A new dicynodont (Anomodontia: Emydopoidea) from the terminal Permian of KwaZulu-Natal, South Africa

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A new taxon of dicynodont (*Thliptosaurus imperforatus* gen. et sp. nov.) is described based on a dorsoventrally-crushed skull from latest Permian (upper *Daptocephalus* Assemblage Zone) strata in KwaZulu-Natal, South Africa. *Thliptosaurus* is distinguished from all other dicynodonts by an elongate intertemporal bar with broad dorsal exposure of the parietals but apparently no pineal foramen. Absence of the pineal foramen in dicynodonts is exceedingly rare; the only other taxa which exhibit this feature either have substantially broader (*Kawingasaurus fossilis*) or narrower (*Kombuisia frerensis*) intertemporal regions. Inclusion of *Thliptosaurus* in a phylogenetic analysis of dicynodonts recovers it as a kingoriid emydopoid, a position supported by its anteriorly-restricted pterygoid keel, elongate, curved anterior process of the lacrimal, relatively posterior position of the median pterygoid plate, and occlusion of the mandibular fenestra by a lateral plate of the dentary. Intriguingly, even in the other kingoriids which retain a pineal foramen (*Dicynodontoides* spp. and *Kombuisia antarctica*), this structure is reduced in size relative to other dicynodonts, suggesting that the pineal eye was less important for thermoregulatory activity in this clade than in other anomodonts. Although part of a local fauna including taxa that are otherwise widespread in the Karoo Basin (*Daptocephalus*, *Lystrosaurus*), the unique presence of *Thliptosaurus* in the relatively poorly-sampled *Daptocephalus* Assemblage Zone deposits of KwaZulu-Natal suggests that this region may preserve endemic taxa, and should be prioritized for future fieldwork.

Keywords: Synapsida, Dicynodontia, Permian, end-Permian mass extinction, South Africa.

INTRODUCTION

Small dicynodonts (i.e. those with skull length <15 cm) are the numerically dominant tetrapods throughout most of the mid-to-late Permian strata in the Karoo Basin of South Africa. In the lowest strata of the Permo-Triassic Beaufort Group (those of the possibly Wordian *Eodicynodon* Assemblage Zone [AZ]), the most abundant taxon is the small basal dicynodont *Eodicynodon oosthuizeni* (Rubidge, 1990, 1995). In the subsequent *Tapinocephalus* AZ (Capitanian), the most abundant taxa are pylaecephalids, a group of small dicynodonts including *Diictodon feliceps*, *Eosimops newtoni*, *Prosictodon dubei*, and *Robertia broomiana* (Boonstra 1969; Angielczyk & Rubidge 2010, 2013; Smith *et al*. 2012; Day 2014). *Diictodon* in particular went on to extreme success even after the extinction of the other pylaecephalids, being far and away the most abundant tetrapod in the later *Pristerognathus* and *Tropidostoma* AZs (early Wuchiapingian) (Smith 1993). Recent research has suggested that the incredible abundance of *Diictodon* in these biozones indicates an unbalanced ecosystem (there are three times as many specimens of *D. feliceps* known from the *Tropidostoma* AZ as of all other taxa put together), and that *D. feliceps* may have been a disaster taxon flourishing in the wake of the mid-Permian mass extinction (much like *Lystrosaurus* following the end-Permian mass extinction) (Day *et al*. 2018). Unlike *Lystrosaurus*, however, which went extinct as soon as ecosystems began to recover in the Triassic, *Diictodon* continued to be a major component of later, more stable ecosystems: it remains the most abundant taxon in the later Wuchiapingian *Cistecephalus* AZ (Smith *et al*. 2012) and survived into the terminal Permian (Changhsingian) *Daptocephalus* AZ (Viglietti *et al*. 2016). Even discounting *Diictodon*, small dicynodonts were the numerically dominant tetrapods in most late Permian biozones: *Pristerodon mackayi* is the second-most abundant taxon in the *Tropidostoma* AZ and *Cistecephalus microrhinus* is the second-most abundant taxon in the *Cistecephalus* AZ, and other taxa such as *Emydops arctatus* are common components of both (Smith *et al*. 2012).

Despite their earlier success, however, small dicynodont fortunes began to founder at the end of the Permian. Small dicynodonts make up only 19.2% of tetrapod specimens in the lower *Daptocephalus* AZ *vs* 40% for large dicynodonts (taxa like *Aulacephalodon*, *Daptocephalus*, *Dicynodon*, and *Oudenodon*), and only 4% in the upper *Daptocephalus* AZ *vs* 64% large dicynodonts (including the aforementioned taxa, but also a preponderance [34%] of the newly-appearing *Lystrosaurus*) (Viglietti *et al*. 2016). Several small dicynodont taxa (e.g. *Compsodon*, *Digalodon*) disappear at

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the boundary between the lower and upper *Daptocephalus* AZ (Viglietti *et al*. 2016; Angielczyk & Kammerer 2017), and some of those that make it into the upper *Daptocephalus* AZ do not have ranges extending all the way to the Permo-Triassic boundary (PTB) (e.g. *Diictodon*; Retallack *et al*. 2003; Smith & Botha-Brink 2014). The only small dicynodont taxon whose range definitely extends to the PTB in South Africa is the kingoriid emydopoid *Dicynodontoides recurvidens* (Smith & Botha-Brink 2014), and it should be noted that the classification of this taxon as a 'small dicynodont' is somewhat questionable; although the majority of collected skulls are in the 10–15 cm range, it reached basal skull lengths of up to 24 cm (Angielczyk *et al*. 2009).

Although small dicynodonts were clearly suffering in the lead-up to the PTB in the Karoo Basin, they were not totally extirpated at the end of the Permian, as small members of two emydopoid families (Kingoriidae and Myosauridae) are known from the earliest Triassic (*Kombuisia antarctica* from the Induan of Antarctica and *Myosaurus gracilis* from the Induan of Antarctica and South Africa; Hammer & Cosgriff 1981; Fröbisch *et al*. 2010). The Permian ancestry of these taxa is currently obscure: although *Dicynodontoides* and *Kombuisia* are sister-taxa (Fröbisch 2007; Kammerer *et al*. 2011), these two genera are so morphologically disparate that a direct ancestor–descendant relationship between the former and the latter is unlikely. *Myosaurus* is the only recognized myosaurid, and though the poorly-known late Permian taxon *Emydorhinus* (Broom 1935) may represent a related genus, the morphological gap between these taxa is not bridged by any known fossils in the Karoo record. Rather, as is also notably the case for the most successful group of Triassic dicynodonts, the Kannemeyeriiformes, it seems that the Permian antecedents of the small dicynodonts in the post-extinction recovery fauna must have been living outside of the well-sampled strata currently known from the Karoo Basin. Even within the Karoo Basin, it should be recognized that sampling of this interval is very uneven: the vast majority of studies are based on a few sections from the Eastern Cape Province and Free State (e.g. Smith 1995; Retallack *et al*. 2003; Ward *et al*. 2005; Smith & Botha-Brink 2014; Viglietti *et al*. 2016). By contrast, the fauna associated with the Permo-Triassic transition in KwaZulu-Natal is relatively poorly known (although the coeval flora is better sampled; Gastaldo *et al*. 2005). Oliviershoek Pass, a *Lystrosaurus* AZ-bearing site at the border between the Free State and KwaZulu-Natal, has been subject to several geological studies (e.g. Turner 1984, 1986) and occasional vertebrate fossil collection (see e.g. Brink 1965; Anderson & Anderson 1970; Rubidge 1997; Shishkin & Rubidge 2000), but this is an exception. The extensive but patchily-exposed Permo-Triassic rocks elsewhere in the province have garnered only rare historical sampling (mostly by James Kitching; see e.g. Kitching 1968).

