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THE OLDEST PROCOLOPHONOID (AMNIOTA: PARAREPTILIA) – NEW DISCOVERY FROM THE LOWER BEAUFORT OF SOUTH AFRICA.

by

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ABSTRACT

Until now the earliest recognised procolophonoid (*sensu* Laurin & Reisz 1995) reptile has been *Owenetta,* which ranges from the *Cistecephalus* assemblage zone (Upper Permian) to the *Lystrosaurus* assemblage zone (Lower Triassic) of the Beaufort Group of South Africa. This paper records the presence of a new even older form from low in the underlying *Tapinocephalus* assemblage zone.

KEYWORDS: Anapsida, Procolophonoidea, Procolophonidae, parareptiles.

INTRODUCTION

The Procolophonoidea are a group of anapsid reptiles which have attracted attention recently as the group most closely similar to turtles. Reisz and Laurin (1991) proposed the procolophonoid *Owenetta* as the sister taxon of turtles, while Lee (1993) has made the same claim for pareiasaurs. The oldest fossils of turtles, of which three genera have been described, occur in Upper Triassic rocks from Germany and Argentina (Rougier *et al* 1995).

The family Procolophonidae Lydekker 1880 (*sensu* Laurin & Reisz 1995) includes the genera *Anomoiodon*, *Burtensia*, *Candelaria*, *Contritosaurus*, *Eumetabolodon*, *Hypsognathus*, *Kapes*, *Koiloskiosaurus*, *Leptopleuron*, *Macrophon*, *Microthelodon*, *Myocephalus*, *Neoprocolophon*, *Orenburgia*, *Paoteodon*, *Procolophon*, and *Thelegnathus* (Laurin & Reisz 1995). As Lee (1995) has pointed out, Reisz and Laurin (1991) previously extended the definition of the family to include *Owenetta*. The family has a cosmopolitan distribution – including Europe, Asia, and Africa. With the exception of *Owenetta*, all of the procolophonoid genera are Triassic in age. In South Africa *Owenetta* occurs in the Triassic *Lystrosaurus* Assemblage Zone, but also occurs in the Upper Permian *Cistecephalus* and *Dicynodon* assemblage zones of the Beaufort Group (Kitching 1995, Kitching & Groenewald 1995, Smith & Keyser 1995). The oldest species is *Owenetta rubidgei* from the *Cistecephalus* assemblage zone of middle Tatarian age.

In this paper the first procolophonoid from the underlying *Tapinocephalus* Assemblage Zone of the Beaufort Group is described, which is thus the earliest known specimen of the group. The specimen was found by Mr. Patrick Bender on the farm Blaaukranz in the Price Albert District which is considered to be low in the *Tapinocephalus* Assemblage Zone (Kitching 1977). In close proximity fossils of the pareiasaur *Bradysaurus*, the dicynodont *Diictodon*, the dinocephalian *Anteosaurus* and fragments of tapinocephalid dinocephalians were recovered.

MATERIAL

The specimen NMQR 3061 in the collections of the National Museum, Bloemfontein, was found in two blocks, one containing an articulated series of nine precaudal vertebrae, and the other thirteen proximal caudals, a partial right pubis, and articulated distal femur plus tibia and fibula. In spite of a thorough search the anterior half of the specimen could not be found. There is no clear fit of the two blocks, but very little appears to be missing as the anteriormost preserved caudal vertebrae are considered to be the first and second caudals. The bones are encased in a fine grained green mudstone containing scattered millimetre cubes of haematite, pseudomorphs after pyrite. The specimen is difficult to prepare as the matrix does not part easily from the bone. Bone surfaces (black) are only well defined where they have been exposed by natural erosion. In preparation it was found that organic acids do attack the matrix, but also adversely affect the bone which is extremely thin-walled, and hence acid preparation was not pursued further. Because of the difficulties experienced in preparation only conservative mechanical preparation has been undertaken.

