CHIGUTISAURID TEMNOSPONDYLS FROM THE LATE TRIASSIC OF INDIA AND A REVIEW OF THE FAMILY CHIGUTISAURIDAE

by DHURJATI P. SENGUPTA

ABSTRACT. Two chigutisaurids (Amphibia, Temnospondyli), *Compsocerops cosgriffi* gen. et sp. nov. and *Kuttycephalus triangularis* gen. et. sp. nov., from the Late Triassic Maleri Formation, Pranhita–Godavari valley, Deccan, India are described. In the past, the only known chigutisaurids have been two genera from Australia and probably two from South America. Relationships within the family are analysed and two groups are recognized. They possess marked differences in their palate and dentition. The Late Triassic beds of the Pranhita–Godavari valley exhibit a rapid faunal change. Two faunal zones are present in the Maleri Formation. The age of the lower zone is possibly Late Carnian and the upper is Early Norian. Chigutisaurids are present in the upper faunal zone only.

TWO new taxa of the family Chigutisauridae, a rare group of temnospondyl amphibians, previously known only from South America and Australia, have been recovered from Late Triassic continental red beds of the Maleri Formation of the Pranhita–Godavari valley, Deccan, India (Text-fig. 1). During the last decade or so, the chigutisaurids have attracted the attention of palaeontologists, as they are known to have crossed the Triassic-Jurassic boundary (Warren and Hutchinson 1983). The new taxa from India have been discovered at a juncture when more information is needed to bridge the geographical gap between the South American and the Australian chigutisaurids. Against this background, the new chigutisaurids seem to be of extreme importance.

The appearance of the chigutisaurids in India is accompanied by the disappearance of the metoposaurids and some reptilian forms. The present work suggests that this change possibly indicates the Carnian–Norian faunal turnover. The discovery of the new chigutisaurids thus adds valuable knowledge not only about this group but also about the Indian Late Triassic.

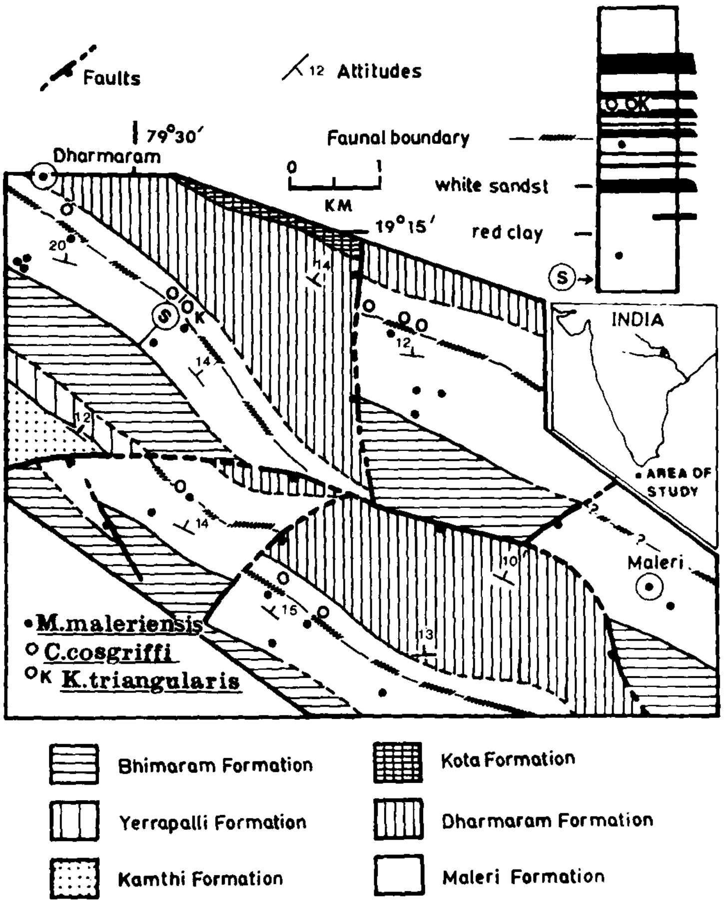
SYSTEMATIC PALAEONTOLOGY

Order TEMNOSPONDYLI Zittel, 1888
Superfamily BRACHYOPOIDEA Säve-Söderbergh, 1935
Family CHIGUTISAURIDAE Rusconi, 1951

Genus COMPSOCEROPS gen. nov.

Derivation of name. From the Greek *compso* (beautiful), *ceros* (horn) and *ops* (face), alluding to an animal with beautiful horns/projections on the skull.

Diagnosis. Large chigutisaurid with parabolic skull, anteriorly placed orbits and a pair of tabular horns; pair of projections present on postparietals, squamosals and quadratojugals; lacrimal absent; pineal foramen anteriorly placed; cultriform process of parasphenoid long and narrow; dentigerous area restricted to anterior region of the skull and lower jaw; complete row of teeth on vomer, palatine and ectopterygoid bones; palatal tooth row separated from marginal row by a



TEXT-FIG. 1. Geological map of area between Dharmaram and Maleri, with significant temnospondyl localities. A schematic section along 'S' is shown at top right. Inset indicates the location of the area studied.

conspicuous groove; dorsal process of clavicle unusually long; pleurocentrum and intercentrum fused in some vertebrae.

Compsocerops cosgriffi sp. nov.

Text-figures 2–14

Derivation of name. The species is named after the late Dr John W. Cosgriff, who first identified as brachyopoids some jaw fragments collected from the Maleri Formation.

Holotype. ISI A 33, an almost complete skull with attached mandibles, in the collection of the Geological Museum of the Indian Statistical Institute (ISI), Calcutta, India.

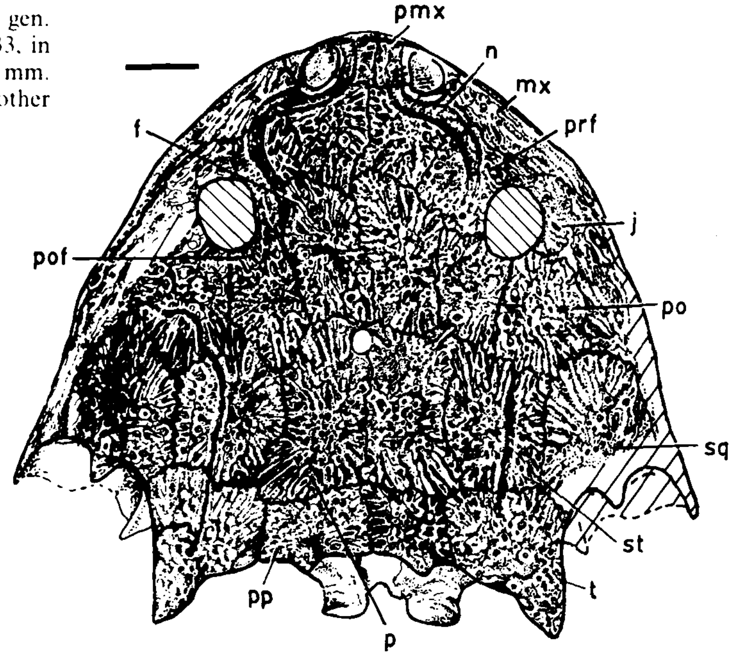
Referred specimens. ISI A 24–27 and ISI A 34–49

Diagnosis. As for the genus.

Horizon and age. All the material described here was collected from the upper part of the Maleri Formation. The type skull was collected from a red clay horizon near Rechni village (Text-fig. 1). An Early Norian age has been assigned to the Upper Maleri fauna in the present work.

Description

Nature of preservation and reconstruction. The type skull is nearly complete with most of the sutures and ornamentation of the skull roof intact (Text-fig. 2). The mandibles were attached to the skull (Text-fig. 3). The



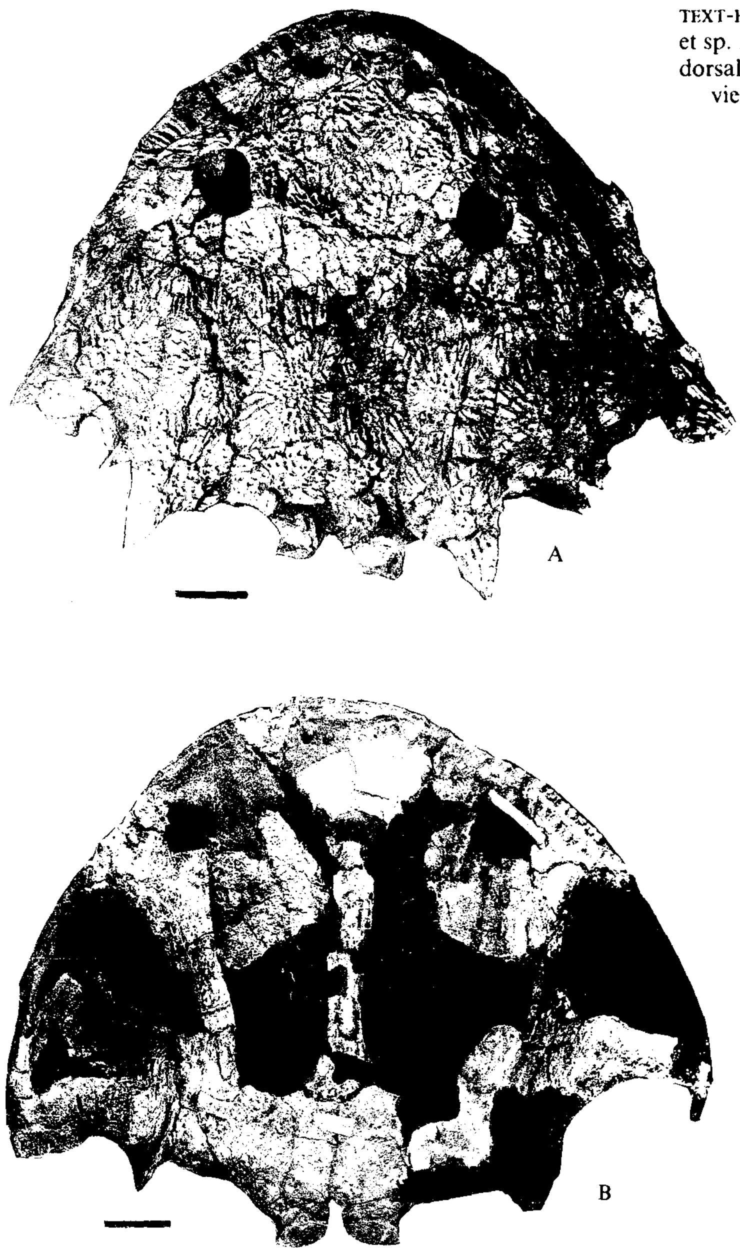
TEXT-FIG. 2. *Compsocerops cosgriffi* gen. et sp. nov. Holotype skull, ISI A 33, in dorsal view. Scale bar represents 50 mm. For abbreviations for this and all other Text-figures, see list on p. 339.

occiput has been flattened. The palate along with the dentition (Text-figs 3–4) is very well preserved in ISI A 34.

A complete left mandible and another fragmentary specimen have been studied, in addition to the mandibles with ISI A 33. A number of postcranial elements have been recovered both from clay and sandstone. Characteristic skull roof bones or vertebrae are always found in association. A list of specimens studied is given in Table 1.

Dorsal surface of the skull (Text-fig. 5). The skull is large and parabolic with conspicuous tabular horns and anteriorly placed dorsolateral orbits. The skull roof is 300 mm long and 400 mm wide with the posterior margin about 170 mm from the rear of the skull roof. A projection is present on the postparietal, squamosal and quadratojugal. The skull is relatively deep (Text-fig. 5B). The skull roof bones show the usual chigutisaurid arrangement. The anterior part of the skull is rounded with the premaxilla at the anteriormost tip. The nasal is broad, expanded anteriorly and strongly ornamented. The frontal is almost rectangular. The parietal is large, rectangular, and shorter than the postparietal. Thicknesses of the bones are at a minimum around the pineal foramen which is relatively anteriorly placed almost at the suture between the parietal and the frontal. The posterior region of the skull is wide and stout and appears to have been the active zone of intensive growth. The tabular horn projects posteriorly. The posterior part of the horn remains unsupported from below as the descending (paroccipital) process of the tabular does not extend posteriorly beneath the horn. The otic notch is marked.

