PHILOSOPHICAL TRANSACTIONS.

I. *The Structure, Evolution and Origin of the Amphibia.—The "Orders" Rachitomi and Stereospondyli.*

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[Plates 1 and 2.]

Contents.

Introduction.

Although Fossil Amphibia have long been known and have been the subject of innumerable and often very excellent works, no systematic attempt to determine their relations to one another and to the living Amphibia has ever been made. Many authors have, of course, discussed the taxonomic position of individual types, and drawn up classifications which express their views of relationships.

Since the time of W. Kovalevski it has been generally realised that the importance of palæontological material entirely depends on the fact that it is of different ages and that the earlier members of any given group will preserve a more primitive fundamental structure than is shown in its later members, although they may, of course, be very specialised, either in adaptation to some special environment or "fortuitously."

It is thus necessary for a satisfactory study of any fossil material to recognise by persistent characters that certain groups are closely related, and then by arranging the members of these groups in their order of appearance and comparing them one with another to determine the evolutionary trend of the group.

That such a study has not yet been undertaken for the early Stegocephalia is owing largely to the following causes:—

1. The fact that the existing material usually allows of a very incomplete description. Of most forms we know only the structure of the dorsal surface of the skull, a region which seems to show no clear direction of evolutionary change.

2. That existing descriptions are usually inadequate because they give no detailed account of the skull base and brain case, in which regions evolutionary changes are obvious.

3. That many existing descriptions and figures are very inaccurate.

4. That with the partial exception of the British and Munich Museums no collections cover the whole field of Amphibia at all fully.

During the last few years I have been able to study the greater part of the material of Fossil Amphibia in existing collections, which is distributed as follows:—

Lower Carboniferous Embolomeri: British Museum, Edinburgh, Manchester.
Upper Carboniferous Embolomeri: British Museum, Newcastle, Manchester.
Permian Embolomeri: Casts from Prague, American Museum, University of Michigan, Munich.
Lower Permian Rachitomi: British Museum, Munich, Tübingen, Paris, American Museum, Chicago.
Upper Permian Rachitomi: South African Museum, Pretoria.
Lower Trias Rachitomi: British Museum, Bloemfontein.
Lower Trias Stereospondyls: British Museum, Munich, South African Museum.
Upper Trias Stereospondyls: British Museum, Munich, Tübingen, Stuttgart, Chicago, Brisbane.
Upper Carboniferous and Lower Permian Phyllospondyli: British Museum, American Museum, Munich, Manchester.
Upper Carboniferous Lepospondyls: British Museum, Manchester, Newcastle, American Museum.
Lower Permian Lepospondyls: British Museum, Munich, Casts from Prague, Diplocaulus at Tübingen, American Museum, Chicago.

I propose in this and subsequent papers to discuss the structure of Amphibia belonging to all orders, firstly pointing out those characters which are common to, and serve to show the real connection between all members of each order, and then treating in greater detail those features which show evolutionary changes.

Such a study, if systematically pursued, allows of the construction of a hypothetical ancestor by the projection backwards of the observed evolutionary trends. Comparison of such hypothetical ancestors of different orders leads easily to a recognition of the real primitive amphibian structure, which can then be compared with that of fish of suitable age.

The Genera of Rachitomous Amphibia.

This section will give a list of all described genera of Rachitomous Amphibia, their age, the extent of our knowledge, and a discussion of doubtful points in the descriptions, especially of the basicranial and occipital regions.

Eryops.

Eryops was originally described by Cope (1), whose work made us acquainted with the shape of the skull and lower jaw, the structure of much of the vertebral column, the limb girdles and limbs.

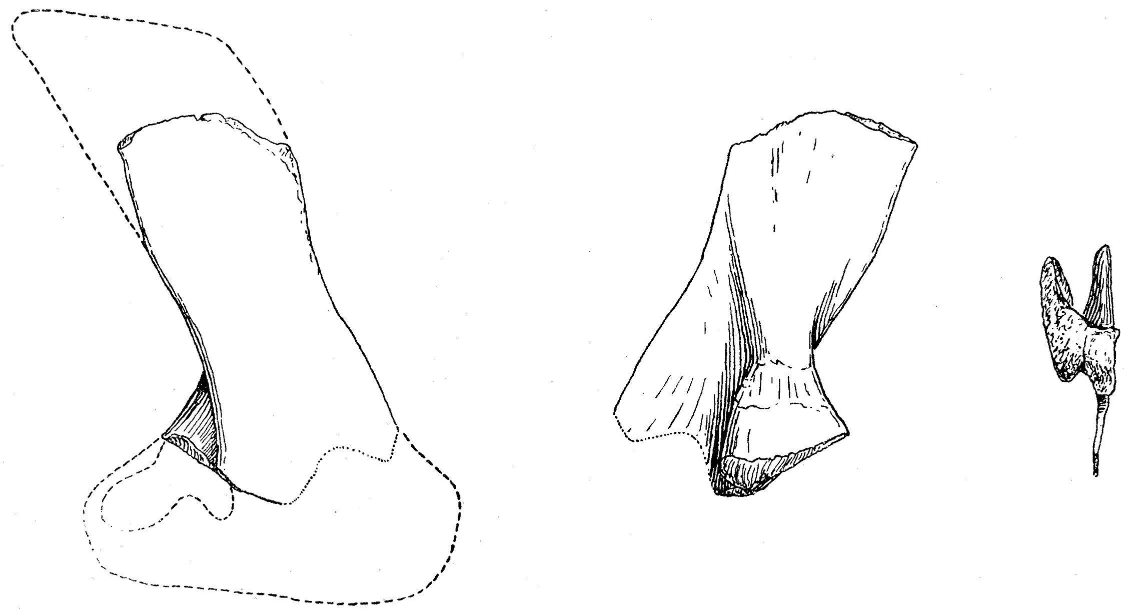


Fig. 1.—Scapula of a young Eryops. $\times \frac{1}{2}$. Brier Creek bone bed, Texas. Specimen given me by Prof. E. C. Case.

Left, external aspect; the dotted outline is that of an adult shoulder girdle; Middle, internal aspect; Right, from below, anterior edge downwards.

In 1899 Broili (2) gave the first description of the palate and occiput and good figures of many other bones.

Branson (3), in 1905, made the first attempt at tracing the sutures on the skull and lower jaw, and in 1910 Case (4) cleared up the rather complicated synonymy; for the first time gave us a good knowledge of the build and general structure of the animal, and added very largely to our knowledge of the palate.

v. HUENE (5) made the first attempt to determine the structure of the brain case, but was unfortunately much misled by the inadequate preparation and preservation of his specimens.

BROOM (6), in 1913, gave an excellent account of the skull structure, first correctly determining all the sutures of the skull roof, occiput, palate, and lower jaw, and correctly determining the structure of the basicranial region. I (7) have given a more complete account of the brain case and stapes (1916), which regions need not be referred to further.

In fig. 1 I have given drawings of an immature scapula of Eryops from the Brier Creek bone bed, which I owe to the generosity of Prof. CASE. This bone is of importance because it agrees in its limits with the scapula of a Pelycosaur, forming the upper part of the screw-shaped glenoid cavity, and showing faces towards the area which in Pelycosaurs is occupied by the two coracoidal elements. (*Cf.* WATSON, 1918.)

The little skull described by CASE (4) as a young Eryops, and by BROOM (6) as *Eryops anatinus,* seems to have been one of the two type specimens of COPE's genus Parioxys, and as, although it is obviously a close ally of Eryops, it seems to deserve generic distinction, it might retain COPE's generic name.

Sclerocephalus, Goldfuss, *and Onchiodon*, Geinitz.

The type species *S. hauseri* was originally described as a fish; v. MEYER (9) recognised that it was a labyrinthodont allied to Archegosaurus and gave a good figure. The type is a nearly complete but somewhat disarticulated skull.

In 1887 BRANCO (10) described as *Weissia bavarica* a fine complete skull which was shown by v. AMMON to belong to the same genus. v. AMMON (11) also described the posterior part of a skull and anterior part of a skeleton as belonging to the type species, an identification which may be correct, although it rests on very slender evidence.

Meanwhile, GEINITZ and DEICHMULLER had described a tooth as *Onchiodon labyrinthica*, and subsequently identified with it a crushed skull which they transferred to the genus Zygosaurus as *Zygosaurus labyrinthicus* (12). v. AMMON (11) recognised this as another species of Sclerocephalus.

To this species CREDNER (13) in 1893 referred some imperfect skulls, a shoulder girdle, femur and hind foot from Niederhasslich. The hind foot is that of a Pelycosaur, and need not be further considered here. Of the other remains all, except the original of Plate XXX, fig. 2, seem to be specifically identical, the skull mentioned differing in the fact that the frontal is shown to enter into the orbital margin.

These animals certainly do not belong to Sclerocephalus. The type skull of that genus has the orbits in the middle of its length. CREDNER's skulls have theirs far back, so that the distance between the orbit and the otic notch is small.

The shoulder girdle described by v. AMMON as belonging to the type species of Sclerocephalus has a large rhomboidal interclavicle and very wide triangular clavicles. CREDNER'S animal has a small interclavicle and narrow clavicles. As CREDNER'S skulls do not seem to belong to any genus described from adequate material I propose to resuscitate GEINITZ'S Onchiodon for them.

Onchiodon is of much interest in that it is very near to, in fact scarcely generically distinct from, Eryops. From the fact that the majority of the specimens from the Plauensch-grund are those of aquatic animals, it is probable that the Onchiodon remains are those of young individuals still largely water-living, whilst Eryops is mostly known from the mainly terrestrial adults.

The only difference in the dorsal surface of the skull is that in Eryops there is an interfrontal which is absent in Onchiodon. The pterygoid and ectopterygoid figured by CREDNER agree exactly with Eryops in most features, including the granular teeth on the former bone, but differ in the shorter length of the post-basipterygoid region, which is crushed out flat, and therefore at first sight differs much from that of Eryops known from uncrushed material.

The lower jaw is much like that of Eryops, so far as known. The neural arches and intercentra are quite similar to those of the American animal.

The ribs agree with those of Eryops in their expansion, but do not show the definite uncinate process of that form. THEVENIN'S account of Actinodon shows that this difference may depend entirely on age.

The shoulder girdle of Onchiodon agrees very closely with Eryops. Comparison of CREDNER'S and CASE'S figures shows that the cleithra and clavicles are identical. The interclavicle differs in having a rather longer stem, if CREDNER'S isolated specimen is rightly referred. The large scapula figured by CREDNER is quite intermediate in structure between the young Eryops scapula figured in this paper and that of the adult.

The ischium and femur and the lower leg are identical, or nearly so, in the two animals. Finally the dermal scutes are similar.

The two genera are thus extremely closely allied, and I only keep them apart because the quadrate condyles of Onchiodon do not project so far behind the occiput as in Eryops and the interpterygoid vacuities seem to be larger.

All the material of Onchiodon comes from the Middle Rothliegende of Niederhasslich Plauensch-grund, and is thus probably rather later than Eryops, of which it seems to be a descendant.

Osteophorus.

This genus is only represented by the single type skull of *O. römeri* described by H. v. MEYER (14) in 1860.

This skull greatly resembles that of Eryops, having an exactly similar interfrontal. The muzzle is, however, somewhat narrowed, and the external nares are long slits and not the round openings of Eryops. The lachrymal also differs in not reaching the nostril.

Osteophorus comes from the Rothliegende of Löwenberg, Silesia.

Actinodon, Gaudry.

This genus was founded by GAUDRY (15) for Rachitomous Amphibia from the Lower Permian of the neighbourhood of Autun; most of the existing material has been described by THEVENIN (16), who has traced the changes which occur with age, showing that the large type described by GAUDRY as Euchirosaurus is specifically the same as the small skulls of *Actinodon frossardi* and *brevirostris.*

The British Museum contains the anterior parts of two skeletons of this type from Autun, one of which is very well preserved and prepared. This specimen shows the following features not well brought out in THEVENIN'S description:

I. There are small and broad occipital lappets of the dermosupra-occipitals, and much larger flanges of the tabulars resembling those of Eryops.

II. There are atlantal ribs in the form of small slightly curved rods. The distal ends of the ribs increase rapidly in size to the pectoral region and then narrow rapidly. They are holocephalus throughout the anterior part of the column.

III. The scapulæ resemble the bone of a young Eryops, shown in fig. 1, and show very clearly the pocket on the inner surface from which the foramina start. The anterior edge of the scapula has a special thickening at the level of the lower end of the cleithrum, which caps the bone in the usual way.

The clavicle differs from that of Eryops in its considerably expanded lower end, but the ascending part of the bone which articulates with the lower end of the cleithrum seems to be extremely similar in the two genera.

The imperfect palate figured by GAUDRY (15) shows clearly that there are not two well-defined exoccipital condyles as represented in THEVENIN'S restoration, but only a single flat surface resembling that of Eryops. The same figure shows the presence of distinct small basipterygoid processes.

All authors who have dealt with Actinodon have recognised its resemblance to "*Archegosaurus latirostris*," Jourdon, from Saarbruck, which is now usually referred to the same genus.

Chelydosaurus, Fritsch (17).

This genus is only known from remains found in the Lower Permian of Bohemia, and described by its author; many of these appear to be imperfectly preserved.

FRITSCH'S restoration of the skull is obviously incorrect in its representation of the relations of the quadrate region to the tabular, and his restoration of the skeleton is certainly not correct in its treatment of the limb girdles. One specimen shows a flat occipital condyle.

The mutual relations of the European genera Onchiodon, Actinodon, Sclerocephalus, Osteophorus and Chelydosaurus are very obscure. They all appear to be close allies, differing so far as the material shows chiefly in the increasing width of the lower end of the clavicle, which in Onchiodon, as in Eryops, is no wider than in many reptiles, whilst in Sclerocephalus it is nearly as expanded as in a Triassic labyrinthodont.

Trimerorachis, Cope.

COPE (1) in various papers made us acquainted with the appearance, though not with the structure, of the top of the skull of Trimerorachis, with the basicranial and ear region, and with parts of its vertebral column.

BROILI (18) first described the clavicular apparatus and a long series of vertebræ. CASE (4) added to our knowledge by a description of the dorsal surface of the skull and of the lower jaw and some limb bones. VON HUENE (19) redescribed the top of the skull, and finally BROOM (6) and WILLISTON (20) gave accurate figures of the structure of the skull and lower jaw, the latter author subsequently (21) describing a nearly complete skeleton.

Trimerorachis is thus very well known. It has been found in the Lower Permian of Texas and Oklahoma, and has no known near allies.

Acheloma, Cope.

Originally described by COPE (22) from a slightly imperfect skull, scapulæ, humeri, fore limb, and many vertebræ. Redescribed by CASE (4) in 1911 from the same material. BROILI, in 1913 (23), published a description of a fragmentary skull of a new species.

The scapula described by COPE and CASE is not really so remarkable as they supposed; it is undoubtedly immature, and comparison of CASE'S figures with fig. 1 of this paper will show that it is structurally very similar to that of Eryops in the same stage.

The absence of an otic notch shows that Acheloma is worthy of a family distinction from Eryops, and it has no known near allies. Acheloma is only known in the Lower Permian of Texas.

Trematops, Williston.

This interesting genus was described by WILLISTON (24) from a skeleton showing everything but the carpus and the length of the tail.

This description is important, for in it Prof. WILLISTON first recognised the presence of basipterygoid processes and of distinct tubera basisphenoidales in a fossil amphibian.

Prof. WILLISTON recognises a distinct basi-occipital, and the basicranial and otic regions are probably very similar in structure to the corresponding parts of Eryops.

Aspidosaurus, *Alegeinosaurus*, and *Broiliellus*.

These genera were described by BROILI (18) in 1904, CASE in 1907 (25), and WILLISTON in 1914 (26) respectively. I agree with WILLISTON that *Aspidosaurus* *cruciger*, *A. glascocki*, and *A. serratus* do not belong to that genus, that the three genera are closely related to each other and to Dissorophus.

The palate of Broiliellus, as figured by WILLISTON, shows slender basipterygoid processes like those of Eryops, that the parasphenoid reaches up behind them, presumably to the fenestra ovalis, and that the condyles are incompletely separated being probably united by a basi-occipital.

Dissorophus and *Cacops*.

Dissorophus was originally described by COPE (27) from two imperfect skeletons, but most of our knowledge of this animal (28) and the whole of that of Cacops we owe to WILLISTON (29).

The two genera are closely allied. The basicranial region has not been described in detail, but it appears that there is an ossified basi-occipital element, although there are distinctly two (exoccipital) condyles. There are distinct basipterygoid processes like those of Eryops.

The two genera are remarkable for the closure of the otic notch behind by a down growth of the posterior corner of the tabular and of the paroccipital connected with it to have a suture with the posterior surface of the suspensorial region just above the quadrate condyle.

Cacops and Dissorophus are only known from the Lower Permian of Texas.

Zygosaurus, Eichwald.

This genus is only known from the single type skull, whose structure has not been correctly understood by any author, although it was well described by EICHWALD (30), 1848. It is extraordinarily like that of Cacops, agreeing in the laterally placed orbits and otic notch, in the closure of the latter by the tabular reaching down to the quadrate, in the deeply cupped occipital surface and in the general build and proportions. Zygosaurus differs from Cacops in the shorter otic notch, the more backward position of the orbit, and the greater depth of the jugal below it.

Zygosaurus seems to me to be an undoubted member of the Dissorophidæ, although, as it is of considerably later date than the typical members of that family, it may be expected to show differences in the basicranial and otic regions.

Zygosaurus lucius, Middle Permian, Orenburg, Russia.

Dasyceps.

Dasyceps is only known from a single skull, which gives a complete knowledge of the dorsal surface and something of the anterior part of the palate.

It was originally well described by HUXLEY in 1851 (31), and redescribed by v. HUENE in 1910 (32).

Lower Permian, Kenilworth, England.

Zatrachys.

Originally described by Cope from some more or less imperfect skulls. To it he referred some peculiar long neural spines with an ornamented apex. The skulls were redescribed by Case (4), who correctly identified many sutures and pointed out their close similarity to Dasyceps. Case removed Cope's neural spines to Aspidosaurus. Broom (6) gave a complete account of the dorsal surface, emphasising the resemblance to Dasyceps.

Finally Williston (33) has shown that Cope's neural spines were correctly referred.

Lower Permian, Texas.

Platyhystrix, Williston.

Known from imperfect skulls and associated neural spines described by Williston (33).

Lower Permian, N. Mexico.

Dasyceps, *Zatrachys* and *Platyhystrix* form a very distinct family, with flat skulls whose margins are produced into points and ridges.

The orbits are small and far back, the muzzle is enormously produced and with a very large internasal opening. The occiput, only known in Zatrachys, seems to resemble a flattened Eryops in most features, but has much more distinctly two condyles.

Cochleosaurus, Fritsch.

This genus was described by Fritsch from a skull and some other fragments. Broili, 1905 (34), gave a good description of the dorsal and palatal surfaces of the skull and of much of the rest of the skeleton.

The palate is remarkable for its small interpterygoid vacuities and the apparent extreme distinction of the exoccipital condyles. The humerus is remarkable for its slender shape and the presence of an entepicondylar foramen. There are no known near allies of this genus.

Lower Permian, Nyran, Bohemia.

Archegosaurus, Goldfuss.

Archegosaurus, originally named by Goldfuss, was subsequently described by Burmeister (35), who gave good figures of the dorsal surface of the skull and pectoral region; and later formed the subject of H. v. Meyer's classical monograph (36). Quenstedt described a good tarsus (37). Credner (38) later published a very imperfect restoration of the palate, and Jaekel (39) made out some further facts about the ribs and lower jaw.

The very large skeleton No. 40162 in the British Museum allows me to add some facts to those previously recorded.

The parasphenoid was well figured by v. Meyer (Plate XIII, figs. 1 and 7).

It is remarkable for the possession of narrow outstanding basipterygoid processes, behind which the bone is contracted, to widen again posteriorly.

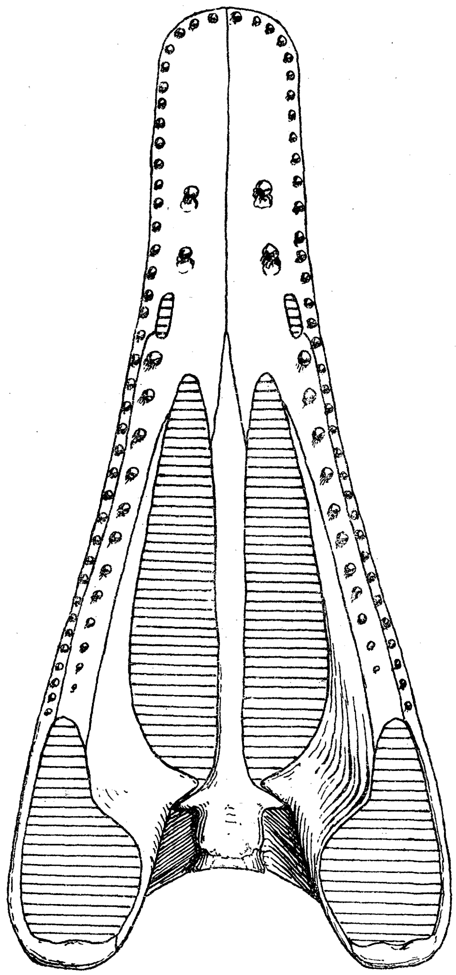


FIG. 2.—*Archegosaurus decheni*, restoration of the palate of a fully adult individual from the figures of H. v. MEYER and the large suite of specimens in the British Museum, Natural History. × ½.

It has always been stated that the occipital region is unossified, but in the old specimen referred to above there are very well developed ossifications in the basi-cranial and otic regions. VON MEYER'S Plate X, fig. 8, represents a similar specimen interpreted by him as showing the skull roof crushed down on the parasphenoid.

The condyle is formed by the fused basi-occipital and exoccipitals, which together form a concave face about twice as wide as high, very much resembling the occipital condyle of Eryops as figured by BROOM (6). The parasphenoid terminates some way in front of this face. From the lateral parts of this great joint-bone the exoccipitals send up stout processes separated from the paroccipital below by a vagus foramen, the details of which are not known.

The paroccipital is not known in detail; it has a stout process passing outwards from the side and front of the exoccipital to the tabular, and at its base has some ossification in the region of the semicircular canals.

There is an ossified pro-otic of which I can give no details. There is good evidence of an ossified basisphenoid, but the bone is too badly preserved for description. There is a large well ossified sphenethmoid.

The pterygoid articulates with the basipterygoid process by a freely movable joint, for in many specimens the whole brain case has fallen away.

The tabular and dermosupra-occipital have rather small occipital flanges resembling those of Eryops, which articulate with the paroccipital and exoccipital respectively.

The atlas consists of a ring whose slender lower part is obviously an intercentrum and the much more massive lateral corners neural arch elements. It closely resembles the atlas of Eryops figured by BRANSOM (3).

Rhinesuchus, Broom, and *Myriodon*, v. Hoepen.

Rhinesuchus was originally described by BROOM (40) from a fragmentary skull from the Pareiasaurus zone of the Gouph, Cape Province. In 1911 BROOM (41) referred to it as *R. major* two imperfect skulls from the Cisticephalus (?) zone of Senekal. Subsequently much more complete material from this locality representing the whole skeleton was described by v. HOEPEN (42) as Myriodon (a name which is pre-occupied). HOUGHTON (43) has given a brief description of a good skull of *Rhinesuchus whaitsi*, the type species, and of a skeleton of *R. major* from Senekal.

Dr. BROOM has most kindly re-examined the material of *R. whaitsi* and sends me the following particulars.

There is a distinct large basioccipital, perforated (or deeply cupped) for the

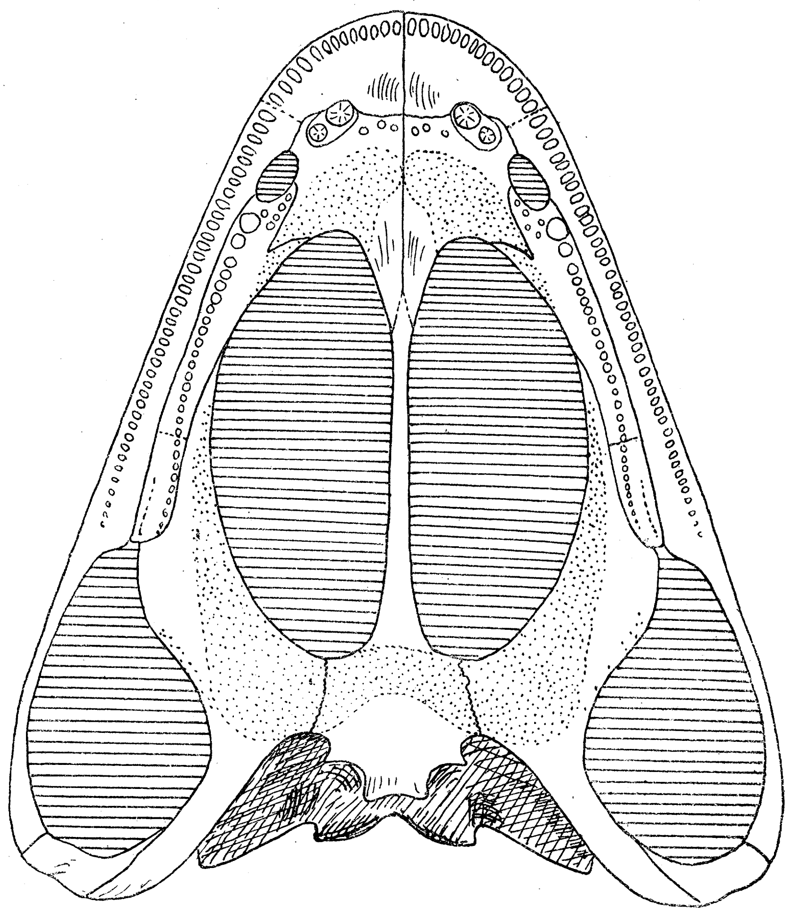


FIG. 3.—*Rhinesuchus whaitsi*. Palate. $\times 1\frac{1}{3}$ approx. This figure is redrawn from a sketch sent me by Dr. BROOM. The original is in the South African Museum, Cape Town.

notochord. The exoccipital part of the condyle is short and the two articular surfaces seem to meet in the middle line at an angle.

The exoccipitals much resemble those of Eryops, reaching up to the occipital flanges of the dermosupra-occipitals and touching in the middle line. The par-occipital is exposed from behind, but the occipital flange of the tabular is very large and extends far downwards.

The epiterygoid is similar to that of Eryops, having a slender ascending ramus and no otic process. There is a twelfth nerve. The palate will be understood from fig. 3, a drawing by Dr. BROOM.

Whether the Senekal animal is generically identical with Rhinesuchus or not cannot be determined from the existing descriptions. It is obviously a close ally, but it is probable that a careful examination of the occiput and brain case will show considerable differences, if I am right in believing that it is of considerably later date.

It may structurally resemble Laccocephalus, but is shown to be generally distinct by the absence in that form of small teeth on the palate.

Lydekkerina, Broom, 1915 (44).

Lydekkerina Huxleyi was originally described by LYDEKKER (45) as Bothriceps, his description making us acquainted with the general shape of the head and clavicular apparatus.

