New and historical specimens of burnetiamorph therapsids, with comments on ontogeny, biogeography, and bizarre structures

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For much of its history, the fossil record of burnetiamorph therapsids was both species poor and known from very few specimens. By contrast, the past two decades have seen a dramatic increase in both measures of the group's fossil record. Here I introduce two new species, *Bondoceras bulborhynchus* gen. et sp. nov. and *Pembecephalus litumbaensis* gen. et sp. nov., from the Guadalupian middle Madumabisa Mudstone Formation of Zambia and the Lopingian Usili Formation of Tanzania, respectively. Both are based on a series of isolated skullcaps that preserve a unique combination of characters that suggest referral to subclades within Burnetiidae. Historical burnetiamorph skullcaps collected in Tanzania in the early 1930s are figured, but these are kept in open nomenclature because not enough information is preserved to warrant assigning them to *Pembecephalus* or another genus. A previously undescribed Russian burnetiamorph is also figured, which is only the third specimen of the clade known from the northern hemisphere, but since the specimen is possibly lost, it is also left unnamed. Specimens referred to *Bondoceras* and *Pembecephalus* suggest that while some morphological features vary predictably with size in these burnetiamorphs, others do not, and that some features previously used to assess ontogenetic status in burnetiamorphs are sometimes similarly problematic. Despite their wide range of shapes, surprisingly little discussion of the function of burnetiamorph cranial adornments has taken place in the literature. Comparing the fossil records of burnetiamorphs and other Permian synapsids to dinosaurs with similar adornments may shed light on the macroevolutionary importance of these traits.

Keywords: Burnetiamorpha, Usili Formation, Madumabisa Mudstone Formation, Luangwa Basin, Ruhuhu Basin, Permian.

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DEDICATION

I first visited South Africa in early 1999. I spent almost four months collecting data for my dissertation at all the major museums and getting a first-hand introduction to the Karoo on a fieldtrip with Bruce Rubidge's team. One of my thesis chapters was a description and analysis of a burnetiamorph skull that was on loan to my Ph.D. supervisor, Jim Hopson. This specimen, which was published in 2004 as *Lobalopex mordax*, was my entrée into the world of burnetiamorph biarmosuchians, a group that I've returned to periodically since then. I brought a cast of *Lobalopex* with me and found that Bruce was happy to share his knowledge of burnetiamorphs, including allowing me to study an unpublished specimen (later described as *Bullacephalus jacksoni*), as well as his photographs and data on the two founding members of the Burnetiamorpha, *Burnetia mirabilis* and *Proburnetia viatkensis*. Bruce and I would go on to publish a revised description of the pair as a prelude to the new taxa we were describing.

The fossil record of burnetiamorphs has come a long way since those days, tripling in its recorded taxonomic diversity and with new species and morphotypes now recognized from across southern Africa. But more specimens oftentimes open up more questions, and in this contribution I will highlight several of the most pressing. It is an honour to contribute to this volume, especially on a topic seminal to my association with Brice Rubidge. I hope he's pleased that there's no cladistic analysis in the paper.

INTRODUCTION

Burnetiamorphs have been known for about a hundred years (Broom 1923), but for most of this time their fossil record was exceptionally sparse (Fig. 1). While still depauperate when compared to other coeval therapsid groups like dicynodonts or therocephalians, the past 20 years have seen a rapid increase in the number of species and specimens recognized, with both Guadalupian and Lopingian records now well established. There have been 13 species of burnetiamorph described through 2021 (3 Guadalupian, 10 Lopingian), eight of which are recorded from the Karoo Basin of South Africa (Table 1). And although burnetiamorph species are known to co-occur

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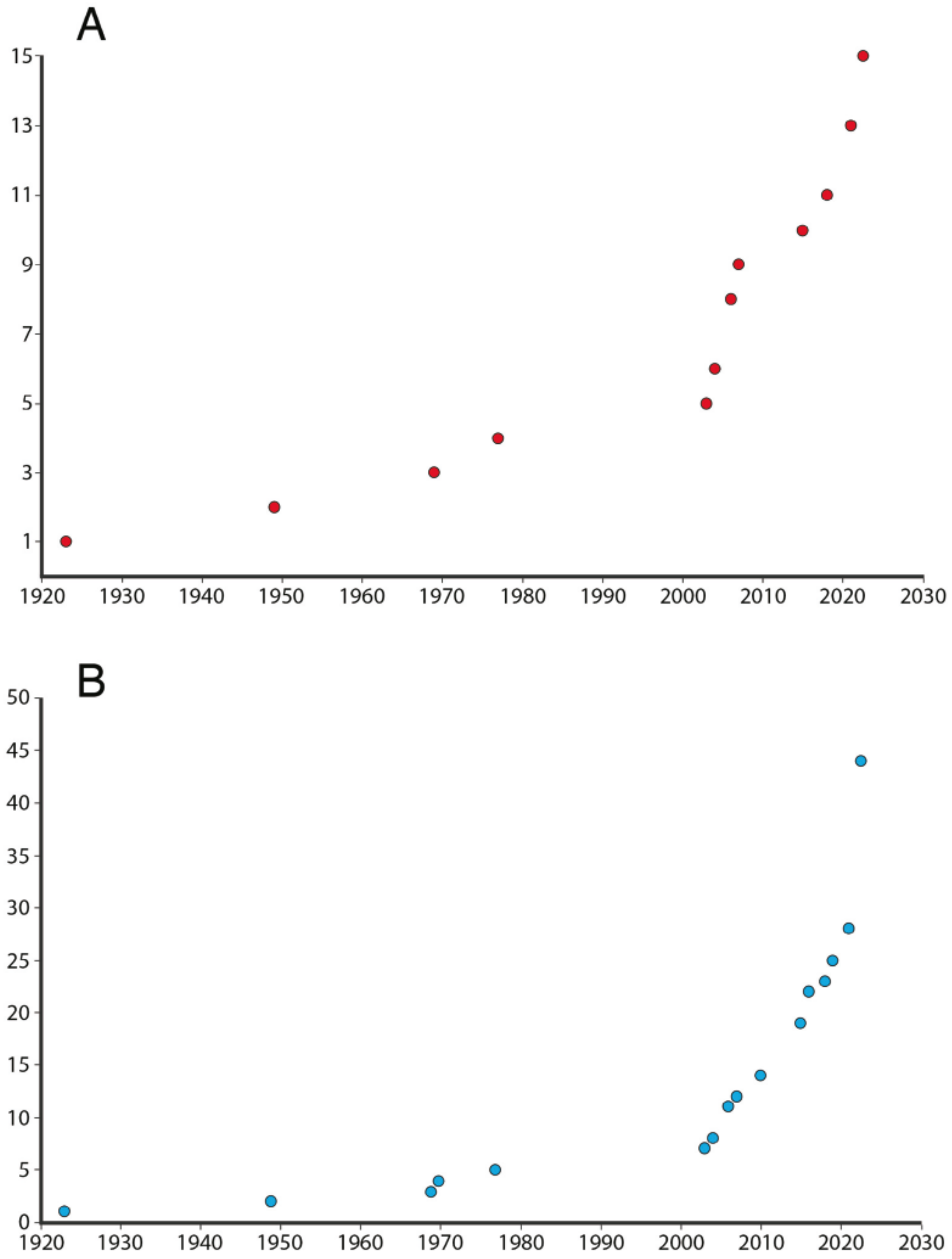

Figure 1. Growth of the burnetiamorph fossil record over time. **A**, Shows how the 15 species of burnetiamorphs recognized here were sequentially named. **B**, Shows the accumulation of the 44 specimens attributed to the clade. In both cases, the fossils described in this contribution are represented by the data points at the top right of each graph. Species are dated by when they were first named, regardless of whether or not they were recognized as belonging to Burnetiamorpha at the time (see Table 1). For example, *Lemurosaurus pricei* was initially described by Broom (1949), but was not recognized as a burnetiamorph until much later (Sidor 2000). The cumulative specimen count includes specimens that were mentioned in the literature but not formally named (e.g. Sidor & Rubidge 2006: table 4.1; Sidor 2015: table 1; Day *et al*. 2016; Kammerer 2016), but does not include the specimens described by Day & Kammerer (2023) elsewhere in this volume.

stratigraphically (e.g. *Lobalopex* and *Leucocephalus*), each of the 13 species is endemic to just one geologic basin, despite otherwise broadscale faunal similarity across southern Pangea during late Permian times (Sidor *et al*. 2013).

The burnetiamorph fossil record almost exclusively comprises cranial material, oftentimes just the durable, pachyostotic skull cap, and its members are understood as medium-sized carnivores that were perhaps crepuscular or nocturnal (Sidor *et al*. 2004; Angielczyk & Schmitz 2014). The suite of bony adornments that decorate the skull of burnetiamorphs has been commented upon since the first specimen was described and has been implicated in the clade's elevated species richness, especially when compared with the low number of specimens recovered (Sidor *et al*. 2021). However, a reliance on these excrescences to diagnose new species, when combined with pachyostosis that tends to obliterate sutural detail, makes a rigorous evaluation of the group's evolution challenging. In particular, ontogenetic variation in boss shape is difficult to estimate in burnetiamorphs, but has been considered highly mutable in similarly adorned pachycephalosaurian dinosaurs (Horner & Goodwin 2009). Duhamel *et al*. (2021) were the first to explicitly address

Table 1. Growth of the burnetiamorph fossil record over time. Fossils are arranged in chronological order based on the year in which they were first described, regardless of whether they were initially recognized as a burnetiamorph. For South African specimens, biostratigraphic zones follow Smith *et al.* (2020). For Russian specimens, the biostratigraphic correlations of Day *et al.* (2018: fig. 10) were used. Additional information can be found in the literature references given. Specimens newly described by Day & Kammerer (2023) elsewhere in this volume not included. Abbreviations: AZ, assemblage zone; Cist, *Cistcephalus*; Dapt, *Daptocephalus*; Endo, *Endothiodon*; Eq, assemblage zone equivalent; M, middle; Tap, *Tapinocephalus*; uncat., uncatalogued specimen; U, upper.

