A new Triassic procolophonoid reptile and its implications for procolophonoid survivorship during the Permo-Triassic extinction event

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A reptile specimen from the *Lystrosaurus* Assemblage Zone of the Beaufort Group, lowermost Triassic of South Africa, represents a new procolophonoid parareptile. *Sauropareion anoplus* gen. et sp. nov. is identified as the sister taxon of Procolophonidae in a phylogenetic analysis of procolophonoids. Stratigraphic calibration of the most parsimonious tree reveals that four of the six procolophonoid lineages originating in the Permian Period extended into the succeeding Triassic Period. This relatively high taxic survivorship (67%) across the Permo-Triassic boundary strongly suggests that procolophonoids were little if at all affected by the mass extinction event that punctuated the end of the Palaeozoic Era (ca. 251 million years ago).

Keywords: mass extinction; palaeontology; phylogeny; procolophonoids; reptiles

1. INTRODUCTION

The Permo-Triassic extinction event is universally regarded as the most severe biological crisis to have occurred during the last 600 million years of earth history. It brought the Palaeozoic Era to a close ca. 251 million years ago (Erwin 1993). The hypothesized causes for this extinction event are varied and include global cooling (Stanley 1988), volcanism (Campbell *et al.* 1992) and extraterrestrial impact (Becker *et al.* 2001). Recent estimates suggest that ca. 90% of marine species were eliminated by this extinction event (Stanley & Yang 1994). The same figures for terrestrial groups range from 60% to almost 80% (Olson 1989; Maxwell 1992).

Estimates of terrestrial vertebrate extinction at the Permo-Triassic boundary can be criticized on the grounds that such studies use low stratigraphic and taxonomic resolutions, thereby generally calibrating diversity at the family level against standard geological stages. King (1990) examined the diversity of tetrapod genera from the Karoo Basin of South Africa using the generic data in Kitching (1977) and his biostratigraphic scheme of land vertebrate assemblage zones. She concluded that the famously low diversity of the earliest Triassic *Lystrosaurus* Zone was merely the final chapter in a gradual reduction in the numbers of Karoo genera that had begun well before the end of the Permian Period. King's (1990) conclusions are drawn from a literal reading of the fossil record of the Karoo and it is possible that a different picture of the diversity patterns of the Karoo fauna could have emerged if her data had been examined from a phylogenetic perspective, which might have allowed her to recover the diversity hidden by preservational and other biases of the fossil record (Norell 1992). Unfortunately, because very few palaeontologists are interested in continental vertebrates of this age, there has been as yet little phylogenetic work on most tetrapod groups that range across the Permo-Triassic boundary.

The recent discovery of a new specimen of procolophonoid reptile from the *Lystrosaurus* Assemblage Zone of South Africa (Modesto & Damiani 2000) has provided the impetus for a reconsideration of the interrelationships of Procolophonoidea. These tetrapods are one of two major groups of reptiles that survived the end-Permian extinctions and underwent taxonomic radiation during the Triassic Period. Recent studies of procolophonoids have focused on their use in biostratigraphy (Sues *et al.* 2000) and in studies of the evolution of herbivory (Reisz & Sues 2000), but have not treated procolophonoid phylogeny in great detail. A rigorous investigation of the interrelationships of these reptiles should permit an assessment of the lineage diversity (*sensu* Norell 1992) of procolophonoids as they weathered what has been termed the 'Mother of Mass Extinctions' (Erwin 1993).

2. MATERIAL AND METHODS

The specimen was preserved on a small block of red mudstone with only the anterior end of the skull exposed. Erosion has resulted in loss of the snout from a point just posterior to the external nares as well as parts of the right side and weathering has removed surface detail from the remaining bones of the antorbital region. Mechanical preparation with an air scribe exposed the protected parts of the skull and a few partial vertebrae and their ribs. This was followed by detailed cleaning of the bones with a pin vice.

