CHIGUTISAURID AMPHIBIANS FROM THE UPPER TRIASSIC OF ARGENTINA AND THEIR PHYLOGENETIC RELATIONSHIPS

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ABSTRACT. A revision of the temnospondyl chigutisaurids from the Upper Triassic of Argentina is presented. The validity of the taxa originally proposed is discussed in the light of new material. The genus *Pelorocephalus* (Chigutisauridae) is diagnosed by the presence of a longitudinally keeled cultriform process, occurrence of the anterior Meckelian fenestra on the suture between splenial and postsplenial, location of the chordatympanic foramen on the contact between angular and prearticular, and exposure of the angular on the lingual mandibular surface. Three species, *Pelorocephalus mendozensis*, *P. tenax* and *P. cacheutensis*, are distinguished mainly by differences in the structure of the occiput. Phylogenetic relationships among all known representatives of this family, including taxa from India and Australia, are discussed.

SEVERAL temnospondyl amphibians have been described from the Upper Triassic of Argentina in the past 50 years (Cabrera 1944; Rusconi 1948*a*, 1948*b*, 1949, 1951, 1953; Bonaparte 1963, 1975). The validity of the different nominal taxa and the families represented has been discussed by various authors (Reig 1961, 1962; Welles and Estes 1969; Bonaparte 1970, 1973, 1978), but without a critical analysis of the specimens involved.

Originally, the taxa described, and the families to which they were assigned, were as follows: *Pelorocephalus mendozensis* Cabrera, 1944 (Brachyopidae); *Otuminisaurus limensis* Rusconi, 1948*a* (Lydekkerinidae); *Icanosaurus rectifrons* Rusconi, 1951 (Trematosauridae); *Promastodonsaurus bellmanni* Bonaparte, 1963 (Capitosauridae); and *Chigutisaurus tunuyanensis* Rusconi, 1948*b*, *Chigutisaurus tenax* Rusconi, 1949, *Chigutisaurus cacheutensis* Rusconi, 1953 and *Pelorocephalus ischigualastensis* Bonaparte, 1975, all included in Rusconi's Chigutisauridae. Recently, most of this temnospondyl material was restudied and its taxonomic status re-evaluated (Marsicano 1993*a*, 1993*b*, 1994, 1996). As a result, only two temnospondyl families are considered to be represented in the Upper Triassic of southern South America, Chigutisauridae and Capitosauridae, with the chigutisaurids, at present, the most important amphibian component of the tetrapod faunas found in that region.

In the last few years, chigutisaurids have also been recognized in other Gondwanan areas, including Australia and India. The Australian chigutisaurid record includes material from the Early Triassic Arcadia Formation (Warren 1981; Damiani and Warren 1996), the Early Jurassic Evergreen Formation (Warren and Hutchinson 1983) and the Early Cretaceous Strzelecki Formation (Warren *et al*. 1997). Indian chigutisaurids are known only from the Late Triassic Maleri Formation (Sengupta 1995). This restricted spatial distribution of chigutisaurids contrasts with their long temporal range (Scythian (Early Triassic) to Aptian (Early Cretaceous)), apparently the longest among temnospondyl families.

In this paper, a redescription of the type specimens of Rusconi's chigutisaurids is presented and their taxonomic assignment is discussed in the light of new material. This new information permits a re-evaluation of the phylogenetic relationships of chigutisaurids (Warren and Hutchinson 1993; Sengupta 1995; Damiani and Warren 1996).

Institutional abbreviations. MCNA, Museo de Ciencias Naturales y Antropológicas, Mendoza; MLP, Museo de Ciencias Naturales de La Plata, Buenos Aires; PVL, Paleontología de Vertebrados Instituto Miguel Lillo, Tucumán.

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SYSTEMATIC PALAEONTOLOGY

'TEMNOSPONDYLI' *sensu* Milner, 1993
Family CHIGUTISAURIDAE Rusconi, 1949

Genus PELOROCEPHALUS Cabrera, 1944

Type species. Pelorocephalus mendozensis Cabrera, 1944.

Diagnosis. Chigutisaurids with a raised longitudinal keel along the ventral surface of the cultriform process of the parasphenoid, a condition not present in other members of the family. In the mandible, there is a well-developed anterior Meckelian fenestra on the suture between splenial and postsplenial, a condition considered derived in relation to the location of the fenestra wholly within the postsplenial, as occurs in brachyopids. A contact between the surangular and prearticular excludes the articular from the postglenoid area (PGA); a prearticular exposure on the PGA is consider plesiomorphic as it is present in brachyopids and also in the basal chigutisaurid *Keratobrachyops*. The chordatympanic foramen is located lingually on the suture between the angular and the prearticular; thus the angular is well exposed on the lingual surface of the mandible, in contrast with other members of Chigutisauridae in which the chordatympanic foramen is located wholly within the prearticular and the angular is not well exposed on the lingual surface of the mandible.

Pelorocephalus mendozensis Cabrera, 1944

Text-figures 1–6

1948*b* *Chigutisaurus tunuyanensis* Rusconi, p. 226, fig. 1.
1951 *Chigutisaurus tunuyanensis* Rusconi, p. 75, figs 4–7.

Holotype. MLP 44-VII-5-1 (Text-fig. 1), the palatine section of a skull preserved in dorsal aspect with its mandible disarticulated, also fragments of vertebrae, ribs and the right humerus. Redescribed by Marsicano (1990).

Locality and horizon. Quebrada de La Mina, south side of Cerro Bayo, Potrerillos locality, Province of Mendoza, Argentina; Cacheuta Formation, dated as early Norian (Kokogian and Mancilla 1989; Kokogian *et al*. 1993; Zavattieri and Papu 1993; López-Gamundi *et al*. 1994).

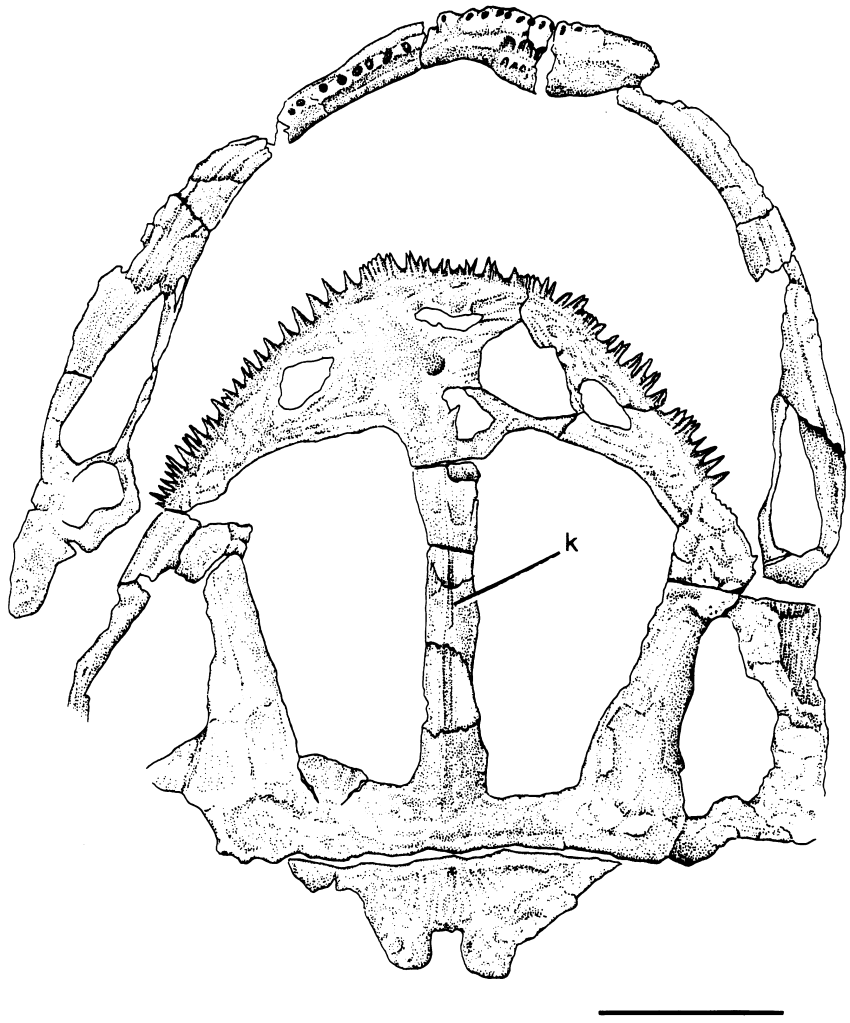
Referred specimens. MCNA 2660 (Text-figs 2–3), two large fragments of a single skull, one of which includes most of the posterior half of the cranium, whilst the other consists of the anterior left half of the palate, and most of the left mandible; PVL 3531, the posterior half of a skull. MCNA 2660 (the holotype of '*C. tunuyanensis*'), was recovered from levels assigned to the Cacheuta Formation (early Norian) in Bajada de la Obligación, north side of Cerro Bayo, El Challao locality, Province of Mendoza. The undescribed specimen, PVL 3531, was collected from the Cacheuta Formation (early Norian) by J. F. Bonaparte on a field trip during 1963. The only locality data available is Estancia San Isidro locality, Province of Mendoza.

Revised diagnosis. Exoccipital condyles located well behind the level of the quadrates; presence of a well-developed semicircular muscle-scar on the ventral surface of the corpus of the parasphenoid; mandible with two symphyseal tooth rows instead of symphyseal tusks.

Description

The following description of MCNA 2660 amends and supplements information and figures in Rusconi (1948*b*, 1951).

Skull roof (Text-figs 2A, 4A). Most of the bones of the skull roof are missing or poorly preserved, so the skull table is observable mainly as an internal mould. The sculpture shows the ridge-groove pattern described in other chigutisaurids

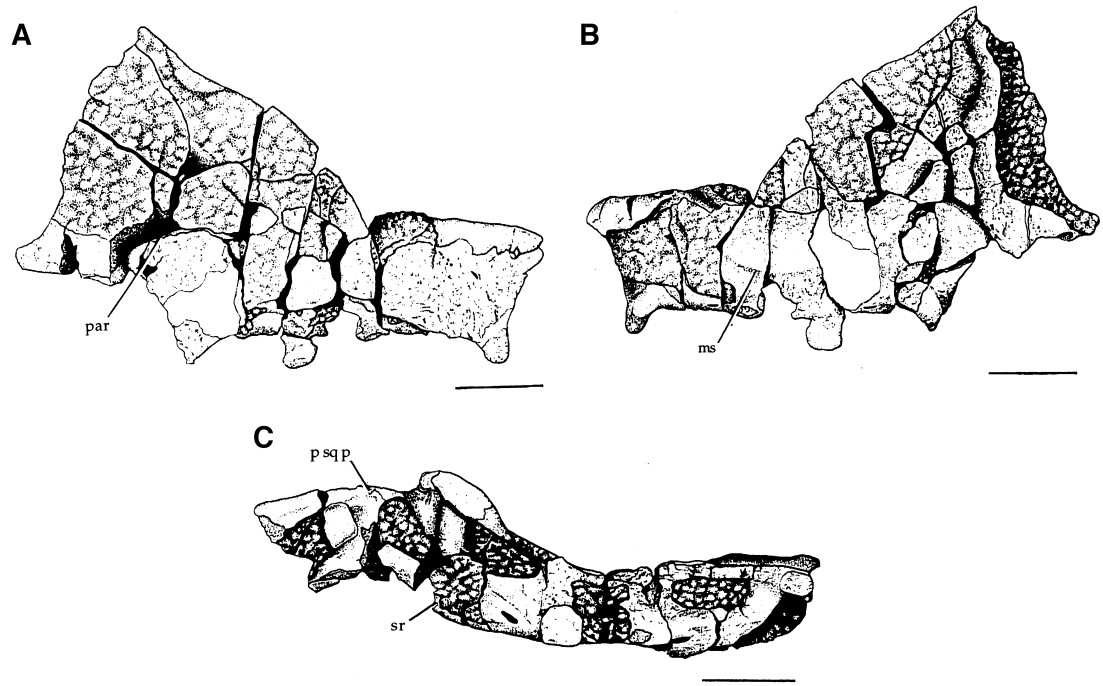


TEXT-FIG. 1. *Pelorocephalus mendozensis* Cabrera, 1944; holotype MLP 44-VII-5-1; skull and mandible in dorsal view. Scale bar represents 50 mm. See Appendix 2 for abbreviations.

and also present in many temnospondyls (Warren and Hutchinson 1983). The skull table, parabolic in dorsal view, has a gently concave posterior border. On this border, each tabular bears a well developed tabular horn. The horns are broad-based, posterolaterally directed and their distal end is unsupported from below by the paroccipital process. The otic notch is poorly incised and broad; in this embayment the squamosal forms a short postsquamosal process (p sq p, Text-figs 2C, 4C). Even though the anterior half of the skull is very damaged, the posterior half of the left orbit is preserved as an impression. The orbit, located in the anterior half of the skull table, is nearly circular and relatively small.

