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Youngest dinocephalian fossils extend the *Tapinocephalus* Zone, Karoo Basin, South Africa

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The dinocephalians (Synapsida, Therapsida) were one of the dominant tetrapod groups of the Middle Permian (Guadalupian Epoch, ~270–260 million years ago) and are most abundantly recorded in the *Tapinocephalus* Assemblage Zone (AZ) of the Main Karoo Basin, South Africa. Dinocephalians are thought to have become extinct near the top of the Abrahamskraal Formation of the Beaufort Group and their disappearance is one criterion used to define the base of the overlying *Pristerognathus* AZ. Because of the abundance of fossils in the Karoo, the Beaufort Group biozones form the biostratigraphic standard for later Permian terrestrial tetrapod ecosystems, so their stratigraphic delineation is of great importance to Permian palaeobiology. We report two new specimens of the rare tapinocephalid dinocephalian *Criocephalosaurus* from the lowermost Poortjie Member, which makes them the youngest dinocephalians known from the Main Karoo Basin and extends the *Tapinocephalus* AZ from the Abrahamskraal Formation up into the Teekloof Formation. The extension of the *Tapinocephalus* AZ relative to the lithostratigraphy potentially affects the biozone or biozones to which a fossil species can be attributed; this extension has implications for biostratigraphic correlations within the Main Karoo Basin as well as with other basins across Gondwana. These discoveries also indicate that a population of herbivorous tapinocephalids survived as rare constituents of the tetrapod fauna after most generic richness within the clade had already been lost.

Introduction

The Dinocephalia are a clade of mostly large basal therapsids[1] that were widely distributed around Pangaea in the Guadalupian. The group is known from Middle Permian basins in Russia, Central Asia, China, Brazil, Tanzania, Zambia and Zimbabwe[2-10], but is best represented in the Abrahamskraal Formation of the South African Beaufort Group[11] (Figure 1). Three dinocephalian families have been found in South Africa: the Anteosauridae, the Titanosuchidae and the Tapinocephalidae. The clade is most abundant and taxonomically diverse in the *Tapinocephalus* Assemblage Zone (AZ) — which has yielded all known species of titanosuchids and 18 of the 22 described species of tapinocephalids — but they are also found in the underlying *Eodicynodon* AZ in which they are represented by only two species, *Tapinocaninus pamelae* and *Australosyodon nyaphuli*.[12,13] Together, the *Eodicynodon* and *Tapinocephalus* AZs are the oldest two biozones of the Beaufort Group.[11]

Although dinocephalians were an important constituent of early therapsid faunas, they disappear from the fossil record at the top of the Middle Permian *Tapinocephalus* AZ[11,14,15] and in the Main Karoo Basin their last occurrence is a major criterion defining the base of the overlying *Pristerognathus* AZ[16]. Lithostratigraphically, the *Tapinocephalus* AZ corresponds to the upper Abrahamskraal Formation, apart from its uppermost strata, while the overlying *Pristerognathus* AZ is considered to extend through the uppermost part of the Abrahamskraal Formation and the Poortjie Member of the Teekloof Formation.[17] Changes in the lithostratigraphic position of the contact between the *Tapinocephalus* and *Pristerognathus* AZs have consequences for stratigraphic correlation, as well as palaeobiodiversity studies, because the biozones of the Beaufort Group represent a global reference for terrestrial tetrapod faunas from the Middle Permian to the Early Triassic.[18-21] Furthermore, radiometric dates have recently been determined for several zircon-bearing volcanic ash horizons within the Beaufort Group,[22] so accurate chronology of tetrapod evolutionary patterns in the Permian is dependent on good biostratigraphic resolution relative to the lithostratigraphy.

Two dinocephalian crania, one with associated postcranial fragments including two articulated vertebrae with a high neural spine, have recently been recovered from the basal Poortjie Member of the Teekloof Formation. These discoveries provide new biostratigraphic data that necessitates a shift in the lithostratigraphic extent of the *Tapinocephalus* AZ.

