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AN AGGREGATION OF JUVENILE *YOUNGINA* FROM THE BEAUFORT GROUP, KAROO BASIN, SOUTH AFRICA

by

Roger M.H. Smith[1] and Susan E. Evans[2]

[1]*Division of Earth Sciences, South African Museum, PO Box 61, Cape Town 8000, South Africa.*
[2]*Dept. Anatomy & Developmental Biology, University College, Gower St., London WC1E 6BT.*

ABSTRACT

An assemblage of five fully-articulated juvenile skeletons of *Youngina* has been recovered from the Late Permian strata of the south-western Karoo Basin. These 12-cm-long skeletons are not only the first articulated juveniles of this taxon, but also the oldest yet found in the Karoo Basin. They are preserved in overbank mudrocks of the Hoedemaker Member (Beaufort Group, Adelaide Subgroup) on the farm Leeukloof 43 in the Beaufort West district. Although they are estimated to be some three million years older than previously described *Youngina*, these specimens show no significant skeletal differences. The high degree of articulation and the spatial arrangement of these skeletons in a dish-shaped hollow is compelling evidence for them having huddled together within an underground burrow. Taphonomic analysis of associated fossils indicates that this was probably a mechanism to reduce water loss during drought on the ancient Karoo floodplains.

KEYWORDS: *Youngina,* juvenile aggregation.

INTRODUCTION

Younginiforms are a small but well-defined clade of Permo-Triassic diapsid reptiles known from the Late Permian of South Africa (*Youngina*), Tanzania (*Tangasaurus*) and Madagascar (*Hovasaurus, Thadeosaurus* and perhaps *Acerosodontosaurus*), and from the Early Triassic of Kenya (*Kenyasaurus*). Once thought to be related to lepidosaurs (lizards, snakes and their relatives), younginiforms are now considered no closer to lepidosaurs than to archosaurs and are therefore placed closer to the base of the diapsid tree (Laurin 1991).

The fossil record of younginid reptiles in the Karoo Basin of southern Africa is comparatively sparse: only 13 highly distorted skulls and a few disarticulated skeletal elements have been collected to date (Gow 1975). Only one of the skulls has an articulated post-cranial skeleton (BPI 2859) and this is incomplete (Gow 1975). All the *Youngina* specimens collected so far are from Beaufort Group strata assigned to the *Dicynodon* Zone (Smith and Keyser, in press), previously known as the *Daptocephalus* Zone (Kitching 1977). These strata immediately underlie the Permian-Triassic boundary in the southern Karoo Basin (Anderson & Cruikshank 1978). Recently, Roger Smith recovered an unusual assemblage of *Youngina* from strata of the *Tropidostoma* Zone (Smith & Keyser in press), previously known as the lower *Cistecephalus* Zone of Kitching (1977). The new locality is some 700m lower in the Beaufort succession than those described to date making this the earliest recorded occurrence of *Youngina* in the Karoo Supergroup. A very rough calculation of the minimum time involved in accumulating these 700m of fluvial strata, based on 2mm/year for the compacted mudrock intervals and 5mm/y for channel sandstone dominated intervals (Smith 1993) is approximately 3 million years. Based on correlation of the associated *Endothiodon* fauna with similar fossils in the Rio-do-Rasto Formation of Brazil (Keyser 1981), the host strata are estimated to be middle to late Tatarian in age (+/-255-253My). The palm-sized specimen contains at least five fully articulated juvenile *Youngina* skeletons preserved in attitudes and orientations that strongly resemble group denning behaviour of modern lizards.

DESCRIPTION OF *YOUNGINA* ASSEMBLAGE AND EVIDENCE FOR IMMATURITY

The five individuals of SAM K7710 are of similar size (snout-vent lengths 86-94mm) and are all at the same level of skeletal development. In the skull, the elongated posterior process of the post-orbital and U-shaped configuration of the frontoparietal suture identify these animals as youginiforms. Comparing the shape of skull elements such as parietal (posterior process angle and orientation; tabular and supratemporal facets), the dentition, the shape of the humerus and the long shallow ectepicondylar groove – these small skeletons show no marked differences from previous descriptions of the genus *Youngina* (Gow 1975) although they are about half the size of previously described specimens. It is possible that they are a new small morph but it is more feasible that they are immature.

