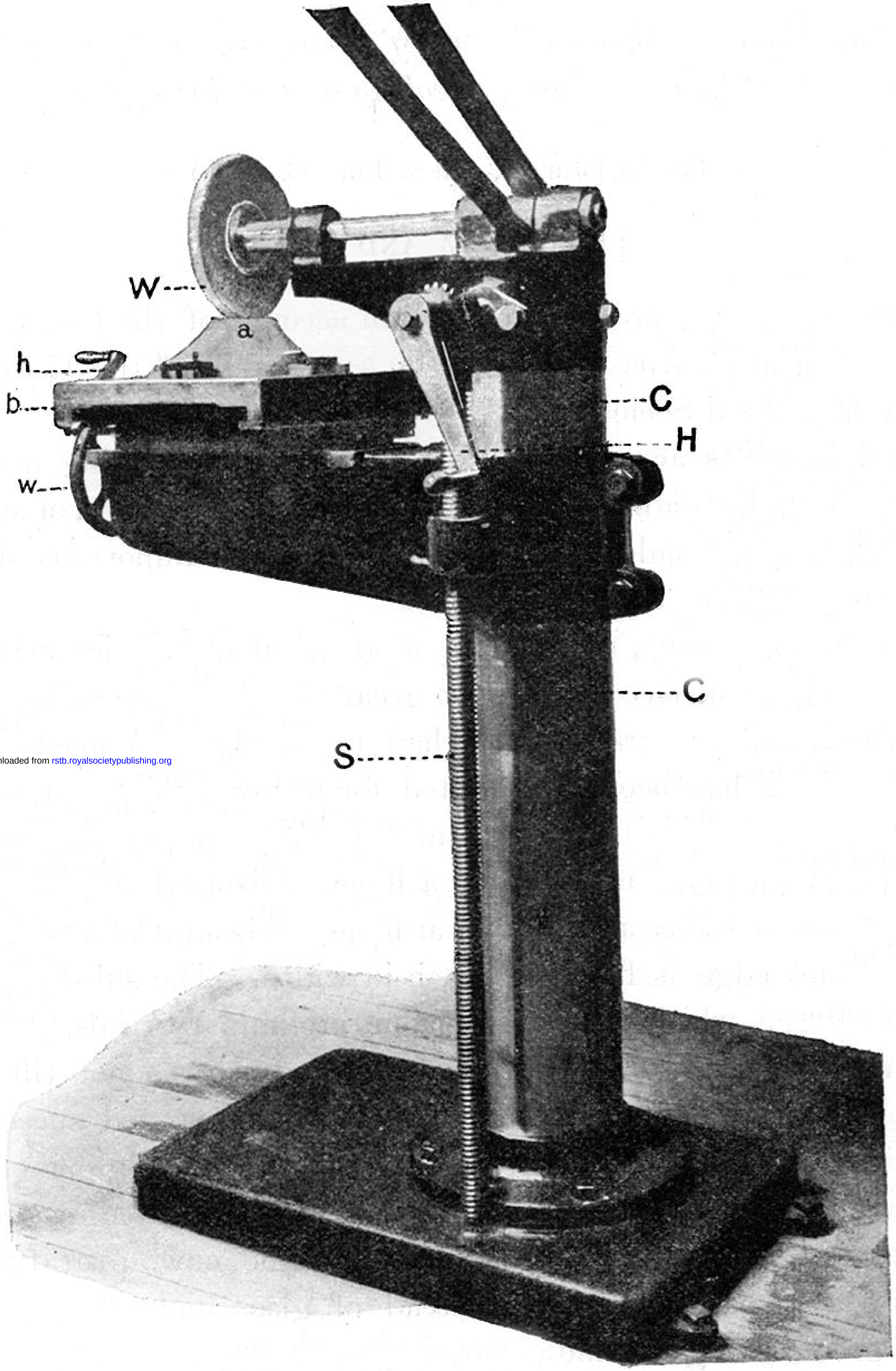
Reconstructions of the Skull of *Dicynodon leoniceps*, Owen, with the Edges of the successive Thin Slices smoothed away. (Nat. size.)

Fig. 1.—The right side of the skull, seen from without.

Fig. 2.—The right side, seen from within. The base is displaced upwards and forwards.

Fig. 3.—The left side, seen from without, after the removal of the ramus of the lower jaw.

Fig. 4.—The left side, seen from within.



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TEXT-FIG. 1.—Machine for Grinding-down large Fossils in order to obtain Serial Sections.

