The first record of late Permian tetrapods from Namibia

Helke B. Mocke[1*] [§], **Christian F. Kammerer**[2], **Roger M.H. Smith**[3,4] & **Claudia A. Marsicano**[5]

[1] *National Earth Science Museum, Geological Survey of Namibia, Private Bag 13297, Windhoek, Namibia*
[2] *North Carolina Museum of Natural Sciences, 11 W. Jones Street, Raleigh, NC 27601, United States of America*
[3] *Evolutionary Studies Institute, University of the Witwatersrand, Private Bag 3, WITS, Johannesburg, 2050 South Africa*
[4] *Iziko Museums of South Africa, P.O. Box 61, Cape Town, 8000 South Africa*
[5] *IDEAN, UBA-CONICET, Departamento de Ciencias Geológicas, Facultad de Ciencias Exactas y Naturales, Universidad de Buenos Aires, Intendente Güiraldes 2160, Ciudad Universitaria C1428EHA, CABA, Argentina*

Received 21 November 2021. Accepted 9 November 2023

The entire Omingonde Formation in Namibia was previously assigned a Triassic age based on the fossil tetrapod fauna discovered southwest of the Waterberg Plateau. However, recently repatriated and newly collected material suggests that the lowermost part of the Omingonde Formation includes late Permian strata, equivalent in age to the upper *Endothiodon* Assemblage Zone of the South African Karoo Basin. In this study, we document the first record of late Permian tetrapod fossils from Namibia, and provide brief descriptions of a gorgonopsian skull collected at Mount Etjo in 1996 and the skull of a small dicynodont collected at the same site in 2019, referable to cf. *Tropidostoma*. This material confirms that there is need for better understanding of the stratigraphy of the Etjo Mountain area, in particular the position and nature of the unconformity between strata of the Permian *Endothiodon* and the Triassic *Cynognathus* assemblage zones.

Key words: *Endothiodon* Assemblage Zone, biostratigraphy, *Tropidostoma*, gorgonopsian, Late Palaeozoic, southern Africa.

INTRODUCTION

Historically, the only Triassic terrestrial vertebrate fauna known from Namibia has been that of the Omingonde Formation (Karoo Supergroup). This formation is a continental, red-bed succession that accumulated in an intermittently active half-graben on the upland plateau of southern Gondwana (Smith & Swart 2002; Holzförster *et al*. 1999). The first purported vertebrate body fossil found in Triassic Namibian outcrops was a single 'mammalian molar with two roots' found by Ernst Reuning in 1913 near Doros crater in southern Kaokoveld, which was later described by Huene (1925a,b) as a new taxon of archaic mammal, *Archaeodon reuningi*. However, subsequent research has demonstrated that this 'tooth' is inorganic in nature and is actually the chalcedony infilling of a gas bubble in igneous rock (Hopson & Reif 1981). More robust early evidence for fossil vertebrates in Namibia came from the ichnological record. Huene (1925c) figured dinosaur tracks from the Early Jurassic Plateau Sandstone/Etjo Formation at two sites on Otjihaenamaperero (see Fig. 1). Gürich (1926) later published additional details of the trackways and possible trace makers, which he concluded were bipedal theropod and quadrupedal sauropodomorph dinosaurs.

What was probably the first actual vertebrate body fossil collected from the Omingonde Formation was found on the farm Breitenbach in the Grootfontein district in 1926 (Gevers 1936). Breitenbach is located at approximately S19°59′53.5″, E17°42′23.8″, roughly 184 km northeast of Mount Etjo and the Otjihaenamaperero trackway site. The Breitenbach fossil was a cast of a partial skull identified by Ernst Stromer as a 'Karroo reptile', which has unfortunately since been lost (Pickford 1995). Further records of Triassic vertebrates from the area were unknown until Keyser (1973a, b) reported the preliminary identifications of 25 tetrapod fossils that his team from the Geological Survey of South Africa had collected at Mount Etjo in 1971 and 1972. These discoveries supported a lower-to-middle Triassic age for the Omingonde Formation, which Keyser (1973a) argued was younger than the *Cynognathus* Zone of the Burgersdorp Formation of South Africa, but older than the Manda Beds of Tanzania. Since the 1970s, various international teams from Namibia, South Africa, Argentina, France, and the United States have discovered numerous Triassic tetrapods in the Omingonde Formation (e.g. Keyser 1973a,b, 1978; Pickford 1995; Smith & Swart 2002; Abdala & Smith 2009; Abdala *et al*. 2013b; Gaetano *et al*. 2018; Mocke *et al*. 2019; Hendrickx *et al*. 2020; Tolchard *et al*. 2021).

Taxa known from the upper Omingonde Formation thus far include a juvenile mastodonsaurid temnospondyl (originally identified as an 'eriopoid'; Keyser 1973a), the 'rauisuchian' archosaur *Etjosuchus* (Tolchard *et al*. 2021), originally identified as an erythrosuchid

---

*Author for correspondence. E-mail: helke.mocke@mme.gov.na

***Palaeontologia africana* 56**: 133–141 — ISSN 2410-4418 [Palaeontol. afr.] Online only
Permanently archived on the 15th of December at the University of the Witwatersrand, Johannesburg, South Africa
The article is permanently archived at: https://hdl.handle.net/10539/37140

(Pickford *et al*. 1995; Smith & Swart 2002), the therocephalian *Herpetogale* (Keyser 1978), which was subsequently synonymized with the South African taxon *Microgomphodon* (Abdala *et al*. 2013a), the kannemeyeriid dicynodonts *Kannemeyeria* and *Dolichuranus* (Keyser 1973a; Bandyopadhyay 1989), and the stahleckeriid dicynodont *Stahleckeria* (Abdala *et al*. 2013b), as well as eight cynodont genera: *Aleodon*, *Chiniquodon*, *Cynognathus*, *Diademodon*, *Etjoia*, *Luangwa*, *Titanogomphodon*, and *Trirachodon* (Keyser 1973a; Abdala & Smith 2009; Abdala *et al*. 2013a; Mocke *et al*. 2019; Hendrickx *et al*. 2020). Based on these taxa, correlations have been made between the Omingonde Formation and the Burgersdorp Formation (*Cynognathus* Assemblage Zone) in South Africa (Keyser 1973a,b, 1978; Holzförster *et al*. 1999; Catuneanu *et al*. 2005; Abdala *et al*. 2005, 2013b; Abdala & Smith 2009; Martinelli *et al*. 2009; Hancox *et al*. 2020), the Chañares and Ischigualasto formations in Argentina (Mocke *et al*. 2019), the Santa Maria Formation (*Dinodontosaurus* Assemblage Zone) in Brazil (Abdala *et al*. 2013b; Martinelli *et al*. 2017; Mocke *et al*. 2019), the Manda beds in Tanzania (Abdala & Smith, 2009; Wynd *et al*. 2018; Tolchard *et al*. 2021), and the Ntaware Formation and Red Marl in Zambia (Wynd *et al*. 2018; Peecook *et al*. 2020; Tolchard *et al*. 2021), with age estimations for the uppermost upper Omingonde ranging from Ladinian to lower Carnian (Martinelli *et al*. 2017; Mocke *et al*. 2019).

