

# A NEW CAPITOSAURID AMPHIBIAN FROM THE EARLY TRIASSIC OF QUEENSLAND, AND THE ONTOGENY OF THE CAPITOSAUR SKULL

by A. A. WARREN and M. N. HUTCHINSON

**ABSTRACT.** Capitosaurid temnospondyls are the most widespread and among the most abundant of the Triassic amphibians, but their phylogenetic relationships are not well understood. The superfamily Capitosauroidae (Capitosauridae, Benthosuchidae, and Mastodonsauridae) appears to be well characterized by several synapomorphies, but taxa within the superfamily are often less firmly established. A new capitosaurid species, *Parotosuchus aliciae*, is described from the earliest Triassic (Scythian A1) of Queensland. The hypodigm of the new species consists of immature animals, including three identified as barely metamorphosed, which provide the first information on the earliest post-larval growth stages of capitosaurids. Many character states present only in juvenile capitosaurids are known to be retained in the adults of several Triassic temnospondyl families, providing strong evidence that paedomorphosis was a dominant mode of evolutionary change in these groups. *P. aliciae* is in some respects one of the most primitive capitosaurids, but it has several unique features which do not indicate a sister-species relationship with any of the known *Parotosuchus* species.

RELATIONSHIPS among capitosaurs have until recently been assessed primarily on the basis of the skull proportions, culminating in the system of indices developed by Welles and Cosgriff (1965). We have commented unfavourably on this approach (Warren and Hutchinson 1983) and have attempted to establish relationships among temnospondyls by searching for shared derived character states. Cladistic theories of relationships among capitosaurid genera have been suggested by Ingavat and Janvier (1981) and Morales and Kamphausen (Kamphausen and Morales 1981; Morales and Kamphausen 1984; Morales 1987). The difficulty of using the cladistic approach with capitosaurs arises in part from the uncertain familial boundaries and lack of knowledge concerning interfamilial relationships in the Superfamily Capitosauroidae. We have used as our starting point the scheme of family-level phylogenetic relationships suggested by Warren and Black (1985), where the Family Capitosauridae is regarded as belonging to a 'capitosaurian' lineage. This lineage also includes the Rhinesuchidae, Benthosuchidae, Mastodonsauridae, Almasauridae, and Metoposauridae, and possibly the Luzocephalidae (not recognized by Warren and Black 1985) and Lydekkerinidae (tentatively assigned by them to the 'trematosaurian' lineage).

Within the capitosaurian lineage the Superfamily Capitosauroidae is usually considered to comprise three families (Capitosauridae, Benthosuchidae, and Mastodonsauridae; Morales 1987). At present none of these three families has been adequately defined by means of derived character states since the few potential apomorphies are all found in parallel elsewhere.

For example, the Benthosuchidae and Mastodonsauridae may be separated from the Capitosauridae by the shared presence of paired, or butterfly-shaped, anterior palatal vacuities (Morales and Kamphausen 1984). This presumed apomorphy is present also in other temnospondyl families, e.g. the Trematosauridae. In adopting it, Morales and Kamphausen have chosen to accept parallel development of the semi-closed and closed otic notch (in the 'capitosaurids' *Parotosuchus* and *Cyclotosaurus* and the 'benthosuchids' *Odenwaldia* and *Eocyclotosaurus*) as more likely than parallel development of paired anterior palatal vacuities, but no case has been presented for preferring the former scenario.

Ingavat and Janvier (1981) defined a select group of genera as 'Capitosauridea *s.str.*' on the basis of their having a well-defined suture between the exoccipital and pterygoid. This excludes *P. gunganj*,

*P. helgolandicus*, and the new parotosuchian described below, in all of which the pterygoid is prevented from suturing with the exoccipital by a foramen (or notch), and also *P. rewanensis* in which the two bones suture on the occiput. While we agree that these three species and some others may form a plesiomorphic group of capitosauroids, we nevertheless include them in the Family Capitosauridae. The fact that this character is also present in some (but not all) rhytidosteids and some (but not all) brachyopids and that those genera lacking the character are the more plesiomorphic members of their families indicates that it is a 'grade' character perhaps associated with increase in size of later genera.

In our opinion, the arguments used by Morales and Kamphausen (1984) for establishing the boundaries of the Benthosuchidae and Capitosauridae, and of Ingavat and Janvier (1981) for grouping the Capitosauridae *s.str.* are unconvincing. The Mastodonsauridae likewise may not be distinct at the family level. However, there is good evidence that the genera included in these families are close relatives, united by several apparently unique apomorphies, and can be discussed together as capitosauroids. These genera were most recently divided by Morales (1987) into Capitosauridae *s.s.* (*Parotosuchus*, *Eryosuchus*, *Paracyclotosaurus*, *Stenotosaurus*, *Cyclotosaurus*), Benthosuchidae *s.l.* (*Benthosuchus*, *Benthosphenus*, *Kestrosaurus*, '*Parotosaurus*' *lapparenti*, *Thoosuchus*, *Trematotegmen*, *Odenwaldia*, *Eocyclotosaurus*), and Mastodonsauridae (*Heptasaurus*, *Mastodonsaurus*). Chief among the genera considered problematic by Morales is *Wetlugasaurus* which, although usually associated with the primitive open-notched capitosauroids with a single anterior palatal vacuity, does not have the frontals entering the orbital margins. He also noted that *Parotosuchus* is almost certainly paraphyletic, since it includes most of the open-otic-notch capitosauroids.

We became particularly aware of these taxonomic problems when confronted with specimens of a new species of capitosaurid recently collected from the Early Triassic Arcadia Formation of Queensland. In determining that the very small juveniles described here were indeed capitosauroids, we identified several other characters which are apomorphic either for the superfamily or for the family. Without using these characters, we could not have determined the smallest specimens as capitosauroids, as their proportions were in no way capitosaurian.

In the following discussion the adjective 'capitosauroid' pertains to the genera included (Morales 1987) in the Families Capitosauridae, Benthosuchidae, and Mastodonsauridae, while 'capitosaurian' refers to the broader assemblage of families regarded as a monophyletic lineage by Warren and Black (1985). 'Capitosaurid' refers to members of the Family Capitosauridae (Morales 1987).

#### CHARACTER STATES USED IN THIS PAPER

##### *Capitosaurians*

*The presence of an oblique ridge on the quadrate ramus of the pterygoid.* This character was used by Warren and Black (1985) as derived for capitosaurians.

##### *Capitosauroids*

*Crista falciformis of the squamosal.* This crest is a flattened flange of bone on the otic-occipital margin of the squamosal, which projects towards the tabular horn. In later capitosauroids the *crista* becomes progressively broader and more horizontal in orientation and contributes to the restriction and eventual closure of the otic notch. In other Triassic temnospondyls the margin of the squamosal does not project or projects only as a low ridge which is rounded in section rather than flattened. The Late Permian rhinesuchoids appear to show a modest development of the squamosal which approaches the state seen in capitosauroids, providing further evidence for the relationship of these two groups of genera.

*The arrangement of muscular crests on the parasphenoid.* The posteroventral face of the parasphenoid bears an area for the attachment of some of the neck musculature, the transverse ridge (Cosgriff 1974; *crista muscularis* of several authors). The attachment area is a depression, set off anteriorly by a ridge which starts at the level of the trailing edge of the pterygoid. The ridge usually curves

posteromedially and the ridges on each side generally meet, forming a V-shaped outline. In some early forms (e.g. *P. orientalis*) the two ridges do not meet, while in some (especially) later forms the posterior curvature disappears and the ridge becomes a straight transverse line. The rhinesuchoids (including *Uranocentron* and *Lydekkerina*) possess a pair of semicircular depressions on the parasphenoid, usually enhanced by a flange of bone which projects around the anterior and lateral margins of the depressions. These were dubbed 'pockets' by Watson (1962) who regarded the ridges of capitosaurids as derived homologues of the rhinesuchoid pockets. Most other families in the capitosaurian lineage (Warren and Black 1985) have lost all trace of pockets or ridges, the only exception apparently being the metoposaur genus *Eupelor* which shows a capitosauroid V-shaped transverse ridge (Colbert and Imbrie 1956).

*Dentary teeth.* Benthosuchids and capitosaurids uniquely share a very large number, fifty or more, of small marginal dentary teeth, and this also seems to be an apomorphy within the capitosaurians.

#### *Capitosaurids*

*Hamate process.* Jupp and Warren (1986) described a number of distinguishing features of the capitosaurid lower jaw. A unique, clearly apomorphic character state is the prearticular or hamate process, defined as a dorsal projection of the prearticular on the anterior margin of the glenoid fossa, which rises above the level of the articular and surangular. Jupp and Warren considered that only the capitosaurids possessed a well-developed hamate process. In this respect, capitosaurids (e.g. *Parotosuchus*) are derived with respect to benthosuchids (e.g. *Benthosuchus sushkini*) in which the prearticular does not rise above the level of the articular.

*Raised orbits.* A further characteristic of *Parotosuchus*, as well as genera such as *Wetlugasaurus* and *Cyclotosaurus*, is the elevation of the orbital rims above the level of the surrounding skull surface. This is especially pronounced anteriorly where the prefrontal slopes down sharply from the leading edge of the orbit. A result of this is that, whatever the degree of flattening or other changes in skull proportions, the orbits always face almost directly upwards.

*Lateral line system.* A last point which seems useful to note is that most capitosaurids, including *Parotosuchus* in particular, have poorly incised lateral line systems. Lateral line grooves are usually only continuous, if at all, on the anterior parts of the supraorbital and infraorbital canals. Grooves on the cheeks, skull table, and interorbital area are often reduced to chains of pits or are absent.

