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LENDE CHIWETA, A NEW THERAPSID FROM MALAWI, AND ITS INFLUENCE ON BURNETIAMORPH PHYLOGENY AND BIOGEOGRAPHY

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ABSTRACT—The Chiweta Beds of Malawi have yielded a diverse late Permian fossil tetrapod fauna that correlates with that of the *Cistecephalus* Assemblage Zone of the South African Karoo Supergroup. Amongst the fossil therapsids from the Chiweta Beds is the well-preserved skull and lower jaw of a burnetiamorph, a group of biarmosuchians with numerous bosses and swellings on the skull. This specimen was reported in a preliminary paper in 2005 as the first burnetiamorph described outside of South Africa and Russia. Reanalysis of the morphology and phylogeny of this specimen places *Lende chiweta*, gen. et sp. nov., as the sister taxon to the clade formed by *Proburnetia* (*Paraburnetia* (*Pachydectes, Bullacephalus, Burnetia, Niuksenitia*)). The greatest diversity of this basal therapsid group is from South Africa, with six of nine described genera and a stratigraphic range that extends from the middle Permian *Tapinocephalus* Assemblage Zone to the upper Permian *Dicynodon* Assemblage Zone. Bearing in mind the constraints that govern fossil preservation, current data suggest that what is now southern Africa may have been the area of origin for burnetiamorphs. Under this premise, what is now central Africa represented a corridor that allowed migration of representatives of the group between the southern and northern portions of Pangea during the late Permian.

http://zoobank.org/urn:lsid:zoobank.org:pub:BB094736-24AE-4B98-A33CBD7B7668DC2F

SUPPLEMENTAL DATA—Supplemental materials are available for this article for free at www.tandfonline.com/UJVP

INTRODUCTION

The basal therapsid clade Biarmosuchia was first proposed by Hopson and Barghusen (1986), but until that time, most genera of this taxon were considered as part of the Gorgonopsia. Sigogneau (1970), in her systematic revision of the Gorgonopsia, recognized five genera (*Hipposaurus, Ictidorhinus, Lycaenodon, Lemurosaurus,* and *Rubidgina*) within the family Ictidorhinidae. After subsequent taxonomic revision of the 'ictidorhinids,' Sigogneau-Russell (1989) recognized four families within the Biarmosuchia: Biarmosuchidae (including *Biarmosuchus*), Hipposauridae (including *Hipposaurus* and *Lycaenodon*), Ictidorhinidae (including *Ictidorhinus, Lemurosaurus,* and *Rubidgina*), and Burnetiidae (including *Burnetia, Proburnetia*, and *Styracocephalus*). Rubidge and van den Heever (1997) subsequently identified *Styracocephalus* as a dinocephalian.

Hopson and Barghusen (1986) considered the Biarmosuchia to be characterized by the possession of primitive therapsid characters but were unsure whether the group was mono- or paraphyletic. Hopson (1991) later proposed several characters supporting the monophyly of biarmosuchians. Over the past two decades, several new biarmosuchian genera have been described

(Sidor, 2000; Rubidge and Kitching, 2003; Sidor and Welman, 2003; Sidor et al., 2004; Jacobs et al., 2005; Sidor and Rubidge, 2006; Smith et al., 2006; Sidor and Smith, 2007). Many of these belong to the Burnetiamorpha, which has become the most species-rich subclade of biarmosuchians.

Originally, the family Burnetiidae was erected for *Burnetia* from South Africa (Broom, 1923). Recent discoveries of more specimens, however, prompted new studies on burnetiamorphs, which have recognized these therapsids as a distinct monophyletic group within Biarmosuchia (Sidor and Rubidge, 2006; Kemp, 2012), which includes all taxa more closely related to *Burnetia* than to *Ictidorhinus* or *Hipposaurus* (Sidor, 2000; Sidor and Welman, 2003). Currently, the Burnetiamorpha comprise nine genera: *Bullacephalus, Burnetia, Lemurosaurus, Lobalopex, Lophorhinus, Paraburnetia,* and *Pachydectes* from South Africa, and *Niuksenitia* and *Proburnetia* from Russia. In addition, Sidor et al. (2010) recently described a partial skull roof including the dorsal margin of orbits and parietal foramen of an unnamed burnetiid from the upper Permian of Tanzania, and Sidor et al. (2014) noted the presence of a burnetiid in the middle Permian of Zambia. Despite the fact that several genera have been described, burnetiamorphs are relatively rare, with each genus being represented by one or two specimens, and most are from the South African Permian beds of the Beaufort Group.

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Jacobs et al. (2005), in a report on the late Permian fauna of the Chiweta Beds of northern Malawi, which they correlated with the *Cistecephalus* Assemblage Zone of the South African Karoo, briefly described an unnamed burnetiamorph skull (MAL 290). Their preliminary phylogenetic analysis recovered it as the sister taxon to *Proburnetia, Burnetia*, and *Bullacephalus*. Subsequent preparation has exposed additional portions of the skull and allowed for a full description and a more comprehensive phylogenetic analysis.

Institutional Abbreviations—BP, Evolutionary Studies Institute (formerly the Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; **CGP**, and also; **WB123**, Council for Geosciences (formerly the Geological Survey of South Africa), Pretoria, South Africa; **MAL**, Malawi Department of Antiquities Collection, Lilongwe and Nguludi, Malawi; **NHMUK**, Natural History Museum, London, U.K.; **NMQR**, National Museum, Bloemfontein, South Africa; **NMT**, National Museum of Tanzania, Dar es Salaam, Tanzania; **RC**, Rubidge Collection, Graaff-Reinet, South Africa; **SAM**, Iziko South African Museum, Cape Town, South Africa.

Anatomical Abbreviations—a, articular; **bo**, basioccipital; **bsp**, basisphenoid; **d**, dentary; **eam**, external auditory meatus; **ec**, ectopterygoid; **f**, frontal; **fb**, frontal boss; **fm**, foramen magnum; **j**, jugal; **lac**, lacrimal; **m**, maxilla; **n**, nasal; **nb**, nasal boss; **op**, opisthotic; **p**, parietal; **pal**, palatine; **pf**, postfrontal; **pin**, pineal foramen; **pm**, premaxilla; **po**, postorbital; **pp**, postparietal; **prf**, prefrontal; **ps**, parasphenoid; **pt**, pterygoid; **q**, quadrate; **qpt**, quadrate ramus of pterygoid; **sm**, septomaxilla; **so**, supraoccipital; **sp**, splenial; **sq**, squamosal; **sur**, surangular; **t**, tabular; **v**, vomer.

