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EDOPS, A PRIMITIVE RHACHITOMOUS AMPHIBIAN
FROM THE TEXAS RED BEDS

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ABSTRACT

A description is given of the skull and such postcranial material as is known of *Edops craigi*, a large labyrinthodont amphibian from the Wichita Permo-Carboniferous beds of Texas. The structure of the *Edops* skull shows this form to be a very primitive member of the Rhachitomi, approaching the embolomerous stage in many structural features.

INTRODUCTION

It was long assumed that the only large amphibian present in the Permo-Carboniferous deposits of the Texas region was the familiar *Eryops*. Some years ago, however, the senior author, while exploring horizons lower than those usually visited by collectors found remains of a rhachitomous amphibian of large size. While exceedingly fragmentary, they obviously represented a form markedly different from *Eryops*; this was described, in preliminary fashion, as *Edops craigi*.¹

The finding of further remains of *Edops* was made a special object of an expedition to these beds by the authors in 1936. By good fortune a specimen was discovered which included a nearly complete

¹ A. S. Romer, "Studies on American Permo-Carboniferous Tetrapods," *Problems of Paleontology*, Vol. I (1936), pp. 85-93.

skull, which forms the basis for much of the description given below. In the course of other recent collecting trips by the Museum of Comparative Zoölogy still other remains have been found. The materials now available include the following specimens:

M.C.Z. 1378.—Most of skull and jaws and a few postcranial fragments. Remains mixed with those of an *Eryops* of smaller size. Terrapin School, Archer County, Texas; Moran Formation. Collected by R. V. Witter. Our skull descriptions are based on this specimen.

M.C.Z. 1235.—Fragmentary remains of skull and jaw and a few postcranial fragments; including valuable jaw and brain-case material. Padgett, Young County; Moran Formation. Collected by L. I. Price and T. E. White.

M.C.Z. 1453.—A large quantity of fragmentary material, collected by various expeditions. Head of Cottonwood Creek, Archer County; Moran Formation.

M.C.Z. 1782.—A number of fragments collected by various expeditions. Padgett.

M.C.Z. 1781.—Humerus. Terrapin School. Collected by L. I. Price.

M.C.Z. 1770.—Partial skeleton of a small individual. Two and one-half miles east of Antelope, Jack County; Pueblo Formation. Collected by L. I. Price and A. S. Romer.

M.C.Z. 1769.—A few remains in a difficult matrix. Same data as for *M.C.Z. 1770*.

Preparation and study of these materials now enables us to give a moderately adequate account of the cranial osteology of *Edops* and some data on the postcranial skeleton. Despite the lack of complete associated material, the identification of fragmentary pieces and isolated elements has not proved difficult in most cases. The nearly complete skull of No. 1378 has rendered easy the recognition of cranial materials. The identification of isolated postcranial elements is somewhat more hazardous. However, except for *Eryops*, all remains of large amphibians in the horizons concerned include, for each element, only a single structural type. In a number of cases the elements are definitely comparable to those of *Edops* specimens Nos. 1235 and 1770. It is therefore reasonable to assume that this material in general pertains to this genus.

The stratigraphic occurrence of *Edops* is not without interest.² Most Texas red-beds collections have been obtained from a series of formations which include the Admiral, Belle Plains, Clyde and Arroyo (in ascending order). In these deposits *Eryops* is exceedingly common, but no trace of *Edops* has ever been found. Below the Admiral are three other formations—Putnam, Moran, and Pueblo, in descending order—which have recently been explored by the Museum of Comparative Zoölogy. (Below this there is a rapid change to marine strata without fossil vertebrates.) In these formations fossils are relatively rare but of interest in that the fauna is rather different from that in higher formations, although a number of familiar types, such as *Eryops*, are present. It is in these deposits that *Edops* occurs. It has not been found thus far in the Putnam. In the Moran, however, it appears to be a common element in the fauna; its remains constitute a large proportion of materials collected from this horizon. In the Pueblo, fossil finds are extremely limited; but, even so, *Edops* is definitely identified from this formation. It seems clear that *Edops* is a component of an early faunal radiation of rhachitomous amphibians and is essentially a Carboniferous rather than a Permian type.

GENERAL DESCRIPTION

SKULL

General structure.—The description and figures are essentially based on No. 1378. This specimen was found broken into numerous fragments. Certain portions were not recovered, but the entire roof structure is determinable except for the tip of the snout; and even here the contour can be inferred readily from that of the lower jaw. The palate is fragmentary; the brain case is nearly perfectly preserved.

Although crushing has flattened the cheek region and introduced some uncertainty in measurements there, the general proportions can be readily determined. The skull is remarkable for its size. The length, as restored, is 63 cm. to a line through the quadrates and 51

² Romer, "Early History of Texas Red Beds Vertebrates," *Bull. Geol. Soc. Amer.*, Vol. XLVI (1935), pp. 1597-1658. In current geological discussions of Texas stratigraphy various suggestions of revision of nomenclature have been advocated; these, however, do not alter the essential picture.

cm. to the occipital condyle; the greatest width as preserved is 48 cm. and was in life presumably about 45 cm. The size is greater than that of any other pre-Triassic amphibian familiar to us. In the red beds, *Eryops* is the nearest competitor; but, of a series of skulls measured by H. J. Sawin,³ the largest measures only 52.5 cm. in greatest length and most are markedly smaller. The skull illustrated is probably close to maximum size; the more fragmentary remains of other skulls in general indicate individuals of smaller proportions.

The proportions are not far from those of *Eryops* and approximate those which Watson believes characteristic of generalized labyrinthodonts. The width is about 70 per cent of the total length, as compared with about 75 per cent in *Eryops*, 80 per cent in *Palaeogyrinus*, about 75 per cent in *Pholidogaster*, etc. The slightly lower figure is to be correlated, perhaps, with the relatively long posterior extension of the suspensorial region. In *Edops* the distance to the tip of the quadrate exceeds that to the condyles by about 10 per cent. In *Eryops* the suspensorium is shorter posteriorly; and still further shortening occurs in more "advanced" rhachitomous forms and stereospondyls; D. M. S. Watson⁴ has discussed the functional significance of this shortening. On the other hand, the posterior extension of the *Edops* suspensorium is rather less than that seen in a number of Carboniferous forms, presumably still more primitive in nature.

In *Edops* the distance from snout to center of orbits is about 60 per cent of the length of the skull roof; the eyes are thus somewhat posteriorly placed, and the relative position is approximately that seen in *Eryops*, *Actinodon*, *Sclerocephalus*, *Palaeogyrinus*, *Pholidogaster*, etc. This condition seems reasonably interpretable as a primitive one for labyrinthodonts in general.

Because of post mortem crushing, the depth of the skull is difficult to determine. It seems probable that the skull is somewhat deeper than in *Eryops* and hence somewhat closer to primitive conditions.

³ "The Cranial Anatomy of *Eryops megacephalus*," *Bull. Mus. Comp. Zool.*, Vol. LXXXVIII, No. 5 (1941), p. 410.

⁴ "The Structure, Evolution and Origin of the Amphibia—the 'Orders' Rachitomi and Stereospondyli," *Phil. Trans. Roy. Soc. London*, Ser. B, Vol. CCIX (1919), p. 57.

Roofing bones.—To depict the skull roof (Fig. 1) we have chosen a photograph of a cast rather than the specimen itself, since the coloration of the original does not lend itself well to photography. The course of the sutures is indicated by India-ink lines. The skull was so cracked and checked in various areas that determination of sutures was by no means an easy task. While we have confidence that the

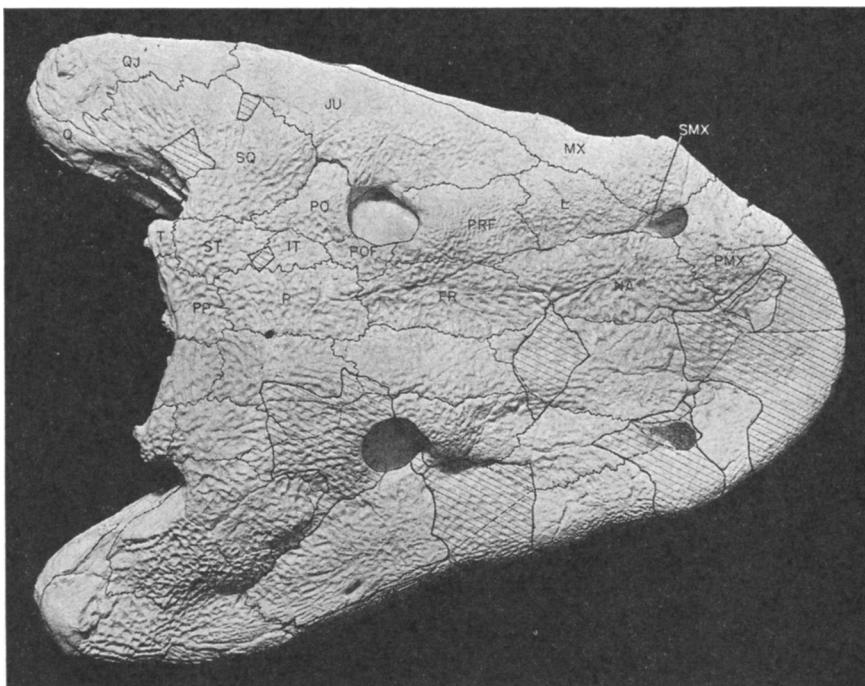


FIG. 1.—Dorsal view of skull. $\times \frac{1}{6}$. Photograph of cast. Restored areas are indicated

sutures indicated are for the most part accurate, it is quite possible that certain details may be erroneous. Most of the sutures have been confirmed by study of the lower surface.

