

A NEW SPECIES OF THE LATE TRIASSIC RHYNCHOSAUR *HYPERODAPEDON* FROM THE SANTA MARIA FORMATION OF SOUTH BRAZIL

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ABSTRACT. A new rhynchosaur, *Hyperodapedon huenei* sp. nov., is described from the Upper Triassic Santa Maria Formation of the Paraná Basin, Brazil. The holotype is an almost complete skull and mandible, collected at Inhamandá, in the state of Rio Grande do Sul, Brazil. The diagnosis of the genus *Hyperodapedon* Huxley is revised to include not only *H. huxleyi* Lydekker and *H. gordonii* Huxley (as generally accepted), but also the new species described here, various specimens usually assigned to '*Scaphonyx fischeri*' Woodward, and '*S. sanjuanensis*' Sill. *H. huenei* sp. nov. exhibits a number of plesiomorphic features and appears to be the least derived species of *Hyperodapedon*, forming a sister taxon to the remaining members of the genus. A preliminary phylogenetic analysis for the more derived rhynchosaurs is presented. '*Scaphonyx sulcognathus*' Azevedo and Schultz represents the sister taxon of *Hyperodapedon*, while '*Rhynchosaurus spenceri*' Benton is considered to be a more derived Middle Triassic rhynchosaur.

KEY WORDS: Rhynchosauria, *Hyperodapedon*, Triassic, Brazil.

RHYNCHOSAURS were herbivorous basal archosauromorphs that colonised most dry-land areas of Triassic Pangea. The oldest representatives of the group are small, rare forms such as *Mesosuchus* and *Howesia* (Dilkes 1995, 1998), known from the Early Triassic *Cynognathus* Assemblage Zone (Karoo Basin), in South Africa. The rhynchosaurs experienced a rapid diversification in the Middle Triassic, and during the Carnian (Late Triassic) they were the dominant first-level consumers in most of the terrestrial ecosystems in which they occurred. Late Triassic rhynchosaurs have been recorded in South and North America, Europe, Africa and India, and are usually assigned to the subfamily Hyperodapedontinae (Chatterjee 1969), which includes the well-known taxa *Hyperodapedon* and '*Scaphonyx*'.

The south Brazilian rhynchosaurs have been known since the beginning of the twentieth century, when Woodward (1907) described some fragmentary remains from the Santa Maria Formation, and coined the name *Scaphonyx fischeri*. Afterwards, a huge collection of these fossil reptiles was recovered from sediments of that stratigraphical unit, including a series of individuals described by von Huene (1929, 1942). Despite this great abundance, *S. fischeri* was believed for a long time to be the only rhynchosaur present in the Brazilian Triassic (Sill 1970), and recently this taxon has been argued to be a *nomen dubium* (Langer 1996). Newly collected specimens indicate, however, that the diversity of the Brazilian Late Triassic rhynchosaur fauna was much higher than previously thought and apart from the classic form (von Huene 1942), three other taxa are known: '*Scaphonyx sulcognathus*', the 'Marinate rhynchosaur' and *Hyperodapedon mariensis* (Tupi-Caldas 1933; Azevedo and Schultz 1987; Schultz and Azevedo 1990; Schultz and Barberena 1991).

The new rhynchosaur taxon described here is thus the fifth now known from the Santa Maria Formation. It appears to be a new species of *Hyperodapedon*, exhibiting most of the derived features of this rhynchosaur genus (Chatterjee, 1974; Benton, 1983a). The new species, however, retains plesiomorphic features, such as two ventral grooves on the maxilla, which indicate that it is more primitive than the previous known species of *Hyperodapedon*. This character, combined with the presence of a single dentary blade, is unique among rhynchosaurs, and provides significant new data for explaining the dental evolution of these reptiles.

LOCALITY AND GEOLOGY

The new *Hyperodapedon* species was collected at the Inhamandá locality, on the embankment of a secondary road, approximately 1 km east of the town of São Pedro do Sul, state of Rio Grande do Sul, Brazil (29°38' south, 54°08' east). The sediments cropping out at this locality belong to the Alemoa Member of the Santa Maria Formation, which is a continental red-bed sequence well known in the central area of Rio Grande do Sul. Mudstones intercalated with fine-grained sandstone layers are the commonest facies of the Santa Maria Formation, and were deposited in the floodplains of a braided fluvial system, under a semi-arid climate (Holz and Barberena 1994).

The Santa Maria Formation is part of the Gondwanan sequence of the Paraná Basin, and is well known for its high diversity of fossil tetrapods (Bonaparte 1982; Barberena *et al.* 1985). Biostratigraphical revisions (Anderson and Cruickshank 1978; Benton 1983b; Anderson and Anderson 1993) have usually assigned this stratigraphical unit, as a whole, to the Late Triassic. Various authors (Chatterjee 1969; Barberena 1977), however, have proposed the presence of at least two faunal assemblages of different ages in the Santa Maria Formation (see also Ochev and Shishkin 1988; Shubin and Sues 1991; Lucas 1998): a dicynodont dominated zone and a rhynchosaur dominated zone.

Sediments at the Inhamandá locality are certainly related to the rhynchosaur zone and are of Carnian age. Their fossil assemblage includes, apart from the new taxon here described, the classic Brazilian rhynchosaur '*Scaphonyx*' (von Huene 1942), as well as the stagonolepid *Aetosauroides*, taxa that are well known from the Santa Maria area, where the rhynchosaur zone was first defined (Barberena 1977). Moreover, these two taxa are also known from the Ischigualasto Formation of Argentina, that has been dated at 228 Ma (Rogers *et al.* 1993). Other tetrapods known from the rhynchosaur zone include the traversodontid *Gomphodontosuchus*, the proterochampsid *Cerritosaurus*, the dinosaur *Staurikosaurus*, the tritheledontid *Therioherpeton*, and several basal archosaurs such as *Rauisuchus* and *Hoplitosuchus* (von Huene 1929, 1942; Price 1946; Colbert, 1970; Bonaparte and Barberena 1975).

Repository abbreviation. UFRGS, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

SYSTEMATIC PALAEOLOGY

Order RHYNCHOSAURIA Osborn, 1903
 Family HYPERODAPEDONTIDAE Lydekker, 1885
 Subfamily HYPERODAPEDONTINAE Chatterjee, 1969
 (nom. trans. ex Lydekker, 1885)
 Genus HYPERODAPEDON Huxley, 1859

Type species. *Hyperodapedon gordonii* Huxley, 1859.

Revised diagnosis. Rhynchosaur with: frontal ornamentation with lateral grooves that have approximately the same depth throughout; ventral process of the squamosal plate-like; only one dentary blade; no primary lingual teeth on the dentary; more than two teeth in transverse sections through the maxillary area lateral to the main groove.

Distribution. Upper Triassic (Carnian) of South America (southern Brazil and north-western Argentina), Africa (Tanzania and Zimbabwe), Europe (northern Scotland), North America (Nova Scotia), and India (Boonstra 1953; Baird 1963; Chatterjee 1974; Benton 1983a; Schultz and Barberena 1991; Raath *et al.* 1992; Contreras 1997).

Hyperodapedon huenei sp. nov.

Text-figures 1–5

Derivation of name. In honour of the famous German palaeontologist Prof. Friedrich von Huene, in recognition of his many important contributions to the study of the Triassic herpetofauna of southern Brazil.

Holotype. UFRGS PV 0132T, a nearly complete skull and mandible.

Diagnosis. Species of *Hyperodapedon* with: unique combination of two maxillary grooves and a single dentary blade; infraorbital foramen (*sensu* Benton, 1983a) absent; supraoccipital and opisthotics fused together.

Locality and horizon. Inhamandá outcrop, east of São Pedro do Sul, Rio Grande do Sul, Brazil. Beds of the rhynchosaur zone (Carnian), Santa Maria Formation, Rosário do Sul Group.

Referred specimens. Remains tentatively referred to this taxon include UFRGS PV 0410T, a fragmentary maxilla and dentary from the 'Cerro da Alema' outcrop and UFRGS PV 0413T, a juvenile dentary from the Inhamandá outcrop.

DESCRIPTION

This description is based only on the holotype (UFRGS PV 0132T);

Skull

The skull does not exhibit any dorsoventral deformation, but was compressed on its anterior left side; thus the left side of the skull is broader than the right (Text-figs 1A, D, 2A, 3A). This compression may also have affected the rostral area of the skull, breaking the anterior edge of the nasals and the posterodorsal region of the premaxillae (Text-figs 1A–C, E, 2). In addition, on the left side of the skull, the more lateral portion of the quadratojugal and the ventral ramus of the squamosal may have been anteroposteriorly compressed, and thus appears to be more laterally extended (Text-figs 1A, C–E, 2, 3A). These distortions have affected the relationship between the maximum breadth and the midline length of the skull. Thus even compared with other species of *Hyperodapedon*, which have very broad skulls (Chatterjee 1974; Benton 1983a), the temporal region of the skull of *H. huenei* is relatively much wider in relation to the midline length (Table 1).

Regardless of the taphonomic distortions, the skull is of average size compared to other described *Hyperodapedon* species (von Huene 1942; Sill 1970; Chatterjee 1974; Benton 1983a), and its general proportions (Table 1) are also not significantly different from those of other derived rhynchosaurs such as '*Rhynchosaurus spenceri*' and '*Scaphonyx sulcognathus*' (Azevedo and Schultz 1987; Benton 1990). It is distinct, however, from more primitive forms such as *Stenaulorhynchus* and *Rhynchosaurus articeps* (von Huene 1938; Benton 1990), in which the skulls are longer than broad.

