A NEW BURNETIID FROM THE MIDDLE PERMIAN OF ZAMBIA AND A REANALYSIS OF BURNETIAMORPH RELATIONSHIPS

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Abstract: A new taxon of burnetiamorph therapsid, *Mobaceras zambeziense* gen. et sp. nov., is described on the basis of a partial skull recovered from the lower Madumabisa Mudstone Formation (Guadalupian) of Zambia. This taxon can be distinguished from all previously known burnetiamorphs by its unique cranial boss morphology, including a bulbous nasal boss on a 'stalk' and highly discretized, exaggerated anterior and posterior supraorbital bosses. Burnetiamorph phylogeny has recently become contentious; here, support for conflicting phylogenetic topologies is evaluated on a character-by-character basis and a revised phylogenetic analysis is presented. The clades Burnetiamorpha and Burnetiidae are supported with their traditional composition, including genera (viz. *Bullacephalus* and *Pachydectes*) recently assigned to a separate family (Bullacephalidae, here considered synonymous with Burnetiidae). The traditional dichotomy within Burnetiidae into Burnetiinae and Proburnetiinae is upheld, with *Mobaceras* recovered as a burnetiine, along with *Bullacephalus*, *Burnetia*, *Niuksenitia*, and *Pachydectes*.

Key words: Synapsida, Therapsida, Burnetiamorpha, Permian, Guadalupian, Zambia.

CRANIAL ornamentation in the form of pachyostosed 'horns', bosses, or crests evolved numerous times in Permian and Triassic therapsids. Nasal bosses are present in most dicynodonts, supraorbital bosses are present in both anteosaurian dinocephalians and rubidgeine gorgonopsians, and median frontal bosses are present in tapinocephalid and some anteosaurian dinocephalians (Angielczyk 2001; Rubidge & Sidor 2001; Kammerer 2011, 2016a). Especially baroque cranial ornamentation is present in the Burnetiamorpha, a subclade of the basal therapsid group Biarmosuchia. All known burnetiamorph skulls feature frontal and supraorbital ornamentation, and most also bear nasal, supratemporal, and zygomatic bosses (Rubidge & Sidor 2002; Smith *et al.* 2006; Kruger *et al.* 2015; Kammerer 2016b). Although functional explanations have been proposed for the supraorbital bosses of some therapsids (Ivakhnenko 2003; Kammerer 2011), the complexity and apparent species-specific morphologies of burnetiamorph cranial ornaments are more suggestive of a display purpose (Sidor *et al.* 2017). Although Kulik & Sidor's (2019) histological examination of two burnetiamorph skull caps failed to show definitive evidence for overlying soft-tissue structures (based on the criteria proposed by Hieronymus *et al.* 2009), cranial ornaments in

this clade would have been highly visible and distinctive even if covered only by a thin layer of skin.

Unfortunately, an understanding of the palaeobiological implications of burnetiamorph cranial ornaments has been hindered by a paucity of fossils. Burnetiamorphs are notoriously rare components of the most intensely sampled Permian tetrapod-bearing beds, those of the South African Beaufort Group (Smith *et al.* 2012; Sidor 2015). Of the eight described species of South African burnetiamorphs (*Bullacephalus jacksoni*, *Burnetia mirabilis*, *Lemurosaurus pricei*, *Leucocephalus wewersi*, *Lobalopex mordax*, *Lophorhinus willodenensis*, *Pachydectes elsi*, and *Paraburnetia sneeubergensis*), only *Lemurosaurus pricei* is known from multiple specimens (Sidor & Welman 2003). Because of this rarity, it is difficult to assess whether burnetiamorph cranial ornaments exhibited intraspecific variation (be it ontogenetic, sexual, or otherwise), which is particularly problematic given the importance of these ornaments both for species diagnoses and phylogenetic analysis (Sidor *et al.* 2017). The only evidence for ontogenetic variation in burnetiamorphs comes from *Lemurosaurus pricei*, in which the holotype (BP/1/816, snout length 41.2 mm) is substantially smaller than the referred specimen (NMQR 1702, snout length 73.3 mm).

Outside of South Africa, burnetiamorph records have historically also been rare, with only three named taxa, each represented by a single specimen (the holotypes of *Niuksenitia sukhonensis* and *Proburnetia viatkensis* from Russia and *Lende chiweta* from Malawi; Ivakhnenko *et al.* 1997; Rubidge & Sidor 2002; Kruger *et al.* 2015). Recent fieldwork in Tanzania and Zambia (Sidor *et al.* 2015) has challenged the notion that burnetiamorphs were always uncommon components of their faunas, however. Sidor *et al.* (2010) reported a burnetiamorph skull cap from the basal conglomerate horizon of the Usili Formation in Tanzania, and an additional six skull caps from this horizon have since been recovered (CAS, pers. obs.) In the lower Madumabisa Mudstone Formation of Zambia, 14 burnetiamorph skull caps have been recovered from 13 localities, a number surpassed only by isolated tapinocephalid teeth as the most commonly encountered vertebrate fossils in this unit (Sidor *et al.* 2014). Kulik & Sidor (2019) described the osteohistology and external anatomy of three of these Zambian skull caps, but left them unnamed because of their incompleteness. Here, we describe the first burnetiamorph specimen from this assemblage preserving more than just the skull roof, recognize it as a novel taxon, and discuss its implications for burnetiamorph phylogeny.

Institutional abbreviations. AMNH FARB, American Museum of Natural History, Fossil Amphibian, Reptile, and Bird Collection, New York, USA; BP, Evolutionary Studies Institute (formerly the Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; CGP/CGS, Council for Geoscience, Pretoria, South Africa; MAL, Malawi Department of Antiquities Collection, Lilongwe and Nguludi, Malawi; NHCC, National Heritage Conservation Commission, Lusaka, Zambia; NHMUK, Natural History Museum, London, UK; 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: South African Museum, Cape Town, South Africa; TM, Ditsong, National Museum of Natural History (formerly the Transvaal Museum), Pretoria, South Africa.

MATERIAL AND METHOD

Comparisons with other biarmosuchians were based on first-hand examination of all published specimens by CFK and CAS. Fossil preparation of NHCC LB133 was accomplished at the University of Washington Burke Museum by Bruce Crowley; matrix surrounding the fossil was removed mechanically with airscribes and pin vices, followed by two acid baths (submersion in sulphamic acid for a total of *c.* 4 hours, followed by overnight rinsing).

SYSTEMATIC PALAEONTOLOGY

THERAPSIDA Broom, 1905
BURNETIAMORPHA Broom, 1923
BURNETIIDAE Broom, 1923
BURNETIINAE Broom, 1923

Genus MOBACERAS nov.

LSID. urn:lsid:zoobank.org:act:EB58B3E8-9FFA-4E87-86FD-37EB4B9F001F

Type species. *Mobaceras zambeziense* sp. nov.

Derivation of name. Genus name *Mobaceras* from *moba*, the name of the knob-thorn acacia tree in the Tonga language (Chitonga) of southern Zambia, and the Ancient Greek κέρᾰς (*ceras*) meaning horn, in reference to the knob-like cranial bosses of this taxon.

Diagnosis. As for the type and only species.

Mobaceras zambeziense sp. nov.
Figures 1–4

LSID. urn:lsid:zoobank.org:act:9BD331C6-39EE-4F35-BC7A-894935BA734D

Derivation of name. Species name *zambeziense* in reference to the Zambezi River valley, where both specimens of this taxon were collected.

Holotype. NHCC LB133, a partial skull missing the anterior portion of the snout and the mandible.

Referred material. NHCC LB593, a skull cap preserving much of the interorbital and intertemporal regions.

Locality and horizon. Collected from locality L157 (type) and L174 (referred specimen), which are part of a cluster of closely spaced sites within a band of outcrop *c.* 18 km southwest of the village of Chamwe, Gwembe District (Southern Province, Zambia). Although not continuous with the outcrop discussed by Sidor *et al.* (2014) or Whitney & Sidor (2016), the inferred stratigraphic position is the same: these rocks are probably part of the informally recognized 'middle calcareous member' of the Madumabisa Mudstone Formation (Gair 1959; Nyambe & Dixon 2000). Based on the presence of tapinocephalid dinocephalian fossils, we consider these rocks to be Guadalupian in age (Olroyd & Sidor 2017).

Diagnosis. A burnetiid burnetiamorph distinguished from all taxa other than *Bullacephalus* and *Burnetia* by the presence of two pairs of large supraorbital bosses (one pair above the dorsal
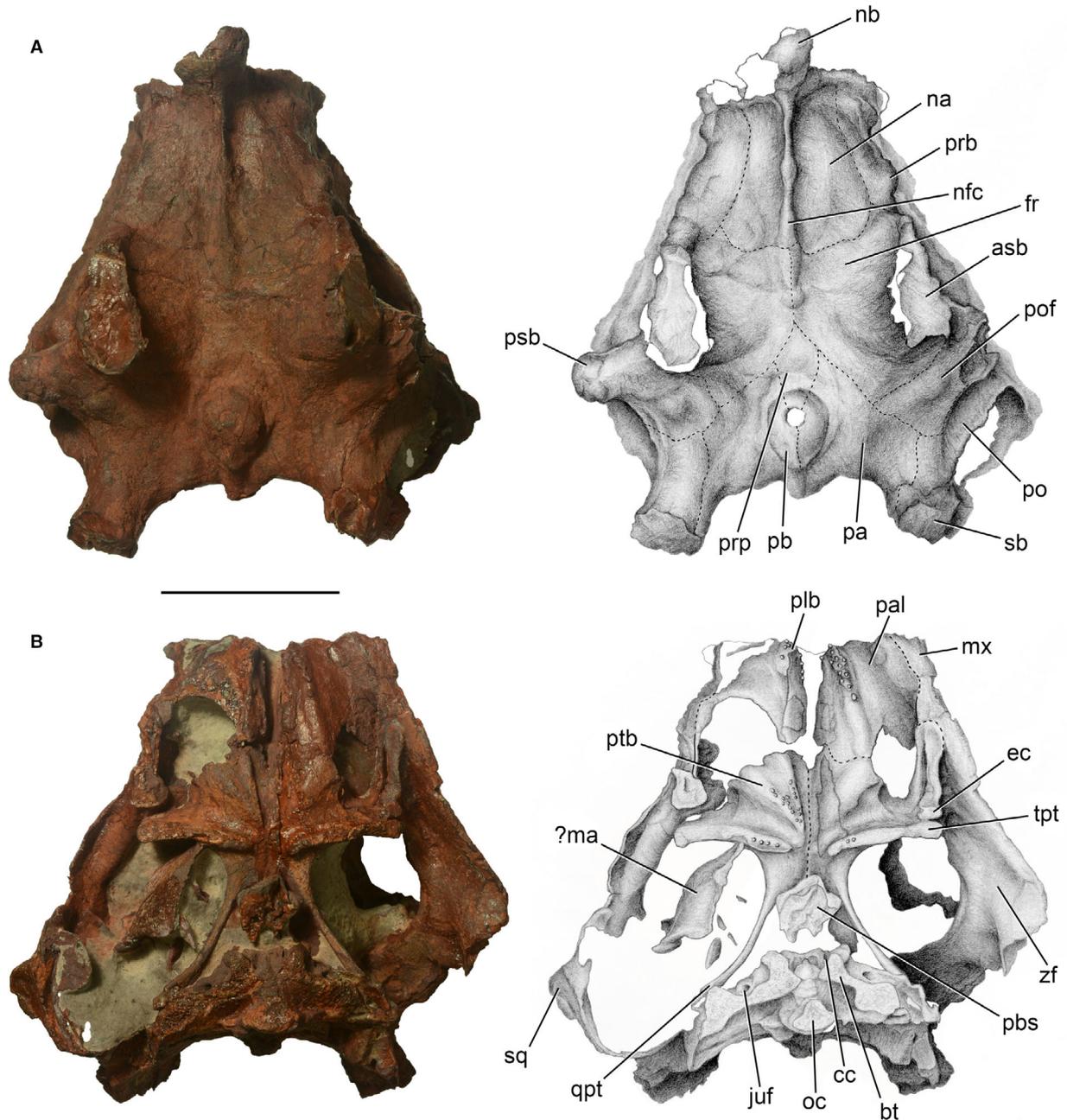
FIG. 1. The holotype of *Mobaceras zambeziense*, gen. et sp. nov. (NHCC LB133). Photographs and interpretative drawings of the skull in: A, dorsal; B, ventral view. *Abbreviations*: asb, anterior supraorbital boss; bt, basal tuber; cc, foramen for carotid canal; ec, ectopterygoid; fr, frontal; juf, jugular foramen; ?ma, possible mandibular fragment; mx, maxilla; na, nasal; nb, nasal boss; nfc, naso-frontal crest; oc, occipital condyle; pa, parietal; pal, palatine; pb, pineal boss; pbs, parabasisphenoid; plb, palatine boss; po, postorbital; pof, postfrontal; prb, prefrontal boss; prp, preparietal; psb, posterior supraorbital boss; ptb, pterygoid boss; qpt, quadrate ramus of pterygoid; sb, squamosal boss; sq, squamosal; tpt, transverse process of pterygoid; zf, fossa on ventral surface of zygomatic arch. Scale bar represents 4 cm.

edge of the orbits and the other above the anterodorsal edge of the postorbital bar). Distinguished from all taxa other than *Burnetia* and *Pachydectes* by the discrete, pachyostosed pineal boss,

which tapers posteriorly to form a narrow ridge extending to the edge of the occiput. Distinguished from all taxa other than *Bullacephalus* by the presence of a massive, rounded median nasal
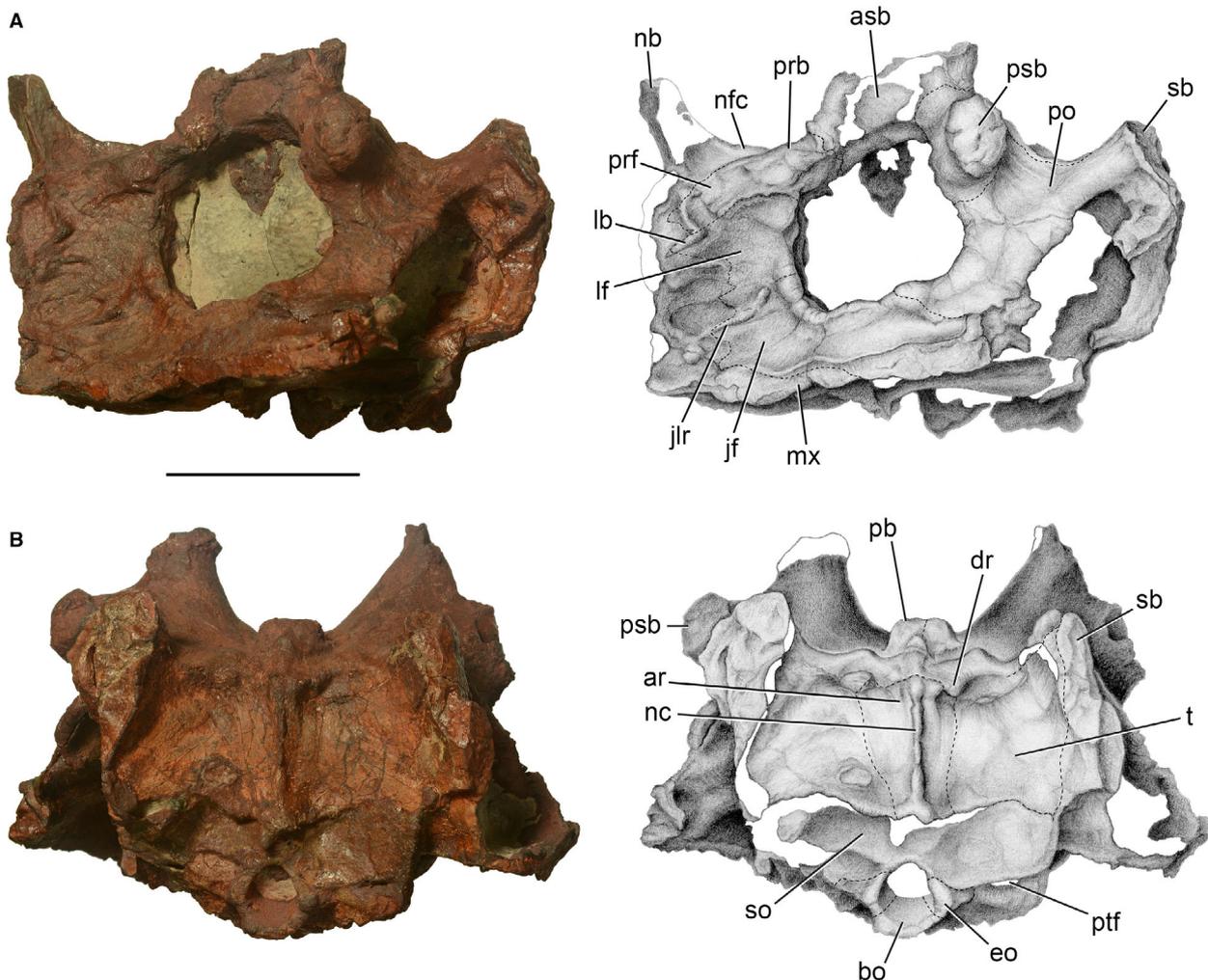
FIG. 2. The holotype of *Mobaceras zambeziense*, gen. et sp. nov. (NHCC LB133). Photographs and interpretive drawings of the skull in: A, lateral; B, posterior view. *Abbreviations*: ar, accessory ridge; asb, anterior supraorbital boss; bo, basioccipital; dr, descending ridge; eo, exoccipital; jf, jugal fossa; jlr, jugal–lacrimal ridge; lb, boss anterodorsal to lacrimal fossa; lf, lacrimal fossa; mx, maxilla; nb, nasal boss; nc, nuchal crest; nfc, nasofrontal crest; pb, pineal boss; po, postorbital; prb, prefrontal boss; prf, prefrontal; psb, posterior supraorbital boss; ptf, post-temporal fenestra; sb, squamosal boss; so, supraoccipital; t, tabular. Scale bar represents 4 cm.

boss. Distinguished from all known burnetiamorphs by the morphology of the median nasal boss, which although incomplete appears to be on a 'stalk', i.e. it is transversely narrow at base and then expands dorsally to form a bulbous tip. (This structure also differs from that of *Bullacephalus* in that the posterior edge of the boss is confluent with a narrow median ridge extending backwards between the orbits.) Further distinguished from all known burnetiamorphs by the morphology of the supraorbital bosses: the anterior supraorbital boss is quadrangular (unlike the triangular bosses of *Lemurosaurus*, *Lende*, *Leucocephalus*, *Lobalopex*, *Paraburnetia*, and *Proburnetia*) and is taller and transversely narrower than that of *Bullacephalus* or *Burnetia*; also, the posterior supraorbital boss is highly discrete, with a distinct, bulbous tip directed posterolaterally, unlike the larger, more diffuse, anterolaterally directed posterior supraorbital bosses of *Bullacephalus* and *Burnetia*.

Description. NHCC LB133 is 11.3 cm in total length from the posterior edge of the squamosal to the anterodorsal tip of the preserved portion of the nasal boss. Estimating the original total length of this skull is difficult because of the high degree of variability in snout length among burnetiamorph taxa, but assuming skull proportions similar to that of *Burnetia mirabilis*, the intact skull would have been *c.* 16 cm in length. This specimen is nearly undistorted and, where intact, the bone surface is reasonably well-preserved, with the pachyostosed elements showing a 'spongy' texture (Figs 1, 2). The skull has suffered several major breaks corresponding to those regions protruding from the nodule in which it was encased. The anterior portion of the snout (from the anterior edge of the lacrimal forwards) is missing entirely (Fig. 3). The tips of both anterior supraorbital, the right posterior supraorbital, and both dorsal squamosal bosses are broken off. The ventral edges of both zygomatic arches and the

prominent midline boss, only the posterior portion of which is preserved. Despite much of it being lost to erosion, the morphology of this boss is clearly unique among burnetiamorphs; it is on a stalk, i.e. the base of the boss is transversely narrow but it expands dorsally, terminating in a bulbous tip. In anterior view (Fig. 3), the boss appears bulb-shaped in cross-section and features the radiating pattern of canals described by Kulik & Sidor (2019) as characteristic of burnetiamorph cranial vascular pachyostosis. The bone surface of the boss, as preserved on its posterior face, has a finely wrinkled texture. A narrow median ridge extends posteriorly from the boss, originating at midheight on the posterior face of the boss (Figs 1A, 2A). This ridge slopes posteroventrally, diminishing in height posteriorly until it disappears entirely at a point roughly midway between the orbits. Paired depressions are present on the skull roof immediately lateral to the ridge and extend throughout its length (Fig. 1A).

