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Two unrecognized burnetiamorph specimens from historical Karoo collections

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Two historical specimens from Permian rocks of the Karoo Basin represent previously unrecognized members of the rare therapsid group Burnetiamorpha. These specimens cannot be referred to any existing burnetiamorph species, but are left in open nomenclature because of their incompleteness (both are isolated skull roofs). The first specimen is from the *Tapinocephalus* Assemblage Zone (AZ) and is characterized by heavily pachyostosed supraorbital bosses and a low nasal crest. The second specimen is from the *Tropidostoma* AZ and is generally similar to the Malawian taxon *Lende*, but is unique among described burnetiamorphs in having a frontoparietal 'dome' that surrounds the pineal foramen. Phylogenetic analysis of burnetiamorphs recovers support for a split between *Proburnetia* and *Burnetia*-like burnetiids, here named Proburnetiinae subfam. nov. and Burnetiinae Broom, 1923.

Key words: Synapsida, Therapsida, Burnetiamorpha, Permian, Karoo Basin.

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INTRODUCTION

Burnetiamorpha is an unusual clade of Permian predatory therapsids whose members are characterized by elaborate ornamentation of the skull, often associated with cranial pachyostosis. Until recently, only two burnetiamorph specimens were known: the holotypes of *Burnetia mirabilis* Broom, 1923 from South Africa and *Proburnetia viatkensis* Tatarinov, 1968 from Russia. The new millennium, however, has witnessed an explosion in burnetiamorph richness, with ten burnetiamorph species currently recognized. Of the new additions to the group, two were previously known but only recently identified as burnetiamorphs (*Lemurosaurus pricei* and *Niuksenitia sukhonensis*; Sidor & Welman 2003), but most have been newly described (*Bullacephalus jacksoni* Rubidge & Kitching, 2003, *Lende chiweta* Kruger *et al*., 2015, *Lobalopex mordax* Sidor *et al*., 2004, *Lophorhinus willodenensis* Sidor & Smith, 2007, *Pachydectes elsi* Rubidge *et al*., 2006, and *Paraburnetia sneeubergensis* Smith *et al*., 2006). Burnetiamorphs have historically been considered very rare components of their respective faunas, as all but one species (*Lemurosaurus pricei*, represented by two definite skulls and an undescribed possible third [Sidor & Welman 2003; Sidor 2015]) are known from a single specimen.

The majority of burnetiamorphs belong to the family Burnetiidae Broom, 1923, defined by Rubidge & Sidor (2002) as the last common ancestor of *Burnetia mirabilis* and *Proburnetia viatkensis* and all of its descendants. Sidor & Smith (2007) recognized two subclades (Fig. 1) of burnetiids: (*Burnetia* + *Bullacephalus* + *Niuksenitia* + *Pachydectes*) and (*Proburnetia* + *Paraburnetia*), with *Lemurosaurus*, *Lobalopex* and *Lophorhinus* representing non-burnetiid burnetiamorphs. A more recent analysis of burnetiamorph phylogeny (Kruger *et al*. 2015) recovered the former clade ('*Burnetia*-line' burnetiids), but with *Paraburnetia* and *Proburnetia* as successive outgroups (and the new taxon *Lende* in an unstable position, typically as a non-burnetiid burnetiamorph).

Phylogenetic analysis of Burnetiamorpha is hampered by the extreme degree of pachyostosis in the group, typically obliterating cranial sutures and making the identity of skull roofing bones questionable. Numerous characters used in analyses of this clade (Rubidge *et al*. 2006; Smith *et al*. 2006; Sidor & Smith 2007; Kruger *et al*. 2015) relate to various bosses and other cranial excrescences on the skull surface. There is reason to be wary of overreliance on such characters, given that they are often intraspecifically variable in other therapsid groups with extensive cranial pachyostosis (e.g. dinocephalians – see Kammerer 2011; Liu 2013; Boos *et al*. 2015). However, boss morphology appears conserved throughout ontogeny in *Lemurosaurus pricei*, in which the holotype is significantly smaller than the referred specimen and likely represents a juvenile (Sidor & Welman 2003), so these characters may be less variable in burnetiamorphs than in other therapsids. Additional specimens of other burnetiamorph taxa are needed to gauge conservatism in boss morphology with growth in the group as a whole.

Another problematic aspect of burnetiamorph evolution is the fact that the most deeply-nested subclade ('*Burnetia*-line' burnetiids) includes the earliest-known representatives of Burnetiamorpha: *Bullacephalus* and *Pachydectes* from the middle Permian *Tapinocephalus* AZ of South Africa (Rubidge & Kitching 2003; Rubidge *et al*. 2006). This

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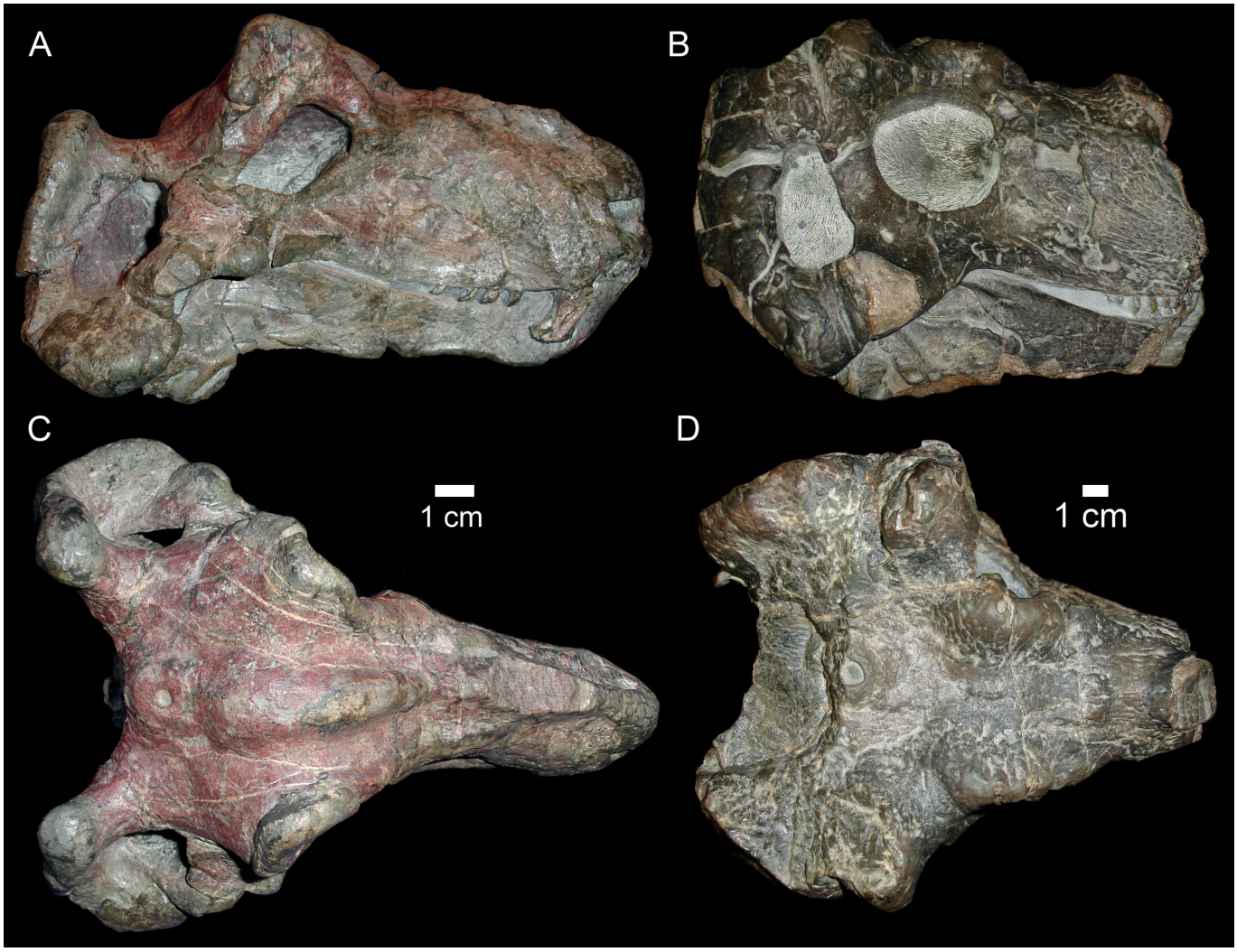


Figure 1. Representative burnetiids, showing exemplars from and characteristics of the two subclades recovered by Sidor & Smith (2007) and the current analysis: *Paraburnetia sneeubergensis* (SAM-PK-K10037) in (**A**) right lateral and (**C**) dorsal views; *Bullacephalus jacksoni* (BP/1/5387) in (**B**) right lateral and (**D**) dorsal views. In *Paraburnetia*, a single, triangular supraorbital boss is present (directly over the orbits), a massive median interorbital boss is present, and the pineal boss abuts the occiput. In *Bullacephalus*, two supraorbital bosses are present (with the larger one situated above the posterior margin of the orbit), no median interorbital boss is present, and the pineal boss is broadly separated from the occiput.

implies a lengthy ghost lineage between these taxa and the other '*Burnetia*-line' burnetiids (*Burnetia* and *Niuksenitia* are from the latest Permian *Daptocephalus* AZ and probable equivalent Russian strata, making them the last known burnetiamorphs [Rubidge & Sidor 2002]) and indicates a significant span of 'hidden' history for the rest of Burnetiamorpha (as the earliest known non-burnetiid burnetiamorphs occur in the late Permian *Tropidostoma* AZ).