Specimens used for comparative purposes included the holotype of *Coletta seca* (GHG 228 in the collections of the Geological Survey, Pretoria) and a referred specimen of *Procolophon trigoniceps* (BP/1/4014 in the collections of the Bernard Price Institute for Palaeontological Research, Johannesburg).

3. SYSTEMATIC PALAEONTOLOGY

Parareptilia Olson, 1947 (*sensu* deBraga & Reisz 1996)
Procolophonoidea Seeley, 1888
Sauropareion anoplus gen. et sp. nov.

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(a) *Diagnosis*

This taxon is distinguished from other procolophonoids by a deep, posteromedian emargination of the skull table, deep occipital shelves of the parietals and supratemporals, a posteroventral facial process of the quadratojugal and a contribution from the prearticular to the dorsal portion of the retroarticular process.

(b) *Holotype*

South African Museum specimen SAM PK-11192 preserves the skull and mandible posterior to the external nares, vertebral fragments and cervical rib fragments.

(c) *Locality and horizon*

The holotype and only known specimen was collected in 1935 by the late L. D. Boonstra from Barendskraal in the Middelburg District, Eastern Cape Province, Republic of South Africa. The strata exposed on Barendskraal belong to the *Lystrosaurus* Assemblage Zone of the Beaufort Group, which is earliest Triassic period in age (Groenewald & Kitching 1995; Kitching 1977).

(d) *Etymology*

The generic name is from the Greek words *sauros* and *pareion*, meaning 'lizard' and 'cheek', respectively and refers to the superficially lizard-like appearance of the temporal region. The specific epithet is from the Greek word *anoplos*, meaning 'without arms or armour' and alludes to the absence of the cheek spines that ornament many of its procolophonoid relatives.

4. DESCRIPTION

SAM PK-11192 is missing the anterior half of the snout and the right side of the skull has been flattened and slightly disarticulated so that the remaining elements can be seen in dorsal view. For this reason, the skull is only illustrated in dorsal and left lateral views (figure 1). In the interests of brevity, only features of phylogenetic interest are documented here. A detailed description, including that of the less informative postcranial remains, will be presented elsewhere.

The dorsoventrally low maxilla preserves seven teeth plus the partial tooth base of an eighth. The well-preserved teeth are essentially conical with sharp, slightly recurved tips. All of the teeth appear to be subcircular in transverse section from base to tip, thereby displaying none of the transverse expansion of the lateral teeth found in procolophonoids such as *Contritosaurus* (Ivakhnenko 1974) and *Procolophon* (Carroll & Lindsay 1985). The teeth are relatively larger than those of the basal procolophonoid *Owenetta* (Reisz & Laurin 1991) and, as in procolophonoids, they are less densely arranged along the ventral margin than in that genus.

The lacrimal has a distinctive interfingering suture with the prefrontal and the entrance to the lacrimal duct is present just lateral to that suture. The posteroventral process of the lacrimal, which is completely hidden in lateral view by the maxilla, overlies the palatine and extends posteriorly to make contact with both the jugal and the ectopterygoid, as in *Procolophon* (Carroll & Lindsay 1985).

The prefrontal resembles those of other procolophonoids in its general structure. The posterior 'spur' on the antorbital margin of the prefrontal, which is seen in other procolophonoids (Reisz & Laurin 1991; Lee 1995), is presumably present but not visible because matrix has been left inside the orbits in order to support the skull table. The postfrontal is a splint of bone that is restricted to the orbital margin. It is broadly separated from the postorbital by the parietal and, thus, it closely resembles the condition seen in procolophonoids such as *Procolophon* (Carroll & Lindsay 1985).

The parietal is very similar to that of *Procolophon*, except for a few details. While the parietal contributes to the posterior margin of the orbit, this edge is not as deeply incised by the orbit as it is in procolophonoids. The pineal foramen lies at the bottom of a shallow subcircular fossa in the dorsal surface of the paired parietals, as in *Owenetta* (Reisz & Laurin 1991) and *Coletta* (S. Modesto, H.-D. Sues, R. Damiani, personal observation). The paired parietals form a deep, median excavation along the occipital margin of the skull table, which is an autapomorphy of *Sauropareion*.

