

## A NEW CAPITOSAURID LABYRINTHODONT FROM EAST AFRICA

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ABSTRACT. Cranial and post-cranial amphibian remains from two localities in the Middle Triassic Manda Formation of the Ruhuhu area of Tanzania are described. A new species of *Parotosaurus*, *P. pronus* is proposed.

In the skull, the pterygoid canal is of particular interest and may have carried the VIIIth nerve. The lower jaw has a well-developed pre-articular (hamate) process with behind it a pre-articular fossa.

The neural arches, intercentra, and ribs show considerable regional variation. Ossified pleurocentra are described for the first time in a capitosaur.

The dermal pectoral girdle is massive. Large trabeculae on the interclavicle and clavicles have been interpreted as a ridge system to resist a forward pull on the dorsal process of the clavicle by a cleidomastoideus muscle. Both fore and hind limbs are poorly ossified.

The problem of jaw opening is discussed in capitosaurs and brachyopids. It is thought that in capitosaurs a cleidomastoideus muscle, attached to the tabular horn and to the clavicle, was used to raise the skull, while the depressor mandibulae muscle was used to lower the mandible. In brachyopids the first part of this system was probably an occipito-vertebral muscle.

The retro-articular process and the stereospondylous vertebral column are considered.

LABYRINTHODONTS have been known since Jaeger in 1824 figured remains of a skull and vertebral column which were later recognized as belonging to the same animal, *Mastodonsaurus giganteus*. Subsequently, labyrinthodonts from Carboniferous, Permian, or Triassic rocks have been recovered from most parts of the world.

Since Jaeger's account of *Mastodonsaurus*, capitosaurs, in the broad sense, have been described by many authors. Contributions other than taxonomic descriptions of new species have been made especially by Watson (1919, 1951, 1958, 1962), Huene (1922), Nilsson (1937, 1943 *a, b*, 1944), and Romer (1947). Welles and Cosgriff (1965) revised the group and placed all members of the Family Capitosauridae in three genera, *Parotosaurus*, *Paracyclotosaurus*, and *Cyclotosaurus*, thus following Romer (1947) in excluding *Mastodonsaurus* from the family.

Capitosaurs arose in the Lower Triassic and became extinct before the Jurassic. Adults range in size from a skull length of 7 cm. in a specimen from Australia being described by Cosgriff, to approximately 70 cm. in the Upper Triassic *Cyclotosaurus hemprichi*, the latter indicating a total length of at least 280 cm.

Watson emphasized various trends associated with the evolution of the capitosaurs from Lower, through Middle to Upper Triassic times. The more obvious are: an increase in size; a decrease in ossification, especially of the brain-case and limbs; an increase in dorso-ventral flattening of the skull; and a tendency to close the otic notch. This last character, especially, divides the family, so that the Lower Triassic forms are parotosaurs with open otic notches, while the Upper Triassic types are cyclotosaurs with closed otic notches. The third capitosaur genus, *Paracyclotosaurus*, is Upper Triassic, and was considered by Watson (1958) to have a closed otic notch. Although post-cranial skeletons have rarely been described in capitosaurs, one noticeable trend throughout the group is a gradual change from a rhachitinous vertebral column to

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a neorhachitinous, and finally to a stereospondylous one at least in the anterior part of the column.

The parotosaurs described here were collected by Dr. F. R. Parrington in the Manda Formation of the Ruhuhu Coalfields in Tanzania. They were mentioned in 1958 and 1962 by Watson who thought they could be ancestral to a line of deep-skulled parotosaurs, and by Welles and Cosgriff in 1965, and are especially noteworthy for the large amount of post-cranial material associated with two of the skulls.

Capitosaurs are thought to have been slow-moving animals, living on the bottom of swamps or shallow streams. The huge size of the later forms, accompanied by a decrease in ossification has led to speculation about the function of various parts of their anatomy. Watson has discussed problems concerning the opening of their jaws, and has emphasized the general flattening, together with the enormous development of dermal pectoral girdle, and several authors have commented on the strange mixture of rhachitomy and stereospondyly in the vertebral column.

The Manda beds are regarded by Watson (1958, 1962), Parrington (1946), and Crompton (1955) as being of Middle Triassic age and a detailed summary of the stratigraphy of the area is given by Charig (1963).

*Material.* The capitosaur material described was collected from two of Stockley's localities in the Manda Formation. Stockley's B 9, Mkongoleko, produced Dr. Parrington's field no. 48 which consists of two labyrinthodont skulls with mandibles, a labyrinthodont pterygoid, and a large amount of labyrinthodont post-cranial material, the holotype of a new pseudosuchian (this specimen is being described by Dr. A. J. Charig), and some problematical bones which are here taken to be two ischia and six sacral ribs of an early Triassic reptile. An additional labyrinthodont skull (field no. 135) of the same species as the above was recovered from Stockley's B 26, Gingama.

The labyrinthodont material will be referred to below by Parrington's field numbers. Thus the two skulls from Mkongoleko become F.R.P. 48 I (the larger) and F.R.P. 48 II (the smaller).

The material from Mkongoleko was preserved in a sandstone, undoubtedly the 'pink and purple felspathic sandstone' noted by Stockley (1932) as characteristic of the Manda Beds. The Gingama specimen is grey in colour and its matrix is a 'consolidated marl'.

Although much of the skull material is fragmented, the pieces are generally well preserved. Skull F.R.P. 48 I has almost perfectly preserved ornament but the individual bones have broken apart at their sutures, so their exact interdigitations are not always clear.

Skull F.R.P. 135 has weathered dorsally. In this specimen it was impossible to follow most suture lines because the bone and matrix were identical in colour, and because the bone is covered with a reticulum of suture-like cracks. However, the skull is particularly well preserved in the brain-case area.

All three skulls are a little dorso-ventrally distorted.

The post-cranial material is equally well preserved although pre-sacral neural arches tend to have their spines separated, while several post-sacral neural arches are split in half longitudinally. Only one intercentrum is longitudinally split.

While the skulls, lower jaws, and post-cranial material from F.R.P. 48 were not found in actual association, they were the only labyrinthodont remains recovered from the particular site, and as they all appear to belong to parotosaur-like labyrinthodonts of a comparable size, the post-cranial material is taken to belong to the two skulls.

Preparation of the specimens was carried out with a dental mallet, and an airbrasive unit, and they were reinforced with glyptal.

*Parotosaurus pronus* sp. nov.

The labyrinthodont material contained in F.R.P. field locality 48 is considered to belong to a new species of parotosaur which is named *P. pronus*, the specific name referring to the fact that the animal is dorso-ventrally flattened.

*Holotype.* A skull, no. 48 I: F. R. Parrington collection, University Museum of Zoology, Cambridge.

*Paratypes.* A second skull, 48 II. Four half mandibles. Labyrinthodont post cranial material designated by letters. All F. R. Parrington collection, University Museum of Zoology, Cambridge.

*Referred specimen.* A skull, no. 135: F. R. Parrington collection, University Museum of Zoology, Cambridge.

*Type locality.* F. R. Parrington field locality B 91, at Stockley's B 9, Mkongoleko, Ruhuhu Valley, Tanzania.

*Horizon.* Manda Formation (K8), *Teleocrater* Zone (as proposed by Charig, 1963), Middle Trias.

*Diagnosis.* A parotosaurus with a skull broad posteriorly (B:L approximately 75) (indices as used by Welles and Cosgriff (1965)—B = breadth of skull across quadratojuggals, L = skull length, S = breadth of snout one-fifth of the skull length from the tip, H = height of the postparietals above the parasphenoid), but tapering anteriorly (S:L approximately 32); skull deep posteriorly (H:B approximately 23); nares elongate, lateral, long axes parallel to skull border; septomaxilla present; orbits close together and separated by a shallow depression, well posterior, oval, long axes parallel to mid-line; frontal and jugal enter orbital margin; pineal foramen rectangular, just posterior to hind border of orbits; otic notches semiclosed with tabular horns distinctive, expanded distally towards squamosal; supratemporal excluded from otic notch; posterior skull border concave.

Anterior palatal vacuity reniform; exoccipitals barely exposed on palate; pterygoids meeting palatines; pterygoid with facet for jaw articulation.

Processus lamellosus of exoccipital present.

Lower jaw with large pre-articular process and pre-articular fossa.

Vertebrae not longitudinally compressed; pre-sacral neural arches with antero-ventral nodules developed; intercentra crescentic; some pleurocentra ossified.

Ribs all with uncinat processes; most with distal expansion; all with 'knee' bend.

Dermal pectoral girdle massive, flattened; dorsal process of clavicle well developed and inclined inwards anterodorsally, scapulocoracoid poorly ossified.

Humerus tetrahedral, poorly ossified.

Pelvic elements separate; pubis apparently unossified.

Hind limb poorly ossified; femur with well-developed adductor ridge.

### *Skull*

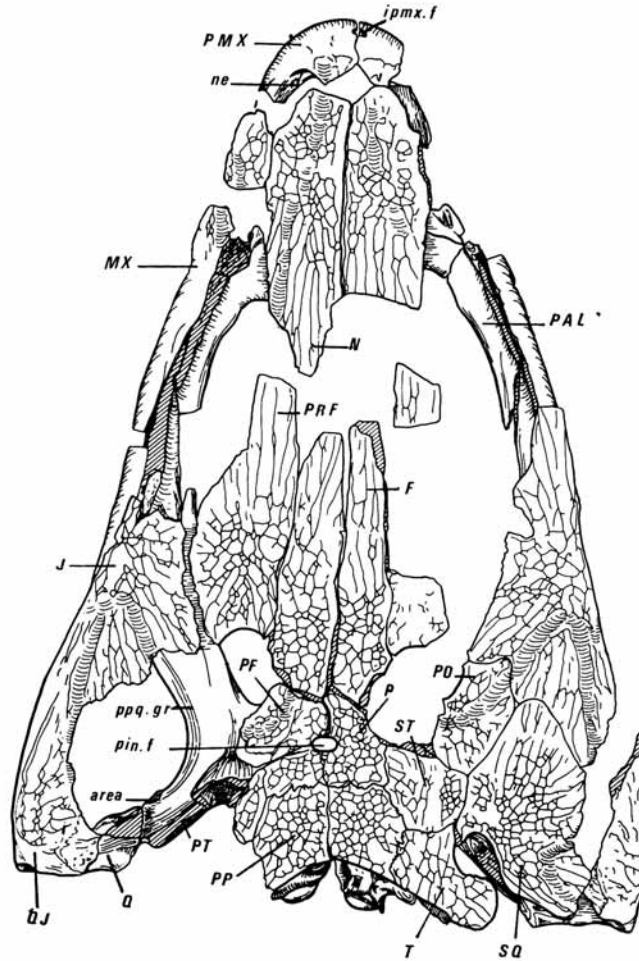
The skull of *Parotosaurus pronus* has the bone complement and shape characteristic of the genus as described for *P. peabodyi* by Welles and Cosgriff (1965).

One character distinguishing *P. pronus* from other parotosaur species is the shape of the tabular horn (text-fig. 1): it is expanded anteriorly as well as laterally towards the squamosal so that distally the horn is nearly one-third wider than the neck which separates it from the body of the tabular.

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#### EXPLANATION OF PLATE 45

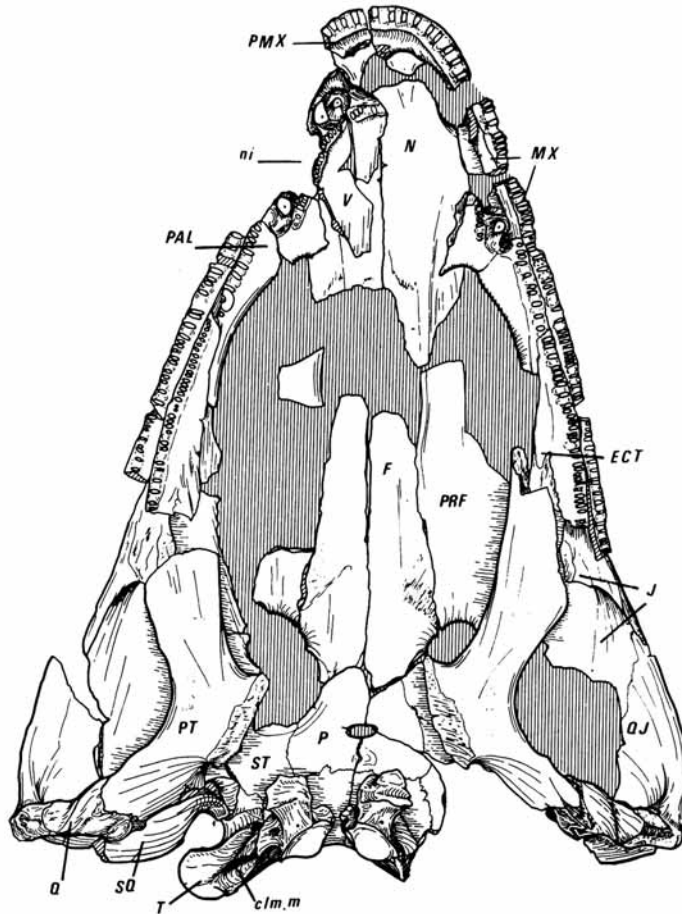
*Parotosaurus pronus* sp. nov. Type skull F.R.P. 48 I. Dorsal view. The exoccipital bones have been displaced posteriorly.



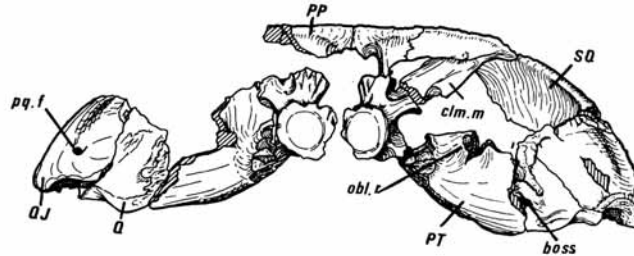
TEXT-FIG. 1. *Parotosaurus pronus* sp. nov. Skull 48 I. dorsal view ( $\times \frac{1}{2}$ ).

A second distinction is a roughened area of bone on the quadrate ramus of the pterygoid in an internal position adjacent to the quadrate (text-figs. 1, 9). This appears to have been a continuation on to the pterygoid of the articular surface of the screw-shaped quadrate condyle.

