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Cranial morphology and phylogenetic relationship of the enigmatic dinocephalian *Styracocephalus platyrhynchus* from the Karoo Supergroup, South Africa

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Styracocephalus platyrhynchus is an unusual dinocephalian therapsid, known only from a handful of specimens from the *Tapinocephalus* Assemblage Zone of South Africa. It has had a chequered taxonomic history, largely because it is characterized by cranial pachyostosis and the presence of horn-like structures that project posteriorly from the temporal region; these features are found in the clades Burnetiamorpha and Dinocephalia. Its affinities have been further obfuscated by a lack of well-preserved material. This paper presents a description of a well-preserved skull referable to *Styracocephalus* from the western Karoo Basin and provides a revised generic diagnosis for the genus. This study – incorporating comparative anatomy, CT scanning, and cladistic analysis – reveals new character information that was not evident from pre-existing *Styracocephalus* material, and incorporates this into a new phylogenetic analysis. Our analysis recovers Styracocephalidae as a well-supported, monotypic family within Tapinocephalia, which is characterized by: prominent pachyostotic nasal and supraorbital bosses; two posteriorly projecting crest-like protuberances comprising contributions by the postorbital, squamosal and tabular bones; weak lingual heels on the incisor and postcanine dentition present with a moderate upper and lower canine. As *Styracocephalus* is restricted to the upper part of the *Tapinocephalus* Assemblage Zone, it may be a useful biostratigraphic index taxon in future.

Key words: Dinocephalia, *Styracocephalus*, Therapsida, Karoo Supergroup, Middle Permian, Guadalupian.

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INTRODUCTION

The Dinocephalia was a group of successful mid-Permian (Guadalupian) basal therapsids, predominantly known from sedimentary deposits in South Africa and Russia (Rubidge 1991; Ivakhnenko 2008), but with a wide geographic distribution across Gondwana and Laurasia (e.g. Li & Cheng 1995; Langer 2000; Cisneros *et al*. 2012; Lepper *et al*. 2000; Simon *et al*. 2010; Sidor *et al*. 2014; Boos *et al*. 2015). They were some of the earliest large land-living vertebrates, evolving into the top predators and largest herbivores of their time (Boonstra 1969; Benoit *et al*. 2017).

The taxonomy of Dinocephalia has received recent attention (e.g. Kammerer 2011; Atayman *et al*. 2009) but, at least for tapinocephalians, the clade remains in a rather chaotic state. South African dinocephalians were traditionally placed into one of four families: Anteosauridae, Titanosuchidae, Tapinocephalidae and Styracocephalidae (Boonstra 1963); additional families, Rhopalodontidae, Deuterosauridae and Estemmenosuchidae, are known from Russia (Ivakhnenko 2003, 2008). Later systematic schemes have recognized two subclades: Anteosauria, comprising the carnivorous taxa of the family Anteosauridae, and Tapinocephalia, including all herbivorous forms in the families Titanosuchidae, Tapinocephalidae, Styracocephalidae and Estemmenosuchidae (Hopson & Barghusen 1986; Rubidge & van den Heever 1997; Rubidge & Sidor 2001; Kammerer 2011). As well as being relatively richer in species than Anteosauria, the clade Tapinocephalia was herbivorous, had large body size and evolved great cranial pachyostosis (Rubidge & Sidor 2001; Modesto *et al*. 2001).

The family Styracocephalidae is one of the most poorly known dinocephalian groups, and is represented by a single species, *Styracocephalus platyrhynchus* (Haughton, 1929). The holotype (SAM-PK-8936) was discovered in 1928 by L.D. Boonstra on the farm Boesmansrivier, near Beaufort West, and when described a year later by Haughton (1929) was considered sufficiently unusual to warrant the erection of a new suborder, Styracocephalia. The specimen comprises a nearly complete skull, which is crushed dorsoventrally, and a partial lower jaw (Haughton 1929; Rubidge & van den Heever 1997) (Fig. 1A,B). The holotype was the only specimen of *Styracocephalus* known until 1959, when Boonstra collected seven poorly preserved partial skulls that he attributed to *Styracocephalus* (Boonstra 1969). A second series of cranial material was collected in the early 1990s, which prompted Rubidge & van den Heever (1997) to undertake a review of *Styracocephalus*. These authors recognized ten referred specimens in addition to the holotype and expanded the diagnosis.

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Although Haughton initially thought *Styracocephalus* distinct from other therapsid suborders, since then it has mostly been considered as a member either of Burnetiamorpha or of Dinocephalia (Broom 1932; Romer 1945, 1966; Haughton & Brink 1954; Boonstra 1963; Tatarinov 1974; Von Huene 1956; Boonstra 1969; Kitching 1977; King 1988). One numerical cladistic analysis indicated a close relationship with Estemmenosuchidae (Sidor 2000, Rubidge & Sidor 2001). Nevertheless, the precise phylogenetic position of *Styracocephalus* remains tentative, mainly because of the lack of well-preserved material and the poor condition of the holotype.

This paper presents a description of a relatively complete specimen of *Styracocephalus* (BP/1/7141), which preserves morphology not yet described for this genus and allows the formulation of a revised diagnosis (Fig. 1C,D). It also provides new character information that elucidates the phylogenetic position of the Styracocephalidae.

MATERIALS AND METHODS

Mechanical preparation

Mechanical preparation of BP/1/7141 was undertaken by Wilfred Bilankulu at the Evolutionary Studies Institute (ESI), University of the Witwatersrand, using a Desoutter VP2-X airscribe fitted with tungsten carbide tips. Paraloid, diluted with acetone, was used as an adhesive.

CT-scanning and segmentation

To provide information on dental morphology, specimens SAM-PK-8936 and BP/1/7141 (the only specimens which preserve tooth-bearing elements), were scanned at the ESI using microfocus X-ray computed tomography (CT) with a Nikon Metrology XTH 225/320 LC dual-source industrial CT system. For scanning, each specimen was individually packed in specially constructed Perspex tubes and positioned with bubble wrapping or packaging foam. The reconstructed scans were segmented as RAW Volumes and segmentation was completed manually using Avizo Lite v.9.0.0 and Wacom Cintiq graphics tablets.

The holotype (SAM-PK-8936) snout and lower jaw were scanned in two parts. The anterior portion of the snout and mandible were scanned, using the parameters 120 kV, 155 uA at an exposure rate of one frame per second, frame averaging every two frames, with a 1 mm thick copper filter. The snout did not reveal dental features, but data from the lower jaw are presented in the description. For BP/1/7141, after several experimental scans, parameters of 140 kV, 150 uA at an exposure rate of one frame per second, frame averaging every two frames with a 1.5 mm thick copper filter, provided the best resolution and contrast.

Phylogenetic analysis

A cladistic analysis was performed using a modified dataset of Liu *et al*. (2009) with the addition of three tapinocephalid taxa (*Moschops capensis*, *Tapinocaninus pamelae*, and *Ulemosaurus svijagensis*) to better determine the position of *Styracocephalus* in relation to other dinocephalians. Coding for three tapinocephalid taxa was based on descriptions by Gregory (1926) for *Moschops*, Efremov (1940) for *Ulemosaurus*, and Rubidge (1991) for *Tapinocaninus*, and augmented with direct observations based on a *Moschops capensis* skull (AM4950), *Ulemosaurus svijagensis* skull (PIN 2207/2), and the holotype skull of *Tapinocaninus pamelae* (NMQR2987). The final dataset comprises 26 taxa, including seven biarmosuchians, three gorgonopsians, three anomodonts, and nine dinocephalians. More derived therapsid clades (therocephalians and cynodonts) were excluded. A complete list of taxa and characters used is provided in Appendix 1, and the data matrix is reproduced in Appendix 2. The characters used in the data matrix were updated, including the omission of four characters used in Liu *et al*., (2009) (thereby reducing the character number to 67) and the ordering of some states (characters 38 and 58 in this analysis). We omitted characters 18 and characters 41–43 of Liu *et al*. (2009), the first because it was made redundant by refining the definition for character 11, and the latter three because they relate to the basicranium, which is not well preserved in BP/1/7141. *Haptodus* was used as the outgroup taxon.

The character matrix was created in Mesquite version 3.2 (Maddison & Maddison 2017), and 'ordered' parsimony rules applied to characters 38 and 58; however, all characters were treated with equal weight. A parsimony analysis applied to the dataset used the heuristic search algorithm tree bisection reconnection (TBR) in TNT. To avoid becoming trapped in a local minimum, 10 000 random addition sequence replicates were calculated. Taxa with missing data or inapplicable characters were coded '?'. Tree Drift, Ratchet, Tree Fusing and Sectorial searches were also applied. The data matrix was also treated under the assumption of the minimal model of unweighted parsimony using PAUP.4b1 (Swofford 2002), with a Branch and Bound search (exhaustive search; addition sequence = furthest). The results were then visualized using WinClada (Nixon 2002). All characters were equally weighted. Characters 38 and 58 were treated as ordered in a first analysis. and in a second, all characters were treated as unordered. Both analyses found similar results. Ordering the characters results in a most parsimonious tree which is one step longer but does not change the strict consensus tree topology.

To calculate the Bremer support values for each node (Bremer 1994), suboptimal trees up to five steps longer were included, yielding a total of 417 trees when analysed using TBR. Bremer support values were calculated in TNT based on the resulting trees.