Year	Current taxonomy	Specimen	Basin	Stratigraphy	Literature
1923	*Burnetia mirabilis*	NHMUK PV R 5697	Karoo	Dapt AZ	Rubidge & Sidor 2002
1949	*Lemurosaurus pricei*	BP/1/816	Karoo	Cist AZ	Duhamel *et al.* 2021
1969	*Proburnetia viatkensis*	PIN 2416/1	Vyatka River	Endo Eq	Rubidge & Sidor 2002
1970	Burnetiamorph indet.	BP/1/818[1]	Karoo	Cist AZ	Sigogneau 1970
1977	*Niuksenitia sukhonensis*	PIN 3159/1	Sukhona River	Tap Eq	Ivachnenko *et al.* 1997
2003	*Lemurosaurus* sp.	NMQR 1702	Karoo	Cist AZ	Duhamel *et al.* 2021
2003	*Bullacephalus jacksoni*	BP/1/5387	Karoo	Tap AZ	Rubidge & Kitching 2003
2004	*Lobalopex mordax*	CGP/1/61	Karoo	Endo AZ	Sidor *et al.* 2004
2006	*Paraburnetia sneeubergensis*	SAM-PK-K10037	Karoo	Cist AZ	Smith *et al.* 2006
2006	*Pachydectes elsi*	BP/1/5735	Karoo	Tap AZ	Rubidge *et al.* 2006
2006	Burnetiamorpha indet.	SAM-PK-K5292[2]	Karoo	Endo AZ	Sidor & Rubidge 2006
2007	*Lophorhinus willodenensis*	SAM-PK-K6655	Karoo	Endo AZ	Sidor & Smith 2007
2015	*Lende chiweta*	MAL 290	Chiweta	Chiweta Beds	Kruger *et al.* 2015
2015	cf. *Lemurosaurus*	SAM-PK-K10906	Karoo	Endo AZ	Sidor 2015
2016	Burnetiamorpha indet.	BP/1/7098	Karoo	Endo AZ	Day *et al.* 2016
2016	Proburnetiinae indet.	NHMUK PV R 871	Karoo	Endo AZ	Kammerer 2016
2016	Burnetiinae indet.	TM 4305	Karoo	Tap AZ	Kammerer 2016
2018	*Leucocephalus wewersi*	SAM-PK-K11112	Karoo	Endo AZ	Day *et al.* 2018
2021	*Mobaceras zambeziense*	NHCC LB133	Mid-Zambezi	M Madumabisa	Kammerer & Sidor 2021
2021	*Mobaceras zambeziense*	NHCC LB593	Mid-Zambezi	M Madumabisa	Kammerer & Sidor 2021
2021	*Isengops luangwensis*	NHCC LB363	Luangwa	U Madumabisa	Sidor *et al.* 2021
2021	Burnetiamorpha indet.	CGS MJF 22	Karoo	Endo AZ	Duhamel *et al.* 2021
2021	cf. *Lophorhinus willodenensis*	SAM-PK-K11126	Karoo	Endo AZ	Duhamel *et al.* 2021
2023[4]	*Bondoceras bulborhynchus*	NHCC LB118	Mid-Zambezi	M Madumabisa	Kulik & Sidor 2019
2023	*Bondoceras bulborhynchus*	NHCC LB124[3]	Mid-Zambezi	M Madumabisa	Sidor 2015
2023	Burnetiamorpha indet.	NHCC LB371	Mid-Zambezi	M Madumabisa	This paper (Fig. 4)
2023	Burnetiamorpha indet.	NHCC LB372	Mid-Zambezi	M Madumabisa	This paper (Fig. 4)
2023[4]	*Bondoceras bulborhynchus*	NHCC LB373	Mid-Zambezi	M Madumabisa	Kulik & Sidor 2019
2023	Burnetiamorpha indet.	NHCC LB376	Mid-Zambezi	M Madumabisa	This paper (Fig. 4)
2023[4]	Burnetiamorpha indet.	NHCC LB410	Mid-Zambezi	M Madumabisa	Kulik & Sidor 2019
2023	*Bondoceras bulborhynchus*	NHCC LB411	Mid-Zambezi	M Madumabisa	This paper (Fig. 8)
2023	Burnetiamorpha indet.	NHCC LB590	Mid-Zambezi	M Madumabisa	This paper (Fig. 4)
2023	*Bondoceras bulborhynchus*	NHCC LB592	Mid-Zambezi	?M Madumabisa	This paper (Fig. 8)
2023	Burnetiamorpha indet.	NHCC LB831	Mid-Zambezi	M Madumabisa	This paper (Fig. 4)
2023	Burnetiamorpha indet.	NHCC LB1154	Mid-Zambezi	M Madumabisa	This paper (Fig. 8)
2023	*Pembecephalus litumbaensis*	NMT RB4	Ruhuhu	Usili	Sidor *et al.* 2010
2023	*Pembecephalus litumbaensis*	NMT RB36	Ruhuhu	Usili	Sidor *et al.* 2010
2023	*Pembecephalus litumbaensis*	NMT RB411[4]	Ruhuhu	Usili	Sidor 2015
2023	*Pembecephalus litumbaensis*	NMT RB451	Ruhuhu	Usili	This paper (Fig. 9)
2023	*Pembecephalus litumbaensis*	NMT RB470	Ruhuhu	Usili	This paper (Fig. 9)
2023	*Pembecephalus litumbaensis*	NMT RB841	Ruhuhu	Usili	This paper (Fig. 9)
2023	*Pembecephalus litumbaensis*	NMT RB842	Ruhuhu	Usili	This paper (Fig. 9)
2023	Burnetiamorpha indet.	SAM uncat.	Ruhuhu	Usili?	This paper (Fig. 3)
2023	Burnetiamorpha indet.	SAM uncat.	Ruhuhu	Usili?	This paper (Fig. 3)
2023	Burnetiamorpha indet.	SAM uncat.	Ruhuhu	Usili?	This paper (Fig. 3)
2023	Burnetiamorpha indet.	SAM uncat.	Ruhuhu	Usili?	This paper (Fig. 3)
2023	Burnetiamorpha indet.	SAM uncat.	Ruhuhu	Usili?	This paper (Fig. 3)
2023	Burnetiamorpha indet.	St. Petersburg?	?	?	This paper (Fig. 2)

NOTES

[1] This specimen (also known as BPI 353) was referred to cf. *Lemurosaurus* by Sigogneau (1989). It was considered to differ sufficiently from *Lemurosaurus* to be excluded from the genus by Sidor & Welman (2003), but Duhamel *et al.* (2021) referred it to *L. pricei*.

[2] SAM-PK-K5292 was first noted by Sidor & Rubidge (2006: table 4.1). It was incorrectly labelled as originating from the *Dicynodon* AZ in Sidor (2015).

[3] This specimen was accidentally listed as LB149 in Sidor (2015). The locality for NHCC LB124 is L149.

[4] NMT RB411 was accidentally referred to as NMT RB169 in Sidor (2015). However, the latter specimen number was previously used in Barrett *et al.* (2015) for a femur of the dinosauriform *Asilisaurus kongwe*.

ontogenetic character variation in burnetiamorphs, but did little to quantify boss growth or to address possible remodelling.

This paper has two main objectives. The first is descriptive: I will introduce two new species of burnetiamorphs based on a series of specimens from the middle Madumabisa Mudstone Formation of southern Zambia and the basal Usili Formation of southern Tanzania. I also include mention of historical burnetiamorph specimens collected during colonial-era geological work in Tanzania in 1930, but left undescribed until now. Finally, I present photographs of what likely represents a novel burnetiamorph from Russia, although I resist naming it because the specimen seems lost. The second objective is to discuss several questions that have vexed our understanding of burnetiamorph paleobiology, namely: 1) how much morphological variation is present in a species and how does that variation relate to ontogeny? 2) what conclusions can be made about the biogeographic history of the group? and 3) why did bony cranial adornments evolve in the group?

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Biarmosuchia Sigogneau-Russell, 1989
Burnetiamorpha Broom, 1923

Definition. The most inclusive clade including *Burnetia mirabilis*, but excluding *Hipposaurus boonstrai*, *Ictidorhinus martinsi*, and *Herpetoskylax hopsoni* (from Day *et al*. 2016).

Taxonomic note. The stem-based definition provided above was proposed by Day *et al*. (2016) as an emendation of the original phylogenetic definition for Burnetiamorpha given by Sidor & Welman (2003; see also Sidor 2000). The original definition included *Biarmosuchus tener* as an additional reference taxon, but excluded *H. hopsoni*. However, given the results of recent cladistic analyses, the original definition would necessitate including several taxa traditionally excluded from Burnetiamorpha (*viz*. *Lycaenodon*, *Herpetoskylax*; Day *et al*. 2016; Kammerer & Sidor 2021; Sidor *et al*. 2021). For the purposes of this contribution, my use of burnetiamorph refers only to taxa with bony excrescences (i.e. *Lemurosaurus* and more derived taxa).

Diagnosis. Biarmosuchians with the following features: (1) preorbital fossae present, (2) pits present on the lateral surface of the snout, (3) median nasal excrescence, (4) median frontal excrescence, as well as (5) anterior and (6) posterior supraorbital bosses (based on the cladistic results of Kammerer & Sidor [2021] when unnamed specimens are excluded). To this list can be added: (7) quadripartite pachyostosis of the skull roof, notably with a compact, lamellar zone located near the endocranial surface, and (8) mid-portion of braincase ossified (possibly by rostral projections of the supraoccipital or prootic).

Comment. Although first recognized in thin section (Kulik & Sidor 2019), quadripartite pachyostosis can be seen in *Isengops* (Sidor *et al*. 2021: fig. 5), *Lemurosaurus* (Duhamel *et al*. 2021: fig. 18), *Lende* (Duhamel *et al*. 2021: fig. 17A), and the Zambian taxon described below (see also Kulik & Sidor 2019: fig. 1), and so seems likely to be widespread throughout the group. Likewise, an ossified mid-portion of the braincase can be seen in the Zambian and Tanzanian taxa described below, *Lemurosaurus pricei* (Benoit *et al*. 2017a: fig. 5), *Lende* (Duhamel *et al*. 2021: fig. 17), and *Leucocephalus* (Benoit *et al*. 2017a: fig. 7). This distribution suggests a relatively early evolution of the feature, with non-ossification in presumed juveniles or taphonomic loss likely accounting for its absence in otherwise well-preserved skulls (e.g. *Lobalopex*; Sidor *et al*. 2004).

Burnetiamorpha indet.

Referred specimen. Unknown institution and catalogue number.

Locality and horizon. Unknown.

Comments. The rarity of burnetiamorphs from the northern hemisphere makes the introduction of this specimen important, despite the fact that no locality information is available and that the specimen is possibly lost. Bruce Rubidge visited several institutions in St. Petersburg in May 1992 to inquire specifically about this specimen, after being shown photographs by Leonid Tatarinov (reproduced here as Fig. 2), but was unable to locate it.

Two features are worth commenting on. First, the development of excrescences and pachyostosis is minimal in the St. Petersburg specimen. For example: 1) the base of a median nasal excrescence is visible in dorsal view (Fig. 2B), but it is relatively ridge-like and only moderately expanded; 2) the parietal foramen is set upon a distinct chimney and not enveloped by more general pachyostosis of the temporal region; 3) the squamosal boss is only moderately developed and the posterior margin of the temporal fenestra lacks thickening altogether (Fig. 2A); and 4) the supraorbital region apparently lacks pachyostosis, although the posterior portion of the dorsal orbital margin is angled strongly posterolaterally. Second, the specimen preserves relatively large postcanine teeth (Fig. 2A). In general, biarmosuchians possess relatively small, simple postcanine teeth (e.g. Rubidge & Kitching 2003: text-fig. 1; Sidor & Welman 2003: fig. 1; Sidor *et al*. 2004: fig. 1; Day *et al*. 2018: fig. 3), with only *Wantulignathus gwembensis* preserving postcanines of comparable size and anatomy (Whitney & Sidor 2016). The combination of features preserved in this specimen indicate a basal phylogenetic position for it among burnetiamorphs, akin to the position for *Lemurosaurus*, *Lobalopex*, or *Lophorhinus*. Compared to the relatively derived positions of the other Russian forms, *Niuksenitia* and *Proburnetia*, the St. Petersburg specimen represents an earlier evolutionary grade and implies that the early evolution of burnetiamorphs was likely more geographically widespread than sometimes considered (Sidor *et al*. 2021).

Burnetiamorpha indet.

Referred specimens. Five uncatalogued specimens housed at the SAM (Fig. 3); NHCC LB371, fragmentary skullcap (Fig. 4C); NHCC LB372, fragmentary skullcap (Fig. 4D); NHCC LB376, skullcap with pronounced median frontal excrescence on interorbital and intertemporal regions (Fig. 4A); NHCC LB410, skullcap that was previously thin-sectioned (Kulik & Sidor 2019); NHCC LB590, skullcap with large pineal opening (Fig. 4B); NHCC LB831, crushed skullcap with part of occiput articulated (Fig. 4E); NHCC LB1154, skullcap preserving interorbital and intertemporal regions, with dorsal portion of occiput attached (Fig. 4F).

Locality and horizon. The SAM specimens come from locality B32, which was noted as occurring, 'Below Usili Mt., near Ngaka-Ruhuhu confluence' and lies within the Lower Bone Bed (now Usili Formation) on Stockley's map (1932: pl. 38). The NHCC specimens come from four

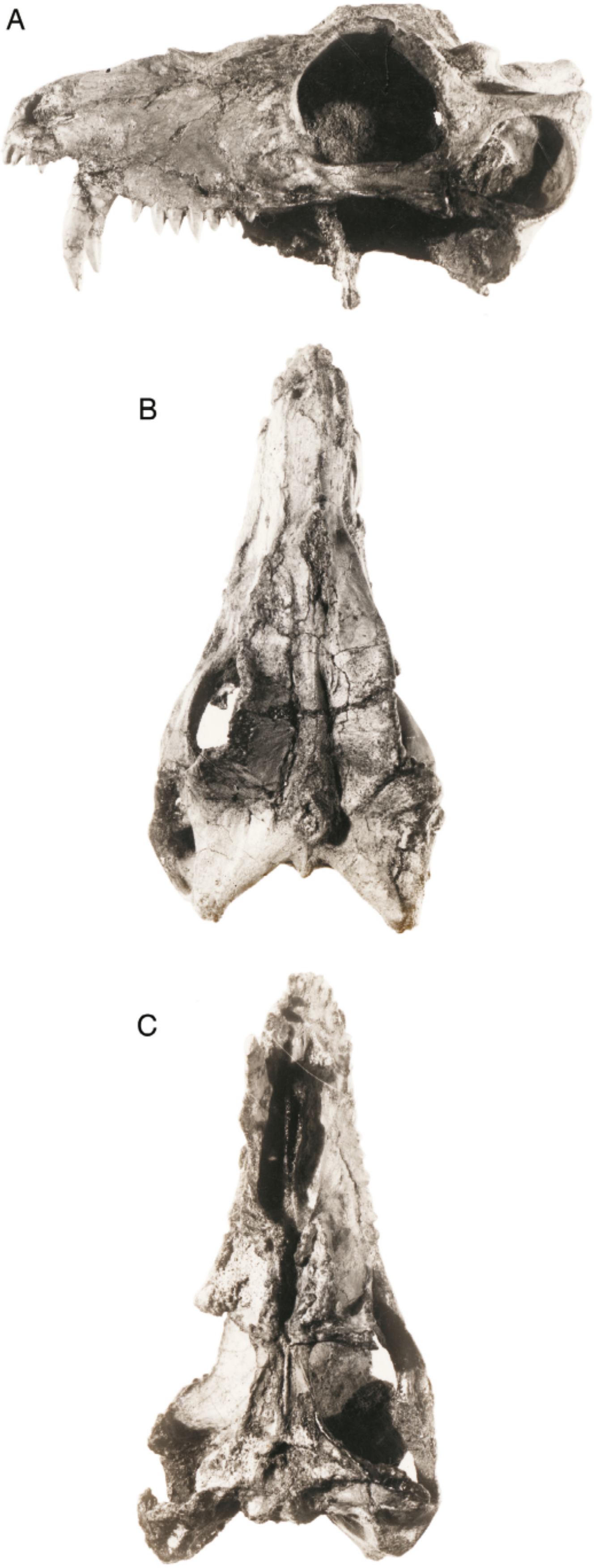

Figure 2. Cranial anatomy of an unidentified burnetiamorph specimen. These photographs were given to Bruce Rubidge by Leonid Tatarinov while visiting the Paleontological Institute in Moscow in 1992. The specimen supposedly resides in St. Petersburg, but was not found when Bruce Rubidge visited several institutions there in 1992. Scale unknown. Skull in (**A**) left lateral, (**B**) dorsal, and (**C**) ventral views.

localities (L186, L198, L212, L213) in the middle Madumabisa Mudstone Formation of the Mid-Zambezi Basin, Gwembe District, Southern Province, Zambia (Sidor *et al*. 2014). Detailed coordinates are available to qualified researchers from the NHCC or by contacting the author.