The skull is roughly triangular in dorsal view, with a very short rostral region. As in all known Mid–Late Triassic rhynchosaurs, the premaxillae are edentulous beak-like structures, with a strong ventral projection. Other features of the skull, however, are as yet only found in Late Triassic rhynchosaurs; for example, the dorsally oriented orbits and the alignment between the occipital condyle and the quadrates. The skull of *H. huenei* is a little deeper (Text-figs 1B, 3C, E) than those of *H. gordonii* (Benton 1983a) and '*Scaphonyx fischeri*' (von Huene 1942), and is thus more similar to the skull of *H. huxleyi* (Chatterjee 1974) in this respect.

The suture arrangement is clearly seen, and the parietal is longer than the frontal, a typical feature of Mid–Late Triassic rhynchosaurs. The supratemporals, however, that are present in the Middle Triassic forms (von Huene 1938; Benton 1990), are absent in *H. huenei*.

Dermal bones of the skull roof. The paired premaxillae (Text-figs 1A–E, 2, 3A) are dorsoventrally oriented, a feature that is apomorphic for Rhynchosauria. The shape of the anterodorsal margin of the maxillae suggests, however, that their ventral portion was originally more anteriorly placed, having been displaced backward by taphonomic compression of the skull. The dorsal portion of each premaxilla fits into a notch posteriorly. The notch crosses the anterior border of the vomer and maxilla, and extends onto the prefrontal and nasal as a superficial groove. The prefrontal-premaxilla contact is also apomorphic for rhynchosaurs, and found in all members of the group. The dorsal portions of the premaxillae are oval in cross section and form the lateral border of the single external naris. Although their dorsal ends are incomplete, their posterior limits can be determined indirectly from the position of the articular grooves into which they fitted. Ventrally, each premaxilla converges medially to meet its opposite through an unsutured symphysis that limits the anterior border of the naris. In this area, the premaxillae reach their greatest breadth, are triangular in cross section, and have a flattened medial face where they meet. The ventral ends of the premaxillae thin abruptly, showing signs of wear, mostly evident on the anterior face. This feature is not present in all rhynchosaur specimens and may indicate that the specimen described here is a relatively old individual. The medial face of the premaxillae do not exhibit the indentation mentioned by Sill (1970, p. 350) for some South American rhynchosaur specimens (von Huene 1942, pl. 31, fig. 1e; Sill 1970, pl. 2, fig. b).

TABLE 1. Main measurements (in mm) of the skull and mandible of *Hyperodapedon huenei*, UFRGS PV 0132T (holotype).

Skull midline length	146
Maximum skull width	289
Maximum skull height	117
Maximum width of maxillary tooth bearing area (left)	37
Maxillary tooth bearing area length (left)	98
Mandible length (left)	251
Mandible depth at the coronoid (left)	71

The limits of the paired nasals (Text-figs 1A, 2A) are difficult to determine, because of a series of fractures at their anterior ends (and on the lateral side of the left bone). As for all rhynchosaurs, their anterior margin forms the posterior border of a single medial external naris, and there is no sign of an anteromedial process as seen in *Mesosuchus* (Dilkes 1998). Each nasal bears an anterolateral process that extends ventrally below the posterior end of the premaxilla and meets the anterior ascending process of the maxilla. The medial portion of this process, which lies medial to the premaxilla, forms part of the posterolateral border of the external naris.

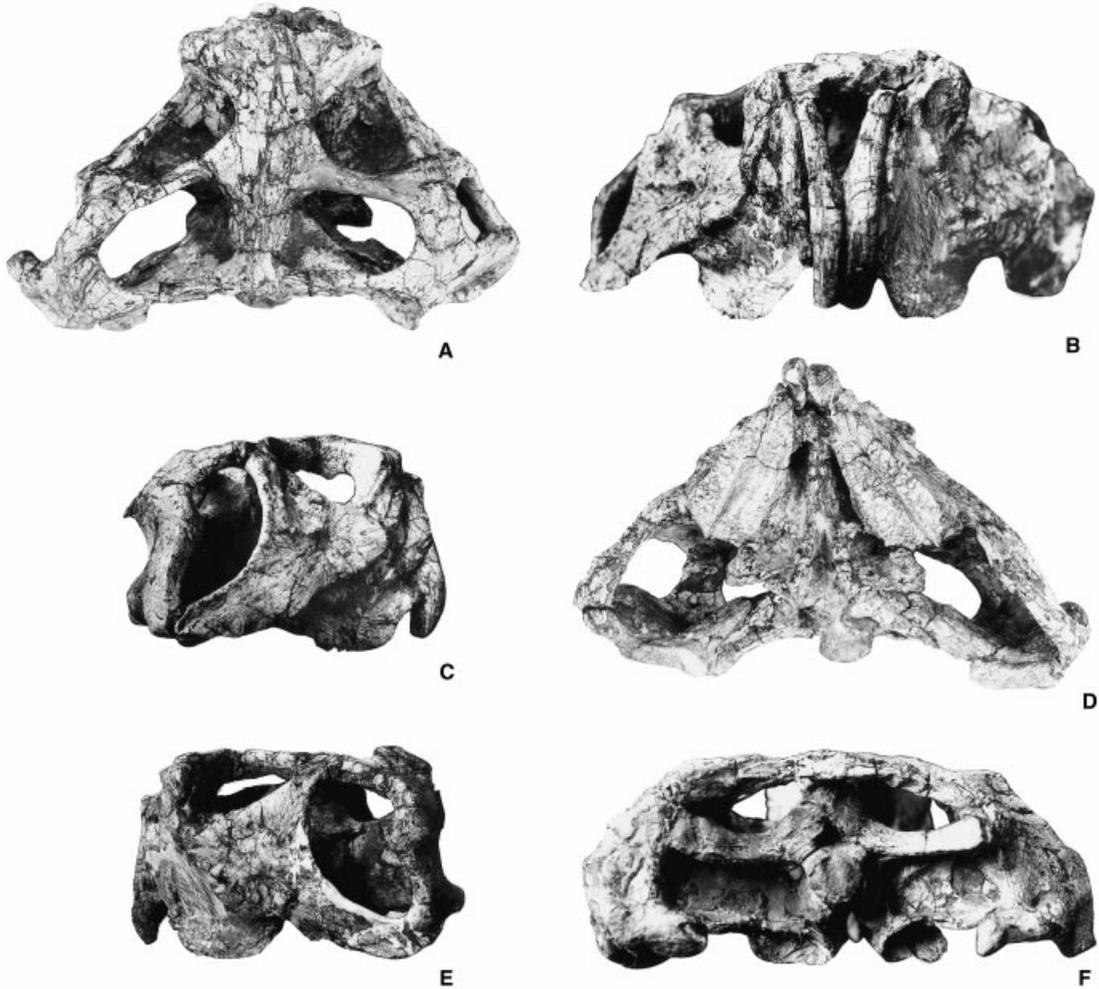
Both frontals (Text-figs 1A, 2) are clearly delimited and form the interorbital region of the skull roof. Along the median suture, the topography of the frontals is quite similar to that of *H. gordonii* (Benton 1983a, fig. 4), with a marked median ridge that appears to be continuous with the sagittal crest of the parietal. Lateral to this suture, each frontal bears an anteroposteriorly oriented shallow groove, identified by Dilkes (1998) as an apomorphic feature of rhynchosaurs. The groove extends along the entire length of the bones and is of the same depth throughout, thus differing from the condition seen in '*Scaphonyx sulcognathus*' and *Stenaulorhynchus* (von Huene 1938; Azevedo and Schultz 1987), in which it deepens posteriorly. A narrow process of the parietal interdigitates with the frontals on their posteromedial margins, as described in *H. gordonii* (Benton 1983a, fig. 4).

The fused parietals (Text-figs 1A, F, 2, 3B) form a T-shaped element, with two laterally diverging wings at their posterior end and a single long ramus directed anteriorly. The anterior ramus bears a prominent sagittal crest, but there is no evidence of a pineal foramen. Anteriorly, this ramus becomes wider and butts firmly against the frontals and the postfrontals. The parietal also articulates with the postorbitals via short, diverging anterolateral processes that take part in the anteromedial border of the upper temporal fenestrae. Ventrally, on the median portion of the sagittal ramus, a pair of flat descending processes of the parietal accommodate the supraoccipital medially and receive the dorsal end of the ascending process of the epipterygoid anteriorly.

Similar to the condition in all other Mid-Late Triassic rhynchosaurs, the posterior wings of the parietal are directed laterally, rather than posterolaterally, as in the Early Triassic forms (Dilkes 1995, 1998). The wings are, however, much longer than those of Middle Triassic rhynchosaurs (von Huene 1938; Benton 1990), and approach the condition found in Late Triassic forms (von Huene 1942; Chatterjee 1974; Benton 1983a). Each wing meets the medial process of the squamosal laterally, overlapping this bone posteroventrally. The posterior surface of the medial portion of each parietal wing has ventral and dorsal borders separated by a shallow groove.

The lacrimal (Text-figs 1A-C, 2) is a small, robust element that forms part of the anterior border of the orbit. This border is well marked by a ridge that, in posterior view, extends dorsoventrally along the whole length of the lacrimal, dividing the bone into lateral and ventromedial portions. The lacrimal is firmly attached to the prefrontal dorsally and medially, and the dorsal limit of its ridge takes part in the composition of a rugose projection on this bone. Its ventral portion is wedge-shaped and firmly attached to the jugal posteriorly and to the maxilla anteriorly. Its ventromedial portion extends dorsally to the medial side of the anterior process of the jugal and meets an ascending process of the palatine. This portion forms part of the inner surface of the orbital cavity and bears a concavity that probably received the openings for the lacrimal duct, though these openings are not visible.