#### *Parotosuchus*

*Frontal bones enter orbital margins.* *Parotosuchus* species are characterized by frontals entering the orbital borders, a derived state also found in most other capitosaurids, but absent from the two species placed in *Wetlugasaurus* (*W. angustifrons* and *W. samarensis*). The latter two species are in all other respects similar, not simply to *Parotosuchus*, but to its Early Triassic species, with tapering horns and relatively narrow pterygoid-parasphenoid contact. It is possible that *Wetlugasaurus* was derived from these primitive *Parotosuchus* species via secondary contact of the prefrontal and postfrontal, rather than retaining a primitive contact of these bones.

*Otic notch.* The most easily observed evolutionary change which occurred within *Parotosuchus* (*sensu* Kamphausen and Morales 1981) was the development of a partly closed otic notch. The plesiomorphic state of the otic area is shown by those species having tapering, pointed, posteriorly directed tabular horns and only a moderate development of the *crista falciformis*. More derived taxa show the development of a rounded lappet on the end of the tabular horn, a more lateral orientation of the horn, and expansion of the *crista* towards the tip of the tabular horn. Many of the later capitosaurids show a marked broadening and flattening of the skull compared with earlier, apparently more primitive species. The broad-skulled forms also show a reduction in the relative size of the orbits, which is accompanied by a reduction in the extent of the jugal bordering the orbit. These evolutionary changes are often found as a mosaic in different species.

## SYSTEMATIC PALAEOLOGY

Superfamily CAPITOSAUROIDEA Säve-Söderbergh, 1935

Family CAPITOSAURIDAE Watson, 1919

Genus PAROTOSUCHUS Otschev and Shishkin, 1968

*Type species. Capitosaurus nasutus* Meyer 1858, by subsequent designation.

*Diagnosis of genus.* Capitosaurid temnospondyls with open otic notches, a single anterior palatal vacuity, and with both the frontals and jugals taking part in the orbital border (Kamphausen and Morales 1981; Morales and Kamphausen 1984). Full discussions of intrageneric variation are provided by Welles and Cosgriff (1965), and Cosgriff and de Fauw (1987).

*Parotosuchus aliciae* n. sp.

Text-figs. 1-10

*Derivation of name.* The species is named in honour of Alice Crosland Hammerly who found the small juvenile specimens referred to this species.

*Type specimens.* Holotype. QM F12281 (text-figs. 1, 2, 4-6A, 7), a partial skeleton consisting of most of the skull and attached lower jaws, parts of the anteriormost vertebrae and ribs, most of the right hind limb, the right ilium, and other fragmentary postcranial remains. The nearly complete dermal pectoral girdle was destroyed in order to expose the palate, but is preserved as a polyester resin cast.

*Paratype.* QM F12282 (text-figs. 3-5, 6B), a skull and lower jaws minus the snout, with a partial shoulder girdle.

*Referred specimens.* QM F12286, a weathered specimen consisting of the skull posterior to the level of the orbits, with the rear portions of both lower jaws and most of the dermal pectoral girdle still in place. QM F12287, a weathered right hand rear quadrant of the skull (plus associated dermal girdle) of a smaller individual. QM F12290-12292 (text-figs. 8-10), three small juvenile skulls with associated mandibles and skeletal fragments.

*Type locality.* Collected by R. Jupp, A. C. Hammerly, A. A. Warren, R. Lane, and D. Harrison at AAW field locality Q6, on Duckworth Creek south-west of the town of Bluff, Queensland. Bluff lies on the Tropic of Capricorn, approximately 195 km west of the coastal city of Rockhampton.

*Horizon.* Lower Upper Arcadia Formation, Rewan Group, Early Triassic (Scythian). Jensen (1975) and Warren (1980) discuss the stratigraphic position of these deposits and their *Lystrosaurus* zone fauna. Based largely on these studies Cosgriff (1984) assigned the Arcadia Formation fauna to his earliest, A1, division of the Scythian. Q6 is also the type locality for three other temnospondyl amphibians: *Xenobrachyops allos* (Howie, 1972) (Brachyopidae), *Keratobrachyops australis* Warren, 1981 (Chigutisauridae), and *Arcadia myriadens* Warren and Black, 1985 (Rhytidosteidae).

*Diagnosis.* Distinguished from all other species of *Parotosuchus* by the following combination of character states: oblique ridge of pterygoid greatly expanded, forming a fan-shaped, dorsomedially directed plate flooring the otic area; *crista falciformis* of the squamosal well developed and oriented nearly vertically, forming a high wall bordering the otic notch laterally and terminating abruptly at the squamosal-quadratojugal suture; posteroventral margins of tabular and postparietal with an unusually well-developed *crista muscularis* which partially occludes the post-temporal fossa; *crista tabularis externa* absent; ectopterygoid tusks present; posterior meckelian foramen of lower jaw exceptionally small, not bordered by the postsplenial. The species is currently known only from small specimens (skull length less than 40 mm) which show such juvenile features as a relatively short, rounded snout, very large orbits, weakly sutured cranial roofing bones, and a parietal foramen centred at the level of the posterior margins of the orbits.

*Description*

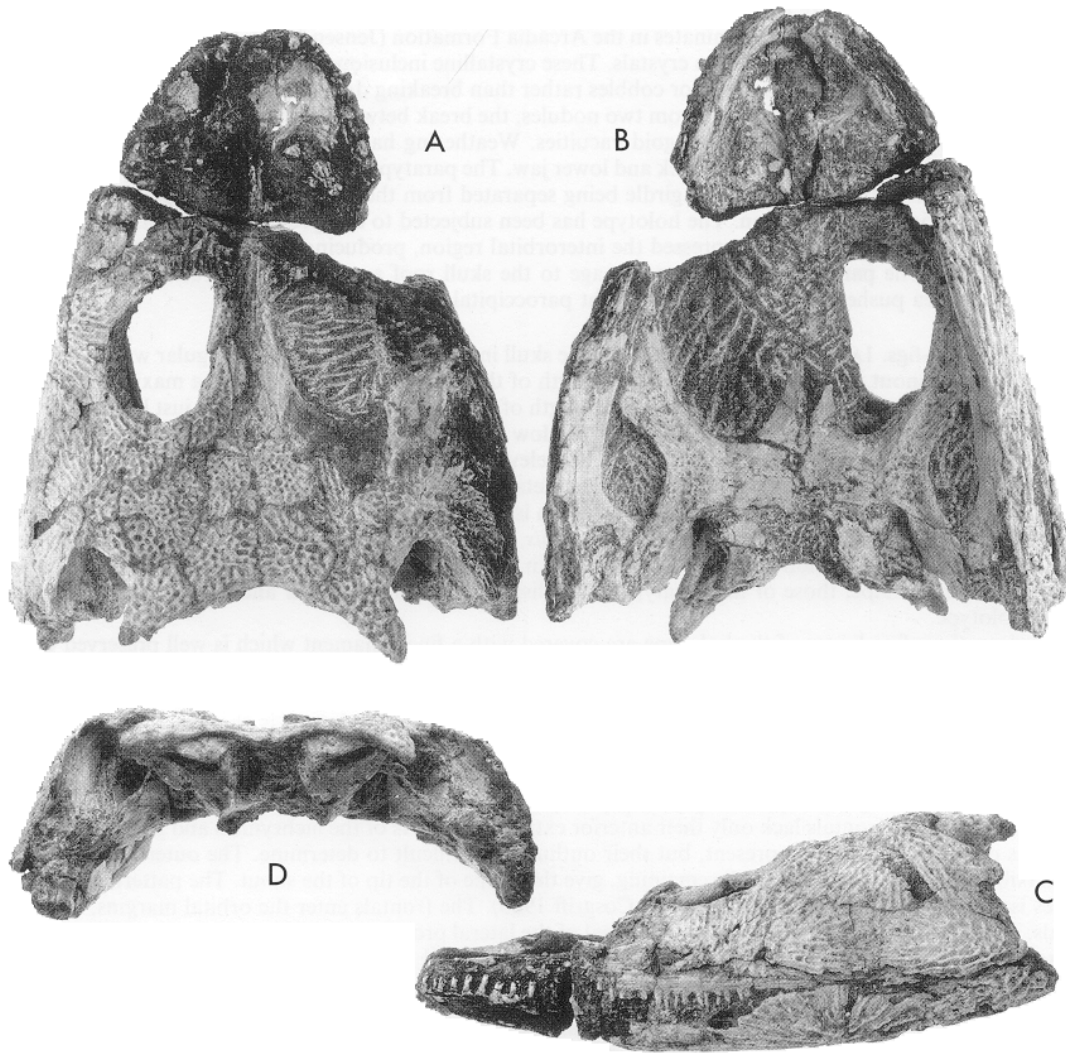
The description of the new species is based on the holotype and paratype specimens.

*Preservation.* The types were collected in small nodules. The matrix surrounding the fossil bone is basically the same red mudstone which predominates in the Arcadia Formation (Jensen 1975), but is distinctive in being heavily impregnated with small gypsum crystals. These crystalline inclusions have apparently given the matrix sufficient solidity to weather as nodules or cobbles rather than breaking down into the silty mud typical of the formation. The holotype was extracted from two nodules, the break between them having occurred at the level of the anterior margins of the interpterygoid vacuities. Weathering had destroyed the dorsal surface of the anterior nodule and abraded the right cheek and lower jaw. The paratype was also in two sections, the posterior right-hand corner of the skull, jaw, and girdle being separated from the rest. Both skulls apparently suffered some damage prior to preservation. The holotype has been subjected to compression which has depressed the right cheek region and laterally compressed the interorbital region, producing a depressed fracture along the mid-line suture. The paratype shows some damage to the skull roof anterior to the orbits and has had the right tabular area pushed down crushing the right paroccipital process.