Here I describe a new taxon of small dicynodont from latest Permian rocks in KwaZulu-Natal. This taxon is represented by only a single skull, so it does not alter the view of small dicynodonts as a declining percentage of faunas in the lead-up to the PTB. However, it does suggest that small dicynodont species richness in the terminal Permian was higher than previously thought, and points towards under-sampled regions like KwaZulu-Natal as a potential source of 'missing diversity' between the Permian and Triassic faunas.

MATERIAL

The specimen BP/1/2796 (in the collection of the Evolutionary Studies Institute [ESI], University of the Witwatersrand, Johannesburg, South Africa) was collected by James Kitching in September 1958 in Stoffelton, northwest of Bulwer in western KwaZulu-Natal. This site encompasses both latest Permian and earliest Triassic rocks of the *Daptocephalus* and *Lystrosaurus* AZs (Kitching 1968). Assemblage zone of origin is reflected in the preservational style of the fossils from this locality: Permian bone (e.g. BP/1/2784, *Daptocephalus leoniceps*) is black-to-grey and preserved in grey matrix, whereas Triassic bone (e.g. BP/1/2793, *Thrinaxodon liorhinus*) is yellowish and preserved in red matrix (Kammerer, pers. obs.), as is seen in the transition from late Permian rocks of the Balfour Formation to those of the boundary-spanning Palingkloof Member elsewhere in the basin (Smith 1995). Despite the geographic and stratigraphic importance of this site, Kitching's collections from Stoffelton have received little attention in the literature (and indeed much of this material remains unprepared). Durand (1991) described a complete skull of the large therocephalian *Moschorhinus kitchingi* (BP/1/2788) from the *Daptocephalus* AZ portion of this collection. Maisch (2002) described a small dicynodont skull (BP/1/2792), also from the *Daptocephalus* AZ portion of this collection, which he made the holotype of a new genus and species of basal lystrosaurid, *Kwazulusaurus shakai*. BP/1/2796, the specimen described herein, was also collected in the *Daptocephalus* AZ strata. Based on the co-occurrence of *Daptocephalus*, *Lystrosaurus*, and *Moschorhinus* in this assemblage it can be recognized as belonging to the upper *Daptocephalus* AZ of Viglietti *et al*. (2016), the latest Permian fauna in South Africa.

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Anomodontia Owen, 1860
Dicynodontia Owen, 1860
Emydopoidea van Hoepen, 1934
Kingoriidae King, 1988

***Thliptosaurus imperforatus* gen. et sp. nov.**

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Holotype. BP/1/2796, a nearly complete but badly compressed skull and lower jaws.

Type locality and horizon. Stoffelton, near Bulwer, KwaZulu-Natal, South Africa. *Daptocephalus* Assemblage Zone, Changhsingian, Permian.

Etymology. Genus name meaning 'compressed lizard', from the ancient Greek θλῖψις (Latinized *thlipsis*) and σαῦρος (Latinized *saurus*), in reference to the highly dorsoventrally compressed nature of the holotype. Also from *thlipsis* in the Biblical sense, in reference to the tribulations accompanying the End Times, alluding to the existence of this taxon immediately prior to the end-Permian mass extinction. Species name meaning 'unpunctured' in Latin, in reference to the great reduction (if not total absence) of the pineal foramen.

Diagnosis. Emydopoid dicynodont characterized by the following combination of characters: absence (or extreme reduction) of the pineal foramen (otherwise only known in *Kawingasaurus fossilis* and *Kombuisia frerensis* among dicynodonts), moderately broad intertemporal bar (narrower than *Kawingasaurus* but broader than *Kombuisia*), absence of the postfrontal (synapomorphy of Kistecephalia), dentary plate occluding the mandibular fenestra (synapomorphy of Kingoriidae), arcing anterior process of lacrimal contacting nasal, eliminating contact between the maxilla and prefrontal (synapomorphy of Kingoriidae), broad, flat exposure of the parietals in the intertemporal bar (symplesiomorphy of Dicynodontia not present in *Dicynodontoides* or *Kombuisia*).

DESCRIPTION

The holotype and only known specimen of *Thliptosaurus imperforatus* (BP/1/2796) is a small skull (8.6 cm basal length; see Table 1) that has suffered extensive postmortem dorsoventral compression (Figs 1–5). It is nearly complete, although the suborbital portions of the zygoma and posterior edges of the temporal fenestrae have been reconstructed in plaster. The bone is light grey in colour and preserved in a grey siltstone matrix, like the other *Daptocephalus* AZ specimens from this locality (Kammerer, pers. obs.) Sutures on this specimen can be discerned dorsally (Fig. 1), but due to poor preservation and over-preparation are difficult to see on the lateral skull surface (Fig. 2). Preservation of the lower jaw in occlusion with the skull and its strong compression unfortunately obscures most of the palate, with only the pterygoids and basicranium clearly visible ventrally (Fig. 3).

Table 1. Cranial measurements of BP/1/2796, holotype of *Thliptosaurus imperforatus*.

BSL = 8.6 cm
DSL = 8.1 cm (assuming plaster reconstruction is accurate)
Snout length = 2.4 cm
Interorbital width = 1.7 cm
Anterior intertemporal width = 2.5 cm
Posterior intertemporal width = 2.1 cm
Median pterygoid plate width = 0.5 cm
Anterior pterygoid keel height = 0.6 cm
Anterior pterygoid ramus height = 0.4 cm
Anterior pterygoid process length = 2.0 cm
Quadrate pterygoid process length = 1.2 cm
Pre-median pterygoid plate length of skull = 6.2 cm
Post-median pterygoid plate length of skull = 2.4 cm
Dentary symphysis height = 2.0 cm
Dentary ramus height = 1.5 cm
Postdentary bone height (left side) =1.0 cm
Temporal fenestra length (left side, more complete) = ~3.5 cm

