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Barendskraal, a diverse amniote locality from the *Lystrosaurus* Assemblage Zone, Early Triassic of South Africa

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A diverse amniote fauna has been recovered from Lower Triassic *Lystrosaurus* Assemblage Zone exposures on the farm Barendskraal, near Middelburg in Eastern Cape Province, South Africa. The fauna includes the dicynodont therapsid *Lystrosaurus* sp., the therocephalian therapsids *Tetracynodon darti, Moschorhinus kitchingi* and *Ericiolacerta parva,* the archosauromorph reptiles *Proterosuchus fergusi* and *Prolacerta broomi,* and the procolophonoid reptiles *Owenetta kitchingorum, Sauropareion anoplus* and *Saurodectes rogersorum.* The locality is remarkable in that although it is fossil-rich, *Lystrosaurus* fossils do not appear to be as abundant as elsewhere in this assemblage zone, and the diversity of taxa at Barendskraal (at least nine species) is surpassed only by that of the famous Harrismith Commonage locality in the northeastern Free State province (at least 13 species). However, the fauna at Harrismith Commonage is typical of most other *Lystrosaurus* biozone localities in being dominated numerically by *Lystrosaurus.* Study of the tetrapod taxa from Barendskraal is providing new insights into procolophonoid phylogeny and survivorship across the Permo-Triassic boundary, as well as the stratigraphic ranges of various taxa in the Lower Triassic deposits of the Karoo Basin.

Keywords: Amniota, Barendskraal, Karoo, Lower Triassic, *Lystrosaurus* Assemblage Zone.

INTRODUCTION

In 1935, a South African Museum field crew led by the late L.D. Boonstra recovered a small collection of Karoo fossils from the farm Barendskraal (an annexe of the original farm Klip Fonteyn 234), approximately 11 km south of Middelburg in Eastern Cape Province, South Africa. This collection consisted mainly of material belonging to the dicynodont therapsid *Lystrosaurus* and the archosauromorph reptile '*Chasmatosaurus*' (= *Proterosuchus*), along with a small, bone-bearing nodule labelled 'amphibian'. That nodule later proved to contain the partial skeleton of a new procolophonoid parareptile, *Sauropareion anoplus* (Modesto *et al.* 2001). In his compilation of tetrapod species distribution in the Karoo, Kitching (1977) listed four species from Barendskraal, namely *Proterosuchus 'vanhoepeni'* (= *P. fergusi*) and three species of *Lystrosaurus,* both index genera for the *Lystrosaurus* Assemblage Zone (Groenewald & Kitching 1995). Successive expeditions to Barendskraal in 2001 and 2002 by the authors, prompted by the description of *S. anoplus,* resulted in the recovery of additional procolophonoid material, which proved to be part of a diverse amniote fauna (Damiani *et al.* 2002) that we report fully in this paper.

The *Lystrosaurus* Assemblage Zone is part of the succession of eight biostratigraphic assemblage zones that comprise the Upper Permian–Middle Triassic Beaufort Group of the Karoo Basin, South Africa (Rubidge *et al.* 1995), a sequence that is generally accepted as the standard for non-marine Permian and Triassic time (Lucas 1998). The *Lystrosaurus* biozone is the type fauna for the Lootsbergian Land Vertebrate Faunachron of Early Triassic age (Lucas 1998), and records the recovery of terrestrial vertebrate faunas following the end-Permian extinction event, the largest such event in Earth history (Erwin *et al.* 2002). Note, however, that the genus *Lystrosaurus* has also been documented in uppermost Permian strata (Smith 1995; Smith & Ward 2001), so that the biozone does not encompass the full stratigraphic range of the genus *Lystrosaurus.* The tetrapod fauna of the *Lystrosaurus* biozone is dominated numerically by the dicynodont therapsid *Lystrosaurus,* which comprises some 95% of its known fossils (Groenewald & Kitching 1995); the remaining fauna consists of dicynodont, cynodont, and therocephalian therapsids, procolophonoid and diapsid reptiles, and temnospondyl amphibians (Groenewald & Kitching 1995).

The fauna recovered to date from Barendskraal, surveyed below, contains typical elements of the *Lystrosaurus* Assemblage Zone but is remarkable for the diversity of amniote taxa, which includes three newly described procolophonoid species (Modesto *et al.* 2001, 2003; Reisz & Scott 2002). In addition, material of *Lystrosaurus* is relatively scarce, in contrast to most other *Lystrosaurus* biozone localities where *Lystrosaurus* is the dominant fossil taxon recovered (Kitching 1977; Groenewald & Kitching 1995). No temnospondyl amphibian material has yet been recovered, despite intensive collecting efforts.

All material recovered during the 2001 and 2002 field seasons is reposited in the Bernard Price Institute for

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Palaeontological Research, Johannesburg (abbreviated 'BP'). Other institutional abbreviations used in the text are as follows: RC, Rubidge Collection, Wellwood, Graaff-Reinet; SAM, South African Museum, Cape Town.

GEOLOGICAL SETTING

General

In the south of the main Karoo Basin the *Lystrosaurus* Assemblage Zone, as currently recognized by the South African Committee for Stratigraphy (SACS 1980), includes the uppermost member of the Balfour Formation (Palingkloof Member), the Katberg Formation, and the lower third of the Burgersdorp Formation (Groenewald & Kitching 1995). However, in the north of the basin the entire Burgersdorp Formation contains a fauna assignable to the lower part of the *Cynognathus* Assemblage Zone (Welman *et al.* 1991; Hancox *et al.* 1995), and Neveling (2002) has restricted the *Lystrosaurus* biozone to the Palingkloof Member and Katberg Formation only.

The Palingkloof Member is a thin, predominantly argillaceous unit characterized by red and maroon mudstones and subordinate, light olive to light grey sandstones (SACS 1980; Hiller & Stavrakis 1984; Smith 1995). The Palingkloof strata broadly represent high-sinuosity channel and floodplain deposits that accumulated under semi-arid climatic conditions (Smith 1995; Groenewald 1996). The overlying Katberg Formation is a predominantly arenaceous unit that consists of stacked, tabular sheets of fine to medium-grained sandstones, with subordinate red and greenish-grey mudstones (SACS 1980; Smith 1995; Groenewald 1996). Deposition of this unit is thought to have occurred within a low sinuosity, braided river system under dry climatic conditions (Hiller & Stavrakis 1984: Smith 1995; Groenewald 1996; Ward *et al.* 2000; Neveling 2002). The rapid change in fluvial style from sinuous channel (Palingkloof) to braidplain (Katberg) deposits has previously been attributed to the combined effects of source area uplift and increasing aridity (Hiller & Stavrakis 1984; Smith 1995). More recently, this transition was attributed to a rapid and basin-wide die-off of floodplain vegetation, leading to increased sediment loads and a weakening of channel banks, and consequently the development of braided channels (Ward *et al.* 2000).

The main bone-bearing exposures on Barendskraal occur on the slopes of a small, isolated hill (referred to locally as a 'koppie') known as 'Maanhaar', and on a nearby larger koppie known as 'Agterkamp'. The strata of the Palingkloof Member and overlying Katberg Formation are exposed on both koppies, and a description of these units at Barendskraal is provided below. All of the fossils discovered come from the finer mudstone/siltstone facies, representing overbank or abandoned channel deposits. Loose, reddish-brown calcareous nodules containing indeterminate and relatively large postcranial bones, probably those of *Lystrosaurus,* also occur throughout the sequence. Figure 1 shows a stratigraphic section of the sequence at the Maanhaar locality. Note that, for convenience, the stratigraphic distribution of fossils on both Maanhaar and Agterkamp are plotted together on this section.

