PROCEEDINGS
of the
# LINNEAN SOCIETY
of
NEW SOUTH WALES

This volume contains a selection of papers dealing with vertebrates or vertebrate fossil sites, arising from a Symposium held by the Linnean Society of New South Wales at Wellington Caves, New South Wales, in December 1995. Papers concerning Holocene vegetation will appear in volume 118.

The opening session of that symposium was held in Cathedral Cave. The cover of this volume is based on a colour photograph, supplied by the Museum of Natural History, London, of an aquatint of nearby Breccia Cave, also known as Mitchell's Cave, by Thomas Mitchell. It was first published in 1831 in Part XIV of the Edinburgh New Philosophical Journal. A version of this drawing was also published by Mitchell in 1838 in his book "Three expeditions into the Interior of Eastern Australia".

The legend to the original states, "The cave in which the fossil bones are found at Wellington Valley is in compact secondary limestone, as described more fully in a memorandum which accompanied a very large bone sent by Mr Rankin to Prof. Jameson. It is near a larger cave* where no breccia has been found, and which is very different in character from that of which this drawing is intended to convey an idea, the appearance of disruption and with unshapely masses overhanging being characteristic of all the situations where the fossil bones have hitherto been discovered in N.S. Wales. 12 Oct 1830. The bone above mentioned is that of an elephant**".

*Cathedral Cave
**It was *Diprotodon*

VOLUME 117
March 1997

# Dedication

## Professor Richard Dehm

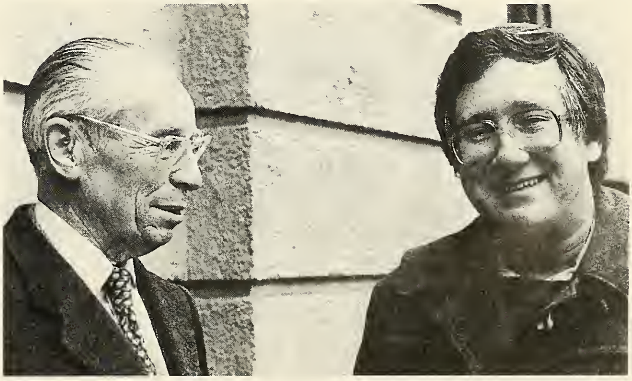
July 1907– March 1996

The contents of this volume would have been noticeably different and the course of research into Australian Quaternary mammals substantially altered had fate not intervened to prevent research begun by Dr Richard Dehm from being concluded. Inspired by lectures and contacts with cave researchers from his teenage years, Dr Dehm jumped at the chance to travel to Australia in 1939 with his colleague Dr Joachim Schröder, supported and encouraged by the director of the Bavarian Collection of Palaeontology and Historical Geology in Munich. The timing was however most unfortunate, and the two scientists found themselves in Australia when war broke out between Germany and Great Britain. The story of their internment and difficult return to Germany has been partly told (Augee at al., 1986, *The Australian Zoologist* **22**, 3–6), and further details and documentation provided by Prof Dehm shortly before his death will, when fully translated, be incorporated into a future publication. The tragic outcome for palaeontology was that fossils collected from Australia, especially from Wellington Caves and Jenolan, were largely destroyed or lost. The few that survived the misfortunes of war remain in the museum at Munich, excellently preserved and stored, but are of little research value. A list which I compiled while on study leave in Munich in 1986 is held in the archives at the Wellington Caves Fossil Studies Center.

Richard Dehm had the view that the remains of small animals, particularly mammals, held the secret to understanding climatic and faunal changes. He studied fossils found in fissure fillings, and therefore Wellington Caves were of particular interest. Prof Dehm had a life-long desire to return to Australia and sites such as Wellington and Jenolan, however a successful career and the added duties from 1958 as Director of the "Universitätsinstitut and Staatssammlung für Paläontologie und Historische Geologie München" intervened and he was never to make the journey. In a way the research he would have carried out was finally begun in the early 80s when the University of NSW began the stratigraphically controlled excavation in Cathedral Cave. A brass plaque at Wellington Caves marks one of the spots from which the remaining Munich collection was obtained, and this is readily viewed by visitors to the Phosphate Mine section.

Prof Dehm remained very active following his retirement as Director of the Munich collection and museum. During my three month study of the Australian mammal fossil in Munich, he was a delightful host, with a keen interest in current Australian palaeontological studies on which he was well informed. His death marked the end of a remarkable career and a sad loss to colleagues around the world.

*M.L. Augee*



*Richard Dehm (left) and Michael Augee on the steps of the Munich museum which houses the Bavarian state fossil collection, winter 1985.*

# Giant Ringtail Possums (*Marsupialia, Pseudocheiridae*) and Giant Koalas (*Phascolarctidae*) from the Late Cainozoic of Australia

MICHAEL ARCHER, KAREN BLACK AND KERRY NETTLE

School of Biological Science, University of New South Wales, Sydney N.S.W. 2052

Archer, M., Black, K. and Nettle, K. (1997). Giant Ringtail Possums (Marsupialia, Pseudocheiridae) and Giant Koalas (Phascolarctidae) from the late Cainozoic of Australia. *Proceedings of the Linnean Society of New South Wales* **117**: 3-16

While seven pseudocheirids have been described from the late Oligocene to early Miocene and five from the Pliocene of Australia, none are known to have been confined to the Pleistocene. We describe here a giant ringtail, *Pseudokoala cathysantamaria* n. sp., from the early Pleistocene Portland Local Fauna (lower Nelson Bay Fm) of Victoria. We review the generic distinction of the Miocene–Pliocene *Corracheirus* Pledge, 1992 and conclude that it is a junior synonym of *Pseudokoala* Turnbull and Lundelius, 1970. The palaeohabitat for all species of *Pseudokoala* appears to have been rainforest. A second pseudocheirid in the Portland Local Fauna is most similar in morphology and size to the still-living *Pseudocheirus peregrinus*, a species whose habitat range also includes rainforest. We describe the first known upper and additional lower molars for the giant koala *Cundokoala yorkensis* Pledge, 1992, from a Pleistocene deposit in Wellington Caves, New South Wales, a taxon previously only known from Pliocene sediments of South Australia. The Portland giant ringtail and Wellington giant koala add two more families to the already extensive list that exhibited Pleistocene gigantism. Previously, only one other lineage (tree kangaroos) of arboreal mammals has been known to have undergone gigantism.

Manuscript received 6 June 1996, accepted for publication 23 October 1996.

KEYWORDS: Koalas, Phascolarctidae, Pleistocene gigantism, Pseudocheiridae, Quaternary, ringtail possums.

## INTRODUCTION

The record for ringtail possums (Pseudocheiridae) begins in the late Oligocene. From sediments of this age in South Australia, Woodburne et al. (1987a) and Pledge (1987b) describe four species of *Pildra*, two of *Marlu* and one of *Paljara*. Archer (1992) reports over twelve additional unnamed taxa from the Oligo-Miocene sediments of Riversleigh, northwestern Queensland. Archer and Bartholomai (1978) note a *Pseudochirops* from the late Miocene of Alcoota, Northern Territory. Turnbull and Lundelius (1970; augmented by Turnbull et al. 1987) describe *Pseudokoala* from the early Pliocene Hamilton Local Fauna as well as two species of *'Pseudocheirus'* which may (Archer 1984) represent the otherwise modern genus *Petauroides*. Another species of *Pseudochirops*, from the early Pliocene Bluff Downs Local Fauna of northeastern Queensland, is under study (B. Mackness and M. Archer). Pledge (1992) describes a giant species of *Corracheirus* from the late Miocene to Pliocene Curramulka Local Fauna of southern South Australia as well as a single tooth of another large pseudocheirid from the Plio-Pleistocene Cement Mills Local Fauna of southeastern Queensland. Until now, however, no giant pseudocheirids have been reported from undoubted Pleistocene sediments. The tooth described here as *Pseudokoala cathysantamaria*, from early Pleistocene deposits at Portland, Victoria, is the only ringtail possum confined to the Pleistocene and the only giant ringtail known from the Quaternary.

Fossil koalas (Phascolarctidae) are similarly known from late Oligocene and younger sediments. Stirton (1957), Stirton, Tedford and Woodburne (1967), Woodburne et al. (1987b) and Springer (1987) describe six species in the Oligo-Miocene genera *Perikoala, Litokoala* and *Madakoala*. Black and Archer (in press) name another Miocene genus from Riversleigh and Black (in prep.) reports additional Miocene taxa from Riversleigh. Pledge (1992) describes a Miocene to Pliocene species of the giant *Cundokoala*. Bartholomai (1968) describes a large Plio-Pleistocene Queensland species of the modern genus *Phascolarctos*. Pledge (1987a) describes another large *Phascolarctos* from the early Pliocene of South Australia. We describe here isolated teeth, from Pleistocene deposits of Wellington Caves, New South Wales, that appear to represent the same Miocene/Pliocene South Australian species described by Pledge (1992) as *Cundokoala yorkensis*. The Wellington material includes the first known upper molars for this taxon.

Material described is registered in the palaeontological collections of three institutions as follows: AM F numbers represent the Australian Museum fossil collection; P numbers represent the palaeontological collections of the Museum of Victoria; SAM P numbers represent the palaeontological collections of the South Australian Museum. Dental terminology used here follows Luckett (1993) for molar homology, Flower (1867) for premolar homology and Archer (1984) and Woodburne et al. (1987a,b) for molar morphology.

## SYSTEMATICS

Class Mammalia Linneaus, 1758
Superorder Marsupialia Illiger, 1811
Order Diprotodontia Owen, 1866
Superfamily Phalangeroidea Weber, 1928
Family Pseudocheiridae Winge, 1893

### *Pseudokoala* Turnbull and Lundelius, 1970

Type species:

*Pseudokoala erlita* Turnbull and Lundelius, 1970

Additional species:

*Pseudokoala curramulkensis* (Pledge, 1992) and *Pseudokoala cathysantamaria* n. sp.

Revised generic distribution:

Corra Lynn Cave, Yorke Peninsula, South Australia; Hamilton Local Fauna, south-western Victoria; Portland Local Fauna, Nelson Bay Formation, Portland, Victoria.

Revised age range for the genus:

The Hamilton Local Fauna is interpreted (Rich et al. 1991) to be early Pliocene in age. The Curramulka Local Fauna is interpreted (Pledge 1992) to be late Miocene to Pliocene in age; the Nelson Bay Formation is interpreted (Flannery and Hann 1984) to be early Pleistocene in age.

Revised generic diagnosis:

Species of *Pseudokoala* are distinguished from *Marlu praecursor* by their continuous postmetacristid and preentocristid, and posthypocristid which does not extend to the lingual side of the crown. They are distinguished from *M. kutjamarpensis* by their continuous postmetacristid and preentocristid, connection of the cristid obliqua to the metacristid and their truncated posthypocristid. They are distinguished from species of *Pildra* and *Paljara* in their lack of an entostylid, presence of a buccal buttress on the protoconid, *en echelon* overlap of the postmetacristid and preentocristid, large size, and truncated posthypocristid. They are distinguished from species of *Pseudocheirus*, *Petauroides* and *Hemibelideus* in having a truncated posthypocristid, being much larger in size, having a second buccal buttress on the protoconid, not having steep entoconid blades and in lacking a protostylid. They are distinguished from species of *Pseudochirops* in having a truncated posthypocristid, being larger in size, having a second buccal buttress on the protoconid, not having steep entoconid blades, having the cristid obliqua connected to the metacristid, and in lacking a protostylid.

### *Pseudokoala curramulkensis* (Pledge, 1992)

Emendation of dental homology for the paratype and referred specimen:

Pledge (1992) notes three specimens including the Holotype. The homology of the teeth (using the M1-4 molar homology system of Luckett 1993) given in table 5 needs emendation as follows. SAM P29901 (referred specimen) is a right dentary fragment with $M_2$ (not $M_1$) and alveoli for $M_1$ and $M_{3-4}$. SAM P31792 (Paratype) is a left dentary fragment with $M_{2-3}$ (not $M_{1-2}$) and alveoli for $M_1$ and $M_4$.

### *Pseudokoala cathysantamaria* n. sp.

Holotype:

P173650, an isolated LM$_1$ (Fig. 1).

Type Locality:

Interpreted to be Nelson Bay, Portland, Victoria, although no specific locality details are recorded in the Museum of Victoria Palaeontology register (B. Thompson, pers. comm. to M. Archer), nor are there any details on the specimen label. However, it is registered within a series of fossils, including P173649 (a dentary of *Pseudocheirus* sp. cf. *P. peregrinus*; see below), for all of which the locality data is Nelson Bay, Portland, Victoria.

Age:

Marine invertebrates from the Lower Nelson Bay Formation, the probable source of the Holotype, are early Pleistocene in age (Flannery and Hann 1984).

Etymology:

In honour of Cathy Santamaria for her constant interest and much appreciated encouragement for palaeontological research in Australia.

TABLE 1

Measurements of *Pseudokoala* material. All measurements in millimetres.

| Specimen | P3 | | M1 | | | M2 | | | M3 | | | M4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L | W | L | AW | PW | L | AW | PW | L | AW | PW | L | AW | PW |
| MV P173650 | | | 10.7 | 5.20 | 5.60 | | | | | | | | | |
| SAM P26542 | | | 10.9 | 4.51 | 5.20 | | | | | | | | | |

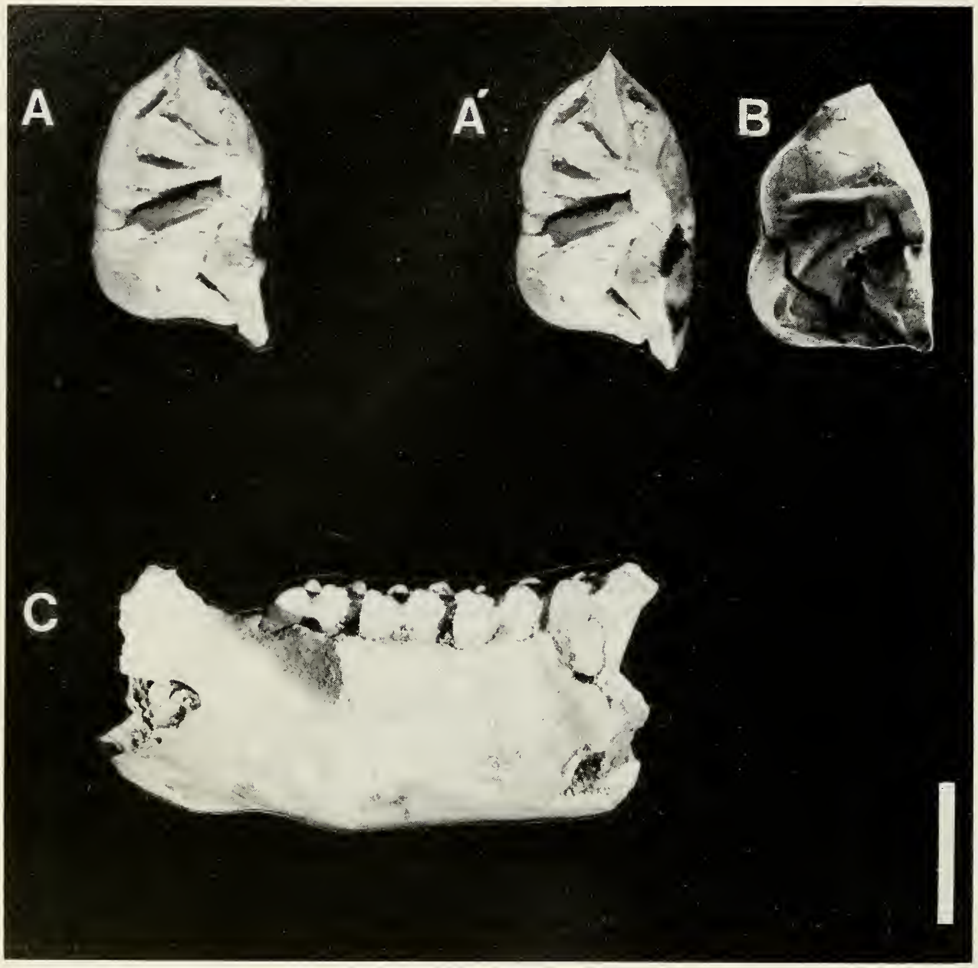


Figure 1. A-A', Holotype of *Pseudokoala cathysantamaria* n.sp, Museum of Victoria P173650, occlusal stereopair of left $M_1$, from the early Pleistocene of Portland, Victoria; B, *Pseudokoala erlita*, NMV P54159, left $M_1$, occlusal stereopair; C, *Pseudocheirus* sp. cf. *peregrinus*, Museum of Victoria P173649, a right dentary fragment with $M_{1-4}$, from the early Pleistocene of Portland, Victoria . Bar indicates 5mm.

Species diagnosis:

*Pseudokoala cathysantamaria* is a giant ringtail possum with molar teeth at least 20% larger than those of *P. erlita* (Turnbull et al. 1987) but comparable in size (Table 1) to *P. curramulkensis* (Pledge 1992; see below). It is also distinguished from *P. erlita* by having an extra anterior vertical buttress (as well as a posterior one) on the buccal flank of the protoconid, an anterobuccal vertical trigonid cleft anterior to the extra vertical buttress, an anterolingual basal cingulum and cingular pocket, a lingually convex metacristid, posterior elongation of the postentocristid, and mesostylids between the bases of the hypoconid and protoconid. Although the missing anterior half of $M_1$ for *P. curramulkensis* prohibits comparisons in this area, the tooth of *P. curramulkensis* is smaller, appears to lack at least the posterior mesostylid, may lack the anterior flexure on the cristid obliqua, and has a much shorter postentocristid. In this feature, the three species appear to form a gradient with the postentocristid of *P. erlita* the least extended and that of *P. cathysantamaria* the most.

Description:

The Holotype (Fig. 1) is the least worn of any *Pseudokoala* specimen known enabling details of dental morphology in the genus to be clarified. $M_1$ has a large, medially situated protoconid (as in *P. erlita*) which is connected by a steep anterior paracristid to a tiny possible paraconid (not evident in *P. erlita* and unknown for *P. curramulkensis*), and by a gently inclined posterior metacristid to a poorly distinguished metaconid (as in at least *P. erlita*). Two prominent, vertical buccal buttresses subtend the protoconid. There is a tiny, anterolingual basin defined by a small, basal anterolingual cingulum, an anterobuccal cingula and a marked, vertical, anterobuccal trigonid cleft. Between the cristid obliqua and posterior buccal buttress are two basal mesostylids.

The following features of *P. cathysantamaria* are also evident (where they can be checked) in the holotype of *P. curramulkensis* and *P. erlita*. There is no protostylid. At the posterior end of the metacristid is a topographically defined metastylid immediately buccal to the anterior end of the preentocristid. The cristid obliqua does not run directly to the metacristid but instead veers anterobucally to tangentially contact the metacristid. There are pronounced crenulations on the lingual side of the cristid obliqua. There is *en echelon* overlap of the postmetacristid over the preentocristid. The paracristid, metacristid and postentocristid are elongate and together define a composite blade that extends the length of the whole tooth. The entoconid blades are not steeply inclined. There is no entostylid. The posthypocristid is truncated at the lingual end before it reaches the postentocristid. It stops far short of the posterolingual corner of the tooth, leaving the posterior end of the postentocristid (which extends posteriorly further than the same crest in the other species of *Pseudokoala*) to define the edge of the crown. In terms of relative height on the crown, the protoconid is just higher than the metaconid which is higher than the entoconid which is higher than the metastylid which is higher than the hypoconid which is higher than the paraconid.

Discussion:

Estimates of body size for *Pseudokoala cathysantamaria*, based on tooth and body size in *Phascolarctos cinereus*, suggest that this ringtail may have weighed 9–10 kg, far larger than any living ringtail possum. However, it is only slightly larger than the Curramulka giant ringtail described by Pledge (1992) as *Corracheirus curramulkensis*. Pledge (1992) suggests that species of *Corracheirus* (viz. *C. curramulkensis*) are differentiated from those of *Pseudokoala* (viz. *P. erlita*) by three features: 1, larger size; 2, having the postprotocristid continuous with the cristid obliqua rather than extending to the metastylid; and 3, having a continuous entocristid with a simple metastylid flexure.

Large size is not normally regarded to be a basis for establishment of a monotypic genus (in this case for *curramulkensis* Pledge). Considering the second feature, there are three specimens of *P. curramulkensis* noted in the type description: the Holotype with part of $M_1$ and $M_{2-4}$, and SAM P29901 with $M_2$ which support the distinction with the postprotocristid appearing to make no contact with the metastylid; and SAM P31792 with $M_{2-3}$ where the postprotocristid bypasses (but is touched by) the cristid obliqua to make contact with the metastylid flexure. Consequently, this feature appears to be variable and does not distinguish species of *Corracheirus* from those of *Pseudokoala*. Considering the third distinguishing feature, the Holotype and SAM P29901 do support the suggestion that the preentocristid is continuous with metacristid via a simple metastylid flexure. However, the condition in SAM P31792 is much closer to the *P. erlita* condition in that there is only a very tenuous direct connection linking the preentocristid and the metacristid via a fine and low bridge of enamel buccal to the metastylid. In this specimen, the preentocristid and metacristid really overlap *en echelon*, with the preentocristid passing anterobuccal to the posterior end of the metacristid to make contact with the postprotocristid, a condition closer to that seen in *P. erlita*.

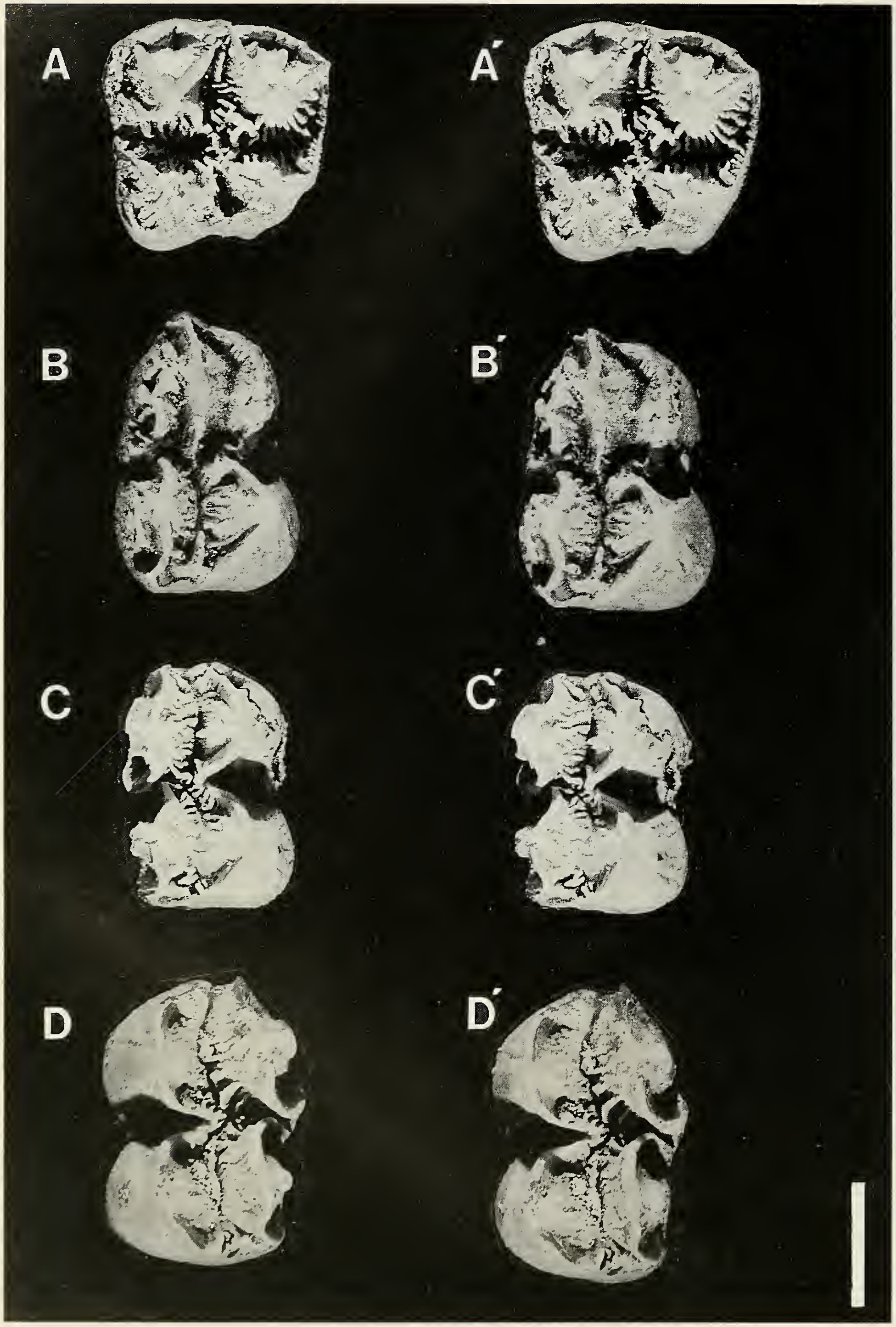


Figure 2. *Cundokoala yorkensis*, referred material from Wellington Caves, New South Wales. A-A', AMF98885, a left $M^1$. B-B', AMF98886, a right $M_1$. C-C', AMF98889, a right $M_2$. D-D', AMF98890, a left $M_3$. Bar indicates 5mm.

Conversely, comparison of SAM P31792 with the $M_3$ or $_4$ of *P. erlita* illustrated in Turnbull, Rich and Lundelius (1987, Fig. 2C) suggests basic overall similarity in all key features (except, possibly, the degree to which the metacristid is lingually concave and the degree of posterior development of the postentocristid; see below). *Corracheirus curramulkensis, P. erlita* and *P. cathysantamaria* also exhibit a striking synapomorphy of $M_1$: truncation of the posthypocristid such that it stops well short of the lingual side of the crown and does not contact any other structure. This condition differs from all other pseudocheirids where the posthypocristid closely approximates the postentocristid (or the entostylid) at or near the lingual margin of the tooth. All three taxa also exhibit a tendency to posteriorly extend the postentocristid, a feature best-developed in $M_1$. Finally, all three taxa appear to be united in their tendency towards gigantism. For these reasons, we suggest that *Corracheirus* Pledge, 1992 is better regarded as junior synonym of *Pseudokoala* Turnbull and Lundelius, 1970 which then contains three species: *erlita* Turnbull and Lundelius, 1970; *curramulkensis* Pledge, 1992; and *cathysantamaria* Archer, Black and Nettle (this paper), *erlita* being the type species of the genus.

Within *Pseudokoala*, *P. cathysantamaria* appears to be the sister-group of *P. curramulkensis*, these two sharing as synapomorphies extreme gigantism and greater posterior development of the postentocristid. Although the trigonid is unknown for *P. curramulkensis*, that of *P. cathysantamaria* shows two prominent buccal buttresses in contrast to one in *P. erlita*, the second buttress being an autapomorphic condition (or perhaps a synapomorphic condition shared with *P. curramulkensis*). The single buttress of *P. erlita* may be the homologue of the vertical protostylid ridge in the same position in species of *Marlu* (or the homologue of the protostylid in, e.g., species of *Pseudochirops, Pseudocheirus, Pseudocheirulus*).

Species of *Pseudokoala* share distinctive features of $M_1$ with species of *Marlu* Woodburne, Tedford and Archer, 1987 including: failure of the cristid obliqua to directly contact the postmetacristid (a deep crevice intervening); a crenulated cristid obliqua; *en echelon* overlapping of the postmetacristid and the preentocristid (in *M. kutjamarpensis* but not *M. praecursor*); a vertical buttress but no protostylid on the buccal flank of the protoconid; no entostylid; and gently inclined (rather than steeply inclined) entoconid blades. This intergeneric relationship was originally suggested by Woodburne, Tedford and Archer (1987; Fig. 23) on the basis of synapomorphies exhibited primarily by the upper molars. The new species *P. cathysantamaria* exhibits the same combination of synapomorphies, lending support to the hypothesis of a *Pseudokoala/Marlu* clade.

Marked differences between species of *Marlu* and *Pseudokoala* include the truncated posthypocristid of species of *Pseudokoala* and their better-developed entoconid blades. Differences in the nature of the connection between the preentocristid and metacristid vary within at least *P. curramulkensis* (see above) making intergeneric contrasts here of questionable value.

In terms of patristic relationships, the early Miocene *Marlu kutjamarpensis* exhibits no features that would preclude it being ancestral to the Pliocene/Pleistocene species of *Pseudokoala*.

### *Pseudocheirus* Ogilby, 1837

### *Pseudocheirus* sp. cf. *P. peregrinus* (Boddaert, 1785)

Specimen:

P173649, a right dentary with $M_{1-4}$ (Fig. 1).

Locality:

Nelson Bay, Portland, Victoria. Label data also records: 'Monash Univ. field trip (1973?)' and '# 280 004'.

Age:

The marine invertebrate assemblage of the Lower Nelson Bay Formation, source of P173649, is early Pleistocene in age (e.g., Flannery and Hann 1984).

Description:

P173649 is a *Pseudocheirus peregrinus*-sized ringtail possum (Table 2) with overall similarity to *P. peregrinus* and *P. occidentalis*. It is, however, distinguished from these modern species (most individuals but not all, these features being somewhat variable in at least *P. occidentalis*) in that: the preentocristid is connected to the metastylid on $M_{2-4}$; and the metaconid on $M_1$ is less distinct. It is distinguished from *Pseudocheirulus herbertensis* in that: the preentocristid is connected to the metastylid; the $M_1$ lingual parastylid is not developed; and there is no notch between the postmetacristid and metastylid. It is distinguished from *P. caroli* and *P. forbesi* in that: the preentocristid is connected to the metastylid; the $M_1$ lingual parastylid is not developed; the preentocristid is strongly bladed; and there is no notch between postmetacristid and metastylid. It is distinguished from *P. canescens* and *P. mayeri* in that: the preentocristid is connected to the metastylid; the preentocristid is strongly bladed; and there is no notch between postmetacristid and metastylid. It is distinguished from *Hemibelideus lemuroides* in that: the buccal shelf is not prominent; and the $M_1$ metaconid is less distinct. It is distinguished from *Petauroides volans* in that: the preentocristid is connected to the metastylid; there is no entostylid ridge; and the $M_1$ metaconid is less distinct. It is distinguished from *Pseudochirops albertisii* in: not having a protostylid basin on $M_1$; lacking a prominent buccal shelf; lacking an entostylid ridge; lacking a posterobuccal trigonid basin; and in having a less distinct $M_1$ metaconid. It is distinguished from *P. corinnae* in that: the preentocristid is connected to the metastylid; it lacks a protostylid basin on $M_1$; it lacks a prominent buccal shelf; it lacks an entostylid ridge; it has no posterobuccal trigonid basin; and the $M_1$ metaconid is less distinct. It is distinguished from *P. cupreus* in: not having a protostylid basin on $M_1$; lacking a prominent labial shelf, the $M_4$ cristid obliqua is not angulate, no entostylid ridge, no posterobuccal trigonid basin; and in having a less distinct metaconid on $M_1$. It is distinguished from *P. archeri* in: not having a protostylid basin on $M_1$; having an $M_4$ cristid obliqua that is not angulate; lacking an entostylid ridge; lacking a posterobuccal trigonid basin; and in having a less distinct metaconid on $M_1$. It is distinguished from *Petropseudes dahli* in: not having a protostylid basin on $M_1$; lacking a prominent buccal shelf; lacking a posterobuccal trigonid basin; and in having a less distinct metaconid on $M_1$. It is distinguished from the species of all extinct ringtail genera in having: a well-developed $M_1$ protostylid; a preentocristid connected to the metastylid; a strongly bladed preentocristid; an entoconid that is positioned anterior to the hypoconid; a protoconid positioned lingual to the midline of $M_1$; and a less distinct metaconid on $M_1$.

TABLE 2

Measurements of *Pseudocheirus* material. All measurements in millimetres.

| Specimen | P3 | | M1 | | | M2 | | | M3 | | | M4 | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | L | W | L | AW | PW | L | AW | PW | L | AW | PW | L | AW | PW |
| MV P173649 | | | 4.16 | 1.96 | 2.22 | 4.06 | 2.15 | 2.30 | 4.05 | 2.15 | 2.27 | 4.36 | 1.88 | 2.15 |
| AM M4046 | 3.51 | 1.58 | 3.98 | 1.74 | 2.29 | 3.84 | 2.12 | 2.54 | 4.03 | 2.37 | 2.60 | 4.74 | 2.43 | 2.30 |

The early Pleistocene habitat of Portland:

The presence of an ektopodontid and *Pseudokoala cathysantamaria* in the Portland assemblage suggests a rainforest component in the palaeoenvironment. All ektopodontids occur in assemblages that have been interpreted (e.g. Archer, Hand and Godthelp 1995) to represent rainforest communities or communities that include rainforest: the late Oligocene Ditjimanka and Ngama Local Faunas, South Australia; the early and middle Miocene assemblages of Riversleigh, Queensland; the ?early or middle Miocene Kutjamarpu LF, South Australia; and the early Pliocene Hamilton LF, Victoria. The late Miocene to Pliocene Curramulka LF of South Australia, which contains *Pseudokoala curramulkensis*, is also regarded (Pledge 1992) to represent wet sclerophyll forest and/or rainforest, as is the Hamilton assemblage (Turnbull and Lundelius 1970, Turnbull, Rich and Lundelius 1987) which contains *P. erlita*. The occurrence in the Portland assemblage of *Pseudocheirus* sp., *cf. P. peregrinus* does not conflict with this interpretation because, although primarily an inhabitant of dense understorey vegetation, some modern populations of *P. peregrinus* extend well into rainforest.

## Order Diprotodontia Owen, 1866

### Suborder Vombatiformes Woodburne, 1984
### Infraorder Phascolarctomorphia Aplin and Archer, 1987
### Family Phascolarctidae Owen, 1839

### *Cundokoala yorkensis* Pledge, 1992

Holotype:

SAM P24904, left dentary with $M_{1-4}$ and alveolus for P3.

Referred material

(Fig. 2) and (Table 3): SAM P24905, partial left $M_4$ in its alveolus.

AM F98885, L $M^1$; AM F98886, R $M_1$; AM F98887, L $M_2$; AM F98888, L $M_2$; AM F98889, R $M_2$; and AM F98890, L $M_3$.

TABLE 3

Measurements of all known specimens of *Cundokoala yorkensis*. All measurements in millimetres. Abbreviations: L, length; AW, anterior width; PW, posterior width.

| Specimen | $P^3$ |  | $M^1$ |  |  | $M^2$ |  |  | $M^3$ |  |  | $M^4$ |  |  |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
|  | L | W | L | AW | PW | L | AW | PW | L | AW | PW | L | AW | PW |
| AM F98885 |  |  | 12.1 | 12.3 | 11.0 |  |  |  |  |  |  |  |  |  |
|  | $P_3$ |  | $M_1$ |  |  | $M_2$ |  |  | $M_3$ |  |  | $M_4$ |  |  |
|  | L | W | L | AW | PW | L | AW | PW | L | AW | PW | L | AW | PW |
| P24904 |  |  | 11.8 | 7.0 | 8.1 | 12.9 | 8.1 | 8.1 | 12.9 | 8.0 | 8.2 | 12.7 | 7.4 | 7.3 |
| AM F98886 |  |  | 11.5 | 6.5 | 8.0 |  |  |  |  |  |  |  |  |  |
| AM F98887 |  |  |  |  |  | 11.5 | 6.9 | 6.8 |  |  |  |  |  |  |
| AM F98888 |  |  |  |  |  | 11.2 | 7.2 | 7.0 |  |  |  |  |  |  |
| AM F98889 |  |  |  |  |  | 11.3 | 7.1 | 6.9 |  |  |  |  |  |  |
| AM F98890 |  |  |  |  |  |  |  |  | 11.4 | 7.3 | 6.7 |  |  |  |

Revised distribution:

*Cundokoala yorkensis* is known from Corra Lynn Cave, the Curramulka Local Fauna, Yorke Peninsula, South Australia and now Wellington Caves, New South Wales.

Revised age range:

The Curramulka Cave site of the typical material is interpreted by Pledge (1992) to be Miocene to Pliocene in age. The exact locality and age for all but one (AM F98886) of the Wellington Caves specimens is unknown. They were collected from the surface of spoils piles dumped outside the newly restored entrance to the Phosphate Mine. The material on these piles had been obtained during excavation of tourist paths in the Wellington Caves complex in late 1995. The source of the material for each pile was not certainly known but thought by excavation workers at the site to be various localities within the Phosphate Mine and Bone Cave. Although most of the taxa recovered to date from the Wellington Caves complex of sediments have been interpreted to be Pleistocene in age, Hand, Dawson and Augee (1988), L. Dawson et al. (in prep.) and Osborne (1983) have demonstrated that some deposits in the Wellington Caves complex (e.g., in the entrance doline of Big Sink and others in the Phosphate Mine) are Pliocene in age. Therefore the age of the *Cundokoala yorkensis* material obtained from the spoils piles could be Pliocene, Pleistocene or both.

AM F98886, however, was obtained by one of us (MA) in company with H. Godthelp, A. Gillespie, A. Musser et al. from a newly-excavated pathway in the Phosphate Mine. Material excavated at the same time included an isolated lower molar of *Diprotodon* sp. *cf. D. optatum* (only known from the Pleistocene), a dentary of *Protemnodon* sp. *cf. P. roechus* (only known from the Pleistocene), abundant dentary and maxilla fragments of *Aepyprymnus rufescens* (Pleistocene and living species) and a dentary of *Onychogalea unguifera* (living species). Although other taxa obtained at the same time have yet to be identified, nothing contradicts a Pleistocene age for this assemblage. We would conclude, pending a thorough analysis of the rest of the fauna from this deposit, that Wellington Caves *C. yorkensis* is Pleistocene in age, giving the species a Pliocene-Pleistocene age range.

Revised diagnosis

*Cundokoala yorkensis* differs from all other phascolarctids: in being larger; having higher-crowned teeth; and in having a relatively short, massive dentary. It differs from all other phascolarctids except species of *Phascolarctos* in having: a larger paraconule and neometaconule on $M^1$; a more lingually positioned protoconid and a larger protostylid on $M_1$; well-developed lingual columnar stylids on the metaconid and entoconid of $M_{1-4}$; and a well-developed buccal cingulum and metastylid fold on $M_{1-4}$. It differs from species of *Litokoala* in: lacking the posterobuccal crest which extends from the apex of the metaconid in $M_{2-4}$; lacking an anteriorly displaced entoconid (relative to the hypoconid) on $M_4$; lacking an anteriorly displaced metaconid (relative to the protoconid) on the $M_4$; and in having the postprotocristid and cristid obliqua of $M_4$ meeting in the transverse median valley on $M_4$ (in contrast to the parallel arrangement seen in *Litokoala kanunkaensis*) It differs from species of *Madakoala* and *Perikoala*: in having: a larger parastyle on $M^1$; a more crenulate, less linearly-oriented paraconule and neometaconule on $M^1$; a paraconule that connects anterobuccally to the anterior cingulum on $M^1$; an entostylid ridge on $M_{1-4}$; a more lingual junction of the postprotocristid and cristid obliqua; and in lacking protoconid-metaconid and hypoconid-entoconid crests.

Description

The new Wellington Caves materials (AM F98885 to AM F98890) augment understanding about the morphology of this species. AM F98885 is an unworn, relatively square selenodont $M^1$ that tapers posteriorly. It is morphologically very similar to the $M^1$ of species of *Phascolarctos* and differs mainly in being relatively wider anteriorly. The paracone and metacone are similar in height and are the tallest cusps on the tooth followed by the metaconule and protocone. The apex of the protocone lies lingually opposite that of the paracone. The apex of the metaconule lies lingually opposite and slightly anterior to that of the metacone. The lingual bases of the paracone and metacone and the anterolingual base of the protocone are highly crenulate. The protocone and metacone and their associated crests are slightly obliquely (anterolingually) oriented. The tooth is bisected bucco-lingually by a deep transverse median valley and antero-posteriorly by a relatively deep longitudinal valley. The buccal tooth margin is mildly convex sloping anterolingually at the anterolingual tooth margin and curving posterolingually around the buccal margin of the metacone. The lingual bases of the protocone and metaconule slope gently towards the base of the crown. The lingual bases of the paracone and metacone slope more steeply into the longitudinal tooth valley. The triangular buccal surface of the paracone is reduced relative to the metacone as is the paracone buccal margin. The buccal basin of the paracone is closed and deep. The buccal basin of the metacone is comparatively shallower but remains closed. A ridge-like stylar shelf extends along the length of the buccal tooth margin. The relative heights of stylar cusps in descending order are as follows: stylar cusp C, B, A, D and E. The preparacrista, postparacrista, premetacrista and postmetacrista which make up the buccal selene of the tooth, are distinct linear crests which extend from the apices of the paracone and metacone respectively. The lingual selene is offset posteriorly and is composed of a relatively linear preprotocrista and premetaconule crista and a crescentic postmetacrista and highly crescentic postprotocrista. The postprotocrista and premetaconulecrista meet in the transverse median valley at a point slightly lingual to the longitudinal valley. The parastyle is poorly developed. It exists as a slight swelling of the anterior cingulum at the anterobuccal corner of the tooth. A shallow pocket is created between the anterior cingulum and the anterior base of the paracone. Lingually, the pocket is defined by a small, crenulate, but distinct paraconule which lies at the anterolingual base of the paracone. A short, non-cuspate, spur-like protostyle which originates from the preprotocrista at a point slightly lingual to the longitudinal valley, extends posteriorly along the buccal base of the protocone, terminating opposite the protocone apex. A well developed anterolingual paracrista connects the paraconule posteriorly to the apex of the paracone. A similarly well-developed posterolingual paracrista extends from the apex of the paracone into the junction of the transverse median and longitudinal valleys wherein it divides into two spurs which become part of the crenulation pattern of the tooth.

A small, crenulate, non-cuspate neometaconule lies in the longitudinal tooth valley at the anterolingual base of the metacone. It is connected to the metacone base by a weak anterolingual metacrista, which originates approximately half way down the base of the metacone. A posterolingual metacrista is absent. A crenulate, cingulum-like shelf runs along the anterior and anterolingual base of the protocone forming a shallow pocket between the cingulum and the protocone base. A weak anterolingually directed crest extends from the apex of the protocone to meet the anterolingual cingulum. A similar, but deeper pocket occupies the anterolingual base of the metaconule and is bounded by the posterior base of the protocone anteriorly, the anterior base of the metaconule posteriorly, the junction of the premetaconule crista and postprotocrista buccally, and a short, crescentic lingual cingulum lingually. The lingual cingulum effectively closes off the lingual exit of the transverse median valley and is continuous with a weak crest that extends anterolingually from the apex of the metaconule. Weak buccally directed spurs extend from the apices of the protocone and metaconule, fading down their respective bases towards the longitudinal valley. A well developed posterior cingulum is continuous with the postmetaconulecrista lingually and buccally and meets stylar cusp E at the posterobuccal tooth corner.

The $M_1$ of the holotype is poorly worn and the anterolingual tooth corner is missing. Consequently, much of the crown morphology of the trigonid has been lost. In AMF98886 the preprotocristid is a well defined, linear crest which terminates anteriorly in a small paraconid. The preprotostylidcristid extends anterolingually to terminate at the base of the paraconid. Pledge (1992), in his description of the holotype $M_1$, suggests that *C. yorkensis* differs from all other phascolarctids in having a fine anterobuccal spur of the preprotocristid meet the preprotostylidcristid at the anterior tooth margin. Its absence in AM F98886 suggests this is a variable feature within the species, and the preprotocristid spur is most probably part of the crenulation pattern of the tooth. A well-developed posterobuccal ridge extends from the protostylid apex in AM F98886. This crest is only vaguely discernible in the holotype. The buccal cingulum is better developed in AM F98886. The postprotocristid meets the anterior base of the cristid obliqua at a slightly more lingual position than in the holotype. The lingual columnar stylids of the metaconid and entoconid are large, crenulate and well preserved in AM F98886 whereas they are only represented by slight swellings in the holotype. The entostylid is a well-developed, cuspate swelling on the terminus of the postentocristid at the posterolingual tooth corner in AM F98886. AM F98887, AM F98888 and AM F98889 ($M_2$) are morphologically similar to but smaller than the $M_2$ of the holotype. Again, the holotype is highly worn, the apices of all major cusps are missing and the lingual tooth margin is damaged such that the columnar stylids are not preserved and the entostylid is missing. In contrast, all of the Wellington Caves $M_2$ specimens show little or no wear. The columnar stylids are large, particularly that of the metaconid. The postentocristid curves lingually to the posterolingual tooth corner where it terminates in a well developed entocristid. The entoconulid, like in the holotype, is poorly developed. Well developed lingually directed crests extend from the apices of the protoconid and hypoconid and terminate just prior to reaching the longitudinal valley. These crests are not present in the holotype. The $M_3$, AM F98890, is largely unworn and is slightly smaller than the $M_3$ of the holotype. The postmetaconid, preentocristid and postentocristid are more arcuate than in the holotype. The lingual buttresses of the metaconid and entoconid are better developed however the buccal bases of these cusps are more greatly expanded in the holotype. The metastylid is larger and the metastylid fold is more pronounced. The lingual faces of the protoconid and hypoconid are more steeply sloping and the lingually directed crests associated with these cusps are well developed (however they are absent in the holotype). Following an analysis of variation in dentitions of the modern species, it is evident that the above mentioned morphological differences between the referred material and the holotype fall within the boundaries of normal intraspecific variation.

## DISCUSSION

*Pseudokoala cathysantamaria* is an enormous ringtail possum and *Cundokoala yorkensis* an enormous koala. With the addition of these two to the Pleistocene of Australia, all families of Australian herbivorous mammals are now known to have had giants in the Pleistocene megafauna. They also significantly increase the ranks of known *arboreal* megafaunal species. Apart from one modestly large koala (*Phascolarctos stirtoni* Bartholomai, 1968), the only undoubted megafaunal arboreal species previously known from the Pleistocene was *Bohra paulae* Flannery and Szalay, 1982, a gigantic tree kangaroo from Wellington Caves, New South Wales.

## ACKNOWLEDGMENTS

We thank the Australian Research Committee, the University of New South Wales, the Queensland Museum, National Estate Programs (Queensland), the Riversleigh Society, Queensland National Parks and Wildlife Service, Australian Geographic Society, Royal Zoological Society of New South Wales, Linnean Society of New South Wales and private individuals for support that has enabled discovery and preparation of the diverse koalas and ringtail possums of Riversleigh. Henk Godthelp, Anna Gillespie and Anne Musser (all of the University of New South Wales) helped collect material from Wellington Caves. Armstrong Osborne (University of Sydney) and Michael Augee (University of New South Wales) organised the opportunity to examine the Wellington deposits. Mathew Crowther (University of New South Wales) confirmed the identifications of other Wellington mammals excavated with the tooth of *Cundokoala yorkensis*. Neville Pledge (South Australian Museum) and Tom Rich (Museum of Victoria) made materials available for study. Betty Thompson (Museum of Victoria) confirmed collection details of Portland materials. Suzanne Hand and Jenni Brammall (University of New South Wales) read and constructively criticised a draft of this paper.

## REFERENCES

Archer, M. (1984). The Australian marsupial radiation. In 'Vertebrate zoogeography and evolution in Australasia' (Eds M. Archer and G. Clayton) pp. 633–808. (Hesperian Press: Perth).

Archer, M. (1992). Ringtail possums (Pseudocheiridae, Marsupialia) from the Tertiary deposits of Riversleigh. *The Beagle* **9**: 257–258.

Archer, M. and Bartholomai, A. (1978). Tertiary mammals of Australia: a synoptic review. *Alcheringa* **2**: 1–19.

Archer, M., Hand, S.J., and Godthelp, H. (1995). Tertiary environmental and biotic change in Australia. In 'Paleoclimate and evolution, with emphasis on human origins' (Eds E.S. Vrba, G.H. Denton, T.C. Partridge, L.H. Burckle) pp. 77–90. (Yale University Press: New Haven).

Bartholomai, A. (1968). A new fossil koala from Queensland and a reassessment of the taxonomic position of the problematical species, *Koalemus ingens* DeVis. *Memoirs of the Queensland Museum* **15**: 65–73.

Black, K. and Archer, M. (in press). *Nimiokoala*, a new genus and species of koala (Marsupialia, Phascolarctidae) from Riversleigh, northwestern Queensland, with a review of *Litokoala* Stirton, Tedford and Woodburne, 1967. *Memoirs of the Queensland Museum.*

Flannery, T.F. and Hann, L. (1984). A new macropodine genus and species (Marsupialia: Macropodidae) from the Early Pleistocene of southwestern Victoria. *Australian Mammalogy* **7**: 193–204.

Flannery, T.F. and Szalay, F. (1982). *Bohra paulae*, a new giant fossil tree kangaroo (Marsupialia, Macropodidae) from New South Wales, Australia. *Australian Mammalogy* **5**: 83–94.

Flower, W.H. (1867). On the development and succession of teeth in the Marsupialia. *Philosophical Transactions of the Royal Society, London* **157**: 631–641.

Hand, S.J., Dawson, L., and Augee, M. (1988). *Macroderma koppa*, a new Tertiary species of false vampire bat (Microchiroptera: Megadermatidae) from Wellington Caves, New South Wales. *Records of the Australian Museum* **40**: 343–351.

Luckett, W.P. (1993). An ontogenetic assessment of dental homologies in therian mammals. In 'Mammal phylogeny: Mesozoic differentiation, multituberculates, monotremes, early therians, and marsupials' (Eds F.S. Szalay, M.J. Novacek, M.C. McKenna) pp. 182–204. (Springer-Verlag: New York).

Osborne, R.A.L (1983). Cainozoic stratigraphy at Wellington Caves, New South Wales. *Proceedings of the Linnean Society of New South Wales* **107**: 131–147.

Pledge, N.S. (1987a). *Phascolarctos maris*, a new species of koala (Marsupialia: Phascolarctidae) from the Early Pliocene of South Australia. In 'Possums and opossums: studies in evolution' (Ed. M. Archer) pp. 327–330. (Surrey Beatty and Sons Pty Ltd: Sydney).

Pledge, N.S. (1987b). Pseudocheirids (Marsupialia: Pseudocheiridae) from the Middle Miocene Ngama Local Fauna of northern South Australia. In 'Possums and opossums: studies in evolution' (Ed. M. Archer) pp. 639–679. (Surrey Beatty and Sons Pty Ltd: Sydney).

Pledge, N.S. (1992). The Curramulka Local Fauna: a new late Tertiary fossil assemblage from Yorke Peninsula, South Australia. *The Beagle* **9**: 115–142.

Rich, T.H., Archer, M., Hand, S.J., Godthelp, H., Muirhead, J., Pledge, N.S., Flannery, T.F., Woodburne, M.O., Case, J.A., Tedford, R., Turnbull, W.D., Lundelius Jr, E.L., Rich, L.S.V., Whitelaw, M.J., Kemp, A. and Rich, P.V. (1991). Appendix 1: Australian Mesozoic and Tertiary terrestrial mammal localities. In 'Vertebrate palaeontology of Australasia' (Eds P. Vickers-Rich, J.M. Monaghan, R.F. Baird, T.H. Rich ) pp. 1005–1058. (Pioneer Design Studio: Melbourne).

Springer, M.S. (1987). Lower molars of *Litokoala* (Marsupialia: Phascolarctidae) and their bearing on phascolarctid evolution. In 'Possums and opossums: studies in evolution' (ed M. Archer) pp. 319–325. Surrey Beatty and Sons Pty Ltd: Sydney.

Springer, M.S. (1993). Phylogeny and rates of character evolution among ringtail possums (Pseudocheiridae: Marsupialia). *Australian Journal of Zoology* **41**: 273–291.

Stirton, R.A. (1957). A new koala from the Pliocene Palankarinna Fauna of South Australia. *Records of the South Australian Museum* **13**: 71–81.

Stirton, R.A., Tedford, R.H. and Woodburne, M.O. (1967). A new Tertiary formation and fauna from the Tirari Desert, South Australia. *Records of the South Australian Museum* **15**: 427–462.

Turnbull, W.D. and Lundelius Jr, E.L. (1970). The Hamilton Fauna, a late Pliocene mammalian fauna from the Grange Burn, Victoria, Australia. *Fieldianna: Geology* **19**: 1–163.

Turnbull, W.D., Rich, T.H.V. and Lundelius Jr, E.L. (1987). Pseudocheirids (Marsupialia: Pseudocheiridae) of the Early Pliocene Hamilton Local Fauna, southwestern Victoria. In 'Possums and opossums: studies in evolution' (Ed. M. Archer) pp. 689–713. (Surrey Beatty and Sons Pty Ltd: Sydney).

Woodburne, M.O., Tedford, R.A. and Archer, M. (1987a). New Miocene ringtail possums (Marsupialia: Pseudocheiridae) from South Australia. In 'Possums and opossums: studies in evolution' (Ed. M. Archer) pp. 681–688. (Surrey Beatty and Sons Pty Ltd: Sydney).

Woodburne, M.O., Tedford, R.A., Archer, M. and Pledge, N.S. (1987b). *Madakoala*, a new genus and two species of Miocene koalas (Marsupialia: Phascolarctidae) from South Australia, and a new species of *Perikoala*. In 'Possums and opossums: studies in evolution' (Ed. M. Archer) pp. 293–317. (Surrey Beatty and Sons Pty Ltd: Sydney).

# Functional Anatomy of the Macropodid Pes

NICOLAS BISHOP
(Communicated by M.L. Augee)

Biological Sciences, Flinders University, GPO Box 2100, Adelaide SA 5001

Bishop, N. (1997). Functional anatomy of the macropod pes. *Proceedings of the Linnean Society of New South Wales*, **117**: 17-50

The functional anatomy of the sthenurine pes was investigated, based on a comparative study of the extant macropodines. Comparisons were made with the possum, koala, and wombat to determine a number of plesiomorphic character states associated with the diprotodontid pes. Dissections were made of the hind limb and pes of a number of extant potoroids and macropodids to determine the functional nature of the actions and insertions of the muscles, as well as the nature of the articulations. A cluster analysis was used to sort a collection of 219 fossilised macropodid calcanea from the Pleistocene Victoria Fossil Cave deposit, Naracoorte southeast South Australia. The morphology of the sthenurine calcanea were compared with *Macropus fuliginosus*. The findings support the previously held view that the sthenurine pes had been selectively modified for its weight bearing function during stand-up browsing. Morphological differences between different sthenurine species suggests that the pedal morphology could be useful in the construction of sthenurine phylogeny.

Manuscript received 1 May 1996, accepted for publication 23 Oct 1996.

KEYWORDS: Functional, anatomy, macropodid, kangaroo, foot, pes, biomechanics, morphology, evolution.

## INTRODUCTION

The aim of this research was to investigate the locomotion of the extinct sthenurine kangaroos (subfamily Sthenurinae) by means of a functional analysis of their pes (hindfoot). The locomotory adaptations of the extinct sthenurines may be inferred from a study of modern functional analogues, in this case the macropodines. The structure and function of many aspects of the macropodine pes have been examined to varying degrees in past studies (Parsons 1896; Windle and Parsons 1897; Barnett 1970; Lewis 1964, 1983; and Hopwood and Butterfield 1990). Neither the form of the macropodine pes, nor that of any other animal, is dictated solely by its functional role. Form may be influenced as much by ancestry as by functional adaptations. Unravelling these interactions is an essential aspect of functional analysis. In this case it was necessary to determine what specific features made the pes macropodine (the derived or apomorphic conditions) as opposed to diprotodontid (ancestral or plesiomorphic conditions). All diprotodont marsupials, which include the Macropodidae, share the same basic foot pattern in which the IV$^{th}$ digit is enlarged, sometimes equalling in size, but usually larger than the V$^{th}$ digit. The V$^{th}$ digit is in turn larger than the syndactylous II$^{nd}$ and III$^{rd}$ digits, which are again larger than the often vestigial or absent hallux or I$^{st}$ digit. This is expressed as the digital formula, IV>V>III=II>I .

At the basis of the concept of modern functional analogues, is the well studied conception of function being reliant on form (Bock and von Wahlert 1965; Gould and Lewontin 1979; Bock 1980, 1981, 1988, 1989; Lauder 1981; Arnold 1983; Gans 1988; Lauder 1990; and Losos 1990). The same authors have expressed the need to use careful consideration of all aspects of the evolution of form when ascribing particular traits to a specific function.

To ascertain the plesiomorphic diprotodontid pes structure from which the macropodine pes has evolved, it was necessary to examine the characteristics of several different marsupial families. Evidence from studies of craniodental characters place the Macropodidae close to, but derived from, the Potoroidae. Together these two are closely related to, but derived from, the Phalangerids (possums), (Dollo 1899, Bensley 1903, Raven and Gregory 1946, Archer 1984, and Flannery 1983). The superfamily Macropodoidea is broken up into two main families, the Macropodidae and Potoroidae.

The muscular anatomy of the hindlimb and pes of the macropodines has previously been examined by Parsons (1896), Windle and Parsons (1897), Craven (1971), Adnams-Hodges (1988), and most recently and comprehensively by Hopwood and Butterfield (1990). Only Parsons (1896) and Lewis (1983) have investigated the anatomy of the binding ligaments of the pes. The osteological remains of the macropodine foot and the nature of the articulations have also been dealt with to various degrees by Owen (1875); Parsons (1896); Windle and Parsons (1897); Barnett (1970); Lewis (1964, 1983); and Hopwood and Butterfield (1990).

The locomotion of the macropodids, initially documented by Muybridge (1887) has been well studied, particularly by Badaux (1965), Windsor and Dagg (1971), Marshall (1974), Bennett (1987), Biewener and Blickhan (1988), and Baudinette (1994). Macropodines progress by a ricochetal saltatory mode of locomotion, where both of the hind-feet are placed on the ground simultaneously. Weight is transmitted through the tibia to the astragalus, the calcaneum, through the cuboid, then through to the elongated fourth metatarsal. Windsor and Dagg (1971) in their study of nineteen macropodine species were able to identify four gaits: 1) the slow progression - pentapedal (four limbs and tail), used mainly during grazing; 2) the walk - the pairs of the limbs are asynchronously placed in contact with the substrate, and expressed only in *Dendrolagus* the tree kangaroo; 3) the quadrupedal bound - the use of the hind feet followed by the forefeet, exhibited only in *Setonix*, *Dendrolagus*, *Petrogale* and the Potoroidae; 4) the bipedal hop - he fastest gait, with synchronous placement of the hind feet on the ground.

Independent studies by Marshall (1974), and previously Badaux (1965), characterised macropodine locomotion as hopping or bipedal ricochetal saltation, where the hind feet are synchronously placed in contact with the ground. Despite macropodines possessing at least four gaits, it seems that the general elongated form of the macropodine locomotor apparatus has been modified primarily in relation to the fastest gait, the bipedal hop. This is supported by evidence associated with the energetic efficiency of this gait at high speeds (Dawson and Taylor 1973, Alexander and Vernon 1975, Cavagna et al. 1977, Baudinette et. al. 1992, Baudinette 1994), which can be primarily explained by the physical return of stored energy in the hindlimb (Alexander and Vernon 1975, Alexander 1984, and Bennett and Taylor 1995).

Based on a study of cranial and dental characters, Raven and Gregory (1946) examined the adaptive branching of the kangaroos and its relation to habitat. The pes can also be used in a similar function as eluded to by Windsor and Dagg (1971). The macropodines have diversified to occupy a wide variety of habitats ranging from open plains (*Macropus rufus*) to tree top canopies (*Dendrolagus*). An examination of the varied pedal morphology of the macropodines from segregated habitats should provide an excellent source of definition for the functional nature of the derived features.

Wells and Tedford (1995) noted some major differences between the sthenurine kangaroos, and the extant (modern) macropodines. The first major difference is in the generally bulkier nature of the animal; the skull and teeth being adapted for tough feed browsing, rather than grazing which predominates in the modern macropodines. The structure of the shoulder facilitated raising the arms above the head, with the associated long digits of the manus (hand) enabling it to reach higher foliage. Structure of the spine and tail vertebrae suggest adaptations to standing upright, also for procuring food. These authors also note that the hindfeet are functionally one-toed or monodactylous, with further reduction of the second, third, and fifth digits differing from the modern generalised macropodine form.

## MATERIALS AND METHODS

All of the fossil bones used in this study were excavated from the "Victoria Fossil cave" at Naracoorte from 1972 to the 1988. Measurements were also taken on various reference skeletons from extant species in Flinders University and South Australian Museum collections. The specimens are listed in Table 1.

TABLE 1

The reference skeletons examined from the South Australia Museum (M) and Flinders University Reseacrh (FUR) collections.

| Specimen | | Reference |
|---|---|---|
| POTOROIDAE | *Hypsiprymnodon moschatus* | M11940 |
| | *Aepyprymnus rufescens* | FUR |
| | *Bettongia lesseur* | FUR 011 |
| | *Bettongia penicillata* | M8286 |
| MACROPODIDAE | *Macropus fuliginosus* | FUR |
| | *Macropus rufus* | FUR 001 |
| | *Macropus eugenii* | FU 010 |
| | *Macropus rufogriseus* | M16370 |
| | *Macropus greyi* | M2121 |
| | *Macropus parma* | M7191 |
| | *Macropus irma* | M16489 |
| | *Macropus robustus* | M3695 |
| | *Macropus parryi* | M14103 |
| | *Macropus dorsalis* | M7967 |
| | *Dorcopsis sp.* | M13754 |
| | *Petrogale lateralis* | M12555 |
| | *Setonix brachyurus* | M14102 |
| | *Wallabia bicolor* | M16469 |
| | *Dendrolagus bennettianus* | M5530 |
| PHALANGERIDAE | *Pseudochirus peregrinus* | FUR 004 |
| VOMBATIDAE | *Lasiorhinus latifrons* | FUR 006 |
| PHASCOLARCTIDAE | Phascolarctos cinereus | FUR 009 |

### Muscles, tendons and ligaments

The hind limbs were removed from a number of kangaroo carcasses for the purpose of dissection. Whole frozen specimens of one female western grey (*M. fuliginosus*) and one female red kangaroo (*Macropus rufus*) were provided by the South Australian

National Parks and Wildlife Service. One Tammar wallaby (*Macropus eugenii*), one burrowing bettong (*Bettongia lesueur*) and one rufous bettong (*Aepyprymnus rufescens*) from the frozen specimen collection at Flinders University were dissected.

All specimens had been frozen soon after death and stored in a freezer room held at -15°C. Two to three days prior to their dissection they were transferred to a refrigerated room held at 4°C. The specimens remained in the refrigerated room for the duration, to minimise deterioration of the flesh. All dissections were carried out using a standard dissection kit. After all of the flesh was dissected away the limbs of the specimens were macerated, cleaned and bleached so that they could be illustrated and examined for muscle and ligament scars.

The measurements taken on the calcaneum are displayed in Fig. 1. The terms used to describe the features of the pes follows Murray (1995). Figure 2 shows the anatomical terms used in the descriptive anatomy.

### Statistical analysis

Twelve measurements were made on the calcanea of both the extinct and extant taxa. A cluster analysis was performed on this data matrix to determine the natural groupings of the specimens measured.

The statistical program SPSS (1989) was used to cluster the fossil bones into natural groupings based on the measurements taken. Recognition of the distribution patterns of operational taxonomic units (OTU) and groups of OTU's (taxa) were carried out in a hyper dimensional (12 dimensions) space (phenetic A space), where a pattern is any discernible property of the distribution and groups of OTU's in A space. I have chosen a cosine measure of similarity. The use of cosine as a similarity measurement is particularly useful in the measurement of shape (Sneath and Sokal 1973). This standardises size so that measurement of similarity is on shape only. The agglomerative clustering technique was used to cluster the OTU's and is the most widely accepted and tested method. There are several methods available to group the specimens, however the most widely accepted, and also default setting for the SPSS program, is the sequential, agglomerative, hierarchical, non-overlapping clustering method (SAHN).

To summarise the differences, a principal component analysis was carried out on the same data set. Principle components analysis measures the variance for the entire group and then displays the variance in the form of major components.

## RESULTS

### Comparative Anatomy and Cladistic Analysis of the Marsupial Pes (Tables 2-4)

### Anatomy of the crus and pes of the western grey kangaroo, Macropus fuliginosus

Osteology

Separate bones of the crus and pes include: tibia, fibula, seven tarsal bones, four metatarsals, twelve phalanges, a plantar sesamoid, four metatarsophalangeal sesamoids (Figs 3 and 4).

i) The crus: (between knee and ankle) comprising of tibia and fibula: On the tibia the condyles are located on the posterior half of the head of the tibia. The tibia articulates with the fibula along the posterolateral aspect of the lateral condyle of the tibia. The tibia is greatly expanded anteroposteriorly compared with its transverse width. Proximally the tibia is expanded, with the shaft roughly triangular in cross section as described by Owen (1874–77). Distally the shaft is circular to ovoid at its extremity, expanding into the medial malleolus. The proximal lateral surface of the shaft is deeply concave to receive the extensor muscle mass of the crus.

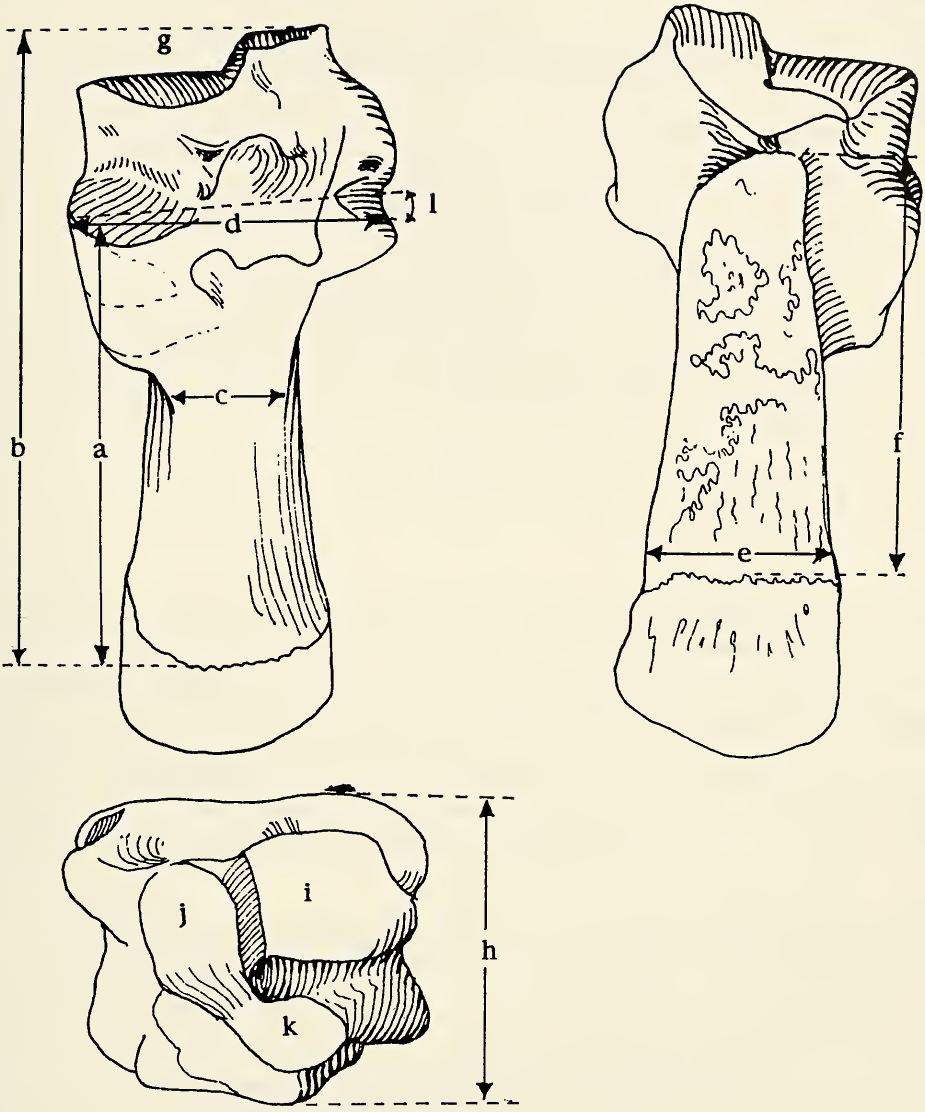


Figure 1. a-The length of the calcaneum from the epiphysial junction to the line of transverse axis of the astragalus: b- The length of the calcaneum from the epiphysial articulation to the distal portion of the dorsolateral cuboid facet on the calcaneum: c- The width of the dorsal portion of the tuber calcanei of the calcaneum measured transversely at the posterior region of the lateral process and the posterior region of the sustentaculum tali: d- Width across the pivot point, or line of transverse axis of the astragalus: e- The width of the plantar surface of the calcaneum measured at the most posterior aspect of the tuber calcanei, not including the epiphysis if present: f- Plantar surface length, measured from the epiphysial arthrosis on the plantar surface to the transverse plantar sulcus on the calcaneum or when not present, to the distal portion of the plantar tuberosity on the calcaneum: g- The prominence of the dorsolateral cuboid facet on the calcaneum, measured from the face of the dorsomedial cuboid facet on the calcaneum to the most distal portion of the dorsolateral cuboid facet on the calcaneum: h- The height of the calcaneum measured dorsoventrally at the most posterior aspect of the tuber calcanei, not including the epiphysis if present: i- The surface area of the dorsomedial cuboid facet on the calcaneum: j- The surface area of the dorsolateral cuboid facet on the calcaneum: k- The surface area of the ventromedian cuboid facet on the calcaneum: l- The angle of transverse axis of the astragalus measured from the central axis of the calcaneum.

TABLE 2

The characters which were determined to be plesiomorphic.

| Character | State |
|---|---|
| 1 | Weak and asymmetrical ridges |
| 2 | Malleolar fossa is situated posteromedially, and not distinct |
| 3 | The medial trochlear crest is greater in length than the lateral trochlear crest |
| 4 | Large scar for the posterior talocalcaneal ligament |
| 5 | Long astragalar head and neck with no distinct notch for the trochlear bursa |
| 6 | The lateral trochlear crest is aligned with the lateral border of the navicular facet on the astragalus |
| 7 | The medial trochlear crest aligns with the lateral border of the navicular facet on the astragalus |
| 8 | The navicular facet is broad, with its longitudinal axis transecting the lateral trochlear crest of the astragalus |
| 9 | Transversely wide sustentaculum tali which tapers medially |
| 10 | Uninformative |
| 11 | The sustentaculum tali is deflected anteromedially, and the base of the sustentaculum tali is rounded posteriorly |
| 12 | The articular surface for the astragalus on the calcaneum is continuous transversely, and shallowly convex anteroposteriorly |
| 13 | The lateral facet for the astragalus on the calcaneum is higher than the medial facet for the astragalus |
| Derived characters of other diprotodontids: | |
| 5 | The wombat possesses both a long astragalar head and neck and a small notch for the trochlear bursa |
| 11 | In the koala, the base of the sustentaculum tali is straight, nearly horizontal |
| 14 | Single smooth surface distally for articulation with the cuboid in other diprotodontids |
| 15 | No transverse plantar sulcus in other diprotodontids |
| 16 & 17 | Single articulating surface for the cuboid in other diprotodontids |

TABLE 3

The shared derived characters of Hypsiprymnodon and Macropus.

| Character | State |
|---|---|
| 1 | The trochlear ridges are symmetrical and well rounded |
| 6 | The lateral trochlear crest is aligned with the lateral portion of the dorsolateral facet (of the calcaneum) when the astragalus is articulated |
| 7 | The medial trochlear crest aligns with the median portion of the navicular facet on the astragalus |
| 9 | Comparatively transversely narrow astragalus |
| 14 | The dorsomedial and dorsolateral facets (for the cuboid) are equal in height in distal aspect |
| 16 | Presence of a groove separating the dorsomedial and ventromedian facets (for the cuboid) on the calcaneum |

TABLE 4

The derived or apomorphic characters of the generalised macropodine pes.

| Character | State |
|---|---|
| 2 | There is a distinct notch on the transversely wider medial malleolar fossa |
| 3 | The parallel trochlear ridges are angled more obliquely |
| 4 | The scar for the posterior talocalcaneal ligament is much reduced |
| 5 | The development of a distinct notch for the trochlear bursa |
| 8 | The navicular facet is broader, and its longitudinal axis transects the medial trochlear crest |
| 10 | The tuber calcanei is relatively narrow and elongated anteroposteriorly |
| 11 | The sustentaculum tali is deflected anteromedially, and curved posteroventrally |
| 12 | There are two separate lobate facets (on the calcaneum) for articulation with the astragalus |
| 13 | The medial and lateral facets (for the astragalus) on the calcaneum are equal in height |
| 15 | The transverse plantar sulcus is anteroposteriorly narrow |
| 17 | The cuboidocalcaneal step is short but distinct |

### The fibula

is a long and slender bone, with the head being the most expanded part, anteroposteriorly. It articulates with the transverse fibular groove on the posterolateral aspect of the tibia. The fibula shaft is thickest proximally, with the lateral surface, convex and the medial surface concave to articulate with the lateral aspect of the tibia, as well as providing area for muscle insertion in proximal region. The distal epiphysis is expanded into the lateral malleolus (Hopwood and Butterfield 1990).

ii) The Pes consists of a number of separate bones:The tarsus consists of seven separate tarsal bones plus one sesamoid (Hopwood and Butterfield 1990): calcaneum, astragalus (talus), and Metatarsal IV make up the bulk of the tarsus.

### The astragalus

(talus) bears a large articulation dorsally with the distal end of the tibia. The bone is subdepressed and triangular , with the base turned forward (Owen 1874–77). In medial or lateral view it is arched, convex dorsally. The dorsal surface is formed mainly by the trochlear articulation with the tibia, which is convex anteroposteriorly and concave transversely. Further, the dorsal surface is divided into medial and lateral portions by the respective medial and lateral trochlear grooves, providing facets for the lateral and medial malleoli. Ventrally the astragalus is concave anteroposteriorly, forming the articular surface for the calcaneum. It is divided into a lateral and medial articulation site, corresponding to articulation sites on the calcaneum. The lateral surface of the head of the astragalus also articulates with a small area on the dorso medial portion of the calcaneum. Distally, the astragalus articulates with the navicular bone as well as a small area on the posteromedial portion of the cuboid.

### The calcaneum

articulates dorsomedially with the astragalus, dorsolaterally with the fibula, and distally with the cuboid. There is a roughened flat surface on the plantar aspect for the insertion of the large plantar calcaneo cuboid ligament. The calcaneum is roughly triangular in cross section, flattened and broad plantarly. The dorsal surface of the tuber calcanei has a smooth surface with a relatively narrow longitudinal ridge extending posteriorly. The sustentaculum tali is narrow transversely but deep dorsoplantarly, and is curved

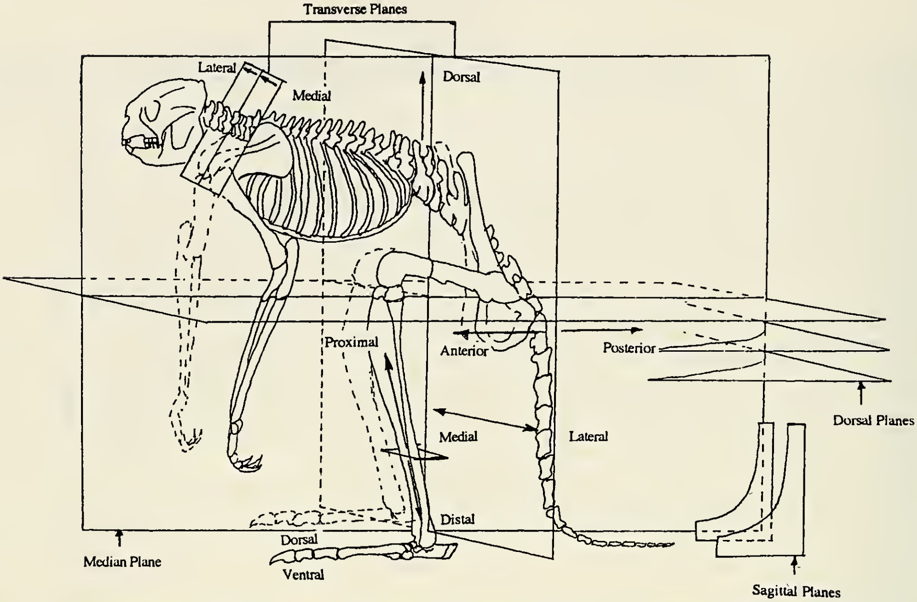


Figure 2. Shows the anatomical and directional terms and planes of the body (Adapted from Leach, 1993)

posteriorly through plantarly. It bears a groove for the flexor digitorum longus. Laterally, the fibular condyle bears an articular facet for the lateral malleolus of the fibula on its posterolateral aspect. Dorsally, the lateral facet for the astragalus is high and rounded, proportioned equally transversely and anteroposteriorly. It is separated from the concave medial facet by a small longitudinal ridge. The ridge of the medial facet sits slightly higher and more anterior to the posterior border of the lateral facet. The fossa for the anterior proximal process of the astragalus is shallow and semicircular. There is a small triangular facet on the dorsomedial aspect of the calcaneum for articulation with the lateral aspect of the neck of the astragalus. Distally, the surface of the dorsomedial facet is transversely broad, rectangular and strongly convex dorsoplantarly. The dorsolateral facet is narrow transversely, but longer dorsoplantarly and narrowing plantarly. This facet is stepped and protrudes more anteriorly than the dorsomedial facet. Ventrally, the dorsolateral facet merges into the ventro median facet, which is of similar size to latter, but broader transversely than dorsoplantarly, and is of sub triangular shape, but with the most plantar aspect not contributing to the plantar surface.

The navicular,

proximally, is concave, articulating with the corresponding convex head of the astragalus. Laterally, it articulates with the medial surface of the cuboid. It is convex and articulates distally with the entocuneiform and ectocuneiform.

The entocuneiform

articulates proximally with the navicular, distally with the II$^{nd}$ metatarsal and mesocuneiform, laterally with the cuboid, and medially with the ectocuneiform (Hopwood and Butterfield 1990).

The mesocuneiform

articulates proximally with the ectocuneiform, distally with the II$^{nd}$ metatarsal, dorsally with the III$^{rd}$ metatarsal, and is the smallest tarsal bone.

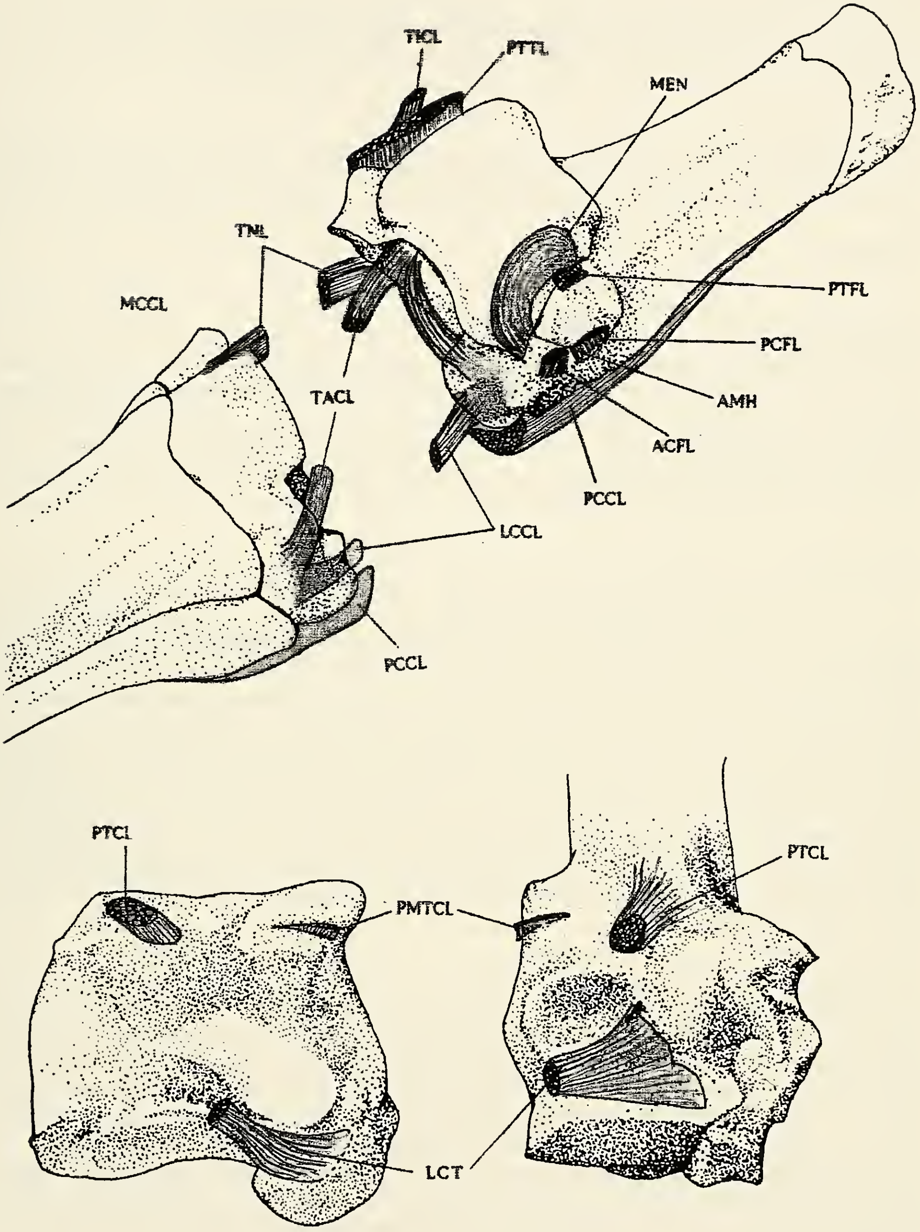


Figure 3. View of the ligaments of the left pes of *Macropus fuliginosus* . **TCL-** tibiocalcaneal ligament ; **PTTL-** posterior tibiotalar ligament ; **MEN-** meniscus ; **PTFL-** posterior talofibular ligament ; **PCFL-** posterior calcaneofibular ligament ; **ACFL-** anterior calcaneofibular ligament ; **AHM-** anterior horn of the meniscus ; **PCCL-** plantar calcaneocuboid ligament ; **LCCL-** lateral calcaneocuboid ligament ; **MCCL-** medial calcaneocuboid ligament ; **TNL-** talonavicular ligament ; **TCL-** talocuboid ligament ; **PTCL-** posterior talocalcaneal ligament ; **PMTCL-** posteromedial talocalcaneal ligament ; **LCT-** ligamentum cervicis tali.

### The ectocuneiform

articulates proximally with the navicular, distally with the mesocuneiform and III$^{rd}$ metatarsal, medially with the entocuneiform, and laterally with the cuboid and IV$^{th}$ metatarsal, extending backward, beyond and overlapping the entocuneiform (Owen 1874–77).

### The cuboid

articulates proximally with the calcaneum accommodating its three facets, distally with IV$^{th}$ and V$^{th}$ metatarsals, and medially with the navicular and ectocuneiform.

### Metatarsal I

Absent

### Metatarsal II and III

Metatarsal II articulates proximally with entocuneiform and mesocuneiform, and distally with the first phalanx of digit II. Metatarsal III articulates proximally with mesocuneiform and entocuneiform, and distally with the first phalanx of digit III. Both metatarsals II and III are reduced greatly in width but not in length. In the middle of the tarsus both lie on the plantar aspect of metatarsal IV, then curve dorsomedially in the distal portion of the metatarsus (Hopwood and Butterfield 1990).

### Metatarsal IV

articulates proximally with the cuboid, and proximomedially with the ectocuneiform. It articulates medially with metatarsal III, laterally with metatarsal V, and plantarly with the tarsal sesamoid bone (Hopwood and Butterfield 1990). Distally metatarsal IV articulates with the first phalanx of digit IV and the medial and lateral metatarsophalangeal sesamoid bones. The dorsal surface is convex transversely, most so at the most proximal part where it articulates with the cuboid. The plantar surface is slightly concave transversely, mainly in the distal two thirds, but with a deep tuberous keel proximally present as a thick ridge. The proximal plantar surface also provides a site for the attachment of the plantar sesamoid, which is grooved for accommodation of the flexor digitorum longus tendon. The distal articulation is convex dorsoplantarly but nearly flat transversely. Ventrally on the distal articular surface is a median ridge forming two concave surfaces for the trochlear articulation of the first phalanx of the metatarsal IV.

### Metatarsal V

articulates proximally with the cuboid, and medially with the lateral surface of metatarsal IV. It articulates distally with the first phalanx of digit V and also plantarly with the metatarsophalangeal sesamoid bones of digit V. A significant portion of metatarsal V is in contact with the ground. Proximally this bone possesses a sigmoidal shape, curving up most proximally at its articulation with the cuboid. The rest of the bone is curved in the opposite direction, very greatly curved concavely. Proximally the bone is roughly triangular in cross section. The lower border is thicker than the upper, and primarily in the proximal portion. In plantar aspect metatarsal V is also curved out laterally so that the distal end of this bone lies ventrolaterally to metatarsal IV. The distal articulation with the first phalanx of digit V is convex dorsoplantarly.

### Digits

There are three digits corresponding to each of the metatarsals, and the size of these digits conforms well with the size of the metatarsal carrying that digit. The metatarsal IV is the longest digit with the distal digits of metatarsal V extends as far as the articulation between the first and second digits of metatarsal IV.

The ligaments of the pes

In the majority of mammals including humans, the ankle consists of only one joint. It is noted that in macropods the ankle has been modelled into two ankles (Lewis 1980). The first joint is considered the articulation of the tibia with the astragalus and the fibula with the calcaneum, with the second joint (sub talar) being formed between the astragalus and the calcaneum. The *Nomina Anatomica* text suggests that the ankle joint is the talocruralis, i.e. the joint between the tibia and the astragalus. While this joint exists in the macropods, the fibula also articulates with the calcaneum. The articulation of the tibia on the astragalus is a "hinge-like" trochlear joint convergent in form and function with the eutherians (Lewis 1980).

i) Articulatio tarsocruralis (tibiotalar/calcaneofibular) (see Fig. 3): The broader lateral part of the tibial surface articulates directly with the large trochlear groove on the astragalus. This area is separated from the medial articulation by the medial trochlear ridge. The well defined astragalar depression accommodates the terminal articular knob on the tibia. The lateral trochlear ridge separates the trochlear groove from the lateral surface of the astragalus where the medial surface of the fibula articulates.

Medially, there is a ligamentous wall, common to congruent joints. The posterior tibiotalar ligament arises from a long ridge, extending longitudinally on posteromedial aspect of the astragalus. More superficial to this and crossing over the tibiotalar ligament, is the tibiocalcaneal ligament which passes down to attach to the tuberosity on the sustentaculum tali. This is in close proximity to the talo-navicular ligament passing from the medial aspect of the neck of the astragalus to a dorso-lateral position on the navicular. A small cartilaginous meniscus intervenes on this surface in between the fibula and the astragalus, but does not extend up in between the tibia and fibula (Lewis 1980).

Anteriorly, the meniscus continues forward between the fibula and the astragalus, terminating as a fibrous horn, and recurves to attach to the calcaneum. Passing from the fibula to the astragalus, protruding from underneath the meniscus is the posterior talofibular ligament which intervenes between the fibula and the exposed projection of the articular facet on the calcaneum. Also protruding from the astragalus near the astragalar neck, the talocuboid ligament divides into two components; one band transversely forming a strap through which the tendons of the flexor muscles pass, and another band over the cuboid to insert into its lateral surface, where it shares its insertion with a small lateral calcaneocuboid ligament. As with the medial side of the tibia, two ligaments, the posterior and anterior ligaments, cross and bind the fibula and calcaneum, both with origins on the lateral projection of the calcaneum and insertions on their respective diagonally opposite anterior and posterior regions on the distal end of the fibula. On the plantar surface there are two main ligaments binding the calcaneum to the more distal tarsals and metatarsals (Lewis 1980). Crossing from the medial side posteriorly on the calcaneum to an insertion into the cuboid and base of metatarsal IV and V on the ventro-lateral aspect is the large plantar calcaneocuboid ligament. Medially is a comparatively smaller calcaneocuboid ligament originating in the base of the sustentaculum tali and passing to an insertion into the navicular, cuneiform bones and metatarsal II and III.

ii) Talocalcaneocentralis (subtalar joint): This is comprised of the articulation of the astragalus on the medial portion of the calcaneum. There are two main articulating surfaces on the plantar aspect of the astragalus corresponding to the lateral and medial articulating surfaces on the calcaneum. Both surfaces have a predominantly transverse axis, are concave on the astragalus and are convex on the calcaneum (Lewis 1980).

Two main ligaments tightly bind the astragalus to the calcaneum, the anterior and posterior talocalcaneal ligaments. The anterior talocalcaneal ligament is the homologue of the ancestral ligamentum cervicis tali. It extends from the neck of the astragalus to a large insertion into the median portion of the calcaneum (Lewis 1983). The large posterior talocalcaneal ligament extends from a large area of insertion on the astragalus to a similar sized tuberosity in the posterolateral region of the articulating part of the calcaneum. There is also a small ligament extending between the postero-medial process of the astragalus to the corresponding postero-medial area on the calcaneum. This ligament is not described in any text, and is probably a second fascia of the main posterior talocalcaneal ligament. Similar remodelling of the subtalar joint such as seen in macropods can also be found in the precursors of the artiodactyls (Lewis 1983).

The muscles and tendons of the crus and pes of the western grey kangaroo, *Macropus fuliginosus*

The complete descriptions of the muscles of the crus of the eastern grey (*Macropus giganteus*) have been succinctly described in a previous study, (Hopwood and Butterfield 1990) and will not be dealt with here.

## Comparative morphology of modern Macropodines

The muscles and tendons of the hindlimb and pes

The muscles and ligaments of a number of modern macropodid and potoroid forms were examined to determine whether there were any differences in the origins and particularly insertions of the muscles, and to see whether these differed significantly from the form of *M. fuliginosus*. The insertion sites of the tendons did not vary between the different macropod species examined in this study. It was noted however that there was a correlation between the size of the tendon entering an insertion site and the size of the resulting scar.

The comparative osteology of *Macropus fuliginosus*, *Macropus rufus*, and *Dendrolagus bennettianus*

To ascertain some of the features which may be related to habitat in the modern kangaroos, I have chosen to describe two species from two different habitats using *Macropus fuliginosus* as a comparative model.

i) Comparative anatomy of the astragalus: Dorsally in *Dendrolagus bennettianus* the astragalus is subdepressed and rectangular in form, greater transversely than anteroposteriorly, compared with *M. fuliginosus* which is slightly more triangular in form, due largely to the angle of the lateral trochlear crest. *Macropus rufus* is the most triangular of the three specimens with the medial trochlear crest greatly elongated posteriorly. The dorsal surface of the astragalus in the three specimens is formed mainly by the trochlear-like articulation with the tibia. The dorsal surface is divided into three portions by the two-medial and lateral trochlear crests providing facets for the lateral and medial malleoli. The astragali of the specimens are curved convexly anteroposteriorly, greatest in Dendrolagus and least curved in *M. rufus* in keeping with the proportions of the relative calcanea. The trochlear of the astragalus is also curved concavely transversely, deepest in *Dendrolagus* and most shallow in *M. rufus* compared with *M. fuliginosus*. The comparative height of the medial and lateral trochlear crests varies between the three specimens. In *M. fuliginosus* and *M. rufus* the medial trochlear ridge is higher than the lateral trochlear ridge viewed in distal aspect, compared with *D.bennettianus* where these ridges are equal in height.

Ventrally the astragalus is concave anteroposteriorly, forming the articular surface for the calcaneum, being approximately equal depth in all three specimens. The transverse width of the articular facets is greater in *D. bennettianus* than *M. fuliginosus* which is in turn greater than *M. rufus* where the facets are longer anteroposteriorly and narrower transversely. The two facets for the calcaneum on the astragalus are more similar in shape in *M. rufus* and *M. fuliginosus* compared with *Dendrolagus*, where in the former two, the lateral facet is roughly circular, compared with the triangular form of the latter. Also in *Dendrolagus*, the medial facet is sub triangular compared with the transversely wide rectangular form of the medial facet for the calcaneum in *M. rufus* and *M. fuliginosus*. A small area of the lateroplantar portion of the head of the astragalus also articulates with a dorsomedial portion of the calcaneum.

Medially, the articulation for the medial malleolus varies slightly between the three specimens. In *Dendrolagus* there is an ovoid pit on the medial malleolus compared with a more circular pit in *M. fuliginosus* and *M. rufus*. The ridge on the medial aspect for the posterior tibiotalar ligament is longer in *M. rufus* than *M. fuliginosus* because of the elongated portion of the medial trochlear ridge. The site for the attachment of the posterior tibiotalar ligament in *Dendrolagus* is more angled, giving a greater area of attachment for the ligament dorsally compared with the nearly flat ridges of *M. fuliginosus* and *M. rufus*. The area for attachment of the anterior tibiotalar ligament is smallest in *Dendrolagus*, but is borne in a deep groove which lies medially and plantarly compared with *M. rufus* and *M. fuliginosus* where the site for attachment is predominantly on the medial surface, and also dorsally as illustrated by a deep pit in *M. rufus*.

Ventrally in medial aspect, the astragalus is curved concavely, most greatly in *Dendrolagus* and least curved in *M. rufus*. The other main distinction is with the articulation on the astragalus for the cuboid and navicular. In *Dendrolagus* the articular surface is curved gently convexly and runs nearly transversely, terminating medially compared with *M. rufus* and *M. fuliginosus* where this articular facet is directed dorsoplantarly. The largest articulation on the astragalus for the cuboid is in *M. rufus* where this articulation encroaches on the anterior or distal face of the head of the astragalus, so that the area on the astragalus for the navicular is reduced and narrow dorsally. This facet is also deflected more plantarly than in *Dendrolagus* and *M. fuliginosus*.

ii) The comparative anatomy of the calcaneum: The tuber calcanei of the calcaneum of *M. fuliginosus* and *M. rufus* is triangular in cross-section, being flattened and broad plantarly compared with *D. bennettianus* which is much shorter and broader and ovoid in cross-section, reminiscent of possums and koalas. The dorsal surface of the tubercalcanei is formed by two surfaces which converge dorsally into a longitudinal ridge which extends posteriorly. In *D. bennettianus* this ridge is very flat and broad, narrowing posteriorly. In *M. fuliginosus* this ridge is relatively narrow, but not as narrow as in *M. rufus*. There is considerable difference in the width of the sustentaculum tali of these three macropods. In *Dendrolagus* the sustentaculum tali is very broad transversely and pointed medially and shallow dorso-plantarly, compared with *M. fuliginosus* and *M. rufus* where the sustentaculum tali is very narrow, particularly so in *M. rufus*. Corresponding with the astragalus, the anteroposterior length of the sustentaculum tali is shorter in *D. bennettianus* than *M. fuliginosus* which is shorter than the very elongated form in *M. rufus*. The sustentaculum tali is deepest and most curved in *M. fuliginosus*. In *D. bennettianus* the plantar process of the sustentaculum tali extends further medially and nearly contacts the ground, compared with the slightly concave nature of the sustentaculum tali dorsoplantarly in the other two specimens. The sustentaculum tali also bears the tuberosity for the ligamentum cervicis tali on the dorsal surface and is larger in *M. rufus* than *M. fuliginosus* compared with *D. bennettianus*, where the deep groove for this ligament extends posteriorly on the medial surface. In *D. bennettianus* the sustentaculum tali bears a very shallow and broad groove for the tendon of flexor digitorum longus compared with the relatively deep groove of *M. fuliginosus* and *M. rufus*, and is more steeply inclined in the former. Laterally, the fibular condyle exhibits similar variation. The calcaneum has least area of contact for the fibula in *Dendrolagus*, and greatest in *M. rufus*. In *D. bennettianus* the lateral malleolar condyle is angled more obliquely than in the other macropods, as in the case with its medial malleolar condyle. Only *M. fuliginosus* and *M. rufus* bear a true condyle for the fibula, posterolaterally in the former and laterally in the latter. In *M. fuliginosus* and *M. rufus* there is an area excavated in the body of the calcaneum underneath the lateral projection which is not present in *D. bennettianus*. Dorsally the lateral border of the most distal portion of the calcaneum is directed medially in *M. fuliginosus* and *M. rufus* compared with *D. bennettianus*, where this section continues in the axial longitudinal plane of the foot.

There are two facets on the calcaneum for the astragalus. The lateral facet is narrowest in *M. rufus*, almost circular, slightly wider in *M. fuliginosus*, and much broader transversely in *D. bennettianus* which narrows medially. This convex facet is separated from the concave medial facet in *M. fuliginosus* by a small longitudinal ridge, compared with *D. bennettianus* and *M. rufus* where it is nearly continuous between the two facets. In *M. rufus* and *D. bennettianus* the ridge of the medial facet is higher than the lateral facet. This ridge, which is curved in *M. fuliginosus* and *M. rufus*, is straight and runs transversely in *D. bennettianus*.

The fossa for the anterior proximal process of the astragalus which is a small circular pit in *M. fuliginosus*, is more ovoid anteroposteriorly in *M. rufus* and divided by a small ridge, and is not discernible in *D. bennettianus* as this portion of the calcaneum is flat and converges with the lateral border. The corresponding fossa in *D. bennettianus* is on the anterior face of the lateral facet for the astragalus. In *M. rufus* and *M. fuliginosus* there is a small triangular facet on the dorsoanterior medial portion of the calcaneum for articulation with the lateral border of the neck of the astragalus.

Distally, the dorsomedial facet on the calcaneum for the cuboid is transversely broad and rectangular in *M. fuliginosus*, equally broad and deep in *M. rufus* and triangular in *D. bennettianus*. This facet is convex dorsoplantarly, only slightly in *D. bennettianus*, moderately convex in *M. fuliginosus*, and strongly convex in *M. rufus*. The dorsolateral facet on the calcaneum for the cuboid in *M. fuliginosus* and *M. rufus* is narrower transversely and elongated dorsoplantarly. However in *D. bennettianus* this facet is transversely broad, and triangular in shape, narrowing laterally. This facet is convex dorsoplantarly and concave transversely only slightly in *D. bennettianus*, moderately in *M. fuliginosus* and strongly in *M. rufus*. There is a step between the dorsolateral and dorsomedial facets on the calcaneum for the cuboid which is subtle in *D. bennettianus* and lies oblique to the axis of the foot, slightly more acute in *M. fuliginosus* and in line with the axis of the foot in *M. rufus*. The dorsolateral facet merges into the ventromedian facet for the cuboid on the calcaneum, which is circular and slightly concave in *M. rufus*, circular and slightly convex in *M. fuliginosus* and barely distinguishable in the flattened surface of *D. bennettianus*. These three aforementioned facets in the three specimens are separated differently from contact with the ground by a sulcus. The plantar portions of the dorsomedial and ventromedian facets are in contact with the ground in *D. bennettianus* and *M. fuliginosus*, compared with *M. rufus* where the facets are separated by a large, deep sulcus.

iii) Comparative anatomy of the cuboid: Dorsally, the cuboid is greater in length medially than laterally in all of the specimens. The medial border is concave slightly in *M. rufus* and moderately in both *M. fuliginosus* and *D. bennettianus*. The fossa for the dorsolateral facet of the calcaneum for the cuboid is visible in dorsal view. This fossa is obscured in *M. rufus*, partly visible in *M. fuliginosus* and entirely visible in *D. bennettianus*. The step between the dorsolateral and dorsomedial facets of the calcaneum for the cuboid is also apparent on the proximal surface of the cuboid, and when viewed dorsally this angle is in line with the long axis of the foot in *M. rufus*, slightly oblique in *M. fuliginosus* and very oblique in *D. bennettianus*. The proximal portion on the medial side in *M. rufus* is deflected posteromedially to articulate with the astragalus, compared with *D. bennettianus* and *M. fuliginosus* where there is only small surface for articulation for the astragalus on the medial side. Also in dorsal view, none of the distal articulating facets can be seen in *D. bennettianus*.

Medially, the cuboids of *M. rufus* and *M. fuliginosus* are vastly different from that of *D. bennettianus*, the latter which is rhomboidal in appearance, while in the former pair they are rectangular, deep and anteroposteriorly compressed. The cuboid as in the calcaneum is greatly compressed dorsoplantarly. The fossa for the dorsomedial facet of the calcaneum can also be seen in cross-section, and it is greatly concave in *M. rufus*, slightly less concave in *M. fuliginosus* and only gently concave in *D. bennettianus*. Also prominent medially in *D. bennettianus* is a deep sulcus bearing the large cubonavicular and mesocuneiform ligament. Medially in *D. bennettianus* the medial plantar process forms part of the plantar surface of the foot, being different from *M. fuliginosus* and *M. rufus* where the medial plantar crest is raised off the plantar surface to make room for the large tendon of flexor digitorum longus.

Anteriorly in medial aspect in *D.bennettianus* the cuboid is expanded dorsally where it is concave, and convex plantarly. In contrast, in *M. fuliginosus* and *M. rufus* the anterior profile of the cuboid is concave dorsally, convex in the median section, then concave again plantarly. Laterally, the cuboid is longest anteroposteriorly and shallowest dorsoplantarly in *D. bennettianus*. The lateral plantar crest is expanded anteroposteriorly in *M. rufus* and *M.fuliginosus*, compared to the very short lateral plantar crest of *D. bennettianus*. All three specimens have a deep tuberous sulcus for the insertion of the tendon of the peroneus longus.

Ventrally the most prominent feature of *M. fuliginosus* and *M. rufus* is their large ovoid lateral plantar process, separated from a smaller and shorter medial plantar process by a sulcus running longitudinally, the path of the ligament attaching the medial side of the cuboid to the base of the fourth and fifth metatarsals. In *D. bennettianus* the two plantar processes, which are of equal sizes, both make contact with the ground and are separated by an oblique sulcus running posterolateral to anteromedial region of the cuboid.

Distally, the cuboid bears three facets; the largest articulating with the fourth metatarsal, a smaller circular facet in *M. fuliginosus* and *M. rufus* or small triangular facet in *D. bennettianus* articulating with the plantar crest of the fourth metatarsal, which is a small rectangular facet in *M. rufus* and *M. fuliginosus* and a semicircular facet in *D. bennettianus*. The facet for the plantar crest of the fourth metatarsal, lying ventromedially is approximately the same size in all specimens, but is barely distinguishable in *D. bennettianus*, and is separated from the larger articular facet for the fourth metatarsal by a thin tuberous section. In *M. rufus* however these facets are separated by a small deep sulcus which channels the medial section of the ligament joining the cuboid to the fourth metatarsal. The size of the facet on the ventrolateral portion of the cuboid is largest in *D. bennettianus* and smallest in *M. rufus* compared with *M. fuliginosus*.

## The Calcanea of extinct and extant Macropods

### Statistical analysis

The results of the cluster analysis can be seen in Fig. 4. This figure is a diagrammatic representation of the output from the SPSS clustering algorithm. This analysis included both the fossil specimens and known extant specimens. If any one of the variables was missing from the measurements of one of the specimens, the respective specimen was excluded from the analysis (approximately 15% of the total sample). As a consequence, it was necessary to include the specimens not used in the analysis after the remainder of the calcanea were sorted out, using these as a guide.

Group “1” contains 14 specimens which are all definitely sthenurine, and most probably *Sthenurus brownei* (Merrilees and Porter 1979). There are two distinct size ranges in this group, and if one species is represented, this may be explained as sexual dimorphism. (see Fig. 6)

Group “2” contains 12 specimens and is also definitely sthenurine, most probably *Sthenurus occidentalis* (Merrilees and Porter 1979). This group contains four very large specimens, two of which still have their astragalus articulated. There are four medium sized calcanea and four smaller specimens, suggesting that this group may contain at least a second species, smaller than *S. brownei* and *S. occidentalis* (see Fig.7).

Group “3” contains 14 macropodine specimens. From examination and comparison with extant specimens, this group contains a majority of specimens attributable to *Macropus fuliginosus*, but also interestingly three specimens which can be identified as

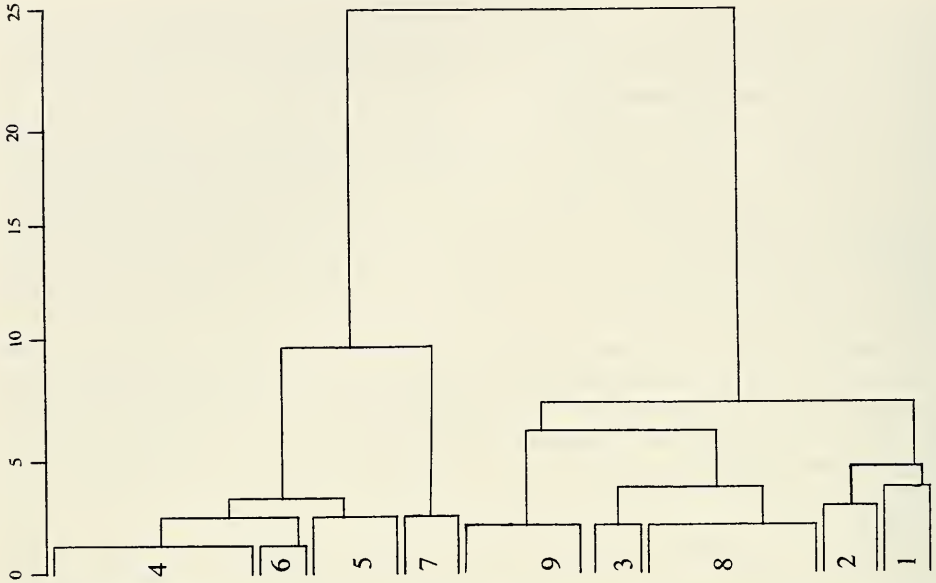


Figure 4. Shows the diagramatically simplified results of the cluster analysis performed on the fossilised calcanea. Left-hand terminations represent the groups separated in the cluster analysis. This diagram gives a representative view of the similarity (indicated by the arbitrary scale of 0–25 on the y- axis) in structure of the groups clustered out in the analysis

*Macropus rufus*, an exclusively plains and desert-dwelling kangaroo. Using the measurements taken, the clustering algorithm assigned *M. fuliginosus* and *M. robustus* to this group. Due to the large size of the specimens, this group most likely contains the fossilised calcanea of *M. fuliginosus* rather than the smaller *M. robustus.*

Group "4" is the largest macropodine group with 57 specimens. Of the extant material, *Macropus parryi*, *Macropus rufogriseus*, and *Wallabia bicolor* were assigned to this group through the cluster analysis. *M. rufogriseus* is one of the best represented macropodine species identified from cranial elements. There are three distinct size ranges in this group, the largest of which most probably represents *M. rufogriseus.*

Group "5" is a large group containing 29 macropodid specimens. *Macropus dorsalis* is the only extant species associated with this group through the cluster analysis. Despite the observation that all of the specimens are roughly equal in size, there are definitely two distinct morphs in this group, varying in only a few characters which were not measured in the analysis. Therefore they did not sort or cluster separately.

Group "6" contains six macropodid specimens. Although similar in size to a female *Macropus fuliginosus*, no modern macropodid sharing the distinctive features of these specimens were found. Their form however is somewhat similar to one of the two morphologically different subgroups of group "5". Many specimens of this group were not included in the analysis because of the poor state of preservation common to the group. Many of the specimens were large yet slender, with many of the processes being broken or abraded.

Group "7" contains three macropodine specimens. Many of the known extant species had been clustered in this group; *Macropus parma*, *Macropus irma*, *Dorcopsus sp*, *Petrogale lateralis, Setonix brachyurus*, and *Macropus eugenii.* On comparison with extant material, only the latter was found to be represented in the fossil collection . It is interesting to note that so many extant macropodid species are found clustered together in one group. This indicates that the genera represented are similar, and that the cluster analysis was not able to discriminate to the genus level in this cluster.

Group "8" contains 25 macropodid specimens. The majority of this group is probably attributable to *Macropus titan* or *Macropus giganteus*, and also possibly *Macropus robustus*. The cluster analysis assigned *Macropus fuliginosus* to this group. However, this is a recent lineage, and any such material pre or during the Pleistocene is often referred to as belonging to *Macropus giganteus*. There do seem to be two separate morphs within this group exhibiting very little size variation.

Group "9" is the largest sthenurine group with 34 specimens. It appears that this group could possibly be divided further into three separate morphs. Based on a comparison of the relative abundance of sthenurine cranial elements from the Victoria fossil cave deposit, the larger part of this group is probably attributable to *Sthenurus gilli*. This is supported by the observation that *Sthenurus gilli* is the smallest species from Victoria fossil cave deposit, which corresponds with the small size of the specimens. One morph may be attributed to *Sthenurus andersoni* (see Fig. 8).

It is now important to understand which factors are causing the main variation of the morphology of the characters measured. This is achieved through examination of the principal components analysis.

TABLE 5

The results of the principle components analysis and the first three factors (as defined in text) which account for the majority of the variation.

| Factor | Eigenvalue | Percent of Variation | Cumulative percentage |
|---|---|---|---|
| 1 | 8.926 | 81.8 | 81.8 |
| 2 | 0.891 | 8.1 | 89.2 |
| 3 | 0.362 | 3.3 | 92.5 |

Usually with a principal components analysis, a great deal of the variation for the entire data set can be explained by only two or three factors. Looking at Table 5 we can see that in this group of calcanea, 92.5% of the variation can be explained by the first three factors, shown in the cumulative percentage column. The majority of the variation is undoubtedly in the first factor, which is usually, and certainly in this case, attributed as size. Hence 81.8% of the variation is accounted for by size.

It can be seen from Fig. 4 that the sthenurine groups cluster separately from the larger macropodid group. This plot indicates that there were no small sized species among the sthenurines as seen in groups "4" and "7" of the macropodids. Only principle components with an eigenvalue greater than '1' are regarded as being statistically significant and hence through principal components analysis, size is the only statistically significant factor.

Comparative morphology of the sthenurine calcanea

As many of the groups sorted out can be assigned to a number of extant taxa, in which functional and morphological characters are well understood (Owen 1875, Parsons 1896, Windle and Parsons 1897, Craven 1971, Hopwood and Butterfield 1990), I will concentrate on the sthenurine groups. Where more than one species has clustered into a single group of the extant macropods, it was possible to discern between the different species through a visual examination. Within each group there are at least two or more morphs. These morphs most probably relate to separate species or perhaps separate sexu-

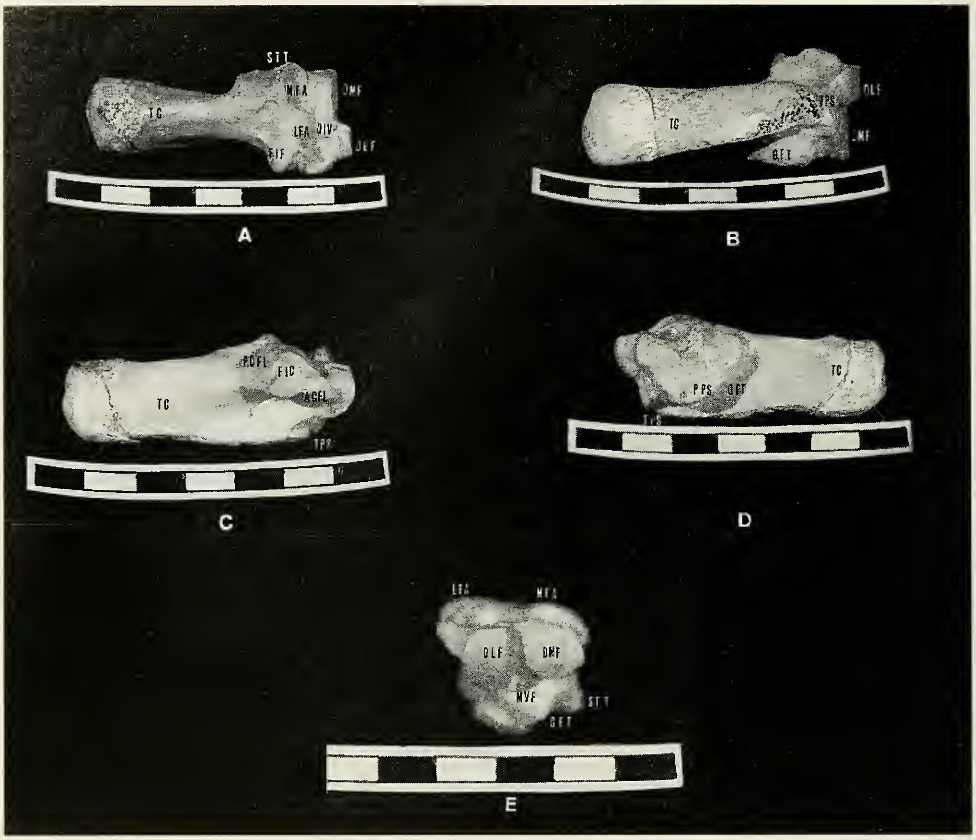


Figure 5. The right calcaneum of *Macropus fuliginosus* in dorsal (A), ventral (B), lateral (C), medial (D), and distal (E) views. **DIV**- longitudinal division of the medial and lateral facets on the calcaneum; **DLF**- Dorsolateral facet; **DMF**- Dorsomedial facet; **FIC**- Fibular condyle of the calcaneum; **FIF**- Facet for the fibula; **GFT**- Groove in the sustentaculum tali for the tendon of the Flexor digitorum longus; **LFA**- Lateral facet for the astragalus; **MFA**- Medial facet for the astragalus; **PPS**- Plantar process of the sustentaculum tali; **STT**- Sustentaculum tali; **TC**- Tuber calcanei; **VMF**- Ventromedian facet; **TPS-** Transverse plantar sulcus.

al morphs of the same species. Marked sexual dimorphism is exhibited in modern kangaroos by way of size (Poole et.al 1984). As the clustering algorithm used removes the factor of size, it is expected that sexually dimorphic species will group into the same cluster. Within group (1) there are at least two morphs; three morphs in group (2); and three morphs in group (9) (see Figs 6–8). The figures follow after the text.

The tuber calcanei of *Macropus fuliginosus* is of sub triangular form. Of the sthenurines, morph (iii) of group (9) possesses an ovoid cross sectional shape of the tuber calcanei (see Figs 5 and 8). The remainder of the sthenurines possess a generally much broader tuber calcanei which is sub triangular in morphs (i) and (ii) of group (1), morph (i) of group (2), and morph (ii) of group (9), compared with the square cross sectional shape of morphs (ii) and (iii) of group (2), and morph (i) of group (9) (see Figs 6–8). All of the specimens narrow dorsally to some extent and are flattened plantarly. The tuber calcanei is flared greatly posteriorly in the sthenurines compared with *M. fuliginosus*. The medial and lateral surfaces of the tuber calcanei apex in a longitudinal ridge which is narrow in morphs (ii) and (iii) of group (9) compared with *M. fuliginosus* (see Figs 5 and 8). Of the other sthenurines, this longitudinal ridge is moderately narrow in group (1),

Figure 6. The right calcaneum of a representative of group "1" in dorsal (A), ventral (B), lateral (C), medial (D), and distal (E) views. **APT**- Accessory plantar tubercle of the calcaneum; **DLF**- Dorsolateral facet; **DMF**- Dorsomedial facet; **FIC**- Fibular condyle of the calcaneum; **FIF**- Facet for the fibula; **GFT**- Groove in the sustentaculum tali for the tendon of the Flexor digitorum longus; **LFA**- Lateral facet for the astragalus; **MFA**- Medial facet for the astragalus; **PPS-** Planter process of the sustentaculum tali; **STT**- Sustentaculum tali; **TC**- Tuber calcanei; **VMF**- Ventromedian facet; **TPS-** Transverse plantar sulcus.

broad in all morphs of group (2), but most broad and nearly continuous with the medial and lateral surfaces in morph (i) of group (9). The tuber calcanei is also deepest in morph (iii) of group (9) relative to its width (see Fig. 8). The tuber calcanei is also shorter in the sthenurines than *M. fuliginosus* with the exception of all in group (1) and morph (iii) of group (9) (see Figs 5, 6 and 8). The sustentaculum tali is relatively narrow transversely in the sthenurines compared with *M. fuliginosus*.

A major difference in the sustentaculum tali in dorsal aspect is that in all of the sthenurines there is a posterior deflection of the plantar portion of the sustentaculum tali compared with *M. fuliginosus*, where the plantar portion of the sustentaculum tali is less angled and deflected medially (see Fig. 5). The sustentaculum tali is very much deeper

Figure 7. The right calcaneum of a representative of group “2” in dorsal (A), ventral (B), lateral (C), medial (D), and distal (E) views. **APT**- Accessory plantar tubercle of the calcaneum; **DLF**- Dorsolateral facet; **DMF**- Dorsomedial facet; **FIC**- Fibular condyle of the calcaneum; **FIF**- Facet for the fibula; **GFT**- Groove in the sustentaculum tali for the tendon of the Flexor digitorum longus; **LFA**- Lateral facet for the astragalus; **MFA**- Medial facet for the astragalus; **PPS-** Planter process of the sustentaculum tali; **STT**- Sustentaculum tali; **TC**- Tuber calcanei; **VMF**- Ventromedian facet; **TPS-** Transverse plantar sulcus.

dorsoplantarly in all of the sthenurine species than in the two macropodine specimens (see Figs 5–8). Another feature common to all of the sthenurines is that the plantar surface of the sustentaculum tali points directly plantarly compared with anteroplantarly in group (6) and *M. fuliginosus* (see Figs 5–8). The plantar process of the sustentaculum tali makes up part of the plantar surface in morphs (i) and (ii) of group (2) as well as morphs (i) and (ii) of group (9) (see Figs 7 and 8). In the remainder of the sthenurine groups the plantar process of the sustentaculum tali is separated from the plantar process by a dorsoplantarly deep groove for the tendon of the flexor digitorum longus. This separation from the plantar surface is most extreme in morph (iii) of group (9). Another main distinction between the sthenurines and the macropodines can be seen in the medial profile of the sustentaculum tali, where in the sthenurines, because of the plantarly deflected plantar process, a right angle or 90° profile is produced. This is in contrast to *M. fuliginosus*,

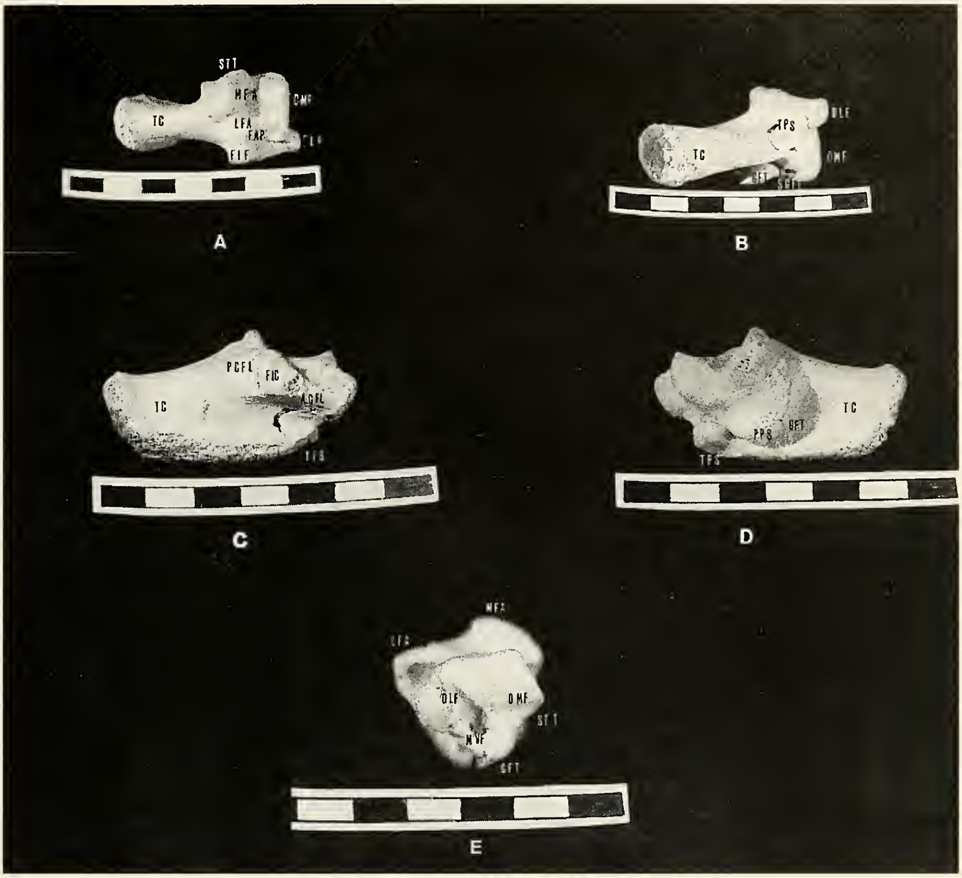


Figure 8. The right calcaneum of a representative of group "9" in dorsal (A), ventral (B), lateral (C), medial (D), and distal (E) views. **APT**- Accessory plantar tubercle of the calcaneum; **DLF**- Dorsolateral facet; **DMF**- Dorsomedial facet; **FIC**- Fibular condyle of the calcaneum; **FIF**- Facet for the fibula; **GFT**- Groove in the sustentaculum tali for the tendon of the Flexor digitorum longus; **LFA**- Lateral facet for the astragalus; **MFA**- Medial facet for the astragalus; **PPS-** Planter process of the sustentaculum tali; **STT**- Sustentaculum tali; **TC**- Tuber calcanei; **VMF**- Ventromedian facet; **TPS-** Transverse plantar sulcus.

where the border is rounded posteriorly and not so steeply inclined, as also noted by Murray (1995) (see Figs 5–8).

Laterally the fibular condyle is not as wide in sthenurines as it is in *M. fuliginosus*. Dorsally, the fibular condyle is substantially variable between the different morphs of the different groups, but generally the origin of the condyle being more abrupt in the sthenurines than macropodines. Laterally the fibular condyle bears two scars; one posteriorly for the posterior calcaneofibular ligament and one anteriorly for the anterior calcaneofibular ligament. In morph (i) of group (1) the scar for this ligament encroaches dorsally on the condyle, also providing an area for the posterior talofibular ligament which intervenes in between the fibula and its condyle (Fig. 6). The angle of the scar for the posterior calcaneofibular ligament is also slightly vertically inclined, but not as much as in *M. fuliginosus* (Fig. 5). The posterior border of the fibular condyle is also more abrupt in morph (i) than morph (ii) of group (1), compared with *M. fuliginosus* where the fibular condyle is curved convexly plantarly and then recurved, demarcating the scar for the attachment of the anterior calcaneofibular ligament. The fibular condyle is also generally deeper in the sthenurines than in *M. fuliginosus*. In all of the sthenurines there is also a greater area for insertion of the lateral calcaneocuboid ligament.

Dorsally, there are two facets on the calcaneum for articulation with the astragalus. The origin of the lateral facet for the calcaneum on the dorsal surface is markedly variable in the different specimens. In morph (i) of group (1), the lateral facet for the astragalus originates from and is continuous with the dorsolateral surface as in morph (iii) of group (9), compared with *M. fuliginosus*, where although the lateral facet for the astragalus originates from the dorsolateral surface of the tuber calcanei, it is interrupted by the higher convex form of the facet. In the remainder of the sthenurines the origin of the lateral facet for the astragalus is dorsally from the tuber calcanei, and is interrupted by its convex form in morph (ii) of group (1), morphs (i) and (ii) of group (2), and morph (i) of group (9), compared with morph (i) of group (1), morph (iii) of group (2), and morph (ii) of group (9) where the origin of the facet is continuous with the dorsal surface of the tuber calcanei. Immediately anterior to the lateral facet for the astragalus is the fossa for the proximal ventrolateral process of the astragalus, which is generally much deeper in the sthenurines. This fossa is also expanded anteroposteriorly in morph (ii) of group (1), and morph (i) of group (2), rather than being transversely broad in the other sthenurines, compared with the shallow circular pit in *M. fuliginosus* (see Fig. 5). In all of the sthenurines, the lateral facet for the astragalus sits lower than the medial facet. The medial facet for the astragalus is similarly variable between the sthenurines and macropodines, as well as within the sthenurines. Generally the medial facet for the astragalus is steeper in the sthenurines than in *M. fuliginosus*, which is shallowly concave on its anterior face and inclined posterodorsally (see Figs 5–8). The lateral and medial facets for the astragalus are separated by a transversely convex ridge which is particularly high and narrow in morph (ii) of group (1), morph (i) of group (2), and morph (i) of group (9), and slightly more shallow but still convex in morph (i) of group (1), morphs (ii) and (iii) of group (2), and morphs (ii) and (iii) of group (9). This feature may allow a slight degree of pronation. However in *M. fuliginosus* the lateral facet sits as high as the medial facet and is separated from the latter by a small longitudinal ridge, restricting pronation and supination. Directly behind the medial ridge which articulates with the astragalus, there is a scar for the posterior talocalcaneal ligament, the main posterior ligament binding the astragalus to the calcaneum. This scar in sthenurines suggests that the ligament, which is deflected dorsally and posterolaterally in *M. fuliginosus*, is deflected only dorsally, restricting any motion of the astragalus rolling forward. The pit for this ligament is greatest in morph (ii) of group (1) and morph (i) of group (9) (see Figs 5–8).

On the posterodorsomedial region of the sustentaculum tali is a large scar for the posteromedial talocalcaneal ligament in the sthenurine groups, perhaps with the exception of morphs (ii) and (iii) of group (9) where the scar is smaller compared with *M. fuliginosus*. The sustentaculum tali bears much of the weight of the astragalus in the majority of sthenurine morphs, with the exception of (ii) and (iii) of group (9). It is elongated anteroposteriorly at its dorsal margin compared with *M. fuliginosus* where it narrows dorsally.

In dorsal aspect it is also possible to see the varying morphology of the dorsolateral facet on the calcaneum for the cuboid. In all of the sthenurine groups, the dorsolateral facet is more narrow transversely, generally shorter anteroposteriorly, but more importantly the medial side of this portion is deflected laterally, i.e. the calcaneocuboid step is not as steep as in *M. fuliginosus* (see Figs 5–8). The dorsolateral facet is shortest in morph (iii) of group(2) and morph (ii) of group (9), which exhibit the shallowest step. This process is steepest and most elongate in morphs (i) and (iii) of group (9) (Fig. 8). The remainder of the sthenurines are somewhat intermediate in this character. The shallower the angle of the calcaneocuboid step on the calcaneum, the greater the ability for supination of the foot at the calcaneocuboid joint.

Ventrally, the plantar surface of the calcaneum is very greatly elongated in *M. fuliginosus*. This is due in great part to the width and position of the transverse plantar sulcus. This is narrowest and situated anterior most among the sthenurines in morphs (i) and (ii) of group(1), and morph (i) of group (9), and hence the greatest plantar surface length. It is also broadest anteriorly in the formerly mentioned morphs and *M. fuliginosus* compared with morphs (i) (ii), and (iii) of group (2) and morphs (ii) and (iii) of group (9). Here the plantar surface is narrow anteriorly and emanates from the lateral side. It is expanded posteriorly, particularly in morphs (i) and (iii) of group (2) and morph (ii) of group (9) and results in the plantar surface being nearly triangular in form (see Figs 7 and 8). In *M. fuliginosus* the plantar surface is nearly uniform in transverse breadth along its length, expanding only slightly posteriorly. The plantar surface is most narrow in morph (iii) of group (9). A large component of variation can also be seen plantarly in the comparative widths of the groove for the tendon of the flexor digitorum longus which is greatest in morph (ii) of group (1), morph (i) of group(2), and morph (i) of group (9) (see Figs 6, 7 and 8). Correspondingly the groove in the aforementioned specimens is only shallowly concave transversely compared with *M. fuliginosus*. Conversely it is deeply excavated and concave in morphs (ii) and (iii) of group (2), morphs (ii) and (iii) of group (9), and to a lesser extent morph (i) of group(1). In all of the sthenurines there is a demarcation at the base of the sustentaculum tali in the form of a narrow longitudinal sulcus which is not present in *M. fuliginosus*.

Distally, there are three facets on the calcaneum which articulate with the cuboid. In general, the dorsomedial and dorsolateral facets on the calcaneum are more narrow transversely, although still quite broad in morph (i) of group(1) and morphs (ii) and (iii) of group(2), compared with *M. fuliginosus* (see Figs 5–8). The medial border of the dorsomedial facet on the calcaneum for the cuboid is steeper in the sthenurine groups and nearly vertical in morph (iii) of group (2) compared with *M. fuliginosus*, which is deflected dorsomedially. The dorsolateral facet on the calcaneum for the cuboid is also more elongated dorsoplantarly in the sthenurine groups than *M. fuliginosus*. Also characteristic of the sthenurines this facet sits lower, or starts more plantarly in distal aspect to the larger dorsomedial facet, compared with *M. fuliginosus* where the dorsolateral facet for the cuboid is equal in height to the dorsomedial facet for the cuboid (see Figs 5–8). The dorsolateral facet is also deflected dorsomedially in morph (ii) of group (1), morph (i) and (iii) of group (2) and morph (i) of group (9). Where the dorsolateral facet for the cuboid is expanded in the sthenurine groups, as in morph (ii) of group(1), morph (i) of group (2) and morph (i) of group (9), it is done so more plantarly, approximately half the way down the distal surface. The lateral border of the lateral facet for the cuboid is curved convexly dorsoplantarly in the dorsal region then recurves concavely more plantarly, most strongly convex dorsally in group (6), morph (ii) of group (1), morph (i) of group (2), and morph (i) of group (9), and most concave plantarly in morphs (i) and (iii) of group (2), and morphs (ii) and (iii) of group (9) (see Figs 5–8). The dorsolateral facet narrows plantarly and merges into the ventromedian facet which is generally larger in the sthenurine groups than *M. fuliginosus*. In morphs (i) and (ii) of group (1), morphs (i) and (ii) of group (2), morph (i) of group (9), the plantar portion of this facet contributes to the plantar surface of the pes. In morphs (i) and (ii) of group (2) and morph (i) of group (9), the apex of the ventromedian facet is situated directly underneath the dorsomedial facet compared with the more medial placement of the facet underneath the step separating the dorsomedial and dorsolateral facets in *M. fuliginosus*, morph (iii) of group(2), and morphs (ii) and (iii) of group (9). It is common to all of the aforementioned morphs that the ventromedian facet plays no direct weight bearing role. Common to all of the sthenurine groups is the curved form of the ventromedian facet, whose dorsal and plantar borders are curved transversely such that the facet is "u" shaped in morphology compared with *M. fuliginosus*, which possesses a small ovoid facet. Also common to the sthenurine groups is the merging of the ventromedian facet on to the dorsomedial facet for the cuboid, making the three facets continuous, and forming a fossa in the centre of the three facets, compared with *M. fuliginosus* where the two facets are separated by a deep groove (see Figs 5–8).