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Dinocephalia Seeley, 1894
Tapinocephalia Broom, 1923
Styracocephalidae Haughton & Brink, 1954
Styracocephalus Haughton, 1929

Styracocephalus platyrhynchus Haughton, 1929

Holotype specimen and locality

SAM-PK-8936, a dorsoventrally compressed skull, with

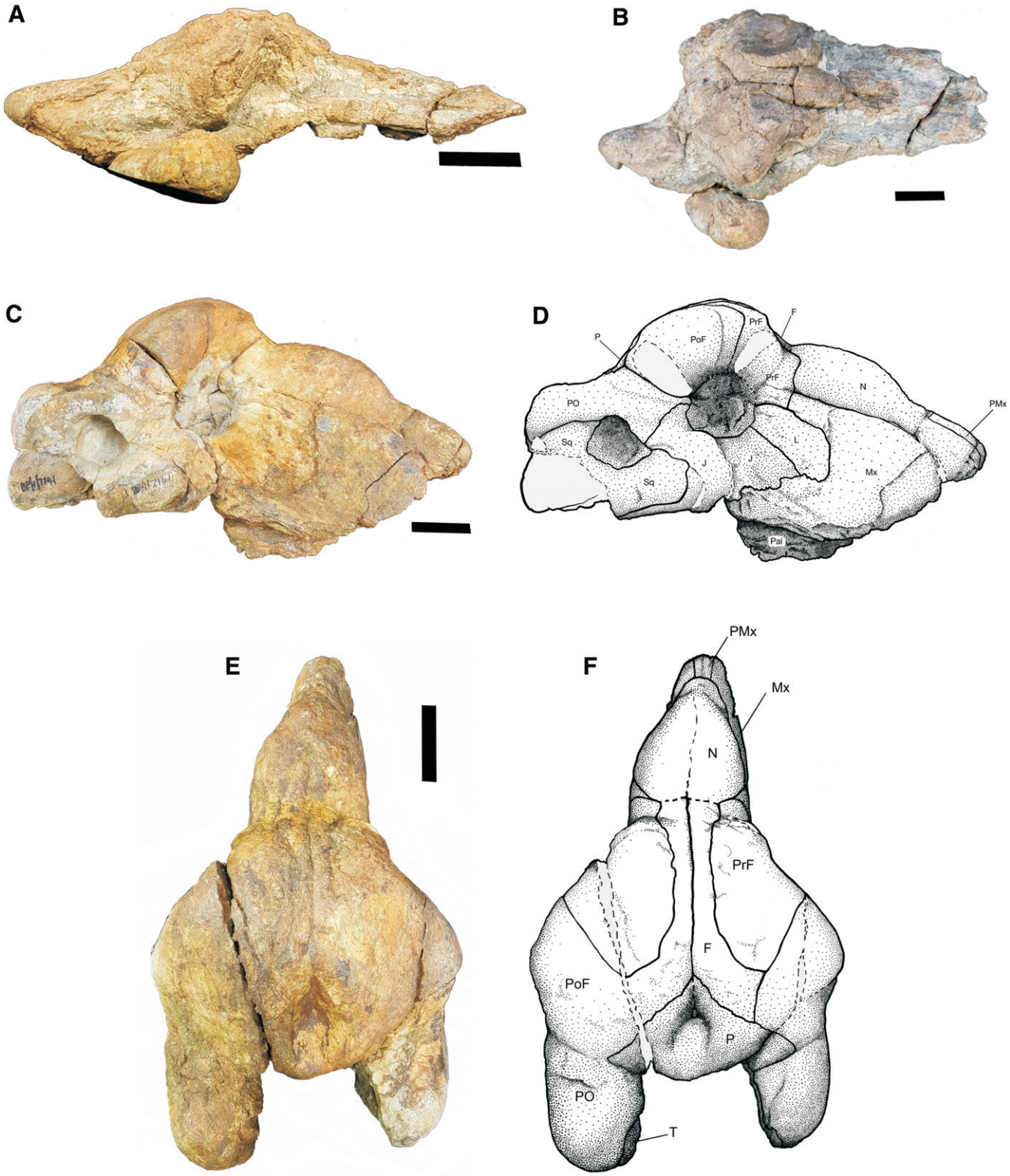


Figure 1. Skull of *Styracocephalus* holotype, SAM-PK-8936: **A**, right lateral view; **B**, dorsal view. Scale bars = 5 cm. *Styracocephalus* specimen BP/1/7141: **C** & **D**, right lateral view; **E** & **F**, dorsal view. Dashed lines indicate areas on BP/1/7141 where material is missing or has been opened by cracks. Scale bars = 5 cm.

the greater portion of the left ramus of the lower jaw. Collected from Boesmansrivier (part of Bushmans River 312), Beaufort West district, Western Cape Province.

Referred material

All referred specimens come from the Western and Northern Cape provinces of South Africa. **BP/1/7141,** an almost complete right side of skull, Tontelbosch (Bastards Berg 35), Sutherland district. Global positioning system (GPS) coordinates for the location on file at the Evolutionary Studies Institute; **BP/1/5433**, the posterior portion of skull roof with left 'horn', Rietfontein (Swaerskraal 40), Laingsburg district; **BP/1/8009,** a portion of skull roof above the orbits with two associated fragments, De Skeur (Riethoek 28), Laingsburg district; **SAM-PK-9346**, the posterior portion of skull roof and separate portion with

heeled incisor teeth (matrix of portion with teeth does not resemble that of skull roof), Abrahamskraal 29, Prince Albert district; **SAM-PK-12181**, the posterior portion of skull roof with right 'horn', Vrederus (Dale Ajalon 322), Beaufort West district; **SAM-PK-12201**, a portion of skull roof, Nelskraal (Flagfontein 308), Beaufort West district; **SAM-PK-12215**, an unprepared skull roof with horns preserved and other skull fragments, Koedoeskop (Leeuwkraal 309), Beaufort West; **SAM-PK-K364**, the posterior portion of skull roof, with right supraorbital region preserved, Leeuskraal (Anysfontein), Fraserburg district.

Age and stratigraphy

All specimens except BP/1/5433 were recovered from the Moordenaars Member of the Abrahamskraal Formation (Upper *Tapinocephalus* Assemblage Zone), Beaufort Group, Karoo Basin, South Africa). BP/1/5433 is likely from the Moordenaars Member but may be from the underlying Swaerskraal Member.

Revised diagnosis

Long-snouted dinocephalian characterized by the following autapomorphies: convex, pachyostosed median nasal boss which is separated from a heavily pachyostosed interorbital region; supraorbital boss projecting laterally over the posterior orbital margin; postorbital that extends far posteriorly above temporal opening to form the dorsal part of the thick, posteriorly projecting horn, the ventral part of which is formed by the squamosal and the medial part by the tabular; narrow frontals bifurcate at the suture with the parietals anterior to the small pineal foramen and extend posterolaterally to meet the postorbitals; square occiput buttressed laterally by thickened squamosal crests; squamosal that extends anteriorly into a boss ventral to the temporal fenestrae. It also defined by the following combination of characters: dentition that comprises a moderate-sized canine in upper and lower jaws, incisors with weak lingual heels, and 8–10 postcanines with weak lingual heels.

Styracocephalus differs from tapinocephalids (except *Tapinocaninus* and *Ulemosaurus*) in the presence of an enlarged canine. *Styracocephalus* differs from titanosuchids in greater pachyostosis of the skull roof, heels on the post-canine dentition and from both tapinocephalids and titanosuchids in the presence of palatal teeth. In *Styracocephalus*, the lacrimal is laterally indented and extends further anteriorly than is seen in other tapinocephalians. The frontal of *Styracocephalus* does not participate in the orbital margin, a condition which is similar to most tapinocephalians but different from anteosaurids and titanosuchids.

Remarks

This diagnosis differs from the diagnosis of Haughton (1929), Boonstra (1963) and King (1988) in the inclusion of a median nasal boss, and confirmation of incisors and postcanines with talon and heel morphology. In addition to the referred specimens above, two other specimens mentioned by Rubidge & van den Heever (1997) are not referable to *Styracocephalus*: specimen SAM-PK-12187 is a fragment of pachyostosed skull roof that shows similarities with burnetiid biarmosuchians in having a narrow intertemporal and a distinct intertemporal boss. BP/1/5428 is a fragment of skull roof that exhibits a strong affinity with Burnetiidae, and may represent a new taxon. For the time being it should be considered Burnetiidae indet.

DESCRIPTION OF BP/1/7141

BP/1/7141 is an almost complete skull preserved in three dimensions, but is mediolaterally compressed, especially in the preorbital region. It was collected from a pebble lag in an interbedded sand- and mudstone horizon from the arenaceous Moordenaars Member of the Abrahamskraal Formation, on the farm Tontelbosch, Sutherland District of Northern Cape Province, South Africa (Fig. 2).

The skull has a length of 376 mm from the tip of the snout to the occiput. In dorsal view specimen BP/1/7141 is broadly triangular with the snout being the apex and is about half as wide as it is long. The right side is mostly complete and allows for good description, whereas the left side of the skull was damaged prior to fossilization so the left maxilla, lacrimal, jugal and squamosal are not preserved. The skull preserves parts of the premaxilla and palate, a large nasal boss, all the supraorbital bones and bones of the skull roof, the ventral process of the postorbital, and the posteriorly projecting horn. The right squamosal boss is missing part of its posteroventral border and small wedges of bone are missing from the supraorbital region at two points, one anterior and one posterior. The basicranium is not well preserved. As a result of compression, the right palatal bones project further ventrally than the left, and a large crack that occurred post-fossilization runs anteroposteriorly through the left orbit and along the skull roof to the occiput. A smaller crack on the right orbit is probably associated with weathering.

The skull has four main regions of cranial pachyostosis: a domed medial nasal boss which is about half as tall as it is long and has a rough dorsal surface; a thick interorbital skull roof that projects laterally into a boss above the posterior margin of the orbit; paired posteriorly projecting pachyostosed and rounded postorbital horns; and a squamosal boss formed by the posterior elements of the jugal and the squamosal that flares out laterally slightly ventral and posterior to the temporal fenestra.

Skull Roof

In dorsal view the *premaxilla* is a narrow strap-like bone forming the tip of the snout. Only the dorsal process of the premaxilla is preserved, as the anterior portion is weathered and the contacts between the premaxilla, maxilla and external nares remain unclear. Its posterior projection is short and terminates in front of the anterior margins of the external nares. The dentulous regions of the premaxilla are not preserved. CT-scans revealed the short premaxillary–nasal suture located just anterior to a straight transverse crack visible across the dorsal surface of the snout, anterior to the nasal boss.

