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A CAPTORHINID WITH MULTIPLE TOOTH ROWS FROM THE UPPER PERMIAN OF ZAMBIA.

by

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ABSTRACT

Captorhinids are some of the best known early amniotes. They range throughout the Permian and occur in North America, Europe, India and Africa. There are several small forms with single rows of marginal teeth, medium sized multiple-rowed forms typified by *Captorhinus*, and large forms most of which possess numerous rows of marginal teeth. As a group, captorhinids are extremely conservative in cranial morphology in most other respects. A small Late Permian, single rowed form has been recorded from the Madumabisa Mudstone of Zambia, equivalent in age to the *Cistecephalus* Assemblage Zone of the Karoo Basin of South Africa. This paper records a multiple-rowed form from these rocks similar in size to *Captorhinus*, but with distinctive dentition.

KEYWORDS: Upper Permian, Captorhinidae, Zambia.

INTRODUCTION

In 1960 and 1961 J W Kitching made a large collection of tetrapod skulls from the upper Luangwa valley, Zambia (then Northern Rhodesia). Two horizons within the Madumabisa Mudstone yielded fossil amniotes, the lower horizon being equivalent to the *Tropidostoma* Assemblage Zone of the South African Karoo, while the upper horizon yielded a typical *Cistecephalus* Assemblage Zone fauna (Kitching1963). This latter assemblage, of Upper Permian age, included the captorhinid described here, which was originally catalogued as a procolophonid.

Gaffney and McKenna(1979) described two small single-toothrowed skulls from the Upper Permian Madumabisa Mudstone of Zimbabwe (then Southern Rhodesia), and referred them to the Lower Permian *Protocaptorhinus* of North America. More recently Modesto (pers. com. and in press) has collected and described a small single rowed captorhinid from the *Cistecephalus* Assemblage Zone of the main Karoo Basin.

MATERIAL AND METHODS

The skull, BP/1/3899, including lower jaw and teeth, is encased in a very hard and brittle haematitic matrix, as is most of the Luangwa Valley material. Most of the superficial bones have been lost to weathering, leaving most of the skull roof represented by steinkern, itself partially weathered. Several features on the steinkern are clearly the result of cracks in the overlying bone, and such internal traces of sutures as exist are not comparable with true surface sutures. Typical captorhinid dermal bone sculpturing is visible in only two places, on a small area of jugal, and on the mid-dorsal surface of the exposed supra-occipital. The occiput and palate having been still encased in matrix responded quite well to airscribe preparation, though as the lower jaw and teeth are present in occlusion and in poor condition, the anteriormost part of the palate has not been prepared. A vexing feature of this specimen is that several sutures have opened up very slightly post mortem, none the less, the overall *Captorhinus*-like shape of the skull is not compromised. Very few tooth tips are exposed, but as several teeth are represented by high fidelity impressions these could be usefully studied with a soft, fast setting dental impression material. A single articulated digit was found lying against the skull and is now stored separately.

SYSTEMATIC PALAEONTOLOGY

Reptilia Laurenti, 1768
Eureptilia Olson, 1947
Family Captorhinidae Case, 1911
Genus *Captorhinus* Cope, 1897

Species. *Captorhinus* sp. indet.

This specimen is some 20 million years younger than the two species of *Captorhinus* (*C. aguti* and *C. laticeps*). In nearly every observable feature apart from detailed morphology of the dentition, it is typical of the genus. Pristine post caniniform multi-rowed cheek teeth are robust, conical, and sharp pointed, as opposed to those of *C. aguti* which have mesio-distally aligned blade-like tips (Modesto 1998 and pers. obs.), and those of *C. laticeps* which are described as triangular with cutting edges (Modesto 1998). The latter is, in any case, a single-rowed form. Several teeth have the tips worn to flat, lingually sloping micro-pitted facets. The absence of scratches on worn crowns indicates that occlusion was purely orthal. These details of wear and occlusion may all prove to be individual characters. Another potentially diagnostic character is the attitude of the paroccipital processes: these angle ventrad distally, whereas in *C. aguti* they angle dorsad.