Only the ascending process of the premaxilla can be seen in BP/1/2796. Although transversely broad anteriorly, it tapers strongly posteriorly where it divides the nasals, terminating near the level of the anterior tip of the lacrimal (Fig. 1). The premaxilla is unpaired throughout its length. The external nares (and with them, the septomaxillae) in this specimen cannot be discerned due to dorsoventral compression, but must have been present at the anterior tip of the snout, as they are clearly not located on the lateral face of the snout above the caniniform process. The maxilla is typical for dicynodonts, making up most of the lateral snout surface and bearing a distinct, ventrally-directed caniniform process (Fig. 2). The caniniform process is located in a very anterior position relative to the orbit (as in *Dicynodontoides*) and is tuskless. No other teeth are visible in this specimen, but overlap of the medial palatal portion of the maxilla by the lower jaw makes it impossible at present to be sure they were absent. The anterior margin of the caniniform process is longer and more gently sloping than the posterior margin, which rises steeply to contact the zygomatic arch. A postcaniniform keel appears to be present behind the left caniniform process, which is the better exposed of the two. Suborbitally the maxilla continues onto the zygomatic arch, but its posterior extent is uncertain due to plaster reconstruction on both sides of the skull; it is unknown whether it contacted the anterior zygomatic process of the squamosal. The nasal bosses are very similar to those of *Dicynodontoides*: although distinctly expanded laterally near the snout tip, where they are separated by the premaxilla, they do unite posteromedially to form a single median swelling (Fig. 1A). The nasal bosses are heavily pitted or foraminated and weakly rugose. Posterior to the nasal boss, the nasal bone has a short length of flat, unornamented bone terminating near the anterior margin of the orbits in a nearly-straight suture with the frontal. The prefrontal and lacrimal are very similar to the condition in *Dicynodontoides*: the prefrontal is a short, roughly triangular element at the anterodorsal corner of the orbit, but the lacrimal is very dorsoventrally thin and anteroposteriorly elongate, with a distinctly curved anterior process contacting the nasal and separating the maxilla from the prefrontal (Fig. 1B).

The jugal is poorly exposed in this specimen, only being visible at the anteroventral corner of the right orbit, anterolateral corner of the temporal fenestra (Fig. 1), and forming the lateral rim of the subtemporal fenestra ventrally (Fig. 3). The zygomatic ramus of the squamosal makes up all of the subtemporal bar in lateral view; this ramus is dorsoventrally extremely thin and transversely broad (although this has likely been exaggerated by taphonomic compression). The occipital ramus of the squamosal is mostly missing in this specimen (and replaced by plaster). Its ventrolateral corner is intact on both sides, however, and show that it was broad and plate-like posteriorly as in most other dicynodonts (Fig. 4). It bears a dorsoventral depression immediately lateral to its contact with the paroccipital process of the opisthotic.

The frontal is a very large bone in *Thliptosaurus*, and forms almost the entirety of the interorbital region and part of the intertemporal region (Fig. 1). The frontal forms most of the dorsal margin of the orbit and is transversely

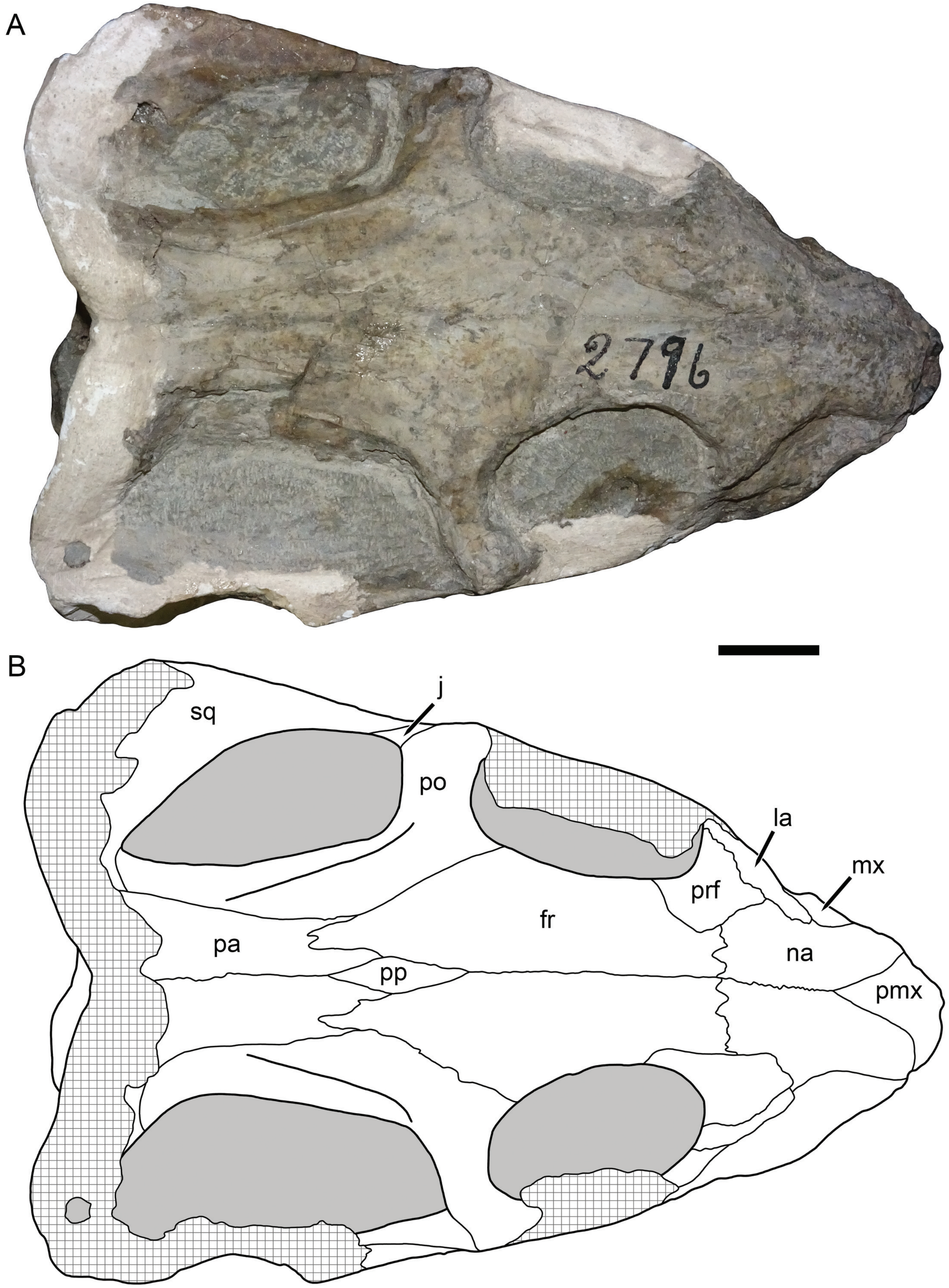

Figure 1. Holotype of *Thliptosaurus imperforatus* (BP/1/2796) in dorsal view: **A**, photograph; **B**, interpretive drawing (grey indicates matrix, hatching indicates plaster reconstruction). fr, frontal; j, jugal; la, lacrimal; mx, maxilla; na, nasal; pa, parietal; pmx, premaxilla; po, postorbital; pp, preparietal; prf, prefrontal; sq, squamosal. Scale bar equals 1 cm.

