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THE MALAGASY CYNODONT *MENADON BESAIRIEI* (CYNODONTIA; TRAVERSODONTIDAE) IN THE MIDDLE–UPPER TRIASSIC OF BRAZIL

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ABSTRACT—The traversodontid cynodont *Menadon besairiei*, previously known from the ‘Isalo II’ group of Madagascar, is reported for the first time from the Triassic of southern Brazil. New material referable to *M. besairiei* was collected in the Schoenstatt outcrop (Santa Cruz do Sul municipality), which belongs to the *Santacruzodon* Assemblage Zone (Carnian) in the Santa Maria Supersequence. Their attribution to the Malagasy taxon is based on the presence of a deep snout; four upper incisors, with procumbent first and second incisors, and three lower, procumbent incisors; five upper postcanines, the first one ‘peg-like’; six lower postcanines, the two most anterior and the most posterior being reduced; the quadrangular form of the postcanines; a pterygoid reaching the jugal and excluding the maxilla from the suborbital fenestra; a mandible with a tall coronoid process covering the last lower postcanine laterally; and a posteriorly projected angular process. A cladistic analysis of traversodontid cynodonts was performed based on a matrix composed of 30 taxa and 78 characters. In the resulting trees, *M. besairiei* nested within the clade Gomphodontosuchinae, the only traversodontid subclade reasonably well supported. Thus, the presence of *M. besairiei* is established in the Santa Cruz do Sul fauna, constituting the first record for South America and confirming the previously proposed biostratigraphic correlation between the ‘Isalo II’ and the *Santacruzodon* Assemblage Zone.

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INTRODUCTION

Traversodontids are one of the most diverse groups of non-mammaliaform cynodonts. The earliest records of this clade are from the Middle Triassic (Anisian) of South America and Africa, and it becomes a cosmopolitan lineage towards the end of the Middle Triassic and into the Late Triassic (Bonaparte, 1962; Chatterjee, 1982; Gow and Hancox, 1993; Sues et al., 1999; Battail and Surkov, 2000; Abdala et al., 2001; Kemp, 2005; Kammerer et al., 2008; Abdala and Ribeiro, 2010). The success of the group is usually interpreted as being related to adaptations for oral processing of food (Hopson, 1984; Goswami et al., 2005), including labiolingually expanded postcanines that show a relatively complex occlusal pattern (Crompton, 1972; Kemp, 1980; Goni and Goin, 1990).

Knowledge about these herbivorous cynodonts has grown considerably since the first contributions by Huene (1928, 1936), who described the first representative of the traversodontids, discovered in the Middle Triassic of Brazil. At least four new species of this group have been recognized from Triassic Brazilian faunas in the last decade (Abdala et al., 2002; Abdala and Ribeiro, 2003; Abdala and Sa-Teixeira, 2004; Reichel et al., 2009). This is more than has been described in the rest of the world during this period (Abdala and Ribeiro, 2010; Liu and Abdala, 2014). Traversodontids underwent a remarkable

diversification during the Middle Triassic, although this was mostly restricted to a Gondwanan faunal event (Abdala and Ribeiro, 2010). Therefore, the study of the diverse traversodontid cynodonts in fossil assemblages from the Santa Maria Supersequence is of prime importance for our understanding of the diversification of this group and also for understanding morphological changes in this lineage seen in the transitional fauna of Santa Cruz do Sul (see below).

The Pinheiros-Chiniquá Sequence of Horn et al. (2014) Zerfass et al. (2003) (= base of the Santa Maria Formation sensu Andreis et al., 1980; base of the Santa Maria 1 Sequence of Zerfass et al., 2003) is represented by the *Dinodontosaurus* Assemblage Zone (Schultz et al., 2000), which includes the following traversodontids: *Traversodon stahleckeri*, *Massetognathus ochagaviae*, *Luangwa sudamericana*, and *Protuberum cabralense* (Huene, 1936; Barberena, 1981a, 1981b; Abdala and Sa-Teixeira, 2004; Liu et al., 2008; Reichel et al., 2009; Kammerer, 2014). In the younger *Hyperodapedon* Assemblage Zone (Candelária Sequence of Horn et al., 2014; = base of the Santa Maria 2 Sequence of Zerfass et al., 2003) there are two traversodontids: the abundant *Exaeretodon riograndensis* and the extremely rare *Gomphodontosuchus brasiliensis*, which is known only from the type specimen (Huene, 1928; Hopson, 1985; Schultz et al., 2000; Abdala et al., 2002). In the more recently proposed *Santacruzodon* Assemblage Zone (Soares et al., 2011a; originally defined as the ‘Traversodontid Biozone’ by Abdala et al., 2001), which is considered to be temporally intermediate between the two previous assemblage zones, there is a remarkable dominance of

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traversodontid cynodonts (Abdala et al., 2001; Soares et al., 2011a; Raugust et al., 2013). From this faunal association *Santa cruzodon hopsoni* (Abdala and Ribeiro, 2003), *Menadon* sp. (Melo et al., 2009), and forms defined as *Massetognathus*-like, which have not yet been formally described, have been identified.

In this contribution we present a detailed description of recently discovered specimens of traversodontids from the *Santa cruzodon* Assemblage Zone, including a nearly complete cranium and several partial lower jaws, previously reported by Melo et al. (2009; UFRGS-PV-1164-T and UFRGS-PV-1165-T). The morphology of these specimens indicates that they belong to *Menadon besairiei*, previously known only from Madagascar.

Institutional Abbreviations—**FMNH**, Field Museum of Natural History, Chicago, Illinois, U.S.A.; **GPIT**, Institut und Museum für Geologie und Paläontologie der Universität Tübingen, Tübingen, Germany; **UA**, Université d'Antananarivo, Antananarivo, Madagascar; **UFRGS-PV**, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil.

STUDY AREA AND BIOSTRATIGRAPHY

A new faunal association with a marked predominance of traversodontid cynodonts was discovered in 1998 on the outskirts of Santa Cruz do Sul City, southern Brazil. This fauna was originally recorded only from the Schoenstatt outcrop, located at the side of the road RS 471 (Fig. 1A).

The Schoenstatt outcrop (UTM zone 22; 359767E, 6709062N) is represented by approximately 20 m of massive mudstones

interpreted as floodplain deposits, followed by 15 m of non-fossiliferous sandstones representing channel facies (Bertoni-Machado and Holz, 2006).

Abdala et al. (2001) recognized four types of traversodontids in the Santa Cruz do Sul fauna (termed types I–IV). Type I traversodontids were interpreted as closely related to *Gomphodontosuchus* (Hopson, 1985), *Menadon* (Flynn et al., 2000), *Scalenodontoides* (Gow and Hancox, 1993), and *Exaeretodon* (Bonaparte, 1962). Type II was considered similar to *Dadadon* (Flynn et al., 2000; Ranimoharimanana et al., 2011; Kammerer et al., 2012); type III was similar to *Massetognathus* (Romer, 1967), and type IV was represented by a small fragment of maxilla with postcanines, resembling the Laurasian traversodontid *Boreogomphodon* (Sues and Olsen, 1990; Liu and Sues, 2010; Sues and Hopson, 2010).

In addition to traversodontid cynodonts, there are also records of chiniquodontid cynodonts (Abdala et al., 2001), cf. *Probatognathus* (Soares et al., 2011a), and the proterochampsian archosauriform *Chanaresuchus bonapartei* (Raugust et al., 2013).

Bertoni-Machado and Holz (2006) interpreted these fossil accumulations as being produced by biogenic action. This assemblage is predominantly composed of skulls and lower jaws without preferential orientation. The authors have interpreted these remains as portions of the skeleton that are generally discarded by vertebrate scavengers or predators.

The co-occurrence of some South American Ladinian forms (e.g., *Massetognathus*-like material) and forms also found in the Ladinian–Carnian ‘Isalo II’ beds from Madagascar (e.g., the