The L-shaped prefrontal (Text-figs 1A-C, E, 2) has a broad posteromedial branch, which forms most of the anteromedial orbital border, and a ventral process. The posteromedial branch bears a conspicuous dorsal groove and is wider and broader anterolaterally. On its dorsal surface, the prefrontal forms most of a strong rugose protuberance that appears to be characteristic of Late Triassic rhynchosaurs, although a similar structure is known for *Stenaulorhynchus* (von Huene 1938). Anterior to that protuberance, the prefrontal extends anteroventrally, bearing an anterior groove for the accommodation of the premaxilla and meeting the ascending process of the maxilla. The ventral process of the prefrontal consists of a flat sheet of bone that makes up most of the anterior part of the orbital cavity and separates it from the nasal capsule. This process abuts the lacrimal anteroventrally and touches the ascending process of the palatine posteroventrally.

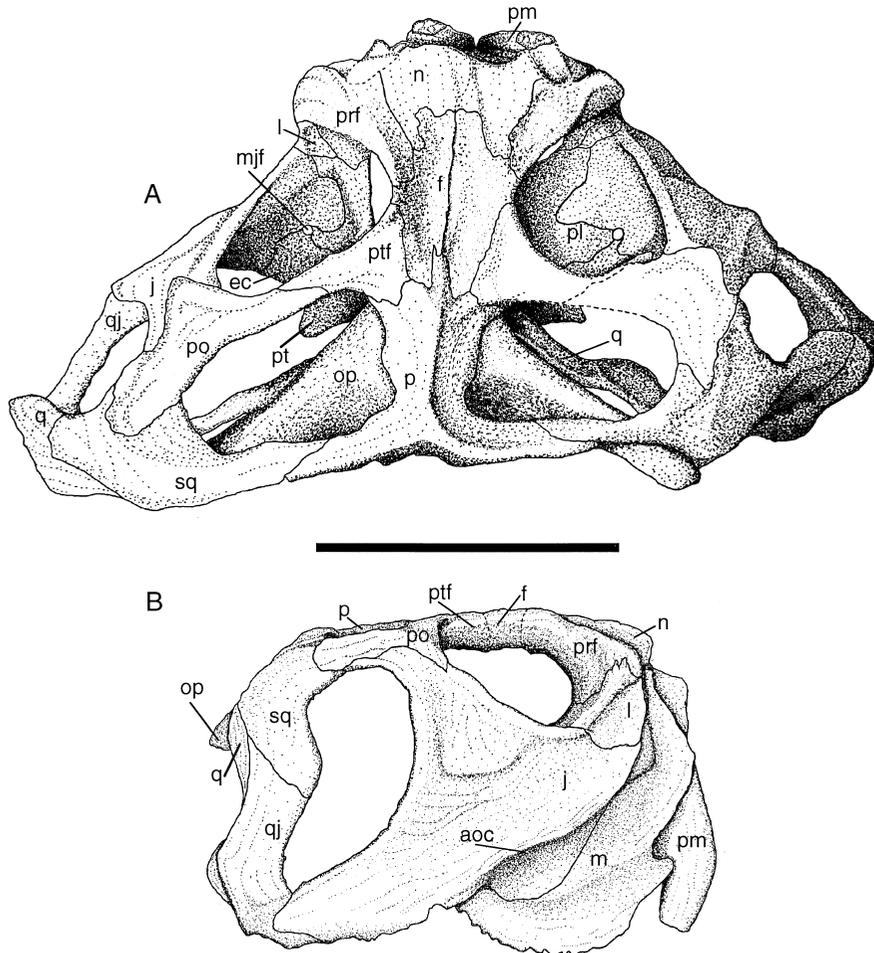


TEXT-FIG. 1. Skull of *Hyperodapedon huenei* sp. nov., UFRGS PV0132T, holotype. A, dorsal view; B, frontal view; C, right lateral view; D, ventral view; E, left lateral view; F, occipital view; $\times 0.25$.

The postfrontal (Text-figs 1A, C, E, 2) is a triangular element composed of an anteroposteriorly directed body and a posterolateral process. The dorsal surface of the main body bears a shallow depression on its anterior portion, apparently a rhynchosaurian apomorphy (Dilkes 1998). Posterior to that depression, the postfrontal bears a protuberance that projects from the parietal and represents laterally divergent extensions of the sagittal crest. Its posterolateral process overlaps the anterior side of the medial process of the postorbital, and takes part in the anteromedial border of the upper temporal fenestra, dorsal to the contact between the parietal and the postorbital.

The postorbital (Text-figs 1A, C, E, 2) is typical of a Mid–Late Triassic rhynchosaur, in that the posterior process is longer than the ventral. In this respect it differs from Early Triassic forms which have a longer ventral process (Dilkes 1998). The short ventral process of *H. huenei* sutures firmly with the ascending process of the jugal, overlapping it externally. The posterior process, on the other hand, overlaps the anterodorsal tongue-like process of the squamosal and forms the external surface of the intertemporal bar. Shallow depressions are seen externally on the central portion of the bone, and extend along the entire length of the posterior process.

The jugal (Text-figs 1A–E, 2, 3A) is a large and complex element that occupies most of the cheek region. The external surface of its anterior process overlaps the maxilla ventrally, and has a well marked *anguli oris* crest (Sill



TEXT-FIG. 2. Skull of *Hyperodapedon huenei* sp. nov., UFRGS PV0132T, holotype. A, dorsal view; B, right lateral view. For explanation of abbreviations, see Appendix. Scale bar represents 100 mm.

1971) which begins in the posterior portion of the maxilla-jugal suture and extends (as an extension of the ventral border of the posteroventral process) anterodorsally along the entire length of the anterior process, reaching the anterior end of the jugal and extending anteriorly along the posterior portion of the maxilla-lacrimal suture. Such a well-developed *anguli oris* crest is typical of more derived rhynchosaurs including '*Rhynchosaurus*' *spenceri* and the Late Triassic forms (Chatterjee 1974; Benton 1983a, 1990). Primitive rhynchosaurs such as *Stenaulorhynchus* and *Rhynchosaurus articeps*, on the other hand, have a shorter *anguli oris* crest, that is restricted to a ventral shelf on the posterior part of the anterior jugal process (von Huene 1938; Benton 1990). The row of foramina that is present below this crest in other species of *Hyperodapedon* (Chatterjee, 1974; Benton, 1983b) is not seen in *H. huenei*.

The inner surface of the anterior jugal process bears a diagonal crest that extends in roughly the same direction as the external *anguli oris*. This crest is more pronounced anterodorsally, where the jugal attaches to the lacrimal. Ventral to that suture, the jugal has a descending ridge (anterior to the diagonal crest) that is overlapped by the ascending process of the palatine. Beneath the palatine, this crest overlaps part of the dorsal surface of the anterior portion of the maxilla, where it meets the lateral projections of the anterior portion of the vomer. More posteriorly, this portion of the jugal forms most of the ventral surface of the orbital cavity, overlapping the maxilla and meeting the palatine

anteromedially and the lateral process of the ectopterygoid posteromedially. The canal extending between the anterior descending ridge of the jugal and the ascending process of the palatine (infraorbital foramen *sensu* Benton 1983b) does not seem to be present in *H. huenei*, although it is seen in other species of *Hyperodapedon* (Chatterjee 1974, fig. 4b; Benton 1983a, fig. 6b).

The dorsal process of the jugal forms the main part of the bar between the orbit and the lower temporal fenestra, and touches the anterior process of the squamosal through a small posterodorsal extension. The inner surface of that process has a vertical crest that marks the posterolateral limit of the orbital cavity. The ventral portion of the crest is more developed medially, has a firm contact with the dorsal surface of the maxilla and is overlapped posteriorly by the lateral process of the ectopterygoid. The medial jugal foramen appears to be located anterior to this crest, at the junction between the jugal, ectopterygoid and palatine, as in *H. gordonii* (Benton 1983a, fig. 6b) but not in *H. huxleyi* (Chatterjee 1974, fig. 4b), in which the palatine does not border that foramen.

On the external surface of the jugal, a second, less well-developed crest is present, dorsal, but almost parallel, to the main *anguli oris* crest. Similar ornamentation also occurs in '*Rhynchosaurus*' *spenceri* (Benton 1990, p. 265), *H. gordonii* (Benton 1983a, p. 620, fig. 5a), and in most South American Upper Triassic rhynchosaurs (von Huene 1942; Sill 1970), but is unknown in more primitive rhynchosaurs (von Huene 1938; Benton 1990).

The quadratojugal is L-shaped (Text-figs 1–3) as in all Mid–Late Triassic rhynchosaurs, with a stout dorsal limb and an anteroventral process. In this respect *H. huenei* differs from Early Triassic rhynchosaurs, which lack the anteroventral process, and thus have an infratemporal fenestra that is open ventrally (Dilkes 1995, 1998). The dorsal limb bifurcates dorsally, forming anterior and posterior plate-like ascending processes that envelop the descending ventral limb of the squamosal. The anteroventral process forms the medial surface of the posterior half of the infratemporal bar, where it is overlapped externally by a tongue-like process of the jugal. Ventrally, the quadratojugal has a short and broad medial process that meets the quadrate, forming the ventral border of a prominent quadrate foramen.

The squamosal (Text-figs 1–3) forms most of the temporal region of the skull. The upper portion of its medial surface bears a depression that accommodates the paroccipital process and is isolated from the lower temporal fenestra by the wings of the parietal. The ventral limb is very broad and bears a well-developed anterolateral extension that forms the posterodorsal border of the lower temporal fenestra. Ventrally, this part of the squamosal extends over the quadrate and fits between the limbs of the quadratojugal.