The ±480 m thick Karoo-aged Omingonde Formation mostly lies unconformably on folded Neoproterozoic rocks of the Damara Supergroup; however, borehole cores containing remnants of the Permo–Carboniferous glaciation (Dwyka Group) and the post-glacial coal-bearing deltaic beds of the Tevrede Formation (equivalent to the early Permian lower Ecca Group) have been reported lying between the base of the Omingonde and the basement (Gunthorpe 1987). At the southwestern end of Mount Etjo, the Damaran basement outcrops around 1500m southeast of the new Permian vertebrate locality, which would indicate that a relatively thin succession of pre-Triassic strata underlies the Omingonde Formation in this area.

In the Mount Etjo area, the Omingonde Formation is informally subdivided into a lower, maroon mudrock-dominated unit overlain by a series of multistoreyed, white-weathering, pebbly sandstone bodies making up the middle unit, which is in turn overlain by an upper unit of red mudstone with interbedded gritstone and laterally-accreted, fine-grained sandstone bodies (Fig.1; Holzförster *et al*. 1999). Smith & Swart (2002) recognized five sedimentological facies in the Omingonde succession at Mount Etjo, which they interpreted as a sequence of changing landscapes from (1) paludal floodplains with marginal alluvial fans, (2) gravel-bed braided rivers with marginal alluvial fans, (3) loessic plains with saline lakes and ponds, (4) gravel-bed meandering rivers on semi-arid floodplains, and (5) sand-bed meandering streams on semi-arid loessic plains with saline ponds.

Only the upper 25 metres or so of the lower Omingonde facies is exposed in the study area, but similar sequences have been documented in nearby boreholes as the infilling of bedrock valleys (Holzförster *et al*. 1999). It comprises a monotonous succession of dark reddish-brown mudrocks with interbedded 3–5 m thick dominantly trough cross-bedded coarse to medium-grained, vertically-accreted and multistoreyed pebbly sandstone bodies. The former are interpreted as overbank and paludal fines deposited by episodic flooding, the latter are the in-channel deposits of wide, shallow, low sinuosity rivers that emanated from the toe of an alluvial fan (Löffler 1998; Smith & Swart 2002).

The entirety of the Omingonde Formation has traditionally been considered Triassic in age, but the lower portions of this unit are poorly known. Stratigraphic sections of the entire Omingonde Formation exposed at Mount Etjo were measured by Holzförster *et al*. (1999) and Smith & Swart (2002). Although neither team found any tetrapod fossils in the lower and middle members of the succession, the lithologies and sedimentary units were similar enough to the upper Omingonde to assign a Triassic age to the entire section. However, while there are no published tetrapod fossils from the base of the section, in 1996, a team from Harvard University led by Farish Jenkins discovered a partial therapsid skull in mottled purple sandstone at the southeastern base of Mount Etjo. This specimen found by Neil Shubin and William Amaral was recently repatriated to Namibia from the Museum of Comparative Zoology (Cambridge, U.S.A.) and thus made available for study. Intriguingly, Jenkins initially identified this skull as belonging to a gorgonopsian, a group of therapsids generally thought to be restricted to the Permian (see e.g. Viglietti 2020; Kammerer *et al*. 2023).

In 2019, one of the authors (R.M.H.S.) led an international team to the geographical coordinates where Jenkins' team had collected this specimen (GSN F1590) to confirm that this was indeed the correct locality for such an apparently anomalous find. They first compared rock samples taken from GSN F1590 with the strata exposed at the locality and found matching lithologies. Follow-up fieldwork resulted in the discovery of several more fossils at the site, including the skull and mandible of a small dicynodont with post-caniniform dentition (GSN F1586) by C. Marsicano. Here, we provide a preliminary description of these specimens and discuss their stratigraphic implications, as well as confirm identification of GSN F1590 as a gorgonopsian. Based on the co-occurrence of a gorgonopsian and a *Tropidostoma*-like dicynodont, we propose that the lowermost part of the Omingonde Formation exposed on Mount Etjo includes late Permian strata equivalent in age to the upper *Endothiodon* Assemblage Zone (*Tropidostoma-Gorgonops* Subzone of Day & Smith 2020) of the South African Karoo Basin.

SEDIMENTARY ENVIRONMENTS OF THE PERMIAN LOCALITY

The new Permian fauna is preserved (coordinates may be obtained from the authors) in the upper part of the middle storey of a channel sandstone complex within dark red (Munsell colour 10R3/6) weakly-cemented massively-bedded medium-grained sandstone (see Fig. 2A). The lower part of each of the three erosively-