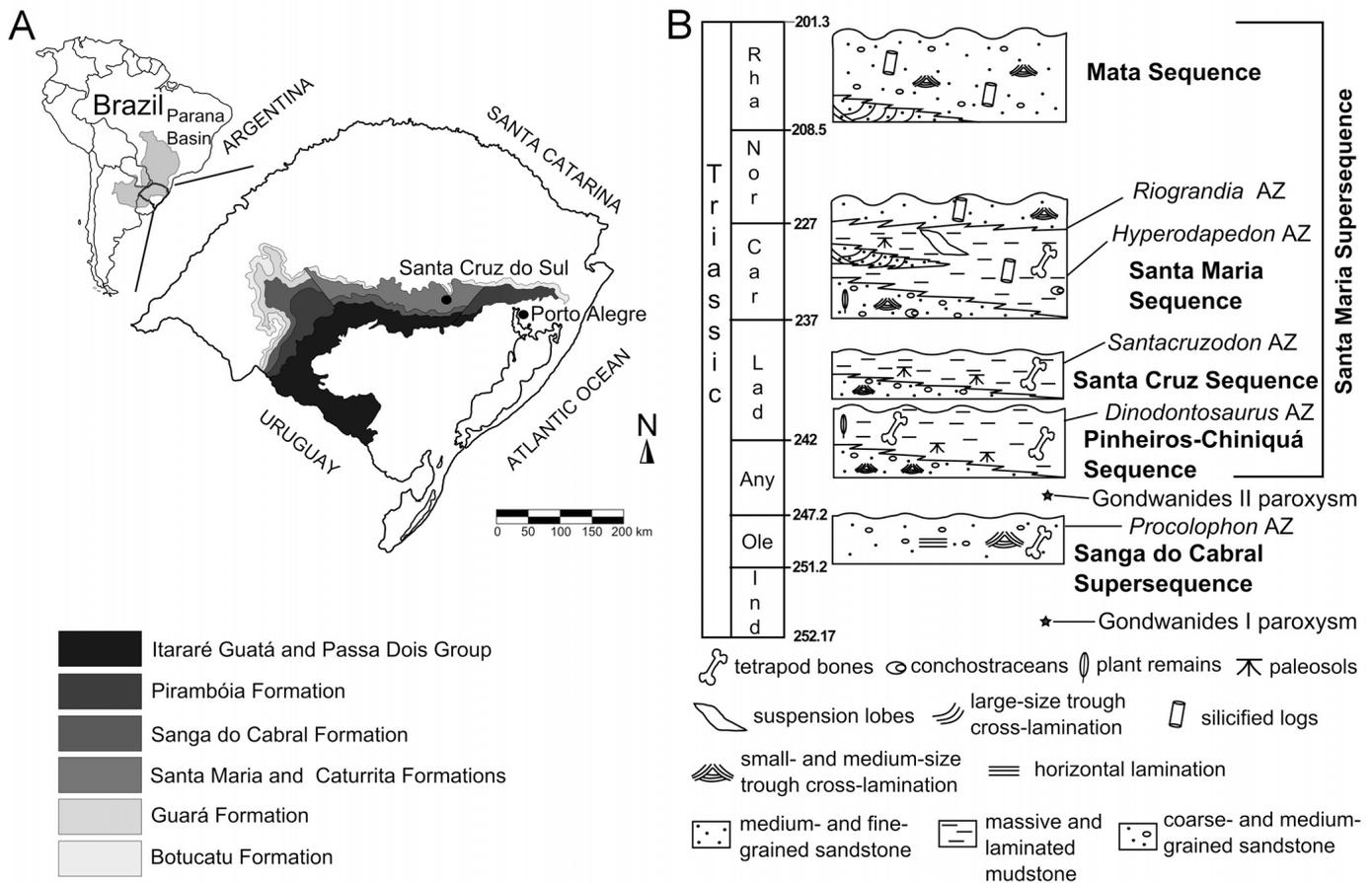


FIGURE 1. **A**, map of the Paraná Basin, South America and lithostratigraphy of the area of study (modified from Soares et al., 2011a); **B**, chronostratigraphy of the southern Brazilian Triassic and depositional sequences (modified from Horn et al., 2014), biostratigraphy after Schultz et al. (2000) and Soares et al. (2011a), ages after Gradstein et al. (2012).

Dadadon-like *Santacruzodon*; Flynn et al., 2000) was considered similar to those found in the fossiliferous deposits of Santa Cruz do Sul, which represent a distinct Ladinian–Carnian biostratigraphic unit. Abdala et al. (2001) defined it as the Traversodontid Biozone. This unit is temporally intermediate between the *Dinodontosaurus* and *Hyperodapedon* assemblage zones (Abdala et al., 2001; Schultz et al., 2000). Modifications to the geological time scale (Gradstein et al., 2012) indicate that the age of the Argentine Ischigualasto Formation (Furin et al., 2006; Rogers et al., 1993) and, by correlation, the *Hyperodapedon* Assemblage Zone, is Carnian/Norian. Thus, the *Santacruzodon* Assemblage Zone could possibly be Early Carnian (Liu and Abdala, 2014). In fact, according to U-Pb dating from the Schoenstatt outcrop, Philipp et al. (2013) have defined an U-Pb isochrone of 236 ± 1.5 Ma, which marks the maximum age limit of the Santa Maria Santa Cruz Sequence in which the *Santacruzodon* Assemblage Zone is recognized.

Of the four originally differentiated traversodontid morphotypes of traversodontids from the Santa Cruz do Sul fauna (Abdala et al., 2001), only type II has been formally described and named *Santacruzodon hopsoni* (Abdala and Ribeiro, 2003), a species endemic to this Brazilian fauna. The single specimen representing type IV was recently also reinterpreted as a specimen of *S. hopsoni* (Soares et al., 2011a). Considering that *S. hopsoni* is unique to this fauna, Soares et al. (2011a) proposed naming this unit the *Santacruzodon* Assemblage Zone, replacing the Traversodontid Biozone originally proposed by Abdala et al. (2001) (Fig. 1B).

More recently, traversodontids with similarities to those from Santa Cruz do Sul were discovered in two other outcrops in the Venâncio Aires and Vera Cruz municipalities in Rio Grande do Sul (Reichel et al., 2005; Melo et al., 2010; Soares et al., 2011b). In addition to the morphological similarities of the traversodontids, the fossils from these three localities show the same diagenetic pattern, with a predominance of quartz permineralization, differing from other Triassic localities (*Dinodontosaurus* and *Hyperodapedon* assemblage zones) where there is a predominance of calcitic permineralization (Reichel et al., 2005; Teixeira et al., 2010). This new information allows for the geographic expansion of the *Santacruzodon* Assemblage Zone.

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905

CYNODONTIA Owen, 1861

EUCYNODONTIA Kemp, 1982

TRAVERSODONTIDAE Huene, 1936 (sensu Kammerer, Flynn, Ranivoharimanana, and Wyss, 2008)

MENADON BESAIRIEI Flynn, Parrish, Rakotosamimanana, Ranivoharimanana, Simpson, and Wyss, 2000

Holotype—UA 10601, partial skull.

Additional Specimens—From Madagascar: FMNH PR 2444, partial skull and postcranial material; FMNH PR 2104, isolated lower jaw. From Brazil: UFRGS-PV-0269-T, dentaries of a juvenile; UFRGS-PV-0434-T, dentaries; UFRGS-PV-0891-T, incomplete lower jaw; UFRGS-PV-0903-T, snout; UFRGS-PV-0905-T, lower jaw; UFRGS-PV-1054-T, dentaries (432 in Abdala et al., 2001); UFRGS-PV-1164-T, nearly complete skull; UFRGS-PV-1165-T, dentaries, right maxilla, and left premaxilla; MCN-PV 0505, dentaries; MCN-PV 2750, skull associated with vertebrae, a scapula-coracoid, and other postcranial bones.

Geographic Provenance and Age—Basal ‘Isalo II’ (= Formação Makay [sensu Razafimbelo, 1987]), Morondava Basin, Madagascar; *Santacruzodon* Assemblage Zone, Santa Cruz do Sul, Paraná Basin, Brazil (Flynn et al., 1999; Abdala et al., 2001). Late Triassic (Gradstein et al., 2012).

Emended Diagnosis—Traversodontid with four large upper incisors, I1 and I2 being procumbent and I3 and I4 caniniform; I4 recurved and serrated; upper canine similar in size to incisors; canine anteriorly tilted, with its alveolus labiolingually narrower than those of the incisors; absence of diastema between last upper incisor and canine; eight upper postcanines; i1 to i3 procumbent; six to seven lower postcanines, quadrangular to trapezoidal in occlusal view; last lower postcanine reduced in size; suborbital process of jugal absent; ventral process of squamosal in the zygoma laterally covering the quadrate-quadratejugal complex.

COMPARATIVE DESCRIPTION

General Morphology of the Skull

The most complete skull, UFRGS-PV-1164-T, is laterally compressed, but is markedly similar to the skull of *Menadon besairiei* (FMNH PR 2444), described by Kammerer et al. (2008). The Brazilian skull, UFRGS-PV-1164-T, is more complete than FMNH PR 2444 and preserves the entire postorbital region, except for the quadrate and quadratejugal. In addition, a nearly complete postcanine dentition is preserved in the Brazilian specimen from Santa Cruz do Sul. In relation to *Exaeretodon*, the skull of UFRGS-PV-1164-T is elevated, with the preorbital region shorter than the postorbital. The lateral platform of the maxilla is less pronounced than in other traversodontids such as *Massetognathus* and *Santacruzodon* (Figs. 2 and 3).

Snout

The snout of UFRGS-PV-1164-T is indistinguishable from that of *Menadon* specimen FMNH PR 2444 (Kammerer et al., 2008). As in the Malagasy specimen, it is quite tall, a trait also present in *Gomphodontosuchus* (Hopson, 1985), *Protuberum* (Reichel et al., 2009), and in juveniles of *Exaeretodon* (Abdala et al., 2002). The snout morphology does not seem to be affected by taphonomic deformation present in the Brazilian specimen from Santa Cruz do Sul.

In palatal view, the anterior margin of the premaxilla is semicircular, with a more marked convexity than in FMNH PR 2444. The holotype (UA 10601) seems to have a more pointed anterior margin, although it may be a result of postmortem deformation.

In lateral view, the narial opening is bordered anterodorsally by the premaxilla and posterodorsally by the septomaxilla. The contact between the premaxilla and maxilla is observed in the posterodorsal margin of the former, at the level of the septomaxillary foramen. The premaxilla is deep below the nares, similar to that of FMNH PR 2444 (Kammerer et al., 2008) and *Protuberum* (Reichel et al., 2009). The holotype of *M. besairiei* (Flynn et al., 2000) has a much shallower premaxilla, as in *Exaeretodon* (Bonaparte, 1962; Abdala et al., 2002), probably due to distortion.

The internarial process of the premaxilla, which forms the anterior border of the external naris, is well developed and nearly complete, anteriorly bordering the external naris. This opening is bordered anteroventrally by the premaxilla, posteroventrally by the maxilla, and dorsally by the nasal.

Sutures of most of the elements in the snout are not clear because of the fracturing of bones in this region. In general, the configuration of the maxilla, nasal, and lacrimal seems to be similar to that of *Menadon* (Kammerer et al., 2008) and also similar to other traversodontids (Barberena, 1974).

The maxilla has a constriction behind the canines, and the postcanine teeth are located medially in relation to the canines. The maxilla-jugal suture is positioned anteroventral to the orbit.

