A new middle Permian burnetiamorph (Therapsida: Biarmosuchia) from the South African Karoo filling a gap in the biarmosuchian record

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Biarmosuchia, the most basal therapsid clade, is represented by relatively few specimens known from Permian deposits in Russia and southern Africa. In both the Guadalupian (middle Permian) and Lopingian (late Permian), biarmosuchians represent less than 1% of the fossil record at the specimen level. Here, we describe a new burnetiamorph biarmosuchian, *Impumlophantsi boonstrai*, based on a partial skull and associated postcrania from the upper *Tapinocephalus* Assemblage Zone. It is characterized by the presence of a low nasal crest with a unique morphology among burnetiamorphs. Inclusion of this taxon in an updated phylogenetic analysis of biarmosuchians indicates that this specimen is one of the most basal burnetiamorphs, representing the only record of this grade from the middle Permian.

Keywords: Synapsida, Burnetiamorpha, Permian, phylogeny, biostratigraphy.

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INTRODUCTION

Biarmosuchians are among the most basal therapsids (Rubidge & Sidor 2001; Kemp 2005; Day *et al*. 2018; Kammerer & Sidor 2021) and are known from the Permian deposits of Russia, South Africa, Malawi, Zambia, and Tanzania (Tatarinov 1968; Kruger *et al*. 2015; Sidor *et al*. 2015; Duhamel *et al*. 2021; Sidor 2023). Historically, biarmosuchian species were considered primitive gorgonopsians (e.g. Boonstra 1952) or dinocephalians (e.g. Broom 1923), and only relatively recently were they recognized as a separate group (Hopson & Barghusen 1986; Hopson 1991). Given their position at the base of the therapsid radiation, understanding the evolution of biarmosuchians is important for understanding therapsid origins generally (Sidor & Rubidge 2002; Kemp 2005). Although there are currently 24 recognized biarmosuchian genera, most of these are known from only a few specimens (Sidor 2015; Kammerer 2016; Whitney & Sidor 2016; Day *et al*. 2018; Kulik & Sidor 2019; Kammerer & Sidor 2021; Sidor *et al*. 2021; Sidor 2023; Day & Kammerer 2023). This has limited our understanding of evolution and relationships within the group, especially since many biarmosuchians are represented by incomplete cranial material (Rubidge & Sidor 2001; Liu *et al*. 2009; Day *et al*. 2018; Duhamel *et al*. 2021).

Biarmosuchian phylogeny has proven contentious, especially regarding the internal relationships of its main sub-clade, the Burnetiamorpha. Recent work on this group has produced two main phylogenetic hypotheses: one proposed by Day *et al*. (2016, 2018) and the other by Kammerer & Sidor (2021) (with the general topology of the latter traceable to the earliest cladistic work on biarmosuchians; e.g. Sidor & Welman 2003). At the time it was published, the hypothesis of Day *et al*. (2018) was more consistent with stratigraphy, as it recovered the majority of middle Permian burnetiamorphs in relatively basal positions. The hypothesis of Kammerer & Sidor (2021) recovered two primary burnetiamorph subclades, Proburnetiinae and Burnetiinae, but with a long gap between middle and late Permian burnetiine records and a notable ghost lineage for proburnetiines (with no middle Permian records). More recently, the two hypotheses have been reconciled into one phylogenetic matrix, which, along with the discovery of new burnetiid taxa, has helped resolve the apparent disconnect between stratigraphy and morphology in this clade (Sidor *et al*. 2021; Day & Kammerer 2023; Sidor 2023). However, support values for biarmosuchian phylogeny are low, and substantial uncertainty as to the precise relationships between individual biarmosuchian species remains. The resolution of biarmosuchian phylogeny could be improved by the discovery of new material – particularly for its middle Permian record, the known burnetiamorph sample consists mainly of isolated 'skull caps' (heavily pachyostosed cranial fragments consisting of extensively fused temporal elements with limited phylogenetic utility). Here, we redescribe a historic 'gorgonopsian' specimen, SAM-PK-12118a, recognizing it as a new burnetiamorph species from the middle Permian

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Tapinocephalus Assemblage Zone (AZ) of South Africa and discuss its implications for biarmosuchian systematics.

MATERIAL AND METHODS

Specimen preparation

Specimen SAM-PK-12118a, which comprises the preorbital portion of a skull and lower jaw, was mechanically prepared by Charlton Dube at the Evolutionary Studies Institute (ESI) of the University of the Witwatersrand using an air scribe fitted with a sharpened tungsten carbide tip. Before the recent preparation work, the block containing the skull had not been prepared (SAM-PK-12118a, Fig. 1a), with only the block containing postcrania having been prepared by Boonstra (SAM-PK-12118b, Fig. 1b). Paraloid glue (B-72) was used as a consolidant and adhesive.

Phylogenetic analysis

The character matrix from the most recent analysis of biarmosuchian phylogeny, that of Day & Kammerer (2023), was updated by scoring SAM-PK-12118a in the software Mesquite (Maddison & Maddison 2017). Cladistic analyses were run using the programs TNT version 3.2 (Goloboff *et al*. 2008), PAUP (Swofford 2002), and Winclada (Nixon 2002). These analyses were performed using maximum parsimony, an exhaustive search in TNT (Traditional Search) and PAUP (Branch and Bound), and a heuristic search in Winclada. All three analyses found consistent results. *Dimetrodon grandis* was used as the outgroup, and the Bremer support was calculated using TNT (Bremer 1994).

Highly incomplete specimens (BP/1/7098, NHMUK PV R 871a, and TM 4305; see Day *et al*. 2016 and Kammerer 2016) were removed from the updated Day & Kammerer (2023) matrix, as recommended in that publication. *Dimetrodon grandis* and SAM-PK-12118 were added to the matrix as novel operational taxonomic units. Character scoring of *Dimetrodon* was based on descriptions by Romer & Price (1940). Scoring of SAM-PK-12118 was based on direct observations. The final updated matrix comprises 26 operational taxa and 27 characters and is provided in the Appendix 1. No characters were added or removed from the matrix.