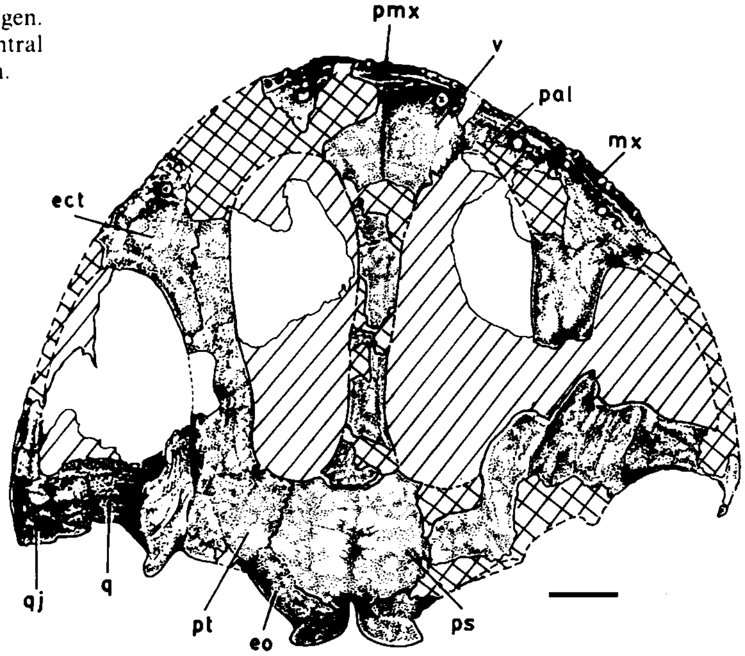
The subcircular orbit is formed by the prefrontal, jugal, postfrontal and postorbital. These bones have fainter sculpturing compared with the posterior skull roof bones. The external naris is elliptical and faces anterodorsally. The unusually deep lateral line canal around the posterolateral border of the naris causes the rim of the naris to be raised except anteriorly, where it is confluent with the skull roof. The rim is conspicuous.



TEXT-FIG. 3. *Compsocerops cosgriffi* gen. et sp. nov. A, holotype skull, ISI A 33, in dorsal view. B, skull, ISI A34, in ventral view. Scale bar represents 50 mm.

The ornamentation on the skull roof has numerous pits at the centre of each bone and radiating ridges near the edges. Narrow U-shaped grooves between the ridges gradually widen towards the periphery of each bone. In places, these ridges bear small uneven pustules. The grooves are very coarse on the tabular horns, while the ridges are longest at the posterior of the quadratojugals.

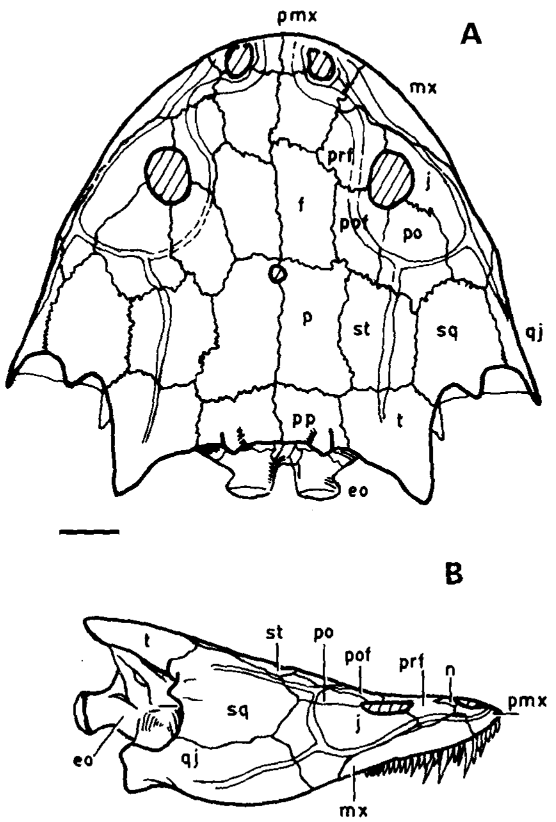
Ventral surface of the skull roof (Text-fig. 6). On the ventral face of the tabular, the descending process starts with a thinning fan of bone which divides the ventral side of the unsupported part of the tabular into two deep



TEXT-FIG. 4. *Compsocerops cosgriffi* gen. et sp. nov. Skull, ISI A 34, in ventral view. Scale bar represents 50 mm.

TABLE 1. List of specimens studied.

Material	Specimen no.
Compsocerops cosgriffi	
Parts of vertebra	ISI A 22
Parts of vertebra	ISI A 24
Right ilium	ISI A 25
An isolated occipital condyle (left) with part of the basal plate of the parasphenoid	ISI A 26
A broken interclavicle	ISI A 27
A complete skull with both mandibles attached	ISI A 33
A mostly complete skull with one side of the palate intact	ISI A 34
Right side of a skull roof	ISI A 35
A complete left mandible	ISI A 36
Left posterior portion of a skull roof with tabular and post-parietal only	ISI A 37
A nearly complete clavicle	ISI A 38
Parts of two vertebrae	
(i) One intercentrum and pleurocentrum fused together	ISI A 39
(ii) One intercentrum	ISI A 40
Parts of humerus	ISI A 41
Parts of neural spines	ISI A 43 to ISI A 49
Kuttycephalus triangularis	
A complete skull with left lower jaw	ISI A 50
Skull fragments	ISI A 51
	ISI A 52

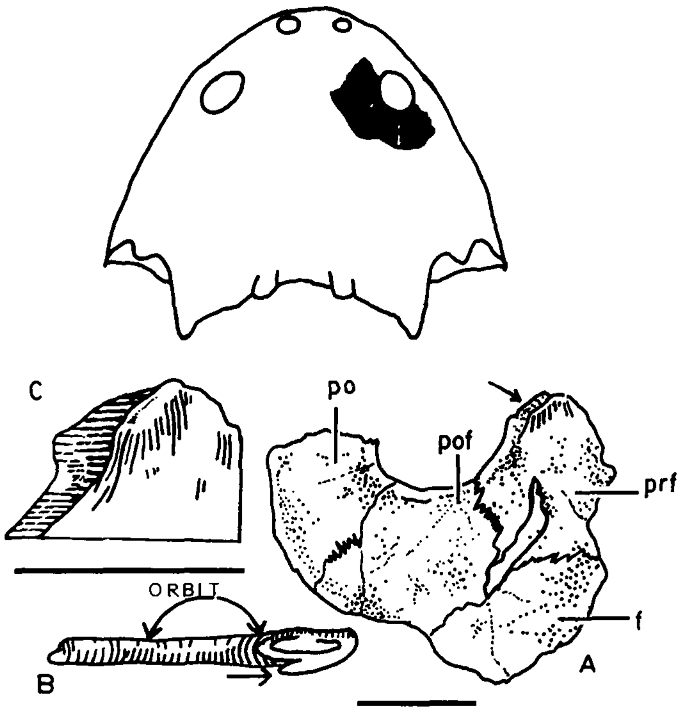


TEXT-FIG. 5. *Compsocerops cosgriffi* gen. et sp. nov. A, reconstruction of the skull in dorsal view. B, reconstruction of the skull in lateral view. Scale bar represents 50 mm.

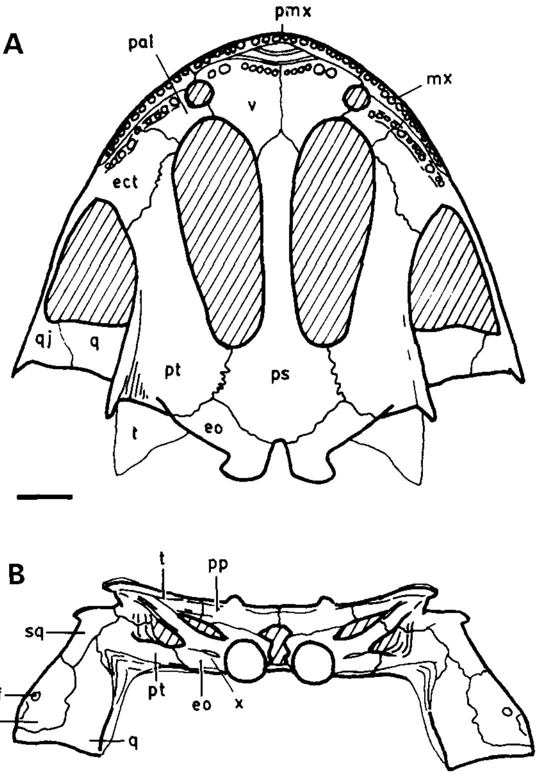
elliptical scars of the internal and external *tabularis*. Beneath the supratemporal, a semicircular ridge of bone may represent the remains of the ascending ramus of the pterygoid. Near the anterior border of the orbit, on the ventral side of the prefrontal, is a small prominence (Text-fig. 6). This type of prominence in this position has not been reported from any other chigutisaurid. It may indicate the presence of a muscular connection between the roof and the more anterior parts of the palate. It is interesting to note that *Benthosuchus sushkini* has a pair of projections, the '*spina lachrymalis*' (Bystrow and Efremov 1940), on the dorsal side of the palatines.

Ventral surface of the palate (Text-fig. 7A). Posteriorly, the palate is essentially a parallel-sided longitudinal vault with a flat roof. The vertical lateral wall of the pterygoid projects posteriorly as far as the occipital condyle with an exceptionally deep development of the pterygoid.

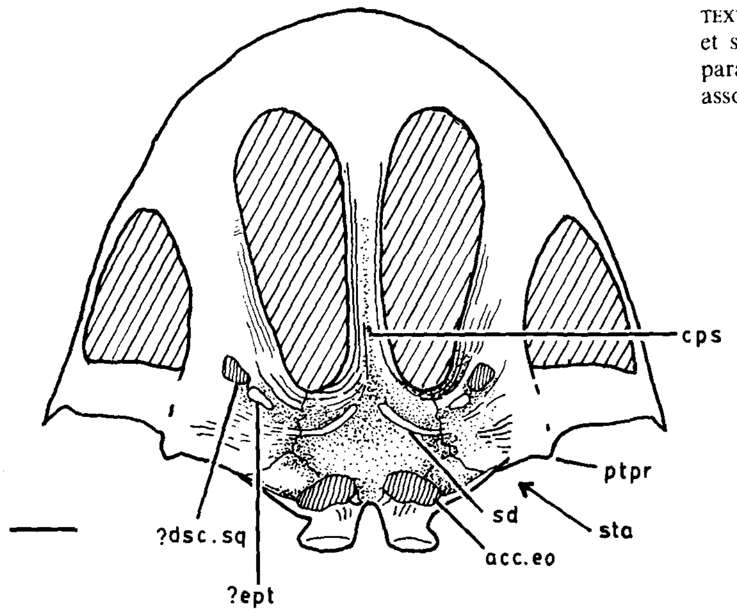
Although the suture is not preserved completely, the posterior parts of the vomers appear to include the anterior tongue of the cultriform process of the parasphenoid, slightly posterior to the level of the anterior borders of the interpterygoid vacuities. The anterior margin of the vomers forms the border of the transversely lenticular anterior palatal vacuity. On the ventral surface of the palate, along the anterior margin of this vacuity, at least two irregular ridges of bone are present. The dentigerous area is restricted to the anterior region of the palate leaving a larger posterior portion, with big subtemporal vacuities, which extends anterior to the centre of the interpterygoid vacuities. The parasphenoid has a large subcircular base and a long and narrow cultriform process with a low ridge-like elevation along its ventral margin at the axis of curvature. The exoccipitals suture with the posterior margin of the body of the parasphenoid. More laterally, the quadrate is exposed between the pterygoid ramus and a flat posterior projection of the quadratojugal. The quadrate condyle is positioned well anterior to the occipital condyle. The quadrate-pterygoid suture is present on the outer side of the downturned wall of the pterygoid.



TEXT-FIG. 6. *Compsocerops cosgriffi* gen. et sp. nov., ISI A 35. Prefrontal prominence in A, ventral view; B, lateral view; C, enlarged. Scale bars represent 50 mm.



TEXT-FIG. 7. *Compsocerops cosgriffi* gen. et sp. nov. A, reconstruction of the skull in ventral view; B, reconstruction of the occiput. Scale bar represents 50 mm.



TEXT-FIG. 8. *Compsocerops cosgriffi* gen. et sp. nov.; ISI A 34; the base of the parasphenoid and the braincase and associated features in dorsal view. Scale bar represents 50 mm.

Dorsal surface of the palate (Text-fig. 8). The cultriform process forms an elongate canal-like depression. This depression gradually flattens on to the basal plate of the parasphenoid as a pair of shallow depressions which fan out symmetrically. They lead to two crescentic canals for the internal carotid arteries within the base of the parasphenoid (Text-fig. 8).