Orbit and Zygoma

The orbits are semicircular, high and located laterally, resembling *Protuberum* and probably *Gomphodontosuchus* and less

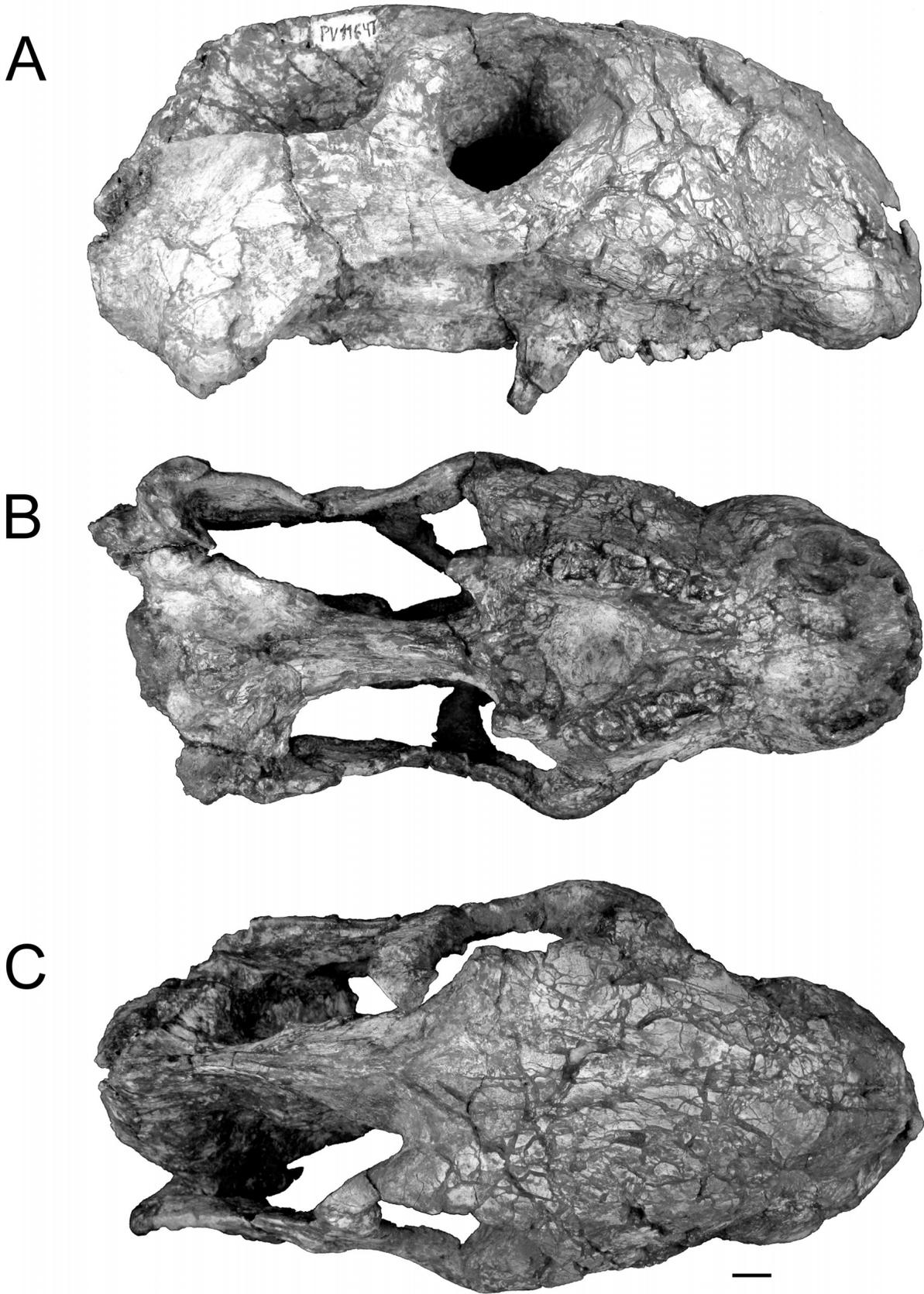


FIGURE 2. Skull of *Menadon besairiei*, UFRGS-PV-1164-T. **A**, right lateral view; **B**, ventral view; **C**, dorsal view. Scale bar equals 1 cm.

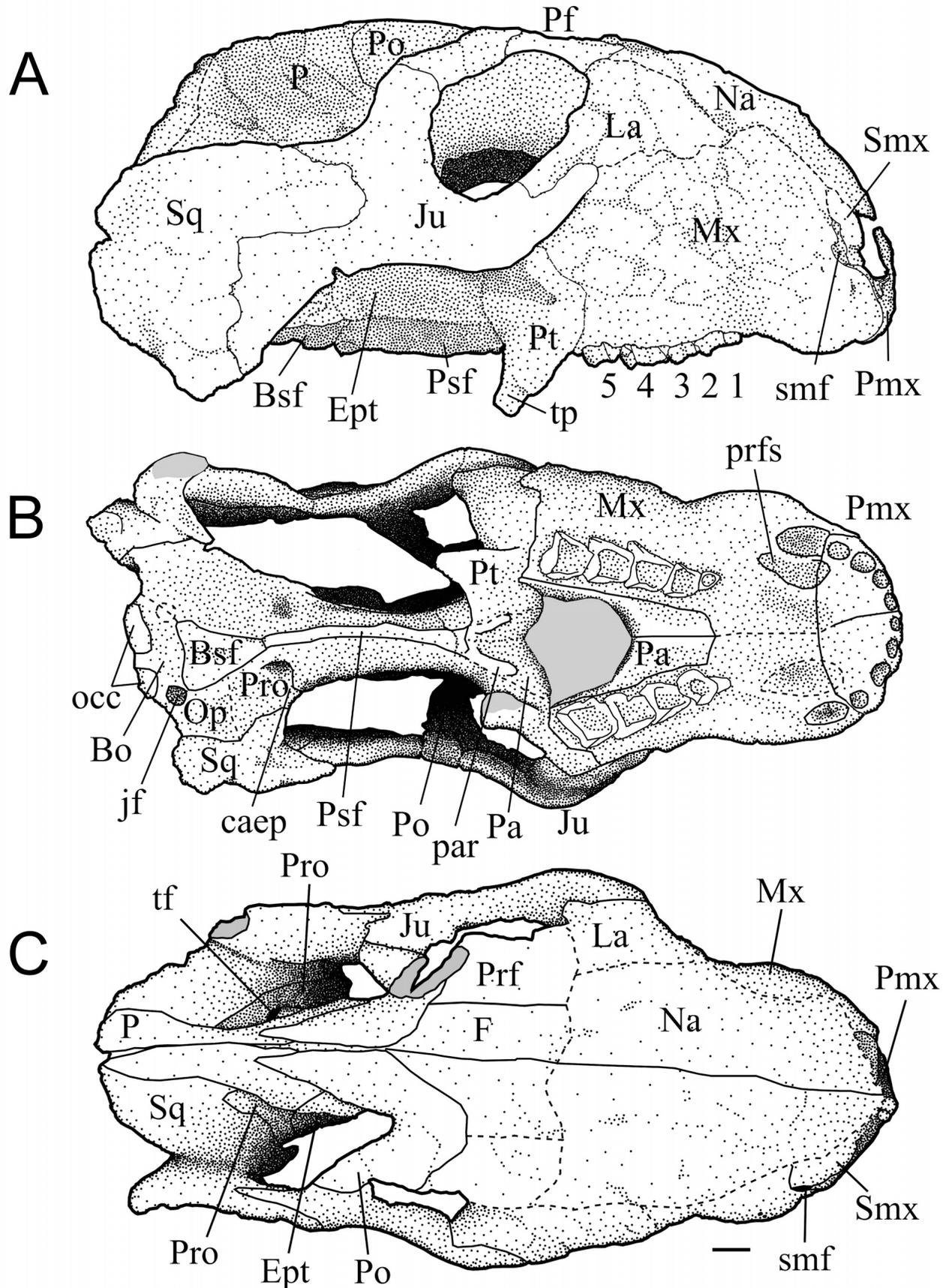


FIGURE 3. Interpretative drawing of the skull of *Menadon besairiei*, UFRGS-PV-1164-T. **A**, right lateral view; **B**, ventral view; **C**, dorsal view. **Abbreviations:** 1–5, postcanine dentition; **Bo**, basioccipital; **Bsf**, basisphenoid; **caep**, cavum epiptericum; **Ept**, epipterygoid; **F**, frontal; **jf**, jugular foramen; **Ju**, jugal; **La**, lacrimal; **Mx**, maxilla; **Na**, nasal; **occ**, occipital condyles; **Op**, opisthotic; **P**, parietal; **Pa**, palatine; **Pf**, prefrontal; **Pmx**, premaxilla; **Po**, postorbital; **prfs**, paracanine fossa; **Pro**, prootic; **Pst**, parasphenoid; **Pt**, pterygoid; **smf**, septomaxillary foramen; **Smx**, septomaxilla; **Sq**, squamosal; **tf**, trigeminal foramen; **tp**, transverse process of the pterygoid. Scale bar equals 1 cm.

dorsally placed than in *Exaeretodon* and *Massetognathus*. The postorbitals form the posterodorsal posterior margin of the orbit, overlapping the prefrontals and covering them anteriorly and extending back over one-third of the sagittal crest. The lacrimal and prefrontals form the anterodorsal portion of the orbit. The prefrontal seems to be a rectangular bone; however, fragmentation of the bone on both sides of the skull makes interpretation of its sutures difficult.

The jugal borders the posteroventral half of the orbit and contacts the postorbital. The anterior portion of the jugal contacts the lacrimal dorsally, the maxilla anteroventrally, and the pterygoid ventrally. As is observed in traversodontids (with the exception of *Exaeretodon*), a dorsolateral projection of the pterygoid excludes the maxilla from the margin of the suborbital fenestra (Kammerer et al., 2008).

The zygoma is elevated, very similar to that of *Exaeretodon* and Malagasy *Menadon* specimens (Bonaparte, 1962; Kammerer et al., 2008). The dorsal margin of the zygoma does not surpass the dorsal margin of the orbit, being located at mid-orbital height, as in *Menadon* from Madagascar (Flynn et al., 2000). Similar to *Menadon* and *Massetognathus* (Romer, 1967; Kammerer et al., 2008; Liu et al., 2008), there is no suborbital process of the zygoma (also termed the descending process of the jugal). On the contrary, this process is strongly developed in *Exaeretodon* (Abdala et al., 2002) and, to a lesser extent, in *Protuberum* (Reichel et al., 2009).

Posterior to the orbit, the jugal is divided by the anterior projection of the squamosal into a short dorsal process and a long and robust ventral one. This condition is similar to that in *Exaeretodon* (Bonaparte, 1962; Abdala et al., 2002) and *Scalenodontoides* (Gow and Hancox, 2003), but with the dorsal projection proportionally smaller and the ventral one less robust and less ventrally directed, as in *Protuberum* (Reichel et al., 2009) and Malagasy *Menadon* (Flynn et al., 2000). The ventral projection of the jugal extends to the sulcus of the squamosal that lodges the quadrate and quadratojugal.

In the squamosal, the zygomatic and cranial portions are separated by a deep 'V'-shaped incision typical of gomphodont cynodonts (Fig. 4). The zygomatic portion of the squamosal represents the posterodorsal half of the zygomatic arch.

Skull Roof

The sutures of the skull roof are difficult to interpret. The frontal is short, of similar anteroposterior length to the prefrontal. It is possible to recognize the sutures between the frontals and between the left prefrontal and frontal of UFRGS-PV-1164-T, which are jagged lines, running parallel to the sagittal plane of the skull.

