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Editors' choice

A new mid-Permian burnetiamorph therapsid from the Main Karoo Basin of South Africa and a phylogenetic review of Burnetiamorpha

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Discoveries of burnetiamorph therapsids in the last decade and a half have increased their known diversity but they remain a minor constituent of middle–late Permian tetrapod faunas. In the Main Karoo Basin of South Africa, from where the clade is traditionally best known, specimens have been reported from all of the Permian biozones except the *Eodicynodon* and *Pristerognathus* assemblage zones. Although the addition of new taxa has provided more evidence for burnetiamorph synapomorphies, phylogenetic hypotheses for the clade remain incongruent with their appearances in the stratigraphic column. Here we describe a new burnetiamorph specimen (BP/1/7098) from the *Pristerognathus* Assemblage Zone and review the phylogeny of the Burnetiamorpha through a comprehensive comparison of known material. Phylogenetic analysis suggests that BP/1/7098 is closely related to the Russian species *Niuksenitia sukhonensis*. Remarkably, the supposed mid-Permian burnetiids *Bullacephalus* and *Pachydectes* are not recovered as burnetiids and in most cases are not burnetiamorphs at all, instead representing an earlier-diverging clade of biarmosuchians that are characterised by their large size, dentigerous transverse process of the pterygoid and exclusion of the jugal from the lateral temporal fenestra. The evolution of pachyostosis therefore appears to have occurred independently in these genera. The resulting biarmosuchian tree is significantly more congruent with the stratigraphic appearance of its constituent taxa than in previous phylogenetic hypotheses and, consequently, does not necessarily constrain the diversification of the Burnetiamorpha to before the Capitanian.

Key words: Therapsida, Burnetiamorpha, Biarmosuchia, Karoo Basin, Poortjie Member, Capitanian extinction, South Africa.

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Introduction

The history of research on the Burnetiamorpha is mostly a recent one. The name was first erected by Broom (1923), concurrently with the family Burnetidae (sic!), in order to house the peculiar and ornamented species *Burnetia mirabilis.* A second genus was added only several decades later with the description of *Proburnetia viatkensis* from Russia (Tatarinov 1968). Initially, most researchers believed *Burnetia* (and by extension the Burnetiamorpha) to be an atypical, or at least potential, gorgonopsian (Broom 1923; Boonstra 1934; Haughton and Brink 1954; Sigogneau 1970) but Sigogneau-Russell (1989) recognised similarities with the "ictidorhinids" and placed Burnetiidae in the basal therapsid clade Biarmosuchia, a group proposed previously by Hopson and Barghusen (1986). Russian palaeontologists, however, have continued to group Burnetiidae with gorgonopsians (e.g., Ivakhnenko 2003, 2008; Ivakhnenko et al. 1997), along with some other taxa such as *Estemmenosuchus* that are elsewhere considered as dinocephalians (Rubidge and Van den Heever 1997; Rubidge and Sidor 2001).

The Burnetiamorpha remained poorly understood and low in abundance and generic richness until the 21st century, when a series of discoveries both in the field and in fossil repositories led to a number of new taxa being described and the solidification of the clade within the broader context of the Biarmosuchia (Sidor 2000; Rubidge and Kitching 2003; Sidor and Welman 2003; Sidor et al. 2004; Jacobs et al. 2005; Rubidge et al. 2006; Smith et al. 2006; Sidor and Smith 2007; Kruger et al. 2015; Kammerer 2016). The ex-

pected increase in understanding resulting from the rapid rate of discovery and concomitant increase in anatomical data is, however, partially obfuscated by the fact that of the ten burnetiamorph genera only one, *Lemurosaurus*, is represented by more than one described specimen. A second specimen of *Lophorhinus* is also known but is as of yet undescribed. This scarce record, combined with the poor preservation of some specimens and the difficulty in determining the position of sutural contacts (e.g., Sidor and Welman 2003; Rubidge et al. 2006) has contributed to a lack of confidence in any phylogenetic reconstruction.

Nevertheless, improvements in the absolute dating of the South African Beaufort Group and its biostratigraphy and the continuing stratigraphic incongruence of hypothesised biarmosuchian phylogenies (most recently in Kruger et al. 2015 and Kammerer 2016) mean that a review of the clade with reference to their stratigraphic occurrence is appropriate. This is especially relevant as extensive fieldwork programs in east and southern Africa are yielding increasing numbers of burnetiamorphs (Sidor et al. 2010; Sidor 2015; Whitney and Sidor 2016). In February 2011 a collecting team from the Evolutionary Studies Institute discovered a partial burnetiamorph skull north of Merweville, Western Cape Province, in strata of the lower Teekloof Formation. Here we describe this new specimen, the first to be definitively found in the *Pristerognathus* Assemblage Zone (AZ), and explore the implications of new phylogenetic hypotheses for models of burnetiamorph diversification.

Institutional abbreviations.—BP, Evolutionary Studies Institute (formerly the Bernard Price Institute for Palaeontological Research), University of the Witwatersrand, Johannesburg, South Africa; CGP, Council for Geoscience, Pretoria, South Africa; MAL, Malawi Department of Antiquities Collection, Lilongwe and Nguludi, Malawi; NMQR, National Museum, Bloemfontein, South Africa; SAM, Iziko South African Museum, Cape Town, South Africa; PIN, Palaeontological Institute, Moscow, Russia.

Other abbreviations.—AZ, Assemblage Zone; GER, gap excess ratio; GER*, modified GER; GERt, topological GER; MIG, minimum implied gap; k, constant of concavity; MSM, manhattan stratigraphic measure; MSM*, modified MSM; RCI, relative completeness index; SCI, stratigraphic consistency index; SRL, simple range length.

Material and methods

Specimen preparation.—This study is based on a newly discovered biarmosuchian skull (BP/1/7098). The surface of the bone is very weathered and shows severe cracking, indicating that the specimen was exposed for a long period on the surface before burial. Preparation was mainly mechanical using an air scribe and was carried out under a stereoscopic microscope, on which the ratio of magnification could be varied from 4× to 40×. As the brittle matrix did not separate cleanly from the bone by mechanical preparation, and because the specimen was quite badly sun-cracked, acid preparation, using the method of Rudner (1972), was employed to remove the remaining thin coating of matrix from the bone. All bone was coated with a thin layer of Paraloid cement to protect it from acid erosion and a solution of 10% acetic acid at approximately 25° centigrade was used. This caused gentle effervescence of the matrix. The specimen was left in the acid bath for one hour intervals before being washed in running water for at least 18 hours after each acid immersion. This was to remove the acid residue and prevent the formation of insoluble salts. The specimen was dried thoroughly with compressed air before preparation was resumed. The whole acid preparation process to the current state of preparation took four weeks.

Cladistic analyses.—In order to determine the relationships of the new specimen we thoroughly re-examined the majority of known biarmosuchian material and then modified the most recent published character matrix for the clade (Kammerer 2016). Although Kammerer reviewed the preceding matrix of Kruger et al. (2015) and made a number of changes to it, we had made independent observations of Kruger et al.'s matrix that led us to different solutions to what we perceived as problematic characters. Kammerer (2016) rectified several inconsistencies in the biarmosuchian character set but we propose further extensive revisions on the basis of our own work (see SOM 2 and 3, Supplementary Online Material available at http://app.pan.pl/SOM/app61-Day_etal_SOM.pdf). This resulted in a revised character list containing three continuous characters and 34 discrete characters for 16 biarmosuchian taxa and specimen RC 20, which was scored separately amid concerns over its referral to *Lycaenodon* (Kammerer 2016; SOM 2).

The following specimens were studied as part of our research: BP/1/3924 (referred specimen of *Herpetoskylax hopsoni*); BP/1/5387 (holotype of *Bullacephalus jacksoni*); BP/1/5735 (holotype of *Pachydectes elsi*); CGP/1/61 (holotype of *Lobalopex mordax*); CGP/1/66 (undescribed specimen of *Hipposaurus boonstrai*); CGP/1/67 (holotype of *Herpetoskylax hopsoni*); MAL290 (holotype of *Lende chiweta*); NHMUK R5397 (holotype of *Burnetia mirabilis*); NMQR 1702 (referred specimen of *Lemurosaurus pricei*); PIN 1758/2 (holotype of *Biarmosuchus tener*); PIN 1758/8, 18 and 255 (referred specimens of *Biarmosuchus tener*); PIN 2159/1 (holotype of *Niuksenitia sukhonensis*); latex and plaster casts of PIN 2416/1 (holotype of *Proburnetia viatkensis*); SAM-PK-8950 (holotype of *Hipposaurus boonstrai*); SAM-PK-K6655 (holotype of *Lophorhinus willodenensis*); SAM-PK-K10037 (holotype of *Paraburnetia sneeubergensis*); SAM-PK-K11126 (undescribed specimen of *Lophorhinus willodenensis*); RC 20 (referred specimen of *Lycaenodon longiceps*). *Ustia atra* Ivakhnenko, 2003 is also probably a burnetiamorph based on the form of its dentary, particularly the posterior margin, but as this is all that is known of it we

do not include it in the phylogenetic analysis. Specimens NHMUK R871 and TM 4305 were excluded from our analyses, the former due to its incompleteness and the latter pending preparation.

The cladistic analysis was conducted using TNT 1.1 (Goloboff et al. 2008b) with all characters non-additive except for characters 0, 1, 2, 6, 11, 18, 21, and 32, which show adjacency of character states (Lipscomb 1992). Because the matrix is small, trees were calculated through implicit enumeration. Trees were generated using both equal weights and implied weights, which reduce the influence of homoplastic characters (Goloboff 1993, 1997) and have been shown to result in increased stability and support when applied to morphological characters (Goloboff et al. 2008a). The search was conducted with variable values of the constant of concavity (k). *Biarmosuchus* and *Hipposaurus* were used alternately as outgroups, which allowed a comparison of inferred burnetiamorph relationships when character states were polarised by either the oldest biarmosuchian (*Biarmosuchus*) or the most basal biarmosuchian to possess basicranial rami of pterygoids narrowly separated by a median trough (*Hipposaurus*). This latter character is highly diagnostic for most biarmosuchians and appears to be a robust synapomorphy for a clade excluding only *Biarmosuchus.* All trees are presented in SOM 1: fig. 1.

Stratigraphic congruence analyses.—Several formulae have been conceived to provide an a posteriori statistical measure of stratigraphic congruence (Norell and Novacek 1992; Benton and Storrs 1994; Huelsenbeck 1994; Siddall 1998; Wills 1999; Pol and Norell 2001; Wills et al. 2008). Most of these use some measure of the length of ghost lineage within a selected tree relative to either the length of known taxon ranges, as in the RCI, or to the minimum amount of ghost lineage possible for a tree bearing the same terminal taxa, such as the MSM and GER.

To test whether the phylogenies presented here demonstrate a better fit to stratigraphy than previous trees we implemented six measures of stratigraphic congruence using the StratPhyloCongruence function of the strap package (Bell and Lloyd 2015) for the statistical programming language R (R Core Team 2015). The StratPhyloCongruence function calculates various measures of stratigraphic congruence for a given tree or set of trees (Bell and Lloyd 2015). Input data include the phylogenetic tree (or trees) to be tested and the first and last appearance dates (FADs and LADs) for the branch-tip taxa, which are presented in SOM 4. Because these measures, other than the GER* and GERt, do not implicitly consider whether the fit of a tree to stratigraphy differs from that obtained by chance, we used the StratPhyloCongruence function to calculate estimated p-values for these metrics from 10 000 randomly generated trees. All twelve new trees were analysed, as were the most recent biarmosuchian phylogenies from the literature, i.e., the strict consensus tree of Kammerer (2016) and the majority-consensus tree of Kruger et al. (2015). In order to present a fair comparison, tip taxa were maintained through all tested trees by removing BP/1/7098 and RC 20 from trees calculated in this study and adding *Biarmosuchus* as a post hoc outgroup to those trees from which it had been omitted.

