Extended procolophonoid reptile survivorship after the end-Permian extinction

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The end-Permian extinction event is regarded as the most severe of the five major extinction events in the history of life. Recent work in the Karoo Basin of South Africa suggests that the extinctions at the Permo-Triassic boundary (PTB) may have been followed by a second pulse of extinctions, one that claimed the few species that crossed the PTB and thus survived the first extinction pulse. We report here a new specimen of the procolophonoid reptile, *Sauropareion anoplus,* which was known heretofore only from a single specimen from Lower Triassic strata of the Palingkloof Member, Balfour Formation. The new specimen comes from the lower part of the overlying Katberg Formation and serves as the last appearance datum for the stratigraphic range of *S. anoplus.* It indicates that *S. anoplus* survived the second pulse of PTB extinctions and reinforces the hypothesis that procolophonoid evolution was not seriously perturbed by extinctions that mark the beginning of the Triassic Period.

The end-Permian extinction, which occurred approximately 251.4 million years ago,[1] is widely regarded as the most catastrophic mass extinction event in Earth's history. An estimated 90% of all marine species[2–5] and 70% of all terrestrial vertebrate families[6] disappeared within 165 000 years[1] and perhaps as few as 10 000 years.[7] Although most research on the end-Permian extinction has focused historically on marine invertebrates (due to the many well-preserved, complete marine Permo-Triassic boundary sequences[8–10]), recent years have seen an increase in studies examining the effects of the extinction on terrestrial vertebrates.[11–20] Several transitional Permo-Triassic boundary (PTB) sequences occurring in terrestrial strata have been described from Australia,[21,22] Antarctica,[12,13,22] South Africa,[6,7,14,23] China[17,24,25] and Russia.[18,20] Research on the terrestrial South African and Russian PTB sequences have shown that there was a massive faunal turnover with most of the dominant Permian vertebrates disappearing at or below the boundary.[7,18,20]

Recent intense fossil collecting at the PTB sections in the South African Karoo Basin indicates an extinction level of 54% among the terrestrial vertebrate species.[26] That research also showed that the post-extinction recovery fauna in the Karoo Basin consisted mostly of temnospondyls, procolophonoids, non-mammalian cynodonts, and species of the dicynodont genus *Lystrosaurus*.[27,28]

Procolophonoids are Permo-Triassic reptiles that were once thought to be the closest fossil relatives of turtles,[29] but are now regarded as the only parareptiles to extend from the Palaeozoic into the Mesozoic. Permian procolophonoids are known only from Africa, Madagascar[30] and Europe,[31] whereas Early Triassic species are known from all major landmasses except North America, which indicates that they were important components of the post-extinction recovery fauna. *Procolophon trigoniceps* is the best-known procolophonoid of the *Lystrosaurus* Assemblage Zone (LAZ), and is restricted to the Katberg Formation[27] and the basal part of the Burgersdorp Formation.[32] Most other Triassic South African procolophonoids (*Sauropareion anoplus, Owenetta kitchingorum, Saurodektes rogersorum*) are known only from the Palingkloof Member (Balfour Formation) portion of the LAZ, which extends no more than 30 m above the Permo-Triassic boundary.[27] The exception is *Coletta seca,*[30] which is known from a single specimen from the Katberg Formation [Early Triassic (Olenekian) in age[33]].

Fig. 1. *Sauropareion anoplus,* NMQR 3544, in dorsal view. Scale bar = 10 mm.

Sauropareion anoplus is a basal procolophonoid that was recently described from the Palingkloof Member (Balfour Formation) portion of the LAZ.[15] It is characterized by a deep, posteromedian emargination of the skull table, deep occipital shelves of the parietals and supratemporals and a posteroventral facial process of the quadratojugal.[15] Here we describe new material of *S. anoplus* (National Museum specimen NMQR 3544), consisting of a skull and articulated anterior portion of the skeleton. This new material is from the Katberg Formation and therefore extends the range of this species upwards in Karoo stratigraphy.

