

A NEW ARMoured AMPHIBIAN FROM THE UPPER PERMIAN OF EAST AFRICA

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[Plate 8]

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Amphibian material collected by Mr F. R. Parrington from an Upper Permian locality in the Ruhuhu Valley of Tanganyika has been prepared with the aid of acid. An account of the technique adopted is given. The remains consist of three imperfect skulls, some skull fragments and about 300 post-cranial bones, most of which were contained in blocks of marly limestone.

The material is assigned to a new genus and species for which the name *Peltobatrachus pustulatus* is proposed and a diagnosis given.

The cranial material is described and a composite restoration is given. The pattern of dermal roofing bones is of the 'temnospondyl' type, but the surface is ornamented with pustules instead of the normal labyrinthodont ornament. The whole skull, including supraoccipital, basioccipital and opisthotic, is heavily ossified. Parts of a jaw ramus, including a well-developed retroarticular process, are described.

The dorsal vertebrae are shown to consist of single, elongate notochordal centra and free 'intervertebral' neural arches. It is concluded that the dorsal vertebrae are not stereospondylous. Caudal vertebrae consisting of neural arches, centra and separate small intercentra with haemal arches are described and a reconstruction is made of the caudal region. The dorsal ribs are adapted to carry the heavy dermal armour: a complete sacral rib and forked caudal ribs are also described.

Imperfect remains of the appendicular skeleton include a scapulocoracoid and cleithrum, humerus, pelvis and femur. The inferred relation of the cleithrum to the clavicle is not of the normal labyrinthodont type. The species has a characteristic massive dermal armour. Two dermal shields are preserved, together with a large number of scutes, some singly and some sutured as transverse bands. The armour is reconstructed as pectoral and pelvic shields connected by neural and costal bands.

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A reconstruction of the whole skeleton is attempted and the possible mode of life, that of a heavy terrestrial form, is discussed.

A relation between *Peltobatrachus* and the Triassic plagiosaurs is postulated on both cranial and postcranial characters. The most significant common features are considered to be the pustular ornament, the ossification of the endochondral bones of the occiput, the form of the vertebrae and that of the dermal armour. Establishment of this relationship removes the plagiosaurs from the stereospondylous labyrinthodonts in agreement with Nilsson (1946).

The taxonomic position of the plagiosaurs is discussed and a case made against their relationship to the brachyopids. It is also concluded that they are not closely related to *Dvinosaurus* or to the metoposaurs. The position of the genera *Plagiosternum* and *Taphrognathus* is discussed in the light of the diagnostic features of the group.

The retention of the plagiosaurs (including *Peltobatrachus*) within the *Labyrinthodontia* as defined by Romer is proposed, but their separation from temnospondyls and anthracosaurs as the order Plagiosauria is endorsed. A new diagnosis of the order is given and diagnostic characters of two constituent suborders, the Peltobatrachi (including only *Peltobatrachus*) and the Plagiosauri are listed.

INTRODUCTION

Following earlier geological surveys by Bornhardt (1900), Dantz (1903) and Gillman (1927), a thorough survey of the Karroo rocks in the Ruhuhu Valley of Tanganyika was undertaken by Stockley (1932). He recognized two wide bone-bearing strata, which he referred to as the Upper and Lower Bone Beds.

Haughton (1932) determined Stockley's vertebrate material, which included the jaw of a small labyrinthodont, a pareiasaur, a gorgonopsid and several dicynodonts from the 'Lower Bone Bed', and on the basis of this material concluded that the stratum was homo-taxial with parts of the *Endothiodon* and *Cistecephalus* zones of South Africa.

Further collections were made by Parrington in 1933 over a wide area in the Ruhuhu Valley, and descriptions of some of the reptilian material collected have been published (Parrington 1936*a, b*, 1946*a, b*, 1955; Crompton 1955).

Additional stratigraphical work was done in the area by Nowack between 1934 and 1936. He endorsed and expanded the work of Stockley and also made extensive collections of vertebrate fossils (Nowack 1937). Some of this material has been described by Broili & Schroeder (1936) and von Huene (1938*a, b*, 1939, 1942*a*, 1944, 1950). Further Tanganyika material has also been described by Boonstra (1953*a, b*).

MATERIALS AND METHODS

The material described in this paper constitutes specimen 35 from Mr Parrington's 1933 collection. The numbering of the localities in this collection follows Stockley's list and B4/5 from which this specimen comes is a 'Lower Bone Bed' locality near Stockley's B4 (Katumvi Viwili). The material, labelled 'amphibian remains', consisted of several blocks containing bones, together with three incomplete skulls and some fragments, with other bony fragments found scattered on the site.

Each specimen has been given an identifying letter which will be referred to throughout this paper. A complete list of the material is as follows:

Specimen	Skulls
A	The most complete skull, associated with a left scapulocoracoid and cleithrum, and a single centrum
B	The postero-medial part of a skull
C	The hind part of a skull, extending laterally to the tabular region

Specimen	Blocks
<i>D</i>	The largest block: dorsal vertebrae and ribs, pelvis and femur, humerus, dermal armour: 103 specimens
<i>E</i>	Articulated series of dorsal vertebrae, ribs and armour: 67 specimens
<i>F</i>	Caudal vertebrae, ribs and scutes: 32 specimens
<i>G</i>	Part of jaw ramus, dorsal vertebrae and ribs, scutes: 21 specimens
<i>H</i>	Scutes and a dorsal rib: 9 specimens
<i>I</i>	Two centra, pelvic fragments, ribs and scutes and a limb bone: 14 specimens
<i>K</i>	Sacral rib, pelvic fragment, ribhead, scutes, 9 specimens.
<i>L</i>	Lower jaw angle, rib fragment, scutes, ? toe bone: 17 specimens
<i>M</i>	Rib and scute fragments: 13 specimens
<i>N</i>	Crushed centrum and neural arch, scutes and rib fragments: 7 specimens
<i>O</i>	Three unidentified bony plates
	Skull fragments
<i>P</i>	Quadrate region with two other dermal fragments
<i>Q</i>	Part of the cheek region
<i>R</i>	Part of interorbital region
	Miscellaneous
<i>S</i>	A single weathered-out scute
<i>T</i>	Microscope slide: bone section
<i>V</i>	Loose bone fragments (ornamented): 12 specimens
<i>X</i>	Loose bone fragments (unornamented): 7 specimens, not identified

The specimens were preserved in a matrix of grey marly limestone. It differs in colour from other 'Lower Bone Bed' matrix, which is frequently stained reddish with iron.

Some development had already been carried out on specimen 35 before the present study was started. In order to expose the sutures, the ornament had been ground away from the dorsal surface of the three skulls, specimen areas being left. Some development with a dental mallet had also been undertaken on the two largest blocks, as well as on the skulls, exposing areas of bone near the surface.

The calcareous nature of the matrix made it ideal for the acetic acid technique of development (Toombs 1948; Rixon 1949), and all the specimens, except skull *A*, have been completely freed of matrix by this method. It was found that a solution of Perspex in chloroform, used for mending, was, if further diluted, suitable for strengthening the bone during and after development; and also providing a permanent protection.

The specimen was left in 15% acetic acid for about twelve hours at a time and then washed and dried. After this Perspex was brushed on the newly exposed bone, which, if at all porous would soak it up. The Perspex thus provided internal strengthening as well as forming an external coating.

In the development of the larger blocks the relative positions and the orientation of the individual bones within the block were preserved by mapping. Plans were made for blocks *D*, *E*, *F* and *G* and the numbers given to bones in these four blocks, which are quite arbitrary, will be used for reference, preceded by the letter of the block, throughout this paper.

Local acid development was carried out on skull *A* using formic acid at various dilutions. Where possible this was poured into a natural cavity, otherwise it was applied with a brush. Alternate applications of water and acid, made in rapid succession, were found to give the best results, and after about an hour of this treatment the whole was washed and dried, and Perspex applied in the usual way.

PELTOTRACHUS PUSTULATUS GEN. ET SP. NOV.

Holotype. Specimen *A* (skull, scapulocoracoid, cleithrum, centrum) of specimen 35: F. R. Parrington collection, University Museum of Zoology, Cambridge.

Paratypes. The remaining specimens from specimen 35, with the exception of 35 *O* and 35 *X* (unidentified bone).

Type locality. F.R.P. locality B4/5, near Stockley's B4 (Katumvi Viwili), Ruhuhu Valley, Tanganyika.

Horizon. 'Lower Bone Bed' (*Endothiodon-Cistecephalus* zones), Upper Permian.

The material to be described is considered to belong to a new genus and species of amphibian, for which I propose the name *Peltotrachus pustulatus*; the generic name referring to the extensive dermal armour and the trivial name to the character of the ornament on the dermal bones.

Specimen 35 obviously represents several individuals and specimen *A*, including the best-preserved skull, has been selected as the holotype. With the exception of the unidentified pieces of unornamented bone not included in blocks with identifiable material, all the specimens are referred to the same species because of the proximity of the finds, the anatomical similarity of individual bones in separate blocks, and especially because of the unusual character of the dermal ornament represented in every block or specimen. The ornament consists of small rounded pustules, about 1 mm in diameter, often raised on a short neck above the general surface of the bone.

A diagnosis of the new species, based on the description of the material which follows, is given below. A more detailed description of the material and the association of the specimens within the various blocks is given in the dissertation on which this paper is based, available in the University Library, Cambridge. *P. pustulatus* is the genotype and only known species of the genus *Peltotrachus*.

Diagnosis

Amphibia with distinctive pustular ornament on the dermal bones.

Skull about 15 cm long, broad, apparently parabolic in outline. Skull table long, the raised orbits being about half way along the length of the skull. Cheek broad and smoothly curved. Occipital condyle single. Occipital surface sloping slightly back from the skull table.

No intertemporal bone. Large supratemporal just reaching the border of the short otic notch, and having a wide suture with the interparietals; so that the tabular is widely separated from the parietal. Tabular bearing a large globular horn. Circumorbital bones large; lacrimal apparently excluded from the orbit. Quadrate articulation apparently slightly anterior to the corner of the skull, so that the latter forms a distinct quadratojugal horn.

Large interpterygoid vacuities separated by a slender processus cultriformis. Short basi-cranial suture between the parasphenoid and pterygoid. Parasphenoid and pterygoid ornamented with small denticles. Distinct backwardly-directed quadrate ramus of the pterygoid.

Neurocranium heavily ossified: massive cylindrical sphenethmoid extending far anteriorly; ossified basioccipital and supraoccipital; tabular and exoccipital separated by a long paroccipital process but meeting dorsal to the deep post-temporal fossa.

Lower jaw ornamented laterally and bearing a well-developed retroarticular process.

Dorsal vertebrae consisting of single elongate, notochordal centra, bearing 'intervertebral' neural arches. Neural spines high and conical. Rib articulation terminates a wide massive transverse process formed by the diapophysis of the neural arch combined with the parapophysis of the centrum in front of it.

Caudal vertebrae of pleurocentra and small crescentic intercentra bearing haemal arches. Anterior pleurocentra open ventrally, posterior pleurocentra complete notochordal rings, finally becoming fused to the neural arches.

Ribs bearing capitulum and tuberculum at the end of an undivided shaft. Dorsal ribs massive, curved, bearing posteriorly a broad surface for the dermal armour. Caudal ribs forked distally.

Scapulocoracoid very broad antero-posteriorly and with a deep coracoid plate. Four foramina in the glenoid region. Cleithrum splint-like ventrally, clasping the front of the scapula blade and overlapping the clavicle anteriorly but not laterally. Humerus broad, tetrahedral and well-ossified. Pelvic girdle with a deep puboischiadic plate and deep symphysis anteriorly. Slender iliac shaft borne on a single highly adapted sacral rib.

Massive dermal trunk armour of dorsal pectoral and pelvic shields, separated by overlapping bands of sutured scutes, divisible for at least some of the trunk into neural and flanking costal series. Apparently a flexible ventral armour of minute gastralia. Tail region also armoured dorsally with sutured scutes.

Skull

Of the three principal skull specimens, skull *A*, the holotype, is the most completely preserved and gives information on the structure of a large part of the skull. This information is supplemented by skulls *B* and *C*, and by several skull fragments.

Dorsal surface

In skull *A* (figure 1) the preservation of the dorsal surface is sufficiently good to allow most of the sutures to be traced, although a number of cracks and fractures, especially anteriorly, make confusion possible. The characteristic dermal ornament had been ground away to a smooth surface before the specimen was received by the writer, to facilitate tracing the sutures, specimen areas of ornament being left round the orbit edge. A natural cast of the cheek region shows the form of the skull well, and although the sutures cannot be traced with absolute certainty, further supporting evidence for their apparent course is provided by radial ridges which appear to have their origin at the centres of ossification.

The shape of the skull is broad and flat, with the skull table and centre snout region forming a plane or slightly concave surface with various raised regions. The orbits are raised prominently and there is a rounded ridge crossing the frontals between them. The side of the snout appears, from the natural cast, to fall away quite sharply at an angle of about forty-five degrees from the somewhat concave central region, so that the latter must have been bordered by distinct ridges. Further back the jugal region descends less sharply and the cheek falls away in a shallow curve to its extreme edge, which descends vertically for a short distance. Nowhere on the surface of any of the skulls is there any sign of lateral line grooves.

The pattern of sutures traced on the roof of skull *A* will be clear from the figure. The only specimen certainly showing the fronto-parietal suture, which is obscured by a large crack in the holotype, is a fragment from the interorbital region, specimen *R*.

The form of the orbit in skull *A* is completely preserved, although the preserved bone is confined to the median side. The whole right orbit is defined as a natural cast, the original space having been filled with a plug of matrix. It is somewhat quadrangular in shape and faces obliquely upwards.

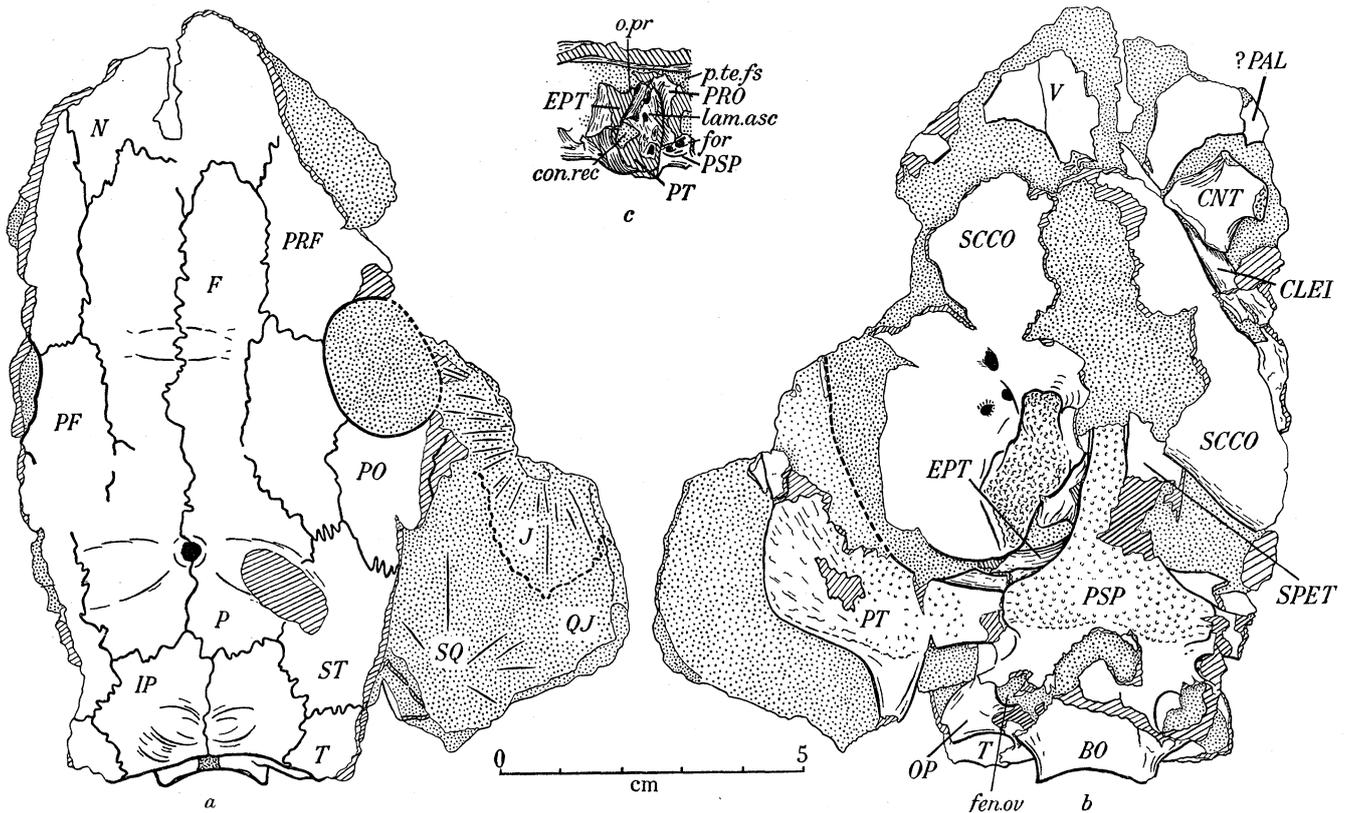


FIGURE 1. Skull *A* (magn. $\times \frac{4}{5}$). Matrix stippled; sutures and edges traced across matrix, heavy broken lines. (For explanation of abbreviations used in figures see p. 281.) *a*: dorsal; *b*: ventral; *c*: view of basiptyergoid region from left side.

Laterally to the orbit in the preserved natural cast, there is a ridge of matrix running vertically downwards, which probably marks the suture at the anterior border of the jugal. In the absence of any traceable prefrontal-lacrimal suture it seems probable that the lacrimal was excluded from the orbit and that the whole anterior part of the orbit was occupied by the prefrontal.

The radiating ridges in the natural cast of the jugal converge to a point just outside the preserved region, and the centre of ossification must therefore have been near to the lateral edge of the bone. In this lateral region the cast of the cheek curves rapidly down to palatal level, and at a point just posterior to the presumed position of the centre of ossification, appears to be wrapping round, becoming continuous with the bones of the palate, suggesting the presence of a palatal ramus of the jugal (processus alaris: Bystrow & Efremov 1940).

No suture between the quadratojugal and squamosal could be traced, although the radii on the cast of the latter bone suggests that the suture ran directly posteriorly. The squamosal probably extended forward almost to the level of the orbit as a tapering bone.

The most distinctive feature of the tabular, seen in skull *C*, is a large tabular horn, broken off posteriorly, which rises about a centimetre above the general level of the roof. This horn extends forward to the supratemporal region and must have originally extended back well behind the skull margin, probably as a large globular mass of bone.

Skull *C* shows that the supratemporal formed part of the border of the otic notch, sending back a thin process between tabular and squamosal to reach the notch margin. A short extent of the notch margin is preserved and the sutures bounding the supratemporal can be traced both dorsally and on the under surface of the roof. About a centimetre of the preserved notch border is formed by the squamosal, and this border runs forward parallel to the direction of the tabular horn. Below it there projects outwards the beginning of a shelf from the squamosal, which, with the quadrate ramus of the pterygoid, would form the hind wall of the subtemporal fossa.

Occiput

In skull *A* most of the occiput itself is preserved, including the single but bipartite condyle and the region between it and the skull roof (figure 2*a*): in skull *B* the occiput is preserved on the right side to a point part way along the paroccipital process and includes a complete right exoccipital. The occiput of skull *C* is much distorted as a result of the horizontal rotation of the skull roof relative to the palate, though the distal tabular region is well preserved.

It seems probable that, due to damage in the parasphenoid region, skull *A* does not give a true idea of the angle of the occipital surface. In skulls *B* and *C* the backward slope of the occiput is much more marked, though this may have been exaggerated by crushing.

The bounding suture of the interparietal of skull *A* was completely traced, and on neither side does the bone reach the foramen magnum. Ventrally the suture crosses the border of a deep excavation in the bone surface on each side near the midline. This pair of pits are presumably for insertion of axial neck musculature. Distal to the pit the right interparietal appears as a thick sheet of bone overlapping the occipital tabular at its edge, and marked with clear radial striae. It is remarkable in not reaching the post-temporal fossa, being separated from it by the tabular and exoccipital.

The region of bone between the interparietals and foramen magnum presumably represents an ossified supraoccipital, though its suture on each side with the exoccipitals could not be made out. After removal from the palate the lower surface of the roof of skull *C* showed a distinct supraoccipital ossification below the interparietals and attached to their ventral surface. Anteriorly, the surface of this ossification is roughened to take cartilage, but posteriorly it is of smooth finished bone (figure 2*d*).

The occipital condyle is single, but has a marked constriction in the middle. Its articular surface is roughened for cartilage and the sutures on this surface separating the lateral exoccipitals from the median basioccipital cannot be made out. The exoccipital-basioccipital suture is, however, visible on the ventral surface of skull *B* (see below). The roughened condylar surface is concave about a vertical axis, but has no curvature from

top to bottom. A similarly roughened concave groove about 0.3 cm wide runs from it along the floor of the foramen magnum, and below this on the articular surface there is a shallow pit of about the same diameter to take the end of the notochord.

The exoccipital reaches the interparietal and tabular in a more or less horizontal suture and has only a short process buttressing the paroccipital. There is a large vagus foramen below the corner of the post-temporal fossa, on about the same level as the top of the condyle in skull *A* and somewhat lower down in skull *B*. In the latter, removal of the skull roof exposed the course of the nerve running obliquely forward and inward at an angle of about forty-five degrees. A smaller foramen, presumably for the hypoglossal (Watson 1919; Säve-Söderbergh 1936), can be seen about 2 mm below and behind the vagus. In skull *B* it is possible, after acid development, to push a bristle through its entire length. It emerged in the lateral corner of the foramen magnum, about 2 mm from the posterior edge, near two similar foramina; and there are three foramina similarly situated within the foramen magnum of skull *A*.

The tabular sutures proximally with the exoccipital, between the interparietal and the post-temporal fossa. It tapers distally, forming a strongly overhanging roof to the oblique post-temporal fossa, and at its end it sends a process down, curving round the end of the fossa, to buttress the end of the paroccipital. This process of the tabular is complete in skull *C*. A small part of the supratemporal is continuous with it and apparently this bone also contacted the paroccipital process to a limited extent.

The paroccipital process tapers markedly towards its contact with the tabular, from about 0.6 cm at the exoccipital to 0.2 cm. The rounded dorsal and ventral surfaces meet posteriorly in a ridge somewhat dorsal to the midline. There is a slight distal expansion for the tabular contact preserved in skull *A* apparently to its true distal end.

Palate

Apart from the parasphenoid and the proximal region of the pterygoid the bones of the palate are preserved only in skull *A*. The scapulocoracoid associated with this skull covered the region of the processus cultriformis of the parasphenoid leaving only the posterior part of the latter, and occupied most of the interpterygoid vacuities. Part of the girdle was later removed, however.

The condition of the bones of the palate is very much poorer than that of the roofing elements. The exposed part of the processus cultriformis is much eroded, and a dent in the basisphenoid region has resulted in the loss of some bone from the body of the parasphenoid. Fortunately, however, the parasphenoid of skull *B* is well preserved and almost complete, including part of the processus cultriformis; and the body of the bone is quite well preserved in skull *C*.

The vomers are present in part on both sides of skull *A*, though medially they are broken away so that the suture between them is not preserved. The right one shows the edge of the interpterygoid vacuity along most of its posterior border, and also what may be the border of the internal naris. The left vomer is preserved to a similar extent though its border along the edge of the vacuity is somewhat more broken. Laterally a small piece of bone is displaced under the main sheet, and this may be the beginning of the palatine.

The right border of the processus cultriformis of the parasphenoid in skull *B* is almost complete throughout the preserved length, but the left is only complete posteriorly. In ventral view it shows a central region of thick, somewhat convex bone covered with fine denticles, which extend on to the body of the parasphenoid. This central region of the process is flanked by lateral flanges. The whole process is remarkably narrow and tapers from about 1.2 cm at its posterior base to an estimated 0.3 cm at the forward limit of preservation. The dorsal side of the process is visible due to complete acid development of skull *B* (figure 2*b*). It is slightly concave becoming more so anteriorly. Posteriorly two rather ill-defined shallow grooves can be made out on the upper surface marking the course of the internal carotids; these diverge anteriorly and finally reach the borders about 1.2 cm from the base of the process.

The main body of the parasphenoid is roughly pentagonal and is connected by a suture, visible in all three skulls, to the basal region of the pterygoid. Its anterior margin is very thick, particularly laterally, and near the suture an additional thickening shows as a vertical wall in front view. The suture is about 0.8 cm wide. Just inside it, on the parasphenoid, there runs a parallel ridge at the level of the back of the basicranial junction. Posterior to this the bone is smooth and the whole surface concave. It underlies both the central part of the otic region and the fenestra ovalis of each side. In this region the body of the bone is produced outwards as a horizontal lappet on each side, partly preserved in skull *A* and completely on the right in skull *B*.

This lappet may be identified with the similar structure described by Watson (1919) as arising from the parasphenoid in *Lydekkerina huxleyi*, and described by Säve-Söderbergh (1936) in *Aphaneramma* and *Lyrocephalus* as the parafenestral crista. Posterior to the crista there is on each side a laterally placed semicircular area, presumably for muscle insertion, bounded by a sharp ridge.

The basal region of the pterygoid is preserved at least in part in all three principal skull specimens. The covering of denticles, present on the anterior part of the parasphenoid, extends on to the pterygoid, although a gap of about 0.5 cm of plain bone is present next to the suture.

This region, seen in skulls *B* and *C* and as a longitudinal section on the left side of skull *A*, is covered dorsally by two laminae which arise from the anterior and posterior edge of the pterygoid. They join about 3 mm above its dorsal surface to form the lamina ascendens and to enclose the conical recess for the reception of the basiptyergoid process of the basisphenoid.

The lamina ascendens, whose true median border is preserved on the right in skull *B*, extends inwards considerably, to overhang the parasphenoid region. In skull *A* it is sandwiched between the epiptyergoid anteriorly and the ossified otic notch region posteriorly. It appears to have been attached or even fused to a forward-projecting part of the otic capsule, which separates it from the skull roof, but the precise structure is difficult to make out (figure 1*c*).

The conical recess takes the form of a shallow pocket, best seen in skull *B*. The anterior part of this pocket is deepened and conical and the anterior wall is quite thin. The floor slopes forward and downward to within 6 mm of the ventral surface of the pterygoid and the recess appears as an equilateral triangle in section.

