

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

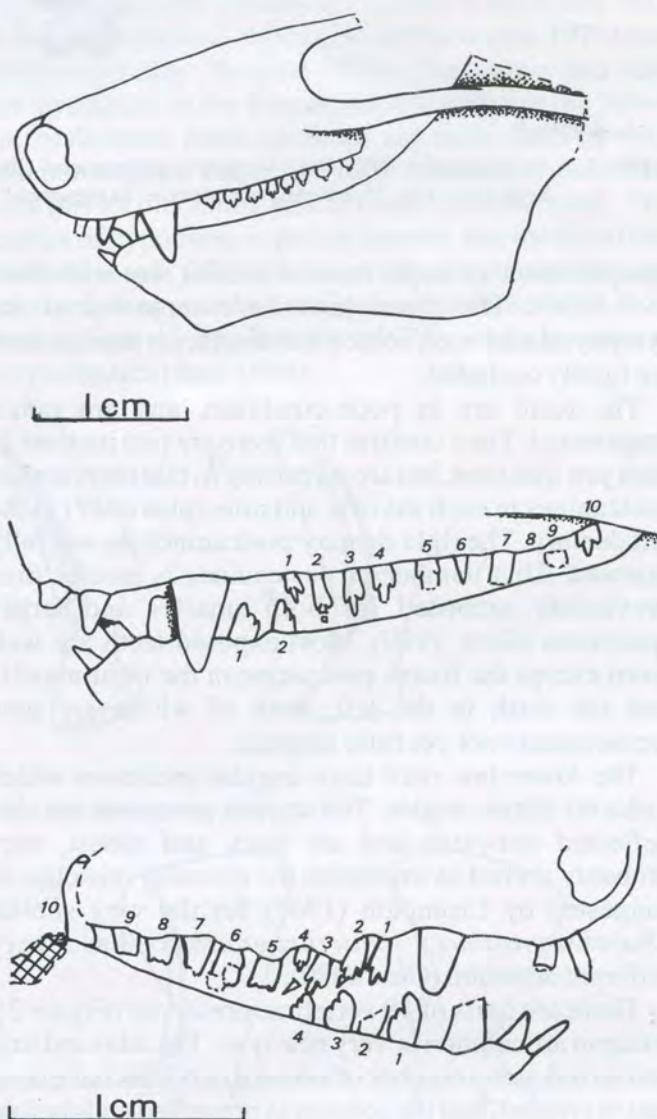


Figure 1. *Pachygenelus* BP/1/5623. Left lateral view of skull as preserved, detail of left and right dentitions. Scale bars = 1 cm.

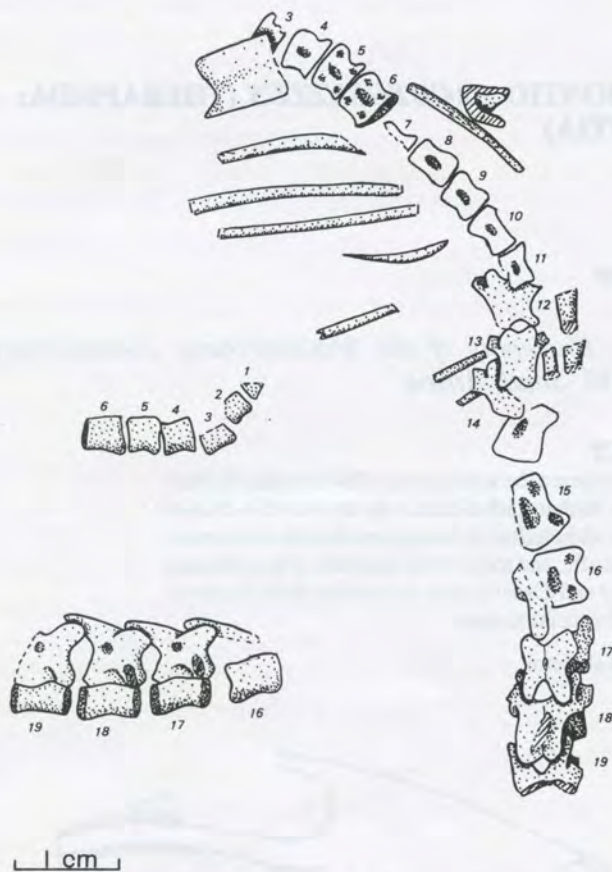


Figure 2. *Pachygenelus* BP/1/5623 Vertebral column and ribs. Scale bar = 1 cm. Numbering of vertebrae "as preserved".