Figure 2. Holotype of *Thliptosaurus imperforatus* (BP/1/2796) in (**A**) right lateral and (**B**) left lateral views. Scale bar equals 1 cm.

broadest just anterior to the postorbital bar. Posteriorly, the frontal forms a ragged, tapering process extending between the preparietal and postorbital and dividing the anterior margin of the parietal at tip. The preparietal is a narrow, lozenge-shaped median element that is flush with the surrounding frontals and parietals. No postfrontal is present; as is typical for kistecephalian emydopoids (Kammerer & Angielczyk 2009), the region where the postfrontal occurs in other dicynodonts is occupied by an anterior portion of the postorbital. It is possible that this is the result of fusion between the postfrontal and postorbital during development, but at present no juvenile kistecephalians showing separation between these elements have been found, unlike the situation in geikiids (Kammerer & Smith 2017) and kannemeyeriiforms (Angielczyk *et al*. 2018) in which juveniles with at least partially discrete postfrontals are known. The postorbital forms the anteroposteriorly thin postorbital bar ventrally, which makes up the posterior margin of the orbit. Dorsally, it forms a posteriorly-directed process rimming the medial edge of the temporal fenestra. The postorbital has a broad, nearly-horizontal dorsal exposure in the intertemporal bar that is offset nearly perpendicularly from the portion of the postorbital making up the wall of the temporal fenestra. This dorsal exposure of the postorbital bears an elongate, posteriorly-tapering depression (originating immediately behind the postorbital bar and terminating at roughly two thirds of the length of the temporal fenestra). This depression would have served as the attachment site for the *M. adductor mandibulae externus medialis* (Angielczyk *et al*. 2018). The parietal is a broad, flat bone exposed dorsally in the posterior intertemporal bar. Anteromedially it contacts the preparietal and anteriorly its margin is split in two by the posterior process of the frontal. Highly unusually for a dicynodont, the midparietal suture appears to extend uninterrupted throughout its length, i.e. there is no pineal foramen apparent. There is a darkened area of the suture at about the midlength of the intertemporal bar (Fig. 1A), but careful microscopic examination of this area suggests that this represents discoloration of the parietal edge and some adhered matrix. If a pineal foramen is present in this region (e.g. obscured by compression of the specimen), it would have to be exceedingly narrow and slit-like and also separated from the preparietal by a substantial length (0.6 cm, 21% of the length of the intertemporal bar), an extreme rarity among dicynodonts.

As mentioned above, little of the palate is exposed on this specimen. The anterior pterygoid rami are elongate and narrow, with the pterygoid keel restricted to their anterior tip (Fig. 3). The anterior rami are nearly straight, as in *Compsodon* and *Dicynodontoides* (Angielczyk & Kammerer 2017). The anterior rami do not seem to converge into a median ridge posteriorly, but as the median pterygoid plate is damaged this is uncertain. The quadrate rami of the pterygoid are relatively short (1.2 cm in length, *vs* 2.0 cm for the anterior rami) and extend towards the quadrate at an angle of ~60° relative to the long axis of the skull (65° on the right side, 56° on the left with differences due to compression), giving the median pterygoid plate a relatively posterior position on the skull. The basal tubera are anteroposteriorly elongate, with the parabasisphenoid contribution greater than that of the basioccipital. No intertuberal ridge is present. The quadrate-quadratojugal complex forms an expanded plate at the anteroventral edge of the squamosal, as is typical for dicynodonts. The occiput is very poorly preserved and no sutures can be delimited, but what is visible is standard for dicynodonts, with a large, tripartite occipital condyle and dorsoventrally expanded paroccipital process of the opisthotic extending laterally and ventrally (Fig. 4). The posterior tip of the paroccipital process is broken off, so the possibility that it had a sharp posterior process as in other emydopoids cannot be excluded.

The dentary symphysis of the lower jaw is long (Fig. 5), with an elongate anterodorsal end ending in a flattened, shovel-like beak tip. There is a weak ridge along the lateral edge of the anterior face of the symphysis. The ventral edge of the jaw symphysis is made up an attenuate anterodorsal process of the fused splenial. No angular contribution to the symphysis is present. Laterally, the dentary forms a tall plate obscuring the mandibular fenestra, a feature otherwise known only in *Dicynodontoides* (in which it partially covers the fenestra) and *Kombuisia* (in which the fenestra is covered completely) among dicynodonts (Fröbisch 2007). The exact degree of occlusion is uncertain, however, due to adhering matrix on the surface of the angular. The dentary of *Thliptosaurus* is unusual in seeming to have a relatively short dorsal (coronoid) process overhanging the surangular; in *Dicynodontoides* and *Kombuisia* this process extends far posterior to the ventral margin of the dentary (Cluver & King 1983; Fröbisch 2007; Fröbisch *et al*. 2010). However, it is possible that the dentary extends further posterodorsally but is obscured by matrix. A weak anteroposteriorly-oriented ridge is present at midheight on the left dentary ramus, representing a greatly reduced lateral dentary shelf. The angular has two broad, concave lateral exposures on the jaw: one anterior to the reflected lamina, forming the ventral edge where the mandibular fenestra