In 1912 I (46) described the lower jaw, not recognising the presence of the post-sphenial, which, however, I noted in 1914. In 1915, Dr. BROOM (44) described the whole structure of the top of the head, correctly determining all the sutures, and founded the genus Lydekkerina.

The British Museum contains seven skulls, one associated with the clavicular arch, scapula, and many vertebræ, other strings of vertebræ and a block with the hinder part of a skeleton. Careful development of this material allows of a nearly complete description of the skeleton.

Skull.—The structure of the dorsal surface has been described by BROOM, whose paper should be referred to. There are distinct "slime" grooves which take the

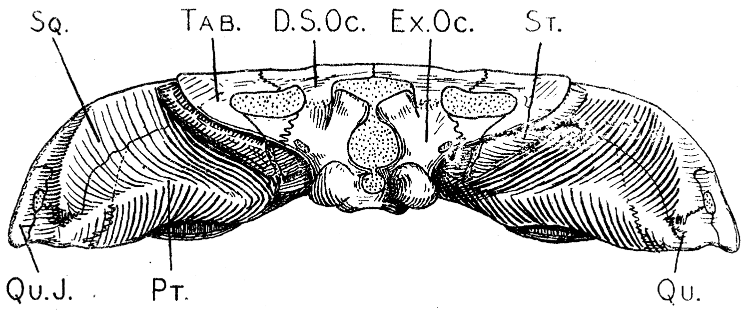


FIG. 4.*—*Lydekkerina huxleyi.* ? Lystrosaurus zone, Edenburg, Orange Free State. Restoration of the occiput. × $1\frac{1}{3}$. Mainly from R. 506, B.M.N.H.

D.S.Oc., dermo-supra-occipital; *Ex.Oc.*, exoccipital; *Pt.*, pterygoid; *Qu.*, quadrate; *Qu.J.*, quadrato-jugal; *Sq.*, squamosal; *St.*, stapes; *Tab.*, tabular.

unusual form of a series of disconnected pits, into the bottom of each of which a small foramen opens. Their distribution will be best understood from the figure.

The occipital surface is well preserved in two specimens, R. 506 and R. 507.

Parasphenoid.—The parasphenoid consists of a narrow processus cultriformis

* Unless otherwise stated all drawings are projections and dotted areas represent unremoved matrix.

which articulates with the prevomers anteriorly, and posteriorly expands into a broad body whose lateral borders have a union with the pterygoid, which in the young specimen R. 507 is a straight abutment, whilst in the old R. 506 it is a jagged and deeply interlocked suture.

The posterolateral corner of this part of the parasphenoid just within its suture with the pterygoid is produced backwards as a special thin lappet which overlies the lower surface of the stapes.

The median part of the posterior end of the bone is separated from the lappet by a deep notch and runs backwards in contact with the exoccipital in a very uncertain suture until it terminates in a jagged suture some distance in front of the lower margin of the foramen magnum.

Basi-occipital.—The bone exposed in the median line between the posterior end of the parasphenoid and the foramen magnum is presumably the basi-occipital, but no sutures separating it from the exoccipitals are visible.

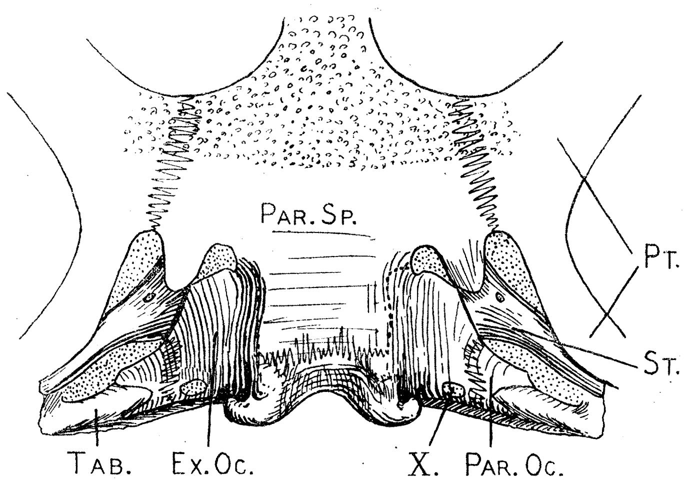


FIG. 5.—*Lydekkerina huxleyi.* Basicranial region. × 2. Slightly restored. From R. 506, B.M.N.H. Reference letters as before, with: *Par.Oc.*, paroccipital; *Par.Sp.*, parasphenoid; *X.*, tenth cranial nerve.

Exoccipital.—The exoccipital forms the condyle, which does not project very strongly, but has a laterally produced outer corner. On the level of the upper surface of the condyle the exoccipital sends in a process towards the middle line which forms the floor of the foramen magnum and roofs a little cavity in which the basioccipital cartilage formerly lay. Above the condyle on the posterior surface the exoccipital extends nearly up to the skull roof as a powerful column, forming the side of the foramen magnum and only separated from its fellow of the opposite side by a small gap above that opening.

A special thin process reaches down from the postparietal to the posterior surface of the exoccipital, but its suture with that bone is not distinct.

Laterally, the exoccipital passes outwards, sheathing the paroccipital; the distinct suture separating these bones passes outside the foramen for the tenth nerve, which opening hence lies entirely within the exoccipital. That this suture is certain, is shown by the fact that on the right side of R. 506 the two bones have separated slightly at the top, allowing of a very distinct tongue of matrix coming between them, and that the same thing has happened at the lower end on the other side.

There is a small foramen for the twelfth nerve, lying on the side of the exoccipital just above the condyle. In front the bone is extended by a process running along the parasphenoid and lying below the lower edge of the inner end of the stapes, so that in the bony skull the fenestra ovalis is surrounded below by the exoccipital, and only to a very small extent by the parasphenoid.

Paroccipital.—The paroccipital is shown as a slender bone extending out from the side of the exoccipital below the post-temporal fenestra. Distally its lower and posterior surfaces are clasped by a special process of the tabular, the sutures being quite distinct in two skulls.

Tabular.—The tabular, so far as concerns its dorsal surface, has been described by BROOM. From its ventral surface a special process arises which curves round the outer end of the post-temporal fenestra and covers the lower and posterior sides of the paroccipital.

Stapes.—The stapes is a proportionately very heavy rod of bone whose proximal end expands gently and fills the fenestra ovalis. It is pierced by a very small foramen. The distal end lies in the otic notch between the tabular and squamosal.

Squamosal.—The general disposition of the squamosal has been described by BROOM. The bone sends a plate down before the otic notch which unites with the pterygoid in a long suture. When viewed from behind it has a strong ridge which lies nearly parallel to the lower margin of the otic notch at the back of the temporal region, and extends down to the quadrate, being ornamented at the junction. The space between this ridge and the outer edge of the pre-otic flange of the squamosal forms a smooth groove for the musculus depressor mandibuli.

Quadratojugal.—This bone articulates with the squamosal and quadrate on the posterior surface of the skull and leaves a small quadrate foramen.

The structure of the palate will be best understood from fig. 6, the only remarkable feature being the presence of an anterior palatal vacuity which is known in no other Rachitomous Amphibian.

Vertebræ.—On account of difficulties of development the vertebral column cannot be described in detail. It is typically rachitomous.

The neural arches are solid; in the early dorsal region they have fairly long thick spines, long and powerful transverse processes, and are short antero-posteriorly. At the sacral region they suddenly lengthen; the spine, which rapidly becomes very small in the caudal series, being placed over the posterior zygapophyses and quite behind the transverse process.

The pleurocentra, represented only by one bone and several sections, are very thin, but not otherwise remarkable.

The intercentra form segments of cylinders; they are very thin, leaving an enormous notochordal cavity; they have anteriorly distinct facets for articulation with each other and a rib facet at the upper posterior corner.

Ribs.—Such ribs as are shown are long, nearly straight, and holocephalous.

Ventral Armour.—Sections across the mid-dorsal region show that there is a thin and feeble armour on the ventral surface, presumably of small scutes, as in Archegosaurus.

Interclavicle.—The interclavicle is a rhomboidal bone whose ventral surface is feebly convex. The antero-lateral margins are produced into thin flanges which are striated for the attachment of clavicles.

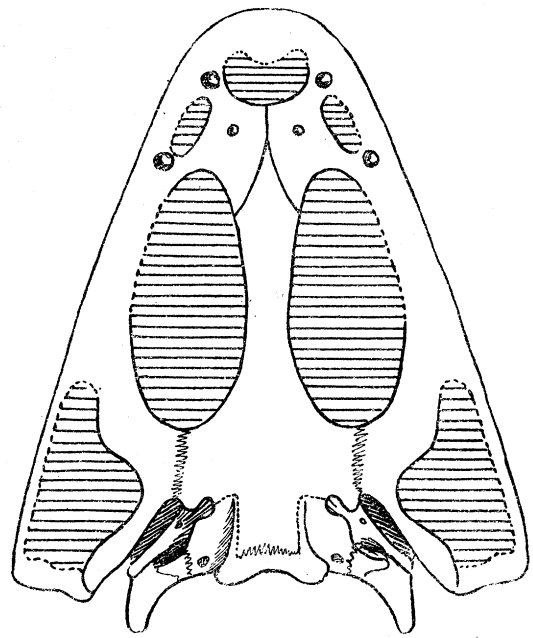


FIG. 6.—*Lydekkerina huxleyi.* Palate of an average specimen. × 1. Mainly from R. 506, B.M.N.H.

Clavicle.—The clavicle consists of a broad expansion on the ventral surface which fits on to the antero-lateral border of the interclavicle, and must very nearly meet its fellow anteriorly. The ascending part of the bone rises at right angles from the postero-lateral corner of this broad plate. It stands quite vertically, and its lower end has a continuation of the ridged ornament of the ventral surface. The posterior surface of the extreme summit has a facet for articulation with the cleithrum.

Cleithrum.—The cleithrum is represented by an isolated example whose lateral surface is exposed. It is a flat bone, bent so as to cap the top of the scapula, and slightly contracted towards the bottom, where it is broken off.

Scapula.—The single scapula preserved is isolated and exposed from the visceral surface. It has a thick lower end, showing traces of a cartilaginous expansion. The blade of the bone, which is thin, and passes directly into the lower portion, has a concave anterior margin. There is no evidence of any foramen piercing it.

Humerus.—The only humerus preserved belongs to the right side and is exposed from the dorsal and posterior aspects. The head forms a slightly expanded region; it is rounded and not screw-shaped like that of Eryops, and very incompletely ossified. There is a short and small pectoral crest, some distance below the head. On the postero-lateral surface is a marked muscular insertion, perhaps for the deltoid. The shaft is not very slender and widens to the lower end, which extremity is incompletely ossified. There is a wide entepicondyle and a pronounced process rising from the ectepicondylar region and passing outward.

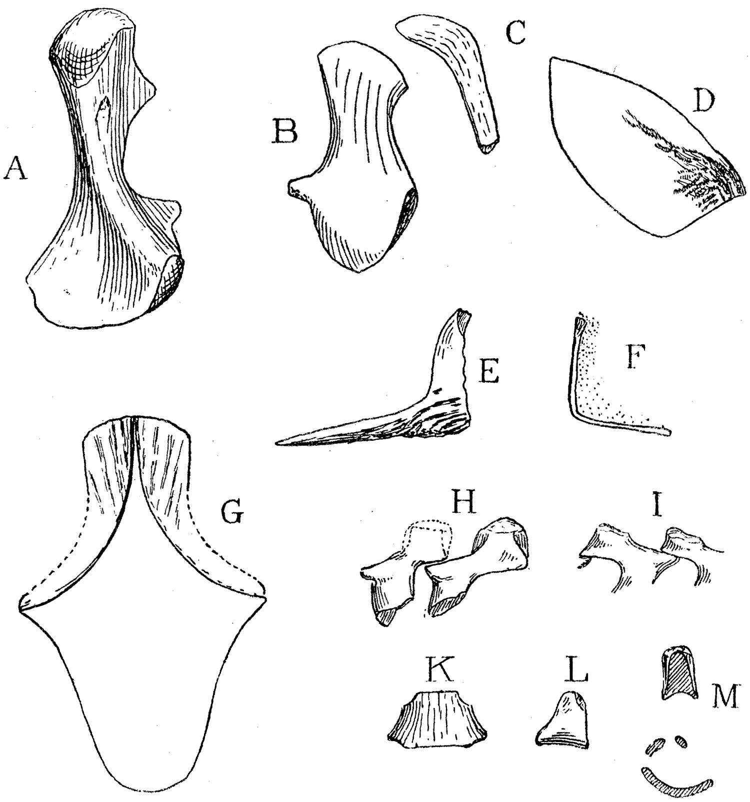


FIG. 7.—*Lydekkerina huxleyi*. × $1\frac{1}{3}$.

A, right humerus, dorsal surface, R. 504; B, left scapula, inner surface, R. 508; C, right cleithrum, outer surface, R. 508; D, E, and F, left clavicle, ventral, lateral and posterior aspects, R. 508; G, interclavicle, ventral surface, R. 508; H, neural arches of sacral and 1st caudal vertebræ, R. 504; I, neural arches of caudal vertebræ, R. 504; K and L, mid-dorsal intercentrum, R. 504; M, transverse section of a mid-dorsal vertebra.

Ilium.—The ilium has a very narrow and slender dorsal blade, presumably in contact with only a single sacral rib. The lower end of the bone, which is much expanded, presents facets for the ischium and pubis. There is a distinct acetabulum, whose rim is as usual raised above the general level of the bone.

Ischium.—The ischium is a large quadrangular bone which articulates with the ilium, and has a very indefinite face for the head of the femur and another for the pubis.

Pubis.—There can be no doubt that the pubis was cartilaginous in the specimen from which the above description of the pelvis is drawn. There is no trace of it on either side.

Femur.—The femur is a somewhat slender bone with slightly expanded ends, which are very incompletely ossified. The head is a comma shaped face, continued on the fibula side down to a low trochanter. The shaft is rounded and from its lower surface a thin but very marked adductor ridge is developed.

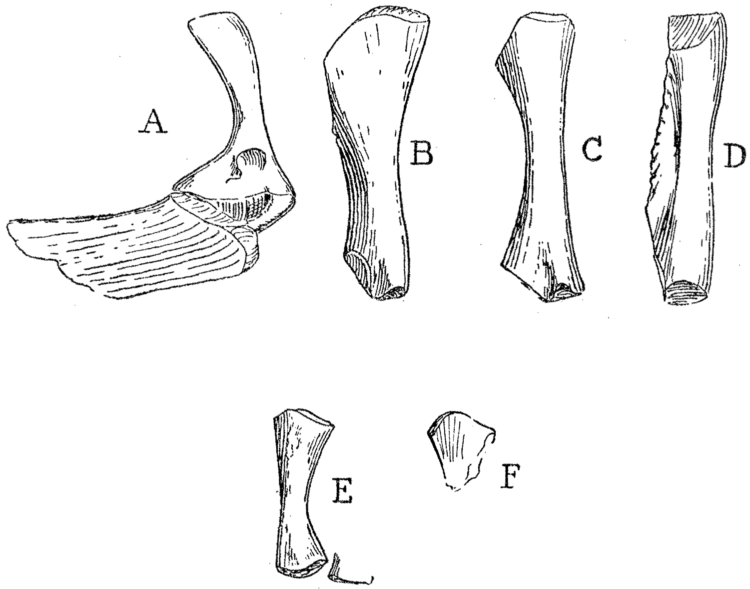


FIG. 8.—*Lydekkerina huxleyi*. All bones of the same individual. × $1\frac{1}{3}$.

A, right ilium and ischium; B and C, left femur; D, right femur; E, left tibia and fibula; F, upper end of right tibia.

The lower end of the bone is divided into two condyles by a very marked groove on its dorsal surface.

Tibia.—The tibia is a short massive bone with a well developed cnemial crest, a contracted shaft and an expanded, distal end.

Fibula.—Only the lower end of the fibula is known; it is a very wide flattened bone.

From the evidence afforded by the bones described above I have drawn a sketch restoration of the skeleton (fig. 9).

The skull is that of a medium-sized individual, and as the actual range in size is not great, it is probable that the proportional size of the bones represented is not widely out. The length is given on the assumption that there were twenty-eight pre-sacral vertebræ; the number is not likely to have been much less or to have greatly exceeded thirty.

The most marked features are the total absence of a neck, the long, broad, and very flat body, and the very short limbs.

The depression of the anterior part of the body is certain. From the shape of the skull and lower jaw it is probable that the animal at the neck was only half as high as it is wide. The whole build is not very different from that of Cryptobranchus. The restoration greatly resembles the photograph of a skeleton of Rhinesuchus published by HOUGHTON (43).

The type and most other specimens of Lydekkerina came from a locality in the Orange Free State which is believed to be near Edenburg. One specimen comes from the van Rienen's Pass between Natal and the Orange Free State. The type has also been found at Harrismith in association with Lystrosaurus.

It is, therefore, one of the latest Rachitomi, probably of very early Triassic age.

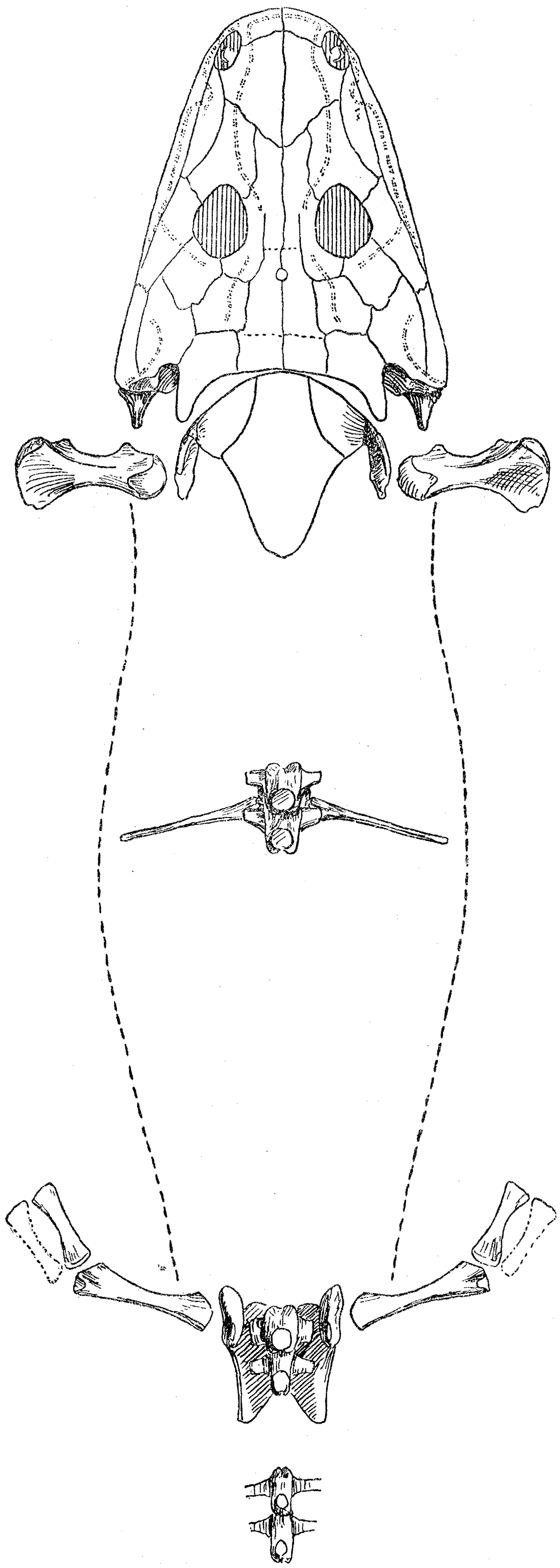


FIG. 9.—*Lydekkerina huxleyi*. Restoration of the dorsal aspect of the skeleton. × $\frac{2}{3}$.

*Laccocephalus insperatus, gen. et sp. nov.**

This new genus and species is founded on the incomplete skull of a large labyrinthodont from "near Mr. Hope's Farm, Orange Free State." The position of this locality is unknown to me, but as the specimen was presented by Dr. ORPEN of Smithfield, it may be near that town. Its horizon is unknown.

The specimen (No. R. 532) consists of the left half of the skull and a little of the right side, the extreme front being missing. It is preserved in an extremely hard, flaggy sandstone. The whole dorsal surface has been weathered away so that the dorsal surface of the palate is exposed.

The posterior part is also exposed by a fracture in the plane of the palate, which has removed the parasphenoid, showing the exoccipitals and basi-occipital which rest on the upper surface of that bone.

The broken condition of the specimen, the softness of the bone, and the extreme intractableness of the matrix, make it impossible to do any preparation, but fractures cut the bones of the brain-case in so many planes that the more important structural features are quite clearly shown. The succeeding description can be checked by the photographs on Plate 2.

Parasphenoid.—The parasphenoid has a long and narrow processus cultriformis whose lower surface has a pronounced

* λακκος = a "Tank," September 15, 1916.

median ridge from which the sides flare outward so that the bone is widest at the dorsal surface. Posteriorly the upper surface of the process is deeply grooved, the basisphenoid lying in it. The processus cultriformis expands slightly at the back of the interpterygoid vacuities, its lateral margins having deeply interlocked sutures with the pterygoids, in the anterior part this junction is thin dorso-ventrally so that the dorsal surface is nearly flat, but posteriorly the surface becomes concave, the edges of the bone being thickened up in bosses which articulate with the upstanding ridge of the quadrate ramus of the pterygoid. Just medial of the posterior end of the suture with the pterygoid, the parasphenoid has a free margin produced into a little process, similar to, but proportionately much smaller than, the lappet in the corresponding position in Lydekkerina.

Still further back the lateral margins have powerful and deeply interlocked sutures with the lower and anterior ends of the exoccipitals. The bone is then broken away, but no doubt extends backwards to the lower margin of the foramen magnum.

Very nearly or quite in the posterior end of the suture between the pterygoid and the parasphenoid a medium-sized foramen enters the latter bone and travels forward and inwards in its substance until it turns upwards towards the brain cavity. Comparison with the skull of Capitosaurus described on p. 22 of this paper shows that this canal must be for the internal carotid artery, for in the latter type the basisphenoid is perforated by obvious carotid foramina, and there is a small foramen at the junction of the exoccipital, pterygoid, and parasphenoid which is the only possible entrance for the carotid, and agrees with the posterior end of the canal in Laccocephalus.

Basi-occipital.—The basi-occipital, shown only from below, is quite a large well ossified bone. It lies on the concave upper surface of the parasphenoid, its postero-lateral corners extending out so that they are overlain by the exoccipitals.

Exoccipital.—The exoccipital is not well shown, the occipital surface being completely concealed by matrix. The bone has a powerful sutural union with the parasphenoid, and stretches far forward below the fenestra vestibuli, but does not reach the pterygoid, so that there is a free parasphenoidal margin left to form part of the bony fenestra. Dorsally, the exoccipital no doubt articulates with the dermosupra-occipital, and is seen to have a suture with the tabular.

Nothing is to be seen of the paroccipital, perhaps only on account of the unfavourable plane of section.

Pro-otic.—The pro-otic is visible in section as a small element, articulated with the upper inner corner of the quadrate ramus of the pterygoid.

Basisphenoid.—The basisphenoid is a large and well ossified bone lying in the groove on the dorsal surface of the parasphenoid, in advance of the articulation of that bone with the pterygoid. It has a large sella turcica, overhung by a very thin dorsum sellæ. Posteriorly, the bone is completely concealed by matrix.

Pterygoid.—The pterygoid has a massive articulation by a deeply interlocked suture with the edges of the parasphenoid. This region of the bone passes out as the palatal ramus, becoming thinner as it does so.

The quadrate ramus is mainly composed of a slender upstanding sheet of bone, which rises towards the skull roof, and whose upper and inner corner has a suture with the pro-otic. Weathering has removed the upper part of this bone, which no doubt joined the squamosal, as in all early Stegocephalia.

Epipterygoid.—The epipterygoid is a bone of considerable size, lying on the front surface of the quadrate ramus of the pterygoid at its base. It has a very tightly interlocked suture with this bone, below which the two separate, so as to leave a large opening, passing directly inwards toward the region between the basi-occipital and basisphenoid. It seems probable that this cavity was filled with a cartilaginous extension from the planum basale during life.

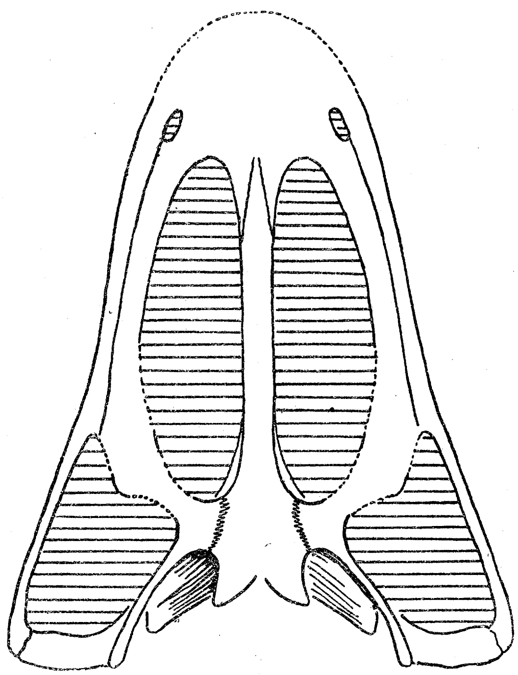


FIG. 10.—*Laccocephalus insperatus*, gen. et sp. nov. Restoration of the outline of palate. B.M.N.H. R. 532. Much reduced. Type specimen. Mr. Hope's Farm, Orange Free State.

The epipterygoid is produced into a powerful ascending process, which forms a massive plate, placed vertically, and extending outwards from the region of the outer surface of the brain case for a considerable distance, about 5 cm.

The inner face of this bone is deeply notched for the Gasserian or semi-lunar ganglion, the first division of the fifth nerve issuing in front of it.

There is no trace of an otic process, and the condition of the specimen makes it certain that there never was one, the second and third branches of the fifth nerve issuing through the large gap between the outer end of the ascending process and the quadrate ramus of the pterygoid.

There is no ossified supra-occipital.

The lower parts of the dermosupra-occipital and tabular are shown; so far as preserved, they differ in no respect from the same bones in Capitosaurus.

No details of the structure of the palate can be made out, but its form and proportions are well shown, and will be understood from fig. 10.

Micropholis, Huxley.

Originally described by HUXLEY in 1859 (47), and subsequently more completely figured by OWEN (48) in 1876 under the name Petrophryme, Micropholis was described as completely as the existing material allowed by WATSON (49) in 1913.

In that description the only alteration to be made is that the "coronoid" in the lower jaw is really the postsplenial, the real coronoid being an extremely thin slip of bone on the oral surface of the jaw.

All the material comes from the Procolophon zone, Lower Trias of Cape Colony.

The following genera are undoubtedly Rachitomi, but are founded on such unsatisfactory material that they afford no evidence bearing on the features discussed later in this paper:—

Nyrania, Fritsch.
Melosaurus, H. v. Meyer.
Chalcosaurus, H. v. Meyer.
Platyops, Twelvetrees.
Sparagmites, Credner.
Discosaurus, Credner.
Acanthostoma, Credner.

The Genera of Stereospondylous Amphibia.

The list of Stereospondyli given by Broili (50) in Zittel's 'Palæontology' includes—

Anthracosaurus, Loxomma, Eosaurus, ? Baphetes, ? Macrerpeton, and *Erpetosuchus*, Moodie.