DESCRIPTION (Figures 1, 2 &3)

A total of 22 vertebrae are preserved, and it is possible to differentiate 9 dorsals and 13 caudals. The anteriormost 5 dorsal vertebrae are reasonably complete and well preserved. In the posterior dorsal vertebrae the pleurocentra have been weathered, thus exposing a horizontal cross-section of some. From this it is evident that the pleurocentra are

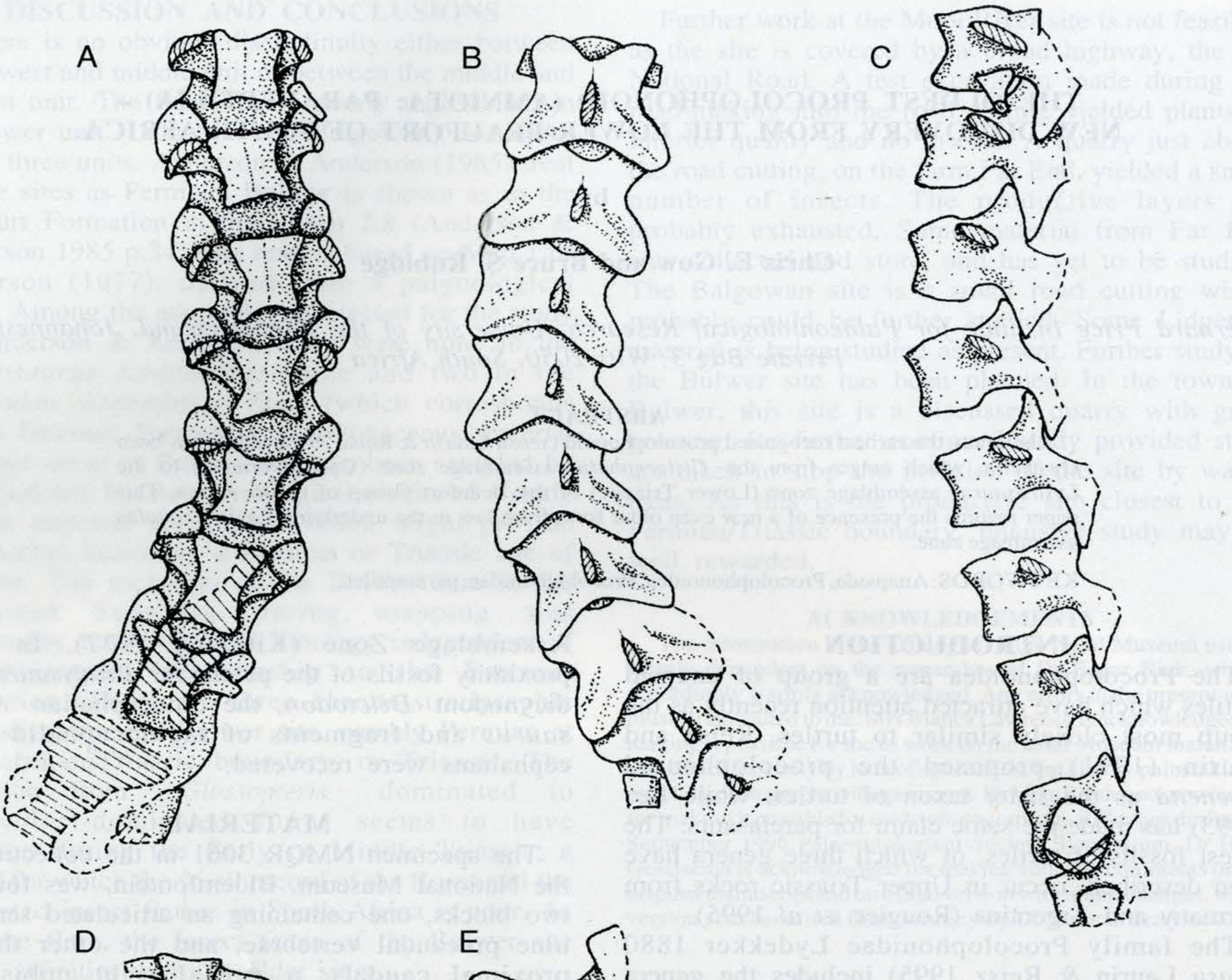

Figure 1: Procolophonoid specimen NMQR 3061: A) trunk vertebrae, ventral view; B) trunk vertebrae, dorsal view; C) trunk vertebra lateral view; D) caudal vetebrae, vental view; E) pubic (?) fragment, ventral view; F) proximal ends of tibia, dorsal aspect, G) articular ends of tibia and fibula; H) tibia ventral view.

