A PARTIAL SKELETON OF THE TRITHELEDONTID PACHYGENELUS (THERAPSIDA: CYNODONTIA)

by

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ABSTRACT

Tritheledontids are advanced cynodonts that are considered the sister group of Mammalia. To date the postcranial skeleton has remained largely unknown, so that cladistic analyses are based on cranial characters only. This paper describes a specimen of the tritheledontid Pachygenelus which has most of the skull and vertebral column, a complete shoulder girdle, and most of the forelimb. The girdle and limb are closely comparable to those of Massetognathus and Eozostrodon, and unlike these elements in tritylodontids, which are more derived for fossorial specialisations.

KEYWORDS: Therapsida, Pachygenelus, postcranial skeleton.

INTRODUCTION

Recent cladistic analyses favour tritheledontids as the sister taxon to Triassic mammals (Hopson 1994; Luo 1994). The morphology of tritheledontids is still poorly known, however, and virtually nothing has been published on the postcranial skeleton. The specimen described here goes some way to fill this gap, and supports the above relationship; Pachygenelus is less derived than the contemporary tritylodontids, which are specialised fossorial herbivores.

MATERIAL AND METHODS

Pachygenelus is the most common tritheledontid. The specimen described herein has enough of the skull preserved, including the dentition, for positive identification and to establish skull length. It also preserves much of the vertebral column and ribs, a nearly complete pectoral girdle, and the left forelimb excluding the distal phalanges. Some unusual aspects of the skull are noted below.

The specimen was collected from the Upper Elliot Formation, now generally considered of Lower Jurassic age (Benton 1994), on Clarens townlands. It was encased in a fine grained sandy matrix cemented with calcium carbonate, and containing hard caliche nodules. The latter imply that lithification was a slow process, which may account for some of the peculiarities of the specimen noted below. A thin, fairly soft ferruginous layer surrounded most of the bone and was separated from it by a very thin amorphous calcitic layer. The specimen was prepared mechanically.

DESCRIPTION

Only the anterior portion of the skull is preserved (Figure 1); this shows the internarial process of premaxilla making contact with the nasal. The skull roof, braincase and occiput have been lost through weathering: a skull length of 50 ± 5 mm is indicated by

Figure 1. Pachygenelus BP/1/5623. Left lateral view of skull as preserved, detail of left and right dentitions. Scale bars = 1 cm.
comparison with a specimen of similar size with skull roof intact. The lower jaws have separated at the symphysis and been somewhat displaced, though they are tightly occluded.

The teeth are in poor condition, and are rather fragmentated. They confirm that there are two incisors in each jaw quadrant, but are surprising in that there are ten postcanines in each maxilla and nine (plus one?) in the left dentary. The right dentary postcanines are not fully exposed. This number of postcanines is greater than previously recorded for both smaller and larger specimens (Gow 1980). Most exposed teeth are well worn except the fourth postcanine in the right maxilla and the sixth in the left, both of which are new replacements not yet fully erupted.

The lower jaw rami have angular processes which make 90 degree angles. The angular processes are also deflected outwards and are thick and robust, they probably served as insertions for masseter muscles, as suggested by Crompton (1963) for the very similar Diarthrognathus. Diarthrognathus has very different dentition (Gow 1980).

There are parts of 19 vertebrae preserved (Figure 2), either in articulation or very nearly so. The atlas and axis and an unknown number of anterior cervicals have been lost to erosion, and the column as preserved ends before the lumbar region. The centra are quite well preserved, increasing in length along the column from cervical to posterior dorsal region. The neural arches are poorly represented and there is no trace of neural spines. This is mostly the result of erosion, but also due to poor preservation. The young age of the individual is also a contributing factor.

Several of the more anterior ribs are present, but are generally badly eroded. They are circular to slightly ovoid in section, with poor differentiation of tuberculum and capitulum. There is no sign of the ribs that were attached to the last five vertebral centra, but the neural arches bear prominent rib facets.

Due to the young age of the individual, the elements of the pectoral girdle were not fused and have become slightly separated (Figure 3). Only the lower half of the right scapula remains and this includes the acromion process. Of the left scapula only the dorsal margin is missing, but the acromion region is badly preserved (a shed maxillary tooth lies beside it on the blade). The scapula is tall and narrow with a deeply concave external surface, the acromion is thickened, with a flat surface for articulation of the clavicle; it is very similar to the scapula of Eozostrodon figured by Jenkins and Parrington (1976), and thus more derived than the scapula of earlier cynodonts and totally lacking the pronounced specialisations of tritylodontids (Sues
Both coracoids are present; these are typical of cynodonts, having a straight suture for the procoracoid (damaged on the right coracoid). Only one procoracoid with a coracoid foramen is preserved, and this appears to be the right element; comparison with the specimen of *Cynognathus* figured by Jenkins (1971) suggests the orientation and relationship with the coracoid depicted here (Figure 3). Both clavicles are present, slightly incomplete, and a little distorted. Their morphology is plesiomorphic for cynodonts and unlike the highly derived condition seen in tritylodontids (Sues 1986). The interclavicle is robust; its broad posterior projection had broken off and could not be found. The cross piece of the T that bears the facets for the clavicles is deflected upwards relative to the shaft of the T through an angle of approximately 44 degrees. This bone is so robust as to cast doubt on the identity of the interclavicle tentatively assigned to *Eozostrodon* by Jenkins and Parrington (1976), which is far more delicate, and which Evans (1981) suggests may belong to the rhynchocephalian *Gephyrosaurus*. The facets on the interclavicle which received the clavicles are finished in smooth periosteal bone, suggesting that movement was possible at these joints.

