

https://dspace.org/

Re-identification and updated stratigraphic context of the holotypes of the late Permian tetrapods Dicynodon ingens and Scymnosaurus warreni from KwaZulu-Natal

Groenewald, David P; Kammerer, Christian F

2023
Evolutionary Studies Institute
https://hdl.handle.net/10539/37143

Downloaded from a DSpace repository. https://dspace.org/

Re-identification and updated stratigraphic context of the holotypes of the late Permian tetrapods *Dicynodon ingens* and *Scymnosaurus warreni* from KwaZulu-Natal

David P. Groenewald[1, 2*] [§] **& Christian Kammerer**[2, 3]

[1]*Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Cerdanyola del Vallès 08193, Barcelona, Spain*

[2]*Evolutionary Studies Institute (ESI), University of the Witwatersrand, Johannesburg, 2050 South Africa*

[3]*North Carolina Museum of Natural Sciences, 11 West Jones Street, Raleigh, NC 27601, U.S.A.*

Received 1 August 2023. Accepted 10 October 2023

Two historical therapsid holotypes held in the collections of the KwaZulu-Natal Museum (*Dicynodon ingens* Broom, 1907 and *Scymnosaurus warreni* Broom, 1907) are redescribed. The holotype of *D. ingens* is a snout tip of a large dicynodontoid that can be re-identified as a specimen of *Daptocephalus leoniceps* based on premaxillary proportions and palatal morphology. The holotype of *S. warreni* consists of a dorsoventrally crushed therocephalian snout, which is here re-identified as that of *Moschorhinus kitchingi* based on size, general proportions, tooth count, and septomaxillary morphology. The localities of both specimens are biostratigraphically assigned to the *Lystrosaurus maccaigi-Moschorhinus* Subzone of the *Daptocephalus* Assemblage Zone (latest Permian).

Keywords: Karoo Basin, Balfour Formation, KwaZulu-Natal Province, *Daptocephalus* Assemblage Zone, biostratigraphy, Lopingian, Broom holotypes.

Palaeontologia africana 2023. ©2023 David P. Groenewald & Christian Kammerer. This is an open-access article published under the Creative Commons Attribution 4.0 Unported License (CC BY4.0). To view a copy of the license, please visit http://creativecommons.org/licenses/by/4.0/. This license permits unrestricted use, distribution, and reproduction in any medium, provided the original author and source are credited.
The article is permanently archived at: https://hdl.handle.net/10539/37143

INTRODUCTION

The Balfour Formation of the Beaufort Group in the province of KwaZulu-Natal, South Africa, has long been known for its richness of tetrapod fossils from the latest Permian *Daptocephalus* Assemblage Zone (AZ) and the Early Triassic *Lystrosaurus declivis* AZ (Ewer 1961; Kitching 1968, 1977; Groenewald 1990; Green 1997; Smith *et al*. 2020). However, when compared to the rest of the main Karoo Basin, these outcrops have received much less attention in terms of focused palaeontological and biostratigraphical investigations (Groenewald *et al*. 2022). Furthermore, many of the historically collected specimens are still unprepared and/or have poor locality data. This means that their stratigraphic context is unclear, limiting their use for biostratigraphy, and they have therefore been overlooked in recent biostratigraphic revisions (Botha & Smith 2020; Viglietti 2020).

Karoo Supergroup fossils have been known in the region now comprising KwaZulu-Natal since at least the 19th century (Anderson 1901), with early reports including records of *Glossopteris* (Tate 1867) and 'saurian' bones (Sutherland 1868). However, more precise identifications of the local tetrapod remains were wanting prior to work by Broom (1907), based on his study of specimens submitted by Drs William Anderson (Government Geologist, Geological Survey of Natal) and Ernest Warren (Director of the Natal Government Museum, Pietermaritzburg). Broom identified Anderson's material as being referable to *Lystrosaurus*. Among Warren's material Broom recognized two new species of therapsid, which he referred to the existing genera *Dicynodon* (Anomodontia) and *Scymnosaurus* (Therocephalia): *D. ingens* and *S. warreni*. As is the case for many of the earliest species established by Broom, these taxa were based on highly fragmentary, largely unprepared fossils and received little attention from subsequent researchers. Later published coverage of these species consisted mainly of their inclusion in comprehensive lists of Karoo fossil taxa (e.g. Haughton 1917; Haughton & Brink 1954; Kitching 1977; Brink 1986; King 1988).

The most substantial attention to these species was by Broom (1932), who had, by this point, much greater basis for comparison than when he originally erected them. Based on the broader sample of therocephalian fossils collected in the intervening decades, he recognized *S. warreni* as belonging to the late Permian genus *Moschorhinus* rather than the middle Permian *Scymnosaurus* (a genus currently considered to be Lycosuchidae indet.; Abdala *et al*. 2014). Broom noted the inadequacy of the *D. ingens* holotype, but stated that a topotype in the collections of the Durban Museum permitted the species to be differentiated, designating it as the neotype for the species. Haughton & Brink (1954) also referred to the

*Author for correspondence. E-mail: david.groenewald@icp.cat

***Palaeontologia africana* 56**: 171–179 — ISSN 2410-4418 [Palaeontol. afr.] Online only
Permanently archived on the 15st of December at the University of the Witwatersrand, Johannesburg, South Africa
The article is permanently archived at: https://hdl.handle.net/10539/37143

Durban specimen as the 'neotype' of *D. ingens* (a designation that can only be made following loss of the holotype or by direct decision of the ICZN), and subsequent workers considered the holotype lost (Kammerer *et al*. 2011). In general, the few later publications addressing *D. ingens* and *S. warreni* based their conclusions on previous papers rather than personal examination of the fossils (e.g. Brink 1954; Mendrez 1974).

Recent research visits to Pietermaritzburg by the authors have, however, confirmed that the holotypes of *D. ingens* and *S. warreni* are in the same place they have been since their discovery: the collections of the KwaZulu-Natal Museum (formerly known as the Natal Government Museum [1904–1910] and Natal Museum [1910–2010]). Here we review and revise the taxonomy of these two species and provide a brief discussion on the biostratigraphy of their localities of origin. Figure 1 shows the localities discussed in the text and provides an overview of the geology and stratigraphy of the area of interest in KwaZulu-Natal.

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Anomodontia Owen, 1860
Dicynodontia Owen, 1859
Dicynodontoidea Olson, 1944

Dicynodon ingens Broom, 1907
Figures 2, 3C

1934 *Daptocephalus ingens* van Hoepen, p. 92

Holotype. NM 175 (Holotype number 742), a weathered and partially prepared palatal portion of a skull comprising the maxillary and premaxillary bones, parts of the palatines, most of the vomer, and large (40 mm diameter) tusks that are broken off where they emerge from the caniniform processes. A second skull from the type locality housed in the Durban Museum was later designated as the neotype of *D. ingens* (Broom 1932), but recent efforts to locate this specimen have failed and it is considered lost for the time being. Note that although the Durban Museum specimen was stated to be the 'neotype' of *D. ingens* by Broom (1932) and Haughton & Brink (1954), under the current edition of the Code (ICZN 1999), this designation was invalid if Broom was aware the holotype was still extant.