The anterior margin of the frontal seems to be located at the level of the anterior border of the orbit, as is the case in *Exaeretodon* (Bonaparte, 1962). As reported by Kammerer et al. (2008) for Malagasy *Menadon*, a prominent interorbital depression is observed in the entire region in which the frontals are located. The posterior portions of both frontals form a wedge between the anterior portions of the parietals. At the junction between the frontal, parietal, and postorbital, the low sagittal crest ascends posteriorly above the level of the interorbital roof. As in most traversodontids, the crest is slightly higher than the skull at the level of the parietal-frontal suture and extends to the lambdoid crests for most of the length of the temporal fenestra, unlike in *Protuberum* (Reichel et al., 2009) and *Scalenodontoides* (Battail, 2005). Only a fragment of the skull of *Menadon* described by Kammerer et al. (2008) preserves part of the sagittal crest, which looks similar to the crest represented in UFRGS-PV-1164-T.

In the first one-third of the parietals, there is a cleft between these elements, at the place where the parietal foramen is usually

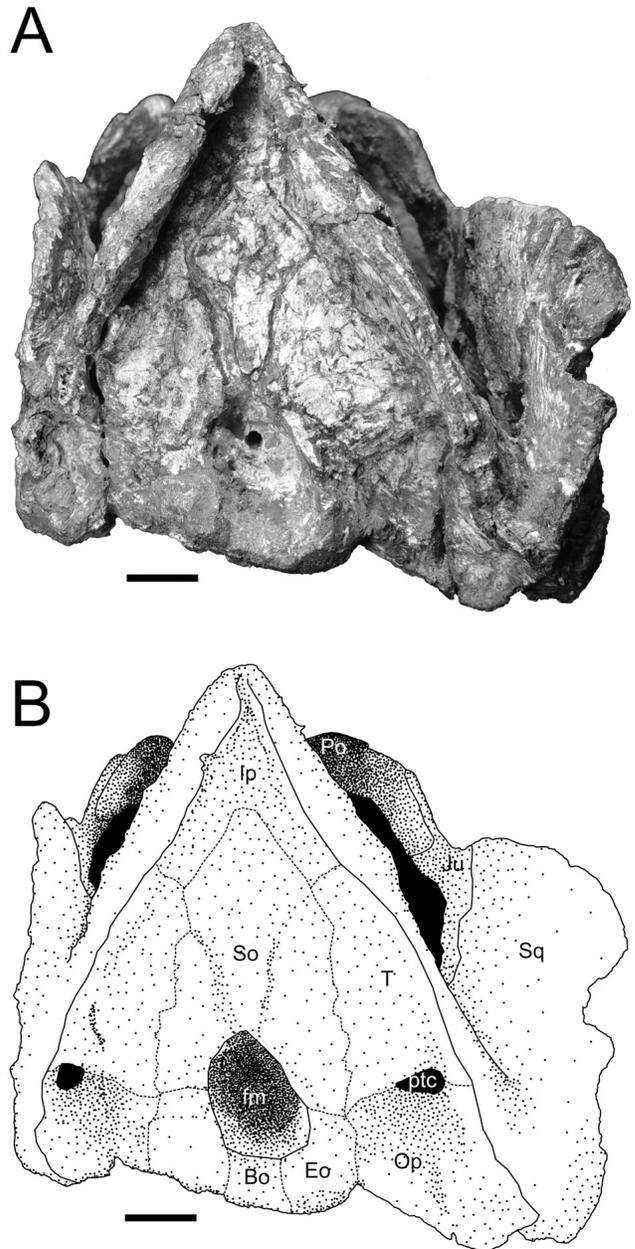


FIGURE 4. **A**, posterior view of the skull of *Menadon besairiei*, UFRGS-PV-1164-T; **B**, interpretative drawing. **Abbreviations:** **Bo**, basioccipital; **Eo**, exoccipital; **fm**, foramen magnum; **Ip**, interparietal; **Ju**, jugal; **Op**, opisthotic; **Po**, postorbital; **ptc**, posttemporal canal; **So**, supraoccipital; **Sq**, squamosal; **T**, tabular. Both scale bars equal 1 cm.

located in other traversodontids (e.g., *Protuberum*, *Traversodon*, *Luangwa*), but there is no defined foramen.

Occiput

The occiput of UFRGS-PV-1164-T is laterally compressed, resembling an isosceles triangle with the angle of divergence of the lambdoid crests being approximately 60 degrees. The foramen magnum is high and ovoid, albeit also deformed by lateral compression. The condition of the occipital plate in the Brazilian

specimen is similar to that in FMNH PR 2444 and different from that in the holotype, in which the foramen magnum is more circular. The occipital condyles are well developed and separated by a sulcus formed by the basioccipital. A short paroccipital process of the opisthotic is in contact laterally with the base of the zygomatic process of the squamosal lateral to the occipital condyle. The narrow lambdoid crest projects posterolaterally, its dorsal margin being formed by the cranial process of the squamosal, which extends ventrolaterally to the base of the crest where it forms a 'V'-shaped angle with the zygomatic process of the squamosal.

An elongated supraoccipital is located above the foramen magnum and is in contact with the tabulars laterally. Dorsal to the supraoccipital there is a suture that indicates the presence of the interparietal, which resembles that described in *Exaeretodon argentinus* by Bonaparte (1962). There is no reference to this bone in the occiput of the Malagasy specimen of *Menadon* (Flynn et al., 2000; Kammerer et al., 2008). The posttemporal canal appears to lie on the border between the tabular and the opisthotic.

Palate

The palate in UFRGS-PV-1164-T is poorly preserved with numerous breaks. The secondary palate exhibits a prominent lateral extension at the level of the canines, presenting a constriction in the region posterior to these teeth. Paracanine fossae are located medially to the canines as in *Gomphodontosuchus* and Malagasy specimens of *Menadon* (Hopson, 1985; Kammerer et al., 2008) and not posteromedially as in the other Gomphodontosuchinae. It was not possible to determine whether the incisive foramina, which seem to be confluent, are completely enclosed by the premaxillae or if the maxillae also participate in their posterior margin (Fig. 2B).

A longitudinal crest formed by the medial portion of the palatine extends from the level corresponding to the first preserved postcanine to that of the fourth postcanine and diverges posteriorly along the lateral borders of the internal choanae to form the posterior margin of the palatal plate. The median crest is remarkably deep, reaching the level of the postcanine crowns, but this is more likely a preservational artifact produced by lateral compression of the skull. The posterior margin of the secondary palate extends back to the level of the anterior margin of the fourth postcanine as in the Malagasy *Menadon* (Abdala, pers. observ.).

The only visible sutures on the palate are those on the midline between the palatines and pterygoids. There is a pair of palatine crests converging posteriorly towards the cultriform process of the parasphenoid. The transverse processes of the pterygoids are located lateral to the palatine crests and projected posteroventrally as in *Exaeretodon* (Abdala et al., 2002). The quadrate ramus of the pterygoid extends to the level of the anterior margin of the cavum epiptericum.

Basicranium

This region is poorly preserved in UFRGS-PV-1164-T. The basicranial morphology is represented by a short basioccipital and a triangular basisphenoid. The paroccipital process seems to be comparatively narrower than is usual for traversodontids, resulting in a narrower occiput, as seen in the Malagasy specimens of *M. besairiei* (Kammerer et al., 2008). In the squamosal portion observed in ventral view, it is possible to recognize the notch for the articulation of the quadrate and quadratojugal. This notch is delimited laterally by the ventral portion of the jugal (Fig. 4).

Lateral Wall of the Braincase

The ascending process of the epipterygoid and the anterior lamina of the prootic are located medial to the ventral margin of the parietal. The anterior lamina of the prootic is less expanded anteroposteriorly than is the epipterygoid. The trigeminal opening, delimited between the prootic and epipterygoid, is observed on the left side of UFRGS-PV-1164-T. The posterior margin of the prootic is in contact with the cranial portion of the squamosal. As in *Exaeretodon*, the lateral projection of the prootic is well defined, having the posterolateral margin in contact with the squamosal and the anterior margin in contact with the quadrate ramus of the epipterygoid.

Mandible

The dentary is anteroposteriorly short and dorsoventrally high, presenting three procumbent incisors, one canine, and six postcanines. The shallowly sloping symphysis between the dentaries is fused and robust, extending posteroventrally to the level of the third postcanine. This region differs from the steeply sloping symphyseal region of *Exaeretodon* and *Gomphodontosuchus*. A midline depression in the back of the symphysis is observed in this region, not so developed as in *Gomphodontosuchus*, but clearly more so than in *Exaeretodon* (Hopson, 1985; Abdala et al., 2002).

The horizontal ramus is robust and transversely expanded. A very tall coronoid process projects posterodorsally, obscuring in lateral view the alveolus of the last postcanine. The angle of the dentary is well developed and posteriorly projecting as in *Exaeretodon* and *M. besairiei* (Bonaparte, 1962; Flynn et al., 2000). There is a deep emargination in the posterior portion of the dentary, dorsal to the angle, similar to *Exaeretodon*. The anterior margin of the prominent masseteric fossa is located at the level of the second postcanine, as in *Gomphodontosuchus*, *Exaeretodon*, *Scalenodontoides*, and Malagasy *Menadon* (Bonaparte, 1962; Hopson, 1985; Flynn et al., 2000). The mental foramen is located on the swelling on the anterodorsal margin of the masseteric fossa (Fig. 6A).

There is no preservation of postdentary bones, but a narrow postdentary sulcus suggests that they were reduced as in *Exaeretodon* (Bonaparte, 1962; Liparini et al., 2013).

Dentition

The upper dentition (Fig. 5) in UFRGS-PV-1164-T is represented by four incisors, one canine, and five postcanines. The first and second incisors are procumbent as in *Menadon besairiei* (Kammerer et al., 2008). Incisor alveoli are ovoid, labiolingually wider but anteroposteriorly shorter than those of the canines. There is no diastema between the incisors and canine, whereas a long diastema separates the latter from the first postcanine. This region is poorly preserved, and it is possible that some anterior postcanines (not preserved here) would imply a shorter diastema.