The lamina ascendens continues laterally then turns sharply back becoming the quadrate ramus of the pterygoid. Just over a centimetre of this is preserved on the right side of skull *A*. Viewed from below it appears as a tapering column 0.9 cm wide at its junction with the body of the pterygoid, 0.4 cm. wide one centimetre back. This ventral exposure,

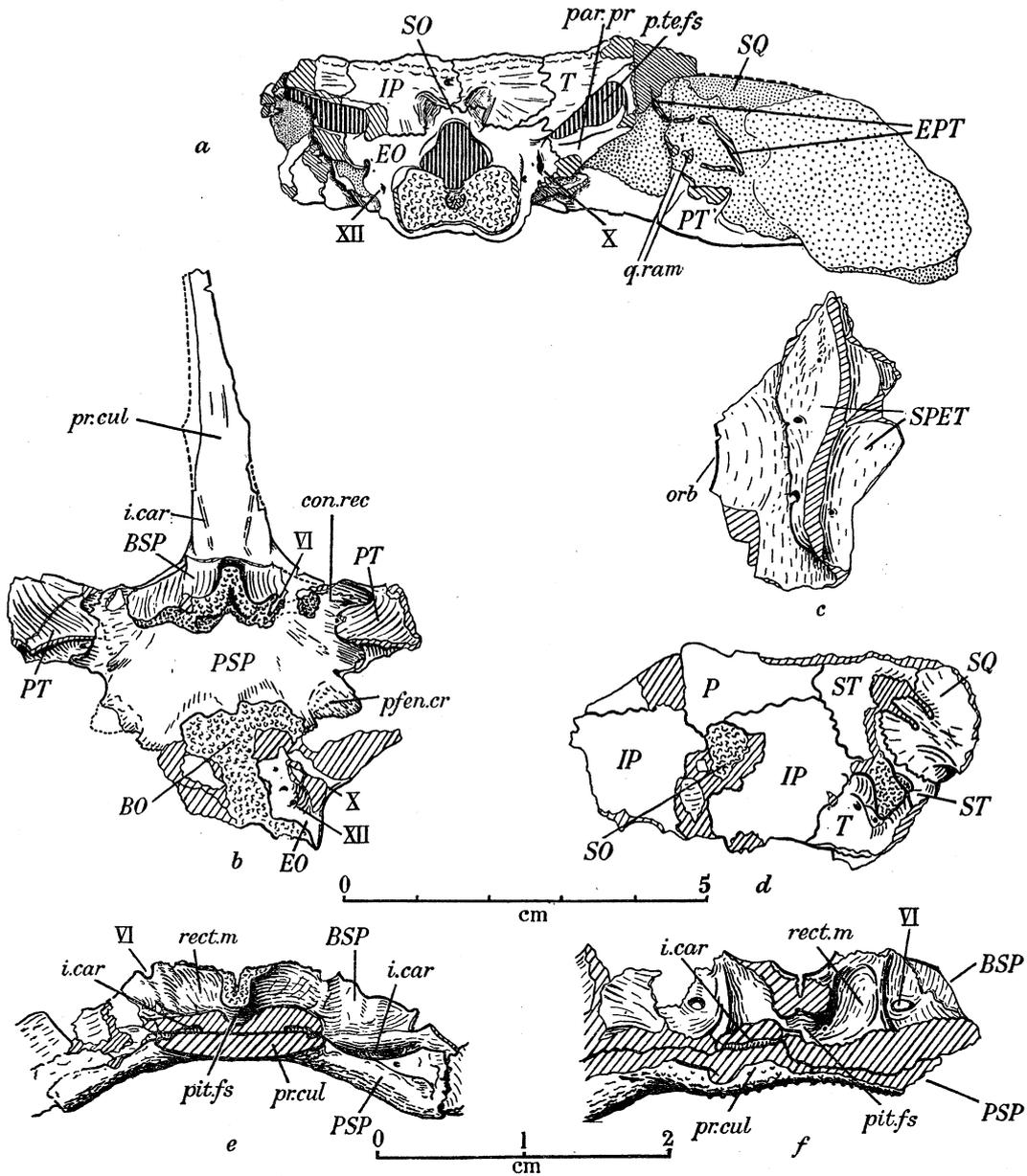


FIGURE 2. Skull. *a-d*: natural size; *e, f*, twice natural size. *a*: skull *A* occiput; *b*: skull *B* after removal of skull roof, dorsal; *c*: specimen *R*, ventral; *d*: skull *C* roof, ventral. *e* and *f*: front view of basi-cranial region from level of base of processus cultriformis, dorsal roof removed; *e*, skull *B*; *f*, skull *C*.

however, merely represents a thick laterally turned rim to a vertical sheet continuous with the lamina ascendens. Part of the sheet is preserved adhering to the matrix of the cheek region of the specimen but it is incomplete dorsally.

The inner margin of the palatal ramus is preserved as bone, somewhat doubtfully, for only a short extent, though the outer edge extends to the front of the subtemporal fossa.

Beyond this for about 3.5 cm its impression is preserved in matrix, though the edge of the cast may not represent the true margin.

The preserved bone shows evidence of considerable crushing and was probably originally at the level, along its outer margin, of the lowest point of the jugal: this outer margin has a distinctly thickened rim. The medial part of the palatal ramus is covered with denticles continuous with those that start a little way out on the basal region. Laterally, however, they merge into a low indistinct ornament of small grooves and ridges.

The epipterygoid is extensively ossified. The large columella cranii was exposed on the right in skull *A* by removal of a part of the scapulocoracoid and development in the sphenethmoid region below it: the whole right epipterygoid seems to have been displaced forwards so that the columella is in front of the basicranial region. It appears as a thick ventro-laterally directed rod of which only the rather flat ventral surface is exposed: laterally this surface twists, so that in the region of the basal articulation it faces posteriorly to some extent, parallel to the lamina ascendens of the pterygoid.

In the section seen at a fracture in the pterygoid just medial to the origin of the quadrate ramus in skull *A*, a bone which is probably the epipterygoid can be seen still running parallel to the lamina but displaced anteriorly away from it. Here the quadrate process of the epipterygoid, if such it be, reaches the skull roof, but is only preserved ventrally to a point 4 mm above the pterygoid. In hind view the lamina, no more than 1 mm thick, can still be seen running parallel and lateral to the quadrate ramus of the pterygoid.

The left epipterygoid is visible from the side of the specimen. Its posterior face is closely applied to the pterygoid and its flat anterior face slopes obliquely forward into the matrix. The transverse section presented is triangular with a concave surface dorsally. At the top hind corner the bone is prolonged into a process, broken off dorsally, which probably contacted the otic capsule. If this was the case the epipterygoid had all three regions, the columella, the otic process and the quadrate process, ossified.

Neurocranium

The form of the otic capsule, which is fully ossified, is preserved only in skull *A*. The structure of the capsule is best seen on the right. The opisthotic extends from the paroccipital process along the floor of the post-temporal fossa. In ventral view the opisthotic is bounded by the border of the fenestra ovalis, which is slightly broken. Laterally to this the wall of the capsule slopes up to the skull roof, gently posteriorly, more steeply anteriorly; so that in the prootic region its side wall appears to be almost vertical, though much of it is concealed by matrix. The ventral surface in this prootic region is a narrow horizontal strip of bone about half a millimetre wide.

Posteriorly the ossification of the otic region extends laterally to the limit of the post-temporal fossa, anteriorly to the region of the basicranial suture. The fenestra ovalis was apparently a large aperture with a diameter of about 0.5 cm. Only the lateral half of its border is preserved and medial to it no otic ossification is visible. No suture could be made out in skull *A* dividing the prootic from the opisthotic.

On the left it is possible to see the post-temporal fossa extending forwards as a sagittal section to a point nearly above the lamina ascendens of the pterygoid: it is thus about 1.5 cm

deep. There is no sign of any neurocranial ossification in the roof of the fossa. As described, the otic capsule comes to overlie and possibly to fuse with the pterygoid anteriorly and also probably contacts the epipterygoid.

The basioccipital has a wide ventral exposure. At the sides it extends far forward, but medially it is underlain by an extension of the parasphenoid so that its midline exposure is narrow. It forms the major part of the ventral border of the condyle, but it is doubtful whether it formed a very great part of the body of that structure.

The dorsal surface of the basioccipital was exposed by development and removal of the skull roof in skulls *B* and *C*, and is well preserved in the former (figure 2*b*). In this skull it extends forward over the upper surface of the parasphenoid to the region of the parafenestral cristae, but in skull *C* it is more completely ossified reaching to within half a centimetre of the basisphenoid ossification at the level of the back of the basicranial articulation. Its whole upper surface is roughened to take cartilage in the same manner as that part which forms the floor of the foramen magnum.

The basisphenoid ossification was exposed by complete development in skull *B* and in skull *C*. It covers the anterior part of the body of the parasphenoid immediately behind the processus cultriformis. The whole of its posterior surface is roughened in typical manner for the attachment of cartilage.

The central region has a vertical posterior surface about 0.4 cm high. In skull *B* (figure 2*e*) this cartilage-roughened surface continues as the dorsal surface, and in the midline, and to a lesser extent laterally, the cartilage surface moves forward to overhang the smooth anterior face of the bone. The latter is markedly concave and is thus divided into two shallow pockets with the forward extension of the cartilage-bearing surface coming to face anteriorly between them. The surface of the smooth bone extends forward to the base of the processus cultriformis, where it is broken off. Between the two pockets there is a deep recess, formed by the overhang of the midline region and depression of the floor; this is the pituitary fossa. The whole concave surface of this central region represents the posterior wall of the canal transmitting the interorbital vein, enlarged as the interorbital fenestration. Its great enlargement and the development of the pockets, is probably for the origin of the rectus musculature of the eyes, as noted by Sawin (1941) for *Eryops* and Säve-Söderbergh (1944) for an unnamed Triassic amphibian. Thus both the anteriorly facing part of the cartilage surface and, below it, the broken edge were originally connected to the sphenethmoid region, the former by cartilage.

The corresponding region of skull *C* (figure 2*f*), though less well preserved, is much more heavily ossified. In the midline the dorsal surface is the actual smooth floor of the braincase, but lateral to it the dorsal surface is cartilage finished.

The greater ossification of the basisphenoid of skull *C* also extends to the lateral regions. In skull *B* it seems probable that there was no ossification of the basitrabecular processes: in skull *C* the right side, though very disrupted, appears to extend very far laterally and in this skull an ossified basiptyergoid process may have been present. On the right in skull *B*, just lateral to the ridge separating off the region of the interorbital fenestration, a groove of smooth bone representing the floor of the course of the sixth nerve passes back over the cartilage surface (cf. *Aphaneramma*: Säve-Söderbergh 1936): in skull *C* the course of this nerve perforates the body of the bone as a large oval foramen.

Anteriorly a deep groove running parallel to their edges separates the parasphenoid from the basisphenoid. Medially this groove terminates at the origin of the carotid groove in the processus cultriformis: laterally it deepens and terminates in a foramen between the two bones, so that it presumably marks the course of the internal carotids.

The sphenethmoid region of the cranium is fairly completely preserved in skull *A*, though the state of preservation is rather poor. Part of the right ventral wall is preserved in skull *B*, and the skull fragment, specimen *R*, shows the contact of the sphenethmoid ossification with the skull roof in the interorbital region.

The sphenethmoid region of the cranium was exceptionally heavily ossified, although separated by about a centimetre from the otic region. A break across the middle of skull *A* gives a section which suggests that the sphenethmoid was a massive, dorso-ventrally flattened cylinder of bone, complete dorsally and probably ventrally, and extending forward to within 2 cm of the front margin of the interpterygoid vacuities.

Posteriorly a narrow ventral ossification on the parasphenoid extends back to the basal region. Near the posterior edge is centred a large foramen for the optic nerve.

In specimen *R* (figure 2*c*) the sphenethmoid ossification is very closely applied to the skull roof, particularly in the midline where in transverse section it is only possible to distinguish the two by the more porous texture of the former. As it progresses anteriorly the outer surface of the lateral wall of the sphenethmoid, which is somewhat concave, becomes less vertical, inclining inwards ventrally. Thus at the front it spreads out laterally over the underside of the roof. At the posterior limit of the specimen only the beginning of the side wall (about 0.3 cm) is preserved; but it appears, unlike the rest of the wall, to slope outwards as it descends, so that a small pocket is enclosed between it and the skull roof. Near the front of the specimen there is a broken area internally, suggesting the existence of a vertical transverse partition in the sphenethmoid.

Quadrate region

The only specimen in which the quadrate region is preserved is from specimen *P*. This consisted of three separate pieces of bone enclosed in the same small piece of matrix. Two of these are pieces of either the margin of the skull or the lower jaw: the third is a right quadrate with part of the quadratojugal and possibly some of the squamosal attached.

The quadrate specimen may be divided into two regions; the quadratojugal region which is ornamented externally and the region which includes the quadrate itself. This latter is at an acute angle to the quadratojugal region and is not ornamented on its external surface. Both branches of the specimen are broken off anteriorly. There is no sign that the junction between them, over which the surface is well preserved both internally and externally, has been in any way distorted.

The quadratojugal branch, which would continue as the cheek region of the skull, is complete along its ventral edge for about 2 cm. The ventral surface is smooth and more or less flat with rounded edges: about 1.5 cm from the hind edge there appears to be a foramen, the accessory quadrate foramen (cf. *Benthosuchus sushkini*, Bystrow & Efremov 1940), but it is blocked with bone and may be artifact. If in orientating the specimen it is assumed that this ventral surface is horizontal, the ornamented side wall is vertical, becoming rounded off dorsally where it joins the quadrate branch. This dorsal edge of the cheek is

preserved for a considerable distance and thus gives the angle of slope down to the lateral corner of the skull.

The quadrate branch, which includes the region of the condyle itself, must form the lateral extremity of the hind surface of the skull. Its external surface, which faces posteriorly and dorsally, is scored and cracked so that it was not possible to trace any sutures

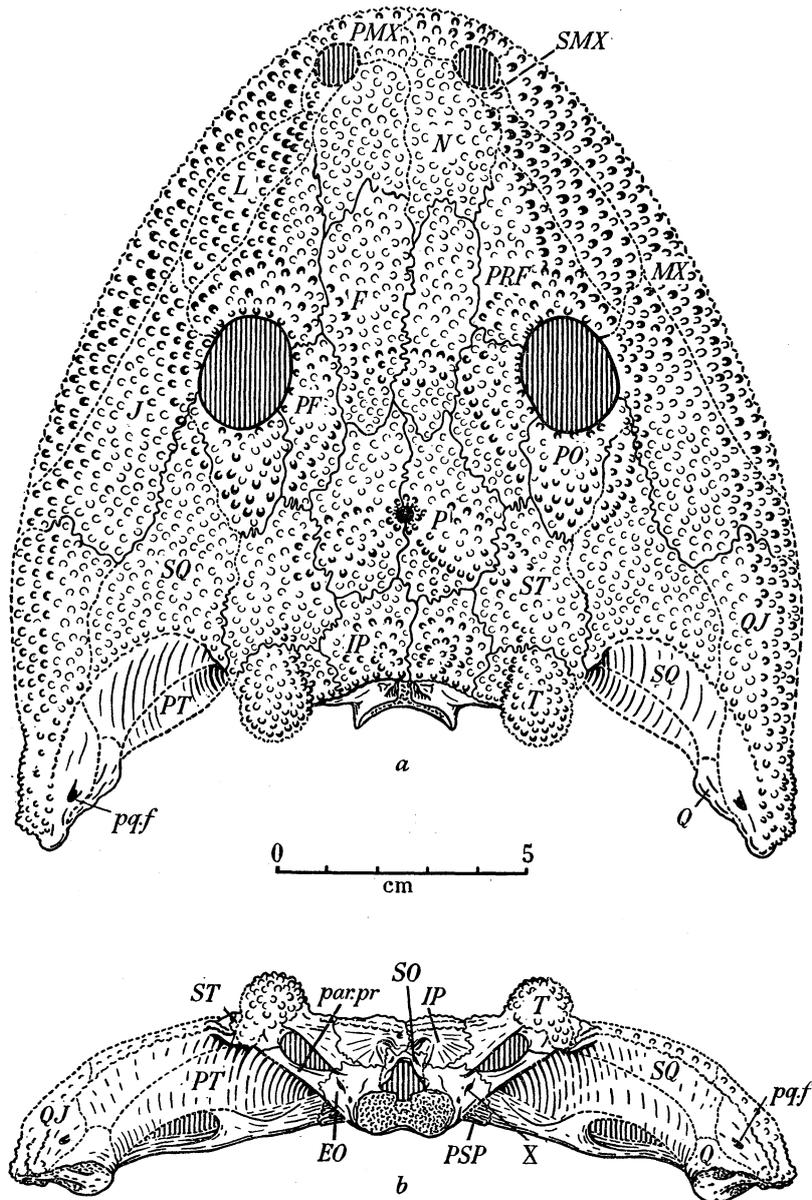


FIGURE 3. Composite restoration of the skull. Two-thirds natural size.
a: dorsal view; *b*: occipital view.

across it. It would be expected, however, to be in part quadratojugal. It is perforated by the paraquadrate foramen which usually either passes between the quadrate and quadratojugal or perforates the quadratojugal. The internal opening of this foramen is probably marked by another situated on the internal surface between the two branches, though no connecting canal was cleared in development.

Medially the bone of the quadrate branch thickens and terminates in two rounded eminences, somewhat damaged, lying internal to the broken edge. The condylar surface is probably formed by these eminences, which in life may have been built up to some extent in cartilage. If the side of the quadratojugal was approximately parallel to the axis of the skull, and so followed the line of the cheek, then the eminences would be well forward of the lateral corner of the skull, and if orientated in this way they are in a suitable position to articulate with the region of the articular in the preserved lower jaw.

Reconstruction of the skull

The holotype skull (specimen *A*) has been used as a basis for restoration (figures 3, 4), but data from the other specimens have been incorporated to give a composite picture. Direct measurement of all specimens in which a sufficient region is preserved suggests that they represent skulls of approximately the same size, so that a direct transfer of data is possible.

The natural cast of the lateral regions in skull *A* are assumed to be near the true depth of the skull border as they reach the level of the lateral palatal elements, and the cheek cast also gives the width and form of the cheek posteriorly. Slightly more anteriorly an isolated fragment of skull, specimen *Q*, which includes part of the orbit edge and extends to the skull margin, gives the curve of the edge lateral to the orbit and the course of the median jugal suture.

The shape of the occiput is from skull *A* proximally and skull *C* in the tabular region. In the former a swing forward *post mortem* due to the damage in the parasphenoid region was allowed for, and the form of the occipital condyle is nearer that of skulls *B* and *C* than the rather rectangular form in skull *A*.

The orientation of the quadrate suggested in the description of specimen *P* has been adopted, and the horizontal lower edge of the quadratojugal region of that specimen then continues the line of the posterior cheek restored from skull *A*. The slope of the top of the quadratojugal region of specimen *P* could then be used to give some idea of the posterior extent of the corner of the skull behind the occiput.

As no suture was found cutting the front of the orbit the prefrontal has been restored excluding the lacrimal from the orbit edge and extending round to the jugal suture found as a natural cast. No junction of the nasal and maxilla in front of the lacrimal has been restored: such a condition, with exclusion of the lacrimal from the orbit as well, is characteristic of very long-snouted species.

As the skull was so highly ossified the quadrate ramus of the pterygoid and the occipital exposure of the squamosal have been restored to give a complete bony hind wall to the subtemporal fossa, but there is no evidence of this.

The relations of the outer palatal bones, the palatine and ectopterygoid, and their junction with the pterygoid, have been restored by comparison with labyrinthodont skulls with a similar development of the vacuities. A small palatal process of the jugal, the processus alaris, has been restored in view of the strongly developed turning under of that bone.

Lower jaw

Two certainly identifiable lower jaw specimens are preserved, both from right rami. One is from the small block *L* and was associated in the block with fragments of scutes, a piece

of rib and several minute scraps including a possible toe bone. It is the posterior end of the ramus and includes the regions of the articular and part of the adductor fossa. The other specimen is a more anterior part of a ramus from block *G* and is numbered *G19*. It was associated with scutes, dorsal vertebrae and ribs.

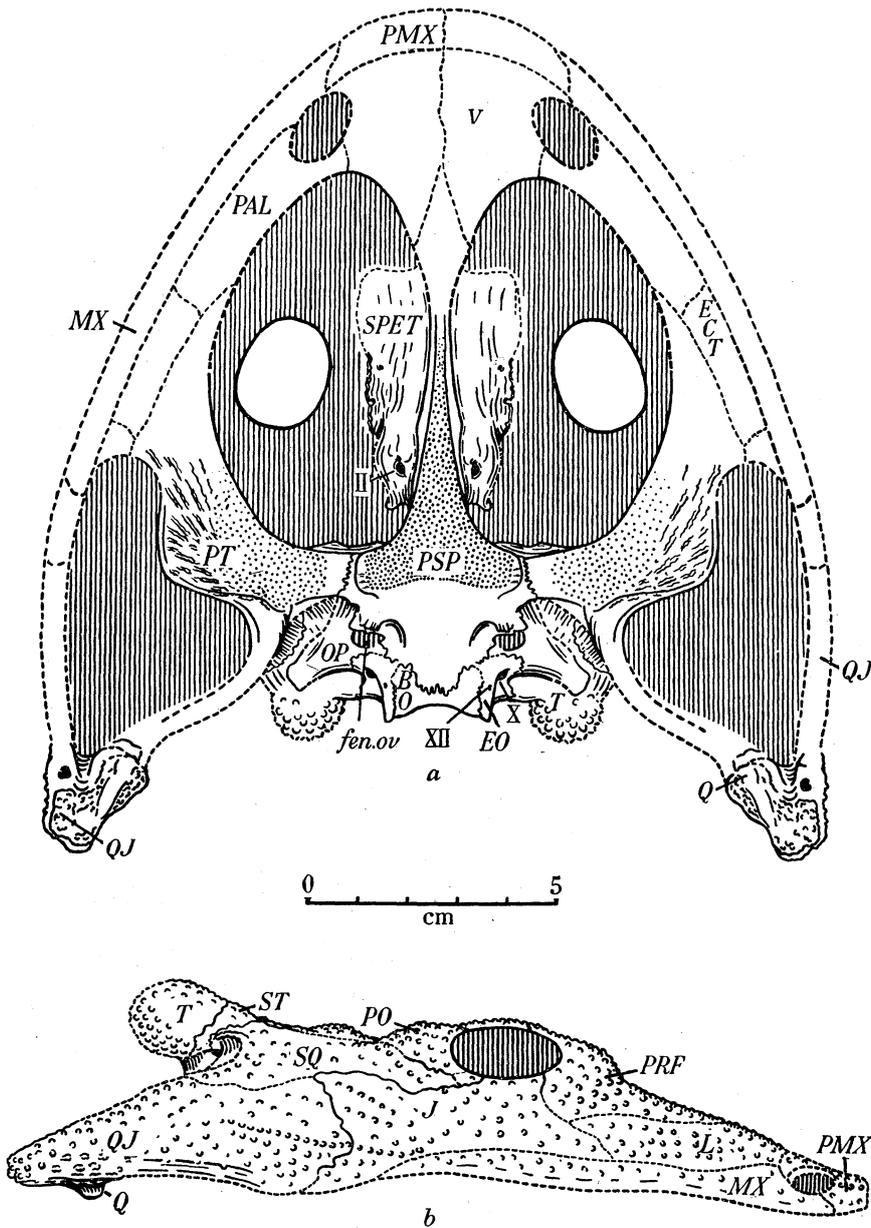


FIGURE 4. Composite restoration of the skull. Two-thirds natural size.
a: palatal view; *b*: side view.

Apart from the surface of the anterior condyle itself, the former specimen is in an excellent state of preservation, and the sutures can be made out easily both internally and externally (figure 5*a-d*). The lateral external surface is ornamented with pustules. These tend to be arranged, particularly on the angular, in single parallel rows along well-marked ridges, but in the retroarticular region the linear arrangement is less marked.

Nowhere on the surface is there any sign of a lateral line canal. The medial surface is smooth and unornamented, though ventrally the ornament extends round beyond the midline on to the medial surface for a short distance.

The retroarticular process, formed from the surangular, has the well-developed rounded point typical of more advanced labyrinthodonts, but medially and slightly anterior to this there is a second well-defined process with a marked ventral keel. This second process projects slightly below the general level of the lower surface and has a thickened, rounded termination.

The posterior end of what is presumably the dentary forms most of the preserved lateral edge of the adductor fossa. A groove in its wall may mark the course of a process from the surangular.

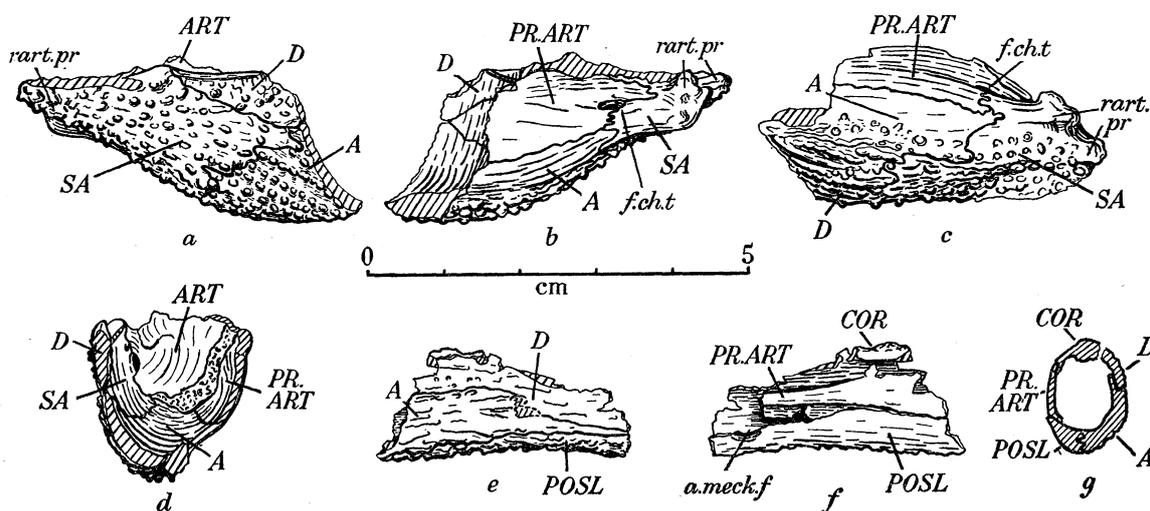


FIGURE 5. Lower jaw. Natural size. *a-d*: rear end of right ramus; *a*, lateral; *b*, medial; *c*, ventral; *d*, anterior. *e-g*: middle region of right ramus: *e*, lateral; *f*, medial; *g*, posterior.

The angular is considerably thicker than the other dermal bones, particularly in the ventro-lateral region, where it forms a strong keel to the jaw ramus. Its bounding sutures were traced completely on the outer surface and as far as possible within the fossa: the amount of overlap with the adjacent bones was thus seen to be very slight.

The articular is completely preserved except for the region of the condyle which is badly eroded. It forms the complete hind wall of the fossa, which faces somewhat laterally and is concave. At the medial wall, formed by the prearticular, the articular terminates in a concave forward-facing roughened surface, to which Meckel's cartilage was attached in life. In the angle between the smooth anterior face of the articular and the inner surface of the surangular there is a large foramen passing back along this inner surface.

Dorsally this junction between the articular and the surrounding dermal bones is visible only along the undamaged articular-surangular surface. Due to the erosion of most of the rest of the dorsal surface, it cannot be determined whether a distinct suture was present or whether some degree of fusion has taken place. The form of the eroded surface suggests that the position of the articulation was on the anteromedial part of this surface, at the level of the tip of the dentary and of the foramen chordae tympani. This is the

normal position in the labyrinthodonts, the main body of the articulation always being somewhat medial to the midline of the ramus (Nilsson 1944).

Specimen *G19* (figure 5*e-g*) originally lay crushed flat in the matrix. It was completely developed and in mending an attempt was made to restore it in the round. The whole specimen is very much cracked, but owing to the considerable overlap of the individual bones it is not difficult to distinguish sutures from cracks. The specimen, as far as can be judged, tapers quite considerably towards the anterior end and so probably comes from a fairly posterior region, but the presence of a thickened region with possible teeth as points on the coronoid suggests that it is anterior to the adductor fossa.

The dermal ornament, present only on the lateral face, again has the pustules drawn out along well-marked ridges. It is much more clearly developed ventrally than dorsally on this surface.

The probable identity of the individual bones is based on the assumption that the specimen is from the region immediately in front of the adductor fossa and is comparable with other fairly advanced labyrinthodonts (Nilsson 1944).

Vertebrae

The largest series of dorsal vertebrae, comprising twelve centra and six neural arches, are preserved, many in perfect condition, from block *D*. They are not, however, articulated and the only articulated series of any length is from block *E* (figure 6), though two centra, with a fragment of a third, articulated with their neural arches, come from block *G*. All these vertebrae are from the dorsal series and to them must be added the single centrum associated with skull *A*, which is unique in appearance, and probably comes from the region immediately behind the skull.

Block *F* contained undoubted caudal vertebrae bearing haemal arches, and two centra from block *I* are probably caudal. A single centrum and a neural arch, both very crushed, are preserved from block *N*.