Occipital surface (Text-figs 2C, 4C). The relatively small and rounded exoccipital condyles are located well behind the posterior border of the skull roof and the level of the quadrates. The vertical process of the exoccipital is short and anteriorly directed, in contrast with the paroccipital process which is long and posterolaterally directed. Close to the base of each paroccipital process, a single large foramen, probably for the vagus (X) nerve, is present.

In posterior view, the corpus of the left pterygoid shows a longitudinal ridge on its dorsal surface. This ridge, the substapedial ridge (*sensu* Warren and Hutchinson 1983) (sr, Text-figs 2C, 4C), runs sagittally and separates the stapedial fossa (externally) from the substapedial fossa (internally). The ascending ramus of the pterygoid (par,



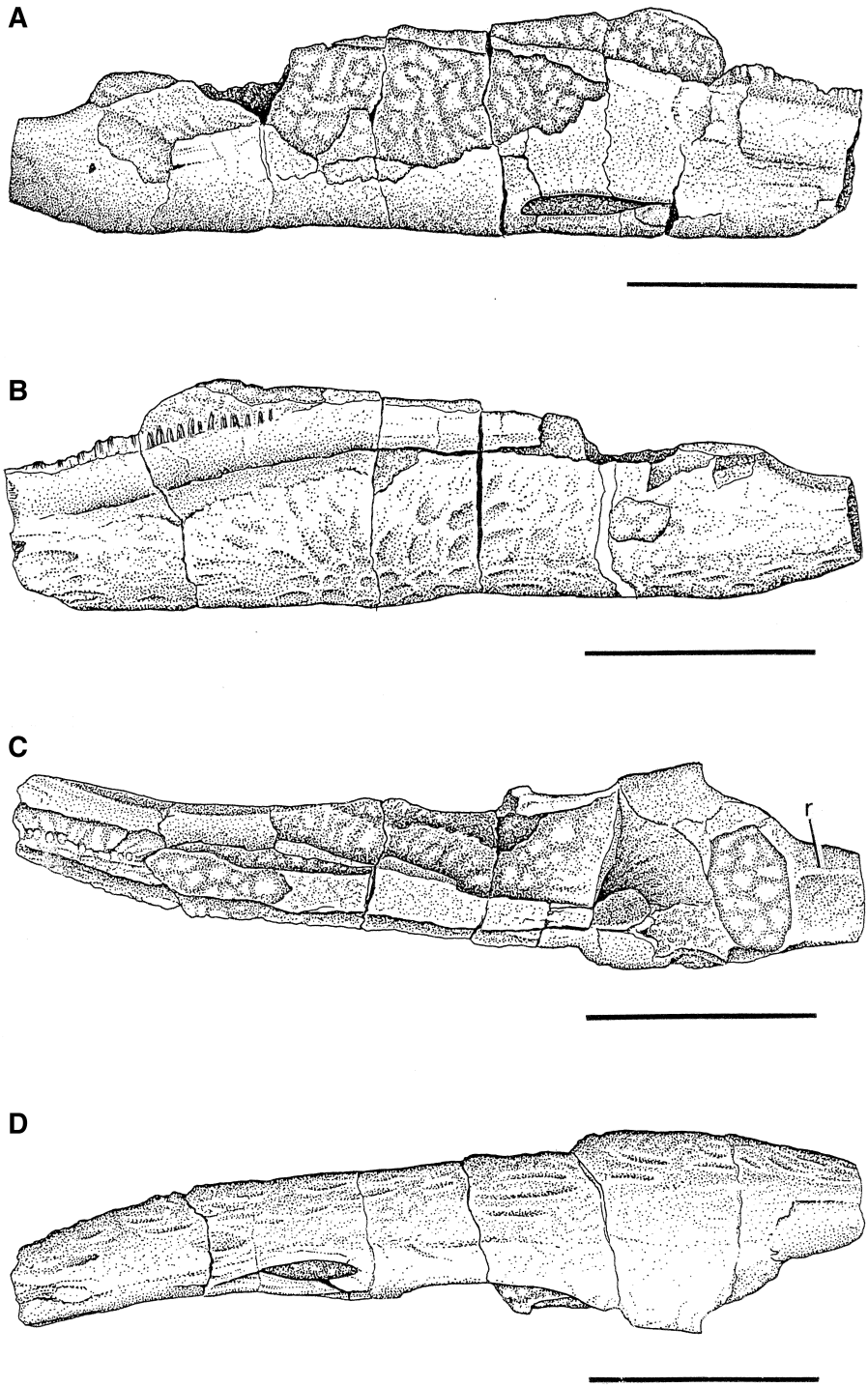
TEXT-FIG. 2. *Pelorocephalus mendozensis* Cabrera, 1944; MCNA 2660 (holotype of '*Chigutisaurus tunuyanensis*'). Skull fragment in A, dorsal, B, ventral, C, posterior view. Scale bars represent 50 mm. See Appendix 2 for abbreviations.

Text-fig. 2A), partially preserved on both sides of the skull, is a slender lamina that forms the anterolateral wall of the stapedial fossa. This lamina is fan-shaped and curves forwards and inwards from its suture with the squamosal to end, approximately, at the level of the substapedial ridge. The lamina is dorsoventrally thickened toward its medial end. Because it contacts the descending portion of the squamosal, no palatoquadrate fissure is present. The ascending ramus of the pterygoid seemingly contacts the bones of the skull table throughout its length. The quadrate ramus of the pterygoid, only partially preserved on the left side of the skull, is clearly deeply downturned. On the left side of the skull and on the posterior lateral wall of the occiput wall, the uppermost part of the squamosal-quadratojugal trough is visible.

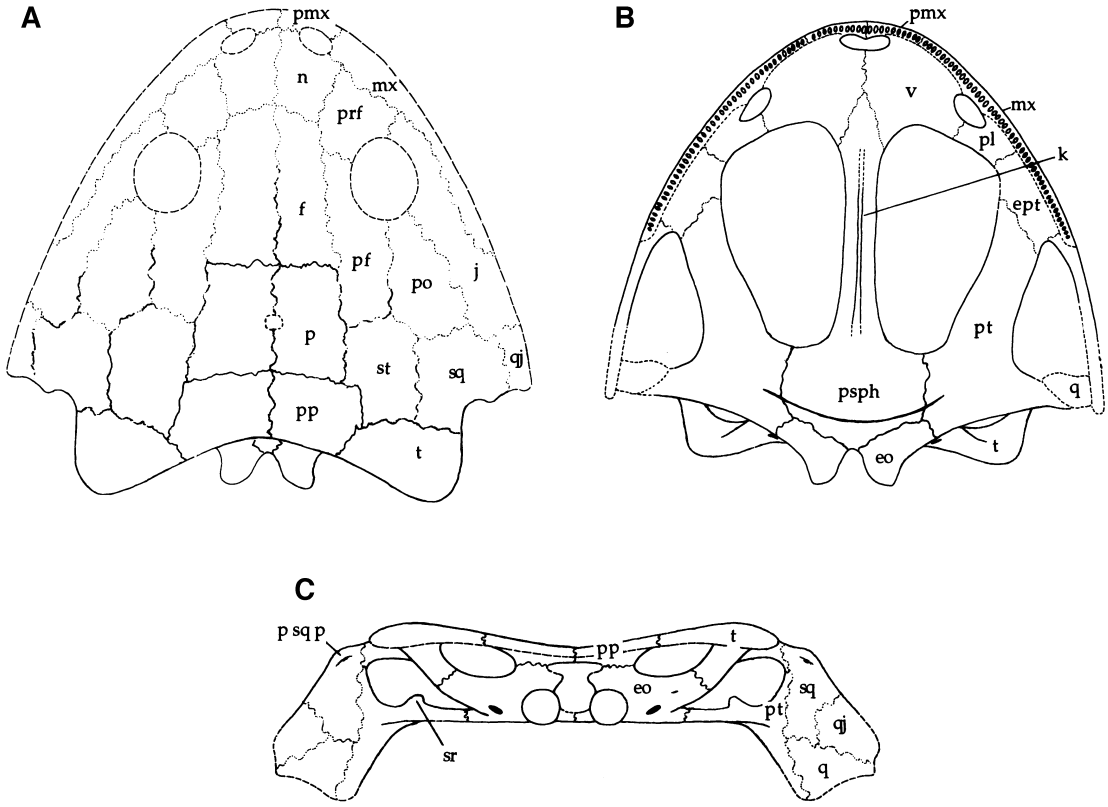
Palatal surface (Text-figs 2B, 4B). The left choana, the internal border of the orbit and part of the cultriform process of the parasphenoid are preserved on a fragment that corresponds to the left anterior half of the palate. The cultriform process of the parasphenoid bears a medial longitudinal keel on its ventral surface (k, Text-fig. 4B), whilst the corpus of the parasphenoid, preserved in the main skull fragment, has a tranverse muscle scar (ms, Text-fig. 2B) close to its posterior margin. This crescent-shaped scar leaves an anteriorly concave surface on the parasphenoid. Behind the scar, the surface of the palate slopes smoothly to the exoccipital condyles.

Dentition. On a fragment comprising part of the left maxilla, left palatine and left ectopterygoid, teeth of the marginal and palatal tooth rows are present. The teeth are laterally compressed and they curve lingually. On the palatal tooth row, a tusk and a row of small teeth are preserved.

Mandible (Text-figs 3, 5–6). A fragment that represents most of the medioposterior part of the left mandibular ramus is preserved. The surfaces of the bones are somewhat damaged so most of the sutures are not visible. The mandibular ramus is laterally compressed and the labial surface is ornamented with the same pattern as the bones of the skull roof. On the labial surface a well developed oral sulcus runs throughout the dentary, just below the tooth row, reaching the posterior glenoid area. Neither the mandibular nor the accessory sulcus are present. On the lingual surface and ventral to the articular area, there is a small chordatympanic foramen on the suture between the angular and the prearticular.