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 fragmented. 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

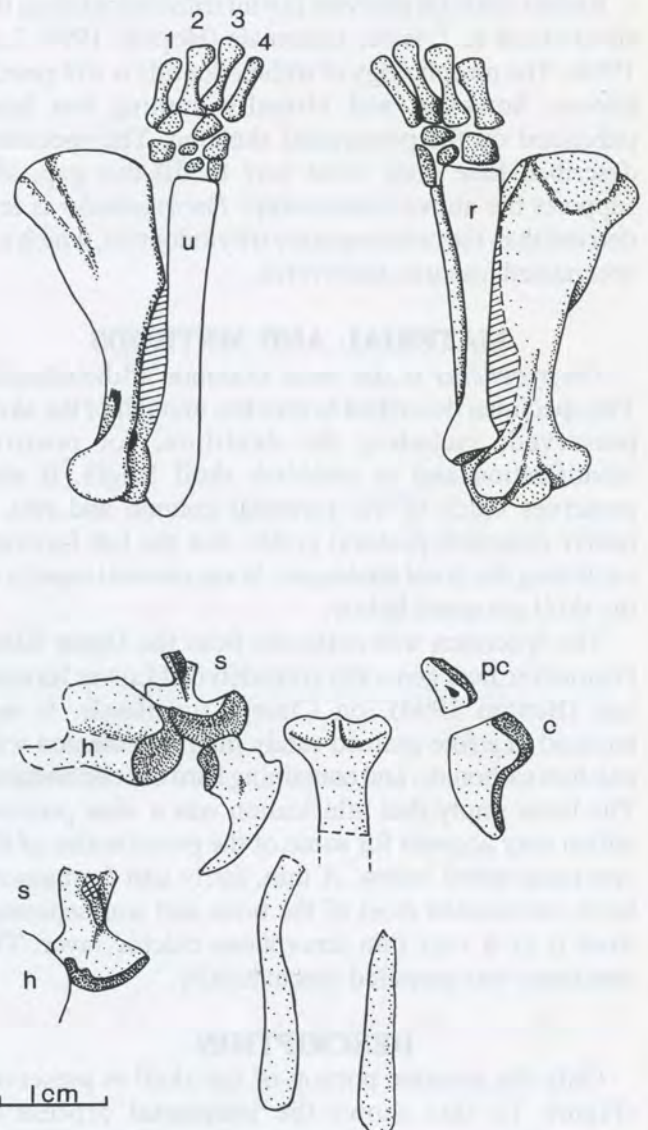


Figure 3. *Pachygenelus* BP/1/5623. Pectoral girdle and forelimb. Scale bar = 1 cm.

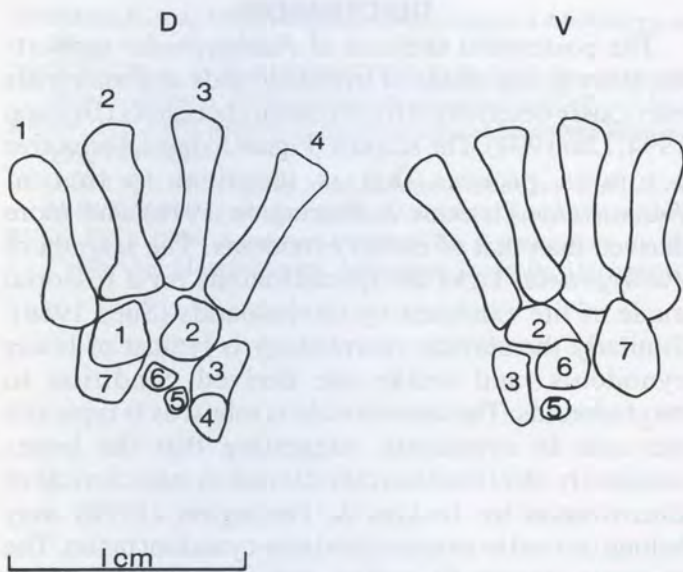


Figure 4. *Pachygenelus* BP/1/5623. Wrist detail, dorsal and ventral. Scale bar = 1cm. Note bones are still supported by matrix.

1986).

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).