Dorsal centra

The typical dorsal centra (figure 6*c-e*) are amphicoelous cylinders, slightly constricted between the ends. Every centrum is clearly notochordal, with a central perforation of about 1.5 mm diameter. A prominent ridge rises near the front on each side of the centrum and runs back to join the postero-dorsal parapophysis, which projects sideways as a massive process. Distally this bears the capitular facet, indicated by an unfinished bone surface. This facet faces laterally, but is continuous with a dorsal facet on the process, which faces slightly back, for contact with the transverse process of the neural arch.

Paired facets for neural arch articulation are situated anteriorly on the dorsal surface of the centrum and slope forwards at about twenty degrees to the horizontal. Their front edges are continuous with the anterior surface of the centrum, and two wide ridges run back from them to the posterior border. The central part of the dorsal surface is markedly convex and bounded by two parallel grooves which extend right along the centrum.

In some of these centra there is a pair of backwardly-facing neural arch facets bordering the posterior edge of the centrum and terminating the ridges from the anterior facets. In others the ridges end as irregular rounded knobs, and conditions intermediate between the

two forms are also present. There appears to be no regional significance in this. There is, however, some slight variation in the length of the centra and also in the span of their transverse processes: two centra from block *D* which are probably from the extreme posterior dorsal region are extremely short in length and span.

They also differ from the typical dorsals in the form of the processes bearing the rib facets, the size of the notochordal perforation and the shape of the ventral surface of the centrum body. The parapophyses are very short in span, situated somewhat lower than in the typical dorsals and have little or no neural arch facet running along their upper surfaces, there being merely an oval capitular facet at the end. The ridge running forwards from the parapophysis is very low, rounded, and difficult to distinguish; but ventrally on the body of the centrum there are signs of a double keel formed by two low ridges running antero-posteriorly about 5 mm apart. The notochordal perforation is rectangular and larger than that of typical dorsals.

The very anterior centrum associated with skull *A* has its left side much eroded, but the dorsal surface and the right side are well preserved. The small posterior neural arch facets are very well developed in this centrum and the body of the centrum is somewhat more constricted than usual; but the most distinctive feature is the form of the parapophysis, which is not dorsally placed, but is situated about half way down the centrum at its posterior end. The process itself, which is somewhat eroded, is very short, and the articular surface, which faces postero-laterally, is continuous with the posterior surface of the centrum; the whole parapophysis being an expansion of the body of the centrum rather than a distinct transverse process. Though small the centrum is elongate as compared to its height and has a very small notochordal perforation.

Dorsal neural arches

Typically the neural arches are high with long spines and wide massive transverse processes at right angles to the axis. The transverse process is deep and expands laterally to a variable degree towards the terminal facet for the tuberculum, which is convex in anterior view and continuous with a ventral facet for the articulation of the parapophysis of the centrum. This ventral facet is inclined slightly forwards and the whole process is set at a slight angle corresponding to that of the parapophysis.

Ventrally on each side of the neural canal are facets for articulation to the body of the centrum, well developed posteriorly, corresponding to the anterior facets on the centrum and facing back; less sharply defined anteriorly corresponding to the incipient posterior centrum facets.

The prezygapophyses typically have a marked slope so that the facets, which are sub-circular in outline, face inwards as well as upwards. They are quite separate from each other and each is connected to the neural spine by a prominent ridge at right angles to the plane of the facet.

The neural spine is high and narrow, but quite deep antero-posteriorly, and tapers dorsally. The three specimens with complete spines from block *D* (figure 6*a, b*) form an interesting morphological series. All were preserved near the pelvis and sacral rib in the block. *D15* has a high, bluntly pointed spine and is similar to those from block *E*. In *D18* the spine is truncated in side view and in front view expands towards the tip. It

terminates in a shallow horizontal groove 6 mm wide, 1 mm deep and 5 mm long, running antero-posteriorly. The function of this groove seems to be to take the median ridge on the under surface of the posterior dorsal dermal armour. The spine of the third block *D* arch,

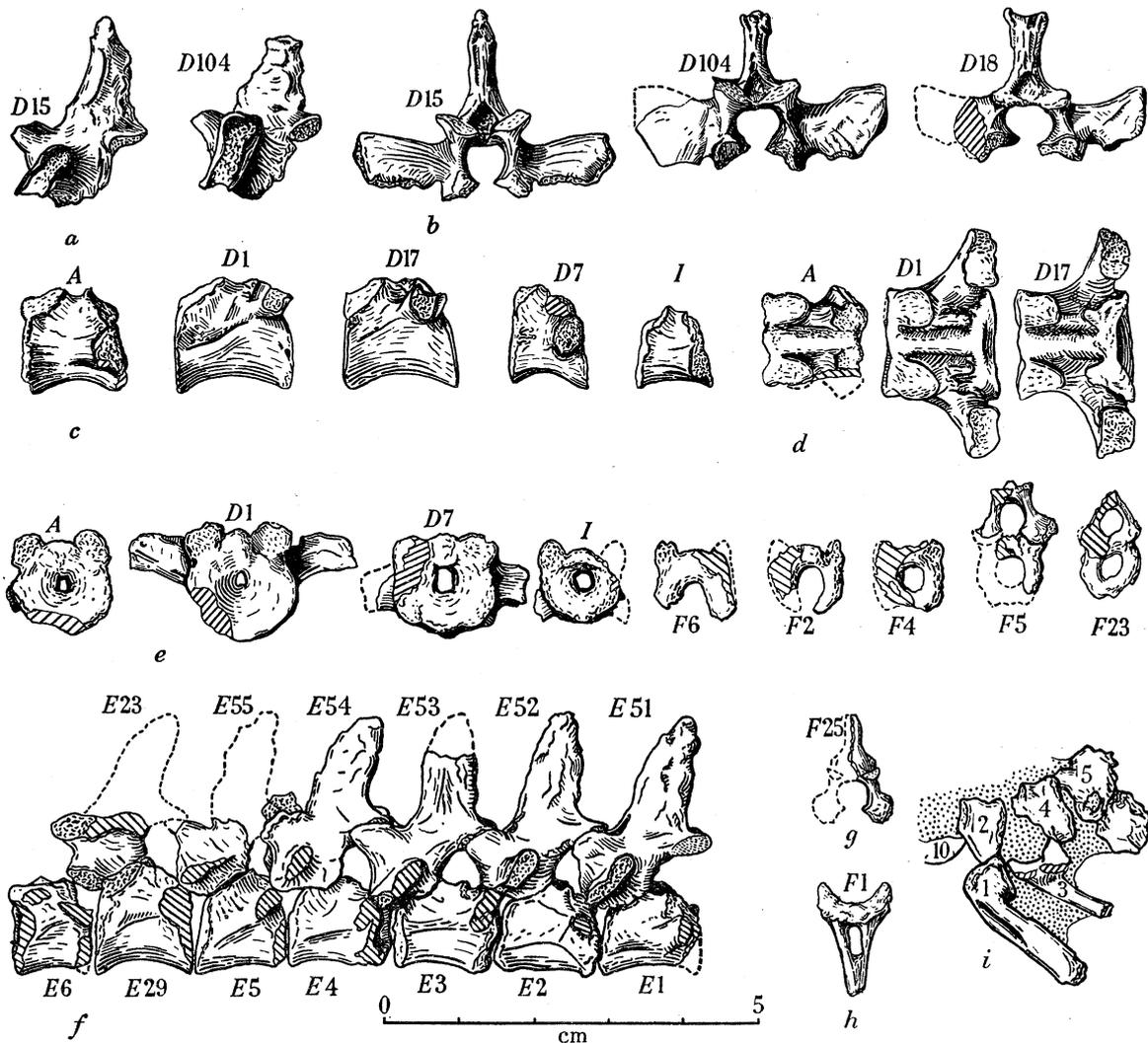


FIGURE 6. Vertebrae. Natural size. *a, b*: posterior trunk neural arches; *a*, lateral; *b*, front view. *c-e*: centra; *c*, 'cervical', mid-dorsal, posterior dorsal, presacral, early caudal in side view; *d*, in dorsal view; *e*, dorsal and caudal centra in front view. *f*: articulated dorsal vertebrae (block *E*). *g*: caudal neural arch, front view. *h*: haemal arch, front view. *i*: block *F* caudal vertebrae, partly developed.

D104, shows an intermediate condition. The spine is truncated but not greatly expanded at the tip and its apical surface, though convex, is bordered laterally by two ridges. The plane of the transverse processes of *D104* and *D18* is much nearer the vertical than that of any other neural arch. Also the transverse process of *D104* is very deep distally though its tubercular facet is not wide enough for the attachment of the large sacral rib.

Neither of the two neural arches from block *G* has its spine preserved, but there is an isolated spine with attached postzygapophyses from that block. This is rather low in comparison with those from *D* and *E*, being thin but very deep antero-posteriorly.

The dorsal series

The centra in the block *E* series were preserved in order and in contact, the posterior five (*E*1–5) retaining their contact with the neural arches (*E*51–55) and the remaining neural arches lying so near the centra that there can be little doubt of their association, and the actual mode of contact can be seen by study of the facets best preserved in the block *D* vertebrae. The neural arches were ‘intervertebral’ in position, each one fitting closely on the broad anterior facets of the body of the centrum behind it and usually just contacting the incipient posterior facets of the centrum in front with no space for additional central elements.

While the principal articulation of the neural arch is with the body of the centrum behind it, there is a strongly developed connexion by the diapophysis to the parapophysis of the centrum in front, so that the processes combine to form a single massive transverse process for the articulation of the rib. Thus it appears that the rib articulation spans two vertebrae.

The close fit of the neural arches between centra and the broadly confluent facets connecting their respective transverse processes must have made the presacral vertebral column a very rigid structure allowing little flexure of the trunk in any plane. Also the plane of the zygapophyses would eliminate the possibility of relative torsion; though the zygapophyses of *D*18, probably the most posterior dorsal neural arch preserved, are nearer the horizontal and would allow more lateral movement between vertebrae in the pelvic region.

From evidence of form and association it is possible to summarize the form of the vertebral elements of different parts of the dorsal series. The most anterior ‘cervical’ centra, represented by that from skull *A*, are elongate and somewhat constricted with a small notochordal perforation. In the ‘thoracic’ region represented by vertebrae from blocks *G* and *E*, the centra are shorter and bear neural arches with pointed spines. The length of the centra would reach a maximum in the middle of the lumbar region, to decline with increasing rapidity towards the sacrum. Posteriorly the dermal armour becomes intimately connected with the vertebral column and the modification of the neural spine for its articulation has been described in the neural arches *D*104 and *D*18.

In the neck region the parapophyses are slightly developed in relation to small cervical ribs. The combined transverse processes in the pectoral region are well developed but the respective parts formed by the centra and neural arches are not extensively bound together, and the rib articulation in this region though strong was probably comparatively loose, presumably to allow for respiratory movements. In the anterior lumbar region the parapophysis and diapophysis are firmly connected and the fit of the rib is also very tight, but towards the pelvic region there comes a second ‘loosening-up’: the area of contact between the parapophysis and diapophysis decreases and the fit of the ribs is probably looser.

Caudal vertebrae

The two centra from block *I*, associated with fragments of pelvis and early caudal ribs, are somewhat more elongate than the most posterior dorsal, *D*7, but in other ways represent a perfect continuation of the morphological series from block *D*.

The parapophyses are situated even lower on the centrum body than those of *D7*, being somewhat ventral to the midline, and are like those of the *A* centrum, being merely expansions of the centrum with their facets continuous with the posterior surface.

The caudal material from block *F* includes five centra, two with neural arches attached, a half neural arch and several fragments, and four haemal arches, associated with caudal ribs and scutes.

The four haemal arches differ from one another in size and form, but are similar in general build. The largest of them, *F1* (figure 6*h*), is complete and perfectly preserved, and another, *F7*, but very slightly damaged. The haemal arches are elongate and when orientated slope back at about forty-five degrees to the axis. Each is fused to a small wedge-shaped intercentrum, which is a shallow crescent in end view, the dorsal surface being roughened and forming the floor of the notochordal canal. This intercentrum is quite distinct in every case from the central element forming the main body of the vertebra and bearing the neural arch.

The five centra preserved from block *F* show considerable difference in form and size. Three of them, *F2*, *F4* and *F5* were preserved in sequence with the haemal arches *F1* and *F3*, the numbers indicating, in this case, the actual order. *F6* is a larger centrum from a more anterior position in the block, which is somewhat similar to *F2*; and *F23* is the smallest preserved centrum from a position in the block posterior to the series. *F5* and *F23* have attached neural arches. All these centra, which form the main body of their vertebrae, are distinct from the intercentra with haemal arches and must therefore be pleurocentra.

Their chief interest lies in the fact that they seem to continue the series of centra seen in the dorsal region and the anterior caudals from block *I*. All but *F23* show steep, widely separated anterior neural arch facets like those of the block *I* centra and have similar wide notochordal canals with convex floors. *F6* and *F2* are crescentic, being open ventrally, and wedge-shaped in side view. In *F6* the two ventral corners are widely divergent and directed downwards, but in *F2* the one completely preserved corner curves under partly to enclose the notochordal canal, though it does not form a complete ring. *F4* lay immediately behind *F2* and in this centrum the closure is complete though the centrum is very short in the ventral midline.

Only part of the left half of the centrum is preserved in *F5*. The attached neural arch is complete except for the postzygapophyses and is well preserved on the left side. It has, in this vertebra, taken up a position directly over the centrum, although the junction surface still faces anteriorly at about thirty degrees to the horizontal. Although the two are preserved attached, the centrum and neural arch are still separate and the neural arch is somewhat displaced upwards.

The neural arch itself is low, and the neural spine does not rise above the level of the prezygapophyses, being merely a median longitudinal ridge. Transverse processes are preserved on both sides antero-ventrally as low conical projections.

F23, from its form and position in the block, appears to be the most posterior vertebra preserved. It is a rather poorly preserved ring-shaped centrum with attached neural arch. Ventrally the centrum has three parallel longitudinal ridges, which probably correspond to the ventral keel and two lateral ridges of more anterior vertebrae. The floor of the neural

canal, formed by the top of the centrum, appears to be somewhat convex, as in other centra. Neither pair of zygapophyses is preserved on the neural arch and owing to its extreme posterior position may not have been present. The neural arch terminates dorsally at a longitudinal ridge, similar to that in *F5*, but this is damaged. A low conical protuberance, terminating in a roughened surface and situated ventrally on one side of the arch, is probably the transverse process.

Complete fusion of the centrum and arch seems to have taken place, though the line of this junction is probably marked by an oblique shallow groove on the side with the preserved transverse process. If, as in other vertebrae, this line slopes forward and downward, it is on the right side.

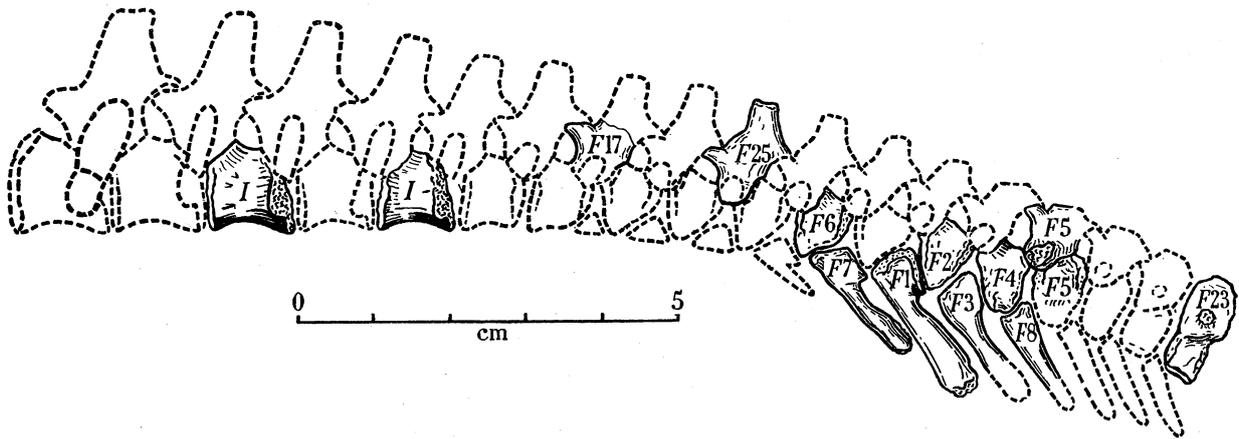


FIGURE 7. Composite reconstruction of the sacral and caudal vertebral column (see text).
Natural size.

F25 (figure 6g) is a well-preserved half neural arch produced by an accurate split down the midline, suggesting that the caudal neural arches, like those of many labyrinthodonts, are easily divided. The size and form of the specimen suggest a position in the vertebral column anterior to those arches already described: it was not, however, preserved in relation to any other vertebral element.

The neural spine rises considerably above the level of the zygapophyses and tapers slightly dorsally: it is, however, flat topped. The transverse process appears as a rounded thickening of the bottom of the lateral surface. The principal centrum facet lies posteriorly to the diapophysis and slopes at an angle of about forty-five degrees, ventro-posteriorly. There is also a small anterior facet below the diapophysis, which is almost horizontal from front to back but faces inwards. The prezygapophysis facet also faces slightly inwards. Several fragments of similar neural arches were also present.

In reconstructing the caudal vertebral column (figure 7) the two block *I* centra have been restored under the pelvic shield and near the sacrum because of their association with pelvic fragments, and the adaptation of their parapophyses to take the deep ribs supporting the shield: the latter would cover four centra and the two preserved have been separated by a restored one because of their disparity in size.

The rest of the tail is restored entirely from material preserved in block *F*. The number of vertebrae restored between the last block *I* centrum and the most anterior one from

block *F* (*F6*) is based on a minimum estimate of the number of caudal ribs behind the shield. Fortunately the smallest and probably most posterior rib was preserved in position between the centra *F2* and *F4* and it is estimated that it is the eighth in the post-shield series.

Ribs

Many dorsal ribs are preserved, but few are complete and only a limited number are associated with the vertebrae to which they belong. The material from block *D* includes the remains of eighteen ribs, seventeen dorsal and one sacral. Of the former, six are from the right side, nine are from the left and the remaining two fragments cannot be determined. Block *E* contained the proximal ends of six right ribs and the remains of five or six left ones together with some fragments, all from the dorsal series. Block *G* has the proximal ends of two right ribs associated with their vertebrae and there is a single well-preserved dorsal rib from block *H*.

The only sacral rib preserved apart from the incomplete *D64* is an almost perfect left rib from block *K*. Three anterior caudal ribs are associated in block *I* with the two described centra and with a ribhead which may belong to one of them. Another rather similar ribhead is preserved from block *K*. A longer series of caudal ribs is preserved from block *F*, and consists of five right ribs, two left and several fragments.

Dorsal ribs

Although there is considerable regional variation, a common pattern may be described for all the dorsal ribs. The head of the rib is divisible into tubercular and capitular regions, but there is no separation into a double head, the two facets, which are confluent though set at an angle to one another, being at the end of a single shaft. This shaft is flattened and in the same plane as the combined transverse process to which it is attached. In those cases where ribs and vertebrae can be fitted together the fit is seen to be very close, and in many it does not seem likely that much movement of the ribs on the vertebrae was possible.

The shaft extends laterally for about 2 cm, at which point the rib begins to broaden out posteriorly to a variable extent. Beyond the shaft it is a sheet of bone facing antero-dorsally, with a thickened leading edge continuous with that of the shaft. The extension of this main surface behind the level of the posterior edge of the shaft changes direction to face dorsally and, with the curve of the rib, laterally. This posterior area, which is very variable in width, represents the main broadening of the rib beyond the shaft and is roughened dorsally by a series of grooves and furrows to take the under surface of the dermal armour. The dorsal surface anterior to this is smooth or scored with fine longitudinal striations. Near the beginning of the scute-bearing surface, about 3 cm out from the ribhead, there is a usually elongate foramen which goes straight through the bone lamina in a horizontal direction, presumably transmitting a nerve or blood vessel. The rib usually tapers distally from the level of this foramen.

The most anterior ribs represented are probably two from block *D* (*D66*, *D68*), both right, which were preserved at the side of the block in close association with the only known humerus.

D68 (figure 8*a*) is remarkably massive and the postero-dorsal edge of the shaft is powerfully thickened along to the level of the raised scute surface. Highly characteristic of this

rib is the fact that the shaft and the main body of the rib meet at a marked angle, so that there is a 'knee' on the antero-dorsal surface at their junction. The shaft is somewhat constricted at this point, the edges being markedly concave. When the ribhead is orientated at a normal angle, the plane of the rib is almost vertical, so that the 'knee' produces a bending back of the main lamina.

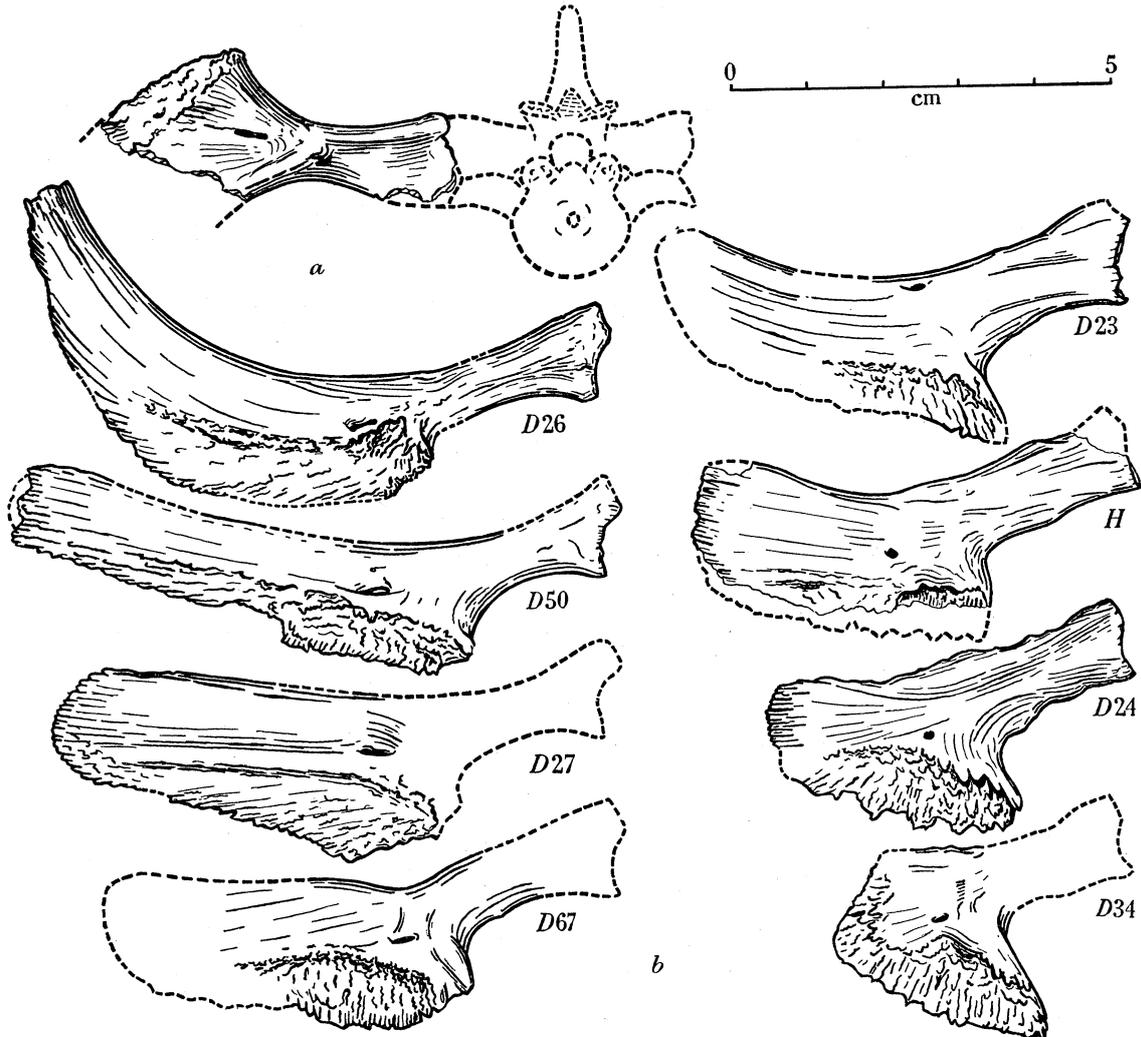


FIGURE 8. Dorsal ribs. Natural size. *a*: pectoral rib, anterior. *b*: a series of left dorsal ribs from blocks *D* and *H* (fourth specimen reversed from a right rib).

The form of this rib, and of *D66*, a similar rib of which more of the lamina is preserved but which has lost the shaft, and their association with the humerus, suggest that they may be adapted to underlie the scapulocoracoid. This would account for the turning back of the rib at the 'knee' and, if any pressure were exerted inwards by the girdle, the massiveness and the vertical plane. Also the unusually high scute surface would carry the dermal armour above the level of the top of the scapula.

The most anterior right rib from block *E* also has the 'knee' slightly developed, though it is not so massive as the two *D* ribs. This feature is also present to a slight extent in the two block *G* ribs. It seems possible, therefore, that the two massive *D* ribs took the main

strain of the pectoral girdle, while those of the type from block *G* and the front of block *E* were situated near to them, perhaps posteriorly, where they were partially covered by the scapula blade.

The remaining ribs from block *D* can be arranged in a morphological series to span the region covered by the vertebrae from that block, ending just in front of the sacral region (figure 8*b*). With decrease in the length from front to back is correlated a series of other changes: (1) increasing extension behind the level of the back edge of the shaft; (2) increasing width of the shaft; (3) increasing acuity of the angle between the proximal edge of the scute-bearing surface and the hind edge of the shaft, and increasing length of the former edge.

*D*26, the first member of this series, when orientated in its natural position, curves round so that the distal end is in a nearly vertical plane. This end is truncated and the surface so formed is of unfinished bone. This terminal surface is also preserved in the right rib *D*21, which pairs with *D*26; suggesting the connexion by cartilage of those two ribs to a sternal ossification.

Sacral ribs

Of the two sacral ribs preserved *D*64 has only the distal end present, including the articular area for the ilium, and is without any of the shaft. It was situated near the anterior end of the pubis in the block, but at some distance from the iliac shaft. The half pelvis from block *D* is a left one, but *D*64 appears to be from the right.

The block *K* rib (figure 9*a*) was associated in the block with scutes, a fragment of pelvis and two fragments of caudal ribs. The ribhead is similar to that of a dorsal rib but wider and deeper, with a slipper-shaped outline in end view. The shaft is short and massive, its section continuing the form of the tubercular facet distally with very little constriction so that the capitulum is a ventral expansion of the shaft.

The articular area for the ilium faces antero-laterally and is concave in dorsal view. It is elliptical in outline and bears a series of ridges and furrows radiating from its slightly thickened upper edge and becoming more marked ventrally. Above the articular area and separated from it by a thickened region there is a roughened bone surface, facing anteriorly and slightly dorsally. This surface, which forms the distal part of the expanded end of the rib, does not contact the ilium, being dorsal to the top of the iliac shaft. When, however, the ilium is placed in position this area continues dorsally a similar area on the top of the iliac shaft, so that together they form a scute-bearing surface.

From the form of the sacral rib and of the ilium there can be little doubt that only one pair of sacral ribs was developed. Though damaged in preparation, the head of the iliac shaft was apparently complete in outline in the block and shows no posterior expansion: also the articular surface on the rib is placed so that it curves right round behind the shaft of the ilium, to cover the head of the latter posteriorly as well as medially.

Caudal ribs

The three ribs from block *I* (figure 9*b*) are very different in form both from the dorsal ribs and from the block *F* caudals. They are characterized by a great expansion, which is almost certainly concerned with the support of the dermal pelvic shield, forming a deep

girder to withstand downward pressure. None of them is preserved as far proximally as the ribhead, and the one with the greatest distal expansion, assumed to be anterior, has none of the shaft present. The three ribs, when arranged in order of decreasing distal area, tend towards the bifurcating type of caudal rib from block *F*: for this reason it may be assumed that they represent an antero-posterior series starting near the sacral rib.