In general the sculpture is of the common labyrinthodont type. It is rather coarse, with areas of finer sculpturing occurring along the dental margins and along a band from orbit to the lateral margins of the nares. There are no indications of lateral-line canals. The roof is somewhat concave along the mid-line, with high ridges along the upper margins of the orbits, where the bone is much thickened;

there is an especially thick and elevated area in the prefrontal region, lateral to which is a marked depression near the prefrontal-jugal suture. Ridges extend anteriorly from the prefrontal thickenings toward the snout and diverge anterolaterally along the lacrimals. Prominent swellings are present on the maxilla external to the nares. These swollen areas are the most massive pieces of bone in the skeleton and have been found isolated on various occasions.⁵

The general region of the tabulars is thickened and swollen, and from the posterior margins of these bones project rounded processes comparable to those seen in loxommids. The otic notch is typically developed, with a well-rounded anterior margin, and, in contrast with presumed primitive conditions, there is a firm union of cheek and table anterior to the notch.

The external nares open as much posteriorly as directly dorsally, the openings being at the anterior end of grooves developed in the septomaxillae. The naris is in great measure bounded by the septomaxilla, although the premaxilla forms the roof of the actual opening; neither maxilla nor lacrimal enters into its margins.

In many respects the pattern of the skull elements follows the "normal" pattern of generalized labyrinthodonts and need not be considered in detail. There is no median interfrontonasal element of the type found in *Eryops*. The postparietals (dermal supraoccipitals) extend far laterally, and the tabulars are small so that there is a broad supratemporal-postparietal contact. The septomaxilla is presumably primitive in that it has a well-developed sculptured surface exposure posterior to the external naris. The lacrimal is of a common rhachitomous type, well developed but not reaching the orbit; it is excluded from the naris because of the presence of a superficial portion of the septomaxilla. The squamosal extends far laterally, and the jugal and quadratojugal meet only in a relatively short transverse suture. The maxilla extends posteriorly to meet the quadratojugal in a short suture. The postfrontal is small.

An unusual feature is the presence of an intertemporal, rare in nonembolomerous forms. This is preserved only on the left side. Its outlines have been carefully checked by a study not only of the outer

⁵ It was incorrectly assumed in the type description that these swellings were premaxillary in position.

surface but of the inner face of the bone, radial growth striations, and the sections shown on the breaks in the specimen. As usual, it occupies the general area covered by the posterior part of the prefrontal and the anterior part of the supratemporal when the intertemporal is absent.

The sutures between various skull-roof elements are seen from the inner side in Figure 2, although portions of the sutures are concealed

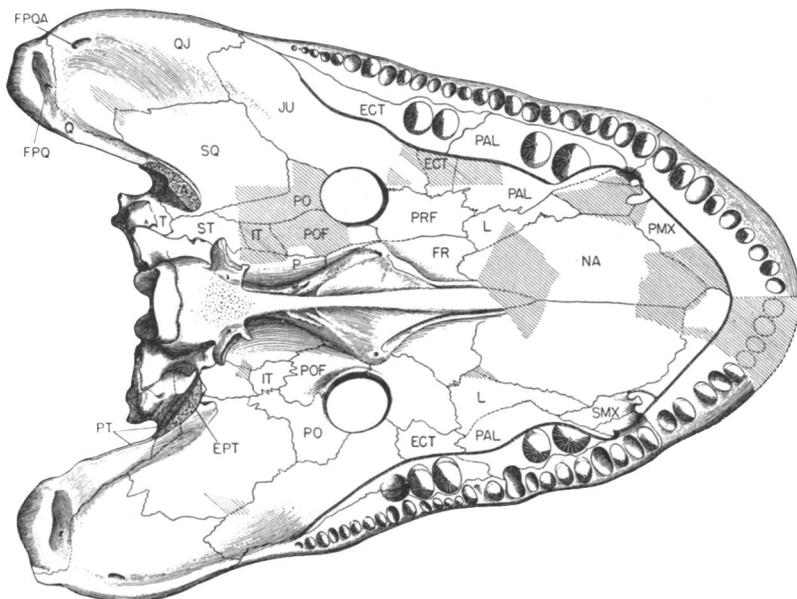


FIG. 2.—Ventral view of dermal roof. $\times \frac{1}{6}$. The palatal elements have been removed, except for their thickened lateral portions. Restored areas shaded. On the right side (*upper side*) the pterygoid and epipterygoid have been removed in their entirety, showing the rough ventral articular surface of the descending squamosal buttress (*A*). On the opposite side the section is at a more ventral level, showing the thickened portion of the epipterygoid which articulates with this flange and the thin sheet of pterygoid which lies posteromedial to it.

by the brain case and the more lateral portions of the roof are in part covered ventrally by palatal elements. It will be noted that in a number of instances there are marked overlaps, so that the internal sutural pattern differs considerably from that seen externally.

Palate and palatoquadrate complex (Figs. 3-6).—In the skull described much of the palate was preserved but broken into pieces,

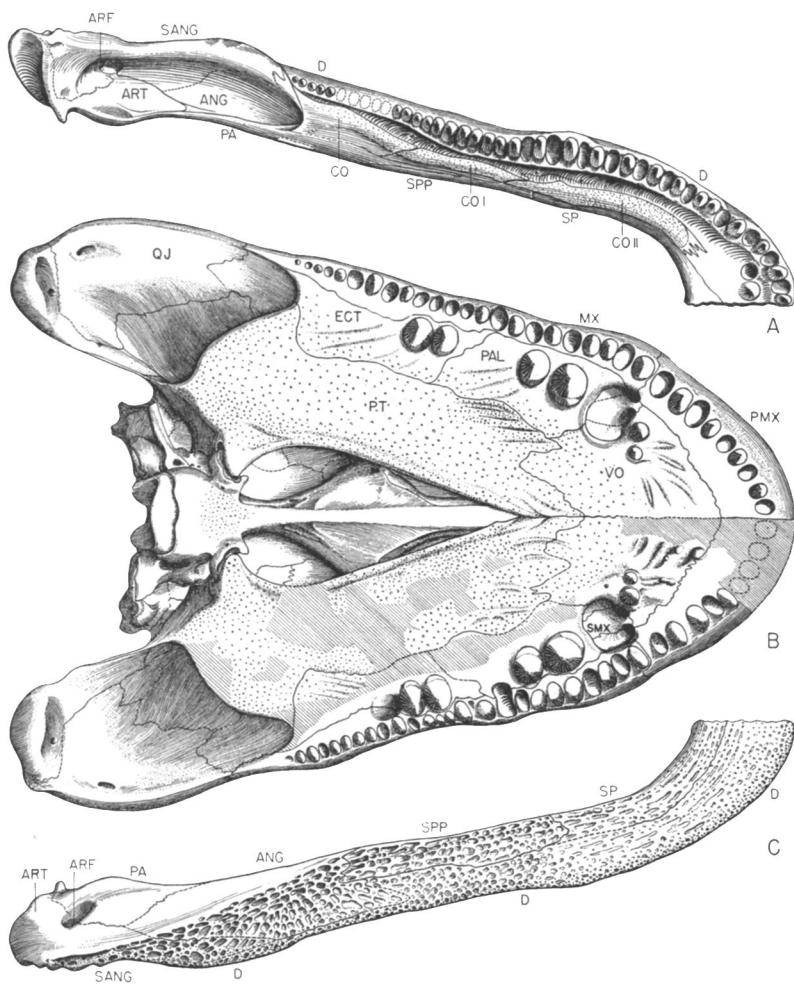


FIG. 3.—*A*, dorsal (internal) view of lower jaw. Crosses mark the position of upper-jaw fangs. *B*, palate; on the left (*lower*) side, only the known portions of the palate are indicated, the remaining areas hatched; on the opposite side the palate has been freely restored. Whether or not vacuities existed anteriorly for the anterior dentary fangs is uncertain. *C*, ventral (external) view of lower jaw. All $\times \frac{1}{6}$.

which were fitted with difficulty. On the left side of the palate in Figure 3, *B*, are shown those portions present in this specimen; on the right is an attempt at restoration of the entire structure.

Laterally are seen the ventral surfaces of marginal roofing elements—premaxilla, maxilla, and quadratojugal (the jugal does not enter the lower margin). The maxilla has little exposure beyond the marginal tooth row. The premaxilla has a moderate ventral exposure. The region of the median suture between the two premaxillae is not preserved, and hence one cannot be sure whether the pit or vacuity characteristic of this region in many labyrinthodonts for the accommodation of lower-jaw teeth was present or not; since, however, each jaw ramus bears a well-developed tooth pair here, such a pit may well have existed.

The marginal teeth are unusually large. They are subquadrate in basal contour and slant markedly outward toward the tips. Probably about 32–33 teeth were present in each ramus. The exact number in the premaxilla cannot be determined; the maxilla carried about 24. There is some evidence of the usual alternation of even and odd series of marginal teeth. The largest marginal teeth are those near the anterior end of the maxillary series, as in many early tetrapods; there is some suggestion of a secondary “peak” in tooth size farther back along the maxilla.