SYSTEMATIC PALAEONTOLOGY

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).

***Impumlophantsi boonstrai* gen. et sp. nov.**

LSIDs. urn:lsid:zoobank.org:act:A9969FFB-FB85-40DB-8ED3-BD64467871EE (*Impumlophantsi*); urn:lsid:zoobank.org:act:BE7EBD94-0702-4897-9D8A-6E477192D082 (*I. boonstrai*).

Holotype. SAM-PK-12118, the almost complete preorbital region of a skull with an occluded lower jaw (SAM-PK-12118a, Fig. 1a), originally identified by Boonstra (1965) as a gorgonopsian. This specimen also includes a pelvis preserved with a portion of the vertebral column, which was damaged during earlier preparation (SAM-PK-12118b, Fig. 1b).

Type locality and stratigraphic horizon. The holotype was found on the Palmietfontein portion (plot 57) of Kruidfontein farm, Prince Albert District. This specimen is from the Abrahamskraal Formation of the Beaufort Group (Fig. 2) in the *Diictodon-Styracocephalus* Subzone of the *Tapinocephalus* AZ, which corresponds to an age of approximately 261 Ma (Day & Rubidge 2020).

Etymology. Genus name meaning 'low nose' in isiXhosa in reference to the low nasal crest that diagnoses this taxon. Species name recognizing Lieuwe D. Boonstra, who first described the specimen and spent most of his life exploring the palaeobiology of the *Tapinocephalus* AZ.

Diagnosis. A burnetiamorph biarmosuchian with a weakly pachyostosed, anteroposteriorly elongate (extending for most of the length of the nasals), dorsoventrally low nasal crest, notably lower in height than the crest in other non-burnetiid burnetiamorphs such as *Lobalopex*,

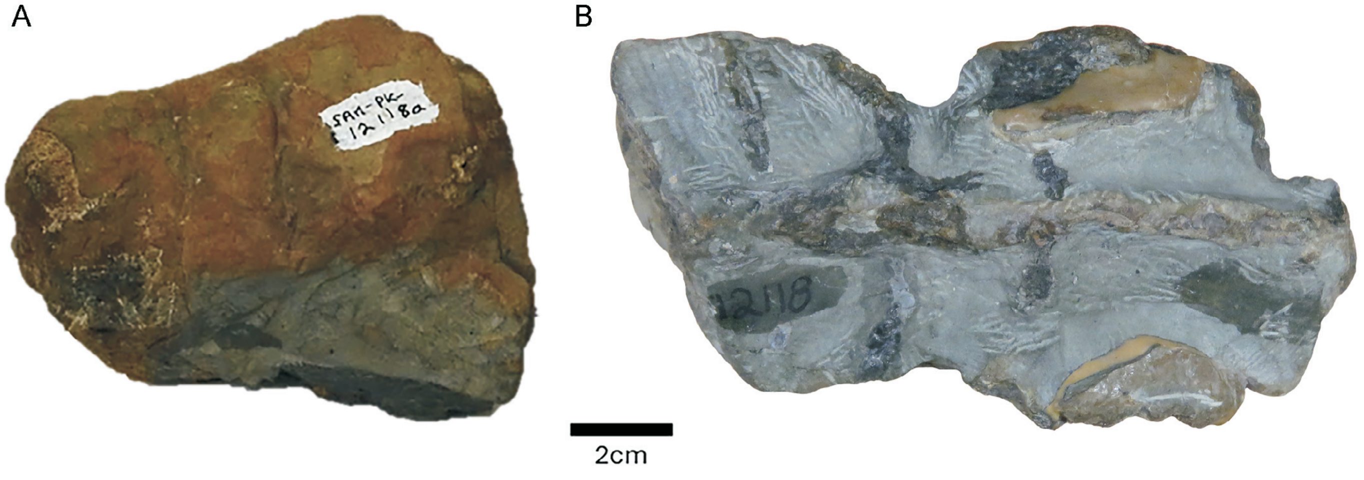

Figure 1. **A**, Left lateral view of the skull of *Impumlophantsi boonstrai* (SAM-PK-12118a) before preparation; **B**, postcranium of *Impumlophantsi boonstrai* (SAM-PK-12118b) as prepared by L.D. Boonstra.

Figure 2. Photograph showing outcrops of the *Diictodon-Styracocephalus* Subzone of the *Tapinocephalus* AZ on Kruidfontein farm, Prince Albert.

Lophorhinus, and *Isengops*. It also lacks deep pits on the lateral surface of the snout (present in other burnetiamorphs in which the snout is known) and has unusually short, transversely wide palatal bosses of the pterygoids.

DESCRIPTION

This description focusses on the snout of SAM-PK-12118a, which was newly prepared for this study. The postcrania (SAM-PK-12118b) were previously described and figured by Boonstra (1965), but his rather destructive preparation hinders further work on these elements.

SAM-PK-K12118a preserves the preorbital region of a relatively well-preserved skull and lower jaw (Fig. 3). The specimen is 100 mm long from the tip of the snout to the posteriormost part of the jugal. The orbit and postorbital region of the specimen are missing, but the palate is well-preserved to the level of the transverse process of the pterygoid.