Though none of them has a preserved ribhead, the ribhead from the same block and that from block *K*, are probably of the type borne by at least the anterior two. Both heads are imperfectly preserved but their form can be made out. They are very deep and narrow in section and their terminal facets would best fit the centra from block *I*.

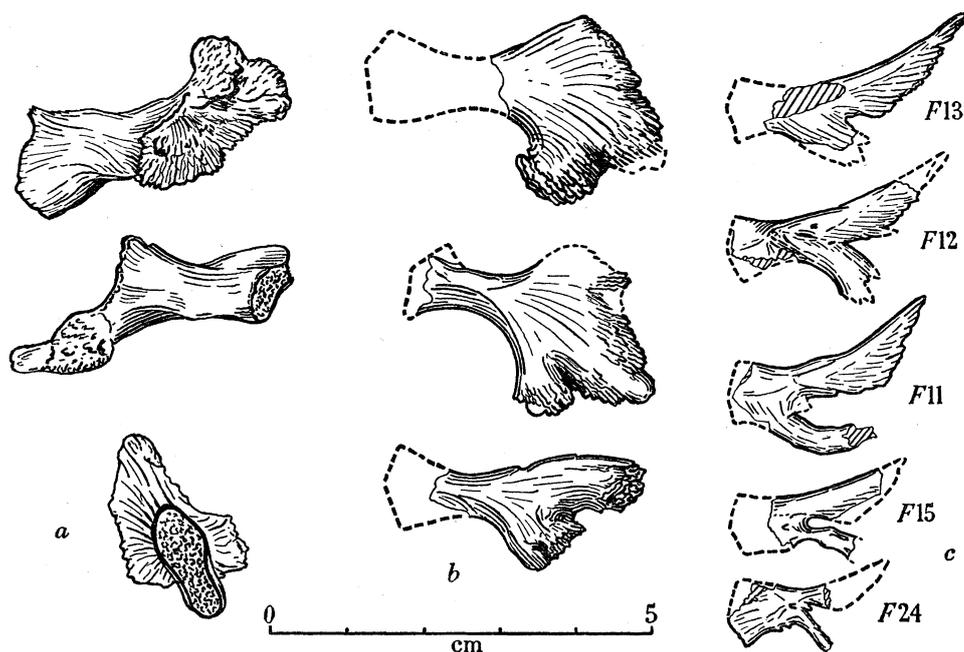


FIGURE 9. Sacral and caudal ribs. Natural size. *a*: left sacral rib; anterior, dorsal, medial. *b*: right caudal ribs from block *I* modified to bear pelvic shield. *c*: right caudal ribs from block *F* (one specimen in both *B* and *C* reversed from a left rib).

In the ribs from block *F* (figure 9*c*) the bifurcation into postero-dorsal and antero-ventral branches is complete. The antero-ventral branch is the principal one, forming the body of the rib and extending much further laterally than the other. The leading edge of the main branch forms a continuous, smoothly rounded curve with the shaft: the trailing edge is roughened to take scutes and the whole branch tapers distally so that the edges meet in a terminal point. The shaft is wide but thin and flat proximally, but thickens to a more or less triangular section further out, so that there is a distinct but variably developed 'knee' before the division into branches.

Appendicular skeleton

The only recognizable remains of the pectoral girdle preserved are the left scapulo-coracoid and cleithrum associated with skull *A*. The complete removal of the girdle from the skull was not attempted, so that over most of the preserved area only the lateral surface

is visible; but a piece of the coracoid region, including the glenoid, is removable and the inner surface may be seen.

The single right humerus from block *D* (*D66a*), touching one of the massive thoracic ribs already described, is the only one preserved. The two specimens lay in the block not far removed from the pelvic girdle. This latter consists of the left side only, with the ilium and pubis fairly complete. The outline of at least part of the ischium region was preserved on the block as a natural cast: also the head of the ilium, from which the postero-dorsal part is now missing was apparently complete but very fragmentary in the block. Other small fragments of pelvis are preserved from block *I* and a piece of bony plate is associated in block *K* with the sacral rib.

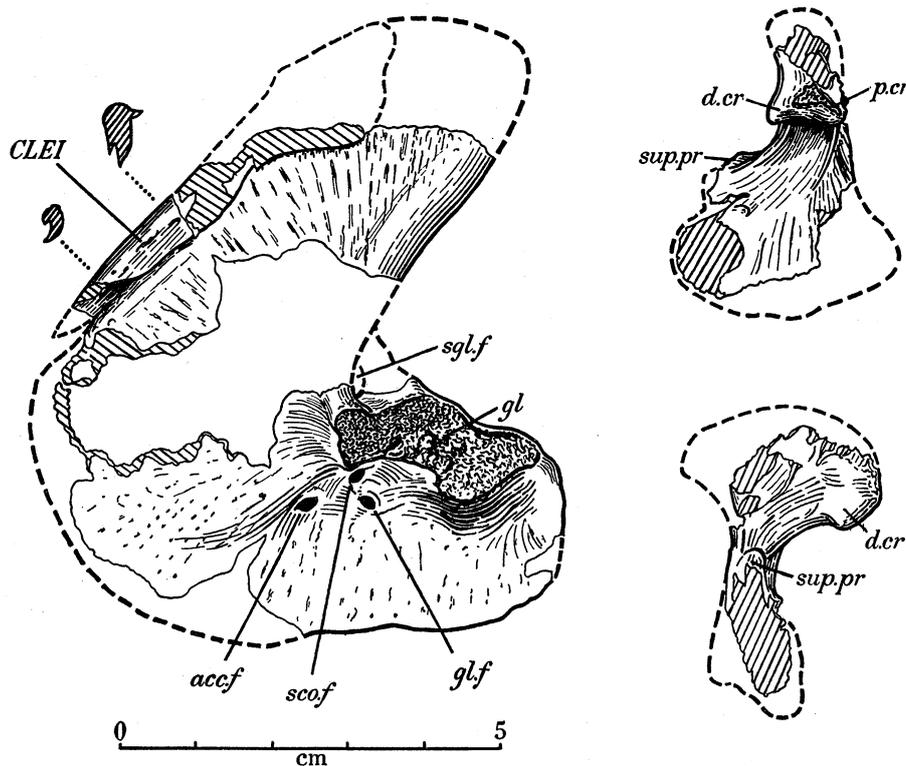


FIGURE 10. Fore limb. Natural size. Scapulocoracoid and cleithrum (sectional views of cleithrum at the points indicated); and anterior and outer views of humerus.

A single left femur (*D61*) was preserved on top of the pelvis in almost its natural position, with the head lying very near the acetabulum, ventral side uppermost. In consequence the ventral surface has been much eroded and the condition of the specimen, with the exception of the upper surface of the shaft, is poor.

Pectoral girdle

The scapulocoracoid is incomplete dorsally and a large part of its central area is missing, but its impression is preserved as a cast in the underlying matrix, and a thin strip of rotted bone anteriorly gives some idea of its extent forwards at this point. The coracoid plate, including the region of the glenoid, is almost complete and is preserved to its true ventral edge. Preservation, however, does not extend forwards to the antero-ventral border.

The cleithrum is well-preserved ventrally and this part is removable from the edge of the scapula which it clasps. More dorsally it is poorly preserved and is incomplete dorsally, being broken off at the same level as the scapula.

The whole scapulocoracoid is remarkably wide from front to back compared to that of a form such as *Eryops*. As far as preserved the anterior and posterior edges of the upper part of the scapula are roughly parallel, though dorsally the anterior edge turns in so that the missing dorsal region must have been much narrower than the rest. The posterior edge is free and can be seen to be thick and rounded. The anterior edge is less thick and sharper, and in this region the thickness of the scapular blade tapers from back to front. Posteriorly the scapula is 4 mm thick, anteriorly about 2.5 mm.

The glenoid is of the screw-shaped form typical in labyrinthodonts and other primitive tetrapods and has a cartilage-bearing surface. Above the glenoid the base of the thick supraglenoid buttress is preserved, and immediately anterior to it the floor of the supraglenoid foramen runs obliquely forward and inward to the inner surface. The base of the posterior edge of the scapular blade forms the anterior wall of the supraglenoid foramen and the antero-dorsal support of the glenoid as in *Eryops* (Miner 1925) and other forms. The thickness in this region, measured as the depth obliquely across the base of the buttress, is about 1 cm. On the inner surface, opposite the anterior end of the glenoid, is the scapular fossa which is triangular in shape with the apex ventrally. It extends from the preserved edge in this region to the level of the supraglenoid buttress posteriorly, thus being at least 1 cm wide. Its dorsal extent is again to the preserved edge so that the supraglenoid foramen opens into it; and it is about 1.2 cm deep, fading out ventrally, but with a well-defined posterior border. It faces inwards and antero-dorsally, being parallel to the most anterior part of the glenoid.

Two more foramina open into the fossa. One of these, opening externally below the front of the glenoid, is probably the supracoracoid foramen; a second foramen, whose external opening is anterior to the latter, has not been described in any other animal. A glenoid foramen (Williston 1909) opens externally below and slightly behind the supracoracoid foramen, and internally opposite the middle of the lower edge of the glenoid.

The coracoid plate below the glenoid region is preserved to its true edge ventrally and for most of its extent posteriorly, though here the edge is slightly damaged. Ventrally the edge appears as a cartilage-bearing surface at least 1 mm wide; so that in life the coracoid plate probably continued in cartilage to near the midline.

The plate itself is a rather thin sheet of bone below the glenoid, being only about 1.5 mm thick. A slightly hollowed area on the inner surface, about 1 cm in diameter, opposite the back of the glenoid and reaching almost to the posterior edge, is probably for muscle insertion.

There is no sign of any suture separating the scapula and coracoid regions of the girdle.

The ventral part of the cleithrum, as in typical labyrinthodonts, is a bony rod clasping the end of the scapula in a deep groove. The lateral wall of this groove decreases in depth towards the ventral tip, to allow for the insertion of the dorsal process of the clavicle. The relation of these two bones in the region of the overlap differs significantly from that on described labyrinthodonts (Nilsson 1939). In temnospondyl labyrinthodonts typified by *Eryops* and *Cacops*, the tip of the clavicle overlaps the process of the cleithrum both laterally

and anteriorly. In *Peltobatrachus*, however, although the clavicle is not preserved, it is clear that it was overlapped by the cleithrum anteriorly, though the former still lay lateral to the latter.

Humerus

The humerus is rather poorly preserved and is very incomplete distally and only partially complete proximally. It is, however, possible to make out some of its structure. The form is that typical of primitive terrestrial tetrapods, and, as in *Eryops* (Romer 1922; Miner 1925), the planes of the proximal and distal bony surfaces are almost at right angles, giving the typical tetrahedral form.

Most of the head of the humerus is missing, but the strongly developed deltoid and pectoral crests are well preserved and together give a strongly overhanging square-shaped end to the head. Above and between them on the anterior end of the head there is a depressed triangular area of cartilage-finished bone, one corner of which stretches as a shallow groove into the pectoral crest. Below (distal to) the deltopectoral crest, which is strongly concave below, the anterior bone surface is defined by two ridges. The outer one from the deltoid is very sharp and runs outwards and distally in a smooth curve, to terminate near the preserved edge of the bone at a point where a low, thick projection, the supinator process, stands out laterally. The inner ridge is very sharp proximally at its origin at the side of the pectoral crest, but as it continues distally roughly parallel to the outer ridge, it fades into the general distal bone surface. The extent of this distal surface is not known due to the poor state of preservation and no clear division into ent- and ectepicondyle is preserved.

In posterior view very little of the true bone surface remains. Part of the posterior surface is preserved and is slightly concave in both directions. It is bounded by a very sharp ridge on the left and forms an acute angle with the inner surface. On the right it is defined by another ridge which runs down posterior to the supinator process. At the level of this process the preserved surface finishes. Dorsal to this main surface, part of a bone mass which may be the processus latissimi dorsi below the head of the humerus is preserved, but this region is damaged and somewhat displaced.

In outer view the form of the remaining part of the anterior region of the head may be seen. Below this the plane of the outer surface twists towards the supinator process, so that the ridge separating it from the anterior edge becomes sharper as the angle between them increases. There is no clearly defined ridge running back transversely to the processus latissimi dorsi at the junction of the head and the outer surface as there is in *Eryops*.

Pelvic girdle

The condition of *D 65* is not good. The outer surface was exposed in the block so that there is some surface erosion and little true edge remains. The surface of the bone is better preserved on the inner face and the surface of the symphysis is perfectly preserved. As restored the plane of the whole structure is at about forty degrees to the vertical, and the two figures in side view have been drawn at this angle so that they appear reduced in height. The greatest depth measured in the plane of the specimen is 7.2 cm and the depth measured vertically when corrected for distortion is 6.5 cm.

The outer surface, therefore, faces ventro-laterally. The ascending shaft of the ilium is very damaged on this side. Towards the top, however, it is fairly complete and the surface is well preserved. At the top of the shaft there is a concave vertical surface roughened by a series of small vertical ridges. As they are on the outer surface they are not to take the sacral rib, and it seems probable that this surface was connected to some of the dermal armour.

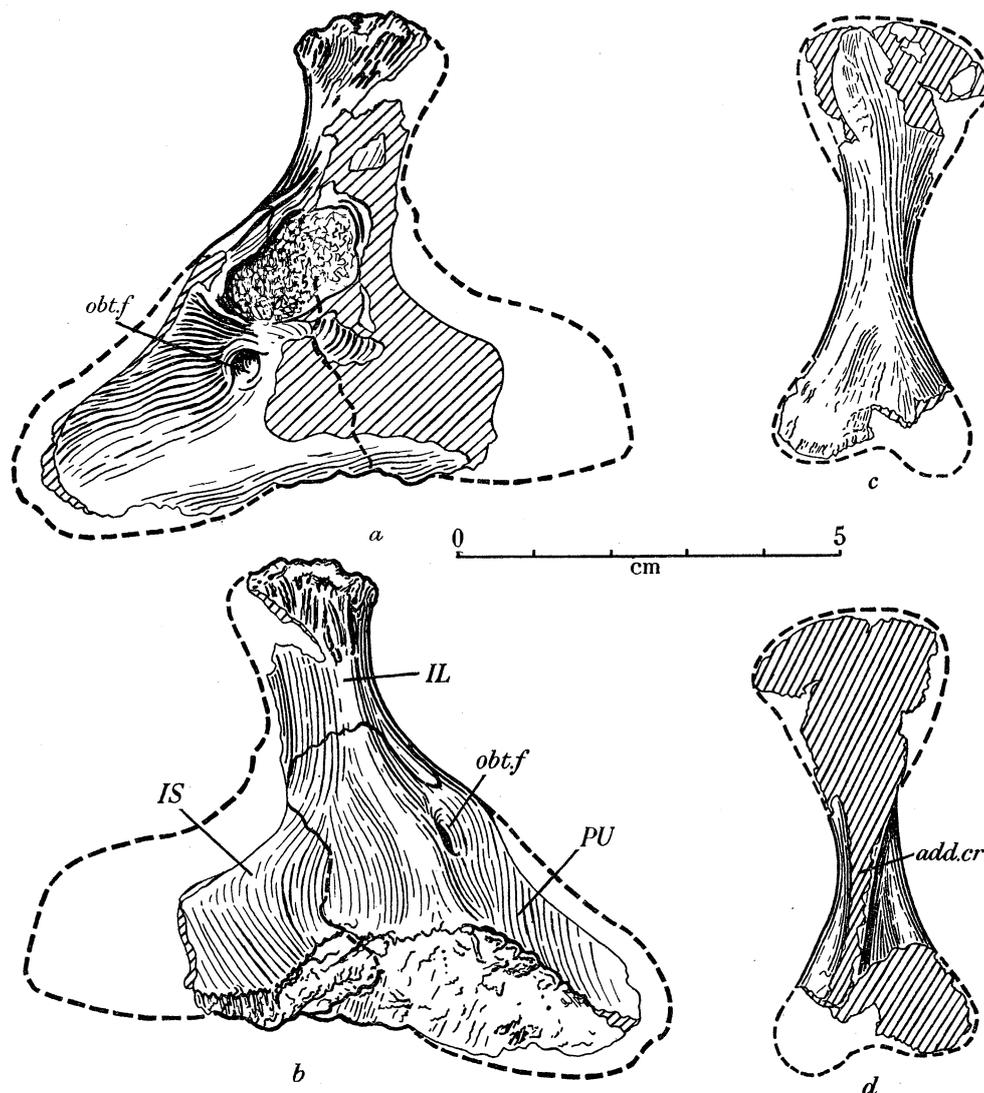


FIGURE 11. Hind limb. Natural size. *a, b*: outer and inner view of left pelvic girdle. *c, d*: dorsal and ventral view of femur.

The large acetabulum is situated at the base of the iliac shaft near the anterior border of the girdle. It is roughly oval in outline with rather poorly preserved borders, but postero-dorsally its margin stands out as a prominent ridge, and the antero-dorsal border is formed by the prominent turning-out of the whole anterior margin of the specimen. Ventrally a sharp ridge separates the acetabulum from the pubic region below it. This region, as far as preserved, is strongly plano-concave, with the axis directed slightly downwards and laterally at the front. The ventral opening of the large obturator foramen, which follows a directly vertical course, is a little below the front of the acetabulum.

The ischium as far as preserved appears to continue the plane of the pubic region and the suture between them cannot be made out on this side. The only suture visible on the outer surface is a short extent of the ilio-pubic suture on the anterior rim of the acetabulum.

On the inner surface the suture between the ilium and the pubis can be easily seen running right across the specimen at the level of the top of the acetabulum. The inner (proximal) surface of the head of the ilium is roughened with vertical ridges, somewhat more prominent than those on the outside, for the articulation of the sacral rib. These stop short of the top edge, however, which is thickened and swollen.

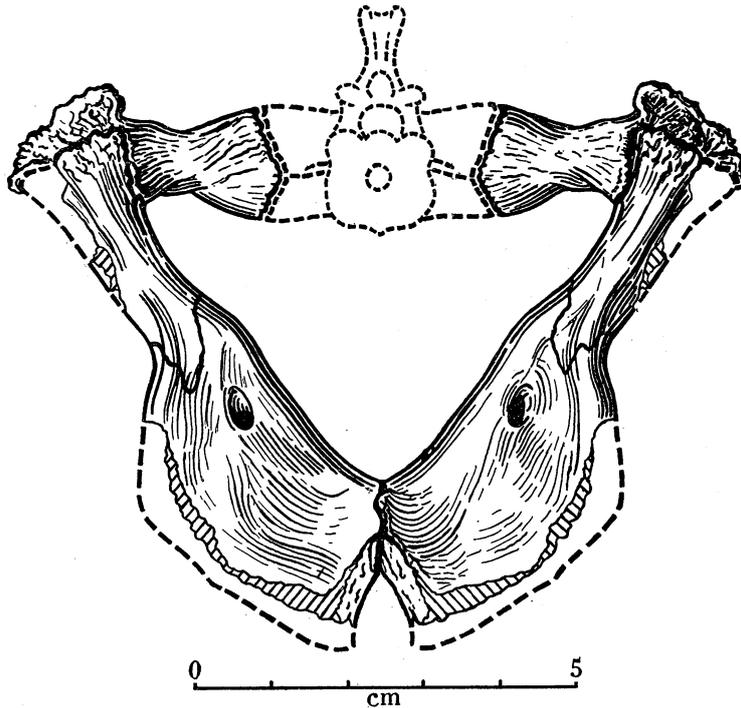


FIGURE 12. Reconstruction of sacrum and pelvic girdle: anterior. Natural size.

The inner surface of the iliac shaft has an aerofoil-like cross-section, and further down this shape becomes a surface divided by a wide, very low ridge into two distinct planes, the main surface of the pubo-ischiadic plate and, anterior to it, a concave surface whose plane is at about forty-five degrees to the sagittal one. The dorsal opening of the obturator foramen lies just in front of the ridge.

The symphyseal surface is very deep in the pubic region but narrows off towards the ischium. Its true ventral border is preserved only posteriorly on the pubic and along the short preserved ischial region. The pubo-ischiadic suture can be traced across its surface and for most of the distance beyond it up to the level of the ilium.

There must have been a large amount of cartilage in the symphysis. The symphyseal surface is not all in one plane and when the specimen is orientated only the narrow ischial region is vertical, even allowing for distortion. In this region the roughening of the symphyseal surface consists of closely packed vertical ridges, but more anteriorly it is sparse and irregular. In the deep anterior region the surface faces slightly ventrally, and at the front

curves round with the front of the main pubic surface to face somewhat anteriorly. It seems therefore that in the whole girdle the bony symphyseal surfaces must have diverged anteriorly and ventrally in the pubic region.

Femur

The shaft of the femur is slender and, as far as preserved, expands in a smooth curve on either side to the region of the head. A slight twisting is apparent in dorsal view so that a low rounded ridge runs from the anterior side of the head to the posterior side of the distal end. Although the femur is not preserved to its distal extremity, the beginning of its division into tibial and fibular regions may be seen on the dorsal surface. The anterior part, leading to the tibial condyles, remains in the same plane as the rest of the shaft, but the region of the fibular articulation is thick and quadrangular in transverse section, and slopes up distally from the general level of the shaft.

In ventral view the powerful adductor crest is visible though eroded, running down to the posterior fibular side of the distal end, thus contributing to the thickness of this region. The region of the proximal end of the crest is badly eroded but the beginnings of its forking proximally can be seen.

Other limb bones

Three small bones may be considered under this heading. The first is from block *L* and is a small quadrangular bone 8 mm in length with cartilage surfaces at each end. The association of this in block *L* with the lower jaw angle, and with part of the distal end of a massive thoracic rib, suggests that it might be part of the carpus. A rather similar but very much smaller bone is preserved from block *E*, which could be a finger bone.

A possible tibia or fibula is preserved from block *I*. One end is apparently almost complete though damaged: the other is obviously broken off. The bone is fairly flat in section, but its plane twists through about thirty-five degrees along its length. One margin is more or less straight, the other strongly indented.

Dermal armour

One of the most characteristic features of the species is the dermal armour which covered at least the dorsal part of the body. This armour consists of scutes, usually elliptical or quadrangular in shape, which are ornamented on the outer surface with the tubercles typical of the species. In most cases it is possible to distinguish at one edge a region overlapped by another part of the armour, and here the ornament is reduced in height and often takes the form of low rounded ridges, in which the individual pustules can still be made out. There is also in the majority of scutes a thickened region, showing dorsally as a rounded boss, at a point probably corresponding to the centre of ossification.

The scutes did not form a flexible armour of separate scales but, with very few exceptions, were rigidly locked together by strong interdigitated sutures. In most cases, where the complete scute is preserved, the sutures are seen to occur at one or both ends of a quadrangular scute leaving the other sides, one of which usually has an overlap surface, free.

It seems therefore that most of the armour was organized in a series of bands, so that the scutes were connected by suture medially and laterally, and by relatively mobile overlap

anteriorly and posteriorly. Though most of the scutes are preserved separately and their arrangement in bands can only be inferred from the sutures, several more or less complete bands are also preserved. In addition there were at least two different arrangements of scutes sutured anteriorly and posteriorly as well as laterally forming shields.

Dermal shields

A pelvic dermal shield was preserved on the side of block *D* on which the dorsal surface of most of the dermal armour was exposed. It lay immediately above the region including the pubic region of the pelvis, the head of the femur, the sacral rib and a group of posterior dorsal vertebrae. The dorsal surface was exposed in the block, so that the ornament is somewhat worn in places, but otherwise the condition is very good.

The shield takes the form of a broad band curved in end view and tapering slightly from front to back. The rear end then has a section forming the arc of a circle: the front is more angular. The posterior edge is rounded and has a large rounded projection in the midline. Antero-laterally on the left side there is a marked shallow emargination and this was probably present on both sides, though in the right anterior corner the poor preservation makes it more difficult to see. In side view the lateral edge is smoothly rounded.

In ventral view the most prominent feature is a sharply defined median ridge, reaching its maximum depth of about 3 mm at 1 cm from the preserved front edge and gradually becoming lower until it merges into the general surface 1.3 cm from the median posterior edge. Apart from some roughening laterally, probably to take the ribs supporting the shield, the rest of the ventral surface is smooth.

The whole shield is made up of five rows of scutes. The median row consists of three scutes, the rounded posterior one being the largest. The right lateral row next to it also has three scutes, the posterior one being exceptionally wide from front to back. The right marginal series has three scutes, but the very small anterior one has been 'crowded out' and is visible only on the ventral surface. On the left some degree of fusion between scutes appears to have taken place.

The evidence for the sacral position of the block *D* shield is its occurrence and position in block *D*, and the presence of a continuous ventral ridge, which would fit a series of grooves similar to that on the posterior dorsal neural arch *D*18. This arch was preserved just below the shield. It is assumed to be post-sacral as the posterior circumference is much too narrow and too deep to fit over any of the dorsal ribs as restored; and it seems unlikely that such a restricting girdle would fit immediately over the sacrum, with the femora projecting sideways in typical early tetrapod fashion.

A thoracic shield is preserved from block *E*. Unlike the pelvic shield this latter is very incomplete and was built up from its constituent scutes by mending the sutures. In all cases there could be no doubt of the correctness of the joins made, and all the scutes were preserved near together in the block. They lay among a group of scutes to the left of the anterior members of the series of articulated vertebrae. The sutures, ornament and ventral surface are all very little eroded.

Four scutes of the median series are preserved, though only one, which is larger and squarer than the others, is complete. Of the two terminal ones that which is probably

posterior appears to be tapering towards the edge of the shield though its own edge is not preserved; but the other (*E44*) has about 5 mm of sutural edge preserved at the front, though the rest of the border is broken off. Thus there must have been at least five scutes in the median series.

Only three incomplete lateral scutes from the presumed left side are preserved, and are sutured together. The posterior two of these extend to the region of the lateral ridge, and in end view the shield is markedly more angular than that from block *D*. It is also slightly narrower, but this may be due to differences in size of the individuals concerned.

The most important difference between the two is the larger number of median and, presumably, lateral scutes in the *E* specimen. As in the block *D* shield, there is a median ventral ridge, but that in the *E* shield seems to be broken at the suture between each successive scute, and the posterior terminal scute *E33* has a shallow pocket at its terminal edge. It is probable, therefore, that in this shield the neural spines fitted between the median scutes as they do in the adjacent block *E* bands described below; whereas in the pelvic shield, whatever the position of the spines relative to the scutes, some at least must have articulated on the ridge.

Among the dermal fragments collected loose are two which are probably from shields, one having two consecutive bosses with a suture between them; the other a ventral ridge on a very thick piece of scute. Neither, however, is large enough to give any useful information.

Trunk armour

The bands of scutes which were situated between the pectoral and pelvic shields were divided, at least near the shields, into separate neural and costal series. Three incomplete bands were preserved behind the scutes of the pectoral shield in block *E*, but each is sufficiently preserved to show that it consisted originally of only three scutes. The middle one, which may be termed a median neural, rested between two consecutive neural arches and its back and front edges are hollowed ventrally to form shallow pockets for the reception of their respective neural spines. Each neural spine thus fitted in a pocket formed at the edges of two consecutive scutes. A lateral neural was situated on each side of the median neural and in the block *E* bands the lateral neurals have no suture distally and must therefore have terminated the band. Comparison with the ribs from block *E* shows that such a short band would not have extended out to the scute-bearing costal surfaces and the bands are thus entirely neural.

In end view the contour of the bands is like that of the pectoral shield with a sharp turn-down of the lateral scutes at the level of their respective bosses: this angled shape is characteristic of neural laterals. The bands were preserved more or less in the natural position and it is evident from the anterior position of the overlap surface that each band overlapped the one behind it.