Institutional Abbreviations

BP, Evolutionary Studies Institute (formerly Bernard Price Institute for Palaeontological Research), Johannesburg; CGS, Council for Geosciences, Pretoria; KM, McGregor Museum, Kimberley; NHMUK, Natural History Museum, London, UK; SAM, Iziko: South African Museum, Cape Town.

Material

SAM-PK-K10888 is a partial skull and some associated postcranial elements that were discovered by J.A. and Madelon Tusenius on the Beaufort West commonage, Western Cape Province, to the southwest of that town (32° 23.25' S, 22° 33.24' E). Although the specimen was found ex situ, the low relief of the area and the sub-horizontal strata constrain the provenance of the specimen to a mudrock horizon exposed on the southern side of the valley (Figure 1). Reference to the published 1:250 000 geological map for the area (1979, Beaufort West Sheet, Geological Survey of South Africa 1:250000 Series), combined with stratigraphic fieldwork in the area by the authors, shows that this locality is within the lower Poortjie Member of the Teekloof Formation. As the combination of low relief and poor rock exposure was not conducive to measuring a stratigraphic section between the locality and the base of the Poortjie Member, a stratigraphic section was instead measured between the locality and

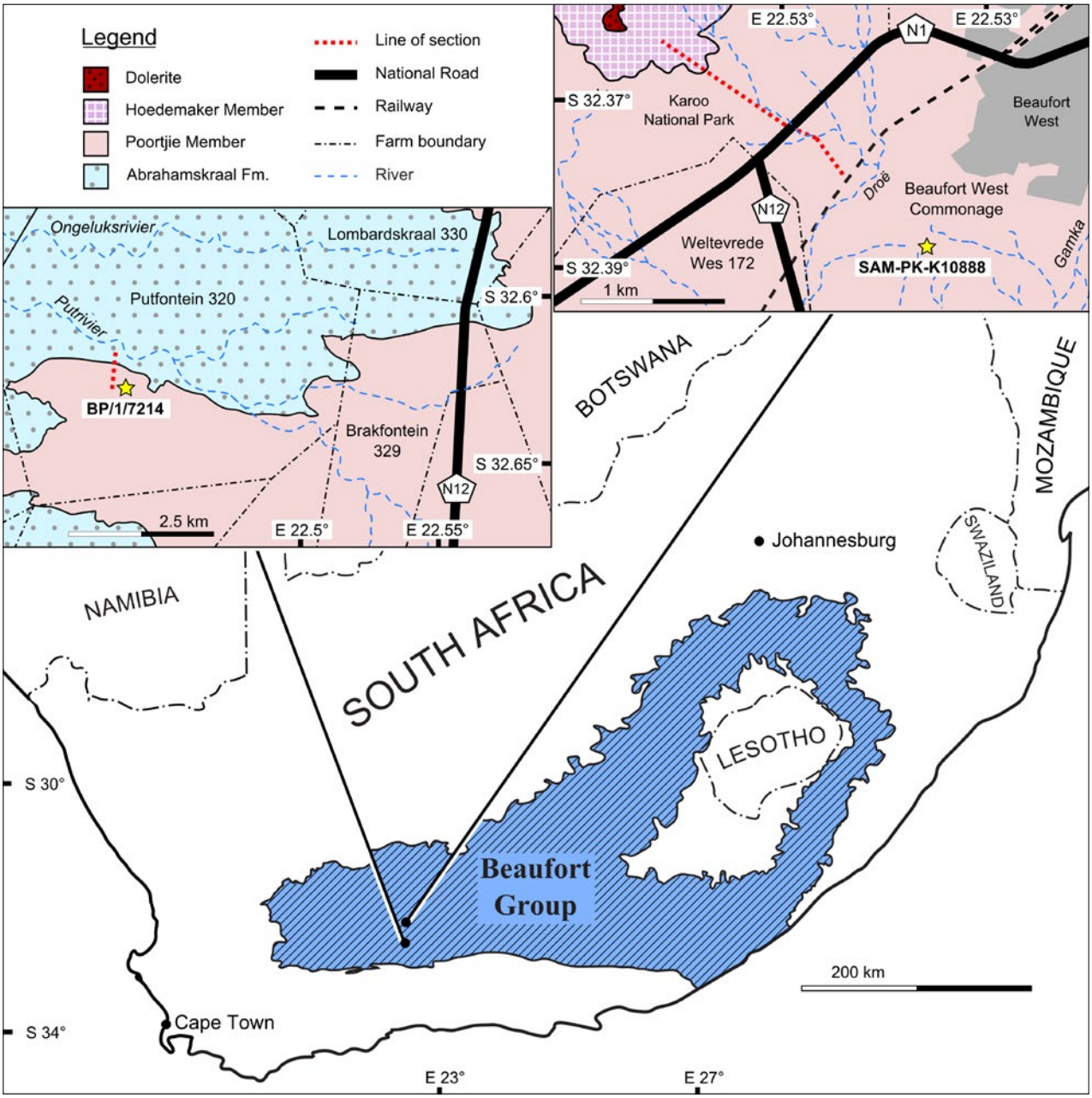


Figure 1: Map of the southwestern Karoo Basin, showing the localities of SAM-PK-K10888 and BP/1/7214 and the line of sections presented in Figure 2.

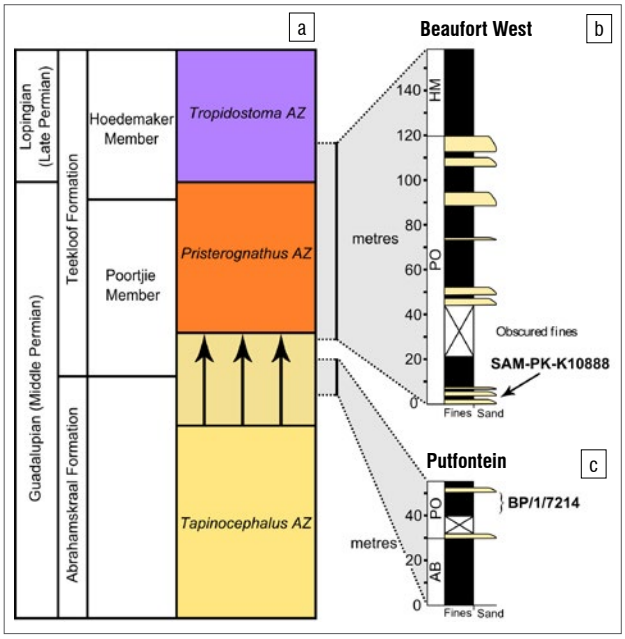