MATERIALS AND METHODS

The specimen MAL 290 was discovered in 1992 as a result of collaborative field work by members of the Malawi Department of Antiquities and Southern Methodist University during a day trip to the Permian Karoo Supergroup rocks near Chiweta (Jacobs et al., 2005). Following a preliminary description, the specimen was further prepared at the Evolutionary Studies Institute, where a detailed study was undertaken.

For comparative purposes, the following specimens were examined: BP/1/816, holotype of *Lemurosaurus pricei*; BP/1/3924, referred specimen of *Herpetoskylax hopsoni*; BP/1/5387, holotype of *Bullacephalus jacksoni*; BP/1/5735, holotype of *Pachydectes elsi*; CGP/1/61, holotype of *Lobalopex mordax*; CGP/1/67, holotype of *Herpetoskylax hopsoni*; NHMUK R5700, holotype of *Lycaenodon longiceps*; cast of NHMUK R5397, holotype of *Burnetia mirabilis*; NMQR 1702, referred specimen of *Lemurosaurus pricei*; NMT RB4, unnamed burnetiamorph; RC55, holotype of *Rubidgina angusticeps*; SAM-PK-K6655, holotype of *Lophorhinus willodenensis*; and WB123, undescribed specimen of *Hipposaurus boonstrai*. Information on *Ictidorhinus* and *Niuksenitia* was obtained after Boonstra (1935), Tatarinov (1977), Sigogneau-Russell (1989), and Ivakhnenko (2002).

A cladistic analysis was undertaken based on a data matrix of 36 characters and 15 taxa (see Supplementary Data). Twenty-three characters in the matrix were previously used by Rubidge et al. (2006); six characters were also included in previous phylogenies (e.g., Rubidge and Kitching, 2003; Sidor and Welman, 2003), and seven characters are proposed here for the first time. Taxa included in the analysis are *Biarmosuchus, Bullacephalus, Burnetia, Herpetoskylax, Hipposaurus, Ictidorhinus, Lemurosaurus, Lobalopex, Lophorhinus, Lycaenodon, Niuksenitia, Pachydectes, Paraburnetia*, and *Proburnetia*, with *Biarmosuchus* representing the outgroup used for character polarization. The main intention of the analysis is to explore the monophyly and internal groups of Burnetiamorpha.

As knowledge of the postcranium of the vast majority of biarmosuchian taxa is poor, the data matrix incorporates only craniodental characters. The data matrix used in the analysis is freely available on Morphobank as project P1190.

The program TNT (Goloboff et al., 2003) was used to search for the most parsimonious trees. All characters were given equal weight, and multistate characters with states representing morphologically adjacent conditions were considered ordered (Lipscomb, 1992). Considering the small size of the data matrix, a search strategy of implicit enumeration, guaranteeing the recovery of the shortest most parsimonious tree(s), was used. Bremer support and resampling were calculated to evaluate the reliability of the monophyletic groups recovered. Sensitivity analyses implying alteration in additivity of characters and using implied weights (Goloboff, 1993) were also considered, and the resulting most parsimonious trees compared with those of our original analysis.

SYSTEMATIC PALEONTOLOGY

THERAPSIDA Broom, 1905
BIARMOSUCHIA Sigogneau-Russell, 1989
BURNETIAMORPHA Broom, 1923

Diagnosis—Supraorbital boss present, antorbital fossa or pit on lateral surface of lacrimal; median frontal ridge present but variably expressed; boss on ventral surface of squamosal lateral to level of quadrate; boss present on lower margin of zygomatic arch at level of postorbital bar (Sidor and Welman, 2003).

LENDE CHIWETA, gen. et sp. nov.
(Figs. 1–3)

Holotype—MAL 290, almost complete skull with lower jaw.

Etymology—MAL 290 was informally referred to as the 'head of the devil' because of reminiscent excrescences on the skull. In recognition of that whimsical reference and more seriously in honor of the culture of Malawi, the generic name is given for a member of Gule wa Mkulu, masked dancers that bridge the spirit world in Chewa culture (Malawi transliterated spelling; UNESCO, 2014). 'Lende' is a notorious figure in the Gule wa Mkulu who appears at night and sometimes disappears from view. The specific epithet refers to the type locality and should be treated as a noun in apposition.

Diagnosis—Small burnetiamorph, with short snout; high and long ridge-like midline nasal boss extending posteriorly up to the anterior margin of the orbit; very robust and high frontal boss (as high as the supraorbital boss); flat to slightly concave dorsal surface of parietal surrounding parietal foramen, lacking chimney and high angulation (105°) between the preorbital and postorbital portions of the cranial roof; midline ridge of postparietal does not extend dorsally onto parietal.

Locality and Age—Lower Bone Bed (B1) of the Chiweta Beds, Malawi. Correlated with the *Cistecephalus* Assemblage Zone of South Africa, and therefore also the Usili Formation of Tanzania, and the Upper Madumabisa Mudstone Formation of Zambia (Jacobs et al., 2005; Sidor et al., 2013). Late Permian.

Comments—The holotype was prepared in a way that new information, especially from the palate, is now available. Considering the exceptionally large orbit, it is possible that the specimen represents a juvenile individual and that diagnostic characters such as snout length may prove to be linked with age. This is also the case with the dorsal skull angulation, because there is evidence that change in the dorsal profile of the skull (calvaria of living mammals) is linked with deflection of the rostrum in relation to the basicranium during ontogeny (Lieberman et al., 2008; Flores et al., 2010).

DESCRIPTION

The skull and lower jaw of *Lende chiweta* is well preserved, only slightly distorted on the left side and almost complete except for damage to the front of the snout and the anterior end of the right ramus of the lower jaw. Because of the pachyostotic nature of the bone, it is difficult to identify sutures. The high and narrow snout of *Lende* makes up approximately one-third of the skull length.

In lateral view, *Lende* exhibits a prominent parietal boss posterodorsal to the temporal opening, a triangular supraorbital boss, and large, elongated frontal and nasal bosses. No parietal chimney is present. The temporal fenestra is positioned behind and somewhat below the orbit, and the postorbital region of the skull is short compared with the length of the snout, features that are reminiscent of pelycosaur-grade synapsids and basal therapsids.