Locus typicus. Ennersdale Hill, Plot Ennersdale 2101, Estcourt, uThukela District, KwaZulu-Natal Province, South Africa.

Remarks. An additional two isolated large tusks (NM 179, NM 180; also Holotype number 742) from the type locality and the nearby locality Willbrook (Plot Weltevreden 1903), respectively, were also considered to belong to *Dicynodon ingens* (but not to the same individuals) (Broom 1907: pl. XXVIII, figs 3 and 4). Haughton (1917) accepted this species as valid. Broom (1932) figured a more complete topotypic specimen housed in the Durban Museum and stated that 'it may be taken as the neotype' of *D. ingens* (p. 178). Van Hoepen (1934) noted similarities between *Dicynodon ingens* and several other species of *Dicynodon*, particularly *Dicynodon leoniceps*, and assigned it to his new genus *Daptocephalus*. The validity of the genus *Daptocephalus* was recognized by Toerien (1953) based on palatal morphology, and this was accepted by Haughton & Brink (1954), although they considered only the type species, *D. leoniceps*, to be definitely attributable to the genus. They stated that other species may eventually prove referable to *Daptocephalus*, but in the interim retained them (including *D. ingens*) in *Dicynodon* until a revision of the latter genus could be accomplished. Kitching (1977) considered several *Dicynodon* species to be synonymous with *Daptocephalus leoniceps* (e.g. *D. daptocephaloides*, *D. dutoiti*), but did not explicitly include *D. ingens* in this group. He recognized that *D. ingens* was involved in the problem of *Daptocephalus* taxonomy, stating that 'the present author has carefully considered the morphology and taxonomic position of *Daptocephalus leoniceps*, *Dicynodon osborni* and *Dicynodon ingens*' (Kitching 1977, p. 18), but elsewhere stated that 'The genus [*Daptocephalus*] is most frequently found in close association with isolated specimens of *Oudenodon* and "*Dicynodon ingens*" [*sic*]' (p. 19), seemingly treating them as distinct taxa, and in his entry for Ennersdale (pp. 74–75), listed three skulls of *Daptocephalus leoniceps* and two skulls of *Dicynodon ingens* as originating from that locality. Following the synonymization of *Daptocephalus* with *Dicynodon* (Cluver & Hotton 1981), *Dicynodon ingens* was retained as a valid species (King 1988). In their revision of *Dicynodon*, Kammerer *et al*. (2011) resurrected the genus *Daptocephalus*, noting several differences other than size distinguishing *Daptocephalus leoniceps* and *Dicynodon lacerticeps*. Kammerer *et al*. (2011) were unable to examine the holotype or 'neotype' of *Dicynodon ingens*, and considered both specimens to be lost. However, based on published figures of the specimens (Broom 1907, 1932), Kammerer *et al*. (2011) considered *Dicynodon ingens* to be a *nomen dubium*, with the holotype likely referable to *Daptocephalus leoniceps* or *Dicynodon lacerticeps* and the 'neotype' possibly referable to *Dinanomodon gilli*.

Although NM 175 and NM 179 are both from the same locality (Ennersdale Hill), NM 180 is from Willbrook (at a similar stratigraphic level ~18 km SE of Ennersdale) and the catalogue of the KwaZulu-Natal Museum records different collectors for all three specimens. Because the anatomy of the palatal portion of the skull is considered to be of more taxonomic significance, the tusks are not discussed further. Specimen NM 175 is relatively poorly preserved. Nonetheless, the secondary palate is sufficiently exposed for it to be identified as a large specimen of *Daptocephalus leoniceps*, based on the long and narrow snout with elongate anterior palatal ridges (Fig. 3). The secondary palates of *Dicynodon lacerticeps* and *Lystrosaurus* spp. are proportionally broader and shorter (the same is true of *Aulacephalodon bainii*, which is present in the lowermost portion of the Balfour Formation [Viglietti *et al*. 2021]). The dimensions of the secondary palate overlap with some specimens of *Dinanomodon gilli*, but NM 175 exhibits a more robust median palatal ridge than is typical of the latter species (but in keeping with identification as *D. leoniceps*). Also, although the tip of the snout is somewhat weathered, the premaxilla displays a blunt