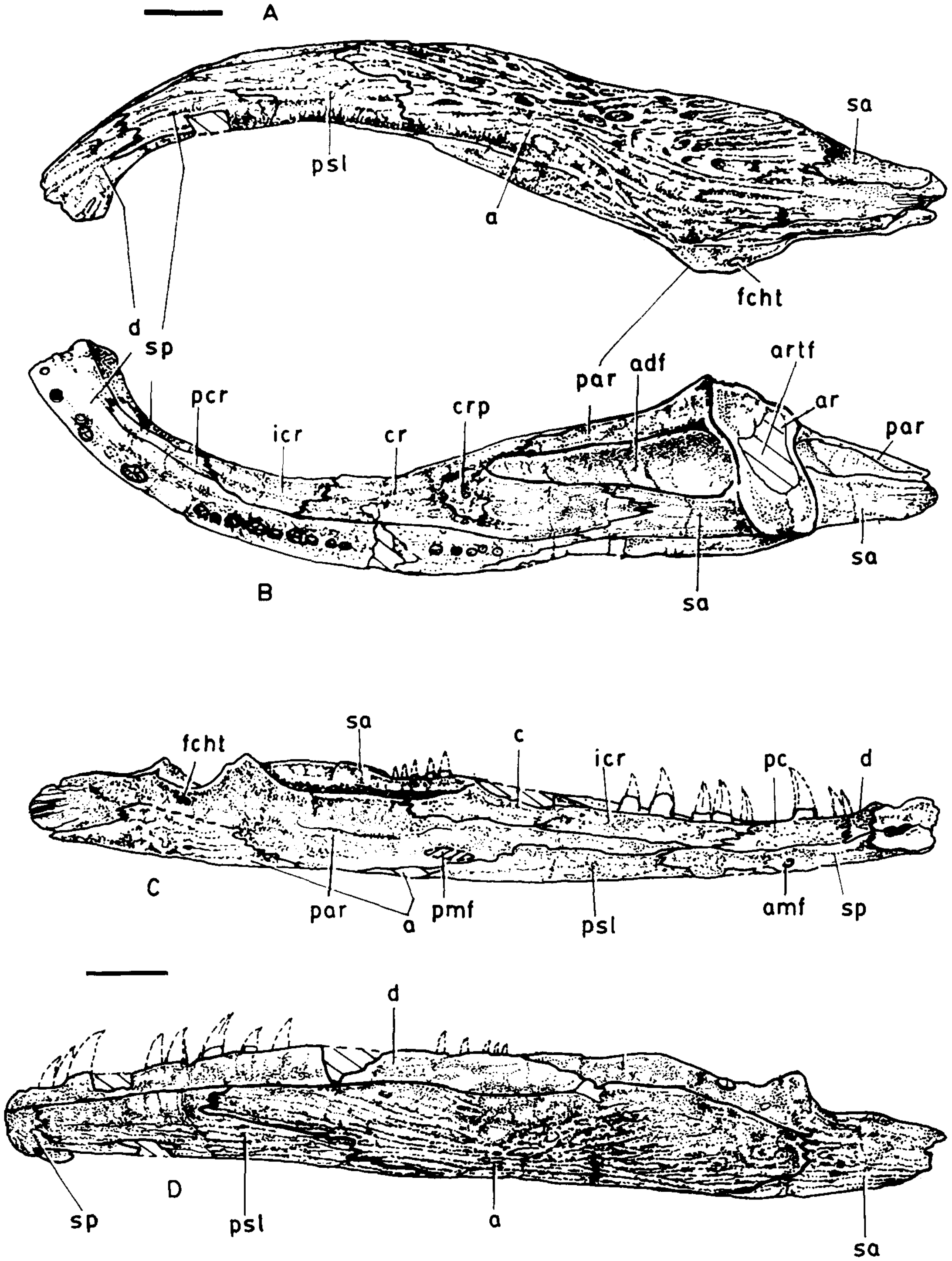
On the dorsal surface of the pterygoid, the base of the ascending process of the pterygoid is preserved. Anterior to this, another lateral canal runs towards the carotid canals. However, it cannot be determined whether an ascending column of the pterygoid (Warren and Hutchinson 1983) was present on the medial margin of this process. It appears that the braincase may have been relatively wide, anteriorly expanded and low.

Occiput (Text-fig. 7B). The occiput is an inverted U-shaped structure with the skull roof and the palate present as a flat table in the middle and flanged by two large squamosal-quadratojugal troughs. The inverted U is formed by the downturned quadrate rami of the pterygoids.

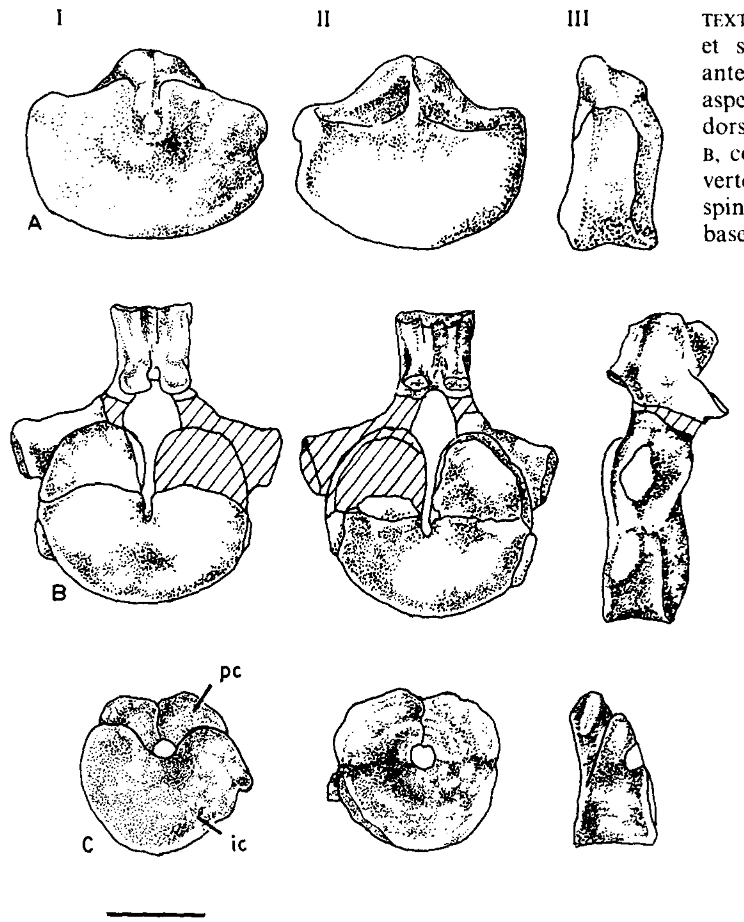
The exoccipitals form the posteriorly directed condyles. They have quite long necks. The columnar part of the ascending process of the exoccipital is flat and inclined, and meets the descending process of the postparietal and the tabular. Ventrally the exoccipital continues up to the pterygoid, forming a plate which is curved inwards. The exoccipital bears a large oval foramen for nerve (x) just at the point where the process of the exoccipital starts ascending. The otic recess is extremely large and so is the otic notch. No stapes is preserved.

At the posterior end, where the quadrate ramus of the pterygoid turns ventrally, a marked posterior projection of the pterygoid is present. Pronounced muscle attachment scars are present on the transverse edge of the postparietal and tabular which are very conspicuous in the occipital view. As mentioned above, a large rectangular trough, formed by the squamosal, quadratojugal and quadrate, is present in *C. cosgriffi*. The trough has its lower part almost infolded, creating a depression at the bottom. This may represent the origin of the *depressor mandibuli* muscle (Welles and Estes 1969). A circular paraquadrate foramen is present on the quadratojugal. The quadrate is seen in occipital view, separating the quadratojugal and the downturned pterygoid. The dorsal part of the quadrate-pterygoid suture extends laterally onto the squamosal-quadratojugal trough, whereas more ventrally this suture runs down the medial wall of the trough.

Mandible (Text-fig. 9A–D). The mandible has the characteristic chigutisaurid shape, as described by Jupp and Warren (1986). In cross-section it is elliptical with a flat top. The dentition is restricted to the anterior half. The ornamentation in the posterior part consists essentially of large elliptical grooves walled by coarse ridges.



TEXT-FIG. 9. *Compsocerops cosgriffi* gen. et. sp. nov., ISI A 36, left mandible in A, ventral view; B, dorsal view; C, lingual view; D, labial view. Scale bars represent 50 mm.



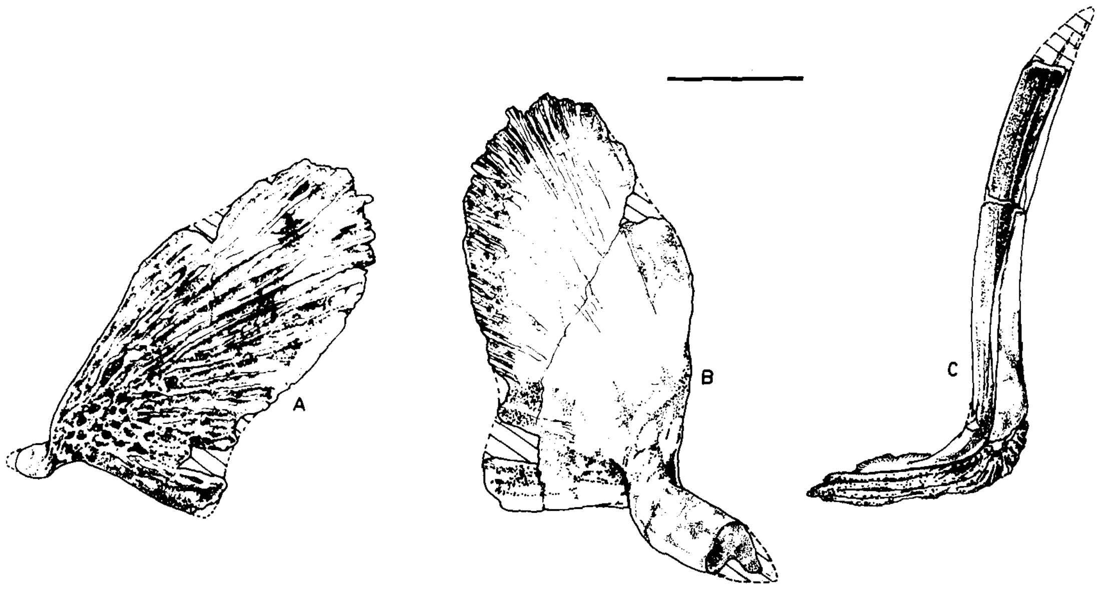
TEXT-FIG. 10. *Compsocerops cosgriffi* gen. et sp. nov. Presacral vertebrae in I, anterior, II, posterior and III, left lateral aspects. A, parts of pseudostereospondyl dorsal vertebra as preserved in ISI A 39. B, composite reconstruction of a dorsal vertebra based on ISI A 43–47 (neural spine) and ISI A 24 (centra). C, axis based on ISI A 22. Scale bar represents 50 mm.

Anteriorly, the ornament consists of anastomosing ridges on the splenial and postsplenial. The articular is exposed on the dorsal surface of the postglenoid area as a triangular bone between the surangular and the prearticular. The posteriormost part of the postglenoid area is pointed but without any marked retroarticular process. Lingually, a small foramen, possibly for the *chorda tympani*, is present in the prearticular. Two openings for the anterior meckelian foramen and a third, opening a little anterior to it, are visible in the splenial. Three coronoids also appear on the lingual surface and a conspicuous coronoid process is present at the posterior coronoid. Dorsally, the dentary has a thin posterior extension. It increases in width anteriorly. The large adductor fossa is pointed near its anterior tip. The articular fossa is bilobed. The symphysis is formed largely by the dentary, with a small ventral inclusion of the anterior splenial.

In the upper jaw, two tooth rows, marginal and palatal are embedded in narrow ridges with a narrow groove in between them. This groove is prominent at the ectopterygoid-maxillary junction. In the maxillary row, the teeth are larger anteriorly and are of uniform shape. All the teeth, including the tusks, are curved lingually. The curvature is probably maximal near the tip.