Here I describe two previously unrecognized burnetiamorph specimens from historical collections in the Karoo Basin of South Africa: one from the middle Permian *Tapinocephalus* AZ and one from the late Permian *Tropidostoma* AZ. Although fragmentary (both specimens are isolated portions of skull roof), these fossils are not referable to any currently-known burnetiamorph species and suggest higher burnetiamorph diversity in the Karoo than currently recognized. These specimens exhibit a mosaic of features highlighting the complexity of boss evolution in the group and help to fill missing sections of burnetiamorph evolutionary history.

MATERIALS AND METHODS

The following specimens were examined by the author for comparative purposes: *Biarmosuchus tener* (PIN 1758/1, 2, 7, 8, 18, 19, 85), *Bullacephalus jacksoni* (BP/1/5387), *Burnetia mirabilis* (NHMUK R5097), *Herpetoskylax hopsoni* (BP/1/3924; CGP/1/67), *Hipposaurus boonstrai* (SAM-PK-8950, 9081), *Ictidorhinus martinsi* (AMNH FARB 5526), *Lemurosaurus pricei* (BP/1/816; NMQR 1702), *Lobalopex mordax* (CGP/1/61), *Lophorhinus willodenensis* (SAM-PK-K6655), *Lycaenodon longiceps* (NHMUK R5700), *Niuksenitia sukhonensis* (PIN 3159/1), *Pachydectes elsi* (BP/1/5735), *Paraburnetia sneeubergensis* (SAM-PK-K10037) and *Proburnetia viatkensis* (PIN 2116/1). Information on *Lende chiweta* was taken from Kruger *et al*. (2015).

The phylogenetic analysis was run in TNT v1.1 (Goloboff *et al*. 2008) using New Technology search parameters (sectorial searching, parsimony ratchet, drift, and tree fusing) set to find minimum tree length at least 20 times. Support metrics were based on symmetric resampling using 10000 replicates. The data matrix for this analysis is included as Supplementary material for this paper.

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Burnetiamorpha Broom, 1923

Burnetiamorph sp. A

Material. TM 4305, a weathered, largely unprepared partial skull comprising the interorbital region, temporal region and dorsal occiput (Figs 2 & 3).

Locality and horizon. Unknown locality, South Africa; *Tapinocephalus* AZ (Guadalupian). Precise locality data for this specimen has been lost. All that is known is that it is from the *Tapinocephalus* AZ, based on a label found with the specimen.

Description. The dorsal skull roof of this specimen is pachyostosed, and the supraorbital bosses are pachyostotic and massive. It appears that a single supraorbital boss was present on each side of the skull, as is the case for most burnetiamorphs (but not *Bullacephalus* and *Burnetia*). Incomplete preparation complicates the already-difficult delimitation of cranial sutures in this specimen, but a mid-parietal suture can be seen on the posterior half of the pineal boss (Fig. 2) and a mid-nasal suture can be seen in anterior cross-section (Fig. 3C). The pineal boss abuts the back of the skull, unlike the condition in *Bullacephalus* or *Burnetia*. The intertemporal region is very broad (Fig. 2), comparable to that of *Paraburnetia* (Fig. 1C) or *Proburnetia*, but not as broad as in *Bullacephalus* (Fig. 1D). The interorbital skull roof is flat (Fig. 2), similar to that of *Bullacephalus* or *Lobalopex* but unlike *Lende*, *Paraburnetia*, or *Proburnetia* in which there is a massive median boss. A narrow boss is present on the probable back of the nasal, as is visible in anterior view (Fig. 3C). The postorbital bar is pachyostosed and very anteroposteriorly expanded (Fig. 3A) compared to most biarmosuchians (including other burnetiids – compare with Fig. 1A, B). Ventrally, paired structures at the base of the orbits (Fig. 3D) may represent sphenoid elements. These elements are poorly known in burnetiamorphs, although Sidor & Smith (2007) described a sphenethmoid for *Lophorhinus*. Unlike the paired structures in TM 4305, the sphenethmoid of *Lophorhinus* is a single median ossification. As such, it is possible that these structures could also represent palatal elements, although this is difficult to reconcile with their position in the skull (i.e. intraorbital; compare their position in Fig. 3D with Fig. 3A, B).

Burnetiidae Broom, 1923
Burnetiinae Broom, 1923

Type genus. *Burnetia* Broom, 1923.

Included genera. *Bullacephalus* Rubidge & Kitching, 2003; *Niuksenitia* Tatarinov, 1977; *Pachydectes* Rubidge *et al*., 2006.

Diagnosis. Burnetiid therapsids characterized by the autapomorphic presence of two supraorbital bosses: a massive, ovoid boss above the anterior edge of the orbit and a more laterally-positioned boss above the posterior edge of the orbit.

Definition. *Burnetia mirabilis* Broom, 1923 and all taxa more closely related to it than *Proburnetia viatkensis* Tatarinov, 1968.

Proburnetiinae subfam. nov.

Type genus. *Proburnetia* Tatarinov, 1968.

Included genera. *Lende* Kruger *et al*., 2015; *Paraburnetia* Smith *et al*., 2006.

Diagnosis. Burnetiid therapsids characterized by the autapomorphic presence of a massive, anteroposteriorly elongate interorbital boss.

Definition. *Proburnetia viatkensis* Tatarinov, 1968 and all

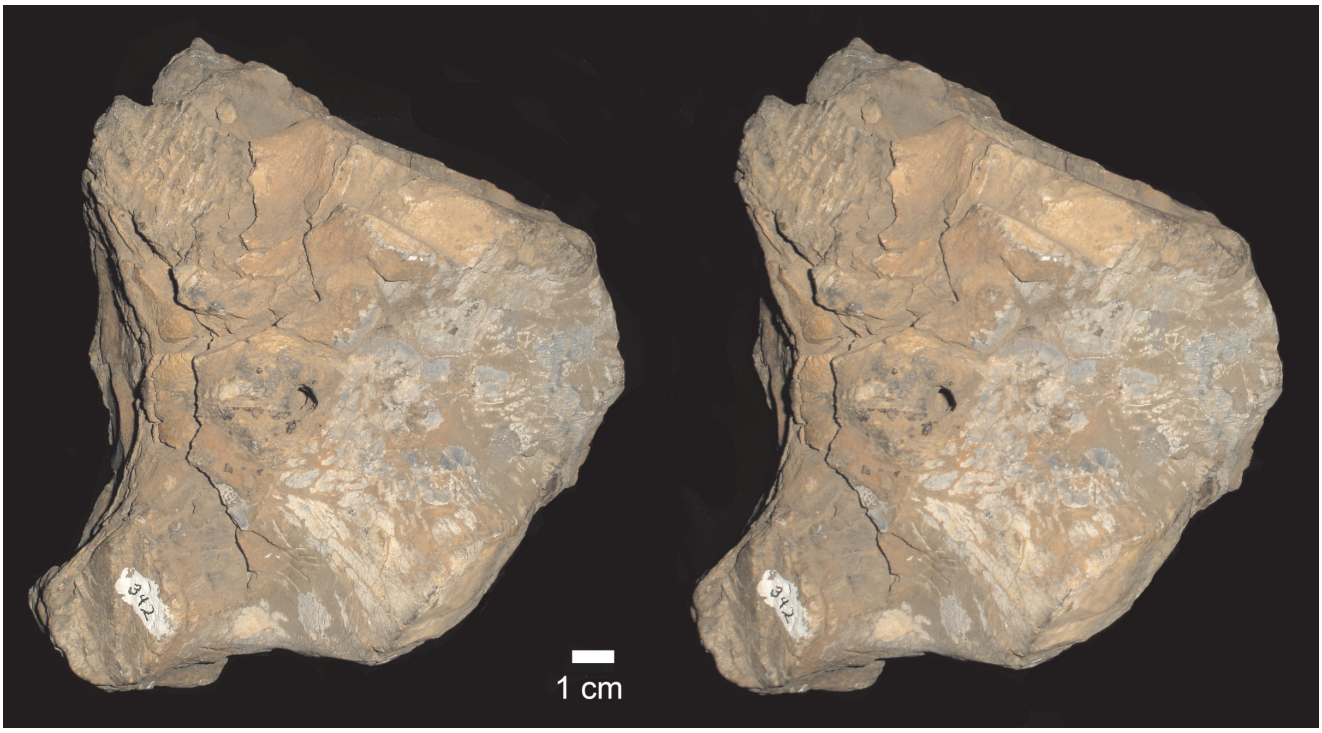


Figure 2. Stereopair of TM 4305 in dorsal view.

