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The first biarmosuchian from the upper Madumabisa Mudstone Formation (Luangwa Basin) of Zambia

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This contribution reports the first occurrence of a biarmosuchian therapsid from the upper Madumabisa Mudstone Formation of the Luangwa Basin of northeastern Zambia. Although incomplete, the fossil preserves diagnostic features of post-*Biarmosuchus* biarmosuchians, such as the presence of a prearietal bone and parasagittal ridges on the basicranial rami of the pterygoids, that allow its unambiguous referral to this group. Based primarily on the record of dicynodonts, the upper Madumabisa Mudstone assemblage can be correlated with the *Cistecephalus* Assemblage Zone of South Africa. During this interval, the tetrapod faunas of the Karoo and Luangwa basins were remarkably similar and likely characterized by frequent biotic interchange.

Keywords: Biarmosuchia, *Cistecephalus* Assemblage Zone, Madumabisa Mudstone Formation, Luangwa Basin, Zambia.

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INTRODUCTION

Boonstra (1938) described the first Permian tetrapods from the Luangwa Valley based on a collection of fossils resulting from fieldwork undertaken by Dixey in 1928 and 1935 (Dixey 1937). Three expeditions in the early 1960s added greatly to the palaeontological information available and suggested that at least two Permian biozones were represented in the upper member of the Madumabisa Mudstone, namely the *Endothiodon* and *Cistecephalus* zones (Drysdall & Kitching 1962, 1963; Kitching 1963; Attridge *et al*. 1964). Rocks of *Tapinocephalus* zone-equivalent age were hypothesized to occur in the lower Madumabisa Mudstone, but confirming fossils were not recovered (Kitching 1963; Utting 1978; but see Sidor *et al*. 2014 regarding pertinent fossils from the Mid-Zambezi Basin).

A decade later, Kemp (1975) collected Upper Permian vertebrates from the Madumabisa Mudstone in the mid-Luangwa Valley, about 230 kilometres southwest of the region of the initial work (Fig. 1). These fossils were typically much better preserved, lacking the red hematite-like coating common among northern Luangwa specimens (Davies 1981), and led to a body of important anatomical work (e.g. Kemp 1979, 1980; King 1981). Notably, King & Jenkins (1997) identified a partial dicynodont skull as pertaining to *Lystrosaurus*, suggesting that it was a Permian representative of the predominantly Triassic taxon and that the upper Madumabisa Mudstone likely contained rocks of latest Permian age. This specimen was subsequently re-identified as a lystrosaurid, but not pertaining to *Lystrosaurus* itself (Angielczyk *et al*. 2014)

A new fieldwork effort was initiated in 2009 with collaborators from the University of Washington, Field Museum of Natural History, Museum National d'Histoire Naturelle, Iziko South African Museum and the National Heritage Conservation Commission (Peecook *et al*. 2013; Sidor *et al*. 2013, 2014; Angielczyk *et al*. 2014). This work has helped to clarify that the northern and mid-Luangwa rocks of the Madumabisa Mudstone Formation preserve essentially the same tetrapod fauna, despite markedly different styles of preservation, and that the upper Madumabisa vertebrate assemblage is most likely *Cistecephalus* Assemblage Zone-equivalent in age (Angielczyk *et al*. 2014). In addition, Sidor *et al*. (2013) showed that *Cistecephalus* zone-equivalent strata in Malawi, South Africa, Tanzania, and Zambia all preserve a broadly distributed fauna that was relatively homogenous in composition and dominated by dicynodonts (particularly *Oudenodon*), pareiasaurs (*Pareiasuchus*), and medium-sized gorgonopsids. Until now, biarmosuchian therapsids were recorded from each of the basins, save Zambia (Rubidge & Sidor 2002; Jacobs *et al*. 2005; Sidor *et al*. 2010).