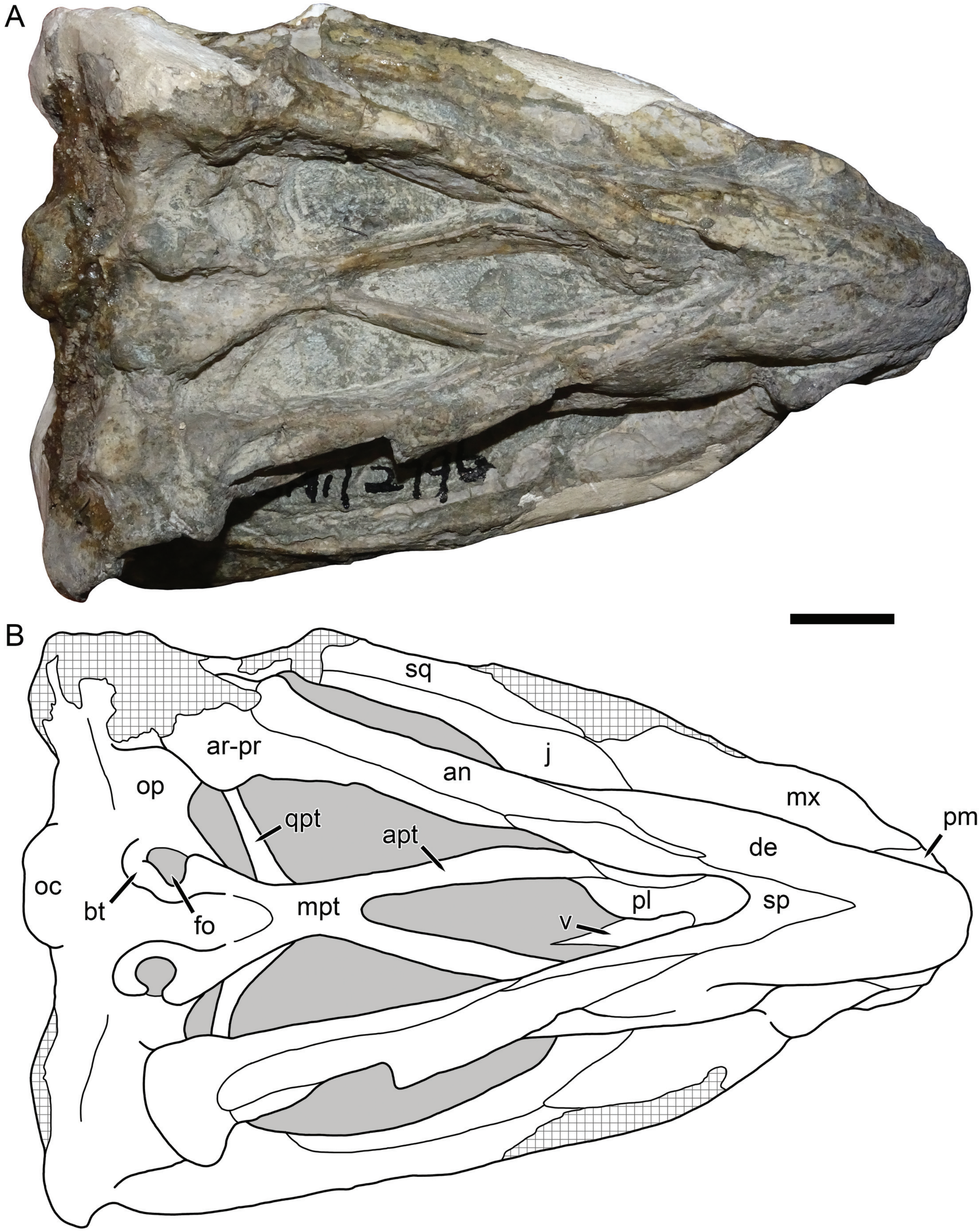

Figure 3. Holotype of *Thliptosaurus imperforatus* (BP/1/2796) in ventral view: **A**, photograph; **B**, interpretive drawing (grey indicates matrix, hatching indicates plaster reconstruction). an, angular; apt, anterior pterygoid ramus; ar-pr, articular-prearticular complex; bt, basal tuber; de, dentary; fo, fenestra ovalis; j, jugal; mpt, median pterygoid plate; mx, maxilla; oc, occipital condyle; op, opisthotic; pl, palatine; pmx, premaxilla; qpt, quadrate pterygoid ramus; sp, splenial; sq, squamosal; v, vomer. Scale bar equals 1 cm.

Figure 4. Holotype of *Thliptosaurus imperforatus* (BP/1/2796) in occipital view. Scale bar equals 1 cm.

would normally be in a dicynodont, and one posterior to the reflected lamina, separating it from the articular region of the jaw. Only the base of the reflected lamina is preserved; it was anteroposteriorly short, similar in proportions to that of *Dicynodontoides* (Cox 1959). The surangular is exposed as a narrow strip running along the dorsal margin of the jaw ramus in the postdentary region. The articular has a curved, convex dorsal surface fitting between the ventral condyles of the quadrate and extending beyond them (to allow palinal jaw motion). The articular ends ventrally in a short, blunt retroarticular process. Medially, the prearticular is visible as a thin lamina making up part of the jaw surface, but is preserved too poorly to note any further detail.

PHYLOGENETIC ANALYSIS

Thliptosaurus imperforatus was coded into the most recent phylogenetic analysis of anomodonts (Kammerer 2018; based on the revised analysis of Angielczyk & Kammerer 2017). The dataset consists of 105 OTUs (98 anomodont taxa and 7 non-anomodont therapsids, with *Biarmosuchus tener* used as outgroup) with 23 continuous and 174 discrete state characters. Seven discrete state characters were treated as ordered (characters 58, 61, 79, 140, 150, 151, 166), following Angielczyk & Kammerer (2017). Continuous characters were treated as additive using the methodology of Goloboff *et al*. (2006). Revised codings for *Sangusaurus parringtonii* were included based on the analysis of Angielczyk *et al*. (2018). The dataset was analysed using TNT v1.1 (Goloboff *et al*. 2008) using New Technology methods (tree drifting, parsimony ratchet, and tree fusing) on a driven search (initial search level = 65, checked every three hits) required to find the shortest tree at least 20 times. Symmetric resampling analysis was done on 1000 replicates and Bremer values were calculated using the bremer.run script in TNT based on stored trees suboptimal by 20 steps.

Three most parsimonious trees of length 1146.601 were recovered, with a consistency index of 0.241 and retention index of 0.716. A consensus tree showing the results of the phylogenetic analysis is presented in Fig. 6. In general, tree topology is similar to that of Angielczyk & Kammerer (2017), Olroyd *et al*. (2017), Angielczyk *et al*. (2018), and Kammerer (2018). Like these recent topologies (and unlike a number of previous analyses based on earlier versions of the data matrix; e.g. Kammerer *et al*. 2011, 2013, 2015a, 2016; Castanhinha *et al*. 2013; Cox & Angielczyk 2014; Angielczyk *et al*. 2016; Kammerer & Smith 2017), Pylaecephalidae is recovered outside of Therochelonia. Bidentalian topology remains volatile. Although a monophyletic Cryptodontia (as in Kammerer 2018) is not recovered; a 'partial Cryptodontia' made up of Rhachiocephalidae+Geikiidae is found, unlike in the analyses of Angielczyk & Kammerer (2017), Olroyd *et al*. (2017), and Angielczyk *et al*. (2018) in which Geikiidae, Rhachiocephalidae, and Oudenodontidae formed successive sister-taxa to the main dicynodontoid radiation (with *Idelesaurus* and *Odontocyclops* as wildcard taxa either recovered as basal geikiids or outside Geikiidae+'traditional' dicynodontoids). Within Dicynodontoidea, the only result of note is the recovery of a clade made up of Lystrosauridae (here restricted to *Lystrosaurus*) and various '*Dicynodon*-grade' taxa (*Daptocephalus*, *Delectosaurus*, *Dicynodon*, *Dinanomodon*, *Peramodon*, *Turfanodon*, *Vivaxosaurus*). The latter group could be recognized as Dicynodontidae if supported by future analyses, with the caveat that dicynodontoid phylogeny needs intense further research before the position of any of the Permian taxa can be considered stable.

Intriguingly, an expansive version of the clade Endothiodontia (*sensu* Kammerer & Angielczyk 2009) is recovered, in which *Pristerodon*, *Brachyprosopus*, and endothiodontids (*Niassodon*+*Endothiodon*) form successive outgroups to Emydopoidea (*sensu* Kammerer *et al.* 2015a). Within Emydopoidea, *Thliptosaurus* is recovered as a kingoriid outside of the clade *Dicynodontoides*+*Kombuisia*, and Kingoriidae is recovered within Kistecephalia (like most recent analyses, but unlike that of Olroyd *et al*. 2017, where they fell outside of *Emydops*+Kistecephalia). Oddly, *Myosaurus* is recovered as the sister-taxon of Kingoriidae; this taxon is usually recovered as the sister-taxon of Cistecephalidae (e.g. Kammerer *et al*. 2011; Angielczyk & Kammerer 2017; Olroyd *et al*. 2017; Angielczyk *et al*. 2018; although see Angielczyk & Kurkin 2003). It must be noted, however, that support for the expansive Endothiodontia and a Myosauridae+Kingoriidae relationship is extremely low (<50 resampling support and <1 Bremer support), requiring only a fractional step to revert to the prevailing topology.

