



## SHORT COMMUNICATION

### EVIDENCE OF A SECOND, LARGE ARCHOSAURIFORM REPTILE IN THE LOWER TRIASSIC KATBERG FORMATION OF SOUTH AFRICA

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Crown-group diapsid reptiles first appeared at the end of the Paleozoic Era (Late Permian, Lopingian), but became conspicuous components of vertebrate faunas only at the dawn of the Mesozoic Era (Early Triassic: Reisz et al., 2000). The diapsid crown is divided into two sister groups: Lepidosauromorpha, consisting of squamates, tuataras, and their fossil relatives, and Archosauromorpha, which consists of crocodylians, birds, and their fossil relatives (Gauthier, 1994). Archosauromorph diapsids exhibited greater taxonomic, morphological, and ecological diversification than lepidosauromorphs during the Mesozoic.

The richest continental vertebrate faunas that include early archosauromorphs comprise the Lower Triassic *Lystrosaurus* Assemblage Zone (LAZ) of the Beaufort Group, South Africa. The LAZ includes two species, *Prolacerta broomi* and *Proterosuchus fergusi*, that have been integral to both anatomical (Clark et al., 1993) and phylogenetic (Dilkes, 1998; Modesto and Sues, 2004) studies of basal Archosauromorpha. Although the seminal biostratigraphic overview of the LAZ fauna by Groenewald and Kitching (1995) posited disjunct stratigraphic ranges for *Prolacerta* and *Proterosuchus*, recent collecting efforts that have concentrated on the lower part of the zone have established that these archosauromorphs overlap in the Palingkloof Member of the Balfour Formation and in lowermost strata of the overlying Katberg Formation (Damiani et al., 2004; Ward et al., 2005; Smith and Botha, 2005; Botha and Smith, 2006). There are no definitive records of *Prolacerta* and *Proterosuchus* from upper Katberg Formation localities of which we are aware.

Recent field work by the authors has led to the discovery of new LAZ localities, which have produced vertebrate fossils with interesting biostratigraphic implications. Initial prospecting of the farm Vangfontein in Middelburg District, Eastern Cape Province, produced the youngest specimen of the procolophonoid reptile *Sauropareion anoplus*, providing support for the hypothesis that the lower Katberg Formation preserves a relatively diverse assemblage of these small parareptiles (Botha et al., 2007). A visit to Vangfontein in 2006 yielded the partial maxilla of a large reptile with a distinctive morphology, one that precludes referral to *Proterosuchus*, *Prolacerta*, or to any other reptile known from the Beaufort Group. This maxilla, despite its fragmentary preservation, exhibits a posterodorsal embayment. Thus, this specimen displays evidence of an antorbital fenestra, which is a synapomorphy of Archosauriformes (Benton and Clark, 1988; Parrish, 1992; = Archosauria of Benton, 1985). We describe the Vangfontein maxilla in this paper, and consider its

biostratigraphic significance for the Early Triassic tetrapod fauna of South Africa.

**Institutional Abbreviations**—NM, National Museum, Bloemfontein; SAM, Iziko South African Museum, Cape Town.

#### SYSTEMATIC PALEONTOLOGY

DIAPSIDA Osborn, 1903

ARCHOSAURIFORMES von Huene, 1946  
ARCHOSAURIFORMES Gauthier et al., 1988

Gen. et sp. indet.

**Material**—NMQR 3570, a partial left maxilla, preserved in sandstone conglomerate.

**Locality and Horizon**—A locality of the farm Vangfontein, Middelburg District, Eastern Cape Province, Republic of South Africa. The fossiliferous levels exposed on Vangfontein are assignable to the lower Katberg Formation (Botha et al., 2007), Beaufort Group, Lower Triassic. Thus, NMQR 3570 is positioned biostratigraphically in the *Lystrosaurus* Assemblage Zone (Groenewald and Kitching, 1995), and can be assigned to the Lootsbergian land-vertebrate faunachron of Lucas (1998).

**Description**—NMQR 3570 is the anterior portion of a left maxilla that consists of the dorsal process and an alveolar portion preserving at least five tooth positions (Fig. 1). As measured from the apex of the dorsal process to the ventral margin, the bone is 30 mm tall, and the preserved length is approximately 38 mm. There is a relatively short, triangular anterior projection of the alveolar margin with a heavily weathered bone surface. The remains of a matrix-filled cavity at the base of this process suggests that there was an alveolus here, for what would be the first tooth position, but there is no evidence of a root. The preserved ventral margin of the alveolar portion, extending from the presumed second to fourth tooth positions, is straight.

