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Angielczyk, Kenneth D.

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First occurrence of the dicynodont *Digalodon* (Therapsida, Anomodontia) from the Lopingian upper Madumabisa Mudstone Formation, Luangwa Basin, Zambia

Kenneth D. Angielczyk[1,2]

[1]*Integrative Research Center, Field Museum of Natural History, 1400 South Lake Shore Drive, Chicago, Illinois 60605, U.S.A.*

[2]*Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa*

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Digalodon is a rare emydopoid dicynodont first described from upper Permian rocks in the Karoo Basin of South Africa. During fieldwork in the upper Madumabisa Mudstone Formation of the Luangwa Basin (Zambia) in 2014, a small dicynodont skull was discovered that conforms very well to the recently revised diagnosis of *Digalodon rubidgei*, although some minor differences between the Zambian and South African specimens are apparent. The Zambian occurrence of *Digalodon* expands the known geographic range of the genus, which was previously limited to a small set of localities in the vicinity of the town of Graaff-Reinet (Eastern Cape). Based on historical specimens, *Digalodon* is thought to have a comparatively short stratigraphic range in the Balfour Formation that spans the boundary between the *Cistecephalus* and *Daptocephalus* assemblage zones. This observation may allow refinement of biostratigraphic correlations between the Karoo and Luangwa Basins, but discovery of more precisely-provenanced specimens in the Karoo is needed to fully assess *Digalodon*'s biostratigraphic utility.

Keywords: Synapsida, Dicynodontia, Emydopoidea, Permian, biostratigraphy, biogeography.

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INTRODUCTION

Digalodon rubidgei Broom and Robinson, 1948 numbers among the last dicynodonts named by Robert Broom (Wyllie 2003). As with much of Broom's taxonomic work, the description of *D. rubidgei* consists of only a few short paragraphs of text and two line drawings of the holotype, and it was nearly four decades before *D. rubidgei* began to be re-assessed. Cluver & King (1983) made a cursory comparison between *D. rubidgei* and *Aulacephalodon*, and King (1988) carried this further by tentatively suggesting that *Digalodon* was a junior synonym of *Aulacephalodon*, echoing Broom and Robinson's suggestion that *Digalodon* and *Aulacephalodon* were 'allied' (1948: 404). In contrast, Brink (1986) considered *Digalodon* a synonym of *Dicynodontoides*, but he did not discuss the rationale behind this conclusion. Angielczyk *et al*. (2009) disagreed with both of these hypotheses in their taxonomic revision of *Dicynodontoides*, instead suggesting that *D. rubidgei* was likely a valid taxon.

Kammerer *et al*. (2015a) undertook the first detailed examination of *Digalodon* since Broom and Robinson named the taxon. They redescribed the holotype, confirmed the validity of *D. rubidgei*, identified additional specimens, discussed the possibility of sexual dimorphism, and investigated its phylogenetic relationships, concluding that *Digalodon* is a member of Emydopoidea. Perhaps most importantly, Kammerer *et al*. (2015a) noted that all of the specimens of *D. rubidgei* known at that time were collected from strata thought to be close to the boundary between the *Cistecephalus* and *Daptocephalus* assemblage zones (also see Viglietti *et al*. 2016) at localities in the vicinity of Graaff-Reinet in the Karoo Basin. Several other therapsids have their only Karoo records in this restricted geographic and stratigraphic interval (Kammerer *et al*. 2015a,b; Kammerer 2016, 2017; Van den Brandt & Abdala 2018), although the underlying causes for this pattern are uncertain (Kammerer 2017).

Dicynodont fossils were first discovered in the Permian rocks of the Luangwa Basin of Zambia in 1925 (Dixey 1937), with the first substantive report of Zambian specimens being provided by Boonstra (1938). Additional fieldwork in the basin was carried out in the early 1960s and early 1970s, with a brief reconnaissance in 2000 (see reviews in Angielczyk *et al*. 2014; Sidor & Nesbitt 2018). Most recently, field crews led by the University of Washington and the Field Museum of Natural History have collected fossils in the Luangwa Basin in 2009, 2011, 2014, and 2018 [2012 Zambian fieldwork mentioned by Sidor & Nesbitt (2018) only occurred in the Mid-Zambezi Basin]. Lopingian fossils occur in the upper Madumabisa Mudstone Formation in the Luangwa Basin (e.g. Drysdall & Kitching 1963),

