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Reappraisal of supposed 'dinocephalian' specimens expands burnetiamorph diversity in the Guadalupian *Tapinocephalus* Assemblage Zone of South Africa

Michael O. Day[1,2*] [§] & Christian F. Kammerer[2,3,4]

[1]*Section of Fossil Reptiles, Amphibians, and Birds, Natural History Museum, Cromwell Road, London, SW7 5BD, United Kingdom*
[2]*Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa*
[3]*North Carolina Museum of Natural Sciences, 11 W. Jones Street, Raleigh, NC 27601, U.S.A.*
[4]*North Carolina State University, Raleigh, NC 27695, U.S.A.*

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Burnetiids are a rare, yet seemingly species-rich family of therapsids in the rocks of the Karoo Basin of South Africa. Discoveries over the past 20 years have provided a greater understanding of the morphological variation within the group and have led to differing hypotheses of burnetiid phylogeny and that of their parent clade, Burnetiamorpha. One posits the existence within Burnetiidae of two subclades, Burnetiinae and Proburnetiinae, but this hypothesis invokes lengthy and thus problematic ghost lineages, particularly for proburnetiines. Here we review and describe cranial material from the Capitanian *Tapinocephalus* Assemblage Zone that was previously referred to the dinocephalian therapsid *Styracocephalus platyrhynchus*, showing that it instead represents two new morphotypes of proburnetiine burnetiids. One of these, *Nierkoppia brucei* gen. et sp. nov., is diagnosed by the autapomorphic presence of a supraorbital boss 'folded over' the dorsal margin of the orbit, giving this structure a roughly 'ear' or 'kidney'-shaped appearance; flattened, posteriorly directed squamosal horns; a median frontal boss taller than the supraorbital bosses, reaching its maximum height anterior to them; and massive, rounded nuchal bosses borne on the postparietal and supraoccipital. The other specimen is left in open nomenclature due to incompleteness, but represents a heavily pachyostosed proburnetiine similar to *Lende* and *Leucocephalus*. The recovery of proburnetiines within the *Tapinocephalus* Assemblage Zone shortens the ghost lineage of this clade and indicates that a diverse burnetiid fauna was present in the Guadalupian Karoo, comparable to that now known from Tanzania and Zambia.

Keywords: Synapsida, Burnetiidae, Permian, taxonomy, biostratigraphy.

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INTRODUCTION

Twenty years ago, the unusual therapsid family Burnetiidae was thought to comprise only two taxa, the South African *Burnetia* and the Russian *Proburnetia*, each known from a single skull (Rubidge & Sidor 2002). Since then, our understanding of the diversity, anatomy, geographic distribution, and stratigraphic range of this family (and its more inclusive clade Burnetiamorpha) has improved dramatically, driven in large part by the research efforts of Bruce Rubidge and Christian Sidor (who have been authors on all but two of the burnetiamorph-focused papers published since the year 2000). Numerous new burnetiamorph taxa, particularly from southern Africa, have been described in recent years, with a total of 16 genera currently recognized (Sidor 2015, 2023; Whitney & Sidor 2016; Day *et al*. 2018; Kammerer & Sidor 2021; Sidor *et al*. 2021). However, this increase in burnetiamorph material, including several morphotypes known only from highly incomplete crania (e.g. Kammerer 2016; Kulik & Sidor 2019), has caused the once fairly simple phylogeny of the group to become more contentious.

*Author for correspondence. E-mail: michael.day@nhm.ac.uk

Particularly uncertain has been the taxonomic composition of (and interrelationships within) Burnetiidae. Defined by Rubidge & Sidor (2002) as the least inclusive clade containing *Burnetia* and *Proburnetia*, Burnetiidae historically contained the bulk of burnetiamorph diversity, including all taxa with heavily pachyostosed skulls (e.g. Smith *et al*. 2006). Within Burnetiidae, two subclades have been recognized, which were formalized as subfamilies by Kammerer (2016): Proburnetiinae and Burnetiinae. The taxa that have been recovered as proburnetiines in previous phylogenetic analyses are exclusively Lopingian in age (with the stratigraphically uncertain *Proburnetia* as the only potential exception) and include records from Russia (*Proburnetia*), Malawi (*Lende*), and South Africa (*Leucocephalus*, *Paraburnetia*) (Kammerer & Sidor 2021). Burnetiines *sensu* Kammerer (2016) include *Burnetia* itself, from the Lopingian *Dicynodon-Theriognathus* Subzone of the *Daptocephalus* Assemblage Zone (AZ) of the South African Beaufort Group (Viglietti 2020), but also two Guadalupian South African taxa (*Bullacephalus* and *Pachydectes* from the *Tapinocephalus* AZ; Day & Rubidge 2020) and one Russian taxon of uncertain but probable Lopingian age (*Niuksenitia*; Ivakhnenko 2008; Arefiev *et al*.

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2015; Sennikov & Golubev 2017). In the Karoo Basin, all non-burnetiid burnetiamorphs (e.g. *Lemurosaurus*, *Lobalopex*, *Lophorhinus*) and the majority of non-burnetiamorph biarmosuchians (e.g. *Herpetoskylax*, *Ictidorhinus*, *Lycaenodon*) are Lopingian in age (Sidor & Smith 2007), so the presence of deeply-nested burnetiines in the Guadalupian is problematic, incurring lengthy ghost lineages for the group (four to six million years separate these Lopingian records from *Bullacephalus* and *Pachydectes* at the base of the *Tapinocephalus* AZ; see Fig. 1).

Noting this stratigraphic disconnect, and highlighting homoplasy in previous phylogenetic analyses of the clade, Day *et al.* (2016, 2018) proposed an alternative hypothesis of burnetiamorph relationships in which the Guadalupian taxa *Bullacephalus* and *Pachydectes* (placed in a separate family Bullacephalidae) fall outside of Burnetiidae (and in some analyses outside of Burnetiamorpha altogether, as some of the earliest-diverging biarmosuchians; see Day *et al.* 2016: fig. 6C). Without these genera, the breakdown of Burnetiidae into two subclades (*sensu* Kammerer 2016) collapses, with *Burnetia* nesting deep within the 'proburnetiines' (either as sister-taxon of *Paraburnetia* or of a *Lende*+*Paraburnetia* clade) and *Niuksenitia* falling out as a non-burnetiid burnetiamorph. Although not completely eliminating ghost lineages within Burnetiamorpha, the topology of Day *et al.* (2016) did yield substantially greater stratigraphic congruity than previous hypotheses of burnetiamorph relationships.

The most recent studies addressing burnetiamorph phylogeny, however, have returned to recovering an expansive Burnetiidae divided into two subclades (Kammerer & Sidor 2021; Sidor *et al.* 2021). These analyses were based on the incorporation of new taxa (notably *Mobaceras* from Guadalupian exposures of the mid-Zambezi Valley of Zambia, which exhibits features intermediate between 'bullacephalids' and *Burnetia*), new characters, and exhaustive revision of existing character sets, and strongly recover *Bullacephalus* and *Pachydectes* as close relatives of *Burnetia* (i.e. as burnetiine burnetiids, with Bullacephalidae placed in synonymy). The return of *Bullacephalus* and *Pachydectes* to a deeply nested position within Burnetiinae carries with it the same stratigraphic problems as before: it extends the ghost lineage for burnetiids (and particularly proburnetiines) back into the early Guadalupian.

In October 1993, a fragment of pachyostosed therapsid skull roof (BP/1/5485) was found by James Kitching on the farm Stellenboschvlei in the Western Cape Province of South Africa, along with several other incomplete fossils (Fig. 2; see Table 1). The assemblage of fossils at this locality suggested the presence of the *Tapinocephalus* AZ (Rubidge pers. comm.) but was otherwise unremarkable. Rubidge & van den Heever (1997) referred BP/1/5485 to the enigmatic, pachyostotic *Tapinocephalus* AZ therapsid taxon *Styracocephalus platyrhynchus* Haughton, 1929, which, like burnetiids, exhibits horn-like projections of the skull roof. This similarity has led to historical uncertainty over the affinities of *Styracocephalus*.

In describing *Styracocephalus*, Haughton (1929) noted

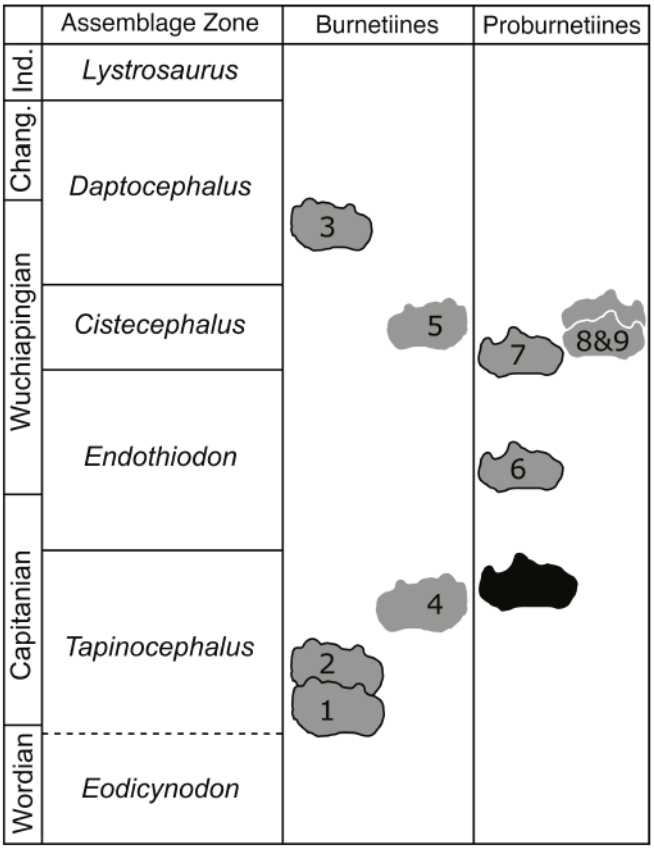

Figure 1. Vertebrate biozones of the Beaufort Group in the main Karoo Basin showing burnetiid occurrences. Black fill = *Nierkoppia brucei* gen. et sp. nov.; black outline = occurrences in the main Karoo Basin. 1, *Pachydectes*; 2, *Bullacephalus*; 3, *Burnetia*; 4, *Mobaceras*; 5, *Niuksenitia*; 6, *Leucocephalus*; 7, *Paraburnetia*; 8 & 9, *Lende* and *Proburnetia*. Chang., Changhsingian; Ind., Induan.