The maxillary tooth row is anteriorly parallel and slightly divergent posteriorly. The first postcanine is considerably smaller than the remaining teeth, with its crown showing signs of wear, and having a rounded-triangular outline with the apex directed anteriorly. This condition strongly resembles that of *Gomphodontosuchus* (Hopson, 1985). The next four postcanines are successively larger, with labiolingually enlarged crowns of quadrangular occlusal outline and implanted slightly obliquely on the maxilla.

Strong postdepositional erosion of the postcanines limits detail, but it is clear that a large posterior buccal main cusp was joined to an anterobuccal accessory cusp by a crest, to form a longitudinal cutting edge. The deepest portion of the occlusal basin is located anterolingually, medial to the sectorial buccal

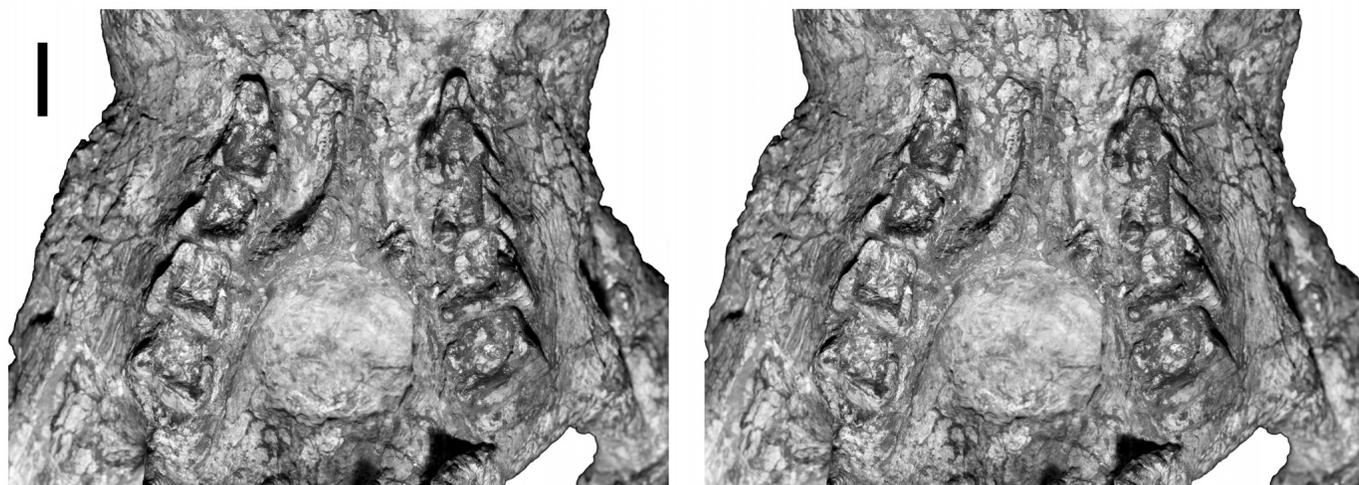


FIGURE 5. Stereo pair of the postcanine dentition of *Menadon besairiei* (UFRGS-PV-1164-T) in occlusal view. Scale bar equals 1 cm.

crest. There is a main posterior lingual cusp connected by a crest to an anterolingual accessory cusp. In addition, an anterior crest connects the anterior lingual and anterior buccal cusps. The posterior transverse crest ascends from the base of the posterior buccal cusp to the posterior lingual cusp without evidence of a central cusp. The posterior crest is slightly concave, allowing only a small imbrication (shouldering sensu Hopson, 1985) between successive postcanines, a condition closer to that of *Gomphodontosuchus* (Hopson, 1985) than *Exaeretodon*.

The three lower incisors are large, strongly procumbent, and have chisel-like, self-sharpening tips, much like in *Exaeretodon* and, especially, in specimens of *M. besairiei* (Bonaparte, 1962; Flynn et al., 2000). Whereas *i1* and *i2* are of equivalent size, *i3* is smaller, the three forming an almost continuous shearing surface. The canine is curved posteriorly, ellipsoid in cross-section and somewhat procumbent, but never markedly longer than the incisors. There is a very short diastema (~2.0 mm) between the canine and the first postcanine (Fig. 6D).

The first lower postcanine is peg-like, without an occlusal basin. The second has the same crown height as successive postcanines and shows an incipient basin. The morphology of the third to fifth postcanines is similar to that of other traversodontids, quadrangular in occlusal view, with an anterior transverse crest and a shallow occlusal basin, although its cusps are not clearly recognizable due to wear. The sixth and last postcanine is much reduced, comparable to the first lower postcanine, as occurs in *M. besairiei* (Flynn et al., 2000). In all specimens, the lower postcanines are canted posteriorly, whereas the upper ones are canted anteriorly (Fig. 6B, C, E).

Discussion

Following the description of the Brazilian material, it is clear that the anatomical details indicate a high degree of similarity to the Malagasy traversodontid *Menadon besairiei*. The major difference is the absence of the three first simple upper postcanines found in the holotype of *M. besairiei* (Flynn et al., 2000). However, these simple anterior postcanines are also not present in specimen FMNH PR 2444 of *M. besairiei*. Discussing this difference, Kammerer et al. (2008) alluded to preservational causes, but another possibility suggested by these authors is ontogeny, and that the three single-crowned, anterior postcanines were lost in FMNH PR 2444 due to growth pattern. *Exaeretodon* is known to reduce the number of postcanines during ontogeny (Abdala et al., 2002) by adding fewer teeth posteriorly than are lost

anteriorly, so it is possible that other Gomphodontosuchinae, such as *Menadon*, displayed the same pattern. This condition is the opposite to that of *Massetognathus* and early diverging traversodontids, which tend to increase the number of postcanines with growth (Abdala and Giannini, 2000; Kammerer et al., 2012). Preservation in the specimens from Brazil is in fact quite poor, so that comparison in detail with the better-preserved specimens from Madagascar (especially the holotype) is hampered. We believe, however, that the close similarity in morphology and size of the lower postcanines (comparing, for example, the lower jaws of UA-10601 and UFRGS-PV-1165-T), the general morphology of the mandible (robust horizontal ramus and well-projected angle), the shallow anterior end of the dentary compared with the deep region below the postcanines and the shallowly sloping symphysis, the short and quite high snout, and, especially, the presence of a high crest in the anterior portion of the upper postcanines warrant taxonomic assignment of the Brazilian material to *Menadon besairiei*.

From our morphological study and phylogeny (see below), it can be seen that *M. besairiei* resembles *Gomphodontosuchus brasiliensis* (Fig. 7). This enigmatic taxon, the first traversodontid described (Huene, 1928), is represented by only the holotype, a poorly preserved partial skull and lower jaw discovered in an outcrop near the city of Santa Maria, corresponding to the *Hyperodapedon* Assemblage Zone of the Santa Maria 2 Sequence and is the first traversodontid ever described (Huene, 1928). We find several features of similarity in our material to *M. besairiei* and *G. brasiliensis*, such as high skull, paracanine fossa medial to canine, simple anterior upper postcanines, and incipient shouldering of the upper postcanines.

Although there are some similarities between these forms, there are also significant differences. Among these, the labiolingually wide posterior upper postcanines appear to be somewhat more expanded (i.e., look more rectangular) in *G. brasiliensis*, differing from the nearly quadrangular crowns of *M. besairiei*. Additionally, the former has small, non-procumbent incisors, whereas the latter has larger, procumbent incisors.

Furthermore, *G. brasiliensis* was collected in a well-established association in Brazil, coeval with the Argentine Ischigualasto Formation, that configures younger stratigraphic units, with no species in common with the *Santacruzodon* Assemblage Zone or Isalo II.

Moreover, the presence of *M. besairiei* in the *Santacruzodon* Assemblage Zone is consistent with other similarities between this fauna and the Isalo II assemblage, both of which possess

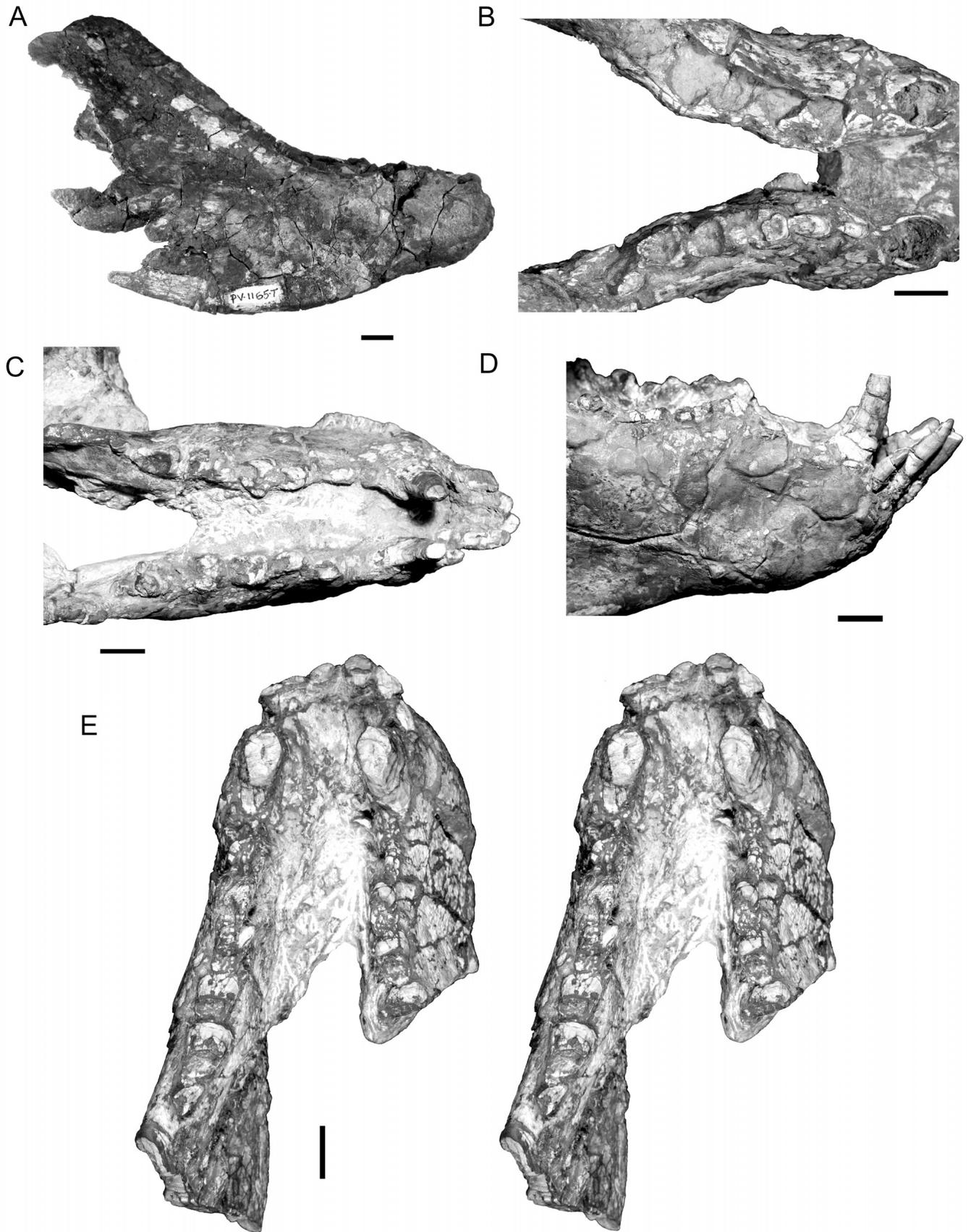


FIGURE 6. Lower jaws of *Menadon besairiei*. **A**, UFRGS-PV-1165-T, in right lateral view; **B**, UFRGS-PV-1054-T in occlusal view; **C**, UFRGS-PV-0434-T, in occlusal view; **D**, UFRGS-PV-0434-T, in lateral view; **E**, stereo pair of UFRGS-PV-0891-T, in occlusal view. Both scale bars equal 1 cm.