The lateral surface of the snout, as preserved, consists of the prefrontal, lacrimal, jugal, and a small ventral portion of the maxilla (Fig. 2A). As is usual for burnetiamorphs, broad fossae are present on the facial surface of the lacrimal and jugal. The lacrimal and jugal fossae are demarcated by a distinct ridge (inferred to follow the path of the jugal–lacrimal suture). This ridge is developed to varying degrees on the two sides of the skull, with the right ridge being notably more robust. Where this ridge meets the orbit, the orbital margin is pachyostosed, forming an irregular swelling with two primary bulges. Posterior to the upper of these two bulges, on the internal surface of the orbit, is a single lacrimal foramen (exposed only on the left side of this specimen). Anterodorsal to the lacrimal fossa is a small, oval, vertically oriented boss (Fig. 2A). Dorsal to the lacrimal fossa, originating at the anterodorsal edge of the orbit, is a horizontally oriented, irregular boss on the prefrontal. This boss is discrete and distinct from the anterior supraorbital boss, although the portion of the orbital margin separating these two bosses is also somewhat pachyostosed.

The zygomatic arch is best preserved on the left side of the skull (although the subtemporal portion of the arch is broken off entirely on that side; Fig. 2A). Suborbitally, its surface is weakly concave laterally. A small, rounded boss is present on the lateral surface of the suborbital zygoma, near its dorsal edge behind the orbital midpoint. The zygomatic bosses present in other burnetiamorphs are usually larger and are either situated on the ventral edge of the zygoma or more broadly extended across its lateral surface (in *Bullacephalus* and *Pachydectes*). The ventral edge of the zygoma is not preserved, so it is uncertain whether larger zygomatic bosses positioned similarly to those of other burnetiids were present. The posteroventral edge of the preserved portion of the left squamosal does show some lateral expansion of the bone, which probably represents the base of a broken zygomatic boss, but this region is too incomplete to be sure. The right subtemporal zygoma is preserved but its lateral surface is completely broken off, so it is unknown which bosses, if any, would have been present. A well-developed, elongate fossa is present on the internal face of the zygomatic arch on both sides, and would have served as an attachment site for jaw adductor musculature (Fig. 1B).

A pair of extremely well-developed supraorbital bosses are present above the dorsal margin of the orbit (Figs 1, 2). The

FIG. 3. The holotype of *Mobaceras zambeziense*, gen. et sp. nov. (NHCC LB133) in anterior view. Grey denotes matrix. *Abbreviations*: m, maxilla; nb, nasal boss; pal, palatine; v, dorsal lamina of vomer. Scale bar represents 1 cm.

occiput are eroded off, as is the lateral surface of most of the right zygomatic arch. Ventrally, the surface of the palate and braincase is eroded, although certain portions are well-preserved (the left palatine, quadrate rami of the pterygoids, and the right lateral wall of the basicranium). Few sutures are visible in this specimen, as the result of a combination of the obliteration of surface detail due to pachyostosis (as is typical for burnetiamorphs; Kulik & Sidor 2019) and the taphonomic effects of hematite encrustation (as is typical of many vertebrate fossils in the Madumabisa Mudstone Formation in the Mid-Zambezi Basin). The sutures we can delimit with reasonable confidence include the mid-frontal, preparietal, and parietal sutures on the skull roof and the parietal, postparietal, and supraoccipital sutures on the occiput.

Because of breakage, in anterior view NHCC LB133 presents a cross-section through the snout (Fig. 3). This section is semi-oval in shape (not including the nasal boss): narrowest at its rounded dorsal margin and broadest ventrally, across the palate. The ventral wall of this section of the snout is made up of the palatine bones. A broad trough, rounded in anterior cross-sectional view, separates the palatines between the palatine bosses. Dorsal to this trough is a paired element we identify as the vomer. It consists of a narrow median lamina (with a midline suture) extending dorsally and paired ventral laminae contacting the palatines. The maxilla is thin (3–4 mm) in section and there is no evidence of pachyostosis. In contrast, at the dorsal edge of the anterior snout section, the nasals are pachyostotic (maximally 9 mm thick, not including the nasal boss) and bear a

FIG. 4. Referred specimen of *Mobaceras zambeziense* gen. et sp. nov. (NHCC LB593) in: A, dorsal; B, ventral; C, right lateral view. D, detail of NHCC LB133 in right lateral view for comparison. *Abbreviations*: asb, anterior supraorbital boss; mt, median trough; nfc, nasofrontal crest; pf, pineal foramen; prp, preparietal; psb, posterior supraorbital boss; r, ridge; tf, temporal fossa. Scale bar represents 1 cm.

anterior supraorbital bosses are broken at their tips on both sides of the skull, but enough is preserved to indicate that they were quadrangular, rather than triangular, in outline in lateral view (Fig. 2A). However, they are proportionally very tall, similar to the best-developed triangular bosses in other burnetiids (e.g. *Proburnetia*) and unlike the shorter bosses of previously known taxa with quadrangular bosses (*Bullacephalus* and *Burnetia*). The anterior supraorbital boss is transversely narrowest anteriorly, expanding posteriorly before terminating in a broadly rounded (in dorsal view) structure above the posterior margin of the orbit (Fig. 1A). The posterior supraorbital bosses are situated at the posterodorsal edge of the orbit, between the anterior supraorbital bosses and the postorbital bar. The left posterior supraorbital boss is almost perfectly preserved and consists of a discrete, ovoid knob at the tip of a lateral projection of bone (presumably the postfrontal, although this is uncertain because of poor sutural visibility; Fig. 2A). The orbital margin is

distinctly indented around the base of this boss. The postorbital bar originates immediately behind the posterior supraorbital boss and is dorsoventrally short but anteroposteriorly expanded. It is broadest dorsally and narrows at mid-height before expanding again at its contact with the zygomatic arch. The posterior margin of the postorbital bar is pachyostosed and the bar is transversely expanded relative to that of non-burnetiamorph biarmosuchians, but not to the extreme degree of many dinocephalians (or even *Bullacephalus*).

In between the supraorbital bosses, posterior to the median nasofrontal ridge, and anterior to the pineal boss, there is a small region where the skull roof is essentially flat. The only topology in this region is a set of weak ridges delimiting the edges of the preparietal and anterior parietal processes (Fig. 1A). The preparietal makes up the anterior portion of the pineal boss and extends forwards onto the flat portion of the skull roof, expanding transversely into a broad structure before narrowing again to terminate

in a sharply tipped anterior process. This morphology can be seen in the holotype, but is more clearly delimited on the skull roof of the smaller referred specimen (Fig. 4). Preparietal morphology in *Mobaceras* is similar to what was shown (based on thin sections) for the otherwise morphologically dissimilar (here considered taxonomically distinct, but left in open nomenclature given their incompleteness) Zambian burnetiamorph specimens described by Kulik & Sidor (2019). Comparable preparietal shape is also present in NHMUK PV R871a (Kammerer 2016b) and appears to be present in *Burnetia* and *Lobalopex*, suggesting that this morphology is typical of burnetiamorphs in general. The preparietal is flanked on each side by an anterior process of the parietal, which terminates immediately posterior to the broadest portion of the preparietal. These processes also make up the remaining portion of the pineal boss. The pineal boss is massively pachyostosed but highly discrete, with very sharp demarcation between its edges and the otherwise flat surrounding portion of skull roof. The boss is roughly teardrop-shaped in dorsal view; it is broadest and rounded anteriorly but narrows in transverse dimension behind the pineal foramen (Fig. 1A). This attenuate posterior portion of the boss extends to the edge of the occiput, terminating immediately above the origin of the nuchal crest. A small nubbin is present on the dorsal surface of the boss at the boundary between its broad circumpineal portion and its attenuate posterior process.

The temporal fenestra is smaller than the orbit, as in all other burnetiamorphs. It is roughly triangular in lateral view: narrowest dorsally and broadest ventrally. Above the apex of the temporal fenestra is a well-developed dorsal squamosal boss. The tip of this boss is broken on both sides of the skull, but it was clearly massive and the preserved portions extend posterior to the occipital plate (Fig. 1).

The most ventrally projecting parts of the palate protruded beyond the nodule encasing the skull and were eroded. In these regions, the palate is poorly preserved, but most of the surface morphology of the palatine and pterygoid is visible (Fig. 1B). The palatine and pterygoid each bear a triangular, dentigerous palatal boss. These bosses are close to one another and oppose each other, such that the apex of the palatine boss is oriented anteriorly whereas that of the pterygoid boss is oriented posteromedially. The palatine boss (best preserved on the left side) is roughly twice the length of the pterygoid boss (best preserved on the right side). Each boss bears a row of tiny, pointed teeth. None of the palatal bosses has a complete tooth row preserved; the most complete (the left palatine) preserves 13 teeth. As is typical for early therapsids, the palatal tooth rows lack stereotyped tooth positions, unlike the marginal dentition. Although roughly forming a line, at any given point along the row multiple teeth in various stages of eruption may be present. However, these rows are restricted to the long edges of the bosses; they do not broadly cover the palatal surface as in *Biarmosuchus* (Ivakhnenko 1999). On the palatine boss, the medial side of the tooth row is directed medially, whereas the lateral side and both sides of the pterygoid boss tooth row are directed ventrally. Posterolateral to the palatal bosses the palatal surface is notably concave ventrally. This region is incomplete on both sides of the skull, but the edge of the ectopterygoid is visible in the concavity on the right side. The transverse processes of the pterygoid are also poorly preserved, with their ventral edges eroded off, but were clearly dentigerous (at least four teeth are present near

the medial edge of the right transverse process). The transverse processes are anteroposteriorly narrow, expand only slightly at their lateral tips (although this may be due in part to breakage), and exhibit only weak posterior curvature towards their edges. There is a sharp change in height between the transverse process and posterior portion of the pterygoid, with the ventral surface of the quadrate ramus being 3–4 mm dorsal to the ventral surface of the transverse process. The quadrate ramus of the pterygoid is broadest anteromedially, attenuating posteriorly and curving posterolaterally as an elongate element that would have terminated at a contact with the quadrate (not preserved). A medially projecting horizontal shelf is visible on the left quadrate ramus, which is a feature common among biarmosuchians (Sidor & Rubidge 2006).

The exposed ventral portion of the basicranium consists of the parabasisphenoid, basioccipital, and opisthotic (Fig. 1B). No sutures between these bones are visible and it is likely that they are fused. The parabasisphenoid is fractured, splitting into anterior and posterior fragments. The posterior fragment is preserved *in situ* and remains in articulation with the basioccipital posteriorly, whereas the anterior fragment has rotated anteroventrally, such that a cross-section through its posterior face is visible in ventral view. Anteriorly, the parabasisphenoid has a tripartite tip, with an attenuate median process that would have inserted between the pterygoids and two short, swollen lateral processes. Although damaged, the ventral edge of the parabasisphenoid appears to have been gently convex. The posterior parabasisphenoid portion is partially obscured by matrix and the displaced anterior fragment. Its ventral surface is complex, with a median ridge flanked by paired grooves situated between the basal tubera anteriorly, and a mound-like mass of bone situated between the basal tubera around mid-length. This mass of bone bears a small anterior projection and becomes irregular posteriorly, probably as the result of damage. Immediately anterior to the basal tuber is a foramen, partially obscured with matrix, representing the carotid canal. The basal tubera themselves are semilunate, as is typical for early therapsids. The fenestra ovalis is relatively small compared with that of dicynodonts or gorgonopsians (Kemp 1969; Surkov & Benton 2004), and the surrounding tuber appears swollen. Immediately posterodorsal to the fenestra ovalis (4 mm distant) is the large, ovoid jugular foramen.

The occiput is only partially preserved, with large portions of its lateral edges and the ventral margins of the opisthotics broken off. The upper half of the occipital plate consists of a pair of concave surfaces separated by the nuchal crest (Fig. 2B). Based on the condition in other biarmosuchians these surfaces probably consist of the postparietal medially and tabulars laterally (the lateral edges, where the squamosal contributions to the occiput would be expected, are mostly missing). The nuchal crest is well-developed and extends from the posterior edge of the parietals dorsally to the dorsal margin of the supraoccipital ventrally. To either side of the nuchal crest are small accessory ridges, extending from the posterior edge of the parietals down the surface of the postparietal for *c.* 4 mm before terminating. The right accessory ridge is better developed (or better preserved) than the left. The supraoccipital is partially disarticulated with the postparietal (along what is presumed to have been its natural suture) and is displaced anteriorly. In posterior view, the supraoccipital is a broad, bow tie-shaped element, narrowest

above the foramen magnum and expanding in height laterally. A pair of small, slit-like, horizontally oriented post-temporal fenestrae are present between the supraoccipital and underlying opisthotics on either side of the foramen magnum. The foramen magnum is nearly circular in outline. At its lateral edges, near mid-height, is a pair of eminences here interpreted as exoccipital processes. Ventral to it is a small, reniform occipital condyle.

One large and numerous smaller bones fragments are preserved in the matrix that fills the right subtemporal fenestra. The smaller fragments are unidentifiable slivers of bone. The larger fragment is a laminar, weakly curved structure bearing a lateral ridge and a prominent foramen. This element may represent a fragment of the lower jaw.

PHYLOGENETIC ANALYSIS

Background

Biarmosuchian phylogeny (Fig. 5) has remained largely stable since the earliest analyses that included multiple members of this clade (Sidor 2000; Rubidge & Kitching 2003; Sidor et al. 2004). All of these analyses have recognized a well-supported clade of taxa with extravagant cranial excrescences, often pachyostosed into bosses, called Burnetiamorpha (Sidor & Welman 2003). Outside of this clade is a paraphyletic assemblage of 'basal biarmosuchians' including Biarmosuchus, Herpetoskylax, Hipposaurus, Ictidorhinus, and Lycaenodon. The exact topology in this part of the tree is highly unstable, but the latter three taxa have generally been recovered as more closely related to Burnetiamorpha than Biarmosuchus and Hipposaurus (e.g. Sidor & Rubidge 2006). Within Burnetiamorpha, nearly every analysis has recovered a large clade (Burnetiidae) that excludes the basal taxa Lemurosaurus, Lobalopex, and Lophorhinus and consists of two subclades that Kammerer (2016b) formalized as Burnetiinae and Proburnetiinae. Burnetiids are characterized by an extreme degree of pachyostosis and the development of additional cranial excrescences absent in non-burnetiid burnetiamorphs such as Lemurosaurus and Lobalopex.

Recently, however, Day et al. (2016) recovered an unorthodox set of topologies for their cladistic analysis of Biarmosuchia. These topologies (here called A, B and C for ease of reference) represented the most parsimonious trees resulting from analyses using implied weighting with Biarmosuchus as the outgroup (A and B, with the concavity constant $k \leq 4$ for A and $k = 5$–7 for B) and equal weighting using Hipposaurus as the outgroup (C; with Biarmosuchus excluded in this analysis). Intriguingly, they recovered a less pectinate topology for non-burnetiamorph biarmosuchians than in previous analyses. In topologies B and C, they recovered a monophyletic Ictidorhinidae containing Ictidorhinus, Lycaenodon, Herpetoskylax, and the problematic specimen RC 20

(holotype of Hipposauroides rubidgei, a taxon usually considered synonymous with Lycaenodon longiceps; Sigogneau-Russell 1989; Sidor 2003). In topology A, they recovered Lycaenodon, Herpetoskylax, and RC 20 in a clade, but with Ictidorhinus outside of a group containing that clade plus Burnetiamorpha. In their sharpest break with previous analyses, Day et al. (2016) recovered Bullacephalus and Pachydectes as non-burnetiids, with these genera forming a clade (named as a new family, Bullacephalidae) either at the base of Burnetiamorpha (as the sister-group of the clade containing all burnetiamorphs except Lemurosaurus in topology A) or outside of Burnetiamorpha entirely (as the sister-group of or one node removed from Hipposaurus in topologies B and C). In all of their topologies, Burnetiidae was restricted to Burnetia, Lende, Paraburnetia, and Proburnetia (with Burnetia always recovered as more closely related to Lende and Paraburnetia than Proburnetia). They also recovered Niuksenitia outside of Burnetiidae, in a novel clade containing this genus, Lophorhinus, and BP/1/7098, an unnamed burnetiamorph specimen from the Pristerognathus Assemblage Zone (AZ) of South Africa. A subsequent paper (Day et al. 2018) using the same underlying dataset recovered a similar topology, with Bullacephalus + Pachydectes outside of Burnetiidae.

The novel results of Day et al. (2016) can be ascribed to the extensive revisions they made to earlier versions of the data matrix, given that their taxon list was largely unchanged from previous studies. They questioned a number of homology statements for biarmosuchians, reformulated character states, and added several new characters. Day et al.'s (2016) critiques of previous phylogenetic datasets for Biarmosuchia are well-considered and worth addressing.

Revised analysis

We concur with Day et al. (2016) that several traditionally utilized biarmosuchian characters are problematic, although we disagree on how best to resolve this. Here, we provide a new phylogenetic analysis for Biarmosuchia, with alternative formulations of many previously utilized characters and thorough explanations where our dataset differs from that of Day et al. (2016).

Our analysis consists of 27 characters and, in the full version of the analysis, 21 operational taxonomic units (OTUs). All the OTUs are biarmosuchians, with Biarmosuchus tener used as the outgroup. Most biarmosuchian taxa are known only from their respective holotypes, so the majority of OTUs are coded from single specimens. The exceptions are Biarmosuchus tener (coded based on PIN 1758/1, 1758/2, 1758/7, 1758/8, 1758/18, 1758/85, and 1758/255), Herpetoskylax hopsoni (coded based on
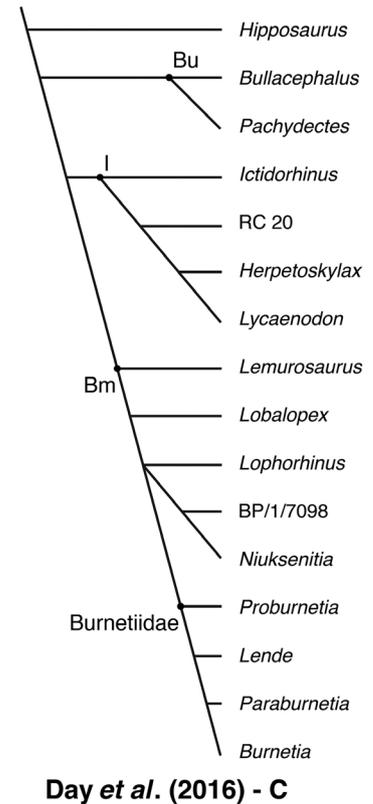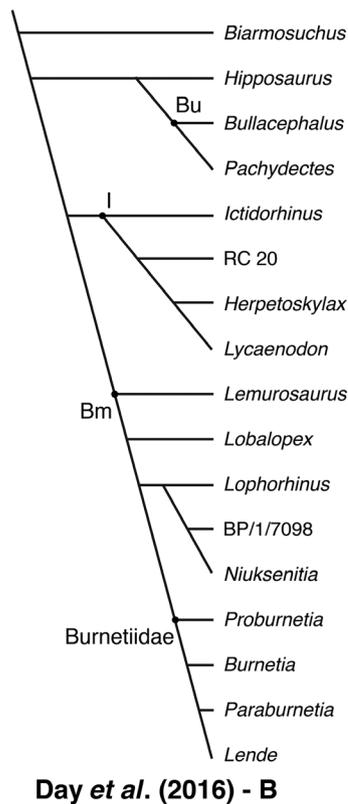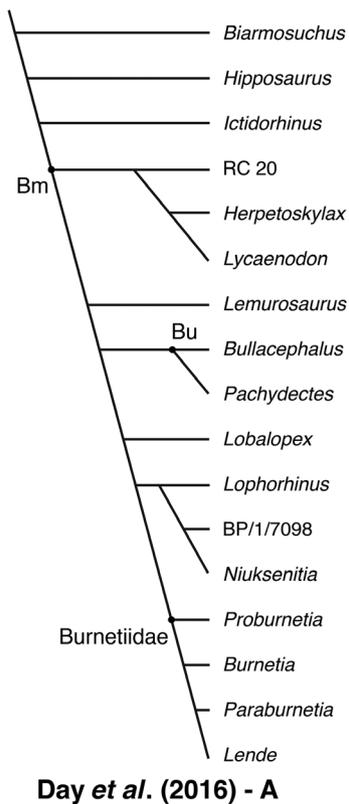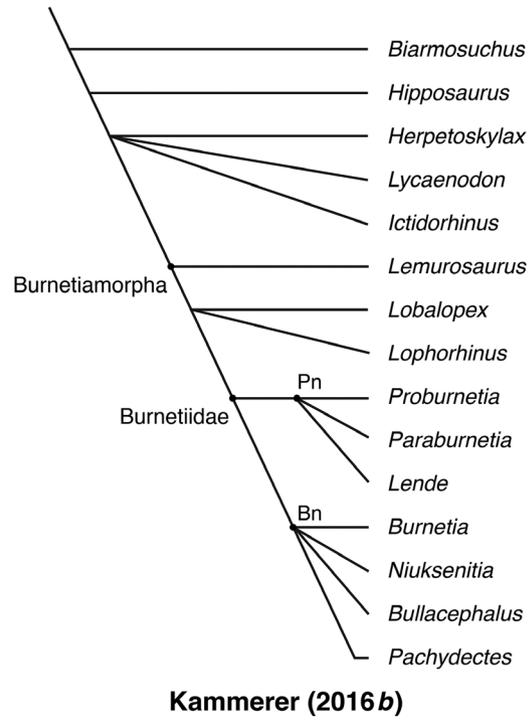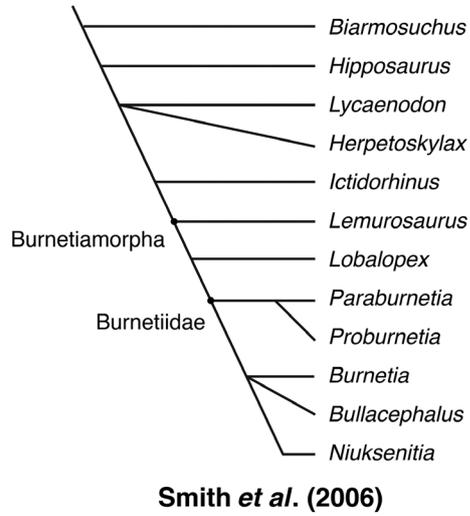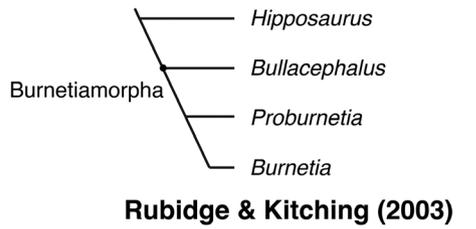
FIG. 5. Comparison of previous cladograms depicting biarmosuchian relationships. *Abbreviations*: Bn, Burnetiinae; Bm, Burnetiamorpha; Bu, Bullacephalidae; I, Ictidorhinidae; Pn, Proburnetiinae.