The StratPhyloCongruence function of the strap package can use several means of assigning relative branch lengths when time-scaling phylogenies. We used the “equal” dating method in our analyses, i.e., an equal division of branch length as per Brusatte et al. (2008). Bell and Lloyd (2015) note that this may affect stratigraphic congruence metrics that rely on the MIG or the length of ghost lineages but that this has not yet been explored. The function was set to randomly sample an age for each terminal taxon from within its apparent duration (randomly.sample.ages = TRUE) to reflect that most taxa are known from one or two specimens assignable only to one assemblage zone, lacking a specific stratigraphic position or age. The root of the tree was set to 2 million years (rlen = 2) in all trees and polytomies were randomly resolved (hard = FALSE). Other variables were kept as default. Trees were plotted against the most recent version of the Permian international timescale (Angiolini and Shen 2015; International Commission on Stratigraphy: Subcommission on Permian Stratigraphy, ICS-SPS 2016) and Beaufort Group biozones (Day et al. 2015; SOM 5) using the DatePhylo and geoscalePhylo functions of strap.

Geological and stratigraphic setting

BP/1/7098 was discovered in the south-western Karoo Basin on the farm Springfontein, Beaufort West district. This locality is situated 110 km west of Beaufort West on the Nuweveld Escarpment and is lithostratigraphically within the Poortjie Member of the lower Teekloof Formation (Fig. 1). The Poortjie Member crops out along the length of the Nuweveld escarpment and is clearly visible at Springfontein as a package of laterally extensive sandstone bodies approximately 120 m thick and bounded by the overlying argillaceous Hoedemaker Member and underlying, largely argillaceous Karelskraal Member of the uppermost Abrahamskraal Formation (Day and Rubidge 2014; Jirah and Rubidge 2014).

The specimen was recovered ex situ on a slope, where a small area of maroon siltstone was well exposed. The specimen was partially encased in grey, calcareous micritic matrix and was situated about 1 m below a horizon of small nodular pebbles formed of the same micritic material. Because of the limited extent of the exposure and the close proximity (within 50 cm) of three dicynodont skulls encrusted with the same micritic matrix, at least one of which is *Diictodon feliceps*, it is highly likely that all three fossils came from this nodular horizon. The extensive lateral continuity and vertical restriction of this bed, combined with the weathered and sun-cracked surface of the fossils, suggests it represents a palaeosol. This horizon lies approximately

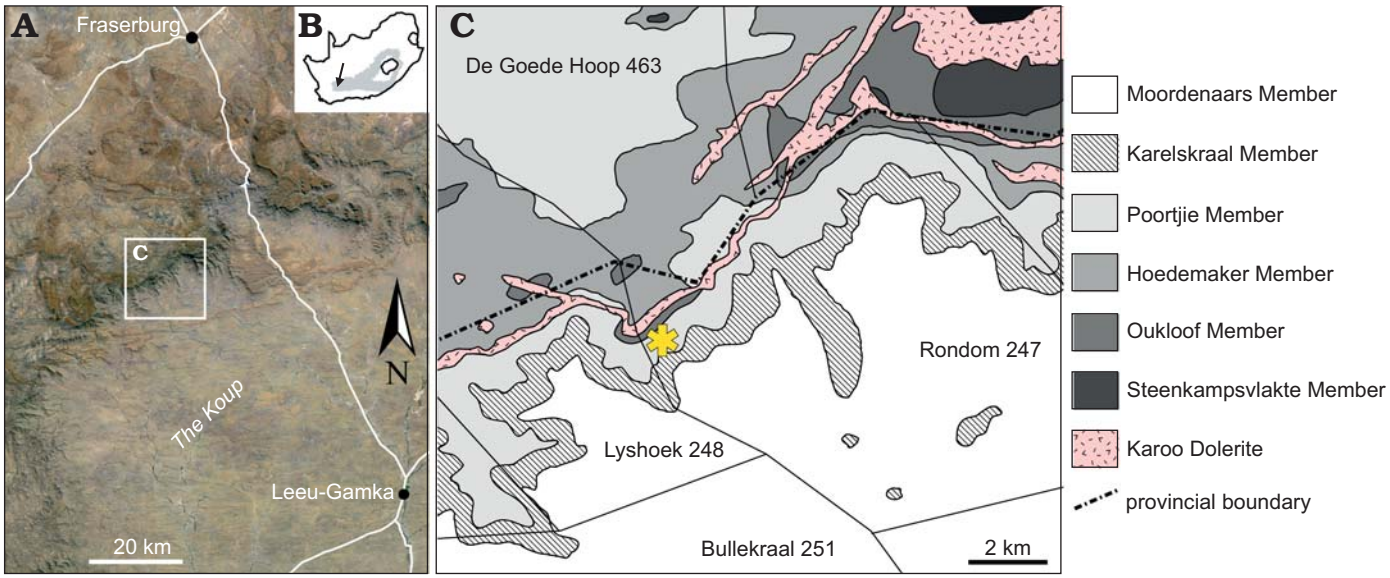


Fig. 1. **A**. Satellite map of the study area on the Nuweveld escarpment, Western Cape Province, South Africa. **B**. Map of South Africa; arrow indicates position of the locality within Main Karoo Basin (grey). **C**. Geological map and stratigraphy of Springfontein locality; asterisk indicates position of BP/1/7098.

70 m above the base of the Teekloof Formation and 2–3 m above the fifth laterally continuous sandstone body above the base of the Poortjie Member at the Springfontein locality (Fig. 2), although the thickness and number of sandstone bodies within the member is locally variable. Although few other fossils were collected from the Poortjie Member at this locality, elsewhere in the basin the middle Poortjie Member hosts a fauna assignable to the *Pristerognathus* AZ (Smith and Keyser 1995).

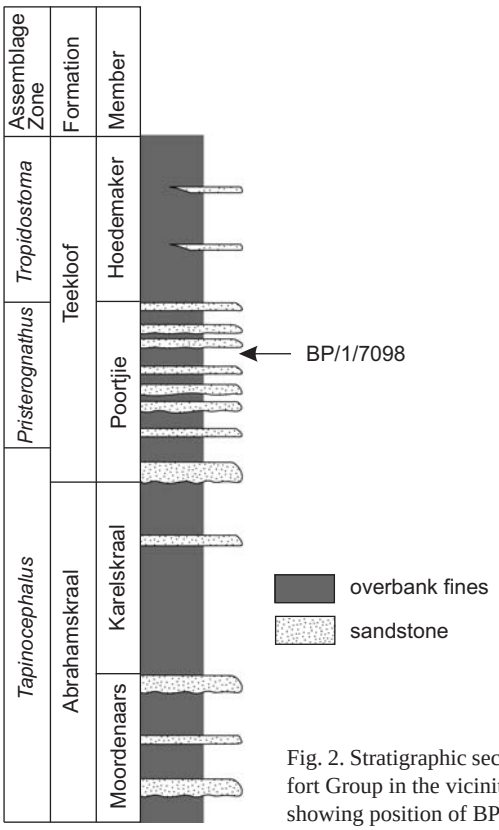


Fig. 2. Stratigraphic section of lower Beaufort Group in the vicinity of Springfontein, showing position of BP/1/7098.

Systematic palaeontology

Therapsida Broom, 1905

Biarmosuchia Sigogneau-Russell, 1989

Family Bullacephalidae nov.

Etymology: After the type genus.

Type genus: *Bullacephalus jacksoni* Rubidge and Kitching, 2003; Middelstevlei, Laingsburg district, South Africa; mid-Abrahamskraal Formation, Tapinocephalus AZ, early Capitanian.

Included genera: Type genus and *Pachydectes elsi* Rubidge, Sidor, and Modesto, 2006.

Diagnosis.—Biarmosuchians characterised by the following characters: skull moderately to greatly pachyostotic; swollen boss present above the postorbital bar formed by the postfrontal and postorbital; deep linear sculpturing of the snout; exclusion of the jugal from the lateral temporal fenestra; row of teeth present on the transverse process of the pterygoid; relatively large size (>20 cm basal skull length. The family may also be characterised by a ventrally offset, sub-triangular platform behind the transverse process of the pterygoid, delineated medially by a line representing an antero-medial continuation of the quadrate ramus (in *Pachydectes* this area is not preserved).

Stratigraphic and geographic range.—Both genera occur in the lower *Tapinocephalus* AZ of the Main Karoo Basin, South Africa; lower–mid-Abrahamskraal Formation; early Capitanian (Guadalupian or mid-Permian; Rubidge 2005; Rubidge et al. 2013; Day et al. 2015).

Burnetiamorpha Broom, 1923

Emended definition.—The most inclusive clade including *Burnetia mirabilis*, but excluding *Hipposaurus boonstrai*, *Ictidorhinus martinsi*, and *Herpetoskylax hopsoni* (adapted from Sidor and Welman 2003).

Emended diagnosis.—Skull moderately to greatly pachyostotic; median ridge-like structures on the skull roof present; supraorbital boss over posterior margin of orbit; one or two twin bosses on the suborbital bar and zygomatic arch; palatal processes of premaxillae long and laterally bounding anterior portion of vomer (modified from Sidor et al. 2004). In all burnetiamorphs except for *Lemurosaurus*: squamosal is swollen into a bulb at the contact of its three rami lateral to the quadrate; posterior margin of the squamosal swollen to form a thickened rim.

Burnetiamorpha gen. et sp. indet.

Material.—BP/1/7098, an obliquely deformed anterior half of a skull, broken at the level of the orbits and lacking lower jaws (Figs. 3–5) from Springfontein portion of the farm Rondom 247, Beaufort West district, Western Cape Province (32°23.572' S, 21°25.008' E). The fossil was encased in grey, calcareous matrix and was collected ex situ from below a palaeosol horizon within maroon siltstones of the upper Poortjie Member of the Teekloof Formation, in strata assigned to the *Pristerognathus* AZ (Smith and Keyser 1995). The only associated fossils collected from this horizon were one specimen confidently (BP/1/7089), and two specimens tentatively (BP/1/7087, BP/1/7088) assigned to the dicynodont taxon *Diictodon feliceps*. The specimen is latest Guadalupian or perhaps earliest Lopingian (Capitanian-Wuchiapingian) in age (Rubidge 2005; Rubidge et al. 2013; Day et al. 2015), postdating the Capitanian extinction event.

Description.—BP/1/7098 comprises the anterior portion of a skull without lower jaw, which has been dorso-ventrally and obliquely compressed towards the left. Some displacement of elements has occurred, particularly at the pterygoid-palatine junction, where the palatines have shifted to the right and the left pterygoid boss has been flattened and folded out laterally. A small, folded sheet of bone bearing a longitudinal sulcus is situated behind the left palatine boss but it is uncertain if this represents the interior of an elongated palatal boss or the "spandrel" of the pterygoid separating the palatal boss from the transverse process. The interchoanal portion of the vomers has rotated about its anterior end, the right maxilla is crushed and the lacrimals are medially displaced. The surface of the bone has been severely sun-cracked suggesting a long period spent on the surface before burial and this makes it difficult to determine some of the sutures. However, the majority of the bones are sufficiently well preserved on at least one side to describe their morphology. The tip of the snout including much of the premaxillae has eroded away but along the midline of the skull roof the specimen measures 109 mm.