In lateral view, the *maxilla* was a large triangular bone when fully preserved and comprises the greater part of

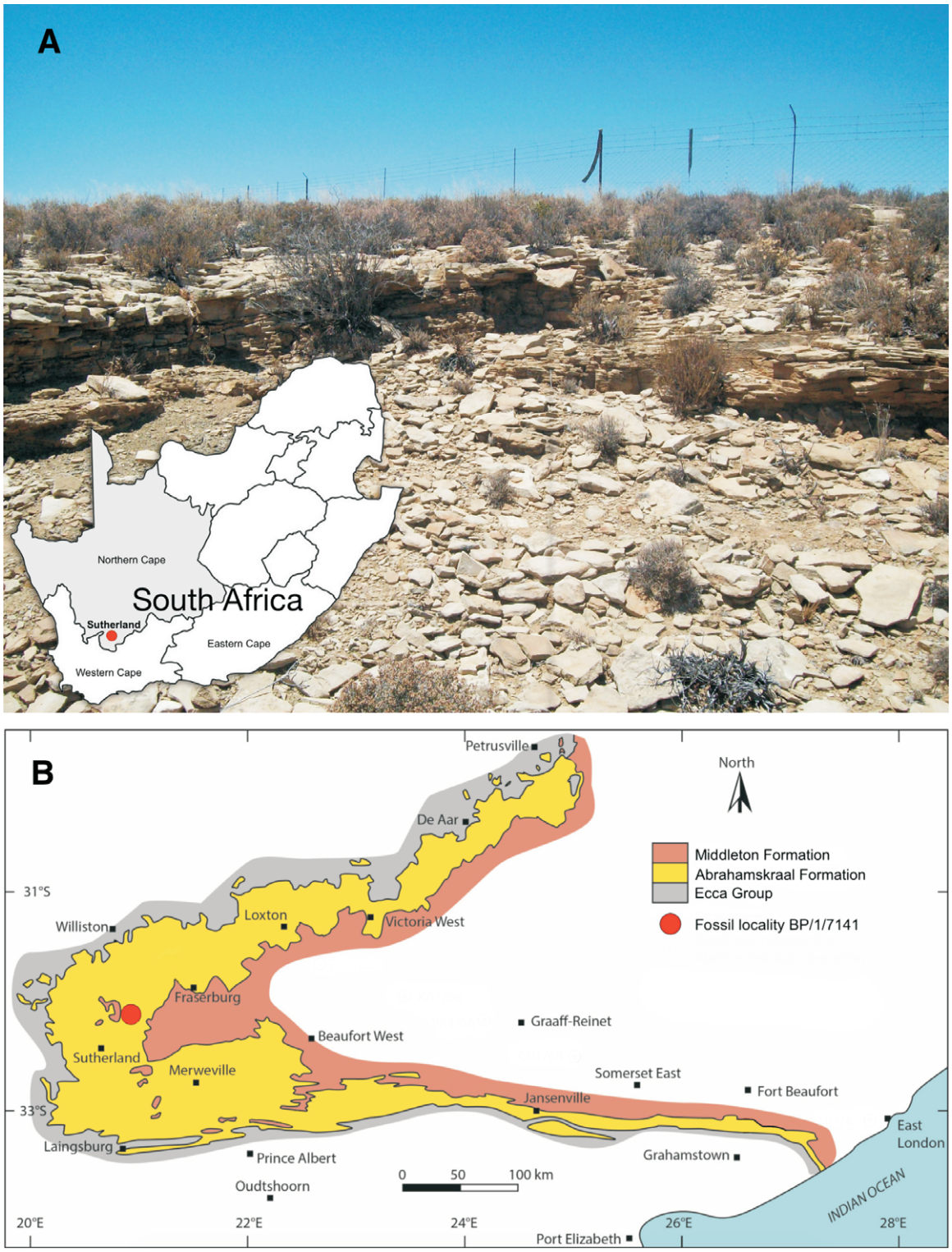


Figure 2. Locality of BP/1/7141. **A**, Photograph of locality on Tontelbosch, Sutherland; inset: map of South Africa showing the locality in the Sutherland district, Northern Cape Province. The precise GPS coordinates of the fossil locality are on file at the Evolutionary Studies Institute. **B**, Lithostratigraphic map shows the position of the fossil locality (red circle) in the Abrahamskraal Formation (yellow). Source: map adapted from Cole *et al*. (2016).

the antorbital region of the skull. Only the posterior portion of the right maxilla is preserved, and the left side has been completely removed. The maxilla contacts the prefrontal posterodorsally, the lacrimal posteriorly, and jugal posteroventrally. Dorsally, it has a long contact with the nasal, and on the left side (where the maxilla has been removed) it is evident that the maxilla laterally overlies the nasal (Fig. 1C–F).

The *lacrimal* is rectangular, forming a small part of the anterior border of the orbit, and is much larger than the estimation figured by Rubidge & van den Heever (1997). It contacts the maxilla anteriorly and ventrally, and the jugal posteroventrally. The lateral surface of the lacrimal is indented to form a trough that extends onto the jugal. No lacrimal foramen can be discerned. Dorsally, the lacrimal meets the prefrontal approximately halfway up the anterior margin of the orbit.

Directly ventral to the orbit, the *jugal* is a thickened,

irregularly shaped bone on the lateral surface of the skull. It forms the ventral margin of the orbit, the lower portion of the postorbital bar, and contributes to a small part of the anterior margin of the temporal fenestra. Anterodorsally it forms an oblique straight sutural contact with the lacrimal, and has an irregular posteroventrally sloping sutural contact with the maxilla ventral to the orbit. Dorsally it overlies the postorbital halfway up the orbit, has a long lunate posterior sutural contact with the squamosal and terminates as a point on the ventral margin of the skull below the temporal fenestra. In the holotype, the suture between the jugal and the postorbital was indeterminate (Rubidge & van den Heever 1997), but this suture is well defined in BP/1/7141 and can be identified on the left side where the postorbital bar has been broken at the level of this suture.

In lateral view, the *squamosal* is roughly 'C'-shaped, making up the ventral and posterior borders of the temporal fenestra. Anteroventrally it is in sutural contact with the jugal, and extends posteriorly well beyond the occiput to form a posteroventrally oriented oblique suture with the postorbital behind the temporal fenestra. Posteromedially, the squamosal sutures with the tabular on the occipital surface. The squamosal boss makes up most of the lateral surface of the skull around the trapezoid temporal fenestra, which is slightly smaller than the orbit. The boss of BP/1/7141 appears less protuberant than that of the holotype, because the skull is not dorsoventrally compressed. The squamosal forms the lateral surface of the horn and its contact with the postorbital extends posteriorly from the dorsal margin of the temporal fenestra; this is not visible in a dorsal view due to pachyostosis of the overlying postorbital, which forms the dorsal surface of the posteriorly projecting horn. The suture between the squamosal and postorbital is recognizable in lateral view as a furrow along the lateral surface of the right horn, leading to the end of the posteriorly projecting horn.

The *nasals* are elongated bones along the midline of the skull on the dorsal surface of the snout. Together, they are pachyostotically thickened (as is evident in cross-section in CT-scanning) to form a prominent domed boss that extends to the level of the maxillo-prefrontal suture. The nasal boss has a rough dorsal surface which makes the midline suture between the nasals less obvious. However, this suture is clear on CT-scans (Fig. 3). Anteriorly, the nasal has a short contact with the dorsal process of the premaxillae. Laterally, it has a large sutural contact with the maxilla and posteriorly it contacts the prefrontal, but its sutural contact with the frontal is unsure. The internarial region at the junction between the dorsal margin of the premaxilla and the nasal bones is broad and reminiscent of the situation in titanosuchid dinocephalians.

The paired *frontal* bones are long and narrow, extending anteroposteriorly along the midline of the skull between the parietal and the nasal, and are laterally flanked by the prefrontals. They are pachyostosed, and do not contribute to the orbital rim. Each frontal extends posterolaterally, towards the posteriorly projecting 'horn', creating a forked 'Y' shape with the base of the 'Y' directed towards the

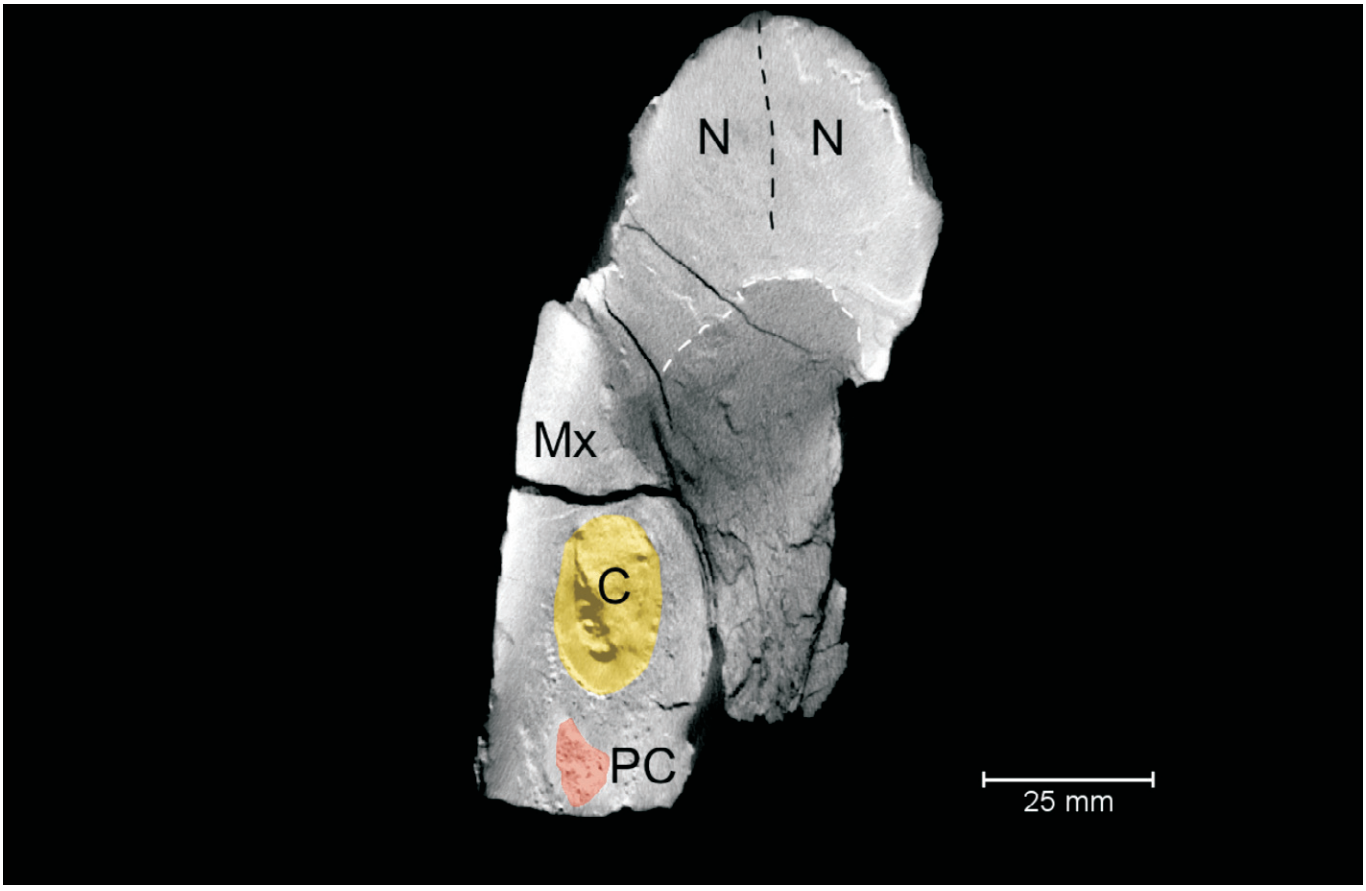


Figure 3. CT image of a vertical section through the snout of BP/1/7141 showing the thickness of the nasal boss at the level of the canine. Black dashed line indicates the position of the midline sutural contact between the nasals. White dashed line indicates the limits of matrix infill.

snout. This bifurcation marks the anterior margin of the parietal (Fig. 1F).

