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A new species of basal rhynchosaur (Diapsida: Archosauromorpha) from the early Middle Triassic of South Africa, and the early evolution of Rhynchosauria

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ABSTRACT

Rhynchosauria was an important clade of herbivorous archosauromorph reptiles during the Triassic, with a worldwide distribution. We describe a new genus and species of early rhynchosaur, *Eohyosaurus wolvaardti*, from the early Middle Triassic (early Anisian) *Cynognathus* Assemblage Zone (Subzone B) of the Karoo Supergroup, South Africa. *Eohyosaurus wolvaardti* is known from a single skull, and is recovered as the sister taxon of Rhynchosauridae in a new phylogenetic analysis,. *Cynognathus* Subzone B has previously yielded the stratigraphically oldest well-understood rhynchosaur species, *Mesosuchus browni* and *Howesia browni*. *Eohyosaurus wolvaardti* increases the rhynchosaur diversity within this stratigraphic horizon to three species. Intriguingly, all currently confirmed rhynchosaur occurrences from the Early Triassic to earliest Middle Triassic are from South Africa. This may suggest a relatively restricted palaeogeographic distribution for early rhynchosaurs, followed by a global dispersal of rhynchosaurids during the Middle Triassic.

ADDITIONAL KEYWORDS: Anisian – Burgersdorp Formation – phylogeny – Rhynchosauridae – South Africa.

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INTRODUCTION

Rhynchosaurs were an important group of herbivorous archosauromorph reptiles that played a key role in many terrestrial ecosystems during the Triassic, particularly in Gondwana. The clade diversified during the Middle Triassic and early Late Triassic, with abundant remains known from Tanzania, South Africa, Madagascar, India, Brazil, Argentina, the UK, and the USA (Huene, 1938; Chatterjee, 1980; Benton, 1983a, 1990; Dilkes, 1995, 1998; Langer *et al*., 2000; Nesbitt & Whatley, 2004; Montefeltro, Langer & Schultz, 2010; Montefeltro *et al*., 2013; Ezcurra *et al*., 2013; Mukherjee & Ray, 2014). The youngest stratigraphic occurrences of rhynchosaurs occur close to the Carnian–Norian boundary (Langer *et al*., 2007; Martinez *et al*., 2011), and the clade has been considered as a victim of the possible Carnian–Norian extinction event (Benton, 1983b, 1990). Most rhynchosaurs (i.e. those belonging to the clade Rhynchosauridae) were squat, pig-like herbivores, with unusual skulls characterized by bony beaks and complex tooth plates.

The earliest rhynchosaur, *Noteosuchus colletti*, is known from the Lower Triassic *Lystrosaurus* Assemblage Zone of South Africa (Carroll, 1976; Dilkes, 1998; Ezcurra, Scheyer & Butler, 2014), shortly after the Permo-Triassic mass extinction. Two basal rhynchosaurs, *Howesia browni* and *Mesosuchus browni*, are known from the middle part (Subzone B) of the overlying *Cynognathus* Assemblage Zone (AZ) (Dilkes, 1995, 1998), of early Middle Triassic (early Anisian) age. These taxa are considered key for understanding the origin and early evolution of rhynchosaurs, as many aspects of their anatomy are intermediate between other early archosauromorphs and more derived rhynchosaurs (Rhynchosauridae). *Mesosuchus browni* is the stratigraphically oldest well understood rhynchosaur, is recovered as the

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most basal rhynchosaur taxon in many phylogenetic analyses (e.g. Dilkes, 1998; Hone & Benton, 2008), and is represented by excellent cranial and postcranial material. It lacks the well-developed tooth plates that are typical of later rhynchosaurs. By contrast, *H. browni* is known from relatively fragmentary material and is considerably less well understood, but does possess tooth plates formed by more than two rows of maxillary and dentary teeth.

Here, we describe a third taxon of basal rhynchosaur from Subzone B of the *Cynognathus* AZ of South Africa (Fig. 1). This taxon provides additional insights into the early evolutionary history of the clade, including cranial evolution, diversity and biogeography.

Institutional abbreviations: BRSUG, University of Bristol, School of Earth Sciences, Bristol, UK; FZB, Fundação Zoobotânica do Rio Grande do Sul, Porto Alegre, Brazil; MACN-Pv, Museo Argentino de Ciencias Naturales "Bernardino Rivadavia", Paleontología de Vertebrados, Buenos Aires, Argentina; PVSJ, Museo de Ciencias Naturales, Universidad de San Juan, San Juan, Argentina; NHMUK, Natural History Museum, London, UK; SAM, Iziko South African Museum, Cape Town, South Africa; SHYMS, Shropshire Museums, Ludlow, UK; UFRGS, Instituto de Geociências, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil; WARMS, Warwickshire Museum, Warwick, UK.

METHODS

COMPUTED TOMOGRAPHIC SCANNING

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SAM-PK-K10159 was scanned in the Museum für Naturkunde Berlin with a Phoenix|x-ray Nanotom (GE Sensing and Inspection Technologies GmbH, Wunstorf, Germany) using a tungsten target and a Cu filter 0.1 mm thick in modus 0, averaging 3, skip 2. The scan comprised 1440 slices with an exposure time of 1s, 85 kV, current of 400 µA, and a voxel size of 22.79 µm. X-ray slices were reconstructed with the software datos|x-reconstruction version 1.5.0.22 (GE Sensing and Inspection Technologies GmbH, Phoenix|x-ray) and analyzed in VG Studio Max 2.1 (Volume Graphics, Heidelberg, Germany). The specimen was too large to be scanned in its entirety, so scans focused on areas of particular interest (tooth rows, endocranium). The endocranial anatomy will be explored in detail elsewhere. A copy of the CT data has been provided to the SAM, to be archived along with the specimen.

CLADISTIC ANALYSES

In order to investigate the phylogenetic position of SAM-PK-K10159, a novel parsimony analysis was conducted based upon a modified version of the data matrix of Montefeltro *et al*. (2013). The matrix of Montefeltro *et al*. (2013) was originally constructed in order to investigate relationships within Rhynchosauridae. For the present analysis we expanded both taxonomic and character sampling in order to allow us to address the relationships of both basal (non-rhynchosaurid) members of Rhynchosauria and Rhynchosauridae.

We added two non-rhynchosaurian outgroups (*Prolacerta broomi* and *Protorosaurus speneri*) and the two currently recognised species of *Rhynchosaurus* (*R. articeps* and *R. brodiei*) as discrete operational taxonomic units. By contrast, the postcranial material EXEMS 79/1992 from the Otter Sandstone of the UK, previously referred to *Fodonyx spenceri* (Hone & Benton, 2008), was not included in the analysis

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given its fragmentary nature and uncertain taxonomic status and phylogenetic position (Langer *et al*., 2010; Montefeltro *et al*., 2013).

We added characters from previously published phylogenetic analyses relevant to the basal relationships of Rhynchosauria and Rhynchosauridae, including proposed synapomorphies of these two clades (Benton, 1983a, 1985; Dilkes, 1998), as well as a number of new characters. Scoring of taxa was based primarily on firsthand examination of specimens, with the exception of *Isalorhynchus genovefae*, which was scored using Langer *et al*. (2000) and Whatley (2005), *Stenaulorhynchus stockleyi* scored based on Huene (1938), Dilkes (1998), Langer & Schultz (2000) and Hone & Benton (2008), and *Fodonyx spenceri* scored based on Benton (1990) and unpublished photographs provided by Max Langer. The final matrix (14 taxa and 93 characters) was analyzed using TNT version 1.1 (Goloboff, Farris & Nixon, 2008) using the implicit enumeration algorithm. Multistate characters 70, 73 and 75 were treated as additive. Zero branch length nodes were collapsed following the search. Absolute and GC bootstrap frequencies were calculated after 10,000 pseudoreplicates.

SYSTEMATIC PALAEONTOLOGY

DIAPSIDA OSBORN, 1903 sensu LAURIN, 1991

ARCHOSAUROMORPHA HUENE, 1946 sensu GAUTHIER *ET AL*., 1988

RHYNCHOSAURIA OSBORN, 1903 sensu DILKES, 1998

***EOHYOSAURUS WOLVAARDTI* GEN. ET SP. NOV.**

(Figs 2–5)

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Etymology: Genus name from the Greek *eos*, meaning "early" or "dawn", *hyos*, meaning "pig" or "hog", and *sauros*, meaning "lizard" or "reptile". Name refers to the common description of rhynchosaurs as "pig-reptiles" and the early stratigraphic occurrence of the new taxon. The species is named for Frederik Petrus Wolvaardt, who discovered the type and only known specimen in December 2000. The name is therefore intended to translate as "Wolvaardt's early pig-reptile".

Holotype: SAM-PK-K10159, partial skull missing the anterior end, with associated incomplete lower jaws (Figs 2–5).

Locality and horizon: Farm Lemoenfontein 44, Rouxville District, Free State Province, South Africa. Burgersdorp Formation, *Cynognathus* Assemblage Zone, Subzone B (early Middle Triassic: early Anisian) (Fig. 1).

The specimen was found as loose float on boulder-strewn slopes at the base of a cliff (coordinates: 30° 36' 43.7" S, 26° 37' 22.9" E). The same locality has also yielded remains of the archosauriform *Erythrosuchus*, the cynodont *Trirachodon*, the kannemeyeriid dicynodont *Kannemeyeria*, procolophonids and the bauriid therocephalian *Microgomphodon oligocynus* (Sheena Kaal pers. comm. 2013; D. Wolvaardt pers. comm. 2013; Abdala *et al*., 2014).