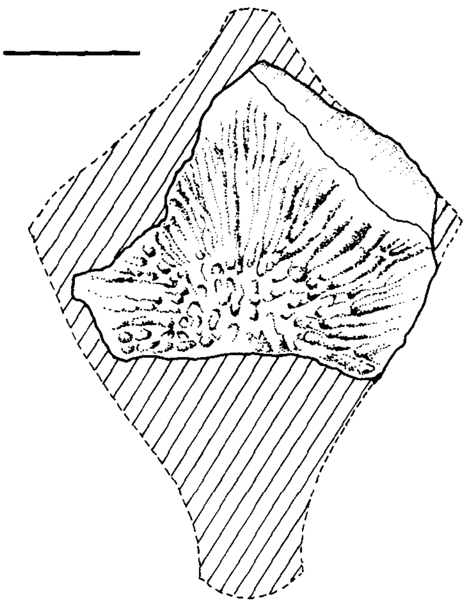
Dentition. A single row of teeth is present in the anterior half of the mandible. No symphysial row is preserved. An indication that a large tusk pit is present near the mandibular symphysis is seen in one specimen, but not in another. The teeth are largest midway along each ramus. At the ectopterygoid-palatine contact, the bite may have been most severe with larger teeth located there. Sixty-four teeth are estimated to have been present in the mandible of ISI A 33.

Vertebrae (Text-fig. 10A–C). All the vertebral elements collected are presacral, but their exact position is difficult to determine. In at least one element, the pleurocentra are fused with the intercentrum to give a pseudo-stereospondyl appearance (Text-fig. 10C). From anterior to posterior the convexity of the intercentra decreases. The pleurocentra are two symmetrical, small, roughly spindle-shaped, bones. Possibly they met to form the floor of the neural canal. Anteriorly, they are fused with the intercentrum, so that a notochordal canal is formed near the centre of each vertebral unit. The canal is U-shaped, with the long arm in the axis, and becomes circular posteriorly. The pleurocentra also become curved posteriorly and, while joined with crescentic intercentra, they become almost spool-shaped. This type of vertebra is known only from a few vertebral elements of *Metoposaurus ouazzoui* and, to some extent, in the entire vertebral column of the almasaurids (Dutuit 1976). The former vertebrae resemble those of *C. cosgriffi*, but the latter look different. The axis is rectangular in shape. It appears that, more posteriorly, the intercentra become heart-shaped. All of them have strong parapophyses. The neural arch is small and blunt. The neural spines are thick, moderately high, and have two symmetrically disposed posterior and anterior zygapophyses. The anterior side of each spine is marked by two thin symmetrical ridges. The neural arches appear to have been intervertebrally placed.

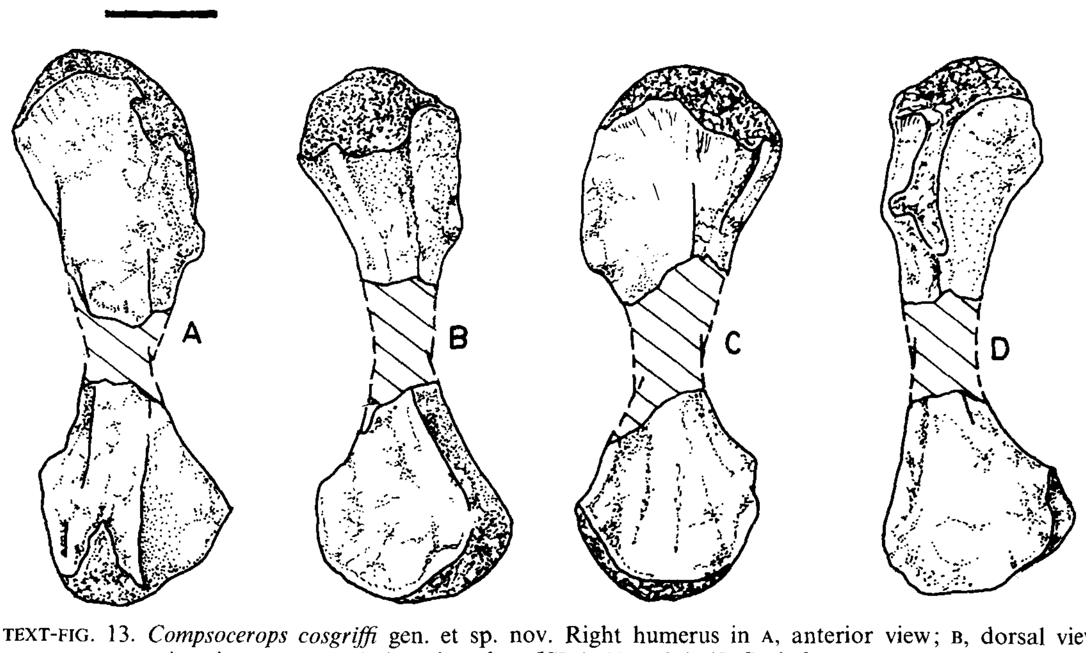


TEXT-FIG. 11. *Compsocerops cosgriffi* gen. et sp. nov. ISI A 38, right clavicle in A, ventral view; B, dorsal view; C, posterior view. Scale bar represents 50 mm.

Appendicular skeleton (Text-figs 11–14). The preserved appendicular elements of *Compsocerops* resemble their counterparts in *Siderops*. The clavicle bears an unusually long cleithral process which begins abruptly and becomes narrow dorsally (Text-fig. 11A–C). Posteriorly, the process is deeply grooved for the cleithrum. The groove continues onto the flat plate of the clavicle where it dies out. The incomplete interclavicle has been reconstructed as a diamond-shaped plate (Text-fig. 12). The clavicle and the interclavicle are very similar to those of *Siderops*. The humerus is also slender and lacks extensive projections. The angle of torsion is almost 90 degrees (Text-fig. 13A–D). The distal articulation is rounded and knob-like in the ectepicondylar region. This was probably the area for the insertion of muscles like the *trochlea* and *capitellum*. The entepicondylar side is somewhat flattened. Both condyles are sharp and pointed. The ectepicondyle merges with the supinator process. There is also a well developed furrow for the supinator muscle. The proximal articulation is thinner on the deltopectoral side. The deltopectoral crest is relatively blunt. The area of attachment of the *pectoralis*

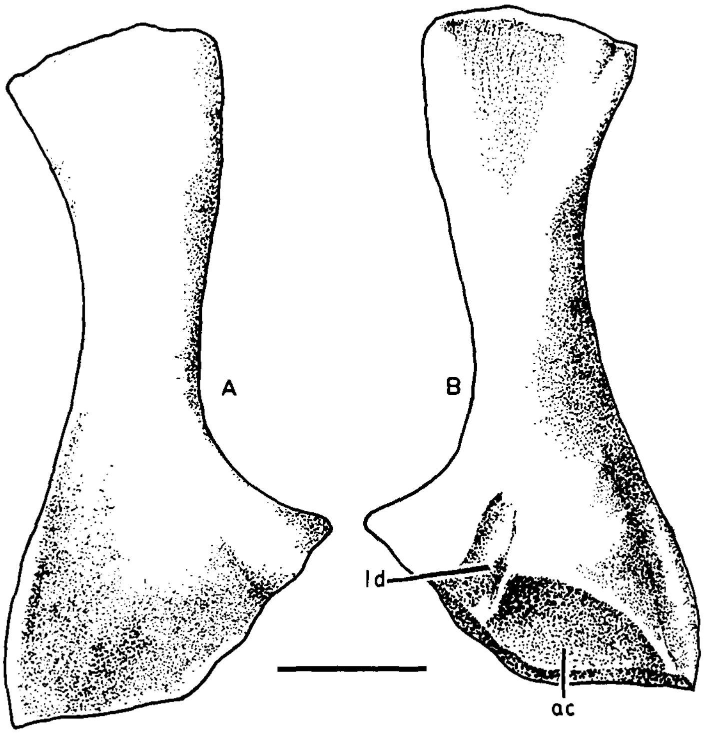


TEXT-FIG. 12. *Compsocerops cosgriffi* gen. et sp. nov. ISI A 27, interclavicle in ventral view. Scale bar represents 50 mm.

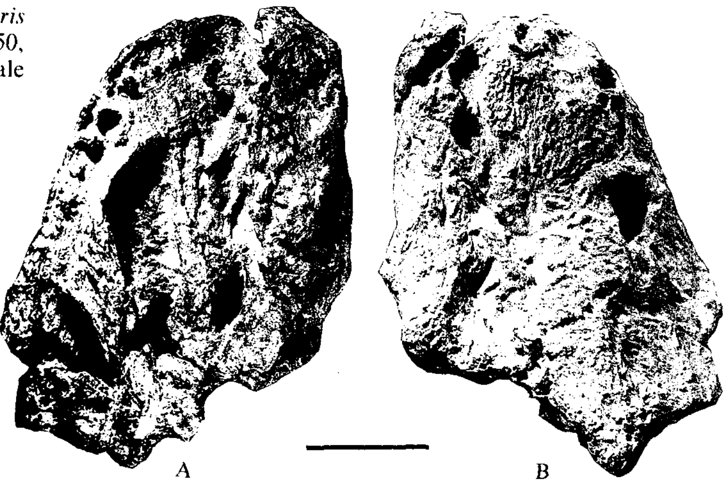


TEXT-FIG. 13. *Compsocerops cosgriffi* gen. et sp. nov. Right humerus in A, anterior view; B, dorsal view; C, posterior view; D, ventral view; based on ISI A 41 and A 42. Scale bar represents 50 mm.

muscle is very distinct as are the attachments for the deltoid muscle. Attachment for the medial head of the *triceps* is also very prominent. The ilium is thin and elongate with prominent ridges dorsally on the external surface (Text-fig. 14A–B). Deep furrows are present on both sides of the dorsal edge of the acetabulum. The acetabulum is a comparatively large knob-like structure with a deep fossa.



TEXT-FIG. 14. *Compsocerops cosgriffi* gen. et sp. nov., ISI A 25, right ilium in A, medial view; B, lateral view. Scale bar represents 50 mm.

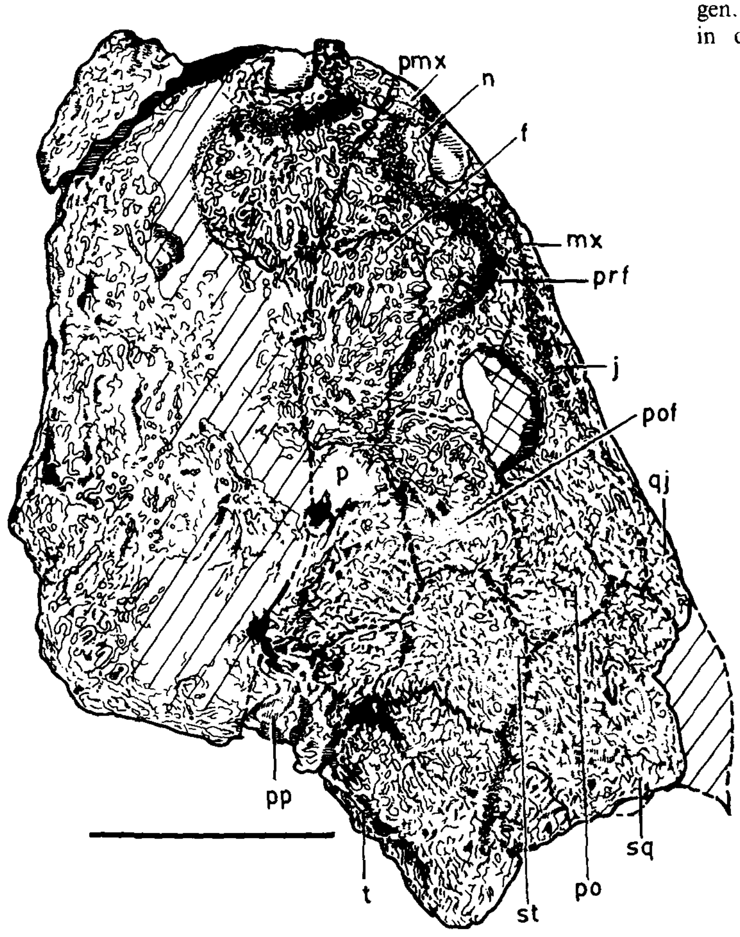


TEXT-FIG. 15. *Kuttycephalus triangularis* gen. et sp. nov., holotype skull, ISI A 50, in A, ventral view; B, dorsal view. Scale bar represents 50 mm.

Genus KUTTYCEPHALUS gen. nov.

Derivation of name. The genus is named after Mr T. S. Kutty of the Geological Studies Unit, Indian Statistical Institute, who discovered most of the material, including the skull.

