

A MIDDLE TRIASSIC CYNODONT FAUNA FROM NAMIBIA AND ITS IMPLICATIONS FOR THE BIOGEOGRAPHY OF GONDWANA

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ABSTRACT—The upper Omingonde Formation of Namibia contains a diverse vertebrate fauna represented by amphibians, dicynodonts, archosaurs, therocephalians, and cynodonts, which is generally considered to be of Anisian age. Four cynodont taxa (*Cynognathus*, *Diademodon*, *Trirachodon*, and *Titanogomphodon*) are currently known from this fauna. Here we document four additional cynodonts, all of which were recovered from the highest levels of the formation: *Luangwa*, an indeterminate traversodontid, *Aleodon*, and *Chiniquodon*. These discoveries allow us to recognize the Omingonde Formation as preserving the most diverse fauna of Middle Triassic cynodonts in the world. Furthermore, we recognize that the formation is a biostratigraphic link among Middle Triassic faunas from South Africa, Tanzania, Zambia, Argentina, Brazil, and Antarctica. *Aleodon* is recorded here for the first time in Anisian faunas of southern Africa, and the unexpected record of *Chiniquodon* poses a biostratigraphic enigma because this taxon is known only from Ladinian–Carnian faunas of South America. We explore some possible scenarios related to the radiation of traversodontid cynodonts in Gondwana during the Anisian.

INTRODUCTION

Vertebrate fossils of Middle Triassic age are known from many localities in the former Gondwanan continents (King, 1993; Bandyopadhyay and Sengupta, 1999; Morel et al., 2001; Rubidge, 2005; Abdala et al., 2005). In south-central Africa the record of Middle Triassic vertebrates is widely accepted as being strictly Anisian in age (Catuneanu et al., 2005), whereas the Ladinian record is particularly well represented in South America (Rogers et al., 2001; Langer, 2005) and Madagascar (Flynn et al., 1999). Faunal links between terrestrial Triassic assemblages from South America and Africa are rare, and until recently were based only on the common presence of the carnivorous cynodont *Cynognathus* (Bonaparte, 1969a). The recent discovery in southern Brazil of the traversodontid cynodont *Luangwa* (Abdala and Teixeira, 2004), previously reported only from Zambia (Brink, 1963; Kemp, 1980), represents a correlation between an African Anisian fauna and an apparently Ladinian fauna from South America. However, the presence of this traversodontid has been used to suggest an Anisian age for some levels of the Santa Maria Formation of Brazil (Abdala and Teixeira, 2004). To these cases should be added the latest discovery of the gomphodont cynodont *Diademodon* in the Middle Triassic of Argentina (Martinelli et al., 2008).

The Omingonde Formation of the Otiwarongo Basin in north-central Namibia is well known for its Triassic terrestrial fauna. The first report of vertebrate fossils in this rock unit was published by Keyser (1973a, 1973b), who described remains of amphibians, dicynodonts, bauriid therocephalians, and cynodonts. The last group was represented by herbivorous gomphodonts (e.g., *Trirachodon* and *Titanogomphodon*) and *Cynognathus*. In his catalogue of synapsids, Brink (1986) mentioned the presence of the traverso-

odontid cynodont *Scalenodon* in levels of the Omingonde Formation. Later, Pickford (1995) assigned the skull of a carnivorous archosauriform from these exposures to *Erythrosuchus*, and more recently Smith and Swart (2002) reported an almost complete armored skeleton associated with this skull. A number of taxa from the Omingonde Formation are also known from the Burgersdorp Formation of the South African Karoo (Keyser, 1973a; Lucas, 1998; Holzförster et al., 1999; Smith and Swart, 2002), whereas some cynodonts such as the gomphodont cynodont *Diademodon* and the carnivorous cynodont *Cynognathus* have been also recorded from other localities of Gondwana. Consequently, the Omingonde fauna has been correlated to subzones B and C of the *Cynognathus* Assemblage Zone of the Karoo Basin, and dated as Anisian (Abdala et al., 2005).

Recent fossil collecting in the upper Omingonde Formation resulted in a notable abundance of non-mammaliaform cynodonts (Smith and Swart, 2002). Re-investigation of these specimens reveals that, in addition to their abundance, taxonomic diversity in the group is unexpectedly high. Besides the previously known records of cynognathids, diademodontids, and trirachodontids (Keyser 1973a; Smith and Swart, 2002), here we document the first occurrence of the cynodont genera *Luangwa*, *Aleodon*, and *Chiniquodon*, plus a traversodontid of uncertain identity in Namibia. These records provide definite links with two faunas from East Africa and two from South America, placing the upper Omingonde Formation as a key source of information for reconstructing the biogeography of southern Gondwana during the Middle Triassic. The Namibian record of *Chiniquodon* is a remarkable biostratigraphic enigma in that this carnivorous cynodont, known before only in South America (Romer, 1969a, 1969b; Martinez and Forster, 1996; Abdala and Giannini, 2002), represents the first Ladinian–Carnian taxon discovered so far in African continental Middle Triassic faunas.

Institutional Abbreviations—BP, Bernard Price Institute for Palaeontological Research, University of the Witwatersrand,

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Johannesburg; **BMNH**, Natural History Museum, London; **CGP**, Council for Geosciences, Pretoria; **GPIT**, Institut und Museum für Geologie und Paläontologie der Universität Tübingen; **GSN**, Geological Survey of Namibia, Windhoek; **MCP**, Museu de Ciências e Tecnologia, Pontifícia Universidade Católica do Rio Grande do Sul, Porto Alegre; **MCZ**, Museum of Comparative Zoology, Harvard University; **OUMNH**, Oxford University Museum of Natural History; **PULR**, Museo de Antropología, Universidad Nacional de La Rioja; **PVL**, Colección Paleontología de Vertebrados Lillo, Universidad Nacional de Tucumán; **PVSJ**, Museo de Ciencias Naturales, Universidad Nacional de San Juan; **UFRGS**, Universidade Federal do Rio Grande do Sul, Porto Alegre; **UMZC**, University Museum of Zoology, Cambridge.

MATERIALS

The majority of the material is poorly preserved, hampering a detailed description. The Namibian cynodonts are succinctly described here, where we mainly point out features relevant to taxonomic identity and for comparison of the taxa. With the exception of one specimen, all those described are housed at the Geological Survey, Windhoek, Namibia. The materials are referred to by field numbers provided by Smith and Swart (2002) and are listed in the Systematic Paleontology section.

The following comparative material was examined: *Aleodon*: UMCZ T906, T920; BMNH R9390, R10048; *Chiniquodon*: BMNH R8429; GPIT 40, 1050; MCP PV1600; MCZ 1533, 3035, 3614, 3615, 3777, 3776, 3779, 3781, 4002, 4020, 4100, 4296, 8823; PULR 12*, 18*, 100, 101, 102; UFRGS PV 66T, 66Tg, 122T, 274, 275T; PVL 4167, 4444, 4448, 4674, 4675; PVSJ 411. *Luangwa*: BP/1/3731; MCP 3167PV; OUMNH TSK121; UFRGS PV 267. An asterisk indicates that the specimen was stolen from the museum. *Probesodon* is considered a junior synonym of *Chiniquodon* following Abdala and Giannini (2002).

STRATIGRAPHY AND SEDIMENTARY ENVIRONMENTS OF OMINGONDE FOSSIL LOCALITIES

The Omingonde Formation is a classic continental redbed sequence that accumulated in one of several E-W trending half grabens that are associated with extension of western Gondwana prior to its break up. The facies reflect an upward trend from humid to arid environments linked to climatic drying. The upward trend was interpreted by Smith and Swart (2002) as a succession of lakes with alluvial fans (lower Omingonde) followed by gravel-bed braided rivers with marginal alluvial fans (middle Omingonde) and loessic plains, and gravel- and sand-bed meandering rivers on semi-arid floodplains (upper Omingonde).

Smith and Swart (2002:fig. 3) list three fossil-rich localities on the farms Rhenosterkloof, Omingonde 96, and Etjo Nord 93. It is safe to conclude (A. Keyser, pers. comm., 2007) that Rhenosterkloof and Etjo Nord 93 correspond to Keyser's (1973a, 1973b) 'western buttress of Etjo Mountain' and 'northern slope of Etjo Mountain,' respectively.

Stratigraphically, vertebrate fossils discovered by Smith and Swart (2002) were mostly from loessic mudrocks of the upper Omingonde Formation, although they also reported very rare and fragmented fossils in the coarse pebbly sandstones of the middle Omingonde. Holzförster et al. (1999) reported fossils coming from all three units of the Omingonde Formation. However, the only fossils reported by these authors from their unit 1 (= lower Omingonde Formation) is the skeleton of *Erythrosuchus* on Etjo North, which is in fact from a downfolded block of the upper Omingonde Formation (Pickford, 1995; Smith and Swart, 2002). The majority of the fossils presented by Holzförster et al. (1999) come from their units 2 and 3 (= middle and base of the upper Omingonde Formation, respectively). It is difficult to position precisely the findings of Keyser (1973a, 1973b) in

the stratigraphic scheme provided by Smith and Swart (2002) and Holzförster et al. (1999). Keyser (1973a) locates the fossils discovered by his team in relation to three arenaceous horizons in the Omingonde Formation. It is not possible to be certain if these horizons are restricted to what Smith and Swart (2002) identified as the upper Omingonde Formation, or if they include middle and lower as well. Holzförster et al. (1999) concluded that the fossils found by Keyser (1973a, 1973b) correspond to their units 2 and 3. Nevertheless, it is clear from Keyser (1973a, 1973b) that the specimens of *Cynognathus*, the amphibian originally identified as the amphibamid *Micropholis*, which is probably a juvenile mastodontosaurid (R. Damiani, pers. comm., March, 2008), and the dicynodont *Dolichuramus* all come from below his 'lower arenaceous horizon' and thus they are the oldest specimens discovered. In contrast, the gigantic diademodontid *Titanogomphodon* and the therocephalian *Herpetogale* come from above the 'upper arenaceous horizons' and are the youngest specimens discovered by him (discussed further below). In addition, Keyser also discovered remains of traversodontids reported as *Scalenodon angustifrons* by Brink (1986), and considered as *Luangwa* in this contribution, that were recovered "very high" in the upper Omingonde Formation (A. Keyser, pers. comm., November, 2007).