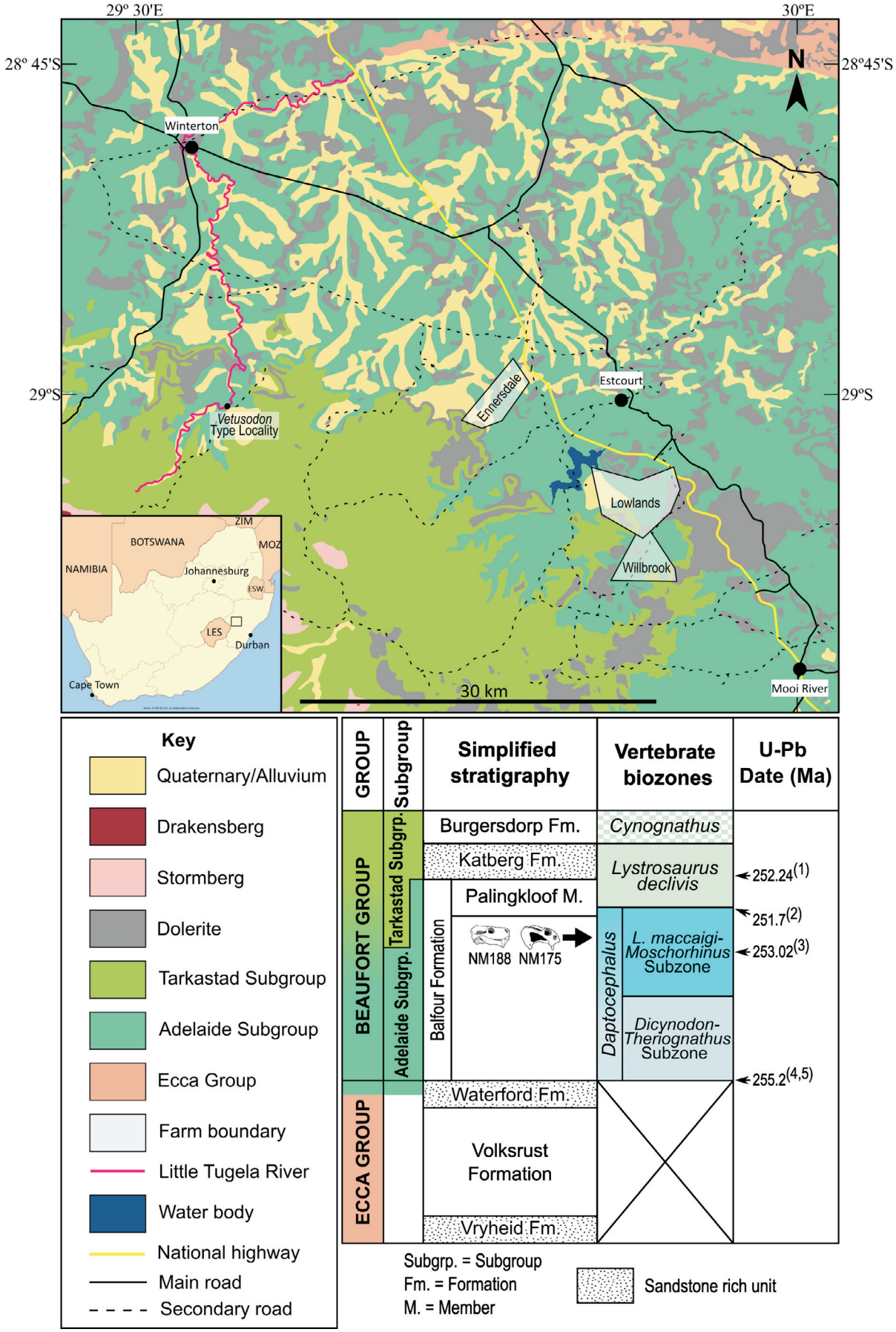

Figure 1. Locality and geological map of the area where type specimens NM 175 and NM 188 were discovered. Localities mentioned in the text are labelled. Geology is based on the 2828 Harrismith (Council for Geoscience 1998) and 2928 Drakensberg (Geological Survey 1981) 1:250 000 geological map sheets. The Waterford Formation includes strata mapped as upper Ecca and lower Beaufort groups (Groenewald *et al*. 2022). Sources for radiometric ages: (1) Gastaldo *et al*. (2020); (2) Botha *et al*. (2020); (3) Gastaldo *et al*. (2015); (4) Rubidge *et al*. (2013); (5) Groenewald (2021). Skull outlines after Kammerer *et al*. (2011) and Abdala *et al*. (2019). Abbreviations: ESW, Eswatini; LES, Lesotho; MOZ, Mozambique; ZIM, Zimbabwe.

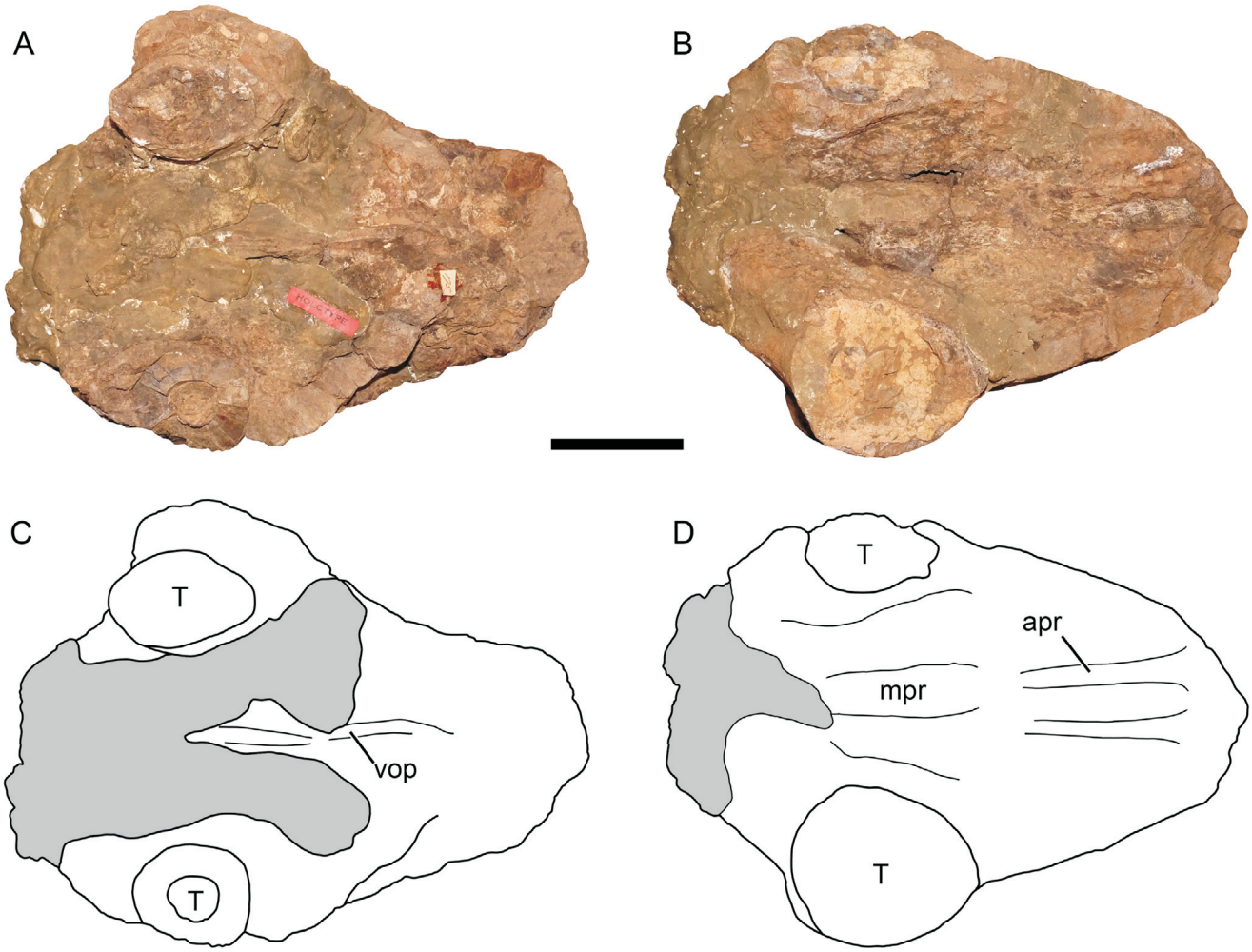

Figure 2. Photographs (**A**, **B**) and interpretive drawings (**C**, **D**) of the holotype of *Dicynodon ingens* NM 175 in dorsal (A, C) and ventral (B, D) views. Abbreviations: apr, anterior palatal ridge; mpr, median palatal ridge; T, tusk; vop, median vomerine plate. Scale bar = 5 cm.

morphology and does not appear to have had the sharp 'hook' characteristic of *Dinanomodon gilli* (Kammerer *et al*. 2011).

Therocephalia Broom, 1903
Eutherocephalia Hopson & Barghusen, 1986
Akidnognathidae Nopcsa, 1928

Scymnosaurus warreni Broom, 1907
Figures 4, 5C,D, 6C,D

1932 *Moschorhinus warreni* Broom, p. 89

Holotype. NM 188, a dorsoventrally crushed partial snout. The anterior portion of the lower jaw was originally preserved in occlusion with the cranium, but was subsequently lost, leaving an impression of the dentary with the crowns of the lower dentition preserved in place and visible as cross-sections in ventral view.

Locus typicus. Little Tugela River, near Winterton, uThukela District, KwaZulu-Natal Province, South Africa.

Remarks. Following Broom's (1932) referral of 'S.' *warreni* to *Moschorhinus*, it was mostly treated as a valid species of that genus (e.g. Brink 1954; Mendrez 1974). Kitching (1972), in his unpublished Ph.D. thesis, considered *M. warreni* to be synonymous with the type species *M. kitchingi*; this synonymy was maintained by Kitching (1977) and Brink (1986).