Diagnosis. Chigutisaurid with relatively triangular skull and fine, reticulate ornamentation; pair of projections on the squamosals and quadratojugals together with tabular horns; postparietal



TEXT-FIG. 16. *Kuttycephalus triangularis* gen. et sp. nov., holotype skull, ISI A 50, in dorsal view. Scale bar represents 50 mm.

projections are absent; dentigerous area of the upper jaw and palate extends to the posterior half of the skull; cultriform process of the parasphenoid broad; anterior tip of the subtemporal vacuity not reaching level of centre of interptergyoid vacuities; numerous small marginal teeth present.

Kuttycephalus triangularis sp. nov.

Text-figures 15–18

Derivation of name. The specific name highlights the triangular shape of the skull.

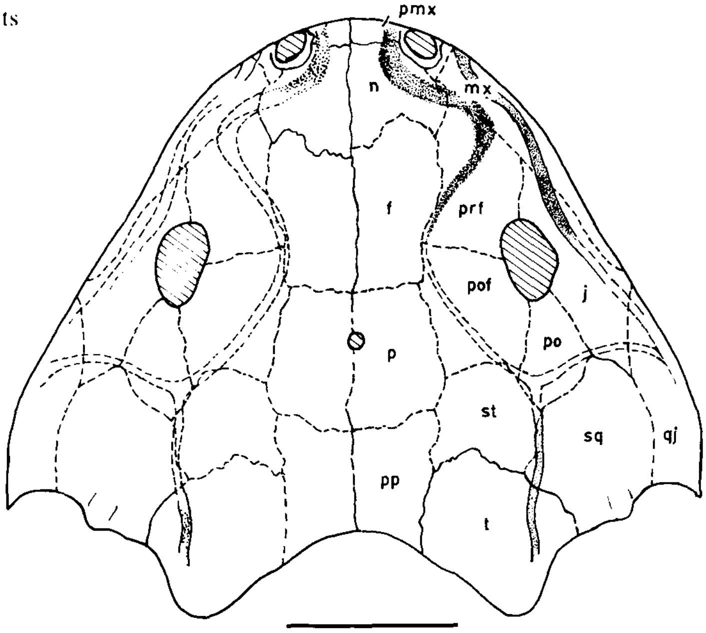
Holotype. ISI A 50. A complete skull with left lower jaw in the collection of the Geological Museum of the Indian Statistical Institute, Calcutta, India.

Referred specimens. ISI A 51, 52.

Diagnosis. As for genus.

Horizon and Age. A surface find from a clay bed in the upper part of the Maleri Formation, assigned to the Early Norian.

Description of the skull (Text-figs 15-18). The nearly complete skull is distorted and had calcareous encrustation on the bone surface. The left mandible is attached to the skull (Text-figs 17-18). Part of the left side of the skull, along with the mandible, is strongly infolded and rides over the palate. The left side of the skull is more complete.



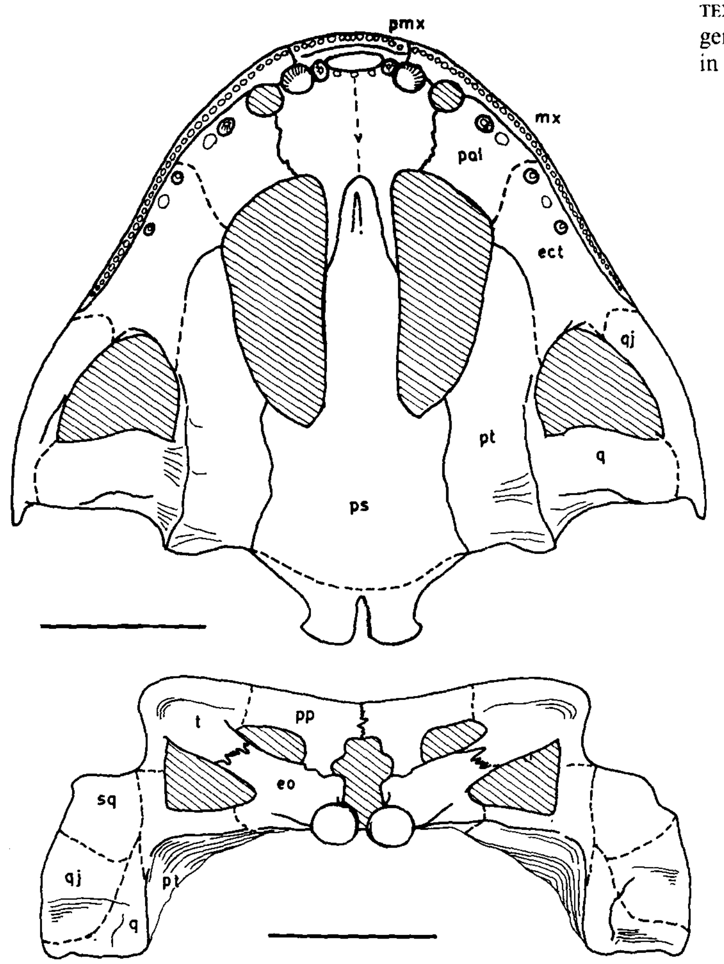
TEXT-FIG. 17. *Kuttycephalus triangularis* gen. et sp. nov. Reconstruction of skull in dorsal view. Scale bar represents 50 mm.

It appears that the skull was distorted by forces acting in more than one direction. The skull roof appears to be shorter and narrower than in other chigutisaurids and, in this, it bears resemblance to a rhytidosteid skull. The skull is 145 mm long and nearly 220 mm wide. The reconstructions of the skull roof, palate and occiput are shown in Text-figures 17-18. The skull shows the usual chigutisaurid bone arrangement. The tabular has a stout large unsupported horn typical of the chigutisaurids. The ornament of *K. triangularis* is composed of fine ridges and wide grooves branching out rapidly in a reticulate pattern. The ridges are markedly thin (less than 0·5 mm in places). The tabular horns and the quadratojugal and squamosal projections look similar to those observed in *C. cosgriffi*. The parietal foramen is more anterior than in other chigutisaurids except *C. cosgriffi*. The border of the naris stands out as a conspicuous rim, as in *C. cosgriffi*. The lacrimal appears to be absent. The postparietal projections are absent. The pterygoid is vaulted as in other chigutisaurids. The vaulting begins more posteriorly than in *C. cosgriffi*.

The cultriform process of the parasphenoid is wider than other chigutisaurids. In ISI A 50 the process is partly folded, the original width having been greater. The anterior tip of the process extends anterior to the interpterygoid vacuities, and becomes spatulate at the anterior end which is enclosed by the vomers. Unlike the situation in *C. cosgriffi*, the anterior palatal vacuity is a single elliptical depression. The anterior tip of the subtemporal vacuity does not extend forward beyond the central portion of the interpterygoid vacuity.

The upper jaw is characterized by numerous, small, uniform marginal teeth which extend posterior to the centre of the interpterygoid vacuity. The palatal tusks and tusk pits are marked. Thus, unlike *C. cosgriffi*, no tooth row is present on the palatine and ectopterygoid apart from the tusks. The vomer bears a pair of tusks and tusk pits along with three other smaller teeth at the border of the posterior edge of the anterior palatal vacuity. The tusk pits are shallow, large and circular. The palatine and ectopterygoid also bear smaller tusks.

The occiput is typically chigutisaurid with deep vaulting of the palate, and the quadratojugal–squamosal flange opens up into a wide trough on two sides. The quadrate ramus of the pterygoid in the angle between



TEXT-FIG. 18. *Kuttycephalus triangularis* gen. et sp. nov. Reconstruction of skull in ventral view and occipital view. Scale bars represent 50 mm.

its horizontal and vertical portion forms a sharp pointed posterior projection as in *C. cosgriffi*. The ascending ramus of the pterygoid is not very well preserved. The otic recess is large.

DISCUSSION

The family Chigutisauridae

The family Chigutisauridae was erected by Rusconi (1951) to include several short-faced Triassic temnospondyls from Argentina. The first chigutisaurid, *Pelorocephalus mendozensis*, was described by Cabrera (1944) from the upper part of the Cacheuta Formation. It was initially placed in the Family Brachyopidae by Romer (1947, 1966). However, Welles and Estes (1969) excluded *Pelorocephalus* from the family Brachyopidae revalidating the distinctiveness of the chigutisaurids. Rusconi (1948) described another chigutisaurid, *Chigutisaurus tunuyanensis*. Subsequently he also described *C. tenax* (Rusconi 1949) and *C. cacheutensis* (Rusconi 1953) as well as a number of other genera and species (see Rusconi 1950, 1951). Bonaparte (1975) recognized another species from the Ischigualasto Formation (Late Triassic) of Argentina and named it *P. ischigualastensis*. Later, Bonaparte (1978) synonymized all Argentinian chigutisaurids with *P. mendozensis*. Recently

Marsicano (1993) has undertaken a revision of the Argentinian chigutisaurids and recognized the presence of more than one taxon. However, the present discussion is based on the assumption that there are two valid genera of Argentinian chigutisaurids, *Pelorocephalus* and *Chigutisaurus*.

Warren (1981) described a chigutisaurid *Keratobrachyops australis* from the Arcadia Formation (Early Triassic) of the Rewan Group of Australia. Subsequently Warren and Hutchinson (1983) described another large chigutisaurid, *Siderops kehli*, from the Evergreen Formation (Early Jurassic) of south-west Queensland, Australia.

Chigutisaurids have been considered as active predators and agile swimmers by Cosgriff (1984). DeFauw (1989) considered chigutisaurids as semiaquatic forms. Warren and Hutchinson (1983) defined the chigutisaurids as having a parabolic skull with anteriorly placed orbits, a deeply vaulted palate, a pair of occipital condyles positioned much posterior to the quadrate condyles, a complete inner row of palatal teeth, an ascending column of the ptergyoid and a pair of tabular horns. The lacrimal is absent.

Relationships within the Chigutisauridae

The following discussion is intended to bring out some salient features of the two new chigutisaurid genera and species erected in the present work. The characters chosen for detailed analysis are those which have been thought to distinguish chigutisaurid genera. Some of them are argued to be derived and shared by different chigutisaurids, while a few characters, treated as significant by Coldiron (1978) and Warren and Hutchinson (1983), are also discussed. Several projections of the skull roof seem to be of particular systematic value and are discussed first.

Tabular horn. Chigutisaurids are distinguished from brachyopids by the presence of a tabular horn and a deep otic notch. Brachyopids, plagiosaurids and some members of the Rhytidosteidae lack tabular horns, and usually possess a small horn with a shallow otic notch. Warren and Black (1985) noticed that, in the 'Capitosaurians', the otic notch is usually deeply incised almost always with a tabular horn. In this group, the tabular horns are always supported from below but in the chigutisaurids they are not similarly supported. The tabular horn is present in almost all chigutisaurids. It is partly preserved in *Keratobrachyops* (Warren 1981) but not preserved in *Siderops* (Warren and Hutchinson 1983). The tabular horn and the posterior part of the skull, consisting of the tabular and the postparietal, are similar in the Argentinian and Indian genera in many respects. Their postparietal and tabular form a flat bony plate which projects out from the squamosal. The deep otic embayment is responsible for this. The lateral side of the tabular horn is long and straight running parallel to the midline. The tip of the tabular horn is always pointed in the Argentinian and Indian genera. The posterior margin of the plate, formed by tabular and postparietal, is concave anteriorly. *Keratobrachyops* also has the latter character. The angle of the horn with the skull margin, the nature of the posterior boundary of tabular and postparietal and also the shape of the otic embayment of *Siderops* were probably like other chigutisaurids, rather as reconstructed by Warren and Hutchinson (1983).