the base of the overlying Hoedemaker Member, using a Jacob's staff and Abney level. This section indicated that the specimen occurred in a horizon 116 m below the top of the Poortjie Member (Figure 2). The Poortjie Member in the Beaufort West area is 160–182 m thick,[23,24] in which case this specimen can be constrained to 40–70 m above the base of the Poortjie Member. This position is consistent with altitude readings for the locality and the mapped base of the Teekloof Formation (1979, Beaufort West Sheet, Geological Survey of South Africa 1:250000 Series), which provides an estimate of 50–60 m, although this may be affected by minor local folding.

The second specimen, BP/1/7214, is also a partial skull and was found by M.D. and Christen Shelton, 70 km further south of Beaufort West on the farm Putfontein, Beaufort West district (32° 37.644' S, 22° 26.366' E). Like SAM-PK-K10888, BP/1/7214 was found ex situ in a stream bed but its provenance can be constrained to a 10-m thick mudrock horizon immediately below the second major sandstone body of the Poortjie Member. The specimen therefore originated 10–20 m above the base of the Poortjie Member (Figure 2).

Description

SAM-PK-K10888 and BP/1/7214 have very similar morphologies (Figure 3). Both comprise the posterior two-thirds of a skull roof up to the posterior border of the orbits and the occiput, although BP/1/7214 is more extensively weathered. SAM-PK-K10888 also preserves the basicranium (Figure 3d). In dorsal view, both specimens display a broadly elliptical shape resulting from the broad frontals being bordered by the narrow interorbital region anteriorly and the narrow temporal roof posteriorly (Figure 3a, 3e).