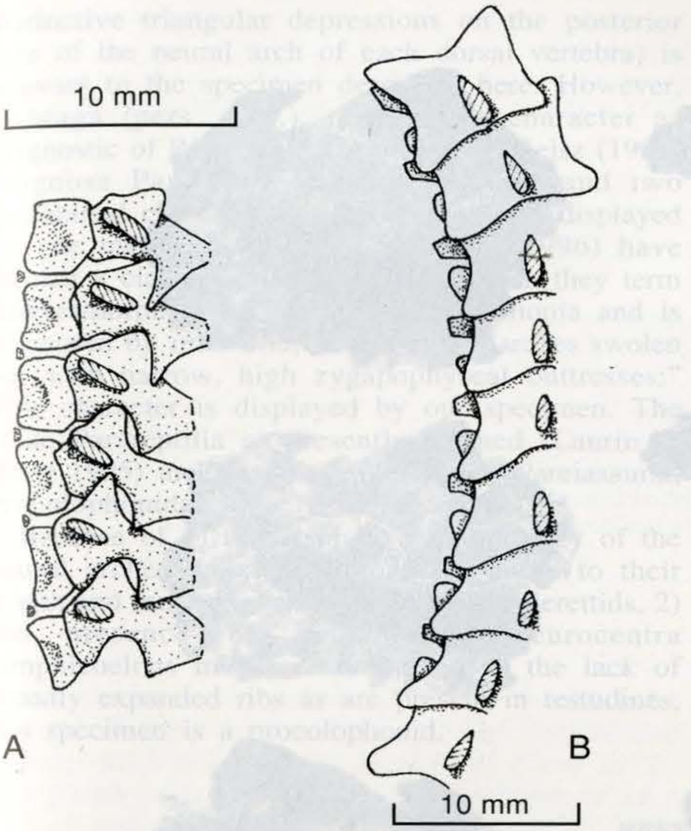

Figure 2: *Procolophon trigoniceps*.
A) Left BP/1/2854. B) Right BP/1/2278.
Both drawn from casts of impressions taken from natural molds.

notochordal. When viewed from the ventral side the pleurocentra are spindle-shaped and both ends of the centra are slightly bevelled; the ventral surfaces are not ridged. From the bevelled nature of the ventral side of the ends of the pleurocentra, as well as the wide spacing between the ventral surfaces of successive articulated vertebrae, it is evident that large intercentra were probably present between all the well preserved vertebrae, but are not preserved now (large intercentral spaces are also present in *Procolophon* – pers. com. Michael Debraga). Where broken it can be seen that the vertebrae are remarkably spongey and thin walled.

The neural arches of the preserved dorsal vertebrae have large, extensively overlapping and horizontally oriented zygapophyses. The dorsal surfaces of the postero-laterally projecting postzygapophyses are swollen, and the postzygapophyses have indentations on their anterior surfaces. In contrast the anterior zygapophyses have an anterolateral orientation, but the dorsal surface is more flattened and slightly concave to accomodate the articular surface of the postzygapophyses of the preceding vertebra with which they make a horizontally oriented articulation. The neural spines are very low and are ovoid in cross-section with the broader end posterior. The postero-dorsal surfaces of the neural arches bear a pair of triangular depressions. The neural arches are fused to the pleurocentra indicating that the animal was mature.

As the posterior dorsal vertebrae have been weathered it is difficult to differentiate between lumbar and sacral vertebrae. However, as the posterior 2 precaudal vertebrae are abruptly smaller and have less prominent zygapophyses than those preceding them, they are considered to be sacral. There is no evidence for a third sacral, though it is possible that the critical area may be missing.