The *premaxilla* forms the anterior tip of the snout (Fig. 4). This element is slightly damaged at the anterior end. It bears five incisors, as is usual for burnetiamorphs (Rubidge & Sidor 2002; Sidor *et al*. 2004); however, no serrations were observed on the incisors, unlike in *Lobalopex* and *Lophorhinus* (Sidor *et al*. 2004; Sidor & Smith 2007). The absence of serrations on the incisors could be the result of poor preservation, however. The upper

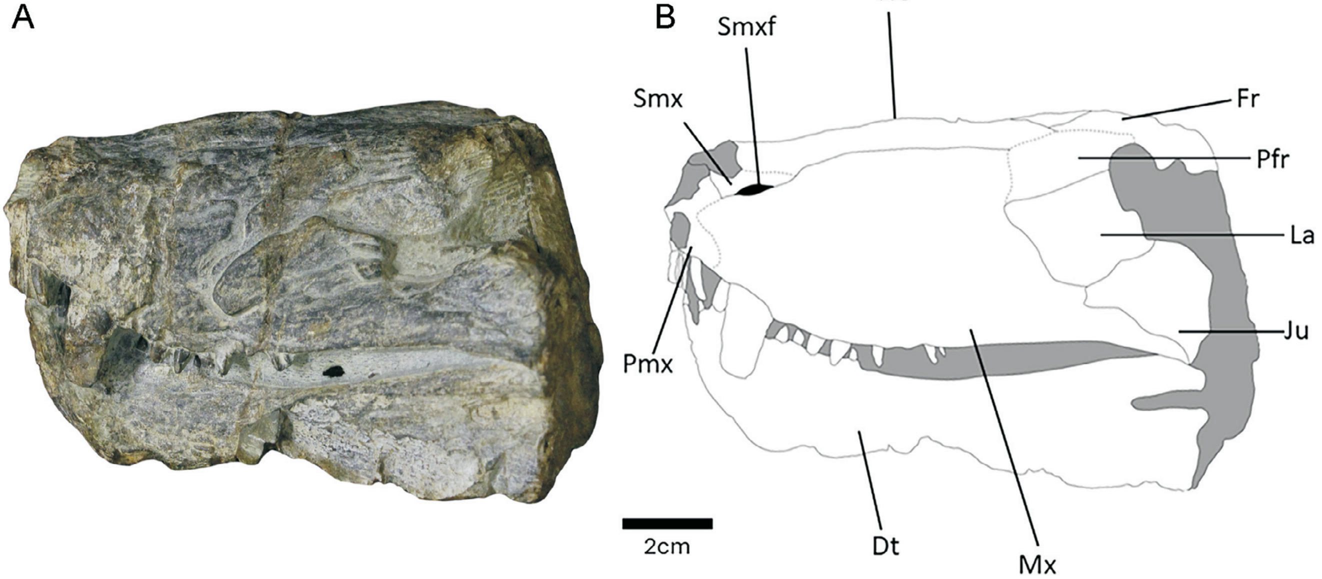

Figure 3. Skull of the holotype of *Impumlophantsi boonstrai* (SAM-PK-12118a) in left lateral view. **A**, photograph of the specimen; **B**, interpretive drawing of the specimen. *Abbreviations:* Dt, dentary; Fr, frontal; Ju, jugal; La, lacrimal; Mx, maxilla; Nc, nasal crest; Pmx, premaxilla; Pfr, prefrontal; Smx, septomaxilla; Smxf, septomaxillary foramen. Grey area represents the matrix. Dotted lines indicate that the suture is not clearly visible.

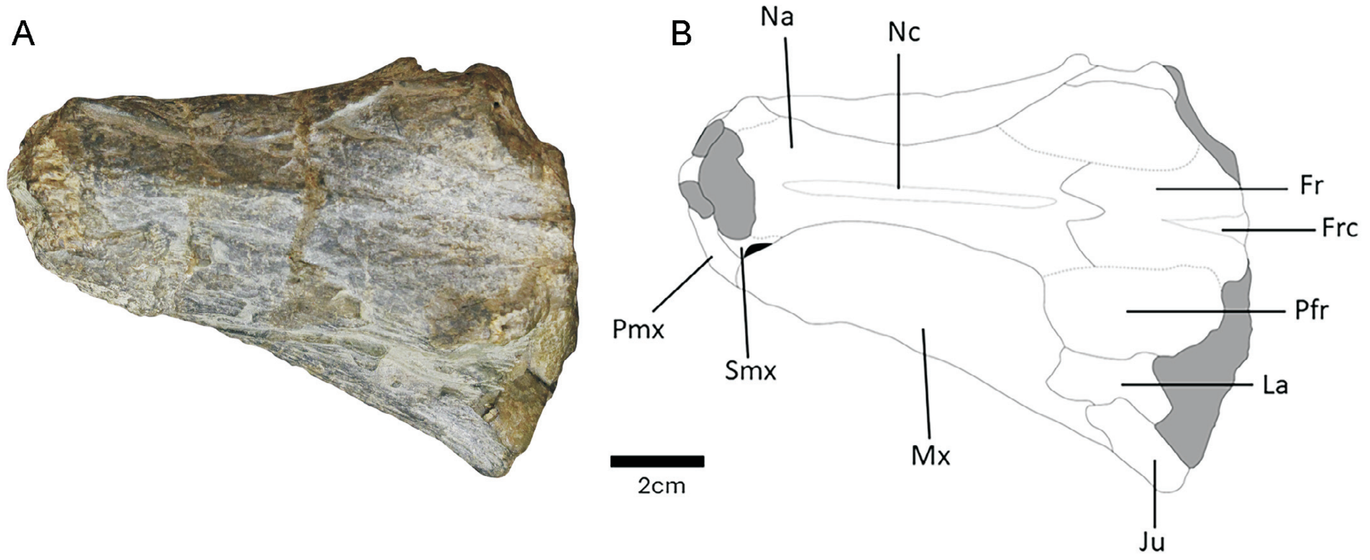

Figure 4. Skull of the holotype of *Impumlophantsi boonstrai* (SAM-PK-12118a) in dorsal view. **A**, photograph of the specimen**;** **B**, interpretive drawing of the specimen. *Abbreviations*: Fr, frontal; Frc, frontal crest; Ju, jugal; Mx, maxilla; Na, Nasal; Nc, nasal crest; Pmx, premaxilla; Pfr, prefrontal; Smx, septomaxilla;. Grey area represents the matrix. Dotted lines indicate that the suture is not clearly visible.