TEXT-FIG. 3. *Pelorocephalus mendozensis* Cabrera, 1944; MCNA 2660 (holotype of '*Chigutisaurus tunuyanensis*'). Fragment of the left mandibular ramus in A, lingual, B, labial, C, occlusal, D, ventral view. Scale bars represent 50 mm.

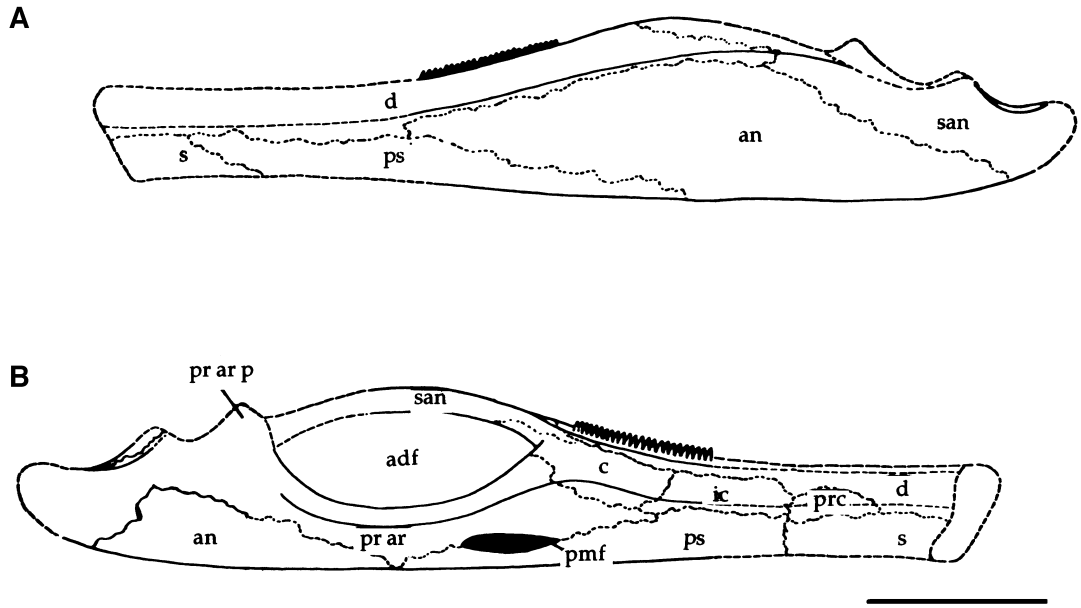


TEXT-FIG. 4. *Pelorocephalus mendozensis* Cabrera, 1944. Composite restoration of the skull in A, dorsal, B, ventral, C, posterior view. Reconstructed outlines are shown by dashed lines and inferred position of the sutures by dotted lines. See Appendix 2 for abbreviations.

Also on the lingual surface an anteroposteriorly elongated posterior Meckelian fenestra is located just below the anterior edge of the adductor fossa and close to the ventral border of the mandible. On the dorsal surface of the prearticular the base of the prearticular process (pr ar p, Text-fig. 5B) is preserved. The postglenoid area (PGA *sensu* Jupp and Warren 1986) is well developed, although its distal end is broken off. On the dorsal surface of the postglenoid area there is a longitudinal ridge (r, Text-fig. 3C) that corresponds to the suture between the prearticular and the surangular; thus the articular is only exposed in a small triangular region just behind the glenoid area (Text-fig. 6A).

Dentition. The fragment of mandible preserved contained 20 teeth; extrapolating from this a single mandibular ramus might bear up to 80 teeth. In shape the teeth are similar to those described for the palate. No coronoid teeth are preserved.

Remarks. '*Chigutisaurus tunuyanensis*' was erected by Rusconi for an assemblage of two different sets of bones: the holotype (MCNA 2660) and a skull fragment associated with several postcranial bones (MCNA 2661). All of the specimens were collected by Rusconi (1948*b*) from the Cacheuta Formation, west of Mendoza city. In a subsequent paper, Rusconi (1951) assigned more material from the same locality to '*Chigutisaurus tunuyanensis*' and also referred the species to a new family, Chigutisauridae (Rusconi 1949). The new specimens included an atlas (MCNA 2678), a nearly complete postcranial skeleton (MCNA 2669), and two very poorly preserved ?juvenile skulls (MCNA 2675 and 2677). Apparently, all these specimens were collected from the same stratigraphical unit (Cacheuta Formation), but were not found in direct association. A review of this material gives a new perspective to the specimens originally



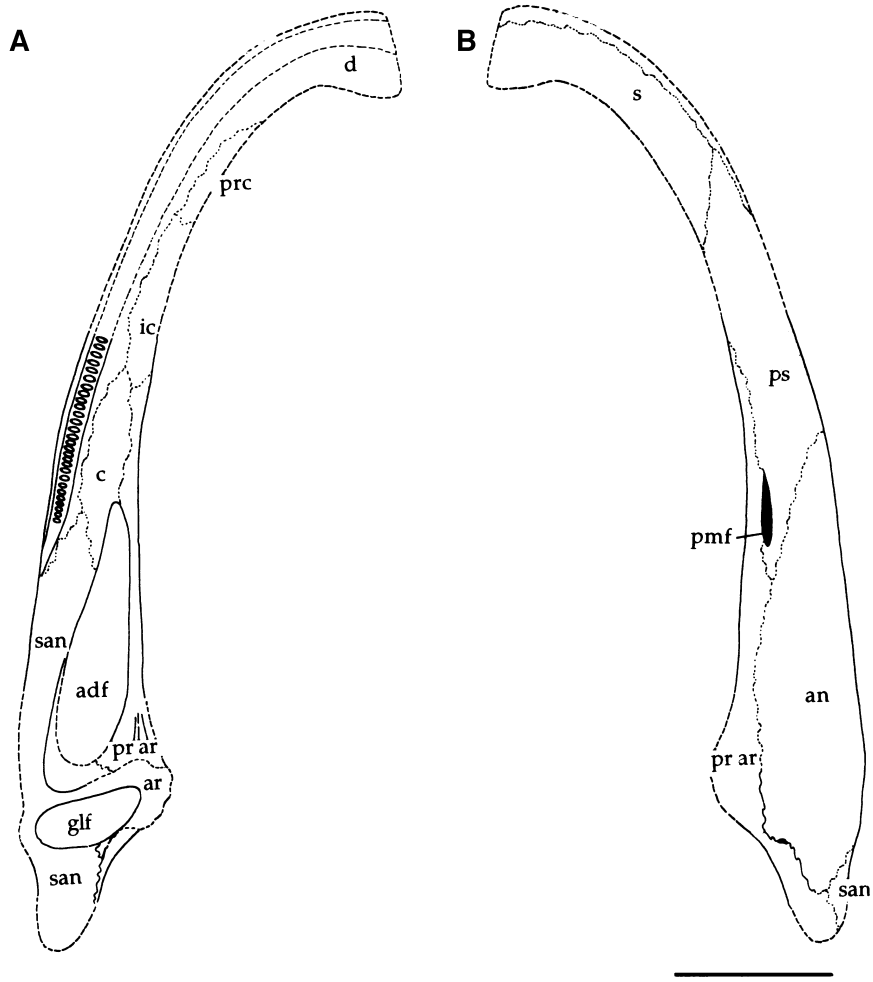
TEXT-FIG. 5. *Pelorocephalus mendozensis* Cabrera, 1944; MCNA 2660 (holotype of '*Chigutisaurus tunuyanensis*'). Restoration of the the left mandibular ramus in A, labial, B, lingual view. Scale bar represents 50 mm. Reconstructed outlines are shown by dashed lines and inferred position of the sutures by dotted lines. See Appendix 2 for abbreviations.

described by Rusconi (1948*b*, 1951): MCNA 2669 (a nearly complete postcranial skeleton) was later regarded by Reig (1961) as representing a new taxon of 'proterosuchian thecodont', *Cuyosuchus huenei*, presently considered an aetosaur (Arcucci, pers. comm. 1994); both juvenile skulls referred to '*Chigutisaurus tunuyanensis*', one of them apparently lost (MCNA 2677), are so poorly preserved that it is impossible to assess their taxonomic identity; and the atlas, described and figured by Rusconi (1951, fig. 8), is also lost. In any case, its taxonomic position would have remained uncertain as, according to the figure, it consisted of part of the right articular facet only. Rusconi (1951) also redescribed the specimen labelled MCNA 2661 and assiged it to a new taxon, *Icanosaurus rectifrons* (Rusconi, 1951), which is now regarded as a *nomen vanum* (Marsicano 1994). Thus, although many remains were originally assigned to '*C. tunuyanensis*', the holotype (MCNA 2660) is the only specimen confidently referable to that taxon.

Description of new material: PVL 3531. Due to the poor preservation of this specimen, most of the sutures between the bones of the skull roof and the sculpture pattern of the dermal bones are barely visible.

The skull table, although incomplete, appears to be parabolic, with its posterior border gently concave. On this border, each tabular projects as a well-developed tabular horn that is triangular in shape, broad-based and posterolaterally directed. Lateral to each tabular projection a broad otic embayment is present. On the left side of the skull it is possible to see part of the postsquamosal process projecting from the posterior border of this otic embayment.

The exoccipitals exhibit small, rounded condyles that project well behind the level of the quadrates. Each exoccipital has a short, anteriorly directed vertical process and a rod-like paraoccipital process. This latter process is posterolaterally directed and has a large single nerve foramen close to its base, probably for the vagus (X) cranial nerve. The left pterygoid has a deeply downturned quadrate ramus. On the dorsal surface of each pterygoid corpus a well developed stapedial ridge is visible (sr, Text-fig. 4C). This ridge runs into the stapedial fossa, and separates it from the substapedial fossa. No palatoquadrate fissure is present. In dorsal view on the left side of the skull it is possible to see the ascending ramus of the pterygoid in section. The ramus takes the form of a thin incurved lamina that, from its suture with the squamosal, runs forward and inward forming the anterolateral wall of the stapedial fossa. The lamina



TEXT-FIG. 6. *Pelorocephalus mendozensis* Cabrera, 1944; MCNA 2660 (holotype of '*Chigutisaurus tunuyanensis*'). Restoration of the the left mandibular ramus in A, occlusal, B, ventral view. Scale bar represents 50 mm. Reconstructed outlines are shown by dashed lines and inferred position of the sutures by dotted lines. See Appendix 2 for abbreviations.