The fossil described herein was illegally collected from North Luangwa National Park sometime in 2009 or 2010 and then exported to the United States, where it was ultimately turned over to the author for repatriation. What is preserved of the specimen does not warrant the recognition of a new species or permit unambiguous referral to a previously known species. However, recording the presence and anatomy of this biarmosuchian will contribute to recent efforts to characterize the evolutionary history of this rare and enigmatic group of therapsids (Hopson & Barghusen 1986; Sigogneau-Russell 1989; Rubidge & Sidor 2001; Sidor & Rubidge 2006; Kammerer *et al*. 2013).

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Figure 1. Geographic distribution of vertebrate fossil localities in Zambia. Circles near (**A**) denote the northern Upper Permian localities of Drysdall & Kitching (1962, 1963) as well as Triassic localities near Sitwe (e.g. Brink 1963; Cox 1969; Chernin 1974; Peecook *et al*. 2013). Circles near (**B**) indicate Upper Permian localities of North Luangwa National Park and the adjoining Munyamadzi Game Management Area (Kemp 1975). Circle near (**C**) indicates Middle Permian localities (Sidor *et al*. 2014), which contain unreported Upper Permian fossils as well.

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Biarmosuchia Sigogneau-Russell, 1989

Biarmosuchia indet.

Referred specimen. NHCC LB181, incomplete cranium missing the occiput, the tip of the snout, and most of the right mandible.

Horizon. Upper member of the Madumabisa Mudstone Formation, Lower Karoo Group, Luangwa Basin (stratigraphic nomenclature from Banks *et al*. 1995). The associated tetrapod assemblage indicates correlation with the *Cistecephalus* Assemblage Zone (AZ) of South Africa, and therefore a Wuchiapingian age (Angielczyk *et al.* 2014; Rubidge *et al.* 2013).

Locality. Collected within 500 metres of locality L39, a new locality discovered in 2009 that is located near the southern border of North Luangwa National Park adjoining some historic localities (Kemp 1975), approximately 30 kilometres northwest of the village of Chitungulu. Detailed coordinates are available to qualified researchers from the NHCC or by contacting the author.

DESCRIPTION

General preservation

The specimen is preserved in three dimensions but is slightly deformed so that the skull roof lies to the right of the palate. It measures 111 mm in maximum length and 69 mm in maximum width. The tip of the snout is eroded and the postorbital region of the specimen is missing because a calcite vein bisects the fossil at the level of the temporal fenestrae. The skull roof is generally well preserved, but has been restored in places with a cleverly painted porous material (in the figures this material is represented by the same gray tone as matrix). Because of this restoration, the skull roof is less complete than it seems on first inspection. Except for the braincase, the palate is essentially complete and preserves the best detail, as it was unexposed prior to preparation.

Lateral view

Figure 2 shows NHCC LB181 in left lateral view, which is the more complete of the two sides. The premaxilla is entirely missing and although the anterior maxilla is weathered off, the root of the upper canine is visible. The maxilla is tall and contacts the nasal, prefrontal, lacrimal, and jugal, as is typical for early therapsids like dinocephalians, anomodonts, gorgonopsids, as well as biarmosuchians (Hopson & Barghusen 1986; Sidor 2000). The lateral surface of the snout is flat and lacks the depressions typically seen in burnetiamorph biarmosuchians near the posterior margin of the maxilla (Sidor & Smith 2007). The maxilla extends posteriorly beneath the orbit, but the jugal forms most of the suborbital bar.

The orbit appears relatively large, but this is partially due to its incomplete margin, especially in the region of the postfrontal and postorbital. As preserved, the left orbit is 41 mm in diameter, measured dorsoventrally. Small flakes of bone are suspended in matrix within the orbit and likely represent disarticulated parts of the sclerotic ring. Such bones have been preserved in several other biarmosuchian specimens, which seemingly represents a greater frequency than in other therapsid groups (e.g. Sigogneau 1970: fig. 191; Sidor & Welman 2003: fig. 2; Smith *et al.* 2006: fig. 2). The left orbit is excavated deeply enough to present the midline sphenethmoid and the underlying cultriform process of the parasphenoid. Also