Although both specimens lack the anterior portion of the skull, they are clearly identified as tapinocephalid dinocephalians by the anteroventral rotation of the occiput and by the presence of pronounced cranial pachyostosis. Furthermore, SAM-PK-K10888 and BP/1/7214 present a set of characters that allow their referral to the tapinocephalid genus *Criocephalosaurus* (replacement name for *Criocephalus* since 2002).[25,26] These include the close proximity of the orbits to one another and their anterior position on the skull compared to other tapinocephalids, a long pineal canal, and an acute angle between the median line of the



AB, Abrahamskraal Formation; HM, Hoedemaker Member; PO, Poortjie Member.

Figure 2: (a) Extension of the *Tapinocephalus* Assemblage Zone (AZ) into the lower Teekloof Formation. Former extent of biozones after Smith et al.[17] Approximate position of the Guadalupian–Lopingian boundary after Rubidge et al.[22] Arrows indicate the extension of *Tapinocephalus* AZ into the Teekloof Formation. (b) Stratigraphic section measured at Beaufort West between the level of the SAM-PK-K10888 locality and the lower Hoedemaker Member. (c) Stratigraphic section on the farm Putfontein.

occiput and the skull roof.[9,25,27,28] Compared with other specimens of *Criocephalosaurus*, the cranial roof of both SAM-PK-K10888 and BP/1/7214 displays moderate pachyostosis that increases the cranial width across the frontals and deepens the parietal along the pineal canal, as is the case in the genotype (KM5138) and the referred specimen (NHMUK R36626). However, the preserved portion of the orbital region in both SAM-PK-K10888 and BP/1/7214 also shows only minor thickening of the prefrontal dorsally and of the postorbital posteriorly (Figure 3b, 3c, 3f and 3g), unlike other examples of *Criocephalosaurus*. This difference may be related to their size, as the two new specimens are the smallest representatives of the genus, with postorbital skull lengths (from the posterior border of the orbit to the posterior tip of the temporal roof) of 160 mm (SAM-PK-K10888) and 169 mm (BP/1/7214).

The parietal in both specimens is a small but deep bone extending across the posteriorly narrowing intertemporal region. In this latter character, SAM-PK-K10888 and BP/1/7214 differ from KM5138, CGP/1/846 and NHMUK R36626, in which the intertemporal region is broad throughout. In SAM-PK-K10888, the posterior portion of the cranium is fractured, creating a roughly sagittal section through the cranial roof, allowing the long pineal canal to be seen (Figure 3h). The canal is orientated parallel to the long axis of the cranium, as in NHMUK R36626. The posteriorly facing pineal opening is large and is surrounded by a thick rim, which is elevated from the parietal surface as in KM5138, CGP/1/846 and NHMUK R36626; this rim contributes to the conical appearance of the posterior end of the skull. The preserved portion of the occiput of SAM-PK-K10888 is formed by the tabular and postparietal bones (Figure 3d), which are elongated dorsoventrally as in the only other specimen of *Criocephalosaurus* that possesses a comparably well-preserved occiput (NHMUK R36626).