The vertebrae in the second block are smaller than the rest and become progressively smaller posteriad. The zygapophyses are less pronounced and from the distinctive morphology of the transverse processes – large, laterally projecting on the first, large and strongly curved posteriad on the second -, they are considered to be the first and second caudals. These vertebrae are visible only in ventral view and like the dorsal vertebrae also have spindle shaped pleurocentra. The ventral surface of the anteriormost two caudal vertebrae is rounded, but those more posteriorly situated have a flattened ventral surface with a narrow midline keel. The lack of spacing between successive pleurocentra, which are preserved in close articulation, suggests that haemal arches if present would have been small.

Only a few fragmentary ribs and very few rib heads are preserved. From these and the single facetted attachments on the transverse processes, it is evident that the ribs were single headed and relatively slender structures.

The bone here identified as a partial pubis is large, plate-like and unfenestrated as is typical of basal parareptiles. Only the distal portion of the right femur is present; it is almost square in cross section at its distal end. In dorsal view it displays a slight depression, the intercondylar fossa, at the distal end.

The distal ends of both the tibia and fibula and most of the foot, except for part of an astragalus or calcaneum, are missing. The proximal articular surface of the tibia displays a central pit which is probably a natural feature which would have afforded purchase to a tendon or ligament. When viewed from the lateral side the tibia is a curved bone which is broad proximally and thins towards the distal end which is weathered. In dorsal view the tibia is crescent shaped, rounded anteriorly with a concavity on the posterior side. The fibula is less robust than the tibia but is not well exposed from the matrix. This bone is also slightly curved and has a prominent articular facet at the distal end.

DISCUSSION

Laurin & Reisz (1995) list 14 synapomorphies of the Parareptilia, ten of which are cranial characters and only four postcranial. However these postcranial characters are all in elements which are not preserved in specimen NMQR 3061. Lee (1995) on the other hand lists 18 characters of which only four pertain to the postcranium and only one (pair of