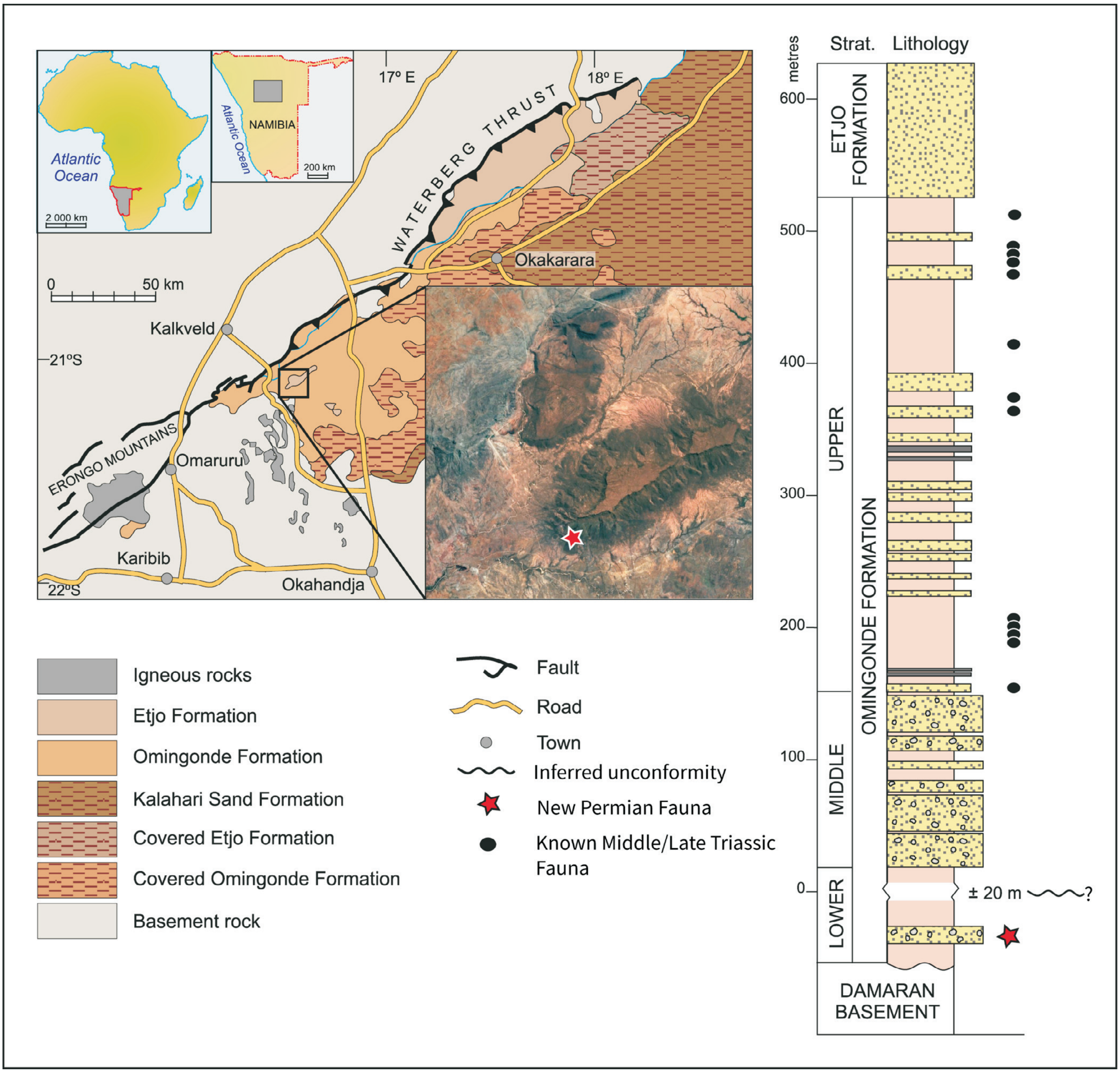

Figure 1. **A**, Geological map of outcrop and sub-outcrop of Omingonde and Etjo formations in the study area with satellite image of Mount Etjo showing the locality of the new Permian fauna (starred). **B**, Generalized stratigraphy and known tetrapod fossil localities from the exposures at the southern end of Mount Etjo. Section from Smith & Swart (2002) was measured close to the new Permian fossil locality (starred).

based storeys comprises more well-cemented trough cross-bedded coarse-grained sandstone (Fig. 2B). The dominance of large-scale trough cross-bedding in the lower parts is indicative of relatively persistent deep turbulent flow confined by a low sinuosity channel. The paucity of lower flow regime structures such as small-scale troughs and ripple cross-lamination also suggests sedimentation in a low sinuosity river system (Horn *et al*. 2018).

The massively-bedded sandstone is in the upper part of each channel fill sequence. It lies conformably atop a large-scale trough cross-bedded unit (Fig. 2B) and it is interpreted as having been rapidly deposited following the sudden loss of competence as sediment-laden flood-waters overtopped their confining riverbanks in what has been termed an overbank splay (e.g. Horn *et al.* 2018; Burns *et al*. 2017). Massive beds in braided stream sequences have been attributed to bank collapse (Martin & Turner 1998) but these are normally of limited width, whereas those of the lower Omingonde extend across the entire 300 m wide outcrop. Extensive bioturbation by infauna can also disrupt the laminae such that the sediment becomes structureless, but this is more common in marine and coastal settings and not considered a viable explanation in this case.

The fossil-bearing level of the massive sandstone bed displays irregularly-shaped light grey mottles, and the white bones are enveloped in a thin but distinctive dark purple haematitic crust (see Fig. 2C). This is a mode of fossilization common to the Triassic-aged fossils higher in the succession, in the upper Omingonde (Abdala *et al.* 2013b) as well as the Santa Maria Supersequence of Brazil (Holtz & Schultz 1998), and is likely a result of the palaeoclimate at the time of burial (Holtz & Souto-Ribeiro

Figure 2. **A**, General view of the outcrop where GSN F1586 was found (arrowed) and in the immediate vicinity of GSN F1590 GPS coordinates. Note the tabular vertically-accreted coarse-grained light brown sandstone units with intervening pale red massive medium to fine-grained sandstone. Arrow indicates position of GSN F1586. **B**, Distinctive trough cross-bedding within the overbank splay facies immediately below the GSN 1590 locality (white arrow). **C**, Close-up of GSN F1586 at the locality. Note the white bone of the skull roof visible on the surface of an elongate smooth surfaced calcareous nodule. Scale bar equals 5 cm. **D**, The terminal section of a siltstone-filled burrow tunnel dipping at a low angle into the upper unit of the channel sandstone below the GSN 1586 locality. Similar structures in the *Endothiodon* AZ strata of the Karoo Basin are interpreted as tetrapod burrows made by the dicynodont *Diictodon*. Geo-pick length equals 33 cm.

2000). A cylindrical burrow structure (Fig. 2D) dipping some 20 degrees from horizontal was observed in the fossil-bearing interval at the new Permian fauna locality. The burrow resembles the dimensions and geometry of *Diictodon* burrow casts recently described from the late Permian Teekloof Formation of the main Karoo Basin in South Africa (Smith *et al*. 2021).

To summarize, the interpreted environment of the new Permian fauna is one of wet floodplains with ponds and marshes fed by streams issuing from marginal alluvial fans along the fault scarp. The paucity of organic remains in the lower Omingonde mudrocks possibly is due to preservation failure rather than an original scarcity, although the scarcity of outcrops suitable for finding macrofossils and the lack of concerted prospecting efforts are more likely.

MATERIAL

The dicynodont specimen GSN F1586 consists of a dorsoventrally compressed skull and partial mandible, eroded at the base to expose an extensive dentary tooth row (Fig. 3A,C,D). The surface of the bone has a densely cracked appearance, but for the most part, sutures are visible. A large crack runs anteroposteriorly through the right side of the skull at the level of the dorsal orbital margin. The lower jaw is pressed up against the cranium, but is not occluded in life position, being displaced somewhat to the left. Most of the ventral surface of the mandible is missing, and portions of the palate, occiput, and right lateral surface of the cranium have also been lost to erosion. The specimen was prepared at the Iziko South African Museum (Cape Town).

The gorgonopsian specimen GSN F1590 is a laterally compressed skull and mandible, with only the left side currently exposed (Fig. 4). Only the snout and dentary appear to be preserved. The snout is badly eroded on the left side, exposing the medial surface of the right maxilla. The only intact bones from the left side of the skull are portions of the premaxilla, septomaxilla, and nasal. Where complete, the bone surface of these elements is reasonably well-preserved, with clear sutural boundaries and well-defined foramina. The left lower jaw ramus is mostly missing, but the symphysial portion from the left lower canine forwards is preserved. The left upper and lower incisors are well-preserved, with intact enamel, showing that these teeth were serrated. Portions of the right incisor tooth rows are also preserved, but they are still largely covered with matrix so little can be said about their morphology. The upper and lower canine and postcanine tooth rows are intact on the right side of the specimen and are exposed lingually. GSN F1590 was prepared at the Museum of Comparative Zoology, Harvard University (Cambridge).

Both specimens are accessioned in the collections of the Geological Survey of Namibia (Windhoek).