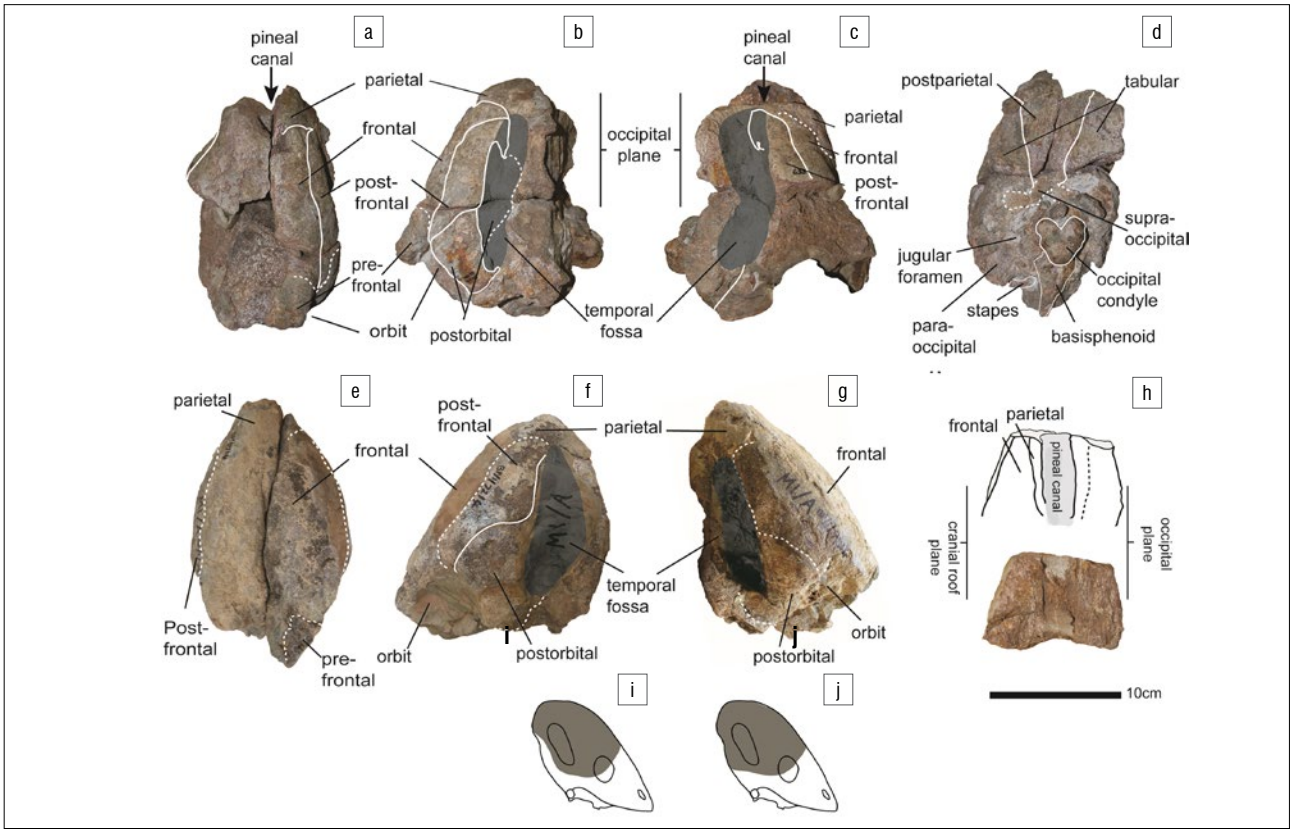


Figure 3: Photos of the specimens (a–d) SAM-PK-K10888 and (e–g) BP/1/7214 showing (a,e) dorsal view, (b,f) left lateral view, (c,g) right lateral view and (d) occipital view. (h) View of sagittal plane on right posterior part of the skull of SAM-PK-K10888, showing the pineal canal orientated parallel to the occipital plane. (i, j) Idealised skull of *Criocephalosaurus* (redrawn from Boonstra[14,28]) showing the portions preserved in (i) BP/1/7214 and (j) SAM-PK-K10888.

Discussion and conclusions

The genus *Criocephalosaurus* has two described species: *C. vanderbyli* Broom 1928, the holotype of which is a weathered cranial roof, and *C. gunyankaensis* Boonstra 1968, which was based on four cranial roofs briefly described by Boonstra[9] and only later referred to *Criocephalus*.[28] The latter specimens are now all missing. A few other incomplete crania were referred to the genus by Boonstra[28], but a survey of museum collections has yielded only four specimens that can reliably be identified as *Criocephalosaurus*: KM5138 (holotype), CGP/1/846, NHMUK R36626 and BP/1/1582. Although specimens SAM-PK-K10888 and BP/1/7214 can be confidently identified as *Criocephalosaurus*, their poor state of preservation does not allow their identification to species level.