## DISCUSSION

### The plesiomorphic characters of the marsupial pes

In constructing the cladistic relations of this group, it was revealed that there were no phylogenetic reversals in the cladogram. The pes of the outgroup expressed fourteen of the seventeen characters that were considered to be symplesiomorphic. This indicated that the morphology of the pes is highly conservative. There were only three characters where the polarity could not be determined. These were: 1 - (Character 10) The tuber calcanei, which was phylogenetically uninformative due to its diverse morphology. Murray (1995) similarly found this character to be uninformative in his study of the phylogenetic relationships of the late Miocene kangaroo, *Hadronomas*. 2 - (Character 5) The possession of a trochlear notch along with the (plesiomorphic) long astragalar head and neck in the wombat can be attributed to parallelism of evolution. Similarly the convergence in form of the sustentaculum tali of the koala and *Hypsiprymnodon* is unlikely to be the result of similar function in these species. The expression of this character state in the koala may be attributed to the retention of an ancestral character state. 3 - (Character 11) Based on a single feature, the Potoroidae would appear to be derived from the Phascolarctidae, contradictory to current phylogenetic placement. The contradictory nature of the cladogram can be explained by the use of a limited character set, i.e. the groupings of the outgroup marsupials are being determined on only one or two characters which are seen to be divergent from the generalised marsupial pes. This is most probably biased through the choice of characters which seemed to be most divergent in the macropodid species. A larger set of characters would have to be used for a more comprehensive study, particularly for the plesiomorphic states.

There were six shared derived features which unite *Hypsiprymnodon* (the most Plesiomorphic of the living kangaroos) with *M. fuliginosus*. This is consistent with the current placement of this family and its contained species, as intermediate in structure between the phalangerids (possums) and the macropodids (kangaroos). Disregarding the uninformative characters (5,10 and 11), there were no reversals of characters between the ancestral marsupial grade and that of *M. fuliginosus*.

The derived features of the macropodine pes are considered to be important, as they define its specific structure in relation to the generalised marsupial pes. Those features which are characteristic of the macropodines are likely to be related to locomotion and habitat preference. A more complete analysis of the features of the generalised macropodine form was attained through an examination of *Macropus fuliginosus* which is considered to be derived relative to *Hypsiprymnodon*. It is necessary to understand the functional nature of unique derived features of the macropodine pes.

### Anatomy of the Hindlimb and Pes of Macropus fuliginosus

The results of this work support earlier findings (Craven 1971, Parsons 1896 Adnams-Hodges 1988, Hopwood and Butterfield 1990) that the main contribution to the muscle mass in the macropodines is in the flexor and extensor muscles of the hindlimb. This reflects the specialised form of locomotion. The actions of the separate muscles of the crus on the pes have been further described. The insertion points of the tendons and ligaments produce scars or rugosities on the surface of the bones. This knowledge has been used to identify homologous features on the bones of the extinct forms.

The functional anatomy of the western grey kangaroo, *Macropus fuliginosus* was used in this study as a general model against which to compare other macropodid species.

Also studied was the anatomy of the binding ligaments of the pes, an area which seems to have been ignored in previous studies. The main muscles acting on the pes have lines of action predominantly in the sagittal plane. Ligaments of the pes also tend to restrict motion to the sagittal plane. Ligaments also restrict the elongated pes from being excessively dorsiflexed. These ligaments are the large posterior and anterior calcaneofibular ligaments in lateral aspect, and the posterior tibiotalar ligament and tibiocalcaneal ligament in medial aspect. Their cruciate (crossed) form stabilises the ankle. Similar results were found by Lewis (1983), and by Parsons (1896) who highlighted the stabilising nature of the "X" formation in the rock wallaby, *Petrogale xanthopus*. Parsons (1896) also identified two calcaneocuboid ligaments, a large plantar ligament, referred to as the '*outer ligament* ' running from the rugose plantar surface of the calcaneum to the lateral tubercle of the cuboid, and on to the base of the fourth and fifth ligaments; '*the medial* ', being smaller but still prominent, passing from the sustentaculum tali to the cuboid and the base of the second and third metatarsals. These results complement the findings of this research. I conclude that the function of these ligaments is to prevent over dorsiflexion of the pes, and allow for the possibility of elastic recoil, loaded when the animal lands.

The most complete description of the macropodine foot to date is by Owen (1875) in his description of the pes of *Macropus rufus*. The work of Owen (1877–1878) supports the current findings, in that the narrow form of the pes is related to its saltatory mode of locomotion. Lewis (1980, 1982) also notes the form of the astragalus (a functionally important bone of the ankle) as being remodelled into a trochlear shape, convergent in function with the placentals, supporting the current findings. Conclusions regarding the splint-like nature of the fibula in macropods and its role in restricting the motion about the ankle to the sagittal plane are supported by Barnett and Napier (1953). One peculiarity of this form in macropods is that while the trochlear ridges of the astragalus are parallel, they are slightly oblique to the long axis of the foot, resulting in internal rotation of the foot. This may be linked to the idea expressed by Barnett and Napier (1953), Parsons (1896), and Wells and Tedford (1995), of the possibility of a spring return of the fibula when loaded as the lateral condyle of the femur forces the head posteriorly during flexion of the knee. With the pes firmly placed on the ground, the tibia, fibula and remainder of the animal passes over the fixed pes, and the angle of the trochlear crests will act to rotate the crus externally, such that the action of the femur on the fibula is magnified. Parsons (1896), Windle and Parsons (1897), and Hopwood and Butterfield (1990) also provide evidence on the general morphology of the macropodine pes which supports the current study. The transverse nature of the subtalar joint complex was identified supporting earlier findings of Owen (1877–1878), Lewis (1964, 1980, 1983), and Barnett (1970).

## Modifications of the macropodine pes.

Despite being restricted by the specialised mode of locomotion and necessary structural modifications associated with it, the modern macropods have managed to occupy a number of diverse habitats; e.g. as *Macropus rufus*, a plains dwelling kangaroo, and *Dendrolagus bennettianus*, a kangaroo adapted for an arboreal lifestyle.

### Modifications of the Macropodid Pes for Open Plains and Arboreal Habitats

The main difference of the pes of *Macropus rufus*, an open plains animal, from that of *Macropus fuliginosus*, is the gracile form of the entire pes. As *M. rufus* inhabits large areas of flat treeless rolling plains of calcareous clay soils it is often referred to as the "open plains kangaroo". *M. rufus* also has the highest recorded speeds among modern macropodines (Bennett 1987).

There are a number of features of the pes of *Dendrolagus bennettianus* which I consider to be adaptations to an arboreal lifestyle. Despite the macropodines having evolved from the arboreal possums, there is little doubt that *Dendrolagus* is a macropodine and not simply an ancestral grade between the possums and the kangaroos. It has clearly secondarily modified a terrestrial hindlimb for an arboreal lifestyle. Those features considered to be derived in the macropodine pes are also expressed in *D. bennettianus*.

i) Modifications of the Astragalus: The main distinction between *Dendrolagus* and *Macropus fuliginosus* is the form of the transversely broad astragalus. This feature is in accordance with the general breadth of the entire pes of this genus. The broad pes is a functional requirement for the arboreal habitat, giving greater stability on narrow tree limbs. The parallel trochlear crests are oblique to the long axis of the foot. In this respect the form is convergent in function with the other arboreal species examined in this study, the possum and koala. The oblique nature of the articulation of the crus on the pes results in one of two actions. With the proximal portions of the hindlimb held close to the body, when climbing, the oblique trochlear ridges cause the foot to be internally rotated, conceivably aiding in climbing tree trunks. Similarly when the feet are closely placed next to each other, such as when sitting on a branch, the knees are externally rotated, lowering the body and centre of gravity, resulting in a more stable posture.

Conforming with the remainder of the pes, in *M. rufus* the astragalus is relatively narrow transversely, and elongated anteroposteriorly. It is probable that the great anteroposterior length of the astragalus and of the trochlear ridges have the effect of restricting motion of the pes to the sagittal plane. The parallel trochlear ridges are in line with the longitudinal axis of the foot, indicating that any movement of the pes is confined to the sagittal plane. Another feature of this articulation in *M. rufus* is the medial trochlear ridge, which is greater in height than the lateral trochlear ridge and associated with a well demarcated and steep medial malleolus. This feature seems to be related to maintaining the pes in the sagittal plane during locomotion. Another factor restricting motion at this joint is the line of action of the main medial ligaments. Medially, the insertion of the two crossed ligaments on the astragalus are defined by a long horizontal ridge. This arrangement limits external and internal rotation of the pes as well as pronation.

The trochlear groove for the tibia is deepest in *Dendrolagus*, which I believe is due to the necessity for greater mobility at the ankle, in particular in being able to pronate and supinate the foot. When viewed in distal aspect, the medial and lateral trochlear ridges are equal in height compared with *Macropus fuliginosus* where the medial trochlear ridge is higher. I believe this is also related to the ability to pronate and supinate the foot. Barnett and Napier (1952), Hicks (1953), Close (1956) and Sarrafian (1993) have examined the nature of the ankle articulations in human specimens. Their results support the findings of this work that flexion and extension of the foot also affects other motions, such as pronation, and supination. Barnett (1970) and Lewis (1980) note the transverse nature of the subtalar joint complex, and Barnett (1970) notes the diverse morphology of this feature among the modern macropodines, but makes no functional interpretations.

Ventrally the articular facets of the calcaneoastragalar articulation are transversely broad, and this is most likely related to the general breadth of the pes. In *Dendrolagus* the medial malleolar tibial articulation is ovoid, expanded anteroposteriorly, and is probably related to greater mobility of the tibia. In *Dendrolagus* the scar for the posterior tibiotalar ligament suggests that the action of this ligament would most likely allow for greater eversion and inversion of the foot. Similarly the area for attachment for the anterior tibiotalar ligament is much reduced, possibly allowing for greater supination when the foot is plantarflexed, although even the reduced ligament would constrain this range of motion. The navicular facet on the astragalus is transversely wide, corresponding with an enlarged fifth digit. Lewis (1980) notes the nature of an intra articular meniscus in possums, which is much reduced in macropodids. Lewis (1980) also suggests the meniscus provides greater mobility at the articulation between the fibula, tibia, and the astragalus. Examination of a dried ligament preparation from the South Australian Museum indicated that the meniscus is enlarged in *Dendrolagus* compared to other macropodines.

ii) Modifications of the Calcaneum: The general morphology of the calcaneum of *Dendrolagus* corresponds with the form of the rest of the pes, being broad and dorsoplantarly compressed. The tuber calcanei is ovoid, reminiscent of the form of the possum, and considering its similar habitat, may also be convergent in function. Similarly, the sustentaculum tali is extremely broad, tapering medially as in the koala and possum, also related to the breadth of the pes. The sustentaculum tali bears a groove for the tendon of the flexor digitorum longus, the function of which is to flex the digits. The morphology of this groove in *Dendrolagus* is such that the tendon would be relatively unconstrained, allowing the digits to be flexed in a greater range of positions. There is a reduced articulation of the fibula with the calcaneum in *Dendrolagus*, as noted by Barnett and Napier (1953). This would suggest greater mobility at the articulatio tarsocruralis (between the crus and the pes) as the constraining nature of the talofibular articulation is minimised. This is associated with only a slight lateral projection for the fibula articulation.

In *M. rufus* the tuber calcanei shows evidence of being adapted to a biomechanical function, associated with an open plains habitat, as it narrows dorsally. Ontogenetic changes of bone are related to the direction and type of forces placed on it (Hildebrand 1988). As the tuber calcanei narrows dorsally, to a shape which is essentially triangular, it is indicative of the unidirectional forces acting upon the calcaneum. The groove for the tendon of the flexor digitorum longus runs under the very narrow sustentaculum tali, suggesting that the digits are only flexed when the foot is in the sagittal plane of the body, i.e. only when there is a direct line of action for this tendon. Dorsally, the large area for insertion of the ligamentum cervicis tali is associated with the strong binding of the astragalus to the calcaneum. This further restricts motion at the subtalar joint.

Another feature of the calcaneum suggesting a restriction of motion to the sagittal plane, is the size of the articular facet for the fibula. The fibula and the associated ligaments ensure the crus is securely braced to the pes, and restricts any internal or external rotation of the foot about the tibia. There are also a number of features of the ankle of *M. rufus* that relate to restriction of lateral movement at the calcaneocuboid articulation. This is supported by the arrangement of the ligaments at this joint. The dorsolateral facet of the calcaneum for the cuboid is anteroposteriorly compressed, but more importantly the step between this and the dorsomedial facet is well defined. This feature constrains any pronatory or supinatory motions of the pes.

Ventrally, the plantar surface of the pes is particularly tuberous, providing a large surface area for insertion of the plantar calcaneocuboid ligament. Medially, the sustentaculum tali is also tuberous for the insertion of a large medial calcaneocuboid ligament. These findings concur with those of Parsons (1896). The areas for insertion of the ligaments binding the cuboid to the fourth and reduced fifth metatarsal are also correspondingly large.

Dorsally, of the two articulating facets for the astragalus, the medial possesses a ridge dorsally which is straight, runs transversely, and is deflected slightly anteriorly. The function of this is probably for greater flexion and extension of the pes at the subtalar ankle joint. Directly behind this ridge is a large scar for the posterior talocalcaneal ligament, suggesting that the astragalus is well bound to the calcaneum posteriorly, resisting excessive pronation of the pes. A further feature of the talocalcaneocentralis joint of *Dendrolagus* is the fossa for the anterior proximal process of the astragalus is not well developed, and hence motion at this articulation is not restricted.

In summary, the features of the subtalar joint complex of *Dendrolagus* allow for greater freedom of movement associated with an arboreal habitat. Distally the main features of the calcaneum that allow for increased motion at the distal joint are related to the shallow gradient of the normally steep facets for the cuboid as expressed in other macropodines. The basic form of the distal articular surface is shallowly convex, both transversely and dorsoplantarly (cup shaped), and corresponds to what Sarrafian (1993) describes as a male ovid surface. The motions generated at a male and female ovid (or ball and socket) joint are those of flexion, extension, pronation, supination, internal rotation, and external rotation (Sarrafian 1993).

iii) Modifications of the Cuboid: The proximal articulating facet of the cuboid corresponds with the calcaneum as the female ovid surface. As with the calcaneum and astragalus, the cuboid is transversely broad and dorsoplantarly compressed. Distally, the separate articulating facets on the cuboid for the fourth and fifth metatarsals take the form of a single facet. In medial or lateral view, the cuboid is rhomboidal in appearance, extended anteriorly dorsally, the function of which would be to prevent excessive dorsoflexion of the foot, being restricted by the protruding dorsal portion. Ventrally, in *Dendrolagus*, the medial plantar crest of the cuboid is enlarged, and in contact with the substrate surface, providing greater stability for the pes.

In summary, the feature of the *Dendrolagus* pes provides greater stability in the width of the pes in addition to greater mobility of the ankle joints, both necessary for an arboreal habitus.

These results suggest the main adaptations for an open plains habitat are an elongated narrow pes with motion restricted to the sagittal plane. The comparison of these two forms (arboreal and terrestrial), clearly indicate a large degree of homoplasticity in the features deemed to be derived within the macropodines. This has allowed the macropodines to radiate into a number of different habitats.

## The Cluster Analysis

One aim of this study was to sort the fossilised calcanea from the Victoria Fossil Cave, Naracoorte. From an examination of both the cluster analysis and principal components analysis it can be seen that sthenurines separate from the macropodines and form three distinct groups. A closer examination of the group revealed a number of features of the calcaneum which were species specific. In a similar fashion, it is possible that the sthenurine groups may include more than one species.

The cluster analysis was an invaluable tool in determining primary structural differences in the large number specimens examined. It was not until after a discrete functional and structural analysis had been carried out that a number of "species specific" characters could be recognised.

## Functional Anatomy of the Sthenurine Pes

Very few studies (Stirton 1963, Tedford 1966, 1967; Adnams-Hodges 1988; Murray 1991, 1995; Wells and Tedford 1995) have attempted to determine the functional nature of the postcranial elements of the sthenurines. Wells and Tedford (1995) examined the postcranial remains of three species of extinct sthenurines and suggested that as there are no modern descendants it was difficult to determine the locomotory habits of these animals for lack of a reliable functional analogue. These authors were however able to relate a number of features relating to the locomotor ability of the sthenurines. Wells and Tedford (1995) suggest that the sthenurine's mode of locomotion was of limited manoeuvrability, and further suggest that adaptations of the hindlimb and pes are related to supporting the weight of the animal, both during locomotion and stand-up browsing.

Just as the modern macropodine forms have diversified into a wide range of habitats, with accompanying differences in foot structure, so it is expected that differences in morphology of the calcaneum of the extinct forms may also be related to habitat.

The morphology of the tuber calcanei is much varied in the sthenurine morphospecies. Despite being generally more robust than *Macropus*, the four morphospecies share a subtriangular form; three of which have a square cross-sectional shape, and the fourth is transversely narrow. The three 'species' where the tuber calcanei is square in cross-section suggest that forces acting on this process of the calcaneum are both in the sagittal and transverse planes. The transversely narrow tuber calcanei is indicative of forces being directed largely in the sagittal plane only. With the exception of four species, the tuber calcanei of the sthenurines is relatively anteroposteriorly compressed. This would suggest that the sthenurines were not as well adapted for fast locomotion as many of the extant macropodines. Their form is divergent from the form of the highly specialised red kangaroo, *Macropus rufus*. As noted by Tedford (1966, 1967), Adnams-Hodges (1988), Murray (1995), and Wells and Tedford (1995), the sustentaculum tali is generally narrower in the sthenurines than the macropodines, with the exception of two morphospecies where the sustentaculum tali is particularly broad posteriorly. This seems to be convergent in function with the possums and koalas, in being an adaptation allowing the digits to be plantar flexed while the foot is internally rotated. This is supported in other features of the sustentaculum tali. In medial aspect, the profile of the sustentaculum tali is dorsoplantarly deep and right-angled, providing two possible functions. While the main extensor muscles, the gastrocnemius and flexor digitorum brevis provide the majority of the power to extend the pes during standing, the flexor digitorum longus may augment this action. As the animal starts to stand, the distal digits are firmly planted on the ground, and the action of the tendon of the flexor digitorum longus running underneath the pes would be to elevate the pes at the point of the sustentaculum tali. The right angled form of the sustentaculum tali would also impede the tendon from dislodging medially. This is supported by another feature of the sustentaculum tali in that it is pointed plantarly, further constraining the tendon with the foot extended, and also possibly providing support medially, as it contributes to the plantar surface of the pes in all but one morphospecies.

Also related to the action of the flexor digitorum longus tendon across the sustentaculum tali is the presence of a small longitudinal groove lateral to the path of the tendon, separating the sustentaculum from the body of the calcaneum plantarly, also reported by Wells and Tedford (1995). Deep within this groove is a small foramen, which suggests that this adaptation is for protection of the blood and nervous innervation of the calcaneum. Another feature of the calcaneum related to raising the body is the degree to which the tuber calcanei is flared posteriorly. On comparison of sthenurine and macropodine specimens of equal size, this feature indicates large areas for insertion of the tendons of the gastrocnemius and flexor digitorum brevis, suggesting that the action of these tendons in extending the pes is particularly important in the sthenurines, supporting earlier findings (Adnams-Hodges 1988, Murray 1989, 1995, and Wells and Tedford 1995).

The fibular condyle is reduced in the sthenurines and relatively flat compared with *M. fuliginosus*, indicating less fibular contact with the calcaneum. On many of the sthenurine calcanea, the fibular condyle is depressed, sitting lower on the lateral face. This may indicate that the foot is able to be pronated to a greater degree, supporting the suggestion of Murray (1995) that the majority of the weight is transferred to the medial side in the sthenurines. This is further supported by a number of features of the calcaneum. If the sthenurines were to distribute the majority of their weight medially, with their foot pronated, we would expect to see a number of mechanisms preventing the astragalus from being displaced from the calcaneum. One of the most notable pieces of evidence for this is the large scar for the calcaneoastragalar ligament, which is similarly large in the arboreal forms, possum, koala, and tree kangaroo. This was also noted by Stirton (1963), and Murray (1995). This ligament restricts anteromedial movement of the astragalus about the calcaneum. The medial articulation for the astragalus is greatly accentuated and bears a deep scar for the posteromedial talocalcaneal ligament, further limiting medial displacement of the astragalus. There is a ridge between the medial and lateral facets for the astragalus, which is very broad in two of the morphospecies. This ridge also forms the medial border of an extremely deep pit which is anteroposteriorly elongated in some species, bearing the anterior proximal process of the astragalus. This feature is similarly related to stabilising the subtalar ankle joint, imperative not only in locomotion, but also to support the huge bulk of the body when standing erect. This provides an explanation for the reduction of the fifth metatarsal as the majority of the weight is being borne on the medial side of the pes.

The fifth metatarsal is expanded proximally (Adnams-Hodges 1988; Murray 1991, 1995; Wells and Tedford 1995), and may relate to morphological differences of the distal lateral portions of the calcaneum. The entire distolateral portion in the calcaneum is depressed in distal aspect, as well as being angled anteroplantarly, transmitting weight through to the expanded proximal portion of the fifth metatarsal. In four of the sthenurine morphospecies, there is a large transverse plantar sulcus on the plantar surface of the calcaneum, convergent in form with the potoroids.

The tuberous section of the plantar surface provides insertion for the plantar calcaneocuboid ligaments, which tightly bind the calcaneum to the base of the cuboid, fourth and fifth metatarsal. The sthenurine's possession of an elongate transverse plantar sulcus may be related to utilisation of the elastic properties of the ligament originating posteriorly on the calcaneum. As the ligament is not bound to the calcaneum at the plantar sulcus, the ligament may act like a bow across the plantar surface between the calcaneum and the cuboid.

In the sthenurines as with *Macropus rufus* there is evidence for large lateral and medial calcaneocuboid ligaments, suggesting reduced lateral movement. Mobility at the calcaneocuboid articulation is also heavily influenced by the morphology of the distal articulating facets for the cuboid. In two of the morphospecies the dorsolateral facet for the cuboid is particularly narrow, but also broad in three of the morphospecies. The most important functional nature of the calcaneocuboidal step, which is shallow in four of the morphs, suggests the foot may be supinated or pronated at the calcaneocuboid articulation. The dorsolateral facet for the cuboid is also anteroplantarly compressed in a few of the sthenurine groups, convergent in form with *M. rufus*, the distinction being in the degree of truncation of the step. A further consistent feature of the sthenurines is that the dorsomedial and ventromedian facets are fused, surrounding a circular fossa suggesting increased rotational mobility at the calcaneocuboid articulation. The ventromedian facet for the cuboid is much larger in all of the sthenurines than the macropodines. This would be attributed to its weight bearing role during stand-up browsing. In three of the morphospecies, the plantar apex of the ventromedian facet is situated directly below the dorsomedial facet, compared with a more lateral placement of the ventromedian facet, below the calcaneocuboidal step in the other morphospecies. The placement of this fossa indicates where the weight is being borne in the foot, and that, in the former group, the foot was stressed in a slightly pronated position.

## Inferred Locomotory and Feeding Habits of the Sthenurines from the Naracoorte Area

On discrete analysis of the sthenurines calcanea, at least eight morphospecies could be identified. The diverse morphology of the calcaneum suggests that they were segregated into a wide range of habitats.

### Inferred Habits of Group (1):

There are two morphospecies within this group which were originally thought to represent two sexual morphs of *Sthenurus browneii* (Merilees and Porter 1979). It was not within the scope of this study to include a complete comparison of the sexual dimorphism present in the modern macropodine species, which should be carried out to test such a hypothesis.

It can be inferred from the pes structure that this sthenurine group is adapted mainly for bearing the large weight of the animal during locomotion. The sthenurines in this group were not able to rotate their feet to the extent of the modern macropodines. Because of the monodactyl nature of the pes, it is concluded that these sthenurines were adapted to a habitat relatively free of obstacles. There are still adaptations apparent to align the foot under the body in the sagittal plane during locomotion.

### Inferred Habits of Group (2):

There are three morphospecies in this group. Because the measurements were not able to discriminate to species level, morph 1 of this group has the same relative proportions as the other two. On further examination morph 1 was found to be anatomically very different. There are a number of features discriminating the second two morphs of group (2) which are probably *Sthenurus occidentalis* based on a comparison with a known specimen from the Green-Water Hole at Tantanoola, S.A.:

It can be inferred from the morphology that the pes of this sthenurine group is adapted for bearing the large weight of the animal (approximately 20% greater in mass compared with the largest of the modern macropodine species) during locomotion, and that there are adaptations for greater mobility at the ankle. It would seem that the sthenurines in this group have compensated for the loss of the stabilising lateral digits by having greater ability to control the motion of the foot. The loss of stability at the ankle however would indicate slow locomotion as much of the action of the muscles would be in control of the foot, particularly through uneven terrain. These sthenurines also would have been well adapted for stand-up browsing.

Morph 1 of group (2) shows many adaptations to keeping the pes in line under the body during locomotion, but also show adaptations for being able to rotate the foot internally and externally. These features are most likely related to control of the foot during stand-up browsing, such as moving the digits and the feet, particularly with the feet externally rotated, providing greater stability. The sthenurines of this morphospecies were probably also moderately well adapted to locomotion through habitats with uneven terrain.

### Inferred Habits of group (9):

The detailed anatomy of the morphs of group (9) is extremely varied. morph (i) is concluded to be a sexual morph of group (1) morph (ii) with the exception of the comparatively short tuber calcanei. Morph (ii) of group (9), which is surmised to be *Sthenurus gilli*, can be distinguished by the following characters:

The features of morph (ii) of group (9) (tentatively *Sthenurus gilli*) suggest that this species was particularly well adapted to stand-up browsing, being able to externally rotate the foot, producing a stable posture. This species also possessed features allowing the foot to be pronated and supinated. This species had stable upper and lower joint complexes, suggesting that during locomotion the feet were able to be placed underneath the body, possibly through internal rotation of the crus about the articulation with the femur. It is evident that this smaller species does not possess the weight bearing adaptations. This is to be expected considering the small size of this species.

Morph (iii) of group (9) diverges significantly from the general robust form of the remaining sthenurines.

It is evident that this species bears few of the adaptations to locomotion and stand-up browsing recognised in the remainder of the sthenurines. It is proposed that this sthenurine species was particularly gracile and had proficient locomotor capabilities. The depth of the tuber calcanei suggests that the animal still had to bear a substantial weight load, which was subsequently directed primarily in the sagittal plane. There was limited mobility of the foot, extraneous to motion in the sagittal plane. Evidence suggests that during locomotion, the feet did not have to be forced underneath the body to support a great weight. It is concluded that this species was adapted to a plains environment, and was the most gracile or slender of the sthenurines. This sthenurine species was not particularly well adapted to stand-up browsing.

## CONCLUSIONS

The shared pedal characters of the diprotodont marsupials were compared with other diprotodont marsupials including the possum, wombat and koala. Using these as an outgroup, the musky rat-kangaroo, *Hypsiprymnodon* was shown to possess the fewest derived characters of the macropodids. The western grey kangaroo, *Macropus fuliginosus* was shown to be very derived relative to the condition expressed in *Hypsiprymnodon.*

A study of the functional anatomy of the hindlimb and pes of *Macropus fuliginosus* demonstrated that the derived morphology related directly to its specialised bipedal mode of locomotion. Some of the macropodines have diverged, and are present in varied habitats. *Dendrolagus bennettianus*, the tree-dwelling kangaroo, possessed a short broad pes, and an ankle structure with high mobility, clearly adaptations to an arboreal habitat. *Macropus rufus*, the plains-dwelling kangaroo showed adaptations such as a narrow elongated pes with a highly constrained ankle, which relate to locomotion in the even terrain plains habitats.

A cluster analysis of the fossil calcanea sorted the sthenurines from the macropodines. The sthenurines could further be broken down into nine distinct morphological groups, some of which could be assigned to particular species.

The main features uniting the sthenurines suggest that the sthenurine pes was adapted for stand-up browsing. While there is no doubt that like the modern kangaroos, the sthenurines utilised the bipedal hop for locomotion, the results support earlier findings that their morphology suggests that the feet were adapted to bearing the great weight of the animal during locomotion.

However, some of the sthenurine calcanea, while still possessing adaptations for stand-up browsing were noted to be particularly slender, and lacked the adaptations related to weight bearing. Evidence suggests that the sthenurines from the Naracoorte area were partitioned into several different habitats, from scrub and uneven terrain to plains environments.

The distinct morphological variance exhibited in the characters of the pes of these sthenurine forms suggest it may be possible to reconstruct the phylogeny of these groups based on anatomy of the foot.

## AKNOWLEDGEMENTS

I wish to thank all of my colleagues at Flinders University who helped me with this study; Assoc. Prof. Rod Wells, Assoc. Prof. Russel Baudinette, Gavin Prideaux, Matthew McDowell, and Pyramo Marianelli. I would also like to thank Lynette Queal and Neville Pledge of the South Australian Museum for providing me with extant and extinct specimens respectively. I would like to thank the Cleland Wildlife Park for provision of a number of carcases for dissection. I would also like to thank Dr. Michael Schwartz for advice and help with the statistical analysis.

## REFERENCES

Adnams-Hodges, W.A.J. (1988). A partial reconstruction of an extinct browsing kangaroo. Honours Thesis, Flinders University, South Australia.

Alexander, R.McN. and Vernon, A. (1975). The mechanics of hopping by kangaroos (Macropodidae). *Journal of Zoology, London.* **177**, 265–303.

Alexander,R.McN.(1984). Elastic energy stores in running vertebrates. *American Zoologist* **24**, 85–94.

Archer, M. (1984). The Australian marsupial radiation. In: 'Vertebrate zoogeography and evolution in Australia: animals in time and space.' (Eds M. Archer and G. Clayton) pp. 728–759 (Hesperian Press, Carlisle, WA)

Badoux, D.M. (1965). Some notes on the functional anatomy of *Macropus giganteus* Zimm with general remarks on the mechanics of bipedal leaping. *Acta Anatomica* **63**, 418–433.

Barnett, C.H. (1970). Talocalcaneal movements in mammals. *Journal of Zoology, London* **160**, 1–7.

Barnett, C.H., and Napier, J.R. (1952). The axis of rotation at the ankle joint in man. Its influence upon the form of the talus and the mobility of the fibula.*The Journal of Anatomy* **86**, 1–9.

Barnett, C.H., and Napier, J.R. (1953). The form and mobility of the fibula in metatherian mammals. *Journal of Anatomy, London* **87**, 207–213.

Barnett, C.H., and Napier, J.R. (1953). The rotary mobility of the fibula in eutherian mammals. *Journal of Anatomy, London* **87**, 11–21.

Baudinette, R.V., Snyder, G.K., and Frappel, P.B. (1992). Energetic cost of locomotion in the tammar wallaby. *American Journal of Physiology*. **262**, RT11–RT18.

Baudinette, R.V.(1994). Locomotion in macropodid marsupials: gaits, energetics and heat balance. *Australian Journal of Zoology* **42**, 103–123.

Bennett, M.B. (1987). Fast locomotion of some kangaroos. *Journal of Zoology London* **212**, 45–464.

Bennett, M.B., and Taylor, G.C. (1995). Scaling of elastic strain energy in kangaroos and the benefits of being big. *Nature*, **378**, 56–59.

Bensley,B.A. (1903). On the evolution of the Australian marsupialia; with remarks on the relationships of the marsupials in general. *Transactions of the Linnean Society London* **Ser.2**, 83–217.

Biewener, A.A., and Blickhan, R. (1988). Kangaroo rat locomotion: design for elastic energy storage or acceleration? *Journal of experimental Biology* **140**, 243–255.

Bock, W.J. (1980). The definition and recognition of biological adaptation. *American Zoologist* **20**, 217–227.

Bock, W.J. (1981). Function-adaptive analysis in evolutionary classification. *American Zoologist* **21**, 5–20.

Bock, W.J. (1988). The nature of explanations in morphology. *American Zoologist* **28**, 205–215.

Bock, W.J. (1989). Organisms as functional machines: a connectivity explanation. *American Zoologist* **29**, 1119–1132.

Bock, W.J., and von Wahlert, G.(1965). adaptation and the form-function complex. *Evolution* **19**, 269–299.

Cavagna, G.A., Heglund, N.C., and Taylor, C.R. (1977). Mechanical work in terrestrial locomotion: two basic mechanisms for minimising energy expenditure. *American Journal of Physiology* **233**, R234–R261.

Craven, H.J. (1971). Functional aspects of the anatomy of the lower limb in *Megaleia rufa* with reference to the ricochetal mode of locomotion. Honours thesis, Monash university, Melbourne.

Dawson, T.J., and Taylor, R.C. (1973). Energetic costs of locomotion in kangaroos. *Nature* **246**, 313–314.

Dollo, L. (1899). Les anâtres des marsupiaux, é taientils arbericoles? *Miscellanées Biologiques*, (Paris) 188–203.

Flannery, T.F. (1983). Revision in the macropodid subfamily Sthenurinae (Marsupiala: Macropodoidea) and the relationships of the species *Troposodon*, and *Lagostrophus* . *Australian Mammalogy* **6**, 15–28.

Gans, C. (1988). Adaptation and the form-function relation. *American Zoologist* **28**, 681–697.

Gould,S.J., and Lewontin, R.C. (1979). The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptionist programme. *Procedings of the Royal Society of London* **205**, 581–598

Hicks, J.H. (1953). The mechanics of the foot: I. *The Joints Journal of Anatomy* **87**, 345–357.

Hildebrand, M. (1988) 'Analysis of vertebrate structure'. (John Wiley and Sons, N.Y.)

Hopwood, P.R., and Butterfield, R.M. (1990). The locomotor apparatus of the crus and pes of the eastern grey kangaroo, *Macropus giganteus* . *Australian journal of Zoology* **38**, 397–413.

Johnson, P.M., and Strahan, R. (1982). A further description of the Musky Rat-Kangaroo, *Hypsiprymnodon moschatus* Ramsay, 1876 (Marsupialia, Potoroidae), with notes on its biology. *Australian Zoologist* **21**, 27–46.

Kirsch, J.A.W., and Poole, W.E. (1972). Taxonomy and distribution of the grey kangaroos, *Macropus giganteus* (Shaw) and *Macropus fuliginosus*(Desmarest), and their subspecies (Marsupialia: Macropodidae). *Australian Journal of Zoology* **20**, 315–339.

Lambert, K.L. (1971). The weight-bearing function of the fibula. A strain gauge study. *The Journal of Bone and Joint surgery* **53**, 507–513.

Lauder, G.V. (1981). Form and function: structural analysis in evolutionary morphology. *Paleobiology* **7**, 430–442.

Lauder, G.V. (1990). Functional morphology and systematics: studying functional patterns in an historical context. *Annual Review of Ecological Systematics* **21**, 317–340.

Leach, D. (1993). Recomended terminology for researchers in locomotion and biomechanics of quadrapedal animals. *Acta Anatomica* **146**, 130–136.

Lewis, O.J. (1964). The homologies of the mammalian tarsal bones. *Journal of Anatomy, London* **98**, 195–208.

Lewis, O.J. (1980). The joints of the evolving foot. Part I. The ankle joint. *Journal of Anatomy* **130**, 527–543.

Lewis, O.J. (1980). The joints of the evolving foot. Part II. The intrinsic joints. *Journal of Anatomy* **130**, 833–857.

Lewis, O.J. (1983). The evolutionary emergence and refinement of the mammalian pattern of foot architecture. *Journal of Anatomy* **137**, 21–45.

Losos, J.B. (1990). The evolution of form and function: morphology and locomotor performance in West Indian anolis lizards. *Evolution* **44**, 1189–1203.

Merilees, D. and Porter, J.K., (1979). 'Guide to the identification of teeth and some bones of native land mammals occurring in the extreme Southwest of Western Australia'. Western Australia Museum, Perth, Australia.

Marshall, L.G. (1974). Why kangaroos hop. *Nature* **248**, 174–175.

Murray, P.F. (1991). The pleistocene megafauna of Australia. In: 'Vertebrate palaentology of Australasia' (Eds.

P. Vickers-Rich, J.M. Monahaghan, R.F. Baird and T.H. Rich) pp. 1071–1164.

Murray, P.F. (1995). The postcranial skeleton of the miocene kangaroo, *Hadronomas puckridgi* Woodburne. *Alcheringa* **19**, 119–170.

Muybridge, E. (1887). 'Animal locomotion'. (University of Pennsylvania).

'Nomina Anatomica Veterenaria' (N.A.V. 1972). International Committee on Veterinary Anatomical Nomenclature of the World Association of Veterinary Anatomists. (Distributed by the Department of Anatomy, New York State Veterinary College, Ithca.)

Owen, R. (1874–1877). On the osteology of the Marsupialia. *Zoological Society of London Transactions* **9**, 417–446.

Owen, C.B. (1875). VIII- On the fossil mammals of Australia- Part X. Family Macropodidae: mandibular dentition and parts of the skeleton of *Palorchestes* ; Additional Evidences of *Macropus titan, Sthenurus* and *Procoptodon* .

Parsons, F.G. (1896). On the anatomy of *Petrogale xanthopus*, compared with that of other kangaroos. *Proceedings of the Zoological Society* **XLVI**, 682–714

Poole, W.E., Carpenter, S.M.m and Wood, J.T. (1984). Growth of grey kangaroos and the reliability of age determination from body measurements iii. interspecific comparisons between eastern and western grey kangaroos, *Macropous giganteus* and *M. fuliginosus. Australian Wildlife Research* **11**, 11–19.

Raven,H., and Gregory,W. (1946). Adaptive branching of the kangaroo family in relation to habitat. *American Museum Novitates* **1309**, 1–33.

Robert Close, J. (1956). Some applications of the functional anatomy of the ankle joint. *The Journal of Bone and Joint Surgery* **38**, 761–781.

Sarrafian, S.K. (1993). Biomechanics of the subtalar joint complex. *Clinical Orthopaedics and Related Research* **290**, 17–26.

Sneath, P.H.A., and Sokal, R.R. (1973). 'Numerical taxonomy'. (W.H. Freeman and Company, San Francisco).

SPSS (1989). SPSS release 6.1 for Macintosh. Novis SPSS incorporated.

Stirton, R.A. (1963). A review of the genus *Protemnodon* . *University of California Publications in Geological Sciences* **44**, 97–162.

Tedford, R.H. (1966). A review of the macropodid genus *Sthenurus* . *University of California Publications in Geological Sciences* **57**, 1–72.

Tedford, R.H. (1967). The fossil Macropodidae from Lake Menindee, New South Wales. *University of California Publications in Geological Sciences* **64**, 1–156.

Wells, R.T., and Tedford, R.H. (1995). Sthenurus (Macropodidae: MARSUPIALIA) from the Pleistocene of Lake Callabonna, South Australia. *Bulletin of the American Museum of Natural History* **225**.

Windle, B.C.A., and Parsons, F.G. (1897). On the anatomy of *Macropus rufus*. *Journal of Anatomy and Physiology* **32**, 119–134.

Windsor, D.E., and Dagg, A.I. (1971). The gaits of the Macropodinae (Marsupialia). *Journal of Zoology, London* **163**, 165–175.

# The Late Quaternary Sediments and Fossil Vertebrate Fauna from Cathedral Cave, Wellington Caves, New South Wales

LYNDALL DAWSON AND M.L. AUGEE

Biological Science, University of New South Wales, Sydney, NSW 2052

Dawson, L., and Augee, M. L. (1997). The Late Quaternary sediments and fossil vertebrate fauna from Cathedral Cave, Wellington Caves, New South Wales. *Proceedings of the Linnean Society of New South Wales* **117**: 51-78

Excavation of the floor of Cathedral Cave, Wellington Caves, was undertaken between 1982 and 1986. Three major phases of deposition are recognised, representing the end of the last interglacial (Phase 1), the last glacial maximum (Phase 2) and a Holocene phase (Phase 3). Radiocarbon dating of small amounts of charcoal in Phase 1 gave dates ranging from 33,800 BP to 21,000 BP, while dates of 2,590 BP and 2,950 BP were obtained from Phase 3 sediments.

Within these Phases stratigraphic, sedimentological and taphonomic changes are apparent. Phase 1 has the characteristics of an attritional entrance facies deposit. Large taxa (>1.5 kg body weight) are represented by juveniles only, except for scavengers and carnivores, suggesting a pitfall trap. The abundance of small mammals is consistent with their accumulation due to owls and the Ghost Bat, which is present in the bottom 1.25 m of the deposit. In Phase 2 a high degree of disturbance is suggested by the inclusion of large limestone boulders and rocks and the highly fragmented nature of the bone. Two distinct heavily indurated 'floors' dip toward the south-east and suggest entry of the sediments from a point in the roof of the cave co-incident with the apex of the present 'altar' formation. The sediments of Phase 3 are not indurated and contain no large boulders or bone fragments, larger species being represented by isolated teeth only. The entrance source of Phase 3 sediments is unknown.

At least 38 marsupial taxa have been identified of which 10 are extinct. Of the remaining 28 extant marsupial taxa only 9 may still occur west of the Great Dividing Range today. Of the non-marsupial taxa rodents are most abundant. Microchiropteran bats are represented in several strata, as are reptiles and small birds. Pleistocene 'megafauna' taxa are represented in Phase 1 and Phase 2. 'Megafaunal' species include *Macropus (Osphranter) altus, M. (M.) titan, M. (M.) ferragus, M. (Notamacropus)* n. sp., *Protemnodon* sp., *Simosthenurus oreas*, and *Thylacoleo carnifex*.

The fauna of medium and smaller sized mammals exhibits disharmonious assemblages typical of other late Pleistocene/Holocene faunas of eastern and south-eastern Australia. The presence of the Ghost Bat, *Macroderma gigas*, in Phase 1 suggests a suitable configuration of the cave and cave entrance at that time, and a warmer, wetter climate than Phase 2. Fauna of Phase 3 lacks extinct species and is representative of conditions which existed at the time of first European settlement of the Wellington region.

Manuscript received 18 June 1996, accepted for publication 23 October 1996.

KEYWORDS: Marsupial, Megafauna, Quaternary, Wellington.

## INTRODUCTION

The Wellington Caves, located 6 km south of Wellington on the western slopes of the Great Dividing Range in New South Wales, have been renown, since their first discovery in 1830, as a rich source of fossil bones, including many taxa of extinct marsupials. The history of their exploration and excavation has been reviewed most recently by Dawson (1985) and Osborne (1991). Descriptions of the caves complex, the associated sediments and stratigraphy have been published by Frank (1971), Francis (1973) and Osborne (1983).

The complex consists of several natural chambers and man-made tunnels which have been excavated from the sediments which fill much of the cave system. Over a period of more than 150 years, fossil bones have been collected from Mitchell Cave,

Figure 1. Map of the floor of Cathedral Cave, Wellington Caves, indicating the position of the University of New South Wales' excavation (1982–1986).

Cathedral Cave, Big Sink, Bone Cave and the Phosphate Mines. It had previously been assumed that all the sediments in the caves were of Pleistocene age because of the predominance in museum collections of the bones of extinct marsupial megafaunal taxa. However, the stratigraphic studies of Frank (1971) and Osborne (1983) suggested that the sediments may possibly range in age from Miocene to late Pleistocene.

To test this hypothesis, a team from the School of Zoology, University of New South Wales, commenced stratigraphically controlled collection of bones from several of the caves. Between 1982 and 1986 bones were collected from Big Sink, the Phosphate Mines, Bone Cave and Cathedral Cave. The first results of this study have indicated an early to mid-Pliocene age for the deposits in the Big Sink, hypothesised by Osborne (1983) to be the oldest stratigraphic units in the complex (Hand et al. 1988). The present paper continues this study and reports on the sediments and fauna from the floor of the Cathedral Cave.

## DESCRIPTION OF CATHEDRAL CAVE

The Cathedral Cave is the largest of the natural caves in the Wellington Caves complex. The cave (Fig. 1) consists of a steeply sloping entrance passage which extends for about 40 metres before expanding into a huge main chamber with dimensions of 45 m long, 20–25 m wide with a domed roof approximately 14 m maximum height. This chamber now has a nearly level compact earth floor, which is approximately 20 m below the ground surface. At the northern-most end of the chamber a huge 'stalagmite' reaches from floor to ceiling. The cave derives its name from the resemblance of this flowstone covered pillar to a cathedral altar.

The chamber has been formed by nothephreatic solution in massive limestone of the Devonian Garra Formation (Osborne 1983). The walls and roof of the chamber are largely devoid of speleothems. The chamber has been formed along a fault between thinly bedded limestone which forms much of the roof and eastern walls, and unbedded massive limestone forming the western roof and walls. The 'altar' occurs on this fault line. Immediately north of the 'altar' there is a vertical drop of approximately 3.5 m to the floor of a second narrower chamber. This floor extends horizontally for approximately 30 m to another vertical drop of 6–7 m terminating in a pond of water. The level of water in this pond varies with rainfall and the flow in the nearby Bell River. During a flood in 1956 the water rose to a level 1 m deep throughout the second chamber (i.e. only about 2.5 m below the floor of the main chamber).

The Cathedral Cave (then known as "the Great Cave") was described and illustrated by Sir Thomas Mitchell, who first entered this cave and surveyed it in 1830 (Mitchell 1838). Mitchell discovered some fossil bones in Cathedral Cave in 1830, but these were considered insignificant in comparison to his discoveries in the nearby "Breccia Cave". Prior to 1881 extensive bone collections of great significance were made from the "Breccia Cave" (now known as Mitchell's Cave) (Dawson 1985). However, there is no record of any collection from Cathedral Cave during that period.

In 1881 at least two shafts were dug in the earthen floor of the main chamber of Cathedral Cave during an exploratory expedition undertaken by the Australian Museum under the direction of the Curator, E. P. Ramsay. The location and depth of these shafts is indicated by Ramsay (1882), the most productive excavation being Shaft No 2, which was sunk near the 'altar' and described as follows:

'At No 2 shaft, which we sunk to the depth of 25 feet, many important bones have been found, and the different floors we went through show that these bones have been washed in at different periods. In the last layer, the red mud-like breccia which characterised this shaft (at present) has become more sandy, the bones being more perfect here and less worn' (Ramsay 1882, p.34).

This tantalising description provided much of the incentive needed to sustain the most recent excavation of the Cathedral Cave floor, the results of which are described in this paper.

## MATERIALS AND METHODS

### The excavation

The position of the UNSW pit, between the "altar" and the south wall of the main chamber is indicated in Fig. 1. A site close to the location of Ramsay's "No. 2 shaft" was preferred because of its promised depth and productivity. Care was taken to avoid the exact location of the previous shaft. The fact that the cave was continuously in use by large groups of tourists further limited the choice of sites for the excavation.

Surface dimensions of the pit were 2.0 m x 1.0 m, with the long axis extending away from the "altar" in a SSE direction. The northernmost edge of the pit was approximately 1 m from the outer rim of the base of the "altar", which is delineated by concentric ridges of flowstone. Surveyed co-ordinates of the pit are Easting 294 294.7 Northing 1 289 237.1 Height 322.6 (Integrated Survey Grid [ISG] of NSW).

Sediments were excavated by hand in 'spits', which were of variable depth, ranging from 10 to 20 cm, depending on the nature of the sediment encountered. Each spit was further divided into 8 horizontal grid segments, labelled A-H. The final depth of the excavation was approximately 7.25 m from the cave floor surface. All material was bagged and labelled before being stored in the cave, or removed from the cave for further treatment, either locally or at the University of New South Wales.

Treatment of the sediments consisted of first drying them, then screen washing (flyscreen) with water. Residual lumps of sediment which were insoluble in water were treated further with dilute acetic acid. However, there was generally poor breakdown of the clay-rich breccia in acid. As far as possible all bone was retrieved and stored for further analysis. Other inclusions such as charcoal, gravels, and limestone pieces were also retained for future examination.

During the excavation samples were collected for detailed sedimentary analysis. Unfortunately most of these samples were inadvertently destroyed.

### Analysis of bone

After screen washing and treatment of the sediments, all bone was collected and labelled according to the spit and grid sector of origin. Only teeth and jaws have been used to identify the taxa present in the deposit. The absolute number of individuals per stratigraphic unit could not be used for comparison between units because each unit represents an unknown (different) volume of sediment. In order to compare the relative abundance of various mammalian taxa, the minimum number of individuals (MNI) and the percentage abundance of each taxon was calculated for each stratigraphic unit. The estimate of minimum number of individuals was based on a count of identifiable right and left dentaries and maxillae. The most numerous element was taken as the MNI. Where a taxon was represented by a few isolated teeth only, it was scored as MNI = 1, except in the case of the peramelids (bandicoots),which were frequently represented by isolated molar teeth. These teeth were identified by position in the tooth row (e.g. $LM^4$, $RM_2$) and the most numerous element was taken as the MNI. The percent abundance of a taxon in each unit was calculated by the formula MNI /Total MNI per unit X 100. Non-mammalian taxa were not included in this analysis.

Dental nomenclature follows Luckett (1993). All specimens are registered in the collections of the Australian Museum, Sydney.

Abbreviations: AM = Australian Museum, QM = Queensland Museum, L = length, AW = anterior width, PW = posterior width, mm = millimetres.

## RESULTS

### Stratigraphy

The present floor of Cathedral Cave is nearly horizontal and has been beaten to a smooth hard surface by tourists over many years. At the site of the excavation the floor was somewhat irregular and sloped slightly away from the altar. The top metre of soil showed evidence of extensive disturbance. Fragments of bottle glass, sawn timber, metal, and even a piece of gramophone record were encountered in Spits 1–3. There was no further evidence of disturbance of the sediments by man below Spit 4, approximately one metre below the present floor. That the sediments beneath Spit 4 were undisturbed was supported by the presence in Spit 5 of a thin discontinuous layer of flowstone, no more than 2 cm thick, below which an orange cemented sediment rich in small bone fragments was encountered.

Over a period of approximately four years the Cathedral Cave excavation was continued to a final depth of 7.25 m below the present floor of the cave. Throughout the pit the sedimentary matrix consisted predominantly of heavy red clay. Inclusions varied in size from large limestone boulders (up to 30 cm in diameter) to gravels, and included both jagged rock fragments and smooth river pebbles. After consideration of the nature of the stratigraphy of the deposit, it became apparent that analysis of 10 cm spits was unwarranted, so samples were pooled for 50 cm intervals for the purpose of faunal analysis.

TABLE 1

Stratigraphic description of excavation in floor of Cathedral Cave, Wellington Caves.

| Depth (m) at base of unit | Spit groups (inclusive) | Description |
|---|---|---|
| Phase 3<br>−1.5 | 4–5 | Matrix of heavy red clay mottled with grey loamy textured silt, containing gravels and limestone nodules of varying size plus occasional small pieces of flowstone. Residue after washing comprised 30–40% original volume of insoluble material including bone and calcified clay aggregates.<br>Bone: low concentration of small fragments of bone, max. fragment length approx 2cm. |
| Phase 3<br>−2.0 | 6–10 | Matrix and inclusions as above. Lens of charcoal in spits 6 and 7 gave $C^{14}$ date of 2,950 ± 80 BP.<br>Bone: as above, larger taxa represented by isolated teeth only. |
| Phase 3<br>−2.5 | 11–15 | Matrix and inclusions as above. Large boulder approx. 20 cm diameter in spits 11–12. At spits 13–14 there was a hardened 'floor' 10 cm thick composed of indurated clay and flowstone, dipping south at approxmiately 20°. A small circular area rich in charcoal occurred immediately below this 'floor' and gave a $C^{14}$ date of 2540±80 BP.<br>Bone: As above, max. fragment length approx. 3 cm. |
| Phase 3<br>−3.0 | 16–19 | Matrix of heavy red clay, less insoluable residue than overlying strata including gravels and limestone fragments.<br>Bone: As above, max. fragment length approx. 4 cm. |
| Phase 2<br>−3.5 | 20–23 | Zone comprises a hard 'floor' approximately 20 cm thick extending the entire length of the pit, dipping south at approximately $20^{0}$ . This consists of heavily cemented clay with inclusions of limestone boulders and fragments, flowstone and bone breccia<br>Bone: Relatively high proportion of bone representing both large and small taxa. Large bone variably preserved, some weathered prior to deposition, fragmented. Max. fragment length approx 23 cm. Largest taxa represented by juvenile individuals. |
| Phase 2<br>−4.0 | 24–28 | Matrix of zone immediately below the 'floor' comprised unconsolidated red clay with few large inclusions. At north-west corner of spits 26 A–27A encountered a limestone boulder >30 cm in diameter with crushed and broken bone cemented to it. Another very large boulder in 28C. Spit 26 represents top of a layer of 'rubble' approx 30 cm deep dipping to the south as above, but less heavily indurated than 'floor' described above.<br>Bone: low concentration of small and larger bone fragments which are thinly encrusted with calcite. Largest taxa represented by juvenile individuals. Max. bone length = 14cm. |
| Phase 2<br>−4.5 | 29–33 | Matrix of heavy red clay, residue after washing comprised from 90% (at top of zone) to 30% (toward base of the zone) of original volume as insoluble calcite nodules and limestone pieces.<br>Bone: Relatively low bone content, small jaws and fragments only, thinly encrusted with calcite. Max. bone length = 5 cm. |

| | | |
|---|---|---|
| Phase 2<br>−5.0 | 34–38 | Matrix of heavy red clay, residue after washing comprised 30–50% original volume of small calcite nodules and flakes. Spit 36 A (nth end) contained thin indurated layer including much small gravel overlying a thin layer of blackened small bone. Spit 36B encountered top of a limestone boulder approx. 30 cm diameter.<br>Bone: Relatively high concentration of large and small bone with largest pieces approx. 12 cm long; partial macropodid cranium 8 x 11 cm. Bone encrusted with red calcite. |
| Phase 1 −5.5<br>−5.5 | 39–42 | Matrix of sandy red clay, gravels and occasional large pieces of limestone, residue after washing containing calcite nodules and flakes. Pooled sample of charcoal from spit 40 gave a $C^{14}$ date of 21,400±700 BP<br>Bone: Very rich in bone, many larger bones (including robust femur 24 cm long) , also rich in bones of small taxa. Bone reddish cream in colour, thinly encrusted in calcite, not abraded or chewed. |
| Phase 1<br>−6.0 | 43–45 | Thin calcite layer on top of spit 43 at north end of pit, petering out towards south. Matrix of sandy reddish clay with higher gravel and bone content. Residue after washing contains many flat grey ?calcite flakes.<br>Bone: Relatively high content of bones of small and larger taxa. Bone well preserved, cream-brown in colour, no calcite encrustation. Largest bone fragment 16 cm long. Associated skeletal elements present. Some bone appears gnawed. |
| Phase 1<br>−6.5 | 46–50 | Matrix of reddish clay with high proportion of sand and gravels. No evidence of dipping strata. Pooled samples of charcoal from Spit 46 gave $C^{14}$ date of 21,350 ±1,700 BP. Pooled samples of charcoal from Spit 50 gave $C^{14}$ date of 26,800±2000 BP.<br>Bone: Relatively low bone content, washed clean with water, lacking calcite encrustation. Bones represent mostly small taxa with larger taxa represented by isolated teeth only. Largest bone fragment 7 cm long. Some bone slightly gnawed. |
| Phase 1<br>−7.0 | 51–54 | Spit 51 as above. Spits 52 and 53 comprised of grey friable matrix. Thin hard calcite layer in spit 54, red matrix below this. Charcoal from Spits 51 and 52 gave $C^{14}$ dates of 33,800±2000 BP and 32,500±2100 BP, respectively.<br>Bone: Extremely rich in large and small bone fragments, longest approx. 17 cm; associated elements present; rich in bones of small taxa. Bone washed clean in water; colour mottled grey, no calcite encrustation, larger bone not gnawed or abraded. |
| Phase 1<br>−7.5 | 55–57 | Matrix red sandy clay, inclusions wash clean in water, not indurated, but contained many flat grey 'flakes' of rock (?calcite ). Many large limestone boulders encountered below spit 55.<br>Bone: Relatively high content of creamy coloured bone, washed clean in water, lacking calcite encrustation; large species represented by isolated teeth and fragmented bone with highly abraded (? gnawed) ends; largest fragment approx 9 cm long. No associated elements. |

Detailed description of the sediments is provided in Table 1. Stratification within the sediments was indicated by variations in degree of induration and cementing of layers to form successive "floors" throughout the deposit. As the excavation proceeded several hardened "floors" of varying thickness were encountered as described in Table 1. Above Spits 30–33 ( -4.25 to -4.5 m) these "floors" dip at a consistent angle of approximately 20 degrees from the north edge of the pit towards the south, i.e. slope away from the base of the "altar", consistent with the hypothesis that they form an extension of the base of a cone of sediment with its apex under the existing stalagmite called the "altar". Below 4.5 m the stratification is nearly horizontal.

The following factors have been considered in formulating a hypothetical interpretation of the history of this deposit:

- the sequence and direction of slope of hardened 'floors' and flowstone layers
- degree of induration of the sediments
- the preservation of bone, including size, colour, fragmentation, association of elements, presence of juveniles etc.
- the nature of inclusions (other than bone) in the sediments
- the information from $C^{14}$ dating of charcoal

Examination of the data presented in Table 1 has indicated three main phases in the deposit. These are described and justified below.

Phase 1

This is the oldest phase of deposition, and extends from the base of the pit (7.5 m) to approximately 5.0 m below the surface (Units 55–57 to Unit 39–42, inclusive). The upper boundary is not delimited by any definite demarcation line; in fact Spit 38 and Unit 39–42 represents a transition zone. However, Phase 1 has several characteristics which define it:

- sediments are approximately horizontal
- predominantly more sandy/gravelly sediments
- much less calcification / induration of sediments than higher levels — almost completely soluble in water
- bone well preserved, less fragmented, including some associated elements and intact skeletal elements of larger taxa
- large taxa represented mainly by juveniles
- fauna contains extinct taxa and "megafauna"

Phase 2

The middle phase of deposition extends from approximately 5.0 m to approximately 3.0 m below the surface (Units 34–38 to 20–23 inclusive). The upper boundary of this phase is demarcated by heavily indurated rubble 'floor' approximately 20 cm thick. Characteristics defining Phase 2 are:

- red clay, generally heavily indurated, does not break down readily in water
- large number of boulder-sized inclusions and many smaller rock
- strata dip at approximately 20° from north to south
- large bones highly fragmented, some weathered prior to deposition
- large taxa represented by small jaw fragments or isolated teeth only
- large taxa mainly represented by juveniles.
- fauna contains extinct taxa and "megafauna"

Phase 3

The most recent phase of deposition is represented from -3.0 m to the surface (the top one metre being disturbed since European settlement). Characteristics of Phase 3 are:

- red clay, variably indurated, mostly breaks down in water
- inclusions consist mainly of gravels, small limestone nodules and small pieces

of flowstone.

- low bone concentration.
- bone fragments small, large taxa represented by isolated teeth only
- little evidence of stratification — some thin flowstone sheets
- no extinct species represented

TABLE 2

Radiocarbon dates obtained from charcoal excavated from the floor of Cathedral Cave, Wellington Caves. Asterisk indicates pooled samples. Depths represent depth below present cave floor.

| Sample no. | Spit | Depth | Age (yrs BP) |
|---|---|---|---|
| SUA 2097 | Spit 6 | 1.6 m | 2950 ± 80 |
| SUA 2098 | Spit 14 | 2.7 m | 2590 ± 80 |
| ANU 4480 | Spit 39 * | 5.1 m | 14,300 ± 730 |
| ANU 4479 | Spit 40 * | 5.2 m | 21,400 ± 700 |
| ANU 4478 | Spit 44 * | 5.8 m | 11,900 ± 790 |
| ANU 5323 | Spit 46 | 6.1 m | 21,350 ± 1700 |
| ANU 5324 | Spit 47 * | 6.2 m | 28,000 ± 1100 |
| ANU 5325 | Spit 49 | 6.4 m | 23,700 ± 1400 |
| ANU 5326 | Spit 50 * | 6.5 m | 26,800 ± 1100 |
| ANU 5327 | Spit 51 | 6.6 m | 33,800 ± 2000 |
| ANU 5328 | Spit 52 | 6.7 m | 32,500 ± 2100 |

## Radiocarbon dating

Charcoal was rare in the Cathedral Cave deposits, but small samples of charcoal were recovered during the excavation and while screen washing. These were collected in sealed plastic bags and submitted for radiocarbon dating. The results are presented in Table 2. The first two samples (Spits 6 and 14) were submitted to the Radiocarbon Laboratory at the University of Sydney (SUA) in 1984. A further 9 samples (from Spits 39 to 52) were submitted to the Radiocarbon Dating laboratory, Research School of Pacific Studies, Australian National University (ANU), in 1985 and 1986. In several of the spits it was necessary to pool small samples of charcoal to obtain a quantity large enough for dating. Dates derived from pooled samples are indicated with an asterisk in Table 2.

The irregularities apparent in the sequence of the dates (Table 2) may be due to a variety of factors, including contamination during handling and pretreatment of small pooled samples of charcoal, lateral facies changes and variable transportation of different elements (Archer 1974, Osborne 1984). The date for Spit 44 (ANU 4478) is most likely to be anomalous and due to younger organic contamination during pretreatment (J. Head, ANU Radiocarbon Dating Laboratory, pers. comm. 1985).

The $C^{14}$ dates presented in Table 2 provide an indication of the probable time span involved in this deposit, from approximately 34,000 BP (the minimum age of the lowest sediments) to approximately 2,500 BP for the undisturbed sediments at the top of the deposit. While there are several inconsistencies in the sequence of the dates throughout the column, the general trend of the dates indicates that the lower levels of the deposit are older than the higher levels, i.e. that there is no major stratigraphic reversal present.

## The fauna

Bone fragments were present throughout the deposit (Table 1). The preservation of the bone varied enormously, ranging from very weathered bone, some crushed bone, some heavily mineralised well preserved elements and some clean, lightly mineralised bone. Generally the larger bones were very fragmented and, with few exceptions, large taxa were represented by small jaw fragments only. No intact jaws or associated skeletal elements were encountered until more than 5 m below the surface, after which depth the bone was generally better preserved.

Teeth and jaws referable to marsupial taxa have been identified to species level where possible. Specific identification of most other non-marsupial remains has not been attempted, with the exception of some of the rodents, the Ghost Bat, *Macroderma gigas*, and the identification of snail shells (Mollusca).

The fauna of the Cathedral Cave deposit is summarised in Table 3, which indicates the presence/absence data for taxa at each stratigraphic level. At least 38 marsupial taxa have been identified in the deposit, of which 10 are extinct, and one, *Sarcophilus harrisii*, is now confined to Tasmania. Of the remaining 27 extant marsupial taxa only 9 may still occur west of the Great Dividing Range today (Dickman 1994). Of the non-marsupial taxa, most are rodents, which are abundant in most strata. Microchiropteran bats are represented in several strata, as are reptiles and small birds.

Table 4 presents the MNI present and % abundance per stratigraphic unit and the total taxa present. The relative abundance of selected taxa has been graphically depicted in Fig. 2. The results must be considered in light of the fact that there was considerable difference between stratigraphic units in the total number of taxa present, thus affecting comparison of percent abundance values throughout the deposit.

## Taphonomy

Preservation of the bone and the observed stratigraphic variations suggest that the fauna present in the Cathedral Cave floor deposit has complex sources, and it is likely that several different agents were responsible for the accumulation of bones. In each stratigraphic unit of this deposit at least 85% of the animals present represent taxa with average body weights of less than 1.5 kg. Bones of small animals (less than 1.5 kg in body weight) are most likely to be derived from owl pellet deposits or the prey of Ghost Bats (Baird 1991), while the remains of larger animals may be accumulated by carnivores or scavengers or accumulate because the cave acts as a natural pit-trap. Analysis of the relatively intact jaw fragments of larger animals in the deposit has revealed that 88% of the macropodines present are juveniles, only three specimens representing adult individuals. Carnivores and scavengers are extremely rare in the deposit (4 jaws only), but in each case these are from adult individuals. These data indicate that large animals mainly entered the cave by falling in, their remains attracting scavengers, some of which also succumbed.

It is considered that the three phases recognised in this study represent periods in which there were different agents of accumulation or sources of the bone.

Phase 1 has the characteristics of an attritional entrance facies deposit (Baird 1991). This profile is characteristic of the distal elements of a talus cone, not markedly reworked since deposition (associated skeletal elements). Large taxa are represented by juveniles only, except for scavengers and carnivores. This is characteristic of a pitfall trap. The abundance of small mammals is consistent with accumulation due to owls and ghost bats. Within Phase 1 stratigraphic horizons are indistinct, with the exception of the unit represented by Spits 51–54 which was grey in colour, rather than the otherwise predominantly red sediments. However, the composition of the fauna varied considerably from spit to spit. For example, Spits 51–54 contained the greatest number of taxa, but fewer individuals than units above and below it (Table 4). Spits 51–54 also contained the highest fraction of bone representing large species (Fig. 3), despite the fact that it also contained the largest number of Ghost Bats.

TABLE 3

Faunal list from the floor of the Cathedral Cave, Wellington Caves, indicating presence/absence of each taxon per strtigraphic unit of the excavation

| | Spits 4–5 | Spits 6–10 | Spits 11–15 | Spits 16–19 | Spits 20–23 | Spits 24–28 | Spits 29–33 | Spits 34–38 | Spits 39–42 | Spits 43–48 | Spits46–50 | Spits 51–54 | Spits 55–57 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sminthopsis crassicaudata* | | — | | | | | | | | | | — | |
| *Sminthopsis murina* | | — | — | — | — | — | — | — | — | — | — | — | — |
| *Sminthopsis* sp indet | | | | | | | | | | | | — | |
| *Antechinus* sp cf *A. flavipes* | | | | | — | — | | — | — | — | — | — | — |
| *Phascogale tapoatafa* | | | | | — | | — | — | — | — | | — | — |
| *Phascogale calura* | | | | | | | | | | | | — | — |
| *Dasyurus viverrinus* | — | | | | | | | | | | | — | |
| *Dasyurus geoffroii* | | | — | | — | — | | — | — | — | — | — | |
| *Dasyurus hallucatus* | | | | | | | — | — | | | | | |
| *Sarcophilus harrisii* | | | | | | | | | | | | — | |
| ?*Dasyuroides* sp. | | | — | | | | | | | | | | — |
| *Perameles gunnii* | — | — | — | — | — | — | — | — | — | — | | — | — |
| *Perameles nasuta* | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Isoodon obesulus* | — | — | | | — | — | — | — | — | — | — | — | — |
| ***Thylacinus cynocephalus*** | | | | | | | | — | | | | a— | |
| *Trichosurus* sp. | — | — | | | | | | | | | — | — | — |
| *Petaurus* sp. cf *P. breviceps* | | | | — | — | | | — | — | — | — | | |
| *Pseudocheirus* sp. | | | | | | | | — | | | | | |
| *Acrobates pygmaeus* | | | | | | | | | | | — | — | |
| *Aepyprymnus rufescens* | — | | | — | — | — | | | | | — | — | — |
| *Bettongia* sp | | | | | | | | | | — | | | |
| *Potorous tridactylus* | | | | | | | | — | — | | | — | |
| *Macropus giganteus* | — | | — | | | | | | | | | | |
| *M. (Osphranter)* sp. | | | | | | | | | | | | | — |
| ***M. (O) altus*** | | | | | | # | | | | | a | | |
| *M.* sp.cf. *M. (N.) agilis* | | | | | | # | | | | | | # | |
| *M.* sp. cf *M. (N.) dorsalis* | | | | | — | | | | | — | | | |
| ***M.* sp. cf. *M. (N.) rankeni*** | | | | | | | | | | #a | # | | |
| ***M. (M.) titan*** | | | | | # | # | | # | | # | | | |
| ***M. (M.) ferragus*** | | | | | | # | | | | | | | |
| ***Protemnodon* sp.** | | | | | | | — | | | | | | — |
| *Petrogale* sp. | | | | | # | # | | | | — | | # | # |
| *Thylogale* sp. | — | | | | | | # | | | | | — | — |
| *Onychogale* sp. | | | | | | | | | | | | — | — |
| *Simosthenurus oreas* | | | | | | | | — | | # | #a | # | |
| ***Diprotodon* sp.** | | | | | x | | | | | | | | x |

| | Spits 4–5 | Spits 6–10 | Spits 11–15 | Spits 16–19 | Spits 20–23 | Spits 24–28 | Spits 29–33 | Spits 34–38 | Spits 39–42 | Spits 43–48 | Spits46–50 | Spits 51–54 | Spits 55–57 |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Thylacoleo carnifex*** | | | | | | — | — | — | | — | | | |
| *Vombatus* sp. | | x | x | | x | | | | | | | x | x |
| *Phascolarctos* sp | | | | | | | | | | | — | — | |
| Rodent indet (med) | — | — | — | — | — | — | — | — | — | — | — | — | — |
| Rodent indet (sm) | — | — | | — | — | — | | — | — | — | — | — | — |
| *Mastacomys fuscus* | — | — | — | | | — | — | | | | | | — |
| ***Conilurus albipes*** | — | — | — | — | — | — | — | — | — | — | — | — | — |
| *Hydromys* sp. | | | | | | | | | | — | | | |
| Small bats indet | | — | — | | — | | | | | | | — | — |
| ***Macroderma gigas*** | | | | | | | | | | | — | — | — |
| *Varanus* sp. | | | | | — | | | | | | | — | |
| *Teliqua* sp. | | | | | — | — | | | | | | | — |
| Small reptiles | | — | | — | | — | | | — | — | | — | |
| Small birds indet | | | | | | — | | — | — | | | — | — |
| Mollusca (snails) | | | — | | | | — | — | — | — | | — | |

Legend: a = associated elements; # = juvenile; x = enamel fragment only; bold italics = extinct.

In Phase 2 a high degree of disturbance is suggested. The large number of limestone boulders and rocks, the highly fragmented nature of bone, and the complete absence of any associated skeletal elements, supports an hypothesis that the bones and sediments have been redeposited here. The sediments of this phase vary in the degree of cementation and include two distinct hardened "floors", each approximately 20 cm deep. The consistent dip of the strata toward the south away from the present 'altar' suggests that the source of the sediments is likely to be from a point above the 'altar'. The total number of taxa and the number of individuals represented is much lower than in Phase 1 (Table 4). The proportion of larger species is also higher than in Phase 1 (Fig. 3). The predominant presence of juveniles among the large fauna indicates that the original deposit acted as a pitfall trap for large animals. Ghost Bats are absent from the fauna of this Phase and it is likely that small mammal remains are derived from owl pellets.

There is little evidence in the upper phase (Phase 3) to suggest the probable source of inclusions. There are no large bone fragments present, and large species are represented by isolated teeth only. This differs markedly from the earlier phases and indicates that the entrance to the cave was restricted. The entrance site above the 'altar', suggested to have been present during Phase 2, had apparently closed by this time, as there is no evidence of large rubble or characteristics of pit-fall accumulation.

It is unlikely that this deposit was an active vadose environment at any time during the period of deposition (i.e. during the last 35,000 years), so water transport is not likely to be responsible for the accumulation of the bones. The highest terraces of the Bell River are considerably lower than the present cave entrance, and probably date from the Pliocene (Francis 1973) and the cave has never been a vadose cave, although the action of groundwater may have contributed to the secondary distribution of the elements in the deposit.

However, it is likely that level of groundwater has intermittently risen to at least the level of the present floor of Cathedral Cave over the period represented by the floor deposits (note 1954 flood level in lower chamber). This intermittent saturation and dry-

Table 4

Faunal list from Cathedral Cave, Wellington Caves, indicating the Minimum Number of Individuals (MNI) and percentage abundance of each taxon per stratographic unit

| | Spits 4–5 | % | Spits 6–10 | % | Spits 11–15 | % | Spits 16–19 | % | Spits 20–23 | % | Spits 24–28 |
|---|---|---|---|---|---|---|---|---|---|---|---|
| *Sminthopsis crassicaudata* | | | 1 | 1.9 | | | | | | | |
| *Sminthopsis murina* | | | 1 | 1.9 | 2 | 5.9 | 1 | 5 | 2 | 3 | 5 |
| *Sminthopsis* sp. indet 1 | | | | | | | | | | | |
| *Antechinus* sp. cf. *A. flavipes* | | | | | | | | | 1 | 1.5 | 2 |
| *Phascogale tapoatafa* | | | | | | | | | 1 | 1.5 | |
| *Phascogale calura* | | | | | | | | | | | |
| *Dasyurus viverrinus* | 1 | 3.7 | | | | | | | | | |
| *Dasyurus geoffroii* | | | | | 1 | 2.9 | | | 1 | 1.5 | 1 |
| *Dasyurus hallucatus* | | | | | | | | | | | |
| *Sarcophilus harrisii* | | | | | | | | | | | |
| ?*Dasyuroides* sp. | | | | | 1 | 2.9 | | | | | |
| *Perameles gunnii* | 1 | 3.7 | 2 | 3.7 | 1 | 2.9 | 1 | 5 | 1 | 1.5 | 2 |
| *Perameles nasuta* | 1 | 3.7 | 1 | 1.9 | 1 | 2.9 | 2 | 10 | 3 | 4.5 | 3 |
| *Isoodon obesulus* | 1 | 3.7 | 3 | 5.6 | | | | | 3 | 4.5 | 1 |
| *Thylacinus cynocephalus* | | | | | | | | | | | |
| *Trichosurus* sp. | 1 | 3.7 | 1 | 1.9 | | | | | | | |
| *Petaurus* sp. cf *P. breviceps* | | | | | | | 1 | 5 | 4 | 6 | |
| *Pseudocheirus* sp. | | | | | | | | | | | |
| *Acrobates pygmaeus* | | | | | | | | | | | |
| *Aepyprymnus rufescens* | 1 | 3.7 | | | | | 1 | 5 | 3 | 4.5 | 1 |
| *Bettongia* sp | | | | | | | | | | | |
| *Potorous tridactylus* | | | | | | | | | | | |
| *Macropus giganteus* | 1 | 3.7 | | | 1 | 2.9 | | | | | |
| *M. (Osphranter)* sp. | | | | | | | | | | | |
| *M.* sp. cf. *M. (O.) altus* | | | | | | | | | | | 1 |
| *M.* sp.cf. *M. (N.) agilis* | | | | | | | | | | | 1 |
| *M.* sp. cf. *M. (N.) dorsalis* | | | | | | | | | 2 | 3 | |
| *M.* sp. cf. *M. (N.) rankeni* | | | | | | | | | | | |
| *M. (M.) titan* | | | | | | | | | 3 | 4.5 | 1 |
| *M. (M.) ferragus* | | | | | | | | | | | 1 |
| *Protemnodon* sp. | | | | | | | | | | | |
| *Protemnodon brehus* | | | | | | | | | | | |
| *Petrogale* sp. | | | | | | | | | 2 | 3 | 1 |
| *Thylogale* sp. | 1 | 3.7 | | | | | | | | | |
| *Onychogale* sp. | | | | | | | | | | | |
| *Sthenurus* sp. cf. *S. oreas* | | | | | | | | | | | |
| *Diprotodon* sp. | | | | | | | | | | | |
| *Thylacoleo carnifex* | | | | | | | | | | | 1 |
| *Vombatus* sp. | | | 1 | 1.9 | 1 | 2.9 | | | 1 | 1.5 | |
| *Phascolarctos* sp. | | | | | | | | | | | |
| Rodent indet (med) | 15 | 55.6 | 38 | 70.4 | 23 | 67.6 | 12 | 60 | 27 | 40.3 | 35 |
| Rodent indet (sm) | 2 | 7.4 | 2 | 3.7 | | | 1 | 5 | 6 | 9 | 4 |
| *Mastacomys fuscus* | 1 | 3.7 | 1 | 1.9 | 1 | 2.9 | | | | | 1 |
| *Conilurus albipes* | 1 | 3.7 | 3 | 5.6 | 3 | 8.8 | 1 | 5 | 7 | 10.4 | 2 |
| *Hydromys* sp. | | | | | | | | | | | |
| Small bats indet | | | 1 | | 1 | | | | 1 | | |
| *Macroderma gigas* | | | | | | | | | | | |
| *Varanus* sp. | | | | | | | | | 1 | | |
| *Teliqua* sp. | | | | | | | | | 1 | | 1 |
| Small reptiles | | | 1 | | | | 1 | | | | 1 |
| Small birds indet | | | | | | | | | | | 1 |
| **Total MNI Non-volant mammals** | **27** | | **54** | | **34** | | **20** | | **67** | | **63** |
| **TOTAL TAXA INCLUDED** | **12** | | **11** | | **10** | | **8** | | **16** | | **17** |

| % | Spits 29–33 | % | Spits 34–38 | % | Spits 39–42 | % | Spits 43–45 | % | Spits 46–50 | % | Spits 51–54 | % | Spits 55–57 | % |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | | | | | | 8 | 4.1 | | |
| 7.9 | 1 | 1.7 | 4 | 1.6 | 9 | 2.3 | 15 | 5.3 | 10 | 13.3 | 28 | 14.4 | 4 | 1.1 |
| | | | | | | | | | | | 3 | 3.1 | | |
| 3.2 | | | 1 | 0.4 | 5 | 1.3 | 8 | 2.8 | 2 | 2.7 | 20 | 10.3 | 4 | 1.1 |
| | 1 | 1.7 | 1 | 0.4 | 2 | 0.5 | 1 | 0.4 | | | 2 | 1 | 1 | 0.3 |
| | | | | | | | | | | | 5 | 2.6 | 2 | 0.6 |
| | | | | | | | | | | | 1 | 0.5 | | |
| 1.6 | | | 3 | 1.2 | 3 | 0.8 | 2 | 0.7 | 1 | 1.3 | 3 | 1.5 | | |
| | 1 | 1.7 | 2 | 0.8 | | | | | | | | | | |
| | | | | | | | | | | | 1 | 0.5 | | |
| | | | | | | | | | | | | | 1 | 0.3 |
| 3.2 | 3 | 5.1 | 5 | 2 | 3 | 0.8 | 4 | 1.4 | | | 2 | 1 | 4 | 1.1 |
| 4.8 | 4 | 6.8 | 6 | 2.4 | 8 | 2 | 16 | 5.6 | 3 | 4 | 3 | 1.5 | 1 | 0.3 |
| 1.6 | 3 | 5.1 | 13 | 5.3 | 9 | 2.3 | 9 | 3.1 | 3 | 4 | 4 | 2.1 | 1 | 0.3 |
| | | | 1 | 0.4 | | | | | | | 2 | 1 | | |
| | | | | | | | | | 1 | 1.3 | 2 | 1 | 1 | 0.3 |
| | | | 1 | 0.4 | 1 | 0.3 | 1 | 0.4 | 1 | 1.3 | | | | |
| | | | 1 | 0.4 | | | | | | | | | | |
| | | | | | | | | | 2 | 2.7 | 14 | 7.2 | | |
| 1.6 | | | | | | | | | 1 | 1.3 | 1 | 0.5 | 2 | 0.6 |
| | | | | | | | 2 | 0.7 | | | | | | |
| | | | 1 | 0.4 | 1 | 0.3 | | | | | 1 | 0.5 | | |
| | | | | | | | | | | | | | | |
| | | | | | | | | | | | | | 1 | 0.3 |
| 1.6 | | | | | | | | | 1 | 1.3 | | | | |
| 1.6 | | | | | | | | | | | 1 | 0.5 | | |
| | | | | | | | 2 | 0.7 | | | | | | |
| | | | | | | | 1 | 0.4 | | | 1 | 0.5 | | |
| 1.6 | | | | | 1 | 0.3 | | | | | | | 1 | 0.3 |
| 1.6 | | | | | | | | | | | | | | |
| | 1 | 1.7 | | | | | | | | | | | | |
| | | | | | | | | | | | | | 1 | 0.3 |
| 1.6 | | | | | | | 1 | 0.4 | | | 1 | 0.5 | 1 | 0.3 |
| | 1 | 1.7 | | | | | | | | | 2 | 1 | 1 | 0.3 |
| | | | | | | | | | | | 1 | 0.5 | 1 | 0.3 |
| | | | 1 | 0.4 | | | 1 | 0.4 | | | 1 | 0.5 | 1 | 0.3 |
| | | | | | | | | | | | | | 1 | 0.3 |
| 1.6 | | | 1 | 0.4 | 1 | 0.3 | | | | | | | 1 | 0.3 |
| | | | | | | | | | | | 1 | 0.5 | 1 | 0.3 |
| | | | | | | | | | 1 | 1.3 | 1 | 0.5 | | |
| 55.6 | 37 | 62.7 | 190 | 77.2 | 308 | 77.4 | 183 | 63.5 | 6 | 8 | 21 | 10.8 | 314 | 85.3 |
| 6.3 | | | 5 | 2 | 19 | 4.8 | 22 | 7.8 | 42 | 56 | 57 | 29.2 | 4 | 1.1 |
| 1.6 | 5 | 8.5 | | | | | | | | | | | 12 | 3.3 |
| 3.2 | 2 | 3.4 | 10 | 4.1 | 28 | 7.1 | 20 | 6.9 | 1 | 1.3 | 5 | 2.6 | 6 | 1.6 |
| | | | | | | | 1 | 0.4 | | | | | | |
| | | | | | | | | | | | 1 | | 1 | |
| | | | | | | | | | | | 45 | | 2 | |
| | | | | | | | | | | | | | 1 | |
| | | | | | 1 | | 1 | | | | 1 | | | |
| | | | 1 | | 1 | | | | | | 1 | | 1 | |
| . | **59** | | **246** | | **398** | | **288** | | **75** | | **195** | | **368** | |
| | **11** | | **17** | | **14** | | **16** | | **13** | | **28** | | **25** | |

ing of the sediments would account for the succession of calcified ‘floors’ and flowstone layers encountered in the deposit. If the water level were to rise above the level of the sediments (as is likely) this would account for the levelling of the cave floor.

A high level of induration and calcification, as is observed in Phase 2 sediments, could result from a long period of stagnation of calcite-rich water — or a prolonged dry period following after a period of saturation.

## SYSTEMATIC ANALYSIS

### Mammalia
### Marsupialia

### Dasyuridae

Larger dasyurids (body weight greater than approximately 1–1.5 kg) are represented by three species of *Dasyurus* and the devil, *Sarcophilus harrisii*, all of which are scavenger / carnivores.

Species of *Dasyurus* have been identified from jaw fragments by comparison with specimens from the modern fauna in the Australian Museum. In the case of maxillary fragments, identification was assisted by the comparison of dental measurements. The ratio of protocone-parastyle length / protocone-metastyle length of $M^4$ distinguishes between *D. geoffroii* and *D. hallucatus. D. viverrinus* is distinguished by being larger than the other two species.

In Phase 1 the Western Quoll, *D. geoffroii* is represented in all units by well preserved jaws. The Eastern Quoll, *D. viverrinus*, is also represented in units 51–54 by well preserved jaws. The Devil, *Sarcophilus harrisii* is represented by a single intact right mandibular ramus. Dental measurements of this specimen place it in the range of overlap in size between the largest individuals of the modern Tasmanian population and the smallest individuals attributed to the Pleistocene species, *S. laniarius* (Dawson 1982a). Given that this specimen comes from the oldest strata of the Cathedral Cave deposit, associated with $C^{14}$ dates of approximately 33,000 BP, it is possible that it represents the Pleistocene species, however, this diagnosis cannot be made without a larger sample.

In Phase 2 *Dasyurus geoffroii* is represented in all but one of the units in this phase. In Spits 34–38 both *D. geoffroii* and *D. hallucatus* (the Northern Quoll) are present, while a single maxillary fragment appears to represent *D. hallucatus* in Spits 29–33.

In Phase 3 large dasyurids are extremely rare, *Dasyurus viverrinus* and *D. geoffroii* being represented by a few isolated teeth only.

The most common species of Quoll represented in the Cathedral Cave deposit is *D. geoffroii*. This species was present in the western division of New South Wales at the time of European settlement, but has not been captured in New South Wales since 1857 (Dickman 1994). *D. viverrinus* has not been recorded in western New South Wales in historic times, being confined to coastal regions of south-eastern Australia and Tasmania (where it is still extant).

At least five species of dasyurid smaller than 1.5 kg body weight have been identified, all of which are extant in the modern fauna of eastern Australia. At least two species of *Sminthopsis* are represented, *S. murina* and *S. crassicaudata*, with the former being almost ubiquitous, while *S. crassicaudata* is rare, being present in two widely separated levels (Phase 1 and Phase 3) only. *Antechinus sp.* cf *A. flavipes* is present below Spit 20. *Phascogale tapoatafa* is present in Phase 1 and Phase 2, while *P. calura* is present in the lower spits of Phase 1 only.

The greater relative abundance of small dasyurids in Phase 1 compared with higher levels of the deposit is marked. Both *A. flavipes* and *S. murina* show dramatic peaks in

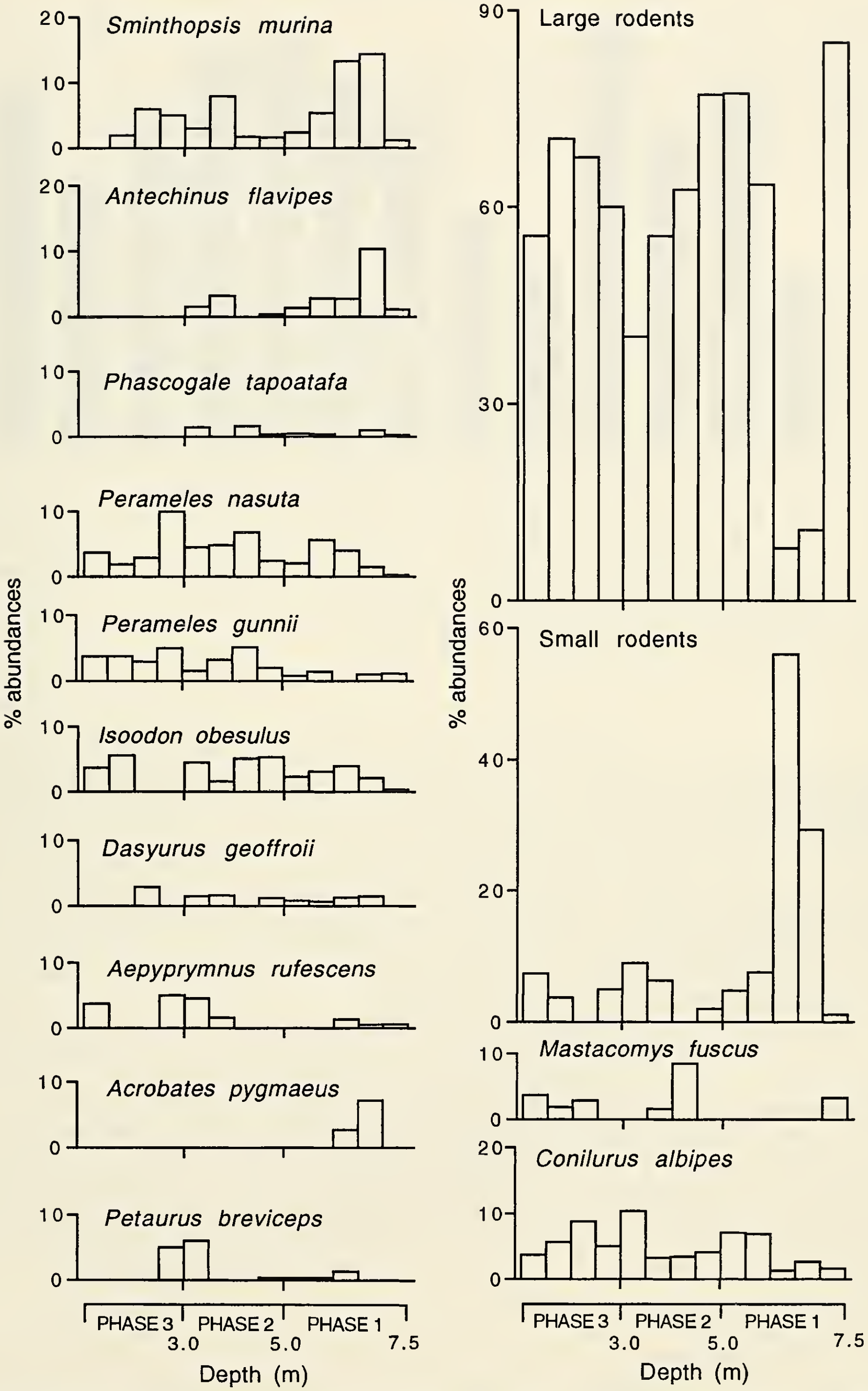


Figure 2. Relative abundance of selected mammal taxa represented in the sediments from the floor of Cathedral Cave, Wellington Caves. Data from Table 4.

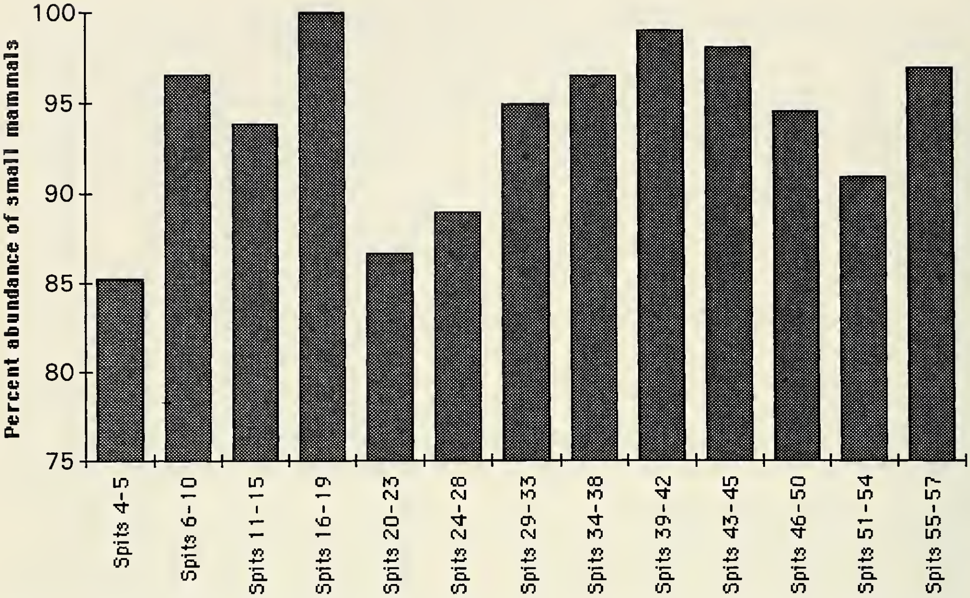


Figure 3. Relative abundance of small mammal taxa with body weight less than 1.5kg in the sediments from the floor of Cathedral Cave, Wellington Caves. Data from Table 4.

the lower units which contain the Ghost Bat, *Macroderma gigas*. These spits also contain the greatest diversity of dasyurid taxa in the deposit. In fact small dasyurids represent nearly 35% of the total number of individual animals recorded from Spits 51–54 (Table 4). While the foraging habits of the Ghost Bat most likely account for the abundance of individuals in that stratigraphic unit, other factors may account for the rich species diversity in the lower spits of Phase 1. The high diversity of small dasyurids in the 'Macroderma' spits of Phase 1 coincides with an increase in relative abundance of small rodents and a sudden sharp decrease in relative abundance of larger rodents (Table 4, Fig. 2). Detailed identification of the rodent taxa present must be undertaken before hypotheses to explain these observations can be developed.

All the species of small dasyurids identified in the Cathedral Cave deposit (with the possible exception of *Phascogale calura* and *?Dasyuroides sp.*) have ranges in the modern fauna which encompass the Wellington Valley, at least peripherally (Strahan 1983). Similarly, all species are common components of other late Pleistocene fossil faunas of eastern Australia (Lundelius 1983). With the exception of *Sminthopsis crassicaudata* and *Phascogale calura*, which have predominantly xeric habitat preferences, the species present are characteristic of woodland habitats, and none has particularly rigid vegetation or climatic limitations, although microhabitat preferences vary between species (Strahan 1983). Fox (1982) suggests, rather, that species separation is effected by body size and life strategies in small dasyurids, rather than climatic limitations.

## Thylacinidae

*Thylacinus cynocephalus* is represented in Phase 2, Spits 34–38, by an isolated upper molar only. The only other occurrence is the presence of two left mandibular rami (adult) referable to *T. cynocephalus* in Phase 1, Spits 51–54. The dental dimensions of these specimens fall in the upper size range of modern *T. cynocephalus* from Tasmania, and within the range of Pleistocene populations from Wellington Caves and Naracoorte Caves (Dawson 1982b).

## Peramelidae

Throughout the deposit peramelids are represented by jaw fragments which rarely retain the molar teeth, but isolated teeth are very common. Isolated teeth have been identified as to position in the tooth row and the estimate of minimum numbers of individuals has been based on the counts of teeth according to the method described earlier in this paper.

*Isoodon obesulus* is present throughout Phase 1 and Phase 2 of the deposit, increasing in relative abundance in Phase 2. In Phase 3 *I. obesulus* occurs in the uppermost units only. Two species of *Perameles* are also represented throughout the deposit. *P. nasuta* and *P. gunnii* were identified by comparison with jaws and dental characteristics of skulls from the modern fauna in the collections of the Australian Museum, Sydney, and with the descriptions and measurements given by Freedman (1967). *P. nasuta* is the most abundant peramelid taxon throughout. Both species of *Perameles* are less abundant in Phase 1 than in higher levels, and the relative abundance of *P. nasuta* over *P. gunnii* is slightly greater in Phase 1. In Phase 2 the relative abundance of both species of *Perameles* shows near parallel fluctuations. In Spits 16–19, at the base of Phase 3 both *P. nasuta* and *P. gunnii* show a sharp increase in relative abundance, at the same time that *I. obesulus* temporarily disappears from the fauna. Subsequently, in the upper units of Phase 3, *P. gunnii* is more abundant and more consistently present than *P. nasuta*. (Fig. 2).

The lower relative abundance in Phase 1 of all bandicoots, and especially of species of *Perameles*, coincides with sharp increases in the relative abundance of small dasyurid taxa and small rodents (Fig. 2). These trends probably reflect the food preferences of the Ghost Bat, *Macroderma gigas*, which is the most likely agent of accumulation of small mammals in the earliest phase of deposition.

Although these three bandicoot species have not previously been identified in the same deposit, their occurrence together is not incongruous. Gordon and Hulbert (1989) cite these species (plus *I. macroura*) as characteristic of the peramelid fauna of the coastal/sub-coastal southern humid zone, extending in part into the semi-arid zone of eastern Australia. This contrasts with the species characteristic of true semi-arid areas (including *I. auratus, P. bougainville, P. eremiana, Chaeropus* sp. and *Macrotis* sp.), none of which have been identified from the Cathedral Cave fauna.

Gordon and Hulbert (1989) note that the habitat requirements of bandicoots are extremely flexible and opportunistic, although each species may have a preferred habitat. They suggest that *P. nasuta* and *P. gunnii* may exhibit competitive exclusion in their modern distribution (e.g. in Tasmania *P. gunnii* thrives in the absence of *P. nasuta*). However, *I. obesulus* occurs with *P. gunnii* in Tasmania and with *P. nasuta* throughout their ranges in the modern mainland fauna and in most late Pleistocene faunas from eastern Australia which contain bandicoots. All three species appear to prefer open forest–grassland habitat.

This is the northernmost record of the occurrence of *P. gunnii* and this species was not recorded from the Wellington area at the time of European occupation. *P. gunnii* is known from mainland late Pleistocene faunas of South Australia ( Smith 1972, Pledge 1990) and Lake Victoria in western New South Wales (Marshall 1973) as well as from the modern fauna of Victoria and Tasmania (Gordon and Hulbert 1989).

### Phascolarctidae

*Phascolarctos cinereus* is represented in Phase 1 by a small mandibular fragment (Spits 51–54) and several isolated molars (Spits 46 and 51–54). In the modern fauna this species inhabits wooded areas and river channels throughout New South Wales, its distribution being dependent on the presence of suitable food trees rather than climatic factors.

### Thylacoleonidae

*Thylacoleo carnifex* is represented in Phase 2 by an isolated left $I_1$ in Spits 24–28 and another isolated left $I_1$ in Spits 34–38. The species is represented in Phase 1 by a left mandibular ramus in Spits 39–42, and by an isolated $I^3$ in Spits 55–57. Well preserved remains of *Thylacoleo* are common in museum collections from Cathedral Cave (Dawson 1985). Many of these were collected by Henry Barnes in 1881 (Ramsay 1882), but unfortunately the original records do not include precise stratigraphic locations for the specimens.

### Acrobatidae

*Acrobates pygmaeus* occurs in Phase 1 only, and then only in Spits 46–54, coincident with the Ghost Bat, which is most likely to be the accumulating agent. In the modern fauna, *A. pygmaeus* has a wide range of climatic tolerance, and inhabits eucalypt forest throughout the eastern coast, ranges and slopes. It is therefore unlikely that its limited distribution in the Cathedral Cave deposit is the result of climatic or vegetation factors.

### Phalangeridae

*Trichosurus vulpecula* is represented by isolated molars in the upper spits of Phase 3. It has not been collected from the Phase 2 levels of the Cathedral Cave floor deposit, but is represented in all spits of Phase 1 below Spit 46 and by associated left and right mandibular rami from Spits 51–54. *T. vulpecula* is a generalist in its dietary preferences and inhabits a wide range of habitats. The species is common in the Wellington area today, and its absence from the Phase 2 levels of the Cathedral Cave is probably due to unknown taphonomic factors rather than indicating its absence from the fauna of the area during this phase of deposition.

### Petauridae

*Petaurus breviceps* occurs only in the upper spits of Phase 1 (in relatively low abundance) and at the top of Phase 2 / base of Phase 3, where there is a sharp peak in abundance of this species (Table 4, Fig. 2). Occurring as they do at times of transition in the deposit, it is tempting to hypothesise that some factor related to those transitions could account for the disjunct distribution of this species in the deposit. It is most likely that they represent the prey of owls, since the species is not represented in the 'Macroderma' spits at the base of Phase 1. Given the modern range of *P. breviceps*, where it inhabits forested areas throughout the entire east coast of the continent, extending inland to the western slopes, it is unlikely that climatic limitations are responsible for the observed distribution. *P. breviceps* has been recorded from late Pleistocene faunas through the eastern margin of the continent, extending from Russenden Cave, Queensland (Archer 1978) to the Naracoorte region of South Australia (Pledge 1990)

## Pseudocheiridae

*Pseudocheirus* sp. is extremely rare in the deposit, being represented by a single maxillary fragment at the base of Phase 2. Ringtail possums are not uncommon in other late Pleistocene faunas, and occur in the Wellington region in the modern fauna, so their virtual absence in the Cathedral Cave deposit is difficult to explain.

## Potoroidae

### Potoroinae

Three potoroine species are represented sporadically through the deposit. The most common, *Aepyprymnus rufescens*, occurs at low abundance at the base of Phase 1, peaks suddenly in the upper levels of Phase 2 and Phase 3, but is absent from the intervening levels (Table 4, Fig. 2). *Potorous tridactylus* is represented by a single mandibular fragment in each of Spits 51–54, Spits 39–42 and in Spit 38. Its distribution is thus effectively restricted to Phase 1 of the deposit. *Bettongia* sp. is represented by two isolated premolars, also in Phase 1. *Aepyprymnus rufescens* inhabits well grassed open forest, and is now almost entirely confined in its distribution to coastal and southeastern Queensland, with a relict population on the Murray River in NSW (Strahan 1983:190). A record of this species from the late Pleistocene fauna of Henscke's Cave in South Australia (Pledge 1990) suggests that its original range extended throughout mesic areas of eastern Australia, although it occurs in few fossil faunas of the late Pleistocene.

TABLE 5

Dental dimensions (mm) of *Macropus titan* from Cathedral Cave, Wellington Caves. a = approximate.

| | | AM F69889 | AM F69890 | AM F69891 | AM F69892 | AM F69893 | AM F69894 |
|---|---|---|---|---|---|---|---|
| $M^2$ | L | 14.5a | | | | | |
| | PW | 12.6 | | | | | |
| $M^3$ | L | 15.8 | | | | | |
| | PW | 12.8 | | | | | |
| $P_2$ | L | | | 8.8 | 8.3 | 8.19.0 | |
| | PW | | | 6.0a | 4.6 | 4.8 | 5.1 |
| $dP_3$ | L | 11.8 | 10.8 | 11.0 | 10.8 | 11.0 | |
| | PW | | 7.5 | 7.3a | 6.9 | 7.0 | 7.1 |

Occlusal length $I^3$ = 16.0 mm (F69888)

## Macropodidae

### Macropodinae

Macropodine species are represented in all units of Phase 1 and Phase 2 of this deposit. However, in Phase 3 only a few isolated teeth have been recovered, most referable to *Macropus giganteus.* This undoubtedly reflects the taphonomy of the Phase 3 deposits, since it would be expected that the larger kangaroos of the modern fauna were present in the Wellington region throughout the Holocene period.

Five specimens from Phase 2 and two from Phase 1 are referable to *Macropus titan.* All jaw fragments represent juvenile individuals. Dimensions of these specimens are given in Table 5. Comparison with published data for populations of *M. titan* from Queensland and Lancefield (Bartholomai 1975, Dawson 1982c), and with data for the old collections from Wellington Caves (Dawson 1982c) indicates that the specimens all fall well within the size range of the Pleistocene species, *M. titan*, rather than the smaller *M. giganteus* .

A single mandibular fragment (juvenile) from Phase 2 (Spits 24–28) represents the giant kangaroo, *Macropus ferragus.* Dimensions of the partially erupted $M_4$ of F69895 are: length = 19.5mm, anterior width = 11.8mm. This species is present in the old collections from Wellington Caves and the recent collections from Bone Cave, and otherwise recorded from Pleistocene deposits of the eastern Darling Downs, Queensland, and Lake Victoria and Lake Menindee in western New South Wales (Dawson and Flannery 1985).

The Pleistocene Wallaroo, *Macropus (Osphranter) altus*, is represented by two specimens, a juvenile maxillary fragment from Phase 2 (Spits 24–28) and left and right maxillae of one adult individual from Phase 3 (Spits 46–50). Although morphologically identical to *M. robustus*, the modern wallaroo or euro, *M. (O.) altus* is considerably larger. Dental dimensions of the Cathedral Cave specimens agree in size with the holotype of *M. (O.) altus* from the eastern Darling Downs, Queensland and with a larger sample from the old collections from Wellington Caves (Dawson 1982c). A species of *M. Osphranter* is also represented by three isolated teeth, an $I_1$, $P_3$ and an upper molar, in Spits 51–54, and two isolated upper premolars in Spits 55–57.

Several species of the *Macropus* wallabies (*M. Notamacropus* spp.) (Dawson and Flannery 1985), are present in the deposit. In Phase 2 *M.* cf. *M. (N.) dorsalis* is represented by two juvenile mandibles in Spits 20–23, while a jaw of a juvenile *M.*cf *M. (N.) agilis* occurs in Spits 24–28. In Phase 1 two juvenile mandibles represent *M.* cf. *M.(N.) dorsalis* (Spits 43–45) and a single jaw fragment is referable to *M.* cf *M. (N.) agilis* (Spits 51–54). Neither of these taxa have occurred in the Wellington region in historic times, being now confined to northern Australia. However, the larger Pleistocene form of *M. (N.) agilis, M. (N.) a. siva,* is relatively common in old collections from Wellington Caves (Dawson 1985) and has been reported from Pleistocene deposits in Victoria (Marshall 1974) and New South Wales (Marshall 1973, Gorter 1977). *Macropus dorsalis* has been reported from the Pleistocene Lancefield Swamp fauna of western Victoria (Gillespie et al. 1978) but was not identified in the old collections from Wellington Caves (Dawson 1985).

A new species of large wallaby referable to *Macropus (Notamacropus)* is present in Phase 1 of the deposit. Remains similar to this species have been recorded, but not yet formally described, from the old collections from Wellington Caves (Dawson 1982c and 1985, as *Macropus rankeni* n.sp.) and from the recent collections from Bone Cave (Dawson in prep). Associated elements from Spit 43 represent the upper and lower dentition, and limb and pedal bones of a juvenile individual. The specimens from Cathedral Cave vary from the Bone Cave material in premolar morphology and in being slightly smaller, and may represent a 'dwarfed' version of the Bone Cave species. This species may have its closest affinities with *Macropus dorsalis*, but varies considerably from that species (and from all other *Notamacropus* wallabies), in being much larger, having a relatively longer, more slender diastema and in premolar morphology. The elongate diastema and relatively high crowns of the molars indicate that this was a grazing animal.

Large extinct wallabies of the genus *Protemnodon* are extremely rare in the deposit, being represented by isolated teeth in Spits 29–33 and Spits 55–57 only. The teeth represented in the present collection are closest to *P. brehus* in size, but there is insufficient material for definite specific determination. Species of *Protemnodon* are well represented in the old collections from Wellington Caves but it is unlikely any of those specimens came from the Cathedral Cave (Dawson 1985).

Rock wallabies (*Petrogale* sp) are represented in Phase 1 and Phase 2 by jaw fragments of juveniles. Although *Petrogale* sp. does not occur in Phase 3 of the deposit, the Wellington region falls within the modern range of *P. penicillata*, which inhabits suitable rocky areas in sclerophyll forest of inland New South Wales (Strahan 1983:211).

The presence of species of *Thylogale* and *Onychogalea* in the lower levels of the Cathedral Cave sediments has been determined on the basis of isolated teeth (the distinctive posteriorly grooved $I^3$ of *Thylogale* sp and the small narrow $I_1$ of *Onychogalea* sp.) The presence of these taxa together in the lower levels of Phase 1 has contradictory ecological implications. *O. fraenata* inhabited shrubland and grassy woodland of the western slopes and plains last century (Strahan 1983:205), but all extant species of *Thylogale* are today confined to densely forested habitats of the east coast and ranges.

### Sthenurinae

This sub-family of extinct macropodids is represented by 6 specimens from Spits below 6 metres. An isolated $I^3$ is the only occurrence in Phase 2 of the deposit (Spits 34–38). In Phase 1 a juvenile left maxillary fragment was found in Spits 43–45, associated left and right mandibular rami of a juvenile individual in Spits 51–54, and three isolated teeth ($P_3$, $I_1$ and $M_2$) in Spits 55–57. Dental dimensions of these specimens are given in Table 6. Identification of these fragments as *Simosthenurus oreas* is based on morphological comparison of the mandibular teeth (AM F69880, F69881, F69883 and F69884) with a cast (AM L1728) of the holotype, QM F2923, from the Darling Downs in Queensland, and with the descriptions of Tedford (1966). *S. oreas* is a poorly known species and the upper dentition has not previously been described. The maxillary fragment, AM 69885, has the following dental dimensions $P^3$ L = 15.3mm, AW = 8.0mm, PW = 9.8mm; $dP^3$ L = 9.5mm, AW = 8.6mm, PW = 9.8mm; $M^1$ L = 11.2mm, AW = 11.0mm, PW = 11.2mm. The teeth of this fragment are in the same size range as the lower molars of *S. oreas*, although size alone would not necessarily distinguish this species from similarly sized *Sthenurus andersoni* or *Simosthenurus orientalis*. The maxillary fragment AM F69885 has therefore been tentatively assigned to *S. oreas* pending comparison with more confidently assigned maxillary dentition of this species.

Three species of *Simosthenurus* and 2 species of *Sthenurus* have previously been recorded in the Old Collections from the Wellington Caves (Dawson 1985). As far as can be determined from their documentation, none of the specimens from the old collections came from Cathedral Cave. It is most likely that the three specimens of *S. oreas* in the old collections came from the Phosphate Mine, since two of the three specimens were originally part of the collections of the NSW Mining Museum, and the third bears documentation indicating it was collected in the "drives put in ..... by a Phosphate Company in search of fertiliser" (Anderson 1932). *S. oreas* is present in the new collections from Bone Cave, but is otherwise only recorded from the Pleistocene deposits of the eastern Darling Downs, and from Bingara in northern New South Wales (Tedford 1966). All species of *Sthenurus* and *Simosthenurus* represent browsing animals. Tedford (1966) has suggested that *Simosthenurus*, with its deep skull, short snout and heavily ankylosed jaws possibly browsed woodland vegetation rather than shrubs.

TABLE 6

Dimensions (mm) of the cheek teeth of specimens referable to *Simosthenurus oreas* from Cathedral Cave, Wellington Caves.

| | | AM F69880 | AM F69882 | AM F69883 | AM F69884 | QM F2923* |
|---|---|---|---|---|---|---|
| $P_2$ | L | 10.0 | | | | |
| | AW | 6.8 | | | | |
| | PW | 8.0 | | | | |
| $P_3$ | L | | | 14.0 | | 14.3 |
| | AW | | | 6.0 | | 6.4 |
| | PW | | | 8.5 | | — |
| $dP_3$ | L | 10.2 | | | | |
| | AW | 9.0 | | | | |
| | PW | 9.0 | | | | |
| $M_1$ | L | 13.2 | | | | 11.8 |
| | AW | 10.5 | | | | 9.8 |
| | PW | 10.7 | | | | 10.0 |
| $M_2$ | L | | | | 14.9 | 14.8 |
| | AW | | | | 11.5 | 11.5 |
| | PW | | | | 11.9 | 11.6 |
| I1 | Depth | 12.0** | 18.2 | | | |

* measurements taken from a cast (AM L1728) of the holotype.

** tooth not fully erupted.

## Other marsupial taxa

Both Vombatidae and Diprotodontidae are represented in the deposit. However no analysis of these groups has been attempted, since they are represented only by small tooth fragments or fragments of dental enamel which are too incomplete to allow identification to genus level.

## Placentalia

### Rodentia

Rodents are by far the most abundant animals represented in the Cathedral Cave deposit, comprising in total more than 70% of the individuals present in all except three spits (Table 4). This study has not included detailed analysis of the rodent fauna, and analysis at species level has been confined to two taxa only, *Conilurus albipes* and *Mastacomys fuscus*.

*C. albipes* occurs throughout the deposit, at relatively low levels of abundance in Phase 1, increasing to moderately high levels in the top of Phase 2 and middle of Phase 3 (Table 4, Fig. 2). Now extinct, *C. albipes* occurred in the Wellington area early last century, and has been recorded from late Pleistocene faunas of mesic eastern Australia from Queensland (Russenden Cave, Archer 1978) to South Australia (Henscke's Cave, Pledge 1990). According to historical records it had a semi-arboreal habitat, and nested in low hollow tree branches (Strahan 1983:382).

*Mastacomys fuscus* has a disjunct distribution in the Cathedral Cave deposit, being present only in the base of Phase 1, and the middle spits of Phase 2 and Phase 3, respectively (Table 4, Fig. 2). *M. fuscus* is abundant in the late Pleistocene fossil faunas of the southeastern highlands such as the faunas from Jenolan Caves (Morris et al., this volume) and Wombeyan Caves (Hope 1982). It is also present in the late Pleistocene of the Naracoorte region (Victoria Cave and Henschkes Cave, Pledge 1990) and in the Seton Rock Shelter on Kangaroo Island (Hope et al. 1977). The distribution of *M. fuscus* in the modern fauna suggests a preference for cool moist climatic conditions and dense ground cover (Seebeck 1981). The occurrence of this species in the middle of Phase 2 corroborates other evidence of a cooler climate in the Wellington region at that time, but the occurrence in Phase 1 appears to be anomalous on climatic grounds because of the associated presence of the Ghost Bat (which implies a warmer climate).

### Chiroptera

#### Microchiroptera

Unidentified microchiropteran bats are represented in the lower spits of Phase 1, where they probably formed part of the diet of the Ghost Bat. They appear to be absent from most of Phase 2, with the exception of the upper spits in the transition zone to Phase 3, where they again occur in the middle spits of this zone. This distribution possibly reflects changing entrances to the cave.

#### Megadermatididae

The Ghost Bat, *Macroderma gigas*, is represented in the lower levels of Phase 1, its relative abundance peaking sharply in Spits 51–54, where it comprises 45% of the individuals present (Table 4, Fig. 2). Coincident with this peak, the sediments changed from predominantly reddish to grey, and positive tests for the presence of phosphates in the sediments indicated a high proportion of guano (G. Hodge, pers comm, 1991). The data suggest that at this period the cave was most probably the home of a breeding colony of Ghost Bats.

## Non-mammals.

Small reptiles and small birds are represented sparsely throughout the deposit (Table 4). A species of *Varanus* is represented at the base of Phase 1 and the top of Phase 2 only.

Of non-vertebrate remains, 11 shells of terrestrial snails (Mollusca) were found in the sediments and identified by Dr J. Stanisic of the Queensland Museum, as follows: In Phase 1 Spit 53, *Nevistitis aridorum*, Spit 43, Charopid sp.; Phase 2, Spits 30–40, *N. ari-*

*dorum, Galidistes* sp. *Elsothera* sp. ; Phase 3, Spit 14, *Galidistes* sp, *Glyptopupoides egregia*. With the exception of the charopid species from Phase 1 all these species are found in the area today and are quite characteristic of limestone outcrops of the central west of New South Wales. The charopid, however is typically found in wetter forests of eastern New South Wales (J. Stanisic, pers comm. 1991).

## DISCUSSION

Osborne (1984) has emphasised the great difficulties involved in interpretation of the depositional events and stratigraphy of cave sediments, particularly noting the importance of recognising lateral facies change, secondary unconformities and reverse stratigraphy. A deposit such as the floor of Cathedral Cave is likely to be the result of a complex sequence of events over the period of deposition and it is to be expected that a section taken through the deposit, such as the section revealed by the present excavation, would not necessarily represent a simple depositional time line. With these considerations in mind, this attempt at interpretation of the stratigraphy and time events of this deposit has combined information from the observed sedimentary sequence with interpretation of other inclusions and the taphonomy of the bones to derive a hypothetical correlation of events. Radiocarbon dates indicate a depositional time span from approximately 35,000 BP to about 2,000 BP (in fact up to the present, since the top meter of the deposit had been too disturbed for analysis).

Taphonomic factors were of prime importance in determining the range of fauna present in the sediments. Fig. 3 indicates that in most spits of the deposit over 90% of the bones represent small mammals (<1.5 kg body weight) suggesting the main source of bone was the remains of prey of owls and, in the case of Phase 1, the Ghost Bat. The general absence of large bone (Table 1 indicates the largest bone fragment, from Phase 2, is approx 23 cm long) suggests that at no time was there a large entrance to the cave. Where large species are present they are represented by fragmentary remains of juveniles, suggesting that pitfall situations only allowed entry of small animals, or previously broken remains of larger animals. These observations could well account for the general absence of many typical late Pleistocene megafaunal species, e.g. *Diprotodon, Zygomaturus, Palorchestes, Phascolonus*, which are present in deposits of approximately the same age from nearby Cuddie Springs (Dodson et al. 1993).

Of the small mammal taxa which have been identified to species level, most could have inhabited the area at the time of first European settlement, although many would have been at the extreme of their known distributions (Strahan 1983). Further analysis of the rodents is currently being undertaken by one of us, M. L. Augee. This group is the most abundantly represented in the fauna and preliminary analysis indicates that considerable species diversity is represented. It is hoped that the rodent fauna may be of greater value in reflecting climatic or vegetation differences over the depositional period.

While differences between the three Phases primarily reflect taphonomic factors rather than climate or ecology, some trends are apparent.

In Phase 1 the presence of the Ghost Bat and the high level of species diversity indicate a warm climate with complex vegetation communities and a high level of productivity. Although the Ghost Bat is now confined to sub-tropical and monsoonal regions of Northern Australia, its fossil record indicates that it could tolerate more temperate climates (Molnar et al. 1984). However, it is suggested that they require breeding caves in which the mean temperature does not drop below 20 degrees C (Nelson 1989). With the exception of a record of two specimens from Cliefden Caves, 30 km south of Wellington (Molnar et al. 1984) this record from Cathedral Cave represents the most southern occurrence of the Ghost Bat in Eastern Australia. Owls may also have contributed to the small mammal fauna of Phase 1, and the different contributions from these two volant carnivores could account for some of the strange shifts in relative abundance of dasyurid and rodent taxa in the lower spits of the deposit (Fig. 2). Although Ghost Bat remains are present throughout the lower 1.5 metres of the deposit they are only abundant in a 50 cm zone of Spits 51–54. Dramatic differences in the proportion of small and larger rodents and dasyurids in these and adjacent spits, and the peak in occurrence of *Acrobates* sp. in Spits 46–54 may reflect the different feeding preferences of the Ghost Bat compared with owls, which probably became the prime contributors to the fauna after the departure of the bats. Associated $C^{14}$ dates suggest that the period of Ghost Bat occupation of the caves ceased prior to approximately 21,000 BP, and that the peak occupations occurred prior to 30,000 BP. These data suggest that cooling climate due to the approaching glacial period may have forced the Ghost Bats to depart.

Among the larger taxa present in Phase 1, *Sthenurus oreas* and *Macropus (Notamacropus)* n. sp. represent Pleistocene species which do not occur later in Phase 2. *Phascolarctos cinereus, Sarcophilus harrisii*, *Phascogale calura* and unidentified species of *Bettongia, Onychogalea* and *Thylogale* are all confined to Phase 1, supporting the suggestion of complex ecological conditions supporting high productivity during that period. The presence of a species of land snail characteristic of wet forest habitats also supports a complex moister environment near the caves during the period represented by Phase 1.

Throughout Phase 2 there is a somewhat higher proportion of large mammals represented (Fig. 3), and the preservation of bone and nature of the sediments suggests a very different mode of deposition from that in Phase 1. Larger species are represented almost entirely by juveniles (Table 3) and by small highly fragmented remains. Extinct Pleistocene species are present, but rare, the grazing macropodines being the most common, with notable absence of browsing taxa (except for one jaw fragment of *Protemnodon* sp. in Spits 29–33). It is difficult to find firm evidence for climatic change during this period since the fauna continues to suggest a complex, relatively productive environment with many microhabitats being sampled. The fauna does not suggest that the Wellington area suffered undue climatic stress during the glacial maximum, the period most likely represented by Phase 2 of the deposit. The absence of *Cercartetus* sp. and of *Burramys parvus*, both of which are commonly present in faunas of similar age from nearby eastern highland regions (e.g. Jenolan Caves, Wombeyan Caves) suggest that the climate was not unduly cold.

While most of the taxa of small mammals from Phases 1 and 2 are still extant, and could have inhabited the Wellington area at the time of first settlement, the macropodine taxa, in particular, indicate significant change since late Pleistocene times. The smaller potoroid and macropodine taxa, e.g. *Aepyprymnus rufescens, Bettongia* sp., *Petrogale* sp, *Onychogale* sp., and possibly *Potorous* sp. and *Thylogale* sp. all now inhabit contracted ranges in the modern fauna but may have been represented in the Wellington area last century, although they were probably always rare (Strahan 1983, Dickman 1993, 1994). However, the larger wallabies and kangaroos (*Macropus* spp.) of the Cathedral Cave fauna are completely different from the species inhabiting the area today (i.e. *M. rufogriseus, M. robustus, M. giganteus* and *Wallabia bicolor*). *M. giganteus* is represented by isolated teeth in Phase 3 of the deposit (Holocene age), but only its 'giant' precursor, *M. (M.) titan* is present in Phase 1 and Phase 2. Similarly the Pleistocene precursor of the Euro, *M. (Osphranter) altus* is represented in Phase 1 and Phase 2.

Of the three species of *M. (Notamacropus)* ('wallabies'), present in the deposit, two, *M.* cf. *M. (N.) agilis*, and *M.* cf. *M. (N.) dorsalis*, are very close to the species now confined to northern and northeastern Australia and have not been recorded from further south in historic times. The third species of *M. (Notamacropus)* is clearly derived from a new species to be described from the early Pleistocene Bone Cave fauna of Wellington Caves (Dawson in prep.), where it forms one of the more abundant elements in that fauna. The Bone Cave species is similar to *M. (N.) dorsalis*, but is much larger and differs in other significant features.

The presence of *M. (M.) ferragus* in the upper part of Phase 2 is of interest, since this taxon appears to have been relatively common in the late Pleistocene of far western New South Wales (Marshall 1973, Merrilees 1973) and of the Pleistocene deposits of the eastern Darling Downs, Queensland (Bartholomai 1975). Its presence in Phase 2 may be an indication of more arid conditions and open grassland spreading eastwards into the Wellington area during the glacial maximum. Overall, the species of *Macropus* in the Cathedral Cave deposit represent a suite of taxa allied most closely with the fauna of northern Australian grasslands, rather than with elements more characteristic of Pleistocene faunas of Victoria or South Australia, or the macropodine fauna of the Wellington region today.

The top 2.5 to 3.0 meters of the deposit (Phase 3) evidently represents a period when the cave had a very restricted opening to the surface, insufficient to allow the entry of large bone. There is no evidence that any animals fell into the cave, nor of scavenger species. The faunal remains consist of small bones and teeth of small taxa, predominantly rodents, with some peramelids and dasyurids, probably accumulated by owls roosting in overhangs or crevices near the entrance. The bones may have washed into the cave with surface soil and debris during periods of rain, or been blown in during high winds.

Although imprecise, associated radiocarbon dates indicate that some elements of the Pleistocene 'megafauna' survived in the Wellington area at least until the glacial maximum (about 17,000 BP) and possibly later, but not into the Holocene. However, this representation is very depleted compared with the old collections from Wellington Caves, most of which are derived from the Mitchell Cave, Bone Cave and the passages of the phosphate mines (Dawson 1985). This observation is supported by new collections from the Bone Cave, yet to be described, which contain a much more diverse array of taxa than described here from Cathedral Cave, and thus support the hypothesis that the sediments in each part of the caves complex at Wellington represent different ages.

## ACKNOWLEDGMENTS

The contribution of many people during the four years when the excavation was underway is gratefully acknowledged. In particular we are grateful to the Wellington Shire Council for permission to dig in the floor of the main tourist cave of the complex, and to Mr Arnold Worboys, the Wellington tourist officer at the time, for his enthusiastic support. Others present at the initiation of the project were Professor Mike Archer and Dr Ken Aplin of the University of New South Wales, and Dr Alex Ritchie, Australian Museum. Many students from the University of New South Wales, and several staff and other volunteers assisted with the dig and with sorting of bones. In particular the contribution of Bill Symons, Chris Brydon, Henk Godthelp and Armstrong Osborne is gratefully acknowledged. Dr Steve van Dyke of the Queensland Museum assisted with identification of the small dasyurids, and Mr Steve Blandford and Ms Giselle Hodge, honours students in Zoology, University of New South Wales, contributed to the interpretation of the rodents and bandicoots, respectively. From 1984 to 1986 the work was supported by a grant from the Australian Research Grants Scheme to M. L. Augee and Lyndall Dawson.

## REFERENCES

Anderson, C. (1932). Unpublished report to the Trustees of the Australian Museum, Sydney, February 1932, ref no. 324/31 in the archives of the Australian Museum.

Archer, M. (1974). Apparent association of bone and charcoal of different origin and age in cave deposits. *Memoirs of the Queensland Museum* **17**, 37–48.

Archer, M. (1978). Quaternary vertebrate faunas from the Texas Caves of southeastern Queensland. *Memoirs of the Queensland Museum* **19**, 61–109.

Baird, R.F. (1991). The taphonomy of late Quaternary cave localities yielding vertebrate remains in Australia. In 'Vertebrate Palaeontology of Australasia' (Eds P.Vickers-Rich, J.M. Monaghan, R.F. Baird and T.H. Rich) pp 267–309. (Pioneer Design Studio: Melbourne).

Bartholomai, A. (1975). The genus *Macropus* Shaw (Marsupialia: Macropodidae) in the upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* **17**, 195–235.

Dawson, L. (1982a). Taxonomic status of fossil devils (*Sarcophilus,* Dasyuridae: Marsupialia) from late Quaternary eastern Australian localities. In 'Carnivorous Marsupials' (Ed M. Archer) Vol. 2 pp 517–525. (Surrey Beatty & Sons: Sydney and Royal Zoological Society of N.S.W: Mosman).

Dawson, L. (1982b). The taxonomic status of fossil thylacines (*Thylacinus*: Thylacinidae: Marsupialia) from late Quaternary deposits in eastern Australia. In 'Carnivorous Marsupials' (Ed M. Archer) Vol. 2 pp 527–536. (Surrey Beatty & Sons: Sydney and Royal Zoological Society of N.S.W: Mosman).

Dawson, L. (1982c). Marsupial fossils from Wellington Caves, New South Wales. Unpublished Ph.D Thesis, University of New South Wales, Kensington.

Dawson, L. (1985). Marsupial fossils from Wellington Caves, New South Wales; the historic and scientific significance of the collections in the Australian Museum, Sydney. *Records of the Australian Museum* **37**, 55–69.

Dawson, L. & Flannery, T.F. (1985). Taxonomic and phylogenetic status of living and fossil kangaroos and wallabies of the genus *Macropus* Shaw (Macropodidae: Marsupialia), with a new subgeneric name for the larger wallabies. *Australian Journal of Zoology* **33,** 473–498.

Dickman, C. (1994). Native mammals of western New South Wales: past neglect, future rehabilitation? In 'Future of the Fauna of Western New South Wales' (Eds D. Lunney, S. Hand, P. Reed and D. Butcher) pp 81–91. (Royal Zoological Society of New South Wales: Mosman).

Dickman, C., Pressey, R. L., Lim, L. & Parnaby, H. E. (1993). Mammals of particular conservation concern in the western division of New South Wales. *Biological Conservation* **65**, 219–248.

Dodson, J., Fullagar, R., Furby, J., Jones, R. and Prosser, I. (1993). Humans and megafauna in a late Pleistocene environment from Cuddie Springs, north western New South Wales. *Archaeology in Oceania* **28**, 94–99.

Fox, B. J. (1982). A review of dasyurid ecology and speculation on the role of limiting similarity in community organization. In 'Carnivorous Marsupials' (Ed. M. Archer) Chapter 11, pp. 97–116. (Royal Zoological Society of New South Wales: Mosman).

Frank, R. (1971). The clastic sediments of the Wellington Caves, New South Wales. *Helictite* **9**, 3–26.

Francis, G. (1973). Evolution of the Wellington Caves landscape. *Helictite* **11**(4), 79–91.

Freedman, L. (1967). Skull and tooth variation in the genus *Perameles*. Part 1: Anatomical Features. *Records of the Australian Museum* **27**(6), 147–166.

Gillespie, R., Horton, D.R., Ladd, P., Macumber, P.G., Rich, T.H., Thorne, R. and Wright, R.V.S. (1978). Lancefield Swamp and the extinction of the Australian megafauna. *Science* **200**, 1044–1048.

Gordon, G. and Hulbert, A. J. (1989). Peramelidae. In 'Fauna of Australia. Mammalia' (Eds D.W. Walton and B.J. Richardson) pp 603–624. Australian Government Publishing Service Vol. 1B: Canberra .

Gorter, J.D. (1977). Fossil marsupials from the Douglas Cave, near Stuart Town, New South Wales. *Journal and Proceedings of the Royal Society of New South Wales*, **110**, 139–145.

Hand, S.J., Dawson, L. and Augee, M. L. (1988). *Macroderma koppa*, a new Tertiary species of false vampire bat (Microchiroptera: Megadermatidae) from Wellington Caves, New South Wales. *Records of the Australian Museum* **40**, 343–351.

Hope, J. (1982). Fossil vertebrates from Wombeyan Caves. *Sydney Speleological Society Occasional Paper* **5**, 155–64.

Hope, J.H., Lampert, R.J., Edmondson, E., Smith, M.J. and van Tets, G.F. (1977). Late Pleistocene faunal remains from Seton rock shelter, Kangaroo Island, South Australia. *Journal of Biogeography* **4**, 363–385.

Luckett, W. P. (1993). An Ontogenetic Assessment of Dental Homologies in Therian Mammals. In 'Mammal Phylogeny: Mezozoic differentiation, multituberculates, monotremes, early therians and marsupials' (Eds F. S. Szalay, M. J. Novacek and M. C. McKenna) pp 182–204. (Springer-Verlag: New York).

Lundelius, E.L. Jr. (1983). Climatic implications of Late Pleistocene and Holocene faunal associations in Australia. *Alcheringa* **7**, 125–49.

Marshall, L.G. (1973). Fossil vertebrate faunas from the Lake Victoria region, S.W. New South Wales, Australia. *Memoirs of the National Museum of Victoria* **34**, 151–172.

Marshall, L.G. (1974). Late Pleistocene mammals from the "Keilor Cranium Site", southern Victoria, Australia. *Memoirs of the National Museum of Victoria* **35,** 63–86.

Merrilees, D. (1973). Fossiliferous deposits at Lake Tandou, New South Wales, Australia. *Memoirs of the*

*National Museum of Victoria* **34,** 177–182.

Mitchell, T.L. (1838). Three expeditions into the interior of eastern Australia, with descriptions of the recently explored region of Australia Felix, and of the present colony of New South Wales. 2 vols. (T. & W. Boone, London).