Comments. In the course of mapping the Ruhuhu Basin in the early 1930s, five burnetiamorph skullcaps and one partial lower jaw symphysis of a dicynodont were collected under field number S559 (Stockley 1932). These fossils were apparently part of a shipment sent to the South African Museum for identification, but were never discussed in the literature (Haughton 1932; Boonstra 1953). These burnetiamorph fossils were recognized in the SAM collections by Brandon Peecook in 2015 and are figured here for the first time (Fig. 3). Unfortunately, since their recognition in 2015, the SAM collections were reorganized and the burnetiamorph specimens have yet to be inventoried; as such, they lack specimen numbers here.

The specimen shown in Fig. 3B retains matrix that matches that of the basal conglomerate of the Usili Formation, which has produced all the skullcaps of Tanzanian burnetiamorphs described thus far (Sidor *et al*. 2010). However, the remaining specimens are essentially devoid of matrix, which would be atypical for fossils from the basal conglomerate, raising the possibility that multiple collecting events were combined under one field number. Interestingly, the most complete specimen (Fig. 3D–F) is unlike the Tanzanian species described below in possessing a very tall and well-developed median frontal eminence alongside a uniformly thickened supraorbital region, suggesting the possibility of a second burnetiamorph from the Ruhuhu Basin. Pending relocation of the original locality/localities and the discovery of more complete material, Stockley's collection is best referred to Burnetiamorpha indet.

The NHCC specimens are figured here for the sake of completeness (Fig. 4). An additional specimen, NHCC LB410, was figured by Kulik & Sidor (2019) and thin-sectioned as part of that study. These specimens preserve a wide range of sizes and styles of preservation, with some clearly very crushed. Supraorbital and median frontal excrescences are uniformly present, but specific features diagnostic of a named burnetiamorph genus are not preserved. Some of these specimens probably pertain to *Bondoceras* (especially NHCC LB376, LB 410, LB590, and LB1154), as they preserve aspects of the anatomy characteristic of that taxon. However, on balance, they do not preserve sufficient anatomy to warrant formal referral.

Burnetiidae Broom, 1923

Bondoceras bulborhynchus **gen. et sp. nov.**

LSID. urn:lsid:zoobank.org:act:6DDBCD99-F920-4742-A076-66E829CB26DB

Holotype. NHCC LB124, the skull roof of a medium-sized burnetiamorph preserving the dorsal part of the snout, interorbital region, and intertemporal region, as well as part of the occiput and braincase (Figs 5–7).

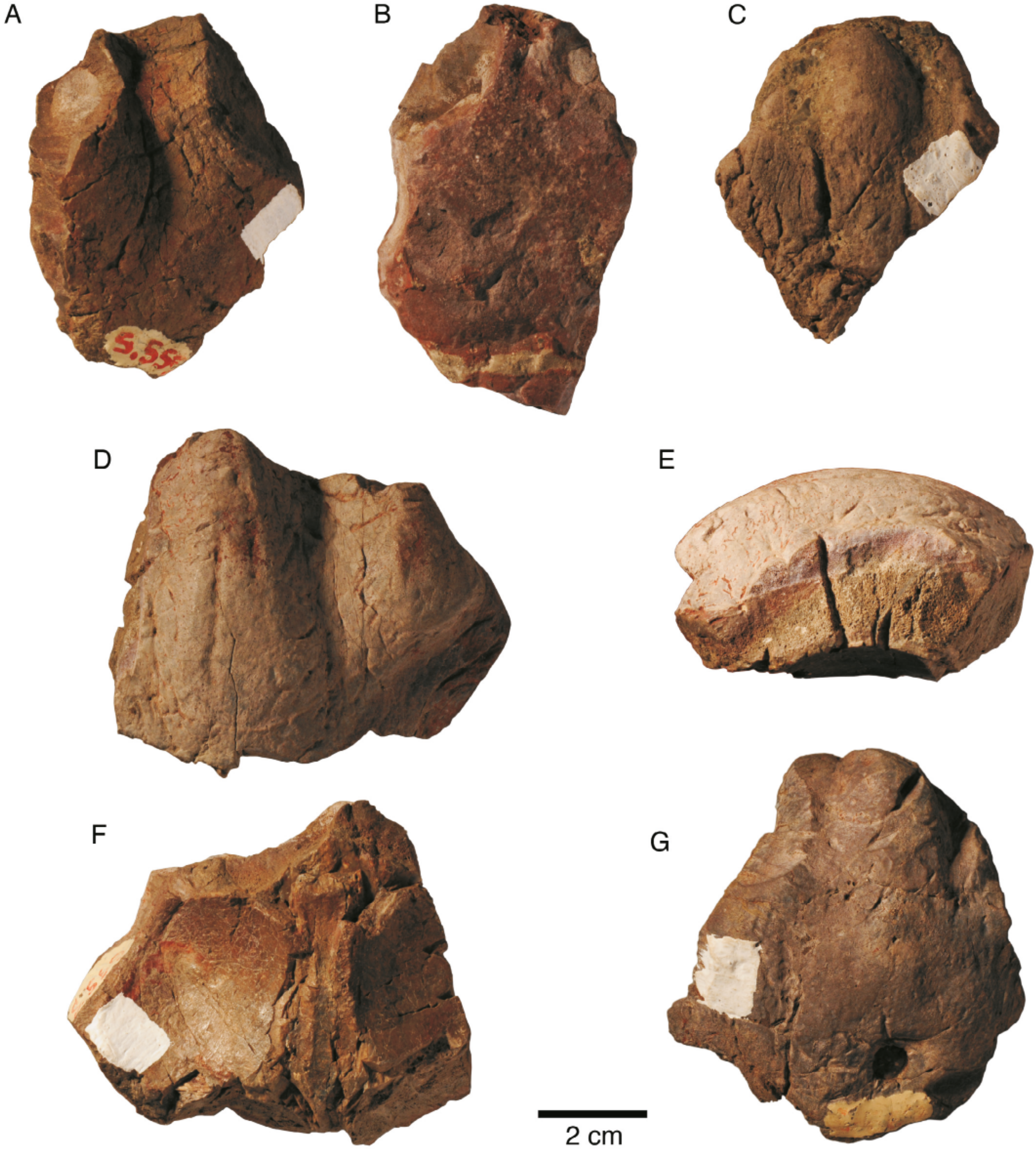

Figure 3. Cranial anatomy of burnetiamorph skullcaps collected by Gordon Stockley from the Ruhuhu Valley of Tanzania. Dorsal view of uncataloged specimens (**A**, **B**, **C**, **G**). The best preserved specimen in (**D**) dorsal, (**E**) left lateral, and (**F**) ventral views. Images provided by Brandon Peecook.

Referred specimens. NHCC LB118, a small skullcap preserving the interorbital and intertemporal regions (Fig. 8C); NHCC LB592, largest specimen with pronounced median frontal excrescence and tall supraorbital bosses (Fig. 8B,E); NHCC LB411, a well-preserved skullcap with dorsal portion of occiput attached (Fig. 8A); NHCC LB373, small skullcap that was previously thin-sectioned (Kulik & Sidor 2019) (Fig. 8D).

Etymology. Bondo, the name of a village in close proximity to the fossil localities producing these specimens; *ceras*, ancient Greek meaning horn and referring to the bony excrescences that typify burnetiamorphs; *bulbus* (Latin), a bulb or knob; *rhynchus*, Greek for snout; the species name references the hemispherical median nasal boss.

Diagnosis. Autapomorphic in possessing a median triangular wedge of bone extending posteroventrally from the posterior skull roof surface, continued ventrally by a strong nuchal ridge and separating the occiput into a pair of deep fossae with dorsolateral pockets. In large specimens, the median frontal excrescence is taller and

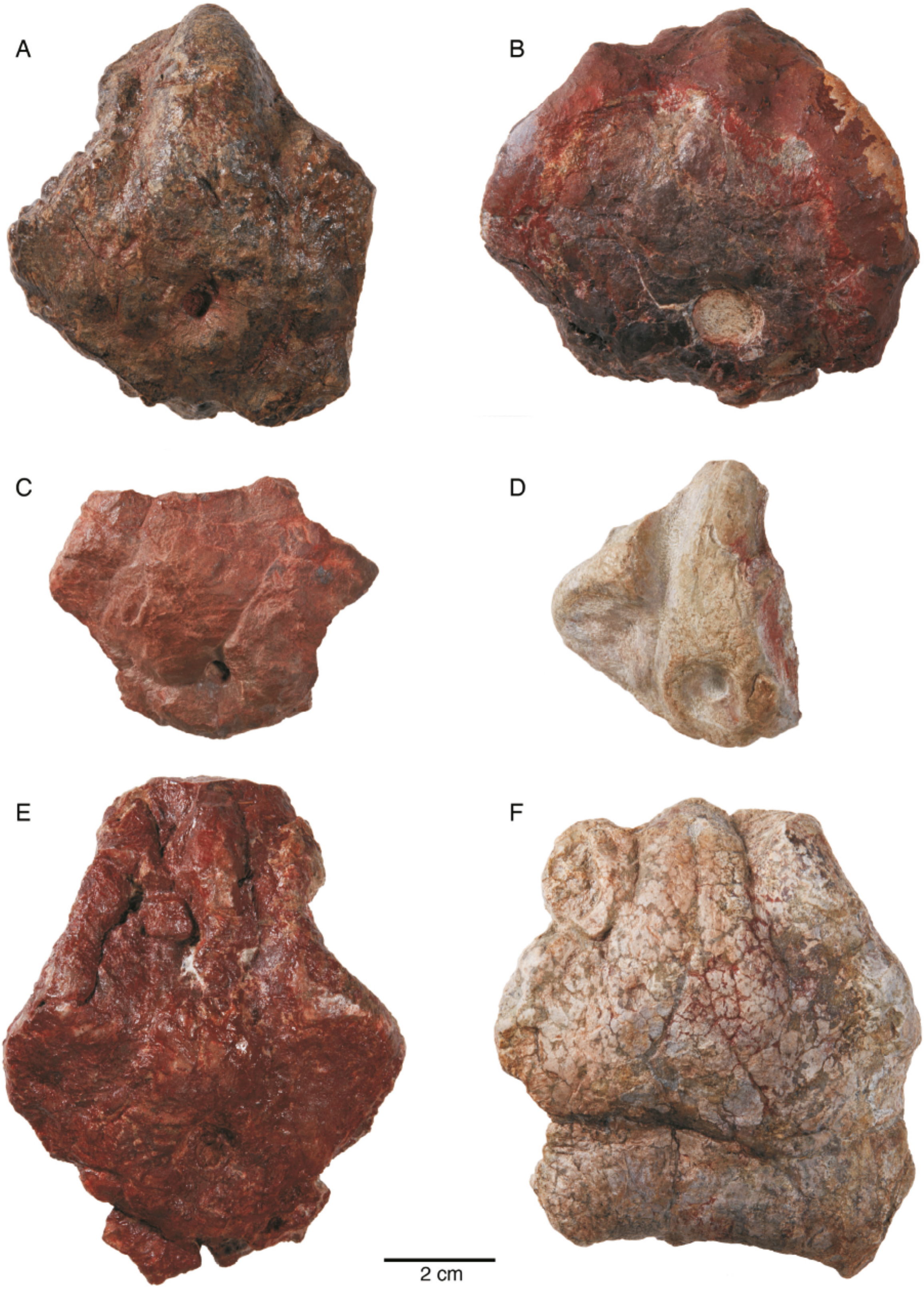

Figure 4. Specimens referred to Burnetiamorpha indet. from the Permian of Zambia. Skullcaps of (**A**) NHCC LB376, (**B**) NHCC LB590, (**C**) NHCC LB371, (**D**) NHCC LB372, (**E**) NHCC LB831, and (**F**) NHCC LB1154, in dorsal view.

more pronounced than the supraorbital bosses. Also characterized by the following unique combination of characters: hemispherical nasal boss; dorsal orbital margin uniformly thickened and not creating a distinct peak in lateral view; pineal region rounded and formed by diffuse pachyostosis, dorsal squamosal boss either absent or comparatively small.