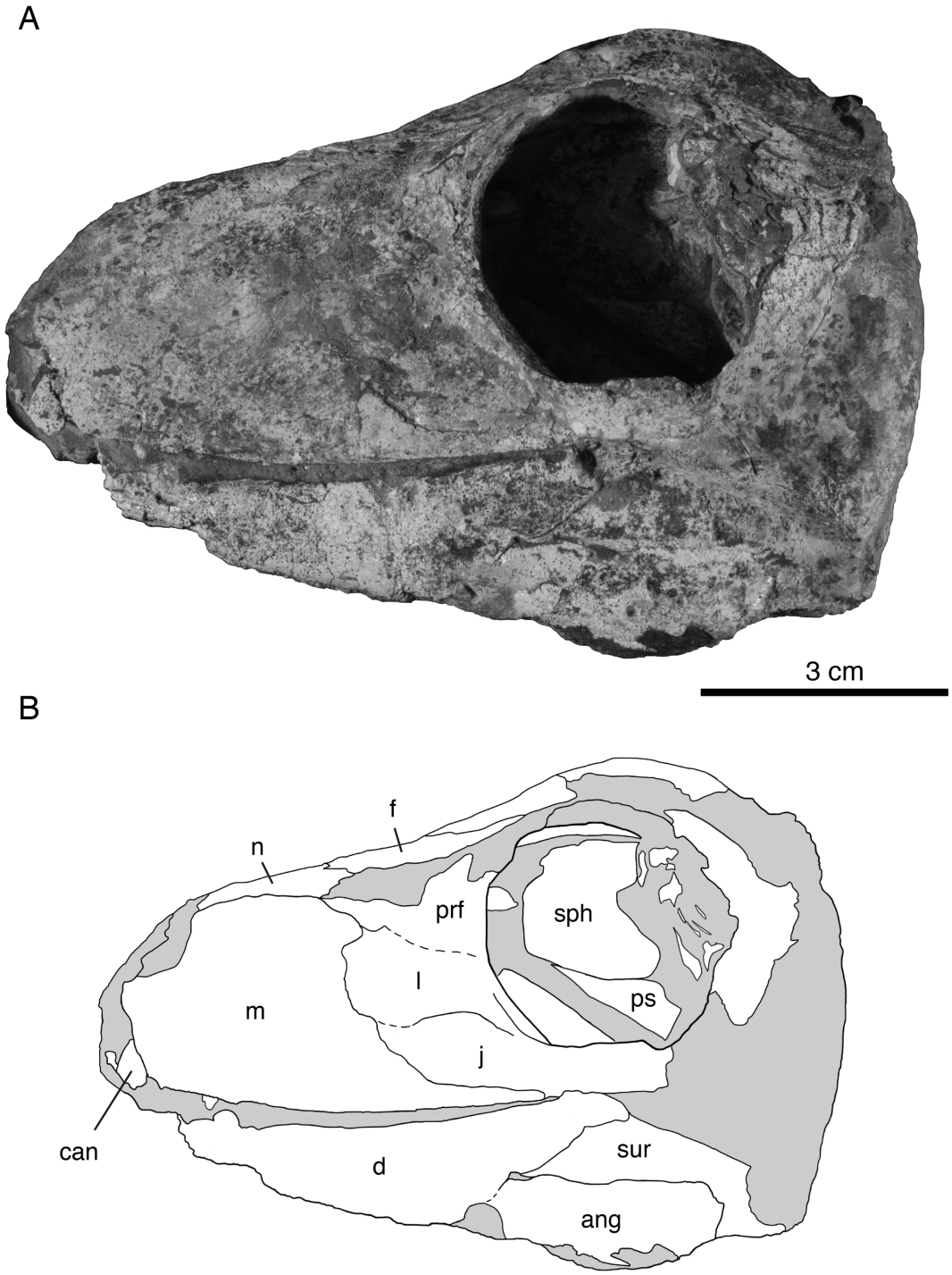


Figure 2. Biarmosuchian skull (NHCC LB181) from the upper Madumabisa Mudstone Formation of Zambia. Photograph (**A**) and line drawing (**B**) of the specimen in left lateral view. Abbreviations: ang, angular; can, canine; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; prf, prefrontal; ps, parasphenoid rostrum; sph, sphenethmoid; sur, surangular.

visible below the cultriform process is a vertical plate of bone that likely represents part of the dermal palate. The dorsal portion of the left postorbital bar is preserved, but the remainder of the margins of the temporal fenestra is missing.