similarities with dinocephalians, gorgonopsians, and therocephalians, as well as *Burnetia* (at the time a therapsid *incertae sedis*). Subsequent studies attempting to classify *Styracocephalus* generally were split between dinocephalian (e.g. Boonstra 1934; Kitching 1977; King 1988) and burnetiid affinities for the taxon (in the latter cases, usually included within an expansive Gorgonopsia, e.g. Broom 1932; Watson & Romer 1956; Tatarinov 1974). Boonstra's (1934) arguments for a dinocephalian identification were based primarily on the morphology of the quadrate-quadratojugal complex, together with details of the palate, basicranium, and the extensive pachyostosis of the skull roof. In a later paper, Boonstra (1963) also noted the presence of 'heels' on the incisors of *Styracocephalus*, which has been considered a synapomorphy of Dinocephalia (Hopson & Barghusen 1986). Rubidge & van den Heever (1997) accepted the identification of *Styracocephalus platyrhynchus* as a dinocephalian based on the combination of cranial pachyostosis and heeled incisors.

BP/1/5485 was among the smallest of the 10 specimens referred to *Styracocephalus platyrhynchus* by Rubidge & van den Heever (1997), along with the similarly-sized SAM-PK-12187. They did not address the possibility that these specimens might instead represent burnetiids, which is understandable given that the group was so poorly known at the time. Despite the lengthy history of taxonomic confusion between *Styracocephalus* and *Burnetia*, by the time of Rubidge & van den Heever's (1997) work,

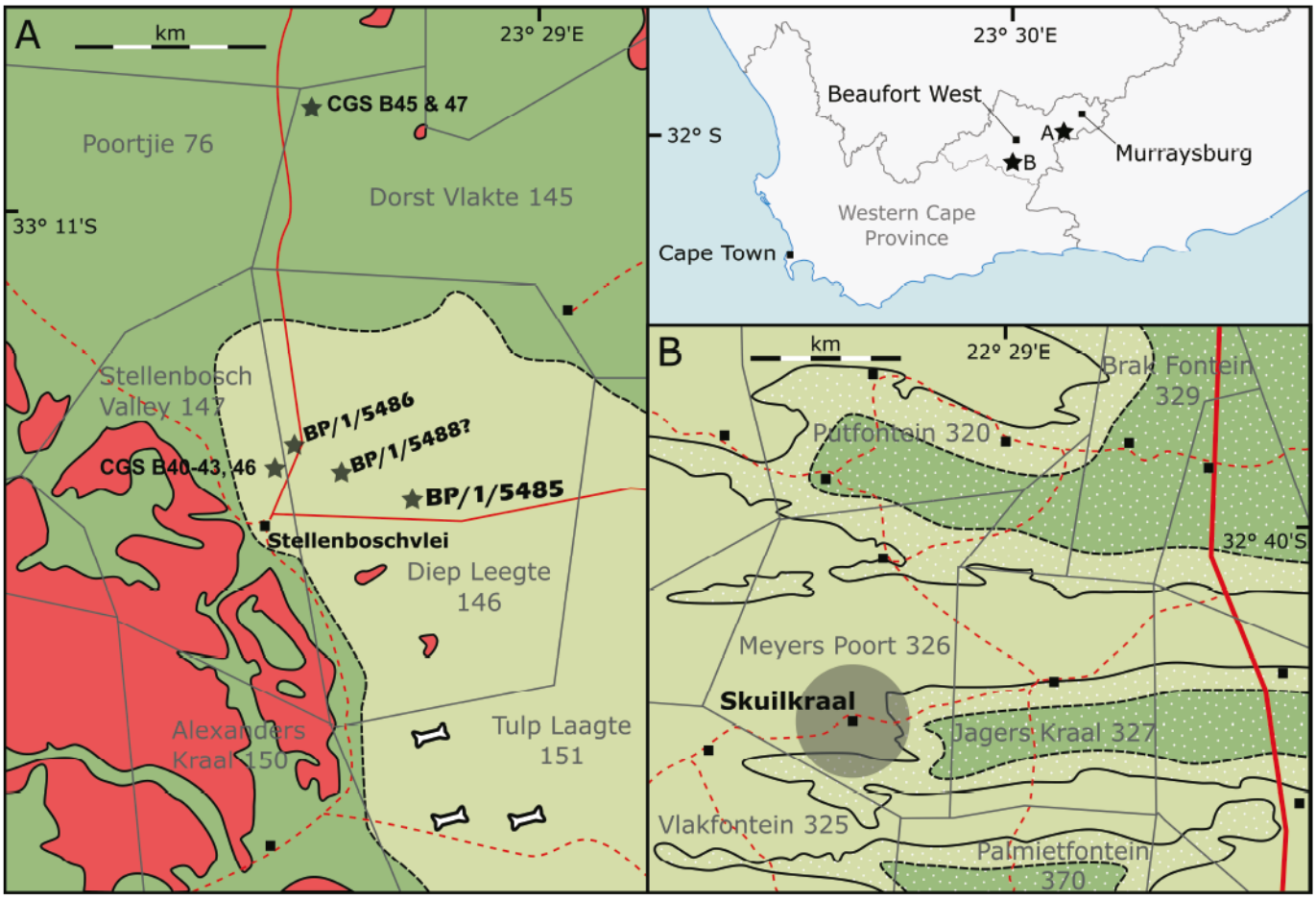

Figure 2. Map of the localities in Western Cape Province of South Africa. Legend for local area maps in part A, Stellenboschvlei, and part B, Skuilkraal: light green = Abrahamskraal Formation; dark green = Teekloof Formation; pink = dolerite; red lines = roads and tracks; grey lines = farm boundaries; black squares = farmsteads; dark stars = fossil localities; dark circle = possible collection area of SAM-PK-12187; bone symbols = large bone (uncollected) indicated on James Kitching's field map. In part B only, the Teekloof Formation is indicated by white stippling.

these genera were considered widely separated both phylogenetically and stratigraphically. As the only known Karoo burnetiid at that time was *Burnetia mirabilis* itself, represented solely by the type skull (NHMUK PV R 5697) from the Lopingian *Daptocephalus* AZ, pachyostosed crania from the *Tapinocephalus* AZ (and the Guadalupian of the Karoo generally) were thought to pertain exclusively to dinocephalians.

However, ongoing discoveries over the last 20 years have revealed the much greater diversity and stratigraphic range of burnetiamorphs in the Karoo Basin. The referral of pachyostosed Guadalupian cranial materials to Dinocephalia is thus no longer a safe assumption and, given the aforementioned problematic ghost lineages in Burnetiamorpha, fragmentary pachyostotic elements from within this Guadalupian gap are deserving of additional scrutiny. In their recent review of *Styracocephalus*, Fraser-King *et al.* (2019) mentioned that both BP/1/5485 (erroneously cited as BP/1/5428) and SAM-PK-12187 showed similarity to burnetiids and excluded them from the *S. platyrhynchus* hypodigm. These authors accepted the identification of the other material referred to *Styracocephalus* by Rubidge & van den Heever (1997), with the exception of two specimens that went unre-

Table 1. Specimens found at Stellenboschvlei and adjacent farms and curated at the Evolutionary Studies Institute and Council for Geoscience.

Specimen number	Repository	Idenfication	Locality
B40	CGS	Dicynodontia cf. *Diictodon*	Stellenboschvlei (Stellenbosch Valley 147)
B41	CGS	*Diictodon feliceps*	Stellenboschvlei (Stellenbosch Valley 147)
B42	CGS	Dicynodontia indet.	Stellenboschvlei (Stellenbosch Valley 147)
B43	CGS	Dinocephalia indet.	Stellenboschvlei (Stellenbosch Valley 147)
B46	CGS	*Diictodon feliceps*	Stellenboschvlei (Stellenbosch Valley 147)
B45	CGS	*Diictodon feliceps*	Dorst Vlakte
B47	CGS	*Endothiodon bathystoma*	Dorst Vlakte
BP/1/5486	ESI	*Eriphostoma microdon*	Stellenboschvlei (Diepleegte 146)
BP/1/5487	ESI	Tapinocephalia indet.	Stellenboschvlei (Diepleegte 146)
BP/1/5488	ESI	Dinocephalia?	Stellenboschvlei (Diepleegte 146)
BP/1/5495	ESI	Dinocephalia?	Stellenboschvlei (Diepleegte 146)
BP/1/8499	ESI	Varanopidae cf. *Heleosaurus*	Stellenboschvlei (Diepleegte 146)

marked upon in their paper: the actual BP/1/5428 (which is indeterminate, but probably dinocephalian) and SAM-PK-K8071 (which we do consider to represent *Styracocephalus*). Two specimens in the hypodigm (SAM-PK-9346 and SAM-PK-K364) are only slightly larger than the specimens that form the subject of this paper, but these are not considered here as they do not display a typically burnetiid morphology of either the supraorbital bosses or the median frontal crest.

Here, we redescribe BP/1/5485 and SAM-PK-12187, confirming that they represent burnetiamorphs rather than dinocephalians. We place these specimens in an updated stratigraphic and phylogenetic context, discussing the evidence for the age of the involved localities and the implications for burnetiamorph evolution.