Diagnosis: Characterized by the following autapomorphy: jugal with elongate dorsal process that forms the entire anterior margin of the infratemporal fenestra and that articulates anteriorly with the entire posterior margin of an elongate ventral process of the postorbital. Distinguished from other rhynchosaurs on the basis of the following unique combination of characters: (1) maxillae and dentaries mediolaterally expanded

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(present in *Howesia browni* and Rhynchosauridae *sensu* Dilkes, 1998; mediolaterally expanded maxillae/dentaries absent in *Mesosuchus browni*); (2) teeth present on the occlusal and lingual surfaces of the maxillae and dentaries (present in *Howesia browni* and Rhynchosauridae; occlusal teeth only present in *Mesosuchus browni*); (3) maxilla lacks a longitudinal occlusal groove and dentary lacks occlusal blade (groove and blade present in Rhynchosauridae; groove and blade also absent in *M. browni* and *H. browni*); (4) occlusal margin of maxilla offset ventrally from the ventral margin of the main body of the jugal (occlusal margin not offset ventrally in *M. browni*; offset ventrally in Rhynchosauridae, and possibly in *H. browni*); (5) presence of a short *anguli oris* crest on the lateral surface of the maxilla (crest absent in *M. browni*; present in Rhynchosauridae but placed on the jugal; condition uncertain in *H. browni*); (6) posterior process of jugal is short and terminates at approximately 50% of the anteroposterior length of the infratemporal fenestra (process proportionately longer in *M. browni*, and contacts quadratojugal in most Rhynchosauridae; process is also short in *H. browni*); (7) elongate posterior process of the postorbital terminates above the anterior margin of the ventral process of the squamosal (posterior process shorter and does not terminate above the ventral process of the squamosal in *M. browni* and *H. browni*; present in Rhynchosauridae); (8) elongate ventral process of the squamosal extends for more than 50% of the posterior margin of the infratemporal fenestra (ventral process does not extend for more than 50% of the posterior margin in *H. browni*; present in *M. browni* and Rhynchosauridae); (9) sagittal crest on parietal (sagittal crest absent in *M. browni*; present in *H. browni* and Rhynchosauridae).

ANATOMICAL DESCRIPTION

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General: SAM-PK-K10159 is relatively complete posteriorly, but the anterior end of the skull is incomplete (Fig. 2, 3). On the left side, the premaxilla and anterior half of the maxilla are entirely missing, the external surface of the posterior half of the maxilla has broken away, the prefrontal and lacrimal are represented by small fragments lacking their external surfaces, and the external surface of the anterior process of the jugal has broken away (Fig. 2B, D). On the right side, the premaxilla and the tip of the maxilla are missing, much of the anterior part of the preserved maxilla is represented by an impression of the medial surface of the element, and only fragments of the lacrimal and prefrontal are preserved (Fig. 2A, C). Dorsally, the nasals, frontals, anterior end of the parietals and much of the postfrontals are missing, although a natural cast of the endocranium and nasal capsule is exposed. In the lower jaw, the anterior end of the dentary is missing on both left and right sides, and much of the external surface of the left mandible is missing, but some details of the morphology of the latter are revealed by a natural mould. The left side of the skull has additionally been displaced ventrally relative to the right side, and also appears to have been compressed anteroposteriorly. Posteriorly, the parietals appear to have been displaced dorsally relative to the occipital region.

As preserved, the maximum anteroposterior length along the sagittal plane of the skull on the left side, from the broken anterior margin of the maxilla to the posterior margin of the quadrate condyles, is 68.2 mm. Based on the dimensions of the orbit and infratemporal fenestra (Table 1), SAM-PK-K10159 is similar in size to a referred specimen of the early rhynchosaur *Mesosuchus browni* (SAM-PK-6536; Dilkes, 1998) that has a basal skull length (premaxilla to quadrate condyles) of 89 mm, and we suggest that the complete length of SAM-PK-K10159 would have been similar. Our estimate of skull length suggests that the skull was longer than broad,

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similar to the condition in *M. browni* (Dilkes, 1998), *Howesia browni* (Dilkes, 1995) and the rhynchosaurids *Rhynchosaurus articeps* (Benton, 1990), *Stenaulorhynchus stockleyi* (Huene, 1938) and *Bentonyx sidensis* (Langer *et al*., 2010).

Although the dorsal rim of the orbit is not preserved on either side of SAM-PK-K10159, the orbit appears to be slightly anteroposteriorly longer than dorsoventrally tall on the right side (that of the left side appears to be anteroposteriorly compressed). Despite deformation, the orbits face mostly laterally, unlike the condition in the hyperodapedontines *Isalorhynchus genovefae* (Whatley, 2005), *Teyumbaita sulcognathus* (UFRGS-PV-0232, UFRGS-PV-0298; Montefeltro, Langer & Schultz, 2010) and *Hyperodapedon* spp. (*H. mariensis*, FZB-PV-1867; *H sanjuanensis*, MACN-Pv 18185; *H. huenei*, UFRGS-0132) in which the orbits face mostly dorsally. Fragments of the right sclerotic ring appear to be present in the right orbit, and some fragments may also be present on the left side (Figs. 2–4: scl).

The infratemporal fenestra has a trapezoidal outline on the right side (the left side is anteroposteriorly compressed), being longer anteroposteriorly at its ventral margin than at its dorsal margin. The supratemporal fenestra has a broadly rounded anterior margin, expands in transverse width posteriorly reaching a maximum width just posterior to the midlength of the parietal, and then tapers to a rounded posterolateral corner.

Maxilla: The maxilla is poorly preserved on both sides of the skull, but its external morphology is best preserved on the right side (Figs. 2, 4: m). As in all other rhynchosaurs and non-archosauriform archosauromorphs, an antorbital fenestra and fossa are absent. The occlusal margin is nearly straight in lateral view, but the preserved part of the anterior end of the left maxilla and the impression of the anterior

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part of the right maxilla suggests that it curved gently dorsally toward the contact with the premaxilla. This curvature is not as marked as typically occurs in rhynchosaurids (e.g. Benton, 1983a, 1984, 1990; Langer & Schultz, 2000; Nesbitt & Whatley, 2004; Montefeltro, Langer & Schultz, 2010; Mukherjee & Ray, 2014), but does differ from the completely straight occlusal margin present in *M. browni* (SAM-PK-6536; Dilkes, 1998). The posterior end of the occlusal margin of the maxilla is offset ventral relative to the ventral margin of the jugal, contrasting with the condition in *M. browni* (SAM-PK-6536; Dilkes, 1998) in which the ventral margin of the jugal is in line with the occlusal margin of the maxilla.

The posteriormost portion of the maxilla tapers dorsoventrally, apparently forming an anterodorsally-to-posteroventrally oriented suture with the jugal, although the exact path of this suture is difficult to establish due to poor preservation. The contact of the maxilla with the lacrimal is unclear on both sides of the skull.

The lateral surface of the maxilla is mostly flat, and is slightly expanded laterally at the occlusal margin. Additionally, the lateral surface of the maxilla bears a distinct ridge (Figs. 2, 4: ao), here proposed to be homologous to the *anguli oris* crest of rhynchosaurids (Sill, 1970; Langer & Schultz, 2000). In *Eohyosaurus wolvaardti* this ridge extends from the contact of the maxilla with the ventral margin of the jugal, along the lateral surface of the former bone, and terminates anteriorly below the anteroventral corner of the orbit. Below this ridge the lateral surface of the maxilla is slightly bevelled inwards. Although we propose that this feature is homologous with the *anguli oris* crest, its position is slightly different from that in most rhynchosaurids, where it is positioned on the boundary between the jugal and the maxilla (Sill, 1970; Langer & Schultz, 2000).

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Where the anterior part of the right maxilla has broken away, an impression of the bone demonstrates that the ventral part of this element is strongly transversely expanded, and that this transverse expansion becomes stronger posteriorly. This transverse expansion forms a nearly horizontal, ventrally facing occlusal surface laterally. Medially the occlusal surface forms a near right angle with the lingual surface of the maxilla. This transverse expansion is very similar to that present in *H. browni* (Dilkes, 1995) and rhynchosaurids (Benton, 1984; Nesbitt & Whatley, 2004; Langer & Schultz, 2000; Montefeltro, Langer & Schultz, 2010), but differs from the transversely narrower occlusal surface present in *M. browni* (Dilkes, 1998).

Jugal: The jugal forms the ventral margin of the orbit and much of the anterior and ventral margins of the infratemporal fenestra (Figs. 2–4: j). The lateral surface of the main body of the jugal possesses several subcircular pits that are irregularly distributed (Figs. 2, 4C). Similar pits are present on the jugal of *H. browni* (SAM-PK-5884). The orbital margin is marked by a low thickening that is continuous with a similar thickened margin on the orbital margin of the postorbital. This thickened orbital margin is present to some degree in all rhynchosaurs, but is particularly marked in the basal rhynchosaurids *R. articeps* (SHYMS G-132/1982), *R. brodiei* (WARMS Gz6097), *S. stockleyi* (Huene, 1938) and *B. sidensis* (BRSUG 27200). However, this orbital thickening is less well developed in *Fodonyx spenceri* (Benton, 1990) and hyperodapedontines (Benton, 1983a; Whatley, 2005; Montefeltro, Langer & Schultz, 2010).

The posterior process of the jugal is short, and terminates at approximately the anteroposterior midlength of the infratemporal fenestra (Fig. 4C: pp.j). This short process is similar to that of *H. browni* (Dilkes, 1995) and *R. articeps* (NHMUK

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R1236), but differs from the proportionately longer process of *M. browni* (Dilkes, 1998) and most rhynchosaurids (Benton, 1983a, 1990; Langer & Schultz, 2000; Montefeltro, Langer & Schultz, 2010), which extends nearly as far as or beyond the anterior margin of the ventral process of the squamosal (e.g. *H. huenei*: UFRGS-PV-0132T). The posterior process of the jugal of SAM-PK-K10159 is oriented almost directly posteriorly, as also occurs in *M. browni* (SAM-PK-6536) and *H. browni* (SAM-PK-5884). By contrast, in rhynchosaurids the posterior process of the jugal is more strongly directed lateroventrally as well as posteriorly and, as a result, the temporal region of the skull is considerably broader than the orbital region (e.g. *R. articeps*: NHMUK R1236, SHYMS G-132/1982).