Despite their size, the new skeletons are too well ossified to represent young hatchlings. Neurocentral sutures are closed; tarsal and carpal elements are ossified; the components of pectoral and pelvic girdles are in close proximity (i.e. there are no large areas of cartilage separating them); and the sacral and caudal ribs are fused to their respective vertebrae (although on one specimen there is the trace of a suture). However, there is also evidence that these small reptiles are not fully mature. In the skull, the roofing bones are unsculptured; the paired frontals and parietals are joined by simple sutures which have separated easily; and the eyes and parietal foramen are proportionally large. The sternal plates are only weakly ossified and remain paired although the coracoid foramen is already enclosed. In the pelvis, the pubis and ischium are separated by a weakly ossified area and the obturator foramen of the pubis is open posteriorly. The ends of the long bones lack joint surfaces. The carpals and tarsals are incompletely preserved. They have ossified centres but are still more rounded than angular in shape; there is no trace of a notch on the calcaneum for the perforating artery.

Developmental stages have been described for two younginiforms- *Hovasaurus* (Currie 1981) and *Thadeosaurus* (Currie & Carroll 1984). *Hovasaurus* was almost certainly aquatic; *Thadeosaurus* at least partially so. Aquatic animals tend to show a retarded level of skeletal development which makes comparison with terrestrial animals difficult. Bearing this in mind, however, the new younginid specimens described here would seem to correspond to age class E or F (H being adult) in the aquatic genera and can be described as juveniles.

SEDIMENTOLOGY AND TAPHONOMY OF YOUNGINA LOCALITY

The new *Youngina* locality is on the border between Beaufort West and Loxton districts of the Cape Province of South Africa within a regionally extensive mudrock sequence (informally termed the Hoedemaker member) that forms part of the Teekloof Formation of the lower Beaufort Group (Adelaide Subgroup). Detailed mapping of sedimentary facies and taphonomic analyses of 243 *in-situ* vertebrate fossils at this locality have been used to reconstruct several floodplain palaeoenvironments (Smith 1993). The younginid fossils were embedded in a 2-metre-thick structureless greenish-grey siltstone, which is interpreted as having accumulated on the proximal floodplain areas flanking a large meandering river (Smith 1987a). Sedimentary structures in the point bars that make up the bulk of the channel sandstones indicate that the rivers were perennial and prone to large discharge fluctuations (Stear 1985). This resulted in flood dominated sedimentation in the main channels and on the channel banks. The structureless siltstone in which the younginids were buried is interpreted as