Palingkloof exposures at Barendskraal

The Palingkloof exposures on Maanhaar consist of greyish-red and greyish-brown mudstones and siltstones, with subordinate, thin (<1.5 m) tabular sandstones. The sandstones are of two types. The first consists of fine to very fine-grained, laterally extensive, 1–1.5-m-thick units that are bounded by erosive bases and grade upwards into massive silt- and mudstones. The presence of basal erosional scours, intra-formational pebbles, horizontal stratification with primary current lineation, and isolated trough cross-stratification, are indicative of deposition in the upper part of the lower flow-regime. However, deposition under lower flow-regime conditions during waning flow is also evident through the presence of ripple cross-stratification and the gradual fining-upwards into siltstones. Based on their erosive bases, tabular geometry, and evidence for rapid, but fluctuating, flow, these sandstones are interpreted as broad, shallow, unconfined channels, similar to the sheetflow sandstones proposed for this interval by Smith (1995) and Ward *et al.* (2000). The second sandstone type is more numerous, thinner (20–600 mm), and tends to pinch out laterally. It contains a larger siltstone component, and is usually massive in nature, although ripple cross-stratification also occurs. These sandstones have abrupt bases, often drape underlying topography, and are interpreted as the distal extremities of crevasse splays.

The mudstones and siltstones of the Palingkloof Member on Maanhaar outcrop as units 2–12 m thick, although they can usually be subdivided into smaller packages based on internal architecture, grain size, and the occurrence of incipient pedogenic horizons. The massive mudstones at the base of the section consist of stacked, thin (<25 mm), interbedded layers of siltstone and mudstone. Higher up in the Palingkloof Member, the siltstone packages are thicker (30–300 mm), and separated by thin, mudstone veneers. As a rule, weathering processes obliterate any original sedimentary structure in the fines. Silt particles predominate, but rare, fining-upward and coarsening-upward trends have also been documented in the mudrocks. Rare incipient pedogenic horizons are characterized by calcareous nodules of various sizes. These nodules occur sporadically throughout the sequence, but in places they amalgamate to form laterally continuous horizons. Subvertical, siltstone-filled *Taenidium* invertebrate burrow casts occur abundantly in both the mudstones and sandstones, as documented within Palingkloof exposures elsewhere in the basin (Smith 1995; Smith & Ward 2001).

The Palingkloof strata exposed on the koppie Agterkamp display the same general sequence as on Maanhaar, except for the absence of thicker (0.5–1.5 m), laterally extensive sandstones. The sequence consists almost exclusively of massive siltstones and mudstones, although they display some vague, tabular internal architecture. In general, the Agterkamp exposures appear to represent a lower energy depositional setting compared to the sequence exposed on Maanhaar.

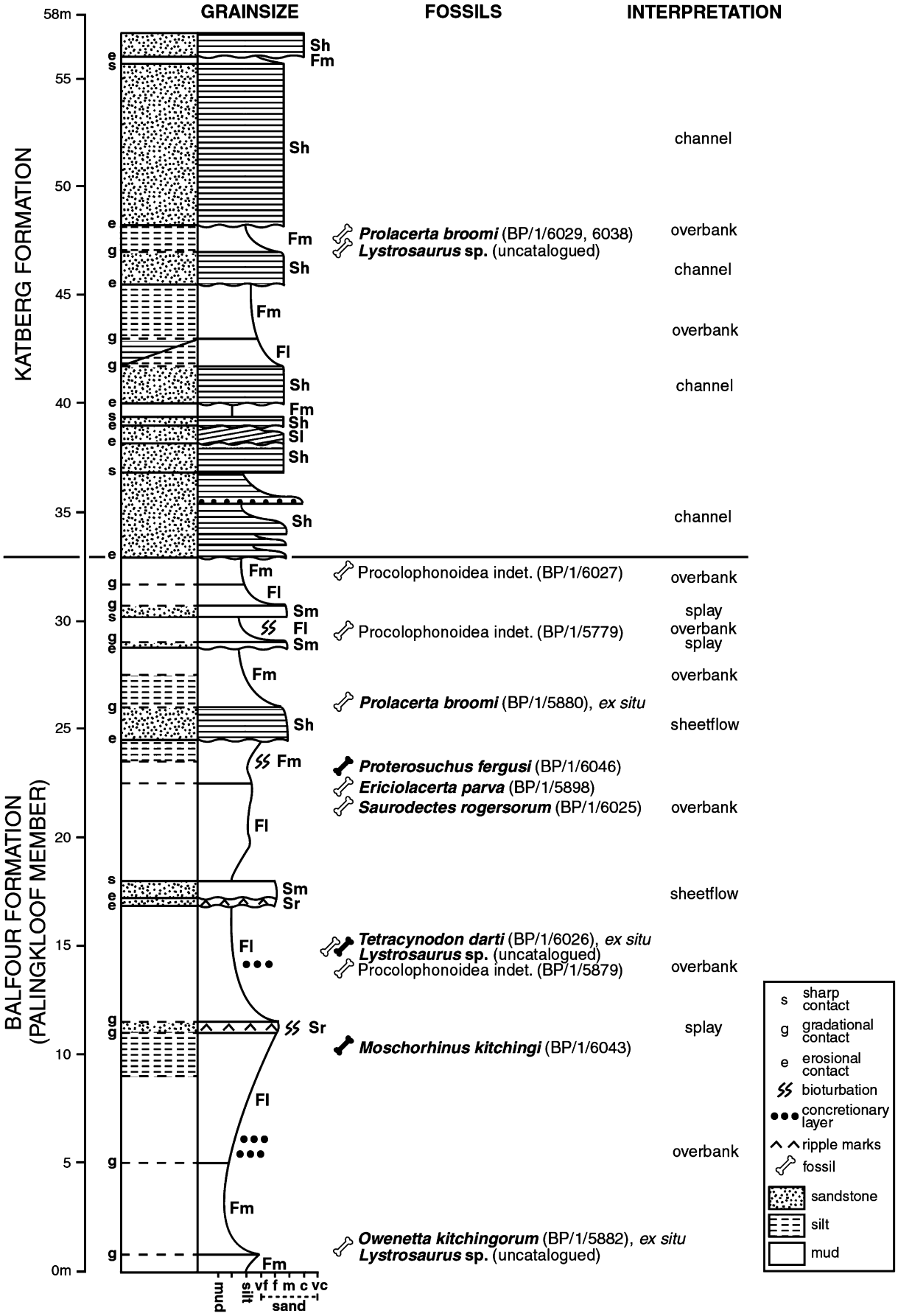

Figure 1. Stratigraphic section of the koppie 'Maanhaar', farm Barendskraal, Eastern Cape Province, South Africa. Strata of the lower part of the Early Triassic *Lystrosaurus* Assemblage Zone are exposed. For the sake of simplicity, fossil occurrences on Agterkamp are also plotted here. Fossil occurrences on Maanhaar are denoted by open bone symbols, whereas those on Agterkamp are denoted by closed (black) symbols. Facies codes (after Miall 2000): Fl, finely laminated sand, silt and mud (interbedded); Fm, massive fines (mudstone, siltstone); Sh, horizontally laminated sandstone; Sl, low-angle cross-bedded sandstone; Sm, massive sandstone; Sr, ripple cross-laminated sandstone.