The paired *parietals* form the posterior end of the skull roof and together form a triangle, with the apex in the midline anterior to a small pineal foramen. They broaden posteriorly from a point formed by the bifurcation of the frontals onto the dorsal portion of the occiput. Apart from a short midline suture anterior to the pineal foramen, the suture between the parietal bones is indeterminate as a result of pachyostosis. In BP/1/7141, as in the holotype, the pineal foramen is situated in a fossa. The parietal meets the frontal anteriorly, and the postfrontal laterally. Posteriorly, the parietal contacts the postorbitals, laterally, and the postparietal, medially. In occipital view, a small process of the parietal participates in the medial surface of the horns, where it overlies the tabular and the medial part of the postorbital bones.

The *prefrontal* forms the anterodorsal margin of the orbit. Ventrally it is in contact with the lacrimal, has a short anteroventral contact with the maxilla, and a long anterior contact with the nasal. It has a medial sutural contact with the frontal and an oblique sutural contact with the postfrontal such that the frontal does not participate in the orbital margin. In dorsal view, the prefrontals appear as two thick wedges on the anterolateral side of the distinctive bifurcating median suture, forming a smooth convex boss surface with the postfrontals.

The *postfrontal* forms the posterodorsal margin of the orbit and in dorsal view is a massive, dense and rectangular bone comprising the lateral portion of the bony boss above and behind the orbit. It has a sutural contact with the prefrontal anteriorly, frontal medially, and the postorbital posteriorly.

As indicated by Rubidge & van den Heever (1997), the *postorbital* is a large pachyostosed bone that forms the posterolateral part of the skull roof and the major portion of the dorsal surface of the horns. Posteroventrally, it has a long sutural contact with the squamosal and forms the dorsal and anterodorsal margins of the temporal fenestra. The postorbital forms only a small part of the posterior margin of the orbit. It has a posteroventrally slanting contact with the jugal. This sutural contact is unclear on the right side, but is obvious on the left and shows that the jugal laterally overlies a large part of the anteroventral part of the postorbital.

Occiput

The occiput of BP/1/7141 exhibits the characteristic square shape described for *Styracocephalus* (Rubidge & van den Heever 1997) but is not well preserved (Fig. 4). The right side is better preserved than the left, and the squamosal is entirely missing on the left. It appears to have a more vertical orientation, more like anteosaurids than is the situation in tapinocephalids. The posteriorly projecting horn forms a sort of vertical ridge of bone that delimits the lateral sides of the occiput. The parietal is exposed along the dorsal margin of the occiput. The occipital condyle and foramen magnum are not preserved.

A thin sliver of the dorsomedial protrusion of the *supraoccipital* is preserved. The single *postparietal* is rectangular and bears a vertical midline ridge and a prominent lateral depression on either side for attachment of nuchal ligaments and muscles. The postparietal meets the tabular laterally in a near-vertical suture that has opened as a crack in BP/1/7141, and is in contact with the supraoccipital along its entire ventral margin.

The dorsal portion of the *tabular* is preserved on the left side, and on the right, the entire tabular is missing, exposing the medial surface of the squamosal and postorbital bones. From the left side, it is evident that the tabular would be an ovoid thin plate that overlies the dorsolateral surfaces of the occiput including the medial surface of each posteriorly projecting horn – as described by Rubidge & van den Heever (1997). It is bounded ventrolaterally by the squamosal and ventromedially by the supraoccipital. Dorsally, the tabular contacts the postorbital along a straight suture, and does not contribute much to the dorsal surface of the posteriorly projecting horn.

The squamosal forms most of the lateral margin of the occiput. Only the right squamosal is preserved, and because the tabular is not present, the medial surface of this bone is visible. The dorsal extent of the triangular external auditory meatus is obvious, and a faint suture between the squamosal and the postorbital extends anteromedially.

Palate

The entire ventral surface of BP/1/7141 is extensively weathered, most of it has been eroded away and as such it does not provide much morphological detail (Fig. 4). The palate is laterally crushed and its primary value is in confirming the description of Rubidge & van den Heever (1997), which reported on the relatively better-preserved palate of the holotype.

The very thin and weathered portion of the dorsal process of the premaxilla with a midline suture is evident at the anterior end of the palate but does not exhibit morphological detail. A thin paired vomer extends posteriorly from the premaxilla to meet the palatine dorsal to the palatine boss, but the ventral surface of the vomer is too weathered to determine morphological detail. Although heavily damaged and somewhat laterally compressed, the palatine and pterygoid bosses are prominent (Fig. 4). An interdigitating suture halfway along the length of the boss marks the contact of the palatine with the pterygoid. It is not possible to determine the structure of the lateral process of the palatine. In ventral view the central portion of the palatine boss is raised and bears the roots of at least 12 teeth on the left, and seven on the right. These are arranged along the anteromedial, anterior and lateral margins of the raised portion of the boss. Apart from the very weathered anterior portion of the pterygoid boss, the rest of the palate is not preserved.

The ventral surface of both the maxilla and premaxilla has been eroded away such that a large part of the anteroventral margin of the skull is not present. There are no tooth sockets visible along the lateral margins, indicating that a significant portion of the ventral surface is missing. The roots of two teeth (a canine and post-canine) have been preserved in the right maxilla.

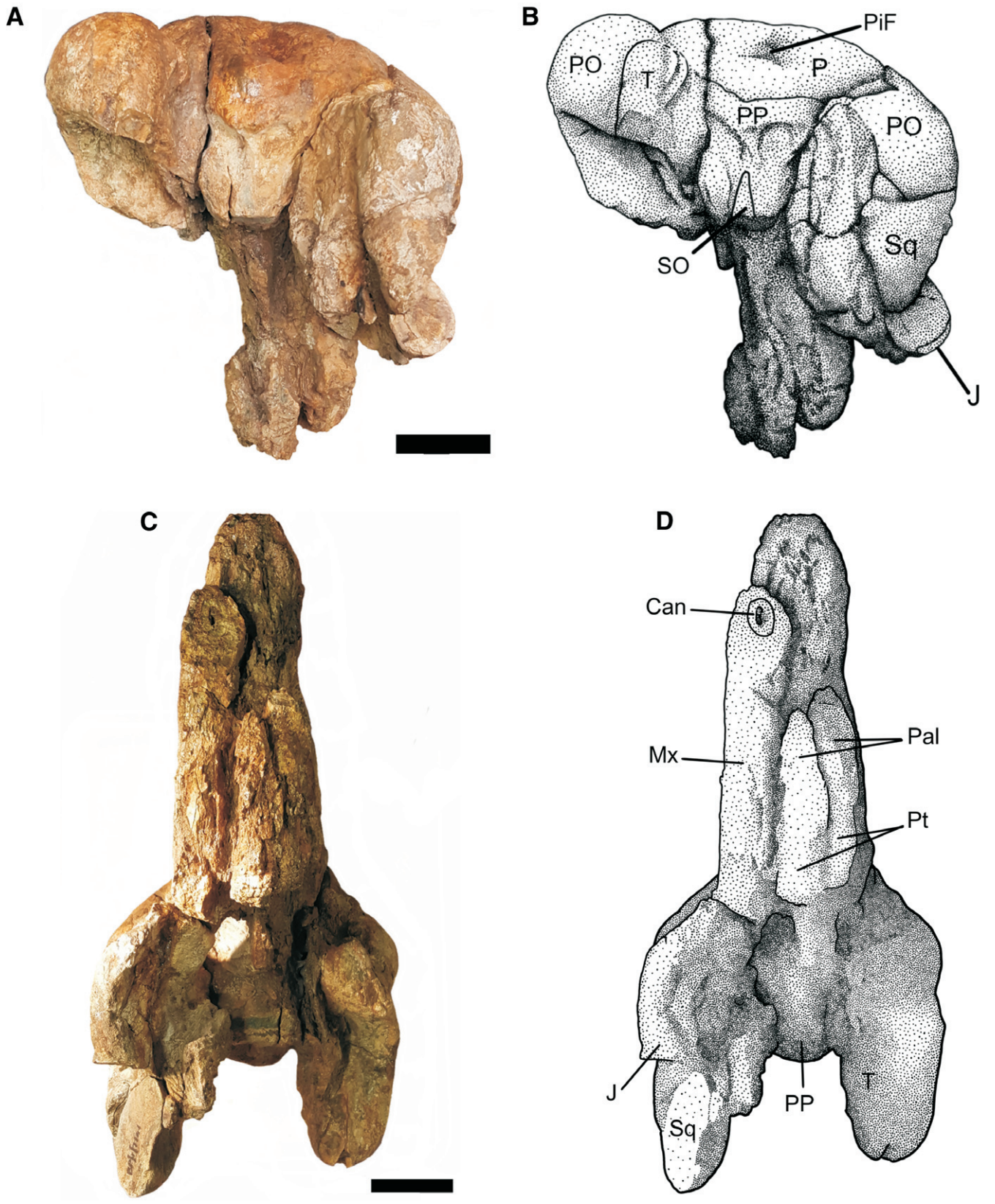


Figure 4. Skull of *Styracocephalus* specimen BP/1/7141. **A** & **B**, Occiput; **C** & **D**, ventral view of the palate. Scale bars = 5 cm.