The external surface of the left lower jaw is lightly weathered. The dentary forms the anterior half of the lower jaw, but the shape of its anterior extent is missing, so it is impossible to determine if an enlarged chin were present, like some other biarmosuchians (e.g. Sidor & Welman 2003: fig. 1). A horizontal contact between the surangular and angular is clearly delineated in lateral view, but the external surface of the latter element does not preserve the reflected lamina typical of therapsids and sphenacodontids (Sidor 2000; Sidor & Rubidge 2006).

Dorsal view

Despite the extensive reconstruction of the left side of the skull roof (Fig. 3), most of the typical complement of sutures for a biarmosuchian can be readily observed. However, the contribution of the frontal to the dorsal margin of the orbit and the size of the postfrontal are both difficult to determine.

Importantly, a median preparietal is clearly present.

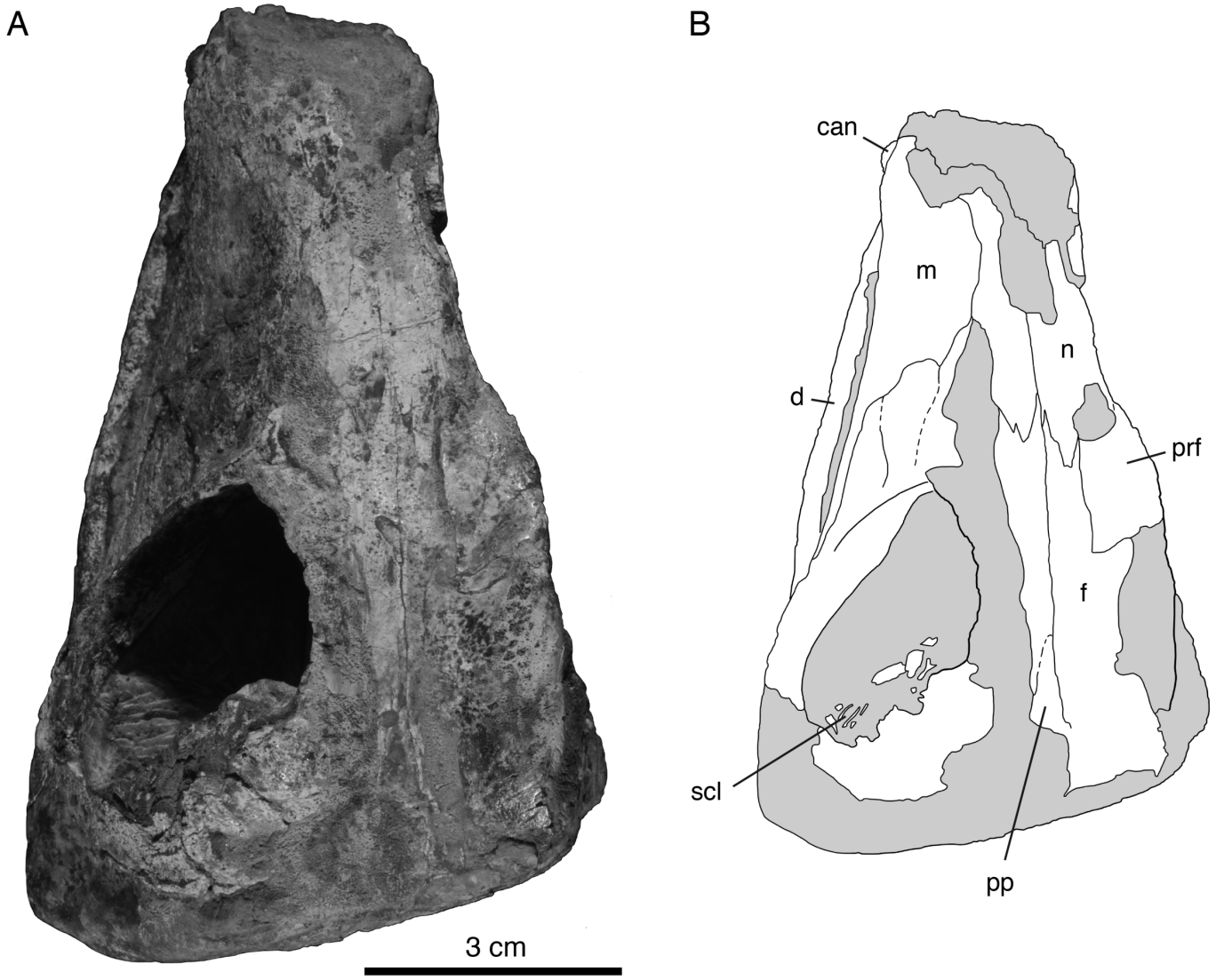


Figure 3. Biarmosuchian skull (NHCC LB181) from the upper Madumabisa Mudstone Formation of Zambia. Photograph (**A**) and line drawing (**B**) of the specimen in dorsal view. Abbreviations: can, canine; d, dentary; f, frontal; m, maxilla; n, nasal; pp, preparietal; prf, prefrontal; scl, sclerotic ring elements.

Among biarmosuchians, this ossification is absent in *Biarmosuchus*, but can be observed in *Herpetoskylax*, *Hipposaurus*, and *Pachydectes* (Sidor & Rubidge 2006; Rubidge *et al*. 2006). Because of their pachyostosis, it has been difficult to determine if most of the burnetiamorph biarmosuchians phylogenetically placed between these taxa had a preparietal (e.g. *Lemurosaurus*, *Paraburnetia*). However, its occurrence in the relatively derived form, *Pachydectes* suggests that this element was retained.