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905

CYNODONTIA Owen, 1861

EUCYNODONTIA Kemp, 1982

CYNOGNATHIA Hopson and Barghusen, 1986

TRAVERSODONTIDAE Huene, 1936

LUANGWA Brink, 1963

Diagnosis—Traversodontid cynodont with short snout and temporal region, and enormous orbits almost of the size of the temporal opening; angle of the dentary slightly projected posteriorly; upper postcanines with oval cross sections; each postcanine exhibits a mesiolabial cingulum and a distal cingulum with tiny cusplules behind the transverse crest; incipient cingulum in front to the anterior transverse crest of the lower postcanines formed by tiny cusplules (Abdala and Teixeira, 2004).

Type Species—*Luangwa drysdalli* Brink, 1963.

Included Species—*L. drysdalli*, *L. sudamericana*.

Age and Distribution—Upper Ntawere Formation, Zambia; Santa Maria Formation, Brazil; upper Omingonde Formation, Namibia. Anisian–?Ladinian (Abdala and Teixeira, 2004).

LUANGWA sp.

(Figs. 1–4)

Referred Material—GSN OM-2, a snout fragment; GSN RK-4a, a distorted skull with mandible; GSN RK-4b skull with articulated mandible; GSN RK-4c, a skull with associated mandible and some postcranial elements; and CGP R 572, a skull associated to mandible and some postcranial bones.

Description—Three skulls and some postcranial remains are represented in GSN RK-4. The basal lengths of these skulls range between 14.5 and 16.2 cm (Table 1). One of the skulls (GSN RK-4a) is completely distorted, and it is possible to recognize only the presence of large orbits and a short snout. In addition, the cross section of the last postcanine indicates it is a traversodontid cynodont. The remaining two skulls (GSN RK-4b and c) exhibit a short snout, a relatively enlarged orbit approximately the same size as the temporal region, and a broad basi-cranial girder (Table 1; Fig. 1A, B). The zygomatic arch is subparallel to the long axis of the skull, and the jugal exhibits a well-developed suborbital process (Fig. 1B) similar to that observed in OUMNH TSK121 (Kemp, 1980). GSN RK-4c preserves four incisor roots (Fig. 1C), the first being circular in outline, whereas the second and third are more ovoid, with the

TABLE 1. Measurements of the skulls of *Luangwa* from the Omingonde Formation (in cm).

Measurement	GSN RK-4a	GSN RK-4b	GSN RK-4c	GSN OM-2	CGP 572
Basal skull length	between 14.0 and 14.5	16.2	15.5e		20.4
Snout length		7.1	7.0e	6.9	9.1
Orbital length		3.6	3.1		4.2
Temporal length		3.9	3.4		6.7

Abbreviation: e, estimate.

long axis oriented bucco-lingually, and somewhat larger than the first tooth. The partially preserved crown of the fourth incisor also seems to be ovoid, but with its larger axis oriented antero-posteriorly. The canines are anteroposteriorly elongated and buccolingually thin. These teeth are broken at their bases, and the right canine is in the process of being replaced by a new tooth that is erupting anterior to the former tooth (Fig. 1C). Serrations on the margins of both incisors and canines are observed in GSN RK-4b. Eight ovoid, buccolingually expanded postcanines are preserved on the right side of GSN-RK-4c, whereas a last left tooth is in eruption (Fig. 1C). Only part of the posterior margin of this tooth is visible, and shows a well-developed lingual cusp, and a crest placed in the posterior margin of the tooth. The anterior teeth are remarkably worn, with the crown showing a deep concave basin. This pattern is visible in the four anterior right postcanines and in the two elements that are visible in the left series (probably representing the fifth and sixth postcanines). In the three posterior left postcanines a posterior crest is observed (Fig. 1D, E). This crest is remarkably worn and is located at some distance from the posterior margin of the tooth. Labial and lingual cusps are present in the last two teeth, whereas fragmentation and poor preservation of these elements hamper the recognition of more cusps in the central portion of the crest. In the laterally expanded labial margin of the final left tooth it is possible to recognize a main posterior cusp and an anterior accessory cusp, both of which are broken (Fig. 1E). A cingulum is barely discernable on the labial margin of the postcanine. In the last two left postcanines a cingular ridge, which crosses the crown transversely, is present in the posterior margin of the teeth. A tiny anterior lingual cusp is separated from the larger posterior cusp in the postcanine in eruption, and a low central cusp, uniting the larger labial and lingual cusps, is present.

An isolated snout (GSN OM-2; Fig. 2A, B), previously identified as *Massetognathus* (Smith and Swart, 2002) and of comparable size to specimens GSN RK-4a–c (see Table 1), is dorsoventrally flattened. The snout shows four upper incisors and minimally six upper postcanines (Fig. 2A). The canines are not preserved and their placement is difficult to assess in the material, although they are most likely positioned in the jaw such that there is a short diastema anterior to the first postcanine, as in GSM RK-4c. The left postcanine series shows poorly preserved teeth. The overall morphology of the postcanines is similar to that of GSN RK-4c, with labial margins expanded laterally (Fig. 2C). The osseous secondary palate is extended in the entire fragment (i.e., to the level of the sixth postcanine) a condition similar to that of GSN RK-4c.

The lower jaw has a fused symphysis, with the dentary exhibiting a well-developed coronoid process directed posterodorsally (Fig. 3A) with a transversely thick anterior margin. The backward projection in the angle of the dentary is absent in GSN RK-4c, whereas this projection seems to be present in the right lower jaw of GSN RK-4a, despite poor preservation of this area. Three incisor alveoli are present in the lower jaw (Fig. 3B) and the observation of a replacement tooth in GSN RK-4b reveals that these teeth are lanceolate and serrated. Nine lower postcanines are preserved in GSN RK-4a (Fig. 3A, C), of which the most anterior is a tiny peg-like tooth and the remaining teeth are

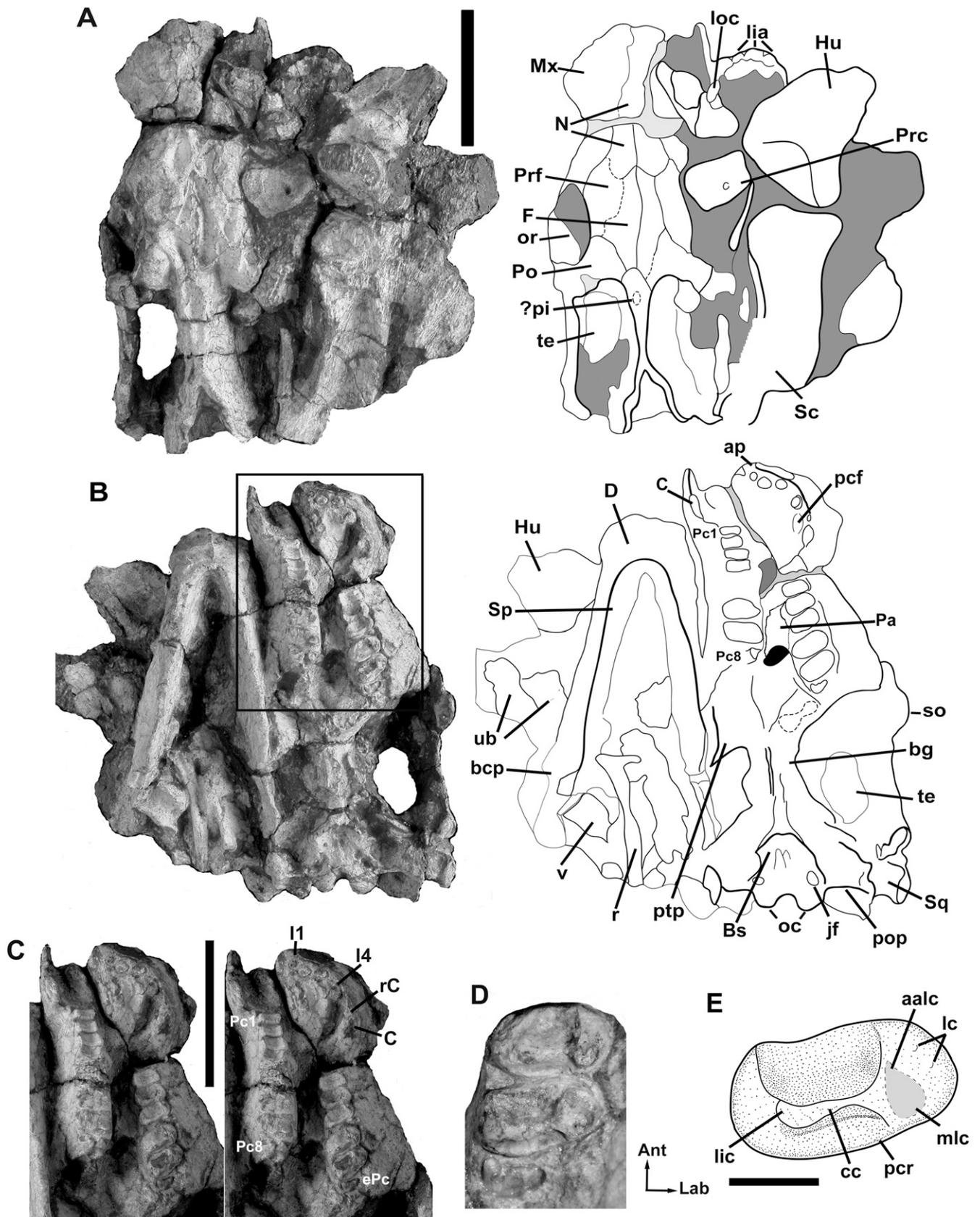
quadrangular in outline. The sizes of the teeth increase gradually towards the back of the row. There is a transverse crest formed by two cusps, followed by a basin. Most posterior postcanines show that the transverse crest is positioned towards the anterior portion of the teeth, but not on the anterior margin (Fig. 3C, D). The presence of a cingular ridge anterior to the main crest of the lower postcanine is observed in the last left element. In the remaining teeth the crown is not preserved completely and part of the enamel is broken, leaving no trace of this ridge. The last right postcanine exhibits a crenulated posterior margin (Fig. 3D).