Locality and horizon. Collected from four localities (L149 [type locality], L152, L167, L177, L234) ranging from approximately 11–18 km southwest of Chamwe, Gwembe District, Southern Province, Zambia. Tapinocephalid teeth, which imply a Guadalupian age (Olroyd & Sidor 2017), were found in the vicinity of all but the last locality. L234 may instead correspond to an overlying *Endothiodon*-

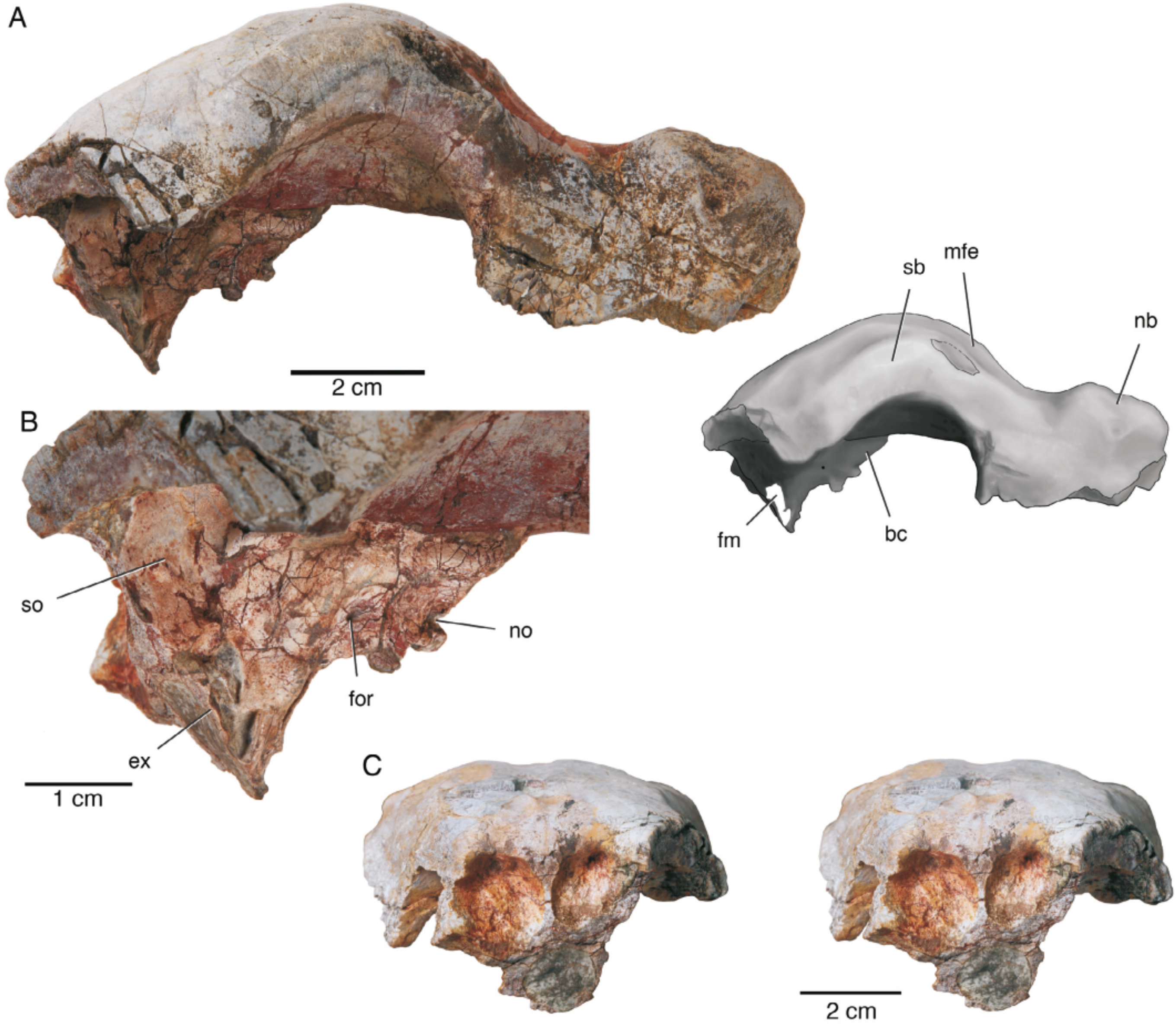

Figure 5. Holotype of *Bondoceras bulborhynchus* gen. et sp. nov. (NHCC LB124). **A**, Skullcap in right lateral view; **B**, enlarged image of braincase in right lateral view with dermal skull roofing bones shaded; **C**, stereopair of occiput in posterior view. Abbreviations: bc, ossified braincase, possibly formed by the supraoccipital; ex, exoccipital; fm, foramen magnum; for, foramen; mfe, median frontal excrescence; nb, nasal boss; no, notch along anterior margin of braincase; sb, supraorbital boss; so, supraoccipital.

equivalent biozone (Sidor, unpubl. data). Detailed coordinates are available to qualified researchers from the NHCC or by contacting the author.

DESCRIPTION

As with most vertebrate fossils collected from the middle Madumabisa Mudstone Formation, the holotype and referred specimens of *B. bulborhynchus* were at least partially preserved in calcareous nodules typical of the middle unit of that formation (Sidor *et al.* 2014). In some cases, the limits of the nodule are clearly visible (i.e. where there is a sharp break between a highly weathered surface and well-preserved bone), but in others, the distinction is much more subtle. Areas with red staining on NHCC LB124 indicate areas originally covered in matrix (Figs 5–7). Even on seemingly pristine specimens, sutural detail is often limited on the external surface, as vascular pachyostosis extends to the ectocranial surface of the skull (Kulik & Sidor 2019).

The following description focuses on the holotype of *B. bulborhynchus* (NHCC LB124), as it preserves the most complete anatomy (Figs 5–7), including the dorsal surface of the snout as well as a partial occiput and braincase. When compared to the full spread of specimens referred to the genus (Fig. 8), this specimen is intermediate in terms of size and its development of pachyostotic features. Some specimens are much smaller and have relatively little pachyostosis (Kulik & Sidor 2019) and are likely to represent juveniles (Fig. 8C,D), whereas one is moderately larger and shows much more pronounced pachyostosis (Fig. 8B,E).

Lateral view – Fig. 5A shows the holotype in right lateral view, which is the more complete of the two sides. The hemispherical nasal boss is weathered dorsally, but is continuous with a low, broad frontal ridge that extends posteriorly towards the interorbital region, where it blends into the dome-like pachyostosed bone. By contrast, the largest specimen (NHCC LB592) shows a massively

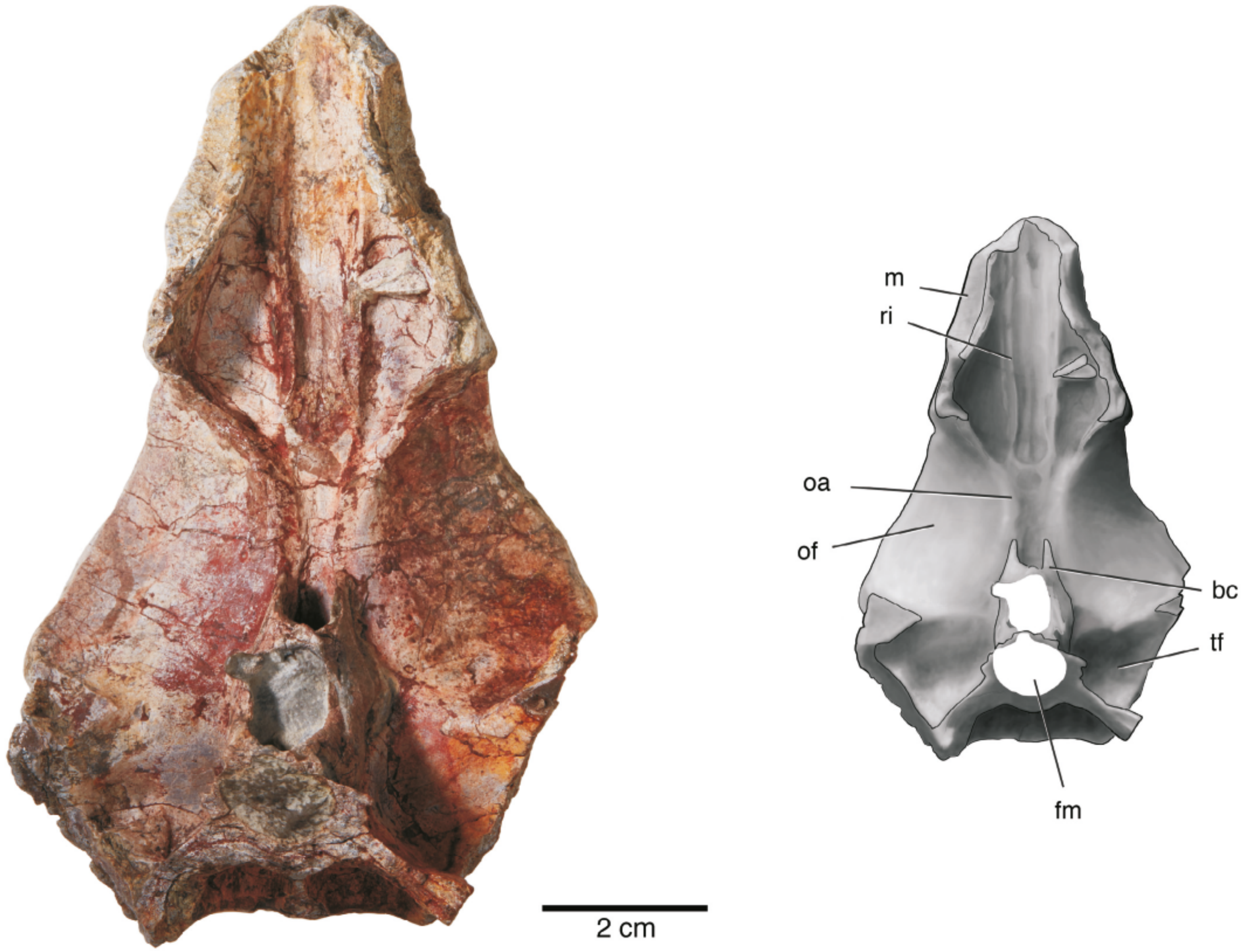

Figure 6. Holotype of *Bondoceras bulborhynchus* gen. et sp. nov. (NHCC LB124). Skull roof in ventral view. Abbreviations: bc, ossified braincase, possibly formed by the supraoccipital; fm, foramen magnum; m, maxilla; oa, articulation surface for orbitsphenoid; of, orbital fossa; ri, ridge on ventral surface of nasal; tf, temporal fossa.

thickened median frontal excrescence with near-vertical sides that is much taller than the adjacent supraorbital bosses (Fig. 8B,E). In the type, the supraorbital region is uniformly thickened along its entire length and its lateral margin, just above the orbit, is oriented vertically. In the largest referred specimen (Fig. 8B,E), increased pachyostosis has reshaped the supraorbital boss to laterally overhang the orbit, but the region just above the orbit retains a curved, vertical surface. None of the referred specimens show a second excrescence at the posterior end of the orbital rim, as seen in the other burnetiamorph species from the middle Madumabisa Mudstone Formation, *Mobaceras zambeziense* (Kammerer & Sidor 2021), but rather the supraorbital thickening is remarkably uniform in height. Anterior to the orbit, the lateral surface of the snout is fractured and poorly preserved (Fig. 5A), making it very difficult to determine if the lacrimal fossa characteristic of burnetiamorphs was present (Kammerer & Sidor 2021). In lateral view, the intertemporal region slopes posteroventrally towards the occipital region (Fig. 5A). Just a small portion of the dorsal end of the postorbital bar is preserved, but no details of its composition can be discerned in the holotype or any of the referred specimens.