SYSTEMATIC PALAEONTOLOGY

Synapsida Osborn, 1903
Therapsida Broom, 1905
Anomodontia Owen, 1860
Dicynodontia Owen, 1859
Oudenodontidae Cope, 1871

cf. *Tropidostoma*

Referred specimen. GSN F1586, a small (dorsal skull length = 11 cm) skull with occluded partial mandible (Fig. 3A,C,D).

Description and comparative remarks. The cranium is cracked to the right of the midline, with a gap in the snout region (Fig. 3A). The posterior edge of the intertemporal bar and the lateral edge of the right temporal arch are eroded and missing large portions. The right mandibular ramus is damaged and largely missing, although a section posterior to the symphysis showing ventral cross-sections through the dentition is present (Fig. 3C,E). The bone surface of this specimen shows fine cracking throughout, but is otherwise reasonably well-preserved, showing clear sutures.

A variety of characters clearly indicate that this specimen is not referable to any of the known groups of Triassic dicynodonts. Chief among these is the presence of a well-developed dentary tooth row (Fig. 3C). Based on the exposed roots visible in ventral view on the right mandibular ramus, at least seven dentary teeth were present (and probably more, as the ramus is broken in the middle of the tooth row). These teeth are present in a single row (unlike that of *Endothiodon*; see Olroyd *et al*. 2021), although a replacement tooth can be seen developing medial to the inferred functional tooth at tooth position six. Dentary teeth are absent in all members of Dicynodontoidea, the group housing the majority of Triassic dicynodont diversity. Two Triassic subclades of Dicynodontoidea are known: Lystrosauridae and Kannemeyeriiformes. The single Triassic lystrosaurid genus is the hyper-abundant 'disaster taxon' *Lystrosaurus*, which did not survive beyond the Early Triassic (Botha & Smith 2007; Smith *et al*. 2020; Viglietti *et al*. 2021). *Lystrosaurus* is one of the most specialized dicynodonts, with a deepened snout offset from the rest of the cranial axis, unlike the snouts of most dicynodonts (including GSN F1586) that are in the same plane as the rest of the skull. Kannemeyeriiforms were mostly large-bodied dicynodonts, which were abundant in terrestrial ecosystems in the Middle and early Late Triassic (Kammerer *et al*. 2013). Members of this group are characterized by the absence of the postfrontal bone, which is present and well-developed in GSN F1586 (Fig. 3A).

The only non-dicynodontoid Triassic dicynodonts are rare members of Emydopoidea, consisting of two species of kingoriids (*Kombuisia antarctica* and *K. frerensis*) and one myosaurid (*Myosaurus gracilis*). Emydopoids often do have postcaniniform dentition (Angielczyk & Kammerer 2017; Olroyd *et al*. 2021), but it is absent in both *Kombuisia* and *Myosaurus*. GSN F1586 also differs from these taxa (and all other known emydopoids) in the absence of paired, groove-like depressions on the palatal surface of the premaxilla, embayment of the palatal rim anterior to the caniniform process, and 'shovel-like' shape of the mandibular symphysis (Kammerer & Angielczyk 2009). Finally, Triassic emydopoids include the smallest known dicynodonts, and GSN F1586 greatly exceeds the largest specimens of *Kombuisia* and *Myosaurus* (dorsal skull length ~4–6 cm) in size.

The combination of nasal bosses present as paired swellings near the dorsal margin of the external nares (Fig. 3A) and a postcaniniform crest (Fig. 3C,E) indicate that GSN F1586 is a cryptodont. Cryptodontia is a group of exclusively late Permian dicynodonts including some of the most abundant taxa in southern African basins (e.g. *Aulacephalodon*, *Oudenodon*; Kammerer *et al*. 2011; Smith *et al*. 2012). Among cryptodonts, the only subclade known to have dentary teeth is Oudenodontidae. Identification of GSN F1586 as an oudenodontid is also supported by its expanded interpterygoid vacuity (the other typical feature of oudenodontids, contribution of the postparietal to the intertemporal bar, cannot be confirmed in GSN F1586 due to damage). In overall skull morphology, GSN F1586 is extremely similar to the abundant South African oudenodontid *Tropidostoma dubium*, which is restricted to the *Tropidostoma-Gorgonops* Subzone of the *Endothiodon* Assemblage Zone (Wuchiapingian) (Day & Smith 2020). At present, we identify GSN F1586 as cf. *Tropidostoma*. Although identification as *Tropidostoma* (and probably *T. dubium* specifically) is likely based on available data, few characters separate this taxon from the other known toothed oudenodontid, the Russian *Australobarbarus*, and additional preparation and study is necessary to confirm its identification. Both *Tropidostoma* and *Australobarbarus* are restricted in age to the early late Permian, however, so regardless of specific identification, this specimen indicates a Permian age for its host rock.

Theriodontia Owen, 1876
Gorgonopsia Seeley, 1894

cf. *Lycaenops*

Referred specimen. GSN F1590, a partial skull and articulated mandible (Fig. 4).