W, grinding wheel; CC, cylindrical column, which supports the bearings for the wheel W and carries the movable bench *b*; H, handle to turn the screw S, which determines the amount of the vertical movement of the bench *b*; *h*, handle which moves the bench horizontally and laterally; *w*, wheel which moves the bench to and fro horizontally; *a*, the object to be ground. ($\times \frac{1}{10}$.)

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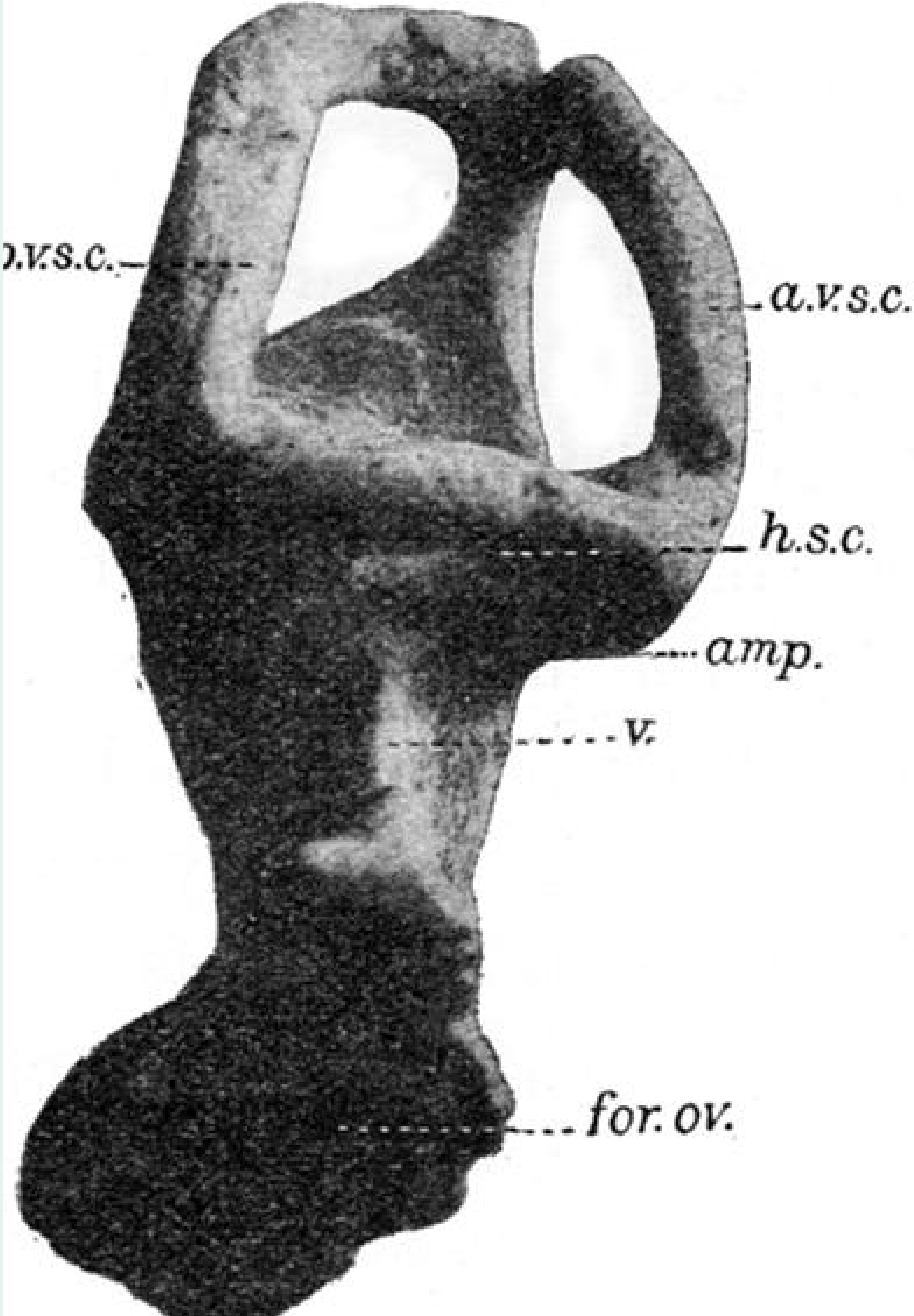

XT-FIG. 9.—The Labyrinth of the Ear. (× about 3.)