CGP R 572 is the largest skull known for this taxon (Fig. 4A, B) and was previously identified as *Scalenodon angustifrons* by Brink (1986). The proportions of some skull regions (such as orbital and temporal lengths) are somewhat different from those of the other specimens of *Luangwa* (Table 1), but the general morphology of the skull is similar, with a quadrangular temporal region, limited by subparallel zygomatic arches. There is no clear evidence on the presence of the pineal foramen. CGP R 572 exhibits nine alveoli for the upper postcanines (Fig. 4B), and the secondary palate extends until the level of the seventh postcanine. The lower jaw is robust, with a fused symphysis and a well-developed coronoid process with its anterior margin remarkably broad mediolaterally. There is no evidence indicating the presence of the posterior projection of the angular region, although the preservation of these regions on both sides is not complete. There are alveoli for three lower incisors, the third one being tiny, followed by an ellipsoid canine. Eight to nine lower postcanine alveoli seem to be present, but part of the occlusal margin of the lower jaw is covered by other bones, hampering a definitive tooth count.

Gen. et sp. indet.
(Fig. 5)

Referred Material—GSN OM-5, skull with mandible.

Description—OM-5 has a skull length of 18.4 cm and is flattened dorsoventrally, such that the postcanine crowns are barely visible in lateral view. Neither orbit is preserved, whereas the temporal region is represented only by the complete sagittal crest (Fig. 5A). The anterior portions of the horizontal rami of the mandible are preserved in occlusal contact with the skull. The snout is robust and exhibits a uniform breadth throughout its length, a feature that can be ascribed to the dorsoventral flattening the skull has undergone. The anterior tip of the snout is not preserved and reveals the presence of three lower incisors (Fig. 5A). The sagittal crest is notably long and has a tiny ellipsoid parietal foramen placed close to the long posterior process of the postorbital. Compression has also badly affected the temporal region, so that the left alisphenoid and the prootics are crushed and distorted. An extremely thin laminar bone is preserved in the interorbital vacuity that probably represents the orbitosphenoid. In ventral view it is observed a long and thin basicranial girder, followed by the typical triangular basicranium of non-mammaliaform cynodonts that ends in rounded occipital condyles posteriorly (Fig. 5B). On the right side an incomplete stapes is preserved, showing that one of the crura (possibly the anterior one) is well developed and expanded in its proximal margin. The anterior portion of the lower jaw is quite robust



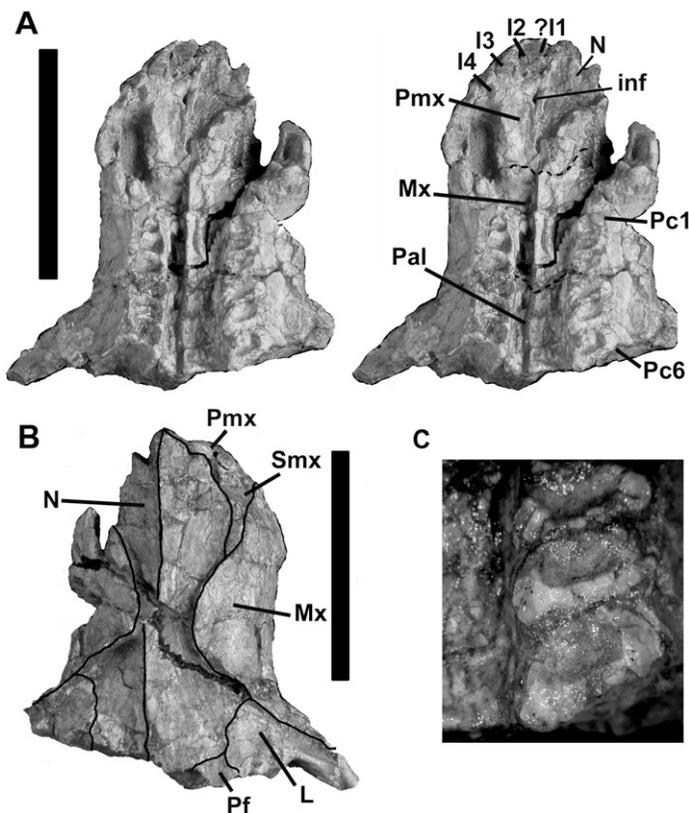


FIGURE 2. *Luangwa*, GSN OM-2. **A**, stereopair of the ventral view; **B**, dorsal view; **C**, detail of the last three left upper postcanines. **Abbreviations:** **I**, incisor; **inf**, incisive foramina; **L**, lacrimal; **Mx**, maxilla; **N**, nasal; **Pal**, palatine; **Pc**, postcanine; **Pf**, prefrontal; **Pmx**, premaxilla; **Smx**, septomaxilla. Numbers indicate first and last postcanines and all incisor alveoli. Scale bar equals 5 cm.

and has a fused symphysis (Fig. 5B). The most posterior portion of the horizontal ramus exhibits a platform lateral to the dental series that is similar to, although clearly less developed than, that of bauriid therocephalians. This condition is unknown in other non-mammaliaform cynodonts and can also be the consequence of the dorsoventral flattening of the skull.

Three lower incisors are represented in both sides by broken teeth that are circular in outline. The right upper canine is also broken at its base and the tooth appears ellipsoid in outline, being long anteroposteriorly and remarkably thin buccolingually. Some of the postcanines are partially visible medial to the lower jaw (Fig. 5C). The crown of one left lower postcanine is broken at its base and somewhat displaced. Its lingual margin has an anterior cusp that forms a crest, followed by a deep basin. The cusp is well developed and rounded, and there is no evidence of the presence of cingulum or of a posterior cusp in the lingual margin of the tooth (Fig. 5D). In addition, on the right side it is possible to observe a quite rounded lingual margin of an upper tooth. A cusp is placed posteriorly and a basin toward the anterior portion of the

tooth. As in the lower tooth, there is no indication of a cingular cusp in the lingual margin of the upper postcanine.

PROBAINOGNATHIA Hopson, 1990
ALEODON Crompton, 1955

Diagnosis—Probainognathian cynodont with a long osseous secondary palate extending to the end of the tooth row (as is common in *Chiniquodon* and other cynodonts; see below) and buccolingually expanded (ovoid to ellipsoid) outline of the upper postcanines, exhibiting a well-developed cingular platform.

Type Species—*Aleodon brachyrhamphus* Crompton, 1955.

Age and Distribution—Manda Formation, Tanzania; upper Omingonde Formation, Namibia. Late Anisian–?early Ladinian (Abdala and Ribeiro, 2003).

ALEODON sp.
 (Fig. 6)

Referred Material—GSN EN-3, a skull.

← FIGURE 1. *Luangwa*, GSN RK-4c. **A**, dorsal view of the skull and some postcranial bones; **B**, ventral view of the skull, lower jaw and some postcranial bones. White rectangle is the palatal portion of the skull presented as stereopair in C. **D**, detail of two left upper postcanines and the last postcanine in eruption. **E**, last left upper postcanine. **Abbreviations:** **aalc**, anterior accessory labial cusp; **ap**, ascending process of the premaxilla; **bcp**, base of the coronoid process; **bg**, basicranial girder; **Bs**, basisphenoid; **C**, canine; **cc**, central cusp; **D**, dentary; **ePc**, post canine in eruption; **F**, frontal; **Hu**, humerus; **I**, incisors; **jf**, jugular foramen; **lc**, labial cingulum; **lia**, lower incisor alveoli; **lic**, lingual cusp; **loc**, lower canine; **mlc**, main labial cusp; **Mx**, maxilla; **N**, nasal; **oc**, occipital condyles; **or**, orbit; **Pa**, palatine; **Pc**, postcanine; **pcf**, paracanine fossa; **pcr**, posterior cingular ridge; **pi**, pineal foramen; **pop**, paroccipital process; **Prc**, procoracoid; **Prf**, prefrontal; **ptp**, pterygoid process; **Po**, postorbital; **r**, rib; **rC**, replacement canine; **Sc**, scapula; **so**, suborbital process; **Sp**, splenial; **Sq**, squamosal; **te**, temporal opening, **ub**, unidentified bone; **v**, vertebra. Numbers indicate first and last incisors and postcanines. Light grey indicates broken bone, dark grey is matrix, and dashed lines are broken bone and inferred sutures. Note that the anterior left portion of the snout is not glued in its natural position. Scale bars equal 5 cm (A, C) and 5 mm (E).