Ventral view

Figure 4 shows NHCC LB181 in palatal view. Parts of both lower jaws are present, although the right side preserves only slivers of the splenial and segments of the angular. The splenial is more complete on the left side, but its symphyseal region is weathered off. Parts of four dentary teeth are suspended in matrix on the right side and show serrations. Roots of two maxillary teeth are also preserved, but lack any meaningful morphology.

The dermal palate is nicely preserved and is formed by the median vomer and paired palatines, pterygoids, and ectopterygoids. Anteriorly, the vomer bears a median trough and thin, down-turned lateral margins, as in *Lophorhinus* and *Lemurosaurus*. The choana extends far posteriorly and the palatine would have contributed to more than one-third of its lateral margin, both of which were noted by Sidor (2003) to be therapsid synapomorphies. The palatal portion of the vomer is concave and contacts the palatines laterally and the pterygoids posteriorly.

The palatine bears a V-shaped area of small palatal teeth. Compared to other biarmosuchians, there are clearly fewer teeth in this area than in *Hipposaurus* and the V-pattern is more elongate than in *Lemurosaurus*. Further posteriorly, the pterygoid also has a small raised area with a patch of very small teeth on its palatal surface. In addition, there are two or three very small teeth present on the medial portion of the transverse flange of the pterygoid. The left transverse flange is complete and teeth are lacking from its lateral half. A tiny disarticulated tooth lies on its side, suspended in matrix on the midline between the