incisors are roughly equivalent in size, with a crown height of 5 mm. As in other biarmosuchians such as *Biarmosuchus*, *Lende*, *Paraburnetia*, and *Proburnetia* (Tchudinov 1960; Rubidge & Kitching 2003; Smith *et al*. 2006; Kruger *et al*. 2015; Kammerer 2016; Day *et al*. 2018), the upper incisors intermesh with the lowers when the jaws are occluded. Laterally, the premaxilla is in contact with the maxilla; however, the suture is not clearly defined. Posterodorsally, this element is overlain by the septomaxilla with a straight suture that extends obliquely for 10 mm. The suture between the premaxilla and nasal is not visible, as the nasal (= ascending) process of the premaxilla is not preserved. In palatal view, the premaxilla delineates the anterior edge of the choana and encloses the anterior margin of the vomer medially.

The posterior and posteroventral margins of the external naris are formed by the *septomaxilla*. This bone is roughly triangular (10 mm long, 5 mm high) with the apex oriented posteriorly (Fig. 3). It contacts the maxilla ventrally at the level of the canines, as in other biarmosuchians (Sidor 2003; Rubidge *et al*. 2006; Kruger *et al*. 2013; Day *et al*. 2018; Sidor *et al*. 2021) and meets the nasal dorsally. A septomaxillary foramen is present at the junction of the ventral edge of the septomaxilla and maxilla (Fig. 3), similar to that in *Lycaenodon* and *Leucocephalus* (Sidor 2003; Day *et al*. 2018).

The *maxilla* is a large element (40 mm long, 30 mm high) forming most of the lateral surface of the snout and preorbital region (Fig. 3). It has a rugose lateral surface texture, albeit less pronounced than in *Hipposaurus* and especially *Bullacephalus* or *Pachydectes* (Haughton 1929; Rubidge & Kitching 2003; Rubidge *et al*. 2006). The maxilla contacts the septomaxilla anterodorsally and meets the nasal dorsally. In lateral view, the ventral margin of the maxilla is slightly curved, as in *Lemurosaurus* and *Lobalopex* (Sidor & Welman 2003; Sidor *et al*. 2004).

Posteroventrally, the suture connecting the maxilla and jugal is slightly meandering and extends obliquely for 16 mm at the base of the jugal (Fig. 3). Slightly further dorsally, the sutural contact between the maxilla and lacrimal is straight and runs obliquely for 20 mm anterior to the orbit. The dorsal border of the maxilla is less clear, but appears to form a straight horizontal contact with the nasal. Posterior to the nasal, the suture connecting the maxilla and prefrontal is visible and extends vertically for 5 mm above the anterior margin of the orbit. Judging from the inferred position of the orbit, *Impumlophantsi* would have had a proportionally long snout relative to taxa like *Lende* and *Leucocephalus*.

The preorbital fossa is a broadly depressed region on the maxilla that expands to the anterior end of the lacrimal. This morphology is similar to that of other burnetiamorphs (Sidor & Welman 2003; Kammerer & Sidor 2021; Duhamel *et al*. 2021). Eight postcanine teeth are visible in the right maxilla and six are present on the left; however, the left maxilla has two empty alveoli, indicating that the postcanine count would also be eight. On either side of the specimen, the maxillary postcanines are separated from the canine by an 8 mm diastema. Maxillary canines are slightly curved and are 15 mm long.

The *nasal* makes up most of the anterodorsal surface of the snout (Figs 3 & 4). Anteriorly, the nasal forms the lateral and posterior margins of the external nares. In lateral view (Fig. 3), the contact between the premaxilla and nasal is not visible, and the nasal contacts the septomaxilla and maxilla along its lateral margin. In dorsal view (Fig. 4), the nasal bone is 55 mm long, but is eroded anteriorly, so would have been slightly longer in life. Dorsally, along the midline, the paired nasals bear a median ridge, but no midline suture is visible between the two nasals.

The nasal ridge is low and roughly triangular in transverse section, unlike the taller crest present in other burnetiamorphs, such as *Lobalopex*, *Lophorhinus*, *Lende*, *Leucocephalus*, *Isengops*, and the unnamed species (BP/1/7098) from the *Endothiodon* AZ (Sidor & Welman 2003; Sidor *et al*. 2004; Sidor & Smith 2007; Kruger *et al*. 2015; Day *et al*. 2018; Sidor *et al*. 2021). The nasal ridge is only weakly pachyostosed, but the bone surface appears dense and rugose. Posteriorly, the nasal ridge does not extend onto the frontal, similar to the condition in *Burnetia*, *Lende*, and *Proburnetia*. A very low, incipient midline ridge is present on the frontals too, but it is well-separated from the nasal ridge in *Impumlophantsi*. In some burnetiamorphs such as *Leucocephalus*, *Paraburnetia*, and *'Lemurosaurus'* (NMQR 1702), the median ridge on the nasals continues posteriorly on the frontals to form a well-defined nasofrontal ridge or crest (Sidor & Welman 2003; Kammerer 2016; Day *et al*. 2018). In *Impumlophantsi*, the nasal ridge extends anteriorly to the external nares, remaining low for the entirety of its length.

The *prefrontal* is a roughly rectangular element forming the anterodorsal margin of the orbit (Figs 3 & 4). Its sutural boundaries with the nasal and frontal are not clearly visible. Anteriorly, this element contacts the maxilla along a vertical suture that runs for 5 mm. Ventrally, it contacts the lacrimal along a curved suture.