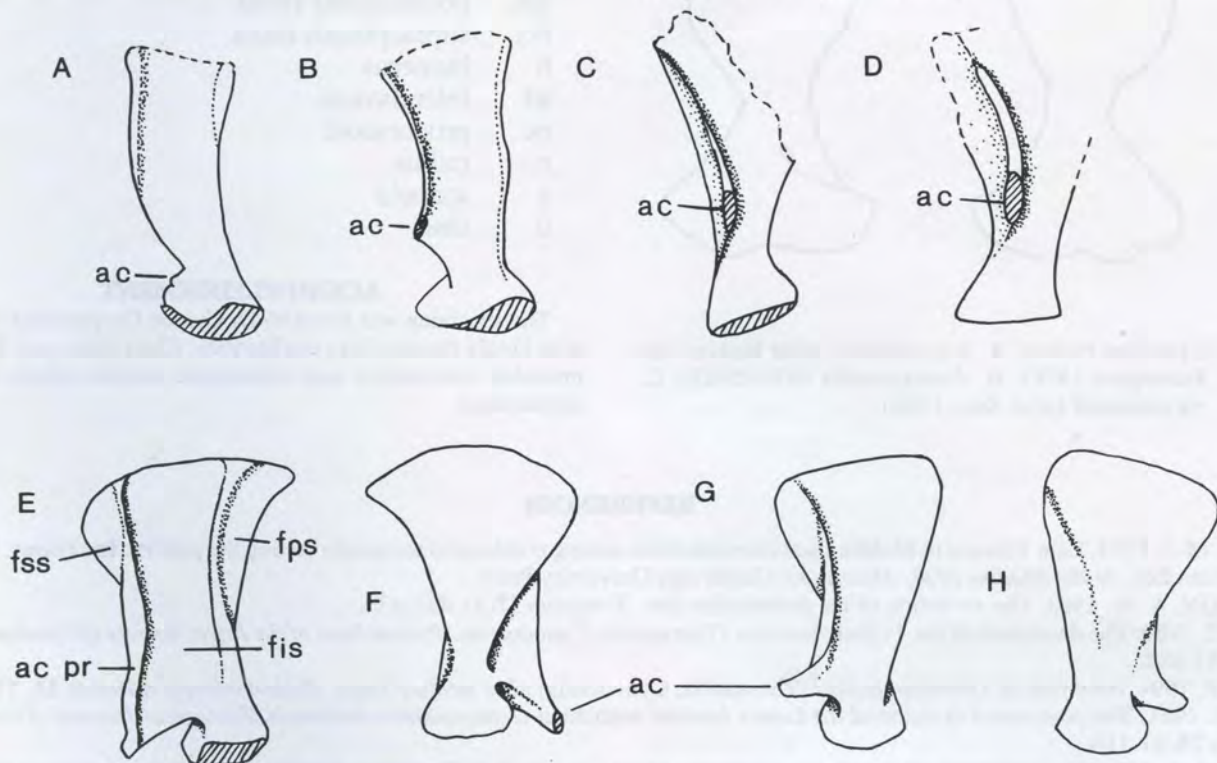


Figure 5. Cynodont scapulae. A, *Cynognathus* (after Jenkins 1971), B, *Luangwa* (after Kemp 1980), C, *Pachygenelus* (BP/1/5623), D, *Megazostrodon* (after Jenkins & Parrington 1976), E & F *Kayentatherium wellsi* (after Sues 1986), G & H, *Tritylodon longaevus* (BP/1/5167).