Skull roof: The tip of the snout is heavily weathered anterior to the external nares and the tooth-bearing ramus of both premaxillae is fragmented beyond recognition. The premaxilla presumably formed the medial and medio-ventral borders of the external naris and would have met the maxilla posterolaterally, though neither of these contacts is clear. The number of premaxillary teeth is unknown. Despite the heavy weathering of this part of the specimen, the midline suture between the premaxillae is visible on the dorsal surface of the snout. On the right side, the nasal-premaxilla suture has opened as a crack, demonstrating that the dorsal process of the premaxilla extends posteriorly as a thin strip from the external naris to the level of the posterior margin of the canine tooth (Fig. 3A). A long dorsal process of the premaxilla is considered a plesiomorphic state for therapsids and in basal biarmosuchians such as *Hipposaurus* can extend as far posteriorly as half way between the tip of the snout and the orbit (Hopson and Barghusen 1986; Sidor and Rubidge 2006). Conversely, in most biarmosuchians for which the character is at least partially preserved, the process is shorter and usually does not extend far beyond the external nares (e.g., *Herpetoskylax*, *Lycaenodon* and *Proburnetia*; Rubidge and Sidor 2002; Sidor 2003; Sidor and Rubidge 2006). In *Lophorhinus* the process extends beyond the external nares and onto the dorsal surface of the snout but does not continue beyond the level of the canine tooth, which led Sidor and Smith (2007) to consider it relatively short. The condition in BP/1/7098 is relatively long but the process does not reach the nasal boss.

The premaxilla forms the anterior margin of the internal naris and the anterior part of each vomerine process of the premaxilla is preserved. These project posteriorly but due to damage the contact between the premaxilla and vomer is not clear; however, the relationship of this contact with the vomers seems to be unusual (see below). As in *Lycaenodon* (Sidor 2003) and *Lophorhinus* (Sidor and Smith 2007) a foramen is present on the ventral surface of the premaxilla anterior to the base of the vomerine process. Although we did not personally examine the holotype of *Lycaenodon*, the foramen as figured by Sidor (2003) for this genus is situated more posteriorly than in either BP/1/7098 or *Lophorhinus*, as is the foramen of *Burnetia*.

The septomaxilla is badly fragmented on both sides of the skull but its posterior portion is indicated on the right side by a wedge of matrix and broken bone between the nasal and maxilla. A fragment of the lateral narial margin on this same side is probably septomaxilla (Figs. 3A, 4A).

The nasals form most of the preserved skull roof. Anteriorly the nasals are separated along the midline by the dorsal processes of the premaxillae but posterior to this come together and, after a short gap, rise to form a midline nasal boss approximately half way between the orbit and the tip of the snout (Fig. 3). Posterior to and adjoining this boss the contact between the nasals continues as a thickened median ridge extending onto the frontals thus forming a well-ossified, contiguous median crest that is thickened throughout, although it reduces in thickness at the point of the naso-frontal contact. This contrasts with the morphology of most burnetiamorphs, except perhaps *Paraburnetia* and *Pachydectes*, where the midline frontal ridge is separated from the nasal boss by a flat gap. Unlike in *Paraburnetia*, *Burnetia*, or *Proburnetia*, the midline ridge does not continue anterior to the nasal boss. On the frontals the crest is transversely rounded but becomes higher and more squared-

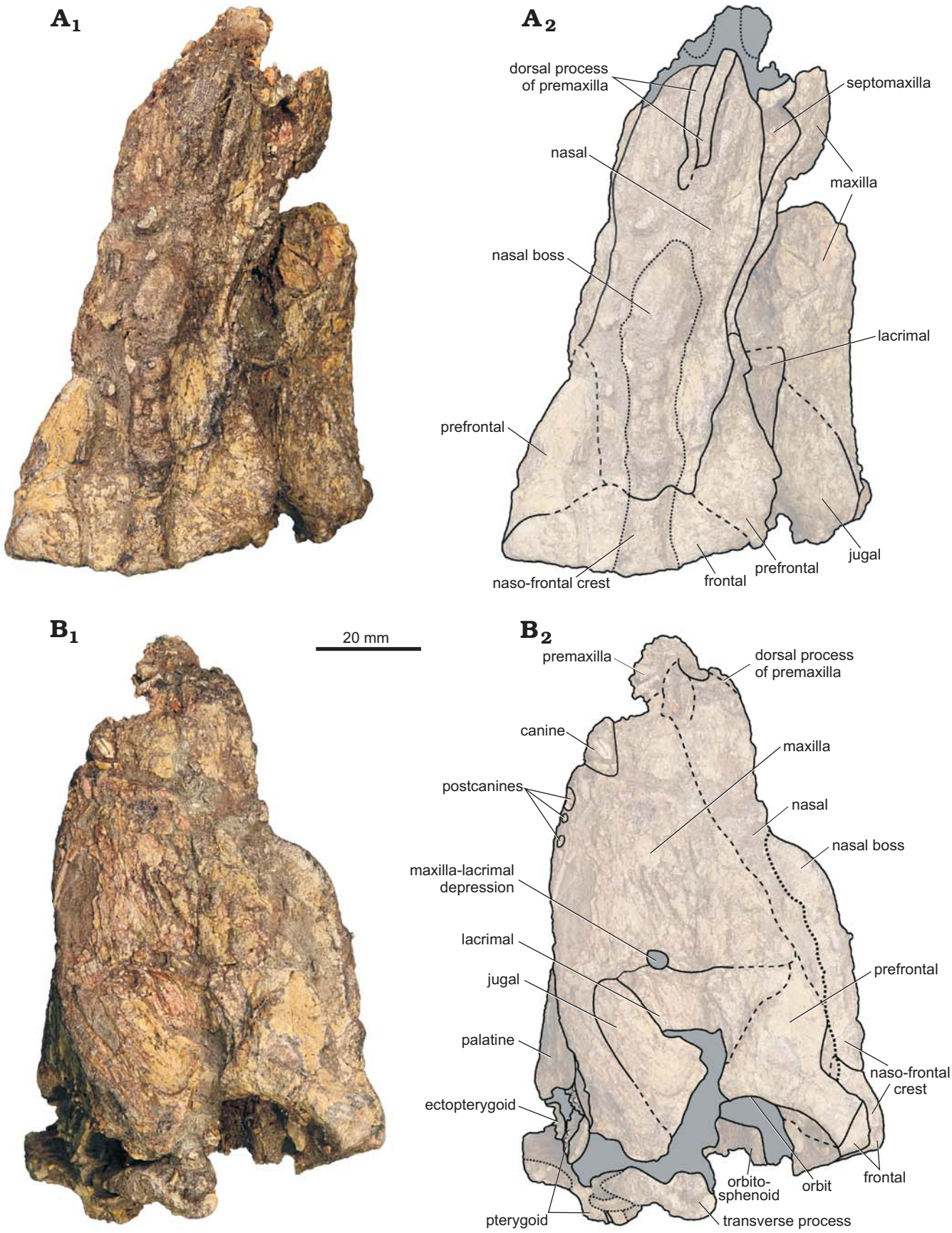


Fig. 3. Burnetiamorpha gen. et sp. indet. (BP/1/7098) from Springfontein, Beaufort West district, South Africa; upper Poortjie Member, *Pristerognathus* AZ, latest Capitanian; in dorsal (**A**) and left lateral (**B**) views. Photographs (A_1, B_1) and explanatory drawings (A_2, B_2).

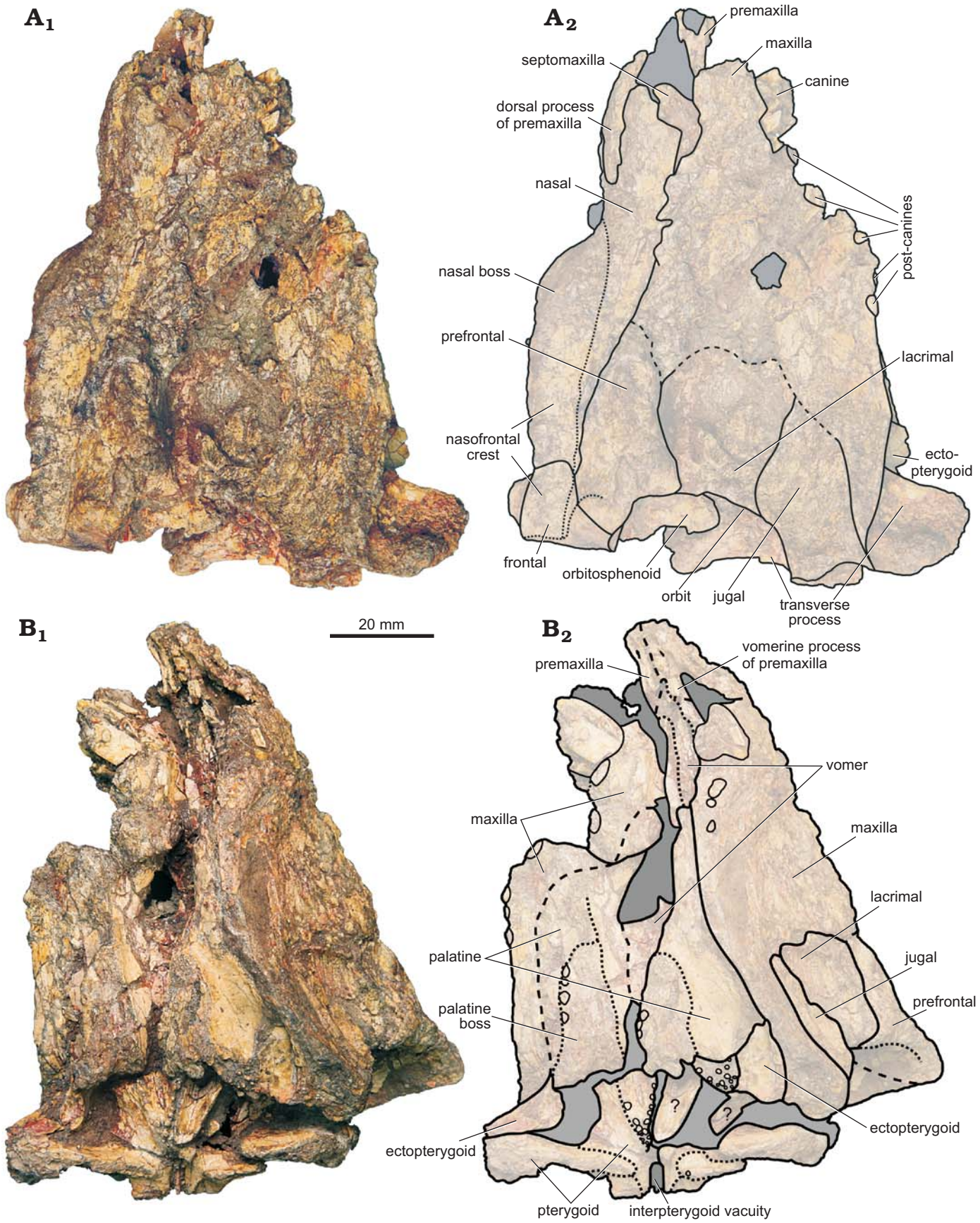


Fig. 4. Burnetiamorpha gen. et sp. indet. (BP/1/7098) from Springfontein, Beaufort West district, South Africa; upper Poortjie Member, *Pristerognathus* AZ, latest Capitanian; in right lateral (**A**) and ventral (**B**) views. Photographs (A_1, B_1) and explanatory drawings (A_2, B_2).

off onto the nasal, culminating in the nasal boss at the anterior end. The nasal boss reaches just over 10 mm at its widest point but its edges remain relatively straight, rather than swelling into a rounded boss as in *Paraburnetia*, *Burnetia*, or *Bullacephalus.*

The posterior border of the nasal contacts the frontal transversely across the median crest (Fig. 3A). Anteromedially the nasal contacts the dorsal process of the premaxilla and anterolaterally the septomaxilla; at its anterior end the nasal surely borders the dorsal margin of the external nares but this is not preserved due to severe weathering of this part of the specimen. Laterally the nasal has a relatively straight contact with the maxilla. At the anterior end of the prefrontal the contact of the nasal with that bone turns posteromedially, leading to a slight narrowing of the nasals towards their posterior end.