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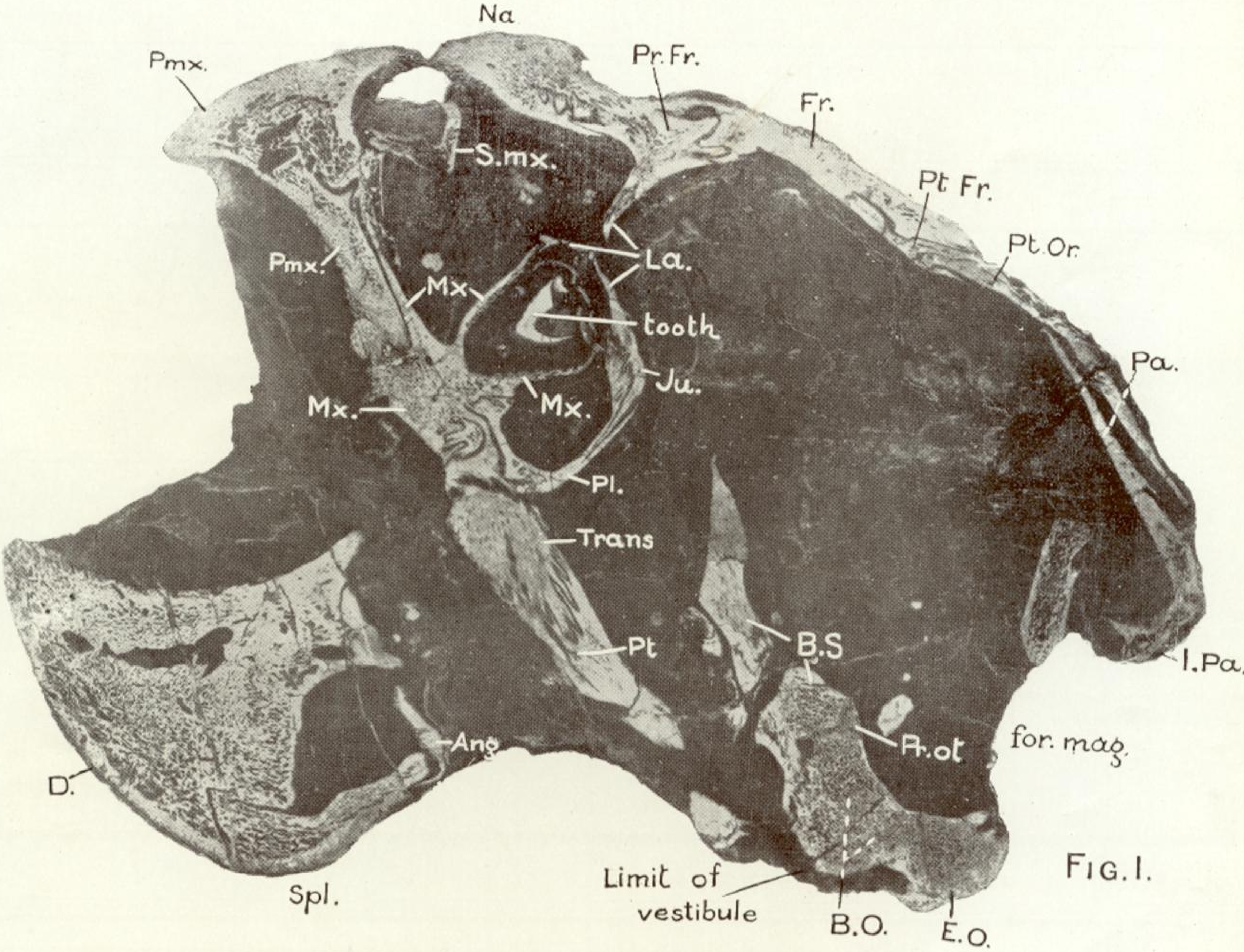