Although the medial surface of the posterior process of the jugal is covered with sediment, it seems highly likely that the jugal-quadratojugal bar was incomplete, as in *H. browni* (Dilkes, 1995), *M. browni* (Dilkes, 1998) and *R. articeps* (NHMUK R1236). The dorsal process of the jugal is elongate, and forms the entire anterior margin of the infratemporal fenestra, tapering to a very slender strip of bone at its dorsal tip (Fig. 4C: dp.j). By contrast, the dorsal process of the jugal is proportionately shorter in *H. browni* (Dilkes, 1995), *M. browni* (Dilkes, 1998), *R. articeps* and *R. brodiei* (Benton, 1990). Moreover, in SAM-PK-K10159 the postorbital bar is formed along its entire length by an articulation between the dorsal process of the jugal and the elongate ventral process of postorbital. This differs from the condition in *B. sidensis* (Langer *et al*., 2010), *S. stockleyi* (Huene, 1938) and hyperodapedontines (Chatterjee, 1974; Benton, 1983a; Langer & Schultz, 2000; Whatley, 2005; Montefeltro, Langer & Schultz, 2010) in which the bar is formed mostly by the dorsal process of the jugal. The very elongate dorsal process combined with the presence of a well-developed ventral process of the postorbital represents an

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autapomorphy of *E. wolvaardti*. The anterior margin of the dorsal process of the jugal contacts the posterior margin of the ventral process of the postorbital, differing from the condition in *T. sulcognathus* and *Hyperodapedon* spp. in which the ventral process of the postorbital fits into a slot in the dorsal margin of the dorsal process of the jugal (Whatley, 2005; Montefeltro, Langer & Schultz, 2010).

Prefrontal/Lacrimal: The anterior border of the orbit is delimited by the mould of the medial projections of the ventral processes of the prefrontal and possibly lacrimal. This mould shows that the anterior wall of the orbit was well extended medially, as also occurs in *R. brodiei* (WARMS Gz6097). There is a nearly horizontal groove that is preserved as a natural mould situated anteroventral to the orbit, and which would most likely have been placed within the lacrimal. This groove appears to have exited on the anterior margin of the orbit, in the same position as the pair of foramina that are present for the exit of the naso-lacrimal duct in the lacrimal of *R. brodiei* (WARMS Gz6097).

Frontal: The frontal is completely missing, but the natural mould of its ventral surface is preserved (Fig. 3A, C). This mould shows the morphology of the olfactory tract and, more anteriorly, the transversely expanded olfactory bulbs. The morphology of the olfactory apparatus resembles that of other basal archosauromorphs (e.g. *Tasmaniosaurus triassicus*: Ezcurra, 2014).

Postorbital: The postorbital is a triradiate bone (Figs. 2–4: po). The posterior process is elongate and extends posteriorly, reaching a point level with the posterior border of the infratemporal fenestra (Fig. 4C: pp.po), as also occurs in all rhynchosaurids (e.g.

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R. articeps: NHMUK R1237, SHYMS G-132/1982; *B. sidensis*: Langer *et al*., 2010; *T. sulcognathus*: Montefeltro, Langer & Schultz, 2010; *Hyperodapedon* spp.: Chatterjee, 1974; Benton, 1983a; Langer & Schultz, 2000). Although not complete on either side, its posterior termination was gently rounded, as shown by the articular surface preserved on each squamosal. By contrast, in *M. browni* (SAM-PK-6536; Dilkes, 1998) and *H. browni* (Dilkes, 1995) the posterior process of the postorbital is proportionally shorter, ending anterior to the posterior border of the infratemporal fenestra, and tapers to a point rather than being broadly rounded. The orbital margin of the postorbital of SAM-PK-K10159 is thickened (Fig. 4C: t.po), and posterior to this thickening the lateral surface of the bone is gently concave.

The ascending process of the postorbital forms a broad transverse suture with the postfrontal. The contacts in the postorbital-postfrontal-parietal region are not clear, but the ascending process appears to continue medially as a broad process that forms the entire anterior margin of the supratemporal fenestra, as in *M. browni* (SAM-PK-6536; Dilkes 1998), *H. browni* (Dilkes 1995), *R. articeps* (SHYMS G-132/1982, Benton, 1990) and *S. stockleyi* (Montefeltro, Langer & Schultz, 2010).

Postfrontal: The lateral part of the postfrontal is preserved on the left side of the skull, contributing to the posterodorsal part of the orbital margin (Figs. 2–4: pf). The postfrontal appears to be excluded from the anterior border of the supratemporal fenestra.

Parietal: The parietals are fused to one another, without any trace of a median suture (Figs. 2–4: p), resembling the condition present in other rhynchosaurs (Dilkes, 1998). The anterior ends of the parietals are damaged, and the presence or absence of a

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pineal foramen cannot be determined. A sagittal crest is present along the full length of the midline of the parietals as preserved (Fig. 4E: sc). This differs from the condition in *M. browni* (SAM-PK-6536; Dilkes, 1998), in which the sagittal midline bears a concavity that is bounded laterally by ridges that define the supratemporal fenestrae, but resembles the condition in *H. browni* (Dilkes, 1995) and rhynchosaurids (Benton, 1983a, 1990; Langer *et al*., 2010; Montefeltro, Langer & Schultz, 2010). As preserved, the posterolateral processes of the parietals are directed posterolaterally in dorsal view. The posterolateral orientation is similar to the condition in *M. browni* (SAM-PK-6536), *H. browni* (SAM-PK-5885), *R. articeps* (SHYMS G-132/1982) and *S. stockleyi* (Montefeltro, Langer & Schultz, 2010), but differs from the laterally oriented processes in *B. sidensis* (BRSUG 27200), *I. genovefae* (Whatley, 2005), *T. sulcognathus* (UFRGS-PV-0232T, UFRGS-PV-0298) and *Hyperodapedon* spp. (e.g. *H. huenei*: UFRGS-PV-0132T; *H. mariensis*: FZB-PV-1867, Montefeltro, Langer & Schultz, 2010). In addition, the distal tips of the posterolateral processes do not curve anteriorly as occurs in *S. stockleyi* (Montefeltro, Langer & Schultz, 2010) and the 'Mariante rhynchosaur' (UFRGS-PV-0168T).

In posterior view the posterolateral processes are ventrally deflected at an angle of nearly 40º from the horizontal (Fig. 3B, D). This ventral deflection is a unique condition among rhynchosaurs in which the posterolateral processes are typically directed nearly directly laterally in posterior view. This may represent an autapomorphy of *E. wolvaardti*, but this is difficult to confirm given the post-mortem deformation that has affected the skull (including the dorsal displacement of the parietals relative to the supraoccipital), and this character is not included in the diagnosis. The posterolateral processes of the parietals are dorsoventrally deep, but

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taper at their distal ends where they fit into a notch within the supratemporal. As in all other rhynchosaurs, there is no postparietal bone.

Supratemporal: The supratemporal is well preserved on the left side and lies between the posterolateral process of the parietal and the medial surface of the squamosal (Figs. 2, 3: st). This condition is different from *T. sulcognathus* and *Hyperodapedon* spp. in which this bone is absent (Benton, 1983a; Langer & Schultz, 2000; Langer *et al*., 2010; Montefeltro, Langer & Schultz, 2010). The supratemporal in SAM-PK-K10159 is transversely broad in occipital view as also occurs in *B. sidensis* (Langer et al. 2010), but also forms a small part of the posterior margin of the supratemporal fenestra as in *M. browni* (SAM-PK-6536). Posteriorly the supratemporal contacts the dorsal edge of the tip of the paroccipital process, and forms most of the dorsal margin of the posttemporal fenestra. This condition differs from that present in *B. sidensis* (BRSUG 27200; Langer *et al*., 2010), in which this bone lacks a ventromedial process and, as a result, is limited to a more lateral portion of the margin of the fenestra.

Squamosal: The squamosal has four distinct processes (Figs. 2, 3: sq). The anterior process is broadly overlapped by the extensive posterior process of the postorbital. The anterior process forms only small portions of the lateral border of the supratemporal fenestra and the dorsal border of the infratemporal fenestra. The ventral process is proportionally elongate, extending for more than 75% of the height of the infratemporal fenestra (Fig. 4C: vp.sq). This is similar to the condition in *M. browni* (SAM-PK-6536; Dilkes, 1998), *F. spenceri* (Benton, 1990) and *T. sulcognathus* (UFRGS-PV-0232T, Montefeltro, Langer & Schultz, 2010), but differs from the abbreviated process that is present in *H. browni* (Dilkes, 1995) and *R.*

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articeps (SHYMS G-132/1982). Additionally, the narrow anteroposterior width of the ventral process is similar to the condition in *M. browni* (Dilkes, 1998), *H. browni* (Dilkes, 1995), *R. articeps* (SHYMS G-132/1982), *S. stockleyi* (Montefeltro, Langer & Schultz, 2010), and *F. spenceri* (Benton, 1990), but differs from the wide ventral process of the squamosal that is present in the hyperodapedontines *I. genovefae* (Whatley, 2005), *T. sulcognathus* (Montefeltro, Langer & Schultz, 2010) and *Hyperodapedon* spp. (Chatterjee, 1974; Benton, 1983a; Langer & Schultz, 2000). The medial process of the squamosal contacts the supratemporal, but it is unclear whether it contacted the parietal. Finally, there is a short posteroventral process that extends between the supratemporal and the head of the quadrate, reaching the paroccipital process. The lateral surface of the squamosal possesses several small subcircular pits.

Quadratojugal: The quadratojugal is a strap-like, slightly posteriorly bowed bone in lateral view (Figs. 2–4: qj), resembling that of *M. browni* (SAM-PK-6536; Dilkes, 1998). The bone is best preserved on the left side, and is damaged slightly at its very anteroventral margin. A short, rounded anterior process of the quadratojugal appears to have been present (Fig. 4: ap.qj), similar to the condition in *R. articeps* (SHYMS G-132/1982), but differing from the condition in *M. browni* in which an anterior process is absent (Dilkes, 1998). The quadratojugal terminates posteriorly adjacent to the quadrate condyles. It forms the lateral margin of an oval quadrate foramen, shared with the quadrate. The size of the quadrate foramen is similar to that of *M. browni* (SAM-PK-6536) and *R. articeps* (SHYMS 3), but differs from the more reduced aperture that is present in *F. spenceri* (Benton, 1990), *T. sulcognathus* (Montefeltro, Langer & Schultz, 2010) and a number of South American specimens of *Hyperodapedon* spp. (PVSJ 680, UFRGS-PV-0408T, UFRGS-PV-0149T).