Skull Roof

The premaxilla, which forms the tip of the snout, is damaged at its anterior end and has a relatively short dorsal process, which does not extend far on the snout. This differs from the basal biarmosuchians *Hipposaurus* and *Biarmosuchus*, which exhibit a relatively long dorsal process of the premaxilla that reaches halfway between the tip of the snout and the orbit (Sidor and Rubidge, 2006). Although five incisors are typical for burnetiamorpha, three small incisors are preserved on the left premaxilla and two are visible on the right side (Fig. 1).

Only a small triangular sliver of the septomaxilla facial process is preserved and is directed posteriorly between the maxilla and the nasal on the left side of the specimen.

The maxilla is a large bone that makes up most of the lateral surface of the snout (Fig. 1B, D). Because of the weathered nature of the anterior end of the skull, it is not possible to recognize the suture between maxilla and premaxilla. The maxilla has a long, dorsal sutural contact with the nasal, a pointed posterodorsal contact with the prefrontal, and a vertical posterior contact with the lacrimal. On the left side of the skull, a large ovoid fossa is present on the contact between the maxilla, the lacrimal, and the jugal, but it is absent on the right side. The maxilla makes up the ventral margin of the snout and forms a long, tapering posterodorsal sutural contact with the jugal until half way along the length of the orbit, where it appears to touch a thin anteroventral extension of the squamosal on the ventral margin of the skull. The jugal is a prominent bone of the zygomatic arch and almost forms the entire ventral margin of the orbit. Its posterior contact with the postorbital is unclear, and it appears to form the anteroventral margin of the temporal fenestra.

The nasals cover a large area on the dorsal side of the snout. Anteriorly they form the roof of the external nares; they have a long lateral contact with the maxilla and respectively meet the prefrontal and frontal posterolaterally and posteromedially. The
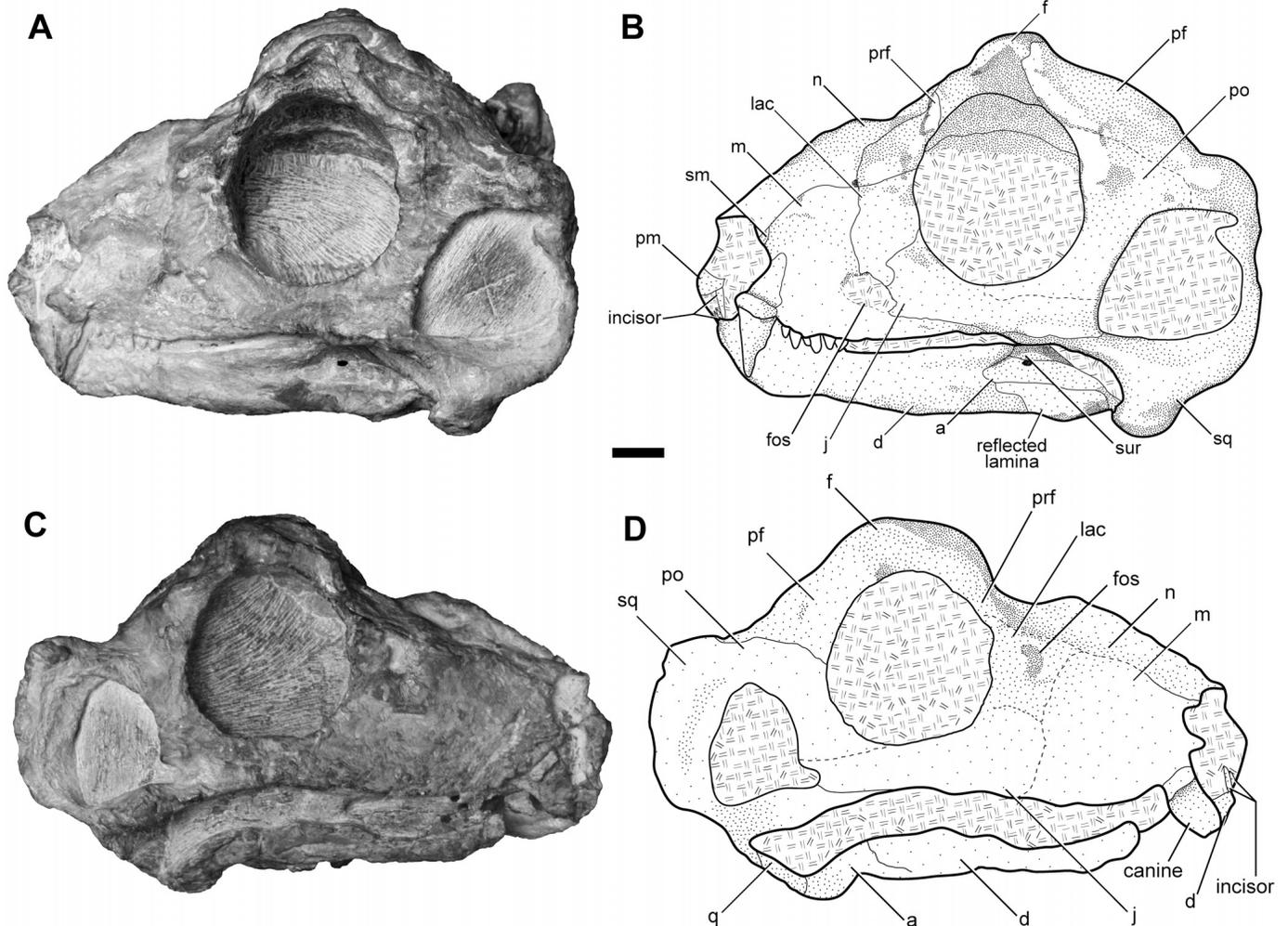

FIGURE 1. *Lende chiweta*, gen. et sp. nov., MAL 290, holotype, skull and mandible. **A**, photograph, and **B**, illustration of specimen in left lateral view; **C**, photograph, and **D**, illustration of specimen in right lateral view. Scale bar equals 1 cm.

nasal has only a short, pointed contact with the lacrimal, which is visible on the left side. A narrow elongated but prominent nasal crest is present and is similar to that of *Lobalopex* (Sidor et al., 2004) and *Lophorhinus* (Sidor and Smith, 2007). Anteriorly, it terminates immediately behind the external naris, and posteriorly above the anterior margin of the orbit.