Most of the *frontal* is missing, with only the anteriormost part preserved (Fig. 3). It is thus not possible to determine whether the frontal contributed to the dorsal margin of the orbit. This element contacts the prefrontals laterally; however, their sutural contact is unclear. Anteriorly, it contacts the nasal along a meandering, transversely oriented suture that is 40 mm long. An incipient ridge seems to be present along the midline suture between the frontals. However, the specimen is broken at this level, so it is unknown whether a more prominent frontal ridge was developed posteriorly.

The *lacrimal* is a quadrangular element forming the anterior margin of the orbit (Fig. 3). This element is recessed within the antorbital depression, and a subtle ridge marks the contact with the jugal ventrally. The antorbital depression is restricted to the lacrimal and does not extend onto the maxilla. The suture with the jugal is positioned ventrolateral to the circumorbital region, and is 15 mm long and roughly horizontal. Anteriorly, the lacrimal contacts the maxilla. The suture between the lacrimal and maxilla is obliquely angled and straight, and extends posteroventrally for 20 mm. The lacrimal exhibits a lacrimal-maxilla fossa similar to that described in *Lophorhinus* and *Proburnetia* (Rubidge & Sidor 2001; Sidor & Smith 2007; Sidor *et al*. 2021).

The *jugal* forms the anteroventral margin of the orbit and contacts the maxilla anteriorly (Fig. 3). The right jugal is not preserved and the posterior part of the left jugal is broken. The anteroposterior length of the preserved part of the left jugal is 35 mm. In lateral view (Fig. 3), the jugal forms the ventral edge of the suborbital bar and has a rugose surface. It is excavated by a shallow longitudinal depression on its lateral surface and bounded dorsally by a raised edge along the orbital margin (Fig. 3). This structure may be homologous to the fossa present on the jugal and lacrimal of other burnetiamorphs (Kammerer & Sidor 2021). The maxilla and jugal share a meandering suture that runs obliquely posteroventrally for 16 mm. In ventral view, this element is not visible as it is masked by the lower jaw.

The *vomer* is a slender bone characterized by an elongated midline trough that extends anteroposteriorly (Fig. 5). This element is located medially on the anteriormost part of the palate. As in other burnetiamorphs, it is excavated by a long sulcus defined laterally by two longitudinal crests (Day *et al*. 2018). The two vomer ridges decrease in height from anterior to posterior, where they ultimately disappear. Anteriorly, the contact between the vomer and

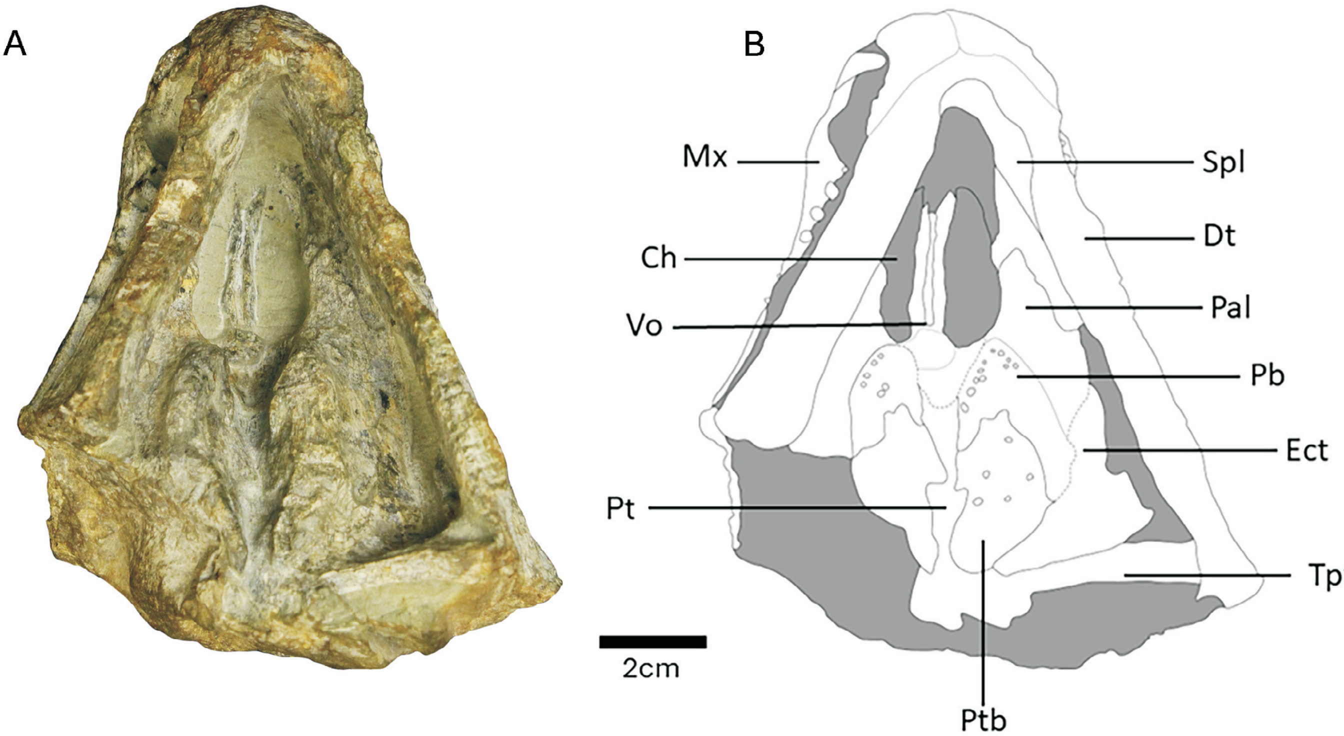

Figure 5. Skull of the holotype of *Impumlophantsi boonstrai* (SAM-PK-12118a) in ventral view. **A**, photograph of the specimen; **B**, interpretive drawing of the specimen. *Abbreviations*: Ch, choana; Dt, dentary; Ect, ectopterygoid; Mx, maxilla; Pal, palatine; Pb, palatine boss; Pt, pterygoid; Ptb, pterygoid boss; Spl, splenial; Tpt, transverse process of pterygoid; Vo, vomer. Grey area represents the matrix. Dotted lines indicate that the suture is not clearly visible.

premaxilla is not visible, and the posterior end of the vomer contacts the palatine posterolaterally and the pterygoid posteromedially, although none of these sutures are clear (Fig. 5). The elongated choanae extend lateral to the vomer and their posterior end reaches the level of the palatine boss. The choana and paracanine fossa are confluent as in many other early therapsids (Martinelli *et al*. 2009).