Dentition

The incisors visible to the naked eye in the lower jaw of the holotype are limited to just two teeth, which are broken close to the base and so provide little morphological information. As the teeth of the holotype of *Styracocephalus* are not well preserved but more of the jaw is present, CT scans were undertaken of both the holotype lower jaw and the snout of BP/1/7141 in an attempt to determine the morphology of unerupted replacement teeth. Segmentation of the lower jaw of the holotype yielded visualization of two generations of replacement incisors, which suggested a weak lingual heel. This was confirmed by segmentation of a first-generation replacement incisor within the upper jaw, which has a character-

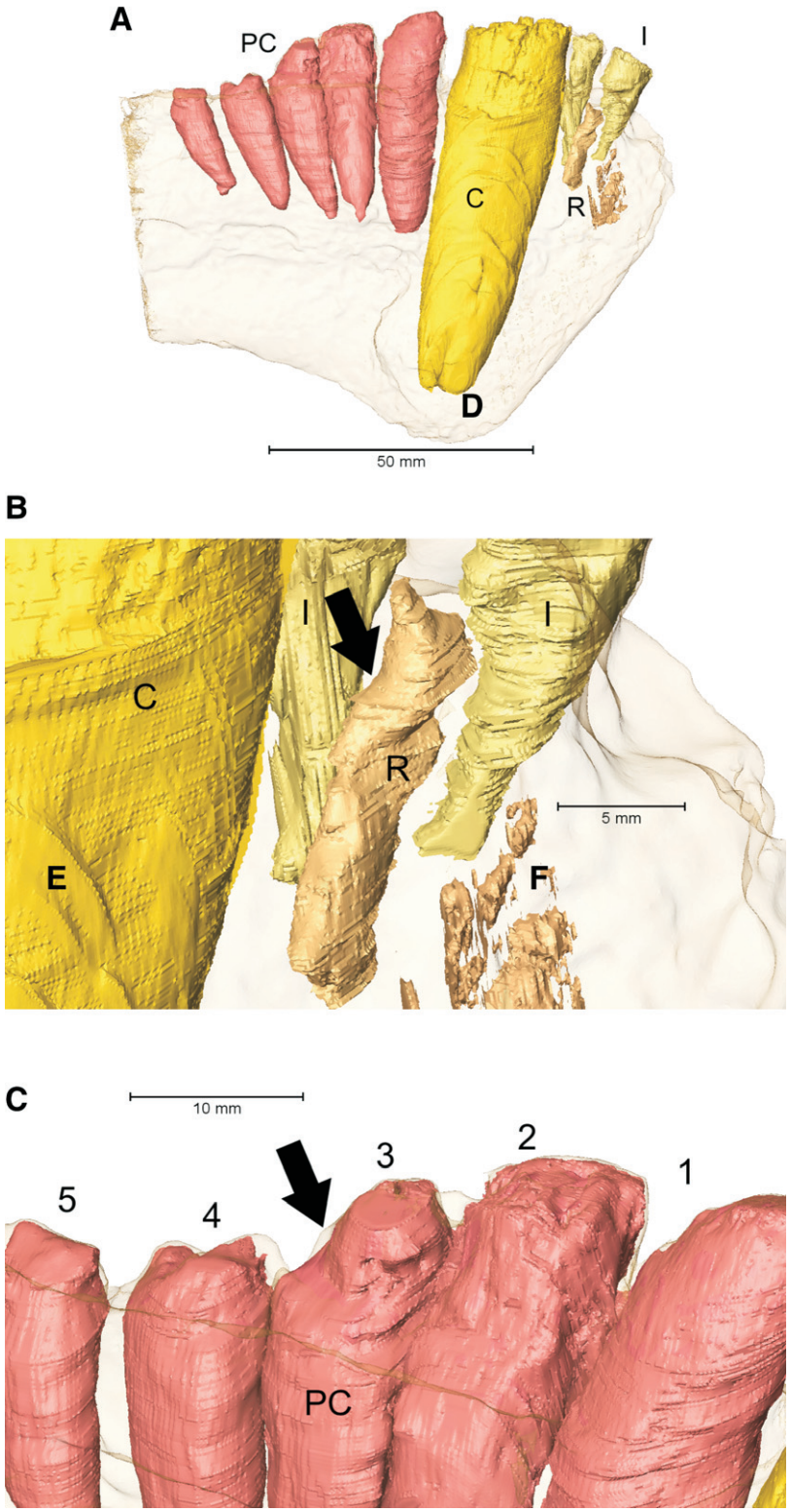


Figure 5. Segmented CT scan reconstruction of the anterior fragment of the left lower jaw of SAM-PK-8936. **A**, Dentition showing two left incisors, canine, postcanines, and two generations of replacement incisors in the mandible; **B**, an unerupted first-generation replacement incisor (labelled 'R') revealed a characteristic dinocephalian talon-and-heel morphology (arrow); **C**, the lingual surface of the postcanines is shown. Most notable is the evidence of lingual heels preserved in the third postcanine (arrow). Note scale bars.

istic dinocephalian talon-and-heel morphology, albeit with a weak heel (Figs 3, 5). All second-generation incisors are too fragmentary to provide conclusive information on tooth morphology.

A row of nine postcanine teeth was segmented in the two preserved fragments of the lower jaw of SAM-PK-8936 (five in the anterior fragment, and four in the posterior fragment). This revealed that the second postcanine is in direct contact with the third postcanine and has the appearance of resorbing the posterior tooth. The third postcanine exhibits a lingual heel (Figs 3, 5).

In the snout of BP/1/7141, the roots of one upper canine and the first postcanine tooth are preserved in the right maxilla but are broken below the level of the alveolar border. The moderately sized canine is oval in cross-section, and the enamel borders of the tooth are of equal

thickness all around the central cavity (Fig. 3). The root of the canine extends well into the maxilla, and both the postcanines and canine have closed roots (evident in CT-scans). While no heel is evident on the first postcanine, on the CT reconstructions the elongate cross-sectional shape of this tooth is suggestive of a lingual heel as in the holotype. Further evidence for this feature is that the enamel on the lingual side of the cross-section was almost twice as thick as the enamel on the buccal side, indicating a strong possibility of a talon and heel morphology for both the upper and lower postcanines of *Styracocephalus* as well as the incisors.

Small broken teeth and even a few small crowns are preserved on the palatine and pterygoid bosses, confirming the observation of Rubidge & van den Heever (1997), who counted 12 teeth on the palatal bosses in the holotype. At least six teeth are visible in two rows on the left palatal boss of BP/1/7141. The diameter of each tooth is between 3.2 mm and 4.8 mm, with the smaller teeth positioned anteriorly and larger ones posteriorly. A tooth crown (3.9 mm high, 4.6 mm length anterior–posterior × 2.9 mm diameter medial–lateral) embedded in matrix attached to the boss shows that the shape of these palatal teeth is roughly triangular, with a rounded anterior side and tapered posterior margin.

DISCUSSION

Revised anatomy of *Styracocephalus*

The characteristic posteriorly projecting bosses ('horns') have previously been described as tabular bosses (Boonstra 1963), but BP/1/7141 reveals that the tabular is a relatively flat bone that is restricted to the occiput where it overlies the postorbital and squamosal bones, medially. Our description confirms the finding of Rubidge & van den Heever (1997) that the posterior projecting 'horns' are formed to a large degree by the postorbitals. However, the postorbital only forms the dorsal part of the 'horn', and does not extend posterior to the squamosal boss; it thus appears that the posterior projection of the postorbital relative to the squamosal boss in the holotype is in fact the result of dorsoventral compression. Similarly, deformation is likely responsible for the lateral splay and anteroventral orientation of the squamosal boss in the holotype. The better preservation of BP/1/7141, even although it has suffered some lateral compression, demonstrates that previous reconstructions were not correct in this regard (Boonstra 1963; Rubidge & van den Heever 1997), and that the thickness of the postorbital bar was previously underestimated.

Boonstra (1934) considered *Styracocephalus* a dinocephalian on the basis of the morphology of its palate and basicranium, the configuration of the bones of the skull roof, and the pachyostosis of the postorbital and supraorbital regions. The pachyostosis in the supraorbital region of BP/1/7141 (62 mm) is comparable with the skull roof thickness of derived Tapinocephalidae such as *Moschops*, which can be 5–6 cm thick at the cranial vault (Gregory 1926; Benoit *et al*. 2017). Whereas some dinocephalians have a pachyostosed naso-frontal boss (Boonstra 1969; Benoit *et al*. 2017), in *Styracocephalus* the nasal boss does not extend onto the frontals. The presence of the nasal boss was previously unknown in *Styracocephalus*, as the anterior skull roof is very poorly preserved in the holotype (the only other specimen to have a snout). This prominent feature is uncommon in dinocephalians and we consider it a character diagnostic of *Styracocephalus*.

Furthermore, CT images of BP/1/7141 and SAM-PK-8936 for the first time confirm that *Styracocephalus* has lingual heels on both the incisor and postcanine teeth immediately posterior to the canine, which is a character normally associated with tapinocephalid dinocephalians (Rubidge 1991; Atayman *et al*. 2009).

Phylogenetic analysis

The phylogenetic analysis of the dataset in Appendix 2 resulted in eleven most parsimonious trees. The strict consensus of these trees is shown in Fig. 6. Each tree had an identical tree length of 188 steps. The consistency index (CI) is 0.452, the homoplasy index (HI) is 0.5479, the retention index (RI) is 0.741 and the rescaled consistency index (RC) is 0.335. Polytomies were recovered for the relationships between *Dimetrodon* and *Tetraceratops*; between *Herpetoskylax*, *Lycaenodon* and the Burnetiamorpha (Biarmosuchia); and between the gorgonopsians included in the analysis; however, the relationships within Dinocephalia were well defined). Dinocephalia is supported by six unambiguous synapomorphies: narrow interparietal (character 18[state 1]), vomerine process of the premaxilla absent in ventral view (27[2]), post-parietal taller than wide in occipital view (41[2]), intermeshing incisors (58[2]), heeled incisors (59[1]) and canines (63[1]); and two ambiguous synapomorphies: short facial exposure of the septomaxilla (7[1]) and vertically oriented occiput (42[1]).

Estemmenosuchus was recovered as the sister taxon to all other tapinocephalians, with Tapinocephalia being supported by two unambiguous synapomorphies (posterior shelf of the pterygoid present, 39[1] and pronounced forward rotation of the occiput, 42[2]) and five ambiguous synapomorphies.