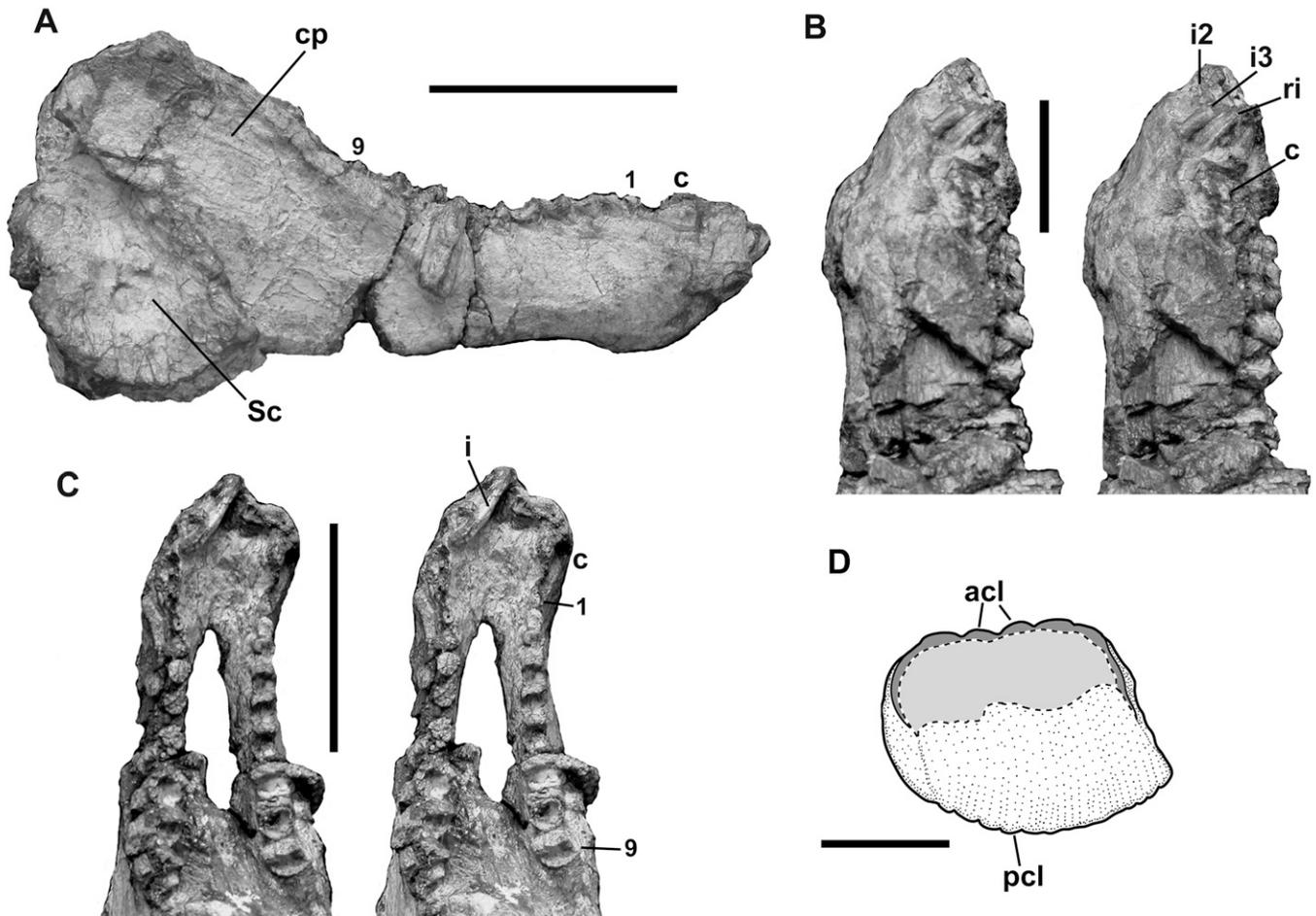


FIGURE 3. *Luangwa*, GSN RK-4a. Mandible. **A**, right lateral view; **B**, stereopair of the left lateral view; **C**, stereopair of the occlusal view. **D**, ninth right lower postcanine. The anterior cingulum was observed in the 8th left lower postcanine. **Abbreviations:** **acl**, anterior cingulum; **c**, canine; **cp**, coronoid process; **i**, incisor; **pcl**, posterior cingulum; **ri**, replacement incisor; **Sc**, scapula. Numbers indicate first and last postcanines and incisor teeth. Light grey is broken surface, dark grey is enamel layer. Scale bars equal 5 cm (A, C), 2 cm (B), and 5 mm (D).

Description—This taxon is represented by a poorly preserved, isolated skull that lacks the lower jaw, with the exception of the right coronoid process, which is pressed against the lateral wall of the skull of the same side. The basal skull length of the new specimen is 15.6 cm, only slightly longer than the estimated skull length (= 14.5 cm) for the specimen described by Crompton (1955). The snout is robust and nearly the same length as the temporal region (Table 2). In dorsal view, the nasals are repositioned slightly ventrally and the sutures with both maxillae and the left lacrimal are clearly discernible (Fig. 6A, B). The nasals, as is usual in most cynodonts, are expanded in their posterior third and the ascending processes of the premaxillae are observed wedging between the anteromedial borders of the nasals (Fig. 6A). In the interorbital area, the frontal bones are depressed in relation to the prefrontal and postorbital bones, which form the dorsal border of the orbit. The postorbital bar is formed in equal proportion by the postorbital bone dorsally and the jugal ventrally. There is a long sagittal crest and there is no vestige of a pineal foramen. This crest is extended so far posteriorly that the occipital plate is totally hidden in dorsal view. However, this condition is probably due to the deformation and poor preservation of the skull. In lateral view, the zygomatic arches of both sides are preserved, lacking only their posterior portion. The zygoma is very robust and dorsoventrally high (Fig. 6B). The ventral margin is not totally preserved on both sides of the skull, but considering the better preserved left side, a

suborbital angulation between the posterior margin of the maxilla and the anterior end of the jugal seems to be absent (Fig. 6B). The elongate osseous secondary palate extends to the level of the last postcanine (Fig. 6C). An incisive foramen is present in the anterior region of the palate, and seems to be limited posteriorly by the maxilla. The basicranial girder appears to be remarkably wide and it is possible to observe a furrow between the medial and lateral pterygoid ridges, posterior to the pterygoid processes. Although poorly preserved, the basicranium is triangular in outline (typical of most non-mammaliaform cynodonts), and exhibits the foramen jugular and the fenestra ovalis. The occipital condyles are not preserved. The preserved portion of the right coronoid process seems to have been quite high and not very extensive anteroposteriorly (Fig. 6A), similar to the condition observed in some specimens of *Massetognathus* (e.g., PVL 3901).

The skull preserves alveoli for four upper incisors, followed by a diastema that forms the lateral margin of the paracanine fossa (Fig. 6C). The canines are broken at their bases, but it is evident that they have oval outlines and protruded lateral to the snout. The postcanine series consists of 11 teeth, which are placed medially in relation to the upper canine, and are remarkably divergent posteriorly. A single postcanine (with a poorly preserved crown) is observed on the right side (Fig. 6D), whereas the crowns of the entire left series of teeth have been lost, revealing only that the teeth are ellipsoidal to circular in outline (Fig. 6E).

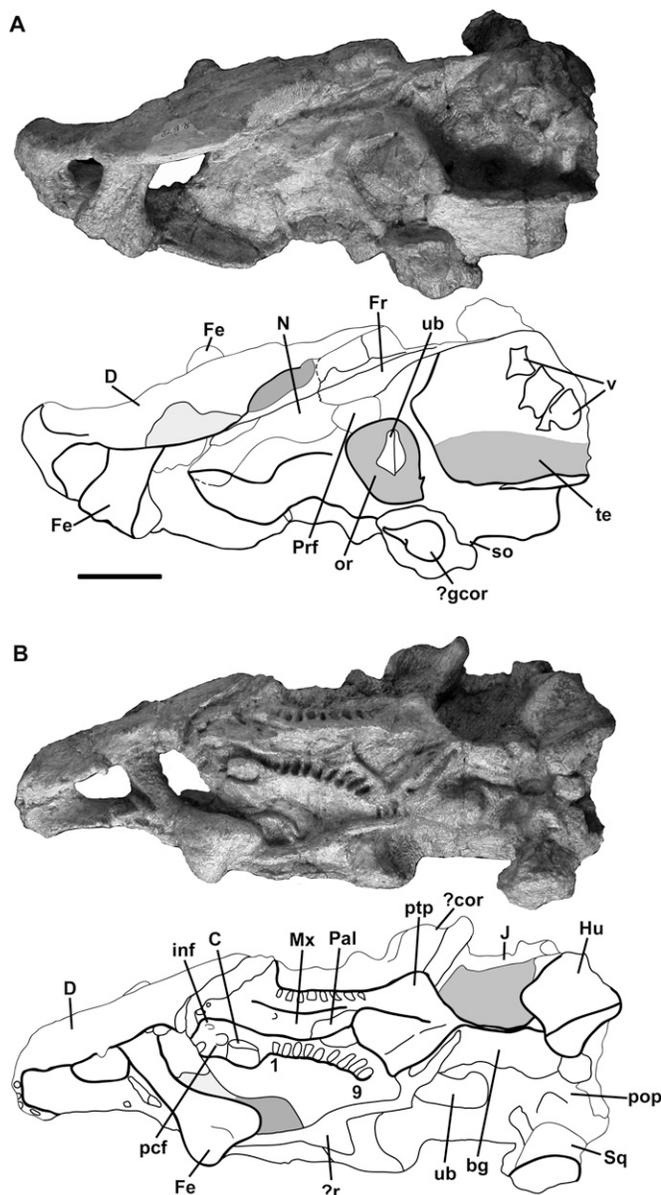


FIGURE 4. *Luangwa*, CGP R572. **A**, dorsolateral view of the skull with mandible and some postcranial bones; **B**, ventral view of the skull with mandible and some postcranial bones. **Abbreviations:** **bg**, basicranial grider; **C**, canine; **cor**, coracoid; **D**, dentary; **gcor**, glenoid facet of the coracoid; **Fe**, femur; **Fr**, frontal; **Hu**, humerus; **inf**, incisive foramen; **J**, jugal; **Mx**, maxilla; **N**, nasal; **or**, orbit; **Pal**, palatine; **pcf**, paracanine fossa; **pop**, paroccipital process; **Prf**, prefrontal; **ptp**, pterygoid process; **r**, rib; **so**, suborbital process; **Sq**, squamosal; **te**, temporal opening; **ub**, unidentified bone; **v**, vertebrae. Numbers indicate first and last postcanine alveoli. Light grey is broken bone (reconstructed with plaster), dark grey is matrix, and dashed lines are inferred sutures. Scale bar equals 5 cm.

PROBAINOGNATHIA Hopson, 1990
 CHINIQUODONTIDAE Huene, 1936
CHINIQUODON Huene, 1936

Diagnosis—Probainognathian cynodont showing a single autapomorphy, pterygoid flanges greatly elongated, ending in a thin projection, directed posteroventrally, and the following combination of characters: overall cranial morphology similar

to that of *Thrinaxodon*, but with a more robust zygomatic arch, which is also conspicuously more flared laterally; characteristic suborbital angulation (approximately 110° or more) between the ventral edge of the maxillary zygomatic process and the anteroventral margin of the jugal (also known in large galesaurid cynodonts); long secondary osseous palate usually extending posteriorly to the end of the postcanine series (also known in *Aleodon*, *Probainognathus*, *Tritheledontia*, and *Mammaliaformes*); posterior sectorial postcanine teeth with strongly posteriorly curved main cusp, lacking cingula or with tiny lingual cingular cusps (postcanines with a similar morphology are the posterior sectorials of the gomphodont *Diademodon*) (modified from Abdala and Giannini, 2002).

Type Species—*Chiniquodon theotonicus* Huene, 1936.