Molnar, R.E., Hall, L.S. and Mahoney, J.H. (1984). New fossil localities for *Macroderma* Miller 1906 (Chiroptera: Megadermatidae) in New South Wales and its past and present distribution in Australia. *Australian Mammalogy* **7**, 63–73.

Morris, D. A., Augee, M. L., Gillieson, D. and Head, J. (1997). Analysis of a late Quaternary mammal fauna from Nettle Cave, Jenolan Caves, New South Wales. (this volume).

Nelson, J.E. (1989). Megadermatidae. In 'Fauna of Australia. Mammalia' (Eds D. W. Walton & B. J. Richardson) pp 852–856. (Australian Government Publishing Service Vol.1B: Canberra).

Osborne, R. A. L. (1991). Red earth and bones: the history of cave sediment studies in New South Wales, Australia. *Earth Sciences History* **10**(1), 13–28.

Osborne, R. A. L. (1983). Cainozoic stratigraphy at Wellington Caves, New South Wales. *Proceedings of the Linnean Society of New South Wales* **107**, 129–145.

Osborne, R. A. L. (1984). Lateral facies changes, unconformities and stratigraphic reversals; their significance for cave sediment stratigraphy. *Transactions British Cave Research Association* **11**, 175–184.

Pledge, N.S. (1990). The upper fossil fauna of the Henschke Fossil Cave, Naracoorte, South Australia. *Memoirs of the Queensland Museum* **28**, 247–262.

Ramsay, E. P. (1882). Reports to the Trustees of the Australian Museum on the exploration of Wellington Caves, 20 September, 1881 and 31 December, 1881. In New South Wales Parliamentary Paper. Exploration of the Caves and Rivers of New South Wales. (Minutes, Reports, Correspondence, Accounts): 34, 44.

Seebeck, J. H. (1981). Distribution and habitat of the broad-toothed rat, *Mastacomys fuscus* Thomas (Rodentia: Muridae) in Victoria. *Victorian Naturalist* **88**, 310–323.

Smith, M.J. (1972). Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. II. Peramelidae, Thylacinidae and Dasyuridae (Marsupialia). *Transactions of the Royal Society of South Australia* **96**, 127–137.

Strahan, R. (Ed.) (1983). 'The Australian Museum Complete Book of Australian Mammals'. Angus & Robertson, Sydney.

Tedford, R.H. (1966). A review of the macropodid genus *Sthenurus*. *University of California Publications in Geological Sciences* **57**, 1–72.

# Taphonomy and Palaeoenvironmental Interpretation of a Late Holocene Deposit from Black's Point Sinkhole, Venus Bay, S.A.

M.C. McDowell

(Communicated by M.L. Augee)

School of Biological Sciences, The Flinders University of South Australia,
Box 2100, Adelaide, SA, 5001.

McDowell, M.C. (1997). Taphonomy and palaeoenvironmental interpretation of a late Holocene deposit from Black's Point Sinkhole, Venus Bay, S.A. *Proceedings of the Linnean Society of New South Wales* **117**: 79-96

The deposit from Black's Point Sinkhole, Venus Bay Conservation Park, SA, represents a continuous 3500 year palaeontological and geological record for the late Holocene. Taphonomic analysis established the sinkhole as a pitfall trap. Palaeoenvironmental settings were deduced by analysing sediments and fauna. Age was assessed using carbon dating. Evidence suggests that around 4000BP precipitation was greater than present and the environment was dominated by closed canopy forests with an understorey and nearby mud flats. During this period fauna including *Isoodon obesulus* and *Bettongia penicillata* accumulated. From approximately 4000BP to 1000BP the climate became warmer, drier and more variable. During this period sea level retreated, forests became more open and the understorey was greatly reduced. Species including *Perameles bougainville*, *Pseudomys bolami*, *Sminthopsis dolichura*, *Sminthopsis hirtipes* and *Thylacinus cynocephalus* appeared and/or became dominant. A carbon date associated with a *T. cynocephalus* tooth suggests an age of 3030±60BP making it the youngest mainland occurrence recorded. Around 1000BP precipitation increased and climate became slightly less variable, resulting in an increase in forest and understorey density. *Macrotis lagotis* appeared and *I. obesulus* returned while *P. bougainville* and many arid zone species retreated. These species changes can be associated with the increase in density of forest and understorey during the period of increased precipitation.

Manuscript received 2 April 1996, accepted for publication 23 October 1996.

KEYWORDS: holocene, taphonomy, palaeontology, pit fall trap, bone accumulation, sinkhole

## INTRODUCTION

Late Pleistocene to Holocene fossil deposits provide a record of faunal communities and, by inference, floral communities that occupied their surrounding area prior to European settlement (Baynes 1987). The study of such fossil deposits is of vital importance, as it increases our knowledge and understanding of past communities, and provides a baseline against which to measure change. The aim of this study was to use the sedimentological and palaeontological evidence from the Black's Point sinkhole within the Venus Bay Conservation Park, Eyre Peninsula, SA to reconstruct the regional history of environmental change before European settlement.

Processes that affect fossils tend to bias against, rather than for, preservation. The *prima facie* assumption therefore, is that all fossil deposits are a biased representation of the community from which they were drawn. Many authors (e.g. Douglas et al. 1966; Voorhies 1969; Peterson 1977; Behrensmeyer 1978, 1982, 1991, 1993; Behrensmeyer et al. 1979; Behrensmeyer and Hill 1980; Behrensmeyer and Kidwell 1985, 1979; King and Graham 1981; Wakefield 1982; Andrews and Nesbit Evans 1983; Hoffman 1988; Andrews 1990; Baird 1991; Lyman 1994a, b; Simms 1994) have investigated the biases

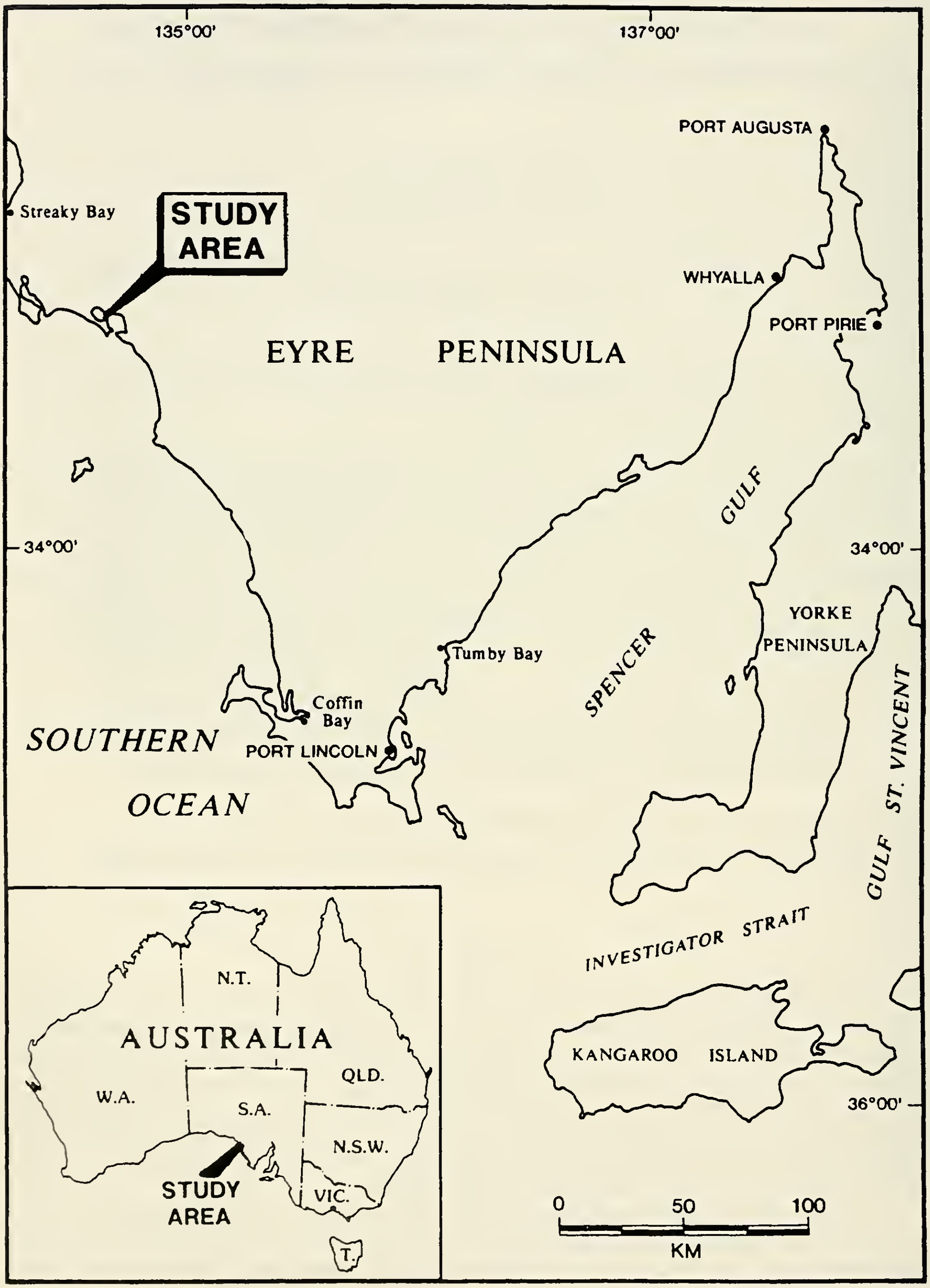


Figure 1. Location map of Black's Point sinkhole, Venus Bay.

affecting bone assemblages and how they can be recognised. Biasing processes include environmental and substrate conditions proximal to a death site, the mode of accumulation, hydraulic transport, weathering, bioturbation, animal size, animal lifespan, time averaging (processes such as erosion and redeposition by which fossils of different age are concentrated so that they appear to be contemporaneous) and excavation practices. This study investigates the taphonomic biases present during accumulation of the Black's Point sinkhole deposit by analysing samples of the fossils and sediments.

This study coincides with a Department of Environment and Natural Resources (DENR) program to reintroduce the brush-tailed Bettong (*Bettongia penicillata*) to the park. It is of interest to DENR to determine what other locally extinct species might also be reintroduced.

### Location

Black's Point Sinkhole is located at latitude 33°(10’95” S and longitude 134°(26’84” E on an island within Venus Bay Conservation Park (established in 1976). Venus Bay is on the upper west coast of Eyre Peninsula near the eastern edge of the Great Australian Bight (Fig. 1). The island lies inside Venus Bay proper and has been connected to the mainland in geologically recent time by a tombolo. It is not named on maps, but is locally known as Black's Point, hence the sinkhole's name.

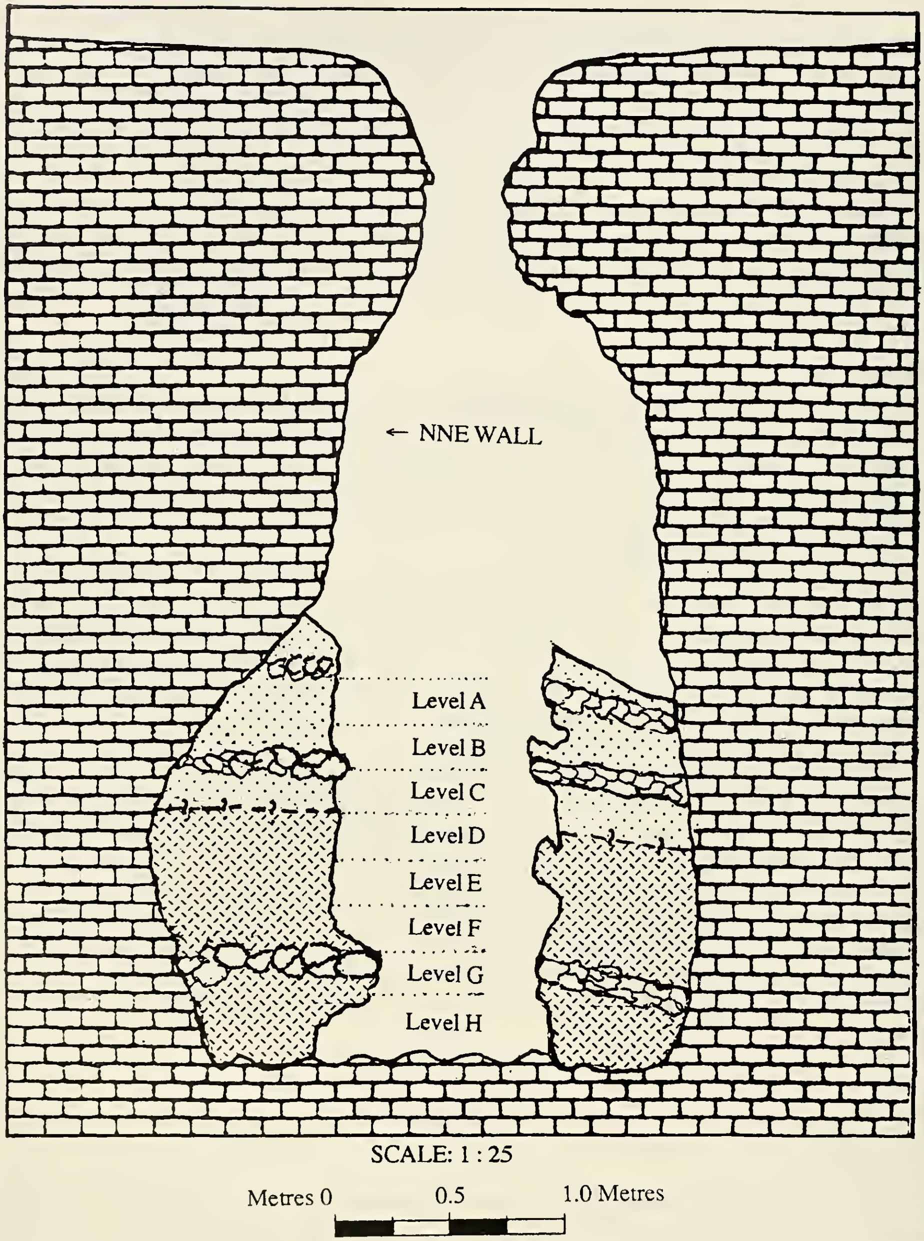
Black's Point sinkhole is approximately 4m deep and somewhat bell shaped (Fig. 2). Its non-parallel walls are about 1.2m apart at the floor but narrow rapidly near the surface to an approximately ovoid entrance measuring 0.6m by 0.9m. The entrance to Black's Point sinkhole lies approximately 6m above mean sea level and 53m from the sheltered bay on a gentle north-westerly slope of approximately 8 degrees. The area is surrounded by water but protected from the open ocean by the 50–100 metre high limestone/calcaranite cliffs of Cape Weyland (Fig. 1).

Black's Point sinkhole has an interesting history. Some time ago a well was dug inside the sinkhole, presumably by a farmer searching for fresh water. The sediment removed was left in a spoil heap near its entrance. The sinkhole entrance was later rediscovered by Conservation Park biologists who covered it with wire mesh in the belief that it posed a danger to the brush-tailed bettongs being released in the park. In the process they noted fossils in the spoil heaps and realised the potential of deducing the park's original (pre-European) fauna. A large proportion of sediment had been removed from the sinkhole by the well sinking operation, but sediment varying in thickness from 100 to 790 mm, was left *in situ* around the walls (Fig. 2) from which samples could be taken.

## METHODS

### Excavation

The strata within Black's Point sinkhole were divided into seven 20cm units and one 30cm unit using the lip of the sinkhole mouth as a datum. Excavation was confined to a 0.5m wide column of sediment from the NEE sinkhole wall that was chosen for its high fossil content. Excavation levels were defined with steel pegs and twine using a spirit level and tape measure to ensure accuracy. The eight levels were then labelled A through to H from top to bottom (Fig. 2). Fossiliferous sediment was excavated using dental picks, trowels, soft brushes and dust pans. A large tray was inserted at the base of the level being excavated to prevent contamination of lower levels. Sediment was lifted to the surface by hand using a 10kg bucket (as an arbitrary unit measure) which were emptied into labelled polythene bags. The fossiliferous sediment was wet sieved by Mr G. Medlin using nested sieves of 5mm, 2.5mm and 1.25mm mesh. Rocks were removed



**LEGEND**

| | |
|---|---|
| ⠿ | - Chocolate brown clays |
| ▨ | - Red brown clays |
| ▦ | - Bridgewater Limestone |
| ○ | - Rockfall |
| --?---?-- | - Inferred boundary |

Figure 2. A cross sectional view of Black's Point sinkhole morphology and infilling sediments with excavation levels indicated.

and fossils were allowed to dry. All skeletal elements were sorted and collected from the remaining sediment and rock using a small brush and forceps, then stored in labelled vials for identification and use in quantitative analysis.

### Faunal Analysis

Small mammal fossil remains were viewed using a binocular microscope following the procedure described in Andrews (1990). Specimens were identified by comparison with published data and reference material accessed from The Flinders University of South Australia (FUSA), the South Australian Museum (SAM) and the collection of Dr M Smith. Once identified, specimens were allocated reference numbers and stored in vials labelled with the species name, level of origin, source and reference number. They have now been lodged with the SAM mammal collection.

### Taphonomic Analysis

Using the methods of Andrews (1990), the numbers of skeletal elements per level (Ni) were counted and their relative abundance (Ri) calculated, based on comparison with the minimum numbers of individuals (MNI) multiplied by the expected numbers of each element (Ei). MNI is calculated by counting the most abundant skeletal element present and dividing it by the number of those elements present in a complete skeleton and Ei is calculated by multiplying MNI by the number of each element present in a complete skeleton.

$$\mathrm{Ri} = \frac{\mathrm{Ni}}{\mathrm{MNI(Ei)}} \times 100\%$$

Proportions of elements are indicated by four indices: (a) post-crania in relation to crania were shown by an index comparing five post-cranial elements (humerus, radius, ulna, femur and tibia) to numbers of mandibles, maxillae and isolated molars; (b) a second index compares numbers of humeri and femora to mandibles and maxillae; (c) loss of distal limbs is shown by an index comparing numbers of tibiae and radii with numbers of femora and humeri; (d) relative proportions of isolated teeth were calculated with reference to numbers of empty alveolar spaces in the jaw such that proportions of more than 100% indicate relative loss of jaws and less than 100% relative loss of teeth; this index was calculated separately for incisors and molars.

Breakage of post-cranial elements was based on separation of each into complete, proximal, shaft and distal segments, with the proportions of each category calculated against the whole.

Breakage of skulls was indicated by proportions of complete skulls, proportions of maxillae retaining the zygomatic process, and molars and incisors lost from the maxilla.

Breakage of mandibles was indicated by proportions of complete half-mandibles (with no distinction made between left and right), proportions of mandibles with inferior borders broken, and molars and incisors lost from the mandible.

The age frequency distribution of small mammals was determined by attributing each cranial specimen to one of five age classes in accordance with the wear observed on teeth. Age classes are defined as: (1) very young, no wear on molars, (2) young, small amount of molar cusp wear, (3) middle aged, molar cusps worn near smooth with dentine clearly visible, (4) old, molar cusps almost worn away completely with only strips of enamel remaining, (5) very old, molars very worn with only a rim of enamel around a basin of dentine remaining. A negligible number of broken teeth and no evidence of element digestion was observed so these categories of information were not investigated.

TABLE 1

Minimum Numbers of Individuals (MNI) for Mammals from different levels in Black's Point Sinkhole, Venus Bay.

| **Stratigraphic Level** | **A** | **B** | **C** | **D** | **E** |
|---|---|---|---|---|---|
| Sample Size (x10kg) | 1 | 4 | 4 | 4 | 1 |
| Muridae Indet.* | 9 | 232 | 111 | 332 | 18 |
| *Rattus sp.* | 2 | | 12 | 8 | |
| *Rattus fuscipes* | 4 | 122 | 93 | 71 | 4 |
| *Pseudomys sp.* | 2 | 28 | 73 | 35 | 4 |
| *Pseudomys australis* | | 21 | 2 | 5 | |
| *Pseudomys shortridgei* | | 9 | 16 | 3 | |
| *Pseudomys gouldii* | | 1 | 2 | 1 | |
| *Pseudomys bolami* | | 2 | | | |
| *Pseudomys occidentalis* | | | 1 | | |
| *Notomys sp.* cf.. *N. mitchelli* | | 2 | 1 | | |
| **Total Muridae MNI** | 17 | 232 | 200 | 332 | 26 |
| *Cercartetus sp.* cf. *C. concinnus* | | 2 | | | |
| **Total Phalangeroidea MNI** | | | 2 | | |
| *Peramelidae indet.* | 2 | 3 | 2 | 17 | |
| *Isoodon obesulus* | 2 | | | 18 | |
| *Perameles bougainville* | | 4 | 9 | | |
| **Total Peramelidae MNI** | 4 | 7 | 11 | 35 | 0 |
| *Macrotis lagotis* | 1 | | | | |
| **Total Thylacomyidae MNI** | 1 | 0 | 0 | 0 | 0 |
| *Bettongia indet.* | 1 | 3 | | | |
| *Bettongia penicillata* | 3 | 6 | 3 | 7 | |
| *Macropus eugenii* | 1 | 4 | 8 | | |
| **Total Macropodoidea MNI** | 5 | 13 | 11 | 7 | 0 |
| *Sminthopsis sp.* | | 5 | 1 | 3 | 1 |
| *Sminthopsis sp.* cf. S *hirtipes* | | 1 | 2 | | |
| *Sminthopsis psammophila* | | 1 | 1 | | |
| *Sminthopsis sp.* cf. *S. dolichura* | 6 | 1 | | | |
| *Parantechinus apicalis* | | | 1 | 1 | |
| *Phascogale tapoatafa* | | | | 1 | |
| *Dasyurus sp.* cf.. *D. geoffroii* | | | 1 | 1 | |
| *Thylacinus cynocephalus* | | | 1 | | |
| **Total Dasyuroidae MNI** | 0 | 13 | 8 | 6 | 1 |
| **Total N$^{o}$ of Species** | 6 | 13 | 16 | 10 | 3 |
| **TOTAL MNI** | **33** | **265** | **232** | **377** | **27** |

* Muridae Indet. MNI is based on individual insisors which often represents the total maximum murid MNI.

## Sedimentological Analysis

Sediment from each surveyed level of Black's Point sinkhole was petrographically analysed in thin section to determine differences in composition grain size and grain shape in attempt to identify the sediment's source of origin.

## Carbon Dating

All charcoal fragments were collected for each level to use in carbon dating. A series of five carbon dates were obtained for levels A, C, D, E and G from the Quaternary Dating Research Centre at the Australian National University (ANU). Several small fragments of charcoal were collected and added together for each level to make a sample large enough for dating.

# RESULTS

## Faunal Analysis

Table 1 presents the mammal fauna and the total number of species identified from each level of Black's Point sinkhole. It also includes the MNI calculated for each species, the MNI calculated for each genus and the total MNI for each level. The discovery of a single thylacine first upper right molar ($M^1/$) and two mandibles from the dibbler (*Parantechinus apicalis*) are of particular interest.

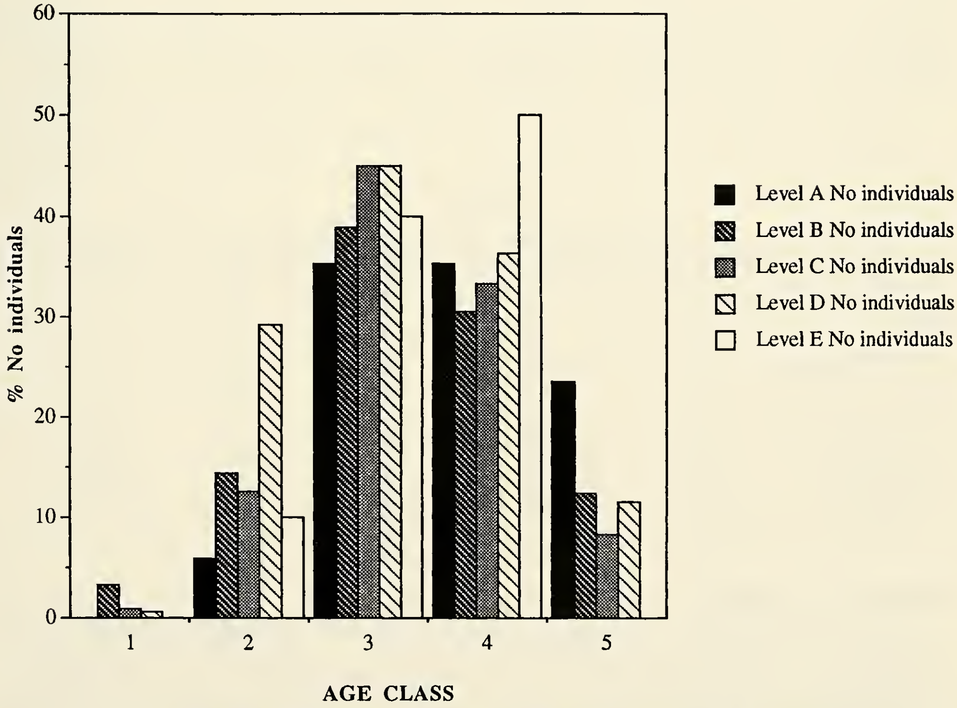


Figure 3. Small mammal age frequency distribution where category 1 = juvenile, 2 = subadult, 3= adult, 4 = old, and 5 = very old.

TABLE 2

The quantity (No) and relative abundances (Ri) of small mammal skeletal elements recovered from different levels of Black's Point sinkhole.

| Level | A | | B | | C | | D | | E | |
|---|---|---|---|---|---|---|---|---|---|---|
| Sample Size (x10kg) | 1 | | 4 | | 4 | | 4 | | 1 | |
| Skeletal Elements | Nº | Ri | Nº | Ri | Nº | Ri | No | Ri | Nº | Ri |
| Mandibles | 12 | 31.60 | 401 | 75.70 | 418 | 90.10 | 390 | 51.80 | 11 | 28.90 |
| Maxillae | 14 | 36.80 | 345 | 65.10 | 336 | 72.40 | 207 | 27.50 | 13 | 34.20 |
| Incisors | 27 | 35.50 | 312 | 29.40 | 315 | 33.90 | 1221 | 81.00 | 61 | 80.30 |
| Molars | 76 | 33.30 | 577 | 18.10 | 375 | 13.50 | 821 | 18.10 | 112 | 49.10 |
| Femora | 12 | 31.60 | 152 | 28.70 | 262 | 56.50 | 125 | 16.60 | 6 | 15.80 |
| Tibia | 16 | 42.10 | 93 | 17.50 | 251 | 54.10 | 166 | 22.00 | 34 | 89.50 |
| Pelvi | 24 | 63.20 | 134 | 25.30 | 194 | 41.80 | 92 | 12.20 | 8 | 21.10 |
| Calcanea | 12 | 31.60 | 19 | 3.40 | 13 | 2.80 | 41 | 5.40 | 11 | 28.90 |
| Astragali | 7 | 18.40 | 23 | 4.30 | 13 | 2.80 | 11 | 1.50 | 5 | 13.20 |
| Humeri | 7 | 18.40 | 148 | 27.90 | 250 | 46.30 | 168 | 22.30 | 12 | 31.60 |
| Radii | 5 | 13.20 | 8 | 1.50 | 26 | 5.60 | 10 | 1.30 | 2 | 5.30 |
| Ulnae | 16 | 42.10 | 91 | 17.20 | 68 | 14.70 | 110 | 14.60 | 5 | 13.20 |
| Scapulae | 14 | 36.80 | 97 | 18.30 | 36 | 7.80 | 28 | 3.70 | 2 | 5.30 |
| Ribs | 51 | 11.20 | 293 | 5.00 | 199 | 3.60 | 373 | 4.10 | 5 | 1.20 |
| Vertebrae | 154 | 20.30 | 258 | 2.40 | 102 | 1.10 | 82 | 0.50 | 51 | 2.00 |
| Mean Ri | | 31.07 | | 22.65 | | 29.80 | | 18.89 | | 27.97 |

TABLE 3

Indices indicating proportions of skeletal elements.

| Stratigraphic Level | A | B | C | D | E |
|---|---|---|---|---|---|
| *Index* | | | | | |
| % post crania/crania | 87.8 | 65.2 | 122.7 | 65.5 | 69.4 |
| %fem.+hum./man.+max | 73.1 | 40.2 | 67.9 | 45.4 | 75.0 |
| % tib.+rad./fem.+hum. | 110.5 | 47.0 | 55.1 | 68.1 | 194.4 |
| % isolated molars | 166.0 | 40.1 | 22.3 | 64.3 | 183.6 |
| % isolated incisors | 135 | 54.4 | 58.4 | 275.6 | 254.2 |

## Taphonomic Analysis

The results for the taphonomic analysis of Black's Point sinkhole fauna are shown in Tables 2–5 and Figs 2 and 3. Levels F, G and H were not included due to small yields and sample sizes. Mammal fossils appear most abundant in the upper levels but are common throughout the sinkhole strata. Level E was the lowest unit analysed and contains mostly isolated teeth and tibia (Table 2). The proportion of post-crania to crania is moderate (Table 3), while breakage for both cranial and post-cranial elements is high (Tables

4 and 5). The proportion of isolated teeth suggest a relative loss of jaws. No elements show the affects of digestive dissolution, polishing or rounding, but many show the effects of mild chemical weathering and some root dissolution.

Fossils appear better preserved in level D than level E, but proportions of post-crania to crania are very similar (Table 3). Mandibles and maxillae are relatively more abundant (Table 2) but the degree of both cranial and post-cranial breakage is similar (Table 4). The proportion of isolated molars is less than 100% suggesting a relative loss of teeth, but the proportion of isolated incisors is much greater than 100% suggesting a relative loss of jaws (Table 3).

TABLE 4

Type and extent of breakages in small mammal long bones extracted from different levels of Black's Point sinkhole.

| Stratigraphic Level | A | | B | | C | | D | | E | |
|---|---|---|---|---|---|---|---|---|---|---|
| *Breakage* | No. | % | No. | % | No. | % | No. | % | No. | % |
| Humeri | | | | | | | | | | |
| Complete | 1 | 14.3 | 81 | 54.6 | 131 | 52.4 | 19 | 14.1 | 0 | 0 |
| Proximal | 4 | 57.1 | 63 | 42.6 | 109 | 43.6 | 110 | 81.5 | 9 | 75 |
| Shaft | 1 | 14.3 | 2 | 1.4 | 6 | 2.4 | 5 | 3.7 | 3 | 25 |
| Distal | 1 | 14.3 | 2 | 1.4 | 4 | 1.6 | 1 | 0.7 | 0 | 0 |
| Ulnae | | | | | | | | | | |
| Complete | 2 | 12.5 | 19 | 20.9 | 10 | 14.7 | 1 | 0.9 | 0 | 0 |
| Proximal | 14 | 87.5 | 72 | 79.1 | 58 | 85.3 | 108 | 98.2 | 5 | 100 |
| Shaft | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0.9 | 0 | 0 |
| Distal | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Femora | | | | | | | | | | |
| Complete | 9 | 75 | 61 | 39.9 | 129 | 49.3 | 21 | 16.4 | 0 | 0 |
| Proximal | 3 | 25 | 82 | 53.6 | 124 | 47.3 | 100 | 78.1 | 5 | 83.3 |
| Shaft | 0 | 0 | 0 | 0 | 0 | 0 | 3 | 2.3 | 1 | 16.7 |
| Distal | 0 | 0 | 9 | 5.9 | 9 | 3.4 | 4 | 3.2 | 0 | 0 |
| Tibia | | | | | | | | | | |
| Complete | 5 | 31.25 | 24 | 15.7 | 37 | 14.7 | 10 | 6.0 | 0 | 0 |
| Proximal | 5 | 31.25 | 54 | 35.3 | 121 | 48.0 | 56 | 33.7 | 8 | 23.5 |
| Shaft | 5 | 31.25 | 27 | 17.7 | 53 | 21.0 | 72 | 43.4 | 25 | 73.5 |
| Distal | 1 | 6.25 | 48 | 31.3 | 41 | 16.3 | 28 | 16.9 | 1 | 3.0 |
| Radii | | | | | | | | | | |
| Complete | 5 | 100 | 8 | 100 | 26 | 83.9 | 10 | 55.6 | 2 | 100 |
| Proximal | 0 | 0 | 0 | 0 | 1 | 3.2 | 3 | 16.7 | 0 | 0 |
| Shaft | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Distal | 0 | 0 | 0 | 0 | 4 | 12.9 | 5 | 27.8 | 0 | 0 |

TABLE 5

Small mammal Cranial Element preservation for different level of Black's Point sinkhole.

| Stratigraphic Level | A | B | C | D | E |
|---|---|---|---|---|---|
| *Skull Breakage:* | | | | | |
| % complete | 0 | 0 | 0 | 0 | 0 |
| % maxillae with zygoma. | 3.6 | 66.4 | 54.7 | 38.8 | 23.1 |
| % maxilla molar loss: | 27.4 | 34.8 | 45.3 | 36.9 | 42.3 |
| % maxilla incisor loss | 85.7 | 99.7 | 100 | 100 | 100 |
| *Mandible Breakage:* | | | | | |
| % complete | 8.3 | 0 | 0.3 | 0 | 0 |
| % inferior border broken | 58.3 | 38.9 | 21.4 | 54.1 | 100 |
| % mandible molar loss: | 33.3 | 32.8 | 31.8 | 35.0 | 42.4 |
| % mandible incisor loss | 66.7 | 79.8 | 48.8 | 60.5 | 100 |

Skeletal element relative abundance is higher for level C than for levels D and E with mandibles showing greater than 90% relative abundance and many other elements showing greater than 40% relative abundance (Table 2). The proportion of post-cranial to cranial elements is significantly higher in level C than levels D and E, but other indices of skeletal element proportions are comparable. The proportion of isolated molars and incisors suggests a relative loss of teeth (Table 3). The degree of breakage is lower in level C than in levels D and E (Tables 4 and 5).

The fossils of level B are well preserved and the proportion of isolated molars and incisors is less than 100% suggesting a relative loss of teeth. The proportion of post-cranial to cranial elements is lower than obtained for level C, but other indices of proximal and distal post-cranial elements are very similar (Table 3). The degree of breakage is comparable to that seen in level C (Table 4 and 5).

The fossils of level A, the uppermost level analysed, show high post depositional weathering and high levels of breakage (Tables 4 and 5). The proportions of isolated molars and incisors are both greater than 100% indicating a relative loss of jaws. This is supported by the degree of mandible and maxillae breakage.

The age frequency distribution attained for all levels (Fig. 3) is slightly skewed toward aged individuals but generally reflects those age group proportions found in a living community.

## Sediments and Stratigraphy

Two major stratigraphic units occur in Black's Point sinkhole. The lower unit which extends from the top of Level D to the floor consists of thick red-brown amorphous clays. No evidence of lamination or reworking was observed. The upper unit which extended from the bottom of Level C to above Level A consists of chocolate brown silty clay which again showed no sedimentary structure. The two units are separated by a very sharp contact.

When petrographically analysed level E was observed to be composed of 58% clay minerals, 32% gypsum, 7% micro-crystalline calcite (micrite) and 3% opaques (charcoal). Non-clay sized grains were fine, sub angular and moderately to poorly sorted. Level D contained 55% clay minerals, 35% gypsum, 5% micrite and 5% opaques (charcoal). Non-clay sized grains were fine, sub-rounded and moderately to well sorted. Some 2–3mm clay nodules and calcite gravel were also observed, as were fossil root casts.

Petrographic analysis showed that level C is composed of 50% clay minerals, 35% gypsum, 5% micrite and 10% opaques (charcoal). Sand sized grains are predominantly fine and sub-rounded to rounded. Some coarse clay nodules and calcite gravel also occur. The sand sized sediments of level B are fine grained, rounded to sub-rounded and moderately sorted. They are composed of 40% clay minerals, 40% gypsum, 15% micrite and 5% opaques (charcoal). Sediments from level A consist of 50% clay minerals, 35% gypsum, 10% micro-crystalline calcite (micrite) and 5% opaques (charcoal). Sand sized grains are fine and moderately sorted. Gypsum grains appear sub-angular to sub-rounded, while all other grains appear well rounded. In all levels gypsum grains are fragmentary suggesting that they have been transported into the sinkhole and are not authigenic.

TABLE 6

Summary of Results obtained for Radiocarbon Dating of Charcoal collected from different levels of Black's Point sinkhole.

| Code Number | Date | Level of Origin |
|---|---|---|
| ANU-9893 | 1160±60 BP | A |
| ANU-9892 | 3030±60 BP | C |
| ANU-9891 | 4440±70 BP | D |
| ANU-9890 | 4040±140 BP | E |
| ANU-9889 | 4300±290 BP | G |

## Dating

The radiocarbon dates obtained from ANU can be seen in Table 6. It shows a partial succession in age from the youngest at the highest stratigraphic level dated, to the oldest in a lower stratigraphic level, but the three lower most dates obtained are not in sequence. Carbon dates obtained for level D and level G are not significantly different, but the age of level D is significantly older than level E. This suggests that the lower strata may have been reworked, although there are no supporting sedimentary structures. Alternatively, contamination of charcoal used to obtain the two lower-most dates with younger material may have occurred. Because several charcoal fragments were used to obtain a workable sample size, spurious grains that originated from higher levels may have been included. Charcoal samples from the lower strata are especially prone to this as their sample sizes were very small.

Contaminated charcoal samples would be subject to an averaging effect that would significantly alter the age estimate obtained. Only a small quantity of 'young' charcoal would be needed to decrease an age estimate obtained from a contaminated sample of 'old' charcoal. Radiocarbon dates indicate that the majority of sediments and fossils sampled from Black's Point sinkhole have not been reworked. It is therefore assumed that any change in fauna, or any disharmonious species pairs do not result from the mixing of non-contemporaneous sediments or time averaging.

Charcoal associated with the thylacine tooth recovered from level C was dated at 3030±60BP suggesting the youngest date of a mainland thylacine.

## DISCUSSION

### Accumulation of Black's Point sinkhole fauna

The morphology of Black's Point sinkhole renders it unsuitable for den use by either mammalian or avian predators. This is supported by the lack of predator tooth marks, digestive dissolution, rounding and/or polishing of fossils. Indices used to compare proportions of skeletal elements (Table 3) show no clear preference in the destruction of cranial elements compared with post-cranial elements, or proximal post-cranial elements compared with distal post-cranial elements. This indicates that the deposit was not accumulated by a mammalian or avian predator, both of which preferentially digest and/or break proportions of their prey skeletons (Andrews and Nesbit Evans 1983, Andrews 1990). The age frequency distribution (Fig. 3) obtained for all levels suggests an accumulative or chance collection mode rather than a selective one expected of predators.

Elements from all three Voorhies groups (Voorhies 1969) are well represented on all levels and no evidence of abrasive wear was observed. This suggests that fluvial transport was not the primary mode of fossil collection.

As can be seen in Table 1 the size and species of animals present for all levels is highly diverse, ranging from large animals (> 20kg) to very small animals (< 20g) (Strahan 1988). Many of the species listed in Table 1 are still thought to inhabit Eyre Peninsula, but it is of particular interest to note the collection of thylacine and dibbler specimens. The deposit was initially considered too recent to collect megafauna specimens, while the dibbler is a threatened species that has not previously been recorded from Eyre Peninsula fossil deposits, but is common in Western Australia.

Some of the species present are nocturnal while others are diurnal. Some are predators while others are herbivores and still others are omnivores. The vast majority of species present are terrestrial ground dwellers with only a few scansorial and arboreal species present in small numbers.

This indicates a collection mode that does not significantly bias for body size, feeding habits or activity schedules, but does bias against species' habitual dwelling areas. The evidence obtained suggests that the primary mode of collection for the fossils excavated from Black's Point sinkhole was a pitfall trap.

In a pifall trap assemblage one might expect to find more articulated or at least associated elements within the undisturbed sediment excavated. The lack of associated skeletons suggests that a degree of secondary taphonomic biasing has occurred. This is believed to be the result of minor hydraulic sorting and compaction. In the winter months after soil saturation has occurred, runoff water cascades into the sinkhole, eroding and transporting the surface sediment a short distance towards the sides of the sinkhole before percolating away. Element disassociation might also result from the activities of trapped animals before their death. The moderate to high levels of chemical weathering observed on all specimens suggests that this water was mildly acidic. This weathering, combined with the occasional root mark and frequent discrete layers of roof fall material (Fig. 2) show that the sinkhole entrance was becoming larger with time.

### Palaeoenvironmental Interpretation

Pitfall traps are extremely useful for interpreting past environmental conditions because unlike other collection modes such as predators or fluviatile systems they are geographically stationary. One can therefore assume that compositional variations will be the result of changing environmental conditions rather than changing collection agents. Assuming uniformitarian principles apply, a record of environmental conditions may be obtained by examining the preferred conditions of animals that once lived proximal to, and were trapped in a pitfall. Through analysing the fossils from each level of Black's Point sinkhole strata, a story of past environmental conditions and changes begins to emerge.

TABLE 7

Preferred habitats of mammals from different levels in Black's Point Sinkhole, Venus Bay.

| Stratigraphic Level | A | B | C | D | E |
|---|---|---|---|---|---|
| Sample Size (x10kg) | 1 | 4 | 4 | 4 | 1 |
| **Ubiquitous species** | | | | | |
| *Thylacinus cynocephalus* | | | ✓ | | |
| **Percentage ubiquitous species** | **0** | **0** | **7** | **0** | **0** |
| **Forest species** | | | | | |
| *Rattus fuscipes* | ✓ | ✓ | ✓ | ✓ | ✓ |
| *Pseudomys occidentalis* | | | ✓ | | |
| *Bettongia penicillata* | ✓ | ✓ | ✓ | ✓ | |
| *Macropus eugenii* | ✓ | ✓ | ✓ | | |
| *Cercartetus sp.* cf. *C. concinnus* | ✓ | | | | |
| *Isoodon obesulus* | ✓ | | | ✓ | |
| *Phascogale tapoatafa* | | | | ✓ | |
| **Percentage forest species** | **66.7** | **30.8** | **28.6** | **40** | **66.6** |
| **Heathland species** | | | | | |
| *Pseudomys shortridgei* | | ✓ | ✓ | ✓ | |
| *Parantechinus apicalis* | | | ✓ | ✓ | |
| **Percentage heathland species** | **0** | **7.8** | **12.5** | **20** | **0** |
| **Desert species** | | | | | |
| *Pseudomys australis* | | ✓ | ✓ | ✓ | |
| *Pseudomys gouldii* | | ✓ | ✓ | ✓ | |
| *Pseudomys bolami* | | ✓ | | | |
| *Notomys sp.* cf.. *N. mitchelli* | | ✓ | ✓ | | |
| *Sminthopsis sp.* cf. S *hirtipes* | | ✓ | ✓ | | |
| *Perameles bougainville* | | ✓ | ✓ | | |
| *Macrotis lagotis* | ✓ | | | | |
| *Sminthopsis psammophila* | | ✓ | ✓ | | |
| *Sminthopsis sp.* cf. *S. dolichura* | ✓ | ✓ | | ✓ | |
| *Dasyurus sp.* cf.. *D. geoffroii* | | | ✓ | ✓ | |
| **Percentage Desert species** | **16.7** | **61.5** | **50** | **30** | **33.3** |

The fossil faunas and sediments of levels D and E are from the same stratigraphic unit and are similar in preservation and breakage patterns, thus suggesting that they were collected under very similar environmental conditions. Level E lacks many of the species recorded in level D, but this is considered a function of level E's sample size (see Table 1). *R. fuscipes* and *P. tapoatafa* both commonly occupy forests. *P. tapoatafa* is arboreal, suggesting the presence of tall trees. *P. shortridgei* populates heath-land, while *I. obesulus* is known to occur in both forests and heathland, and like *B. penicillata*, prefers areas with a low shrubby ground cover or understorey. *P. gouldii* inhabits hummocky grassland, while *P. australis* prefers rocky desert and *D. geoffroii* is considered ubiquitous (Walton 1988) (Table 7).

Several allopatric species pairs occur in level D (Appendix I). Several tropical to temperate heath and forest dwelling species coexisted with rocky desert and hummock grassland species, suggesting the environment was more equitable than at present and that a greater range of niches were available (Lundelius 1983). The assimilation of these different ecologies indicate an environment composed of broken temperate forest-woodland with a low shrubby understorey, interspersed with grassland-heathland and rocky or alluvial surfaced patches, that requires a higher level of precipitation than is available under present conditions. The high proportion of detrital gypsum present in the sediments of these levels suggests that an evaporitic setting also existed nearby. This may have taken the form of a sabkha mudflat or a playa lake from which gypsum was eroded by the wind.

The fauna identified in levels C and B indicate a change in palaeoenvironmental conditions. *D. geoffroii* and *T. cynocephalus* are considered ubiquitous, and are therefore of little interpretive use, but *R. fuscipes*, *N. mitchelli* and *P. occidentalis* are known to mainly populate temperate forests and shrublands. *M. eugenii*, *S. dolichura* and *P. bougainville* have been seen to inhabit similar environments, but are also known to occur in heathlands where *P. shortridgei* and *P. apicalis* both predominate. Walton (1988) reports that *P. bougainville* prefers to hunt on stony ridges and sandhills, or plains behind beaches. *P. australis* occupies a temperate rocky desert while *P. gouldii* inhabits hummocky grasslands. *S. hirtipes* and *S. psammophila* are also known to inhabit grasslands, but are common to sandhills and plains. *S. hirtipes* has also been recorded in woodlands and on alluvial plains and is adapted for locomotion on sandy surfaces (Walton 1988) (Table 7). These species suggest a more arid palaeoenvironmental setting. This is supported by the sharp change in clay mineral type from the gypsiferous red-brown clays to the gypsiferous chocolate brown clays. The change indicates a drying and erosion of nearby mudflats previously indicated by detrital gypsum only. Several pre-European disharmonious species pairs have again been observed at this stratigraphic level (Appendix I). Allopatric species pairs suggest a more equitable environment than exists at present (Lundelius 1983). Temperate heath and forest dwelling species are seen to have coexisted with several sandy and rocky desert dwelling species, hummock grassland dwelling species and open heath dwelling species. The faunal assemblage deduced from level C suggests a more arid variable environment dominated by open woodlands that lack an under storey and are interspersed with grassland-heathland and rocky or alluvial surfaced patches.

The faunal composition of level B is similar to the previous level with the addition of *P. bolami*, an arid zone species, and the loss of *P. occidentalis*, *P. apicalis* , *D. geoffroii* and *T. cynocephalus*, scrubland/heathland and ubiquitous species (Walton 1988). These species have only been recorded in small numbers so their presence or absence may be a chance event. Several allopatric species pairs similar to level C exist on level B (Appendix I). The addition of more arid species supports the hypothesis that the environment became drier, and that forests become more open, losing its understorey while grassland, heathland and sandy or alluvial surface patches become more prominent.

The fauna of level A suggests another change in palaeoenvironmental conditions (Table 7). The continued presence of *R. fuscipes*, *B. penicillata* and *M. eugenii* suggests a patchy temperate coastal forest still exists. The reappearance of *I. obesulus* may be interpreted as a shift in the understorey vegetation from the open community preferred by *P. bougainville* to a more closed community with greater ground cover. The presence of a single *Macrotis lagotis* individual suggests that a sandy or alluvial plain may still exist nearby. No disharmonious pairs exist at this stratigraphic level suggesting the environment may be approaching those characteristics seen in the present. The faunal composition for this level suggests a shift towards a more dense vegetation community as was previously inferred for Level D and E.

## CONCLUSIONS

The evidence compiled from the study of the sedimentology and palaeontology of Black's Point sinkhole has enabled a palaeoenvironmental reconstruction spanning the last 4500 years. It indicates three major periods of accumulation. Prior to 4000BP the fauna present suggest that the climate for the Venus Bay region was wetter, more temperate and less variable than at present. The vegetation was dominated by forest-woodlands with a thick understorey, while a mudflat area existed within the bay. Around 4000BP evidence suggests that effective precipitation or water availability decreased and environmental conditions became drier and more variable. This resulted in a more open woodland with a decreased understorey density, and drying and erosion of mudflats. Around 1000BP it appears the region became slightly wetter and environmental conditions became less variable. This would allow forests to recover slightly, becoming more closed with a thicker understorey.

Evidence in the literature relating to sites across Australia lends support the palaeoenvironmental synthesis proposed from the Black's Point sinkhole data. Several authors (Bowler 1981; Kershaw 1983; Bowler and Wasson 1984; Chivas et al. 1985; COHMAP 1988; Shulmeister 1992; Chivas et al. 1993; Barnett 1994; Williams 1994) report wetter periods from 7500–4500BP for the Australian region, with drier conditions occurring between 3500–2000BP, and a climatic recovery taking place 2000–1000BP.

The community composition of the Black's Point sinkhole fauna appears to be a mixture of western and eastern species, but it most closely resembles the Nullarbor Plain and associated coastal fauna deduced by Baynes (1987). This implies a greater range for the Nullarbor coastal community, extending it to the eastern side of the Great Australian Bight.

Taphonomic analysis indicates that Black's Point sinkhole has operated as a pitfall trap during the Late Holocene. The fossil fauna identified in the sinkhole is considered a good representation of the terrestrial palaeocommunity that populated the Venus Bay coastal regions prior to European settlement.

The Black's Point sinkhole fauna includes the youngest occurring mainland specimen of *Thylacinus cynocephalus*. It suggests that Thylacine populations that once ranged across southern Australia began to retreat eastward approximately 3000BP before becoming extinct on the mainland and later in Tasmania. An Accelerator Mass Spectrometer carbon date from the tooth enamel would confirm its age.

Further palaeoenvironmental information could be obtained from the study of pollen and land snail shells in the Black's Point sinkhole strata. This could test and/or improve the resolution of the palaeoenvironmental interpretation that has been constructed from the palaeontological and sedimentological data collected. More fossil sites should also be sought out and investigated in the Eyre Peninsula region to better determine the regional pre-European faunal composition. This will be of use to DENR in their attempts to re-establish at least part of Eyre Peninsula's pre-European fauna within the Venus Bay Conservation Park.

## ACKNOWLEDGMENTS

I would like to firstly acknowledge the aid of Prof R. T. Wells, Prof C. C. von der Borch and Dr M. J. Smith, all of whom provided critical comment, encouragement, and advise during the work on this project. I also thank Mr. D. Armstrong for his aid in accessing and excavating the site, and Mr. G. Medlin who introduced me to the study, and gave freely of his time, aiding with excavation, advice, identification of dasyurid species, and arranged funds, supplied by the Department of Environment and Natural Resources 'Wildlife Research Fund' for the carbon dating of five charcoal samples.

## REFERENCES

Andrews, P. (1990). 'Owls, Caves and Fossils'. University of Chicago Press, Chicago.

Andrews, P. and Nesbit Evans, E. M. (1983). Small mammal bone accumulations produced by mammalian carnivores. *Paleobiology* **9**, 289–307.

Baird, R. T. (1991). The taphonomy of late Quaternary cave localities yielding vertebrate remains in Australia. In Vickers-Rich, P., Monaghan, J. M., Baird, R. F. and Rich, T. H. (Eds.). (1991). 'Vertebrate Palaeontology of Australasia'. Monash University Publication Committee, Melbourne. pp 267–310.

Barnett, E. J. (1994). A Holocene paleoenvironmental history of Lake Alexandrina, South Australia. *Journal of Paleolimnology* **12**: 259–268.

Baynes, A. (1987). The original mammal fauna of the Nullarbor and southern peripheral regions: evidence from skeletal remains in superficial cave deposits. In McKenzie, N. L. and Robinson, A. C. (*Eds.*) (1987). 'A biological survey of the Nullarbor Region South and Western Australia in 1984'. South Australian Department of Environment and Planning, Adelaide. pp 139–152.

Behrensmeyer, A. K. (1978). Taphonomic and ecological information from bone weathering. *Paleobiology* **4**, 150–162.

Behrensmeyer, A. K. (1982). Time resolution in fluvial vertebrate assemblages. *Paleobiology* **8**, 211–227.

Behrensmeyer, A. K. (1991). Terrestrial vertebrate accumulations. In Allison, P. A. and Briggs, D. E. G. (Eds.). (1991). 'Taphonomy. Releasing the data locked in the fossil record'. Plenium Press, New York. pp 291–335.

Behrensmeyer, A. K. (1993). The bones of Amboseli. *Research and Exploration* 402–421.

Behrensmeyer, A. K. and Hill, A. P. (1980). 'Fossils in the making. Vertebrate Taphonomy and Paleoecology'. The University of Chicago Press, Chicago.

Behrensmeyer, A. K. and Kidwell, S. M. (1985). Taphonomy's contribution to paleobiology. *Paleobiology* **11**, 105–119.

Behrensmeyer, A. K., Western, D. and Dechant Boaz, D. E. (1979). New perspectives in vertebrate paleoecology from a recent bone assemblage. *Paleobiology* **5**, 12–21.

Bowler, J. M. (1981). Australian salt lakes. *Hydrobiologia* **82**: 431–444.

Bowler, J. M. and Wasson, R. J. (1984). Glacial age environments of inland Australia. In Vogel, J. C. (Ed.) (1984). 'Late Cainozoic palaeoclimates of the Southern Hemisphere'. Balkema, Rotterdam, pp 183–208.

Chivas, A. R., De Deckker, P and Shelly, J. M. G. (1985). Strontium content of ostracods indicates lacustrine palaeosalinity. *Nature* **316**: 251–253.

Chivas, A. R., De Deckker, P., Cali, J. A., Chapman, A., Kiss, E. and Shelly, J. M. G. (1993). Coupled stable-isotope and trace-element measurements of lacustrine carbonates as palaeoclimatic indicators. In Swart, P. K., Lohmann, K. C., McKenzie, J. and Savin, S. (Eds.). (1993). Climate change in continental isotopic records. *American Geophysics Union Geophysical Monograph* **78**: 113–121.

COHMAP (1988). Climatic changes of the last 18, 000 years: observations and model simulations. *Science* **241**: 1043–1052.

Douglas, A. M., Kendrick, G. W. and Merrilees, D. (1966). A fossil bone deposit near Perth, Western Australia, interpreted as a carnivore's den after feeding tests on living Sarcophilus (Marsupialia, Dasyuridae). *Journal of the Royal Society of Western Australia* **49**, 88–90.

Hoffman, R. (1988). The contribution of raptorial birds to patterning in small mammal assemblages. *Paleobiology* **14**, 81–90.

Kershaw, A. P. (1983). The vegetation record of northeastern Australia 7±2 KA. In Chappell, J. and Grindrod, A. (Eds.). (1983). Proceedings First CLIMANZ, Feb. 1981. pp 100–101.

King, F. B. and Graham, R. W. (1981). Effects of ecological and paleoecological patterns on subsistence and paleoenvironmental reconstructions. *American Antiquity* 128–142.

Lundelius, E. (1983). Climatic implications of Late Pleistocene and Holocene faunal associations in Australia. *Alcheringa* **7**, 125–149.

Lyman, R. L. (1994a).Relative abundances of skeletal specimens and taphonomic analysis of vertebrate remains. *Palaios* **9**, 288–298.

Lyman, R. L. (1994b). 'Vertebrate Taphonomy'. Cambridge University Press, Great Britain.

Peterson, C. H. (1977). The palaeoecological significance of undetected short term temporal variability. *Journal of Palaeontology* **51**, 976–981.

Shulmeister, J. (1992). A Holocene pollen record from lowland tropical Australia. *The Holocene.* **2** (2): 107–116.

Simms, M. J. (1994). Emplacement and preservation of vertebrates in caves and fissures. *Zoological Journal of the Linnean Society* **112**, 261–283.

Strahan, R. (1988). 'The Australian Museum complete book of Australian mammals'. Angus and Robertson Publishers, New South Wales.

Voorhies, M. R. (1969). Taphonomy and population dynamics of an early Pliocene vertebrate fauna, Knox County, Nebraska. *Contributions to Geology Specific Paper* No 1.

Wakefield, N. A. (1982). Palaeoecology of mammals from some Australian caves, *Proceedings of the Royal Society of Victoria* **85**, 1–29.

Walton, W. D. (1988). 'Zoological catalogue of Australia. Vol. 5: Mammalia'. Brian Prior Anderson Pty. Ltd. Burwood, Victoria.

Williams, M. A. J. (1994). Some implications of past climatic changes in Australia. *Transactions of the Royal Society of South Australia* **118** (1): 17–25.

## APPENDIX I

Allopatric species present on different levels in Black's Point Sinkhole, Venus Bay

| Species Present | Allopatric pairs (Pre-Europeans) |
|---|---|
| **(1)** *Rattus fuscipes* | 5 and 14 |
| **(2)** *Pseudomys australis* | 3, 5, 6, 17 and 9 |
| **(3)** *P. shortridgei* | 2, 5, 6, 14 and 15 |
| **(4)** *P. gouldii* | 5 and 17 |
| **(5)** *P. bolami* | 1, 2, 3, 4 and 7 |
| **(6)** *P. occidentalis* | 2, 3, 14 and 15 |
| **(7)** *Notomys mitchelli* | 5 and14 |
| **(8)** *Cercartetus concinnus* | |
| **(9)** *Isoodon obesulus* | 2 and17 |
| **(10)** *Perameles bougainville* | |
| **(11)** *Macrotis lagotis* | |
| **(12)** *Bettongia penicillata* | |
| **(13)** *Macropus eugenii* | 14 |
| **(14)** *Sminthopsis hirtipes* | 1, 3, 6, 7 and 13 |
| **(15)** *S. psammophila* | 3 and 6 |
| **(16)** *S. dolichura* | |
| **(17)** *Parantechinus apicalis* | 2, 4 and 9 |
| **(18)** *Phascogale tapoatafa* | |
| **(19)** *Dasyurus geoffroii* | |
| **(20)** *Thylacinus cynocephalus* | |

# Some Smaller Macropod Fossils of South Australia

J.A. McNamara
(Communicated by M.L. Augee)

South Australian Museum, North Terrace Adelaide SA 5000

McNamara, J.A. (1997). Some smaller macropod fossils of South Australia. *Proceedings of the Linnean Society of New South Wales* **117**: 97-106

Bones of *Lagostrophus fasciatus*, *Lagorchestes asomatus*, *L. leporides*, *Onychogalea lunata*, *O. fraenta*, are reported. Old records of *Caloprymnus campestris* and *Lagorchestes conspicillatus* are rejected. Juvenile material of *L. asomatus* is described and *Bettongia pusilla* sp. nov. is described from the Nullarbor.

Manuscript received 19 April 1996, accepted for publication 24 July 1996

KEYWORDS: *Lagostrophus*, *Lagorchestes asomatus*, *Lagorchestes*, *Onychogalea*, *Caloprymnus*, *Bettongia pusilla*.

## INTRODUCTION

The bulk of the South Australian Museum's fossil collections are mammal bones of late Pleistocene to Holocene age. Since 1988 systematic sorting and data collation of these vertebrate fossils has yielded interesting observations. The new information generated relates to, past distributions of extant or recently extinct species, new material of rare forms and some new forms that have been brought to light, and some of it is reported here.

Sound determinations of smaller macropod taxa appear difficult but repay the effort. *Lagostrophus fasciatus*, more readily associated with southern Western Australia, may be extended with specimens from near Ceduna, the River Murray and the South East. The modern extinction of *Lagorchestes* species must be anthropogenic but may well involve synergistic stressors. For *Lagorchestes asomatus* the second skull known, first juvenile material, first South Australian record and a huge extension of range were discovered among material from the enigmatic, ?late Pleistocene Mairs Cave deposit of the Flinders Ranges. The recently exterminated *Lagorchestes leporides*, although poorly known as a living species, is present in Pleistocene and Holocene deposits in the South East, River Murray, Yorke Peninsula and Flinders Ranges. Some earlier determinations of *Lagorchestes conspicillatus* appear to be in error. *Onychogalea lunata* is recorded from the Nullarbor, Flinders Ranges and Yorke Peninsula. *Onychogalea fraenata* may now be recorded from Kangaroo Island in an apparently Holocene assemblage of mammals including *Lasiorhinus latifrons*.

*Bettongia pusilla* sp. nov. is described from material of Koonalda and Weekes Caves, Nullarbor Plain. It appears to be the taxon, misidentified as *Caloprymnus campestris*, sensu Lundelius and Turnbull and known informally as 'Thompson's unnamed potoroid'.

## MATERIALS AND METHODS

All material referred to is part of the fossil collections held by the South Australian Museum, wherein all registered specimens bear numbers with the prefix P. or part of the mammal collections where the prefix M is used. Teeth are numbered according to my whim, favouring a system in which adult cheek teeth of macropods are, P3 M1, M2, M3, M4, with P2 and dP3 shed earlier in life.

All measurements are in millimetres. All localities are within South Australia, unless otherwise stated. Published measurements of Finlayson's holotype of *Lagorchestes asomatus* were checked against the specimen so that the fossil material could be measured in a comparable manner.

## SYSTEMATICS

### *Family MACROPODIDAE Gray, 1821*

***Bettongia pusilla*** sp.nov. (Fig. 1) = *Caloprymnus campestris*, sensu Lundelius and Turnbull, 1984, non (Gould, 1843)

Holotype

P35450 right dentary, juvenile with $P_2$, $dP_3$, $M_1$ and $M_2$, lacking $M_3$, $M_4$ and $I_1$, top of coronoid process and tip of the angular process.

Type Locality

Koonalda Cave, Nullarbor Plain, South Australia, specifically, spit 6 of trench A of the Gallus site (see Wright 1971).

Age

Holocene from faunal association, although published dates suggest the deposit may be near 20,000 years old (Thorne 1971).

Etymology

From the latin referring to its small size.

Referred Specimens

Koonalda Cave, Nullarbor Plain: P35446, right maxilla with $P^2$, $dP^3$, $M^1$ and $M^2$; P35447 part left dentary with $M_2$ and $M_3$; P35448, right dentary with $I_1$, $P_3$ in crypt and $M_2$ unerupted; P35449, left dentary with $I_1$, and $M_2$; P35451 right dentary with $I_1$, $P_2$ and $dP_3$.
Weekes Cave, Nullarbor Plain: P35442, left dentary fragment with $M_3$.
Old Homestead Cave, Nullarbor Plain, Western Australia: P35443 part left dentary with $P_3$ loose, $M_1$, $M_2$, $M_3$ and $M_4$; P35444, part left dentary with no teeth; P35445, right $I_1$.

Diagnosis

A small bettong with the dentary more lightly built and teeth smaller. The molars are less bulbous, more straight sided, with the crowns proportionately higher with more loph-like development than the living species of *Bettongia*. $P_2$ has fewer (3) cuspules and associated ridgelets, between the anterior and posterior cusps, than *B. penicillata, B. gaimardi* and *B. lesueur.* The condyle is clavate in dorsal aspect, but sub-ovoid in *Caloprymnus* and more or less T-shaped in *Hypsiprymnodon, Bettongia, Aepyprymnus*, and *Potorous*. It differs from *Caloprymnus* in being less robust, and in having, the ramus less markedly bowed ventrally, the angular process bent inward more markedly, the molars smaller and less bulbous, $P_2$ finer with three cuspules and ridgelets rather than just one. *B. pusilla* compares with *Hypsiprymnodon* in dentary size but its, premolars are not flared outward, diastema is shorter, ramus less bowed ventrally and it lacks the distinct hip on the posterior margin of the masseteric fossa. While it resembles *Potorous platyops* in jaw size and tooth size, it

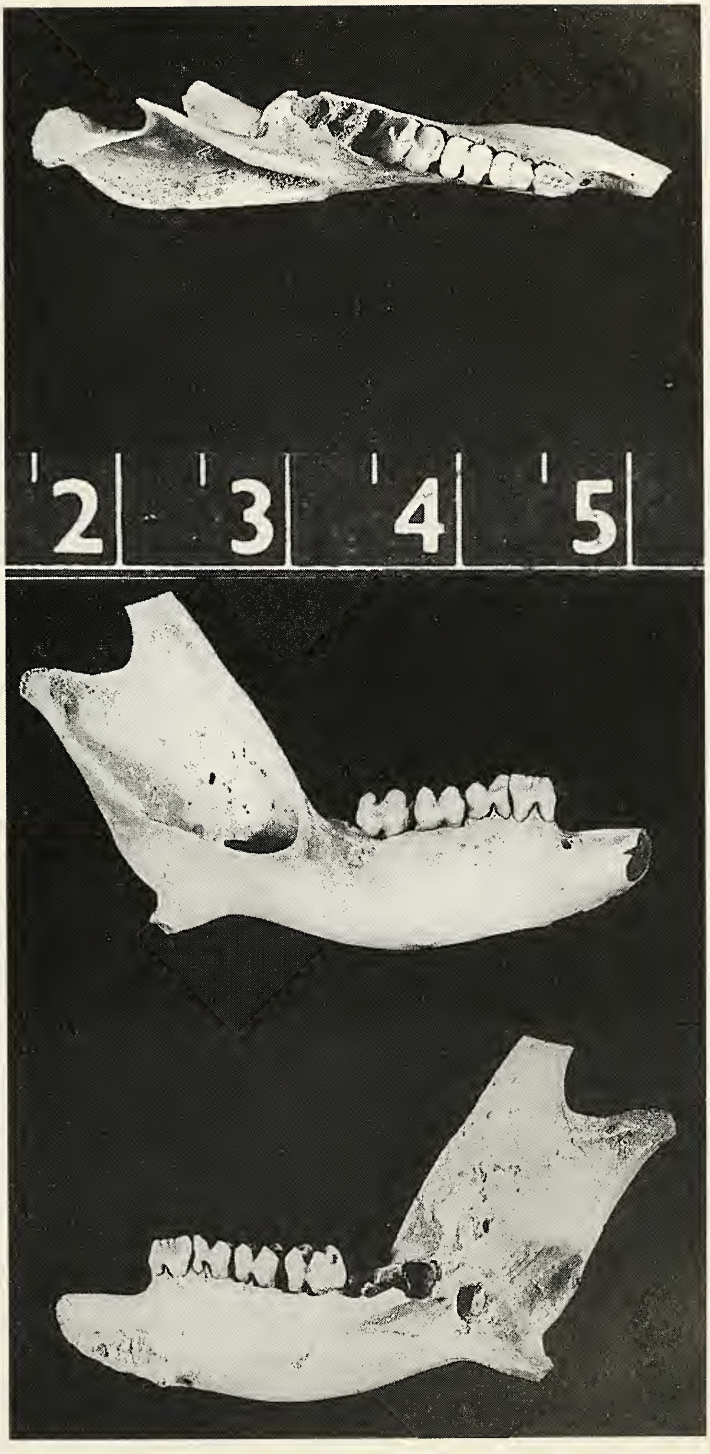


Figure 1. *Bettongia pusilla* sp. nov., holotype dentary, P35450, in dorsal, lateral and medial view, scale = 1 cm.

does not have the dentary form, with ascending ramus swept back at a low angle, the low-crowned molars, simpler premolar and primitive $I_1$ enamel pattern of the potoroo.

Description

The dentary (Fig. 1), 34.2 mm long, is lightly built with a short diastema of 4.6 mm and a depth under $M_1$ of 6.4 mm. In lateral aspect the horizontal ramus appears straight and forms an angle of 60°(with the ascending ramus. The line of the ventral margin bows downward to its lowest point below the point between $M_1$ and $M_2$. This even curve is interrupted by a slight eminence at the posterior end of the symphysis. The highest, most concave portion of the curve is below the masseteric foramen and just before the angular process which curves downward, inward and backward (to a point below the condyle in P35451). The posterior margin of the masseteric fossa is produced laterally only slightly to form a low hip before rising , in a near parallel of the anterior margin, to the condyle which is clavate in dorsal view. The coronoid process is swept back (to a point in P35451). The teeth have lengths and maximum widths of: $P_2$, L2.42, W1.80; $dP_3$, L2.41, W1.87; $M_1$, L2.80, W2.38; $M_2$, L3.24, W2.57. $P_2$ is a small tooth convex labially and concave lingually with a single crest formed by anterior and posterior cusps with 3 interposed cuspules and their associated ridgelets. The deciduous $dP_3$ is similarly small with a blade-like trigonid and loph-like talonid. $M_1$ is a little smaller than $M_2$ but both have similar form with the crown tops nearly as broad as their bases, their four cusps forming distinct protolophid and hypolophid. The type specimen has the alveoli of the remaining molars indicating an $M_3$ similar to $M_2$ and an $M_4$ which is smaller with a distinctly narrower hypolophid (and these may be seen as such in P35443). $I_1$ is not retained in the type but the alveolus indicates a smaller more slender version of the tooth seen in other bettongs. This tooth removed from juvenile dentary, P35448, has enamel on the lateral and lower surfaces and extending well down toward the open root. It does not extend as a ridge back along the dorsal lateral edge as in *Potorous*. The worn $I_1$, P35445, shows a remarkable extension of enamel down along the ventral edge to the root tip which is not closed, indicating an extreme hypsodont condition. I note that this tooth is a good match for the exposed alveolus of jaw fragment, P35443, allowing that they are from opposite sides of the animal.

Remarks

I am satisfied that the taxon described and figured well by Lundelius and Turnbull (1984) under the name *Caloprymnus campestris* is this taxon and note that they found 'no overlap in any measurement' (Lundelius and Turnbull 1984: 29) between their sample from Madura Cave and those quoted by other authorities. Their extensive descriptive work may be read in conjunction with this formal description of *B.pusilla*.

The name *Calopymnus campestris* should be removed from the mammalian record of the Nullarbor region until verifiable evidence is produced. Tate (1879) listed *Bettongia campestris* with a presumed native name of weelba, as a common species while he did not list *Bettognia lesueur*, which was perhaps more likely. Finlayson (1932:150) provides some evidence that 'Weelba' does not support Tate's claim. In this context three old specimens, M1705, M1706, M1710, all registered in 1922 with locality given only as SA and no collector named, are now correctly identified as *B. lesueur*, but each is branded *B. campestris*, in pencil, across the top of the skull. These indicate the possibility of early misidentification.

Lundelius (1963) lists *C. campetris* from Webb's and Snake Pit Caves but particular specimens are not identified. Archer (1974) lists *C.campestris* in the fauna of the Hampton Tableland but does not allow verification by specifying the material in question. My own brief inspection of Western Australian Museum material revealed only *B.pusilla* and no *C. campestris*. True *Caloprymnus campestris*, such as M3256 and M3257, is a distinctive form with distinctly bowed dentary with fat *Bettongia*-like molars and cruder potoroo-like premolars. $P_2$ has one ridgelet and $P_3$ has two, whereas *B. pusilla* has 3 and 3 respectively.

Baynes is familiar with *B.pusilla* (pers.comm.) and has referred to it as 'Thomson's unnamed Potoroid' or 'Unnamed potoroid' (Baynes 1987). I consider these are one and the same. While I recognised this taxon independently in South Australia, this was at a later date than the original work by Peter Thompson (Baynes 1987) and I wish to encourage the recognition of true discoverers. I favour the use of names that relate directly to the animal and are mnemonic, and so I suggest Nullarbor Dwarf Betttong for *Bettongia pusilla*. I can see no practical purpose served by assigning this form to a new genus. I keenly await the bold cladist who may place it clearly in a diagrammatic phylogeny of the potoroids.

The ecological description of this species cannot be given at the moment, but the tantalising possibility exists that well preserved mummies may provide some of this information. Well known from some Nullarbor caves, mummies can preserve pelage, soft-tissues and gut contents. I urge the collection and proper deposition of such material.

### ***Lagostrophus fasciatus*** (Péron, 1807)

Specimens

Henschke's Quarry Cave, Naracoorte, South East: P31639, right dentary; P31640, left and right maxillae and matching dentaries; P31641, right dentary; P31642, part left dentary; P31643 and P31644, part left maxillae; P31645, left, $I_1$; P31646, left $I_1$, and $M_1$, as loose teeth; and seven unregistered loose teeth.

Jimmy's Well, north of Tintinara, South East: P35460, right dentary.

Overland Corner Quarry, River Murray: P33474, right maxilla.

Albert Brown's Cave, Rocky Point between Ceduna and Penong, West Coast: P31647, right dentary; P31648, right dentary, juvenile; P31649; right dentary; P31650, broken skull, adult.

Charra Plains, near Ceduna, West Coast: P31651, skull and right dentary, juvenile.

Point De Mole, Gascoigne Bay, West Coast: P31653 and P31654, a pair of maxillae belonging to same skull; P31652, left dentary; P31655 and P31656, right dentaries.

Remarks

To the published archaeological evidence from the lower Murray (Wakefield 1964), an early record (Poole 1979) and one specimen reported by Flannery (1990), there can be added the hard palaeontological evidence of the existence of this species in South Australia. Its bones have been recovered from a late Pleistocene deposit (Pledge 1990) in the South East and Holocene deposits from the South East to West Coast.

This taxon may be overlooked in samples of rabbit-sized macropods. It has not been recorded from the South East (Wells and Pledge 1983) or from Henschke's (Pledge 1990). In a large sample from Henschke's Quarry Cave material, in this size range, minimum numbers of individuals of three species were found; 94 *Lagorchestes leporides* (left dentaries), 4 *Onychogalea lunata* (left dentaries) and 4 *Lagostrophus fasciatus* (left maxillae, there were 3 left dentaries). So *Lagostrophus* comprises near 5 percent of this class from that locality.

This form is easily recognised by the lower molars, with distinctive L-shaped forelink lying proud of the anterior cingulum and upper molars with prominent postlink. The skull, particularly the dentary and lower incisors, present an unusual *Sthenurus*-like facies.

### ***Lagorchestes asomatus*** Finlayson, 1943

Specimens

All from Mairs Cave, Buckalowie, lower Flinders Ranges: P14513 and P35453, skulls, juvenile; P35454, part skull, juvenile; P14516 and P35455, right dentaries; P35452, P35456, P35457, P35458, left dentaries. All specimens are juveniles with the oldest tooth-stage having the $M_2$ or $M^2$ newly erupted and $P_2$ or $P^2$ in occlusion.

Remarks

As this is the first juvenile material reported some further observations follow. The holotype described and figured by Finlayson (1943) is an adult skull with worn molars and the new fossil specimens conform closely to it. Some measurements of P14513 followed by Finlayson's measurements of the type, M3710, in brackets, for comparison are: greatest length, 62.3 (65.8); zygomatic breadth, 41.6 (42.9);nasals greatest breadth, 9.2 (9.9);diastema, 10.5 (7.1); palate length 33.7 (36.7). The usual age-related differences are noted with the older skull a little longer and higher with greater crest development, deeper zygomae and bigger bullae. A discrepancy in diastema length results from the cheek teeth being forward of the orbit by 6.1 (13.5), and of the masseteric process 9.0 (15.3). This may be explained by forward migration of the teeth, as predicted by Finlayson, and evidenced by the dentary of the holotype where $M_4$ is about 5 mm forward of its original position and $P_3$ is rotated forward in a manner characteristic of the condition found in macropodines in which tooth progression occurs without loss of that premolar.

The teeth of P14513 measure: $P^2$ length 4.2, width 2.5; $dP^3$, length 4.3, width 3.5; $M^1$ length 4.2, width 3.8. Compared to the type, the first cheek tooth, $P^2$, is shorter than $P^3$, Finlayson's $P^4$ (6.3mm), tapers more markedly, anteriorly, and the lingual cingulum is less well developed.

The juvenile skull, P14513, of *L. asomatus*, resembles that of a similiar aged skull of *L. hirsutus*, M3102, apart from the posterior breadth and depth of the former, probably associated with the greater otic development. A comparison of the teeth of these two species reveals differences. In the first, $P_2$ has two distinct cuspules and associated ridgelets between the anterior and posterior cusps and is longer than the corresponding tooth in *L. hirsutus*, which has just one cuspule and ridgelet. The $dP_3$ is more molariform, broader anteriorly with a distinct trigonid basin, whereas in *L. hirsutus* the trigonid is blade like. $M_1$ is similar in form but broader and higher crowned in *L. asomatus*. Of the upper teeth, $P^2$ is longer with 2 cuspules and ridgelets compared with one in *L. hirsutus*, and the lingual cingulum is more developed. $dP^3$ is broader and more molariform. $M^1$ is broader and higher crowned, while closely matching in form, that of *L. hirsutus*.

Initial determination and registration in 1968 as *Bettongia*, submerged this material in the South Australian Museum and Mr Merv Anderson's private collection until redetermination by the author in June 1994.

### *Lagorchestes leporides* (Gould, 1841)

Specimens

Hereford Stream Cave, lower South East: P29143, an almost complete skull.

Unnamed Cave L106, lower South East: P29144, P29145, P29146, three near complete skulls.

Dene Kilsby's Cave, lower South East: P35596, juvenile skull.

Blanche Cave, Naracoorte, South East: P35597, skull.

Henschke's Quarry Cave, Naracoorte, South East: P17681, right dentary; P17814, left dentary; P17826, left dentary; P17798, left dentary, juvenile; P18658, part left dentary; P17626, part left maxilla; P35598 right dentary; P35599, left maxilla; P35600, P35602, P35603, left dentaries; P35604 right dentary; P35605 right dentary; P35606, left dentary; P35607, right maxilla, adult; P35608, left maxilla, juvenile; P35609, right dentary; P35610, left dentary; and a large collection of unregistered material.

Victoria Fossil Cave, Naracoorte South East; P20275, near complete skull; P25552, part skull.

Curramulka Town Cave, central Yorke Peninsula: P12921, cemented and crushed skull in two parts.
Mairs Cave, Buckalowie, lower Flinders Ranges: P35459, left dentary.

Remarks

Historical records indicate that this species was tolerably abundant in the southern settled areas of South Australia (Strahan 1983) and it is not surprising to find its fossil bones across a wide range. The name *L.* cf. *conspicillatus* has appeared on lists for the South East (Wells and Pledge 1983) but I have seen no specimens to support this. P17626 was registered as *Lagorchestes* cf. *conspicillatus* in early 1972, and indicates a possible source of confusion. The label was amended to '*leporides*' at some time but the register entry was not corrected until this year when the number was assigned to a single specimen, previously several unnumbered specimens of mixed taxa were together under the one label. Two teeth of *Macropus rufogriseus* were removed during a later phase of sorting, probably 1989–90. *Lagorchestes*, P17814 registered later in 1972, was not given a specific identification and was subsequently sorted as one left dentary of *L. leporides*, bearing the number and one left dentary of *Onychogalea lunata* now numbered P35470. Confusion of similar sized taxa is discussed elsewhere. Uncertainty was not confined to the Henschke's material, P20275 from Victoria Cave is still registered as *Largochestes*? [*sic*] only. In the absence of supporting evidence, *L. conspicillatus* should be struck from the fossil record of South Australia.

### ***Onychogalea lunata*** (Gould, 1840)

Specimens

Henschke's Quarry Cave, Naracoorte, South East: P35467, left maxilla; P35468, part right maxilla; P35473, part left maxilla with $P^3$, $M^1$, P35469, left dentary, juvenile, P35470, left dentary, juvenile; P35474, part left dentary, and some unregistered loose teeth.
Curramulka Town Cave, Yorke Peninsula: P35466, right dentary.
Corra Lynn Cave, Curramulka, Yorke Peninsula: P35464, juvenile skull, left dentary and some associated post-cranial bones.
Baldina Creek, near Burrra: P35465, complete juvenile left dentary with $P_3$ exposed in crypt.
Dempsey's Lake, Port Augusta: mostly fragmentary material including, P19470, P19493, P35484, P35486, P35487; and more complete dentaries, P22488 and P35485.
Mairs Cave, Buckalowie, Southern Flinders Ranges: P35461, right dentary juvenile; P35462 part right dentary, juvenile.
Koonalda Cave, Nullarbor Plain, (Gallus site): P35476, P35477, P35478, P35479, P35480, P35482, P35483, dentary fragments; P35481, part maxilla.
Purple Goringe Cave, Nullarbor Plain, Western Australia: P35463, mummified upper thorax with skull and right dentary.

Remarks

Poorly known as a living animal *O. lunata* seems to have favoured the drier northern and western regions and this is reflected in the occurrence of its bones from the Nullarbor to the Flinders Ranges. If we can say anything definite about the ecology of this species, its presence in Pleistocene deposits of the South East, may indicate that these samples record, at least in part, a drier episode of regional climate.

This species was overlooked in samples of rabbit-sized macropods, as noted elsewhere, or simply misidentified. Although its arched tooth-rows, elegantly flaring molar crests and lophs and vestigial premolars should distinguish it and the following species. It was not distinguished in various South Australian Museum samples, and Williams (1982) tentatively discussed material of this and the following species under the heading of *Macropus eugenii.*

***Onychogalea fraenata*** (Gould, 1841)

Specimens

Kelly Hill Caves, Kangaroo Island, P35491, skull; P35492, part skull; P35493, left and right maxillae; P35494, left maxilla; P35490, left maxilla; P35495, P36496, P35497, P35498, P35499, P35500, dentaries.

Lake Fowler, Southern Yorke Peninsula: P18918, left maxilla; P18919, part left maxilla; P18920, right dentary with $P_3$ excavated.

Baldina Creek, near Burra: P35488, right maxilla; P21023, part left maxilla; P21090, part left dentary; P22458, part left dentary.

Dempsey's Lake, Port Augusta: P18243, P19426, P19469c, fragments with teeth.

Remarks

Some comments for the preceding species apply here, although *O. fraenata* still allows ecological study of populations in a tiny part of its former range.

This report seems to include the first record of the species for Kangaroo Island, where its remains were mixed with those of *Lasiorhinus latifrons*, now extinct on the Island, too, but well entrenched on the mainland where it has been well studied ecologically.

We have evidence of coincidence of the two *Onychogalea* species from the lower Flinders Ranges area, but as usual with fossil deposits this should not be taken as proof of synchrony and, therefore sympatry.

## DISCUSSION

The purpose of this paper is to report the results of sorting and systematic reorganisation of about half the South Australian Museum fossil mammal bone material. Reports of fossils are all too often associated with speculative interpretation of biological, ecological and climatological implications. I can only indicate the potential there may be for such information to be gleaned from the Quaternary deposits of South Australia. If reliable determinations of well curated specimens can be married to sound stratigraphies with secure, consistent dates of actual bone material and then considered together with a deeper ecological understanding (if it can be gained from the remaining rabbit-sized macropods), this may allow detailed explanation of the Pleistocene and Holocene climate changes as they affected this continent. However, trying to survive as a museum palaeontologist in an environment increasingly influenced by adverse financial and intellectual conditions, one should perhaps be content with the modest and achievable goal of completing the second half of the sort. One hint of what might be undetected is provided by specimen M1828, associated with labels suggesting that it was collected in October 1872 by F.W. Andrews in sandhills near Lake Gairdner — it is a skull of *Setonix brachyurus*.

## ACKNOWLEDGEMENTS

I wish to express my appreciation to all those who collected bone material and lodged it at the South Australian Museum, including: Peter F. Aitken, Merv Anderson, Fred W. Aslin, Albert H. Brown, Cave Exploration Group of S. Aust. Inc., A. Gallus, C. Hales, P. Harper, W.A. Head, Ken Heynes, Jack Howard, J. MacLucas, J. Miekel, H.W. Moeller, G. Pilkington, N.S. Pledge, Ron Simms, D.J. Taylor, A.E. Vigar, Dom L.G. Williams and Adam Yates. The gestation of a scientific contribution requires a certain sequence of events, these people were the vital initiator, without whom there would be no knowledge gain. Unlike the biological model, timing in science is not so definite and in one case, forty years does not seem over long. My thanks to Lynette Queale for bringing the *Setonix* skull to my attention, Robyn Cherrington and Lucy Ramsden for typing and Trevor Peters for photography.

## REFERENCES

Archer, M. (1974). New information about the Quaternary distribution of the thylacine (Marsupialia, Thylacinidae) in Australia. *Journal of the Royal Society of Western Australia* **57,** 43–50.

Baynes, A. (1987). The original mammal fauna of the Nullarbor and southern peripheral regions: evidence from skeletal remains in superficial cave deposits. In 'A biological survey of the Nullarbor Region South and Western Australia in 1984' (Eds N.L. McKenzie and A.C. Robinson) pp. 139–52, 401–2. (S. Aust. Dept. Environment and Planning: Adelaide).

Finlayson, H.H. (1932). *Caloprymnus campestris*. Its recurrence and characters. *Transactions of the Royal Society of South Australia* **56**, 148–167.

Finlayson, H.H. (1943). A new species of *Lagorchestes* (Marsupialia) *Transactions of the Royal Society of South Australia* **67**, 319–321.

Flannery, T.F. (1990). 'Australia's vanishing mammals'. (RD Press: Surry Hills).

Lundelius, E.L. (1963). Vertebrate remains from the Nullarbor Caves, Western Australia. *Journal of the Royal Society of Western Australia* **46**, 75–80.

Lundelius, E. L. and Turnbull W.D. (1984). The Mammalian Fauna of Madura Cave, Western Australia Part IV: Macropodidae: Potoroinae. *Fieldiana* : Geology New Series, No 14.

Pledge, N.S. (1990). The Upper Fossil Fauna of the Henschke Fossil Cave, Naracoorte, South Australia. *Memoirs of the Queensland Museum* **28,** 247–261.

Poole, W.E. (1979). Australian Kangaroos. In 'The Status of endangered Australasian Wildlife'. Proceedings of the Centenary Symposium (Ed. M.J. Tyler) pp 13–27. (Royal Zoological Society of South Australia: Adelaide).

Strahan, R. (ed) (1983). 'The Australian Museum Complete Book of Australian Mammals' (Angus and Robertson: Sydney).

Tate, R. (1879). The Natural history of the country around the head of the Great Australian Bight. *Transactions Royal Society South Australia* **2**, 94–128.

Thorne, A.S. (1971). The Fauna. In 'Archaeology of the Gallus site, Koonalda Cave'. Australian Aboriginal Studies No. 26, Prehistory Series No. 5 (Ed. R.V.S. Wright) chap. 5. (Australian Insitute of Aboriginal Studies: Canberra).

Wakefield, N.A. (1964). Appendix 1 Mammal Remains. In 'Archaeological excavation of rock shelter No. 6 Fromm's Landing, South Australia' (Eds D.J. Mulvaney, G.H. Lawton and C.R. Twidale) pp 494–498. *Proceedings of the Royal Society of Victoria* **77.**

Wells, R.T. and Pledge, N.S. (1983). 16 : Vertebrate Fossils. In 'Natural History of the South East' (Eds M.J. Tyler, C.R. Twidale, J.K. Ling and J.W. Holmes) pp. 169–176. (Royal Society of South Australia Inc. :Adelaide).

Williams, D.L.G. (1982). Late Pleistocene vertebrates and palaeoenvironments of the Flinders and Mount Lofty Ranges, South Australia. (Unpublished thesis, Flinders University, School of Biological Sciences: Adelaide).

Wright, R.V.S., ed. (1971). The archaeology of the Gallus site, Koonalda Cave. Australian Aboriginal Studies No. 26, Prehistory Series No. 5. (Australian Institute of Aboriginal Studies: Canberra).

# The Distribution of Pleistocene Vertebrates on the Eastern Darling Downs, Based on the Queensland Museum Collections

R.E. MOLNAR[1] AND CORNELIA KURZ[2]
(communicated by M.L. Augee)

[1] Queensland Museum, P.O. Box 3300, South Brisbane, Qld., 4101, and
[2] Institut für Paläontologie, Universität Bonn, Nussallee 8, 53115 Bonn, Germany

Molnar, R.E. and Kurz, C. (1997). The distribution of Pleistocene vertebrates on the eastern Darling Downs, based on the Queensland Museum collections. *Proceedings of the Linnean Society of New South Wales* **117**: 107-134

Pleistocene tetrapods have been collected from the eastern Darling Downs of Queensland for about a century and a half. A search of the registers and audit of the collections permits a set of faunal lists to be compiled for specific localities for the first time. Among the tentative conclusions — tentative because of lack of control for collecting bias in the past, among other factors — are the following. The eastern Darling Downs seems to have had a uniform vertebrate fauna. Few taxa are found at many localities, and these uncommon taxa were widespread and either actually rare when alive or subject to preservational bias. Sthenurine kangaroos were less common than macropodines. Some taxa, including monotremes, ninja turtles and lungfish seem to actually have been rare when alive. Crocodiles seem to have been more common and diverse in the northwestern (Dalby) region of the eastern Downs. Dromornithid birds, medtsoine snakes and ziphodont crocodilians seem to have been absent altogether.

Manuscript received 27 March 1996, accepted for publication 18 September 1996.

KEYWORDS: Darling Downs, diprotodontids, distribution, macropodids, *Megalania*, ninja turtle, Pleistocene, taphonomy.

## INTRODUCTION

### Historical background

Pleistocene fossils have long been known from the Darling Downs. Australian Pleistocene fossils were first brought to the attention of the scientific world by discoveries in central New South Wales around 1830. Although the Darling Downs was not settled until 1840, Thomas Mitchell had already collected material from the Downs by 1842 (Owen, 1877:240). From that period to 1870 further fossils were found and are included in Owen (1877), who also published an extract of a letter from Leichhardt describing the Downs and the occurrences of fossils there (p. 241, also included in Bennett, 1876). About 25% of the Australian fossil marsupials in the British Museum noted in Lydekker (1887), 236 of the 835 entries, come from the Darling Downs. This is a minimal estimate as some entries for material collected by Bennett are located only as "Queensland" and since Bennett, and his employees, did much collecting on the Downs (Bennett 1876) some of this material probably derives from the Downs. In fact, the area of the Downs that produced fossils as given by Bennett is basically the same as that recognised now, except that it has been extended southeast to include Freestone Creek and Warwick. However, Bennett noted that few bones had been found in the Dalby region and nothing was reported from that area in Lydekker (1887). In spite of this long history, the only attempt to present an overall picture of the region during the Pleistocene is that of Bartholomai (1976).

## Geography

The Darling Downs comprises low, rolling hills and plains in southeastern Queensland bounded by the Great Dividing Range on the northeast. It extends from the Bunya Mountains (and the Main Range to their south), south to the granite belt at the border with New South Wales, west to the Herries Range and the hilly country west of the Condamine and north to the hills of the Dividing Range (French, 1989). Topographically the land gradually descends from the hills, slopes and valleys of the Main Range in the east, to the plains of the Condamine in the west. In the early nineteenth century the Downs was covered with grass and herbs, with open woodland on the hills (Leichhardt in Owen, 1877). The fossil-bearing part of the Darling Downs is a roughly rectangular region about 200 km long by 80 km wide orientated with its long axis parallel to the Great Dividing Range, that is northwest to southeast (Fig. 1). The region east of the Condamine is known as the eastern Darling Downs, and provides a Pleistocene fauna, whilst the area to the west (including Chinchilla) is the western Downs: the Pliocene Chinchilla fauna is sometimes known as the western Downs fauna.

This study is restricted to the Darling Downs east from Macalister and the Condamine River, and hence the term 'Downs' as used here refers to the eastern Darling Downs not the Chinchilla region or the trans-Condamine portion, with two exceptions. The two Pleistocene localities west of the Condamine River (Kupunn and Boiley's property), so technically not on the eastern Downs, are included. The sites discussed are given in Fig. 1, except for a few that can no longer be located.

## Stratigraphy

Woods (1960) provided an overview of the eastern Downs Pleistocene sediments. They consist largely of dark clays, sands and grits derived from the basalts of the Dividing Range, although the sands may also derive from weathering of the underlying Mesozoic beds (Gill, 1978). Calcareous nodules are common and carbonate lenses may be found. Judging from the discoveries of fossils in wells, the fossiliferous sediments are at least 50 metres deep in places but, as pointed out by Bartholomai (1976), these are probably of Pliocene age at that depth. Pleistocene sediments are, however, at least 42 metres thick in the northwest (Bennett, 1872). The fossils generally derive from the dark clay soils but, especially in the northwest along the Condamine, may also be abundant in the yellowish quartz sands.

Macintosh (1967) and Gill (1978) gave a stratigraphy of the region between Kings and Dalrymple Creeks introducing the 'Toolburra Silt' and overlying 'Talgai Pedoderm' and 'Ellinthorpe Clay', names which have not subsequently seen general use. Gill gave a chronology of depositional events in the Dalrymple Creek region. The Toolburra silt was deposited with brief intervals of lower energy (marked by clay deposition) and higher energy (marked by sand) flows. This deposition was followed by a dry period that oxidised the Toolburra, and produced some carbonate nodules about 26,000 years old. The Talgai and Ellinthrope were then deposited, and record periods of dryness and flooding respectively. Gill interpreted the climate as having generally been wetter than at present. Macintosh suggested that the intermediate and sporadically occurring 'Talgai Fossil Soil' was deposited about 12,000 years ago, based on carbonate dates from the Toolburra and Ellinthorpe. Gill provided dates for Kings Creek sites as old as 40,000 years. These two workers made the only attempts at dating the Downs fossils or deposits.

Gill discussed the dates based on the carbonate nodules (and Gill reports that most dating laboratories were reticent about using these), although in his Fig. 2 he indicated that comparable dates were also obtained from charcoal (Gill, 1978). Some dates were also derived from bone and shell according to the figure. Terrestrial carbonates are now regarded as the least reliable material for radiocarbon dating with whole bone and shells not greatly better, but charcoal is regarded as probably the best (inorganic) material for

Figure 1. Pleistocene fossil localities of the eastern Darling Downs. The diamonds represent selected major towns (four of which are also localities) and the dots (other) localities. The Condamine River and major creeks are also shown. By region, the localities are: **Dalby region**: 1, Jimbour; 2, Brimblecomb's and Jimbour Ck. c. 1.5 km S of Jimbour; 3, Pirrinuan and Jimbour Ck. c. 4.5 km S of Jimbour; 4, 'Wyoming'; 5, c. 3 km downstream from 'Armour' and 'Darrington'; 6, Macalister; 7, 'The Myalls'; 8, Boiley's; 9, Kaimkillenbun; 10, 'Crystal Brook'; 11, Mocatta's Corner; 12, Kapunn; 13, Loudon's bridge; 14, 'Territ'; and Dalby. **Cecil Plains region**: 15, 'Cardoch'; 16, 'Springvale; 17, St. Ruth; 18, Irongate; 19, Bongeen; 20, 'Cecil Downs'; 21, Braemar. **Toowoomba region**: 22, Balgowan; 23, Goombungee; 24, Oakey; 25, near Kingsthorpe (Gowrie Ck.); 26, Kingsthorpe (Westbrook Ck.); 27, Gowrie; 28, Wellcamp; 29, 'Eton Vale'; 30, Cambooya; 31, 'Harrow'; 32, 'Woodstock' and 'Cowarrie'; and 33, Greenmount. **Clifton region**: 34, Hirstglen; 35, 'Ravensthorpe'; 36, Brown's, Bell's, 'Greenfields' and Pilton; 37, 'Manapouri'; 3, Pearson's and Budgie Creek; 39, Nobby; 40, 'Bundah'; 41, Clifton; 42, Sutton's; 43, College Green; 44, O'Mara's bridge; 45, Spring Creek; 46, Talgai; 47, 'Ebley'; 48, 6.5 km W of 'Goomburra'; 49, 'Goomburra'; 50, Eastwill's; 51, Freestone; 52, Yangan. In addition the locality at Gore is also shown. Not all of these localities are known with comparable accuracy, e.g., 'Ebley' cannot now be located, other than that it was near Allora, so the dot marks Allora. Glengallen Plains could not be located. The regions defined in the text are shown by dashed lines.

dating (Meltzer and Mead, 1985). However the strength of the association of the charcoal (and shells and nodules) with the bones is not given. In view of these considerations it is very desirable to replicate these dates.

### Aims of this work

This study was intended to achieve five aims:

1). to provide a general introduction to the Downs and its fossils for paleontologists,

2). to collect together the data in the Queensland Museum on vertebrate fossils from the eastern Downs,

3). to test regionalism in the region,

4). to check whether there was one, or more, local fauna, and finally,

5). to see if there were any interesting conclusions to be drawn from the previously uninspected data.

It has been generally assumed that the distribution of fossil taxa on the eastern Downs is uniform, i.e. that there is no regionalism. Because of the importance of this area for the understanding of Pleistocene Australia, it is desirable to check this assumption. This study was undertaken in part in response to the comment of Archer (1984) that eastern Darling Downs local fauna might actually be more than a single fauna. And because the fauna is undated, it has also been assumed that the fossils were all more or less of the same age, although admittedly several workers have emphasised that this may not be the case. Dating the material and taphonomic observation, such as whether the sites represent high or low energy deposition, unfortunately cannot be addressed here. Even so it is clear that some sites, e.g. Sutton's and Pearson's, seem to represent low energy deposition while others, e.g. 'Bundah', had at least some episodes of high energy deposition.

### Caveats of this work

Several other caveats of this study must be noted. It is restricted to the eastern Downs and is based only on material (including casts) in the Queensland Museum collections. This is probably the largest collection of eastern Downs material, and so lends confidence to the conclusions, but still the study is indicative rather than comprehensive. In view of the large number of specimens involved, by and large the collection identifications were not verified but simply accepted. The mammalian nomenclature has been updated following Archer et al. (1984). However, all register entries were checked in a thorough audit of all specimens not presently on loan.

In view of the lack of taxonomic revision of Pleistocene diprotodontids (now underway by B. Mackness) these have been put into three categories: identifications as *Diprotodon australe, D. australis* and *D. optatum* are given here as "*Diprotodon*, large form"; *Diprotodon minor* as "*Diprotodon*, small form", and all other, non-*Diprotodon* diprotodontids as "small diprotodontids" (which probably includes several species). Likewise crocodilians (almost invariably recorded as *Pallimnarchus pollens*) have been given as "crocodilian" except where diagnostic features have been preserved. Chelonians, unless clearly referable to the Meiolaniidae or the Trionychidae, have been given as chelids.

Similarly locality identifications have been assumed to be accurate. Some of the early localities, such as 'Gowrie' or 'Pilton', probably refer to regions rather than to discoveries at those specific locations. Hence some taxa in the lists for these localities may actually be referable to other, more specific localities included here such as, e.g., Brown's property at Pilton. Thus some taxa may be included in the wrong lists, or some of the localities given as separate may be identical. For much of the early work this would seem prohibitively difficult or impossible to determine now, and it is hoped that this does not greatly alter the conclusions. It should be remembered that these lists are lists of fossils found at the localities. Faunal lists, of which taxa lived in these regions, may be compiled from the lists of fossils but we have not done so. Thus discrepancies between lists for nearby localities reflect differences in the fossils (so far) found, but do not necessarily imply differences in the kinds of animals that lived there.

Most sites have not been systematically collected, and collecting before 1970 was probably restricted to collecting vertebrates of moderate to large size, about the size of *Sarcophilus* and larger. Recently, systematic collecting has been done at some sites, specifically Sutton's, Pearson's, O'Mara's Bridge and 'Bundah'. The last site, 'Bundah', has been exhaustively collected including everything uncovered at the locality since its discovery.

Because of the lack of control over early collecting and other constraints a detailed statistical analysis of the faunal lists is unwarranted. Such an analysis would seem to provide an uncomfortably large possibility of 'garbage in, garbage out'. Therefore only a general set of suggested conclusions — working hypotheses — based on inspection of the data for the distribution of Pleistocene taxa on the eastern Downs is presented. A list of the tetrapod material in the British Museum in the late 19th century from the eastern Downs localities, taken from Lydekker (1887, 1888, 1889) but with the nomenclature updated, is given in the Appendix 1. Since there has not been much collecting on behalf of the British Museum on Downs since then, this probably gives a reasonably complete list of their eastern Downs collection.

## FOSSIL LISTS FOR EASTERN DARLING DOWNS LOCALITIES

Synonymies from Archer, et al., (1984), Ingram, (1990), Van Tets and Rich (1990). The number in parentheses before most localities is the locality number in Fig. 1. Note that nearby localities are not individually represented by dots on the figure, and that imprecise localities,such as "Jimbour Creek", and major towns, such as Warwick, are not numbered. The number in parentheses after the locality name gives the number of taxa found at that locality.

### DALBY Region: 20 localities + "Jimbour Creek"

**Site 1** — Jimbour (2):
Macropodinae
- *Macropus ?ferragus*
- *Protemnodon anak*

**Site 2** — Jimbour Ck., c. 1.5 km S of Jimbour (1):
Diprotodontidae
- *Diprotodon*, large form

**Site 2** — Brimblecomb's property, Jimbour Creek (3):
Macropodinae
- *Macropus titan*
- *Protemnodon anak*

Diprotodontidae
- *Diprotodon*, large form

**Site 3** — Jimbour Ck., c. 4.5 km S of Jimbour (1):
Sthenurinae
- *Procoptodon goliah*

**Site 3** — Pirrinuan, Jimbour Creek (1):
Sthenurinae
    *Troposodon minor*

**Site 4** — 'Wyoming' (2):
Macropodinae
    macropod
Diprotodontidae
    ?*Diprotodon*, large form

**Site 5** — Condamine River, c. 3 km downstream from 'Armour' (2):
Diprotodontidae
    *Diprotodon*, large form
    small diprotodontid

**Site 5** — near 'Darrington', Condamine River (1):
Diprotodontidae
    *Diprotodon*, large form

**Site 6** — Macalister, Condamine River (16):
Vombatidae
    *Phascolomys* sp.
    *Vombatus* sp.
Macropodinae
    *Macropus ferragus*
    *Macropus pearsoni*
    *Protemnodon anak*
    *Protemnodon roechus*
Sthenurinae
    *Procoptodon pusio*
    *Troposodon minor*
Diprotodontidae
    *Diprotodon*, small form
    *Diprotodon*, large form
    small diprotodontid
Palorchestidae
    *Palorchestes azael*
Crocodylidae
    *Crocodylus porosus*
    *Pallimnarchus pollens*
Meiolaniidae
    meiolaniid
Chelidae
    chelid

**Site 7** — 'The Myalls' (and vicinity) (3):
Macropodinae
    *Protemnodon anak* (c. 1 km N.)
Diprotodontidae
    *Diprotodon*, large form
    small diprotodontid

**Site 8** — Boiley property, near 'Daandine' (1):
Macropodidae
    macropod

**Site 9** — Kaimkillenbun (3):
Vombatidae
    *Vombatus* sp.
Macropodinae
    *Protemnodon brehus*
Sthenurinae
    *Sthenurus andersoni*

**Site 10** — 'Crystal Brook', Myall Creek (2):
Macropodinae
    macropod
Diprotodontidae
    diprotodontid

**Site 11** — Mocatta's Corner, Bunya Creek (1):
Varanidae
    *Megalania prisca*

**Site 12** — Kupunn (given "Kapunn") (1):
Vombatidae
    *Phascolonus gigas*

**Site 13 —** 'Greenbank' (Loudons Bridge) (1):
Diprotodontidae
    diprotodontid

**Site 14** — 'Territ', Oakey Creek (1):
Vombatidae
    *Phascolomys medius*

**Dalby region, Cattle Creek** (9)
Vombatidae
    wombat
Hypsiprymnodontinae
    *Propleopus oscillans*
Macropodinae
    *Macropus ferragus*
    *Macropus titan*
    *Protemnodon anak*
    *Protemnodon roechus*
Diprotodontidae
    *Diprotodon*, large form
Dasyuridae
    *Sarcophilus laniarius*
Thylacoleonidae
    *Thylacoleo carnifex*

**Dalby** (12):
Vombatidae
    *Phascolomys magnus*
Macropodinae
    *Macropus titan*
    *Protemnodon anak*
    *Wallabia indra*

Diprotodontidae
    *Diprotodon*, large form
    small diprotodontid
Palorchestidae
    *Palorchestes azael*
Thylacoleonidae
    ?*Thylacoleo carnifex*
Dromaiidae
    *Dromaius* sp. cf. *D. novaehollandiae*
Crocodylidae
    crocodilian
Varanidae
    *Megalania prisca*
Chelidae
    chelid

**"Jimbour Creek"** (6):
Macropodinae
    *Macropus agilis*
    *Macropus titan*
    *Protemnodon anak*
    *Protemnodon roechus*
Diprotodontidae
    *Diprotodon*, large form
Thylacoleonidae
    *Thylacoleo carnifex*

**Myall Creek** (1):
Macropodidae
    macropod

**'CONDAMINE RIVER'**
Macropodinae
    *Macropus ferragus*
Diprotodontidae
    *Diprotodon*, large form
    small diprotodontid
Dromaiidae
    *Dromaius* sp.
    Crocodylidae
    crocodilian
Varanidae
    *Megalania prisca*
Chelidae
    *Chelodina* sp. (given "*Chelonia*")

**CECIL PLAINS Region: 8 localities**
**Site 15** — 'Cardoch', Condamine River (1):
Macropodinae
    *Protemnodon anak*

**Site 16** — 'Springvale', near Tipton (5):
Macropodinae
    *Macropus pearsoni*
    *Protemnodon anak*

Diprotodontidae
- *Diprotodon*, small form
- small diprotodontid

Palorchestidae
- *Palorchestes azael*

**Site 17** — St. Ruth (2):
Diprotodontidae
- *Diprotodon*, large form

Palorchestidae
- *Palorchestes azael*

**Site 18** — Irongate (1):
Diprotodontidae
- *Diprotodon*, small form

**Site 19** — Bongeen (2):
Macropodinae
- *Macropus titan*
- *Osphranter altus*

**Site 20** — 'Cecil Downs', Linthorpe Creek(7–8):
Macropodinae
- *Macropus* sp.
- *Protemnodon roechus*

Sthenurinae
- *Procoptodon* sp.

Diprotodontidae
- *Diprotodon*, large form
- small diprotodontid

Thylacoleonidae
- *Thylacoleo* sp.

family not known
- ?bird

Agamidae
- agamid[a]

**Site 21** — 'Braemar', near Southbrook (1):
Diprotodontidae
- *Diprotodon*, large form

**Cecil Plains** (1):
Diprotodontidae
- *Diprotodon*, large form

[a] The condition of the specimen suggests that it may be recent or of different age from the rest of the taxa listed.

### TOOWOOMBA Region: 14 localities + "Gowrie Creek"

**Site 22** — Balgowan colliery (2):
Macropodinae
- *Protemnodon anak*

Diprotodontidae
- *Diprotodon*, large form

**Site 23** — Goombungee (1):
Macropodinae
- *Protemnodon anak*

**Site 24** — Oakey, Gowrie Creek (1):
Diprotodontidae
    *Diprotodon*, large form

**Site 25** — near Kingsthorpe, Gowrie Creek (1):
Macropodidae
    macropod

**Site 26** — Kingsthorpe, Westbrook Creek (4):
Macropodinae
    *Macropus titan*
    *Protemnodon anak*
Diprotodontidae
    *Diprotodon*, small form
    *Diprotodon*, large form

**Site 27** — Gowrie (25):
Vombatidae
    *Phascolomys angustidens*
    *Phascolonus gigas*
    *Vombatus ursinus*
Potoroinae
    *Aepyprymnus rufescens*
Macropodinae
    *Macropus agilis*
    *Macropus dryas*
    *Macropus thor*
    *Macropus titan*
    *Onychogalea unguifera*
    *Osphranter altus*
    *Protemnodon anak*
    *Protemnodon brehus*
    *Protemnodon devisi*
    *Protemnodon roechus*
    *Wallabia indra*
Sthenurinae
    *Procoptodon pusio*
    *Sthenurus andersoni*
    *Troposodon minor*
Diprotodontidae
    *Diprotodon*, large form
    small diprotodontid
Thylacinidae
    *Thylacinus cynocephalus*
Thylacoleonidae
    *Thylacoleo carnifex*
Rallidae
    *Gallinula mortierii*
Crocodylidae
    crocodilian
Chelidae
    chelid

**Site 28** — Wellcamp and vicinity (5):
Macropodinae
  *Macropus* sp.
  *Protemnodon anak*
  *Protemnodon roechus*
Diprotodontidae
  *Diprotodon*, large form
  small diprotodontid

**Site 29** — 'Eton Vale' (2):
Macropodinae
  *Macropus* sp.
Diprotodontidae
  *Diprotodon*, large form

**Site 30** — Cambooya region (3):
Macropodinae
  *Macropus titan*
  *Protemnodon anak*
Diprotodontidae
  *Diprotodon*, large form

**Site 31** — 'Harrow' ("Sharrow") (7):
Macropodinae
  *Macropus pearsoni*
  *Macropus titan*
  *Protemnodon anak*
Sthenurinae
  *Troposodon minor*
Diprotodontidae
  *Diprotodon*, large form
  small diprotodontid (*Prochoerus celer*)
Crocodylidae
  crocodilian

**Site 32** — 'Cowarrie', near Southbrook (1):
Diprotodontidae
  *Diprotodon*, large form

**Site 32** — 'Woodstock', Hodgsons Creek (4):
Diprotodontidae
  *Diprotodon*, large form
family not known
  bird
Varanidae
  *Megalania prisca*
family not known
  lizard

**Site 33** — Greenmount, Emu Creek (6):
Macropodinae
  *Macropus titan*
  *Protemnodon anak*
Sthenurinae
  ?*Procoptodon* sp.

- Diprotodontidae
  - *Diprotodon*, large form
- Peramelidae(?)
  - bandicoot
- family not known
  - bird

**"Gowrie Ck"** (9):

- Macropodinae
  - *Macropus* sp.
  - *Protemnodon anak*
  - *Protemnodon roechus*
- Diprotodontidae
  - *Diprotodon* sp.
  - diprotodontid (*Sthenomerus charon*)
- Dasyuridae
  - *Sarcophilus* sp.
- Thylacinidae
  - *Thylacinus cynocephalus*
- Thylacoleonidae
  - *Thylacoleo carnifex*
- family not known
  - teleost

**Toowoomba** (1):

- Diprotodontidae
  - *Diprotodon*, large form

**CLIFTON Region: 25 localities + "Kings Creek"**

**Site 34** — Longe's property, Hirstglen (1):

- Macropodinae
  - *Macropus titan*

**Site 35** — 'Ravensthorpe' (19–20):

- Vombatidae
  - *Vombatus* sp.
- Macropodinae
  - *Macropus agilis*
  - *Macropus ferragus*
  - *Macropus pan* or *faunus*
  - *Macropus piltonensis*
  - *Macropus thor*
  - *Macropus titan*
  - *Osphranter woodsi*
  - *Protemnodon anak*
  - *Protemnodon ?devisi*
  - *Protemnodon roechus*
- Sthenurinae
  - *Sthenurus pales?*
  - *Troposodon minor*
- Diprotodontidae
  - *Diprotodon*, large form
- Rallidae
  - large rail

Ardeidae
    *Ardea* cf. *A. novaehollandiae*
Megapodidae
    *Progura gallinacea*
Crocodylidae
    crocodilian
Varanidae
    *Megalania prisca*
Trionychidae
    trionychid

**Site 36** — Bell's property, Pilton (1):
Palorchestidae
    *Palorchestes parvus*

**Site 36** — Brown's property, Pilton, Kings Ck. (7):
Macropodinae
    *Macropus agilis*
    *Macropus* cf. *M. giganteus*
    *Protemnodon anak*
    *Protemnodon roechus*
Diprotodontidae
    *Diprotodon*, large form
    small diprotodontid
Chelidae
    chelid

**Site 36 —** 'Greenfields', Pilton (4):
Vombatidae
    *Phascolonus gigas*
Macropodinae
    *Macropus ferragus*
    *Macropus* sp. cf. *M. titan*
    *Protemnodon anak*

**Site 36** — Pilton, Kings Creek (17):
Vombatidae
    *Phascolomys angustidens*
    *Phascolonus gigas*
    *Vombatus ursinus*
Macropodinae
    *Macropus ferragus*
    *Macropus titan*
    *Protemnodon anak*
    *Protemnodon roechus*
Sthenurinae
    *Sthenurus andersoni*
Diprotodontidae
    *Diprotodon*, large form
Dasyuridae
    *Dasyurus* sp.
    *Sarcophilus laniarius*
Thylacinidae
    *Thylacinus cynocephalus*

Thylacoleonidae
  *Thylacoleo carnifex*
Ornithorhynchidae
  *Ornithorhynchus anatinus*
Dromaiidae
  *Dromaius novaehollandiae*
Varanidae
  *Megalania prisca*
family not known
  teleost

**Site 37** — 'Manapouri', Kings Creek (3):
Macropodinae
  *Macropus titan*
Diprotodontidae
  *Diprotodon*, large form
Chelidae
  chelid

**Site 38** — Budgie Creek (1):
Macropodinae
  macropod

**Site 38** — Pearson's Locality, Kings Creek (22):
Vombatidae
  *Phascolomys medius*
  *Phascolonus gigas*
Macropodinae
  *Macropus agilis*
  *Macropus ferragus*
  *Macropus pearsoni*
  *Macropus titan*
  *Onychogalea unguifera*
  *Protemnodon anak*
  *Protemnodon brehus*
  *Protemnodon roechus*
  *Thylogale* sp.
Sthenurinae
  *Procoptodon pusio*
  *Procoptodon rapha*
  *Sthenurus andersoni*
  *Troposodon minor*
Diprotodontidae
  *Diprotodon*, large form
Palorchestidae
  *Palorchestes azael*
Dasyuridae
  *Dasyurus* sp.
Thylacinidae
  *Thylacinus cynocephalus*
Phasianidae
  quail
Varanidae
  *Megalania prisca*

Plotosidae
    *Tandanus tandanus*

**Site 39** — Nobby (1):
Rallidae
    *Gallinula* (*G. mortierii*?)

**Site 40** — 'Bundah', Neds Gully (9):
Vombatidae
    wombat
Macropodinae
    *Macropus titan*
Sthenurinae
    *Procoptodon goliah*
Diprotodontidae
    *Diprotodon,* large form
Dasyuridae
    *Sarcophilus* sp.
Thylacoleonidae
    *Thylacoleo* sp.
family not known
    rodent
family not known
    ?bird
family not known
    ?teleost

**Site 41** — Clifton, Kings Creek (17):
Vombatidae
    *Lasiorhinus* sp.
    *Phascolomys* sp.
Macropodinae
    *Macropus agilis*
    *Macropus titan*
    *Protemnodon affinis*[c]
    *Protemnodon anak*
    *Protemnodon devisi*
    *Protemnodon roechus*
    *Osphranter altus*
Sthenurinae
    *Procoptodon goliah*
    *Procoptodon pusio*
    *Troposodon minor*
Diprotodontidae
    *Diprotodon,* small form
    *Diprotodon*, large form
    small diprotodontid
Thylacoleonidae
    *Thylacoleo carnifex*
Rallidae
    *Gallinula mortierii*

**Site 42** — Sutton's site, Kings Creek (18):
Vombatidae
    *Phascolonus gigas*

Macropodinae
    *Macropus titan*
    *Protemnodon roechus*
Diprotodontidae
    *Diprotodon*, large form
Palorchestidae
    *Palorchestes* sp.
Peramelidae(?)
    ?bandicoot
Dasyuridae
    *Dasyurus* sp.
family not known
    ?monotreme
family not known
    rodent
family not known
    bird
Crocodylidae
    crocodilian
Varanidae
    *Megalania prisca*
    other varanid
family not known
    snake
Agamidae
    agamid
Chelidae
    chelid
family not known
    ?frog
family not known
    teleost

**Site 43** — near College Green, Kings Creek (1):
Diprotodontidae
    diprotodontid

**Site 44** — O'Mara's Bridge, Kings Creek (12):
Macropodinae
    *Macropus agilis*
    *Protemnodon anak*
Sthenurinae
    *Troposodon kenti*
    *Troposodon minor*
Diprotodontidae
    *Diprotodon*, large form
Dasyuridae
    *Dasyurus* sp.
Thylacoleonidae
    *Thylacoleo* sp.
Crocodylidae
    crocodilian

Varanidae
    *Megalania prisca*
    other varanid
Chelidae.
    chelid
family not known
    teleost

**Site 45** — near Clifton, Spring Creek (5):
Macropodinae
    *Macropus agilis*
    *Macropus ferragus*
    *Macropus titan*
Diprotodontidae
    diprotodontid
Thylacoleonidae
    *Thylacoleo carnifex*

**Site 46** — Talgai (1):[d]
Macropodinae
    *Protemnodon anak*

**Site 47** — 'Ebley', near Allora (1):
Diprotodontidae
    *Diprotodon*, large form

**Site 48** — 6.5 km W. of 'Goomburra' (1):
Vombatidae
    *Phascolonus* sp

**Site 49** — 'Goomburra', near Allora (1):
Palorchestidae
    *Palorchestes* sp.

**Site 50** — Eastwill's property, Glengallen Creek (1):
Sthenurinae
    *Procoptodon goliah*

**Site 51** — Freestone, Freestone Creek (14):
Vombatidae
    *Phascolonus gigas*
    *Vombatus ursinus*
Macropodinae
    *Macropus agilis*
    *Macropus titan*
    *Osphranter altus*
    *Protemnodon anak*
Sthenurinae
    *Procoptodon goliah*
    *Procoptodon rapha*
    *Sthenurus* sp. (nov.?)
Diprotodontidae
    *Diprotodon*, large form
    small diprotodontid

Peramelidae
    *Perameles* sp. (nov.?)
Dasyuridae
    *Dasyurus* sp
Ciconiidae
    *Ephippiorhynchus asiaticus*

**Site 52** — Yangan (given "Yangau") (1):
Diprotodontidae
    *Diprotodon*, large form

**Glengallen Plains** (1):
Vombatidae
    *Lasiorhinus latifrons*

**"King Creek":**
Vombatidae
    *Phascolonus* sp.
    *Vombatus* sp.
Hypsiprymnodontinae
    *Propleopus oscillans*
Macropodinae
    *Macropus agilis*
    *Macropus ferragus*
    *Macropus titan*
    *Protemnodon anak*
    *Protemnodon brehus*
    *Protemnodon roechus*
Sthenurinae
    *Procoptodon goliah*
    *Procoptodon rapha*
    *Troposodon minor*
Diprotodontidae
    *Diprotodon*, large form
    small diprotodontid
Thylacoleonidae
    *Thylacoleo carnifex*
family not known
    monotreme
Dromaiidae
    *Dromaius novaehollandiae*
Anatidae
    duck
Accipitridae
    buteonine (*Taphaetus brachialis*)
Varanidae
    *Megalania prisca*
    "*Varanus dirus*"
Meiolaniidae
    *Ninjemys oweni*
Chelidae
    chelid
Ceratodontidae
    *Ceratodus palmeri*

**Warwick** (2):
Diprotodontidae
    small diprotodontid
Columbidae
    *Phaps* sp.

[b] Locality uncertain.

[c] The label makes clear that this is a reference to the *Macropus affinis* of Owen (1845; cf. Mahoney and Ride, 1975).

[d] We agree that the human skull wasn't contemporaneous with *Protemnodon* (cf. Gill, 1978).

## DISCUSSION

### Size bias

Almost half of the taxa identified in the lists are recorded from only one locality. This obscures any geographical patterns that might be present. Such patterns, if any, are probably not reliable for the small taxa (e.g., birds, *Dasyurus*, bandicoots, rodents, monotremes, small lizards, frogs). Collecting experience, especially at Sutton's site and 'Bundah', suggests that these small forms have been overlooked and actually may have been much more widespread, as would be expected from ecological considerations.

Contrawise any geographical patterns are probably more reliable for the larger forms so suggested conclusions here are restricted (largely) to these large forms.

### Regionalisation

In order to discern any geographical patterns the eastern Downs, west to (and including) the region around Macalister, was divided somewhat arbitrarily into four portions (Fig. 1): around Dalby; around Cecil Plains; around Oakey and Toowoomba; and around Clifton and Warwick, respectively called the Dalby, Cecil Plains, Toowoomba, and Clifton regions. Taxa found in each region are given in Appendix 2. The variety of taxa was greatest in the Clifton region, then progressively less in the Toowoomba and Dalby regions and least in the Cecil Plains region. This is proportional to the numbers of localities in each region. There seems to be no obvious indication of regionalization (except possibly for crocodilians as discussed below), so we tentatively suggest that the eastern Darling Downs Pleistocene fauna is a single local fauna.

### Rarity

The number of sites at which each taxon was recorded are given in Appendix 3. Of the 68 taxa identified there, only 14 are found at more than five localities and only five (*Macropus titan, Protemnodon anak, P. roechus*, 'large *Diprotodon*', 'small diprotodontid') at more than 10. Thus there seem to be few widespread taxa and many restricted ones, e.g., *Palorchestes parvus, Sthenurus, Aepyprymnus, Propleopus, Onychogalea, Osphranter* and *Thylogale* which all seem to have been uncommon or restricted in range. However, this may be misleading as large numbers of fossils have only vague locality data such as "Darling Downs" so, for example, although only a single *P. parvus* is recorded from any specific site, 11 other specimens (without specific locality data) are in the QM collections. This example is the worst, and the other taxa here listed are represented by few or no (*Aepyprymnus, Onychogalea, Osphranter* and *Thylogale)* other Pleistocene specimens from the Downs in the QM collections. Neither are they recorded (at least from specific localities) by Lydekker (1887).

Although we regard those taxa found at several localities as having been widespread animals on the Pleistocene Downs, "restricted" is used here to indicate taxa found at few localities. We may interpret these taxa as having been uncommon, having had small population sizes, and most are actually represented by few specimens in the collections. In fact, even the creatures with widespread distributions are represented by few specimens, and the minimum number of individuals represented per locality is usually 1. Whether the animals represented by uncommon fossils were rare in the sense of today's rare animals is a matter requiring taphonomic analysis.

Were these restricted taxa found all over the Downs in low numbers (actually rare) or were they perhaps in large numbers restricted to specific locations, i.e., localized? If they were widely distributed in low numbers we might expect to find them preferentially at localities with large numbers of taxa (ranging to 25 taxa per locality), i.e., the larger sample sizes. Of these restricted taxa (defined in this context as those found at 1–5 localities) some, such as *Macropus thor* and *Onychogalea unguifera* are indeed found only in the large sample sizes. Only one, *Phaps* sp., is found only in a small sample size (<5) but others, such as *Procoptodon goliah* and *Megalania prisca*, are found in both large and small sample sizes. Being a bird *Phaps*, we think, was probably subject to both preservational and collecting bias. Hence it may well have been more common than here indicated. So it seems likely there weren't any localized populations but we would recommend more systematic collecting, especially in the western regions, before drawing any further conclusions on this point.

Only a single human fossil, the Talgai skull, has been found on the Downs. Even human artifacts contemporaneous with the megafauna are probably nonexistent as there is only a single, unconfirmed report of their existence (Klaatsch, 1904), and we have seen none in our collecting on the Downs. This may imply that the Downs fossils and deposits date to a time before the entry of humans into Australia. Gill (1978) thought the Talgai skull clearly postdated the extinct marsupials. Ninja turtles are also uncommon, which is unexpected in view of their size and exuberant armor. In addition to the holotype of *Ninjemys oweni*, their presence is confirmed by a single meiolaniid vertebra from near Macalister. This suggests that they were widespread — the holotype is from "Kings Creek" — but quite rare.

## Pliocene taxa

Several species considered to be Pliocene (e.g., by Archer, *et al.*, 1984) have been recorded in the QM collections from the eastern Downs. These include *Macropus dryas, Osphranter woodsi, Protemnodon devisi, Euryzygoma dunense* and possibly *Macropus pan*. Four possibilities exist: i) there are some unrecognized Pliocene deposits in the eastern Downs; ii) some Pliocene species persisted, perhaps in reduced numbers, into the Pleistocene, iii) they are simply mis-identified; and iv) the locality data are incorrect. Even though detailed Pleistocene stratigraphy has yet to be carried out on the Downs, the fact that all of putative Pliocene taxa derive from localities with large sample sizes (17–25 taxa) suggests that the first possibility is unlikely. In order to very roughly assess the likelihood of misidentification, we looked at the specimens of *Euryzygoma* reported. These included an incomplete temporal from Macalister, nine isolated and worn incisors (some of which may be macropod) from Freestone Ck. and Dalby and two dentaries with very worn cheek teeth from Gowrie. Since we are not aware that diprotodont genera can be accurately distinguished from fragmentary cranial elements or the roots of incisors we feel that these identifications may be in error. From the amount of wear on the teeth — which are usually considered the more diagnostic structures in mammals — in the Gowrie specimens we hesitate to take these to be confidently identifiable. As for the remainder of the taxa concerned, we cannot distinguish between the remaining possibilities at this time, but our experience with the reported *Euryzygoma* material suggests that misidentification cannot be ruled out as an explanation.

## Specific groups

Looking at the specific groups present on the eastern Downs, further comments are warranted. Of the wombats, *Phascolonus* was the most widespread. This may be the result of its large size, but the smaller *Vombatus* is also (moderately) widespread, suggesting that both of these forms were actually prominent in the Downs mammalian fauna.

Potoroines and hypsiprymnodontines seem to have been rare but are also small, so caution is advised. Of course if *Propleopus* was a predator, as has been suggested (Archer and Flannery, 1985), its rarity is to be expected. Large macropodids, on the other hand, were common; most sites have *Macropus titan, Protemnodon anak* and *P. roechus*. Other macropods are found at fewer than ten sites, although *M. agilis, M. ferragus* and *Troposodon minor*, found at eight to nine sites, are reasonably common. Sthenurines (except *T. minor*) are found at fewer sites, suggesting that they (even *T. minor*) were generally rarer than macropodines. But their presence does suggest that some of the eastern Downs was wooded to a greater extent than when visited by Leichhardt in the early 19th century.

Of the diprotodontids, the 'large *Diprotodon*' is found at almost all sites ranging across the Downs up and into the dividing range. It is approximately eight times as common as the smaller form, which may imply that the smaller individuals were juveniles or simply that the large and robust bones of larger animals were more easily preserved and discovered than those of the smaller form. The smaller diprotodontids are still poorly understood taxonomically so no conclusions about them are presently warranted.

Palorchestids seem only moderately widespread and monotremes seem to have been rare. This is supported by our field experience — very few monotremes have been found after much searching by both professionals and amateurs. As mentioned previously carnivores are expected to be rare. The most widespread were *Thylacoleo* and *Megalania*, the latter confirming the significant role of reptilian predators in Australian Pleistocene faunae.

Teleost fossils are rare and restricted to the eastern and southeastern regions. But in our opinion, based on collecting experience, this is due to collecting bias. Teleost fossils have been found at all of the systematically collected localities, except 'Bundah' (which produced no certain fossils of aquatic or amphibious animals at all), and almost none of the other sites. Dipnoans are a different matter, and have been known from the Pliocene at Chinchilla since the nineteenth century. Those from the eastern Downs belong to the same species, *Ceratodus palmeri*, as that from Chinchilla and are all recorded from Kings Creek. We suspect that this accurately reflects their distribution when alive, although why they have not been recorded from deposits on the Condamine, where they lived during the Pliocene, is unknown. It may be that the Kings Creek population was a relict population during the Pleistocene.

## Absent taxa

Several forms that might reasonably have been expected are not in fact present in the QM collections nor, to our knowledge, in any other collections from the eastern Downs. Since these are animals of moderate to large size, we are reasonably confident that they were actually absent, although we don't know why. These are madtsoine snakes (such as *Wonambi*), dromornithid birds and ziphodont crocodilians. The first two might be expected on the basis of size — both emus and smaller snakes have been found — and shed teeth of ziphodont crocs might be expected to have been collected, even if mistaken for teeth of *Megalania*. But none are present.

Possums do not occur in the QM (or London) collections from the Downs. This might be attributed to their small size, except that they have not been found at systematically collected localities nor in searches specifically for them (Godthelp, pers. comm, 1995).

Crocodilians are more common and diverse in the Dalby region and this is borne out by field experience. So while crocs were not actually absent in eastern regions they seem to have been decidedly rare. *Megalania*, on the other hand, seems to have been widely spread. It is not known from the Cecil Plains region, but this may be simply a matter of the small sample from that region.

## SUMMARY

There is presently no evidence for faunal regionalization or the existence of more than a single local fauna in the eastern Darling Downs Pleistocene. Few taxa (14 out of 63) are found at more than five (of 68) localities and even fewer (five) at more than 10. The uncommon taxa seem to have been widespread over the Downs, and may have had small population sizes, or may have been subject to preservational bias. Sthenurines seem to have been less common than macropodines, but their presence suggests that the Pleistocene Downs did support some woodland. Ninja turtles almost certainly had small populations. Species considered to be Pliocene are recorded, but whether they represent remnant populations or simply mistakes is unknown. The large form of *Diprotodon* was widespread and seems to have been common, whereas palorchestids were less common, and monotremes seem to have been rare. The most common carnivorous forms were *Megalania* and *Thylacoleo*. Crocodiles seem to have been most common and diverse in the Dalby region. The rarity of teleost fossils is probably due to collecting bias, but lungfish seem to have been restricted to Kings Creek, perhaps as a relict population. There is no indication that possums, ziphodont crocodiles, dromornithid birds or madtsoine snakes inhabited the Pleistocene Downs.

## ACKNOWLEDGMENTS

We appreciate the assistance of Bernard Cook, Angela Hatch, Henk Godthelp and Ian Sobbe in the course of this research, and of Bevan and Debra Byers, John Mahon, Gary and Neville Rannfeldt, Julian Ridgeway and Grantleigh Wolf in drawing our attention to and providing access to localities. Cornelia Kurz was funded by the Deutscher Akademischer Austauschdienst.

## REFERENCES

Archer, M. (1984). Background to the search for Australia's oldest mammals. In 'Vertebrate Zoogeography and Evolution in Australasia'. (Eds M. Archer and G. Clayton) pp. 517–565. (Hesperian Press: Australia).

Archer, M. and Flannery, T. F. (1985). Revision of the extinct gigantic rat kangaroos (Potoroidae: Marsupialia), with descriptions of a new Miocene genus and species and a new Pleistocene species of *Propleopus*. *Journal of Paleontology* **59**, 1331–1349.