DISCUSSION

Taxonomic distinction of *Thliptosaurus*

The compressed state, small size, and singleton nature of BP/1/2796 raise the question of whether its distinctive features could be the result of ontogenetic and/or taphonomic variation. Discrete characters such as the absence of the pineal foramen and occlusion of the mandibular fenestra by the dentary are not known to be variable with ontogeny in dicynodonts. However, intertemporal width is notably ontogenetically variable in this clade (Kammerer *et al*. 2011, 2015b), and it is conceivable that compression could obscure the pineal foramen in a taxon in which it is already small. As such, further comparison with other kingoriids (the only dicynodont clade in which

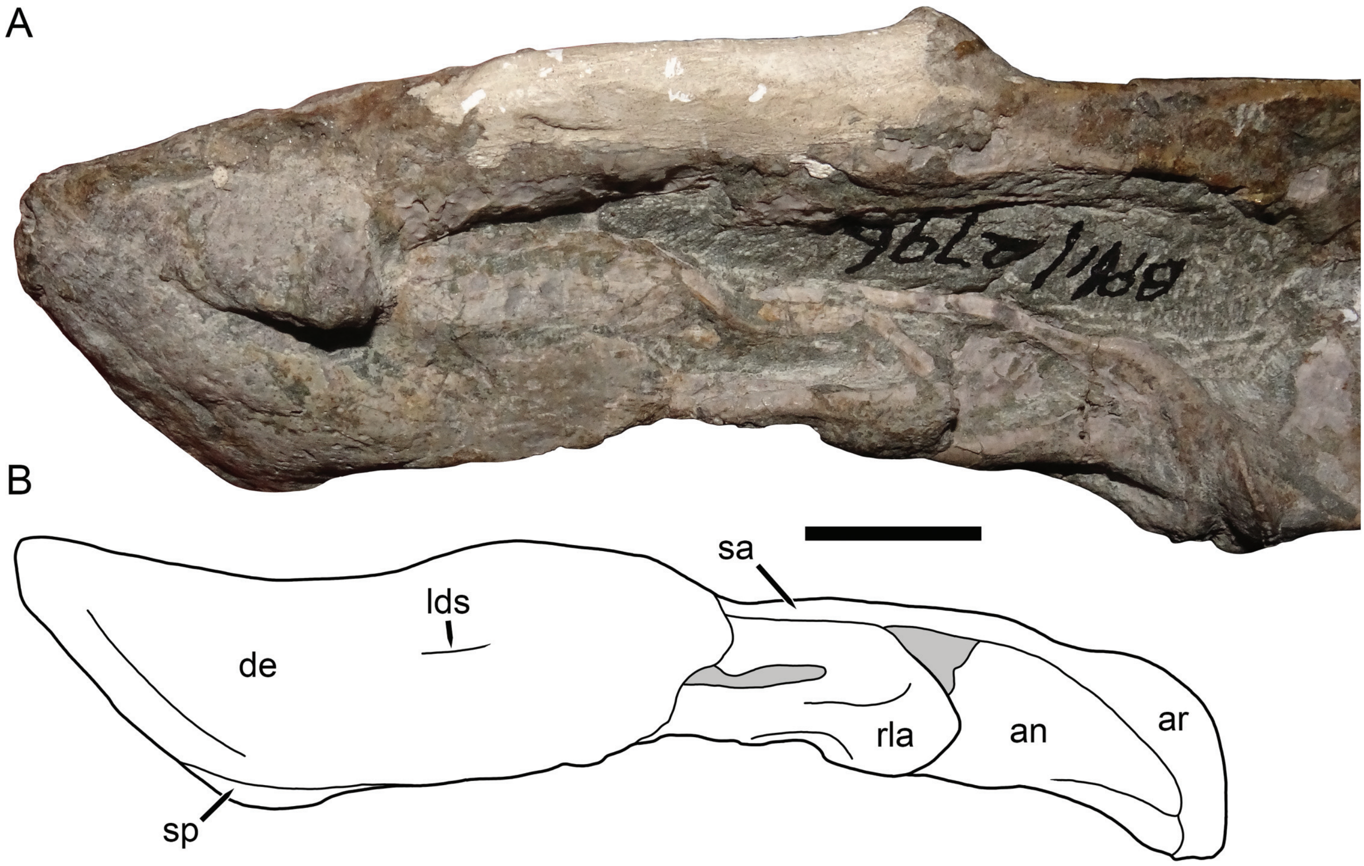

Figure 5. Holotype of *Thliptosaurus imperforatus* (BP/1/2796) in left lateral view; detail illustrating mandibular morphology. **A**, Photograph; **B**, interpretive drawing (grey indicates matrix). an, angular; ar, articular; de, dentary; lds, lateral dentary shelf; rla, reflected lamina of angular; sa, surangular; sp, splenial. Scale bar equals 1 cm.

the mandibular fenestra is occluded, whose members also tend to have small pineal foramina; see below) is warranted. Of particular import in this regard is *Dicynodontoides*, which also occurs in rocks of latest Permian age (Smith & Botha-Brink 2014).

BP/1/2796 can readily be distinguished from both species of *Kombuisia* based on intertemporal morphology. The intertemporal region in *Kombuisia* is generally narrow and very sharply constricted near its posterior end (Fröbisch 2007; Fröbisch *et al*. 2010). The parietals of *Kombuisia* are exposed as only a thin sliver between the large, overlapping postorbitals, unlike in BP/1/2796 where they are broadly exposed (Fig. 7). Furthermore, the holotype of *Kombuisia frerensis* (Fig. 7B), which shows the most extreme narrowing of the intertemporal bar in the genus, is both slightly smaller (7.7 cm basal length) than and just as dorsoventrally crushed as BP/1/2796 (Fröbisch 2007).

Comparisons with similarly-sized and preserved specimens of *Dicynodontoides* also indicate that their differences from BP/1/2796 are not attributable to ontogenetic or taphonomic variation. USNM 25176 (in the collections of the National Museum of Natural History, Washington DC, U.S.A.) is a small skull (9.6 cm basal length) of *D. recurvidens* from Doornplaas, Graaff-Reinet (Fig. 7C). Although only slightly larger than BP/1/2796, it already exhibits the comparatively narrow intertemporal bar typical of larger *Dicynodontoides* specimens, with broad overlap of the parietals by the postorbitals (as in *Kombuisia*). Nor can taphonomic distortion explain differences in intertemporal proportions between BP/1/2796 and *Dicynodontoides*. BP/1/22 is another skull of *D. recurvidens* from Doornplaas, which has experienced extreme dorsoventral crushing (Fig. 7D) comparable to that of BP/1/2796, yet its intertemporal bar is recognizably more similar to the somewhat laterally-compressed USNM 25176 than to BP/1/2796. Also of note is that the pineal foramina remain evident despite distortion in both USNM 25176 and BP/1/22, and dorsoventral compression is unlikely to obscure this foramen in any case (although extreme lateral compression could do so). Given these consistent differences between BP/1/2796 and other kingoriids, it is here considered justified to establish a new taxon (*Thliptosaurus imperforatus*) for the former despite the crushed state of the holotype.

A final point of consideration is whether BP/1/2796 represents the adult of a late-surviving small-bodied dicynodont taxon (as argued here) or is a juvenile for which the adult morphology is currently unknown. Although a definite answer is not possible in the absence of further material, several features suggest that BP/1/2796 is indeed a mature individual. The snout in BP/1/2796 is well-ossified, with none of the fontanelles or irregular sutures observed in juveniles of larger dicynodonts (e.g. Kammerer *et al*. 2015b). There is no evidence of a postfrontal bone in BP/1/2796; loss of this bone is usually interpreted as occurring via fusion with the postorbital during ontogeny (Kammerer & Smith 2017). Finally, the preparietal of BP/1/2796 is small relative to skull size.

Figure 6. Results of the phylogenetic analysis. *Thliptosaurus imperforatus* highlighted in bold. Numbers at nodes represent symmetric resampling values (above nodes) and Bremer supports (below nodes). Resampling values <50 and Bremer values <1 not shown. Higher taxa of importance vis-à-vis *Thliptosaurus* are labelled.