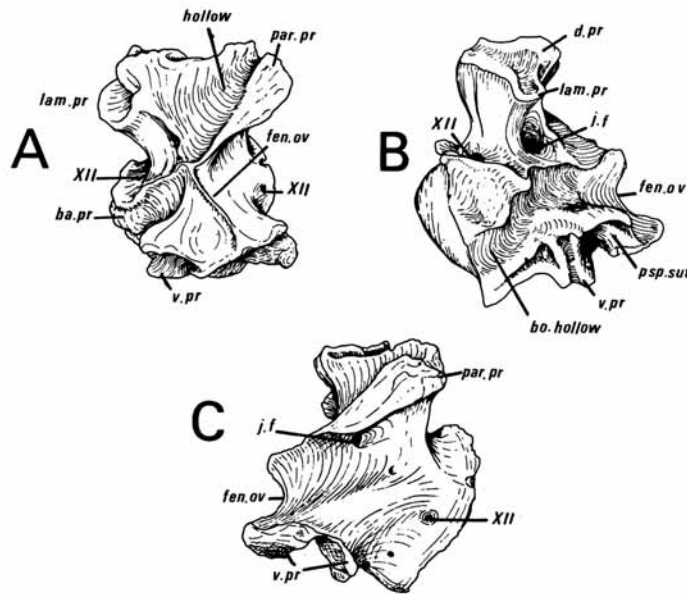
Excellent preservation in some parts of the occiput and the area around the brain-case reveal several new features of capitosaur anatomy. Particularly prominent on the occiput are a pair of tabular ridges. Below the postero-medial edge of each tabular is a

TEXT-FIG. 2. Skull 48 I. palatal view ( $\times \frac{1}{2}$ ).

rugose ridge which runs across the occiput, narrows, and is continued on to the post-parietals. This would have served, together with a small rugosity immediately below the distal end of the tabular, as an insertion point for some of the occipito-vertebral muscles. However, the most conspicuous ridge on the tabular runs along the paroccipital process (text-figs. 3, 5) and was the insertion for the cleidomastoideus muscle (see below). In anterior view (that is, from inside the otic notch) it can be seen that this ridge is confluent with the anterior wall of the paroccipital process. Also in this view, a further ridge can be seen running down the paroccipital process along what appears to be the posterior border of the subtympenic area.



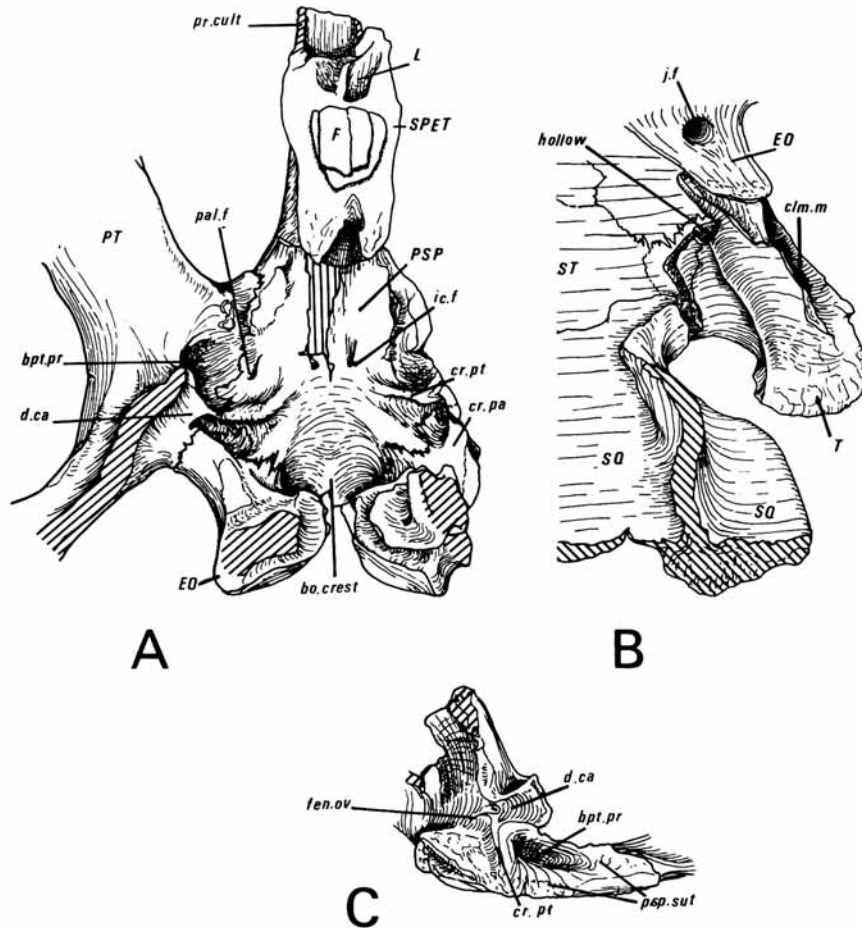
TEXT-FIG. 3. Skull 48 I. occipital view ( $\times \frac{1}{4}$ ).



TEXT-FIG. 4. Skull 48 I. Left exoccipital ( $\times \frac{3}{4}$ ). A, anterior view; B, medial view; C, lateral view.

At their suture on the paroccipital process both the tabular and exoccipital are hollowed: this space was filled in life by the cartilaginous opisthotic which was not exposed on the occiput. An antero-ventral expansion of the tabular has an unfinished surface and a space between it and the paroccipital process is hollowed and presumably also contained opisthotic.

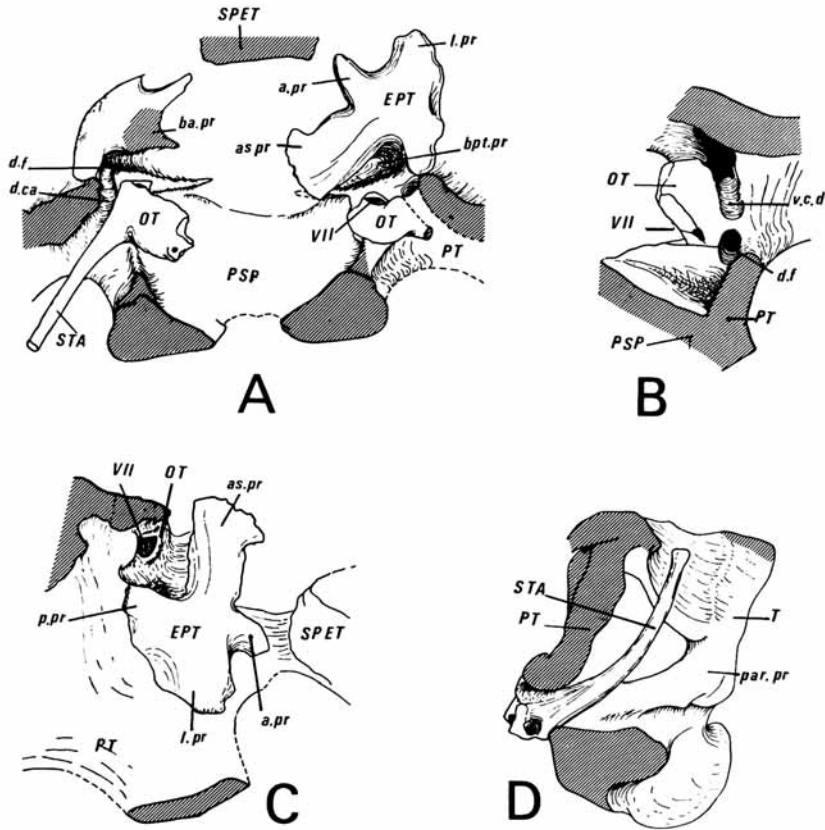
The exoccipitals of the type skull are shown in three views in text-fig. 4. Text-fig. 4A shows the jugular foramen and the foramen for nerve XII entering the exoccipital from the cavity occupied by the medulla oblongata while text-fig. 4C shows their exits. Also in text-fig. 4A can be seen a longitudinal hollow for the lateral edge of the basioccipital



TEXT-FIG. 5. Skull ( $\times \frac{1}{2}$ ). A, Skull 48 II, dorsal view of parasphenoid area; B, Skull 48 I, ventral view of otic notch; C, Skull 48 I, medial view of pterygoid body.

cartilage, and below this an area of suture with the parasphenoid. Anteriorly, beneath the base of the paroccipital process, an oblique ridge which connects the lateral external part of the exoccipital with the inner brain-case area is the median edge of the fenestra ovalis.

Beside the exoccipital, the pterygoid curves anteriorly to form a cupped region beneath the otic notch—the subtympanic cavity—whose postero-lateral edge is the beginning of an oblique ridge. This ridge projects less than the 'otic flange' described by Watson (1962) and in specimen 135 is recurved so that it just fails to meet the ptery-



TEXT-FIG. 6. Skull 135 ( $\times \frac{1}{2}$ ). A, dorsal view of parasphenoid area; B, anterior view of left otic area; C, antero-latero-dorsal view of right epipterygoid; D, antero-latero-ventral view of left stapes and surrounding area.

goid dorsally to form a canal. From the front of the subtympanic cavity a semicircular groove leads inwards above the exoccipital suture and ends dorsal to the conical recess in the pterygoid for the basiptyergoid process of the basisphenoid. This groove is referred to as the dorsal canal of the pterygoid and its opening above the conical recess is the dorsal foramen (text-figs. 5, 6). Watson (1919, fig. 16) shows a similar groove but does not describe it.

A foramen for the vena capitis dorsalis enters skull 135 just above the dorsal canal, while in the type skull immediately below the canal and behind the parapterygoid crista, is a sharp lip of bone which marks the lateral edge of the fenestra ovalis.

In addition to the sphenethmoid complex, specimen 135 has part of the stapes, otic regions, and epipterygoids preserved on both sides (text-fig. 6). The right epipterygoid



is almost complete and differs from that of *P. peabodyi*, rather resembling the ones described by Wilson (1941) in *Buettneria*. A medial basal process of the epipterygoid (text-fig. 6A) is pierced by a foramen which probably carried the profundus nerve ( $V_1$ ) and also the palatine branch of nerve VII. Just posterior to this basal process nerve V must have divided so that  $V_1$  passed in front of the ascending process of the epipterygoid, and  $V_2$  behind it, but there is no trace of a groove for the gasserian ganglion found in this area by Watson (1958).

Little interpretable structure can be seen in the stapes (text-fig. 6D) as its proximal end cannot be separated from the otic ossification. The head of the stapes is thus fused into the fenestra ovalis which is formed by the otic bones dorsally, the pterygoid laterally, and the exoccipital medially.

The otic ossification attached to the stapes is probably the pro-otic but it has a less well-defined shape than the pro-otic described by Welles and Cosgriff in *P. peabodyi*. It lies medially to the quadrate ramus of the pterygoid and postero-dorsally to the parapterygoid crista (which forms the rear wall of the conical recess for the basipterygoid process of the basisphenoid). On the left, laterally, the dorsal canal between the pro-otic and the underlying pterygoid marks the lateral limit to the otic area. The more antero-medial section of the pro-otic, above the parapterygoid crista is thin antero-posteriorly, and is perforated by a foramen which probably carried part of the VIIth nerve before it curved posteriorly to exit from the skull. Bystrow and Efremov (1940) in their restoration of the brain and cranial nerves in *Benthosuchus* show nerve VII passing into the pro-otic in a similar position as does Francis (1934, plate X) in the salamander.

Separate from and posterior to the otic region joined to the stapes is an opisthotic ossification which still forms a core to the paroccipital process.

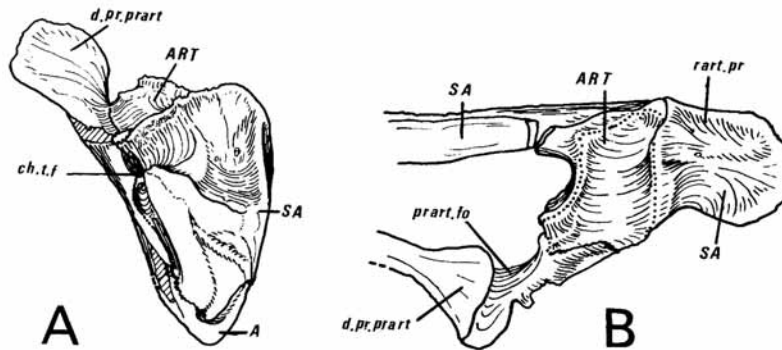
#### *Lower jaws* (text-fig. 7)

The bones of the lower jaw largely follow the typical parotosaurian pattern as shown by Welles and Cosgriff. One difference is that in lateral view in *P. pronus* the most posterior part of the postsplenial lies ventral to the anterior wedge of the angular, the reverse of the condition in *P. peabodyi*.

The pre-articular in *P. pronus* occupies all the median edge of the adductor fossa, and here its hinder end is drawn dorsally into an extensive pre-articular (hamate) process which rises 3.5 cm. above the fossa. The process is transversely thickened and is excavated medially by the leading edge of a pre-articular fossa. A flange of the hamate process forming the dorso-medial wall of the pre-articular fossa is continued forward inside the jaw parallel to, but a centimetre below, the margin of the adductor fossa. The pre-articular fossa has not been described in other labyrinthodonts although it was present in an unidentified mandible cf. *Parotosaurus* in Cambridge (F.R.P. 116). In other better-ossified labyrinthodonts which have a hamate process (e.g. *Paracyclotosaurus*, *Rhineceps*, *Mastodonsaurus* (Wepfer 1923)) the fossa has been filled by a more anterior ossification of Meckel's cartilage than is seen in *P. pronus*. It seems likely, as suggested by Nilsson (1943b) that there was also a posterior extension of Meckel's cartilage running beneath the angular and ending just medial to the most posterior point of the retro-articular process. An interior flange of the angular noted by Nilsson in *Aphaneramma* is present in *P. pronus* as a nodule of bone on the floor of the Meckelian space at the centre of ossification of the angular.

The articular forms a screw-shaped glenoid fossa for articulation with the double quadrate condyle of the skull, the articular area being increased by the hamate process which articulates with the roughened patch on the pterygoid adjacent to the quadrate.

Teeth on the skull and mandible have the typical capitosaur shape and arrangement. Alternation of teeth with replacement pits is regular on the premaxillae of all three specimens, but becomes less regular in more posterior areas. Here there seems little obvious order of teeth and pits, sometimes as many as twenty-three teeth appearing without a gap. In skull F.R.P. 48 II and in one of the mandibles work with an airbrasive



TEXT-FIG. 7. Lower jaw ( $\times \frac{1}{2}$ ). A, posterior view; B, dorsal view of posterior end.

unit revealed tiny replacing teeth in some of the pits. These occurred in areas where pits regularly alternate with fully formed teeth and usually several replacing teeth are found in a series. Often the mature teeth between pits containing replacement teeth are old and appear to be being resorbed, showing the characteristic pattern described by Bystrow (1938) for aged teeth. The enamel in the small replacing teeth is unconvoluted.

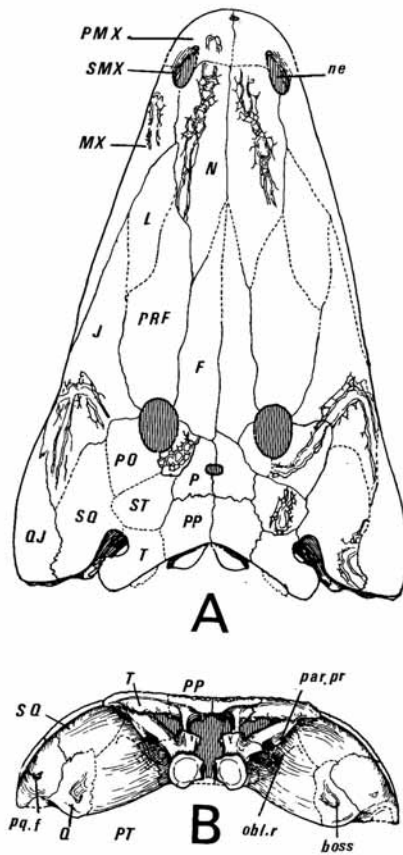
Preparation of a section of left mandible for *Lydekkerina* sp. (specimen F.R.P. 1964/34) revealed replacement teeth in almost every pit. These were found in all stages of development from minute to mature teeth. One tooth was emerging from a partly resorbed mature tooth, while in at least five instances, two teeth were found in a single pit. One replacement tooth was found on a coronoid bone.