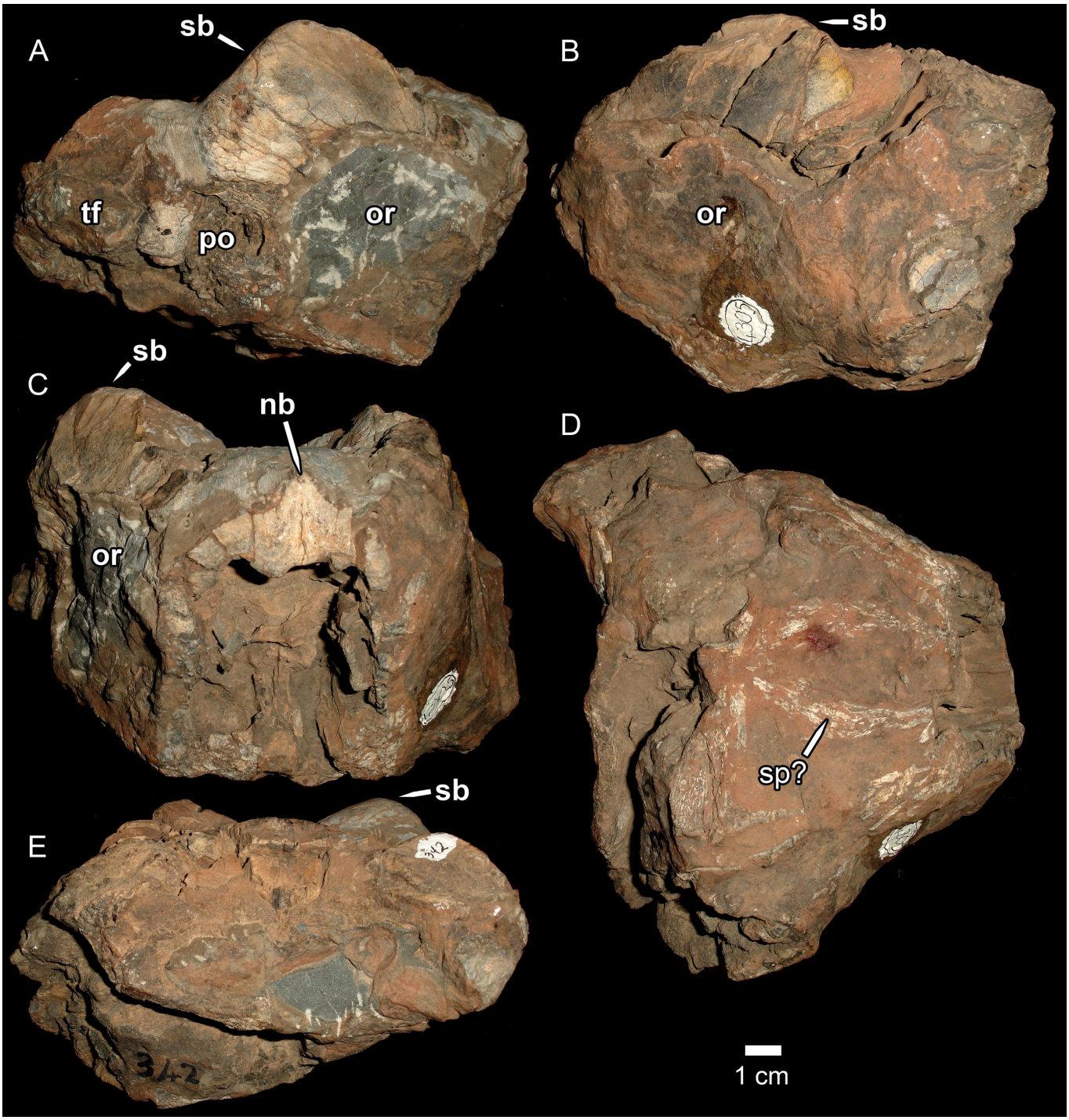


Figure 3. TM 4305 in (**A**) right lateral, (**B**) left lateral, (**C**) anterior, (**D**) ventral and (**E**) posterior views. nb, Nasal boss; or, orbit; po, postorbital bar; sb, supraorbital boss; sp, sphenoid element; tf, temporal fenestra.

taxa more closely related to it than *Burnetia mirabilis* Broom, 1923.

Burnetiamorph sp. B

Material. NHMUK R871, a fragment of skull roof preserving the interorbital region and temporal roof to the anterior edge of the pineal foramen (Figs 4–6).

Locality and horizon. Tafelberg, Beaufort West; *Tropidostoma* Assemblage Zone (Lopingian). This specimen was collected by Thomas Bain, at the same locality where he collected the type series of *Tropidostoma* (i.e. the holotypes of *T. dunnii*, *T. microtrema*, and topotypic material [Seeley 1889], all currently considered referable to *Tropidostoma dubium* [Kammerer *et al*. 2011]). Tafelberg consists of steep exposures near Teekloof Pass spanning (in descending order) the *Cistecephalus*, *Tropidostoma*, *Pristerognathus* and a small portion of the *Tapinocephalus* AZs (B. Rubidge, pers. comm.). As for most historical Karoo collections, precise stratigraphic data for Bain's Tafelberg material is not available. Given that all of this material other than NHMUK R871 is referable to *Tropidostoma*, however, it is reasonable to conclude that this collection originated in the *Tropidostoma* AZ.

Description. This fragment of skull roof was originally labeled 'Theriodont? Reptile' and subsequently relabeled 'Deinocephalian.' The collection of this specimen with