Juvenile dicynodonts usually have proportionally large preparietal bones (Kammerer *et al*. 2011; see also Fig. 7C), but this bone is relatively small in most dicynodont adults (with some exceptions, e.g. *Diictodon*), including other emydopoids (see Fig. 7B).

Pineal foramen reduction in Kingoriidae

Loss of the pineal foramen is a very rare occurrence within Anomodontia, and previously characterized only the cistecephalid *Kawingasaurus fossilis* (Laaß 2014) and the kingoriid *Kombuisia frerensis* (Fröbisch 2007) (i.e. only

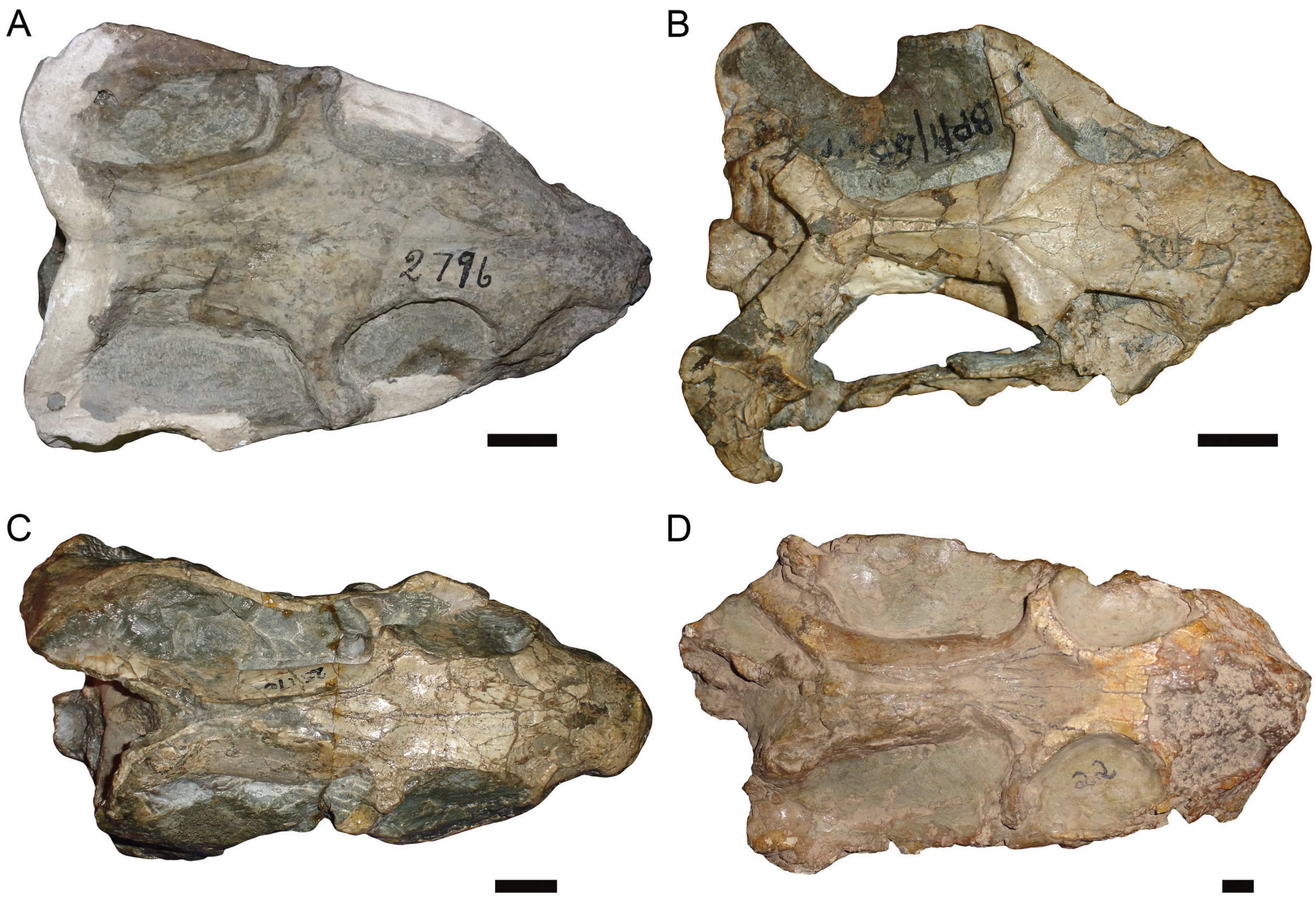

Figure 7. Kingoriids compared in dorsal view. **A**, BP/1/2796, holotype of *Thliptosaurus imperforatus*. **B**, BP/1/5344, holotype of *Kombuisia frerensis*. **C**, USNM 25176, referred specimen of *Dicynodontoides recurvidens*. **D**, BP/1/22, referred specimen of *Dicynodontoides recurvidens*. Scale bars equal 1 cm.

in these taxa do all known specimens lack the pineal foramen. Rare intraspecific variability in presence/absence of the foramen has also been reported by Benoit *et al*. 2016 for *Cistecephalus*, *Diictodon*, *Lystrosaurus*, and *Oudenodon*. It should be noted that the available samples for both *Ka*. *fossilis* and *Ko*. *frerensis* are very small, however, so potential variability in this feature is uncertain.) Although only absent in *Kombuisia frerensis* and *Thliptosaurus imperforatus*, the pineal foramen is also reduced in all other known kingoriids: in *Kombuisia antarctica* it is present as only a narrow slit (Fröbisch *et al*. 2010) and in both species of *Dicynodontoides* it is relatively small (compared to other dicynodonts) and seemingly constricted by the medial expansions of the postorbitals (Cox 1959). In other dicynodonts in which the intertemporal bar is very narrow, with the postorbitals overlapping the parietals, the pineal foramen is usually positioned right behind the postorbital bars, with the constricted portion of the intertemporal bar occurring posteriorly (e.g. *Daptocephalus*, *Dicynodon*; Kammerer *et al*. 2011). In *Dicynodontoides*, however, the pineal foramen is near the mid-length of the intertemporal bar (Angielczyk *et al*. 2009), in the area where overgrowth of the postorbitals reduces dorsal exposure of the parietals to a thin crest.

In extant reptiles, the pineal complex (pineal eye and/or gland) is involved in thermoregulation, with the pineal gland producing melatonin governing thermoregulatory behaviours (e.g. basking) and circadian rhythms (Underwood 1990). A pineal foramen housing a pineal eye, as would have been the case in most dicynodonts, is retained in *Sphenodon* and a variety of lizards, whereas only the underlying pineal gland (covered by the parietal bones) is present in turtles and snakes (the pineal complex is absent altogether in crocodilians) (Tosini 1997). A pineal gland, but no pineal eye, is also present in modern mammals, and loss of the pineal foramen is recognized as a synapomorphy of probainognathian cynodonts (Hopson & Kitching 2001). Benoit *et al*. (2016) recently reviewed the distribution of pineal foramina in therapsids leading up to its loss, and noted convergent reduction of this feature in both therocephalians and cynodonts during the Permo-Triassic transition. They argued that this loss could have been correlated with the evolution of endothermy in Therapsida, potentially involving convergent origins of endothermy in cynodonts and therocephalians.