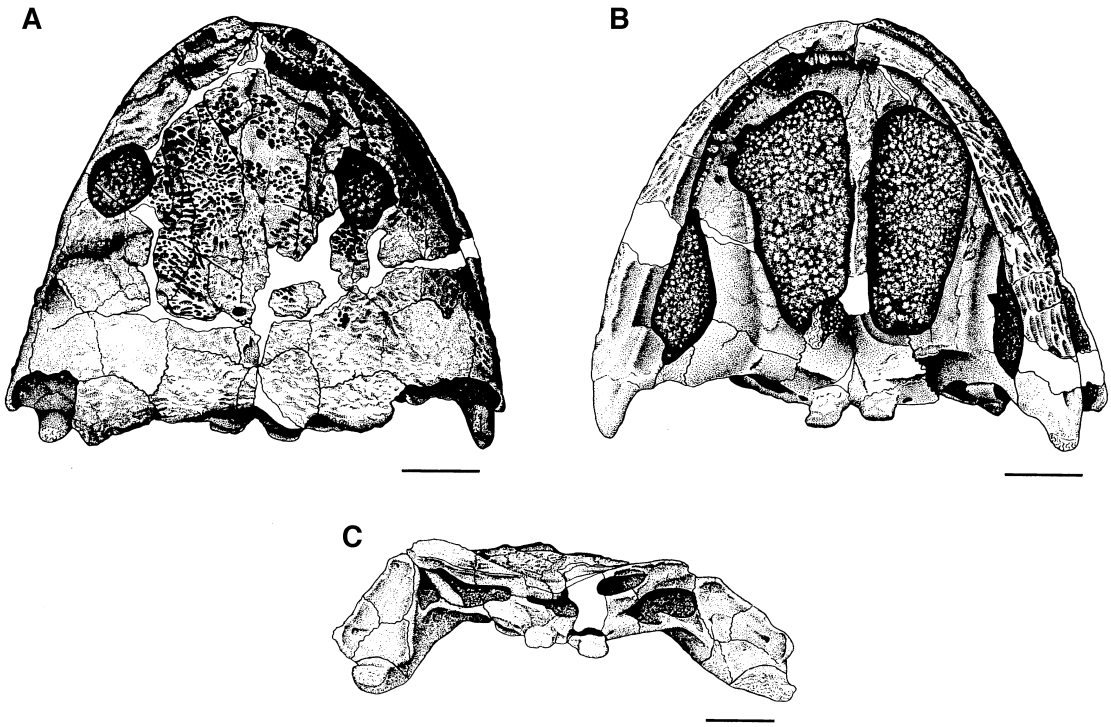
has a dorsoventral thicknening close to its medial end, and is apparently sutured throughout its length with the bones of the skull roof. On the lateral wall of the occiput a well-developed squamosal-quadratojugal trough is present.

The interpterygoid vacuities are almost quadrangular in shape (Text-fig. 4B). The parasphenoid has a narrow cultriform process which bears a longitudinal ventral keel (k, Text-fig. 4B). The corpus of the parasphenoid is hexagonal and has a well-developed muscle scar close to its posterior border. The scar is crescentic, resulting in an anteriorly concave surface on the corpus. Posterior to the scar, the surface of the palate slopes smoothly to the exoccipital condyles. The palatal ramus of the pterygoid, partially visible on the left side of the skull, is longitudinally concave and its external border projects more ventrally than does the internal.

Pelorocephalus tenax (Rusconi, 1949)

Text-figures 7–9

1949 *Chigutisaurus tenax* Rusconi p. 93.
1951 *Chigutisaurus tenax* Rusconi, p. 136, figs 65–71.



TEXT-FIG. 7. *Pelorocephalus tenax* (Rusconi, 1949); MCNA 2752 (holotype of '*Chigutisaurus tenax*'). Skull in A, dorsal, B, ventral, C, posterior view. Scale bars represent 50 mm.

Holotype. MCNA 2752 (Text-figs 7–9), a complete skull with the mandibles articulated.

Locality and Horizon. Bajada de la Obligación, north side of Cerro Bayo, El Challao locality, Province of Mendoza; Rio Blanco Formation, upper Norian (Kokogian and Mancilla 1989; Kokogian *et al.* 1993; López-Gamundi *et al.* 1994).

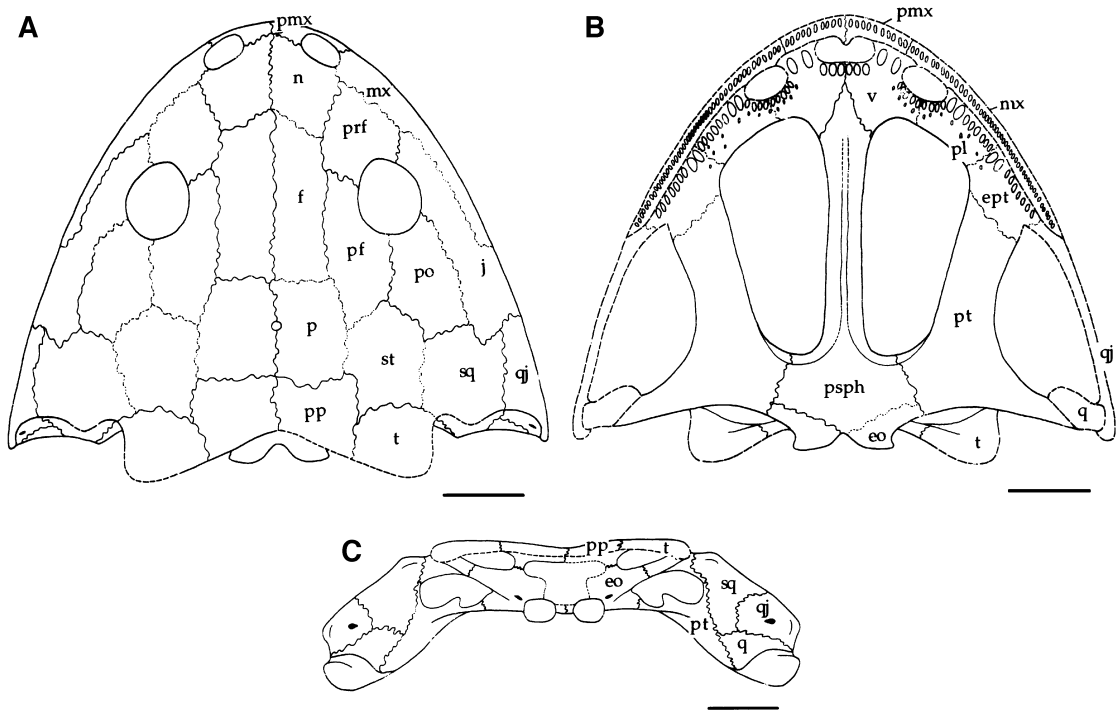
Diagnosis. Chigutisaurid with a very narrow vertical process of the exoccipital. The left and right vertical processes are well separated from each other, thus the supratemporal fossa is transversely elongate, reaching the level of the external border of the exoccipital condyles. The exoccipital condyles are short and do not project posterior to the level of the quadrate condyles.

Description

The following description of MCNA 2752 amends and supplements information and figures from Rusconi's (1949, 1951) descriptions.

Skull roof (Text-figs 7A, 8A). The skull is parabolic in outline and the arrangement of the dermal bones of the skull roof is the same as in other chigutisaurs, particularly the Australian forms (Warren 1981; Warren and Hutchinson 1983), with the absence of the lacrimal and the inclusion of the maxilla in the border of the external naris. As in all Mesozoic temnospondyls, no intertemporal is present. The tabulars exhibit posterolaterally directed projections (tabular horns) that are triangular, broad-based and unsupported from below by the paroccipital process. Lateral to each tabular horn there is a broad otic embayment delimited by the tabular, squamosal and quadratojugal. The squamosal develops a short postsquamosal process that projects into this embayment. In addition, each quadratojugal bears a projection on the posteroventral corner of the skull, the postquadratojugal process.

The orbits are rounded and located in the anterior half of the skull roof. The external nares are oval and lie close to



TEXT-FIG. 8. *Pelorocephalus tenax* (Rusconi, 1949); MCNA 2752 (holotype of '*Chigutisaurus tenax*'). Restoration of the skull in A, dorsal, B, ventral, C, posterior view. Scale bars represent 50 mm. Reconstructed outlines are shown by dashed lines and inferred position of the sutures by dotted lines. See Appendix 2 for abbreviations.

the anterior border of the table; the posterior border of the nares is thick and raised. The pineal foramen lies in the midlength of the parietal bones.

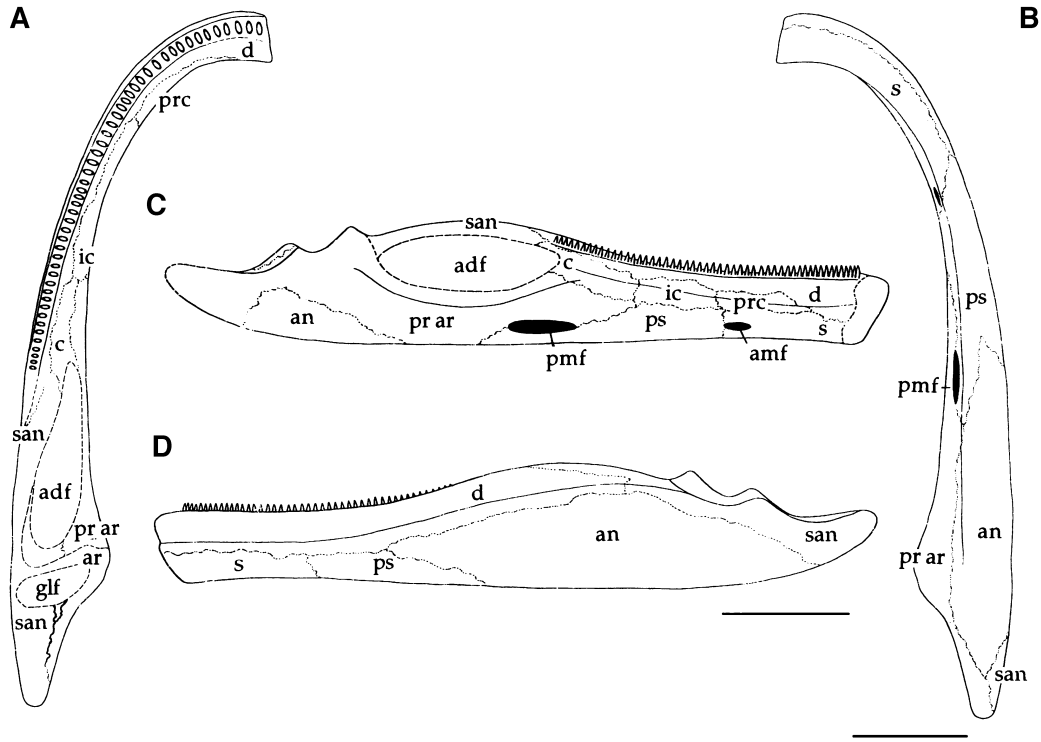
The bones of the skull roof bear a coarse, pitted ornament at the centre of ossification of each bone. This pattern becomes a ridge-groove ornament away from the centre, and no zones of intensive growth are present. The sensory canals are well developed, especially on the anterior half of the skull. The supraorbital canal, in the region of the naris and medial to the orbits, consists of a row of large pits.

Occiput (Text-figs 7C, 8C). In occipital view, the skull exhibits the brachyopoid inverted U-shape as a result of the deeply downturned nature of the quadrate ramus of the pterygoids. The posterior border of the ascending ramus of the pterygoid sutures with the descending flange of the squamosal; thus no palatoquadrate fissure is present. The pterygoid bears a longitudinal ridge (substapedial ridge *sensu* Warren and Hutchinson 1983) that runs sagittally on the corpus and enters the stapedial fossa. As this fossa is full of matrix that would be difficult to remove without damaging the specimen, it is not possible to observe details of the internal structure of the pterygoids, especially the shape of the ascending ramus.

Each exoccipital bears a small rounded condyle that does not project posteriorly as in other chigutisaurs. This condition appears to be genuine as the posterior wall of the exoccipital is almost perpendicular to the skull midline and does not slope anteriorly as in *P. mendozensis*. The vertical process of each exoccipital is short, laterally narrow and located beyond the level of the external border of the condyle. This results in a very elongated supraoccipital fossa. The lamellar processes are well developed, but do not project from the corpus of the exoccipital. The paraoccipital processes are long and thin, and posterolaterally directed. A single nerve foramen (probably for the vagus (X) nerve) is present on the exoccipital just lateral to each condyle.