Postparietal projection. As already mentioned, *Compsocerops* is characterized by a postparietal projection. This is a narrow, symmetrical, elongate ridge with pointed ends, concave towards the midline and extending a little beyond the posterior margin of the skull roof. The functional significance of this projection is not clear. Somewhat irregular dermal projections are also present in the zatrachydids. They also have a raised ridge at the posterior mid-skull (Langston 1953). *Acanthostomatops vorax*, considered to be the most primitive zatrachydid, has no postparietal projections. Other members of the family Zatrachydidae have them, and hence the origin of those projections is thought to be within this family (Boy 1989). *Keratobrachyops* and the Argentinian forms do not have this projection (though Bonaparte's 1975 reconstruction of *Pelorocephalus ischigualastensis* depicts a depressed area in the posterior part of the skull at the midline flanged by two raised portions of the postparietal bones). Shishkin (1987) also mentioned that all chigutisaurids have postparietal projections. However, the postparietal horn is absent in *Kuttycephalus*. Outside the Chigutisauridae, postparietal lappets are known in *Cochleosaurus* (Steen 1938; Rieppel 1980) and have also been reported by Warren (pers. comm.) in *Parotosuchus rewanensis* (a capitosaurid) and in two rhytidosteids (*Arcadia myriadens*; Warren and Black 1985; and in an undescribed juvenile). Rieppel (1980) differentiated *Cochleosaurus florensis* from *C. bohemicus* by the size of the postparietal lappets. In the present work the postparietal projection is noted as a derived character in *Compsocerops cosgriffi* (as the size, shape and position of the horn is different from that present in the zatrachydiids, *Cochleosaurus* or in other Australian temnospondyls) and is used here as an autapomorphy (*sensu* Eldredge and Cracraft 1980) for the genus. Steen (1938, fig. 32) noticed that the postparietal lappets of *Cochleosaurus* show allometric growth during ontogeny. *Compsocerops*, however, does not display this. In the present work no taxonomic significance, above generic level, has been assigned to the postparietal projections.

Squamosal projection. A squamosal projection is present in *Compsocerops*, *Kuttycephalus*, *Pelorocephalus* and *Chigutisaurus*. The former two genera have spatulate, blunt projections at the posterior border of the squamosal. In *Compsocerops*, the projection is more conspicuous than in *Kuttycephalus* and is present in all individuals where the squamosal is preserved. The squamosal projection in *Compsocerops* does not show any definite pattern of growth.

The squamosal projection has not been observed in any other Triassic temnospondyls. It is not present in zatrachydids. This is basically a chigutisaurid character though not present in *Keratobrachyops*. It is not preserved in *Siderops*.

Quadratojugal projection. A quadratojugal projection is present in the Indian and Argentinian genera. In *Siderops* this region is not preserved. *Keratobrachyops* does not have any quadratojugal projection. The quadratojugal projection is most conspicuous in *Chigutisaurus* and *Compsocerops*. At the posteriormost tip of the quadratojugal, a squarish lappet, with coarse ridges, projects out posteriorly in the latter genus from the squamosal-quadratojugal trough. This projection is also visible in *Kuttycephalus*.

Dentition. The basic dentition is similar in all chigutisaurid genera. A row of small marginal teeth and another row of palatal teeth are present in all genera. A similar sized double row of teeth aligned in parallel is present in the maxilla-ectopterygoid of *Compsocerops* and *Siderops*. In *Pelorocephalus*, *Keratobrachyops*, *Kuttycephalus* and in the various species of *Chigutisaurus*, the double row is present but they are not parallel. Nor are the maxillary and ectopterygoid teeth embedded in narrow ridges as they are in *Compsocerops* and *Siderops*. This character is used here as an apomorphy linking these two genera. In *Siderops* and *Compsocerops* the dentition of the palate and the upper jaw is restricted to the anterior half of the skull. In *Pelorocephalus*, the dentigerous area of the upper jaw and palate is positioned further anteriorly. In the lower jaw, the teeth are usually larger and curved lingually.

Mandible. The features of the mandible of *Compsocerops*, as discussed earlier, confirm Jupp and Warren's (1986) character assignments for previously known chigutisaurid mandibles. In all chigutisaurids, the adductor fossa is large and deep while the articular fossa is shallow, feebly bilobed and lingually widening. The postglenoid ridge is not very high in any chigutisaurid. The postglenoid area is relatively longer in all chigutisaurids though the ratio of the total mandibular length and the length of the postglenoid area may vary from genus to genus. This ratio is highest in *Chigutisaurus tunuyanensis* (2·8) and lowest in *Siderops kehli* (1·5). In *Compsocerops cosgriffi* the ratio is 1·8 and in *Keratobrachyops australis* it is 1·76. A distinct coronoid process is present in the lower jaw of *Compsocerops* as well as in *Siderops* and *Keratobrachyops*. Following Warren and Hutchinson (1983), this is thought to be a derived character.

Cultriform process of the parasphenoid. The width of the cultriform process of the parasphenoid was taken as an important apomorphy by Coldiron (1978) for some temnospondyls. This process is generally believed to be narrower in the chigutisaurids. Among the Indian forms, *Kuttycephalus* has a wide cultriform process similar to that of *Keratobrachyops*. Warren and Hutchinson (1983) noted that only *Keratobrachyops* has the anterior border of the interpterygoid vacuities placed posterior to the anteriormost tip of the cultriform processes among all the chigutisaurids. *Kuttycephalus* has this character and it also shows the inverted 'V'-like grooves running parallel to the vomer-parasphenoid suture as in *Keratobrachyops*. The comparatively narrow cultriform processes of *Siderops*, *Compsocerops* and *Pelorocephalus* are similar on the other hand. The position of the suture between vomer and parasphenoid, as present in *Keratobrachyops* and *Kuttycephalus*, is considered in the present work to be a derived character. The wide cultriform process of *Kuttycephalus* and *Keratobrachyops* is also used in the phylogenetic reconstruction.

Palatal vacuities. Two major palatal vacuities, the subtemporal vacuity and the interpterygoid vacuity, vary both in shape and size among the chigutisaurid genera. The subtemporal vacuity in *Keratobrachyops*, *Chigutisaurus* and *Kuttycephalus* is less than half of the length of the interpterygoid vacuity. *Compsocerops*, *Siderops* and *Pelorocephalus* have subtemporal vacuities with anterior tips extending beyond the centre of the interpterygoid vacuity. This is considered here to be a derived character.

Postcranial elements. Postcranial elements are known only in *Siderops*, *Compsocerops* and *Chigutisaurus*. The clavicle-interclavicle complex and the humerus of the first two are very similar. *Compsocerops* has fused inter- and pleurocentrum to give the vertebrae a pseudostereospondyl appearance. This is unique within the family. The long dorsal process of the clavicle is a derived character, shared by *Compsocerops* and *Siderops*.

There are some other characters which have either been thought by earlier authors as important for construction of relationships or show some variations. These characters are discussed below. The polarities of some of these characters are uncertain.

Parietal–postparietal ratio. Triassic temnospondyls commonly have the postparietal shorter than the parietal. Metoposaurids, brachyopids, rhytidosteids, capitosaurids and plagiosaurids all have shorter postparietals. Warren and Hutchinson (1983) claimed that this condition prevailed in *Keratobrachyops* and *Siderops* but not in *Pelorocephalus*. *Compsocerops* and *Kuttycephalus* also have shorter postparietals. There is no clear indication in Warren and Hutchinson's work whether the postparietal of *Pelorocephalus* is equal to its parietal or longer. All available drawings and photographs of *Chigutisaurus* and *Pelorocephalus* show that the parietal is roughly equal in length to the postparietal. Warren and Hutchinson's cladogram, however, depends heavily on the parietal–postparietal ratio for splitting the Australian and Argentinian genera.

Anterior palatal vacuity. The shape and size of the anterior palatal vacuity vary widely among chigutisaurids. Coldiron (1978) used the bilobed anterior palatal vacuity as an apomorphy. He considered the single lobed anterior palatal vacuity of the brachyopids as a primitive condition or a secondary development for that group. Chigutisaurids also have an unpaired anterior palatal vacuity. The type of *Pelorocephalus* (Cabrera 1944) shows a feebly bipartite anterior palatal vacuity (see Bonaparte 1978). The presence of two deeper depressions at two ends gives rise to this type of structure which is visible also in *Kuttycephalus*. The anterior palatal vacuity of *Compsocerops* is a complicated structure with ridges and grooves running parallel to both anterior and posterior borders of the vacuity. The shape of the vacuity in *Compsocerops* is also lenticular.

Ornamentation. The ornament of *Compsocerops* and *Siderops* is strikingly similar. Both have circular pits present at the centre of ossification and elongate ridges radiating away from the centre. There are grooves between two ridges which widen towards the margin of the bones. The ridges anastomose locally. The ridges do not have symmetrical cross sections. *Kuttycephalus*, in contrast, has finer straight ridges with close reticulations. This type of ornamentation resembles that in

TABLE 2. Derived characters used to construct the relationships of the chigutisaurid genera (Text-fig. 19); characters 1 to 11 after Warren and Hutchinson (1983).

(1) Short, broad, parabolic skull
(2) Zones of intensive growth in cheek region only
(3) Lacrimal absent
(4) Basicranial joint firmly sutured
(5) Pterygoid with a deep vertical ventrally-directed plate forming an inverted 'U'-shaped palate; quadrate condyles well below the level of the occipital condyles
(6) Squamosal-quadratojugal trough lateral to occiput
(7) Retroarticular process long
(8) Posterior meckelian foramen and angular-prearticular suture on the ventral surface or very low on lingual surface of lower jaw
(9) Articular exposed on dorsal surface of the retroarticular process
(10) Quadrate condyles anterior to the occipital condyles
(11) Ascending column of pterygoid present
(12) Complete row of small marginal palatal teeth present
(13) Suture between the cultriform process of the parasphenoid and the vomer situated anterior to the anterior borders of the interpterygoid vacuities
(14) Paraquadrate foramen on the quadrate-quadratojugal suture
(15) The ratio of maximum palatal width to that of the cultriform process of the parasphenoid very low (10·50)
(16) Presence of tabular horns and squamosal and quadratojugal projections in the posterior part of the skull
(17) Cultriform process of the parasphenoid long, narrow
(18) The anterior tip of the subtemporal vacuity positioned anterior to the centre of interpterygoid vacuity
(19) A similar-sized double row of teeth embedded on narrow ridges particularly in the ectopterygoid-maxilla
(20) Lower jaw with coronoid process
(21) Exceptionally long dorsal process of the clavicle
(22) Presence of a pair of projections on the postparietals
(23) Posteriorly placed pineal foramen

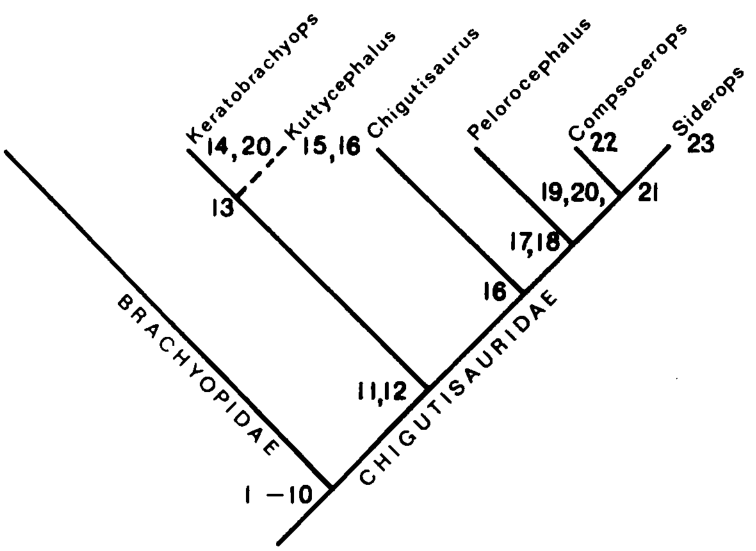
Keratobrachyops (Warren 1981). The ornamentation of *Chigutisaurus* appears to be similar to the *Kuttycephalus-Keratobrachyops* type. The ornament of the Argentinian chigutisaurids, however, has not been described adequately.

Vomerine pit and shagreen. Only *Siderops* has a vomerine pit. *Chigutisaurus tenax* also has a vomerine shagreen (Rusconi 1951).

Quadrate condyles. Quadrate condyles placed anterior to and well below the level of the occipital condyles vary within the family. *Chigutisaurus* and *Pelorocephalus* illustrate this variation among the Argentinian forms. The latter and *Compsocerops* have long cylindrical quadrate condyles. In *Siderops* and, to some extent, in *Chigutisaurus*, the condyles appears to have a screw-like appearance (see Howie 1970 for details of this character in capitosaurids). In *Kuttycephalus* the quadrate condyles are not well preserved.

Orbits. The orbit of *Chigutisaurus* is placed slightly dorsally relative to other genera. In *Compsocerops* the orbit always remains anterior and lateral. *Keratobrachyops*, has comparatively larger orbits.

Occiput. In the occiput, the height of the skull and the angle of the vaulting of the pterygoid vary from genus to genus. These parameters seem to be highly susceptible to deformation because the combination of the heavy squamosal-quadratojugal flanges with the thinner skull table and basal



TEXT-FIG. 19. Cladogram depicting relationships of chigutisaurids. Characters used are listed in Table 2.

plate of the parasphenoid in between, created a situation in which pressure from above or from the sides may have changed the height of the skull. Minor variations in these characters are not suitable for phylogenetic consideration.