There is definite evidence that Anthracosaurus and Loxomma are Embolomerous forms [Watson (51), 1912]. Baphetes is very similar in all respects to Loxomma, and Erpetosuchus to the Embolomerous Pteroplax. Macrerpeton is completely indeterminable. Eosaurus is of more interest. The complete identity of the two centra preserved shows that it is not an Embolomerous form. The central position of the notochordal pit, and the uniformity in length of the upper and lower parts of the centra, show that it is not a Stereospondylous type. It is really quite indeterminate, but may perhaps be a fish.

The only other Carboniferous animal which has been referred to the typical Labyrinthodonts, *i.e.*, the Stereospondyli, is the tooth from the coal measures of Kansas, described by Williston (52) as Mastodonsaurus. This was badly preserved and only a small part of its section is figured, but is stated to be quite similar to the section of a Mastodonsaurus tooth.

Sections of Loxomma teeth, although not quite so complicated as those of Mastodonsaurus, have still very strongly-folded dentine and show that in the complete absence of any corroborative evidence it is impossible to accept the evidence of Prof. Williston's tooth for the occurrence of Stereospondyls in the Carboniferous.

All other animals which have been referred to the Stereospondyli are of Triassic age. They are as follows:—

1. *Capitosaurus.*

Originally described by MUNSTER for *C. arenaceus*, the type and only known specimen of which is not generically determinable, as it shows only the anterior part of the skull, the term is now used by all authors for *C. nasutus*, described by H. v. MEYER (53), from Bernberg.* VON MEYER described the dorsal and ventral surfaces of the skull incompletely but accurately. VON ZITTEL in his text-book gives a good new restoration of the dorsal surface. JAEKEL (54) gave a fair figure of the dorsal surface. SCHROEDER (55) gave an excellent account of the dorsal surface, palate, and occiput of the genus founded partly on *C. nasutus* and partly on the new *C. helgolandiæ*. Unfortunately he did not describe any sutures on the palate, and his interpretation of the occiput is not quite correct, although his description and figure are excellent.

A large skull which I collected on the farm Watford, Dist. Albert, Cape Province, South Africa, from the Cynognathus zone allows me to add considerably to our knowledge of the skull of this genus.

The material is at present preserved in five blocks and some fragments. These are as follows :

Block 1 contains the left quadrate, the impression of the corresponding part of the pterygoid, and the entire left half of the brain case behind the pro-otic notch ; the brain case is exposed from within and the back ; the stapes is in position in the fenestra vestibuli. Block 2 fits into Block 1 and contains the left pterygoid, epipterygoid and the outer surface of the left side of the sphenethmoid. Block 3 has the right side of the brain case beautifully exposed from above, the outer side and the bottom ; it crosses the middle line and shows much of the basi-occipital ; it fits into Blocks 1 and 2. Block 4 contains much of the exoccipital condyles and a wedge-shaped bit of the basis cranii ; it connects Blocks 1 and 3. Block 5 fits into Block 3 and shows the left face of the sphenethmoid, mostly as an impression with an adherent film of bone.

There is thus no actual median longitudinal section, but the complete development allows of the construction of one which cannot possibly be inaccurate in any essential point, as the whole side wall is clearly exposed and the dorsal and ventral surfaces of the basis cranii are known.

The bone is white, hard, and very brittle, the sutures infiltrated with red iron oxide. The matrix is a very hard and tough cornstone, really a "Fontainebleau sandstone" with, however, some rather disconcerting soft patches. It leaves the bone cleanly and has allowed of a very satisfactory preparation.

* BROILI has recently figured the type of *C. arenaceus*, but his excellent description does not permit of a comparison of the otic and basicranial region with that of Capitosaurus and Cyclotosaurus. It is probable that the form is really a Cyclotosaurus. Evidence brought forward in this paper will show that the two genera are distinct, although related as parent and child. 'Centralb. für Min. Geol. u. Pal.,' pp. 569, 1915.—D. M. S. W., 1.1.19.

The specimen is a typical *Capitosaurus sensu auct.* of large size but specifically undeterminable.

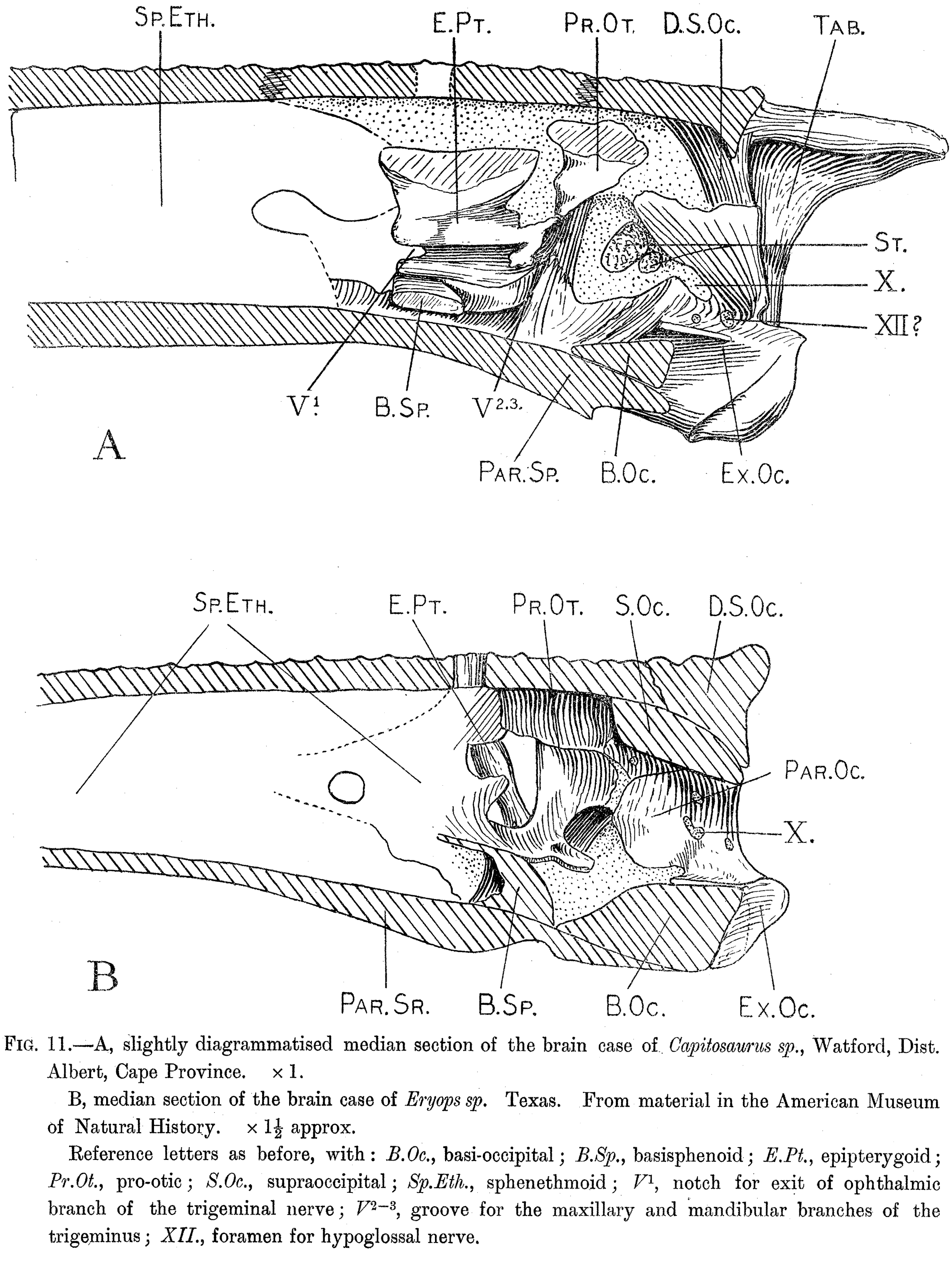


Fig. 11.—A, slightly diagrammatised median section of the brain case of *Capitosaurus sp.*, Watford, Dist. Albert, Cape Province. × 1.

B, median section of the brain case of *Eryops sp.* Texas. From material in the American Museum of Natural History. × 1½ approx.

Reference letters as before, with: *B.Oc.*, basi-occipital; *B.Sp.*, basisphenoid; *E.Pt.*, epipterygoid; *Pr.Ot.*, pro-otic; *S.Oc.*, supraoccipital; *Sp.Eth.*, sphenethmoid; V^1, notch for exit of ophthalmic branch of the trigeminal nerve; V^{2-3}, groove for the maxillary and mandibular branches of the trigeminus; *XII.*, foramen for hypoglossal nerve.

The structure of the dorsal surface of the head and of the palate of a member of the genus has long been known, and excellent figures of the occipital surface have been published, although their interpretation has been inaccurate. Nothing whatever has been known of the characters of the brain case, and the following description of my South African skull will be mainly concerned with that region.

Parasphenoid.—As the parasphenoid forms the foundation of the whole skull it is convenient to begin by describing that bone.

The anterior stem of the parasphenoid is broken off just in advance of the pterygoid articulation; here its upper surface is markedly channelled, the lateral borders forming free edges. The bone is thick, its lower surface being nearly flat.

Behind this region the parasphenoid suddenly widens to the pterygoid articulation; at this the edge of the bone rapidly thickens so that a powerful ridge, which does not extend across the middle line, is formed, the inner margin of the quadrate ramus of the pterygoid continues this ridge upwards.

At its maximum the edge is quite thick, and articulates with the pterygoid by a very deeply interlocked suture.

Behind the pterygoid articulations the bone narrows rapidly, its outer margin having a suture with the exoccipital.

Finally, it ends in a free margin at the back of the skull between the condyles.

Basi-occipital.—The basi-occipital is represented by a small ossified tract lying on the dorsal surface of the parasphenoid just in advance of its posterior end; it is thickest posteriorly, and thins to a feather edge both in front and at the sides.

Exoccipital.—The exoccipital is a large and remarkable bone. Posteriorly, it forms the condyle, in advance of which its body articulates with the parasphenoid, sending out a special process, which forms the lower border of the bony fenestra ovalis, along the outer side of the upstanding outer margin of that bone. At the level of the top of the condyle the exoccipital sends inwards a thin plate, which nearly meets its fellow of the opposite side, the two forming the floor of the brain cavity and overhanging the basi-occipital. From the body of the bone rises the great process which forms the side wall of the foramen magnum; seen from within, this process has a large exposure, and is perforated by two foramina where it turns out to the floor, the posterior for the twelfth nerve running right through the bone, the other, which lies in front of the hypoglossal foramen, merely transmitting a vein. The upper anterior corner of the endocranial face of the exoccipital runs forwards towards the pro-otic, and is separated by a very deep notch from the lower part of the bone; this notch transmitted the tenth nerve.

The posterior surface of the exoccipital widens rapidly above the condyles, and is faintly divided into two wings, the inner having a good deal of the posterior surface covered by the dermosupra-occipital, and the outer covering the posterior surface of the descending process of the tabular. The posterior surface of the exoccipital is pierced by three small nutritive foramina.

The outer surface of the exoccipital forms a large area nearly flat antero-posteriorly and gently convex dorso-ventrally; posteriorly it forms the condyle, in the middle it

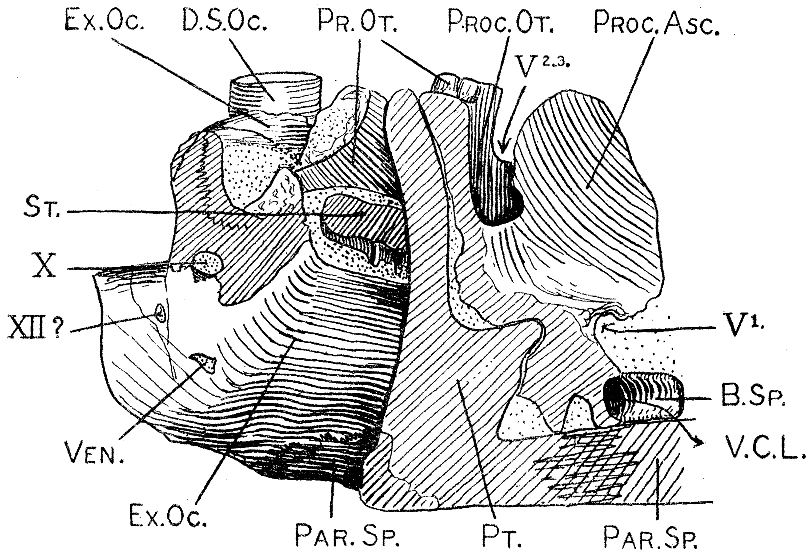


Fig. 12.—*Capitosaurus sp.* Watford, Dist. Albert, Cape Province, South Africa. × 1. The right side of the brain case from without. Block 3 of the specimen.

Reference letters as before, with: *Proc.Ot.*, otic process of the epipterygoid; *Proc.Asc.*, ascending process of the epipterygoid; *V.C.L.*, foramen for the vena capitis lateralis; *Ven.*, a small venous foramen.

reaches out below the tabular, and is pierced by three foramina, a large one for the tenth nerve, considerably below which are two much smaller foramina for the twelfth nerve posteriorly and for a vein anteriorly. The upper surface of the

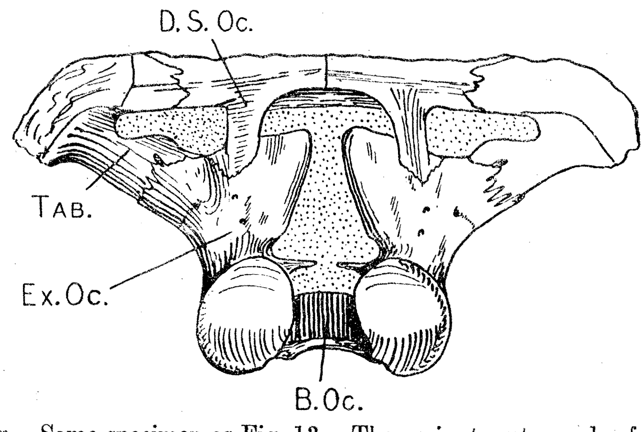


Fig. 13.—*Capitosaurus sp.* Same specimen as Fig. 13. The occiput, outer ends of the tabulars broken off. Blocks 1, 3, and 4. × $\frac{2}{3}$.

exoccipital in this region supports the paroccipital, in advance of which it forms the lower border of the fenestra ovalis, and terminates in a powerful contact with the pterygoid. The meeting place of the pterygoid, parasphenoid, and exoccipital is the site of a small foramen for the internal carotid, which opens backward.

Paroccipital.—The paroccipital is a very small bone lying on the dorsal surface of the exoccipital, from which it is clearly separable by its structure, though not by suture. The inner end is exposed in the plane of the membrana vestibuli, from here it extends outwards about a centimetre, its posterior border being in contact with the tabular ; its anterior face touches the pro-otic over the fenestra ovalis.

Pro-otic.—The pro-otic is a bone of considerable size. On the inner surface, which is somewhat mutilated, it has a triangular exposure, crossed by a well marked groove leading forwards and outward. The dorsal surface of the bone is very complicated, its inner margin is a shallow vertically placed plate in contact with the roof of the

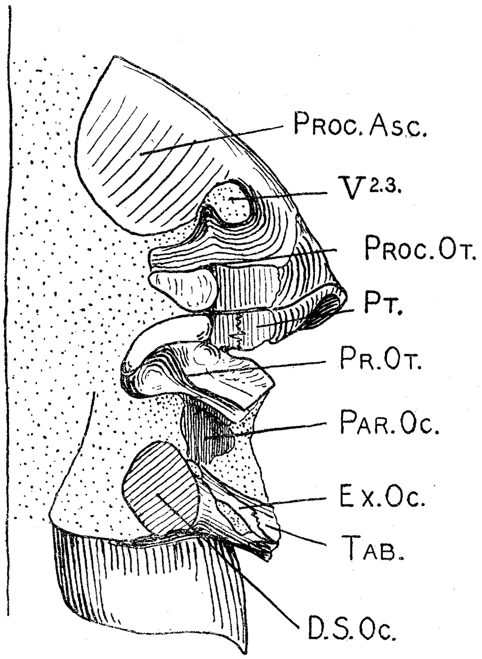


FIG. 14.

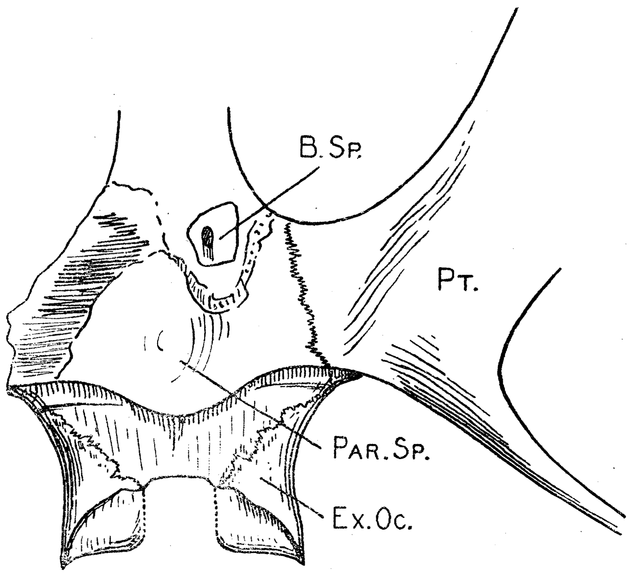


FIG. 15.

FIG. 14.—*Capitosaurus sp.* Same specimen as Fig. 13. Right side of the brain case from above. Block 3. The straight line on the left is the median plane of the skull. × 1.

Reference letters as before with : *Par.Oc.*, paroccipital.

FIG. 15.—*Capitosaurus sp.* Same specimen as Fig. 13. Basi-cranial region from below. × $\frac{2}{3}$.

Reference letters as before.

skull, and directed outwardly and forwards at an angle of nearly 45° with the principal plane of the skull. The outer end of the plate is suddenly depressed (forming the lower margin of a foramen to be described later), and articulates by suture with the upper and inner corner of the quadrate ramus of the pterygoid.

This same region is in contact with the hinder surface of the otic process of the epipterygoid.

From this part of the pro-otic a powerful process runs outwards, with its hinder edge in contact with the paroccipital, and forms the upper margin of the fenestra ovalis and the anterior part of the paroccipital process.

There is no trace of any cartilage bone lying above the brain.

Basisphenoid.—The basisphenoid is represented by a paired ossification. The left of these small bones is exposed from below and the outer edge, the right from the outer edge. Each bone lies on the dorsal surface of the parasphenoid, and is quite well ossified; it is perforated vertically by a foramen, from which a groove on the ventral surface leads to the posterior edge of the bone. The outer corner of the bone touches the epipterygoid. The outer surface is channelled, the extreme lower lateral border touching the pterygoid.

Pterygoid.—The pterygoid articulates with the parasphenoid by very deeply interdigitating sutures. Externally to this connection it forms a flat plate on the bottom of the skull, being directly continued forwards and outwards as the anterior ramus, which has a long suture with the transverse bone. No. 40041,

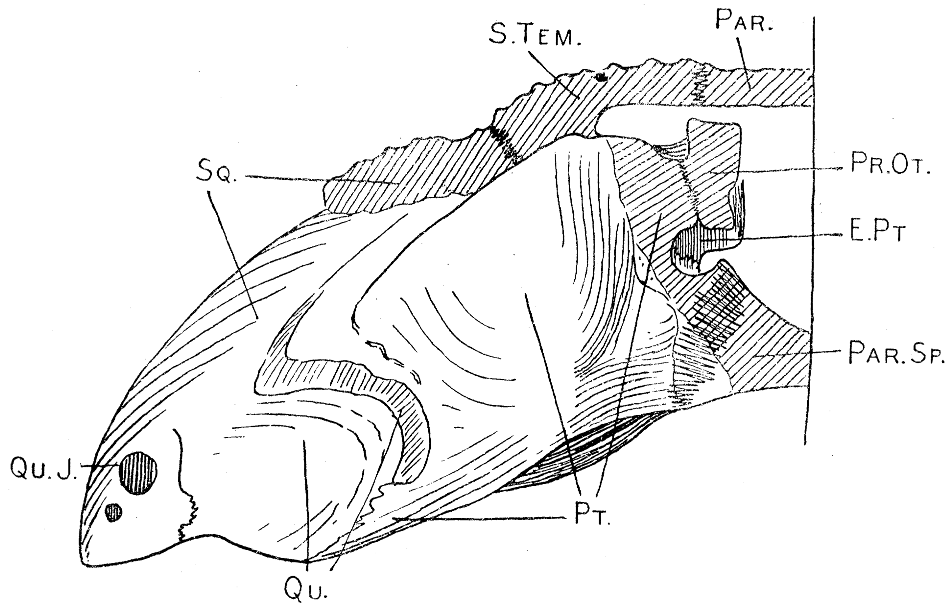


FIG. 16.—*Capitosaurus sp.* Same specimen as Fig. 13. The left quadrate region and the brain case in transverse section through the pro-otic. × $\frac{2}{3}$. Block 2.
Reference letters as before, with: *Par.*, parietal; *S.Tem.*, supratemporal.

B.M.N.H., a skull of *Capitosaurus nasutus* from Bernburg, shows that the anterior end of the ramus reaches the palatine. In the South African skull this ramus bears a sculpture similar to that of the skull roof, as SCHROEDER has described it doing in *C. nasutus* and *C. helgolandiæ*.

The quadrate ramus arises from the part of the pterygoid which is in contact with the parasphenoid. It forms a thin plate, rising nearly vertically, to have a long and close connection with the supratemporal and squamosal. Its upper inner corner has a sutural union with the pro-otic, with which bone and the supratemporal it forms a large foramen leading forwards over the pro-otic and epipterygoid to the anterior part of the skull. This opening must transmit the vena capitis dorsalis and a lymphatic duct. Just above its articulation with the parasphenoid and below the pro-otic the inner margin of the quadrate ramus of the pterygoid is notched for the passage of the vena capitis lateralis and the seventh nerve.

The quadrate ramus passes backwards behind the quadrate, its lower margin extending very nearly to the condyle. The angle between the inner part of the quadrate ramus and the basal part of the bone houses the epipterygoid.

Epipterygoid.—The epipterygoid is a large and very remarkable bone, which lies in the angle between the quadrate ramus and the horizontal part of the pterygoid. It has an otic process reaching up in close contact and in some regions in sutural connection with the inner end of the quadrate ramus of the pterygoid to the pro-otic. The inner part of the dorsal end of the otic process reaches up to the skull roof, or very nearly so; laterally it is depressed to form with the pro-otic and pterygoid the lower border of the foramen of the vena capitis dorsalis.

Viewed from the outer aspect, the otic process gives origin to the main mass of the bone, which runs forwards and inwards and upwards as a processus ascendens, separated by a deep narrow notch, widening into a foramen, from the otic process.

On the endocranial surface the ascending process forms a large area lying outside the original cranial wall (whose position is indicated by the posterior end of the sphenethmoid). The bone articulates with, may in fact be fused to, the antero-lateral corner of the basisphenoid. Just above the dorsal surface of this bone the inner surface of the epipterygoid is crossed by a very deep and narrow groove, whose outer end opens by a notch at the front border of the bone. Posteriorly, this groove is overhung by a delicate process which joins or nearly joins the anterior and lower corner of the pro-otic. Lateral to and behind this process the groove turns outwards and upwards, leading to the deep groove and foramen which separate the otic and ascending processes. Into the groove at this point opens the large foramen for the vena capitis lateralis. The groove is undoubtedly for the Gasserian ganglion, the first part of the fifth nerve passing out from the notch in front of the bone, and the second and third branches between the otic and ascending processes. All appearances suggest that the main trunk of the vena capitis lateralis passes through the foramen and receives a vena cerebralis media coming out of the cranial cavity over the pro-otic notch, subsequently running forwards through a distinct notch left between the pterygoid and the back of the epipterygoid, issuing from a foramen formed by a notch in the lower margin of the epipterygoid, the pterygoid and the grooved outer edge of the basisphenoid. The palatine branch of the seventh nerve may perhaps have passed forward with the vein.

Sphenethmoid.—The sphenethmoid is only represented by the impressions of its lateral surfaces, to which a little bone adheres, and its extreme posterior ends. It begins just in front of the epipterygoid, lying closer to the middle line than the inner face of that bone, and extends forward for 8 cm. at least. The upper edge of the bone is in contact with the cranial roof, the lower with the parasphenoid. The posterior end of the bone is deeply notched for the second nerve.

Palate.—This skull shows very well the suture between the pterygoid and the ectopterygoid. This passes through a somewhat down-turned corner of the pterygo-transverse bar which is a relic of the familiar flange applied to the inner face of the lower jaw.

Two skulls of *Capitosaurus nasutus* from Bernburg, in the British Museum, Natural History No. 36344 and No. 40041, show the sutures between some of the palatal bones. As all these sutures are very deeply interlocked, their position varies according to the plane at which they are viewed.

These specimens show that the anterior end of the external ramus of the pterygoid reaches the palatine, the ventral surface of the union being largely covered by the anterior end of the ectopterygoid.

The anterior end of the palatine forms part of the border of the internal naris and has a long suture with the prevomer. Part of the outer border of the internal naris seems to be formed by the maxilla.

The only other feature of this skull which requires special notice is that the foramen which appears to correspond with the quadrate foramen lies entirely in the quadratojugal.

The only definitely determinable remains of Capitosaurus, that is, of forms which agree with *C. nasutus*, are :—

C. nasutus, H. v. M., Bunter, Bernburg.
C. fronto ,, ,, ,,
C. helgolandiæ, Schroeder, Bunter, Heligoland.
C. africanus, Broom, Cynognathus zone, C.P.
C. sp., described above ,, ,,

Capitosaurus arenaceus, the original type, from the Keuper of Schleswig, is indeterminate, as is *C. polaris*, Wiman, M. Trias, Spitzbergen.

Capitosaurus stantonensis, A.S.W., is not a Capitosaurus in the sense of this paper.

All Capitosaurus skulls which are definitely determinable, and of which the horizon is known, are Lower Trias.

2. *Cyclotosaurus.*

This quite distinct genus was founded by E. Fraas (56), for *Capitosaurus robustus*, H. v. Meyer, in 1889. Von Meyer (57) correctly described the structure of much of the dorsal surface, but in 1850 F. A. Quenstedt (58), in his work, 'Die Mastodonsauria im grünen Keupersandstein Würtembergs sind Batrachia,' gave a magnificent description of the whole structure, including something of the brain case. This still remains the best and most complete account of the structure of a Stegocephalian skull.

In 1889 E. FRAAS (56) redescribed *C. robustus*, adding little to QUENSTEDT'S description except as to the anterior part of the palate. In 1904 A. SMITH WOODWARD (59) described as *Capitosaurus stantonensis* a skull from the English Trias which showed much of the upper surface and a very good occiput. BROILI and SCHROEDER (55) pointed out that this skull is a Cyclotosaurus.

Finally E. FRAAS (60) gave a brief description of a fine skull as *Cyclotosaurus postumus*, and of the anterior part of another, *C. mordax*.

FRAAS' (56) figure of the palate of *C. robustus* is inconsistent with his figure of the dorsal surface, and comparison of it with QUENSTEDT'S figures and a cast of his specimen shows that it is inaccurate in representing the quadrate condyles as extending back behind the exoccipital condyles, in the position of the pterygo-transverse suture, in the exaggerated notch between the exoccipitals, and in the shape and position of the quadrate condyle.