In lateral view, the maxilla is a large sub-triangular bone forming most of the antero-lateral portion of the snout. Both maxillae are heavily distorted due to the oblique deformation of the specimen but the better preserved left side suggests that the ventral surface of the maxilla was ventrally convex and that the premaxillary tooth row would therefore have been dorsally offset from the maxillary tooth row (Fig. 3B). Because of the weathering of the anterior snout, it is difficult to ascertain with certainty whether BP/1/7098 displayed a gentle elevation of the premaxillary tooth row above the postcanines as in *Hipposaurus*, *Lophorhinus*, and *Proburnetia* or the much more pronounced offset present in *Lobalopex* or *Lemurosaurus.*

The maxilla would have contacted the premaxilla anteriorly but this is not well preserved in BP/1/7098. Anterodorsally the maxilla contacts the septomaxilla, while dorsally it borders the lateral margin of the nasal (Figs. 3A, 4A). Posterior to the nasal the right maxilla appears to have a relatively extended (13 mm) contact with the anterolateral margin of the prefrontal that resembles the extent present on the right side of *Herpetoskylax* (Fig. 4A). However, on the left side the prefrontal-lacrimal suture appears to continue antero-dorsally to the nasal, suggesting a much shorter contact. An antero-dorsal spur of the lacrimal limiting (but not excluding) the contact of the maxilla and prefrontal would be consistent with other burnetiamorphs, while the holotype of *Herpetoskylax* actually displays asymmetry for this character similar to the condition perceived in this specimen. The central part of the right maxilla is badly crushed but it is evident that the posterior sutural contact of the maxilla descends ventrally from the prefrontal to the anterior margin of the lacrimal (Fig. 4A). The posterior margin of the maxilla extends postero-ventrally beneath the lacrimal and then the jugal, from where it attenuates posteriorly to a thin spur that pinches out between the jugal and the ventral margin of the skull beneath the anterior portion of the orbit.

The maxilla forms the postero-lateral margin of the expanded anterior portion of the internal naris and about half of the lateral margin of the internal naris posterior to this, after which the palatine overlaps it medially (Fig. 5A, B). The triangular shape of the anterior part of the internal naris (for accommodation of the lower canine) is seen in other biarmosuchians including *Lycaenodon*, *Lobalopex*, and *Burnetia* but the degree to which the corner of this vacuity has reduced the thickness of the external surface of the skull most closely resembles *Lophorhinus.* The lateral expansion of the internal naris would have accommodated the lower canines as other biarmosuchians, gorgonopsians and therocephalians (Hopson and Barghusen 1986; Sidor et al. 2004; Sidor and Smith 2007). Posterior to this, the medial side of the maxilla forms a moderately swollen ridge that projects into the internal naris, the crista choanalis. This ridge is rounded dorsally but on its ventral side possesses a slight ridge that forms a depression between this ridge and the tooth-row. Posteriorly, the choanal spur of the palatine fits into this depression. After being excluded from the lateral margin of the internal naris the maxilla shares a long medial contact with the palatine and, more posteriorly, with the ectopterygoid (Fig. 4B).

The maxillae bear the worn roots of both canine teeth, of which the right one is mediodistally elongated giving an ovoid cross-section (Fig. 5A, B). Conversely, the left canine is more circular, possibly due to deformation or deeper weathering of the root. Just anterior to the right canine is the root of a small tooth. It is uncertain whether this represents a precanine or a distal incisor as the tooth is not within its alveolus but precanines are not known in other burnetiamorphs, which would suggest the latter is more likely. Posterior to the canine the left maxilla preserves the roots of three postcanine teeth, the anteriormost of which is larger than the posterior two (Figs. 4B, 5A, B). No other teeth are visible on the ventral margin of the left maxilla, presumably because of the heavy weathering suffered by this area. Immediately posterior to the canine, the right maxilla bears the root of a single large postcanine so no postcanine diastema is present in BP/1/7098. Further posteriorly the maxilla has been crushed but the medially displaced maxillary block bears the worn root of another postcanine tooth. A further five teeth are evident on the maxilla posterior to this such that the tooth row extends as far as the level of the anterior margin of the palatine boss. At least seven postcanines were thus present. Postcanine 4 still retains a portion of the crown and preserves three small serrations on its distal surface, whereas the anterior surface of this tooth is rounded and bears no serrations.

In lateral view the prefrontal forms the antero-dorsal margin of the orbit and in dorsal view appears as a diamond-shaped bone on the lateral part of the skull roof (Figs. 3A, 4A). On the skull roof the prefrontal has an oblique contact with the nasal anteromedially and with the frontal posteromedially, the latter of which runs from the frontonasal contact to the dorsal rim of the orbit where the prefrontal contributes to the thick interorbital skull roof. The posterior margin of the prefrontal is slightly swollen in a way that suggests a similarity to *Lende*, where the supraorbital margin is pinched upwards at the junction of the prefrontal and frontal. Anterior to the orbit the prefrontal has a sutural contact with the lacrimal

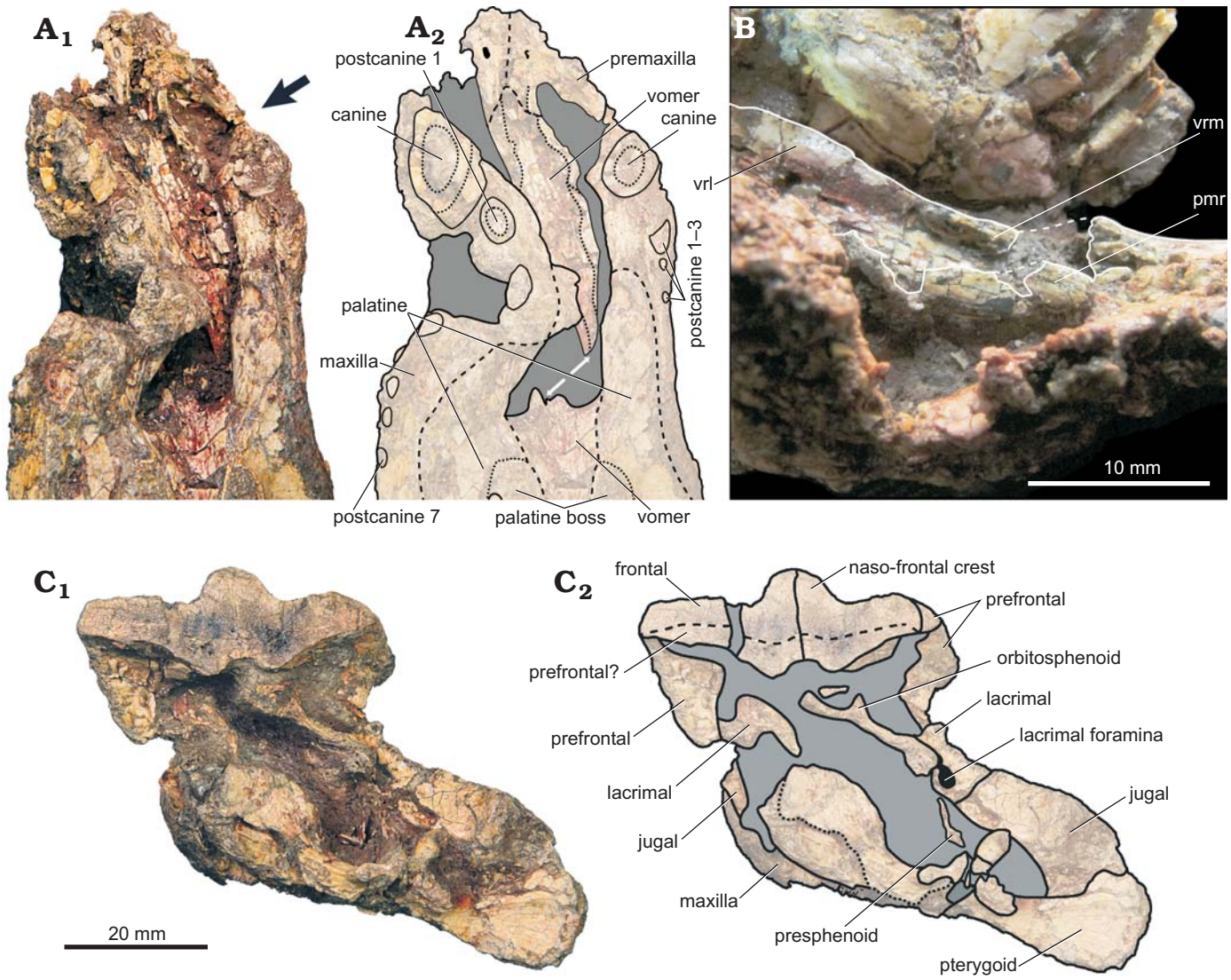


Fig. 5. Burnetiamorpha gen. et sp. indet. (BP/1/7098) from Springfontein, Beaufort West district, South Africa; upper Poortjie Member, *Pristerognathus* AZ, latest Capitanian. **A**. Anterior palate in ventral view, black arrow shows direction of view in B; white arrows show lateral displacement of interchoanal portion of the vomers. **B**. Interchoanal portion of vomers in right ventral view (**B**), showing the continuation of the downturned edges of the vomer extending anteriorly onto the premaxilla; pmr, ventral ridge of premaxilla at anterior margin of choana; vrl, ventral ridge of vomer laterally flared; vrm, ventral ridge of vomer medially folded. **C**. Specimen in posterior view. Photographs (A_1, C_1) and explanatory drawings (A_2, C_2).

ventrally and contacts the maxilla anteroventrally, although the extent of this is hard to determine. A small projection of bone perhaps evident on antero-dorsal part of the orbit just anterior to the break may correspond to the pinched antero-dorsal margin of the orbit seen in most burnetiids.

As is evident on the right side of the skull, the lacrimal is a large quadrangular bone forming the anterior margin of the orbit. The lacrimal has a ventral contact with the jugal, an anterior contact with the maxilla and meets the prefrontal dorsally (Fig. 3B). On both sides of the skull the lacrimal has collapsed medially, presumably as this bone is thinner than those surrounding it and represents a point of weakness, but the concave surface of this area on both sides demonstrates the existence of an antorbital depression as is common to all burnetiamorphs and *Herpetoskylax* (Sidor and Rubidge 2006; Sidor et al. 2006).