Much of the mid-portion of the braincase (i.e. the area roughly corresponding to the midbrain and including the pineal organ) remains in articulation with the skull roof, which presents a rare opportunity to study this region in a burnetiamorph (Fig. 5B). Tatarinov (1968) described this region based on the natural mould that is the holotype of *Proburnetia* and, more recently, Benoit *et al.* (2017a) used CT data to analyse the braincase in *Lemurosaurus* and *Leucocephalus* as part of a study on brain evolution (see also Duhamel *et al.* 2021). These differing modes of preservation and analysis have resulted in differing interpretations of the bones surrounding the brain, which makes describing the anatomy in *Bondoceras* less than straightforward.

In lateral view, the mid-portion of the braincase has the outline of a right triangle, with the two orthogonal sides attaching to the underside of the skull roof and the occipital region (Fig. 5B). The hypotenuse is an irregular bony margin coursing diagonally from anterodorsal to posteroventral. The dorsal part of the braincase is nearly vertical, but its lateral surface bows slightly laterally in coronal section and then curves ventromedially, especially where the two sides contact one another anteriorly. In lateral view, an oval, anteriorly-directed foramen is visible on the

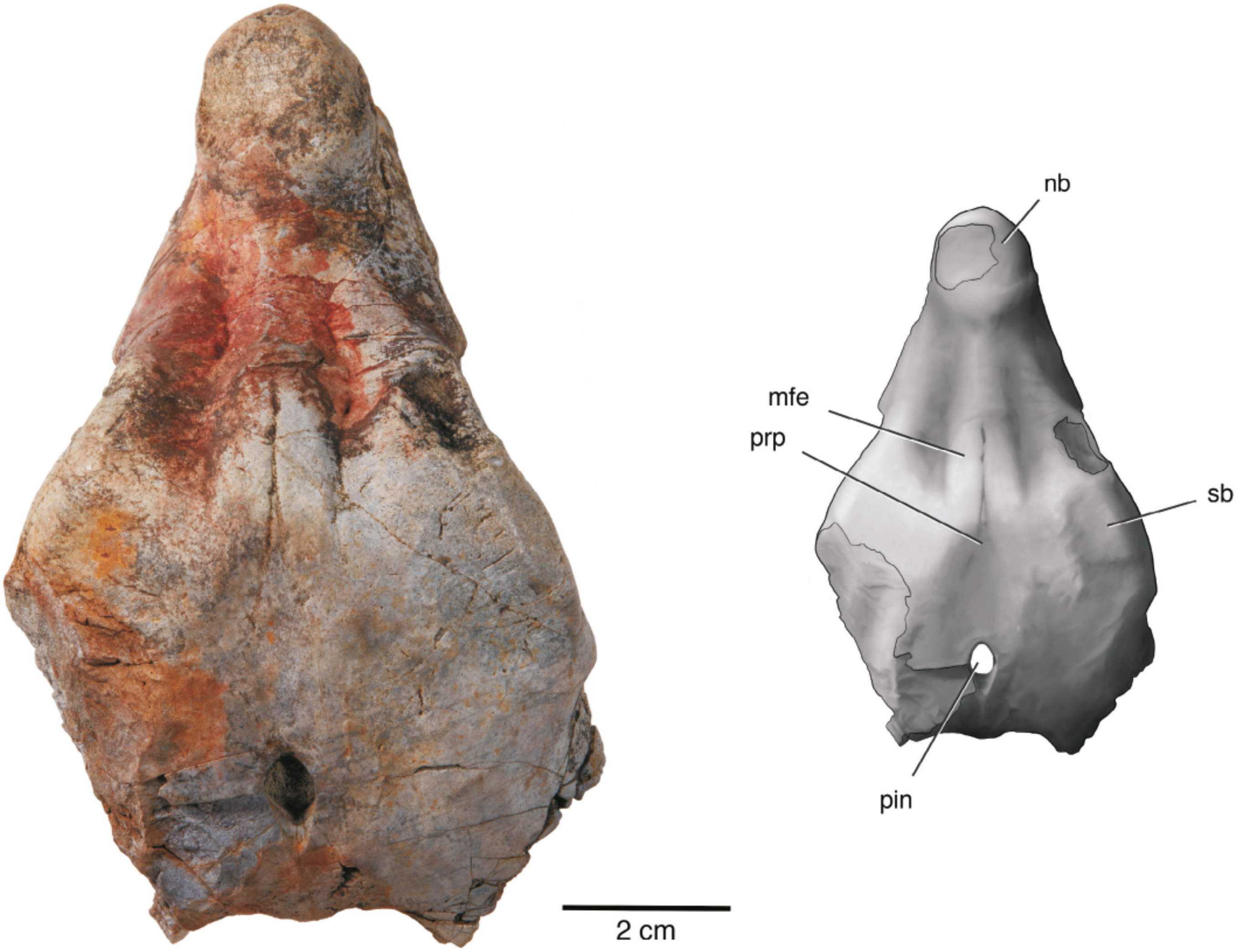

Figure 7. Holotype of *Bondoceras bulborhynchus* gen. et sp. nov. (NHCC LB124). Skull roof in dorsal view. Abbreviations: mfe, median frontal excrescence; nb, nasal boss; pin, pineal foramen; prp, preparietal; sb, supraorbital boss.

right side and is positioned posterior to a notch in the anterior margin of the element (Fig. 5B). Posteriorly, the braincase deepens and contacts the supraoccipital and, ventral to a matrix-filled gap, a small sliver of the exoccipital.

Identifying which elements form the triangular mid-portion of the braincase in *Bondoceras* is difficult, and this difficulty is compounded by an inconsistent use of terms among therapsid workers. Tatarinov (1968: fig. 3) showed the sphenethmoid and an anterior process of the basisphenoid forming the anterior braincase, separated by a wide, matrix-filled gap from the epipterygoid, basicranium, and an ossified capsule surrounding the parietal organ more posteriorly. Ivakhnenko (2008: fig. 28) reinterpreted the braincase of *Proburnetia*, showing a mesethmoid, orbitosphenoid, and presphenoid anteriorly, but not the ossified capsule. Sidor & Smith (2007) figured a partial sphenethmoid in the anterior part of the interorbital region in *Lophorhinus* (based on comparisons with *Dimetrodon*; Romer & Price 1940), but the anatomy and position of this element suggests that it would correspond to what Castanhinha *et al.* (2013) and Laaß (2015) termed 'ethmoid' in their descriptions of dicynodont braincases. In *Lemurosaurus* and *Leucocephalus*, Benoit *et al.* (2017a) identified a similar braincase element as the orbitosphenoid, although Day *et al.* (2018) noted an interorbital septum ventral to it as well as a mesethmoid ossification more anteriorly. Benoit *et al.* (2017a) were non-committal when identifying more posterior elements (i.e. the mid-portion of the braincase), which were often simply labelled as 'braincase wall'. The preserved braincase in *Bondoceras* does not correspond anatomically to an orbitosphenoid (*sensu* Benoit *et al.* 2017a), which would have been present more anteriorly. Similarly, I consider the epipterygoid as not preserved in *Bondoceras*, as this element has been described in both *Lobalopex* and *Proburnetia* where it conforms to the columnar shape seen in pelycosaur-grade synapsids as well as gorgonopsians and anomodonts (Tatarinov 1968; Sidor *et al.* 2004; Kemp 1969; Castanhinha *et al.* 2013; Kammerer 2015; Laaß 2015). The triangular braincase element in *Bondoceras* corresponds most closely to what Tatarinov (1968) labelled the parietal organ capsule, but it is much more extensive and CT data will likely be needed to corroborate this hypothesis or suggest an alternative, like an anterior process of the supraoccipital and/or prootic.

Ventral view – Sidor *et al.* (2010) described a burnetiamorph interorbital and intertemporal region in ventral

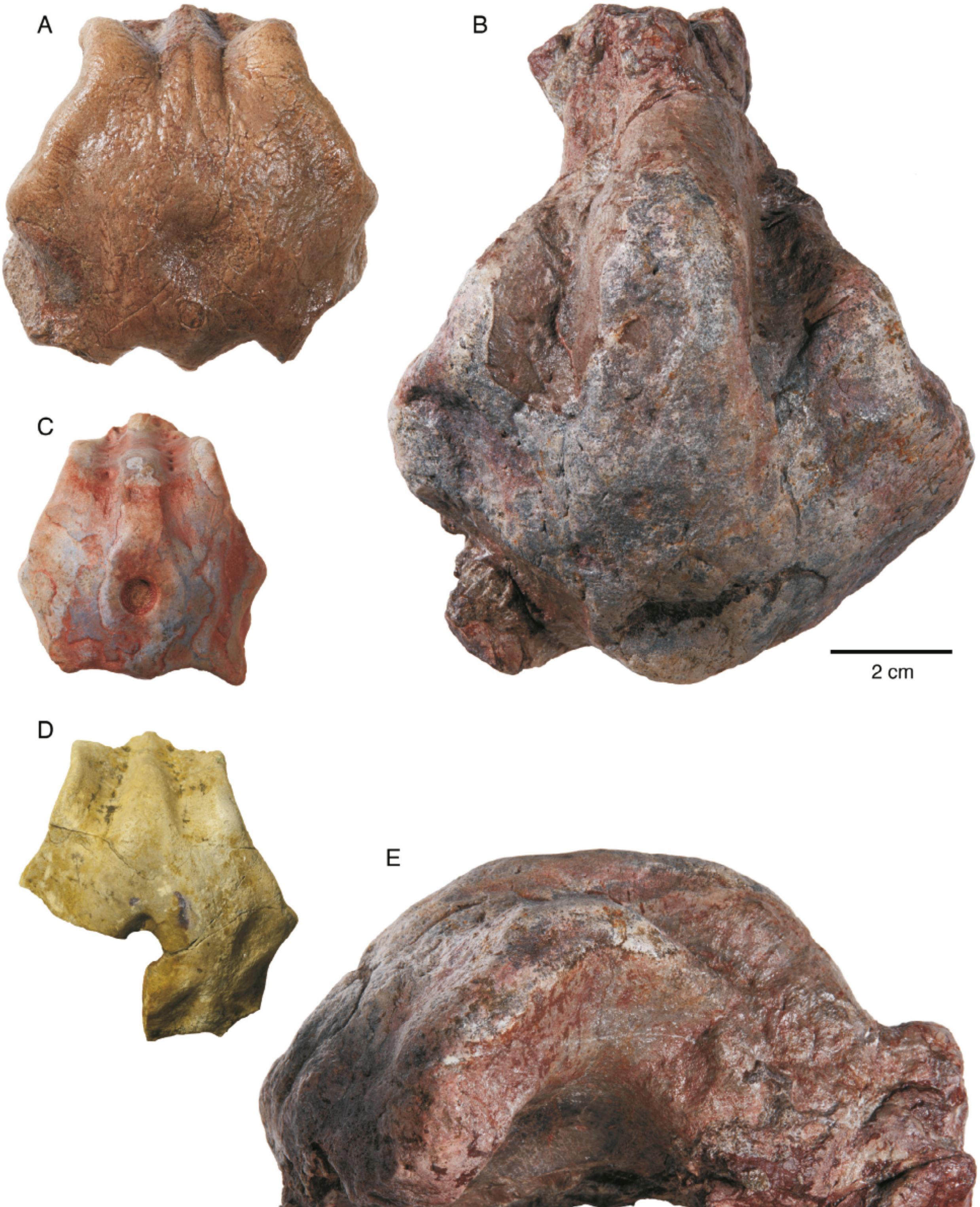

Figure 8. Burnetiamorph skullcaps from the Permian of Zambia. Skullcaps of *Bondoceras bulborhynchus* gen. et sp. nov. Dorsal view of (**A**) NHCC LB411, (**B**) NHCC LB592, (**C**) NHCC LB118, and (**D**) NHCC LB373. Right lateral view of (**E**) NHCC LB592.

view and, despite the current specimen being relatively narrower, much of that description applies to the anatomy of *Bondoceras*. However, the holotype of *B. bulborhynchus* provides new information anteriorly (Fig. 6). The ventral surface of the nasals and prefrontals is well-preserved and features a pair of longitudinal ridges that slightly diverge anteriorly, where they become less prominent. The bone between the ridges forms a shallow depression, but at its midline there is the faint hint of a ridge posteriorly and a midline suture near its mid-length. At their posterior end, the ridges flare laterally to create a U-shaped depression or pocket in combination with the medial margin of the orbit. In this region, each ridge splits into thin medial and lateral ridges, with a sutural surface for a ventral element, likely the orbitosphenoid, in between (Fig. 6). This sutural surface can be traced along the medial margin of the curved ridges that separate the orbital fossa from the midline trough. Anteriorly, at the level of the anterior orbit, a circular depression is formed in the ventral midline surface of the skull roof.