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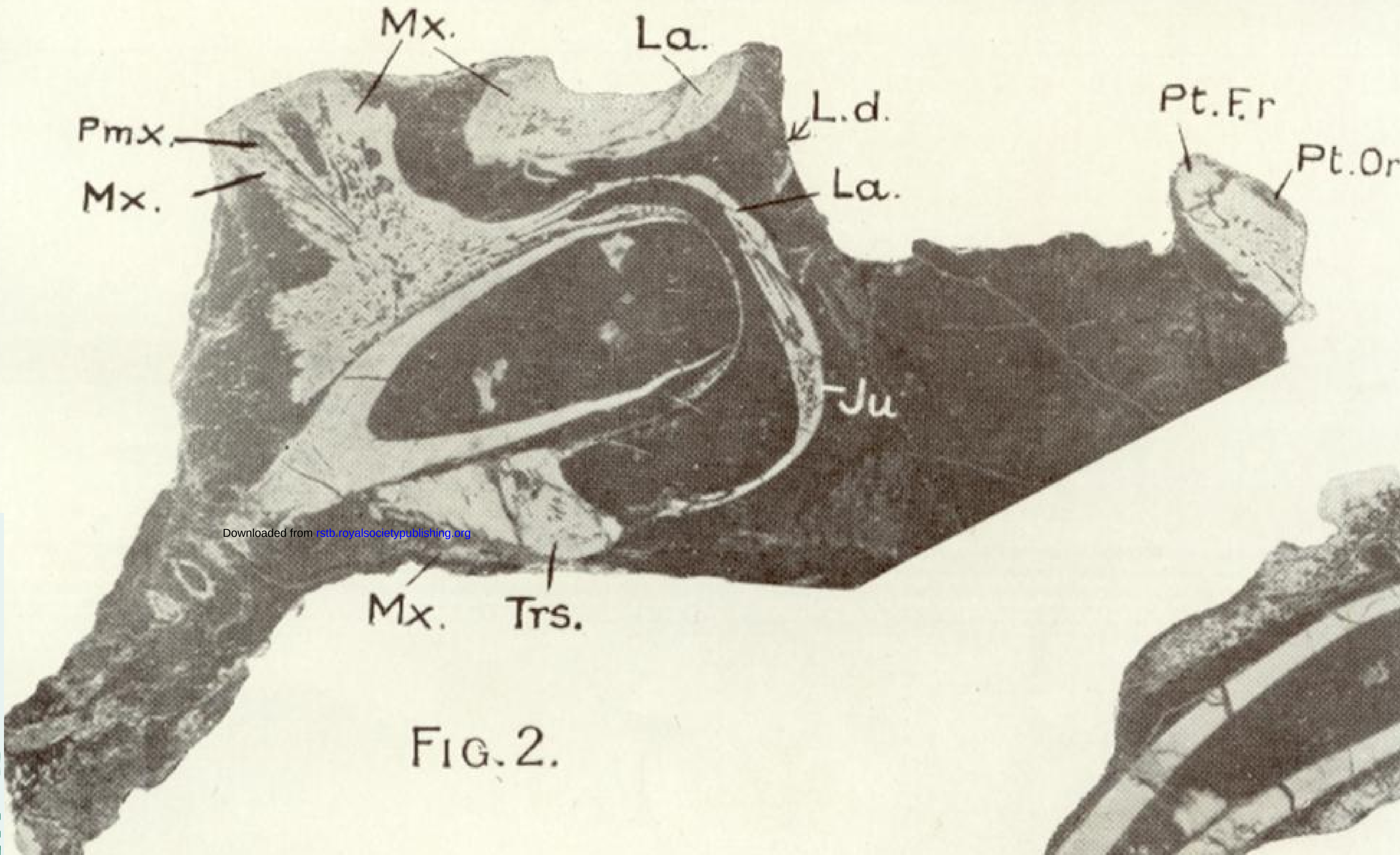