Description and comparative remarks. The left side of the

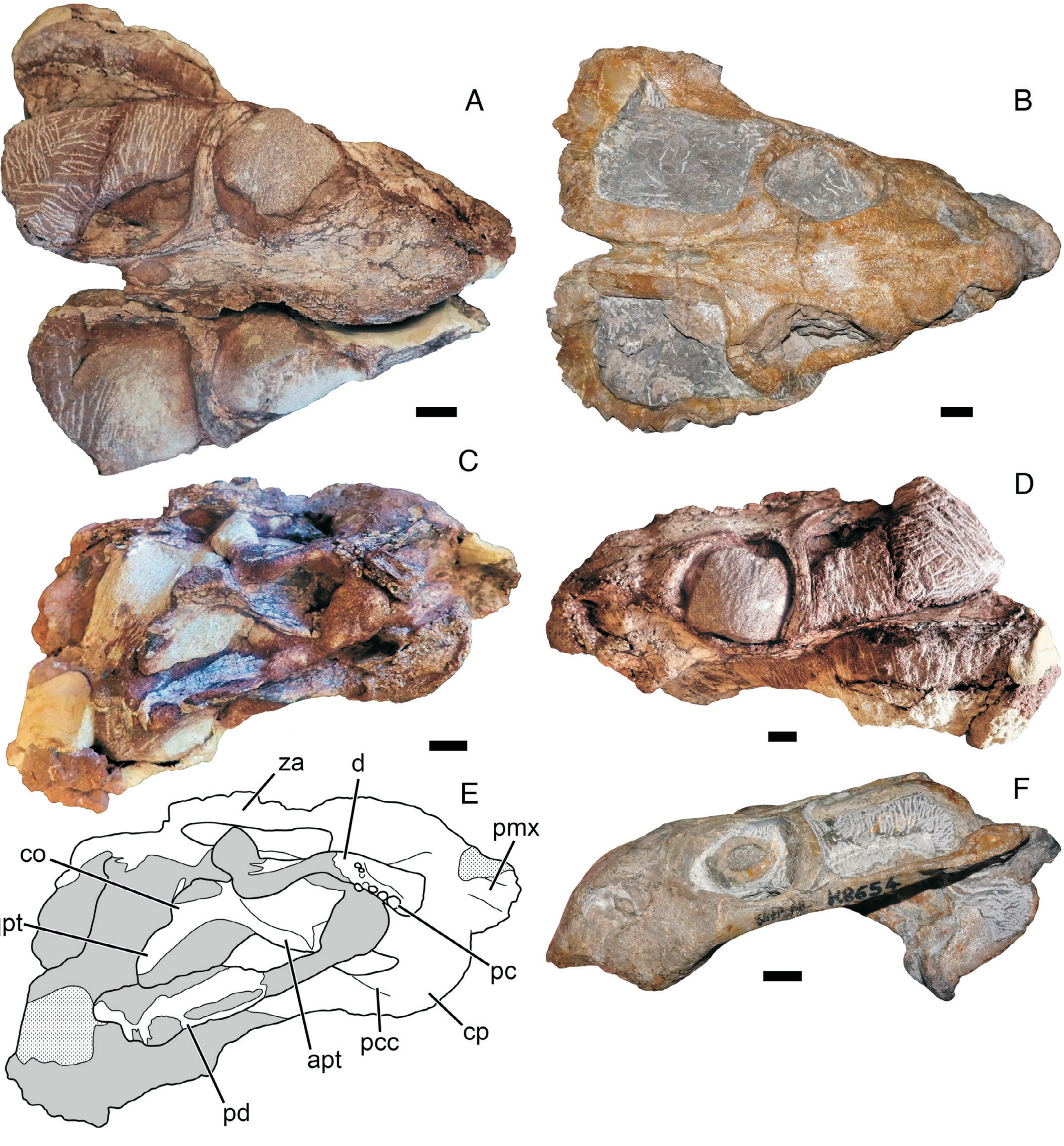

Figure 3. GSN F1586, cryptodont dicynodont (cf. *Tropidostoma*) from the base of the Omingonde Formation. Specimen in (**A**) dorsal, (**C**) ventral, and (**D**) left lateral views with (**E**) interpretive drawing of ventral view. Karoo Basin specimens of *Tropidostoma dubium* included for comparison: **B**, SAM-PK-K6901 in dorsal view; **E**, SAM-PK-K8654 in left lateral view. Abbreviations: apt, left anterior ramus of the pterygoid; co, crista oesophagea; cp, caniniform process of the left maxilla; d, exposed fragment of right dentary; pc, lower postcaniniform tooth row exposed in section; pcc, postcaniniform crest; pd, post-dentary portion of left mandibular ramus; pmx, anterior tip of premaxillary 'beak'; qpt, left quadrate (or posterior) ramus of the pterygoid; za, right zygomatic arch. Scale bars equal 1 cm.

skull is exposed but badly eroded, such that most of the lateral surface of the snout and the left mandibular ramus are missing (Fig. 4B). The right side is still embedded in matrix. The specimen is broken around the orbital region and appears to preserve little of the temporal region of the skull. Information on this specimen comes largely from the medial view of the right mandibular ramus, partial palate, and snout tip (the only exposed part preserving a substantial amount of external bone surface). The specimen has clearly suffered intense lateral compression, but the bone quality is otherwise good and the sutures are well defined.

The combination of five upper and four lower incisors, serrated canines, a tall, steep mandibular symphysis, and septomaxilla with a broad footplate on top of the premaxilla (Fig. 4C) confirm that this specimen is a gorgonopsian. Gorgonopsian alpha taxonomy has historically been problematic, although recent studies have begun to

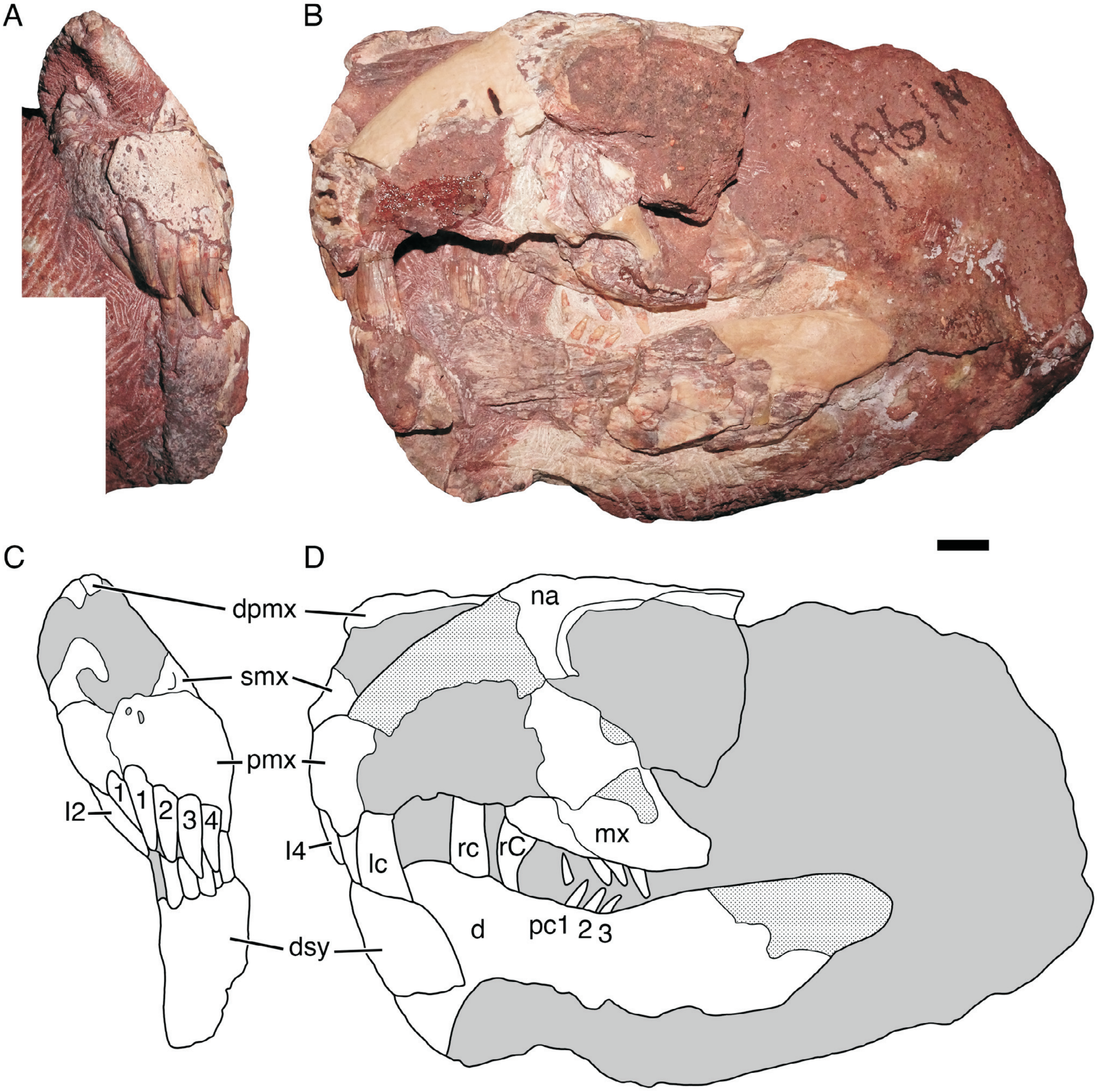

Figure 4. GSN F1590, partial gorgonopsian skull from the base of the Omingonde Formation. Specimen in (**A**) anterior and (**B**) left lateral views with interpretive drawings (**C** and **D**, respectively). Abbreviations: d, dentary; dpmx, dorsal process of premaxilla; dsy, dentary symphysis; I, upper incisor; lc, left lower canine; mx, maxilla; pc, lower postcanine; pmx, premaxilla; rc, right lower canine; rC, right upper canine; smx, septomaxilla. Scale bar equals 1 cm.