The only comment which can be made about QUENSTEDT'S description is that his "felsenbein" (pro-otic) is really the epipterygoid, its position in relation to the pterygoid being identical with that held by this bone in the Capitosaurus skull described above.

As shown by its relations in *C. postumus*, where it was described as epiotic by FRAAS, this bone differs from that of Capitosaurus in being exposed from the posterior side by the reduction of the quadrate ramus of the pterygoid.

QUENSTEDT'S tympanica interna is really only a part of the squamosal. Otherwise, allowing for nomenclatural changes, his determinations are quite accurate.

Cyclotosaurus stantonensis.

Examination of the type skull in the light of more recent knowledge allows me to extend and in some degree modify Dr. SMITH WOODWARD'S description (59).

The object which Dr. WOODWARD described as a basioccipital cannot be a bone in its natural position, because it is unsymmetrically placed and extends up between the faintly indicated flanges from the exoccipitals which floor the brain, into the middle of the foramen magnum.

Examination of it with a binocular dissecting microscope (an instrument which I regard as indispensable for critical palæontological work) suggests that it is not really bone at all, but a peculiarly cracked mass of clay.

On the posterior surface of the exoccipital just below the post-temporal fossa there is a small foramen, presumably for the twelfth nerve, the vagus foramen, as already described by WOODWARD, lying on the under surface of the lateral wing of the exoccipital.

The exoccipital is very clearly shown to extend forward to have a suture with the pterygoid, but on the ventral surface this is much shorter proportionately than in the large *C. robustus*.

The quadratojugal foramen is much smaller than it is represented in

Dr. WOODWARD'S restored figure, which is derived from the left side of the specimen where the bone is broken away, its impression on the stone being, however, clearly distinct. On the right side the bone is mostly present, but is somewhat mutilated. This foramen lies entirely in the quadratojugal, the suture cutting off that bone from the quadrate being quite clear on both sides but especially on the left.

The pterygoid is well shown from behind and the upper edge of its quadrate ramus shown in fig. 17 seems to be natural, as on the right side the matrix is excavated behind its plane somewhat above it and shows no bone. There is no doubt that the upper outer corner of the bone touches the squamosal.

In all ways *C. stantonensis* seems to be a perfect intermediate form between Capitosaurus and *Cyclotosaurus robustus*. The more important changes between these two types are discussed on p. 55 of this paper, some other less important features in which it is intermediate are recorded here.

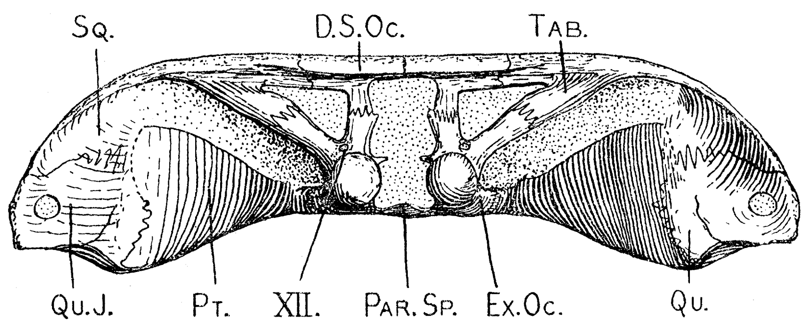


FIG. 17.—*Cyclotosaurus stantonensis* (Smith Woodward). Occiput. $\times \frac{2}{3}$. Slightly diagrammatised from the type specimen.

Reference letters as before.

In Capitosaurus the quadrate has quite a large exposure on the posterior surface, although it is so far overlapped by the quadratojugal that the quadrate foramen lies entirely in that bone. In *C. stantonensis* the quadratojugal is still further expanded, so that in addition to the condylar surface only a small strip of quadrate is visible between the pterygoid and quadratojugal. In *Cyclotosaurus postumus* the quadratojugal has a large suture with the pterygoid and only the condylar edge of the quadrate is visible from behind.

The hypoglossal foramen of Capitosaurus lies on the outer surface of the exoccipital at the upper side of the condyle, and cannot be seen from behind. In *C. stantonensis* it is placed in the middle of the posterior surface of the exoccipital, so that its canal only just passes through that bone. In *C. postumus* and *C. robustus*, if we may trust the existing descriptions, the hypoglossal must pass out behind the skull, there being no foramen for it.

The definitely determinable remains of Cyclotosaurus are—

C. robustus, H. v. Meyer, the type of the genus; Keuper, Wurtemberg.

C. posthumus, E. Fraas; Keuper, Wurtemberg.

C. stantonensis, a small and aberrant form retaining primitive features; Keuper, Staffordshire.

C. albertyni, Broom, Upper Cynognathus zone, C.P.

C.sp., Wianamatta shales, N.S.W.

C. mordax, E. Fraas, although not definitely determinable, probably belongs here; Keuper, Wurtemberg.

C. ? spitsbergensis, Wiman, is quite indeterminable; M. Trias, Spitzbergen.

All definitely determined Cyclotosauri are of Upper Triassic age.

Metoposaurus diagnosticus.

Metoposaurus diagnosticus was originally described by H. v. MEYER, who figured a considerable part of the upper surface of the skull, and subsequently (61) a still better, though similar, example. Later, MIALL (62) published a reconstruction, which showed the distribution of the sensory grooves quite accurately. Finally, E. FRAAS (56) gave a complete description of the dorsal surface, of the general structure of the lower surface, of the occiput, and of a fine fragment of the anterior part of the skeleton.

This description made us better acquainted with the structure of Metoposaurus than of any other Trias labyrinthodont, except, perhaps, Mastodonsaurus.

The British Museum specimen No. 37, which is said by FRAAS to have come from the Feuerbacher Haide, near Stuttgart, and is a young and small individual, has been recently redeveloped by Mr. HALL, and allows me to add to and in part correct FRAAS' description.

The actual preservation of the specimen is quite perfect, but the premaxillæ had fallen away before burial, and a break nearly parallel to the palate has separated the right posterior corner of the upper surface, which has been replaced about 3 mm. from its true position. Finally, the exoccipital condyles are broken off and are missing.

Parasphenoid.—The parasphenoid is a very long bone, with an unusually broad processus cultriformis, whose upper surface bears a pair of ridges well within the margin, which must have given origin to the walls of the anterior part of the brain case. Posteriorly, the parasphenoid expands somewhat, but its lateral margins are here not markedly thickened, as they are in Capitosaurus. They articulate by jagged sutures with the pterygoids and exoccipitals. In this region the upper surface of the bone is slightly excavated and roughened for the entirely cartilaginous basi-occipital. The parasphenoid ends freely at the back of the skull in the notch between the two condyles.

Exoccipital.—The exoccipital is only incompletely preserved, the condylar part being broken off. The remaining portion of the bone, however, has a powerful

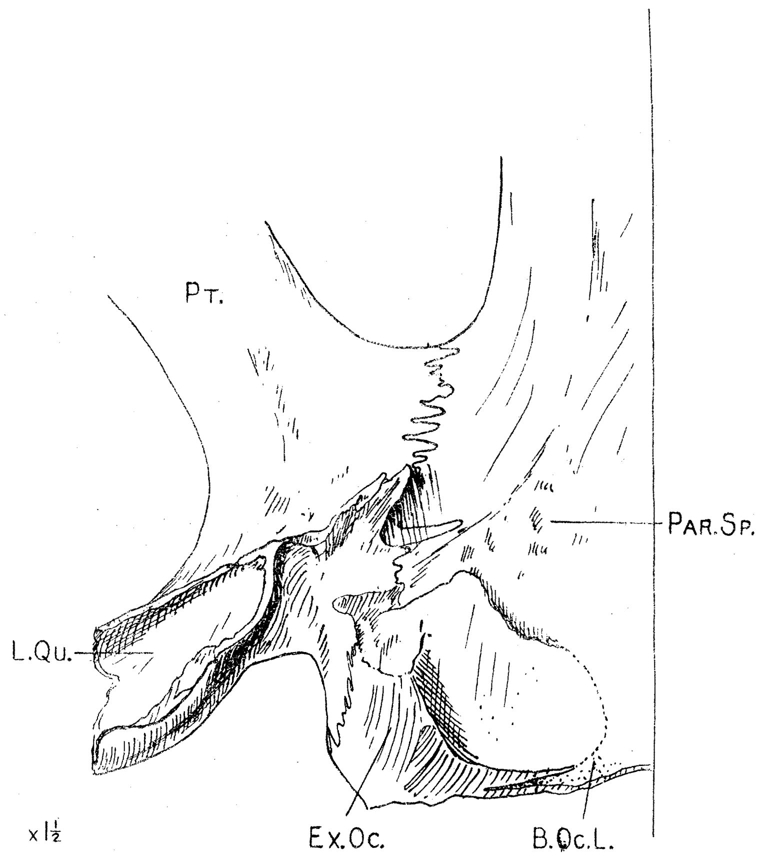


FIG. 18.—*Metoposaurus diagnosticus.* The dorsal surface of the left basicranial and otic region, the roof of the skull being removed. × 1. The straight line on the right is the median plane. *B.Oc.L*, space for the basioccipital; *Ex.Oc.*, exoccipital; *L.Qu.*, groove in the pterygoid for the reception of the quadrate; *Par.Sp.*, parasphenoid.

suture with the parasphenoid, and also with the pterygoid. The bone sends in the usual plate over the basi-occipital to form the floor of the brain cavity, but in this individual the flange does not nearly reach the middle line, and the basi-occipital space, although about 25 mm. across, is only 3 mm. high at the maximum.

The outer edge of the bone is raised in a ridge, which is only incompletely preserved, but must be a production from that part of the bone which reaches up on the occiput to the skull roof. This ridge dies down at the suture with the pterygoid.

Although the specimen is so preserved as to show the regions where a pro-otic and opisthotic, like those of Capitosaurus, would occur, no trace of any other bone in relation to the brain cavity is to be seen.

Pterygoid.—The pterygoid articulates with the parasphenoid and exoccipital by a long suture, immediately outside of which lies the body of the bone; from this the external ramus runs forward, to have a suture with the ectopterygoid alone, being widely separated from the palatine. The quadrate ramus is short, much broader than it is high, and not nearly reaching up to the squamosal. Its upper surface is grooved, presumably to allow it to surround the lower edge of the quadrate.

Quadrate.—The quadrate seems to have been entirely cartilaginous in this individual, although, as FRAAS' figures show, it was thoroughly ossified in adults. Its position is clearly shown by the faces on the quadratojugal and pterygoid, which face the gap which it formerly occupied.

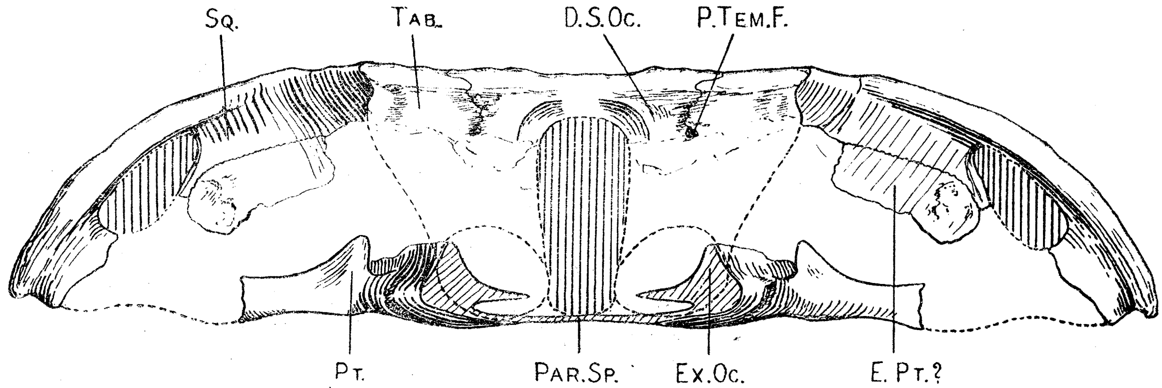


FIG. 19.—*Metoposaurus diagnosticus.* Skull from the Lower Keuper of the Feuerbacher Haide, Stuttgart. $\times \frac{2}{3}$. Occiput restored, every part shaded is clearly shown on one side or the other of the British Museum No. 37938.

There is a very large quadrate foramen, whose outer margin lies partly in the quadratojugal and partly in the squamosal. Medial of this foramen, the squamosal sends down a flange behind the otic region. This flange has a suture with an incompletely preserved bone whose lower edge faces the upper edge of the quadrate ramus of the pterygoid, and, like that bone, is grooved and has a peculiar surface. It seems very improbable that this bone, which is separated from the quadrate ramus of the pterygoid by more than a centimetre, can be part of the quadrate, and I am inclined to believe that it is really epipterygoid. As shown by QUENSTEDT'S figures, the epipterygoid occupies just this position in Cyclotosaurus, except that there it does articulate directly with the upper edge of the quadrate ramus of the pterygoid.

Of the rest of the occipital surface little can be said. The descending portions of the tabulars and dermosupra-occipitals are well preserved, and lie in close contact, separated only by a very small triangular foramen, which represents the post-temporal fossa. The sutures with the exoccipitals must have lain below the region where these bones are broken off.

The general structure of this occiput will be intelligible from fig. 19, which represents the portions actually preserved in the British Museum specimen, except that the exoccipital where shown in broken lines is restored.

This illustration shows that FRAAS' figure, which is admittedly founded as a restoration on two specimens, is very inaccurate in the lateral parts, and it will, I expect, prove to be not quite correct for the central region.

The general structure of the palate has already been accurately described by FRAAS. The sutures between the various elements are shown with diagrammatic clearness in my specimen, and will be best understood from fig. 21.

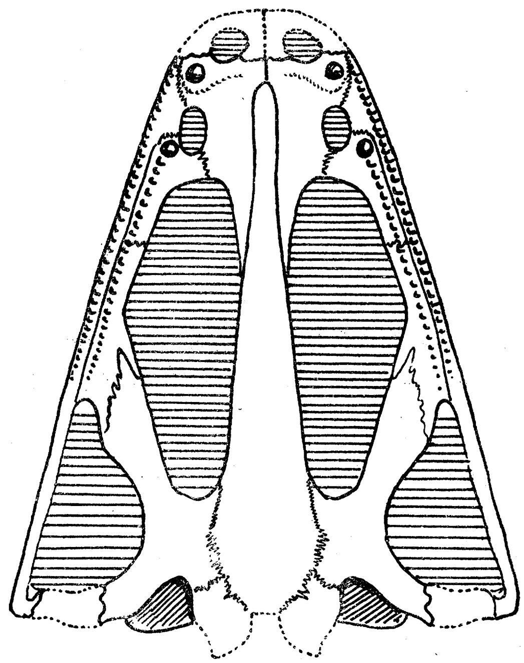


FIG. 20. — *Metoposaurus diagnosticus.* Palate. B.M.N.H., No. 37938. Parts in dotted outline restored. Much reduced.

Anaschisma, Bransom.

Anaschisma was well described by BRANSOM (3) from two excellent skulls and lower jaws.

Prof. WILLISTON has kindly checked certain doubtful points for me. There is clear evidence that the parasphenoid, instead of stopping short as BRANSON represented it, extends to the extreme back of the skull, being bounded by parallel sutures with the pterygoid anteriorly and the exoccipital behind. The suture between the exoccipital and pterygoid is not visible, but I think that there can be no possible doubt that the structure is quite as in Metoposaurus. Prof. WILLISTON tells me that the epipterygoid is as in a sketch of the conditions of the quadrate otic region in Metoposaurus (fig. 19).

A more satisfactory knowledge of the structure of Metoposaurus shows that, as BRANSOM suspected, the two genera are exceedingly closely allied, agreeing in all structural points and being perhaps scarcely generically distinct.

Rhytidosteus capensis.

The type and only known material from Beersheba, O.F.S., was well described and figured by OWEN (63), who, however, did not recognise the importance of certain fragments belonging to the specimen. The part of the skull described by OWEN only reaches as far back as the middle of the orbit and the anterior part of the large palatal vacuity. An additional fragment includes part of the right tabular, dermosupra-occipital, supratemporal and parietal. It shows that these bones are long and that the post-orbital part of the skull must have considerably exceeded the pre-orbital part in length.

The most interesting of the new fragments consists of the right exoccipital, broken off above, and the neighbouring regions of the parasphenoid and right pterygoid.

The exoccipital has the very short and slightly concave condyle preserved. From the front of this the occipital part of the bone rises as a transversely placed plate,

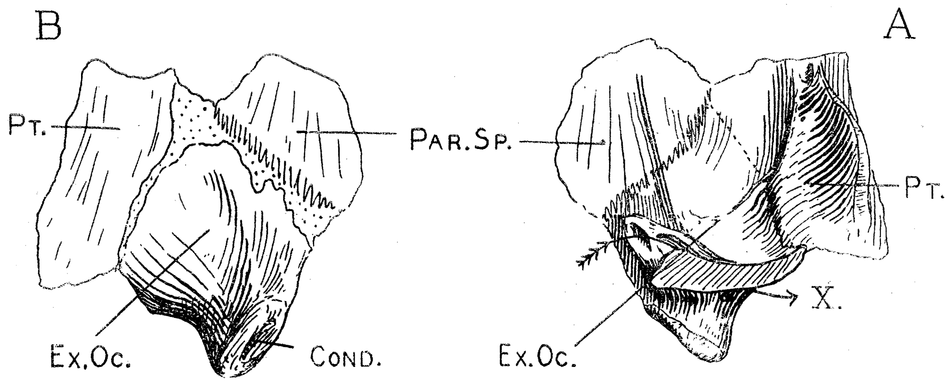


FIG. 21.—*Rhytidosteus capensis.* Type skull No. R. 503, B.M.N.H. Part of the right side of the basicranial region. $\times \frac{2}{3}$. A, dorsal aspect; B, ventral aspect.
Reference letters as before.

which is, however, soon broken off. It is pierced by the foramen jugulare, which lies just on the level of the upper edge of the condyle and passes out at right angles to the major axis of the skull, piercing the posterior plate of the exoccipital nearly longitudinally. The outer edge of this plate has a long and powerful suture with the pterygoid.

The lower end of this part of the exoccipital is turned forwards, unites with the parasphenoid and forms part of the floor of the skull on which the cartilages of the otic and basicranial region must have rested. The exoccipital plate roofing the basioccipital is only represented by a short stump just medial to the inner opening of the jugular foramen.

The small fragment of pterygoid remaining shows a little of the ascending plate of the quadrate ramus.

The basi-occipital must have been exceedingly reduced and unossified.

There was certainly no foramen for the twelfth nerve.

Mastodonsaurus.

This genus was originally described by JAEGER (64) from a tooth, a separated occipital region described at the same time as Salamandroides being subsequently shown by him to belong to the same genus. In 1844, v. MEYER and PLEININGER gave a good general description of the upper and under surfaces of the skull, not, however, determining any sutures, and figured and described many bones of the post-cranial skeleton. They correctly determined the atlas, vertebræ and ribs. They called the interclavicle Brustbein, the clavicle Schulterblatt, and the lower end of the real scapula-coracoid, coracoid. The humerus they determined correctly but with doubt. They correctly determined the pelvis, femur and lower leg bones.

In 1889 E. FRAAS (56) gave a good description of the dorsal surface and palate of

Mastodonsaurus giganteus and *M. acuminatus*, but in his discussion of the postcranial skeleton he wrongly identified many bones and his account is by no means so good as that of MEYER and PLEININGER written 40 years before.

FRAAS' ischium is a complete scapulo-coracoid, agreeing extremely closely with that

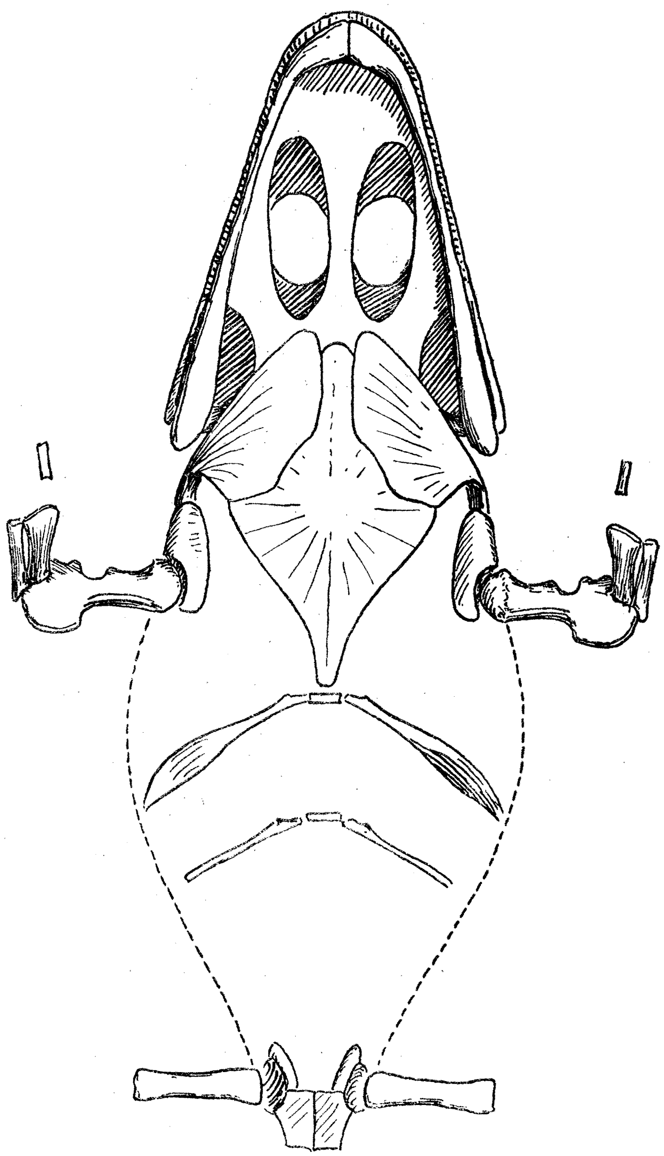


FIG. 22.—*Mastodonsaurus giganteus.* Restoration of the ventral side of the skeleton, from the bones figured by PLEININGER and FRAAS. $\times \frac{1}{12}$.

of Eryops. It has the same screw-shaped glenoid cavity, the same depressions on both inner and outer aspects for the glenoid, supraglenoid and coracoid foramina, although the crushing of the specimen prevents observation of the actual openings.

Dr. FRAAS' pubis is really an ischium and agrees exactly with the example of that bone still in natural articulation with the ilium figured by v. MEYER, Plate V, fig. 3.

There is no bone which could be a pubis amongst the Stuttgart material which I examined and it is most probable that the bone was never ossified, a view supported by the conjoined ischium and ilium figured by v. MEYER.

There is in the Stuttgart collection a bone which appears to be a cleithrum, showing an expansion similar to but not so broad as that which caps the scapula in Eryops.

From this material I have made the sketch restoration, fig. 22, in which the only point about which there is any doubt is the length of the vertebral column. In the drawing I have allowed for thirty pre-sacrals, a number suggested by the fragments apparently belonging to one column in Stuttgart.

The only definitely recognisable species of Mastodonsaurus are :—

M. giganteus, Lettenkohle, Wurtemberg.
M. acuminatus, Fraas, Wurtemberg.
M. keuperianus, Fraas, L. Keuper, Wurtemberg.

The other fragments referred to in this genus either belong to other types or are quite indeterminable.

Trematosaurus Brauni.

Trematosaurus Brauni, which is very common in the middle Bunter Sandstone of Bernberg, was excellently described by H. BURMEISTER (65) in 1844. The restored figure of the dorsal surface published by this author is nearly perfect and his palatal and occipital views are both good; although in the latter the sutures between the exoccipital and the dermosupra-occipital and tabular, which are correctly shown in the dorsal view, are not introduced. Subsequent figures by v. MEYER added nothing to BURMEISTER'S description. In 1897, v. ZITTEL (66) in his text-book published a restored figure of the dorsal aspect reputedly after BURMEISTER, but which shows a pair of perforations in the dorsal surface of the premaxillæ in front of the nares which do not occur in the original figure.

O. JAEKEL has published a new and fair figure of the dorsal surface in FRECK'S 'Lethæa Geognostica.'

The fine series of specimens from the type locality in the British Museum allows me to add some details to the existing descriptions of this form.

Parasphenoid.—The parasphenoid consists of a very narrow processus cultriformis which expands to a wide bone where it joins the pterygoids. Its lateral margins are here much thickened, so that, as the lower surface is nearly flat, the upper (endocranial) surface forms a wide groove.

Posteriorly, the walls of this groove fall away, their upper surfaces being covered by the exoccipitals. The parasphenoid terminates in a thin free margin at the extreme back of the skull.

Exoccipital.—The exoccipital has a body which articulates with the upper side of the lateral margin of the posterior part of the parasphenoid.

This body ends behind in the large, nearly circular condyle, which appears to be slightly concave. It is continued forwards below the fenestra vestibuli by a thin plate presumably of perichondral bone lying without the cartilaginous otic capsule. From the body of the bone the occipital part rises to the lower margin of the post-temporal fenestra. On each side of this it sends out a process, the inner forming the

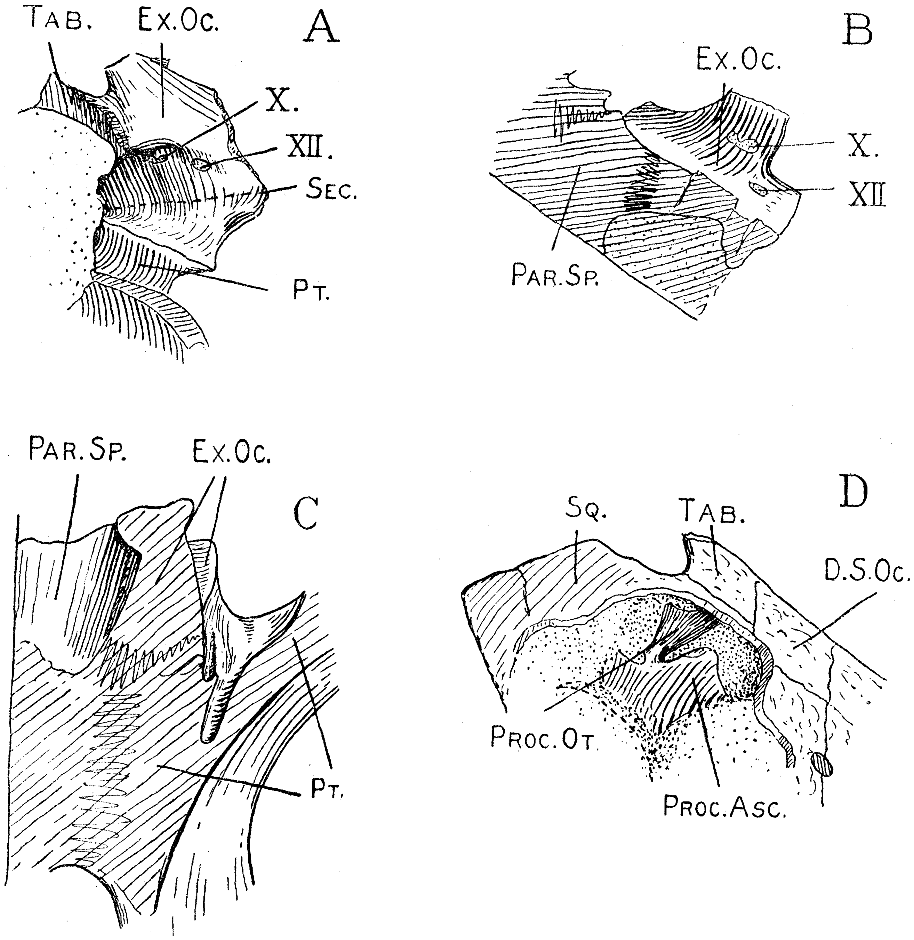


FIG. 23.—*Trematosaurus Brauni.* Middle Bunter, Bernburg.