Dermal bones of the palate. The maxilla (Text-figs 1B–E, 2B, 3A) consists of a blunt body, its ventral face bearing teeth, and a thin anterolateral ascending process. The medial surface of the ascending process forms most of the lateral surface of the nasal cavity, while its posterior surface attaches firmly to the lacrimal dorsally and to the anterior process of the jugal ventrally. This process becomes wider dorsally, meeting the nasal dorsomedially and the prefrontal dorsolaterally. At the base of this process, where it meets the body of the maxilla, there is an anterior invagination, as is found in all Mid–Late Triassic rhynchosaurs.

The heavily-built portion of the maxilla is anteromedially to posterolaterally oriented. The tooth-bearing area is ventrally convex and broader posteriorly, with the medial margin convex and the lateral concave. Its ventral surface is composed of two main tooth-bearing areas separated by a longitudinal groove into which the blade of the dentary fitted during occlusion.

On its medial margin, the basal portion of the maxilla receives the vomer anteriorly and the palatine posteriorly. Between these two articulations, it forms part of the lateral border of the choana. Anteriorly, the dorsal surface of the maxilla paves most of the bottom of the nasal cavity, and is not overlapped by other bones. Posteriorly, parts of this dorsal surface are overlapped by medial projections of the anterior process of the jugal laterally, by the palatine anteromedially and by the lateral process of the ectopterygoid posteromedially. There is a groove between the posterodorsal margin of the maxilla and the overlying portions of the jugal and ectopterygoid.

Each of the paired vomers (Text-figs 1D, 3A) consists of a deep, anteroposteriorly directed body, and a small flat process extending laterally from its anterior portion. Its posterior surface makes up the anteromedial border of the choana, and the posterior end is firmly connected to the palatal ramus of the pterygoid, meeting the palatine laterodorsally. The lateral process of the vomer forms the anterolateral border of the choana and is firmly clamped to the anteromedial face of the maxilla. It overlaps a small area of that bone dorsally, touching a medial projection of the descending process of the jugal. The dorsal surface of the vomers forms the bottom of the nasal cavities and has a low medial crest that appears to have supported a cartilaginous nasal septum.

The palatine (Text-figs 1D, 3A) is a very complex bone that does not seem to contact its opposite at any point. Its anterior portion bears a plate-like process that overlaps the anterior process of the pterygoid laterally and touches the vomer anteriorly. This process lines the upper part of the medial surface of the choana. Dorsally, it has a plate-like extension that is folded laterally, roofing the posterior part of the internal naris. The posterodorsal portion of the palatine has a pronounced lateral extension that overlaps the maxilla, borders the medial jugal foramen, enters the

inferior orbital foramen posteriorly and meets a descending crest of the dorsal process of the jugal laterally. Its anterodorsal portion, on the other hand, is much thicker. It is firmly attached to the prefrontal and lacrimal and forms a strong ascending process that overlaps the vertical inner crest of the anterior process of the jugal. In this feature, *H. huenei* seems to differ from *H. gordonii*, in which the anterior border of the lateral extension of the palatine overlaps the anterior end of the maxilla and meets the lateral process of the anterior portion of the vomer (Benton 1983a).

The posteroventral portion of the palatine has two divergent processes: one extends posteromedially, overlapping the pterygoid and forming the posterior border of the choana. The other extends anterolaterally, overlapping the posterior portion of the medial surface of the maxilla. It also meets the ectopterygoid posteriorly, excluding the maxilla from the border of the inferior orbital foramen. Although the exclusion of the maxilla from that opening is a characteristic feature of most Mid–Late Triassic rhynchosaurs (von Huene 1938, 1942; Chatterjee 1974; Benton, 1983a, 1990), the arrangement of its border is variable. In '*Scaphonyx sulcognathus*' the palatine is excluded from that aperture by the ectopterygoid (Azevedo 1982), while in *Stenaulorhynchus* this last bone does not appear to enter the foramen (von Huene 1938).

The ectopterygoid (Text-figs 1A, D, 2A, 3A) is an L-shaped element, with one process directed posteroventrally and the other dorsolaterally. The first process overlaps the lateral portion of the ectopterygoid process of the pterygoid ventrally, meeting the maxilla anteriorly. The dorsolateral process is firmly attached to the inner crest of the dorsal process of the jugal, overlapping it dorsally. Following the direction of the jugal crest, it forms the posterior corner of the orbital cavity, which divides the process into two surfaces. The posterior surface extends ventrally, fitting against the posterior border of the maxilla on its ventral margin. The anterior surface overlaps the posterodorsal portion of the maxilla, bordering the inferior orbital foramen and the medial jugal foramen, and meets the palatine anteriorly.

Each pterygoid (Text-figs 1A, D, F, 2A, 3) has a deep and heavily built, anteroposteriorly directed palatal ramus and two laterally directed plate-like processes arising from its posterior portion: the ectopterygoid and the quadrate process. The posterior portions of the palatal rami descend under the neurocranium, forming two lateral branches that delimit a narrow interpterygoid vacuity. In dorsal view, the single septum that is present on the anterior portion of the rami splits into two interorbital septa that extend laterally to make up the medial portion of the posterior border of the orbital cavity.

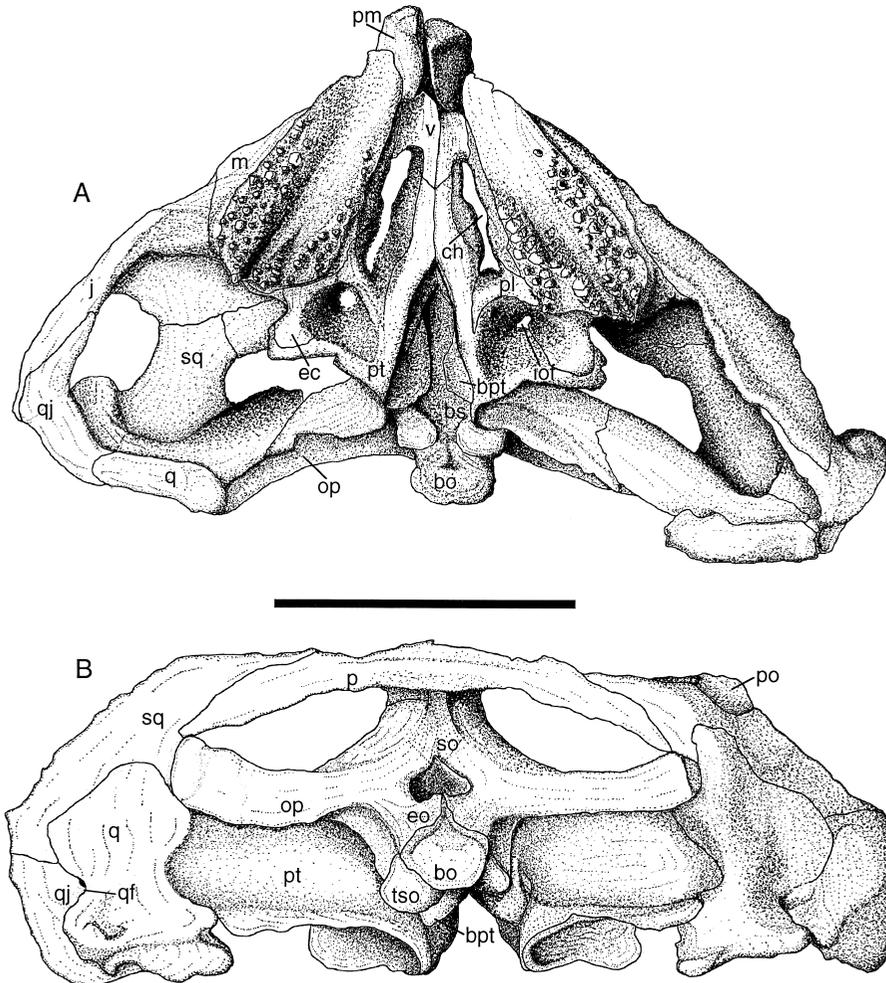
The small ectopterygoid process extends laterally from the posterior portion of the palatal ramus and its lateral portion is overlapped ventrally by the ectopterygoid. The quadrate process is a thin sheet of bone, well developed dorsoventrally, with a deep concavity on its posterior surface. It extends posterolaterally from the articulation surface between the posterior edge of the palatal ramus and the neurocranium. Its medial surface articulates with the basisphenoid ventrally and the basal portion of the epipterygoid and the ventral part of the pro-otic dorsally. Laterally, this process is elongated, meeting the paroccipital process along its entire dorsal margin and overlapping the quadrate posteriorly.

Quadrate and epipterygoid. The epipterygoid has a thin triangular base and a rod-like ascending process. The ventral portion of the plate-like base is applied to the dorsal portion of the anteromedial margin of the quadrate process of the pterygoid, while its dorsal portion overlaps the anterior area of the suture between the basisphenoid and the pro-otic. The ascending process borders the anterolateral surface of the pro-otic and supraoccipital, touching the ventral face of the parietal at its dorsal end.

The quadrate (Text-figs 1–3) is a large, vertically elongated bone with a stout, pillar-like median portion (posterior crest of Benton 1983a, p. 624) that extends along its entire dorsoventral length. Laterodorsal to the pillar-like area, the quadrate has a thinner lateral expansion that overlaps the ventral base of the squamosal and the dorsomedial portion of the posterior surface of the quadratojugal. The quadrate foramen is located ventral to that expansion, between the quadrate and the quadratojugal. Medial to the pillar-like area, the quadrate has a thinner medial extension, more developed ventrally and excavated posteriorly. The ventral portion of the quadrate is massive, forming a long mediolaterally directed condyle, with the more developed medial portion directed ventrally.