Included Species—*C. theotonicus*, *C. sanjuanensis*.

Age and Distribution—Chañares and Ischigualasto formations, Argentina; Santa Maria Formation, Brazil; upper Omingonde Formation, Namibia. Early Ladinian–early Carnian (Abdala et al., 2001; Rogers et al., 2001, but see Lucas, 1998).

CHINIQUODON sp.
 (Figs. 7, 8)

Referred Material—GSN OM-3, a skull with articulated mandible and unprepared postcranial remains.

Description—The basal skull length is approximately 19.1 cm, but the skull is deformed and has a notably shortened the left side with respect to the right side (see arrows in Fig. 7A). The right orbit and temporal region are covered by remains of the hind limb. Although the condition of the bone is fairly good, deformation of the material and exposure to pre-fossilization weathering has resulted in numerous cracks and bone loss. In dorsal view it is possible to recognize a small fragment anteriorly, where the tips of the ascending processes of the premaxillae lie between the anterior tips of the nasals (Fig. 7A). Most of the anterior parts of both nasals are missing and only the middle and posterior portions remain. Only the sutures between the maxilla and the nasal, the maxilla and the lacrimal, and the lacrimal and the prefrontal are discernible on the snout (Fig. 7A, C). The lacrimal has a large protuberance anterior to the orbit. On the left side it is possible to see the suture between the prefrontal and the postorbital, with the anterior margin of the latter bone placed above the posterior margin of the prefrontal. The portion of the frontal forming the interorbital region is notably depressed with respect to the postorbital, a condition that has probably been accentuated by the deformation of the skull. In addition, the sagittal crest appears remarkably high in relation to the interorbital region, but this is also likely the result of deformation. It should be mentioned, however, that a similar raised sagittal crest was also described in chiniquodontids from Brazil (see Romer, 1969a: figs. 3, 7). There is no evidence of a pineal foramen. In ventral view, the anterior portion of the long osseous palate is obscured by the attached lower jaw. The palate extends until the level of the last upper postcanine and shows a large contribution by the palatines, whereas the pterygoid processes are well developed and end in a very long and thin projection (Fig. 7B). In right lateral view (Fig. 7C) the zygomatic arch is practically complete and the suture between the jugal and the squamosal along the zygoma is similar to the condition observed in some specimens of *Chiniquodon* from the Chañares Formation (see in Abdala and Giannini, 2002:fig. 5A). Although the ventral margin of the anterior portion of the zygomatic arch is not completely preserved, it is clear that there was an angulation present between the posterior margin of the maxilla and the anterior margin of the jugal (see dashed lines in Fig. 7C). The lower jaw exhibits a fused symphysis and the ventral margin of the dentary is slightly convex back to the angle of the dentary. The posterior margin of the dentary (i.e., from the angle to the

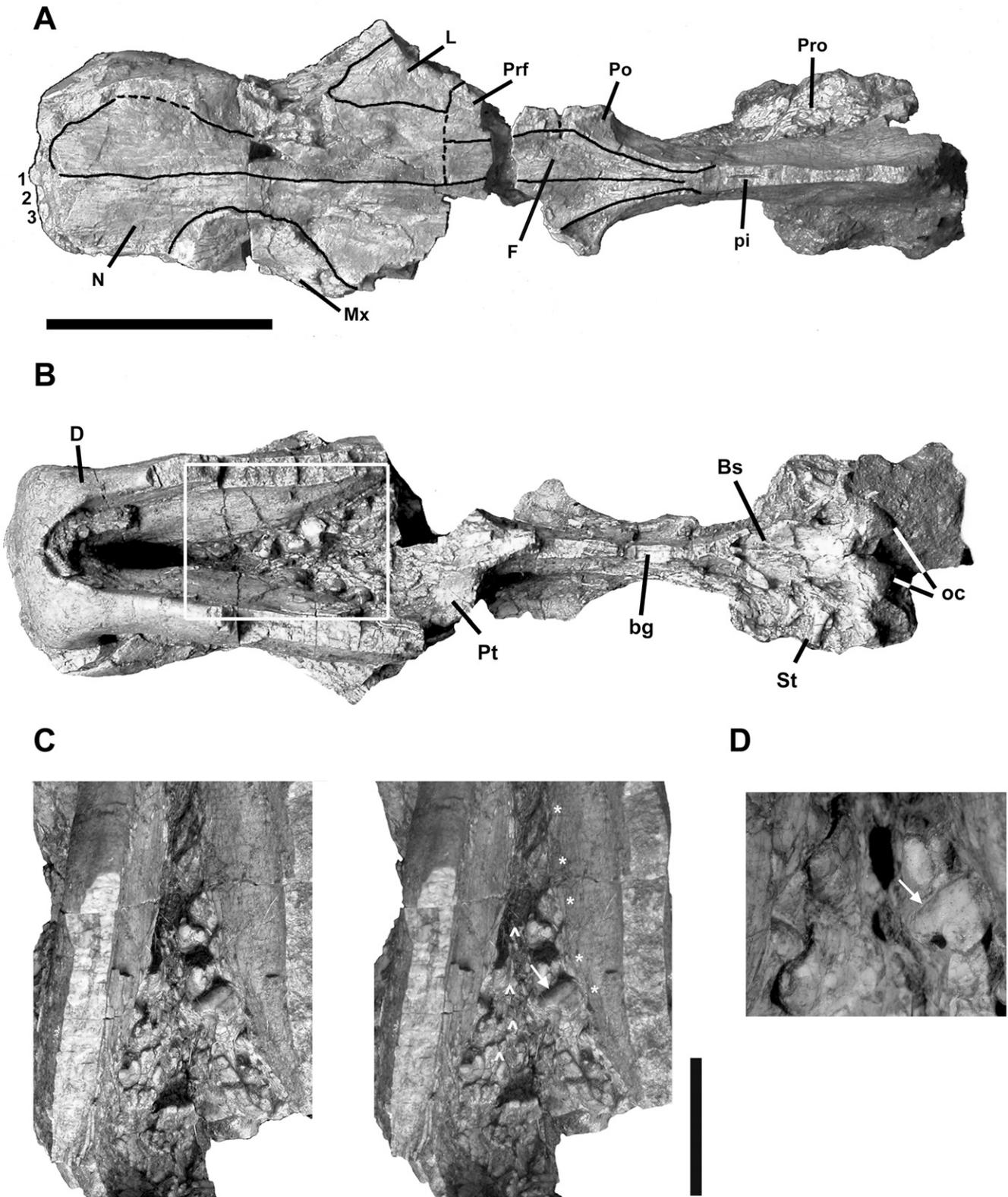


FIGURE 5. Traversodontidae, gen. et sp. indet., GSN OM-5. **A**, dorsal view; **B**, ventral view. White rectangle is the palatal portion of the skull presented as stereopair in **C**. **D**, detail of the lingual margin of a lower postcanine, indicated by an arrow in **C**. **Abbreviations:** **bg**, basicranial girder; **Bs**, basisphenoid; **D**, dentary; **F**, frontal; **L**, lacrimal; **Mx**, maxilla; **N**, nasal; **oc**, occipital condyles; **pi**, pineal foramen; **Po**, postorbital; **Prf**, prefrontal; **Pro**, prootic; **Pt**, pterygoid; **St**, stapes. Numbers in **A** indicate lower incisors. Asterisks (*) and chevrons (^) in **C** indicate lower and upper postcanines, respectively. Scale bars equal 5 cm (**A**, **B**) and 2 cm (**C**).

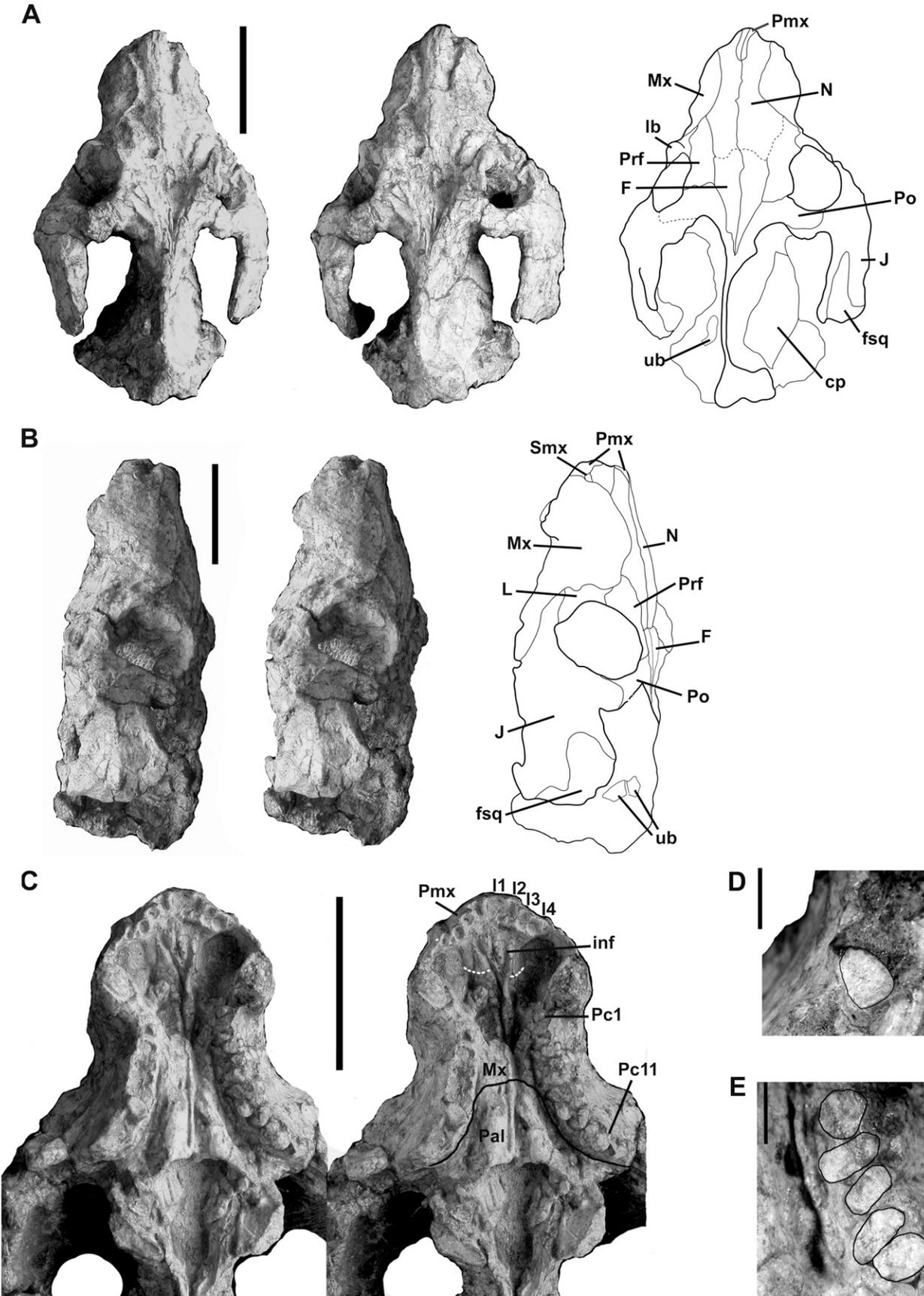


TABLE 2. Measurements of the skull of *Aleodon* (in cm).