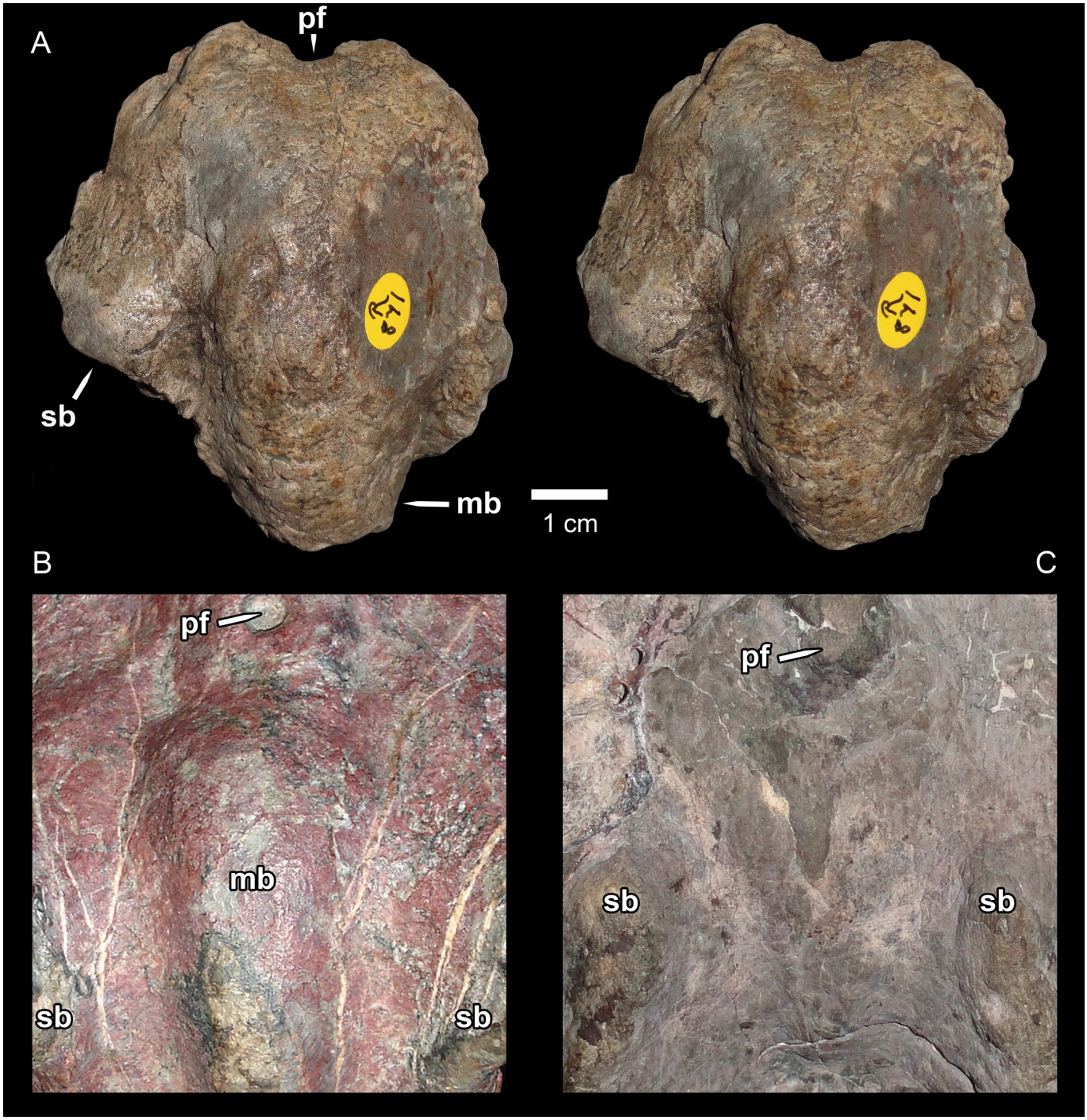


Figure 4. Burnetiid interorbital regions: **A**, Stereopair of NHMUK R871 in dorsal view; close-ups of the interorbital regions of (**B**) *Paraburnetia sneeubergensis* (SAM-PK-K10037) and (**C**) *Burnetia mirabilis* (NHMUK R5097). Note shared presence of a massive median boss in *Paraburnetia* and NHMUK R871 (absent in *Burnetia*), and separation between the median, supraorbital, and pineal bosses in *Paraburnetia* (distinguishing it from NHMUK R871). mb, Median boss; pf, pineal foramen; sb, supraorbital boss.

definitive specimens of *Tropidostoma* makes a dinocephalian identification very unlikely based on established biostratigraphic distributions (Rubidge 1995). Additionally, the high degree of pachyostosis in such a small skull (the preserved portion is 6.3 cm sagittal length, 5.6 cm maximum width) would be remarkable in a dinocephalian, but is typical of burnetiids. In *Anteosaurus* skulls of similar size, there is no development of the frontal boss or supraorbital 'horns' (Kammerer 2011), whereas a median boss and paired, presumed supraorbital bosses are clearly present in NHMUK R871. Among dinocephalians, NHMUK R871 is somewhat similar to *Styracocephalus platyrhynchus*, but differs from that taxon in the presence of a large median interorbital boss separated from the supraorbital bosses by a narrow channel anteriorly (Fig. 4). In *Styracocephalus*, the massive supraorbital bosses become confluent with a weaker frontal boss located anterior to the orbits (Rubidge & van den Heever 1997).

Among burnetiamorphs, NHMUK R871 is most similar to *Lende*, *Paraburnetia* and *Proburnetia*, which share a massive, anteroposteriorly elongate median boss in the interorbital region. The endocast of *Proburnetia viatkensis* (PIN 2116/1) confirms that this boss overlies the mid-frontal suture (Rubidge & Sidor 2002). In *'Burnetia*-line' burnetiids

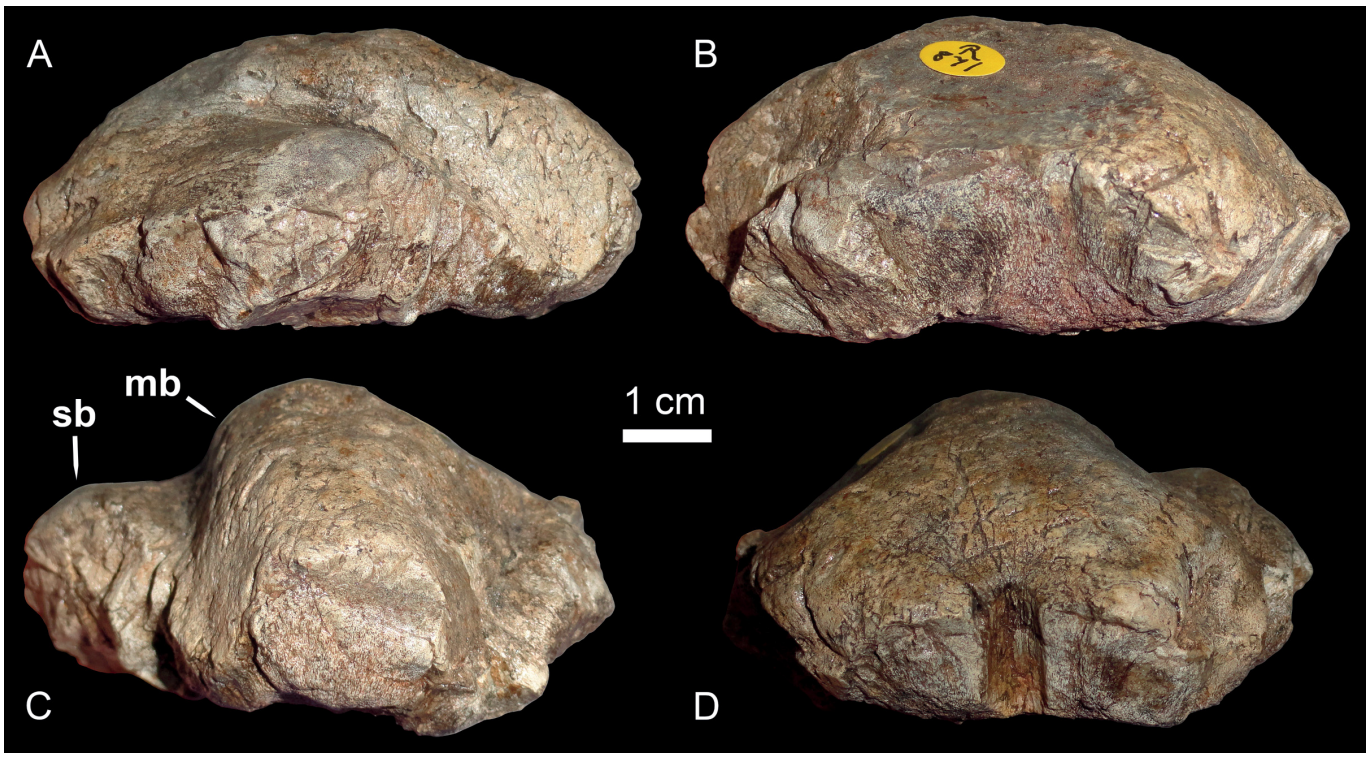


Figure 5. NHMUK R871 in (**A**) right lateral, (**B**) left lateral, (**C**) anterior and (**D**) posterior views. mb, Median boss; sb, supraorbital boss.

(at least *Burnetia*, *Bullacephalus* and *Pachydectes* – this region is not preserved for *Niuksenitia*), the interorbital region typically bears a weak median ridge (Figs 1D & 4C), but not a massive boss as in NHMUK R871. A broader, but still relatively low, median ridge is also present in the Tanzanian burnetiamorph NMT RB4 (also known solely from an isolated skull roof), which has been considered most similar to *Burnetia* (Sidor *et al*. 2010). The median frontal ridge is extremely weak in *Lobalopex*, and posterior to the contact with the nasals the interorbital region of this taxon becomes almost flat. Although only the anterior edge of the interorbital region is known for *Lophorhinus*, this taxon clearly lacked the sort of massive median boss present in NHMUK R871 – only a weak median ridge is present. In the other taxa (*Lende*, *Paraburnetia* and *Proburnetia*) with massive interorbital bosses, this structure extends anterior to the orbits, and would be evident in the preserved portion of *Lophorhinus* if present. Finally, *Lemurosaurus* has a distinct median interorbital boss, but it is transversely narrower and anteroposteriorly shorter than that of NHMUK R871 and the other taxa with massive median bosses.

In addition to sharing a massive median interorbital boss, NHMUK R871 also closely resembles *Lende* in the absence of a pineal boss (present in all other burnetiamorphs) and in the morphology of the supraorbital boss.