MATERIAL AND METHODS

BP/1/5485 was first recognized as part of a burnetiamorph skull roof in 2016 (independently by the two authors), during examination of mid-Permian fossils at the Evolutionary Studies Institute (ESI) in Johannesburg. It had been collected on the farm Stellenboschvlei (Fig. 2A) as part of palaeontological work by Bruce Rubidge and James Kitching commissioned by the Atomic Energy Corporation. For the most part, the bone surface of this specimen was exposed by natural weathering rather than laboratory preparation.

SAM-PK-12187 consists of an isolated skull roof found in 1959 on the farm Skuilkraal (southern portion of the cadastral farm Meyers Poort 326), south of Beaufort West (Fig. 2B), by Lieuwe Boonstra and Humphrey Zinn from the South African Museum in Cape Town. It has similarly not been subject to laboratory preparation, but the bone is mostly free of matrix.

The specimens described herein were added as new operational taxonomic units to the most recent phylogenetic matrix of burnetiamorphs, that of Kammerer & Sidor (2021) (with the addition of codings for *Isengops* from Sidor *et al.* 2021). The data matrix consists of 24 operational taxonomic units and 27 characters and is provided in Appendix 1. The analysis was run in TNT (Goloboff *et al.* 2008) using all New Technology search parameters, with initial value set at 15 and required to find shortest tree at least 20 times. Two versions of the analysis were run: one including all previously coded burnetiamorph specimens, and a second in which unnamed, fragmentary specimens (BP/1/7098, NHMUK PV R 871a, TM 4305; see Day *et al.* 2016; Kammerer 2016) were excluded. Bootstrap values were based on 1000 replicates of the analyses.

The first analysis recovered 94 most parsimonious trees (MPTs) of length 51 (consistency index [CI] = 0.706, retention index [RI] = 0.877). In the strict consensus (Fig. 3A), the base of Burnetiidae is a large polytomy including BP/1/5485, SAM-PK-12187, BP/1/7098, *Isengops luangwensis*, and all previously recognized proburnetiines (*sensu* Kammerer 2016). Burnetiinae is recovered, but with its contents in a polytomy. The 50% majority rule tree from this analysis shows greater resolution within Burnetiidae, with Proburnetiinae, Burnetiinae, and *Isengops luangwensis* recovered in a polytomy. Within Proburnetiinae, BP/1/7098, *Leucocephalus wewersi*, *Paraburnetia sneeubergensis*, and *Proburnetia viatkensis* form a basal polytomy out-

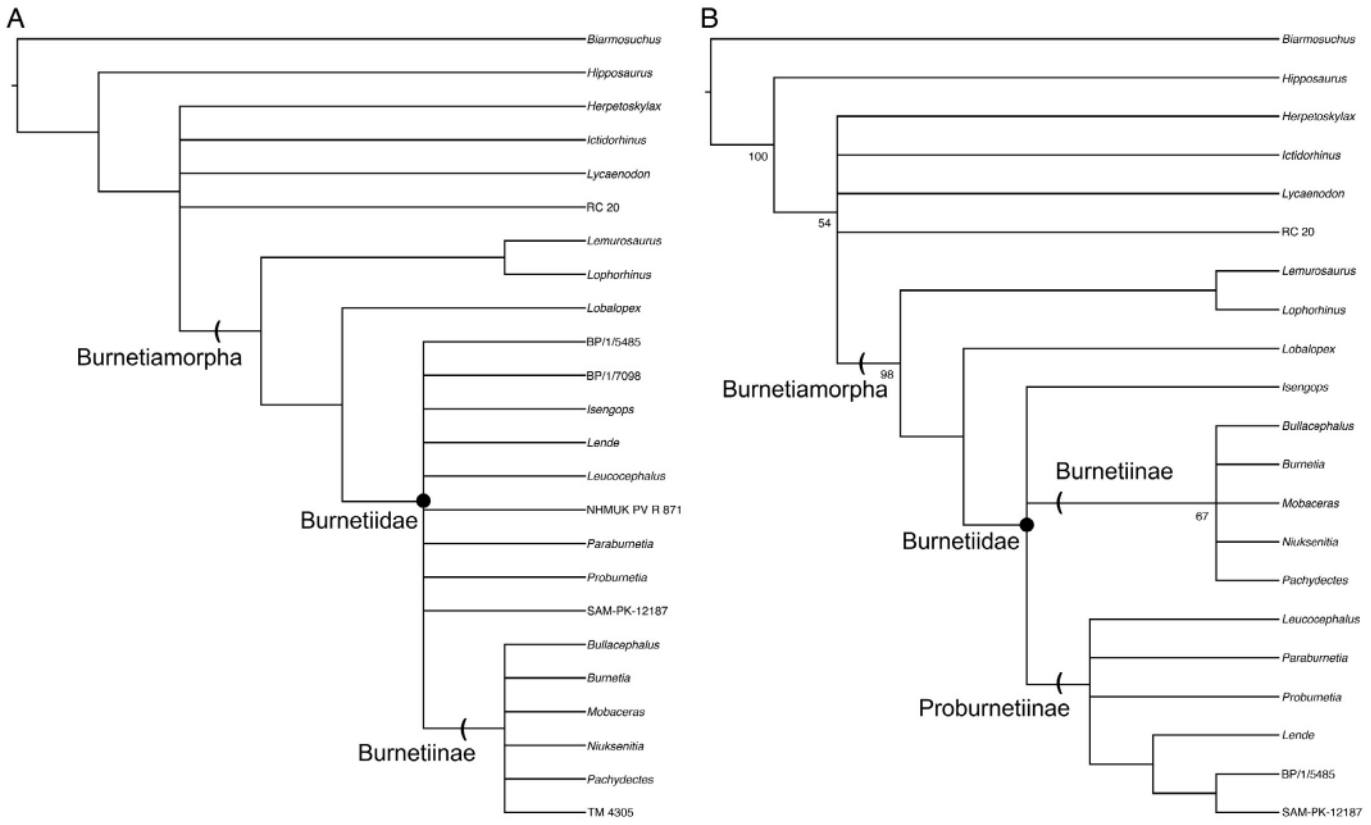

Figure 3. Results of the phylogenetic analysis. **A**, Analysis including all OTUs. **B**, Analysis with unnamed, fragmentary specimens (BP/1/7098, NHMUK PV R 871a, TM 4305) excluded. Numbers below nodes in B represent bootstrap values (1000 replicates).

side of a clade containing BP/1/5485, NHMUK PV R 871a, SAM-PK-12187, and *Lende chiweta*.

The second analysis recovered 15 MPTs of length 50 (CI = 0.720, RI = 0.885) (Fig. 3B). The strict consensus tree is similar to the 50% majority rule tree of the first analysis, with Burnetiidae consisting of a polytomy of Proburnetiinae, Burnetiinae, and *Isengops*, and Proburnetiinae consisting of a basal polytomy of *Leucocephalus*, *Paraburnetia*, *Proburnetia*, and a clade consisting of (*Lende* (BP/1/5485+SAM-PK-12187)). The 50% majority rule tree differs only in adding resolution within Burnetiinae, finding sister-taxon relationships for *Bullacephalus*+*Pachydectes* and *Burnetia*+*Niuksenitia*. Bootstrap values for most recovered clades are low, however. Among burnetiamorph clades, only Burnetiamorpha as a whole (bootstrap value = 98) and Burnetiinae (67) are well-supported (values>50).

STRATIGRAPHIC CONTEXT

In the southwestern Main Karoo Basin, the lower, Permian part of the fluvio-lacustrine Beaufort Group comprises the Abrahamskraal and Teekloof formations. These formations are in turn divided into members, although those of the Abrahamskraal Formation are not clearly differentiable east of Prince Albert (22° E). The localities from which the two specimens described here were collected lie between 22.4° and 23.5° E (Fig. 2). The boundary between these two formations has been dated to ~260 Ma using CA-TIMS zircon U-Pb geochronology and corresponds with a peak in extinctions associated with the Capitanian mass extinction (Day *et al*. 2015; Day & Rubidge 2021). The uppermost Abrahamskraal Formation yields tetrapod fossils of the *Diictodon-Styracocephalus* subzone of the *Tapinocephalus* AZ, which continues a short distance into the lowest member of the Teekloof Formation (the Poortjie Member), where it is succeeded by the *Lycosuchus-Eunotosaurus* subzone of the *Endothiodon* AZ (Day & Rubidge 2020; Day & Smith 2020).

The localities that produced both specimens are biostratigraphically within the upper *Tapinocephalus* AZ, close to the boundary with the overlying *Endothiodon* AZ. SAM-PK-12187 very likely comes from the upper Abrahamskraal Formation, which crops out around the (now ruined) Skuilkraal homestead and along the slopes of the rise to the east (Geological Survey 1979; note that Skuilkraal does not appear by name on this map). The lower Poortjie Member is exposed to the south and east along the higher ground, but is less well exposed and thus less likely to have yielded this fossil. Other fossils from this locality listed in the catalogues of the South African Museum and the Council for Geoscience (Pretoria) include the holotype of the therocephalian *Zinnosaurus paucidens* (=Lycosuchidae *incertae sedis*; Abdala *et al*. 2014), indeterminate therocephalian, gorgonopsian and dicynodont therapsids, a rhinesuchid temnospondyl, and *Eunotosaurus*. Unfortunately, such an assemblage does not permit distinction between the *Diictodon-Styracocephalus* and *Lycosuchus-Eunotosaurus* subzones.