A portion of the lateral surface of the snout is preserved on both sides and these are continuous with the anterior border of the orbit along a broken edge of bone. Unfortunately, even in cross-section there is no indication of sutural contacts between the bones. It is worth noting, however, that the right maxilla is somewhat thickened in cross-section (Fig. 6), suggesting that this part of the skull was also subject to pachyostosis in *Bondoceras*.

The ossified braincase is visible in ventral view (Fig. 6). Its left and right sides are broadly separated anteriorly and posteriorly, but near the centre fold towards the midline to form a bridge. However, matrix obscures the details of this connection and an irregular thickening of bone lies just ventral to the bridge. It is unclear if this thickened lump of bone is a natural feature or a piece of bone that was moved into its current location. Matrix fills the space directly anterior to the foramen magnum and obscures the location of the pineal foramen, which Sidor *et al.* (2010) showed was positioned roughly in line with the transverse ridges separating the orbit and temporal fossae.

Dorsal view – In dorsal view (Fig. 7), the intertemporal region of the holotype of *B. bulborhynchus* is relatively flat, with a broad area of eroded bone on the left side. Indeed, the flatness of the region likely reflects at least a moderate degree of weathering, as most of the referred specimens show this area to be more domed from side to side and from front to back (Fig. 8). The anterior margin of the preparietal is visible as a steep-sided, inverted V in several specimens (Figs 7, 8), where it projects anteriorly to a level roughly in line with the anteroposterior midpoint of the orbit. Curiously, the preparietal is not visible in either of the smallest specimens (Fig. 8C,D), despite their otherwise excellent preservation.

The pineal foramen has an oval outline when seen in dorsal view (Fig. 7). It is relatively large compared to the condition in the other specimens available, suggesting that the external surface of the skull roof actually represents a deeper section through the parietal canal. This is reinforced by the observation that the dorsal end of the canal has a smaller diameter than its ventral end in several specimens where both can be observed. In dorsal view, the posterior margin of the pineal foramen forms a shallow angle to the skull roof (Fig. 7). By contrast, the lateral and anterior portions of the pineal foramen have vertical walls. The reason for the sloping posterior wall of the pineal foramen is unknown, but Sidor *et al.* (2010) noted a similar anatomy on the internal face of a burnetiamorph skull cap from Tanzania and CT data for a referred specimen of *Bondoceras* (NHCC LB411) shows the same posteroventral slope to the posterior wall of the pineal canal when seen in sagittal section. Although preliminary, based on these observations, I suggest that a relatively large pineal foramen and an oval pineal opening likely indicate a relatively immature individual (or that the skull roof has suffered substantial weathering) and that a small, circular foramen indicates relative maturity. Table 2 includes measurement data showing that

Table 2. Cranial measurements for selected burnetiamorph specimens.
All measurement in millimetres. Abbreviations: BSkullL, skull length measured from the anterior tip of the premaxillary to the posterior end of the occipital condyle; InterOrb, interorbital width, taken transversely across the midpoint of the orbital fossa in ventral view; MFE, thickness of the median frontal excrescence, taken dorsoventrally from the midline trough on the ventral skull roof to the dorsal margin of the boss; OrbD, orbital diameter, reported as the average of anteroposterior and dorsoventral measurements; PinL, pineal foramen anteroposterior length taken at the dorsal margin of the skull; PinW, pineal foramen mediolateral width taken at the dorsal margin of the skull; SupOrb, maximum thickness of supraorbital boss, measured dorsoventrally.

Taxon	Specimen	PinL	PinW	InterOrb	OrbD	SupOrb	MFE	BSkullL
Bondoceras	NHCC LB118	6.4	6.2	34.0	–	11.3	18.7	–
Bondoceras	NHCC LB124	7.3	6.1	59.9	–	18.6	27.4	–
Bondoceras	NHCC LB411	3.5	3.5	48.2	–	17.2	–	–
Bondoceras	NHCC LB592	3.7	3.7	68.0	–	26.1	51.5	–
Burnetia	NHMUK PV R 5697	3.9	3.4	69.0	29.0	20.0	–	145.0
Bullacephalus	BP/1/5387	6.5	6.0	63.0	45.5	19.0	–	–
Isengops	NHCC LB363	3.9	3.4	46.0	36	19.8	–	130*
Lemurosaurus	NMQR 1702	3.3	2.9	37.6	32.5	13.1	–	113.1
Lende	MAL 290	6.6	5.2	34.0	34	10.8	–	104
Lobalopex	CGP/1/61	4.7	4.1	37.2	27	6.5	–	142.0
Mobaceras	NHCC LB133	4.1	3.9	51.8	38.9	22	–	–
Paraburnetia	SAM-PK-K6655	4.0	4.0	58.5	34.5	23.2	–	171
Pembecephalus	NMT RB4	5.5	5.0	74.9	–	16.1	17.8	–
Pembecephalus	NMT RB36	–	–	49.6	–	10.4	17.0	–
Pembecephalus	NMT RB411	3.3	3.3	92.6	–	21.4	31.0	–
Pembecephalus	NMT RB451	–	–	–	–	23.7	–	–
Pembecephalus	NMT RB470	4.7	4.7	64.0	–	16	20.6	–
Pembecephalus	NMT RB841	4.0	4.6	72.4	–	10.4	15.7	–
Pembecephalus	NMT RB842	–	–	68.8	–	–	16.2	–
Proburnetia	PIN 2116/1	5.8	5.8	–	35.9	40.5	–	160

– Measurement unavailable.
*Estimated.

relatively small specimens generally have relatively large pineal openings.

In the holotype (NHCC LB124), the median frontal excrescence is relatively low and broad and is bounded by a shallow longitudinal fossa to either side (Fig. 7). In the smallest, presumably juvenile specimens, Kulik & Sidor (2019) were able to document an irregular series of small foramina at the base of these fossae, but similar foramina could not be recognized in any of the other specimens, likely because of poor matrix separation. Anteriorly, the nasal boss is nearly circular in dorsal view (Fig. 7), but its longitudinal axis is slightly longer than its transverse axis. Much of the boss' dorsal surface is weathered, especially on the left side, so it is likely that it would be slightly taller than shown in Fig. 5. Except for about 1 cm to either side of the midline, the posterior and posterolateral margins of the holotypic skull are eroded off. However, the central section is well preserved and forms a gentle W-shape in dorsal view (Fig. 7). NHCC LB411 preserves the dorsal end of the skull roof above the occipital plate more completely and shows that the midline is formed into a posteroventrally tapering wedge (Fig. 8A). NHCC LB118 preserves the dorsolateral corner of the skull roof, which forms an acute angle and is unexpanded and unthickened (Fig. 8C). Even though the latter specimen is among the smallest, and so the lack of a dorsal squamosal boss could be interpreted as a juvenile feature, what is preserved on the remainder of the specimens suggests that *Bondoceras* lacked a substantial squamosal boss.

Posterior view – The occiput is only partially preserved (Fig. 5C), as much of it was weathered off, leaving a flat erosional plane passing through the foramen magnum, exoccipitals, supraoccipital, and postparietal. A well-developed, vertical nuchal ridge is present on the midline of the supraoccipital and interparietal, which separates the occipital surface into two broadly concave surfaces. The contact between the parietal and interparietal is unclear, but likely took place near the junction between the skull roof and occipital faces of the skull. Lateral to the interparietal, a deep pocket is present on either side, but descending ridges (*sensu* Kammerer & Sidor 2021) are not present. NHCC LB411 preserves more of the occipital surface, including the supraoccipital and part of the dorsal margin of the foramen magnum, but additional preparation is needed to understand any sutural connections.

Pembecephalus litumbaensis **gen. et sp. nov.**

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Holotype. NMT RB4, skullcap preserving interorbital region and intertemporal regions (Fig. 9E).

Referred specimens. NMT RB36, fragmentary skullcap preserving the right supraorbital region and part of the median frontal boss (Fig. 9C); NMT RB411, large skullcap with partial occiput and braincase in articulation (Fig. 9G,H); NMT RB451, isolated left supraorbital region of a large individual (Fig. 9F); NMT RB470, skullcap preserving interorbital region and pineal boss (Fig. 9D); NMT RB841, skullcap preserving interorbital region and pineal boss (Fig. 9A); NMT RB842, fragmentary skullcap preserving right supraorbital region and part of the median frontal boss (Fig. 9B).

Etymology. *Pembe*, Kiswahili for horn; *cephalus*, ancient Greek for head; *Litumba*, the name of the village near the type locality; *-ensis*, Latin meaning from or belonging to.

Diagnosis. Diagnosed by a unique combination of skull roof characters: anterior supraorbital boss parasagittally oriented and slightly sigmoidal in dorsal view with concave medial surface next to thickened posterior half of dorsal orbital margin, which likely represents a diffuse posterior supraorbital boss; thickening surrounding the parietal foramen narrows caudally (i.e. is somewhat teardrop-shaped in dorsal view, because of posterolateral depressions on intertemporal skull roof); median frontal eminence relatively muted and diminishes anteriorly towards nasofrontal suture.

Locality and horizon. All localities (Z10 [type locality], Z24, Z49, Z150, Z229) are closely clustered about 4.4 km northwest of the village of Litumba Ndyosi and represent where strata of the highly resistant basal conglomeratic unit of the Usili Formation crop out (Sidor *et al*. 2010; Angielczyk *et al*. 2014b: fig. 1). Detailed coordinates are available to qualified researchers from the NMT or by contacting the author.

DESCRIPTION

The holotype of *Pembecephalus litumbaensis* (NMT RB4) was previously described by Sidor *et al*. (2010) but referred to Burnetiidae indet. at the time, pending the collection of further material. Fieldwork in 2008, 2012 and 2017 yielded additional isolated skullcaps, mostly preserving the interorbital and intertemporal portions of the skull roof (Fig. 9). A single specimen, NMT RB411, has part of the occiput and braincase attached (Fig. 9G,H). All of the specimens show similar preservation, with areas of robust, pachyostotic bone preferentially preserved and the snout broken off at the junction of the frontals and prefrontals. Preservation in the conglomeratic unit of the Usili Formation resulted in poor separation during preparation, especially on the 'spongy' dorsal surface of the skullcaps.

The anatomy of the supraorbital region is a key feature of *Pembecephalus*. In all specimens, the anterior supraorbital boss forms a parasagittal ridge that is progressively more inset from the orbital margin posteriorly. In burnetiines such as *Burnetia* and *Mobaceras*, an enlarged posterior supraorbital boss is present at the posterodorsal margin of the orbit, but in *Pembecephalus* this region is more diffusely thickened. In dorsal view, the latter region causes the orbital margin to angle posterolaterally, but Fig. 9 demonstrates that this angle becomes progressively reduced in larger specimens, so that in the largest specimen this angulation is nearly gone (NMT RB451; Fig. 9F). This presumed ontogenetic change is due to the two supraorbital bosses merging with increased size. Interestingly, however, the smallest specimen (NMT RB36; Fig. 9C) lacks any thickening in the region of the posterior supraorbital boss, at least in what is preserved. This may suggest a complex pattern of growth for the supraorbital region in *Pembecephalus*.