In lateral view, the lacrimal is rectangular and has a clear dorsal sutural contact with the prefrontal. The anterior margin contacts the maxilla, and posteroventrally it meets the jugal. A fossa is present on the dorsal margin of the lacrimal, but it is larger on the right side of the skull than it is on the left.

The prefrontal is a large, broadly triangular, flattened bone, which forms the anterodorsal margin of the orbit but does not contribute to thickening of the orbital margin. It contacts the maxilla anteroventrally, the nasal dorsally and anteriorly, and the frontals at the basal margin of the supraorbital boss. As is evident on the left side of the skull (Fig. 1B), the prefrontals contact the lacrimal ventrally by means of a long, horizontally oriented suture positioned half way down the anterior orbital margin.

The paired frontals make up most of the skull roof (Fig. 2A, B). Anteriorly they meet the nasals but the suture is unclear, and they meet the prefrontals anterolaterally. The nasals make up a large part of the dorsal margin of the orbit and have a long curved posterolateral contact with the postfrontals. The nature of the posterior contact with the parietals is uncertain. Laterally the frontals are thickened and contribute to two slightly pachyostosed supraorbital bosses on either side of the skull, in contrast to the condition in other burnetiamorphs such as *Lophorhinus* and *Lemurosaurus,* where the prefrontals contribute to the formation of the supraorbital boss (Sidor and Welman, 2003; Sidor and Smith, 2007). Between the supraorbital bosses of the frontals, a large elongated midline frontal boss is present. This boss is of comparable height to the supraorbital bosses and is slightly pachyostotic. In dorsal view, the midline boss is broadly triangular, displaying its greatest width posteriorly and tapering anteriorly to a point that is in line with the anterior margin of the orbits. The highest point of the frontal boss is situated in line with the midpoint of the orbits and is relatively much larger than that of *Lemurosaurus*. At the posterior end, the frontal boss flattens without secondary thickening and apparently terminates in front of the parietal, but the contact between the frontal and the parietal is not clear. The postfrontals form a small portion of the posterodorsal margin of the orbit, contacting the frontals and contributing to the pachyostosed supraorbital boss in a similar way to that of *Lobalopex* (Sidor et al., 2004). This protuberance is of comparable height to the median frontal boss. The postfrontals extend posteriorly as they form the posterodorsal margin of the orbit and have a sutural contact with the postorbitals posterior to the orbit.

The postorbital is a large bone forming a substantial part of the posterior margin of the orbit and the anterior and dorsal margins of the temporal fenestra. In lateral view, the postorbital contacts the jugal on the posteroventral border of the orbit and the postfrontal on its posterodorsal margin. Dorsomedially the postorbital contacts the parietal on the skull roof. The tabular and squamosal bones contact the postorbital posteriorly.

The squamosal is a large bone forming the posterior and ventral margins of the temporal opening. Anteromedially, it is in sutural contact with the postfrontal and likely the postorbital. In lateral and occipital views, the squamosal forms a 'squamosal horn' (Figs. 1, 3), located on the posterodorsal margin of the temporal fenestra. Below the temporal fenestra, the squamosal forms a prominent boss on the ventral margin of the zygomatic arch. Anterodorsally it meets the jugal by means of a horizontal suture below the postorbital bar, and it appears to extend anteriorly as a thin wedge along the ventral margin of the zygomatic arch to contact the maxilla below the orbit.

As in most other biarmosuchians, the presence of a preparietal is difficult to determine because of the pachyostotic nature of the bones of the skull roof. In many biarmosuchians, this bone is believed to form the anterior margin of the parietal foramen, being part of the raised chimney (Sidor and Welman, 2003, Sidor et al., 2004). In *Lende*, the pineal foramen is located posterior to the base of the frontal boss, but no pineal boss is present. In *Paraburnetia, Proburnetia*, and *Bullacephalus*, the parietals create a broad swelling around the pineal foramen but do not create a chimney, whereas *Lemurosaurus, Hipposaurus*, and *Herpetoskylax* have a distinctive parietal chimney (Rubidge and Sidor, 2002; Rubidge and Kitching, 2003; Sidor and Welman, 2003; Sidor and Rubidge, 2006).

The parietal makes up a large portion of the posterodorsal surface of the skull and quite certainly extends onto the occiput, although the sutures of the bony elements on the occipital area are very difficult to trace (Fig. 2A, B). Anteriorly the parietal contacts the frontals and postfrontals, whereas laterally it contacts the postorbitals. In dorsal view, it is evident that the parietal is situated between the postorbital and the dorsal margin of the tabular.

Palate

The palate of MAL 290 (Fig. 2C) is reasonably preserved; however, it is difficult to place palatal sutures with confidence. The vomer is a long, thin bone with an elongated, anteroposteriorly extending trough, produced by the downturned lateral margins. Because no midline suture is visible, it appears that the vomer is unpaired. Posteriorly it narrows to meet the palatine behind the internal nares, but the nature of this contact is unclear.

The paired palatine forms a large proportion of the palatal surface. Anterolaterally, it overlies the maxilla and extends posteriorly from the level of the canine along the posterolateral and posterior margins of the internal nares to meet the vomer medially. The left and right palatines are separated by a long trough between the prominent dentigerous palatine bosses. Three and four small teeth are visible on the left and right bosses, respectively. These teeth are difficult to see, and there is no apparent pattern of tooth distribution. On its lateral side, the palatine boss slopes in a dorsal direction and forms a horizontal platform close to its lateral contact with the maxilla.