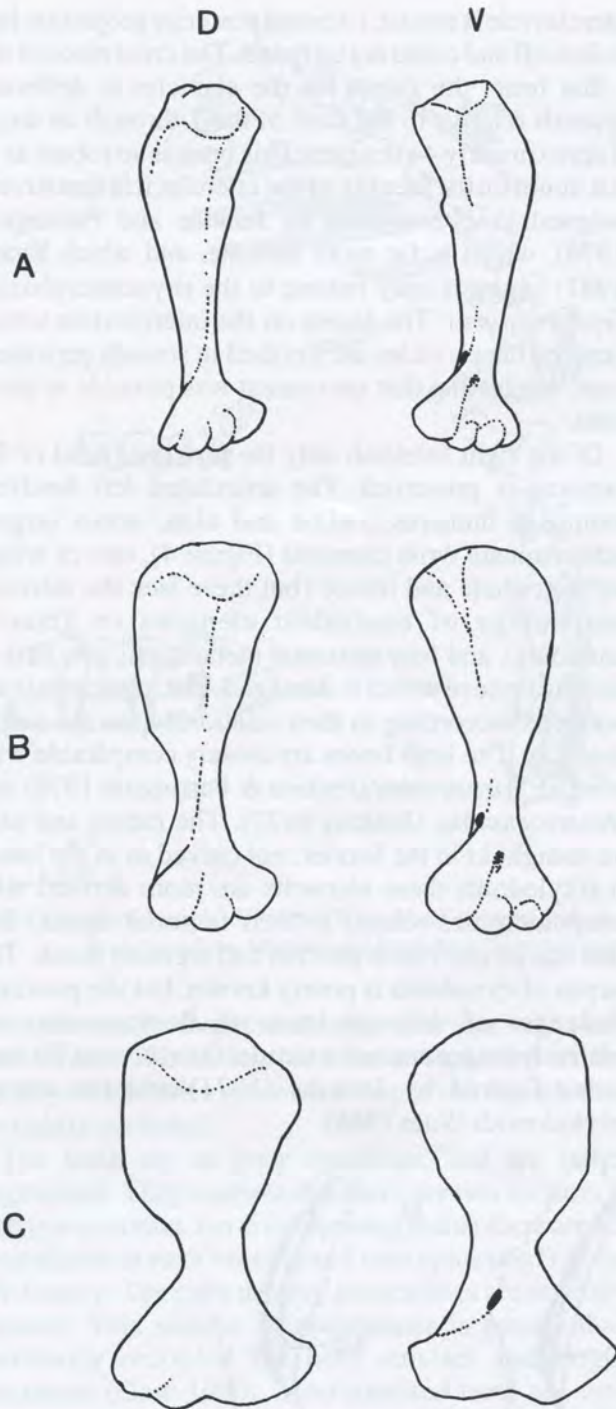


Figure 6. Cynodont humeri. A, *Eozostrodon* (after Jenkins and Parrington 1976), B, *Pachygenelus* (BP/1/5623), C, tritylodontid (after Sues 1986).

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.

ABBREVIATIONS

ac	acromion
ac pr	acromion process
c	coracoid
cl	clavicle
fis	infraspinous fossa
fps	postscapular fossa
fss	supraspinous fossa
h	humerus
icl	interclavicle
pc	procoracoid
r	radius
s	scapula
u	ulna

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ABSTRACT

A new genus and species of viverrid of modern type, *Orangicetus garrispensis*, is described from the basal Middle Miocene locality of Arrisdrift in southern Namibia. It is the earliest known representative of the subfamily Viverrinae from Africa. Detailed examination of the molarized-like carnivorans of the early Miocene of Africa, hitherto all assigned to the family Viverridae, reveals that most of them are related to this group.

KEYWORDS: Middle Miocene, Namibia, Viverridae, Carnivora, Arrisdrift

INTRODUCTION

In a recent publication, Morales *et al.* (1998) described the carnivore fauna from Arrisdrift, 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 assemblage. The aim of this paper is to describe a new genus of viverrid from this early Middle Miocene site.

SYSTEMATIC DESCRIPTION

Family Viverridae Gray, 1821

Subfamily Viverrinae Gill, 1872

Genus *Orangicetus* nov.

Species *Orangicetus garrispensis* nov.

Etymology: The genus is named for the Orange River with the suffix *cetus* which is often used in composing the names of small carnivores. *Garrisp* is the Khoi name for the Orange River.

Holotype: AD 613/98, hemi-mandible with C-M₂ (Figure 1), housed at the Geological Survey of Namibia Museum, Windhoek.

Paratype: AD 119/98, right mandible with C-M₁ (Figure 2), housed at the Geological Survey of Namibia Museum, Windhoek.

Diagnosis: Primitive viverrine intermediate in size between *Viverricula indica* and *Viverra zibetha*. Robust dentition: P₂ with greatly reduced anterior cusplet, M₁ short with high and closed trigonid, in which the metaconid is important and the paraconid is in a very lingual position. Small talonid with very well developed entoconid, attaining the height of the hypoconid. M₂ relatively large, with open trigonid in that there remains

a small paraconid and the metaconid is slightly higher than the protoconid, the talonid is deeply notched and like that of M₁, but the hypoconid is higher than the entoconid and is separated from it and the hypoconid.

Type locality: Arrisdrift, Spangkop, Namibia.

Age: Basal Middle Miocene (Fornal Set P 61a) (approximately MN 4) ca 17.5 Ma.

DESCRIPTION OF THE HOLOTYPE

The canine is poorly preserved, but would have been robust with an oval section. The P₁ is unisulcate and very reduced. The P₂ has a voluminous main corp., a small low anterior cusplet and a small but high distal cusplet, and there is a small basal cingulum posteriorly (Figure 1). The P₃ is similar to the P₂ but the cusplets and cingulum are better developed. The P₄ is more robust than the other premolars and possesses a large posterior cusp in a more buccal position, and an enlarged posterior cingulum which lingually develops two medium sized cusplets. The anterior cusplet is small. The M₁ is slightly concoid on its external wall at the height of the hypoconid and on the internal wall of the paraconid. Nevertheless, the structure of the tooth is clearly visible. The trigonid has an v-shaped occlusal morphology with a high, voluminous metaconid situated close to the protoconid which occupies a very lingual position. The talonid is well developed, possessing a strong entoconid which is possibly slightly lower than the hypoconid, but in any case almost the same height as it. The entoconid is joined to the hypoconid by a low but well developed hypoconulid which closes the posterior margin of the talonid. The entoconid is clearly separated from the metaconid, so much so that a small, low, low-let exits between them. The lingual wall of the hypoconid is oblique to the axis of the tooth, being oriented towards