Neurocranium. The ossified neurocranium has a solid base composed of the basisphenoid anteriorly and the basioccipital posteriorly. The basioccipital is longer than the basisphenoid, as is typical for Late Triassic rhynchosaurs (Chatterjee 1974; Benton 1983a). The anterior margin of the neurocranium is not preserved and the relations between the parasphenoid (if separate) and the basisphenoid, as well as the cultriform process, are not clear. The paired pro-otics, opisthotics and exoccipitals make up the otic capsules and the lateral walls of the brain cavity, while the roof of this cavity is formed by the supraoccipital. A well-developed paroccipital process is present, and most of it is composed of the opisthotic.

The basioccipital (Text-figs 1D, E, 3) is a heavily-built, compact bone, that expands posteriorly to form the major portion of the single round occipital condyle. Its dorsal portion is almost completely overlapped by the paired exoccipitals, and, apparently, is excluded from the base of the brain cavity. Anterior to the condyle, the basioccipital



TEXT-FIG. 3. Skull of *Hyperodapedon huenei* sp. nov., UFRGS PV0132T, holotype. A, ventral view; B, occipital view. For explanation of abbreviations, see Appendix. Scale bar represents 100 mm.

becomes thinner, but at its most anterior end it becomes more laterally developed, with diverging *tubercula sphenoccipitales* that meet the anterior surface of the basisphenoid. The dorsolateral surface of the bone receives a small ventral process of the opisthotic. Behind that contact, the basioccipital forms the ventral border of an aperture identified by Benton (1983a, p. 632) as the metotic foramen.

The basisphenoid (Text-figs 1D, 3) articulates with the anterior surface of the *tubercula sphenoccipitales* via two plate-like expansions of its posterior margin. Anterior to those expansions, the paired basiptyergoid processes extend ventrally and contact the pterygoid articular facets on the dorsal border of the interptyergoid vacuity. These processes are blunt elements that differ clearly from the elongated structures found in Middle Triassic rynchosaurs, but are similar to the processes of Late Triassic forms (Benton 1983a, 1990). In comparison to these last forms, the basiptyergoid processes of *H. huenei* are directed somewhat laterally and posteriorly as in *H. huxleyi* (Chatterjee 1974, fig. 6a), but are otherwise a little more developed than in that taxon and thus more like those of *H. gordonii* (Benton 1983a, fig. 10c).

The anterior face of the basisphenoid is not well preserved and the structures of the *dorsum sellae* are not well delimited. The anterolateral surface of the basisphenoid is, also, not clearly seen, since it is overlapped by the eptyergoid anteriorly and the quadrate process of the pterygoid more posteriorly. The dorsal surface of the

basisphenoid appears to form the anterior part of the base of the brain cavity medially. More laterally, it accommodates the entire ventral surface of the pro-otics, which appear to isolate it from the fenestra ovalis.

The paired exoccipitals (Text-figs 1F, 3B) are small bones that form the posterolateral surfaces of the braincase. Each is composed of a thin ventral plate that overlaps the basioccipital dorsally, and a lateral ascending process. The ventral plates compose almost all of the posterior part of the base of the brain cavity and each meets its opposite medially. These plates expand posteriorly and form the dorsolateral portion of the occipital condyle. The ascending processes apparently contribute to the ventrolateral borders of the foramen magnum and the more posterior part of the lateral walls of the brain cavity, but the dorsal limits of these processes are not clear. Each ascending process also appears to give rise to a ventrolateral extension that overlaps the posterior side of the opisthotic and forms the posteromedial part of the paroccipital process, as is evident in *H. gordonii* (Benton 1983a, fig. 10c). However, there is no sign of a suture between that structure and the opisthotic, and its existence is inferred based on comparison with *H. gordonii*, in which it is placed behind the lagenar crest of the opisthotic (Benton 1983a, p. 632).

The medial portion of the opisthotic (Text-figs 1A, C–F, 2A, 3) contributes to the lateral wall of the brain cavity and has a descending crest (lagenar crest *sensu* Benton 1983a, p. 632) that meets the dorsal surface of the *tuberculum spheeno-occipitale* of the basioccipital ventrally. This crest also forms the posterior border of the otic capsule, bordering the fenestra ovalis anteriorly and the metotic foramen posteriorly. The relationship between the opisthotic, the supraoccipital (dorsally) and the exoccipital (posteriorly) is not clear, and these elements appear to be fused together. Among the other species of *Hyperodapedon*, such fusions are only seen between the opisthotic and the exoccipital of *H. huxleyi* (Chatterjee, 1974, p. 223; Benton, 1983b). As in the other species of *Hyperodapedon*, the posterior surface of the spatulate paroccipital process bears a longitudinal stapedial canal, that is limited posteriorly by a lateral extension of the lagenar crest (*sensu* Benton 1983a, p. 632).

The pro-otic forms the entire anterodorsal portion of the neurocranium, including the anterior portion of the lateral walls of the brain cavity. The ventral portion is only partially visible in the specimen, and it is overlapped by the epipterygoid and by the quadrate process of the pterygoid. However, it lies dorsal to the basisphenoid, its posteroventral margin forming the anterior border of both the otic capsule and the fenestra ovalis. The posterodorsal surface of the pro-otic overlaps the opisthotic and its lateral projection takes part in the anteromedial surface of the paroccipital process. Its anterior surface is not preserved.

The supraoccipital (Text-figs 1F, 3B) is a pyramidal arch-shaped element, as in all Mid–Late Triassic rhynchosaurs, and is clearly distinct from the plate-like structures of Early Triassic forms (Dilkes 1995, 1998). It forms the dorsal border of the foramen magnum and the roof of the brain cavity and is attached to the pro-otics anteroventrally and to the opisthotics posteroventrally by means of ventrolateral projections. Its relation to the exoccipitals is not clear. Dorsally, it fits into a concavity on the ventral surface of the anterior ramus of the parietal.

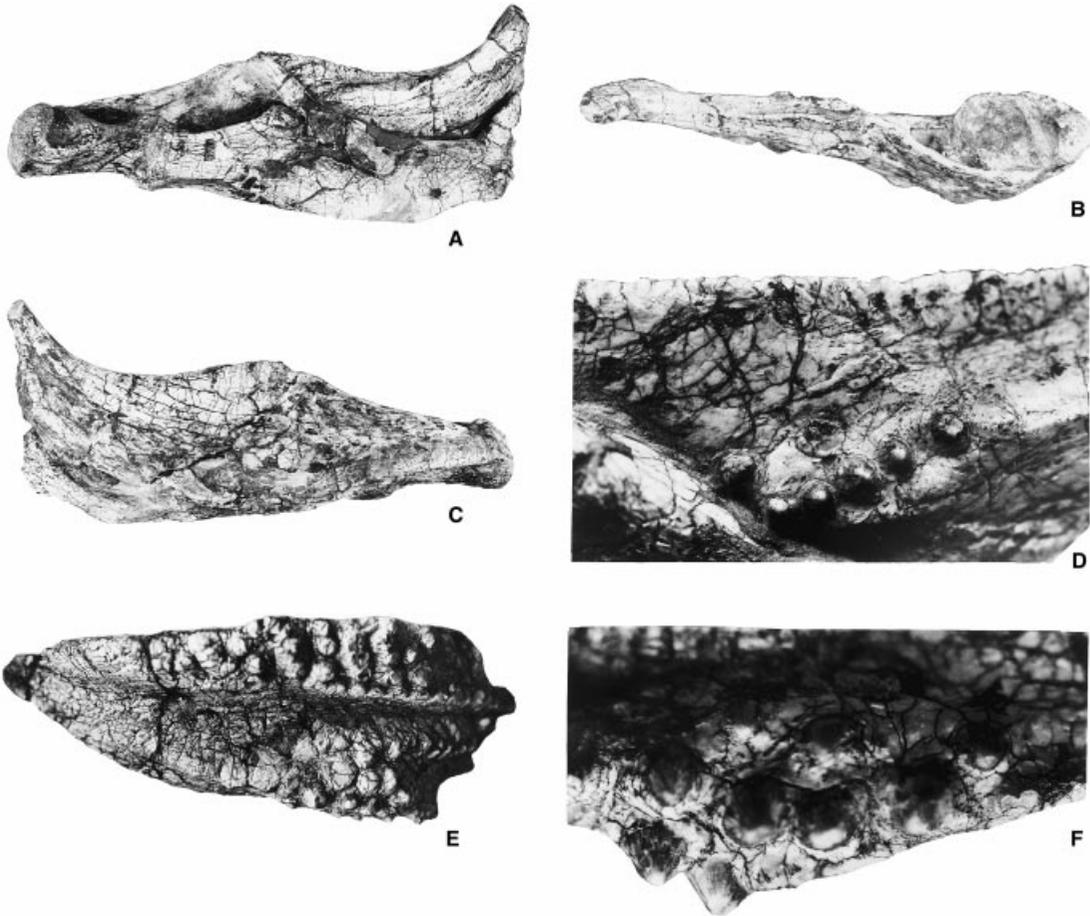
Mandible

Both rami of the mandible are well preserved. The right, however, is incomplete, lacking the splenial, the coronoid and part of the surangular. The more complete left ramus is used as the basis for this description, but it also lacks parts of the coronoid and surangular (the lateral border of the adductor fossa).

The general construction of the mandible of *H. huenei* (Text-figs 4A–C, 5; Table 1) is similar to that of other Upper Triassic rhynchosaurs (Benton 1983a; Azevedo and Schultz 1987), its depth being equivalent to more than 25 per cent of the total length. The posterior portion is flat and broad, and there is a large adductor fossa and an anteriorly developed meckelian canal. The angle between both rami is estimated as 80 degrees.