The general nature of the bony structures in the narial region may be seen from the palatal view and that of the under surface of the roof. The choanae are subcircular in outline and mainly bounded by the vomers and palatines, the maxillae form a small part of the outer wall, and the premaxillae barely enter the anterolateral corners. The inner half of the opening, mainly the vomerine portion, is a thickened rim of bone which has no connection with the roofing elements. Laterally the maxilla forms a continuous vertical wall; this wall is continued posteromedially by the palatines, which for much of their extent form a solid mass of bone extending dorsally to be firmly attached to the maxilla below the skull roof. As seen through the choana, the upper boundary of the choanal region is formed by the roofing elements, with the maxilla laterally, the nasal medially. Between the two is seen the ventral surface of the septomaxilla. As noted above, this bone dorsally becomes deeply grooved

toward its anterior end. The ventral surface, in corresponding fashion, develops a marked ridge anteriorly; this articulates at the anterior edge of the choana with the vomer. Between this point and the lateral margin there is a small opening leading forward to the region of the external naris. It will be noted that the external naris lies anterior to the position of the choana, and it is obvious that air in passing from surface to palate first passed forward and downward through the external naris and then had to be directed sharply backward to reach the choana. The lateral opening between septomaxilla and maxilla is too small to have accommodated such an air channel and presumably was utilized only by a branch of Nerve V and associated vessels; the air passage must have been medial to the septomaxilla. Unfortunately, the bones surrounding the nares have nearly smooth surfaces which give little evidence as to the structure of the cartilages of the nasal capsule. However, the undersurface of the roof shows a marked ridge, rounded in section, which crosses the middle of the septomaxilla and extends posteriorly and medially to the nasal; a second, less marked ridge lies posterior to and parallel to this on the lacrimal and nasal, and there is some evidence of a corresponding ridge on the adjacent upper surface of the palatine. These structures may indicate the posterior boundary of the nasal capsule.

The interpterygoid vacuities are notable for their small size; they are smaller than in any other described member of the Rhachitomi. Unique for this group is the structure at their anterior ends. In all other Rhachitomi their anterior margins are curved, and they are bordered here by the vomers with which the parasphenoid articulates. In *Edops* the anterior margins are V-shaped, and the two pterygoids meet in a median suture ventral to the anterior end of the parasphenoid. This is an embolomerous, rather than a typically rhachitomous, condition.

Three pairs of palatal fangs are present on each side of the palate, arranged, as is frequently the case in labyrinthodonts, as single pairs on vomers, palatines, and ectopterygoids. The palatine teeth are the largest of the series; the ectopterygoid teeth nearly as large; the vomerine pair much smaller.

In addition to these fangs, much of the palate is covered with a shagreen of smaller teeth. These cover most of the palatal aspect of

the pterygoid and extend on to the adjacent regions of the other bones. The skull illustrated showed a mass of partially ossified tooth-bearing tissue underlying the basal articulation, so that in life the tooth-bearing areas of pterygoid and parasphenoid appear to have been continuous in this specimen. In other smaller, and apparently less mature, specimens this tissue appears to be absent. A curious feature is the fact that the denticulation of the pterygoid is not restricted to the palatal aspect of the pterygoid but extends some distance on to the quadrate ramus of the bone (Fig. 4).

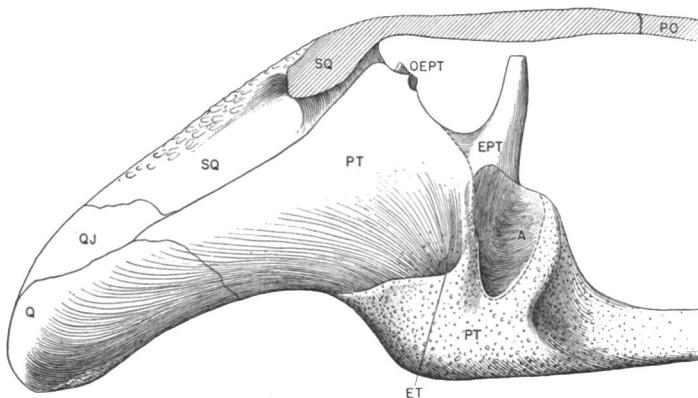


FIG. 4.—Medial view of the suspensorial region; the lateral wall of the skull omitted. $\times \frac{5}{8}$. The epipterygoid is in great measure concealed by the pterygoid; and the only parts visible are the tip of the otic process, the columnella cranii, and the concave articular surface (*A*) for the basipterygoid process.

The palatal elements show a series of low ridges which radiate from the fang pairs in the case of the lateral elements. Such ridges are also present on the adjacent portions of the pterygoid.

The median margin of the pterygoid is a thickened ridge adjoining the interpterygoid vacuity. The pterygoid flange is moderately thickened. Owing to the small size of the vacuities, the palatal rami of the pterygoids are broadly expanded. The vomer is a platelike structure with a thickened area beneath the fangs and a thickened rim extending back around the choana to the palatine articulation. This rim is pierced by a small foramen which passes forward from dorsal to ventral surfaces; presumably this carried a branch of the palatine nerve. Much of the palatines and ectopterygoids are thick

masses of bone which are in contact with the maxillae dorsally as well as laterally. In Figure 2 these elements are represented as if cut off medially close to the edge of the thickened portions. Palatine and ectopterygoid further send upward and medially thin flanges of bone, apparently rather variable in development, underlying the bones of the dermal roof. On the palatal surface palatine and ectopterygoid extend medially to articulate with the pterygoid and, in the case of the palatine, to meet the vomer behind the choana. On the dorsal surface of the palate the pterygoid is more restricted anteriorly, for both vomer and palatine considerably overlap it dorsally. On the other hand, the pterygoid overlaps the posteromedial border of the ectopterygoid to some extent dorsally.

As far as can be determined from sections seen in breaks in the material, a canal leading forward from the quadratojugal passes through the maxilla beneath the tooth row. Anteriorly this comes to lie between maxilla and the thickened portion of the palatine to open, funnel-shaped, into the posterolateral corner of the choana. The palatine is pierced medially by a foramen whose course cannot be definitely traced. These two openings have been interpreted by Säve-Söderbergh as filled by cartilaginous extensions of the nasal capsule. It seems more reasonable, however, to assume that the medial opening in the palatine carried nutrient vessels, while the funnel and the connecting canal in the maxilla contained the maxillary nerve and artery. The medial surface of the ectopterygoid is penetrated by a branching set of foramina which presumably afforded entrance for portions, at least, of the maxillary artery and nerve, although we have not determined the connections (if any) of these foramina with the longitudinal canal contained in the maxilla.

The broken condition of the palate makes it difficult to determine the possible extent of the cartilaginous palatal ramus of the palatoquadratus or the complete extent of the ossification of this ramus by the epipterygoid. This ossification, however, was unusually extensive for a rhachitomous amphibian, for one of the palatal fragments shows that the bone extended at least one-third of the distance forward from the region of the basal articulation to the narial region.

The thickest portion of the epipterygoid lies adjacent to the basal articulation. This element forms a deep socket for the reception of

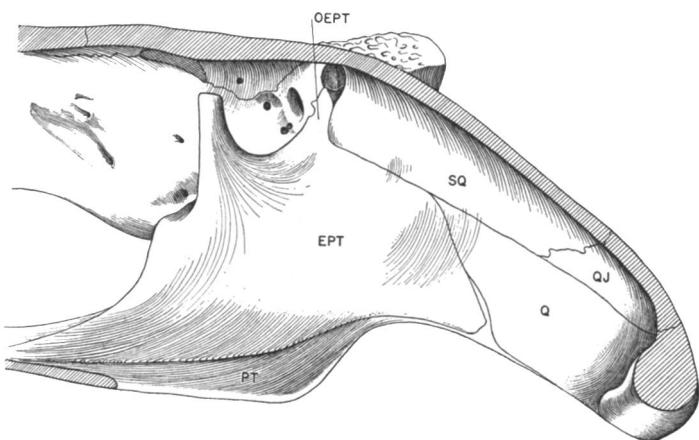


FIG. 5.—Lateral view of the suspensorial region, the dermal bones sectioned longitudinally through the quadrate. $\times \frac{2}{3}$.

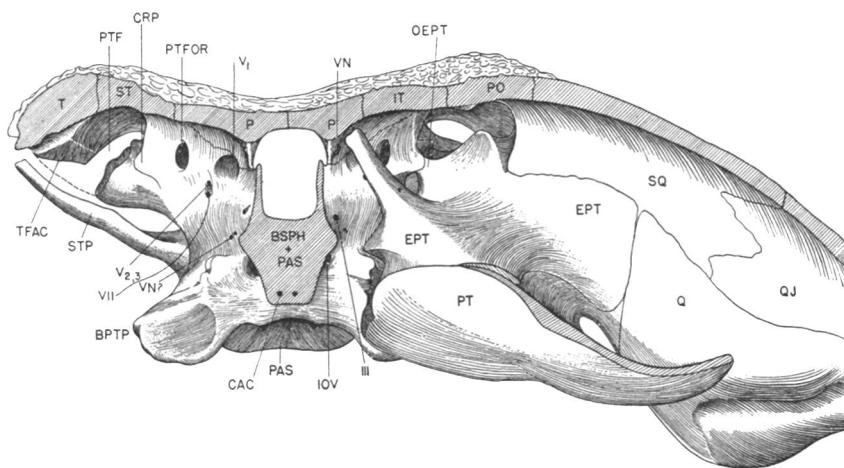


FIG. 6.—Anterior view of the posterior portion of the skull. $\times \frac{2}{3}$. The brain case is represented as sectioned just anterior to the pituitary fossa, and this transverse plane is continued to the right. On the left side of the figure the palatoquadrate has been removed and the roof sectioned diagonally backward to the otic-notch region. Details of the interior of the brain cavity are omitted. At the left the broken line indicates the ventral margin of the cartilaginous extension of the paroccipital process, which in life would have concealed the posttemporal fossa from view.

the basipterygoid; as in many early tetrapods, this socket includes two essentially plane surfaces approximately at right angles to one another, one surface facing downward and inward, the other rather dorsally and posteriorly, as well as inward. The epipterygoid socket is nearly completely surrounded by thick margins formed by the pterygoid. The two elements are well fused here but can be distinguished by differences in bone texture.