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Quadrate: The quadrate is strongly bowed along its length with a concave posterior margin in lateral view (Figs. 2–4: q). Ventrally, the articular surface for the mandible is divided into two strongly convex condyles. The medial condyle is moderately better developed transversely and extends further ventral than the lateral condyle, resembling the condition present in *M. browni* (SAM-PK-6536), but differing from the condition in rhynchosaurids in which the condyles are equally well developed (e.g. *R. articeps*, NHMUK R1236; *B. sidensis*, BRSUG 27200; *T. sulcognathus* UFRGS-PV-0232). The lateral flange of the quadrate forms the dorsal margin of the quadrate foramen and overlaps the posterior margin of the ventral process of the squamosal (Figs. 3, 4: lf.q, qf).

Occiput: The supraoccipital is plate-like (Fig. 3: so) and similar to that of *M. browni* (Dilkes, 1998) and *H. browni* (Dilkes, 1995), but differs from the pillar-like supraoccipital that is present in Rhynchosauridae (e.g. *R. articeps*, Benton, 1990; *B. sidensis*, Langer *et al*., 2010; *T. sulcognathus*, Montefeltro, Langer & Schultz, 2010). The supraoccipital has a very low midline ridge. The paroccipital process is strap-like, and as preserved is posterolaterally oriented, but appears to have been displaced from its articulation with the supraoccipital. Its ventral margin is straight as in *M. browni*, *T. sulcognathus* (Montefeltro, Langer & Schultz, 2010) and some specimens of *Hyperodapedon* (e.g. UFRGS-PV-0149T), differing from the convex ventral margin that is present in *R. articeps* (SHYMS G-132/1982), *S. stockleyi* (Huene, 1938), the 'Mariante rhynchosaur' (UFRGS-PV-0168T), *B. sidensis* (BRSUG 27200), and *H. huenei* (UFRGS-0132). The paroccipital process forms the ventral margin of the slit-like posttemporal fenestra.

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Lower jaw, general: The dentary, surangular, angular and articular are preserved (Fig. 2). The mandibular anatomy is generally very similar to that of *M. browni* (SAM-PK-6536; Dilkes 1998). There is no mandibular fenestra, as in all rhynchosaurs. The maximum dorsoventral height of the mandible is less than a quarter of mandibular length, differing from hyperodapedontines in which the mandible is higher than a quarter of mandibular length (Benton, 1990; Dilkes, 1998; Whatley, 2005; Montefeltro, Langer & Schultz, 2010).

Dentary: The dentary is incomplete anteriorly on both sides, but a natural mould on the right side indicates that the bone tapered in dorsoventral height towards its anterior end, and would probably have ended approximately level with the anterior margin of the maxilla (Fig. 2: d), as in *M. browni* (SAM-PK-6536; Dilkes, 1998). Our estimation suggests that the dentary comprises less than half of the total length of the mandible, similar to the condition in *M. browni* and *S. stockleyi* (Benton, 1984, 1990; Dilkes, 1998). Natural moulds indicate that, as in the maxilla, the dentary was transversely expanded, and further show that multiple tooth rows were present, and that teeth were present on the lingual as well as occlusal surfaces. Posteriorly, the dentary has an elongate posterodorsal process that overlaps the lateral surface of the surangular.

Surangular: The surangular is a large element that dominates the mandible in lateral view, extending for more than 70% of mandibular length, and extending posterior to the glenoid fossa, forming the lateral surface of the retroarticular process (Figs. 2, 3: sa). The surangular has strongly convex dorsal and ventral margins, and a gently

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concave lateral surface. The lateral border of the glenoid fossa (which is not exposed) forms a low tuberosity. Immediately below this tuberosity there is a small posterior surangular foramen (Fig. 2: sf).

Angular: The angular is exposed as a narrow strip of bone ventral to the surangular (Fig. 2: a).

Articular: The articular is poorly preserved, but it can be determined that it contributed to a well posteriorly developed and upturned retroarticular process (Fig. 2: ar), resembling the condition in *H. browni* (Dilkes, 1995).

Hyoid apparatus: The right ceratobranchial of the hyoid apparatus is preserved, and is a slender, rod-like element (Fig. 2: hy). As preserved, it extends posteriorly beyond the level of the cranio-mandibular joint, and is missing its posterior end.

Dentition: Micro-CT data demonstrate that the maxillae and dentaries are transversely expanded, forming dental plates with multiple rows of conical teeth, with teeth present both on occlusal and labial surfaces of the bones (Fig. 5: d.occ, m.occ). This condition resembles the jaw apparatus of *H. browni* (Dilkes, 1995). The tooth bearing surfaces of the maxilla and dentary are divided into a nearly horizontally orientated occlusal surface, and a nearly vertical, medially facing surface, which bears the lingual teeth (Fig. 5: d.t, m.t). This condition is different from the lingual margin of the tooth plates of *H. browni* in which the occlusal surface more gradually merges into the lingual surface (Dilkes, 1995). As in *H. browni* (Dilkes, 1995), there is no occlusal groove, but in some places the occlusal surface of the maxilla appears to be

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gently concave. The presence of dental plates in both maxilla and dentary in SAM-PK-K10159 is different from the groove and blade jaw apparatus of all rhynchosaurids, including the fragmentary Middle Triassic form *Ammorhynchus navajoi* and the 'Chañares form' (Benton, 1983a, 1984, 1990; Langer *et al*., 2000; Nesbitt & Whatley, 2004; Montefeltro, Langer & Schultz, 2010; Ezcurra *et al*., 2013).

The most clearly distinguishable and most complete, teeth are the most lingual. These teeth are clearly set within shallow sockets and appear to be fused to the surrounding bone, although they are still distinguishable. More labially positioned teeth, and teeth on the occlusal surface, are more completely fused and difficult to distinguish from the surrounding bone, with those on the occlusal surface likely completely worn completely level with the bone.

As in *M. browni* there is clearly a single row of tightly packed teeth on the vomer (Fig. 5: v.t), and slightly smaller teeth are also present along the thickened medial parts of the pterygoids (Fig. 5: ptg.t). It is unclear whether or not palatine teeth are present. The palatal teeth of the vomer and pterygoid are similar in size to the lingual teeth present on the maxilla and dentary.

Possible tibia and fibula: There is a partial long bone preserved adjacent to the posterior end of the right side of the skull that partially obscures the craniomandibular joint (Fig. 2A, C: lb). Next to it, there is a natural mould of a long bone shaft that possesses the same longitudinal orientation (Fig. 2A, C: lbm). The size, curvature of the shaft, and morphology of the preserved articular end suggest that the preserved long bone is the distal half of a fibula and the natural mould next to it may be of a tibia. The probable fibula is bowed along its length and the distal articular surface is sub-circular.

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PHYLOGENETIC ANALYSIS

The parsimony analysis yielded a single most parsimonious tree of 146 steps with a consistency index (CI) of 0.6781 and a retention index (RI) of 0.7565. *Eohyosaurus wolvaardti* is recovered as the sister taxon of Rhynchosauridae (*sensu* Dilkes, 1998) (Fig. 6). Under suboptimal constrained topologies one additional step is necessary to recover *E. wolvaardti* as the sister taxon of *H. browni* (Templeton's test p=1.000), five additional steps for a position as the sister taxon of *M. browni* (Templeton's test p=0.2891), and eight additional steps for a position as a member of Rhynchosauridae (Templeton's test p=0.0078).

DISCUSSION

PHYLOGENETIC IMPLICATIONS

Our phylogenetic results place *Eohyosaurus wolvaardti* as closer to rhynchosaurids than are *Mesosuchus browni* and *Howesia browni* on the basis of one synapomorphy: the elongated posterior process of the postorbital that reaches the level of the posterior border of the infratemporal fenestra (character number 29: 0→1). However, the *E. wolvaardti* + Rhynchosauridae node is weakly supported (Table 2), and an alternative position as the sister taxon to the morphologically similar *H. browni* is not a significantly worse explanation of the data (Templeton test results).

Rhynchosauridae is supported to the exclusion of *M. browni*, *H. browni* and *E. wolvaardti* on the basis of eight synapomorphies: orbit with elevated rim along the jugal, postorbital, frontal, prefrontal and lacrimal (character number 5: 0→1); jugal without multiple pits on the lateral surface of its main body (character number 17: 1→0); jugal subtemporal (= posterior) process with a distinct lateroventral orientation

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with respect to the sagittal axis of the snout (character number 19: 0→1); squamosal with a very long medial process, forming the entire or almost the entire posterior border of the supratemporal fenestra (character number 40: 0→1); supraoccipital with an inverted V-shape ("pillar-like"; character number 48: 0→1); blade and groove jaw apparatus, where dentary blade(s) fit precisely into maxillary groove (character number 60: 1→2); and absence of vomerine and pterygoid teeth (character numbers 61 and 63: 0→1). Several of the synapomorphies recovered here for Rhynchosauridae are recognised here for the first time, and the clade is one of the best supported in our analysis (i.e. Bremer support=8, bootstrap frequencies=99%; Table 2).

The overall topology of the tree is consistent with that recovered by Montelfeltro *et al*. (2013) (Fig. 6), including the sister grouping of the 'stenaulorhynchines' *Stenaulorhynchus stockleyi* and the 'Mariante rhynchosaur', and the placement of *Fodonyx spenceri* as the sister group of a monophyletic Hyperodapedontinae (*Isalorhynchus genovefae*, *Teyumbaita sulcognathus* and *Hyperodapedon* spp.). In the present analysis *Bentonyx sidensis* was unambiguously recovered as closely related to hyperodapedontines, rather than in a polytomy among derived rhynchosaurids. However, the support for this clade is low (Table 2).

The addition of *Rhynchosaurus articeps* and *R. brodiei* to the phylogenetic analysis resulted in a paraphyletic genus *Rhynchosaurus*, with the latter species being recovered as more closely related to hyperodapedontines than to *R. articeps*. The clade composed of *R. brodiei* and other rhynchosaurids to the exclusion of *R. articeps* is supported by three synapomorphies: jugal higher than maxilla below the ventral border of the orbit (character number 11: 0→1); prefrontal with a deeply concave dorsomedial surface near the orbital rim (character number 21: 0→1); and frontal without a groove on its dorsal surface (character number 23: 1→0). This clade

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possesses relatively high bootstrap support (>75%, Table 2). *Rhynchosaurus brodiei* is recovered in a polytomy together with 'stenaulorhynchines' and more derived rhynchosaurids. Although the results of our phylogenetic analysis suggest that *R. brodiei* may need to be transferred to a new genus, further anatomical and taxonomic work is necessary on the hypodigm series of *Rhynchosaurus* to confirm this, and is beyond the scope of the present work.