The anterodorsal margin, which would have contacted the posterodorsal process of the premaxilla, extends posteriorly at an angle of about 55°. About a third of the way from the anterior tip of the bone, there is a slight step in the anterodorsal margin, and another step about one-quarter of the length of the margin from the apex of the bone, serving to form a shallow, trapezoidal embayment in the anterodorsal margin. The apex of the dorsal process is broadly rounded and tongue-like in lateral aspect. There is no evidence of a facet or sutural surface for the lacrimal. The dorsal process comprises approximately 55% the height of the maxilla. Posterodorsally the maxilla exhibits a deep triangular embayment, of which the anterior border is formed by the posterior margin of the dorsal process and the ventral border is formed by the dorsal margin of the alveolar portion. The poste-

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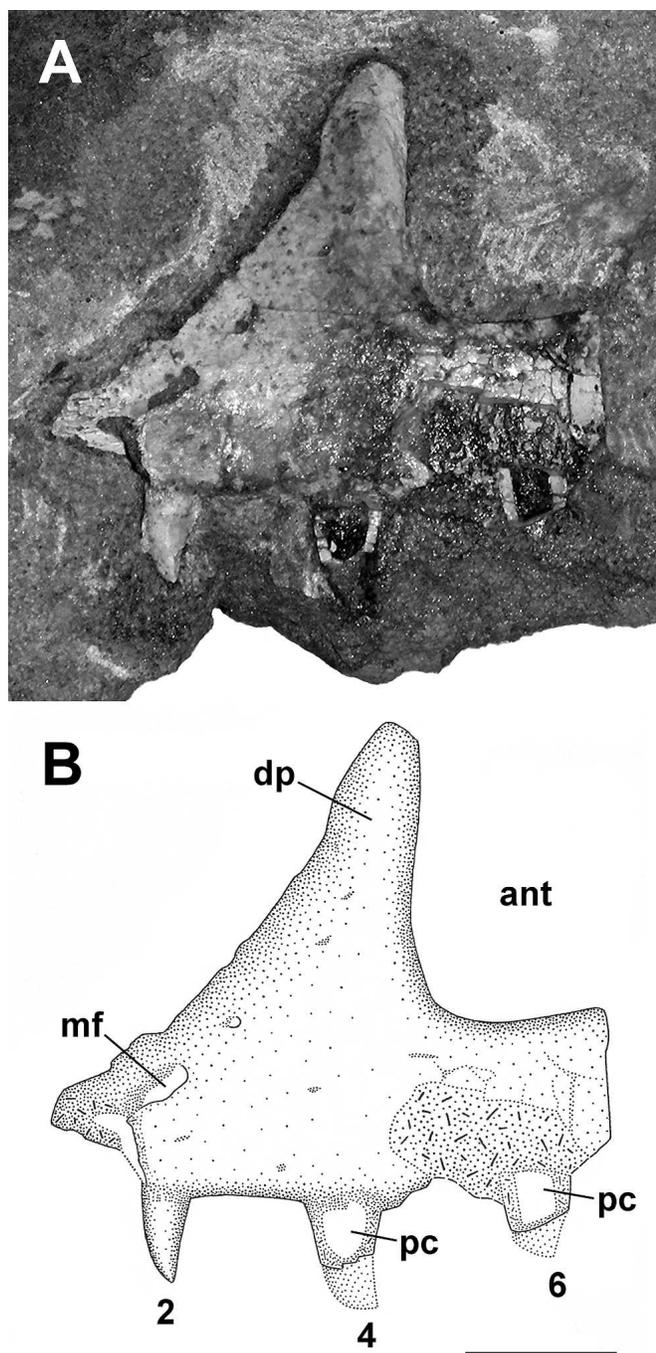


FIGURE 1. NMQR 3570, Archosauriformes indet. **A**, photograph and **B**, camera-lucida drawing of partial left maxilla in lateral view. **Abbreviations:** ant, antorbital fenestra; dp, dorsal process; mf, maxillary foramen; pc, pulp cavity. Numbers refer to tooth positions. Scale bar equals 10 mm.

rior margin of the dorsal process is straight for most of its length, except where it curves abruptly anteriorly at the apex and curves gently ventrally where it merges with the alveolar portion. The lateral surface of the dorsal process descends gently to a sharp edge that would contact the premaxilla anteriorly, and does the same posterodorsally. Half way down the posterior margin, however, the edge becomes rounded, and this rounded margin continues ventrally and then posteriorly along the dorsal margin of the alveolar portion of the maxilla, to form the anteroventral

corner of an antorbital fenestra. There is no evidence that the maxilla contributed to an antorbital fossa.