Phylogenetic relationships within Tapinocephalia are weakly supported by ambiguous synapomorphies and Bremer values of 1 only. This implies that the hypothetical relationships discussed below are likely to change in the future, pending discovery of more complete material as well as redescription of specimens in museum collections. Our analysis recovers *Styracocephalus* as the sister group to a clade consisting of *Jonkeria* (Titanosuchidae) and Tapinocephalidae. This occurs in spite of the apparent close relationship of *Styracocephalus* to the Tapinocephalidae suggested by the talon-and-heel morphology of the postcanines and great degree of cranial pachyostosis. The sister-group relationship between *Styracocephalus* and the clade Titanosuchidae + Tapinocephalidae is supported by three ambiguous characters: the presence of a low, weakly defined pineal boss (17[1]), a vomer internarial part parallel-sided (29[0]) and the loss of the stapedial foramen (45[1]). The clade gathering Titanosuchidae

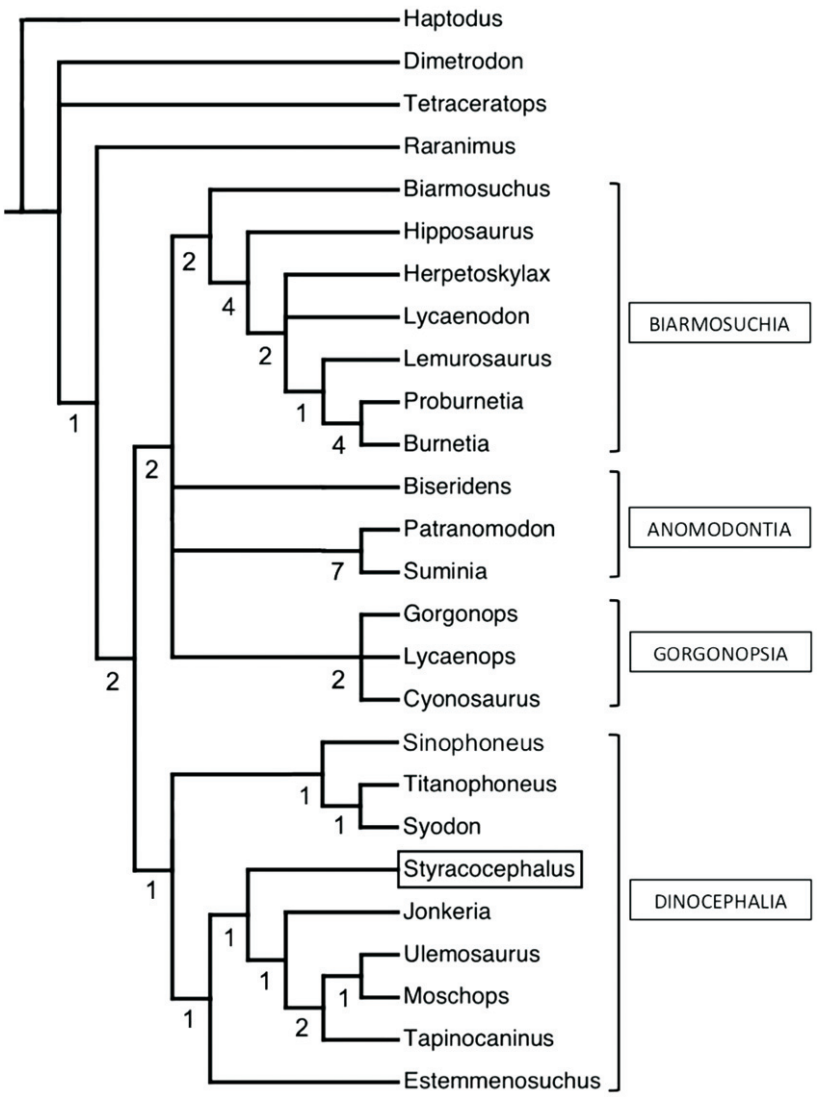


Figure 6. Results of the phylogenetic analysis of *Styracocephalus* amongst basal therapsids. Tree (tree length = 188, consistency index = 0.452, retention index = 0.741) is the strict consensus tree of eleven shortest trees resulting from our PAUP and TNT analysis of 67 cranial and dental characters. Numbers on tree indicate decay index of the respective clade.

and Tapinocephalidae is supported by three characters relating to the loss of palatal dentition: teeth on the palatine bosses, pterygoid bosses, and lateral flange of the pterygoid, respectively (35[2], 36[1], 37[1]).

These results do not support a close relationship between *Styracocephalus* and Burnetiidae. More generally, Biarmosuchia is defined by several characters that also apply to Dinocephalia, such as a moderately forward-rotated occiput (Rubidge & Sidor 2001), intermeshing incisors (Rubidge & Sidor 2001), and cranial pachyostosis (Benoit *et al*. 2016, Rubidge & Sidor 2001). Burnetiamorph skulls, like dinocephalians, also exhibit protuberances and bosses, including a nasal boss (Rubidge & Sidor 2001; Rubidge & Sidor 2002). However, *Styracocephalus* appears excluded from the Burnetiamorpha in our analysis as the Biarmosuchia is supported by two unambiguous synapomorphies that are absent in dinocephalians (including *Styracocephalus*): the dorsal notch of the reflected lamina of the angular is located near the articular (51[0]) and the upper incisors are roughly equivalent in size to the post-canine teeth (60[1]). The above-mentioned similarities between burnetiamorph taxa and *Styracocephalus* are therefore better interpreted as homoplasies.

Our study supports the existence of the family Styracocephalidae, which can be distinguished from other dinocephalian families in possessing all the following synapomorphies: incisor and postcanine dentition having weak heels; long postcanine tooth row of 8–10 teeth in line with the canine; moderately sized canine in both upper and lower jaws; specialized cranial pachyostosis in the supraorbital and postorbital regions; distinctive posteriorly projecting postorbital and squamosal crests, and a thick median nasal boss. Though some of these characters are present in other dinocephalian families, their combined presence is unique to Styracocephalidae. To these characters, the cladistic analysis identifies five additional autapomorphies of *Styracocephalus*, all ambiguous: a short dorsal process of the premaxilla (4[0]), temporal fossa smaller than the orbit (11[0]), posterior process of the post-orbital that does not extend beyond the level of the temporal fossa laterally (14[1]), post-parietal is wider than tall (41[0]) and a pronounced difference in dentary height between the canine and post-canine regions of the lower jaw (46[1]).

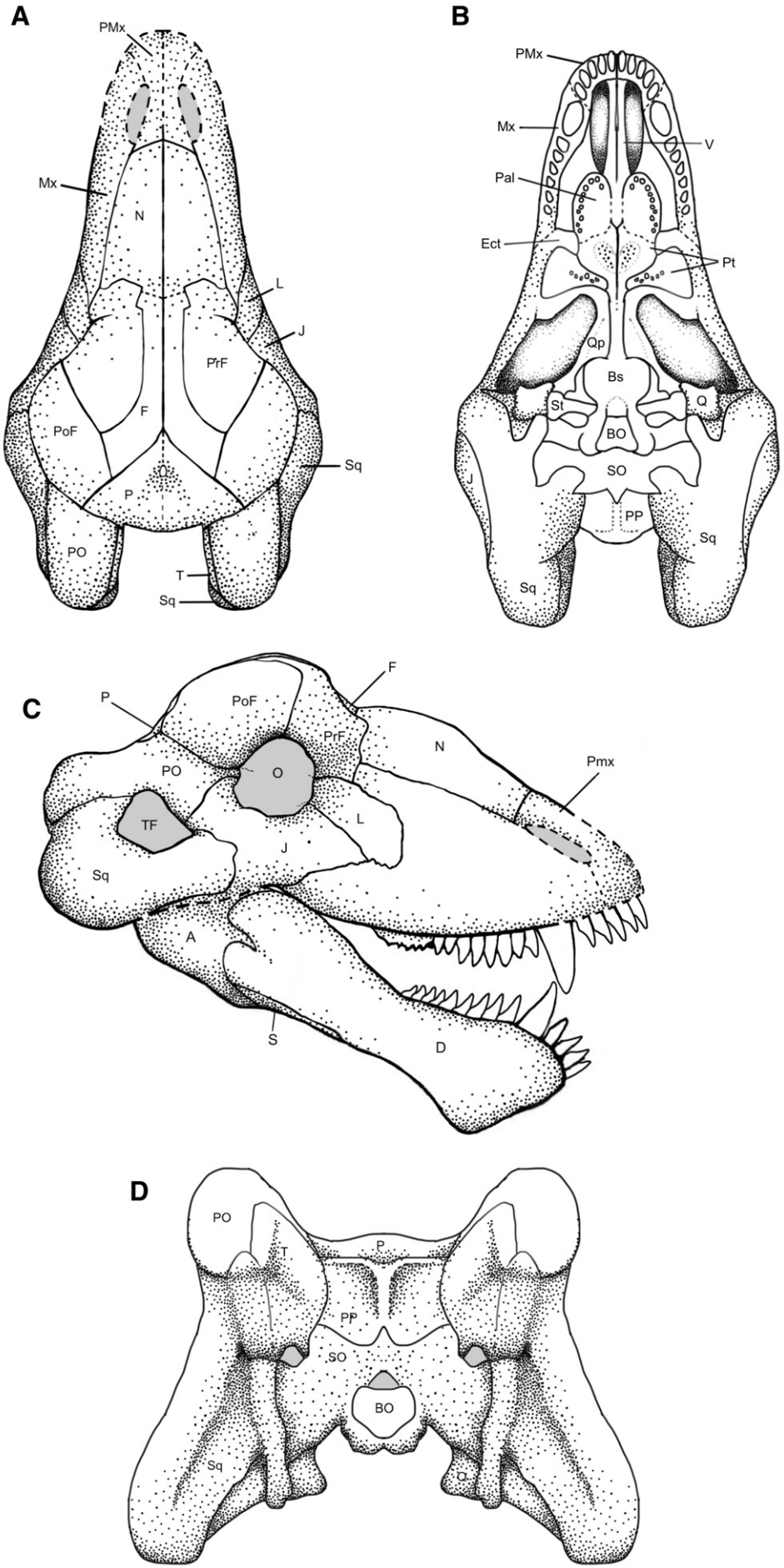


Figure 7. Composite diagrams of *Styracocephalus* skull. **A**, Dorsal view; **B**, ventral view; **C**, lateral view; **D**, occiput.