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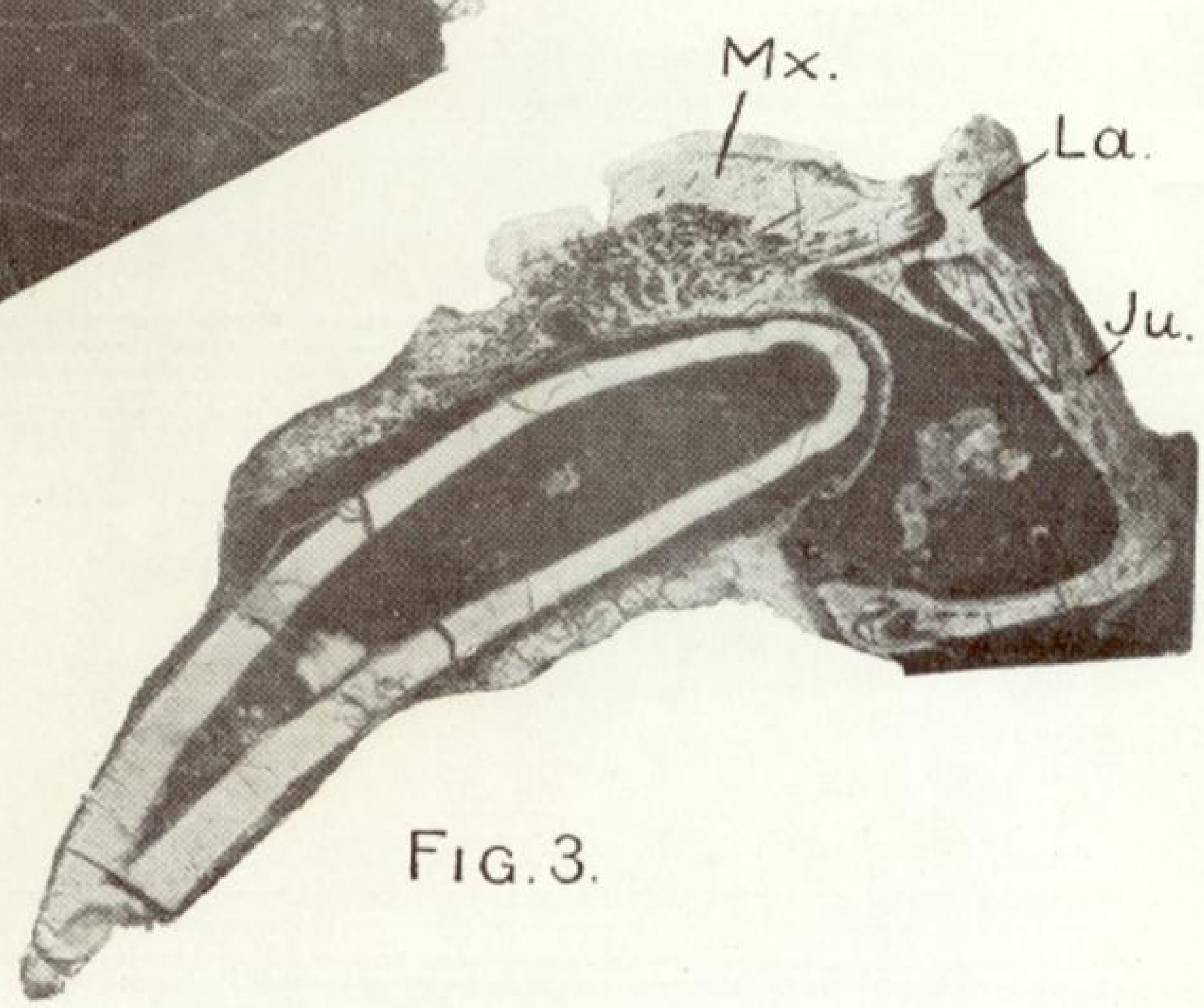

FIG. 3.

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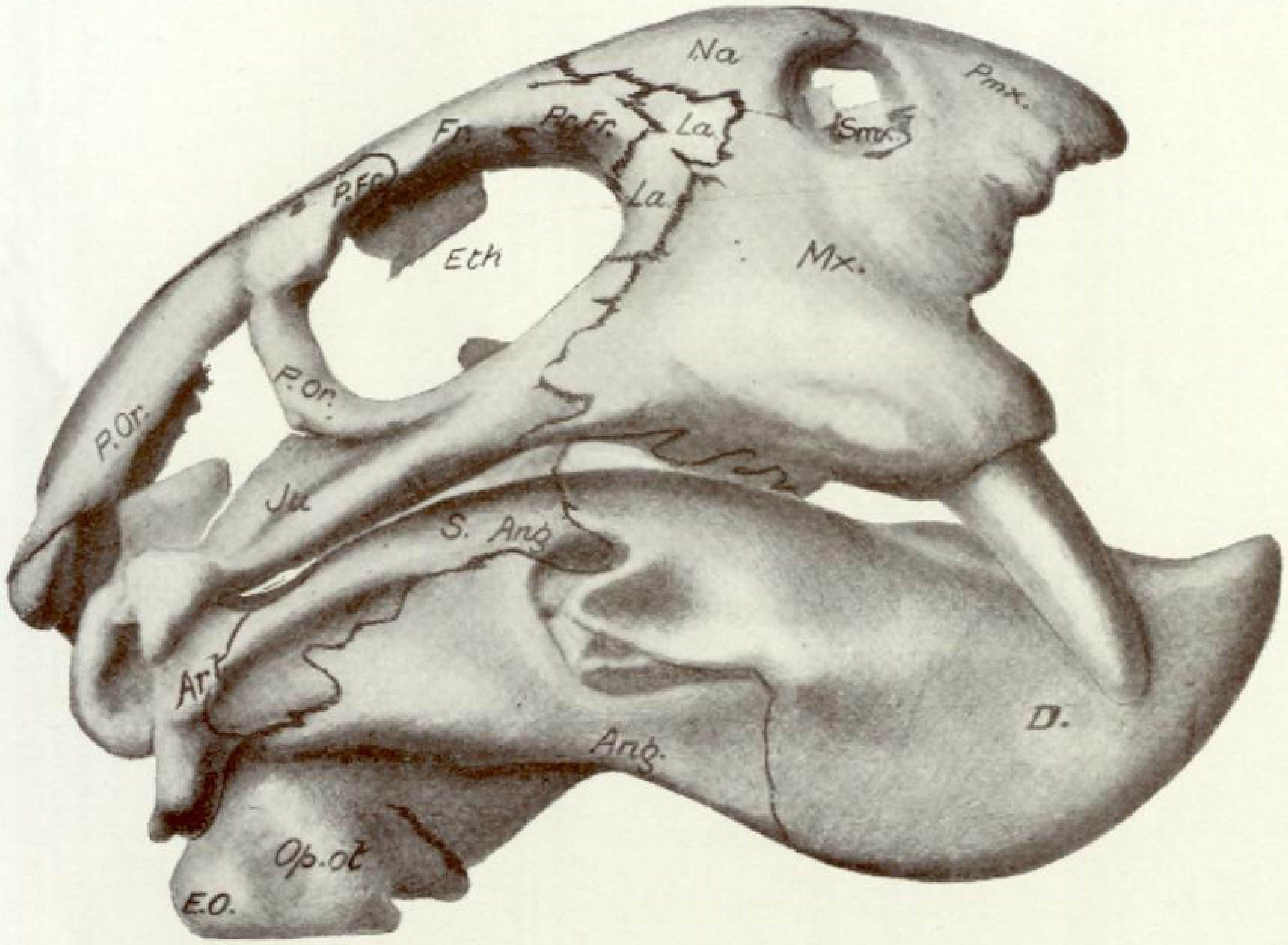