*Reconstruction of the skull and mandible (text-figs. 8, 9)*

In the skull reconstruction the parasphenoid and septomaxilla, missing in the type skull, were restored from skull 48 II.

With the articular in place against the quadrate it can be seen that the teeth of the lower jaw must fit in between the two upper tooth rows. It is evident that in this position the upper and lower jaw margins will be separated by at least the depth of the lower teeth, so that in the jaw closed position the three rows are aligned. It can be seen in the present reconstruction that the dentary tusks clear the palate without needing the extra depth afforded by the anterior palatal vacuity. Text-fig. 9 shows that the tooth rows do not meet posteriorly: this region was probably enclosed laterally by a flap of

skin which would prevent food escaping from the mouth. A similar situation can be seen in Watson's reconstruction of *Paracyclotosaurus*.



TEXT-FIG. 8. *Parotosaurus pronus* sp. nov. Restoration of skull 48 I ( $\times \frac{1}{2}$ ). A, dorsal view; B, occipital view.

facet (which Watson (1958) notes is for articulation with the pleurocentrum), while, almost continuous with this but on the anterior surface of the arch, is a further facet. This is deep medially beside the neural canal, but tapers laterally, and is separated from the prezygapophysis by a marked recess. This anterior facet is apparently absent in *Paracyclotosaurus* but is present in other rhachitomes and neorhachitomes and some stereospondyls. It is said (Nilsson 1943a) to be an articular facet for the pleurocentrum belonging to the vertebra in front. A pronounced ridge bounds both ventral and anterior

#### Post-cranial skeleton

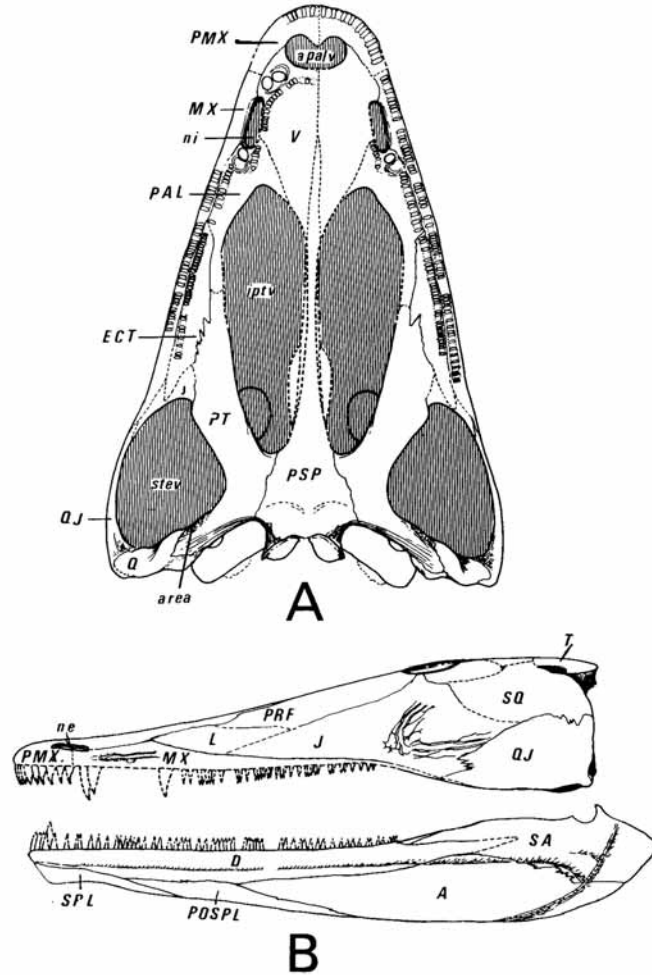
**Vertebral column.** Among the capitosaur, *Paracyclotosaurus* and *Mastodonsaurus* (Huene 1922) have been preserved with their vertebral columns almost intact, but in other forms only scattered, dissociated elements remain.

The vertebrae in specimen F.R.P. 48 probably belonged to two animals but for descriptive purposes they are treated as a single, incomplete vertebral column. Neural arches, intercentra, and pleurocentra are present, and some regional differentiation can be seen in them, especially in the neural arches. The latter have been lettered and the intercentra and pleurocentra numbered to prevent them being inadvertently linked.

Atlas and axis are not represented in the collection.

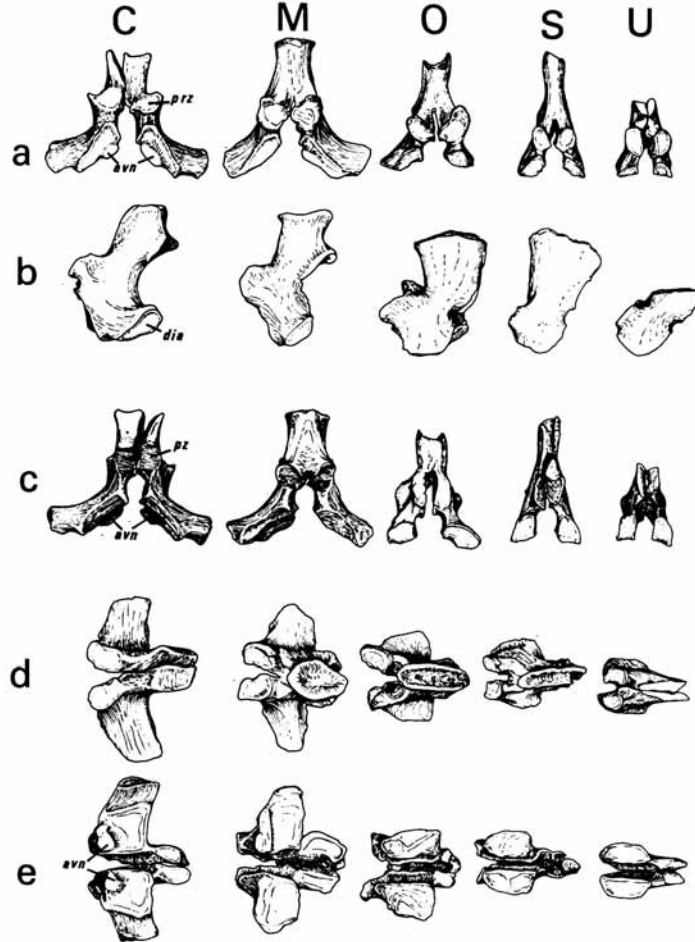
**Neural arches.** One of the more anterior presacral neural arches, arch C (text-fig. 10), probably supported a massive rib above the pectoral girdle. Its spine is split longitudinally and laterally bears a vertical roughened area which marks the position of the segmental boundary (Olsen 1936, Panchen 1967). Beneath the neural spine the limits of the neural canal are clearly defined by dorsal and ventro-lateral ridges: midway along the canal on each side is a small foramen.

On the underside of the body of the neural arch on either side of the neural canal, and extending laterally as far as the transverse processes, is an almost rectangular



TEXT-FIG. 9. *Parotosaurus pronus* sp. nov. Restoration of skull 48 I ( $\times \frac{1}{3}$ ). A, palatal view; B, lateral view of skull and lower jaw.

facets and separates them from the neural canal medially, from the dorsal parts of the arch body anteriorly and posteriorly, and from the transverse process laterally. Both facets are cartilage finished, but in a slight depression between them, towards the midline on each side, is a projecting nubbin which has a surface of finished bone. The bone lamellae of this knob lie in the same plane as the body of the arch, almost at right angles to the longitudinal axis of the vertebra. These antero-ventral nubbins are developed to



TEXT-FIG. 10. Neural arches. C, M, O, S, U. ( $\times \frac{1}{2}$ ). *a*, anterior views; *b*, left lateral views; *c*, posterior views; *d*, dorsal views; *e*, ventral views. Where necessary in this and the following figures bones have been reversed so that all views are of the left side.

some extent in most presacral vertebrae. They vary in size and shape from a small (4 mm.) rounded nubbin, to a raised strip of bone tapering from the midline and completely separating the ventral and anterior neural arch facets. No reference can be found to them in other labyrinthodonts and they were not found in specimens of *Eryops* and *Lydekkerina* examined, or in *Paracyclotosaurus*.

The sacral neural arch, K (text-fig. 11B) has a low spine with poorly ossified zygapophyses, strongly developed body arches, and small antero-ventral bone nubbins. There is a precocious development of the diapophyses so that they are almost circular in lateral view and the transverse processes are correspondingly thickened.

Neural arch O (text-fig. 10), from the anterior caudal area, is remarkable for the altered shape of its neural spine. This is taller, longer, and better ossified than in the more anterior arches, and is narrower at the base than it is dorsally. Its post-zygapophyses are poorly developed and appear merely as swellings of the posterior wall of the neural spine immediately above the neural canal. Laterally the arch body is reduced so that it hardly exceeds the neural canal in width. On the left, the ventral and anterior facets have almost merged, with only a low swelling between. There is no transverse process, but a raised, down-facing, triangular facet lateral to the ventral articular area probably represents the diapophysis.

In the more posterior caudal arches like arch S (text-fig. 10), the post-zygapophyses have disappeared, but in the appropriate place the lower edges of the neural spine bend outwards as if to form a lateral boundary to a pair of wholly cartilaginous facets.

The more helpful criteria used in arranging the presacral neural arches are as follows: from anterior to posterior there can be seen

1. An increase in the angle between the neural spine and the body of the vertebra carrying the transverse process,
2. A decrease in length of the transverse process,
3. 1 and 2 together produce a narrowing of the total width of the neural arch,
4. A decrease in length and width of the diapophyses: this follows from a decrease in size of the ribs,
5. A slight over-all decrease in size,
6. On these criteria, presacral vertebrae with split arches fall anteriorly. This position is supported by observation of the arrangement of *Paracyclotosaurus* in which arches 1–12 are wholly or partially split.

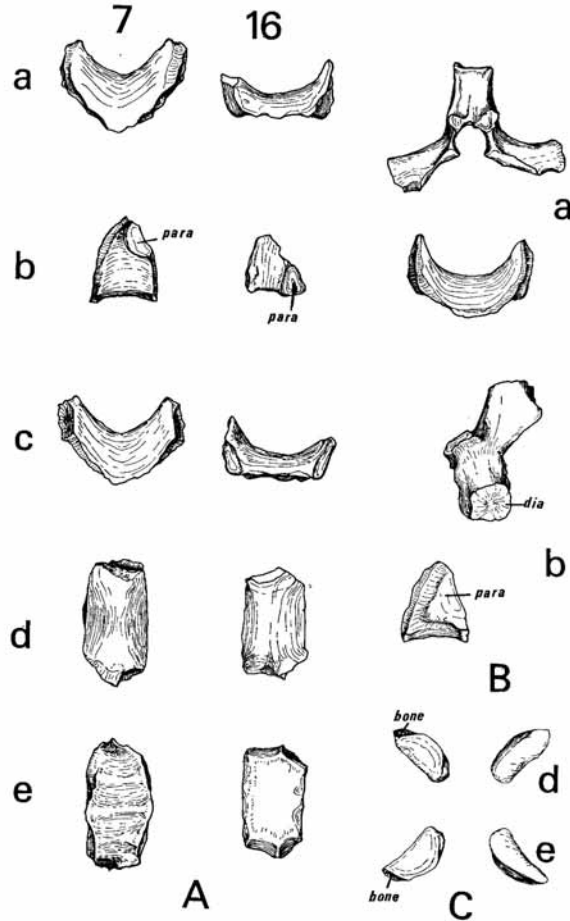
Characters used in ordering the caudal neural arches are as follows:

1. A decrease in over-all size accompanied by a decrease in ossification, especially of the post-zygapophyses,
2. A decrease in the size of the body of the arch and transverse processes, until the latter disappear,
3. An increase in length of the spine in those arches with transverse processes, and, thereafter, its gradual decrease.

The most posterior caudals are graded purely on size.

*Intercentra.* It was found that *P. promus*'s intercentra could be divided into two categories, the first containing the more anterior intercentra, and the second, the more posterior ones.

An example of the first category is intercentrum no. 7 (text-fig. 11A). This is characteristically wedge shaped in lateral view and crescentic in anterior and posterior views. Seen from in front, the intercentrum is much less massive than anterior intercentra of *Paracyclotosaurus*, its dorsal-most parts being pointed, not dorsally flattened. There



TEXT-FIG. 11. A, Intercentra 7, 16. *a*, anterior view; *b*, lateral view; *c*, posterior view; *d*, dorsal view; *e*, ventral view. B, Sacral arch K and intercentrum. *a*, anterior view; *b*, lateral view. C, Pleurocentra 1 and 2. *d*, dorsal view; *e*, ventral view. ( $\times \frac{3}{8}$ ).

are no indications that the element is beginning to ossify around a notochord as it was in the anterior vertebrae of some Upper Triassic capitosaur.

The ventro-lateral surface of the intercentrum is of finished bone and is concave antero-posteriorly. It is traversed by three longitudinal ridges which are similar to, though much smaller than, ridges seen beneath *Eryops* intercentra.

Between this ventral surface and the dorsal convex one there is often a groove which

runs on the anterior margin of the intercentrum. Posteriorly, a similar groove borders the intercentrum below the level of the parapophyses.

The parapophysis, the oval facet for articulation with the capitulum of the rib, is much better developed than its equivalent in *Eryops*, but less well developed than anterior *Mastodonsaurus* parapophyses. The facet in *P. pronus* lies at the back of the intercentrum in a dorso-lateral position. It is surrounded by a ridge which is especially well developed anteriorly, so that there is often a distinct groove between the parapophysis and the anterior edge of the bone. All surfaces of the intercentrum except the concave ventral and lateral ones were finished in cartilage.

An example of the second category of intercentrum is seen in no. 16 (text-fig. 11A). It differs markedly from no. 7 in being flattened ventrally so that its lateral faces have become distinct from the ventral face. It is shallower, and less well ossified than the more anterior intercentra, and only a small area on its ventral surface appears to be of finished bone. The parapophyses have moved ventrally so that their lower edges project below the ventral line of the bone and have become triangular, with the base of the triangle lying ventrally and the hypotenuse lying posteriorly. In this position the parapophysis is lying in a wider part of the intercentrum, and so the groove between it and the anterior border of the bone has become correspondingly wider.

No. 14 may belong to the sacral vertebra (text-fig. 11B). It is flattened, but not to such an extent as the apparently more posterior caudals, and its parapophyses, which are already triangular, are larger than any others in the column.

Trends used to position the intercentra are as follows: from anterior to posterior

1. There is a decrease in over-all size of intercentra.
2. There is a change in shape from deeply crescentic and ventrally pointed anteriorly to ventrally flattened and shallow posteriorly.
3. The parapophysis changes in position from dorsal to ventral, in shape from oval to triangular, and its size first decreases and then increases again with the change to triangular shape.

