Two unrecognized burnetiamorph specimens from historical Karoo collections

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Received 5 January 2016. Accepted 9 March 2016

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 species 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 *Niuksentia sukhonensis*; Sidor & Welman 2003), but most have been newly described (*Bullacephalus jacksoni* Rubidge & Kitching, 2003, *Lende chiweta* Liu 2013; *Bullaeccephalus* jacksoni Rubidge & Kitching, 2003, *Lende chiweta* Kruger et al., 2015, *Lobalopex mordax* Sidor et al., 2004, *Lophorhinus willdenensis* Sidor & Smith, 2007, *Pachydecetes 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 Burnetiiidae 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* + *Niuksentia* + *Pachydecetes*) 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 *Pachydecetes* from the middle Permian *Tapinocephalus* AZ of South Africa (Rubidge & Kitching 2003; Rubidge et al. 2006). This
implies a lengthy ghost lineage between these taxa and the other ‘Burnetia-line’ burnetids (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 boonstraui (SAM-PK-K8950, 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 sneeuwbergensis (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.
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

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

**Figure 6.** NHMUK R871 in (A) ventral view with (B) interpretive drawing. fr, Frontal; pa, parietal; pc, pineal canal; pof, postfrontal; pp, prefrontal; 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 burnetid. 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 willodonensis* 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. willodonensis* (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 *Lycaeodon 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 *Lycaeodon 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 chiveta* 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*. 

70 ISSN 2410-4418 *Palaeont. afr.* (2016) 50: 64–75
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 endocard 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 Lophornius, 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 Pachydeces, 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 sneeburgensis as uncertain. In neither of these taxa does the temporal fenestra under-cut 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 (‘preparietal’) 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 Lycocodon longiceps coded as having state 1. However, in Ictidorhinus, the preparietal clearly forms the anterior margin of the pineal foramen. For Lycacodon, 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 Lycocodon (Sidor & Rubidge 2006), for the purposes of the current analysis the codings for Ictidorhinus martinsi and Lycocodon longiceps are based solely on their respective holotypes. Because the pineal region is absent in NHMUK R5700, Lycocodon is here coded as uncertain (?) for preparietal morphology. In RC 20, however, the preparietal forms the anterior margin of the pineal foramen, so even if this specimen was included in the Lycocodon 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 preparietal. It must be noted, however, that in the only taxon coded as lacking a preparietal (Biarmosuchus tener), this absence may be autapomorphic. The broad distribution of preparietals 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 Niuksentitza 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 Pachydeces 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 Lictidorhinus 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 chitwa 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 ?), 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 parietales 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 autopomorphy 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, Pachydecetes and Proburnetia as having ‘elongate’ squamosal bosses (Paraburnetia and Niuksenitida 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 Niuksenitida 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 Niuksenitida or Paraburnetia, there is clearly a boss on the squamosal below the temporal fenestra. In Pachydecetes 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 Lycacenodon 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 dention’).

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 Burnetidae (in a polytomy with Paraburnetia and Proburnetia) and the non-burnetioid morphs Herpetoskylax and Ictidorchinus collapsed into a polytomy with Lycacenodon (Fig. 8B).

Within Burnetidae, 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, Niuksenitida and Bullacephalus to the exclusion of other burnetioids (Sidor & Welman 2003; Sidor et al. 2004; Smith 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’
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 Pachydecetes). As such, it could lie immediately outside of Burnetidae 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 proburnetine, representing the oldest African record of the group (Paraburnetia is from low in the Cistecephalus AZ and, although the correlation is somewhat uncertain, the Chweta 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, Pachydecetes), east Africa (Lende, NMT RB4) and Russia (Proburnetia, Niukensitia). 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.
REFERENCES