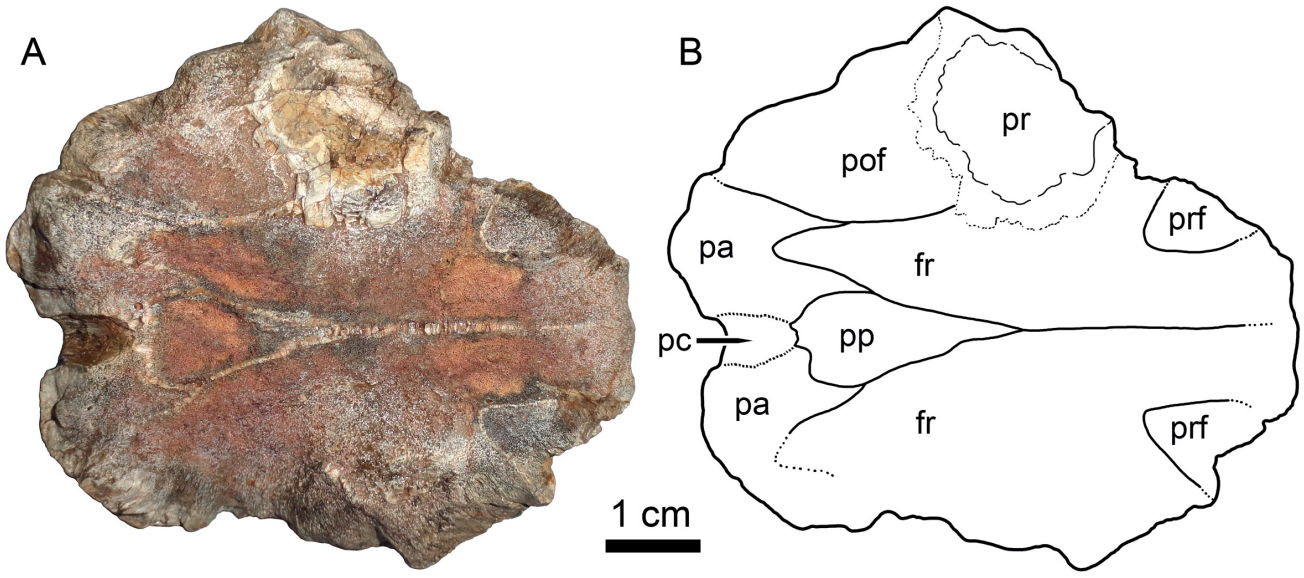


Figure 6. NHMUK R871 in (**A**) ventral view with (**B**) interpretive drawing. fr, Frontal; pa, parietal; pc, pineal canal; pof, postfrontal; pp, preparietal; pr, pachyostosed region at base of supraorbital boss; prf, prefrontal.

In *Paraburnetia* and *Proburnetia*, the supraorbital boss, although massive, is topologically restricted to the orbital rim (Fig. 1C), whereas in *Lende*, an attenuate portion of the supraorbital boss extends posteromedially in the direction of the pineal foramen (Kruger *et al*. 2015). The same condition is present in NHMUK R871 (Fig. 4A). However, despite these similarities, NHMUK R871 differs from *Lende* (as well as *Paraburnetia* and *Proburnetia*) in an important regard. In these other taxa, the median, supraorbital, and (in *Paraburnetia* and *Proburnetia*) pineal bosses are all discrete structures, separated from one another by shallow troughs (Figs 1C & 4B). In NHMUK R871, the supraorbital bosses extend far enough posteromedially to fuse with the median boss, forming a diffuse cranial 'dome' in the intertemporal region (Fig. 4A). This 'dome' is penetrated by the pineal foramen, which unlike all burnetiamorphs except *Lende* lacks a raised boss around it. In *Lende*, the pineal foramen is located on a flat surface posterior to the median boss, whereas in NHMUK R871 the median boss (as part of the 'dome') slopes gradually posteriorly, enveloping the foramen. This morphology is similar to that of tapinocephalid dinocephalians, in which the pineal boss becomes absorbed by a pachyostotic dome during ontogeny (Boos *et al*. 2015), and also vaguely resembles the frontoparietal dome of pachycephalosaurian dinosaurs. NHMUK R871 is also unusual in that it appears the median interorbital boss was slightly taller than the supraorbital bosses (Fig. 5C). This is probably an artefact of damage, as the orbital edges of the latter (typically where these bosses are tallest; see Fig. 1C) are not preserved. This said, it is worth noting that the median boss of *Lende* is also unusually tall, proportionally, being nearly equal in height to the supraorbital bosses (Kruger *et al*. 2015).

No sutures are visible dorsally on this specimen (Fig. 4); they have been completely obliterated by pachyostosis. Ventrally, however, clear sutures are visible (Fig. 6), providing some of the only information on the precise positions of the skull roofing bones in a burnetiid. Most of this specimen is made up of the frontals, although a large portion of the left postfrontal is also preserved, making up the supraorbital boss. The posterior tips of the prefrontals are preserved at the anterolateral edge of the specimen, indicating substantial posterior extension of this bone (as is typical of biarmosuchians). Most remarkably, a definite preparietal is present. This element originates immediately anterior to the pineal foramen and is broadest posteriorly, where it is flanked on both sides by anterior processes of the parietals. It strongly attenuates anteriorly between the frontals, giving an elongate triangular shape to the element as a whole. Previously, a preparietal had only been reported for *Pachydectes* within Burnetiamorpha (Rubidge *et al*. 2006), but it is likely that this element was present in many (possibly all) members of the group. Although obscured by pachyostosis, a preparietal-shaped depression is present anterior to the pineal foramen in *Lobalopex* (Sidor *et al*. 2004), and an attenuate element between the frontals in *Burnetia*, although not distinct from the parietals dorsally (Rubidge & Sidor 2002), is very similar in shape to the preparietal of NHMUK R871.

PHYLOGENETIC ANALYSIS

TM 4305 and NHMUK R871 were included in a modified version of the most recent phylogenetic analysis of burnetiamorphs (Kruger *et al*. 2015; itself modified from the analyses of Rubidge & Kitching [2003], Rubidge *et al*. [2006] and Sidor & Welman [2003]) to test their relationships. The analysis of Kruger *et al*. (2015) included 36 characters and 15 operational taxonomic units (OTUs), whereas the current analysis includes 30 characters and 17 OTUs. The following alterations were made to the Kruger *et al*. (2015) matrix for the current analysis:

For character 1 ('length of dorsal process of premaxillae'), Kruger *et al*. (2015) coded *Ictidorhinus martinsi* as having a short dorsal process of the premaxilla (i.e. not extending posterior to the level of the upper canine). However, this portion of the snout is not preserved in the holotype of *I. martinsi* (AMNH FARB 5526) – a damaged section covered in matrix extends between the premaxillae and nasals dorsally. This damaged section extends past the upper canine, so the posterior extent of the premaxilla dorsally is unclear. *Ictidorhinus martinsi* has been recoded as uncertain (?) for this character. Kruger *et al*. (2015) coded *Lophorhinus willodenensis* as being uncertain for this character, but it has been recoded as having a short dorsal process of the premaxilla (state 0). The posterior suture of the premaxilla is preserved in the holotype of *L. willodenensis* (SAM-PK-K6655) and is clearly anterior to the upper canine, as figured by Sidor & Smith (2007).

For character 2 ('lateral surface of lacrimal bears one or more deep fossae'), Kruger *et al*. (2015) coded the non-burnetiamorph biarmosuchians *Lycaenodon longiceps* and *Herpetoskylax hopsoni* as possessing lacrimal fossae, *contra* previous studies (e.g. Sidor & Welman 2003; Sidor & Smith 2007) that considered this fossa autapomorphic for Burnetiamorpha. In my examination of this material (NHMUK R5700, holotype of *Lycaenodon longiceps*, and CGP/1/67 and BP/1/3924, holotype and referred specimen of *Herpetoskylax hopsoni*), no lacrimal fossae were evident, and this character has been recoded as absent (state 0) for these taxa. Kruger *et al*. (2015) coded *Lende chiweta* as lacking a lacrimal fossa, but indicate in their description that this structure is present; this has been recoded accordingly.

For character 3 ('external surface of maxilla'), Kruger *et al*. (2015) coded *Burnetia mirabilis* as having a smooth external maxillary surface. While probably correct, the external bone surface of the holotype of *B. mirabilis* (NHMUK R5697) is so overprepared that this should be considered uncertain (?), and this taxon has been recoded as such.

For character 4 ('shape of dorsal surface of nasals'), Kruger *et al*. (2015) coded *Lende chiweta* and *Proburnetia viatkensis* as having a 'narrow median boss' (state 1). However, the breadth of the nasal boss in *Proburnetia* is nearly equal to (albeit anteroposteriorly shorter than) that of *Paraburnetia* (coded as state 2, 'with transversely expanded median boss') and significantly more transversely expanded than in taxa such as *Lophorhinus* or *Lobalopex* in which it forms a narrow crest. As such, *Proburnetia* has been recoded as state 2 for this character. The nasal boss of *Lende* is also more transversely expanded than that of *Lophorhinus*

or *Lobalopex*, so it has also been recoded as state 2. This character and character 5 ('shape of dorsal surface of frontals') have been changed to ordered in the current analysis, to reflect the fact that they represent a continuum of increasingly robust cranial bosses.