The lateral surface is smoothly surfaced for the most part. Small nutritive foramina pierce the lateral surface sparsely, and anteriorly there is a relatively large opening positioned directly dorsal to the second tooth, about as far from the ventral margin as the second tooth is tall. The opening is shallow and broad, with its long axis aligned with the anterodorsal margin. This conspicuous opening appears in the same relative position as the maxillary foramen (sensu Modesto and Sues, 2004:338) of *Prolacerta*, and nearly identical openings in the maxillae of taxa such as *Mesosuchus* (Dilkes, 1998:fig. 5) and *Proterosuchus* (Welman, 1998:fig. 8). In NMQR 3570, however, the opening is formed entirely in the maxilla, and does not border the margin that contacted the premaxilla, as it does in the aforementioned archosauriforms. In one specimen of *Prolacerta*, the left maxillary foramen (Modesto and Sues, 2004:fig. 3A) of BP/1/471 appears to display a morphology similar to that we describe in NMQR 3570. BP/1/471, however, was prepared in the mid-Twentieth Century by grinding, which resulted in the obliteration of the surface sculpturing and heavy polishing of the anterior end of the left maxilla, such that it appears that this bone formed the entire border of the maxillary foramen (SPM, pers. obs., 2001). The right maxilla of BP/1/471 exhibits a well-preserved maxillary foramen, in which the maxilla does not form the entire margin of the maxillary foramen (Modesto and Sues, 2004:fig. 3B), and this is the morphology seen on all other well prepared specimens of *Prolacerta*.

A complete tooth occupies the second tooth position. It is almost 7 mm tall, moderately recurved, and slightly compressed labiolingually. The mesial surface of the tooth is smooth, whereas the distal or trailing edge forms a cutting edge. No serrations are visible on the cutting edge under light microscopy. The tooth is anchored to the maxilla by bone of attachment. The presumed third and fifth tooth positions are empty, whereas the fourth and sixth positions are occupied by fragmentary tooth bases. The apex and the labial (or lateral) half of the fourth tooth have been lost to weathering, but the lingual face of the apex is preserved as impression in the matrix, showing that this tooth is a slightly larger version of the presumed second tooth. The pulp cavity is relatively large and the walls of the tooth base are approximately 0.75 mm in thickness. The mesodistal diameter of the base of the sixth tooth is equal to that of the fourth tooth, suggesting that these teeth are subequal in size. The depth of the alveoli cannot be discerned, despite abrasion to the alveolar portion of the maxilla just lateral to the fifth and sixth alveoli. Tooth implantation is either subthecodont or ankylothecodont (sensu Chatterjee, 1974).

## DISCUSSION

NMQR 3570 can be assigned to Archosauriformes on the basis of the presence of an antorbital fenestra. The presence of this fenestra and the large size of the bone precludes assignment to *Prolacerta*. The straight, vertical posterior margin of the dorsal process of the maxilla distinguishes NMQR 3570 from *Proterosuchus*, the only archosauriform known from the LAZ (Cruikshank, 1972; Welman, 1998). NMQR 3570 can also be distinguished from the archosauriforms *Erythrosuchus* (Gower, 2003) and *Euparkeria* (Ewer, 1965) from the overlying *Cynognathus* Assemblage Zone, because the maxillae in both those taxa exhibit a posterodorsally-curving dorsal process and an antorbital fossa. Among other Early Triassic archosauriforms, only *Osmolskina czatkoviensis* from Europe (Borsuk-Białynicka and Evans, 2003) exhibits a vertically-aligned dorsal process of the maxilla. This process, however, is relatively narrow throughout its length, displays a slight but definite posterodorsal curvature, and exhibits a posterior lateral shelf, which indicates the presence of an antorbital fossa.