Archer, M., Clayton, G. and Hand, S. (1984). A checklist of Australasian fossil mammals. In 'Vertebrate Zoogeography and Evolution in Australasia.' (Eds M. Archer and G. Clayton) pp. 1027–1086. (Hesperian Press: Australia).

Bartholomai, A. (1976). Notes on the fossiliferous Pleistocene fluviatile deposits of the eastern Darling Downs. *Bureau of Mineral Resources, Geology and Geophysics, Bulletin* **166**, 153–154.

Bennett, G. F. (1872). A trip to Queensland in search of fossils. *Annals and Magazine of Natural History* ser. 4, **9**, 314–321.

Bennett, G. F. (1876). 'Notes of rambles in search of fossils on the Darling Downs'. (Government Printer: Australia).

French, M. (1989). 'Conflict on the Condamine'. (Darling Downs Institute Press: Australia).

Gill, E. D. (1978). Geology of the late Pleistocene Talgai cranium from S.E. Queensland, Australia. *Archaeology and Physical Anthropology in Oceania* **13**, 177–197.

Ingram, G. J. (1990). The works of Charles Walter de Vis, Alias 'Devis', alias 'Thickthorn'. *Memoirs of the Queensland Museum* **28**, 1–34.

Klaatsch, H. (1904). Übersicht über den bischerigen Verlauf und die Errungenschaften seiner Reise in Australien bis Ende September 1904. *Zeitschrift für Ethnologie* **1904**, 211–213.

Lydekker, R. (1887). 'Catalogue of the fossil Mammalia in the British Museum (Natural History). Part V. The Group Tillodontia, the Orders Sirenia, Cetacea, Edentata, Marsupialia, Monotremata and Supplement'. (British Museum: England).

Lydekker, R. (1888). 'Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History). Part I. The Orders Ornithosauria, Crocodilia, Dinosauria, Squamata, Rhynchocephalia, and Protorosauria'. (British Museum: England).

Lydekker, R. (1889). 'Catalogue of the fossil Reptilia and Amphibia in the British Museum (Natural History). Part III. The Order Chelonia'. (British Museum: England).

Macintosh, N. W. G. (1967). Fossil man in Australia. *Australian Journal of Science* **30**, 86–98.

Mahoney, J. A. and Ride, W. D. L. (1975). Index to the genera and species of fossil Mammalia described from Australia and New Guinea between 1838 and 1968 (including citations of type species and primary type specimens). *Western Australian Museum, Special Publication* **6**, 3–249.

Meltzer, D. J. and Mead, J. I. (1985). Dating late Pleistocene extinctions: theoretical issues, analytical bias, and substantive results. In, 'Environments and extinctions: man in late glacial North America' (Eds J. I. Mead and D. J. Meltzer) pp. 145–173 (Center for the Study of Early Man, University of Maine: U.S.A.).

Owen, R. (1845). 'Descriptive and illustrated catalogue of the fossil organic remains of Mammalia and Aves contained in the Museum of the Royal College of Surgeons of England'. (Richard and John E. Taylor: England).

Owen, R. (1877). 'Researches on the fossil remains of the extinct mammals of Australia; with a notice of the extinct marsupials of England'. (J. Erxleben: England).

Van Tets, G. F. and Rich, P. V. (1990). An evaluation of de Vis' fossil birds. *Memoirs of the Queensland Museum* **28**, 165–168.

Woods, J. T. (1960). Fossiliferous fluviatile and cave deposits. In, D. Hill and A. K. Denmead, eds., 'The Geology of Queensland'. *Journal of the Geological Society of Australia* **7**, 393–403.

## APPENDIX 1: FAUNAL LISTS FROM LYDEKKER (1887, 1888, 1889):

Clifton list includes 'Clifton Plains' and Kings Creek list, excludes those given as 'King Ck., Clifton'

**Condamine River**:
Diprotodontidae
    *Diprotodon*, large form
    small diprotodontid
Thylacoleonidae
    *Thylacoleo carnifex*
Crocodylidae
    crocodilian
Varanidae
    *Megalania prisca*

### CECIL PLAINS REGION:

**St. Ruth:**
Diprotodontidae
    *Diprotodon*, large form
Vombatidae
    *Phascolomys medius*
    *Phascolonus gigas*
    *Vombatus ursinus*
Macropodinae
    *Macropus ferragus*
    *Osphranter altus*
    *Protemnodon brehus*
    *Protemnodon roechus*
Sthenurinae
    *Procoptodon rapha*
    *Troposodon minor*

### TOOWOOMBA REGION:

**'Eton Vale'**:
Vombatidae
    *Phascolomys magnus*
    *Phascolonus gigas*
Macropodinae
    *Osphranter altus*
    *Protemnodon roechus*
Diprotodontidae
    *Diprotodon*, large form
Thylacoleonidae
    *Thylacoleo carnifex*
Chelidae
    chelid

**Gowrie**:
Vombatidae
    *Phascolomys magnus*
    *Phascolomys medius*
    *Phascolonus gigas*
    *Vombatus ursinus*
Macropodinae
    *Macropus titan*
    *Osphranter altus*
    *Osphranter robustus*
    *Protemnodon anak*
    *Protemnodon roechus*
Sthenurinae
    *Procoptodon rapha*
    *Sthenurus atlas*
Diprotodontidae
    *Diprotodon*, large form
    small diprotodontid
Dasyuridae
    *Dasyurus viverrinus*
    *Sarcophilus laniarius*
Thylacoleonidae
    *Thylacoleo carnifex*
Crocodylidae
    crocodilian
Varanidae
    *Megalania prisca*

**Hodgsons Creek**:
Thylacoleonidae
    *Thylacoleo carnifex*

**Westbrook Creek**:
Chelidae
    chelid

### CLIFTON REGION:

**Clifton**:
Vombatidae
    *Phascolonus gigas*
Macropodinae
    *Macropus giganteus*
    *Macropus titan*
    *Protemnodon brehus*
    *Protemnodon roechus*
Sthenurinae
    *Procoptodon pusio*
Diprotodontidae
    *Diprotodon*, large form
Crocodylidae
    *crocodilian*
**Kings Creek**:
Vombatidae
    *Phascolonus gigas*

Macropodinae
  *Protemnodon brehus*
Diprotodontidae
  *Diprotodon*, large form
Thylacoleonidae
  *Thylacoleo carnifex*
Varanidae
  *Megalania prisca*
Meiolaniidae
  *Ninjemys oweni*

## APPENDIX 2

Distribution of taxa on the eastern Darling Downs.
DR = Dalby region; CPR = Cecil Plains region; TR = Toowoomba region; CR = Clifton region.

| | DR | CPR | TR | CR |
|---|---|---|---|---|
| *Lasiorhinus latifrons*/sp. | | | | x |
| *Phascolomys angustidens* | | | x | |
| *P. medius* | | | x | x |
| *Phascolonus gigas*/sp. | | x | x | x |
| *P. magnus* | x | | | |
| *Vombatus ursinus* | | | x | x |
| *V.* sp. | x | | | |
| *Aepyprymnus rufescens* | | | x | |
| *Propleopus oscillans* | x | | | x |
| *Macropus agilis* | x | | x | x |
| *M. dryas* | | | x | |
| *M. ferragus* | x | | x | x |
| *M. giganteus* | | | | x |
| *M. pan* (or *faunus*) | | | | x |
| *M. pearsoni* | x | x | x | x |
| *M. piltonensis* | | | | x |
| *M. thor* | | | x | x |
| *M. titan* | x | x | x | x |
| *Onychogalea unguifera* | | | x | x |
| *Osphranter altus* | | x | x | x |
| *O. woodsi* | | | | x |
| *Procoptodon goliah* | x | | | x |
| *P. pusio* | x | | x | x |
| *P. rapha* | | | | x |
| *Protemnodon anak* | x | x | x | x |
| *P. affinis* | | | | x |
| *P. brehus* | x | | x | x |
| *P. devisi* | | | x | x |
| *P. roechus* | x | x | x | x |

| | | | | |
|---|---|---|---|---|
| *Sthenurus andersoni* | x | | x | x |
| *S. pales* | | | | ? |
| *Thylogale* sp. | | | | x |
| *Troposodon kenti* | | | | x |
| *T. minor* | x | | x | x |
| *Wallabia indra* | x | | x | x |
| *Diprotodon* small form | x | x | x | x |
| *Diprotodon* large form | x | x | x | x |
| small diprotodontid | x | x | x | x |
| *Palorchestes azael* | x | x | | x |
| *P. parvus* | | | | x |
| *Dasyurus* spp. | | | | x |
| *Sarcophilus laniarius*/sp. | x | | x | x |
| *Thylacinus cynocephalus* | | | x | x |
| *Thylacoleo carnifex*/sp. | x | x | x | x |
| *Perameles* sp. | | | ? | x |
| *Ornithorhynchus anatinus* | | | | x |
| rodent | | | | x |
| *Dromaius novaehollandiae* | x | | | x |
| *Ardea* cf. *A. novaehollandiae* | | | | x |
| *Ephippiorhynchus asiaticus* | | | | x |
| *Phaps* sp. | | | | x |
| *Progura gallinacea* | | | | x |
| *Gallinula mortierii* | | | x | x |
| duck | | | | x |
| quail | | | | x |
| buteonine | | | | x |
| *Crocodylus porosus* | x | | | |
| *Pallimnarchus pollens* | x | | | |
| crocodilian | | | x | x |
| *Megalania prisca* | x | | x | x |
| varanid | | | | x |
| agamid | | ? | | x |
| snake | | | | x |
| meiolaniid | x | | | x |
| chelid | x | | x | x |
| trionychid | | | | x |
| frog | | | | ? |
| *Ceratodus palmeri* | | | | x |
| *Tandanus tandanus* | | | | x |
| teleost | | | x | x |

## Appendix 3

Ranking of taxa (mostly monospecific genera or species) by the number of sites at which they occur. Those sites for which identifications were only to category higher than genus, or to genus for multispecific genera, and "Jimbour Creek", "Condamine River" and "Kings Creek" were excluded, as being too extensive for single localities in this context. 68 localities (not all with taxa identified to genus) are included. Numbers on the right are the total number of taxa found at the sites at which the listed taxa occurred (given only for those that occurred at fewer than 10 sites). *: species recorded as Pliocene in age.

| Taxon | No. of sites | No. of taxa from each site |
|---|---|---|
| *Lasiorhinus latifrons*/sp. | 2 | 17, 1 |
| *Phascolomys angustidens* | 2 | 25, 17 |
| *P. medius* | 2 | 22, 1 |
| *Phascolonus gigas*/*magnus*/sp. | 8 | 25, 22, 18, 17, 14, 4, 1, 1 |
| *Vombatus ursinus*/sp. | 6 | 25, 19, 17, 16, 14, 3 |
| *Aepyprymnus rufescens* | 1 | 25 |
| *Propleopus oscillans* | 1 | 9 |
| *Macropus agilis* | 8 | 25, 22, 19, 17, 14, 12, 7, 5 |
| *M. dryas* * | 1 | 25 |
| *M. ferragus* | 7 | 22, 19, 17, 16, 9, 5, 4 |
| *M.* cf. *M. giganteus* | 1 | 7 |
| *M. pan* (or *faunus*) * | 1 | 19 |
| *M. pearsoni* | 4 | 22, 16, 7, 5 |
| *M. piltonensis* | 1 | 19 |
| *M. thor* | 2 | 25, 19 |
| *M. titan* | 21 | – |
| *Onychogalea unguifera* | 2 | 25, 22 |
| *Osphranter altus* | 4 | 25, 17, 14, 2 |
| *O. woodsi* * | 1 | 19 |
| *Procoptodon goliah* | 5 | 17, 14, 9, 1, 1 |
| *P. pusio* | 4 | 25, 22, 17, 16 |
| *P. rapha* | 2 | 22, 14 |
| *Protemnodon affinis* | 1 | 17 |
| *P. anak* | 27 | – |
| *P. brehus* | 3 | 25, 22, 3 |
| *P. devisi* * | 2–3 | 25, 19?, 17 |
| *P. roechus* | 12 | – |
| *Sthenurus andersoni* | 4 | 25, 22, 17, 3 |
| *S. pales* | 1? | 19 |
| *Thylogale* sp. | 1 | 22 |
| *Troposodon kenti* | 1 | 12 |
| *T. minor* | 8 | 25, 22, 19, 17, 16, 12, 7, 1 |
| *Wallabia indra* | 2 | 25, 12 |
| *Diprotodon* small | 5 | 17, 16, 5, 4, 1 |
| *Diprotodon* large | 39 | – |
| small diprotodontid | 15 | – |

| | | |
|---|---|---|
| *Palorchestes azael* | 5 | 22, 16, 12, 5, 2 |
| *P. parvus* | 1 | 1 |
| *P.* sp. | 2 | 18, 1 |
| *Dasyurus* sp. | 5 | 22, 18, 17, 14, 12 |
| *Sarcophilus laniarius*/sp. | 4 | 17, 9, 9, 9 |
| *Thylacinus cynocephalus* | 4 | 25, 22, 17, 9 |
| *Thylacoleo carnifex* | 9 | 25, 17, 17, 12, 9, 9, 7, 5, 4 |
| *Perameles* sp./bandic. | 3 | 18, 14, 6 |
| *Ornithorhynchus anatinus* | 1 | 17 |
| rodent | 2 | 18, 9 |
| *Dromaius novaehollandiae*/sp. | 2 | 17, 12 |
| *Ardea* cf. *A. novaehollandiae* | 1 | 14 |
| *Ephippiorhynchus asiaticus* | 1 | 19 |
| *Phaps* sp. | 1 | 2 |
| *Progura gallinacea* | 1 | 19 |
| quail | 1 | 22 |
| *Gallinula mortierii*/sp. | 3 | 25, 17, 1 |
| *Crocodylus porosus* | 1 | 16 |
| *Pallimnarchus pollens* | 1 | 16 |
| crocodilian | 6 | 25, 19, 18, 12, 12, 7 |
| *Megalania prisca* | 8 | 22, 19, 18, 17, 12, 12, 4, 1 |
| varanid | 2 | 18, 12 |
| agamid | 1–2 | 18, 7? |
| snake | 1 | 18 |
| meiolaniid | 1 | 16 |
| chelid | 7 | 25, 18, 16, 12, 12, 7, 3 |
| trionychid | 1 | 19 |
| frog? | 1 | 18 |
| *Tandanus tandanus* | 1 | 22 |
| teleost | 4 | 18, 17, 12, 9 |

# Analysis of a Late Quaternary Deposit and Small Mammal Fauna from Nettle Cave, Jenolan, New South Wales.

DEBORAH A. MORRIS[1], M.L. AUGEE[1], D. GILLIESON[2] AND J. HEAD[3].

[1]School of Biological Science, University of NSW, Sydney NSW 2052;
[2]School of Geography and Oceanography, University College, University of NSW,
Australian Defence Force Academy, Canberra ACT 2600;
[3]Radiocarbon Laboratory, Australian National University, Canberra ACT 2601.

Morris, D.A., Augee, M.L., Gillieson, D. and Head, J. (1997). Analysis of a late Quaternary deposit and small mammal fauna from Nettle Cave, Jenolan, New South Wales. *Proceedings of the Linnean Society of New South Wales* **117**: 135-162

A deposit of small mammal bones in Nettle Cave, part of the Jenolan Caves system, was excavated. The bone deposit appears to be the result of owl pellet accumulation. A pair of Sooty Owls (*Tyto tenebricosa*) currently inhabits a roosting site within the cave. The deposit was excavated to a depth of 68 cm, which represents an accumulation throughout the last glacial recession in the late Pleistocene to the present. Two radiocarbon dates (7,140 ± 280 and 8,730 ± 280 BP) were obtained from discrete charcoal lenses in the middle layers of the deposit. Analyses of small mammal remains and sediments indicate climatic conditions during the late Pleistocene were colder and drier than at present, becoming warmer and wetter in the Holocene. The apparent abrupt extinction of *Burramys parvus* and the rapid decline in abundance of *Mastacomys fuscus* in the Jenolan area are attributed to a brief humid period that occurred in southeastern Australia at around 15,000 to 14,000 BP.

Manuscript received 1 June 1996, accepted for publication 23 October 1996.

KEY WORDS: Nettle Cave, owl pellet accumulation, *Tyto tenebricosa*, late Quaternary, *Burramys parvus*, sediments, climate.

## INTRODUCTION

Fossil deposits have long been used as a basis for the interpretation of past environments. In Australia, various Quaternary cave deposits have been analysed and used to reconstruct the faunal and climatic history of the surrounding area (e.g., Balme et al. 1978, Baynes 1987, Baynes et al. 1976, Hope et al. 1977, Porter 1979, Wakefield 1972). Deposits containing small mammal remains have been found to be particularly useful (Lundelius 1963).

Little fossil material had been found in Jenolan Caves until a collection of bones was analysed from a small cave overlooking the lower carpark (Hope 1979). Infrequent discoveries of isolated skeletal remains from various caves have been reported in subsequent years. This study involved excavation of a fossil deposit in Nettle Cave, part of the Jenolan Caves system. The excavation yielded an abundance of intact small mammal bones, including those belonging to now locally extinct taxa, together with avian postcranial material and a few agamid and scincid mandibles (which are not discussed in this paper).

## MATERIALS, METHODS AND STUDY AREA

The Jenolan Caves Reserve is situated on the Great Dividing Range (33°47'S,

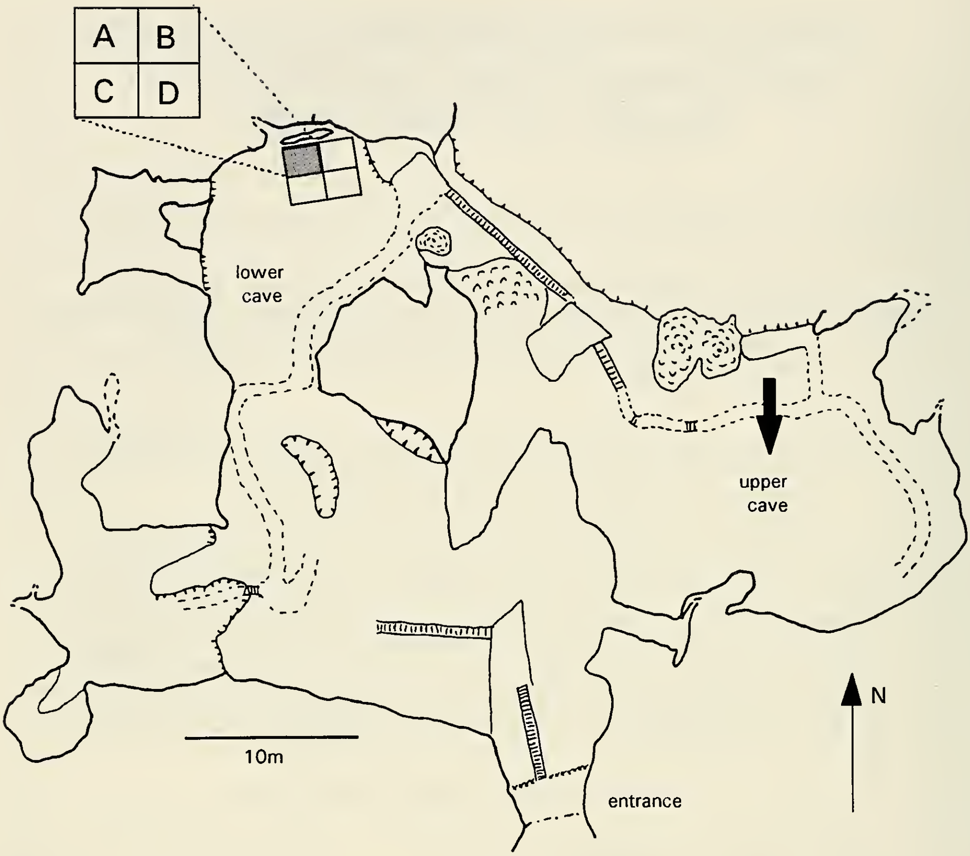


Figure 1. Plan of Nettle Cave, Jenolan, with the area of heaviest deposition of owl pellets outlined (lower cave). The highlighted area is the quadrat selected randomly for excavation. This area was further subdivided into quarters as shown in the insert. The quadrat and the subdivided areas are not to scale. The current Sooty Owl roost is indicated by the arrow (upper cave). (modified from Cox et al. 1989).

150°02'E; 1,100–1,200 m a.s.l.) approximately 110 km west of Sydney. This area has a maximum yearly mean temperature of 16.6°C and a minimum of 8.0°C (recorded at Katoomba - approximately 30 km from Jenolan). The average annual precipitation is 1,412 mm with the greatest rainfall occurring between December and June. The vegetation within the Jenolan Caves Reserve supports eight major vegetation communities (Lembit 1988) ranging from open forest to cleared land.

Nettle Cave is a high-level entrance into the Devil's Coach House, which is itself a natural tunnel approximately 80 m high and 40 m wide (Cox et al. 1989). Flowstone forms a false floor in Nettle Cave (Anon. 1988). Cave conditions are dry (Nettle Cave is about 20 m above modern flood levels), with an annual temperature range from below zero to 30°C (Cox et al. 1989). The cave receives light from the entrance in the south, from a roof-hole in the northeast and from Arch Cave in the southwest (Fig. 1).

The fossil deposit examined in this study is concentrated beneath a rock ledge in the roof of Nettle Cave close to the northern wall of the lower cave (Fig. 1). A pair of Sooty Owls (*Tyto tenebricosa*) currently occupies a nocturnal roosting site in the north-facing wall of the upper Nettle Cave (Fig. 1). Sooty Owls were first reported roosting in

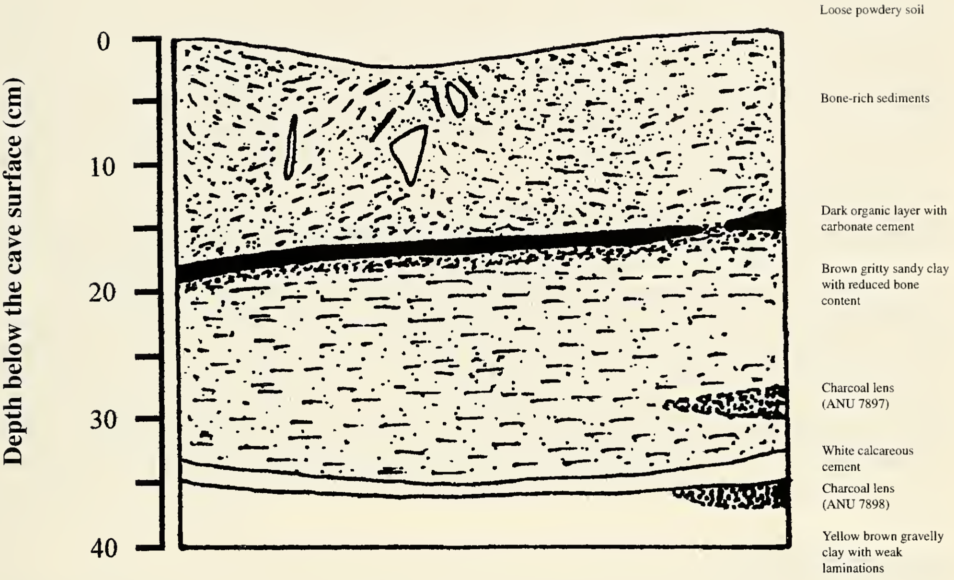


Figure 2. Stratigraphy of the upper levels of the southern wall of the excavated pit in the owl pellet deposit, Nettle Cave.

Nettle Cave late last century by Jeremiah Wilson (the first official guide at Jenolan) (E. Holland, pers. comm.). The nocturnal roosting site is thought to communicate with the rock ledge in the lower cave by a tunnel in the roof of the cave (E. Holland, pers. comm.). The pair of Sooty Owls appears to roost diurnally in the roof of the Devil's Coach House.

In July 1990, owl pellets and bone material associated with disintegrated pellets were collected from the surface of an area of approximately 2 x 2 m directly beneath the rock ledge in the roof of the lower Nettle Cave. On 10 January 1991, three fresh pellets were collected approximately 4.5 m from the northwestern wall of the lower cave.

## Excavation

Excavation of the deposit began in January 1991. An area measuring 1.5 x 1.5 m was pegged over the site of heaviest deposition with one side abutting the northeastern wall (Fig. 1). A test dig was begun adjacent to the pegged area; its dimensions were about 50 x 50 cm and 58 cm deep. The dig proved to be rich in bone to this depth. Charcoal lenses were found at 28 cm and 35 cm.

A quadrant measuring roughly 75 x 75 cm was chosen at random for excavation (Fig. 1). A section drawing of the southern wall of the excavation is shown in Fig. 2. Spits (defined in this paper as arbitrary vertical divisions, with respect to the stratigraphy in the deposit) from 0–5 cm, 5–13 cm, 13–25 cm and 25–35 cm were excavated. The deposit to 35 cm below the present cave floor was rich in bone.

Below 35 cm the main excavation was subdivided into four areas of roughly equal size (A, B, C and D) (Fig. 1) and excavated separately. Two centimetre layers (here defined as natural vertical intervals of sediments, in which conditions of formation in each layer appear to have been consistent) were removed, following the line of the sediment, from 35 to 41 cm. These layers contained less bone than above. The bones were found in association with small aggregates of sediment cemented by calcium carbonate. A limestone outcrop was apparent at 37 to 41 cm on the eastern wall of the pit, but receded beyond the wall of the pit below 41 cm.

The sediment was heavily cemented by calcium carbonate below 41 cm. Excavation of quadrants A and C (Fig. 1) became impossible. Excavation of quadrants B and D from 41 to 44 cm was possible by using the sharp end of a trowel to break up the sediment.

At 44 cm the sediment from quadrant D and the outer part of quadrant B was so firmly cemented that further excavation of this section of the pit with the hand-held implements available was impossible. The remainder of quadrant B contained bone in a relatively soft sediment. This area was excavated to a depth of 68 cm. Spits ranging from 2 to 5 cm in depth were removed from 44 to 68 cm of the excavation. Excavation ceased in April 1991 at a depth of 68 cm, despite bone being visible below this point. The excavation was not backfilled as is customary because the Jenolan Caves Scientific Advisory Committee plans to line the walls of the excavation with perspex covers and use the pit as an exhibit.

### Sediment Samples

Sediment samples were taken every 5 cm, or every 2 cm if the stratigraphic layer was narrower, from the inner part of the southern wall of quadrant B (Fig. 1). A total of 16 samples was taken to a depth of 64 cm. The pH of each sample was determined in the field by using a CSIRO test kit. The method of measuring particle size and the particle size classification follow Folk (1968).

### Carbon Samples

Although minor amounts of charcoal were present throughout the levels (here defined as any point on the vertical axis of the deposit) of the excavation, usable quantities were only located in two lenses at 28–29 cm and 35–36 cm depth in the western wall of the main pit. The lenses were sampled for radiocarbon dating using the methods of Gupta and Polach (1985) and submitted to the Australian National University Radiocarbon Laboratory. For sample ANU-7897 (Nettle Cave 28–29 cm), possible contaminants were removed and the sample washed in hot 10% HCl, rinsed and dried to remove possible carbonate. For sample ANU-7898 (Nettle Cave 35–36 cm), the sample was wet sieved and the fraction <500 um taken for dating. After solvent extraction, the sample was washed in boiling HCl, and NaOH insoluble residue (non-humic) was re-acidified, rinsed and dried.

### Preparation of the Bone Remains

All surface material and subsamples from 0–5 cm were washed in water and air-dried. Material from 13 cm downwards required acid treatment (10% acetic acid for seven days) for separation of bone from matrix. Levels 5–13 cm and 39–41 cm were not analysed because of time constraints.

### Identification of Mammalian Material

Each depth interval (here defined as a vertical division between two measured levels within the excavation, e.g. 0–5 cm) was analysed separately. The upper levels of the deposit contained relatively more intact maxillary and dentary specimens than the lower levels. All maxillary and dentary material bearing teeth or with tooth sockets, and isolated teeth were identified.

Marsupials and rodents were identified by comparing maxillary and dentary fragments and isolated teeth with published descriptions (Appendix A) and with reference specimens held at the University of NSW and the Australian Museum. Microchiropteran specimens were identified by S.J. Hand.

Dental nomenclature of marsupials follows Luckett (1993). Marsupial specimens were considered to be juvenile if the P3 and/or M4 had not fully erupted. Edentulous mandibular specimens were regarded as juvenile according to size variation recorded in the literature and by comparison with reference material.

Nomenclature generally follows that of Walton (1988) and Walton and Richardson (1989). *Pseudocheirus peregrinus* and *Petauroides volans* are referred to Pseudocheiridae (Archer 1984), and *Acrobates pygmaeus* to Acrobatidae (Aplin and Archer 1987).

The identified mammalian and unidentified avian material will be lodged at the Australian Museum (the reptile specimens were sent to the South Australian Museum for identification and cataloguing, and are lodged there).

### Quantitative Methods

In order to make inferences regarding the composition of the mammalian assemblage, the minimum number of individuals (MNI) of each taxon represented in each analysed depth interval was determined. Estimation of the MNI follows Baynes et al. (1976). Identifiable right and left dentaries and maxillae were counted separately. The most numerous element was taken as the MNI. Relative abundance was taken as the percentage of all species occurring in each depth interval. (These percentages give a more accurate representation of each species from depth interval to depth interval than does the MNI.)

## RESULTS

### Sedimentary Analyses

#### Stratigraphy

A section drawing of the southern wall of the excavated pit is shown in Fig. 2. Because cementation by calcium carbonate made definition of the stratification of the lower layers difficult, only the top 40 cm of the excavation are shown. The gross stratigraphy of the bone-rich sediment suggests these sediments had formed as a result of a series of deposits of air-fall debris. The dark organic layer indicates a stable surface. The sediment changed below this layer to a brown, gritty, sandy clay that contained an increased amount of charcoal and soil particles, but a reduced amount of bone. Two discrete lenses of charcoal were evident. Between these lenses was a white, calcareous, cemented layer which may represent a former water saturation level. The sediment below this cemented layer to the base of the pit contained a yellow-brown, gravelly clay which may have been the result of water ponding in the cave. There was no clear stratification below 40 cm.

#### Sediment Chemistry

The field pH measurements were uniformly 9.5 for the 16 sediment samples. An alkaline environment promotes the precipitation of calcium carbonate out of solution and the rapid decomposition of organic material by bacteria and fungi (Levinson 1982).

#### Radiocarbon Dates

Radiocarbon ages are reported in Table 1 as conventional years BP. $d^{13}C$ values were estimated and given an error of 2.0 permil. The two radiocarbon ages are significantly different (p>0.05).

TABLE 1 Radiocarbon ages of charcoal from the Nettle Cave deposit.

| Sample code | Depth (cm) | d14C (permil) | δ13C (permil) | D14C (permil) | age (years BP) |
|---|---|---|---|---|---|
| ANU-7897 | 28–29 | - 587.8 ± 13.7 | - 24.0 ± 2.0 | - 588.6 ± 13.8 | 7,140 ± 280 |
| ANU-7898 | 35–36 | - 661.9 ± 11.4 | - 24.0 ± 2.0 | - 662.6 ± 11.5 | 8,730 ± 280 |

## Source of the Sediment

Mineral magnetic results from the Nettle Cave sediment samples are compared with data from other sites in the Jenolan Caves catchment (Stanton 1989) in Table 2. The results indicate that the Nettle Cave sediments are distinct from these possible sources and especially from the Mammoth Cave fluvial sediments.

TABLE 2 Mean magnetic parameters for different sediment source areas, Jenolan catchment. SIRM denotes saturation isothermal remanent magnetisation. Data other than that for Nettle Cave from Stanton (1989).

| Source area | Mean susceptibility | Mean frequency dependent susceptibility | Mean SIRM |
|---|---|---|---|
| Nettle Cave | 1.43 | 9.9 | 20.6 |
| Terrace Creek | 4.24 | 6.9 | 41.4 |
| Jenolan-Bindo Creek Divide | 4.41 | 7.9 | 49.6 |
| Western Ridge | 9.24 | 4.2 | 109 |
| Mammoth Cave Fines | 4.24 | 5.4 | 39.9 |
| Mammoth Cave Coarse | 3.7 | 5.2 | 32.5 |

Particle size analysis can provide some information on sediment transport and deposition (Krumbein and Sloss 1963). The relative amounts (by weight) of gravel, sand, silt and clay in each sample from the Nettle Cave deposit are illustrated in Fig. 3. (Unfortunately, bone was included in the gravel fraction; if bone had been excluded, the relative proportions of sand, silt and clay would be greater than that suggested in Fig. 3.) The greatest fluctuations, albeit minor, were in the proportions of gravel and then sand. An increase in the amount of fine material occurred around 37 cm. This increase was coincident with water ponding of the top layer in the lower zone of the deposit. The preponderance of coarser, angular particles in the sediment samples suggests that the sediment is of local origin and has not been subjected to lengthy fluvial transport.

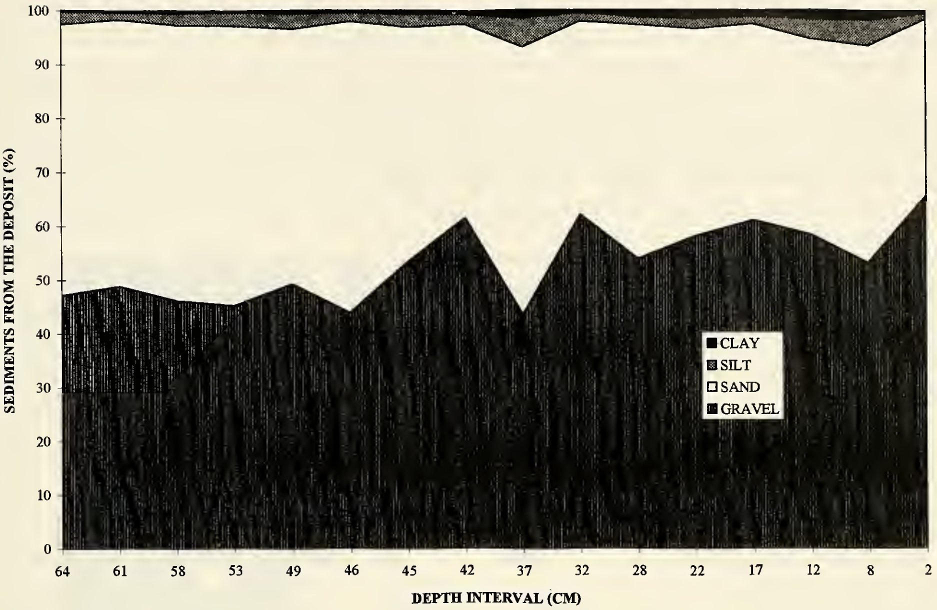


Figure 3. Graphical representation of the amount of gravel, sand, silt and clay (by weight) in the sediments from the Nettle Cave deposit.

Considering the mineral magnetic data and particle size of the Nettle Cave sediments, these sediments are likely to have originated from local soil above the cave. Moreover, the relatively minor fluctuations in the proportions of the sediments throughout the depth of the deposit suggest there was little variation in the source of the sediments.

## Mammal Fauna from the Nettle Cave Deposit

Thirty-five species of mammals were identified in the Nettle Cave deposit (Appendix B). Of these species, 74% are extant and 26% are extinct either locally or in southeastern Australia.

If a species is present in an upper or lower level of the deposit, it tends to appear throughout the upper or lower zone of the deposit, respectively (Table 3). The distribution of some species at 41 to 44 cm appears to be discontinuous.

The majority of the species occurring throughout the deposit (Table 3) are small animals weighing less than 200 g. All these specimens are adult. The larger species present, e.g. *Dasyurus* sp., *P. peregrinus*, *Isoodon obesulus* and *Perameles nasuta*, are represented by subadults.

Species with restricted habitat requirements and range of distribution are the most useful indicators of environmental conditions (Baynes et al. 1976). The changes in relative abundance with time of selected non-volant, small mammal species from the Nettle Cave deposit are illustrated in Fig. 4. These species were selected as indicators of possible environmental change in the Jenolan area for the following reasons:

1. the species showed a change in distribution over time or,
2. the species showed a change in abundance over time and

TABLE 3 Summary of Appendix B: Presence or absence of specimens identified from each depth interval from the Nettle Cave deposit. Presence of species in a depth interval is indicated by a black block. Depth intervals 13–5 cm and 41–39 cm were not analysed, and are represented as narrow, blank bars. S = number of non-volant mammal species in the deposit. n=sum of the MNIs of non-volant mammal species, excepting *A.* spp., *S.* sp., *P.* spp. and *R.* spp. 1. Presence of bats in a depth interval is indicated by a dashed block, but the MNI is not included in n. 2. Presence of birds is indicated by a dashed block; specimens were not identified above order. 3. Skinks were present in depth intervals 5–0 cm and 25–13 cm; agamids were present in depth intervals 5–0, 25–13, 35–25, 37–35 and 39–37 cm.

| *SPECIES* | 68–66 cm | 66–64 cm | 64–59 cm | 59–54 cm | 54–50 cm | 50–46 cm | 46–44 cm | 44–43 cm | 43–41 cm | 39–37 cm | 37–35 cm | 35–25 cm | 25–13 cm | 5–0 cm | Surface |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *Antechinus stuartii* sensu lato | | | | | | | ■ | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A. swainsonii* | | ■ | ■ | ■ | ■ | ■ | ■ | | | ■ | ■ | ■ | ■ | ■ | |
| *A. flavipes* | | | | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *A.* spp. | ■ | | | ■ | | ■ | ■ | ■ | | | ■ | ■ | ■ | ■ | ■ |
| *Sminthopsis murina* | | | ■ | | ■ | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *S.* sp. | | | | | | ■ | | | | | ■ | ■ | ■ | ■ | |
| *Phascogale tapoatafa* | | | ■ | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | |
| *Dasyurus* sp. cf. *D. viverrinus* | | ■ | | | | ■ | | | | | ■ | ■ | | ■ | |
| *Isoodon obesulus* | | | ■ | | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| *Perameles nasuta* | ■ | | ■ | ■ | ■ | ■ | ■ | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Pseudocheirus peregrinus* | | ■ | | | | ■ | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Petauroides volans* | | | | | | | | | ■ | ■ | | ■ | ■ | ■ | ■ |
| *Petaurus breviceps* | ■ | | | | ■ | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Cercartetus nanus* | | | | | | | | | ■ | ■ | ■ | ■ | | ■ | |
| *C. lepidus* | | | ■ | ■ | | | ■ | ■ | | | | | | | |
| *Burramys parvus* | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | | | | | | | |
| *Acrobates pygmaeus* | | | | | | | | | | ■ | ■ | ■ | | ■ | |
| *Potorous* sp. cf. *P. tridactylus* | | | | | | | ■ | | | ■ | ■ | ■ | ■ | ■ | |
| *Bettongia* sp. | | | | | | | | | | ■ | ■ | ■ | ■ | ■ | |
| *Thylogale thetis* | | | | | | | | ■ | | | ■ | | | | |
| *Conilurus albipes* | | | | | | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Pseudomys oralis* | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *P. gracilicaudatus* | | | | | | | | | | | | ■ | | | |
| *P. australis* | | ■ | ■ | ■ | ■ | | ■ | | ■ | ■ | ■ | ■ | ■ | ■ | |
| *P. novaehollandiae* | | | | | | | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| *P. fumeus* | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| *P.* spp. | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | |
| *Mastacomys fuscus* | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *Rattus fuscipes* | | ■ | ■ | | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ | ■ |
| *R. rattus* | | | | | | | | | | | | | | ■ | ■ |
| *R.* spp. | | | | ■ | | ■ | ■ | | ■ | ■ | ■ | ■ | ■ | ■ | |
| *Mus musculus* | | | | | | | | | | | | | | ■ | ■ |
| *Oryctolagus cuniculus* | | | | | | | | | | | | | | ■ | ■ |
| Bats[1] | | | | | | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| Birds[2] | | | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ | ▨ |
| Lizards[3] | | | | | | | | | | ▨ | ▨ | ▨ | ▨ | ▨ | |

| Depth interval | S | n |
|---|---|---|
| Surface | 14 | 119 |
| 5–0 cm | 25 | 1400 |
| 25–13 cm | 19 | 717 |
| 35–25 cm | 23 | 911 |
| 37–35 cm | 22 | 452 |
| 39–37 cm | 21 | 371 |
| 43–41 cm | 16 | 101 |
| 44–43 cm | 12 | 35 |
| 46–44 cm | 14 | 76 |
| 50–46 cm | 9 | 41 |
| 54–50 cm | 10 | 37 |
| 59–54 cm | 8 | 33 |
| 64–59 cm | 12 | 28 |
| 66–64 cm | 9 | 14 |
| 68–66 cm | 4 | 11 |

3. the species' habitat requirements are both well-documented and restricted.

### Modern Mammal Fauna in the Jenolan Area

The term 'modern mammal fauna' is used to describe the fauna inhabiting, or thought to inhabit, the Jenolan area since European settlement. Of the 35 mammal species recovered from the Nettle Cave deposit (Table 3), one (*Conilurus albipes*) is presumed to be extinct (Watts and Aslin 1981); eight (*Dasyurus viverrinus*, *Cercartetus lepidus*, *Burramys parvus*, *Bettongia* sp., *Pseudomys fumeus*, *Pseudomys australis*, *Pseudomys oralis* and *Mastacomys fuscus* are extinct in the area (Strahan 1995; Watts and Aslin 1981); *Pseudomys gracilicaudatus* had previously occurred this far south (remains were found in superficial deposits at Walli Caves near Canowindra and Wombeyan Caves [Mahoney and Posamentier 1975]); the status of *Phascogale tapoatafa* and *Pseudomys novaehollandiae* in this area is uncertain (Strahan 1995; Watts and Aslin 1981); the remaining 23 are locally extant (Strahan 1995).

## DISCUSSION

### Age of the Deposit

The age of specimens in the Nettle Cave deposit can be estimated when associated with stratigraphy, other fauna, radiometric dates and the appearance of the material (after the manner of Baynes (1987)).

Two radiocarbon dates based on charcoal samples were obtained from the middle levels of the deposit (Fig. 2). If one assumes a constant rate of accumulation of sediments to the base of the excavation at 68 cm, then this level may represent 16,000–14,000 years BP. However, ponding and a change in the nature of sedimentation is evident below 35–36 cm (Fig. 2). In addition, abrupt changes in the faunal assemblage around 41–43 cm may indicate either a hiatus in deposition, or a minor unconformity (period of nondeposition or erosion) in the deposit (Krumbein and Sloss 1963). Conversely, changes in the composition of the material being deposited may have produced the change in stratification (Dunbar and Rodgers 1963). For example, changes in grain size may cause pronounced layering. Therefore, this time frame on the basis of sedimentation should be treated with caution, since charcoal was not available at the base of the pit to allow more precise dating.

### Environmental History at Jenolan based on Nettle Cave Sediments

Although real precipitation at the end of the Pleistocene was reputedly low (Dodson 1977; Galloway 1965), seasonal melting of the snow would have made available free water. A study by one of us (D.G., unpublished data) suggests the influx of subsoil particles to the lower levels of the Nettle Cave deposit indicates erosion of the topsoil overlying the cave either due to hillslope instability (Gillieson et al. 1985) or thawing of the ground and subsequent washing away of this surface material. Wind activity would have contributed to the erosion to some degree. More importantly, wind activity is a selective barrier in the transport of particular grains. Coarse particles such as gravel are left behind or deposited close to the source forming a local accumulation. Fine grains (silt and clay) are kept in suspension and transported over long distances (Krumbein and Sloss 1963; Pettijohn 1957; Reineck and Singh 1975). These conditions are reflected in the relatively low amounts of silt and clay in the Nettle Cave sediments (Fig. 3).

The sediment in the levels of the deposit around 44–41 cm consists of a yellow-brown, gravelly clay which was probably the result of local water ponding in the cave.

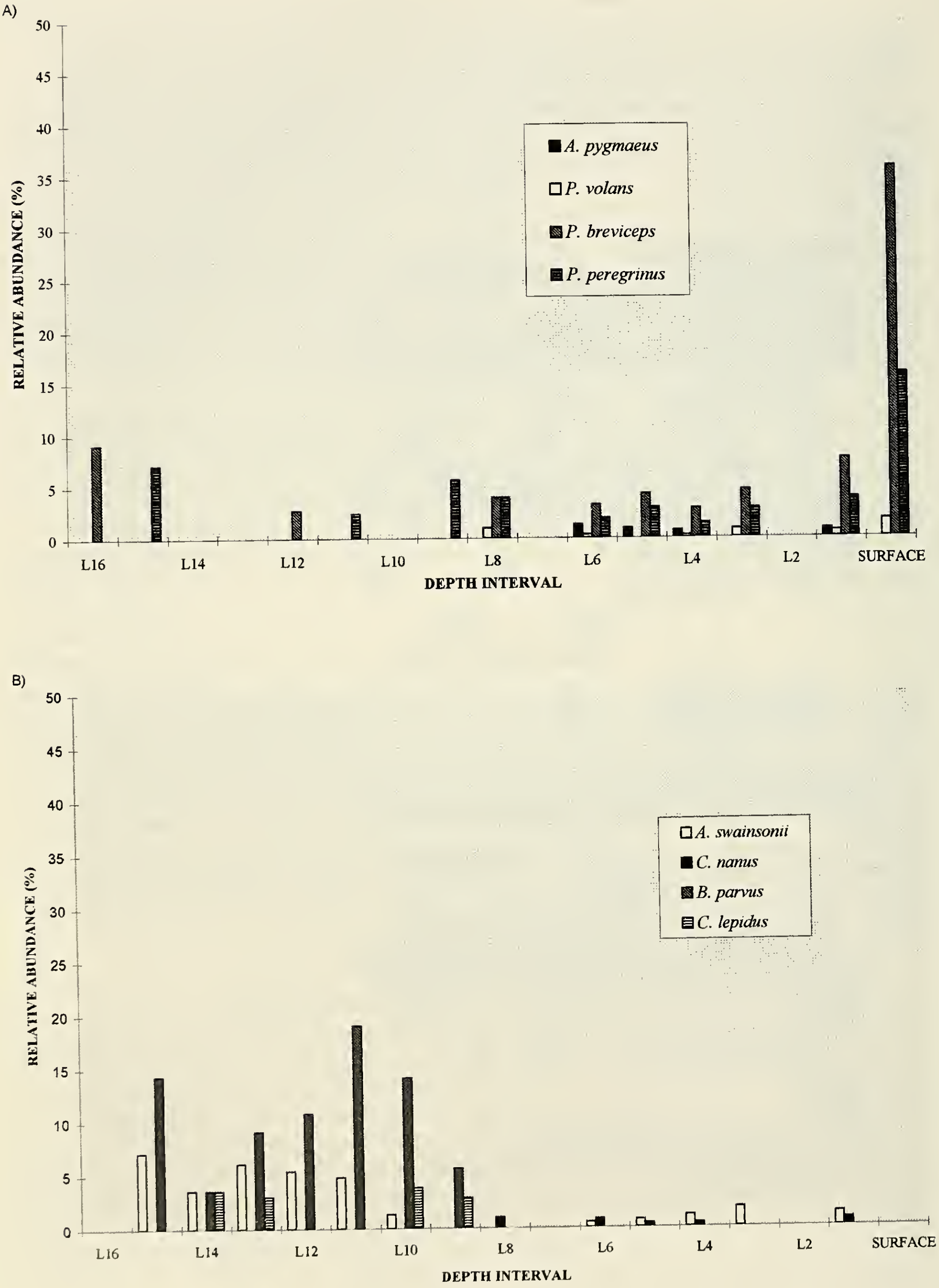


Figure 4. The relative abundance of selected non-volant, native mammal species from the Nettle Cave deposit. The species represented are possible indicators of climatic change. Levels L2 and L7 were not analysed. See Appendix B for the corresponding depth interval to each level. Continued on following page.

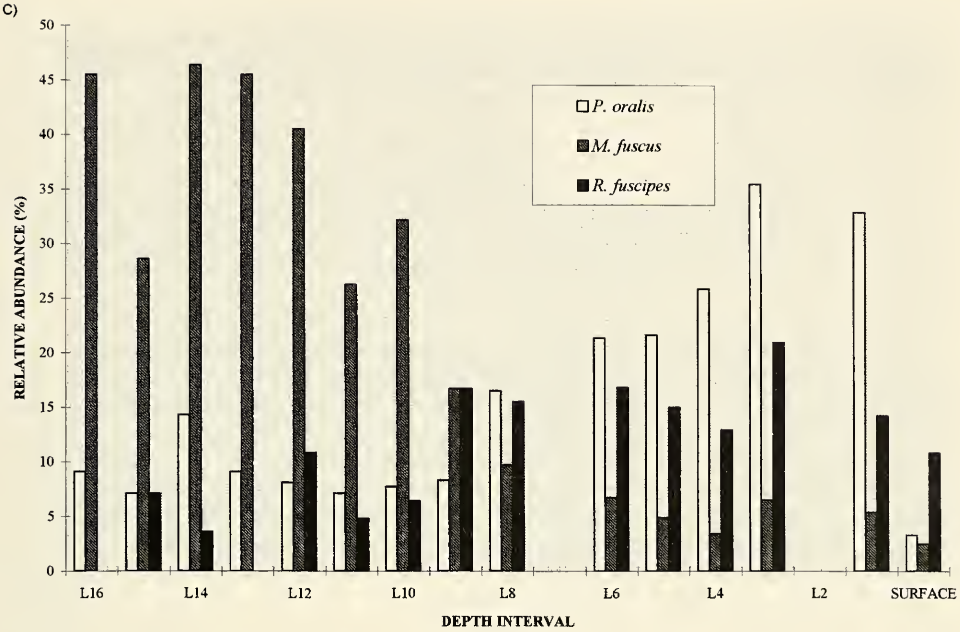


Figure 4. Continued from previous page.

Ponding may have occurred from surface water seeping into the limestone and accumulating behind the cave wall. Numerous runnels on the wall behind the excavation suggest water inflowing. Leaching to the lower layers would have followed. An increase in the amount of fine material (Fig. 3) at these levels corresponds with more humid conditions, a phenomenon reported by Wells et al. (1984) for Victoria Cave. Consolidation of parts of these levels may have been due to the introduction of cementing material in the early stages of diagenesis, rather than from compaction (Krumbein and Sloss 1963). In fact, alkaline conditions and an increase in temperature would enhance the precipitation of calcium carbonate which in turn would promote cementation of the sediment (Pettijohn 1957; Reineck and Singh 1975).

The radiocarbon dates of 7,140 ± 280 and 8,730 ± 280 BP agree well with the sedimentary analyses. Between the two charcoal lenses was a white, calcareous, cemented layer (Fig. 2). Its formation appears to have coincided with the wettest period at 7,500 to 5,000 BP (Bowler et al. 1976). Relative increases in the proportion of fine particles at 37 cm (Fig. 3) indicate wetter conditions. These conditions seem to correlate with the early to mid-Holocene humid period (Bowler et al. 1976; Colhoun et al. 1982). Drier conditions throughout the remainder of the Holocene (Bowler et al. 1976; Hooley et al. 1980) are reflected in the proportionately low amounts of clay and silt in the upper levels of the Nettle Cave sediments (Fig. 3). However, particle size analysis of these sediments indicates the drier conditions of the late Holocene were still wetter than the conditions experienced in the late Pleistocene.

## Mode of Deposition

Sooty Owls are the current source of small mammal bone deposits in Nettle Cave. We consider that owls of some species have been the source of the deposit over the entire period of deposition covered by our excavation for the following reasons:

1. Long bones are intact; skulls are either intact (except for a damaged or absent occiput) or broken into their component bones; mandibles are rarely heavily fragmented; and little erosion of bone and tooth has taken place.

2. There is a bias towards smaller animals, particularly murids and small dasyurids; the larger species are represented by subadults or juveniles.

3. Evidence for collection by diurnal raptors, e.g. kestrels, such as heavy digestive erosion of bones and tooth enamel (Andrews 1990; Kusmer 1990) is absent. Evidence for mammalian carnivores, e.g. *Sarcophilus* or *Thylacinus*, such as highly fragmented bones (especially skulls), eroded teeth and bone-bearing coprolites (Lundelius 1966) is also absent.

4. There is no evidence for fluvial deposition from the sedimentological data.

While the material from the Nettle Cave deposit fulfils the requirements of an owl accumulation (Lundelius 1966), it is impossible to conclude that Sooty Owls have been responsible for the entire deposit. Occupation of the roosting site may have alternated between Masked Owls (*Tyto novaehollandiae*) and Sooty Owls for the duration of pellet deposition. Both species have been found living in caves (Anon. 1988; J. Calaby, pers. comm., in Wakefield 1960; pers. obs.) and take similar prey items of comparable sizes (Table 4). Powerful Owls (*Ninox strenua*) may also have contributed to the deposit. However, the Powerful Owl habitually roosts in trees rather than caves (Fleay 1944) and is a more specialist predator, taking mid- to large-size arboreal species almost exclusively (Fleay 1944; James 1980; Kavanagh 1988; Tilley 1982) (Table 4). The almost total absence of moderate-size arboreal mammals in the lower levels of the deposit (Table 3), prey known to be taken by Sooty Owls and Masked Owls, suggests a lack of trees in the Jenolan area at this time. A lack of trees would also make it unlikely that Powerful Owls would have been present, given their habitat preference for forests (Kavanagh 1988) and therefore, they were unlikely to have contributed to the Nettle Cave deposit.

## Environmental History at Jenolan based on Mammal Remains

The Nettle Cave faunal assemblage containing *B. parvus* (Table 3) appears to be late Pleistocene in age. The presence of *B. parvus* together with *M. fuscus* and *Antechinus swainsonii* throughout this early phase of the deposit indicates a colder environment than at present in the Jenolan area (Table 5). Modern *B. parvus* is physiologically intolerant of high temperatures (Fleming 1985) and is restricted to high alpine areas in NSW and Victoria. The presence of these species and the virtual absence of arboreal mammals suggest the vegetational formation was dominated by open areas with a dense ground cover of grasses and low shrubs. Conversely, the low representation of arboreal mammals may be due to a smaller owl as predator, rather than a lack of trees. However, the absence of *A. pygmaeus* and the low abundance of *Petaurus breviceps* in the lower zone of the deposit probably reflects the available vegetation at the time rather than predator bias, given that owls will take arboreal mammals if they are present (Table 4). The presence of *M. fuscus* may indicate the immediate presence of water (Hope et al. 1977), either as snow, running streams or wet microhabitats in the grasslands. Small pockets of forest or woodland were likely to have been present at lower altitudes.

The faunal composition of the lower levels of the Nettle Cave deposit appears to broadly correspond to the assemblage described in the Pleistocene fraction of the Pyramids deposit at Buchan (Wakefield 1969, 1972) and the entire Wombeyan breccia (Ride 1960). The relatively higher abundance of *M. fuscus* and *B. parvus* and lower abundance of *A. swainsonii* and arboreal species in the lower Nettle Cave deposit compared with the relative abundances of these species in the older fraction of the Pyramids deposit, suggest a less heavily forested vegetation in the Jenolan area, although sampling

TABLE 4 A list of the recorded prey items of the Sooty Owl, Masked Owl and Powerful Owl from the literature. a = adult, j = juvenile, yes denotes that the species is taken as prey by that particular owl, ? = this prey is possibly taken. 1. Howe (1935); Hyem (1979); Loyn et al. (1986); Schodde and Mason (1980); Smith (1984). 2. Hyem (1979); Mooney (pers. comm.). 3. Hyem (1979); James (1980); Kavanagh (1988); Seebeck (1976); Tilley (1982).

| Prey species | Sooty Owl[1] (*Tyto tenebricosa*) | Masked Owl[2] (*T. novaehollandiae*) | Powerful Owl[3] (*Ninox strenua*) |
|---|---|---|---|
| *Petaurus breviceps* | yes | yes (a, j) | yes (a) |
| *P. australis* | | | yes |
| *Pseudocheirus peregrinus* | yes (a, j) | yes (a) | yes (a, j) |
| *Petauroides volans* | yes (j) | | yes |
| *Trichosurus vulpecula* | | yes (j) | yes (j) |
| *Cercartetus nanus* | yes | yes (a) | |
| *C. lepidus* | | yes (a) | |
| *Acrobates pygmaeus* | yes | | |
| *Antechinus stuartii* | yes | | yes |
| *A. swainsonii* | yes | | yes |
| *A. minimus* | | yes (a) | |
| *Sminthopsis leucopus* | | yes | |
| *Phascogale tapoatafa* | | | yes |
| *Dasyurus maculatus* | | yes (a) | |
| *D. viverrinus* | | yes (a, j) | |
| *Isoodon obesulus* | | yes (j) | |
| *Perameles gunnii* | | yes (a, j) | |
| *Bettongia gaimardi* | | yes (a) | |
| *Potorous tridactylus* | | yes (a) | |
| *Thylogale thetis* | | | ? |
| *T. billardierii* | | yes (j) | |
| *Hydromys chrysogaster* | | yes (a) | |
| *Mastacomys fuscus* | yes | yes (a) | |
| *Pseudomys fumeus* | yes | | |
| *P. higginsi* | | yes (a, j) | |
| *Rattus fuscipes* | yes | | yes (a) |
| *R. lutreolus* | | yes (a) | |
| *R. rattus* | yes | yes (a) | |
| *R. norvegicus* | | yes (a) | |
| *Mus musculus* | | yes (a) | |
| *Felis cattus* | | yes (j) | |
| *Lepus capensis* | | yes (j) | |
| *Oryctolagus cuniculus* | | yes (j) | yes |
| Bats | | yes | yes |
| Insects | ? | yes | yes |
| Birds | yes | yes | yes |
| Frogs | | yes | |

TABLE 5 Habitat data on the native, non-volant mammal species which occur in the Nettle Cave deposit. M.A.R. = mean average rainfall, ? denotes no rainfall data for that species. yes denotes the species is present in that habitat, yes ++ denotes the species is abundant in that habitat. For generic names, see Table 3. 1. Aitken (1977); 2. Braithwaite (1979); 3. Broome (1995); 4. Broome and Mansergh (1989); 5. Calaby (1988); 6. Calaby and Wimbush (1964); 7. Cockburn (1995); 8. Covacevich and Easton (1974); 9. Cuttle (1988); 10. Dickman (1982, 1995); 11. Fox (1995); 12. Godsell (1995); 13. Green (1995); 14. Happold (1989, 1995); 15. Heinsohn (1966); 16. Johnston (1995); 17. King and Mackowski (1986); 18. Lunney (1995); 19. Mahoney and Posamentier (1975); 20. Marlow (1958); 21. McKay (1988); 22. Ride (1970); 23. Soderquist (1995); 24. Stodart (1995); 25. Turner (1988); 26. Wakefield (1969, 1972); 27. Wakefield and Warneke (1967); 28. Watts and Aslin (1981).

| Species | Associated with water | Ground cover/ Understorey | Dry sclerophyll forest | Wet sclerophyll forest | Woodland | Rainforest | Alpine heathland | Alpine shrubs | Heathland | Scrub | Dry shrubland | Grassland | Cultivated land | M.A.R. (mm) | References |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| *A. stuartii* | | thick ground cover | yes | yes ++ | | | | | | | | | | 500–1,900 | 2, 26, 27 |
| *A. swainsonii* | yes | dense understorey | | yes | | | yes | | | | | | | >1,000 | 10, 26 |
| *A. flavipes* | | | yes | yes | yes | yes ++ | | | | | | | | ? | 20, 27 |
| *S. murina* | | | yes | | yes | | | | yes | | | | | ? | 11, 20 |
| *P. tapoatafa* | | thin ground cover | yes | | yes | | | | | | | | | 500–1,300 | 9, 20, 23, 26 |
| *D. viverrinus* | | rocky | yes | | yes | | | | yes | yes | | | yes | 500–900 | 12, 20, 26 |
| *I. obesulus* | | good cover | yes | | yes | | | | yes | | | | | 800–1,000 | 15, 22, 26 |
| *P. nasuta* | | little ground cover | yes | yes | | yes | | | | | | | | 800–1,900 | 20, 24, 26 |
| *P. peregrinus* | | dense shrubs | yes | yes | yes | yes | | | | | | | | 500–1,900 | 20, 21, 22, 26 |
| *P. volans* | | | yes | yes | yes | | | | | | | | | 1,000–1,800 | 20, 21, 22, 26 |
| *P. breviceps* | | | yes | yes ++ | yes | | | | | | | | | 500–1,900 | 20, 22, 26 |
| *C. nanus* | | | yes | yes | | yes | | | | | | | | 500–1,300 | 20, 22, 25, 26 |
| *C. lepidus* | | | yes | yes | | | | | | yes | yes | | | 300–1,200 | 1, 13, 26 |
| *B. parvus* | | rocky with sparse ground cover | | yes | | | | yes | yes | | | | | 1,300–2,400 | 3, 4, 5, 26 |
| *A. pygmaeus* | | | yes | yes | yes | | | | | | | | | 250–1,900 | 20, 22, 26 |
| *P. tridactylus* | | thick ground cover | yes | yes | yes | yes | | | yes | yes | | | | 760–1,300 | 16, 20, 22, 26 |
| *T. thetis* | | | | yes | | yes | | | | | | | | ? | 20, 22 |
| *C. albipes* | | | | | yes | | | | | | | | | 500–900 | 26, 28 |
| *P. oralis* | yes | dense ground cover | yes | yes | | | | | | | | | | ? | 8, 17, 28 |
| *P. gracilicaudatus* | | dense understorey | yes | yes | | | | | yes ++ | | | | | ? | 8, 19, 28 |
| *P. australis* | | | | | | | | | | | | yes | | ? | 8, 28 |
| *P. novaehollandiae* | | well-developed understorey | yes | | | | | | yes | | | | | 650–1,150 | 26, 28 |
| *P. fumeus* | | diverse understorey | yes | yes | yes | | | | yes | | | | | 900–1,900 | 7, 26, 28 |
| *M. fuscus* | yes | dense ground cover | | yes | yes | | yes | | | | | | | 1,500–2,500 | 6, 14, 26, 28 |
| *R. fuscipes* | yes | dense ground cover | | yes | yes | yes | | | | yes | | | | ? | 18, 28 |

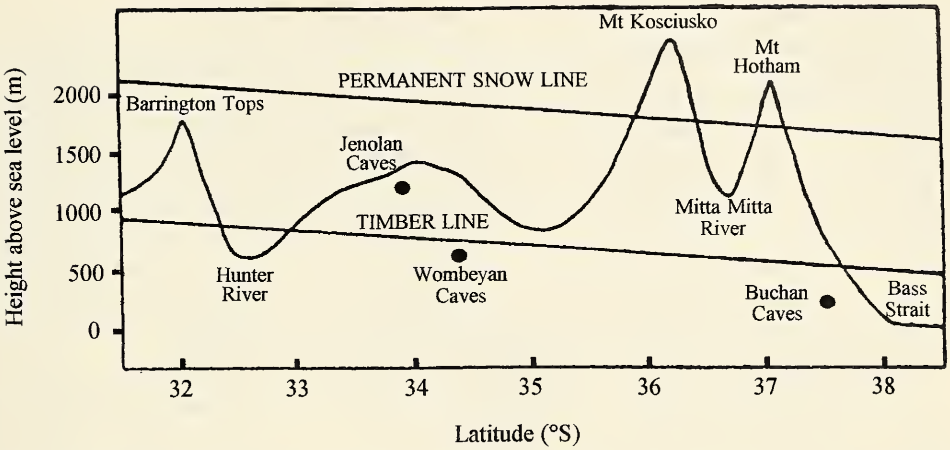


Figure 5. An altitude profile from Barrington Tops to Bass Strait with the location of *Burramys parvus* fossils from the Pleistocene, and the estimated position of the tree-line and permanent snowline during the height of glaciation at that time. However, the position of the snowline should be higher. The positions of the Buchan and Wombeyan Caves have been lowered from that indicated by Caughley (1986) to that stated by Wakefield (1969). The scale on the ordinate axis has been lowered so Bass Strait is at sea level. (modified after Caughley 1986).

bias from different predators at the two sites cannot be ruled out. The higher altitude of Nettle Cave lends support to the former scenario. Caughley (1986) estimated the position of the tree-line at the height of glaciation during the late Pleistocene to be below the Jenolan, Wombeyan and Buchan Caves (Fig. 5). However, altitudinal data from Wakefield (1969) indicate the tree-line would have been above the Buchan and Wombeyan Caves at this time. While periglacial activity did not reach the southern flanks of the Blue Mountains (Peterson 1968), the ground may have been seasonally frozen (Gillieson et al. 1985). The apparent presence of trees at Jenolan indicates the tree-line had shifted up and climatic warming in the highlands of southeastern Australia had begun. Wakefield (1969, 1972) identified the older fraction of the Pyramids deposit as having accumulated over the period covering most of the glacial recession phase at the termination of the Pleistocene. This agrees well with the climatic and vegetational sequences indicated by the faunal composition and sedimentological data of the lower Nettle Cave deposit.

The age of the Nettle Cave deposit cannot be estimated with any certainty on the rate of sedimentation alone. However, from the faunal evidence and comparison with the Pyramids deposit and the climatological data from southeastern Australia (Bowler et al. 1976; Galloway and Kemp 1981), the lower levels of the Nettle Cave deposit appear to have accumulated after the glacial maximum, about 20,000 years ago (Frakes et al. 1987), to around 15,000 BP.

Following this early phase was a transition period, represented by approximately 44–41 cm of the deposit, and correlating with the period 15,000 to 10,000 BP. This period was marked by an abrupt change in the composition and/or abundance of the faunal assemblage in the deposit (Table 3, Appendix B) along with a change in the sediments (Fig. 3). *Burramys parvus* and *C. lepidus* were no longer represented, the abundance of *A. swainsonii* and *M. fuscus* was greatly reduced while the numbers of *Rattus fuscipes*, *P. peregrinus*, *P. volans* and *P. breviceps* suddenly increased. While absence from the deposit and discontinuity of distribution of some species at around 44–41 cm (Table 3) may indicate a change of predator, the presence of other species throughout the deposit, such as *Dasyurus* sp., *I. obesulus*, *P. nasuta* and most native murids, suggests changes in abundance of most species were the result of changing climatic conditions.

As previously mentioned, *B. parvus* is physiologically intolerant of high temperatures (Fleming 1985). The presumed abrupt local extinction of *B. parvus* may therefore indicate a sudden increase in temperature. The zoogeographic range of *B. parvus* may have started to narrow during the brief period of humidity at 15,000 to 14,000 BP (Bowler et al. 1976). The presence of *A. swainsonii* and *M. fuscus* indicates cold conditions (Table 5). The lower abundance of these species in the 44–41 cm of the deposit suggests warmer conditions than previously experienced. An increase in abundance of *R. fuscipes* occurred at around the same time (Appendix B). Changes in vegetation at the close of the Pleistocene from grasslands, with grasses being a major food source for *M. fuscus*, to a ground cover dominated by ferns and shrubs, the preferred habitat of *R. fuscipes*, may have given *R. fuscipes* a competitive advantage, thereby maintaining a lower population of *M. fuscus* in the Jenolan area throughout the Holocene.

The local extinction of *C. lepidus* cannot be explained by climatic change alone. The modern distribution of this species includes hot and dry conditions (Aitken 1977; Dixon 1978). The coexistence of *B. parvus* and *C. lepidus* throughout the late Pleistocene suggests the latter species is capable of tolerating climatic extremes. The disappearance of *C. lepidus* from the Jenolan area may be attributed to a possible lack of floristic diversity at the time. It has been claimed that modern *C. lepidus* is highly mobile, and follows plants as they flower throughout the year (Ward 1992). As the Jenolan area became more heavily forested towards the end of the Pleistocene, *C. lepidus* may have been replaced by its larger congener, *C. nanus*.

The presence of arboreal species in the upper levels of the deposit suggests the presence of open forest and woodland. These vegetational communities were well established by 11,500 to 9,000 BP (Kershaw 1981). A combination of increased real precipitation (Bowler et al. 1976; Kershaw 1981) and an increase in temperature (Binder and Kershaw 1978) around this period may have contributed to the forestation. Increased wetness is evident from the nature of the sediments in the deposit (Fig. 3), while the continued low representation of *A. swainsonii* and *M. fuscus* is suggestive of warmer conditions.

The upper levels of the Nettle Cave deposit (c. 41– 0 cm) appear to have accumulated throughout the Holocene. The mammal species in the deposit indicate both wet and dry sclerophyll forest and woodland with varying amounts of ground cover (Table 5). The vegetation in the Jenolan area throughout the Holocene therefore appears to have been much the same as that found in the area today.

The upper levels of the Nettle Cave deposit broadly resemble the younger fraction of the Pyramids deposit. The species composition from this fraction of the Nettle Cave deposit gives no indication of an arid period, as proposed by Wakefield (1969, 1972) for the Pyramids deposit, but rather a change to perhaps slightly drier conditions. The faunal assemblage from the final phase of the transition period in the Nettle Cave deposit is comparable with the assemblage from the most recent Pleistocene sediments of the Pyramids deposit.

The cave surface mammal fauna (Table 3) closely resembles the modern mammal fauna in the Jenolan area with a few notable exceptions. Introduced species are found with species no longer extant in the area (*P. oralis* and *M. fuscus*) or extinct (*C. albipes*). Mixing of the deposit, possibly by rock-wallabies, or humans when the cave was open to tourists, may have occurred at the surface and top level of excavation (0–5 cm). Mixing is quite likely because the appearance of the bone from the surface differs from white to pale grey for the introduced species, to a yellow-cream for the native species. The colour of the bones from 0–5 cm varies from pale to dark grey for the introduced species, compared with yellow-cream to dark orange for the native murids. Wakefield (1972) concluded that variation in colour is correlated with age, whereby the lighter coloured bones represent a more recent age than the darker coloured bones. Differential colouration of

TABLE 6 Proposed correlation of events from the Nettle Cave data.

| Years BP | Levels of the deposit | Mammals in the deposit | Events at Nettle Cave | Vegetation | Climate | Contemporaneous events |
|---|---|---|---|---|---|---|
| c.20,000–15,000 | 68–44 cm | Small mammal fauna: *B. parvus*, *C. lepidus*, *M. fuscus* & *A. swainsonii* | Erosion of topsoil above cave. Low amounts of silt & clay in the deposit | Dominated by grasses; small pockets of forest & woodland at lower altitudes | Conditions were very cold & dry; maximum aridity 17,500–16,000 BP | Deglaciation began before 15,000 BP Accumulation of the Pleistocene fraction of the Pyramids Cave deposit & the entire Wombeyan breccia |
| 15,000–10,000 | 44–41 cm | *B. parvus* & *C. lepidus* locally extinct; *M. fuscus* & *A. swainsonii* nos reduced; *R. fuscipes* & arboreal spp. nos increased | Water ponding in the cave; increased amounts of silt & clay; possible hiatus in deposition | Open forest & woodland established by 11,500–9,000 BP | Period of humidity from 15,000–14,000 BP; wetter, warmer conditions; becoming slightly drier towards the end of this period | Accumulation of the most recent Pleistocene level of the Pyramids deposit corresponds with the final phase of this period |
| 10,000– present | 41–0 cm | Small mammal fauna similar to that found in the area today; abundance of arboreal spp. increased, while abundance of native murids decreased in modern times | Radiocarbon dates of 7,140 & 8,730 BP from these levels; increase in amount of silt & clay corresponding to period of humidity; low amounts in other levels | Wet & dry sclerophyll forest & woodland, much the same as at present | Period of humidity from 7,500–5,000 BP; wetter, warmer conditions; drier conditions followed, but still wetter than late Pleistocene | Accumulation of the Holocene fraction of the Pyramids deposit |

bone occurred according to the depths at which the bones were initially deposited. The presence of different coloured bones together suggests mechanical mixing of layers after colour alteration of the bones had taken place, that is, the darker, older bones from a lower level were mixed with the lighter coloured, younger bones from a more superficial level. Therefore, by using Wakefield's (1972) colour-age criterion, it may be assumed that there was limited temporal overlap between these introduced and native species. However, this assumption should be treated cautiously given that stratigraphic control of the excavation was not sufficient to detect this overlap. Therefore, *C. albipes*, *P. oralis* and *M. fuscus* may have been contemporaries of the introduced species. It is possible that the local extinction of these three native mammals was a result of the introduction of non-native mammals associated with European settlement (Wakefield 1960; Watts and Aslin 1981), e.g., rodents and rabbits. Distributional data on *P. australis* (Watts and Aslin 1981), *P. novaehollandiae* (Keith and Calaby 1968; Strahan 1995) and *P. fumeus* (Watts and Aslin 1981) in conjunction with the colour of the bones of these species from 0–5 cm, suggest they were not contemporaneous with the introduced species.

On the basis of the Nettle Cave data, major extinctions of the small mammal fauna in the Jenolan area at the end of the Pleistocene do not appear to have occurred. Two species (*B. parvus* and *C. lepidus*) probably became locally extinct at this time. The most parsimonious explanation for most of the faunal changes at the end of the Pleistocene is that of climatic change, particularly an increase in temperature. Local extinction of *M. fuscus*, *P. oralis* and *C. albipes* at the time of European settlement was possibly the result of competition from introduced species.

## A Summary of the Chronology of Events

The available geomorphological and palaeontological evidence from the Nettle Cave deposit and the proposed correlation with other events is summarised in Table 6.

The small mammal assemblage represented in the lower Nettle Cave deposit (68–c. 44 cm) appears to be late Pleistocene in age. We suggest this fraction of the deposit was accumulated during the glacial recession at the terminal phase of the Pleistocene, i.e. after 20,000 to 15,000 BP. Conditions were colder and with less real precipitation than at present. The vegetation was dominated by shrubs and a dense ground cover, with pockets of wet sclerophyll forest. The disappearance of *B. parvus* from the Nettle Cave deposit is attributed to the increase in temperature in southeastern Australia over the period 15,000 to 14,000 BP. A brief hiatus in deposition may have followed. The appearance of arboreal species may signify the revegetation of the area by forest and/or woodland. This event corresponds with the period of increased precipitation from 11,500 to 9,000 BP. This transition period of increased wetness is represented by ponding at roughly 44–41 cm of the deposit.

The small mammal assemblage represented in the upper levels (41–0 cm) of the Nettle Cave deposit is identified as Holocene. A wet forest fauna is suggested to have inhabited the area during the early to mid-Holocene. Drier conditions, much the same as the modern vegetational communities in the Jenolan area today, followed this early Holocene humid phase. However, this period was wetter than that in the late Pleistocene.

The surface of the deposit is modern. Mixing with the upper levels of the Holocene fraction occurred. Modern specimens could be distinguished from specimens deposited prior to European settlement largely on the basis of discolouration of the bone. Local extinctions, most notably of rodents, possibly occurred after European settlement as a consequence of competition from introduced mammals.

## ACKNOWLEDGEMENTS

Our thanks go to Dr Suzanne Hand for identification of the bat material, Mr Henk Godthelp for making available comparative fossil material and assisting with identification of rodents and Mr Ernst Holland for advice and information about the Sooty Owl and geomorphology of Nettle Cave. Thanks also to Drs Alex Baynes, Rod Wells and Suzanne Hand for critically reading earlier drafts of this paper. The Jenolan Caves Scientific Advisory Committee gave permission for the excavation in Nettle Cave.

## REFERENCES

Aitken, P.F. (1977). The Little Pygmy Possum (*Cercartetus lepidus* [Thomas]) found living on the Australian mainland. *South Australian Naturalist* **51**, 63–66.

Andrews, P. (1990). 'Owls, caves and fossils'. (University of Chicago Press: Chicago).

Anon. (1988). 'Jenolan Caves Reserve; Draft Plan of Management, volume 2 Specialist Papers'. (Draft Plan prepared by Cameron McNamara, Sydney; published by Tourism Commission of New South Wales and Crown Lands Office: Sydney).

Aplin, K.P. and Archer, M. (1987). Recent advances in marsupial systematics with a new syncretic classification. In 'Possums and opossums: studies in evolution' (Ed. M. Archer) pp. 15–72. (Surrey Beatty and Sons and the Royal Zoological Society: Sydney).

Archer, M. (1981). Results of the Archbold Expeditions, number 104. Systematic revision of the marsupial dasyurid genus *Sminthopsis* Thomas. *Bulletin of the American Museum of Natural History* **168**, 61–224.

Archer, M. (1984). The Australian marsupial radiation. In 'Vertebrate zoogeography and evolution in Australasia' (Eds M. Archer and G. Clayton) pp. 633–808. (Hesperian Press: Carlisle, Western Australia).

Balme, J., Merrilees, D. and Porter, J.K. (1978). Late Quaternary mammal remains, spanning about 30,000 years, from excavations in Devil's Lair, Western Australia. *Journal of the Royal Society of Western Australia* **61**, 33–65.

Baynes, A., (1987). The original mammal fauna of the Nullarbor and southern peripheral regions: evidence from skeletal remains in superficial cave deposits. In 'A biological study of the Nullarbor Region South and Western Australia in 1984' (Eds N.L. McKenzie and A.C. Robinson) pp. 139–152. (South Australian Department of Environment and Planning: Adelaide).

Baynes, A., Merrilees, D. and Porter, J.K. (1976). Mammal remains from the upper levels of a late Pleistocene deposit in Devil's Lair, Western Australia. *Journal of the Royal Society of Western Australia* **58**, 97–126.

Binder, R. and Kershaw, A.P. (1978). A late Quaternary pollen diagram from the southeastern highlands of Australia. *Search* **9**, 44–45.

Bowler, J.M., Hope, G.S., Jennings, J.N., Singh, G. and Walker, D. (1976). Late Quaternary climates of Australia and New Guinea. *Quaternary Research* **6**, 359–394.

Braithwaite, R.W. (1979). Social dominance and habitat utilization in *Antechinus stuartii* (Marsupialia). *Australian Journal of Zoology* **27**, 517–528.

Broome, L.S. (1995). Mountain Pygmy-possum, *Burramys parvus*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 208–210. (Reed Books: Chatswood, NSW).

Broome, L.S. and Mansergh, I.M. (1989). The Mountain Pygmy Possum *Burramys parvus* (Broom) an alpine endemic. In 'The scientific significance of the Australian Alps' (Ed. R. Good) pp. 241–264. (Australian Alps National Parks Liaison Committee: Canberra).

Calaby, J.H. (1988). Mountain Pygmy-possum, *Burramys parvus*. In 'Australian Museum complete book of Australian mammals' (Ed. R. Strahan) pp. 168–169. (Angus and Robertson: Sydney).

Calaby, J.H. and Wimbush, D.J. (1964). Observations on the Broad-toothed Rat, *Mastacomys fuscus* Thomas. *CSIRO Wildlife Research* **9**, 123–133.

Caughley, J. (1986). Distribution and abundance of the Mountain Pigmy-possum, *Burramys parvus* Broom, in Kosciusko National Park. *Australian Wildlife Research* **13**, 507–516.

Cockburn, A. (1995). Smoky Mouse, *Pseudomys fumeus*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 598–599. (Reed Books: Chatswood, NSW).

Colhoun, E.A., van de Geer, G. and Mook, W.G. (1982). Stratigraphy, pollen analysis, and paleoclimatic interpretation of Pulbeena Swamp, northwestern Tasmania. *Quaternary Research* **18**, 108–126.

Covacevich, J. and Easton, A. (1974). 'Rats and mice in Queensland'. (Queensland Museum: Brisbane).

Cox, G., James, J.M., Osborne, R.A.L. and Leggett, K.E.A. (1989). Stromatolitic crayfish-like stalagmites. *Proceedings of the University of Bristol Spelaeological Society* **18**, 339–358.

Cuttle, P. (1988). Brush-tailed Phascogale, *Phascogale tapoatafa*. In 'Australian Museum complete book of Australian mammals' (Ed. R. Strahan) pp. 34–35. (Angus and Robertson: Sydney).

Davison, A. (1986). Dentition of Victorian *Antechinus* species (Marsupialia: Dasyuridae). *Australian Mammalogy* **9**, 73–85.

Dickman, C.R. (1982). Some ecological aspects of seasonal breeding in *Antechinus* (Dasyuridae, Marsupialia). In 'Carnivorous marsupials' (Ed. M. Archer) pp. 139–150. (Royal Zoological Society of NSW:

Sydney).

Dickman, C.R. (1995). Dusky Antechinus, *Antechinus swainsonii*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 98–99. (Reed Books: Chatswood, NSW).

Dixon, J.M. (1971). *Burramys parvus* Broom (Marsupialia) from Falls Creek area of the Bogong High Plains, Victoria. *Victorian Naturalist* **88**, 133–138.

Dixon, J.M. (1978). The first Victorian and other Victorian records of the Little Pigmy Possum *Cercartetus lepidus* (Thomas). *Victorian Naturalist* **95**, 4–7.

Dodson, J. (1977). Late Quaternary palaeoecology of Wyrie Swamp, southeastern South Australia. *Quaternary Research* **8**, 97–114.

Dunbar, C.O. and Rodgers, J. (1963). 'Principles of stratigraphy'. (John Wiley and Sons, Inc.: New York).

Fleay, D. (1944). Watching the Powerful Owl. *Emu* **44**, 97–112.

Fleming, M.R. (1985). The thermal physiology of the Mountain Pygmy-possum *Burramys parvus* (Marsupialia: Burramyidae). *Australian Mammalogy* **8**, 79–90.

Folk, R.L. (1968). 'Petrology of sedimentary rocks'. (Hemphill's: Austin, Texas).

Fox, B.J. (1995). Common Dunnart, *Sminthopsis murina*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 150–151. (Reed Books: Chatswood, NSW).

Frakes, L.A., McGowran, B. and Bowler, J.M. (1987). Evolution of Australian environments. In 'Fauna of Australia' (Eds G.R. Dyne and D.W. Walton) pp. 1–16. (Australian Government Publishing Service: Canberra).

Freedman, L. (1967). Skull and tooth variation in the genus *Perameles*. Part 1: Anatomical features. *Records of the Australian Museum* **27**, 147–166.

Freedman, L. and Joffe, A.D. (1967). Skull and tooth variation in the genus *Perameles*. Part 2: Metrical features of *P. nasuta*. *Records of the Australian Museum* **27**, 183–195.

Freedman, L. and Rightmire, G.P. (1971). Skull and tooth variation in Australian bandicoots (Peramelidae, Marsupialia): the genus *Isoodon* and multivariate comparisons with *Perameles*. *Journal of the Royal Society of Western Australia* **54**, 21–31.

Galloway, R.W. (1965). Late Quaternary climates in Australia. *Journal of Geology* **73**, 603–618.

Galloway, R.W. and Kemp, E.M. (1981). Late Cainozoic environments in Australia. In 'Ecological biogeography of Australia' (Ed. A. Keast) pp. 51–80. (Dr W. Junk bv Publishers: The Hague).

Gillieson, D., Spate, A. and Head, J. (1985). Evidence for cold-climate processes at Wombeyan Caves, Southern Tablelands, New South Wales. *Search* **16**, 46–47.

Godsell, J. (1995). Eastern Quoll, *Dasyurus viverrinus*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 70–71. (Reed Books: Chatswood, NSW).

Green, R.H. (1983). 'An illustrated key to the skulls of the mammals in Tasmania'. (Queen Victoria Museum and Art Gallery: Launceston).

Green, R.H. (1995). Little Pygmy-possum, *Cercartetus lepidus*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 215–216. (Reed Books: Chatswood, NSW).

Gupta, S.K. and Polach, H.A. (1985). 'Radiocarbon dating practices at A.N.U'. (Australian National University, Radiocarbon Dating Research Laboratory: Canberra).

Happold, D.C.D. (1989). Small mammals of the Australian Alps. In 'The scientific significance of the Australian Alps' (Ed. R. Good) pp. 221–239. (Australian Alps National Parks Liaison Committee: Canberra).

Happold, D.C.D. (1995). Broad-toothed Rat, *Mastacomys fuscus*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 562–564. (Reed Books: Chatswood, NSW).

Heinsohn, G.E. (1966). Ecology and reproduction of the Tasmanian bandicoots (*Perameles gunni* and *Isoodon obesulus*). *University of California Publications in Zoology* **80**, 1–96.

Hooley, A.D., Southern, W. and Kershaw, A.P. (1980). Holocene vegetation and environments of Sperm Whale Head, Victoria, Australia. *Journal of Biogeography* **7**, 349–362.

Hope, J.H. (1979). 'Quaternary fossil mammal localities in southeastern New South Wales and eastern Victoria'. (Unpublished manuscript: Research School of Pacific Studies, Australian National University, Canberra).

Hope, J.H., Lampert, R.J., Edmondson, E., Smith, M.J. and van Tets, G.F. (1977). Late Pleistocene faunal remains from Seton rock shelter, Kangaroo Island, South Australia. *Journal of Biogeography* **4**, 363–385.

Howe, F.E. (1935). Some field notes on the Sooty Owl. *Emu* **34**, 317–318.

Hyem, E.L. (1979). Observations on owls in the upper Manning River district, New South Wales. *Corella* **3**, 17–25.

James, J.W. (1980). Food of the Powerful Owl, *Ninox strenua*, in southeastern Queensland. *Emu* **80**, 34–35.

Johnston, P.G. (1995). Long-nosed Potoroo, *Potorous tridactylus*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 301–302. (Reed Books: Chatswood, NSW).

Jones, B. and Baynes, A. (1989). Illustrated key to Australian Mammalia to generic level. In 'Fauna of Australia. Mammalia, volume 1B' (Eds D.W. Walton and B.J. Richardson) pp. 1075–1157. (Australian Government Publishing Service: Canberra).

Kavanagh, R.P. (1988). The impact of predation by the Powerful Owl, *Ninox strenua*, on a population of the Greater Glider, *Petauroides volans*. *Australian Journal of Ecology* **13**, 445–450.

Keith, K. and Calaby, J.H. (1968). The New Holland Mouse, *Pseudomys novaehollandiae* (Waterhouse), in the Port Stephens district, New South Wales. *CSIRO Wildlife Research* **13**, 45–58.

Kershaw, A.P. (1981). Quaternary vegetation and environments. In 'Ecological biogeography of Australia' (Ed. A. Keast) pp. 81–101. (Dr W. Junk bv Publishers: The Hague).

King, G.C. and Mackowski, C.M. (1986). Two new localities for *Pseudomys oralis* Thomas (Rodentia: Muridae) in New South Wales. *Australian Mammalogy* **9**, 63–65.

Krumbein, W.C. and Sloss, L.L. (1963). 'Stratigraphy and sedimentation'. (W.H. Freeman and Co.: San Francisco).

Kusmer, K.D. (1990). Taphonomy of owl pellet deposition. *Journal of Paleontology* **64**, 629–637.

Lembit, R. (1988). Vegetation and weed management issues. In 'Jenolan Caves Reserve; Draft Plan of Management, volume 2' (Ed. Cameron McNamara) pp. 1–21. (Tourism Commission of New South Wales and Crown Lands Office: Sydney).

Levinson, M. (1982). Taphonomy of microvertebrates - from owl pellets to cave breccia. *Annals of the Transvaal Museum* **33**, 115–121.

Loyn, R.H., Traill, B.J. and Triggs, B.E., (1986). Prey of Sooty Owls in east Gippsland before and after fire. *Victorian Naturalist* **103**, 147–149.

Luckett, W.P. (1993). An ontogenetic assessment of dental homologies in therian mammals. In 'Mammal phylogeny' (Eds F.S. Szalay, M.J. Novacek and M.C. McKenna) pp. 182–204. (Springer-Verlag: New York).

Lundelius, E.L. (1963). Vertebrate remains from the Nullarbor Caves, Western Australia. *Journal of the Royal Society of Western Australia* **46**, 75–80.

Lundelius, E.L. (1966). Marsupial carnivore dens in Australian caves. *Studies in Speleology* **1**, 174–181.

Lunney, D. (1995). Bush Rat, *Rattus fuscipes*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 651–653. (Reed Books: Chatswood, NSW).

Lyne, A.G. and Mort, P.A. (1981). A comparison of skull morphology in the marsupial bandicoot genus *Isoodon*: its taxonomic implication and notes on a new species, *Isoodon arnhemensis*. *Australian Mammalogy* **4**, 107–133.

Mahoney, J.A. and Posamentier, H. (1975). The occurrence of the native rodent, *Pseudomys gracilicaudatus* (Gould, 1845) (Rodentia: Muridae), in New South Wales. *Australian Mammalogy* **1**, 333–346.

Marlow, B.J. (1958). A survey of the marsupials of New South Wales. *CSIRO Wildlife Research* **3**, 71–114.

McKay, G.M. (1988). Common Ringtail Possum, *Pseudocheirus peregrinus* and Greater Glider, *Petauroides volans*. In 'Australian Museum complete book of Australian mammals' (Ed. R. Strahan) pp. 126–127, 134. (Angus and Robertson: Sydney).

Merrilees, D. (1967). Fossil bandicoots (Marsupialia, Peramelidae) from Mammoth Cave, Western Australia, and their climatic implications. *Journal of the Royal Society of Western Australia* **50**, 121–128.

Merrilees, D. and Porter, J.K. (1979). 'Guide to the identification of teeth and some bones of native land mammals occurring in the extreme south west of Western Australia'. (Western Australian Museum: Perth).

Musser, G.G. (1981). The giant rat of Flores and its relatives east of Borneo and Bali. *Bulletin of the American Museum of Natural History* **169**, 67–176.

Peterson, J.A. (1968). Cirque morphology and Pleistocene ice formation conditions in southeastern Australia. *Australian Geographical Studies* **6**, 67–83.

Pettijohn, F.J. (1957). 'Sedimentary rocks'. (Harper and Row: New York).

Porter, J.K. (1979). Vertebrate remains from a stratified Holocene deposit in Skull Cave, Western Australia, and a review of their significance. *Journal of the Royal Society of Western Australia* **61**, 109–117.

Reineck, H.-E. and Singh, I.B. (1975). 'Depositional sedimentary environments'. (Springer-Verlag: Berlin).

Ride, W.D.L. (1960). The fossil mammalian fauna of the *Burramys parvus* breccia from the Wombeyan Caves, New South Wales. *Journal of the Royal Society of Western Australia* **43**, 74–80.

Ride, W.D.L. (1970). 'Native mammals of Australia'. (Oxford University Press: Melbourne).

Schodde, R. and Mason, I.J. (1980). 'Nocturnal birds of Australia'. (Lansdowne Editions: Melbourne).

Schram, F.R. and Turnbull, W.D. (1970). Structural composition and dental variations in the murids of the Broom Cave fauna, late Pleistocene, Wombeyan Caves area, New South Wales, Australia. *Records of the Australian Museum* **28**, 1–24.

Seebeck, J.H. (1976). The diet of the Powerful Owl, *Ninox strenua*, in western Victoria. *Emu* **76**, 167–170.

Soderquist, T. (1995). Brush-tailed Phascogale, *Phascogale tapoatafa*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 104–106. (Reed Books: Chatswood, NSW).

Smith, P. (1984). Prey items of the Sooty Owl and the Barn Owl at Bega, New South Wales. *Corella* **8**, 71–72.

Stanton, R. (1989). Sediment transport in the McKeowns Creek valley and the northern caves system at Jenolan, New South Wales. BSc (Hons.) thesis, Australian National University, Canberra.

Stodart, E. (1995). Long-nosed Bandicoot, *Perameles nasuta*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 184–185. (Reed Books: Chatswood, NSW).

Strahan, R. (1995). 'The mammals of Australia'. (Reed Books: Chatswood, NSW).

Tate, G.H.H. (1951). Results of the Archbold Expeditions, number 65. The rodents of Australia and New Guinea. *Bulletin of the American Museum of Natural History* **97**, 183–430.

Taylor, J.M. and Horner, B.E. (1973). Results of the Archbold Expeditions, number 98. Systematics of native Australian *Rattus* (Rodentia, Muridae). *Bulletin of the American Museum of Natural History* **150**, 1–130.

Tilley, S. (1982). The diet of the Powerful Owl, *Ninox strenua*, in Victoria. *Australian Wildlife Research* **9**, 157–175.

Turnbull, W.D. and Schram, F.R. (1973). Broom Cave *Cercartetus*, with observations on Pygmy Possum dental morphology, variation, and taxonomy. *Records of the Australian Museum* **28**, 437–464.

Turner, V. (1988). Eastern Pygmy-possum, *Cercartetus nanus*. In 'Australian Museum complete book of Australian mammals' (Ed. R. Strahan) p. 160. (Angus and Robertson: Sydney).

Van Dyck, S.M. (1982). The relationships of *Antechinus stuartii* and *A. flavipes* (Dasyuridae, Marsupialia) with special reference to Queensland. In 'Carnivorous marsupials' (Ed. M. Archer) pp. 723–766. (Royal Zoological Society of NSW: Sydney).

Wakefield, N.A. (1960). Recent mammal bones in the Buchan district - 2. *Victorian Naturalist* **77**, 227–240.

Wakefield, N.A. (1967). Some taxonomic revision in the Australian marsupial genus *Bettongia* (Macropodidae), with description of a new species. *Victorian Naturalist* **84**, 8–22.

Wakefield, N.A. (1969). An investigation of late Pleistocene and Recent cave deposits insoutheastern Australia. MSc thesis, Monash University, Melbourne.

Wakefield, N.A. (1972). Palaeoecology of fossil mammal assemblages from some Australian caves. *Proceedings of the Royal Society of Victoria* **85**, 1–26.

Wakefield, N.A. and Warneke, R.M. (1967). Some revision in *Antechinus* (Marsupialia) -2. *Victorian Naturalist* **84**, 69–99.

Walton, D.W. (1988). 'Zoological catalogue of Australia, volume 5 Mammalia'. (Australian Government Publishing Service: Canberra).

Walton, D.W. and Richardson, B.J. (1989). 'Fauna of Australia. Mammalia, volume 1B'. (Australian Government Publishing Service: Canberra).

Ward, S.J. (1992). Life history of the Little Pygmy-possum, *Cercartetus lepidus* (Marsupialia: Burramyidae), in the Big Desert, Victoria. *Australian Journal of Zoology* **40**, 43–55.

Watts, C.H.S. and Aslin, H.J. (1981). 'The rodents of Australia'. (Angus and Robertson: London).

Wells, R.T., Moriarty, K. and Williams, D.L.G. (1984). The fossil vertebrate deposits of Victoria Fossil Cave Naracoorte: an introduction to the geology and fauna. *Australian Zoologist* **21**, 305–333.

## APPENDIX A

A list of the published descriptions used in identifying the non-volant, native mammal species from the Nettle Cave deposit. The illustrated key to Australian Mammalia (Jones and Baynes 1989) was used to check all specimens.

| Taxon | Reference |
|---|---|
| *Antechinus* | Davison (1986); Merrilees & Porter (1979); Van Dyck (1982); Wakefield & Warneke (1967) |
| *Sminthopsis* | Archer (1981); Merrilees & Porter (1979) |
| *Phascogale* | Merrilees & Porter (1979) |
| *Dasyurus* | Green (1983); Merrilees & Porter (1979) |
| *Isoodon, Perameles* | Freedman (1967); Freedman & Joffe (1967); Freedman & Rightmire (1971); Green (1983); Lyne & Mort (1981); Merrilees (1967); Merrilees & Porter (1979) |
| *Pseudocheirus* | Green (1983); Merrilees & Porter (1979) |
| *Petaurus* | Green (1983) |
| *Petauroides* | Archer (1984) |
| *Cercartetus* | Green (1983); Merrilees & Porter (1979); Turnbull & Schram (1973) |
| *Burramys parvus* | Dixon (1971) |
| *Acrobates pygmaeus* | Archer (1984) |
| *Potorous* | Green (1983); Merrilees & Porter (1979) |
| *Bettongia* | Green (1983); Merrilees & Porter (1979); Wakefield (1967) |
| *Thylogale thetis* | Green (1983) |
| *Rattus* | Green (1983); Merrilees & Porter (1979); Musser (1981); Tate (1951); Taylor & Horner (1973) |
| *Pseudomys* | Green (1983); Merrilees & Porter (1979); Schram & Turnbull (1970) |
| *Mastacomys* | Green (1983) |

## Appendix B

The minimum number of individuals (MNI) of small mammals and skinks identified from the Nettle Cave deposit. Birds and agamids are listed as present (yes) from the depth intervals of the deposit in which they were found. Depth intervals are in cm. The relative abundance (%) and aggregate (AGG), i.e. the total number of specimens of the mammal species in each depth interval is also given. L1, L2, etc. represents levels 1, 2 and so on. Depth intervals 41–39 cm and 13–5 cm were not analysed. 1. These do not represent new species in the relevant genus; the specimens were broken or lacking teeth, thus could not be assigned to a species with certainty. 2. If generic identification is correct, the species would be *M. schreibersii*. 3. If generic identification is correct, the species would be *C. gouldii*.

| Depth interval | 68–66 (L16) | 66–64 (15) | 64–59 (L14) | 59–54 (L13) | 54–50 (L12) | 50–46 (L11) | 46–44 (L10) |
|---|---|---|---|---|---|---|---|
| Species | MNI (%) AGG | MNI (%) AGG | MNI (%) AGG | MNI (%) AGG | MNI (%) AGG | MNI (%) AGG | MNI (%) AGG |
| **DASYURIDAE** | **1 (9.1) 1** | **2 (14.3) 2** | **3 (10.7) 3** | **3 (9.1) 4** | **3 (8.1) 6** | **7 (16.7) 9** | **8 (10.3) 12** |
| *Antechinus stuartii* sensu lato | 0 | 0 | 0 | 0 | 0 | 0 | 1 (1.3) 1 |
| *A. swainsonii* | 0 | 1 (7.1) 1 | 1 (3.6) 1 | 2 (6.1) 3 | 2 (5.4) 4 | 2 (4.8) 4 | 1 (1.3) 1 |
| *A. flavipes* | 0 | 0 | 0 | 0 | 0 | 0 | 2 (2.6) 4 |
| *A.* spp.[1] | 0 | 0 | 0 | 1 (3) 1 | 0 | 3 (7.1) 3 | 2 (2.6) 3 |
| *Sminthopsis murina* | 0 | 0 | 1 (3.6) 1 | 0 | 1 (2.7) 2 | 0 | 1 (1.3) 2 |
| *S.* sp.[1] | 0 | 0 | 0 | 0 | 0 | 1 (2.4) 1 | 0 |
| *Phascogale tapoatafa* | 0 | 0 | 1 (3.6) 1 | 0 | 0 | 0 | 1 (1.3) 1 |
| *Dasyurus* sp. cf. *D. viverrinus* | 0 | 1 (7.1) 1 | 0 | 0 | 0 | 1 (2.4) 1 | 0 |
| **PERAMELIDAE** | **1 (9.1) 1** | **0** | **2 (7.1) 2** | **1 (3) 1** | **1 (2.7) 1** | **1 (2.4) 1** | **1 (1.3) 1** |
| *Isoodon obesulus* | 0 | 0 | 1 (3.6) 1 | 0 | 0 | 0 | 0 |
| *Perameles nasuta* | 1 (9.1) 1 | 0 | 1 (3.6) 1 | 1 (3) 1 | 1 (2.7) 1 | 1 (2.4) 1 | 1 (1.3) 1 |
| **PSEUDOCHEIRIDAE** | **0** | **1 (7.1) 1** | **0** | **0** | **0** | **1 (2.4) 1** | **0** |
| *Pseudocheirus peregrinus* | 0 | 1 (7.1) 1 | 0 | 0 | 0 | 1 (2.4) 1 | 0 |
| *Petauroides volans* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **PETAURIDAE** | **1 (9.1) 1** | **0** | **0** | **0** | **1 (2.7) 1** | **0** | **0** |
| *Petaurus breviceps* | 1 (9.1) 1 | 0 | 0 | 0 | 1 (2.7) 1 | 0 | 0 |
| **BURRAMYIDAE** | **0** | **2 (14.3) 3** | **2 (7.1) 3** | **4 (12.1) 7** | **4 (10.8) 7** | **8 (19) 18** | **14 (17.9) 33** |
| *Cercartetus nanus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *C. lepidus* | 0 | 0 | 1 (3.6) 1 | 1 (3) 1 | 0 | 0 | 3 (3.8) 3 |
| *Burramys parvus* | 0 | 2 (14.3) 3 | 1 (3.6) 2 | 3 (9.1) 6 | 4 (10.8) 7 | 8 (19) 18 | 11 (14.1) 30 |
| **ACROBATIDAE** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| *Acrobates pygmaeus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **POTOROIDAE** | **0** | **0** | **0** | **0** | **0** | **0** | **1 (1.3) 1** |
| *Potorous* sp. cf. *P. tridactylus* | 0 | 0 | 0 | 0 | 0 | 0 | 1 (1.3) 1 |
| *Bettongia* sp. | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **MACROPODIDAE** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| *Thylogale thetis* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **MURIDAE** | **8 (72.7) 14** | **9 (64.3) 19** | **21 (75) 46** | **25 (75.8) 60** | **28 (75.7) 62** | **24 (57.1) 53** | **52 (66.7) 138** |
| *Conilurus albipes* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Pseudomys oralis* | 1 (9.1) 1 | 1 (7.1) 2 | 4 (14.3) 7 | 3 (9.1) 8 | 3 (8.1) 7 | 3 (7.1) 4 | 6 (7.7) 16 |
| *P. gracilicaudatus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *P. australis* | 0 | 1 (7.1) 1 | 1 (3.6) 1 | 2 (6.1) 3 | 2 (5.4) 2 | 0 | 2 (2.6) 4 |
| *P. novaehollandiae* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| 44–43 (L9) MNI (%) AGG | 43–41 (L8) MNI (%) AGG | 39–37 (L6) MNI (%) AGG | 37–35 (L5) MNI (%) AGG | 35–25 (L4) MNI (%) AGG | 25–13 (L3) MNI (%) AGG | 5–0 (L1) MNI (%) AGG | SURFACE MNI (%) AGG |
|---|---|---|---|---|---|---|---|
| **6 (16.7) 10** | **14 (13.6) 33** | **51 (13.6) 115** | **92 (20.3) 198** | **175 (19.1) 324** | **90 (12.4) 197** | **235 (16.6) 564** | **13 (10.8) 32** |
| 0 | 3 (2.9) 5 | 16 (4.3) 38 | 17 (3.8) 40 | 26 (2.8) 48 | 20 (2.8) 51 | 74 (5.2) 202 | 5 (4.2) 17 |
| 0 | 0 | 2 (0.5) 2 | 3 (0.7) 3 | 10 (1.1) 12 | 13 (1.8) 19 | 18 (1.3) 30 | 0 |
| 2 (5.6) 3 | 3 (2.9) 7 | 9 (2.4) 18 | 7 (1.5) 15 | 15 (1.6) 28 | 18 (2.5) 41 | 45 (3.2) 101 | 2 (1.7) 3 |
| 2 (5.6) 3 | 0 | 0 | 23 (5.1) 55 | 45 (4.9) 78 | 18 (2.5) 35 | 50 (3.5) 118 | 4 (3.3) 10 |
| 2 (5.6) 4 | 8 (7.8) 21 | 22 (5.9) 55 | 27 (6) 63 | 46 (5) 114 | 15 (2.1) 43 | 31 (2.2) 86 | 2 (1.7) 2 |
| 0 | 0 | 0 | 12 (2.6) 19 | 17 (1.9) 26 | 3 (0.4) 4 | 10 (0.7) 15 | 0 |
| 0 | 0 | 2 (0.5) 2 | 2 (0.4) 2 | 10 (1.1) 12 | 3 (0.4) 4 | 6 (0.4) 11 | 0 |
| 0 | 0 | 0 | 1 (0.2) 1 | 6 (0.7) 6 | 0 | 1 (0.1) 1 | 0 |
| **1 (2.8) 1** | **3 (2.9) 3** | **11 (3) 16** | **22 (4.8) 27** | **31 (3.4) 45** | **21 (2.9) 38** | **34 (2.4) 43** | **1 (0.8) 1** |
| 1 (2.8) 1 | 1 (1) 1 | 4 (1.1) 4 | 7 (1.5) 8 | 14 (1.5) 20 | 3 (0.4) 3 | 16 (1.1) 23 | 0 |
| 0 | 2 (1.9) 2 | 7 (1.9) 12 | 15 (3.3) 19 | 17 (1.9) 25 | 18 (2.5) 35 | 18 (1.3) 20 | 1 (0.8) 1 |
| **2 (5.6) 3** | **5 (4.9) 5** | **8 (2.2) 12** | **13 (2.9) 33** | **15 (1.6) 31** | **26 (3.6) 65** | **62 (4.4) 136** | **21 (17.5) 56** |
| 2 (5.6) 3 | 4 (3.9) 4 | 7 (1.9) 11 | 13 (2.9) 33 | 13 (1.4) 29 | 20 (2.8) 58 | 54 (3.8) 127 | 19 (15.8) 54 |
| 0 | 1 (1) 1 | 1 (0.3) 1 | 0 | 2 (0.2) 2 | 6 (0.8) 7 | 8 (0.6) 9 | 2 (1.7) 2 |
| **0** | **4 (3.9) 8** | **12 (3.2) 24** | **19 (4.2) 44** | **26 (2.8) 60** | **33 (4.6) 70** | **107 (7.6) 306** | **43 (35.8) 136** |
| 0 | 4 (3.9) 8 | 12 (3.2) 24 | 19 (4.2) 44 | 26 (2.8) 60 | 33 (4.6) 70 | 107 (7.6) 306 | 43 (35.8) 136 |
| **3 (8.3) 6** | **1 (1) 1** | **3 (0.8) 3** | **2 (0.4) 2** | **4 (0.4) 4** | **0** | **10 (0.7) 15** | **0** |
| 0 | 1 (1) 1 | 3 (0.8) 3 | 2 (0.4) 2 | 4 (0.4) 4 | 0 | 10 (0.7) 15 | 0 |
| 1 (2.8) 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| 2 (5.6) 5 | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **0** | **0** | **5 (1.3) 7** | **4 (0.9) 6** | **6 (0.7) 6** | **0** | **11 (0.8) 16** | **0** |
| 0 | 0 | 5 (1.3) 7 | 4 (0.9) 6 | 6 (0.7) 6 | 0 | 11 (0.8) 16 | 0 |
| **0** | **0** | **4 (1.1) 4** | **5 (1.1) 5** | **5 (0.5) 5** | **6 (0.8) 6** | **8 (0.6) 9** | **0** |
| 0 | 0 | 3 (0.8) 3 | 4 (0.9) 4 | 3 (0.3) 3 | 4 (0.6) 4 | 7 (0.5) 8 | 0 |
| 0 | 0 | 1 (0.3) 1 | 1 (0.2) 1 | 2 (0.2) 2 | 2 (0.3) 2 | 1 (0.1) 1 | 0 |
| **1 (2.8) 1** | **0** | **0** | **1 (0.2) 1** | **0** | **0** | **0** | **0** |
| 1 (2.8) 1 | 0 | 0 | 1 (0.2) 1 | 0 | 0 | 0 | 0 |
| **22 (61.1) 49** | **74 (71.9) 192** | **277 (73.8) 755** | **294 (64.9) 839** | **649 (71) 1833** | **541 (74.8) 1485** | **932 (65.8) 2920** | **40 (33.3) 83** |
| 0 | 1 (1) 1 | 2 (0.5) 2 | 6 (1.3) 7 | 23 (2.5) 57 | 2 (0.3) 2 | 1 (0.1) 1 | 2 (1.7) 2 |
| 3 (8.3) 8 | 17 (16.5) 44 | 80 (21.3) 253 | 98 (21.6) 320 | 236 (25.8) 740 | 256 (35.4) 860 | 465 (32.8) 1602 | 4 (3.3) 9 |
| 0 | 0 | 0 | 0 | 1 (0.1) 1 | 0 | 0 | 0 |
| 0 | 3 (2.9) 4 | 7 (1.9) 11 | 9 (2) 11 | 3 (0.3) 3 | 4 (0.6) 5 | 6 (0.4) 6 | 0 |
| 1 (2.8) 1 | 5 (4.9) 14 | 28 (7.5) 82 | 33 (7.3) 84 | 132 (14.4) 391 | 40 (5.5) 104 | 35 (2.5) 75 | 0 |

| Depth interval<br>Species | 68–66 (L16)<br>MNI (%) AGG | 66–64 (15)<br>MNI (%) AGG | 64–59 (L14)<br>MNI (%) AGG | 59–54 (L13)<br>MNI (%) AGG | 54–50 (L12)<br>MNI (%) AGG | 50–46 (L11)<br>MNI (%) AGG | 46–44 (L10)<br>MNI (%) AGG |
|---|---|---|---|---|---|---|---|
| *P. fumeus* | 0 | 1 (7.1) 1 | 1 (3.6) 1 | 2 (6.1) 4 | 2 (5.4) 2 | 2 (4.8) 5 | 5 (6.4) 16 |
| *P.* spp.[1] | 2 (18.2) 2 | 1 (7.1) 4 | 1 (3.6) 1 | 2 (6.1 6 | 2 (5.4) 2 | 5 (11.9) 11 | 7 (9) 22 |
| *Mastacomys fuscus* | 5 (45.5) 10 | 4 (28.6) 8 | 13 (46.4) 35 | 15 (45.5) 38 | 15 (40.5) 39 | 11 (26.2) 28 | 25 (32.1) 62 |
| *Rattus fuscipes* | 0 | 1 (7.1) 3 | 1 (3.6) 1 | 0 | 4 (10.8) 6 | 2 (4.8) 4 | 5 (6.4) 15 |
| *R. rattus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *R.* spp.[1] | 0 | 0 | 0 | 1 (3) 1 | 0 | 1 (2.4) 1 | 2 (2.6) 3 |
| *Mus musculus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **VESPERTILIONIDAE** | **0** | **0** | **0** | **0** | **0** | **1 (2.4) 1** | **2 (2.6) 2** |
| *Nyctophilus* sp. cf. *N. gouldi* | 0 | 0 | 0 | 0 | 0 | 0 | 1 (1.3) 1 |
| *N.* sp. cf. *N. geoffroyi* | 0 | 0 | 0 | 0 | 0 | 1 (2.4) 1 | 1 (1.3) 1 |
| *Miniopterus schreibersii* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| cf. *Miniopterus*[2] | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Chalinolobus gouldii* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *C. morio* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| cf. *Chalinolobus*[3] | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| Falsistrellus tasmaniensis | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **LEPORIDAE** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| *Oryctolagus cuniculus* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| **TOTAL MNI (%)** | **11 (100)** | **14 (100)** | **28 (99.9)** | **33 (100)** | **37 (100)** | **42 (100)** | **78 (100.1)** |
| TOTAL AGGREGATE | 17 | 26 | 54 | 72 | 77 | 83 | 187 |
| **AVES** | **yes** | **yes** | **yes** | **yes** | **yes** | **yes** | **yes** |
| **AGAMIDAE** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| **SCINCIDAE** | **0** | **0** | **0** | **0** | **0** | **0** | **0** |
| *Egernia* sp. cf. *E. whitii* | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| *Eulamprus quoyii* sp.-group | 0 | 0 | 0 | 0 | 0 | 0 | 0 |
| New taxon | 0 | 0 | 0 | 0 | 0 | 0 | 0 |

| 44–43 (L9) MNI (%) AGG | 43–41 (L8) MNI (%) AGG | 39–37 (L6) MNI (%) AGG | 37–35 (L5) MNI (%) AGG | 35–25 (L4) MNI (%) AGG | 25–13 (L3) MNI (%) AGG | 5–0 (L1) MNI (%) AGG | SURFACE MNI (%) AGG |
|---|---|---|---|---|---|---|---|
| 2 (5.6) 4 | 8 (7.8) 17 | 14 (3.7) 32 | 15 (3.3) 34 | 8 (0.9) 13 | 2 (0.3) 3 | 12 (0.8) 20 | 0 |
| 4 (11.1) 10 | 13 (12.6) 35 | 35 (9.3) 89 | 25 (5.5) 71 | 54 (5.9) 145 | 21 (2.9) 50 | 72 (5.1) 182 | 0 |
| 6 (16.7) 16 | 10 (9.7) 24 | 25 (6.7) 63 | 22 (4.9) 57 | 31 (3.4) 69 | 47 (6.5) 139 | 77 (5.4) 213 | 3 (2.5) 4 |
| 6 (16.7) 10 | 16 (15.5) 51 | 63 (16.8) 184 | 68 (15) 220 | 118 (12.9) 339 | 151 (20.9) 292 | 201 (14.2) 701 | 13 (10.8) 31 |
| 0 | 0 | 0 | 0 | 0 | 0 | 42 (3) 83 | 16 (13.3) 32 |
| 0 | 1 (1) 1 | 23 (6.1) 39 | 18 (4) 35 | 43 (4.7) 75 | 18 (2.5) 30 | 19 (1.3) 33 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 2 (0.1) 4 | 2 (1.7) 5 |
| **1 (2.8) 1** | **2 (1.9) 2** | **4 (1.1) 4** | **1 (0.2) 1** | **3 (0.3) 4** | **6 (0.8) 6** | **16 (1.1) 25** | **1 (0.8) 1** |
| 0 | 0 | 0 | 0 | 0 | 1 (0.1) 1 | 3 (0.2) 3 | 0 |
| 1 (2.8) 1 | 1 (1) 1 | 2 (0.5) 2 | 0 | 2 (0.2) 3 | 0 | 2 (0.1) 3 | 0 |
| 0 | 0 | 0 | 0 | 0 | 5 (0.7) 5 | 8 (0.6) 12 | 1 (0.8) 1 |
| 0 | 0 | 0 | 0 | 1 (0.1) 1 | 0 | 0 | 0 |
| 0 | 0 | 1 (0.3) 1 | 0 | 0 | 0 | 1 (0.1) 3 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 (0.1) 1 | 0 |
| 0 | 1 (1) 1 | 0 | 1 (0.2) 1 | 0 | 0 | 0 | 0 |
| 0 | 0 | 1 (0.3) 1 | 0 | 0 | 0 | 1 (0.1) 3 | 0 |
| **0** | **0** | **0** | **0** | **0** | **0** | **1 (0.1) 1** | **1 (0.8) 2** |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 (0.1) 1 | 1 (0.8) 2 |
| **36 (100.1)** | **103 (100.1)** | **375 (100.1)** | **453 (99.9)** | **914 (99.8)** | **723 (99.9)** | **1416 (100.1)** | **120 (99.8)** |
| 71 | 244 | 940 | 1156 | 2312 | 1867 | 4035 | 311 |
| **yes** | **yes** | **yes** | **yes** | **yes** | **yes** | **yes** | **yes** |
| **0** | **0** | **yes** | **yes** | **yes** | **yes** | **yes** | **0** |
| **0** | **0** | **0** | **0** | **0** | **2** | **1** | **0** |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 |
| 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 |

# *Perameles bowensis*, a New Species of *Perameles* (Peramelemorphia, Marsupialia) from Pliocene Faunas of Bow and Wellington Caves, New South Wales

JEANETTE MUIRHEAD, LYNDALL DAWSON AND MICHAEL ARCHER

School of Biological Science, University of New South Wales, Sydney 2052

Muirhead, J., Dawson, L., and Archer, M. (1997). *Perameles bowensis*, a new species of *Perameles* (Peramelemorphia, Marsupialia) from Pliocene faunas of Bow and Wellington Caves, New South Wales. *Proceedings of the Linnean Society of New South Wales* **117**: 163-174

*Perameles bowensis* n. sp. is described from the early Pliocene Bow Local Fauna and is phylogenetically compared to other species of *Perameles*. This species is the second species of Tertiary *Perameles*. It appears to be closer to Recent species of *Perameles* than to the early Pliocene *Perameles allinghamensis*. Specimens from Pliocene sediments of Wellington Caves are also considered to represent *P. bowensis*. The presence of this species in both the Bow and Big Sink Local Fauna (Wellington) provides further support to the correlation of these faunas.

Manuscript received 17 June 1996, accepted for publication 23 October 1996.

KEYWORDS: Bandicoot, *Perameles*, Pliocene, Wellington Caves, Bow Local Fauna, Big Sink Local Fauna

## INTRODUCTION

*Perameles allinghamensis* Archer, 1976 was the first species described from the fossil record of the otherwise modern genus *Perameles*. It was recovered from the early Pliocene Bluff Downs Local Fauna in north Queensland (Archer 1976). Other Tertiary occurrences of *Perameles* have been reported, e.g. the Miocene Tarkarooloo and Kutjamarpu Local Faunas (Rich et al. 1982), however, none of these have been formally described and re-examination of this material indicates that these specimens have been incorrectly attributed to *Perameles* (Rich et al. 1991). *Perameles bowensis* from the Bow Local Fauna of northern New South Wales is the second species of Tertiary *Perameles* described.

There are currently five recognised species of *Perameles*. These are *P. nasuta* Geoffroy, 1804, *P. gunnii* Gray, 1838, *P. bougainville* Quoy and Gaimard, 1824, *P. eremiana* Spencer, 1897 and the Pliocene *P. allinghamensis* Archer, 1976. While Tate (1948) regards *P. bougainville*, *P. eremiana*, *P. fasciata* and *P. notina* to be possible local races of a widespread southern species, Marlow (1962) considers all of these to be distinct species. Here these forms are collectively regarded as *P. bougainville* except for *P. eremiana* which is considered distinct following Mahoney and Ride (1988) and Seebeck et al. (1990). All comparative specimens used in this work representing *P. bougainville* were collected as subfossil specimens from the Nullarbor Plains in Western Australia and therefore do not necessarily represent all possible races and variants of this species.

Dental nomenclature used follows that of Flower (1864) and Luckett (1993) where the adult (unreduced) tooth formula of marsupials is P1-3 and M1-4. Tooth morphology nomenclature follows Muirhead (1994). Classification follows Aplin and Archer (1987). Catalogue number abbreviations are AMF; Australian Museum palaeontological collection.

Figure 1. *Perameles bowensis* type material. A and A' = AMF98810 stereo occlusal views. B and B' = AMF98809 stereo occlusal views. C and C' = AMF98811 stereo occlusal views. D = AMF98811 lateral view of lingual side. Scale bar at A = 1mm. Scale bar at B = 2mm. Scale bar at C and D = 1mm.

## SYSTEMATICS

Supercohort: Marsupialia (Illiger, 1811) Cuvier, 1817
Cohort: Australidelphia Szalay, 1982
Order: Peramelemorphia (Kirsch, 1968) Aplin and Archer, 1987
Family: Peramelidae (Gray, 1825), (sens. Groves and Flannery,1990)
*Perameles bowensis* n. sp.

### Holotype

AMF98809 (Fig. 1B) Right $M^3$

### Paratypes

AMF98810 (Fig. 1A) $RM^2$; AMF98811 (Fig. 1C and D) $RP^3$; AMF98812 (Fig. 2C and D) $RM_3$; AMF98813 (Fig. 2A and B) $LM_1$.

### Specific etymology

The species name is in reference to the type locality.

### Type locality and age

The Bow Local Fauna lies within unnamed roadcut sediments in northeastern New South Wales. This fauna has been dated at early Pliocene based on biocorrelation with the radiometrically dated Bluff Downs Local Fauna (Skilbeck 1980, Flannery and Archer 1984, Rich et al. 1991).

### Diagnosis

*Perameles bowensis* differs from all other species of *Perameles* in the following combination of features: 1) small size, 2) greater development of metastylar region on $M^3$, 3) shallow ectoflexus on $M^3$ and none on $M^2$, 4) small hypocone on $M^3$, 5) large lingual displacement of stylar cusps on $M^2$, 6) small development of parastylar region on $M^2$, 7) strongly curved preparacrista on $M^2$, 8) anterobuccal cingulum on $M^3$ and $M^2$ but not connecting to preprotocrista, 9) $P^3$ ovoid in shape with well developed posterior heel not continuing anteriorly beyond lingual side of primary cusp, 10) no anterior cusp on $P^3$, and 11) posthypocristid on $M_1$ not continuous to posterolingual corner of crown.

*Perameles bowensis* is phenetically most similar to *P. eremiana* in terms of size and general shape of the molars. It differs from *P. eremiana* in the following features: 1) more continuously thick cingulum between lingual to posterior corners of $P^3$, 2) less well developed and shallow trough between St B and St D and associated crests on $M^2$ 3) larger $M^3$ formed by the wider stylar shelf region and larger metastylar corner, 4) stylar cusps larger and wider on $M^3$, 5) postmetacrista entirely straight and not curved posterobuccally, 6) hypocone much smaller, 7) angle of posthypocristid orientated more oblique to the tooth length and not perpendicular, and 8) paracristid and metacristid of $M_1$ and $M_3$ are more distant.

### Description

$P^3$ crown is short and ovoid in occlusal shape. The posterior dimension of the crown is wider than the anterior. The primary cusp is anteriorly positioned. One major crest extends posteriorly from the primary cusp to a small posterior cusp. Expansion of the crown is present as a heel from the lingual side of the primary cusp to a posterior cusp. Slight development of a heel is also present on the buccal side of the crest.

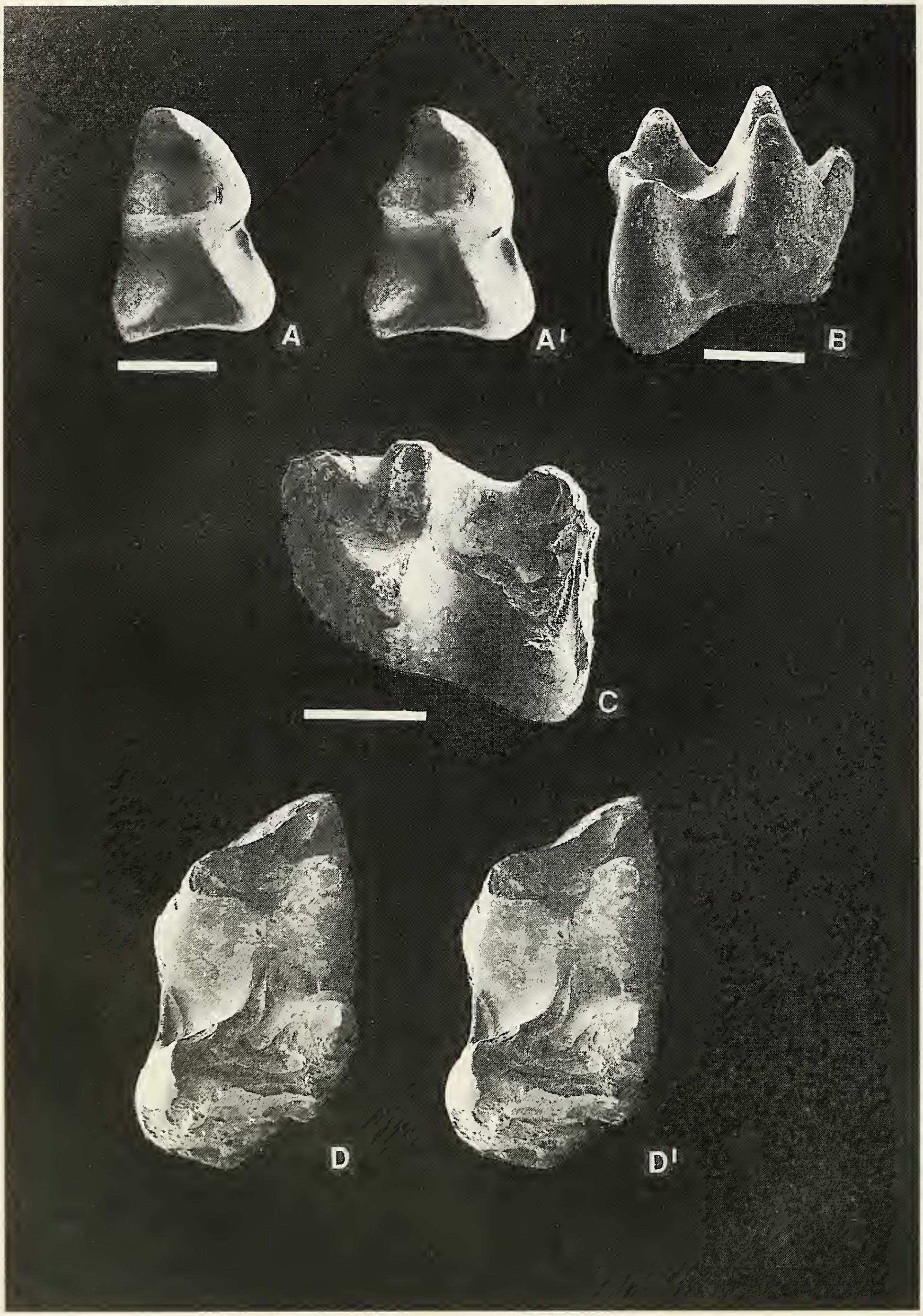


Figure 2. *Perameles bowensis* paratype material. A and A'–AMF98813 stereo occlusal views. B = AMF98813 lateral view. C = AMF98812 lateral view. D = AMF98812 stereo occlusal views. All scale bars = 1mm. C and D to same scale.

$M^2$ crown is roughly square in occlusal outline. The posterobuccal corner is broken. The anterior cingulum terminates below the midpoint of the preparacrista. No contact exists between the anterior cingulum and the preprotocrista. The preprotocrista terminates at the anterolingual corner of the paracone base. The crown is worn. The largest cusp is St D, followed (in decreasing height) by St B, metacone, anterior cingulum tip, paracone, protocone and hypocone. The preparacrista is short and curves to connect to the anterior cingulum tip without connection to St B. The postparacrista is slightly shorter in length, terminating around the posterior base of St B. The premetacrista is slightly longer than the preparacrista and parallel to this crest, terminating at the anterolingual base of St D. The postmetacrista is very worn and broken posterobuccally. A slight inflection exists between the protocone and hypocone. The posthypocristid terminates at the posterior base of the metacone. St B and D are the only stylar cusps present. These have strong lingual curvature. The paracone is located midway between the buccal and lingual sides of the crown. The metacone is positioned at a more lingual position. The protocone and hypocone are equidistant from the buccal edge.

$M^3$ crown is triangular in occlusal view. The buccal surface is the shortest of the three crown dimensions. All cusps and crests are worn. Morphology follows that of $M^2$ except as follows. Ectoflexus is stronger on the buccal side. The posterobuccal corner of the crown is prominently extended. St B and D do not curve lingually as much as on $M^2$. The anterior cingulum is shorter. The position of the paracone is more lingual and lies directly anterior to the metacone. The paracristae are longer. The postparacrista connects directly to St B rather than to the base of this cusp. The trough between St B and D is deeper at the shelf. The hypocone is small. The crest from the hypocone terminates at the lingual base of the metacone. The parastylar region is developed to a greater degree, with a larger distance between St B and the anterior cingulum tip.

The protoconid and metaconid of $M_1$ are approximately equal in height, followed (in decreasing height) by the entoconid, hypoconid, hypoconulid and paraconid. Of the primary cusps, the metaconid and protoconid are closer to each other than either is to the paraconid. The metaconid is directly posterior to the paraconid. The entoconid lies directly posterior to the metaconid and not connected by a preentocristid. The entoconid is conical in shape. The hypoconid is positioned almost twice as far buccally as is the protoconid. The posthypocristid is the longest crest on the crown connecting to the hypoconulid at the posterobuccal base of the entoconid. The cristid obliqua is curved, terminating at the posterior base of the protoconid and buccal to the valley in the metacristid. The entoconid lies directly lingual to the hypoconid. No anterior or posterior cingulum is present.

Morphology of $M_3$ follows that of $M_1$ except as follows. The metaconid is higher than the protoconid. The anterior cingulum is wide and without a notch, terminating at the anterior base of the protoconid. The metaconid is closer to the paraconid than to the protoconid. The protoconid is higher than the hypoconid. The protoconid is almost buccally level with the hypoconid. The cristid obliqua terminates at the base of the valley in the metacristid. No hypoconulid is present. The posthypocristid terminates at the base of the entoconid. A wear facet along the crest of the entoconid lies oblique to the anteroposterior length of the tooth.

Measurements of *P. bowensis* type material are found in Table 1.

## *PERAMELES BOWENSIS* FROM WELLINGTON CAVES

Material collected from the Phosphate Mine Beds of Wellington Caves (NSW) during excavations by A. Osborne, M. Archer and L. Dawson in 1982–1983, has produced two bandicoot taxa (Dawson and Augee this volume). Five of these specimens appear to be *Perameles bowensis*.

All five specimens are isolated molars. Three specimens are from the Big Sink Unit and include two broken $M^3$s (AM F69887 [formerly WC1678], Fig 3B and AM F69899, Fig 3A) and an $RM_1$ (AM F69804 [formerly WC1677], Fig 3C). The remaing two specimens, a broken $RM^1$ (AM F69897, Fig 3E) and a $RM^2$ (AM F69896, Fig 3D), were retrieved from the lower 'Graded-Bedded Unit' (Osborne 1982).

The 'Graded-Bedded Unit' is separated from the Big Sink Unit by the disconformably overlying 'Conglomerate Unit' (Osborne 1983). The unconformity separating the Big Sink Unit from the overlying Mitchell Cave Beds has been estimated by Osborne (1983) to be at least late Pliocene in age. Teeth from both of these deposits appear to represent the same taxon.

TABLE 1

Measurements of specimens of *Perameles bowensis* from the Bow Local Fauna and Wellington Caves. All measurements are maximum distances in mm. Width is lingual-buccal distance on crown. Length is antero-posterior distance. Para = paracone, meta = metacone, proto = protocone, ento = entoconid, hypo = hypoconid, metad = metaconid, parad = paraconid, protod = protoconid, – = information missing or not appropriate.