Our examination of NM 188 confirms Kitching's proposed synonymy: the anatomy of this specimen accords with specimens of *Moschorhinus* in all regards and shows a suite of characteristic features of *M. kitchingi*: extremely broad and robust snout, greatly enlarged facial process of septomaxilla, a dental formula of I5:prC1:C1:PC3/i4:c1:pc4, with the first four upper incisors being strongly mesiodistally compressed and the first three showing a distinct 'hourglass' shape in cross-section.

'*Scymnosaurus*' *warreni* Broom, 1907 has priority over *Moschorhinus kitchingi* Broom, 1920 if the two are considered synonymous. However, we consider it premature to establish *warreni* as the accepted species name for this therocephalian, pending comprehensive revision of akidnognathid alpha taxonomy (in prep.) and redescription of certain yet-earlier-named species that may have seniority (see e.g. Mendrez 1974).

DISCUSSION

Biostratigraphy of the Balfour Formation in KwaZulu-Natal

The type series of *Dicynodon ingens* comes from the localities Ennersdale Hill and Willbrook, which are roughly 18 km from one another but are both at approximately the same stratigraphic level. In the surrounding area are

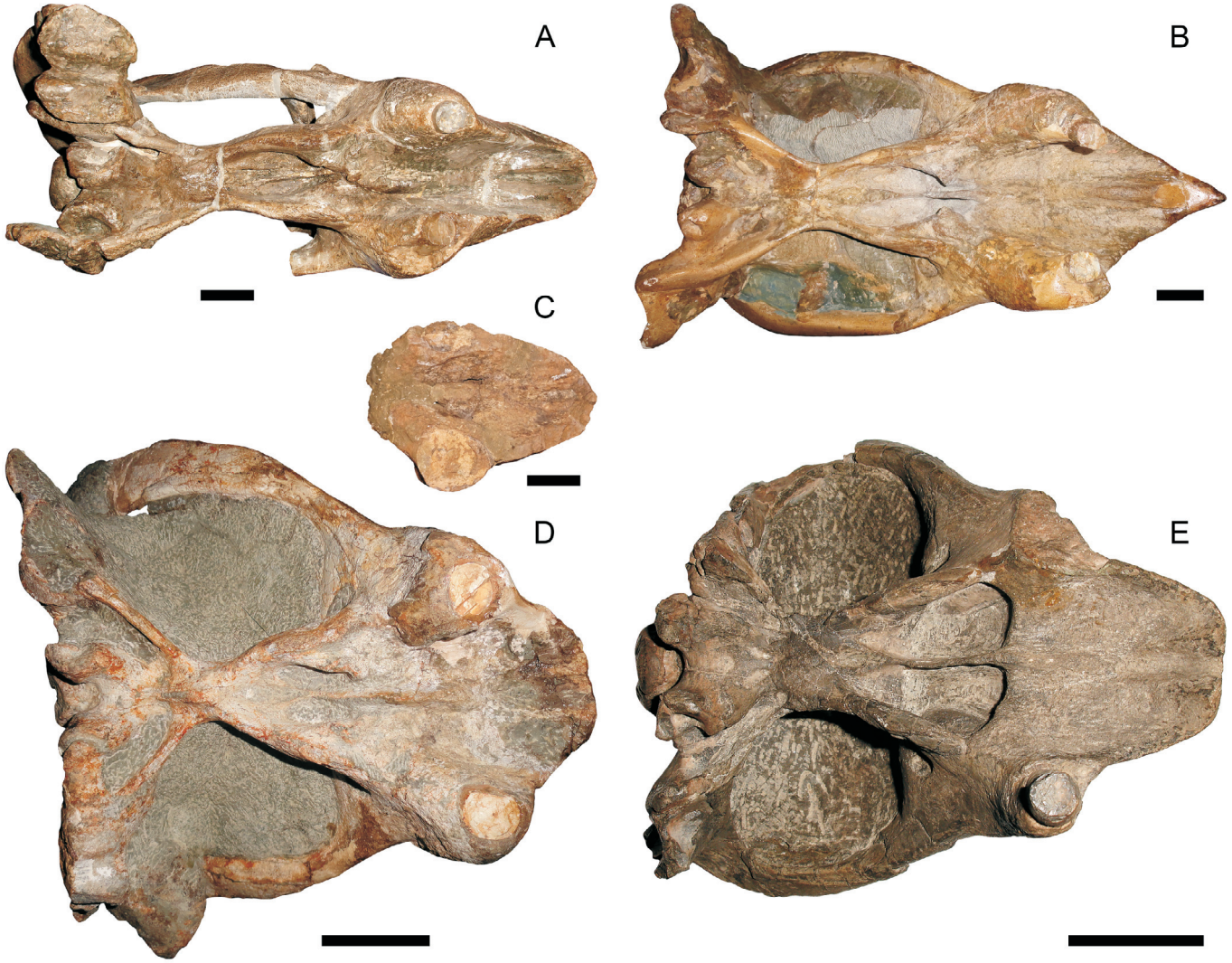

Figure 3. Comparison of dicynodontoid skulls in ventral view. **A**, *Daptocephalus leoniceps* (UCMP 33431); **B**, *Dinanomodon gilli* (RC 9); **C**, *Dicynodon ingens* (NM 175); **D**, *Dicynodon lacerticeps* (RC 85); **E**, *Lystrosaurus curvatus* (NHMUK PV R 3597). Scale bars = 5 cm.

several more localities that have produced tetrapod fossils proving that strata of the *Daptocephalus* and *Lystrosaurus declivis* assemblage zones are present (Kitching 1977; Green 1997; Groenewald *et al*. 2022, 2023). The collections catalogue of the Evolutionary Studies Institute at the University of the Witwatersrand in Johannesburg also records both *Daptocephalus leoniceps* (BP/1/1712; BP/1/3927) and *Lystrosaurus maccaigi* (BP/1/6158) from Ennersdale. The most recent fieldwork in this area was carried out by Green (1997), who noted that fossils of large (>30 cm) skulls, isolated large tusks, and fragmentary postcrania were recovered from olive-green mudstones, whereas smaller skulls and skeletons of *Lystrosaurus* and the amphibian *Lydekkerina* were discovered in the overlying maroon mudstones of the Palingkloof Member. Green (1997) also reported a partial maxilla with four serrated incisor teeth from *Daptocephalus* AZ strata at the locality Lowlands (Plot Roode Poortspruyt 1005), the neighbouring plot to Willbrook. This likely represents a gorgonopsian, rather than one of the large late Permian eutherocephalians (i.e. *Moschorhinus kitchingi* or *Theriognathus microps*), as the latter do not have serrated incisors (Huttenlocker & Abdala 2015). However, it is uncertain where the specimen is currently housed and a more confident identification is not possible at this time. In the case of the Palingkloof Member, most of the fossil remains, from limb bones to skulls, are peri-mineralized with calcareous nodular material (Green 1997). This form of preservation is generally quite common elsewhere in the Karoo for fossils from the *Lystrosaurus declivis* AZ (Smith *et al*. 2022). Based on the co-occurrence of *Daptocephalus leoniceps* and *Lystrosaurus maccaigi* at these localities, we can confidently assign the strata to the *Lystrosaurus maccaigi-Moschorhinus* Subzone of the *Daptocephalus* AZ.