Posterolaterally, the palatine meets a small triangular ectopterygoid, which is positioned on the anterior flank of the lateral process of the pterygoid. The tripartite pterygoid comprises an anterior medial process, the lateral processes, and the posterior process, which extends posterolaterally to form the quadrate ramus. The anterior process makes up the dentigerous pterygoid boss, which is confluent with the palatine boss but is much smaller. The suture between the palatine and pterygoid is not visible. Four teeth are present on the pterygoid boss, two on each side, but no pattern can be ascertained. A broad anterolaterally oriented trough is present between the pterygoid boss and the lateral process. In ventral view, the edentulous lateral process of the pterygoid is broad laterally and tapers posteromedially to form a narrow ridge that curves posteromedially to the interpterygoidal vacuity, from where it runs posteriorly, parallel to the midline, to the posterior end of the pterygoid. Another ridge extends down the lateral side of the pterygoid. Anteriorly, it begins as a low ridge immediately behind the pterygoid process, and becomes more accentuated as it extends onto the quadrate ramus. Only the anterior portions of the quadrate rami on either side are preserved, and at this point the quadrate ramus is a flat horizontally oriented bone. A narrow interpterygoid vacuity is present, with its anterior margin in line with the anterior
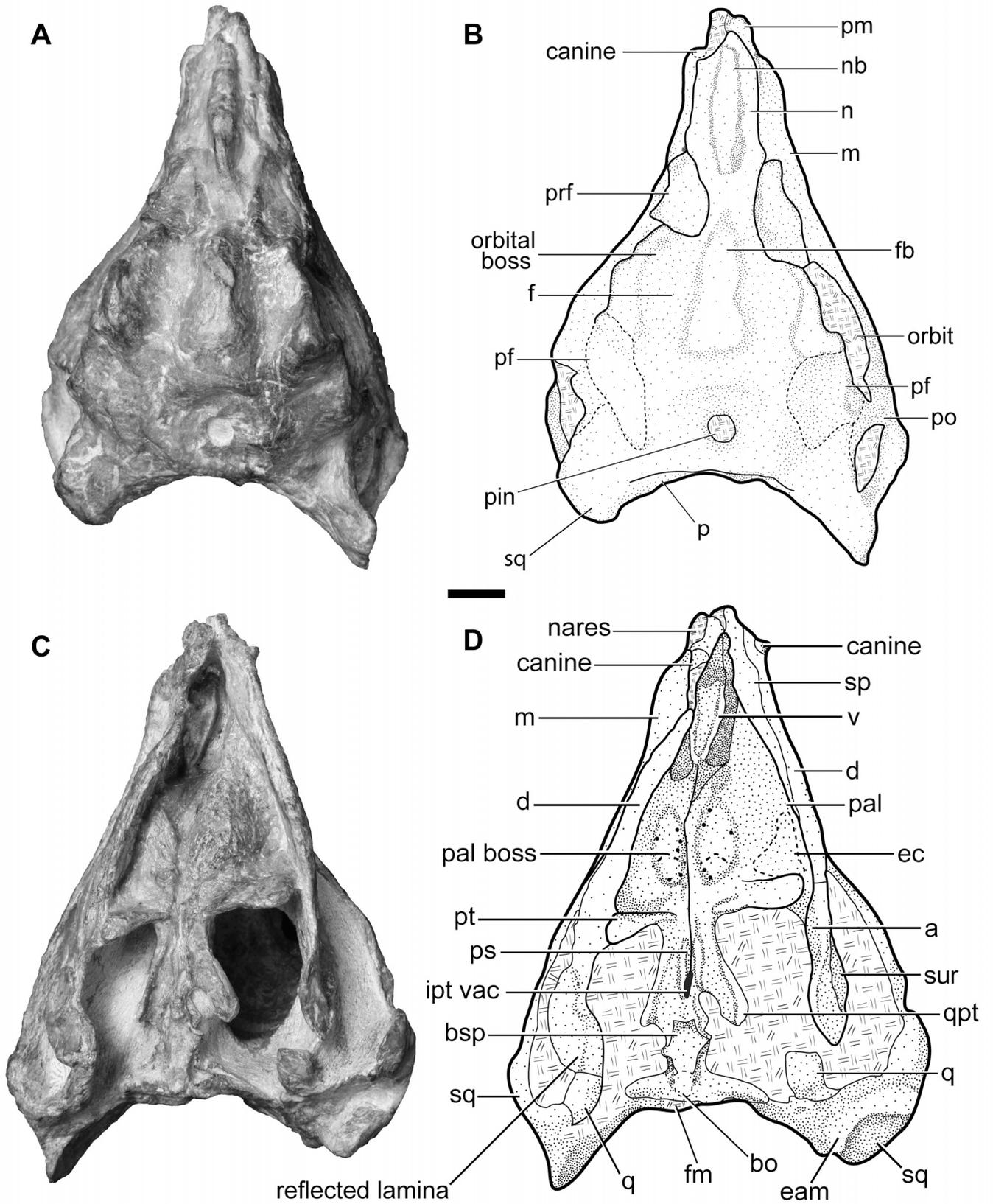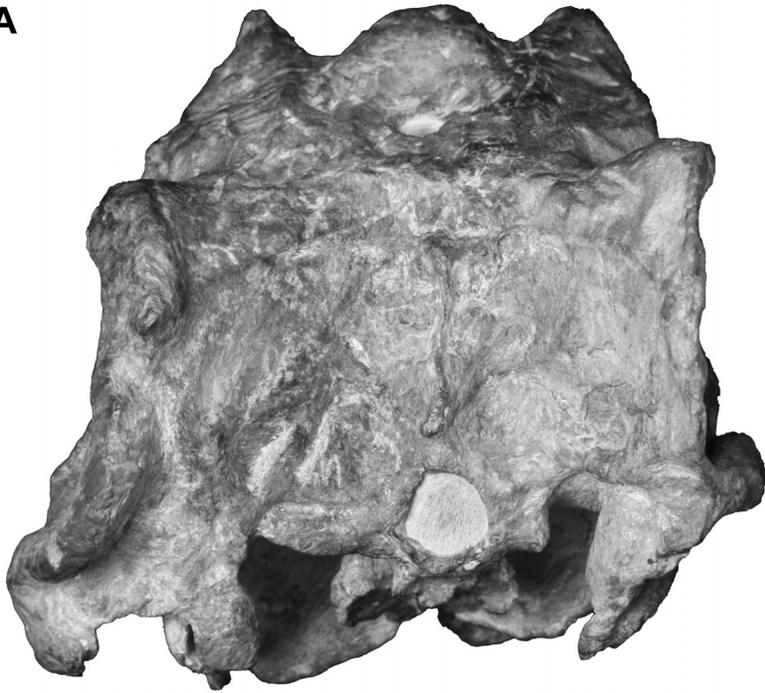
FIGURE 2. *Lende chiweta*, gen. et sp. nov., MAL 290, holotype, skull and mandible. **A**, photograph, and **B**, illustration of specimen in dorsal view; **C**, photograph, and **D**, illustration of specimen in ventral view. Scale bar equals 1 cm.
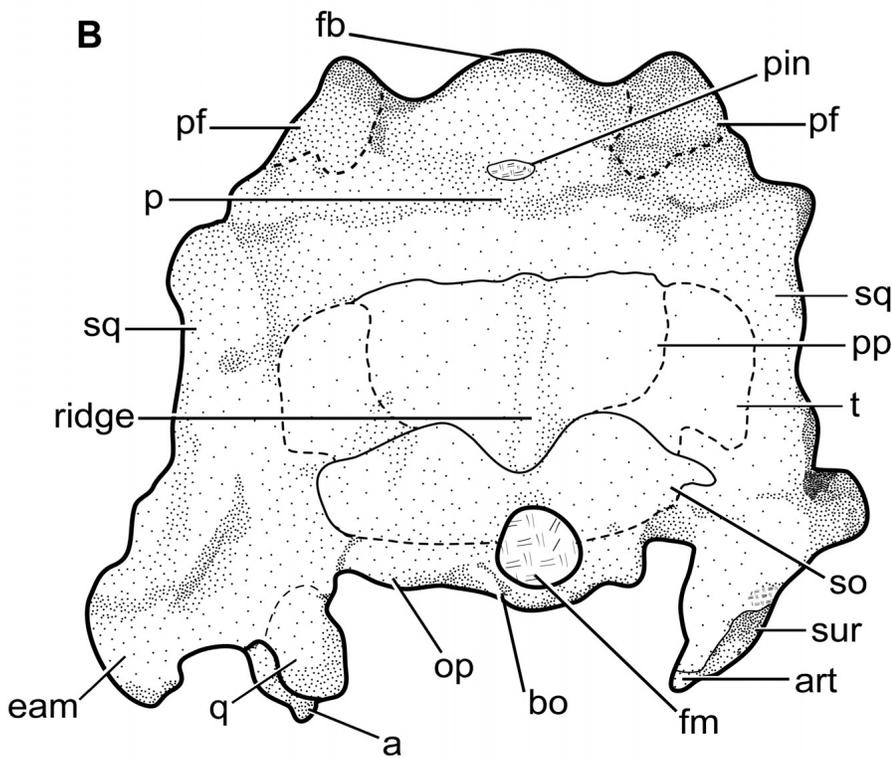
FIGURE 3. *Lende chiweta*, gen. et sp. nov., MAL 290, holotype, skull and mandible. **A**, photograph, and **B**, illustration of specimen in occipital view. Scale bar equals 1 cm.