In the case of BP/1/5485, associated fossils provide greater biostratigraphic constraints. Its locality of origin, the farm Stellenboschvlei, is currently mapped as exposing rocks of the Teekloof Formation (Geological Survey 1979) and, due to a paucity of fossils from much of the area between Beaufort West and Aberdeen, had previously been assumed to predominantly expose the *Endothiodon* AZ (formerly the *Pristerognathus* and *Tropidostoma* AZs; Keyser & Smith 1979; Rubidge 1995; van der Walt *et al*. 2010). Rubidge & van den Heever (1997) considered the locality to expose at least some *Tapinocephalus* AZ, but did not make explicit whether this was founded on the identification of BP/1/5485 as a dinocephalian (*Styracocephalus*) or on associated fossils. Although we do not support a dinocephalian identification for BP/1/5485, additional specimens collected in 1993 from Stellenboschvlei (covering cadastral farm plot Stellenbosch Valley 147 and Diepleegte 146 in the Murraysburg district) are referable to that group, indicating the presence of *Tapinocephalus* AZ exposures at the locality (Table 1). Notably, they include a skull fragment identifiable as a tapinocephalian dinocephalian (BP/1/5487; Fig. 4B) and two other pieces of large bone that likely represent dinocephalians (BP/1/5488 and BP/1/5495). A skull of the small gorgonopsian *Eriphostoma microdon* (BP/1/5486; Fig. 4A) was also recovered.

1:50 000 topographic field maps annotated by James Kitching (stored in the Evolutionary Studies Institute map collection) show the localities of the specimens collected at the time, although only a few, including BP/1/5485, are identified by their eventual registration number. The locality was revisited by the lead author in March 2020, confirming that Kitching's 1993 collections all came from a similar horizon comprising 15 m of predominantly mudrocks below a sandstone capping the hill on which BP/1/5485 was found. In addition, this recent fieldwork recovered a large rib likely attributable to a dinocephalian from 1 m below this upper sandstone (Fig. 4D) and, from almost exactly the same spot as BP/1/5485, a small partial skeleton likely to be the varanopid *Heleosaurus scholtzi* (Fig. 4C). These taxa are all consistent with the *Diictodon-Styracocephalus* Subzone of the *Tapinocephalus* Assemblage Zone (Day & Rubidge 2020).

A separate set of 1:50 000 topographic field maps is held at the Council for Geoscience in Pretoria. These show the localities of some material collected by palaeontologists working for the Geological Survey of South Africa in 1978 from just inside the farm boundary of Stellenbosch Valley, west of the dirt road (Fig. 2A). The map also mentions the occurrence there of *Eunotosaurus* and a gorgonopsian, but we could not locate these in the collections of the Council for Geoscience and so they remain unverified. A 'medium-sized humerus' is indicated to have been found on the southern side of Nierkoppie. Nine and a half kilometres to the north, the maps indicate a specimen of *Endothiodon* from a small hill east of the dirt track on the farm Dorst Vlakte (Fig. 2A); this is present in the collections with field number B47 and is a confirmed individual of *Endothiodon bathystoma*.

The precise stratigraphic distance between the localities at Stellenboschvlei and Dorst Vlakte is uncertain, but the strata are relatively horizontal and we estimate that the locality at Dorst Vlakte is approximately 40 m higher in the

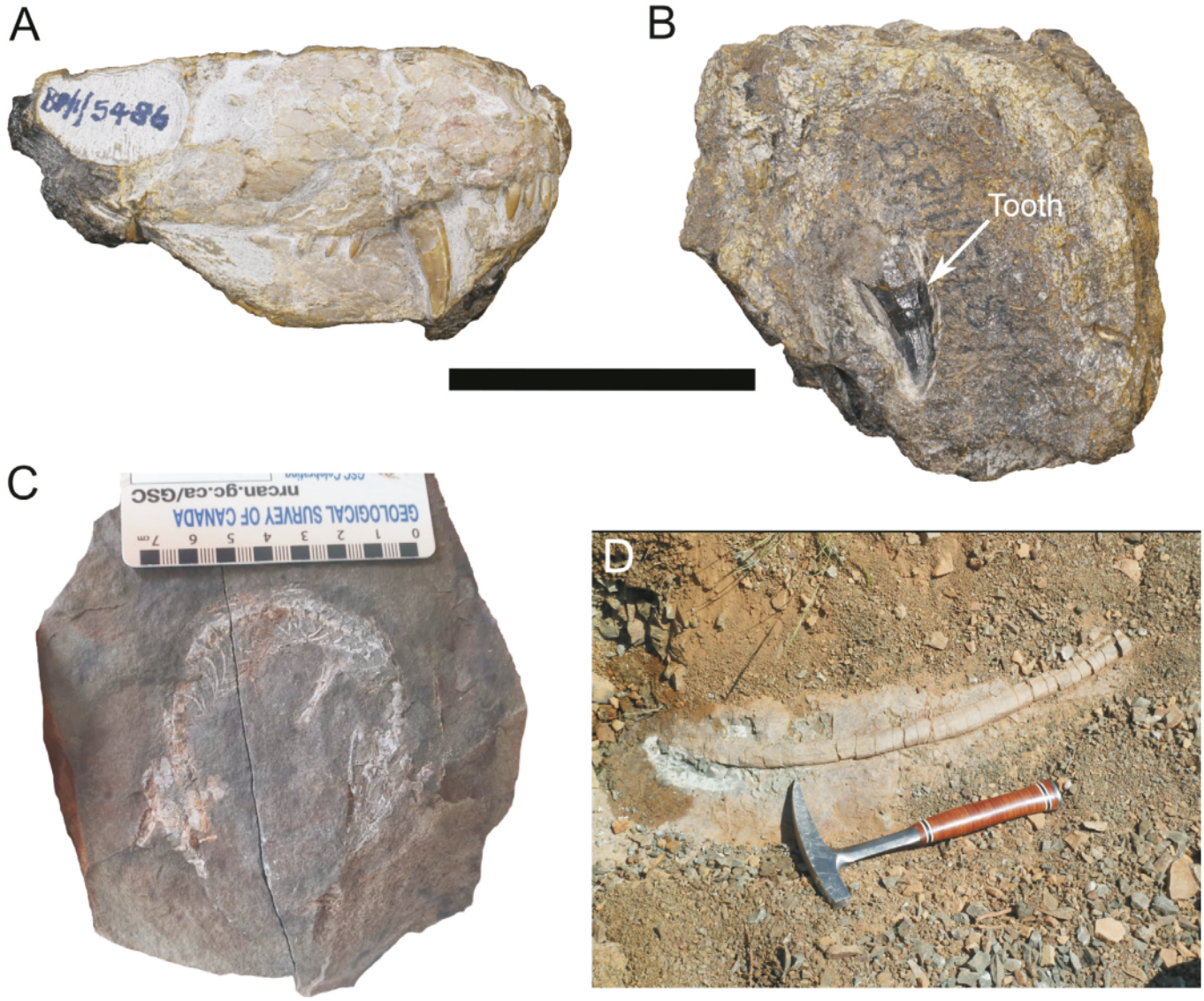

Figure 4. Other specimens from the Stellenboschvlei locality. **A**, BP/1/5486 (*Eriphostoma microdon*); **B**, BP/1/5487 (Tapinocephalia indet.); **C**, BP/1/8499 (*Heleosaurus*?); **D**, Dinocephalian rib *in situ*. Scale bars in A and B = 5 cm.

section than the highest localities at Stellenboschvlei. This proximity indicates that the assemblage from Stellenboschvlei comes from close to the top of the *Tapinocephalus* AZ.

SYSTEMATIC PALAEONTOLOGY

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

Proburnetiinae Kammerer, 2016

Diagnosis. Burnetiid therapsids characterized by the presence of a massive, anteroposteriorly elongate interorbital boss and a single, usually triangular supraorbital boss.

Nierkoppia **gen. nov.**

LSID. urn:lsid:zoobank.org:act:2EE597DA-598E-4373-B8C7-1D5C4C128E6F

Type species. *Nierkoppia brucei* sp. nov.

Etymology. Named for the small hill on which the specimen was found, known as Nierkoppie (meaning 'Kidney Hill'). This can also be taken as a reference to the autapomorphic, reniform shape of the supraorbital bosses in this taxon.

Diagnosis. As for type and only species.

Nierkoppia brucei **sp. nov.**

Figures 5–7

LSID. urn:lsid:zoobank.org:act:9A8CBF11-DDB8-48C6-8882-42EF2B4980EF

Holotype. BP/1/5485, a relatively well-preserved fragment of skull roof, preserving the interorbital and intertemporal regions and dorso-medial portion of the occiput.

Type locality. Southern side of 'Nierkoppie' on the farm Stellenboschvlei (cadastral farm Diepleegte 146), Murraysburg area, Central Karoo District Municipality, Western Cape Province, South Africa (32°14′24.4″S 23°27′03.2″E).

Type horizon. Uppermost Abrahamskraal Formation or (possibly) lowermost Poortjie Member of the overlying

Teekloof Formation, Beaufort Group. Late Capitanian, Guadalupian, Permian. Upper *Diictodon-Styracocephalus* Subzone of the *Tapinocephalus* AZ (Day & Rubidge 2020).

Etymology. Species named to honour Bruce Rubidge in recognition of his manifold contributions to the palaeontology of the Karoo Basin, particularly concerning Burnetiamorpha and the fauna of the *Tapinocephalus* AZ.

Diagnosis. A burnetiid therapsid distinguished by the following autapomorphies: supraorbital boss with triangular apex (as in other proburnetiines) but 'folded over' the dorsal margin of the orbit, giving this structure a roughly 'ear' or 'kidney'-shaped appearance; median frontal boss very well developed and taller than the supraorbital bosses, reaching its maximum height anterior to them; squamosal horns flattened and posteriorly directed; and massive, rounded nuchal bosses borne on the postparietal and supraoccipital. Differs from *Leucocephalus* in that the frontal crest is much more strongly developed, terminates posteriorly flush with the skull roof medial to the supraorbital bosses, and does not reach the pineal, as well as the presence of a swelling posterior to the pineal foramen.