The epipterygoid has a well-developed ascending process, subcircular in section, which approaches but does not reach the dermal roof. More posteriorly there is a well-defined otic process which articulates over a very limited area with the parotic process of the otic capsule. Posterior to this point the epipterygoid rises still higher and thickens to present a broad dorsal surface which articulates with a thick buttress descending from the squamosal. Posteriorly the epipterygoid extends back as a wide but thin sheet of bone which gains a broad contact with the quadrate.

Applied medially to the epipterygoid is the still more expanded quadrate ramus of the pterygoid. In the region of the parotic process the pterygoid approaches the otic capsule closely, but there is no actual contact. There is a long contact dorsally with the squamosal and more posteriorly with the quadratojugal. Its distal portion overlaps medially the "otic" process of the quadrate. Just behind the basipterygoid articulation is a pronounced pocket in the medial surface of the pterygoid, which A. P. Bystrow and J. A. Efremov⁶ have termed the "excavatio tympanica." There is no well-defined indication of the crista obliqua, which both these authors and Säve-Söderbergh have noted on the quadrate ramus in advanced labyrinthodont types.

The relations of the squamosal to the suspensorial region are shown in somewhat diagrammatic sections in Figure 2. From the inner end of the squamosal descends a thick buttress with a broad ventral articular surface; more distally the articular surface becomes much thinner. The buttress is met ventrally by a thickened ascending process of the epipterygoid. This is bounded medially by a thin sheet of pterygoid, which fuses with the squamosal on the medial

⁶ "*Benthosuchus sushkini* Efr.: A Labyrinthodont from the Eotriassic of Sharjenga River," *Trav. Inst. Paleont. Acad. Sci. U.S.S.R.*, Vol. X (1940), pp. 1-152.

surface of the buttress. More distally, beyond the buttress, the area of epipterygoid articulation is reduced, and the contact of squamosal with pterygoid becomes broader.

The quadrate is well ossified, with a thickened articular portion and a long and relatively thin "otic process" which, as has been noted, is in contact with the epipterygoid, although there is no well-developed suture and cartilage tended to persist between them. The usual paraquadrate (quadrate) foramen was present and in addition an accessory paraquadrate foramen, noted otherwise, as far as I am aware, only in *Benthosuchus*.⁷ Unfortunately, the main skull described is badly fractured in this area, and there appears to be considerable variation in other available fragments of this region so that details here are somewhat uncertain. Apparently, however, the paraquadrate foramen lies mainly in the quadrate rather than between that bone and the quadratojugal. The accessory foramen enters the quadratojugal from the inner surface but does not reach the outer side. Instead, it continues as a canal, which passes forward through the thickened lower margin of the quadratojugal and, as suggested by sections seen in fractures, may be continuous with the canal present in the lateral margin of the maxilla. In one instance, at least, the two foramina are connected by a further canal lying within the substance of the quadratojugal. A. P. Bystrow⁸ has suggested that these foramina transmitted arterial vessels, but we do not feel certain of the details of his interpretation.

Brain case (Figs. 4-11).—The brain case is nearly completely preserved in No. 1378, and a number of fractures have fortunately allowed us to explore the internal surface. In many regions confirmatory evidence is afforded by other, more fragmentary remains. The side walls of the fore- and midbrain regions were somewhat damaged, but between the two sides almost the whole of this region could be satisfactorily determined.

The general proportions of the brain case are in many regards those seen in typical Rhachitomi, such as *Eryops*, with an expanded sphenethmoidal region, a constriction to a "waist" near the basi-

⁷ *Ibid.*

⁸ "Blutgefäßsystem der Labyrinthodonten," *Acta zool.*, Vol. XX (1939), Fig. 15.

pterygoid articulations, and a broad posterior expansion into otic and occipital regions. The brain case is, however, proportionately deeper, less platybasic, and hence closer to the presumed primitive type than in the flatter structural type seen in *Eryops* and later labyrinthodonts. Although it may be reasonably assumed that a number of ossification centers were present, there are no visible sutures except in portions of the occipital region.

As always, a well-developed parasphenoid is closely fused with the brain case ventrally. The cultriform process is little expanded anteriorly, and here the line of demarcation between parasphenoid and replacement bone of the brain case is readily visible. More posteriorly, the parasphenoid expands laterally so that it nearly completely ensheathes the basisphenoid core of the basipterygoid process (much as the pterygoid ensheathes the corresponding articular area of the epipterygoid). Posteriorly, the ventral portion of the parasphenoid ends with a broad free rim, of which the raised lateral corners are essentially tubera for the attachment of ventral neck musculature. The lateral borders of the parasphenoid behind the basipterygoid processes fuse into the sides of the otic capsule so that no definite boundary can be marked. The bone carries a shagreen of small teeth in the region adjacent to the basipterygoid processes; more anteriorly the surface is not preserved.

The dorsal surface of the brain case is nearly flat and for the most part has a complete roof beneath, and closely applied to, the dermal elements. In the supraoccipital region there is an unossified dorsal area, which was presumably filled by cartilage. In front of this region there is for a considerable distance a complete, although thin, roof in the position of a typical synotic tectum, and laterally this roof extends outward to cover the inner portion of the posttemporal fossa. More anteriorly there is a large fontanelle, reaching forward to the roots of the olfactory nerves. From this point forward the sphenethmoid region is solidly roofed, although in No. 1378 brain-case roof and dermal bones do not gain close contact for about 1 cm. anterior to this point. At the sides of the fontanelle region the brain-case walls do not reach the skull roof. Anteriorly and posteriorly the gap is closed by short descending flanges from the parietals; there persists, however, a longitudinal slit opposite part of the fore- and

midbrain regions, which may have afforded passage for Nerve IV and possibly a vein but appears to have been otherwise unimportant.

The sphenethmoid region is diamond-shaped, as seen in dorsal or ventral view. It is mainly a solid mass of bone, pierced by a pair of large divergent canals for the olfactory nerves; in contrast to *Eryops*, there is no subdivision of these canals. Anterior to the broadest portion of the sphenethmoid, these canals open into gradually fading grooves on the lateral surface of the bone. At its broadest portion the bone is pierced by short canals, which appear to have carried the profundus nerve forward into the ethmoid region. The brain case was obviously continued anteriorly and laterally in cartilage, the continuations of the curving lateral margins forming a planum antorbitale; as noted earlier, however, there are few data upon which to base any reconstruction of nasal and ethmoidal regions.

In *Eryops*⁹ the internal carotid artery, palatine artery, and palatine nerve appear to have passed forward beneath the basipterygoid process in a groove on the under surface. In *Edops* the latter two structures appear to have followed a similar course, but the internal carotid enters a foramen in the parasphenoid near the back margin of the basipterygoid process—a situation apparently present in a large proportion of the older amphibia. Thence the artery runs forward (as clearly seen in fragmentary specimens) between parasphenoid and basisphenoid, the two carotids converging but not meeting anteriorly. At a point somewhat anterior to the basipterygoid processes and pituitary fossa the carotids enter the primary carotid foramina, turning sharply upward in the substance of the basisphenoid to enter paired pockets beneath the forebrain, where branching occurs. Two pairs of openings from these pockets reach the surface of the sphenethmoid region, and the further, forward course of the contained vessels is indicated by grooves. The upper vessel presumably was an optic artery, the lower an ophthalmic (in contrast to the modern anuran condition of a single artery taking the place of these two).

There is a well-developed transverse canal of primitive type for the anastomotic (interorbital, pituitary, or hypophysial) vein con-

⁹ Cf. Sawin, *op. cit.*

necting the two surfaces of the brain case immediately anterior to the basipterygoid processes and curving slightly internally to pass just back of the pituitary fossa. In *Eryops* this channel is present in somewhat flattened form; in modern Anura it is absent, perhaps in relation to the highly platybasic condition.

The optic nerve appears to have emerged from an area of the lateral wall which was quite thin and has been damaged so that the exact contours of the opening are not preserved. Farther posteriorly are foramina which appear to have carried Nerves III and VI. Above, at the contact between brain case and parietal, there is on one side of the specimen one small opening, on the other a pair of similar openings; these may have carried small veins. More posteriorly, in the position of the pro-otic foramen of a modern anuran, we find three openings, which we may interpret as carrying Nerves V₁, V₂₋₃, and VII (there is no indication of a separate opening for the palatine branch of the facial nerve).

The stout basipterygoid processes were, as noted, articulated with the palate and consist of a core of endochondral bone, surrounded, except dorsally, by bony tissue continuous with the parasphenoid. As on the corresponding portion of the epipterygoid, the articular surface consists of two areas; one faces downward, outward, and forward and the other rather dorsally and posteriorly. The depression over the top of the process at its base appears to represent the course of the lateral head vein; a groove on the posterior margin of the process may indicate the downward course of the palatine branch of Nerve VII.