Of the right forelimb only the proximal head of the humerus is preserved. The articulated left forelimb comprises humerus, radius and ulna, seven largely indeterminate wrist elements (Figure 4), two of which are the radiale and ulnare (but these lack the intricate morphology of equivalent elements in Triassic mammals), and four proximal metacarpals (the fifth is missing), one of which is damaged. The metacarpals are numbered according to their relationship to the carpal elements. The limb bones are closely comparable with those of *Eozostrodon* (Jenkins & Parrington 1976) and *Massetognathus* (Jenkins 1970). The radius and ulna are straight as in the former, not curved as in the latter. In tritylodonts these elements are more derived with autapomorphies related to their fossorial habits. The ulna has an olecranon process and sigmoid notch. The carpus of cynodonts is poorly known, but the proximal phalanges of this specimen of *Pachygenelus* are relatively longer and more slender than those of Triassic forms figured by Jenkins (1971) and the coeval tritylodontids (Sues 1986).
DISCUSSION

The postcranial skeleton of Pachygenelus supports the sister group status of tritheledontids and mammals previously determined from cranial characters (Hopson 1994; Luo 1994). The scapula (Figure 5) has a distinctive acromion process that is identical to that of Eozostrodon (Jenkins & Parrington 1976) and more derived than that of earlier cynodonts. The scapula of Pachygenelus lacks the specialisations for a fossorial mode of life exhibited by tritylodontids (Sues 1986). Similarly the clavicle morphology is typical of lower cynodonts, and unlike the derived condition in tritylodontids. The interclavicle is robust as is typically the case in cynodonts, suggesting that the bones tentatively identified as a clavicle and an interclavicle of Eozostrodon by Jenkins & Parrington (1976) may belong instead to an associated non-cynodont taxon. The humerus (Figure 6), radius, and ulna are essentially identical to those of Eozostrodon and lack the specialisations seen in tritylodontids. The wrist elements are more plesiomorphic than those of Triassic mammals. The preserved metacarpals are relatively longer and more slender than those of Triassic cynodonts and tritylodontids. The skull confirms the presence of only two incisors in each jaw quadrant, and compared with previously described dentitions (Gow 1980), suggests that the number of postcanines varied intraspecifically.

ABREVIATIONS

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REFERENCES

INTRODUCTION

In a recent publication, Morales et al. (1998) described the specimens from Arradistrift, Namibia. Excavations that were undertaken in the past few years have led to the discovery of additional taxa which were not represented in the earlier sample. The aim of this paper is to describe the postcranial remains of these new specimens from the early Middle Jurassic of Namibia.

SYSTEMATIC DESCRIPTION

Family Theropoda Owen, 1861
Genus Omosuchus n. gen.
Species O. deinostratus n. sp.

Eymology. The genus is named for the Orange River, with the suffix -saurus which is often used in naming the remains of extinct carnivorous mammals in the Klerksdorp area of the Orange River.


Diagnosis: Primitive sphenosuchian, intermediate in size between Therapsida and Proterotheria. Characteristic of the parietal element M, short with high and broad trigonid in which the metastylid is important and the proconid is in a very anterior position. Small talonid with very well developed hypoconulid, retaining the height of the hypoconid, M relatively large, with open trigonid in that there remains a small paracristid and the metastylid is slightly anterior than the procanid; the talonid is very well developed, more anterior than the hypoconid, and is separated from it and the hypoconid.

DESCRIPTION OF THE HOLOTYPE
The specimen is poorly preserved, but would have been robust with a wide section. The P1 is the most complete and very reduced. The P2 has a somewhat more cusp, a small low anterior cusp and a small but high posterior cusp, and there is a small basal cusp in the posterior cusp. The P3, is more robust than the other processes and possesses a large posterior cusp, which is more anterior and is separated from it and the hypoconid.

Type Locality Arradistrift, Southern Namibia, in the basal Middle Jurassic (Frasnian, Set. 1) approximately MN 1254 b.