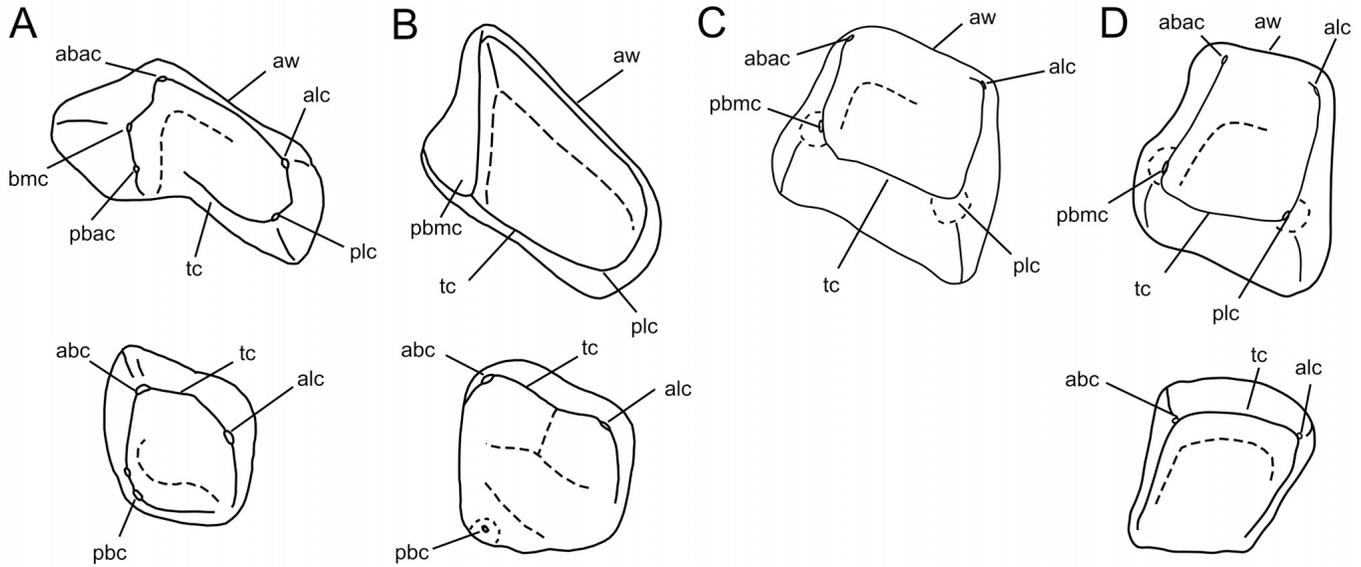


FIGURE 7. Comparative drawing of right upper and left lower postcanines of **A**, *Exaeretodon*; **B**, *Gomphodontosuchus*; **C**, Malagasy *Menadon* (based on the holotype); **D**, Brazilian *Menadon* (based on UFRGS-PV-1164-T). **Abbreviations:** **abac**, anterior buccal accessory cusp; **abc**, anterior buccal cusp; **alc**, anterior lingual cusp; **aw**, anterior wall; **bmc**, buccal main cusp; **pbac**, posterior buccal accessory cusp; **pbmc**, posterior buccal main cusp; **plc**, posterior labial cusp; **tc**, transverse crest. Modified from Hopson (1985).

closely related massetognathine (sensu Kammerer et al., 2012) and chiniquodontid cynodonts: *S. hopsoni* (Abdala and Ribeiro, 2003) and *D. isaloi* (Flynn et al., 2000); and Chiniquodontidae indet. (Abdala et al., 2001) and *Chiniquodon kalanoro* (Kammerer et al., 2010), respectively.

Phylogenetic Analysis

We present a cladistic analysis of traversodontid cynodonts with the aim of exploring whether additional scores for characters present in the Brazilian material of *Menadon* have any significant result on its placement among traversodontids. For this analysis, we used the data matrix of 78 characters and 30 taxa compiled by Liu and Abdala (2014) with an additional character (character 78 in the present analysis; originally character 48 of Gao et al., 2010). We also updated the scoring of *Dadadon* after Kammerer et al. (2012). Characters 8, 50, and 66 were coded according to the new Brazilian material. Characters 30, 31, and 55 were coded differently from previous matrices and 64 and 65 were considered not applicable to *Menadon*. The data matrix is project P1223 in Morphobank. The software TNT (Tree analysis using New Technology) was used for the phylogenetic analyses (Goloboff et al., 2008).

Figure 8 shows the strict consensus of nine equally parsimonious trees resulting from an analysis in which the multistate characters 2, 10, 25, 31, 32, 48, 52, 54, and 73 were scored as additive (Lipscomb, 1992). The placement of *Menadon* in the clade Gomphodontosuchinae is as recovered in previous phylogenetic analyses (Kammerer et al., 2008, 2012; Liu and Abdala, 2014). Several interesting points result from this analysis. The most basal traversodontid is the European *Nanogomphodon* from the Ladinian, a taxon known by an isolated lower postcanine. This is followed by a polytomy including *Scalenodon angustifrons*, a clade formed by *Pascualgnathus* and *Andescynodon*, and a second clade including the remaining traversodontids. This analysis recovered the Massetognathinae as recently defined by Kammerer et al. (2012), but the two species of *Massetognathus* do not form a monophyletic group. The clade with two Laurasian

traversodontids is placed between Massetognathinae and Gomphodontosuchinae, somewhat resembling the topology obtained by Liu and Abdala (2014). To evaluate monophyletic groups we present values of Bremer support, which is the number of extra steps necessary that will result in the loss of a monophyletic group from the strict consensus tree (Bremer, 1994), and of relative Bremer support, which also takes into account evidence in favor of, and against, a monophyletic group (Goloboff and Farris, 2001). Bremer support (Bs) values were poor for the majority of the monophyletic groups: traversodontids have Bs 3/relative Bs support 44; the clade formed by *Protuberum* (*Scalenodontoides*, *E. argentinus*, *E. riograndensis*) has Bs 3/relative Bs 44, whereas Gomphodontosuchinae has Bs 2/relative Bs 56. Massetognathinae is poorly supported: Bs 1/relative Bs 17.

A second analysis was performed excluding *Nanogomphodon* from the data matrix, because the basal position of this form was, in our understanding, a result of a lack of information (or else the presence of three cusps in the lower postcanines). The strict consensus tree, resulting from 22 trees, also considers the multistate characters with adjacent states as additive. The results of this analysis do not differ significantly from the previous analysis (only the absence of *Nanogomphodon* at the base of traversodontids) but support values were slightly higher: traversodontids (Bs 4/rBs 44), *Protuberum* (*Scalenodontoides*, *Exaeretodon argentinus*, *Exaeretodon riograndensis*) (Bs 6/rBs 50), and Gomphodontosuchinae (Bs 4/rBs 45). Support for Massetognathinae continued to be the same than as in the previous analysis. The clade formed by *Pascualgnathus* and *Andescynodon* has support of Bs 2/rBs 25, and the group formed by two species of *Mandagomphodon* has Bs 2/rBs 22.

We also performed sensitivity analyses by considering all multistate characters as non-additive and by implementing implied weighting (with values of K coefficients set to 3; see Goloboff, 1993). These analyses are referred to below with the following abbreviations: o, ordered; uo, unordered (non-additive); iw, implied weight; wN, without *Nanogomphodon*. The major modifications obtained from the comparison of the strict consensus resulting from this experimentation are as follows: (a) *Scalenodon*