CONCLUSIONS

1. BP/1/7141 is an almost complete skull of the tapinocephalian *Styracocephalus*, and provides useful new information on the morphology and position of cranial bones and the nature of their contacts, especially in the circumorbital and preorbital regions. New characters such as the swollen median nasal boss and thick postorbital bar, previously unknown for *Styracocephalus*, are recognized for the first time, as well as the relationship between the postorbital, squamosal and tabular bones described by Rubidge & van den Heever (1997). An updated composite cranial figure of *Styracocephalus* is presented in Fig. 7.
2. CT images of the holotype (SAM-PK-8936) and BP/1/7141 confirm the existence, previously mooted but not demonstrated by Boonstra (1969), of weak lingual heels on both the incisors and postcanines of *Styracocephalus*.
3. Scanning also enabled updated and more precise coding of the character matrix for a phylogenetic analysis. *Styracocephalus* is recovered as the sister-group to a clade composed of Titanosuchidae and Tapinocephalidae. The analysis suggests that Styracocephalidae can be considered as a distinct monotypic family.
4. *Styracocephalus* appears to be restricted to the upper part of the *Tapinocephalus* Assemblage Zone, and may prove to be a useful biostratigraphic indicator.

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ABBREVIATIONS

Institutional

BP	Evolutionary Studies Institute (formerly Bernard Price Institute), Johannesburg, South Africa.
SAM	Iziko, South African Museum, Cape Town, South Africa.

Anatomical

A	articular	PMx	premaxilla
C	canine	PP	postparietal
D	dentary	PO	postorbital
F	frontal	PC	postcanine
I	incisor	PoF	postfrontal
J	jugal	PrF	prefrontal
L	lacrimal	Pt	pterygoid
Mx	maxilla	R	replacement incisors
N	nasal	S	splenial
O	orbit	SO	supraoccipital
P	parietal	Sq	squamosal
Pa	prearticular	T	tabular
Pal	palatal	TF	temporal fenestra
PiF	pineal foramen	V	vomer

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REFERENCES

ATAYMAN, S., RUBIDGE, B.S. & ABDALA, F. 2009. Taxonomic re-evaluation of tapinocephalid dinocephalians. *Palaeontologica africana* **44**, 87–90.

BENOIT, J., MANGER, P.R., FERNANDEZ, V. & RUBIDGE, B.S. 2016. Cranial bosses of *Choerosaurus dejageri* (Therapsida, Therocephalia): earliest evidence of cranial display structures in eutheriodonts. *PLOS ONE* **11**(8), e0161457.

BENOIT, J., MANGER, P.R., NORTON, L., FERNANDEZ, V. & RUBIDGE, B.S. 2017. Synchrotron scanning reveals the palaeoneurology of the head-butting *Moschops capensis* (Therapsida, Dinocephalia). *PeerJ* **5**, e3496; DOI: 10.7717/peerj.3496

BOONSTRA, L.D. 1934. On an aberrant gorgonopsian *Burnetia mirabilis*. *South African Journal of Science* **31**, 462–470.

BOONSTRA, L.D. 1963. Diversity within the South African Dinocephalia. *South African Journal of Science* **59**, 196–206.

BOONSTRA, L.D. 1969. The fauna of the *Tapinocephalus* Zone (Beaufort beds of the Karoo). *Annals of the South African Museum* **56**, 1–73.

BOOS, A.D.S., KAMMERER, C.F., SCHULTZ, C.L., PAES NETO, V.D. 2015. A tapinocephalid dinocephalian (Synapsida, Therapsida) from the Rio do Rasto Formation (Parana Basin, Brazil): taxonomic, ontogenetic and biostratigraphic considerations. *Journal of South American Earth Sciences* **63**, 375–384.

BREMER, K. 1994. Branch support and tree stability. *Cladistics* **10**, 295–304.

BROOM, R. 1932. *The Mammal-like Reptiles of South Africa and the Origin of Mammals*. London, HF & G Witherby. 376 pp.

CISNEROS, J.C., ABDALA, F., ATAYMAN-GÜVEN, S., RUBIDGE, B.S. & CELÂL SENGÖR, A.M. 2012. Carnivorous dinocephalian from the Middle Permian of Brazil and tetrapod dispersal in Pangaea. *Proceedings of the National Academy of Sciences of the United States of America* **109**(5), 1584–1588.

COLE, D.I., JOHNSON, M.R. & DAY, M.O. 2016. Lithostratigraphy of the Abrahamskraal Formation (Karoo Supergroup), South Africa. *South African Journal of Geology* **119**(2), 415–424.

EFREMOV, I.A. 1940. *Ulemosaurus svijagensis* Riab., Ein Dinocephale aus den Ablangeungen des Perm. De U.S.S.R. *Nova Acta Leopoldina*, n. Folge, 9, 12–205 (German, English summary).

GREGORY, W.K. 1926. The skeleton of *Moschops capensis broom*, a dinocephalian reptile from the Permian of South Africa. *Bulletin of the American Museum of Natural History* **56**, 179–288.

HAUGHTON, S.H. 1929. On some new therapsid genera. *Annals of the South African Museum* **28**, 55–78.

HAUGHTON, S.H. & BRINK A.S. 1954. A bibliographical list of Reptilia from the Karoo beds of Africa. *Palaeontologica africana* **2**, 1–187.

IVAKHNENKO, M.F. 2003. Eotherapsids from the East European Placket (Late Permian). *Palaeontological Journal* **37(**4), 339–465.

IVAKHNENKO, M.F. 2008. Cranial morphology and evolution of Permian Dinomorpha (Eotherapsida) of Eastern Europe. *Paleontological Journal* **42**(9), 859–995.

KAMMERER, C.F. 2011. Systematics of the Anteosauria (Therapsida: Dinocephalia). *Journal of Systematic Palaeontology* **9**(2), 261–304.

KEMP, T.S. 2005. *The Origin and Evolution of Mammals*. Oxford, Oxford University Press.

KING, G.M. 1988. Anomodontia. **In**: Wellnhofer, P. (ed.), *Encyclopedia of Paleoherpetology*. 174 pp. Stuttgart, Gustav Fischer.

KITCHING, J.W. 1977. The distribution of the Karroo vertebrate fauna. *Memoirs of the Bernard Price Institute for Palaeontological Research, University of the Witwatersrand* **1**, 1–131.

LANGER, M.C. 2000. The first record of dinocephalians in South America: Late Permian (Rio do Rasto Formation) of the Paraná basin, Brazil. *Neues Jahrbuch für Geologie und Paläontologie Abhandlunge* **215**(1), 69– 95.

LEPPER, J., RAATH, M.A. & RUBIDGE, B.S. 2000. A diverse dinocephalian fauna from Zimbabwe. *South African Journal of Science* **96**, 403–405.

LI, J. & CHENG, Z. 1995. A new Late Permian vertebrate fauna from Dashankou, Gansu with comments on Permian and Triassic vertebrate assemblage zones of China. **In**: Sun A.L. & Wang Y.Q. (eds), *Short Papers of Sixth Symposium on Mesozoic Terrestrial Ecosystems and Biota*, 33–37. Beijing, China Ocean Press.

LIU, J. 2013. Osteology, ontogeny, and phylogenetic position of *Sinophoneus yumenensis* (Therapsida, Dinocephalia) from the Middle Permian Dashankou fauna of China. *Journal of Vertebrate Paleontology* **33**(6), 1394–1407.

LIU, J., RUBIDGE, B.S. & LI, J. 2009. New basal synapsid supports Laurasian origin for therapsids. *Acta Palaeontologica Polonica* **54**(3), 393–400.
LIU, J., RUBIDGE, B.S & LI, J. 2010. A new specimen of *Biseridens qilianicus* indicates its phylogenetic position as the most basal anomodont. *Proceedings of the Royal Society B: Biological Sciences* **277**, 285–292.
MADDISON, W. & MADDISON, D. 2017. Mesquite version 3.3.2 (build 801).
MODESTO, S.P., RUBIDGE, B.S., DE KLERK, W.J. & WELMAN, J. 2001. A dinocephalian therapsid fauna on the Ecca–Beaufort contact in Eastern Cape Province, South Africa. *South African Journal of Science* **97**, 161–163.
NIXON, K.C. & CARPENTER, J.M. 2002. WinClada ver. 1.00. 08. Published by the author, Ithaca, NY, 2002. On simultaneous analysis. *Cladistics* **12**(3), 221–241.
ROMER, A.S. 1945. *Vertebrate Paleontology* (2nd edn). Chicago, University of Chicago Press.
ROMER, A.S. 1966. *Vertebrate Paleontology* (3rd edn). Chicago, University of Chicago Press.
RUBIDGE, B.S. 1991. A new primitive dinocephalian mammal-like reptile from the Permian of southern Africa. *Palaeontology* **34**(3), 547–559.
RUBIDGE, B.S. & SIDOR, C.A. 2001. Evolutionary patterns among Permo-Triassic therapsids. *Annual Review of Ecolological Systems* **32**, 449–480.
RUBIDGE, B.S. & SIDOR, C.A. 2002. On the cranial morphology of *Burnetia* and *Proburnetia* (Therapsida: Burnetiidae). *Journal of Vertebrate Paleontology* **22**, 257–267.
RUBIDGE, B.S. & VAN DEN HEEVER J.A., 1997. Morphology and systematic position of the dinocephalian *Styracocephalus platyrhynchus*. *Lethaia* **3**, 157–168.
SIDOR, C.A. 2000. *Evolutionary trends and relationships within the Synapsida*. Unpublished Ph.D thesis, University of Chicago, Chicago. 370 pp.
SIDOR, C.A., ANGIELCZYK, K.D., SMITH, R.M.H, GOULDING, A.K., NESBITT, S.J., PEECOOK, B.R., STEYER, J.S. & TOLAN, S. 2014. Tapinocephalids (Therapsida, Dinocephalia) from the Permian Madumabisa Mudstone Formation (Lower Karoo, Mid-Zambezi Basin) of southern Zambia. *Journal of Vertebrate Paleontology* **34**(4), 980–986.
SIMON, R.V., SIDOR, C.A., ANGIELCZYK, K.D. & SMITH, R.M.H. 2010. First record of a Tapinocephalid (Therapsida: Dinocephalia) from the Ruhuhu Formation (Songea Group) of Southern Tanzania. *Journal of Vertebrate Paleontology* **30**(4), 1289–1293.
SWOFFORD, D. L. 2002. PAUP*. *Phylogenetic Analysis Using Parsimony (and Other Methods)*. Version 4. Massachusetts, Sinauer Associates, Sunderland.
TATARINOV, L.P. 1974. *Teridonty SSSR [Theriodonts of the USSR]*. Moscow, Nauka.
VON HUENE, F.R. 1956. *Paläontologie und Phylogenie der Niederen Tetrapoden*. Jena, Gustav Fischer. 716 pp.