***Specimens from Bow***

**Uppers**

| AMF number | width | length | para-meta | meta-proto | proto-para |
|---|---|---|---|---|---|
| 98810 | 2.54 | 2.50 | 1.27 | 1.18 | 0.77 |
| 98809 | 2.76 | 3.14 | 1.53 | 1.74 | 0.77 |
| 98811 | 1.69 | 1.88 | – | – | – |

**Lowers**

| AMF number | width | length | ento-meta | meta-hypo | metad-parad | parad-protod | protod-metad |
|---|---|---|---|---|---|---|---|
| 98813 | 1.61 | 2.52 | 0.92 | 1.12 | 1.02 | 1.07 | 0.69 |
| 98812 | 1.84 | 2.81 | 1.14 | 1.42 | 0.71 | 1.27 | 1.16 |

***Specimens from Wellington Caves***

**Uppers**

| AMF number | width | length | para-meta | meta-proto | proto-para |
|---|---|---|---|---|---|
| 69896 | 2.83 | 2.61 | 1.63 | 1.79 | 0.95 |
| 69899 | – | 3.17 | 1.59 | – | – |
| 69887 | – | – | – | – | – |
| 69897 | – | 3.34 | 1.78 | – | – |

**Lowers**

| AMF number | width | length | ento-meta | meta-hypo | metad-parad | parad-protod | protod-metad |
|---|---|---|---|---|---|---|---|
| 69804 | 1.63 | – | 1.01 | 1.30 | – | - | 0.79 |

These bandicoots specimens from Wellington Caves are clearly a *Perameles* rather than an *Isoodon* due to the lack of complete anterior and posterior cingulum on the upper molars (particularly the posterior molars). These specimens are within the size range of *P. bougainville* and *P. eremiana*; however they differ in morphology from these species. The only remaining species of *Perameles* of this size range is *P. bowensis* from the Bow Local Fauna.

No $M^1$s are available in the Bow Local Fauna attributed to *P. bowensis*. This there-

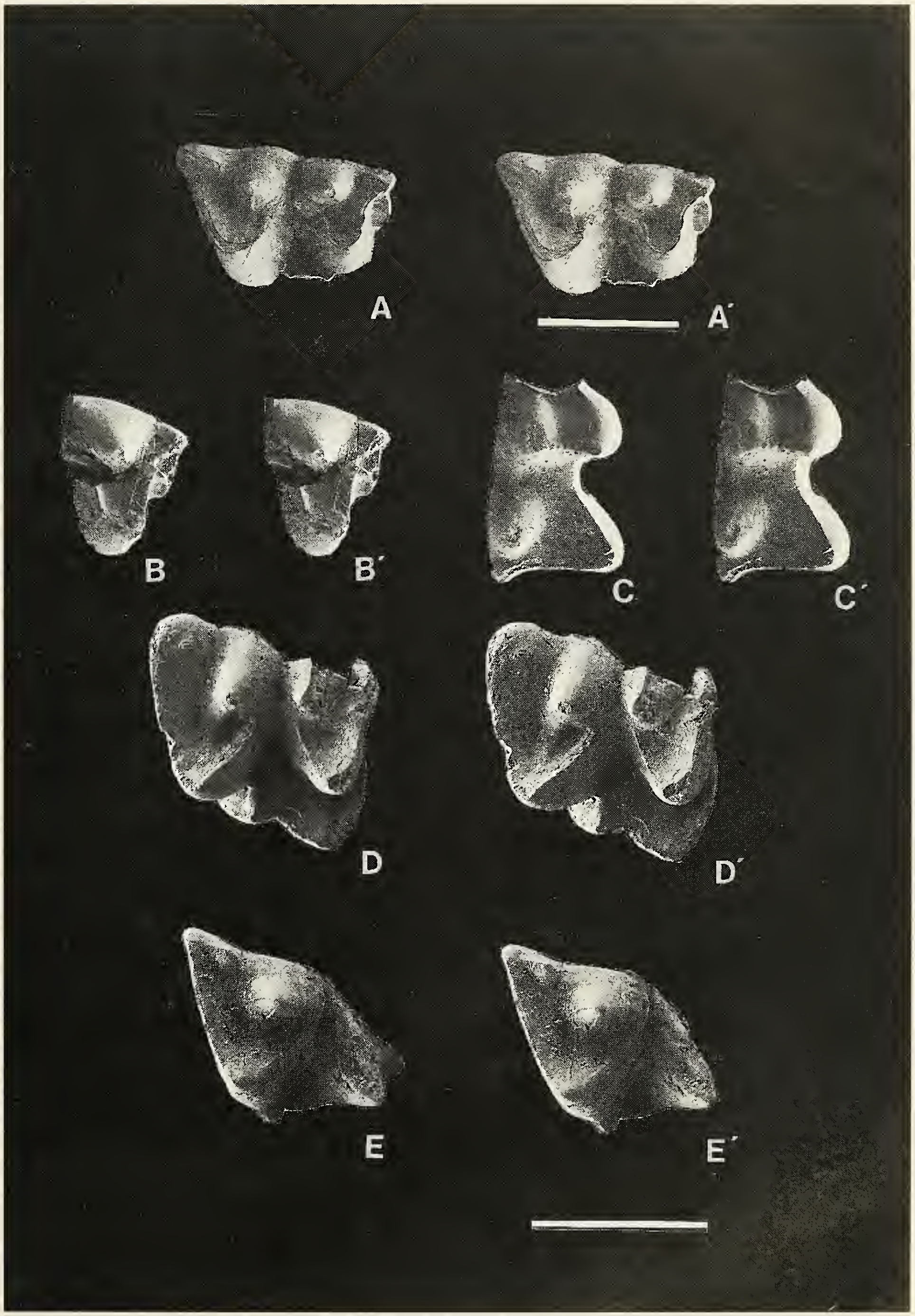


Figure 3. *Perameles bowensis* from Wellington Caves. Stereo occlusal views of specimens. A and A' = AMF69899. B and B' = AMF69887. C and C' = AMF67804. D and D' = AMF69896. E and E' = AMF69897. Scale bars = 2mm. Lower scale bar refers to all specimens except A.

fore prevents direct comparison between the $M^1$ from Wellington Caves and this species. The morphology of the broken $M^1$, however, is within the range exhibited by other species of *Perameles* and within that expected following the morphological trends of the more posterior molars of this species.

The $M^2$ from Wellington Caves is very similar to the corresponding tooth from *P. bowensis* in having no ectoflexus, no anterior cingulum, the same development of the posterior cingulum, the same degree of lingual displacement of the stylar cusps and a similar height of all of the cusps on the tooth. The metastylar region cannot be compared because this area has been broken in the Bow sample. The Wellington $M^2$ differs from the corresponding tooth from Bow in having a less concave preparacrista and greater dissimilarity in size between the protocone and hypocone. This difference in morphology between the $M^2$ from these sites is easily attributed to wear. The $M^2$ from Bow shows greater wear at the back of the lingual tip of the protocone. These is little reason to doubt the inclusion of this tooth within the morphological and size range expected for *P. bowensis*.

The $M^3$s from Wellington Caves are represented by two broken fragments. The larger of these includes the paracone, metacone and the stylar region of this tooth. The smaller fragment represents the paracone and parastylar region and in all respects duplicates the morphology and size shown by the more completely preserved specimen. The $M^3$s from Wellington are similar to the corresponding tooth of *P. bowensis* in all respects except for the lesser ectoflexus with less extension of the postmetacrista and the greater size of the St E. The size difference of St E may be attributed to wear. The extent of morphological variation for this species is unknown because of the very limited number of samples, but this degree of dfference is unlikely to be beyond that exhibited within a species.

The $RM_1$ differs from that of *P. bowensis* from the Bow Local Fauna only by a slightly smaller hypoconid.

There is little to preclude specimens from the Big Sink Unit and the 'Graded Bedded Unit' of Wellington Caves from being considered representative of *P. bowensis*. All differences between specimens may be attributed to wear or intraspecific variation. Because specimens from the type locality do not include an example of the $M^1$, this tooth of *P. bowensis* is described from Wellington Caves.

## Description of $M^1$

The buccal portion of the $M^1$ is the only part preserved. The highest cusp on the crown is the metacone, followed (in decreasing height) by the St D, St E, paracone and St B. The parastylar region includes a small, unnotched tip on the anterobuccal corner of the crown. The paracrista does not connect to the parastylar tip but instead runs posterobuccally from the paracone to connect with St B. The postparacrista runs parallel to the preparacrista from the paracone to connect at the posterior flank of the St B. There is no ectoflexus on the crown and the buccal face of the tooth is slightly rounded. The trough between St B and St D is shallow. St D is conical in shape and there is no connection by way of a crest to the St B. The premetacrista is straight and terminates at the anterior base of St D. The postmetacrista is the longest crest on the tooth, terminating at the posterobuccal metastylar tip of the crown. It is slightly convex around the metastylar region. St E lies on the posterobuccal region of the stylar shelf. It has a short anterior and posterior crest connecting to the St D and metastylar tip respectively. The broken region at the base of the metastylar portion of the tooth indicates a triangular shape of the complete tooth with the presence of a hypocone. The posterior cingulum would, if present, not have connected to the base of the metastylar corner of the crown.

## PHYLOGENETIC DISCUSSION

Aplin and Archer (1985) recognise the presence of both *Isoodon* and *Perameles* within the Bow Local Fauna. Part of the material described here as *Perameles bowensis* was that referred to as *Isoodon* (Aplin and Archer 1986, Archer 1984, Rich et al. 1991). There is no material from Bow that shares apomorphies with *Isoodon* that are not also shared with *Perameles* (e.g. enlargement of the hypocone on $M^2$). Apomorphies that distinguish *Isoodon* from *Perameles* are not apparent in this material such as the complete (or almost complete) and well developed anterior and posterior cingula on $M^2$ and $M^3$, and enlarged roots with a lack of distinction between root and crown. These specimens are therefore precluded from *Isoodon*. The specimens previously considered to represent *Isoodon* are now included with material referred to as *Perameles* and described here as the one species, *P. bowensis*.

Material refered to here as *Perameles bowensis* shares no apomorphies with any other genus not also shared with other species of *Perameles*. Features that *P. bowensis* has in common with other genera that are not also shared with other species of *Perameles* are symplesiomorphies. The morphology of *P. bowensis* appears to fall well within the range of diversity exhibited by modern species of *Perameles* and is therefore placed within this genus.

In general, *P. bowensis* appears to be slightly more plesiomorphic in most regards than modern species of *Perameles* but is likely to be closer to these than to *P. allinghamensis*. Of the modern species, *P. bougainville* is considered to show more plesiomorphic features of the dentition (but not cranial characters). *Perameles bougainville*, unlike *P. eremiana*, *P. nasuta* and *P. gunnii*, retains the plesiomorphic characteristics of less caniniform $I^5$, more linear $P^3$, smaller hypocones, less developed posterior cingulum, less elongated snout, retention of the hypoconulid on $M_2$, more equidistant paraconids, metaconids, and protoconids and an incomplete anterior cingulum on $M_1$.

*Perameles bowensis* is more plesiomorphic than all Recent species in having a smaller hypocone on the $M^3$, more equidistant paraconids, metaconids and protoconids on $M_{1-3}$ with the paraconid and metaconid wider apart on $M_1$ than on Recent species. Of the Recent species, *P. bowensis* is phenetically similar to *P. eremiana* in having similar sized $P^3$ and molars except for the $M^3$, which is slightly larger in *P. bowensis*. The morphology of the $P^3$ and $M^2$ does not differ between these two species except that the metastylar region is smaller in *P. bowensis* and in this feature is more similar to *P. bougainville*. The lower molars of *P. eremiana* are more apomorphic in their concave cristid obliquas producing a narrower talonid. *Perameles eremiana* is also more apomorphic than *P. bowensis* in the overall smaller width of the trigonid basin produced by reduction of the distance between the paraconid and metaconid and orientation of associated crests more perpendicularly to the long axis of the tooth row. *Perameles bowensis* is plesiomorphic in this regard in having a wider trigonid which is also wider than in any other Recent species. *Perameles bowensis* is also more plesiomorphic than *P. eremiana* in having a smaller hypocone on the $M^3$, a feature in which it is also more plesiomorphic than all Recent species of *Perameles*.

Comparison to *P. eremiana* is restricted due to the few available samples of this species and therefore intraspecific variation for *P. eremiana* cannot be adequately assessed. However, variation to the degree needed to include *P. bowensis* into this species is much wider than that known for any other species. No species is known to vary the orientation of crests of the molars to such a degree. The variation between samples of *P. eremiana* and *P. bowensis* is therefore considered to be outside of that for a single species, and *P. bowensis* is therefore separated from *P. eremiana*. The kind of variation between these two species in some characters (e.g. crest orientation, basin width) represents the two extremes shown within the entire genus.

*Perameles bowensis* retains some of the plesiomorphies seen in *P. bougainville*. These are the small hypocone on $M^3$ and roughly equidistant paraconid, metaconid, and protoconids. The $P^3$ is more apomorphic than that of *P. bougainville*, with posterior thickening and a posterior heel. The poor trough development between the stylar cusps on the $M^2$ and the buccal termination of the cristid obliqua on the lowers are plesiomorphic features lost by all modern species.

*Perameles bowensis* is more apomorphic than *P. allinghamensis*. This Pliocene species is represented only by a broken isolated upper molar. The arrangement of the preparacrista and parastylar corner of the crown is entirely different to that of other species of *Perameles*. In all other species of *Perameles*, the preparacrista on the $M^2$ and $M^3$ continue past the stylar cusps to terminate at the parastylar corner. This region is of equal height or even higher than the stylar shelf and functions as an akis (a pointed cusp at the terminal end of a sharp-edged blade, [Every 1975]). This region extends anteriorly past the remainder of the crown and overlaps the proceeding molar. No anterior cingulum is present on the anterobuccal side of the tooth. The morphology of this region on *P. allinghamensis* is considered to be plesiomorphic because it is similar to that seen in dasyurids and relatively plesiomorphic bandicoots. Here the preparacrista terminates at the parastylar corner, but in addition the buccal portion of the anterior cingulum is low lying and anterior to the parastylar corner of the crown. The preparacrista bends anteriorly at this corner in other species of *Perameles*, while in *P. bowensis* the preparacrista is straight so that these regions remain separate on two levels. Further finds from the Allingham Formation representing *P. allinghamensis* may realise the possibility suggested by Archer (1976) that it represents a new genus of bandicoot.

The presence of *P. allinghamensis* in the early Pliocene Allingham Local Fauna (Archer 1976) is the earliest formally described member of this genus. Reports of the presence of *Perameles* from the Tarkarooloo and Kutjamarpu Local Faunas of the middle Miocene (Rich et al. 1982) are unsupported by more recent review (Rich et al. 1991) where these specimens have been re-classified as “Perameloidea” and appear to represent other taxa. *Perameles* sp. is also reported to be present in the Pliocene Dog Rocks Local Fauna together with *Isoodon* sp. (Whitelaw 1989, Rich et al. 1991).

*Perameles bowensis* is phylogenetically closer to Recent species than is *P. allinghamensis*. In most features it is more plesiomorphic than *P. nasuta* and *P. eremiana*; however, its relationships to *P. bougainville* and *P. gunnii* are unresolved. Considering its close phenetic similarity to *P. eremiana,* it may be the sister species to a *P. eremiana* — *P. nasuta* clade. Alternatively, it may lie outside of all Recent species of *Perameles* as their sister-species.

## ACKNOWLEDGEMENTS

The Big Sink material was collected by M. Archer, A. Osborne and L. Dawson in October 1982. Phosphate Mine material from Wellington Caves was collected by A. Osborne and L. Dawson in May 1983. We are grateful of useful comments and advice provided by Ken Aplin and referees, and the assistance of Henk Godthelp, Mike Augee (University of New South Wales), Linda Gibson, Robert Jones (The Australian Museum) and the Wellington and Bow Shire Councils for permission to collect.

## REFERENCES

Aplin, K. and Archer, M. (1985). Fossil bandicoots of the mid-Pliocene Bow Local Fauna. *Australian Mammal Society Bulletin,* p 29.

Aplin, K. and Archer, M. (1987). Recent advances in marsupial systematics with a new syncretic classification. In ‘Possums and opossums: studies in evolution’ (Ed M. Archer) ppxv-lxxii. (Surrey Beatty and Sons and the Royal Zoological Society of New South Wales, Sydney).

Archer, M. (1976). The Bluff Downs Local Fauna. In ‘The Allingham Formation and a new Pliocene vertebrate fauna from northern Queensland’ (M. Archer and M. Wade). *Memoirs of the Queensland Museum* **17**, 383–395.

Archer, M. (1984). The Australian marsupial radiation. In 'Vertebrate zoogeography and evolution in Australasia' (Eds M. Archer and G. Clayton) pp. 633–808. (Hesperian Press, Perth).

Dawson, Lyndall and Augee, M.L. (this volume). The Late Quaternary sediments and fossil vertebrate fauna from Cathedral Cave, Wellington Caves, New South Wales. *Proceedings of the Linnean Society, New South Wales* **117**, 163-174.

Every, R.G. (1975). Significance of tooth sharpness for mammalian, especially primate, evolution. In 'Approaches to primate paleobiology' (Ed. F.S. Szalay) pp. 295–325. *Contributions to Primatology* Vol 5. (Karger, Basel).

Flannery, T.F. and Archer, M. (1984). The Macropoids (Marsupialia) of the early Pliocene Bow Local Fauna, central eastern New South Wales. *The Australian Zoologist* **21**, 357-383.

Flower, W.H. (1869). Remarks on the homologies and notation of the teeth in the Marsupialia. *Journal of Anatomy and Physiology* **3**, 262-278.

Luckett, W.P. (1993). An ontogenetic assessment of dental homologies in therian mammals. In 'Mammal phylogeny, Vol 1' (Eds F.S. Szalay, M.J. Novacek and M.C. McKenna) pp. 182–204. (Springer-Verlag: New York).

Mahoney, J.A. and Ride, W.D.L. (1988). Peramelidae. In 'Zoological catelogue of Australia vol. 5 Mammalia' (Ed. D.W. Walton) pp. 36–42. (Bureau of Flora and Fauna: Canberra).

Marlow, B.J. (1962). 'Marsupials of Australia'. (Jacaranda Press: Brisbane).

Muirhead, J. (1994). Systematics, evolution and palaeobiology of Recent and Fossil bandicoots (Peramelemorphia, Marsupialia). PhD Thesis, Unviersity of New South Wales, Sydney.

Osborne, R.A.L. (1983). Cainozoic stratigraphy at Wellington Caves, New South Wales. *Proceedings of the Linnean Society of New South Wales* **107**, 131–147.

Rich, T.H., Archer, M., Hand, S.J., Godthelp, H., Muirhead, J., Pledge, N.S., Lundelius, E.L.Jr., Flannery, T.F., Rich, L.S.V., Woodburne, M.O., Case, J.A., Whitelaw, M.J., Tedford, R.H., Kemp, A., Turnbull, W.D. and Rich, P.V. (1991). Australian Mesozoic and Tertiary terrestrial mammal localities, Appendix 1. In 'Vertebrate palaeontology of Australia' (Eds P. Vickers-Rich, J.M. Monaghan, R.F. Baird and T.H. Rich) pp. 1005–1058. (Pioneer Design Studio and Monash University Publications Committee: Melbourne).

Rich, T., Archer, M., Plane, M., Flannery, T., Pledge, N., Hand, S. and Rich, P. (1982). Australian Tertiary mammal localities. In 'The fossil vertebrate record of Australiasia' (Eds P.V. Rich and E.M. Thompson) pp. 526–572. (Monash University, Clayton: Victoria).

Seebeck, J.H., Brown, P.P., Wallis, R.L. and Kemper, C.M. (1990). The Bandicoot and Bilby species. In 'Bandicoots and bilbies' (Eds J.H. Seebeck, P.P. Brown, R.L. Wallis and C.M. Kemper) pp 377. (Surrey Beatty and Sons: Sydney).

Skilbeck, C.G. (1980). A preliminary report on the Late Cenozoic geology and fossil fauna of Bow, New South Wales. *Proceedings of the Linnean Society of New South Wales* **104**, 171-181

Tate, G.H.H. (1948). Results of the Archbold Expeditions, no 60. Studies in the Peramelidae (Marsupialia). *Bulletin of the American Museum of Natural History* **92**, 317–46.

Whitelaw, M.J. (1989). Magnetic polarity, stratigraphy and mammalian fauna of the Late Pliocene (Early Matuyama) section at Batesford (Victoria), Australia. *Journal of Geology* **97**, 624–31.

# Rehabilitation of the Wellington Caves Phosphate Mine: Implications for Cainozoic Stratigraphy

R.A.L. Osborne

School of Teaching and Curriculum Studies, A22, University of Sydney, Australia, 2006

Osborne, R.A.L. (1997). Rehabilitation of the Wellington Caves Phosphate Mine: implications for Cainozoic stratigraphy. *Proceedings of the Linnean Society of New South Wales* **117**: 175-180

Rehabilitation work on the Wellington Caves Phosphate Mine has revealed stratigraphic sections and boundaries which were not exposed when Frank (1971) and Osborne (1983) undertook their studies. As a consequence the Cainozoic stratigraphy at Wellington Caves is now seen to be in need of revision.

Preliminary investigations have revealed the presence of a previously unrecognised stratum of Pleistocene clay, up to 4 m of undifferentiated strata of probable Pliocene age and the presence of a second major unconformity within the sequence.

The newly-recognised unconformity separates strata of known Pliocene age from an older sequence whose fauna has yet to be studied. Given that the unconformity is likely to represent a significant time break, the older sequence is likely to be significantly older than Pliocene.

Manuscript received 20 March 1996, accepted for publication 19 June 1996.

KEYWORDS: Cainozoic, stratigraphy, Wellington Caves, Phosphate Mine

## INTRODUCTION

The Wellington Caves Phosphate Mine (Fig. 1) operated between 1914 and 1918 during which time some 6,000 tonnes of phosphate rock were extracted from workings in sediment-filled limestone cave passages at Wellington Caves in central western New South Wales. The mine intersected significant deposits of bone-bearing strata, particularly red cave earth, which have formed the basis for most 20th century palaeontological studies at Wellington Caves.

Fossils from the Phosphate Mine and from Bone Cave, which has now been shown to be an abandoned early section of the mine, have been extracted and studied by Anderson (Anderson 1926) and Brown (Brown 1926) in the 1920s, Anderson and Schevill (Anderson 1933) and Schroeder and Dehm in the 1930s (Augee et al. 1986), Marcus (Marcus 1962), Mahoney and Lundelius (Lundelius 1966) in the 1950s, Hope in the 1960s and Augee and Dawson in the 1980s and 1990s.

The exposures in the mine have been the most instructive of all in elucidation of the Cainozoic stratigraphy at Wellington Caves and formed the basis for unpublished work by J. Mahoney in the 1950s and the major stratigraphic studies of Frank (1971) and Osborne (1983).

## THE PHOSPHATE MINE RESTORATION PROJECT

The condition of the Wellington Caves Phosphate Mine deteriorated significantly during the 1980s and 1990s and it became clear by 1994 that some sections of the mine

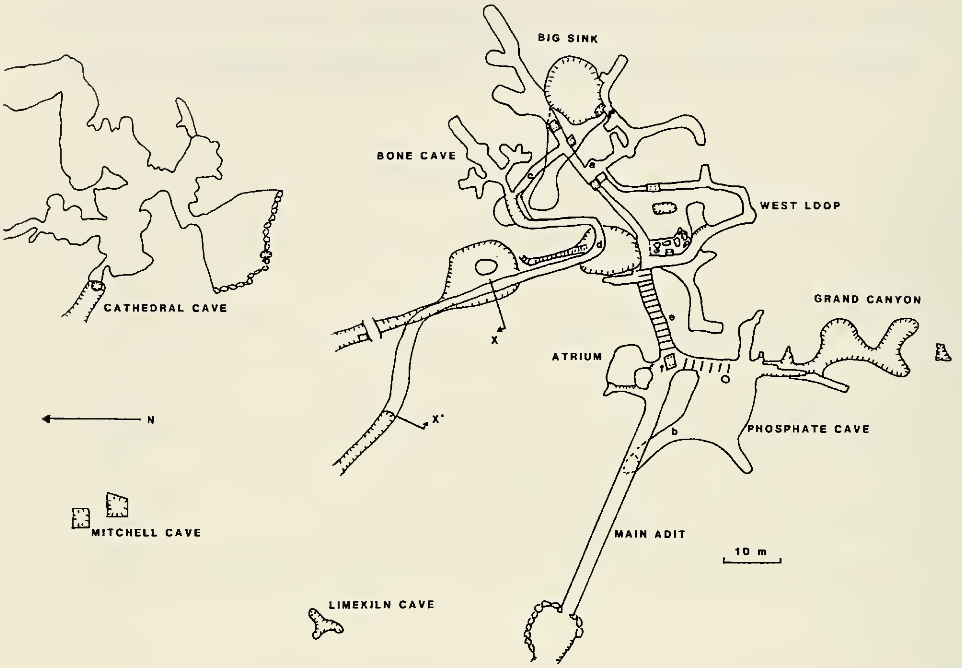


Figure 1. The Wellington Caves Phosphate Mine. (a) 'Shaft Cave' fossil locality of Schroeder and Dehm, (b) 'Phosphate Cave' fossil locality of Schroeder and Dehm, (c) Adit connecting Bone Cave to the mine, reopened during rehabilitation in 1995, (d) Cut and fill passage joining Bone Cave to minor adit, formed in early 1996, (e) Timber platform used to mine phosphate, (f) North Shaft, (X-X') New adit through massive limestone constructed in 1995 to provide second tourist entrance to mine.

were in imminent danger of collapse, in particular the passage that provided access to Schroeder and Dehm's 'Shaft Cave' fossil locality.

During the early 1990s some members of the Wellington Caves Advisory Committee, which assists Wellington Council in management of Wellington Caves, in particular Campbell Gregory, came to believe quite strongly that the Phosphate Mine had considerable potential for development as an additional tourist attraction at the caves. As a result Wellington Council was strongly lobbied to take action to prevent further deterioration of the mine and to begin a process that could eventually result in the mine being rehabilitated and developed as a tourist attraction.

In mid 1994 Wellington Council commissioned a series of studies to assess the feasibility of rehabilitating and developing the mine. These examined: the bat population (Dovey 1994), geological and palaeontological features (Osborne 1994) and mining heritage and archaeology (Godden Mackay 1995). A mining survey and estimate of rehabilitation costs were undertaken (Donnelly Mining and Civil Pty Ltd. 1994) and in July 1994 the most unstable section of the mine was given temporary support using expandable metal props.

In July 1995 Wellington Council received funding under the New Work Opportunities Scheme through the Department of Employment Education and Training to employ up to thirty people for six months on the Phosphate Mine project. From July 1995 to April 1996 Wellington Council provided funding to cover supervision, capital materials, an interpretation study (Hamilton-Smith and Osborne 1995) and all other necessary works to bring the project to completion.

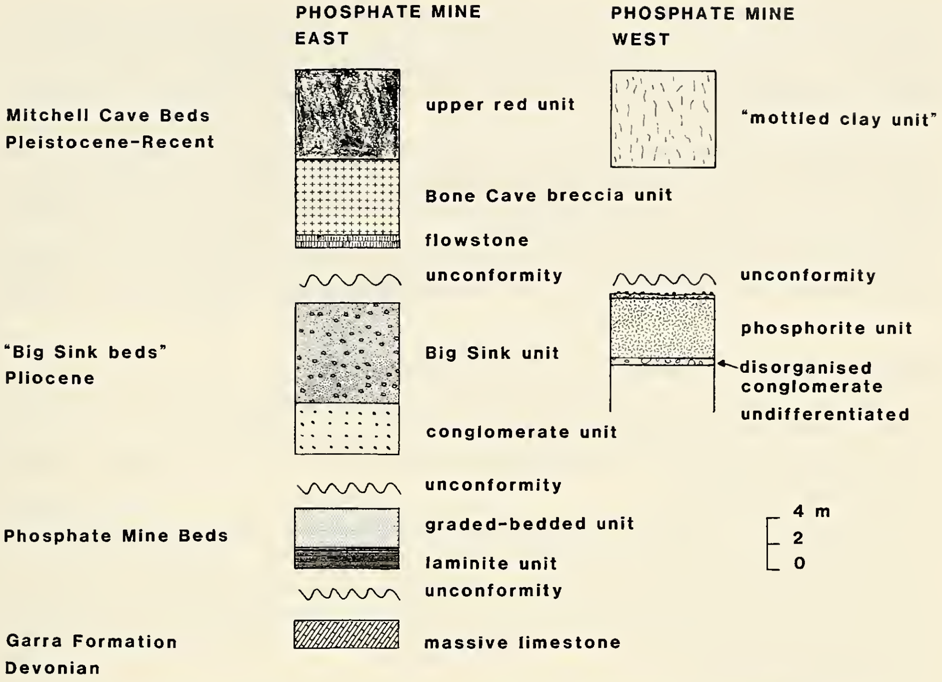


Figure 2. Tentative stratigraphic columns for strata exposed in the Wellington Caves Phosphate Mine.

Rehabilitation and development work on the mine has included removal of fallen mullock from the mine passages, replacement of all unsafe timbering, installation of a new collar on the North Shaft, reopening of the tunnel between the mine and Bone Cave (discovered during the rehabilitation work) and excavation of a new entrance tunnel. The work has also revealed indications that mining commenced in the Big Sink area, that the Grand Canyon began as a shaft and was exhumed as the mining proceeded, that the the mine was electrically lit and that an extensive rail system was used in the mine, probably in conjunction with a hand cart.

Tourist development has involved the laying of paths to disabled access specifications, installation of lighting and services, followed by cleaning of features and passage walls by dry vacuuming.

The removal of mullock from the passages, and of material falling during re-timbering, was carried out so that original mine walls remained undisturbed. Spoil from these operations, which contains significant amounts of out-of-context bone fragments, has been stockpiled in labelled dumps which can be identified with the part of the mine from which they were extracted.

## NEW STRATIGRAPHIC OBSERVATIONS

The cleaning and restoration work has revealed whole sequences of strata and significant stratigraphic boundaries which were obscured when Frank (1971) and Osborne (1983) undertook their stratigraphic studies. Opening of the connection between the mine and Bone Cave, restoration of passages in the Big Sink area and the installation of paths has also meant that it is now much easier to determine level relationships between stratigraphic sections in different parts of the mine. From observations made up till the time of writing (March 1996) it is clear that the stratigraphy of the deposits in the mine is in need of significant revision.

A tentative comparison between the stratigraphic schemes of Frank (1971) and Osborne (1983) and details available from initial examination of the mine after rehabilitation is given in Figure 2. Except where specifically stated, stratigraphic terminology used here follows that of Osborne (1983).

It must be stressed that the work reported here is preliminary and that a detailed reexamination of the mine's stratigraphy will be undertaken later in 1996.

**Major points of this new tentative interpretation are :**

a) an unconformity between the Big Sink unit, on which flowstone (Unit 2 FS of Frank 1971) is deposited, and the Bone Cave breccia unit.

b) correlation of the Big Sink unit of Osborne (1983) with Unit 1 BG of Frank (1971), as per Osborne (1983).

c) recognition of an unconformity between the Big Sink and conglomerate units (here now grouped as the Big Sink beds) and the graded-bedded unit. Osborne (1983) proposed that the boundary between the conglomerate unit and the graded-bedded unit was likely to be disconformable. Boundaries now revealed in the Bone Cave indicate that the Big Sink unit has an unconformable (in places vertical) boundary with the graded-bedded unit.

It would seem likely that the Big Sink and conglomerate units together form a distinct sequence of strata likely to be of Pliocene age, tentatively named the 'Big Sink beds'.

d) a new stratum, the 'mottled clay unit', which disconformably overlies the phosphorite unit is recognised in the western part of the mine. Fossils collected by H. Godthelp (UNSW, pers. comm.) suggest that this unit is of Pleistocene age.

e) the sequence of strata below the phosphorite unit in the western part of the mine:
    - may not be correlated with the graded-bedded and laminate units as was suggested by Osborne (1983)
    - has unclear relationships with the Big Sink unit
    - contains at least 4m of strata not previously described.

f) the phosphorite unit probably does not conformably overlie the graded-bedded unit as was suggested by Osborne (1983).

g) the Bone Cave breccia unit is far better stratified than has previously been recognised and contains discontinuous thin layers of flowstone.

## IMPLICATIONS OF PRELIMINARY OBSERVATIONS

The new stratigraphic observations suggest that the Cainozoic record in the Phosphate Mine contains at least three distinct sequences separated by significant unconformities representing phases of erosion and exhumation of the phosphate mine cave system. The simplest interpretation now possible is shown in Table 1.

The stratigraphic interpretation of Osborne (1983) suggested that the sequence at Wellington Caves had the potential to extend well back into the Tertiary. The emerging new interpretation would lead to a similar conclusion.

Studies of the fauna from the Big Sink unit by Hand et al. (1988) and L. Dawson (UNSW, pers. comm.) have indicated an Early Pliocene age.

The recognition of an unconformity between the graded-bedded unit and the Big Sink and conglomerate units suggests that the older parts of the sequence may be considerably older than Pliocene.

Although bones or bone fragments are found in significant quantities in all of the strata marked with an asterisk, there has yet to be any systematic palaeontological study of the units lower in the sequence than the Big Sink unit.

It is thus highly likely that a detailed revision of the stratigraphy, coupled with palaeontological studies will show that the sequence in the Wellington Caves Phosphate Mine extends well back into the Tertiary.

TABLE 1

A stratigraphic interpretation of sequences at Wellington Caves

| Phosphate mine east, | Bone cave and big sink | Phosphate mine west |
|---|---|---|
| Mitchell Cave beds | upper red unit * | 'mottled clay' unit *# |
| (Pleistocene-Recent) | Bone Cave breccia unit *# | |
| | flowstone | |
| | UNCONFORMITY | UNCONFORMITY |
| 'Big Sink' beds | Big Sink unit *# | phosphorite unit |
| (Early Pliocene) | conglomerate unit* | disorganised conglomerate |
| | | 4m undifferentiated* |
| | UNCONFORMITY | |
| Phosphate Mine beds | graded-bedded unit* | |
| (age unknown) | laminate unit | |
| | ?UNCONFORMITY | ?UNCONFORMITY |
| | phosphate rim rock | phosphate rim rock |
| | UNCONFORMITY | UNCONFORMITY |
| Garra Formation (Devonian) | massive limestone | massive limestone |

* = bone and bone fragments present

# = fossils studied from this unit in Phosphate Mine

## ACKNOWLEDGEMENTS

The new observations reported here were made while the author was engaged as scientific consultant to Wellington Council during the course of the Phosphate Mine project. Particular credit must be given to Stan Donnelly, mining engineer; Brian Palmer, overseer; R and R Fraser, mining contractors and the workers employed under the New Work Opportunities Scheme for the care with which they undertook the work and for their assistance with observations in the mine.

## REFERENCES

Anderson, C. (1926). The Wellington Caves. *Australian Museum Magazine* **2,** 367–374.

Anderson, C. (1933). Presidential address: The fossil mammals of Australia. *Proceedings of the Linnean Society of New South Wales*. **48**, ix-xv.

Augee, M., Dehm, R., and Dawson, L. (1986). The Munich collection of Wellington cave fossil marsupials. *Australian Zoologist* **22**, 3–5.

Brown, C. (1926). In touch with a lost world, part 1. *The Sydney Mail*. June 2, 1926: 8–10.

Donnelly Mining and Civil Contracting Pty Ltd. (1994). Report on the Wellington Caves Phosphate Mine: infrastructure, safety and refurbishment. Unpublished report to Wellington Council, July 1994. 11p.

Dovey, L. (1994). Wellington Caves Reserve- Proposal to open Phosphate Mine to the public: Issues relating to the endangered species Common Bent-wing Bat, *Miniopteris schreibersii*. Unpublished report to Wellington Council, 1994. 4 p.

Frank, R. (1971). The clastic sediments of Wellington Caves, New South Wales. *Helictite* **9**, 3–26.

Godden Mackay Pty Ltd. (1995). Wellington Phosphate Mine Conservation Study, New South Wales. Unpublished report to Wellington Council, May 1995. 57p.

Hamilton-Smith, E. and Osborne R.A.L. (1995). Travelling through time at Wellington Caves, New South Wales. Unpublished report to Wellington Council, July 1995. 50p.

Hand, S., Dawson, L. and Augee, M.L. (1988). *Macroderma koppa*, a new Tertiary species of False Vampire Bat (*Microchiroptera, Megadermatidae*), from Wellington Caves, New South Wales. *Records of the Australian Museum* **40**, 343–351.

Lundelius, E.L. Jr. (1966). Marsupial Carnivore Dens in Australian Caves. *Studies in Speleology* **1**, 174–180.

Marcus, L.F. (1962).A new species of *Sthenurus* (*Marsupialia, Macropodidae*) from the Pleistocene of N.S.W. *Records of the Australian Museum* **25**, 299–304.

Osborne, R.A.L. (1983). Cainozoic stratigraphy at Wellington Caves, N.S.W. *Proceedings of the Linnean Society of New South Wales* **107**, 129–145.

Osborne, R.A.L. (1994). Geological, geomorphological and palaeontological features of the Wellington Caves Phosphate Mine. Unpublished report to Wellington Council, June 1994. 21p.

# New *Sthenurus* Species (Macropodidae, Diprotodontia) from Wellington Caves and Bingara, New South Wales

GAVIN J. PRIDEAUX AND RODERICK T. WELLS
(Communicated by M.L. Augee)

School of Biological Sciences, Flinders University of South Australia, GPO Box 2100,
Adelaide SA 5001.

Prideaux, G.J. and Wells, R.T. (1997). New *Sthenurus* species (Macropodidae, Diprotodontia) from Wellington Caves and Bingara, New South Wales. *Proceedings of the Linnean Society of New South Wales* **117**: 181-196

Two new species of the extinct macropodid genus *Sthenurus* are described from vertebrate deposits in eastern and northeastern New South Wales. Although its exact stratigraphic origin is uncertain, *Sthenurus brachyselenis* sp. nov. displays an early stage of evolution, only slightly more derived than the plesiomorphic early Pliocene *S. cegsai*. Its molars are low crowned and relatively simple, and $P^3$ bears a very short buccal crest. *S. euryskaphus* sp. nov. is from the Pleistocene Bingara deposit and is morphologically intermediate between the late Pliocene *S. antiquus* and two widespread Pleistocene species. *S. oreas*, within which the two new species were previously included, is deemed to be a very derived member of the genus, and may reside phylogenetically close to the origin of *Procoptodon*.

Manuscript received 1 May 1996, accepted for publication 23 October 1996.

KEYWORDS: Sthenurine kangaroo, *Sthenurus, Simosthenurus, Sthenurus brachyselenis* sp. nov., *Sthenurus euryskaphus* sp. nov., *Sthenurus oreas*, Wellington Caves, Bingara, Pliocene, Pleistocene.

## INTRODUCTION

Sthenurine kangaroos (subfamily Sthenurinae) are considered to have diverged from macropodine kangaroos (subfamily Macropodinae) in the mid-late Miocene (Flannery 1989). Although rare in Pliocene deposits, they are diverse and abundant in Pleistocene faunas, and distributed across much of southern and eastern Australia (Tedford 1966). This paper describes a new species of *Sthenurus*, probably of Pliocene age from Wellington Caves, eastern New South Wales, and another species from a Pleistocene deposit near Bingara in northern New South Wales.

Following Tedford's (1966) subgeneric division of *Sthenurus*, both new species described here would be referred to *Simosthenurus*, based on their relatively low crowned molars, upturned lower incisors and shortened mandibles. However, current research by one of us (GJP) questions the validity of the subgeneric or generic (*sensu* Flannery 1983) distinction within *Sthenurus*.

## MATERIALS AND METHODS

Material referable to the new species is housed in the Australian Museum (prefix AM). Dental homology employed is that of Flower (1867) following Luckett (1993) and Ride (1993). Dental nomenclature follows Tedford and Woodburne (1987) and Ride (1993). Mensuration follows Tedford (1966) and Wells and Murray (1979), with all measurements in millimetres and listed in Table 1: Anterior Width = width of protolophid; Posterior Width = width of hypolophid; Anterior Height = height of protolophid crown on buccal side; Posterior Height = height of hypolophid crown on buccal side. Comparisons have generally been made with those taxa that appear most similar to the two new species.

Specimens and localities used for comparisons are listed in the Appendix.

TABLE 1

Cheek teeth dimensions of *Sthenurus brachyselenis* and *S. euryskaphus*. Values in millimetres.

| Tooth | Species | Length | Anterior Width | Posterior Width | Anterior Height | Posterior Height |
|---|---|---|---|---|---|---|
| $P_2$ | *S. brachyselenis* | 8.1 | 5.1 | 6.1 | 5.7 | 5.5 |
| $dP_3$ | *S. brachyselenis* | 10.2 | 7.8 | 8.2 | 6.2 | 7.0 |
| | *S. euryskaphus* | 9.4 | 7.8 | 7.9 | 6.5 | 6.5 |
| $P_3$ | *S. brachyselenis* | 13.8 | 6.3 | 8.0 | 7.3 | 6.7 |
| | *S. euryskaphus* | 13.9 | 7.0 | 8.7 | 9.5 | 8.7 |
| $M_1$ | *S. brachyselenis* | 13.9 | 9.9 | 10.3 | 9.3 | 9.4 |
| | *S. euryskaphus* | 12.9 | 9.7 | 9.7 | 8.4 | 8.4 |
| $M_2$ | *S. brachyselenis* | – | – | – | – | – |
| | *S. euryskaphus* | *14.4* | *10.8* | *10.9* | *9.0* | *8.5* |

## SYSTEMATICS

Order DIPROTODONTIA Owen 1866
Suborder PHALANGERIDA Aplin and Archer 1987
Superfamily MACROPODOIDEA (Gray 1821)
Family MACROPODIDAE Gray 1821
Subfamily STHENURINAE (Glauert 1926)
Genus *STHENURUS* Owen 1874
Subgenus *SIMOSTHENURUS* Tedford 1966

### *Sthenurus (Simosthenurus) brachyselenis* sp. nov.

(Figs 1–3)
1966 *Sthenurus oreas* Tedford, p. 39–40.

### Holotype

AM F31026, right juvenile ramus with $I_1$, $P_2$, $dP_3$, $M_1$ erupted; $M_2$ in early stage of eruption; and $P_3$ excavated from body of mandible. Only ventral portion of ascending ramus is preserved.

### Type locality and age

The holotype is from Wellington Caves, eastern New South Wales (32°31'S, 148°51'E) and was collected in 1932 by C. Anderson and W. Schevill from a phosphate

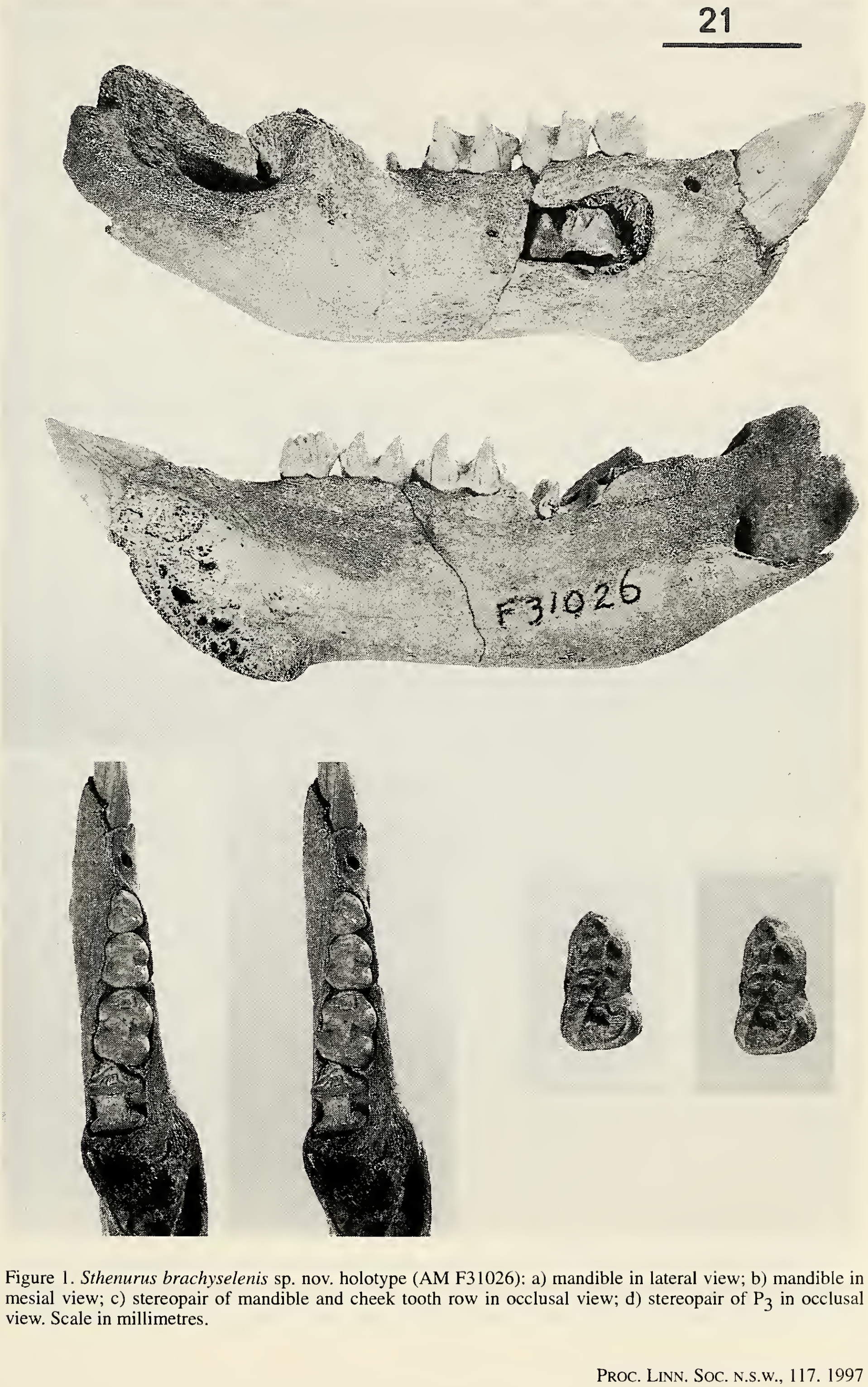


Figure 1. *Sthenurus brachyselenis* sp. nov. holotype (AM F31026): a) mandible in lateral view; b) mandible in mesial view; c) stereopair of mandible and cheek tooth row in occlusal view; d) stereopair of $P_3$ in occlusal view. Scale in millimetres.

mining drive (Anderson 1932, Dawson 1985). The stratigraphic provenance of the specimen is unknown, although the species appears to exhibit a Pliocene stage of evolution.

## Diagnosis

$I_1$ robust with relatively straight occlusal surface, only very slightly curved dorsally at anterior extreme. $P_2$ short relative to length of $dP_3$, possessing very short, crescentic buccal crest. This crest extends from posterior extremity of main (lingual) crest, terminates in posterobuccal corner and extends only very slightly anteriorly. $P_3$ short, equal in length to $M_1$, narrow and only inflated in posterobuccal corner below very short, crescentic buccal crest. This crest extends only one-third length of tooth. Anterior cingulum of lower molars symmetrically tapered, from both buccal and lingual extremities of protolophid.

## Etymology

Gr. *brachys* 'short', *selenis* 'crescent', in reference to the short crescentic nature of the buccal crest on $P_2$ and $P_3$.

## Description

Juvenile mandible with ramus relatively deep and narrow for much of its length. Prominent boss extends below level of ventral border of ramus at base of symphysis. Symphysis extends posteriorly below circular genial pit. Digastric sulcus very shallow and digastric eminence only moderately formed. Diastema very short and orientated in same plane as $I_1$ occlusal surface. Buccinator sulcus narrow, deep and positioned close to dorsal border of ramus, extending from between anterior mental foramen and half-way point on diastema, to below hypolophid of $dP_3$. Dorsal border of anterior mental foramen located immediately below anterior extreme of buccinator sulcus. Posterior mental foramen positioned directly below protolophid of $M_1$, on a horizontal plane that lies just below ventral border of masseteric fossa. Masseteric foramen elongate when viewed dorsally, leading into slightly anteroventrally trending masseteric canal. Inferior mandibular foramen moderately sized and ovally-shaped.

$I_1$ robust and upturned relative to cheek tooth row, with occlusal surface long and straight, and orientated in same plane as diastema. Anterior extreme of occlusal surface only very slightly curved dorsally.

$P_2$ short relative to length of $dP_3$, with main (lingual) crest consisting of four prominent cuspules, posteriormost largest. Transverse ridge directed buccally from posterior extreme of main crest and confluent with a very short crescentic buccal crest. Posteriorly directed ridgelet descends from second cuspule on main crest, terminating immediately anterior to buccal crest and resulting in a small notch.

$dP_3$ completely molariform, with protolophid tapering more toward narrower occlusal surface than hypolophid. Cristid obliqua and paracristid fine and low. Lophid faces lack enamel crenulations. Paracristid relatively short, descending anterolingually from protoconid apex, then trending more anteriorly and bifurcating. Main component of this curves lingually, while minor short ridge extends anteriorly to edge of anterior cingulum. A weak premetacristid folds across anterior face of protolophid into trigonid basin, terminating before reaching anterolingually directed component of paracristid. Posterior face of hypolophid bears a weak, centrally positioned, triangular-shaped inflation, with point of triangle uppermost.

Unerupted $P_3$ short and equal in length to $M_1$, although not yet bearing full complement of enamel. $P_3$ narrow and dominated by main (lingual) crest, except for expanded posterobuccal corner upon which short, crescentic buccal crest is borne. Buccal crest extends one-third length of tooth. Main crest divided into five cuspules, with posteriormost twice size of any of anterior four. Three anteriormost cuspules accompanied by finer lingual and coarser buccal vertical ridgelets. Two transverse ridgelets cross median valley between main and buccal crests, arising from buccal face of posteriormost cuspule on main crest, then extending to base of lingual face of buccal crest. A transverse ridge connects posteroventral extreme of main crest to buccal crest with which ridge is confluent.

$M_{1-2}$ low crowned with protolophid and hypolophid occlusal surfaces linear and close to parallel. Cristid obliqua and paracristid low, but well-formed, and remaining close to buccal side of tooth. Anterior cingulum short anteroposteriorly and symmetrically tapered, extending anteriorly from buccal and lingual extremities of base of protolophid. Paracristid arises ventrolingual to protoconid apex, descending anterolingually onto anterior cingulum. Paracristid then bifurcates, with main component curving lingually and thickening into a rounded eminence, while a short ridge continues anterolingually to edge of anterior cingulum. Lingual extreme of paracristid met by a very slight premetacristid descending anteriorly from metaconid apex, then folding buccally across anterior face of protolophid. Two anteroposteriorly orientated enamel crenulations are present on anterior face of $M_1$ protolophid. Four fine, barely separable crenulations descend from anterior face of $M_2$ protolophid into trigonid basin. Anterior face of hypolophid with several very fine anteroposteriorly orientated enamel crenulations descending into interlophid valley. Posterior face of hypolophid bears a similar triangular inflation to $dP_3$, but is more marked, with distinct shelves formed on buccal and lingual sides.

## Comparison with other taxa

Due to the juvenile nature of the *S. brachyselenis* holotype, it is not useful to compare the mandibular characters with those in the descriptions of most other sthenurines as they are largely based on adult specimens. The holotype was therefore compared with the only *Sthenurus* species for which similarly aged specimens are known, namely *S. occidentalis* Glauert 1910, *S. brownei* Merrilees 1967, *S. maddocki* Wells and Murray 1979, *S. pales* DeVis 1895, *S. andersoni* Marcus 1962 and *S. gilli* Merrilees 1965. Dental comparisons were also made with adult specimens of *S. cegsai* Pledge 1992 and *S. oreas* DeVis 1895 (see Appendix 1). In both size and shape of the mandible, *S. brachyselenis* is most similar to *S. occidentalis,* but the ramus is relatively deeper for most of its length (Fig. 2). Morphology of the symphysial union, the degree to which $I_1$ is upturned and relative length of the diastema are also similar to *S. occidentalis.* However, the unworn occlusal surface is quite straight in *S. brachyselenis,* a characteristic only observed previously in the very slender and elongate $I_1$ of *S. maddocki* (Wells and Murray 1979; Fig. 2).

$P_2$ is very similar in morphology to $P_3$, although it is only around half the length and relatively wider. The $P_3$ of *S. brachyselenis* is most similar (Fig. 3) to the plesiomorphic early Pliocene *S. cegsai,* from Corra Lynn Cave, Yorke Peninsula, South Australia (Pledge 1992), and is shorter relative to $M_1$ than any other *Sthenurus* species. Both *S. brachyselenis* and *S. cegsai* have a relatively narrow $P_3$ dominated by the main crest divided into five cuspules. The buccal crest is very short in both species, although the crest appears to have been straighter in *S. cegsai,* and is positioned very close to the posterior extremity of the main crest. This results in a very narrow median valley, unlike *S. brachyselenis,* and also means that the *S. cegsai* $P_3$ is only slightly wider posteriorly than anteriorly. *S. brachyselenis,* in contrast to the holotype of *S. oreas* (QM F2923) and the only other conspecific for which $P_3$ is known (AM MF90 — see Tedford 1966, Fig. 14), possesses a very short buccal crest which does not join with the main crest anteriorly, has a main crest that is markedly curved posteriorly and two transverse ridgelets which dominate the median valley. The very limited degree to which these characters vary within species known from large samples (20 to 150 individuals of *Sthenurus occidentalis, S.*

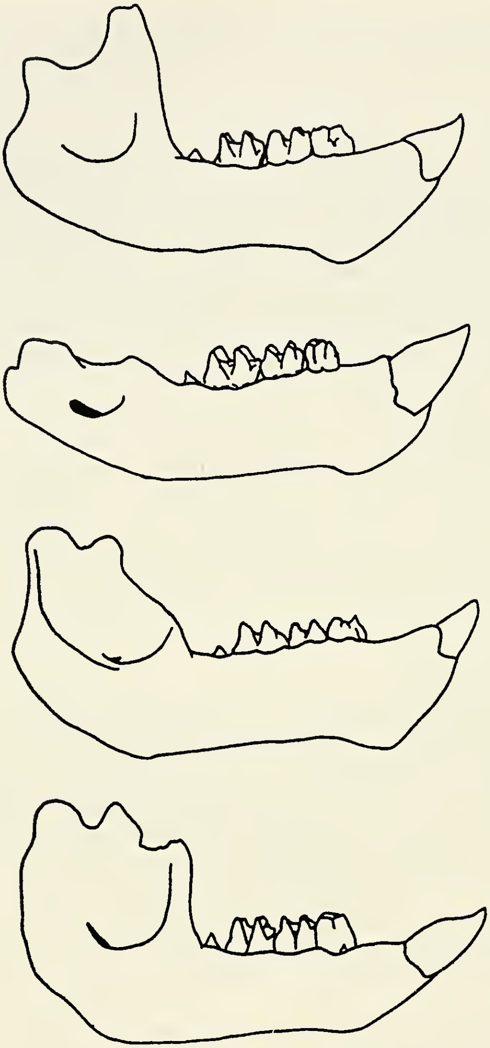


Figure 2. Juvenile mandible outlines of a) *S. occidentalis*, b) *S. brachyselenis*, c) *S. maddocki* and d) *S. brownei*, scaled to a common length.

*brownei, S. gilli, S. andersoni, S. maddocki* ) suggests that the differences between *S. brachyselenis* and *S. oreas* are unlikely to be a result of intraspecific variation (cf. Tedford 1966).

In morphology and size, the molariform teeth of *S. brachyselenis* are most similar to *S. brownei* (Fig. 3). The teeth are similarly low crowned, lophids are linear and close to parallel, the anterior cingulum is relatively narrow (laterally), the cristid obliqua and paracristid are low, but well-formed and aligned on the buccal side of the tooth, and the posterior face of the hypolophid bears a marked triangular-shaped inflation. However, in contrast, the anterior cingulum is shorter and not symmetrically tapered in *S. brownei,* and the lophid faces are more coarsely crenulated. The manner in which the paracristid bifurcates anteriorly also differs between these species. In *S. brownei* and *S. pales* the

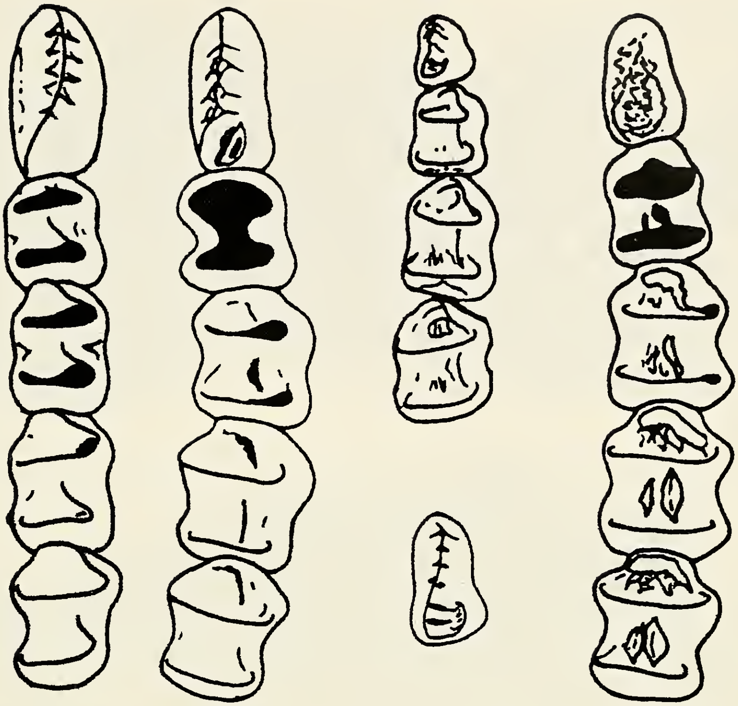


Figure 3. Comparison of cheek teeth of a) *Hadronomas puckridgi* P3, Ml-4; b) *Sthenurus cegsai* P3, Ml-4; c) *S. brachyselenis* P2, dP3, Ml-2, P3; and d) *S. oreas* P3, Ml-4.

transverse component of the paracristid is either thickened anteroposteriorly forming a lozenge shape, or reduced to tiny cuspules. The anteriorly directed fork is only slight and variably present in these two species. In *S. maddocki* and *S. euryskaphus* a bifurcated paracristid is also evident, but the transverse component is larger and more completely formed than the aforementioned species, curving across the anterior cingulum. Among sthenurines, the anteriorly directed fork is expressed to the greatest degree in *Procoptodon,* its function appearing to be as a buttress for the typically high paracristid.

On comparison with *S. oreas,* a triangular-shaped inflation on the posterior face of the hypolophid is incipient in one of the three mandibular specimens referable to that species, AM F88541 (= MF1). The manner in which the *S. brachyselenis* paracristid bifurcates anteriorly is also expressed to a similar, but slightly lesser degree in AM F88541. However, the lower molars of *S. oreas* can be separated in the following ways:

1. The anterior cingulum is not symmetrically tapered and does not extend to the lingual extremity of the base of the protolophid. Additionally, in the holotype, it does not extend to the buccal extremity of the base of the protolophid.
2. The paracristid and cristid obliqua are thicker and higher.
3. A thick accessory crest is positioned lingual and parallel to the cristid obliqua.

## Phylogenetic affinities

Using the late Miocene sthenurine *Hadronomas puckridgi* for comparison, all species of *Sthenurus* bear a buccal crest (raised buccal cingulum) adjacent to the main crest on $P_3$, molars that are wider relative to their length, lophids orientated very close to perpendicular to the longitudinal axis of the tooth, and at least a few very fine enamel crenulations on the molar lophid faces. Within *Sthenurus,* there is a general evolutionary trend toward elongation of the buccal crest on $P_3$. This is barely more than a posterobuccal cusp in the early Pliocene *S. cegsai,* but runs most of the length of the tooth in derived Pleistocene species, such as *S. pales.* Likewise, the pairing of low crowned molars with a few fine or no enamel crenulations on the lophid faces is characteristic of *S. cegsai* and *Hadronomas,* but all of the Pleistocene species have either low crowned molars with many fine or a varying number of coarse enamel crenulations (eg., *S. occidentalis, S. brownei* ), or high crowned molars with very few fine or no enamel crenulations (eg., *S. andersoni, S. stirlingi* ). Low crowned, heavily crenulated molars combined with brachycephaly, are adaptations to heavier browsing, while high crowned, weakly crenulated molars combined with dolichocephaly, and hypertrophy of the paracristid and cristid obliqua led Tedford (1966) to suggest a reversion to a largely grazing habit in these species.

Therefore, possession of low crowned molars with few fine enamel crenulations, a low paracristid and cristid obliqua positioned close to the buccal side of the molar, and a narrow $P_3$ with a very short, buccal crest must suggest that *S. brachyselenis* occupies a relatively plesiomorphic phylogenetic position among *Sthenurus,* and is only derived relative to the early Pliocene *S. cegsai.* It is conceivable that *S. brachyselenis* could be a precursor to *S. oreas,* but presence of a strong paracristid, cristid obliqua and interlophid accessory crest, and long buccal crest on $P_3$ joining to the main crest anteriorly, suggest that a direct ancestor-descendant relationship is most unlikely.

## *Sthenurus (Simosthenurus) euryskaphus* sp. nov.

(Figs 4–6)

1966 *Sthenurus oreas* Tedford, p. 39–41, fig. 15.
1976 *Sthenurus oreas* Marcus, p. 69–70.

### Holotype

AM MF2, left juvenile ramus, with $dP_3$, $M_1$, $M_2$, $P_3$ excavated from body of mandible. Associated $I_1$ described and figured by Tedford (1966) appears to be lost. $P_2$, $M_3$ not preserved, although alveoli indicate both teeth were fully erupted.

### Type locality and age

The holotype was collected in 1887 by W. Anderson from Bone Camp Gully, adjacent to Myall Creek, near Bingara in northeastern New South Wales (29°50'S, 152°30'E). Age of the type locality is middle Pleistocene (Marcus 1976).

### Diagnosis

$P_3$ short relative to width, with median valley very wide and rather circular due to very lingually convex posterior component of main (lingual) crest and buccally convex buccal crest. Lower molars very similar in size and morphology to eastern *Sthenurus occidentalis,* but with slightly narrower anterior cingulum and fewer fine enamel crenulations on lophid faces. Juvenile mandible differs from *S. occidentalis* in bearing large digastric eminence and sulcus, and large, deep symphysis with long posterior extension below genial pit.

Figure 4. *Sthenurus euryskaphus* sp. nov. holotype (AM MF2): a) mandible in lateral view; b) mandible in medial view; c) stereopair of mandible and cheek tooth row in occlusal view; d) stereopair of $P_3$ in occlusal view. Scale in millimetres.

### Etymology

Gr. *eury-* 'broad', *skaphe* 'basin, trough', in reference to the broad nature of the median valley or basin formed between the main (lingual) and buccal crests on $P_3$.

### Description

Juvenile ramus deep for width, particularly in region of symphysis and digastric eminence. Anterior region of symphysial union not preserved, but deep and rugose central and posterior regions indicate strong mandibular ankylosis. Posterior region of symphysis extends well below genial pit forming a prominent boss. Digastric eminence long and deep, with sulcus large and deep, extending anteriorly to below $M_2$ protolophid. Posterior portion of $I_1$ alveolus large and orientation of longitudinal axis indicates tooth was very upturned relative to cheek tooth row (see also Tedford 1966, fig. 15). Little of diastema preserved, but appears to have been relatively short. Only deep, anteriormost portion of buccinator sulcus is preserved. Anterior mental foramen circular in cross-section, opening more dorsally than laterally, with dorsal border immediately below anterior extreme of buccinator sulcus. Posterior mental foramen positioned relatively high on mandible, below hypolophid of $M_1$. Most of posterior region of mandible broken away, preserving only broken anterior root of ascending ramus, small part of anteroventral border of masseteric fossa and large, near vertical masseteric canal. Posteriorly, on mesial side of mandible, a sharp anterodorsally orientated process is present and appears to have partially overhung mylohyoid groove.

Alveolus of $P_2$ indicates tooth was slightly shorter than $dP_3$. $dP_3$ completely molariform, with protolophid markedly tapered buccally toward relatively narrow occlusal surface. Cristid obliqua low, descending anterolingually from hypoconid, then curving more anteriorly to posterior face of protolophid, before trending buccally to terminate at protoconid apex. Very low pre-entocristid directed anterobuccally from entoconid apex met in interlophid valley by low postmetacristid descending posterobuccally from metaconid apex. Posterior extreme of paracristid shifted slightly lingually along anterior face of protolophid from protoconid apex. Anteroposteriorly orientated component of paracristid short, and turning into longer tranverse component which terminates near to lingual extreme of anterior cingulum. Premetacristid directed buccally across anterior face of protolophid, which also bears two central, anteriorly directed, fine enamel crenulations. Anterior face of hypolophid bears no enamel crenulations. Posterior face of hypolophid with low, barely detectable postentocristid which descends ventrobuccally from entoconid apex to about one third of way down tooth crown, then curves up centrally, then trends ventrobuccally once again. This produces a very shallow, rather sinusoidal inflation across the posterior hypolophid face.

$P_3$ wide relative to length and nearest to, although slightly shorter than $M_2$ in length. Posterobuccal aspect of tooth slightly inflated and bearing a buccally convex, crescentic crest. Main crest divided into four cuspules linked to one another by short ridgelets. Prominent, anteriormost cuspule bears two thick posteroventrally directed ridgelets descending from apex; one lingual, one buccal. Main crest extends posterolingually, curving even more lingually toward posterior extreme, then descending to terminate posterior to median valley. At this point, posterolingual extreme of buccal crest also terminates, resulting in a V-shaped notch when viewed posteriorly. Median valley is very wide and rather circular, with many fine ridgelets descending into centre of valley. Anterior extreme of buccal crest connected to buccal side of second cuspule of main crest by low transverse ridgelet.

$M_{1-2}$ low crowned with protolophid and hypolophid occlusal surfaces linear and close to parallel. Anterior turn on lophid ends emphasised buccally. Cristid obliqua and paracristid low, but well-formed, and shifted slightly lingually along anterior lophid faces from buccal extreme of tooth. Anterior cingulum not extended across entire base of protolophid and only tapered anteriorly on buccal side. Paracristid trends anteriorly from position on protolophid anterior face slightly ventrolingual from protoconid apex, before turning lingually. Anteroposteriorly orientated component of paracristid slightly shorter than transverse component, which terminates at lingual extreme of anterior cingulum. Several fine enamel crenulations descend into trigonid basin from anterior protolophid face. Similarly, several anteroposteriorly orientated enamel crenulations arise from anterior hypolophid face, but these are very fine and terminate before reaching interlophid valley. Posterior face of hypolophid is characterised by a triangular-shaped inflation, much more pronounced than in $dP_3$. A very shallow and barely detectable postentocristid descends to a position in ventrolingual region of posterior hypolophid face. From here, shelf-like crest turns and trends dorsobuccally to a point, before trending to ventrobuccal corner of posterior hypolophid face. In this region, shelf becomes less distinct and more of an inflation.

## Comparison with other taxa

As with *S. brachyselenis,* it is most useful to compare the juvenile holotype of *S. euryskaphus* with similarly aged specimens in order to elucidate any unique features of the mandible. The holotype was compared with juvenile specimens of *S. occidentalis, S. brownei, S. pales, S. gilli,* and a widespread species referred to herein as *Sthenurus* 'P17250' (see Appendix 1). The latter species is currently under description elsewhere. A comparison was also made with adult representatives of *S. antiquus* and *S. oreas,* and Tedford's (1966) sketch of AM MF90, which is a juvenile *S. oreas* mandible slightly older ontogenetically than the *S. euryskaphus* holotype.

In size and general shape, the juvenile mandible is most similar to *S. occidentalis* and *S.* 'P17250' (Fig. 5). *S. euryskaphus* differs from *S. occidentalis* in its greater ramus depth relative to width, longer and deeper extension of the posterior region of the symphysis below the genial pit, more pronounced digastric eminence, and possession of a sharp process overhanging the mylohyoid groove. *S. euryskaphus* differs from *S.* 'P17250' in being slightly more robust, possessing a relatively shorter ramus, a longer and deeper extension of the posterior region of the symphysis below the genial pit, and more upturned $I_1$. On comparison with Tedford's sketch of MF90, it appears that the anterior border of the mandible is more steeply inclined and straighter in *S. oreas,* the digastric eminence is less prominent and the ventral border of the masseteric fossa is higher. Although only one adult ramus is known for *S. antiquus,* considering the differences in their ontogenetic age, the general dimensions (size, shape, development of the digastric sulcus) are not unlike what might be predicted for an adult *S. euryskaphus.*

In morphology, absolute size, and size relative to the succeeding molars, the $P_3$ of *S. euryskaphus* is similar to *S.* 'P17250', but also bears some resemblance to *S. oreas.* Like *S.* 'P17250', the $P_3$ is short relative to $M_1$ and bears a relatively short buccal crest. *S. euryskaphus* can be distinguished from *S.* 'P17250' by its large lingual convexity of the main crest posteriorly, the slightly longer buccal crest, and much wider, open median valley. In size, *S. euryskaphus* differs from the holotype of *S. oreas* in its greater size, but cannot be separated from the species on this basis because it is very similar to AM MF90 in premolar dimensions (measurements from Tedford 1966). Morphologically though, the $P_3$ of *S. euryskaphus* is slightly wider relative to its length, has a shorter, more crescentic buccal crest without a strong connection with the main crest anteriorly, and a more circular and slightly wider median valley (Fig. 6). The *S. euryskaphus* $P_3$ is easily distinguishable from *S. antiquus,* being much smaller in size, shorter relative to molars, wider relative to length, and bearing a shorter, wider median valley and a shorter, more curved buccal crest. *S. euryskaphus* is easily separable from *S. occidentalis, S. brownei, S. gilli* and *S. pales,* as the $P_3$ of these species is longer relative to molar size, they have a narrower median valley bordered by a much straighter main crest, and a longer buccal crest

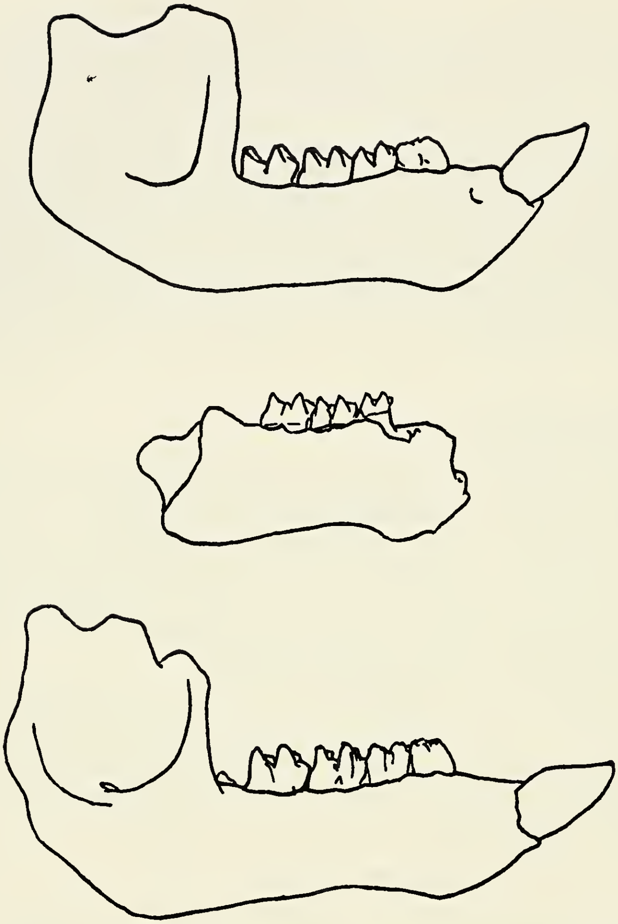


Figure 5. Juvenile mandible outlines of a) *S. occidentalis*, b) *S. euryskaphus* and c) S. 'P17250', scaled to a common depth below the $M_2$ protolophid.

which joins with the main crest anteriorly.

The molariform teeth of *S. euryskaphus* are most similar to *S. occidentalis* and *S. antiquus* in almost all characters observable (Fig. 6). The cristid obliqua and paracristid are similarly positioned and orientated, but not quite as shifted lingually. The anterior cingulum and transverse component of the paracristid are most similar to *S. occidentalis,* but the cingulum is slightly narrower overall. In *S. antiquus,* the cingulum is wider, and shorter anteroposteriorly. The morphology of the posterior hypolophid face in *S. euryskaphus* is characterised by a triangular-shaped inflation, with a short shelf formed along its dorsal border. This is similar to *S. occidentalis,* but a dorsal shelf is only barely detectable. In this feature, it is intermediate between *S. occidentalis* and *S. brownei.*

A few fine vertical enamel crenulations are present lingual to the paracristid in *S. euryskaphus,* which is intermediate in morphology between the many fine crenulations on the anterior protolophid face of *S. occidentalis* and the very few fine crenulations present in *S. antiquus.* Similarly, there are a few fine enamel crenulations lingual to the cristid obliqua on the anterior hypolophid face of *S. occidentalis,* few very fine crenula-

Figure 6. Comparison of cheek teeth of a) *S. euryskaphus* $dP_3$, $M_{1-2}$, $P_3$; b) *S. antiquus* $P_3$, $M_{1-4}$; c) *S. occidentalis* $P_3$, $M_{1-4}$; d) S. oreas $P_3$, $M_{1-4}$.

tions on the *S. euryskaphus* hypolophid, and only the barest remnant of very fine crenulations in *S. antiquus.* Previously, Marcus (1976) referred to the similarity between the enamel crenulations of MF2 and *S. occidentalis,* although observed that the molars of the latter were smaller. However, the comparison was made with the typically small topotypic material from Western Australia, not specimens from eastern Australia with which *S. euryskaphus* compares favourably in size. Work in progress indicates that *S. occidentalis* may be synonymous with *S. orientalis* Tedford 1966, each representing the morphological extremes of a geographic cline. Overall, in general molar outline and width relative to length, *S. euryskaphus* is similar to both *S. antiquus* and *S. occidentalis.*

*S. euryskaphus* is separable from *S. oreas* in that the posteriormost component of the paracristid is orientated almost directly anteroposteriorly, not anterolingually; the transverse component of the paracristid is larger; the enamel crenulations on the anterior lophid faces are much finer and there is no thick accessory crest positioned lingual to the cristid obliqua.

## Phylogenetic affinities

While doubt is an inherent part of the description of new morphological species from very limited material, especially where well-represented related taxa display a significant amount of intraspecific variation, an appreciation of the most variable characters minimises the chances of future synonymy. *S. euryskaphus* bears a resemblance to the variable *S. occidentalis,* but the characters by which it is distinguishable are not highly variable within *S. occidentalis.* Most variation in mandibular and dental characters is size-based, either absolute or proportional. Tedford (1966) attributed MF2 to *S. oreas* because he considered it within the probable morphological range of that species. However, disparity in the morphology of the mandible, $P_3$ and molars, strongly suggest that MF2 does not belong within *S. oreas,* or within any other previously named taxon.

The overriding number of similarities shared with *S. occidentalis, S.* 'P17250' and *S. antiquus* is likely to imply a relatively close phylogenetic relationship with these species. Low crowned, low complexity molars and a short, wide anterior cingulum appear to be plesiomorphic characters within the genus, as exemplified by *S. cegsai* and *S. brachyselenis.* Although the molars are larger and higher crowned, these features are similar in *S. antiquus,* known from the late Pliocene of southeastern Queensland (Bartholomai 1963). As molars tend to be more conservative evolutionarily, this may indicate that *S. euryskaphus* is more derived than *S. antiquus.* Although the $P_3$ of *S. antiquus* is considerably larger, and the buccal crest longer and straighter, if this crest were simply curved buccally, then posterior premolar width would be increased and the median valley widened, producing a very similar form to *S. euryskaphus.* It appears very likely that *S. occidentalis* is more derived, given its more complex molar morphology, and presence of a long buccal crest connected to the main crest anteriorly on $P_3$. Although the phylogenetic position of *S.* 'P17250' is uncertain and currently under consideration elsewhere, it is likely to be less derived than *S. euryskaphus,* given the very short buccal crest on $P_3$, close proximity of the cristid obliqua and paracristid to the hypoconid and protoconid, paucity of molar enamel crenulations, and absence of a shelf on the posterior hypolophid face.

Bartholomai (1963, 1972) and Tedford (1966) have suggested a close phylogenetic association, perhaps even ancestor-descendant relationship between the late Pliocene *S. antiquus* and Pleistocene *S. oreas.* The latter is certainly more derived, but a close alliance is unlikely given the disparity in molar complexity, premolar morphology and premolar length relative to the molars. *S. oreas* is clearly a very derived member of the genus and it is not surprising that De Vis (1895) synonymised *Procoptodon* with *Sthenurus* based on these dental characters. Tedford (1966) considered the dental similarities between *S. oreas* and, in particular, *Procoptodon pusio* a likely result of parallel evolutionary trends, but *S. oreas* also resembles *Procoptodon* in the robustness of its ramus and massive opening for the insertion of the deep masseter. These craniodental similarities and the absence of pre-Pleistocene *Procoptodon* remains seem more likely to indicate that the genus has arisen from within *Sthenurus,* possibly in the vicinity of *S. oreas.*

## CONCLUSIONS

*Sthenurus brachyselenis* bears closest affinity with the early Pliocene *S. cegsai* from Corra Lynn Cave, Yorke Peninsula, South Australia, possessing low crowned, simple molars and a narrow $P_3$ bearing a very short, buccal crest. It is more derived than *S. cegsai,* but plesiomorphic relative to all other *Sthenurus* species. As such, it displays a stage of evolution hitherto unrepresented by any described taxon.

Characters shared or intermediate in expression between *S. occidentalis, S.* 'P17250' and *S. antiquus* imply that *S. euryskaphus* is phylogenetically close to these taxa. *S. antiquus* appears to be more plesiomorphic, possessing low complexity molars with short, wide anterior cingula, characters shared with the plesiomorphs *S. cegsai* and *S. brachyselenis.* In contrast, *S. occidentalis* is considered more derived than *S. euryskaphus,* due to its greater molar complexity and long buccal crest connected to the main crest anteriorly on $P_3$.

The removal of both AM F31026 and MF2 from *S. oreas* has impelled a reconsideration of the phylogenetic position of that species. *S. oreas* appears to represent a very derived species of *Sthenurus,* sharing several important dental and mandibular similarities with *Procoptodon,* in particular *P. pusio.* This may point to a paraphyletic origin for *Procoptodon* from within *Sthenurus,* a view supported by the absence of *Procoptodon* remains from pre-Pleistocene deposits.

## ACKNOWLEDGMENTS

Sincere thanks to Drs Richard Tedford, Peter Murray and Lyndall Dawson for their very constructive comments on the manuscript. We are appreciative to Mr Nic Bishop for producing the illustrations for Figures 2 and 4. Specimens used in the study were kindly loaned by Mr R. Jones (Australian Museum), Dr R. Molnar (Queensland Museum), Mr N. Pledge and Mr J. McNamara (South Australian Museum).

## REFERENCES

Anderson, C. (1932) Unpublished report to the Trustees of the Australian Museum, Sydney, Feb., 1932, Ref. No. 324/31 in the archives of the Australian Museum. (cited in Dawson 1985.)

Bartholomai, A. (1963) Revision of the extinct macropodid genus *Sthenurus* Owen in Queensland. *Memoirs of the Queensland Museum* **14**, 51–76.

Bartholomai, A. (1972) Aspects of the evolution of the Australian marsupials. *Proceedings of the Royal Society of Queensland* **82**, v-xviii.

Dawson, L. (1985) Marsupial fossils from Wellington Caves, New South Wales; the historic and scientific significance of the collections in the Australian Museum, Sydney. *Records of the Australian Museum* **37**, 55–69.

De Vis, C.W. (1895) A review of the fossil jaws of the Macropodidae in the Queensland Museum. *Proceedings of the Linnean Society of New South Wales* **10**, 75–133.

Flannery, T.F. (1983) Review of the subfamily Sthenurinae (Marsupialia) and the relationships of the species of *Troposodon* and *Lagostrophus. Australian Mammalogy* **6**, 15–28.

Flannery, T.F. (1989) Phylogeny of the Macropodoidea; a study in convergence. In 'Kangaroos, Wallabies and Rat-kangaroos' (Eds G.C. Grigg, P. Jarman and I.D. Hume) pp. 1–48. (Surrey Beatty and Sons: Sydney).

Flower, W.H. (1867) On the development and succession of teeth in the Marsupiala. *Philosophical Transactions of the Royal Society of London B* **157**, 631–641.

Luckett, W.P. (1993) An ontogenetic assessment of dental homologies in therian mammals. In 'Mammal Phylogeny' (Eds F.S. Szalay, M.J. Novacek and M.C. McKenna) pp. 182–204. (Springer-Verlag: New York).

Marcus, L.F. (1976) The Bingara Fauna, a Pleistocene vertebrate fauna from Murchison County, New South Wales, Australia. *University of California Publications in Geological Sciences* **114**, 1–145.

Osborne, R.A.L. (1983) Cainozoic stratigraphy at Wellington Caves, New South Wales. *Proceedings of the Linnean Society of New South Wales* **107**, 131–147.

Pledge, N.S. (1992) The Curramulka Local Fauna: a late Tertiary fossil assemblage from Yorke Peninsula, South Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* **9**, 115–142.

Ride, W.D.L. (1993) *Jackmahoneya* gen. nov. and the genesis of the macropodiform molar. *Memoirs of the Association of Australasian Palaeontologists* **15**, 441–59.

Tedford, R.H. (1966) A review of the macropodid genus *Sthenurus. University of California Publications in Geological Sciences* **57**, 1–72.

Tedford, R.H. and Woodburne, M.O. (1987) The Ilariidae, a new family of vombatiform marsupials from Miocene strata of South Australia and an evaluation of the homology of molar cusps in the Diprotodontia. In 'Possums and Opossums: Studies in Evolution' (Ed. M. Archer) pp. 401–418 (Surrey Beatty and Sons: Sydney).

Wells, R.T. and Murray, P.F. (1979) A new sthenurine kangaroo (Marsupiala, Macropodidae) from southeastern South Australia. *Transactions of the Royal Society of South Australia* **103**, 213–19.

# APPENDIX I

Material used for comparison with *S. brachyselenis* and *S. euryskaphus*. AM = Australian Museum, FU = Flinders University, QM = Queensland Museum, SAM = South Australian Museum.

| Species | Registration Number | Locality |
|---|---|---|
| *Sthenurus andersoni* | SAM P20636, FU0463 | Victoria Fossil Cave, Naracoorte SA |
| *S. brownei* | SAM P20713, P25604, P27796, P27798, FU0273 | Victoria Fossil Cave, Naracoorte SA |
| *S. cegsai* | SAM P31800 (holotype) | Corra Lynn Cave, Curramulka SA |
| *S. gilli* | FU0008, FU0102 | Victoria Fossil Cave, Naracoorte SA |
| *S. maddocki* | SAM P16518, P16674, P27357 | Victoria Fossil Cave, Naracoorte SA |
| *S. occidentalis* | SAM P16534, P16536, P16624, P16664 | Victoria Fossil Cave, Naracoorte SA |
| *S. oreas* | QM F2923 (holotype)<br>QM F3814,<br>AM F88541 (= MF1) | Darling Downs QLD<br>Cement Mills, Gore QLD<br>Wellington Caves NSW |
| *S. pales* | SAM P27797 | Victoria Fossil Cave, Naracoorte SA |
| *Sthenurus* 'P17250' | SAM P17250<br>SAM P28671, P28996 | Greenwater Hole Cave, Tantanoola SA<br>Victoria Fossil Cave, Naracoorte SA |

# Origins and Setting: Mammal Quaternary Palaeontology in the Eastern Highlands of New South Wales

W.D.L. Ride and A.C. Davis

Department of Geology, Australian National University, Canberra ACT 0200

Ride, W.D.L. and Davis, A.C. (1997). Origins and setting: mammal Quaternary palaeontology in the Eastern Highlands of New South Wales. *Proceedings of the Linnean Society of New South Wales* **117**: 197-222

Fossil mammal faunas found in the early years of Australian cave exploration were primarily regarded as a source of information on the diversity and anatomy of the extinct megafauna although they certainly played an important part in shaping the awareness that led to ideas of evolutionary biogeography. Thomas Mitchell, who had a leading role in their early discovery, also suggested correlations of the Wellington deposits with climatic fluctuations, with sea levels, with lunette formation and with the development of landscape. Later palaeoclimatic speculations by Owen and Darwin were based on faunal analogy. At that time, it was not possible to extend these speculations further.

Interest in finding fossil ancestors led to some Pleistocene forms being regarded as ancestral to modern taxa but it was generally agreed that, as "Ice Age" equivalents, they only illustrated the demise of megafauna as did cave faunas in Europe and South America.

Now, because of extensive palaeoclimatic information derived from a wide range of disciplines, and realization that the caves of eastern Australia contain deposits extending back into the Tertiary, and the recognition that by far the greater part of the characteristic modern Australian marsupial radiation (and much of the murid radiation) is arid adapted, it seems likely that the caves have the potential to illustrate the spectacular and rapid Australian radiation after the loss of most of the rainforests.

The topographic and ecological diversity of eastern Australia also highlights the sensitivity of the Eastern Highland cave faunas as indicators of faunistic and climatic change, but currently, very few reliably dated mammal-bearing deposits are known in the highlands. However, studies made recently of both cave and fluviatile deposits indicate the occurrence of faunal change and turnover during the Pleistocene, and well before the last glacial maximum, followed by progressive faunal depauperization. The loss of megafauna occurred before climatic amelioration following the glacial maximum. The reason is not apparent.

Fossil faunas reveal unexpected associations that indicate that our knowledge of the evolution of physiological and behavioural responsiveness of animal species to environmental factors (such as climate, soils, and topography) may not be as closely correlated with morphological evolution as is required to enable palaeofaunal distributions to be used as the basis of faunal predictions of the effects of global warming. Alternatively, it may be that distributions that currently seem to be discordant are, in fact, the product of imprecise morphotaxonomy as is suggested by recent work on *Burramys*.

Manuscript received 19 June 1996, accepted for publication 23 October 1996.

KEYWORDS: Cave fossils, megafauna, Mitchell, Owen, paleoclimatology, Quaternary

## ORIGINS: DISCOVERY, SCIENCE AND COMMITMENT

Although there is evidence that other caves were found in the years immediately before the caves in the Wellington Valley, none was reported as being fossiliferous and if one were to designate any place in Australia as being the founder site of Australian vertebrate palaeontology, we have no doubt that it would be the caves in which this opening address of our symposium is being given — the great Cathedral Cave (and the nearby "Breccia Cavern" = Mitchell's Cave, see cover), at Wellington (Lane and Richards 1963, Dawson 1985).

Figure 1. George Ranken: settler and magistrate of Bathurst, NSW. Discoverer of the Breccia Cave: Mitchell's Cave, Wellington. Reproduced by permission of Mrs M. Suttor.

The discovery was first announced, in Sydney, on the 25th May 1830 in a letter and editorial in the *Sydney Gazette and New South Wales Advertiser,* that Mr George Ranken (Fig. 1), colonist and magistrate, had found a deposit of fossil bones in these caves (Anon 1830a, b). A few months later the discovery was made known to the scientific world in the *Edinburgh New Philosophical Journal* by Colonel Patrick Lindesay, who was then stationed with the 39th Regiment in New South Wales (Lindesay 1830) and *de facto* Lieutenant Governor. Lindesay was an active naturalist and promoter of natural history. Educated at the University of Edinburgh, he was a friend and correspondent of the editor of the journal, Professor Robert Jameson (Regius Professor of Natural History at the University of Edinburgh) (Wittell 1954, Chisholm 1967).

Palaeontological interpretations accompanied the announcement in the *Sydney Gazette*. The correspondent observed that the deposit seemed to contain extinct forms only, and speculated on the aetiology of the deposit and its relation to the universal Deluge (see below). Ranken had made a small collection and, as indicated in the *Sydney Gazette*, it was sent abroad for examination. Lindesay sent it to Jameson by the Rev John Dunmore Lang who travelled to Britain in 1830 (Anon. [Jameson] 1831a, Pentland in Anon. [Jameson] 1831b, Baker 1967). From the collection, Jameson and a colleague, Dr Adam (Jameson 1831), identified wombat and kangaroo teeth and an animal "larger than any of the living species in the Australian world" which appeared to resemble the radius of a specimen of hippopotamus in the Edinburgh College Museum. Jameson then sent the bones to William Clift of the College of Surgeons, London, who added the Tasmanian devil to Jameson and Adam's list. Clift agreed that the large bone bore a resemblance to the radius of a hippopotamus and commented that 'It does not belong to the elephant ...' (Clift 1831, p. 394).

From Clift, the much-travelled bones went to Cuvier in Paris and were reported on there by Cuvier's colleague, Pentland, who provided a new list of identifications. As well as the marsupials identified previously (to which Pentland added a species of rat kangaroo and a wallaby one third larger than the kangaroo), he listed "Elephant, one species" (Pentland in Anon. [Jameson] 1831b). He later (Pentland 1832) considered this bore a closer resemblance to the fossil elephant "common in the valley of the Arno" than to either the African or Indian elephant. Ranken's collection then returned to Edinburgh and was deposited in the Edinburgh College Museum (now the Royal Scottish Museum, Andrews 1982, p. 56). In the three years from its discovery, study in Edinburgh, London and Paris had revealed the occurrence of an extinct fauna in Australia of mammals belonging to the same groups as the modern fauna, and which, like those of other continents, included gigantic forms (the 'hippopotamus/elephant' seems now to have been a gigantic Australian dromornithid, Rich 1985, p.191). Its study had made a significant contribution to the debate over the universality of the Deluge and to the beginnings of a historical perspective in biogeography.

Although Ranken's collection was an important beginning, it was the very lively interest and energy of his friend, Major Thomas Mitchell, the Surveyor General of New South Wales (Fig. 2), his careful field observations, his published geological descriptions and inferences (Mitchell 1831a, b), the wide public reached through his book of explorations in New South Wales (1838) and, most importantly, from 1837 onwards his relationship with Richard Owen (Fig. 3) at the Royal College of Surgeons in London, that were instrumental in developing the scientific potential of the caves and their bones.

Like Ranken, Mitchell had also made and sent a collection of bones from Wellington Caves to Britain in 1831 (he also sent a second collection to Cuvier in Paris (Pentland 1833, Foster 1936)). Mitchell donated the collection to the Geological Society of London (Anon. 1831) of which he was a Fellow. It was an extensive collection consisting of three large boxes of bones accompanied by ten plans and drawings and a "report of 36 pages" (Ranken 1916, p.23). The report was published in abridged form (Mitchell 1831b) and, later, more extensively in his *Three Expeditions...* (Mitchell 1838). The contribution by Richard Owen on the specimens in the latter work was to provide the first detailed anatomical descriptions and naming of the fossils. Moreover, the research on this collection generated a lasting commitment to the study of Australian fossil mammals by the greatest anatomist of the time — to be followed by succeeding generations both in Britain and Australia.

The "philosophical" setting in which the discovery of Wellington Caves and its fossils took place is important for an understanding of what, as well as sheer love of exploration, encouraged people like Mitchell to go out of their way to spend time and energy not only on exploring caves for fossils but, more importantly, to take considerable trouble to preserve and pass on their finds to experts eager to interpret them. In the eye of the edu-

Figure 2. Major Thomas Mitchell: Surveyor General of New South Wales. First describer of the fossil-bearing Wellington Cave deposits. Reproduced by permission of the Mitchell Library, State Library of NSW.

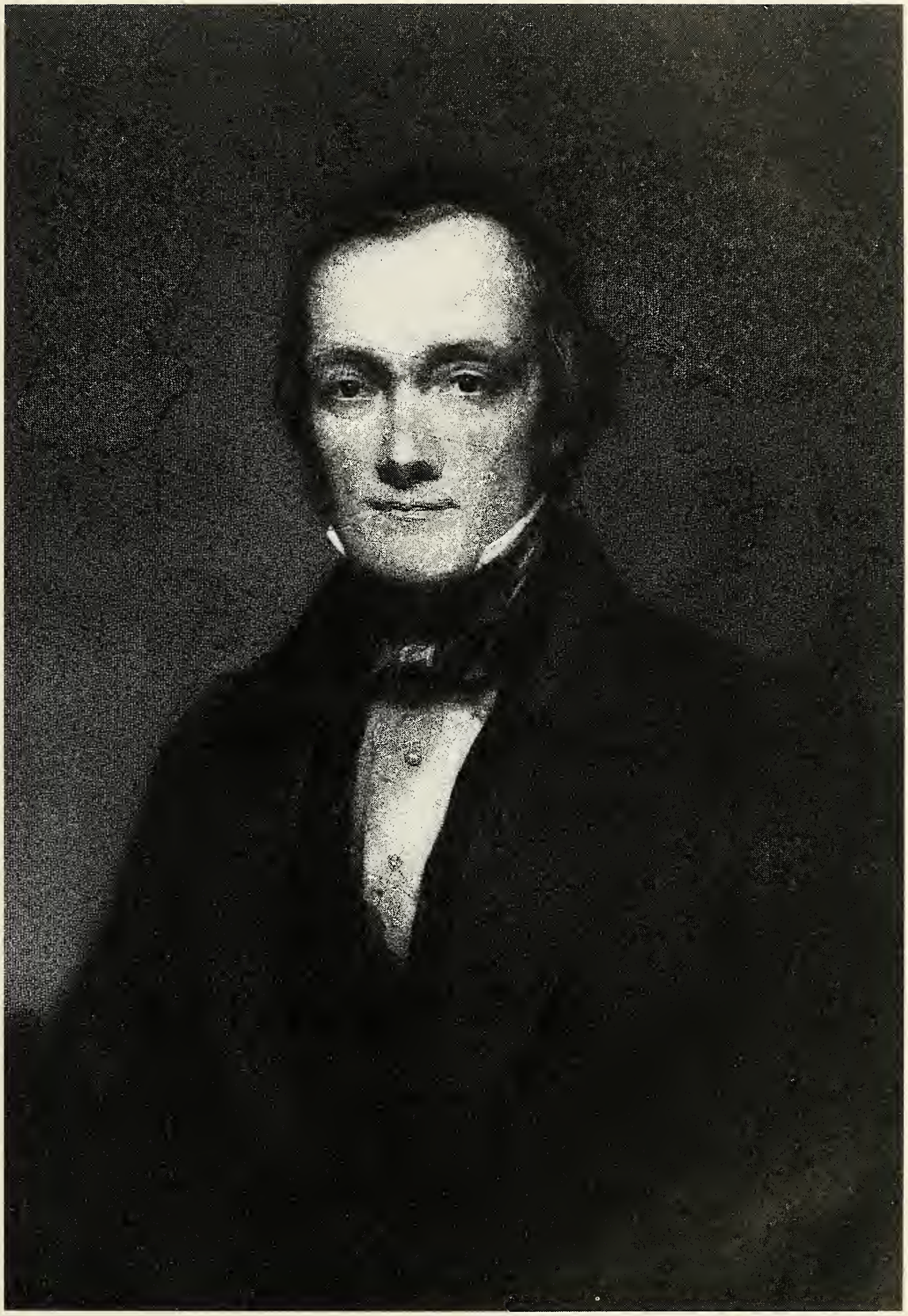


Figure 3. Professor Richard Owen, Hunterian Professor, Royal College of Surgeons, London. c 1844 from a mezzotint by W. Walker from a portrait by H.W. Pickersgill. Reproduced by permission of the Trustees of the Wellcome Institute: from the collection of the Wellcome Institute Library, London (no. 2197.2).

cated public cave fossils were the stuff of controversy at the time and people in New South Wales, like George Ranken and Thomas Mitchell, were very aware of divergent interpretations that were being placed on them in Europe (Ranken 1916, Foster 1936, Rudwick 1972, Dawson 1985). Fossils held an interest that extended well beyond scientific circles because they were the centre of a widening public awareness that biblical literalism was under renewed challenge as the result of the new discoveries of geology.

Although in scientific and theological circles the challenge to the inerrancy of the Scriptures had been an ongoing debate from the time of Copernicus (see Brooke 1991) and was widely accepted by intellectuals on scientific and other grounds (both textual and historical), it was elevated into public consciousness by current findings in geology (see Rudwick 1972). More particularly, discoveries in palaeontology, and especially of extinct mammal faunas in European and British caves, caught the public imagination. Discoveries were effectively publicised by the Rev Dr Buckland, Reader in Geology at Oxford, who, as a geologist–theologian was both influential and a popular public speaker. Initially, in opposition to such distinguished scientists as Linneaus and Cuvier, he interpreted the discoveries as proofs of the Noachian flood (Buckland 1824: 221–228), but this view was contested by contemporary geologists (and especially by his influential pupil Charles Lyell 1830–33). Within a decade, in his second major work, Buckland stated that the facts now contradicted his earlier view (Buckland 1836: 94–5). He went further and, as a senior churchman, presented an unmistakable challenge to literalist interpretation of Scripture in favour of what the rocks reveal of the historical past (including evidence of design). Buckland said

> "If the suggestions I shall venture to propose require some modification of the most commonly received and popular interpretation of the Mosaic narrative, this admission neither involves any impeachment of the authenticity of the text, nor of the judgement of those who have formerly interpreted it otherwise, in the absence of information as to facts which have but recently been brought to light; and if, in this respect, geology should seem to require some little concession from the literal interpreter of scripture, it may fairly be held to afford ample compensation for this demand, by the large additions it has made to the evidences of natural religion, in a department where revelation was not designed to give information.[1]
>
> The disappointment of those who look for a detailed account of geological phenomena in the Bible, rests on a gratuitous expectation of finding therein historical information, respecting all the operations of the Creator in times and places with which the human race has no concern ..."
>
> (Buckland 1836, p.14)

Buckland's second major work (the *Bridgewater Treatise on geology and mineralogy*, 1836) was immensely influential, both in Britain and in continental Europe through its translation by Agassiz (Rudwick 1972: 203). This later view of the origin of the fossil cave faunas and their impact on the Mosaic account of creation was also held by many of Buckland's contemporaries, both ecclesiastical and scientific (see Rudwick 1972: 168–172). But they were opposed strongly by others. Public awareness was torn between authorities who, both churchmen and scientists, were challenging the simplistic biblical literalism that was the comfortable faith of the educated public (and of many, if not the majority, of the clergy).

From Mitchell's correspondence with his friend George Ranken (in Ranken 1916) it is clear that these issues motivated him. Certainly the anonymous 'L' (Anon. 1830b), had published in Sydney his Diluvial interpretation of the Wellington fossils before Mitchell entered the caves. Even before the Wellington discovery, Mitchell had searched caves at Bungonia (Fig. 4) for bones (Holland 1992), and this enthusiasm for the search for fossil bones permeates his writing. The words of his description (1838, vol. 2) of Ranken's discovery are as vivid today as when they were written.

Figure 4. Locality map showing vertebrate fossil localities mentioned in the text.

> "The pit had been first entered only a short time before I examined it, by Mr Rankin [sic.], to whose assistance in these researches I am much indebted. He went down by means of a rope, to one landing place, and then fixing the rope to what seemed a projecting portion of rock, he let himself down to another stage, where he discovered, on the fragment giving way, that the rope had been fastened to a very large bone and thus these fossils were discovered." (p. 362)

Mitchell was determined to extend his discoveries and, having seen for himself the circumstances under which the cave fossils occurred, and having learned of the existence of other caves in the vicinity of Buree (Borenore), he and Ranken went to look for yet more bones. So riding along Oakey Creek

> "We soon found one, which I considered to be of the right sort, viz. a perpendicular crevice with red tuff about the sides. Being provided with candles and ropes, we descended perpendicularly first, about six fathoms to one stage, then obliquely, about half as far to a sort of floor of red earth; Mr Rankin [sic.], although a large man, always leading the way into the smallest openings. By these means, and by crawling through narrow crevices, we penetrated to several recesses, until Mr Rankin found some masses of osseous breccia beneath the limestone rock…" (p. 7)

Shortly after the initial discoveries at Wellington, which stirred scientific interest in Europe (and seem to have contributed to Buckland's change of mind over the Diluvial age of cave fossils, see Mitchell in Ranken 1916), exploration northwards by

Mitchell and others, and pastoral and agricultural expansion, led to the finding of the prolifically bone-bearing alluvial deposits of the Condamine River and its associated streams and in turn to a steady flow of material to European scientists (and particularly to the young and energetic Richard Owen, at the Royal College of Surgeons, who was then building his reputation as the "British Cuvier", see Owen 1894, MacLeod 1965, Rupke 1994).

It was not long before many other caves and alluvial deposits became known throughout eastern Australia from the Darling Downs to western Victoria (Owen 1858). In extending these discoveries, the interest of Dr George Bennett (see Bennett 1834 1: 226 — description of Goodradigby Caves) and the early development of the Colonial Museum, in which he was closely involved (Strahan 1979), played an important part and which, together with the direct role later played by the able and turbulent Gerard Krefft, laid the foundations of indigenous mammal palaeontology.

From the very beginning of Owen's involvement by Mitchell in the Wellington Cave fossils, Owen made the Australian fossils very much his province and this interest continued throughout his life resulting in both the publication of numerous papers and his monumental *Researches on the fossil remains of the extinct mammals of Australia* (Owen 1877). He also persuaded the New South Wales Colonial Government to fund exploration of the Wellington Caves by Gerard Krefft and Professor A.M. Thomson in 1867 (New South Wales, Parliamentary Papers 1870, Owen 1877: 239–40).

We make no apologies for dwelling on this aspect of the role played by the "philosophical" issues motivating the beginnings of cave palaeontology in Australia, because it explains both why and how these early players could create, from the outset, the interest and support that they received both within the Colony and in Europe; but it must not be thought from it that people like Mitchell, Owen and Bennett were not also driven to enquiry by scientific curiosity.

If we look at the results of their researches — and their conjectures — we see that almost all the questions that we are asking of our material today are questions that they were also asking 160 years ago.

In their writings we find that they were moved by curiosity about taxonomy, anatomy, biogeography, extinction, evolution, stratigraphy, dating, palaeoclimatology, and landscape evolution. And at that time, most such questions could find no answers — only conjecture, nevertheless they were being asked.

We will also find, as we do today, that their conclusions and conjectures, themselves, motivated challenge by others. So that now, at a time when the "philosophical" issues of the mid-19th Century produce little more than a yawn, except among dogma-driven creationists, other philosophies have taken over the scientific mind (such as environmental sustainability, biodiversity, and cladism). But to most of us the forces that drive our curiosity remain the same basic scientific questions — being asked with more sophistication and being answered from a perspective of a century and a half of accumulated knowledge, and with greater technical capacity than our predecessors had.

### Taxonomy and anatomy

It is of no surprise that most of the early interest in the Pleistocene faunas was anatomical and taxonomic (in the sense that their relationships with the fauna of the known world had to be clarified and described).

In the early period, anatomical interpretation and relationships were argued and established by such people as Pentland, Owen and Clift, and later, in Britain, by Huxley and Flower, and by Krefft in Australia. Thus, initially, there was debate as to whether *Diprotodon* had been hippopotamus, dugong or elephant (see Mitchell 1843 MS., published in Mahoney and Ride 1975: 222–3). And once its marsupial status established, whether it was syndactyl like other diprotodonts.

The debate that followed the discovery in 1846 of the first remains of *Thylacoleo* raised issues about its carnivory — an issue only recently settled beyond dispute (Finch

1982, Wells et al. 1982). Owen, in philosophical mode four years before, in 1842, had argued that among so many large herbivores there must also be a large carnivore to control their populations (Owen 1858). From slender material, he diagnosed the newly discovered remains as marsupial, dasyurid and, on functional "Cuvierian" grounds, carnivorous. Subsequent discoveries revealed its diprotodonty and an argument against the "carnivorous hypothesis" was generated in opposition (in this Owen's principal opponents were Flower and Krefft who argued primarily from the taxonomic grounds that a diprotodont marsupial could not be a carnivore).

Even today, this area of debate continues over similar questions in connection with the morphology of *Palorchestes* and *Propleopus* (see Ride et al. this volume).

### Biogeography and evolution

But biogeographical and evolutionary implications were seen even at this early stage. Thus, as mentioned already, in 1833 Mitchell wrote to Ranken and mentioned the effect that the Australian bones were having on Buckland's expectation that they would be of hyaenas and cave bears.

Jameson (1831) had drawn attention to the fact that it follows from the Wellington fossils "That New Holland was, at a former period, distinguished from the other parts of the world, by the same peculiarities in the organisation of its animals, which so strikingly characterize it at the present day." (p. 395). In 1833 Lyell drew attention to the same phenomenon. He commented in *The Principles of Geology* that "These facts are full of interest; for they prove that the peculiar type of organization that now characterises the marsupial tribes has prevailed from a remote period in Australia ..." (p. 144).

Not only did these discoveries lead Owen and others to challenge the view held on literalist scriptural grounds that the "post-Diluvian" faunas must have originated from a single centre of dispersal in Asia, but led both Darwin (as one of the results of his voyage in the Beagle between 1831 and 1836) and Owen, (who received Darwin's South American Pleistocene fossils in 1835, the year after he received a second collection of Wellington Caves fossils from Mitchell), to enunciate the "laws" of animal distribution that Darwin (1839) called "the law of succession of types" and Owen (1845) a "law of distribution of extinct Mammalia" (and later (Owen 1858) the "law of succession of organizational types"). Moreover, it led them both, inexorably, to their separate and different convictions that species had a natural origin (Dugan 1980; Rupke 1994, p. 220, 223–225).

Despite the fact that possible mechanisms of evolution were under discussion well before the time of the discovery of the Wellington fossils, that the concept of progressive geological change was well accepted, and that it was recognized that proofs of progressive and directional change in organisms must be looked for in the fossil record, there seems to have been no early attempt to interpret the Australian fossils in evolutionary terms.

The Australian cave faunas contained both unknown species and many that appeared to be close to modern forms. Among these were some which, although recognized as distinct species, were much larger than their modern counterparts (e.g. *Thylacinus, Sarcophilus*, and *Macropus*). Yet at that time no one seems to have regarded them as evolutionary forerunners and it is only in modern times that the question of "dwarfing" has been raised (e.g., Marshall 1973, Marshall and Corruccini 1978, Dawson 1985). Instead, they were regarded in the same way as the "Ice Age" mammoths and cave bears of European caves had come to be regarded once the "diluvial debate" was over, namely to represent an antique fauna which had become extinct[2] in the last cycle of extinctions and replaced by the modern fauna.

However, it was not long before the evolutionary debate was fuelled in the public arena by the publication of the *Origin of Species*, and natural selection proposed as its cause. Fossil evidence in support of gradual evolutionary change soon followed in Gaudrey's demonstration in 1866 of gradual horse evolution in deposits from Pikermi in Greece; in 1868 Huxley demonstrated the presence in the fossil record of intermediates between classes in *Compsognathus* (a "bird-like reptile") and *Archaeopteryx* (a "reptile-like bird") (see Rudwick 1972: 245–252). It then became only a matter of time before Australian fossil mammals were being described and studied in those terms. Thus, in 1888, De Vis in describing *Triclis oscillans (*i.e., *Propleopus)*, suggested that *Hypsiprymnodon* could be "a continuation of a stock" (the "Propleopodidae") "whence has arisen the Phalangistidae [Phalangeridae] on the one hand, the Hypsiprymnidae [Macropodidae] on the other" (De Vis 1888: 8). Shortly afterwards in 1896, Robert Broom in describing the fossil mammals of the Wombeyan fauna, remarked of *Burramys parvus* that "On the whole it would seem that we have in *Burramys* one more link in the chain binding the Kangaroos and Phalangers. The main links would thus be — *Macropus, Aepyprymnus, Hypsiprymnodon, Burramys*" (Broom 1896a), and of *Palaeopetaurus elegans* that "In many respects it stands intermediate between the two genera [*Gymnobelideus* and *Petaurus*], and not improbably may be the common ancestor of both" (Broom 1896b).

### Dating the bones

Mitchell and others were not able to suggest any particular age for the faunas from Wellington and Borenore. In the light of his observations Mitchell did not see anything "likely to throw any light on the history or age of the breccia, but the phenomena they present seem to indicate more than one change in the physical outline of the adjacent regions, and probably of more distant portions of Australia, at a period antecedent to the existing strata of the country".

Today, dating (together with a lack of stratigraphic understanding) remains the single most pressing impediment to the interpretation of the cave faunas.

### Palaeoclimatic framework and landscape evolution

Mitchell speculated that the position of the breccia in Wellington Caves, and other caves, indicated that the bone breccia formed during a long dry period between two more humid periods. He reasoned that during these humid periods sea levels would have been higher and inland Australia inundated (Mitchell 1838, vol 2: 370 et seq). He argued that the lunettes on the north-eastern shores of inland lakes that he had discovered in the Wimmera, and the grassy plains between the lunettes and the lakes, supported this conclusion; he also correlated the periods of inundation with the period of lunette formation (p. 373).

From the fact that the bone breccias occurred also as surface outcrops exposed by erosion, he concluded that their exposure had occurred as new drainage formed on the slopes following the most recent retreat of the water body (Mitchell 1838, p. 371). Even today the age of these cave breccias exposed on the surface, and the time required for their exposure, remain problems (Osborne 1992).

Richard Owen reached a different palaeoclimatic conclusion from that of Mitchell. He considered that the fauna accumulated under wetter conditions than at present — not drier. He argued that the bulk and similarity of the megafaunal marsupials to such forms as the elephant and hippopotamus indicated a luxuriantly vegetated environment.

That conclusion was shared widely and led to general acceptance that megafaunal extinction resulted from the subsequent aridity. Darwin dissented (Darwin 1845, p. 98). He pointed out that modern savannah megafauna in Africa occurs abundantly in arid environments. Nowadays it is recognized that megafaunal bulk may confer physiological advantages in situations where dietary nitrogen and energy are low, but under those conditions may also be disadvantageous unless cool refuges (shade) or ample water for evaporative cooling are available (Main 1978). In short, the Australian megafauna occurred under a wide range of climatic conditions but individual species (e.g. *Diprotodon optatum, Zygomaturus trilobus)* may have responded in different ways (Hope 1982).

## THE SETTING

Today, our palaeontology is conducted within a very different framework of knowledge of geology, the timing of events, and palaeoclimatology which, if we are palaeozoologists (as we are) is derived from outside our field. This framework of knowledge provides not only an environmental and temporal structure to which our observations can relate, but it also provides a control on our speculations. No longer do we look to the fossils to provide proofs of evolution, or (except in cases where there is no modern survivor) of relationships of major groups. Instead, we look to the fossils to fill in the gaps (both taxonomically and structurally), to fill out our knowledge of past radiations and palaeobiogeography, to provide their own comments on environmental change, and to exercise controls on hypotheses of the timing of evolutionary events based on biomolecular constructs.

But within that new framework, the questions that Mitchell posed in 1838 about wider issues remain cogent.

### Geology and landscape evolution

With our knowledge of the evolution of the Eastern Highlands and their cave systems (e.g. Osborne and Branagan 1988) we now recognize temporal complexity, and in particular that their fossils may represent faunas and their evolution over a period far greater than the Quaternary.

The prolific occurrence of caves and their variety are the result of the events that produced extensive sequences of weathering limestone rocks along the Eastern Highlands that are the product of uplift and subsequent continuous weathering.

The highlands owe their origin to a swelling in the mantle that occurred along an approximately meridional line during the Cretaceous (at some time between 96 and 84 Ma (Veevers et al. 1991, figs 6, 7) commencing the development of the sea floor spreading episode that opened the Tasman Sea and continued through with slow spreading until about 55.5 Ma (Veevers et al. 1991, fig. 9). The western side of the ridge that developed, in consequence, is represented by the elevated eastern side of the continent as it is today and crosses all the old geological boundaries from south to north resulting in exposure of a variety of basement rocks including extensive sequences of limestones.

In New South Wales the sequence from south to north is as follows (Packham et al. 1969): The basement rocks of the Southern Highlands are Cambrian–Late Devonian in age, mostly either marine sediments or igneous rocks; they are intruded by granites of Ordovician–Carboniferous age. Northwards the basement rocks of the Hunter Valley are marine shallow water sediments and coal measures of Permian age, overlain by fresh water Triassic sediments. The basement rocks of the New England Tableland are Devonian–Permian in age and consist mainly of sediments and volcanics laid down offshore; they have been intruded by granites of Permian–?Traissic age.

Between 96 and 84 Ma , northward movement of the Australian plate commenced (Veevers et al. 1991, figs 6 and 7), accelerated during the Tertiary (Veevers et al. 1991, figs 9–14), and has continued to the present. As it did so, eastern Australia moved over hotspots in the mantle with the result that volcanic flows penetrated the surface during the Tertiary and Quaternary. Some were very extensive (Duncan and McDougall 1989). The New England, Monaro, and Victorian Highlands basalts piled up great thicknesses (Voisey 1969, Wilkinson 1969, Knutson and Brown 1989, Day 1989), thus increasing the height of the highlands.

The significance of these events to the Tertiary and Quaternary palaeontology of cave and fissure fills lies in the development of karst in the uplifted limestones and its timing. Extensive caves and fissures developed and filled possibly in the Late Cretaceous and probably through much of the Tertiary and up to the present day (Osborne 1992, 1993); some speleogenesis resulted from altered drainages from basalt fills in the valleys (Osborne 1986).

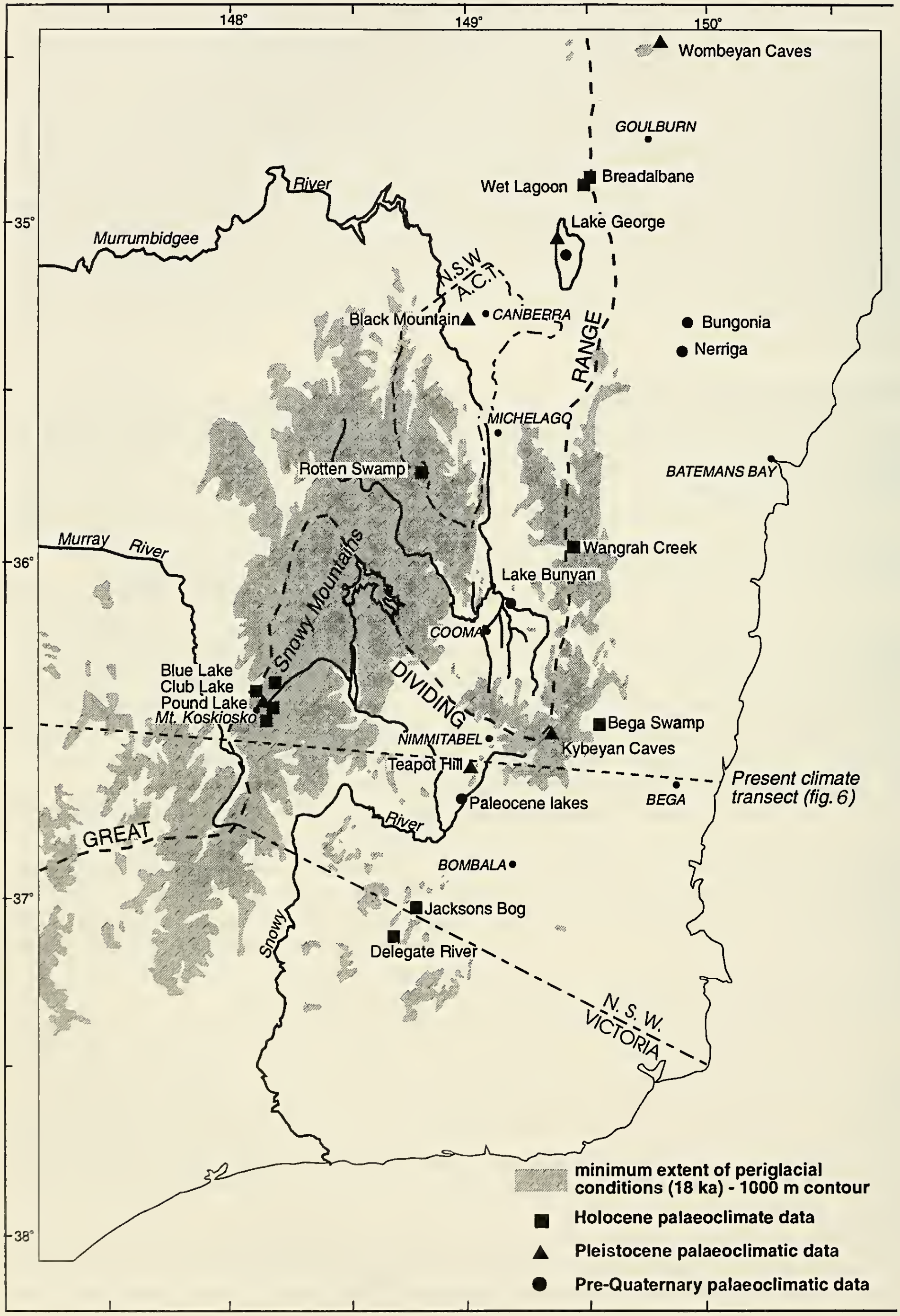


Figure 5. Localities of palaeoclimatic data in the Southern Highlands.

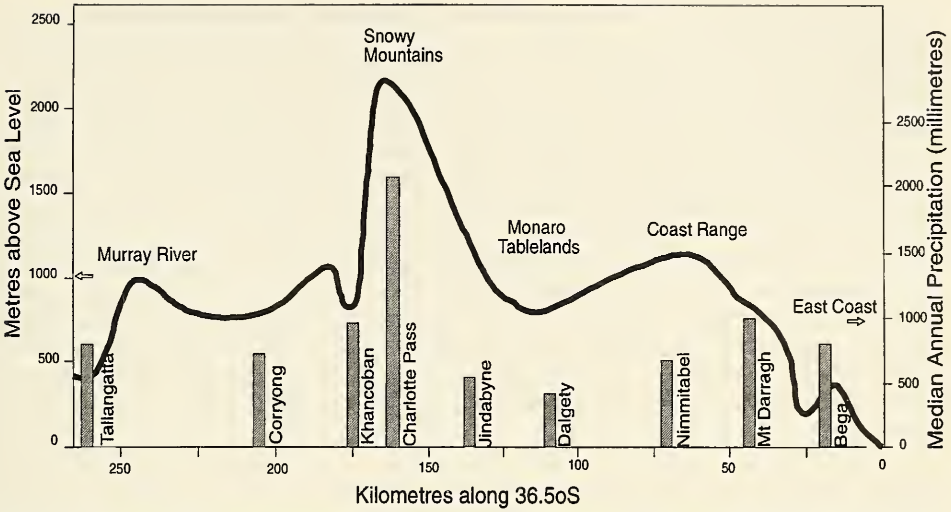


Figure 6. Elevation and annual precipitation across the Monaro Tablelands indicating the rainshadow in the lee of the Snowy Mountains (modified from Atlas of Australian Resources 1986). Median annual precipitation (mm.) at Western Plains, N.S.W. localities comparable with Dalgety (410) is Nyngan (411), Condobolin (423), Leeton (430), Forbes (487) (data from Bureau of Meteorology, 1988, Climatic Averages Australia, A.G.P.S. Canberra).

These events are important in understanding other fossil sites as well. The extrusion of Tertiary and Quaternary basalts over an old landscape covered fluviatile and lacustrine deposits in both the Mesozoic and Tertiary erosional surfaces (Vallance et al. 1969, Pratt et al. 1993). Mammal-containing deposits in the deep leads at Gulgong and at the nearby Canadian Lead (see Woodburne et al. 1985) are good examples from the Eastern Highlands. The basalt flows filling deep-lead valleys on the Gulgong Surface average 14.3 Ma in age; the valley gravels were buried beneath basalt flows in middle Miocene times (Dulhunty 1971).

Because of their weathering and calcium richness, many of the basalts produced conditions in channel fills and terraces favourable to the preservation of bone — as we find in the Monaro.

Finally, as the present landscape formed during the climatic changes and as the uplift continued, river and lake deposits accumulated in the valleys and flood plains from the detritus produced by weathering the exposed highlands. Examples are seen in the valleys of the Bow River and the McLaughlin River where terraces containing mammal fossils extend from the Tertiary to the present, and in the Quaternary sequences of the Monaro (such as at Pilot Creek, Davis 1996).

### Palaeoclimatic framework

A general framework of the sequence of palaeoclimatic changes during the Quaternary (and in particular for the Late Pleistocene (120 ka–10 ka), and Holocene) is now available for eastern Australia including the Eastern Highlands of New South Wales.

This part of the palaeoclimatic record is primarily derived from pollen records from a large number of sites, including sites in the Eastern Highlands (see Fig. 5). A few sequences extend back before the last glacial cooling (35 ka–15 ka), and one (Lake George) to before 350 ka, containing evidence of at least four glacial periods (Singh and Geissler 1985, McEwen Mason 1991). Other evidence of climatic change in the period comes from direct evidence of glacial and periglacial features (which in Tasmania provides evidence of 3 glaciations), sedimentology (including evidence from the Riverina, which reflects activity of the adjacent catchment), and the palaeoecology of aquatic non-marine invertebrates (such as ostracods).

Although lacking the detail of modern deep-sea records of the same period derived from isotope studies, and allowing for the fact that parts of the interpretation are probably influenced by local topographic factors, the general sequence of events in the terrestrial climatic framework accords well with the oceanic record (for comprehensive palaeoclimatic summaries see Chappell 1991, Truswell 1993, Hill 1994, Kershaw 1995).

While the environmental consequences of this sequence are a major factor to be considered in interpreting observed differences between faunas, in the context of highland faunas, local palaeoenvironmental variation at any one time must also be expected to have had marked consequences — even over very short distances.

Today altitudinal variation (topography and erosion surfaces resulting from uplift), aspect, geology, soils, and the availability of surface waters from run-off, all have local effects. For instance, in the Monaro, the local effect of a rainshadow in the lee of the Australian Alps results in environments in the Tableland as arid as those in the western plains of New South Wales (see Fig. 6), yet, despite the aridity, the country is well watered by such rivers as the Murrumbidgee and the Snowy, fed by run-off from the adjacent mountains.

These factors combine to produce environments unique to eastern Australia, such as the alpine zone, as well as a varied and disjunct patchwork of mesophyllic and xeric habitats.

There is good evidence that, even in the Tertiary and Quaternary, this environmental patchiness existed even to the extent that the Monaro rainshadow existed in the Miocene (Ride et al. 1989). The consequence has been that during extremes of aridity in adjacent southern and central Australia the highlands were potential refugia for a wide range of differently adapted mammals that must be expected to occur in contemporary deposits.

As Hope (1982) has pointed out, proximity of arid to well-watered environments has enabled the unexpected, and apparently disharmonious, sympatry of some species in deposits, such as those at Wellington, of forms such as *Diprotodon* and *Zygomaturus* that appear from their distributions to be otherwise ecologically incompatible. In places where environmental patchiness is represented within the hunting ranges of predators inhabiting a cave (such as owls) mixed "pseudosympatry" may be expected in a deposit.

As well as resulting in environmental patchiness, altitudinal variety also has direct consequences to faunal evolution and movement over time. It may result in distributional disjunctions. Thus, populations dependent upon alpine habitats (such as populations of *Burramys parvus)* become isolated as temperatures rise, and become reunited with falling temperatures. The drowning of Bass Strait at the end of the Pleistocene produced a major disjunction and barrier to faunal dispersal.

Highland caves and small valley systems are extremely sensitive indicators of faunistic change over relatively small time-spans but, in these complex environmental situations, differences between adjacent faunal assemblages may be due to a number of factors, both ecological and chronological. Unless stratigraphic relations are very clear and dates reliable, faunistic and palaeoenvironmental interpretation is hazardous. Extreme caution must be exercised in attributing biostratigraphic conclusions to them, as we have found in the Monaro.

As an example, until six months ago, on the basis of radiocarbon dates, we thought that the Bunyan Siding and Pilot Creek faunas in the northern Monaro (see below) were contemporary. We concluded that the observed difference reflected ecological responses at the two localities. Instead of which, we now find, from improved dating techniques, that they are separated in time by at least 100 ka (or even 750 ka), and by at least one climatic fluctuation. We now regard differences between them as an example of faunal turnover during the Pleistocene.

Interpretive consequences of the palaeoclimatic record

From different sources of information a dramatic shift in Australian climate took place about eight million years ago (see Kershaw et al. 1991, Truswell 1993, Hill 1994). Although Megirian has argued for the presence of mesic, and even xeric, environments across Northern Australia even earlier, in Miocene (Carl Creek Limestone) times (Megirian 1992), a change of climate occurred from non-seasonal and warm humid conditions, probably supporting extensive rainforest faunas (possibly through a period of shrinking refugia), towards conditions that by five million years ago had become arid and seasonal (Bowler 1982). Moreover, over much of Australia the seasonality of rainfall shifted from summer to winter. During this shift, except in patchy remnants, vegetation became dominated by sclerophyll and other arid adapted plants such as grasses, acacias and chenopods. Yet in the highlands where mesic environments persisted (Hill 1994), traces continued to survive, in wet sclerophyll, in heaths, and downslope in coastal scrubs, of the humid adapted elements of the late Pliocene mammal fauna (such as the ring-tail possums and *Burramys*) which we know from the transitional period at about 4.5 Ma (Hamilton, Bow, and Chinchilla), as well as in much earlier Tertiary faunas (Riversleigh).

The palaeoclimatic record also indicates that in the last two million years there were 20 marked climatic shifts (Chappell and Shackleton 1986, Hope 1994). There is terrestrial evidence that at least three of these resulted in glaciations (Colhoun 1985). At the height of these the arid threshold was passed, sand deserts formed and dune building occurred (Wasson 1986, Hope 1994). Major expansion of dunes occurred after 700 ka.

The most striking characteristic of the modern Australian mammal fauna is its remarkable adaptation (anatomical, physiological and behavioural) to aridity and climatic instability. From the palaeoclimatic sequence outlined above, it is now apparent that this adjustment must have generated an extremely rapid faunistic response over much of Australia; and that there was a succession of extinctions culminating in the final extinction of the remaining megafauna. The whole sequence, from the start of the aridity to the present day, taking little more than five million years.

As a late Tertiary and Quaternary phenomenon this period of adaptation to arid and semi-arid conditions (by evolution and by faunal movement), probably took place within the time span covered by the eastern highland deposits and, because of this, these deposits should, once we are able to determine their stratigraphy and date them, provide us with a remarkably detailed record of it.

At present there are few data of eastern Australian cave mammal faunas that can be securely positioned within the palaeoclimatic record until we reach the end of the penultimate interstadial at about 30 ka (and even then, records are inadequate).

Of lower- to mid-Pleistocene eastern highland faunas, only Bunyan Siding is securely dated to this period (i.e., to more than 100 and less than 780 ka). Dawson (1985) has argued that part of the Wellington Cave deposit (the Phosphate Mine Beds and Big Sink) is late Pliocene. On the basis of the contained macropod species, she has also argued that the bones in the Wellington red earths (Bone Cave, Mitchell's Cave) may be as old as 128 ka (also see Osborne 1983, p. 143–4, for an evaluation of studies bearing on the ages of these units at Wellington).

In support of Dawson's contention that the Wellington red cave earths may be older than the last glacial cycle, on faunistic grounds alone, there can be no doubt that the Wellington Caves deposits cover a number of replacing faunas. At least 27 species of Macropodidae are represented in historic collections from the caves. By comparison, the richest modern fauna of Macropodidae recorded (that of the Upper Richmond and Clarence Rivers — Calaby 1966) contains 11 species — and even that occurs over a very diverse catchment of some 4000 km$^2$. Bunyan Siding, that we assume contains a single fauna, contains at least 7 species of Macropodidae.

Of earlier deposits, there is now no doubt that Dukes cave system at Buchan contains bone bearing deposits formed in a period of magnetic reversal. These are at least older than the end of the Matuyama chron which finished 0.73 Ma ago (Osborne 1983, Webb et al. 1992, Cande and Kent 1992), but nothing is yet known of the fauna.

As the climate of the eastern highlands moved towards the last glaciation after about 30 ka, it changed from cool temperate and moist interstadial conditions, through increasing aridity and reduced temperatures until the glacial maximum was reached at about 18 ka when temperatures were probably about 9 C below the present (Barrows 1995).

The glacial maximum was followed by climatic amelioration with increased humidity and a temperature that at 6 ka probably reached about 1–2 C above the present. From then until the present, temperatures fell again and it became slightly more arid (Kershaw 1995).

Many of the morphological changes in animals, and changes in species composition, particularly those brought about by gradual responses to changing climates, will be expressed only by changes in ranges of variation, and abundance of species, and will only be detected statistically and as a result of detailed quantitative and stratigraphic study. Some cave deposits are ideal for this and a fine example is provided by the detailed study made by Deborah Morris and colleagues (Morris 1992, Morris et al. 1996) at Jenolan. In other parts of Australia similar studies have been made by Alex Baynes at Hastings Cave in Western Australia (Baynes 1979), and are currently being made by Rod Wells and his colleagues at Naracoorte.

As collections made in former times from caves at Wellington attest, collections made before the need for rigorous localization was recognized, present almost insuperable difficulties in interpretation (see Dawson 1985).

Dated mammal-containing sites from the period of maximum aridity (i.e. immediately before and after the last glacial maximum) are known from throughout the region. In the southern highlands, as well as those we have dated in the Monaro, dated deposits occur at Lake George (21–27 ka, Sanson et al. 1980) and at Cloggs Cave, Buchan (17–25 ka, Flood 1974, 1980), and Pyramids Cave, Buchan (33–30 ka, Wakefield given in Flood, 1980); and in northern New South Wales at Lime Springs, Gunnedah (20–18 ka, Gorecki et al. 1984).