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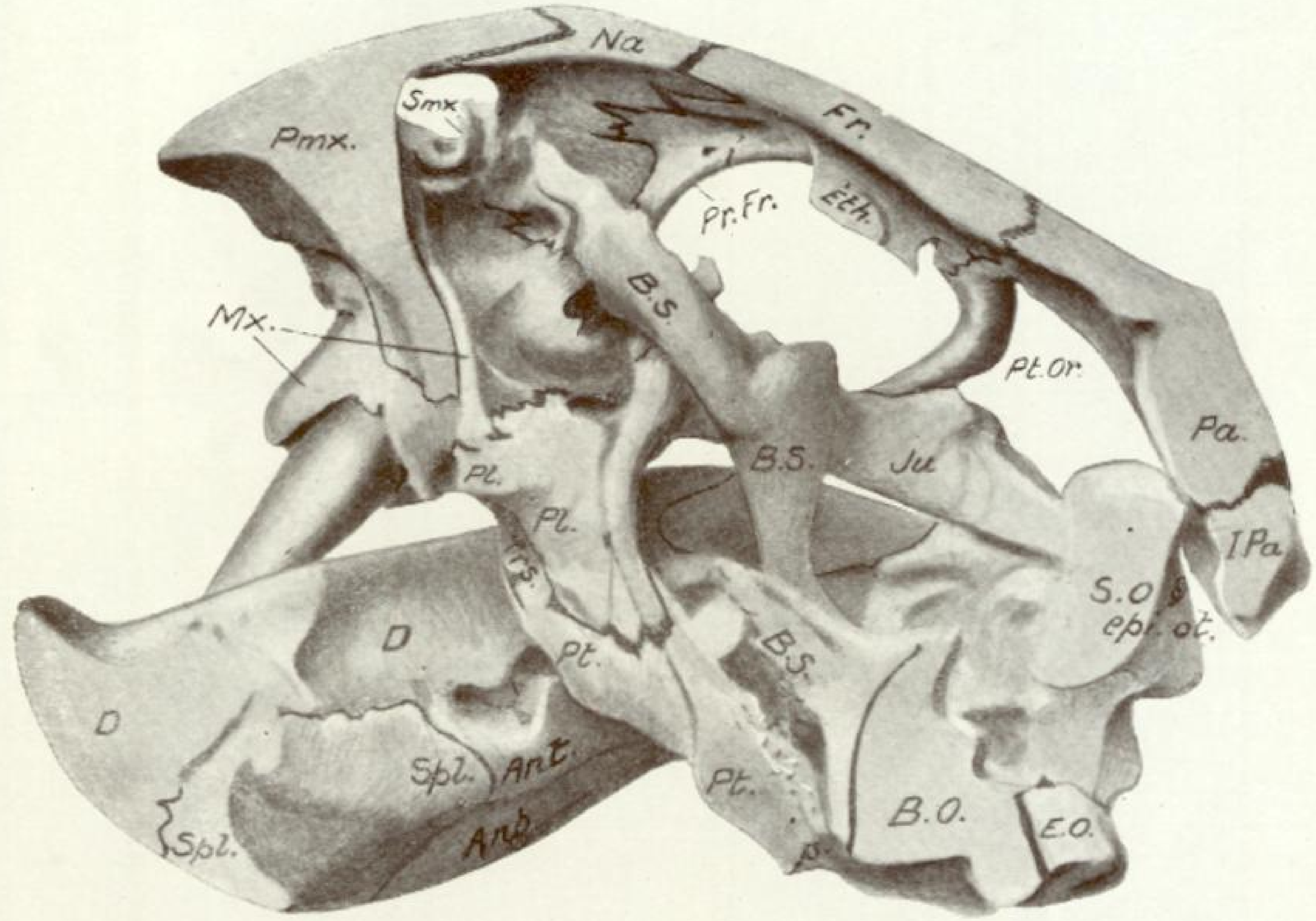