DESCRIPTION

The skull (Figure 1) is the typical size and shape of *Captorhinus aguti*. As can be seen from the Figure the skull is badly eroded: a small patch of jugal and the dorso-medial projection of supraoccipital are the only parts which show the typical dermal bone pitting. Apart from the midline, naso-frontal, and fronto-parietal (and the impression of the pineal opening), sutures on the steinkern are uninformative with the exception of the posterior edge of jugal, which is typically captorhinid (Figure 1 C).

The elements of the palatal surface are all standard captorhinid, the stapes (Figure 1 B) and the median projection of the jugal being the most diagnostic elements. The basal articulations, the contact of the median projection of the jugal with the palatine and pterygoid, and the pterygo-palatine sutures, have all opened up slightly postmortem. An important consequence of this is that the depressions visible on the palatines (Figure 1 B) are actually where the pterygoids would normally lie (Fox and Bowman 1966, describe this sutural relationship in detail). Palatal teeth are sparse. None can be seen on what is exposed of the palatines. Teeth are present on the pterygoids, including their flanges, absent from the basiparasphenoid. However, but palatal teeth are known to be variable in number and distribution in *C. aguti*, so this has no taxonomic significance. The parasphenoid rostrum is directed steeply upwards, as is typical in captorhinids. A single hyoid element lies on the right side on the palatal surface (Figure 1 B). Of possible significance is the shape of the quadrate ramus of pterygoid: this is visible only on the left side where it is seen to terminate in a narrow ventral projection. No details of the corresponding surface of