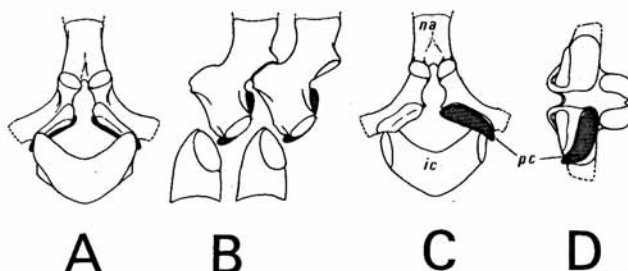
No haemal arches are preserved.

*Pleurocentra* (text-fig. 11C). Although their presence has often been postulated, and the structure of the intercentra indicate that they were present, though probably cartilaginous, ossified pleurocentra have not previously been described in the Capitosauridae. Watson (1958) has dotted them in in *Paracyclotusaurus*. According to Romer (1947) they were ossified in *Benthosuchus*, but Bystrow and Efremov (1940) noted their absence in that animal. Pleurocentra are present in many of the neorhachitomous Rhinesuchidae, especially notable examples being *Uranocentron* (van Hoepen 1915), *Lydekkerina*, and *Sclerothorax* (Huene 1932). However, descriptions of pleurocentra have usually been brief, and they are commonly illustrated in side view only. Nilsson (1943a) does illustrate pleurocentra of the trematosaur, *Lyrocephalus*, in several views, and, except that they are less elongate, their shape is similar to the pleurocentra of *P. pronus*.

Although they were probably present throughout the column, only nine pleurocentra were found. The condition of preservation and degree of ossification of these varies, but it is possible to establish a common structure. Most surfaces are of unfinished bone. The better-formed elements have the median end expanded, the lateral end bluntly



pointed, and are narrow dorso-ventrally, so that they are roughly lens-shaped. The dorsal face is flat for articulation with the postero-ventral facet on the neural arch, while the ventral face bulges a little especially towards the midline. These two faces are separated laterally by a narrow convexly curved surface, but medially they meet in a line which is a little concave, presumably to curve around the dorsal part of the notochord. On the larger pleurocentra is a small area of finished bone which faces antero-laterally: in the smaller pleurocentra this facet is often unfinished. In some cases this area is concave and in one case it seems to be double, with one area lying above and



TEXT-FIG. 12. Reconstruction of presacral vertebra ( $\times \frac{1}{3}$ ). A, anterior view; B, lateral view of two vertebrae; C, posterior view; D, ventral view. Pleurocentra are hatched.

behind the other. In one pleurocentrum the lateral strip of bone also has a partly finished surface. It seems that the pleurocentral element was probably only exposed on its lateral face, at the 'facet' and at the lateral facing strip of bone, all other surfaces being covered with cartilage.

#### *Reconstruction of the vertebrae*

*Presacral region* (text-fig. 12). Placing the neural arches in articulation shows that the presacral vertebrae were arranged in units which averaged 3.3 cm. in length. This leaves a gap of 0.6 cm. between successive intercentra which seems rather large in view of Watson's 1958 restoration in *Paracyclotosaurus davidi* 'with a minimum of ligament between them', but no other arrangement is possible. The intercentra are situated in front of the neural arches with their dorsal points being level, in lateral view, with the transverse processes. It can be seen from the anterior view in text-fig. 12 that the dorsal points of the intercentra are also level with the lateral edges of the anterior neural arch facets.

It follows from this loose arrangement of the neural arch and intercentrum and the small size of the pleurocentrum, that the latter could be placed in one of two ways. It could form the central core of a cartilaginous block which fills the gap between the larger elements: a rhachitomous condition; or it could adhere closely to the neural arch so that the intercentrum fills the gap: an almost stereospondylous condition. It is probable that the neorhachitomous vertebra is almost stereospondylous, the pleurocentra being placed dorsally against the ventral neural arch facet, with a minimum of cartilage between the two. In this position the rounded median end of the pleurocentrum

projected postero-medially towards the anterior neural arch facet of the vertebra behind, while its pointed lateral end extended a little below the level of the transverse process.

*Caudal region* (text-fig. 12). As no haemal arches are preserved there is little evidence on which to base a reconstruction of this area. However, the neural canals can be aligned, and the regions which held their cartilaginous post-zygapophyses can be placed above the prezygapophyses of the arch behind. Haemal arches probably lay between but below the neural arches, separated from them by a great deal of cartilage (as they were in *Uranocentron*).

#### *Ribs* (text-fig. 13)

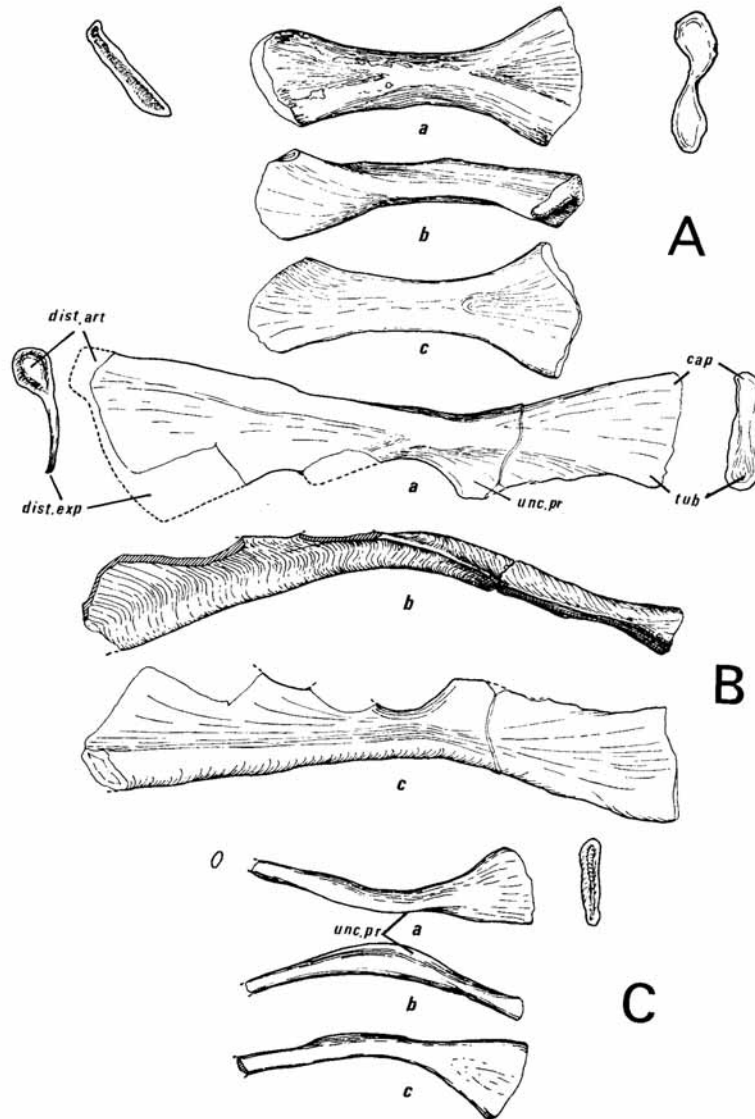
Few rib series of the larger Triassic labyrinthodonts have been described. Among these, ribs are best known in *Paracyclotosaurus* (Watson 1958) which has an almost complete set. Huene (1922) figured a series of ribs of the large neorhachitome *Sclerotherax*. Bystrow (1944) showed a full series of ribs for the Permian seymouriamorph, *Kotlassia*, as did White (1939) for *Seymouria*. Finally, the ribs of *Eryops* are well known, and Olsen (1936) has restored their musculature.

Although there is tremendous individual variation in the ribs it is possible to establish a basic morphological plan. The ribs are single headed but the head is clearly divided into ventral capitular and dorsal tubercular areas, so that it appears slipper-shaped in proximal view. The end was cartilage capped and in life the cartilage probably divided to give a double head. One rib, probably a posterior dorsal, with two heads supports this supposition. From the tuberculum and capitulum, shafts of bone lead laterally to merge on the antero-ventral border of the rib, forming its main shaft. Just distal to this point is a 'knee' bend, so that the remainder of the bone curves postero-ventrally. The 'knee' is present in all ribs (although it is not sharp in the most posterior caudals), unlike the situation in *Paracyclotosaurus* where the posterior thoracic ribs are straight. The rib shaft terminates distally in an unfinished oval facet (the distal articulation) which would have continued as a cartilaginous connection to the sternum. Postero-dorsally, the shaft is drawn out to form a thin shelf of bone which in some cases runs the length of the rib from the tuberculum to the distal articulation, while in others it is a mere indication of a ridge. A cross-section of the rib anywhere along this shelf has a comma shape, the main shaft forming the head of the comma, and giving off the dorsal shelf as its tail. From the shelf develop the characteristic uncinatè processes which are found in most larger labyrinthodonts. These processes are fairly small in F.R.P. 48a, but in addition to them the distal end of the shelf is expanded so that there are usually two (and in one certain case (text-fig. 13B), three) posteriorly directed processes on each rib. Thus all ribs have two heads, a shaft with a 'knee' bend, and some sort of expansion of the shaft.

Cervical ribs are apparently missing in the collection, but a cervical rib count of two seems likely.

Rib A is like rib 4 of *Paracyclotosaurus* and is the largest of all ribs preserved. Remarkable for the massiveness of its shaft and especially for the great distal expansion of the dorsal shelf, it is placed as the first thoracic rib so that it acts as a support for the shoulder girdle.

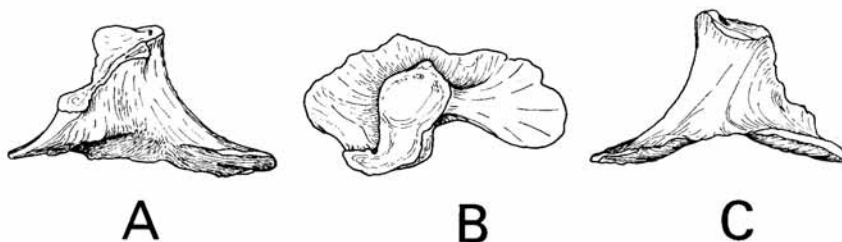
Of the ribs illustrated in text-fig. 13, rib D is fairly typical of anterior thoracic ribs,



TEXT-FIG. 13. *Parotosaurus pronus* sp. nov. A, sacral rib; B, rib D; C, rib X ( $\times \frac{1}{2}$ ). *a*, antero-dorsal views; *b*, posterior views; *c*, postero-ventral views. On the right are proximal and on the left distal outlines of the rib ends.

while rib X resembles the 32nd rib of *Paracyclotosaurus davidi* (the 4th posterior to the sacrum). Moving posteriorly along the series from rib D to rib X there is a gradual decrease in over-all size of the rib accompanied by a more distal position of the uncinat process and the reduction and eventual loss of the distal expansion.

*P. pronus* sacral rib (text-fig. 13) resembles both the cervical and sacral ribs of *Paracyclotosaurus davidi*. The rib has well-developed capitular and tubercular areas. Its distal end is expanded to almost the same extent as its proximal end but has twisted to face anteriorly while the proximal end faces antero-dorsally. On its anterior face, prominent ridges run from all four corners of the bone to meet near the middle of the shaft.



TEXT-FIG. 14. Largest sacral rib of ? reptile ( $\times \frac{1}{2}$ ). A, ventral view; B, medial view; C, dorsal view.

This rib is remarkably like the sacral rib of *Benthosuchus sushkini* (Bystrow and Efremov 1940, fig. 41) although the extremities of the latter are less well ossified: the same muscular 'cristae' are present, and the distal ends of the two ribs are almost indistinguishable. The rib lacks the double processes for articulation with the ilium seen in *Paracyclotosaurus*, but this region was restored by Watson. A similar rib was restored in *Buettneria's* pelvis by Sawin (1945).

In the collection from field locality F.R.P. 48 is another series of sacral ribs.

The largest of these is the best preserved (text-fig. 14). It has an extremely short, thick shaft, and the proximal and distal ends are greatly expanded at right angles to the shaft. Two proximal articular areas are apparent: a rounded capitulum, and running from this, a narrow, elongate tuberculum. Both were finished by cartilage. A strong rounded spine runs laterally from the capitulum to end medial to the anterior part of the distal expansion, while a shorter spine connects the tuberculum with the posterior part of the expansion. This distal expansion for articulation with the ilium is slipper-shaped and curves a little dorsomedially, this 'instep' leading dorsally on to the bone shaft. The proximal end of the rib is twisted roughly  $50^\circ$  relative to the distal end.

This second type of rib is like the one described by Romer (1947) as being typical of labyrinthodonts. Certainly, variations of this rib are seen, for example, in *Pelto-batrachus* (Panchen 1959), *Parioxys* (Shawki Moustafa 1955), *Cacops* (Williston 1910), and *Kotlassia* (Bystrow 1944). However, this type of sacral rib is also seen in reptiles, especially dinosaurs and in the present case it seems more likely that the shorter type of sacral rib belonged to a reptile associated with the remains. Supporting this conclusion is the presence of two elongate bones which can only be interpreted here as ischia of a large Triassic reptile, probably an early member of the Sauropodomorpha

(Huene 1932). The sacral rib series and ischia are of a comparable size and could well have come from the same pelvic girdle.

It seems that in labyrinthodonts the sacral rib may be one of two types. The squat type described by Romer tends to be associated with mainly terrestrial labyrinthodonts with fairly well-developed locomotory powers and expanded iliac blades. In this case the animal has a deep-sided pelvis. The second, elongate type of sacral rib is found in labyrinthodonts which are larger, but flattened, and are probably totally aquatic. These have unexpanded ilia and much cartilage in the pelvis, the pubis being rarely ossified. The ischia in this case incline outwards so the pelvic girdle is dorso-ventrally flattened.

#### *Reconstruction of the ribs*

The ribs as preserved are incomplete both proximally and distally and most have some part of the dorsal shelf missing. The latter has been restored in the figures as described above. No attempt has been made to envisage the restored distal end of the ribs except to note that there was probably some cartilaginous connection to a sternum, at least in the more anterior ribs.

However, some attempt has been made to restore the proximal end of the rib, and to fit the ribs to the vertebral column. It is apparent that the rib head as preserved will not fit the arrangement of a diapophysis and parapophysis on the vertebra, and that to make this fit a greater length of cartilage will have to be added to the capitulum than to the tuberculum. The fit of the tuberculum to the diapophysis is remarkably good in *P. pronus*, and Watson has noted a similarly good fit between these facets in *Paracyclotosaurus*. Thus it seems likely that the cartilaginous caps on the tuberculum and diapophysis were thin. If it is assumed that the cartilage between the capitulum and the parapophysis belonged entirely to the capitulum then it can be seen that the capitulum of an anterior thoracic rib would need to be extended by over a centimetre of cartilage. This is approximately the situation reported by Watson in *Paracyclotosaurus*, and ribs of *Mastodonsaurus* have been preserved with an ossified capitulum which extends medially in this manner (Wepfer 1923).