Katberg exposures at Barendskraal

Earlier workers considered the contact between the mudstone-dominated Palingkloof Member and the sandstone-dominated Katberg Formation to represent an erosional unconformity (Hotton 1967; Anderson & Cruickshank 1978). However, outcrops of the Palingkloof Member in the south of the basin display a gradual upwards increase in average grainsize (*cf.* Fig. 1), prompting some workers to define the Palingkloof-Katberg contact as gradational (Smith 1995; Groenewald 1996; Ward *et al.* 2000). Nevertheless, in the study area, thicker (>4 m) sandstone packages, bounded by sharp or erosional contacts at the base, appear abruptly in the sequence. The appearance of these sandstones coincides with a significant upward increase in the sandstone to mudstone ratio. We consider the horizontal, erosional surface bounding the base of the first thick sandstone package (Fig. 1) to be the contact between the Balfour (Palingkloof Member) and Katberg formations. In the study area, this surface is laterally extensive and serves as a correlatable marker horizon. The contact is overlain by a 7-m-thick sandstone sequence consisting of several stacked, fining-upward packages, each 0.4–1.5 m thick. Each package typically consists of horizontally stratified sandstone that grades into thin (<250 mm) siltstones or mudstones at the top. A horizontal, erosional or sharp surface, which is in some cases draped by an intra-formational conglomerate, bounds each package at the base. The individual silty to very fine-grained sandstones are laterally extensive. These lower Katberg sandstones are interpreted as having been deposited in ephemeral, shallow, unconfined channels.

Higher in the section, sandstone bodies show an increase in thickness, with a concomitant increase in grain size. Both koppies in the study area are capped by stacked sheets of fine- to very fine-grained sandstone, 0.7–1.5 m thick. The lower bounding surfaces of individual sandstone bodies are sharp to erosional, and often draped by mud-pebble conglomerates. Internal architecture is simple, with stacked sandsheets and no evidence of lateral accretion. Mudstones and siltstones overlie the sandstone bodies and are thin and laterally inextensive. Sedimentological data is consistent with deposition by ephemeral, low sinuousity channels (McKee *et al.* 1967; Stear 1985; Miall 1996), although the increase in grain size and thickness relative to the lower Katberg sandstones suggests that these sandstones were deposited in a higher energy environment, with deeper and more permanent channels. Palaeocurrent trends were recorded from parting lineation. Palaeocurrent readings show a change from almost due north (15–195°) at the base, to east-northeast (50–230°; 70–250°) at the top.

Position of the Permo-Triassic boundary

The *Lystrosaurus* Assemblage Zone is widely considered to be Early Triassic in age (e.g. Lucas 1998), although the position of the Permo-Triassic boundary has been the subject of some debate (see review in Hancox 2000). Currently, the boundary is drawn at the base of a distinctively laminated mudrock horizon, some 3–5 m thick, that occurs near the base of the Palingkloof Member in the central and southern Karoo Basin (Ward *et al.* 2000; Smith & Ward 2001). The boundary is palaeontologically defined by the last appearance datum of the dicynodont *Dicynodon,* whose range overlaps that of *Lystrosaurus* in an interval of some 40 m below the boundary (Smith 1995; Ward *et al.* 2000; Smith & Ward 2001). This zone of overlap occurs within the uppermost part of the *Dicynodon* Assemblage Zone, so that the base of the *Lystrosaurus* Assemblage Zone does not coincide with first appearance datum of *Lystrosaurus* (Smith 1995; Smith & Ward 2001). In contrast, Steiner *et al.* (2003) considered the Permo-Triassic boundary to coincide with a 1 m thick fungal spike zone that occurs within the uppermost part of the Palingkloof Member, just below the base of the Katberg Formation, in a studied section near Carlton Heights in the southern Karoo. However, in that section, fossils of *Dicynodon* appear to be restricted to the lower part of the Palingkloof Member (*cf.* Smith 1995; Smith & Ward 2001), well below the fungal spike zone considered to mark the Permo-Triassic boundary. In addition, collecting by the authors at Carlton Heights in the 2002 field season yielded abundant *Lystrosaurus* remains, but no fossils indicative of an uppermost Permian age. Given the paucity of *Dicynodon* Assemblage Zone fossils at this locality, we favour the proposal of Ward *et al.* (2000) and Smith & Ward (2001) for placement of the Permo-Triassic boundary.

At Lootsberg Pass, the stratotype locality for the *Lystrosaurus* Assemblage Zone (Groenewald & Kitching 1995) that is located 20 km southwest of Barendskraal, a total thickness of some 35 m has been documented for the Palingkloof Member (Ward *et al.* 2000). As the uppermost 30 m of the Palingkloof Member is exposed on Maanhaar, the Permo-Triassic boundary may be located some 5–10 m below the base of the koppie. The Early Triassic age of the Barendskraal exposures is supported by the presence of characteristic pedogenic horizons, subvertical *Taenidium* invertebrate burrow casts, and the vertebrate taxa *Lystrosaurus, Prolacerta* and *Proterosuchus,* all of which are typical of Early Triassic *Lystrosaurus* Assemblage Zone deposits of the Karoo Basin (Kitching 1977; Keyser & Smith 1979; Groenewald & Kitching, 1995; Smith 1995; Smith & Ward 2001).

SYSTEMATIC PALAEONTOLOGY

Synapsida
Therapsida
Dicynodontia

***Lystrosaurus* sp.**

Material. SAM-PK-11191, 11195–11206, 11209–11210, cranial and postcranial remains collected by L.D. Boonstra and team in 1935; BP/1/5893, a mandible; and further uncatalogued cranial and postcranial material from the Palingkloof Member and Katberg Formation on Maanhaar and Agterkamp (Fig. 1).

Remarks. Kitching (1977) listed three species of *Lystrosaurus* from Barendskraal, namely *L. declivis, L. murrayi* and *L. oviceps,* presumably through inspection of the South African Museum material (which is listed as '*Lystro-*

saurus sp.' in their catalogue). However, as the genus *Lystrosaurus* is in dire need of taxonomic revision, and as distortion is so prevalent amongst large Karoo dicynodonts (Renaut 2000), we do not feel confident in assigning *Lystrosaurus* material to species level.

Therocephalia

Moschorhinus kitchingi Broom, 1920

Material. BP/1/6043, a large skull with associated postcranial elements, from the Palingkloof Member on Agterkamp (Fig. 1).

Remarks. The moschorhinid *Moschorhinus kitchingi* is known from a number of localities in both the *Dicynodon* and *Lystrosaurus* assemblage zones, and, with the possible exception of species of *Lystrosaurus,* is the sole tetrapod species that crosses the Permo-Triassic boundary in the Karoo (Kitching 1977; Smith 1995). Nevertheless, Smith & Ward (2001) did not report any specimens of *M. kitchingi* in their study of the stratigraphic ranges of vertebrate taxa spanning the Permo-Triassic boundary in the Karoo. Fossils of *M. kitchingi* are relatively rare, and according to Groenewald & Kitching (1995), the species range in the Triassic is restricted to the Palingkloof Member and the lower part of the Katberg Formation.

Ericiolacerta parva Watson, 1931, Fig. 2

Material. BP/1/5898, a complete skull and partial skeleton, from the Palingkloof Member on Maanhaar (Fig. 1).

Remarks. The holotype of the scaloposaurid *Ericiolacerta parva* consists of a small skull and partial skeleton from the *Lystrosaurus* Assemblage Zone at Harrismith Commonage, Free State province. This species has also been reported from the coeval lower part of the Fremouw Formation of Antarctica (Colbert & Kitching 1981). Kitching (1977) and Colbert & Kitching (1981) considered *E. parva* to be a possible juvenile of the scaloposaurid *Scaloposaurus constrictus* (Owen 1876), which occurs at a number of localities in the *Lystrosaurus* biozone, including Harrismith Commonage (Kitching 1977). However, the skulls of *E. parva* and *S. constrictus* are of a similar size, which suggests that their differences are not growth-related. Furthermore, the two species were considered distinct by Crompton (1955) and Mendrez-Carroll (1979) in their respective analyses of scaloposaurid relationships. BP/1/5898 can be referred to *E. parva* on the basis of its incomplete postorbital bar, broad intertemporal region, concave maxillary margin, small temporal fenestrae, the absence of a parietal foramen, teeth of small and uniform size, and the absence of a distinct canine (Watson 1931; Mendrez-Carroll 1979). A forthcoming description of BP/1/5898 by the authors should help to consolidate the taxonomic validity of *E. parva.*