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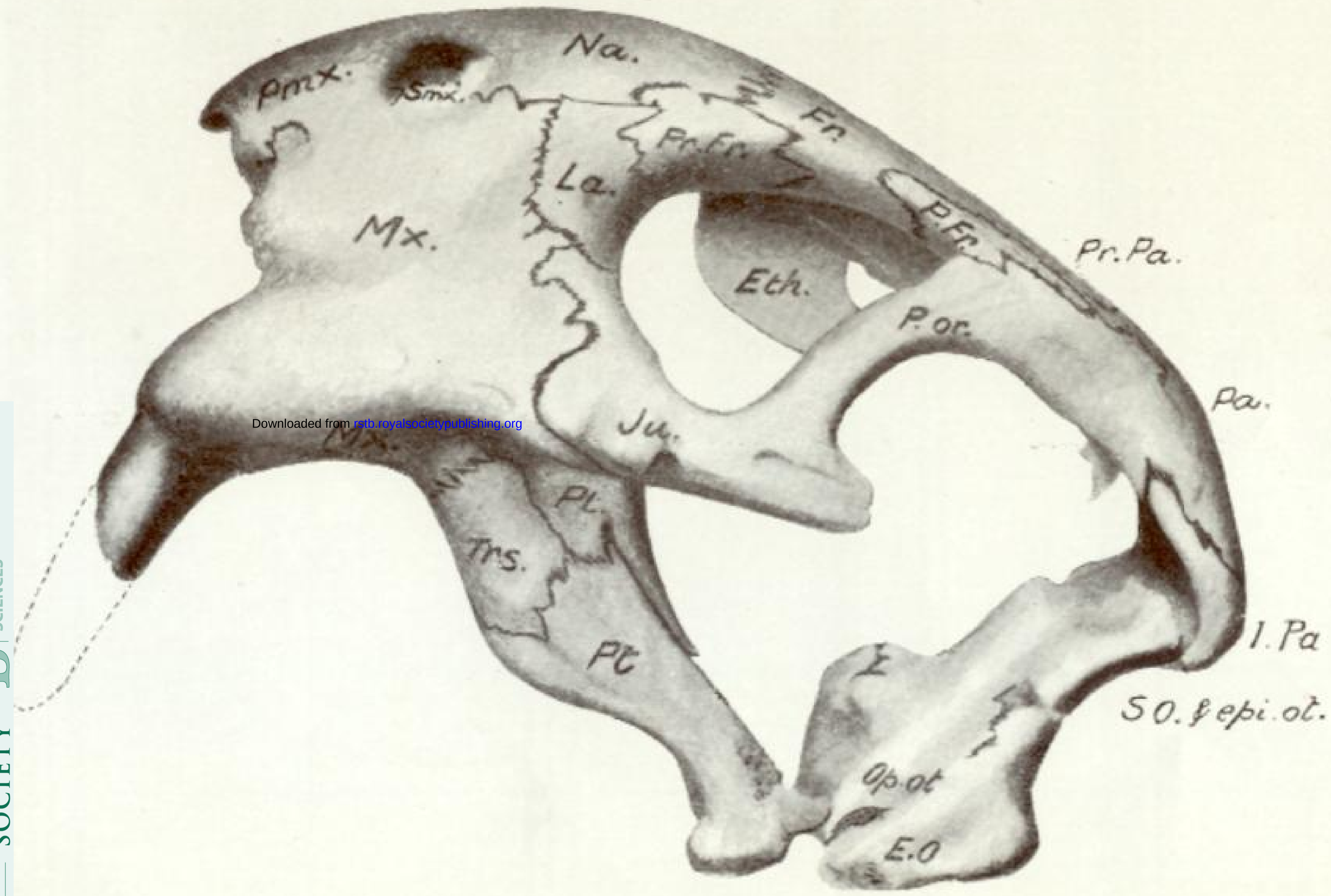