EARLY RHYNCHOSAUR DIVERSITY AND BIOGEOGRAPHY

Our description of *Eohyosaurus wolvaardti* demonstrates the presence of three different rhynchosaur species in the tetrapod assemblage of Subzone B of the *Cynognathus* AZ. This species richness of rhynchosaurs resembles that present in some younger rock sequences such as the Santa Maria Sequence 2 of southern Brazil (Langer *et al*., 2007), and shows that rhynchosaurs were already rather taxonomically diverse by the early Middle Triassic, at least in South Africa (Fig 6). The only rhynchosaur known from rocks older than Middle Triassic is *Noteosuchus colletti*, from the earliest Triassic of South Africa (Carroll, 1976), which has been supported as a member of Rhynchosauria by recent phylogenetic analysis (Ezcurra, Scheyer & Butler, 2014).

Intriguingly, the stratigraphically oldest known rhynchosaurs (*N. colletti*), and the three most basal rhynchosaur (non-rhynchosaurid) taxa in the present phylogenetic analysis (which did not include *N. colletti*) all come from South Africa. Although the impacts of incomplete sampling must be considered, this is suggestive that the early rhynchosaur radiation during the Early and earliest Middle Triassic may have been geographically restricted, and that rhynchosaur origins may lie in southern Pangaea. An important test of this hypothesis would be the restudy of the material of

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Eifelosaurus triadicus, an overlooked reptile from the early Middle Triassic (early Anisian) of Germany (Jaekel, 1904), which has occasionally been identified as rhynchosaurian (e.g. Huene, 1929).

Early rhynchosaurid rhynchosaurs achieved a global distribution during the Anisian, being known from the USA (Nesbitt & Whatley, 2004), Tanzania (Huene, 1938), and the UK (Benton, 1990). This global distribution was also obtained by hyperodapedontine rhynchosaurids during the early Late Triassic, occurring in the UK, Madagascar, Zimbabwe, India, Brazil, Argentina, Canada and the USA (Baird 1963, Chatterjee, 1980; Benton, 1983a; Langer *et al*., 2000; Montefeltro, Langer & Schultz, 2010; Montefeltro *et al*., 2013; Mukherjee & Ray, 2014). The success of hyperodapedontines was, however, relatively short-lived, with the clade apparently suffering extinction somewhere close to the Carnian–Norian boundary.

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FIGURE CAPTIONS

Figure 1. Geographic and stratigraphic setting of the type specimen of *Eohyosaurus wolvaardti*. map of South Africa and surrounding regions showing the location of the farm Lemoenfontein 44 (marked with a star) (A); and simplified stratigraphy of the upper portion of the Beaufort Group (stratigraphic level of *Eohyosaurus wolvaardti* marked with a star) (B).

Figure 2. *Eohyosaurus wolvaardti*, SAM-PK-K10159. Photographs of holotype skull in right (A) and left (B) lateral views; and interpretive line drawings of holotype skull in right (C) and left (D) lateral views. Hatched areas represent broken surface. Dashed lines represent missing bones and uncertain sutural contacts. Arrows indicate tooth impressions in rock matrix. Asterisks indicate approximate planes of the CT cross sections shown in Figure 5. Abbreviations: a, angular; ao, *anguli oris* crest; d, dentary; j, jugal; hy, hyoid bone; lb, long bone; lbm, long bone mould; m, maxilla; p, parietal; pf, postfrontal; po, postorbital; q, quadrate; qj, quadratojugal; sa, surangular; scl, sclerotic plates; sf, surangular foramen; sq, squamosal; st, supratemporal.

Figure 3. *Eohyosaurus wolvaardti*, SAM-PK-K10159. Photographs of holotype skull in dorsal (A) and occipital (B) views; and interpretive line drawings of holotype skull in dorsal (C) and occipital (D) views. Hatched areas represent broken surface. Dashed lines represent missing bones and uncertain sutural contacts. Abbreviations: j, jugal; op, opisthotic; p, parietal; pf, postfrontal; po, postorbital; q, quadrate; qf, quadrate foramen; qj, quadratojugal; sa, surangular; scl, sclerotic plates; so, supraoccipital; sq, squamosal; st, supratemporal.

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Figure 4. *Eohyosaurus wolvaardti*, SAM-PK-K10159, close-up photographs. Anterior end of the skull as preserved in left (A) and right (B) lateral views; temporal region of the skull in right lateral view (C); left squamosal, quadrate and quadratojugal in lateral view (D); and parietals and posterior skull roof in dorsal view (E). Abbreviations: ao, *anguli oris* crest; ap.qj, anterior process of the quadratojugal; d, dentary; dp.j, dorsal process of the jugal; j, jugal; m, maxilla; lf.q, lateral flange of the quadrate; p, parietal; pf, postfrontal; po, postorbital; pp.j, posterior process of the jugal; pp.po, posterior process of the postorbital; q, quadrate; qf, quadrate foramen; qj, quadratojugal; sc, sagittal crest; scl, sclerotic ring; shm, impression of the horizontal occlusal shelf of the maxilla; t.po, thickened orbital margin of the postorbital; vp.sq, ventral process of the squamosal.

Figure 5. *Eohyosaurus wolvaardti*, SAM-PK-K10159, Micro-CT cross sections through the tooth-bearing bones. Approximate positions of the CT sections are shown in Figure 2. Abbreviations: d, dentary; d.occ, occlusal surface of the dentary; d.t, dentary lingual tooth; l.m, left maxilla; m.occ, occlusal surface of the maxilla; m.t, maxillary lingual tooth; ptg.t, pterygoid tooth; r.m, right maxilla; v, vomer; v.t, vomerine tooth. Scale bars equal 2 mm.

Figure 6. Time calibrated single most parsimonious tree showing the phylogenetic relationships of *Eohyosaurus wolvaardti* and other rhynchosaurs recovered in the phylogenetic analysis presented here. The length of the vertical bar representing each terminal taxon represents chronostratigraphic uncertainty rather than true stratigraphic range. Abbreviations: Ans, Anisian; Crn, Carnian; Chx, Changhsingian; E., Early;

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Hynae, Hyperodapedontinae; Ind, Induan; Lad, Ladinian; Nor, Norian; Ole, Olenekian; PER., Permian; Rht, Rhaetian; Wuc, Wuchiapingian.

TABLES

Table 1. Selected measurements of the holotype specimen of *Eohyosaurus wolvaardti* (SAM-PK-K10159), in millimetres. Values between brackets indicate incomplete measurements, and the value given is the maximum measurable. Maximum deviation of the digital calliper equals 0.02 mm but measurements were rounded to the nearest 0.1 millimetre.

	Length	Height	Width
Skull	(68.2)	ca. 39	-
Jugal	(36.2)	19.8	-
Jugal posterior process	9.8	-	-
Jugal posterior process base	-	3.9	-
Jugal ascending process	-	13.9	-
Orbit	24.4	20.5	-
Postorbital posterior process	12.7	-	-
Postorbital ventral process	11.4	-	-
Squamosal	18.4		
Squamosal ventral process	-	13.4	-
Squamosal ventral process at base	-	-	8.0
Infratemporal fenestra	25.1	21.4	-
Supratemporal fenestra	20.4	-	13.0
Quadratojugal height	-	17.4	-
Quadratojugal ventral margin	7.6	-	-
Quadrate height	-	24.6	-
Quadrate distal end	-	-	8.9
Parietals maximum	-	-	25.9
Parietals minimum	-	-	9.2
Lower jaw length	(83.8)	-	-
Surangular height	-	12.4	-
Hyoid length	(52.4)	-	-

Table 2. Bremer index and bootstrap frequency supports for the nodes of the single most parsimonious tree recovered in the phylogenetic analysis.

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Node	Bremer index	Absolute bootstrap frequency	GC bootstrap frequency
Rhynchosauria	5	93%	92%
Howesia + Rhynchosauridae	1	56%	35%
Eohyosaurus + Rhynchosauridae	1	64%	58%
Rhynchosauridae	8	99%	99%
R. brodiei + Hyperodapedontinae	2	79%	74%
Stenaulorhynchinae	2	47%	35%
Bentonyx + Hyperodapedontinae	1	26%	14%
Fodonyx + Hyperodapedontinae	2	64%	55%
Hyperodapedontinae	8	99%	99%
Teyumbaita + *Hyperodapedon*	6	95%	95%

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APPENDICES

APPENDIX 1

Character list arranged in anatomical order for the phylogenetic analysis conducted here. Characters adapted from previously published analyses are acknowledged accordingly. The numbering of characters used in the present analysis is shown between square brackets and that of Montefeltro *et al*. (2013) is shown between parentheses. Character 28 from the original character list of Montefeltro *et al*. (2013) was not included in the current analysis because of the poor distinction between its character states.

[1] (1) Skull dimensions: longer than broad (0); broader than long (1) (Benton, 1984).

[2] (2) Skull height: <50% of the midline length (0); >50% of the midline length (1) (Hone & Benton, 2008).

[3] External nares: separate (0), single medial naris (1) (Benton, 1985).

[4] (3) Orbit orientation: mostly lateral (0); mostly dorsal (1) (Langer & Schultz, 2000).

[5] Orbit with elevated rim along the jugal, postorbital, frontal, prefrontal and lacrimal: absent (0); present (1) (new character).

[6] (4) Orbital medial margin: rounded (0); forming a marked angle (1) (Montefeltro, Langer & Schultz, 2010).

[7] Lower temporal fenestra: open ventrally (0), closed ventrally (1) (Dilkes, 1998).

[8] Premaxilla ventral margin: horizontal (0), down-turned (1) (Benton, 1985).

[9] Premaxilla and prefrontal contact: absent (0), present (1) (Dilkes, 1998).

[10] Shape of cranial margin of nasal at midline: strongly convex with anterior process (0) or transverse with little convexity (1) (Dilkes, 1998).