A, the side of the basicranial region. R. 1733 and 1750. *Sec.* = the plane of the fracture separating the upper part, R. 1733, from the lower, R. 1750. × 1; B, the upper part of the right side of the brain case viewed obliquely from below. × 1. R. 1733; C, the basicranial region viewed directly from above. × 1. R. 1750; D, the right temporal region with the roof of the skull removed to show the epipterygoid. × $\frac{2}{3}$. 36374.

side wall of the foramen magnum, articulating with the descending flange of the dermosupra-occipital, and having a face towards the space for the cartilaginous supra-occipital.

The lateral wing of the exoccipital extends outwards to overlap the hinder surface of the descending process of the tabular and have a deeply interlocked suture with that bone. The lower surface of the lateral wing is placed nearly horizontally and passes smoothly into the side of the body of the bone; at its root it is pierced by a small vagus foramen which is distinctly divided into two. Behind and slightly below this foramen is another smaller opening which agrees with the hypoglossal foramen of Capitosaurus.

The inner surface of the exoccipital is produced into the usual process above the basi-occipital space. This lies very high up, the bone being much excavated below it, so that the basi-occipital cartilage must have been both high and wide.

Above the flooring process the exoccipital extends forwards along the side of the brain for a very small distance, only a few millimetres.

Pterygoid.—The pterygoid articulates with the lateral margin of the parasphenoid through a very long region, posteriorly it passes below the exoccipital, having a suture with the lower surface of that bone.

From this articular region the quadrate ramus rises as a slender plate, articulating with the squamosal above and the posterior surface of the quadrate distally. It passes forwards along that margin of the bone which bounds the sub-temporal fossa, so that the posterior part of the articular region of the bone forms a shelf under the region occupied by the middle ear. This shelf is dorsally channelled for a blood vessel (the vena capitis lateralis ?). The anterior ramus of the bone passes forward and outwards to a long suture with the ectopterygoid.

Epipterygoid.—The epipterygoid is shown from its outer side in No. 36374. It greatly resembles that of Capitosaurus, having a large ascending process separated by a deep notch from the otic process, which nearly reaches up to the skull roof. The whole is applied to the anterior face of the quadrate ramus of the pterygoid. In R. 1733 the epipterygoid appears not to have been ossified.

There are no traces of the basioccipital, basi-sphenoid, pro-otic, opisthotic, and supra-occipital as bones.

Tabular.—The dermosupra-occipitals have the usual descending flange on the occipital surface. The tabulars have a very large descending flange which forms a deep area on the occipital surface. The lower outer corner of the bone is extremely thin and is only preserved in R. 1733.

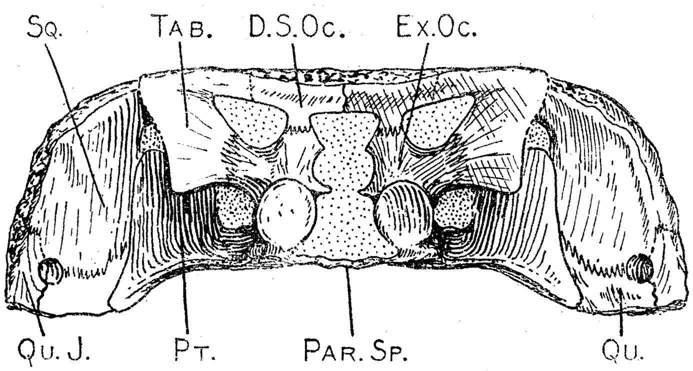


FIG. 24.—*Trematosaurus Brauni.* The occiput restored from B.M.N.H. 36374, R. 1750 and R. 1733. × $\frac{3}{4}$. Reference letters as before.

Squamosal.—The squamosal has the usual exposure on the dorsal surface, whose boundaries are correctly represented in BURMEISTER'S figure.

It sends a deep flange which has a long suture with the pterygoid and possibly with the outer edge of the epipterygoid, down in front of the otic notch; its lower end covers the posterior surface of the quadrate and forms the upper margin of the small quadrate foramen.

Quadratojugal.—The quadratojugal is a small bone on the outer surface of the skull, which articulates by a powerful suture with the outer end of the quadrate. It forms the outer margin of the quadrate foramen.

BURMEISTER'S figures made us acquainted with the general structure of the palate. Fig. 25 shows the whole structure, all the sutures being clearly visible in the various British Museum specimens.

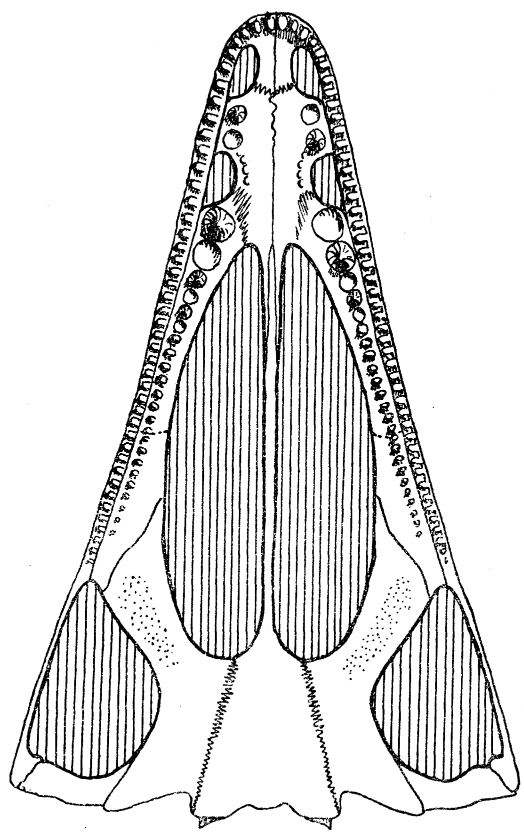


FIG. 25.—*Trematosaurus Brauni.* Restoration of the palate. Two-thirds natural size of a small individual. General outline from 36366 B.M.N.H. Detail from 36375 and R. 1750 and R. 1733.

Trematosaurus brauni is the only described species certainly belonging to the genus.

No. 36369, B.M.N.H., from the Middle Bunter of Bernburg, represents a distinct species with much smaller and more widely separated orbits, whose margins are strongly everted. The skull is contracted behind the orbits.

This may be H. v. MEYER'S, T. ocella.

Trematosaurus sobeyi, Houghton (67), from the Cynognathus? beds of Queenstown, Cape Province, S.A., does not belong to that genus, differing in having no anterior palatal vacuities between the premaxillæ and prevomers, in lacking the corresponding perforations of the dorsal surface of the premaxillæ and in the distribution and character of the palatine and ectopterygoid teeth.

I am inclined to doubt the accuracy of the position of the suture between the pterygoid and transverse bone figured by HOUGHTON.

For the distinct genus represented by this form I propose the name Trematosuchus. It is probably a near ally of Trematosaurus. Whether *Trematosaurus Kannemeyeri*, Broom, belongs to that genus it is impossible to say. Its locality suggests that it may really be a Trematosuchus.

Lyrocephalus.

The occipital surface was originally described by WIMAN (68) in 1913. In 1915, WIMAN (69) gave an excellent and very complete description of the skull, recognising the epipterygoid for the first time in a Stereospondyl (it had previously been described as pro-otic by QUENSTEDT, and correctly determined by BROOM in Rhinesuchus and Eryops). WIMAN also recognised the pro-otic, again for the first time in any Stereospondyl; unfortunately, this bone seems to have been very incompletely ossified, and shows no morphological features. In position and relation to the pterygoid it agrees with the much larger bone in Capitosaurus.

Only known in the M. Trias of Spitzbergen.

Lonchorhynchus.

Originally described by WIMAN (70) in 1909. Much more completely described by the same author in 1915 (69).

The most interesting feature of this form is the apparent presence of a large ossified basi-occipital.

M. Trias, Spitzbergen.

Aphanerrama.

Originally described by A. S. WOODWARD (59) in 1904. This description is of importance as including the first correct account of the quadrate of a Stegocephalian.

Subsequently more completely described by WIMAN in 1915 (69).

M. Trias, Spitzbergen.

Platystega.

A good deal of the skull of this form was described by WIMAN in 1915.

M. Trias, Spitzbergen.

Tertrema.

A very fragmentary skull is also described by WIMAN in 1915.

M. Trias, Spitzbergen.

The five genera just listed from the Middle Trias of Spitzbergen are found in marine deposits. They form an interesting group, all with a somewhat narrowed snout, which may be very elongated.

Certain features :—

1. The position of the orbits.
2. The presence of a pair of openings on the palate in advance of the nares in two forms.
3. The large teeth succeeding the tusks on the palatines.
4. The extension of the pterygoidal flange back to the exoccipitals (in the majority of them if I interpret the figures correctly).
5. The very narrow palatal exposure of the processus cultriformis of the parasphenoid;

seem not to be due merely to a similar environment but to imply that they are really all rather closely related. As the characters listed above also occur in Trematosaurus they may be connected with that form.

The very definite marking and great development of the grooves for lateral line sense organs is interesting, and to have been expected in thoroughly aquatic animals.

Bothriceps australis.

Bothriceps australis was well described by HUXLEY (47) in 1859. In 1915 BROOM (44) gave a new description with a quite accurate diagram of the structure of the cranial roof, and a good description of the rather fragmentary occiput.

The palate is quite well preserved and partially exposed ; it shows certain features of interest which are recorded here.

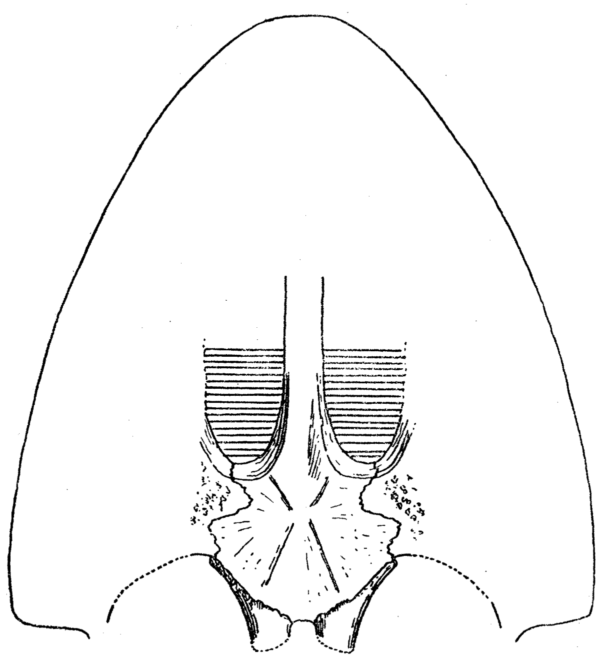


FIG. 26.—*Bothriceps australis.* The palate, slightly diagrammatised from the type specimen, B.M.N.H. 23110. $\times \frac{2}{3}$.

The parasphenoid has the usual suture with the pterygoid, which terminates freely behind. Further back the parasphenoid covers the lower surface of the exoccipitals, having clear sutures with these bones.

The exoccipital has the usual body, which is exposed as a large flat area in side view, and from which a process runs forward below the fenestra ovalis to touch the pterygoid. Dorsally the exoccipital reaches up to articulate with the tabular and dermosupraoccipital in the usual way. There is a medium-sized vagal foramen lying above the condylar root and opening outward on the lateral surface of the bone. Some distance below the vagus foramen is a small opening for the hypoglossal.

The pterygoid just laterally to its articulation with the parasphenoid has on its ventral surface a rather faint ornament, similar in pattern to that of the dorsal skull bones.

Bothriceps australis is known to have come from Australia, probably from New South Wales, but the exact locality and of course the horizon are unknown.

"*Bothriceps*" *huxleyi*, from S. Africa, belongs to the genus Lydekkerina, and is quite distinct.

Bothriceps major, A.S.W., from the oil shales of Airley, N.S.W., is not determinable.

Brachyops.

Brachyops, from the Magli formation of India, is extremely similar to Bothriceps, and, as Dr. BROOM has already suggested, may not be generically distinct.

Batrachosuchus.

This genus was described by BROOM (71) in 1903 from a complete skull from the Cynognathus beds of Aliwal North. This specimen shows nearly the whole structure of the dorsal surface and a good deal of that of the palate.

R. 3589 is a perfectly preserved skull in the British Museum which appears to belong to a different species, differing in proportions and some other details.

The general structure of the top of the head will be obvious from Plate 1.

The interesting features are the almost complete suppression of the otic notch, now only recognisable in a slight concavity of the posterior margin at the junction of the tabular and squamosal: and the extreme anterior position of the orbits, which leads to changes, which are here described, in the relations of the bones between the orbit and the nostril.

The prefrontal forms about a quarter of the inner and anterior parts of the margin of the orbit, extending from its suture with the postfrontal to a deep overlap of the maxilla. Anteriorly the bone is bounded by its sutures with the nasal and maxillæ, these bones meeting in front of it. The nasal forms the posterior and much of the inner border of the nostril, having a suture with the premaxilla in front. The maxilla has a suture with the outer corner of the nasal, but is excluded from the margin of the nostril by a very small bone which is apparently the lachrymal.

The maxilla is perforated by a canal which begins in the prefrontal maxillary suture on the orbital margin and terminates in a small foramen just behind the meeting place of the nasal, lachrymal, and maxilla. The canal is no doubt for a ductus naso-lachrymalis, only previously known in fossil Amphibia in Micropholis.

The small bone which I take to be the lachrymal forms the outer border of the nostril, and has sutures with the nasal, maxilla, premaxilla, and with an even smaller element, which appears to be a septomaxilla.

This element, whose anterior part only is exposed, lies below the nostril in contact with the premaxilla and lachrymal. The doubt as to its determination arises from the fact that it might conceivably, though I think improbably, be a bit of the prevomer.

The palate may be described in more detail, as it was not very completely shown in Dr. BROOM'S original specimen.

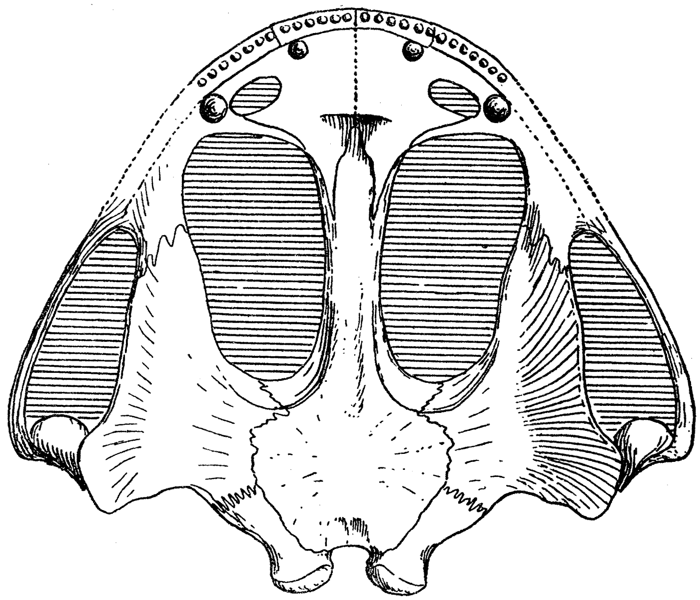


FIG. 27.—*Batrachosuchus sp.* The palate. $\times \frac{1}{3}$. B.M.N.H., R. 3589.

Parasphenoid.—The parasphenoid is a large bone forming a broad processus cultriformis, whose lower surface is nearly flat, but whose lateral margins are sharply bevelled off posteriorly.

The parasphenoid expands to a broad plate behind the pterygoid vacuities, its lateral margins having powerful sutures with the pterygoids and exoccipitals. The bone extends to the back of the skull between the condyles.

Pterygoid.—The pterygoid is an unusual bone ; articulating in the usual way with the parasphenoid and exoccipital in a very long suture, it spreads outwards as a single flat plate which passes rapidly into a deep descending flange placed nearly vertically, whose posterior end covers the inner surface of the quadrate and forms a free edge parallel to, but not touching, a similar edge of the squamosal, which will be described later. The anterior corner of the pterygoid articulates with the posterior end of a bone which is either the ectopterygoid or the palatine ; a break on both sides has removed the bone from the specimen at the point where a suture might be expected, so that this point cannot be decided. The anterior end of the palatine forms the lateral and posterior border of the internal naris, mesial to which it has a suture with the prevomer. The palatine is shown to carry one large tooth.

The prevomers are largely concealed by matrix. Each bears a single tooth, forms part of the border of the internal naris, has a suture with the palatine, and is scarfed on to the lower surface and outer edge of the anterior end of the parasphenoid.

The exoccipital forms a large condyle supported on a short peduncle. Its lower surface is partially covered by the parasphenoid, but its outer edge has a large exposure from below and extends forward to have a long suture with the pterygoid.

This part of the two bones forms a floor to the cavity of the middle ear. Above the condyle on the occipital surface the exoccipital rises to the space for the suprà-occipital and to articulate with the occipital processes of the dermosupra-occipital and tabular. These two processes and the upper edge of the exoccipital enclose an extremely small post-temporal fossa.

The posterior surface of the exoccipital just above the condyle shows a small hypoglossal foramen, in front of which is a much bigger foramen for the vagus. On the right side only there is another small venous foramen.

The posterior edge of the pterygoid, when seen from behind, turns outward and downwards, as already described, along the inner face of the quadrate.

The quadrate is a remarkable bone of triangular horizontal section. The inner flat face of the bone is covered by the pterygoid. The anterior face is slightly convex and faces the infra-temporal fossa. The third face is concave and is covered by the squamosal above and the quadratojugal below. This latter bone is, in fact, split so as to cover some of the anterior face as well. The quadrate ends below in a very remarkable nearly hemispherical condyle.

Squamosal.—The squamosal, so far as it appears on the posterior surface, is described here. It has a suture with the tabular, below which it forms a somewhat triangular area, terminating below in a suture with the quadratojugal. This posterior surface is concave, so that its inner margin is turned backwards as a flange with a free edge parallel to that formed by the pterygoid, from which it is separated by the posterior edge of the quadrate.

The quadratojugal on the posterior surface continues the squamosal, but does not contribute to the flange, its split lower and inner edge clasps the outer corner of the quadrate. The bone is pierced by a small and incompletely shown quadrate foramen.

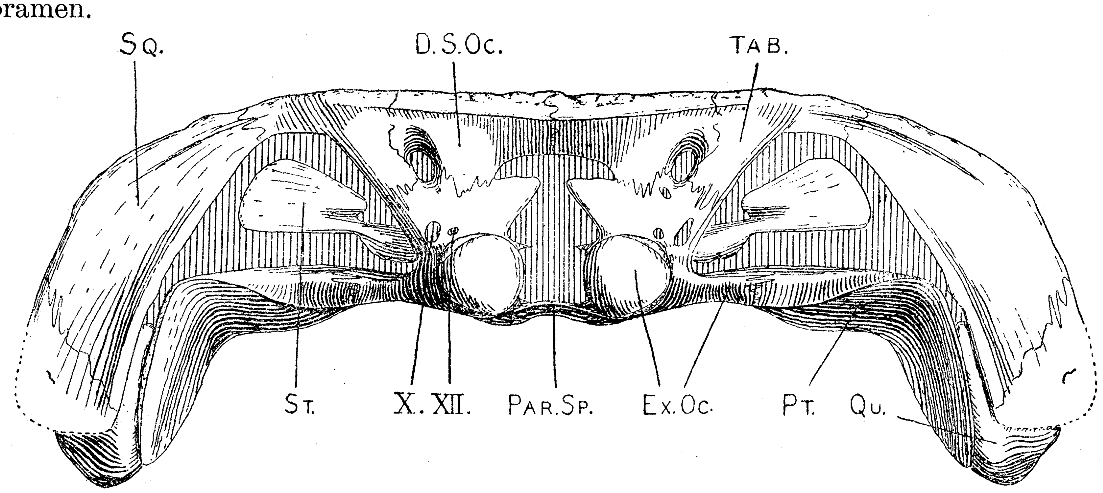


FIG. 28.—*Batrachosuchus sp.* The occiput. × $\frac{2}{3}$. B.M.N.H., R. 3589. Reference letters as before.

Stapes.—The stapes is a large and very massive bone. The inner end is rounded and lies in the fenestra vestibuli, further out its upper surface becomes flat and from it arises a large, flat, vertically situated plate which forms the outer end of the bone. The point of junction of these two regions is marked by a very deep groove, crossing the upper surface, which no doubt transmitted a stapedial artery.

The outer border of the stapes lies parallel to and not far distant from the inner edge of the squamosal, and was in all probability united to that bone by ligaments as it is in many living Urodeles.

The only known remains of Batrachosuchus are :—

Batrachosuchus browni, Broom, Cynognathus beds, Aliwal North, Cape Province.

Batrachosuchus sp., described above, Cynognathus beds, Cape Province, South Africa.

Plagiosaurus, Jaekel (72), 1914.

This genus is founded for FRAAS' type skull of *Plagiosternum pulcherrimum*, and a fragmentary skull, lower jaws, and vertebræ of *P. depressus.*

In FRAAS' (60) description of *P. pulcherrimum*, the upper foramen marked "v" in the occipital view is really the reduced post-temporal fossa, the skull being extremely remarkable, in that the tabular reaches so far down that it touches that flange of the exoccipital which reaches the pterygoid.

In JAEKEL'S description, the element figured as a vertebra is merely a neural arch, whose large facets for articulation with the intercentrum show that that bone must be extraordinarily similar to an ordinary reptilian centrum in appearance.

P. pulcherrimum, Fraas, U. Trias, Wurtemberg.

P. depressus, Jaekel, U. Trias, Prussia.

Plagiosternum, Fraas.

Is only known from clavicles and interclavicles and fragments of the skull. It is in all ways extremely close to Plagiosaurus.

Plagiosternum granulosum (Fraas), Middle Trias, Wurtemberg.

There can be no doubt that Brachiops, Bothriceps, Batrachosuchus, Plagiosternum, and Plagiosaurus are closely allied Amphibians forming the family Brachyopidæ of BROOM.

They resemble one another, and differ from all other known Stereospondyl types in the following ways :—

1. The broad parabolic skulls, with large anteriorly situated orbits.
2. The unusual way in which the pro-otic flange of the squamosal wraps round the outer side of the quadrate, and, having formed a laterally concave face on the occipital surface, ends in a ridge, separated from an exactly similar ridge of the pterygoid by the quadrate.

3. The downturning of the lateral wings of the pterygoids inside the basi-temporal fossæ, so that the palate forms a broad U-shaped channel.
4. The unusual way in which the posterior edge of the pterygoid is applied to the flat inner face of the quadrate.
5. The fact that the occipital condyles lie far behind the dermosupra-occipitals, so that the occipital surface slopes forwards.

The genera even resemble one another in such little features as the general shape of the suture between the parasphenoid and pterygoid.

The whole family seems to have been descended from the Upper Permian type Dwinasaurus, found by Prof. AMALITZKI on the Dwina. I have not found any description of this animal, and only know it by certain photographs and casts presented by its discoverer to the British Museum. I do not therefore feel entitled to give a description of it, but, on account of its great importance, give here a few notes on its relations.

It shows in the most typical manner the five characters which I have shown above to characterise the Brachyopidæ, but it is a Rachitomous type, with the exoccipital condyles ill-defined and united by a basi-occipital. The pterygo-parasphenoid suture seems to have been short, and was not tightly interlocked, as in one individual it is disarticulated. The exoccipital seems not to have reached the pterygoid.

Other undeterminable remains of large Amphibia, which are probably Stereospondyls, have been described as follows :—

Diadetognathus varvicensis, Miall, '74, Keuper, Warwick.
Dictyocephalus elegans, Leidy, '56, U. Trias, N. Carolina.
Ekhainacanthus tschernichevi, Yakowlev, M.T., Spitzbergen.
Eupelor durus, Cope, '66, U. Trias, Pennsylvania.
Eurycervix postumus, v. Huene, '02, U. Trias, Pennsylvania.
Glyptognathus fragilis, Lyd, '82.
Gonioglyptus huxleyi, Lyd., '82, Trias, India.
Gonioglyptus longirostris, Hux., '65, Trias, India.
Labyrinthodon lavisi, Seeley, '76, Keuper, Sidmouth.
Labyrinthodon leptognathus, Owen, '42, Keuper, Warwick.
Pachygonia incurvata, Hux., '65, Trias, India.
Pariostegus myops, Cope, '78, Trias, N. Carolina.
Petrophryne major, Owen, '76 (not Petrophryne, but Stereospondyl), Trias, S. Africa.
Platyceps wilkinsoni, Stephens, '87, Trias, N.S.W.
Ptychosphenodon browni, Seeley, '07, Trias, S. Africa.
Xestorhytias perrini, v. Meyer, Trias, Germany.

Many of these forms are founded on material which may be specifically recognisable on the discovery of more complete specimens, but none of them is ordinarily determinable ; they might be Rachitomi, or even Embolomeri, instead of Stereospondyls, so far as the structures shown in the existing fragments go.

General Discussion of the Forms Described Above.

It is difficult, from an inspection of the literature, to determine what view of the relationships of the Rachitomi and Stereospondyli has been held by previous authors.

Many writers, of whom the late Prof. E. Fraas was perhaps the first, have pointed out that the Stereospondyl vertebra could have been derived from a rachitomous type by the reduction of the pleurocentra and the exaggeration of the intercentrum. This view leads naturally to the idea that the Stereospondyls have actually been derived from the Rachitomi, but, so far as I can discover, this view has only been stated definitely by Cope and Thevenin (19).

The *résumé* of the whole series of animals belonging to these orders which is included in this paper shows that the Rachitomi range in time from the very bottom of the Permian or perhaps the top of the Upper Carboniferous to the top of the Permian and are represented by somewhat remarkable forms as high as the Procolophon zone (Lower Trias ?) of South Africa.

The Stereospondyli, however, are first found in the Lower Trias and range on into the Rhætic, where they disappear.

The time relations of the two groups are thus quite in agreement with the possibility of their mutual connection.

That the Stereospondyls are related to the Rachitomi is indicated by the following series of resemblances :—

1. It is impossible to tell from the dorsal surface of the skull to which order a given form belongs.
2. That the structure of the lower jaw is identical in the two groups.
3. That the clavicular arrangement of such a Rachitomous type as Rhinesuchus is identical with that of such a Stereospondyl as Mastodonsaurus.
4. That the scapulo-coracoid of Eryops is extremely similar to that of Mastodonsaurus.
5. That the humerus of Mastodonsaurus resembles that of Eryops in all its more important morphological features, such as the screw-shaped head, and only differs in its lesser degree of twisting and its more slender form, in which it resembles other Rachitomous types such as Rhinesuchus, Trimerorachis and Lydekkerina.
6. That the pelvis of Mastodonsaurus resembles that of Lydekkerina in all important features and only differs from that of the Lower Permian Rachitomi in the non-ossification of the pubis.
7. That the Stereospondyl femur resembles that of the Rachitomi.