The locality 'Little Tugela River', where NM 188 was found, is harder to relocate precisely and Kitching (1977) considered the locality information too vague to be reliable. The specimen probably comes from exposures along the Little Tugela River (also known as the Injisuthi River), a tributary of the Tugela River that flows from the Injisuthi region of the Drakensberg Mountains past the town of Winterton (Fig. 1). Other important taxa that have been recovered from the river course include *Lystrosaurus maccaigi* and the holotype of the late Permian cynodont *Vetusodon elikhulu* (BP/1/7971) (Abdala *et al*. 2019). Although rare, *Moschorhinus* is also present in the lowermost *Lystrosaurus declivis* AZ (Botha & Smith 2020), strata of which do crop out along the river course further upstream (Kitching 1977; Groenewald 1996). Regardless, we consider that NM 188 most likely comes from exposures of the *Lystrosaurus maccaigi-Moschorhinus* Subzone between the *Vetusodon* type locality and the confluence of the Little Tugela and Tugela rivers, as the collections catalogue of the KwaZulu-Natal Museum mentions that it comes from the 'Lower Beaufort Beds', i.e. below the *Lystrosaurus declivis* AZ (Broom 1906; Day 2013), which is

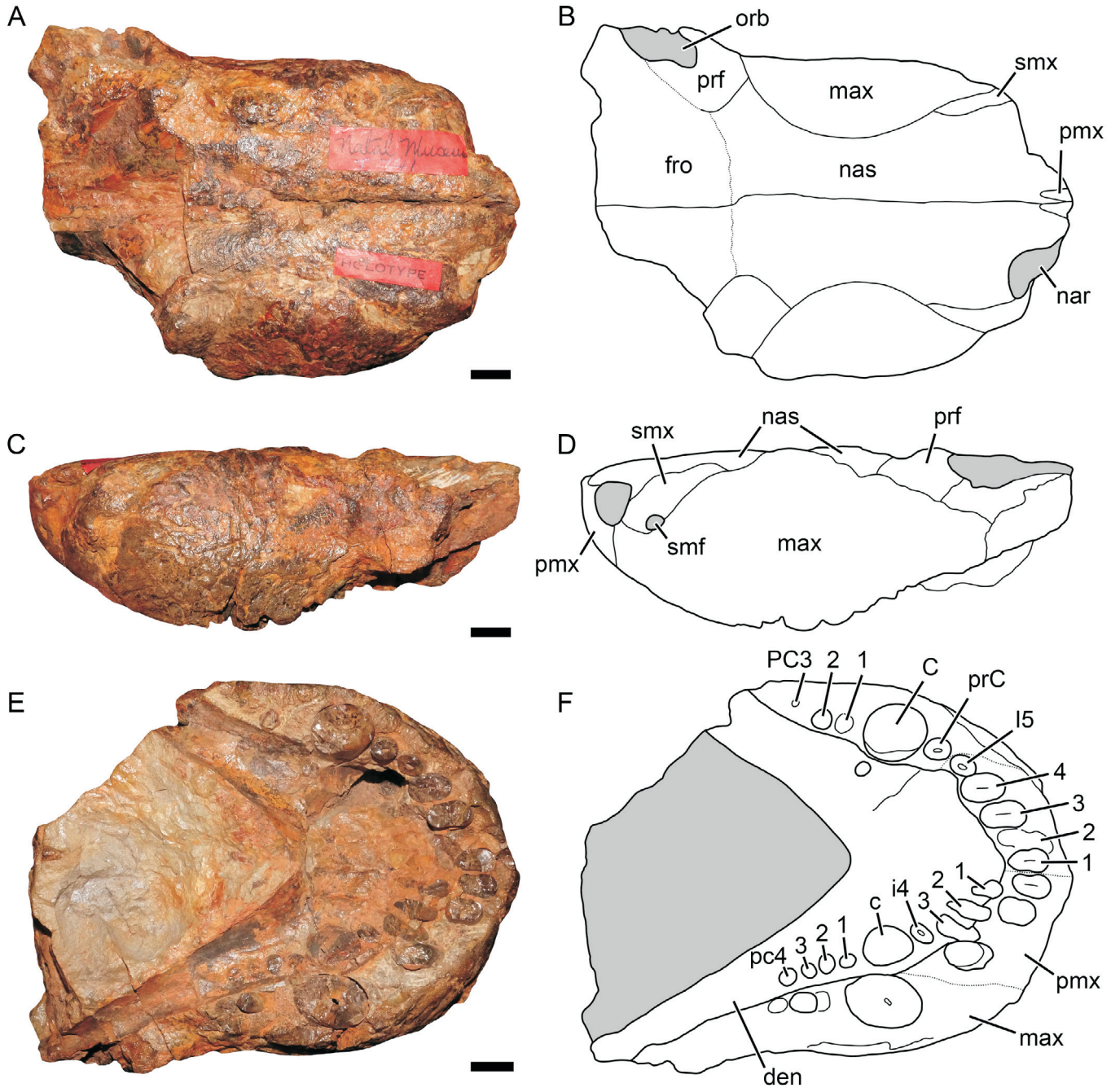

Figure 4. Photographs (**A**, **C**, **E**) and corresponding interpretive drawings (**B**, **D**, **F**) of the holotype of *Scymnosaurus warreni* NM 188 in dorsal (A, B), left lateral (C, D), and ventral (E, F) views. Abbreviations: c, lower canine; C, upper canine; den, dentary; fro, frontal; i, lower incisor; I, upper incisor; max, maxilla; nar, external naris; nas, nasal; orb, orbit; pc, lower postcanine; PC, upper postcanine; pmx, premaxilla; prC, precanine; prf, prefrontal; smf, septomaxillary foramen; smx, septomaxilla. Scale bar = 1 cm.

further supported by the colour of the host matrix and style of preservation of the fossil.

Groenewald (2021) obtained a maximum depositional age (based on the average of the three youngest detrital zircon grains with overlapping uncertainty) of 255.2 ± 6.8 Ma for the base of the Balfour Formation at Estcourt. This is very similar to the two youngest CA-TIMS $^{206}Pb/^{238}U$ dates of 255.24 ± 0.16 Ma and 255.22 ± 0.16 Ma obtained by Rubidge *et al*. (2013) for the base of the *Daptocephalus* AZ in the southwest of the main Karoo Basin. Considering that the localities where the holotypes of *Dicynodon ingens* and *Scymnosaurus warreni* were discovered are in the upper part of the Balfour Formation, near to the base of the Palingkloof Member, it is possible that strata of the underlying *Dicynodon-Theriognathus* Subzone of the *Daptocephalus* AZ also outcrop in this part of the basin, but further fieldwork is required to demonstrate this.