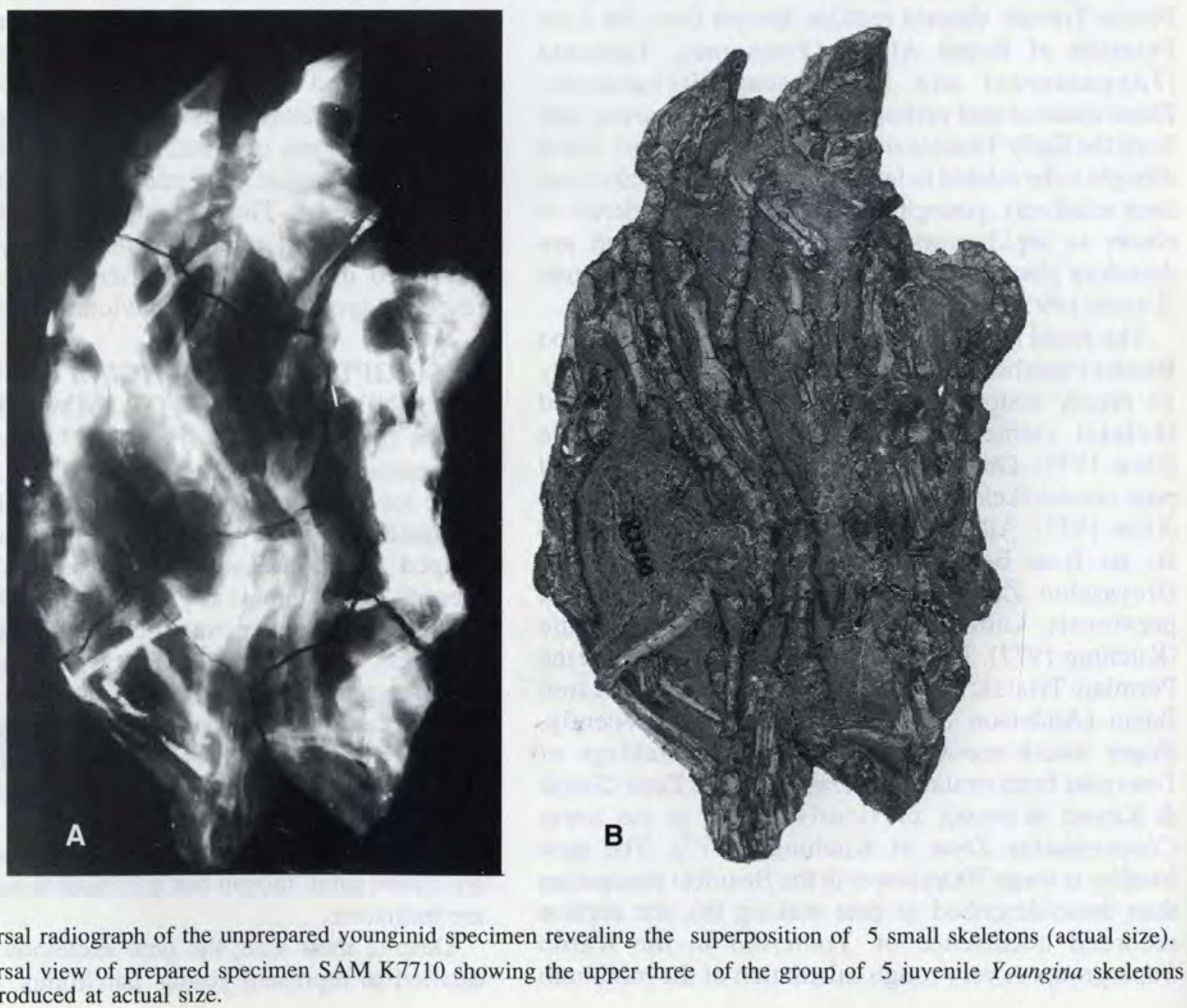

Figure 1A. Dorsal radiograph of the unprepared younginid specimen revealing the superposition of 5 small skeletons (actual size).
Figure 1B.Dorsal view of prepared specimen SAM K7710 showing the upper three of the group of 5 juvenile *Youngina* skeletons reproduced at actual size.

sheetflood alluvium rapidly deposited by sediment-laden floodwaters that overtopped the channel banks (Smith 1987a). Calcic palaeosols in the associated sediments confirm that floodplain sedimentation was highly episodic and the climate was semi-arid in this part of the basin with highly seasonal rainfall (Smith 1990).

When found, the new younginid specimen (SAM K7710) was completely encased in a thin layer (5mm) of micrite cemented siltstone. Such preferential peri-mineralisation of fossil bone is common in the proximal floodplain facies of the Hoedemaker Member and is interpreted to be of pedogenic origin (Smith 1990). Both dorsal and ventral surfaces were mechanically prepared with dental drill and needle under magnification (Figure1b). Anatomical details were recorded on transparent film using radiographs (Figure1a) to maintain positional accuracy. These drawings were enlarged in a photocopier and reversed onto clear film thus making it possible to superimpose dorsal on ventral views (and vice versa) to reveal the intricacies of their taphonomic mode (Figures 2 & 3). The five skeletons are preserved in a dorsal-up attitude along the floor of a spoon-shaped depression. Their skeletons are superposed on each other but show no evidence of disturbance other than that attributable to vertical compaction. The high degree of articulation of these very delicate skeletons and the presence of free-floating sternal plates indicate that they were buried with their flesh intact. This, coupled with the spatial arrangement of limbs and parallel orientation of the skeletons in a dish-shaped depression, is compelling evidence for them having been preserved in "life position" as a behaviourally arranged aggregation of juveniles within an underground burrow (Figure3).