The occipital aspect of the brain case is seen in Figure 7. The condyle structure is comparable to that of an embolomere rather than a typical rhachitomous form. The lateral portions are situated on the exoccipitals, but the basioccipital also contributes a ventral portion continuous with them. The condyle is thus a single subcircular structure, although the lateral margins project somewhat more prominently. The center of the condyle is hollowed out in funnel fashion, so that notochordal material was obviously present. The basioccipital is incompletely ossified dorsally in its anterior portion, and the two exoccipitals, which (in presumably primitive fashion) form a partial floor to the posterior end of the brain case, do not meet

in the midline; a plug of cartilage persisted here between the three elements. Ventrally the basioccipital, shaped rather like a large intercentral element of the column, was sheathed in its more anterior portion by the parasphenoid; a specimen in which the two are separated shows that they interlocked in a system of parallel ridges and grooves such as are sometimes seen on the parasphenoid in forms in which the basioccipital is unossified.¹⁰ Anteriorly the basioccipital is feebly ossified, so that (as in *Eryops*) a deep cleft, presumably

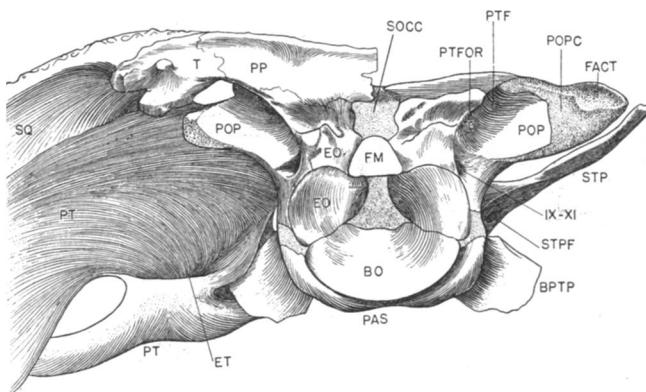


FIG. 7.—Occipital view. $\times \frac{3}{4}$. On the left the dermal roofing bones are present, and part of the suspensorial region is indicated. On the right the dermal bones have been removed. Cartilaginous areas above and below the foramen magnum are restored. On the left the paroccipital region is shown as preserved; on the right its cartilaginous portion is restored. The stapes is shown on the right side.

filled in life by cartilage, was present between the basioccipital and the basisphenoid region (cf. Fig. 10). This unossified gap is a characteristic feature of skulls as far removed as crossopterygians, on the one hand, and such primitive reptiles as pelycosaurs, on the other.

Above the region of the condyles the two exoccipitals extend upward as stout pillars on either side of the foramen magnum and reach the skull roof, where they extend forward beneath the postparietals to merge into the upper surface of the otic region of the brain case; there is no appreciable development of occipital flanges of the postparietals. The posterior surface of the exoccipital is sculp-

¹⁰ Bystrow, "Dvinosaurus als neotenische Form der Stegocephalen," *Acta zool.*, Vol. XIX (1938), Fig. 2, facies cristata.

tured in an irregular fashion which varies in different specimens; in general, however, there is a distinct transverse ridge at about the level of the top of the foramen magnum. There is no distinct evidence of a proatlantal articulation. Medially the exoccipitals form, in their lower portions, a smooth wall for the postvagal region of the medulla. Dorsally the two elements converge to some extent but do not meet, leaving a space above the foramen magnum filled in life with a block of supraoccipital cartilage. At the junction of wall and floor each exoccipital is pierced by two small foramina, reasonably

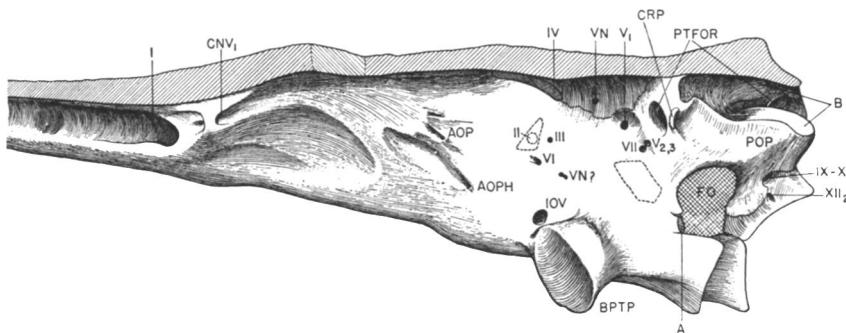


FIG. 8.—Lateral view of the brain case. $\times \frac{2}{3}$. The walls of the sphenoid region were incomplete in the specimen, but between the two sides all areas were present except the two enclosed in broken lines. *A*, perichondral bone sheet continuous with stapes. *B*, unfinished surface of paroccipital process, presumably continued in cartilage.

interpreted as for the hypoglossal roots; the more posterior reaches the lateral surface of the occiput independently, the anterior one fuses with the vagus canal. This latter, presumably carrying Nerves IX–XI, as well as a posterior cerebral vein, is definitely placed between the exoccipital and the posterior margin of the osseous ear capsule. The two elements concerned are readily separable below the foramen. Above the foramen, however, they are fused in the available material. The exoccipital spreads out to some extent at its upper end over the posttemporal fossa.

The brain case is greatly expanded in the otic region. Presumably pro-otic and opisthotic elements were present, but they are not separable by suture, and, further, there are no sutures clearly separating the otic region from other portions of the brain case except for the suture with the lower part of the exoccipital.

Low down on the lateral aspect is the large fenestra ovalis. The dorsal and lateral margins of this opening are clearly defined and well ossified; ventrally, however, the margins are incomplete. Here

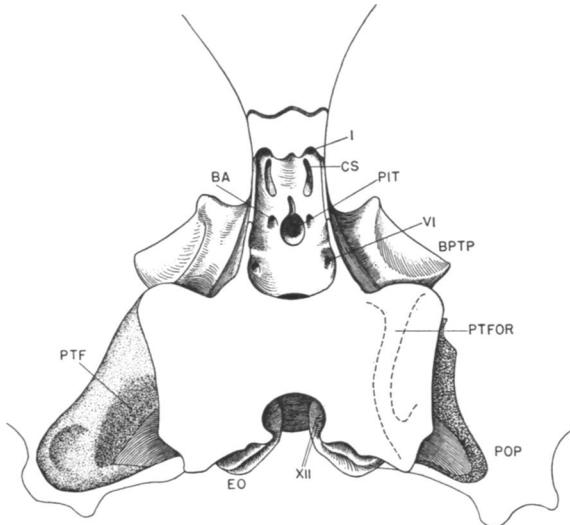


FIG. 9.—Dorsal view of posterior portion of brain case. $\times \frac{2}{3}$. On the left the cartilaginous extension of the paroccipital process is restored. The course of the posttemporal foramen is indicated on the right by broken lines. The outlines of the dermal skull table are indicated.

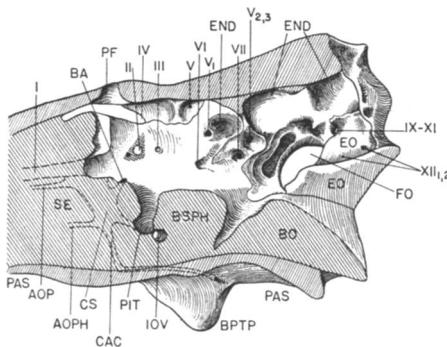


FIG. 10.—Median section of the posterior portion of the brain case. $\times \frac{2}{3}$

there is a ventral extension of the otherwise subcircular fenestra, bounded ventrally, as the specimen is preserved, by the rim of the parasphenoid. This area was occupied by a corresponding ventral expansion of the stapedial footplate. At the anterior edge of this re-

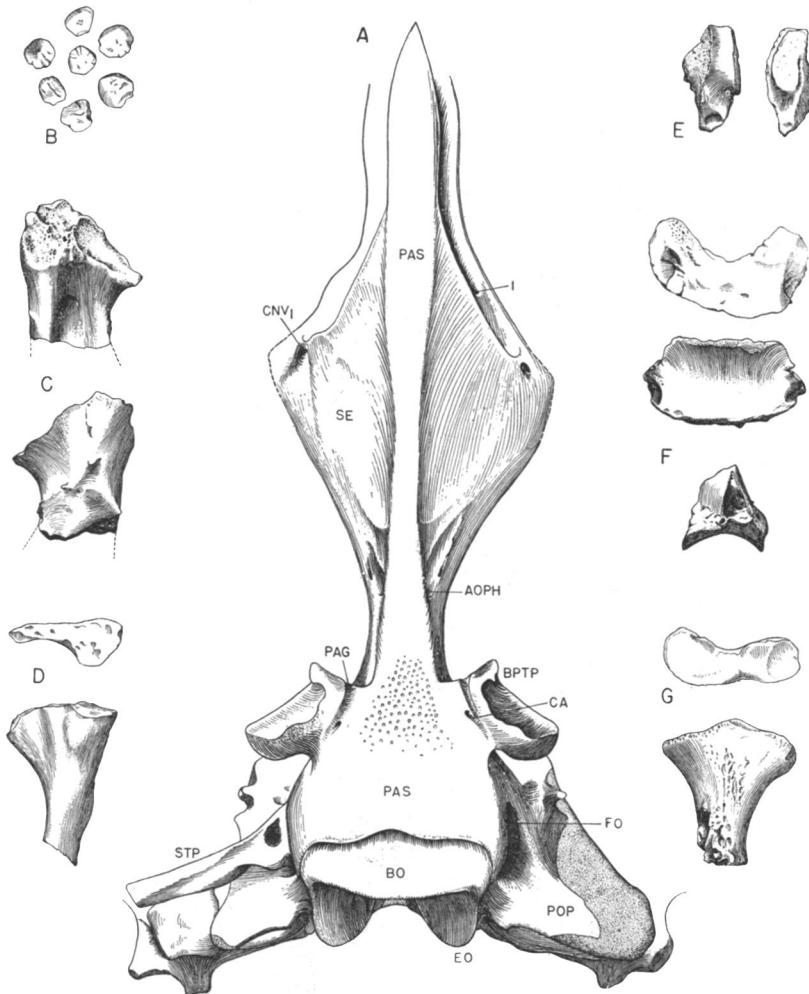


FIG. 11.—*A*, ventral view of brain case. The stapes is present on the left side of the figure. On the opposite side the cartilaginous portion of the paroccipital process is restored. *B*, dermal ossicles. *C*, head of left sacral rib, inner and outer views. *D*, *G*, rib heads, lateral and proximal views. *E*, right pleurocentrum, lateral and anterior views. *F*, intercentrum, anterior, ventral and left lateral views. All $\times \frac{2}{3}$.

gion the stapes was continuous with the superficial portion of the adjacent area of the brain case. A comparable condition of an incomplete ventral ossification of the margins of the fenestra is found in pelycosaurs and probably in other early reptiles.