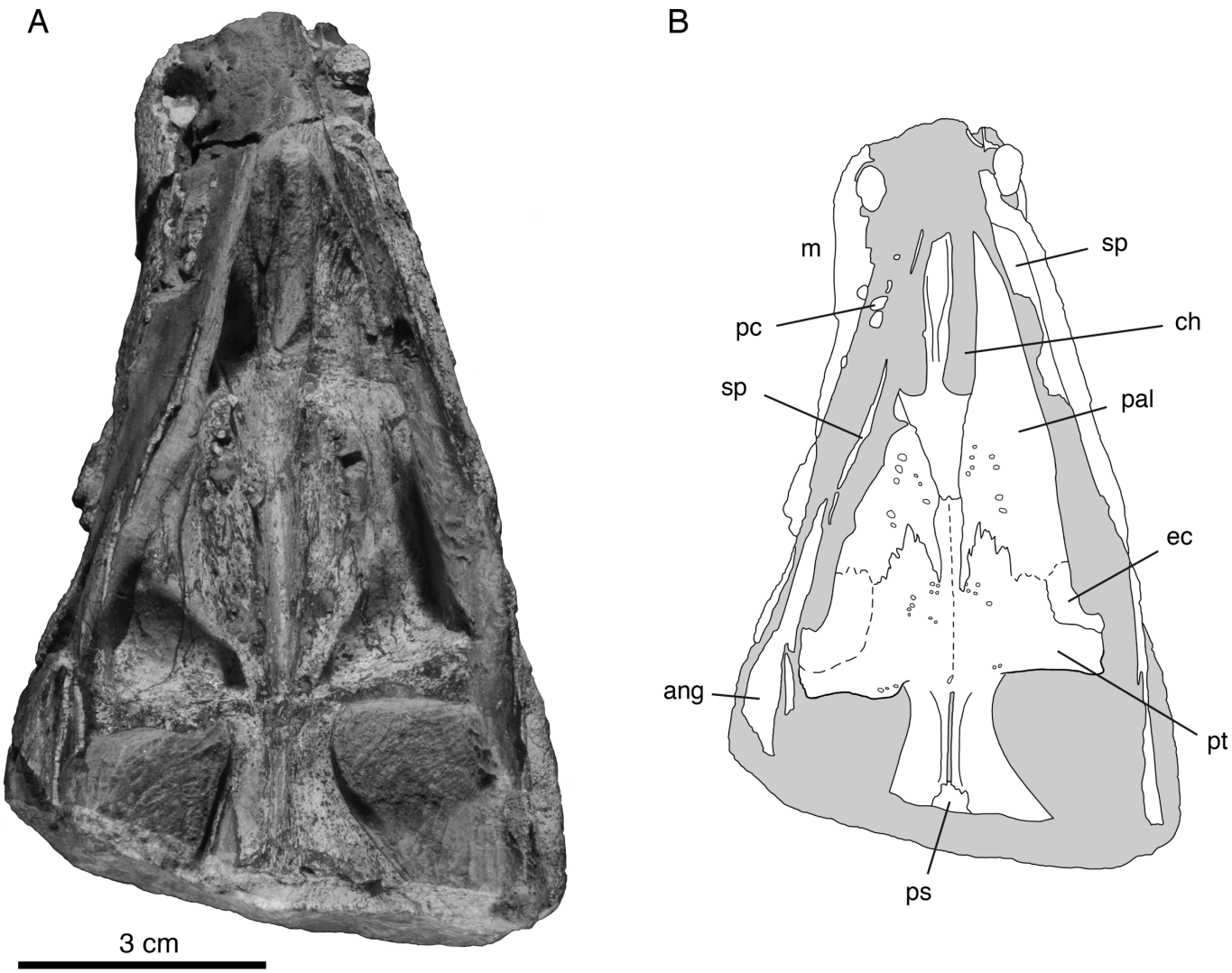


Figure 4. Biarmosuchian skull (NHCC LB181) from the upper Madumabisa Mudstone Formation of Zambia. Photograph (**A**) and line drawing (**B**) of the specimen in ventral view. Abbreviations: ang, angular; ch, choana; ec, ectopterygoid; m, maxilla; pal, palatine; pc, postcanine teeth from dentary; ps, parasphenoid (or basiparasphenoid); pt, pterygoid; sp, splenial.

transverse flanges. The shape and extent of the ectopterygoid is poorly defined, but is better understood on the left side, where is laps up against the anterior face of the transverse flange.