To date no fossil eggs or nesting sites have been found in the Beaufort Group although burrow casts containing curled-up skeletons of the small dicynodont *Diictodon* do occur in the vicinity of the younginid locality (Smith 1987b). Interestingly, an aggregation of ten juvenile skeletons of *Diictodon* (SAM K1650) was found within 100m of the younginids and ten more isolated juvenile skulls of *Diictodon* were collected along the 1300m cliff section. The relatively common occurrence of articulated juvenile skeletons of a variety of groups preserved in the proximal floodplain facies possibly indicates that this was a preferred "nesting" area. However, the wide range of disarticulation classes and "clustering" of skeletal elements into shallow scours suggests that the periodicity of flood events and the net floodplain accretion rate in this part of the floodplain were optimal for the preservation of small skeletons.

DISCUSSION OF EVIDENCE FOR JUVENILE AGGREGATION

Possibly the most interesting feature of the new *Youngina* specimens is that they appear to provide evidence for juvenile aggregation in this taxon. This raises questions of why they aggregated and what killed

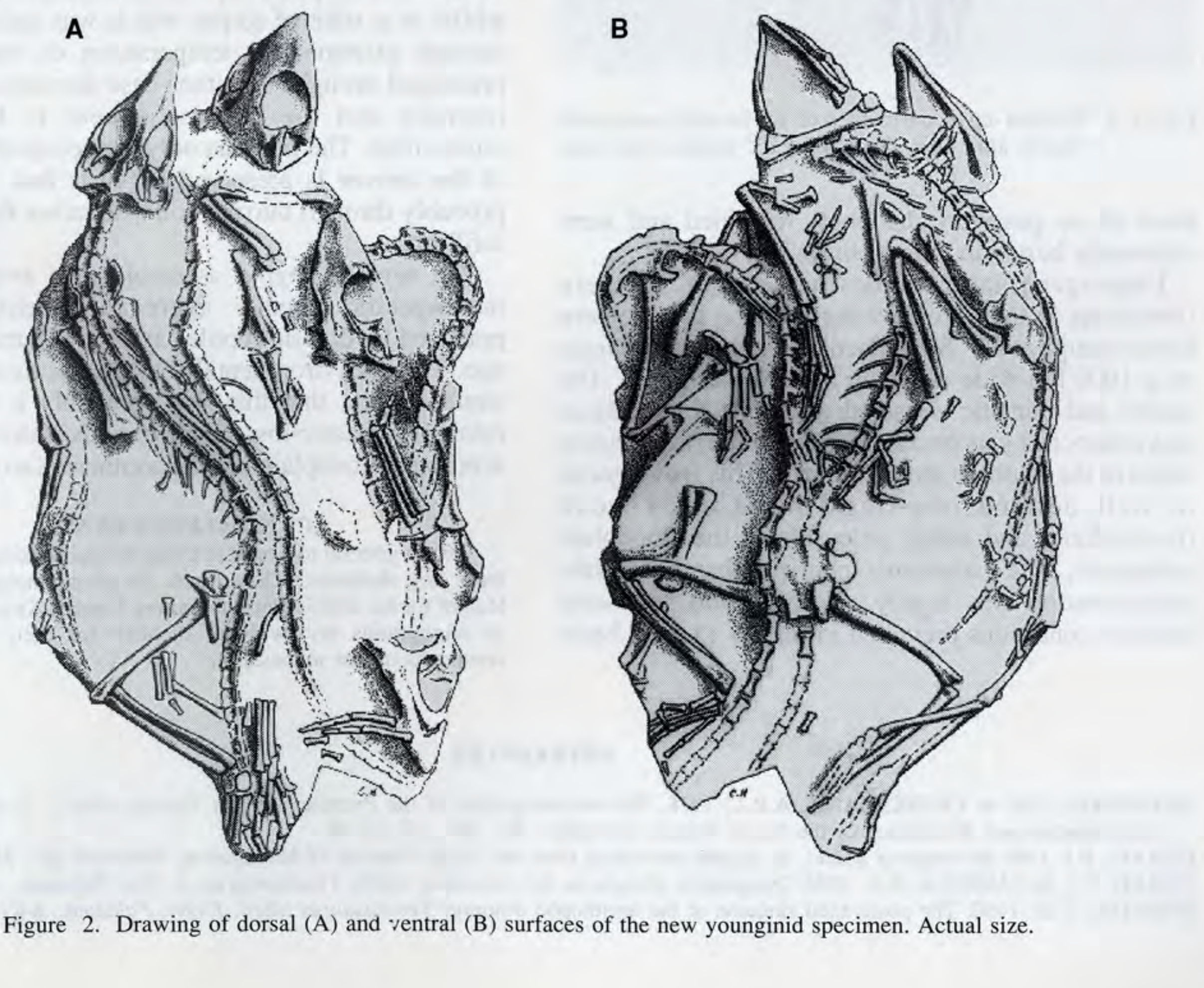

Figure 2. Drawing of dorsal (A) and ventral (B) surfaces of the new younginid specimen. Actual size.

Figure 3. Fleshed -up reconstruction of the juvenile younginids shortly after their death some 255 million years ago.

them all so passively that they remained and were eventually buried in "life position"?.

Palaeogeographic reconstructions of southern Gondwana in the Late Permian position the southern Karoo trough at 55 ° S bounded on the southern margin by a 1000 km-wide orogenic belt (Visser 1991). The aridity and climatic seasonality of the Karoo Basin was enhanced by its continentality and the rain-shadow effect of the southern mountainlands. This is evidenced in well defined tree-rings of silicified wood (*Dicroidium*) and calcic paleosols in the floodplain sediments. The palaeosols confirm that floodplain sedimentation was highly episodic and semi-arid climatic conditions prevailed in this part of the basin (Smith 1990). Comparison of the palaeosol profiles with those of modern soils allows an estimate of mean annual