[11] (5) Jugal and maxillary heights bellow the ventral border of the orbit: maxilla higher (0); jugal higher (1) (Benton, 1984).

[12] (6) Jugal-lacrimal contact: minimal (0); extensive contact of the jugal anterior process (1) (Whatley, 2005).

[13] (7) Anguli oris crest: absent (0); present (1) (modified from Benton, 1984).

[14] Anterior extension of the anguli oris crest: restricted to the main body of the jugal (0); extending onto the anterior process of the jugal, but not the maxilla (1); extending onto the maxilla, but not the anterior process of the jugal (2) (modified from Benton, 1984).

[15] (8) Jugal surface dorsal to anguli oris crest: lacking a secondary crest (0); with a secondary anguli oris crest (1) (Langer & Schultz, 2000).

[16] (9) Lateral overlap of maxilla by jugal: absent or minimally expanded (0); well developed (1) (Whatley, 2005).

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[17] Jugal with multiple pits on the lateral surface of its main body: absent (0); present (1) (taken from Dilkes, 1995; used here for the first time in phylogenetic analysis).

[18] (10) Jugal subtemporal process: height >50% of the length (0); height <50% of the length (1) (Dilkes, 1995).

[19] Jugal subtemporal process with a distinct lateroventral orientation with respect to the sagittal axis of the snout: absent (0); present (1) (new character).

[20] (11) Relative widths of postorbital bar and lower temporal fenestra: <0.4 (0); >0.4 (1) (Langer & Schultz, 2000).

[21] (12) Dorsomedial surface of prefrontal near the orbital rim: flat or slightly concave (0); deeply concave (1) (Whatley, 2005).

[22] (13) Procumbent lacrimal and prefrontal anterolateral margin: absent (0); present (1) (Whatley, 2005).

[23] (14) Groove on the dorsal surface of the frontal: absent (0); present (1) (Dilkes, 1995).

[24] Dorsal groove on frontal: longitudinally extended along most of the surface of the frontal (0); anterolaterally-to-posteromedially extended along the posterior half of the frontal (1) (new character).

[25] (15) Well-marked 'V'-shaped crest along frontal-postfrontal contact, anterior to the margin of the supratemporal fossa: absent (0); present (1) (Montefeltro, Langer & Schultz, 2010).

[26] (16) Frontal and parietal midline lengths: frontal longer (0); parietal longer (1) (Benton, 1987).

[27] (17) Postfrontal: excluded from upper temporal fenestra border (0); forming the upper temporal fenestra border (1) (Dilkes, 1998).

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[28] (18) Postfrontal dorsal surface: flat (0); markedly concave (1) (Dilkes, 1995).

[29] Posterior extension of the posterior process of the postorbital: considerably anterior to the level of the posterior border of the infratemporal fenestra (0); at level with the posterior border of the infratemporal fenestra (1) (modified from Dilkes, 1998).

[30] (19) Postorbital anteroventral process: expanding ventral to the level of the orbital midpoint (0); expanding dorsally to orbital height midpoint (1) (Dilkes, 1998).

[31] (20) Postorbital ventral process: expands anterior to the jugal (0); fits dorsal to the jugal (1) (Whatley, 2005).

[32] (21) Postorbital-parietal suture: visible in dorsal view (0); hidden in dorsal view (1) (Dilkes, 1998).

[33] Parietals: separate (0), fused (1) (Benton, 1985).

[34] Parietal foramen: always, or sometimes, present (0), always absent (1) (Benton, 1985).

[35] Parietal table: broad (0), constricted and with sagittal crest (1) (Dilkes, 1998).

[36] (22) Parietal body: not expanded laterally at midlength (0); expanded laterally at midlength (1) (Montefeltro, Langer & Schultz, 2010).

[37] (23) Parietal transverse process: posterolaterally directed (0); laterally directed (1) (Montefeltro, Langer & Schultz, 2010).

[38] (24) Distal tip of parietal transverse process: not anteriorly curved (0); anteriorly curved (1) (Montefeltro, Langer & Schultz, 2010).

[39] (25) Squamosal ventral process: thinner than 50% of dorsoventral length (0); broader than over 50% of dorsoventral length (1) (Benton, 1990).

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[40] Squamosal medial process: short, forming less than half of the posterior border of the supratemporal fenestra (0); long, forming entire or almost entire posterior border of the supratemporal fenestra (1) (new character).

[41] (26) Relative position of quadratojugal and squamosal processes: squamosal ventral process anterior to quadratojugal dorsal process (0); squamosal ventral process overlapping the quadratojugal dorsal process (1) (Whatley, 2005).

[42] Quadratojugal anterior process: completely absent (0), present (1) (Dilkes, 1998).

[43] (27) Supratemporal: present (0); absent (1) (Benton, 1984).

[44] Supratemporal with a bifurcated medial border, in which a ventromedial process extends underneath the posterolateral process of the parietal: present (0); absent (1) (new character).

[45] (29) Pterygoid midline suture length: greater than or equal to the distance between the posterior margin of the suture and the basipterygoid articulation (0); less than the distance between the posterior margin of the suture and the basipterygoid articulation (1) (Whatley, 2005).

[46] Ectopterygoid reaches lateral corner of transverse flange of pterygoid: no (0), yes (1). (Dilkes, 1998)

[47] (30) Elements forming the border of the suborbital fenestra: ectopterygoid, palatine, and maxilla (0); ectopterygoid and palatine only (1) (Dilkes, 1995).

[48] Supraoccipital shape: plate-like (0); inverted V-shape (1). (Dilkes, 1995)

[49] (31) Occipital condyle position: anterior to craniomandibular articulation (0); aligned to craniomandibular articulation (1) (Benton, 1984).

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[50] (32) Basioccipital and basisphenoid/parasphenoid lengths: basisphenoid/parasphenoid longer (0); basioccipital longer (1) (Langer & Schultz, 2000).

[51] (33) Relative positions of the basipterygoid process of the basisphenoid and the ectopterygoid process of the pterygoid: at the same level (0), basipterygoid process of the basisphenoid posterior to ectopterygoid process of the pterygoid (1) (Dilkes, 1995).

[52] (34) Basipterygoid process dimensions (dorsoventral length, anteroposterior width): longer than wide (0); wider than long (1) (Langer & Schultz, 2000).

[53] Jaw symphysis: formed largely by dentary (0), formed only by splenial (1) (Dilkes, 1998).

[54] Divergence of dentaries in front of symphysis: absent (0), present (1) (Dilkes, 1998).

[55] (35) Mandible depth: <0.25 of the total length (0); >0.25 of the total length (1) (Benton, 1984).

[56] (36) Dentary length: half, or less, than the total mandibular length (0); greater than half of the total mandibular length (1) (Benton, 1990).

[57] Premaxillary teeth: present (0), absent (1) (Benton, 1985).

[58] Tooth implantation: subthecodont or thecodont (0), ankylothecodont (1) (Benton, 1985).

[59] Maxilla occlusal ventral margin: horizontal (0), convex (1). (modified from Dilkes, 1998).

[60] Tooth occlusion: single sided overlap (0), flat occlusion (1), blade and groove jaw apparatus, where dentary blade(s) fit precisely into maxillary groove(s) (2) (Benton, 1985).

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[61] Vomerine teeth: present (0), absent (1) (Dilkes, 1998).

[62] Palatine teeth: present (0), absent (1) (Dilkes, 1998).

[63] Pterygoid teeth: present (0), absent (1). (Benton, 1983a)

[64] (37) Medial maxillary groove: absent (0); present but not reaching the anterior half of the maxilla (1); present and reaching the anterior half of the maxilla (2) (Benton, 1984).

[65] (38) Maxillary area lateral to main groove: narrower than the medial area (0); same width or broader than the medial area (1) (Benton, 1990).

[66] (39) Maxillary cross-section lateral to main groove: crest-shaped (0); cushion-shaped (1) (Langer, Ferigolo & Schultz, 2000).

[67] (40) Tooth rows lateral to main maxillary groove: a single clear row (0); more than one clear row (1) (Langer & Schultz, 2000).

[68] (41) Number of tooth rows medial to main maxillary groove: two rows and scattered teeth (0); three or more tooth rows (1) (Langer, Ferigolo & Schultz, 2000).

[69] (42) Occlusal tooth rows on the anterior half of the maxilla: four or more tooth rows (0); fewer than four tooth rows (1) (Whatley, 2005).

[70] (43) Maxillary lingual teeth: absent (0); scattered teeth (1); large number of teeth on the medial surface of the bone (2) (Benton, 1984), ORDERED.

[71] (44) Maxillary teeth: only conicals (0); conicals and 'pyramidal' (1) (Whatley, 2005).

[72] (45) Dentary teeth: only conicals (0); conical and anteroposteriorly compressed (1) (Whatley, 2005).

[73] Number of rows of teeth on dentary: one (0), two (1), more than two full rows (2). (Benton, 1983a), ORDERED.

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[74] (46) Posterior-most dentary teeth: on the anterior half of lower jaw (0); on the posterior half of lower jaw (1) (Langer & Schultz, 2000).

[75] (47) Lingual dentary teeth: absent (0); present and forming one row (1); present and forming more than one row (2) (Benton, 1984), ORDERED.

[76] (48) Dentary teeth on the dentary lingual surface: scattered (0); crowded (1) (Benton, 1985).

[77] (60) Axis ventral keel: present (0); absent (1) (Montefeltro *et al*., 2013).

[78] (61) Axial parapophysis: present (0); absent (1) (Montefeltro *et al*., 2013).

[79] (62) Cervical postaxial vertebrae ventral keel: absent (0); present (1) (Montefeltro *et al*., 2013).

[80] (49) Truncal vertebrae with ossified intercentrum: present (0); absent (1) (Evans, 1988).

[81] (50) Epipophyses on cervical postzygapophyses: spine-shaped (0); crest-shaped (1) (Whatley, 2005).

[82] (63) Position of the transverse process of cranial truncal vertebrae: at the level of prezygapophysis (0); posteriorly located in the vertebra centrum (1) (Montefeltro *et al*., 2013).

[83] (51) Second sacral vertebra: with a notch between the iliac articular surface and the posterior process (0); posterior process continuous to the iliac articular surface (1) (Dilkes, 1998).