*Author for correspondence. E-mail: kangielczyk@fieldmuseum.org

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and various authors biostratigraphically correlated parts or all of this assemblage with equivalents of the modern *Tropidostoma*, *Cistecephalus*, and *Daptocephalus* assemblage zones of the Karoo (see review in Angielczyk *et al*. 2014). Based on their comprehensive study of the dicynodont component of the Madumabisa faunal assemblage, Angielczyk *et al*. (2014) proposed a correlation with the *Cistecephalus* Assemblage Zone, and Angielczyk & Kammerer (2017) suggested that a further refinement to upper *Cistecephalus* to lower *Daptocephalus* Assemblage Zone might be warranted. Although some of the taxa in the Madumabisa assemblage are endemic or have affinities with other biogeographic provinces (Angielczyk *et al*. 2014; Huttenlocker *et al*. 2015; Huttenlocker & Sidor 2016), the assemblage as a whole displays a strong degree of similarity to that of the Karoo Basin (Fröbisch 2009; Sidor *et al*. 2013; Bernardi *et al*. 2017).

In the course of fieldwork in 2014, Sterling Nesbitt discovered a small dicynodont skull in upper Madumabisa Mudstone Formation strata exposed in North Luangwa National Park. Preparation of this specimen has revealed that it represents *Digalodon*, the first occurrence of this genus outside of the Karoo Basin. Here, I detail the justification for this identification and discuss the specimen's biostratigraphic and biogeographic implications.

SYSTEMATIC PALAEONTOLOGY

THERAPSIDA Broom, 1905
ANOMODONTIA Owen, 1860
DICYNODONTIA Owen, 1860
THEROCHELONIA Seeley, 1894
EMYDOPOIDEA van Hoepen, 1934

Digalodon* cf. *Digalodon rubidgei Broom and Robinson, 1948

Referred material. NHCC LB830, a nearly complete but somewhat dorsoventrally flattened skull (Fig. 1), parts of four vertebrae, and an elongate bone fragment that may be a partial clavicle. Although the postcranial elements were found in association with the skull, it is unclear whether they represent the same individual or even the same species because they were collected loose on the surface and were not in direct contact with the skull.

Locality and Horizon. NHCC LB830 was collected near the southern border of North Luangwa National Park (Northern Province, Zambia) along the banks of a seasonal tributary of the Mulondoshi River (a tributary of the Luangwa River). This locality (L322) also produced a skull of a new burnetiamorph that is currently under study (C.A. Sidor, pers. comm.; also see Sidor *et al*. 2015), and is about 175 m north of the locality of NHCC LB116 (L94), a specimen of *Compsodon helmoedi* described by Angielczyk & Kammerer (2017). Detailed locality information is available to qualified researchers only from the author or NHCC because of past fossil poaching in the area (Sidor 2015). This locality falls in the Mid-Luangwa Basin of Barbolini *et al*. (2016) and exposes strata of the upper Madumabisa Mudstone Formation. The faunal assemblage preserved in these strata correlates with the *Cistecephalus* and/or lower *Daptocephalus* assemblage zones of the Karoo Basin (Angielczyk *et al*. 2014; Angielczyk & Kammerer 2017).

IDENTIFICATION

Kammerer *et al*. (2015a) included the following characters in their revised diagnosis of *D. rubidgei*: 1) small size (basal skull length <10 cm); 2) precaniniform embayment present; 3) paired anterior palatal ridges present; 4) long, horizontal beak that is sharply demarcated from the caniniform process; 5) tall zygomatic ramus of the squamosal with a folded over dorsal margin; 6) raised parietal 'lips' along the lateral edges of the pineal foramen; 7) short frontal contribution to the orbital margin; 8) broad posterolateral expansion of the parietal that excludes the postorbital from the back of the skull roof.