Tetracynodon darti Sigogneau, 1963, Fig. 3

Material. BP/1/6026, an incomplete but articulated skull and postcranial skeleton, from the Palingkloof Member on Agterkamp (Fig. 1). Although found as surface float, BP/1/6026 had most likely weathered from a low rock ledge some 1–2 m above the point where the specimen

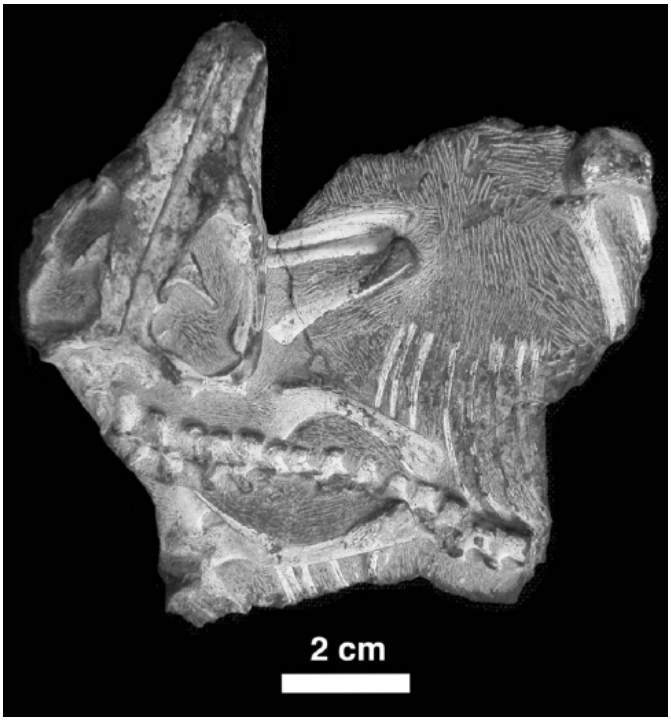

Figure 2. *Ericiolacerta parva* (Therapsida, Therocephalia), BP/1/5898, referred specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in dorsal view.

was found. This is supported by the lithology of the enclosing matrix which is closest to that of the Palingkloof Member.

Remarks. The type species of *Tetracynodon, T. tenuis* (Broom & Robinson 1948), is based on a small skull from the *Dicynodon* Assemblage Zone. Sigogneau (1963) described a new, larger species, *T. darti,* based on a skull and associated postcranial elements from *Lystrosaurus* Assemblage Zone deposits near Bergville, KwaZulu-Natal. BP/1/6026 can be referred to *T. darti* as it is of a comparable size and has a skull morphology identical to *T. darti* in all observable aspects, especially the long and narrow snout and correspondingly slender mandible. The exceptional preservation of BP/1/6026 should provide insight into the otherwise poorly known postcranial anatomy of *Tetracynodon* and of therocephalians in general (Fourie 2001).

Reptilia
Diapsida
Archosauromorpha

Proterosuchus fergusi Broom, 1903

Material. RC 59, a complete skull, the holotype of '*Elaphrosuchus rubidgei*' (Broom 1946), of unknown horizon; SAM-PK-11207–11208, cranial and postcranial remains of '*Chasmatosaurus*' collected by L.D. Boonstra and team in 1935, of unknown horizon; BP/1/6046, a skull and associated partial skeleton, from the Palingkloof Member on Agterkamp (Fig. 1).

Remarks. Kitching (1977) lists *Proterosuchus 'vanhoepeni'* as the senior synonym for the proterosuchid species from the Karoo. However, '*Chasmatosaurus vanhoepeni*' and '*Elaphrosuchus rubidgei*' are now considered subjective

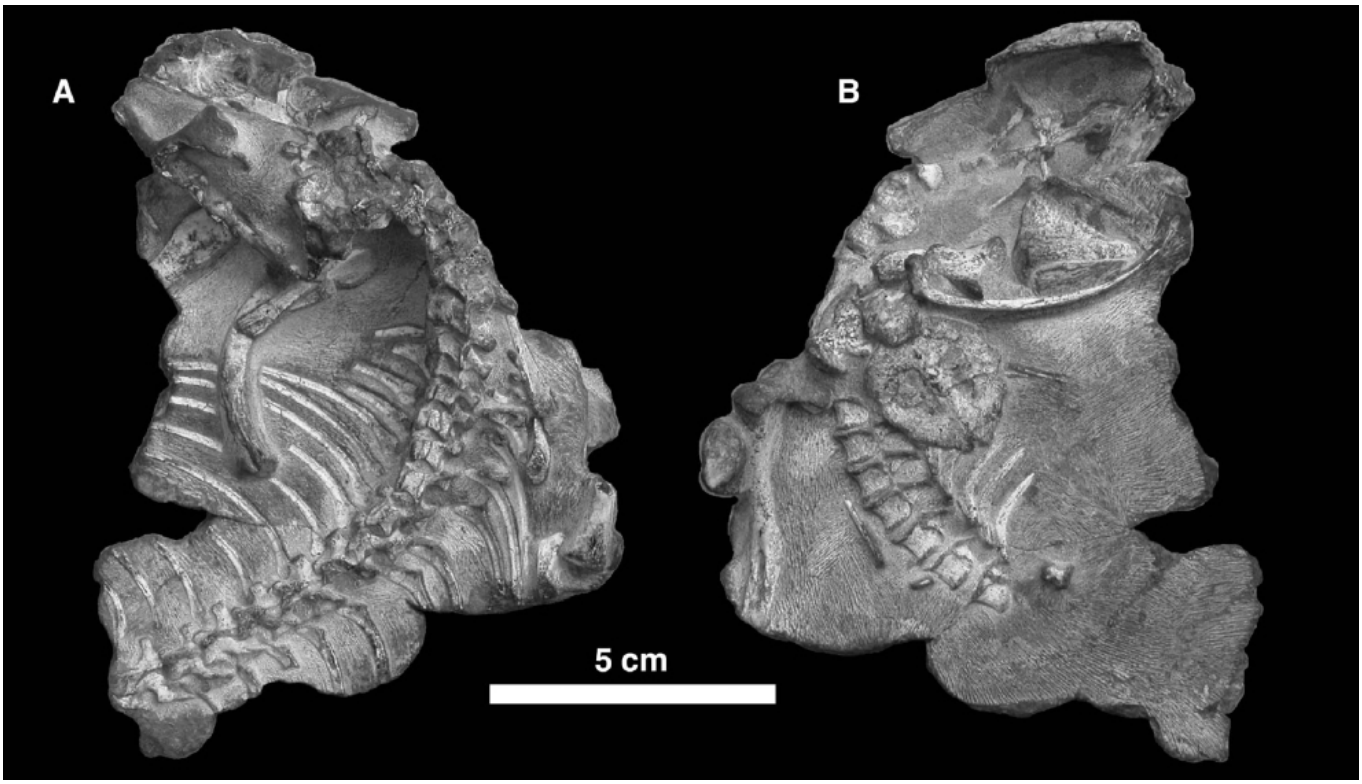

Figure 3. *Tetracynodon darti* (Therapsida, Therocephalia), BP/1/6026, referred specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in (**A**) dorsal and (**B**) ventral views.