Thus restored the rib head fits on to the vertebra with its dorsal shelf sloping backwards. In the anterior ribs successive uncinat processes probably overlapped, possibly so that their surfaces touched.

It was noted in reconstructing the vertebrae that while the tubercular rib head was almost the same size and shape as the diapophysis, the capitular head was much smaller than the parapophysis and seemed to lie across its long axis. Now the proximal ends of the ribs lie in an almost horizontal longitudinal plane, so that any movement made by the rib would be expected to occur in a dorso-ventral direction rather than an antero-dorsal direction. Assuming that the rib was involved in dorso-ventral movements, it becomes possible to explain the larger size of the parapophysis. As the capitulum is longer than the tuberculum it can be seen that if the rib is depressed or raised using the tuberculum-diapophysis facet as a pivot, the capitulum will move a greater distance than the tuberculum. This movement will be along an antero-dorsal to postero-ventral line, that is, in the same line as the long axis of the parapophysis. Thus, if the rib is depressed the capitulum would move dorsally on the parapophysis. Movements of ribs used, for example, in respiration are more likely to be in a downwards direction but it is probable that a little dorsal movement was also possible. The capitulum has therefore

been placed in a resting position a little above the lower limit of the diapophysis. If this interpretation is correct, and the intercentra have been arranged in their correct order, then the anterior ribs seem to have moved less than the posterior ones.

#### *Pectoral girdle*

Two interclavicles, two left and two right clavicles, one left and one right cleithrum, and one primary girdle element, a right scapulo-coracoid, were found. By inspection of their articular facets it can be shown that the interclavicles and clavicles form two complete sets, one a little larger than the other. It is less easy to fit the cleithra to their respective clavicles, but the approximate clavicle-cleithrum relationship can be deduced. The scapulocoracoid is small and badly preserved, and could belong to either of the dermal girdles. All pectoral girdle elements are reasonably well known in Triassic labyrinthodonts.

*Interclavicle* (text-fig. 16). The interclavicles have the typical parotosaur shape as shown by Welles and Cosgriff (1965).

The lateral interclavicular trabeculae on the ventral surface of the bones (Bystrow and Efremov 1940, Welles and Cosgriff 1965) are particularly prominent, but the sternal trabeculae are small. In the smaller specimen, an anterior trabecula arises opposite the sternal trabecula, and leads anteriorly to the base of the interclavicle's stem.

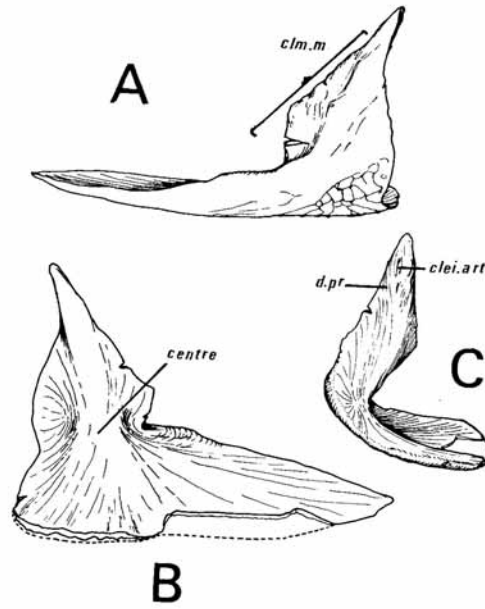
The ventral areas for articulation with the clavicles are deeply ridged especially above the lateral trabeculae. Similar ridges on the dorsal surface of the clavicles undoubtedly intermeshed with these, a system which apparently restricted movement between the elements.

*Clavicle* (text-fig. 15). The general shape of the clavicles is similar to that seen in *Paracyclotosaurus davidi*.

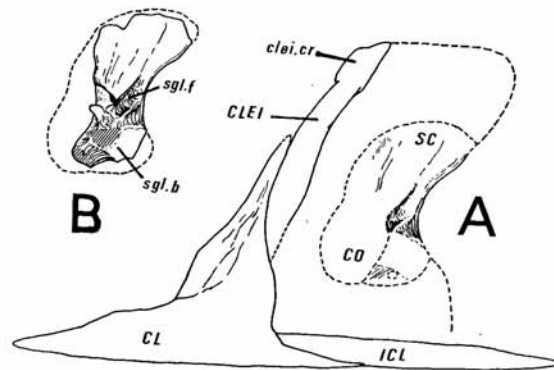
The clavicles also have well-developed trabeculae. These stretch from the median border of the clavicle, from a position below the lateral interclavicular trabeculae, to the base of the dorsal process at which point the thickened bone of the trabeculae is continued upwards and a little medially as a dorsal spine. This spine runs postero-dorsally to draw out the upper corner of the dorsal process into a backwards-facing ridged articulation for the cleithrum. On the external surface of the dorsal process an extensive antero-dorsally facing area in front of the spine is roughened according to Watson (1958) for the cleidomastoideus muscle.

*Cleithrum* (text-fig. 16). The cleithra show similar features to cleithra of *Benthosuchus sushkini* described by Bystrow and Efremov (1940).

In their natural orientation each cleithrum continues the postero-dorsal slope taken by the dorsal spine of the dorsal process on the clavicle. An area for attachment to the clavicle is shown by a system of coarse longitudinal ridges on the ventral half of the anterior face. Above the clavicular articulation the crista cleithralis (Bystrow and Efremov 1940) is represented by a pair of small hooked processes which expand the head of the cleithrum. Diametrically opposite this crista is a posteriorly directed flange, the lamina suprascapularis (Bystrow and Efremov 1940) which leads into a deep, vertically elongated recess in the head of the bone. The recess is continued ventrally as



TEXT-FIG. 15. Smaller right clavicle (reversed) ( $\times \frac{1}{4}$ ). A, antero-lateral view; B, postero-medial view; C, posterior view.



TEXT-FIG. 16. *Parotosaurus pronus* sp. nov. A, reconstruction of the smaller pectoral girdle, lateral view; B, unreconstructed scapulocoracoid, lateral view ( $\times \frac{1}{4}$ ).

a groove which is at first narrow but later broadens to fill the whole width of the median surface. This area undoubtedly clasped the cartilaginous anterior border of the scapulocoracoid.

*Scapulocoracoid* (text-fig. 16). If, as seems likely, this bone resembled the scapulocoracoid of *Parotosaurus peabodyi* (Welles and Cosgriff 1965) or *Wetlugasaurus* sp. (Riabinin 1930) then the thinner, lateral coracoid portion of the bone is missing.

The actual glenoid region is unossified but the articular facet was undoubtedly just postero-lateral to the expanded base of the scapulocoracoid. This expanded area, the supraglenoid buttress, is more extensive than it is in *Paracyclotosaurus*, and shows an antero-ventromesial process divided from the characteristically flattened rectangular buttress by a shallow recess.

The extent of the coracoid process is variable in related types. In *Paracyclotosaurus* it is narrow. In *Parotosaurus peabodyi*, on the other hand, the process is wide ventrally, but narrow dorsally. Close examination of the area of origin of the coracoid process in the present case reveals that only a small section of bone is actually broken, the rest of the roughened surfaces being finished in cartilage. Thus, the coracoid process was probably like the smaller one in *Wetlugasaurus* sp., and even more like the immature scapulocoracoid of *Benthosuchus* (Bystrow and Efremov 1940, fig. 76, D). It is not surprising that *P. pronus* scapulocoracoid probably resembled an immature form as the whole skeleton is poorly ossified when compared with earlier or more terrestrial labyrinthodonts.

As the ventral part of the coracoid plate is missing, the lateral view of the bone is almost a longitudinal section. Thus the supracoracoid foramen is seen in section as a deep recess arising posteriorly near the middle of the bone, and extending antero-ventrally across it. The canal would probably have been closed laterally by bone (as it is in *Wetlugasaurus* sp.) and was rounded, unlike the elongate foramen closed (presumably) by cartilage in *Benthosuchus*.

The narrow dorsal and anterior edges of the scapula blade apparently supported an extensive cartilaginous cap. Dorsally this occupied the position of a suprascapula, while laterally it formed a connection with the posterior face of the cleithrum.

The posterior margin is a true edge which curves forward from just below the dorsal cartilage cap to the median edge of the supraglenoid buttress.

Medially, the existing surface is vertically flat, but falls away slightly anteriorly as the subscapular fossa (Sawin 1945). Vento-medially, behind the supraglenoid buttress is a deep, rounded groove which was presumably finished by cartilage to form the glenoid foramen (Riabinin 1930).

*Reconstruction of the pectoral girdle* (text-fig. 16). In reconstructing the pectoral girdle of *P. pronus* the position of all dermal elements was easily established. It seemed best to restore the scapulocoracoid in a high position. This allows a characteristic overlap of the cleithrum dorsally, and sufficient room for the glenoid cavity to be placed so that the head of the humerus can be clear of the ground.

The girdle as a whole is extensively dorso-ventrally flattened with relatively enormous dermal elements and reduced primary girdle. The clavicles-interclavicle complex forms an immense, ventral plate beneath the pectoral region.

The poor state of ossification of the scapulocoracoid of *P. pronus* indicates a weakly



developed fore limb, a theory supported by the equally poorly ossified condition of the fore limb bones. Thus it seems that the massive dermal shoulder girdle had little to do with locomotion: consideration (below) of the thickened trabeculae on the clavicles and interclavicle indicates a function for it other than limb muscle support.

#### *Fore limb*

The fore limb bones consist of a left and a right humerus, radius, and ulna. Proximal and distal ends of all the limb bones were finished in cartilage.

*Humerus* (text-fig. 17). The humerus is of the reduced tetrahedral type described by Watson in *Paracyclotosaurus* (the humerus illustrated by Watson is a left one and has been incorrectly labelled right). Thus the strong muscular processes seen in *Eryops* (Miner 1925) or *Acheloma* (Romer 1922) have been reduced, and less of the distal and proximal ends of the bone are ossified. There are no ectepicondylar or entepicondylar foramina.

On the proximal-dorsal surface the deltoid crest is prominent as is the antero-distal supinator crest.

*Radius* (text-fig. 17). The radius has an almost straight shaft which is flattened ventrally (posteriorly) and has its ends expanded and cupped to house their terminal cartilages. The proximal end is rounded except ventrally, while the distal end is also flattened postero-dorsally so that it is almost triangular in cross-section. Low ridges lie laterally, anteriorly and medially on the shaft, and the last named forms a distal process directed towards the ulna. There are no easily identified muscle origins or insertions.

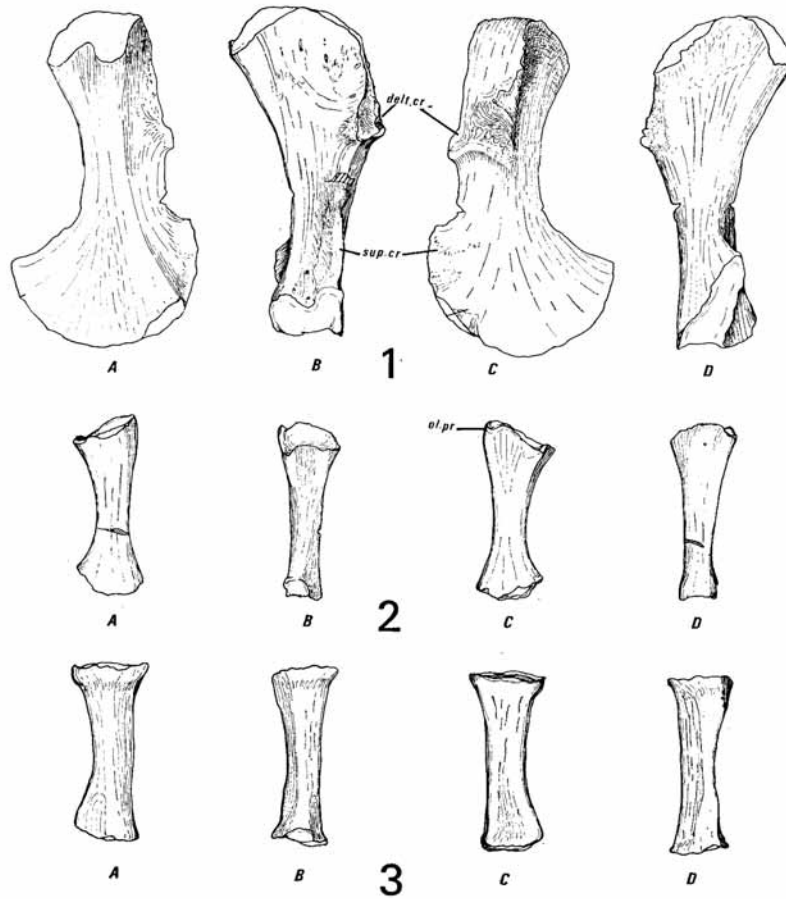
*Ulna* (text-fig. 17). The lateral edge of the ulna is almost vertical, but the medial border is concave, so that the proximal and distal ends of the bone are expanded towards the radius. In proximal view, the cap of the ulna is rhomboidal, and the postero-lateral corner of the rhombus is raised above the other corners as a short olecranon process. Opposite the process, on the median edge of the rhombus is a characteristic depression. The distal end is almost rectangular but narrows on the radial side and is sub-divided into median and lateral facets. The shaft of the ulna is squared proximally, becomes thin and rounded in the middle, and is expanded distally in an anterior-posterior plane. Proximally, the lateral, medial and flexor faces of the shaft are depressed and roughened for muscle attachment.

#### *Pelvic girdle*

The pelvic girdle is represented by a left and a right ilium and a left and a right ischium. As these are of comparable size it seems likely that they are from the same girdle. There is no evidence of pubes but these are rarely ossified in contemporary related forms.

*Ilium* (text-fig. 18). The two ilia resemble those of *Paracyclotosaurus* but the blade shows a greater posterior slope. Dorsally on the antero-medial surface of the ilium is a vertical series of ridges, presumably for ligamentous attachment.

*Ischium* (text-fig. 18). The ischia are unremarkable. They are almost identical, though a

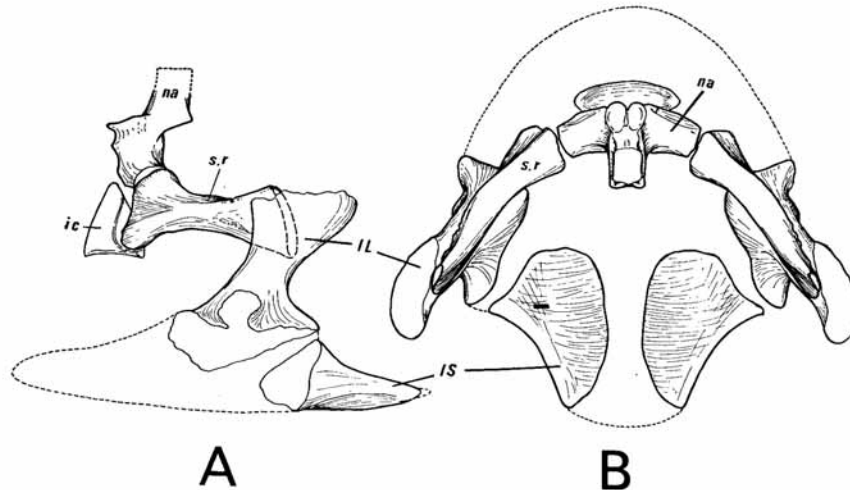


TEXT-FIG. 17. *Parotosaurus pronus* sp. nov. 1. Humerus. A, distal dorsal view; B, proximal ventral view; C, distal ventral view; D, proximal ventral view. 2, Ulna; 3, Radius. A, dorsal view; B, anterior view; C, ventral view; D, posterior view. All  $\times \frac{3}{8}$  approx.

little larger, to those of *Buettneria* (Sawin 1945). *Paracyclotosaurus* has similar ischia, but they are more antero-posteriorly elongate.