The vacuities of the occiput also show some variation. The descending plate of the tabular (posterior to the slender process which comes to the exoccipital) descends down on the dorsal surface of the pterygoid, just at the line of its vaulting in *Compsocerops*. This plate is wide and thin in *Compsocerops*, *Kuttycephalus*, *Pelorocephalus* and *Chigutisaurus*. The paraquadrate foramen is housed in the quadratojugal, near its suture with the squamosal, in all the chigutisaurids except *Keratobrachyops*, where the foramen is on the quadrate-quadratojugal suture.

From the above discussion, several apomorphies have been noted for different chigutisaurid genera (Table 2). Some are thought to be typical brachyopid characters (Watson 1956; Cosgriff 1969, 1974; Chernin 1977), shared by chigutisaurids (Warren and Hutchinson 1983). Others are exclusively chigutisaurid characters. A cladogram (Text-fig. 19) has been constructed to depict the relationships of the chigutisaurid genera.

It is important to note here that some authors prefer to include *Siderops* in the family Brachyopidae (Carroll 1987; Morales 1990; Shishkin 1990). The tabular horn is not preserved in *Siderops* which seems to be the root of the confusion. Shishkin (1990), however, mentioned the absence of other chigutisaurid characters in *Siderops*, such as the axial trough of the skull. Axial troughs are present in the Indian taxa but not yet noted in the Argentinian ones. Similarly, a keel at the ventral surface of the cultriform process of the parasphenoid has been noted by Marsicano (1990) in the type specimen of *Pelorocephalus*. This feature is not present in any other chigutisaurid genera. *Siderops* has all the chigutisaurid characters identified in the present work. Moreover, *Siderops* has a substantial similarity to *Compsocerops*, and the presence of the tabular, squamosal and quadratojugal projections is predicted in *Siderops*. Similarly, the presence of a firmly sutured basicranial joint and the ascending column of pterygoid cannot be verified in the Indian genera. The relevant areas are not well preserved.

In several characters, such as orbit size and position of the paraquadrate foramen, *Keratobrachyops* seems to be distinct from other chigutisaurids. In the shape of the skull and in several palatal characteristics, it resembles *Kuttycephalus* and *Chigutisaurus*. All three have a wide

TABLE 3. The Gondwana succession of the Northern Pranhita–Godavari valley (after Kutty and Sengupta 1989).

Formation	Main lithologies	Important fossils	Age
Deccan traps			Late Cretaceous and Early Tertiary
Chikiala	Highly ferruginous sandstones and conglomerates	?	? = Gangapur Formation
Gangapur	Coarse gritty sandstones; grey white to pinkish mudstones with interbedded ferruginous sandstones and concretions	*Gleichenia* *Pagiophylum* *Ptilophyllum* *Elatocladus*	Early Cretaceous
Kota	Sandstones, silstones and clays with limestone bands	Holostean fish Sauropods Pterosaurs early mammals	Early Jurassic
Dharmaram	Coarse sandstones and red clays	Prosauropods (small and large) Sphenosuchid	Late Late Triassic
Maleri	Red clays, fine to medium sandstones and peloidal calcirudites/ calcarenites	Chigutisaurids Metoposaurid Rhynchosaurs Phytosaurs Aetosaurs	Early Late Triassic
Bhimaram	Medium to coarse and fine sandstones, calcareous above and ferruginous below; some red clays	Labyrinthodont Dicynodont	? Late Middle Triassic
Yerrapalli	Red and violet clays; sandstones; calcirudites/ calcarenites	Stahleckeriid and Kannemeyeriid dicynodonts Capitosaurid	Early Middle Triassic
Kamthi	Ferruginous nonfeldspathic or slightly feldspathic sandstones and purplish siltstones	Dicynodont from basal beds	Late Late Permian to Early Triassic
Infra-Kamthi	Sandstone, carbonaceous and red mudstones; limonitic shales	Endothiodontid Cistecephalid (from lithozone 3)	Late Permian
Barakar	Feldspathic sandstones, carbonaceous shales and coal	*Glossopteris* flora	Late Early Permian
Talchir	Tillites, greenish shales and sandstones		Early Early Permian

cultriform process of the parasphenoid (widest in *Kuttycephalus*; see character 15, Table 2), with more posteriorly positioned dentition. The parasphenoid-vomer suture in *Keratobrachyops* and *Kuttycephalus* is positioned anterior to the interpterygoid vacuities. This character is not observed in *Chigutisaurus*. The ornament of the skull roof and the proportions of the subtemporal vacuity are also similar. The early separation of *Keratobrachyops* (Early Triassic) thus seems to be significant. On the other hand, *Pelorocephalus*, *Siderops* and *Compsocerops* are more similar. The cladogram clearly depicts the two different types of chigutisaurid palate. The *Keratobrachyops*, *Kuttycephalus* and *Chigutisaurus* palate differs from the *Siderops*, *Pelorocephalus* and *Compsocerops* palate by the posteriorly extended dentigerous area. The latter type has the anterior tip of the subtemporal vacuities positioned anterior to the centre of the interpterygoid vacuities (which makes the palate more capacious) and a long, narrow cultriform process of the parasphenoid. *Keratobrachyops*, however, has a coronoid process like that of *Compsocerops* and *Siderops*, while *Kuttycephalus*, unlike *Keratobrachyops*, has posterior projections on the squamosal and quadratojugal. Representatives of the two types of chigutisaurids are found together in one horizon in India and in Argentina. These two types possibly had differences in feeding style and occupied separate niches, as the pattern of dentition and the structure of the palate are different. This may explain the co-existence of these two chigutisaurid morphs in the upper parts of the Maleri and in the Cacheuta formations where no other temnospondyl has so far been reported.

Vertebrates and the age of the Maleri Formation

The Pranhita–Godavari valley of Deccan, India provides a relatively complete succession of Late Triassic continental strata rich in fossil vertebrates (Table 3). The Maleri Formation consists essentially of elongate sandstone ridges and clay valleys. The fossils collected from successive clay valleys have greatly helped the recognition of the faunal change from the base to the top (Text-fig. 1). There are two faunal zones present in the Maleri Formation. Kutty and Sengupta (1989) argued that the age of the lower fauna is Late Carnian and the upper fauna, Early Norian.

The lower Maleri fauna includes the metoposaurid *Metoposaurus maleriensis*, the rhynchosaur *Paradapedon huxleyi*, and the phytosaur *Parasuchus hislopi*. Two species of dipnoan, *Ceratodus hunterianus* and *C. virapa*, are also common. A cynodont, *Exaeretodon statisticae*, an eosuchian, *Malerisaurus robinsonae*, and a small coelurosaur, *Walkeria maleriensis*, are restricted to the lower Maleri fauna. An aetosaur similar to *Typothorax* (Huene 1940), a prosauropod and a dicynodont are also believed to be present. In the upper Maleri fauna, the first three elements of the lower fauna are absent. A different species of *Ceratodus*, *C. nageswari* Shah and Satsangi, 1970, is present. Two chigutisaurids, *Compsocerops cosgriffi* and *Kuttycephalus triangularis*, appear in place of the metoposaurids. Among the phytosaurs, instead of *Parasuchus hislopi*, a long-snouted primitive form and an advanced *Rutiodon*-like form have been noticed. Dicynodonts and aetosaurs are still present.

A comparison of these two faunas indicates that the lower fauna has metoposaurids while the chigutisaurids are restricted to the upper fauna. In North America and Europe, metoposaurids continued up to the Norian (Roychowdhury 1965; Benton 1986; Chatterjee 1986; Long and Padian 1986; Murry 1986; Hunt and Lucas 1990). In Morocco the picture is not clear as no temnospondyls, except almasaurids and metoposaurids, are found there. On the other hand, chigutisaurids are noted in the Gondwanas and are known from the upper part of the Late Triassic Maleri Formation of the Pranhita–Godavari valley, India, the Late Triassic Cacheuta and Ischigualasto Formations of the Mendoza Province, South America (Bonaparte 1982) and the Early Triassic Arcadia Formation (Rewan Group) and Early Jurassic Evergreen Formation of Queensland, Australia. Though the metoposaurids and the chigutisaurids help to distinguish the lower and upper fauna of the Maleri Formation, their stratigraphical ranges do not help to fix the age of boundary between the two faunas. India is the only country where both metoposaurids and chigutisaurids have been found so far.

Apart from the appearance of chigutisaurids, two other events also occurred in the interval between the two Maleri faunas. The rhynchosaurs are absent from the upper fauna and their disappearance may indicate the end of the Carnian (Chatterjee 1974; Tucker and Benton 1982; Benton 1983; Hunt and Lucas 1991). The phytosaurs evolved into advanced forms, evidence of which is very conspicuous in the successive clay valleys of Maleri (T. S. Kutty, pers. comm.).

The demise of the rhynchosaurs at the end of Carnian is also noted in Wyoming, Arizona and Texas and in Argentina and Scotland. The progressive change in the phytosaurs, as noted in Maleri, has been described from several parts of the world. Kutty and Sengupta (1989) noted that the lower Maleri fauna has the primitive *Parasuchus* (= *Paleorhinus*, see Chatterjee 1978) while the upper Maleri fauna has a primitive as well as a specialized *Rutiodon*-like form, and the immediately overlying lower Dharmaram Formation has only the advanced *Nicrosaurus*. They noted that, on the basis of the phytosaurs, the lower Maleri can be correlated with the lower part of the Dockum and Chinle formations while the upper Maleri can be equated with the middle part of these formations. The *Nicrosaurus*-bearing lower Dharmaram Formation can similarly be equated with the upper parts of the Dockum and Chinle formations.

The fauna of the Petrified Forest National Park, Arizona and in the Chinle Formation has been described by Murry and Long (1989). They considered the Norian *Nicrosaurus* to be an advanced phytosaur and *Rutiodon* to be primitive. In the Placerias and Downs quarries of the St John's area, Arizona, they found *Rutiodon* and *Paleorhinus* together with *Metoposaurus*. Elsewhere, either *Metoposaurus*, or *Anaschisma*, or both, are present with *Rutiodon* and the age of the assemblage has been considered to be Late Carnian. *Nicrosaurus* and *Rutiodon*-like forms have not been found to occur together. The faunal assemblages of the Dockum Formation, characterized by *Rutiodon*, *Nicrosaurus* and *Metoposaurus perfecta*, were thought to be of a later age than the *Paleorhinus*-bearing fauna (Gregory 1972). The fauna found at Otis Chalk, Howard County, in the lower Dockum Formation (see Murry 1989) has similarities with the lower Maleri fauna. It contains both *Metoposaurus* and *Latiscopus* (not found in Maleri), and also *Paleorhinus*, *Angiostorhinus*, *Rhynchosaurus* and protorosaurids like *Malerisaurus*. If the lower Maleri fauna is thought of as Late Carnian, that would corroborate its correlation with the basal part of the Chinle and Dockum formations. So far, no vertebrates have been collected from the lower Maleri inconsistent with that age. The upper Maleri, with advanced phytosaurs, could be Early Norian (Kutty and Sengupta 1989).

As noted by Chatterjee (1974), Chatterjee and Roychowdhury (1974) and Kutty and Sengupta (1989), the correlation of the Maleri faunas with those of the German Keuper is not very straightforward. The last-named authors placed the *Franchosuchus*-bearing Buntemergel in equivalence with the lower Maleri, because *Franchosuchus* and *Parasuchus* were considered by Chatterjee (1978) to be synonyms. The Stubensandstein, on the other hand, contains advanced *Mystriosuchus*, *Nicrosaurus* and *Rutiodon* (Chatterjee 1986).

Acknowledgements. I thank the following staff of the Indian Statistical Institute, Calcutta: Professor T. K. Roychowdhury for guidance and help; Mr T. S. Kutty for his help; and Dr S. N. Sarkar who kindly allowed me to consult his unpublished map. I am indebted to Dr A. Warren of La Trobe University, Victoria, and Dr A. R. Milner of Birkbeck College, London, for critically appraising the manuscript. I also thank Dr A. L. Panchen of the University of Newcastle-upon-Tyne, Dr T. S. Kemp of the University Museum, Oxford, and Dr J. F. Bonaparte of Museo Argentino de Ciencias Naturales for their constructive suggestions. Mr D. Pradhan and K. BopuRao helped with fossil collection. Finally, I gratefully acknowledge the encouragement and financial assistance received from the authorities of the Indian Statistical Institute.