The general structure of the paroccipital region is comparable to that of *Eryops*; but, although the tabular has no occipital flange, the distal end of the process is unossified, suggestive of conditions in later types of labyrinthodonts. On the left side of Figure 7 the bones are shown as preserved. The distal and anterior edges of the process are unfinished and indicative of a cartilaginous continuation reaching up laterally beneath the tabular and thence forward and inward. It thus formed an anterior wall to the fossa between the upper surface of the paroccipital and the skull roof—a wall found in ossified condition in *Eryops*. This cartilage is restored on the right side in Figures 7 and 11 and on the left in Figure 9.

The fossa so enclosed has usually been termed the “posttemporal fenestra.” It is, however, not simply a “window” as in reptiles, but a deep pocket extending far forward over the otic region, which may be, as Säve-Söderbergh suggests, homologous with the “fossa Bridgei” of fishes—an area of origin for neck musculature. The term “posttemporal fossa” appears to be an appropriate one for this structure.

The fossa communicated with the temporal region (much as in *Eryops*) by a foramen which may be termed the “posttemporal foramen,” leading forward from the inner portion of the fossa to open on the anterior face of the capsule lateral to the foramen for Nerve V. As is usually assumed, this channel may have carried a dorsal vein draining the blood forward from part of the occipital musculature. Bystrow¹¹ assumes that the vena capitis lateralis passed back through this foramen. This seems to be due to a misinterpretation of conditions in the urodeles, upon which his reconstruction is based; the urodele vein appears to follow the normal course backward ventrally between palatoquadrate and capsule in the cranoquadrate passage.¹² The opening is, nevertheless, one of considerable size—

¹¹ “Blutgefäßsystem der . . . ,” *op. cit.*, p. 138 and Fig. 13.

¹² E. T. B. Francis, *The Anatomy of the Salamander* (Oxford: Clarendon Press, 1934), p. 222, antrum petrosomum laterale.

larger than would be expected for a vein merely draining a small area of musculature.

On the anterior surface of the capsule lateral to the opening of the posttemporal foramen is the small but distinct crista parotica articulating with the otic process of the epitylgoid.

The internal structure of the brain case is shown in Figure 10 but will not be discussed here in detail, since the endocast derived from it is described elsewhere.¹³

STAPES

The stapes is well preserved in No. 1378. The main portion of the footplate is essentially oval in contour; ventrally, however, there is

an additional area corresponding to the ventral portion of the fenestra, at the anterior margin of which the stapes is in continuity with the bone of the adjacent margin of the brain case. This condition is reported in other labyrinthodonts and may well be a primitive one. A stapedial foramen of good size is present. The upper surface of the shaft is incised diagonally by a large channel which

FIG. 12.—Right stapes, postero-medial and anterolateral views. $\times \frac{1}{2}$.

presumably formed the lower margin of the passage through which passed the vena capitis lateralis and the hyomandibular trunk of the facial nerve. The distinct crest at the distal edge of this channel appears to have been closely applied to the paroccipital process of the otic capsule and hence corresponds to the dorsal head of the stapes seen in much more highly developed form in both crossopterygians and pelycosaurs. Its reduced form in this type of labyrinthodont is, of course, due to the fact that the shaft passes close to the paroccipital, and hence no elongation is necessary to produce such a dorsal contact (presumably ligamentous). When articulated, the shaft is seen to be directed into the otic notch. The tip of the shaft is unfinished and hence may have been continued in cartilage.

¹³ Romer and T. Edinger, "Endocranial Casts and Brains of Living and Fossil Amphibia," *Jour. Comp. Neurol.*, Vol. LXXVII (1942), pp. 355-89.

LOWER JAW (FIG. 3, A, C)

One nearly complete ramus and part of the other are present in No. 1378; this, with numerous fragments from other specimens, shows the nearly complete jaw structure except for details at the level of the anterior part of the mandibular fossa, where the only specimen preserving this region is badly crushed and broken. In its general anatomy and the nature and mutual relations of the elements present, the jaw is that of a characteristic member of the Rhachitomi. The one major peculiarity is the fact that the jaw is greatly flattened anteriorly, so that the morphologically external surface faces ventrally.

The marginal dentition includes about 44 teeth. The dentary also bears, close to the symphysis, a pair of fangs of moderate size—rather larger than those of *Eryops*. In correlation with the anterior flattening, the symphysis is moderately elongate; the splenials form a substantial part in the symphysis. The usual series of three coronoids is present. These elements bear numerous small teeth of the type seen on the palate. The tooth-bearing areas are raised and sharply demarcated from the rest of the coronoid surface. Between the tooth-bearing area of the coronoids and the marginal tooth row is a well-defined longitudinal groove of irregular width. Expansions of this groove correspond to the position of the palatine and ectopterygoid fangs of the upper jaw.

The prearticular appears to have extended well forward, although imperfections, as noted, make it impossible to be sure of the exact contours of this bone in its middle portion or of the outlines of the infra-Meckelian fenestra.

Posteriorly the jaw shape changes from the flattened condition seen in front to a more normal upright build. In larger and more mature specimens the articular is well fused with all three adjacent dermal elements—prearticular, surangular, and angular—but numerous fragmentary specimens, some rather small and immature, enable us to make out most of the structure. The articular is well ossified, forms the transversely placed, concave articular surface and the "lips" surrounding it (there is no retroarticular process), and extends as a flattened, triangular process well forward in the floor of the mandibular fossa. The margins of this process are well defined

except at its narrow tip. The outlines, as well as a prominent groove on the angular which continues forward its lateral margin, indicate that there was but a small extent of Meckelian cartilage anterior to the ossified area. The articular is widely overlapped anterodorsally in the fossa by the surangular, which forms a stout buttress in front of the bone in the articular region and runs down into the floor of the mandibular fossa. The prearticular, angular, and surangular join to sheathe the ventral surface of the Meckelian process of the articular. In contrast, however, with many later labyrinthodonts, the articular is widely exposed on the surface of the jaw posteriorly. The canal common in this region in all early tetrapods is present, passing diagonally inward and backward on the medial surface and then curving forward to open laterally in the floor of the mandibular fossa. For the most part, at least, the foramen follows a course between the articular and the adjacent dermal bones—surangular and prearticular. This foramen is generally assumed to be for the chorda tympani nerve. It is here, however, of large size and may reasonably have carried blood vessels as well as nerve. We, therefore, prefer to use for it the noncommittal term of "para-articular foramen" (by analogy with the closely comparable paraquadrate [or quadrate] foramen of the upper jaw).

The senior author has elsewhere¹⁴ commented on the mirror-image relationship of upper and lower jaw structures in early tetrapods. In *Edops* the elements of the posterior end of the lower jaw are highly comparable to those of the suspensorial region—articular to quadrate, surangular to quadratojugal, prearticular to quadrate ramus of pterygoid. There is, however, no observable structure in the lower jaw comparable to the accessory paraquadrate foramen.

NOTE ON RECONSTRUCTIONS OF SOFT ANATOMY

In the preceding sections considerable information has been given which is of aid in the interpretation of the soft anatomy of the cranial region. We have not, however, attempted to present a detailed reconstruction of the cranial angiology or neurology. Two attempts at such reconstructions of labyrinthodonts are available, those of G.

¹⁴ Romer, "Mirror Image Comparison of Upper and Lower Jaws in Primitive Tetrapods," *Anat. Rec.*, Vol. LXXVII, No. 2 (1940), pp. 175-79.

Säve-Söderbergh¹⁵ and Bystrow,¹⁶ the latter confining himself to angiography. We believe heartily in attempts to restore the soft parts of fossil forms, for they are likely to lead to valuable results in the study of the general evolution of the nervous system, circulatory system, musculature, etc. The value of any reconstruction, however, depends upon (1) the amount of pertinent osteological data available and (2) the breadth of the comparisons made with living types.

The studies cited may be criticized on both grounds. Both authors have perforce used advanced labyrinthodonts as the bases for their reconstructions. In these forms there is almost no ossification in the endochondral skeleton, and hence most of the important landmarks by which the course of soft structures may be plotted are absent. If, for example, one seeks the evidence upon which Säve-Söderbergh's detailed figure of the labyrinthodont cranial nerves is based, it is found to be almost nonexistent. He has reconstructed the cartilaginous endocranum, supplied it with hypothetical foramina, and in turn filled these with an appropriate series of nerves.

Further, in neither case has comparison been made with other than a single type of modern amphibian. Säve-Söderbergh's figures are of the frog's nervous and arterial system, slightly modified to fit into a labyrinthodont skull; Bystrow's reconstructions are frankly based on the urodele. The frogs are probably related to labyrinthodonts but may well have become as highly modified in their soft structure as in their skeletons, and the urodeles may well be even further from the ancestral stock. Properly, the interpretation of the soft anatomy of early tetrapods should be based on a comparison with both major modern amphibian groups, a consideration of the features present in the early reptiles, likewise of labyrinthodont descent, and, finally, of antecedent conditions, as far as they may be deduced, in the fish ancestors of the tetrapods.

AXIAL SKELETON

No adequate articulated material of the axial skeleton has been discovered, but numerous isolated vertebral elements exist. These

¹⁵ "On the Morphology of Triassic Stegocephalians from Spitzbergen, and the Interpretation of the Endocranum in the Labyrinthodontia," *Svenska Vet. Akad. Handl.*, Vol. XVI, No. 1 (3d ser., 1936), pp. 1-181.