This series of resemblances cannot be matched by any comparison between the Stereospondyls and any other order of Amphibia except the Embolomeri, and shows that the Rachitomi and Stereospondyli are really genetically related. The similar resemblances to the Embolomeri depend on the fact that the Rachitomi are derived from that group.

It follows that by comparing a Stereospondyl with a Rachitomous type we shall obtain an idea of the evolutionary trend proper to the groups.

Trend of Evolutionary Changes in the Rachitomi and Stereospondyli.

Shape of Skull.

One remarkable feature of the two orders is the occurrence at different times of animals with a very similar skull shape.

1. It seems obvious that the primitive or at any rate the central shape of skull is that of Capitosaurus. This type alone is found in all horizons, Lower Carboniferous, Anthracosaurus; Upper Carboniferous, Pteroplax; Lower Permian, Eryops; Middle and Upper Permian, Rhinesuchus; Lower Trias, Capitosaurus; Upper Trias, slightly modified in Cyclotosaurus.

The characteristic features are the wide muzzle, posterior position and nearness to the middle line of the small orbits, and small otic notches not very widely separated.

2. Animals with elongated rostra, all aquatic fish-eaters.

L. Permian, Cricotus (Embolomerous form), Archegosaurus; Upper Permian, Platyoposaurus; L. Trias, Trematosaurus; M. Trias, ? Aphanerramma, Lonchorhynchus; the last found in marine deposits.

All these types are easily derived from forms with a Capitosaurus-shaped skull by the extension of the pre-orbital part of the face so as to elongate the gape. That they are all aquatic is shown by the occurrence of well-defined sensory grooves and the deficient ossification of the limb bones and girdles when known. An elongated gape always occurs in fish-eating aquatic animals, *cf.* Cetacea, Mesozoic marine Crocodiles, Ichthyosaurus, Choristodera, etc.

3. Animals with very depressed skulls, the dorsally situated orbits being placed more anteriorly than in Capitosaurus. Trimerorachis, L. Permian; Lydekkerina, L. Trias ?; Metoposaurus and Anaschisma, U. Trias. All these animals are obviously aquatic.

4. Animals with a flat-topped head, laterally placed orbits and otic notches.

L. Permian, Aspidosaurus, Broiliellus; L. Trias, Micropholis.

All these types are obviously land forms.

5. Similar to 4, but with the otic notches closed behind by a process from the tabular meeting the quadrate.

L. Permian, Cacops and Dissorophus; Middle Permian, Zygosaurus. All land forms.

Many more types and individuals might be mentioned, but those listed above will show that the general range in shape was similar at different times. In a subsequent stage of this paper it will have to be considered whether these groups are quite unnatural, or whether such a type as Aphaneramma has been derived directly from an earlier form like Archegosaurus, or has appeared as an adaptive modification from a Stereospondylous type with a Capitosaurine skull.

Comparison of Rachitomi and Stereospondyls.—As the members of the first group with Capitosaurine skulls show no special adaptations, direct comparison of them, *inter se*, will give those characteristic changes which I call advances as clearly as possible without the admixture of specialisations.

Fig. 29 represents on the same absolute width a series of Capitosaurus-shaped skulls arranged in order of age. The very remarkable increase in size of the great palatal vacuities lying between the pterygoids and parasphenoid is well shown by this figure. Connected with it is the fact that whilst in Eryops the pterygoids reach to the prevomers, owing to the expansion of the vacuity, they only just succeed in touching the palatines in Capitosaurus, and in Metoposaurus, which is of the same age as Cyclotosaurus in which genus the facts are not known, they do not even reach these elements, but articulate solely with the transverse bones.

Another change well brought out by this series is that there is a steady reduction in the length of the quadrate ramus of the pterygoid, so that the lower jaw articulation, which at first lies far behind the connection of the skull with the neck, finally comes to lie in front of that plane.

These changes are common to all types of large Amphibia, although they proceed at very different rates in the different stocks. For example, Micropholis, the latest known Rachitomous Amphibian, has far larger palatal vacuities than any other member of that order.

All Lower Permian Rachitomi have palatal vacuities very appreciably smaller than those found in Triassic Stereospondyls, and the few known Upper Triassic forms have them larger than those of any Lower Triassic types.

Another change which occurs progressively through the large Amphibia is a gradual flattening of the dorsal surface of the skull and a decrease in depth. This change is obvious in the first three drawings of fig. 31, and that it is general is shown from the fact that there are far more high skulls amongst the Lower Permian forms than in those of any later period; by the Upper Trias, in fact, all the known forms are very flattened. At the same time considerably flattened forms such as Trimerorachis do occur in the Lower Permian in aquatic animals.

Far more interesting, however, are the changes in the basicranial region and in the brain case. These are most readily explained by comparing together Eryops, the best known of the Lower Permian forms, and Capitosaurus.

Capitosaurus differs from Eryops in the following ways (*cf.* fig. 11):—

1. The great reduction in size and degree of ossification of the basi-occipital and basisphenoid, which results in the complete withdrawal of the former bone from the condyle, so that the tripartite condyle of Eryops is converted into the double condyle of Capitosaurus.

2. The replacement of basipterygoid processes whose core is formed of basisphenoid by expansions of the edges of the parasphenoid.
3. The loss of all ossification in the supra-occipital.
4. The great reduction of the pro-otic and paroccipital.
5. The great extension of thin processes of the exoccipital over the outer and inner surfaces of the auditory capsule, so that the paroccipital no longer appears on the endocranial surface, the outer opening of the vagus foramen lies entirely in the exoccipital, and that bone forms the lower margin of the bony fenestra vestibuli and reaches forward to the pterygoid.
6. The development of the descending occipital process of the tabular into a large bone surrounding the posterior surface of the paroccipital, completely hiding that bone in a posterior view, and having a powerful suture with the exoccipital.

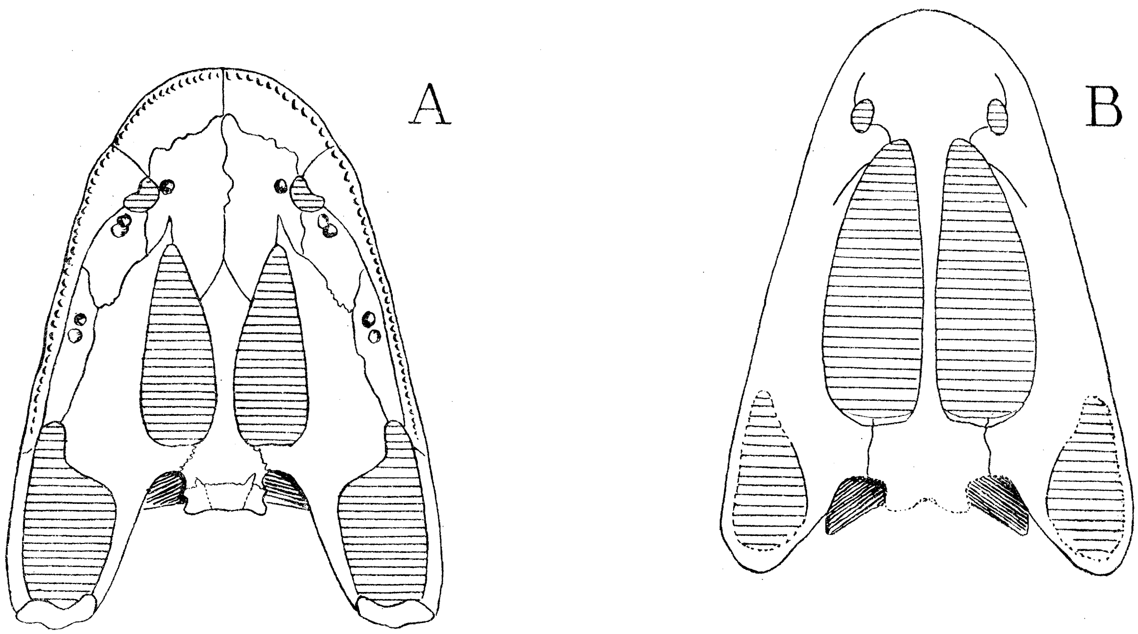


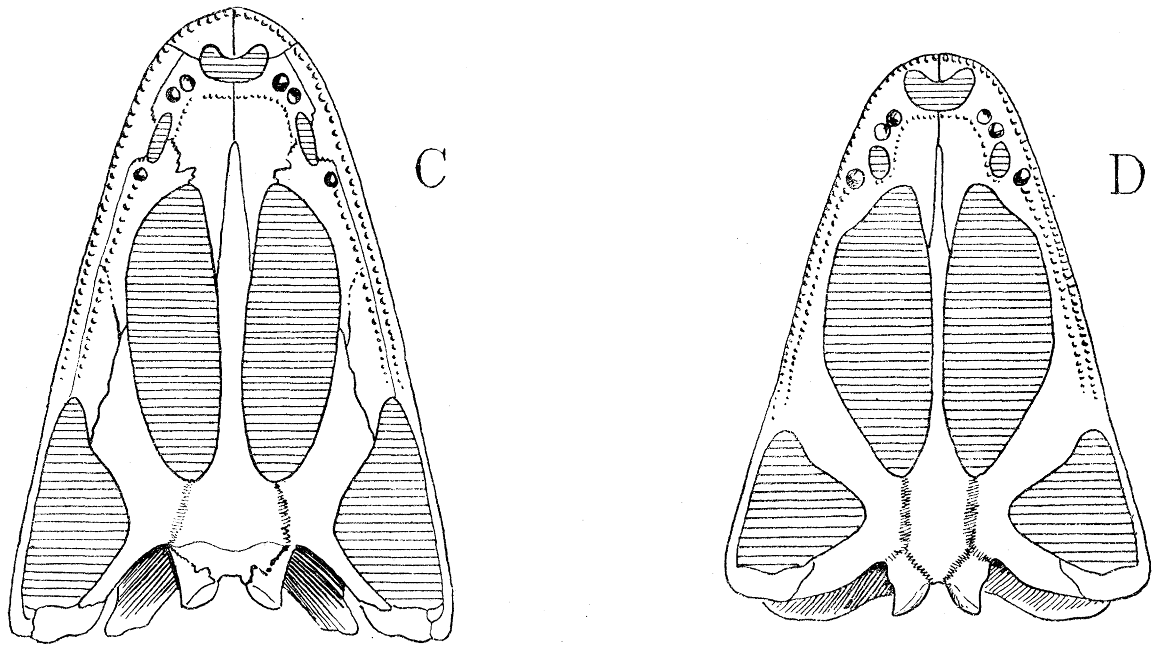
FIG. 29.—Palatal views of A, Eryops, after BROOM; B, *Rhinesuchus major*, from the figures of BROOM, v. HOEPEN,

7. The enormous expansion of the epipterygoid and the development of very distinct ascending and otic processes, the latter of which has acquired a powerful contact with the pro-otic.
8. The development of a contact and, indeed, sutural union between the upper inner corner of the quadrate ramus of the pterygoid and the pro-otic.

The only other Lower Permian form which is sufficiently well known to be compared with Capitosaurus is Trimerorachis, a very specialised aquatic type. This animal differs just as does Eryops in most characters, but it has already a very reduced basisphenoid, and the apparent basipterygoid processes which have distinct articular facets for the pterygoids seem to be mainly or entirely parasphenoid.

That Eryops is typical of the general structure of Rachitomi of its time is indicated by the following facts :—

1. That a single occipital condyle, the middle portion of which is formed by the basi-occipital, is known to occur in Archegosaurus, Chelydosaurus, Actinodon, Trematops.
2. That definite slender basipterygoid processes are known in Archegosaurus, Actinodon, Broiliellus, Cacops, Onchiodon, all of Lower Permian age.
3. That small descending processes of the tabular are known in Archegosaurus and Actinodon.



Capitosaurine skulls.
and HAUGHTON ; C, *Capitosaurus nasutus ;* D, *Cyclotosaurus postumus*, after FRAAS.

I have personally examined no material of L. Permian Rachitomi which, in these and other significant features of the brain case, does not agree with Eryops, so far as the facts are shown.

Laccocephalus is intermediate between Eryops and Capitosaurus in the following ways :—

1. The basi-occipital, though larger and better ossified than in Capitosaurus, is much smaller than in Eryops, and there are distinctly two exoccipital condyles.

2. The basisphenoid is much larger than in Capitosaurus, but differs from that of Eryops in not forming definite ossified basipterygoid processes, although cartilaginous extensions of it seem to have passed outwards above the flat parasphenoidal expansions to the epipterygoid and pterygoid.
4. The pro-otic is far more reduced than in Eryops, but so far as known is larger than in Capitosaurus. The paroccipital is not known.
5. The exoccipital seems to articulate with the tabular very much as in Capitosaurus, but does not reach forward to the pterygoid, so that the parasphenoid does form a very small part of the border of the bony fenestra vestibuli as it does largely in Eryops.
6. The occipital process of the tabular is more greatly developed than in Eryops but its exact size is unknown.

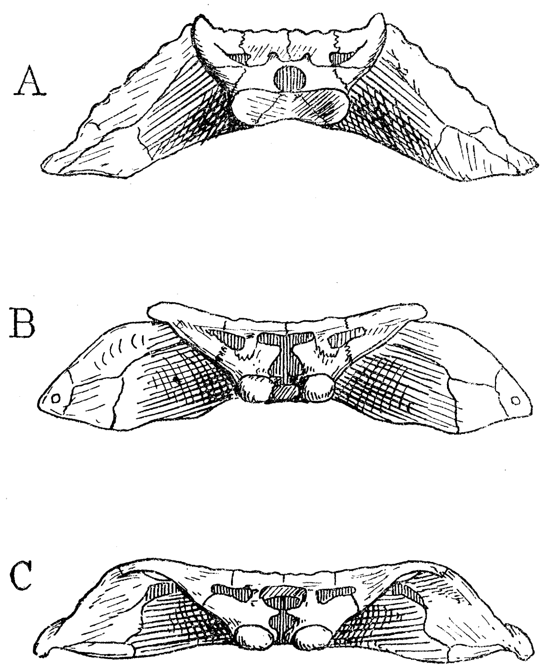


FIG. 30.—Occipital views of three Capitosaur-shaped skulls.
A, Eryops, after CASE and BROOM ; B, Capitosaurus, after SCHROEDER, modified by the S. African specimen described in this paper; C, *Cyclotosaurus postumus*, after FRAAS.

7. The epipterygoid is a far larger bone than in Eryops, and its ascending process, though smaller, is similar to that of Capitosaurus in being deeply grooved for the Gasserian ganglion. It resembles Eryops in that the otic process is still undeveloped.
8. The inner upper corner of the quadrate ramus of the pterygoid articulates with the pro-otic as it does in Capitosaurus.

This animal, therefore, forms a remarkably good intermediate between Eryops and Capitosaurus, standing morphologically, as its probably late age would have suggested, nearer to the latter than the former type.

The new description which Dr. BROOM has sent me (see p. 11) shows that Rhinesuchus in these characters, as in the palate, stands intermediate between Laccocephalus and Eryops.

The only other rachitomous amphibian of age intermediate between Eryops and Capitosaurus of which anything of the brain case is known is Lydekkerina. This animal is intermediate between those two types in the following ways :—

1. The basi-occipital is not completely ossified and there are distinctly two (mainly) exoccipital condyles.
2. The pterygoids articulate by long sutures with flat expansions of the parasphenoid. (The basi-sphenoidal arrangement is not known.)
4. The pro-otic and paroccipital are by no means so well developed as in Eryops or Trimerorachis.
5. The exoccipital sends a long process forwards, so that the vagus foramen is just completely surrounded by that bone, which forms part of the lower border of the fenestra vestibuli, to which, however, the parasphenoid contributes.
6. The lower occipital process of the tabular reaches far down the paroccipital.

7 and 8. The epipterygoid region is not known in Lydekkerina.

As Lydekkerina is a specialised type far off the line of descent of Capitosaurus, this series of characters in which it is intermediate is a very satisfactory one.

Comparison of Capitosaurus with its successor should show a continuance of this series of changes. It would be most satisfactory to compare Cyclotosaurus, which has every appearance of being a direct descendant of Capitosaurus, with that genus, but as our knowledge of this genus is not quite satisfactory I use in addition Metoposaurus and Rhytidosteus, which appear to be of very similar structure.

The Upper Triassic Stereospondyls differ from Capitosaurus as follows :—

1. In the great reduction in size of the basi-occipital (*Cyclotosaurus robustus*, Metoposaurus), its lack of ossification and the absence of any trace of a basisphenoid.
2. In the great extension of the suture between the pterygoid and parasphenoid and the appearance of an additional suture between the pterygoid and the exoccipital, visible in a palatal view.
3. Not only is there no ossified supra-occipital, but in Metoposaurus and Anaschisma the absence of any step for its cartilage on the exoccipital suggests that it has disappeared as completely as it does in modern Amphibia.
4. In the still further reduction of the pro-otic and paroccipital, of which no trace remains as bone.

5. In the continued growth of the exoccipital shown in its large suture with the pterygoid, and in the moving outwards of the suture between the exoccipital and tabular to the outer end of the post temporal fossa in Cyclotosaurus.
7. In Cyclotosaurus the epipterygoid shows a great extension outwards on the quadrate ramus of the pterygoid and has a long suture with the squamosal. The cranial end of the bone is not known in detail.

Other very important changes are :—

a. The reduction of the quadrate ramus of the pterygoid so that it no longer reaches the squamosal.

b. The loss of the foramen for the hypoglossal nerve.

In all these characters *Cyclotosaurus stantonensis* seems to be exactly intermediate between Capitosaurus and the large typical Cyclotosauri.

These changes are in exactly the same direction as those between Laccocephalus and Capitosaurus and between Eryops and Laccocephalus. The series of comparisons shows that in the whole group of large Amphibia with Capitosaurus-shaped skulls, there is a definite trend of evolutionary change in the basicranial and otic regions of the skull, which continues throughout the history of the group.

Study of the very distinct and obviously natural group of the Brachyopidæ shows that that family includes a series of forms displaying an exactly similar series of changes, each step being apparently taken at a rather earlier period.

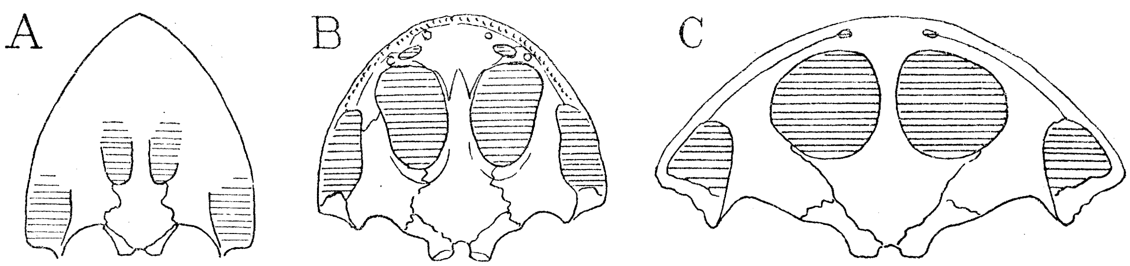


FIG. 31.—Palatal views of Brachyopid skulls.
A, *Bothriceps australis ;* B, *Batrachosuchus sp. ;* C, *Piagiosaurus pulcherrimum*, after FRAAS.

The series Dwinasaurus, Bothriceps, Batrachosuchus, and Plagiosaurus shows a gradual passage forwards of the quadrate condyles from a position just on a level with the occipital condyle in the earliest genus to the extremely anterior place which they hold in Plagiosaurus. The series shows also a steady increase in size of the palatal vacuities, although this change is masked by the progressive widening of the skull, and is most clearly shown in the narrowing of the palatine.

In Dwinasaurus, as in Laccocephalus, the exoccipital does not reach the pterygoid. In Bothriceps the two bones just meet exactly as in Capitosaurus ; Batrachosuchus agrees in this feature with Cyclotosaurus, and Plagiosaurus shows a still further stage of the same change, not reached by any known Capitosaurine type.

In Bothriceps the hypoglossal foramen is on the outer side of the exoccipital condyle, as in Capitosaurus; in Batrachosuchus it is in the middle of the posterior surface of the bone, as in *C. stantonensis;* whilst in Plagiosaurus it has disappeared altogether, as in the typical Cyclotosauri.

It is possible to give a plausible mechanical explanation of one of this series of changes—the gradual travelling forward of the quadrate condyles.

I have called attention to the fact that the large Amphibia show a progressive flattening of the head and anterior part of the body; such an animal as Mastodonsaurus, with an enormous flat head and very small limbs, must have lived in ponds or rivers, lying flat on the bottom and being practically incapable of raising its head off the ground.

Its only possible method of opening its mouth was to raise the head, leaving the lower jaw on the ground, very much as a crocodile does. If the articulation of the head and neck lies in advance of that of skull and lower jaw, such a method of opening the mouth involves raising the whole anterior end of the body to an extent depending directly on the amount of the projection of the quadrate condyle behind the skull-neck joint.

When the two are in the same plane, the head can be raised without raising the anterior part of the body.

This method of opening the mouth also explains the development of the pair of exoccipital condyles as an adaptation to allow great dorsoventral flexibility at this point. Finally, it explains the gradual development of a long postarticular part of the lower jaw, which was the first evolutionary change recognised in the large Stegocephalia. An extremely flattened animal like Metoposaurus must have had very great difficulty in raising its very large head, because, owing to the shallowness of the occiput, the nuchal muscles act at a great mechanical disadvantage, and, furthermore, there can be no elongated neural spines for their insertion. If the lower jaw rests on the ground, however, powerful musculi depressores mandibuli arising from the tabulars and passing behind the otic notch to be inserted into a long retro-articular process of the lower jaw will give very material assistance in raising the head.

Although this explanation is plausible, inasmuch as the mechanical improvements desired are obtained by the changes which actually took place, it is probably not a complete explanation or even an important factor in the initiation of the series of changes, because a similar migration forward of the quadrate condyles undoubtedly occurred in the Cotylosauria, which are not flattened, and paired exoccipital condyles are independently developed in an exactly similar manner in the Cynognathidæ, which are also not depressed forms.

The explanation may, however, be correct for the retro-articular portion of the lower jaw.

Now inspection of the structure of the Upper Triassic Stereospondyls shows that in all ways they resemble the modern Amphibia far more closely than do their earlier ancestors. In fact all the features which have previously been regarded as characteristically amphibian characters may be seen to be gradually developed in the series of large Amphibia which I have discussed in this paper.

These are :—

1. The presence of two distinct exoccipital condyles.
2. The great reduction of the basicranial cartilages and the absence of basi-occipital and basisphenoid bones.
3. The presence of very large interpterygoid vacuities.
4. The junction of the pterygoids with a widened posterior part of the parasphenoid.
5. The presence of an otic process of the palatoquadrate cartilage, which articulates with the pro-otic region of the skull.
6. The absence of a hypoglossal foramen and the position of that nerve behind the skull.

The extreme development of the exoccipital so that its perichondral extensions surround the auditory capsule seems to be characteristic of the Urodeles, judging from W. K. PARKER's figures.

It is certain that this great series of characters must have been independently acquired in the large Amphibia with which this paper deals, and in the Urodeles and Ecaudata, for these latter types have a very different though uncertain ancestry.

These structures, or at least such of them as are known in that form, have had an independent origin in the Lower Permian animal Diplocaulus, belonging to the Lepospondyli, which at that early period had acquired a structure which is in many ways extremely similar to that of such an Upper Triassic Stereospondyl as Plagiosternum, a structure which amongst the large Amphibia does not occur until that period.

This case of the parallel evolution of diverse branches of the same class is perhaps the most striking that palæontology has yet revealed to us, not only from the accuracy of the parallel, but from the fact that the structures whose independent origin has been traced are of such importance that since the time of CUVIER they have been recognised as diagnostic characters of the class Batrachia.

It is my intention in subsequent papers to deal with the earlier history of the Rachitomi-Stereospondyli stock and to discuss the structure and, as far as material allows, the evolutionary history of the Lepospondyli and Phyllospondyli, and the embryonic history of the skull in living Amphibia, when I shall return to the consideration of this great instance of parallelism.

Some parallels to these changes can be found amongst reptiles, although the series as a whole is restricted to the Amphibia.

The mode of development of the paired exoccipital condyles of later Amphibia by the gradual reduction, first of all in length and ossification and then in depth, of the basioccipital which forms the middle part of the large tripartite condyle of Eryops, is quite similar to that in which the paired exoccipital condyle of Diademodon is developed by the gradual retraction and thinning of the middle basioccipital portion of the tripartite condyle of a Gorgonopsid such as Scymnognathus.

The great development of the outer part of the epipterygoid in Cyclotosaurus, and the reduction in height of the quadrate ramus of the pterygoid in that group, is also not altogether unparalleled amongst the Gorgonopsids and Cynogathids.

Perhaps the fact of greatest general morphological importance established in this paper is that a hypoglossal nerve was an almost constant feature of the early large Amphibia. In Trimerorachis, Lydekkerina, Capitosaurus, Trematosaurus, etc., there is a foramen which in its position agrees exactly with the hypoglossal foramen of early Reptiles; it leaves the skull in the same manner, and in Trimerorachis joins the vagal foramen in a way only consistent with its having transmitted that nerve.

In Cyclotosaurus and Rhytidosteus, however, this opening is absent, and the vagal foramen is placed very near the posterior surface of the exoccipital.

It has long been known that the living Amphibia are remarkable in having very few post-otic cranial segments. A review of the literature, and a detailed description of the facts in Amblystoma, has recently been given by GOODRICH (11), who, in agreement with Miss PLATT, finds that there are only three occipital segments in Urodeles. In Reptilia there are probably five post-otic segments, and in fish at least as many, and probably more.

The facts recorded above suggest that the Amphibia had originally the same number of meta-otic segments as the Reptiles, but that the posterior end of the occipital region has migrated forwards, so that the hypoglossal nerve, which belongs to the last two of the original segments, now issues as a spinal nerve between the neural arches of the anterior vertebræ.

The post-cranial skeleton of the Stereospondyls is so badly known that very little can be said of its evolutionary history.

Vertebral Column.

The atlas of Trimerorachis has been clearly described and figured by CASE, whose observations show that it has the following structure. There is a pair of neural arch elements; these articulate with the upper outer corners of the large condyle, which we know, through the work of BROOM and WILLISTON, to be formed by the exoccipitals. Below these elements are a pair of bones, together forming an intercentrum. These articulate with the lower part of the condyle, which is basioccipital. The posterior surface of the atlas articulates with the front of the succeeding vertebra.

In Eryops the atlas has been described by BRANSON and by CASE, whose specimen seems to me to be complete and in its natural articulation.

There are a pair of neural arch elements which articulate by large faces with those lateral and upper parts of the broad occipital condyle which are formed by the exoccipitals. The first intercentrum is comparatively small, and lies close up below the neural elements; it must have articulated with the basi-occipital part of the condyle.

These two animals thus agree in the mode of articulation of the skull with the vertebral column. The notochord ran ventral to the neural elements and dorsal to the intercentra, so as to enter the pit in the condyle, which lies in Trimerorachis above the basi-occipital and below the exoccipitals.