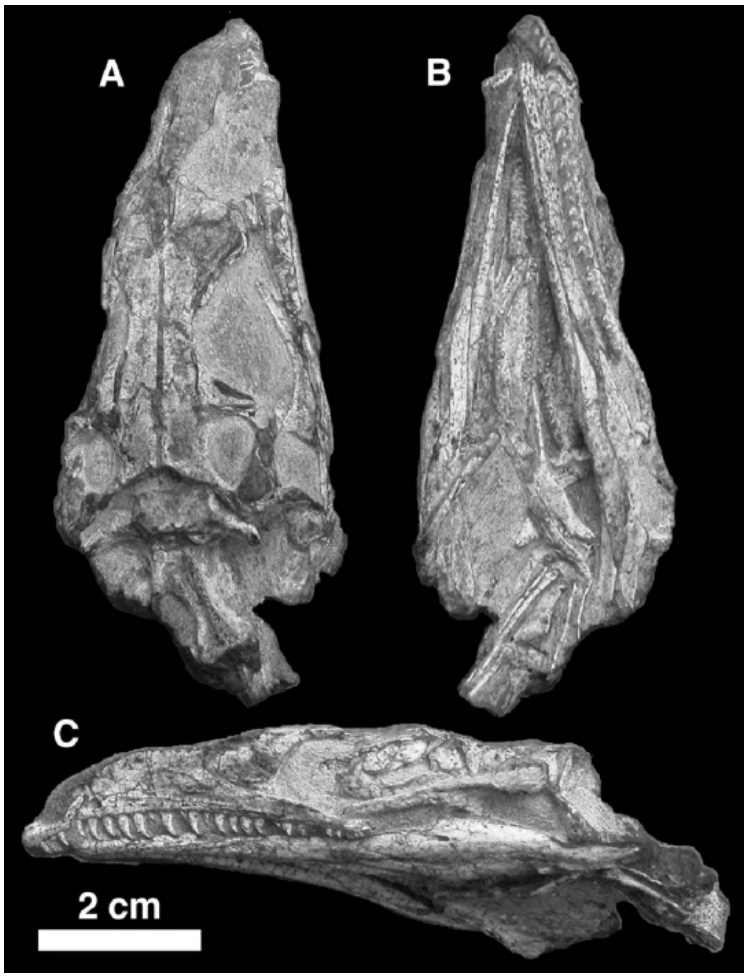

Figure 4. *Prolacerta broomi* (Reptilia, Archosauromorpha), BP/1/5880, referred specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in (**A**) dorsal, (**B**) ventral and (**C**) left lateral views.

junior synonyms of *Proterosuchus fergusi* (Welman 1998). Although the taxonomy of the South African proterosuchids has now been clarified (Welman 1998; Welman & Flemming 1993), a detailed redescription of the anatomy of *P. fergusi* is needed, especially in light of the continuing debate with regard to archosauromorph phylogeny.

Prolacerta broomi Parrington, 1935, Fig. 4

Material. BP/1/5880, a complete skull, from the Palingkloof Member on Maanhaar but found as surface float (Fig. 1); BP/1/6029 and BP/1/6038, partial skulls and associated postcranial elements, from the Katberg Formation on Maanhaar (Fig. 1).

Remarks. Like its larger archosauriform relative *Proterosuchus fergusi,* the small archosauromorph *Prolacerta broomi* requires a detailed reappraisal. Gow's (1975) study added much detail to our understanding of the anatomy of *P. broomi*, in particular his description of a complete skeleton (BP/1/2675), but his description of the skull is inaccurate in a number of respects. The skull is the subject of a forthcoming reappraisal by S.P. Modesto & H-D. Sues.

Parareptilia
Procolophonoidea

Sauropareion anoplus Modesto *et al.,* 2001, Fig. 5

Material. SAM-PK-11192 (holotype), a skull and associated postcranial elements, of unknown horizon. A number of additional, unprepared procolophonoid specimens (BP/1/5779, 5879, 6027),

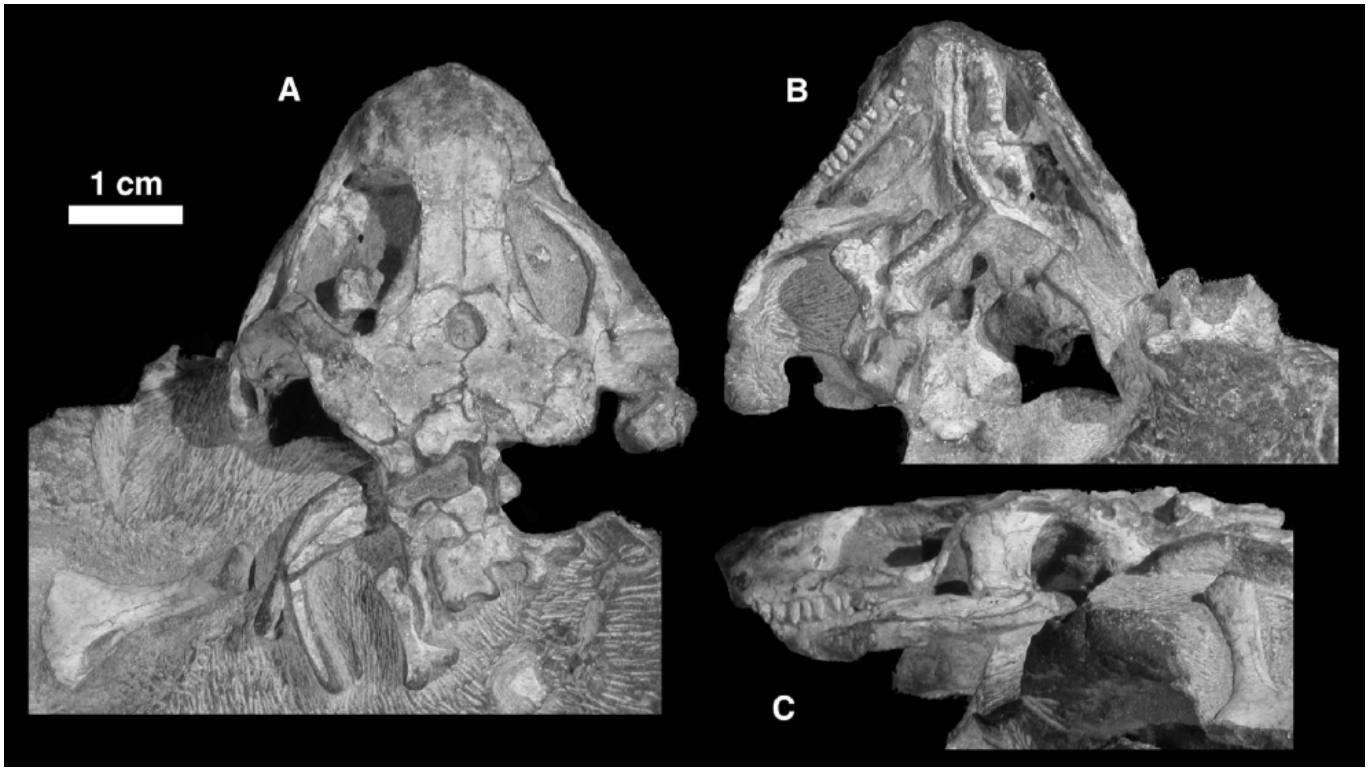

Figure 5. *Sauropareion anoplus* (Reptilia, Procolophonoidea), SAM-PK-11192, holotype specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in (**A**) dorsal, (**B**) ventral and (**C**) left lateral views.

represented by cranial and postcranial remains, were collected from the Palingkloof Member on Maanhaar (Fig. 1). Preliminary observation suggests that they are basal procolophonoids probably referrable to established taxa from Barendskraal, but full preparation of these specimens is still pending.

Remarks. Phylogenetic analysis identifies *Sauropareion anoplus* as the sister-taxon of the Procolophonidae. Thus, it is more derived than the owenettid taxa from the same strata, *Owenetta kitchingorum* and *Saurodectes rogersorum* (Modesto *et al.* 2001, 2003). Stratigraphic calibration of procolophonoid phylogeny is suggestive of ghost lineages (*sensu* Norell 1992) extending back into the Permian for all three procolophonoid taxa from Barendskraal (Modesto *et al.* 2003). We may therefore expect to discover these species in the uppermost Permian strata of the Karoo.

Owenetta kitchingorum Reisz & Scott, 2002, Fig. 6

Material. BP/1/5882, the anterior half of a skull and associated postcranial elements, from the Palingkloof Member on Maanhaar, but found as surface float (Fig. 1).