temperatures between 16-20 °C and highly seasonal rainfall of 500-700mm/y (McPherson & Germs 1979; Smith 1990). In such a setting, large diurnal temperature fluctuations and drought would have been commonplace. It is therefore predictable that ectotherms such as *Youngina* would have some behavioural adaptations, such as aggregating, to regulate their body temperatures. It is also reasonable to assume that these reptiles would aestivate in underground burrows during drought to preserve moisture. Taphonomic analysis of the other 242 *in-situ* fossils found at the younginid locality led to the conclusion that many of the disarticulated dicynodont skeletons had accumulated, during prolonged drought, at watering holes around the margin of a floodplain lake (Smith 1993). Thus it is concluded that drought was the most likely reason that the juvenile younginids went to ground.

The juveniles of some modern species of viviparous lizards, the skinks, huddle together with very similar intertwining and side-by-side disposition. These aggregations involve members of a single brood and are usually found in confined cavities beneath fallen logs or within underground burrows (Shine 1994). Within warm semi-arid climatic conditions the advantages of such behaviour are improved diurnal thermoregulation (Gregory 1982) and more efficient aestivation during drought (Seidel 1978).

It is conceivable that juveniles of both *Youngina* and *Diictodon* died passively within underground burrows whilst in a state of torpor which was induced either through extreme low temperatures or, more likely, prolonged drought. In either case decomposition was retarded and the corpses appear to have been mummified. The fact that only the scoop-shaped floor of the burrow is preserved suggests that burial was probably through burrow collapse rather than gradual infilling.

The new *Youngina* assemblage is evidence that monospecific juvenile aggregation behaviour was practised by diapsid reptiles at least 255 million years ago. Palaeoenvironmental interpretations of the host strata suggest that this was probably a method of minimising water-loss during periods of drought on the semi- arid floodplains of the southern Karoo Basin.

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