For character 6 ('posterolateral extension of frontal reaching the level of the midpoint to behind pineal foramen'), Kruger *et al*. (2015) coded *Ictidorhinus martinsi* and *Proburnetia viatkensis* as uncertain. Examination of the holotype of *I. martinsi* (AMNH FARB 5526) and endocast of the *P. viatkensis* type (PIN 2116/1; see also Rubidge & Sidor 2002) indicates that a posterolateral extension of the frontal is present (state 1) in both of these taxa.

The former characters 7 ('supraorbital margin') and 10 ('boss above postorbital bar') of Kruger *et al*. (2015) have been altered to better capture morphological variation among burnetiamorph taxa. These characters are dealing with two related issues: the presence or absence of a supraorbital horn and the shape of that structure. Presence of a supraorbital horn is a burnetiamorph synapomorphy, and is present in all burnetiamorphs in which the skull roof is known. In most taxa this horn is pachyostosed to form a massive boss, but even in *Lobalopex* and *Lophorhinus*, in which the dorsal orbital margin is not pachyostosed, there is a distinct triangular flange above the orbits. Among burnetiamorphs with extensive cranial pachyostosis, two basic supraorbital boss morphologies are present: there is either a single large, triangular boss directly above the orbits (present in *Lemurosaurus*, *Lende*, *Paraburnetia* and *Proburnetia*) or two supraorbital bosses, with a low, massive, ovoid boss above the anterior edge of the orbit and a second, more laterally-positioned boss above the posterior edge of the orbit and the postorbital bar (present in *Bullacephalus* and *Burnetia*; a boss is present above the postorbital bar in *Pachydectes*, but the orbital region of this taxon is too badly damaged to confidently code this character). The new characters 8 ('supraorbital horn') and 9 ('supraorbital boss morphology') reflect these distinctions. For new character 9, taxa lacking a pachyostosed supraorbital boss are coded as not applicable (–).

Character 8 of Kruger *et al*. (2015) ('adductor musculature originates on dorsal surface of postorbital') has been deleted because it was parsimony uninformative (all taxa were coded as either 0 or ?).

For character 11 ('postorbital bar scoop-shaped because temporal fenestra undercuts it'), Kruger *et al*. (2015) coded *Lende chiweta* and *Paraburnetia sneeubergensis* as uncertain. In neither of these taxa does the temporal fenestra undercut the orbit (an anterior expansion of the right temporal fenestra in MAL 290, holotype of *L. chiweta*, represents damage), and they have been recoded as absent (state 0) for this character.

Character 15 ('prearietal') of Kruger *et al*. (2015) previously had three states ('absent', 'present but is narrowly separated from pineal foramen by parietals', and 'present and forms anterior margin of pineal foramen'), with only *Ictidorhinus martinsi* and *Lycaenodon longiceps* coded as having state 1. However, in *Ictidorhinus*, the prearietal clearly forms the anterior margin of the pineal foramen. For *Lycaenodon*, previous analyses have utilized a composite coding based on the holotype (NHMUK R5700) and a referred specimen (RC 20; referred to *L. longiceps* by Sigogneau-Russell 1989). However, NHMUK R5700 and RC 20 differ in several regards: for example, RC 20 has broader palatines and significantly narrower choanae than NHMUK R5700. In this feature RC 20 is very similar to *Ictidorhinus*, and it is possible that RC 20 actually represents an adult skull of *I. martinsi*. Given continued uncertainty surrounding the distinction between *Ictidorhinus* and *Lycaenodon* (Sidor & Rubidge 2006), for the purposes of the current analysis the codings for *Ictidorhinus martinsi* and *Lycaenodon longiceps* are based solely on their respective holotypes. Because the pineal region is absent in NHMUK R5700, *Lycaenodon* is here coded as uncertain (?) for prearietal morphology. In RC 20, however, the prearietal forms the anterior margin of the pineal foramen, so even if this specimen was included in the *Lycaenodon* hypodigm it would not warrant use of character state 1 of Kruger *et al*. (2015). This character has been changed to simply reflect presence/absence of the prearietal. It must be noted, however, that in the only taxon coded as lacking a prearietal (*Biarmosuchus tener*), this absence may be autapomorphic. The broad distribution of prearietals among basal therapsids (being common in gorgonopsians and anomodonts in addition to biarmosuchians) suggests that the absence of this element in *Biarmosuchus* may not accurately reflect the ancestral condition for Biarmosuchia.

Character 16 ('vomer') of Kruger *et al*. (2015) has been deleted because it was parsimony uninformative. All known biarmosuchians possess an unpaired vomer. Kruger *et al*. (2015) coded a number of non-burnetiid taxa as uncertain for this character, but an unpaired vomer is clearly present in *Biarmosuchus*, *Hipposaurus* and *Ictidorhinus* and appears to be present in *Herpetoskylax*, *Lemurosaurus* and *Lobalopex* as well. The only taxon Kruger *et al*. (2015) coded as having a paired vomer was *Bullacephalus jacksoni*. However, there is no evidence for a paired vomer in this taxon: although the preserved portion of the vomer is made up of paired ventral ridges, similar structures are present in many other biarmosuchians that have a fused vomer, representing ventral extensions of the lateral vomerine margins. Examining the vomer of the *B. jacksoni* holotype (BP/1/5387) in anterior view, there is no clear suture between these ridges, and I interpret this element as unpaired. Even if this interpretation is incorrect and there is a paired vomer in *Bullacephalus*, this would then be an autapomorphy of that genus. So regardless of the condition in this taxon, this character is parsimony uninformative.

For character 17 ('palatine dentition'), Kruger *et al*. (2015) coded *Niuksenitia sukhonensis* as uncertain. Although the anterior palate is largely missing in the holotype of *N. sukhonensis* (PIN 3159/1), the left palatine boss is well preserved and shows that dentition on this element was limited to a single tooth row along the lateral and medial edges of the boss (state 1). Kruger *et al*. (2015) coded *Bullacephalus* and *Pachydectes* as having extensive palatine dentition (state 0). While these taxa have a dense cluster of palatal teeth on the pterygoid, they have only narrow tooth rows on the palatine, and as such have been recoded (to state 1) for this character.

Character 21 ('shape of postparietal') of Kruger *et al*. (2015) has been deleted because it was parsimony uninformative. Of the three character states ('wider than tall', 'approximately square', and 'taller than wide'), only *Ictidorhinus martinsi* was coded as 'wider than tall' and no taxa were coded as 'taller than wide.'

For character 22 ('ratio of dentary height in canine versus anterior postcanine regions'), Kruger *et al*. (2015) coded *Lende chiweta* as showing a pronounced difference between the canine and postcanine heights of the dentary. The dentary proportions of *Lende* are comparable to those of *Proburnetia*, however, so the former taxon has been recoded as showing nearly equivalent heights for these measures (state 1).

For character 23 ('dentary-angular suture'), Kruger *et al*. (2015) coded *Paraburnetia sneeubergensis* as being uncertain. The mandible of *Paraburnetia* is well preserved and the posterior margin of its dentary is clearly incised (state 1), so this taxon has been recoded accordingly.

Character 24 ('palatine boss size') of Kruger *et al*. (2015) has been deleted because it is vague (no quantitative bounds were provided for the distinction between 'small', 'medium' and 'large' bosses) and inconsistently coded. For example, Kruger *et al*. (2015) code *Hipposaurus* as having a large boss, *Lobalopex* as having a medium-sized boss, and *Lycaenodon* as having a small boss, but the palatine boss is not preserved in *Lycaenodon* (i.e. NHMUK R5700; the palatine boss in RC 20 is present, but too badly damaged to accurately measure) and the relative length of this structure (measured as boss length relative to basal skull length) is very similar in *Hipposaurus* (0.14 in SAM-PK-9081) and *Lobalopex* (0.15 in CGP/1/61) (note also that the boss is actually somewhat smaller in *Hipposaurus* than in *Lobalopex*).

Character state 1 ('nubbin-like boss') has been deleted from character 26 ('squamosal horns') of Kruger *et al*. (2015), because in the only taxon with this character state (*Lemurosaurus pricei*) the boss in question is on the lateral surface of the postorbital, not the squamosal. The coding for *Pachydectes* has been changed from present to uncertain (?), because the back of the skull is damaged in the holotype (BP/1/5735) of this taxon.

Character 27 ('crest on the postparietal') of Kruger *et al*. (2015) has been deleted because this structure (the nuchal crest) is present in all biarmosuchians and the different states ('absent to slight', 'moderate' and 'large') are not readily differentiable. From my examination of these specimens, the primary sources of variation in this character are degree of taphonomic wear and overall skull size. This character has been replaced with a new postparietal character (new character 20), based on the presence or absence of a pair of descending ridges lateral to the nuchal crest, extending from the posterior edge of the parietal onto the postparietal. These ridges are well developed in burnetiids; they are clearly present in *Burnetia*, *Lende*, *Paraburnetia* (Fig. 7A) and *Proburnetia*, and are exceptionally well developed (with rugose surface texture) in *Bullacephalus* (Fig. 7B). Very small but distinct descending ridges are present in the same position in *Lobalopex* but appear to be absent in *Lemurosaurus*.