Two small quadrangular elements situated between the parietals and the supraoccipital are interpreted here as postparietals, which previously were only known among procolophonoids in Triassic specimens of *Owenetta* (Reisz & Scott 2001). The postparietals of *Sauropareion* appear to have been more or less confluent with the occipital shelves of the parietals.

The large supratemporal consists of a dorsal, rectangular portion that forms the posterolateral corner of the skull table and a smaller, wedge-shaped occipital shelf that is confluent with that of the parietal. The occipital shelf of the supratemporal is relatively large, comprising at least 33% of the bone.

Posteroventrally the jugal forms the anterodorsal margin of an acute and relatively deep subtemporal emargination. As seen on the right side, the jugal has a very narrow contact with the squamosal.

The quadratojugal has a small posteroventral superficial process that continues posteriorly beyond the quadrate foramen to cover the condylar region of the quadrate in lateral view. No other procolophonoid has this feature, making it the second autapomorphy for *Sauropareion*. Most of the squamosal lies deep to the superficial component of the quadratojugal and, judging from what can be seen of both sides, it appears to have had a narrow superficial exposure between the quadratojugal, postorbital and supratemporal. Medially the squamosal extends almost to the ventral margin of the quadratojugal.

The palatine is notched along its lateral margin for the suborbital foramen, but it is unclear whether this element also forms the lateral margin of this foramen or whether it is replaced here by the lacrimal. The ectopterygoid borders the subtemporal opening anteriorly and has firm contacts with the jugal and the lacrimal laterally and forms the posterior margin of the suborbital foramen.

The supraoccipital is plate-like with a well-defined concavity on its ventral margin bordering the foramen magnum. Its occipital surface bears paired excavations that meet along a faint nuchal ridge. The dorsal margin of the supraoccipital is a slight concavity that presumably contacted the skull roof; it is unclear whether this contact

Figure 1. *Sauropareion anoplus* gen. et sp. nov. SAM PK-11192: (a) dorsal and (b) left lateral views of the skull. an, angular; ar, articular; co, coronoid; d, dentary; ect, ectopterygoid; epi, epipterygoid; f, frontal; j, jugal; la, lacrimal; m, maxilla; n, nasal; op, opisthotic; p, parietal; pal, palatine; pf, postfrontal; po, postorbital; pp, postparietal; pra, prearticular; prf, prefrontal; q, quadrate; qf, quadrate foramen; qj, quadratojugal; sa, surangular; so, supraoccipital; sq, squamosal; st, supratemporal.

was via the postparietals, the parietals or both. The opisthotic has a well-developed paroccipital process, which has a slightly expanded tip that presumably contacted the lower margin of the occipital shelf of the supratemporal.

The dentary is dorsoventrally deep posteriorly. Its teeth are deeply inset with respect to the upper tooth row and little detail is visible because they are almost completely overlain by the latter. Both the surangular and the angular are dorsoventrally low elements, closely resembling those of *Owenetta* (Reisz & Laurin 1991). As in that genus, the angular of *Sauropareion* extends posteriorly beyond the articular to sheathe most of the ventrolateral surface of the retroarticular process, which forms

approximately half of the length of the articular in lateral view. In dorsal view the retroarticular process receives a major contribution from the prearticular. The articular surface for the quadrate is raised slightly above the dorsal margin of the retroarticular process, as in *Procolophon* (Carroll & Lindsay 1985).