The dentary (Text-figs 4A–C, 5), as in all Late Triassic rhynchosaurs (Benton 1983a; Azevedo and Schultz 1987), forms more than half of the lateral surface of the mandible. Its edentulous anterior end has an upwards and slightly lateral curvature that occludes medially with the premaxilla. The dorsal surface bears a well-developed, toothed, cutting blade, laterally placed and more developed posteriorly, that extends along the posterior two-thirds of the bone. The dorsal surface of the dentary also has a well-marked, protruding medial border that extends along the entire length of the bone. The posterior portion of this border bears a few teeth. On the anterior third of the dentary, the medial border is even more prominent than the main cutting crest, and in this aspect the specimen is more similar to *H. gordonii* (Benton 1983a, fig. 14) than to *H. huxleyi* (Chatterjee 1974, fig. 8c). This medial border is presumably homologous to the medial crest described for some Mid–Late Triassic rhynchosaurs (von Huene 1938; Azevedo and Shultz 1987; Benton 1990).

The ventral portion of the dentary is composed of two descending laminae, medial and lateral to the meckelian canal. The lateral lamina is more ventrally developed than the medial. It descends laterally to an ascending lamina of the splenial and fits into a well-marked concavity on the dorsolateral surface of that bone. The medial lamina is overlapped ventrally by the splenial and posteriorly by the coronoid. Its posterior margin appears to meet the prearticular, although this contact is also overlapped by the splenial and the coronoid. The medial lamina has a shallow and elongated groove ventral to the medial tooth line, which presumably accommodated the tongue (Chatterjee 1974,



TEXT-FIG. 4. *Hyperodapedon huenei* sp. nov., UFRGS PV0132T, holotype. Left mandibular ramus: A, medial view; B, dorsal view; C, lateral view; D, lingual teeth. Right maxilla: E, ventral view; F, lingual teeth. A–C, $\times 0.3$; D, $\times 1.75$; E, $\times 0.75$; F, $\times 2.20$.

p. 226). On the anterior portion of the dentary the groove formed between the medial and lateral descending laminae curves upwards, becomes shallower, and faces medially, owing to the anterior development of the lateral lamina.

The splenial (Text-figs 4A, C, 5A–B) consists of a thick ventral body and a medial ascending lamina. The anterior portion of the bone is slightly displaced medially and bears a clear meckelian foramen in its medial surface. The splenials articulate with one another along their entire anteromedial margin, forming the complete mandibular symphysis. The ventral portion of this articular surface is formed from a rugose projection, and dorsally to it an ascending process fits into the anteromedial groove of the dentary. Posteriorly, the splenial is firmly attached to the angular, and its ascending lamina overlaps the prearticular, contacting the coronoid.

The coronoid (Text-figs 4A–D, 5) lying medial to the most posterior teeth of the dentary cutting blade is a small element that lacks its posterior end. Its ventral margin is not well preserved, but it seems to overlap part of the splenial-prearticular contact, allowing the splenial to take part in the anterior border of the adductor fossa.

The angular (Text-figs 4A, C, 5A–B) forms a large part of the ventral portion of the mandible behind the splenial, lining most of the meckelian canal ventrally. Its anterior portion contacts the splenial medially and expands dorsally, entering the lateral surface of the mandibular ramus. The posterior portion of the angular is broader and does not enter the lateral or medial surfaces of the mandible, but overlaps the anteroventral portions of the surangular laterally and the prearticular medially. The posterior limit of the angular is marked by the junction between those two bones, and it does not reach the posterior end of the mandibular ramus.

The surangular (Text-figs 4B–C, 5A, C) consists of a deep and broad ventral portion and a lamina that extends anterodorsally from its lateral margin. The ventral portion forms the lateral half of the posterior base of the mandibular ramus and its ventrolateral border is marked by a strong longitudinal keel, that extends further forwards, entering the angular. The anterolateral margin of the articular is bordered by a thin ascending lamina of the surangular, also reported by Benton (1983a, p. 640) in *H. gordonii*, and which forms the posterolateral border of the adductor fossa. The lateral ascending lamina lacks its dorsal end, but comparison with other species of *Hyperodapedon* suggests that it formed the lateral border of the adductor fossa and contacted the coronoid anterodorsally. The preserved part of the lamina extends forwards, dorsolateral to the angular, forming part of the lateral wall of the meckelian canal. The surangular has a clear posterior supra-angular foramen (*sensu* Benton 1983a) on the posterior part of its lateral surface. As in *H. huxleyi* (Chatterjee 1974, p. 229, fig. 8b), though unlike *H. gordonii* (Benton 1983a, p. 640), the surangular does not seem to take part in the retroarticular process, except by supporting it laterally.

The prearticular (Text-figs 4A–B, 5B–C) has a broad and wide posterior portion that is firmly attached to the posterior part of the surangular medially. Its anterior portion forms the medial border of the adductor fossa and the posteromedial wall of the meckelian canal. A meckelian foramen is not preserved.

The articular (Text-figs 4A–C, 5) is a flat and broad element that forms that glenoid fossa. It lies above the posterior portions of the surangular laterally and the prearticular medially, and its medial border does not contact other bones. The glenoid fossa is shallow, transversely elongate, and deeper on the lateral and medial portions. Anterior to the glenoid fossa the articular is bordered laterally by an ascending lamina of the surangular and has a medial prominence that forms the posterolateral border of the adductor fossa. The posterior margin of the glenoid is marked by a low crest, bordered by a deep transverse groove that is more developed medially, forming a strong and posteriorly expanded cavity. Lateral to that cavity, the articular rises abruptly to form the retroarticular process, which has a smoothly inclined lateral side. The posteriormost part of the articular projects down between the prearticular and the surangular, and bears a descending ridge derived from the retroarticular process.

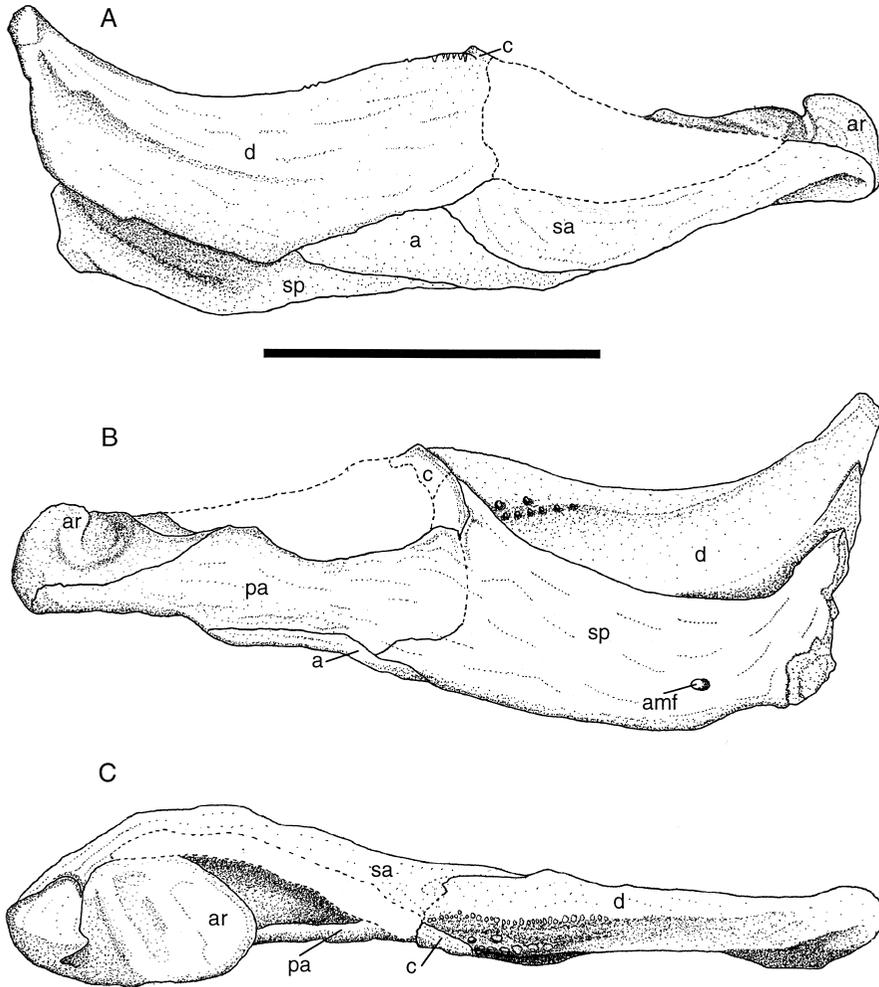
Dentition

Maxillary dentition (Text-fig 3A, 4E–F). The maxillary teeth of *H. huenei* occur in distinct lateral and medial areas, which are separated by a well-developed longitudinal groove. As in other Mid–Late Triassic rhynchosaurs (Benton 1984), there are two different types of teeth on the maxilla: the ‘pyramidal’ type is compressed anteroposteriorly and roughly elliptical in transverse section, while the conical type has a circular transverse section. Although the medial tooth-bearing area is shorter, it is clearly wider than the lateral area on the posterior portion of the maxilla. In this respect, *H. huenei* is similar to more primitive rhynchosaurs (von Huene 1938; Azevedo and Schultz 1987; Benton 1990), and differs from *H. gordonii*, which has tooth-bearing areas of equal width (Benton 1983a), and from *H. huxleyi*, ‘*Scaphonyx sanjuanensis*’ and ‘*S. fischeri*’ which have wider lateral areas (von Huene 1942; Sill 1970; Chatterjee 1974).