BP/1/3924 and CGP/1/67), *Hipposaurus boonstrai* (coded based on CGS WB123, SAM-PK-8950, and SAM-PK-9081), and *Lemurosaurus pricei* (coded based on BP/1/816 and NMQR 1702). Our data matrix is given in the Appendix and available to download (Kammerer & Sidor 2020). For a detailed character list, see below. The analysis was run in TNT (Goloboff *et al.* 2008) using full New Technology searching (required to find shortest tree at least 20 times), and bootstrap analyses were based on New Technology searching using 1000 replicates.

Character list

Abbreviations indicate character numbers in previous papers addressing biarmosuchian relationships: RK, Rubidge & Kitching 2003; SW, Sidor & Welman 2003; SHK, Sidor *et al.* 2004; RSM, Rubidge *et al.* 2006; SR, Sidor & Rubidge 2006; SRS, Smith *et al.* 2006; SS, Sidor & Smith 2007; KR, Kruger *et al.* 2015; K, Kammerer 2016*b*; and DRA, Day *et al.* 2016.

1. Length of dorsal process of premaxilla. 0: long, extends posterior to the level of the upper canine; 1: short, does not extend posterior to the level of the upper canine. The plesiomorphic state in therapsids is to have a long dorsal process of the premaxilla, extending posterior to the external naris and reaching minimally the level of the upper canine. The plesiomorphic state is present in *Biarmosuchus* and *Hipposaurus*, but in most biarmosuchians (including non-burnetiamorphs such as *Herpetoskylax* and *Lycaenodon*) the dorsal process of the premaxilla is relatively short. The only burnetiamorph in which the dorsal process of the premaxilla is known to extend beyond the level of the canine is the fragmentary *Pristerognathus* AZ specimen BP/1/7098. However, the condition in this specimen can be attributed to the fact that its maxillary canines are unusually far forward on the snout; the actual length of the dorsal process of the premaxilla (relative to snout length) is comparable to that of other basal burnetiamorphs (e.g. *Lophorhinus*). The singleton nature of this exception is here not considered sufficient grounds to reformulate the entire character, but this should be considered if additional examples are discovered in the future. The premaxillae are not preserved in NHCC LB133 or in NHCC LB593, so *Mobaceras* was scored as ? for this character. Scorings otherwise following Day *et al.* (2016). (Modified from SW2, RSM2, SR2, KR1, K1, DRA3.)

2. Ornamentation on lateral surface of maxilla. 0: absent or consisting only of pits and foramina; 1: highly rugose with a series of well-developed parallel striations running posterodorsally to anteroventrally immediately anterior to the lacrimal. Most previous versions of this character (Rubidge *et al.* 2006) formulated the states as 0: smooth versus 1: deeply sculptured. This formulation is not entirely accurate, given that the lateral surface of the maxilla in most biarmosuchians shows some degree of sculpturing or pitting (i.e. none is truly smooth; Fig. 6C). The original purpose of this character was to distinguish the unique style of maxillary sculpturing present in *Bullacephalus* and *Pachydectes* (Fig. 6B, D) from other burnetiamorphs; the character states are reworded here to reflect this. The most striking shared aspect of the maxillary ornamentation in *Bullacephalus* and *Pachydectes* is not simply the depth of the sculpturing, but also the unusual parallel striations near the contact with the lacrimal (Fig. 6). NHCC LB133 is broken immediately posterior to where this ornamentation would have been visible, so *Mobaceras* was scored ? for this character. (Modified from RSM8, KR3, K3, DRA5.)

3. Preorbital fossae. 0: absent; 1: present as broadly depressed regions of facial surface of lacrimal and jugal, separated by ridge. Day *et al.* (2016) questioned the utility of this character, long considered a burnetiamorph synapomorphy (Sidor & Welman 2003). They noted that in some burnetiamorph specimens, a lacrimal fossa is present only on one side of the skull, is present on non-lacrimal bones (jugal or maxilla), or is difficult to code due to surface damage to the bone. Previous studies (Kruger *et al.* 2015; Kammerer 2016*b*) also discussed problems with this character. Issues with this character are in part due to the conflation of two different sets of fossae on the burnetiamorph snout: 1. broadly depressed facial surfaces of the lacrimal and jugal, separated by a ridge running along the lacrimal–jugal suture; and 2. discrete, deep, rounded pits on the lateral surface of the lacrimal, jugal, and/or maxilla. Kammerer (2016*b*) and Day *et al.* (2016) were referring to the latter structures in their critiques of this character, but the 'lacrimal fossa' as originally described by Rubidge & Sidor (2002) referred to the shallow depression. Here these structures have been separated out as two distinct characters. Broadly depressed facial surfaces of the lacrimal and jugal are most prominent in *Pachydectes* (Fig. 7B), in which they are bounded anteriorly by snout bosses and highly rugose maxillary bone, but these structures are present in all known burnetiamorphs. Although weakly developed in *Lemurosaurus*, *Lobalopex*, and *Lophorhinus*, in all three of these taxa the lacrimal facial surface is somewhat depressed relative to both the maxilla and orbital margin. These fossae and the associated sutural ridge can be difficult to see in specimens with damaged bone surface, but their presence was confirmed in *Burnetia*, *Lende*, and *Paraburnetia* through

FIG. 6. Character 2 (ornamentation on lateral surface of maxilla), shown in details of preorbital region of representative skulls. A, C, state 0 (absent or consisting only of pits and foramina) illustrated in: A, the non-burnetiid burnetiamorph *Lemurosaurus pricei* (NMQR 1702); C, the proburnetiine burnetiid *Leucocephalus wewersi* (SAM-PK-K11112). B, D, state 1 (highly rugose with a series of well-developed parallel striations running posterodorsally to anteroventrally immediately anterior to the lacrimal) illustrated in the burnetiid burnetiamorphs: B, *Bullacephalus jacksoni* (BP/1/5387); D, *Pachydectes elsi* (BP/1/5735). Note that the snout of (C) *Leucocephalus* is pitted, but lacks the distinct striations seen in the bone texture of (B) *Bullacephalus* and (D) *Pachydectes*. A, B, D, in right lateral view; C in left lateral view but mirrored for comparative purposes. *Abbreviation*: ms, maxillary striations. Scale bars represent 1 cm.
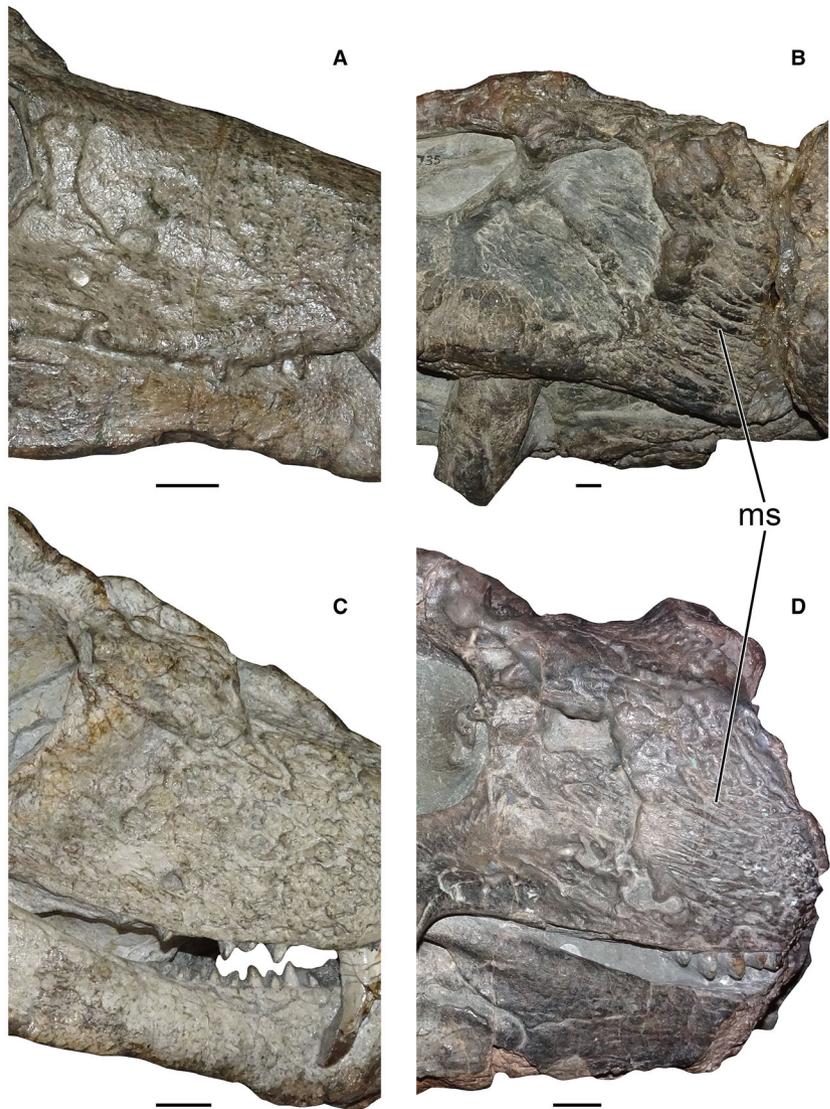
tactile examination of their respective specimens by CFK. These depressions and the ridge separating them are well-developed in NHCC LB133, so *Mobaceras* was scored as 1 for this character. (Modified from SW4, SHK1, RSM6, SR7, SRS1, SS1, KR2, K2, DRA4.)

4. Deep pits on lateral surface of snout. 0: absent; 1: present on lacrimal, jugal, and/or maxilla. As discussed above, we treat these structures as distinct from the broad, usually shallow depressions on the lacrimal and jugal (although they sometimes overlap). These pits appear to be fossae rather than foramina (i.e. they are blind-ended, not perforating the bone) based on external observation, although computed tomography is required for confirmation. Two pits are usually present, one on the sutural border between the lacrimal and maxilla and one between the jugal and maxilla (Fig. 8B), although there are

exceptions (only the lacrimal–maxillary pit is present in *Lophorhinus*, Fig. 8C; pits are restricted to the maxillary surface in *Pachydectes* and *Leucocephalus*, Fig. 8D). Despite this variation, including cases such as *Lende* where the pits vary in number and position even between different sides of the skull, we consider the general presence of these unusual pits on the facial surface of the snout to be homologous across Burnetiamorpha. No snout pits are visible in NHCC LB133, but the regions where they occur in most burnetiamorphs are not preserved in this specimen, so *Mobaceras* was coded as ? for this character. (Modified in part from SW4, SHK1, RSM6, SR7, SRS1, SS1, KR2, K2, DRA4.)

5. Median nasal excrescence. 0: absent; 1: present. See below for discussion of this character. A very prominent nasal boss is present in NHCC LB133, so *Mobaceras* was
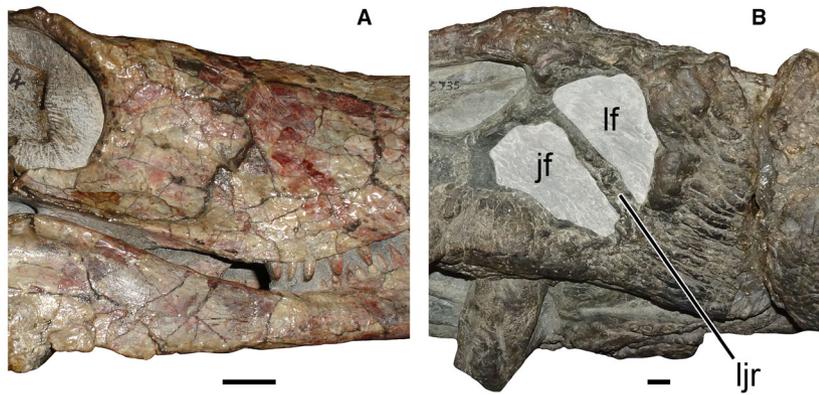
FIG. 7. Character 3 (preorbital fossae), shown in details of preorbital region of representative skulls. A, state 0 (absent) illustrated in the non-burnetiamorph biarmosuchian *Herpetoskylax hopsoni* (CGP/1/67). B, state 1 (present as broadly depressed regions of facial surface of lacrimal and jugal, separated by ridge) illustrated in the burnetiid burnetiamorph *Pachydectes elsi* (BP/1/5735; fossae highlighted). Both specimens in right lateral view. *Abbreviations:* jf, jugal fossa; lf, lacrimal fossa; ljr, lacrimal–jugal ridge. Scale bars represent 1 cm.

coded as 1 for this character. (Modified from RK7, SW6, SHK2, RSM9, SR9, SRS2, SS2, KR4, K4, DRA6.)

6. Morphology of median nasal excrescence. 0: narrow ridge; 1: pachyostosed ridge, of nearly equal transverse width throughout its length; 2: bulbous, rounded boss, with greatest transverse width at its mid-length. The presence of a median nasal excrescence is one of the most characteristic features of burnetiamorphs, but this structure varies extensively in morphology between taxa. Previous analyses have tried to capture shape variation in this structure in different ways: some have treated presence/absence of a nasal excrescence and the shape of that excrescence as separate characters (Sidor *et al.* 2004; Smith *et al.* 2006; Sidor & Smith 2007), whereas others have combined these aspects of nasal morphology into a single multistate character (Rubidge & Kitching 2003; Sidor & Welman 2003; Rubidge *et al.* 2006; Kruger *et al.* 2015). The problem with most multistate formulations for this character is that they treat the different forms of the nasal excrescence as non-homologous for the purposes of analysis (i.e. having an unpachyostosed vs pachyostosed median nasal ridge is analytically equivalent to having either of these morphologies vs none). To address this problem, the most recent phylogenetic analyses of burnetiamorphs have treated this character as ordered multistate, with 'pachyostosed ridge' (i.e. boss) considered a derived state of 'unpachyostosed ridge' (Kammerer 2016*b*; Day *et al.* 2016, 2018). However, this solution is not perfect, because it fails to capture the substantial degree of variation among pachyostosed nasal bosses, specifically the difference between taxa with elongate and narrow (exemplified by *Lende*; Fig. 9D) versus short and rounded nasal bosses (exemplified by *Bullacephalus*; Fig. 9C). Day

et al. (2016) considered the nasal boss of *Bullacephalus* to be non-homologous with those of other burnetiamorphs. They noted that although the nasal boss of *Burnetia* is also short and transversely broad, in that taxon the anterior and posterior edges of the boss are still attenuate, indicating derivation from a median nasal ridge. In contrast, the boss in *Bullacephalus* is a perfectly discrete, almost circular structure, which they considered unlikely to be derived from an ancestral ridge. We consider the nasal boss in *Bullacephalus* to be homologous with that of *Burnetia*, based on the elucidative morphology of NHCC LB133. Although unique in certain aspects (notably the stalk), the nasal boss of *Mobaceras* is more similar to that of *Bullacephalus* than any other burnetiamorph, with both being highly discrete, tall, rounded structures (probably circular in *Mobaceras* as well, although this is uncertain because of breakage). However, the boss in *Mobaceras* originates at the anterior edge of an elongate, narrow median ridge, refuting Day *et al.*'s (2016) argument that a *Bullacephalus*-like boss could not have evolved from such a structure. The fact that the ridge in *Mobaceras* is a narrow, unpachyostosed structure (similar to that of *Lobalopex*) does cast doubt on the homology of elongate versus rounded nasal bosses in burnetiids; it is possible that these structures were independently derived from the ancestral unpachyostosed ridge of basal burnetiamorphs. To reflect this possibility, we have reverted to using two separate characters to capture variation in nasal morphology in biarmosuchians: (1) presence versus absence of any kind of nasal excrescence (because we consider the unpachyostosed ridge of non-burnetiid burnetiamorphs and the median nasal bosses of burnetiids to be homologues); and (2) unpachyostosed ridge only (*Lemurosaurus, Lobalopex, Lophorhinus*) versus elongate boss/

FIG. 8. Character 4 (deep pits on lateral surface of snout), shown in details of the preorbital region of representative skulls (pits highlighted where present). State 0 (absent) illustrated in: A, the non-burnetiamorph biarmosuchian *Herpetoskylax hopsoni* (CGP/1/67). State 1 (present on lacrimal, jugal, and/or maxilla) illustrated in: B–C, the non-burnetiid burnetiamorphs: B, *Lemurosaurus pricei* (NMQR 1702; pits present at lacrimal–maxilla and jugal–maxilla sutures); C, *Lophorhinus willodenensis* (SAM-PK-K6655; single pit present at lacrimal–maxilla suture); D–E, the proburnetiine burnetiids: D, *Leucocephalus wewersi* (SAM-PK-K11112; single pit present on maxillary surface); E, *Lende chiweta* (MAL 290; pits present at jugal–maxilla suture); and the burnetiine burnetiid: F, *Bullacephalus jacksoni* (BP/1/5387; pits present on lacrimal, jugal, and maxillary surfaces). A, B and F in right lateral view; C–E in left lateral view but mirrored for comparative purposes. *Abbreviation:* fp, facial pit. Scale bars represent 1 cm.
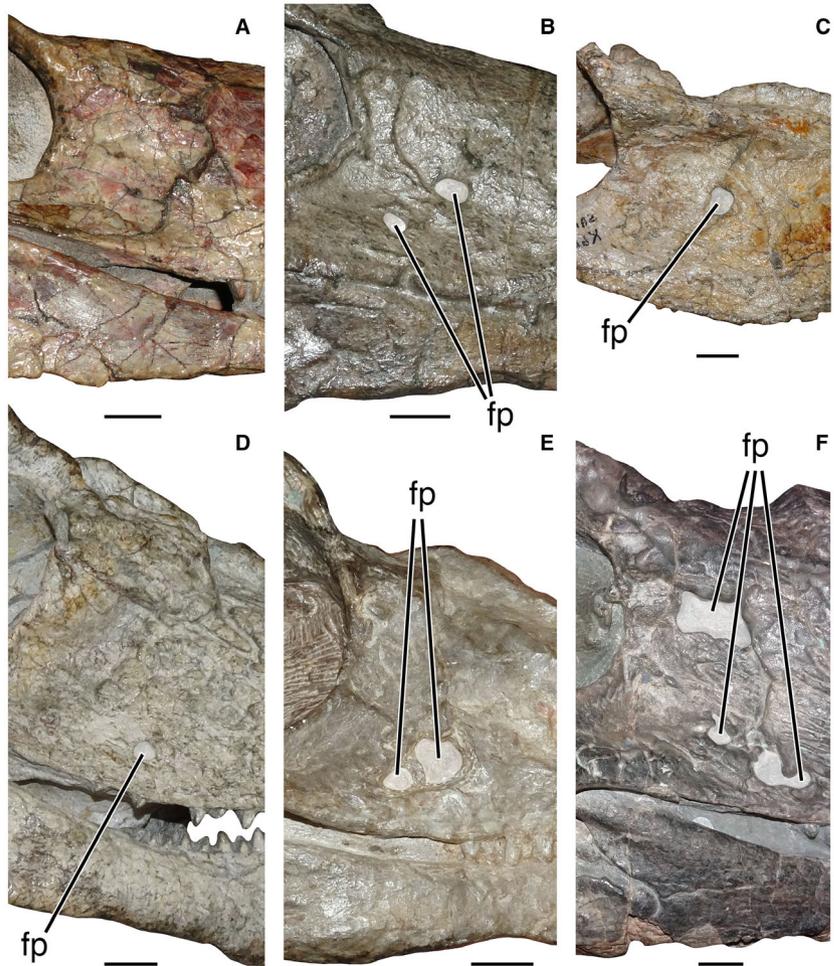
pachyostosed ridge (*Lende*, *Leucocephalus*, *Paraburnetia*, *Proburnetia*) versus rounded boss (*Bullacephalus*, *Burnetia*, *Mobaceras*; accounting for the latter two states being probable derivations of the former, but not necessarily of each other). (Modified from RK7, SW6, SHK3, RSM9, SR9, SRS3, SS3, KR4, K4, DRA6.)