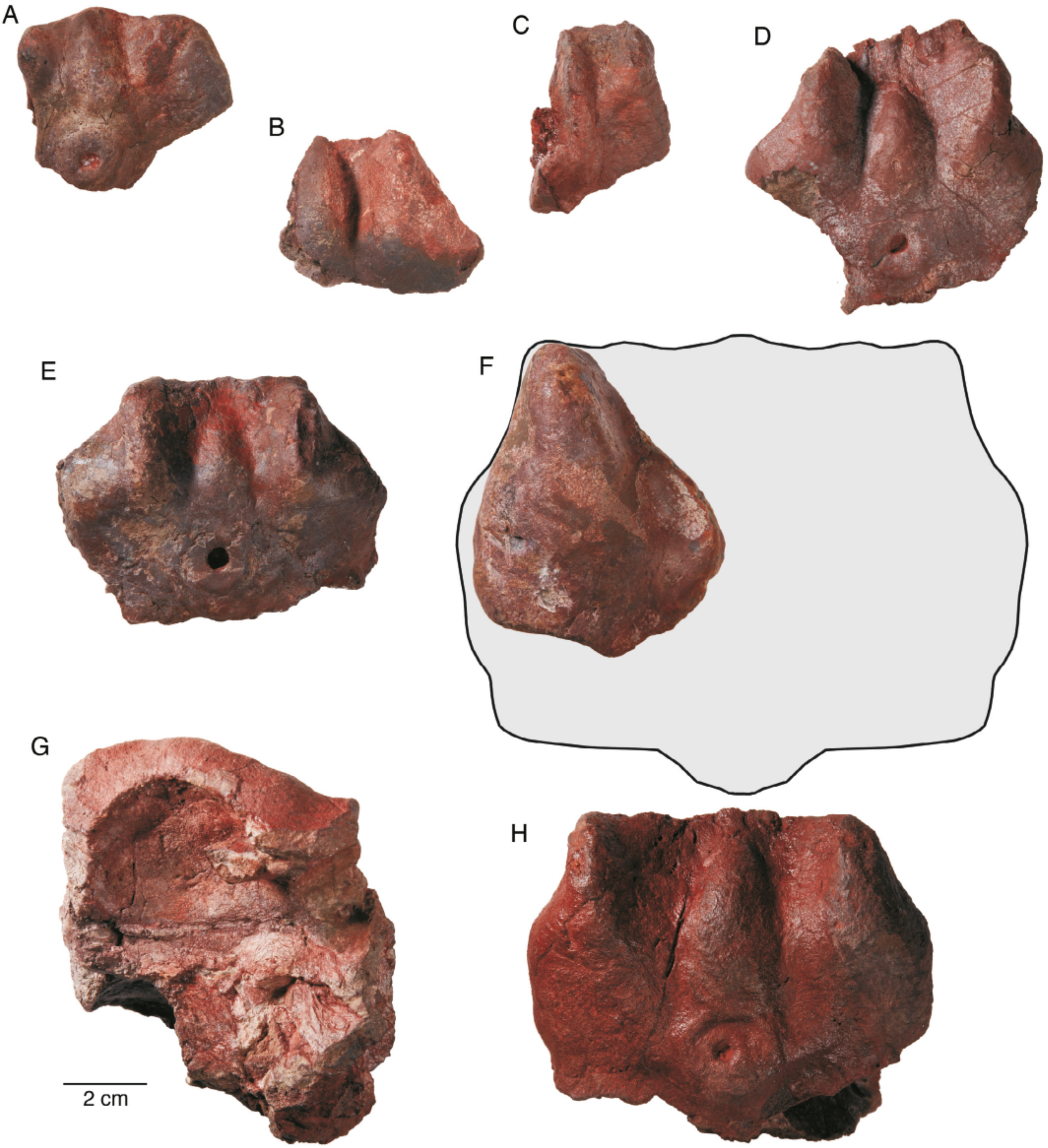

Figure 9. Cranial anatomy of *Pembecephalus litumbaensis* gen. et sp. nov. Dorsal view of **(A)** NMT RB841, **(B)** NMT RB842, **(C)** NMT RB36, **(D)** NMT RB470, **(E)** NMT RB4, holotype, **(F)** NMT RB451, and **(H)** NMT RB411. Ventrolateral view of **(G)** NMT RB411 showing ossified braincase. Outline in **(F)** shows reconstructed size.

One other feature seems similarly ontogenetically variable in *Pembecephalus*. In smaller, presumably less mature individuals, the anterior part of the frontals is flat (i.e. the median frontal excrescence stops posterior to the anterior border of the supraorbital crest; NMT RB4, RB470), whereas the median frontal eminence extends more anteriorly in larger specimens. Importantly, the latter pattern is based on only a single large specimen (NMT RB411; Fig. 9H), so confirming this trend with additional specimens will be necessary. By contrast, the development of the median frontal excrescence lacks a straightforward relationship with overall size. The holotype (NMT RB4; Fig. 9E) and one of the referred specimens (NMT RB470; Fig. 9D) have nearly the same interorbital width, but the median frontal excrescence is about twice as tall in the latter. Furthermore, NMT RB36 (Fig. 9C) is the smallest specimen in the collection, but its frontal ridge is nearly as tall as in the type. Measurement data in Table 2 reinforces the latter statement, but shows that the total thickness of the median frontal excrescence, when measured from the interorbital trough on the ventral surface of the skull roof, is much less dramatically different in NMT RB4 and RB470 than when just the external surfaces of the skullcaps are observed.

NMT RB411 preserves the only available braincase material for *Pembecephalus* (Fig. 9G). A complete description would benefit from CT data and is beyond the scope of this contribution, but it is worth noting that this specimen compares favourably to *Bondoceras* in preserving bilateral ossifications anterior to the supraoccipital, although these are less well defined in *Pembecephalus* (compare Figs 5B and 9G). In addition, NMT RB411 preserves a tall, rectangular median ossification that connects the basisphenoid region to the underside of the skull roof. Anterior to this, a narrow orbitosphenoid appears to be preserved, but this must be confirmed with additional preparation or CT data demonstrating the presence of a tubular cavity for the forebrain (Fig. 9G). Based on NMT RB411 and comparisons with *Bondoceras* and *Lophorhinus*, it seems clear that in ventral view the bowed ridges that medially bound the orbital fossae articulated with the orbitosphenoid for the anterior half of the orbit, and with the posterior braincase element (possible prootic/supraoccipital) for the posterior half of the orbit, as well as in most of the temporal fossa. In posterior view, the supraoccipital, exoccipitals, and basioccipital, as well as the paroccipital processes of both opisthotics, are preserved as a unit, but deformation has rotated and shifted this unit laterally from the overlying postparietal.

DISCUSSION

Phylogenetic position of *Pembecephalus* and *Bondoceras*

Sidor *et al.* (2010) suggested that NMT RB4 (here made the holotype of *Pembecephalus litumbaensis*) could be compared most closely with *Burnetia mirabilis* among burnetiamorphs, citing the presence of a secondary thickening of the posterodorsal margin of the orbit, as well as the low midline ridge on the frontals and the sigmoidal curvature of the supraorbital thickening in dorsal view. However, a midline frontal ridge is absent in *Bullacephalus* and *Mobaceras*, and this feature is typically better expressed in proburnetiines (e.g. *Leucocephalus* and *Paraburnetia*). In addition, the secondary supraorbital thickening in *Pembecephalus* does not take the form of a discrete boss, which is present in all burnetiines where this region is preserved. The mosaic of features seen in *Pembecephalus* make a definitive phylogenetic placement difficult, but overall, a burnetiine relationship seems likely.

The phylogenetic placement of *Bondoceras* is likewise difficult to establish. It has an expanded median nasal excrescence in the shape of a rounded boss with greatest width at its midlength, a character otherwise seen only in burnetiines like *Bullacephalus*, *Burnetia*, and (possibly) *Mobaceras*. However, a burnetiine-like posterior supraorbital boss is absent in *Bondoceras* and this taxon preserves other features that are more in line with a proburnetiine assignment (e.g. a well-developed median frontal excrescence and pachyostosis surrounding the pineal region that blends into the surrounding areas). On balance, the available data suggest that *Bondoceras* is likely a proburnetiine.

I have declined to add the new burnetiamorph taxa named here to a formal cladistic analysis because of the lack of resolution they would undoubtedly engender. For example, Sidor *et al.* (2021) published the most recent phylogenetic analysis of burnetiamorphs and noted that when three similarly incomplete specimens were included, over 18 000 most parsimonious trees were found. My proposals identifying *Bondoceras* as a possible proburnetiine and *Pembecephalus* as a possible burnetiine await future testing, but if verified, would suggest that both subclades of Burnetiidae have representatives in the middle Permian (also argued on the basis of material from the *Tapinocephalus* AZ of the Karoo Basin by Day & Kammerer [2023]).

Morphological and ontogenetic variation

Sidor *et al.* (2021, p. 12) noted that, 'almost every time a new burnetiamorph specimen is found, it is recognized as a new species' and pointed to the farrago of bony bosses and excrescences, combined with the requisite use of morphospecies by palaeontologists, as a contributing factor. While the recognition of *Bondoceras* and *Pembecephalus* as two new species appears no different on the surface, the comparatively large collection of fossils for each should permit addressing questions concerning morphological and ontogenetic variation that have been impossible to address to date, given the history of sampling shown in Table 1. For example, Duhamel *et al.* (2021) analysed two specimens of *Lemurosaurus* and decided that they were better considered to represent two species (contra Sidor & Welman 2003), since the smaller specimen preserved some features thought to be indicative of maturity that were absent in the larger specimen. As discussed below, some of these features are valid, but others are likely misinterpretations or oversimplifications. Nonetheless, a better understanding of the expected degree of morphological variation in features related to pachyostosis and the development of bony bosses would be helpful when assessing species-level variation, or deciding whether or not a certain specimen represents a juvenile (e.g. the holotype of *Lende*; Kruger *et al.* 2015).

All of the material referred to *Pembecephalus* comes from the type horizon and within an area less than 200 metres long (Sidor *et al.* 2010). Combined with the relatively consistent morphology preserved (i.e. presence of median frontal excrescence, shape of supraorbital region, shape of pineal region), this collection seems like a reasonable snapshot of species-level variation spanning roughly a doubling in size. As noted above, some features related to pachyostosis seem to vary predictably with overall size (e.g. straightening of the dorsal orbital margin), but others do not (e.g. degree of development of the median frontal excrescence). Table 2 provides measurement data to help quantify some of this variation, but without assuming a direct relationship between size and degree of maturity, even this sample can shed little light on ontogenetic variation. Likewise, using this sample to test for positive allometry in potentially sexually selected traits (Petrie 1992; O'Brien *et al.* 2018) is difficult without an appropriate standardizing measurement, such as basal skull length. It seems worth entertaining the possibility that the unpredictably variable shape of the median frontal excrescence is related to sexual dimorphism in *Pembecephalus*, but more data are clearly needed (Angielczyk & Kammerer 2018).

Compared to *Pembecephalus*, the material referred to *Bondoceras* is much more heterogeneous in terms of provenance and the anatomy preserved. The smallest specimens referred to *Bondoceras* (NHCC LB118, LB373) represent the second smallest burnetiamorphs reported to date (excluding BP/1/818, which has been variably aligned with the clade; see Sidor & Welman 2003), with an estimated skull length of 100 mm, and the anatomy they preserve agrees with what one might predict a juvenile of *Bondoceras* – given what is preserved in the holotype – to look like (i.e. low supraorbital bosses, weakly developed median frontal excrescence). However, the largest specimen (NHCC LB592) preserves such a hypertrophied median frontal excrescence that it would likely have been enough to suggest generic separation had the collection of specimens not been found in roughly the same stratigraphic horizon and with additional overlapping features of the skullcap. In sum, the morphological variation present in the new, comparatively rich sample from Tanzania and Zambia suggests that while most diagnostic characters vary predictably with size, both genera possess at least one feature that lacks such predictability.

Duhamel *et al.* (2021) reported on six characters that could be used to assess ontogeny in biarmosuchians: 1) orbit size; 2) canine replacement; 3) cranial bosses/pachyostosis; 4) radial vasculature; 5) braincase ossification; and 6) fusion of preparietal/ internal parietals. Of these, only the third, fourth, and sixth are possible to evaluate in the current collection of specimens of *Bondoceras* and *Pembecephalus*. As noted above, the degree of pachyostosis shows a general positive relationship with size in both genera, but some specific features buck this pattern, so caution is certainly warranted when using this feature to assess ontogenetic status.

Duhamel *et al.* (2021) suggested the presence of a radial vasculature indicated juvenile status, but radial vasculature is likely the default pattern for the formation of pachyostosis in burnetiamorphs. Indeed, Kulik & Sidor (2019) showed that the only cranial tissue that was not radially organized was 'Zone B,' which might represent the remnants of early embryonic development. Later ontogenetic stages show infilling of vascular canals peripherally, as shown for pachycephalosaurian dinosaurs (Goodwin & Horner 2004), but the bone matrix remains radially organized. Importantly, current CT technology may not always provide the resolution needed to assess infilling, which could make infilled radially-organized bone look like non-infilled radially-organized bone. To date, no specimens of *Pembecephalus* have been thin-sectioned to assess radial vasculature or its infilling. In *Bondoceras*, one small specimen was histologically sampled and showed very little peripheral infilling (NHCC LB373; Kulik & Sidor 2019). A larger specimen (NHCC LB410) was also sampled and showed increased peripheral infilling, but not enough to suggest more than a subadult status for the specimen (Kulik & Sidor 2019). Since that study, the largest specimen of *Bondoceras* (NHCC LB592) was CT-scanned, but the results could not determine the presence or absence of infilling.