The longitudinal main groove extends along the entire length of the maxilla and narrows posteriorly. In this region, the groove does not show any signs of wear, and does not seem to have contacted the mandibular cutting blade on occlusion. On the other hand, the groove widens in the middle of the maxilla, where it occludes with the dentary crest. The groove becomes even wider anteriorly, but there is no occlusion at this point, and its extensive development seems to be a result of wear during younger stages in the life of the animal, when the maxilla was shorter and occlusion took place more anteriorly on the jaws (Benton 1984). A medial secondary, shallow wear groove is present on the median portion of the maxilla, and it is also found in some specimens of *H. gordonii* (Benton 1983a, fig. 15b).

The medial tooth-bearing area of *H. huenei* exhibits one or two longitudinal rows of ‘pyramidal’ teeth. The rows are adjacent to the main groove and restricted to the posterior end of the bone. Medial to these teeth there is a shallow secondary groove, a feature that is unknown in other species of *Hyperodapedon* (Chatterjee 1974; Benton 1983a). This is a primitive feature of *H. huenei* that is otherwise present only in less derived rhynchosaurs such as *Stenaulorhynchus*, *Rhynchosaurus* and ‘*Scaphonyx sulcognathus*’ (von Huene 1938; Azevedo and Schultz 1987; Benton 1990). Based on their location, between the main and the secondary grooves, it is possible to homologise the medial ‘pyramidal’ teeth of *H. huenei* with the tooth elements that occur on the median maxillary crest of less derived rhynchosaurs.

The secondary groove limits the lateral distribution of the medial conical teeth. These teeth are organised into transverse rows, as is typical for Late Triassic rhynchosaurs (Chatterjee 1974, fig. 13), with two or three teeth in each row. Unlike the ‘pyramidal’ form, the conical teeth do not reach the posterior end of the maxilla. Instead, they appear to arise more medially on the margin of the tooth-bearing area, showing a certain degree of continuity with the lingual teeth. Notably, the medial edge of the tooth-bearing area of *H. huenei* does not terminate abruptly as it does in *H. huxleyi* (Chatterjee 1974, fig. 13) and ‘*Scaphonyx fischeri*’ (von Huene 1942, pl. 31, fig. 1b). As a consequence, the



TEXT-FIG. 5. Left mandibular ramus of *Hyperodapedon huenei* sp. nov., UFRGS PV0132T, holotype. A, lateral view; B, medial view; C, dorsal view. For explanation of abbreviations, see Appendix. Scale bar represents 100 mm.

more medially placed teeth extend on to the lingual surface of the maxilla, similar to the condition in *H. gordonii* (Benton 1983a, fig. 15), and lingual teeth are clearly seen. Based on their medial position in relation to the secondary groove, the medial conical teeth of *H. huenei* appears to be homologous with the tooth elements that occur on the medial maxillary crest of less derived rhynchosaurs (von Huene 1938; Azevedo and Schultz 1987; Benton 1990).

The tooth-bearing area lateral to the main groove is made up of approximately 11 transverse rows of conical teeth (Chatterjee 1974, fig. 13), the more posterior rows containing up to five teeth. 'Pyramidal' teeth are also present, forming a longitudinal row on the lateral side of the main groove. As found on the medial tooth bearing area, the 'pyramidal' teeth of the lateral maxillary tooth-bearing area arise from the posterior end of the bone, while the conical teeth seem to originate from a more laterally placed area.

The lateral 'pyramidal' teeth of *H. huenei* appear to be homologous with tooth elements that occur on the lateral maxillary crest of less derived rhynchosaurs including *Stenaulorhynchus* and *Rhynchosaurus* (Benton 1984, 1990). Indeed, the lateral area of the maxilla of those forms does not possess transverse rows of teeth, but bears just one or two longitudinal rows. Only more derived rhynchosaurs appear to have transverse rows of conical teeth extending on to the lateral area of the maxilla. These teeth are found in all species of *Hyperodapedon*, which also have a longitudinal row

of 'pyramidal' teeth on the lateral side of the main groove (von Huene 1942; Sill 1970; Chatterjee 1974; Benton 1983a).

Mandibular dentition (Text-fig. 4A–D). The mandibular teeth of rhynchosaurs are usually classified into two different types (Benton 1984, p. 744): buccal and lingual. The buccal teeth of *H. huenei* are small, anteroposteriorly compressed, and distributed along a well-defined longitudinal row. This row extends along the posterior half of the dorsal surface of the cutting blade of the dentary, but is worn down in the anterior half. Owing to their extensive wear and proximity to each other, more anterior buccal teeth are not easily distinguished.

The lingual teeth of *H. huenei* are conical and larger than the buccal teeth; they are also well spaced and not as numerous. On the right dentary they make up a diagonal row of five teeth that lie on the posterior portion of the medially projecting border of the dentary. This projecting border probably originally bore more anterior teeth, now obliterated by occlusion of this area against the maxilla. Two other lingual teeth, medial to the main row, are also present. The presence of lingual teeth on the dentary differentiates *H. huenei* from '*Scaphonyx fischeri*' and '*S. sanjuanensis*', which do not possess these elements (von Huene 1942; Sill 1970).

The lingual teeth described for *H. huenei* seem to be homologous with teeth that occur on the medial crest of less derived rhynchosaurs including '*Scaphonyx sulcognathus*', *Rhynchosaurus* and *Stenaulorhynchus* (Azevedo 1982; Benton 1984; 1990). However, these less derived forms also have their own lingual teeth, located medial to that crest. These lingual teeth are not homologous with those described here and we propose that they should be referred to as primary lingual teeth. These teeth were presumably lost in more derived rhynchosaurs, and are absent in all species of *Hyperodapedon* (Sill 1970; Chatterjee 1974), a notable exception is an 'anomalous' specimen of *H. gordonii* (Benton 1983a, fig. 2D).

PHYLOGENETIC ANALYSIS

The monophyly of the more derived rhynchosaurs, usually included in the subfamily Hyperodapedontinae (Benton 1985, 1990), has been clearly established by previous cladistic work (Benton 1985, 1988; Dilkes 1995, 1998) that stressed their morphological differences in relation to the less derived Middle Triassic members of the group including *Rhynchosaurus* and *Stenaulorhynchus*. The diversity of that group is, however, frequently underestimated in terms of operational taxonomic units, and only the two better known taxa are usually included in cladistic analyses: *Hyperodapedon*, representing the Indian and Scottish Late Triassic rhynchosaurs, and '*Scaphonyx*' representing the South American forms.

More detailed cladistic studies (Benton 1990; Wilkinson and Benton 1995; Langer 1996) included other derived rhynchosaurs such as *Hyperodapedon mariensis* (Tupi-Caldas, 1933), '*Scaphonyx sanjuanensis*' Sill, 1970, '*Scaphonyx sulcognathus*' Azevedo and Schultz, 1987, and '*Rhynchosaurus spenceri*' Benton, 1990. All of these forms were found to have a set of derived features that justified their inclusion in a monophyletic group together with the traditional *Hyperodapedon*-'*Scaphonyx*' forms. Their phylogenetic interrelationships are, however, still uncertain.

In order to answer this question a cladistic study was carried out with 29 characters (Appendix), an ingroup consisting of eight derived rhynchosaur taxa, and a two-taxon outgroup (Table 2). The data matrix (Appendix) was analysed using PAUP version 3.1.1 (Swofford 1993) on a Macintosh Power PC computer. The branch-and-bound search option was utilised, and three most parsimonious trees with 32 steps (CI: 0.906, excluding uninformative transformations; RI: 0.940) were found. The trees differ only in the relative position of *Hyperodapedon mariensis*, placed either as the sister taxon of the clades composed of '*Scaphonyx fischeri*' plus '*Scaphonyx sanjuanensis*', or *Hyperodapedon gordonii* plus *H. huxleyi*, or all four forms together. A strict consensus tree showing the result of the analysis is shown in Text-fig. 6A.

DISCUSSION AND TAXONOMIC DEFINITIONS

The name *Hyperodapedon* was coined by Huxley (1859), who identified the presence of 'numerous series of subcylindrical palatal teeth' (in fact the maxillary teeth lying medial to the main groove) as the most important feature of the new taxon. In later works, Huxley (1869, 1887) differentiated *Hyperodapedon* from *Rhynchosaurus articeps*, the only other rhynchosaur known at that time, based on the presence, in the

TABLE 2. Ingroup and outgroup operational taxonomic units used in the present analysis, indicating main descriptive accounts and stratigraphic provenance of each taxon.

Outgroup

Rhynchosaurus articeps Owen, 1841; Taporley Siltstone Formation (Anisian), English Midlands (Benton 1990).
Stenaulorhynchus stockleyi Haughton, 1932; Manda Formation (Anisian), Tanzania (Huene 1938).

Ingroup

Hyperodapedon gordonii Huxleyi, 1859; Lossiemouth Sandstone Formation (Carnian), northern Scotland (Benton 1983a).

Hyperodapedon huxleyi Lydekker, 1881; Lower Maleri Formation (Carnian), central Peninsular India (Chatterjee 1974).

'*Scaphonyx fischeri*'; Santa Maria Formation (Carnian), southern Brazil (Huene 1929, 1942; Sill 1970).

Hyperodapedon mariensis (Tupi-Caldas, 1933); Santa Maria Formation (Carnian), southern Brazil (Tupi-Caldas 1933; Schultz and Barberena 1991; Langer 1998).

'*Scaphonyx sanjuanensis* Sill, 1970; Ischigualasto Formation (Carnian), north-western Argentina (Sill 1970).

'*Scaphonyx sulcognathus* Azevedo and Schultz, 1987; Santa Maria Formation (Carnian), southern Brazil (Azevedo 1982; Azevedo and Schultz 1987).

'*Rhynchosaurus spenceri* Benton, 1990; Otter Sandstone (Anisian), Devon, England (Benton 1990).