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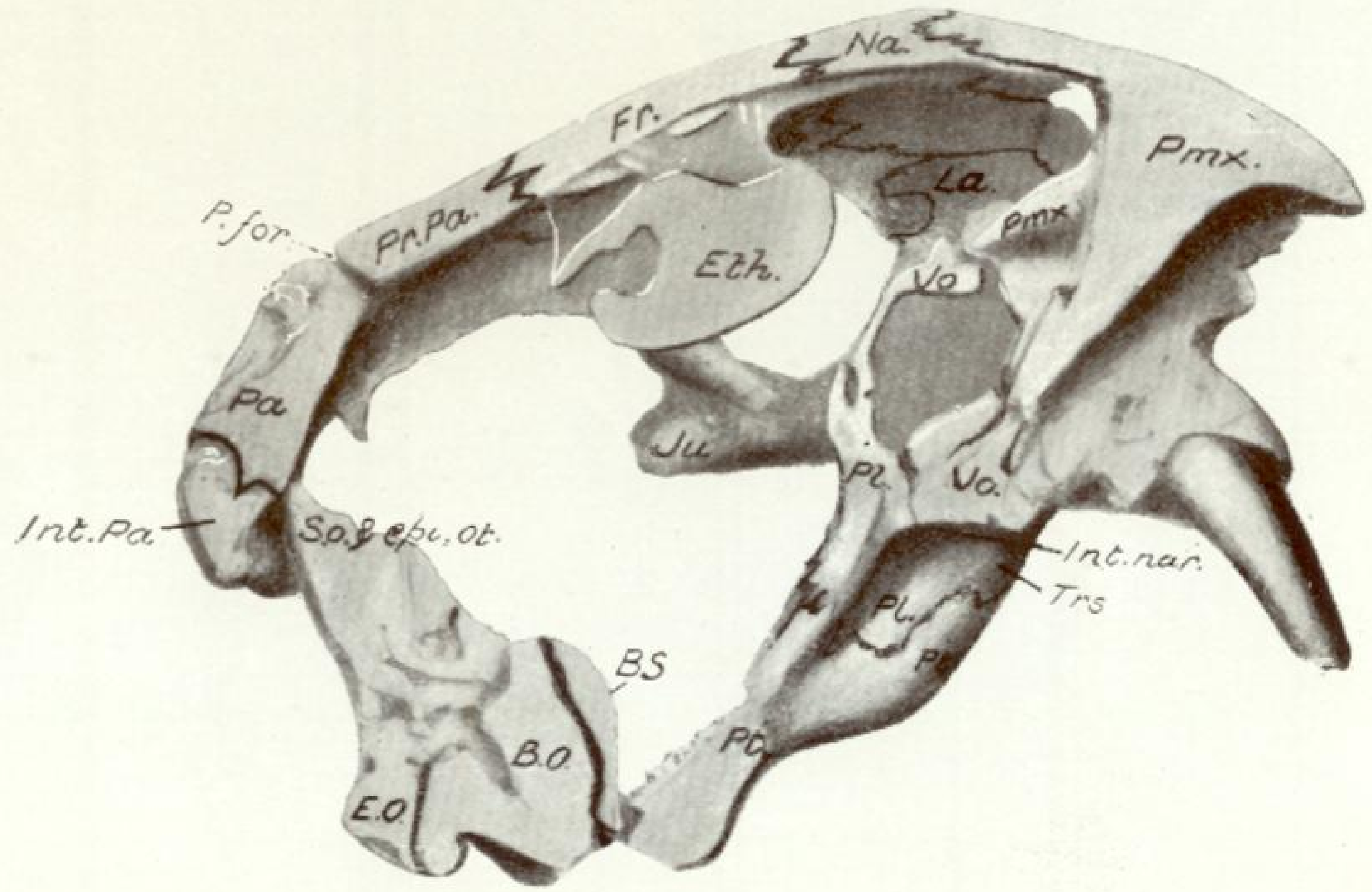

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