5. DISCUSSION

A phylogenetic analysis of procolophonoid interrelationships indicates that *Sauropareion* is the sister taxon of the clade Procolophonidae (*sensu* Laurin & Reisz 1995), as shown in figure 2. Stratigraphic calibration of this phylogeny reveals ghost lineages for three Triassic taxa

Figure 2. Strict consensus of the two most parsimonious trees found in a PAUP 4.068 (Swofford, 2001) analysis of procolophonoid interrelationships. The two trees differ only in the position of *Owenetta rubidgei* (it is the sister taxon of the new owenettid *Owenetta* sp., in one tree, whereas it is the sister taxon of *Barasaurus* in the other). Tree length = 43, consistency index = 0.79 and rescaled consistency index = 0.65.

(figure 3) because a Tatarian origin for Procolophonidae is implied by the Russian taxon *Microphon*. We have not included this genus in the phylogenetic analysis because it is only represented by an isolated maxilla, but the procolophonoid identity of that specimen is based on the presence of labiolingually expanded teeth (Ivakhnenko 1983). *Microphon* may well be a junior synonym of *Contritosaurus* or of another Russian procolophonoid; it lacks unequivocal autapomorphies (Spencer & Benton 2000).

The stratocladogram (figure 3) indicates that four (Procolophonidae, *Coletta*, *Sauropareion* and the Triassic species of *Owenetta*) of the six terminal taxa originated during the later part of the Late Permian Period and extended into the Triassic Period. This translates into a survival rate of 67% for procolophonoids through what has been described as the greatest mass extinction in earth's history. This implies an unexpectedly low level of extinction (33%) for these reptiles when the consensus has been that relatively few Permian tetrapod lineages survived into the Triassic Period (e.g. Rubidge *et al.* 1995).

It is possible that the survival rate for procolophonoids is even higher (five out of six lineages) (83%) because the age of *Barasaurus* is not well constrained with respect to the Permo-Triassic boundary. *Barasaurus* is known from numerous specimens from a locality near Ranohira, in the Sakamena Formation of Madagascar (Smith 2000). The fossiliferous horizons at Ranohira are regarded as uppermost Permian Period by most workers, but this stratigraphic assignment is because of the presence of *Barasaurus*. This genus has long been recognized as a close relative of *Owenetta* (Piveteau 1955), which for most of the last century was thought to have been restricted to the Permian Period. However, a Triassic species of *Owenetta* is now known (Reisz & Scott 2001). Hence, the latest Permian age of Ranohira is now uncertain; it is possible that *Barasaurus* is an earliest Triassic procolophonoid with a ghost lineage that extends well into the Permian Period.

Figure 3. Stratocladogram of procolophonoid phylogeny showing ghost lineages (white extensions of black bars). Procolophonidae includes *Contritosaurus*, *Tichvinskia*, *Procolophon* and *Hypsognathus* from the tree shown in figure 2. The first appearance datum for Procolophonidae is the Russian taxon *Microphon*. Biozone abbreviations: Trop., *Tropidostoma*; Ciste., *Cistecephalus*; Dicyn., *Dicynodon*; Lyst., *Lystrosaurus*; Cyno., *Cynognathus*.

Our findings of high procolophonoid survivorship across the Permo-Triassic boundary compare closely with the results of recent phylogenetic work on a coeval reptile group, which suggest that diapsid reptiles, particularly the archosauromorphs, similarly experienced a relatively low extinction level (ca. 22%, according to Figure 30 in Dilkes (1998)) during the Permo-Triassic extinctions. The growing phylogenetic database for Permo-Triassic reptiles suggests that these terrestrial vertebrates were little if at all affected by the mass extinctions that appear to have devastated marine invertebrate groups (Stanley & Yang 1994). The disparity in survivorship between terrestrial and marine animals is intriguing and it may provide clues regarding the cause(s) of the Permo-Triassic extinctions. For example, it is difficult to explain how an extra-terrestrial impact (Becker *et al.* 2001) could have had such a catastrophic effect on marine communities yet left coeval reptile faunas comparatively unscathed. Clearly, much more work, particularly using phylogenetic approaches, is needed on all tetrapod groups ranging across the Permo-Triassic boundary. If future studies determine similarly low levels of extinction for most tetrapod groups, then explorations for the cause of the Permo-Triassic extinctions might best be restricted to the marine realm.