Despite the deformation and the heavy weathering of the bone surface there appears to be a small pit between the anterior margin of the left lacrimal and the maxilla (Fig. 3B). While unobtrusive by itself, the suggestion that all burnetiamorphs except *Paraburnetia* possess such pits or fossae (Sidor and Smith 2007) gives it greater significance. Two deep pits are visible in the posterior border of the right lacrimal inside the anterior margin of the orbit that presumably host paired foramina connecting to the lacrimal duct (Fig. 5C). The presence of paired lacrimal foramina was described as an autapomorphy of *Lophorhinus* by Sidor and Smith (2007) but this appears to be the case in several biarmosuchian genera including *Lemurosaurus* (Sidor and Welman 2003), *Proburnetia* (Rubidge and Sidor 2002), BP/1/7098 and *Herpetoskylax* (personal observation of referred specimen BP/1/3924). Sidor and Rubidge (2006)

recognised only one elongated foramen in the holotype of *Herpetoskylax* (CGP/1/67) but the pit in which the foramen is situated is not fully prepared and likely contains two foramina separated by a thin septum, as in the aforementioned taxa.

The jugal forms the antero-ventral margin of the orbit in BP/1/7098 but is truncated by the break at the back of the specimen. On the right side, where it is better preserved, the jugal meets the transverse process of the pterygoid ventrally, the posterior spur of the maxilla antero-ventrally, and the lacrimal anterodorsally (Fig. 3B). Along the orbital margin and its border with the lacrimal the jugal is raised to form a lip, with the dorsal surface of the bone bearing a depression. The antorbital depression was therefore probably partitioned by a small ridge as in *Lemurosaurus* or, more strikingly, in *Pachydectes.* The same may be true of *Burnetia* but the difficulty in determining sutures on the holotype, and confusion over the discrepancy between the antorbital depression and the anterior lacrimal fossa, prevent an unambiguous diagnosis.

The paired frontals comprise the medial part of the skull roof between the orbits. No midline suture is evident on the surface of the bone along the median crest but the cross-section through frontals at the broken posterior end of the specimen shows a clear midline suture (Fig. 5C). This is probably true for the nasals as well. The prominent midline crest enters onto the anterior part of the frontals from the nasals and reaches its minimum width around the naso-frontal contact (Fig. 3A).

From the orbital margin the sutural contact between the prefrontal and frontal extends posteroventrally round onto the interior ceiling of the orbit at the broken posterior end of the specimen (Fig. 3B). A similarly orientated suture occurs on the broken surface of the right supraorbital region (Fig. 5C). As no sutures are visible medial to this we conclude that the frontal contributes to the orbital margin posterior to the prefrontal as has been described for *Lophorhinus* and *Lemurosaurus* (Sidor and Welman 2003; Sidor and Smith 2007), rather than being excluded from this area by the meeting of the prefrontal and postfrontal as in *Bullacephalus* and probably as in *Pachydectes* (MOD personal observation). The transversely broken posterior end of BP/1/7098 shows a suture than runs transversely through the skull roof, excluding the frontals from the ventral surface of the skull roof at that point; the identity of this bone is uncertain.

The transverse section of the skull roof provided by the break also shows an anteroposteriorly oriented midline depression along the ventral surface of the frontals (Fig. 5C), formed by the presence of two rounded ventral ridges, one on each frontal bone. These ridges are situated approximately ventral to the lateral edges of the midline naso-frontal crest. A break at the same interorbital level in *Lophorhinus* reveals similar ridges that connect to the wings of the sphenethmoid (orbitosphenoid) to form a central tunnel or canal (Sidor and Smith 2007).

Braincase: The posterior break in the specimen shows that one or more sheet-like median ossifications are present. The first extends from close to the ventral surface of the skull roof down to the level of the lacrimal foramina; the second may be a continuation of the first, extending further ventrally almost to the pterygoid, but is very thin and very poorly preserved; a third can be seen as a beam of bone just dorsal to the interpterygoid vacuity, although it has been displaced along with the pterygoids themselves (Fig. 5C). Median ossifications representing the anterior extensions of the braincase are well documented in synapsids but terminology differs due to the difficulty in identifying homology with extant mammalian bones. In some cases the lamina are considered together as the sphenethmoid or sphenethmoid complex (e.g., Reisz, 1986; Sidor, 2001; Sidor and Smith, 2007), but separate ossifications have been recognised in gorgonopsians and dicynodonts (e.g., Sigogneau 1970; Cluver 1971; Sigogneau-Russell 1989; Sullivan and Reisz 2005).

The first and most dorsal of these median bones is narrowest centrally and thickens towards its dorsal margin where it appears to have bifurcated, though the right wing is broken. The dorsal part of a similar median ossification is preserved in *Lophorhinus* (SAM-PK-K6655), where it clearly possesses two dorso-lateral "wings" enclosing a median canal between this bone and the skull roof. This is interpreted as the orbitosphenoid, possessing similar morphology to same bone in gorgonopsians, therocephalians and dicynodonts (Sigogneau-Russell 1989; Sullivan and Reisz 2005; Sigurdsen et al. 2012). Ventral to this upper ossification, a thin lamina of bone continues ventrally to the pterygoids. This may be a continuation of the orbitosphenoid but appears to be distinct in that it is noticeably thinner. A distinct ossification has been recognised ventral to the orbitosphenoid in the gorgonopsian *Gorgonops* (Sigogneau 1970) but was not named. In dicynodonts the septum in this area has been called the presphenoid (Agnew 1959; Cluver 1971; Sullivan and Reisz 2005) and this may be equivalent to the structure observed in BP/1/7098.

The third and ventral-most median ossification may represent the cultriform process of the parasphenoid. In pelycosaurs and several therapsids including *Biarmosuchus*, this structure is found to be grooved on its dorsal surface to accommodate an ossified or cartilaginous presphenoid or ventral extension of the orbitosphenoid (Agnew 1959; Ivakhnenko 2008; King 1988; Reisz 1986; Sigogneau 1970; Sigogneau-Russell 1989). However, the presence of a dorsal groove is not clear in BP/1/7098 and its identification is therefore more circumstantial. In any case, the ossification of the sphenethmoid was considered an autapomorphy of *Lophorhinus* (Sidor and Smith 2007) but its occurrence in *Biarmosuchus*, BP/1/7098 and *Lobalopex* indicates that it is more common amongst biarmosuchians.

Palate: The elongated vomer meets the premaxilla anteriorly from where it extends posteriorly forming the medial border of the choana. Laterally, the interchoanal portion of the vomer is typically downturned along the choanal margin

to form a ventrally projecting ridge, which together form a medial trough. In other biarmosuchians for which this area is known the trough becomes shallower anteriorly before it reaches the premaxilla but in BP/1/7098 the downturned edge of the vomer continues on to meet the premaxilla (Figs. 4B, 5A, B). The taxonomic significance of this character is unclear as its presence cannot be ruled out for some other burnetiamorphs such as *Bullacephalus*. Posterior to the canine the downturned edge of the vomer is flared outwards on both sides but anterior to the canine it is folded medially. Deformation could certainly be responsible for these structures but the fact that the folding changes direction longitudinally and is mirrored on both sides suggests that they represent genuine morphology. Folding of the raised edges of the vomers is known in anteosaurs, notably in *Syodon efremovi* and *Titanophoneus adamanteus*, where they fold medially to the point they nearly contact each other (see Kammerer 2010). This contrasts with the condition in BP/1/7098, where the medial folding is limited to the anterior end of the choana and, as far as is preserved, where the edges do not curl so far as to almost contact one another. Anteriorly the vomer is broad and becomes narrower posteriorly as the trough becomes shallower. Due to a break in the vomers at the posterior end of the choana it is not clear if the downturned edges of the vomers meet to form a median ridge as in *Lemurosaurus*, *Proburnetia*, *Lende*, *Paraburnetia* and perhaps *Lycaenodon* (Rubidge and Sidor 2002; Sidor 2003; Sidor and Welman 2003). The fragmentary surface preservation of the vomers makes it difficult to ascertain if the vomer is paired.

The palatal bones between the palatine bosses are not well preserved rendering it difficult, as is the case in most biarmosuchians, to identify sutural contacts. However, the displacement of a thin sheet of bone up the medial side of the left palatine boss suggests that the vomer widens out posteriorly to form the posterior margin of the choana and the roof of the interpalatine trough, contacting the palatines laterally. The posteriormost portion of the vomers is not preserved but likely contacted the pterygoids thus excluding the palatines from the midline, as is posited for other biarmosuchians (Rubidge and Sidor 2002; Sidor 2003; Sidor and Welman 2003; Sidor et al. 2004) and, indeed, as is typical of all non-gorgonopsian therapsids.

Both palatines are preserved. On the left side a tongue like anterior process extends forwards from the level of the palatine boss along the ventromedial side of the maxilla, thereby forming the posterolateral margin of the choana. The anterior extent of this process may not be entirely preserved but it is unlikely to have extended much further given its similarity to the same structure in *Lophorhinus*. Laterally to its large boss, the palatine expands to form the smooth shelf of the palate that borders the maxillary tooth row. This shelf is bordered posteriorly by the ectopterygoid (Fig. 4B). Posteromedially the palatine borders the pterygoid, posterior to its boss, where the bone has broken at approximately the level of the contact. Medially, the palatine encloses the postchoanal portion of the vomer.

The large, ventrally projecting palatine bosses are separated by a deep depression, which appears shallower due to the ventral displacement of the postchoanal portion of the left vomer. The deepness of the depression is similar to *Lobalopex*, *Lophorhinus*, *Lemurosaurus*, and *Bullacephalus* (Rubidge and Kitching 2003; Sidor and Welman 2003; Sidor et al. 2004; Sidor and Smith 2007) rather than *Burnetia* and *Proburnetia*, where this depression is shallower (Sidor and Rubidge 2002). *Herpetoskylax* also has a deep vacuity between its palatine bosses as evident in the referred specimen BP/1/3924. In ventral view the medial border of the palatine boss is relatively straight whereas the anterolateral border is more rounded (Fig. 4B). The surface of both bosses is heavily weathered ventrally but the worn roots of four small teeth are present on the anterolateral margin of the right palatine boss, while the left bears the roots of three small teeth along its medial edge. Though weathering has rendered it unclear, the anterior end of the boss also likely bore a peripheral row of teeth as in *Lemurosaurus*, *Herpetoskylax*, *Lophorhinus*, and *Niuksenitia* but the posterolateral margin of the palatine boss was evidently edentulous. As is visible on the right of the skull, the palatine bosses would have projected far ventrally from the level of the lateral palatal shelf as in most other biarmosuchians.

The ectopterygoid is preserved on both sides but is more complete on the right. It manifests as a thin sheet of bone that borders the palatine anteromedially. Although the right ectopterygoid appears displaced, comparison with the same bone in *Herpetoskylax* suggests that it had a similar morphology and has not been massively deformed. In this case the ectopterygoid shares a posteroventrally orientated contact with the palatine along the lateral side of the palatine boss before it meets the pterygoid. The ventromedial part of the ectopterygoid is missing on both sides but on the right it is seen to descend ventrally to meet the lateral end of the transverse process of the pterygoid (Fig. 4B). The lateral edge of the bone carries a sharp ridge, as in *Lobalopex* (Sidor et al. 2004) and *Herpetoskylax* (MOD personal observation). Anterolaterally the ectopterygoid borders the maxilla.