*Skull roof.* (Text-figs. 1A, C, 2A, C, 3A, C, D, F, 4A.) The skull in dorsal view is bluntly triangular with a relatively broad, rounded snout. We estimate the mid-line length of the holotype as 39 mm and the maximum width as 36 mm. The orbits are elongate ovals, 27 % of the length of the skull, and they are centred just behind the mid-point of the skull length and are separated by a shallow trough running along the skull mid-line. They are raised above the level of the adjacent skull roof, the elevation being most pronounced anteriorly where the prefrontal slopes markedly downwards. A circular parietal foramen is centred on a line level with the posterior extremities of the orbits. Each deeply incised otic notch is bounded laterally by a well-developed flange on the occipital edge of the squamosal (the *crista falciformis*, Bystrow and Efremov 1940), which appears as a pronounced fin-like projection when the skull is seen in lateral view. The tabular horns of the paratype and holotype differ in shape, those of the paratype being disproportionately smaller and more slender than those of the holotype.

The dermal roofing bones of the holotype are covered with a fine ornament which is well preserved on the newly exposed surfaces. On the skull table and between the orbits the ornament consists primarily of pits, but becomes a ridge-groove on the cheeks. In the paratype the ridge-groove pattern extends more on to the dorsal surface of the skull; presumably the more pitted pattern seen in the holotype is the result of cross-bridge development during ontogeny, as discussed by Bystrow (1935). Sensory canals are not obvious on the skull bones preserved. Taken together, the type skulls provide complete outlines of the postparietals, tabulars, squamosals, supratemporals, quadratojugals, jugals, postorbitals, postfrontals, and parietals, while the maxillae, prefrontals, and frontals lack only their anterior extremities. Parts of the lacrymals and probably the rear portions of the nasals are also present, but their outlines are difficult to determine. The outer margins of the premaxillae, with several of the teeth remaining, give the shape of the tip of the snout. The pattern of the skull bones is typically parotosuchian (Welles and Cosgriff 1965). The frontals enter the orbital margins, as do the jugals. There is only a small intrusion into the jugal of the lateral process of the postorbital. The supratemporal is excluded from the otic margin by the contact of the squamosal and tabular.

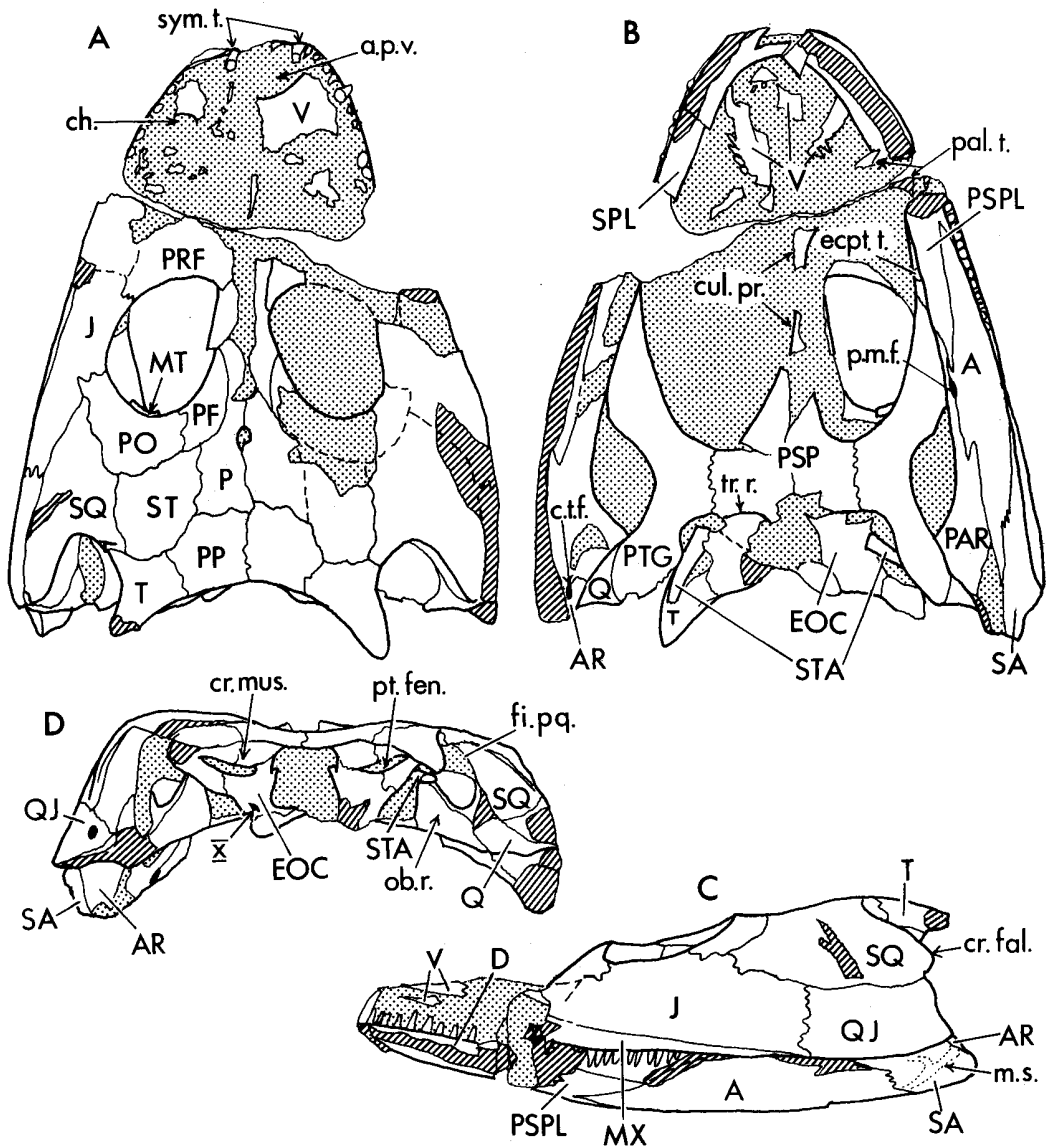
*Occiput.* (Text-figs. 1D, 2D, 4C.) In occipital view the skull is moderately deep, with the cheeks descending more abruptly than in many *Parotosuchus* species. A prominent feature of the rear of the skull table is a descending flange of bone, borne by both the tabular and postparietal on each side. This *crista muscularis* (Bystrow and Efremov 1940; Cosgriff and de Fauw 1987) partly overgrows the post-temporal fossa which, as a result, takes the form of an obliquely oriented slot. The paroccipital processes are made up of the tabulars and exoccipitals with no exposure of the opisthotic between them. The ventral surface of the tabular portion of the paroccipital process lacks any trace of the *crista tabularis externa* (Bystrow and Efremov 1940) which is normally present in capitosaur (Cosgriff and de Fauw 1987). A relatively well-developed *crista tabularis interna* is present on the otic margin of the tabular. The exoccipital bone bears a large foramen (cranial nerve X) at the base of the paroccipital process while the inner margin of its ascending ramus gives rise to a well-developed *processus lamellosus*. The occipital condyle is set off laterally from the body of the exoccipital by a strongly incurved neck of bone. Its articular surface is elliptical and is directed posteromedially. The occipital portions of the squamosal and quadratojugal provide a convex surface for the origin of the *depressor mandibulae* muscle. On its occipital surface the squamosal is bordered laterally by the *crista falciformis* which is not continued along the quadratojugal but ends abruptly at the squamosal-quadratojugal suture. A feature unusual in capitosaur, but possibly present in all juveniles, is the failure of the ascending ramus of the pterygoid to meet the skull roof, so that a gap is present. This represents the more dorsal part of a palatoquadrate fissure, the ventral part being obliterated by a suture between the squamosal and the ascending ramus. The oblique ridge of the pterygoid is exceptionally well developed, its trailing edge being oriented diagonally upwards so that its dorsal limit is



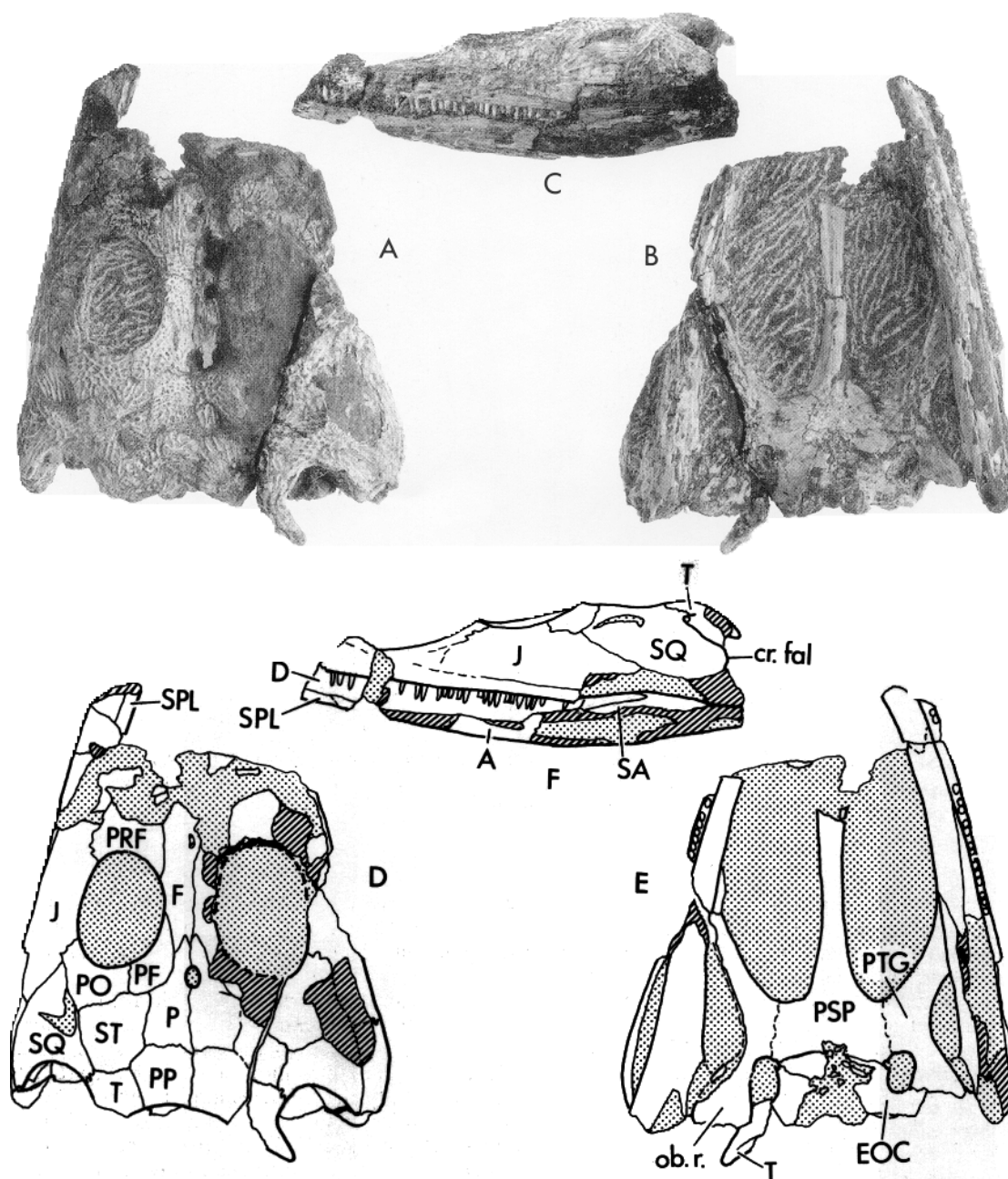
TEXT-FIG. 1. *Parotosuchus aliciae* sp. nov., holotype skull and mandible, QM F12281. A, dorsal view; B, ventral view; C, left lateral view; D, posterior view.  $\times 2$  natural size.