REFERENCES

BENTON, M. J. 1983. The Triassic reptile *Hyperodapedon* from Elgin: functional morphology and relationships. *Philosophical Transactions of the Royal Society of London, Series B*, **302**, 605–720.

—— 1986. The Late Triassic tetrapod extinction events. 303–320. *In* PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic-Jurassic boundary*. Cambridge University Press, 378 pp.

BONAPARTE, J. F. 1975. Sobre la presencia del laberintodonte *Pelorocephalus* en la Formacion de Ischigualasto y su significado estratigrafico. *Actas 1 Congress Argentinoda Paleontologia y Biostratigrafica, Tucuman*, **1**, 537–544.

—— 1978. El Mesozoico de America del Sur y sus tetrapodos. *Tucuman: Fundacion Miguel Lillo, Opera Lilloana*, **26**, 596 pp.

—— 1982. Faunal replacement in the Triassic of South America. *Journal of Vertebrate Paleontology*, **2**, 362–371.

BOY, J. A. 1989. Über einige Vertreter der Eryopoidea (Amphibia: Temnospondyli) aus dem europaischen Rotliegend (?hochstes Oberkarbon Perm) 2. *Acanthostomatops*. *Paläontologische Zeitschrift*, **63**, 133–151.

BYSTROW, A. P. and EFREMOV, J. A. 1940. *Benthosuchus sushkini* Efr. a labyrinthodont from the Eotriassic at Sharzhenga river. *Travaux de l'Institut Paléontologique*, **10**, 1–152. [In Russian with extended English summary].

CABRERA, A. 1944. Sobre un estegocephalo de la Provincia de Mendoza. *Notas del Museo de La Plata*, **9**(69), 421–429.

CARROLL, R. L. 1987. *Vertebrate paleontology and evolution*. W. H. Freeman and Company, New York, 698 pp.

CHATTERJEE, S. 1974. A rhynchosaur from the Upper Triassic Maleri Formation of India. *Philosophical Transactions of the Royal Society of London, Series B*, **267**, 209–261.

—— 1978. A primitive parasuchid (phytosaur) reptile from the Upper Triassic Maleri Formation of India. *Palaeontology*, **21**, 83–127.

—— 1986. The Late Triassic Dockum vertebrates: their stratigraphic and paleobiogeographic significance. 139–150. *In* PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, 378 pp.

—— and ROY-CHOWDHURY, T. 1974. Triassic Gondwana vertebrates from India. *Indian Journal of Earth Sciences*, **1**, 96–112.

CHERNIN, S. 1977. A new brachyopid, *Batrachosuchus concordi* sp. nov., from the Upper Luangwa valley, Zambia with a recapitulation of *Batrachosuchus browni* Broom, 1903. *Palaeontologia Africana*, **20**, 87–109.

COLDIRON, R. W. 1978. *Acroplous vorax* Hotton (Amphibia, Saurerpetontidae) restudied in the light of new material. *American Museum Novitates*, **2662**, 1–27.

COSGRIFF, J. W. 1969. *Blinasaurus*, a brachyopid genus from Western Australia and New South Wales. *Proceedings of The Royal Society of Western Australia*, **52**, 65–88.

—— 1974. Lower Triassic Temnospondyli of Tasmania. *Geological Society of America Special Papers*, **149**, 1–134.

—— 1984. The temnospondyl labyrinthodonts of the earliest Triassic. *Journal of Vertebrate Paleontology*, **4**, 30–46.

DEFAUW, S. 1989. Temnospondyl amphibians: a new perspective on the last phases in the evolution of Labyrinthodontia. *Michigan Academician*, **21**, 7–32.

DUTUIT, J. M. 1976. Introduction à l'étude paléontologique du Trias continental marocain. Description des premiers stégocéphales recueillis dans le couloir d'Argana (Atlas Occidental). *Mémoires du Muséum National d'Histoire Naturelle, New Series C*, **36**, 1–255.

ELDREDGE, N. and CRACRAFT, J. 1980. *Phylogenetic pattern and evolutionary process*. Columbia University Press, 349 pp.

GREGORY, J. T. 1972. Vertebrate faunas of the Dockum Group, Triassic, Eastern New Mexico and West Texas. *New Mexico Geological Society Guidebook, 23 Field Conference*, 120–123.

HOWIE, A. A. 1970. A new capitosaurid labyrinthodont from East Africa. *Palaeontology*, **13**, 210–253.

HUENE, F. von, 1940. The tetrapod fauna of the Upper Triassic Maleri beds. *Palaeontologia Indica, New Series*, **32**, 1–42.

HUNT, A. P. and LUCAS, S. G. 1990. The status of 'Jurassic' metoposaurs in the American South West. *Stegocephalian Newsletter*, **1**, 16.

———— 1991. A new rhynchosaur from the upper Triassic of West Texas and the biochronology of Late Triassic rhynchosaurs. *Palaeontology*, **34**, 927–938.

JUPP, R. and WARREN, A. A. 1986. The mandible of the Triassic temnospondyl amphibians. *Alcheringa*, **10**, 99–124.

KUTTY, T. S. and SENGUPTA, D. P. 1989. Late Triassic formations of the Pranhita–Godavari valley and their vertebrate faunal sequence – a reappraisal. *Indian Journal of Earth Science*, **16**, 189–206.

LANGSTON, W. 1953. Permian amphibians from New Mexico. *University of California Publications in Geological Sciences*, **29**, 344–416.

LONG, R. A. and PADIAN, K. 1986. Vertebrate biostratigraphy of the Late Triassic Chinle Formation, Petrified Forest National Park, Arizona: preliminary result. 161–169. *In* PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, 378 pp.

MARSICANO, C. M. A. 1990. Redescription del craneo del holotipo de *Pelorocephalus mendozensis* Cabrera 1944 (Amphibia, Temnospondyli) de Triasico del Cerro Bayo, Provincia de Mendoza. *Ameghiniana*, **27**, 39–44.
—— 1993. Evolutionary relationships in the Triassic Gondwana family Chigutisauridae (Amphibia, Temnospondyli). *Journal of Vertebrate Paleontology*, **13** (3 Supplement), 48A.
MORALES, M. 1988. A brief review of post Triassic labyrinthodonts. *Journal of Vertebrate Paleontology*, **10** (3 Supplement), 36 A.
MURRY, P. A. 1986. Vertebrate paleontology of the Dockum Group, Western Texas and Eastern New Mexico. 109–137. *In* PADIAN, K. (ed.). *The beginning of the age of dinosaurs: faunal change across the Triassic–Jurassic boundary*. Cambridge University Press, 378 pp.
—— 1989. Geology and paleontology of the Dockum Formation (Upper Triassic), West Texas and Eastern New Mexico. 102–145. *In* LUCAS, S. G. and HUNT, P. H. (eds). *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History, 414 pp.
—— and LONG, A. R. 1989. Geology and paleontology of the Chinle Formation, Petrified Forest National Park and vicinity, Arizona and a discussion of vertebrate fossils of the Southwestern Upper Triassic. 29–65. *In* LUCAS, S. G. and HUNT, P. H. (eds). *Dawn of the age of dinosaurs in the American Southwest*. New Mexico Museum of Natural History, 414 pp.
RIEPPEL, O. 1980. The edopoid amphibian *Cochleosaurus* from the Middle Pennsylvanian of Nova Scotia. *Palaeontology*, **23**, 143–149.
ROMER, A. S. 1947. Review of the Labyrinthodontia. *Bulletin of the Museum of Comparative Zoology, Harvard*, **99**, 1–352.
—— 1966. *Vertebrate paleontology*. 3rd ed. Chicago University Press, Chicago and London, 468 pp.
ROYCHOWDHURY, T. 1965. A new metoposaurid amphibian from the Upper Triassic Maleri Formation of Central India. *Philosophical Transaction of the Royal Society of London, Series B*, **250**, 1–52.
RUSCONI, C. 1948. Nuevos laberintodontes del Triassico de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **2**, 225–229.
—— 1949. I. Presencia de ictiosaurios en el liasico de San Juan. II. Otra especie de la laberintodonte triasico de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **3**, 89–94.
—— 1950. Presencia de laberintodontes en varias regiones de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **4**, 3–8.
—— 1951. Laberintodontes Triasicos y Permicos de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **5**, 33–158.
—— 1953. Nuevo laberintodonte de Mendoza Nova Presia. *Boletin Paleontológico de Buenos Aires*, **26**, 1.
SÄVE-SÖDERBERGH, G. 1935. On the dermal bones of the head in labyrinthodont Stegocephalians and primitive reptilia with special reference to Eotriassic Stegocephalians from East Greenland. *Meddelesler om Grønland*, **98**, 1–211.
SHAH, S. C. and SATSANGI, P. P. 1970. A *Ceratodus nageswari* sp. nov. from Kota–Maleri beds of Andhrapradesh. *Records of the Geological Survey of India*, **98**, 751–752.
SHISHKIN, M. A. 1987. *Evolution of the fossil amphibians Plagiosauroidea*. Nauka, Moscow, 142 pp. [In Russian].
—— 1990. A labyrinthodont from the Jurassic of Mongolia. *Paleontologicheshii Zhurnal*, **1**, 78–91. [In Russian].
STEEN, M. C. 1938. On fossil Amphibia from the Gas Coal of Nýřany and other deposits in Czechoslovakia. *Proceedings of the Zoological Society of London, Series B*, **108**, 205–283.
TUCKER, M. E. and BENTON, M. J. 1982. Triassic environments, climates and reptile evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **40**, 361–379.
WARREN, A. A. 1981. A horned member of the labyrinthdont Superfamily Brachyopoidea from the Early Triassic of Queensland. *Alcheringa*, **5**, 273–288.
—— and BLACK, T. D. 1985. A new rhytidosteid (Amphibia, Labyrinthodontia) from the Early Triassic Arcadia Formation of Queensland, Australia and a consideration of the relationships of Triassic temnospondyls. *Journal of Vertebrate Paleontology*, **5**, 303–327.
—— and HUTCHINSON, M. N. 1983. The last labyrinthodont? A brachyopid (Amphibia, Temnospondyli) from the Early Jurassic Evergreen Formation of Queensland, Australia. *Philosophical Transaction of the Royal Society of London, Series B*, **303**, 1–62.
WATSON, D. M. S. 1956. The brachyopid labyrinthodonts. *Bulletin of the British Museum (Natural History), Geology Series*, **2**, 317–391.
WELLES, S. P. and ESTES, R. 1969. *Hadrokkosaurus bradyi* from the Upper Moenkopi Formation of Arizona. *University of California Publications in Geological Sciences*, **84**, 1–56.

ZITTEL, K. von, 1888. *Handbuch der Paläontologie Abteilung 1. Paläozoologie Band III. Vertebrata (Pisces, Amphibia, Reptilia, Aves)*. R. Oldenbourg, Munich and Leipzig, 900 pp.

DHURJATI P. SENGUPTA

Geological Studies Unit
Indian Statistical Institute
203 Barrackpore Trunk Road
Calcutta 700035, India

Typescript received 28 July 1993
Revised typescript received 25 May 1994

ABBREVIATIONS USED IN THE FIGURES

a	angular
ac	acetabulum
acr	ascending ramus of the pterygoid
adf	adductor fossa
amf	anterior meckelian foramen
ar	articular
artf	articular fossa
acc. eo	ascending process of the exoccipital
cr	coronoid
crp	coronoid process
cps	canal on the dorsal side of the cultriform process of the parasphenoid
d	dentary
dsc, sq	descending process of the squamosal
ect	ectoptergyoid
eo	exoccipital
ept	epipterygoid
f	frontal
fcht	chorda tympanic foramen
ic	intercentrum
icr	intercoronoid
j	jugal
ld	lateral depression
mx	maxilla
n	nasal
p	parietal
pal	palatine
par	prearticular
pc	pleurocentrum
pcr	precoronoid
pmf	posterior meckelian foramen
pmx	premaxilla
po	postorbital
pof	postfrontal
pp	postparietal
prf	prefrontal
ps	parasphenoid
psl	postsplenial
pt	pterygoid
ptpr	posterior projection of the pterygoid
q	quadrate
qj	quadratojugal
sa	surangular
sd	semicircular depression on the dorsal surface of the base of the parasphenoid
sp	splenial
sq	squamosal
st	supratemporal
t	tabular
v	vomer