The pterygoids are broken 5–6 mm behind the transverse processes and so the portion posterior to this is not preserved. Anteriorly, the specimen has been sheared at approximately the level of the contact between the pterygoids and palatines with the snout and palate having been displaced right relative to the pterygoids (Fig. 4B). The left pterygoid boss is laterally displaced and poorly preserved but bears the crowns of thirteen small conical teeth in an apparently random distribution. Conversely, the right pterygoid boss is better preserved and is closer to its original position; it shows that the boss peaked at its posteromedial end with two ridges, one extending anteriorly and the other anterolaterally, which would have met the lateral edges of the palatine bosses to form a single palatal structure. Each ridge bears a line of small teeth that converge at the posterior peak of the boss into a cluster but, while the tooth row on the medial ridge continues almost to the border of the

palatine, the lateral ridge does not extend far anterior to the tooth cluster on the peak of the boss.

Between these ridges is a concave and edentulous fossa that begins just anterior to the divergence of the tooth rows and becomes wider and deeper anteriorly (Fig. 4B). This character is not known in any other biarmosuchian except *Niuksenitia* and possibly *Lophorhinus* (this area is not preserved in the holotype but appears to be the case in the juvenile referred specimen), although a concave depression on the palatine boss is found in several taxa (*Herpetoskylax*, *Lemurosaurus*, *Lophorhinus*, *Lobalopex*). A wide, anterolaterally-expanding trough is present between the boss and transverse process of the pterygoid. The transverse process of both pterygoids is preserved but the ventral surface of these bones has been lost to erosion and so it is impossible to determine if they bore teeth or were blade-like. However, the medial end of the left process appears to preserve a very small tooth. The dorsal surface of the transverse process flares out dorsolaterally so that it becomes over 17 mm tall (excluding any missing ventral surface lost to weathering) at its lateral end. Its posterior surface is concave. From the medial end of the transverse process of the pterygoid, a thin ridge extends posteromedially in an arc that, if its trajectory was extrapolated, would probably run just lateral to narrow interpterygoid vacuity. A thin slice of the left pterygoid has entered into that vacuity, giving it the appearance of a median lamina.

Discussion

Identity and relationships of BP/1/7098.—The structure of the palate of BP/1/7098 is clearly biarmosuchian: the prominent and elongated palatal bosses projecting ventrally from the palatal shelf; the long choanae; interchoanal portion of the vomer bearing a downturned lateral flange and broadest at the level of the canine (not anteriorly as in gorgonopsians); and the presence of a narrow interpterygoid vacuity. The pachyostosis of the skull roof and median ridge-like crest on the nasals and frontals further suggests its inclusion within the Burnetiamorpha (Sidor et al. 2004). The anterior margin of the palatine boss and the anteriorly broad vomer of BP/1/7098 alludes to a possible affiliation with *Lophorhinus*, known from the succeeding *Tropidostoma* AZ. However, BP/1/7098 and the holotype of *Lophorhinus* differ in several characters that suggest that they are not congeneric. Pachyostosis of the skull is greater in BP/1/7098, which possesses a well-developed midline nasal boss that is transversely swollen and lacks evidence of a suture, followed by a thickened median crest that extends posteriorly onto the frontals. This more closely approximates the condition in the burnetiid *Paraburnetia*, being rather different from the "low", blade-like semi-circular nasal crest and low frontal ridge in *Lophorhinus*. The postcanine teeth of BP/1/7098 differ in their relative sizes, whereby pc1 is relatively large and situated directly behind the canine, pc2 and pc3 are moderately sized and pc4–7 are small. This contrasts with *Lophorhinus* in which the postcanines are all moderately-sized with the exception of the posterior two, which are smaller. We doubt this is the result of replacement due to the unilateral decrease in size distally, as well as the consistent size of the teeth in *Lophorhinus*. BP/1/7098 also differs from *Lophorhinus* in its possession of a long dorsal process of the premaxilla, the tooth arrangement on the pterygoid bosses and the anterior continuation of the downturned lateral edge of the vomer to the premaxilla. New specimens, including BP/1/7098, have also shown that several characters thought to be autapomorphies of *Lophorhinus* (doubled lacrimal foramina and ossified sphenethmoid) and *Lobalopex* (ectopterygoid with thin lamina) are in fact more widespread.

BP/1/7098 shows a nasal crest morphology that is intermediate between the thin crest of *Lophorhinus* and the continuous naso-frontal ridge, laterally expanded into a boss, of *Paraburnetia*. Although closer to the latter, the nasal crest of BP/1/7098 does not extend anteriorly as far as the external nares as it does in burnetiids. In ventral view, the palatine bosses of BP/1/7098 are similar to those of both *Lophorhinus* and *Niuksenitia*, but its pterygoid bosses closely resemble the latter in tooth organisation and in the presence of a sulcus between the two anteriorly-projecting peripheral tooth rows. It is unfortunate that this area is the only overlap in preserved morphology between the two taxa but, given the variability in palatal boss morphology among burnetiamorphs, it suggests a close relationship between *Niuksenitia* and BP/1/7098.

Although it appears that BP/1/7098 may possess a unique combination of characters, we have decided to refrain from assigning it to a new burnetiamorph taxon. The reasons for this include the generally poor preservation of the specimen and the fact that particularly interesting characters, such as the anterior extent of the downturned edges of the vomer, are not clear in some other biarmosuchian taxa and so their significance is ambiguous. The arrangement of cranial ornamentation is also an important factor in burnetiamorph taxonomy and the lack of the posterior part of the skull in BP/1/7098 makes comparison with other taxa difficult.

Phylogenetic analysis.—When *Biarmosuchus* was included and used to root the tree with character states given equal weighting, three most parsimonious trees were recovered. These trees differ only in the placement of *Lophorhinus* but otherwise suggest the early branching of a monophyletic clade including most non-burnetiamorph biarmosuchians at various times considered members of the family Ictidorhinidae, namely *Herpetoskylax* (= *Rubidgina*), *Lycaenodon*, *Ictidorhinus*, and specimen RC20 (cf. *Lycaenodon*). They also support the grouping of *Hipposaurus* with (*Bullacephalus* + *Pachydectes*) as a sister clade to all other burnetiamorphs. Conversely, under implied weighting for all values of k parsimony analysis recovered a single most parsimonious tree, though these differ in topology. When $k \leq 4$, *Hipposaurus* and *Ictidorhinus* appear as successive taxa at the base of the tree and *Bullacephalus* + *Pachydectes* are

situated within a monophyletic Burnetiamorpha, just above *Lemurosaurus* (Fig. 6A). Increasing values of k, thereby reducing the down-weighting of characters perceived to show high levels of homoplasy, leads to a stable topology in which *Hipposaurus* and (*Bullacephalus* + *Pachydectes*) form the first branching subclade, then the "ictidorhinids", followed by all other burnetiamorphs (Fig. 6B). The only change thereafter is the position of *Lende* and *Burnetia* relative to *Paraburnetia*.

When *Biarmosuchus* was removed and *Hipposaurus* selected as the outgroup taxon, two shortest trees were recovered under equal weighting that again only differed in the position of *Lophorhinus* (Fig. 6C). Under implied weighting a single shortest tree was consistently produced that resolved the position of *Lophorhinus* as sister to (*Niuksenitia* + BP/1/7098) and for which increasing the values of k led only to the closer relationship of *Burnetia* to *Paraburnetia*, to the exclusion of *Lende*. Figure 6 presents a set of trees selected on the basis of stratigraphic congruence but all twelve trees, including consensus trees, are shown in SOM 1: fig. 1.

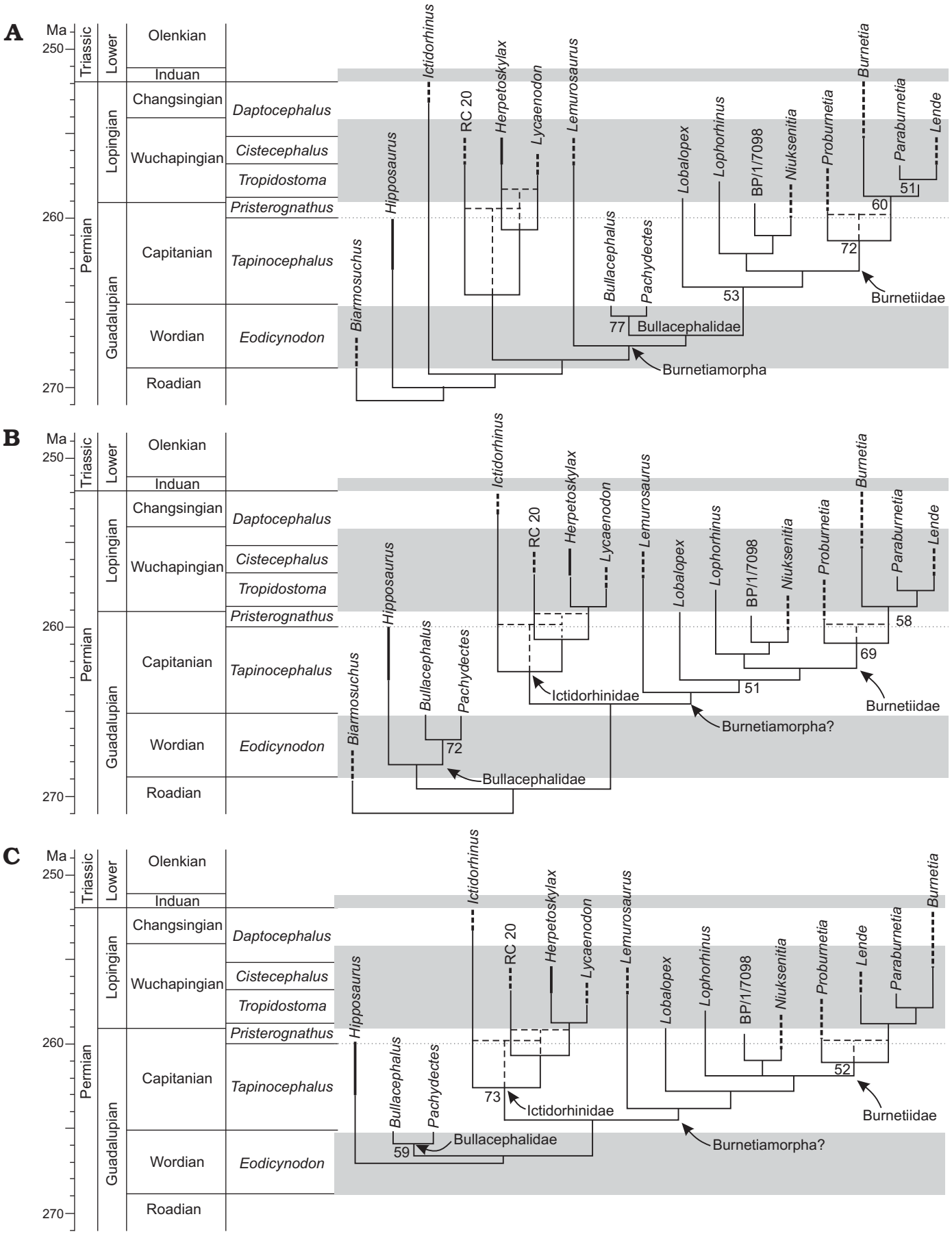
The main results are twofold. Firstly, *Bullacephalus* and *Pachydectes* are returned as sister taxa and are positioned outside Burnetiamorpha as currently defined in all trees except one (*Biarmosuchus* root, implied weights where $k \leq 4$; SOM 1: fig. 1). In this last case they are still at the base of Burnetiamorpha, just above *Lemurosaurus*. When *Biarmosuchus* is used as the outgroup, (*Bullacephalus* + *Pachydectes*) form a clade with *Hipposaurus*, thereby encompassing all Middle Permian biarmosuchians from South Africa. This represents a major shift in biarmosuchian systematics as in all previous studies *Bullacephalus* and *Pachydectes* are not only recovered within Burnetiamorpha but within the family Burnetiidae (Sidor and Welman 2003; Sidor et al. 2004; Sidor and Rubidge 2006; Rubidge et al. 2006; Smith et al. 2006; Sidor and Smith 2007; Kruger et al. 2015; Kammerer 2016).