Dated deposits from the north and south of the region also indicate changes in mammal faunas over this time. The southernmost dated records are from the Florentine Valley, Tasmania (20–10 ka, Goede and Murray 1979), northwestern Tasmania (Pulbeena Swamp, 22 ka, Banks et al. 1976) and Hunter Island (Cave Bay Cave, 23–14 ka, Bowdler 1975). From southern Victoria, dated late interglacial deposits from before the last glacial maximum are Lancefield (c 26 ka, Gillespie et al., 1978), and Spring Creek (>30 ka. White and Flannery 1995). In southern Queensland a dated deposit is known in the western Darling Downs at Kings Creek, Clifton (over 21 ka, Gill 1978).

Of these series, Baynes (1995; pers. comm.) considers that only the dates from Cloggs Cave, Buchan; Kings Creek, Clifton; and the Lancefield Channel have values of 8 or more in the Meltzer and Mead (1985) classification (i.e. can be considered reliable). But in the case of the Lancefield Channel, there is subsequent indication that the fossils within the site have been redeposited (Van Huet 1994). Baynes has not commented on the date given on Pyramids Cave (in Flood 1980), while our most recent dates for the Bunyan Siding and Pilot Creek deposits were obtained after his survey and have not been commented on, either.

Dated mammal-containing deposits from the post-glacial period of climatic amelioration, including the warm moist phase of the early Holocene, are less abundant. In the Eastern Highlands dates have been obtained from Nettle Cave, Jenolan (7.1 and 8.7 ka, Morris 1992) and by us for Coronation Cave, Wombeyan (8.2 ka — but we do not consider this date reliable for the contained fauna). We have also dated post-glacial sediments in the Monaro (Davis 1996).

Southwards, post-glacial dates are known for mammal-containing deposits at Cave

Bay Cave, Hunter Island (c.7 ka, Bowdler 1975), Pyramid Cave, Buchan (c.2.5 ka, Wakefield 1967a), and numerous archaeological sites containing mammal remains such as Capertee Valley (with a dated succession from 7.4 ka–2.9 ka) and Burrill Lake (younger than 1.6 ka). Some dated faunas from this later period are parts of sequences from which the dates of older parts of the same sequences can be inferred. These include Pryamids Cave, Buchan (2.5 ka, Wakefield 1967a) and McEachern's Cave in Western Victoria (15 ka, Wakefield 1967b).

## REFLECTIONS: ON CURRENT DIRECTIONS

### Stratigraphic correlations of open sites

The temporal and palaeoclimatic setting described above has given new possibilities to Quaternary mammal palaeontology. Providing dates can be obtained it should now be possible to correlate palaeoclimatic events and faunal changes such as faunal turnover, extinction, or morphological changes and give ecological meanings to them.

Woodburne et al. (1985), in their survey of the biochronology of the continental mammal record of Australia and New Guinea, point out that, as the result of correlating late Tertiary and Pleistocene faunas of arid Australia with such events as dune building, we know that major faunal changes have taken place during the Quaternary and not only at its end. They say

> "In addition, certain Tertiary groups (for example, diverse diprotodontines) fail to persist into late Pleistocene time and give evidence of important faunal change within the Quaternary that needs better documentation. Integrated palaeontological and geological studies are badly needed to chart the Quaternary faunal changes and determine their causes against the background of Australia's unusual Pleistocene history."
>
> (Woodburne et al. 1985, p. 360)

In the Eastern Highlands numbers of open sites (i.e. sites accumulated under fluviatile or lacustrine conditions) containing mammals have been described. Jeanette Hope (MS. pers. comm.) and Paul Willis (MS. pers. comm.) have listed these from thorough surveys of the literature and museum collections. Most of these sites, with further work, have the potential to be placed within the framework but none, except those we have studied in the Monaro and the Governors Hill site, are dated. We conclude that, in the absence of dates, attempts to incorporate them in a general biostratigraphy of the region would be hazardous. Of relevant sites to the northwards, Bingara, of which the fauna was revised by Marcus (1976), is the richest and has great potential for further study. Weetaliba, which we have surveyed, although rich in numbers of species represented, is very dispersed and appears to lack concentrations of fossils, and we have not found it to have potential for dating.

Over the last 10 years we, with Leanne Dansie (now Armand), Prof. Graham Taylor and Dr Pat Walker, have investigated three alluvial Quaternary sites in the Monaro (Dansie 1992, Davis 1996). Faunistically, our aim was to clarify what happened to the high country faunas in eastern Australia during the decline of the megafauna. We have attempted to find causes by seeking correlations with other factors, such as the palaeoclimatic events that have been revealed by studies from other disciplines.

The sites studied are Bunyan Siding and Pilot Creek, both on tributaries of the Murrumbidgee River near Cooma, and Teapot Creek, a tributary of the Maclaughlin River near Nimmitabel. At Bunyan Siding there are two faunas, both now considered to be Middle Pleistocene. Pilot Creek provides a record of the last 25 ka represented in four stratigraphically distinct faunas with radiocarbon ages of 25, 11, 6 to 2, and 4.5 ka. At Teapot Creek there are two faunas, the younger dated at 4.5 ka and the other which occurs in a series of terraces is yet undated and is, from the species represented, probably

Pleistocene. At the Maclaughlin River, close by, a fauna contains species apparently equivalent to Pliocene Chinchilla. Between them, these sequences in the Monaro give a picture of faunal turnover between the Middle and Late Pleistocene (and possibly the late Pliocene), followed by progressive faunal impoverishment since immediately before the last glacial maximum to the present.

The Middle Pleistocene fauna of Bunyan Siding contains at least 17 species of mammal (11 extinct, 6 extant). Of the 11 extinct, 7 are Macropodidae (i.e. as in Wellington faunas (Dawson 1985), all Bunyan Macropodidae are replaced). The other four species are possibly *Zygomaturus trilobus*, a species of *Diprotodon*, a new vombatid, and a small murid of the *Pseudomys australis*-group. The 6 extant species are *Aepyprymnus rufescens, Vombatus ursinus, Perameles gunnii, Dasyurus viverrinus, Ornithorhynchus anatinus* and *Mastacomys fuscus* (Davis 1996).

The older (25 ka) fauna of Pilot Creek, from immediately prior to the last glaciation, contains both modern species such as *Macropus robustus* and *Vombatus ursinus* as well as large megafaunal species *(Protemnodon anak, Protemnodon roechus/brehus, Thylacoleo carnifex, Sarcophilus laniarius, M. titan*, and species of *Sthenurus* and *Diprotodon*) that are not present in the younger deposits. The post-glacial deposits contain no megafauna, but do contain species that are not found in the modern fauna of the area, although occurring elsewhere. These are *Aepyprymnus rufescens, Perameles gunnii* and *Mastacomys fuscus.* Extinct species represented in these post-glacial faunas include *Thylacinus cynocephalus* and *Conilurus albipes.*

It is instructive to compare the result at Pilot Creek with that obtained by Deborah Morris at Nettle Cave, Jenolan (Morris et al. 1996), and that of Norman Wakefield at Pyramids Cave, Buchan (Wakefield 1967a, tables 1 and 2). In both cases they obtained a distinct faunal transition that probably represents the same climatic event but, unlike the megafauna, in the case of the faunas of small mammals that they describe, while clearly there has been an ecological shift, there have been no extinctions.

Did the megafauna have nowhere to go as the climate warmed and conditions improved, or was there some factor other than climate involved. We now have evidence from Bunyan that species had been lost earlier than the last glacial maximum, and local extinction both before and after the last glacial maximum involved more than the megafauna. Certainly, humans had occupied the highlands by 21 ka and maybe long before. The Lake George core has been interpreted as giving evidence of a human-caused increase in burning from before 100 ka (but this interpretation is not accepted universally (Wright 1986, Ladd 1988).

Through the very small window we now have in Bunyan Siding and Pilot Creek, it is possible to see that considerable faunal change occurred between the time represented by Bunyan (somewhere between 780 and 100 ka) and the colder conditions that immediately preceded the glacial maximum represented at Pilot Creek and, probably, Teapot Creek. Of the 41 species of megafauna known from Australian deposits considered to be Pleistocene (Flannery 1990), only 16 occur in deposits known with reasonable certainty to be late Pleistocene (i.e., 25 ka or younger). Have we enough information yet to suggest that only the very end of megafaunal extinction was coincident with a major adverse climate change, and that it may well have commenced before Aboriginal settlement?

Even Owen, in his time, was asking that question.

> In the extinction of Diprotodon, as of Megatherium, there seems to be an additional exemplification of the fruitful and instructive principle which, under the phrases "contest for existence", or "battle of life", embodies the several circumstances , such as seasonal extremes, generative power, introduction of enemies, &c., under the influence of which a large and conspicuous quadruped is starved out, or falls a prey, while the smaller ones migrate, multiply, conceal themselves, and escape.
>
> We infer from the fact of remains of young and inexperienced Diprotodons occur-

> ring in Australian Caverns with those of Thylacoleo, that the large Marsupial herbivore had its enemy in, and occasionally fell a victim to, the large Marsupial Carnivore; as at the present day the Kangaroo is laid in wait for by the Thylacyne, or "Native Wolf", and by the Dasyure, or "Native Cat".
>
> We may speculate upon the possible relation of the first introduction of the Human kind into Australia, and of the subsequent insulation of that land from the rest of the Papuan Continent, to the final extinction in the so restricted territory of all the characteristic Mammals which happened to surpass in bulk the still existing, swift-retreating, saltatorial and nocturnal Kangaroos.
>
> (Owen 1877, p. 233)

## Impact upon conservation biology

As precise knowledge of the ages and compositions of the faunas increases, we are going to find that there are many faunistic associations that are not explicable on present ecological knowledge. Lundelius (1989, pp 410–411) gives a number of examples from fossil faunas from different parts of Australia.

In Pilot Creek at the Poplars site (4.5 ka) the three bandicoot species *Isoodon obesulus, Perameles nasuta* and *P. gunnii* are sympatric (Davis 1996), assuming that one can discount the possibility that they were collected by a predator from different, but adjacent, habitats. *P. gunnii* occurs nowhere today with *P. nasuta*. The same species association was found by Wakefield (1964, 1967b) in south-eastern Victorian cave faunas.

The three small possums *Burramys parvus, Gymnobelideus leadbeateri* and *Cercartetus lepidus* provide a similar example. All three occur together in the Broom fauna of Wombeyan Caves. Today, these species have widely separate distributions and seem to differ from each other in ecological requirements. On the basis of current knowledge, their presence in a single fauna would be improbable. A similar difficulty is posed by the palaeodistribution of the native mice *Mastacomys fuscus* and *Pseudomys higginsi.*

*Burramys parvus*, the mountain pygmy possum, is today confined to high altitudes, living principally in periglacial conditions above the tree line. It is confined to a few localities in the Australian Alps in Victoria and New South Wales. Its principal habitat (Mansergh and Scott 1990) is alpine and subalpine *Podocarpus* heathland over periglacial rock screes and boulder fields.

The palaeodistribution of *Burramys* (see Ride et al. 1989, p 105) includes Kandos (undated), Nettle Cave, Jenolan (undated but probably immediately before the last glaciation), Wombeyan (Broom Deposit and Coronation Cave — both undated), Wombeyan Quarry (undated), Tuglow Downs (undated), and Pyramids Cave, Buchan (between 33 and 30 ka). Tertiary species of *Burramys* occurred in rainforest environments in the Miocene (Riversleigh) and Pliocene (Hamilton).

Other mammals in the modern habitat are *Mastacomys fuscus, Antechinus stuartii, A. swainsonii* and *Rattus fuscipes*. These species seem to be less successful than *Burramys* in that habitat and appear to be approaching their ecological limits.

The major food resource of *Burramys* is the Bogong Moth which congregates in that habitat in large numbers during the summer when the possums are building up energy reserves for the winter when the animal enters extended bouts of torpor between May and early September (Mansergh et al. 1990).

Its behaviour, as well as its physiology, is highly specialized. In addition to hibernating, the females maintain territories in the preferred habitat the year round and the males leave in the autumn to return in the following summer. Breeding is highly synchronized and there is one litter only. They give birth to supernumerary young. They have a greater longevity than any other small Australian mammal species and this, combined with very efficient breeding, gives them a very high lifetime fecundity.

This information all indicates that *Burramys parvus* has very narrow environmental tolerances (i.e. is dependant upon periglacial conditions) and that it should be very sensitive to climatic change. Recent BIOCLIM analysis ( Bennett et al. 1991) supports this view. On that basis a few degrees rise in temperature should result in its extinction. Yet the palaeoclimatic framework and palaeodistributional records are inconsistent with that contention. Moreover the species did not become extinct despite the climatic amelioration of the Holocene.

*Gymnobelideus leadbeateri, Cercartetus lepidus, Mastacomys fuscus* and *Pseudomys higginsi*, pose similar problems in connection with rise in temperature (see Lindenmayer et al. 1991, Bennett et al. 1991).

Does this mean that the use of modern distributions and their inferred ecological "drivers" alone, as in BIOCLIM analysis, is not an effective methodology for predicting distributional consequences of global warning? Bennett et al. (1991, p. 9) make an important caveat that interactions between species may give rise to responses to climate change that may vary from those predicted by BIOCLIM. Graham and Lundelius (1984) suggest that an explanation of apparently disharmonious distributions might be that they reflect the distribution of evolutionary interactions.

Does it mean that physiological evolution can proceed much more rapidly than the morphological changes with the consequence that we cannot assume that past behaviour and physiological responses of modern morphospecies are those of their seeming palaeo-representatives?

Or does it mean that our morphotaxonomy is not sufficiently precise to enable us to detect the differences that are reflected in ecological responses?

Certainly, in the case of *Burramys* recent research by Jenni Brammall has shown that in the Quaternary more than one taxonomically distinguishable form is involved in the puzzle (and therefore are, possibly, physiologically distinct).

It may be any of these things, but Brammall's current study of the *Burramys* populations (pers. comm.), suggests that our principal barriers to understanding in this area stem from a taxonomy that has still a long way to go and the lack of dated sites that would enable us to assign species distributions to positions within the palaeoclimatological framework.

◆

We have come far in understanding since fossils were collected from these caves in 1830, but, even 166 years later, we still have far to go …

## ACKNOWLEDGMENTS

We are grateful to all who helped us in our research that provided a large part of the background for this paper. In the case of one of us (W.D.L.R.) this help extends through continents and nearly a lifetime. For the paper itself we acknowledge the contribution of Deborah Morris, Jenni Brammall, Mike Augee, Alex Baynes, Jeanette Hope and Paul Willis who freely discussed their research in progress with us, and the curators of the collections, especially Alex Ritchie and Bob Jones of the Australian Museum, who made the collections in their care available. Julian Holland gave helpful advice on the literature on the relationship between Mitchell and Ranken.

The portrait of Professor Sir Richard Owen is published with the permission of the Trustees of the Wellcome Trust (who hold the copyright) and is from the Wellcome Institute Library, London; that of George Ranken is published with the permission of his great granddaughter Mrs Margaret Suttor of Kelloshiel, Hargraves, NSW; and that of Major Sir Thomas Mitchell is published with the permission of the Mitchell Library, State Library of NSW. We are grateful to William Schupbach who selected the portrait of the young Richard Owen for us from the collection of the Wellcome Institute Library, London, that he curates; to Christina S. Wright for locating the portrait of George Ranken; and to Elizabeth Ellis (librarian) and Jennifer Broomhead (copyright and permissions librarian) of the Mitchell Library for locating the portrait of T. Mitchell.

We are grateful for the support of our colleagues, Graham Taylor, Pat Walker, Ken Campbell, Leanne Armand, and others involved directly in our research on the Monaro deposits referred to here. Geoff Hope, Peter Pridmore and Alex Baynes commented on drafts for us and helped us with many suggestions. We are most grateful to them and to Armstrong Osborne and Lyndall Dawson for their most constructive reading of the manuscript.

We gratefully acknowledge that our research on the fossil mammal-bearing deposits of the eastern highlands was supported by a grant from the Australian Research Council to Ride and G. Taylor.

## ENDNOTES

1. A view later echoed by Wilberforce, Bishop of Oxford, in his 1860 review of *The origin of species* in which he gave his view of the proper attitude to scientific truth. Wilberforce said "We have no sympathy with those who object to any facts or alleged facts in nature, or any inference logically deduced from them, because they believe them to contradict what it appears to them is taught by Revelation ... To oppose facts in the natural world because they seem to oppose Revelation ... is ... but another form of the ever-ready feebleminded dishonesty of lying for God ..." (Quoted by Lack 1961, p.14).

2. It should not be assumed that the scientists involved had simply left the issue to rest there. The problem of whether extinction, as a natural process, had occurred at all, had featured prominently in the "philosophical debate" over creation (see Rudwick 1972; e.g., pp 105–9, 171–3). For the Australian fauna this aspect became replaced by speculation over causal factors that might also have operated world-wide (e.g. Darwin 1845, p 178 ) and by the quest to determine whether humans had had a part in Australian megafaunal extinction (Owen 1877, pp 238–240).

## REFERENCES

Andrews, S.M. (1982). The discovery of fossil fishes in Scotland up to 1845 with checklists of Agassiz's figured specimens. *Royal Scottish Museum Studies* (especially 12–13, 56–57 for notes on Jameson and the Edinburgh College Museum).

Anon. (1830a). Interesting discovery of fossil bones [Editorial]. *Sydney Gazette and New South Wales Advertiser* vol. **28**, (no. 1818, 25 May 1830), p. 2.

Anon. (1830b). Interesting discovery [Letter to the editor, signed L., and dated 21st May 1830]. *Sydney Gazette and New South Wales Advertiser* vol. **28** (no. 1818, 25 May 1830), p. 2. [This letter is usually attributed to the Rev J.D. Lang ("this can be assumed", see Lane and Richards 1963, p. 10), confirmation quoting Lang is given in Anon (1832), where Lang's transport of the collection to Jameson is also confirmed.]

Anon. (1831). [List of foreign specimens added to the Museum of the Geological Society of London and list of names of donors to the Museum in 1831]. *Proceedings of the Geological Society of London* **1**, 352–3.

Anon. [Jameson, R.] (1831a). Account of the discovery of bone caves in Wellington Valley, about 210 miles west from Sydney in New Holland. In Anon. *Edinburgh New Philosophical Journal, exhibiting a view of the progressive discoveries and improvements in the sciences and the arts* **10**, 364–368.

Anon. [Jameson, R.] (1831b). Further notices in regard to the fossil bones found in Wellington Country, New South Wales. By Major Mitchell, Surveyor-General of New South Wales. In Anon. *Edinburgh New Philosophical Journal, exhibiting a view of the progressive discoveries and improvements in the sciences and the arts* **11**, 179–80.

Anon (1832). Fossil remains of the elephant in New Holland. *The Penny Magazine of the Society for the Diffusion of Useful Knowledge* **1** (34), 274.

Baker, D.W.A. (1967). Entry: Lang, John Dunmore. In 'Australian Dictionary of Biography' (General Ed. D. Pike) pp. 76–83. (Melbourne University Press: Carlton, Victoria).

Banks, M.R., Colhoun, E.A. and Van de Geer, G. (1976). Late Quaternary *Palorchestes azael* (Mammalia, Diprotodontidae) from northwestern Tasmania. *Alcheringa* **1**, 159–66.

Barrows, T.T. (1995). 'Three aspects of Late Quaternary palaeoclimatic reconstructions in Eastern Australia'. Hons Thesis, Geology, Australian National University.

Baynes, A. (1979). 'The analysis of a late Quaternary mammal fauna from Hastings Cave, Jurien, Western Australia'. PhD Thesis, University of Western Australia: Perth

Baynes, A. (1995). The question "Why did the Australian Pleistocene megafauna become extinct?" currently is unanswerable because there are no reliable dates for any of the species. Abstract, p. 12, *Taphonomy Symposium* 95, held 28–29 April, 1995, Department of Archaeology and Anthropology, Australian National University.

Bennett, G. (1834). 'Wanderings in New South Wales, Batavia, Pedir Coast, Singapore and China; being the journal of a naturalist in those countries during 1832, 1833, and 1834', 2 vols. (Richard Bentley: London).

Bennett, S., Brereton, R., Mansergh, I., Berwick, S., Sandiford, K. and Wellington, C. (1991). The potential effect of the enhanced greenhouse climate change on selected Victorian Fauna. *Arthur Rylah Institute Technical Report Series* No. 123. i–vii, 1–224.

Bowdler, S. (1975). Further radiocarbon dates from Cave Bay Cave. *Australian Archaeology* **3**, 24–26.

Bowler, J.M. (1982). Aridity in the late Tertiary and Quaternary of Australia. In 'Evolution of the flora and fauna of arid Australia' (Eds. W.R. Barker, and P.J.M. Greenslade) pp. 35–45. (Peacock Publs: Frewville: South Australia).

Brooke, J.H. (1991 'Science and religion Some historical perspectives'. Cambridge History of Science Series. (Cambridge University Press, Cambridge).

Broom, R. (1896a). On a small fossil marsupial with large grooved premolars. *Proceedings of the Linnean Society of New South Wales* (2) **10**, 563–7.

Broom, R. (1896b). On a small fossil marsupial allied to *Petaurus. Proceedings of the Linnean Society of New South Wales* (2) **10**, 568–70.

Buckland, W. (1824). 'Reliquiae Diluvianae; or observations on the organic remains contained in caves, fissures and diluvial gravel, and on other geological phenomena attesting the action of an universal deluge'. (John Murray: London) (2nd Edition, 1824, pp. viii, 303. Page nos quoted from the 2nd edn).

Buckland, W. (1836). 'Geology and mineralogy considered with reference to natural theology', Treatise VI, The Bridgewater Treatises on the power wisdom and goodness of God as manifested in the Creation. 2 vols, (2nd edn 1837).

Calaby, J.H. (1966). Mammals of the Upper Richmond and Clarence Rivers, New South Wales. *Technical Paper, Division of Wildlife Research, C.S.I.R.O.* no. 10, 1–55.

Cande, S.C. and Kent, D.V. (1992). A new geomagnetic polarity time scale for the Late Cretaceous and Cenozoic. *Journal of Geophysical Research* **97**, 13917–51.

Chappell, J. (1991). Late Quaternary environmental changes in eastern and central Australia, and their climatic interpretations. *Quaternary Science Reviews* **10**, 377–90.

Chappell, J.M.A. and Shackleton, N.J. (1986). Oxygen isotopes and sea level. *Nature* **334**, 137–40.

Chisholm, A. (1967). Entry: Lindesay, Sir Patrick. In 'Australian Dictionary of Biography' (General Ed. D. Pike) **p.** 119. (Melbourne University Press: Carlton, Victoria).

Clift, W. (1831). Report by Mr Clift, of the College of Surgeons, London, in regard to the fossil bones found in the bone-caves and bone-breccia of New Holland. In Jameson, R. On the fossil bones found in the bone-caves and bone-breccia of New Holland. *Edinburgh New Philosophical Journal, exhibiting a view of the progressive discoveries and improvements in the sciences and the arts* **10**, 394–5.

Colhoun, E.A. (1985). Glaciations of the West Coast Range, Tasmania. *Quaternary Research* **24**, 39–59.

Dansie, L.K. (1992). 'Stratigraphy and Palaeontology of Teapot Creek, Sherwood and Boco Stations, near Nimmitabel, N.S.W'. BSc Hons. Thesis, Geology Department, Australian National University, Canberra.

Darwin, C. (1839). 'Journal of researches into the geology and natural history of the various countries visited by H.M.S. Beagle, under the command of Captain Fitzroy, R.N., from 1832 to 1836'. (Henry Colburn: London).

Darwin, C. (1845). 2nd Edn of Darwin, 1839. Page nos quoted are from the 1894 reprint. ( Ward, Lock and Bowden: London).

Davis, A.C. (1996). 'Quaternary Mammal Faunas and their Stratigraphy in the Northern Monaro Region, Southeastern Australia', PhD Thesis, Geology Department, Australian National University, Canberra.

Dawson, L. (1985). Marsupial fossils from Wellington Caves, New South Wales; the historic and scientific significance of the collections in the Australian Museum. *Records of the Australian Museum* **37**, 55–69.

Day, R.A. (1989). Victoria and South Australia, Older Volcanics. In 'Intraplate volcanism in Eastern Australia and New Zealand' (Ed. R.W. Johnson) pp 133–136. (Cambridge University Press: Cambridge).

De Vis, C.W. (1888). On an extinct genus of the marsupials allied to *Hypsiprymnodon. Proceedings of the Linnean Society of New South Wales* (2) **3**, 5–8.

Dugan, K.G. (1980). Darwin and Diprotodon: The Wellington Caves fossils and the Law of Succession. *Proceedings of the Linnean Society of New South Wales* **104**, 265–272.

Dulhunty, J.A. (1971). Potassium-argon basalt dates and their significance in the Ilford-Mudgee-Gulgong region. *Journal and Proceedings of the Royal Society of New South Wales* **104**, 39–44.

Duncan, R.A. and McDougall, I. (1989). Volcanic time-space relationships. In 'Intraplate volcanism in Eastern Australia and New Zealand' (Ed. R.W. Johnson) pp 43–54. (Cambridge University Press: Cambridge).

Finch. M.E. (1982). The discovery and interpretation of *Thylacoleo carnifex* (Thylacoleonidae, Marsupialia). In 'Carnivorous Marsupials' (Ed. M. Archer) pp. 537–51. (Royal Zoological Society of New South Wales: Sydney).

Flannery, T.F. (1990). Pleistocene faunal loss: implications of the aftershock for Australia's past and future. *Archaeology in Oceania* **25**, 45–67.

Flood, J. (1974). Pleistocene man at Clogg's Cave: His tool kit and environments. *Mankind* **9**, 175–88.

Flood, J. (1980). 'The Moth Hunters; Aboriginal prehistory of the Australian Alps'. (Australian Institute of Aboriginal Studies: Canberra).

Foster, W. (1936). Colonel Sir Thomas Mitchell, D. C.L., and fossil mammalian research. *Royal Australian History Society Journal* **22**, 433–443

Gill, E.D. (1978). Geology of the late Pleistocene Talgai cranium from SE Queensland. *Archaeology and Physical Anthropology in Oceania* **13**, 177–97.

Gillespie, R., Horton, D.R., Ladd, P., Macumber, P.G., Rich, T.H., Thorne, R. and Wright, R.V.S. (1978). Lancefield Swamp and the Extinction of the Australian Megafauna. *Science* **200**, 1044–48.

Goede, A. and Murray, P. (1979). Late Pleistocene bone deposits from a cave in the Florentine Valley, Tasmania. *Papers and Proceedings of the Royal Society of Tasmania* **113**, 39–52.

Gorecki, P.P., Horton, D.R., Stern, N. and Wright, R.V.S. (1984). Coexistence of humans and megafauna in Australia: improved stratified evidence. *Archaeology in Oceania* **19**, 117–19.

Graham, R.W. and Lundelius, E.L. Jnr. (1984). Coevolutionary disequilibrium and Pleistocene extinctions. In 'Quaternary extinctions — a prehistoric revolution' (Eds. P.S. Martin and R.G. Klein) pp. 223–249. (University of Arizona Press: Tucson).

Hill, R.S. (1994). 'History of the Australian vegetation: Cretaceous to Recent'. (Cambridge University Press).

Holland, J. (1992). Thomas Mitchell and the origins of Australian palaeontology. *Journal and Proceedings of the Royal Society of New South Wales* **125**, 103–106.

Hope, G.S. (1994). Quaternary vegetation. In 'History of the Australian vegetation: Cretaceous to Recent'. (Ed. R.S. Hill) pp. 368–389. (Cambridge University Press).

Hope, J.H. (1982). Late Cainozoic vertebrate faunas and the development of aridity in Australia. In 'Evolution of the flora and fauna of arid Australia' (Eds. W.R. Barker and P.J.M. Greenslade) pp. 85–100. (Peacock Press: Frewville, South Australia).

Jameson, R. (1831). On the fossil bones found in the bone-caves and bone-breccia of New Holland. *Edinburgh New Philosophical Journal, exhibiting a view of the progressive discoveries and improvements in the sciences and the arts* **10**, 393–96.

Kershaw, A.P. (1995). Environmental change in Greater Australia. *Antiquity* **69** (Special Number 265), 656–75.

Kershaw, A.P., D'Costa, D.M., McEwen Mason, J.R.C., and Wagstaff, B.E. (1991). Palynological evidence for Quaternary vegetation and environments of mainland southeastern Australia. *Quaternary Science Reviews* **10**, 391–404.

Knutson J. and Brown, M.C. (1989). Central and Southern New South Wales. Monaro, Snowy Mountains and South Coast. In 'Intraplate volcanism in Eastern Australia and New Zealand' (Ed. R.W. Johnson) pp 130–131. (Cambridge University Press: Cambridge).

Lack, D. (1961). 'Evolutionary theory and Christian belief'. (Methuen: London).

Ladd, P.G. (1988). The status of Casuarinaceae in Australian forests. In 'Australia's Ever Changing Forests' (Eds. K.J. Frawley and N. Semple) pp. 63–85. (Department of Geography and Oceanography, ADFA: Canberra).

Lane, E.A. and Richards, A.M. (1963). The discovery, exploration and scientific investigation of the Wellington Caves, New South Wales. *Helictite* **2**, 3–52.

Lindenmayer, D.B., Nix, H.A., McMahon, J.P., Hutchinson, M.F. and Tanton, M.T. (1991). The conservation of Leadbeater's Possum, *Gymnobelideus leadbeateri* (McCoy): a case study of the use of bioclimatic modelling. *Journal of Biogeography* **18**, 371–83.

Lindesay, P. (1830). Bone caves discovered in New Holland. *Edinburgh New Philosophical Journal, exhibiting a view of the progressive discoveries and improvements in the sciences and the arts* **11**, 179–180.

Lundelius, E.L. Jnr. (1989). The implications of disharmonious assemblages for Pleistocene extinctions. *Journal of Archaeological Science* **16**, 407–417.

Lyell, C. (1830–1833). 'Principles of Geology: being an attempt to explain the former changes of the earth's surface, by reference to causes now in operation'. (J. Murray: London) [for the Wellington Fossils see Vol III, Chapter XI, especially pp. 143–44].

MacLeod, R.M. (1965). Evolutionism and Richard Owen, 1830–1868: An episode in Darwin's Century. *Isis* **56**, 259–80.

Mahoney, J. and Ride, W.D.L. (1975). 'Index to the genera and species of fossil Mammalia described from Australia and New Guinea between 1838 and 1968'. Western Australian Museum Special Publication No 6, 1–250.

Main, A.R. (1978). Ecophysiology: Towards an understanding of Late Pleistocene marsupial extinction. In 'Biology and Quaternary environments', pp. 169–183. (Australian Academy of Science: Canberra).

Mansergh, I. and Scotts, D. (1990). Aspects of the life-history and breeding biology of the Mountain Pygmy-possum, *Burramys parvus,* (Marsupialia: Burramyidae) in alpine Victoria. *Australian Mammalogy* **13**, 179–191.

Mansergh, I., Scotts, D., Brady, T., Baxter, B. and Jolley, D. (1990). Diet of the Mountain Pygmy-possum *Burramys parvus*, (Marsupialia: Burramyidae) and other small mammals at Mt Higginbotham, Victoria. *Australian Mammalogy* **13**, 167–177.

Marshall, L.G. (1973). Fossil vertebrate faunas from the Lake Victoria Region of southwestern New South Wales. *Memoirs of the National Museum of Victoria* **34**, 151–71.

Marshall, L.G. and Corrucini, R.S. (1978). Variability, evolutionary rates and allometry in dwarfing lineages. *Palaeobiology* **4**, 101–19.

Marcus, L.F. (1976). The Bingara fauna. A Pleistocene vertebrate fauna from Murchison County, New South Wales, Australia. *University of California Publications in Geological Sciences* **114**, 1–145.

McEwen Mason, J.R.C. (1991). The late Cainozoic magnetostratigraphy and preliminary palynology of Lake George, New South Wales. In 'The Cainozoic of the Australian region: a reassessment of the evidence' (Eds. M.A.J. Williams, P. DeDeckker and A.P. Kershaw) pp. 195–209. (Geological Society of Australia Special Publication No.18).

Megirian, D. (1992). Interpretation of the Miocene Carl Creek Limestone, northwestern Queensland. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* **9**, 219–48.

Meltzer, D.J. and Mead, J.I. (1985). Dating Late Pleistocene extinctions: theoretical issues, analytical bias, and subjective results. In 'Environments and Extinctions: Man in Late Glacial North America' (Eds. J.I Mead and D.J. Meltzer) pp: 145–173. (University of Maine, Center for the Study of Early Man: Orono).

Mitchell, T.L. (1831a). Additional information illustrative of the natural history of the Australian bone-caves and osseous breccia. In Anon. [communicated by Lang], *Edinburgh New Philosophical Journal, exhibiting a view of the progressive discoveries and improvements in the sciences and the arts* **10**, 368–371. [the authorship by Mitchell is stated in Anon. [Jameson] 1831b].

Mitchell, T.L. (1831b). An account of the limestone caves at Wellington Valley, and of the situation, near one of them, where fossil bones have been found. [Abridged] *Proceedings of the Geological Society of London* **1**(21), 321–2.

Mitchell, T.L. (1838). 'Three expeditions into the interior of eastern Australia, with descriptions of the recently explored region of Australia Felix and of the present colony of New South Wales'. 2 volumes. (T. and W. Boone: London) (page nos quoted from the 2nd, 1839 edn).

Morris, D. (1992). 'Analysis of a late Quaternary small mammal fauna from Nettle Cave, Jenolan Caves, NSW'. Unpublished BSc (Hons) thesis, School of Biological Sciences, University of New South Wales.

Morris, D., Augee, M.L., Gillieson, D. and Head, J. (1996). Analysis of a Late Quaternary Small Mammal Fauna from Nettle Cave, Jenolan, New South Wales. *Proceedings Linnean Society of New South Wales*, this volume.

New South Wales (1870). 'New South Wales Parliamentary Paper, Wellington Caves' [see entry under Owen, 1870, in Mahoney and Ride, 1975, 230]

Osborne, R.A.L. (1983). Cainozoic stratigraphy at Wellington Caves, New South Wales. *Proceedings of the Linnean Society of New South Wales* **107**, 131–147.

Osborne, R.A.L. (1986). Cave and landscape chronology at Timor Caves, New South Wales. Journal and Proceedings, *Royal Society of New South Wales* **119**, 55–75.

Osborne, R.A.L. (1992). Australian red earth and bones. *Journal and Proceedings, Royal Society of New South Wales* **125**, 111.

Osborne, R.A.L. (1993). A new history of cave development at Bungonia, New South Wales. *Australian Geographer* **24**, 62–74.

Osborne, R.A.L. and Branagan, D.F. (1988). Karst landscapes in New South Wales. *Earth Science Reviews* **25**, 467–480.

Owen, R. (1845). Report on the extinct mammals of Australia, with descriptions of certain fossils indicative of the former existence of the former existence in that continent of large marsupial representatives of the Order Pachydermata. *14th Report of the British Association for the Advancement of Science*, 223–240. [Also see Mahoney and Ride 1975, 225 for what seems to have been a change in the title of this paper.]

Owen, R. [in Anon.] (1858). Professor Owen's lecture on Monday evening. The extinct quadrupeds of Australia. *The Leeds Mercury*, no. 6854, September 30th, 1858, vol. 95, p. 4, cols 2,3 [republished in Mahoney and Ride (1975)].

Owen, R. (1877). 'Researches on the fossil remains of the extinct mammals of Australia; with a notice of the extinct marsupials of England'. Vol 1 (text), vol 2 (plates). (J. Erxleben: London).

Owen, R.[Jnr]. (1894). 'The life of Richard Owen by his grandson the Rev. Richard Owen, M.A. with the scientific portions revised by C. Davies Sherborn also an essay on Owen's position in anatomical science by the Right Hon. T.H. Huxley, F.R.S.'. 2 vols. (John Murray: London).

Packham, G.H. (ed) with numerous contributors, (1969). The Geology of New South Wales, *Journal of the Geological Society of Australia* **16**, 1–654.

Pentland, W. (1831). Further notices in regard to the fossil bones found in Wellington Country, New South Wales. In Anon. [Jameson, R.]. *Edinburgh New Philosophical Journal, exhibiting a view of the progressive discoveries and improvements in the sciences and the arts* **11**, 180.

Pentland, W. (1832). On the fossil bones of Wellington Valley, New Holland, or New South Wales. *Edinburgh New Philosophical Journal, exhibiting a view of the progressive discoveries and improvements in the sciences and the arts* **12**, 301–8.

Pentland, W. (1833). Observations on a collection of fossil bones sent to Baron Cuvier from New Holland. *Edinburgh New Philosophical Journal, exhibiting a view of the progressive discoveries and improvements in the sciences and the arts* **14**, 120–1.

Pratt, G.W., Lewis, P.C., Taylor, G., Brown, M.C., Roach, I.C. and McQueen, K.G. (1993). The Monaro volcanics of the Cooma District. *Geolological Survey NSW Quarterly Notes* **92**, 1–10.

Ranken, C.G. (1916). 'The Rankens of Bathurst. Compiled by Mrs W.B. Ranken'. (S.D. Townsend: Sydney).

Rich, P.V. (1985). *Genyornis newtoni* A Mihirung In 'Kadimakara Extinct Vertebrates of Australia' (Eds. P.V. Rich, G.V. Van Tets and F. Knight) pp. 188–194. (Pioneer Design Studio: Lilydale Victoria).

Ride, W.D.L., Taylor, G., Walker, P.H. and Davis, A.C. (1989). Zoological history of the Australian Alps — The mammal fossil-bearing deposits of the Monaro. In 'The Scientific Significance of the Australian Alps' (Ed. R. Good) pp: 79–110. (Australian Alps Liaison Committee: Canberra).

Ride, W.D.L., Pridmore, P.A., Barwick, R.E., Wells, R.T. and Heady, R.D (1997). Towards a Biology of *Propleopus oscillans* (Marsupialia: Propleopinae, Hipsiprymnodontidae). *Proceedings Linnean Society of New South Wales*, this volume.

Rudwick, M.J.S. (1972). 'The meaning of fossils. Episodes in the history of palaeontology'. (Macdonald: London).

Rupke, N.A. (1994). 'Richard Owen Victorian Naturalist'. (Yale University Press: New Haven and London).

Sanson, G.D., Riley, S.J. and Williams, M.A.J. (1980). A late Quaternary *Procoptodon* fossil from Lake George, New South Wales. *Search* **11**, 39–40.

Singh, G. and Geissler, E.A. (1985). Late Cainozoic history of fire, lake levels and climate at Lake George, New South Wales, Australia. *Philosophical Transactions of the Royal Society of London* **311**, 379–447.

Strahan, R. (1979). 'Rare and Curious Specimens An Illustrated History of the Australian Museum 1827–1979'. (Australian Museum: Sydney).

Truswell, E.M. (1993). Vegetation changes in the Australian Tertiary in response to climate and phytogeographic forcing factors. *Australian Systematic Botany* **6**, 533–57.

Vallence T.G., Wilkinson, J.F.G., Abbott, M.J., Saulks, I.G., Stewart, J.R., and Bean, J.M. (1969). Mesozoic and Cainozoic igneous rocks. In 'The Geology of New South Wales ' (Ed. G.H. Packham) Chapter 9, pp 513–541. *Journal of the Geological Society of Australia* **16**, 1–654.

Van Huet, A.M.S. (1994). 'Taphonomy of a late Quaternary site: Lancefield Swamp, Victoria'. MSc Thesis, Monash University: Clayton, Victoria.

Veevers, J.J., Powell, C.McA. and Roots, S.R. (1991). Review of seafloor spreading around Australia. I. Synthesis of the patterns of spreading. *Australian Journal of Earth Sciences* **38**, 373–389.

Voisey, A.H. (1969). The New England region; Introduction to Chapter 4, pp 227–29 in Packham, G.H. (ed) The Geology of New South Wales, *Journal of the Geological Society of Australia* **16**, 1–654.

Wakefield, N.A. (1964). Recent mammalian sub-fossils of the basalt plains of Victoria. *Proceedings of the Royal Society of Victoria* **77**, 419–25

Wakefield, N.A. (1967a). Mammal bones in the Buchan District. *Victorian Naturalist.* **84**, 211–14.

Wakefield, N.A. (1967b). Preliminary report on McEachern's Cave S.W. Victoria. *Victorian Naturalist* **84**, 363–83.

Wasson, R.J. (1986). Geomorphology and Quaternary History of the Australian Continental Dunefields. *Geographical Review of Japan* **59**, 55–67.

Webb, J.A., Fabel, D., Finlayson, B.L., Ellaway, M., Li Shu and Spiertz, H.-P. (1992). Denudation chronology from cave and river terrace levels: the case of Buchan Karst, southeastern Australia. *Geological Magazine* **129**, 307–317.

Wells, R.T., Horton, D.R. and Rogers, P. (1982). *Thylacoleo carnifex* Owen (Thylacoleonidae): Marsupial carnivore? In 'Carnivorous Marsupials' (Ed. M. Archer) pp. 573–86. (Royal Zoological Society of New South Wales: Sydney).

White, J.P. and Flannery, T. (1995). Late Pleistocene fauna at Spring Creek, Victoria: A re-evaluation. *Australian Archaeology*, no. **40**, 13–17.

Whittell, H.M. (1954). Entries: Jameson, Robert (Prof.) and Lindesay, Patrick (Lieut.-Colonel). 'The literature of Australian Birds: A history and a bibliography of Australian ornithology', pp. 374–5, 446 [also see p. 87].

Wilkinson, J.F.G. (1969). Intrusive rocks. Pp 540–41 in Packham, G.H. (ed) with numerous contributors, 1969. The Geology of New South Wales, *Journal of the Geological Society of Australia* **16**, 1–654.

Woodburne, M.O., Tedford, R.H., Archer, M., Turnbull, W.D., Plane, M.D., and Lundelius, E.L. (1985). Biochronology of the continental mammal record of Australia and New Guinea. *Special Publications, South Australian Department Mines and Energy*, no. 5, 347–63.

Wright, R. (1986). How old is Zone F at Lake George? *Archaeology in Oceania* **21**, 138–39.

# A Review of the Plio-Pleistocene Crocodilian Genus *Pallimnarchus*

PAUL. M.A. WILLIS[1] AND RALPH E. MOLNAR[2]

[1]Quinkana Pty Ltd, 3 Wanda Cres., Berowra Hts., N.S.W. 2082, and
[2]Queensland Museum, PO Box 3300, South Brisbane, Qld, 4101

Willis, P.M.A. and Molnar, R.E. (1997). A Review of the Plio-Pleistocene crocodilian genus Pallimnarchus. *Proceedings of the Linnean Society of New South Wales* **117**: 224-242

The Plio-Pleistocene crocodilian genus *Pallimnarchus* is revised and new material is included in this revision including some material previously assigned to *Crocodylus porosus*. Species of *Pallimnarchus* inhabited most of northern Australia, extending as far south as northern New South Wales and South Australia, and as far west as Windjana Gorge in northern Western Australia. A new species of *Pallimnarchus* is recognised from Plio-Pleistocene deposits of northern Queensland.

Manuscript received 2 April 1996, accepted for publication 18 September 1996

KEYWORDS: Crocodilian, Mekosuchine, Pliocene, Pleistocene, *Pallimnarchus*

## INTRODUCTION

The genus and species *Pallimnarchus pollens* has a chequered history. The name was first coined by De Vis (1886) as a cabinet name for particularly large and robust crocodilian fossils from the Darling Downs. The name gained acceptance through popular and scientific literature (eg. Longman 1925a, 1925b; Anderson 1937). It was not until Molnar (1982) revised the genus that types were nominated and the species and genus formally diagnosed and described.

*Pallimnarchus* was first suggested to be part of the Australian Tertiary radiation of crocodiles by Willis et al. (1990) and subsequent analyses (Willis 1993, 1995; Megirian et al. 1991) confirmed this. *Pallimnarchus* was formally included in the Mekosuchinae when that taxon was established by Willis et al. (1993).

## SYSTEMATICS

Order Crocodilia Gmelin, 1700
Suborder Eusuchia Huxley, 1875
Family Crocodylidae Cuvier, 1807
Subfamily Mekosuchinae Balouet and Buffetaut 1987

### *Pallimnarchus* (De Vis 1886)

The new species, *P. gracilis*, is similar to *P. pollens* and should be included in the genus *Pallimnarchus*. Because only a single species was assigned to *Pallimnarchus*, separate generic and specific diagnoses were not given. Molnar's (1982) specific (and generic) diagnosis for *P. pollens* is; "Symphyseal portion of mandibles broader than in any living species of *Crocodylus*; angle between ramus of mandible and plane of symphyseal surface greater than in either *C. porosus* or *C. johnstoni*." (Molnar 1982:659). Of these features, the first cannot be assessed on any of the type material of *P. gracilis* and, with the inclusion of *P. gracilis*, the second is now recognised as of dubious value as a diagnostic feature of *Pallimnarchus* (see below).

## Generic Diagnosis

Mekosuchines with a short, broad symphyseal region; symphyseal portion of mandibles broader than in any other Mekosuchine; low alveolar process on the dentary; low but very broad snout; small supratemporal fenestrae; quadratojugal-quadrate contact in ventral view extends anterolaterally from lateral quadrate condyle; distance from medial quadrate condyle to exoccipital buttress exceeds width of quadrate condyles. These latter two characters cannot be seen on any material referred to *P. gracilis* and thus may be specific characters of *P. pollens*.

## Discussion

Of the two characters given by Molnar (1982) for the generic (and specific) diagnosis of *P. pollens*, the first cannot be seen in any material of the new species described here and the second becomes of dubious diagnostic value. The second character is: "angle between ramus of mandible and plane of symphyseal surface greater than in either *C. porosus* or *C. johnstoni*." Molnar measured this angle for 2 specimens of *Pallimnarchus* and 18 specimens of *Crocodylus porosus*. From this data the average measurement of this angle in *P. pollens* is 24.5 degrees (n = 2, s.d. = 2.1 degrees) while for *C. porosus* the average measurement is 17.3 degrees (n = 18, s.d. = 2.4 degrees). This measurement on QM F17069 (*P. gracilis*) is 20.5 degrees. While it would be imprudent to attempt statistical comparisons from such a small data set, it is apparent that QM F17069 could well fall within two standard deviations of the average measurements of both *P. pollens* and *C. porosus*. Such a continuous set of measurements makes this feature ambiguous as a generic diagnostic feature. This judgement should be reviewed when a larger data set becomes available. However, until then we regard this part of Molnar's original diagnosis as a specific diagnostic feature for *P. pollens*.

Molnar (1982) referred the large crocodilian snout from Lansdowne Station (QM 1752) to *C. porosus* for the following four reasons. (1). The breadth was not outside the range of variation of *C. porosus* contrary to Longman's (1924) belief. (2). The posterior part of the narial margin was inclined as in *C. porosus* rather than transversely directed. (3). Although the region was crushed and lachrymal ridges were not apparent, the sulci thought to have bounded them were seen. (4). The form of the snout did not match that of a mandible (QM F2025) of *P. pollens*. A reassessment of the snout by the authors revealed that it has two characteristics of the mekosuchine radiation: it lacks the anterior palatine process and shows a marked disparity in the sizes of the alveoli.

With this in mind Molnar's original features were re-examined and the first was obviously inconclusive (both *C. porosus* and *Pallimnarchus* have broad snouts). The second feature was also shown to be inconclusive by comparison of the premaxillae of the Geoff Vincent specimen (a collection of skull fragments from a single, large individual, collected by Mr Geoff Vincent and currently housed in the Queensland Museum), QM F11626, QM F1151 and QM F1154. These all matched in three features, robustness, size of alveoli (and sequences of size differences) and disparity in alveolar size, and so all are referred to *Pallimnarchus*. Two of them however had inclined posterior narial margins (Geoff Vincent's and QM F11626) and the other two had transversly directed margins. The third feature, the sulci, do seem to be present but are here considered — unlike the lachrymal ridges — to be of no taxonomic value (and lachrymal ridges are clearly absent in the Lansdowne snout regardless of the crushing). Finally the discrepancy with the mandible of *P. pollens* is to be expected because the Lansdowne snout derived not from that species but from *P. gracilis*.

In 1982 Molnar referred Longman's (1924) *Crocodylus nathani* to *C. porosus* in view of the apparent absence of distinguishing characteristics. This is now considered incorrect (in part; QM F11609 is still referred to *Crocodylus*) because QM F1512 and QM F1513 both show two diagnostic features of *P. gracilis* (a step in the posterior margin of the symphysis and a fossa behind the ventral part of the symphysis). Both specimens are now referred to *P. gracilis*.

We do not accept that *C. nathani* is the senior synonym of *P. gracilis* for four reasons. (1) *C. nathani* was established on a collection of specimens representing at least two taxa with no clear designation of a holotype specimen. (2) Molnar (1982) did designate QM F1513, a dentary fragment, as a lectotype but proceeded to place *C. nathani* into junior subjective synonomy with *C. porosus*. The holotype of *P. gracilis* is a premaxilla with an associated dentary fragment. This material allows the unambiguous definition of the new taxon and comments on the association of cranial and dentary characters. Reversion to *P. nathani* would entail the renomination of a lectotype specimen that is of limited taxonomic value. (3) Characters used in the definition of *P. gracilis* are completely different from those originally used in the definition of *C. nathani*. (4) Because of the fragmentary nature of both QM F1513 and the holotype material of *P. gracilis*, there is minimal overlap of bones represented with no shared diagnostic features. Thus there could be true synonomy between *C. nathani* and *P. gracilis* but we cannot be certain. We therefore maintain that *C. nathani* does not constitute an appropriate senior synonym of *P. gracilis* and that recognition of the new taxon avoids taxonomic confusion that could arise from redesignating uninformative lectotype specimens.

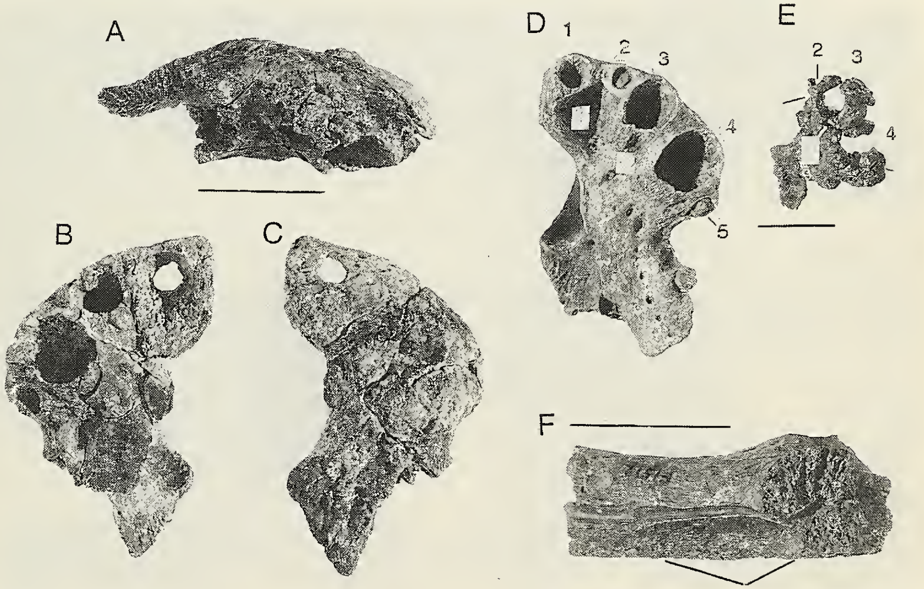


Figure 1. A-C. Right premaxilla of *Pallimnarchus gracilis*, sp. nov. (QM F17065, holotype), from Terrace Site, Riversleigh, Qld. (A) lateral view, (B) ventral (palatal) view, (C) dorsal view. Scale bar 50 mm. (D-E) comparison of Windjana crocodilian premaxilla (E, CPC 17122) with that of *Pallimnarchus pollens* (D, QM F11626), to identify the alveoli and accommodation pits for dentary teeth in the Windjana premaxilla. Numerals along the margins designate the alveoli, all 1–5 in QM F11626, but only 2–5 (2 and 5 have only the medial walls preserved) in CPC 17122. Italic numerals designate accommodation pits for the 1st and 2nd dentary teeth in both specimens. The patterns of both alveoli and accommodation pits are the same in both specimens, indicating that CPC 17122 is referable to *Pallimnarchus*. Scale Bar 50 mm. (F) anterior dentary piece of *Crocodylus nathani* (QM F1512) showing two diagnostic features of P. gracilis, the medial fossa located ventral to the Meckelian groove (indicated on figure with lines) and the 'stepped' posterior margin of the symphysis. Scale bar 50mm.

### *Pallimnarchus gracilis* sp. nov. (Fig 1)

#### Diagnosis

*Pallimnarchus gracilis* has a broadly ovate first dentary alveolus, the width of which is approximately equal to the depth of the symphysis; symphysis extending backward to the fourth or fifth dentary alveolus; the posterior margin of the symphysis with a distinctly stepped profile such that the portion dorsal to the Meckelian canal extends posterior to that ventral to the Meckelian canal by about twenty percent of the length of the symphysis; regular spacing of the fifth to seventh alveoli; a shallow concavity on the medial surface of the dentary ventral to the Meckelian canal and immediately posterior to the symphysis; a splenial contact on the dentary that is poorly marked and difficult to delineate; a flattened premaxilla with the anterior part of the dorsal surface at a low angle to the palate; larger supratemporal fenestrae than *P. pollens*; supratemporal fenestrae separated from the base of the postorbital bar by a wide shelf.

#### Differential diagnosis

Differential diagnosis for *P. pollens* and *P. gracilis*: *Pallimnarchus pollens* is more robust than *P. gracilis*. *Pallimnarchus pollens* has a subcircular first dentary alveolus; the width of this alveolus is less than half the depth of the symphysis; symphysis extends posteriorly to the fifth or sixth dentary alveolus; the posterior margin of the symphysis lacks a distinctly stepped profile; bunching of the fifth to seventh alveoli; no concavity on the medial surface of the dentary ventral to the Meckelian canal and immediately posterior to the symphysis; a splenial contact that is well marked and incised into the dentary; a bulbous premaxilla with the anterior dorsal surface set at a high angle to the palate; smaller supratemporal fenestrae than *P. gracilis*; supratemporal fenestrae separated from the base of the postorbital bar by a wide shelf. Figure 3 clearly shows the separation of *P. pollens* and *P. gracilis* by the depth relative to the width of the premaxilla. This difference in snout depth is also shown by a comparison of QM F17065 (*P. gracilis*) with QM F11626 (*P. pollens*) (Fig. 5).

#### Etymology

The specific name is derived from the Latin *gracilis* and refers to the less robust nature of this animal.

#### Material

Holotype

QM F17065, right premaxilla , Terrace Site, Riversleigh, Qld (Fig. 1 A-C).

Paratypes

QM F17066, left dentary fragment. Terrace Site, Riversleigh; QM F17069, left dentary, Leichhardt River; QM F1752, snout, Lansdowne Station; QM F1512, left dentary. Tara Creek; QM F1513, left dentary, Tara Creek; Mirani Museum 89-1072, Mirani shire skull.

#### Discussion

The association of the distinctive premaxilla, QM F17065, with the even more distinctive dentary, QM F17066, indicates that both probably derived from the same taxon and quite probably the same individual. This is important because it is the only association of cranial with mandibular material among the *P. gracilis* specimens, and so allows identification of both cranial and mandibular material.

Material designated as belonging to *P. gracilis* has previously been assigned to three other species. The Lansdowne snout (QM F1752, Fig. 6) was originally assigned to *P. pollens* by Longman (1925a). Molnar (1982) disagreed with Longman's designation and ascribed this specimen to *Crocodylus porosus*. QM F1512 and QM F1513 both formed part of the type material of *C. nathani* (Longman 1924). Molnar (1982) recognised this taxon as a junior synonym of *C. porosus* and explained how Longman had confused specimens of both *C. porosus* and *P. pollens* in his taxon. Molnar identified QM F1512 and QM F1513 as *C. porosus*.

## Localities, sediments and associated faunas

Terrace Site, Riversleigh, Qld (Fig 2)

The "Terrace Site" is a perched and dissected river terrace deposit 5 km downstream from the crossing of the Gregory River and the Lawn Hill road, along the west bank of the Gregory River, Riversleigh Station, northwestern Queensland. The unnamed sediments at this site are freshwater fluviatile deposits containing mostly unconsolidated sands, clays and conglomerates but which are locally indurated with a light carbonate cement.

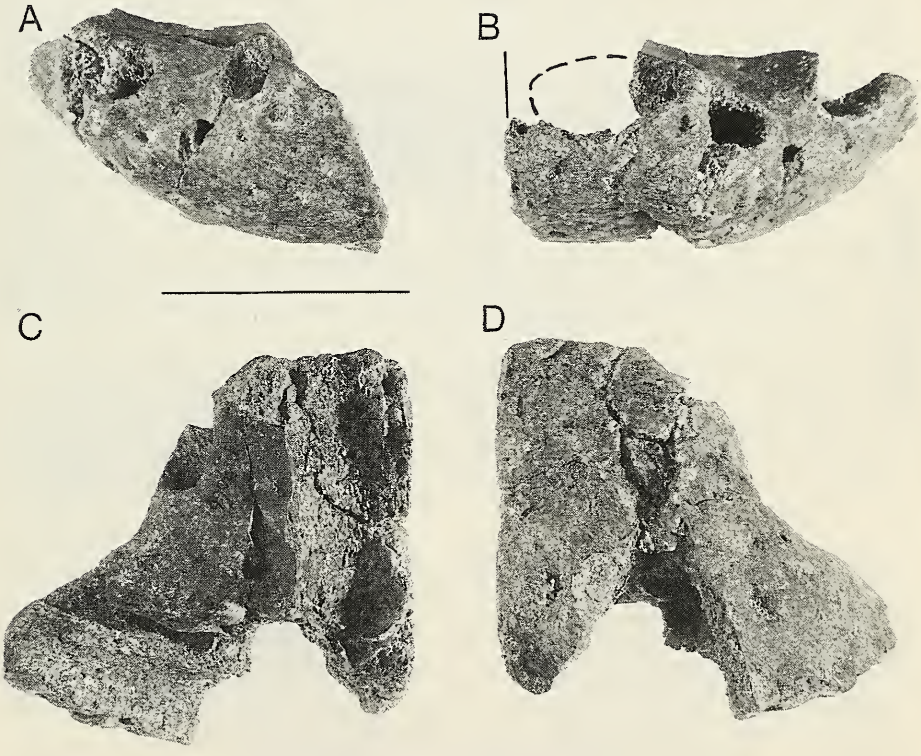


Figure 2. Anterior fragment of the left dentary referred to *Pallimnarchus gracilis*, sp. nov. (QM F17066), from Terrace Site, Riversleigh, Qld. (A) lateral view, (B) anterior view, (C) dorsal view, (D) ventral view. Scale bar 50 mm. Bar in B represents the midline and the presumed form of the 1st alveolus is dotted in to make the elongate form of the first alveolus more clear. This form can also be seen in C.

Two species of crocodile are known from fossils recovered from Terrace Site: *Crocodylus johnstoni* (Willis and Archer 1990) and the new species *P. gracilis*. The Terrace Site material is referred to the Terrace Site Local Fauna (Archer et al. 1989) that also includes freshwater molluscs, *Emydura lavarackorum* (White and Archer 1994), a varanid, *Palorchestes* sp. cf. *P. azael* (Davis in press), *Diprotodon optatum*, unidentified macropodids, and an unidentified rodent.

### Leichhardt River, Qld (Fig 4)

A relatively complete left dentary, QM F17069, comes from "Ernie's Croc Jaw Site", part of a dissected flood plain of the Leichhardt River. It is located on Floraville Downs Station, 13 km south of the homestead and 500m west of the river. The unnamed fluviatile sediment is mostly sands and conglomerates with calcrete and ferrocrete concretions.

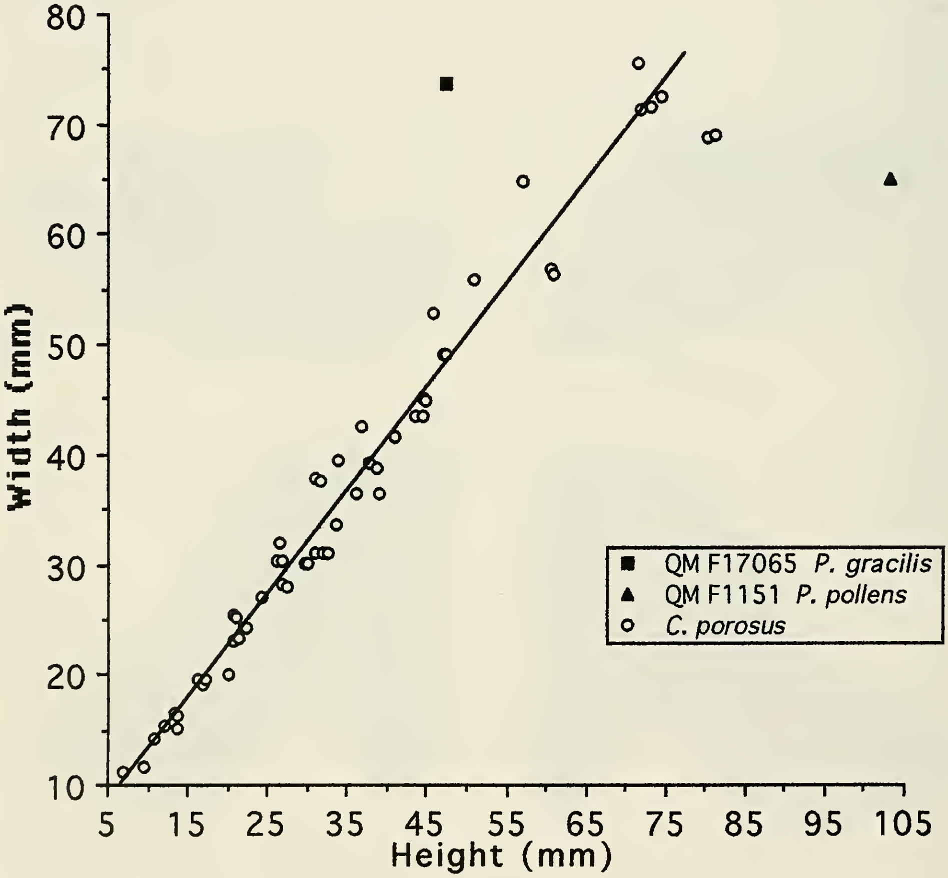


Figure 3. Comparison of the snout depths at the snout notch; *P. gracilis*, *P. pollens* and *C. porosus*.

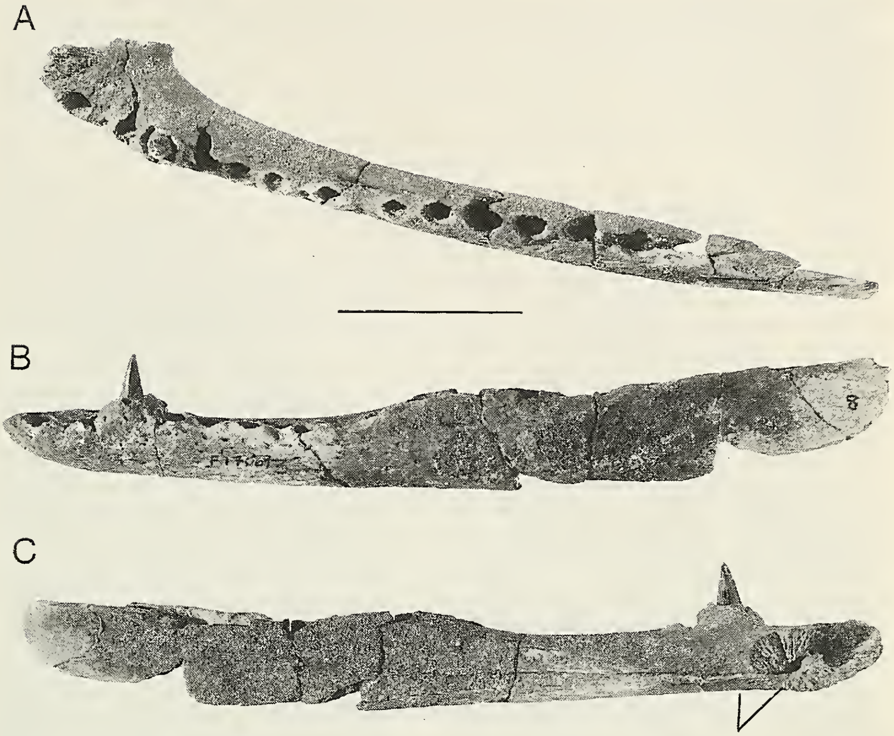


Figure 4. Juvenile left dentary referred to *Pallimnarchus gracilis*, sp. nov. (QM F17069) from the Leichhardt river. (A) dorsal view, (B) lateral view, (C) medial view. Scale bar 50 mm. The characteristic fossa below the Meckelian groove is indicated on C and the 'step' in the posterior margin of the symphysis may also be seen.

Molnar (1982) refers some specimens from the Leichhardt River, northwestern Queensland, to *P. pollens*. Other unidentified crocodilian material was collected in 1987 and a dentary of *C. johnstoni* has also been collected from the Leichhardt River (Willis and Archer 1990). All the crocodilian material is referred to the Floraville Local Fauna along with crustaceans, varanids, snakes, turtles and mammals.

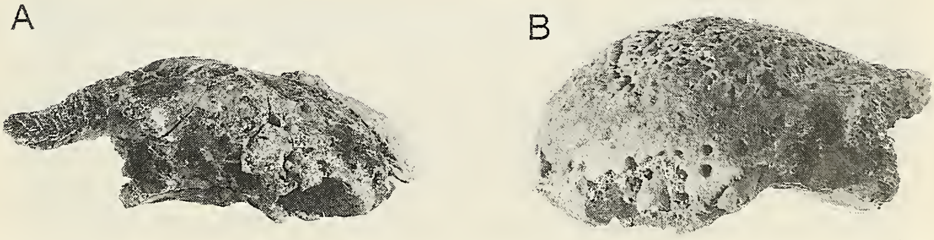


Figure 5. Premaxillae of (A) *Pallimnarchus gracilis*, sp. nov. (QM F17065, holotype) and (B) *P. pollens* (QM F11626) in lateral view to show the lower, more flattened form in *P. gracilis* and the higher more robust form in *P. pollens*. Anterior to the right in A, but to the left in B.

Lansdowne, Qld (Fig 6)

The Lansdowne snout (QM F1752) was collected from Lansdowne Station near Tambo, south central Queensland (Longman 1925b, Molnar 1982a). It was found during excavation for a dam from clays overlying a soft sandstone (Longman 1925a) but more precise geological information is not available. Fossils of *Palorchestes azael* and *Protemnodon anak* were also collected during the excavations (Longman 1925b).

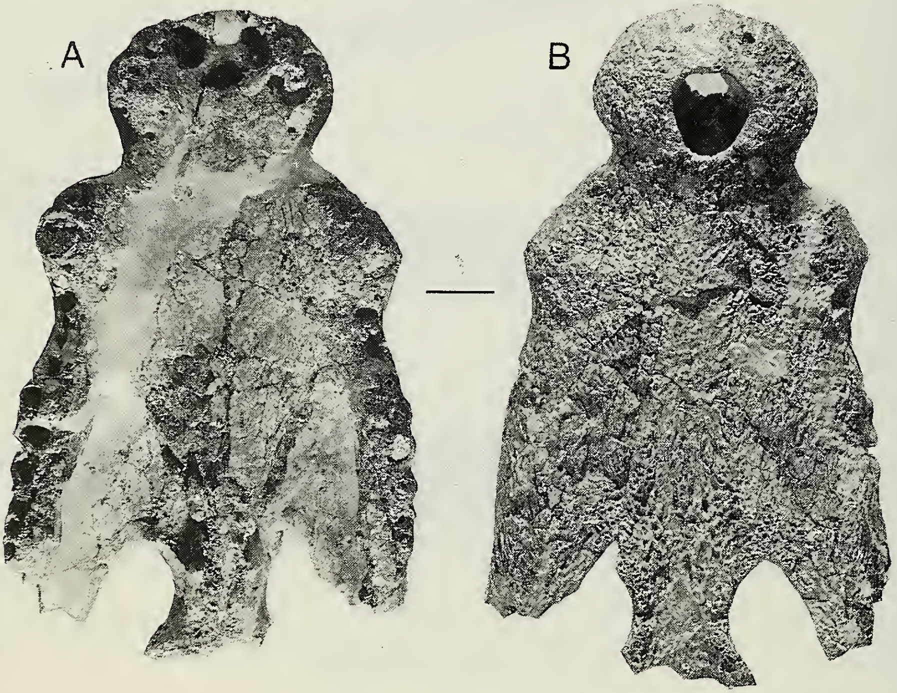


Figure 6. The Lansdowne snout (QM F1752), here referred to *Pallimnarchus gracilis*, sp. nov., in ventral (palatal) (A) and dorsal (B) views. Scale bar 50 mm.

Tara Creek, Qld

Material collected from Tara Creek, inland of Townsville, north Queensland, was recorded only as having come from sediments under the Nulla Basalt. The only comment Longman made regarding the geology here was that these were probably alluvial deposits, based on the grit adhering to the specimens.

Longman (1924) reported turtle and crocodilian fossils from Tara Creek. He referred the turtle material to *Chelodina insculpta* and erected a new taxon, *Crocodylus nathani,* for the crocodilian material. Some unidentified diprotodontids have also been reported from Tara Creek (Rich et al. 1983).

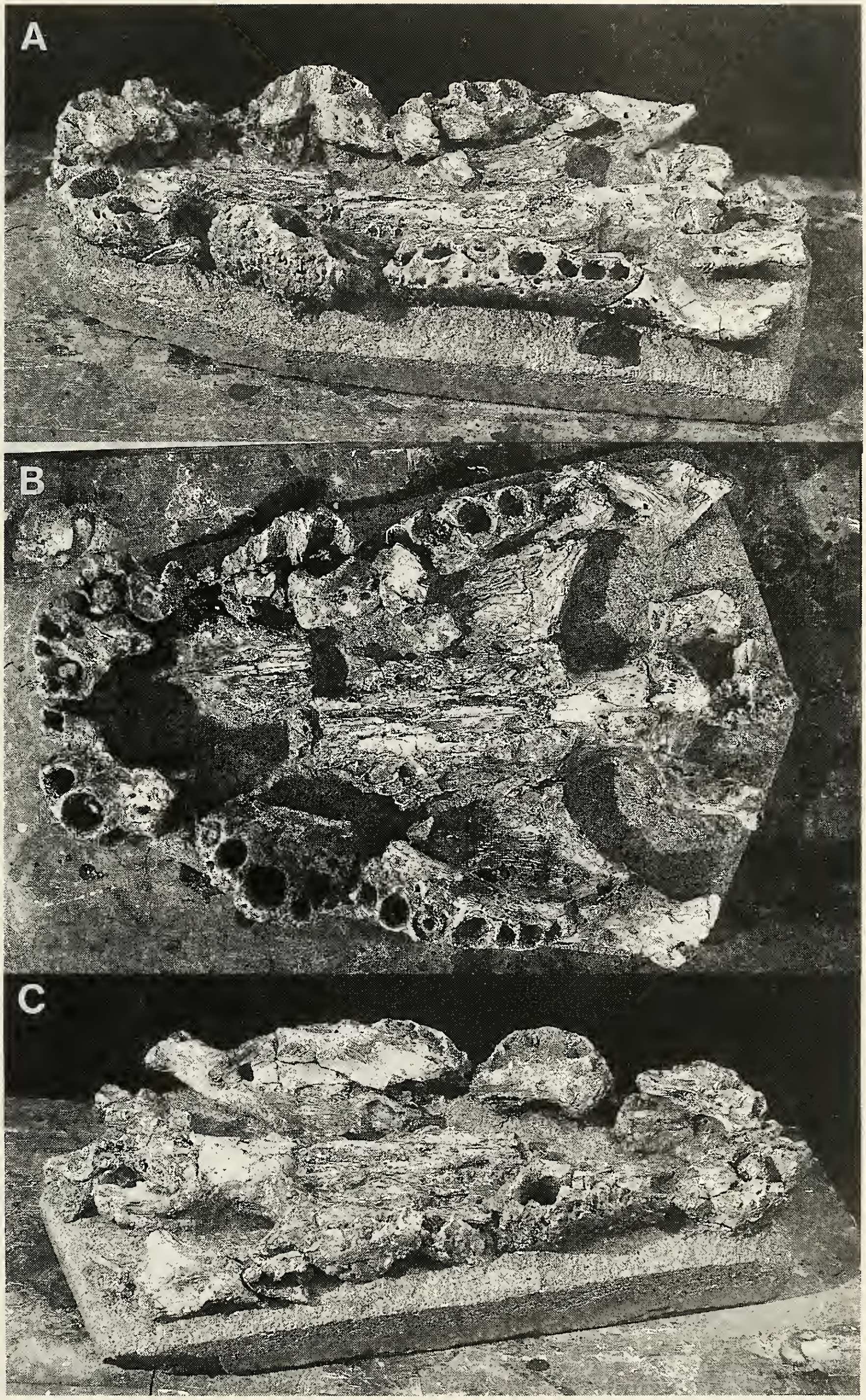


Figure 7. The Mirani Museum skull of *Pallimnarchus gracilis*, sp. nov. (Mirani Museum 89-1072). (A) right lateroventral view (skull inverted), (B) ventral (palatal) view, (C) left lateroventral view (skull inverted).

Mirani Shire, Qld (Fig 7)

Mirani Museum 89-1072 is probably the most complete skull referred to this species, but was encased in concrete (to prevent damage) by its previous owner (Fig. 7). The specimen was purchased by the Mirani Shire Council for the Mirani Museum as part of the collection of Mr J. Williams. It derives from the Nebo district, near Mackay, and is believed to have been found near the top of Mt Robert. Mt Robert consists of Permian sandstones capped with a Tertiary basalt (Malone 1969). The basalt however appears to be a plug (J. Draper, pers. comm., 1996) of Oligocene age (Sutherland et al. 1978). Thus we believe it unlikely that the skull did come from Mt Robert. It may derive from the Sutton Formation, a late Tertiary fluvial deposit.

## Age

The oldest site from which material referred to *P. gracilis* has been collected is Tara Creek, dated at 4.0–4.5 Ma (Rich et al. 1983). The youngest site that has been reliably dated is the Terrace Site, Riversleigh. Carbon from this site has given a $C^{14}$ date of 23,900 years (+4,100, -2,700 years; Angela Davis pers. comm.). It seems, therefore, that *P. gracilis* has a Plio-Pleistocene distribution.

Terrace Site is interpreted as Pleistocene based on the presence of premolars and molars of *Diprotodon optatum,* a taxon that is restricted to Pleistocene deposits (Archer 1984). Charcoal and shell material suitable for radiocarbon dating was retrieved from the level containing the vertebrates and gave a $C^{14}$ date of 23,900 years (+4,100, -2,700 years; Angela Davis pers. comm.). However, there is some doubt as to the accuracy of this date and a more accurate one is expected from shell material obtained from the site (Davis pers. comm.). The Terrace Site deposit can be referred to as late Pleistocene pending further radiocarbon dates.

The age of the Floraville Local Fauna is ambiguous due to the lack of fossil taxa suitable for age correlation. This fauna is tentatively accepted as Plio-Pleistocene (Archer 1982, Archer and Hand 1984), and geological data suggests an early Pleistocene age for this locality (Grimes and Doutch 1978).

Material from Lansdowne Station is suggested to be Pleistocene due to the presence of *Palorchestes azael* and *Protemnodon anak* (Longman 1925b).

The Nulla Basalt has been dated at between 4.0 and 4.5 Ma (Wyatt and Webb 1970) and hence the Tara Creek fauna is regarded as Pliocene (Rich et al. 1983).

## Description

Because QM F1752 has previously been described (Molnar 1982), only new characters seen on this specimen will be described here. The Mirani Shire skull has been set in concrete with only its ventral surfaces visible. Thus this specimen is of limited descriptive value.

Premaxillae

QM F17065 (Fig. 5A) is an almost complete right premaxilla of a large, shallow-snouted, brevirostrine crocodile. The palatal portion, part of the internal wall of the narial canal, and a small piece near the dorsal side of the premaxilla-maxilla suture are missing. The specimen is extensively fractured and calcarenitic matrix adheres to some surfaces. The specimen shows some slight crushing.

The premaxilla has five alveoli. The first and second alveoli are small and of subequal size. The third alveolus is twice as large as the first two but the fourth alveolus is huge, about 1.5 times as large as the third. The fifth alveolus is intermediate in size between the third and second. All alveoli are more or less circular in cross section. The margins of the third, fourth and fifth alveoli are built up into collars that interconnect to form a low alveolar process.

The pit for the reception of the first dentary tooth is large and penetrates through to the dorsal surface of the premaxilla. This pit separates the first and second premaxillary teeth. Pits for the second and third dentary teeth are less distinct and do not occlude between the upper series by the massive fourth premaxillary alveolus. There is a constriction at the premaxilla-maxilla suture for the reception of the fourth dentary tooth. A distinct nutrient foramen occurs slightly lingual to the constriction for the fourth dentary tooth.

The external naris is tear-shaped and pointed posteriorly. The nasals participated in the external nares which reached posteriorly past the anterior termination of the maxilla.

The sculpture consists of indistinct pits, better defined toward the margins.

### Other Cranial Elements

The following cranial features are noted: all elements are heavily built, but not as heavily as in *P. pollens*; the supratemporal fenestrae (seen on the Mirani Shire skull only in ventral view) are small, but not as small as in *P. pollens*; there is a wide shelf of bone between the anterior margins of the supratemporal fenestrae and the base of the postorbital bar.

### Dentaries

QM F17066 (Fig. 2) is an anterior fragment of dentary representing the symphyseal region from the first to the fourth alveoli. Most of the dorsal surface is missing as is part of the medial portion of the symphyseal region. Its proportions are consistent with being part of the lower jaw of the same individual represented by QM F17065. QM F17069 (Fig. 4A-C) is the left dentary of a juvenile. It is generally complete except for a portion of the symphyseal region antero-medial to the first alveolus and much of the ventral surfaces posterior to the twelfth alveolus. QM F1512 and QM F1513 are left dentary fragments. QM F1512 (Fig. 1F) is complete from the third to the seventh alveolus and QM F1513 is complete from the third to the eighth alveolus.

The mandibular body is moderately developed and the dentary becomes more shallow in the symphyseal region. The symphyseal region is sub-triangular in dorsal aspect.

Fifteen alveoli are preserved on QM F17069 representing the complete complement of lower teeth. The first and fourth alveoli are huge but the second and third alveoli are much smaller and subequal in size. The first alveolus is compressed and presumably held a flattened, spade-like tooth. The sequence of tooth enlargement is typically mekosuchine and strongly pseudoheterodont. The alignment of dentary teeth shows a distinct angle about the fourth tooth. Anterior alveoli are nearly circular but they become progressively more ovate posterior to the eighth alveolus in a typically mekosuchine manner.

The fourth tooth is preserved in its alveolus on QM F17069 (Fig. 4), the only tooth preserved in situ in the specimens studied. This tooth has distinct anterior and posterior carinae and the lingual surface has prominent vertical ridges. Less prominent ridges adorn the labial surface. The tooth is slightly compressed to an ovate cross section.

Pits for the reception of maxillary teeth are poorly developed. They indicate that the posterior dentary teeth partially interlock on the lingual side of the upper series. There are no pits for the reception of premaxillary teeth.

The symphysis extends posteriorly to the mid-line of the fourth alveolus in QM F17069 and to between the fourth and fifth alveoli on both QM F1512 and QM F1513. The splenial contact is difficult to delineate on some specimens but reaches anteriorly to the sixth alveolus on QM F17069. The splenial contact can not be determined on either QM F1512 or QM F1513.

The symphysis in medial aspect is quite distinctive. The position of the symphysis ventral to the Meckelian canal ends more anteriorly than does the dorsal portion. Thus the dorsal portion extends more to the posterior than the ventral portion by about twenty percent of the total length of the symphysis. Immediately posterior to the symphysis and ventral to the Meckelian canal there is a shallow concavity on the medial surface of the dentary.

Sculpture consists of well spaced pits and grooves aligned antero-posteriorly.

### Comparisons

Except for the overall shallowness and the specific differences mentioned above, QM F17065, the premaxillae of QM F1752 and the Mirani Shire skull are similar to QM F1151, a premaxilla designated as *P. pollens* by Molnar (1982). Another difference between the premaxillae of *P. gracilis* and *P. pollens* is the shape of the external nares. Molnar stated that QM F1151 has a round external narial opening that does not taper posteriorly. The external narial opening of QM F17065 does taper posteriorly and thus apparently differs from *P. pollens*. However, inspection of the specimen Molnar described reveals that the external nares do taper posteriorly in the same manner as they do in QM F17065 but not to the extent seen in *C. porosus*. This difference in interpretation is a result of misinterpreting the correct orientation of the specimens. Slight rotation in the horizontal plane produces the apparent taper. Such rotation is justified if the vertical suture posterior to the nares is interpreted as contacting the tapering end of the nasals. Another problem in orientating QM F1151 is that it is incomplete both anteriorly and posteriorly. Regardless of the differing interpretations of the correct orientation of the premaxilla, it is apparent that the form of the external nares is similar in both specimens. Further, the shape of the external nares varies considerably within *P. pollens*, as discussed below.

### Pallimnarchus pollens

Molnar (1982) discussed the occurrence of *P. pollens* within Queensland. The following introduces material referable to this species from South Australia and new material from Queensland.

### Revised diagnosis

*Pallimnarchus pollens* is a species of *Pallimnarchus* that has: robust proportions; subcircular first dentary alveolus; width of that alveolus less than half the depth of the symphysis; symphysis extending to the fifth or sixth dentary alveolus; the posterior margin of the symphysis without a distinctly stepped profile; bunching of the fifth to the seventh alveoli; no concavity on the medial portion of the dentary ventral to the Meckelian canal and immediately posterior to the symphysis; splenial contact well marked and incised into the dentary; a bulbous premaxilla with the anterior dorsal surface inclined at a high angle to the palate; small supratemporal fenestrae; supratemporal fenestrae separated from the base of the postorbital bar by a wide shelf.

### Material

As given in Molnar (1982) plus the material given below.

South Australia

A number of specimens recovered from Pleistocene sediments in South Australia can be referred to *Pallimnarchus* cf. *P. pollens*.

1). Dentaries. Two dentary fragments in the collections of the South Australian Museum are identified as *Pallimnarchus* cf. *P. pollens* . SAM P17352 is the anterior portion of the left dentary of a large individual. This specimen is from Coopers Creek in South Australia and is thought to be Pleistocene. It is generally robust and of massive proportions. SAM P17353 is a dentary fragment of a smaller individual than that represented by SAM P17352. It is from the Warburton River in South Australia. Only four alveoli are present, the sixth through to the ninth. The bases of the seventh and ninth teeth are preserved within their alveoli. These alveoli are subequal in size.

The first eight alveoli are preserved in SAM P17352 but no teeth except for the bases of the first, fourth and seventh. The alveoli indicate that this crocodile was strongly pseudoheterodont with the first and fourth teeth greatly enlarged and subequal in size. There is a slightly developed alveolar process corresponding in development to tooth size. The mandibular symphysis reached anteriorly to the level of the fifth alveolus. The extent of the splenial contact cannot be determined.

2). Other material. The palaeontological collection of Flinders University, Adelaide, SA, includes an anterior snout and a posterior cranium with posterior mandibles both collected from the Tirari Formation, Warburton River. Both are crushed and distorted and their preservation obscures many details. However, both can be referred to *Pallimnarchus* cf. *P. pollens*. Both specimens are currently being studied by Dirk Megirian. Other specimens in the vertebrate palaeontological collections of Flinders University that may be referred to *Pallimnarchus* include: P 25086 and P25087, two large teeth from the Katipiri Formation of Coopers Creek; P 25212 a right dentary fragment, P 25213 and P 25214 are posterior maxillary fragments, P25215 a small skull fragment from the Tirari Formation at Waralamanko on Coopers Creek; P 25490 a posterior fragment of a left maxilla, P 25481 a fragment of skull deck including the right parietal and squamosal, and P 25482 an anterior fragment of skull deck including parts of the left postorbital, frontal and parietal, all from the Tirari Formation at Pompapillina on the Warburton River.

Swinton (ca 1924) identified crocodilian remains recovered by Gregory from Central Australia as *Crocodilus* or *Crocodilus porosus* (sic). This material can also be referred to *Pallimnarchus* cf. *P. pollens*.

A specimen of a crocodilian snout and anterior mandible in the collections of the Australian National University (ANU Geol 49071) also appears to be *P. pollens*. Its provenance is unknown but is believed to be from South Australia (Tim Munsum pers. comm.). Portions of the specimen are rebuilt in plaster and many details are obscured by crystal growth and poor preservation.

### The Geoff Vincent specimen

Fragments of the skull of a large specimen of *P. pollens* were recovered by Mr Geoff Vincent and are currently housed in the Queensland Museum. These fragments relate to the same individual. They were collected from a site not far from Chinchilla. The following is a brief description. It is unclear whether this specimen derived from the early to medial Pliocene Chinchilla Sands or the Pleistocene sediments of the Darling Downs. *Pallimnarchus pollens* has been recorded from both of these sediments (Molnar 1982).

Fragments recovered include both premaxillae, the anterior portions of both maxillae, anterior fragment of nasals, posterior portions of nasals, posterior fragment of left maxilla, small fragment of the posterior of the right maxilla, anterior fragment of the left jugal, anterior process of the frontals, left lacrimal, left quadrate, half of the skull deck (includes left frontal, left postorbital, left parietal and left squamosal) and a basicranial fragment (including the basioccipital, exoccipital, opisthotics and basisphenoid). There may be more of this specimen in the deposit that has not yet been recovered.

The supratemporal fenestrae are small and enclosed, elliptic and angled to the midline. The skull deck is basically flat or slightly concave with no raised margin around the supratemporal fenestrae. The margins of the orbits are slightly raised. The jugal fragment is larger and deep anteriorly. The jugal-postorbital bar contact does not have a distinct step.

The lateral sutured margin on the quadrates for the quadratojugal is very deep dorso-ventrally. The medial condyle of the mandibular articulation is half the width of the lateral. The squamosal contact of the quadrate forms a distinct plinth.

On the left maxilla the first and second alveoli are inside (medial to) the fourth dentary tooth reception pit.

Gregory River, Qld

Anderson (1937) described an anterior mandibular fragment of a large crocodilian from the Gregory River, north Queensland, as *Pallimnarchus pollens*. This specimen (AM F36947) is of uncertain provenance but the preservation suggests that it is not from the Terrace Site on the Gregory River at Riversleigh. Examination of the specimen confirms Anderson's original identification as *P. pollens*.

## Pallimnarchus sp.

The following material can be identified as *Pallimnarchus* but not to species. This material comes from Queensland, Western Australia and New South Wales.

### Bluff Downs, Qld

Queensland Museum specimens QM F 17067 and QM F11623 and a specimen collected by Brian Mackness (QM F23240), all from Bluff Downs, north Queensland, are different from both *Pallimnarchus pollens* and *P. gracilis*. However, insufficient material is available to quantify these differences and erect a new species. Until such material is available, the *Pallimnarchus* material from Bluff Downs is referred to *Pallimnarchus* sp.

A mature dentary from Bluff Downs (QM F11623) has a symphysis extending to the posterior margin of the fourth tooth. A more juvenile dentary from this locality (QM F17068) has a symphysis that extends to between the fourth and fifth teeth. Mackness's specimen (QM F23240) has the symphysis extending to the fifth alveolus. In *P. gracilis* the symphysis extends to the fourth or fifth alveolus and in *P. pollens* it extends to the fifth or sixth alveolus. In general proportions the Bluff Downs *Pallimnarchus* is similar to *P. pollens* and is not as lightly built as *P. gracilis*. However, the Bluff downs *Pallimnarchus* differs from *P. pollens* in details of the symphysis and alveolar grouping (see the next section for more details).

Description

The following description is based on the Mackness specimen (QM F23240). This specimen is a fragmentary right dentary. It lacks the extent anterior to the second alveolus and posterior to the tenth alveolus. It is a robust, heavily built dentary similar to that of *P. pollens*. However, it has a slightly stepped symphysis (not as strongly stepped as *P. gracilis*), a splenial contact that is distinct but not incised into the dentary and a shallow concavity on the ventral part of the medial surface immediately posterior to the symphysis. The symphysis is relatively deep, it extends posteriorly to the fifth alveolus and there is no bunching of the fifth, sixth and seventh alveoli. In the expression of these characters, the Mackness specimen (QM F23240) could be seen as being a structural intermediate between *P. gracilis* and *P. pollens*.

### Windjana Gorge, WA

Gorter and Nicoll (1977) described crocodilian and turtle material from Windjana Gorge, north Western Australia. Among the crocodilian material was CPC 17122 (Commonwealth Palaeontological Collections, BMR, Canberra), an incomplete left premaxilla (Fig. 1E). Gorter and Nicoll (1977) also described some scutes (CPC 17113 and CPC 17114) and fragmentary crocodilian bones. However, when comparing the Windjana Gorge crocodilian to other crocodilians, they appear to have confused dentary tooth reception pits with alveoli in the comparative specimens of *Pallimnarchus*. Thus they describe *Pallimnarchus* as having six (not five) premaxillary alveoli and use this character to exclude the Windjana Gorge specimen from that genus. Significantly Gorter and Nicoll used the large difference in alveolar size as a character excluding the Windjana Gorge crocodilian from extant species of *Crocodylus*. Understandibly confused, Gorter and Nicoll finally relegated the premaxilla to "?*Crocodylus* sp. indet.".

Gorter and Nicoll (1977) identified CPC 17113 as a dorsal scute and CPC 17114 as a collection of ventral scutes. They considered that these scutes were distinct from those of members of the Crocodylinae and from Gavials but were more similar to Alligatorinae (except *Alligator*). They also considered that these scutes could be distinguished from those of all extant crocodilians.

Gorter and Nicoll (1977) provided the following diagnosis for the Windjana Gorge crocodilian: "Diagnosis: a brevirostrine form, with five premaxillary teeth, pseudoheterodont, a premaxillary-maxillary notch, mandibular teeth occluding inside the upper series, dorsal and ventral scutes, scutes without crests or angulations but having an anterior bevelled edge and laterally sutured edges."

Study of this material reveals that it can be referred to *Pallimnarchus* and it appears to be very similar to *P. pollens*. However, the premaxilla is very fragmentary and it is difficult to assign it to this species with confidence. Its overbite dentition and huge tooth disparity demonstrate mekosuchine affinities and the massive proportions identify it as *Pallimnarchus*. Until more crocodilian material is recovered from this site, this crocodilian can only be identified as *Pallimnarchus* sp.

### Cuddie Springs, NSW

Numerous large crocodilian teeth from Cuddie Springs, New South Wales are held in the collections of the Australian Museum. These can all be referred to either *Pallimnarchus* sp. or (the ziphodont teeth) to *Quinkana* sp.

### Myrtle Vale, NSW

Thompson (1980) reported on two Pleistocene river bank deposits in western New South Wales, one of which (Myrtle Vale) contained a crocodilian tooth. Thompson (1980) describes the conical tooth as being 15mm across the base. Based on the size as described this tooth could represent a large *C. porosus* but would more likely represent *Pallimnarchus* sp. The present location of the fossils Thompson collected is unknown and the Myrtle Vale site has been submerged under the waters of a weir. Thus there appears to be little chance of correctly determining the identity of this crocodilian or of collecting more material.

## PALAEOECOLOGY AND PALAEOBIOGEOGRAPHY

At Cuddie Springs isolated teeth of *Pallimnarchus* and *Quinkana* have been recovered suggesting sympatry between these two species. The ecomorphic forms of these two taxa suggest a clear niche separation; *Quinkana* was a ziphodont, terrestrial carnivore whereas *Pallimnarchus* was a broad-snouted, semi-aquatic or aquatic ambush predator.

The occurrence of *P. gracilis* at the Terrace Site, Riversleigh coincides with the occurrence of *Crocodylus johnstoni* (Willis and Archer 1990), both being found very close to each other in the same deposit. The deposits on the Leichhardt River at Floraville Downs have also produced both *C. johnstoni* (Willis and Archer 1990) and *P. gracilis*. At Macalister on the Darling Downs (Molnar 1982) *P. pollens* and *C. porosus* coincide and at Bluff Downs *Pallimnarchus* sp. and *C. porosus* (Molnar 1979) also occur together. This suggests sympatry between a species of *Pallimnarchus* and *Crocodylus* at each of these sites.

At Terrace Site and on the Leichhardt River the coexistence of *P. gracilis* and *C. johnstoni* can be explained by the differing ecomorphs. *Pallimnarchus gracilis* is a broad snouted crocodilian, an ecomorph usually associated with a generalised diet, whereas *C.*

*johnstoni* is a longirostrine crocodilian with a piscivorous diet.

The occurrence of *P. pollens* and *C. porosus* at Macalister and the occurrence of *Pallimnarchus* sp. and *C. porosus* at Bluff Downs are more problematic. Both crocodilians have the broad snout of generalist crocodilians, although the snout of *Pallimnarchus* is considerably more broad than that of *C. porosus*. It is not clear how a particularly broad snout can separate the niche occupation of *Pallimnarchus* species from *C. porosus* but the occurrence of these species in the same deposits suggests sympatry and some form of niche separation must have occurred. Meyer (1984) concluded that niche separation in sympatric crocodilians is reflected in snout form. The heavily-built, broad snout of *Pallimnarchus* species would be particularly useful to a semi-aquatic or aquatic ambush predator that includes particularly large and heavy prey species in its diet. Macalister has produced fossils of *Diprotodon optatum*, the largest known marsupial with masses up to an estimated 1500 kg. The Bluff Downs fauna includes mammals that range in size up to 1,000 kg (*Euryzygoma*). However, modern individuals of *C. porosus* have been known to take prey items such as water buffalo, horses and cattle up to 700kg in mass. Thus it appears likely that *C. porosus* was capable of taking larger prey items known from these fossil faunas.

Previously, *Pallimnarchus* was known as a single species restricted to numerous Plio-Pleistocene sites throughout Queensland. Two species are now recognised and a third is suggested. The recognition of the new material described here extends the range of the genus into Western Australia (Windjana Gorge), South Australia (Coopers Creek and Warburton River) and New South Wales (Cuddie Springs and possibly Myrtle Vale). The temporal range for the genus is pushed back to the early Pliocene deposits of Bluff Downs and established from sites as young as a 20–30 thousand years at Cuddie Springs and Terrace Site (Dodson et al. 1993, Davis in press).

Both Coopers Creek and the Warburton River drain into Lake Eyre. It is likely that the Pleistocene waterways inhabited by these crocodiles also drained into a large inland lake. *Pallimnarchus pollens* has previously been recognised from the inland drainage basins of eastern Australia from localities such as the Darling Downs, Lansdowne and Chinchilla (Molnar 1982). However, the South Australian specimens push the geographic range of this species much further west. The identification of the Windjana Gorge specimens as *Pallimnarchus*, possibly *P. pollens*, suggests an even greater geographic range for this species but certainly for the genus.

There does seem to be a clear geographic separation between *P. pollens* and *P. gracilis* (Fig. 8). *Pallimnarchus pollens* is known from the northern portions of the Darling River drainage and the Diamantina-Coopers Creek drainage whereas *P. gracilis* appears to be confined to drainage systems associated with the Gulf of Carpentaria. However, this is not entirely the case. The Mirani Shire skull of *P. gracilis* and Anderson's specimen of *P. pollens* attributed to the Gregory River may be exceptions to this geographic division.

The temporal distributions of the species of *Pallimnarchus* (Fig. 8) is generally uninformative. Both *P. pollens* and *P. gracilis* have been recovered from sediments dated from early Pliocene through to late Pleistocene. The Bluff Downs species appears to be restricted to the early Pliocene and undesignated material referred to *Pallimnarchus* occurs in mid to late Pleistocene deposits. Clarifying the apparent geographic relationships and temporal patterns of the species of *Pallimnarchus* will require better information on the exact location of these specimens and more refined dating of all *Pallimnarchus* material. Neither of these requirements are likely to be immediately fulfilled.

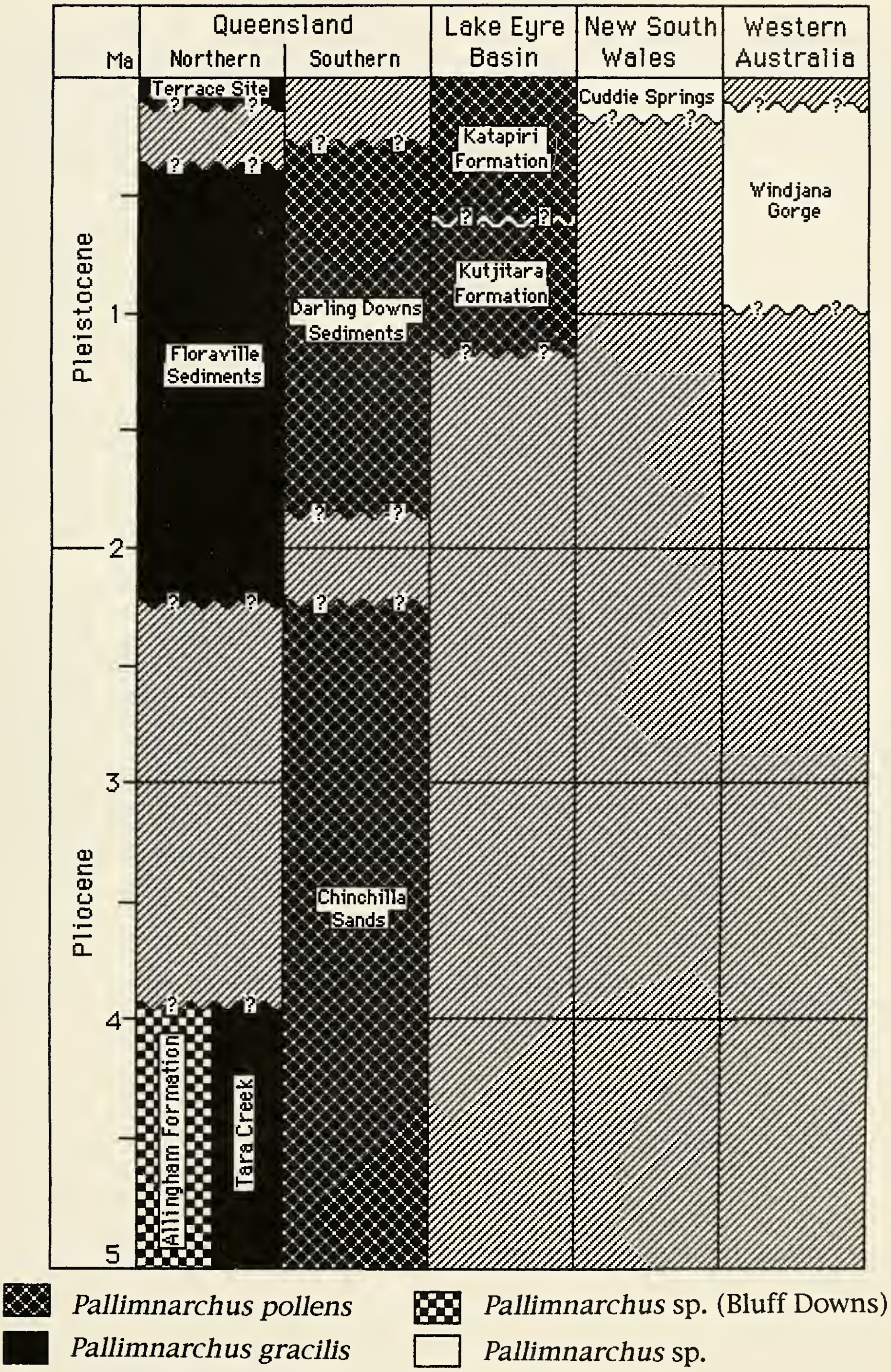


Figure 8. Biocorrelation of sites containing *Pallimnarchus* species.

## FUNCTIONAL MORPHOLOGY

*Pallimnarchus* exhibits certain unusual features that suggest an unusual lifestyle, at least for Australasian crocodilians. The Mirani Shire skull, which includes the snout, jugal arches and dorsal braincase (with skull deck) in articulation, differs from other crocodilian skulls in that the jugals are orientated in the horizontal, rather than the parasagittal, plane. This is also the case on the (uncrushed) right side of the Lansdowne snout. Thus the orbits are directed dorsally rather than dorsolaterally. Together with the very broad, low snout these features give different — broader and flatter — aspects to the skull of *Pallimnarchus* than those of most other crocodilians. Such an appearance is matched by the skulls of the extant *Crocodylus palustris* of India and *Caiman neivensis* from the late Miocene of Colombia (Langston 1965) with *C. neivensis* having the most similar skull. *Caiman neivensis* was the largest species of *Caiman* and Langston (1965) estimated its length as 7–9 metres with a skull comparable in size to that of *Pallimnarchus*. Unfortunately *C. neivensis*, like *Pallimnarchus*, is extinct so its lifestyle cannot be directly observed. *Crocodylus palustris* is, of course, a different matter. It inhabits lakes, rivers, marshes and swamps including, rarely, coastal marshes (Neill 1971) and feeds on fish, water birds, turtles and mammals as large as pigs, goats and deer (Guggisburg 1972). If the similarity in cranial proportions implies a similarity in feeding habits, we might expect *Pallimnarchus* to have fed on fish, turtles, birds and moderately large marsupials. The habitat of *Pallimnarchus* seems to have corresponded to that of *C. palustris*, as *Pallimnarchus* are unknown from coastal regions similar to those inhabited today by *C. porosus*.

The small supratemporal fenestra in both species of *Pallimnarchus* relative to most other crocodilians suggests that the internal and external adductors were less extensively developed than the pterygoid musculature. This in turn suggests that the jaws were capable of being powerfully closed from a fairly wide gape. We suggest that *Pallimnarchus*, like many crocodilians, was an aquatic or semi-aquatic ambush predator. The flat skull and dorsally directed orbits suggest that it lay in wait on the bottom of shallow water bodies, and the robust mandible (in *P. pollens*) and large teeth suggest that it was capable of feeding on relatively large prey. The function of the (presumably) flattened first dentary tooth of *P. gracilis* remains unknown, but the more gracile mandibles and relatively larger supratemporal fenestrae than found in *P. pollens* suggests that this species was less specialised in this direction (although more so than either of the native species of *Crocodylus*).

## ACKNOWLEDGEMENTS

We would like to thank Prof Michael Archer and Stephen Salisbury for reading early drafts and providing constructive comments. Robert Jones provided access to material held in the Australian Museum, Dr Rod Wells allowed access to material held in the collections of Flinders University, Dr Neville Pledge provided access to material held in the collections of the South Australian Museum and Mrs L. Lane and D. Neville assisted with access to and information on the Mirani Shire Skull. Thanks also to Mr Geoff Vincent and Mr Brian Mackness for access to material in their possession. Dr J. Draper of the Geological Survey of Queensland provided useful instruction on aspects of the geology of the Mirani area.

## REFERENCES

Anderson, C. (1937). Palaeontological notes No. IV. *Record of the Australian Museum* **20**, 73–77.

Archer, M. (1982). Review of the dasyurid (Marsupialia) fossil record, intergration of data bearing on phylogenetic interpretation and suprageneric classification. In 'Carnivorous marsupials' (Ed. M. Archer). Pp 397–443. (Royal Zoological Society of New South Wales, Sydney).

Archer, M., and Hand, S.J. (1984). Background to the search for Australia's oldest mammals. In 'Verterbate zoogeography and evolution in Australasia' (Eds M. Archer and G. Clayton). Pp 517–567. (Hesperian Press, Carlisle, Western Australia).

Archer, M., Godthelp. H., Hand, S.J., and Megirian, D. (1989). Fossil Mammals of Riversleigh, Northwestern Queensland: Preliminary Overview of Biostratigraphy, Correlation and Environmental Change. *Australian Zoologist*. **25**, 27–65.

Davis, A.C., and Archer, M. 1996 (in press). *Palorchestes azael* (Mammalia, Diprotodontidae) from the late Pleistocene Terrace Site Local Fauna, Riversleigh Station, northwestern Queensland. *Memoirs of the Queensland Museum*. (in press).

De Vis, C.W. (1886). On the remains of an extinct saurian. *Proceeding of the Royal Society of Queensland* **2**, 181–191.

Dodson, J., Fullagar, R., Furby, J., Jones, R. and Prosser, I. (1993). Human and megafauna in a Late Pleistocene environment from Cuddie Springs, northwestern New South Wales. *Archaeology in Oceania* **28**, 94–99.

Gorter, J.D., and Nicoll, R.S. (1977). Reptilian fossils from Windjana Gorge, Western Australia. *Proceeding of the Royal Society of Western Australia* **60**, 97–104.

Grimes, K. G., and Doutch, H. F. (1978). The late Cainozoic evolution of the Carpentaria Plains, north Queensland. *Bureau Mineral Resourses Journal of Australian Geology and Geophysics*. **3**, 101–112

Guggisberg, C.A.W. (1972). 'Crocodiles; their natural history, folklore and conservation'. (Wren: London).

Langston, W., Jr. (1965). Fossil crocodilians from Colombia and the Cenozoic history of the Crocodilia in South America. *University of California Publications in Geological Sciences* **52**, 1–157.

Longman, H.A. (1924). Some Queensland fossil vertebrates. *Memoirs of the Queensland Museum* **8**, 16–24.

Longman, H.A. (1925a). A crocodilian fossil from Lansdowne Station. *Memoirs of the Queensland Museum* **8**, 103–108.

Longman, H.A. (1925b). A large jaw of *Pallimnarchus pollens. Memoirs of the Queensland Museum* **9**, 158–159.

Malone, E.J. (1969). Mount Coolon, Qld. 1:250,000 Geological Series — Explanatory Notes SF/55–7.

Megirian, D., Murray, P.F. and Willis, P.M.A. (1991). A new crocodile of the gavial ecomorph morphology from the Miocene of northern Australia. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* **8**, 135–158.

Meyer, E.R. (1984). Crocodilians as living fossils. In 'Living fossils' (Eds N. Etheridge and S.M. Stanley) pp. 105–131. (Springer Verlag: New York).

Molnar, R.E. (1979). *Crocodylus porosus* from the Pliocene Allingham Formation of north Queensland. *Memoirs of the Queensland Museum* **19**, 357–365.

Molnar, R.E. (1982). *Pallimnarchus* and other Cenozoic crocodiles of Queensland. *Memoirs of the Queensland Museum* **20**, 657–673.

Neill, W.T. (1971). 'The Last of the Ruling Reptiles; alligators, crocodiles and their kin'. (Colombia University Press: New York).

Rich, T.H., Archer, M., Plane, M., Flannery, T.F., Pledge, N.S., Hand, S., and Rich, P.V. (1983). Australian Tertiary mammal localities. In 'The Fossil Vertebrate Record of Australia' (Eds P.V. Rich and E.M. Thompson) pp. 525–572. (Monash University Printing Unit: Melbourne).

Sutherland, F.L., Stubbs, D. and Green, D.C. (1978). K-Ar ages of Cainozoic volcanic suits, Bowen-St Lawrence hinterland, north Queensland (with some implications for petrologic models). *Journal of the Geological Society of Australia*. **24**, 447–460.

Swinton, W.E. ms (c. 1924). Description of the vertebrate remains collected by professor J.W. Gregory, D. Sc., PRS, in the Lake Eyre district of South Australia. Hunterian Museum, University of Glasgow, 33p.

Thompson, P. (1980). Report on investigation of Myrtle Vale and Redbank; two fossil bone sites; Darling River Weir No. 20 North-west N.S.W.. Report for N.S.W. National Parks and Wildlife Service.

White, A.W., and Archer, M. (1994). *Emydura lavarackorum*, a new Pleistocene turtle (Pleurodire: Chelidae) from fluviatile deposits at Riversleigh, northwestern Queensland. *Records of the South Australian Museum* **27**, 159–169.

Willis, P.M.A. (1993). *Trilophosuchus rackhami*, gen. et sp. nov., a new crocodilian from the early Miocene Limestones of Riversleigh, northwestern Queensland. *Journal of Vertebrate Paleontology* **13**: 90–98.

Willis, P.M.A. (1996). The phylogenetic systematics of Australian crocodilians. Unpublished doctoral thesis, University of New South Wales.

Willis, P.M.A., and Archer, M. (1990). A Pleistocene longirostrine crocodilian from Riversleigh: first fossil occurrence of *Crocodylus johnstoni* Kreft. *Memoirs of the Queensland Museum* **28**, 159–163.

Willis, P.M.A., Murray, P.F. and Megirian, D. (1990). *Baru darrowi gen. et sp. nov.*, a large, broad-snouted crocodyline (Eusuchia: Crocodylidae) from mid-Tertiary freshwater limestones in Northern Australia. *Memoirs of the Queensland Museum* **29**, 521–540.

Willis, P.M.A., Molnar, R.E. and Scanlon, J.D. (1993). An early Eocene crocodilian from Murgon, southeastern Queensland. *Kaupia* **3**, 25–32.

Wyatt, D.H., and Webb, A.W. (1970). Potassium-Argon ages of some northern Queensland basalts and an interpretation of late Cainozoic history. *Journal of the Geological Society of Australia*. **17**, 39–51.

# Towards a Biology of *Propleopus oscillans* (Marsupialia: Propleopinae, Hypsiprymnodontidae)

[1]W.D.L. Ride, [1]P.A. Pridmore, [1]R.E. Barwick, [2]R.T. Wells
and [3]R.D. Heady

[1]Department of Geology, Australian National University, Canberra, ACT 0200; [2]School of Biological Sciences, Flinders University, South Australia 5001; [3]Electron Microscope Unit, Australian National University, Canberra, ACT 0200

Ride, W.D.L., Pridmore, P.A., Barwick, R.E., Wells, R.T. and Heady, R.D. (1997). Towards a biology of *Propleopus oscillans* (Marsupialia: Propleopinae, Hypsiprymnodontidae). *Proceedings of the Linnean Society of New South Wales* **117**, 243-328.

*Propleopus oscillans* is one of the rarest and anatomically least known members of the megafauna of the Australian Pleistocene. Under current interpretations this large hypsiprymnodontid marsupial is usually considered to have been either a predatory carnivore or an omnivorous member of a largely carnivorous clade. Recent discoveries in South Australia extend our knowledge of the cranial and dental anatomy of *P. oscillans*. The post-cranial skeleton is also known from two humeri. The latter, although not directly associated with dental remains, are from a *P. oscillans*-containing deposit and fit no other species known in the deposit. They are also morphologically similar to, but much larger than, the humerus of *Hypsiprymnodon moschatus*, the Musky Rat Kangaroo, the only living representative of the Hypsiprymnodontidae.

Here we give an account of the previously undescribed material and give a fuller account of the material previously reported. The known material now consists of several mandibular rami (including two pairs), a rostrum and facial portion of a cranium (to which one of the pairs of rami belong), many separate teeth representing the complete juvenile and adult dentitions (excepting the second and third upper incisors) and two partial humeri.

On the basis of the morphology of the teeth of and, in particular on the interpretation of scanning electron micrographs of the sectorial premolars and the molars, the hypothesis that *P. oscillans* was a carnivorous kangaroo is reviewed. It is concluded that although diprotodont, *P. oscillans* was a carnivorous marsupial analogous with canids in being long-faced, but as in marsupial carnivores (Dasyuridae and Thylacinidae), the entire molar row has shearing, as well as crushing, specializations distributed along its length. Like *Thylacinus* and *Sarcophilus*, *P. oscillans* had a wide gape enabling it to exert bite force far posteriorly and a mandibular condyle at the level of the tooth row. It was probably an opportunistic feeder like the present-day arid zone long-faced carnivores (*Canis* and *Vulpes*).

Based on the humerus and its inferred musculature, we conclude that unlike kangaroos and wallabies, and despite its size (slightly smaller than the largest extant macropodiform marsupials of the genus *Macropus*), the animal was quadrupedal like *Hypsiprymnodon moschatus*. *P. oscillans* was not arboreal or fossorial and its ability to run fast was evidently less than that of *Canis* or *Thylacinus*. Similarities with the humerus of *Gulo* (wolverine) suggest that it might have had some capacity for endurance running.

Manuscript received 30 August 1996, accepted 11 December 1996.

KEYWORDS: *Propleopus*, skull, dentition, mastication, humerus, forelimb, musculature, locomotion, lifestyle.

## INTRODUCTION

### Myth or Hypothesis?

> 'The notion of predatory potoroid kangaroos was created by both Archer (1984) and Flannery (1984) on reflection of the habits of living potoroids and their possession of large, serrated shearing premolars ...' (Murray 1991, p. 1111)
>
> '*Propleopus oscillans*, killer kangaroo, or strange, but peaceful, herbivore? These are some of the possibilities facing the scientist studying remains of the extinct Giant Rat Kangaroo. There is evidence supporting both interpretations' (Flannery 1985, p. 246).

The myths that presently surround *Propleopus*, may seem fanciful – but are they? Was *Propleopus* a 'killer kangaroo' (Flannery 1985, p. 246) or a 'marsupial cheetah counterpart' (Vickers-Rich and Rich 1993, p. 197)? Did this member of the Pleistocene megafauna survive long enough to 'gobble up any of Australia's first humans'? (Archer et al. 1991, p. 120). Or, most fancifully, could it have been 'trained as an "attack roo"' (Archer et al. 1991, p. 120).

*Propleopus oscillans* has been known for more than 100 years, yet it and its two congeneric species (*P. chillagoensis* and *P. wellingtonensis*) remain the rarest of the large mammals of the Australian Pleistocene. Of the three species, there is most material of *P. oscillans*. Nevertheless, remains of *P. oscillans* are fragmentary and anatomically limited.

As a result of recent discoveries in South Australia we now have a snout, much of the face, and two pairs of mandibles (adult and juvenile) of *P. oscillans*. All of the teeth except for the second and third upper incisors are known. We also have two partial humeri (one almost complete).

The new skeletal material (including some that has been briefly described previously) serves as the basis of the present attempt to move towards a sounder understanding of the biology of *P. oscillans*. In our efforts to clarify its possible diet and environmental niche, morphology must be the prime consideration. However, other factors, such as its ancestry, its distribution and its rarity (Archer and Flannery 1985, Flannery 1985) are also relevant.

We commence this re-examination of *P. oscillans* with a brief restatement of the lines of argument upon which rest the two currently most widely advanced hypotheses; i.e. the view that this species was a carnivore and the view that it was possibly an omnivorous member of a carnivorous clade (the Propleopinae), some other members of which were more carnivorous and others less so. Following that, we describe the new material and discuss its significance for the current hypotheses, and thereby, although admittedly dependent upon information about only a small part of its anatomy, take one step further towards developing an image of the whole animal that was *Propleopus oscillans*.

The most complete statement of the hypothesis of carnivory is by Archer and Flannery (1985). This was modified later by Wroe (1996) who expanded the omnivorous alternative.

## FOUNDATIONS OF THE CURRENT HYPOTHESES

### Heritage

Two other species of the genus (also very rare) have been described. These, *P. chillagoensis* (Archer et al. 1978) and *P. wellingtonensis* (Archer and Flannery 1985), have been regarded as Pleistocene. *P. chillagoensis* is known only from a maxillary fragment and two isolated premolars collected from a fissure at Chillagoe Caves, N.E.

Queensland (Archer et al. 1978), and *P. wellingtonensis* from a part mandibular ramus from the Bone Cave, Wellington Caves, N.S.W. (Archer and Flannery 1985). L. Dawson (pers. comm.) considers that the Bone Cave deposit may be Pliocene. An isolated lower left premolar from Boxlea coal mine, near Bacchus Marsh, Victoria (Woodburne et al. 1985), corresponds closely with one of the *P. chillagoensis* specimens and is certainly Pliocene (probably >4.1 mya, Whitelaw 1991). It is also comparable in size with the alveolus of the premolar of *P. wellingtonensis*. Since the premolars of *P. wellingtonensis* are unknown, the Boxlea specimen cannot be assigned to either species with certainty. The premolar is much too large to be *P. oscillans*.

Further evidence that the lineage of *Propleopus* (i.e., the Propleopinae) extends back well into the Tertiary (Archer and Flannery 1985) is provided by the Pliocene genus *Jackmahoneya* (Bow River, Ride 1993; Hamilton, Flannery et al. 1992) and the middle Miocene genus *Ekaltadeta* (Riversleigh, Archer and Flannery 1985; Wroe 1996). The sister clade Hypsiprymnodontinae is represented today by the morphologically very similar (except for size) living *Hypsiprymnodon moschatus* and occurs also in the Riversleigh Miocene Gag (*H. bartholomaii*, Flannery and Archer 1987) and Camel Sputum Sites. Together the two clades form the Hypsiprymnodontidae (see Ride 1993).

Of the four genera of Hypsiprymnodontidae, the living *H. moschatus* is the smallest species, weighing 0.36 to 0.68 kg when adult (Dennis and Johnson 1995). Unlike Potoroidae and all Macropodidae it does not have a sacculated stomach necessary for foregut fermentation (see Freudenberger et al. 1989). Its diet consists of high-energy foods such as insects, fruit, nuts, etc.

Proportional differences in the premolar-molar row of the two other *Propleopus* species indicate that there was some dietary diversity in the genus (Wroe 1996, Ride 1993). Further comparisons between the different *Propleopus* species are not made in this study.

If it can be assumed that *H. moschatus* is archetypal of the Hypsiprymnodontidae and that the other members of the family, in retaining a hypsiprymnodontine dentition, would have also retained its unspecialized gut, this would be an argument in favour of the hypothesis of carnivorous (or at least non-herbivorous) habits in the other members. But it is commonly held that all macropodiforms were derived from an *Hypsiprymnodon*-like ancestor. If this is so, there can be no logical reason why larger Hypsiprymnodontidae could not also have become foregut fermenters, but see Ride (1993) for a view that *Hypsiprymnodon* and the other genera of the Hypsiprymnodontidae may not be macropodiforms.

Thus, while it is plausible to attribute the dietary requirements of *H. moschatus* for high-energy foods (including animal protein) to *P. oscillans*, the argument if based on relationships alone cannot be regarded as more than suggestive.

## Rarity

*P. oscillans* is a rare fossil. Most occurrences are of fragments of single individuals. In all less than 30 individuals are known. While it is characteristic of predator numbers that they are low compared with prey species, it is not the only factor that results in rarity in the fossil record, even in the case of Quaternary fossils where most species are abundantly represented. For instance *Palorchestes*, certainly a herbivore, and the termite-eating *Tachyglossus* are even rarer than *P. oscillans*, while the Tasmanian Devil (*Sarcophilus*) is not uncommon, although nowhere nearly as common as kangaroos. This evidence suggests that *P. oscillans* was solitary but, while its rarity is not inconsistent with it being a predator, many other reasons could account for the lack of fossils.

## Distribution and inferred palaeoecology

Of the seven deposits that have yielded *P. oscillans* only three are dated: Lancefield Swamp near Melbourne (26 ka = 26,000 years BP), Lake Menindee, NSW (26 ka – 18 ka), and Henschke's Fossil cave (40 ka – 32 ka). Pollen at Lancefield indicates a treeless savannah and a colder and drier climate than at present but there is some doubt about the relevance of the date to the fossils and it is possible that the deposit is secondarily derived and hence that the pollen data do not apply to the *P. oscillans* remains (Van Huet 1994a, 1994b; White and Flannery 1995). There can be no doubt that Menindee between 26 ka and the glacial maximum at 18 ka was arid (but there is doubt that the date of the deposit applies also to the faunal remains, Balme and Hope 1990). Other mammals in both faunas were grazers and browsers (for faunal lists and dates of the deposits see Gillespie et al. 1978; Tedford 1967). The browsers, such as the *Sthenurus* species of kan-

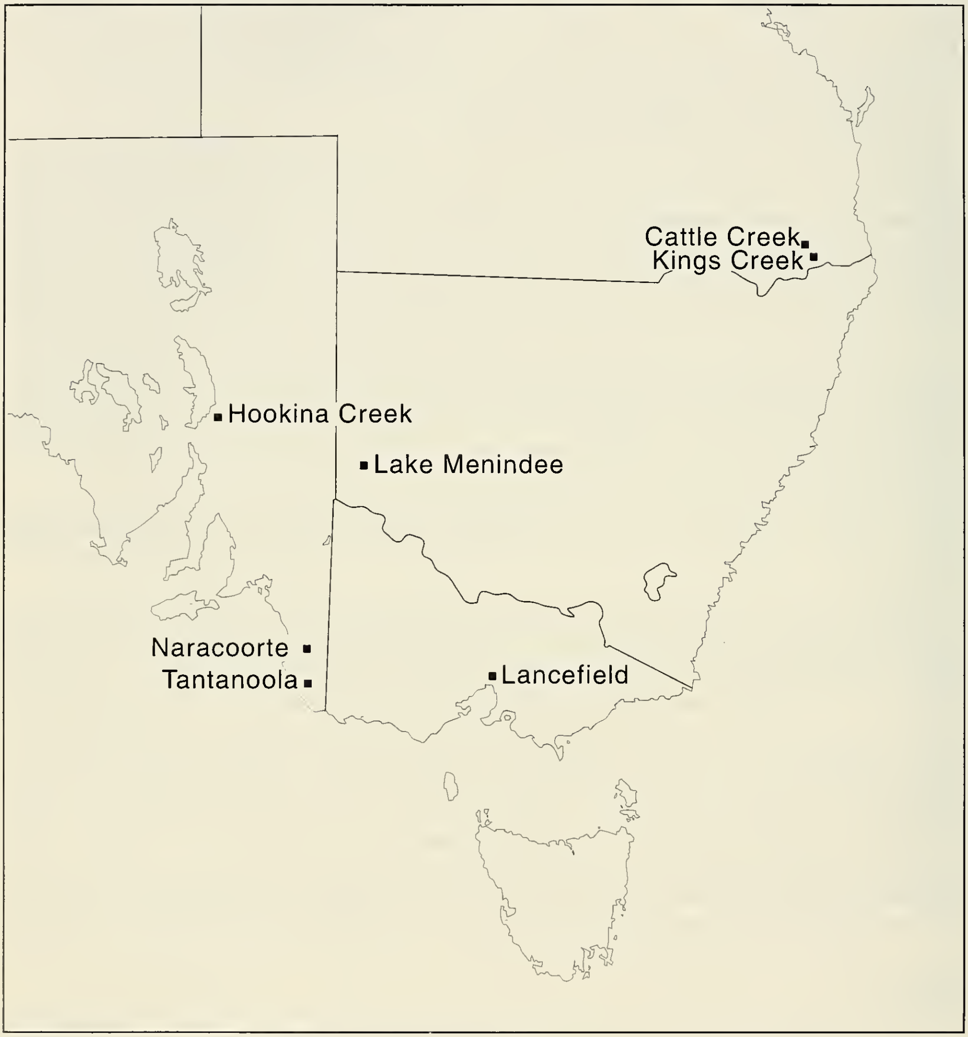


Figure 1. Localities at which *Propleopus oscillans* has been collected.

garoos, presumably browsed on such shrubs as Chenopodiaceae (salt-bush, bluebush) and low trees (Wells and Tedford 1995). The fauna of the Henschke's Fossil Cave deposit (Pledge 1990) indicates a well watered but semi-arid savannah environment, possibly swamps, with open sclerophyll forest and heaths.

In all deposits from which *P. oscillans* has been recovered, grazing and browsing Macropodidae are common. From this it is clear that a major high-energy resource present in the original environment would have been the tissue of herbivorous mammals. However, other high energy food sources, such as birds, reptiles, arthropods, fruits, roots, nuts and seeds, would also have been present (e.g. in the same way in which arid and semi-arid Australia provided sufficient resources to sustain Aboriginal populations). The question as to whether various plant foods could have made a significant contribution to the sustenance of an animal the size of *P. oscillans*, depends upon their abundance and the species' ability to harvest them. Thus, taken by itself and without consideration of masticatory morphology, the occurrence of *P. oscillans* in the arid zone during the maximum aridity of the late Pleistocene, provides only equivocal support for a hypothesis of carnivory.

## Morphology

Prior to the discovery of Henschke's Fossil Cave near Naracoorte, South Australia, the morphology of *Propleopus oscillans* was known only from a partial adult mandibular ramus with its teeth, the holotype (De Vis 1888; see Woods 1960, fig. 1, and Archer and Flannery 1985, fig. 3.1), a portion of a left ramus with P3-M3 (Tedford 1955, 1967; figd Archer and Flannery 1985, fig. 3.3); a lower incisor (Woods 1960), two premolars, a molar and a number of dental fragments (Tedford 1967; Gillespie et al. 1978), and a maxillary fragment with a contained premolar and two molars (Bartholomai 1972, pl. 8). All were from sites believed to be Pleistocene (eastern Darling Downs, southern Queensland; Menindee, western New South Wales; Lancefield, southern Victoria) (Fig. 1).

From this material, Archer and Flannery (1985, p. 1346) pointed to the stout lower incisors with a ventral enamel border, wearing to a sharp anterior edge and the ridged, cusped, non-slip premolars as features that can be interpreted as adaptations to carnivory. Large ridged premolars in smaller animals (*H. moschatus, Bettongia,* and *Burramys*) are used to 'slice insect integument and plant matter (i.e., seed coat)'. They also drew attention to the possession of a notch between the premolars and molars that could have functioned in much the same way as the carnassial notch in Carnivora, and to low crowned molars unsuited to grazing, coupled with the possession of prominent molar cingula that in other mammals function to protect the gums from splinters. In addition Archer and Flannery reported that scanning electron micrographs that they had taken of an upper premolar showed very course wear striae which were larger than those present on the premolars of most carnivores and approached only in size by those of *Thylacoleo carnifex* examined by Wells et al. (1982). They advanced their conclusions as follows:

> 'In summary, the giant rat kangaroos show many dental similarities with much smaller omnivores/insectivores. Where they differ, the specializations present in the species of *Propleopus* can be interpreted as adaptations to carnivory' (Archer and Flannery 1985, p. 1347)

Then, taking into account the apparent reduction in molar row, and premolar hypertrophy, in *P. chillagoensis*, they suggested of *Propleopus oscillans*, that:

> '...its retention of a large molar area and smaller premolars may indicate that it was more omnivorous, perhaps taking a range of food similar to that taken

by baboons in Africa today.' (Archer and Flannery 1985, p. 1347)

Subsequently, Wroe, as a result of a study of the species of *Ekaltadeta*, as well as *Propleopus*, brought together the hypotheses of omnivory and carnivory to conclude that within the clade of Propleopinae, extending back into *Ekaltadeta*, there may be 'two extremes of propleopine adaptation. *Propleopus oscillans* with premolar hypotrophy' (i.e. relatively reduced premolars) 'and an extended molar battery possibly included more plant material in its diet' while the other lineage 'with a reduced molar array and premolar hypertrophy appears better adapted for a carnivorous niche' (Wroe 1996 p. 689).

## MATERIAL OF *P. OSCILLANS* STUDIED[1]

Henschke's Fossil Cave was discovered in 1969 and between 1969 and 1981 numerous specimens of *P. oscillans* were recovered by the South Australian Museum (Pledge 1981, 1990). The excavation was extended by John and Julie Barrie and their associates (Barrie 1990). The first collection of separate teeth of *P. oscillans* from Henschke's Fossil Cave were described by Pledge (1981). He suggested that a humerus from the same deposit was also of *P. oscillans*. Here we report additional discoveries from the same deposit. These specimens consist of the rostral portion of a juvenile skull from the premaxilla to the orbit and zygomatic arch, and an almost complete mandible found separately, but undoubtedly of the same individual and a partial humerus. There are also a large number of separate teeth (additional to those reported previously by Pledge 1981). Except for the second and third upper incisors and the lower canine[2], the specimens from Henschke's Fossil Cave represent the complete juvenile and adult dentitions. Coincident with these discoveries, an almost complete adult mandible was recovered by R.T. Wells and colleagues from the Green Waterhole at Tantanoola, S.A. (containing, as well as the other teeth, the lower canine not found at Henschke's Fossil Cave), and a fragment of a ramus and a number of molars at Hookina Creek to the west of the Flinders Ranges (Williams 1980 p.105). The material from the Naracoorte localities, together with the holotype mandible and a partial maxilla, both from the Darling Downs (Table 1), provide the basis for the present study.

Pledge (1981) tentatively identified the first of the humeri as that of *P. oscillans* on the basis of its similarities to the equivalent bone in *Hypsiprymnodon moschatus*. A fuller description and analysis of this bone is presented below along with a brief account of a second less complete humerus collected by the Barries. The post-cranial anatomy of members of the genus *Propleopus* is is otherwise entirely unknown. Reconstructions of the entire animal (Knight in Flannery 1985, Schouten in Archer 1987) seem to be based on analogy with potoroids, to which *Propleopus*, as a "rat kangaroo", was thought to be most closely related.

TABLE 1

Mandibular and dental measurements of *P. oscillans* specimens.
All in mm. l = length, aw = anterior width, pw = posterior width.