The *palatine* is a prominent bone that makes up a large portion of the lateral and posterolateral margins of the internal naris as well as the palatal surface. The palatines are well-preserved on both sides of the specimen and they expand anteriorly to the level of the upper canine. The anterior part of the palatine is V-shaped in ventral view. Posterolaterally, the palatine should have sutural contact with the ectopterygoid, but this suture is unclear (Fig. 5). Posteromedially, the palatine exhibits a well-developed boss which forms a raised platform confluent with the pterygoid boss. This bean-shaped palatine boss has a rugose texture as in other biarmosuchians (Day *et al*. 2018), and is separated from its counterpart by a deep median trough. The ventral surface of the palatine boss is flat and its general shape is more similar to that of *Leucocephalus*, *Lende*, and *Lemurosaurus* (Sidor & Welman 2003; Kruger *et al*. 2015; Day *et al*. 2018) than to the long and narrow bosses of *Lobalopex*, *Paraburnetia*, *Mobaceras*, and *Isengops* (Sidor *et al*. 2004; Kammerer & Sidor 2021; Sidor *et al*. 2021).

The palatine and pterygoid bosses together are 30 mm long (anteroposteriorly) and 8 mm high (dorsoventrally). Each palatine boss bears small teeth arranged in a V-shaped formation on the anterior margin of the boss (Fig. 5). Unlike in *Biarmosuchus* and *Hipposaurus*, these teeth do not broadly cover the palatal surface (Kammerer & Sidor 2021).

The *ectopterygoid* is a triangular element occupying the posteriormost part of the lateral palatal rim (Fig. 5). This element meets the palatine anteriorly and pterygoid medially, as in *Lemurosaurus*, and likely shares sutures with the maxilla and jugal laterally, although the latter two contacts are concealed by the attached lower jaw. The ectopterygoid lacks teeth, which is true of most therapsids (Sidor & Welman 2003).

The *pterygoid* is a large, intricate element that constitutes the posterior portion of the palate (Fig. 5). The preserved portion of the pterygoid constitutes two parts: the palatal boss and transverse process (the quadrate ramus is missing). Poor sutural preservation makes the precise morphology of its contacts with the vomer and palatine uncertain. Its contact with the vomer likely occurred midway between the palatine and pterygoid dentigerous bosses, similar to the condition in most basal therapsids (Ivachnenko 2000; Rubidge & Sidor 2002; Sidor *et al*. 2021). The anterior portion of the pterygoid boss is widest and narrows posteriorly. Anteromedially, the pterygoid boss is confluent with the palatine boss. Five teeth are present on the left pterygoid boss; however, no pattern can be ascertained. On the right pterygoid boss, teeth are not visible due to the weathering of the bone. The bosses are separated from their counterparts by a narrow median trough. Posterior to the bosses, the pterygoid forms a transverse process that is 30 mm long and is preserved on the left side only (Fig. 5). This transverse process reaches the medial margin of the lower jaw. No teeth are preserved on the transverse process, although this is most likely due to erosion of its ventral surface as they are present in most other basal biarmosuchians (Sidor & Rubidge 2006).

The preserved portion of the lower jaw in SAM-PK-12118a comprises only the dentary and splenial. The preserved dentary is 80 mm long and 20 mm high anteriorly. At the level of the last postcanine, the dentary is 10 mm high and increases in height toward its posterior end.

The *dentary* extends posteriorly to approximately the level of the anterior margin of the orbit (Fig. 3). This element is dorsoventrally thin at the level of the posterior end of the tooth row. The mandibular symphysis is unfused, similar to the condition in *Lende*, *Wantulignathus*, *Leucocephalus*, *Lobalopex*, and *Lemurosaurus* (Sidor & Welman 2003; Sidor *et al*. 2004; Kruger *et al*. 2015; Whitney & Sidor 2016; Day *et al*. 2018; Kammerer & Sidor 2021; Sidor *et al*. 2021). The dorsal edge of the dentary in *Impumlophantsi* is thickened and projects laterally, as is typical in biarmosuchians (Smith *et al*. 2006).

The incisors on the lower jaw are heavily eroded, with only two of them partially preserved on each ramus, and they are narrower and straighter than those of the upper jaw. The dentary postcanines are not well exposed on the right side of the specimen, and only seven are visible on the left side.

As biarmosuchians usually have more postcanines on the dentary than the maxilla (e.g. *Herpetoskylax* has five to six maxillary postcanines and at least eight dentary postcanines; *Leucocephalus* has six maxillary postcanines and eight to nine dentary postcanines (Sidor & Rubidge 2006; Day *et al*. 2018)), it is possible that, as the jaws of *Impumlophantsi* are occluded, some dentary postcanines are not visible.

The *splenial* is a flat bone on the anteromedial aspect of the lower jaw (Fig. 3). This element is wide anteriorly and narrows posteriorly. Anteriorly, the splenial is positioned medial to the dentary and does not contribute to the ventral margin of the lower jaw, as in other biarmosuchians (Sidor 2000) except *Leucocephalus*, which has the splenial contributing to the ventral margin (Day *et al*. 2018).