margin of the lateral process, and a further vacuity is present at the posterior end of the pterygoid.

The basisphenoid is a relatively small quadrangular bone, which has a bulbous midline, pointed contact with the pterygoid, and posteriorly has a broad transverse sutural contact with the basioccipital half way along the fenestra ovalis. The stapes is not preserved. A broad trough extends down the midline of the basisphenoid.

Occiput

The occiput of *Lende* (Fig. 3) is transversely rectangular, oriented vertically, and curves posterolaterally. Sutural borders of the postparietal, parietal, tabular, and supraoccipital bones are clearly delineated. Both quadrates are preserved. The single postparietal has the form of an inverted triangle with the apex pointing down the midline of the occipital surface. It overlies the

supraoccipital and extends ventrally to a point immediately dorsal to the foramen magnum. Dorsally the postparietal has a long contact with the parietal on the occipital surface, and laterally it meets the tabular. A prominent midline ridge extends the entire length of the postparietal but not onto the parietal. This differs from the situation in other biarmosuchians, where the ridge extends along the parietal from the posterior surface of the parietal chimney.

The tabulars are square, flat bones, but the sutures are not clear. Dorsomedially the tabular is in contact with the posterior side of the parietal, whereas dorsolaterally, laterally, and ventrolaterally it has a long contact with the squamosal.

The supraoccipital is a large, transverse bone at the base of the occipital surface and forms the dorsal and a portion of the lateral margin of the foramen magnum. Dorsolaterally, it has a short contact with the tabular.

The opisthotic is preserved on the left side by its paroccipital process, which is a flat and transversely triangular bone, positioned ventral to the supraoccipital. The paroccipital process of the opisthotic contacts the basioccipital medially.

The exoccipitals could not be discerned, and the basioccipital, which forms the entire ventral margin of the foramen magnum, meets the basisphenoid anteriorly on the ventral surface of the skull. What appears to have been a single occipital condyle has been largely eroded away.

The quadrate and quadratojugal are preserved on the left side but are not well exposed. In occipital view (Fig. 3), the quadrate is dorsally broad and partially overlain dorsally by the squamosal, and thins ventrally to form the quadrate condyles.

Lower Jaw

The left lower jaw is complete, but the right ramus is damaged anteriorly and weathered posteriorly such that portions of the dentary are not preserved. Accordingly, this description is based largely on the left ramus (Fig. 1A, B). The mandible is deep posteriorly and shallows towards its thinnest point just behind the canine tooth.

The dentary forms most of the lateral surface of the mandible. In lateral view, the canine and postcanine teeth are not visible, but three incisors are present toward the anterior end. The lateral surface of the dentary is flat and smooth, but its surface changes ventral to the orbit, where the dorsal margin swells and forms an overhanging dentary ledge that extends posteriorly onto the surangular. This feature is also present in *Proburnetia* (Rubidge and Sidor, 2002), *Herpetoskylax* (Sidor and Rubidge, 2006), and *Lemurosaurus* (Sidor and Welman, 2003). The posterior margin of the dentary slopes anteroventrally. Posterodorsally the dentary contacts the surangular, which makes up the posterodorsal end of the lower jaw. Medially the dentary is largely overlain by the splenial anteroventrally and by the prearticular slightly more dorsally.

The angular is a relatively small bone forming the posteroventral portion of the lateral side of the mandible and contacting the dentary anteriorly. A small, reflected lamina is present and its lateral surface is devoid of ornamentation (Fig. 1A, B).

The splenial is a relatively large flat bone on the anteromedial side of the lower jaw. It is wide anteriorly and thins posteriorly to wedge out on the ventral margin of the jaw ramus posterior to the lateral process of the pterygoid. The articular is not preserved on the left ramus and on the right side it is not visible, but the prearticular is well exposed on the left ramus, where it extends as a thin flat rod from the posteroventral margin of the lower jaw to wedge out along the dorsal margin of the splenial at the level of the anterior margin of the palatine boss.