obscured by the paroccipital process. Between the ascending ramus of the pterygoid and the edge of the oblique ridge is a smoothly curved trough underlying the tympanic area. The quadrate is poorly ossified and has a pointed dorsal process wedged between the squamosal and the ascending ramus of the pterygoid.

**Palate.** (Text-figs. 1B, 2B, 3B, E, 4B.) The palate shows the usual suite of vacuities seen in temnospondyls. Parts of the dorsal surface of both vomers are exposed on the holotype snout and contain much of the shallow convex posterior margin of the anterior palatal vacuity. The marginal teeth of the premaxilla and maxilla are small, lanceolate, even in height (1.1 to 1.3 mm), and number between fifty and fifty-five. In ventral view the snout fragment shows the dentition of the right vomer. Following a pair of vomerine tusks (each about 1.5 times the size of a maxillary tooth) is a series of six slender teeth running almost directly posteriorly and apparently delimiting the inner margin of the choana. Two teeth situated posterolaterally to these vomerine teeth probably represent palatine teeth, although no vomer-palatine suture was preserved. The snout has broken along a line

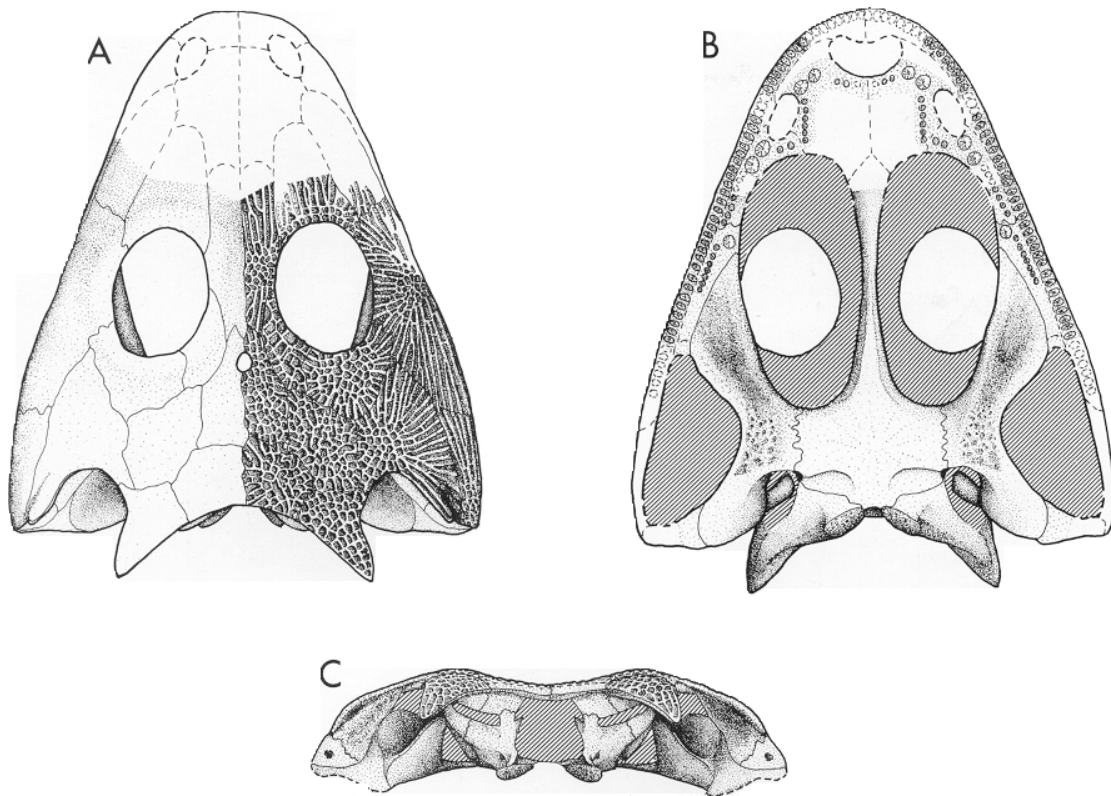


TEXT-FIG. 2. *Parotosuchus aliciae* sp. nov., holotype, skull and mandible, QM F12281. A, dorsal view; B, ventral view; C, left lateral view; D, posterior view.  $\times 2$  natural size. Broken bone surface hatched. Matrix stippled. Abbreviations: A, angular; a.p.v., anterior palatal vacuity; AR, articular; ch, choana; cr.fal., crista falciformis; cr.mus., crista muscularis; c.t.f., chorda tympanic foramen; cul.pr., cultriform process; D, dentary; ecpt.t., ectopterygoid tusk; EOC, exoccipital; fi.pq., palatoquadrate fissure; J, jugal; m.s., mandibular sulcus; MT, metatarsal; MX, maxilla; ob.r., oblique ridge; P, parietal; pal.t., palatine tusk; PAR, prearticular; PF, postfrontal; p.m.f., posterior meckelian foramen; PO, postorbital; PP, postparietal; PRF, prefrontal; PSP, parasphenoid; PSPL, postsplenial; pt.fen., post-temporal fenestra; PTG, pterygoid; Q, quadrate; QJ, quadratojugal; SA, surangular; SPL, splenial; SQ, squamosal; ST, supratemporal; STA, stapes; sym.t., symphysial tusk; T, tabular; tr.r., transverse ridge; V, vomer; X, foramen for tenth cranial nerve.



TEXT-FIG. 3. *Parotosuchus aliciae* sp. nov., paratype, skull and mandible, QM F12282. A, D, dorsal view; B, E, ventral view, C, F, left lateral view.  $\times 2$  natural size. Broken bone surface hatched. Matrix stippled. Abbreviations: F, frontal; remainder as in text-fig. 2.



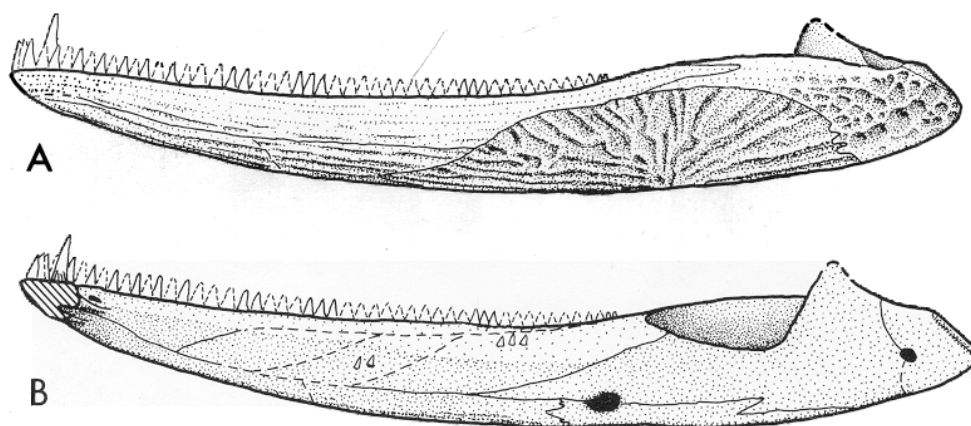


TEXT-FIG. 4. *Parotosuchus aliciae* sp. nov., restoration of skull based mainly on holotype, QM F12281, with details of interorbital and parasphenoid regions added from paratype, QM F12282. A, dorsal view; B, ventral view; C, posterior view.  $\times 2$  natural size.

running through the palatine tusks. The palatal dentition is distinctive in including an ectopterygoid tusk at the front of each ectopterygoid tooth row. An expansion of the ectopterygoid in the region of the tusk contacts the margin of the interpterygoid vacuity, separating the pterygoid and palatine bones. The teeth on the palatines and ectopterygoids are smaller than the marginal teeth, and their crowns are angled lingually.

The palatal ramus of the pterygoid has a sharply downturned flange on its trailing edge which borders the subtemporal fossa. A mid-line strip of the palatal ramus bears a coarse ornament which becomes more elaborate on the body of the pterygoid. The greatly expanded oblique ridge of the pterygoid has already been described. In ventral view it can be seen to merge with the quadrate ramus at a low ridge which is confluent with the posterior edge of the body of the pterygoid. The pterygoid forms a sinuous medial suture with the parasphenoid but does not make ventral contact with the exoccipital. The parasphenoid bears a pair of shallow, transversely aligned grooves ('transverse ridge' of Cosgriff 1974; 'pockets' of Watson 1962; *crista muscularis* of e.g. Otschev 1972) posteriorly. The cultriform process has a flattened median crest posteriorly which reduces to a narrow ridge anteriorly. The stapes is preserved on both sides of the holotype and appears to have been of the usual, rather massive capitosaurian type. Both left and right stapes are slightly displaced.