PHYLOGENETIC ANALYSIS

Phylogenetic analysis using the updated Day & Kammerer (2023) matrix resulted in 50 most parsimonious trees of length 55. The strict consensus tree is presented in Figure 6 and has a consistency index of 0.6727, retention index of 0.8537, homoplasy index of 0.3455, and rescaled consistency index of 0.5743. The tree is well resolved at the base, with *Biarmosuchus* and *Hipposaurus* as the earliest-diverging biarmosuchians.

Impumlophantsi is recovered as the most basal burnetiamorph, with Burnetiamorpha supported by two synapomorphies: presence of a low nasal ridge (5 [0]) and the presence of a frontal ridge that does not widen posteriorly (14 [0]). *Lophorhinus* and *Lemurosaurus* are sister taxa, and

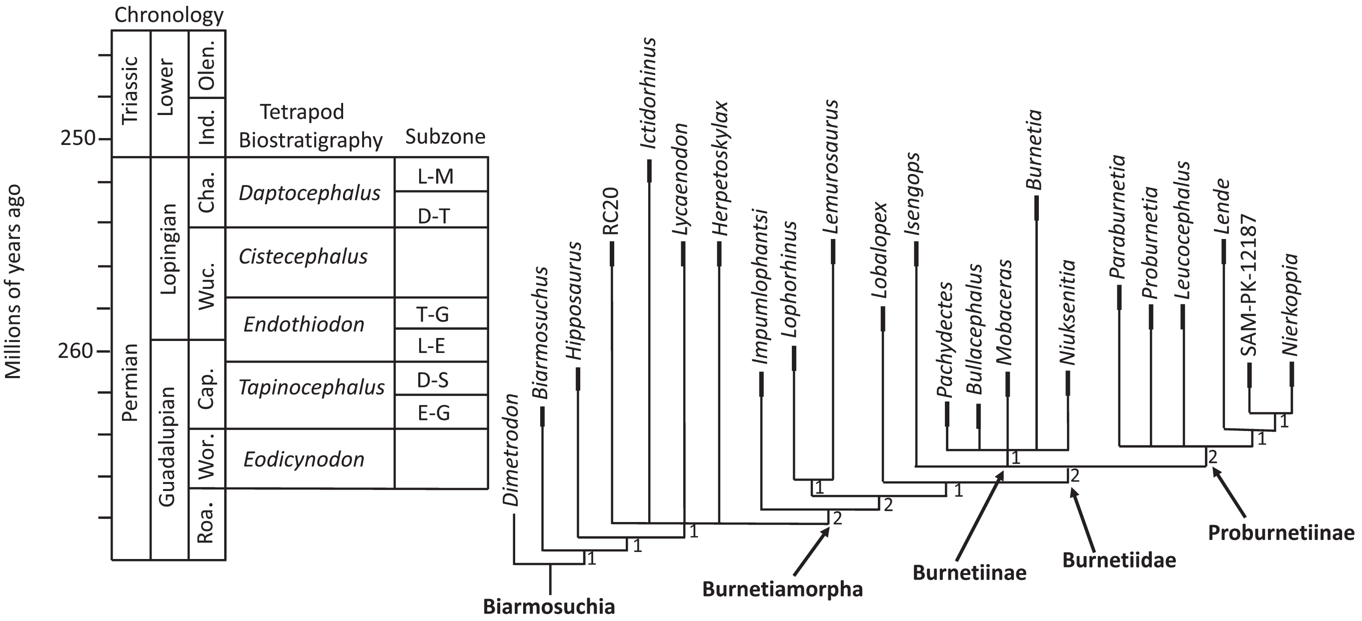

Figure 6. Strict consensus tree of biarmosuchians recovered by updating the Day & Kammerer (2023) phylogenetic matrix. Values at nodes indicate Bremer support. *Abbreviations*: Roa., Roadian; Wor., Wordian; Cap., Capitanian; Wuc., Wuchiapingian; Cha., Changhsingian; Ind., Induan; Olen., Olenekian; E-G, *Eosimops-Glanosuchus* Subzone; D-S, *Diictodon-Styracocephalus* Subzone; L-E, *Lycosuchus-Eunotosaurus* Subzone; T-G, *Tropidostoma-Gorgonops* Subzone; D-T, *Dicynodon-Theriognathus* Subzone; L-M, *Lystrosaurus maccaigi-Moschorhinus* Subzone.

the clade they form is supported by one synapomorphy: the presence of a lateral tooth row on the palatine boss that has a reniform shape (25 [1]). *Lobalopex* forms a clade with Burnetiidae, and the clade Burnetiidae is supported by four synapomorphies: the preorbital fossae that are present as broadly depressed regions of the lacrimal (3 [1]), and the presence of deep pits on the lateral surface of the snout (4 [1]), a median frontal excrescence (8 [1]), and an anterior supraorbital boss (10 [1]).

Burnetiidae is subdivided into two subclades, Burnetiinae and Proburnetiinae. Burnetiinae is not well resolved internally, but is supported by eight synapomorphies: a medial nasal excrescence that is bulbous and rounded (6 [2]), presence of a prefrontal boss (7 [1]), quadrangular morphology of the anterior supraorbital boss (11 [1]), presence of a posterior supraorbital boss and an elongated boss above the posterodorsal margin of the orbit (13 [2]), a pineal boss that is highly pachyostosed (15 [1]), a ventral squamosal boss (17 [3]), a nuchal crest that extends to the dorsal margin of the foramen magnum (22 [1]), and the presence of dentition on the transverse process of pterygoid (27 [0]).

Proburnetiinae has *Paraburnetia*, *Proburnetia*, and *Leucocephalus* in an unresolved polytomy. This subclade is supported by one synapomorphy: median nasal excrescence forming a pachyostosed ridge of nearly equal transverse width throughout its length (6 [1]). The only resolved subclade within the Paraburnetiinae comprises the Malawian *Lende chiweta* and the recently described morphotypes from the upper *Tapinocephalus* AZ: SAM-PK-12187 and *Nierkoppia brucei* (Day & Kammerer 2023). This subclade is supported by one synapomorphy: the absence of the pineal boss and depression of the circumpineal region (15 [3]). *Nierkoppia* and SAM-PK-12187 are recovered as sister taxa to one another, as in Day & Kammerer (2023).