One complete neural band of three scutes is preserved from block *D* and was situated in its natural orientation in front of but overlapped by the pelvic shield. In this case therefore the direction of overlap is opposite to that of the block *E* bands and a change in the direction of overlap must have taken place somewhere in the neural series. An isolated median neural from block *D* which has no overlap surface front or back suggests how this might

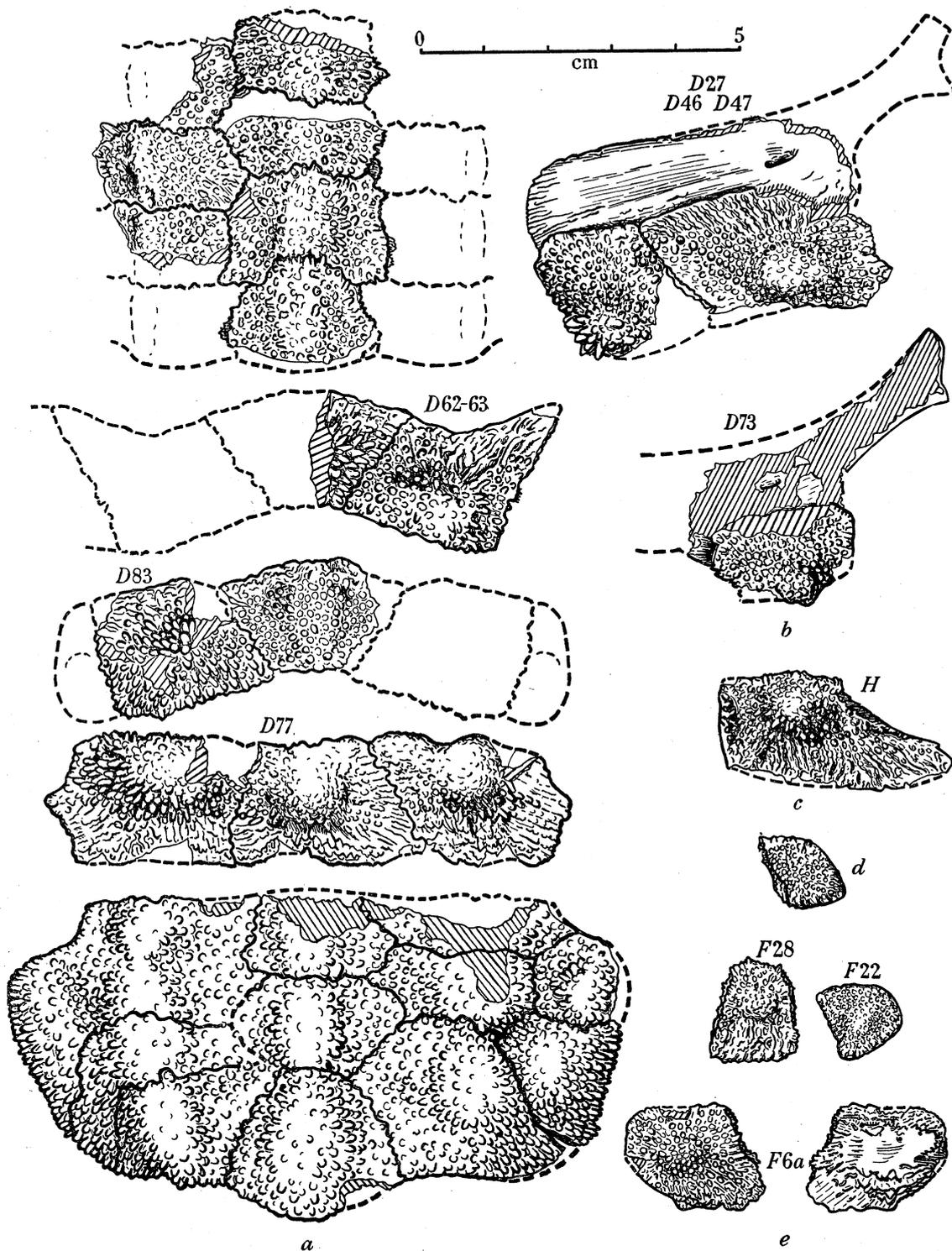


FIGURE 13. Dermal armour. Natural size. *a*: the neural series: pectoral shield, two bands of more than three scutes, three-scute band and associated pelvic shield. *b*: incomplete costal bands preserved on ribs. *c*: floating scute. *d*: block *I* caudal scute. *e*: block *F* caudal scutes.

have occurred. Like the block *E* bands the pelvic band would not have extended far enough laterally to reach the scute-bearing surfaces of the ribs. Another difference from the block *E* bands is the absence of 'half-pockets' for the neural spines, but the presence of a median neural ridge, similar to that under the pelvic shield, which would fit into the groove present in posterior trunk neural spines.

Another similar three-scute band is preserved from block *D* but this has 'half-pockets'. In addition to these two there are two incomplete bands preserved which consisted originally of more than three scutes and thus may have extended right over the costal region. Each consists of an imperfect median neural and an almost complete lateral with a distal suture. The three median scutes of one of these must have formed a shallow V-shape while those of the other would have formed a W. Four isolated neural laterals from block *D* form a morphological series between those of the two bands.

It is not known how these two bands were terminated. Several small marginal scutes are preserved which if sutured directly to the laterals would still confine the band to the neural series. Several rhomboid short lateral scutes are preserved in block *D* with sutures at each edge and these would then carry the bands in one piece to the costal region. It is possible that the separation into neural and costal bands occurred only in the region of the girdles where limb movements would necessitate some bodily flexure, and three-scute bands are only known from these regions.

There are, apart from minute fragments, only two cases in which scutes can be associated with the ribs on which they lay in life, and both of these are from block *D* (figure 13*b*). The first of these consists of a well-preserved rib-blade with two scutes which fit closely on its scute surface, a costal lateral and a marginal. The former bears the remains of a proximal suture and extends slightly beyond the median edge of the scute surface. It is not known, however, whether it was terminated proximally by a short marginal or was continuous with a neural band.

The other specimen, however, though poorly preserved, shows a scute in the same position with no proximal suture. This scute must have terminated a costal band quite separate from the neural band of the same segment. Both these costal bands have anterior overlap surfaces, each therefore was overlapped by the band in front.

Few other costal scutes, distinguished by their smoothly curved contour in end view, are preserved, but two incomplete bands, each consisting of a marginal and a lateral sutured at each end, come from block *D*.

There is one case of a 'floating' scute, complete, but without any suture preserved from block *H* (figure 13*c*).

Tail armour

Those scutes from block *F*, and more tentatively, those from block *I* and block *K* may be assigned to the caudal region behind the pelvic shield. Ten scutes or fragments of scutes are preserved from block *F* (figure 13*e*) of which two are apparently 'floaters'. Both were preserved near the series of posterior tail vertebrae. The remaining scutes have at least one sutural edge: one is like a short trunk lateral with opposite sutures and was preserved not far from the 'floaters'; another is thick and massive and bears a distinct sutural edge on one side with ventrally facing rather ill-developed sutural interdigitations

round the rest of the scute. It was preserved somewhat anterior to the other scutes, and may have formed part of a rather loosely-knit small proximal shield on the tail.

The scute fragments from blocks *I* and *K* are similar to small trunk scutes (figure 13*d*).

Gastralia

All the armour so far described is assumed to be dorsal in position and, if its lower limit was at the distal end of the ribs, would only have reached to the side of the flank. The only evidence of ventral armour preserved is a series of minute bones scattered through several blocks. In each case these were preserved on the 'ventral' side of the block; that is on the side opposite that on which the dorsal surface of the majority of the scutes was exposed.

The bones themselves are mostly fragmentary but appear to reach about 1 cm in length and are usually less than 1 mm wide. The commonest type is pointed at one end and elliptical or kidney-shaped in section, though other shapes are also present.

The largest collection of these objects comes from block *E*. Most of these were fragments of the elongate needle type, but there were also a few wider forms of various shapes.

There were also numerous scattered fragments from block *G* and thirteen were developed, almost all being of the elongate needle type and somewhat smaller than those from block *E*. Three specimens were recorded from block *D* and one small fragment occurred in block *L*.

It seems likely that all three small bones represent units in a flexible gastral armour, of the type common in primitive tetrapods. All those preserved are from blocks containing vertebrae with the exception of that from block *L*, and in each case they were preserved on the ventral surface not far from the vertebrae. This position might be expected for the remnants of a ventral covering. None is preserved from any block containing caudal material.

Reconstruction and mode of life

An attempt has been made to reconstruct the whole skeleton of *Peltobatrachus pustulatus* from all the available material (figure 14). In all cases those parts of the skeleton represented by actual material have been shaded in: the restored or reconstructed regions have been left white.

The normal number of dorsal vertebrae for a terrestrial labyrinthodont is about twenty-five and this was borne in mind in restoring the dorsal column. The material from block *D* extends forward to thoracic ribs underlying the pectoral girdle and the vertebral series from block *E* has therefore been made to coincide with the front of the restored *D* series of vertebrae and ribs: the latter have been drawn in graded series as suggested in their description. Similarly, the *G* series probably coincides with the front of the *E* series. The slight parapophysis of the *A* centrum, together with its association with the skull suggests a very anterior position in the 'neck' region.

The distal parts of the limbs are entirely hypothetical: as far as possible they represent a generalized terrestrial labyrinthodont condition.

The median dermal armour has been indicated as though in sagittal section over the neural spines. The restoration of the pectoral shield and its succeeding bands from block *E* has been used in relation to the vertebral series with which they were preserved. The

pelvic shield has been placed in the immediately post-sacral position suggested for it, so that the band *D77* comes to lie on the sacral neural spine.

In the absence of any dentition and of the distal parts of the limbs conclusions about the mode of life of the species can be in general terms only. All the evidence suggests that *Peltobatrachus* was a thoroughly terrestrial form, as fully adapted to life on land as was *Eryops*.

No trace of lateral line grooves has been found on any of the skull or jaw specimens, and there is thus every reason to believe that they were completely absent. The humerus and femur are well ossified and the humerus is of the tetrahedral type which reaches its highest development in primitive terrestrial tetrapods.

There is no sign in skull or skeleton of the reduction of ossification which accompanied the labyrinthodont return to water, and in particular the bones of the neurocranium are well ossified. Nor is there any sign of the bodily flattening characteristic of the Triassic Amphibia and reaching its climax in the plagiosaurs.

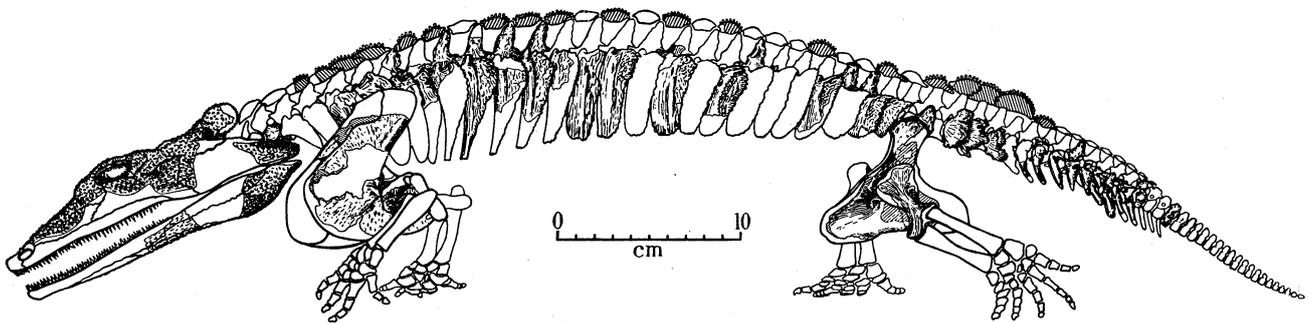


FIGURE 14. *Peltobatrachus pustulatus*: composite reconstruction of the skeleton in left lateral view (magn. ca. $\times \frac{1}{4}$). Dermal armour shown as though in sagittal section over the neural spines.

With this flattening of the plagiosaurs goes an adaptation of the vertebral column to flexure in the vertical plane, shown by the very steep angle of the zygapophyses, whose facets are almost vertical. In contrast the apparent rigidity of the dorsal vertebral column in *Peltobatrachus*, with oblique zygapophyses, has already been remarked upon, and this must be seen as one of the many adaptations to carry the heavy dermal armour resting on very firmly articulated ribs. The great width of the scapulocoracoid and the deep coracoid plate are probably both signs of the powerful musculature necessary to support a massive skull and body. In the pelvic region also, the deep pubo-ischiadic plate and powerful symphyseal region indicate a similar adaptation.

It seems probable that the tail was short and had no propulsive function. Romer (1922) correlated a well-developed posterior process of the ilium with a long tail, contrasting the long tailed '*Cricotus*' (*Archeria*) with *Eryops* in which this process is little developed and the tail short: it seems very unlikely that there was such a process in *Peltobatrachus*. The rapid decline in the size of the haemal arches over a short range in block *F* also suggests a short tail, as does the great range of vertebral form within a few consecutive centra.

It seems, therefore, that *Peltobatrachus* was a ponderous terrestrial amphibian relying on the dermal armour for complete dorsal protection. Even at the base of the skull the tabular

horns protected the vulnerable neck region, and it is probable that a nuchal plate fitted between them.

Among the contemporary fauna preserved from the region there were many species of carnivorous theriodonts of which the gorgonopsids were numerous and reached a considerable size. It is against these that the armour of *Peltobatrachus* presumably gave protection.

The difference between the matrix of the locality *B4/5* and other *B4* localities has already been remarked on. Most of the specimens collected from *B4* sites by Mr Parrington are surrounded by matrix which is partly buff coloured and partly dark red and very hard. There is one other specimen from *B4/5*, a small unidentified dicynodont skull, and the matrix of this is partly deep chocolate brown and partly of the grey type of specimen 35. As in specimen 35 there are numerous seams of calcite crystals. There is only one other *B4* specimen in which the matrix has no reddish or buff colour, this is a large dicynodont skull (no. 33) from *B4/4*, and as in specimen 35 the matrix reacts more vigorously with acid than does the usual buff-coloured matrix.

It is possible, therefore, that the grey matrix represents some difference in terrain from the normal type, perhaps a drying muddy pond or swamp in which the animal bred, and the incidence of the find supports this. Most of the large blocks were found together within a few square yards at the head of a 'donga' and only the small fragments were scattered over a larger area below these. Thus several individuals were confined within a small area at their death and subsequent interment.

THE AFFINITIES OF *PELTOBATRACHUS*

The description of *Peltobatrachus* demonstrates that it is a labyrinthodont in the broad sense of that term used by Romer (1947): when considered in detail, however, the structure of the species, notably the form of the dermal ornament and of the dorsal vertebrae, sets it apart from typical labyrinthodonts.

In a discussion of its affinities, therefore, features in which it differs from contemporary labyrinthodonts must be considered in two categories; those characters which are unexpected in a labyrinthodont from the Upper Permian, and those characters which are surprising in any labyrinthodont.

The structure of the skull

The pattern of dermal bones on the skull roof of *Peltobatrachus* is of the 'temnospondyl' type possessed by the labyrinthodont Rhachitomi and Stereospondyli. This character combined with many others, such as the platybasic condition, the loss of the intertemporal, the large interpterygoid vacuities and the well-developed basicranial suture, shows that the species has evolved in a direction similar to that of the contemporary rhachitomes and separates it quite clearly from the anthracosaur and amniote line of evolution.

The skull appears primitive, however, in the persistent ossification of the elements of the cartilaginous neurocranium. There is a heavily ossified sphenethmoid bone extending far forward, the basisphenoid is extensively ossified, the otic capsule is still completely ossified and has a long occipital exposure as the paroccipital process. Also the supraoccipital and the basioccipital still contribute to the roof and floor of the braincase, and the latter bone forms part of the primitively single occipital condyle. In most contemporary rhachitomous forms these ossifications are reduced or absent.

Upper Permian labyrinthodonts have been described mostly from the African continent (Broom 1908; Haughton 1915, 1925, 1926; Huene 1931; Boonstra 1940), and, apart from *Peltobatrachus* itself, all these African species belong to an assemblage near the *Eryops-Capitosaurus* 'central line' of temnospondyl evolution described by Watson (1919).

In none of these forms is there an ossified supraoccipital: a space above the foramen magnum was presumably occupied by the cartilaginous element. All of them also have a widely spaced pair of exoccipital condyles, though a small ossified basioccipital exists between them: in *Laccosaurus* this is minute and is visible only in section. In *Rhinesuchus* the ossified opisthotic is still visible on the occiput between the tabular and exoccipital: in *Laccosaurus*, however, the tabular and exoccipital meet to cover it and form the visible part of the paroccipital process. Nothing is known of the internal condition of the braincase in these forms except that in an undescribed skull of *Rhinesuchus nyasaensis* collected by Mr Parrington a small sphenethmoid ossification is visible in ventral view. The basicranial suture in all of them is considerably longer than in *Peltobatrachus* and the parasphenoid forms a more extensive floor to the region.

The only other Upper Permian labyrinthodont in which the condition of the braincase is known is the neotenous and aberrant *Dvinosaurus* from zone IV of the Russian Permian (Amalitsky 1924; Sushkin 1923, 1936; Bystrow 1935, 1938). In this form the tabular and exoccipital are widely separated but there is no ossified opisthotic between them, though this was presumably present in cartilage. The supraoccipital is ossified in some old individuals and there is a small basioccipital ossification, though this took no part in the formation of the paired condyles.

Apart from the primitive features just considered the special features of *Peltobatrachus* include the distinctive pustular ornament, quite unlike the 'pit-and-ridge' reticulate ornament common to nearly all labyrinthodonts; the apparently short and broad form of the skull, particularly in the preorbital region (if the assumptions made in restoring the outline are correct); the slope of the occipital surface and the long retroarticular process of the lower jaw. Of less significance are the tabular horns and, if the orientation has been understood correctly, the projection of the quadratojugal corner of the skull beyond the level of the quadrate to form a distinct horn.

Anomalies in the dermal ornament are very few amongst the labyrinthodonts and the only group having an ornament which is in any way similar to that of *Peltobatrachus* are the Triassic plagiosaurs, though Langston (1953) has recently reported a similar ornament in the poorly known and aberrant form *Platyhystrix* from the Lower Permian of New Mexico.

Four genera of plagiosaurs (*Gerrothorax*, *Plagiosaurus*, *Plagiosuchus*, *Plagiosternum*: figure 16) are generally recognized. Of these *Plagiosternum* is unique in not having the pustular ornament: it is atypical in several other features, which are discussed at length in a later section.

One of the most interesting features of the plagiosaurs is the persistent ossification of the endochondral bones of the occiput. A small ossified supraoccipital has been reported in *Gerrothorax rhaeticus* (Nilsson 1937) and in *G. pulcherrimus* (Huene 1922; Nilsson 1937). Huene reported the absence of the supraoccipital in *Plagiosternum*, but Nilsson, after re-study of the same specimen, concluded that it was not possible to interpret the critical region: the condition in *Plagiosaurus* and *Plagiosuchus* is not known.

An ossified basioccipital lying between the condyles was reported in *Gerrothorax pulcherrimus* by Huene and confirmed by Nilsson. The region of the condyles is also preserved in *G. rhaeticus*, but here an ossified basioccipital is absent: a space situated between the exoccipitals and partially floored by them was probably occupied by the element in cartilage. There is reason to believe, however, that the skull specimen is juvenile, as post-cranial remains of a much larger individual are also preserved.

An ossified opisthotic, defined by its sutures with the tabular and exoccipital, has been reported in *G. pulcherrimus* by Nilsson. Huene seems to think that, in the same specimen, the opisthotic is present but fused to the exoccipital, and an ossified opisthotic is mentioned and figured by Fraas (1913). In *G. rhaeticus* Nilsson restores an ossified opisthotic behind the post-temporal fossa from the remnants of a bone quite distinct from the exoccipital and tabular. The same author reports the bone, defined by sutures, in *Plagiosaurus depressus*. The relevant region is not exposed in the skull of *Plagiosuchus*. In *Plagiosternum* Huene asserts that the tabular meets the exoccipital, but in his revised figure of the same specimen Nilsson shows the region behind the post-temporal fossa to be missing and restores an opisthotic in this position.

It is seen, therefore, that of the three endochondral bones the supraoccipital is known in two of the plagiosaurs, the basioccipital in one and an ossified opisthotic probably in three. With the exception of the basioccipital in the apparently juvenile specimen of *Gerrothorax rhaeticus*, not one of these bones is known to be absent in any species. Their presence is surprisingly primitive in a group extending from the Middle Triassic to the Rhaetic. The primitive condition of these structures in *Peltobatrachus* would, therefore, provide strong supporting evidence for a suggested relationship between this form and the Triassic group.

If the restoration of the skull of *Peltobatrachus* is correct it would seem very different in outline from that of the central capitosaur type of labyrinthodont skull. It seems unlikely that there were any transverse regions of intensive growth of the type which Bystrow (1935) has shown to occur postorbitally in *Metoposaurus* and preorbitally in the capitosaurs and all long-snouted forms. Skulls without the zones of growth are characteristic of larval and neotenus forms or very small species. Apart from the latter this skull form occurs in *Dvinosaurus* (Bystrow 1938) and the brachyopids (s.s.) (Watson 1956), as well as in the 'branchiosaurs'. If the *Peltobatrachus* skull is without the zones of elongation, it provides an example of a skull form from which the unique evolution of the fantastically widened plagiosaur skull, again without transverse zones of growth, could begin.

Other similarities to the plagiosaurs include the sloping occiput, the large interpterygoid vacuities and the platybasic skull; both the latter being advanced labyrinthodont characters. The very long retroarticular process of the lower jaw, known in *Plagiosternum* and *Plagiosuchus*, is, though not so fully developed, also a feature of *Peltobatrachus*. The quadratojugal horn apparently existing in *Peltobatrachus* is best seen in the type of *Plagiosaurus depressus* (figured Jaekel 1914; Nilsson 1937). Here the ornamented external part of the quadratojugal extends backwards as a distinct process beyond the quadrate and the occipital exposure of the squamosal. Unfortunately this region is not fully preserved in any other described plagiosaur. It is unknown in *Gerrothorax rhaeticus* and not described in *Plagiosternum*, though the Bear Island skull described below probably pertains to this latter genus and has enormous horns. In *Plagiosuchus* the quadrate and part of the quadrato-

jugal are preserved detached from their correct position and their form is rather difficult to make out in Huene's figure (1922). He states, however, that the quadratojugal forms a lateral and somewhat posteriorly-projecting shield round the quadrate. The corner of the quadratojugal is broken off in *Gerrothorax pulcherrimus* at the general level of the back of the skull roof, but the form of the bone at this point suggests that it projected considerably further back.

The differences between the skull of *Peltobatrachus* and those of the plagiosaurs may again be divided into those in which *Peltobatrachus* represents a more primitive condition in relation to the general trends of labyrinthodont evolution, and those differences which represent unusual specializations in one form or the other.

The extreme flattening of the skull in plagiosaurs might perhaps be included in both these categories. A tendency to flatten the skull is common to most lines of temnospondyl evolution. In plagiosaurs, however, this flattening reaches its maximum and affects the lower jaw as well as the skull.

Characters which remain primitive in *Peltobatrachus* include the single occipital condyle and the presence of a hypoglossal foramen, the short basicranial suture and the absence of an exoccipital-pterygoid suture, the form of the pterygoid with a distinct backwardly-directed quadrate ramus and probably the high degree of ossification of the neurocranium. All these characters are represented in plagiosaurs by a more advanced condition, but would not debar *Peltobatrachus* from relationship to them.

The special characteristics of the plagiosaurs not shared by *Peltobatrachus* are the very large orbits, the extreme widening of the skull, the elimination of the otic notch and the form of the cheek region bordering the subtemporal fossa.

The very large orbits, present in all other plagiosaurs in which the skull roof is known, are a character unique to the group amongst labyrinthodonts, but paralleled in modern Amphibia. Correlated with this character are several features of the pattern of the dermal bones of the skull roof in which the plagiosaurs differ from *Peltobatrachus*. Thus according to Nilsson the frontals border the orbits in *Gerrothorax pulcherrimus* and in *Plagiosternum*. It is probable that the loss of contact between the parietal and supratemporal, demonstrated as a morphological series by *Gerrothorax pulcherrimus*, *Plagiosternum* and *Plagiosaurus* owes more to the enlargement of the orbits than to the widening of the skull.

The elimination of the otic notch is a character which may perhaps be related to the mode of life of the plagiosaurs and particularly to the perennibranchiate condition demonstrated in *Gerrothorax rhaeticus*. All labyrinthodonts known to be perennibranchiate, except the probably larval branchiosaurs, have reduced or eliminated the otic notch. These include *Trimerorhachis* (Williston 1916; Case 1935), *Dvinosaurus* and '*Platycephalus*' *wilkinsoni* (Stephens 1887*a, b*; Watson 1956). This latter is a brachyopid, all of which have a reduced otic notch. Though small and probably larval it has heavily ossified ceratobranchials: these were probably retained in the adult, as bony structures are unlikely to be lost at metamorphosis (Watson).

The loss of the otic notch suggests the loss of the tympanum and this is paralleled in modern Amphibia which are persistently aquatic. Amongst recent Anura the tympanum is hidden in both genera of the Aglossa (*Xenopus* and *Pipa*), and in the stream-living form *Ascaphus* not only the tympanum but also the stapes is lost, and the tympanum is missing in

all urodeles (Noble 1931). Stages in the concealment and degeneration of the tympanum are seen in the various species of the bufonid genus *Telmatobius* from mountain lakes in the Andes (Barbour & Noble 1920).

The form of the pterygoid and cheek region, which is used by Watson (1956) among a series of characters to unite brachyopids and plagiosaurs, is probably inevitable in a skull as wide and flat as that of a plagiosaur, if the temporal musculature is to be accommodated. This argument will be further developed when the relationship of the brachyopids and plagiosaurs is discussed.

In *Peltobatrachus* the lateral wing of the pterygoid is not well preserved and its form is by no means certain, so that an effective comparison with plagiosaurs cannot be made in this region. This also applies to the profile of the skull, which is characterized by the very flattened snout and, following the form of the pterygoid, turned down cheek in brachyopids and plagiosaurs.

Apart from the tabular horns, a feature of minor taxonomic significance, there are no specialized features of the skull of *Peltobatrachus* which separate it from plagiosaurs. The absence of lateral lines may be mentioned but this is a feature reflecting the general difference between Permian terrestrial and Triassic aquatic labyrinthodonts. *Peltobatrachus*, however, is unusually late compared with the typical terrestrial temnospondyls such as *Eryops*, and its temnospondyl contemporaries are assumed to be aquatic.

Current opinion on the plagiosaurs places them in a group with the brachyopid labyrinthodonts (Watson 1919, 1956; Säve-Söderbergh 1935; Nilsson 1937, 1939, 1946; Romer 1947) and the neotenous form *Dvinosaurus* has been included as more or less closely related by Watson and Säve-Söderbergh, and by Kuhn (1939) and Sushkin (1936). In view of this a comparison between *Peltobatrachus* and these latter forms seems necessary.

The brachyopids have been revised by Watson in a recent paper (1956) and an early Permian form described. Thus it is possible to make the comparison in the light of evolutionary trends in the brachyopids and of the geological horizon of *Peltobatrachus*.

The most significant contrast is therefore in the condition of ossification of the neurocranium. In no brachyopid is an ossified sphenethmoid known and in all of them, including the Lower Permian *Eobrachyops townendae*, the paroccipital process is formed by the junction of the tabular and exoccipital, covering the opisthotic. An ossified supraoccipital and basioccipital are known in *Eobrachyops* but in no other brachyopid in which the occiput is known: these are, with the possible exception of *Bothriceps australis* (Huxley) all late Permian or Early Triassic forms.

All the brachyopids were probably aquatic and like the poorly preserved larval form '*Platyceps*' *wilkinsoni* may have been perennibranchiate: even *Eobrachyops* has traces of lateral line grooves and these are developed in all the later forms. *Eobrachyops* is primitive in having a mobile articulation in the basicranial region, but *Bothriceps* and *Batrachosuchus* have both reached an advanced condition in which the long basicranial suture includes the exoccipital. Another advanced feature of all brachyopids is in the position of the quadrates in relation to the occipital condyles. *Bothriceps* is the only brachyopid in which the quadrates are not well in front of the level of the condyles, and in *Batrachosuchus browni* this advancement reaches an extreme condition. This feature, much more extreme than in other advanced labyrinthodonts, is correlated with the slope of the occiput, which though

present in *Peltobatrachus*, is quantitatively different from that of the brachyopids. Its probable function is discussed in a later section.