NHCC LB830 conforms very well to this diagnosis. The basal skull length of the specimen is 77.9 mm. The anterior tip of the snout is slightly damaged but the remains of the anterior median palatal ridges are clearly present (Fig. 2a), although they are roughly parallel for their entire length instead of bowing laterally at their posterior ends as in the holotype (RC 76) (Kammerer *et al*. 2015a). Lateral anterior palatal ridges also are present, helping to confirm a character state that was somewhat uncertain in the type but was visible in one of the referred specimens (B 42). The precaniniform embayment is visible on both sides of the skull (Fig. 2a). The original edge of the palatal rim is eroded, but the long, horizontal beak formed by the premaxilla and maxilla is obvious (Fig. 1c). Similar to the holotype, this portion of the palatal rim meets the anterior edge of the caniniform process at close to a ninety-degree angle (Fig. 1c), and an enlarged vascular foramen is present on the posterior surface of the caniniform process (Fig. 2e). A postcaniniform keel is present in NHCC LB830, but its ventral edge is more broadly rounded than the comparatively narrow keel present in the type. The bone surface in this area is somewhat cracked and damaged on both sides of the skull, however, so the difference may be an artefact of preservation.

NHCC LB830 is unique among known specimens of *Digalodon* in its possession of complete caniniform tusks. The tusks are conical and taper to a fine point. There is no evidence of wear facets near the tips of the tusks, but the bases of the tusks bear low longitudinal ridges and shallow grooves near the margins of the alveoli. This ornamentation appears to be related to the growth of the tusks, not a result of wear. The visible (erupted) portions of the tusk are not infolded to the degree seen in the pathological specimens described by Whitney *et al*. (2019), but it is important to note that the degree of infolding they observed was highest within the alveolus and decreased towards the tip of the tusk. This raises the possibility that the tusk roots of NHCC LB830 also may be infolded to a greater degree than is visible on the external surfaces of the specimen. Unlike the holotype, where the tusks are angled anteriorly, the tusks of NHCC LB830 are very straight and near-vertically oriented (Fig. 1c). The tusks are also broken off at the alveolar margin in B 42, but they seem to be more vertically oriented, so the anterior