Remarks. BP/1/5882 is a small procolophonoid that can be referred to *O. kitchingorum* (Owenettidae) because it possesses the autapomorphy of a midline contact between the prefrontals that separates the nasals from the frontals (Reisz & Scott 2002). All previously known specimens of *O. kitchingorum* (listed by Reisz & Scott 2002) were recovered from the *Lystrosaurus* Assemblage Zone on the farm Tweefontein, Bethulie District, Free State province. Note, however, that one of the specimens referred by Reisz & Scott (2002) to *O. kitchingorum*, BP/1/4196, is actually a crushed, partial *Prolacerta* skull (Gow 1975; Damiani, pers. obs.). Two other specimens are known that may be referrable to *O. kitchingorum.* The first is represented by a crushed skull and partial skeleton uncovered during recent preparation of an undescribed galesaurid cynodont (RC 845) from the farm Fairydale, Bethulie District (Damiani pers. obs.). The second is based on the supposed early lizard *Colubrifer campi* (Carroll 1982), questionably

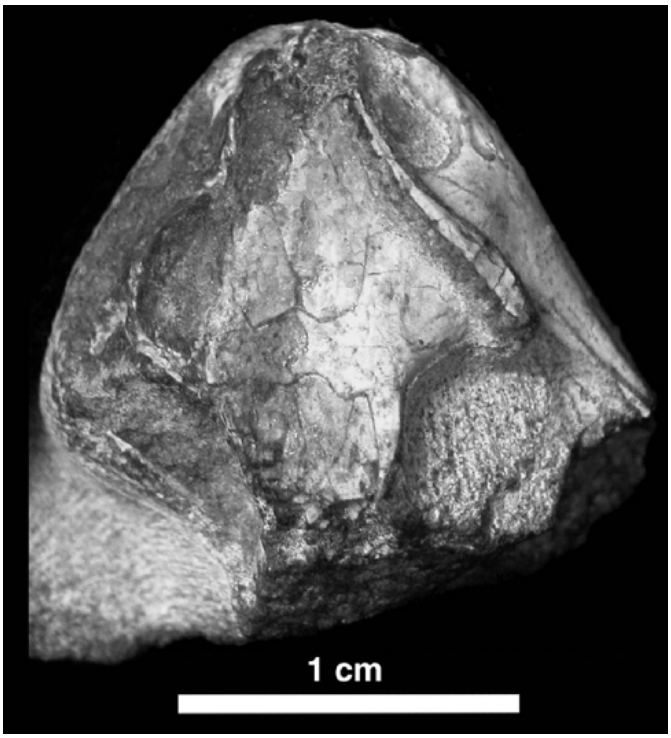

Figure 6. *Owenetta kitchingorum* (Reptilia, Procolophonoidea), BP/1/5882, referred specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in dorsal view.

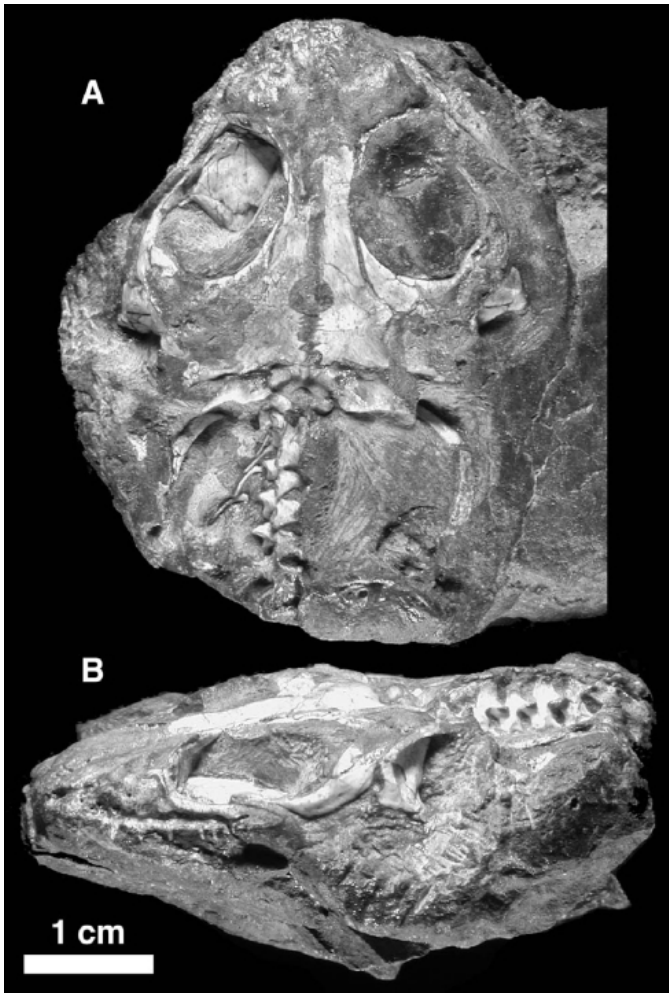

Figure 7. *Saurodectes rogersorum* (Reptilia, Procolophonoidea), BP/1/6025, holotype specimen from Barendskraal (Middelburg District; *Lystrosaurus* Assemblage Zone) in (**A**) dorsal and (**B**) left lateral views.

from the *Lystrosaurus* Assemblage Zone at Thaba N'chu, Free State Province. The holotype of this taxon was recently reinterpreted as a specimen of *Owenetta*, although a specific determination was not possible because of poor preservation (Evans 2001). If the horizon is correct, attribution to *O. kitchingorum* seems likely. For the moment, BP/1/5882 remains the only undoubted specimen of *O. kitchingorum* collected outside of the Bethulie District.

Saurodectes rogersorum Modesto *et al.,* 2003, Fig. 7

Material. BP/1/6025 (holotype), a partial skull with associated postcranial elements, from the Palingkloof Member on Maanhaar (Fig. 1). BP/1/6044, 6045 and 6047 are small, unprepared procolophonoids represented by partially articulated cranial and postcranial remains that were collected from the same excavation point as BP/1/6025. They may be referrable to *S. rogersorum* but require additional preparation.

Remarks. Saurodectes rogersorum is a procolophonoid referrable to the Owenettidae, and is most closely related to *Owenetta rubidgei* and *Barasaurus besairei* from the Upper Permian of South Africa and Madagascar, respectively (Modesto *et al.* 2003). This suggests that the genus *Owenetta,* currently with two nominal species, may be polyphyletic.

DISCUSSION

Intensive collecting over two field seasons on Barendskraal has resulted in the recovery of nine tetrapod species from this locality. With few exceptions, this count far exceeds the norm of two to three species found at most other *Lystrosaurus* Assemblage Zone localities, where *Lystrosaurus* is by far the dominant taxon (Kitching 1968, 1977). In addition, the four tetrapod genera that cross the Permo-Triassic boundary in the Karoo (Rubidge *et al.* 1995), namely *Lystrosaurus, Moschorhinus, Tetracynodon* and *Owenetta,* are present at Barendskraal. Note that for the present discussion we do not distinguish among the various species of *Lystrosaurus* because of taxonomic uncertainty. According to Kitching (1977), only the famous collecting grounds of Harrismith Commonage in the northeastern Free State have yielded a more diverse fauna, with at least 13 species. However, that count includes three cynodonts (*Galesaurus planiceps, Platycraniellus elegans, Thrinaxodon liorhinus*) and two temnospondyls (*Lydekkerina huxleyi, Broomulus dutoiti*; see Shishkin *et al.* 1996), two groups not currently recorded from Barendskraal. Given the relative abundance of cynodonts (particularly *Thrinaxodon*) and temnospondyls (particularly *Lydekkerina*) at Harrismith and other *Lystrosaurus* biozone localities, their absence at Barendskraal may indicate that these animals were not living in the depositional area, or that there was a bias against their preservation.