Duhamel *et al.* (2021) suggested that an unfused preparietal and multipartite parietal were likely indicators of juvenile status in biarmosuchians. Marilao *et al.* (2020) suggested the same for the preparietal in dicynodonts. I agree that fusion of these elements very likely occurs once, relatively early in ontogeny, given that paired preparietals are almost never observed (the multipartite parietal has only ever been observed in section). Duhamel *et al.* (2021, p. 45) also suggested that 'the development of cranial pachyostosis occurs after complete ossification of the preparietal and parietal,' but this statement is contradicted by Kulik & Sidor's (2019: fig. 1) observation of over 7 mm of ectocranial pachyostotic bone in a small specimen of *Bondoceras* that retained intraparietal sutures (although the preparietal was unpaired). A preparietal is not visible (macroscopically) on any specimen of *Pembecephalus*, and no sections (physical or virtual) have been made of the parietal in this taxon.

The ontogenetic assessment proposed by Duhamel *et al.* (2021) is a useful starting point, but the fossil record of individual burnetiamorph genera will need substantial improvement before the evolution of the clade as a whole will be thoroughly understood. For example, most specimens of burnetiamorphs are about 200 mm in basal skull length, but both very small and very large specimens remain extremely rare. The smallest specimen known has a basal skull length of 77 mm (Duhamel *et al.* 2021), whereas for the largest, the holotype of *Pachydectes elsi*, this value is approximately 310 mm (Rubidge *et al.* 2006). Given the generally poor sampling of burnetiamorphs, we are far from getting a sense of average size for the vast majority of species, let alone knowing the maximum/adult skull length.

Biogeography

Day *et al.* (2018) suggested that the main Karoo Basin of South Africa might have been on the periphery of the geographic range of the burnetiamorph species it records, which could explain the rarity of specimens in the basin. They went on to suggest that a test of their hypothesis would be to see if those same species were present in higher abundances in adjacent regions, presumably to the north. However, recent fieldwork in Tanzania and Zambia (Sidor & Nesbitt 2018) as well as Malawi (Kruger *et al.* 2015) has failed to discover any additional records of known Karoo burnetiamorphs, despite finding many of the same Permian therapsid genera from other clades (Sidor *et al.* 2013; Angielczyk *et al.* 2014a).

An alternative explanation for the rarity of burnetiamorphs in the Karoo Basin could be that the clade as a whole represents a mid-latitude radiation and that higher palaeo-latitudes were peripheral. *Pembecephalus* and *Lende* are the lowest latitude burnetiamorphs known (palaeolatitude ~55°S), but to date there has been no evidence to suggest that the basins in which they are found hosted more than one burnetiamorph species each. The same goes for the Luangwa Basin (*Isengops*), but the Mid-Zambezi Basin contains two middle Permian species (*Mobaceras* and *Bondoceras*). Co-occurring species are also known from two assemblage zones within the Karoo Basin (*Bullacephalus* + *Pachydectes* in the *Tapinocephalus* Assemblage Zone; *Lobalopex* + *Lophorhinus* + *Leucocephalus* in the *Endothiodon* Assemblage Zone), suggesting that there is no signal that taxonomic diversity tracks latitude. However, it is worth noting that the relatively high abundance of specimens from the Ruhuhu and Mid-Zambezi basins is extraordinary by burnetiamorph standards (Table 1). The basal conglomerate of the Usili Formation probably acted as sorting mechanism, concentrating resistant hard parts like pachyostotic skullcaps (Sidor *et al.* 2010), but no similar taphonomic rationale can explain the abundance of burnetiamorph fossils in the middle calcareous member of the Madumabisa Mudstone of the Mid-Zambezi Basin, which has been interpreted as lacustrine in origin (Nyambe & Dixon 2000; Sidor *et al.* 2014).

A more significant problem with the mid-latitude origin hypothesis is that the lowest latitude therapsid-bearing localities of Guadalupian age lack burnetiamorphs altogether. The Rio do Rasto Formation of Brazil (~46°S) and the Dashankou locality of China (~33°N) are currently the lowest palaeolatitude therapsid-bearing localities, but have yet to produce any biarmosuchians despite the recovery of anomodont and dinocephalian fossils (Liu *et al.* 2010; Liu 2013; Boos *et al.* 2015). The Moradi Formation of Niger (~17°S) has produced fragmentary gorgonopsian fossils, but its vertebrate assemblage is otherwise very different from others in Africa during the Permian and is usually suggested to be Lopingian in age (Sidor *et al.* 2005; Smiley *et al.* 2008). A direct reading of the occurrence data would therefore suggest that burnetiamorphs preferred higher latitudes and that southern Pangea was their centre of diversity, especially during late Permian times. However, as noted by Sidor *et al.* (2021), the fossil record of burnetiamorphs is unlikely to be at a level where any meaningful inferences can be made about their evolutionary biogeography.

The evolution of bizarre structures in burnetiamorph synapsids

Padian & Horner (2011) reviewed bizarre structures in dinosaurs and proposed that their evolution was typically explained as either one or a combination of four potential causes: 1) mechanical function; 2) sexual selection; 3) social selection; and 4) species recognition. Of these, they suggested that species recognition was probably an important, general force driving the evolution of such features. Several authors have cast doubt on the importance of species recognition (e.g. Knell & Sampson 2011; Mendelson & Shaw 2012; Hone & Naish 2013), but nonetheless, many of the points raised by Padian & Horner (2011) apply equally well to the fossil record of burnetiamorphs and so below I review and apply the criteria suggested. Ultimately, determining why the cranial adornments of burnetiamorphs evolved, and what function(s) they served, are important questions that need to be addressed before a thorough understanding of the group can be achieved.

Despite the wide range of cranial adornments and embellishments seen within burnetiamorphs, workers have been surprisingly agnostic when evaluating their evolution. For example, only Ivakhnenko (2008) has suggested that cranial pachyostosis in *Proburnetia* (and other taxa like *Estemmenosuchus*) was associated with 'primitive thermoregulation' (i.e. a mechanical function). A defensive function has yet to be proposed and no evidence for head-to-head combat has been noted (e.g. lesions; Peterson *et al.* 2013). Padian & Horner (2011) suggested that selection for a mechanical trait could be tested by using a phylogeny to check for the progressive elaboration of structures or improvement of proposed function (but see Knell & Sampson 2011). For burnetiamorphs, there does appear to be a general trend for the intensification of pachyostosis, at least early in the evolutionary history of the group, suggestive of 'improvement'. For example, the degree of pachyostosis in the temporal region in non-burnetiid burnetiamorphs like *Lemurosaurus* or *Lobalopex* is clearly substantially less than within the burnetiid subclade. Within burnetiids, however, levels of pachyostosis seem consistently high and each species tends to emphasize a different combination of bosses, rather than develop additional pachyostosis in general. For example, the height of the supraorbital boss relative to orbit diameter varies unpredictably with respect to the phylogenetic position (based on Sidor *et al.* 2021: fig. 6), with the highest values in *Burnetia* and *Paraburnetia* and reduced values in *Bullacephalus* and *Lende* (Table 2).

Explanations related broadly to display, which are oftentimes the default when evidence for mechanical function is lacking (Padian & Horner 2011), have also been lacking in burnetiamorphs. For example, sexual dimorphism has never been studied. Of course, meaningfully addressing this topic has been hampered by the lack of multiple specimens attributed to a given burnetiamorph species, with only *Lemurosaurus* previously known from more than one specimen (Sidor & Welman 2003; Angielczyk & Kammerer 2018; Duhamel *et al.* 2021). The one reference to a display function in the evolution of burnetiamorph adornments was by Sidor *et al.* (2021), who suggested a macroevolutionary relationship between cranial ornamentation and speciation rate. Sidor *et al.* (2021) showed that, when compared with Permian gorgonopsians or therocephalians, burnetiamorphs were more diverse than might be expected based on the number of specimens and species currently recognized, and that this could be evidence for enhanced speciation rates (see also Vrba 1984; Sampson 1999). Furthermore, they pointed to social selection or enhanced species recognition as possible underlying mechanisms.

Padian & Horner (2011, p. 3) proposed that under the species recognition model 'morphology should be expected to evolve without obvious directional trends' and that 'several contemporaneous species should overlap in geographic range'. Both of these proposals receive some support from the burnetiamorph fossil record, but a more systematic analysis is needed. For example, quantifying the complex shapes of burnetiamorph bosses would allow for directional trends to be tested statistically.

The study of bizarre structures in synapsids lags far behind those of dinosaurs, where mechanical tests of crests, domes, horns, clubs, etc., have a long pedigree (e.g. Sues 1978; Weishempel 1981; Vickaryous *et al.* 2004; Farke *et al.* 2009). Among therapsids, dicynodonts have been occasionally examined for sexual dimorphism (e.g. Sullivan *et al.* 2002; Kammerer *et al.* 2015) and headbutting in tapinocephalids was proposed by Barghusen (1975) and re-examined by Benoit *et al.* (2017b). Comparing evolutionary patterns between similarly adorned dinosaurs and early therapsids might lead to new insights. For example, cranial embellishments evolved independently in at least four different lineages of therapsids during the middle Permian (derived anteosaurids, burnetiamorphs, *Estemmenosuchus*, and tapinocephalids + *Styracocephalus*) – is such stratigraphic/temporal clumping unsurprising or anomalous? In addition, the vast majority of dinosaur species with bizarre structures are herbivores, but burnetiamorphs (as well as anteosaurs and rubidgeine gorgonopsians) were carnivorous – does this ecological difference have any significance? Renewed interest in the function of bizarre structures in therapsids would benefit our understanding of the palaeobiology of individual species (e.g. Benoit *et al.* 2016), as well as for macroevolution more generally (Knell *et al.* 2013).

The fossils described in the paper are the result of long term projects in Tanzania and Zambia, and I am very fortunate to have worked with a great group of colleagues in both countries. Fossils of *Pembecephalus* were collected in Tanzania over several field seasons and I thank the team members for their assistance and companionship (Ken Angielczyk, John Fortner, Jackie Lungmus, Laurent Nampunju, Sterling Nesbitt, Savannah Olroyd, Bill Simpson, Roger Smith, Seb Steyer, Michelle Stocker, Anthony Tibaijuka and Linda Tsuji). The Zambian specimens were collected in 2012 and 2014, with help from the following individuals: Ken Angielczyk, Natasha Barbolini, Chuck Beightol, Adam Goulding, Joseph Museba, Sterling Nesbitt, Brandon Peecook, Roger Smith, Seb Steyer, Neil Tabor and Steve Tolan. In addition, I thank the relevant permitting agencies for allowing us to conduct this work. Funding was provided by the following grants: NGS 7787-05, NGS 8962-11, NSF EAR-1337569 to CAS and NSF DBI-0306158, NSF EAR-1337291, Field Museum/IDP Foundation Inc., and The Grainger Foundation to K. Angielczyk. The drawings of *Bondoceras* in Figs 5–7 are by April Neander and I thank her for exceptional efforts. Kelsie Abrams, Bruce Crowley, and Gary Livingston skillfully prepared the African specimens figured here, and I thank Mike Rich for photography. For access to specimens over the years, I thank the South African Karoo vertebrate palaeontology community. This paper, for example, would not have been possible without the help of Roger Smith and Zaituna Skoskan at the SAM. In addition, Brandon Peecook found Stockley's collection of burnetiamorphs from Tanzania and provided the photographs used here. Aliénor Duhamel, Michael Day, and Christian Kammerer provided useful feedback on the manuscript. Finally, Bruce Rubidge encouraged publishing photographs of the St. Petersburg burnetiamorph and has been a wonderful host during my visits to Johannesburg.

ABBREVIATIONS

Institutional

BP	Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa
CGP, CGS	Council for Geoscience, Pretoria, South Africa
MAL	Malawi Department of Antiquities Collection, Lilongwe, Malawi
NHCC	National Heritage Conservation Commission, Lusaka, Zambia
NHMUK	Natural History Museum, London, United Kingdom
NMQR	National Museum, Bloemfontein, South Africa
NMT	National Museum of Tanzania, Dar es Salaam, Tanzania
PIN	Paleontological Institute, Moscow, Russia
SAM	Iziko South African Museum, Cape Town, South Africa
TM	Ditsong National Museum of Natural History, Pretoria, South Africa

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NOTE ADDED IN PROOF: New data on the stratigraphic horizon of NHCC LB592 suggests that it comes from *Endothiodon* Assemblage Zone-equivalent beds in the Mid-Zambezi Basin, thus higher than the remaining specimens of *Bondoceras* and implying that this genus spanned the Guadalupian-Lopingian transition. As additional material of *Bondoceras* becomes available, the taxonomic assignment of NHCC LB592 should be reevaluated.