This raises problems for the diagnosis of Burnetiamorpha as, although *Bullacephalus* and *Pachydectes* have been consistently found to be deeply nested within Burnetiamorpha on the basis of their pachyostotic skulls and cranial bosses, closer inspection shows that these characters may be more subject to homoplasy than previously appreciated. For instance, while most burnetiamorphs except *Lobalopex* possess two bosses on the ventral side of their suborbital bar and zygomatic arch (character 21; with an additional posterior flange present in *Lemurosaurus*), *Bullacephalus* has only one; *Pachydectes* has at least one but is too damaged posteriorly to tell if another was present. It appears that *Bullacephalus* also lacks the swelling of the squamosal at the junction of its three rami lateral to the quadrate (character 19), present in all burnetiamorphs except *Lemurosaurus*. The posterior margin of the squamosal is pachyostosed to a far greater degree in *Bullacephalus* than in any other burnetiamorph (character 25), where it manifests as a swollen rim. In contrast, the posterior margin of the temporal fenestra in *Bullacephalus* forms a thick bar anteriorly that narrows posteriorly. This unique morphology, unlike the shared condition in other burnetiamorphs, suggests that these characters are not homologous. The supraorbital bosses of *Bullacephalus* do bear similarities to those of *Burnetia* but its palate is far more primitive and shares character states with both *Pachydectes* and *Hipposaurus*. All three taxa have relatively large palatine bosses with a row of teeth on the transverse process of the pterygoid (character 29), while *Bullacephalus* shares with *Hipposaurus* a triangular shelf on the anterolateral side of the quadrate ramus of the pterygoid (character 34), a pterygoid trough between the quadrate rami (character 35) and multiple rows of peripheral teeth on the palatine boss (character 27). *Pachydectes* also possesses a pineal chimney as in *Hipposaurus* and the "ictidorhinids", while in *Bullacephalus* the pineal foramen is slightly rimmed despite its great level of pachyostosis (character 18); this contrasts with later burnetiamorphs where the pineal foramen is flush with the surrounding parietals and situated on a wide low swelling or, in the case of *Lende*, in a wide depression.

Bullacephalus and *Pachydectes* are reasonably well supported as sister taxa in all trees. Because of this and the recognition that they share a number of character states that are likely convergent on burnetiids, they are considered here as members of the new family Bullacephalidae (see Systematic palaeontology). The suite of primitive characters, the differences in the manifestation of cranial ornamentation, and the fact that both taxa existed several million years before the appearance of all other burnetiamorphs (see next section) provide strong evidence that the bullacephalids fall outside of Burnetiidae, and potentially of Burnetiamorpha. In either case it suggests that pachyostosis of the skull roof developed twice in biarmosuchians.

Excluding these taxa, the relationships within Burnetiamorpha are mostly poorly supported outside Burnetiidae, but the clade is generally united by the presence of median ridge-like structures on the skull roof (characters 7 and 11), the twin bosses on the suborbital bar and zygomatic arch (character 21), and, with the notable exception of *Burnetia* itself, the presence of a triangular boss above the posterior margin of the orbit (character 13). In burnetiamorphs other than *Lemurosaurus*, the swollen bulb of the squamosal at the contact of its three rami lateral to the quadrate (character 19) and the thickened rim of the posterior margin of the squamosal (character 25) are shared features.

Problems in the diagnosis of Burnetiidae have arisen with the increasing number of recognised burnetiamorph taxa. Almost all features of Burnetiidae described in the diagnosis of Rubidge and Sidor (2002) have now been recognised in non-burnetiid burnetiamorphs, albeit in various combinations. Furthermore, several burnetiamorphs are represented only by partial skulls that do not preserve key parts of their anatomy (e.g., posterior orbital region and zygomatic arch). Combined with the difficulty of recognising sutural contacts in the pachyostosed skull roofs of most burnetiamorphs, at present it is almost impossible to reliably determine if BP/1/7098 or taxa like *Lophorhinus* or *Niuksenitia* truly rep-



resent burnetiids. While this problem cannot be completely overcome, the current definition of the Burnetiidae defines a relatively well supported group including *Proburnetia*, *Burnetia*, *Paraburnetia*, and *Lende*. It can be diagnosed by two distinct bosses on the ventral surface of the zygomatic arch/suborbital bar beneath the postorbital bar; squamosal strongly swollen to a bulb at the contact of its three rami lateral to the quadrate; high midline nasal ridge with lateral swelling into boss (except in *Lende*) extending anteriorly to level of external nares (except in *Burnetia*); presence of developed squamosal "horns"; midline frontal ridge that expands posteriorly; and a low and diffuse swelling surrounding the pineal opening. This revised diagnosis incorporates characters that are visible in most specimens and better allows the assignment of known material, though some characters may overlap with other burnetiamorphs or differ only in degree. BP/1/7098 and *Niuksenitia*, which are consistently grouped by the single synapomorphy of a sulcus on their pterygoid boss, are currently excluded from this family but neither is particularly complete and additional specimens could easily affect their affinity.

The second major difference is that, apart from in the same exception as for the position of the bullacephalids, the Ictidorhinidae is found to be monophyletic, which is also unprecedented. The clade is weakly supported by lack of midline ridges on the skull roof (characters 6 and 11) and, excluding *Ictidorhinus*, by an oblique contact of the nasal with the frontal (character 8), particularly small palatine bosses and a relatively long snout (character 2). This latter character was not actually measured for RC 20 or *Lycaenodon* due to dorso-ventral crushing, but it was no doubt long in both. Nevertheless, the low support for this clade casts doubt on its veracity. In fact, overall support for nodes is rather low (Fig. 6) with resampling support rarely above 50. This results from a number of phenomena including: missing data for many biarmosuchian taxa, poor preservation, variability in many characters, the existence of several one-specimen taxa, the difficulty of identifying sutural contacts in the skull roof of burnetiamorphs and the consequent difficulty in recognising good characters. Only the addition of new specimens can improve this.

Stratigraphic congruence.—Poor support for its subclades has dogged biarmosuchian systematics since the increase in discoveries began just over a decade ago. But a further concern regarding proposed biarmosuchian phylogenies is their stratigraphic incongruence, as observed by Kruger et al. (2015) and Kammerer (2016). In all published trees, the Capitanian-aged bullacephalids from the *Tapinocephalus* AZ are nested within Burnetiidae, despite being the oldest biarmosuchians other than *Biarmosuchus* itself. Conversely, the non-burnetiamorph genera *Ictidorhinus* (*Daptocephalus* AZ; late Wuchiapingian/Changsingian), *Herpetoskylax* and *Lycaenodon* (*Cistecephalus* AZ; late Wuchiapingian) are among the youngest. This implies the existence of long ghost-lineages within the clade and, because well supported phylogenies are expected to be stratigraphically congruent (e.g., Angielczyk and Fox 2006), may suggest that phylogenies where *Bullacephalus* and *Pachydectes* are deeply nested within Burnetiidae do not represent the relationships between biarmosuchians well.

To provide an independent, quantitative test of our phylogenetic hypotheses we compared the stratigraphic congruence of all twelve new trees with those of Kammerer (2016; Fig. 7A) and Kruger et al. (2015; Fig. 7B). Table 1 shows stratigraphic congruence results for the new trees presented in Fig. 6, including the trees with the worst (Fig. 6A) and best (Fig. 6C) fit. Because *Lende* shows great similarity to *Paraburnetia* and the characters differentiating them (ratio of snout height to length, ridge on dorsal surface of nasals,

Table 1. Comparison of stratigraphic congruence metrics for trees shown in Fig. 6 (new trees A–C) and Fig. 7. P-values for individual metrics calculated from 1000 randomly constructed trees bearing the same end taxa. The new trees are better fitted to stratigraphy for all metrics and are the only one significantly different from random for the GER and MSM*. Bold indicates that a stratigraphic congruence metric is significantly different from random at p = 0.05 or p = 0.01. Abbreviations: GER, gap excess ratio; GER*, modified GER; GERt, topological GER; MIG, minimum implied gap; MSM, manhatten stratigraphic measure; MSM*, modified MSM; RCI, relative consistency index; SCI, stratigraphic consistency index; p.Wills, probability as calculated by the position of the MIG for the tree in question compared to the MIG of random topologies (see Bell and Lloyd 2015).

	Metric				Estiamted p-value				Metric			
Tree	SCI	RCI	GER	MSM*	SCI	RCI	GER	MSM*	GER*	GERt	MIG	p.Wills
New Tree A	0.385	-335.877	0.561	0.229	0.256	**0.005**	**0.016**	**0.008**	0.986	0.759	86.304	0.014
New Tree B	0.385	-232.576	0.696	0.301	0.256	**0.003**	**0.000**	**0.000**	1.000	0.951	65.850	0.000
New Tree C	0.500	-219.697	0.713	0.313	**0.041**	**0.003**	**0.000**	**0.000**	1.000	0.974	63.300	0.000
Kammerer	0.286	-510.173	0.333	0.164	0.629	**0.012**	0.507	0.585	0.620	0.437	120.814	0.380
Kruger et al.	0.125	-575.926	0.247	0.148	0.987	**0.015**	0.818	0.818	0.303	0.315	133.833	0.697

← Fig. 6. Three new phylogenies for Biarmosuchia scaled to time and plotted against Permian Beaufort biostratigraphy. **A**. Single most parsimonious tree calculated using implied weights (k ≤ 4) and when *Biarmosuchus* is used as the outgroup. **B**. Single most parsimonious tree calculated using implied weights (k = 5–7) and when *Biarmosuchus* is used as the outgroup. **C**. Strict-consensus of the two shortest trees recovered using equal weights and when *Hipposaurus* was used as the outgroup. A is the least congruent of the twelve trees calculated from the new dataset and is the only one in which *Bullacephalus* and *Pachydectes* are nested within Burnetiamorpha and in which the Ichtidorhinidae is not monophyletic. Numbers at nodes indicate symmetric resampling values based on 10 000 replicates with a cutoff of 50; dotted line indicates the Capitanian extinction horizon as recorded in South Africa; dashed lines indicate cladogenic events that could have occurred after this horizon.