Measurement	EN-3
Basal skull length	15.6
Snout length	6.7
Orbital length	3.1
Temporal length	7.1
Palate length	6.9
Transverse process width	4.5
Upper postcanine series length	4.3
Maximum height of the zygoma	3.6
Interorbital distance	4.3
Maximum skull width	11.0e

Abbreviation: e, estimate.

posterior portion of the lower jaw) is notably concave and similar to the condition present in *Chiniquodon* (see Romer 1969b:fig. 6). On the right side it is possible to observe the coronoid process with its dorsal tip directed somewhat posteriorly. The postdentary bar is partially preserved on both sides, with the lateral projection of the surangular contacting the squamosal posteriorly. A prominent lateral ridge is observed on the dentary, which corresponds medially to the trough for the postdentary bones.

There are four conical upper incisors, which lack serrations. They are succeeded by a short diastema that is bounded posteriorly by a large canine. The number of upper postcanines is not clear; on the left side there seem to be eight, plus the last tooth in eruption, whereas on the right side there seem to be seven. Most of the postcanines are poorly preserved, but the two posterior left teeth show a recurved main cusp (Fig. 8A), followed by a small posterior accessory cusp. In the erupting tooth it is possible to observe that the postcanines are clearly sectorial, lacking cingular cusps on the lingual side (Fig. 8B).

DISCUSSION

The upper Omingonde Formation contains the only terrestrial Triassic fauna known from Namibia, and it shows clear faunal affinities with the *Cynognathus* Assemblage Zone of South Africa (Keyser, 1973a; Holzförster et al., 1999; Catuneanu et al., 2005; Abdala et al., 2005). The first records of cynodonts from the Namibian deposits were reported by Keyser (1973a, 1973b) and included four taxa, *Cynognathus*, *Diademodon*, *Trirachodon*, and *Titanogomphodon*. The first three taxa are known from the Burgersdorp Formation in the South African Karoo. *Cynognathus* is also known from the Puesto Viejo Formation in Argentina (Bonaparte, 1969a) and the upper Fremouw Formation in Antarctica (Hammer, 1995). *Diademodon* is also recorded from the lower Ntawere Formation in Zambia, the Manda beds in Tanzania and more recently from Argentina (Brink, 1963; Crompton, 1955; Martinelli et al., 2008). *Trirachodontids* are known from the Manda Formation (i.e., *Cricodon*; Crompton, 1955), the Yerapalli Formation of India (Bandyopadhyay and Sengupta, 2006) and the upper Ermaying Formation of China (i.e., *Sinognathus*; Sun, 1988). A lower jaw with teeth from the Donguz Gorizont of Russia was also assigned to *Trirachodontidae* (i.e., *Neotrirachodon expectatus*; Tatarinov, 2002); the postcanines of this specimen, however, are similar to those of bauriid therocephalians (Battail and Surkov, 2000; F. Abdala, pers. obs.). Thus, *Trirachodontidae* and *Traversodontidae* (see below) represent the only

Anisian commonality in the cynodont records from Laurasia and Gondwana. *Titanogomphodon* is a large diademodontid known only from the Namibian fauna (Keyser, 1973a, 1973b) and reported, with doubt, from Antarctica (Hammer, 1995).

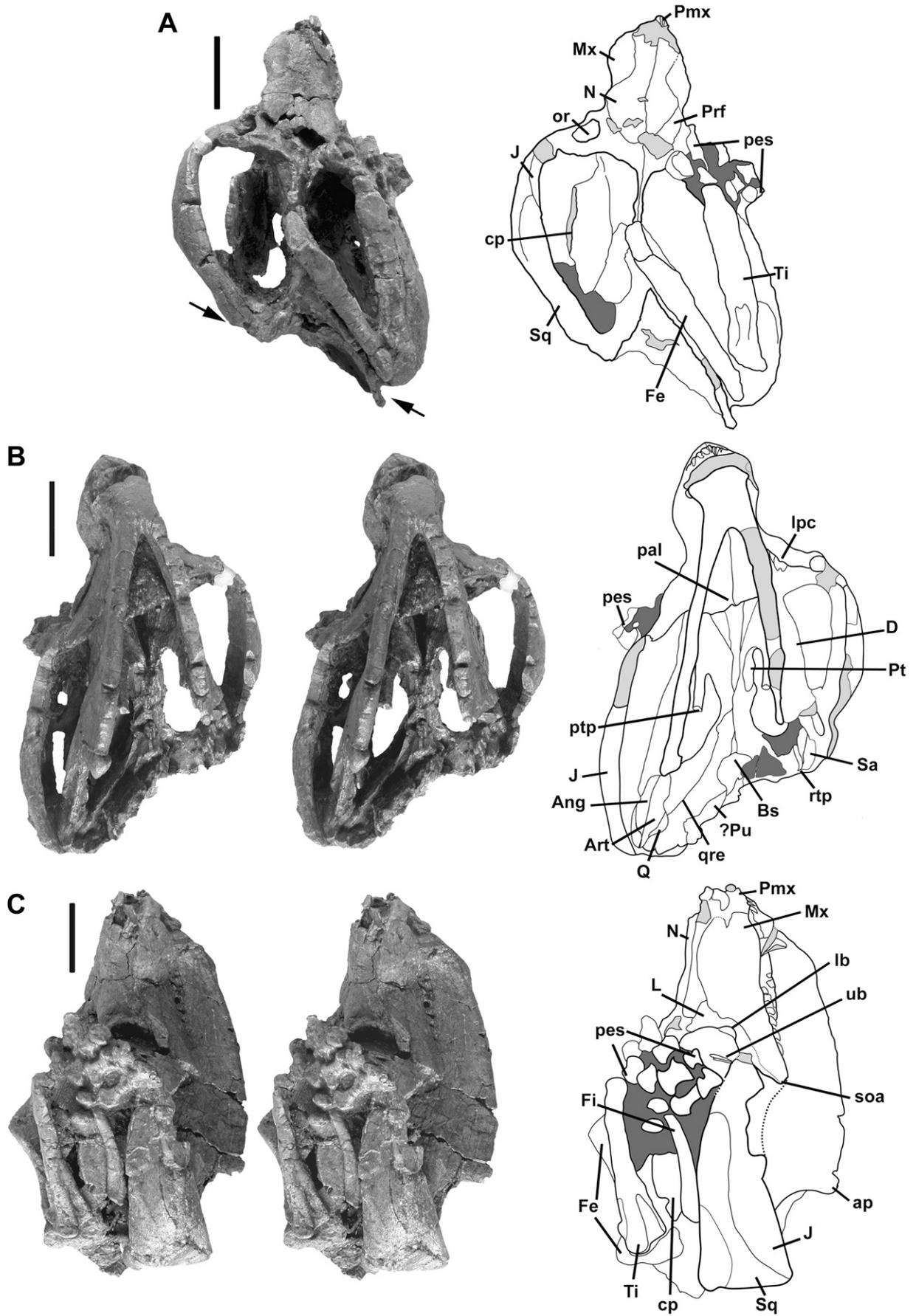
The new records of *Luangwa*, *Aleodon*, *Chiniquodon*, and an undetermined traversodontid double the diversity of cynodonts in the Namibian Middle Triassic, which can now be recognized as preserving the most diverse cynodont fauna from the Gondwanan Middle Triassic. *Luangwa* is a traversodontid cynodont that exhibits a short snout and relatively enlarged orbit that is almost as large as the temporal opening (Brink, 1963; Abdala and Teixeira, 2004; Fig. 9). These particular cranial features are observed in specimens GSM RK-4b and RK-4c. The skull GSM RK-4b is poorly preserved and partially prepared but features of the lower jaw, especially the similarity of the last lower postcanine with that of OUMNH TSK 121, allow assignment to this taxon. The dorso-ventrally distorted partial snout GSM OM-2 is included in *Luangwa* because of the correspondence in size of the snout and number of postcanines with GSM RK-4 (Table 1). In addition, the upper postcanines do not show abrupt changes in size between the teeth, and the crowns are oval-to-ellipsoid in cross section, the last feature being typical of basal *Traversodontidae* (including *Luangwa*, see Abdala et al., 2006). CGP 572 is the largest representative known for this taxon, and suggests that remaining individuals assigned to the same were juveniles. The major difference between its skull and others of *Luangwa* (including the holotype of *Luangwa drysdalli*) is the more extended temporal length (Fig. 9).

GSN OM-5 is assignable to the *Traversodontidae*. Unfortunately, information on the postcanines that would provide a more precise identification for this specimen is only partially accessible. The morphology of the lingual margin of the lower postcanine indicates the presence of an anterior cusp forming a crest followed by a deep basin. In the upper postcanines, the main lingual cusp is located in the posterior portion of the crown with the occlusal basin anterior to it. The absence of any cingular cusps in the medial margins of upper and lower postcanines precludes a *trirachodontid* identity for this specimen (Hopson, 2005). GSN OM-5 is slightly smaller than CGP 572 but it has a remarkably longer and thinner basicranial girder, suggesting that GSN OM-5 is not representative of *Luangwa*.