*Hyoid Element.* (Text-fig. 6A.) A small dumb-bell-shaped bone was found in the oral cavity of both type specimens and the largest referred specimen (QM F12286). The bone in each case lay just in front of the anterior extremity of the interclavicle. We have tentatively identified this as a median hyoid element, probably the copula. No other remains referable to the hyoid apparatus were found, and there was no trace of any branchial bars.



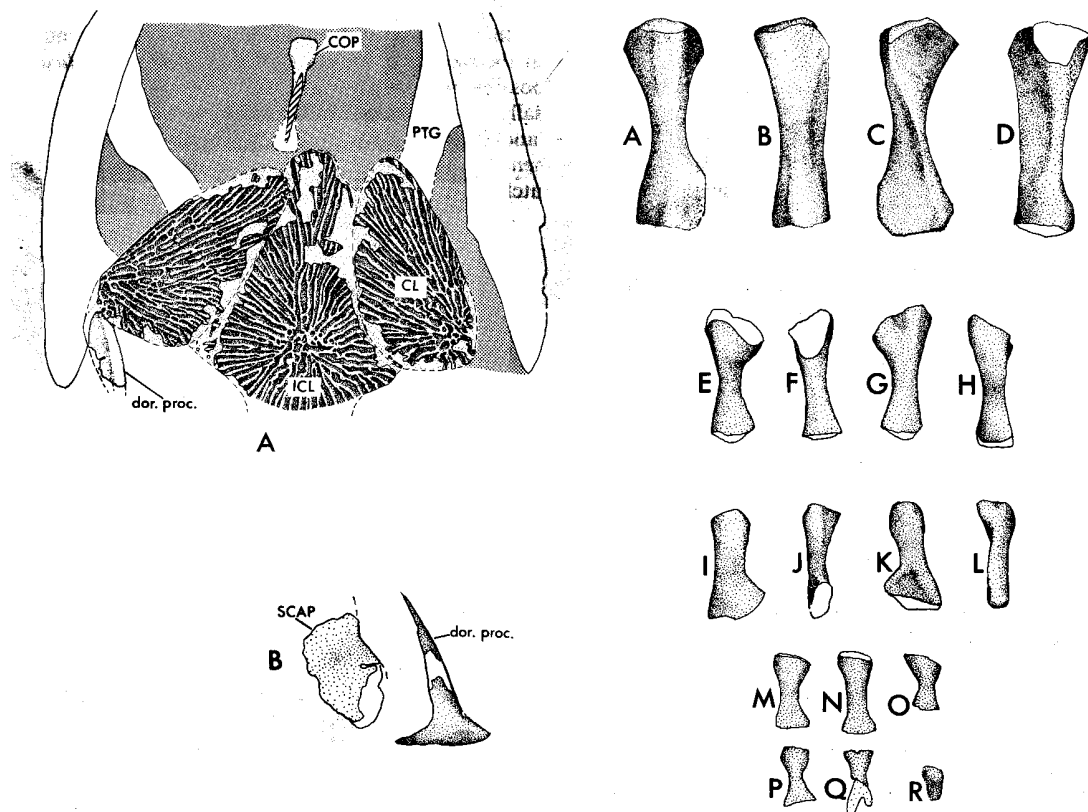
TEXT-FIG. 5. *Parotosuchus aliciae* sp. nov., restoration of mandible (oriented parasagittally) based on holotype and paratype specimens. A, labial view; B, lingual view.  $\times 4$  natural size.

**Lower Jaw.** (Text-figs. 1c, 2c, 3c, F, 5.) No complete mandibular ramus was recovered, but enough partial jaws are available for many of the mandibular features to be described. The mandible resembles that of other capitosaurids (see Jupp and Warren 1986) in many respects, including overall shape, relative tooth size, presence of a well-developed hamate (prearticular) process preceding the glenoid area, a Type 1 postglenoid area (PGA, Jupp and Warren 1986), and a single row of teeth on the posterior coronoid. There are several features which differentiate *P. aliciae* from some or all other capitosaurids. The labial surface of the rear of the mandible shows no extension of the angular on to the PGA, the surangular meeting the angular along a vertical suture at the level of the glenoid area. In lingual view, some unique features are visible. The chorda tympanica foramen is large and situated on the articular-prearticular suture about midway between the glenoid cavity and the ventral margin of the jaw. The posterior meckelian foramen is exceptionally small and fails to contact the postsplenial, so that it is bordered solely by the prearticular and the angular. Damage to the jaw prevents us from determining the presence or absence of an anterior meckelian foramen, although if present it must have been small. The posterior coronoid bore a series of at least three small teeth. The surfaces of the lower jaw covered by the middle and anterior coronoids were difficult to prepare and much of this area remains covered by a thin layer of matrix. However, at least two small teeth are present in this region and have been tentatively restored in text-fig. 5 as lying on the middle coronoid. At the point where the left ramus of the holotype mandible is broken, there is a thickened bump of bone which we interpret as the origin of an enlarged tusk-like tooth.

**Pectoral Girdle.** (Text-fig. 6.) The pectoral girdle is represented in the holotype by a nearly complete dermal girdle and a partial scapulocoracoid, while fragments of the dermal girdle and scapulocoracoid are also present in the paratype. In both specimens the girdles were preserved in almost their natural positions, and had to be removed in order to expose the posterior palate and basicranium. The description of the dermal elements is based principally on a polyester resin cast made of the holotype girdle prior to its destruction.

The ventral plate of the clavicle is roughly triangular with a relatively narrow, concave posterior margin and shallow convex, elongate anterior and medial margins. Ridge-groove ornamentation radiates from a pitted centre of ossification situated at the posterolateral corner of the clavicle. The dorsal process of the clavicle is preserved in external view in the paratype and in posterior view in the holotype cast. The dorsal process is slender and tapering, and lacks any sigmoid flexure or cleidomastoideus scar. In posterior view the process can be seen to consist of a columnar shaft bordered laterally by a flange of bone which merges with the shaft about half-way up. The interclavicle is rhomboidal with an extended anterior arm. The ornament of its ventral surface is similar to that of the clavicles. No specimen retains an intact posterior edge to the interclavicle, although the missing portion does not appear to have been large.

All capitosaurids for which the clavicle has been described have a dorsal process which is markedly different from that of *P. aliciae*. Clavicles of *Paracyclotaurus davidi* (Watson 1958), *Parotosuchus peabodyi* (Welles and Cosgriff 1965), *P. pronus* (Howie 1970), *P. orenburgensis*, *P. tverdochlebovi*, and *P. garjainovi* (Otschev 1966, 1972) all have a dorsal process, the base of which runs forward along the anterolateral edge of the



TEXT-FIG. 6. (left). *Parotosuchus aliciae* sp. nov., pectoral girdle and hyoid elements as preserved.  $\times 2$  natural size. A, clavicles, interclavicle, and copula of holotype, QM F12281, based on polyester resin cast; B, lateral view of right partial clavicle and scapulocoracoid of paratype, QM F12282. Abbreviations: CL, clavicle; COP, copula; dor.proc., dorsal process of clavicle; ICL, interclavicle; SCAP, scapula; remainder as in text-fig. 2.

TEXT-FIG. 7. (right). *Parotosuchus aliciae* sp. nov., right hindlimb elements of holotype, QM F12281. A-D, femur; A, dorsal view; B, anterior view; C, ventral view; D, posterior view. E-H, tibia; E, posterior view; F, lateral view; G, anterior view; H, medial view. I-L, fibula; I, anterior view; J, medial view; K, posterior view; L, lateral view. M-O, three metatarsals in dorsal view. P-R, three proximal phalanges in dorsal view.  $\times 2$  natural size.