[84] (52) Caudal vertebrae neural spines: height twice the length (0); height less than twice the length (1) (Dilkes, 1998).

[85] (53) Interclavicle: posterior process longer than twice the lateral processes (0); posterior process shorter than twice the lateral process (1) (Dilkes, 1998).

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[86] (64) Supinator process on the external surface of humeral ectepicondyle: absent (0); present and hook-shaped (1); present and formed by a low supinator ridge and ligament groove (2) (Montefeltro *et al*., 2013).

[87] (54) Posterior process of the coracoid: present (0); absent (1) (Benton, 1984).

[88] (55) Dorsal margin of the ilium: anterior process <15% of the length of the posterior process (0); anterior process >15% of the length of the posterior process (1) (Dilkes, 1995).

[89] (56) Pubic tubercle on the lateral surface of the pubic shaft: present (0); absent (1) (Whatley, 2005).

[90] (57) Internal trochanter: continuous with the femoral head (0); separated from femoral head (1) (Whatley, 2005).

[91] (65) Crest on anteromedial region of tibial shaft: absent (0); present (1) (Montefeltro *et al*., 2013).

[92] (58) Relative size of astragalar articular facets: tibial facet greater than centrale facet (0); centrale facet greater than tibial facet (1) (Langer & Schultz, 2000).

[93] (59) Metatarsal I: longer than broad (0); broader than long (1) (Hone & Benton, 2008).

APPENDIX 2

Synapomorphies of the single most parsimonious tree recovered in the present analysis.

Rhynchosauria: 3: 0→1; 9: 0→1; 23: 0→1; 60: 0→1; 73: 0→2.

Howesia+Rhynchosauridae: 10: 0→1; 34: 0→1; 59: 0→1; 70: 0→1.

Eohyosaurus+Rhynchosauridae: 13: 0→1; 29: 0→1.

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Rhynchosauridae: 5: 0→1; 17: 1→0; 19: 0→1; 40: 0→1; 48: 0→1; 60: 1→2; 61: 0→1; 63: 0→1.

R. brodiei+Hyperodapedontinae: 11: 0→1; 21: 0→1; 23: 1→0.

Stenaulorhynchinae: 25: 0→1; 38: 0→1; 64: 0→2; 68: 0→1; 70: 1→2; 76: 0→1.

Bentonyx+Hyperodapedontinae: 12: 0→1.

Fodonyx+Hyperodapedontinae: 1: 0→1; 2: 0→1; 5: 1→0; 66: 0→1.

Hyperodapedontinae: 14: 0→1; 16: 0→1; 39: 0→1; 41: 0→1; 55: 0→1; 71: 0→1; 72: 0→1; 74: 0→1.

Teyumbaita+*Hyperodapedon* spp.: 30: 0→1; 31: 0→1; 52: 0→1; 67: 0→1; 68: 0→1; 69: 1→0; 81: 0→1.

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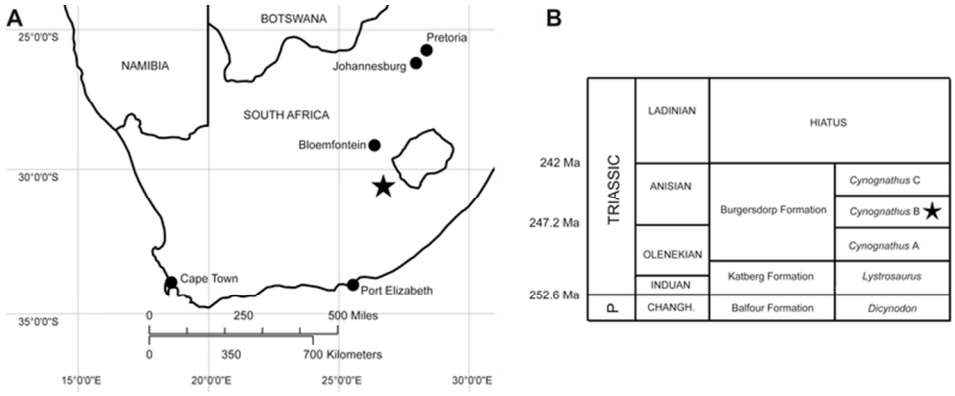

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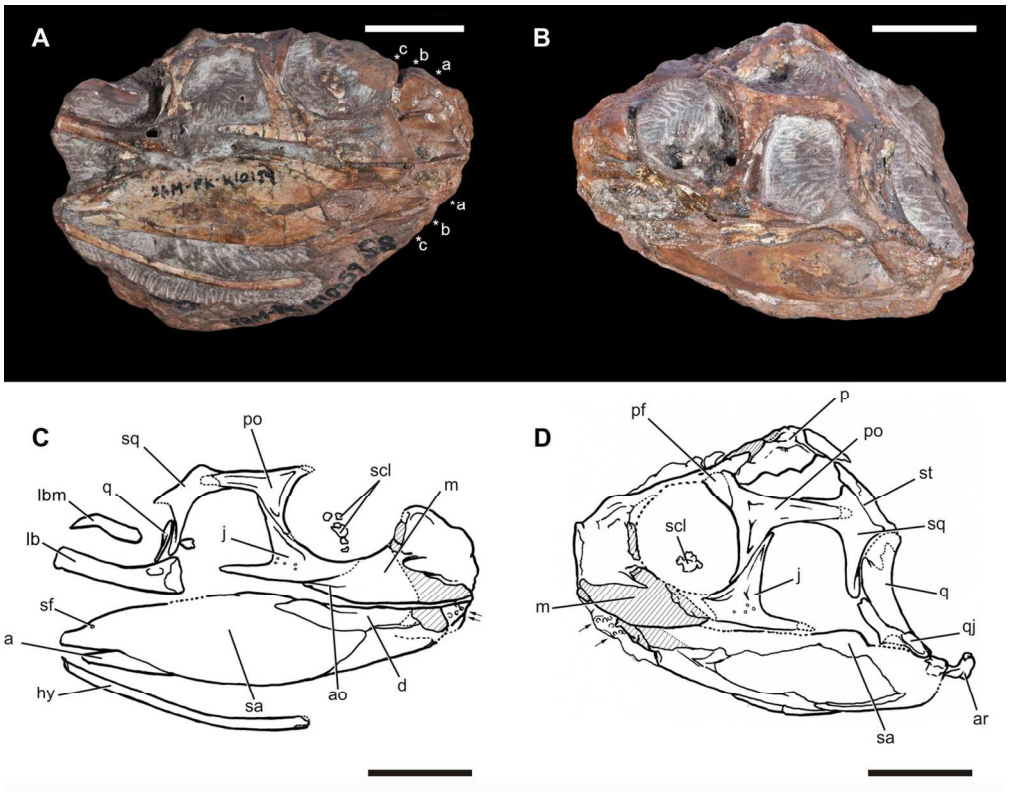

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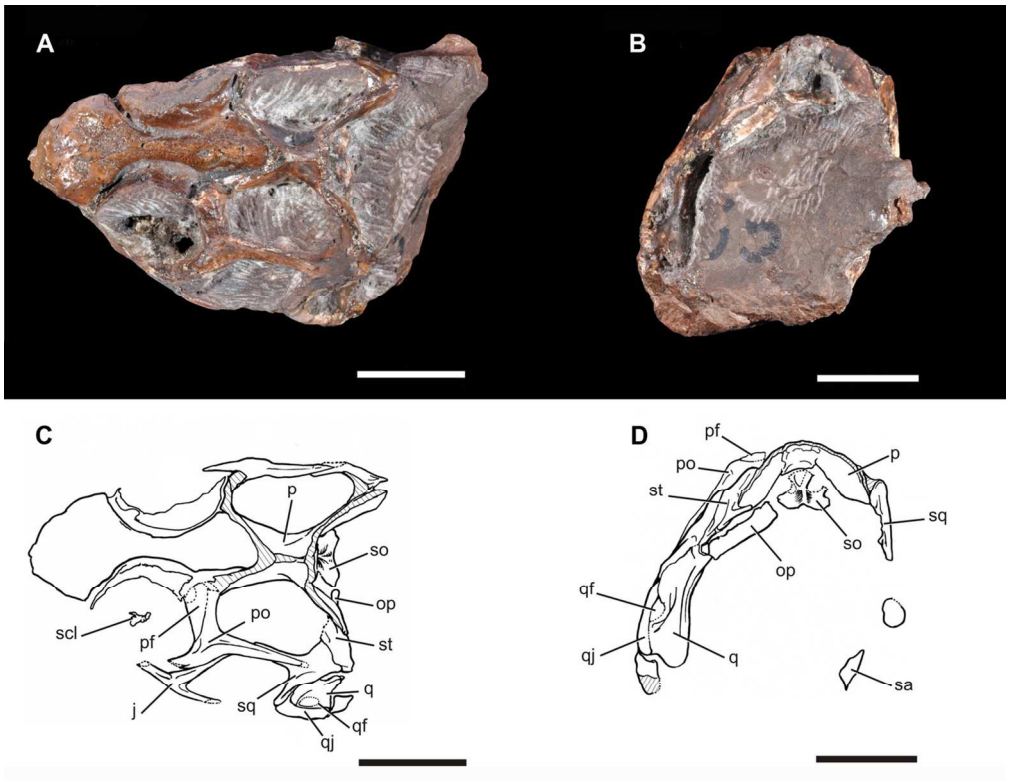