Appendix 1. List of characters and character states used to construct the cladogram using a modified dataset of Liu *et al*. (2009). We added three tapinocephalid taxa (*Moschops*, *Tapinocaninus* and *Ulemosaurus*) to define more precisely the position of *Styracocephalus* in relation to other dinocephalians. Coding for three tapinocephalid taxa was based on descriptions by Gregory (1926) for *Moschops*, Efremov (1940) for *Ulemosaurus*, and Rubidge (1991) for *Tapinocaninus*, and augmented with direct observations based on a *Moschops capensis* skull (AM4950), *Ulemosaurus* skull (PIN 2207/2) and the holotype skull of *Tapinocaninus* (NMQR2987). The number preceding the character definition corresponds to that of the columns in the data matrix (Appendix 2).

1. Dorsal surface of snout: oblique convex (0), near straight and flat (1).
2. Snout width/height ratio: height greater than width (0), height equal to width (1), height less than width (2).
3. External nares: terminal (0), retracted (1).
4. Length of dorsal process of premaxillae: short (0), long, reaching to a level posterior to that of the upper canine (1).
5. Premaxilla alveolar margin shape: downturned (0), horizontal or slightly upturned (1), greatly upturned (2).
6. Antorbital region: long (0), short (1).
7. Septomaxilla: contained within external naris (0), escapes to have a short (1) or long facial exposure (2).
8. Maxilla contacts prefrontal: absent (0), present (1).
9. Shape of dorsal surface of nasals: flat (0), with median boss (1).
10. Supraorbital margin: thin (0), moderately to greatly thickened (1).
11. Temporal fenestra relative to orbit: smaller than orbit (0), larger than orbit (1)
12. Adductor musculature originates on lateral surface of postorbital: absent (0), present (1), on both postorbital and postfrontal (2).
13. Postorbital bar: thin (A-P length less than one-third of height) (0), thickened such that A-P length is greater than 40% of its height (1).
14. Length of posterior process of postorbital: stops above lateral temporal fenestra (0), descends onto posterior margin of lateral temporal fenestra (1).
15. Boss above postorbital bar: absent (0), present (1).
16. Postfrontal: without (0) or with (1) posterior extension along its medial contact with the frontal.
17. Shape of dorsal surface of parietal surrounding parietal foramen: flat (0), low and diffuse swelling (1), forms well-defined chimney (2).
18. Intertemporal region: wider (0), narrower (1), than interorbital region.
19. Ventral surface of zygomatic arch and suborbital bar: smooth (0), with bosses (1).
20. Zygomatic arch elevated above margin of upper tooth row so as to fully expose quadrate and quadratojugal in lateral view: absent (0), present (1).
21. Anterior extension of anterior ramus of squamosal: stops under temporal fenestra (0), beyond the anterior margin of the temporal fenestra (1).
22. Squamosal external auditory meatus groove: absent (0), present (1)
23. Preparietal: absent (0), present (1).
24. Supratemporal: present (0), absent (1).
25. Tabular: contacts paroccipital process of opisthotic (0), restricted dorsally (1).
26. The position of the posterior border of choana: close to the incisor (0), far behind the incisor (1).
27. Length of vomerine process of premaxilla: short (0); long, extending posteriorly and forming part of the medial margin of the inner choana (1); absent in ventral view (2) so that vomer abuts body of premaxilla.

Continued on p. 28

Appendix 1 (continued)

28. Vomer: paired (0), unpaired (1).
29. Vomer internarial part: nearly parallel-sided or slightly ex- panded backward (0), widest nearly middle (1), strongly constraining backwards (2).
30. Interchoanal portion of vomer where it meets the postchoanal portion: broad (0), forms median ridge (1).
31. Vomer ventral surface: flat to convex (0), lateral ridges and median trough (1).
32. Choanal and postchoanal portions of vomer: meet at similar level on palate (0), choanal portion is offset ventrally from postchoanal portion (1).
33. Lateral margin of the choana formed by the palatine: less than 1/3 (0), over 1/3 (1)
34. Two palatines: separated by the vomer and pterygoid (0), join in midline (1)
35. Palatine dentition: broadly distributed (0), restricted to small area (1), absent (2).
36. Dentition on palatal ramus of pterygoid: present (0), absent (1).
37. Row of teeth on transverse flange of pterygoid: present (0), absent (1).
38. Position of transverse flange of pterygoid: under posterior half of orbit (0), under anterior half of orbit (1), preorbital (2).
39. Pterygoid: without (0) or with (1) shelf posterior to its transverse flange.
40. Ectopterygoid teeth: present (0), absent (1).
41. Shape of postparietal: wider than tall (0), approximately square (1), or taller than wide (2).
42. Forward rotation of occiput: none (0), moderate (= vertical) (1), pronounced (2).
43. Paroccipital process orientation: strongly posteroventral and lateral (0), moderately posteroventral and lateral (1), transverse (2).
44. Quadrate contact: primarily paroccipital process (0), about equal paroccipital process and squamosal (1), mostly squamosal (2).
45. Stapedial foramen: present (0), absent (1).
46. Dentary height in canine versus anterior postcanine regions: nearly equivalent (0), shows pronounced difference (1).
47. Dentary: coronoid eminence (0), coronoid process (1).
48. Dentary-angular suture: runs diagonally across lateral surface of mandible (0), posterior margin of dentary deeply incised (1).
49. Coronoid (posterior): present (0), absent or greatly reduced (1).
50. Lateral mandibular fenestra: absent (0), present (1).
51. Angular reflected lamina dorsal notch: near articular (0), midway between articular and dentary (1), close to dentary (2).
52. Angular with pattern of ridges and fossae on its lateral surface: absent (0), present (1).
53. Dorsal edge of surangular just posterior to dentary with laterally projecting ridge: absent (0), or present (1).
54. Foramen between prearticular and angular (sometimes bordered by splenial as well) on medial surface of lower jaw: absent (0), present (1).
55. Articular dorsal process: absent (0), present (1).
56. Differentiation of upper tooth row: more than one caniniform teeth (0), one canine (1), barely differentiated (2).
57. Premaxillary teeth number: 5 (0), 4 or less (1), 6 (2).
58. Upper and lower incisors intermesh: absent (0), present in anterior incisors (1), present in all incisors (2).
59. Incisor heels: absent (0), present (1).
60. Upper incisors: much larger (0) or roughly equivalent in size to postcanines (1).
61. Precanine maxillary teeth: present (0), absent (1).
62. Lower canine: fits into choana (0), or into fossa roofed by premaxilla and maxilla (1), or passes anterior and external to upper canine (2).
63. Upper and lower canines: without heels (0) or small heels present (1).
64. Postcanine diastema on upper jaw: absent (0), present (1).
65. Number of upper postcanines: twelve or greater (0), fewer than 12 (1).
66. Postcanine teeth with triangular crown bearing coarse serrations along both anterior and posterior carinae: absent (0), present (1).
67. Upper postcanine teeth confluent with upper incisor row medial to canine: absent (0), present (1).

Appendix 2. Character matrix used to analyse the phylogenetic position of *Styracocephalus*.

Taxon	1 1234567890	1111111112 1234567890	2222222223 1234567890	3333333334 1234567890	4444444445 1234567890	5555555556 1234567890	66666 12345
Haptodus	0000000000	0000000000	0000??0000	0000000000	?0000?0000	?000000000	0?000
Dimetrodon	0000000000	0000000000	0000000000	0000000000	0000000000	?000001000	01000
Tetraceratops	000000000?	??0000????	??????00??	????000001	?????0?0?0	??0??01000	0000?
Raranimus	00010?2100	??????????	?????00000	1000??????	??????????	?????02?0?	0?00?
Biarmosuchus	0001102100	0100002000	0101000?1?	?01?000101	1111010?0	011??10?01	1?011
Hipposaurus	0001102100	0001012?0	?11101??11	1?1?000101	1111110100	01?1110101	1?011
Herpetoskylax	0000102100	000?012001	111101?1??	111?101101	1111?10100	0110110101	1?011
Lycaenodon	00001?2100	000?0120??	??1??11111	1110101101	??????????	?????10?01	1?011
Lemurosaurus	000??02101	00010?2010	11??01??11	111?101101	1111110?0	0110?1?101	1?011
Proburnetia	0000111?11	200?1?1010	11??111?01	11?0101101	1112?1?100	?1???1?101	1?0?1
Burnetia	00???1??11	100?1?1010	?1??111?1?	11?010?101	?11???????	?????1????	1????
Syodon	0111201100	1200002100	0101012010	'110?10?101	2111000100	1001010210	11101
Titanophoneus	0111201101	1200002100	0101012010	1100110101	2111000000	1001?10210	11101
Sinophoneus	0001201100	0200002100	0101??????	?????00?0?	211??0?0?0	10???10210	1?1?1
Styracocephalus	0110?0?111	0111111000	110111?000	1??0100211	021111?100	?0????10?1?	1?001
Jonkeria	0111101101	1100101100	1101?12000	1100211211	?211?0010?	1000010210	12101
Estemmenosuchus	0101101?11	1?0?102000	?101?12110	110?00021?	?211000 1?0	1001?10210	02000
Biseridens	????1111?1	1101002001	0101011000	0010000 1?1	0000??01??	01?1010001	01011
Patranomodon	0110?1?100	1100000001	1111110011	1110211001	0022100011	211002????	????1
Suminia	0111111100	11000?2001	1101110 1??	?110211001	1022100111	2101021?00	????1
Gorgonops	1100102100	1100002000	0111011121	1111100101	0022011000	110?100000	10011
Lycaenops	1000102100	1100002000	0111011121	1111211201	0022011000	110?100000	10011
Cyonosaurus	1100102100	1100002000	0111011121	1111101101	0022011000	110?100000	1?011
Ulemosaurus	0111111101	1210111100	1101112002	1110211211	2211100100	1000010210	11101
Moschops	0111111101	0210111000	1101112002	1110211211	2211100100	1000020210	12101
Tapinocaninus	0111111101	121011?100	1101112002	1110211211	1211100100	1000010210	11001