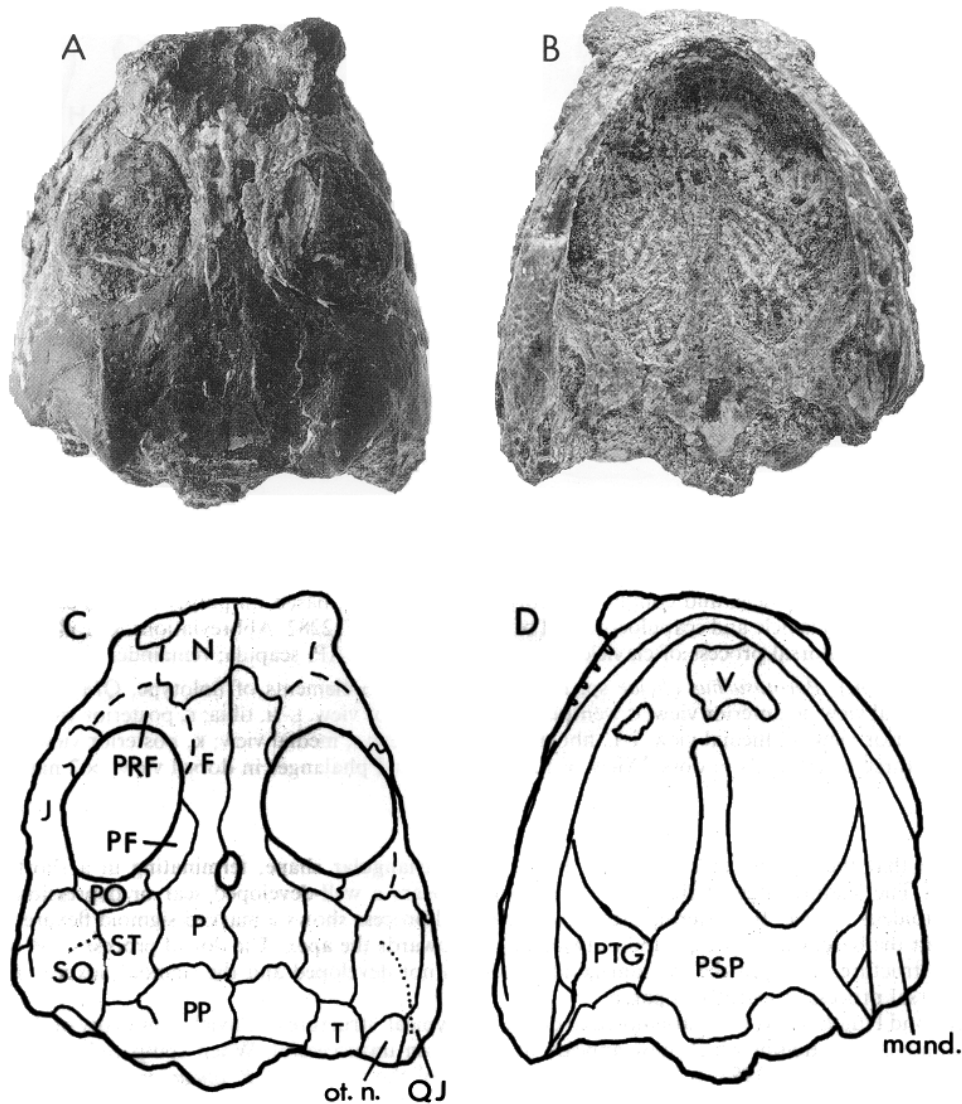
clavicle, so that the process in lateral view has a squat, triangular shape, terminating in a short slender projection. The leading edge of the base of the process bears a well-developed scar or depression for the cleidomastoideus muscle. In posterolateral view, the dorsal process shows a marked sigmoid flexure, curving outwards at the base, then inwards, and outwards again towards the apex. The dorsal process of *P. aliciae* is a simpler structure, in which the cleidomastoideus area is not developed and the sigmoid flexure of the tall slender dorsal process is scarcely apparent.

Warren and Hutchinson (1983) attempted to define the 'typical' structure of clavicles for many of the Triassic temnospondyls, an attempt which now appears to have been unsuccessful. When compared with fig. 27 in Warren and Hutchinson (1983, p. 42), the dorsal process of the clavicle of *P. aliciae* is most similar to the brachyopoid *Siderops*. Recently Snell (1986) has described the clavicle of an Arcadia Formation capitosaur (QM F12278) which can be referred, on the basis of an associated skull, to *P. rewanensis*. This specimen (skull length approx. 150 mm) includes a partial right clavicle with an almost complete dorsal process which is slender, tapering, lacks a sigmoid curvature and, in short, resembles that of *P. aliciae* very closely.

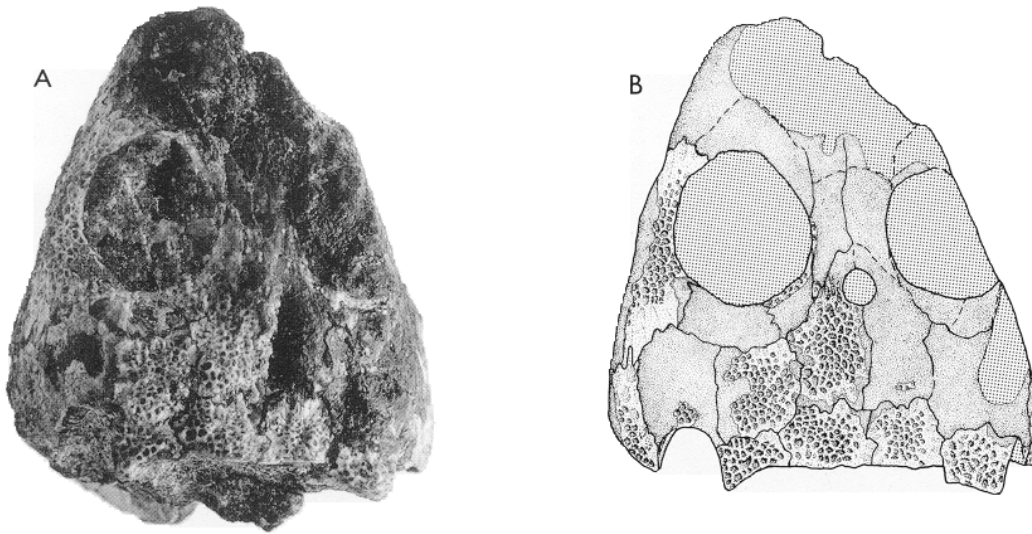
In the series of juvenile to adult clavicles of *Benthosuchus sushkini* (Bystrow and Efremov 1940, fig. 77) the

dorsal process is hardly visible. However, in a second illustration (fig. 78) which shows individual variation in the dorsal processes of eight specimens, it is apparent that those of the smaller individuals are more slender and have a less-developed muscle scar. This indicates that the slender unscarred dorsal process of *P. aliciae* and QM F12278 may be related to their small size and possible immaturity.

The scapulocoracoid of the paratype is incomplete dorsally and ventrally, but the holotype fragment shows the posterior margin and the ventral limits of the coracoid and the supraglenoid buttress. The latter two regions were unfinished ventrally, so that the supraglenoid foramen was open. Such unfinished scapulocoracoids are the rule in the Australian Early Triassic (Warren and Hutchinson 1983).



TEXT-FIG. 8. *Parotosuchus aliciae* sp. nov., referred small juvenile skull, QM F12290. A, dorsal view showing impressions of the ventral surface of the cranial roof; B, ventral view; C, sketch of specimen shown in A, indicating bone outlines; D, sketch of specimen shown in B, indicating bone outlines. Abbreviations: mand., mandible; N, nasal; ot.n., otic notch; remainder as text-fig. 2.  $\times 5$  natural size.



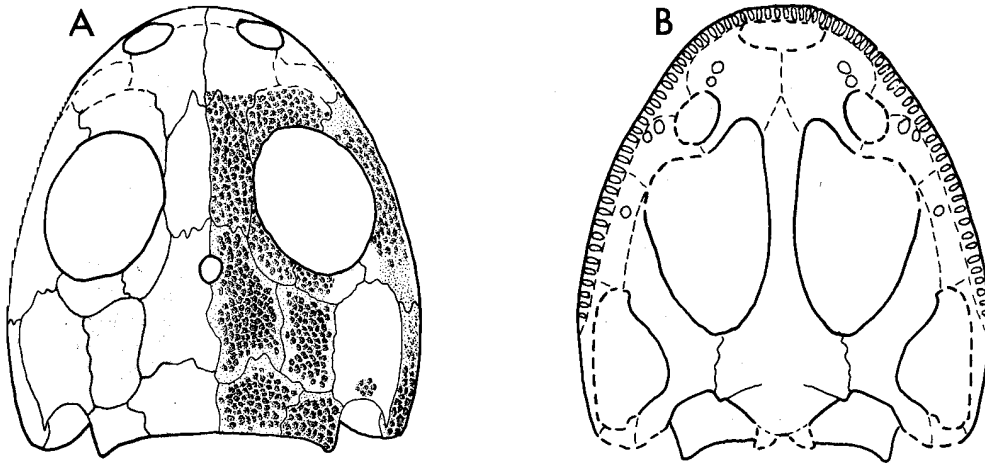
TEXT-FIG. 9. *Parotosuchus aliciae* sp. nov., referred small juvenile skull, QM F12291. A, skull seen in dorsolateral view, B, interpretive drawing of specimen shown in A.  $\times 5$  natural size.

**Pelvic Girdle.** The right ilium and both ischia were preserved as counterparts in the nodule containing the main part of the holotype skull. The ilium is 12 mm long and is notable for its gracile proportions, with a narrow subcylindrical shaft becoming flattened and slightly swept back at its dorsal extremity and with a thickened basal area behind the acetabulum. In posterior view the ilium is bowed outwards. The ischia appear to have been poorly ossified and are visible only as indistinct but bony impressions, each roughly trapezoidal in shape with the narrow end facing posteriorly. No traces of the pubes are visible.

The few capitosaurid ilia which have been described (Watson 1958; Howie 1970) are from larger animals and are considerably more robust in shape than that of *P. aliciae*. The principal difference seen in the larger species is that the expanded dorsal blade of the ilium extends much further ventrally so that the shaft is reduced to a 'waist' separating expanded dorsal and ventral regions.

**Limbs.** (Text-fig. 7.) An almost complete right hind limb was found with the holotype skull. The femur, tibia, fibula, three or four metatarsals, and several phalangeal bones were preserved draped across the left cheek and orbit of the skull, some of the metatarsals having fallen into the matrix which filled the orbit. Apart from their more slender build, the limb bones are very similar to those described by Howie (1970) for *P. pronus*. No trace of ossified tarsals was detected, and in view of the good preservation of the rest of the limb, it seems likely that the tarsal region was not ossified.

**Vertebrae and Ribs.** Several neural arches and associated proximal rib fragments were attached to the holotype skull. Their preservation was not good and the very thin bone proved difficult to separate from the matrix. As far as can be determined the neural arches are similar in shape to those of other capitosaurids such as *P. pronus* (Howie 1970) or *Paracyclotossaurus davidi* (Watson 1958). The ribs are broad-based without any ossified bicipitate structure, but, like the vertebrae, they are preserved in a very fragile state which makes detailed study difficult. No determinable remains of intercentra were recovered, apart from several impressions associated with the ischial remains. No traces of pleurocentra were identified.



TEXT-FIG. 10. *Parotosuchus aliciae* sp. nov., restoration of referred small juvenile skull, based on QM F12290 and F12291, in dorsal (A) and ventral (B) views.  $\times 5$  natural size.