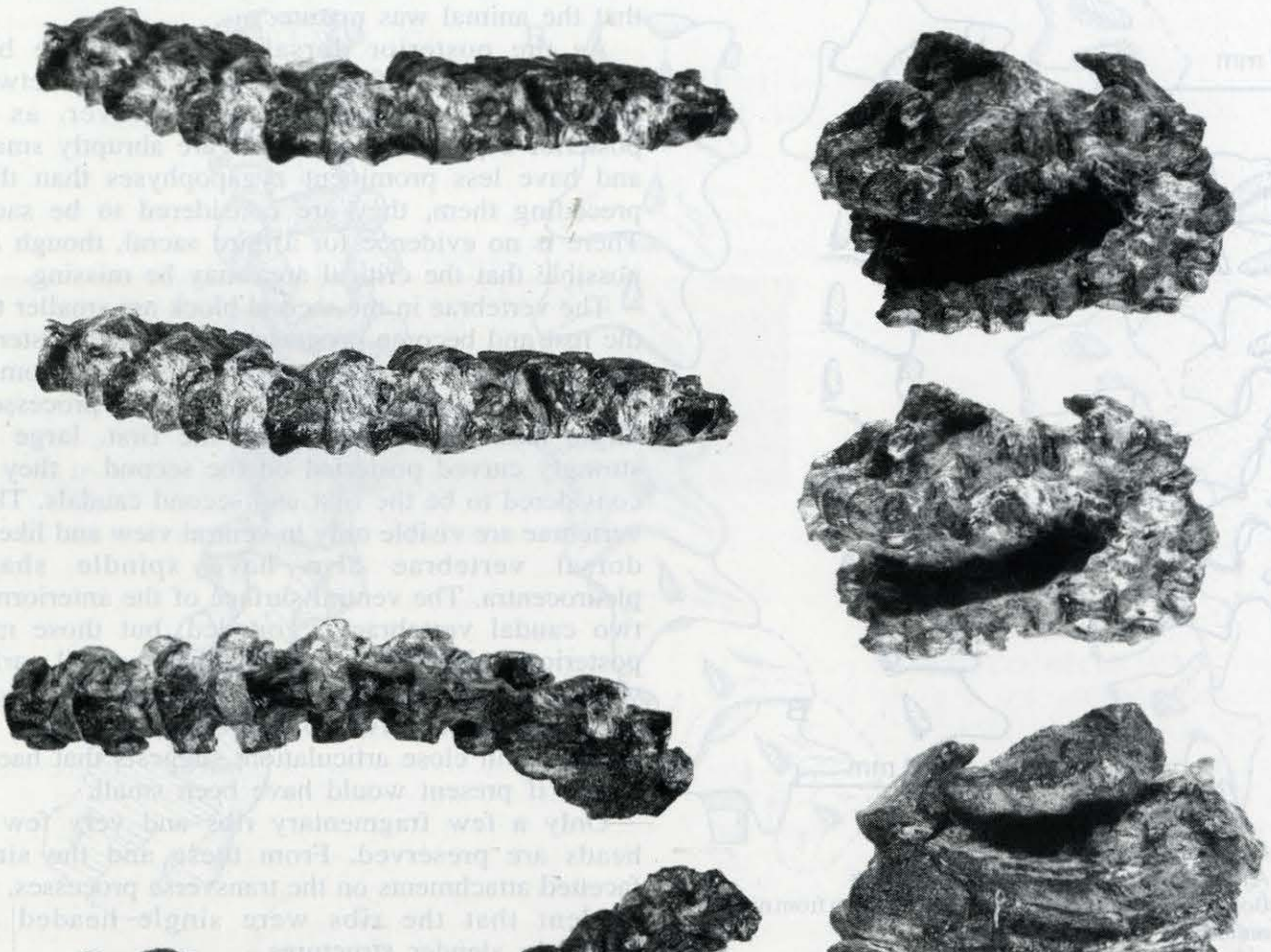

Figure 3: NMQR 3061. Stereophotographs. Left, dorsal vertebrae in dorsal, ventral, and left lateral views. Right, limb bones and caudal vertebrae. Scale bar = 10 mm.

distinctive triangular depressions on the posterior face of the neural arch of each dorsal vertebra) is relevant to the specimen described here. However, Debraga (pers. com.), rejects this character as diagnostic of Parareptilia. Debraga and Reisz (1996) diagnose Parareptilia on five cranial and two postcranial characters, none of which are displayed by our material. Debraga and Reisz(1996) have erected a clade within Parareptilia which they term Ankyramorpha; this includes Procolophonia and is diagnosed by *inter alia*," trunk neural arches swolen but with narrow, high zygapophyseal buttresses;" This character is displayed by our specimen. The clade Parareptilia as presently defined (Laurin & Reisz 1995) includes the Millerettidae, Pareiasauria, Procolophonidae and Testudines.

Because of 1) the distinctive morphology of the neural arches which are broader relative to their length and much bigger than those of millerettids, 2) the presence of notochordal pleurocentra (amphicoelous in pareiasaurs), and 3) the lack of broadly expanded ribs as are present in testudines, this specimen is a procolophonid.

The specimen is much larger than *Owenetta,* but falls within the size range of *Procolophon.* The pleurocentra are notochordal but they are not "pinched" laterally as is the case in *P. trigoniceps.*

Because of the fragmentary nature of the specimen it is difficult to assign it to a particular genus. It probably represents a new taxon but we feel that it would be undesirable to name such an undiagnostic specimen. So far the only parareptiles from the *Tapinocephalus* assemblage Zone are the pareiasaurids *Bradysaurus* and *Embrithosaurus*, the millerettid *Broomia* ((Watson 1914, Thommason & Carroll 1981), and *Eunotosaurus* (which is clearly a parareptile, Gow in prep.). Specimen NMQR 3061 is the first procolophonoid from this zone and shows that the group is not as young as previously supposed (Laurin & Reisz 1991).

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