¹⁶ "Blutgefäßsystem der . . . , " *op. cit.*

are mainly from the Cottonwood Creek locality. At that place there have been recovered many elements of rhachitomous vertebrae. These readily sort into two series. One includes elements of relatively smaller size, which obviously pertain to *Eryops*. The second includes larger elements, different in morphological structure, which are reasonably interpretable as pertaining to *Edops*. This seems to be rendered certain through the finding of a few elements of similar nature with specimens 1235, 1770, and 1378. The intercentra (Fig. 11, *F*) differ notably from those of *Eryops*. They are much flatter ventrally, and the facets for rib articulation are much larger and more distinct. In *Eryops* the anterior and posterior margins of the ventral surface are sharply downturned, rendering this surface markedly concave; in *Edops* little of this downturning is seen. Further, they are less well ossified internally. A typical *Eryops* intercentrum, when seen in anterior or posterior view, is but slightly notched centrally between the two ascending "horns"; the *Edops* intercentra are more crescentic in shape, with a large central cavity. This may indicate a larger notochord but, more probably, means merely that a greater amount of basiventral cartilage persisted. From the caudal region there are intercentra with the bases of the haemal arches, but none is complete.

The pleurocentra (Fig. 11, *E*) have a structure essentially similar to that of *Eryops*, but there are readily distinguishable features. As in the intercentra, the margins of the superficial surface are much less outturned in *Edops* than in the former genus. The thin ventral extension of the pleurocentrum is more developed than in *Eryops*. The flattened facet opposed to the arch pedicel is relatively narrower but more elongated dorsoventrally.

The neural-arch elements are incompletely preserved and are not figured here. It appears that the spine differs from that in *Eryops*, but better material is needed before a diagnosis of value can be made. In the pedicel of the arch in the presacral series the rib facets are much broader than in *Eryops* and approach a subcircular form, rather than the long, thin, rectangular shape seen in that genus. On the other hand, the area beneath the rib articulation, which faces the pleurocentrum, is relatively poorly ossified and smaller in area than in *Eryops*.

Ribs are known only from their heads, of which several are figured (Fig. 11, D, G). The typical dorsal ribs appear to have been less flattened in the proximal portion of the shaft than in *Eryops* and are nearly circular in section. The capitular and tubercular facets are more rounded in contour than in *Eryops*.

Two examples of the articular portion of the sacral rib are preserved (Fig. 11, C). This element appears to have been fundamentally similar to the type seen in *Eryops* but is readily distinguishable. On the medial surface of the head region the rib of *Eryops* is gently concave; this region in *Edops* forms a deep depression, and, conversely, the external surface is much more convex than in *Eryops*. A marked external rugosity near the capitular border of the "neck" of the rib has no parallel in *Eryops*.

APPENDICULAR SKELETON

Only fragments of the appendicular skeleton are available. The pectoral girdle is almost unknown. Of the pelvic girdle, the basal portion of the ilium is present in a well-preserved fragment from Cottonwood Creek, and No. 1770 includes a specimen with a good part of the acetabular area (Fig. 14, D); in this, however, little detail can be seen. The acetabular area and the "neck" above it are of characteristic primitive tetrapod pattern and not dissimilar to *Eryops*. The base of the iliac blade, as preserved, expands rapidly both anteriorly and posteriorly. The fragment may be so articulated as to suggest an iliac blade, shaped like that of *Eryops*. However, the posterior margin ceases at about the position in which in *Eryops* one finds the tip of a posteriorly directed process. But in *Edops* this area is thick, and there may have been a broader type of iliac blade or a more highly developed posterior process.

The humerus (Fig. 13) is best known from No. 1781, a nearly complete element which appears to have belonged to a large individual; the greatest length is about 18 cm. A nearly complete but smaller specimen (with a length of 16 cm.) is included in No. 1770; this has preserved certain portions of the bone not present in No. 1781, but the difficult matrix obscures much detail. The element is of the typical, primitive tetrahedral type common to most contemporary tetrapods but differs markedly from *Eryops*. In general, one may

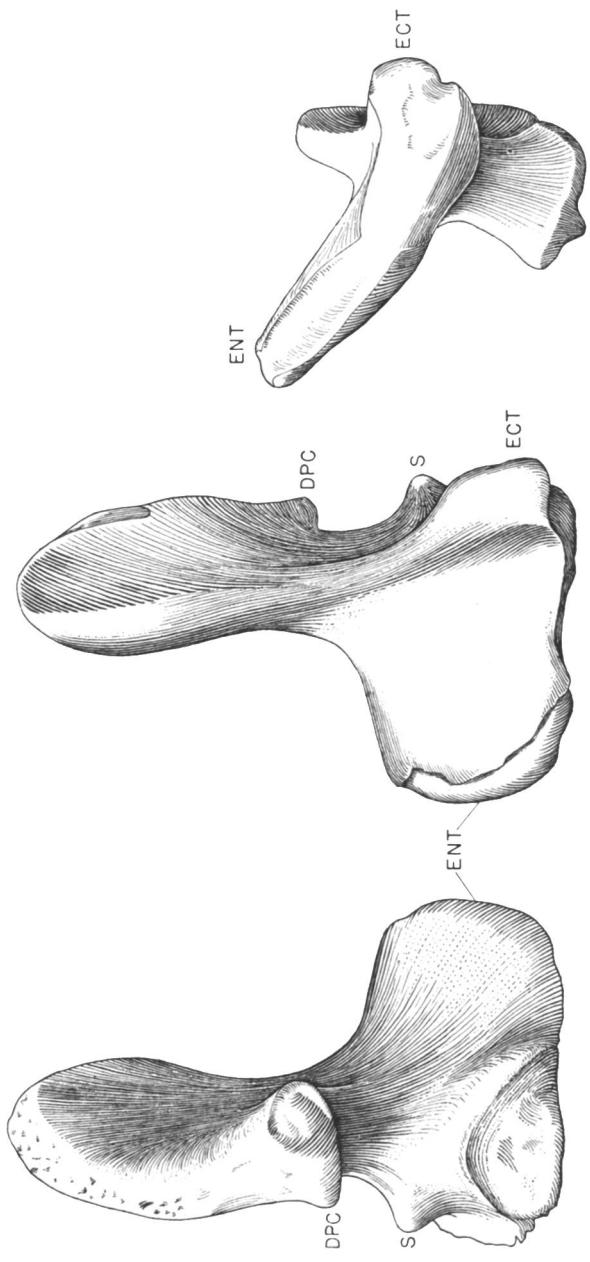


FIG. 13.—Right humerus, ventral, dorsal, and distal views. *DPC*, deltopectoral crest; *ECT*, ectepicondyle; *ENT*, entepicondyle; *S*, supinator process. $\times \frac{3}{4}$.

say that the bone is much less "bumpy," with less pronounced muscular processes and rugosities. The distal end is less sharply twisted on the proximal than in *Eryops*, and there is more development of a shaft region. The supinator crest is less prominent than in *Eryops* and is connected by a continuous ridge with the deltopectoral crest; the condition is intermediate between that seen in *Eryops* and that seen in *Cricotus*. The ectepicondyle is much less elevated than in *Eryops*.

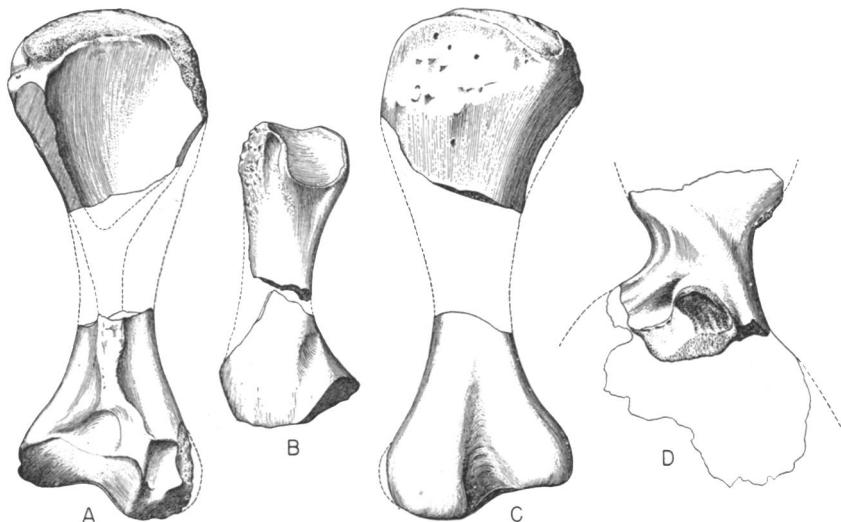


FIG. 14.—*A*, right femur, ventral surface. *B*, right fibula, external view. *C*, right femur, dorsal surface. *D*, incomplete right ilium. The shaded portion based on a specimen from Cottonwood Creek; the unshaded area is present in a second specimen in which, however, the surface is not preserved. All $\times \frac{1}{2}$.

Radius and ulna are almost unrepresented except for No. 1770, where these elements are present, articulated with the humerus noted above. These have lengths of approximately 75 and 97 mm., respectively. They are enclosed in a film of refractory matrix which has not been removed, and little can be said of their detailed characters.

The femur (Fig. 14, *A*, *C*) is known only from fragments of the ends, from which a composite restoration is figured. The bone is obviously flatter distally than in *Eryops* and with the longitudinal ad-

ductor ridge ("linea aspera") much less elevated. In relation to the relative flattening of the distal end, the fibular articular area faces much more ventrally than in *Eryops*; proximal to this area is a deep pocket not present in that genus. Unfortunately, little can be said of the state of development of the proximal part of the ventral-ridge system.