7. Discrete prefrontal boss. 0: absent; 1: present. In all biarmosuchians, the margin of the orbit is somewhat raised relative to the surrounding bone, and this raised area generally continues onto the surface of the prefrontal (forming a 'brow' above the orbit). In taxa where the dorsal margin of the orbit is pachyostosed, the prefrontal continuation of this raised area is generally also pachyostosed (as in *Lende*, *Lobalopex*, *Lophorhinus*, *Paraburnetia*, and *Proburnetia*). Day *et al.* (2016) restricted their definition of the prefrontal boss to an 'independent, ridge-like boss on the dorsal side of the prefrontal', in reference to the structure in *Bullacephalus* and *Burnetia* here termed the anterior supraorbital boss. However, this structure would also have been situated in large part on the frontal

(compared with other biarmosuchians), so calling it the 'prefrontal boss' is problematic. In the current formulation of this character, 'prefrontal boss' does not refer to the anterior portions of the supraorbital bosses, but rather to a small, discrete boss situated entirely on the prefrontal, anterior or anteromedial to the orbits. Such a boss is present in *Bullacephalus* and *Burnetia* (Fig. 10B). A discrete prefrontal boss, very similar to that of *Bullacephalus*, is present in NHCC LB133, so *Mobaceras* is coded as 1 for this character. (Modified in part from RK13, KR34, K5, DRA9.)

8. Median frontal excrescence. 0: absent; 1: present. Like the median nasal excrescence, the structure on the midfrontal suture in burnetiamorphs varies extensively in morphology between taxa. Kammerer (2016b) formulated this as an ordered multistate character, treating 'transversely expanded median boss' as a derived state of 'narrow median boss'. Day *et al.* (2016) also treated this character as ordered multistate, but recognized a more finely differentiated set of states, distinguishing 'low
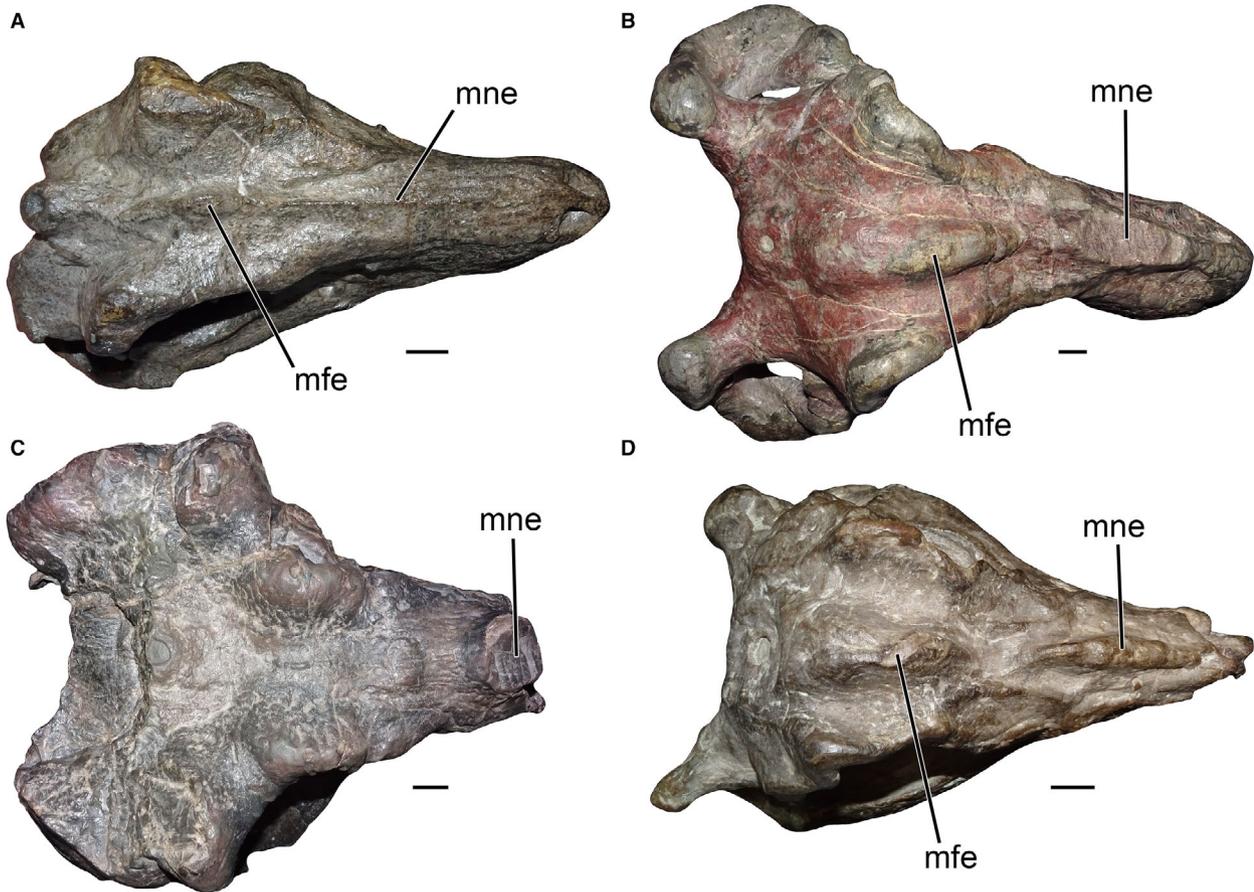
FIG. 9. Characters 5 and 6 (median nasal excrescence) and 8 (median frontal excrescence), shown in representative skulls in dorsal view. A, Character 5, state 0 (median nasal excrescence absent) illustrated in the non-burnetiid burnetiamorph *Lemurosaurus pricei* (NMQR 1702). B, D, Character 6, state 1 (pachyostosed median nasal ridge, of nearly equal transverse width throughout its length) illustrated in the proburnetiine burnetiids: B, *Paraburnetia sneeubergensis* (SAM-PK-K10037); D, *Lende chiweta* (MAL 290). C, Character 6, state 2 (bulbous, rounded nasal boss, with greatest transverse width at its mid-length) illustrated in the burnetiine burnetiid *Bullacephalus jacksoni* (BP/1/5387). Note variable thickness and length of the median frontal excrescence in (A) *Lemurosaurus*, (D) *Lende*, and (B) *Paraburnetia*, and its absence (Char. 8, state 0) in (C) *Bullacephalus*. *Abbreviations*: mfe, median frontal excrescence; mne, median nasal excrescence. Scale bars represent 1 cm.

and narrow median ridge', 'narrow boss set on median ridge', and 'thick median ridge that is widest posteriorly'. We consider this solution to be overly complicated, and to represent arbitrary separation of a continuously variable character. While it is true that the frontal boss of *Lemurosaurus* is transversely narrower than other burnetiamorphs that exhibit this structure (Fig. 9), it is merely the end member in a continuum of variation (with the order of increasing frontal boss thickness being: *Lemurosaurus* < *Lende* < *Proburnetia* < *Leucocephalus*/*Paraburnetia*; note also that the probable juvenile state of the *Lende chiweta* holotype complicates characters likely to show ontogenetic signal, such as degree of cranial boss development). We would argue that the crucial point of distinction for this character is whether a frontal excrescence is present at all, rather than precise degree of thickening. Differentiating between a pachyostosed boss and a totally unpachyostosed ridge, as was done by Kammerer (2016b) for this character and is done for the nasal excrescence above, could be useful in the future. However, at present only the skull of *Pachydectes* among biarmosuchians bears an unexpanded median frontal ridge, rendering a separate character state for this morphology parsimony uninformative. No evidence of any median frontal ridge or boss is present in *Bullacephalus* or *Burnetia*. NHCC LB133 and NHCC LB593 bear a weak median boss towards the anterior edge of the frontal. Although this appears to be a posterior extension of the median nasal ridge rather than a discrete frontal excrescence as is present in proburnetiines, in recognition of this raised

region, we code *Mobaceras* as 1 for this character. (Modified from SW14, SHK12, RSM10, SR10, SRS12, SS14, KR5, K6, DRA11.)

9. Posterolateral process of frontal. 0: does not reach midpoint of pineal foramen; 1: extends to at least the midpoint of the pineal foramen. An elongate posterior process of the frontal, reaching to or beyond the level of the pineal foramen, is present in all non-burnetiamorph biarmosuchians other than *Biarmosuchus* and *Hipposaurus*. This character is difficult to code in most burnetiamorphs (given that they rarely exhibit distinct sutures in this part of the skull), but an elongate frontal process is present in taxa in which sutures can be discerned. An apparent exception is *Mobaceras*; we have interpreted the faint ridges on the skull roof of NHCC LB133 to correspond to sutures, and if this is correct, the posterolateral process of the frontal reaches only the anterior edge of the pineal foramen. On this basis, *Mobaceras* has been coded as 0 for this character. (Modified from RSM11, SR11, KR6, K7, DRA12.)

10. Anterior supraorbital boss. 0: absent; 1: present. All known burnetiamorphs possess exaggerated supraorbital excrescences (variously called 'bosses' or 'horns') that extend across the orbital margin of the prefrontal, frontal, postfrontal, and, in some taxa, the postorbital. The size, shape, and number of these bosses vary between taxa (Fig. 11). As with the mid-nasal and mid-frontal bosses, previous analyses have utilized different character formulations in attempts to capture the morphological variation in this structure. The primary source of conflict between these analyses has been in their treatment of cases in which there are two discrete supraorbital

bosses on each side of the skull (as in the taxa *Bullacephalus* and *Burnetia*; Fig. 11B, D). Kruger *et al.* (2015) treated these bosses separately in two characters: 'supraorbital margin' (with states 0: 'thin' and 1: 'moderately to greatly thickened') for the anterior boss and 'boss above postorbital bar' (with states 0: 'absent' and 1: 'present') for the posterior. Kammerer (2016*b*) also devoted two characters to these structures, but with a different formulation: first, presence/absence of supraorbital bosses in general; and second, boss morphology if present (with states 0: 'large triangular boss directly above orbit' and 1: 'two bosses, one above anterior edge of orbit and other at posterior edge/postorbital bar'). Day *et al.* (2016) not only treated the anterior (which they termed 'prefrontal') and posterior supraorbital bosses as separate characters, but also questioned the homology of the posterior supraorbital boss between *Burnetia* and *Bullacephalus*, noting that this structure is situated over the posterior half of the orbit in *Burnetia*, but over the postorbital bar in *Bullacephalus*. Also, the posterior boss in *Burnetia* is a horizontally elongate, laterally directed structure, whereas that of *Bullacephalus* is taller and more vertically directed.

The condition in NHCC LB133 helps to fill the morphological gap between *Bullacephalus* and other burnetiids (much as it does for the nasal boss). The posterior supraorbital boss in *Mobaceras* is intermediate in position between that of *Burnetia* and *Bullacephalus*: it originates anteriorly over the posterior half of the orbit but terminates above the postorbital bar. This boss is somewhat intermediate in morphology between that of *Burnetia* and *Bullacephalus* as well: it is a tall (in terms of distance from base to tip), anteroposteriorly short structure, but is directed laterally. Given this intermediate morphology, we
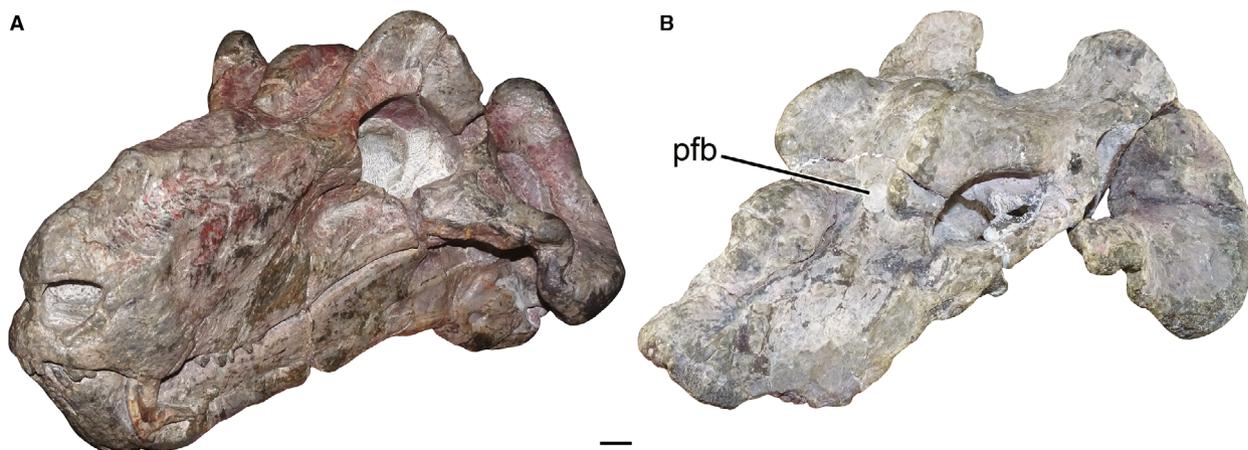
FIG. 10. Character 7 (discrete prefrontal boss), shown in representative skulls in three-quarter view. A, state 0 (absent) illustrated in the proburnetiine burnetiid *Paraburnetia sneeubergensis* (SAM-PK-K10037). B, state 1 (present) illustrated in the burnetiine burnetiid *Burnetia mirabilis* (NHMUK PV R5698; boss highlighted). *Abbreviation*: pfb, prefrontal boss. Scale bar represents 1 cm.
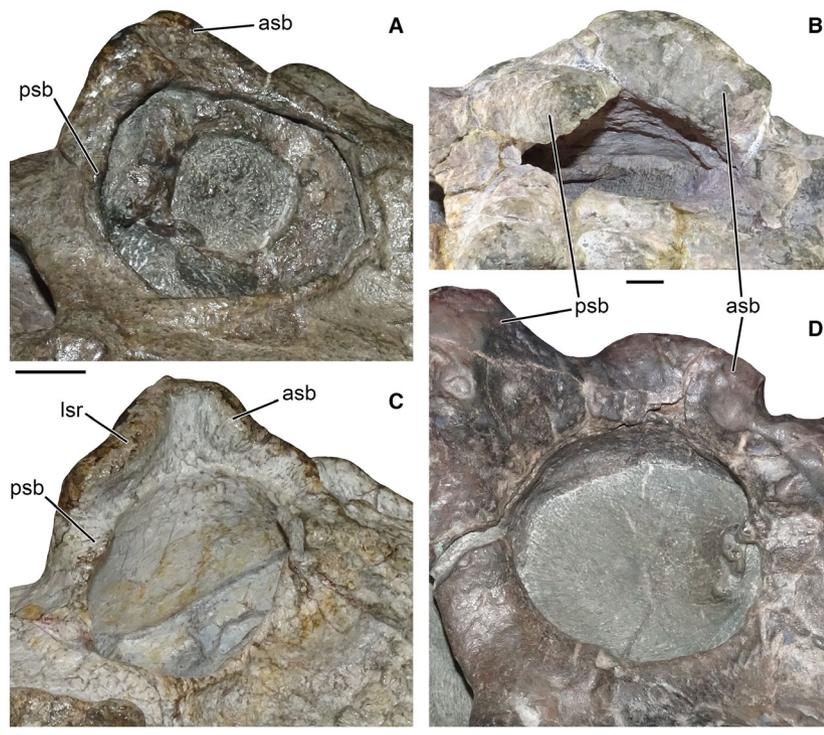
FIG. 11. Character 11 (anterior supraorbital boss), shown in details of circumorbital region of representative skulls. A, C, state 1 (triangular) illustrated in: A, the non-burnetiid burnetiamorph *Lemurosaurus pricei* (NMQR 1702); C, the proburnetiine burnetiid *Leucocephalus wewersi* (SAM-PK-K11112). B, D, state 2 (quadrangular) illustrated in the burnetiine burnetiids: B, *Burnetia mirabilis* (NHMUK PV R5698); D, *Bullacephalus jacksoni* (BP/1/5387). Also, Character 12 (curved lateral ridge at edge of supraorbital boss) illustrated in C and 13 (posterior supraorbital boss) in B and D. A, B, and D in right lateral view; C in left lateral view but mirrored for comparative purposes. *Abbreviations*: asb, anterior supraorbital boss; lsr, lateral supraorbital ridge; psb, posterior supraorbital boss; sb, supraorbital boss. Scale bars represent 1 cm.

do not recognize phylogenetic distinction between the posterior supraorbital bosses of *Burnetia* and *Bullacephalus*, and revert to treating the condition of both genera as the same character state. Day *et al.* (2016) devoted four characters (their chars 9 and 13–15) to the supraorbital bosses: 9, 'prefrontal boss' (with states 'absent' and 'present'); 13, 'supraorbital boss above posterior margin of orbit' (with states 'absent', 'present as a peak above posterior margin of orbit', and 'present as a laterally projected swelling'); 14, 'postfrontal along orbital margin pinched anteroventrally' (with states 'absent' and 'present'); and 15, 'postorbital-postfrontal boss' (with states 'absent' and 'present'). We identify several problems with these formulations, and utilize an alternative four characters to capture variation in supraorbital boss morphology: two involving simple presence/absence of bosses and two describing morphological variation in the anterior supraorbital boss (see below for details). An anterior supraorbital boss ('prefrontal boss' *sensu* Day *et al.* 2016, but not equivalent to the prefrontal boss in our Char. 7) is clearly present in NHCC LB133, so *Mobaceras* is scored

as 1 for this character. (Modified from SRS4, SS6, KR7, K8, DRA9.)

11. Morphology of anterior supraorbital boss. 0: triangular; 1: quadrangular. In the non-burnetiid burnetiamorphs *Lemurosaurus* (Fig. 11A) and *Lobalopex*, the supraorbital boss takes the form of a distinctly peaked, roughly triangular structure over the posterior half of the orbit. In burnetiids with a single large supraorbital boss (*Lende*; *Leucocephalus*, Fig. 11C; *Paraburnetia*; and *Proburnetia*) this general shape is retained, although the boss is generally more heavily pachyostosed and taller, with its apex above a more anterior portion of the orbit. In contrast, the anterior supraorbital boss in *Bullacephalus* (Fig. 11D) and *Burnetia* (Fig. 11B) is a much lower, roughly quadrangular structure, with a weakly convex dorsal margin. This boss is situated mostly above the anterior half of the orbit, and slopes posterodorsally to anteroventrally along its length. As discussed above, sorting out homology among the various supraorbital bosses of burnetiamorphs is problematic. Here, we consider the anterior

supraorbital boss of *Bullacephalus* and *Burnetia* to be homologous with the large, triangular supraorbital boss of other burnetiamorphs, based on their shared origins on the prefrontal and extension across the anterodorsal orbital margin. Also suggestive in this regard is the presence of a small but discrete secondary boss along the posterodorsal margin of the orbit in *Lemurosaurus* (Fig. 11A), distinct from the main supraorbital boss and in a similar position to the posterior supraorbital boss in *Burnetia* (Fig. 11B). For further discussion of this feature see Character 13 below. Although taller than in *Bullacephalus* and *Burnetia*, the anterior supraorbital boss is also quadrangular in *Mobaceras*, so it has been scored as 1 for this character. (Modified from K9.)

12. *Posterior margin of anterior supraorbital boss. 0: uniformly swollen; 1: with curved lateral ridge, giving folded appearance to boss in lateral view.* Day *et al.* (2016) introduced a new character, 'postfrontal along orbital margin pinched anteroventrally', to describe the condition in *Lende* and *Paraburnetia* (and later *Leucocephalus*; Day *et al.* 2018) where the posterior margin of the supraorbital boss bears a curved lateral ridge, giving the edge of the boss a folded appearance. We retain a version of this character here, albeit agnostic to the exact bone involved in this fold (Day *et al.*'s 2016 identification of this region as postfrontal is probable, but clear postfrontal sutures not preserved in the taxa in question). A folded boss characterizes a subset of the burnetiamorphs with triangular supraorbital bosses: it is clearly present in *Lende* and *Leucocephalus* (Fig. 11C) and visible in *Paraburnetia* despite damage, but absent in *Lemurosaurus*, *Lobalopex*, and *Proburnetia* (this region is not preserved in *Lophorhinus*). Although the anterior supraorbital boss is damaged on both sides in NHCC LB133, enough of the right boss is preserved to show that this folded morphology is absent, so we have coded *Mobaceras* as 0 for this character. (Modified from DRA14.)