Hyperodapedon huenei sp. nov.; Santa Maria Formation (Carnian), southern Brazil.

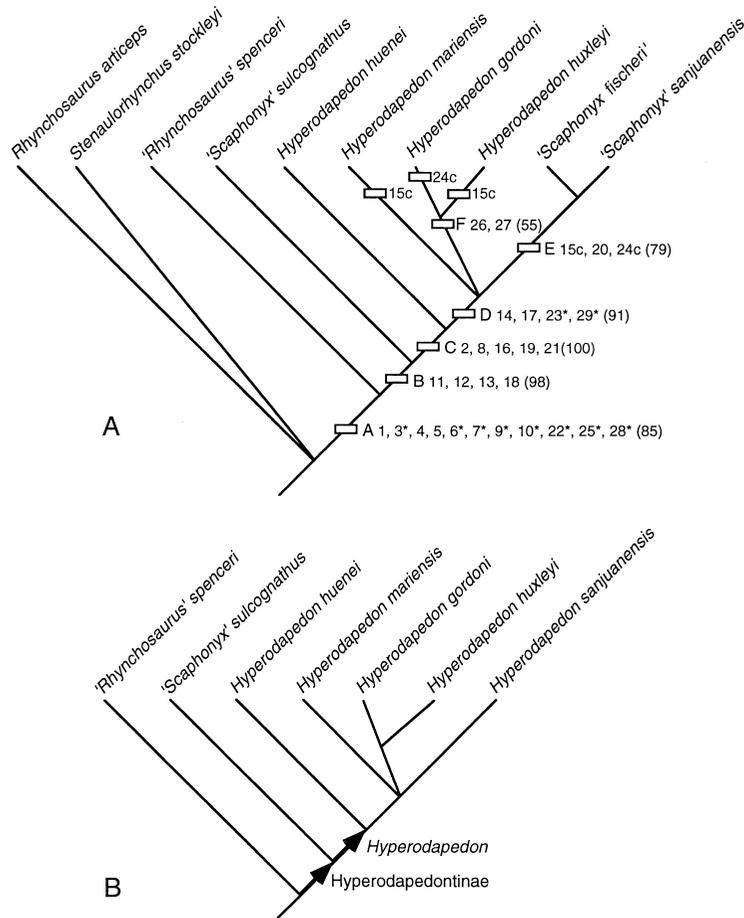
former, of maxillary tooth rows (in reality the maxillary teeth lying lateral to the main groove). Lydekker (1888) recognised the presence of such maxillary teeth in *Rhynchosaurus* and redefined *Hyperodapedon* as having more than two rows of teeth in both 'maxilla and palate' (in fact lateral and medial maxillary tooth-bearing areas).

The definition of *Hyperodapedon* adopted here is in accordance with its early definitions (especially Lydekker 1888). All components of clade 'C' (Text-fig. 6A) have more than two teeth in transverse sections through the lateral tooth-bearing area of the maxilla (character 16), and based on this the genus *Hyperodapedon* is defined as a stem-based taxon (De Queiroz and Gauthier 1990, 1992) consisting of all rhynchosaurs closer to *Hyperodapedon gordonii* (the type species of the genus) than to '*Scaphonyx sulcognathus* (Text-fig. 6B).

Using this definition, most Late Triassic rhynchosaurs are included in the genus *Hyperodapedon*. This is not an unexpected situation, since the majority of the morphological distinctions between those forms rely on dental features that are not always easy to differentiate. Moreover, these different morphologies seem to be just stages of a single morphological trend leading to the reduction of dental structures of the medial area of the dentary and maxilla, and enlargement of the lateral areas (Benton 1983a; Langer *et al.* 1997).

Hyperodapedon huenei is clearly the least derived species of *Hyperodapedon*, and constitutes the sister taxon of the other species of the genus. *H. huxleyi* has a derived maxillary tooth arrangement that is similar to the condition in the South American representatives of the genus, but some postcranial features indicate that it belongs in a monophyletic group with *H. gordonii* (Text-fig. 6). Apart from *H. huenei*, two other species of *Hyperodapedon* are present in the South American Upper Triassic: *H. mariensis*, which includes forms that retain teeth on the lingual side of the dentary, and *H. sanjuanensis*, which is distinguished by loss of those teeth. Both forms occur together in the Ischigualasto Formation of Argentina and the Santa Maria Formation of Brazil, although *H. mariensis* seems to be rare in Argentina (Contreras 1981). *H. sanjuanensis* comprises specimens originally assigned to '*Scaphonyx fischeri*' (von Huene 1942) and to '*Scaphonyx sanjuanensis* (Sill 1970); these were not distinguished by any characters analysed in the present study, and so were grouped together in a single species.

The family Hyperodapedontidae was erected by Lydekker (1885) to include *Hyperodapedon gordonii* and *H. huxleyi*, clearly excluding *Rhynchosaurus articeps* (the only other rhynchosaur known at that time). The stem-based meaning of this definition will be used here, and Hyperodapedontidae is defined as all rhynchosaurs closer to *Hyperodapedon* than to *Rhynchosaurus*. The composition of this taxon is uncertain, since there is no consensus regarding the relative phylogenetic position of *Stenaulorhynchus* and



TEXT-FIG. 6. Phylogenetic hypothesis for the relationships of derived rhynchosaurs. A, Strict consensus of three most parsimonious trees found by analysis of the data matrix given in the Appendix. Apomorphies are indicated for each clade, together with the respective bootstrap value (Felsenstein 1985) in parentheses. All characters were optimised using DELTRAN; ambiguous characters are indicated by an asterisk and convergences by 'c'. B, Taxonomic arrangement of derived rhynchosaurs based on the phylogenetic hypothesis. Stem-based taxa indicated by arrow.

Rhynchosaurus (Benton 1990; Dilkes 1998). All the components of the ingroup studied here, however, are clearly member of Hyperodapedontidae, since they are components of the phylogenetic branch leading to *Hyperodapedon* rather than to *Rhynchosaurus ariceps* (Text-fig. 6A).

Chatterjee (1969) proposed the only known coordinate name of Hyperodapedontidae, Hyperodapedontinae (*nom. trans. ex* Lydekker, 1985), to include all Late Triassic rhynchosaurs known at that time: *H. gordonii*, *H. huxleyi* and '*Scaphonyx fischeri*'. Chatterjee (1969) also proposed a morphological diagnosis for Hyperodapedontinae, in which the least inclusive character, the absence of maxillary lingual teeth, defines clade 'D' of the present study (Text-fig. 6A). Following this morphological definition, two Late Triassic rhynchosaurs ('*S. sulcognathus*' and *H. huenei*) would be excluded from the taxon, and Hyperodapedontinae would be nested within *Hyperodapedon*. Therefore, to preserve this subfamilial name at least in its original stratigraphical meaning, a stem-based phylogenetic definition of Hyperodapedontinae is proposed here (Text-fig. 6B) as: all rhynchosaurs closer to *Hyperodapedon* than to '*Rhynchosaurus' spenceri*'.

Based on this definition, the subfamily Hyperodapedontinae comprises two genera: *Hyperodapedon* Huxley, 1859 and a new monospecific taxon that includes only the form currently known as '*Scaphonyx sulcognathus* Azevedo and Schultz 1987. '*Rhynchosaurus*' *spenceri* Benton, 1990 is proposed as the sister taxon of Hyperodapedontinae. It does not belong to the genus *Rhynchosaurus*, and should be included in a new, more derived, taxon.

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APPENDIX

List of abbreviations

a	angular	op	opisthotic
amf	anterior meckelian foramen	p	parietal
aoc	<i>anguli oris</i> crest	pa	prearticular
ar	articular	pl	palatine
bo	basioccipital	pm	premaxilla
bpt	basipterygoid process	po	postorbital
bs	basisphenoid	prf	prefrontal
c	coronoid	pt	pterygoid
ch	choana	ptf	postfrontal
d	dentary	q	quadrate
ec	ectopterygoid	qf	quadrate foramen
eo	exoccipital	qj	quadratojugal
f	frontal	sa	surangular
iof	inferior orbital foramen	so	supraoccipital
j	jugal	sp	splénial
l	lacrimal	sq	squamosal
m	maxilla	tso	tuberculum spheno-occipitales
mjf	medial jugal foramen	v	vomer
n	nasal		

Characters used in the present analysis

Plesiomorphic (0) and apomorphic (1) states determined by comparison with the outgroups (*Stenaulorhynchus* and *Rhynchosaurus*).

1. Shape of the skull: (0) longer than broad; (1) broader than long.
2. Frontal longitudinal groove: (0) much deeper posteriorly; (1) almost same depth throughout.
3. Orbital orientation: (0) mainly lateral; (1) mainly dorsal.
4. *Anguli oris* crest: (0) short, does not reach the anterior portion of the orbit; (1) long, reaching the anterior portion of the orbit.
5. External surface of the jugal: (0) not ornamented; (1) ornamented with crests or elevations dorsal to the *anguli oris* crest.
6. Width of the bar between orbit and infratemporal fenestra: (0) less than 40 per cent of the maximum opening of the orbit; (1) more than 40 per cent of the maximum opening of the orbit.
7. Supratemporal: (0) present; (1) absent.
8. Ventral process of the squamosal: (0) straight; (1) plate-like.
9. Basipterygoid process: (0) longer than broad; (1) broader than long.
10. Relative length of basioccipital and basisphenoid: (0) basisphenoid longer; (1) basioccipital longer.
11. Position of the occipital condyle: (0) well in front of the quadrates; (1) in line with the quadrates.
12. Mandibular depth: (0) less than 25 per cent of mandibular length; (1) more than 25 per cent of the mandibular length.