CONCLUSIONS

The holotypes of *Dicynodon ingens* Broom, 1907 and *Scymnosaurus warreni* Broom, 1907 were recently rediscovered in the collections of the KwaZulu-Natal Museum in Pietermaritzburg and are redescribed. Based on premaxillary proportions and palatal morphology, the holotype of *Dicynodon ingens* is identified as a specimen of *Daptocephalus leoniceps*. The holotype of *Scymnosaurus warreni* is identified as a specimen of *Moschorhinus kitchingi* based on size, general proportions, tooth count,

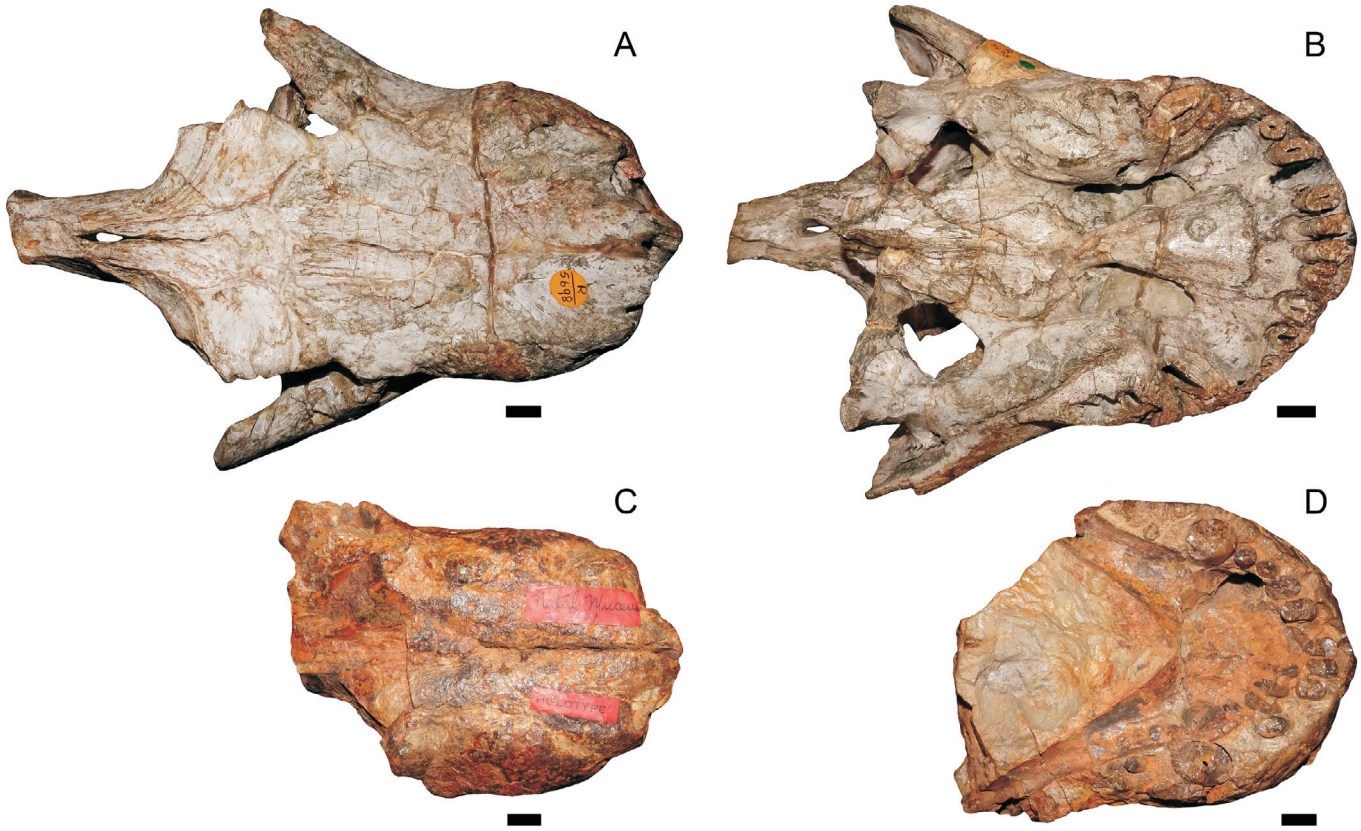

Figure 5. Comparison of the holotype of *Moschorhinus kitchingi* (NHMUK PV R 5698) in dorsal (**A**) and ventral (**B**) views with that of *Scymnosaurus warreni* (NM 188) (**C**, **D**). Scale bars = 1 cm.

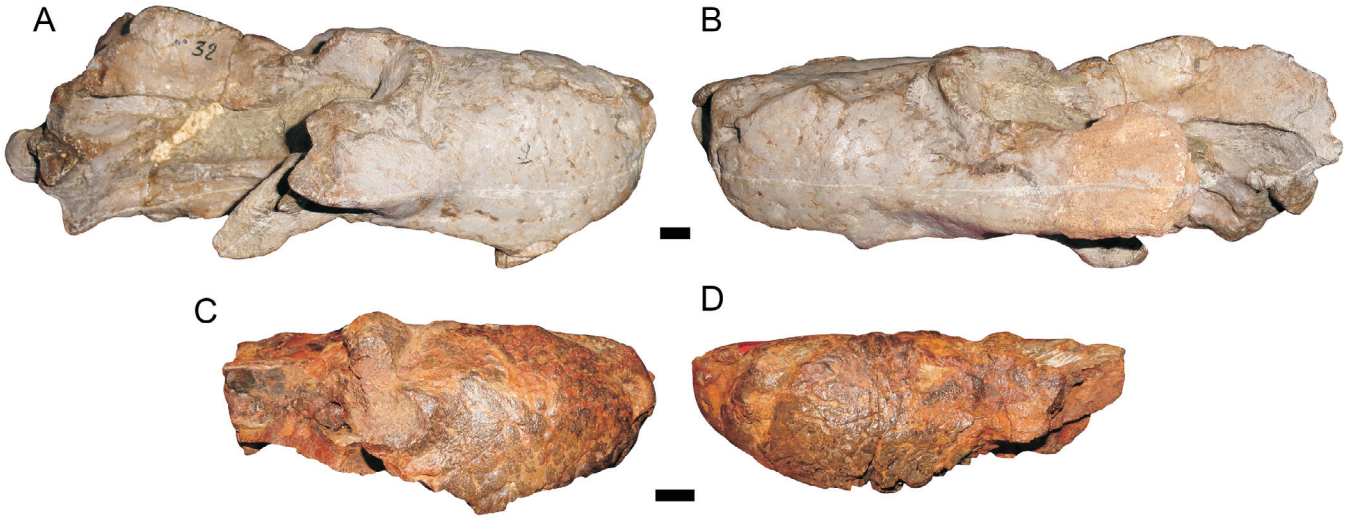

Figure 6. Comparison of a referred specimen of *Moschorhinus kitchingi* (RC 32, holotype of M. *esterhuyseni*; **A**, **B**) with the holotype of *Scymnosaurus warreni* (NM 188; **C**, **D**) in left (A, C) and right lateral (B, D) views. Scale bars = 1 cm.

and septomaxillary morphology. Their co-occurring taxa allow confident biostratigraphic correlation of their strata of origin with the latest Permian (Changhsingian) *Lystrosaurus maccaigi-Moschorhinus* Subzone of the *Daptocephalus* Assemblage Zone.