13. *Posterior supraorbital boss. 0: absent; 1: present as a small but discrete swelling along the posterodorsal margin of the orbit; 2: present as an enlarged boss above the posterodorsal margin of the orbit (ORDERED).* Although we disagree with Day *et al.*'s (2016) assertion that the posterior supraorbital bosses in *Bullacephalus* and *Burnetia* are non-homologous, we agree that it is more phylogenetically informative to treat this structure as a separate character from the anterior supraorbital boss (contra Kammerer 2016*b*), because this approach allows *Pachydectes* to be coded. The dorsal margin of the orbit is badly damaged in the holotype of *Pachydectes elsi* and it is uncertain whether an anterior boss was present, but a boss is preserved above the postorbital bar on the right

side of the skull. In all three of these taxa the posterior supraorbital boss is a very large, heavily pachyostosed structure (in *Bullacephalus* it is larger than the anterior supraorbital boss). Although this boss is absent in other burnetiamorphs, in *Lemurosaurus* (Fig. 11A) there is a small, weakly developed swelling in the same position as the posterior supraorbital boss in *Burnetia* (Fig. 11B), and a comparable structure appears to be present in all proburnetiines in which this region is well-preserved (e.g. *Leucocephalus*; Fig. 11C). Here, we tentatively consider these structures homologues based on position, with the thickened boss treated as a derived state of an ancestral smaller swelling. The posterior supraorbital boss is very well-developed in NHCC LB133, so *Mobaceras* is coded as 2 for this character. (Modified from K9, DRA15.)

14. *Preparietal. 0: absent; 1: present, does not contact pineal foramen; 2: present, makes up anterior margin of pineal foramen.* Kammerer (2016*b*) included only presence/absence in his preparietal character. Kruger *et al.* (2015) and Day *et al.* (2016) also included states for whether the preparietal contacted the pineal foramen in this character. This is a problematic formulation in general because it does not allow the basic presence of a preparietal to affect tree topology (i.e. this treats 'preparietal contacting pineal foramen' and 'preparietal not contacting pineal foramen' as independent character states that can have independent origins from a preparietal-less ancestor; a few millimetres of parietal separating the preparietal from the pineal rim is sufficient to make the entire element non-homologous for purposes of analysis). In future analyses of basal therapsid relationships, it would be worthwhile to separate this into two characters: a simple presence/absence character and a second character concerning preparietal position. This is not necessary for the current analysis, however, because the outgroup (*Biarmosuchus*) is the only taxon that lacks a preparietal (and thus separating out presence/absence would be parsimony uninformative). Based on our examination of the holotype of *Bullacephalus jacksoni*, we were unable to confirm the coding of Day *et al.* (2016; 'narrowly separated from pineal foramen by parietals') and have recoded this taxon as ?. *Burnetia* is recoded as 2 for this character: in NHMUK PV R5697 the anterior margin of the pineal boss is damaged, but the underlying bone shows that the preparietal contributed to the margin of the pineal canal. In NHCC LB133, the weak ridges that we have identified as corresponding to the preparietal sutures disappear at the edge of the pineal boss, but in NHCC LB593 the posterior tip of the preparietal more clearly contributes to the margin of the pineal foramen (Fig. 4). As such we have coded *Mobaceras* as 2 for this character. (Modified from SW17, RSM24, SR24, KR15, K13, DRA17.)

15. Pineal boss. 0: raised, unpachyostosed rim; 1: highly discrete, teardrop-shaped, pachyostosed boss; 2: diffuse, rounded, pachyostosed boss; 3: absent, circumpineal region depressed. The plesiomorphic morphology of the pineal boss in therapsids is a well-developed, raised rim around the pineal foramen, sometimes exaggerated into a tall, chimney-like structure (Hopson & Barghusen 1986). Early analyses (Sidor & Welman 2003; Rubidge *et al.* 2006; Sidor & Rubidge 2006) recognized three states for this character: 'flat', 'well-defined chimney', and 'low and diffuse swelling'. In these analyses, only the non-therapsid outgroup taxa *Haptodus* and *Dimetrodon* were coded as 'flat'; some sort of raised edge to the pineal foramen was recognized in all ingroup biarmosuchian taxa. Analyses of biarmosuchian relationships that included only biarmosuchian taxa usually reduced the states of this character to two: 'flat or low swelling' and 'well-defined chimney' (Sidor *et al.* 2004; Smith *et al.* 2006; Sidor & Smith 2007). Kruger *et al.* (2015) and Kammerer (2016*b*), however, returned to a three-state formulation, using 'flat' to describe the pineal morphology of *Lende* (and the skull roof fragment NHMUK PV R871a in the latter analysis) in which there is not a distinct pineal boss, because the area around the pineal foramen is depressed relative to the pachyostosed intertemporal surface. Day *et al.* (2016) added an additional character state (for a total of four): 'low swelling with rimmed foramen', which they considered unique to *Bullacephalus*, but the lack of other taxa sharing that character state limits its phylogenetic utility. Previous formulations of a pineal boss character for biarmosuchians generally recognized a break between the narrow, 'chimney' or 'collar'-like bosses of non-burnetiids (Fig. 12A, B) and the pachyostosed bosses of burnetiids (Fig. 12C, D). However, none of these formulations properly captures the striking morphological distinction in boss morphology within Burnetiamorpha. For example, in taxa such as *Proburnetia* (proburnetiines *sensu* Kammerer 2016*b*), the pineal boss is a roughly circular structure with diffuse edges (state 2), i.e. it does not have a discrete margin, but rather grades into the surrounding surface of the skull roof (except posteriorly, where it does have a distinct margin at the occipital border). The condition in *Lende* and in NHMUK PV R871a may represent an extreme version of this state, in which the boss has essentially been 'absorbed' by surrounding pachyostotic bone and only the central depression housing the pineal foramen remains. Thin sections showing this condition were figured by Kulik & Sidor (2019) in two unidentified burnetiamorph skull caps from the middle Permian of Zambia. Regardless of evolutionary or developmental origin, however, the circumpineal surface in these taxa is not flat, so this state has been rephrased here (state 3). In taxa such as *Burnetia* (burnetiines *sensu* Kammerer 2016*b*), the pineal boss is not diffuse (contra most previous analyses), instead it is a highly discrete structure with distinct edges (state 1). Furthermore, it is rounded only at its anterior margin; posterior to the pineal foramen, the boss is attenuate and ends in a pointed tip, giving the boss as a whole a teardrop shape in dorsal view. This morphology is best-preserved in *Pachydectes*, but is also present in *Burnetia* (Fig. 12D), TM 4305 (see Kammerer 2016*b*, fig. 2), and NHCC LB133/LB593 (Fig. 1A; the boss of *Bullacephalus* is also consistent with this state as preserved, but was coded as ? because its posterior half is broken off). *Mobaceras* was coded as 1 for this character. (Modified from SW16, SHK14, RSM19, SR18, SRS14, SS16, KR13, K14, DRA18.)

16. Zygomatic bosses. 0: absent; 1: present as one or two oval bosses at the ventral margin of the zygomatic arch; 2: present as a large, circular boss extending across the lateral face of the zygomatic arch (ORDERED). The presence of bosses on the zygomatic arch has long been recognized as a characteristic feature of burnetiamorphs (Rubidge & Sidor 2002), but variation in these structures has only rarely been captured in phylogenetic analyses (Sidor *et al.* 2004, Smith *et al.* 2006, and Sidor & Smith 2007 being exceptions). Day *et al.* (2016) recognized that while the majority of burnetiamorphs have a pair of small bosses at the ventral margin of the zygoma, generally near the base of the postorbital bar (Fig. 13A, C), some taxa have only a single boss. Accordingly, they formulated their states for this character based on boss number (zero, one, or two). However, this formulation does not capture the major source of variation in burnetiamorph zygomatic bosses, which is not simply their number but rather their morphology. Day *et al.* (2016) noted two taxa with only a single zygomatic boss (*Lobalopex* and *Bullacephalus*), but the boss morphology of these two taxa varies markedly. In *Lobalopex*, the zygomatic boss is a small, oval, horizontally oriented structure at the ventral edge of the zygomatic arch, very similar to those of most other burnetiamorphs. In contrast, the boss of *Bullacephalus* is an enormous, roughly circular structure that extends across the entire lateral surface of the zygomatic arch below the anterior margin of the temporal fenestra (Fig. 13B). A similar boss is otherwise known only in *Pachydectes* (Fig. 13D) among biarmosuchians (although it is unknown whether one or two bosses were present in *Pachydectes*, because the zygoma is broken posterior to the boss). Here, we recognize this morphological distinction as of phylogenetic importance, separating the condition in *Bullacephalus* and *Pachydectes* from that of other burnetiamorphs. We formulate state 1 as including either one or two small oval bosses to encompass the condition in *Lobalopex*, but would note that it is actually uncertain whether it had only a single zygomatic boss; the specimen is now broken in this region, but casts of the skull made before it was broken show a swelling adjacent to the boss that may

FIG. 12. Characters 15 (pineal boss) and 18 (dorsal squamosal boss), shown in details of left temporal region of representative skulls. A–D, Character 15: A–B, state 0 (raised, unpachyostosed rim) illustrated in the non-burnetiid burnetiamorphs: A, *Lemurosaurus pricei* (NMQR 1702); B, non-burnetiid burnetiamorph *Lobalopex mordax* (CGP/1/61); C, state 2 (diffuse, rounded, pachyostosed boss) in the proburnetiine burnetiid *Leucocephalus wewersi* (SAM-PK-K11112); D, state 1 (discrete, teardrop-shaped, pachyostosed boss) in the burnetiine burnetiid *Burnetia mirabilis* (NHMUK PV R5698). Character 18: A, state 0 (absent); B–D, state 1 (present). All specimens in dorsal view; C mirrored for comparative purposes. Note weaker development of the boss in (B) *Lobalopex* compared with burnetiids. *Abbreviations*: dsb, dorsal (supratemporal) boss; pf, pineal foramen. Scale bars represent 1 cm.
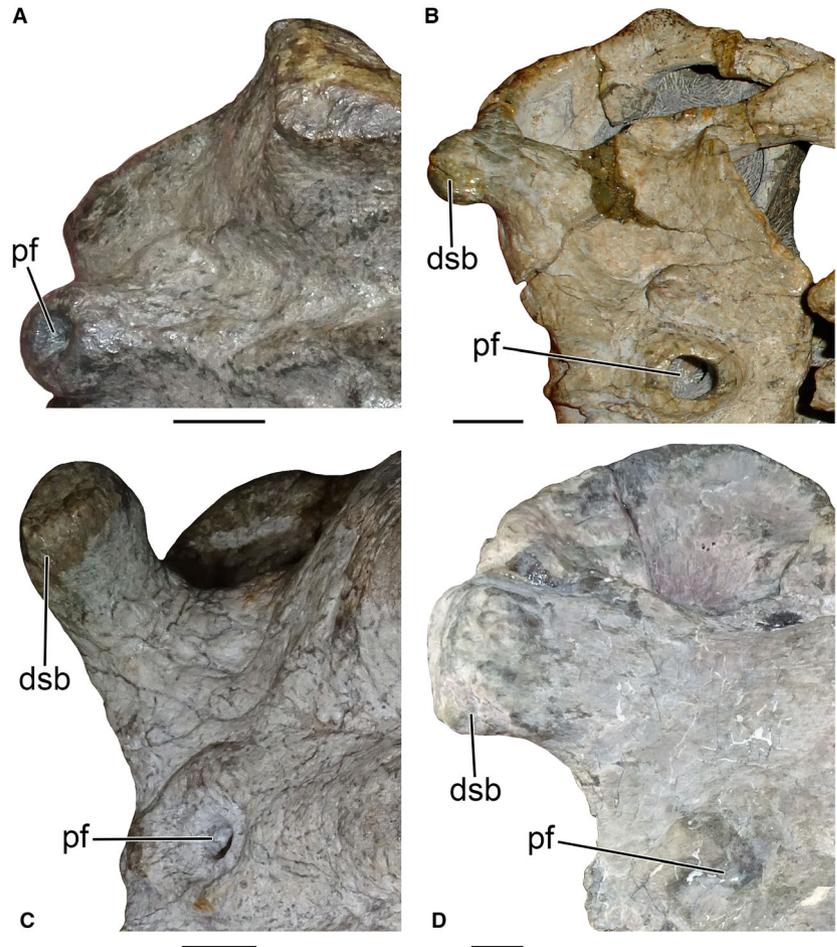
have represented a second boss (Sidor *et al.* 2004). We treat this character as ordered, and consider the single enlarged boss in *Bullacephalus* and *Pachydectes* to represent a derived version of the small, paired bosses in other burnetiamorphs (with the condition in *Burnetia* being a possible intermediate, given that it has a proportionally larger, more dorsoventrally expanded zygomatic boss than most other burnetiamorphs). We recognize that this is a questionable homology statement, but would argue that the heart of this question is whether the simple presence of bosses on the zygomatic arch should be given phylogenetic value. The Day *et al.* (2016) formulation for this character does not; in their analysis the single zygomatic boss of *Lobalopex* is treated as a unique feature unrelated to the anatomy seen in other burnetiamorphs. We argue that the presence of bosses on the zygomatic arch in burnetiamorphs is phylogenetically important. This could be reflected in two ways: (1) create two characters (similar to what we have done for the mid-nasal boss), one for the presence/absence of zygomatic bosses and the other dealing with morphology of the bosses; or (2) create a single multistate character encompassing both presence/absence

and boss morphology, but treat it as ordered so as to recognize the presence of bosses as potentially homologous across taxa with different boss morphologies. We opt for the latter formulation solely for ease of analysis: if future workers do not consider the bosses of *Bullacephalus* and *Pachydectes* homologous with those of other burnetiamorphs, they can simply treat this character as unordered. The squamosal is damaged on both sides of the skull in NHCC LB133, so *Mobaceras* is coded ? for this character. (Modified from RK9, SW9, SHK6–7, RSM22, SR21, SRS6–7, SS8–9, KR14, K16, DRA21.)

17. *Ventral squamosal boss. 0: absent; 1: present as small, ventrally directed process; 2: present as large, pachyostosed boss; 3: present as a transversely expanded, elongate, pachyostosed boss (ORDERED)* . As for most other burnetiamorph boss characters, the majority of previous analyses dealt primarily with boss presence/absence rather than boss morphology. Day *et al.* (2016) noted the difficulty in disentangling the various aspects of subtemporal bar morphology in burnetiamorphs, including boss development, pachyostosis of the bar itself, and angulation of the bar.
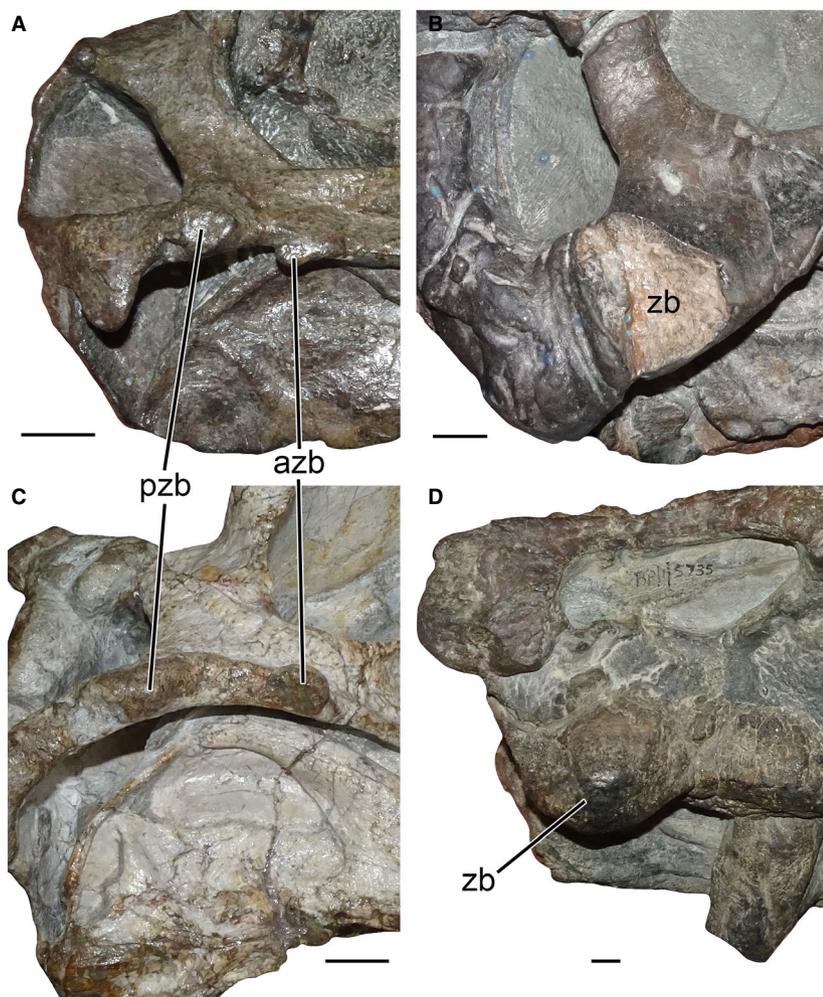
FIG. 13. Character 16 (zygomatic bosses), shown in details of temporal region of representative skulls. A, C, state 0 (paired, small oval bosses on the ventral edge of the zygoma) illustrated in: A, the non-burnetiid burnetiamorph *Lemurosaurus pricei* (NMQR 1702); C, the proburnetiine burnetiid *Leucocephalus wewersi* (SAM-PK-K11112). B, D, state 1 (large, rounded boss covering the lateral surface of the zygoma) illustrated in the burnetiine burnetiids: B, *Bullacephalus jacksoni* (BP/1/5387; surface of boss damaged in this specimen); D, *Pachydectes elsi* (BP/1/5735). A, B, and D in right lateral view; C in left lateral view but mirrored for comparative purposes. *Abbreviations*: azb, anterior zygomatic boss; pzb, posterior zygomatic boss; zb, zygomatic boss. Scale bars represent 1 cm.

Many of these aspects are correlated, however, and here we recognize most of them as part of a series of increasingly elaborated structures. Subtemporal squamosal bosses are present in all burnetiamorphs for which this part of the skull is preserved. In its simplest form (state 1; present in *Lemurosaurus*, Fig. 14B; and *Lobalopex*), the boss ('bulb' of Day *et al.* 2016) is an anteroposteriorly narrow, ventrally directed squamosal process anterolateral to the quadrate. In burnetiids, this boss takes many forms, but in almost all cases is distinctly a boss emerging from the ventral edge of the subtemporal bar (state 2). In *Lende*, it is a very discrete structure with a bulbous tip, although this may be an artefact of overpreparation. In *Leucocephalus* and *Proburnetia*, the boss is anteroposteriorly broader at base but is still distinct from the comparatively poorly pachyostosed subtemporal bar (but the shape of the boss differs between these taxa, being more

bulbous anteriorly in *Paraburnetia*). Distinct from this is the condition in *Burnetia* (Fig. 14D) and *Niuksenitia* (state 3): in these taxa, the entire subtemporal bar is dorsoventrally and transversely expanded, and the subtemporal boss takes the form of a massively thickened lateral edge to this expanded region. This morphology represents the endpoint of a series of character states with increasing pachyostosis and boss size, and as such this character is treated as ordered. Damage to the subtemporal bar in NHCC LB133 makes it impossible to tell whether a boss was present in this region, so *Mobaceras* is coded as ? for this character. (Modified from SW10, SHK8, SRS11, SS10, KR33, K17, DRA19.)