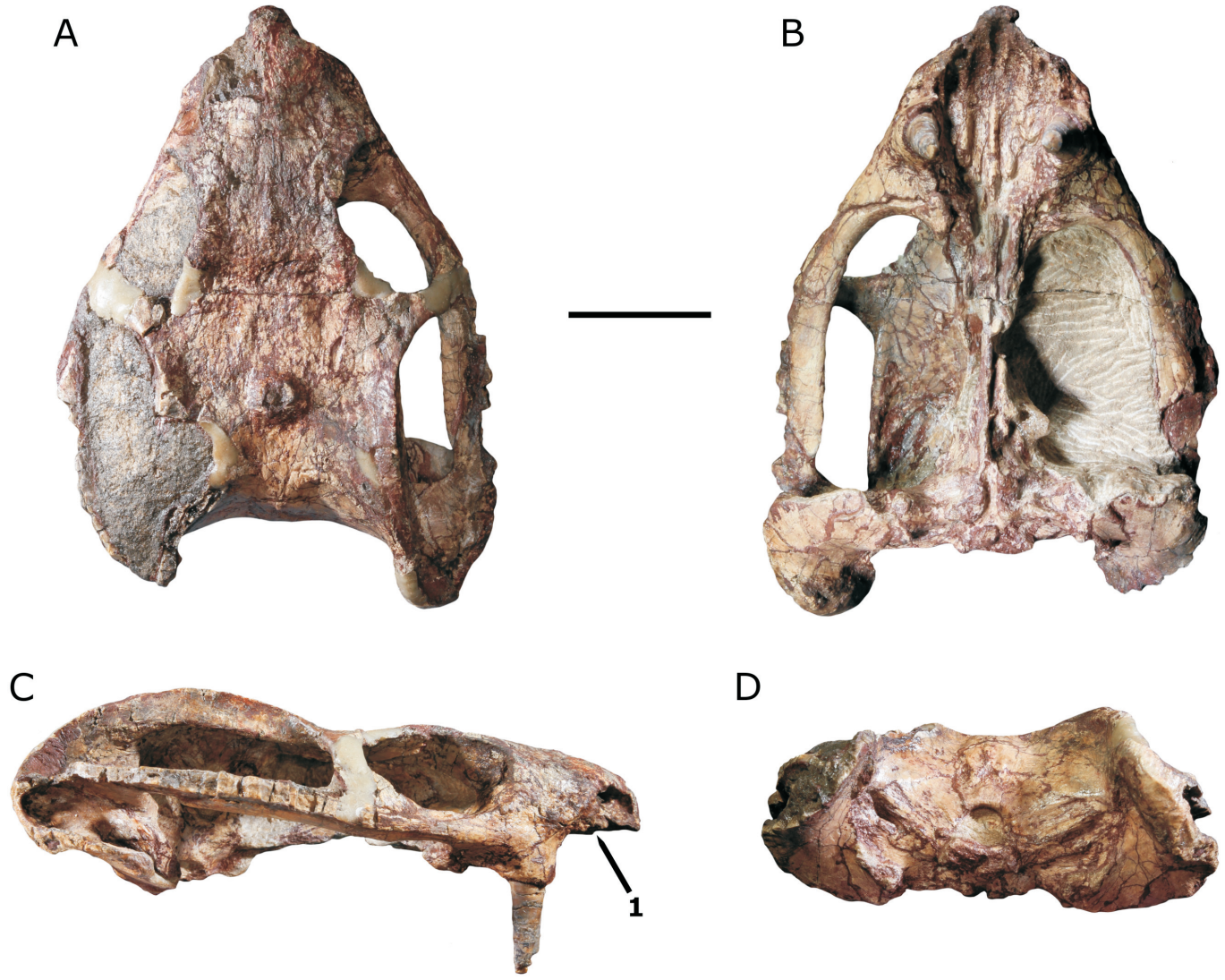


Figure 1. Zambian specimen of *Digalodon* cf. *D. rubidgei* (NHCC LB830) in dorsal (**A**), ventral (**B**), right lateral (**C**), and posterior (**D**) views. The long, horizontal beak that is sharply demarcated from the caniniform process (1) is diagnostic of *Digalodon*. Scale bar is 2 cm.

angulation of the tusks in the holotype may be a result of deformation.

The lateral edge of the zygomatic ramus of the squamosal is damaged on both sides of NHCC LB830 (Figs. 1a–b), making it impossible to assess whether the dorsal margin was folded over. However, enough of the right squamosal is preserved to indicate that the zygomatic ramus was relatively broad. It is more horizontal than in the type, but this may in part reflect the dorsoventral compression that NHCC LB830 has undergone (also evidenced by the anterior curling of the ventral edge of the occipital plate and the breakage and lateral displacement of the ascending ramus of the epipterygoid on both sides of the skull).

The cortical surface of the skull roof is eroded and highly cracked, obscuring many sutural details. Because of this damage, the size of the frontal contribution to the orbital margin is uncertain. However, part of the frontal–postorbital suture is preserved on the left side of the skull, and it indicates that the postorbital had an anterior process that extended beyond the level of the postorbital bar (Fig. 2b). This resembles the morphology present on the right side of the holotype, and is consistent with a relatively small frontal contribution to the orbit.

The pineal foramen is circular and surrounded by a raised eminence. The dorsal edge of the eminence is broken, and this breakage reveals that the walls of the eminence were widest laterally and narrowed both anteriorly and posteriorly (Fig. 2c). This resembles the condition in the type, although as preserved the eminence of NHCC LB830 forms more of a complete raised rim around the pineal foramen instead of lateral thickenings separated by distinct anterior and posterior grooves. Grooves may have been more apparent when the walls of the eminence reached their original height, but it is also possible the NHCC LB830 had a more dome-like pineal boss, comparable to that seen in *Diictodon* or *Eosimops* (Sullivan & Reisz 2005; Angielczyk & Rubidge 2013).

As in the holotype, the posterior ramus of the postorbital is strongly bi-planar, with distinct dorsal and lateral surfaces that are perpendicular to each other. The parietals are widely exposed on the dorsal surface of the intertemporal bar, as in South African specimens of *D. rubidgei*, although the temporal bar itself is proportionally wider.