As in all other biarmosuchians, save *Biarmosuchus*, the medial edge of the basicranial ramus of the pterygoid bears a parasagittal ridge. Between the basicranial rami, a median furrow is formed and is filled by matrix in NHCC LB181. A very small section of the median parasphenoid is present posteriorly, nestled between the basicranial ramus of each pterygoid. Its ventral surface is flat and unkeeled.

DISCUSSION

Biarmosuchia, which includes most genera previously assigned to Ictidorhinidae (*sensu* Sigogneau 1970), has been considered a monophyletic group by most recent authors (Hopson 1991; Rubidge & Sidor 2001; Sidor & Rubidge 2006; but see Sidor 2000 and Kammerer *et al*. 2013). Of the characteristics typically used to diagnose the group, NHCC LB181 preserves relatively large orbits and the suggestion of a small temporal fenestra, based on the impression preserved on the left side of the specimen. Within Biarmosuchia, Sidor & Rubidge (2006) found that the presence of a preparietal and a parasagittal ridge on basicranial ramus of each pterygoid was characteristic of the grade they termed 'post-*Biarmosuchus* biarmosuchians.' The combination of the four aforementioned features occurs only in biarmosuchians, supporting the assignment of NHCC LB181 to this group. There are no autapomorphies or diagnostic features that allow the specimen to be referred to a previously known biarmosuchian genus. It is therefore possible that better-preserved material will show that the Zambian biarmosuchian represents a distinct species. However, dicynodonts and other therapsids from the upper Madumabisa Mudstone Formation of Zambia show remarkable fidelity to the *Cistecephalus* AZ of the Karoo (Sidor *et al*. 2013; Angielczyk *et al*. 2014), so alternatively it is possible that the Zambian biarmosuchian will turn out to be referable to *Herpetoskylax* or *Lycaenodon*.

Biarmosuchian fossils are exceedingly rare, with only 30 specimens currently known from southern Africa (Table 1). In the Karoo Basin, which is undoubtedly the

Table 1. A comprehensive tally of biarmosuchian specimens from southern Africa, organized by biostratigraphic horizon.

Institutional abbreviations: AMNH, American Museum of Natural History, New York; BP, Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg; CGS, Council for Geosciences, Pretoria; MAL, Malawi Department of Antiquities, Lilongwe; NHCC, National Heritage Conservation Commission, Lusaka; NHMUK, Natural History Museum, London; NMQR, National Museum, Bloemfontein; NMT, National Museum of Tanzania, Dar es Salaam; RC, Rubidge Collection, Graaff-Reinet; SAM, Iziko South African Museum.