18. Dorsal squamosal boss. 0: absent; 1: present. Dorsally or posterodorsally directed 'horns' above the temporal fenestra are present in all burnetiamorphs other than *Lemurosaurus*. These horns are usually presumed to be on the squamosal, although direct sutural evidence for this is lacking in most taxa. The small ('nubbin-like' as described by

Kruger *et al.* 2015) postorbital boss above the apex of the temporal fenestra in *Lemurosaurus* (Fig. 14B) has not traditionally been considered homologous with the 'squamosal horns' (see discussion in Kammerer 2016*b*). However, given that the postorbital usually extends to the posterodorsal corner of the temporal fenestra in non-burnetiamorph biarmosuchians, there is a real possibility that the squamosal horns of burnetiamorphs could be composed at least partially of postorbital. Given that the condition in *Lemurosaurus* is unique among burnetiamorphs, however,

we here retain the traditional formulation of this character, while recognizing that the homology of this boss requires further study. The dorsal squamosal boss varies in morphology across all burnetiamorphs, but not in a way that can be easily interpreted as showing phylogenetic structure: its precise shape appears to be species specific (e.g. Fig. 14C, D). Well-developed supratemporal bosses are present in NHCC LB133, so *Mobaceras* is coded as 1 for this character. (Modified from RK6, SW12, SHK10, SRS10, SS12, KR26, K19, DRA23.)
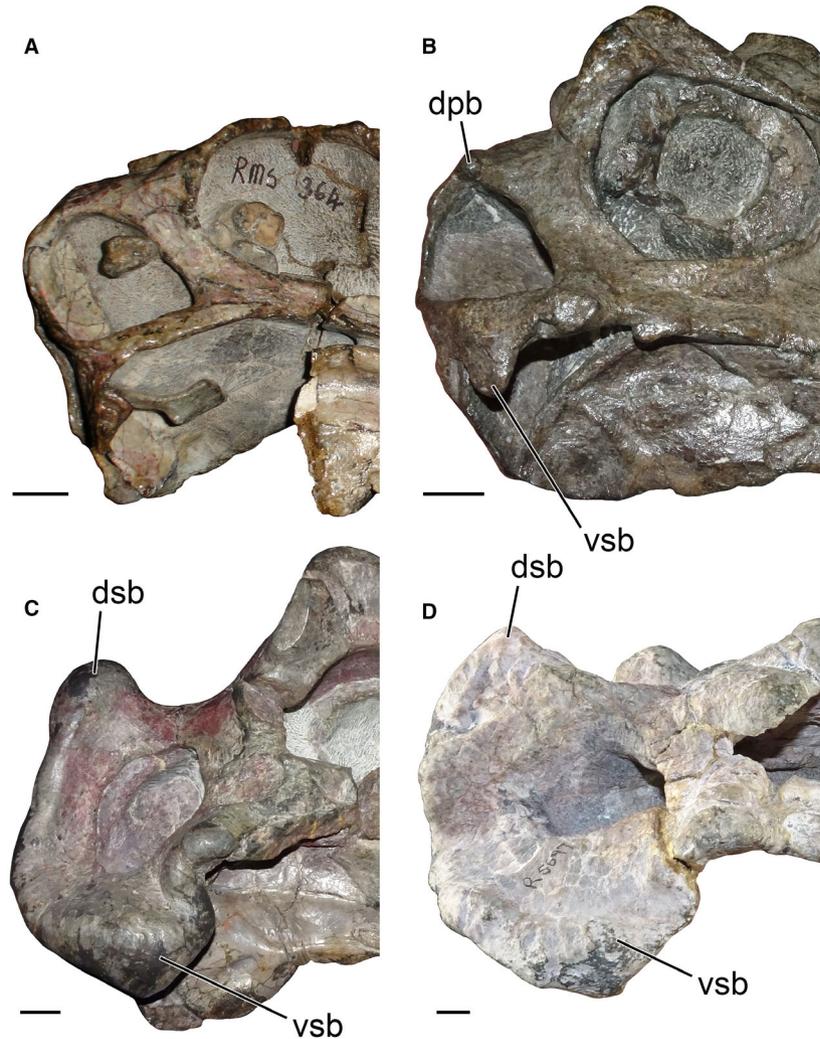
FIG. 14. Characters 17 (ventral squamosal boss) and 18 (dorsal squamosal boss) shown in details of the temporal region in representative skulls. Character 17: A, state 0 (absent) illustrated in the non-burnetiamorph biarmosuchian *Herpetoskylax hopsoni* (CGP/1/67); B, state 1 (small, ventrally directed process) illustrated in the non-burnetiid burnetiamorph *Lemurosaurus pricei* (NMQR 1702). C, state 2 (large, pachyostosed boss) illustrated in the proburnetiine burnetiid *Paraburnetia sneeubergensis* (SAM-PK-K10037); D, state 3 (transversely expanded, elongate, pachyostosed boss) illustrated in the burnetiine burnetiid *Burnetia mirabilis* (NHMUK PV R5698). Note increasing size and degree of pachyostosis through the ascending character states. Character 18: A, state 0 (absent); C–D, state 1 (present); *Lemurosaurus* (B) is unique among biarmosuchians in that only a 'nubbin'-like supratemporal boss is present on the postorbital. Here this taxon is treated as being state 0 for this character, with the recognition that further study of the homology of the dorsal 'squamosal' boss is necessary. All specimens in right lateral view. *Abbreviations*: dpb, dorsal postorbital boss; dsb, dorsal squamosal boss; vsb, ventral squamosal boss. Scale bars represent 1 cm.

19. Contact between the skull roof and occipital plate. 0: sharply angled, with clear demarcation between posterior edge of skull roof and dorsal edge of occiput; 1: weakly angled, skull roof slopes posteroventrally to join occiput. In most biarmosuchians, the planes of the dorsal skull roof and the occiput are sharply offset from one another at nearly a 90° angle, such that the surface of the skull roof is not visible in occipital view (e.g. Fig. 15A, D). In proburnetiines, however, the posterior skull roof is more gradually sloping posteroventrally. Although the extent of the skull roof and occiput in these taxa can still be differentiated by the degree of pachyostosis (high on the parietals and squamosals, not on the tabulars and postparietal), they do not form distinct planes, and much of the posterior skull roof (usually including the intertemporal region and frontal bosses) is visible in occipital view (e.g. Figs 15B, 16B). The posterior skull roof is also not distinct from the occipital plane in *Biarmosuchus tener*, although this may be related to the probable juvenile nature of the specimens preserving the occiput (such as the holotype PIN 1758/2; greater posteroventral angulation of the intertemporal region is typical in juvenile biarmosuchians and likely to be a correlate of the enormous orbits in these individuals, although there is still a break between the plane of the skull roof and occiput in the juvenile holotype of *Lemurosaurus*, despite this angulation). In *Mobaceras*, there is a clear break between the skull roof and occiput, so this taxon is coded as 0 for this character. (New)

20. Occipital dimensions. 0: height of occiput >40% of width; 1: height of occiput <35% of width. In most biarmosuchians, the occipital plate is only slightly wider than tall (height of occiput 67–80% of width in non-burnetiamorph biarmosuchians), although it tends to broaden in burnetiamorphs (52–70%). *Burnetia* (Fig. 15D) and *Niuksenitia* (Fig. 15C) exhibit an extreme condition where the occipital plate is markedly wider than tall (*c.* 24% in *Burnetia* and *c.* 32% in *Niuksenitia*, even when not including the ventrolateral projection of the squamosal in the subtemporal bar). The only specimen showing a morphology even approaching this condition is the holotype of *Lobalopex mordax* (*c.* 45%), but that specimen is badly dorsoventrally compressed, so its apparent breadth is probably an artefact. The postparietal, tabular, supraoccipital, and opisthotic of NHCC LB133 are similar in dimensions to those of *Bullacephalus* or *Proburnetia*, not *Burnetia*, but given that the lateral edges of the squamosal are broken off we must code *Mobaceras* as ? for this character.

21. Paired ridges on occipital surface of postparietal lateral to nuchal crest. 0: absent; 1: present. Kammerer (2016*b*) introduced this character to describe the unusual postparietal ridges flanking the nuchal crest in burnetiids (Fig. 15) and probably *Lobalopex*. Day *et al.* (2016) argued that the occipital ridges in *Proburnetia* were morphologically divergent from those of other burnetiamorphs, and created a new character state to encompass the condition in that taxon. In most burnetiamorph specimens where occipital sutures are visible, these ridges are relatively short and confined to the posterior face of the postparietal, between the suture with the tabular and the median nuchal crest. In *Proburnetia*, these ridges are at the postparietal edge (at the tabular suture) and are elongate, extending ventrally to reach the dorsal margin of the supraoccipital. Here we retain a single character state (1) for the presence of these ridges. The condition in *Proburnetia* may be autapomorphic, but we do not believe its ridges should be treated as non-homologous with those of other burnetiamorphs because of their greater length and slight difference in position. Also, the exact position of these ridges in other burnetiamorphs is not always clear (because of pachyostosis or poor preservation), and it is possible that they occur at the postparietal–tabular suture in other taxa. NHCC LB133 has a well-developed postparietal ridge at least to the right of the median nuchal crest, so *Mobaceras* is coded as 1 for this character. (Modified from K20, DRA24.)

22. Nuchal crest length. 0: nuchal crest largely restricted to postparietal, separated from foramen magnum by broad flat section of supraoccipital; 1: nuchal crest extends to dorsal margin of foramen magnum. The nuchal crest is a median ridge on the occiput serving as a muscular attachment site and is well developed in most carnivorous therapsids. Primitively, the nuchal crest is borne mainly on the postparietal, and this is the case in non-burnetiamorph biarmosuchians (e.g. *Herpetoskylax*; Fig. 16A). In burnetiids, the dorsoventral extent of the nuchal crest is expanded such that it nears the dorsal margin of the foramen magnum, and in some taxa becomes confluent with the swollen dorsal rim of the foramen magnum (e.g. *Burnetia*). In burnetiids the postparietal bears a well-developed ventral process that in some taxa (e.g. *Paraburnetia*; Fig. 16B) nearly bisects the supraoccipital in posterior view. The mid-section of the supraoccipital is more pinched in *Lemurosaurus* and *Lobalopex* than in non-burnetiamorph biarmosuchians, but the nuchal crest is still clearly separated from the foramen magnum by a length of flat supraoccipital surface, so these taxa are coded as 0 for this character. In NHCC LB133, the ventralmost tip of the postparietal is damaged, but the underlying articular surface on the supraoccipital shows that the nuchal crest reached the dorsal rim of the foramen magnum. (New)
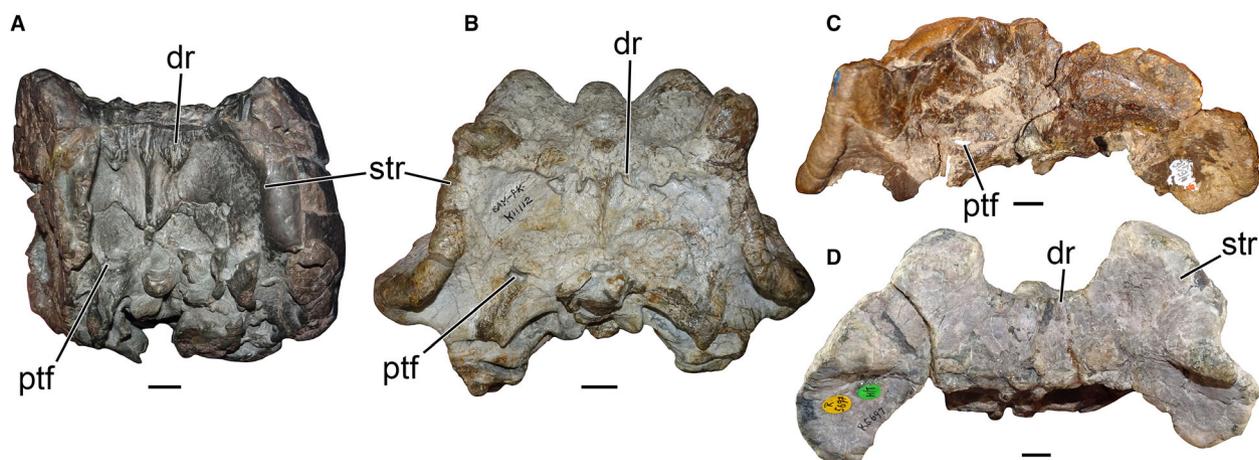
FIG. 15. Burnetiid occiputs, illustrating Characters 19–21, 23 and 24. Character 19 (occipital dimensions), state 0 (height of occiput >40% of width) illustrated in: A, the burnetiine burnetiid *Bullacephalus jacksoni* (BP/1/5387); B, the proburnetiine burnetiid *Leucocephalus wewersi* (SAM-PK-K11112). State 1 (height of occiput <35% of width) illustrated in the burnetiine burnetiids: C, *Niuksenitia sukhonensis* (PIN 3159/1); D, *Burnetia mirabilis* (NHMUK PV R5698). *Abbreviations*: dr, descending ridge on postparietal; ptf, post-temporal fenestra; str, squamosal–tabular ridge. Scale bars represent 1 cm.

23. Squamosal–tabular border. 0: without thickening of squamosal; 1: squamosal pachyostosed to form dorsoventrally elongate swelling along border with tabular. The burnetiamorph occiput exhibits a sharp break between the variably pachyostosed squamosal (making up the lateral edge of the occiput) and the uniformly unpachyostosed tabular (medial to the squamosal in the dorsal portion of the occipital plate). The associated break in surface topology yields a prominent, dorsomedially to ventrolaterally directed ridge on the posterior to posteroventral edge of the squamosal. This ridge is relatively low in *Lemurosaurus* and *Lobalopex*, but is extremely well-developed in burnetiids (Fig. 15). Day *et al.* (2016) questioned the homology of this structure in *Bullacephalus* relative to other burnetiamorphs, arguing that this genus does not have a distinct squamosal–tabular ridge because the entire squamosal is heavily pachyostosed. They created a new state, 'present between tabular and temporal fenestra', unique to *Bullacephalus*. We disagree with this approach for multiple reasons. First, the presence of greater pachyostotic expansion of the squamosal in *Bullacephalus* compared with other burnetiamorphs does not negate the fact that these taxa all share pachyostosis of the occipital portion of the squamosal. Second, *Bullacephalus* is not actually unique in having pachyostosis of the post-temporal squamosal beyond the squamosal–tabular ridge: in *Paraburnetia*, the immediate posterior rim of the temporal fenestra is not pachyostosed, but extensive swelling of the squamosal is present even on its lateral surface, well-separated from its contact with the tabular. For these reasons, we reject Day *et al.*'s (2016) formulation of the condition in *Bullacephalus* as non-homologous with that of other burnetiamorphs, and

recode this genus as 1 for this character. The lateral edges of the squamosal are largely broken off on the occiput of NHCC LB133, but there is a distinct break in height between the preserved margin and the tabular, so *Mobaceras* is coded as 1 for this character. (Modified from SW10, SHK11, SRS11, SS13, K22.)

24. Post-temporal fenestra. 0: large; 1: small. The post-temporal fenestra is plesiomorphically a large, ovoid-to-circular opening between the supraoccipital and opisthotic. In most burnetiamorphs, it is reduced to a thin slit (Fig. 15). This is the case in NHCC LB133, so *Mobaceras* is coded as 1 for this character. (Modified from KR30, K21, DRA26.)

25. Palatine boss morphology. 0: elongate, broadly dentigerous boss; 1: delta-shaped boss with marginal tooth row; 2: reniform boss with marginal tooth row. In sphenacodontids, an elongate, weakly raised dentigerous patch extends across much of the palatal surface of the palatine and pterygoid. In early therapsids, in contrast, the palatal dentition is generally restricted to two discrete bosses, one on the palatine and the other on the pterygoid (Fig. 17). Therapsid palates have substantially fewer teeth than those of sphenacodontids; the latter have hundreds of denticles on each side of the palate, whereas therapsid palatal teeth are typically in single rows or patches of reduced size. Therapsid palatal teeth are also generally individually larger than those of sphenacodontids, so fewer are present even in patches of equivalent area. *Biarmosuchus* appears to exhibit an intermediate morphology between sphenacodontids and most basal therapsids, in which the dentigerous portions of the palate are
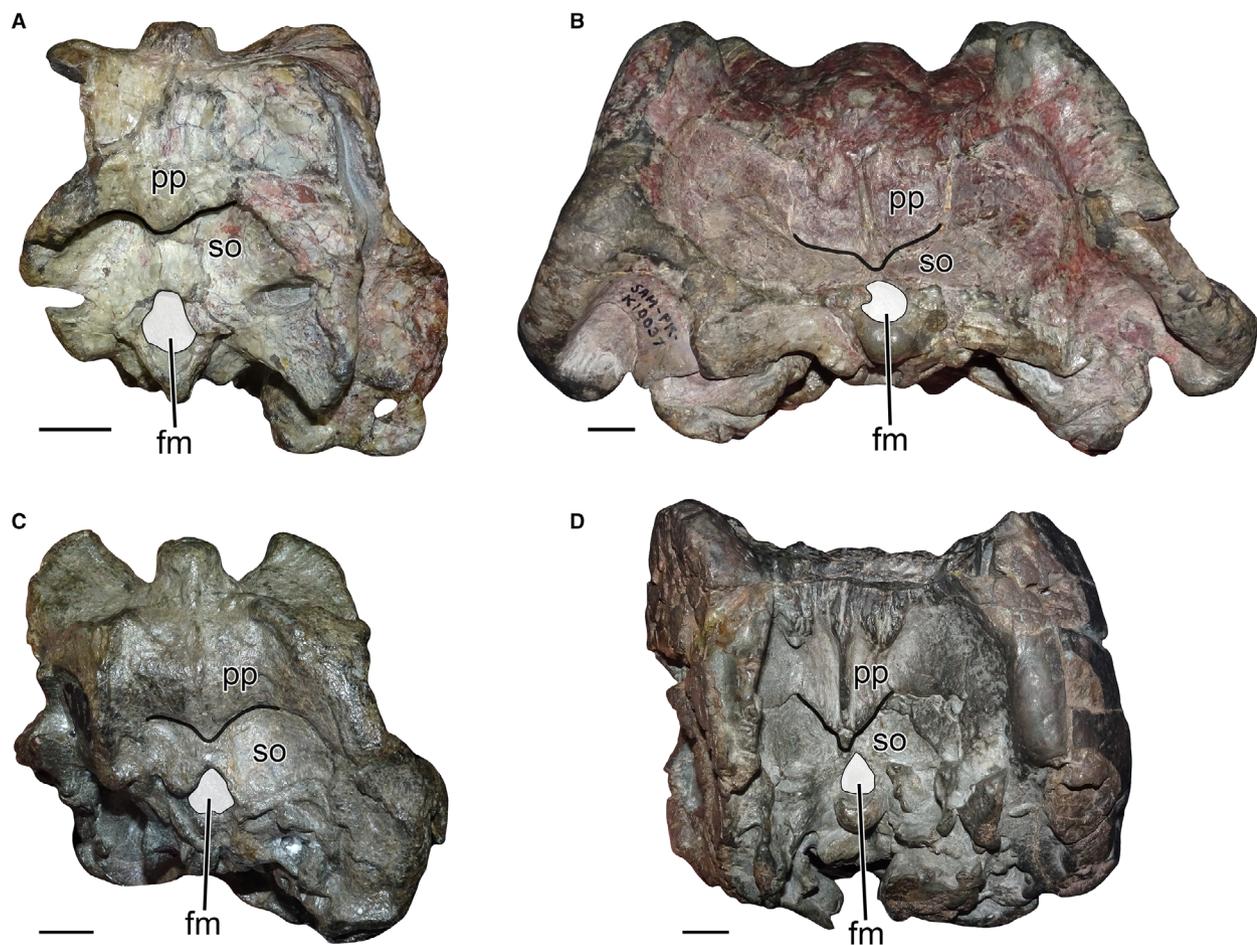
FIG. 16. Character 22 (nuchal crest length) illustrated in: A, the non-burnetiamorph biarmosuchian *Herpetoskylax hopsoni* (CGP/1/67); B, the proburnetiine burnetiid *Paraburnetia sneeubergensis* (SAM-PK-K10037); C, the non-burnetiid burnetiamorph *Lemurosaurus pricei* (NMQR 1702); D, the burnetiid burnetiamorph *Bullacephalus jacksoni* (BP/1/5387). Foramen magnum and postparietal–supraoccipital suture highlighted. *Abbreviations*: fm, foramen magnum; pp, postparietal; so, supraoccipital. Scale bars represent 1 cm.

discretized into distinct palatine and pterygoid bosses, but the palatal teeth are still extremely numerous and spread across these bosses (Fig. 17A). On the pterygoid boss of *Biarmosuchus* there are clearly numerous teeth uniformly spread across the boss surface, without organization into distinct rows. The condition of the palatine is more controversial; Kammerer (2016a) considered the palatine boss to have teeth spread across its surface, and although Day *et al.* (2016) tentatively retained this coding, they noted that previous authors (Sigogneau & Chudinov 1972; Ivakhnenko 1999, 2003) reconstructed the palatine boss of *Biarmosuchus* with discrete marginal tooth rows. Examination of all known cranial material of *Biarmosuchus* (CFK, pers. obs.) was unable to definitively resolve this issue. Kammerer's (2016a, b) coding of the palatine boss of *Biarmosuchus* was based on the condition in the best-preserved specimen, PIN 1758/1 (the holotype of *Eotitanosuchus olsoni*, considered to be a mature

specimen of *Biarmosuchus tener* by Ivakhnenko 1999 and Kammerer 2014). The tooth-bearing surface of the left palatine boss is damaged posteriorly in PIN 1758/1, but the right boss is complete. The entire surface of this boss is covered with teeth; a distinct break in tooth rows between the lateral and medial boss margins cannot be discerned. However, it is possible that this is a taphonomic artefact: PIN 1758/1 has clearly suffered some lateral compression, and this may have crushed the lateral and medial edges of the palatine bosses together. Possible evidence for this interpretation comes from the *Biarmosuchus* specimens PIN 1758/7, 1758/18, and 1758/85, in which the anterior tip of the palatine boss appears to show diverging tooth rows along its edges, with a non-dentigerous depression between them. With this noted, the palatine bosses in these specimens are very badly damaged and worn compared with those of PIN 1758/1, preserving very few teeth and featuring many non-

dentigerous depressions that are clearly the result of breakage (e.g. between the anterior and posterior portions of the lateral boss margin on the left side of PIN 1758/85). Furthermore, at its greatest width the tooth patch on the boss of PIN 1758/1 is seven teeth across, so regardless of whether they form tooth rows this is a more densely dentigerous palatine than in any other therapsid. As such, a distinct state for *Biarmosuchus* is retained here, although we echo Day *et al.* (2016) in hoping for better preparation of *Biarmosuchus* palates in the future to resolve this issue. Among non-*Biarmosuchus* biarmosuchians, two general palatine boss morphologies can be discerned: those in which the boss takes the form of an elongate, triangular structure with an anterior apex (with raised, dentigerous lateral and medial edges, creating a delta shape; Fig. 17B, D); and those in which it is anteriorly rounded (with the raised, dentigerous margin broadly curving across its anterior edge, creating a reniform shape; Fig. 17C, E). Outside of the extreme condition in *Biarmosuchus*, we do not distinguish between number of tooth rows per boss edge as character states, as was done by Day *et al.* (2016). Our examination of basal therapsid palatal bosses indicates that for the most part, the appearance of multiple tooth rows on these structures is an artefact of replacement, with replacement palatal teeth emerging medial to the functional teeth, sometimes with multiple replacements for a single tooth position. Given the difficulty in distinguishing this condition from persistent multiple tooth rows, we err on the side of ignorance. Finally, we would note that although we would recommend separating the three states of the current character into two distinct characters in a broader analysis of synapsid relationships (so as to recognize possible homology of reduction in palatine dentition among non-*Biarmosuchus* therapsids), for the purposes of the current analysis it is computationally unnecessary, given that reduction in dentition would resolve as uniformly present in the ingroup and thus be equivalent to the current coding of *Biarmosuchus* having a unique character state, at least for purposes of tree construction. The palatine boss in NHCC LB133 (best preserved on the left side) is very elongate and definitely pointed at its tip, so *Mobaceras* is coded as 1 for this character. (Modified from RK24, SW23, SHK17, RSM28, SR29, SRS17, SS19, KR17, K22, DRA27–28.)