Both SAM-PK-K10888 and BP/1/7214 fall within the lower size range of tapinocephalids and are the smallest known examples of *Criocephalosaurus*. Both specimens show only a moderate degree of pachyostosis of the postorbital bar and cranial roof. The latter is steadily reduced posteriorly from the level of the mid-temporal fenestra leading to the conical appearance of the back of the skulls (best illustrated in Figure 3e). Both the overall lesser extent of pachyostosis and the pronounced conical form of the skull differentiate SAM-PK-K10888 and BP/1/7214 from larger specimens, although CGP/1/846 demonstrates a slight tapering of the posterior skull roof towards the pineal opening. Because the degree of pachyostosis is associated with ontogeny in tapinocephalids,[29,30] it is possible that these two specimens represent sub-adults; however, their incompleteness prevents the definitive identification of unambiguous juvenile morphology (e.g. unfused sutures). The fact that both specimens bearing the more gracile morphology occur in the lower Poortjie Member, whereas all larger existing specimens occur in the underlying Abrahamskraal Formation, may also be of significance but this can only be elucidated by the discovery of further material.

The stratigraphic position of the *Tapinocephalus–Pristerognathus* AZ boundary relies on the current definition of the *Pristerognathus* AZ, which is described as 'low diversity dominated by [the dicynodont] *Diictodon* in association with [the therocephalian] *Pristerognathus* and the absence of dinocephalian fossils that are a prominent component of the underlying fauna'[16]. Because both *Diictodon* and *Pristerognathus* are known from the underlying *Tapinocephalus* AZ and the dominance of *Diictodon* continues into the overlying *Tropidostoma* AZ,[17] the *Pristerognathus* AZ can only maintain its integrity when described as an 'interval zone'[31] between the last appearance of dinocephalians and the first appearance of the dicynodont *Tropidostoma*. This lack of new taxa in comparison with the *Tapinocephalus* AZ has in fact led to doubt over the validity of the *Pristerognathus* AZ.[21]

Although it is acknowledged that a biostratigraphic review is required for this interval, the work for which has already begun,[32] the last occurrence of the previously dominant dinocephalians remains a biostratigraphically important event. Despite reservations over the definition of the *Pristerognathus* AZ, we therefore recognise a biostratigraphic distinction between the dinocephalian bearing *Tapinocephalus* AZ and the dinocephalian deficient assemblages above, at least within the Main Karoo Basin. The discovery of tapinocephalids in the lowermost Poortjie Member demonstrates that the dinocephalian record extends into the Teekloof Formation of the Beaufort Group (Figure 2a), and this notion is supported by a probable titanosuchid (BP/1/7184) from the lowermost Poortjie Member near Sutherland.[32] Consequently, the *Tapinocephalus* AZ should be extended by a commensurate degree into the lower Poortjie Member, meaning its upper boundary is therefore correspondingly younger than previously understood.

Regionally, an upward shift in the stratigraphic position of the *Tapinocephalus–Pristerognathus* AZ boundary has implications for the biozone designation of fossil material in existing collections and thus of individual genera. For instance, the extension of the *Tapinocephalus* AZ up into the lower Poortjie Member could constrain the therocephalian *Scylacosaurus* (through specimen SAM-PK-10530) and varanopid synapsids (through specimen SAM-PK-K10407) to the *Tapinocephalus* AZ.[32,33] Globally, this shift could potentially impact palaeobiological studies of Permian tetrapods because biozones are often used as approximations of 'time bins' in calculations of taxonomic diversity trends and those of other biological variables.[17,34-37] Because they represent the youngest dinocephalian fossils from the Main Karoo Basin, the new fossils may also help to elucidate the mode by which dinocephalians became extinct, and, by extension, the cause of the global disappearance of the clade.[38] In particular, the presence of *Criocephalosaurus* in the Teekloof Formation, above the range of any other dinocephalian genus, suggests that a loss of species richness within dinocephalians preceded their extinction.

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Authors' contributions

M.O.D. determined the stratigraphic position of the fossils; S.G. described and identified the fossil material; B.R. was the project leader, provided funding for and intellectual input to the study and co-supervised S.G.; F.A. co-supervised S.G.; J.A. and M.D. discovered the new specimens of *Criocephalosaurus* examined in the study; M.D. and S.J. measured the stratigraphic sections; M.D. and S.G. wrote the first draft of the manuscript; and all authors contributed to the preparation of the final draft.

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