Taxon	Specimen	Basin	Publication
***Dicynodon* AZ**			
Burnetia mirabilis	NHMUK R5397	Karoo	Rubidge & Sidor 2002
Ictidorhinus martinsi	AMNH 5526	Karoo	Sigogneau-Russell 1989
Burnetiamorpha indet.	SAM-PK-K5292	Karoo	Undescribed specimen
***Cistecephalus* AZ**			
Biarmosuchia indet.	NHCC LB181	Luangwa	Present paper
Biarmosuchia indet.	RC 55	Karoo	Sidor & Rubidge 2006
Burnetiidae indet.	NMT RB4	Ruhuhu	Sidor *et al*. 2010
Burnetiamorpha indet.	NMT RB36	Ruhuhu	Sidor *et al*. 2010
Burnetiidae indet.	NMT RB169	Ruhuhu	Undescribed specimen
Burnetiamorpha indet.	BP/1/353	Karoo	Sidor & Welman 2003
Herpetoskylax hopsoni	CGS/1/67	Karoo	Sidor & Rubidge 2006
Herpetoskylax hopsoni	BP/1/3294	Karoo	Sidor & Rubidge 2006
Lemurosaurus pricei	BP/1/816	Karoo	Sigogneau-Russell 1989
Lemurosaurus pricei	NMQR 1702	Karoo	Sidor & Welman 2003
Lemurosaurus pricei	SAM-PK-K10906	Karoo	Undescribed specimen
New species	MAL 290	Chiweta	Kruger *et al*. in press
Lycaenodon longiceps	NHMUK R5700	Karoo	Sigogneau-Russell 1989
Lycaenodon longiceps	RC 20	Karoo	Sigogneau-Russell 1989
Paraburnetia sneeubergensis	SAM-PK-K6655	Karoo	Smith *et al*. 2006
cf. *Paraburnetia*	SAM-PK-K11112	Karoo	Undescribed specimen
***Tropidostoma* AZ**			
Lobalopex mordax	CGS/1/61	Karoo	Sidor *et al*. 2004
Lophorhinus willodenensis	SAM-PK-K6655	Karoo	Sidor & Smith 2007
***Tapinocephalus* AZ**			
Bullacephalus jacksoni	BP/1/5387	Karoo	Rubidge & Kitching 2003
Burnetiidae indet.	NHCC LB118	Mid-Zambezi	Undescribed specimen
Burnetiidae indet.	NHCC LB133	Mid-Zambezi	Undescribed specimen
Burnetiidae indet.	NHCC LB149	Mid-Zambezi	Undescribed specimen
Hipposaurus boonstrai	SAM-PK-8950	Karoo	Sigogneau-Russell 1989
Hipposaurus boonstrai	SAM-PK-9081	Karoo	Sigogneau-Russell 1989
Hipposaurus boonstrai	CGS/1/66	Karoo	Sigogneau-Russell 1989
Hipposaurus? *brinki*	SAM-PK-12252	Karoo	Sigogneau-Russell 1989
Pachydectes elsi	BP/1/5735	Karoo	Rubidge *et al.* 2006

most intensely sampled, Smith *et al*. (2013) reported 3755 fossils from the *Cistecephalus* AZ, only four of which are biarmosuchians. However, the true number of specimens is more like 11, as some unidentified specimens were by necessity not included in the database of Nicolas & Rubidge (2010). By comparison, expeditions to the Luangwa Basin in 2009 and 2011 have yielded a minimum of 420 specimens (cataloguing is ongoing), and only one biarmosuchian. In terms of taxonomic diversity, at least five valid biarmosuchian species (*viz*. *Herpetoskyax*, *Lemurosaurus*, *Lycaenodon*, *Paraburnetia*, and a newly recognized species from Malawi; Kruger *et al*., in press) are recognized from *Cistecephalus* AZ-age rocks, which is a diversity maximum paralleling similar maxima in dicynodonts and therapsids as a whole, at least when sampling standardization is not considered (Irmis *et al*. 2013).

This fossil would not have been available for study without the determination of Steve Tolan (Chipembele Wildlife Trust, Mfuwe). His work with the Zambian Wildlife Authority and NHCC, particularly Kagosi Mwamulowe and Collins Chipote, was instrumental in the eventual return of this important specimen. In addition to those previously mentioned, I am very fortunate to have worked in Zambia with a great group of colleagues, including Adam Goulding, Joseph Museba, Justin Bwalya, Jack Menke, Ken Angielczyk, Roger Smith, Seb Steyer, Sterling Nesbitt, Brandon Peecook, and Robin Whatley. I thank Bob Masek for the excellent preparation of NHCC LB181 and Bruce Crowley (Burke Museum, University of Washington) for molding and casting. Research on the Permian vertebrate fauna of Zambia has been supported by the National Geographic Society (grant 8571-08 to Sebastien Steyer and 8962-11 to CAS), The Grainger Foundation and Field Museum/IDP Foundation, Inc. African Partners Program (to Ken Angielczyk), and the National Science Foundation (EAR-1337569 to CAS; EAR-1337291 to Ken Angielczyk; EAR-1336986 to Peter Roopnarine). Ashley Kruger, Fernando Abdala, and Jonah Choiniere provided helpful reviews of the manuscript. Lastly, I thank the collector of the fossil for appreciating its scientific value and returning it for repatriation.

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