resolve this (e.g. Kammerer 2015, 2016, 2017). Unfortunately, limited information pertinent to lower-level identification is currently exposed in GSN F1590. The relatively short postcanine tooth rows (3–4 upper postcanines and 3 lowers) exclude most small-bodied gorgonopsian taxa (e.g. *Aelurosaurus*, *Cyonosaurus*) as well as some larger taxa (e.g. *Aelurognathus*, *Arctognathus*, *Dinogorgon*). The lack of cranial pachyostosis suggests this specimen is not a rubidgeine. The relatively tall snout (even taking compression into consideration) would seem to exclude *Gorgonops* from consideration. In general, this specimen is most similar to the array of gorgonopsians currently housed in the genus *Lycaenops*. However, this taxon seems to be a 'wastebasket' for a variety of non-rubidgeine African gorgonopsians and is in need of revision (C.F.K. pers. obs.). At present, we refer this specimen to cf. *Lycaenops* pending additional preparation and alpha taxonomic review of the genus.

DISCUSSION AND CONCLUSIONS

Day & Smith (2020) formally resurrected the *Endothiodon* Assemblage Zone (AZ) of the Beaufort Group in South Africa as the stratigraphic interval characterized by the co-occurrence of the dicynodonts *Endothiodon*, *Diictodon*, *Emydops*, and *Pristerodon* and the gorgonopsian *Gorgonops*. They further subdivided the *Endothiodon* AZ into two subzones, a lower *Lycosuchus*-*Eunotosaurus* Subzone and an upper *Tropidostoma*-*Gorgonops* Subzone. This assemblage zone records the early recovery of ecosystems from the Capitanian (end-Gudalupian) mass extinction and spans a period from approximately 258 Ma to ±256.8 Ma (Rubidge *et al*. 2013; Day *et al*. 2015).

The fossils introduced herein were found in an outcrop at the base of Etjo Mountain of strata that was previously logged as lower Omingonde Formation (Smith & Swart 2002). Both the gorgonopsian (GSN F1590) and the dicynodont (GSN F1586) specimens are preserved in the same dusky red medium to fine-grained sandstone with light-grey mottles. These two taxa occurring together now confirm the presence of early late Permian strata at the base of what is currently mapped as Omingonde Formation and highlight the need for more detailed investigation of the overlying stratigraphy, which should contain an unconformity representing a depositional hiatus of approximately 20 Ma.

Other possible equivalents of this subzone on the African continent outside of the main Karoo Basin are fossil rich units of the upper Ruhuhu Formation of Tanzania (Angielczyk *et al*. 2014), some Mid-Zambezi exposures of the Madumabisa Mudstone Formation (Sidor *et al*. 2023), and the *Endothiodon*-bearing K5b and K5c units of the Metangula Graben of Mozambique (Macungo *et al*. 2019). Thus, the newly identified late Permian fauna in Namibia suggests that during the late *Endothiodon* AZ times, there was a lowland connection with breeding populations of Karoo tetrapods between the main foreland basin of South Africa and the Waterberg-Erongo rift basins of central Namibia as well those of Tanzania and Mozambique. However, a more detailed understanding of the local faunal assemblages in all of these regions is required.

Although many details of the ecological and stratigraphic context of the new Namibian specimens remain unknown, they represent a tantalizing indication of a previously unknown Permian fauna. To better understand this fauna and the stratigraphy of the lower Omingonde Formation, it is vital to continue fossil prospecting in the area of Etjo Mountain, extensively map out the area, search for the unconformity between the *Endothiodon* AZ and the *Cynognathus* AZ strata, and determine whether it is structural, non-depositional, or erosional. Furthermore, the inter-connectedness of all southern Gondwanan basins during various time periods in the Permian and Triassic needs additional study and contextualization through more rigorous dating of the strata. Although therapsid fossils remain of crucial importance for understanding broad-level correlations between faunas in the various African basins, geochronological data from radiometric analysis of their host rocks is needed to refine index-fossil based age estimates.

We thank Jessica Cundiff, curator at the Museum of Comparative Zoology (Cambridge, U.S.A.) for assisting with the repatriation of material collected in Namibia by the late Farish Jenkins and the MCZ crew. Thanks also to Tiffany van Zyl for preparation of GSN F1586. Research was supported by grants from Universidad de Buenos Aires Ciencia y Técnica (UBACyT 20020170100643), AGENCIA PICT-2019-01127, the Palaeontological Scientific Trust (PAST), and the University of the Witwatersrand. This is C.A.M.'s contribution R-407 to the Instituto de Estudios Andinos Don Pablo Groeber.

---

§ORCID iDs

H.B. Mocke:	orcid.org/0000-0002-1674-8369
C.F. Kammerer:	orcid.org/0000-0002-0596-623X
R.M.H. Smith:	orcid.org/0000-0001-6806-1983
C.A. Marsicano:	orcid.org/0000-0002-0121-6730

REFERENCES

ABDALA, F., HANCOX, P.J. & NEVELING, J. 2005. Cynodonts from the uppermost Burgersdorp Formation, South Africa, and their bearing on the biostratigraphy and correlation of the Triassic *Cynognathus* Assemblage Zone. *Journal of Vertebrate Paleontology* **25**, 192–199.

ABDALA, F. & SMITH, R.M.H. 2009. A middle Triassic cynodont fauna from Namibia and its implications for the biogeography of Gondwana. *Journal of Vertebrate Paleontology* **29**, 837–851.

ABDALA, F., JASHASHVILI, T., RUBIDGE, B.S. & VAN DEN HEEVER, J. 2013a. New material of *Microgomphodon oligocynus* (Eutherapsida, Therocephalia) and the taxonomy of southern African Bauriidae. **In**: Kammerer, C.F., Angielczyk, K.D. & Fröbisch, J. (eds), *Early Evolutionary History of the Synapsida*, 209–231. Dordrecht, Springer.

ABDALA, F., A.M. MARSICANO, R.M.H. SMITH & SWART, R. 2013b. Strengthening western Gondwanan correlations: a Brazilian dicynodont (Synapsida, Anomodontia) in the Middle Triassic of Namibia. *Gondwana Research* **23**, 1151–1162.

ANGIELCZYK, K.D. & KAMMERER, C.F. 2017. The cranial morphology, phylogenetic position and biogeography of the upper Permian dicynodont *Compsodon helmoedi* van Hoepen (Therapsida, Anomodontia). *Papers in Palaeontology* **3**, 513–545.