Benoit *et al*. (2016) also considered the possibility that environmental changes leading into the Triassic (such as increased global temperatures and continental drift towards the equator) could have led to decreased importance of the pineal eye in therapsid thermoregulation. In extant lizards, there is a trend towards reduction or loss of the pineal eye towards the equator, as precise monitoring of daylight and seasonal cycles is less important for ectotherms in the warm tropics (Gundy *et al*. 1975). However, Benoit *et al*. (2016) disfavoured this explanation because of diachronous patterns of reduction in therocephalians *vs* cynodonts and the apparent absence of this pattern in coeval dicynodonts and gorgonopsians. Nevertheless, the presence of a similar pattern in Kingoriidae, a dicynodont clade noted for crossing the Permo-Triassic boundary, suggests that they may have been overly hasty in discounting this hypothesis (the extinction of gorgonopsians at the end of the Permian also makes their retention of a pineal eye something of a moot point). Canalized absence of the pineal foramen in Probainognathia may well have been related to the origin of endothermy, but the possibility that the original reduction of the foramen was driven by environmental pressures in mesothermic ancestors deserves additional consideration.

Small dicynodonts at the Permo-Triassic boundary and their distribution

Thliptosaurus joins a highly restricted contingent of small dicynodonts in the latest Permian. Within the Karoo Basin, *Dicynodontoides*, *Diictodon*, *Emydops*, *Emydorhinus*, and *Pristerodon* have been recorded in the upper *Daptocephalus* AZ (Viglietti *et al*. 2016). However, *Diictodon* is limited to the lowest part of the upper *Daptocephalus* AZ, and the other taxa are represented by very little and sometimes questionable material. Viglietti *et al*. (2016, supplemental material) noted that BP/1/89, the sole upper *Daptocephalus* AZ record of *Emydops arctatus*, was from a locality whose precise stratigraphy was 'unreliable but most likely Upper DAZ'. *Dicynodontoides* and *Emydorhinus* are also known from only single specimens in the upper *Daptocephalus* AZ. The only record of *Pristerodon* from the upper *Daptocephalus* AZ is erroneous, and instead comes from *Tropidostoma* AZ rocks in Esterville (P. Viglietti, pers. comm., 2018). Outside of the Karoo Basin, latest Permian dicynodonts are known from China and Russia, and also show a paucity of small-bodied taxa. In China, the Cangfanggou Group of the Junggur Basin has yielded numerous fossils of '*Dicynodon*-grade' Permian dicynodontoids (e.g. *Jimusaria*) and *Lystrosaurus* (Metcalfe *et al*. 2009; Kammerer *et al*. 2011), but only a single small dicynodont skull, representing the sole extra-African record of *Diictodon* (Angielczyk & Sullivan 2008). Changhsingian dicynodont records of any kind are rare in Russia, but there as well, small taxa (*Delectosaurus*, *Elph*, and *Interpresosaurus*) seem to be rarer than larger dicynodontoids (e.g. *Vivaxosaurus*) (Angielczyk & Kurkin 2003; Kurkin 2011).

Smith & Botha-Brink (2014) argued that the first phase of the end-Permian mass extinction in the Karoo Basin coincided with lowering of the water table, reducing the vegetative groundcover upon which small dicynodonts fed. It is uncertain whether similar environmental factors were driving small dicynodont decline outside of the basin. Clearly, however, small dicynodont habitat was not totally eliminated, as some small dicynodonts survived into the Early (*Myosaurus gracilis*) and Middle Triassic (*Kombuisia frerensis*) of South Africa. Fröbisch *et al*. (2010) suggested that Antarctica might have acted as a refugium for small dicynodonts during this time. They noted that kingoriids are present in South Africa in the late Permian and Middle Triassic, but while missing in the South African Early Triassic recovery fauna, they are present in coeval beds in the Antarctic Fremouw Formation. Further sampling is required to test this hypothesis (unfortunately, pre-Triassic vertebrate fossils have not yet been found in the Fremouw Formation), but the idea of geographically variable survival of small dicynodonts during this time is worth considering.

Although faunal variation between the successive Permo-Triassic assemblage zones in the Karoo Basin has been studied for over a century (see review in Rubidge 1995), relatively little attention has been given to geographic variation within the assemblage zones. In part, this is due to the tight correlation between geography and stratigraphy: because of the original depositional and subsequent erosional history of the basin, older assemblage zones are mainly exposed in the south and west (with the oldest *Eodicynodon* AZ being limited to a thin strip at the southwestern edge of the basin) (Catuneanu *et al*. 2005; Smith *et al*. 2012). However, the later *Daptocephalus–Cynognathus* AZs are exposed as broadly concentric rings surrounding the Triassic-Jurassic Stormberg Group (centred in Lesotho), giving them expansive coverage in the Eastern Cape, Free State, and KwaZulu-Natal (with *Daptocephalus* AZ exposures also appearing in the Western Cape and Mpumalanga) (van der Walt *et al*. 2010). There has been intense recent debate in the Permo-Triassic extinction literature focusing on geographic variation in lithology and paleobotanic records, with potential implications for the uniformity of the PTB event bed across the basin (Gastaldo *et al*. 2009, 2017; Gastaldo & Neveling 2012; Ward *et al*. 2012). However, even these studies were quite limited in their geographic coverage (largely re-examining classic PTB sites in the Free State and Eastern Cape) and incorporated little data concerning the distribution of vertebrate fossils.

Kammerer *et al*. (2015a) noted that within the *Daptocephalus* AZ, some taxa seem to be restricted to the area surrounding Graaff-Reinet (near the boundary between the Eastern and Western Cape provinces), but were uncertain whether this represents real geographic endemism or local exposure of a particular time slice. More extensive stratigraphic study (Viglietti *et al*. 2016) has resolved at least some of this variation between localities as faunal turnover between the lower and upper *Daptocephalus* AZ, but not all of it; nor does this explain the presence of some therapsid taxa with very limited records in South Africa that are more abundant in probable coeval beds in Zambia (see e.g. Angielczyk & Kammerer 2017). Historically, the Permo-Triassic therapsid fauna from KwaZulu-Natal seemed unremarkable, with published records largely representing common taxa known elsewhere in the basin (e.g. *Daptocephalus* [Ewer 1961]; *Lystrosaurus* [Broom 1907; Haughton 1917; Kitching 1968]; *Moschorhinus* [Brink 1959; Durand 1991]). However, these records only scratch the surface: as the index taxa for their assemblage zones, taxa like *Daptocephalus* and *Lystrosaurus* are expected to be present throughout the basin. It is the rarer taxa that are of greater interest, and in this regard *Thliptosaurus* is intriguing, as a new, small-bodied, latest Permian dicynodont.

Considering how well-sampled coeval strata are elsewhere in the basin, discovery of a new South African dicynodont taxon of this age is surprising. A second small dicynodont taxon (*Kwazulusaurus*) is also known only from the Stoffelton locality (although the distinction of this genus from *Lystrosaurus* requires additional study), suggesting that the second-order components of this fauna may differ markedly from those in their better-sampled western counterparts. Further study of this locality is clearly needed, and in general, end-Permian and earliest Triassic exposures in KwaZulu-Natal should be a priority for future fieldwork in the region.

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