In general it may be said that *Peltobatrachus*, considering its geological horizon, is primitive with respect to the brachyopid line of evolution as it is with respect to the capitosaur line, and this is more emphatically the case if Watson's tentative placing of *Bothriceps* in the Middle Permian is correct. The only primitive feature shared by *Peltobatrachus* with all brachyopids is the presence of a hypoglossal foramen.

The only special features shared by *Peltobatrachus* and the brachyopids are the broad parabolic skull without transverse zones of intensive growth, the sloping occiput and the long retroarticular process. The sloping occiput has already been commented upon and the probable function of the long retroarticular process in brachyopids is discussed in a later section: in *Peltobatrachus* as in other labyrinthodonts it is probably related to the flatness of the skull and thus the strength and oblique angle of the depressor mandibulae (Watson 1951).

The remaining significant feature is therefore the shape of the skull in dorsal view. In this the brachyopids depart from the typical 'neotenus' shape in the extreme shortness of the preorbital region and in this they also differ from *Peltobatrachus*. Other diagnostic features of the brachyopids are listed by Watson (1919, 1956) and one of the most important is the very deep cheek region together with the U-shaped palate formed by the sharp turning down of the lateral wings of the pterygoid. To this are added the absence of an otic notch, the long retroarticular process, the slope of the occiput and the form of the skull in dorsal view, already discussed, and the relation of the squamosal and pterygoid to the quadrate, the condition of which is unknown in *Peltobatrachus*.

Peltobatrachus differs from the brachyopids in its own special features as well as in the form of the pterygoids and cheek region, which is the most characteristic brachyopid feature. Thus the brachyopids have a normal labyrinthodont ornament and no tabular or quadrate-jugal horns.

Comparison of *Peltobatrachus* with *Dvinosaurus* gives the same set of common features that the former has with the brachyopids; though the skull shape of *Dvinosaurus* may be more certainly attributed to neoteny. The slope of the occiput of *Dvinosaurus*, judging from published figures, is very slight and more like that of *Peltobatrachus* than that of brachyopids.

Special features in which *Dvinosaurus* differs from *Peltobatrachus* are the persistent intertemporal fused to the postorbital, a unique condition amongst labyrinthodonts, and the form of the dermal ornament. The dermal ornament of *Dvinosaurus* is unusual in consisting of a series of ridges radiating from the centres of ossification of the roofing bones. These ridges are not connected by cross ridges to give the honeycomb appearance of typical labyrinthodont ornament, nor are they broken up into pustules to give the plagiosaur type. Bystrow (1938) has concluded that the condition of the ornament in *Dvinosaurus* is a neotenus one.

The form of the pterygoid of *Dvinosaurus*, apart from the absence of a basicranial suture, could be considered in the lateral region as intermediate between the brachyopid and *Peltobatrachus* condition, and is in superficial form rather like that of the plagiosaur. The lateral wing does not descend abruptly like that of the brachyopid pterygoid to give the characteristic deep cheek: it, however, descends distally, the ventral outline being, to

judge from figures, uniformly concave in posterior view. Also, although the quadrate condyles are slightly in front of the occipital ones, the quadrate ramus of the pterygoid lies in a more nearly vertical plane than the anterior part of the lateral pterygoid. In brachyopids, but not in the plagiosaurs, the two regions are coplanar and thus not distinguishable. The quadrate ramus of *Dvinosaurus* is nevertheless different from that of *Peltobatrachus*: in the latter form it is a distinct, backwardly-directed process of the pterygoid whose plane is at right angles to that of the lateral wing; but in *Dvinosaurus* (and in the plagiosaurs) the quadrate ramus is merely a backward extension of the lateral wing, the plane of which has twisted through rather less than a right angle.

In conclusion it may be said that the skull of *Peltobatrachus* is atypical when compared with that of contemporary labyrinthodonts, and those features which distinguish it from them suggest some sort of affinity with the plagiosaurs. The differences between the skull of *Peltobatrachus* and that of the plagiosaurs may reasonably be related to the very different mode of life of the two, *Peltobatrachus* being terrestrial and the plagiosaurs benthonic, and, in the case of *Gerrothorax* and probably the others, perennibranchiate. Many of these differences may be paralleled in other forms of labyrinthodont evolution, as when the terrestrial Permian form *Eryops* is compared with the late Triassic *Cyclotosaurus* within the capitosaur series (Watson 1919, 1951). Other differences not paralleled in other lines of labyrinthodont evolution may be related to the extreme widening of the skull and enlargement of the orbits, which are unique to the plagiosaurs and would be unlikely in a terrestrial form, and to their perennibranchiate condition.

It does not seem possible, however, to make a case for the relationship of *Peltobatrachus* to either the brachyopids or *Dvinosaurus*, in spite of their much closer position in geological time. In both cases the outline of the skull is the only significant common feature and this represents a generalized condition, while the differences in ornament and neurocranial ossification seem of considerable importance, and the most characteristic feature of brachyopids, the arched palate, is absent in *Peltobatrachus*.

The nature of the vertebrae

The most distinctive feature of *Peltobatrachus* is the unique structure of the dorsal vertebrae, which have the following diagnostic characters: (1) single elongate, centrally notochordal centra; (2) free intervertebral neural arches; (3) laterally projecting, massive, posterior parapophyses on the centrum, confluent in articulation with the diapophyses of the neural arch behind; (4) articulation of the body of the centrum to that of the neural arch in front of it.

Among the labyrinthodonts, using that term in the broadest sense, the only other forms having a single centrum are the stereospondyls. Stereospondylous vertebrae are described from three groups of Triassic labyrinthodonts; the capitosaurs, the metoposaurs and, according to current opinion, the plagiosaurs.

The dorsal vertebrae of the capitosaurs are most fully developed in the genus *Mastodonsaurus* from the Upper Trias of Europe (figure 15). Here the anterior dorsal vertebrae are disks and the only remaining trace of the notochord is a small pit placed dorsally on one or both articular faces. Further back along the dorsal series, and in the caudal region, the centra become wedge-shaped in side view and there is a dorsal notochordal groove. Finally

crescentic centra are found in the posterior caudal region. In the genera *Capitosaurus* and *Cyclotosaurus* the centra are crescentic wedges throughout. It is generally agreed that these centra are derived from the intercentra of earlier rhachitomous forms.

Nilsson (1937) claims that in *Mastodonsaurus* the neural arch lies slightly posterior to the centrum, a view supported by a figure given by Meyer & Pleininger (1844) of part of the vertebral column with its components apparently in their true relation. Also Watson (1951) shows the centrum of *Cyclotosaurus* situated in front of its neural arch. Huene (1922), however, claims that he has seen a few *Mastodonsaurus* centra with facets indicating that the neural arches were intervertebral. Nilsson's view, supported by a well-preserved vertebra showing centrum and neural arch facets, would seem to accord better with expectation, as in the rhachitomous forms from which the capitosaurians are agreed to have evolved the neural arch lies between the intercentrum and the pleurocentrum, and is thus postero-dorsal to the intercentrum.

The vertebrae of the American metoposaurs, all of which may be generically indistinguishable from the main genus *Buettneria*, have been described by Huene (1926), Branson & Mehl (1929), Case (1932) and Sawin (1945). They seem to have reached a more advanced condition than those of capitosaurians: the dorsal centra are all cylindrical and in many cases no trace of the notochord remains. Case, however, describes centra of *Buettneria bakeri* in which a notochordal pit, high up on the articular face, is connected to the dorsal surface by a groove, thus indicating a late closure of the notochordal canal dorsally. There is also from the same site a small juvenile or embryonic centrum in which this closure is not complete, the notochordal canal being open at the top. The European genus *Metoposaurus* has centra which are aberrant in consisting of nothing but a ventral hemicylindrical shell, though this may be merely an age character as suggested by Romer (1947).

In *Peltobatrachus* a strong case can be made for saying that the centrum is posterior to its own neural arch. The posterior central facets of the neural arch form a close and extensive junction with the well-developed anterior facets on the centrum. The anterior facets on the neural arch are less well defined and the corresponding areas on the posterior dorsal surface of the centrum have merely small facets or the rounded ridges described. The position of the parapophyses is peculiar, however, and their articulation with the diapophyses of the neural arch immediately behind makes it appear that, if the association of the neural arch and centrum suggested is correct, the rib articulation spans two vertebrae.

This would not be the case if it were postulated that the centrum of *Peltobatrachus* is the intercentrum and thus lies in front of its own neural arch. The rib articulation would then be of the capitosaur type. This hypothesis, however, creates more problems than it solves. The dorsal notochordal pit in true stereospondyl centra suggests their formation from the intercentral crescents of rhachitomous forms and the intermediate stages are present in the Upper Permian and Lower Triassic neorhachitomes and early stereospondyls, as well as in the caudal vertebrae of more advanced forms. The centrally notochordal condition in *Peltobatrachus*, however, is like that in the seymouriamorphs and primitive reptiles. The elongate form of the centra and the disposition of the neural arch facets are also in striking contrast to typical stereospondyls and there is no sign of any dorsal 'wedging' to suggest an originally crescentic condition.

Also *Peltobatrachus* is from the Upper Permian. If the dorsal vertebrae are to be regarded as stereospondylous, they would represent an advanced stage in which all trace of the pleurocentra had disappeared and the intercentra had become elongate and closely articulated. It would be necessary, therefore, to postulate a stereospondylous ancestor from an earlier period in the Permian. In fact no Permian amphibian from any horizon is known to have evolved beyond the neorhachitomous stage.

It must be concluded, therefore, that whatever the structure of the dorsal vertebrae of *Peltobatrachus* may be, they are not stereospondylous in the accepted sense of the term.

The vertebrae of plagiosaurs (figure 15*b*) are very different from those of the typical stereospondyls and doubts have been expressed by Nilsson and by Romer as to their stereospondylous condition: Piveteau (1928) and Watson (1956) have remarked on the resemblance of their centra to those of amniotes. The vertebrae have been described by Jaekel (1914) (*Plagiosaurus depressus*), Huene (1922) (*Plagiosternum*, *Plagiosuchus*) and Nilsson (1934, 1937, 1946) (*Gerrothorax rhaeticus*). Vertebrae, together with other postcranial remains,

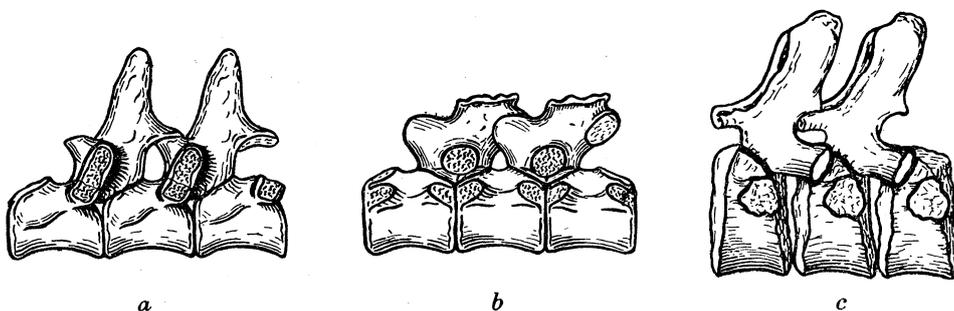


FIGURE 15. Dorsal vertebrae from the left side (somewhat diagrammatic). *a*: natural size. *b*: ca. $\times \frac{1}{2}$. *c*: ca. $\times \frac{1}{4}$. *a*: *Peltobatrachus*. *b*: a plagiosaur. *c*: *Mastodonsaurus*. (*b*, *c* after Nilsson 1937).

have been attributed to *Gerrothorax pulcherrimus* by Huene and other vertebrae have been ascribed to the genus *Plagiosaurus* by Huene (*P. striopustulatus*) and by Piveteau (1928). The vertebrae of *Plagiosternum* are atypical, being short and in some cases unossified dorsally, but all the others conform to the same general type.

The dorsal centra are elongate cylinders bearing intervertebral neural arches. In articulation they leave no space for additional central elements, and there is no sign of a notochordal canal, or the manner of its occlusion. The rib articulation is normally intervertebral, so that the parapophyses are shared by two consecutive centra, though a few individual centra may have only one pair of facets.

This vertebral type resembles that of the new species in the cylindrical close-fitting centra and in the position of the neural arches. In both cases the facets on the centrum for the articulation of the neural arch stand on ridges above the cylindrical body of the centrum, so that the space between these ridges forms the neural canal.

The principal features in which the dorsal vertebrae of *Peltobatrachus* differ from those of the plagiosaurs are as follows: (1) all the centra are notochordal; (2) the anterior and posterior neural arch facets are very differently developed on the body of the centrum, the anterior ones being large and clearly defined, the posterior ones incipient or small; (3) the whole vertebral column is less depressed, the neural spines are high and the

zygapophyses more nearly horizontal; (4) The parapophyses, which project strongly, are confined to a single centrum and, with the diapophyses, form powerful transverse processes.

Bearing in mind that *Peltobatrachus* is from the Upper Permian, the first three of these characters might be seen as earlier stages in the line of plagiosaur evolution. Closure of the central notochordal canal, as occurs in the evolution of amniotes, could result in the amphicoelous or platycoelous centra typical of the plagiosaurs. An intermediate stage must be postulated in the evolution of the completely intervertebral position of the neural arches, in which the articulation of the neural arch to its own centrum was stronger than that to the adjacent centrum. The differential development of the neurocentral facets in *Peltobatrachus* could well represent such a stage. Similarly, the general flattening of the vertebral column and the angle of the zygapophyses in plagiosaurs is related to the very depressed form and mode of life of these animals (Nilsson 1946). This extreme depression is characteristic of all Triassic labyrinthodonts and, as in the skull, would be expected to be less marked in a related terrestrial Permian form.

The massive structure of the transverse process formed by articulation of parapophyses and diapophyses in *Peltobatrachus* may be seen as a specialized character related to the supporting function of ribs bearing heavy armour. In this connexion the striking resemblance of the centrum with skull *A* of *Peltobatrachus* to the excellent photographs of plagiosaur vertebrae published by Piveteau should be noted. The *A* centrum, being from the neck region, does not carry a heavy rib.

The anomalous position of the rib articulation is a more difficult problem. It could well be postulated that the intervertebral position of the parapophyses in plagiosaurs arose by a backward migration from the position in *Peltobatrachus* (as occurs within the American metoposaurs), but it is not easy to see how the position of the parapophyses in this species evolved.

It seems probable that the primitive position of the capitular facet is on the intercentrum. It appears in this position in the typical rhachitomes *Edops* (Romer & Witter 1942) and *Eryops*, in the embolomere *Eogyrinus attheyi* (Watson 1926), and probably in the cross-apterygian *Eusthenopteron* and the Devonian or earliest Carboniferous amphibian *Ichthyostega* (Jarvik 1952). In other forms, however, there is a tendency for it to shift into a position between the intercentrum and the pleurocentrum, as in the embolomere *Archeria* (*Cricotus*) (figured in Williston 1925) and in the rhachitomous *Trimerorhachis* (e.g. Case 1935).

If the parapophyses of *Peltobatrachus* retain this primitive position, the centrum must be formed, at least in part, from the intercentrum, but the presumed anterior position of the neural arch and the notochordal condition of the centrum suggest the homology of the latter with the pleurocentrum of the early rhachitomes and embolomeres: this is very strongly supported by the apparent serial homology of the dorsal centra with the pleurocentra of the tail. Alternatively it may be suggested that, with the reduction of the intercentrum, the parapophyses might have shifted on to the next anterior pleurocentrum.

In comparison to the apparently specialized condition of the dorsals, the caudal vertebrae of *Peltobatrachus* are surprisingly primitive. The free haemapophyses are borne on crescentic wedges lying between successive centra. These crescentic wedges must be intercentra lying between crescentic or ring-shaped pleurocentra, and the resemblance of the

latter to the single centra of the dorsal and early caudal (block *I*) region has already been remarked on. The condition of the posterior tail region is comparable with that in the tail of seymouriamorphs and some rhachitinous labyrinthodonts, such as the old individuals of *Eryops*, in which the pleurocentral blocks fuse dorsally to form a crescent. The two caudal pleurocentra of *Peltobatrachus* which are unfinished ventrally strongly suggest this condition.

The caudal centra of capitosaurians are also more primitive in structure than the dorsals, but the intercentrum remains the principal central element (Huene 1922), and capitosaur intercentra carrying fused haemapophyses have been described by Wepfer (1923). Ossified pleurocentra have never been described from any definitely associated caudal vertebrae of capitosaurians, though they were probably present as small cartilaginous blocks. A caudal intercentrum with attached haemal arch has been described from the metoposaur *Buettneria bakeri*.

It will be seen that the relative development of caudal pleurocentra and intercentra is very different in *Peltobatrachus* from that in true stereospondyls. This alone is sufficient to exclude the possibility of close relationship, and the conclusion reached that the dorsal vertebrae of *Peltobatrachus* could not be considered stereospondylous is therefore further reinforced by the structure of the caudals.

The only plagiosaur caudal vertebrae described are from *Gerrothorax rhaeticus* (Nilsson 1946). Here an intervertebral position of the neural arches is affirmed as 'indicated at least in the foremost caudal vertebrae'. Nilsson then goes on to describe, 'at least on the sixth to eighth caudal centra', long low arches which lack spines and are fused to the whole length of the centrum. These structures, described as haemal arches, are quite unlike the haemapophyses of stereospondyls or those of *Peltobatrachus*, but Nilsson's 'haemal arches' do resemble the fused neural arch on the most posterior preserved centrum of *Peltobatrachus*. Their mode of preservation is equivocal, for, according to Nilsson, the centra 'have been somewhat rotated in the fossil so that the haemal arches come into view on the left side'. It appears very possible, therefore, that since the posterior caudal vertebrae of Nilsson's *Gerrothorax* have undergone rotation, their neural arches have been misinterpreted as haemal arches.

If this is so, the specimen provides no evidence that the caudal vertebrae of *Gerrothorax* were stereospondylous, and it seems not unlikely that the structure of the tail region was very similar to that of *Peltobatrachus*. In the latter the anterior caudal vertebrae have intervertebral neural arches, but more posteriorly the neural arches move back relative to the centra, so that towards the back of the tail they come to lie over the centra and eventually to fuse with them.

Thus nothing in the structure of the tail vertebrae of either *Peltobatrachus* or of the plagiosaurians invalidates the relationship suggested by the structure of the skull and supported by the form of the dorsal vertebrae.

Appendicular skeleton

Comparative accounts of the appendicular skeleton of fossil amphibians are few, but the account by Nilsson (1939) of the cleithrum and humerus is of great value and these two elements will therefore be considered first.

Nilsson's account is supplementary to a description of the cleithrum and humerus of *Plagiosaurus depressus*. In it he distinguishes four main types of cleithrum; the primitive

plate-like condition reconstructed from comparison of the crossopterygian girdle with that attributed by Watson to *Eogyrinus*; the slender rod which may be expanded to cap the scapulocoracoid dorsally, which is found in all temnospondyls and typified by that of *Eryops*; the lepospondyl cleithrum, and that of the plagiosaurs.

The cleithrum of lepospondyls, unlike that of *Eryops*, is usually ornamented laterally and is either T-shaped (e.g. *Batrachiderpeton*) or low and broad (e.g. *Diceratosaurus*). The plagiosaur cleithrum is known in *Plagiosaurus* and in *Gerrothorax pulcherrimus* and *G. striopustulatus* (Huene 1922). It is a large and complex bone ornamented laterally and dorsally and having a long horizontal joint with the clavicle. In this respect it is similar to that of *Diceratosaurus* but it differs from the lepospondyl type of girdle in the relation of its clavicular process to the dorsal cleithral process of the clavicle.

This character is considered by Nilsson to be of some taxonomic importance. In the *Eryops* type the clavicle overhangs the cleithrum ventrally, anteriorly and laterally where their splint-like processes meet on the scapular edge. In the lepospondyl type the clavicle is medial to the cleithrum at their junction and in the plagiosaur type, while the main cleithral process of the clavicle is medial to the cleithrum, the lower end of the clavicular process of the cleithrum is covered laterally by part of the clavicle.

The cleithrum of *Peltobatrachus* is similar in general form to that of temnospondyls (the *Eryops* type) though it may have been ornamented dorsally. The relation of the cleithral and clavicular processes, however, is certainly different. The tip of the cleithrum is hollowed laterally to take the clavicle, but anteriorly the cleithrum overlaps the clavicle, the tip of the latter fitting between the posterior border of the cleithrum and the anterior border of the scapulocoracoid, on the lateral side of the former.

This is essentially the relation of the clavicular process of the cleithrum to the clavicle in *Plagiosaurus*. In this form the lower end of the clavicular process of the cleithrum is covered by part of the clavicle laterally, but the anterior edge of the clavicular process lies in front of the process from the clavicle: the only important difference is therefore the dorsal extension of the cleithral process medially to the cleithrum. It seems, therefore, that in this relation there is another taxonomic detail uniting *Peltobatrachus* and the plagiosaurs. The difference in form of the cleithrum may reasonably be explained on functional grounds. Expansion of the dermal girdle is a common feature of aquatic amphibia, though in typical labyrinthodonts this does not extend to the cleithrum. In terrestrial forms the dermal girdle is reduced, and the different relation to the clavicle of the cleithra of *Eryops* and *Peltobatrachus* shows that they were probably convergent.

It must be noted, however, that Nilsson regards the expanded condition of the plagiosaur cleithrum and its ornamented surface as primitive features and that the reversal of evolution suggested by the re-expansion of the temnospondyl dermal girdle on the return of the group to water never includes the cleithrum. If Nilsson is right *Peltobatrachus* cannot be considered as directly ancestral to the Triassic plagiosaurs, but the evidence of the cleithrum enhances rather than diminishes the probability of relationship of some sort.

The humerus of *Plagiosaurus* described by Nilsson is the only plagiosaur humerus known. It differs from that of *Peltobatrachus* chiefly in the longer shaft, incompletely ossified ends and absence of a deltopectoral crest. Unlike that in some aquatic genera (e.g. *Trimero-rhachis*, *Trematops*, *Lydekkerina*) the ends of the bone stand at right angles to one another.

The humerus of *Peltobatrachus* in general, and as far as preserved, corresponds to the *Eryops* type, as expected in a heavy terrestrial form, though it is doubtful whether the supinator process was as distinct as in *Eryops*.

The strong deltopectoral crest in *Eryops* and *Peltobatrachus* probably acted as an insertion for three muscles concerned with terrestrial locomotion and support of the body on the land; the deltoideus, brachialis inferior and pectoralis. The humerus of *Plagiosaurus* did not have this supporting and terrestrial locomotor function, and the lack of the deltopectoral crest, the poorly ossified ends and the more distinct shaft is merely due to a less great expansion of the flat proximal and distal ends of the bone, which in a form like *Eryops* leave no distinct corpus humeri at all.

The great width of the endochondral girdles of *Peltobatrachus* has already been commented upon, as has the unusual depth of the coracoid and pubo-ischiadic plate. Again these must be seen as adaptations inherent in a heavily built terrestrial form and give little information as to its relationships.

In general the femur of *Peltobatrachus*, though showing little detail, approaches the *Eryops* type (Romer 1922) rather than the somewhat aberrant form described by Nilsson (1946) from *Gerrothorax*. The femur of *Gerrothorax* is characteristically curved in dorsal view and unlike that of *Eryops* or *Peltobatrachus* the tibial side is thicker and more prominent distally. These features of the plagiosaur femur are probably related to the unusual posture of the hind limbs described by Nilsson: they are turned back for swimming like those of a seal. The *Peltobatrachus* femur differs from both that of *Eryops* and that of *Gerrothorax* in its shallow and ill-defined sulcus extensorius between the distal expansions to the tibial and fibular condyles: this is long and deep in *Gerrothorax* and is shorter but deep with a sharp bounding ridge in *Eryops*.

Dermal armour

The presence of dermal armour in labyrinthodonts is probably more common than the existing records would suggest. A ventral covering of elongate scales seems a primitive feature occurring in crossopterygian and palaeoniscid fishes as well as in a wide range of labyrinthodonts. A ventral squamation of this type has been recorded in embolomeres (e.g. *Archeria* ('*Cricotus*'), Case 1911), in ichthyostegids (*Colosteus*, Cope 1875), in *Eryops*, in *Uranocentrodon* (van Hoepen 1915) and in *Gerrothorax* (Nilsson 1946).

Various records exist of dorsal armour in labyrinthodonts. Thin disks of bone, presumably embedded in a thick dermis, have been described in *Eryops* (Romer & Witter 1941) and *Discosaurus* (Credner 1890). Small dermal scales, which were separate and did not form a continuous covering are described from *Archegosaurus* by Broili (1927*b*): in another animal, however (cf. *Scelocephalus*) he describes scales which form a continuous mosaic, and overlapping scales are described from *Trimerorhachis* (Williston 1916: Case 1935; Colbert 1955). In *Uranocentrodon* reduction in ossification appears to have occurred and the scales seem to be horny (van Hoepen 1915).

In all these cases, however, the individual scales of the armour were small, and probably in most cases embedded in a thick dermis. The development of thick large scutes, ornamented externally and forming a dorsal carapace has been described in the Russian seymouriamorph *Kotlassia* (Bystrow 1944), in a family of Permian rhachitomes, the *Dissorophidae* and in the plagiosaurs amongst fossil Amphibia.

In *Kotlassia* the armour consists of a median series of large rectangular scutes flanked by similar lateral ones. Each median scute has a descending lamellate process in the midline, which must have been inserted deeply into the connective tissue between the epaxial musculature. The armour differs from that of *Peltobatrachus* in several points. First, the individual neural scutes did not correspond to the vertebrae below them, their length being greater than that of the vertebrae; secondly the plates seem to have been closely applied at their junctions rather than sutured or overlapped; and lastly the ornament on the outer surface is a curious rectangular mesh of ridges.

In those dissorophids in which the armour is known (*Cacops*, Williston 1910*a*; *Dissorophus*, Williston 1910*b*, Case 1911; *Broiliellus*, Williston 1914; *Aspidosaurus*, Broili 1904; *Alegeinosaurus*, Case 1911) the scutes do correspond individually to the vertebrae. The armour is confined, however, to a single median series, one scute or transverse pair of scutes resting on each spine, and does not as far as is known extend to the costal region or to the tail. The ornament is well developed in all, but unlike that of *Peltobatrachus* consists of small rounded pits.

The armour of plagiosaurs has been fully described only within the genus *Gerrothorax* though Jaekel reports the presence of a number of ornamented scutes found near the type material of *Plagiosaurus depressus* and Schmidt (1931) has attributed to *Plagiosternum* as a scute a single piece of ornamented dermal bone. The armour of *Gerrothorax pulcherrimus* has been described and figured by Huene (1922) and that of *G. rhaeticus* by Nilsson (1934, 1937, 1946).

Nilsson described a ventral armour of elongate scales of somewhat irregular form, arranged in chevron formation about the midline, and a deeper series of elongate rods which he compared to the gastral ribs of reptiles. Dorsally the armour consists of irregular scutes ornamented with the characteristic pustules, with larger more regular scales laterally. There is a median series of 'large . . . dorsal plates overlapping each other to an unusually large extent (an anterior plate as a rule overlapping the succeeding one)'. It is not said whether each of these plates was related to an individual neural spine, but Huene reports a similar median series in *G. pulcherrimus* in which one scute lies over each neural spine.

The lateral scutes in both species show less evidence of regular segmental arrangement, though Huene describes the lateral scutes as organized into transverse series, but not occurring as discrete bands. The block preserved from *G. pulcherrimus* does not extend to the tail region, but a dorsal covering of caudal scutes is reported from *G. rhaeticus*.