DISCUSSION

Identification of *Impumlophantsi* as a burnetiamorph

Specimen SAM-PK-12118a was originally described by Boonstra (1965) as a galesuchid gorgonopsian, but further preparation revealed that it lacks the most common gorgonopsian characteristics: its canines are relatively small, it has a low chin, many postcanine teeth, pterygoid bones that appear to be separate rather than fused, palatines that do not meet at the midline, and a vomer bearing two rather than three ridges (Kammerer 2017; Liu 2022). Accordingly, the identification of *Impumlophantsi* as a gorgonopsian can be safely excluded.

Features that identify *Impumlophantsi* as a burnetiamorph are the presence of a nasal crest and the preorbital fossae (Kammerer 2016). The low nasal crest suggests a basal position for *Impumlophantsi* among burnetiamorphs, as this structure tends to be exaggerated in later members of the group. A similarly low nasal crest is also present in an unnamed, now lost Russian burnetiamorph specimen that Sidor (2023) states possesses characters supporting a basal phylogenetic position among burnetiamorphs. The cranial sutures in *Impumlophantsi* are closed, and the proportions of the snout suggest it was not significantly deformed, so the low aspect of the crest is not readily attributable to ontogeny or diagenesis.

Impumlophantsi as a distinct taxon

Impumlophantsi differs from other basal African burnetiamorphs (e.g. *Lemurosaurus*, *Lycaenodon*, *Lophorhinus*, *Lobalopex*) in having a very low nasal crest, which is more weakly developed than in more derived taxa (Sidor & Welman 2003; Rubidge & Kitching 2003, Day *et al*. 2018) and by the absence of deep pits on the lateral surface of the snout (Sidor & Welman 2003; Day *et al*. 2018; Kammerer & Sidor 2021). *Impumlophantsi* closely resembles the lost 'St. Petersburg specimen' figured by Sidor (2023), as they share the presence of a low nasal crest separated from the frontal crest, the same number of postcanine teeth, palatal teeth forming a 'V' at the margin of the boss, and the absence of a lateral pit on the snout. However, they differ by the size of their postcanine teeth, which are smaller in *Impumlophantsi* than in the St. Petersburg specimen. *Impumlophantsi* has a single row of palatine teeth limited to the margin of the boss (30 [2]), unlike the condition in *Burnetia*, *Paraburnetia*, *Proburnetia*, *Pachydectes*, and *Bullacephalus* (Day *et al*. 2018; Sidor *et al*. 2021). The presence of an incipient frontal excrescence and possible absence of teeth on the transverse process of the pterygoid are characters shared between *Impumlophantsi* and burnetiids; however, this relationship is not supported by our analysis and they are best interpreted as convergence or taphonomic artefact.

Impumlophantsi represents the most basal burnetiamorph from the *Tapinocephalus* AZ and one of the only middle Permian records of a non-burnetiid biarmosuchian (with the only other definite representative of this grade in the *Tapinocephalus* AZ being *Hipposaurus*). Substantial stratigraphic incongruence with biarmosuchian phylogeny remains, with most non-burnetiamorph biarmosuchians (e.g. *Herpetoskylax*, *Ictidorhinus*, *Lycaenodon*) and non-burnetiid burnetiamorphs (e.g. *Lemurosaurus*, *Lobalopex*, *Lophorhinus*) being of late Permian age (Fig. 6). Recently described taxa such as *Bondoceras* and *Nierkoppia* have helped eliminate ghost lineages in the burnetiid subclades (Day & Kammerer 2023; Sidor 2023); now, *Impumlophantsi* has helped resolve the ghost lineage for Burnetiamorpha as a whole. The recognition of this under-described, incompletely prepared specimen as a burnetiamorph rather than a gorgonopsian highlights the importance of historical specimens in expanding our understanding of palaeobiodiversity.

CONCLUSION

Impumlophantsi is of importance as very few burnetiamorph fossils are known from the middle Permian *Tapinocephalus* AZ deposits of the Karoo Basin and it expands the taxonomic and phylogenetic diversity represented in this assemblage. Its low nasal crest and generally weakly developed cranial excrescences accord with our recovery of this taxon as a very basal burnetiamorph. This specimen indicates that mid-Permian biarmosuchian diversity has been underestimated and helps to fill in a major ghost lineage in the evolution of this group. Its resemblance to the unnamed St. Petersburg specimen suggests a broad Pangaean distribution for this very poorly represented grade of basalmost burnetiamorphs.

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ABBREVIATIONS

Institutional

BP	Evolutionary Studies Institute, University of the Witwatersrand, Johannesburg, South Africa
NHMUK	The Natural History Museum, London, United Kingdom
SAM	Iziko South African Museum, Cape Town, South Africa
TM	Ditsong National Museum of Natural History, Pretoria, South Africa

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Appendix 1. Data matrix used for the phylogenetic analysis. The raw TNT data matrix is in the online supplement.

Dimetrodon grandis	00100?0000??000000110001100
Biarmosuchus tener	0[0 1]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?212110111?111
Niuksenitia sukhonensis	????????????????3?01111111?
Burnetia mirabilis	101?1210?11022113101111120?
Mobaceras zambeziense	??1?121101102 21??10?1111110
Bullacephalus jacksoni	?1111210?1102??221001111110
Pachydectes elsi	?111??11???2212?????????100
TM 4305	???????0??????1??10???1????
NHMUK PV R 871a	???????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????????
Impumlophantsi boonstrai	11001000????????????????111