Dentition

The left upper canine is complete, whereas the right one exhibits a damaged tip (Figs. 1, 2). The long recurved canines, which are oval in cross-section and lack serrations, extend almost as far as the ventral margin of the dentary when the jaws are occluded. Six small, pointed upper postcanine teeth, which lack serrations, are present on the left side, but none are preserved on the right (Fig. 1). Three incisors, which also lack serrations, are preserved on the left premaxilla, and two slightly eroded incisors are present on the right. Only the basal portion of the lower incisors is preserved, and as a result it is not possible to determine whether intermeshing of the incisors occurred during occlusion.

DISCUSSION

Because of the presence of the following characters, it is evident that *Lende* is a burnetiamorph biarmosuchian (Jacobs et al., 2005): lateral surface of lacrimal bears one or more deep fossae; dorsal surface of frontals are thickened; presence of bosses on ventral surface of zygomatic arch and suborbital bar; the presence of a squamosal boss; large midline frontal ridge; and small boss on anterior margin of squamosal.

Phylogenetic Analysis

Our analysis yielded 32 most parsimonious trees (MPTs), with the majority-rule consensus shown in Figure 4A. In the majority-rule tree, *Lende* is sister to the (*Proburnetia* (*Paraburnetia* (*Burnetia, Bullacephalus, Pachydectes, Niuksenitia*))) clade. *Herpetoskylax* and *Lycaenodon* form a polytomy with burnetiamorphs. Most of the lack of resolution in the majority-rule tree is concentrated within the Burnetiamorpha. Indeed, there are two polytomies, one including *Lophorhinus, Lobalopex*, and the remaining burnetiamorphs (excluding the basal *Lemurosaurus*), and a second that includes *Burnetia, Bullacephalus, Pachydectes*, and *Niuksenitia* (Fig. 4A). Bremer support is 1 for all the groups, and there are no bootstrapping values higher than 40. Therefore, monophyletic groups are poorly supported in the most parsimonious trees.

Placement of the Malawian taxon in this analysis is consistent with the results of the cladistic analysis of Jacobs et al. (2005). The differences are the result of enhanced sampling, e.g., *Paraburnetia* and *Pachydectes* were not yet described at the time of Jacobs et al. (2005), and *Bullacephalus* is recovered as sister taxon of *Burnetia* in the analysis of those authors.

Four MPTs resulted from an analysis in which all multistate characters were considered as unordered (Fig. 4B). The resolution of the consensus is enhanced with the recovery of a monophyletic clade including *Lophorhinus* and *Lobalopex*, and resolution of the major polytomy in the previous analysis: *Niuksenitia* (*Burnetia* (*Pachydectes, Bullacephalus*)). There is no further resolution of polytomies in non-burnetiamorph biarmosuchians. Similar to Rubidge et al. (2006), our analysis indicates that the clade of *Pachydectes* and *Bullacephalus* is nested deeply in the burnetiamorphs.

Analysis using implied weights (K function = 3) with ordered multistate characters resulted in three MPTs. With regard to burnetiamorphs, the consensus tree in this analysis is similar to that of the main analysis, but *Herpetoskylax* is recovered as the sister taxon to burnetiamorphs.

Finally, the consensus of the three MPTs obtained in an analysis with implied weights (K function = 3) and unordered multistate characters shows some differences to the other results, viz., the sister-group relationship between *Lende* and *Lobalopex* and the polytomy represented by node 'a' (Fig. 4C).
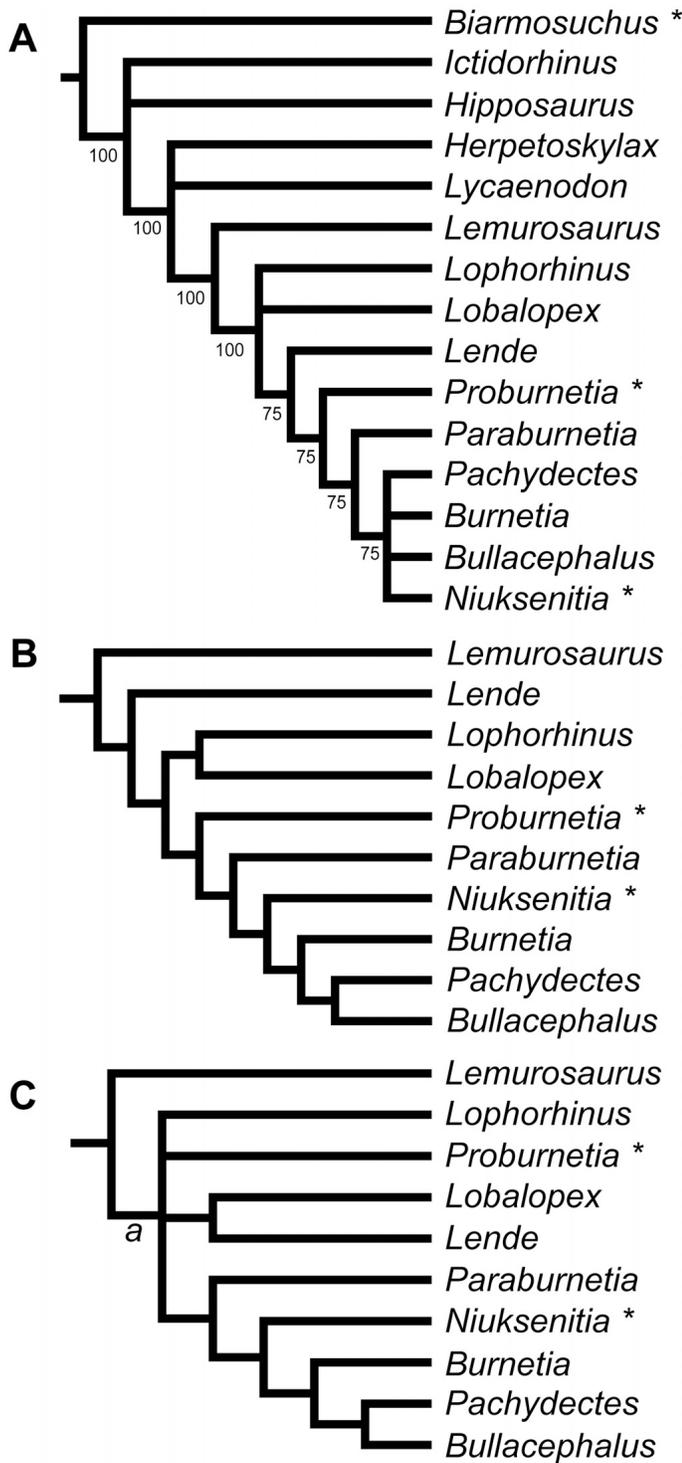
FIGURE 4. **A**, majority-rule consensus tree of the main analysis (equally weighted and ordered multistate characters). Numbers indicate the frequency a clade is represented in the most parsimonious trees; **B**, strict consensus tree from analysis with unordered multistate characters; **C**, strict consensus tree from analysis with unordered multistate characters and implied weights. The 'a' indicates the polytomy discussed in the text. Only burnetiamorph taxa are represented in **B** and **C**. Asterisks denote Laurasian taxa.