NMQR 3544 consists of the anterior half of an articulated skeleton (to the fifteenth presacral vertebra) (Figs 1, 2). The skull is slightly dorso-ventrally compressed and the tip of the snout

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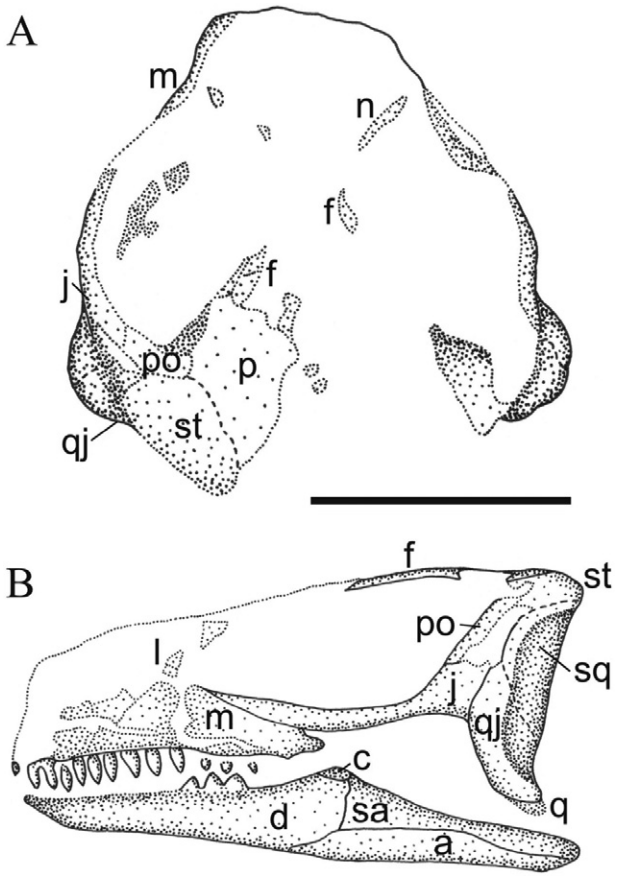

Fig. 2. *Sauropareion anoplus*, NMQR 3544: **A**, skull in dorsal view; **B**, skull in left lateral view. Abbreviations: a, angular; c, coronoid; d, dentary; f, frontal; j, jugal; l, lacrimal; m, maxilla; n, nasal; p, parietal; pf; postfrontal; po, postorbital; q, quadrate; qj, quadratojugal; sa, surangular; sq, squamosal; st, supratemporal. Scale bar = 10 mm.

and much of the skull roof is missing. We assign NMQR 3544 to *Sauropareion anoplus* on the basis of a posteroventral process of the quadratojugal that extends beyond the quadrate foramen in lateral view, and the absence of a supinator process.[15,34] In addition, what remains of the skull roof suggests that, as in the holotype, the posterior margin of the skull table was conspicuously emarginated. NMQR 3544 also has a narrow interpterygoid vacuity and a full complement of palatal teeth, features that are characteristic of *Sauropareion* but not of *Coletta.*

NMQR 3544 was found *ex situ,* enclosed in a nodule of very dusky red (10R2/2) mudrock at the base of a hill on the farm Vangfontein, an annexe of Nooitgedacht 25, Middelburg District in the Eastern Cape province. We have determined that Vangfontein is stratigraphically positioned in the lower half of the Katberg Formation. The outcrops here consist of fine-to-medium-grained pale olive (10YR6/2) sandstone bodies separated by very dusky red (10R2/2) fissile mudrock. The sandstone bodies have a 'gullied' basal contact containing pedogenic glaebules, and scouring of the interchannel facies is evident: both features indicate flash flooding. The succession is capped by a major sandstone body, which possibly represents the base of the informal Swartberg member of Neveling.[32] NMQR 3544 was found approximately 30 m below numerous *in situ* specimens of *Procolophon trigoniceps* and approximately 1 m below *Lystrosaurus* fossils (both taxa are biozone indicators for the LAZ; First Appearance Datum of *Procolophon* 116 m above PTB[26]). The presence of abundant *P. trigoniceps* specimens and the massive sandstone body of the 'Swartberg Member' 44 m above where the specimen was recovered, allows us to position NMQR 3544