***a. Mandible:***

| | Tip of $I_1$ to condyle | $P_3$-$M_4$ | $P_3$-condyle crest of $P_3$ | Depth at crest of $P_2$ | Depth at | $P_2$-condyle |
|---|---|---|---|---|---|---|
| P20815 | 175.8 | 57.5 | 119.2 | 42.6 | - | - |
| P35633 | c. 147.5 | - | - | - | 32.6 | 101.8 |

**b. Premolars:**

| | $P_2$ length | $P_2$ breadth | $P_3$ length | $P_3$ breadth | $P_2$ length | $P_2$ breadth | $P_3$ length | $P_3$ breadth |
|---|---|---|---|---|---|---|---|---|
| P35633 | 9.4 | 7.9 | - | - | - | - | - | - |
| P20815 | - | - | 14.5 | 9.9 | - | - | - | - |
| P35632 | - | - | - | - | 8.6 | 8.3 | - | - |
| F6675 | - | - | - | - | - | - | 15.6 | 11.4 |

**c. Lower molariform teeth:**

| | Specimen No. | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|
| | P35633 | P35641 | P34153 | P34155 | P22814 | P34152 | P22813 | P35644 | P35647 | P22735 |
| $dp_3$ l | 7.6 | 7.9 | - | - | - | - | - | - | - | - |
| pw | 6.7 | 6.2 | - | - | - | - | - | - | - | - |
| $M_1$ l | 9.9 | - | 10.6 | - | - | - | - | - | - | - |
| aw | 8.5 | - | 9.0 | - | - | - | - | - | - | - |
| $M_2$ l | 11.1 | - | - | 11.8 | 10.8 | 11.4 | 11.1 | 11.1 | - | - |
| aw | 9.6 | - | - | 9.5 | 8.6 | 9.6 | 9.1 | 9.8 | - | - |
| $M_3$ l | - | - | - | - | - | - | - | - | 10.6 | - |
| aw | - | - | - | - | - | - | - | - | - | - |
| $M_4$ l | - | - | - | - | - | - | - | - | - | 10.8 |
| aw | - | - | - | - | - | - | - | - | - | - |

**d. Upper molariform teeth:**

| | Specimen No. | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | P35632 | P22736 | P22734 | P35642 | P22815 | P18541 | P24678 | P22826 | P34151 | P35645 | P35646 | P24681 |
| $dp^3$ l | 8.2 | 8.0 | - | - | - | - | - | - | - | - | - | - |
| pw | 7.8 | - | - | - | - | - | - | - | - | - | - | - |
| $M^1$ l | 10.3 | - | 10.0 | 10.0 | - | - | - | - | - | - | - | - |
| aw | 10.6 | - | - | 9.1 | - | - | - | - | - | - | - | - |
| $M^2$ l | 11.8 | - | - | - | 11.9 | 11.3 | 11.2 | - | - | - | - | - |
| aw | 10.5 | - | - | - | 10.2 | 9.7 | 9.9 | - | - | - | - | - |
| $M^3$ l | - | - | - | - | - | - | - | 10.6 | 9.8 | 10.6 | 11.5 | - |
| aw | - | - | - | - | - | - | - | - | - | 9.4 | 9.5 | - |
| $M^4$ l | - | - | - | - | - | - | - | - | - | - | 11.0 | - |
| aw | - | - | - | - | - | - | - | - | - | - | 7.9 | - |

### ***Propleopus oscillans*** (De Vis 1888)

*Triclis oscillans* De Vis 1888, *Proceedings of the Linnean Society of New South Wales* (2)**3**: 5-8, pl. 1. Combined with *Propleopus* Longman 1924, nom. nov. to replace *Triclis* De Vis 1888, junior homonym of *Triclis* Leow 1851 (Arthropoda) (Longman 1924, *Memoirs of the Queensland Museum* **8**: 20 -21).

### Skull

Qd Mus. F6675. – Portion of a left maxilla (Figs 5A, 9; figd Bartholomai 1972, pl. 8) with $P^3$, $M^1$-$M^2$, area of palate and portion of the maxillary root of the zygomatic arch present. Cattle Creek nth of Dalby, eastern Darling Downs, southern Queensland.

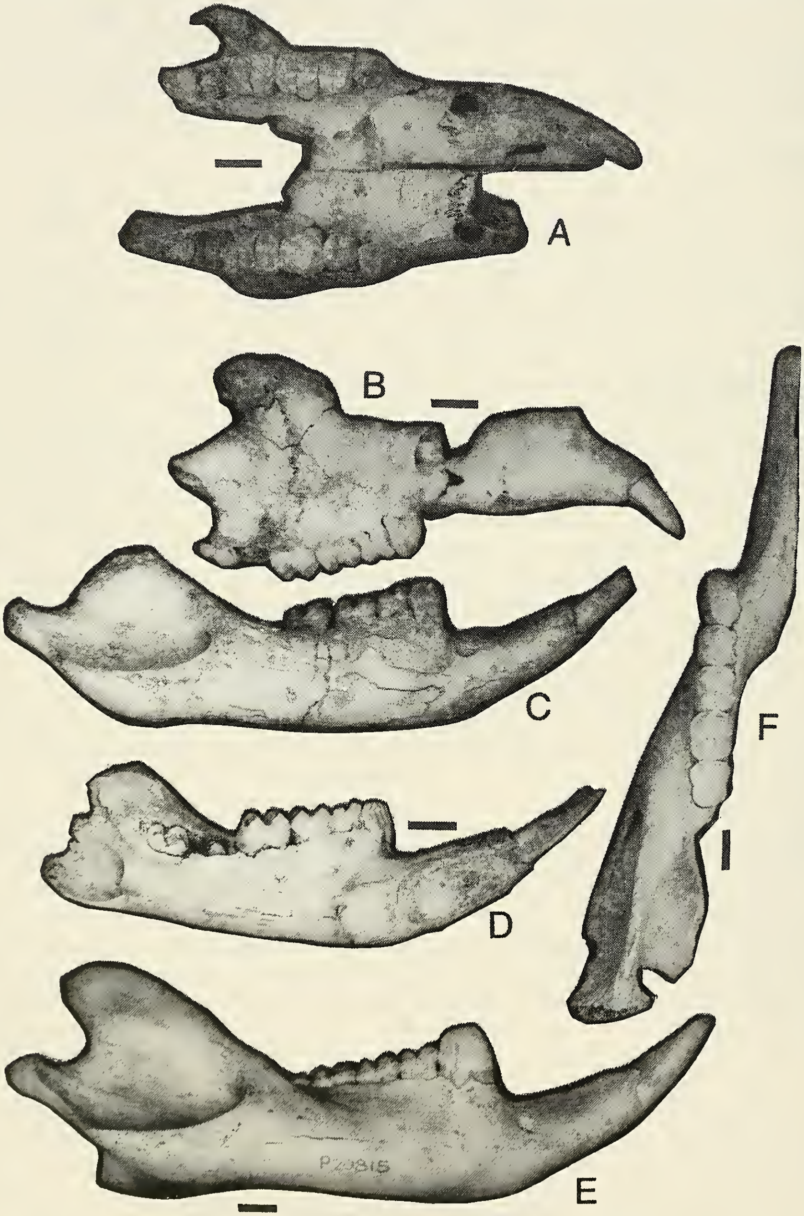


Figure 2. Skull material of *P. oscillans*. A-D: views of rostral portion of P35632 and mandible of P35633, Henschke's Fossil Cave, Naracoorte, South Australia. A: occlusal view, B: right lateral view, C: lateral view of right ramus, D: mesial view of left ramus. E-F: mandibular rami of P20815, Green Waterhole, Tantanoola, South Australia. B and C are roughly in occlusal alignment. Scale bars = 1 cm.

P35632. – Rostral portion of skull (Figs 2A, B; 3) consisting of incomplete right premaxilla with $I^1$ and alveoli of $I^2$ and $I^3$ and canine; right premaxillary palate complete to median suture; left premaxilla present only as palatal fragment anterior to the maxillo-premaxillary suture; both maxillae present but incomplete; $P^2$, $dP^3$, $M^1$, $M^2$, alveolus of $M^3$, $M^4$ erupting and exposed in crypt on both sides; posterior part of maxillary palate incomplete from immediately anterior to the palatal suture; facial portion damaged on both sides and not reaching the naso-maxillary suture; anterior edge of zygomatic arch present on right and includes the eminence representing the masseteric process; on the

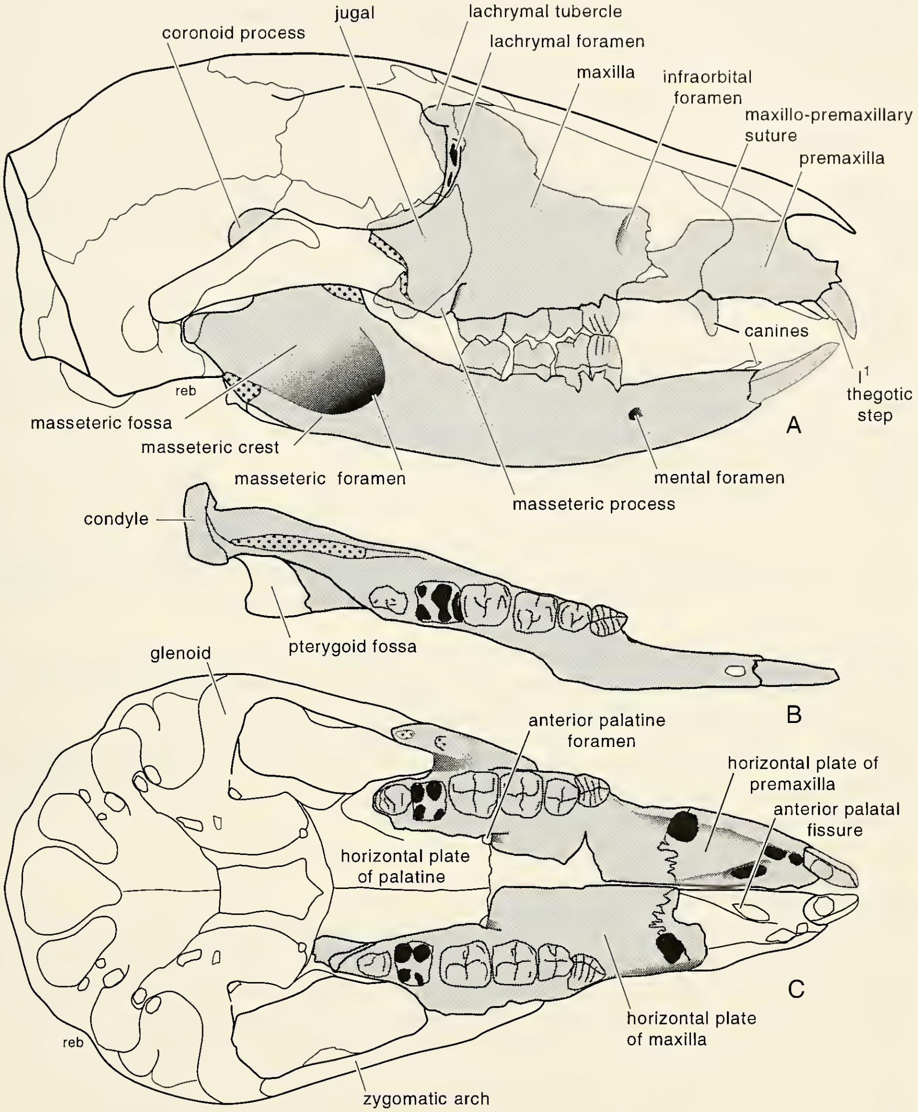


Figure 3. The Henschke's Fossil Cave specimens set within an outline of the restored skull. Terminology as used in the text. For premaxillary sutures see Fig. 19F.

right the lachrymal is present but incomplete within the orbit, its facial exposure is complete including the lachrymal tuberosity and both foramina; anterior edge of orbit present on both sides; within the left orbit a portion of the orbital plate of the palatine is present to its sutures with the jugal and lachrymal. Facial portion of maxillo-premaxillary suture present (but incomplete on left); infraorbital foramen also present (but incomplete on left); right and left portions were disarticulated along the median palatal suture when found, the right portion was fractured immediately anterior to the infraorbital foramen but the junction between the parts on both palatal and facial surfaces is in no doubt. Henschke's Quarry Fossil Cave[3], Naracoorte, S.A.; Barrie locality HJD III ('high in terra rossa filling a vertical fissure between two levels' in 'upper sandy material, fossils sparse compared with lower silty deposit' - see figs 3 and 4 of Barrie 1990, vertical fissure located between i and i in section in fig. 4). Collected J. & J. Barrie and associates, Aug 1983.

P35633. – Mandible (paired rami, Fig. 2C, D) with $I_1$, alveolus of minute canine, $P_2$, $dP_3$, $M_1$, $M_2$, alveolus of $M_3$, $M_4$ erupting and exposed in crypt in both rami; both rami broken away across pterygoid fossa; ascending rami broken across but entire condyle remains on right ramus; teeth of both rami occlude perfectly with corresponding maxillary tooth rows (P35632). Henschke's Quarry Fossil Cave, Naracoorte, S.A.; Barrie locality HJD5 ('found after excavating when sorting material in block adjacent to HJD III'). Collected J. & J. Barrie and associates, Sept 1983.

P20815. – Mandible (paired rami, Fig. 2E, F; $P_3$, Fig. 5B) with $I_1$ (figd Vickers-Rich and Rich 1993, fig. 309); canine present on left side, alveolus on right, $P_3$-$M_4$; right ramus lacks only tip of incisor and small portion of pterygoid shelf lateral to the angular process; left ramus lacks angular process, posterior end of masseteric shelf, and articular surface of condyle. Collected R.T. Wells and associates, Green Waterhole, Tantanoola nr Mt Gambier, S.A.

Qd Mus. F3302. – Left ramus (figd Woods 1960, fig. 1; Archer and Flannery 1985, fig. 3-1) extending from the incisor to the anterior edge of the masseteric fossa, with $I_1$, $P_3$, $M_{1-4}$. Holotype. Kings Creek, eastern Darling Downs, southern Queensland.

P22425a. – Portion of right ramus from mental foramen to anterior edge of pterygoid fossa; roots of $P_2$, $dP_3$, $M_1$ (broken posterior moiety only), $M_2$ shattered (hypoconid lost), $M_3$ partly erupted, $M_4$ exposed in crypt (entoconid broken off). Hookina Creek, west of Flinders Ra., S.A.

## Separate Teeth

All separate teeth studied were collected at Henschke's Quarry Fossil Cave. Those collected by Barrie et al., were collected between 1982 and 1986 from the cave locality HJD (Barrie 1990, figs 3 and 4); those collected by S.A. Mus. party and Pledge et al. were collected between 1969 and 1981 at localities S.A.M. and HNXI in Barrie (1990) (see Pledge 1981, table 1 and fig. 1 for a section through the S.A. Mus. excavation with areas and levels from which the teeth were collected, and Pledge 1990 for a plan of a part of the areas excavated; also see Barrie, loc. cit. for the relative positions of the two excavations). Locations within the cave at which specimens were excavated are recorded here employing the notations used by Pledge and Barrie (op. cit); in the former case they are given in the form 'area/level', in the latter the area is HJD followed by a Roman numeral indicating the 'dig lot' – see Barrie (1990, p. 141).

Most of the separate teeth are no more than 'crowns' (i.e., teeth in which the enamel fully invests the tooth and dentine has formed within, but roots may not be preserved) or caps (i.e., teeth consisting only of a thin skin of enamel, with or without a dentine lining); in the latter, although cusp development is complete, margins may be at various stages of development (from 'margins unformed' to 'margins almost fully formed'). In the case of crowns, there may be some degree of wear.

All separate teeth examined are in the collection of the South Australian Museum.

Incisors: I1: P35634 (left) and P35635 (right).– Pair of I$^1$s (right tooth split, fragment of lateral portion only); freshly erupted but with slight wear. Barrie locs HJD/X and HJD/IV. P22816.- Left I$_1$, crown (i.e., exposed portion) with root broken off well below alveolar margin, loc. A11X/14+ (see Pledge 1981, table 2 legend, for explanation of his notation), collected G. Kilsby, 6.1.80, (figd Pledge 1981, fig. 2).

Canines: C: P35636.- Right upper canine, wear commenced at tip, Barrie loc. HJD/IIV.

Sectorial Premolars (P2, P3): P2: P24677.- Right P$^2$ (Fig. 5C) in fragment of maxilla, much worn, N.S. Pledge et al. 1970s, loc. data lost; P35637.- Right P$^2$ crown, roots broken away, Barrie loc. HJD/X; P35638.- Right P$^2$ crown, fragment only, Barrie loc. HJD/X. P34154.- Left P$^2$ crown (Fig. 5D), roots broken, S.A. Mus. party, loc. slumped sediment centred on area 11 (i.e., loc. A11x/14+ - see Pledge 1981, table 2 legend, for explanation of this notation), 6.1.80.

P3: P24679.- Right P$^3$ cap (unerupted, margin almost fully formed), Pledge et al. 1970s, loc data lost; P22733.- Left P$^3$ cap (unerupted, margin unformed), N.S. Pledge et al., loc A6/10, 22.6.77, (figd Pledge 1981, fig. 2, as P3, P24680.- Right P$^3$ cap (unerupted, margin not fully formed), Pledge et al. 1970s, loc. data lost; P35639.- Right P$^3$ cap (unerupted, margin not formed), loc. HJD/X; P35640.- Right P$^3$ cap (unerupted, margin not formed), loc. ?

Deciduous (Molariform) Premolars (dP3): P22736.- Right dP$^3$ (Fig. 6) cap (unerupted, margin not fully formed), Pledge et al., loc. A7/9, 23.1.77, (figd Pledge 1981, fig. 2, as rM$^1$). P35641.- Left dP$_3$ (Fig. 6) crown, without roots, loc. HJD/X.

Molars (M1-M4): M1: P22734.- Right M$^1$ cap (unerupted), Pledge et al., loc. A7/9, 23.1.77; P35642.- Right M$^1$ (Figs 6, 20, 22) crown, roots broken away, virtually unworn, Barrie et al., loc. HJD/X; P34151.- Left M$^1$ cap (unerupted, margin not fully formed), loc. D6/1+2, excavated A. Rundall, 13.10.79; P34153.- Left M$^1$ (Figs 6, 20) cap (unerupted), Pledge et al., loc. F08, excavated J. Bernards, 17.3.79; P35643.- Left M$_1$ cap (unerupted), trigonid broken away from across crest of protocristid, Barrie loc. HJD/X.

M2: P22815.- Right M$^2$, crown (unerupted), loc. A6/11, coll. D. Leslett (figd Pledge 1981, fig. 2, as rM$^3$ or $^4$); P24678.- Right M$^2$, tooth in maxillary fragment, Pledge et al. 1970s. P18541.- Left M$^2$ (Figs 6, 22) crown (unerupted), N.S. Pledge 12.10.74, loc. A3/11 [= A3/ depth 60”-66”]; P34155.- Right M$_2$ (Figs 6, 22) crown (unerupted), loc. A2/11, coll. 15.11.80; P22813.- Right M$_2$, cap (unerupted, margin not fully formed), loc. A10/12, (figd Pledge 1981, fig. 2); P22814.- Right M$_2$, cap (unerupted, margin not fully formed), loc. A7/11, (figd Pledge 1981, fig. 2); P35644.- Right M$_2$, Barrie et al., loc. HJD/IV; P34152.- Left M$_2$, coll. N.S. Pledge et al. (J. & J. Barrie) 1.3.81, loc. X1E/2.

M3: P22826.- Right M$^3$, cap (unerupted, margin not fully formed), loc. A11x/14+ (see Pledge 1981, table 2 legend, for explanation of this notation), 6.1.80; P35645.- Right M$^3$, cap (unerupted, margin not fully formed), Barrie et al., loc. HJD/X; P35646.- Right M$^3$ (Fig. 6) crown, roots broken away, Barrie loc. HWW (this location is not indicated in Barrie (1990, fig. 3); it lies within the then unexcavated area south of the ‘pitfall’ (indicated to the south-east of the area shown as S.A.M.) between the ‘pitfall’ and the tunnel leading to HJDX. The location is about 6m south of the ‘pitfall’ – J. Barrie pers. comm.). P35647.- Right M$_3$ (Fig. 6) cap (unerupted, margin not formed), Barrie loc. HJD/X.

M4: P24681, Left M$^4$ (Fig. 6), cap (unerupted, margin not fully formed), Pledge et al. 1970s, loc. data lost; P22735.- left $M_4$ (Fig. 6) cap (unerupted), loc. A7/9, coll. N.S. Pledge et al., 23.1.77.

### Humeri

P18846. – Almost complete right humerus (Fig. 7) comprising most of the diaphysis but lacks part of the diaphyseal contribution to the head and the distal portion of the ectepicondyle. Collected L. and G. Henschke 1969, prob. from surface in vicinity of areas X1-X3 (Pledge pers. comm. 29.3.96), Henschke's Quarry Fossil Cave, Naracoorte, S.A. (figd Pledge 1981, fig. 3).
P35648. – Distal portion of right humerus (Fig. 8), lacks distal epiphysis. Collected J. and J. Barrie et al., Henschke's Quarry Fossil Cave, Naracoorte, S.A., Barrie loc. HJD/III.

## METHODS

### Preparation of SEMs and SEM illustrations

Specimens were coated with a 10 nm layer of pure gold using a Polaron E5000 sputter coating unit, and viewed in a Cambridge Instruments S360 scanning electron microscope (SEM) fitted with a high-brightness lanthanum hexaboride (LaB6) electron source. A 30 µm diameter final aperture, a working distance of approximately 15 mm, electron beam current of 70 pA and an accelerating voltage of 20 kV were used as the standard operating conditions. SEM images were recorded on 70 mm (220) roll film and simultaneously digitised and output as 1024 by 768 pixel, 256 grey level, TIFF files using an Image-SlaveÆ (Meeco Pty Ltd, Sydney) slow-scan image acquisition board mounted in a 486 PC.

Selected TIFF files were placed in Adobe Photoshop® 3.0 to create photographic mosaics after some image processing adjustment. These mosaic images and other isolated SEM TIFF files were imported into Adobe Illustrator® version 6.0 to make up individual plates with lettering and accompanying figures.

### Radiography

Radiographs were prepared by xeroradiography in positive mode. X-ray factors were set at 100 kV and 10 mA and exposure times of 1 second (Fig. 4) and 1.5 seconds (Figs 19-31).

## CRANIO-DENTAL MORPHOLOGY

Cranial descriptions, except where indicated, are based on P35632; mandibular descriptions on P35633 and P20815. Since indications of the size of anatomical elements are mostly derived from a single individual, only approximate values are given in the text (for measurements of specimens see Table 1). Except where stated otherwise and defined in the text or illustrations (Figs 3, 19, 23), osteological terminology follows Wells and Tedford (1995); dental terminology follows Ride (1993) and Figs 18, 20 and 21.

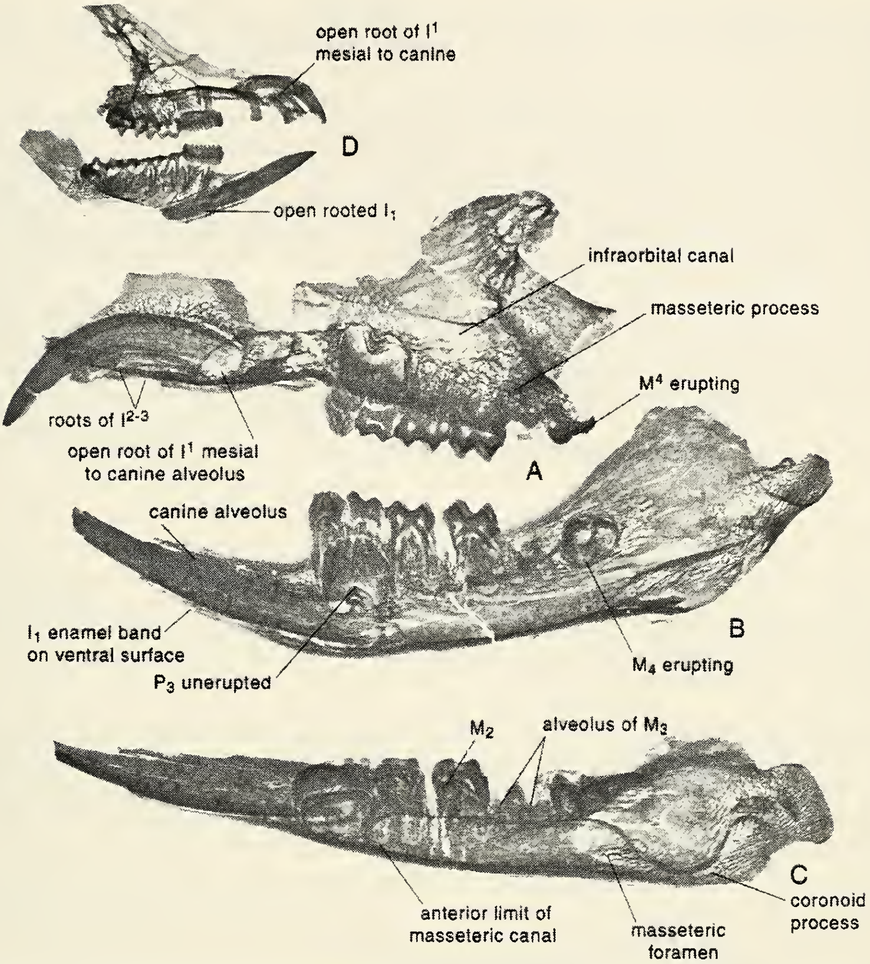


Figure 4. A, B: lateral radiographs of the cranial specimen (P35632) and left ramus (P35633) of *P. oscillans* with (D) the equivalent portions of *Aepyprymnus rufescens*. C: Oblique dorso-lateral view of the mandible showing the extent of the masseteric canal. The masseteric canal is not visible in D, its dorsal surface is exposed in the fractured ventral surface of the ramus where it extends no further forwards than $M_2$.

**Cranium** (Figs 2-4)

Premaxilla: Ventral surface of palatal plate with distinct antero-posterior channel with edges sub-parallel with the medial suture of the palatal surface, the palatal fissure ('incisive foramen'[4]) lying within the channel and wholly enclosed within the premaxilla; the posterior end of the fissure is about 1/3 of the distance from the palatal maxillo-premaxillary suture to the alveolus of $I^1$; the mesial and lateral wings of the premaxilla meet (Fig. 19) and are closely sutured posterio-mesial to the fissure. The junction between them is barely visible and very close to the median interpremaxillary suture, the mesial wing continuing posteriorly as a narrow slip as far as the maxillo-premaxillary suture. The inter-premaxillary and palatal part of the maxillo-premaxillary sutures are serrate (the latter also being a scarf joint); the bone is thickened at the sutured margins. From the palatal aspect the opening of the canine alveolus lies anterior to the maxillo-premaxillary suture, but facially the suture emerges from the alveolus about midway on the alveolar margin. The alveolus of $I^1$ lies mesial to the canine alveolus and extends into the maxilla (Fig. 4).

Maxilla: On the facial surface the infraorbital foramen opens dorsal to the anterior root of the sectorial premolar and about midway between the edge of the orbit and $I^1$. The root of the canine lies wholly within the maxilla. The cheek teeth are positioned forward along the maxilla, all but $M^3$ and $M^4$ anterior to the orbit and the masseteric process of the zygomatic. The orbit, viewed dorsally, is narrow latero-mesially. The masseteric process, although broken in the specimen, was short and rounded, sutured with the jugal almost at its tip, and lay lateral to the anterior part of $M^3$.

The maxillary palate is entire (not fenestrated) and terminates at the level of the maxillo-palatine suture the position of which is indicated by the pair of channels of the anterior palatine foramina (which, when present in macropodiforms, are located at or close to the anterior edge of the palatines through which they pass dorso-posteriorly).

The palatal plane is virtually flat and without the flexure anterior to the maxillary tooth row as occurs in similarly-sized species of Macropodidae (Bartholomai 1973, fig. 4).

Palatine: Only a trace of the horizontal (palatal) plate of the palatine is preserved but the presence of the channels of the anterior palatine foramina close to the posterior edge of the maxillary palate indicates that the horizontal plate was probably unfenestrated. The orbital plate of the palatine forms the antero-mesial surface of the orbit and extends anteriorly to form the mesial margin of the large orbital opening of the infraorbital canal through the maxilla, part of which opens to the face through the infraorbital foramen (see above).

Lachrymal: The lachrymal bone forms the antero-dorsal margin of the orbit; the small portion remaining indicates that it was not rounded, forming a supraorbital ridge. There is a prominent lachrymal tubercle projecting from the antero-dorsal rim of the orbit. Two lachrymal ducts lie within a depression on the orbital rim. The lachrymal forms a suture with the jugal ventro-laterally immediately below the lachrymal foramina.

Jugal: The jugal forms the ventral rim of the orbit and constitutes virtually the entire depth of the anterior part of the zygomatic arch, extending ventrally almost to the tip of the rounded masseteric process. Sufficient of the anterior part of the zygomatic arch remains to indicate that it was not laterally bowed.

### **Mandible** (Figs 2-4).

Dentary: Robust. In the adult, on the lateral face, equally deep below all cheek teeth; on the mesial face, deepest below the posterior end of $P_3$. In the young animal, deepest below the posterior end of $P_2$ in both surfaces. Symphysis rugose, extending the full length of the diastema and fully across the mesial surface. Genial pit well marked. Anteriorly of the genial pit the mandible inclines dorsally and the incisor is elevated above the diastema so that the incisor tips are about in the plane of the molar tooth row. Small canine present immediately posterior to the incisor alveolus. It is flattened occlusally and projects anteriorly. A small rugose area is present in the ramus anterior to $P_3$ in the adult (P20815), but no specimens give any indication that $P_2$ is retained after the eruption of $P_3$ as in the related genera *Hypsiprymnodon* (Ride 1961) and *Ekaltadeta* (Archer and Flannery 1985; Wroe and Archer 1995) and probably also in *Jackmahoneya* (Ride 1993). Radiographs (Fig. 4) indicate that $P_2$ and $dP_3$ are replaced together by $P_3$.

Mandibular condyles are cylindrical, taper mesially and are transversely elongate (i.e. they are not dorsally flattened ovoids as in Macropodidae). The articular surface of each occupies a hemicylinder extending over dorsal and posterior facing surfaces from anterodorsal to posteroventral. A line drawn at right angles to the transverse axis of each condyle lies approximately in the axis of the crest of the sectorial $P_3$. Mesial to the condyle, there is a prominent tubercle for the attachment of the lateral pterygoid muscle. The mandibular condyle lies approximately in the plane of the molar row (Fig. 3A) instead of being elevated well above it as in Potoroidae (e.g. *Potorous, Bettongia, Aepyprymnus*) and Macropodidae (e.g. *Macropus, Lagorchestes, Setonix, Protemnodon, Wallabia, Dorcopsulus* and *Dendrolagus*). It is placed lower than in other Hypsiprymnodontidae (*Ekaltadeta, Jackmahoneya* and *Hypsiprymnodon*).

The ascending process is wide antero-posteriorly and with a wide, rounded, coronoid process. The lateral masseteric crest of the masseteric fossa is low, raised only little above the ventral border of the mandible. Pterygoid fossa with only slightly raised rims. Masseteric fossa communicates widely antero-ventrally by the masseteric foramen into the masseteric canal. Inferior dental canal opening broadly into the masseteric canal. In radiographs (Fig. 4), the masseteric canal extends forward within the ramus to the level of the rear of the $P_3$.

Mental foramen for the exit of the inferior dental canal large, single, placed immediately anterior to and ventral to both $P_2$ and $P_3$.

## Dentition:

Incisors: $I^1$ recurved, obliquely chisel-shaped; enamel covers the anterior surface and extends part way around the sides; on the lateral side it covers about 80% of the thickness of the unworn tooth; on the mesial side it only covers about 50%. In the worn tooth (i.e., the tooth sharpened in use) there is a marked 'thegotic step' inclined across the lingual (posterior) surface where the dentine is worn away resulting in a sharp, laterally angled, chisel-like tip. The distance from the 'step' to the sharp incisive edge is about 10 mm. Radiographs (Fig. 4) indicate that the tooth is open rooted and that the anterior enamel band continues along the full length of the tooth in its alveolus. When first erupted (P35634, 5) enamel forms an apical cap which covers all surfaces, extending along the lingual surface for some 3.5 mm from the tip. Wear commences in the dentine on the posterior surface below the apical cap.

The alveolar portion of the tooth (the 'root') extends posteriorly along the full length of the premaxilla, lying mesial to and overlapping the canine alveolus and extending into the maxilla.

$I^2$ and $I^3$ are represented only by their alveoli which slope posteriorly. From these, the teeth were small and arranged antero-posteriorly immediately behind the first beak-like pair. The antero-posterior diameters of the three incisor alveoli are: 7.7, 2.5 and 4.5 mm.

$I_1$ chisel-shaped. Enamel confined to the anterior, mesial and lateral surfaces. On the lateral surface the enamel extends about midway across the surface. Wear produces a basined, sharp, inclined, chisel edge. The tooth is open rooted and, in radiographs of both the adult P20815 and the young individual P35633 (Fig. 4), the enamel band is seen to extend the full length of the ventral surface of the tooth within the alveolus.

Canine: Upper canine curved and bucco-lingually compressed; lingual and buccal surfaces meet posteriorly at a ridge. Enamel on the buccal surface extending about 10 mm from the tip; on the lingual surface for about 3 mm. Lower canine$^2$ very small, located closely behind the incisor. In specimen P20815 the occlusal surface projects forward from the root and is flattened dorsally (possibly by wear).

Premolars (P2 and P3)(Figs 5, 9): Sectorial, robust, anteriorly out-turned at about 15° to the molar row; premolars are ridged, and channelled between the ridges ('fluted').

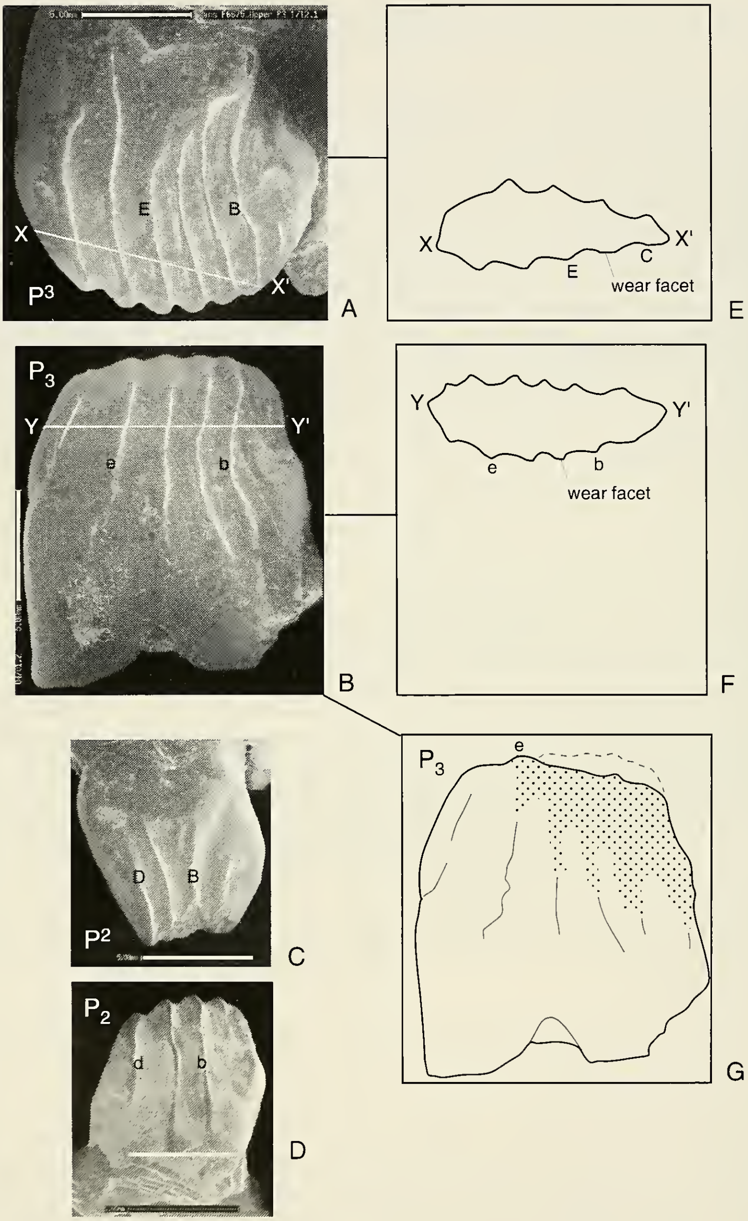


Fig 5 12/6/96

Figure 5. Sectorial premolars of *P. oscillans*: A-D, occlusal faces of A: $P^3$ (F6675), B: $P_3$ (P20815 epoxy cast), C: $P^2$ (P24677), D: $P_2$ (P34154). The crest of the $P^2$ is greatly chipped. E-F: transverse sections of casts of premolars F6675 and P20815, respectively. In each, the occlusal face is towards the lower edge of the figure. G: wear in $P_3$; the wear facet in the worn premolar of the holotype, Qd Mus. F3302 is shown in stipple. Superimposed as a broken line is an outline of the crest of the relatively unworn premolar of P20815 to indicate the area of the tooth that becomes worn by tooth-on-tooth apposition. White scale bars in A to D = 5 mm.

Detailed descriptions of premolar surfaces and their wear features are given in the text accompanying SEM figures (Figs 10-18). In the descriptions, cusps and ridges are lettered sequentially from posterior to anterior (upper teeth **A**, **B**, **C**, etc., lower teeth **a**, **b**, **c**, etc.).

$P^3$ and $P_3$ (Fig. 5A, B) are compressed, with cuspidate crests proud to the level of the molars (Fig. 9), and continuous along the full length of the tooth, ridged on both buccal and lingual surfaces. $P^2$ and $P_2$ (Fig. 5C, D) are shorter, less compressed, in plan are wedge shaped (roughly as broad as long), and with fewer ridges. Neither has a basal cingulum. Along the crest each ridge terminates in a cusp and is separated from the ridge anterior and posterior to it by a channel. Posteriorly, there is a facet for the receipt of the adjacent molariform tooth; anterior to the most anterior cusp the crest curves lingually in both upper and lower premolars.

In the maxilla Qd Mus. F6675, the tips and anterior edges of the cusps are extensively abraded[5] by hard inclusions within food (Fig. 10); in the mandibular cusps of P20815 abrasion grooving occurs mostly at the posterior edges of cusps (Fig. 11).

If it is assumed that planar wear can only result from attrition[5] produced by tooth-on-tooth contact, attrition is initially confined to facets along the hindmost ridges and in the vicinity of cusps and posterior facets, although attrition facets show abrasion as well. In both upper and lower premolars, following a narrow posterior abraded 'shoulder' of the more-or-less planar facet, the edge falls away from the ridge sharply into the succeeding channel providing an abrupt rear face to each ridge (Fig. 14). Towards the crest (Fig. 10), the descent into the channel is more gradual. Within the channels there are no planar wear facets or other evidence of tooth-on-tooth contact (Fig. 16) until adjacent ridges are obliterated by wear (Fig. 5G). Channels contain abrasion features.

The series of $P_3$s demonstrates several stages in the development and spread of wear facets from the unworn tooth to the worn condition. Initially, facets form anterior to the posterior edges of the hindmost ridges; in the most worn specimen (the holotype, Qd Mus. F3302, Fig. 5D), the facets in the posterior part of the tooth have widened into each other, obliterating the ridges over a wedge-shaped area extending from the tip of cusp e to much of the lengths of ridges **a** and **b**.

In all $P^3$s examined, there are 7 cusps and ridges (**A-G**). The occlusal face has the following features: The surface behind ridge **A** bears a wear facet facing slightly obliquely towards $M^1$. It extends to the crest where it makes a notch with the paracrista and preprotocrista of $M^1$ which are abraded. Ridge **A** is short and extends only about 1/3 of the distance from the crest. It has only a low, rather indistinct cusp. An anterior-facing wear facet extends along the full length of the ridge and onto the extensive non-ridged and protruding area that lies between it and the enamel margin at the base of the tooth. Ridge **B** has a large anterior wear facet that is widest on the 1/3 of the ridge closest to the crest (its apical third); after that the ridge curves sharply forward to terminate close to ridge **C**.

Ridges **C, D,** and **E** are similar to each other. They are crescentic (convex anteriorly) and more or less parallel with each other; each has an anterior wear facet widest along its apical third. They terminate on a rounded projection (the 'lingual boss' – Fig. 18) a short distance from the enamel margin. The channels between ridges **C, D** and **E** come together at the boss. The ends of the channels at the boss, and the boss itself, show extensive abrasion grooves and pits.

Ridges **F** and **G** lie anterior to and do not terminate at the lingual boss; their course is almost vertical. Their cusps are extensively damaged by abrasion pitting. Wear, but not the facetting of attrition, occurs along their length and anterior on the surface anterior to ridge **G**.

All the $P_3$s examined have 6 ridges (**a-f**). The occlusal face has the following features: Ridge **a** is short. Posterior to it there is a postero-buccal wear surface forming a notch with an antero-buccal surface (the worn trigonid basin) of $M_1$ bounded dorsally by the premetacristid and the protocristid. Ridge **b** traverses the full height from the crest to the enamel margin. Leaving the crest, it curves slightly anteriorly and then posteriorly. Abrasion grooving on the wear facet is more-or-less vertical (Fig. 12). Ridges **c** and **d** are more-or-less parallel. Ridges **e** and **f** diverge from **d** basally. In the extensively worn holotype, only the cusps at **e** and **f** remain; the others are obliterated (Fig. 5G).

In all $P^2$ examined there are 4 ridges (**A-D**). The occlusal face has the following features: Ridges **A** and **B** are more-or-less parallel (Fig. 5C, D) and before **B** reaches the enamel margin it terminates on a lingual projection smaller, but functionally similar to the boss of $P^3$. Ridge **C** runs parallel **D** which curves anteriorly and then posteriorly away from the leading edge of the tooth. In the very worn tooth (P24677) there is extensive chipping of the crest behind cusp **D**.

All $P_2$s examined have 4 ridges (**a-d**). The crest is parallel with the parametacristid of $dP_3$ and at the same height. In occlusion with the maxillary toothrow, these two crests together match the posterior end of the crest of $P^2$. The occlusal face has the following features: Ridge **a** is very short terminating at a swelling where the postero-buccal margin follows the shape of $dP_3$ which abuts it. The widest part of the tooth is at ridge **b**. Ridges **c, d** are parallel and diverge from ridge **b** as they depart from the crest.

Molariform teeth (dp3, M1-M4; Figs 6, 20-22; Table 1): Both upper and lower molariform teeth are quadritubercular and rounded in outline at their enamel margins. Each has a mid-longitudinal valley which passes between the buccal and lingual cusps and is continuous from tooth to tooth, extending along the entire molar row. Although the molars are not lophodont, each is divided into three basins by transversely directed crests which fall away from near the apex of each cusp to a point of least relief at the mid-longitudinal valley. Anterior and posterior basins are only about half the length of the central basin. Since both anterior and posterior basins of each molar are only separated from the basins of the adjacent molars by very low crests, the entire molar row appears to consist of a regular series of squarish basins, contributed to by adjacent teeth. Progressing along the tooth rows, lingual and buccal marginal crests fall from the cusps into inter-molar embrasures between the teeth and, in the centre of each tooth, to a sulcus between the anterior and posterior pairs of cusps. Viewed from the lingual or buccal surface, the occluding molar rows present a margin of interlocked dentate crests.

The dental gradient is dP3<M1<M2<M3>M4. Lower molars are only slightly narrower than the uppers.

The molariform deciduous premolars ($dP^3$, $dP_3$) (Fig. 6), although smaller than $M^1$, $M_1$, are almost fully molarized, only the trigonid of $dP_3$ being somewhat compressed where the parametacristid forms a crest continuous with the serrate crest of $P_2$. The last molars ($M^4$, $M_4$) taper posteriorly; the posterior cusps being slightly closer together than the anterior cusps and the postero-lingual cusps (metaconule and entoconid) are positioned slightly anterior to the postero-buccal cusps (metacone and hypoconid).

In the unworn upper molars (Fig. 6) there is little difference in the relative heights of the cusps. In $M^1$, the paracone is the tallest cusp, followed by the metacone, protocone, and metaconule; but in $M^2$ the protocone and metaconule are taller than the buccal cusps. The remaining upper molars are only known from separate teeth of which relative cuspal heights of the implanted condition cannot be determined precisely.

Upper buccal cusps (paracone and metacone) (Figs 20, 21D, B) are more or less pyramidal with three sharp ridges, two extending antero-posteriorly (preparacrista, postparacrista; premetacrista, postmetacrista) and the other (paracrista and metacrista) transversely towards the bottom of the mid-longitudinal valley of the tooth. The antero-posterior ridges that form the centrocrista (premetacrista and postparacrista) are barely continuous across the transverse sulcus.

Upper lingual cusps (protocone and metaconule Figs 20, 21D, A, F) also have transverse ridges. But these are shorter and less pronounced than those from the paracone

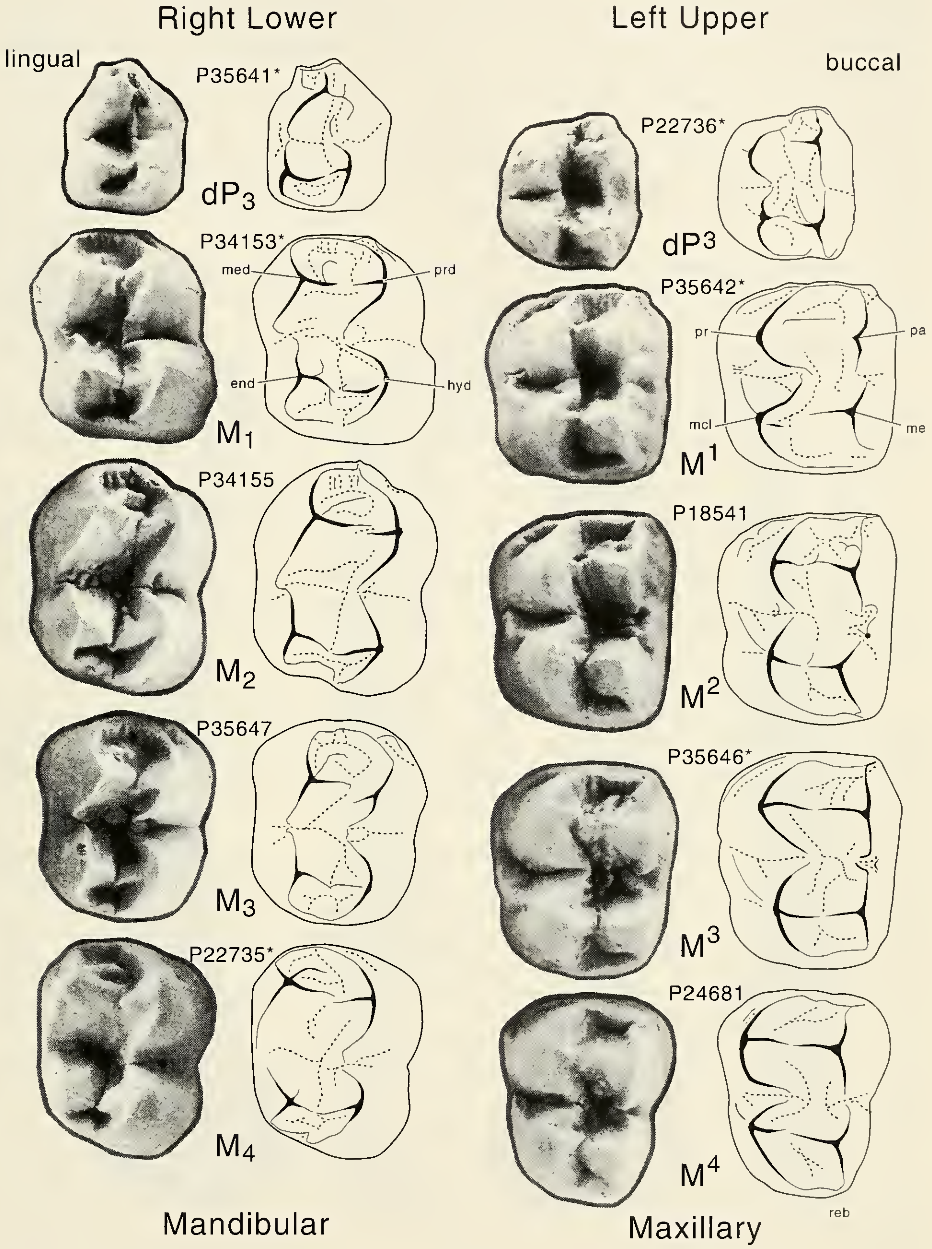


Figure 6. Unworn molarform teeth of *P. oscillans*. The teeth shown are crowns and enamel caps from Henschke's Fossil Cave (as listed in text). *Teeth so indicated are presented as mirror images to enable comparable orientation within tooth rows. Explanatory drawings use the same conventions as in Fig. 20, in which cristae and cristids are labelled with terms used in the text. Abbreviations for the principal cusps are: uppers – pa (paracone), me (metacone), pr (protocone), mcl (metaconule); lowers – prd (protoconid), hyd (hypoconid), med (metaconid), end (entoconid).

and metacone and contribute little to the partitions across the central basin. In unworn teeth, they remain unfused in transverse ridges, their junction is marked by a fissure. The crests that run anteriorly and posteriorly from the apices of the protocone and metaconule (postprotocrista and premetaconulecrista), when unworn, follow the rounded margins of the molar with the result that lingual crests appear selenoid. Like the buccal crests, they also remain unfused across the sulcus. With wear, the tips of the lingual cusps also become low and rounded. Dentine becomes exposed at their tips (cavitation through enamel commencing at the tips of the protocone and metaconule; Fig. 21A, F). The antero-posterior ridges develop inward facing facets aligned along the mid-longitudinal valley.

The surface within the basins of both upper and lower molars (including the central basin) contains low irregular rounded projections and a few accessory spurs from surrounding crests. The parametacristid into the trigonid basin of lower molars is the most prominent of these.

On the buccal surface of upper molars only stylar cusp C is a raised stylar cusp, it is most prominent on $M^2$ and $M^3$ (Fig. 6). The positions of stylar cusps A and E are indicated by angular junctions of cristae at the antero-buccal and postero-buccal margins; raised cusps do not form at these points, except, possibly, in $dP^3$ (Fig. 6).

On the lingual margins of the upper molars anterolingual cingula are present on each tooth, diminishing posteriorly along the tooth row. A metaconule accessory crista (Figs 20, 21E) slopes antero-lingually towards the lingual margin of each metaconule from near to its tip. Together the series of anterolingual cingula and the channels between the metaconule accessory cristae and the metaconules 'nest' the metaconid and entoconid as they occlude with the lingual surfaces of the protocone and metaconule (facets 4 and 5 of Fig. 21D, E; Fig. 22).

By contrast with the upper molars, in the mandible it is these lingual cusps (metaconid and entoconid) that are taller, sharper, and more acutely ridged than the buccal protoconid and hypoconid (Fig. 6). The sharper lingual cusps are more or less pyramidal with three sharp ridges, two extending obliquely antero-posteriorly (postmetacristid and preentocristid) and the other transversely (posthypocristid, entohypocristid) into the central basin of the tooth.

In the lower molars, the selenoid series of crests is on the buccal cusps (protoconid and hypoconid) (Fig. 20). The selenoid crest between the hypoconid and the protoconid probably represents the cristid obliqua. It is disjunct where its two components reach its lowest point. The buccal cusps become rounded (and ultimately, cavitated) with wear. Short transverse crests (protocristid, posthypocristid) run mesially from the buccal cusps into the mid-longitudinal valley originating somewhat mesial to the crescentic tips of the cusps. As in the upper molars, in the unworn tooth these short transverse crests do not unite with the longer transverse crests (metacristid, entohypocristid) originating from the apices of the sharp lingual cusps (metaconid and entoconid). Anterior and posterior basins have marginal crests as in the upper molars. On all lower molariform teeth a parametacristid (Ride 1993) is present; in $dP_3$, $M_1$ and $M_2$ it originates on the transverse crest (metacristid) close to the metaconid (a raised parametaconid occurs only on $dP_3$); posteriorly, in $M_3$ and $M_4$, the parametacristid originates at the metaconid. Only in $dP_3$ does it provide a functional crest continuous with the crest of $P_2$. In the molars it is truncated and, although running anteriorly into the trigonid basin, it terminates before reaching the paracristid.

Viewed from the rear, the mandibular toothrow twists clockwise so that the rounded buccal cusps of $M_3$ and $M_4$ become elevated. The mid-longitudinal valley of the molar tooth row as a whole follows in the plane of the occlusal surface of the sectorial premolar. In the most worn toothrow examined (the holotype mandibular ramus Qd Mus F3302), the rounded buccal cusps of the anterior molars wear almost to the level of the mid-longitudinal valley; in all but $M_4$ a basin of dentine is exposed on the tips of the buccal cusps. The Lake Menindee specimen which we have not examined personally (UCMP51697, figd by Archer and Flannery 1985, fig. 3.3) shows a more advanved state of dental wear than the holotype.

## POST-CRANIAL MORPHOLOGY

### Humeri

The humerus P18846 (Fig. 7) was briefly described by Pledge (1981). As it is the more complete of the two humeri, it is considered first here.

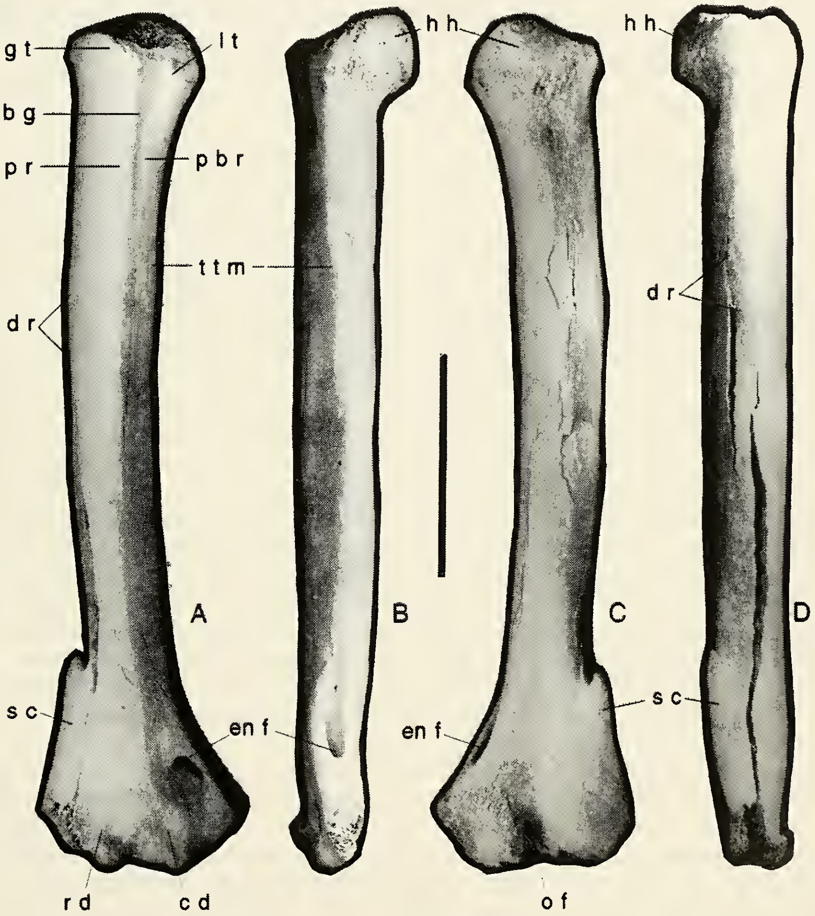


Figure 7. Right humerus (P18846) attributed to *P. oscillans*. The bone is shown in A. anterior; B. mesial; C. posterior; D. lateral view. b.g. = bicipital groove, c.d. = coronal depression, d.r. = deltoid ridge, en.f. = entepicondylar foramen, g.t. = greater (lateral) tuberosity (remnant), h.h. = humeral head (remnant), l.t. = lesser (medial) tuberosity (remnant), o.f. = olecranon (anconeal) fossa, p.b.r. = posterior bicipital ridge, p.r. = pectoral (anterior bicipital) ridge, r.d. = radial depression, s.c. = supinator (supracondylar, ectocondylar) crest, t.t.m. = tubercle for insertion of m. teres major. The specimen has been whitened with ammonium chloride. Scale bar = 5 cm.

Although the proximal and distal epiphyses of P18846 are missing, the diaphysis is largely intact. Proximally the diaphyseal contribution to the humeral head is incomplete; distally the outermost point of the ectepicondyle is broken away. The present length of the bone (195 mm) is less than in life and we estimate that the total length of the bone was originally close to 210 mm. The width of the bone is greatest distally where the maximum transverse dimension is presently 47 mm. Before the corner of the ectepicondyle was lost this measurement would have been greater by some 2 to 3 mm.

Proximally the bone bears evidence of a well developed head (Fig. 7B). This is very closely applied to the shank so that no narrowed neck region can be recognized. The diaphyseal contribution to the head is complete except for a small mesial portion and its terminal part. Despite the missing material it is evident that, relative to the rest of the humerus, the articular surface of the head would have been directed terminally and posteriorly (Fig. 7D). The proximal portions of both the greater (lateral) and lesser (medial) tuberosities are missing. The diaphyseal base of the greater tuberosity is larger than that of the lesser, but both tuberosities seem to have been well developed. A shallow and relatively broad bicipital groove separates these tuberosities anteriorly and although this becomes decreasingly distinct distally it can be traced down the bone over its proximal quarter.

The anterior surface of the main portion of the humeral shaft is incompletely divided by a low and rather indistinct pectoral (or anterior bicipital) ridge (Fig. 7A). The more proximal and sharp-edged portion of this extends from the base of the greater tuberosity and forms the lateral margin of the bicipital groove. It passes down over the first quarter of the bone before becoming indistinct. After a short gap, the distal portion of the pectoral ridge continues down the bone along the same alignment. The latter is a low flat-topped structure extending over the middle third or so of the anterior humeral surface.

A second low inconspicuous ridge arises on the lateral margin of the humerus about a quarter of the way down the shaft and extends a little over halfway down its antero-lateral surface. As it passes distally this ridge gradually curves anteriorly so that its most distal part lies on the anterior surface of the humerus. In living macropodiforms a ridge, which is generally more robustly developed, occupies the same general area of the antero-lateral surface of the humerus. In some larger forms the proximal and most lateral part of this ridge is locally modified to form a substantial laterally-directed tubercle (Fig. 25B). This tubercle is the structure which Owen (1876, p. 431) has referred to as an insertion of the 'pectoralis' in *Macropus rufus*. This entire second ridge is evidently homologous to the deltoid ridge of placental mammals. In many extant macropodiforms the distal extension of this ridge joins that of the pectoral ridge and together these form two sides of a triangular area (Fig. 25). This triangular area marks the site of insertion of the deltoid muscles in *H. moschatus* (Heighway 1939), *M. giganteus* (Hopwood 1974, fig. 15), *M. rufogriseus* (Pridmore and Ride unpub. data), and presumably in other macropodiform species where it occurs.

Anteriorly the base of the lesser tuberosity bears a broad ridge of low relief (Fig. 7A). This posterior bicipital ridge merges over a very short distance into the anteromesial surface of the shaft so that it is only discernible as a separate entity over the proximal eighth of the shaft. Distal to this ridge and centred about a third of the way down the mesial surface of the bone is another low proximo-distally elongate ridge. Immediately posterior to this latter ridge and lying parallel to it, is a shallow elongate depression. By comparison with the condition in *Macropus giganteus* (Hopwood 1974), ridge and depression are thought to mark the area where the teres major and latissimus dorsi muscles inserted.

When viewed from the anterior or posterior (Fig. 7A, C) the shaft of the humerus is seen to be moderately curved (concave mesially). There is no sign of curvature from a lateral or medial perspective over the proximal three fifths of the shaft, although the posterior surface becomes very slightly convex about two thirds of the way down (Fig. 7B, D). Aside from its proximal and distal expansions, the diaphysis is for most of its length relatively constant in diameter and approximately cylindrical in form. At mid-length the humeral shaft is 18.5 mm wide and has an antero-posterior thickness of 17 mm.

Much of the posterior surface of the humeral shaft is evenly convex, although over the distal third it gradually flattens and then becomes slightly concave due to the olecranon fossa. The antero-mesial and antero-lateral surfaces of the shaft are convex over their proximal third but show locally flattened or slightly concave regions about midway down the shaft. A flat triangular area occurs on the second quarter of the antero-lateral surface between the pectoral ridge and the deltoid one. A flattened and slightly convex area occupies the middle third of antero-mesial surface of the shaft between the pectoral ridge and internal border of the humerus. Distally both these surfaces of the shaft are convex, each akin in form to a longitudinally-sectioned cylinder.

The distal end of the humerus is laterally expanded and its anterio-posterior thickness reduced. The extent of the lateral expansion is much less than occurs in humeri of similar length from *Macropus giganteus* whereas the anterio-posterior thinning is relatively much greater in the fossil. Because of the absence of the distal epiphysis, it is impossible to determine whether the entepicondyle was weakly or strongly developed. However, the entepicondylar ridge is preserved and this is a weaker structure than the corresponding structure found on humeri of similar length from *M. giganteus*. On the other hand, the entepicondylar foramen which passes beneath this is as large in the fossil as in similar-sized specimens of *M. giganteus*.

The ectepicondyle is incomplete distally, but was clearly less developed than in similar-sized specimens of *M. giganteus*. It bears a supinator (supracondylar) crest that extends up the diaphysis from the ectepicondyle. This crest is formed by a shelf of bone that thins laterally over a short distance. It terminates proximally as a small peg-like process. The crest is much narrower in the fossil than in similar-length humeri from *M. giganteus*. The posterior surface of the distal humerus is marked by a large olecranon (or anconeal) fossa. On the anterior surface two small very shallow depressions can be identified; a radial depression which lies laterad of the slight convexity that represents the reverse surface of the olecranon fossa and a coronal depression which lies mediad of this.

Humeral torsion, an angular measure of the orientation of the distal humerus relative to the proximal (see Evans and Krahl 1945 for definition), is difficult to measure in P18846 because of the absence of both epiphyses. Nevertheless, a reasonable estimate of the range within which it is likely to have fallen can be obtained using as the distal reference, a line passing mesially along the distal surface of the bone, and as the proximal one, a line passing though the most posteriorly directed part of the diaphyseal contribution to the humeral head and the proximal part of the lateral margin of the bicipital groove (i.e. the transition between this groove and the pectoral ridge). Measured in this way humeral torsion in this specimen lies between 12° and 27°. Comparison with values given by Evans and Krahl (1945) is not possible because the proximal reference line used in making this estimate is not the same as that used by them. Needless to say, it can be compared with measurements obtained from other species using these same reference lines (Table 3).

The second less complete humerus comes from an individual which was somewhat larger than the animal that provided the humerus of Fig. 7. Specimen P35648 is the distal half of a right humeral diaphysis (Fig. 8). It is abraded distally so that it lacks both the lateral margin of the supinator crest and the bridge of bone that closes the entepicondylar foraman medially. Despite its incompleteness, enough of the bone is available to establish that its anterior surface lacked a well developed pectoral ridge. Viewed from a proximal perspective this diaphysis is seen to be rounded-triangular in cross-section over its third quarter with flattened antero-medial and antero-lateral surfaces and a evenly curving posterior surface. These are features it shares with the more complete humerus and which set both apart from similar-sized specimens of *Macropus* and *Sthenurus*. To the extent that this humerus can be compared with the more complete one, the two bones are very similar. Measurement of the shafts of the two bones at a level immediately adjacent to the proximal termination of the supinator crest indicates that P35648 is approximately 10% wider than P18846.

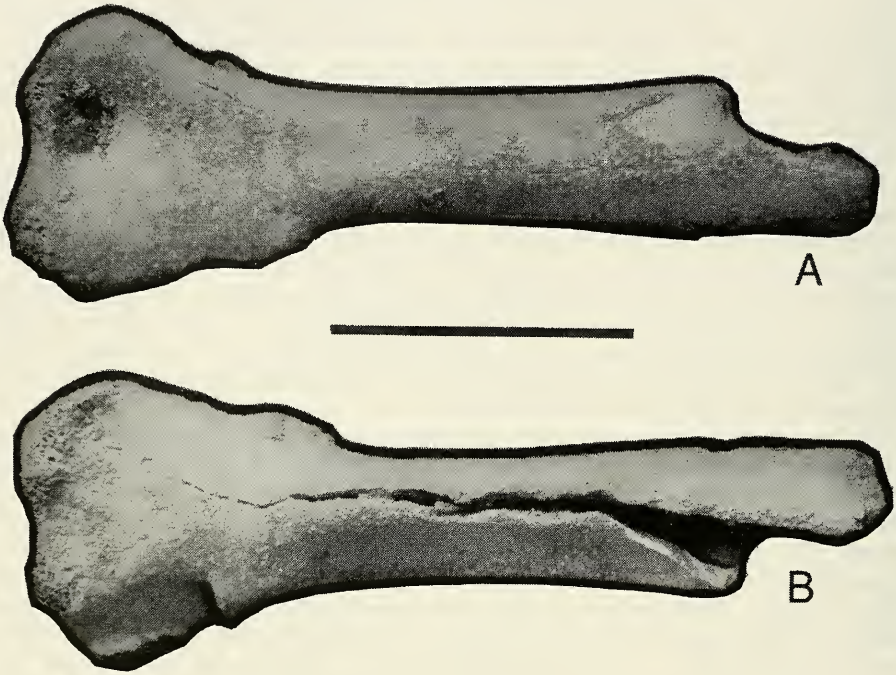


Figure 8. Additional partial humeri P35648 attributed to *P. oscillans*. The bone is shown in A. anterior view; B. posterior view. The specimen has been whitened with ammonium chloride. Scale bar = 5 cm.

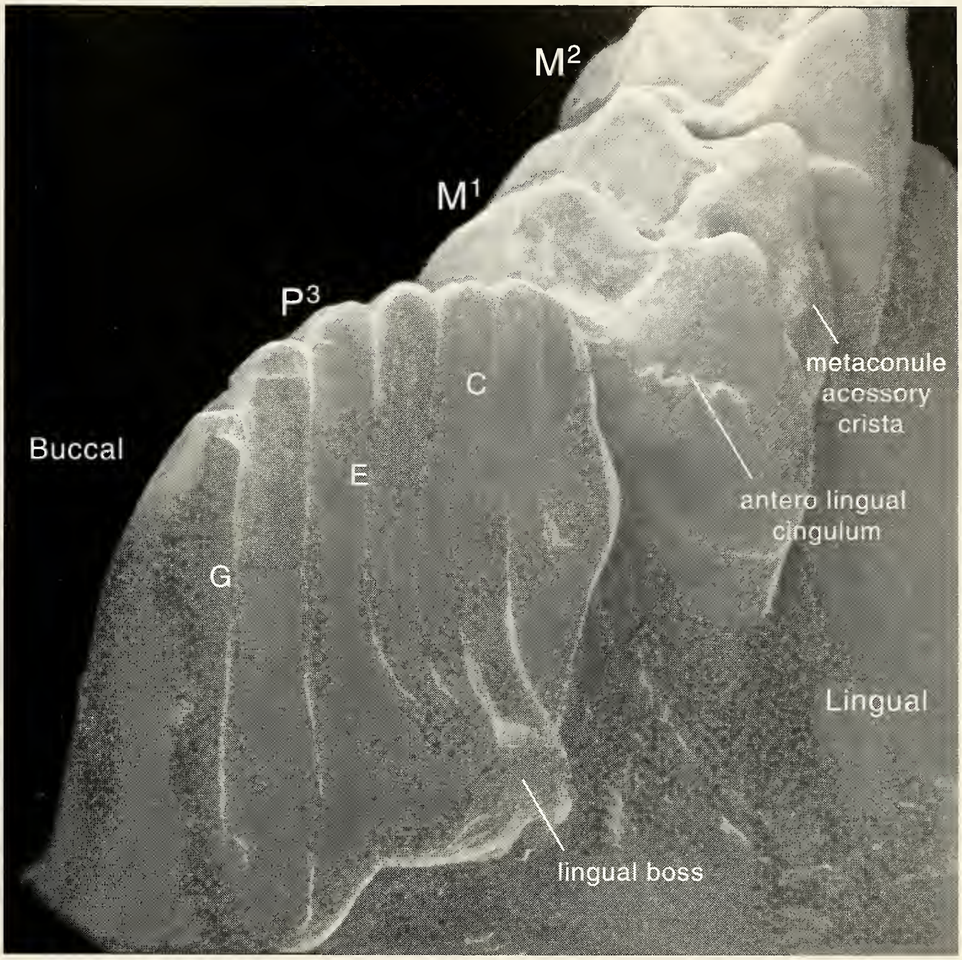


Figure 9. SEM of the left maxillary premolar $P^3$ and the anterior molars of Qd Mus. F6675, Cattle Creek, nr Dalby, Darling Downs, Queensland. The image is from the antero-mesial aspect and shows the occlusal features of the upper tooth row of *P. oscillans*.

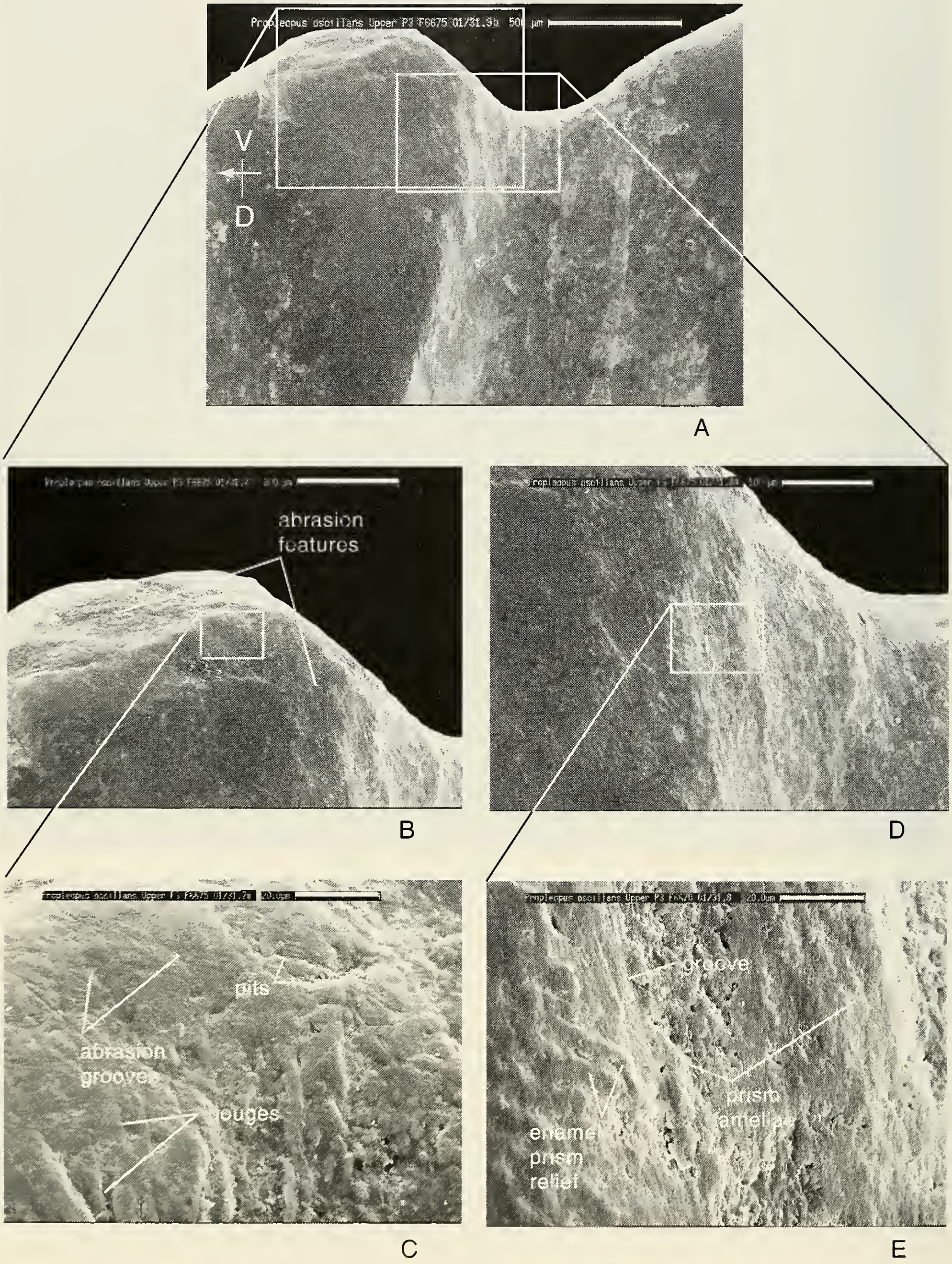

Propleopus oscillans Upper P3 F6675 01/31.3b 500 µm
V
D
A
abrasion features
B
D
pits
abrasion grooves
gouges
C
groove
prism lamellae
enamel prism relief
E

Figure 10. *P. oscillans*, $P^3$, F6675, abrasion features of part of crest between cusps **D** and **E** viewed from the lingual (occlusal) surface. White scale bar in A = 500 µm, B = 200 µm, C = 20 µm, D = 100 µm, and E = 20 µm.

Interpretation.- A: Cusp **E** in upper left. Wear facet **E** is the dark area on the left, wear facet **D** on the right. The paler area extending obliquely downwards from the saddle between the cusps is the commencement of the channel (**E/D**) between ridges (see Figs 15, 16). Shallow abrasion features towards the right in Fig. A (some more than 100 µm in width) may be post-mortem artefacts caused in cleaning.

B and C: Detail of the tip and lingual surface of cusp **E** showing abrasion features – chipping on the antero-ventral face (upper left) of the tip of the cusp, pits (non-linear), gouges (short linear), and abrasion grooves (long linear). D and E: The wear surface at the commencement of the posterior edge of wear facet **E** showing prism relief exposed on the surfaces and some abrasion grooves transecting the linear patterns of prism features.

Interpretation.- Diazonal prism relief exposed on the shoulder of the ridge indicates a radial arrangement of prisms on the wear facet, a wear resistant feature; the edges of enamel lamellae appear in the channel (see Fig. 15). Chipping of the antero-ventral edge of the cusp, and pits and gouges in that area, indicates that objects may be crushed at the premolar crest, but the small amount of major damage to the cusps which are vulnerable to such fracture in both this specimen and the Green Waterhole mandible (Fig. 11) probably indicates that puncture-crushing of large hard objects at the premolar crest is not frequent. However, in much worn specimens (e.g. the holotype, Fig. 5G) and in the worn deciduous premolar (perhaps due for replacement – Fig. 5C), the cusps may be virtually chipped away. The position of this fracture relative to the cusp apex, and similar fractures on cusps **F** and **G** of this tooth, indicate that the fracturing pressure was applied to it from the mandible pressing posterodorsally. The common occurrence of small pits, gouges and abrasion grooves on the antero-lingual surface of upper cusps indicates that material subject to premolar shear frequently contained small hard inclusions.

Exposure of prism features in areas of possible tooth-tooth and tooth-food-tooth contact of mammal teeth has been interpreted as indicating fine polishing by tough but non-scratching materials (e.g. leaves, Walker, et al. 1978, fig. 3A and C), etching by dietary acids (Teaford 1988a), regurgitated stomach acids (Van Valkenburgh, Teaford and Walker 1990, pp. 325 and Pl. III), possibly tooth grinding (Teaford 1988a, fig. 1), and shown experimentally may be produced by polishing by substances softer than enamel (gas propelled $NaHCO_3$, Boyde 1984). The concentration of exposed prism relief on certain worn surfaces in the teeth of *P. oscillans* argues against a general explanation, such as chemical etching, being the cause. It seems likely that both the exposure of prisms on the shoulders (ridges) of the wear facets, and the exposure of laminar structure along the edges and within the channels, have a common cause, namely polishing by relatively soft but tough materials. Koenigswald and Clemens (1992, p. 206) have suggested that arrangements like the prism relief observed on the ridges argue that, where the angle of prism incidence to a tooth surface is largest, as when prisms are radially arranged, wear will occur at the slowest rate, but that such surfaces are vulnerable to fracture.

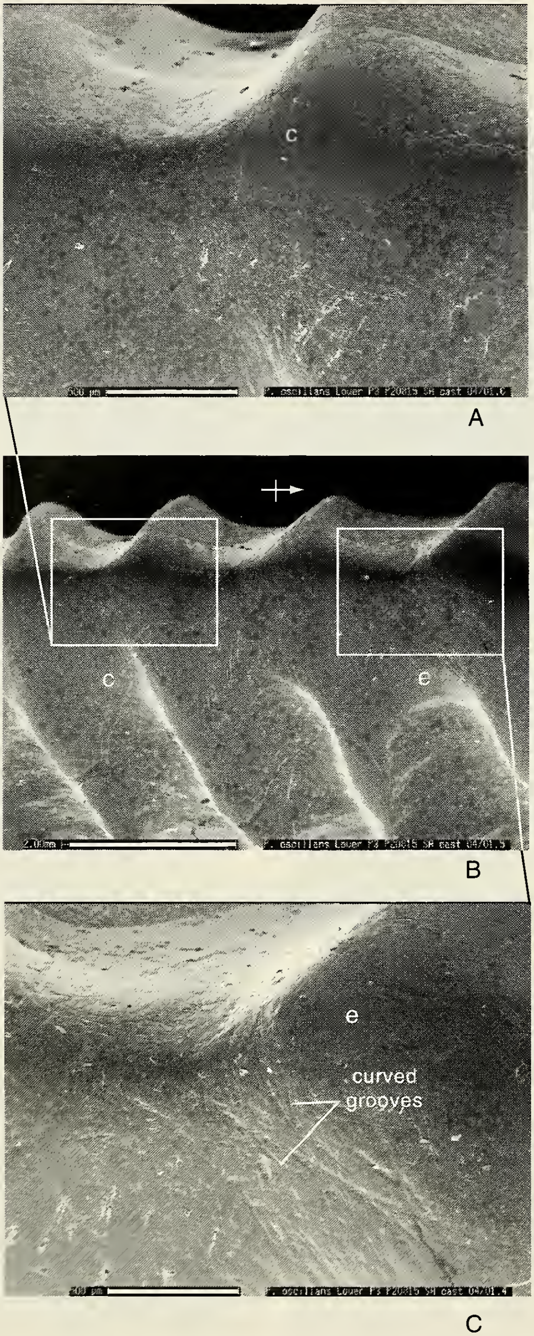


Figure 11. *P. oscillans*, $P_3$, (epoxy cast of P20815) abrasion features of part of crest from cusps **b** to **e** viewed obliquely from the dorso-buccal (occlusal) surface. White scale bar in A = 500 µm, B = 2 mm, and in C = 500 µm.

Interpretation.- A and C illustrate abrasion features immediately behind the cusps **c** and **e** respectively. In this specimen, although fully adult, there has been no major chipping of cusps. Pits, gouges and abrasion grooves mostly occur behind the cusps; from there, abrasion grooves run diagonally forward and ventrally onto the wear facets of the ridges beneath the cusps indicating that the cusps of the lower premolar are moved in a postero-dorsal direction.

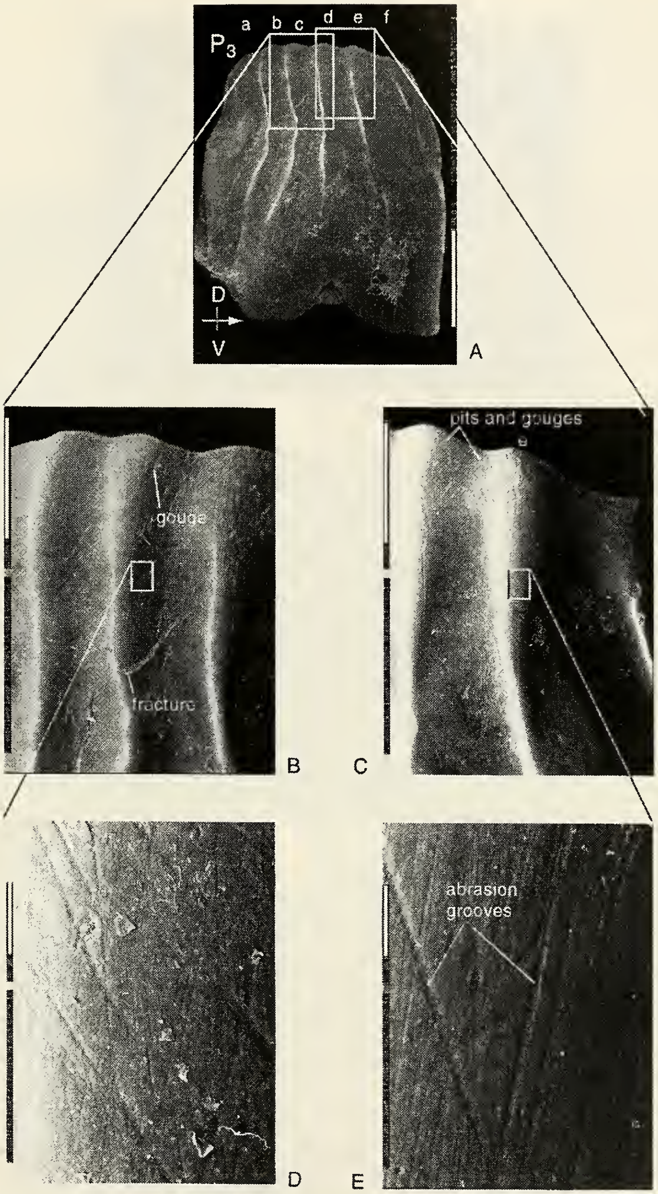


Figure 12. *P. oscillans*, $P^3$, (epoxy cast of P20815), abrasion features of wear facets **c** and **e**. Abrasion grooves on the facets are long parallel-sided features much more regular than those in the channels (Fig. 16). White scale bar in A = 5 mm, B = 2 mm, C = 2 mm, D = 100 µm, and E = 100 µm.

Interpretation.- Regular grooving is typical of shearing facets of extant animals feeding on substances containing hard inclusions. Teaford (1988a, fig. 7b and d) describes it in leaf eating primates where the examples are characterized by low variation in groove width. Van Valkenburgh, Teaford and Walker (1990) illustrate it in Carnivora. There, in cheetah (pl.1, fig. a), a flesh-eater, variation is low as compared with lion, pl. 1, fig. b) a moderate bone-eater. Feature density, as measured by the number of linear features transected by a line drawn at right angles to the general direction of the features, is comparable with lion as illustrated by Van Van Valkenburgh, Teaford and Walker (1990). In *P. oscillans*, as in the shearing facets of lower carnassials of Carnivora, there is variation in groove orientation, although the range in orientation indicates a general directional trend (more-or-less orthal). Fig. 34 illustrates comparable groove variation in the postero-lingual wear facet of $P^2$ of *P. oscillans*.

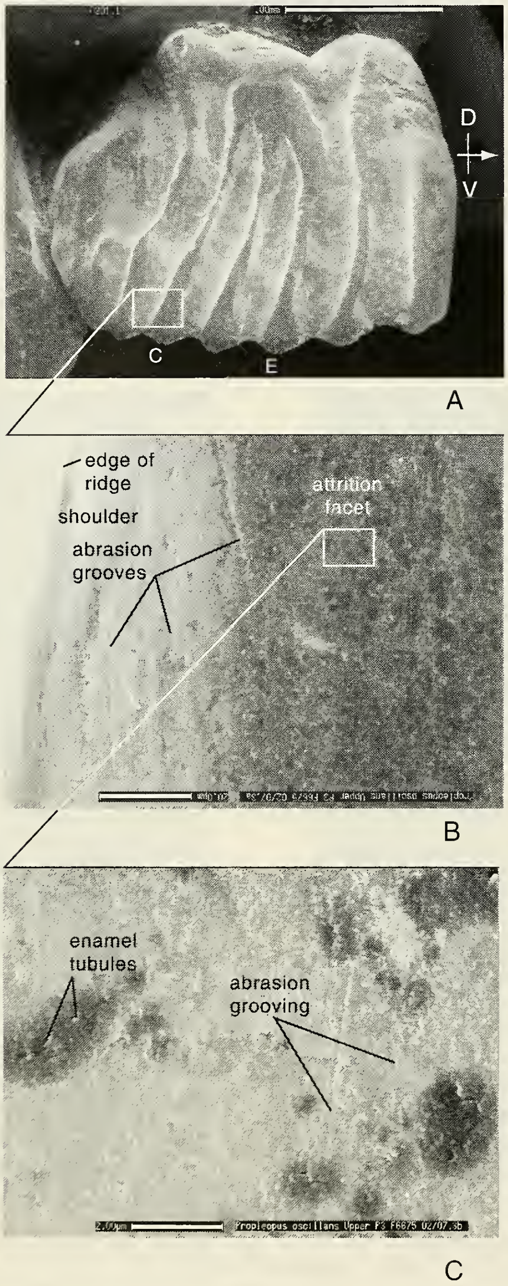


Figure 13. *P. oscillans*, $P^3$, F6675. Abrasion features of the surface of an upper attrition facet (wear-facet **C**). White scale bar in A = 5 mm, B = 20 µm, and in C = 2 µm.

Interpretation.- Abrasion grooves in the surface indicate movement slightly diagonally towards the top left of the frames (posterodorsally) from the planar attrition facet across the shoulder of the ridge, and thence over the edge of the ridge into the channel. While the planar attrition surface of the facet has a polished surface without visible prism relief, the presence of clusters of openings of enamel tubules in the polished surface indicates that the area (like the shoulder, see Fig. 15) is a diazone with wear-resistant radial orientation of prisms (see Boyde and Lester 1967, for the distribution of tubules in relation to prism boundaries within marsupial enamel).

Figure 14. *P. oscillans*, A, B: $P_3$, epoxy cast of P20815 (reversed image). C, D: $P^3$, F6675. Oblique SEM frames of the ridges and channels showing the abrupt transition between facets and their succeeding channels at the posterior edges of ridges. These face posteriorly in both upper and lower premolars. The diamond-shaped object on the shoulder of the ridge in Fig. B (left of frame) is a casting imperfection. White scale bar in A = 2 mm, B = 200 µm, C = 2 mm, and in D = 20 µm.

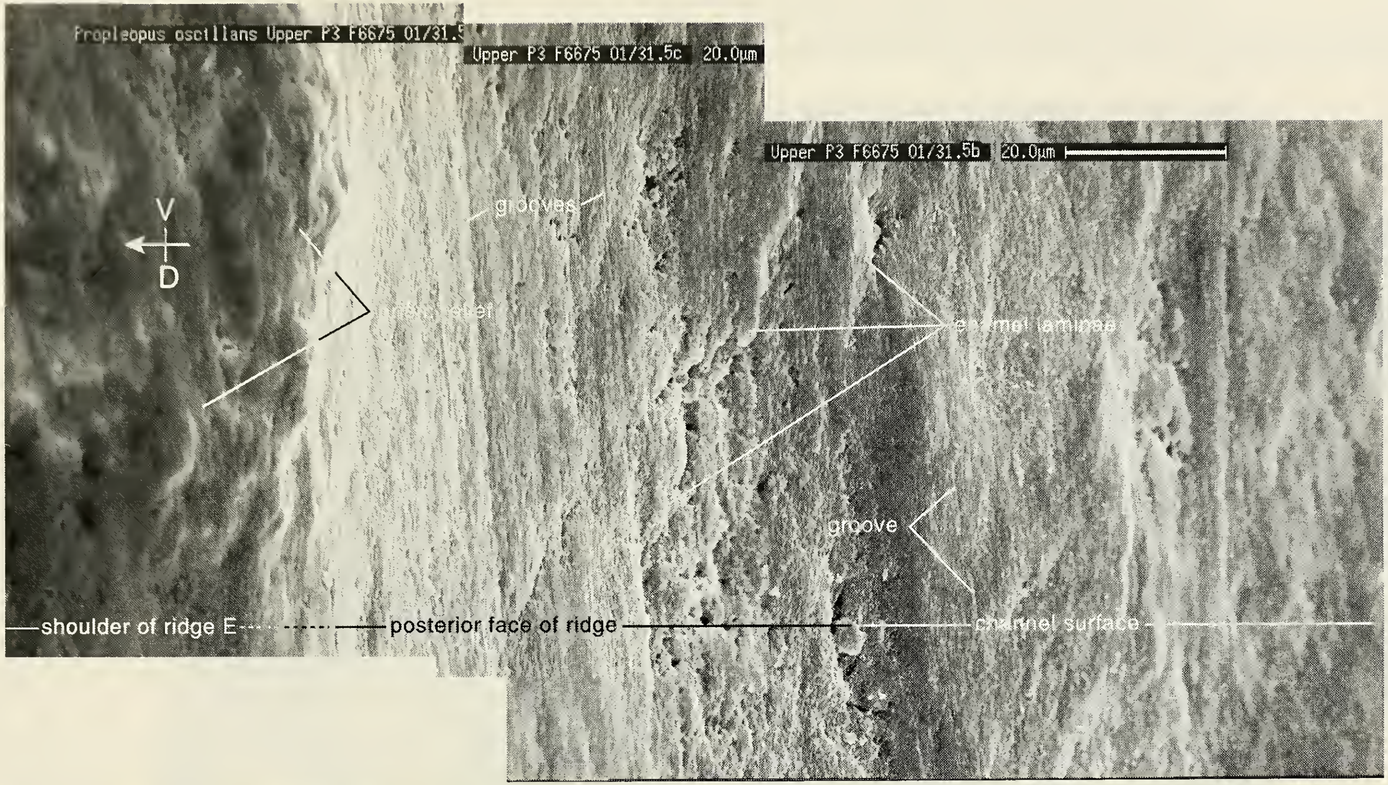


Figure 15. *P. oscillans*, $P^3$, F6675, abrasion features of the posterior edge of ridge **E** on the occlusal (lingual) face. Mosaic of 3 frames from a traverse. White scale bar = 20 µm.

Interpretation.- From left to right, the dark area on the left is prism relief exposed on the shoulder of ridge **E**, then followed by the face of the posterior edge (see Fig. 14) with the edges of enamel laminae exposed along its length. The change from dark to light is partly due to the angle at which the electron beam strikes the edge as well as the nature of the surface; focus was maintained instrumentally during traversing, so the image appears as though it is of a flat surface. The more gently sloping surface of channel extends from the centre of the mosaic to the right edge. Long linear abrasion grooves of different widths can be observed running more or less parallel with the edge of the ridge and independent of the linearity imposed by the laminar arrangement exposed along the edge and within the channel.

The lamellar arrangement within the channel (as distinct from the more wear-resistant radial arrangement of prisms on the ridges) reflects microstructural complexity not explained from surface detail. The detail observed may reflect an arrangement in which prisms are tangential to the surface; such arrangements are thought to be stress-resistant as distinct from wear resistant (Koenigswald and Clemens 1992). Alternatively, apparent absense of prism detail may indicate loss of prism demarkation in radial enamel towards the outer enamel surface similar to that observed in some marsupials (including the propleopine *Ekaltadeta ima*) by Gilkeson and Lester (1989); or it may indicate that the surface of the channels is aprismatic (Koenigswald and Clemens 1992, p. 199, fig. 4).

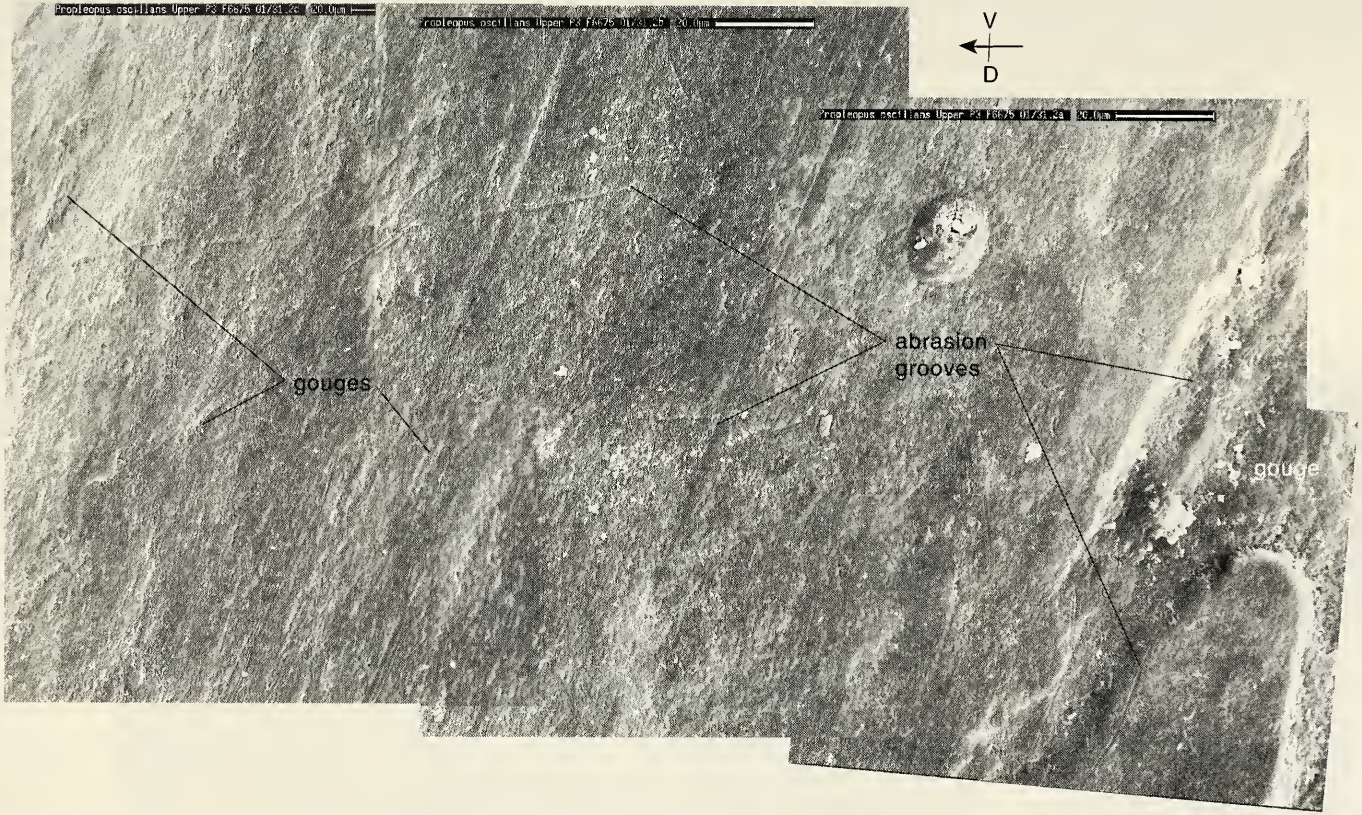


Figure 16. *P. oscillans*, $P^3$, F6675, occlusal (lingual) face, abrasion features of the channel between ridges **E** and **D**. Mosaic of two traverses of 6 SEM frames in the plane of and posterior to the transect in Fig. 15. Long abrasion grooves running diagonally across the mosaic are approximately parallel with the posterior edge of ridge **E** anterior to the channel. The left of the mosaic is approximately 1/3 of the distance across the channel towards ridge **D** (480 µm of approx. 1420 µm). The circular object in the upper right frame is not identified. White scale bar = 20 µm.

Interpretation.- Linear abrasion features are of different widths and change in width and depth along their lengths. This probably indicates both that that incising particles vary in size and that pressure applied to them changed during incision. Large, wide but short, abrasion features (appearing like large gouges) occur. The feature in the lower right of the mosaic is the anterior edge of such a gouge (gouge approximately 50 µm in width) where a piece of enamel lamina has been removed. Grooves in this mosaic range in width from approximately 15 µm to less than 1 µm. Long parallel grooves in the centre of the mosaic are 2-3 µm across. There is no similarity between this surface and that resulting from incision by opaline phytoliths (see Walker et al. 1978, fig. 3E). Apart from the much lower feature density, the pattern of gouges and grooves (some very large) of variable width and length, and rather variable orientation, is comparable with that illustrated in the carnassials of moderate bone-eaters by Van Valkenburgh Teaford and Walker, (1990) but the carnassials of Carnivora studied by these workers showed a much higher density of features than occurs in the grooves of premolars of *P. oscillans*. However, they studied the shearing facet between the paraconid and protoconid of the lower carnassial where shearing is concentrated (as is postulated for the postero-lingual wear facet in *P. oscillans* premolars – see Fig. 34). Feature density on the ridges of *P. oscillans* is more comparable (Fig. 12) although there are few pits away from the crest.

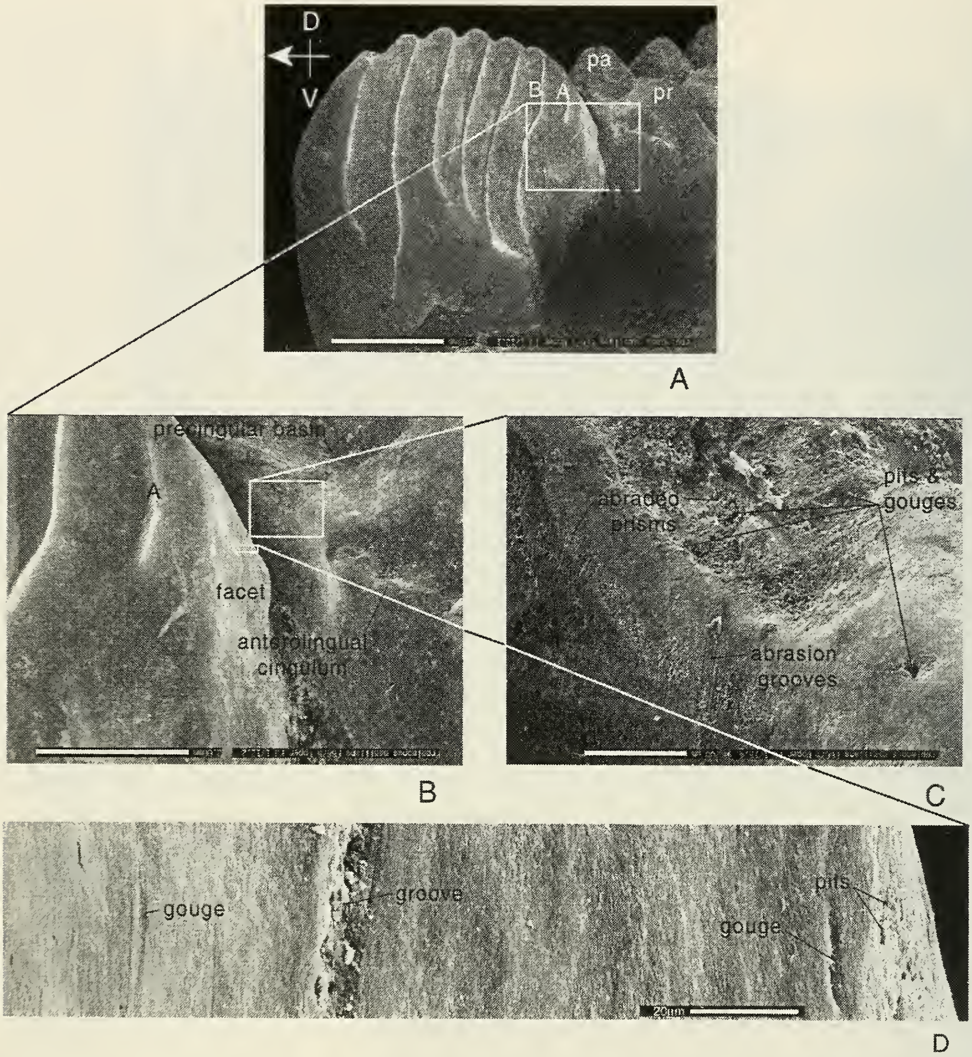


Figure 17. P. *oscillans*, $P^3$, F6675, abrasion features at the molar/premolar junction. A, orientation; B, wear facet and edge of ridge **B**, ridge **A** and the postero-lingual facet of $P^3$ forming the antero-lingual face of the embrasure between $P^3$ and $M^1$. Cavitation in the precingular basin antero-lingual to the protocone, and in the anterolingual cingulum, is visible in the upper right of the frame (for terminology see Fig. 20). C and D abrasion features of the two areas indicated in B. White scale bar in A = 5 mm, B = 2 mm, C = 200 µm, and D = 20 µm.

Interpretation.- Cavitation and pitting in C is typical of crushing facets. Prism exposure anterior to the precingulum is similar to that illustrated by Teaford 1988b, in the interproximal facet of *Proconsul major*. D, abrasion groove and gouges in the anterior face of the embrasure between the premolar and molar also indicate that the postero-lingual facet of $P^3$ is a shearing facet (also see Fig. 34).

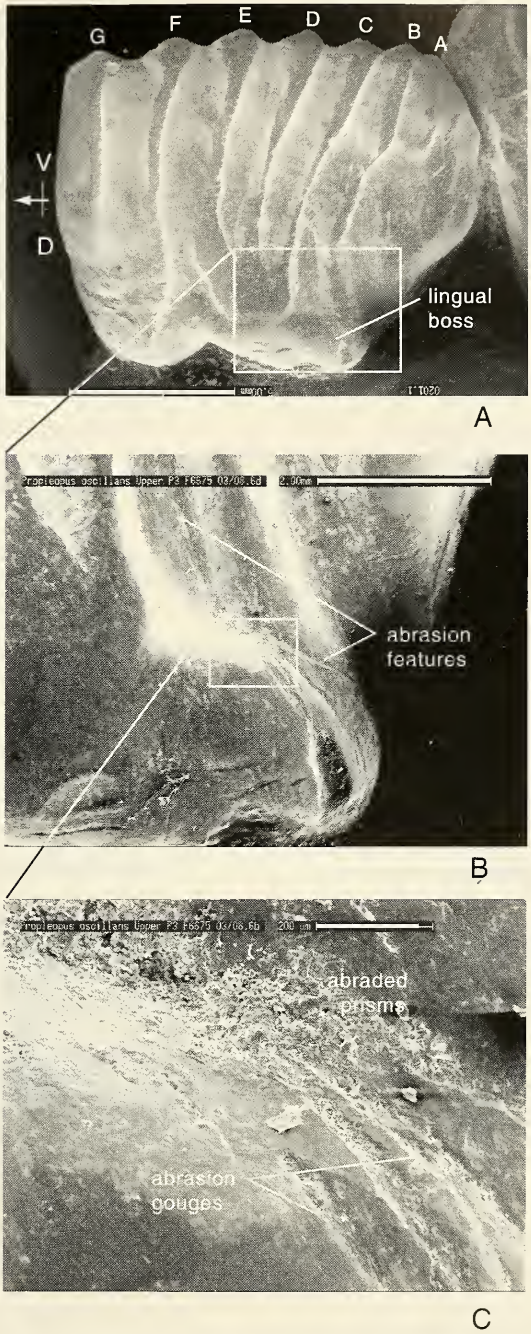
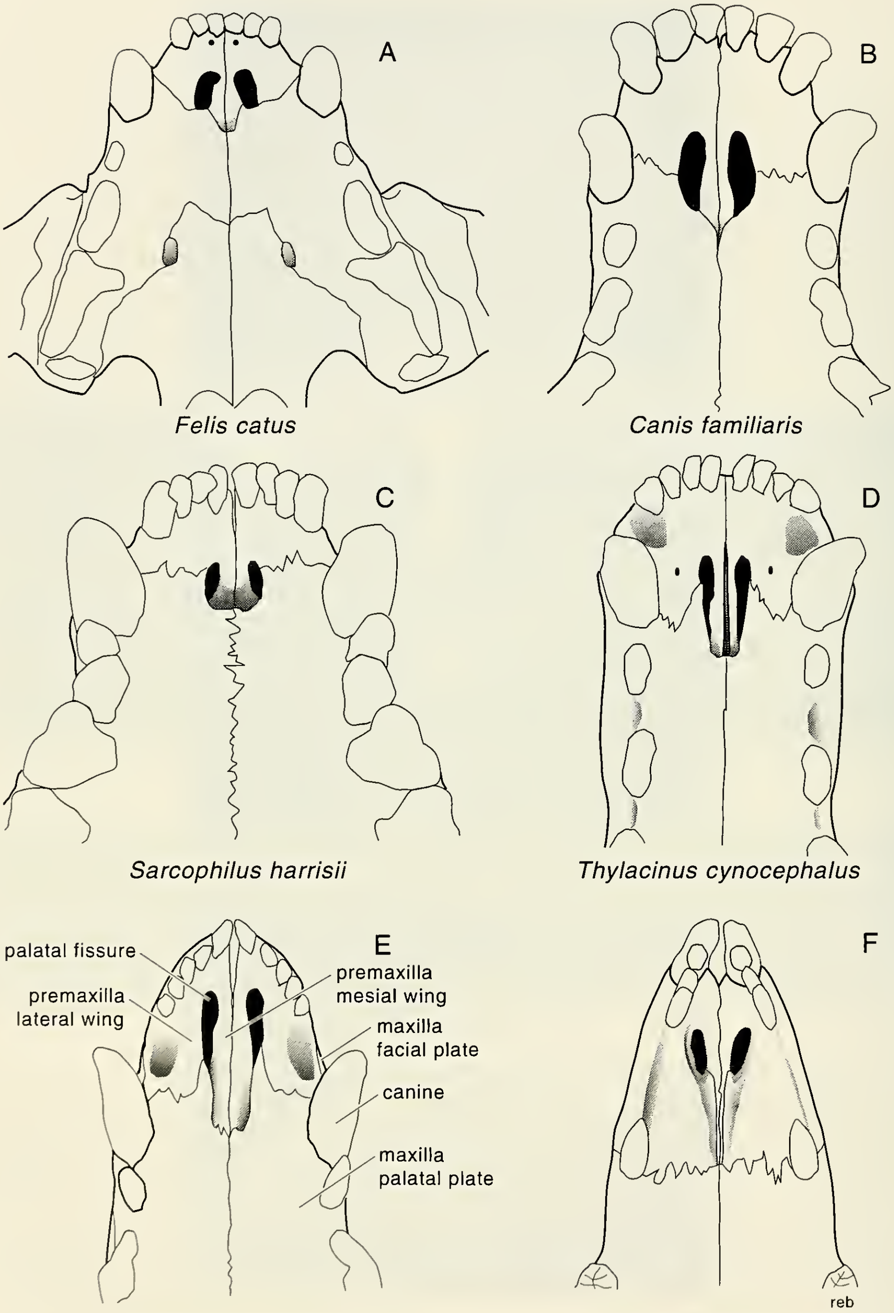


Figure 18. *P. oscillans*, $P^3$, F6675, lingual face; abrasion features at the lingual boss. Abrasion features (including a very large gouge) are concentrated on the boss and particularly at the posterodorsal end of the channel between **D** and **C** where material forced along the channel would have been deflected from the gingival margin. White scale bar in A = 5 mm, B = 2 mm, and in C = 100 µm.


*Felis catus*

*Canis familiaris*

*Sarcophilus harrisii*

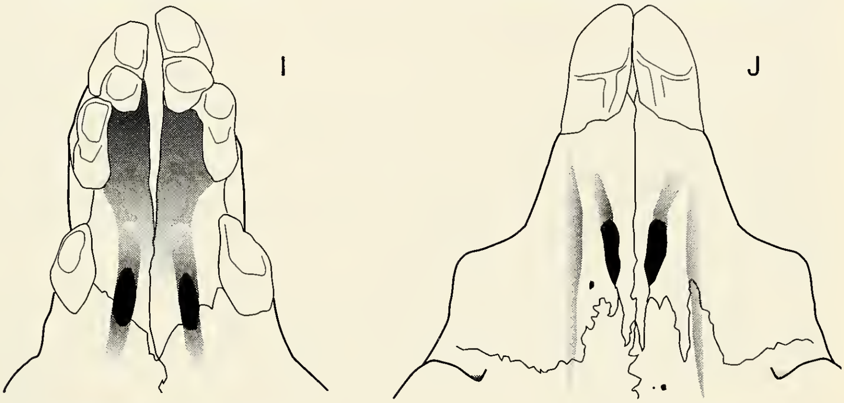
*Thylacinus cynocephalus*

*Didelphis virginiana*

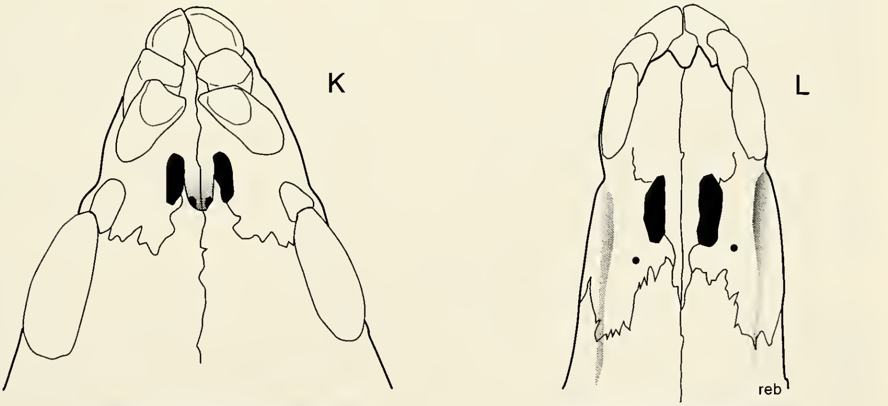
*Propleopus oscillans*

Figure 19. The premaxillary palate of *P. oscillans* (F ) compared with short-faced and long-faced Carnivora (A, *Felis catus*; B, *Canis familiaris*); short-faced and long-faced polyprotodont marsupial carnivores (C, *Sarcophilus harrisii*; D, *Thylacinus cynocephalus*); a short-faced diprotodont carnivore (G, *Thylacoleo carnifex*), and short-faced and comparatively long-faced diprotodonts of different lineages

*Thylacoleo carnifex* *Hypsiprymnodon moschatus*



*Phascolarctos cinereus* *Vombatus ursinus*



*Aepyprymnus rufescens* *Macropus giganteus*

(I, *Phascolarctos cinereus* and J, *Vombatus ursinus*; K, *Aepyprymnus rufescens* and L, *Macropus giganteus*). H, *Hypsiprymnodon moschatus*, illustrates the possible plesiomorphic condition in Hypsiprymnodontidae. *Didelphis virginiana*, E, (with very similar sutural relations to *Hypsiprymnodon*) illustrates the probable ancestral condition of all marsupials.

## DISCUSSION

### Functional inferences from cranio-dental morphology

Premaxilla, incisors and the diastema (Figs 2, 19):

The premaxilla, although elongate, is strongly united with the maxilla by a deeply serrate scarf joint. The break in left maxillary fragment of P35632 just anterior to the suture, instead of separating along the sutural line, demonstrates its robustness. Regrettably, insufficient of the facial surface of the premaxilla is preserved to provide useful information on its facial junction with the maxilla.

Palatal fissures are positioned about mid-way along the premaxilla and separated from the maxillo-premaxillary suture (Fig. 19F). Each fissure lies within a groove bounded by ridges. The interpremaxillary suture is finely serrate. The lateral and mesial wings of the premaxilla are closely sutured posterior to the fissure. Posterior to the fissure the mesial wing is a very slender bone interposed between the lateral wing and the interpremaxillary suture.

The ancestral condition in marsupials (exemplified by *Didelphis* and *Hypsiprymnodon* in Fig. 19E, H) seems, on the basis of its wide distribution[6] among members of the major marsupial taxa, to be one in which fissures are elongate and the lateral and mesial wings do not meet behind them. Moreover, the mesial wings do not suture laterally with the maxilla. Thus, the median part of the premaxillary palate, along the maxillo-premaxillary suture, from one fissure to the other (about 1/3 of the width of the palate in *Didelphis* and *Dasyurus*) is a major zone of weakness in the junction between the four elements; presumably its strength depends to a great extent upon the scarf joint between the elements facially. The premaxillae of marsupial fossils are frequently detached from the skull at this point.

In both short and long-faced Carnivora (exemplified by cats and dogs, Fig. 19 A, B) the incisors, which are placed wholly in the premaxilla, are used for pulling and some cutting, while the canines placed immediately behind the maxillo-premaxillary suture are used for pulling, slicing (i.e. shearing) (Van Valkenburgh 1996) and holding. In both groups of carnivores, the incisors are placed transversely and the palatal plate of the premaxilla is shortened bringing the incisors close to the canines. Both the lateral and mesial wings of the premaxilla are firmly sutured with the maxilla. Polyprotodont marsupials appear to adopt the same solution as Carnivora when incisors and canines are required for similar use. Thus, a similar arrangement of the incisors and a shortening of the premaxillary palate (but without as close a suture between the mesial wings of the premaxilla and the maxilla) occurs in *Sarcophilus* and *Thylacinus* (Figs 19 C, D).

In diprotodont marsupials, because of the form of the mandible, canines have no interlocking partners with the result that the canine function of polyprotodonts, if required, must also be performed by the anterior incisors with concommitant strengthening of the palate between the premaxilla and the maxilla.

Different clades have accomplished this in different ways. Thus, in the carnivorous marsupial lion *Thylacoleo* (Fig. 19G), which is structurally analogous with the cats, the maxilla is shortened and broadened but, comparatively, the premaxilla is less reduced than in cats and accommodates the enlarged $I^1$ which becomes greatly elongate dorsally within a tall premaxilla which is sutured facially with the maxilla closely behind the $I^1$; both this suture and the naso-premaxillary suture are closely serrate. The palatal maxillo-premaxillary suture is broad and serrate also. The posterior ends of the mesial wings of the premaxilla are united in the palatal suture.

The wombats retain a wide diastema (and in that sense are long-faced) but possess greatly enlarged $I^1$s that insert deeply within the premaxillae. There are also strong longitudinal ridges lateral to the recessed palatal fissures. On the basis that palatal ridges and recessed fissures are possessed by both long-faced (e.g. *Vombatus*, Fig. 19J) and short-faced vombatiforms (e.g. *Phascolarctos*, Fig. 19I) it is probable that these ridges are synapomorphic in vombatiforms. In the wombats the palatal fissures are deeply recessed, the most extreme development occurring in *Phascolonus* (see Ride 1967, fig. 2B). The mesial wings of the premaxilla are also united with the maxillae at a short but strong suture. In *Phascolarctos*, with relatively small $I^1$s, the posterior ends of the mesial wings are less strongly united, the palatal fissures are less recessed, and the $I^1$s do not extend postero-laterally to the maxilla. The three pairs of incisor, together, function as a grasping unit extending posteriorly along most of the premaxilla.

In *Aepyprymnus* (Fig. 19K), a short-faced rhizophagous potoroid macropodoid, the $I^1$ is elongate posteriorly and lies mesial to the canine as in *P. oscillans* (Fig. 4A, D). The palate is without ridges but parallels the structure in *Thylacoleo* in being broad. The mesial wings of the premaxilla are united with the maxilla at the maxillo-premaxillary suture. In the long-faced macropodiforms (e.g. *Macropus* Fig. 19L) the $I^1$s are short, do not extend posteriorly, but, presumably to meet the requirements of grasping with the $I^2$ and $I^3$, in large long-faced species (e.g. *M. giganteus, M. fuliginosus* and *M. antilopinus*) the premaxilla is strengthened in an analogous manner. The palatal fissures are anterior to the maxillo-premaxillary suture and the mesial and lateral wings of the premaxillae fuse behind them.

Like the incisors of *Vombatus* and *Aepyprymnus*, the $I^1$s of *P. oscillans* are elongate within the premaxillae (extending posteriorly to the maxillae). Strengthening of the premaxilla (Fig. 19F) is also achieved by the development of vombatiform-like lateral ridges and recessed palatal fissures, but even more than in other diprotodonts, the palatal fissures are distanced from the premaxillo-maxillary suture and strengthened behind as well by the firm union of the lateral and mesial wings. The maxillo-premaxillary suture is not interrupted by the mesial wings as it is in *Macropus*. If *Hypsiprymnodon* is taken to represent the ancestral condition of the Hypsiprymnodontidae, all these features listed in *P. oscillans* (elongated first incisors, recessed palatal fissures, lateral ridges, anterior placement of the palatal fissures, strongly united lateral and mesial wings) constitute adaptational responses to a specialized masticatory function in an animal which did not become short-faced but to which considerable incisor force was necessary.

$I^1$ and $I_1$ have sharp chisel edges maintained by a combination of differential hardness of dental tissues and wear. The teeth are open rooted (probably persistently erupting). Enamel and dentine is distributed in a manner that, on wearing (and possibly also by thegosis) maintains the edges[7]. Macroscopically, they appear only slightly damaged, implying either that food substances are soft and relatively grit-free, or that the sharp edges are maintained as the result of rapid replacement of tooth substance from the open roots together with active incisor thegosis. $I^1$ are more proodont than in rhizophagous forms such as *Aepyprymnus* and *Vombatus*. In *Vombatus* the single pair are flattened; in *Aepyprymnus* the flat surface area of the upper incisors as a group is increased by flattening of the broad $I^1$ and $I^2$. In both genera they serve as excavating and pulling tools. In feeders on hypogeal fungi such as *Bettongia* and *Potorous*, incisor edges are more obtuse and possibly less liable to damage by grit while excavating.

$I^{2,3}$ of *Propleopus oscillans* are small and placed closely behind $I^1$, roots are angled posteriorly, and (from the small size of their alveoli) were much less tall, probably resulting in a sharp beak-like incisor complex which occluded with the sharp, anteriorly directed, edges of the upward-facing $I_1$ in the mandible which, from the genial pit, is angled upwards. This angle carries the incisor tips almost to the level of the molar row. Unlike the larger grazing and browsing Macropodidae, the premaxilla is not flexed downwards to meet horizontally placed lower incisors as in kangaroos and wallabies (Ride 1959) in which maximum surface for grasping is achieved by opposing the antero-posteriorly elongate edges of the group of upper incisors to the lateral edges of the procumbent lower incisors.

The anterior incisors are also quite unlike those of placental chisel-tooth diggers (Hildebrand 1985b) and it seems clear that *P. oscillans* was not specialized for excavating food from soil with these teeth. On the other hand, incisors could certainly have combined the piercing, shearing and holding functions of the incisors and canines of the Carnivora (Van Valkenburgh 1996).

The upper canines are rooted in the maxillae. They are not elongate (Table 1) and would have been only approximately as tall as $I^1$ and $P^3$. Nevertheless, they are anteroposteriorly ridged and robust and were placed mid-way in the short diastema. They have no opposing lower equivalents and their function must have been in holding rather than shearing as in Carnivora.

The infraorbital canal is large and placed midway along the face above the anterior edge of the premolar. It transmits branches of cranial nerves V2 (sensory from skin and rostrum) and VII. Both the large size of the infraorbital foramen and the anterior palatal fissures imply that the muzzle had important sensory functions.

The cheek teeth, commencing with the sectorials, follow shortly after the canine, implying that capacity to manipulate numerous ingested particles (as in Macropodinae, Ride 1959) was of less importance than the ability to grasp and hold larger items. However, despite the shortened diastema, the face is long both to the orbit and to the anterior edge of the adductor attachments of the mandible (the masseteric process), probably enabling wide gape characteristic of high amplitude jaw movement and enabling-puncture crushing (crack-propogation in hard brittle food materials) to take place well back in the unreduced molar row. Sectorial function is carried well forward in the open mouth and well anterior of the orbit.

High amplitude jaw movement has been shown in experimental studies to be characteristic of opportunistic feeders (omnivores) and carnivores such as the opossum (*Didelphis*), tenrec and cat, and not of herbivores (see Hiiemae and Crompton 1985, p. 282). From photographs, *Thylacinus* has an exceptionally wide gape and on the basis of its unreduced molar row and dental topography had a similar high amplitude of movement.

Occlusal relationships of cheek-teeth:

Premolars:

Large ridged sectorial premolars, which originally suggested carnivorous habits for *P. oscillans*, occur widely among the modern Australian marsupial fauna. Among modern macropodiforms they occur in *Hypsiprymnodon* and all genera of Potoroidae; among Burramyidae they are characteristic of *Burramys*. Recent studies of the diet of these animals indicate that it is unwarranted to infer a carnivorous habit from the possession of ridged sectorials alone. Moreover, closer examination reveals that to emphasize size, ridging and lateral compression, as is done when speaking of such teeth as a class of "plagiaulacoid premolars", conceals fundamental morphological differences between the teeth in different groups and in their functioning (Ride and Heady in prep.) Studies by Bennett and Baxter (1989), Scotts and Seebeck (1989), Claridge et al. (1993), Christiansen (1980), Taylor (1992), and Seebeck et al. (1989) indicate that potoroids are, mostly, primarily mycophagous, the exception being *Aepyprymnus* which is primarily rhizophagous. All take some arthropods and some (*Bettongia lesueur* and *B. penicillata*) are known to take flesh. The much smaller *Burramys parvus* (c. 40 g) is an insectivorous omnivore (Mansergh et al. 1990). Its major food is the Bogong moth, *Agrotis infusa*. Vegetative material amounts to about 16% of the diet. Bogong moths are seasonal and seeds with hard seed coats are cached and eaten in winter. The sectorials have been observed in use in cracking the seed coats.

From the evidence of microwear, it is clear that the sectorials of *P. oscillans* were used both in shearing and crushing and that these functions were primarily carried out in different parts of the tooth.

No paired adult tooth rows are available for articulation, but the molars of specimens P20815 and Qd Mus F6675 occlude virtually perfectly. In these, the height of the crest of P3 above the molar cusps enables a tooth-on-tooth contact between opposing premolar ridges from ridge **E**, posteriorly, to be obtained by rotating the ventral border of the ramus mesially accompanied by slight condylar displacement. The shape and distribution of the articular surface on the transversely cylindrical condyle indicates that it could have moved forward in an anteriorly unrestricted glenoid, but suggests that movement of the mandible would have been restricted posteriorly by a closed bearing concavity on the anterior surface of the post-glenoid process. The extensive rugose mandibular symphysis indicates that relative rotational movement between the rami was possible. Tooth-on-tooth contact can be made also at the lingual boss. The worn wear facet of the $P^3$ of the holotype (Qd Mus. F3302) corresponds with the area of premolar tooth-on-tooth contact estimated from occluding the premolars of the other two specimens.

In the younger animal P35632, in which both upper and lower tooth rows are present, when the molars are occluded, the upper and lower sectorial premolars are separated by a distance equal to about half their widths. At this stage of growth, the crests of the sectorial premolars (P2) are at the same level as the cusps of the deciduous premolars and only a small area of the sectorial is brought into tooth-on-tooth contact by rotating the rami.

Evidence of puncture crushing of brittle items whereby cracks are propagated occurs along the premolar crest, at the molar-premolar junction (Fig. 17) and particularly on the rounded cusps of the molars (see interpretation of Figs 21 and 22). However the principal function of the cuspidate crests of the premolar was probably that of high amplitude shearing[8] of tough fibrous material such as hide, tendon or aponeurosis, while abrasional damage incidentally resulting from puncture crushing at the cusps is probably the result of the inclusion of hard resistant material (such as grit or bone) within the material shorn. In this way the crests would have been used in a manner functionally analogous to the shearing carnassials of fissipede carnivores. However, the relatively small number of short features (pits and gouges) and the relatively high degree of long feature orientation (Ride and Heady in prep.), indicate a diet such as that of flesh eaters or moderate bone eaters in which puncture-crushing occurs only at, and deliberately in, a different part of the tooth row as illustrated for the wolf by Van Valkenburgh, Teaford and Walker (1990).

At first sight, the premolar ridges suggest that the tooth had a file-like multi-bladed shearing capability. However, in both upper and lower premolars the acute edges of ridges face posteriorly (Figs 14, 15) and are not opposable. At the wear facets of ridges where tooth-on-tooth contact is obtained, the principal effect seems to have been grinding (analogous to milling) in which flat surfaces adpress material between them without sharp edges shearing past each other. Although tooth-on-tooth contact is not obtained within the channels between the ridges, tough fibrous material shorn at the crest and pressed into, and being forced along, a channel of $P^3$ to the lingual boss would probably have been intersected obliquely by the sharp edge of a ridge of $P_3$ even though the edges of ridges may not cross each other. Within the channels (Figs 15, 16), directional wear demonstrated by abrasion grooves is mostly along the channels. Anteriorly on the premolars, where there was no tooth-on-tooth contact, abrasion features of the sort that can be interpreted as wear of enamel by soft material indicates that soft-tissues may have been parted by penetration by this part of the tooth in extension of the aperture made in the food by the posterior part of the blade.

The uniform width of abrasion grooves and a general trend along the wear facets of the ridges (Fig. 12) imply uniform pressure on inclusions and orthal occlusion, whereas the irregularity of grooves in the channels imply that the inclusions were less rigidly held. It is possible that a function of the channels was to accommodate such irregularities.

The development of wear facets along the apical part of the hindmost ridges of the premolars of *P. oscillans*, followed by extension of wear both forward and away from the crest, is similar to the pattern of wear described by Stirrat (1981) in *Burramys parvus*, a small phalangeroid with very similar premolars. As in *P. oscillans*, the relative movement of the occluding premolars is orthal in the direction of the ridges. At the posterior end of the premolar, topographic differences produce differently-shaped facets. In wild-caught specimens of *B. parvus* there is very little wear of the cusps – even in the case of individuals with extensive wear facets (captive specimens develop considerable cuspal wear). The sequence of facet development in *Hypsiprymnodon moschatus* is also similar (Ride and Heady in prep.). In $P_3$ it is virtually identical, but in $P^3$ the facet commences as a depression "scooped out" of the surfaces of the posterior ridges about a third of the distance below the crest (the development of wear facets in $P^3$ of *P. oscillans* is not yet known). In *H. moschatus* posterior cusps and ridges are abraded extensively as in *P. oscillans*. The general trend of movement is also orthal (Ride and Heady in prep.).

By contrast, development of premolar wear facets in Potoroidae is different, although in all species studied the direction of occlusal movement is also orthal. Morton (1981) has studied *Potorous tridactylus, Aepyprymnus rufescens* and *Bettongia gaimardi*. In *P. tridactylus*, which has elongated premolars oriented in line with the molar row, and dominant anterior and posterior premolar cusps (higher than those between) and rounded ridges, wear is initially confined to the tips of the anterior and posterior cusps of the occluding surfaces and then spreads to the cusps between. Facets develop on the ridges. Cavitation commences immediately below the cusps and exposed dentine surfaces spread along the planar facets developed on the ridges. The area of exposed dentine becomes continuous and a bevelled edge develops along the length of the tooth. The process continues until both cusps and ridges are obliterated. In *A. rufescens*, the premolars are "toed inwards", their anterior ends being directed mesially. Ridges are numerous and more acute than in *P. tridactylus*. A wear facet develops, but instead of spreading along the ridges as in *P. tridactylus* and then becoming continuous along the tooth, the facet develops as a bevelled surface on which dentine is exposed. As it wears the tooth retains its cuspal margin resulting from the tips of the ridges of the non-occluding face being exposed progressively along the edge. In *Bettongia gaimardi* the development of the facet is as in *A. rufescens*, but becomes wedge shaped, narrowing anteriorly. The premolars are "toed outwards" i.e. set at an angle to the molar rows, with their anterior ends angled buccally. Morton considered that the shape of the facet is due to the posterior part of the tooth coming into occlusion first.

In all Potoroidae studied, premolar facet development is accompanied by dentine exposure and the development of a bevelled edge which Morton argues is to enable a "relief angle" to be maintained between opposing edges of the blades. She also regards the presence of crenulations and cusps in such teeth as enabling bite force to be more effectively applied at a reduced occlusal area.

Confirmation that premolar function in Potoroidae is orthal and combines both puncture crushing and shearing is supplied by cinefluroscopic studies of mastication in *B. penicillata* (Parker 1977). In crushing, Parker observed that blades are approximated directly in line with each other. Approximation coincides with anteriorwards condylar movement at the contralateral condyle accompanied by some relative movement at the symphysis. During crushing there may be slight anteriorwards movement of the ipsilateral condyle. The puncture crushing movement may be repeated several times in succession. In shearing, the mandibular blade passes on the median side of the maxillary blade. Observations did not distinguish whether puncture crushing was confined to a particular part of the tooth, which we postulate in *P. oscillans*, but Parker did observe careful manual positioning, and repositioning, of objects for puncture crushing which implies that a particular part of the premolar is favoured.

*B. penicillata*, like *P. oscillans*, has "toed out" premolars and the general form of wear facet development is similar. It seems probable, despite differences in morphological detail, that the dual functions of shearing and crushing were performed in a similar manner and in similar parts of the tooth. SEM studies of *B. penicillata* directly comparable with those reported here for *P. oscillans* are in progress (Ride and Heady, in prep).

Molars:

The molar row is scarcely reduced posteriorly. There is no indication of a transverse or antero-transverse component in chewing as in frugivores and folivores (*Aeteles*, Kay and Hiiemae 1974; *Colobus*, Teaford 1986; *Oryctolagus*, Ardran et al. 1958; *Macropus*, Ride 1959; *Macropus, Wallabia*, Sanson 1980), granivores (*Rattus*, Hiiemae and Ardran 1968) or mycophagous animals (Potoroinae, Parker 1977; Morton 1981); rather the power stroke of the gape cycle seems to have been more or less vertical in direction in both premolars and molars (Figs 12, 13, 21) - closer to that found in carnivores but not herbivores (Hiiemae and Crompton 1985, p. 280) (Fig. 23).

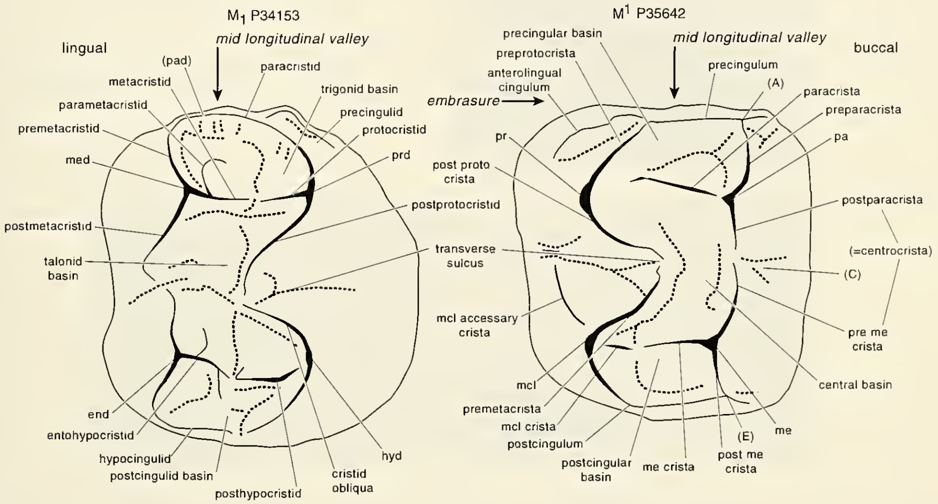


Figure 20. *P. oscillans*, molar cusps and crests. Key to conventions for cusps, crests, and grooves, and to topographical nomenclature employed.
Abbteviations: end = entoconid, hyd = hypoconid, pa = paracone, pad = paraconic, pr = protocone, mcl = metaconule, me = metacone, med = metaconoid, prd = protoconoid.