Description. In dorsal view, BP/1/5485 comprises an approximately pentagonal portion of pachyostosed skull roof that is 114.7 mm long and 109 mm wide. The right supraorbital region is broken and the snout is missing anterior to the approximate position where the contact of the frontals and nasals should occur. In order to estimate the overall skull size we use a ratio calculated from the complete skull of *Proburnetia*: the distance between the dorsal part of the occiput at the midline and the anterior margin of the supraorbital boss relative to the distance between the same point on the occiput and the tip of the snout in *Proburnetia* (72.8 mm/170.8 mm) suggests a ratio of around 0.43. The former distance in BP/1/5485 is 90 mm, so we tentatively estimate its occipital-snout length to be approximately 211 mm (see Table 2 for all measurements).

Sutures are not readily visible on the external surface of the bone, which has a rugose texture, so bone identities have been inferred largely by comparison with other taxa. The skull is distinguished by large, flange-like supraorbital bosses that project laterally above the orbits and the presence of a massive frontal crest (Fig. 5). In lateral view, the supraorbital boss has a sub-triangular appearance, whereby the two dorsal surfaces meet at an apex over the anterior of the orbit (Figs 5C, 7B). The posterior of these surfaces lies in the same plane as the posterior skull roof. Anterior to the apex of this boss, the skull roof flexes ventrally so the apex of this boss is dorsally offset from the medial skull roof. The boss projects up to 25 mm laterally over the orbit and a ridge runs posteromedially from the apex to meet the lateral side of the frontal crest (Figs 5A, 6A). The lateral edge of the posterior part of the boss is folded ventrally, giving it more of a zig-zag profile in lateral view. The lateral margin of the supraorbital boss is slightly 'pinched' dorsally at its anterior end (visible on both sides), in a very similar fashion to *Lende* and *Leucocephalus*. Although they cannot be discerned, it is likely that the frontals extend laterally to form the anterior part of the supraorbital boss, while the postfrontal forms the majority of the posterior portion.

The frontal crest is situated along the midline on the anterior part of the frontal region (Figs 5A, 6A). It is exceptionally tall and thick (18 mm wide and 21 mm tall at its broken anterior end) and curves posteroventrally, widening as it goes, to terminate at the level of the posterior orbit; it does not extend as a low ridge towards the pineal foramen and the skull roof is in fact approximately flat for at least 20 mm anterior to the latter. It has nearly vertical sides anteriorly, with a rounded dorsal surface. The height of the crest is both greater than the apex of the supraorbital bosses (Fig. 5C) and increases anterior to them, unlike in any other known burnetiid.

The degree of cranial pachyostosis in this specimen is high: the skull roof is 25 mm thick medial to the posterior shelf of the supraorbital boss and lateral to the pineal opening, which is remarkably thick even for a burnetiid (*cf.* 13 mm in *Paraburnetia* and 13–15 mm in *Burnetia*). The posteriorly-directed supratemporal horns are incomplete, with the left broken at base and the right preserving only a basal portion (Fig. 5A,D). However, what is preserved indicates that these horns had an unusual morphology among burnetiids, being highly dorsoventrally flattened.

Despite being mostly obscured by weathering, there is some evidence on the broken posterior surface of the horns for differentiation in bone architecture. There appears to be a slight concentration of linear (i.e. dorsoventrally orientated) bone fibres around the dorsomedial margin of the temporal cavity, separated from the more chaotic cancellous bone structure in the rest of the horn by a thin portion of more compact, avascular bone. The former two are similar to the Zone C of Kulik & Sidor (2019), whereas the dividing region may correspond to their Zone B. Physical or virtual sectioning would be

Table 2. Measurements for BP/1/5485, holotype of *Nierkoppia brucei* gen. et sp. nov. Abbreviations follow those used by Sidor (2023) where appropriate. **InterO**: interorbital width, taken transversely across the midpoint of the orbital fossa in ventral view. *This is not possible in BP/1/5485 due to the broken left supraorbital boss; instead, a range was estimated from a) doubling the transverse distance between the midline and the lateral margin of the left boss (which is 59.5 mm) and b) extrapolating the position of the broken margin of the right boss. **InterT**: intertemporal width, measured dorsally. **MFE**: thickness of the median frontal excrescence, taken dorsoventrally from the midline trough on the ventral skull roof to dorsal margin of the boss. In BP/1/5485, this ventral trough is mostly obscured by the ossifications of the forebrain but this measurement was captured anterior to the mesethmoid where the median frontal excrescence is in any case thickest. **OccOrb**: length from occipital to anterior margin of supraorbital boss. **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. **SupOrbL**: anterodorsal supraorbital boss length, measured dorsally.

Specimen	PinL	PinW	InterO	SupOrb	MFE	InterT	SupOrbL	OccOrb
BP/1/5485	6.6	7	110.4–119*	24	38.8	87.5	68	90
SAM-PK-12187	7.9	6	101.7	36.4	20.1	–	57.6	86.9

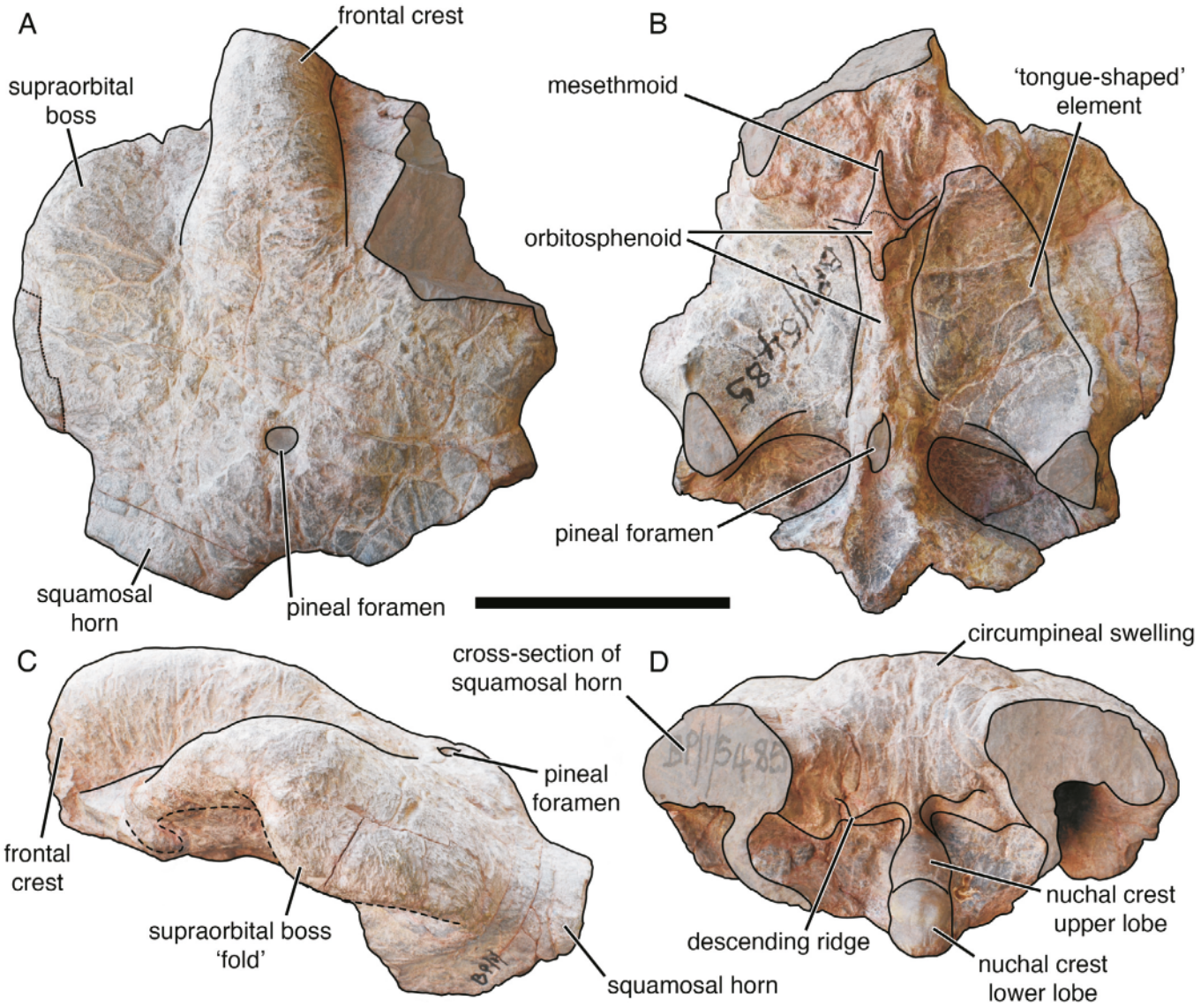

Figure 5. BP/1/5485, holotype of *Nierkoppia brucei* gen. et sp. nov., with line drawings overlain to highlight important morphological features. **A**, Dorsal view (anterior up); **B**, ventral view (anterior up); **C**, left lateral view; **D**, occipital view. Scale bar = 5 cm.

required to confirm correspondence to the Kulik & Sidor (2019) model.

The pineal foramen is situated on the anterior slope of a low but distinct swelling (Figs 5A,D, 6A), and the foramen itself is flush with the surface of the surrounding bone, as in *Leucocephalus* and NHMUK PV R 871a. Posterior to the peak of the swelling, the parietals curve ventrally until their surface is vertically orientated. The occiput is anteriorly offset from this edge so that the skull roof forms a shelf above it. One median and two lateral nuchal crests (the 'descending ridges' of Kammerer [2016]) descend ventrally onto the postparietal (Figs 5D, 7A).

The preserved portion of the occiput consists of the postparietal, much of the supraoccipital, and likely parts of the tabulars, laterally. The contact of the postparietal with the parietal and the supraoccipital can be approximated, but the borders of the occipital bones are not clearly defined. The deep indent of the postparietal suggests that some deformation of the dorsal occiput may have occurred, but this is not certain. The medial spur of the parietal narrows into a vertical lamina that descends onto the ventral portion of the postparietal, but this expands massively as it continues onto the supraoccipital to form a thick, rounded median ridge (Fig. 7A). The thickness of the median nuchal crest is quite remarkable, because its size has been linked to its function as an insertion point for muscles supporting the head, yet even in large and robust burnetiamorphs such as *Bullacephalus jacksoni* this structure remains a thin lamina on the supraoccipital (Kammerer 2016: text-fig. 7; Sidor 2023: fig. 5C). Also unusually, the expanded ventral part of the ridge is not a single structure but is composed of two massive swellings (Fig. 5D), and a third, much smaller swelling is present dorsally, at the base of the median nuchal spur of the parietal.