The three skulls were found embedded in small nodules. Two (QM F12290 and F12291) were found one on top of the other within the same nodule and are better preserved than the third specimen (QM F12292) which has suffered more weathering and distortion. QM F12290 (text-fig. 8) became detached from its nodule, leaving the skull roof attached to the matrix. After a sketch was made of the bony sutures, the exposed underside of the skull roof was filled with polyester resin to provide support while the nodule was mechanically prepared to expose the dorsal side. During this preparation the second skull (QM F12291; text-fig. 9) was discovered lying on its left side on top of the skull of QM F12290. It was also noted during this preparation that numerous postcranial bones were present, including girdles, limbs, neural arches, and possible ribs. These were little more than fragile films of bone and could not be saved but were sketched before being destroyed as preparation of the skulls proceeded.

In making the reconstructions of the skull shown in text-fig. 10, information from QM F12290 and F12291 was combined. QM F12290 retained a detailed impression of most of the internal surface of the skull roof and provided the most complete palatal surface, as well as the overall proportions of the skull and orbits. The dorsal surface of its skull roof, which could only be partially prepared, gave additional information on the sutures and ornament of the interorbital area. QM F12291 preserved the rear of the skull table including the external surfaces of the tabular horns and otic notches, and provided the surfaces of the lateral skull bones and a complete labial view of the right mandibular ramus. This specimen also provided extra detail of the palate, including the parasphenoid ridges and the ectopterygoid tusk.

*Description.* The mid-line length of QM F12290 is 12.5 mm, and the less complete QM F12291 and QM F12292 are of similar size. The skull is broadly rounded, with a short, blunt snout and very large orbits (length of orbit 36% of skull length). The orbital borders are raised above the level of the adjacent skull bones, especially anteriorly. The mid-line region of the skull is shallowly concave. The parietal foramen is large and centred on a line level with the posterior margins of the orbits. The otic notches are deeply incised but broadly open posteriorly. The bones of the skull roof bear a pitted ornament which is absent from the sutural margins of the bones, especially on the skull table. No impressions of sensory canals are evident. The arrangement of the skull bones is typical of many Triassic temnospondyls, with the following exceptions: the frontals enter the orbital margins and the jugals broadly border the orbits laterally; there is a broad jugal-prefrontal suture running to the ventrolateral rim of the orbit; the otic margin of the squamosal bears a distinct *crista falciformis*; the tabular horn projects only slightly beyond the body of the tabular, and it is well buttressed ventrally by

the tabular portion of the paroccipital process; the tabular and squamosal contact to exclude the supratemporal from the otic margin.

In palatal view, the choanal openings are large and their posteromedial borders bulge into the interpterygoid vacuities. The anterior palatal vacuity is not preserved, but it is restored here as single. Tusks are present on the vomers, palatines, and ectopterygoids; it is not possible to determine if smaller palatal teeth were also present. The body of the pterygoid is flat and in moderately broad contact with the parasphenoid. The cultriform process of the parasphenoid is relatively broad. The body of the parasphenoid bears a pair of transverse ridges which start just posterior to the pterygoid–parasphenoid suture and run anteromedially. The exoccipitals were apparently poorly ossified and have not been adequately preserved, as is true also of the quadrates.

The lower jaw is known primarily from its external surface as preserved in QM F12291. The pattern of sutures completely matches that seen in the lower jaw of *P. aliciae* QM F12281 (text-fig. 5), and the pattern of ornamentation, with a pitted surangular and ridged angular, is also very similar. The postglenoid area is Type I (Warren and Black 1985). The internal surfaces of the jaws show few sutural details, but it is clear from QM F12290 that the prearticular gave rise to a pronounced hamate process.

*Allocation to P. aliciae.* The following character states collectively indicate that QM F12290–12292 are small capitosaurids, and should probably be allocated to *P. aliciae*.

1. Otic notches distinct and semicircular. A primitive character state which characterizes the capitosaurian lineage but is lost by trematosaurians, the other major Triassic temnospondyl assemblage (Warren and Black 1985).

2. Tabular horn well buttressed ventrally by the paroccipital process. Again a primitive character state, but one which is typical of capitosaurians.

3. Frontals enter orbital borders. A derived state found in most capitosaurids although also occurring in other families (e.g. Dissorophidae).

4. Parasphenoid with transverse ridges. The form of the ridges in the small specimens is somewhat aberrant in that the ridges are directed anteriorly as well as medially but in this respect they resemble the smaller *P. aliciae* (paratype) specimen (QM F12282).

5. Parasphenoid–pterygoid suture. The referred specimens resemble early capitosaurids, including *P. aliciae*, in possessing an intermediate stage of this character, in which the corpus of the pterygoid has a flattened ventral surface and the suture with the parasphenoid is sinuous but not greatly extended posteriorly. This is derived with respect to more archaic groups such as eryopoids and dissorophoids, in which the pterygoid corpus is narrow and curved ventrally and in virtual point contact with the parasphenoid. Later capitosaurids, as well as most other Triassic families, show a more derived state in which there is a posterior lengthening of the pterygoid–parasphenoid suture.

6. Orbital borders raised above the level of the adjacent skull surface.

7. Squamosal with flattened, fin-like *crista falciformis*. Such a *crista* is diagnostic for capitosaurids. The form of the *crista*, well preserved in QM F12291, is very similar to that seen in the *P. aliciae* types, and it differs only in its relatively smaller size.

8. Ectopterygoid tusks present. The only capitosaurids known to retain ectopterygoid tusks are *P.* (= *Benthosuchus*) *madagascariensis* (Warren and Hutchinson, in press) and *P. aliciae*.

9. Mandibular features. The Type I PGA and hamate process, both indicate a capitosaurid.

The characters discussed above all suggest that QM F12290–12292 are capitosaurids, and in particular a species of *Parotosuchus*. Characters 4, 7, and 8 indicate a special resemblance to *P. aliciae*, and in view of the fact that the small specimens were apparently preserved at the same time and place as the *P. aliciae* types, we are confident that QM F12290–12292 should be regarded as very young specimens of *P. aliciae*.

#### CAPITOSAURID ONTOGENY AND TEMNOSPONDYL PHYLOGENY

Boy's (1974) analysis of temnospondyl ontogeny, based on the Permian eryopid *Sclerocephalus*, summarized the changes occurring during larval development to early postmetamorphic stages. Our

capitosaurid specimens appear to complement Boy's material, and extend his staging of temnospondyl ontogeny through to the adult.

Boy's criteria for determining the point of metamorphic climax were loss of gills (including gill rakers), development of a sclerotic ring, ossification of the exoccipital, and definite presence of vertebral centra. Both latest larva and earliest adult showed a complete dermatocranium, labyrinthine teeth, ossified copula, lateral line grooves, and ossified limbs and girdles (except coracoid and pubis). Our very small specimens (QM F12290–12292) appear to be at this stage and show, where it is possible to ascertain, a combination of late larval and early adult character states. Adult features include apparent loss of gills, no traces of which (or their more durable branchial teeth) were found, and partial ossification of the exoccipitals. However, a sclerotic ring was not preserved, nor were any remains of centra, although neural arches were preserved in partial articulation. Thus, these small specimens represent the starting point for postmetamorphic ontogenetic changes in capitosaurids.

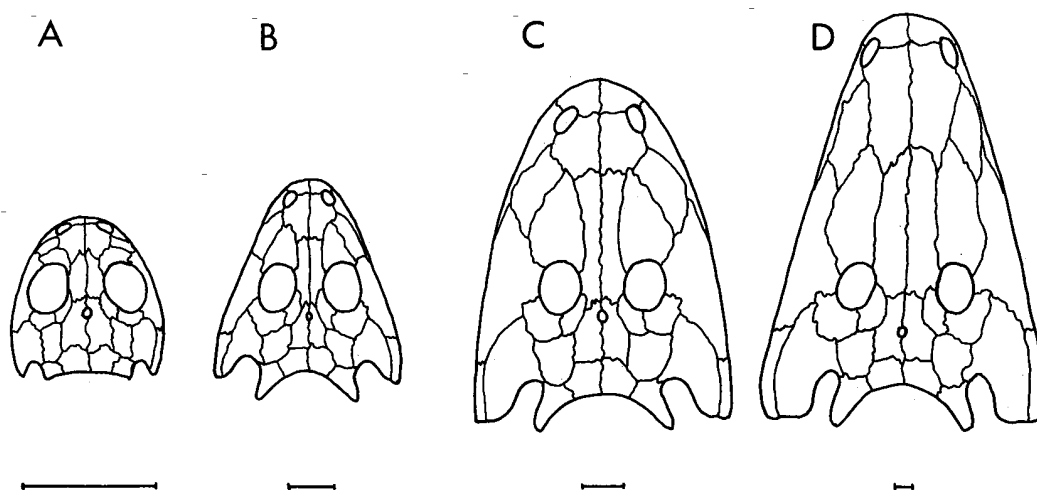
TABLE 1. Characteristics of the skull of capitosaurids at metamorphosis.

- 
1. Bones weakly sutured.
  2. Ornament of coarse pits not extending to sutural boundaries.
  3. Short, broadly rounded snout.
  4. Palatine and ectopterygoid relatively short and 'crowded' towards the front of the interpterygoid vacuities.
  5. Very large orbits (> 30% of skull length) centred in anterior half of skull.
  6. Pineal foramen centred level with the rear margins of the orbits.
  7. Tabular horns not strongly projecting; otic notches not deeply incised and widely separated.
  8. Cultriform process relatively broad.
  9. Transverse ridges of parasphenoid directed anteromedially but not contacting medially.
  10. Poorly ossified exoccipitals and quadrates.
  11. Palatoquadrate fissure present.
  12. Occiput deep.
- 

At the end of metamorphosis the capitosaur skull was evidently very different from that of a mature individual (Table 1). In many respects, such as the broad, parabolic skull outline, anteriorly centred orbits, weakly projecting tabular horns, broad cultriform process, and presence of a palatoquadrate fissure, the skull of a juvenile capitosaur resembled that of a mature brachyopoid or trematosaurid (Warren and Black 1985). However, all of these features were lost during subsequent growth, via positive allometry of the antorbital and cheek regions and increased ossification.