Character 28 ('dorsal skull angulation above the orbital region') of Kruger *et al*. (2015) has been deleted because variation in this character is primarily due to miscoding or taphonomic distortion. This character refers to the characteristic angle in the dorsal profile of biarmosuchian skulls, which forms an apex above the orbits, with downward slope of both the snout and temporal regions. Kruger *et al*. (2015) coded five taxa as lacking this angulation: *Herpetoskylax*, *Lobalopex*, *Proburnetia*, *Burnetia* and *Bullacephalus*. In *Lobalopex mordax*, the absence of this angulation can be attributed to the extreme dorsoventral crushing suffered by the holotype (CGP/1/61). In the holotype of *Herpetoskylax hopsoni* (CGP/1/67), there is a relatively weak posterior slope to the temporal region, but the characteristic biarmosuchian angulation is definitely present in the referred specimen BP/1/3924. In the burnetiids *Bullacephalus*, *Burnetia* and *Proburnetia*, this angulation is absent, but only because the dorsal margin of the temporal region is expanded due to the presence of pachyostosed squamosal horns. In the absence of these horns, the skull would have the typical

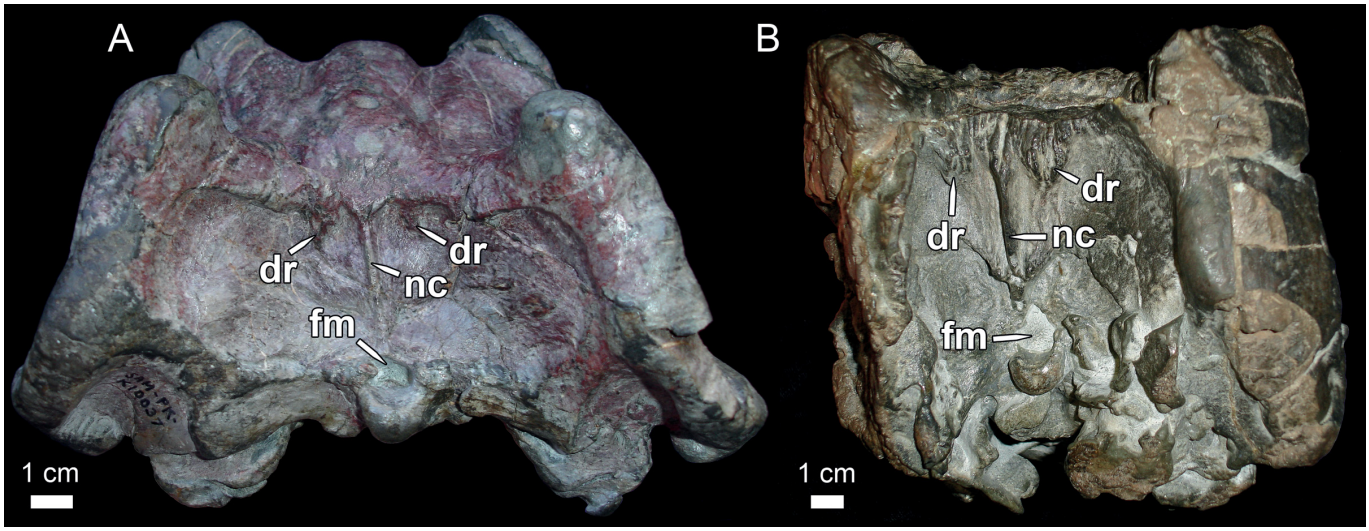


Figure 7. Burnetiamorph occiputs, illustrating presence of paired descending ridges extending between the parietals and postparietal, lateral to the nuchal crest (new character 20): **A**, *Paraburnetia sneeubergensis* (SAM-PK-K10037); **B**, *Bullacephalus jacksoni* (BP/1/5387). dr, Descending ridge; fm, foramen magnum; nc, nuchal crest.

biarmosuchian morphology (as indicated by the relatively ventral position of the temporal fenestra relative to the orbit). As such, the only real morphological variation being captured by this character is redundant with character 26 ('squamosal horns') of Kruger *et al*. (2015).

Character 31 ('arcant ridge extending from anterodorsal margin of orbit towards external naris') of Kruger *et al*. (2015) has been deleted because it was parsimony uninformative. Kruger *et al*. (2015) coded this character as being present in two taxa: *Lobalopex mordax* and *Lende chiweta*. However, the apparent ridge between the orbit and naris in the holotype of *L. mordax* (CGP/1/61) is artefactual – it is the result of dorsoventral crushing creating apparent biplanarity between the maxilla and nasal. There is a real ridge on the lateral surface of the snout in *Lobalopex*, but it corresponds to the underlying canine root and does not extend to the naris. As such, this character is, at best, interpreted as an autapomorphy of *Lende*.

Character 32 ('posterior extension of the postfrontal') of Kruger *et al*. (2015) has been deleted because it was parsimony uninformative. The only taxon for which Kruger *et al*. (2015) coded this as absent is *Biarmosuchus tener*. In the holotype of *Biarmosuchus tener* (PIN 1758/2), the temporal region is poorly preserved and the extent of the postfrontal is difficult to determine. In multiple referred specimens, however (PIN 1758/1, PIN 1758/7, PIN 1758/18), there is clearly a posterior extension of the postfrontal present.

Character 33 ('boss on anterior margin of squamosal') of Kruger *et al*. (2015) previously had three states ('absent', 'small' and 'elongated'). Kruger *et al*. (2015) coded *Lemurosaurus*, *Lende* and *Lobalopex* as having 'small' squamosal bosses and *Burnetia, Pachydectes* and *Proburnetia* as having 'elongate' squamosal bosses (*Paraburnetia* and *Niuksenitia* were coded as '?', but these taxa have very prominent squamosal bosses). While this boss is indeed weakly developed in *Lemurosaurus* and *Lobalopex*, the squamosal boss of *Lende* is rather larger relative to its skull size. The squamosal boss morphology among burnetiids varies extensively – 'elongated' does not accurately describe the low bosses of *Proburnetia* or the complex curved structure in *Paraburnetia*, for example. Only in *Burnetia* and *Niuksenitia* are the squamosal bosses nearly identical in morphology. Given the difficulty in firmly demarcating 'small' from 'elongate' bosses in this sample of taxa, this character has been changed to simply reflect presence/absence of the squamosal boss. Kruger *et al*. (2015) coded *Bullacephalus* as lacking a squamosal boss, but although this taxon lacks an anteriorly-projecting boss like that of *Niuksenitia* or *Paraburnetia*, there is clearly a boss on the squamosal below the temporal fenestra. In *Pachydectes* the subtemporal squamosal is not preserved, so its coding has been changed to uncertain (?).

For character 34 ('prefrontal boss'), Kruger *et al*. (2015) coded *Paraburnetia sneeubergensis* as uncertain. A swollen portion of the prefrontal is present at the anterior margin of the orbit in this taxon, so it has been recoded as present (state 1).

For character 35 ('zygomatic arch elevated in lateral view'), Kruger *et al*. (2015) coded *Hipposaurus boonstrai* and *Paraburnetia sneeubergensis* as uncertain. This is a problematic character; although the zygoma is clearly more elevated in, e.g. *Herpetoskylax* than in *Bullacephalus*, there is not a clear demarcation between these end-members. This character is tentatively retained; as *Paraburnetia* exhibits a morphology comparable to burnetiids in which this character is listed as absent (state 0), it has been recoded as such. Similarly, the morphology of *Hipposaurus* is comparable to that of *Herpetoskylax*, so it has been recoded as elevated (state 1). Kruger *et al*. (2015) coded *Lycaenodon longiceps* and *Lobalopex mordax* as having an elevated zygomatic arch, but this part of the skull is missing in the former and badly crushed in the latter; these have been recoded as uncertain (?).

Character 36 ('palatine teeth') of Kruger *et al*. (2015) has been deleted because it was redundant with their character 17 ('palatine dentition').

Characters 11 ('pachyostosis of zygomatic arch') and 13 ('squamosal thickened along its posterior border with the tabular') of Sidor & Smith (2007) have been added as new characters 16 and 22 in the present analysis. The latter is treated as ordered.