ABBREVIATIONS

Institutional

NHMUK	Natural History Museum, London, U.K.
NM	KwaZulu-Natal Museum, Pietermaritzburg, South Africa
RC	Rubidge Collection, Graaff-Reinet, South Africa
UCMP	University of California Museum of Paleontology, Berkeley, U.S.A.

We dedicate this paper to Bruce S. Rubidge, who has contributed so much to South African palaeontology, and without whom D.P.G. may well have chosen a different career path, and thank him for all his support and encouragement over the years. We thank John Midgley and Matabaro Ziganira for access to the specimens in the collections of the KwaZulu-Natal Museum. Thanks also to the reviewers, Kenneth Angielczyk and Roger Smith, for their helpful comments that greatly improved the manuscript, and Kimberley Chapelle for her editorial work. Financial support provided by GENUS (DSI/NRF Centre of Excellence in Palaeosciences); the National Research Foundation (NRF); the Palaeontological Scientific Trust (PAST); the South African National Biodiversity Institute (SANBI); CERCA Programme/ Generalitat de Catalunya; and the European Union's Horizon Europe Marie Skłodowska-Curie actions (GA: 101060666 to D.P.G.) are acknowledged. D.P.G. is a member of the Consolidated Research Group (GRC) 2021 SGR 01184 (Generalitat de Catalunya). Opinions expressed and conclusions arrived at are those of the authors and are not necessarily to be attributed to GENUS, the NRF, SANBI, Generalitat de Catalunya, or the European Union.

§ORCID iDs

D.P. Groenewald: orcid.org/0000-0001-6570-0436
C. Kammerer: orcid.org/0000-0002-0596-623X

REFERENCES

ABDALA, F., GAETANO, L.C., SMITH, R.M.H. & RUBIDGE, B.S. 2019. A new large cynodont from the Late Permian (Lopingian) of the South African Karoo Basin and its phylogenetic significance. *Zoological Journal of the Linnean Society* **186**(4), 983–1005. DOI: 10.1093/zoolinnean/zlz004

ABDALA, F., KAMMERER, C.F., DAY, M.O., JIRAH, S. & RUBIDGE, B.S. 2014. Adult morphology of the therocephalian *Simorhinella baini* from the middle Permian of South Africa and the taxonomy, paleobiogeography, and temporal distribution of the Lycosuchidae. *Journal of Paleontology* **88**(6), 1139–1153. DOI: 10.1666/13-186

ANDERSON, W. 1901. *First Report of the Geological Survey of Natal and Zululand*. Pietermaritzburg, South Africa, P. David & Sons. 138 pp.

BOTHA, J., HUTTENLOCKER, A.K., SMITH, R.M.H., PREVEC, R., VIGLIETTI, P.A. & MODESTO, S.P. 2020. New geochemical and palaeontological data from the Permian-Triassic boundary in the South African Karoo Basin test the synchronicity of terrestrial and marine extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* **540**, 109467. DOI: 10.1016/j.palaeo.2019.109467

BOTHA, J. & SMITH, R.M.H. 2020. Biostratigraphy of the *Lystrosaurus declivis* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**(2), 207–216. DOI: 10.25131/sajg.123.0015

BRINK, A.S. 1954. On the Whaitsiidae, a family of therocephalian mammal-like reptiles. *Transactions of the Royal Society of South Africa* **34**(1), 43–59. DOI: 10.1080/00359195409518978

BRINK, A.S. 1986. *Illustrated Bibliographic Catalogue of the Synapsida. Geological Survey of South Africa Handbook 10: J212A251A*. Pretoria, South Africa, Geological Survey of South Africa.

BROOM, R. 1903. On the classification of the theriodonts and their allies. *Report of the South African Association for the Advancement of Science* **1**, 286–294.

BROOM, R. 1905. On the use of the term Anomodontia. *Records of the Albany Museum* **1**, 266–269.

BROOM, R. 1906. The classification of the Karoo beds of South Africa. *Geological Magazine* **3**(1), 36. DOI: 10.1017/S001675680012271X

BROOM, R. 1907. On two new reptiles from the Karroo Beds of Natal. *Annals of the Natal Government Museum* **1**, 167–172 pl. xxviii, 1–4.

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

CLUVER, M. A. & HOTTON, N. 1981. The genera *Dicynodon* and *Diictodon* and their bearing on the classification of the dicynodontia (Reptilia, Therapsida). *Annals of the South African Museum* **83**(6), 99–146.

COUNCIL FOR GEOSCIENCE 1998. 2828 Harrismith 1:250 000 Geological Map Series. Pretoria, South Africa, Council for Geoscience.

DAY, M. 2013. Charting the fossils of the Great Karoo: a history of tetrapod biostratigraphy in the Lower Beaufort Group, South Africa. *Palaeontologia africana* **48**, 41–47.

EWER, R.F. 1961. The anatomy of the anomodont *Daptocephalus leoniceps* (Owen). *Proceedings of the Zoological Society of London* **136**(3), 375–402. DOI: 10.1111/j.1469-7998.1961.tb05881.x

GASTALDO, R.A., KAMO, S.L., NEVELING, J., GEISSMAN, J.W., BAMFORD, M. & LOOY, C.V. 2015. Is the vertebrate-defined Permian-Triassic boundary in the Karoo Basin, South Africa, the terrestrial expression of the end-Permian marine event? *Geology* **43**(10), 939–942. DOI: 10.1130/G37040.1

GASTALDO, R.A., KAMO, S. L., NEVELING, J., GEISSMAN, J.W., LOOY, C.V. & MARTINI, A.M. 2020. The base of the *Lystrosaurus* Assemblage Zone, Karoo Basin, predates the end-Permian marine extinction. *Nature Communications* **11**(1), 1428. DOI: 10.1038/s41467-020-15243-7

GEOLOGICAL SURVEY 1981. 2928 Drakensberg 1:250 000 Geological Map Series. Compiled by: Linström, W., 1979. Pretoria, South Africa, Government Printer.

GREEN, D. 1997. *Palaeoenvironments of the Estcourt Formation (Beaufort Groups), KwaZulu-Natal*. Unpublished M.Sc. thesis, University of KwaZulu-Natal, Durban, South Africa.

GRINE, F.E., FORSTER, C.A., CLUVER, M.A. & GEORGI, J.A. 2006. Cranial variability, ontogeny, and taxonomy of *Lystrosaurus* from the Karoo Basin of South Africa. **In**: Carrano, M.T., Gaudin, T.J., Blob, R.W. & Wible, J.R. (eds.), *Amniote Palaeobiology: Perspectives on the Evolution of Mammals, Birds, and Reptiles*, 432–506. Chicago, Illinois, University of Chicago Press.

GROENEWALD, D.P. 2021. *A litho- and biostratigraphic analysis of the lower Beaufort Group in the distal sector of the main Karoo Basin, South Africa – implications for the depositional history of the distal foredeep to back-bulge basin*. Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg, South Africa.