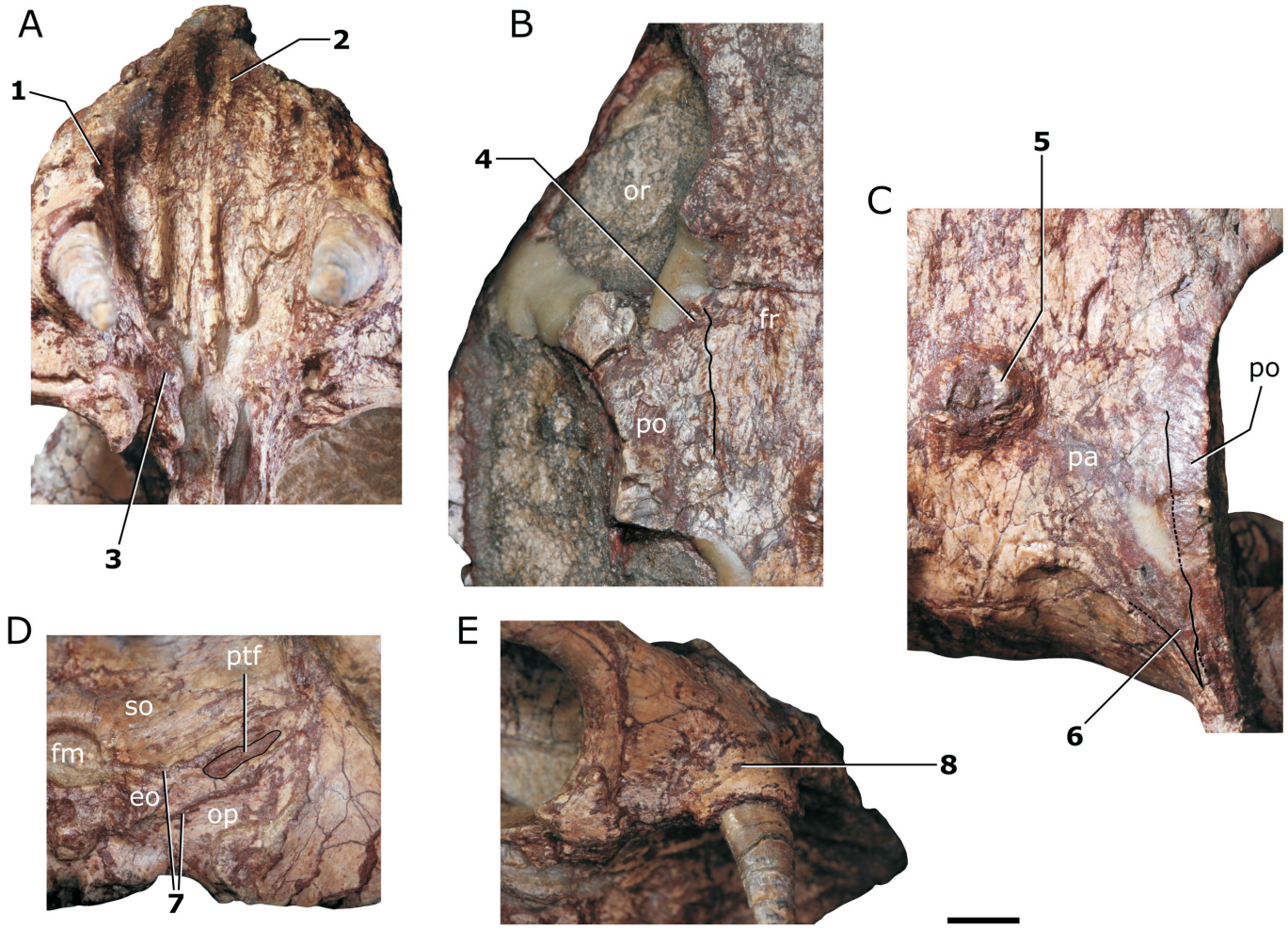


Figure 2. Close-ups of the Zambian specimen of *Digalodon* cf. *D. rubidgei* (NHCC LB830) showing characters important for identification. **A**, secondary palate in ventral view showing precaniniform embayment (1), anterior median palatal ridges (2), and absence of a palatine foramen (3). **B**, left side of skull roof in dorsal view showing the anterior process of the postorbital that extends past the postorbital bar (4), suggestive of a small frontal contribution to the orbit. **C**, right side of intertemporal region in dorsal view showing parietal lips around the pineal foramen that are widest laterally (5), and the broad posterloateral expansion of the parietal that excludes the postorbital from the back of the skull roof (6). **D**, Right side of occipital plate in posterior view showing matrix-filled cracks (7) in the vicinity of the exoccipital that may represent areas of weakness associated with unfused sutures. **E**, right maxilla in ventrolateral view showing the enlarged vascular foramen (8) on the posterior surface of the caniniform process. Scale bar is 5 mm. Abbreviations: eo, exoccipital; fm, foramen magnum; fr, frontal; op, opisthotic; or, orbit; pa, parietal; ptf, posttemporal fenestra; po, postorbital; so, supraoccipital.