GSN EN-3 shows a series of features that are known only in the probainognathian *Aleodon*, including the general morphology of the snout, the long osseous palate extending posteriorly to the end of the tooth row, and the buccolingually expanded (ovoid to ellipsoid) outline of the upper postcanines. In addition, the skull size of the specimen (Table 2) approximates the 14.5 cm estimated for the holotype (UMCZ T.906) of *Aleodon brachyrhamphus* (Crompton, 1955). The morphology of the snout of GSN-EN-3 is very similar to the referred specimen BMNH 9390 (Abdala and Giannini, 2002). The general morphology of this taxon is not well known and GSN EN-3, although poorly preserved, offers evidence of cranial regions previously unknown, such as the zygomatic arch. The only feature that contrasts GSN EN-3 with UMCZ T.906 is the presence of a pineal foramen in the latter specimen (Crompton, 1955). After recent examination of the latter specimen, the senior author could not confirm the presence of the pineal foramen.

GSN OM-3 displays a long secondary palate, sectorial postcanine teeth with the main cusp curved posteriorly, long and thin

← FIGURE 6. *Aleodon*, GSN EN-3. **A**, stereopair and interpretative drawing in dorsal view; **B**, stereopair and interpretative drawing in left lateral view; **C**, stereopair palatal view. **D**, detail of the only right postcanine preserved in dorsal view; **E**, detail of the last five left postcanines in dorsal view. Numbers indicate first and last postcanine and incisor teeth. **Abbreviations:** cp, coronoid process; F, frontal; fsq, facet on the jugal for the squamosal; I, incisor; inf, incisive foramina; J, jugal; L, lacrimal; lb, lacrimal boss; Mx, maxilla; N, nasal; Pal, palatine; Pc, postcanine; Pmx, premaxilla; Prf, prefrontal; Po, postorbital; Smx, septomaxilla; ub, unidentified bone. Dashed lines indicate interpreted sutures. Outline of the postcanine crowns are highlighted in D and E. Scale bars equal 5 cm (A–C) and 7 mm (D, E).



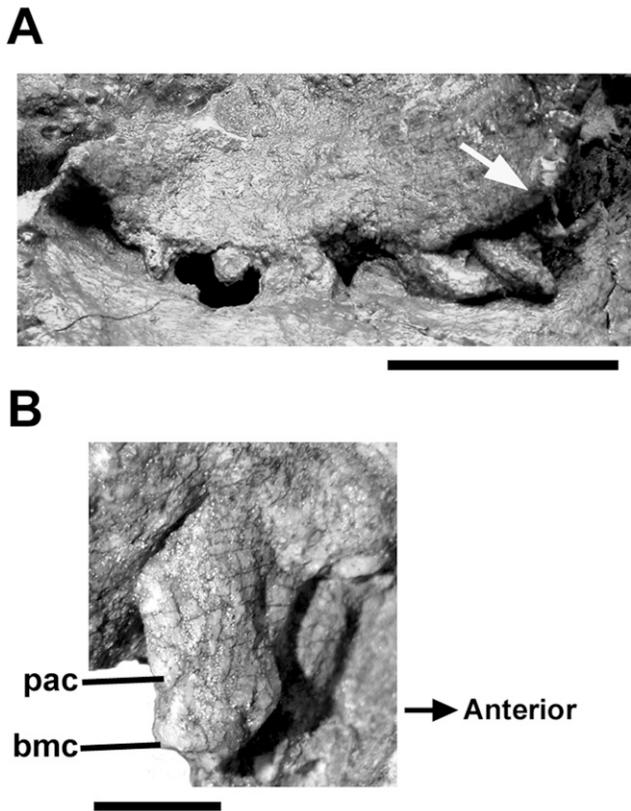


FIGURE 8. *Chiniquodon*, GSN OM-3. **A**, lateral view of the left postcanine series. Arrow indicates position of the last upper postcanine. **B**, detail of the last left upper postcanine in medial view. **Abbreviations:** **bmc**, broken main cusp; **pac**, posterior accessory cusp. Scale bars equal 2 cm (A), and 5 mm (B).

pterygoid processes, and the zygoma, although incompletely preserved, shows evidence of a suborbital angulation between the maxilla and jugal. This particular combination of features is known only in *Chiniquodon* (Abdala and Giannini, 2002).

Prior to these discoveries, *Luangwa* was known from the upper Ntawere Formation in Zambia (Brink, 1963; Kemp, 1980) and, more recently, from the Brazilian Santa Maria Formation (Abdala and Teixeira, 2004); *Aleodon* was restricted to the Manda Formation in Tanzania (Crompton, 1955); and *Chiniquodon* was known from the Middle Triassic Santa Maria Formation of Brazil and from the Middle Triassic Chañares and Upper Triassic Ischigualasto formations of Argentina (Abdala and Giannini, 2002). These new records of Namibian fossils position the upper Omingonde Formation as a biostratigraphic link between Middle Triassic faunas from Antarctica, Argentina, Brazil, South Africa, Tanzania, and Zambia (Fig. 10A, B). The record of *Chiniquodon* in the Omingonde fauna represents the

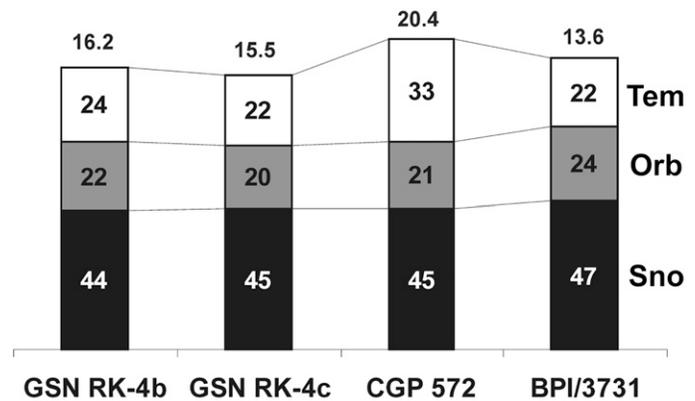


FIGURE 9. Percentage proportion of skull regions in specimens of *Luangwa*. Length of each region is considered in relation to the basal skull length (indicated in cm on the top of each bar). The proportions of GSN RK-4c are approximated because the specimen does not preserve the tip of the snout. **Abbreviations:** **Orb**, orbital length; **Sno**, snout length; **Tem**, temporal length.

fourth evidence of genus-level commonality between cynodonts from South America and Africa. Furthermore, the other three taxa shared between these continents, *Cynognathus* (Bonaparte, 1969a), *Luangwa* (Abdala and Teixeira, 2004) and *Diademodon* (Martinelli et al., 2008), are also known in the Namibian fauna.

Vertebrate Faunas from the Upper Omingonde Formation

It is interesting to note that records of all new cynodonts from the upper Omingonde Formation are located in the highest levels of the unit (Fig. 11). Besides the cynodonts, there are also recorded in these levels a dicynodont tibia and the skeleton of an archosauriform assigned to *Erythrosuchus* (Pickford, 1995). The character of the cynodont records of these levels is remarkably different from that of the *Cynognathus* Assemblage Zone of South Africa, not only by the presence of *Aleodon*, *Chiniquodon*, and traversodontids, but by the lack of *Cynognathus* and *Diademodon*, common representatives of the South African fauna. Interestingly, these taxa are represented in middle and lower levels of the upper Omingonde Formation (Fig. 11). Possible explanations for these faunal differences can be ecological or temporal. The depositional environment and climatic conditions where these faunal clusters are found do not seem to be so remarkably different (Fig. 11) as to produce such a notable contrast in the cynodonts represented in the faunas. The temporal alternative is that at least two different ages are represented in the upper Omingonde Formation, the older one including *Diademodon* and *Cynognathus* and perhaps correlative of Subzone B of the *Cynognathus* Assemblage Zone (AZ) (Hancox, 2000). The putative younger fauna can be correlated with the Manda Formation and the upper Ntawere Formation in East Africa, as well as perhaps part of the Santa Maria Formation in southern Brazil. Also, Subzone C of the *Cynognathus* AZ could be part of this younger faunal association (see Abdala et al., 2005 and

← FIGURE 7. *Chiniquodon*, GSN OM-3. **A**, photo and interpretative drawing in dorsal view. Arrows indicate posterior margin of the skull on both sides to highlight deformation. **B**, stereopair and interpretative drawing in ventral view; **C**, stereopair and interpretative drawing in right lateral view. **Abbreviations:** **Ang**, angular; **ap**, angular process; **Art**, articular; **Bs**, basisphenoid; **cp**, coronoid process; **D**, dentary; **Fe**, femur; **Fi**, fibula; **J**, jugal; **L**, lacrimal; **lb**, lacrimal boss; **lpc**, last upper postcanine; **Mx**, maxilla; **N**, nasal; **or**, orbit; **pal**, secondary osseous palate; **Pmx**, premaxilla; **Prf**, prefrontal; **Pt**, pterygoid; **ptp**, pterygoid process; **Pu**, pubis; **Q**, quadrate; **gre**, quadrate ramus of the epipterygoid; **rtp**, retroarticular process; **Sa**, surangular; **soa**, suborbital angulation; **Sq**, squamosal; **Ti**, tibia; **ub**, unidentified bone. Light grey is broken bone, dark grey is matrix, and dashed lines are broken bone and inferred sutures. Scale bars equal 5 cm.