On the lateral wall of the occiput, the squamosal, quadrate and quadratojugal develop a dorso-ventral squamosal-quadratojugal trough. The paraquadrate foramen lies close to the centre of the occipital part of the quadratojugal.

Palate (Text-figs 7B, 8B). As the mandibles are preserved in articulation, the lateral margins of the palate remain



TEXT-FIG. 9. *Pelorocephalus tenax* (Rusconi, 1949); MCNA 2752 (holotype of '*Chigutisaurus tenax*'). Restoration of the mandible in A, occlusal, B, ventral, C, lingual, D, labial view. Scale bars represent 50 mm. Reconstructed outlines are shown by dashed lines and inferred position of the sutures by dotted lines. See Appendix 2 for abbreviations.

unknown. The interpterygoid vacuities are quadrangular, with the borders nearly parallel-sided. The presence of an anterior palatal fenestra and the position of the choanae are denoted by the position of the palatal tooth row.

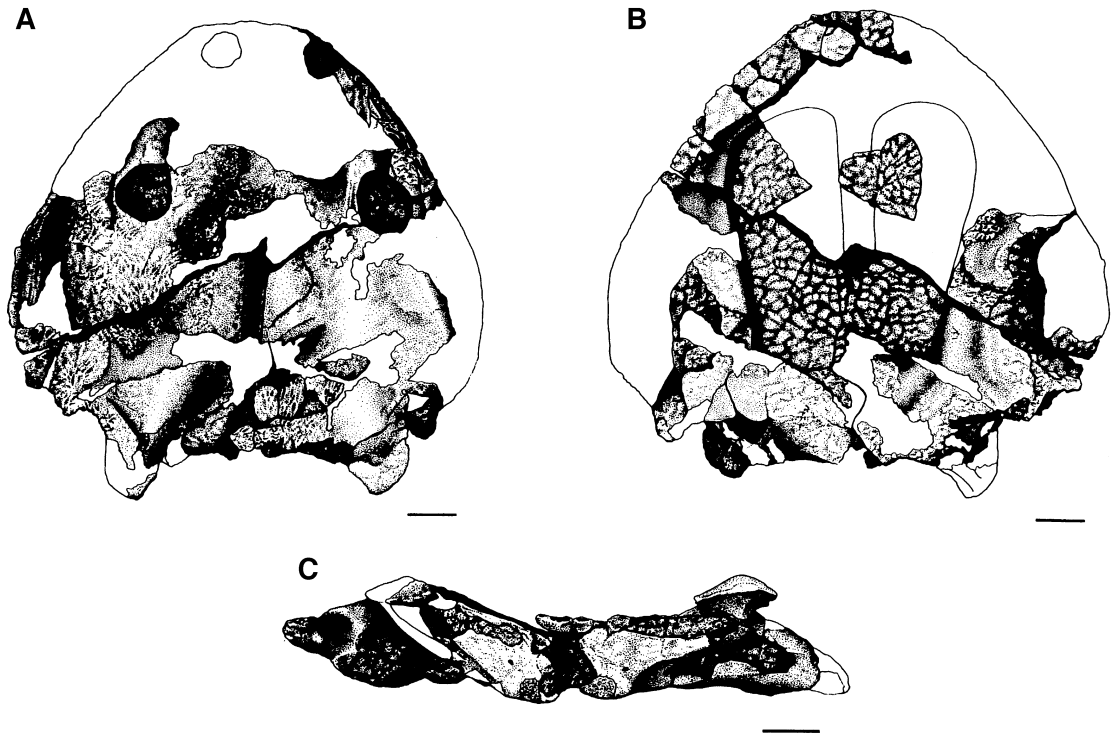
The pterygoid has a longitudinally grooved palatal ramus and a deeply downturned quadrate ramus. It also has a long suture with the parasphenoid and a ventral contact with the exoccipital. The parasphenoid consists of a flat hexagonal body with a long parallel-sided cultriform process that bears a ventral keel.

Dentition. The marginal tooth row comprises *c*. 160 small, striated teeth. The palatal teeth form a continuous row on the vomers, palatines and ectopterygoids and continue medial to the choana. This row contains approximately half the number of teeth present in the marginal tooth row, and exhibits a greater range of tooth sizes. Tusks are present on the vomers, palatines and ectopterygoids. On some areas of the palate (cultriform process, left vomer and left ectopterygoid) it is possible to see patches of small denticles embedded in sediment but not attached to the underlying bones. It is possible that the denticles occupied the entire surface of the palate, but were removed during preparation.

Mandible (Text-fig. 9). As the mandible is attached to the skull, it is not possible to see its dorsal surface. Moreover, the nature of its preservation precludes clear identification of the sutures. Each ramus has a well-developed post glenoid area (PGA), although both distal ends are broken off. Seen from the lingual surface, the prearticular extends on to the PGA and has a longitudinal suture with the surangular on the dorsal surface of this region. The suture is raised so that it forms a longitudinal ridge. A prearticular process is visible on the prearticular. On the lingual surface, anterior and posterior Meckelian fenestrae are visible. Both are close to the ventral border of the mandible, and the latter is located at the anterior level of the adductor fossa. The labial surface is covered by ornament, and a well-developed oral sulcus is present along the surangular and dentary.

The dentition is obscured by the position of the mandible, but it is possible to recognize teeth on the middle and posterior coronoids.

Remarks. Originally, the holotype material (MCNA 2752) also included some vertebral elements (Rusconi



TEXT-FIG. 10. *Pelorocephalus cacheutensis* (Rusconi, 1953); MCNA 2966 (holotype of '*Chigutisaurus cacheutensis*'). Skull in A, dorsal, B, ventral, C, posterior view. Scale bars represent 50 mm.

1951) that are apparently lost. However, judging from the figures of the bones in Rusconi (1951), they might represent reptile remains.

Pelorocephalus cacheutensis (Rusconi, 1953)

Text-figures 10–13

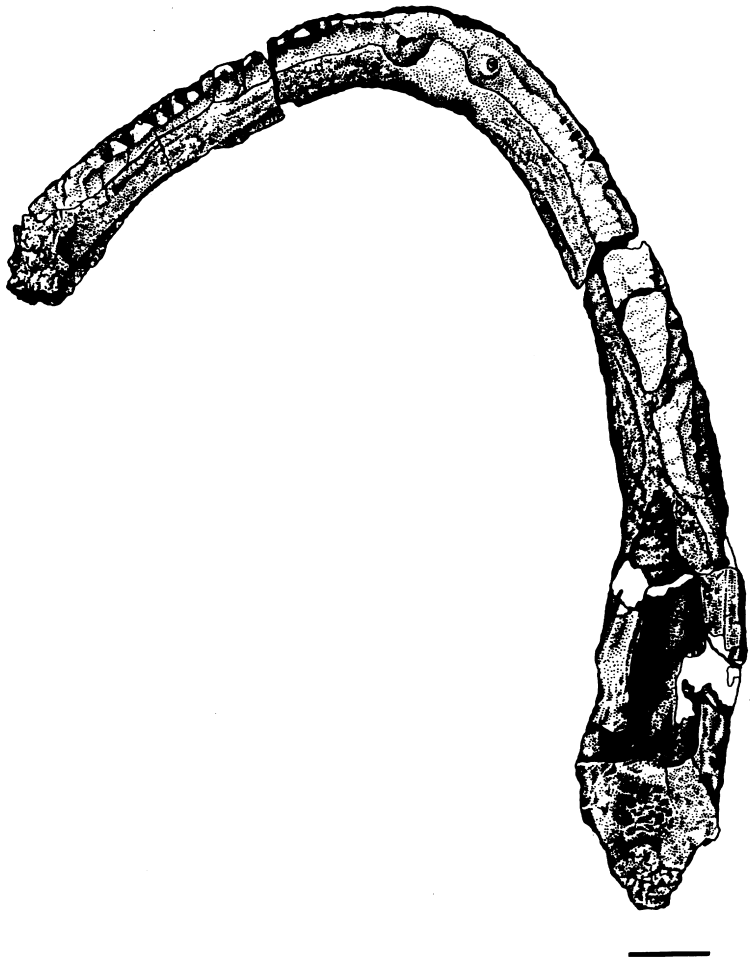
1953 *Chigutisaurus cacheutensis* Rusconi, p. 1.
1955 *Chigutisaurus cacheutensis* Rusconi, p. 86, figs 1–3.

Holotype. MCNA 2966, a partially preserved skull, mandible and a right humerus.

Locality and Horizon. South side of Cerro Cacheuta, Cacheuta locality, Province of Mendoza; Cacheuta Formation, lower Norian (Kokogian and Mancilla 1989; Kokogian *et al*. 1993; Zavattieri and Papu 1993; López-Gamundi *et al*. 1994). PVL 3463 was collected 1 km further south from Cerro Cacheuta; Cacheuta Formation.

Diagnosis. Chigutisaurid with a distinct, laterally expanded vertical process on the exoccipital, which continues as a lamina to merge with the paraoccipital process forming a dorsoventrally narrowed posttemporal fenestra. An extremely thick substapedial ridge is present. In the mandible, the symphyseal tusks are well separated from each other by the presence of a rounded protuberance.

Referred specimens. MCNA 2968, a nearly complete mandible; PVL 3463, a skull with the mandible preserved in articulation.

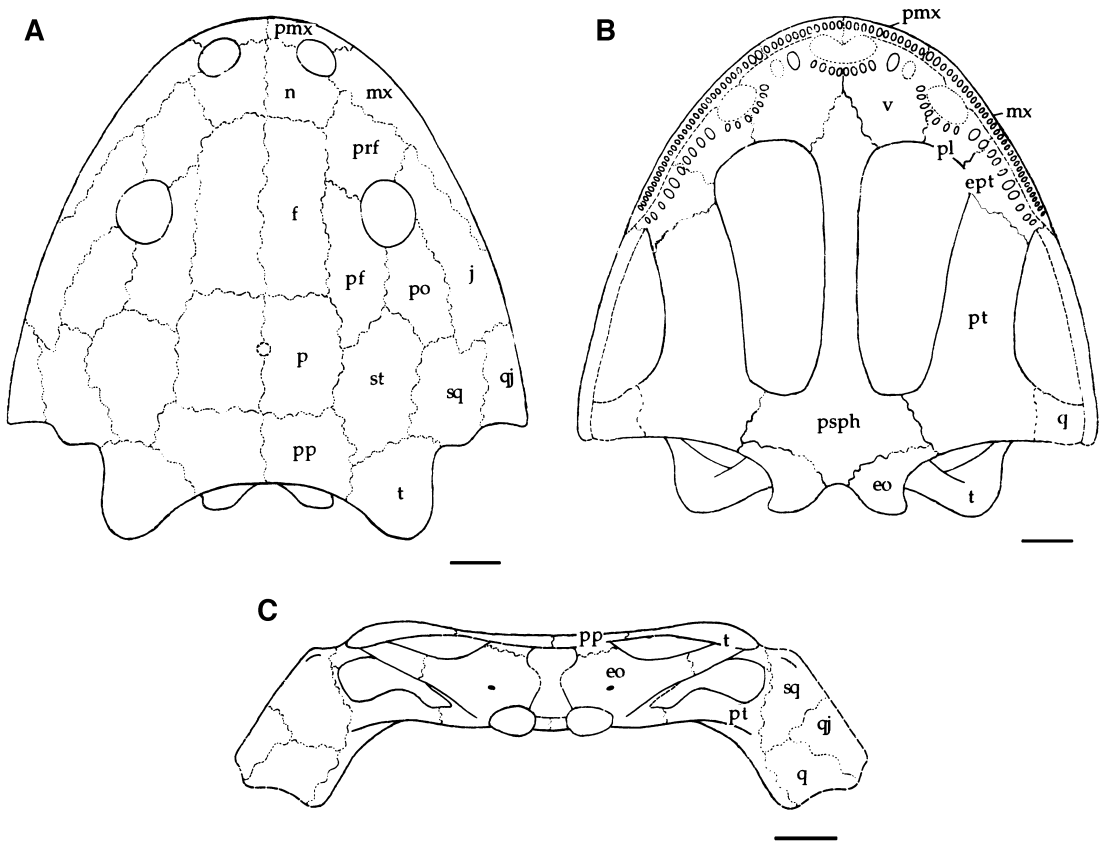


TEXT-FIG. 11. *Pelorocephalus cacheutensis* (Rusconi, 1953); MCNA 2968. Mandible in dorsal view. Scale bar represents 50 mm.