In Mastodonsaurus, the earliest Stereospondyl in which the atlas is known, the exoccipital condyles are large and well separated and the basi-occipital reduced. The atlas consists of a single bone surrounding the spinal chord, and having a pair of cotyli for the exoccipital condyles. The body of this bone is perforated by a notochordal canal, which enters high up at the back and leaves low down in front. There can be no doubt that the greater part of this bone is of neurapophysial origin, though it seems by no means improbable that there is a small intercentrum included in the lower part of its posterior surface below the notochord.

The mode of articulation of the atlas with the skull in Eryops and Trimerorachis makes it appear possible that the basi-occipital is an intercentrum and the exoccipitals pleurocentra. This view is supported by the fact that the occipitals in the large Amphibia always meet or nearly meet below the brain, so as to exclude the basi-occipital from the brain cavity, and that the notochordal pit always lies on the upper edge of the basi-occipital. The intercentra are the only subnotochordal elements of the ordinary rachitomous vertebra.

All Lower Permian reptiles in which the structure of the occipital condyle is known agree with Trimerorachis in having the exoccipitals meeting below the brain and the notochordal pit at the junction of the two exoccipitals with the basi-occipital.

No intermediate condition between the typical rachitomous and stereospondylous vertebral columns is definitely known, but Gondwanosaurus may perhaps be an example.

The Mastodonsaurus vertebral column in Stuttgart suggests the presence of small pleurocentra, but without further study and preparation of this material I should not like to be certain of their presence.

That the main elements of the column of this animal are intercentra, as is now generally recognised, is shown by the fact that they are often horseshoe-shaped, the notochord notching the upper edge, and by the fact that the hæmapophyses arise from them in the caudal region.

Shoulder Girdle.

Prof. WILLISTON, in his description of the osteology of Trimerorachis, has pointed out that that animal is secondarily aquatic and that its expanded clavicles are related to the mode of life; with this conclusion I am in perfect agreement.

The only direct evidence that the wide triangular clavicles which are so noticeable a feature of Triassic Stereospondyls have been derived from narrow clavicles like those of Reptiles is derived from the family Brachyopidæ, where the Upper Permian Dwinasaurus, the oldest known member of the family, has quite narrow clavicles like those of Eryops, whilst in the Upper Triassic Plagiosaurus and Plagiosternum the clavicles are extremely widened. Additional evidence in support of this view is afforded by the fact that narrow clavicles are very common in Lower Permian Rachitomous forms, whilst no Triassic Stereospondyl is known which has not large widely expanded clavicles.

It might, in the absence of Dwinasaurus, have been argued that after all the wide type is the primitive one, and that from it Eryops, etc., were derived as short-lived side branches.

This view, however, will not meet the case ; the clavicles described by HANCOCK and ATTLEY (19) which belong to Pteroplax are totally different from those of Eryops and the expanded type of Metoposaurus, and certainly represent the primitive, primarily aquatic, large amphibian type. I propose to discuss these bones and the methods and causes of the origin of the Eryops clavicle from them in a later paper.

It must be pointed out here that the dorsal part of the clavicle of such a rachitomous type as Rhinesuchus or of a Stereospondyl is structurally identical with the same region in Eryops, articulating with the front edge of the lower end of the cleithrum in quite the same way.

This narrow dorsal process, similar to that of a reptile clavicle, seems to me to have arisen in Eryops, etc., as an adaptation to terrestrial life, and I am, therefore, driven to conclude that the later, entirely aquatic Stereospondyls have descended from more terrestrial ancestors.

The cartilaginous shoulder girdle is so badly known in Stereospondyls that no evolutionary change can be discovered. The flattening of the body makes the scapula short and its extreme wideness leads to the complete separation of the two bones.

It is possible that the necessity of supporting the two widely separated halves of the cartilaginous shoulder girdle has been a contributing factor to the development of the expanded clavicles and interclavicle.

Fore Limb.

So little is known of the fore limb in most Fossil Amphibia that its evolutionary changes are obscure. The humerus in Mastodonsaurus is clearly a reduction from that of Eryops, and in the less development of its muscular insertions and twist is apparently a more aquatic type.

Eryops seems to have had five fingers in the hand, most other large Amphibia (Archegosaurus, Actinodon, "Rhinesuchus") have four. It seems to me much more probable that most forms have lost one digit than that Eryops should have developed one.

The development of a four-fingered hand has thus probably been independent in the large Amphibia and the Lepospondyls and Phyllospondyls, groups which have certainly not been derived from Rachitomous Amphibia.

Pelvic Girdle.

The only change in the pelvic girdle is that in the later forms the pubis is never ossified, whilst in the majority of Lower Permian Amphibia it is as thoroughly ossified as the ischium.

No recognisable changes except the reduction of the adductor ridge are visible in the hind limb.

General Form and Habits.

The complete skeleton is known in so few large Amphibia that discussion of its changes and adaptations is difficult.

There can be no doubt that there is a gradual depression of the skull and anterior part of the body from the round-bodied Eryops to the extraordinary flat Cyclotosaurus. It is also obvious that this change is connected with a gradual return to an aquatic life, which in the Late Triassic forms is probably quite complete, for it is difficult to conceive that Mastodonsaurus can ever have been capable of effective movement on land, and the extreme development of the canals for lateral line sense organs on the skulls of all Triassic forms is only intelligible if these organs were of great functional importance, which implies that they were in water.

Probable Structure of an Ancestor of the Rachitomi.

In this work I have shown that there is a great series of changes in the skull and skeleton of the large Amphibia which do not seem to conduce directly to life under any special conditions but to be of that type which I call " advances."

Advances in this special sense take place in regions of the animal where they seem to be largely protected from direct contact with the environment, and proceed in definite directions unaffected by the changes of habit of the stock, and hence by projecting them backwards we should be able to reconstruct a hypothetical ancestor.

The advances in the large Amphibia are :—

1. The gradual flattening of the skull and body.
2. The gradual reduction of the basi-occipital and its retreat from the occipital condyle.
3. The reduction of the basipterygoid processes largely formed by basisphenoid and their replacement by expansions of the parasphenoid.
4. The increase of the exoccipitals, so that they finally form the whole occipital articulation, reach forward to the pterygoids below the fenestræ ovales, and up to the dermosupra-occipitals and tabulars.

5. The reduction of the paroccipitals and pro-otics.
6. The reduction of the supra-occipital.
7. The development of the occipital plates from the tabulars and dermosupra-occipitals.
8. The shallowing of the quadrate ramus of the pterygoid.
9. The great increase in size of the epipterygoid, and the development of an otic process reaching the pro-otic.
10. The exaggeration of the interpterygoid vacuities and the reduction of the palatal ramus of the pterygoid.
11. The reduction of the suspensory part of the skull, so that the quadrate condyles come to lie in front of the occipital condyles.
12. The loss of a twelfth nerve.
13. The development of a large retro-articular part of the lower jaw.
14. The increase in importance of the neural elements of the atlas.
15. The decrease of the pleurocentra throughout the vertebral column.

An ancestor of the Rachitomi should, therefore, have the following structure :—A round body and deep skull, a single condyle formed by the basi-occipital, well-ossified basi-occipital and basisphenoid, with definite basipterygoid processes formed by the latter bone. Small exoccipitals, lying entirely behind the paroccipitals and not reaching the skull roof. Large well-ossified paroccipitals, pro-otics, and supra-occipital. Tabulars and dermosupra-occipitals restricted to the skull roof, and not provided with occipital flanges. A well-developed quadrate ramus of the pterygoid and a small epipterygoid without an otic process. Small interpterygoid vacuities and a long suspensory region carrying the quadrate back behind the occiput. A twelfth nerve should be present. There should be no retro-articular process of the lower jaw. The atlas should have a large intercentrum articulating with the basi-occipital condyle and small neural elements with the exoccipitals. Finally, the pleurocentra should be large.

In a subsequent paper, I shall be able to show that this structure is completely realised in the Carboniferous Embolomerous amphibian Pteroplax.

Classification of the Labyrinthodontia.

The survey of the whole series of Rachitomous and Stereospondylous Amphibia, which forms the first part of this paper, shows that even with known forms there is a complete gradation of structure between the orders, which merely mark evolutionary stages.

It is necessary to found a large order or superorder to include all the large Amphibia, Embolomerous, Rachitomous, and Stereospondylous, for which the old term Labyrinthodontia may be used in an extended sense.

The classification of these animals will stand as follows :—

Order *Labyrinthodontia.*

Amphibia with a roofed skull, a lower jaw consisting of at least eight bones on each side, and vertebræ consisting of neural arches and intercentra in all forms, with pleurocentra in addition in most.

Grade *Embolomeri.*

Labyrinthodonts with large well-ossified basi-occipital and basisphenoid. Occipital condyle single or triple. Pterygoids with a large palatal part, articulating by movable facets with definite basipterygoid processes of the basisphenoid. Interpterygoid vacuities very small. Tabulars and dermosupra-occipitals without occipital extensions.

Vertebræ embolomerous, *i.e.*, with pleurocentra and intercentra complete discs.

Grade *Rachitomi.*

Labyrinthodonts with ossified basioccipital and basisphenoid. Occipital condyle triple or double. Pterygoids usually with a medium sized palatal part, interpterygoid vacuities of medium to large size. Pterygoids articulating with both parasphenoid and basisphenoid.

Tabulars and dermosupra-occipitals with occipital flanges. Paroccipital always visible from behind.

Vertebræ rachitomous, *i.e.*, with small paired pleurocentra and half-moon-shaped intercentra.

Family *Eryopidæ*, Cope.

Rachitomi with not very depressed skulls, orbits small and far back, pterygoids reaching the prevomers, interpterygoid vacuities of medium size, definite basipterygoid processes. Occipital condyle triple. Clavicles not expanded on the ventral surface. Pubis ossified.

Eryops, Cope; Artinskian, Texas.

Parioxys, Cope; Artinskian, Texas.

Onchiodon, Geinitz; M. Rothliegende, Saxony.

Family *Actinodontidæ*, nov.

Rachitomi with not very depressed skulls, orbits small and in the middle of the skull, interpterygoid vacuities of medium size, definite basipterygoid processes. Occipital condyle triple. Clavicles expanded on the ventral surface, pubis ossified.

Actinodon, Gaudry; Lower Permian, France, Saarbruck.

Sclerocephalus, Goldfuss; L. Permian, Bavaria.

Chelydosaurus, Fritsch; L. Permian, Bohemia.

? *Osteophorus*, H. v. Meyer; L. Permian, Silesia.

Family *Rhinesuchidæ*, nov.

Rachitomi with somewhat depressed skulls, orbits small and far back, pterygoids not reaching the prevomers, interpterygoid vacuities of large size, no definite basipterygoid processes. Occipital condyle double. Clavicles expanded. Pubis ossified.

Rhinesuchus, Broom; M. Permian, Cape Province.

"*Myriodon*," v. Hoepen; U. ? Permian, Orange Free State.

Laccocephalus, Watson; U. Permian or L. Trias, Orange Free State.

Family *Achelomidæ*, nov.

Rachitomi with a high skull with a narrowed muzzle; orbits large and in the centre of the skull. Otic notches obliterated.

Acheloma, Cope; Artinskian, Texas.

Family *Dissorophidæ*, Boulenger.

Rachitomi with a dorsal dermal armour. Skull high, short, with large orbits in the middle of its length and large laterally placed otic notches.

Interpterygoid vacuities of medium size. Definite basipterygoid processes. Occipital condyle triple or double ? Clavicles not expanded. Pubis ossified.

Sub-family *Aspidosaurinæ*, Williston.

With the otic notch not closed behind.

Aspidosaurus, Broili; Artinskian, Texas.

Alegeinosaurus, Case; Artinskian, Texas.

Broiliellus, Williston; Artinskian, Texas.

Sub-family *Dissorophinæ*, Williston.

With the otic notch closed behind.

Cacops, Williston, Artinskian, Texas.

Dissorophus, Cope; Artinskian, Texas.

Zygosaurus, Eichwald; M. Permian, Russia.

Family *Trematopsidæ*, Williston.

Rachitomi with a high skull, contracted muzzle, orbits in the middle of its length, enlarged nostrils, an inter-premaxillary opening, small dorsally placed closed otic notches.

Interpterygoid vacuities of medium size. Definite basipterygoid processes.

Occipital condyle triple ?

Clavicles not expanded, pubis ossified.

Trematops, Williston; Artinskian, Texas.

Family *Zatrachydæ*, Williston.

Rachitomi with a depressed skull, orbits small and far back. A very large internasal opening; small otic notches. Interpterygoid vacuities of medium size. Occipital condyle double?

Neural spines of vertebræ elongated and ornamented.

Zatrachys, Cope; Artinskian, Texas.

Dasyceps, Lloyd; L. Permian, England.

Platyhistryx, Williston; L. Permian, New Mexico.

Family *Archegosauridæ*, Fritsch.

Rachitomi with a much elongated skull, orbits small and far back. Pterygoids reaching the prevomers, interpterygoid vacuities of medium size, definite basipterygoid processes. Occipital condyle triple, only ossified in old individuals. Clavicles expanded on lower surface. Pubis not ossified.

Archegosaurus, Goldfuss; Lower Permian, Germany, ? Kashmir.

Family *Trimerorachidæ*, Cope.

Rachitomi with depressed skulls, orbits small and far forward. Interpterygoid vacuities of considerable size, apparent basipterygoid processes formed by the parasphenoid. Occipital condyle triple. Clavicle expanded. Pubis unossified.

Trimerorachis, Cope; Artinskian, Texas.

Family *Lydekkerinidæ*, nov.

Rachitomi with depressed skull, orbits small and in the middle of the length.

Interpterygoid vacuities large, no definite basipterygoid processes. Occipital condyle double. Clavicle expanded, pubis unossified.

Lydekkerina, Broom; L. Trias, Orange Free State.

Family *Micropholidæ*, nov.

Small Rachitomi with a depressed skull. Large laterally placed orbits and otic notches. Interpterygoid vacuities very large. Definite basipterygoid processes. Occipital condyle double. Clavicle not expanded.

Micropholis, Huxley; L. Trias, Cape Province.

Family *Dwinasauridæ*, nov.

Rachitomi with a broad skull, small dorsally placed orbits. Small otic notches. Interpterygoid vacuities large. No definite basipterygoid processes. Occipital condyle triple? Clavicle not expanded.

Dwinasaurus, Amalitzki; U. Permian, Russia.

Rachitomi incerta sedis.

Sparagmites, Fritsch ; Discosaurus, Credner ; *Cochleosaurus, Fritsch ; Melosaurus, v. Meyer ; Calcosaurus, v. Meyer ; and *Platyops, Trauschold.

Those starred are definitely distinct families.

Grade *Stereospondyli.*

Labyrinthodonts with reduced basi-occipital and basisphenoid. Occipital condyle double. Pterygoids with a reduced palatal ramus, interpterygoid vacuities large or very large. Pterygoids supported by the parasphenoid. Exoccipital meeting the occipital flange of the tabulars so as to hide the paroccipital in an occipital view.

Vertebræ stereospondylous, *i.e.*, with very reduced or absent pleurocentra and large intercentra.

Family *Capitosauridæ*, nov.

Stereospondyls with elongated skulls with a comparatively broad snout. Orbits small, near the middle line and far back.

Capitosaurus, Munster ; Lower Trias, Germany, S. Africa.

Cyclotosaurus, Fraas ; Upper Trias, Wurtemberg, England, South Africa (?), New South Wales.

Family *Trematosauridæ*, nov.

Stereospondyls with relatively high skulls with narrow elongated snouts. Orbits of small or medium size, placed laterally. Processus cultriformis of the parasphenoid very narrow. Posterior end of the parasphenoid carried very far back and with the pterygoid forming a floor to the middle ear region.

Trematosaurus, Braun ; L. Trias, Germany.

Trematosuchus, Watson ; L. Trias ?, S. Africa.

Lyrocephalus, Wiman ; M. Trias, Spitzbergen.

Lonchorhynchus, Wiman ; M. Trias, Spitzbergen.

Aphaneramma, A. S. Woodward ; M. Trias, Spitzbergen.

Platystega, Wiman ; M. Trias, Spitzbergen.

Tertrema, Wiman ; M. Trias, Spitzbergen.

Family *Metoposauridæ*, nov.

Stereospondyls with broad elongated skulls. The orbits small and very anteriorly placed. The palatal surface nearly flat. The processus cultriformis very broad. Quadrate foramen very large.

Metoposaurus, Lyd. ; U. Trias, Wurtemberg and Alps.

Anaschima, Branson ; U. (?) Trias, Wyoming.

Family *Mastodonsauridæ*, nov.

Stereospondyls with triangular skulls with enlarged orbits placed close together.

Mastodonsaurus, Jaeger ; M. and U. Trias, Wurtemberg.

Family *Brachyopidæ*, Broom.

Stereospondyls with short parabolic skulls, orbits of medium or large size placed anteriorly. Pterygoids turned downwards at the sides so that the palate is trough shaped.

Brachyops, Owen ; L. Trias (?), India.

Bothriceps, Huxley ; (?), New South Wales.

Batrachosuchus, Broom ; L. (?) Trias, Cape Province.

Plagiosternum, Fraas ; M. Trias, Wurtemberg.

Plagiosaurus, Jaekel ; U. Trias, Germany.

I have to acknowledge my indebtedness to the following gentlemen and institutions, through whom I was enabled to make the observations recorded in this paper :—

To Mr. WALKER, of Watford, Dist. Albert, Cape Province, S. Africa, I am indebted for the opportunity of collecting the Capitosaurus skull, study of whose structure provided the key to that of all other Stereospondyls.

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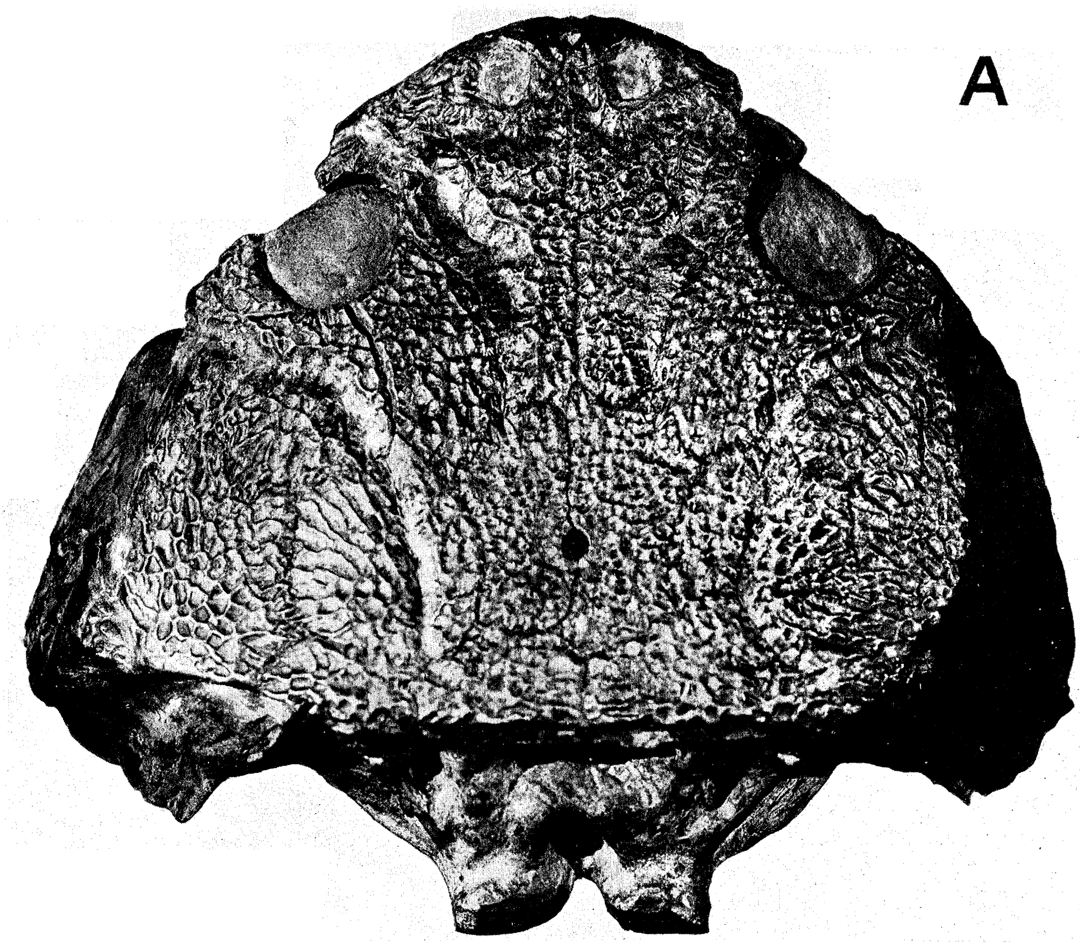

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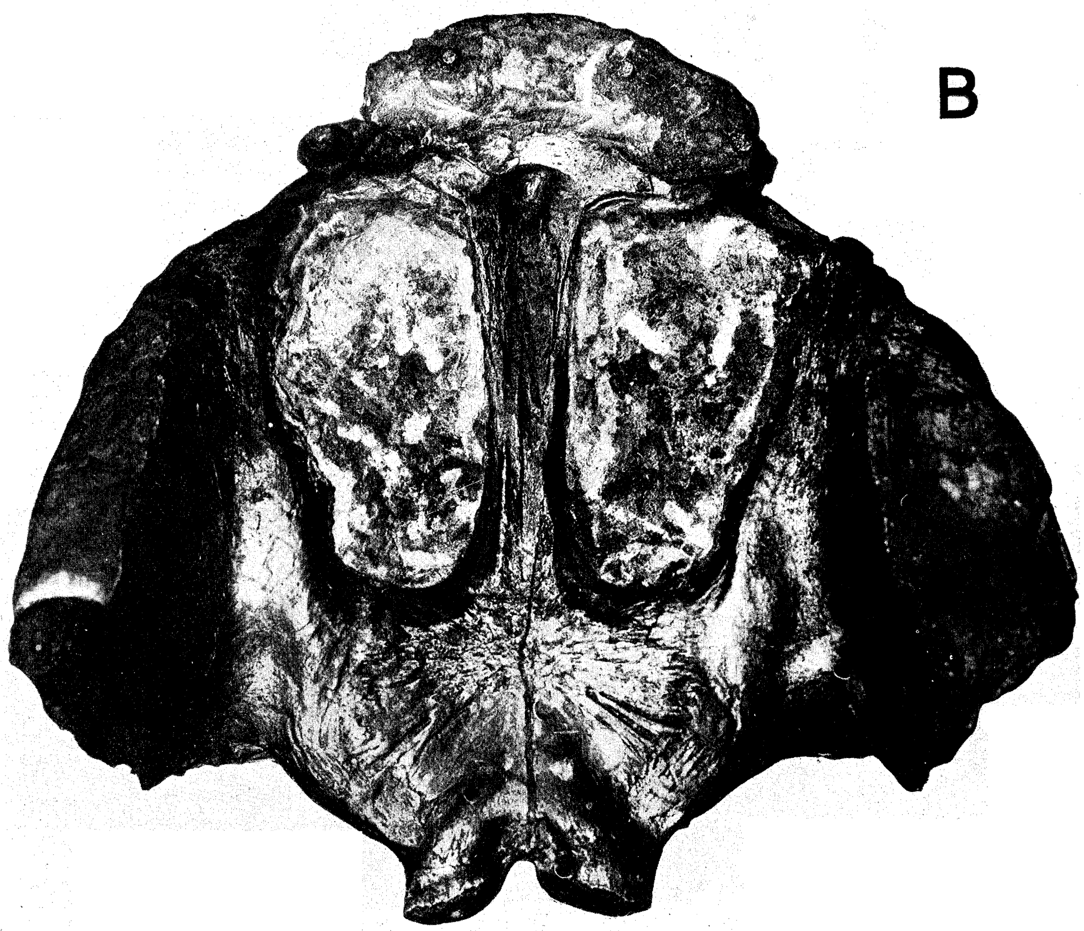