There is a suggestion of the pectoral shield of *Peltobatrachus* in the remains of two large antero-lateral scutes firmly sutured together, reported by Nilsson in the pectoral region of *G. pulcherrimus*. Apart from this the resemblances between the armour of *Peltobatrachus* and that of *Gerrothorax* may be summarized thus: (1) dorsal armour of massive scutes covering trunk and tail; (2) scutes ornamented with pustules; (3) a median series of neural scutes, connected by overlap, corresponding individually to the neural spines; (4) lateral scutes connected by overlap or suture; (5) ventral armour of both irregular shaped and elongate elements.

The differences between the armour of *Gerrothorax* and that of *Peltobatrachus* lie, as far as is known, entirely in the form and arrangement of those dorsal scutes lateral to the median

neurals. To some extent this may be correlated with the mode of life of the two forms. The armour of *Gerrothorax* must of necessity have been flexible if it swam, as Nilsson suggested, by vertical undulations passing along a very flat body; whereas the more rigid system of *Peltobatrachus* would have afforded greater protection to a terrestrial animal, in which flexibility of the body was not so important.

Conclusion

The conclusion has been reached on discussion of the structure of the skull that the only forms which may be nearly related to *Peltobatrachus* are the plagiosaurs. Discussion of the vertebrae also leads to the conclusion that the dorsals of *Peltobatrachus* represent, in their principal characters, an antecedent stage to those of plagiosaurs, but do not correspond to any other known type of labyrinthodont vertebra. Scanty evidence from the tail region does nothing to invalidate this conclusion.

Study of the appendicular skeleton, and of the dermal armour, adds supporting evidence to that derived from the skull and the vertebrae for a taxonomic connexion with the plagiosaurs, and a separation from all other labyrinthodonts. It emphasizes, however, the very different mode of life of *Peltobatrachus* from the Triassic plagiosaurs, a difference also reflected in the specialized features of the skull and vertebrae. This is paralleled to some extent by the difference between the terrestrial rhachitomous labyrinthodonts and the aquatic stereospondylous forms; but the expanded cleithrum of Triassic plagiosaurs may indicate that they are a primarily aquatic group. If this is so *Peltobatrachus* cannot represent a directly ancestral condition.

Peltobatrachus is such a remarkable amphibian that, apart from its numerous common characters with the plagiosaurs, its structure gives little idea as to its possible position in the scheme of amphibian evolution. In many characters it and they have evolved in a direction parallel to that of the temnospondyl labyrinthodonts; and the structure of the skull together with the form of the caudal vertebrae of *Peltobatrachus* places both it and the plagiosaurs within the Labyrinthodontia in the broad sense of that term as used by Romer (1947). The structure of the dorsal vertebrae, however, excludes both *Peltobatrachus* and the plagiosaurs from the order Temnospondyli (*Ichthyostegalia*, *Loxommoidea*, *Rhachitomi* and *Stereospondyli*) of that author, and nothing in the known evolutionary history of the group suggests the origin of vertebrae of the plagiosaur type. The structure of the cleithrum, the form of the ornament and the presence of a fully developed dorsal armour are also significant characters not typical of temnospondyls, but uniting *Peltobatrachus* and the plagiosaurs.

Current opinion, relying entirely on cranial characters unites the plagiosaurs with the brachyopid labyrinthodonts, either within the Labyrinthodontia (Romer 1947; Watson 1956) or as a separate group (Nilsson 1946). Comparison of the brachyopids and *Peltobatrachus* has led to the conclusion that no good case can be made for their close relationship. The affinity between the plagiosaurs and *Peltobatrachus* therefore necessitates a detailed comparison between the former and the brachyopids, and a critical re-appraisal of the taxonomic position of the plagiosaurs.

THE TAXONOMIC POSITION OF THE PLAGIOSAURS

The early finds of plagiosaurs were referred by Jaekel (1911) to his 'Nebenklasse' Hemi-spondyli, a group containing phyllospondyls as well as rhachitomous and stereospondylous labyrinthodonts, in a new 'Nebenordnung' the Plagiosterni. In 1914, however, following the description of *Plagiosaurus depressus*, the same author widely separated the two genera *Plagiosternum* (s.s.) and *Plagiosaurus* (including '*Plagiosternum pulcherrimum*' and '*Plagiosternum pustuliferum*'). The new family Plagiosauridae and order Plagiosauri were erected for the latter genus and on the character of the vertebrae the order was placed in the subclass Microsauria. Broili (in Zittel 1911, 1918) placed the genus *Plagiosternum* within the Stereospondyli, and retaining Jaekel's separation, placed the genus *Plagiosaurus* in the family Microsauridae of the lepospondyls. The two genera were reunited by Abel (1919) as the family Plagiosauridae and placed in the order Rhachitomi, which included rhachitomous and stereospondylous forms.

Watson (1919) was the first to suggest an affinity between the plagiosaurs and the brachyopids described by Broom. He grouped the two together as the family Brachyopidae within his 'Grade' Stereospondyli. Watson also suggested the descent of the brachyopid line from the then little-known *Dvinosaurus*. Huene (1922) accepted Watson's classification but preferred the name Plagiosauridae for the brachyopid-plagiosaur family on priority grounds.

Säve-Söderbergh (1935) retained the brachyopids and plagiosaurs (superfamily Brachyopoideae) and the Dvinosauroidae (comprising only *Dvinosaurus*) together as the suborder Brachyopoidea within the Labyrinthodontia. This arrangement was followed by Nilsson (1937) who advanced, however, reasons for the separation of brachyopids and plagiosaurs as separate families. In the same paper he asserted that the vertebrae of plagiosaurs could not be regarded as stereospondylous in the normal sense of that term.

This fact, together with the description of the unusual cleithrum of *Plagiosaurus depressus* led Nilsson (1939) to erect a separate order Plagiosauria, equal in rank to the Labyrinthodontia, comprising the families Brachyopidae and Plagiosauridae. The structure of *Dvinosaurus* had also become more fully known (Sushkin 1936; Bystrow 1938) and Nilsson questioned its relationship to the Plagiosauria. In 1946 the same author gave a diagnosis of this order in which the postcranial characters were derived from the plagiosaurs alone. He also rejected the idea of any relationship between the group and *Dvinosaurus*.

Romer, in his review of the labyrinthodonts (1947), retains the plagiosaurs within the stereospondylous labyrinthodonts while expressing doubts as to the true nature of the vertebrae: he places them, together with the families Brachyopidae and Metoposauridae, in the superfamily Brachyopoidea, chiefly characterized by the abbreviated facial region and sloping occiput. *Dvinosaurus* he removes entirely from the assemblage, placing it in a separate family near *Trimerorhachis* and related rhachitomous forms.

In a recent paper Watson (1956) reaffirms the view first expressed in 1919 that the brachyopids and plagiosaurs form a natural group within the labyrinthodonts and are closely related to *Dvinosaurus*. The description of a Lower Permian brachyopid, however, and the neotenuous condition of *Dvinosaurus* now certainly debar the latter from a position ancestral to the other forms.

Comparison of brachyopids and plagiosaurs

In the paper in which he first postulated the relationship of brachyopids and plagiosaurs Watson (1919) gave the following diagnostic characters uniting both groups of genera:

1. The broad parabolic skulls, with large anteriorly situated orbits.
2. The unusual way in which the prootic 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 down-turning of the lateral wings of the pterygoid inside the basitemporal fossae, 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 condyle lies far behind the dermo-supraoccipitals, so that the occipital surface slopes forwards.

In his recent paper, in a discussion of the plagiosaurs, Watson adds three more common features (Watson 1956, pp. 341-342):

6. The absence of an otic notch.
7. The existence of a very large retroarticular process of the lower jaw.
8. The extreme shallowness of the anterior part of the skull to the hinder end of the maxilla, and the deepening seen in side view, from a point behind the orbit to the quadrate condyle.

The diagnosis of the order Plagiosauria (brachyopids and plagiosaurs) gave the following additional cranial characters (Nilsson 1946):

1. No transverse zones of intensive growth on the skull.
2. Lamina ascendens of the pterygoid low or absent (contrast *Dvinosaurus*).
3. Lateral outline of the pterygoid slightly concave or convex in ventral view (contrast *Dvinosaurus*).

Other common features are those to be expected in advanced Upper Permian or Triassic labyrinthodonts, and some of them are not present in the newly-described Lower Permian *Eobrachyops*.

Of the eight common features put forward by Watson only the last four apply to both brachyopids and plagiosaurs and the significance of these may be considered now.

Two of the similar features have been discussed already. A correlation between the loss of the otic notch and the perennibranchiate condition has been noted and its significance discussed: also it has been shown that the absence of transverse zones of intensive growth in the skull is a generalized condition, from which the various forms of labyrinthodont skull diverge, either by allometric growth as in plagiosaurs, or by development of the zones in various regions as in typical labyrinthodonts (Bystrow 1935; Bystrow & Efremov 1940).

The long retroarticular process is known in the lower jaw of *Bothriceps* and *Plagiosuchus*, and has been reconstructed by Watson in *Eobrachyops* and in a jaw which has been associated by him with *Batrachosuchus*. Common to other advanced labyrinthodonts (Nilsson 1944), it has been explained by Watson (1951) as correlated with the flattening of the skull and advance of the quadrates in aquatic forms. With the quadrates level with, or in front of, the occipital condyles, the mouth in these forms could open by lifting of the skull itself; while the lower jaw merely slid forward slightly. This could be accomplished without

lifting the body at all but a very large depressor mandibulae was necessary: this was inserted on the retroarticular process. The occipital muscles combine with the depressor to lift the skull.

In the plagiosaurs the depression of the skull has reached such an extreme condition that it seems that muscles of sufficient power could not be accommodated vertically. The shallow slope of the occiput and the projecting process for the quadrate are probably parallel to, and to some extent surfaces of origin for, the neck musculature and depressor respectively. It is as though, with the flattening of the skull, the skull table had slid forwards relative to

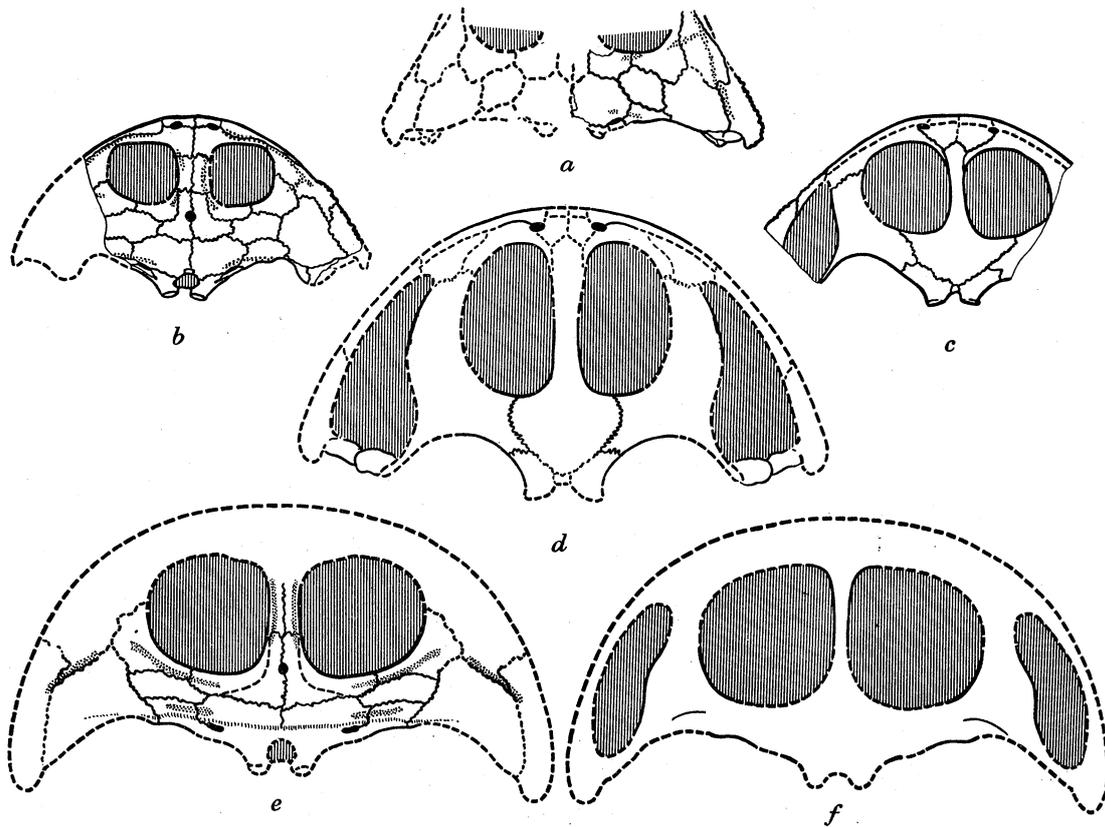


FIGURE 16. Plagiosaur skulls (magn. $\times \frac{1}{6}$). *a*: *Plagiosaurus depressus*, dorsal. *b*, *c*: *Gerrothorax pulcherrimus*, dorsal and ventral. *d*: *Plagiosuchus pustuliferus*, ventral. *e*, *f*: *Plagiosternum granulosum*, dorsal and ventral. (*a-c*: after Nilsson 1937; *d-f*: new reconstructions: *d*, from Huene's figure of original material; *e*, *f*, data from Nilsson, Schmidt, Huene; outline from Bear Island specimen (figure 19, plate 8).)

the occipital and quadrate condyles to preserve the areas of insertion and length of action of the muscles involved. It will also be noticed that the greater the depression of the skull, the more nearly the horizontal axes of rotation of the occipital and quadrate condyles approach one another; with the result that, in opening the mouth, the amount of movement of the lower jaw forwards with the raising of the skull is diminished (figure 17*a*).

The condition in the brachyopids is very different. Although the quadrates are either level with (*Bothriceps*), or in front of, the occipital condyles, the very deep cheek would cause the jaw to move forwards very markedly as the skull was raised from it. Also the axis of the depressor mandibulae must have been nearly vertical when viewed in profile,

and the concave squamosal-quadratojugal surface suggests that this muscle was very large and powerful (figure 17*b*).

Thus the very flat, wide skull of the plagiosaurs, having the depressor mandibulae nearly horizontal and thus working at a considerable mechanical disadvantage, but with the protrusion of the lower jaw reduced to a minimum, may be contrasted with the very deep-cheeked skull of brachyopids, with a very powerful depressor mandibulae and a lower jaw which shot forwards as the mouth was opened.

The plagiosaurs might perhaps be compared to the angler fish *Lophius*, in which the mouth is a trap with powerful adductors but weak depressors. The brachyopids, on the other hand, are better compared to an active predatory fish such as the cod, in which a sudden opening of the mouth and protrusion of the lower jaw aids in securing the prey. Both the former condition and the latter represent adaptations of aquatic predators, but of a very different type.

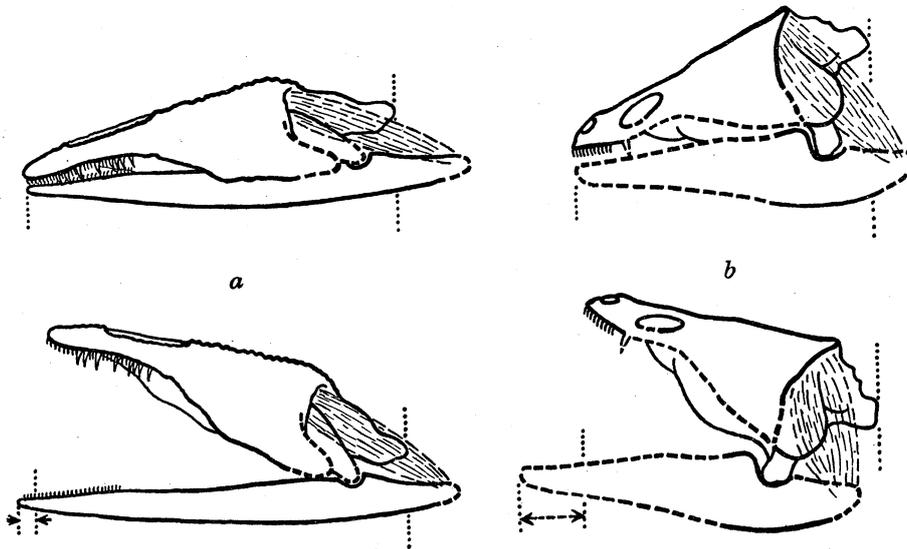


FIGURE 17. Reconstructed skulls of a plagiosaur and a brachyopid in profile to show opening of the mouth by raising the skull. *Depressor mandibulae* indicated. *a*: ca. $\times \frac{1}{3}$. *b*: ca. $\times \frac{1}{4}$. *a*: *Gerrothorax*: note slight protrusion of jaw. *b*: *Batrachosuchus*: note marked protrusion of jaw. (*a*, skull after Watson, jaw data from Huene; *b*, skull and jaw after Watson.)

It also follows that the loss of the otic notch in both brachyopids and plagiosaurs, apart from the aquatic correlations already suggested, may be advantageous when the position of the origin of the depressor mandibulae is considered. The axis of the concave squamosal surface in *Batrachosuchus* ends dorsally at the suture between the squamosal and the tabular, the normal position of the otic notch, and the skull roof overhangs slightly at this point. It seems probable, therefore, that part of the origin of the muscle lay under the overhanging skull roof, in the position from which the otic notch had disappeared.

In *Gerrothorax* there is a considerable cavity under the region of the tabular-squamosal suture and this again was probably for the origin of the depressor mandibulae. In this case, however, the very lateral position of the muscle would be consequent upon the widening and flattening of the skull table; the muscle moving out to retain its position over the lower jaw.

The form of the pterygoids in plagiosaurs, dealt with in detail below, and the corresponding turn-down of the cheek region, are probably to accommodate the very powerful adductor muscles: the subtemporal fossa in *Gerrothorax* has a considerable volume for such a flat skull. The powerful adductor muscles would then secure a rapid snap of the 'rat-trap' jaw. Also it may be seen that in a very flat skull the buccal cavity, if flat along its roof and turned down only at the edges, would have a much greater volume for the same depth of skull than one whose roof was uniformly curved.

It seems, therefore, that the similarities in skull form between brachyopids and plagiosaurs can all be attributed to functional adaptation. This might be taken as some evidence of relationship, except that many of the adaptations, though producing analogous skull features are probably towards different modes of life in the two groups; so that the similarities are superficial.

The first four points which Watson claims as common features of brachyopids and plagiosaurs must now be considered. The first concerns the shape of the skull and the size of the orbits. As the skull table of brachyopids is of typical 'temnospondyl' type both in the general shape and in the arrangement of the dermal bones, the distinctive outline of the skulls in dorsal view is due almost entirely to the very short facial region; that region which in most labyrinthodonts is elongated by means of zones of growth. There seems nothing exceptional about the size of the orbits of brachyopids.

The uniquely expanded skull table in plagiosaurs, combined with the enormous orbits, gives the plagiosaur skull its very distinctive appearance. The facial region, known certainly only in *G. pulcherrimus*, is also abbreviated, but it is difficult to say whether this abbreviation is caused by the enlargement of the orbits, or preceded this in the evolution of the group.

Watson's second character concerns the form of the occipital squamosal and its relation to the quadrate and the pterygoid. This character is shown very clearly in those brachyopids in which the occiput is well known (*Eobrachyops*, *Bothriceps*, *Batrachosuchus*: Watson 1956). The squamosal (and ventrally the quadratojugal) forms a surface concave about a vertical axis, and has a proximal edge which projects as a ridge. This ridge is parallel to a similar ridge formed by the pterygoid, but the two are separated by the quadrate.

The critical region is known in the plagiosaurs only in *Gerrothorax rhaeticus*, *G. pulcherrimus* and *Plagiosaurus depressus*. In all three the quadrate is carried back on a process formed dorsally by the squamosal and quadratojugal and ventrally by the quadrate ramus of the pterygoid, to a position well behind the general level of the skull table. Because of the general flattening of the skull, the occipital squamosal and quadratojugal are almost horizontal, and, in contrast to brachyopids, that part of them which forms the body of the process is convex. Judging from Nilsson's description of these forms (1937), from his figures and from a cast of the typeskull of *Gerrothorax pulcherrimus* in Cambridge, it seems certain that there is no distinct vertical axis of concavity of the occipital squamosal; nor is any ridge described. Furthermore, the squamosal is described in *G. rhaeticus* as contacting the pterygoid (Nilsson 1937), and the squamosal of *G. pulcherrimus* is figured by Fraas (1913), Huene (1922) and Nilsson (1937) as having a long slightly irregular suture with the pterygoid. A similar suture is figured by Nilsson in *Plagiosaurus depressus*. Another point of difference from the brachyopids shown by the latter two species is the projection of the quadrate well behind the squamosal.

Watson's next two points (3 and 4) concern the form of the pterygoids and their relation to the quadrates. The unique form of the pterygoid in brachyopids is caused by the abrupt turning down of the whole lateral part at an angle of about sixty degrees to give the characteristic U-shaped palate. Because of the advanced position of the quadrate condyles and the fact that they are at the bottom of the very deep cheek, a distinct quadrate ramus of the pterygoid is not present: the part of the pterygoid applied to the quadrate is merely the back of the almost vertical lateral wing. The only change in the plane of the latter is due to its very slight convexity inwards. This remarkable form of the pterygoid is well shown in *Eobrachyops*, *Bothriceps* and *Batrachosuchus* and is essentially the same in all three.

The form of the plagiosaur pterygoid, best shown in *Gerrothorax pulcherrimus*, is somewhat different. Because the quadrates are thrust back behind the skull table, there is, in contrast to the brachyopids, a distinct quadrate ramus of the pterygoid lying in a different plane from the rest of the bone. This ramus is formed by a backward extension of the lateral wing behind the body of the pterygoid. As it progresses backwards the plane of the ramus twists, eventually going past the vertical so that its medial surface faces dorsally.

The lateral wing itself is also different in form from that of the brachyopid pterygoid. A comparison of the respective forms of the pterygoids can be made from the study of casts of the type skulls of *G. pulcherrimus* and *Batrachosuchus watsoni* in Cambridge. The lateral wing in *Batrachosuchus* is turned down throughout its length, but in *Gerrothorax* this is certainly not the case. In the latter genus, the edge of the pterygoid bordering the subtemporal fossa is convex ventrally and the wing of the pterygoid between this edge and the lateral border of the interpterygoid vacuity is arched to a variable degree in a smooth curve, to conform to the ventral bulge occurring laterally.

Thus, discussion of Watson's first four diagnostic features of brachyopids and plagiosaurs demonstrates several features which may be used to separate the two groups: these differences (numbers 1-6) may be tabulated together with those noted by Nilsson (1937) most of which have been mentioned in the comparisons with *Peltobatrachus* (table 1).

In addition to these two further differences may be noted. The first is the possession by the plagiosaurs of a quadratojugal horn: the second is of more significance and concerns the form of the palatal dentition.

The dentition of the palatal bones is more or less known in *Eobrachyops*, *Bothriceps* and *Batrachosuchus* amongst the brachyopids and in *Plagiosuchus* and *Gerrothorax pulcherrimus* of the plagiosaurs. All the brachyopids bear typical labyrinthodont tusks, either singly or two together on each side, on the vomers and palatines. In *Batrachosuchus* there are six smaller teeth between the single pair of vomerine tusks, but apart from this the palatine dentition is confined to these tusks.

In plagiosaurs the condition is very different. The vomers of *Plagiosuchus* are covered with small denticles and the palatines, as far as exposed, show three fairly large teeth forming a row parallel to the maxillary row. The extent of this inner palatine row is not known, but in *Gerrothorax* a somewhat irregular row of about ten large teeth extends right round the palatine and on to the region of the ectopterygoid on each side. There is also a scatter of large teeth on the vomers of *Gerrothorax*, in addition to a single row of small teeth behind them.

Of the differences listed a few may be taken to demonstrate a more advanced condition in the plagiosaurs, to be expected from their geological horizon. These include the loss of the hypoglossal foramen and the flattening of the skull. The ossification of the endochondral bones of the occiput, on the other hand, represents a more primitive condition than that in the brachyopids, a fact noted by Nilsson (1937). *Eobrachyops*, described since Nilsson's paper, still lacks an occipital exposure of the opisthotic and is the only brachyopid with an ossified basioccipital and supraoccipital. Thus in the condition of the opisthotic the Upper Triassic and the Rhaetic plagiosaurs are more primitive than the earliest brachyopid, which comes from the Lower Permian.

TABLE 1

Brachyopidae	Plagiosauridae
1 orbits normal	orbits greatly enlarged
2 occiput deep, cheek very deep	whole skull greatly flattened
3 skull table not expanded	skull table enormously widened
4 quadrates vertically below back of skull table	quadrates projecting behind back of skull table in a horizontal process
5 quadrate ramus of pterygoid absent	quadrate ramus well developed
6 occipital squamosal vertical, concave, separated from the pterygoid by the quadrate	occipital squamosal nearly horizontal, convex, contacting the pterygoid
7 opisthotic concealed by junction of tabular and exoccipital	ossified opisthotic exposed and forming the paroccipital process
8 basioccipital and supraoccipital unossified (except <i>Eobrachyops</i>)	supraoccipital (and sometimes basioccipital) ossified
9 hypoglossal foramen present	hypoglossal foramen absent
10 central region of pterygoid and body of parasphenoid long ant.-post.	central body of pterygoid and body of parasphenoid short
11 ornament reticulate	ornament pustular (except <i>Plagiosternum</i>)

All the remaining differences represent divergent specializations of the brachyopids and plagiosaurs and seem strongly to refute any relationship between the two groups of genera, even when balanced against the resemblances already discussed. There is, however, one other line of evidence from skull structure which must be considered: a claim to relationship might be established if it could be shown, as is stated by Watson (1956) that the brachyopids are tending in their evolution towards the plagiosaur condition.

There are a few features in which the plagiosaurs, in common with other Triassic labyrinthodonts, have reached a more advanced condition than the earlier brachyopids, and in some of these the brachyopids may be said to show a series tending towards the plagiosaur condition. The clearest case is in the evolution of the basicranial junction: a movable articulation occurs in *Eobrachyops* (and in *Dvinosaurus* considered a brachyopid by Watson); in *Bothriceps* there is a basicranial suture which includes a short exoccipital-ptyerygoid suture; the latter is longer in *Batrachosuchus* and the plagiosaurs.

The loss of the intertemporal in all the later brachyopids, though tending towards the plagiosaur condition, cannot be described as an evolutionary trend as the bone is only known in the very early *Eobrachyops* (and in *Dvinosaurus*). The loss of the hypoglossal foramen in plagiosaurs is again an advanced character, but it is not clear from Watson's description of the individual types that the brachyopids are tending towards this condition.

In two further general labyrinthodont trends the plagiosaurs show an extreme exaggeration of the advanced condition; they are the flattening of the skull, and correlated with it, the extreme length of the retroarticular process. While the existence of a retroarticular

process is known in *Eobrachyops*, *Bothriceps* and claimed in *Batrachosuchus*, its full extent is known only in *Bothriceps*; so that the postulation of a series tending towards the form of the enormous process known in *Plagiosuchus* is somewhat speculative.

Watson (1956, p. 385) states that 'the occipital aspect of the skull of *Eobrachyops* shows a deep occiput and very ventrally placed quadrate condyles, *Bothriceps*, *Batrachosuchus* and *Gerrothorax* show a progressive flattening, both of the lateral suspensory parts of the skull and of the occiput'. This should be demonstrable firstly by measurement to give the ratio of overall width to overall depth of the skull, and secondly the ratio of the width of the skull table measured across the tabulars to the occipital depth. In the tables the measurements for the brachyopids are taken from Watson's figures: *Gerrothorax* was measured from the cast of the type skull (tables 2 and 3).