GROENEWALD, D.P., DAY, M.O., PENN-CLARKE, C.R. & RUBIDGE, B.S. 2022. Stepping out across the Karoo retro-foreland basin: improved constraints on the Ecca-Beaufort shoreline along the northern margin. *Journal of African Earth Sciences* **185**, 104389. DOI: 10.1016/j.jafrearsci.2021.104389

GROENEWALD, D.P., KRÜGER, A., DAY, M.O., PENN-CLARKE, C.R., HANCOX, P.J. & RUBIDGE, B.S. 2023. Unique trackway on Permian Karoo shoreline provides evidence of temnospondyl locomotory behaviour. *PLOS ONE* **18**(3), e0282354. DOI: 10.1371/journal.pone.0282354

GROENEWALD, G.H. 1990. The use of palaeontology in the correlation of lithostratographic units in the Beaufort Group, Karoo Sequence of South Africa. *Palaeontologia africana* **27**, 21–30.

GROENEWALD, G.H. 1996. *Stratigraphy and Sedimentology of the Tarkastad Subgroup, Karoo Supergroup of South Africa*. Unpublished Ph.D. thesis, University of Port Elizabeth [Nelson Mandela University], Port Elizabeth, South Africa.

HAUGHTON, S.H. 1917. Descriptive catalogue of the anomodontia, with special reference to the examples in the South African Museum. *Annals of the South African Museum* **12**, 127–174.

HAUGHTON, S.H. & BRINK, A.S. 1954. A bibliographic list of Reptilia from the Karroo Beds of Africa. *Palaeontologia africana* **2**, 1–171.

HOPSON, J.A. & BARGHUSEN, H. 1986. An analysis of therapsid relationships. **In**: Hotton, N., MacLean, P.D., Roth, J.J. & Roth, E.C. (eds.), *The Ecology and Biology of the Mammal-like Reptiles*. 83–106. Washington, U.S.A., Smithsonian Institution Press.

HUTTENLOCKER, A.K. & ABDALA, F. 2015. Revision of the first therocephalian, *Theriognathus* Owen (Therapsida: Whaitsiidae), and implications for cranial ontogeny and allometry in nonmammaliaform eutheriodonts. *Journal of Paleontology* **89**(4), 645–664. DOI: 10.1017/jpa.2015.32

ICZN. 1999. *International Code of Zoological Nomenclature*. Fourth edition. London, U.K., The International Trust for Zoological Nomenclature.

KAMMERER, C.F., ANGIELCZYK, K.D. & FRÖBISCH, J. 2011. A comprehensive taxonomic revision of *Dicynodon* (Therapsida, Anomodontia) and its implications for dicynodont phylogeny, biogeography, and biostratigraphy. *Journal of Vertebrate Paleontology* **31**(sup1), 1–158. DOI: 10.1080/02724634.2011.627074

KING, G.M. 1988. *Anomodontia. Handbuch der Paläoherpetologie (Encyclopedia of paleoherpetology)*, Vol. **17C**. Stuttgart, Germany, Gustav Fischer Verlag. 174 pp.

KITCHING, J.W. 1968. On the Lystrosaurus Zone and its fauna with special reference to some immature Lystrosauridae. *Palaeontologia africana* **11**, 61–76.

KITCHING, J.W. 1972. *On the distribution of the Karroo vertebrate fauna with special reference to certain genera and the bearing of this distribution on the zoning of the Beaufort beds*. Unpublished Ph.D. thesis, University of the Witwatersrand, Johannesburg, South Africa.

KITCHING, J.W. 1977. The distribution of the Karroo vertebrate fauna: with special reference to certain genera and the bearing of this distribution on the zoning of the Beaufort Beds. *Bernard Price Institute for Palaeontological Research, Memoir* **1**, 131.

MENDREZ, C.H. 1974. A new specimen of *Promoschorhynchus platyrhinus* Brink 1954 (Moschorhinidae) from the *Daptocephalus*-zone (Upper Permian) of South Africa. *Palaeontologia africana* **17**, 69–85.

NOPCSA, F. 1928. The genera of reptiles. *Palaeobiologica* **1**, 163–188.

OLSON, E.C. 1944. Origin of mammals based upon cranial morphology of the therapsid suborders. *Geological Society of America Special Papers* **55**, 1–136.

OSBORN, H.F. 1903. On the primary division of the Reptilia into two sub-classes, Synapsida and Diapsida. *Science* **17**(424), 275–276.

OWEN, R. 1859. On some reptilian remains from South Africa. *The Edinburgh New Philosophical Journal* **10**, 289–291.

OWEN, R. 1860. On the orders of fossil and recent Reptilia, and their distribution in time. *Report of the Twenty-Ninth Meeting of the British Association for the Advancement of Science* **1859**, 153–166.

RUBIDGE, B.S., ERWIN, D.H., RAMEZANI, J., BOWRING, S.A. & DE

KLERK, W.J. 2013. High-precision temporal calibration of Late Permian vertebrate biostratigraphy: U-Pb zircon constraints from the Karoo Supergroup, South Africa. *Geology* **41**(3), 363–366.
SMITH, R M.H., BOTHA, J. & VIGLIETTI, P.A. 2022. Taphonomy of drought afflicted tetrapods in the Early Triassic Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **604**, 111207. DOI: 10.1016/j.palaeo.2022.111207
SMITH, R.M H., RUBIDGE, B.S., DAY, M.O. & BOTHA, J. 2020. Introduction to the tetrapod biozonation of the Karoo Supergroup. *South African Journal of Geology* **123**(2), 131–140. DOI: 10.25131/sajg.123.0009
SUTHERLAND, P.C. 1868. *On the Geology of Natal. Natural History Association of Natal*. Durban, South Africa, Adams and Co. 26 pp.
TATE, R. 1867. On some secondary fossils from South Africa. *Quarterly Journal of the Geological Society* **23**, 139–175.
TOERIEN, M.J. 1953. The evolution of the palate in South African Anomodontia and its classificatory significance. *Palaeontologia africana* **53**, 49–117.
VAN HOEPEN, E.C.N. 1934. Oor die indeling van die Dicynodontoidae na aanleiding van nuwe vorme. *Paleontologiese Navorsing van die Nasionale Museum* **2**, 67–101.
VIGLIETTI, P.A. 2020. Biostratigraphy of the *Daptocephalus* Assemblage Zone. *South African Journal of Geology* **123**(2), 191–206.
VIGLIETTI, P.A., BENSON, R.B.J., SMITH, R.M.H., BOTHA, J., KAMMERER, C.F., SKOSAN, Z., BUTLER, E., CREAN, A., ELOFF, B., KAAL, S., MOHOI, J., MOLEHE, W., MTALANA, N., MTUNGATA, S., NTHERI, N., NTSALA, T., NYAPHULI, J., OCTOBER, P., SKINNER, G., STRONG, M., STUMMER, H., WOLVAARDT, F.P. & ANGIELCZYK, K.D. 2021. Evidence from South Africa for a protracted end-Permian extinction on land. *Proceedings of the National Academy of Sciences* **118**(17), e2017045118. DOI: 10.1073/pnas.2017045118