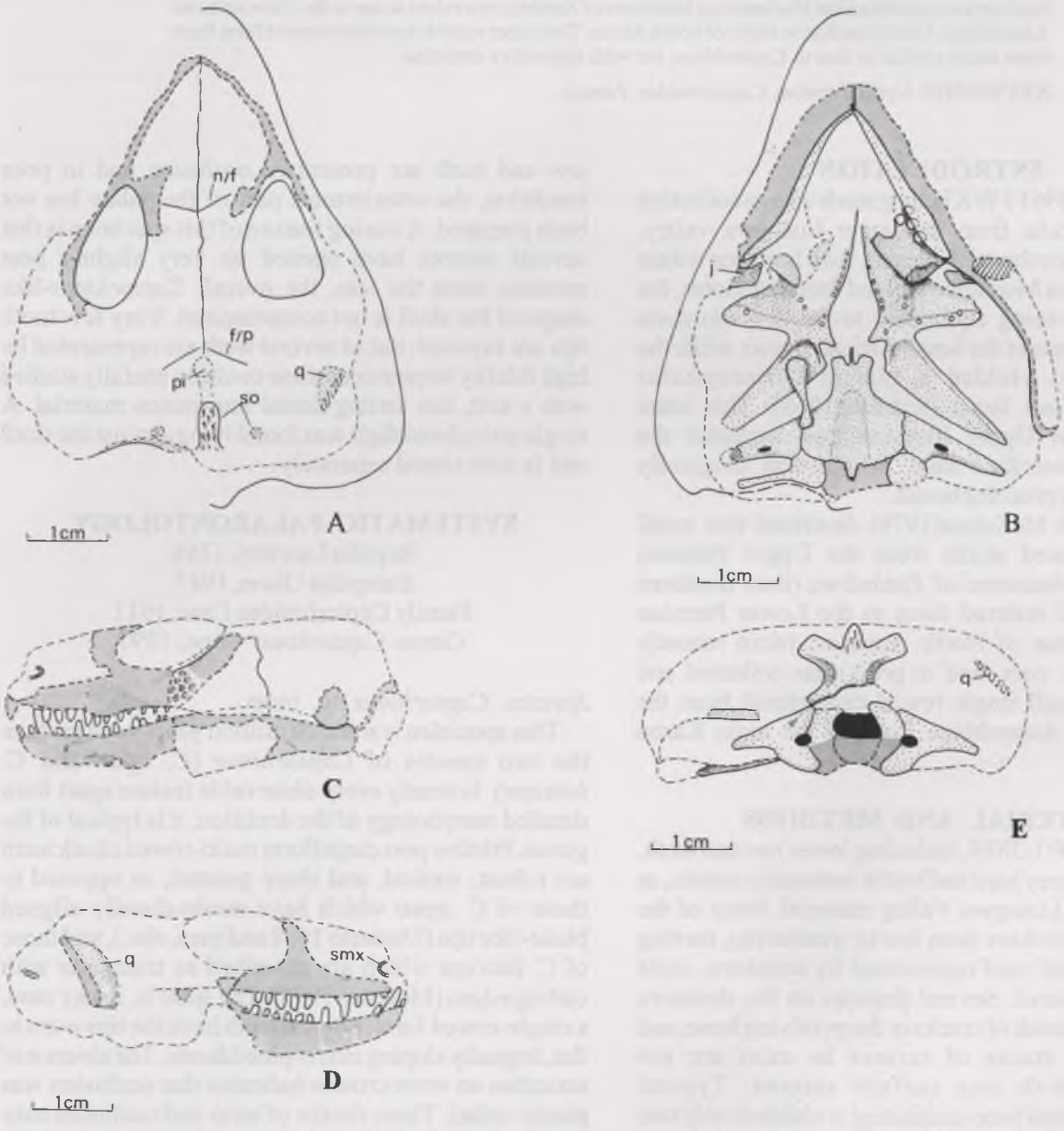


Figure 1. Skull of *Captorhinus sp.* from Zambia. In A dorsal, B ventral, C left lateral, D right lateral, and E occipital views. Dense shading indicates broken bone. Estimated original outline of skull is indicated.

the quadrate are exposed. The pterygoid ramus of quadrate is typically tall: it has been partially prepared on the right side where the rest of the bone is missing; further preparation would compromise other details (Figure 1 D & E).

On the occiput the supratemporal is well dispayed and just as described for *C. aguti* (Modesto 1998). Though the occipital condyles have been eroded off, the opisthotics and exoccipitals are quite well preserved. The paroccipital processes project slightly ventrad: this may be a real difference between this taxon and *C. aguti*, in which the paroccipital processes project somewhat dorsad (Modesto 1998, Figure 6 D), and cannot be due to any distorting postmortem effects.

The left lower jaw ramus is sufficiently complete to show the typical sigmoidal flexure of this structure in ventral aspect, but erosion makes it impossible to determine the morphology of the articular region. The splenials can be seen to participate in the symphysis.

The dentition (Figure 2) is uncannily similar to that of *C. aguti*. All the premaxillary teeth have been lost to erosion. The maxillary and dentary marginal rows contain a minimum of 13 and 17 teeth respectively, in a manner very similar to *C. aguti*. The surfaces of both maxillae and both dentaries have been completely eroded off and most of the exposed teeth are damaged. Thus it is likely that those visible are not marginal rows. However, the right maxilla contains a perfectly preserved caniniform tooth in the fourth tooth position which even displays typical theco-acrodont attachment. This tooth is symmetrically pointed in labial view. In mesial or distal view it is convex labially and concave distally on the lingual surface, with blunt mesial and distal edges, just as in *C. aguti*. Subsequent teeth are symmetrically conical and robust, becoming very small at the posterior end of the row. With the exception of the right caniniform, all exposed upper teeth are damaged.

Each dentary has a small procumbent tooth anteriorly, followed by the two largest teeth in the row; these are followed by a series of stout conical teeth, again becoming very small at the posterior end of the row. Two adjacent intact teeth have been prepared out on the ligual side of the left dentary (shown schematically in Figure 1 B): these are sharply pointed, robust cones. High fidelity impressions of two worn teeth are preserved in the right dentary: these exhibit wear facets dipping linguad at aproximately 30 degrees. The facets are finely pitted, not scratched, and the extremely thin enamel, being harder than the dentine, forms an uninterrupted, slightly raised rim. This wear indicates that jaw movements were purely orthal: it could have resulted from tooth-to-food contact as easily as tooth-to-tooth contact. The simple captorhinid jaw mechanism would generate maximun speed with the adductor muscles near full stretch and maximum force when the jaws were nearly closed. Multiple tooth rows seem "designed" to exploit the force component, either for crushing and cutting plant food in the case of *C. aguti* (Dodick and Modesto 1995; Modesto 1998), or in the case of *C. zambiensis*, for crushing invertebrate prey.