This can be easily visualized by the fact that the edges of the intertemporal bar are approximately aligned with the margins of the interorbital skull roof in most South African specimens (e.g. RC 498), whereas in NHCC LB830 the edges of the intertemporal bar extend farther laterally than the orbital margins. The posterior portion of the suture between the postorbital and the parietal is well preserved on the right side of the skull roof. There, it is clear that the parietal had a well-developed posterior process that excluded the postorbital from the posterior edge of the skull roof (Fig. 2c).

Although they did not include them in their formal diagnosis of *D. rubidgei*, Kammerer *et al*. (2015a) described two other unusual characters in the holotype that also are apparent in NHCC LB830. First, in contrast to most other emydopoids (Angielczyk 2001; Angielczyk & Kurkin 2003), the palatine pad of RC 76 is not pierced by a palatine foramen and this is also the case in NHCC LB830 (best preserved on the right side of the skull; Fig. 2a). Second, the exoccipitals of the holotype do not appear to have been fully fused with the other bones of the occiput, with an open suture between the exoccipital and the opisthotic being especially clear. Sutures delineating the margins of the exoccipital are not clear on the occiput of NHCC LB830. However, as noted above, the occiput of the specimen has been deformed in response to dorsoventral compression. Some of the buckling associated with this deformation, especially on the right side of the skull, resulted in pieces of bone in the vicinity of the exoccipitals being displaced slightly posteriorly relative to the rest of the occiput, with raised areas of matrix filling the surrounding cracks (Fig. 1d). Although it is uncertain how precisely this breakage followed the sutures surrounding the exoccpitals, it does suggest an area of weakness existed in this part of the skull, as would be expected if the sutures were not fully co-ossified.

In summary, NHCC LB830 displays almost all of the diagnostic features of *D. rubidgei* that were enumerated by Kammerer *et al*. (2015). Even in cases where damage prevents a definitive assessment of a character state (e.g. small frontal contribution to the orbital margin, downturned edge of the zygomatic ramus of the squamosal),

the preserved parts of the specimen are suggestive of the states expected for *D. rubidgei* originally being present. NHCC LB830 also possesses characters found in *D. rubidgei* that are otherwise rare among emydopoids (e.g. absence of a palatine foramen). However, several differences also are apparent, including anterior median palatal ridges that do not diverge posteriorly, more vertical tusks, more rounded postcaniniform keel, more horizontal zygoma, more continuous raised rim of the pineal foramen, and proportionally broader intertemporal bar. Based on these observations, I consider the identification of NHCC LB830 as a member of the genus *Digalodon* to be well justified, but its referral to the species *D. rubidgei* is less certain.

The differences between NHCC LB830 and the South African specimens may represent intraspecific variation that would be more apparent if a larger sample of *D. rubidgei* was available, but it could also indicate a species-level divergence between Zambian and South African populations of *Digalodon*. The situation is further complicated by the dorsoventral flattening experienced by NHCC LB830, which may explain some differences (e.g. more horizontal zygoma in NHCC LB830) but not others (e.g. the wider intertemporal bar is unlikely an artefact of deformation because the interorbital skull roof also is proportionally narrower relative to basal skull length). A larger number of specimens from both the Karoo and Luangwa basins (and ideally other southern African basins) is needed to fully resolve these issues, and in light of this uncertainty I consider it most conservative to identify NHCC LB830 as *Digalodon* cf. *D. rubidgei* instead of formally referring it to the species *D. rubidgei* or erecting a new species.

DISCUSSION

The upper Madumabisa Mudstone Formation of the Luangwa Basin preserves an important late Permian tetrapod assemblage that has strong similarities to contemporary assemblages from the Karoo Basin (Fröbisch 2009; Sidor *et al*. 2013; Angielczyk *et al*. 2014; Bernardi *et al*. 2017). However, the Madumabisa assemblage displays lower species richness than the *Cistecephalus* or *Daptocephalus* assemblage zones of the Karoo, and Roopnarine *et al*. (2018) hypothesized that this was likely the result of incomplete sampling of the Luangwa Basin fossil record. *Digalodon* clearly was a rare dicynodont, with fewer than ten specimens identified worldwide (Kammerer *et al*. 2015a). Its discovery in Zambia in the course of recent fieldwork corroborates Roopnarine *et al*.'s (2018) hypothesis that less abundant elements of the Madumabisa assemblage remain unrecognized, underscoring the importance of continued collecting in this formation.