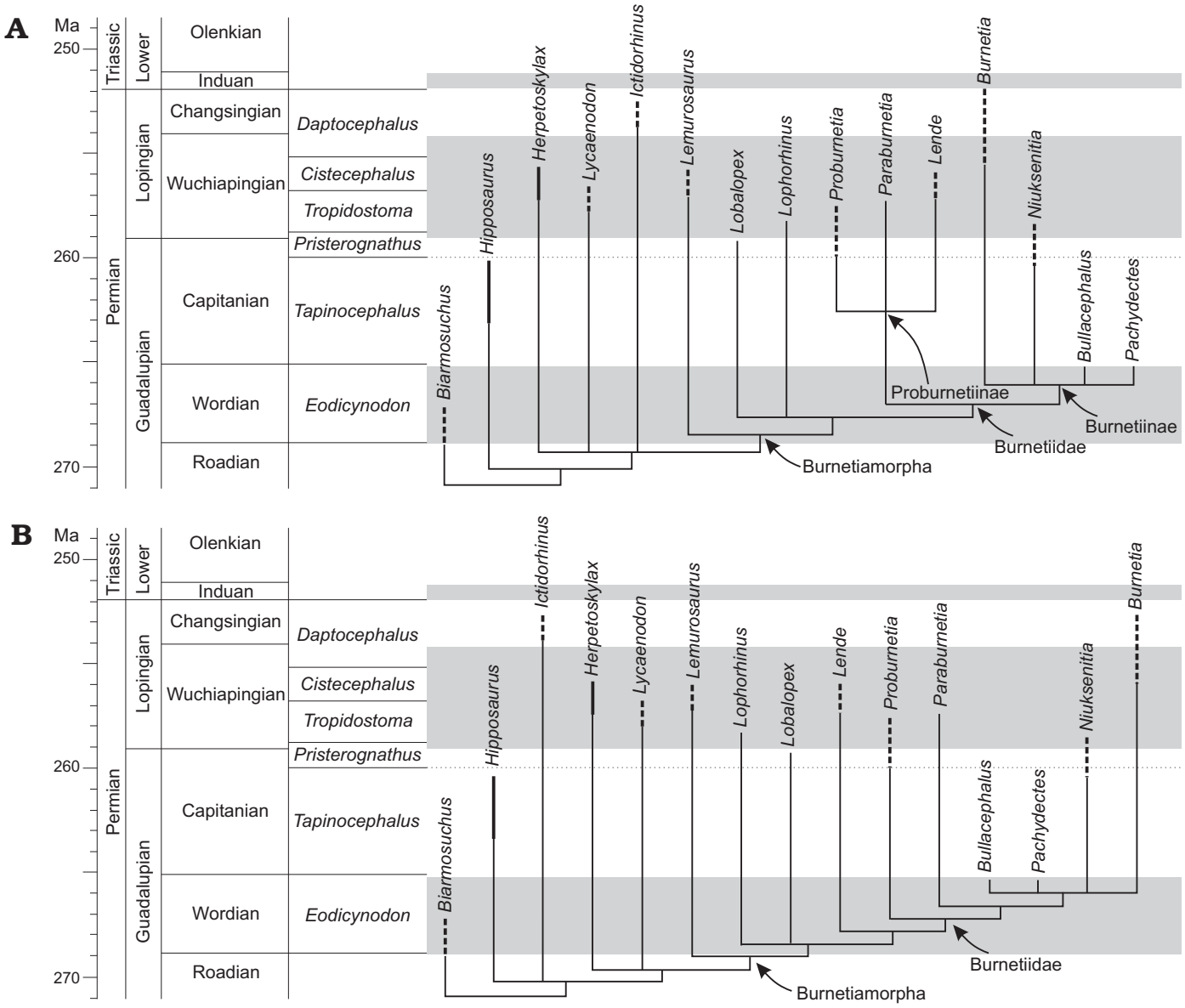


Fig. 7. Previous phylogenies for the Biarmosuchia scaled to time and plotted against Permian Beaufort biostratigraphy. **A**. The strict-consensus tree of Kammerer (2016). **B**. The majority-consensus tree of Kruger et al. (2015). Dotted line indicates the Capitanian extinction horizon as recorded in South Africa.

shape of dorsal surface of parietals surrounding pineal foramen) may be related to ontogeny, we suspect that *Lende* could be a juvenile of *Paraburnetia* or is at least congeneric. If we select a tree in which *Lende* is sister to *Paraburnetia*, it is only marginally suboptimal stratigraphically (Fig. 6B). All new trees fit the stratigraphy better than that of Kruger et al. (2015) or Kammerer (2016) for all metrics, with the minimum required amount of ghost lineage or minimum implied gap (MIG) reduced by 29–49% and 36–54%, respectively (Table 1; see SOM 1: table 1 for all output data). Furthermore, only the new phylogenies are significantly more congruent with stratigraphy for the GER and MSM* metrics than 10 000 randomly generated trees for the same taxa, at the $p = 0.05$ level.

It is worth noting that the RCI values retrieved for all trees are negative due to experimental bias. This is due to the RCI's use of the Simple Range Length (SRL) of terminal taxa, i.e., their temporal duration, as an input variable to estimate coverage of the true phylogeny by the fossil record. However, in the StratPhyloCongruence script we state that randomly.sample.ages = TRUE, meaning that temporal ranges given for each genus are assumed by the program to be an uncertainty. This is appropriate as most taxa are represented by a single specimen and/or are not known from a precise stratigraphic position but this results in point data for taxonomic occurrences and therefore very low SRLs, thus implying poor stratigraphic coverage of the true phylogeny. Because of the way the RCI works, the low SRL values calculated for the biarmosuchian data lead to negative RCI values; however, the output values for the new trees are still less negative than that for the majority-consensus tree of Kruger et al. (2015) or Kammerer (2016).

The primary reason for variance in stratigraphic congruence within the new trees is the position of the bullacephalids and *Hipposaurus*. In the one case where the former is included within Burnetiamorpha congruence is reduced, whereas when equally weighted and rooted with *Biarmosuchus* the position of the (*Hipposaurus* + Bullacephalidae) clade as sister to the Burnetiamorpha slightly reduces congruence. The relationship of *Paraburnetia* to *Burnetia* and *Lende* and the unresolved position of *Lophorhinus* are responsible for the other minor differences. Although none of these relationships is well supported by osteological character data stratigraphic congruence can still provide evidence for the preference of one phylogenetic hypothesis over another. In this case, there is strong stratigraphic support for the more basal position of Bullacephalidae (*Bullacephalus* and *Pachydectes*) outside Burnetiamorpha and to a lesser degree for the monophyly of Ictidorhinidae.

Timing and patterns of biarmosuchian diversification. — BP/1/7098 is the first definite record of a biarmosuchian from the Poortjie Member of the Teekloof Formation, and thus from the *Pristerognathus* AZ. It is possible that *Lobalopex* may also come from this assemblage zone; although it was described as coming from the overlying Hoedemaker Member (*Tropidostoma* AZ; Sidor et al. 2004) the coordinates assigned to the specimen by both these authors and the CGP collections catalogue suggest that it was in fact found in the uppermost part of Poortjie Member, following the published 1 : 250 000 geological map (geological sheet 3122 Victoria West, 1989, Council for Geoscience, Pretoria). In either case, the *Eodicynodon* AZ is now the only Permian biozone of the Beaufort Group that has not yet delivered a biarmosuchian.

When scaled to time, the difference in the phylogenetic position of *Bullacephalus* and *Pachydectes*, as well as the ictidorhinids, has implications for biarmosuchian diversification patterns. In the previous phylogenies, the deeply nested position of these early taxa constrains either all, or at least most biarmosuchian diversification to before the Capitanian, including that of the burnetiids (Fig. 7). This would be consistent with an "early burst" model of diversification within the clade (e.g., Gavrilets and Losos 2009; Slater 2015), perhaps as part of the initial radiation of therapsids in the early Guadalupian (e.g., Kemp 2006; Benton 2012; Brocklehurst et al. 2013) but would be an extreme example with practically no speciation occurring thereafter within the known tree. This model would also suggest high standing diversity of biarmosuchians over the Capitanian and early Wuchiapingian.

Alternatively, the new phylogenies allow for a more even distribution of speciation events within the Capitanian and Wuchiapingian (Fig. 6) and thus could fit several models of diversification. Importantly, this has wide palaeobiological implications as it would have a direct impact upon the perceived phylogenetic severity of the Capitanian extinction event (see Day et al. 2015) and the role of biarmosuchian diversification in the subsequent recovery: later speciation means potentially fewer lineages would have had to pass through the *Tapinocephalus–Pristerognathus* AZ boundary and evolutionary rates could be more variable. In the tree of Kruger et al. (2015) 11 lineages pass through the Capitanian extinction event (excluding RC 20 and BP/1/7098; Fig. 7B), while in that of Kammerer (2016) this could be reduced to nine with the later branching of his "proburnetiines" (Fig. 7A). With the new trees the number of range-through lineages could be reduced to only six (excluding BP/1/7098) due to the potential for the diversification of the ictidorhinids and burnetiids after the Capitanian extinction event and the removal of necessary ghost lineages in the Guadalupian (Fig. 6).

The new phylogenies still suggest diversification of non-burnetiid burnetiamorphs within the Guadalupian prior to the Capitanian extinction event, constrained by BP/1/7098 and the potentially latest Capitanian or early Wuchiapingian age for *Niuksenitia* from the Russian *Proelginia* AZ (Lucas 2006; Smith et al. 2006; c.f. Sidor and Smith 2007; Arefiev et al. 2015; see SOM 4 and 5), as well as mid-Permian "burnetiamorphs" from the Mid-Zambezi Basin of the Zambia (Sidor 2015; Whitney and Sidor 2016). The significance of Zambian fossils is dependent on their currently uncertain phylogenetic affinities, but the large size of the recently described *Wantulignathus gwembensis,* and more circumstantially its association with dinocephalians, suggests it may be a bullacephalid. If this is the case then it provides fewer constraints on the timing of burnetiamorph diversification. Whatever the affinity of the mid-Permian Zambian biarmosuchians, the first appearance of burnetiamorphs, now excluding the bullacephalids, in South Africa and Russia only in the latest Capitanian or earliest Wuchiapingian suggests that they successfully colonised higher latitude basins only after the Capitanian extinction event. This may point to origins in lower latitude regions, possibly in sub-tropical Gondwana.

Conclusions

BP/1/7098 is the first burnetiamorph to be definitively recognised from the *Pristerognathus* AZ of South Africa. Phylogenetic analysis using a modified character list suggests a close relationship between BP/1/7098 and the Russian genus *Niuksenitia*, outside of the Burnetiidae. It also finds that the family Bullacephalidae, consisting of *Bullacephalus* and *Pachydectes*, is not nested within Burnetiidae or even within Burnetiamorpha and instead represents an earlier, independent development of cranial pachyostosis. This hypothesis is based on characters of the palate in the bullacephalids and their similarities with *Hipposaurus*, as well as differences in the development of their cranial ornamentation compared with burnetiamorphs. A monophyletic Ictidorhinidae is also recovered in a modified form, as is Burnetiidae, the latter of which shows no evidence of a split into burnetiines and proburnetiines as per Kammerer (2016). Poor support for most nodes highlights the continuing limitations imposed

on burnetiamorph phylogenetic reconstruction as a result of their scarce record, poor preservation, the difficulty of identifying sutures in many burnetiamorphs and apparently high levels of homoplasy. Further clarification of biarmosuchian evolutionary patterns may be provided by the application of CT scanning methods to better identify sutures and observe internal cranial structures, as well as the increasing number of burnetiamorph discoveries in Permian basins of southern and eastern Africa (e.g., Sidor et al. 2010; Sidor 2015; Whitney and Sidor 2016).

Support for the earlier branching of the bullacephalids is provided by stratigraphic congruence: because these taxa are some of the oldest biarmosuchians, phylogenies constructed from the amended character matrix are invariably more congruent with stratigraphy than the most recently published alternatives and, unlike them, are significantly more congruent for the GER and MSM* metrics than 10000 randomly-generated trees with the same tip taxa. The new topologies postulated here are consistent with later diversification within Burnetiamorpha and Ictidorhinidae and allow for a lower standing diversity of burnetiamorph lineages in the Guadalupian. Depending on the age of the Russian forms *Niuksenitia* and *Proburnetia*, as well as the affinities of the Zambian biarmosuchian fossils, Burnetiamorpha and particularly Burnetiidae could potentially have diversified rapidly in the aftermath of the Capitanian extinction event. Burnetiamorphs dispersed into high latitude basins only at this time.

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