DISCUSSION

Results of the phylogenetic analysis

The full analysis, including the two new specimens, yielded 22 most parsimonious trees of length 45 (consistency index=0.778, retention index=0.882). In the strict consensus (Fig. 8A), TM 4305 is recovered as a burnetiamorph more derived than *Lemurosaurus*, in a polytomy with *Lobalopex*, *Lophorhinus*, all *'Burnetia*-line' burnetiids, and a clade made up of the *'Proburnetia*-line' burnetiids. NHMUK R871 is recovered in a polytomy with *Lende*, *Paraburnetia* and *Proburnetia* in the *'Proburnetia*-line' clade. Deletion of the extremely incomplete new specimens (TM 4305 could be coded for only 4 of 30 characters; NHMUK R871 for 6) from the analysis yielded three most parsimonious trees of length 45. The strict consensus of these trees is a topology similar to that of Sidor & Smith (2007), albeit with *Lende* included within the Burnetiidae (in a polytomy with *Paraburnetia* and *Proburnetia*) and the non-burnetiamorphs *Herpetoskylax* and *Ictidorhinus* collapsed into a polytomy with *Lycaenodon* (Fig. 8B).

Within Burnetiidae, two subclades are formally recognized here, corresponding to the *'Proburnetia*-line' and *'Burnetia*-line' burnetiids. All previous phylogenetic analyses of Burnetiamorpha have recovered a close relationship between *Burnetia*, *Niuksenitia* and *Bullacephalus* to the exclusion of other burnetiamorphs (Sidor & Welman 2003; Sidor *et al*. 2004; Smith *et al*. 2006), and all analyses that included *Pachydectes* also recovered it as a member of this group (Rubidge *et al*. 2006; Sidor & Smith 2007; Kruger *et al*. 2015). Sidor *et al*. (2004), Smith *et al*. (2006) and Sidor & Smith (2007) also previously recovered *Paraburnetia* and *Proburnetia* as sister-taxa (with this clade in turn forming the sister of *'Burnetia*-line' burnetiids). Although Kruger *et al*. (2015) did not recover a monophyletic group of *'Proburnetia*-line' burnetiids, this portion of their topology was influenced by character codings disputed here (see above). Here, the *'Burnetia*-line' and *'Proburnetia*-line'

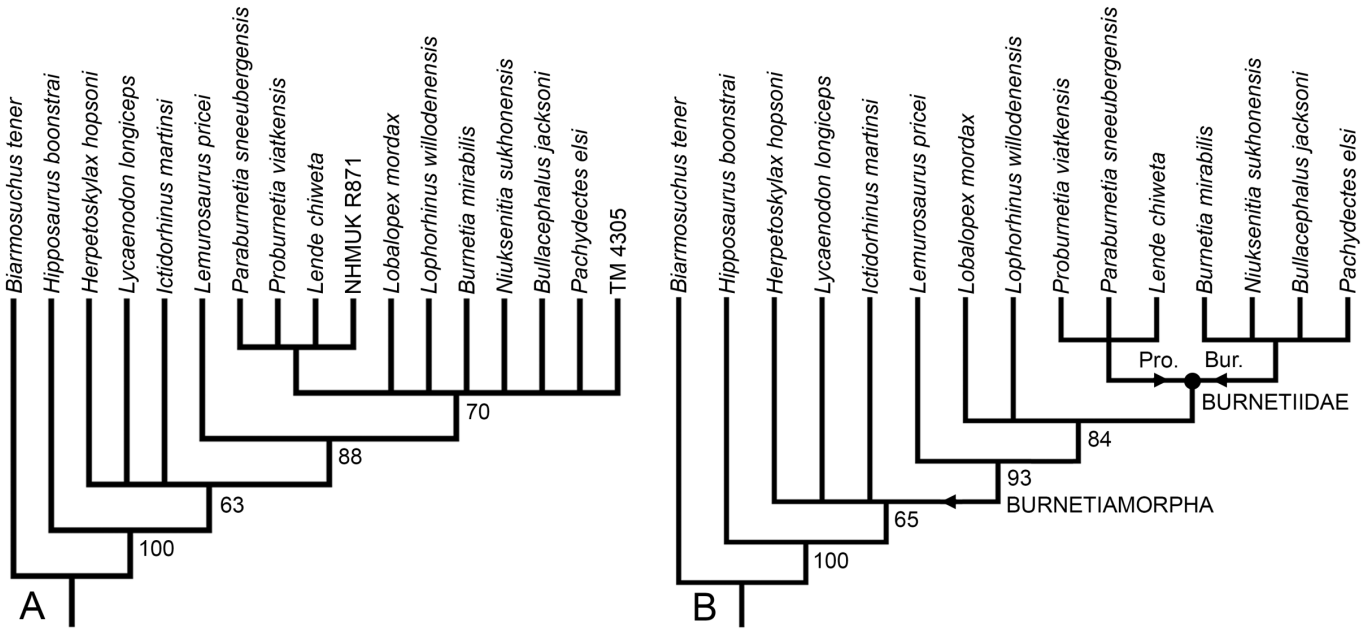


Figure 8. Results of the phylogenetic analysis. **A**, Strict consensus of complete taxon set; **B**, strict consensus with TM 4305 and NHMUK R871 excluded from the analysis. Numbers at nodes represent symmetric resampling values. Pro., Proburnetiinae; Bur., Burnetiinae.

burnetiid subclades are called Burnetiinae Broom, 1923 and Proburnetiinae nov., and make up a node-stem triplet with Burnetiidae.

Burnetiamorph diversity and distribution

Although fragmentary, the new specimens TM 4305 and NHMUK R871 differ from all previously described burnetiamorphs in their overlapping morphology. Because of their incompleteness, these specimens are left in open nomenclature, but they are likely to represent distinct taxa and indicate even higher burnetiamorph richness in the Karoo than currently thought. Although recovered in somewhat uncertain positions in the phylogenetic analysis, these specimens help fill in significant ghost lineages in South African Burnetiamorpha. Though it was recovered in a polytomy with burnetiids, *Lobalopex* and *Lophorhinus*, TM 4305 is likely to be more closely related to Burnetiidae than the latter two genera based on its high degree of cranial pachyostosis, including massive supraorbital bosses and anteroposteriorly expanded postorbital bar. This specimen lacks the median interorbital boss characteristic of proburnetiines and the double supraorbital bosses, very broad intertemporal region, and anteriorly-positioned pineal foramen characteristic of burnetiines (though these characters may also be absent in *Pachydectes*). As such, it could lie immediately outside of Burnetiidae or represent a basal member of either subfamily. This specimen requires additional study (with either new preparation or CT scanning) to solidify its relationships, as it could represent the only proburnetiine or non-burnetiid burnetiamorph known from the *Tapinocephalus* AZ.

NHMUK R871 is recovered as a proburnetiine, representing the oldest African record of the group (*Paraburnetia* is from low in the *Cistecephalus* AZ and, although the correlation is somewhat uncertain, the Chiweta beds that produced *Lende* are generally considered *Cistecephalus* AZ equivalents; Jacobs *et al*. 2005; Smith *et al*. 2006). Though recovered in a polytomy with all other proburnetiines, several features (absence of a pineal boss, posteromedial expansion of the supraorbital bosses) suggest that NHMUK R871 is most closely related to *Lende* among described burnetiamorphs. Burnetiid biogeography is difficult to assess given their spotty record, but they appear to be broadly distributed even within subclades, with both proburnetiines and burnetiines being present in South Africa (*Paraburnetia*, NHMUK R871, *Bullacephalus*, *Burnetia*, *Pachydectes*), east Africa (*Lende*, NMT RB4) and Russia (*Proburnetia*, *Niuksenitia*). In addition to the published records of east African burnetiamorphs (Sidor *et al*. 2010; Kruger *et al*. 2015), there are currently a number of undescribed specimens referable to this group from the Madumabisa Mudstone Formation of Zambia (Sidor 2015; Sidor *et al*. 2015; Whitney & Sidor in press). Although no burnetiamorphs have yet been recovered from other Permian therapsid-bearing regions (e.g. Brazil, China, India, Scotland), given the general rarity of this group, their absence from these areas should be considered questionable (especially considering that significantly more abundant clades such as Gorgonopsia and Therocephalia have yet to be found there). Greater exploration of these understudied regions will be vital to improving our understanding of early therapsid evolution, but as the specimens described herein indicate, there is clearly still much to be discovered even in the South African fossil record.

ABBREVIATIONS

Institutional

AMNH FARB	American Museum of Natural History, Fossil Amphibian, Reptile, and Bird Collection, New York, U.S.A.
BP	Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa;
CGP	Council for Geoscience, Pretoria, South Africa
MAL	Malawi Department of Antiquities Collection, Lilongwe and Nguludi, Malawi
NHMUK	the Natural History Museum, London, U.K.

NMQR	National Museum, Bloemfontein, South Africa
NMT	National Museum of Tanzania, Dar es Salaam, Tanzania
PIN	Paleontological Institute of the Russian Academy of Sciences, Moscow, Russia
RC	Rubidge Collection, Wellwood, Graaff-Reinet, South Africa
SAM	Iziko Museums of South Africa, Cape Town, South Africa
TM	Ditsong National Museum of Natural History, Pretoria, South Africa.

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