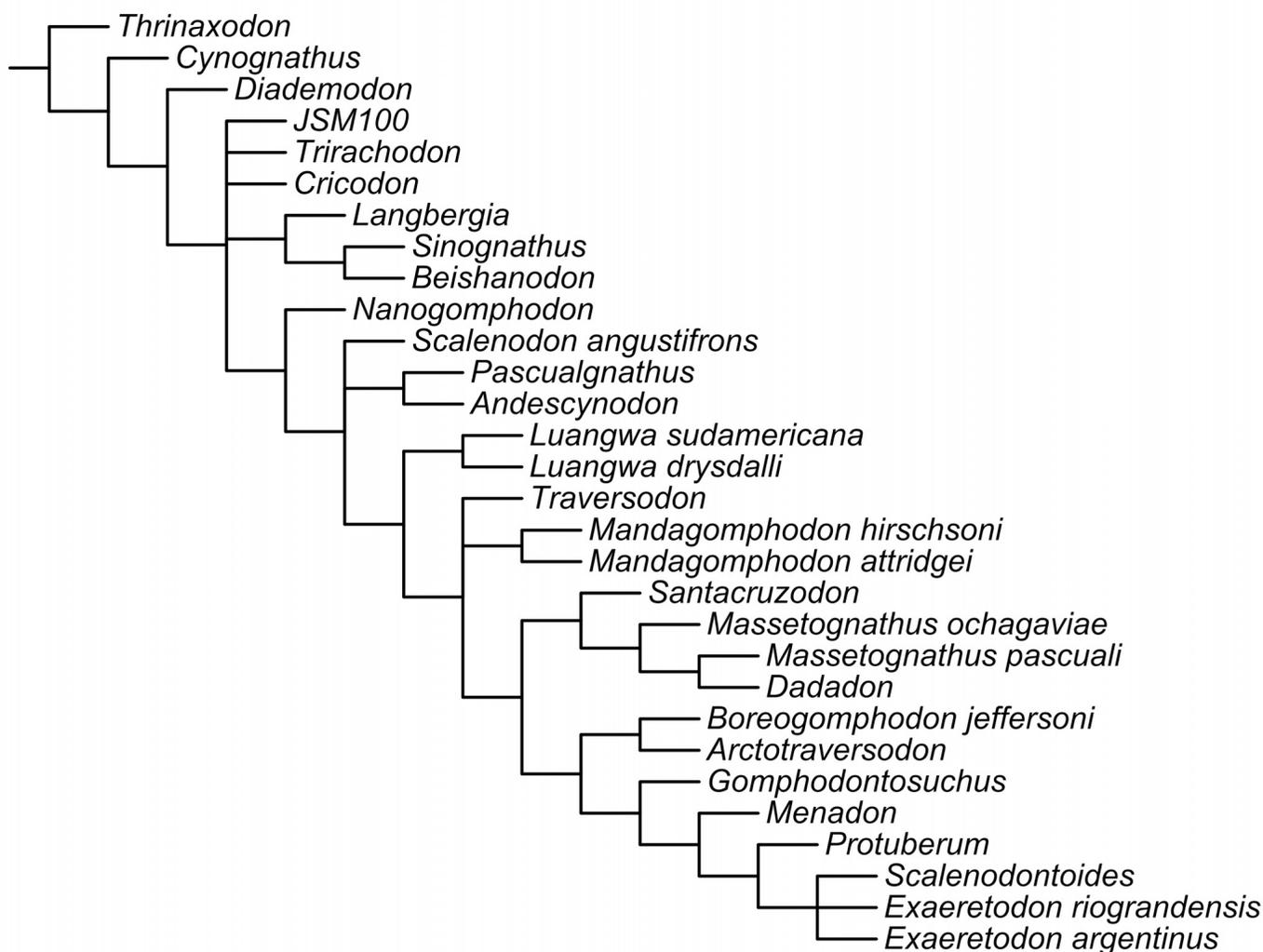


FIGURE 8. Cladogram of traversodontid relationships derived from the dataset modified after Liu and Abdala (2014). Strict consensus of nine most parsimonious trees.

angustifrons is the most basal traversodontid (uo iw wN; uo iw); (b) *Pascualgnathus* and *Andescynodon* do not form a monophyletic group and are placed between *S. angustifrons* and remaining traversodontids (uo iw; uo iw wN); (c) *Pascualgnathus* and *Andescynodon* form the most basal clade of traversodontids (o iw wN); (d) *Traversodon* forms a monophyletic group with the two species of *Luangwa* (uo iw; uo iw wN); (e) the clade *Boreogomphodon jeffersoni*, *Arctotraversodon* has a basal position between *Andescynodon* and the *Mandagomphodon* clade (uo iw; uo iw wN); and (f) *Massetognathinae* was not recovered as monophyletic group in any of the consensus trees obtained from the sensitivity analyses.

In summary of these analyses, the only clade recovered with a reasonable support in Traversodontidae is Gomphodontosuchinae (which includes, among others, *Menadon*). *Massetognathinae* is also recovered in our main analyses, although with poor support. Species of *Mandagomphodon*, *Luangwa*, and, to some degree, *Exaeretodon* appear as sister taxa, whereas the species of *Massetognathus* are recovered as paraphyletic. The basal-most traversodontid continues to be undefined, with some resolution suggesting the African *Scalenodon angustifrons* and others in the clade formed by the South American traversodontids *Pascualgnathus* and *Andescynodon*.

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LITERATURE CITED

- Abdala, F., and N. P. Giannini. 2000. Gomphodont cynodonts of the Chañares Formation, the analysis of an ontogenetic sequence. *Journal of Vertebrate Paleontology* 20:501–506.
- Abdala, F., and A. M. Ribeiro. 2003. A new traversodontid cynodont from the Santa Maria Formation (Ladinian-Carnian) of southern Brazil, with a phylogenetic analysis of Gondwanan traversodontids. *Zoological Journal of the Linnean Society* 139:529–545.

- Abdala, F., and A. M. Ribeiro. 2010. Distribution and diversity patterns of Triassic cynodonts (Therapsida, Cynodontia) in Gondwana. *Palaeogeography, Palaeoclimatology, Palaeoecology* 286:202–217.
- Abdala, F., and A. M. Sa-Teixeira. 2004. A traversodontid cynodont of African affinity in the South American Triassic. *Palaeontologia africana* 40:11–22.
- Abdala, F., M. C. Barberena, and J. Dornelles. 2002. A new species of the traversodontid cynodont *Exaeretodon* from the Santa Maria Formation (Middle/Late Triassic) of southern Brazil. *Journal of Vertebrate Paleontology* 22:313–325.
- Abdala, F., A. M. Ribeiro, and C. L. Schultz. 2001. A rich cynodont fauna of Santa Cruz do Sul, Santa Maria Formation (Middle-Upper Triassic), in southern Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 2001:669–687.
- Andreis, R. R., G. E. Bossi, and D. K. Montardo. 1980. O Grupo Rosário do Sul (Triássico) no Rio Grande do Sul; pp. 659–673 in XXXI Congresso Brasileiro de Geologia, Anais, volume 2, Camboriú, Santa Catarina.
- Barberena, M. C. 1974. Contribuição ao Conhecimento dos Cinodontes Gonfodontes (Cynodontia, Tritylodontoidea) do Brasil. Ministério de Educação e Cultura, Universidade Federal do Rio Grande do Sul, Porto Alegre, Brazil, Tese Livre Docente, 194 pp.
- Barberena, M. C. 1981a. Novos materiais de *Traversodon stahleckeri* da Formação Santa Maria (Triássico do Rio Grande do Sul). *Pesquisas* 14:149–162.
- Barberena, M. C. 1981b. Uma nova espécie de *Massetognathus* (*Massetognathus ochagaviae*, sp. nov.) da Formação Santa Maria, Triássico do Rio Grande do Sul. *Pesquisas* 14:181–195.
- Battail, B. 2005. Late Triassic traversodontids (Synapsida: Cynodontia) in southern Africa. *Palaeontologia africana* 41:67–80.
- Battail, B., and M. V. Surkov. 2000. Mammal-like reptiles from Russia; pp. 86–119 in M. J. Benton, M. A. Shishkin, D. M. Unwin, and E. N. Kurochkin (eds.), *The Age of Dinosaurs in Russia and Mongolia*. Cambridge University Press, Cambridge, U.K.
- Bertoni-Machado, C., and M. Holz. 2006. Biogenic fossil concentration in fluvial settings: an example of a cynodont taphocoenosis from the Middle Triassic of southern Brazil. *Revista Brasileira de Paleontologia* 9:273–282.
- Bonaparte, J. F. 1962. Descripción del cráneo y mandíbula de *Exaeretodon frenguelli* Cabrera, y su comparación con *Diademodontidae*, *Tritylodontidae* y los cinodontes sudamericanos. *Publicaciones del Museo Municipal de Ciencias Naturales y Tradicional de Mar del Plata* 1:135–202.
- Bremer, K. 1994. Branch support and tree stability. *Cladistics* 10:295–304.
- Broom, R. 1905. On the use of the term Anomodontia. *Records of the Albany Museum* 1:266–269.
- Chatterjee, S. 1982. A new cynodont reptile from the Triassic of India. *Journal of Paleontology* 56:203–214.
- Crompton, A. W. 1972. Postcanine occlusion in cynodonts and tritylodontids. *Bulletin of the British Museum (Natural History), Geology* 21:29–71.
- Flynn, J. J., J. M. Parrish, B. Rakotosamimanana, L. Ranivoharimanana, W. F. Simpson, and A. R. Wyss. 2000. New traversodontids (Synapsida, Eucynodontia) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology* 20:422–427.
- Flynn, J. J., J. M. Parrish, B. Rakotosamimanana, W. F. Simpson, R. L. Whately, and A. R. Wyss. 1999. A Triassic fauna from Madagascar, including early dinosaurs. *Science* 286:763–765.
- Furin, S., N. Preto, M. Rigo, G. Roghi, P. Gianolla, J. L. Crowley, and S. A. Bowring. 2006. High-precision U-Pb zircon age from the Triassic of Italy: implications for the Triassic time scale and the Carnian origin of calcareous nannoplankton and dinosaurs. *Geology* 34:1009–1012.
- Gao, K.-Q., R. C. Fox, C.-F. Zhou, and D.-Q. Li. 2010. A new nonmammalian eucynodont (Synapsida, Therapsida) from the Triassic of northern Gansu Province, China, and its biostratigraphic and biogeographic implications. *American Museum Novitates* 3685:1–25.
- Goloboff, P. A. 1993. Estimating character weights during tree search. *Cladistics* 9:83–91.
- Goloboff, P. A. and Farris, J. S. 2001. Methods for quick consensus estimation. *Cladistics* 17:S26–S34.
- Goloboff, P. A., J. S. Farris, and K. C. Nixon. 2008. TNT, a free program for phylogenetic analysis. *Cladistics* 24:774–786.
- Goñi, R., and F. J. Goin. 1990. Morfología dentaria y biomecánica masticatoria de los cinodontes (Reptilia, Therapsida) del Triásico argentino; II, *Exaeretodon frenguelli* Cabrera; Traversodontidae. *Ameghiniana* 27:327–336.
- Goswami, A., J. J. Flynn, L. Ranivoharimanana, and A. Wyss. 2005. Dental microwear in Triassic amniotes: implications for paleoecology and masticatory mechanics. *Journal of Vertebrate Paleontology* 25:320–329.
- Gow, C. E., and P. J. Hancox. 1993. First complete skull of the Late Triassic *Scalenodontoides* (Reptilia, Cynodontia) from southern Africa. *New Mexico Museum of Natural History and Science Bulletin* 3:161–168.
- Gradstein, F. M., J. G. Ogg, M. D. Schmitz, and G. M. Ogg. 2012. *The Geologic Time Scale 2012*. Elsevier, Oxford, U.K., 1176 pp.
- Hopson, J. A. 1984. Late Triassic traversodont cynodonts from Nova Scotia and southern Africa. *Palaeontologia africana* 25:181–201.
- Hopson, J. A. 1985. Morphology and relationships of *Gomphodontosuchus brasiliensis* von Huene (Synapsida, Cynodontia, Tritylodontoidea) from the Triassic of Brazil. *Neues Jahrbuch für Geologie und Paläontologie, Monatshefte* 1985:285–299.
- Horn, B. L. D., T. M. Melo, C. L. Schultz, R. P. Philipp, H. P. Kloss, and K. Goldberg. 2014. A new third-order sequence stratigraphic framework applied to the Triassic of the Paraná Basin, Rio Grande do Sul, Brazil, based on structural, stratigraphic and paleontological data. *Journal of South American Earth Sciences* 55:123–132.
- Huene, F. von. 1928. Ein Cynodontier aus der Trias Brasiliens. *Centralblatt für Mineralogie, Geologie und Paläontologie, Abteilung B* 1928:251–270.
- Huene, F. von. 1936. Lieferung 2 (Cynodontia); pp. 93–159 in *Die fossilen Reptilien des südamerikanischen Gondwanalandes. Ergebnisse der Sauriergrabungen in Südbrasilien 1928/1929*. Franz F. Heine, Tübingen, Germany.
- Kammerer, C. F. 2014. Theriodontia: introduction; pp. 165–169 in C. F. Kammerer, K. D. Angielczyk, and J. Fröbisch (Eds.), *Early Evolutionary History of the Synapsida*. Springer, Dordrecht, The Netherlands.
- Kammerer, C. F., J. J. Flynn, L. Ranivoharimanana, and A. R. Wyss. 2008. New material of *Menadon besairiei* (Cynodontia, Traversodontidae) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology* 28:445–462.
- Kammerer, C. F., J. J. Flynn, L. Ranivoharimanana, and A. R. Wyss. 2010. The first record of a probainognathian (Cynodontia: Chiniquodontidae) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology* 30:1889–1894.
- Kammerer, C. F., J. J. Flynn, L. Ranivoharimanana, and A. R. Wyss. 2012. Ontogeny in the Malagasy Traversodontid *Dadadon isaloi* and a reconsideration of its phylogenetic relationships. *Fieldiana Life and Earth Sciences* 5:112–125.
- Kemp, T. S. 1980. Aspects of the structure and functional anatomy of the Middle Triassic cynodont *Luangwa*. *Journal of Zoology* 191:193–239.
- Kemp, T. S. 1982. *Mammal-like Reptiles and the Origin of Mammals*. Academic Press, London, 363 pp.
- Kemp, T. S. 2005. *The Origin and Evolution of Mammals*. Oxford University Press, Oxford, U.K., 331 pp.
- Langer, M. C., A. M. Ribeiro, C. L. Schultz, and J. Ferigolo. 2007. The continental tetrapod-bearing Triassic of south Brazil. *Bulletin of the New Mexico Museum of Natural History and Science* 41:201–218.
- Liparini, A., T. V. Oliveira, F. A. Pretto, M. B. Soares, and C. L. Schultz. 2013. The lower jaw and dentition of the traversodontid *Exaeretodon riograndensis* Abdala, Barberena and Dornelles, from the Brazilian Triassic (Santa Maria 2 Sequence, *Hyperodapedon* Assemblage Zone). *Alcheringa* 37:331–337.
- Lipscomb, D. L. 1992. Parsimony, homology and the analysis of multistate characters. *Cladistics* 8:45–65.
- Liu, J., and F. Abdala. 2014. Phylogeny and taxonomy of the Traversodontidae; pp. 255–279 in C. F. Kammerer, K. D. Angielczyk, and J. Fröbisch (Eds.), *Early Evolutionary History of the Synapsida*. Springer, Dordrecht, The Netherlands.
- Liu, J., and H.-D. Sues. 2010. Dentition and tooth replacement of *Boreogomphodon* (Cynodontia, Traversodontidae) from the Upper Triassic of North Carolina, USA. *Vertebrata Palasiatica* 48: 169–184.
- Liu, J., M. B. Soares, and M. Reichel. 2008. *Massetognathus* (Cynodontia, Traversodontidae) from the Santa Maria Formation of Brazil. *Revista Brasileira de Paleontologia* 11:27–36.