The reconstructed pelvic girdle is flattened dorso-ventrally, with the iliac blades well separated dorsally. The sacral rib slopes backwards along the same lines as its neighbouring ribs: its area of contact with the ilium is vertical and narrow, but was apparently extended by cartilage in the living animal. This positioning of the sacral rib so that its iliac contact lies well behind the level of the sacral vertebra seems a weak arrangement, but other species such as the salamander *Megalobatrachus* are similarly built.

An area in front of the ischia was presumably filled by cartilaginous pubes: Watson has found impressions of flat oval elements with ossification in this region in *Paracyclotosaurus*.



TEXT-FIG. 18. Reconstruction of the pelvic girdle ( $\times \frac{1}{3}$ ). A, lateral view; B, dorsal view.

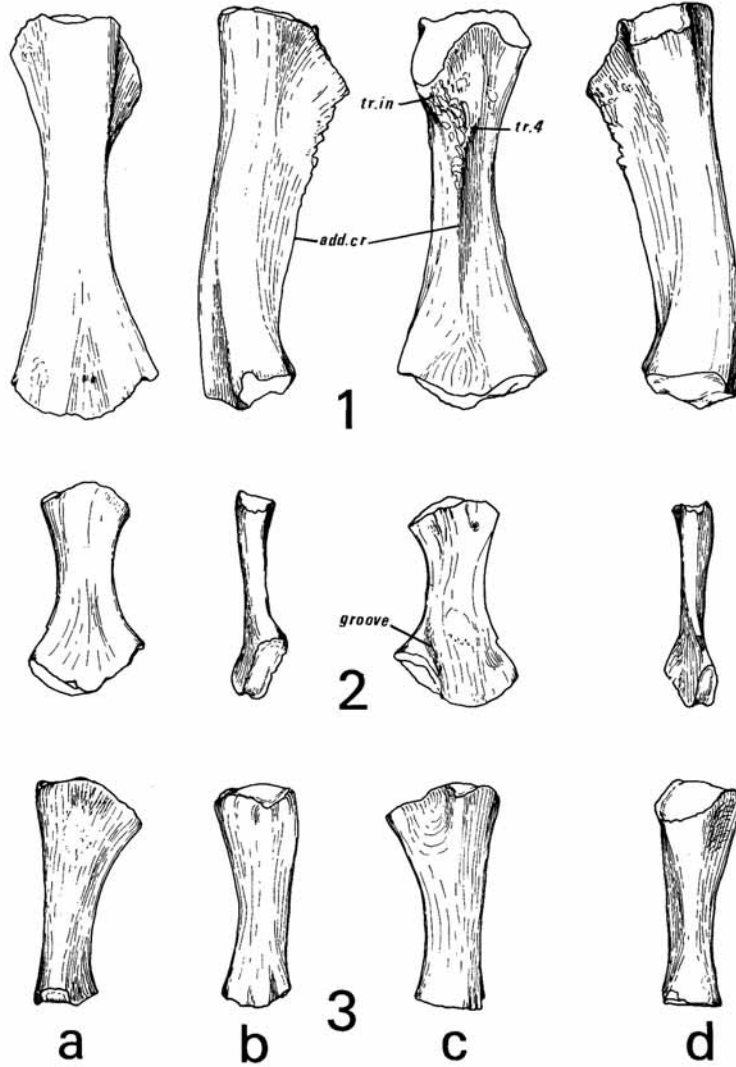
#### *Hind limb*

The collection contains one left and two right femora, a left and a right tibia, and a right fibula.

*Femur* (text-fig. 19). Except for its smaller size the femur resembles the *Paracyclotosaurus* femur described by Watson.

*Tibia* (text-fig. 19). Proximally, the tibia is greatly expanded anteriorly (dorsally), medially and laterally but posteriorly (ventrally) the surface is concave. This massive head tapers to form a shaft which is circular but for a broad dorsal ridge leading distally from the 'knee' region to the smaller distal end. One especially prominent muscle scar covers the proximal and anterior 'knee' region and is equivalent to the tuberositas tibiae of Bystrow and Efremov (1940): their ventral crista posterior is present proximally as a sharp, low ridge anterior to the posterior concavity mentioned above, but fails to extend further along the shaft.

*Fibula* (text-fig. 19). The fibula is remarkably like the ones described by Bystrow and Efremov (1940) in *Benthosuchus* and Case (1932) in *Buettneria*. The most characteristic feature of this and fibulae of related types is a reflection of the distal medio-ventral corner of the bone forming a groove (the sulca fibularis of Bystrow and Efremov) between it and the shaft. Muscle scars are concentrated about the extremities of the fibula, but posteriorly there is one large scar in the middle of the shaft.



TEXT-FIG. 19. *Parotosaurus pronus* sp. nov. 1, Femur; 2, Fibula; 3, Tibia. ( $\times \frac{1}{2}$ ). *a*, dorsal view; *b*, anterior view; *c*, ventral view; *d*, posterior view.

*Other limb bones*

Fourteen smaller limb bones were found. Twelve of these are of roughly the same shape but of varying sizes and are probably phalangeal bones, metacarpals, and metatarsals. These are elongated, a little dorso-ventrally (antero-posteriorly) flattened, and have their ends expanded. The two remaining bones are paired and could be carpals or tarsals. They are smaller and thicker than the above and have one end compressed at right angles to the other.

## DISCUSSION

*Dermal pectoral girdle*

Prominent on the interclavicle are the lateral trabeculae which lead from the centre of ossification of the bone to its lateral corners. It is evident that the trabeculae are thickest where they meet and underlie the postero-lateral edge of the clavicles. Here is the region of maximum contact between interclavicle and clavicles with maximum interlocking between their articular surfaces. The clavicles in their turn are thickest in this region. This is the lateral limit of the clavicular trabeculae which lead to the centre of ossification of the clavicle at the base of the dorsal process and are continued dorsally as the clavicular spine. This series of trabeculae is a system of struts well sited to counteract an upwards and forwards pull on the dorsal process of the clavicle. The cleidomastoideus muscle (if Watson's interpretation of the scar on the external antero-dorsal corner of the dorsal process of the clavicle is correct) is in a position to create just such a pull. In support of this theory is the fact that only the larger, flattened, aquatic labyrinthodonts with similar interclavicles to *P. promus* have well-developed trabeculae, and in all these types the dorsal process of the clavicle has an enlarged cleidomastoideus muscle scar (especially *Buettneria* (Sawin 1945, fig. 9a), *Benthosuchus* (Bystrow and Efremov 1940, figs. 44, 45), *Paracyclotosaurus* (Watson 1958, figs. 10, 11)). A possible reason for the enlarged cleidomastoideus muscle in these flattened forms will be discussed below.

It is evident that a strong framework in this area would also be necessary because the animal is large and flat. A flattened girdle means that the legs are far apart. In this position the fore limbs, working together, could, theoretically, raise the anterior part of the body off the ground, but only if the area between them was stiff. In fact if the girdle was stiff, it would take no more effort to lift the weight above it from two points near the girdle's edges, than from two points near its centre. To prevent the animal collapsing, a system of struts would be required similar to that needed to resist the pull of a strong cleidomastoideus muscle. But in this case the pull would act on the back of the dorsal process of the clavicle, via the scapulocoracoid and cleithrum.

The girdle undoubtedly also functioned to protect thoracic organs from pressures from the ground.

The flattened dermal pectoral girdle of capitosaur is thus of use in three ways: as a framework for a system of ridges backing up the cleidomastoideus muscle, as a strut for the pectoral region, and as a protection for the anterior viscera.

*Jaw opening*

When discussing the jaw musculature of *Paracyclotosaurus davidi* in 1958, Watson noted: 'The relative position of the occipital and quadrate condyles shows that if the

lower jaw rested on the ground, as must often have been the case, it would move forward as the mouth was opened by raising the skull.' In 1962 he postulates, in the same animal, a 'great muscle, the musculus depressor mandibulae', attached to the retro-articular process of the lower jaw and 'inserted onto the posterior edge of the dermal skull roof at the highest possible point, contraction of which will raise the skull *if the lower jaw rests on the ground*' (my emphasis). Panchen (1959) also uses the depressor mandibulae to raise the skull in brachyopids and plagiosaurs. But he suggests that occipital muscles combined with the depressor to lift the skull. However, there is an alternate system of muscles which could be used in jaw opening to overcome some of the difficulties inherent in the above schemes.

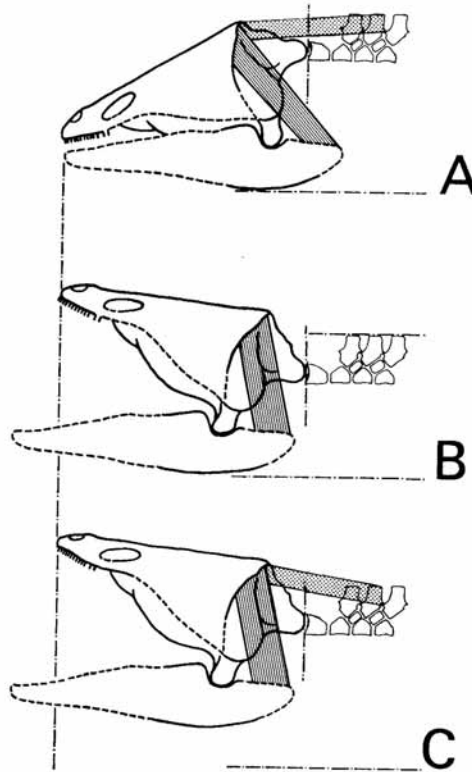
Watson's scheme employs both the occipital condyles and the quadrate condyles in a movement governed by a single muscle. This could function only if the two sets of condyles were in the same transverse line, otherwise, if it is assumed that the atlas does not move posteriorly when the skull is raised against the atlas using the articular as fulcrum then:

- (a) If the occipital condyles were in the same transverse plane as, but above the quadrate condyles, the vertebral column would be depressed as the skull was raised,
- (b) If the occipital condyles were in the same horizontal plane as, but in front of the quadrate condyles, the column would be elevated as the skull was raised, or
- (c) If the occipital condyles were in the same horizontal plane as, but behind the quadrate condyles, the vertebral column would again be depressed as the skull was raised.

Watson realized this and employed point (b) when he showed that *Eryops* could not raise its skull (1951). But he disregarded it when he noted (1951) that in capitosaur the lower jaw would move forward as the skull was raised. True, capitosaur are approaching the ideal situation for Watson's scheme, and some of them (especially *Parotosaurus orenbergensis*, Konzhukova 1965), seem to have reached it.

Brachyopids, however, are far from it. In them, the occipital condyles are well behind and above the quadrate condyles, and it can be seen (text-fig. 20) that using the depressor mandibulae muscle to raise the skull (as shown by Panchen) must force the occipital condyle ventrally, and with it the whole vertebral column. In brachyopids this depression is considerable (more than one-quarter of the body depth) and implies that either the pectoral girdle was very loosely connected to the vertebral column, or that the pectoral area was held clear of the ground, a most unlikely position if the mandible must be grounded.

Brachyopids, having their occipital condyles behind and above the quadrate condyles, better illustrate a second difficulty: than an animal whose lower jaw shoots forward as it must in a brachyopid when it raises its skull, is unlikely to be relying on that jaw for leverage against the ground. Panchen likens the brachyopid jaw movement to that of an active, predatory fish, implying a rapid action. But for the skull to be raised by a depressor muscle, the lower jaw must be on the ground; if it was not, contraction of the depressor would lower the jaw, not raise the skull. No other system supports the lower jaw except the adductor muscles, and these are antagonistic to the depressor: if they were relaxed, and the jaw was not on the ground, again the depressor would lower the

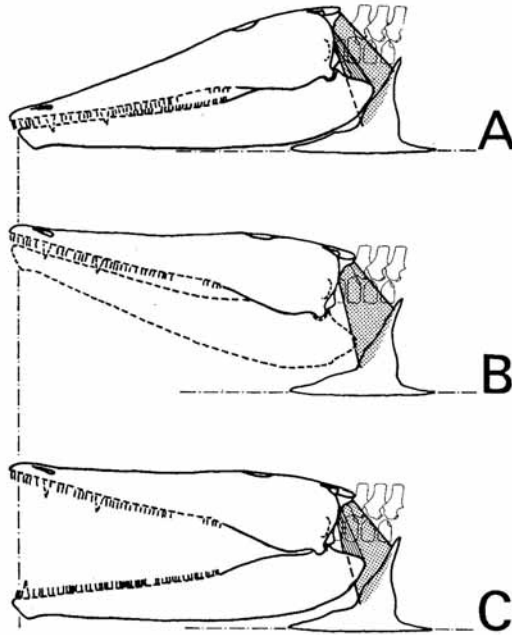


TEXT-FIG. 20. A brachyopid skull (*Batrachosuchus*) in profile. A, Skull with jaws closed. B, Skull to show the method of opening the jaws by raising the skull by contraction of the depressor mandibulae muscle as depicted by Panchen (1959). Note depression of the vertebral column. C, Skull to show method of opening the jaws by 1, contraction of the muscles between the occiput and the vertebrae to raise the skull, and 2, contraction of the depressor mandibulae muscle to lower the lower jaw. Note that the vertebral column has not been depressed and that the lower jaw is clear of the ground. Skull outline from Watson's figure of *Batrachosuchus* (1956, text, fig. 5). Lower jaw from Panchen's (1959) reconstruction. Occipito-vertebral muscles stippled. Depressor mandibulae muscle hatched. *Batrachosuchus*'s vertebrae are restored following discussion with Dr. S. P. Welles who has a collection of inter-centra which show that the brachyopids had rhachitomous vertebrae.

jaw. (Of course, when the animal was swimming it could feed by lowering the jaw, but the rapid forward movement of the jaw characteristic of predatory fish could only occur if the skull was raised.)

Finally, it is illuminating to consider the nature and attachments of the depressor mandibulae muscle itself. Watson says that the muscle should be inserted on the highest possible point of the skull roof. In capitosaur this is the tabular. From the side, a

muscle inserted here looks feasible (Watson 1951, fig. 27). From behind, however, the angle at which the muscle would have to function is poor: the depressor would have almost as high a horizontal component as a vertical one. The situation in this case is worsened by the nature of the quadrate condyles which are slightly screw-shaped, the thread of the screw running from postero-lateral to antero-medial. A lower jaw rotating about this condyle must necessarily move laterally so that the two rami separate slightly



TEXT-FIG. 21. *Parotosaurus pronus* skull in profile. A, skull with jaws closed. B, C, the method of opening the jaws divided into two stages. B, contraction of the cleidomastoideus muscle to raise the skull (depressor muscles omitted); C, contraction of the depressor mandibulae muscle to lower the lower jaw. Cleidomastoideus muscle stippled. Depressor mandibulae muscle hatched.

at their median symphysis. This action would oppose the inward pull from the depressor which would then be working at a double disadvantage. (However, it should be noted that in brachyopids a depressor would have a better working angle as the cheek is deeper, and the muscle could act from directly above the lower jaw.)