Whereas the presence of an antorbital fenestra supports an archosauriform identity for NMQR 3570, determination of a more precise position within Archosauriformes is complicated by the limited information afforded by its fragmentary preservation. The absence of an antorbital fossa suggests that NMQR 3570 represents a basal stem archosauriform; the presence of an antorbital fossa is a synapomorphy of the unnamed archosauriform clade that includes erythrosuchids, *Euparkeria*, and archosaurs (clade 'A' in fig. 11 of Gower and Sennikov, 1997). With the elimination of a higher placement within Archosauriformes, there are four possibilities for the phylogenetic position of NMQR 3570: (1) it is a proterosuchid; (2) it is the sister taxon of Proterosuchidae; (3) it is the sister taxon of the unnamed archosauriform clade that excludes Proterosuchidae; or (4) it is the sister taxon of a clade comprising all other archosauriforms.

The available dental morphology suggests that NMQR 3570 may be a close relative of *Proterosuchus*. Most early archosauriforms, like the archosauromorph *Prolacerta* (Modesto and Sues, 2004), have cutting edges on both mesial and distal margins of the marginal teeth. The cutting edges of most archosauriforms, including *Erythrosuchus* (Gower, 2003) and *Euparkeria* (Senter, 2003), exhibit fine serrations on both mesial and distal edges. The Middle Triassic proterosuchid *Sarmatosuchus* also exhibits serrated mesial and distal cutting edges (Gower and Sennikov, 1997). The maxillary teeth of *Proterosuchus*, however, possess only distal cutting edges with fine serrations, and the mesial margins of the marginal teeth are rounded (pers. obs. of SAM-PK-K140, NMQR 1484, and NMQR 880). NMQR 3570 shares with *Proterosuchus* the absence of cutting edges on the mesial (leading) margins of the marginal teeth. Although the one complete tooth in NMQR 3570 appears to lack serrations on its (distal) cutting edge, it is possible that serrations may have been present in life but were removed during normal feeding activities or by post mortem weathering. NMQR 3570 may represent a proterosuchid with a slightly modified antorbital region, one in which the maxilla and the lacrimal might have been separated along the dorsal margin of the antorbital fenestra, as suggested by the straight posterior margin of the dorsal process of the maxilla and the absence of a facet for the reception of the lacrimal.

Our description of NMQR 3570 adds a noteworthy component to the fauna of the Triassic of the Karoo Basin. This is largely because of its biostratigraphic position in the LAZ relative to other archosauromorph reptiles. Groenewald and Kitching (1995) included three archosauromorph genera in their biostratigraphy of the LAZ. One of these, *Noteosuchus*, is represented solely by its holotype, which is from an unreliable locality (Kitching, 1977). The other two genera are *Prolacerta* and *Proterosuchus*. They are represented by numerous enough specimens to allow us to establish plausible stratigraphic ranges for these two archosauromorph genera. As mentioned previously, both are present in the upper part of the Palingkloof Member and in the lower part of the Katberg Formation (Botha and Smith, 2006). Intense collecting by Roger M. H. Smith and colleagues (Ward et al., 2000, 2005; Smith and Botha, 2005; Botha and Smith, 2006) at Permian-Triassic-boundary localities indicates that neither *Prolacerta* nor *Proterosuchus* appear below that boundary. Lack of attention to LAZ localities higher in the Katberg Formation is a challenge, and we are uncertain as to the last appearance datum (LAD) for both taxa. We conservatively place LADs for *Prolacerta* and *Proterosuchus* in the lower Katberg Formation.

The productive levels at Vangfontein consist of lower Katberg Formation strata that include, near the top of the exposures, the informal 'Swartberg Member' (Neveling, 2004), a major sandstone bed that is present in the Katberg Formation throughout the southern part of the Karoo Basin. NMQR 3570 was found *ex situ* on a slope just below the occurrence of abundant *in situ* nodules containing *Procolophon* and above the occurrence of

*Sauropareion*. This positions the Vangfontein archosauriform in the approximate middle of the lower part of the Katberg Formation, and above the possible LAD of *Proterosuchus* (Fig. 2). NMQR 3570 thereby reduces the large stratigraphic gap for Archosauriformes in the Beaufort Group, between the last appearance of *Proterosuchus* in the lower Katberg Formation and the undescribed archosauriform from the lower third of the *Cynognathus* Assemblage Zone (Neveling et al., 2006).