Description

The following description of MCNA 2966 and MCNA 2968 amends and supplements information and figures from Rusconi's (1953, 1955) descriptions. The holotype material (MCNA 2966) originally included a skull, a mandible and a humerus. The mandible was only mentioned in the original description of the taxon (Rusconi 1955) and is apparently lost. In the same paper Rusconi (1955) also mentioned two other skulls with mandibles (MCNA 2968 and 2967), recovered by him at a nearby locality, at the same stratigraphical level as the holotype material, and assigned by him to '*C. cacheutensis*'. Only the mandible of one of the specimens (MCNA 2968) was described by Rusconi and it was the only element available for redescription in the present work as the other remains are lost.

Skull roof (Text-figs 10A, 12A). The bones of the skull roof are poorly preserved so that most of the table is visible only as an internal mould. The ornamentation, where present, seems not to differ from that described for other members of the genus. No sensory canals are preserved. The skull is parabolic with the orbits located in the anterior half. The orbits are rounded and relatively small, and the external naris is oval and located on the anterior border of the roof. No pineal foramen is preserved. On the posterior border of the skull table the tabulars have broad-based tabular horns, the lateral surface of which forms the border of a broad otic embayment. In each embayment, a short postsquamosal process is



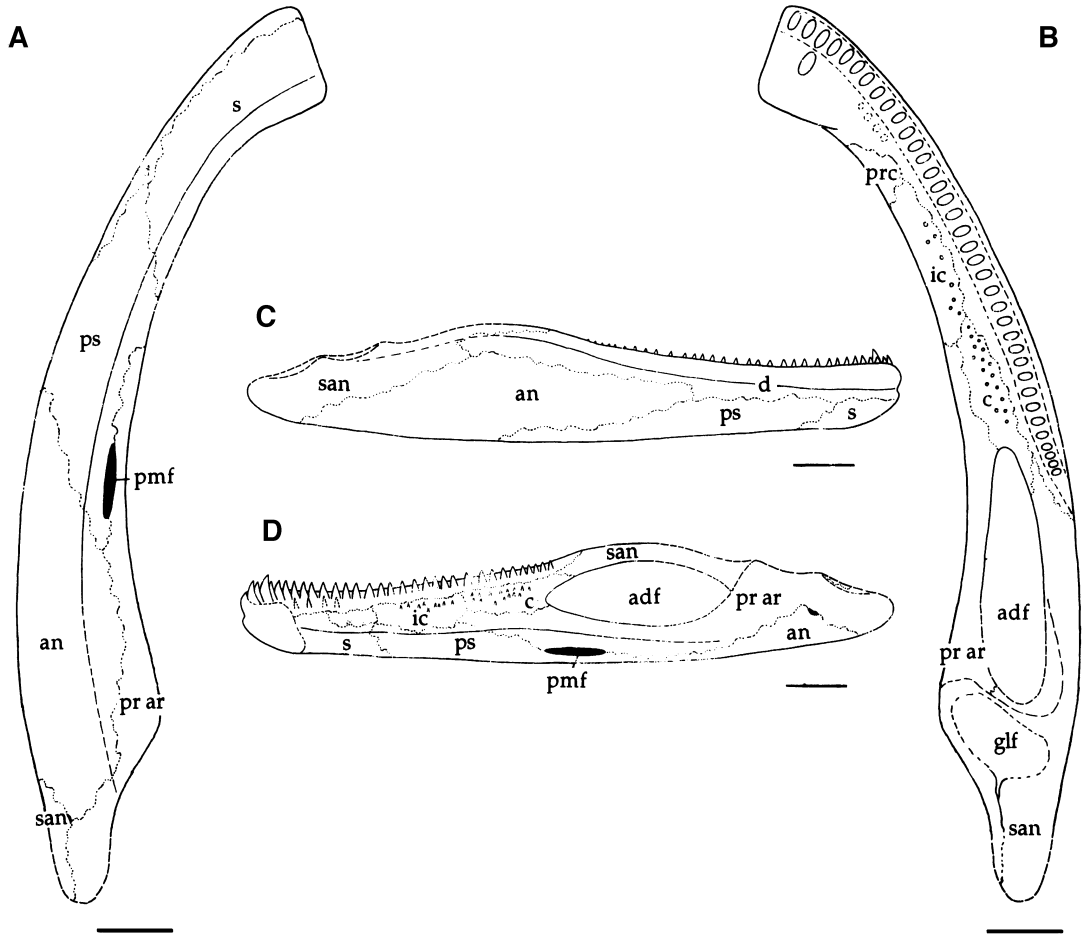
TEXT-FIG. 12. *Pelorocephalus cacheutensis* (Rusconi, 1953). Composite restoration of the skull in A, dorsal, B, ventral, C, posterior view. Scale bars represent 50 mm. Reconstructed outlines are shown by dashed lines and inferred position of the sutures by dotted lines. See Appendix 2 for abbreviations.

present and on the left quadratojugal a postquadratojugal process is developed. A deep narrow canal, that might correspond to the position of the sphenethmoid, is partially preserved in the skull midline.

Occiput (Text-figs 10C, 12C). Both pterygoid quadrate rami are missing, although the base of the left one is downturned. The substapedial ridge is present on the body of the right pterygoid. The ridge is particularly thick laterally, forming a blunt elevation on the corpus of the pterygoid in posterior view. A palatoquadrate fissure is absent as the ascending ramus of the pterygoid sutures with the descending portion of the squamosal. The exoccipitals have a vertical process that is strongly expanded laterally. These processes are continuous with the distal part of the paraoccipital process, forming a laminar area, and resulting in a dorsoventrally narrow posttemporal fenestra. The lamellar processes were apparently small, resulting in a small supraoccipital fossa. Both condyles are missing. A single small foramen is visible dorsolateral to each condyle, and probably represents the exit for the vagus (X) nerve. A squamosal-quadratojugal trough is present on the lateral wall of the occiput.

Palate (Text-figs 10B, 12B). The palate is only partially preserved. The interpterygoid vacuities are large with the borders nearly parallel-sided. The pterygoid has a longitudinally grooved palatal ramus and a long suture with the parasphenoid and the exoccipital. The parasphenoid has a relatively small, flat body.

Dentition (Text-fig. 12B). The marginal and palatal tooth rows are visible only on the right half of the palate as the teeth were preserved in the sediment that occupies that area. In the marginal row, the teeth diminish in size posteriorly and



TEXT-FIG. 13. *Pelorocephalus cacheutensis* (Rusconi, 1953). Composite restoration of the mandible in A, ventral, B, occlusal, C, labial, D, lingual view. Scale bars represent 50 mm. Reconstructed outlines are shown by dashed lines and inferred position of the sutures by dotted lines. See Appendix 2 for abbreviations.

are also more closely spaced. The marginal teeth are striated, curved lingually, and have a medial keel as described in the chigutisaurid *Siderops kehli* (Warren and Hutchinson 1983) (= xiphoid teeth of Warren and Davey 1992). The palatine teeth form a continuous row on the vomers, palatines and ectopterygoids, between the tusks and also medial to the choana.

Mandible (Paratype MCNA 2968; Text-figs 11, 13). Almost the entire mandible is preserved, although most of the sutures are not visible. The right ramus has a well-developed postglenoid area (PGA), which is broken off distally. The mandible is laterally compressed, but with a very thick symphyseal portion that bears a rounded protuberance separating the symphyseal tusks. The labial surface of the right ramus is ornamented and has a well-developed oral canal on the dentary and surangular. No mandibular and accessory sulci are present. On the lingual surface, the posterior Meckelian fenestra is located on the ventral border of the ramus at the level of the anterior border of the adductor fossa. Neither the anterior Meckelian fenestra nor the chordatympanic foramen are preserved. Part of the prearticular process is present on the right side, but no coronoid process is present.

The teeth preserved have the same shape as those previously described in MCNA 2966. Lateral to the symphysis, there is an additional tooth row on the dentary that follows the same line as the tusks. Also, there are patches of teeth on the middle and posterior coronoids.

Humerus. The element does not differ from other isolated humeri described by Marsicano (1994) from the same stratigraphical unit.

Description of new material: PVL 3463 (Text-fig. 12A–C). The specimen consists of a fairly complete skull with the mandible articulated. The sutures are not visible on the skull table and the labial surface of the mandible. The sculpture shows the same pattern exhibited by other specimens of the genus described here. As in *P. tenax*, the sensory canals are well developed, especially in the anterior half of the table where the supraorbital forms a deep canal around the nares and internal to the orbits. The nares are oval and their posterior border is raised above the surface of the skull roof. The orbits are nearly round and located in the anterior half of the skull, relatively close to the lateral border of the table. The pineal foramen is in the midline between the parietals. The posterior border of the table and the dorsal part of the exoccipitals are not preserved.

On the lateral wall of the occiput a well-developed squamosal-quadratojugal trough is present and no paraquadrate foramina are visible. The exoccipitals are partially preserved with only the ventral portions including the condyles present. They are rounded, relatively small and posteriorly projected. Both pterygoids are almost complete and, because the posterior border of the table is missing, the ascending ramus is visible. The ramus has the form of a thin lamina that curves forwards and inwards from its suture with the squamosal. The lamina is fan-shaped and ends slightly anterior to the substapedial ridge. It does not differ from those described in other South American chigutisaurs and the Australian chigutisaurid *Siderops kehli* (Warren and Hutchinson 1983). The substapedial ridge is nearly triangular when seen from above and remarkably broad when viewed from behind. The quadrate ramus of the pterygoid is deeply downturned and does not bear posterior projections.

As the mandibles are preserved in position, the external border of the palate is not visible. The interpterygoid vacuities are large and quadrangular. The corpus of the parasphenoid is flat and has a long suture with the pterygoids, which also contact the exoccipitals. The cultriform process is narrow and parallel-sided and has a longitudinal raised keel, although only the mid portion of this is preserved. The palatine rami of the pterygoids are longitudinally grooved. There is a continuous tooth row on the vomers, the palatines and the ectopterygoids, including large tusks on the vomers and palatines, and smaller ones on the ectopterygoids. Small denticles similar to those described for *P. tenax* are also present on the vomers.