The proposed solution to these problems has two aspects (text-fig. 21B, C). First, the skull is raised by specially developed occipital muscles using the occipital condyles as the fulcrum, and, second, the lower jaw is lowered by contraction of the depressor mandibulae muscle. In practice, the two muscles would work simultaneously (text-fig. 21C). The most obvious advantage of this system is that raising the skull against the occipital condyles will elevate the quadrate condyles as well (that is, the opposite effect



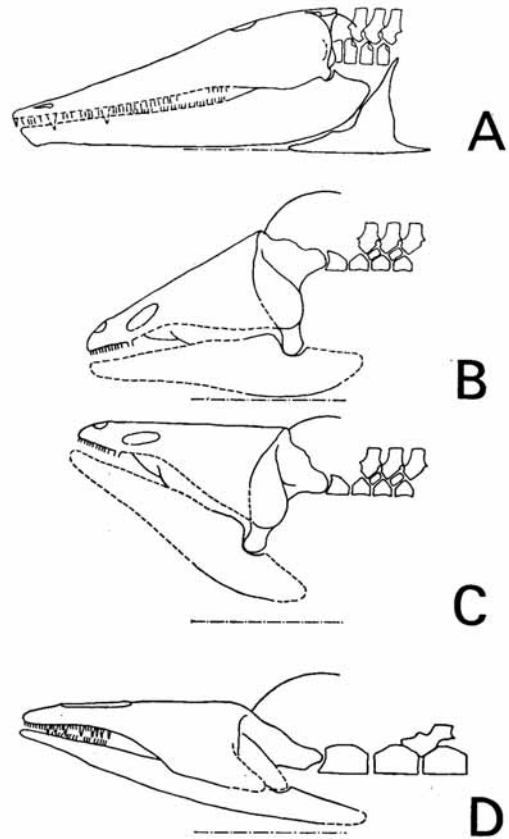
to the depression of the vertebral column resulting from Panchen's scheme) and so the lower jaw will be freed from the ground. Subsequent contraction of the depressor does not need ground support as it is a lowering not a raising action. Under these conditions the brachyopid jaw will shoot forward without interference from the ground.

There is evidence for a suitable occipital muscle in capitosaur. Consideration of the dermal girdle in *Parotosaurus pronus* (above) has indicated a well-developed system of ridges which were interpreted as a support for an upwards and forwards pull by the cleidomastoideus muscle. If the girdle is placed behind the skull it can be seen that the area of attachment for the cleidomastoideus muscle on the dorsal process of the clavicle is in the same plane (but behind and below) a pronounced ventro-lateral flange of the tabular (text-figs. 3, 5). This flange runs from the tabular horn postero-ventro-medially along the paroccipital process, ending just dorsal to the suture between the tabular and the exoccipital. It is proposed that in capitosaur this flange was the insertion of the cleidomastoideus muscle which contracted to raise the skull. In this position, the cleidomastoideus muscle would be working at an angle very similar to the depressor muscle as visualized by Watson, but the lateral component would be reduced. However, unlike the depressor, the cleidomastoideus muscle will not have to counteract the lateral movement of the lower jaw. Miner (1925) restored part of the cleidomastoideus in *Eryops*, attaching it to the squamosal and posterior part of the skull generally, with its other end on the cleithrum, clavicle, and scapula, but he did not attempt a functional explanation for it. It is interesting to note that Watson (1926) postulated, in embolomeres, a bony articulation between the tabular horn and the shoulder girdle via a post-temporal element but Romer later (1947) considered that this was more likely to be a ligamentous connection.

Use of this muscle in a skull-raising capacity may help to explain the (evolutionary) lateral movement of the tabular horns (which eventually closed the otic notch in cyclotosaurs), and the accompanying inward movement of the dorsal process of the clavicle in these flattened forms, so that the origin and insertion of the cleidomastoideus came to lie more in a longitudinal-vertical plane.

Occipito-vertebral muscles could have assisted the cleidomastoideus, but they are unlikely to have formed the main skull-raising system in a capitosaur. A capitosaur has a vertical occiput, so that the point of attachment of the occipital muscles is in the same transverse plane as the occipital condyles. Consideration of text-fig. 22 shows that a muscle attached between the occiput and the vertebral column could raise the skull a certain amount, but it would only be really effective at the very beginning of its contraction, and it is doubtful whether this would be sufficient to account for the whole range of opening. The clavicle, however, is positioned better in relation to the occiput, and, if a muscle attached to it was used to raise the skull, the muscle would be at its most effective position when the occiput had travelled backwards through approximately 25°, resulting in a narrow gape which will be shown below to be that most used by a capitosaur. It thus seems highly probable that the cleidomastoideus formed the main skull-raising muscle in a capitosaur, with the occipito-vertebral muscles perhaps assisting at the start of the movement.

The situation is different in the brachyopids. Here the occiput slopes forward (text-fig. 22) giving an occipito-vertebral muscle a greater effective range. It is probable, therefore, that the brachyopid skull was at least partly raised by occipito-vertebral



TEXT-FIG. 22. Diagrams of lateral views of the skull and anterior vertebrae of various labyrinthodonts to show the relationship of the occiput to the vertebral column and pectoral girdle. The arcs which would be described by the point of attachment of the occipital muscles on the skull when the latter is raised, are indicated. No attempt is made to indicate the extent of the gape in the brachyopid or plagiosaur but the capitosaur skull would probably not have opened further than the arc suggests. Note that in A the dorsal process of the clavicle is in a better position than the vertebrae for the attachment of a skull-raising muscle; in B the vertebral column is in a better position than a (presumably) more ventral clavicle, but that in C where the skull is held with its dorsal surface parallel to the vertebrae the position is better still; in D the plagiosaur skull is held in a similar position. A, *Parotosaurus pronus*; B, C, *Batrachosuchus* as in text-fig. 20; D, *Gerrothorax* after Panchen (1959) —vertebrae reconstructed from Nilsson's (1937) figures of *Gerrothorax rhaeticus*.

muscles (as suggested by Panchen): these would certainly have a better initial moment than a more ventral muscle from the pectoral girdle. Whether a pectoral or a vertebral muscle was used cannot be determined until the vertebrae and pectoral girdle of brachyopids are better known. It is evident that if a muscle from the clavicle was used in an animal with a forward-sloping occiput, then the dorsal process of the clavicle would have to be tall, at least as high as the vertebrae. Reconstruction of the clavicle of *Eobrachyops*, an early brachyopid, from Watson's (1956) figure and description, shows that in that animal at least, the dorsal process was too short. Watson's (1956) observation that in the brachyopid *Platyceps wilkinsoni* 'the first three vertebrae seem to be somewhat more massively ossified than those farther back, but curiously there seem to be no ossifications in the exoccipital condyles' may lend support to the case for a vertebral muscle.

The pectoral girdle is known in metoposaurs where the occiput is intermediate between capitosaur and brachyopids, the occipital condyles projecting a little behind the quadrate condyles, but being almost on a horizontal level with them. Here the area for the cleidomastoideus muscles' attachment to the clavicle is exceptionally well developed (Sawin 1945, figs. 8e, 9a) and the muscle could apparently have been used to raise the skull.

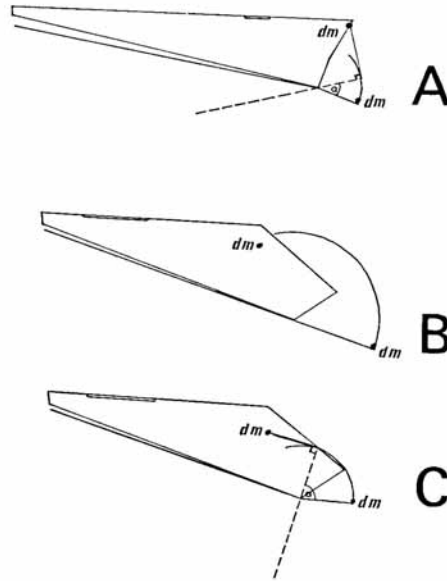
One point which becomes obvious when studying text-fig. 22 is that in order to increase the mechanical advantage of the occipital muscles in the brachyopid and plagiosaur skulls it would be necessary to increase the height of the neural arches. But neural spines of these labyrinthodonts, where preserved, are low. However, the same result would be achieved if, instead of the dorsal surface of the skull facing anteriorly, it was horizontal, so that the vertebral column was parallel to the skull (text-fig. 22b). This position is not unknown in aquatic animals: fish such as the herring have the skull facing dorsally and the lower jaw facing antero-ventrally. This position of the skull seems a more satisfactory arrangement for labyrinthodonts such as brachyopids and plagiosaurs, with anteriorly sloping occiputs, but it would hold little advantage for a capitosaur.

#### *Retro-articular process*

It is apparent in these labyrinthodonts that, for the depressor mandibulae muscle to be effective, the greater the slope of the occiput, the longer must be the retro-articular process. A better solution would be to have a shorter process which turned upward (text-fig. 23) (as it does in capitosaurs). This would have the same effect as a long retroarticular process except that the length of the muscle would be a little less.

Text-fig. 23 illustrates the position of the mandible in capitosaurs and plagiosaurs at which the depressor mandibulae would be most effective. This indicates a narrow gape in capitosaurs and a wide one in plagiosaurs (brachyopids being intermediate). If the retro-articular process was turned dorsally (text-fig. 23c) in plagiosaurs it would be possible for the depressor muscle to reach a point of maximum efficiency, but with a straight process (text-fig. 23b) the point would not be reached. In the only brachyopid jaw preserved with the retro-articular process intact, *Bothriceps australis* (Watson 1956), the tip is turned up. In *Batrachosuchus watsoni* (Watson 1956), the retro-articular process appears to turn up, but its tip is missing. Although the retro-articular process is often said to be long in advanced Triassic labyrinthodonts no jaw has been described

where the process is complete and is longer than it is in *Bothriceps*. Panchen (1959) has reconstructed a straight retro-articular process on the lower jaw of *Gerrothorax* from Huene's (1922) figures and description of the lower jaw of *Plagiosuchus* and *Plagiosternum* but the posterior half of the process is missing in both these forms, and it is possible that they did, in fact, turn dorsally.



TEXT-FIG. 23. Diagrammatic representations of the skulls and lower jaws of a capitosaur and a plagiosaur to show the difference in their gapes with different retro-articular processes.  $a$  is the angle through which the lower jaw will move before the depressor mandibulae muscle meets the lower jaw at a right angle. According to Parrington (1955) this is the position where the depressor muscle achieves the greatest leverage on the lower jaw.  $dm$  are the points of origin and insertion of the depressor muscle. Note that in A, a capitosaur, the gape is narrow when angle  $a$  is reached. In B, a plagiosaur, the angle is never reached. In C, a plagiosaur, the retro-articular process has been turned dorsally: now the position of greatest leverage can theoretically be attained.

It was shown above that in capitosaurids the depressor mandibulae muscle would appear to be most efficient when the gape was small. Additional factors actually prevent the jaws opening far. It seems that in most capitosaurids the ventro-postero-lateral corners of the quadratojugals are not preserved, presumably because they were cartilaginous. But in one or two cases (e.g. *Cyclotosaurus posthumus*, Fraas 1913) ossification persists and it appears that the quadratojugals projected below the level of the quadrate condyle. Now, the capitosaur condylar system is screw-shaped which necessitates an outward movement of the articular along the quadrate as the jaws open. The ventro-postero-lateral projection of the quadratojugals would prevent this movement beyond

a certain point. Also limiting the gape is the post-condylar process of the surangular. There are indications that this was tall, and if so, it would have prevented too great a movement of the quadrate relative to the lower jaw.

The lateral screwing of the jaws, while not great, must increase with the gape and this movement would have been against the action of the depressor muscles which tend to pull the retro-articular process inwards as well as upwards. While the disadvantage of this action has largely been removed by using the depressor to lower the jaw rather than raise the skull, it would undoubtedly become a limiting factor were the jaws to try to open wide.

It seems, therefore, that the capitosaur cranial anatomy is adapted for keeping the gape of the jaws fairly small, rather than for allowing them to open far.

The position of the eyes may have some bearing on this question. As the eyes are placed far back and close together on the capitosaur skull, it is manifest that were the jaw to open widely (by raising the skull), the animal would be unable to see. True, the eyeball could probably be protruded as it is in modern frogs, but it is doubtful if this protrusion would be enough to enable a capitosaur to see if its skull was raised far. It seems significant that in many labyrinthodonts which are thought to have a wider gape such as brachyopids and plagiosaurs, the eyes are larger and further forward on the skull and would probably have been able to project sufficiently. Metoposaurs seem intermediate: they undoubtedly had a wider gape than capitosaurs, and their eyes were well forward.

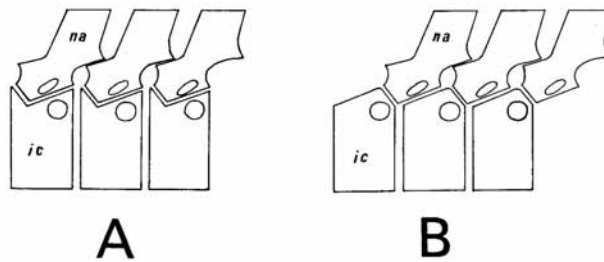
#### *Dorsal pterygoid canal*

The floor of this canal can be seen in specimen 48 I (text-fig. 5A) and more of the canal is shown in specimen 135 (text-fig. 6A). It runs from behind to enter the skull at an abrupt face beside the stapes and above the conical recess and it is probable that the canal carried the VIIth nerve with its accompanying blood vessels. If this dorsal foramen and canal did carry nerve VII then the path of the nerve may have continued behind the ascending oblique ridge of the pterygoid which begins near the posterior section of the canal. This ridge rises obliquely and then turns laterally along the quadrate ramus of the pterygoid to end at the quadrate. On the left of specimen 135 the distal lip of the ridge almost meets the pterygoid to form a canal. On the right of the same skull, a groove above the quadrate leads down and laterally to end near the paraquadrate foramen in the quadratojugal, and this foramen has been postulated by Bystrow and Efremov (1940) as the point where the hyomandibular branch of nerve VII re-enters the skull. If this system of canals did house VII it would adequately protect that nerve from the depressor muscles. Watson (1962) describes in *Rhineceps* and *Wetlugasaurus* a stapedia groove which corresponds in position to the oblique ridge on the pterygoid and suggests that this groove housed the stapes. This may have been the case in other forms but in *P. pronus* the groove is much too small and extends too far laterally. Watson notes this lateral elongation and suggests that the outer section of the groove was to carry the ligamentous attachment of the stapes to the quadrate. But if this was its sole purpose, the groove should have run towards the quadrate 'boss', shown by Westoll (1943) to be the probable point of attachment of the quadrate ligament from the stapes. This is not the case, as study of the same specimen of *Rhineceps* shows a distinct shallow groove which originates at the lateral limit of the oblique ridge and by-passes

the quadrate boss, passing above it in just the position predicted for a nerve stretching from the end of the oblique ridge of the paraquadrate foramen. There seems no reason why in species where the oblique ridge obviously was large enough and in a position to carry the stapes it should not have also carried the VIIIth nerve.