Biogeography

Burnetiamorphs have long been known from South Africa and Russia, and more recently a fragment of skull roof (NMT RB4) was described from Tanzania (Sidor et al., 2010). *Lende* is the first burnetiamorph reported from Malawi (Jacobs et al., 2005), but as pointed out by Sidor et al. (2010:702), the faunal similarity and geographic proximity of the Tanzanian and Malawian localities suggests that the "two sets of exposures might represent parts of the same original basin." The unnamed Tanzanian specimen (NMT RB4; Sidor et al., 2010) is a larger individual than the *Lende* holotype and has two larger and more pachyostosed supraorbital bosses, but surprisingly, the frontal boss of *Lende* is much larger than that of the Tanzanian specimen. The Tanzanian NMT RB4 thus appears to belong to a different taxon to *Lende*, but because of the fragmentary nature of the latter specimen, further comparison between the two skulls is not possible at this stage and is dependent on finding better-preserved specimens.

The results of our phylogenetic analysis and the paleodistribution of burnetiamorph taxa suggest that what is now southern Africa was a potential area of origin for burnetiamorphs. This proposal is supported by the following observations: (1) the most basal taxon in our phylogeny (Fig. 4B, C), and those identified in previous phylogenetic analyses of burnetiamorphs (Sidor and Wellman, 2003; Rubidge et al., 2006; Sidor and Smith, 2007), is known from South Africa; (2) the oldest burnetiamorphs are known from South Africa; and (3) the majority of the known species (six of nine) are from the Karoo Basin. Alternatively, because burnetiamorphs are now known from South Africa, Malawi, Tanzania, Zambia, and Russia, they could have had a Pangea-wide distribution and the biogeographic pattern evident from the cladogram results from biased sampling because of problems relating to non-preservation in the fossil record, as was suggested by Sidor and Welman (2003).

The South African Karoo Basin preserves the longest temporal distribution of the Burnetiamorpha, which ranges from the middle Permian *Tapinocephalus* Assemblage Zone (AZ) until the late Permian *Dicynodon* AZ. Each of the described genera (apart from *Lemurosaurus*) is represented by only a single specimen. Currently, the only named middle Permian genera (*Bullacephalus* and *Pachydectes*) are from South Africa, and Sidor et al. (2014) mentioned the presence of this group in middle Permian deposits of Zambia, but this material has not been described. Of the late Permian taxa, five (*Lobalopex, Lophorhinus, Niuksenitia, Proburnetia*, and *Paraburnetia*) are from the stratigraphic equivalent of the *Tropidostoma* AZ; two (*Lemurosaurus* and *Lende*) are from the *Cistecephalus* AZ; and one (*Burnetia*) is from the *Dicynodon* AZ. Therefore, at this stage of knowledge, the heyday of burnetiamorphs was in *Tropidostoma* AZ times, at which stage they were widely distributed in Pangea. Of importance is the fact that the phylogeny presented in this work is not in agreement with the geological record of burnetiamorphs, because the basal representative *Lemurosaurus* is from the *Cistecephalus* AZ (Sidor and Welman, 2003), whereas *Pachydectes* and *Bullacephalus* from the older *Tapinocephalus* AZ are sister taxa in a polytomy following *Lemurosaurus* (see Fig. 4). The record of the large burnetiamorph *Pachydectes* (skull length of 318 mm) in the *Tapinocephalus* AZ indicates that in the middle Permian, burnetiamorphs and basal biarmosuchians (of the large size of *Hipposaurus*) were members of the large predator guild of the time, in conjunction with anteosaurid dinocephalians and basal therocephalians. The middle Permian burnetiamorphs have strongly pachyostotic cranial bones, a condition that is greatly reduced in the medium to small burnetiamorphs from the *Tropidostoma* and *Cistecephalus* AZs. Cranial pachyostosis regains importance in the latest Permian *Burnetia* from the *Dicynodon* AZ.

Discovery of late Permian burnetiamorphs in at least four basins in Africa (Jacobs et al., 2005; Sidor et al., 2010, 2014; this work) suggests that this geographic region was part of a corridor permitting the migration of the clade between 'Gondwana' and

'Laurasia,' where the group is represented by two Russian species during the late Permian. This supports the idea of a broadly distributed and highly connected therapsid community during the Permian (Sidor et al., 2013).

CONCLUSIONS

Lende chiweta, a new genus and species, is the first burnetiamorph from Malawi, and because the specimen is relatively well preserved, it adds to morphological, stratigraphic, and biogeographic understanding of the taxon. Burnetiamorph relationships are poorly understood, and this can be attributed to three main reasons. The paucity of specimens means that, of the known genera, only one (*Lemurosaurus*) is represented by more than one specimen. Secondly, because of the pachyostosed nature of the skull roof, sutural contacts are difficult to place with certainty (Rubidge and Sidor, 2002; Sidor and Welman, 2003). Finally, knowledge of some species (e.g., *Pachydectes elsi*) is based on extremely poorly preserved material that provides low-quality anatomical information.

Our phylogeny (Fig. 4) confirms that *Lemurosaurus* is the most basal burnetiamorph and that *Lende* is member of that group. Considering the poor support of monophyletic groups in our hypothesis, it is expected that the phylogenetic position of *Lende*, as well as other members of the group, will change as additional biarmosuchian specimens are discovered and improve the quality of information. The occurrence of the oldest burnetiamorphs, an enhanced diversity, as well as results of our phylogeny, suggests that southern Africa could be the area of origin for the lineage. The presence of this clade together with other therapsid genera in different Permian localities in what is now central Africa as well as in eastern Europe (Sues and Boy, 1988; Angielczyk and Kurkin, 2003; Kammerer et al., 2011; Sidor et al., 2013) suggests that central Africa was part of a corridor that allowed migration of burnetiids and other therapsids between southern Gondwana and Laurasia.

ACKNOWLEDGMENTS

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