The Zambian record of *Digalodon* expands the geographic range of the genus. Prior to this, it was known only from a restricted set of Karoo localities in the vicinity of Graaff-Reinet (Kammerer *et al*. 2015a), and it now becomes another example of the surprisingly good dispersal abilities of small dicynodonts (e.g. Angielczyk & Sullivan 2008; Angielczyk *et al*. 2014; Angielczyk & Kammerer 2017). Several other therapsid taxa seem to be largely limited in their occurrences to this area of the Karoo (Kammerer *et al*. 2015a,b; Kammerer 2016, 2017; Van den Brandt & Abdala 2018), and among these taxa *Kitchinganomodon* and *Compsodon* also are present in the Madumabisa assemblage (Angielczyk *et al*. 2014, Angielczyk & Kammerer 2017). It is not clear whether the geographically-restricted Karoo occurrences are an artefact of sampling or if they reflect a genuine pattern resulting from factors such as an unusual palaeoenvironment or short time interval being represented at the localities (Kammerer 2017). Further collecting and research on the sedimentology, geochemistry, and geochronology of the Balfour Formation near Graaff-Reinet and the upper Madumabisa Mudstone Formation will be necessary to explain the reason for the biogeographic link between the Karoo sites and the Luangwa Basin. Nevertheless, the presence of *Digalodon* in the Luangwa Basin is one more point of similarity between its Lopingian dicynodont fauna and that of the Karoo, and further differentiates it from the geographically proximal Ruhuhu Basin of Tanzania (also see discussion in Angielczyk *et al*. 2014).

The currently-recognized stratigraphic range of *Digalodon* in the Balfour Formation spans the upper *Cistecephalus* and lower *Daptocephalus* assemblage zones (Kammerer *et al*. 2015a; Viglietti *et al*. 2016). If this range is delineated correctly, it is additional evidence suggesting that the upper Madumabisa Formation assemblage is better correlated with this interval (also see Angielczyk & Kammerer 2017) instead of only the *Cistecephalus* Assemblage Zone, as suggested by Angielczyk *et al*. (2014). However, all but one (SAM-PK-K11551) of the Karoo specimens of *Digalodon* are parts of historical collections whose geographic and stratigraphic provenance data lack modern levels of precision.

SAM-PK-K11551 (Fig. 3) was collected in 2017 on the farm Riverdene (formerly Steilkrans), about 480 m below the Permo-Triassic boundary in the upper Oudeberg Member of the Balfour Formation. This farm is the type



Figure 3. Dorsal view of a *Digalodon rubidgei* skull (SAM-PK-K11551) collected from a measured stratigraphic section in the Karoo Basin, South Africa, in 2017. This specimen establishes the presence of *D. rubidgei* in the *Daptocephalus* Assemblage Zone.

locality of the *Cistecephalus* Assemblage Zone, which traditionally included all of the Oudeberg Member (Smith & Keyser 1995). Recent research suggests that the uppermost Oudeberg Member actually hosts a lower *Daptocephalus* Assemblage Zone fauna, however (Viglietti *et al.* 2016, 2017). We use this correlation between the regional litho- and biostratigraphy, but it is important to note that this is an area of on-going active research (R. Smith, pers. comm.). Therefore, the stratigraphic position of SAM-PK-K11551 places the specimen near the base of the lower *Daptocephalus* Assemblage Zone, helping to confirm the previously hypothesized range of *Digalodon* in the Karoo. If additional specimens can be found in measured stratigraphic sections, it should be possible to more rigorously constrain its full stratigraphic range in that basin. Our on-going fieldwork in Zambia complements this process because it is generating an increasingly large database of geographically and stratigraphically well-provenanced specimens, particularly for North Luangwa National Park and the Munyamadzi Game Management Area of the Mid-Luangwa Basin. Work is now underway using this resource to test the hypothesis that a single faunal assemblage is present in the upper Madumabisa Mudstone Formation in this region (B. Peecook, pers. comm.). Taken together, advances of this kind will provide the data needed to further refine biostratigraphic correlations between the Luangwa and Karoo basins.

INSTITUTIONAL ABBREVIATIONS

B	Bremner Collection, Graaff-Reinet Museum, Graaff-Reinet, South Africa
NHCC	National Heritage Conservation Commission, Lusaka, Zambia
RC	Rubidge Collection, Graaff-Reinet, South Africa
SAM	Iziko Museums of South Africa, Cape Town, South Africa

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