- Melo, T. P., M. B. Soares, and B. L. D. Horn. 2010. The traversodontid biozone of the Santa Maria Formation (Middle-Upper Triassic), Paraná Basin, Southern Brazil: geographic distribution and biostratigraphic refinement; p. 24 in XXV Jornadas Argentinas de Paleontología de Vertebrados, Libro de Resúmenes, San Luis, San Luis.
- Melo, T. P., M. B. Soares, and T. V. Oliveira. 2009. Primeiro registro do traversodontídeo *Menadon* sp. (Flynn et al., 2000) na Biozona de Traversodontídeos da Formação Santa Maria, Triássico Médio do Rio Grande do Sul, Brasil; p. 16 in PALEO 2009, Reunião Anual da Sociedade Brasileira de Paleontologia, Livro de Resumos, São João do Polêsine, Rio Grande do Sul.
- Owen, R. 1861. Paleontology or a Systematic Summary of Extinct Animals and Their Geological Relations. Adam and Charles Black, Edinburgh, U.K., 420 pp.
- Philipp, R. P., H. Closs, C. L. Schultz, M. Basei, B. L. D. Horn and M. B. Soares. 2013. Proveniência por U-Pb LA-ICP-MS em zircão detrítico e idade de deposição da Formação Santa Maria, Triássico da Bacia do Paraná, RS: evidências da estruturação do Arco do Rio Grande; pp. 154–157 in VIII Symposium International on Tectonics—XIV Simpósio Nacional de Estudos Tectônicos, 2013. Anais VIII Symposium International on Tectonics—XIV Simpósio Nacional de Estudos Tectônicos, Cuiabá, Mato Grosso.
- Ranivoharimanana, L., C. F. Kammerer, J. J. Flynn, and A. R. Wyss. 2011. New material of *Dadadon isaloï* (Cynodontia: Traversodontidae) from the Triassic of Madagascar. *Journal of Vertebrate Paleontology* 31:1292–1302.
- Raugust, T., M. Lacerda, C. L. Schultz. 2013. The first occurrence of *Chanaresuchus bonapartei* Romer 1971 (Archosauriformes, Proterochampsia) of the Middle Triassic of Brazil from the *Santacruzodon* Assemblage Zone, Santa Maria Formation (Paraná Basin). *Geological Society, Special Publications* 379:303–318.
- Razafimbelo, E. 1987. Le bassin de Morondava (Madagascar). Synthèse géologique et structurale. Ph.D. dissertation, Université Louis Pasteur, Strasbourg, France.
- Reichel, M., C. L. Schultz, and V. P. Pereira. 2005. Diagenetic pattern of vertebrate fossils from the Traversodontidae Biozone, Santa Maria Formation (Triassic) Southern Brazil. *Revista Brasileira de Paleontologia* 8:173–180.
- Reichel, M., C. Schultz, and M. B. Soares. 2009. A new traversodontid cynodont (Therapsida, Eucynodontia) from the Middle Triassic Santa Maria Formation of Rio Grande do Sul, Brazil. *Palaeontology* 52:229–250.
- Rogers, R. R., C. C. Swisher, P. C. Sereno, A. M. Monetta, C. A. Forster, and R. N. Martínez. 1993. The Ischigualasto Tetrapod Assemblage (Late Triassic, Argentina) and ⁴⁰Ar/³⁹Ar Dating of Dinosaur Origins. *Science* 260:794–797.
- Romer, A. S. 1967. The Chañares (Argentina) Triassic reptile fauna. III. Two new gomphodonts, *Massetognathus pascuali* and *M. terugii*. *Breviora* 264:1–25.
- Schultz, C. L., C. M. Scherer, and M. C. Barberena. 2000. Biostratigraphy of southern Brazilian Middle–Upper Triassic. *Revista Brasileira de Geociências* 30:491–494.
- Soares, M. B., F. Abdala, and C. M. Bertoni-Machado. 2011a. A sectorial toothed cynodont from the Triassic Santa Cruz do Sul fauna, Santa Maria Formation, Southern Brazil. *Geodiversitas* 33:265–278.
- Soares, M. B., C. L. Schultz, T. V. Oliveira, and T. P. Melo. 2011b. Os cinodontes não-mamaliaformes e sua contribuição para o refinamento bioestratigráfico do Triássico Médio-Superior do Rio Grande do Sul, Brasil; p. 731 in XXII Congresso Brasileiro de Paleontologia, Boletim de resumos, Natal, Rio Grande do Norte.
- Sues, H.-D., and J. A. Hopson. 2010. Anatomy and phylogenetic relationships of *Boreogomphodon jeffersoni* (Cynodontia, Gomphodontia) from the Upper Triassic of Virginia. *Journal of Vertebrate Paleontology* 30:1202–1220.
- Sues, H.-D., and P. E. Olsen. 1990. Triassic vertebrates of Gondwanan aspect from the Richmond Basin of Virginia. *Science* 249:1020–1023.
- Sues, H.-D., P. E. Olsen, and J. G. Carter. 1999. A late Triassic traversodontid cynodont from the Newark Supergroup of North Carolina. *Journal of Vertebrate Paleontology* 19:351–354.
- Teixeira, G. V., B. L. D. Horn, and M. B. Soares. 2010. Comparação entre padrões fossil diagenéticos de três localidades da Formação Santa Maria, Triássico do Rio Grande do Sul, e sua contribuição na ampliação geográfica da Biozona de Traversodontídeos; p. 9 in XXII Salão de Iniciação Científica da UFRGS, CD de resumos, Porto Alegre, Rio Grande do Sul.
- Zerfass, H., E. L. Lavina, C. L. Schultz, A. J. V. Garcia, U. F. Faccini, and F. Chemale Jr. 2003. Sequence stratigraphy of continental Triassic strata of Southernmost Brazil: a contribution to Southwestern Gondwana palaeogeography and paleoclimate. *Sedimentary Geology* 161:85–105.

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