It is noteworthy that Harrismith Commonage has been intensively prospected by both local and foreign researchers for over 75 years. In contrast, most other *Lystrosaurus* biozone localities, including Barendskraal, have, to our knowledge, received relatively little attention. This suggests that the high species counts at Harrismith and Barendskraal may represent a collection bias. Although most of the Barendskraal fauna belongs to established taxa, it contains two new procolophonoid species, *Sauropareion anoplus* and *Saurodectes rogersorum,* that shed light on the diversity and survivorship of procolophonoid reptiles in post-extinction, earliest Triassic time (Modesto *et al.* 2001, 2003). Clearly, there remains the potential for future discovery of new taxa from Barendskraal and other relatively unexplored localities in the *Lystrosaurus* biozone.

Our work at Barendskraal also sheds light on the stratigraphic distribution of some taxa within the *Lystrosaurus* Assemblage Zone. First, our documentation of *Lystrosaurus* in the Palingkloof Member (Fig. 1) corroborates the findings of Smith (1995) and Smith & Ward (2001), who first confirmed the occurrence of *Lystrosaurus* below the Katberg Formation (*cf.* Hotton 1967; Keyser & Smith 1979; Groenewald & Kitching 1995). Second, previous authors have suggested that *Prolacerta broomi* was present only in the upper Katberg Formation or the middle-upper part of the *Lystrosaurus* biozone (Kitching 1977; Groenewald & Kitching 1995). However, *Prolacerta* has been documented by Kitching (1977) on the farms Tweefontein and Fairydale in the Bethulie District, Free State province, where it co-occurs with *Owenetta* (Reisz & Scott 2002; this paper). At these localities, the strata exposed is the Paling-

kloof Member and lower part of the Katberg Formation, hence the lower part of the *Lystrosaurus* Assemblage Zone (Ward *et al.* 2000, and field observations by the authors). Thus, the occurrence of *Prolacerta* at these localities, combined with our field observations at Tweefontein and Fairydale, suggests a much earlier appearance in the *Lystrosaurus* biozone for this reptile. The presence of *Prolacerta* in the Palingkloof Member at Barendskraal (Fig. 1) confirms that the stratigraphic range of *Prolacerta* extends from the Palingkloof Member to the middle or upper horizons of the Katberg Formation. Third, the stratigraphic occurrence of the therocephalian *Ericiolacerta parva* in the *Lystrosaurus* Assemblage Zone was tentatively identified as being within the Katberg Formation (Groenewald & Kitching 1995). The Barendskraal specimen of *E. parva* (Fig. 1) indicates a more extensive stratigraphic range for this therocephalian, one approximately equal to that now identified for *Prolacerta,* which builds on the former, single occurrence at the type locality of Harrismith Commonage.

It is interesting to note that the Palingkloof exposures at Barendskraal have yielded three genera of basal procolophonoids, but no remains of the well-known and otherwise relatively abundant procolophonid *Procolophon.* The lowest stratigraphic occurrence of *Procolophon* is at present speculative because of insufficient data, although it has apparently been documented from localities (e.g. Fairydale, Bethulie District) in which strata of both the Palingkloof Member and Katberg Formation are exposed (Kitching 1977; Smith & Ward 2001). Nevertheless, fossils of *Procolophon* appear to be rare in the lower part of the *Lystrosaurus* Assemblage Zone, but increase in abundance toward the upper reaches of the biozone (Keyser & Smith 1979; Neveling 2002). On the other hand, there is no evidence for the occurrence of the basal procolophonoid *Owenetta* in the upper part of the *Lystrosaurus* biozone (contra Rubidge *et al.* 1995 and Smith 1995), whereas its presence in the lower part of the biozone, as postulated by Kitching (1977), is now firmly established by its occurrence in the Palingkloof Member at Barendskraal (Fig. 1).

Based on available evidence, including our data from Barendskraal, it appears that *Owenetta* and other basal procolophonoids are restricted to the Palingkloof Member, and that *Procolophon* is the only procolophonoid that is present in the Katberg Formation. It is tempting to conclude that *Procolophon* succeeded *Owenetta, Sauropareion* and *Saurodectes* during *Lystrosaurus* Assemblage Zone 'time'. However, the possible occurrence of *Procolophon* in the Palingkloof Member (Smith & Ward 2001), and its co-occurrence with *Owenetta* on the farm Fairydale in Bethulie (Kitching 1977; this paper), suggests that *Procolophon* may have been partially contemporaneous with its more basal procolophonoid relatives. As the transition from the Palingkloof Member to the Katberg Formation marks a major, basin-wide change in fluvial conditions (Ward *et al.* 2000), the presence of *Procolophon* but not its more basal procolophonoid relatives in the Katberg Formation may be interpreted in two ways. The first is a result of different selective pressures imposed by the two fluvial regimes, allowing some procolophonids such as *Procolophon* to survive, whereas more basal procolophonoids perished. Alternatively, the preservation of some procolophonoid reptiles in the *Lystrosaurus* Assemblage Zone is facies-specific. At present, there is insufficient evidence for either hypothesis, and more intensive collecting efforts in the *Lystrosaurus* biozone are needed to investigate both this issue and the related problem of terrestrial vertebrate extinctions around the Permo-Triassic boundary.

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REFERENCES

ANDERSON, J.M. & CRUICKSHANK, A.R.I. 1978. The biostratigraphy of the Permian and the Triassic. Part 5. A review of the classification and distribution of Permo-Triassic tetrapods. *Palaeontologia africana* **21**, 15–44.

BROOM, R. 1903. On a new reptile (*Proterosuchus fergusi*) from the Karroo Beds of Tarkastad, South Africa. *Annals of the South African Museum* **4**, 159–164.

BROOM, R. 1920. On some new therocephalian reptiles from the Karroo beds of South Africa. *Proceedings of the Zoological Society of London* **1920**, 343–355.

BROOM, R. 1946. A new primitive proterosuchid reptile. *Annals of the Transvaal Museum* **20**, 343–346.

BROOM, R. & ROBINSON, J.T. 1948. On some new types of small carnivorous mammal-like reptiles. *Royal Society of South Africa Robert Broom Commemorative Volume,* 29–44.

CARROLL, R.L. 1982. A short limbed lizard from the *Lystrosaurus* zone (Lower Triassic) of South Africa. *Journal of Paleontology* **56**, 183–190.

COLBERT, E.H. & KITCHING, J.W. 1981. Scaloposaurian reptiles from the Triassic of Antarctica. *American Museum Novitates* **2709**, 1–22.

CROMPTON, A.W. 1955. A revision of the Scaloposauridae with special reference to kinetism in this family. *Navorsinge van die Nasionale Museum* **1**, 149–183.

DAMIANI, R.J., MODESTO, S.P., NEVELING, J. & YATES, A.M. 2002. A rich amniote fauna from the Early Triassic *Lystrosaurus* Assemblage Zone of South Africa. *Palaeontological Society of Southern Africa 2002, Bloemfontein, Abstracts,* 13–14.

ERWIN, D.H., BOWRING, S.A. & YUGAN, J. 2002. End-Permian mass extinctions: a review. *Geological Society of America, Special Papers* **356**, 363–383.

EVANS, S.E. 2001. The Early Triassic 'lizard' *Colubrifer campi*: a reassessment. *Palaeontology* **44**, 1033–1041.

FOURIE, H. 2001. *Morphology and function of the postcrania of selected genera of Therocephalia (Amniota: Therapsida).* Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.

GOW, C. E. 1975. The morphology and relationships of *Youngina capensis* Broom and *Prolacerta broomi* Parrington. *Palaeontologia africana* **18**, 89–131.

GROENEWALD, G.H. 1996. *Stratigraphy of the Tarkastad Subgroup, Karoo Supergroup, South Africa.* Unpublished PhD thesis, University of Port Elizabeth, Port Elizabeth.