The entire surface of the mandible is badly damaged, sutures are not visible, and neither the anterior nor the posterior Meckelian fenestra are preserved. Only the chordatympanic foramina are present on the lingual surface, below the glenoid area. On the dorsal surface of the PGA, a longitudinal ridge is preserved, as in other South American chigutisaurid mandibles, indicating the presence of a suture between the prearticular and the surangular. Dorsally, the symphysis bears a rounded protuberance that projects inside the anterior palatal vacuity when the mandible is in articulation with the skull.

PHYLOGENETIC ANALYSIS

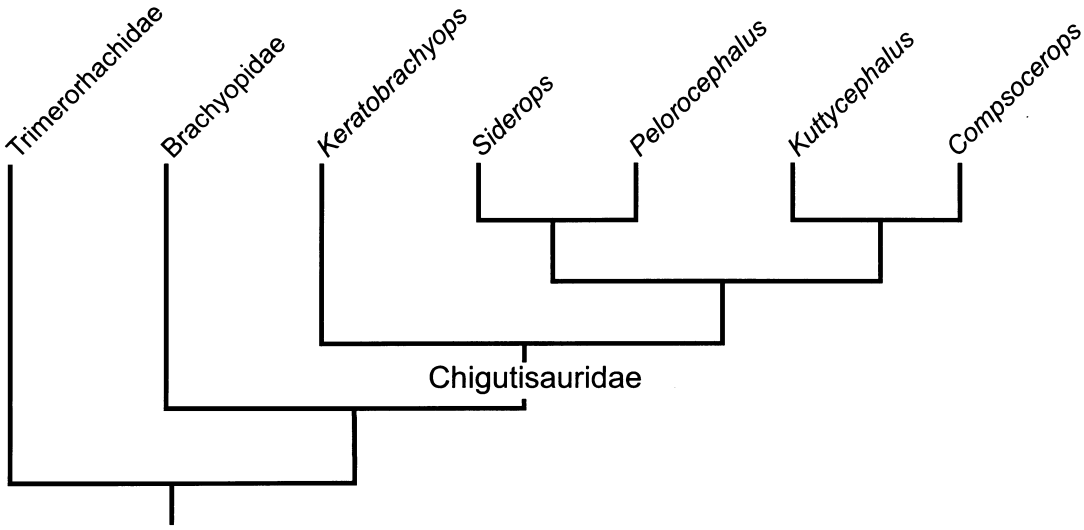
Materials and methods

The chigutisaurid genera *Pelorocephalus*, *Keratobrachyops*, *Siderops*, *Compsocerops* and *Kuttycephalus* were included as terminal taxa in the present analysis. The fragmentary temnospondyl material from the Cretaceous of Australia, *Koolasuchus cleelandi* (Warren *et al*. 1997) is discussed after the analysis. Two outgroups, Trimerorhachidae (Broom 1913; Nilsson 1944; Olson 1955; pers. obs.) and Brachyopidae (pers. obs.), were chosen following more inclusive analyses by Warren and Black (1985) and Milner (1990). Characters presented in Appendix 1 were analysed using both Hennig86 (Farris 1988) and PAUP 3.1 (Swofford 1993). Characters were treated as of equal-weight and multistate characters as unordered, except for character 12 that was treated as ordered.

Phylogenetic results

The same single shortest tree of 27 steps (Consistency index = 89 and Retention index = 80; see Appendix 1; Text-fig. 14) was found using both the exhaustive search option of Hennig86 (Farris 1988) and of PAUP 3.1 (Swofford 1993) to analyse the 19 character matrix of seven taxa.

Monophyly of Chigutisauridae is supported by four unequivocal synapomorphies: presence of a substapedial ridge (9); ascending ramus of the pterygoid strongly recurved inwards (12); absence of palatoquadrate fissure (10); and absence of a septomaxilla (2). The substapedial ridge was originally



TEXT-FIG. 14. Cladogram showing the phylogenetic relationships of chigutisaurids.

described by Warren and Hutchinson (1983) for the Australian *Siderops* and already identified as a chigutisaurid apomorphy by those authors. Previously, the same structure was figured by Rusconi (1951) for '*Chigutisaurus tenax*', but not labelled, and was described as a 'pterygoid thickening' in *Keratobrachyops* (Warren 1981). The substapedial ridge shows some variation, forming a single narrow ridge in *K. australis*, *P. mendozensis* and *P. tenax*, a double ridge in *S. kehli* and a thick, raised bar in *P. cacheutensis*. The presence of a markedly recurved, fan-shaped ascending ramus of the pterygoid is a unique condition of chigutisaurids and is present at least in the South American and Australian forms and in an isolated pterygoid described by Warren *et al*. (1997) for the Cretaceous temnospondyl *Koolasuchus*. The condition for both characters is unknown in the Indian chigutisaurids owing to the poor preservation of this area in the specimens, although in *C. cosgriffi* there is a 'thickening' on the pterygoid corpus that might suggest the presence of a substapedial ridge in that taxon (Sengupta, pers. comm. 1995). The absence of a palatoquadrate fissure in chigutisaurids has already been used by Warren (1981) and Warren and Black (1985) as a diagnostic character of the family.

The monophyletic group ((*Pelorocephalus* + *Siderops*) + (*Compsocerops* + *Kuttycephalus*)) is supported by two unequivocal synapomorphies (the presence of postsquamosal and postquadratojugal projections (5), and the absence of ornament on the palate (14)), and by the presence of a prearticular process on the mandible, a condition also present in the Permian Trimerorhachidae.

The Indian chigutisaurids (*Kuttycephalis* + *Compsocerops*) form a monophyletic group that is strongly supported by five synapomorphies: maxilla excluded from the border of the external nares (1); blunt projections on the posterior border of the postparietals (postparietal process) (6); postpterygoid processes (a projection of the posterior border of the pterygoid corpus) (7); a contact between the tabular and the parietal (3); and, in the mandible, the anterior Meckelian fenestra is located in the splenial (19). The presence of a reduced palatine tooth row (13), at least not continuous medial to the choana, is an equivocal synapomorphy of Indian chigutisaurids because it also occurs in Brachyopidae. The presence of a postparietal process (6) (considered by Sengupta (1995) as an autapomorphy of *Compsocerops*) is unknown in *Siderops*.

The clade (*Pelorocephalus* + *Siderops*) is supported by one unequivocal synapomophy: the presence of a suture between the surangular and prearticular on the postglenoid area of the mandible (17). This condition also occurs in the mandible of the Cretaceous temnospondyl *Koolasuchus* (Warren *et al*. 1997).

The monophyletic taxon Brachyopoidea (Brachyopidae + Chigutisauridae) is supported by four synapomorphies: presence of a vaulted palate (11), a coronoid process on the mandible (15), an ascending ramus of the pterygoid developed on the dorsal surface of the pterygoid corpus and curved inwards (12), and projected occipital condyles (8), although this last condition is reversed in *Siderops*.

DISCUSSION

The first attempt to analyse cladistically the relationships of chigutisaurids was carried out by Warren and Hutchinson (1983), although the Indian chigutisaurid material was not included since it was unknown at that time. Later, Marsicano (1993*a*, 1993*b*) performed a new phylogenetic analysis of the family (including the Indian taxa *Kuttycephalus* and *Compsocerops*) and related groups, which confirmed its position as the sister group to the Brachyopidae, as suggested by Warren and Hutchinson (1983). In Marsicano's analysis, the South American chigutisaurid *Pelorocephalus* and the Australian forms (*Keratobrachyops* + *Siderops*) are sister-groups, and the clade (*Kuttycephalus* + *Compsocerops*) the sister-group of (*Pelorocephalus* + (*Keratobrachyops* + Siderops)). Recently, Sengupta (1995) carried out another review of chigutisaurids which resulted in a cladogram exhibiting a different topology from that of Marsicano (1993*a*, 1993*b*), particularly in relation to the position of the Indian chigutisaurids, which do not form a monophyletic group in Sengupta's analysis. A more recent study by Damiani and Warren (1996) in which they analysed the phylogenetic relationships of brachyopoids (Brachyopidae + Chigutisauridae) supports a sister-taxa relationship for the Indian taxa *Kuttycephalus* and *Compsocerops*, although the remaining chigutisaurid relationships were unresolved in their analysis.

The results of the analysis presented herein support the inclusion of the Cretaceous *Koolasuchus* in Chigutisauridae, as proposed by Warren *et al*. (1997), based on the presence of the unique chigutisaurid type of pterygoid (shape of the ascending ramus and presence of substapedial ridge) in that specimen. Moreover, the Cretaceous taxon might be closely related to the clade (*Pelorocephalus* + *Siderops*) because it also exhibits a contact between the surangular and prearticular along the dorsal surface of the PGA in the mandible, a synapomorphy of that clade. The cladogram also shows a sister-taxa relationship between the Indian forms *Kuttycephalus* and *Compsocerops* which is strongly supported by several derived character states.

If the branching pattern revealed by the present cladogram is compared with the order of occurrence of chigutisaurid taxa in the fossil record, an equivalence of age and cladistic information is observed (Norell and Novacek 1992); thus the oldest records occupy the most basal positions in the cladogram and the youngest records the most derived. The oldest known representative of the family, the Australian *Keratobrachyops* from the Lower Triassic, appears to be the basal-most chigutisaurid and thus suggests an Australian origin for the group. The sister-taxon relationship of the Late Triassic Indian chigutisaurids supports the hypothesis of a relatively independent history of this group from the remaining chigutisaurids, probably related to the early isolation of the Indian plate from the rest of Gondwana during the Triassic (Wopfner 1991). By contrast, the Late Triassic South American chigutisaurids are closely related to the Australian post-Triassic chigutisaurids (*Siderops* and *Koolasuchus*), thus indicating a close connection between western Argentina and eastern Australia presumably via the Panthalassan margin of Gondwana (Veevers *et al*. 1994) during the early Mesozoic.

The South American chigutisaurids, represented by three different species, were apparently not contemporary forms. Stratigraphical evidence suggests that whilst *P. mendozensis* and the larger species *P. cacheutensis* may have been contemporary forms living in a lacustrine environment, *P. tenax* was collected from somewhat younger levels related to flood-plain deposits (Toledo 1987).

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REFERENCES

BONAPARTE, J. 1963. *Promastodonsaurus bellmanni*, capitosáurido del Triásico medio de Argentina. *Ameghiniana*, **3**, 67–78.

—— 1970. Annotated list of South American Triassic tetrapods. *Proceedings of the II Gondwana Symposium*, **3**, 665–682.

—— 1973. Edades reptil para el Triásico de Argentina y Brasil. *Actas del V Congreso Geológico Argentino*, **3**, 93–129.

—— 1975. Sobre la presencia del laberintodonte *Pelorocephalus* en la Formación Ischigualasto y su significado estratigráfico. *Actas del I Congreso Argentino de Paleontología y Bioestratigrafía*, **1**, 537–544.

—— 1978. El Mesozoico de América del Sur y sus tetrápodos. *Opera Lilloana*, **26**, 1–596.

BROOM, R. 1913. Studies on the Permian temnospondylous stegocephalians of North America. *Bulletin of the American Museum of Natural History*, **32**, 563–595.

CABRERA, A. 1944. Sobre un estegocéfalo de la provincia de Mendoza. *Notas Museo Universidad Nacional de La Plata IX, Paleontología*, **69**, 421–429.

DAMIANI, R. and WARREN, A. A. 1996. A new look at members of the Superfamily Brachyopoidea (Amphibia, Temnospondyli) from the Early Triassic of Queensland and a preliminary analysis of brachyopoid relationships. *Alcheringa*, **20**, 277–300.