Posterior to the orbits, the postorbitals descend from the skull table to separate the orbit from the temporal fenestra. The contacts of this bone with its neighbours are difficult to discern, but its contact with the postfrontal appears to run anteroventrally from the posterior end of the supraorbital boss (Fig. 5C). No boss is present on the postorbital above the postorbital bar.

On the ventral surface of BP/1/5485, several elements of the braincase are preserved (Figs 5B, 6B). Anteriorly,

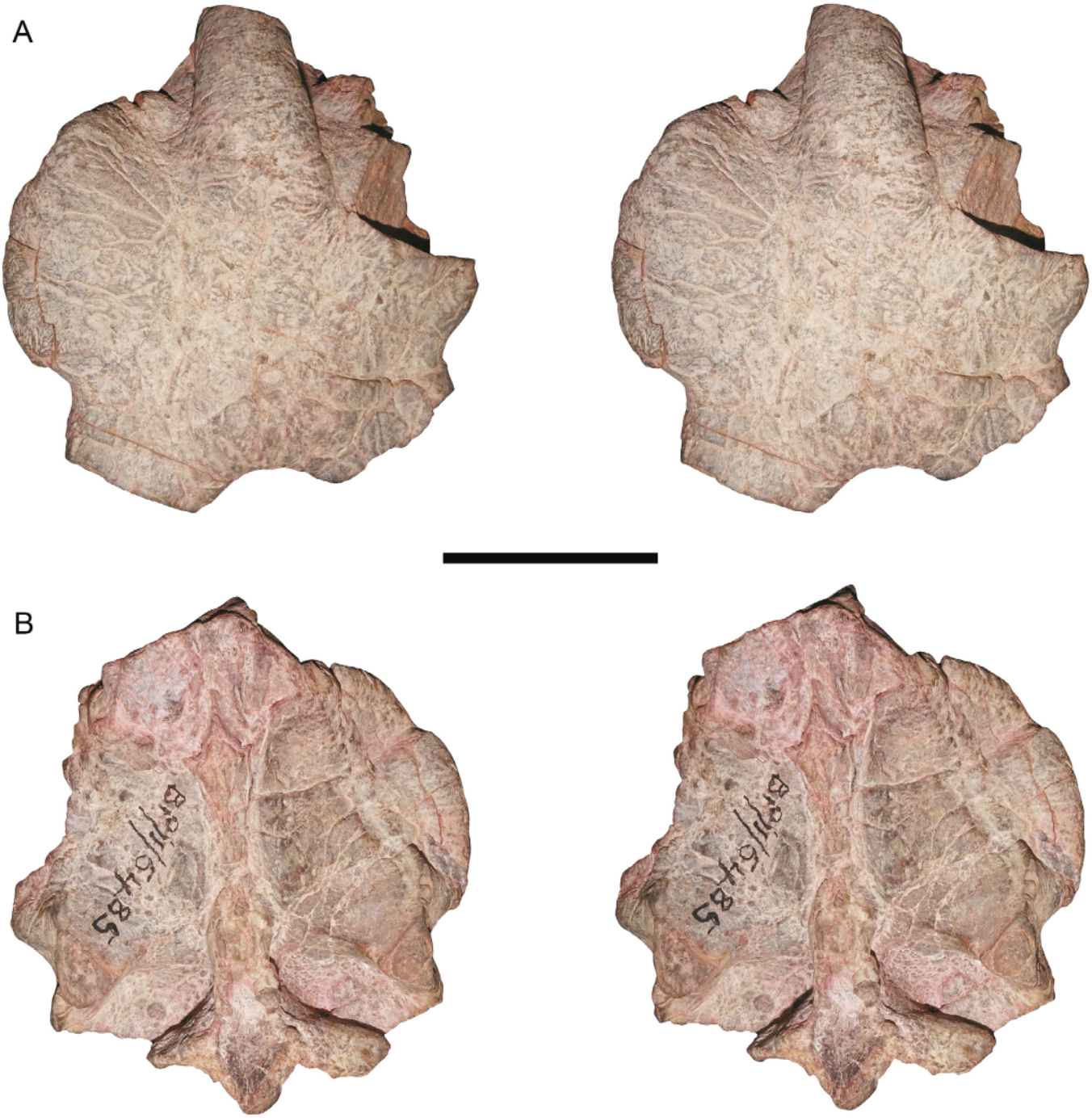

Figure 6. Stereophotographs of BP/1/5485, holotype of *Nierkoppia brucei* gen. et sp. nov. **A**, Dorsal view (anterior up); **B**, ventral view (anterior up). Scale bar = 5 cm.

the osseous casing of the forebrain is present, which comprises: 1) a sheet-like bone enclosing an anteroposteriorly orientated canal against the skull roof that broadens slightly anteriorly, and which bears a ventral midline lamina that is broken; and 2) a median, anteriorly-facing, wedge-shaped bone that mostly plugs the anterior opening of the canal except for a small foramen on each side. The posterior element occurs in other burnetiamorphs, where it has been identified as the sphenethmoid or sphenethmoidal complex (Sidor & Smith 2007; Benoit *et al*. 2017) or individually as its presumed major component, the orbitosphenoid (Day *et al*. 2016, 2018; Duhamel *et al*. 2021). We interpret the anterior element to be the mesethmoid, which was also noted in *Leucocephalus* by Day *et al*. (2018: fig. S1-E). The combined structure has been referred to as the anterior plate in dicynodonts, where the involved bones are fused (Sullivan & Reisz 2005; Castanhinha *et al*. 2013). The sphenethmoidal complex affixes to ventral ridges on the ventral surface of the skull roof to form a fully ossified anterior braincase in adult burnetiamorphs (Benoit *et al*. 2017), although it appears to have been cartilaginous in juveniles (Duhamel *et al*. 2021).

In a posterior direction, the canal formed by the orbitosphenoid narrows then widens just anteriorly to a ridge that runs medially from the postorbital bar along the ventral surface of the skull roof. The hindbrain cavity is exposed due to weathering but appears to have had an

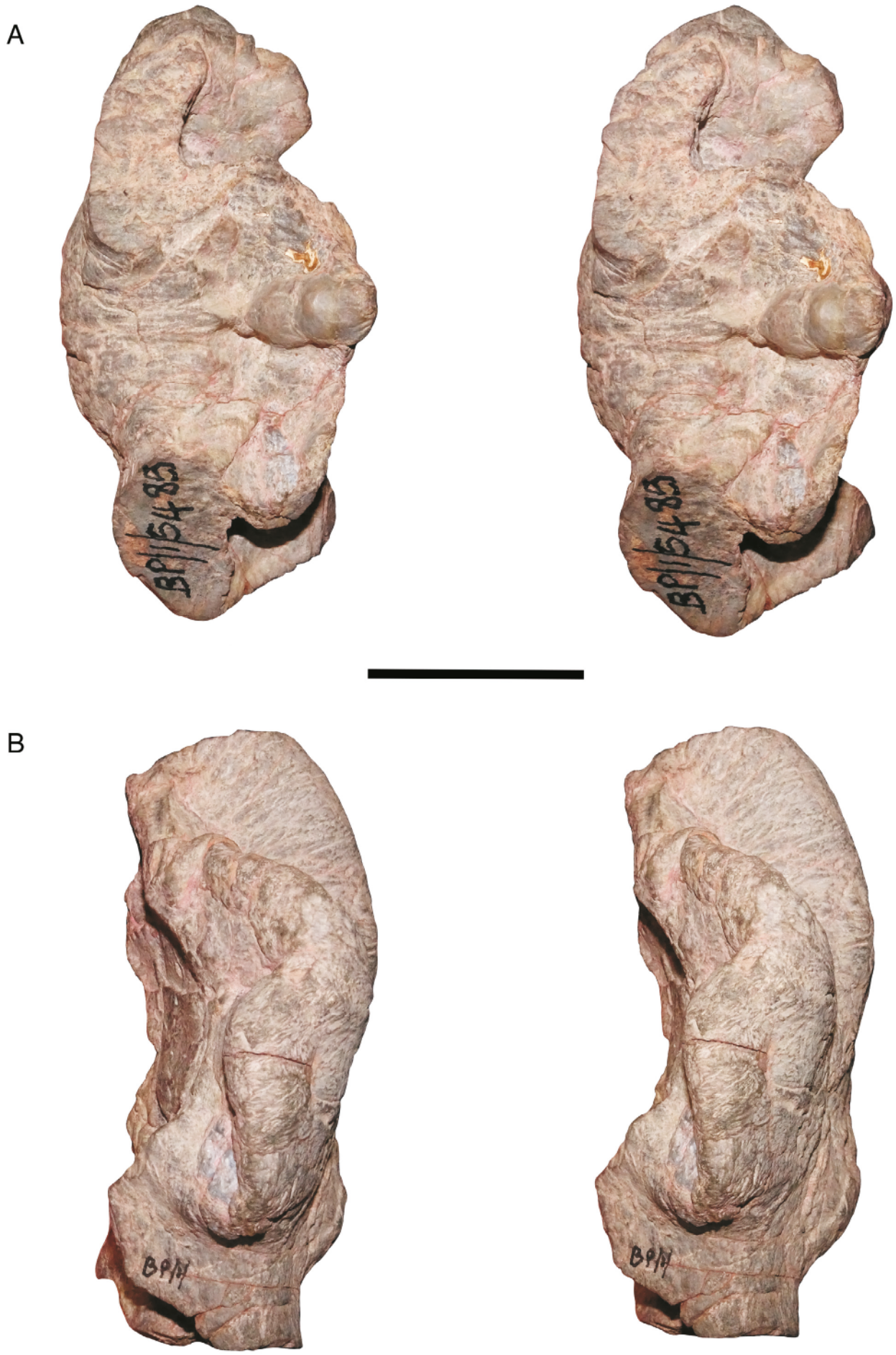

Figure 7. Stereophotographs of BP/1/5485, holotype of *Nierkoppia brucei* gen. et sp. nov. **A**, Occipital view; **B**, left lateral view. Scale bar = 5 cm.

intact osseous casing, though the contacts of individual bones are not visible. Anteriorly, the walls of the hindbrain were postulated to be formed by the epipterygoid by Benoit *et al.* (2017), but an epipterygoid contribution was later considered doubtful by Sidor (2023). Two small ventral ridges are present at the anterolateral edges of the hindbrain cavity in BP/1/5485 but their significance is uncertain. Posteriorly, the dorsal part of the prootic likely forms the lateral wall of the braincase, while the supraoccipital forms its posterodorsal surface. Anteriorly, the hindbrain cavity is filled with matrix, but the intact part of the wall suggests a slight ventral depression that may be the hypophyseal fossa for the pituitary.