DISCUSSION

Dodick and Modesto (1995) present a useful cladogram of captorhinid relationships. Of the characters they use to diagnose Captorhinidae the Zambian specimen has the following three: 1) caniniform region present anteriorly on dentary, 2) pineal foramen anterior to midpoint of interparietal suture, and 3) maxillary dentition reduced to 25 or fewer teeth. Only one character places it in *Captorhinus*, namely, anterior teeth procumbent - true of the lowers but inferred for the premaxillary teeth which have all been lost.

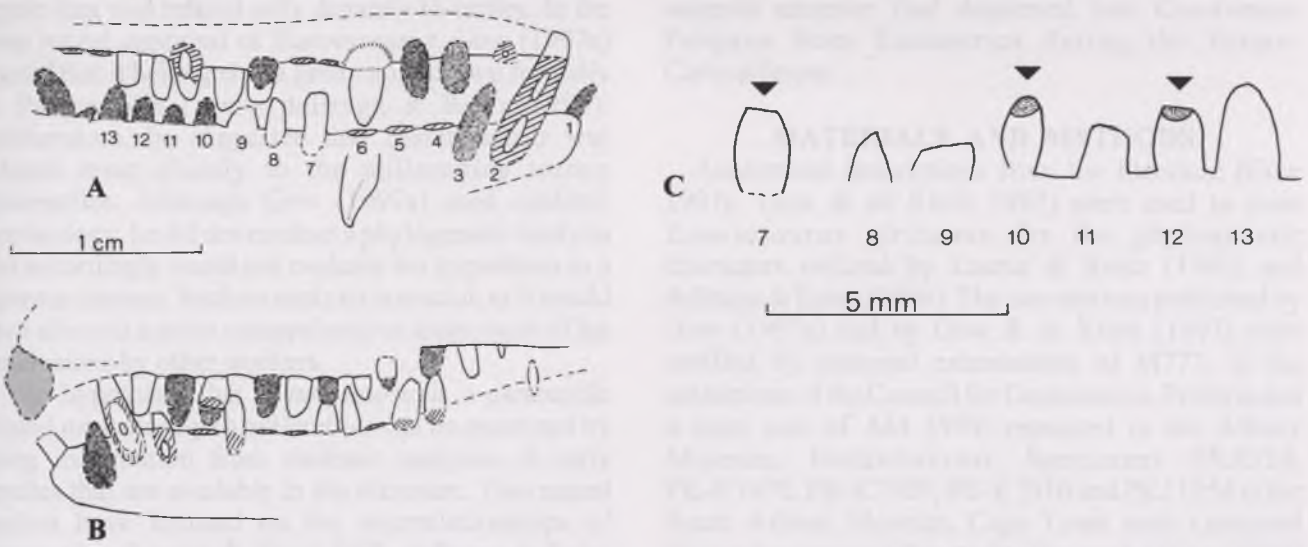


Figure 2. Dentition of *Captorhinus sp.* from Zambia drawn with the dentition horizontal. Shading indicates impressions, oblique lines indicate damaged teeth.A right side; maxillary caniniform sketched in mesial view beneath the number 6; B left side, disruption of maxillary row due to bone being broken at different depths; C three dentary teeth exhibiting crown tip wear (10 and 12 are impressions).

In the new Zambian specimen the only tooth which may be described as having anterior and posterior cutting edges is the maxillary caniniform, the rest of the teeth are conical and pointed. Modesto (1996) suggests that "teeth with cutting edges" is probably a synapomorphy of captorhinids. If this is so, then *C. zambiensis* with its connical pointed teeth is more derived than its sister taxon of *C.aguti* plus *C.laticeps* both of which have cutting cheek teeth.

ABBREVIATIONS

bo	basioccipital
f/p	fronto-parietal suture
hy	hyoid
j	jugal
n/f	naso-frontal suture
pi	pineal
ptgd	pterygoid
q	quadrate
smx	septomaxilla
so	supraoccipital
st	stapes

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