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

FARRIS, J. S. 1988. *Hennig86. Version 1.5 software and documentation*. Port Jefferson Station, New York.

KOKOGIAN, D. A., FERNANDEZ SEVESO, F. and MOSQUERA, A. 1993. Las secuencias sedimentarias triásicas. 65–78. *In* RAMOS V. (ed.). *Geología y recursos naturales de Mendoza*. Relatorio del XII Congreso Geológico Argentino y II Congreso Exploración de Hidrocarburos, Buenos Aires, 762 pp.

—— and MANCILLA, O. 1989. Análisis estratigráfico secuencial de la Cuenca Cuyana. 169–201. *In* CHEBLI, G. and SPALLETTI, L. (eds). *Cuencas sedimentarias argentinas*. Serie Correlación Geologica N6, Instituto Superior de Correlación Geológica, Universidad Nacional de Tucumán, 1–512.

LOPEZ-GAMUNDI, O. R., ESPEJO, I. S, CONAGHAN, P. J. and POWELL, C. McA. 1994. Southern South America. 281–329. *In* VEEVERS, J. J. and POWELL, C. McA. (ed.). Permian–Triassic Pangean basins and foldbelts along the Panthalassan margin of Gondwanaland. *Memoir of the Geological Society of America*, **184,** 1–368.

MARSICANO, C. A. 1990. Redescripción del cráneo del holotipo de *Pelorocephalus mendozensis* Cabrera, 1944 (Amphibia, Temnospondyli) del Triásico del Cerro Bayo, Provincia de Mendoza. *Ameghiniana*, **27**, 39–44.

—— 1993*a*. Revisión de los anfibios chigutisáuridos ('Temnospondyli') del Triásico de Argentina. Relaciones evolutivas y aspectos paleobiogeográficos. Unpublished Ph.D. thesis, Universidad de Buenos Aires, Buenos Aires.

—— 1993*b*. Evolutionary relationships in the Triassic Gondwanan family Chigutisauridae (Amphibia, Temnospondyli). *Journal of Vertebrate Paleontology*, **13,** supplement 3, 48A.

—— 1994. Postcranial skeleton of a brachyopoid (Amphibia, Temnospondyli) from the Triassic of Mendoza (Argentina). *Alcheringa*, **17**, 185–197.

—— 1996. *Otuminisaurus limensis* Rusconi, 1948: a problematic temnospondyl amphibian from the Triassic of Argentina. *Journal of Vertebrate Paleontology*, **16**, 785–786.

MILNER, A. R. 1990. The radiations of temnospondyl amphibians. 321–349. *In*, TAYLOR, P. D. and LARWOOD, G. P. (eds). *Major evolutionary radiations*. Systematics Association Special Volume 42, 1–437.

—— 1993. The Paleozoic relatives of lissamphibians. *Herpetological Monographs*, **7**, 8–27.

NILSSON, T. 1944. On the morphology of the lower jaw of the Stegocephalia, with special reference to Eotriassic Stegocephalians from the Spitsbergen. II. General Part. *Kibugka Svenska Vetenskapsakad Handl, Series 3*, **21**, 3–70.

NORELL, M. A. and NOVACEK, M. J. 1992. Congruence between superpositional and phylogenetic patterns: comparing cladistic patterns with fossil records. *Cladistics*, **8**, 319–337.

OLSON, E. C. 1955. Fauna of the Upper Vale and Choza: 10. *Trimerorhachis*: including a revision of pre-Vale species. *Fieldiana, Geology*, **10**, 225–274.

REIG, O. A. 1961. Acerca de la posición sistemática de la familia Rauisuchidae y del género *Saurosuchus* (Reptilia, Thecodontia). *Publicaciones del Museo Municipal de Ciencias Naturales y Tradición*, **1**, 73–114.

—— 1962. Nuevos datos y nuevas hipótesis sobre la cenogénesis de los tetrápodos sudamericanos. *Physis*, **23**, 157–162.

RUSCONI, C. 1948*a*. Nuevo reptil estegocéfalo del triásico de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **2**, 203–206.

—— 1948*b*. Nuevos laberintodontes del triásico de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **2**, 225–229.

—— 1949. Otra especie de laberintodonte del triásico de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **3**, 93–94.

—— 1951. Laberintodontes triásicos y pérmicos de Mendoza. *Revista del Museo de Historia Natural de Mendoza*, **5**, 33–158.
—— 1953. Nuevo laberintodonte de Mendoza. Nota previa. *Boletín Paleontológico de Buenos Aires*, **26**, 1.
—— 1955. Acerca de los grandes laberintodontes de Cacheuta. *Revista del Museo de Historia Natural de Mendoza*, **8**, 85–101.
SENGUPTA, D. P. 1995. Chigutisaurid temnospondyls from the Late Triassic of India and a review of the family Chigutisauridae. *Palaeontology*, **38**, 313–339.
SWOFFORD, D. L. 1993. *PAUP: Phylogenetic Analysis Using Parsimony, version 3.1*. Computer program distributed by the Illinois Natural History Survey, Champaign, Illinois.
TOLEDO, M. 1987. Análisis de facies e interpretación paleoambiental de las sedimentitas triásicas del área Co. Bayo-Co. Melocotón, Departamento de Las Heras, Provincia de Mendoza. Unpublished Licenciatura degree thesis, Universidad de Buenos Aires, Buenos Aires.
VEEVERS, J. J., POWELL, C. McA., COLLINSON, J. W., LOPEZ-GAMUNDI, O. R. 1994. Syntesis. 331–353. *In* VEEVERS, J. J. and POWELL, C. McA. (eds). Permian–Triassic Pangean basins and foldbelts along the Panthalassan margin of Gondwanaland. *Memoir of the Geological Society of America*, **184**, 1–368.
WARREN, A. A. 1981. A horned member of the labyrinthodont superfamily Brachyopoidea from the Early Triassic of Queensland. *Alcheringa*, **5**, 273–288.
—— and BLACK, T. 1985. A new rhytidosteid (Amphibia, Labyrinthodontia) from the early Triassic Arcadia Formation of Queensland, Australia, and the relationships of Triassic temnospondyls. *Journal of Vertebrate Paleontology*, **5**, 303–327.
—— and DAVEY, L. 1992. Folded teeth in temnospondyls – a preliminary study. *Alcheringa*, **16**, 107–132.
—— and HUTCHINSON, M. 1983. The last labyrinthodont? A new brachyopoid (Amphibia, Temnospondyli) from the early Jurassic Evergreen Formation of Queensland, Australia. *Philosophical Transactions of the Royal Society of London, Series B*, **303**, 1–62
—— RICH, T. H. and RICH, P. V. 1997. The last last labyrinthodonts? *Palaeontographica*, *Abteilung A*, **247**, 1–24.
WELLES, S. P. and ESTES, R. 1969. *Haddrokosaurus bradyi* from the upper Moenkopi Formation of Arizona, with a review of the brachyopid labyrinthodonts. *University of California Publications in Geological Sciences*, **84**, 1–56.
WOPFNER, H. 1991. Permo-Triassic sedimentary basins in Australia and East Africa and their relationship to gondwanic stress pattern. 133–146. *In* ULBRICH, H. and ROCHA-CAMPOS, A. (eds). *Gondwana Seven Proceedings*, Seventh International Gondwana Symposium, Instituto de Geociencias, U.S.P., San Pablo.
ZAVATTIERI, A. M. and PAPU, O. H. 1993. Microfloras mesozoicas. 309–316. *In* RAMOS V. (ed.). *Geología y recursos naturales de Mendoza*. Relatorio del XII Congreso Geológico Argentino y II Congreso Exploración de Hidrocarburos, Buenos Aires, 762 pp.

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APPENDIX 1

Character List

1. External nares: maxilla included in the border (0); maxilla excluded (1).
2. Septomaxilla: present (0); absent (1).
3. Contact between tabular and parietal: absent (0); present (1).
4. Tabular horns: present (0); reduced or absent (1).
5. Postsquamosal and postquadratojugal processes: absent (0); present (1).
6. Postparietal process: absent (0); present (1).
7. Postpterygoid process: absent (0); present (1).
8. Occipital condyles: do not project (0); project (1).
9. Substapedial ridge on the dorsal surface of the corpus of the pterygoids and enters inside the substapedial fossa sagittally: absent (0); present (1).
10. Palatoquadrate fissure: present (0); absent (1).

11. Vaulted palate: absent (0); present (1).
12. Ascending ramus of the pterygoid: does not arise from the dorsal surface of the corpus of the pterygoid (0); the ascending ramus arises from the dorsal surface of the corpus of the pterygoid and curves slightly inwards (1); arises from the dorsal surface of the corpus of the pterygoid and recurves markedly inwards (fan-shaped) (2).
13. Palatal tooth row continuous on the palatal bone series and medial to the choana: present (0); absent (1).
14. Ornamented palatal bones: present (0); absent (1)
15. Coronoid process on the mandible: absent (0); present (1).
16. Prearticular process on the mandible: present (0); absent (1).
17. Prearticular in the PGA (= postglenoid area, *sensu* Jupp and Warren (1986), = retroarticular process): prearticular covers the lingual and part of the dorsal surface of the PGA, but does not form a suture with the surangular in the PGA (0); prearticular does not extend onto the PGA (1); prearticular occurs on the lingual and dorsal surface of the PGA and forms dorsally a suture with the surangular in the PGA (2).
18. Chordatympanic foramen: wholly within the prearticular (0); on the angular-prearticular suture (1); absent (2).
19. Anterior Meckelian fenestra: one or more fenestra in the postsplenial (0); one or more fenestra in the splenial (1); single fenestra on the splenial-postsplenial suture (2); absent (3).

Taxon-character state matrix

	CHARACTER																	
TAXON	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19
Trimerorhachidae	0	0	0	0	0	0	0	0	0	?	0	0	0	0	0	0	?	0	0
Brachyopidae	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	1	0	2	0
Pelorocephalus	0	1	0	0	1	0	0	1	1	1	1	2	0	1	?	0	2	1	2
Siderops	0	1	0	?	?	?	0	0	1	1	1	2	0	1	1	0	2	0	0
Keratobrachyops	0	1	0	0	0	0	0	1	1	1	1	2	0	0	1	1	1	0	3
Kuttycephalus	1	1	1	0	1	1	1	1	?	1	1	?	1	1	?	?	?	?	?
Compsocerops	1	1	1	0	1	1	1	1	?	1	1	?	1	1	1	0	0	0	1

APPENDIX 2

Abbreviations. adf, adductor fossa; amf, anterior Meckelian foramen; an, angular; ar, articular; c, coronoid; d, dentary; eo, exoccipital; ept, ectopterygoid; f, frontals; glf, glenoid fossa; ic, intercoronoid; j, jugal; k, keel on cultriform process; ms, muscle scar; mx, maxilla; n, nasal; p, parietal; par, ascending ramus of the pterygoid; pf, postfrontal; pl, palatine; pfm, posterior Meckelian fossa; pmx, premaxilla; po, postorbital; pp, postparietal; pr ar, prearticular; pr ar p, prearticular process; prc, precoronoid; prf, prefrontal; ps, postsplenial; psph, parasphenoid; p sq p, postsquamosal process; pt, pterygoid; q, quadrate; qj, quadratojugal; r, ridge; s, splenial; san, surangular; sq, squamosal; sr, substapedial ridge; st, supratemporal; t, tabular; v, vomer.