Figure 3. Eohyosaurus wolvaardti, SAM-PK-K10159. Photographs of holotype skull in dorsal (A) and occipital (B) views; and interpretive line drawings of holotype skull in dorsal (C) and occipital (D) views. Hatched areas represent broken surface. Dashed lines represent missing bones and uncertain sutural contacts. Abbreviations: j, jugal; op, opisthotic; p, parietal; pf, postfrontal; po, postorbital; q, quadrate; qf, quadrate foramen; qj, quadratojugal; sa, surangular; scl, sclerotic plates; so, supraoccipital; sq, squamosal; st, supratemporal.
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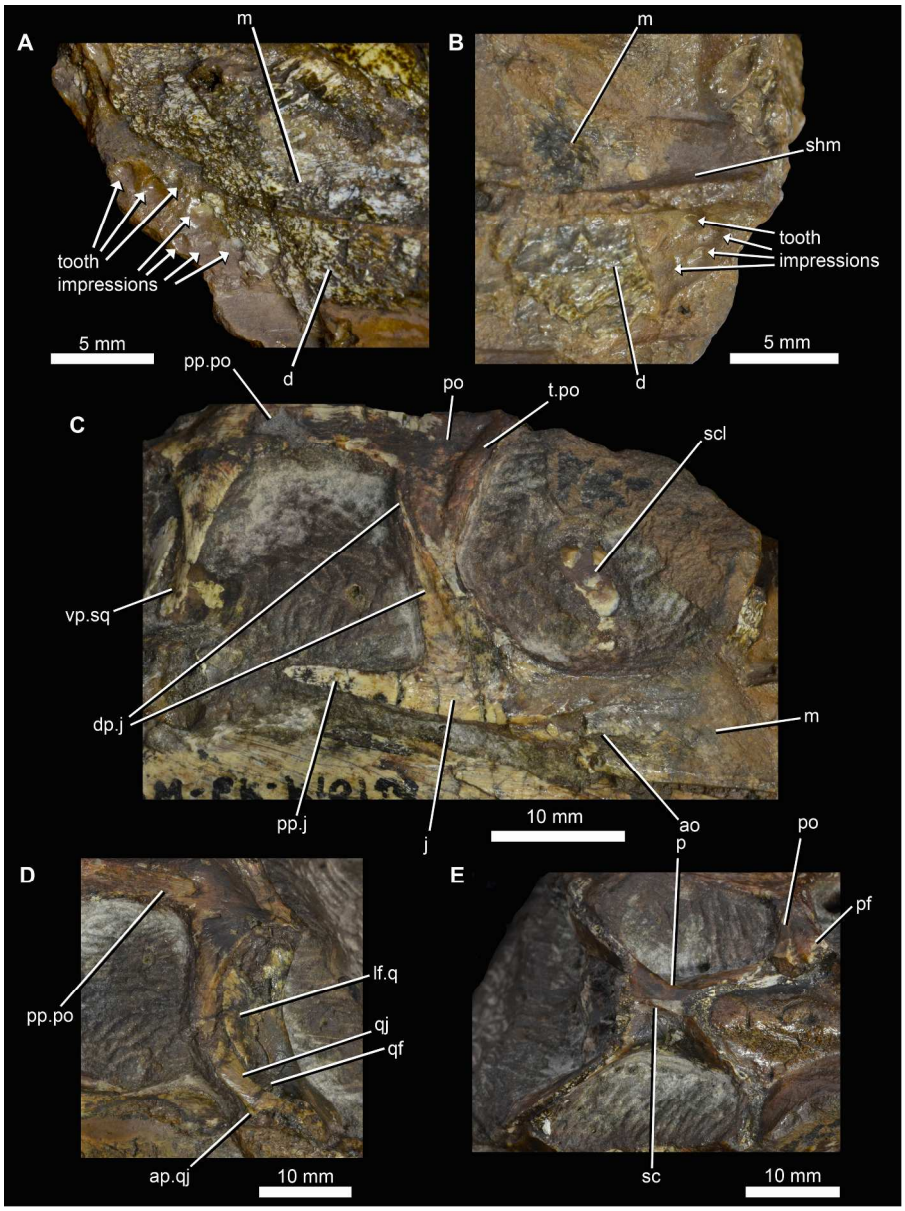

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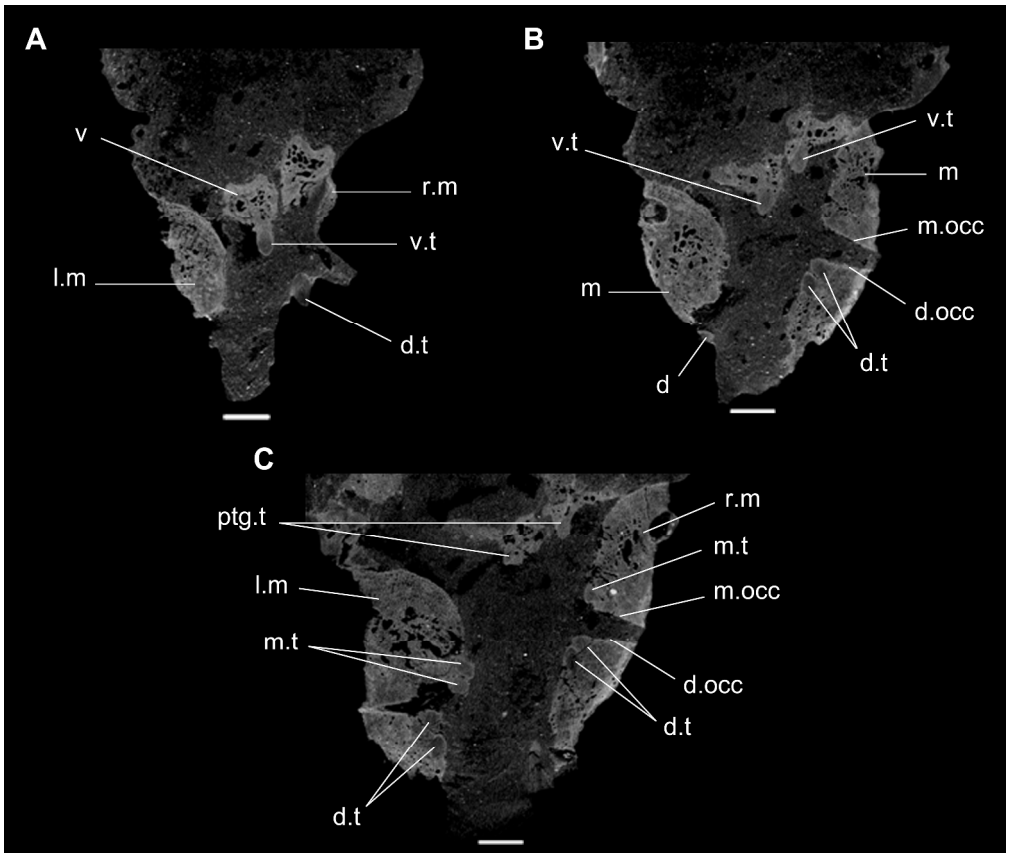

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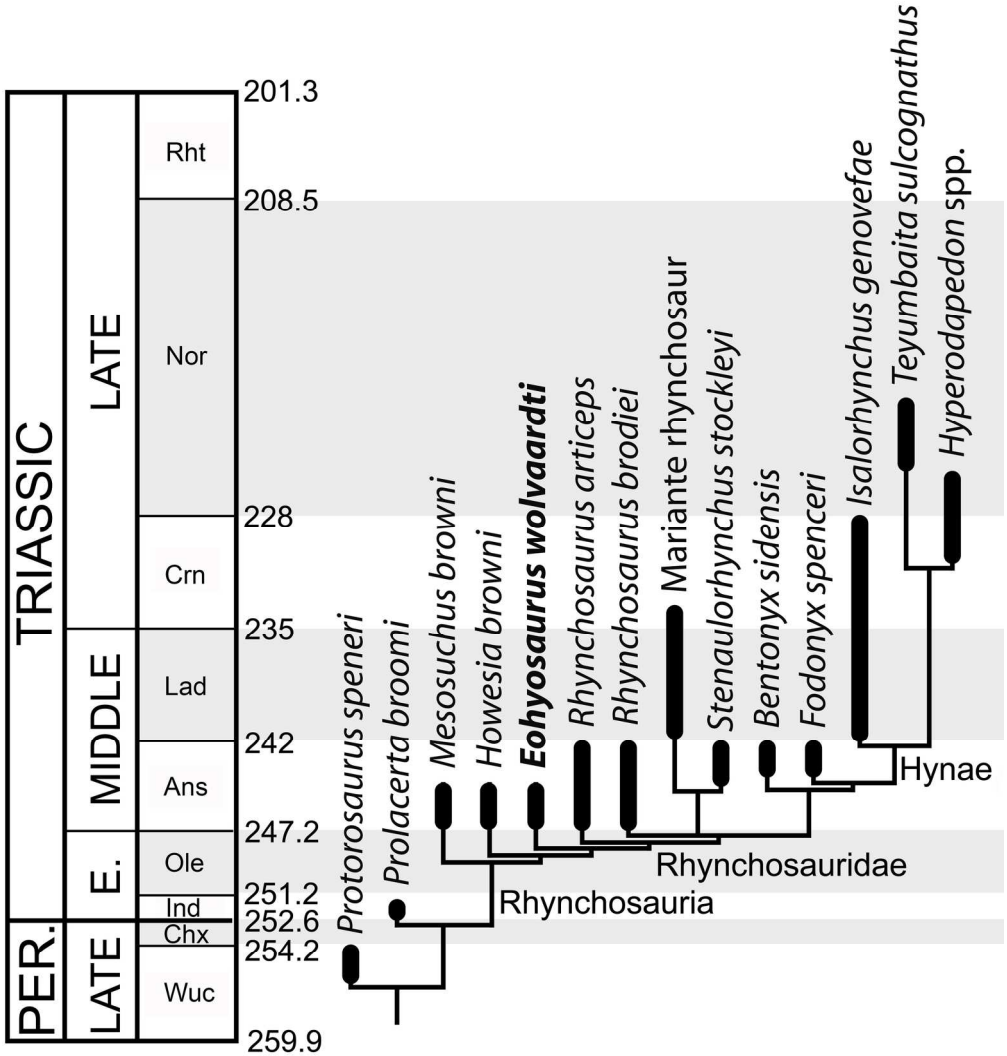

Figure 6. Time calibrated single most parsimonious tree showing the phylogenetic relationships of Eohyosaurus wolvaardti and other rhynchosaurs recovered in the phylogenetic analysis presented here. The length of the vertical bar representing each terminal taxon represents chronostratigraphic uncertainty rather than true stratigraphic range. Abbreviations: Ans, Anisian; Crn, Carnian; Chx, Changhsingian; E., Early; Hynae, Hyperodapedontinae; Ind, Induan; Lad, Ladinian; Nor, Norian; Ole, Olenekian; PER., Permian; Rht, Rhaetian; Wuc, Wuchiapingian.
174x185mm (300 x 300 DPI)