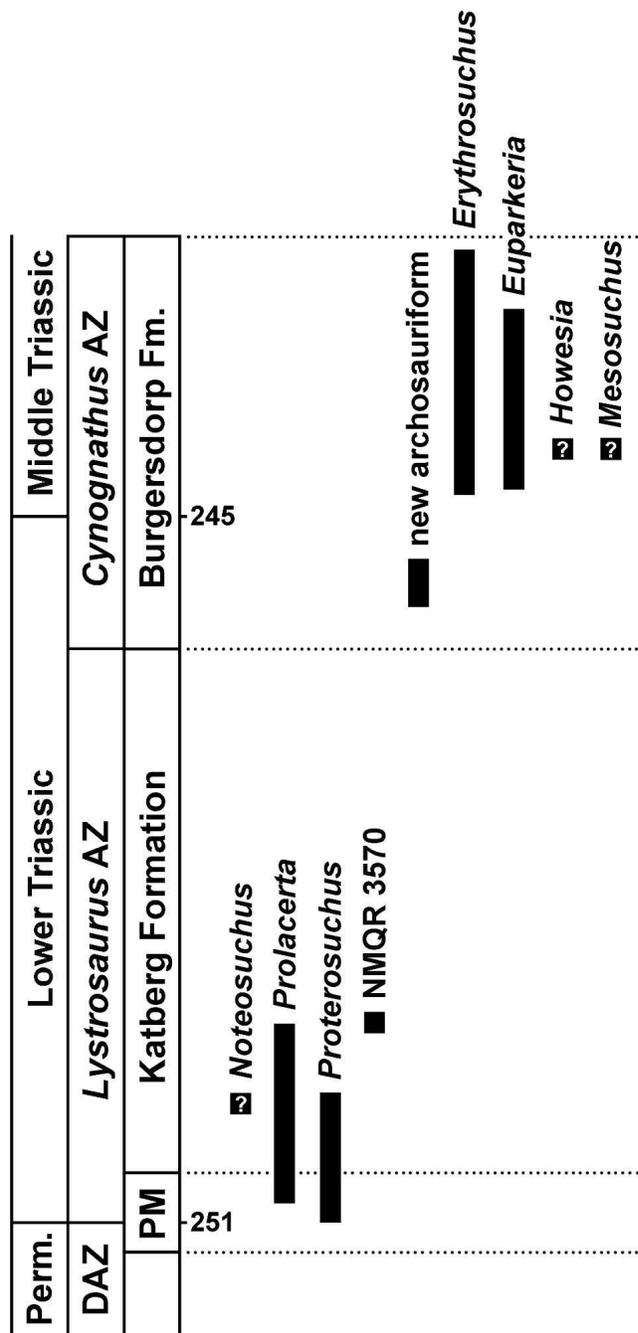


FIGURE 2. Stratigraphic ranges of archosauromorph taxa in the *Lystrosaurus* and *Cynognathus* assemblage zones of South Africa. Ranges enclosing a question mark indicate poor stratigraphic control for the taxon. The 'new archosauriform' is an undescribed form ('archosauriform gen. nov.') reported in Neveling et al. (2006:fig. 3). Ranges from Kitching (1995), Botha and Smith (2006), Neveling et al. (2006), and Modesto and Botha-Brink (unpubl.). Numbers are dates in millions of years. **Abbreviations:** AZ, Assemblage Zone; DAZ, *Dicynodon* Assemblage Zone; Fm., Formation; Perm., Permian; PM, Palingkloof Member.

The ecological niche of the Vangfontein archosauriform in the LAZ is difficult to reconstruct with the limited information afforded by its fragmentary preservation. *Proterosuchus*, as a large (1.5 m long) carnivorous reptile, shared the role of top LAZ predator with the synapsid genus *Moschorhinus* during the time recorded by the rocks of the upper Palingkloof Member. In the time recorded by the lowermost rocks of the Katberg Formation, it appears to have been the only large predator in the LAZ fauna, with *Moschorhinus* disappearing from the record before the onset of that formation. Although there is no consensus on the paleoecology of *Proterosuchus*—Broili and Schröder (1934) considered *Proterosuchus* a crocodylian analog, whereas Cruickshank (1972) regarded it as facultatively aquatic—the numerous specimens of *Proterosuchus* (e.g., Welman [1998:341] lists twelve) contrasts starkly with NMQR 3570, a single bone fragment. Given these numbers, it seems doubtful that the Vangfontein archosauriform inherited the mantle of top LAZ predator from *Proterosuchus*, yet there is no record of any other large carnivorous tetrapod in the upper three-quarters of the Katberg Formation.

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