*The stereospondylous vertebra*

It is generally agreed that the stereospondylous centrum is an intercentrum (that is, it corresponds to the intercentrum of amniotes), and that it lies beneath, but a little in front of, the neural arch. Nilsson (1937, fig. 16) places the neural arch of *Mastodonsaurus* in this position and Watson (1958) does the same with *Paracyclotosaurus*.



TEXT-FIG. 24. Diagrams of stereospondylous vertebrae showing the two possible arrangements of the neural arch on the intercentrum. A, conventional position, B, correct position. Note 1. The necessity to notch the intercentrum dorsally in A. 2. The relationships of the diapophysis to the parapophysis in A which would make it impossible to fit the type of rib found in stereospondylous labyrinthodonts to the vertebra.

However, Chowdhury (1965, fig. 7) notes the presence of both anterior and posterior facets in stereospondylous intercentra which he assumes belong to *Metoposaurus*, but he also suggests articulating the centrum with only the ventral (posterior) facet of the neural arch. This position agrees with conclusions reached (above) about the arrangement in *Parotosaurus pronus*. However, in this position the intercentrum is articulating with the smaller, anterior, neural arch facet, while the larger more posterior, ventral facet is not accounted for.

Watson, in 1958, notes that this ventral neural arch facet is for the pleurocentrum, a statement undoubtedly true for rhachitomes and neorhachitomes, including *P. pronus*. But in view of the fact that Chowdhury shows two articular facets on a stereospondylous intercentrum (even labelling them anterior neural arch facet and posterior neural arch facet), it seems likely that the neural arch of stereospondyls is morphologically intervertebral, so that the anterior facet of the intercentrum actually articulated with the large posterior facet of the neural arch anterior to it (text-fig. 24).

*The vertebral column*

Parrington (1967) has noted the disproportionate size of the head in typical labyrinthodonts and the fact that this must have resulted in a forward displacement of the centre of gravity with resulting problems when the mode of walking is considered. And

he has suggested that a rhachitinous vertebral column served the purpose of allowing considerable twist to the short presacral vertebral column enabling the animal to raise the front end of the body on the appropriate side at each step of a fore limb, and so reposition the centre of gravity of the body above the triangle of support offered by the three legs remaining on the ground. He notes, however, that the principle may not have applied to the larger Triassic forms which may have lived largely in water and never have walked with the body clear of the ground. In addition, Watson (1958) has suggested that *Paracyclotosaurus* may have been of almost neutral buoyancy and that it moved in water by touching the ground with its digits (much as does the 'walking' lungfish). It seems therefore that in capitosaur and stereospondyls the rhachitinous type of vertebra is no longer essential for locomotion (in Parrington's sense).

It was once thought that all capitosaur were truly stereospondylous, but work by Bystrow and Efremov and others recognized in them the neorhachitinous condition of well-developed intercentrum with reduced bony or cartilaginous pleurocentrum. Watson (1958) has dotted pleurocentra in *Paracyclotosaurus* but none have been found ossified in capitosaur other than in *P. pronus*. These are obviously mere remnants of the true rhachitinous pleurocentra, and it seems clear that the vertebrae are becoming stereospondylous. If it is accepted that the rhachitinous condition has become unnecessary for locomotion it becomes important to try to explain the advantage of the stereospondylous condition.

Among labyrinthodonts two types of vertebrae are particularly associated with aquatic life: embolomerous and stereospondylous. Parrington (1967) has suggested that the embolomerous condition allows an eel-like form of locomotion in long-bodied types, the greater number of central units allowing a greater flexibility in a lateral plane. As far as they are known the stereospondyls were comparatively short-bodied and therefore could not have swum by lateral undulations, and so some other method must have sufficed. Probably the capitosaur and other typical stereospondyls swam by flexion of the tail which propelled the animal forward while the body remained largely stiff, much as do tadpoles. Although Watson restored *Paracyclotosaurus* with a fairly short tail of about twenty-five vertebrae, there is evidence that some neorhachitomes at least may have had a longer tail. According to van Hoepen (1915) the neorhachitome *Uranocentron senekalensis* had 'at least thirty-six caudal vertebrae and may have had forty-six'. Huene (1922) figured the intercentra of *Mastodonsaurus giganteus*, only showing a representative number of caudal vertebrae but noting that in all probability the tail was very long.

Often in capitosaur the anterior vertebrae are almost stereospondylous, but the development of the intercentra decreases towards the tail, the posterior presacral and caudal vertebrae remaining in the rhachitinous condition. This is shown in Huene's figure of *M. giganteus* (1922, fig. 2) and is also present in *Paracyclotosaurus*, and, to a much lesser extent in *Parotosaurus pronus*. In short, it seems that, during the Trias, in capitosaur-like labyrinthodonts there is a gradual tendency towards stereospondylous in the presacral vertebrae, while the tail tends to remain rhachitinous. Force produced by a tail used as a propulsive organ must be transmitted through the vertebral column, and a reasonably rigid strut will best serve to transmit this force. The tail, however, would be more flexible if it remained rhachitinous. Flexibility is no doubt increased by a large core of cartilage in the tail and Van Hoepen's photograph of *Uranocentron*

tail vertebrae, preserved in what appears to be their natural position, shows neural arches and haemal arches well separated, presumably by cartilage.

It seems, then, that the neorhachitinous tail could have been a flexible structure with isolated dorsal and ventral ossifications, perhaps providing a framework for the attachment of a tail fin; while the neorhachitinous presacral vertebral column was a fairly rigid strut which transmitted the propulsive force produced by the tail to the body.

#### *Taxonomic position*

As is well known, the type specimen of *Capitosaurus*, *C. arenaceus*, is indeterminate as its otic region is not preserved and, as an Upper Triassic form, it is probably a cyclotosaur. Jaekel (1922) recognized this and coined the term *Parotosaurus* to refer to capitosaur. Romer (1947) concurs, suggesting that *Capitosaurus* be confined to the type, while *Parotosaurus* should refer to the Early Triassic '*Capitosaurus*' with open otic notch, and *Cyclotosaurus* to the Upper Triassic closed otic notch type. Welles and Cosgriff, in their much-needed (1965) revision of the family Capitosauridae, decided to follow this scheme, but dropped *Capitosaurus* altogether, the type becoming *Parotosaurus arenaceus*. Further, they lump the twenty-nine genera of Triassic 'capitosaur' into four, of which three, *Cyclotosaurus*, *Parotosaurus*, and *Paracyclotosaurus*, are Capitosauridae.

It is manifest that the present specimens are parotosaurs, but they cannot be fitted into any of the eight parotosaur species retained by Welles and Cosgriff, nor to *P. orenbergensis* (Konzhukova 1965). They are thus deemed to belong to a new species, *Parotosaurus pronus*. The species is defined by both cranial and post-cranial material, although Welles and Cosgriff use only cranial characters (post-cranial material is not available for most parotosaur species). It is felt that the separation of a species on characters of the skull roof only, as has been done in the past, is a needless generalization when description of post-cranial bones will often clarify a species.

*Parotosaurus pronus* is distinguished from other parotosaurs chiefly by the shape and position of its tabular horn. In four of the ten species of *Parotosaurus* the tabulars have grown laterally towards the squamosal, like they have in *P. pronus*. Of these, *P. semiclausus* (Swinton 1927) is obviously different: the tabular is unexpanded distally, and only just fails to meet the squamosal; the choanae and orbits are more rounded, the former parallel the midline, while the latter parallel the skull margins; the pineal foramen is rounder; the jugal is excluded from the orbital margin; and the sculpture is large and coarse. Some of these characters could apply to a young individual of *P. pronus*, but in that case the otic notch could be expected to be less, not more, closed in the younger specimen.

Although the tabular horn of *P. birdi* (Brown 1933) and *P. peabodyi* have moved laterally, they still have no distal expansion. In addition, *P. peabodyi* has a much shallower occiput. Its vertebrae differ from those of *P. pronus*, both intercentrum and neural arch being extensively antero-posteriorly compressed in the former. The occiput of *P. birdi* is much nearer to *P. pronus*. However, *P. birdi* has a greater exposure of exoccipital on the palate; the orbits are far apart and slope towards the otic notch; the cultriform process is sharply keeled; and the occipital area extends farther posteriorly, behind the level of the quadrates.

The last of the four is *P. brookvalensis* (Watson 1958). This is the only other



partosaur where the tabular is expanded distally as it is in *P. pronus*, but Watson's reconstruction shows this as a bulbous swelling of the horn, increasing its surface area rather than causing it to approach the squamosal. *P. brookvalensis* could be thought a juvenile *P. pronus* but for the character of its ornament and the length of its snout, which are both adult in proportion.

In 1958, Watson divided the Capitosauridae into shallow-skulled and deep-skulled lines. The latter contained *Paracyclotosaurus davidi* and '*Paracyclotosaurus*' *hemprichi*, and he suggested that *Parotosaurus pronus* could well be their ancestor. Welles and Cosgriff dissolved this grouping, returning '*Paracyclotosaurus*' *hemprichi* to *Cyclotosaurus*. Indeed, there seems little to link the former species apart from their depth of skull, and *Parotosaurus birdi* and *P. angustifrons* seem just as deep.

It is possible that *P. pronus* is ancestral to *Paracyclotosaurus davidi*. Curiously, *Paracyclotosaurus davidi* is the only form where the otic notch is closed by unornamented bone, this area being delimited from the tabular and squamosal by well defined ridges which follow the lines of these bones. It seems possible that the notch is open, the gap being filled by matrix. Certainly, it is unlike the semiclosed *Parotosaurus semiclausus* where tabular and squamosal closely approach one another with their opposing edges parallel. No closed otic notch type has a similar concavity in the posterior skull margin behind the notch, and, if the link between tabular and squamosal be removed, *Paracyclotosaurus davidi* looks remarkably like a parotosaur. In dorsal view, its skull bone arrangement is similar to *Parotosaurus pronus*, but the tabular differs in being expanded proximally as well as distally. Such a character could, however, be advanced, and would not preclude a relationship between the two. Other advanced characters of *Paracyclotosaurus davidi* which could have come from *Parotosaurus pronus* are: a greater exposure of exoccipital on the palate, and a reduction in ossification of the brain-case region, the latter being especially noticeable in the absence of a processus lamellosus to support the supra-occipital. It is harder to envisage the evolution of the *Paracyclotosaurus davidi* rounded nostril from the oval in *Parotosaurus pronus*, or the unusually broad cultriform process from *P. pronus* narrow, almost keeled one. One curious feature of Watson's reconstruction of *Paracyclotosaurus davidi* is the absence of an anterior palatal vacuity, and a (possibly related) absence of tusks in the mandible. This would set *P. davidi* apart from all other capitosaurids, but inspection of casts of the areas shows that they were missing in the original. Unless Watson has other evidence for their absence, it seems more likely that they were present.

The post-cranial skeleton is better ossified in *P. davidi* than *Parotosaurus pronus*, and most differences in shape can be attributed to this. Intercentra have advanced towards the stereospondylous condition. Rib structure, however, distinguishes the two as *P. pronus* ribs all carry some development of uncinatous process, usually accompanied by a distal expansion, while *Paracyclotosaurus davidi* ribs have no process or expansion beyond the seventh or eighth thoracic rib.

These comparisons lead to the conclusion that *Parotosaurus pronus* and *Paracyclotosaurus davidi* are remarkably similar, but, while *Parotosaurus pronus* may be more closely related to *Paracyclotosaurus davidi* than to other parotosaurids, there are some features which preclude the former being directly ancestral.

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## LIST OF ABBREVIATIONS USED IN THE FIGURES

Nerve	Roman numerals	avn	antero-ventral bone nubbin
foramina		ba. pr	basal process
A	angular	bo. crest	basi-occipital crest
add. cr	adductor crest	bo. hollow	hollow in exoccipital for the basi-occipital cartilage
a. pal. vac	anterior palatal vacuity	bone	area of finished bone on the pleurocentrum
a. pr	anterior process	boss	quadrate boss
area	area of pterygoid which articulates with the pre-articular process	pt. pr	conical recess for the basipterygoid process of the basisphenoid
ART	articular		
as. pr	ascending process		

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C	coronoid	pal. f	foramen for the palatine branch of the internal carotid artery
cap	capitulum	para	parapophysis
centre	centre of ossification	par. pr	paroccipital process
ch. t. f.	chorda tympanic foramen	pc	pleurocentrum
CL	clavicle	PF	post-frontal
CLEI	cleithrum	pin. f	pineal foramen
clei. art	area for articulation with the cleithrum	PMX	premaxilla
clm. m	area of attachment of the cleido-mastoideus muscle	PO	post-orbital
CO	coracoid	POSPL	post-splenial
cr. pa	paroccipital crest	PP	post-parietal
cr. pt	parapterygoid crest	ppq. gr	groove on the pterygoid for the palato-ptyergo-quadrate cartilage
D	dentary	p. pr	posterior process
d. f	dorsal foramen	pq. f	paraquadrate foramen
d. ca	dorsal canal	pr. cult	cultriform process of the parasphenoid
delt. cr	deltoid crest	PRF	prefrontal
dia	diapophysis	prz	prezygapophysis
dist. art	distal articulation	PSP	parasphenoid
dist. exp	distal expansion	PT	pterygoid
d. pr	dorsal process	psp. sut	area for suture with the parasphenoid
d. pr. prart	dorsal process of the pre-articular	pz	post-zygapophysis
ECT	ectopterygoid	Q	quadrate
F	frontal	QJ	quadratojugal
fen. ov	fenestra ovalis	rart. pr	retro-articular process
hollow	hollow in tabular or exoccipital for the opisthotic	SA	surangular
ic. f	foramen for the internal carotid artery	SC	scapula
ICL	interclavicle	sgl. b	supraglenoid buttress
IL	ilium	sgl. f	supraglenoid foramen
IS	ischium	SMX	septomaxilla
ipmx. f	interpremaxillary foramen	SPET	sphenethmoid complex
ipt. v	interpterygoid vacuity	SPL	splenial
J	jugal	SQ	squamosal
j. f	jugular foramen	ST	supratemporal
L	lachrymal	STA	stapes
l. pr	lateral process	ste. v	subtemporal vacuity
lam. pr	lamellar process	sup. cr	supinator crest
MX	maxilla	T	tabular
N	nasal	tr. in	internal trochanter
n. a.	neural arch	tr. 4	fourth trochanter
ne	external nostril	tub	tuberculum
ni	internal nostril	V	vomer
obl. r	oblique ridge	v. c. d.	groove for vena capitis dorsalis
ol. pr	olecranon process	v. pr	ventral process
OT	pro-otic ossification	unc. pr	uncinate process
P	parietal		
PAL	palatine		

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