ANGIELCZYK, K.D., STEYER, J-S., SIDOR, C.A., SMITH, R.M.H., WHATLEY, R.L. & TOLAN, S. 2014. Permian and Triassic dicynodont (Therapsida: Anomodontia) faunas of the Luangwa Basin, Zambia: taxonomic update and implications for dicynodont biogeography and biostratigraphy. **In**: Kammerer, C.F, Angielczyk, K.D. & Fröbisch, J (eds), *Early Evolutionary History of the Synapsida*, 93–138. Dordrecht, Springer.

BANDYOPADHYAY, S. 1989. The mammal-like reptile *Rechnisaurus* from the Triassic of India. *Palaeontology* **32**, 305–312.

BOTHA, J. & SMITH, R.M.H. 2007. *Lystrosaurus* species composition across the Permo-Triassic boundary in the Karoo Basin of South Africa. *Lethaia* **40**, 125–137.

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

BURNS, C.E., MOUNTNEY, N.P., HODGSON, D.M. & COLOMBERA, L. 2017. Anatomy and dimensions of fluvial crevasse-splay deposits: examples from the Cretaceous Castlegate Sandstone and Neslen Formation, Utah, U.S.A *Sedimentary Geology* **351**, 21–35.
DOI: 10.1016/j.sedgeo.2017.02.003

CATUNEANU, O., WOPFNER, H., ERIKSSON, P.G., CAIRNCROSS, B., RUBIDGE, B.S., SMITH, R.M.H. & HANCOX, P.J. 2005. The Karoo basins of south-central Africa. *Journal of African Earth Sciences* **43**, 211–253.

COPE, E.D. 1871. On the homologies of some of the cranial bones of the Reptilia, and on the systematic arrangement of the class. *Proceedings of the American Association for the Advancement of Science* **19**, 194–247.

DAY, M.O., GÜVEN, S., ABDALA, F., JIRAH, S., RUBIDGE, B. & ALMOND, J. 2015. Youngest dinocephalian fossils extend the *Tapinocephalus* Zone, Karoo Basin, South Africa. *South African Journal of Science* **111**(3/4), 1–5.

DAY, M.O. & SMITH, R.M.H. 2020. Biostratigraphy of the *Endothiodon* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**, 165–180.

GAETANO, L.C., MOCKE, H. & ABDALA, F. 2018. The postcranial anatomy of *Diademodon tetragonus* (Cynodontia, Cynognathia). *Journal of Vertebrate Paleontology* **38**, e1451872.
DOI: 10.1080/02724634.2018.1451872

GEVERS, T.W. 1936. The Etjo Beds of northern Hereroland, South West Africa. *Transactions of the Geological Society of South Africa* **39**, 317–329.

GUNTHORPE, R.J. 1987. Final report, Samoa and Tevrede prospecting grants (M46/3/1240 and 12411), Otjiwarongo District, South West Africa/Namibia. Unpublished Report. Tsumeb, Namibia, Tsumeb Corp. Ltd. 14 pp.

GÜRICH, G. 1926. Über Saurier-Fährten aus dem Etjo Sandstein von Südwestafrika. *Paläontologische Zeitschrift* **8**, 112–120.

HANCOX, P.J., NEVELING, J. & RUBIDGE, B.S. 2020. Biostratigraphy of the *Cynognathus* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**, 217–238.

HENDRICKX, C., GAETANO, L.C., CHOINIERE, J.N., MOCKE, H. & ABDALA, F. 2020. A new traversodontid cynodont with a peculiar postcanine dentition from the Middle/Late Triassic of Namibia and dental evolution in basal gomphodonts. *Journal of Systematic Palaeontology* **18**, 1669–1706.

HOLZ, M. & SCHULTZ, C.L. 1998. Taphonomy of the South-Brazilian Triassic herpetofauna: fossilization mode and implications for morphological studies. *Lethaia* **31**, 335–345

HOLZ, M. & SOUTO-RIBEIRO, A. 2000. Taphonomy of the South-Brazilian Triassic vertebrates. *Revista Brasileira de Geociências* **30**(3), 491–494

HOLZFÖRSTER, F., STOLLHOFEN, H. & STANISTREET, I.G. 1999. Lithostratigraphy and depositional environments in the Waterberg Erongo area, central Namibia, and correlation with the main Karoo Basin, South Africa. *Journal of African Earth Sciences* **29**, 105–123.

HOPSON, J.A. & REIF, W-E. 1981. The status of *Archaeodon reuningi* von Huene, a supposed late Triassic mammal from southern Africa. *Neues Jahrbuch für Geologie und Paläontologie – Monatshefte* **5**, 307–310.

HORN, B.L.D., GOLDBERG, K. & SCHULTZ, C.L. 2018. Interpretation of massive sandstones in ephemeral fluvial settings: a case study from the Upper Candelária Sequence (Upper Triassic, Paraná Basin, Brazil). *Journal of South American Earth Sciences* **81**, 108–121.
DOI: 10.1016/j.jsames.2017.10.009

HUENE, F. VON. 1925a. Triassischer Säugetierzahn aus Südwestafrika. *Centralblatt fuer Mineralogie, Geologie und Paläontologie* **1925**, 174–181.

HUENE, F. VON. 1925b. *Archaeodon* statt *Archaeotherium*. *Centralblatt fuer Mineralogie, Geologie und Paläontologie* **1925**, 303.

HUENE, F. VON. 1925c. Ausgedehnte Karroo-Komplexe mit Fossilführung im nordöstlichen Südwestafrika. *Centralblatt fuer Mineralogie, Geologie und Paläontologie* **1925**, 151–156.

KAMMERER, C.F. 2015. Cranial osteology of *Arctognathus curvimola*, a short-snouted gorgonopsian from the Late Permian of South Africa. *Papers in Palaeontology* **1**, 41–58.

KAMMERER, C.F. 2016. Systematics of the Rubidgeinae (Therapsida: Gorgonopsia). *PeerJ* **4**, e1608.
DOI: 10.7717/peerj.1608

KAMMERER, C.F. 2017. Anatomy and relationships of the South African gorgonopsian *Arctops* (Therapsida, Theriodontia). *Papers in Palaeontology* **3**, 583–611.

KAMMERER, C.F. & ANGIELCZYK, K.D. 2009. A proposed higher taxonomy of anomodont therapsids. *Zootaxa* **2018**, 1–24.

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. *Society of Vertebrate Paleontology Memoir* **11**, 1–158.

KAMMERER, C.F., FRÖBISCH, J. & ANGIELCZYK, K.D. 2013. On the validity and phylogenetic position of *Eubrachiosaurus browni*, a kannemeyeriiform dicynodont (Anomodontia) from Triassic North America. *PLOS ONE* **8**(5), e64203.
DOI: 10.1371/journal.pone.0064203

KAMMERER, C.F., VIGLIETTI, P.A., BUTLER, E. & BOTHA, J. 2023. Rapid turnover of top predators in African terrestrial faunas around the Permian-Triassic mass extinction. *Current Biology* **33**, 2283–2290.