GROENEWALD, G.H. & KITCHING, J.W. 1995. Biostratigraphy of the *Lystrosaurus* Assemblage Zone. **In**: Rubidge, B.S., Ed, *Biostratigraphy of the Beaufort Group (Karoo Supergroup),* 35–39. SACS Biostratigraphic Series No. 1. Pretoria, Council for Geoscience.

HANCOX, P.J. 2000. The continental Triassic of South Africa. *Zentralblatt für Geologie und Paläontologie Teil I* **1998**, 1285–1324.

HANCOX, P.J., SHISHKIN, M.A., RUBIDGE, B.S. & KITCHING, J.W. 1995. A threefold subdivision of the *Cynognathus* Assemblage Zone (Beaufort Group, South Africa) and its palaeogeographical implications. *South African Journal of Science* **91**, 143–144.

HILLER, N. & STAVRAKIS, N. 1984. Permo-Triassic fluvial systems in the southeastern Karoo Basin, South Africa. *Palaeogeography, Palaeoclimatology, Palaeoecology* **34**, 1–21.

HOTTON, N. 1967. Stratigraphy and sedimentation in the Beaufort Series (Permian–Triassic), South Africa. *University of Kansas Department of Geology Special Publication* **2**, 390–428.
KEYSER, A.W. & SMITH, R.M.H. 1979. Vertebrate biozonation of the Beaufort Group with special reference to the western Karoo Basin. *Annals of the Geological Survey of South Africa* **12**, 1–35.
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. 1977. The distribution of the Karroo vertebrate fauna. *Bernard Price Institute for Palaeontological Research, Memoir* **1**, 1–131.
LUCAS, S.G. 1998. Global Triassic tetrapod biostratigraphy and biochronology. *Palaeogeography, Palaeoclimatology, Palaeoecology* **143**, 347–384.
McKEE, E.D., CROSBY, E.J. & BERRYHILL, H.L. 1967. Flood deposits, Bijou Creek, Colorado. *Journal of Sedimentary Petrology* **37**, 829–851.
MENDREZ-CARROLL, C.H. 1979. Nouvelle étude du crâne du type de *Scaloposaurus constrictus* Owen, 1876, spécimen jeune, Therocephalia, Scaloposauria, Scaloposauridae, de la zone à *Cistecephalus* (Permien supérieur) d'Afrique australe. *Bulletin du Museum national d'Histoire naturelle, Paris* (4e sér.) **1**, 155–201.
MIALL, A.D. 1996. *The Geology of Fluvial Deposits: Sedimentary Facies, Basin Analysis and Petroleum Geology.* Berlin, Springer-Verlag.
MIALL, A.D. 2000. *Principles of Sedimentary Basin Analysis* (3rd edn). Berlin, Springer-Verlag.
MODESTO, S., SUES, H-D. & DAMIANI, R. 2001. A new Triassic procolophonoid reptile and its implications for procolophonoid survivorship during the Permo-Triassic extinction event. *Proceedings of the Royal Society of London B* **268**, 2047–2052.
MODESTO, S., DAMIANI, R.J., NEVELING, J. & YATES, A.M. 2003. A new Triassic owenettid parareptile and the mother of mass extinctions. *Journal of Vertebrate Paleontology* **23**, 715–719.
NEVELING, J. 2002. *Biostratigraphic and sedimentological investigation of the contact between the* Lystrosaurus *and* Cynognathus *assemblage zones (Beaufort Group: Karoo Supergroup).* Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.
NORELL, M.A. 1992. Taxic origin and temporal diversity: the effect of phylogeny. **In:** Novacek, M.J. & Wheeler, Q.D., Eds, *Extinction and Phylogeny,* 89–118. New York, Columbia University Press.
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.
PARRINGTON, F.R. 1935. On *Prolacerta broomi,* gen. et. sp. n., and the origin of lizards. *Annals and Magazine of Natural History* (Ser. 10) **16**, 197–205.
REISZ, R.R. & SCOTT, D. 2002. *Owenetta kitchingorum* sp. nov., a small parareptile (Procolophonia: Owenettidae) from the Lower Triassic of South Africa. *Journal of Vertebrate Paleontology* **22**, 244–256.
RENAUT, A. 2000. *A re-evaluation of the cranial morphology and taxonomy of the Triassic dicynodont genus* Kannemeyeria. Unpublished PhD thesis, University of the Witwatersrand, Johannesburg.
RUBIDGE, B.S., JOHNSON, M.R., KITCHING, J.W., SMITH, R.M.H., KEYSER, A.W. & GROENEWALD, G.H. 1995. An introduction to the biozonation of the Beaufort Group. **In**: Rubidge, B.S., Ed, *Biostratigraphy of the Beaufort Group (Karoo Supergroup),* 1–2. SACS Biostratigraphic Series No. 1. Pretoria, Council for Geoscience.
SHISHKIN, M.A., RUBIDGE, B.S. & KITCHING, J.W. 1996. A new lydekkerinid (Amphibia, Temnospondyli) from the lower Triassic of South Africa: implications for evolution of the early capitosauroid cranial pattern. *Philosophical Transactions of the Royal Society of London B* **351**, 1635–1659.
SIGOGNEAU, D. 1963. Note sur une nouvelle espece de Scaloposauridae. *Palaeontologia africana* **8**, 13–37.
SMITH, R.M.H. 1995. Changing fluvial environments across the Permian–Triassic boundary in the Karoo Basin, South Africa and possible causes of tetrapod extinctions. *Palaeogeography, Palaeoclimatology, Palaeoecology* **117**, 81–104.
SMITH, R.M.H. & WARD, P.D. 2001. Pattern of vertebrate extinctions across an event bed at the Permian–Triassic boundary in the Karoo Basin of South Africa. *Geology* **29**, 1147–1150.
SOUTH AFRICAN COMMITTEE FOR STRATIGRAPHY (SACS) 1980. Stratigraphy of South Africa. Part 1 (Comp. by L.E. Kent). Lithostratigraphy of the Republic of South Africa, South West Africa/Namibia, and the Republics of Bophuthatswana, Transkei and Venda. *Handbook of the Geological Survey of South Africa* **8**.
STEAR, W.M. 1985. Comparison of the bedform distribution and dynamics of modern and ancient sandy ephemeral flood deposits in the southwestern Karoo region, South Africa. *Sedimentary Geology* **45**, 209–230.
STEINER, M.B., ESHET, Y., RAMPINO, M.R. & SCHWINDT, D.M. 2003. Fungal abundance spike and the Permian–Triassic boundary in the Karoo Supergroup (South Africa). *Palaeogeography, Palaeoclimatology, Palaeoecology* **194**, 405–414.
WARD, P.D., MONTGOMERY, D.R. & SMITH, R.M.H. 2000. Altered river morphology in South Africa related to the Permian–Triassic extinction. *Science* **289**, 1740–1743.
WATSON, D.M.S. 1931. On the skeleton of a bauriamorph reptile. *Proceedings of the Zoological Society of London* **1931**, 1163–1205.
WELMAN, J. 1998. The taxonomy of the South African proterosuchids (Reptilia, Archosauromorpha). *Journal of Vertebrate Paleontology* **18**, 340–347.
WELMAN, J. & FLEMMING, A. 1993. Statistical analysis of the skulls of Triassic proterosuchids (Reptilia, Archosauromorpha) from South Africa. *Palaeontologia africana* **30**, 113–123.
WELMAN, J., GROENEWALD, G.H. & KITCHING, J.W. 1991. Confirmation of the occurrence of *Cynognathus* Zone (*Kannemeyeria-Diademodon* Assemblage-zone) deposits (uppermost Beaufort Group) in the northeastern Orange Free State, South Africa. *South African Journal of Geology* **94**, 245–248.