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APPENDIX A: PHYLOGENETIC CHARACTERS

1. Premaxillary nasal process extends dorsally (0) or anterodorsally (1).
2. Premaxillary teeth number five (0), four (1), three (2), two (3) or eight (4).
3. Maxilla pre-maxillary (subnarial) process present (0) or absent (1).
4. Maxillary depression absent (0) or present (1) on the maxilla and nasal.
5. Maxillary teeth number 12 or more (0) or nine or less (1).
6. Maxillary teeth subcircular (0) or labiolingually expanded (1) in basal cross-section.
7. Maxillary teeth crowns subcircular (0) or labiolingually expanded (1).
8. Lateral marginal teeth bases mesodistally narrow (0) or mesodistally broad (1).
9. Maxillary 'cheek' teeth not inset (0) or inset (1) from lateral surfaces of the cheek and jaws.
10. Lacrimal separated from (0) or contacts the ectopterygoid (1).
11. Orbit terminates at the level of the anterior margin of the pineal foramen (0), extends posteriorly to the level of the posterior-most point of the pineal foramen (1) or extends posteriorly well beyond the pineal foramen (2).
12. Pineal foramen flush with the dorsal surface of the skull table (0) or positioned in shallow fossa (1).
13. Postfrontal in contact with the post-orbital (0), in contact with the supratemporal also (1), separated from both elements (2) or absent and area occupied by the parietal (3).
14. Squamosal ventral margin terminates dorsal to (0) or extends at least as far ventrally as (1) that of the quadratojugal in the tympanic notch.
15. Quadratojugal lateral surface lacking processes (0) or with one or more spines (1).
16. Supratemporal longer anteroposteriorly than broad transversely (0) or vice versa (1).
17. Supratemporal lateral margin roughly straight (0) or notched (1).
18. Postparietal present (0) or absent (1).
19. Vomerine dentition consisting of shagreen of small denticles (0), consists of two or three rows of larger parachoanal teeth instead of denticles (1) or dentition entirely absent (2).
20. Suborbital foramen formed ventrally by the palatine and ectopterygoid alone (0) or by the palatine, ectopterygoid and maxilla (1).
21. Pterygo-palatine teeth present and aligned anterolaterally (0), present and aligned anteromedially (1) or absent (2).
22. Pterygoid quadrate process extends posterodorsally to but does not contact (0) or makes broad contact with (1) the occipital flange of the squamosal.
23. Temporal ventral margin roughly straight (0), acutely emarginated (1) or broadly excavated (2).
24. Quadratojugal anteroposteriorly narrow (0) or broad, extending anteriorly as far as the frontal contribution to the orbit (1).
25. Entepicondylar foramen on the humerus present (0) or absent (1).

APPENDIX B: DATA MATRIX

Character states for nine procolophonoid taxa and the outgroup taxon *Macroleter*. '*O. rubidgei*' is the type species of *Owenetta* and '*Owenetta* sp.' is a second species that was referred to this genus by Reisz & Scott (2001). Uncertainty for states 0 and 2 is coded as A.

<i>Macroleter</i>	00000	00000	00000	00000	00000
<i>O. rubidgei</i>	04000	00000	01100	1110?	?010?
<i>Owenetta</i> sp.	00000	00000	01100	11000	00101
<i>Barasaurus</i>	00000	0000?	0?100	1010?	00101
<i>Coletta</i>	01010	0000?	01000	???10	??10?
<i>Contritosaurus</i>	02111	10101	0?A??	???11	1????
<i>Tichvinskia</i>	02111	11101	20310	00111	11200
<i>Procolophon</i>	11111	11011	10211	00111	11210
<i>Hypsognathus</i>	13101	1111?	20311	00121	??010
<i>Sauropareion</i>	?????	00001	11210	0001?	1?10?

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