26. Pterygoid boss morphology. 0: broadly dentigerous boss; 1: delta-shaped boss with marginal tooth row. As mentioned above, *Biarmosuchus* clearly has a broad, undifferentiated tooth patch covering the entire surface of the pterygoid boss (Fig. 17A). A broadly dentigerous pterygoid boss is also present in some other early therapsids, including other biarmosuchians (although in no other taxa is the boss as large or bearing as many teeth as in *Biarmosuchus*). A broad tooth patch on the pterygoid boss is definitely present in *Hipposaurus* (Fig. 17B), *Ictidorhinus*, *Herpetoskylax*, and *Lemurosaurus* (Fig. 17C) among non-burnetiid biarmosuchians. The condition in *Lycaenodon* is uncertain because this region is badly damaged in the holotype. In most burnetiamorphs, however, the pterygoid boss dentition is restricted to the boss margins, and the boss as a whole is delta shaped (Fig. 17D). This boss mirrors the palatine boss, so that its apex points posteriorly (whereas the palatine boss, if delta shaped, has an anteriorly directed apex). This morphology is present in *Lobalopex* and all burnetiids with the unusual exceptions of *Burnetia* (Fig. 17E) and *Pachydectes*, which exhibit a *Biarmosuchus*-style pterygoid tooth patch (although the total area of this patch is much smaller in *Burnetia* than that of other biarmosuchians; this taxon generally has unusually small palatal bosses). NHCC LB133 has what is clearly a delta-shaped tooth row on the right pterygoid boss, so *Mobaceras* is coded as 1 for this character. (Modified from RK25, SR33, DRA30.)

27. Dentition on transverse process of pterygoid. 0: present; 1: absent. Although often ontogenetically variable in therapsids (Kammerer 2011), there does seem to be phylogenetic structure to the distribution of transverse process dentition in biarmosuchians. Teeth on the transverse process of the pterygoid are known only in *Biarmosuchus* and *Hipposaurus* (Fig. 17B) among non-burnetiamorph biarmosuchians. Uniquely among burnetiamorphs, a tooth row on the transverse process is also present in *Bullacephalus* (Fig. 17D), *Pachydectes*, and *Mobaceras*. (These teeth might also be present in *Burnetia* and *Niuksenitia*, but their holotypes are too damaged to be certain.) A single tooth root is present on the left transverse process in the presumed mature specimen (NMQR 1702; Fig. 17C) of *Lemurosaurus* (Sidor & Welman 2003) and at least three teeth are present on the right transverse process in the presumed juvenile holotype (BP/1/816). This is consistent with the pattern of loss of the transverse process dentition throughout ontogeny seen in other therapsids (e.g. *Titanophoneus*; Kammerer 2011); as such *Lemurosaurus* has been coded as 'absent' for this character. This is also the case for *Herpetoskylax*, in which teeth are present on the transverse process in the smaller referred specimen (BP/1/3924), but are absent in the larger holotype (CGP/1/67). The large size of the holotypes of *Bullacephalus* and especially *Pachydectes* make it extremely unlikely that the presence of transverse process teeth in these taxa is the result of immaturity; although not as large, the holotype of *Mobaceras* does not exhibit other juvenile burnetiamorph features, so this taxon is coded as 0 for this character. (Modified from SW21, SHK16, RSM29, SR30, SRS16, SS18, KR18, K25, DRA29.)
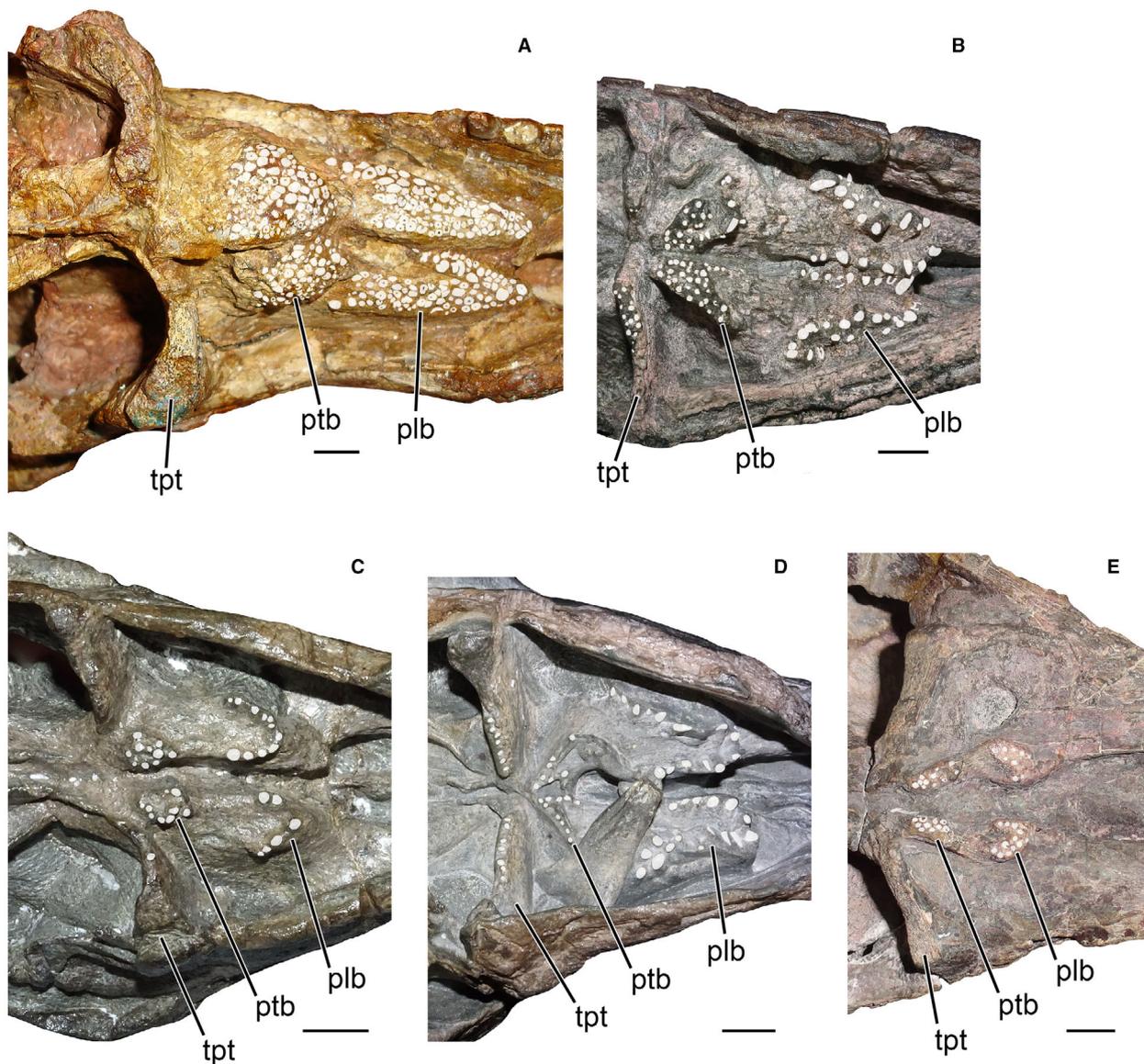
FIG. 17. Biarmosuchian palates, illustrating Characters 25–27. Palatal dentition highlighted to improve visibility. A, the non-burnetiamorph biarmosuchian *Biarmosuchus tener* (PIN 1758/1). B, the non-burnetiamorph biarmosuchian *Hipposaurus boonstrai* (CGS WB123). C, the non-burnetiid burnetiamorph *Lemurosaurus pricei* (NMQR 1702). D, the burnetiine burnetiid *Bullacephalus jacksoni* (BP/1/5387). E, the burnetiine burnetiid *Burnetia mirabilis* (NHMUK PV R5698). Character 25 (palatine boss morphology): A, state 0 (elongate, broadly dentigerous boss); B, D, state 1 (delta-shaped boss with marginal tooth row); C, E, state 2 (reniform boss with marginal tooth row). Character 26 (pterygoid boss morphology): A–C, E, state 0 (broadly dentigerous boss); D, state 1 (delta-shaped boss with marginal tooth row). Character 27 (dentition on transverse process of pterygoid): B, D, state 0 (present); A, transverse processes damaged in PIN 1758/1 but dentition known to be present on this structure in *Biarmosuchus* based on other specimens. *Abbreviations*: plb, palatine boss; ptb, pterygoid boss; tpt, transverse process of pterygoid. Scale bars represent 1 cm.

Deleted characters

Several characters from the analysis of Day *et al.* (2016) have been deleted from the current analysis. Characters were deleted if they were parsimony uninformative or restructured into new or modified characters (detailed above). Below we provide our reasoning for deleting each of the characters noted.

DRA0: ratio of preorbital to basicranial length. We deleted this character because its coding primarily reflects ontogenetic state (the holotype of *Ictidorhinus martinsi*, generally regarded as a juvenile, is a particularly notable outlier).

DRA1: upper postcanine number. This character provided no phylogenetic signal in the analysis of Day *et al.* (2016) and is also variable with ontogeny (Sidor & Welman 2003).

DRA2: ratio of snout height at anterior border of lacrimal (excluding nasal ridge or boss) to snout length. This character provided no phylogenetic signal in the analysis of Day *et al.* (2016) and is probably variable with ontogeny, given general allometric trends of shorter faces in juvenile tetrapods.

DRA5: median nasal ridge extends to level of external nares. Deleted as part of the restructuring of nasal ornamentation characters into current Characters 5 and 6.

DRA8: contact of frontals and nasals. This character is listed in the TNT file for the Day *et al.* (2016) analysis, but was not mentioned elsewhere in that paper or in its supporting online materials. The derived state ('anteromedial', as opposed to 'transverse') was coded only for *Herpetoskylax* and RC 20. However, some other biarmosuchian specimens also exhibit an anteromedially to posterolaterally angled nasofrontal suture, and this feature appears to be variable even within species (in *Biarmosuchus* specimens, for instance, PIN 1758/1 has an angled suture, but PIN 1758/7 has a mostly transverse, but interdigitated, suture). Given this variability, this is not considered a useful character for the current analysis.

DRA16: posterolateral constriction of the postfrontal by postorbital results in a narrow posterior process. Day *et al.* (2016) rephrased this character (formerly 'postfrontal posterior extension along its medial contact with the frontal'; Sidor & Rubidge 2006) in order to include the condition in *Hipposaurus*, where the posterior process of the postfrontal contacts the parietal, not the frontal, medially (*Hipposaurus* had been coded as having the derived state for this character in all previous analyses). This character has been deleted for two reasons. One, in the context of the current analysis, it is not parsimony informative; only the outgroup taxon has the plesiomorphic state, so it does not provide any information on ingroup relationships. Two, the absence of a posterior postfrontal process in *Biarmosuchus* is debatable. In *Biarmosuchus* skulls (e.g. PIN 1758/85) the postfrontal is definitely narrower at its posteromedial edge than at the orbital margin, albeit to a lesser degree than that of *Hipposaurus* (which in turn is to a lesser degree than that of *Herpetoskylax* and so forth). Some degree of posterior constriction of the postfrontal by the postorbital is plesiomorphic for Therapsida (and further stemward: it is constricted in *Dimetrodon*; Romer & Price 1940). Incorporation of this aspect of postfrontal morphology into a reformulated continuous character may be useful in future analyses of therapsid relationships, but given the small percentage of biarmosuchians for which postfrontal preservation is sufficient for coding, this would have limited utility for the current analysis (i.e. Day *et al.* 2016 could code it for only five taxa, of which only one was a burnetiamorph).

DRA20: jugal contribution to lateral temporal fenestra. Deleted because Day *et al.*'s (2016) codings could not be replicated during our examination of the relevant material. Although their identifications of jugal position are likely, in most burnetiamorphs there are not clear sutures delimiting this element, so we considered its extent uncertain.

DRA32: basicranial rami of pterygoids. Deleted because it is parsimony uninformative, with all ingroup taxa being coded identically.

DISCUSSION

Referral of NHCC LB593 to Mobaceras zambeziense

NHCC LB593 consists of a partial skull cap preserving the majority of the interorbital and intertemporal regions of the skull (Fig. 4). It is 5.72 cm in total length from the anterior preserved edge of the nasofrontal crest to the posterior edge of the pineal boss, making it somewhat smaller than NHCC LB133 (in which the same region measures 6.43 cm). NHCC LB593 shares several unique features with NHCC LB133 that distinguish them from all other burnetiamorphs, such as a narrow median nasofrontal crest terminating anterior to the contact with the preparietal and a highly discrete, knob-like, laterally directed posterior supraorbital boss. NHCC LB593 does differ from NHCC LB133 in a few regards, in that the margins of the preparietal are more clearly delimited, with the surrounding portions of the frontal being more swollen. The shape of the anterior supraorbital boss also differs between these two specimens. In NHCC LB133, it is very tall and nearly vertically directed (Fig. 4D), whereas in NHCC LB593 it appears somewhat lower (although the dorsal edge of the boss is damaged, so this could be a taphonomic artefact) and is angled more anteriorly (giving it a more *Burnetia*-like appearance in lateral view; compare with Fig. 11B).

NHCC LB593 is clearly more similar to NHCC LB133 than it is to the other burnetiamorph skull caps described from the lower Madumabisa Mudstone Formation (Kulik & Sidor, 2019). Those specimens have a more domed intertemporal region, without a distinct pineal boss (similar to the South African specimen NHMUK PV R871a), an unusually low, rim-like supraorbital boss, and a broad median nasofrontal eminence comparable to that of proburnetiines. Whether NHCC LB593 and NHCC LB133 are conspecific or merely closely related is somewhat uncertain; as previously discussed, an understanding of

individual variation in burnetiamorphs has been hindered by the rarity of specimens. However, the differences between NHCC LB593 and NHCC LB133 are similar to those observed intraspecifically in members of other therapsid clades characterized by extensive cranial pachyostosis (i.e. dinocephalians and rubidgeine gorgonopsians; Kammerer 2011, 2016a). Based on this, we consider these specimens to most parsimoniously be interpreted as conspecific, but caution that a larger sample (ideally with more complete skulls) is needed to evaluate this. Of the 14 burnetiamorph skull caps collected from the lower Madumabisa Mudstone Formation, the majority are comparable in morphology to the specimens sectioned by Kulik & Sidor (2019); only NHCC LB133 and NHCC LB593 appear to be burnetiine.

The ventral surface of the skull cap in NHCC LB593 (Fig. 4B) is similar to that described for other burnetiids (Sidor et al. 2010; Kammerer 2016b; Kulik & Sidor 2019), suggesting that this region is morphologically conservative in the clade. A prominent median trough (probably housing part of the dorsal portion of the brain) is present on the underside of the skull, bounded by ridges that curve laterally at their anterior and posterior ends. These ridges also bound the lateral edges of the preparietal in ventral view. Lateral to the pineal foramen, well-developed temporal fossae are present on the underside of the postorbitals, each bounded by an anterior transverse ridge (separating it from the orbital wall) and a medial anteroposterior ridge (separating it from the parietal).

Burnetiamorph phylogeny and stratigraphy

Figure 18 shows the results of our phylogenetic analysis. The initial run of the analysis, including all OTUs, recovered 89 most parsimonious trees (MPTs) of length 47 (consistency index [CI] = 0.766; retention index [RI] = 0.899). This run included several extremely fragmentary specimens (BP/1/7098, NHMUK PV R871a, and TM 4305) that are too incomplete to be named but which probably represent distinct taxa based on their stratigraphic position (Day et al. 2016; Kammerer 2016b). These specimens are recovered as burnetiids in our analysis, but the large amount of missing data for these OTUs results in substantial instability (Fig. 18A). In this analysis, both Burnetiidae and Burnetiinae (containing *Bullacephalus*, *Burnetia*, *Mobaceras*, *Niuksenitia*, *Pachydectes*, and TM 4305) are recovered in the strict consensus tree, but a monophyletic Proburnetiinae is not, with the proburnetiines (*sensu* Kammerer 2016b) forming a polytomy with Burnetiinae. In the Adams consensus tree derived from this analysis, both Burnetiinae (including TM 4305) and Proburnetiinae (including NHMUK PV R871a, as the sister taxon of *Lende*) are recovered, with

BP/1/7098 in an unresolved basal polytomy with these two subclades. When the unnamed, fragmentary specimens are excluded from the analysis, five trees of length 46 (CI=0.783, RI=0.905) are recovered, yielding a more resolved strict consensus in which Burnetiidae includes a monophyletic Proburnetiinae as the sister taxon to Burnetiinae (Fig. 18C). Topology within Burnetiinae is unresolved in the strict consensus tree from both analyses, but in the second analysis, *Proburnetia* is recovered as the sister-taxon of (*Lende* + *Leucocephalus* + *Paraburnetia*) within Proburnetiinae.

We find that the cladistic conclusions of Day et al. (2016, 2018) do not withstand a detailed restudy of the constituent characters and character states. Instead, our study bolsters earlier proposals of burnetiamorph phylogeny that recognize an expansive Burnetiidae divided into the subclades Proburnetiinae and Burnetiinae. Burnetiidae is supported by the following unambiguous synapomorphies: Characters 6 (state 1, median nasal excrescence in the form of a thickened ridge), 17 (state 2, large, pachyostosed ventral squamosal boss), 22 (state 1, nuchal crest extends near foramen magnum), and 24 (state 1, small post-temporal fenestra). Proburnetiinae is supported by Characters 15 (state 2, diffuse, pachyostosed pineal boss) and 19 (state 1, posteroventrally sloping posterior skull roof joining occiput). In all versions of the analysis, *Bullacephalus* and *Pachydectes* are recovered within Burnetiinae, which is one of the strongest-supported clades in our analysis (Fig. 18C). Burnetiinae is supported by Characters 6 (state 2, median nasal excrescence a rounded boss), 7 (state 1, prefrontal boss present), 11 (state 1, anterior supraorbital boss quadrangular), and 13 (state 2, posterior supraorbital boss present as a large swelling).