Of the tibia only the head has been identified. This exhibits the general rhachitomous type of structure but with less development of depth in the medial articular region. A fibula (Fig. 14, B) apparently associated with M.C.Z. 1378 is nearly complete, and details missing can for the most part be supplied from other fragments. The bone is in some features comparable to that of *Eryops* but is relatively broader. At the head the structure is markedly different from that of *Eryops*. The articular area extends farther down the inner (or tibial) aspect and tends to a subcircular form rather than the elongate oval seen in *Eryops*. The usual rugosity on the external aspect of the head is found at the postaxial margin; and beneath this area, on the flexor aspect, is a distinct longitudinal groove not seen in *Eryops*.

A few carpal and tarsal elements and numerous metapodials and phalanges are present in the material from the Cottonwood and Padgett localities. We cannot, however, clearly distinguish at present the *Edops* specimens from those pertaining to *Eryops*.

DERMAL ARMOR

We have not found in our material any trace of normal ventral dermal scales of the type usually found in labyrinthodonts. This, however, is not surprising in view of the lack of undisturbed postcranial material and the delicate nature of isolated scales. (We may note that even in the case of *Eryops* the dermal scales are but rarely found.) Evidence of a second type of dermal armor is, however, present. In the Cottonwood Creek locality, where fragmentary remains of *Edops* are plentiful, there are found numerous lens-shaped bony ossicles with an average diameter of 8–10 mm. (Fig. 11, B). One surface tends to be relatively flattened but with irregular furrows and tiny openings presumably for nutrient vessels. The other side is much more convex, often with a distinct raised area, and rela-

tively smooth. A majority are subcircular in outline, others have varied, more distinctive contours. Presumably these elements are dermal ossicles, situated in the corium of the back and flanks and very probably superficially situated, the convex surface external. There is, of course, no evidence as to details of their arrangement. That these ossicles are associated with *Edops* seems certain from the fact that they are abundantly represented in No. 1769, a specimen definitely ascribable to *Edops*.

PHYLOGENETIC POSITION OF "EDOPS"

From the description above it is obvious that *Edops* is a very primitive member of the Rhachitomi, to which group it may be definitely assigned on the basis of vertebral structure. It is comparable to *Eryops*, *Actinodon*, and other characteristic Lower Permian rhachitomes rather than to more advanced or more specialized forms in a number of regards, such as general skull shape, lack of multiplication of lateral palatal teeth, well-ossified brain case, etc. The only feature in which *Edops* is further "evolved" (in the direction of degeneracy) than *Eryops* is the incomplete ossification of the paroccipital and supraoccipital regions. On the other hand, *Edops* is much more primitive than typical rhachitomes in a number of features. These include, among others, (1) presence of an intertemporal, (2) retention of a sculptured septomaxilla, (3) movable basipterygoid articulation, (4) unusually small interpterygoid vacuities, with (5) the pterygoids meeting anteriorly, (6) unusually well-ossified epipterygoid, (7) less platybasic brain case, with which is associated (8) a deep pituitary fossa and (9) a single occipital condyle. In all these features *Edops* approaches or reaches conditions presumably present in ancestors of the rhachitomes in an "embolomerous" stage of morphological development.

Of Permian types, *Trimerorhachis* has kept certain of these primitive features, including retention of the intertemporal and, apparently, a persistence of the movable basipterygoid articulation. This form is, however, quite degenerate in other regards, although it may well have been derived from an *Edops*-like ancestor.

For closer relatives of *Edops* we must turn to Carboniferous forms.

Most closely comparable of well-described types is *Dendrerpeton* of the Joggins of Nova Scotia.¹⁷ This is likewise rhachitomous, although the vertebral structure is not of the usual type. The skull roof is comparable to that of *Edops*, but in the fact that the lacrimal still reaches the orbit *Dendrerpeton* is slightly more primitive. The occiputs are closely comparable; particularly noteworthy is the common presence of the primitive single condyle. In both the basal articulation is movable, and in *Dendrerpeton* the interpterygoid vacuities are unusually small for a rhachitome. Here, however, *Edops* is much more primitive, for in *Dendrerpeton* the anterior end of the palate is figured as being formed in typical rhachitomous fashion, with the pterygoids separated and with curved anterior margins of the vacuities formed by the vomers.

In the same general category as *Edops* and *Dendrerpeton* may be placed *Cochleosaurus* of Nýřany, as redescribed by Steen.¹⁸ Here the brain case is unfortunately poorly known; the intertemporal is still present; the lacrimal is barely excluded from the orbit. The palate, however, shows a more developed pair of interpterygoid vacuities, the condyle appears to be attaining the double condition, and on the whole *Cochleosaurus* is rather more advanced toward the typical rhachitomous condition.

Several other forms from the Joggins and Nýřany, described by Steen, exhibit a skull-roof pattern which, in the presence of an intertemporal and a tabular of small size, is comparable to that of the primitive Rhachitomi already mentioned. For the most part, however, these are too poorly known to render further discussion profitable. Of interest, however, is *Capetus*, a Nýřany genus described by Steen¹⁹ on the basis of a skull table. To this, she notes, may well be assigned an imperfect skull described by F. Broili²⁰ in error as *Sclero-*

¹⁷ M. C. Steen, "The Amphibian Fauna from the South Joggins, Nova Scotia," *Proc. Zool. Soc. London*, Part III (1934), pp. 465-504.

¹⁸ "On the Fossil Amphibia from the Gas Coal of Nýřany and Other Deposits in Czechoslovakia," *Proc. Zool. Soc. London*, Ser. B, Vol. CVIII, Part II (1938), pp. 205-83.

¹⁹ *Ibid.*, pp. 241-42, Fig. 27.

²⁰ "Über *Sclerocephalus* aus der Gaskohle von Nürschan und das Alter dieser Ablagerungen," *Jahrb. geol. Reichsanst. Wien*, Vol. LVIII (1908), pp. 49-70.

cephalus credneri. A still better specimen, which is probably assignable likewise to *Capetus*, although omitted by Steen from her discussion of the Nýřany material, is a skull roof repeatedly figured by O. Jaekel²¹ and compared by him with *Chelydosaurus vranii*. The skull table is closely comparable with that of the Steen and Broili skulls of *Capetus*. The entire roof pattern is almost identical with that of *Edops*, and it is reasonable to believe the two closely related.

Edops, then, is a very primitive member of the Rhachitomi. Except for the withdrawal of the lacrimal from the orbit, it shows every major feature to be expected in the ancestor of any rhachitomous or stereospondylous labyrinthodont and in skull structure bridges much of the gap between the Rhachitomi and their ancestors in a morphologically embolomerous (although non-anthracosauroid) condition. *Dendrerpeton* is related but more advanced in palatal structure; *Cochleosaurus* is apparently somewhat more advanced toward typical rhachitomes, and *Trimerorhachis* represents a degenerate side branch from the *Edops* stage. Since forms of more advanced type were already present in Westphalian or early Stephanian times, the genus *Edops*, which is apparently late Stephanian in appearance, cannot be considered as generically ancestral to them. We have noted that *Edops* is confined to the lowest levels of the Texas red-beds deposits. It thus appears to have been a late survivor of a group of Pennsylvanian ancestral rhachitomes.

²¹ *Die Wirbeltiere* (Berlin: Borntraeger, 1911), Fig. 124; and "Über den Bau des Schädels," *Verh. anat. Gesellsch* (1913), Fig. 5.

ABBREVIATIONS FOR FIGURES

ANG.	angular	NA.	nasal
AOP.	optic artery	OEPT.	otic process of epitypoid
AOPH.	ophthalmic artery	P.	parietal
AP.	anterior process of stapes	PA.	prearticular
ARF.	para-articular foramen	PAG.	groove for palatine artery and nerve
ART.	articular	PAL.	palatine
BA.	basilar artery	PAS.	parasphenoid
BO.	basioccipital	PF.	foramen for parietal organ
BPTP.	basitypoid process	PIT.	pituitary fossa
BSPH.	basisphenoid	PMX.	premaxilla
CAC.	canal for carotid artery	PO.	postorbital
CNV.	canal carrying n. ophthalmicus profundus forward through sphenethmoid	POF.	postfrontal
CO, CO. I,		POP.	paroccipital process
CO. II	coronoid elements	POPC.	cartilaginous region of paroccipital process
CRP.	crista parotica	PP.	postparietal (dermal supraoccipital)
CS.	pocket in which internal carotid branches	PRF.	prefrontal
D.	dentary	PT.	pterygoid
DP.	dorsal process of stapes	PTF.	posttemporal fossa
ECT.	ectopytoid	PTFOR.	posttemporal foramen
END.	position of endolymphatic sacs	Q.	quadrate
EO.	exoccipital	QJ.	quadratojugal
EPT.	epitypoid	SANG.	surangular
ET.	"excavatio tympanica"	SE.	sphenethmoid
FACT.	restored facet on paroccipital process for tabular	SMX.	septomaxilla
FM.	foramen magnum	SOCC.	supraoccipital cartilage
FO.	fenestra ovalis	SP.	anterior splenial
FPQ.	paraquadrate foramen	SPP.	posterior splenial
FPQA.	accessory paraquadrate foramen	SQ.	squamosal
FR.	frontal	ST.	supratemporal
G.	groove in stapes for vena capititis lateralis	STP.	stapes
IOV.	interorbital anastomotic vein	STPF.	stapedial foramen
IT.	intertemporal	T.	tabular
JU.	jugal	TFAC.	facet on tabular for paroccipital process
L.	lacrimal	VN.	presumed venous foramina
MX.	maxilla	VO.	vomer
			Nerve exits are indicated by roman numerals