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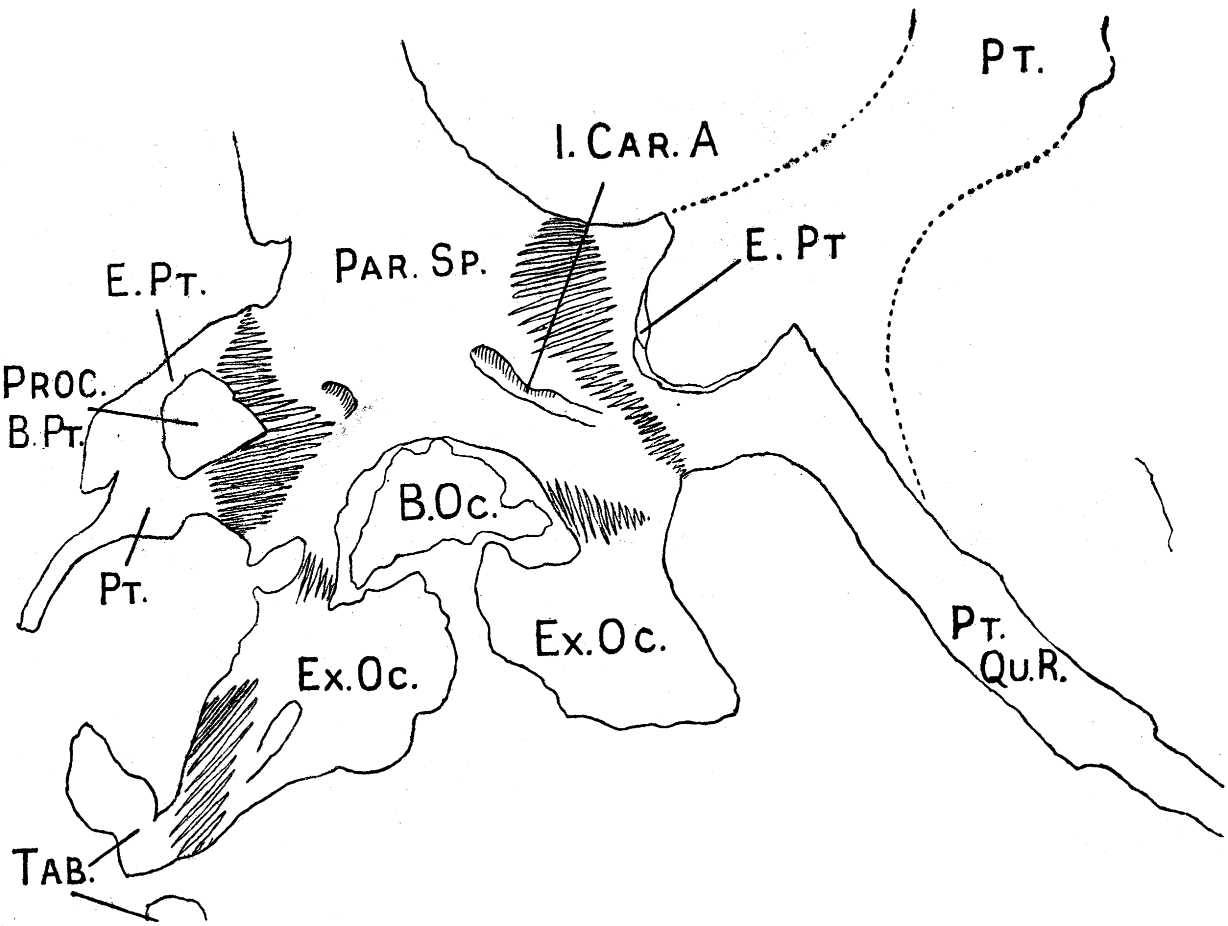
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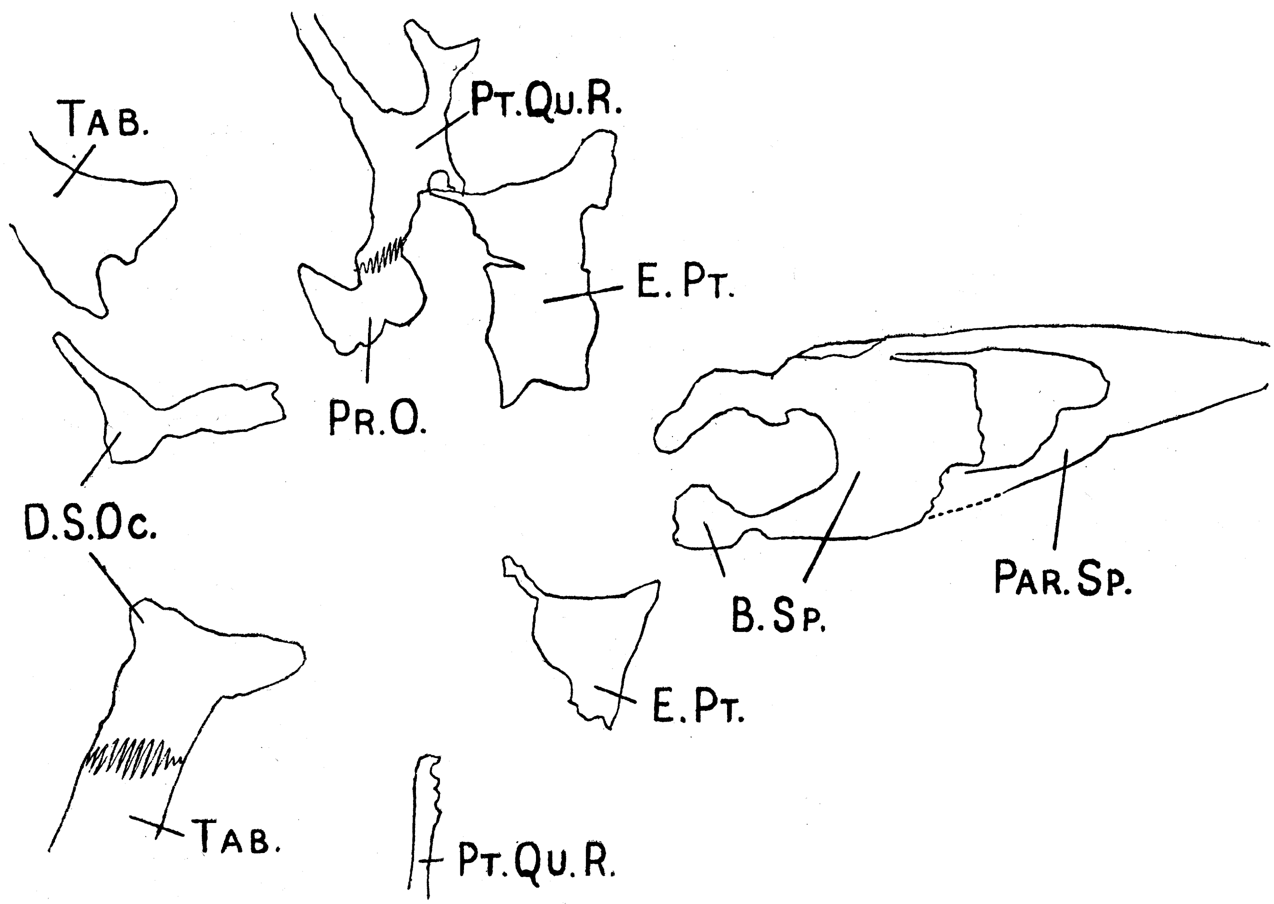
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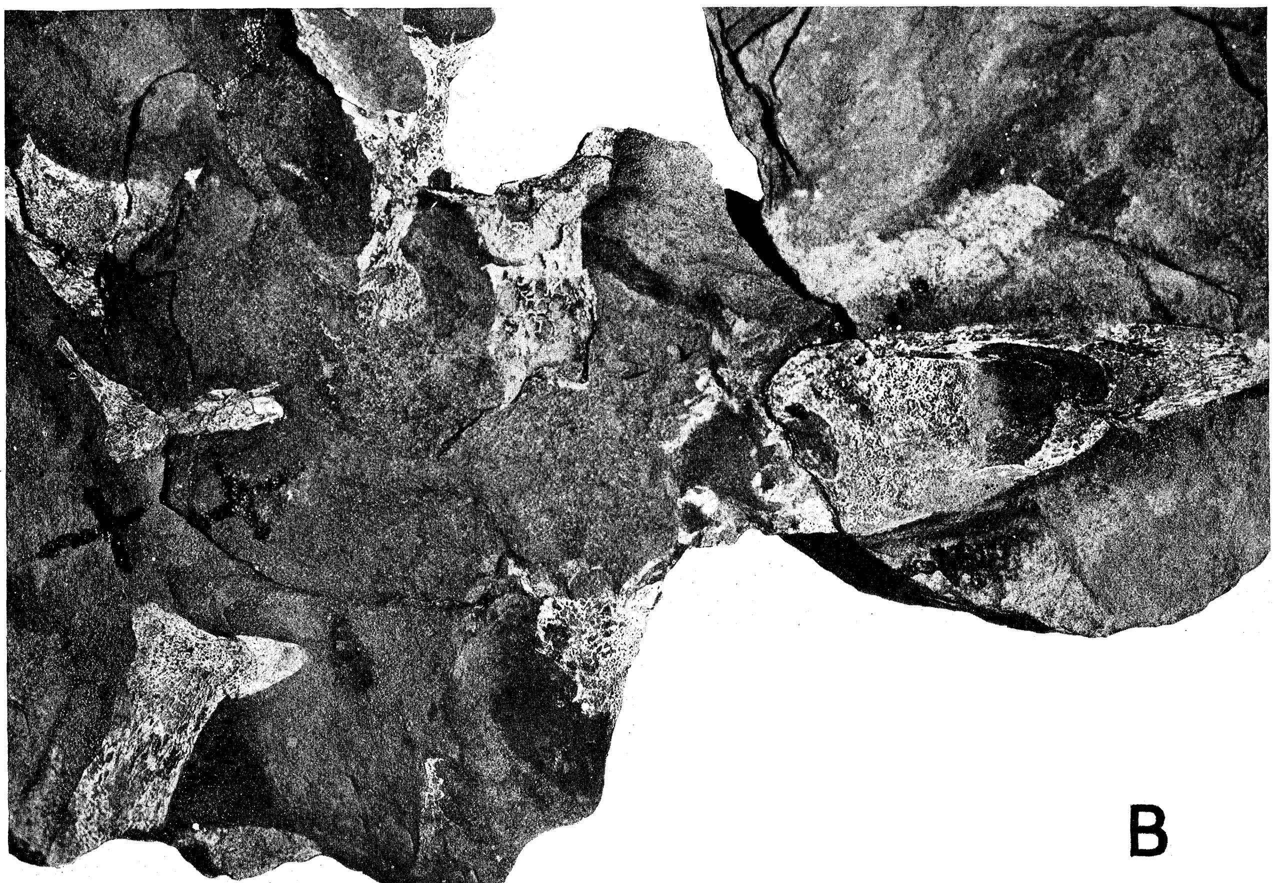

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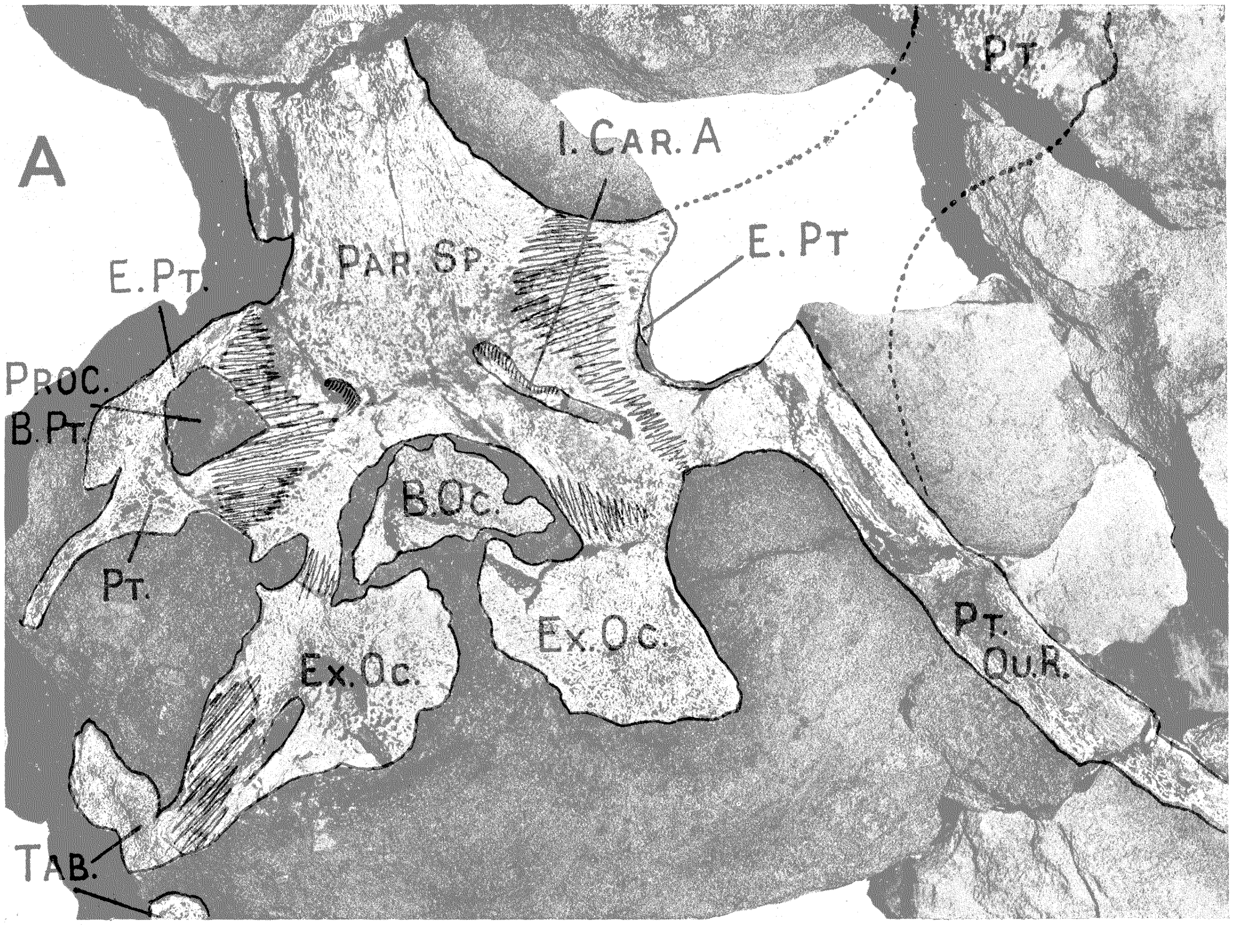
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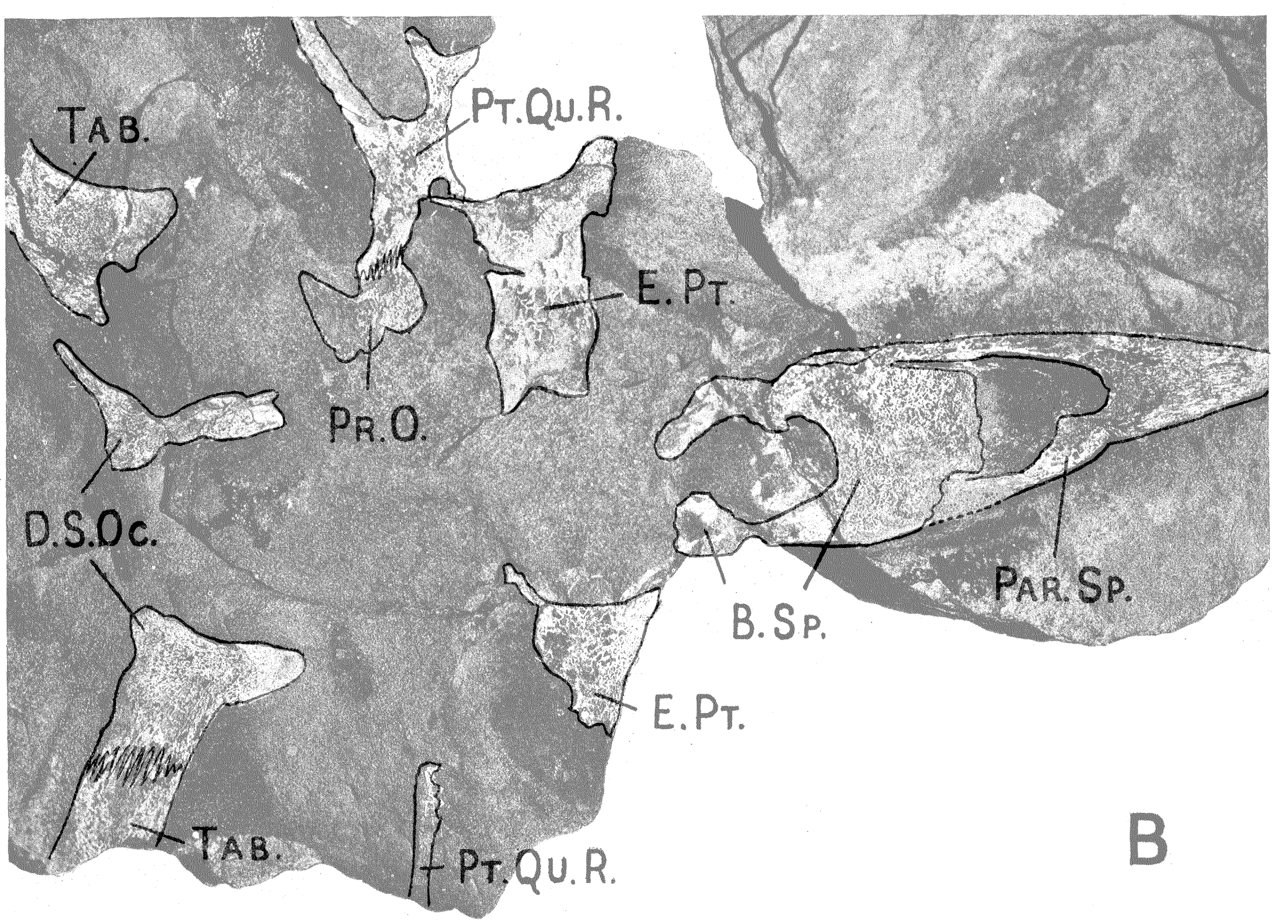
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EXPLANATION OF PLATES.

PLATE 1.

Batrachosuchus sp. Cynognathus zone, South Africa.

Skull, No. R. 3589, B.M.N.H. from the dorsal and palatal aspects. $\times \frac{1}{2}$ approx.

PLATE 2.

Laccocephalus insperatus, gen. et sp. nov.

Type Specimen, No. R. 532, from "near Mr. Hope's Farm," Orange Free State.

Upper figure. Photograph of the posterior part of the palate from below shown on a fractured surface.

B.OC., basioccipital; E.PT., epipterygoid; EX.OC., exoccipital; I.CAR.A., canal for the internal carotid artery; PAR.SP., parasphenoid; PROC.B.PT., cavity for a cartilaginous basipterygoid process; PT., pterygoid; PT.QU.R., quadrate ramus of the pterygoid.

Lower figure. Photograph of the bones of the brain case seen from above on a fractured surface.

B.SP., basisphenoid; D.S.OC., dermo-supraoccipital; E.PT., epipterygoid; PAR.SP., parasphenoid; PR.O., pro-otic; PT.QU.R., quadrate ramus of the pterygoid; TAB., tabular.

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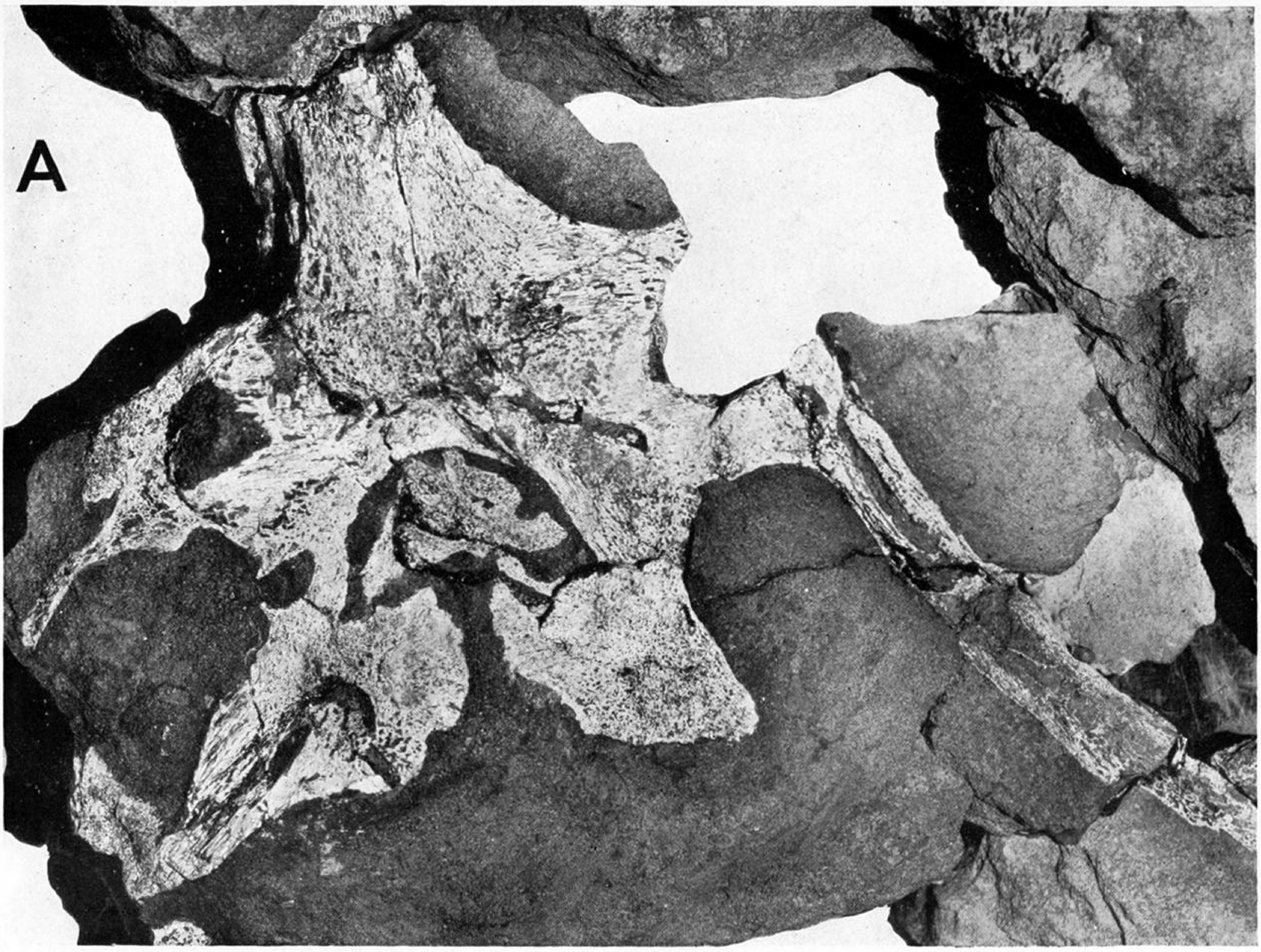
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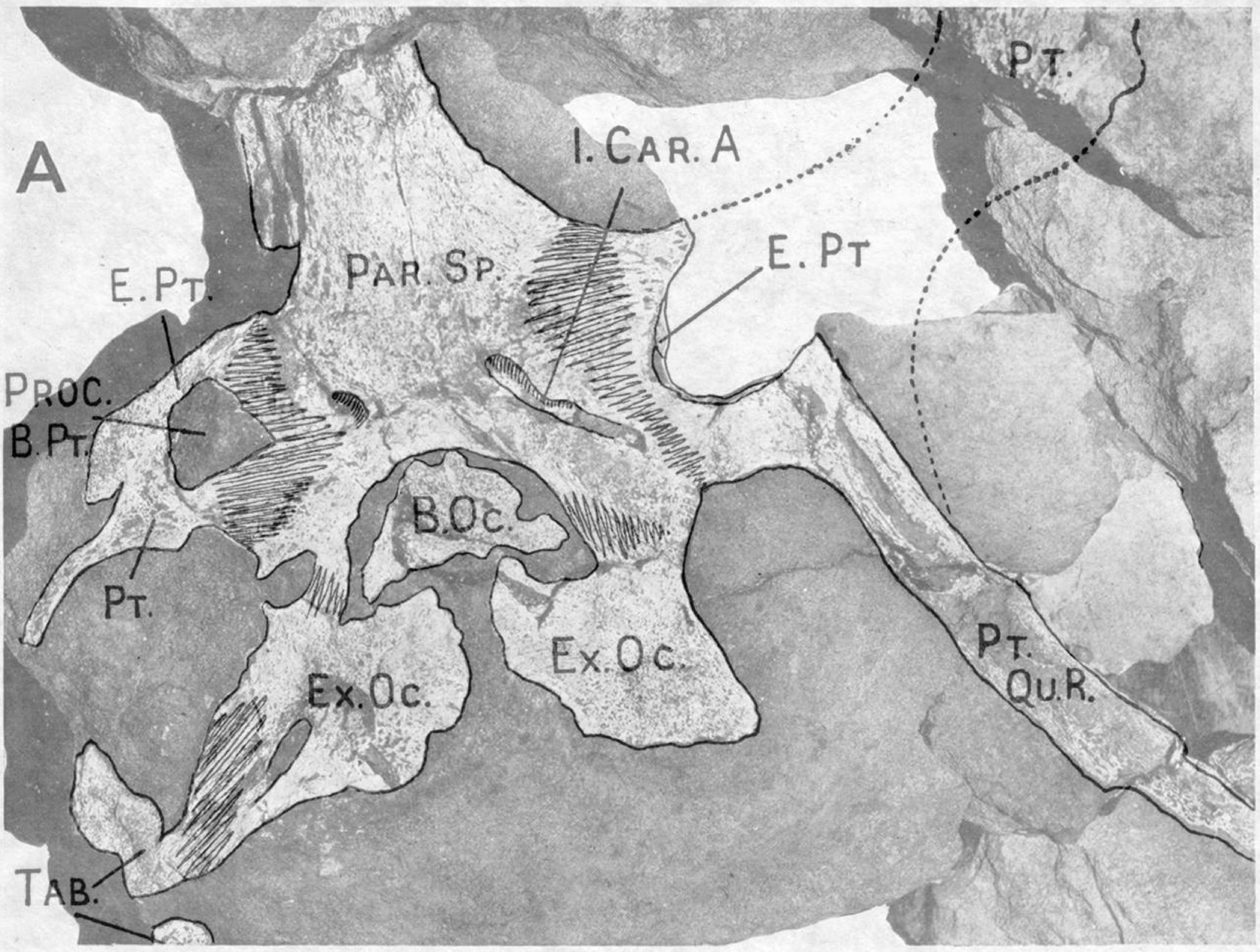

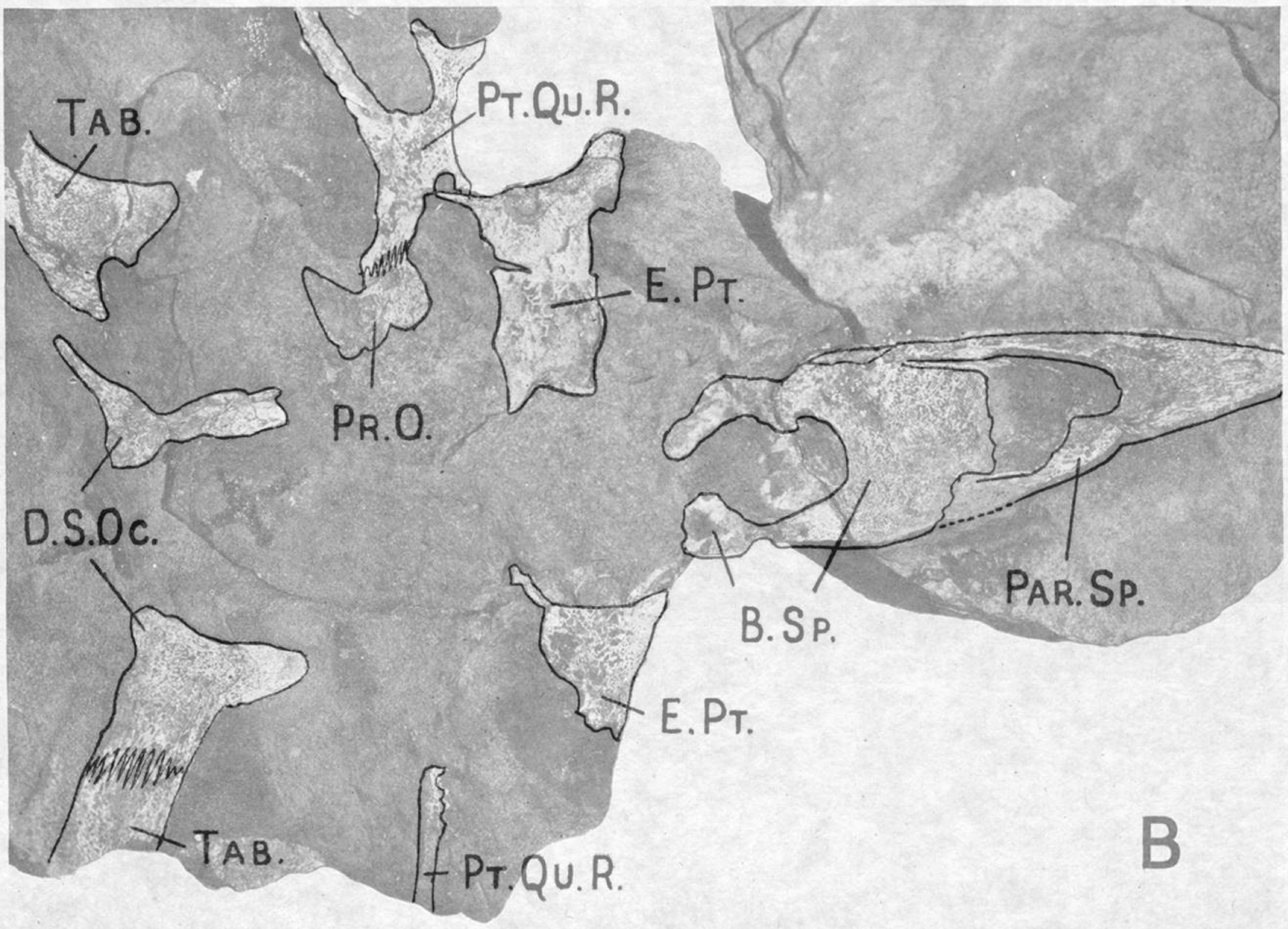

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