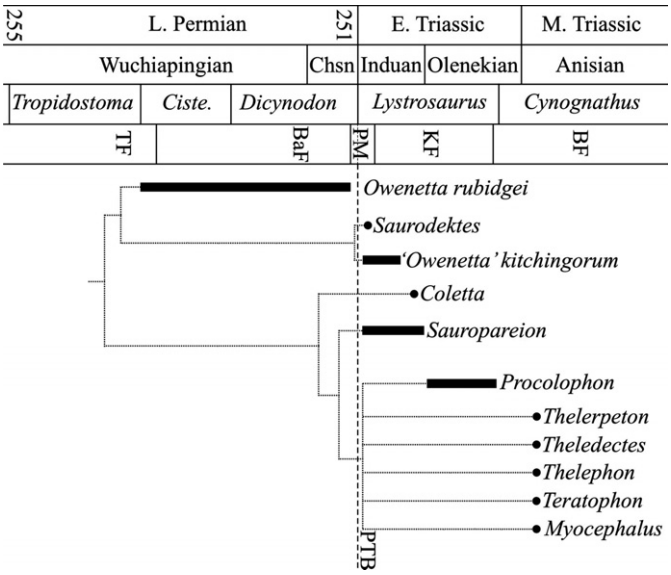

Fig. 3. Phylogenetic position of *Sauropareion anoplus* plotted against the South African Permo-Triassic biostratigraphy. Stratigraphic ranges from refs 15, 16, 26, 35, and this study. Vertical bars and solid circles indicate taxon ranges and single specimen occurrences, respectively. Abbreviations: Chsn, Changhsingian; *Ciste., Cistecephalus* Assemblage Zone; PTB, Permo-Triassic boundary. Numbers indicate millions of years ago. Stratigraphic chart follows Catuneanu *et al.*[33]

stratigraphically in the lower third of the Katberg Formation, approximately 120 m above the PTB.

Although most of the vertebrates affected by the end-Permian extinction disappeared at or just below the Permo-Triassic boundary, a second, smaller pulse of extinctions has recently been recognized, just after the main extinction event in the Karoo Basin.[27] This second pulse claimed taxa that survived the initial extinctions, and includes the dicynodont *Lystrosaurus curvatus* and the therocephalians *Moschorhinus* and *Ictidosuchoides.* Smith and Botha[27] also regarded the therocephalian taxon *Tetracynodon* as a member of the survivor fauna. Recent phylogenetic work by Modesto *et al.* indicates that the two species assigned to *Tetracynodon* are indeed sister taxa. The observation that they are found on either side of the PTB (Modesto in prep.) requires a ghost lineage for the Triassic species, *T. darti,* to cross the PTB. *Tetracynodon darti* is restricted to the Lower Triassic portion of the Palingkloof Member[26,27] and appears to have succumbed to the second extinction pulse.

NMQR 3544 significantly extends the biostratigraphic range of *Sauropareion* from the Palingkloof Member upwards into the Katberg Formation (Fig. 3). This discovery is important because it allows us to recognize that three basal procolophonoid lineages in South Africa (*Coletta seca, 'Owenetta' kitchingorum,* and now *Sauropareion anoplus*) did not succumb to a second pulse of extinctions. However, the available evidence indicates that a stratigraphic gap still exists between owenettids and other basal procolophonoids on the one hand and *Procolophon trigoniceps* on the other (Fig. 3).

Although traditionally it was thought that the South African procolophonoids were as severely affected by the end-Permian extinction as other vertebrate taxa, it now appears as though they were virtually unaffected by the extinction. By contrast, they radiated during the Early Triassic and taxa such as *Procolophon trigoniceps* became one of the most abundant and widely distributed vertebrates of the Early Triassic.

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