TABLE 2

Ratio: overall width/overall depth of skull.	
<i>Eobrachyops townendae</i> L. Permian	2.3
<i>Bothriceps australis</i> ? horizon	3.0
<i>Brachyops laticeps</i> U. Permian	2.5
<i>Batrachosuchus watsoni</i> L. Trias.	2.7
<i>Gerrothorax pulcherrimus</i> U. Trias.	7.5

TABLE 3

Ratio: width of skull table/occipital depth.	
<i>Eobrachyops townendae</i> L. Permian	2.4
<i>Bothriceps australis</i>	2.9
<i>Batrachosuchus watsoni</i> L. Trias.	2.9
<i>Gerrothorax pulcherrimus</i> U. Trias.	7.8

It does not seem established, from consideration of these figures, that the brachyopids were evolving towards the extreme plagiosaur condition. In table 2 a steady but very slight trend towards overall flattening is apparent, though the condition of *Bothriceps* is surprising: the trend demonstrated is probably somewhat less than would be that of a similar series of labyrinthodonts selected from the same horizons but otherwise random. It should also be borne in mind that the very deep cheek of *Eobrachyops* is reconstructed, the original being incomplete. In table 3 it is true that the two later forms show a slight decrease of occipital depth compared with *Eobrachyops*, but again this does not suggest a trend towards the extreme occipital flattening of *Gerrothorax*.

One further general trend is mentioned by Watson: the advance of the quadrate condyles relative to the occipital condyles. Within the brachyopids a chronological series can be distinguished, though *Bothriceps*, while advanced in other respects has the most posterior position of the quadrates. In *Eobrachyops* the quadrates are slightly in front of the occipital condyle, and a progressive series runs through *Brachyops* and *Batrachosuchus watsoni*, to the extreme condition in *B. browni*, in which the quadrates lie far in front of the occiput.

When the plagiosaurs are considered, it is found that the quadrates of *Plagiosaurus* are level with, or even slightly behind the occiput condyles; those of *Gerrothorax pulcherrimus* are somewhat in front, and those of *G. rhaeticus* reach a position comparable to that of *Batrachosuchus*. Thus while the brachyopid and plagiosaur series show parallel trends, it cannot be said that the brachyopids are evolving towards the plagiosaur condition.

All the trends considered so far are common to all temnospondyl labyrinthodonts (Watson 1919, 1951), and even if fully established would not necessarily indicate a close relationship between the two groups. Also the remarkable condition of the occipital bones of the plagiosaurs, a condition from which the brachyopids diverge as do all other labyrinthodonts should be weighed against the positive trends.

When the special features of the plagiosaur skull are considered the evidence that the brachyopids are evolving towards them is even more unsatisfactory. No claim has ever been made that the orbits of brachyopids tend to enlarge towards the plagiosaur condition, nor that there is a progressive widening of the brachyopid skull towards the extreme expanse of that of plagiosaurs. In the latter case, however, measurements were made of the figures of the five brachyopid skulls and from the skull cast of *Gerrothorax pulcherrimus* in an attempt to find such a trend. The ratios taken were of the overall width to the length of the skull table, the region of maximum expansion in the plagiosaurs, and the overall width to overall length. In both cases the figures for the brachyopids showed no trend at all and were remarkably constant, 2.4 ± 0.3 in the first case, 1.2 ± 0.1 in the second. The corresponding figures for *Gerrothorax* were 5.6 and 2.3 respectively.

All previous comparisons of brachyopids and plagiosaurs have been made on the skulls alone, though Nilsson recognized the importance of unique features of the postcranial skeleton of plagiosaurs. Little useful information is obtainable from the postcranial skeleton of brachyopids for a comparison with the plagiosaurs.

There is, however, a significant difference in the form of the interclavicle. The dermal shoulder girdle is fairly well preserved in '*Platyceps wilkinsoni*' and in *Eobrachyops* (Watson 1956), and is well known in plagiosaurs. In all known plagiosaur interclavicles the posterior end is truncated at the level of the back of the clavicles (figure 18), while the interclavicle of stereospondylous labyrinthodonts extends well behind them. This backward extension also occurs in *Eobrachyops* and its outline has been restored by Watson as triangular with concave sides. In '*Platyceps*' a similar extension is present, but appears to be truncated instead of reaching a point.

In conclusion it must be said that the evidence for the relationship of brachyopids and plagiosaurs seems inadequate when the skull is considered. In the characters of the skull and of the dermal ornament the brachyopids appear as a rather specialized, but fundamentally 'orthodox' group of temnospondyls, while the plagiosaur skull is highly aberrant. No skull is known which shows a structure intermediate between the two: Huene (1922) restored the skull of *Plagiosuchus* in a form which suggested an intermediate stage; but after re-study of the specimen, Nilsson (1937) corrected Huene's interpretation of the parasphenoid region and in consequence denied the possibility of *Plagiosuchus* representing such a stage.

The few known postcranial remains of brachyopids give no warrant for assuming that the group possessed the special characters which distinguish the plagiosaurs from the stereospondylous labyrinthodonts and which caused Nilsson to remove them from the labyrinthodonts as a separate order.

The geographical distribution of the two groups of genera is also very different. Apart from *Peltobatrachus* all the plagiosaurs are European while no brachyopid has been recorded from Europe in spite of their occurrence in five other continents.

Dvinosaurus and the metoposaurs

Discussion of the relationships of *Dvinosaurus* has been undertaken by Sushkin (1936), Bystrow (1938), Nilsson (1937, 1946), Romer (1947) and Watson (1956). It has been related to both brachyopids and plagiosaurs by Watson and Sushkin on the structure of the skull, but this has been contested by the other authors, of whom Nilsson (1946) gives a long series of differences from both brachyopids and plagiosaurs.

The common characters of *Dvinosaurus* and the plagiosaurs include the ossification of the supraoccipital and basioccipital, the lack of transverse zones of growth, absence of the otic notch, the perennibranchiate condition, and the form of the lateral wing of the pterygoid. Probably the most significant of these is the ossification of the occipital bones, in which *Dvinosaurus* differs from the brachyopids. It should be noted, however, that while this feature is unknown in any Triassic stereospondyl it persists in many Upper Permian forms apart from *Dvinosaurus*, and is surprising only if the latter is considered to be a brachyopid. Most of the other features have been discussed and related to an aquatic and perennibranchiate mode of life. The similar form of the pterygoid and cheek region is probably due to the same problems of accommodation of the temporalis muscles in a flat wide skull. The quadrate region of *Dvinosaurus*, as Watson (1956) notes, is of the brachyopid type, and thus is different from that of the plagiosaurs.

While the evidence of relationship to the plagiosaurs on skull structure is unsatisfactory and the curious dermal armour already mentioned in the discussion of *Peltobatrachus* represents a neotenous condition and thus is equivocal, the postcranial skeleton of *Dvinosaurus* is that of a typical labyrinthodont.

The cleithrum is of the normal labyrinthodont type, both in its form and in its relation to the clavicle; the interclavicle has a long slender process posteriorly, and the clavicles are not greatly widened. No dermal armour is recorded, and in spite of a probably similar mode of life to the plagiosaurs, the humerus has a well-developed deltopectoral crest, absent in the latter. Finally the vertebral column is rhachitomous, though some co-ossification of the vertebral elements may take place in the anterior dorsal region.

The characters of plagiosaurs, many of which they share with *Peltobatrachus*, which caused Nilsson to separate them from the labyrinthodonts were mostly postcranial. The postcranial skeleton of *Dvinosaurus* is typically labyrinthodont and in the absence of important skull characters uniting the two a close relationship cannot be assumed.

A similar argument may be applied to the metoposaurs, which were included by Romer (1947) with the brachyopids and plagiosaurs in a common superfamily within the stereospondyls. The inclusion of the metoposaurs in this group is based chiefly on a comparison of the form of the skull with that of brachyopids, and there are many striking resemblances: the relatively short face and long postorbital region, the elongate parietals and posteriorly situated pineal, the broad processus cultriformis, and particularly the long exoccipital-ptyergoid suture. There is some slope of the occiput in metoposaurs, though this is not so marked as that in brachyopids and plagiosaurs, and the otic notch is much reduced.

The skull, though considerably flattened, does not show the extreme flattening present in the plagiosaurs and there is no sign of any great widening. The distinctive plagiosaur features, pustular ornament, wide skull, large orbits and ossified endochondral bones of

the occiput, are absent in metoposaurs; also the broad processus is a brachyopid rather than a plagiosaur character. One point separates the metoposaurs from both brachyopids and plagiosaurs: the very long skull table in the former is produced by zones of intensive growth in the postorbital region (Bystrow 1935), and in this respect the skull has diverged from the generalized 'neotenous' skull form in a manner different from that of the plagiosaurs.

The postcranial skeleton of metoposaurs is fairly well known (Fraas 1889; Case 1932; Sawin 1945). The vertebrae have already been discussed and seem to represent the culmination of the stereospondylous type. The dermal shoulder girdle is broadly expanded. It approaches the plagiosaur type in the form of the interclavicle, which though not truncated posteriorly, has a comparatively short broad posterior part; and the broad expansion of the clavicles, which meet in front of the interclavicles. The cleithrum, however, is small and has the normal labyrinthodont relation to the clavicle (Nilsson 1939; Sawin 1945).

The metoposaurs thus seem in many respects to represent the culmination of aquatic stereospondyl development and, while they may be related to the brachyopids, cannot be included in a group with the plagiosaurs outside the stereospondylous labyrinthodonts.

Plagiosternum and Taphrognathus

It has already been pointed out that the ornament in *Plagiosternum granulosum* is not like that of the rest of the plagiosaurs, and when the other features of the species are considered, several anomalies appear.

The genus *Plagiosternum* was founded by Fraas (1896) for his '*Mastodonsaurus*' *granulosus* (1889), described from skull fragments, pieces of dermal shoulder girdle and centra from an Upper Muschelkalk locality at Creilsheim, Swabia. A large piece of skull, extending to the quadratojugal laterally and from the occiput to the mid-orbital region anteriorly, was described by the same author in 1913. Fraas's *Plagiosternum* material has been re-described by Huene (1922) and the skull by Nilsson (1937). Other material has been ascribed to the genus by Huene (1922), Broili (1927*a*), Corroy (1928) and Schmidt (1931).

The ornament of *Plagiosternum* consists, like that of typical labyrinthodonts, of a series of pits and ridges, but there is little elongation of the pits in the direction of bone growth. The difference between this type of ornament and that in typical labyrinthodonts such as *Mastodonsaurus* seemed very marked to Fraas and the trivial name *granulosus* refers to this. It should be noted, however, that confusion is possible and a jaw fragment referred by Fraas to *Plagiosternum* in fact pertains to *Mastodonsaurus* (Nilsson 1937, p. 47, footnote).

The occiput is poorly known in *Plagiosternum*: the opisthotic region is missing in the main skull specimen, and the area above the foramen magnum is not sufficiently well-preserved, according to Nilsson, to determine whether an ossified supraoccipital was present, though Huene reported its absence. The basioccipital region is not preserved, nor is the dentition of the upper jaw.

The most important skull feature shared by *Plagiosternum* with the other plagiosaurs is the form of the skull. The widening of the skull probably reaches a higher degree in *Plagiosternum* than in the other genera, and the orbits are of comparatively enormous size, so that the frontal region between them is extremely narrow. The occiput slopes very

markedly and is separated from the posterior border of the orbits by an exceptionally narrow skull table. The anterior and lateral borders of the skull are not known from Fraas's original material, nor is the form of the quadrate region. A recent find, however, may supply some of the missing information.

During the summer of 1948 an enormous labyrinthodont skeleton was found by two Cambridge undergraduates on Bear Island, Spitsbergen, in shales considered to be of immediately pre-Carnian age. Unfortunately the skeleton was in an extremely fragmentary condition and could not be collected, though sample fragments, now in Norway, were brought back. The find was reported (Lowy 1949) but none of the photographs taken was published. The whole skeleton was 2.6 m long, and the skull 21 cm long by 70 cm wide.

The form of the skull (figure 19, plate 8) and the reticulate ornament seen over parts of its surface, make it likely that the animal was of the genus *Plagiosternum*, though not necessarily *P. granulatum*. On this assumption a new restoration of the skull of the latter has been made using the Bear Island skull as a guide to the overall form (figure 16e-f). It will be noticed that enormous quadratojugal horns are present, extending well behind the occiput. While this is a plagiosaur character it leads to some doubt about the position of the quadrates, which in the Bear Island skull may well lie behind the level of the occipital condyles, a surprising feature.

Three vertebral centra preserved from the same site as the type material of *Plagiosternum granulatum* and of a size compatible with the skull and dermal girdle were described by Fraas. Each centrum was about twice as wide as its length and very low: finished bone surface was present only ventrally and laterally and the form suggested the tail vertebrae of *Mastodonsaurus* to Fraas. Huene's revision of Fraas's material includes a brief description of 'several' centra. Of these some specimens were unossified dorsally, the rest apparently crushed dorso-ventrally. Two of the latter are said to show facets for intervertebral neural arches. One of these appears from Huene's figure to resemble the centrum of an American metoposaur rather than that of a plagiosaur (cf. Branson & Mehl 1929) and the other, though more elongate, appears low and featureless. Fraas's material includes the only *Plagiosternum* vertebrae described.

The dermal armour is a characteristic feature of plagiosaurs: no dermal armour at all is described amongst Fraas's material of *Plagiosternum*. The only piece recorded is a scrap of dermal bone doubtfully identified as a *Plagiosternum* scute on the character of the ornament (Schmidt 1931).

With the exception of the cleithrum the elements of the dermal shoulder girdle of *Plagiosternum* are well known: clavicle and interclavicle were among the type material and most of the finds attributed to the genus are parts of the dermal girdle. The interclavicle is exceptionally wide and differs in form from that of the other plagiosaurs (figure 18). The interclavicle is more or less well known in *Plagiosuchus pustuliferus*, *Plagiosaurus depressus*, *Gerrothorax rhaeticus* and *G. pulcherrimus*, and all the remaining species include parts of the interclavicle amongst the type material: the interclavicle of *Plagiosaurus* is typical.

In all other plagiosaurs in which the full extent is known, the ventrally exposed and ornamented part of the interclavicle is roughly as broad as it is long: that of *Plagiosternum* is approximately twice as broad as its length. The anterior end of the interclavicle is



FIGURE 19. Skull of (?) *Plagiosternum* sp. from Bear Island, Spitsbergen, (approximately one-third natural size) dorsal surface. Original photograph by N. Creasey (see Lowy 1949).

(Facing p. 272)

known in *Plagiosuchus*, *Gerrothorax rhaeticus*, and *G. pulcherrimus* and tapers to a blunt point: in *Plagiosternum* the anterior edge is wide and concave, though the lateral edges do converge somewhat anteriorly.

The difference in form and ornamentation of the interclavicle between *Plagiosternum* and *Plagiosaurus* so impressed Jaekel (1914) that he proposed a very wide separation of the two genera. *Plagiosternum* was retained in the labyrinthodonts while *Plagiosaurus* was placed in a new order Plagiosauri referred to the microsaur.

The clavicles of *Plagiosternum* give little useful information. They are flat sheets of bone crescentic in outline, and their orientation on the interclavicle is difficult to make out (Fraas 1913; Huene 1922; Nilsson 1937). The cleithrum is not known and its relations to the clavicle cannot be inferred from the latter.

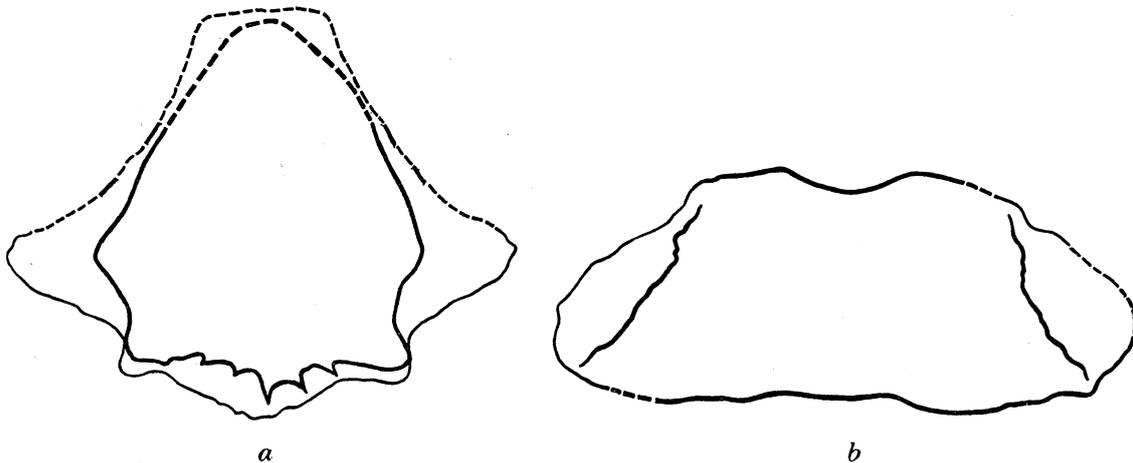


FIGURE 18. Plagiosaur interclavicles in ventral view (magn. $\times \frac{1}{4}$). *a*: *Plagiosaurus depressus*.
b: *Plagiosternum granulosum*. (*a*, after Nilsson; *b*, after Fraas.)

In conclusion it may be said that the evidence for the relationship of *Plagiosternum* to the other plagiosaurs is unsatisfactory. It has specialized even further than they in the flattening and widening of the skull and enlargement of the orbits, but many of the diagnostic features are missing and the very short skull table is a unique feature. Important taxonomic characters are unrecorded in the absence of any description of a cleithrum or dermal armour and the form of the dermal shoulder girdle is unique.

It seems probable therefore that Jaekel was right in his original separation of *Plagiosternum* from the other then known plagiosaurs: the reticulate ornament and vertebrae more nearly referable to the stereospondylous than the plagiosaur type are significant but not certain indicators of its affinities, but its anatomy is not sufficiently well known to make the separation certain.

Another labyrinthodont species that has been referred to the plagiosaurs is *Taphrog-nathus bradyi* from the Upper Moenkopi Formation of Northern Arizona (Welles 1947). The type specimen is a right jaw ramus, complete but for the articular region: referred specimens include jaw fragments, an exoccipital, a right clavicle, a scapula and a humerus.

The type is referred to the plagiosaurs on general form, the short tooth row and the long retroarticular process. It is remarkable in being almost totally without dermal

ornament: this is present only faintly on the surangular and unfortunately is not described.

This fact, together with the total absence of lateral line grooves on the jaw and the lack of pustular ornament on any of the referred specimens, makes its reference to the plagiosaurs somewhat doubtful, and in the absence of further cranial material or vertebrae its taxonomic position remains uncertain.

THE ORDER PLAGIOSAURIA

In the foregoing discussion it has been established that the plagiosaurs may be distinguished from all contemporary stereospondylous labyrinthodonts on important cranial and postcranial characters. This separation was first proposed by Jaekel (1914) who erected a new order, the Plagiosauri, and later by Nilsson (1939), though his order Plagiosauria also included the brachyopids. Comparison of the brachyopids and plagiosaurs shows that they cannot be considered at all closely related and that the brachyopids are to be included amongst the temnospondylous labyrinthodonts.

Nilsson's new order was separated from, and ranked equally with, the Labyrinthodontia, chiefly because of the very different vertebrae and the rather lepospondyl-like dermal shoulder girdle of the plagiosaurs. The pattern of dermal bones on the skull and many other cranial features show, however, that the plagiosaurs have evolved in a manner closely parallel to the temnospondyls, and that they probably have temnospondyl origins. Such wide separation from labyrinthodonts does not therefore seem justified.

The description of *Peltobatrachus* demonstrates that it has many characters distinguishing it from the temnospondylous labyrinthodonts and allying it with the plagiosaurs. Furthermore, the structure of the vertebrae suggests the mode of evolution of the distinctive plagiosaur vertebrae. The tail of *Peltobatrachus* is comparable, however, to the labyrinthodont type and indicates that the species is a labyrinthodont in the broad sense of that term as used by Romer (1947).

Peltobatrachus may therefore be included with the plagiosaurs in the order Plagiosauria. This group then ranks equally with the principal subdivisions of the superorder Labyrinthodontia. The position of the Plagiosauria in the framework of Romer's classification may be indicated thus:

CLASS AMPHIBIA

SUBCLASS APSIDOSPONDYLI

Superorder Labyrinthodontia

1. Order Temnospondyli
2. Order Plagiosauria
3. Order Anthracosauria

While it seems certain that *Peltobatrachus* should be included within the order Plagiosauria, when this is modified to exclude the brachyopids, it is very different from the Triassic plagiosaurs in a number of characters. These features reflect the different geological horizons and very different modes of life of the two. The differences seem as fundamental as those between, for example, the suborders Rhachitomi and Stereospondyli, as defined by Romer, and I propose, therefore, the division of the order Plagiosauria into

two suborders. The first is to include *Peltobatrachus* as the only known form and to be called Peltobatrachi; the second is to include all the remaining described plagiosaurs, with the probable exception of the genus *Plagiosternum* and the problematic *Taphrognathus*. For this second suborder I propose the use of Jaekel's term Plagiosauri in its original sense.

A detailed diagnosis of the revised order Plagiosauria and the two suborders proposed is as follows:

Order Plagiosauria

Amphibia in which the dermal bones have a pustular ornament. Skull parabolic, platybasic, apparently without transverse zones of intensive growth; intertemporal absent, tabulars separated from the interparietals; occiput sloping, quadrates anterior to skull corners which form projecting quadratojugal horns; interpterygoid vacuities large, basicranial suture between parasphenoid and pterygoid; basioccipital and supraoccipital ossified, tabular and exoccipital separated by an ossified opisthotic forming the paroccipital process; lower jaw with well-developed retroarticular process.

Dorsal vertebrae consisting of single elongate centra bearing free 'intervertebral' neural arches; rib articulation spanning two vertebrae; posterior caudal vertebrae of free intercentra or none, and pleurocentra with fused neural arches. Ribs bearing capitulum and tuberculum at the end of an undivided shaft.

Ventral part of clavicular process of cleithrum overlapped laterally by the clavicle, but overlapping the cleithral process of the clavicle anteriorly. Humerus tetrahedral.

Dermal armour dorsally and ventrally—dorsal armour ornamented with pustules and consisting of a median series of neural scutes related to the vertebral neural spines, and flanked by scutes of somewhat different form; sutured scutes in pectoral (and ? pelvic) region at least sometimes forming shields. Ventral armour of elongate scales; tail armoured.

A. *Suborder Peltobatrachi*

1. Skull not greatly flattened or widened, having turned-down cheek and lateral snout region.
2. Orbits of normal size with raised margins.
3. Circumorbital bones large, separating frontals from orbit.
4. Occipital condyle single, including a large basioccipital.
5. Slope of occiput slight.
6. Quadrates probably behind occipital condyle.
7. Otic notch present, including supratemporal in its border.
8. Tabular bearing large globular horns.
9. Hypoglossal foramen present.
10. Quadrate ramus distinct from main pterygoid, which has a marked corner posterolaterally.
11. No exoccipital-ptyerygoid suture; parasphenoid-ptyerygoid suture short.
12. Lateral line grooves absent.
13. Retroarticular process of lower jaw of moderate length.
14. Centra notochordal with weakly developed posterior neural arch facets.
15. Neural spines high, zygapophyses nearly horizontal.
16. Strongly projecting parapophyses confined to a single centrum and forming a massive transverse process with the diapophyses.

17. Caudal centra short.
18. Dorsal ribs curved, broadly expanded backwards to carry armour.
19. Humerus bearing a strongly developed deltopectoral crest.
20. Cleithrum slender, only expanded dorsally.

B. *Suborder Plagiosauri*

1. Skull greatly flattened and widened.
2. Orbits greatly enlarged, margins not raised.
3. Postfrontal reduced; frontals form part of orbit edge.
4. Occipital condyles paired; basioccipital small.
5. Slope of quadrate very marked.
6. Quadrates level with, or in front of, occipital condyles.
7. Otic notch absent: supratemporal excluded from skull margin.
8. Tabulars flat and without horns.
9. Hypoglossal foramen absent.
10. Quadrate ramus a backward extension of the main plane of the lateral pterygoid: lateral outline of the pterygoid smoothly curved.
11. Parasphenoid-ptyerygoid suture long, continued laterally as an exoccipital-ptyerygoid suture.
12. Lateral line grooves well developed.
13. Retroarticular process very long.
14. Centra without trace of notochordal perforation, platycoelous or slightly amphicoelous; anterior and posterior neural arch facets more or less equally developed.
15. Neural spines low, zygapophyses nearly vertical.
16. Parapophyses formed by adjacent centra; no strongly projecting transverse processes.
17. Caudal centra elongate.
18. Dorsal ribs straight, not expanded.
19. Humerus without deltopectoral crest.
20. Cleithrum broadly expanded, ornamented laterally.

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EXPLANATION OF ABBREVIATIONS USED IN FIGURES

<i>A</i> , angular	<i>P</i> , parietal
<i>ART</i> , articular	<i>PAL</i> , palatine
<i>BO</i> , basioccipital	<i>PF</i> , postfrontal
<i>BSP</i> , basisphenoid	<i>PMX</i> , premaxilla
<i>CLEI</i> , cleithrum	<i>PO</i> , postorbital
<i>CNT</i> , centrum	<i>POSL</i> , postsplenic
<i>COR</i> , coracoid	<i>PR.ART</i> , prearticular
<i>D</i> , dentary	<i>PRF</i> , prefrontal
<i>ECT</i> , ectopterygoid	<i>PRO</i> , prootic
<i>EO</i> , exoccipital	<i>PSP</i> , parasphenoid
<i>EPT</i> , epipterygoid	<i>PT</i> , pterygoid
<i>F</i> , frontal	<i>PU</i> , pubis
<i>IL</i> , ilium	<i>Q</i> , quadrate
<i>IP</i> , interparietal	<i>QJ</i> , quadratojugal
<i>IS</i> , ischium	<i>SA</i> , surangular
<i>J</i> , jugal	<i>SCCO</i> , scapulocoracoid
<i>L</i> , lacrimal	<i>SMX</i> , septomaxilla
<i>MX</i> , maxilla	<i>SO</i> , supraoccipital
<i>N</i> , nasal	<i>SPET</i> , sphenethmoid
<i>OP</i> , opisthotic	<i>SQ</i> , squamosal
	<i>ST</i> , supratemporal
	<i>T</i> , tabular
	<i>V</i> , vomer
<i>acc.f.</i> , accessory foramen	<i>o.pr.</i> , otic process
<i>add.cr.</i> , adductor crest	<i>orb.</i> , orbit edge
<i>a.meck.f.</i> , anterior meckelian foramen	<i>par.pr.</i> , paroccipital process
<i>con.rec.</i> , conical recess	<i>p.cr.</i> , pectoral crest
<i>d.cr.</i> , deltoid crest	<i>pfen.cr.</i> , parafenestral crista
<i>f.ch.t.</i> , foramen chordae tympani	<i>pit.fs.</i> , pituitary fossa
<i>fen.ov.</i> , fenestra ovalis	<i>pq.f.</i> , paraquadrate foramen
<i>for.</i> , foramen	<i>pr.cul.</i> , processus cultriformis
<i>gl.</i> , glenoid	<i>p.te.fs.</i> , post-temporal fossa
<i>gl.f.</i> , glenoid foramen	<i>q.ram.</i> , quadrate ramus of pterygoid
<i>i.car.</i> , course of internal carotid artery	<i>rant.pr.</i> , retroarticular process
<i>lam.asc.</i> , lamina ascendens	<i>rect.m.</i> , origin of rectus musculature of eye
<i>obt.f.</i> , obturator foramen	<i>sco.f.</i> , supracoracoid foramen
	<i>sgl.f.</i> , supraglenoid foramen
	<i>sup.pr.</i> , supinator process

Nerve foramina in skull indicated by Roman numerals: II, optic; VI, abducens; X, vagus; XII, hypoglossal.



FIGURE 19. Skull of (?) *Plagiosternum* sp. from Bear Island, Spitsbergen, (approximately one-third natural size) dorsal surface. Original photograph by N. Creasey (see Lowy 1949).