KEYSER, A.W. 1973a. A new Triassic vertebrate fauna from South West Africa. *Palaeontologia africana* **16**, 1–15.

KEYSER, A.W. 1973b. New Triassic vertebrate fauna from South West Africa. *South African Journal of Sciences* **69**, 113–115.

KEYSER, A.W. 1978. A new bauriamorph from the Omingonde Formation (Middle Triassic) of South West Africa. *Palaeontologia africana* **21**, 177.

LÖFFLER, T. 1998. Fluvial facies and palaeo-environments of Triassic Karoo deposits in Central Namibia: Abstracts of Epicontinental Triassic International Symposium, Halle. *Hallesches Jahrbuch für Geowissenschaften*, Reihe B, Beiheft **5**, 103–104.

MACUNGO, Z., LOIDE, I., ZUNGUZA, S., NHAMUTOLE, N., MAHARAJ, I.E.M., MUGABE, J., ANGIELCZYK, K.D. & ARAÚJO, R. 2019. *Endothiodon* (Therapsida, Anomodontia) specimens from the middle/late Permian of the Metangula Graben (Niassa Province, Mozambique) increase complexity to the taxonomy of the genus. *Journal of African Earth Sciences* **163**(1-2), 103647.
DOI: 10.1016/j.jafrearsci.2019.103647

MARTIN, C.A.L. & TURNER, B. R. 1998. Origins of massive-type sandstones in braided river systems. *Earth-Science Reviews* **44**(1-2), 15–38.
DOI: 10.1016/s0012-8252(98)00019-1

MARTINELLI, A.G., DE LA FUENTE, M. & ABDALA, F. 2009. *Diademodon tetragonus* Seeley, 1894 (Therapsida: Cynodontia) in the Triassic of South America and its biostratigraphic implications. *Journal of Vertebrate Paleontology* **29**, 852–862.

MARTINELLI, A.G., KAMMERER, C.F., MELO, T.P., PAES NETO, V.D., RIBEIRO, A.M., DA-ROSA, Á.A.S., SCHULTZ, C.L. & BENTO SOARES, M. 2017. The African cynodont *Aleodon* (Cynodontia, Probainognathia) in the Triassic of southern Brazil and its biostratigraphic significance. *PLOS ONE* **12**(6), e0177948.
DOI: 10.1371/journal.pone.0177948

MOCKE, H.B., GAETANO, L.C. & ABDALA, F. 2019. A new species of the carnivorous cynodont *Chiniquodon* (Cynodontia, Chiniquodontidae) from the Namibian Triassic. *Journal of Vertebrate Paleontology* **39**, e1754231.
DOI: 10.1080/02724634.2019.1754231

OLROYD, S.L., LEBLANC, A.R., ARAÚJO, R., ANGIELCZYK, K.D., DUHAMEL, A., BENOIT, J. & AMARAL, M. 2021. Histology and μCT reveal the unique evolution and development of multiple tooth rows in the synapsid *Endothiodon*. *Scientific Reports* **11**, 16875 1–23.
DOI: 10.1038/s41598-021-95993-6

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

OWEN, R. 1859. On some reptilian remains from South Africa. *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 29th Meeting of the British Association for the Advancement of Science (1859)*, 153–166.

OWEN, R. 1876. *Descriptive and Illustrated Catalogue of the Fossil Reptilia of South Africa in the Collection of the British Museum*. London, Taylor and Francis, xii + 88 pp., 70 pls.

PEECOOK, B.R., ANGIELCZYK, K., KAMMERER, C.F., LUNGMUS, J.K., McINTOSH, J., SIDOR, C.A., SMITH, R.M., TOLAN, S., VIGLIETTI, P.A. & WHITNEY, M. 2020. A new stratigraphic framework for the Permo-Triassic Strata of the mid-Luangwa Basin, Zambia: Upper Permian Turnover and Middle-Upper Triassic Vertebrate Assemblages. *80th Annual Meeting of the Society of Vertebrate Palaeontology, Program and Abstracts*. 266.

PICKFORD, M. 1995. Karoo Supergroup palaeontology of Namibia and brief description of a thecodont from Omingonde. *Palaeontologia africana* **32**, 51–66.

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**, 363–366.

SEELEY, H.G. 1894. Researches on the structure, organisation, and classification of the fossil Reptilia. Part IX, Section 1. On the Therosuchia. *Philosophical Transactions of the Royal Society of London, Series B, Biological Sciences* **185**, 987–1018.

SIDOR, C.A., MANN, A. & ANGIELCZYK, K.D. 2023. *Gorgonops* and *Endothiodon* (Synapsida: Therapsida) from the Madumabisa Mudstone Formation: evidence of a previously unreported tetrapod biozone in the Mid-Zambezi Basin of southern Zambia. *Journal of Vertebrate Paleontology* **43**, e2256812.
DOI: 10.1080/02724634.2023.2256812

SMITH, R.M.H., ANGIELCZYK, K.D., BENOIT, J. & FERNANDEZ, V. 2021. Neonate aggregation in the Permian dicynodont *Diictodon* (Therapsida, Anomodontia): evidence for a reproductive function for burrows? *Palaeogeography, Palaeoclimatology, Palaeoecology* **569**, 110311.
DOI: 10.1016/j.palaeo.2021.110311

SMITH, R.M.H. & SWART, R. 2002. Changing fluvial environments and vertebrate taphonomy in response to climatic drying in a Mid Triassic rift valley fill: the Omingonde Formation (Karoo Supergroup) of central Namibia. *Palaios* **17**, 249–267.

SMITH, R.M.H., RUBIDGE, B.S. & VAN DER WALT, M. 2012. Therapsid biodiversity patterns and paleoenvironments of the Karoo Basin, South Africa. **In**: Chinsamy-Turan, A. (ed.), *Forerunners of Mammals: Radiation, Histology, Biology*, 31–62. Bloomington, Indiana University Press.

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**, 131–140.

TOLCHARD, F., SMITH, R.M.H., ARCUCCI, A., MOCKE, H. & CHOINIERE, J. 2021. A new 'rauisuchian' archosaur from the Middle Triassic Omingonde Formation (Karoo Supergroup) of Namibia. *Journal of Systematic Palaeontology* **19**, 595–631.

VIGLIETTI, P.A. 2020. Biostratigraphy of the *Daptocephalus* Assemblage Zone (Beaufort Group, Karoo Supergroup), South Africa. *South African Journal of Geology* **123**, 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. *The Proceedings of the National Academy of Sciences* **118**(17), e2017045118.
DOI: 10.1073/pnas.2017045118

WYND, B.M., PEECOOK, B.R., WHITNEY, M.R. & SIDOR, C.A. 2018. The first occurrence of *Cynognathus craterous* (Cynodontia: Cynognathia) in Tanzania and Zambia, with implications for the age and biostratigraphic correlation of Triassic strata in southern Pangea. *Society of Vertebrate Paleontology Memoir* **17**, 228–239.