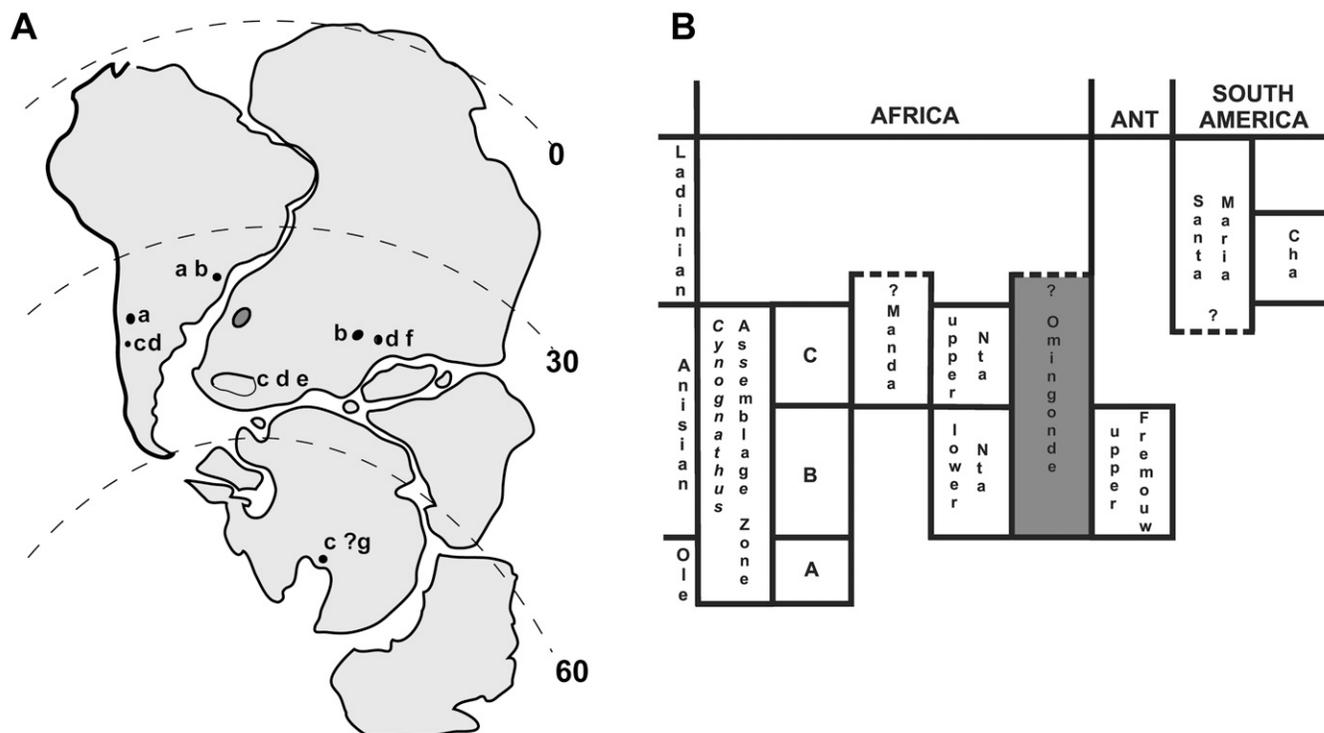


FIGURE 10. **A**, paleoposition of Gondwanan continents during the Early-Middle Triassic and shared cynodonts between the upper Omingonde fauna (in dark grey) and others Gondwanan faunas from South Africa, East Africa, South America, and Antarctica. Paleomap modified after Smith and Swart (2002); **B**, stratigraphic chart showing the temporal range of the different Gondwanan faunas discussed in the text. **Abbreviations:** **a**, *Chiniquodon*; **ANT**, Antarctica; **b**, *Luangwa*; **c**, *Cynognathus*; **Cha**, Chañares; **d**, *Diademodon*; **e**, *Trirachodon*; **f**, *Aleodon*; **g**, ?*Titanogomphodon*; **Nta**, Ntawere; **Ole**, Olenekian. A, B, and C refers to subzones of the *Cynognathus* Assemblage Zone.

discussion below), but the fauna does not display any of the cynodont groups recorded in the higher levels of the upper Omingonde Formation. The presence of *Erythrosuchus*, known from Subzone B of the *Cynognathus* AZ, in this upper cluster of the upper Omingonde fauna seems to contradict the younger age proposed for this cluster of the Namibian fauna. However, we should mention that some features observed in the archosauriform from the Omingonde fauna, such as the morphology of the cervical ribs and of the osteoderms from the sacral region, are similar to those of the raiusuchid *Ticinosuchus* (Krebs, 1965, 1976; A. Arcucci, pers. comm., 2007) from the Anisian/Ladinian Grenzbitumenhorizont of Switzerland and northern Italy (Gower, 2000). Therefore the presence of a raiusuchid archosauriform instead of *Erythrosuchus* seems to be possible for the Omingonde fauna.

This new evidence from the cynodont fauna seems to consolidate a late Anisian age for the later fauna of the upper Omingonde Formation (Keyser, 1973a, 1973b; Smith and Swart, 2002). Finally, the record of *Chiniquodon* in Namibia, apart from representing an expansion of the known geographic range of this taxon, has two possible interpretations: (1) a temporal extension of this Ladinian-Carnian genus (Romer, 1969a, 1969b; Martinez and Forster, 1996; Abdala and Giannini, 2002) to the late Anisian, thereby representing one of the longest-lived cynodont known (more than 9 Ma), or (2) an indication of a younger age for part of the Namibian fauna, which can thus be extended into the earliest Ladinian. In the latter case, the uppermost fauna of the upper Omingonde Formation would not only have been geographically closest to South America during the Middle Triassic, but also would have been the African continental vertebrate fauna closest in age to the Middle Triassic (Ladinian)

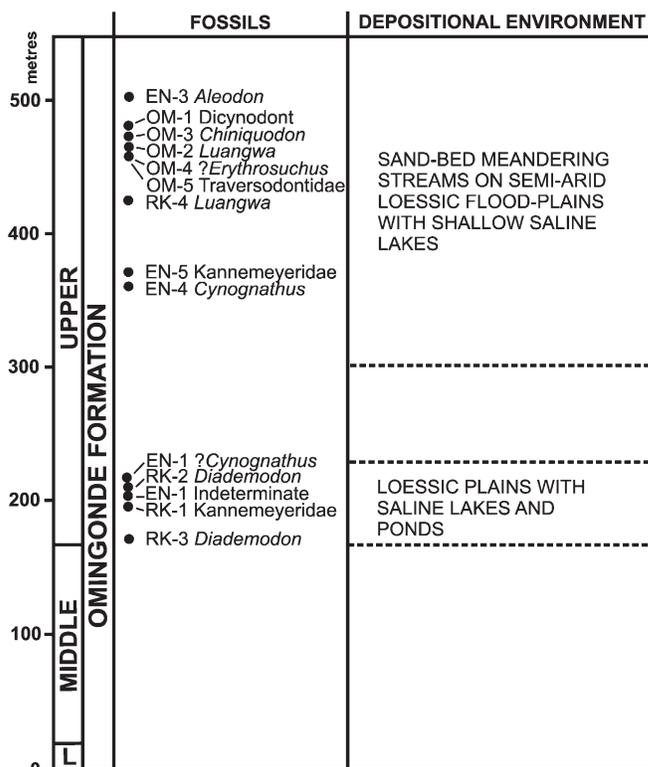


FIGURE 11. Fossils and environment of the upper Omingonde Formation (modified after Smith and Swart, 2002). **Abbreviation:** **L**, lower.

faunas from the Ischigualasto Basin in Argentina and the Paraná Basin in Brazil.

As presented by Keyser (1973a), the cynodont *Titanogomphodon* and the bauriid therocephalian *Herpetogale* were found in the upper levels of the Omingonde Formation (above the third sandstone level) and are therefore the youngest faunal representatives found by him. The discovery of *Herpetogale* high up in the Omingonde Formation is confirmed in Keyser and Brink (1977–78) who mention that it was discovered near the contact with the Etjo Formation. If these forms were contemporaneous with the upper faunal cluster of Smith and Swart (2002) (Fig. 11), then *Herpetogale* would represent the youngest record of therocephalians in Gondwana (Keyser, 1978).

Paleobiogeography of Anisian Gondwanan Traversodontids

Traversodontidae is one of the most diverse families of non-mammaliaform cynodonts, the first records of which are already widespread in Gondwanan Middle Triassic (Anisian) faunas of Tanzania, Manda, Namibia, Argentina, and, possibly, Brazil (Abdala and Ribeiro, 2003; Abdala and Teixeira, 2004). Approximately seven to eight taxa were represented in Anisian times in Gondwana: four species currently assigned to *Scalenodon* in the Manda Formation, Tanzania (some of these taxa should be allocated to different genera, and others may prove to be invalid; Hopson and Kitching, 2001; Abdala and Ribeiro, 2003); *Luangwa* in the upper Ntawere Formation, Zambia, the upper Omingonde Formation, Namibia, and the Santa Maria Formation, Brazil (Abdala and Teixeira, 2004); and, from Argentina, *Pascualgnathus* in the Puesto Viejo Formation (Bonaparte, 1966) and *Andescynodon* and *Rusconiodon* in the Cerro de las Cabras Formation (Bonaparte, 1969b; Goñi and Goin, 1988; Goñi and Abdala, 1989). These faunas are paleolatitudinally restricted to land areas between 35° and 45° south, corresponding to regions of arid or semi-arid climate but adjoining areas of warm, temperate climate (Scotese, 2000; Spalletti et al., 2003; Sellwood and Valdes, 2006). Traversodontids are known from two isolated upper postcanines from the ?Upper Anisian-Ladinian of Russia (Tatarinov, 1973; Battail and Surkov, 2000; Shishkin et al., 2000) and have recently been recorded, also on the basis of an isolated lower postcanine, from the Ladinian of Germany (Hopson and Sues, 2006), but they are unknown in other Middle Triassic faunas of Laurasia (e.g., in China), as well as in Antarctica, India and, surprisingly, the Karoo Basin of South Africa. Considering the proposed correlation of terrestrial Middle Triassic faunas from Gondwana, traversodontids are expected to be present in, at least, Subzone C of the *Cynognathus* AZ. This subzone outcrops only in the Bamboeshoek Valley of the Karoo Basin (Hancox, 1998; Abdala et al., 2005), being comparatively more restricted than the typical Subzone B (that provides most of the known fossils of the *Cynognathus* AZ) and the basal Subzone A. In addition, the fauna recorded in Subzone C is depauperate, and this can perhaps explain the lack of record of traversodontids. The paleolatitudinal position of this part of Gondwana may account for the absence of this particular group. The faunas from the *Cynognathus* Assemblage Zone of South Africa, lying approximately at 55° S, and the even more austral upper Fremouw Formation from Antarctica, are the most southerly Middle Triassic faunas that contain cynodonts (Fig. 10A), and, in both cases, traversodontids are absent. It is possible therefore that the earliest representatives of this family were less tolerant of climatic conditions in higher latitudes than other cynodonts.

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