The recognition of Burnetiinae as a deeply nested clade including middle Permian forms entails a ghost lineage for the proburnetiine subclade as well as many individual non-burnetiamorph biarmosuchian lineages (alleviated, but not eliminated, if the majority of these late Permian taxa make up a monophyletic Ictidorhinidae). Day et al. (2016) cited the Guadalupian age of *Bullacephalus* and *Pachydectes* as support for their basal position, broadly separating them from the latest Permian *Burnetia* both phylogenetically and temporally. Based on the age dates given by Rubidge et al. (2013), the biarmosuchian fossil record spans c. 10 myr. Sidor (2015) noted c. 30 known biarmosuchian specimens within this span (including NHCC LB133, there labelled 'Burnetiidae indet.', and several other undescribed Tanzanian and Zambian fossils). Such a small number of individuals over such a broad temporal range constitutes sampling much too poor for robust stratocladistic conclusions (Sumrall & Brochu 2003), and does not require the invocation of unorthodox topologies to account for the current ghost lineages.
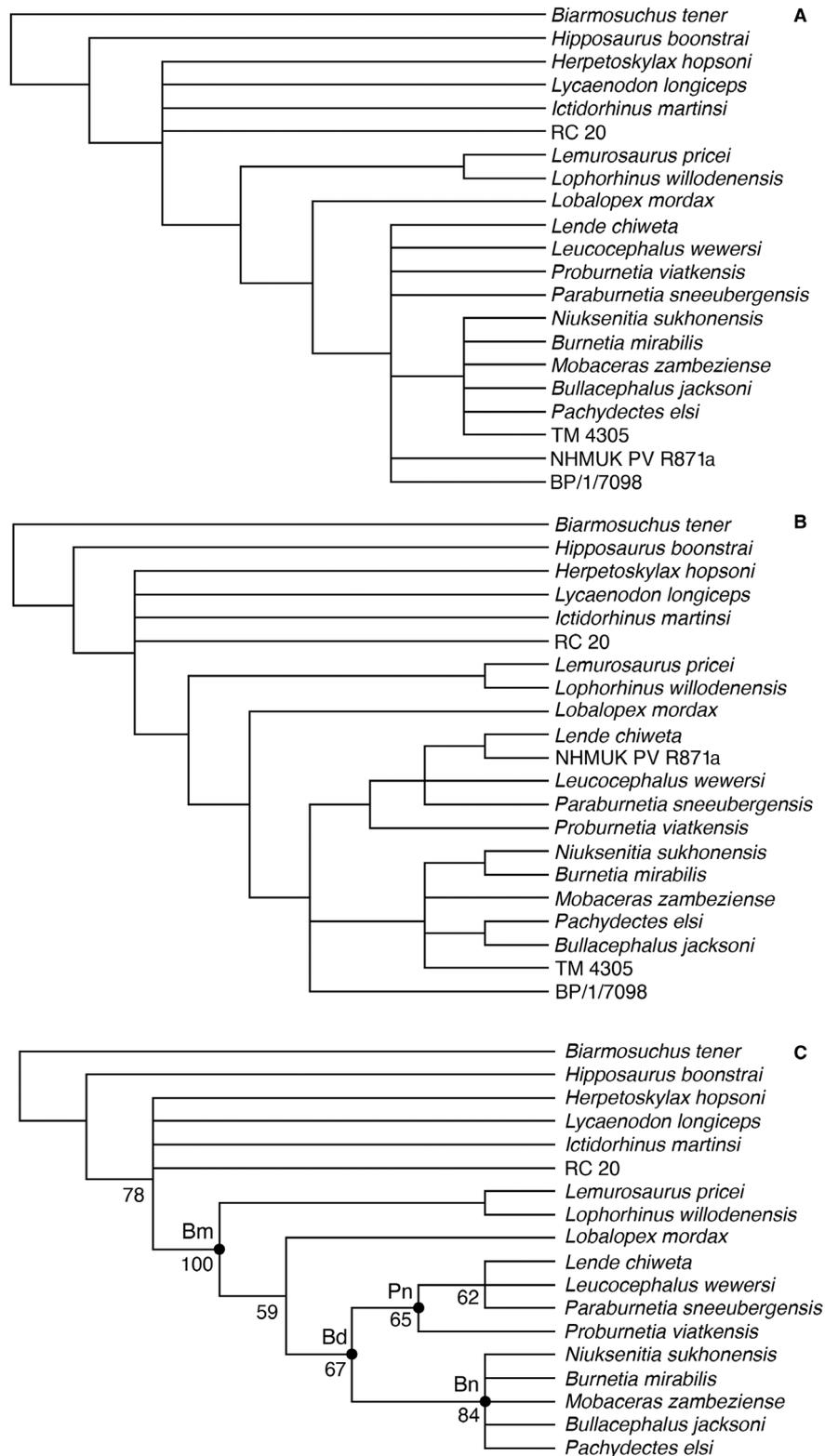
FIG. 18. Updated cladogram of burnetiamorph relationships found after the review and revision of character argumentation discussed herein. A, strict consensus topology resulting from the full analysis including the highly fragmentary, unnamed specimens BP/1/7098, NHMUK PV R871a, and TM 4305. B, Adams consensus topology resulting from the full analysis. C, strict consensus topology resulting from the analysis in which the unnamed specimens are excluded. Numbers at nodes indicate bootstrap values, labelled nodes in C represent Burnetiamorpha (Bm), Burnetiidae (Bd), Proburnetiinae (Pn), and Burnetiinae (Bn).

Review of characters supporting Bullacephalidae

Day *et al.* (2016) erected a new family, Bullacephalidae, based on their recovery of the clade (*Bullacephalus* + *Pachydectes*) outside of Burnetiidae (*sensu* Rubidge & Sidor 2002) in all iterations of their analysis (and even outside of Burnetiamorpha in one of their analyses). Day *et al.* (2016) argued that the burnetiid-like features of *Bullacephalus* were superficial convergences, and listed nine characters distinguishing *Bullacephalus* (and to a lesser degree *Pachydectes*) from all other burnetiamorphs. We consider the interpretations of Day *et al.* (2016) for all of these characters to be problematic.

1. Single boss on ventral side of postorbital bar. Day *et al.* (2016) suggested that this was a feature of Bullacephalidae. However, they also noted that the condition in *Pachydectes* was not definitive (as the relevant area is damaged) and that *Lobalopex* has a single boss in this region, indicating that this feature is variable even within taxa they considered firmly supported burnetiamorphs. We would argue that the unusual zygomatic boss morphology of *Bullacephalus* and *Pachydectes* (greatly enlarged) does indicate a close relationship between these two genera, but does not support their exclusion from Burnetiidae (unless the zygomatic bosses of *Bullacephalus*/*Pachydectes* are assumed *a priori* to be non-homologous with those of other burnetiamorphs).

2. Absence of swelling of squamosal at junction of three rami lateral to quadrate. We disagree with the coding of Day *et al.* (2016) for this feature. Although this part of the skull is somewhat damaged, our examination of the holotype of *Bullacephalus jacksoni* indicates that there is a swelling in this region.

3. Posterior edge of squamosal pachyostosed to greater degree than any other burnetiamorph. We agree that this feature is present in *Bullacephalus*, but regard it as an autapomorphy of the genus, which does not contribute to the inference of cladistic relationships. The fact that this boss is more extremely developed than those of other burnetiamorphs does not necessarily indicate that it evolved independently.

4. Large palatine bosses. Features of the palate figure prominently in the assessment of Day *et al.* (2016) that *Bullacephalus* should be considered a relatively primitive biarmosuchian. It is true that the palatine bosses in *Bullacephalus* and *Pachydectes* are substantially larger than those of *Burnetia* (in which the palatal bosses are unusually small, an autapomorphy of the genus; see Fig. 17E), but are not outside the range known in other burnetiamorphs. For example, *Paraburnetia*, *Lobalopex*, and *Mobaceras* all have bosses of equal or greater proportional length. Moreover, large palatine bosses probably represent the plesiomorphic condition for biarmosuchians (based on the condition in *Biarmosuchus*; Fig. 17A), so do not support *Bullacephalus* and *Pachydectes* as a clade.

5. Row of teeth on transverse process of pterygoid. It is unknown whether teeth are present on the transverse process of the pterygoid in *Burnetia*, because this region is badly worn in the holotype (Fig. 17E). Teeth are present on the transverse process in *Lemurosaurus* (three in BP/1/816, one in NMQR 1702; Fig. 17C) and *Mobaceras* (Fig. 1B), but are absent in all non-burnetiamorph biarmosuchians (e.g. *Herpetoskylax*), so their presence in *Bullacephalus* does not necessarily support a non-burnetiamorph position.

6. Triangular shelf on anterolateral side of the quadrate ramus of pterygoid. An anterolateral shelf on the quadrate ramus of the pterygoid is indeed well-developed in both *Hipposaurus* and *Bullacephalus*, and this kind of shelf is absent in some burnetiamorphs (e.g. *Proburnetia*). However, a shelf in this position (of varying degrees of extent) is also present in other burnetiamorphs (e.g. *Niuksenitia* and *Lobalopex*, in which it is small, or *Mobaceras*, in which it is comparable in size to that of *Bullacephalus*; Figs 1B, 17D) and is absent in some non-burnetiamorph biarmosuchians (e.g. *Herpetoskylax*).

7. Pterygoid trough between the quadrate rami. This character is mentioned as 'Character 35', which is not listed in the supporting online material of Day *et al.* (2016). Presumably this refers to the median trough along the basicranial girder between the pterygoids, which is present in all biarmosuchians other than *Biarmosuchus* itself. It is also present in all burnetiamorphs for which this region is preserved, so it indicates no particular relationship between *Bullacephalus* and *Hipposaurus*. *Hipposaurus* is unusual in that the trough forms a broad depression, not a clearly demarcated channel with raised edges as in burnetiamorphs. However, *Bullacephalus* clearly has the typical burnetiamorph channel.

8. Multiple rows of peripheral teeth on palatine boss. Our examination suggests that only a single tooth row (delta shaped and extending medially and laterally) is present in *Pachydectes*. On the delta-shaped palatine bosses of *Bullacephalus*, medially there is a single tooth row and on the right palatine boss the same is true laterally. On the left palatine boss, however, the posterolateral end of the tooth row shows a jumble of five teeth (Fig. 17D). Rather than representing persistent tooth positions, we interpret this patch as representing the typical style of palatal tooth replacement in early therapsids (with replacement teeth erupting irregularly to the side of the previous functional teeth), which is also seen in numerous gorgonopsian taxa with a single palatine tooth row

(Kammerer 2016*a*). This is a different condition to the broad rows of palatine teeth that are plesiomorphic for synapsids and (arguably) seen in *Biarmosuchus* (Fig. 17A). Even taking the condition in *Bullacephalus* at face value, however, rows of multiple 'peripheral teeth' are also present in *Burnetia* (Fig. 17E), so this feature would not support Bullacephalidae.

9. Pineal chimney. Day *et al.* (2016, p. 713) stated that this is present in *Pachydectes* (implied to be, uniquely among burnetiamorphs, identical to that of *Hipposaurus* and 'ictidorhinids') and still is 'slightly rimmed' in *Bullacephalus* 'despite its great level of pachyostosis', in contrast with 'later burnetiamorphs where the pineal foramen is flush with the surrounding parietals and situated on a wide low swelling or, in the case of *Lende*, in a wide depression'. However, this latter statement is not accurate. The only burnetiamorphs in which the pineal foramen is nearly flush with the surrounding parietal are *Lende* (in which the whole region is depressed, as they noted) and NHMUK PV R871a. In *Leucocephalus*, *Paraburnetia*, and *Proburnetia*, the pineal boss is part of a generally swollen intertemporal region anterior to the pineal foramen, but its posterior edge still has a rim demarcating the position of the boss. In other taxa there is clearly a distinct pineal boss. The pineal foramen in *Lemurosaurus* (based on NMQR 1702) and *Lobalopex* is situated on a tall, chimney-like structure immediately comparable to that of many non-burnetiamorph basal therapsids (indeed, much more so than that of *Pachydectes*, in which the boss is notably swollen and pachyostosed). The holotype of *Burnetia* is a badly overprepared specimen, and little of the actual bone surface of the dorsal skull roof is intact. Much of the area around the pineal foramen is clearly broken or overprepared, as indicated by trabecular bone visible at the surface at the immediate anterior edge of the foramen. However, enough is preserved of the posterior rim of the pineal foramen to show that a discrete boss surrounded it, rather than a uniformly broad parietal swelling. The preserved portion of this boss is notable for having a distinct teardrop shape, with the posterior margin extending and attenuating posteriorly into a median ridge. The same morphology is present in *Pachydectes*, *Mobaceras* and TM 4305 (what is preserved of the pineal boss in *Bullacephalus* also matches this morphology). The results of our phylogenetic analysis indicate that this character supports inclusion of *Pachydectes* in Burnetiinae. (See discussion of Char. 15 above for further information.)

To summarize, none of the characters cited by Day *et al.* (2016) in support of Bullacephalidae clearly indicates a non-burnetiamorph or non-burnetiid position, and indeed, close examination of these characters reveals that they generally support a burnetiid identification for *Bullacephalus* and *Pachydectes*, as originally proposed (Rubidge *et al.* 2006).

Mobaceras zambeziense *and* Wantulignathus gwembensis

Two carnivorous therapsids with craniomandibular excrescences are currently recognized from the lower Madumabisa Mudstone Formation of Zambia: *Mobaceras zambeziense* (described herein) and *Wantulignathus gwembensis* (Whitney & Sidor 2016). Fossils assigned to these species come from approximately the same horizon within a kilometre of each other, so potential synonymy between them requires careful consideration. Whitney & Sidor (2016) determined that *Wantulignathus* was probably a biarmosuchian based on a variety of dentary features (thickening in the coronoid region to form a dorsal ridge, a nearly vertical symphysis, and a notch along the posterior dentary margin). Although they did not assign this taxon to a lower-level clade, they considered Burnetiamorpha a possibility based on the presence of pachyostosed bosses. However, the boss in *Wantulignathus* is unlike those of other known burnetiamorphs, taking the form of a prominent oval swelling at the posteroventral margin of the dentary. Although the ventral margin of the dentary is thickened in many burnetiamorphs, the only other taxon with a distinct boss at the dentary angle is *Proburnetia* (although the boss is smaller and not angled posterodorsally in *Proburnetia*).

Unfortunately, because of the lack of overlapping material between *Wantulignathus* and *Mobaceras* it is currently impossible to be certain of their distinction. However, available evidence indicates that they are most likely to be separate taxa. In addition to its unique boss morphology, *Wantulignathus* is characterized by a proportionally short, tall dentary dissimilar to those known in other biarmosuchians. The shortness of the jaw is also reflected in the tooth row: *Wantulignathus* has only four lower postcanine teeth. In other biarmosuchians where the lower tooth row is preserved, that number is much higher (e.g. at least eight in *Herpetoskylax*, 8–9 in *Leucocephalus*; Sidor & Rubidge 2006; Day *et al.* 2018). No complete mandibles are known for burnetiines, but most of the jaw is preserved in BP/1/5387 (holotype of *Bullacephalus jacksoni*) and it is generally similar to those of other burnetiamorphs (with four preserved teeth, but given that this is only the posteriormost section of the tooth row, more were probably present). It is worth noting that biarmosuchians generally have greater lower than upper tooth counts (e.g. 5–6 uppers vs ≥8 lowers in *Herpetoskylax*, six uppers vs 8–9 lowers in *Leucocephalus*), suggesting that *Burnetia* (five upper postcanines;

Rubidge & Sidor 2002) and *Pachydectes* (eight upper post-canines; Rubidge *et al.* 2006) had more than four lower postcanines, and the same is likely to be true of the more incomplete but broadly comparable *Bullacephalus* and *Mobaceras*. We cannot exclude the possibility that *Mobaceras* had highly aberrant proportions relative to the otherwise-similar *Bullacephalus*, *Burnetia*, and *Pachydectes* (given that the jaws of *Wantulignathus* should correspond to an unusually short-snouted animal), but regard this as unlikely. Until more complete specimens are found, however, some uncertainty will remain.

CONCLUSION

Mobaceras zambeziense represents the first diagnosable burnetiid taxon from Zambia, but is part of what is clearly a broader assemblage of burnetiamorph morphotypes from the Madumabisa Mudstone Formation (Sidor *et al.* 2017; Kulik & Sidor 2019). Burnetiamorph species richness and specimen abundance is notably higher in the Zambezi Basin than in the historically better-sampled Karoo Basin of South Africa, suggesting that the previous rarity of this clade may owe more to local conditions than to an accurate reflection of their roles in ecosystems globally.

Mobaceras shows a number of similarities to the Karoo taxa *Bullacephalus* and *Burnetia*, including some characters intermediate between these two genera. In this regard, *Mobaceras* helps to clarify several previously problematic characters used in analyses of biarmosuchian phylogeny, and provides novel support for the inclusion of all of these taxa in the burnetiid subclade Burnetiinae. Although this topology invokes a ghost lineage for proburnetiines (an issue previously discussed by Day *et al.* 2016, 2018), we regard this as an artefact of limited sampling. While of uncertain taxonomic attribution, it is worth noting that the isolated Zambian burnetiamorph skull caps sampled by Kulik & Sidor (2019) exhibit characters here considered diagnostic for proburnetiines (diffuse, extensive swollen circumpineal region, posterodorsally sloping skull roof). Further study and more extensive material is required, but if these specimens are proburnetiines it would serve to eliminate their ghost lineage (given that the lower Madumabisa Mudstone Formation has been identified as Guadalupian on the basis of tapinocephalid dinocephalian records; Sidor *et al.* 2014; Olroyd & Sidor 2017). The substantial novel Zambian and Tanzanian burnetiamorph records should greatly improve our understanding of this unusual clade, and additional fieldwork in these regions holds great potential for future biarmosuchian discoveries.

DATA ARCHIVING STATEMENT

This published work and the nomenclatural acts it contains have been registered in ZooBank: http://zoobank.org/References/993f67b7-37ff-48b8-9a55-d829d4a5ba41
The data matrix for this paper is archived in MorphoBank: https://doi.org/10.7934/P3785

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APPENDIX

Character matrix used in the phylogenetic analysis (Nexus file available in Kammerer & Sidor 2020). Characters 13, 16, and 17 are ordered.

	01	02	03	04	05	06	07	08	09	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	27
Biarmosuchus tener	0	[0 1]	0	0	0	–	0	0	0	0	–	–	0	0	0	0	0	0	1	0	0	0	0	1	0	0	0
Hipposaurus boonstrai	0	0	0	0	0	–	0	0	0	0	–	–	0	1	0	0	0	0	0	0	0	0	0	1	0	0
Herpetoskylax hopsoni	1	0	0	0	0	–	0	0	1	0	–	–	0	1	0	0	0	0	0	0	0	0	0	1	0	1
Lycaenodon longiceps	1	0	0	0	0	–	0	0	0	?	0	–	–	0	?	?	?	?	?	?	?	?	?	?	?	?	1
Ictidorhinus martinsi	?	0	0	0	0	–	0	0	1	0	–	–	0	?	0	0	0	0	0	0	0	0	0	?	?	?	?
RC 20	1	0	0	0	0	–	0	0	1	0	–	–	0	1	0	0	?	?	?	?	?	?	?	?	1	0	1
Lemurosaurus pricei	?	0	1	1	1	0	0	1	?	1	0	0	1	?	0	1	1	0	0	0	0	0	1	?	2	0	1
Lobalopex mordax	?	0	1	?	1	0	0	1	1	1	0	0	1	?	0	1	1	1	0	0	1	0	1	0	1	1	1
Lophorhinus willodenensis	1	0	1	1	1	0	0	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	2	?	?
Lende chiweta	1	0	1	1	1	1	0	1	?	1	0	1	1	?	3	1	2	1	1	0	1	1	1	1	1	1	1
Leucocephalus wewersi	1	0	1	1	1	1	0	1	?	1	0	1	1	2	2	1	2	1	1	0	1	1	1	1	1	1	1
Proburnetia viatkensis	1	0	1	1	1	1	0	1	1	1	0	0	1	?	2	1	2	1	1	0	1	1	1	1	2	1	1
Paraburnetia sneeubergensis	?	0	1	1	1	1	0	1	?	1	0	1	1	?	2	1	2	1	1	0	1	1	1	?	1	1	1
Niuksenitia sukhonensis	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	?	3	?	0	1	1	1	1	1	1	1	?
Burnetia mirabilis	1	0	1	?	1	2	1	0	?	1	1	0	2	2	1	1	3	1	0	1	1	1	1	1	2	0	?
Mobaceras zambeziense	?	?	1	?	1	2	1	1	0	1	1	0	2	2	1	?	?	1	0	?	1	1	1	1	1	1	0
Bullacephalus jacksoni	?	1	1	1	1	2	1	0	?	1	1	0	2	?	?	2	2	1	0	0	1	1	1	1	1	1	0
Pachydectes elsi	?	1	1	1	?	?	?	1	1	?	?	?	2	2	1	2	?	?	?	?	?	?	?	?	1	0	0
TM 4305	?	?	?	?	?	?	?	0	?	?	?	?	?	?	1	?	?	1	0	?	?	?	1	?	?	?	?
NHMUK PV R871a	?	?	?	?	?	?	?	1	1	?	?	?	?	2	3	?	?	?	?	?	?	?	?	?	?	?	?
BP/1/7098	0	0	1	1	1	1	0	1	?	1	?	?	?	?	?	?	?	?	?	?	?	?	?	?	1	1	?