Lateral to the anterior plate, the ventral side of the skull roof is covered by what appears to be a 'tongue'-shaped layer of bone forming the roof of the orbital cavity (Fig. 5B). The medial edge of the tongue terminates lateral to the mesethmoid at the anterior margin of the orbit, but posteriorly it appears to sweep back along the medial surface of the postorbital bar. The lateral margin of this bone is demarcated by a rugose fissure, clearly visible on the left side, that suggests it is distinct from the bones of the skull roof contributing to the supraorbital boss. The same structure was noticed in other burnetiamorph specimens by Day *et al.* (2016, 2018), who interpreted it as an extension of the postorbital. However, on the right side it appears that the posterior margin of this ossification runs along the transverse ridge separating the orbital fossa from the temporal cavity, thus limiting it to the former. Thus, it is possible that it could represent a separate ossification unique to burnetiamorphs.

Alternatively, it may be the result of developmental zonation in the bones of the skull roof. Kulik & Sidor (2019) observed two layers of compact or low porosity bone (their zones A and B) in the ventral skull roof of a burnetiamorph from Zambia (NHCC LB373). These layers, primarily zone A, were shown to form the dorsomedial surface of the orbital cavity in NHCC LB373, whereas their more vascular Zone C forms the dorsolateral part. With this in mind, the tongue of bone observed in BP/1/5485 could have formed through endocranial growth of the corresponding skull bones dorsal to it, with the illusion of a distinct element arising from the absence of visible sutures between the component bones combined with the external expression of their osteological 'zones'. External distinction on the bone surface of the orbit is also visible (albeit in a different configuration) in the skull figured by Kulik & Sidor (2019: fig. 1B), which shows a transverse difference in bone surface texture between the lateral and medial halves of the orbital roof.

Kulik & Sidor (2019) interpreted their zone B to represent the first deposition of bone in the embryonic burnetiamorph from which surrounding layer expanded throughout the growth of the animal. Because they determined their specimens to be immature on the basis of overall histology, it may be that the appearance of a distinct element becomes greater as the surrounding bone continues to grow out from zone B in mature individuals. Indeed, a second rugose fissure running just within the dorsal surface of the left orbital cavity in BP/1/5485 (Figs 5B, 6B) may represent the boundary between the vascular zone C and the more compact zone D that Kulik & Sidor (2019) showed to extend across the dorsal skull roof.

Remarks. When this specimen was collected in 1993, few burnetiids were known. Its occurrence with dinocephalian remains and the presence of supraorbital bosses combined with a frontal ridge suggested an affinity with the dinocephalian genus *Styracocephalus*, to which it was ultimately referred (Rubidge & van den Heever 1997). However, the many new discoveries of burnetiid crania and additional material of *Styracocephalus* (see Fraser-King *et al.* 2019) have now permitted a more refined identification of this specimen.

BP/1/5485 differs from the holotype and other referred specimens of *Styracocephalus platyrhynchus* in several key features. Firstly, the supraorbital bosses and skull roof are less pachyostosed, manifesting more as a dorso-lateral projection of the orbital margin than the thick, rounded swelling of the *S. platyrhynchus* holotype (SAM-PK-8936) or the referred specimens BP/1/7141 and BP/1/8009. The frontal crest is markedly more pronounced than in *Styracocephalus* and is different in shape: instead of a low ridge of even width that appears to be pinched by the swollen supraorbital bosses at its posterior end, as in SAM-PK-8936, the frontal crest of BP/1/5485 is a tall, thickened ridge that lowers in height and widens posteriorly, and is separated from the supraorbital bosses by a distinct channel. The median frontal crest also shows no evidence of a sagittal suture, which is typical of burnetiids but unlike *Styracocephalus*, where even heavily pachyostosed specimens like BP/1/7141 display a thin midline trough at the pairing of the frontal and the nasals (see Fraser-King *et al.* 2019: fig. 1E-F).

BP/1/5485 is smaller than most other specimens of *Styracocephalus*, but we discount the possibility of its unique features being attributable to immaturity. The frontal crest in this specimen is relatively much taller than in the larger specimens, which would not be expected in vertebrate ontogeny (whereby structures assumed to have sexual or combat roles become more pronounced throughout growth). Ontogenetic variation would also not explain the presence in this specimen of several characters unique to burnetiamorphs among therapsids, including descending ridges on the occiput lateral to the median nuchal crest (Kammerer 2016) and lateral zonation of the bone surface (or a separate ossification) on the dorsal surface of the orbital cavity (Day *et al.* 2016, 2018; Kulik & Sidor 2019). These structures have never been observed in specimens generally accepted as juvenile dinocephalians (see e.g. Kammerer 2011).

Other than in the autapomorphic 'folding' of the tips, the supraorbital bosses of BP/1/5485 are essentially similar to those of *Leucocephalus* and *Lende*, with the thickened anterior rim of the orbit projecting laterally, being pinched along the anterior edge, and with the postfrontal slightly folded ventrally. The folding of the postfrontal produces the same notch at its posterior contact with the postorbital along the orbital margin (Day *et al.* 2018). It is remarkable, however, in possessing a far more prominent frontal crest

and in its size, being the largest proburnetiine yet known (as inferred by interorbital dimensions relative to other members of this clade).

Despite being merely an isolated skull roof, the suite of highly distinctive features of this specimen permits confident diagnosis as a new species (and hopefully, referral of more complete materials in the future).

Proburnetiinae indet.

Material. SAM-PK-12187, a partial skull roof including the interorbital region. Several fragmentary pieces of snout bearing weathered tooth roots and unerupted crowns are also attached to this number, as are some unidentifiable pieces of possibly postcranial bone. However, these are not described in detail here, as their attribution to the same individual as the skull roof is highly doubtful (see below).

Locality. Skuilkraal (cadastral farm plot Meyers Poort 326), Beaufort West, Central Karoo, Western Cape Province, South Africa. Old farmhouse is present only on older maps (e.g. Geological Survey 1952), situated at 32°43′21.7″S 22°25′40.2″E.

Stratigraphy. Probably uppermost Abrahamskraal Formation, Beaufort Group. Late Capitanian, Guadalupian, Permian. Upper *Diictodon-Styracocephalus* Subzone of the *Tapinocephalus* AZ (Day & Rubidge 2020).

Description. The skull roof is weathered around the edges and had clearly been exposed for a time after exhumation. It is within the size range of known burnetiids, including BP/1/5485, but the bones of the skull roof are even thicker than in that specimen. The supraorbital bosses reach an apex above the mid-orbit and are heavily pachyostosed, particularly on the posterior slope (Fig. 8B). Anteriorly, each boss thins rapidly and has an abrupt, vertical termination against the anterior skull roof. A slight lateral shelf projects from the postfrontal portion of the supraorbital boss and shows some anteroventral folding. The frontal crest is low and reduces in height to become a low mound at the level of the anterior margin of the orbits. Posterior to this, it increases in width and is separated from the supraorbital boss by a shallow channel (Fig. 8A). The pineal foramen is situated in a very shallow and wide depression. The posterior edge of the skull roof is not preserved, so the presence and form of squamosal horns cannot be determined. Likewise, the zygomatic arch and occiput are not preserved, and the ventral side of the skull table is heavily weathered and no morphology can be discerned.

Remarks. The anteroventral folding of the postfrontal on the posterior slope of the supraorbital boss is a burnetiid character, though this is obscured somewhat by the high degree of pachyostosis; the thickness of the boss is beyond anything yet observed in any other burnetiamorph, except perhaps the largest specimen (NHCC LB592) referred to *Bondoceras bulborhynchus* by Sidor (2023), which is most similar to SAM-PK-12187 among known burnetiamorph material. The thickness of the posterior slope of the boss and the abrupt anterior termination of the boss resemble the condition in NHMUK PV R 871a (though the anteriormost portion of the latter is damaged) but the overall shape of the skull differs between these specimens; SAM-PK-12187 also lacks a pineal boss but displays greater thickening of the skull roof, to the same level as the apex of the supraorbital bosses.

The morphology of the frontal crest is more burnetiid than dinocephalian, in that it increases in width and decreases in height posteriorly and extends between the supraorbital bosses onto the posterior skull roof. In general, the boss morphology accords with that of proburnetiines (heavily pachyostosed median crest that reduces in height posteriorly towards the pineal foramen, situated in a diffuse, heavily pachyostosed region and with only the posterior edge of the pineal boss discernible). As in BP/1/5485, there is no evidence of a midline suture on the midline frontal crest as would be expected for *Styracocephalus*.