The next stages in growth are shown by the *P. aliciae* types (QM F12281–12282), as well as in the smaller individuals of several growth series of *B. sushkini* (Bystrow and Efremov 1940), *Archegosaurus decheni* and *Actinodon latirostris* (Romer 1939), and *Zatrachys serratus* (Steen 1937, as *Acanthostoma vorax*). In these, the proportions are intermediate between the metamorphling and adult, although the skull is well ossified and family characteristics more obvious. Based on the growth series reported for *P. peabodyi* (Welles and Cosgriff 1965), and on the proportions of the small Australian species *P. wadei* (Cosgriff 1972), both described from later in the Triassic than *P. aliciae*, capitosaurids seem to have attained almost adult proportions by a skull length of 60 to 70 mm, although growth proceeded to a much larger adult size (in excess of 250 mm for *P. peabodyi*). Thus by this stage, ossification of the skull was complete, and allometric growth had become much less important. A similar pattern of growth also seems to have been the case for the well-documented *B. sushkini* series described by Bystrow and Efremov (1940). A more recent study of benthosuchid ontogeny (Getmanov 1981) was based on skulls said to belong to two species, *B. korobkovi* and *Thoosuchus jakovlevi*. Getmanov identified two phases of positive allometric growth in these skulls which were of much larger (older?) individuals than the biggest





TEXT-FIG. 11. Diagrammatic drawings of the changes in skull roof proportions seen in the post-metamorphic growth of capitosaurids. A, at metamorphosis; B, juvenile; C, immature; D, adult. Scale bar in all drawings equals 10 mm.

specimen of *P. aliciae*. As Getmanov does not describe the character states by which he identified his specimens as capitosauroids, benthosuchids, or members of their respective genera and species, we are unable to determine whether he was indeed studying a growth series or just a collection of different-sized temnospondyls.

In summary, temnospondyls appear to have gone through four post-metamorphic stages, starting with (1) recently metamorphosed individuals, retaining larval cranial proportions; (2) juveniles, during which allometric growth is pronounced; (3) immatures, in which adult proportions are essentially achieved, grading into (4) adults, in which maximum size is reached. Allometry continues in these last two stages but to a much reduced extent.

Text-fig. 11 shows a series of four generalized early capitosaurid skulls, based on *P. aliciae*, *P. wadei*, and *P. rewanensis*, showing the ontogenetic changes occurring during the post-metamorphic growth of a capitosaur.

The juvenile characteristics of young capitosauroids include several which have been regarded as significant for phylogenetic investigations. Among these are skull outline, anteriorly centred orbits, and palatoquadrate fissure, and these now appear to be the result of paedomorphosis. A change in the timing of the development of a character is a relatively 'simple' evolutionary step (Hecht and Edwards 1977), and therefore more prone to parallel evolution. In addition, character reversal, with the re-establishment of a more developed 'adult' condition, would be expected to be an easily acquired source of confusion. The fact that most Triassic temnospondyl families appear to possess unique mosaics of juvenile and adult character states supports the idea that similar juvenile character states have been independently retained by unrelated lineages. It should, therefore, be clear that such retained juvenile character states are not likely to be sufficient to diagnose monophyletic taxa; rather, they must correlate with a number of other, ideally non-paedomorphic, derived character states before they can contribute to the recognition of natural groups.

#### RELATIONSHIPS OF *P. ALICIAE*

The capitosauroids with the greatest phenetic similarity to *P. aliciae* are the other Early Triassic species. Those which we consider determinable are *P. madagascariensis* (Lehman 1961; Warren and Hutchinson, in press) from Madagascar; the Australian forms *P. wadei* (Cosgriff 1972) and the

two other parotosaurs from the Arcadia Formation, *P. gunganj* Warren 1980 and *P. rewanensis* Warren 1980; the type capitosaurid, *P. nasutus* (Meyer 1858) and the other European species *P. helgolandicus* (Schröder 1913), *P. orientalis* (Otschev 1966), and *P. orenburgensis* (Konzhukova 1965); and the southern African *P. haughtoni* (Broili and Schröder 1937) and *Wetlugasaurus magnus* Watson 1962. These are the more primitive, often deeper skulled capitosaurs with tapering posteriorly directed tabular horns and quadrate condyles aligned behind the level of the occipital condyles. They differ from the similar species usually included in *Wetlugasaurus* (e.g. *W. angustifrons* (Riabinin 1930), *W. samarensis* Sennikov 1981) in having the frontal included in the orbital margin.

*P. aliciae* can be distinguished from all of the early species of *Parotosuchus* using the diagnostic features given earlier, especially the greatly fanned hypertrophied oblique ridge of the pterygoid and the absence of a *crista tabularis externa*. Its skull topography is closest to that of *P. madagascariensis* with which it shares the otherwise unique (for capitosauroids) presence of ectopterygoid tusks. This overall similarity to *P. madagascariensis* may reflect the immature nature of the holotypes of *P. madagascariensis* and *P. aliciae*, but the presence of ectopterygoid tusks is probably not a juvenile feature of capitosauroids as they are absent in the smallest specimens of *B. sushkini* (Bystrow and Efremov 1940).

The relatively broad skull of these two species is found in another small capitosaur, *P. wadei*, from the Early Triassic of the Sydney Basin (Cosgriff 1972). Although *P. wadei* is small, it contrasts with *P. aliciae* and *P. madagascariensis* in that its proportions are essentially adult with small orbits centred well posterior to the mid-point of the skull and closely spaced otic notches. It also differs from *P. aliciae* in having a less abruptly defined *crista falciformis*. Cosgriff (1972) noted that the frontal entered the right orbital margin of the holotype of *P. wadei* but was excluded from the left orbit. We consider this asymmetry unproven as the specimen is not well preserved.

Of the two larger Australian forms, *P. rewanensis* has a markedly heart-shaped anterior palatal vacuity bordered by a V-shaped transvomerine tooth row; in this respect it is similar to *P. madagascariensis* but not to *P. aliciae* which resembles the other Queensland capitosaur, *P. gunganj*, in having a kidney-shaped vacuity and a straight transvomerine tooth row. *P. aliciae* and *P. madagascariensis* share with *P. gunganj* a 'notch' on each side of the parasphenoid lateral to the transverse ridges ('ventral notch' of Warren 1980, figs. 3, 4, 6, 7). This has been illustrated in two other Early Triassic species, *P.* (= *Eryosuchus*) *tverdochlebovi* (*foramen ventrale* of Otschev 1972, fig. 18) and *P. helgolandicus* (Welles and Cosgriff 1965, fig. 24).

*P. aliciae* differs from *P. gunganj* in the shape of the transverse ridges on the parasphenoid. In *P. aliciae* each ridge turns sharply posteriorly leaving a raised median area separating them. In *P. gunganj* and most other capitosaurids these two posterior deflections meet, forming a V. In some capitosaurids, especially the African species, the posterior deflection is lacking so that a single straight ridge runs across the parasphenoid. The only large capitosaurid to have transverse ridges shaped like those of *P. aliciae* is *P. orientalis* which has a skull approximately 470 mm long, indicating that the feature is not a juvenile one.

Among the Australian Early Triassic forms, *P. aliciae* is closest to *P. gunganj*. As the former is small (skull length 39 mm) and the latter much larger (skull length 227 mm) and as both specimens come from the Arcadia Formation, it seems possible that *P. aliciae* is a partly grown *P. gunganj* and that the features which separate them are in fact juvenile characters of *P. aliciae*. However, if we consider these characters as shown by the juvenile to adult series in *B. sushkini* (Bystrow and Efremov 1940), it is apparent that the two Queensland forms are not conspecific. In fact those characters which are larger in *P. aliciae* than in *P. gunganj* (the oblique ridge on the pterygoid and the *crista muscularis* above the occiput) are smaller in the juvenile *B. sushkini* than in the adult. The transparasphenoid ridges of *P. aliciae* do not meet in the mid-line whereas in *P. gunganj* they meet to form a V. In *B. sushkini* they are more widely separated medially in the adult than in the juvenile. Ectopterygoid tusks, present in *P. aliciae* but not *P. gunganj*, are absent from all specimens of *B. sushkini*. It is, therefore, apparent that those characteristics used by us to distinguish *P. aliciae* from *P. gunganj* are not those of juvenile capitosauroids nor are they related to allometric growth.

*Acknowledgements.* We thank our field assistants, in particular Alice Hammerly, Rob Jupp, and Ruth Lane who discovered the site where the *P. aliciae* types and the small juveniles were found. Reg Goodwin of 'Colorado', Bluff, kindly allowed access to his property. Most of the drawings in this paper were painstakingly executed by David Keen. David Walsh (La Trobe University Department of Zoology) took the photographs. We thank Dr Philippe Janvier (Museum Nationale D'Histoire Naturelle, Paris) for casts of the type material of *P. madagascariensis*, and Dr Sam Welles (University of California, Berkeley) for a cast of *P. peabodyi*. Dr Alex Ritchie (Australian Museum, Sydney) loaned us the *P. gunganj* paratype and Dr Max Banks (University of Tasmania, Department of Geology) loaned us some small specimens from Tasmania. Field-work and support for M. N. H. were funded by an Australian Research Grants award to A. A. W. We are grateful to Dr Andrew Milner and an anonymous reviewer for comments on an earlier draft of this paper. Their advice has greatly improved it.

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A. A. WARREN

Department of Zoology  
and

M. N. HUTCHINSON

School of Biological Sciences  
La Trobe University  
Bundoora  
Victoria 3083, Australia

Typescript received 5 May 1987

Revised typescript received 9 December 1987