The associated fragments of snout possess large teeth with characteristically tapinocephalian crown morphology: mesiodistally elongated crowns with a 'talon' bearing a scooped posterior surface curving into a wide

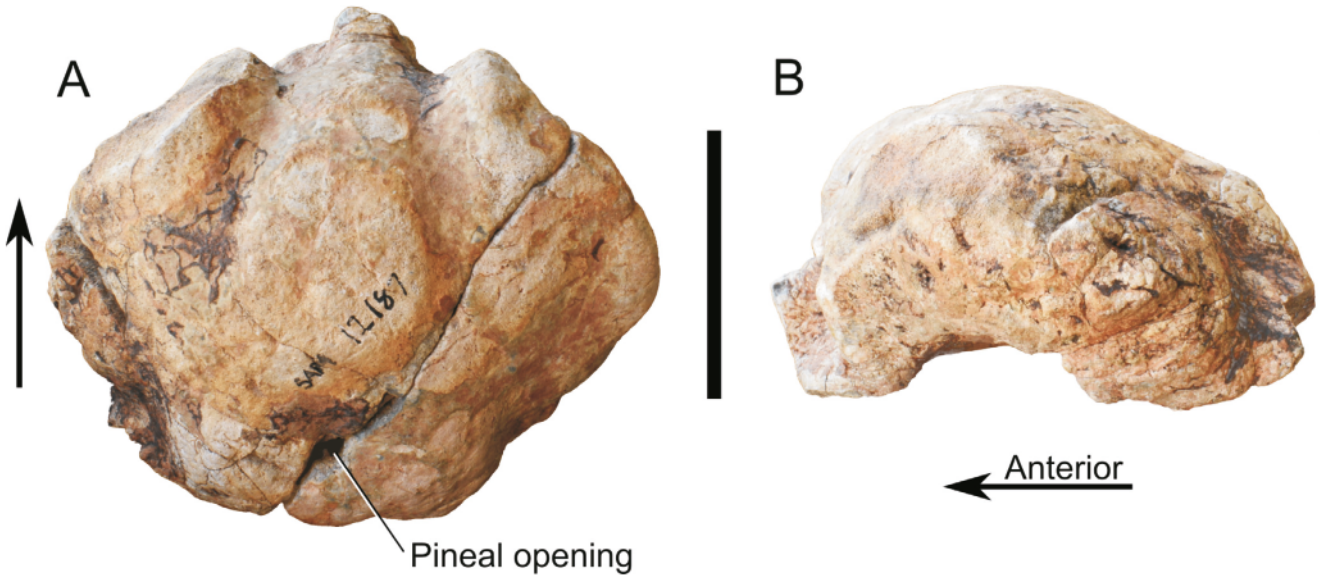

Figure 8. Photographs of SAM-PK-12187, Proburnetiinae indet. **A**, Dorsal view (anterior up); **B**, left lateral view. Scale bar = 5 cm.

'heel' at the base. However, although these fragments have the same catalogue number as the skull roof described above, they are clearly far too large to be part of the same individual.

DISCUSSION

The results of the phylogenetic analysis align with those of recent studies (Kammerer & Sidor 2021; Sidor *et al.* 2021) using the same underlying data matrix, supporting the division of Burnetiidae into two subclades, Burnetiinae and Proburnetiinae. Both BP/1/5485 (*Nierkoppia brucei*) and SAM-PK-12187 are recovered as proburnetiines, and as sister-taxa to one another (Fig. 3B). Together with the Malawian taxon *Lende chiweta* they form the only resolved subclade within Proburnetiinae (in the second analysis, with other fragmentary, unnamed specimens excluded). Inclusion of BP/1/5485 and SAM-PK-12187 in Proburnetiinae is supported by Character 12 (state 1, posterior margin of anterior supraorbital boss with curved lateral ridge, giving folded appearance to boss in lateral view; present in all known proburnetiines other than *Proburnetia*) and Character 19 (state 1, contact between the skull roof and occipital plate weakly angled, skull roof slopes posteroventrally to join occiput; present in all known proburnetiines). An additional character supporting Proburnetiinae, Character 6 (state 1, median nasal excrescence forms pachyostosed ridge of nearly equal transverse width throughout its length), could not be coded for BP/1/5485 or SAM-PK-12187 because of incompleteness, but what is preserved of these specimens is consistent with a proburnetiine-style expanded median frontal crest. Within Proburnetiinae, a close relationship between BP/1/5485, SAM-PK-12187, and *Lende* to the exclusion of other taxa is supported by Character 15 (state 3, pineal boss absent, circumpineal region depressed), and a sister-taxon relationship between BP/1/5485 and SAM-PK-12187 is supported by Character 13 (state 0, posterior supraorbital boss absent; reversal to the pre-burnetiamorph condition).

Nierkoppia and SAM-PK-12187 represent the first Guadalupian records of proburnetiines as supported by cladistic analysis. Sidor (2023) described burnetiid material from the Guadalupian of Zambia that he considered most likely proburnetiine, but they were not included in a phylogenetic analysis because of incompleteness. Combined with the presence of Guadalupian burnetiines (*Bullacephalus*, *Mobaceras*, and *Pachydectes*), these records help to eliminate the middle Permian ghost lineages of the two burnetiid subclades and suggest an early Guadalupian origin for the family as a whole. Biarmosuchian sampling remains low compared to coeval major therapsid clades in the Karoo Basin (see e.g. Smith *et al.* 2012), so gaps in their observed record are expected. However, records from outside the basin (e.g. Kruger *et al.* 2015; Kammerer & Sidor 2021; Sidor *et al.* 2021; Sidor 2023) as well as increased scrutiny of fragmentary material within the basin (e.g. Kammerer 2016; this paper) are beginning to resolve some of these gaps, demonstrating that current phylogenies and the fossil record are not vastly discrepant.

With this said, the addition of extremely fragmentary, mostly skull cap-based burnetiamorph specimens to the group's record is also problematic from a phylogenetic standpoint. Addition of such highly incomplete fossils has proven to be deleterious to phylogenetic resolution in some circumstances (compare results of the first analysis, including several fragmentary specimens, *versus* the more restrictive second analysis). And although recent discoveries outside of the Main Karoo (e.g. Kulik & Sidor 2019; Sidor 2023) have been important in demonstrating that burnetiamorphs were not uniformly rare in their environments, the skull cap-centric nature of these records complicates detailed understanding of their relationships and palaeobiology. Work, such as that presented here, providing alpha taxonomic refinement of the therapsid skull cap record is important from a biostratigraphic standpoint and can help inform tests of phylogenetic congruence at a rough scale. However, additional targeting at the type localities for these specimens is desirable, in the hopes of recovering more complete and potentially character-rich remains of the taxa in question.

CONCLUSIONS

Two therapsid skull roofs that were formerly referred to the dinocephalian *Styracocephalus* are shown to instead represent burnetiids. This fact does not undermine the interpreted exposure of the *Tapinocephalus* AZ at Stellenboschvlei (Murraysburg), which is proven by other associated fossils from this locality. The two specimens we describe here confirm the presence of proburnetiines in the Capitanian and reduce the ghost lineage for this clade. Their relatively large size also supports a shift towards smaller body size within Biarmosuchia across the Capitanian mass extinction.

We would like to thank Schalk Fourie for access to the locality, and to J.C. Loock for providing access to field notes from the 1992 fieldwork during which BP/1/5485 was collected. We wish to thank the Palaeontological Scientific Trust, GENUS, and the Percy Sladen Fund of the Linnean Society for their generous funding, and the field team of 2020. We are grateful to Zaituna Skosan (Iziko SAM) for access to SAM-PK-12187 and for providing measurements, and Sifelani Jirah and Bernard Zipfel (Wits) for access to BP/1/5485. Lastly, we would like to express our gratitude to Bruce Rubidge for his stalwart support of Karoo palaeontology and his contributions to the study of burnetiids.

REPOSITORIES AND INSTITUTIONAL ABBREVIATIONS

BP	Evolutionary Studies Institute (formerly the Bernard Price Institute for Palaeontology), University of the Witwatersrand, Johannesburg, South Africa;
CGS	Council for Geoscience, Pretoria, South Africa;
NHCC	National Heritage Conservation Commission, Lusaka, Zambia;
NHMUK	Natural History Museum, London, United Kingdom;
SAM	Iziko South African Museum, Cape Town, South Africa;
TM	Ditsong National Museum of Natural History (formerly the Transvaal Museum), Pretoria, South Africa.

§ORCID iDs

M.O. Day: orcid.org/0000-0002-7947-8204
C.F. Kammerer: orcid.org/0000-0002-0596-623X

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Appendix 1. Data matrix used for the phylogenetic analysis.

Biarmosuchus tener	0[01]000-0000--000000100001000
Hipposaurus boonstrai	00000-0000--010000000000100
Herpetoskylax hopsoni	10000-0010--010000000000101
Lycaenodon longiceps	10000-00?0--0?????????????1
Ictidorhinus martinsi	?0000-0010--0?000000000????
RC 20	10000-0010--0100????????101
Lemurosaurus pricei	?0111001?1001?011000001?201
Lobalopex mordax	?01?100111001?0111001010111
Lophorhinus willodenensis	10111001?1??????????????2??
Lende chiweta	10111101?1011?3121101111111
Leucocephalus wewersi	10111101?101122121101111111
Proburnetia viatkensis	1011110111001?2121101111211
Paraburnetia sneeubergensis	?0111101?1011?2121101111?111
Niuksenitia sukhonensis	????????????????3?011111111?
Burnetia mirabilis	101?1210?110221131011111120?
Mobaceras zambeziense	??1?12110110221??10?1111110
Bullacephalus jacksoni	?1111210?1102??221001111110
Pachydectes elsi	?111???11???2212????????100
TM 4305	???????0??????1??10???1????
NHMUK R871	???????11????23????????????
BP/1/7098	00111101?1??????????????11?
Isengops luangwensis	?0111001?1010?2??1001?0?111
Nierkoppia brucei	??????01?101023??11?1?1????
SAM-PK-12187	???????1?1010?3???1????????