When the molars of the paired mandibles and maxillae (P35632, P35633; and also P20815, F6675) are occluded so that the protocones of the upper teeth lie in the trigonid basins of the lower molars (Fig. 22), the cusps and basins interlock. The buccal cusps of each lower tooth (protoconid and hypoconid) insert into the basins of the mid-longitudinal valley of the opposing tooth row (i.e., the buccal cusps of $M_2$ insert into the postcingular basin of $M^1$ and the central basin of $M^2$ respectively). The lingual cusps occlude within accessory structures (the metaconule accessory crista and anterolingual cingulum) along the lingual margin of the upper molars (i.e., the metaconid of M2 bites into the mesial embrasure between the metaconule of $M^1$ and the anterolingual cingulum of $M^2$, while the entoconid bites into the sulcus of $M^2$ antero-mesial to the metaconule, fitting between its postprotocrista and metaconule accessory crista).

This rather precise fit and interlocking of cusps in *P. oscillans* seems to indicate only limited transverse or antero-transverse molar movement occurred as is observed in

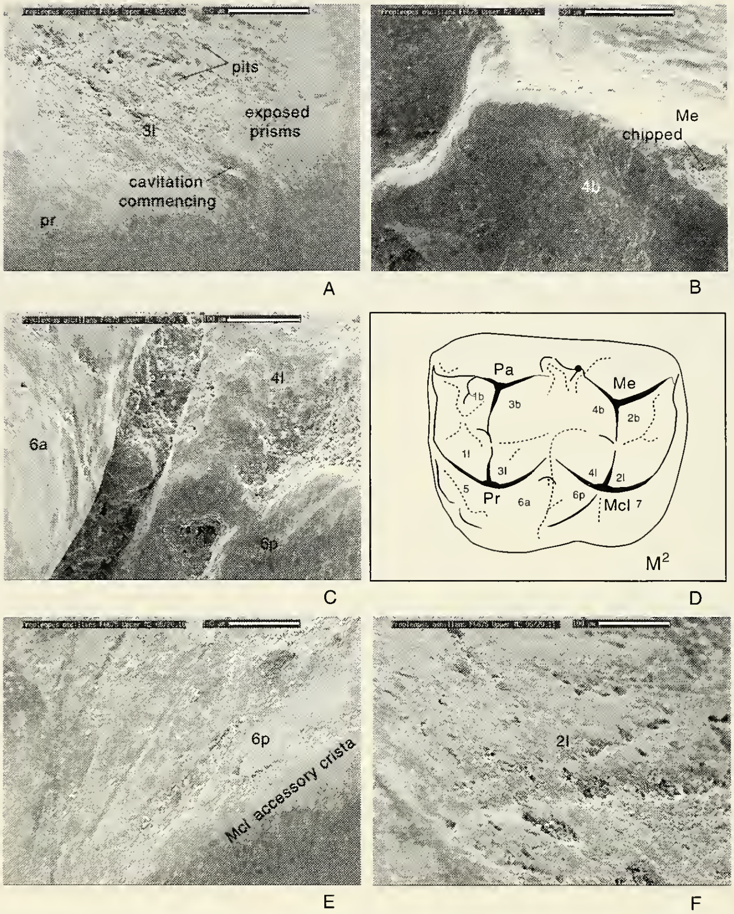


Figure 21. Shearing and crushing features in the *P. oscillans* molar ($M^2$ of F6675). D: diagram based on outline of unworn P18541 to indicate the positions of areas of wear relative to cusps and crests. The numerical designation of the areas adopted here is an extension of the facet designations of Hiiemae and Crompton (1970, fig. 4) for *Didelphis marsupialis* (probably *D. virginiana*) and Kay and Hiiemae (1974) for fossil and modern primates. Numbering on the primary cusps (Pa, Me) and on the lingual face of the protocone (Pr) is the same. Other areas are numbered differently from the facet notation of these authors, to avoid any inference that the hypocone of primates and the metaconule of quadricuspid diprotodont marsupials are homologues. Accordingly areas on the buccal surface of the protocone (Pr) and metaconule (Mcl) are numbered as though the facets on the primary cusps of *Didelphis* had been divided. Thus, the letters b (buccal), l (lingual), a (anterior), p (posterior) are added to facet number to designate the components. Facet 9 of primates may be equivalent to all of areas 1l-4l. Other abbreviations: Pa (paracone), Me (metacone). White scale bar in A = 200 μm, B = 500 μm, C = 100 μm, E = 100 μm, and F = 100 μm.

Interpretation.- A: buccal surface of protocone (lower left corner) and area 3l; the protocone is a rounded crushing cusp. Cavitation is commencing on the postprotocrista close to the apex, abrasion pits are evident. Abrasion grooving extending onto the lingual surface on area 6a (a shearing surface) is visible along the postprotocrista (compare with Teaford 1988b, fig. 8). B: lingual face of premetacrista and area 4b; fracture of the tip of the pointed metacone indicates the vulnerability of pointed cusps to damage; abrasion grooves extend vertically from the ridge of the premetacrista onto the face of area 4b (a shearing surface); pits towards the base of the surface show where the rounded hypoconid occludes (a crushing surface). C: wear surfaces on either side of the sulcus between protocone and metaconulid. Pits and exposed prisms occur on the anterobuccal surface of 4l (a crushing surface), grooves extend vertically from the edge of the premetaconulecrista (bottom right) onto surface 6p (a shearing surface), and on surface 6a anterior to the sulcus. E: Parallel abrasion grooves and gouges in area 6p (a shearing surface) on the buccal face of the metaconule accessory crista. F: buccal surface of metaconule and area 2l (a crushing surface); as in the protocone, the metaconule is a rounded crushing cusp; cavitation is commencing at the tip (bottom left), abrasion pits and gouges from crushing on surface 2l are evident.

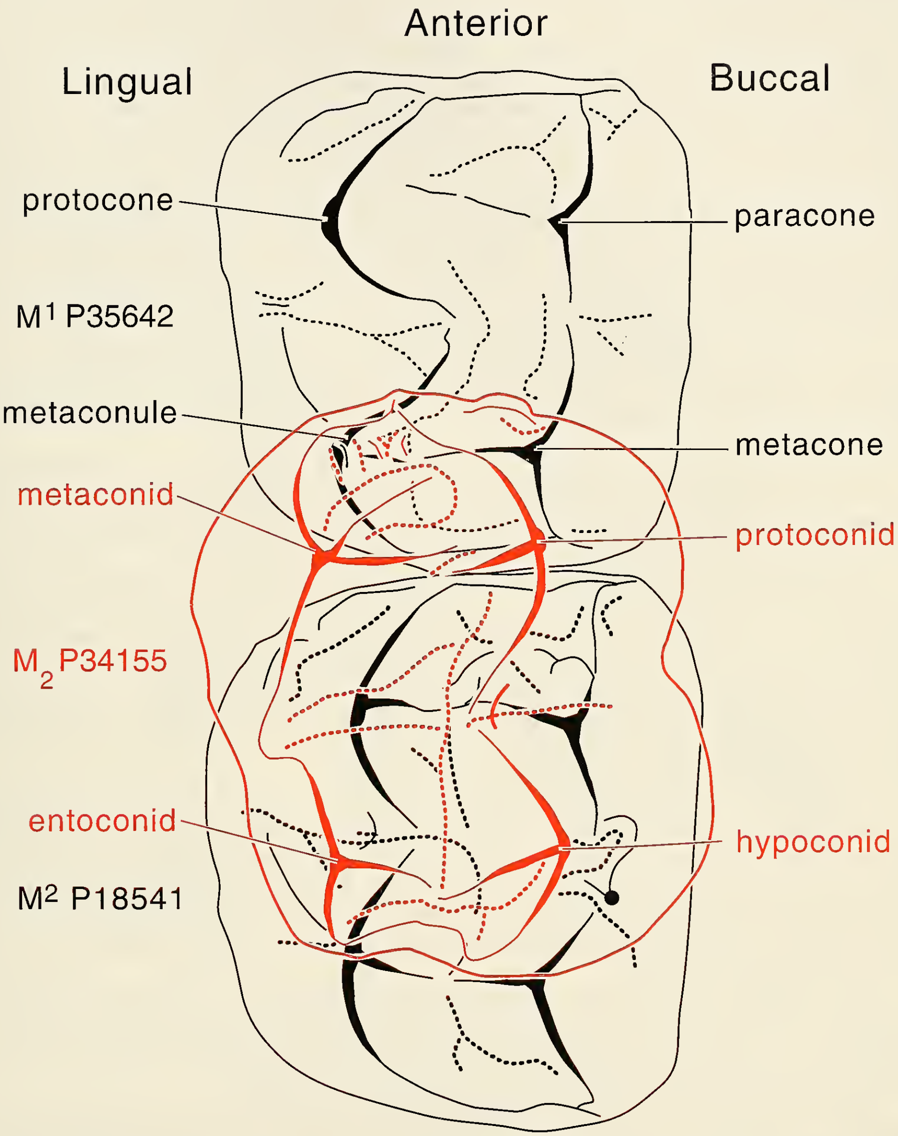


Figure 22. Occlusal relationships between the upper and lower molars of *P. oscillans*. The molars are aligned approximately representing the commencement of the power stroke (Phase I) (see Fig. 21 for SEM illustrations of the different forms of shearing and crushing cusps and wear surfaces). Rounded crushing cusps are aligned so that they occlude within the mid-longitudinal valleys of opposing teeth. Shearing crests of both upper and lower molars are aligned along the external (lingual and buccal) margins of the tooth-rows. Thus, in the upper molar, shearing surfaces on the acute anteroposterior ridges of the paracone and metacone shear against surfaces on the buccal faces of the rounded protoconid and hypoconid. The latter rounded cusps occlude within the rugose basins of the median longitudinal valley. The similarly rounded protocone and metaconule occlude in the same manner.

folivores, frugivores and omnivores. In animals with such diets the power stroke contains two phases defined by Kay and Hiiemae (1974). Phase I begins as the buccal surfaces of the lower molars are brought into contact with the buccal surfaces of the upper molars, and continues until the protocone is located in the talonid basin (the position of centric occlusion). From centric occlusion the movement continues until the antero-mesial movement of the lower molars carries them out of occlusion. This second, post-centric phase is defined as Phase II. Both cinefluoroscopic and microwear studies of a wide range of folivores, frugivores and omnivores (referred to above) have revealed that Phase II of the power stroke is extended into an anterolingual grinding movement (Kay and Hiiemae 1974). Thus the upper lingual cusps of leaf-eating and fruit-eating monkeys become flattened and wear facet 9 buccal to the protocone becomes greatly extended in area (see *Ateles*, fig. 4D of Kay and Hiiemae, loc. cit., also see Teaford 1986; for analogue of wear facet 9 in *P. oscillans* see text Fig. 21). In other folivores, especially grazers and browsers, serial arrangement of cutting crests (as in lophodont and selenodont animals) provide shearing and grinding mechanisms.

In carnivores, Phase II of the power stroke is greatly reduced (Hiiemae and Crompton 1985, p. 280). Anterior movement is virtually eliminated and movement during the power stroke is confined to Phase I and is more or less vertical in direction (Fig. 23).

In *P. oscillans*, due to its rarity, it has only been possible to study the molar microwear in a single maxilla (F6675) but conclusions from this agree so closely with the conclusions derived from the gross morphology that there is little doubt that they will be found to be generally applicable (see text accompanying Fig. 21).

The function of the buccal cusps and cristae are exemplified by the metacone and premetacrista illustrated in Fig. 21B; its anteromesial face has exposed enamel prisms while the crest along its margin is grooved with vertical abrasion; the metacone is chipped. The lingual cusps and their surfaces (protocone and metaconule, Fig. 21A, F) reveal pits and gouges typical of puncture crushing surfaces. The trend of the gouges is back into the median longitudinal valley. Despite the fact that the specimen is fully adult the rounded buccal cusps are not diminished in height as compared with the pointed buccal cusps although cavitation is commencing at their tips.

The function of the lingual accessory structures is exemplified by anterolingual abrasion grooving in the channel between the premetaconulecrista and the metaconule accessory crista (Fig. 21E). The abrasion grooves run along the channel – not across the metaconule accessory crista. The sulcus between the protocone and the metaconule (Fig. 21C) is not traversed by abrasion grooves or gouges as they would be if it was subject to the passage of a lower cusp moving anteromesially through it. Instead, it presents a typical crushing abrasion surface.

In conclusion, the features of the microwear support the contention that relative movement of the molars was orthal with a slight anteromesial component as would be expected in an occlusal cycle with the power stroke virtually confined to Phase I and in which both lingual and buccal cusps were simultaneously engaged.

In the occluded tooth rows, the lingual-most and buccal-most rows of cusps would have been primarily shearing in function (although, inevitably, some crushing must have taken place in them as revealed by the chipping of the metacone in Fig. 21B). The two rows of rounded cusps occluding between them were specialised crushing eminences; they also provided rounded shearing surfaces against which the crests of the "shearing" cusps worked.

The combination of both shearing and crushing capability along the tooth row is analogous to that found in Thylacinidae, but not directly comparable because *P. oscillans* also possessed a "carnassial equivalent". It is also possible that the facet on the posterolingual face of the premolar and its junction with M1 may have provided it with a dental position at which particularly large objects might have been puncture crushed

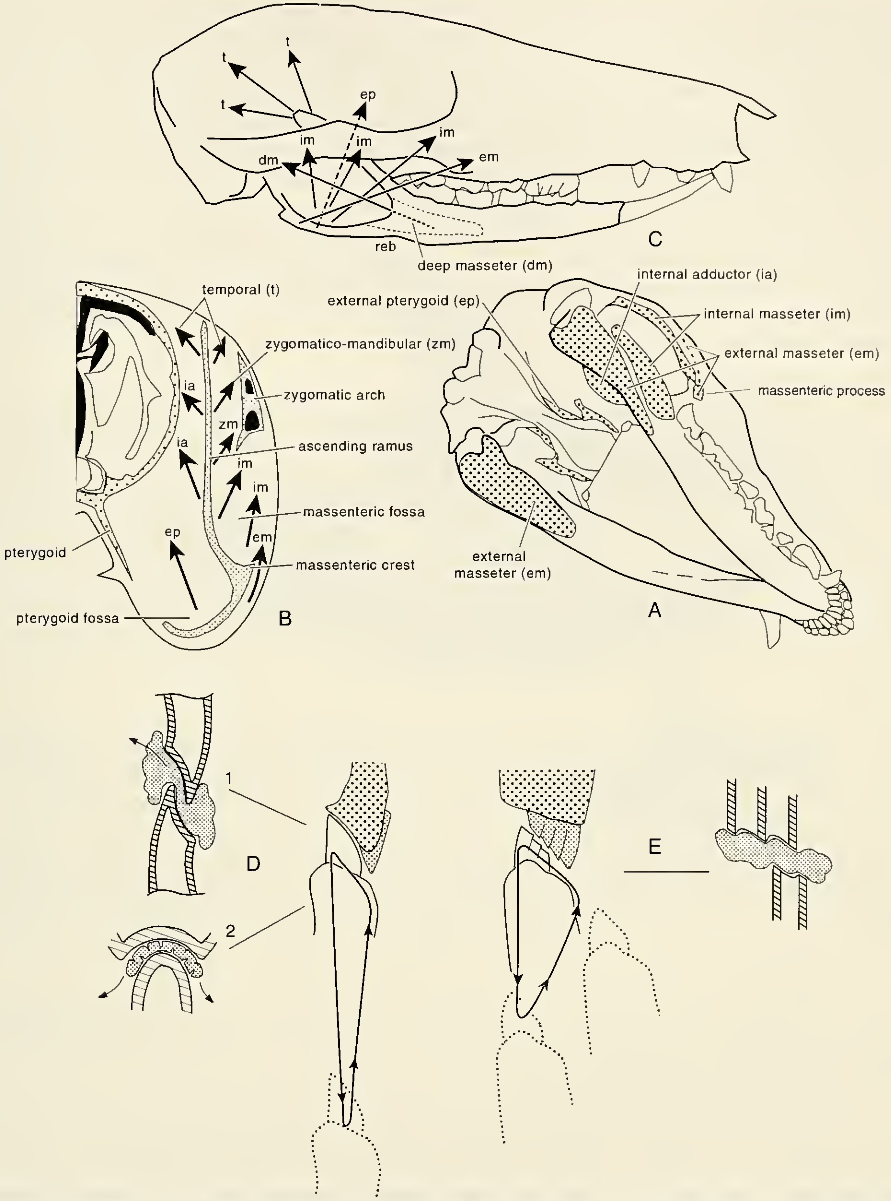


Figure 23. Adductor muscles of mastication in marsupials; the gape cycle; and the elements of tooth design (for shearing and crushing). A: *Didelphis virginiana*, origin and insertion of the components of the masseter-pterygotemporal mass; stipple indicates areas of attachment (modified from Hiiemae and Jenkins 1969). B: *Macropus agilis*, directions of action of muscle components in the transverse plane at the level of the ascending ramus (after Ride 1959). C: *Potorous tridactylus*, directions of action of muscle components in the longitudinal plane; the insertion of the deep masseter within the masseteric canal, and the external pterygoid mesial to the ramus, are shown in broken line (constructed from Morton 1981). D: high amplitude gape cycle typical of carnivores with small lateral component in the power stroke; 1.- shearing of soft, tough, materials between crests and facets (e.g., hide, muscle, or leaves); 2.- crushing hard, brittle or turgid materials between blunt cusp and basin (puncture-crushing involves propagating a crack from an initial crush fracture, e.g., as in bone). E: low amplitude gape cycle with large mesial component in the power stroke typical of mammals that feed on tough fibrous material (e.g. vascular bundles in leaves and grasses) by shearing it between series of sharp edges (D and E modified from Hiiemae and Crompton 1985).

preferentially. It is also probably relevant that studies of free-ranging long-faced Carnivora (dogs) revealed that the carnassials (here the analogue of the part of the sectorial premolars anterior to ridge A) are used to cut skin and muscle while bones are cracked by the blunt cusps of the postcarnassial molars (Van Valkenburgh 1996).

On the basis that *P. oscillans* possessed an elongate molar row and proportionately smaller premolars than other *Propleopus* [and *Ekaltadeta*], Wroe (1996) considered that *P. oscillans* was more herbivorous and less carnivorous than the others. This view is not supported. Wroe (and all those engaged in the controversy over the diet of *Thylacoleo*) based arguments on short-faced Carnivora (e.g. *Felis*), but carnivores can equally be long-faced (e.g. *Vulpes, Canis*, etc.), and as demonstrated by *Thylacinus*, shearing and puncture-crushing may be distributed along the entire unreduced molar row. In view of the high placement of the mandibular condyle in *Ekaltadeta ima* (see below) that species may have been less carnivorous than *P. oscillans*.

Masticatory musculature and gape cycle:

The deep but short and narrow zygomatic arches, the low, rounded, masseteric processes of the maxillo-jugals, and the rather shallow masseteric fossae and crests of the dentaries, when taken together with the wide coronoid processes, that is *Thylacinus*-like in shape, and the well developed pterygoid fossae, imply that the external masseter[9], and the superficial layers of the internal masseter (see Fig. 23) muscles played a relatively small part in mandibular adduction as compared with the temporal and external pterygoids. In macropodine and potoroine mastication in which the mesial component of the power stroke is large (Phase II), the external masseters play an important part (Ride 1959; Morton 1981; Parker 1977); their direction of action is such that they must have a major role in centralizing the mandible through the power stroke into minimum gape (Fig. 23C).

On the other hand, the great size of the masseteric canal within the body of the dentary, and its forward extension to the level of the posterior end of the premolar, implies that the deep masseter within it strongly reinforced the rearward closing action of the temporal on the mandible and the maintenance of pressure on the occlusal faces of the premolars during the power stroke. Together with the temporal, external pterygoid, relatively small external masseter, and median layer of the internal masseter and the internal adductor and zygomatico-mandibular (Fig. 23B), it would also have played an important part in controlling the vertical orientation of the lower premolar (see Sanson 1989).

Although the glenoid fossa is not known, these inferred muscular proportions, together with the cylindrical posterior face of the condyle, imply strong rearwardly directed muscular forces acting on the condyle during the power stroke requiring a robust post-glenoid process. The direction of abrasion features at the cusps of the premolars (Figs 10, 11) support this interpretation.

The low position of the condyle relative to the mandibular tooth row (at the level of the crest of the sectorial premolar) implies both wide gape and a capacity to apply point shearing as occurs in Carnivora where particularly resistant objects are shorn or puncture-crushed at particular positions along the tooth row defined by the different morphologies of different teeth (see Van Valkenburgh 1996). *Thylacinus* and *Sarcophilus* with little morphological difference between anterior and posterior molars have the same capacity. This may indicate that, even though shearing and puncture-crushing may have taken place anywhere along the molar row, there may have been preferred positions according to the gape and force required to crush any particular object.

It is characteristic of mammals with transverse (or semi-transverse) shearing distributed over large areas of tooth surface, that there is a large mesial component in the power stroke of the gape cycle (Phase II). This occurs especially in herbivores (Fig. 23E). In cases where much of the molar row can be occluded more-or-less simultaneously, the condyle is located above the molar row (see Sanson 1989 figs 4-7). In herbivores the widths of upper and lower molars are usually widely discrepant also (but not always e.g. *Phascolarctos*). Among Hypsiprymnodontidae the position of the condyle appears primitively to have been moderately high. *H. moschatus, H. bartholomaii* (see Flannery and Archer 1987, fig. 2), *Ekaltadeta* (Archer et al. 1991, fig. on p. 121) and *Jackmahoneya*, all exhibit a moderately high position of the condyle relative to the tooth row.

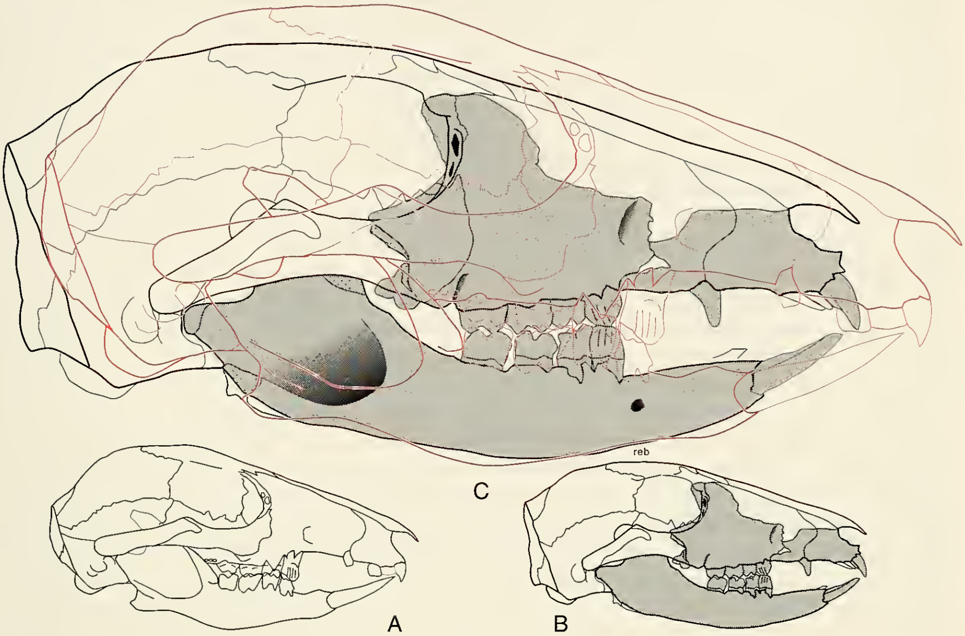


Figure 24. A: lateral view of skull of *Hypsiprymnodon moschatus* at similar stage of dental eruption to the Henschke's Fossil Cave specimen of *P. oscillans*. B: lateral view of reconstructed skull of Henschke's Fossil Cave specimen of *P. oscillans*. C: lateral view of reconstructed skull of *P. oscillans* overlain with outline of skull of *H. moschatus* drawn to the same size (see below for explanation).

### Overall proportions:

If comparison of skull proportions (Fig. 24) are made with the plesiomorphic condition, changed functions may be inferred from observed differences. *Hypsiprymnodon moschatus* and *Hypsiprymnodon bartholomaii* from the Miocene Dwornamor Local Fauna of Riversleigh (Flannery and Archer 1987) indicate possible plesiomorphic conditions for Hypsiprymnodontidae. *Ekaltadeta* from the same formation, with very much enlarged premolars, reduced molars, and short face, is clearly not plesiomorphic.

Osteological features available for comparison with the material available include the shape of the zygomatic arches, the height of the glenoid above the molar row, and some features anterior to the orbit, and the mandible. Other features of the wall of the braincase, the glenoid and the basicranium are not yet observable in *Propleopus*.

The danger of selecting a phylogenetically distant modern species without fossil intermediates to act as a structural ancestor (or an outgroup from which to determine plesiomorphy and, hence, polarity in apomorphy) is that the characters regarded as plesiomorphic, and hence useful to serve as the start point to a sequence of functional changes, may be apomorphic adaptations and, hence, misleading. However, in this case, there are good ecological grounds as well as morphological grounds (similarity to *H. bartholomaii*), for considering *H. moschatus* as persistently plesiomorphic. Its meager fossil record supports the assumption that *H. moschatus* continues to occupy its ancestral environment rain forest (whether gallery forest, as suggested by Megirian 1992, or extensive rainforest, as suggested by Archer et al. 1991, is irrelevant).

In its diet and general ecology (see Johnson and Strahan 1982) modern *H. moschatus* also seems almost archetypal of macropodiforms. Considering the alternative possibility that its limb proportions (and hence by implication its general ecology) might be secondarily acquired, Johnson and Strahan (op. cit., p. 42) say, 'when viewed in the context of its other unspecialized characters, it seems much more likely that the Musky Rat-kangaroo is representative of an early stage of evolution of macropods from an arboreal, possum-like stock.'

To examine proportional differences, the skulls of *H. moschatus* and *P. oscillans* were brought to the same size using a ratio between them of 1:3.7. For illustration (Fig. 24) they are aligned on the $M^2$. The ratio by which the size of *H. moschatus* was increased for comparison is, firstly, the ratios of the lengths of the entire mandibular rami and, secondly, of the $M^2$s. The specimen of *H. moschatus* used for comparison (ANWC CM15551) is at the same stage of dental eruption as *P. oscillans* specimen F35632/3.

The use of the whole mandibular ramus to derive the ratio is open to objection because the structure contains several functional components (length of incisor, length of diastema, size of premolar, length of mandibular cheek-tooth row, breadth of ascending process, length of masseteric fossa), any of which might vary separately to reflect different adaptational needs. Comparison of a single homologous element can be used to test for this disadvantage. Of the characters available $M^2$ was used because of the molars it is least affected by modifications at the opposite ends of the tooth row (i.e. sectorial specialization and $M^4$ reduction); it has also been used as a standard for comparison of hypsiprymnodontid dental characters previously (see Ride 1993, fig. 9); Wroe (in press) also independently selected $M^2$ for a standard of comparison in a study of the evolution of propleopine dental proportions. Comparisons of premolars would have been inappropriate because the premolar has been shown to be evolutionarily labile (Ride, and Wroe, same references). The two methods tried gave closely comparable results (mandibles, 1:3.66; M2s, 1:3.7).

From the figure the following proportional differences are apparent. These are expressed as ratios calculated from projections to a line parallel with the palate, or at right angles to that line (values for *P. oscillans* are given first):

length of premaxilla, not different (44:42);
length of diastema from centre of canine to anterior edge of premolar, shorter in *P. oscillans* (28:38);
length from infraorbital foramen to lachrymal foramen, longer (52:28);
length from infraorbital foramen to masseteric process, longer (58:41);
length from front of premaxilla to masseteric process, slightly longer (130:121);
length from front of premolar to masseteric process, longer (58:41);
zygomatic length, from masseteric process to the posterior edge of the condyle, shorter (84:91);
zygomatic depth at the masseteric process, much deeper (40:25);

From this comparison, it is seen that *P. oscillans* has a slightly longer face than *H. moschatus* measured from the front of the premaxilla to the masseteric process, but within that, the premaxillary length remains unchanged, the diastema is shorter and the premolars and molars comparatively further forward in the mouth; probably an indication that gape was wider. The anterior part of the jugal at the maxilla is very deep implying, in the absence of strong muscular attachments in the area, a need for distribution of stress from force applied vertically at the cheek teeth (especially on the molar row) greater than in *H. moschatus*.

The evidence from the masseteric processes that the external masseter muscle had a small antero-posterior action suggests that the structural increase in the depth of the jugal was an adaptation to distribute compressional forces from about the mid point along the molar row. Finch (1982, p. 200) has described bone thickening with a similar implied stress-shedding function from the premolar alveolus on to the anterior border of the orbit and thence to the cranial vault in *Thylacoleo*. If the thickness was maintained along the length of the zygomatic arch it would also have helped to withstand tension stress from the superficial masseter acting vertically on the beam to a much greater extent than in *Hypsiprymnodon*.

The narrow breadth across the zygomatic arches predicted by projecting the surviving anterior portion rearwards (when taken in conjunction with wider zygomatic arch of *H. bartholomaii* than *H. moschatus*, and the much larger ridge on the zygomatic arch for the insertion of the superficial layer of the internal masseter, as compared with *H. moschatus*), suggests also that the external masseters and, probably also the superficial layers of the deep masseter and zygomatico-mandibularis, are secondarily reduced in length in *P. oscillans*. Since these muscles contribute to the production of lateral mandibular movements and the glenoid in *H. bartholomaii* is well dorsal to the molar row, as figured in Flannery and Archer (1987, fig. 2), it is implied that the plesiomorphic condition had an appreciable lateral component and a lesser amplitude shear in the gape cycle.

## Attribution of humeri

Pledge (1981 p.46) described the partial humerus shown in Fig. 7 as straighter, more slender and more cylindrical than those of kangaroos and potoroines, and noted that it has markedly reduced deltoid and pectoral ridges and a shorter supinator crest. He pointed out that it bears a much greater resemblance to the humerus of *Hypsiprymnodon moschatus* than to the equivalent element in a range of other marsupials including *Macropus, Bettongia, Sthenurus, Thylacinus, Thylacoleo* and *Phascolarctos*.

Our attribution of this bone to *P. oscillans* is based upon similar lines of argument. Firstly, the negative evidence that it is unlike the humeri of any other form presently known from the fossiliferous sediments of Henschke's Fossil Cave. Secondly, the positive evidence that it is morphologically similar to the humeri of *H. moschatus*, the closest living relative of *P. oscillans*.

Aside from *Propleopus* the following marsupial genera are presently known from Henschke's Fossil Cave by cranial material: *Antechinus, Dasyurus, Phascogale, Sarcophilus, Sminthopsis, Thylacinus, Isoodon, Perameles, Cercartetus, Petaurus, Pseudocheirus, Trichosurus, Thylacoleo, Phascolarctos, Lasiorhinus, Vombatus, Diprotodon, Zygomaturus, Palorchestes, Aepyprymnus, Bettongia, Potorous, Lagorchestes, Macropus, Procoptodon, Protemnodon, Sthenurus* and *Wallabia* (Pledge 1990; John Barrie pers. comm.). Also known from the deposit are the monotreme *Megalibgwilia* (Griffiths et al. 1991) and several genera of murid rodents (Pledge 1990).

Members of most of these genera are far too small to have contributed the humerus shown in Fig. 7. However, nine of the listed marsupial genera include forms in which the humerus approaches or exceeds this bone in size. These genera are now considered.

The humerus of *Thylacinus cynocephalus*, is rather smaller than the bone of Fig. 7, but the Henschke's Cave material contains evidence of a larger form of *Thylacinus*. However, as with *T. cynocephalus*, the humerus of this larger form can be distinguished from the humerus illustrated in Fig. 7 by the very poor development of the supinator crest and greater curvature in the parasagittal plane in *Thylacinus*.

The lack of curvature and/or the very limited development of the pectoral ridge and deltoid crest serve to separate the humerus of Fig. 7 from those of *Thylacoleo*

(Murray 1991, fig. 24), *Diprotodon* (Murray 1991, fig. 21C; Gregory 1951, fig. 18.36), *Zygomaturus* (Scott and Harrisson 1911, fig. 1; Murray 1991, fig. 22), *Palorchestes* (Flannery and Archer 1985), *Macropus* (Murray 1991, fig. 26A) and *Sthenurus* (Wells and Tedford 1995). Size and morphology preclude *Procoptodon goliah* (Tedford 1967, fig. 16a; Murray 1991, fig. 26), and as the humeri of the two smaller species of this genus (*P. rapha* and *P. pusio*), which have not so far been described, are likely to be morphologically similar to those of *P. goliah*, we assume that they too are quite unlike the humerus of Fig. 7.

So far as we are aware no illustrations or descriptive accounts have been published of the humerus of *Protemnodon*. However, a Museum of Victoria humerus (NMV P39105) collected from Morwell, and which is almost certainly *P. anak* (Rich pers. comm.), exhibits a number of features which set it far apart from the humeri we attribute to *P. oscillans*. The Morwell specimen, which we have examined, is approximately 255 mm long, but much more massively constructed than the bone of Fig. 7. It has a very strongly developed pectoral ridge which bends mesially over the bicipital groove proximally. The entepicondyle of this bone is well developed and includes a very robust entepicondylar ridge. When this Morwell specimen is viewed from a lateral or medial perspective dual curvature is very evident. Scott and Lord (1924) mention a pair of large humeri (total length 224 mm and 228 mm) that were found in association with a left mandibular ramus collected from King Island which they identified as *P. anak*. Efforts to relocate these bones in the collection of the Queen Victoria Museum (Launceston) have so far been unsuccessful (Tassell pers. comm.), but the fact that Scott and Lord made no mention of any peculiarities of form in these bones suggests that, like the Morwell humerus, they were essentially similar in form to, but much bigger than, those of a large extant species of *Macropus*.

Another large form which is not so far known from this site, but which occurs in other Pleistocene sites in south-eastern Australia is the vombatid *Phascolonus*. Greater size and the extreme development of ridges and crests (Stirling 1900, plate 49 (1); Murray 1991, fig. 17) distinguish the humerus of *Phascolonus* from the bone shown in Fig. 7.

Thus by a process of elimination *P. oscillans* appears to be the only large form presently known from (or likely to turn up in) Henschke's Fossil Cave that might have yielded a humerus of this type.

Support for this interpretation is provided by features which ally the humerus of Fig. 7 with the equivalent bone in *Hypsiprymnodon moschatus*. This positive evidence is now considered.

In comparison with the humeri of extant macropodiform (and most other) marsupials the outstanding feature of the Henschke's Cave humeri shown in Figs 7 and 8 is the very simple contouring of the shaft surface. As we shall see this is one of the features that the humerus of Fig. 7 shares with *H. moschatus*. However, it should be noted that it is bipedal members of the macropodiforms, rather than *H. moschatus*, that exhibit the 'standard' humeral morphology that obtains in generalized quadrupedal marsupials such as *Didelphis, Antechinus* and *Trichosurus* and in most bandicoots.

In the potoroids *Potorous tridactylus* (Figs 25G, 26G), *Aepyprymnus rufescens* (ANWC MAMS-9), *Bettongia penicillata* (Figs 25I, 25O), *B. lesueur* (Figs 25J, 26J), the macropodids *Dendrolagus bennettianus* (Figs 25E, 26E), *Petrogale penicillata* (ANWC CM 13571), *P. xanthopus* (Figs 25D, 26D), *Setonix brachyurus, Lagorchestes, Onychogalea* (Merrilees and Porter 1979 p. 90, p. 81, p. 85), *Wallabia bicolor* (ANU PL), *Macropus parma* (Figs 25C, 26C), *Macropus eugenii* (Merrilees and Porter 1979 p. 99), *Macropus rufogriseus* (ANU DBZ), *Macropus fuliginosus* (Merrilees and Porter 1979 p. 109), *Macropus giganteus* (Figs 25B, 26B), the pectoral ridge is a very pronounced feature of the anterior surface of the humeral shaft. However, this structure is quite weakly developed in both *H. moschatus* (Figs 25J, 26J) and the very small macropodid *Dorcopsulus vanheurni* (Figs 25F and 26F).

The humeri of *H. moschatus* and *D. vanheurni* are further distinguished from those of most other macropodiforms by weak development of the deltoid ridge (Fig. 25J, F). In *Hypsiprymnodon* a relatively low weakly developed ridge can be found on the antero-lateral margin of the proximal humerus (Fig. 25J). As in several other macropodiforms this continues distally and makes contact with the pectoral ridge producing an elongate triangular area on the anterior surface of the proximal humerus which was described by Heighway (1939 p. 16). (Note however, that Heighway uses the name deltoid crest to refer to the structure which we identify as the pectoral ridge.) In *Dorcopsulus* the deltoid ridge is less extensive, and for the most part even more weakly developed, although it rises to a sharp narrow crest about a quarter of the way down the lateral surface of the bone (Fig. 25F). The deltoid ridge can be traced some way beyond this crest distally, but not as far as the pectoral ridge so that *Dorcopsulus* has no triangular area on the front of the humerus. In most other macropodiform marsupials the deltoid ridge is a very obvious feature of the lateral or antero-lateral surface of the humerus. In the rat-kangaroos *Aepyprymnus rufescens* (ANWC MAMS-9), *Bettongia lesueur* (Fig. 25H) and *B. penicillata* (Fig. 25I), its conjunction with the pectoral ridge is associated with the formation of a large triangular-shaped and very strongly protruded crest which is evidently a more robust version of the triangular area found in *H. moschatus*. A somewhat similar situation seems to exist in *Petrogale* and *Dendrolagus* (Fig. 25D and E), but in most other macropodiform species, including *Potorous tridactylus* (Fig. 25G), the two ridges do not join to form a robust crest. As already noted the deltoid ridge is very poorly developed in the Henschke's Fossil Cave humerus of Fig. 7.

In the extinct sthenurine kangaroos the pectoral ridge is said by Wells and Tedford (1995) to be less well developed than in *M. giganteus* but longer, while in comparison with the latter form the deltoid crest is said to be relatively larger in *Sthenurus stirlingi* but relatively smaller in *S. tindalei* and *S. andersoni*. However, both structures are clearly better developed in sthenurines of all sizes than in *H. moschatus* or *D. vanheurni* (Wells and Tedford 1995, fig. 26a, f).

The superficial similarity in form of the humeri of *Hypsiprymnodon* and *Dorcopsulus* is somewhat surprising, but though the articular surface of the humeral head is essentially spheroidal in both forms, in *H. moschatus* it is quite clearly elongate antero-posteriorly (Fig. 27B), whereas in *D. vanheurni* it is slightly more elongate transversely (Fig. 27D). Proximally the margin of the pectoral ridge is wrapped mesially in *D. vanheurni* so that it partly obscures the bicipital groove. This feature is shared by a number of macropodids including *M. parma* (Fig. 27E), but is completely lacking in *H. moschatus* (Fig. 27B).

*D. vanheurni* and *H. moschatus* show a most interesting difference in humeral torsion. In *D. vanheureni*, the articular axis of the elbow joint lies nearly at right angles to a line passing antero-proximally through the humeral head and the proximal pectoral ridge-bicipital groove transition, so that humeral torsion measures around 6° – 7° (n=2). In *H. moschatus* these two lines of reference are not orthogonal but offset from this such that humeral torsion measurements vary between 14° – 24° (mean = 18.7°, n = 6). One consequence of this is that in *H. moschatus* the lateral portion of the distal humerus is more cranially situated and its medial portion more caudally situated than in the macropodid. A strong backward curvature of the proximal part of the supinator crest which further distinguishes *H. moschatus* from *D. vanheureni* (and from other living macropodiforms) seems to be related to this torsional difference. Finally it can be noted that, relative to the condition in *D. vanheurni* (Fig. 25F), the capitulum of *H. moschatus* appears to be abbreviated laterally and the entepicondyle somewhat reduced in size (Fig. 25J).

The humerus of macropodiform marsupials generally shows obvious curvatures in both the parasagittal and transverse planes; the mesial surface being concave (Fig. 25), and the posterior surface being concave proximally and convex distally (Fig. 26). These

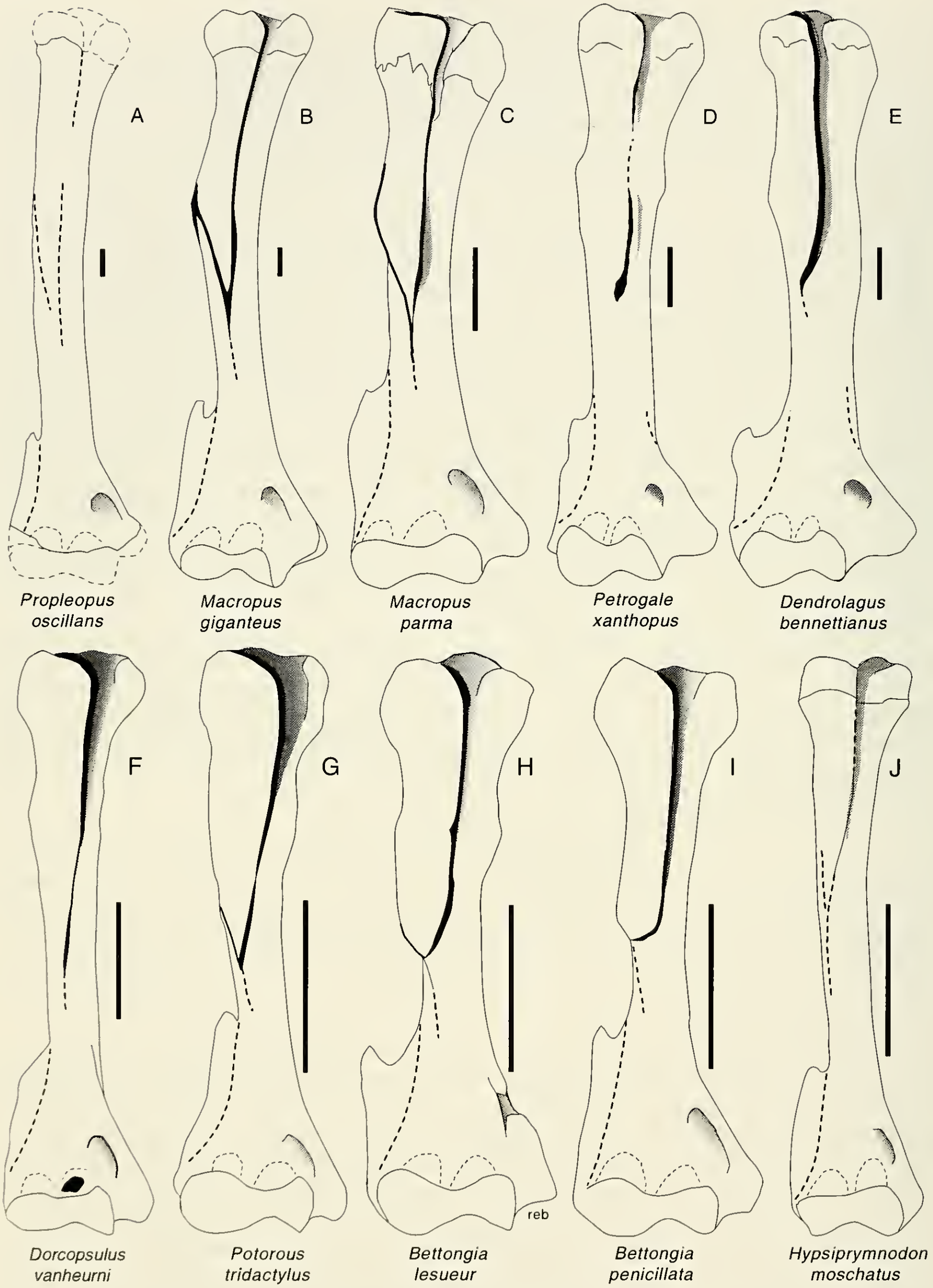


Figure 25. Right humeri of various macropodoid marsupials in anterior view. The illustrated humeri are from: A. Henschke's Fossil Cave specimen attributed to *P. oscillans* (P18846); B. *Macropus giganteus* (ANU PL); C. *M. parma* (ANU PL); D. *Petrogale xanthopus* (M11470); E. *Dendrolagus bennettianus* (M5530); F. *Dorcopsulus vanheurni* (ANWC CM15124); G. *Potorous tridactylus* (ANWC MAMS207); H. *Bettongia lesueur* (ANWC CM12873); I. *B. penicillata* (ANWC CM11458); J. *Hypsiprymnodon moschatus* (ANWC CM6051 and QM JM6187). The humeri have been brought to a common size to facilitate comparison. Scale bars = 10 mm. Epiphyseal reconstruction in A is based largely on the condition in *H. moschatus* (J).

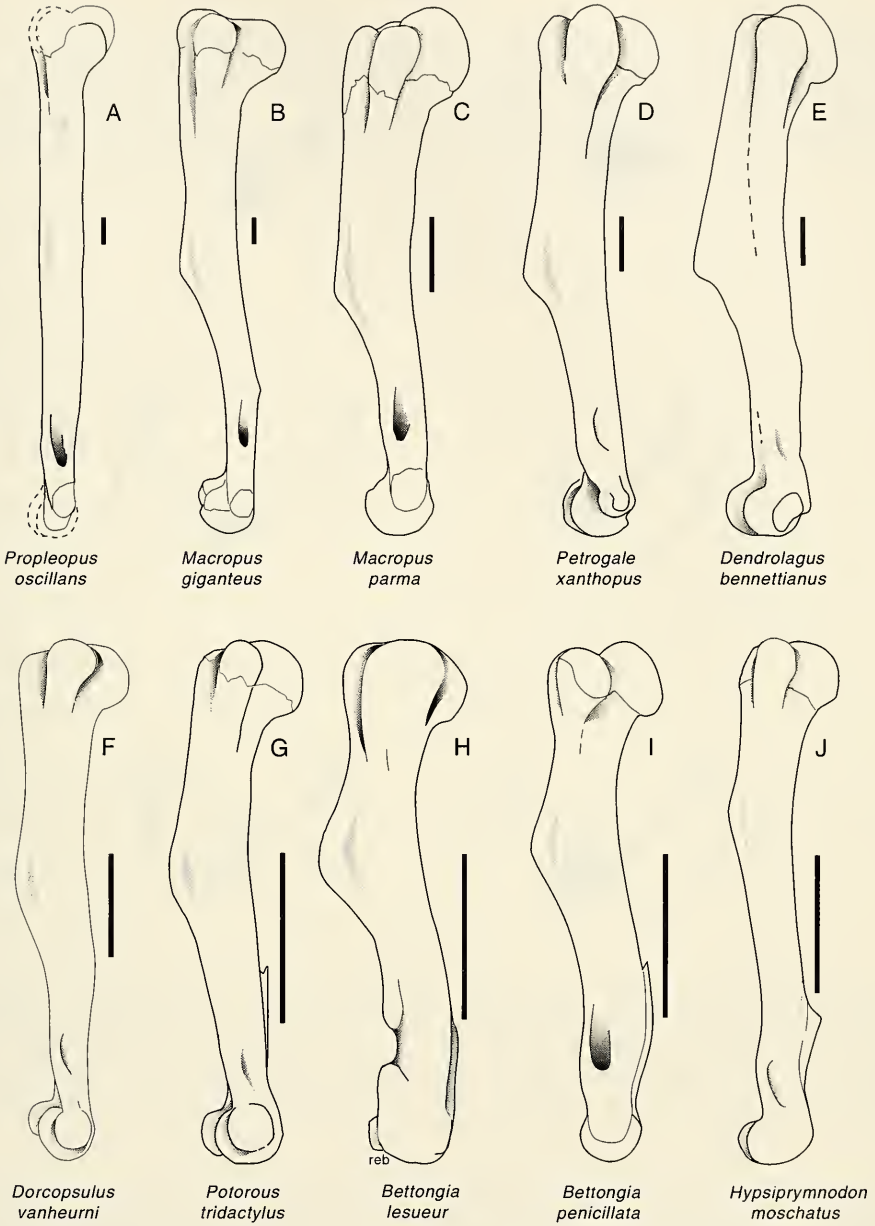


Figure 26. Right humeri of various macropodoid marsupials in medial view. The illustrated humeri are from: A. Henshke's Fossil Cave specimen attributed to *P. oscillans* (P18846); B. *Macropus giganteus* (ANU PL); C. *M. parma* (ANU PL); D. *Petrogale xanthopus* (M11470); E. *Dendrolagus bennettianus* (M5530); F. *Dorcopsulus vanheurni* (ANWC CM15124); G. *Potorous tridactylus* (ANWC MAMS207); H. *Bettongia lesueur* (ANWC CM12873); I. *B. penicillata* (ANWC CM11458); J. *Hypsiprymnodon moschatus* (ANWC CM 6051 and QM JM6187). The humeri have been brought to a common size to facilitate comparison. Scale bar = 10 mm. Epiphyseal reconstruction in A is based largely on the condition in *H. moschatus* (J).

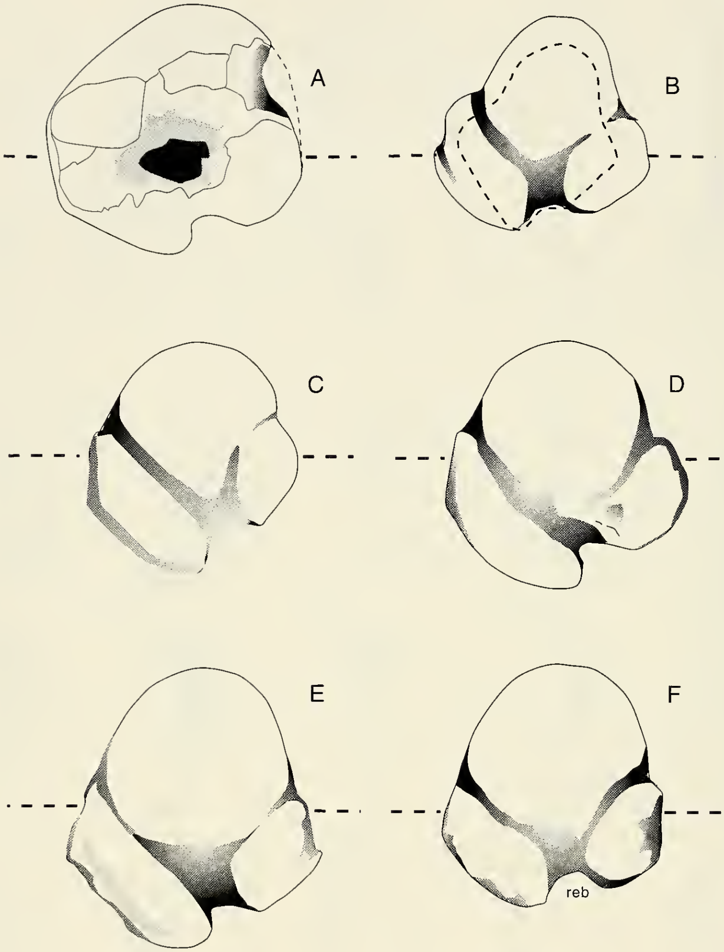


Figure 27. Proximal portions of the right humeri in end view of A. Henshke's Fossil Cave specimen attributed to *P. oscillans* (P18846); B. *Hypsiprymnodon moschatus* (QM JM 6187); C. *Potorous tridactylus* (ANWC MAMS207); D. *Dorcopsulus vanheurni* (ANWC CM15124); E. *Macropus parma* (ANU PL); F. *Macropus giganteus* (ANWC MAMS343). In each instance the bone is drawn with its anterior face directed towards the bottom of the figure and its posterior face towards the top. The approximate alignment of the articular axis of the elbow joint is indicated by a broken line. In B a broken line indicates the shape of a cross-section just below the head. The drawings have been brought to a common size to facilitate comparison.

curvatures are readily apparent in the humeri of large specimens of *Macropus giganteus*, with that in the transverse plane being more pronounced than that in the parasagittal one. All three curvatures are also evident in the humeri of the macropodids *Macropus parma* (Fig. 26C), *M. eugeni* (ANWC CM11450) and *Setonix* (ANWC MAMS 196) and, at least in the transverse plane, in *Onychogale* (Merrilees and Porter 1979 p. 85). In *Dendrolagus bennettianus* (Fig. 26E) and *Petrogale xanthopus* (Fig. 26D), there is no clear indication of curvature in the transverse plane and only slight evidence of it in the parasagittal one. The same would seem to be true of *Lagorchestes* (Merrilees and Porter 1979 p. 81). The three curvatures are evident in members of the genus *Sthenurus* (Wells and Tedford 1995, fig. 26).

Table 2

Humeral torsion in various marsupials. Extreme estimates are given for the single most complete humerus of *P. oscillans* and the real value undoubtedly lies within these. With the other species single estimates were obtained from each humerus. All values were obtained by placing the bone upright with the axis of rotation of the elbow joint set along a previously drawn line and then establishing a second line through the most posterior part of the articular surface of the humeral head and the proximal part of the lateral margin of the bicipital groove. The method is imprecise and may involves errors of up to 5 degrees; nevertheless, data trends are considered reliable. Where left and right humeri were available two values have been given.

| **Species** | **Number of humeri examined** | **Values** |
|---|---|---|
| *Propleopus oscillans* (P18846) | 1 | $12^0 - 27^0$ |
| *Hypsiprymnodon moschatus* Qd Mus. JM6915 | 2 | $18^0$, $24^0$ |
| *Hypsiprymnodon moschatus* Qd Mus. JM6187 | 2 | $16^0$, $20^0$ |
| *Hypsiprymnodon moschatus* CM6051 | 2 | $14^0$, $20^0$ |
| *Aepyprymnus rufescens* | 2 | $2^0$, $2^0$ |
| *Potorous tridactylus* | 2 | $8^0$, $10^0$ |
| *Bettongia penicillata* | 2 | $4^0$, $9^0$ |
| *Bettongia lesueur* | 2 | $3^0$, $7^0$ |
| *Dorcopsulus vanheurni* | 2 | $6^0$, $7^0$ |
| *Macropus parma* | 1 | $6^0$ |
| *Macropus giganteus* | 1 | $10^0$ |
| *Trichosurus vulpecula* | 2 | $7^0$, $9^0$ |
| *Phascolarctos cinereus* | 2 | $2^0$, $4^0$ |
| *Vombatus ursinus* | 2 | $1^0$, $2^0$ |
| *Thylacinus cynocephalus* | 2 | c. $2^0$ |
| *Sminthopsis leucopus* | 1 | c. $13^0$ |
| *Dasyurus maculatus* | 2 | $7^0$, $10^0$ |
| *Isoodon macrourus* | 2 | $3^0$, $7^0$ |
| *Perameles sp.* | 2 | $7^0$, $8^0$ |

Humeral curvature is weakly developed in the transverse plane in potoroids, but the double curvature of the sagittal plane is very evident in the humeri of the potoroids *Potorous tridactylus* (Fig. 26G), *Aepyprymnus rufescens* (ANWC MAMS-9), *Bettongia lesueur* (Fig. 26H) and *B. penicillata* (Fig. 26I). All three curvatures are relatively weakly developed in *Dorcopsulus vanheurni* (Figs 25F, 26F) and very weakly developed in *Hypsiprymnodon* (Figs 25J, 26J). As noted above, the Henschke's Fossil Cave humerus described by Pledge shows no evidence of proximal curvature and very little evidence of distal curvature in the parasagittal plane, while in the transverse plane it is moderately curved outward. The virtual absence of curvatures in the parasagittal plane is responsible for apparent straightness of this bone when viewed from a mesial or lateral perspective (Figs 7B, D, 25A, 26A).

Torsion measurements (Table 2) separate this bone and the humeri of *H. moschatus* from those of living potoroids and macropodids (including *Dorcopsulus*), and indeed from various quadrupedal marsupials as well. Whether such torsion is a feature of the humerus shared by all members of the Hypsiprymnodontidae remains to be established. As in *H. moschatus*, the proximal part of the supinator crest is turned caudally, although not so strongly as in the living form.

Overall P18846 is quite similar to the humeri of *H. moschatus* and *D. vanheurni*. All three humeral types share a simple form that is apomorphic among marsupials. However, when humeral torsion and other more subtle features of morphology are taken into account it is evident that P18846 and the humeri of *H. moschatus* share some derived features that are lacking in the humeri of *D. vanheurni*. This suggests that *H. moschatus* and the species from which P18846 came are are closely related and, in conjunction with other evidence (see below), suggests that the simplified form of the humerus in these animals was acquired independently from that found in *D. vanheurni*.

In so far as the fossil humerus is essentially a scaled-up version of that of *H. moscatus* and in so far as features of cranial anatomy mentioned earlier in this study demonstrates that *Hypsiprymnodon* and *Propleopus* are morphologically similar forms, and since in our view they are quite closely related, we conclude that Pledge (1981) was right and that the humerus P18846 is attributable to *P. oscillans*. On the basis of its similarity to this bone we attribute the less complete, but larger, humerus, P35648 (Fig. 8), to *P. oscillans* as well.

The size of these humeri is not inconsistent with this attribution. The length of the skull of *P. oscillans* is some 3.6 to 3.7 times greater than that of *H. moschatus* whereas the presumed humeri are some 5.7 to 6.2 times larger than the equivalent element in *H. moschatus*. However, the skull tends to be proportionately smaller relative to the humerus in both large macropodoid (bipedal) and large dasyuroid (quadrupedal) marsupials than in small members of these groups, so that such differential scaling of skull and humerus is not unexpected.

## Humeral morphology and life style

The humerus alone provides a very limited basis for assessing life style in *P. oscillans*. Nevertheless, there are three lines of investigation that can provide some insight into the likely habits of the fossil form to the extent that these are reflected in humeral morphology. One involves comparison of the form of the humerus of *P. oscillans* with that of its nearest relative (i.e. *H. moschatus*). The second involves comparison of the form of this bone with the equivalent element in suites of mammals that represent particular habitus types (e.g. digging mammals, cursorial mammals, etc.). The third involves consideration of areas of muscle attachment on the humerus of *P. oscillans* and the inferences that can be drawn from these.

### Comparison of *P. oscillans* with *H. moschatus*

Recent studies of captive specimens of *H. moschatus* confirm that it is consistently quadrupedal (Johnson and Strahan 1982; Johnson pers. comm.), as reported earlier by Le Soeuf and Burrell (1926 p. 238) who noted that *H. moschatus* 'proceeds on all four feet like a rat' Such behaviour sets *H. moschatus* apart from all living potoroid and macropodid marsupials which usually move quadrupedally at low speeds (this may not be true of forest wallabies), but are invariably bipedal at moderate to high speeds (Frith and Calaby 1969; Windsor & Dagg 1971; Morton and Burton 1973; Buchmann and Guiler 1974; Maynes 1974; Lundie-Jenkins 1993).

The considerable morphological similarity of the humeri of *P. oscillans* and *H. moschatus* suggests that the extinct form was not greatly dissimilar in its locomotor behaviour to the smaller living one. This implies that *P. oscillans* was probably quadrupedal at all speeds during normal terrestrial locomotion.

Two further questions arise immediately from this. Firstly, what are the locomotor capabilities of *H. moschatus*? In particular how capable a runner is it? Secondly, was *P. oscillans* more or less capable in this respect than *H. moschatus*?

Despite recent observations, we are relatively ignorant of the performance capabilities of *H. moschatus*. We do not know, for example, how its top speed compares with that of *Aepyprymnus, Bettongia* or *Potorous*. When travelling at maximum speed is it faster or slower than these small bipedal potoroids? Neither do we have any appreciation as to whether its capabilities run to brief bouts of relatively high speed or are more attuned to extended bouts of running at a more moderate pace. Likewise, the capacity of *H. moschatus* for other forms of locomotion remains little known. Dennis and Johnson (1995) note that it occasionally climbs in low vegetation such as fallen trees or branches and Johnson (pers. comm.) reports that it climbs well on thick branches that are inclined at angles of up to 45°. In such climbing it uses not only the whorled pads of its feet, but also its narrow and recurved claws which are surprisingly sharp (Johnson pers. comm.).

There remains the question as to whether the capacity of *P. oscillans* for terrestrial locomotion was more or less than that of *H. moschatus*. Two features which seem to be relevant to assessing the relative terrestrial locomotor capabilities of *P. oscillans* are the greater straightness of the shaft of its humerus when viewed from a lateral perspective, and the even weaker development on this bone of various ridges and processes that are not strongly developed on the humerus of *H. moschatus*.

As noted below greater straightness of the humerus in the parasagittal plane is rather equivocal as it appears to be characteristic not only of cursorial animals but also of larger ones. Less equivocal is the weak development of ridges in *P. oscillans*. As noted below, humeral morphology is generally simplified in cursors. Thus the simpler morphology of its humerus suggests that *P. oscillans* was capable of running relatively faster and/or longer than *H. moschatus*.

### Comparison of *P. oscillans* with various habitus types

The relation between humeral form and life style is not well understood in mammals and in the absence of information on the more distal elements of the forelimb or other parts of the postcranium it is very difficult to advance positive views about the life style of *P. oscillans*. Given this, our aim has been to narrow the range of possible life styles of *P. oscillans* by ruling out certain broad habitus types. To achieve this the humerus of *P. oscillans* is compared with the equivalent elements in a range of other mammals.

#### Comparison with bipedal saltators:

The morphological features that distinguish the humerus of *P. oscillans* from those of bipedal potoroids and macropodids strongly suggests that the fossil form did not use its forelimbs in a manner comparable to that of any living bipedal macropodiform. As already noted the superficial similarities that exist between this bone in forest wallabies of the genus *Dorcopsulus* on the one hand, and *H. moschatus* and *P. oscillans* on the other, occur in conjunction with several subtle but significant differences which indicate that the humerus has been modified for quite different roles in the two groups. Simplification of the humeral shaft presumably reflects alterations in the character of the forces that are applied to it by the attaching muscles and, as we shall see, such simplification is common to several groups of mammals that are locomotively specialized in quite divergent ways.

That we are dealing with a divergent specialization in *Dorcopsulus* is indicated not only by the differences in humeral morphology just alluded to, but additionally by the very different proportions of the fore and hindlimbs in *Dorcopsulus* and *Hypsiprymnodon*, and by the very different form of the scapula in these two genera. Relative to femoral length, the humerus in *Dorcopsulus* is very similar in length to that of *Setonix*. In both these forms the humerus is relatively longer than in *Aepyprymnus* and *Lagorchestes hirsutus*, but relatively shorter than in *Potorous tridactylus*. In *Hypsiprymnodon*, in contrast, the humerus is proportionately much longer than in any of these forms. Indeed, relative to the femur, humeral length in *H. moschatus* closely approaches that of some peramelids and vombatids, although from this perspective the bone of *H. moschatus* is still proportionately much shorter than in dasyurids (Pridmore unpub. data). The scapula of the *H. moschatus* is a long and relatively rectangular bone (Heighway 1939, fig. 5; Johnson and Strahan 1982, fig. 10) which is essentially similar in outline to the same element in *Potorous, Trichosurus, Sarcophilus* (Merrilees and Porter 1979) and *Caenolestes* (Osgood 1921). It lacks the sharp rise in the anterior border immediately adjacent to the scapular notch which is found in *Dorcopsulus* and in other forms with short fan or trapezial-shaped capulae, such as *Setonix* and members of the genus *Macropus* (Merrilees and Porter 1979).

We suspect that the form of the humerus in *Dorcopsulus* reflects minimal use by this form of quadrupedal locomotion. Slow quadrupedal crawling has obvious importance for forms that grub amongst soil or leaf litter for food (most potoroids), and for forms that browse or graze on low growing leaves (most macropodids). However, it is likely to be of little use to small very manoeuvrable forms which obtain leaves that are growing well above ground. For an animal that has to extend its head upwards to grasp food items, the ability to use the bent tail as a third support (supplementary to the hindlimbs) would seem to be of far greater value than any capacity it might possess for supporting itself on its short forelimbs. George (pers. comm.) indicates that specimens of *Dorcopsulus* rarely, if ever, use quadrupedal locomotion. This suggests that the primary roles of the forelimbs in forest wallabies may have been reduced to manipulation of food at the mouth (Menzies 1991 p. 111), to use in toilet and to use in pouch manipulation.

Whether our interpretation is correct or not, the view of Lord and Scott (1924, p. 244) that the essential similarity of the humerus of *Macropus* to that of other marsupials is due to 'the urgent need for the manipulation of the pouch', would seem to be untenable since the pouch is well developed in both *Dorcopsulus* and *Hypsiprymnodon* (Menzies 1991; Dennis and Johnson 1995; Johnson pers. comm.).

Differences between the humeri of *P. oscillans* and *H. moschatus*, on the one hand, and those of other macropodiform marsupials, on the other, are evident in radiographs. These show the shaft of the humerus of *P. oscillans* to be supported by a dense cortical layer of bone which extends along almost the entire length of the diaphysis on all sides (Figs 29A, 30A). A similar situation is found in *H. moschatus* (Figs 29B, 30B), although the cortical layer is markedly less developed in the smaller form. Extended cortical thickening does not characterize the entirety of the humeral shaft in potoroid or macropodid marsupials, including *Dorcopsulus*. In these forms dense cortical bone is found on the posterior, mesial and lateral surfaces of the shaft, but not on the anterior surface, at least proximally (Figs 29C-I, 30C-I). The same is true of the phalangerid *Trichosurus* (Figs 31A, 32A).

Comparison with digging, swimming and typical climbing mammals:

The relatively straight form and smooth surface of the humeral shaft in *P. oscillans* would seem to exclude from consideration life styles in which much time was spent in digging, swimming or climbing in trees in the usual mammalian quadrupedal manner. In mammals that habitually undertake such activities, the deltoid crest is developed to a much greater extent than in *P. oscillans*. However, the ridges of the humeral shaft are weakly developed in certain atypical types of arboreal mammals, in cursorial mammals and in some ambulatory mammals.

Comparison with certain atypical arboreal mammals:

To some extent the condition of the humerus of *P. oscillans* is approached in the vertical-clinging-and-leaping lemuroid primate *Indri*. In this form the shaft of the humerus is akin to a simple cylinder and except for a small anterior crest is largely free of significant protuberances over its length (Vallois 1955, fig. 1860). However, the humerus of *Indri* is at once both too gracile and equipped with too large an anterior crest (see Hill 1953, plate 30) to serve as a credible model for *P. oscillans*. Moreover, to the extent that *Indri* and its relatives exhibit any transverse curvature, it involves lateral concaveness (Demes et al. 1991, fig. 3); exactly the reverse of the situation in *P. oscillans*.

Humeri that are superficially similar to that of *P. oscillans* are encountered also in those primates that habitually use an upright posture. These animals are sometimes termed brachiators, semibrachiators and modified brachiators (e.g. Napier and Napier 1967), but as Andrews and Groves (1975) have pointed out what they share is use of an upright posture and a tendency to employ their mobile forelimbs to reach widely during feeding. These primates which belong to several different lineages, all have straight cylindrical humeri in which the shafts are devoid of all but the most minute protuberances. Humeri of this type are also found in humans.

When compared with the humeri of other primates, those of forms that are upright-postured are characterized by changes in the relative size and position of the humeral head and of the adjacent pair of tuberosities. In the upright-postured forms the head of the humerus is spheroidal rather than ovoid and very much larger relative to the diameter of the shaft than in forms that rarely use an upright posture (Fig. 28A, B). In the former the head is centrally placed at the proximal terminus of the bone, whereas in the latter it is terminal but somewhat offset from the long axis so that it projects posteriorly as well as terminally. In forms that rarely use an upright posture, one of the tuberosities is often sufficiently large to project above the summit of the humeral head (e.g. *Papio* – Swindler and Wood 1973, plate 15), whereas the relatively smaller tuberosities of those that habitually use such a posture do not project above the summit of the head at any point (e.g. *Ateles* – Figs 31E, 32E; *Hylobates* – Giebel and Leche 1874-1900, plate 81; *Pan* – Figs 31F, 32F). Another difference concerns the bicipital groove, which is narrow and sometimes partly closed in members of the former group (Fig. 28B), but broad and quite open in members of the group that do not habitually use an upright posture (Fig. 28A). Moreover, there is a tendency for the lesser tuberosity to atrophy in forms that commonly use an upright posture (Fig. 28B), whereas the proximal tuberosities are generally subequal in size in forms that rarely use an upright posture (Fig. 28A).

Several of these features of the proximal humerus of upright-postured primates are shared by sloths (Miller 1935, fig. 1; Beddard 1958, fig. 98; DeBlase and Martin 1981, fig. 8.15). Like gibbons and spider monkeys, sloths use their forelimbs as suspensory supports. Unlike gibbons, they obtain support in suspension from their hind as well as their forelimbs. In the three-toed sloth *Bradypus* the globular head, which is similar in diameter to the humeral shaft, is sited terminally on the axis of the bone and projects well above the proximal humeral tuberosities (Lessertiseur and Saban 1967, fig. 524A). In this form also, the lesser tuberosity is considerably smaller than the greater and very much smaller than the humeral head (Fig. 26C). In a specimen of the two-toed sloth

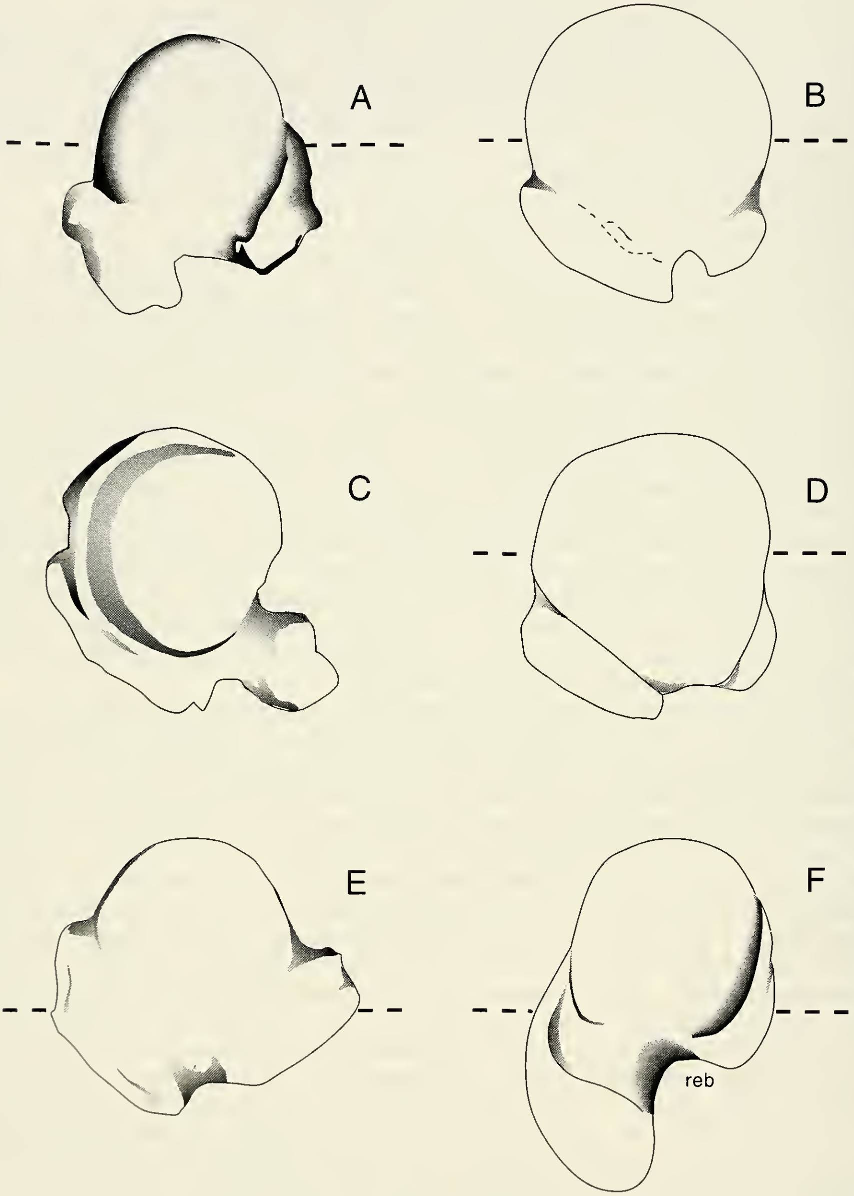


Figure 28. Proximal portions of the right humeri in end view from: A. baboon *Papio*; B. spider monkey *Ateles* sp.; C. three-toed sloth *Bradypus*; D. opossum *Didelphis* sp.; E. brushtail possum *Trichosurus* (ANU PL); F. thylacine *Thylacinus* (NMA IAC). In each instance the bone is drawn with its anterior face directed towards the bottom of the figure and its posterior face towards the top. The approximate alignment of the articular axis of the elbow joint is indicated by a horizontal broken line. The diagram of *Papio* is based on plate 15 of Swindler and Wood (1973), that of *Bradypus* on plate 76 (7a) in Giebel and Leche (1874-1900) and that of *Didelphis* on fig. 5 of Evans and Krahl (1945). The other three are original. The drawings have been brought to a common size to facilitate comparison.

*Choloepus* which we have examined, the humeral head is terminal but directed dorsally as well as terminally. It projects well above the proximal tuberosities and has a somewhat greater diameter than the shaft of the bone. However, the proximal tuberosities are more equally developed than in *Bradypus*. As in the humerus of *P. oscillans* the pectoral and deltoid ridges are very weakly expressed and the entepicondylar foramen well developed. However, the humerus of *Choloepus* which exhibits no obvious curvature in the transverse plane, exhibits obvious dual curvature in the parasagittal plane (Fig. 32G) and has a rather well developed supinator crest (Fig. 31G).

While the humerus of *P. oscillans* exhibits some similarity to those of upright-postured primates and of sloths, it is much less gracile than the equivalent element in these forms. This more stout configuration and the obvious curvature of the humerus in the transverse plane argue against the forelimbs of *P. oscillans* having served in a similar fashion to those of these non-marsupials.

Further evidence against such use is provided by radiographs. Although extended cortical thickening of the humeral shaft is evident also in the primates *Ateles* and *Pan* (Figs 31E, F, 32E, F), relative to humeral length, cortical bone is proportionately much thicker in *P. oscillans* than in the two primates. Moreover, whereas cortical bone is somewhat more thickly developed on the mesial surface of the humeral shaft in *P. oscillans*, the reverse seems to be the case with *Pan* and the sloth.

Comparison with quadrupedal cursorial mammals:

Quadrupedal cursorial adaptations are widespread amongst the Mammalia and mammals that travel far and/or fast share a suite of postcranial characteristics that generally includes a humerus in which the shaft appears largely free of bony protuberances. Indeed, in most cursors the humeral shaft has the form of a tapered ovoid cylinder. It should be noted, however, that the apparent absence of protuberances is a feature which shows some tendency to disappear at large body size. Thus while the humeral shaft seems to have been relatively smooth in the Eocene equid *Hyracotherium* (est. 24 to 35 kg) and to have carried a small deltoid crest in both the Oligocene form *Mesohippus* (est. 42 to 48 kg) and the Miocene form *Merychippus* (est. 85 to 101 kg) (Simpson 1951; MacFadden 1986), this configuration no longer obtains in the modern riding horse (c. 200 kg). In such forms of *Equus caballus* the deltoid crest is very robustly developed (Smythe and Goody 1975, fig. 13).

The weight of *P. oscillans* is unknown, but several authors have suggested that the animal was similar in size to a modern red or gray kangaroo of similar mandibular length (e.g. Woods 1960; Pledge 1981; Archer et al. 1991). Flannery (1985 p. 245 , 1989 p. 17 ) has estimated that the weight of *P. oscillans* was close to 70 kg. These estimates of size and weight are based on analogy with large bipedal macropodids. However, given that *P. oscillans* was most probably quadrupedal, an estimate of weight can also be obtained by using regression equations that relate humeral length to body weight in a large size range of quadrupedal placental mammals (Alexander et al. 1979). Of the four equations relating humeral length and body weight obtained by Alexander et al., that which best fits data for *H. moschatus* is the one that uses values for all placental mammals. Substituting a length of 210 mm into this equation yields a body weight estimate for *P. oscillans* of 51 kg with 95% confidence limits of 34 and 78 kg. The 210 mm long bone lacks epiphyses and so is probably from a sub-adult animal, which suggests that this is likely to be an underestimate of adult weight in *P. oscillans*. Taking this into account an adult weight similar to that estimated by Flannery (1985, 1989) is suggested. Evidently, *P. oscillans* exceeded in weight, not only the dingo, but also *Thylacinus cynocephalus* (15 – 35 kg) (Rounsevell and Mooney 1995).

From a lateral perspective the humeri of most mammals appear sigmoid (Fig. 32B-D). A larger curve, involving concaveness of the anterior surface, occupies the proximal two thirds or so of the bone and the smaller concave-posterior curve uses the remainder.

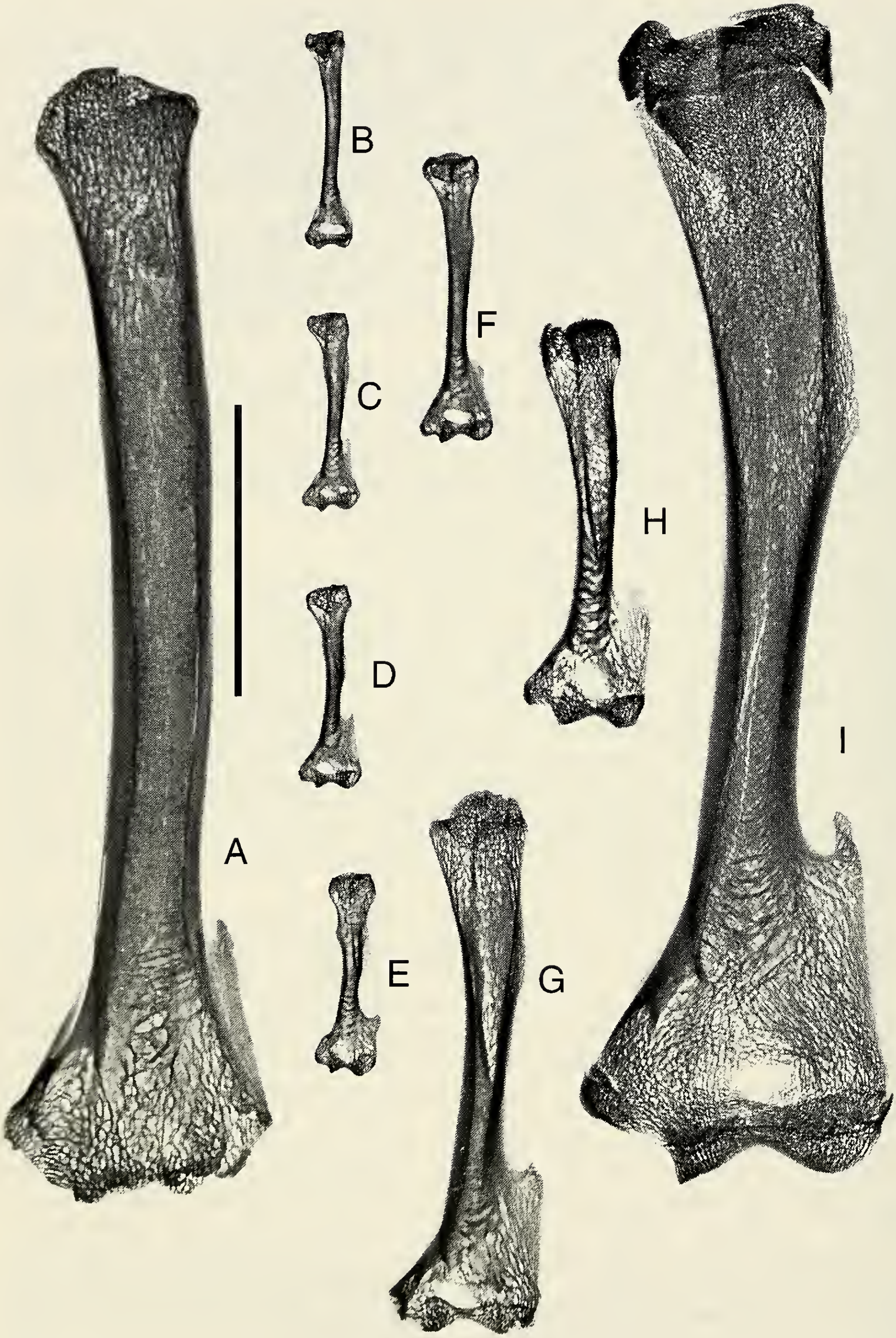


Figure 29. Antero-posterior projection radiographs of right humeri from: A. Putative *P. oscillans* (lacking proximal and distal epiphyses); B. *Hypsiprymnodon moschatus*; C. *Potorous tridactylus*; D. *Bettongia penicillata*; E. *B. lesueur*; F. *Dorcopsulus vanheurni*; G . *Wallabia bicolor* (lacking proximal epiphysis); H. *Macropus parma*; I. *Macropus giganteus*. Note that due to image reversal mesial is to the left. Scale bar = 5 cm

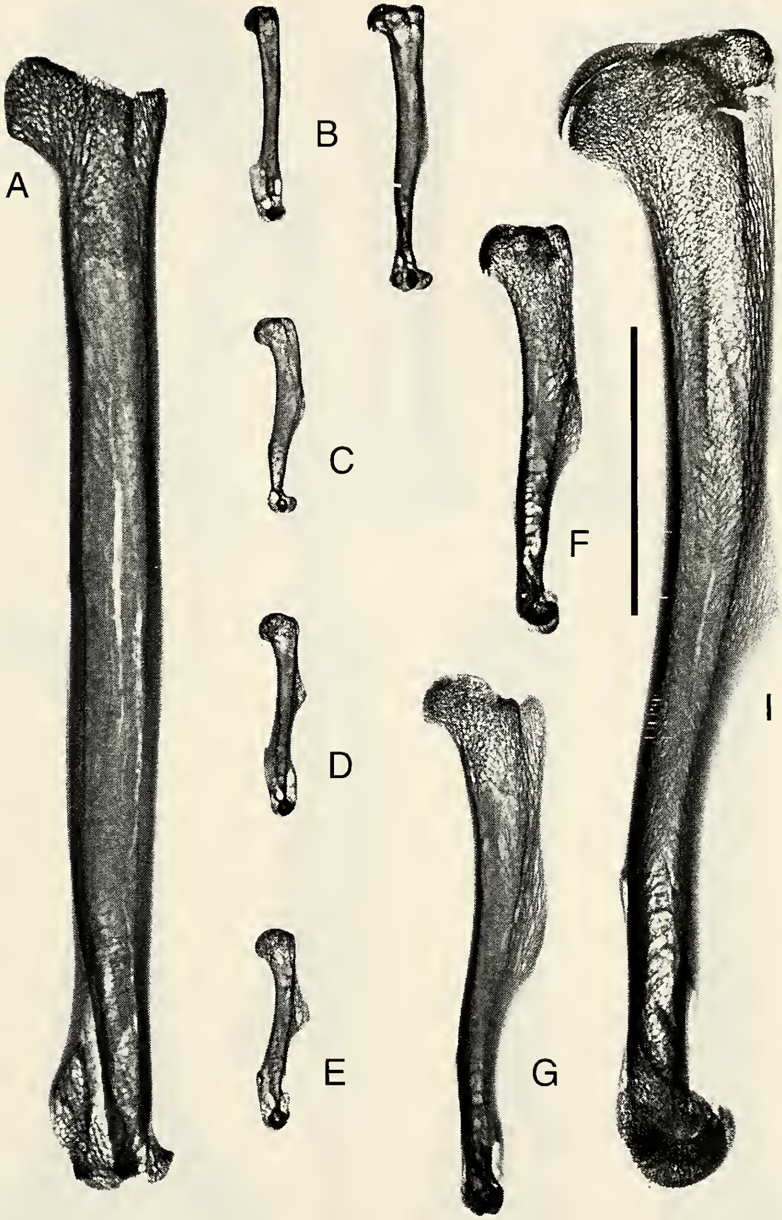


Figure 30. Transverse projection radiographs of right humeri from: A. Putative *P. oscillans* (lacking proximal and distal epiphyses); B. *Hypsiprymnodon moschatus*; C. *Potorous tridactylus*; D. *Bettongia penicillata*; E. *B. lesueur*; F. *Dorcopsulus vanheurni*; G. *Wallabia bicolor* (lacking proximal epiphysis); H. *Macropus parma*; I. *Macropus giganteus*. Scale bar = 5 cm.

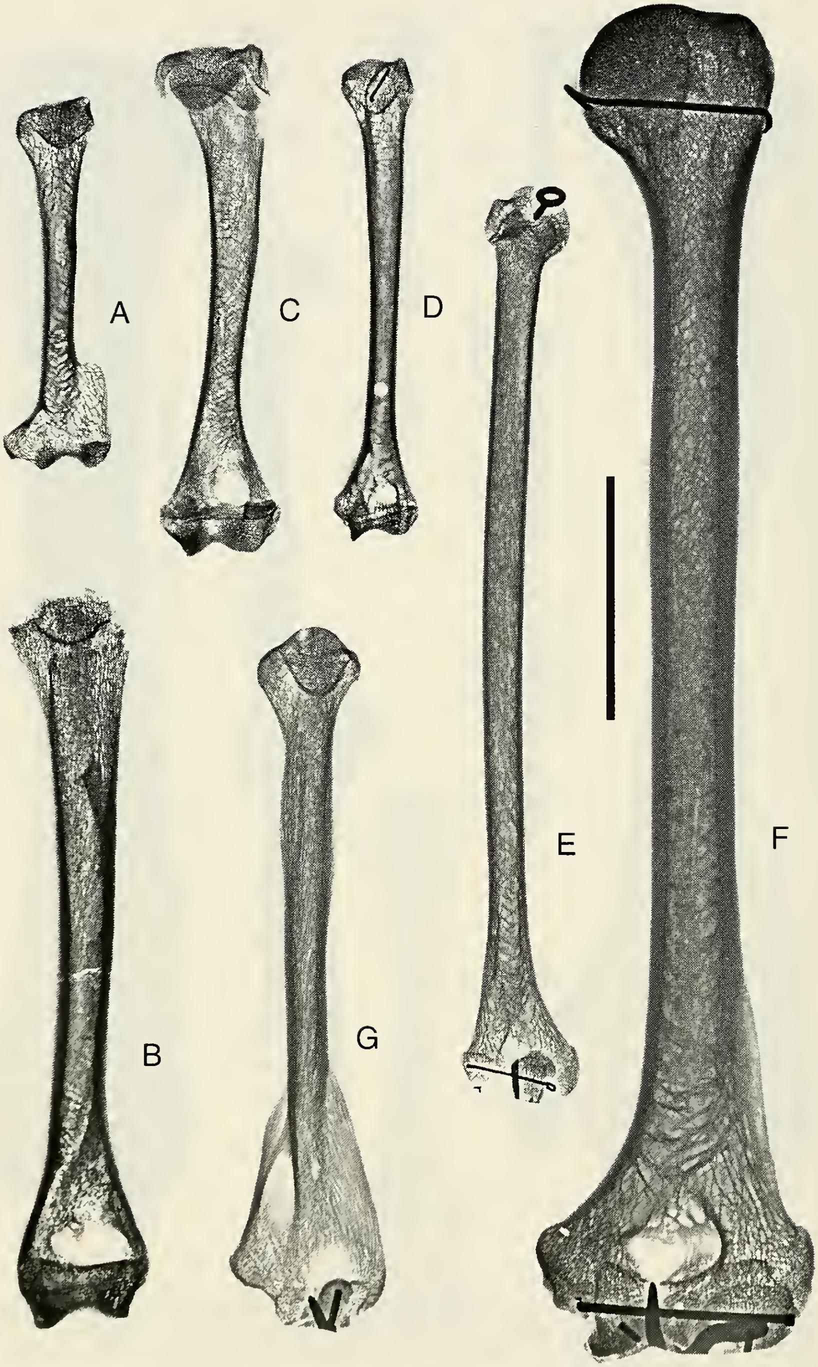


Figure 31. Antero-posterior projection radiographs of humeri from: A. *Trichosurus vulpecula*; B. *Thylacinus cynocephalus* (NMA IAC)(proximal portion lacking); C. *Canis familiaris* (ANU PL); D. *Felis catus* (ANU PL); E. *Ateles* sp. (NMA IAC); F. *Pan troglodytes* (NMA IAC); G. *Choloepus* sp. (NMA IAC). All are right humeri except E. Note that due to image reversal mesial is to the left in all but E. Scale bar = 5 cm.

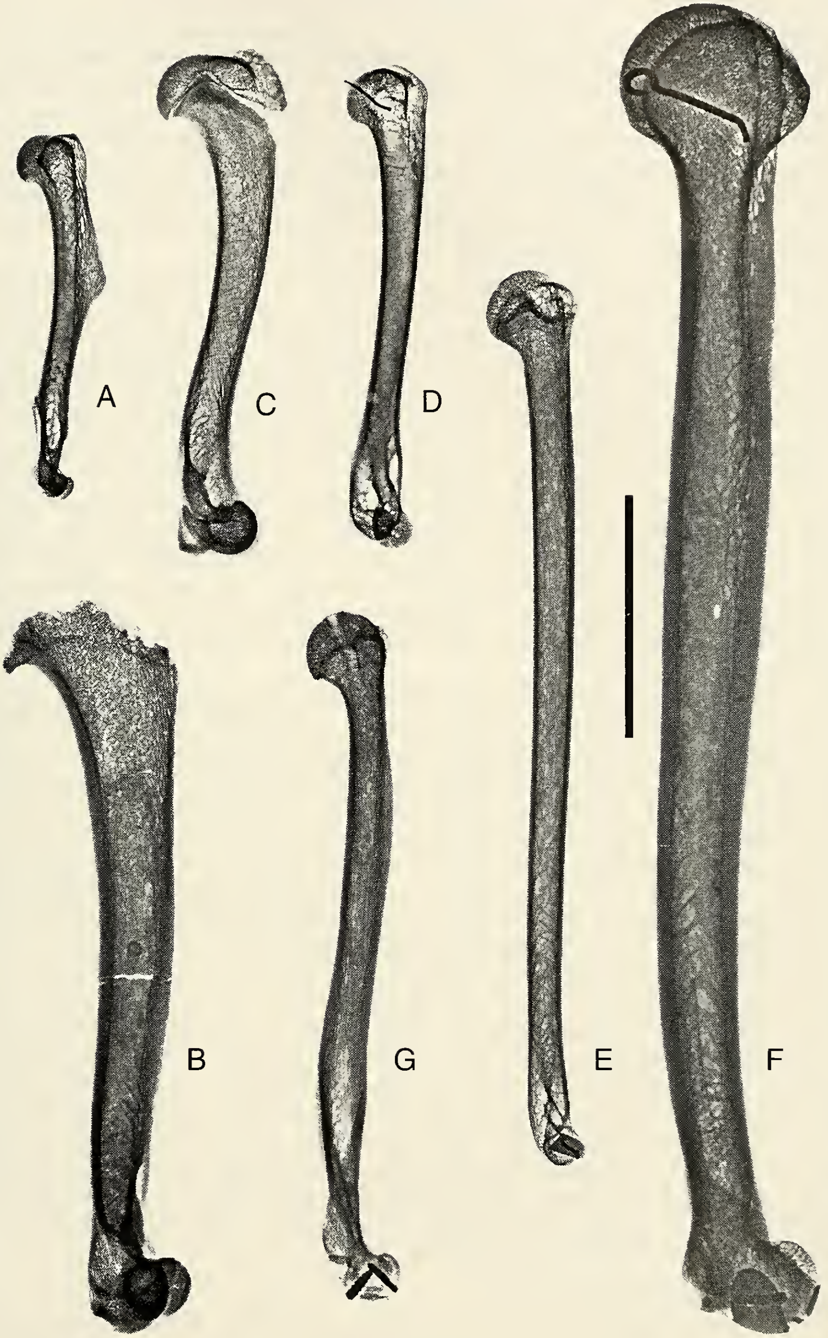


Figure 32. Transverse projection radiographs of humeri from: A. *Trichosurus vulpecula*; B. *Thylacinus cynocephalus* (proximal portion lacking); C. *Canis familiaris*; D. *Felis catus*; E. *Ateles* sp.; F. *Pan troglodytes*; G. *Choloepus* sp. All are right humeri except E. Scale bar = 5 cm.

This dual curvature in the parasagittal plane seems to be affected by body size; data on humeri from a variety of ungulates, carnivorans and rodents indicate that curvature in the parasagittal plane tends to reduce with increasing body size (Biewener 1983, fig. 6). It appears to be influenced by locomotor habits as well; examination of the data provided by Biewener reveals that all of the forms in which curvature is relatively slight are ground-dwellers and that most are at least moderately cursorial. Support for the view that reduced curvature is a feature of cursors is provided by Hopwood's drawings (Hopwood 1947, fig. 2) of the humeri of lion, leopard and cheetah. These indicate that the humerus of the cheetah is less curved in the parasagittal plane than are those of the lion or leopard, despite the greater body weight of the latter two species.

Unfortunately, because of the great difference in size of *P. oscillans* and *H. moschatus*, it is impossible to tell whether the greater straightness of the humerus of the fossil form is due solely to greater size, or whether it also reflects greater running ability.

Viewed from an anterior or posterior perspective the humeri of cursors are straight or very slightly curved (Fig. 31B-D). Curvature in the transverse plane is lacking in *Felis catus* (Fig. 31D), *Acinonyx jubatus* (Van Valkenburgh, Grady and Kurten 1990, fig. 5) and in *Equus* (Smythe and Goody 1975, fig. 13) and *Rhinoceros* (Lessertisseur and Saban 1967, fig. 529). Its absence in these last two cursorial forms would seem not to be attributable to size since curvature in the transverse plane is evident in the larger ambulator *Elephas* (Lessertisseur and Saban 1967, fig. 529). However, the humerus is weakly bowed (concave medially) in *Canis* (Fig. 31B), *Crocuta* (Giebel and Leche 1874-1900, plate 79 (5) and *Thylacinus* (Fig. 31C). Thus, if *P. oscillans* was a cursor, the bowing of its humerus which is evident from an anterior or posterior perspective (Fig. 7A, C), would seem to place it with endurance cursors of the canid-hyaenid type rather than with sprint cursors of the felid type.

As in *P. oscillans* extended cortical thickening of the humeral shaft is evident in *Thylacinus* (Figs 31B, 32B) and in various placental cursors (Figs 31C, D, 32C, D) and, relative to humeral length, the cortical bone in all these forms appears to be of proportionately similar thickness. Moreover, in both *P. oscillans* and these cursors cortical bone is somewhat more thickly developed on the mesial wall of the humeral shaft.

At midshaft the humerus of *P. oscillans* is ovoid in cross-section; the transverse dimension of the bone being greater than the anterio-posterior one. This is exactly the reverse of the situation in many living cursors in which the humerus is laterally compressed at midshaft (Table 3). It is unlikely that the broad condition of the humerus evident in *P. oscillans* is a heritage feature since the midshaft is laterally compressed in *H. moschatus* and in most other diprotodont marsupials (Table 3).

This evidently derived feature of the humerus of *P. oscillans* is not easily explained. Some transverse broadening is evident in *Thylacinus* (Table 3), but since we do not understand the significance of this it shines little light on the condition in the fossil form. Broadening suggests that the humerus of *P. oscillans* was more substantially loaded with transverse forces than is the case with the humeri of most mammals. Such loading could have been imposed during locomotion if the animal frequently changed direction. Alternatively, midshaft shape might reflect some other use of the forelimbs in *P. oscillans*; perhaps a role for the forelimbs in dealing with prey as Vickers-Rich and Rich (1993 p. 197) conjectured, although in the absence of distal limb elements this interpretation is as yet without real foundation.

Comparison with ambulatory mammals:

The general condition of the humeral shaft seen in *P. oscillans* is approached to some extent in a few relatively slow moving terrestrial (or largely terrestrial) mammals of medium size. These medium-sized ambulators include *Erinaceus, Erithizon, Procyon, Mephites* and *Sarcophilus*. They lack the capacity for fast running (Garland 1983) and avoid predators either through use of a defensive covering of spines or quills (*Erinaceus*

TABLE 3

Ratio of medio-lateral to antero-posterior dimension of humerus at midshaft in *P. oscillans, H. moschatus* and in various cursorial (c) and other quadrupedal mammals. The values Hopwood (1947) were taken at the level of the deltoid tuberosity (i.e. slightly more proximally than values collected in the present study).

| **Species** | **Number of humeri examined** | **Mean ratio** | **Source** |
|---|---|---|---|
| *Propleopus oscillans* (P18846) | 1 | 1.09 | this study |
| *Propleopus oscillans* (P35648) | 1 | >1.00 | this study |
| *Hypsiprymnodon moschatus* Qld Mus. JM 6187 | 2 | 0.74 | this study |
| *Hypsiprymnodon moschatus* Qld Mus. JM 6915 | 2 | 0.69 | this study |
| *Antechinomys laniger* (c) | 1 | 0.67 | this study |
| *Sminthopsis leucopus* | 2 | 0.72 | this study |
| *Dasyurus maculatus* M6187 | 2 | 0.66 | this study |
| *Dasyurus maculatus* M2085 | 2 | 0.72 | this study |
| *Sacrophilus harrisii* | 2 | 0.65 | this study |
| *Sacrophilus harrisii* | 1 | 0.86 | this study |
| *Thlacinus cynocephalus* M1960 (c) | 2 | 0.83 | this study |
| *Thlacinus cynocephalus* M5245 (c) | 2 | 0.82 | this study |
| *Isoodon macrourus* | 1 | 0.48 | this study |
| *Perameles* sp. | 1 | 0.54 | this study |
| *Chaeropus ecaudatus* (c) | 1 | 0.70 | this study |
| *Lasiorhinus latifrons* | 2 | 0.93 | this study |
| *Trichosurus vulpecula* | 1 | 0.84 | this study |
| *Gulo gulo* 1 | 2 | 0.74 | this study |
| *Gulo gulo* 2 | 2 | 0.85 | this study |
| *Felis catus* (c) | 1 | 0.81 | this study |
| *Panthera pardus* (c) | ? | 0.75 | Hopwood (1947) |
| *Panthera leo* (c) | ? | 0.70 | Hopwood (1947) |
| *Acinonyx jubata* (c) | ? | 0.57 | Hopwood (1947) |
| *Cabis familiaris* (c) | 1 | 0.80 | this study |
| *Equus caballus 1* (c) | 1 | 0.82 | this study |
| *Equus caballus* 2 (draught) | 1 | 0.78 | this study |

and *Erithizon*), threats and climbing ability (*Procyon* and *Sarcophilus*), or the release of noxious odours (*Mephites*).

In *Erinaceus* the humerus is a stocky bone, quite out of proportion to the equivalent element in *P. oscillans* (Lessertisseur and Saban 1967, fig. 529L; Gregory 1910, fig. 27.16). In *Procyon* the humerus is a relatively straight bone which shows little evidence of curvature in the transverse plane. It appears to be quite weakly ridged anteriorly (Giebel and Leche 1874-1900, plate 78 (6, 7)), although without a specimen to hand this cannot be confirmed. In *Sarcophilus* (ANU PL) the humerus is relatively straight in anterior or posterior view, but unlike the equivalent bone in *P. oscillans*, is clearly sigmoid when viewed laterally. The surface contours of the shaft are generally simple although there is a moderately developed deltoid ridge. Other features which distinguish the humerus of *Sarcophilus* from that of *P. oscillans* include moderately strong development of the greater tuberosity, 'lateral compression' of the shaft at midlength (Table 3), and negligible development of the supinator crest. In general, the form of the humerus in all these animals, to the extent that we have been able to investigate it, suggests that they do not provide a good model for *P. oscillans*.

The wolverine, *Gulo gulo* is in some respects intermediate to cursors and ambulators. Available accounts provide no indication that *Gulo* is capable of rapid running. On the other hand, it possesses very considerable ability as an endurance runner. Its usual running gait is described as a loping gallop (Nowak and Paradiso 1983 p. 1004) and, according to Stroganov (1969), it can maintain this for 10-15 km without stopping. In posterior view the humerus of *Gulo* is slightly concave mesially and its shaft is without obvious posterior protuberances (Giebel and Leche 1874-1900, plate 79 (1), UWZS 21655, 21897). From a lateral perspective it is clearly sigmoid. Its anterior surface bears weakly developed pectoral and deltoid ridges; these are more evident on the humeri of the larger male specimen (UWZS 21655) than in the adult female (UWZS 21897), but still far from robust in the former. Contrary to the condition in *Canis, Felis, Thylacinus* (Fig. 28F) and *Sarcophilus*, the greater tuberosity is weakly developed and extends very little craniad of the anterior face of the bone. Medially there is an obvious teres tubercle about a third of the way down the bone. At mid-shaft the humerus of *Gulo* the anteroposterior dimension is slightly greater than the transverse one (Table 3). The supinator crest is similar in relative extent to that of *P. oscillans*. Thus, aside from its sigmoid curvature and laterally compressed cross-section at mid-shaft the humerus of *Gulo* appears to be a good analogue for the equivalent element in *P. oscillans*.

Overall morphological comparisons confirm that *H. moschatus* provides the best model for interpreting locomotion in *P. oscillans*. Additionally they reveal that, *H. moschatus* aside, the humerus of *P. oscillans* most resembles those of quadrupedal forms that are capable runners but of the slow endurance (*Gulo*) type rather than the fast sprint (*Acinonyx*) type. Thus, the assumption (Vickers-Rich and Rich 1993) that *Propleopus* was saltatorial (i.e. was a bipedal leaper like a kangaroo) appears to be wrong and the suggestion that it might have been a cheetah counterpart is, at least with regard to locomotor ability, very much called into question.

### Muscles attaching to the humerus of *P. oscillans*

The task of comparing the development of humeral muscles in *P. oscillans* with those in forms belonging to all of the habitus types just considered is too a large task to be undertaken here. Some useful comparisons can be made, however, between certain muscles in *P. oscillans* and in *H. moschatus* and between the same muscles in the fossil and in extant potoroids and macropodids. Such comparisons provide some basis for independent assessment of the extent to which *P. oscillans* was likely to have been quadrupedal and cursorial.

It has long been held (Gregory 1912; Maynard Smith and Savage 1956; Hildebrand 1974, 1985) that the limbs of cursors differ from those of non-cursors in having muscles more proximally inserted. This grows out of the view that faster movement of the distal limb can be achieved if the insertion of any limb muscle promoting such motion is moved closer to the joint about which this movement is occurring.

Following this line of argument we had initially sought to compare the location of particular areas of muscle insertion on the humerus of *P. oscillans* with the equivalent areas of insertion in *H. moschatus*. Our hope was that such comparisons would clarify the relative capabilities of the two forms. However, doubts arise about the utility of such comparisons because it is evident that the relative positions of insertion sites do not necessarily relate in a simple fashion to locomotor performance. Thus, although Hildebrand (1985a, p. 46) states that 'it is commonly recognized that many limb muscles of mammalian cursors do insert closer to the associated pivots than the same muscles of their less swift relatives', Howell (1944), in his review of specializations of the forelimb musculature for speedy quadrupedal progression, came to what would seem to be exactly the opposite conclusion. He asserted (op. cite, p. 94) that cursors show 'a tendency toward the distal migration of the insertion of certain muscles' This apparent contradiction may be due to the fact that cursors do not always move at top speed, so that in all probability they possess what Maynard Smith and Savage (1956) and Hildebrand (1985a) call 'low gear' muscles as well as 'high gear' ones. However, the effects of loading on muscle performance further complicate the matter. As Hildebrand (1985a) notes, very high 'gear ratios' may not benefit cursors at all since by increasing the load that a muscle must bear they reduce both the muscle's rate of shortening and distance of shortening. Moreover, recent considerations of muscle architecture (Gans and deVree 1987; Gans 1988) suggest that many widely espoused views about the effects of varying muscle insertion may be overly simplistic.

Given this there would seem to be little to be gained at present from any comparison of the relative positioning of areas of insertion, per se, of humeral muscles in *P. oscillans* and *H. moschatus*.

Nevertheless, an examination of the areas of muscle insertion in *P. oscillans* is not without value. It is possible to compare the areas of insertion of a few muscles in *P. oscillans* with the equivalent areas in *H. moschatus* and other extant macropodiform marsupials, and by focusing on features related to the bone-tendon connection at these sites, rather than their position up and down the shaft, we can make some informative inferences about the relative development of the muscles concerned in *P. oscillans*.

Although some 20 or so muscles or muscle groups attach to the humerus in marsupials, only three seem amenable to this approach. These are the teres major and latissimus dorsi (together), and the supinator longus (= brachioradialis). Most other muscles are either too broadly attached for their sites of attachment to show clearly or too small and weakly attached for these sites to be recognised. A different problem arises with the deltoid musculature. The site of attachment of this muscle complex (the deltoid crest) is clear enough (Fig. 33), but examination of the literature suggests that there is no obvious relation between the size of the muscle complex and the deltoid crest in mammals.

### Latissumus dorsi and teres major muscles

The latissimus dorsi and teres major are considered together here because in *H. moschatus* and *M. giganteus*, and indeed in many other mammals, they share a common insertion onto the mesial surface of the humerus. The former arises from the spines of the caudal thoracic vertebrae and lumbodorsal fascia and in some forms from the ribs as well. The teres major arises from the caudal angle of the scapula. The latissimus dorsi is much the larger muscle and because of its very important role in quadrupedal locomotion it is accorded most attention here.

Both the latissimus dorsi and teres major muscles act as humeral retractors (Walker 1980; Hopwood 1947; Howell 1944) and the importance of the former for rapid locomotion arises from its ability to propel the trunk forward and through the shoulder girdle; a

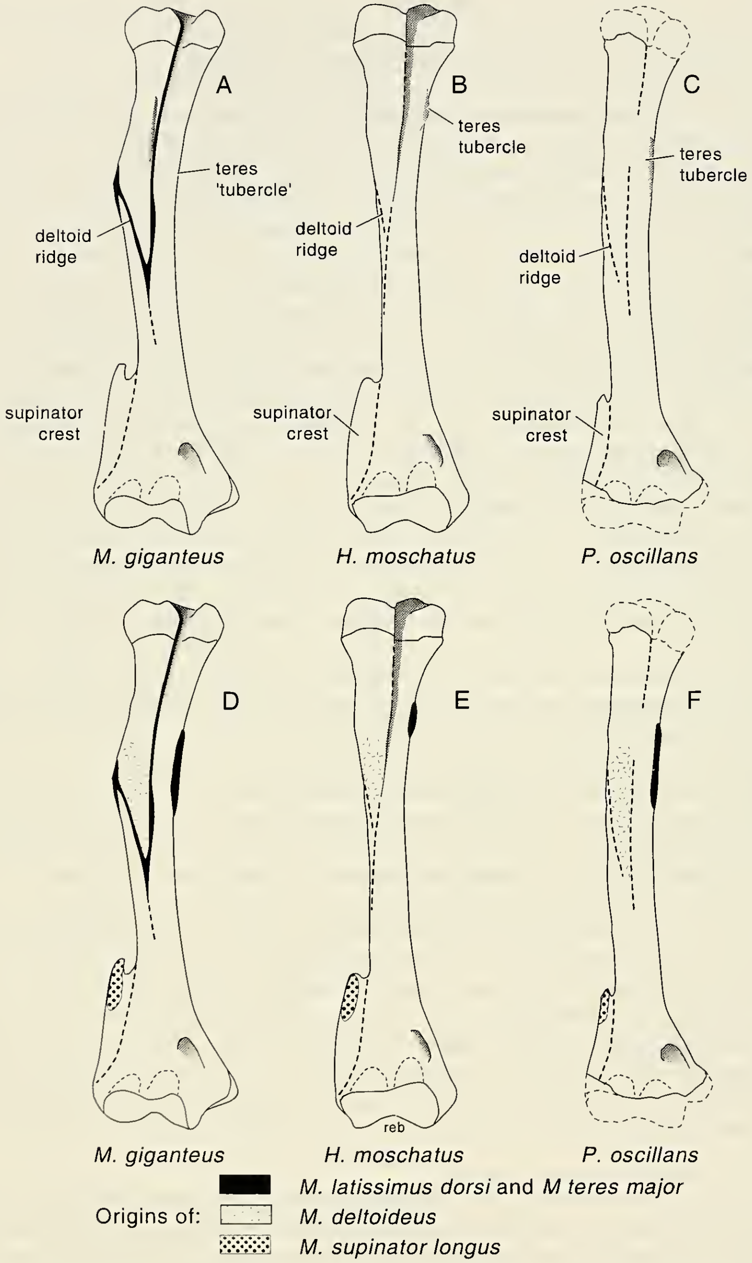


Figure 33. Anterior view of right humerus of A. *Macropus giganteus* (ANU PL); B. *H. moschatus* (based on ANWC CM6051 and QM JM6187); C. Putative *P. oscillans* (P18846). D, E and F; same humeri as in A, B and C, respectively, but with areas of origin and insertion of latissimus dorsi and teres major (together), and supinator longus muscles indicated. The sites of muscle attachment shown in D are based on Hopwood (1974). Those shown in E are based upon information given in Heighway (1939) and Carlsson (1915) and should be regarded as indicative rather than definitive. Those shown in F are inferred from C in conjunction with D and E.

capacity otherwise restricted to the posterior portion of the pectoralis muscle (Jenkins and Weijs 1979; Hopwood 1947). The latissimus dorsi is more strongly developed in the cheetah than in other felids, and is proportionately larger in *Canis lupus* and *Lycaon pictus* than in less cursorial canids (Gambaryan 1974, table 19). A similar, but more equivocal trend, is found in the teres major in these animals. In the cursorial antelopes *Procapra (Gazella) subgutturosa* and *Saiga tatarica* the latissimus dorsi is proportionately much larger than in the similar-sized but less cursorial chamois (*Rupicarpa rupicarpa*) (Gambaryan 1974, table 10). However, in hares (*Lepus* spp.) the latissimus dorsi is somewhat smaller than in the pika (*Ochotona alpina*) (Gambaryan 1974, table 25).

According to Heighway (1939) and Carlsson (1915) the common tendon of insertion of these two muscles in *H. moschatus* attaches into the bicipital groove (sulcus) of the humerus. The exact location of this attachment is not described by either author, but a small low ovate ridge is found about a quarter of the way down the mesial surface on several humeri available to us. We take this to be the site of insertion of the common tendon (Fig. 33B, E). In *M. giganteus* the site of insertion lies on the mesial or antero-mesial surface of the humerus about a third of the way down the bone (Fig. 33D; Hopwood 1974, fig. 17). In specimens of *M. giganteus* available to us this area is weakly pitted, but not marked by any local elevation or depression of the humeral surface.

In comparison with *M. giganteus* the common site of insertion of these two muscles (the so-called teres tubercle) is much more clearly marked in *P. oscillans*. In the fossil form a low ridge and a shallow groove extend in parallel down the mesial surface of the second quarter of the humerus (Figs 7A, B, 33C). The extent of the ridge cannot be determined with any precision but is estimated to be some 28 – 35 mm long in the fossil. Similar difficulty is experienced in determining the length of this tubercle in *H. moschatus*, but in the specimens available to us its length is around 2 to 5 mm.

Information is not available to allow us to establish unequivocally whether the development of the teres tubercle reflects the size of the muscles that insert onto it, although there are indications that this may be the case. A major problem in attempting to assess development of the latissimus dorsi concerns the extent to which the 'muscle' is fleshy as opposed to being made up of connective fascia. The teres tubercle is well developed in *Thylacinus* (NMA IAC), in various African antelopes (Hopwood 1936) and evidently also in the cheetah, the leopard and lion (Hopwood 1947). In *Thylacinus* the latissimus dorsi appears to be quite well developed (Cunningham 1882) and this muscle is certainly very well developed in the three carnivores just mentioned (Gambaryan 1974, table 19), but we are unable to assess whether this is true of the ungulate taxa. In *Trichosurus* (ANU PL) the tubercle rises very slightly above the surrounding bone. The latissimus dorsi of this form originates from the eight thoracic spines and caudal to this from a lumbar fascia. The muscle seems to be quite well developed in so far as the fleshy portion appears to extend quite far back along the dorsal surface of the trunk (Barbour 1963, fig. 21).

In *H. moschatus* the latissimus dorsi has a fairly extensive origin that takes in the spines of seven or eight thoracic vertebrae, the lumbar fascia and the last three ribs (Heighway 1939; Carlsson 1915). How much of the area of the muscle between these sites and its origin is fleshy and how much is connective fascia cannot be determined from the available accounts.

Amongst potoroids the teres tubercle is quite strongly developed in *Aepyprymnus* (CM MAMS 9) and *Bettongia lesueur* (CM 12873), both of which are habitual diggers, but more weakly developed in *B. penicillata* (CM 11458) and *Potorous tridactylus* (MAMS 207), which are not. We have no access to information on the development of the latissimus dorsi in any of these forms aside from the remark (Carlsson 1914) that in *Aepyprymnus* the muscle originates on five thoracic spines and several ribs and her observation that the origin is the same in *Petrogale*, but more extensive in both *Dendrolagus* and *Trichosurus*.

Amongst most macropodids both tubercle and muscle seem to be poorly developed. In *Macropus giganteus* the tubercle is, as previously noted, barely discernible, and the same is true of *M. rufogriseus* (ANU DBZ), *M. parma* (ANU PL), *W. bicolor* ANU PL), *Petrogale penicillata* (ANWC CM13571) and *D. vanheurni* (ANWC CM 15124). The development of the latissimus dorsi seems not to have been described in any of these forms, although Boardman (1941) has given a good account of it in *M. robustus*. According to him the origin of the muscle is relatively lengthy and extends over the spines of ten thoracic vertebrae in this form. However, it is important to note that the proportion of the 'muscle' that is fleshy is relatively small and does not overlap onto the abdomen as is usually the case in mammals. In *Petrogale xanthopus*, in which the teres tubercle is moderately developed, the vertebral origin of the latissimus dorsi is less extensive; it arises from four or five thoracic spines, although contrary to the situation in *M. robustus* it also originates from (three) ribs (Parsons 1896; Carlsson 1915). In *Dendrolagus* the teres tubercle is also moderately developed and the origin of the *latissimus dorsi* extends over the spines of eight thoracic vertebrae and onto the ribs (Carlsson 1914; Boardman 1941). This presumably reflects the importance of the muscle in climbing.

It is evident that further studies are needed to establish whether the development of the teres tubercle does indeed reflect the size of the muscles that insert onto it. However, if it does, the relatively robust and elongate teres tubercle of *P. oscillans* would suggest that the latissimus dorsi was somewhat better developed in the fossil than in *H. moschatus* and considerably better developed than in living macropodids. A relatively larger latissimus dorsi muscle would be consistent with, amongst other things, slightly greater running ability in *P. oscillans* than in *H. moschatus*. While greater development of this muscle relative to the condition in *Macropus* would give strong support to the view that *P. oscillans* was habitually quadrupedal.

Supinator longus muscle:

The other muscle to be considered here is the supinator longus (= brachioradialis). This is one of a series of muscles associated with the supinator crest. It is the most proximally attaching of the muscles originating on this crest and inserts, in marsupials, onto the carpus. Cursorial forms generally exhibit reduced rotation of the forearm (pronation-supination) and reduced ability to manipulate the manual digits (Hildebrand 1974; Hopwood 1947) and these losses of capability are reflected in a reduction in size of the muscles that bring about such movements, including the supinator longus. Thus the supinator longus is absent in most ungulates (Windle and Parsons 1901), in rabbits (Walker 1980) and lacking also in the Patagonian cavy *Dolichotis* (Windle 1897). Amongst canids it is lacking in the cursors *Canis lupus* and *Lycaon pictus*, but present in the sub-cursorial Raccoon dog *Nyctereutes* (Gambaryan 1974, table 19). In most felids the supinator longus is present, but it is absent in the cheetah (Gambaryan 1974, table 19) and it is absent or vestigial amongst hyaenids (Windle and Parsons 1897).

The supinator longus is generally present in marsupials and the extent to which it is developed appears to be reflected in the size of the supinator crest from which it takes its origin. In *Sarcophilus* the muscle is lacking (Macalister 1872) and the bony crest is barely detectable (ANU PL). In *Thylacinus* the supinator crest is short and narrow (NMA IAC) and in accord with this the supinator longus is 'very feebly developed' (Cunningham 1882). In *Dasycercus* and *Trichosurus* both crest and muscle are reasonably well developed (Jones 1949; Barbour 1963) and in *Phascolarctos* both are developed to an extreme (Young 1882).

From this brief review it would seem to be the case that the acquisition of cursorial capabilities is generally associated in mammals with a reduction in size of the supinator longus muscle. Reduction may also occur in response to the adoption of other life styles (e.g. *Notoryctes*). Nevertheless, reduction of the supinator crest would seem to provide good corroboration of cursoriality in forms where such capability is indicated by other morphological features.

According to Carlsson (1915) the supinator longus is well developed in *H. moschatus*; indeed comparably to the situation in *Trichosurus* and *Phalanger*. Heighway (1939) also indicates that the muscle is well developed in *H. moschatus*. This is not surprising given the relatively strong development of the supinator crest in this form (Fig. 25J).

In *Dendrolagus dorianus* the supinator longus is also strongly developed; Carlsson (1914) compares its development in this form with the situation in *Trichosurus* and notes that it has a broad origin on the supinator crest. According to her (op. cite) this muscle is very weakly developed in *Petrogale* in which form it has a less extensive origin on the humerus. Thus muscular development is reflected in the size of the supinator crest in these two genera (Fig. 25D, E).

There are few useful accounts of the supinator longus in other macropodiforms, but those that are available tend to confirm this correlation. Thus the muscle and bony crest appear to be moderately developed in *Macropus giganteus* (Hopwood 1974, fig. 4; Fig. 25B), while in *Aepyprymnus*, according to Carlsson (1914) the muscle has an especially broad origin, which is in good accord with the size of the bony crest in this form (ANWC MAMS-9).

In *P. oscillans* (Fig. 25A) the supinator crest is relatively smaller than in *H. moschatus* (Fig. 25J). This suggests that the supinator longus was reduced relative to the condition in *H. moschatus* (Fig. 33) and is consistent with the fossil form having been more cursorial than the living one. By the same token the reduction in size of this crest has proceeded to a far smaller degree than in *Thylacinus* (or even *Sarcophilus*) so that, unless the muscles of the supinator crest had some special non-running function (e.g. manipulation of food), it is difficult to believe that *P. oscillans* possessed more than semi-cursorial capabilities.

Development of the supinator crest in *P. oscillans* is obviously uninformative with respect to the question of whether the fossil form was habitually quadrupedal or partially bipedal.

Overall, what little we can infer about the development of muscles attaching to the humerus in *P. oscillans* is consistent it having been quadrupedal and having possessed some capability for running, although more appropriate for moderate speed endurance ability rather than any capacity for bouts of high speed locomotion as is sometimes implied.

## CONCLUSIONS

The hypothesis that *P. oscillans* was a carnivorous or omnivorous member of the Propleopinae can now be reviewed in the light of the additional material. As a consequence of being able to assess information from the dentition as part of a functioning masticatory complex, a number of alternative scenarios can be examined.

From our results, the following dietary life-styles open to mammals subsisting in the Australian arid and semi-arid zones, indicated by the distribution of *P. oscillans* fossils, can be eliminated:

Grazing and browsing – The incisors are unlike those of any grazing or browsing diprotodont mammal; in particular the reduction of $I^{2-3}$ (as evidenced by their alveoli) indicates that they probably did not provide a flattened grasping platform for occlusion with the $I_1$. The sharpened beak-like $I^1$ would not have been opposable for grasping and indicates a piercing function. In grazing diprotodonts, the $I_1$s are procumbent. The molar structure indicates that there was no expansion of the power stroke into Phase II. Molars of *P. oscillans* are not lophodont or selenodont and give no evidence of capability for shearing-grinding a high fibrous diet. Grazing is excluded by absence of abrasion typical of phytolithic inclusions in the diet and of adaptations to counter the wear produced by an abrasive diet (hypsodonty, dental progression). The masseteric complex is reduced as compared with the temporalis. The mandibular condyle is cylindrical rather than flattened and is placed at the level of the tooth row unlike any diprotodont herbivore.

Rhizophagy – On the basis of the above characters, as well as the absence of dental wear (both macroscopic and microwear features) that would indicate the presence of extensive grit from soil in the diet, rhizophagy can be excluded. The humerus also indicates that it was unlikely that the animal had fossorial capability.

Frugivory and selective leaf-eating. – While there is an apparent similarity to the molar morphology of leaf-eating monkeys (e.g. *Colobus guereza*), in the molars a major difference lies in the absence of structures in *P. oscillans* for the accomodation of the grinding phase (Phase II) of mastication used in mammals to disrupt plant fibres. Moreover, in all mammals in which there is extensive antero-mesial movement in the power stroke, the condyle is set high above the molar row (it is noteworthy that in the part-carnivorous baboon, *Papio*, the condyle is set much lower than in folivores). Frugivory (e.g. in *Ateles*) is also characterized by the presence of widened crushing molar facets and an extension of Phase II. Phase II of the masticatory cycle is matched dentally by the extensive development of transverse, complex shearing crests in diprotodont leaf-eaters (e.g. *Pseudocheirus, Phascolarctos*) brought into use in the antero-mesial grinding stroke. Transverse shearing crests are of low relief in *P. oscillans*.

Mycophagy – The Potoroinae exemplify the mycophagous niche among diprotodont marsupials. All exhibit more extensive microwear than *P. oscillans*, almost certainly as a result of grit inclusions in the fungal diet. All have wear facets typical of mammals in which Phase II plays a significant part in the power stroke. The mandibular condyle is set above the molar row and the masticatory musculature does not have the temporalis large as compared with the masseteric complex, as in *P. oscillans* and Carnivora.

On the other hand, the morphological characteristics of *P. oscillans* do not deny the hypothesis that it was carnivorous.

## The structure of *P. oscillans*

The premolars and the molars, in themselves, confirm what was previously known of their structure and, as the result of more intensive examination (especially of the Cattle Creek specimen by scanning electron microscopy; Figs 9, 10, 13-18), the mode of their operation is now clear.

The premolars are shearing teeth which wear differentially in various parts of the teeth. Abrasion damage to the cusps is variable and there is no indication that these were used consistently for crack propagation in hard materials such as bone or the hard shells of fruit such as *Santalum*. The area of the premolar that is involved in direct tooth-on-tooth occlusion is small and is confined, certainly into full adult life, to the upper parts of the posterior ridges. Food material moved down the channels, but under less pressure than on the tops of the ridges. Some puncture crushing took place at the crest and its orientation is such as to indicate that the force was applied rearwards. The postero-lingual facet, which faces rearwards towards the first molar, exhibits crushing abrasion. In the both adult and juvenile dentitions abrasion in this part of the tooth indicates that it formed part of the shearing surface. This combination of features of the premolars of both adult and juvenile are consistent with the view that they were primarily used to shear tough material with hard inclusions of irregular size (some large enough to do considerable inadvertent damage). The appearance of these teeth is consistent with the shear-

Figure 34. Abrasion grooving on the postero-lingual wear facet of $P^2$ of *P. oscillans* (P24677). The variation in groove diameter and the presence of gouges illustrated is typical of carnivore carnassials (c.f. Van Valkenburgh, Teaford and Walker 1990, plate 1b, lion). Scale bar = 20 µm.

ing surfaces of the carnassials of Carnivora. In the case of the Carnivora, the irregularity and considerable size of the inclusions is attributed to grit inclusions in hide and fragments of bone rather than to damage resulting from bone crushing.

The gross morphology of the molar row, supported by the microstructure of its abrasion features, indicates that when occluded, the outer rows of cusps (upper, buccal; lower, lingual) functioned as shearing elements with antero-postero ridges (cristae) bearing abrasion that indicates vertical or near-vertical shear. Damage to some cusps of these outer rows indicate that they may also have been inadvertently damaged by puncture-crushing. The inner rows of cusps that occlude within the median longitudinal valleys of their opposite partners are rounded, bearing abrasion features typical of elements used in crack propagation. The molar row does not diminish to any extent posteriorly indicating that both puncture crushing and shearing functions may have been applied locally or simultaneously over much of its length. Such tooth rows are found in *Thylacinus* and *Sarcophilus*[10]. *P. oscillans* differs from both in possessing a specialized shearing tooth in front; an inheritance from its diprotodont ancestry.

In conclusion, the morphology of its teeth, although atypical of any known living marsupial carnivore, are those that functionally fit an animal which fed on high energy foods (such as flesh) that did not require the grinding of tissues to break cell walls before they could be digested (as with plant tissues). In such a scenario, the primary food of *P.*

*oscillans* would have been one which required both piercing and holding, shearing, and crushing (both puncture crushing to propagate cracks through hard, brittle, inclusions, and crushing of soft tissues to separate structure (as in mechanical tenderizing)).

It is important to emphasize that the conclusions advanced here, although heavily influenced by dentition, do not depend upon dental morphology alone. The most significant new information (admittedly incomplete) derives from the cranial specimen. This indicates that *P. oscillans* was long faced; its premaxilla was strengthened in comparison with that of *H. moschatus*; the diastema was furnished with a canine that would have been useful as a holding device (but being without a functional opponent was probably not used to pierce); the molar row (with its dual crushing-shearing capability) was positioned forward in relation to the anterior root of the zygomatic; and the distance between the glenoid and masseteric process was shortened. The zygomatic arch was narrow but dorso-ventrally thick, especially above the middle of the molar row. The infraorbital foramen was large. By comparison with the mandible, the glenoid was located in approximately the palatal plane. In the upper jaw dentition, the first incisors were large and sharp and although succeeded by posterior incisors, these would have been small in height and probably did not share the piercing function of the anterior pair. The coronoid process of the mandible was wide antero-posteriorly (not slender or hooked) indicating a broad insertion of the temporal element of the adductor musculature. As in carnivores (but not herbivores or omnivores) the mandibular condyle was at the level of the molar row and was laterally elongate and cylindrical (the form of the glenoid is not known but with these features of the condyle it is anticipated that it would have had a strong postglenoid process and have been open anteriorly).

Together, these features indicate an animal with a relatively long face and sensitive muzzle. It had the capacity to tightly grasp, pierce and hold. It had a wide gape and powerful vertically and posteriorly-acting masticatory muscles and a capacity to shear through and puncture crush tissue anywhere along the molar row. Its teeth give no indication that it ground its food.

Taken alone, the structure of the teeth may point in more than one direction. Thus, for example, a molar capable of Phase I crushing (as the molars of *P. oscillans* are) could certainly be used to crack nuts or crush fruit, but in a complex that points to hypertrophy of the temporalis, strengthened premaxilla, piercing and holding incisors, and cylindrical and low-set mandibular condyles, such a diet is unlikely to be primary. Moreover, if the arid and semi-arid Pleistocene was ecologically similar to the modern arid and semi-arid zones, it is likely that such foods could have formed part of the diet of an animal that was otherwise non-vegetarian. As a consequence, we consider that the data now point towards *P. oscillans* having been an opportunistic carnivore, i.e., a carnivore which, while being primarily carnivorous, was nevertheless capable of subsisting on a wide range of food materials. The diet of the fox (*Vulpes vulpes*: Carnivora) in arid Australia provides a modern example (Martensz 1971; Bayley 1978; Catling 1988).

The humeri attributed to *P. oscillans* are clearly distinguished from the humeri of bipedal macropodiform marsupials by the form and disposition of the pectoral and deltoid ridges and by degree of humeral torsion. In these and other features there is considerable similarity to the humerus of *H. moschatus*, which suggests that *P. oscillans* was, like the living form, quadrupedal at all speeds when travelling over-ground.

There are indications that the animal was somewhat more cursorial than *H. moschatus*, although since the relative running capabilities of the latter are not well understood, it is difficult to assess what this means relative to other forms. For a variety of reasons muscle insertion sites in *P. oscillans* are difficult to interpret. Nevertheless, the nature of the sites of insertion of the few humeral muscles that are amenable to assessment suggests that *P. oscillans* was less cursorial than *Canis* or *Thylacinus* and that it likely possessed capabilities for endurance rather than high speed running.

A peculiarity of the humerus of *P. oscillans* that distinguishes it from *H.*

*moschatus*, and other mammals, is its relatively broad cross-section at mid-shaft. This feature may be related to a role in prey capture (perhaps by ambush) or manipulation, but more distal limb elements are needed to assess this.

From a broader perspective this bone shows none of the characteristics evident in aquatic or semi-aquatic mammals, forelimb burrowers or arboreal forms that climb in trees in the quadrupedal mode adopted by most such mammals. Some similarities to the humeri of upright postured primates and sloths are evident, but these do not stand up to detailed comparison. Relative to the humeri of these forms the bone attributed to *P. oscillans* is less gracile, possesses a different distribution of cortical bone within the shaft and is distinguished also by curvature in the transverse plane. Greater similarities exist between the humerus attributed to *P. oscillans* and the humeri of quadrupedal cursors and fast ambulators. Of the forms we have been able to examine, it is the slow endurance cursor (or fast ambulator) *Gulo gulo* that most resembles *P. oscillans* in humeral form.

### *Propleopus oscillans*: the animal

All of these features contribute to an image of a wolf-sized animal that was primarily carnivorous, but probably a flesh-eater rather than a crusher of large bones (like, say, the large cats and *Thylacoleo*). In the arid and semi-arid environment it was probably a fox-like opportunist in its feeding habits. As we visualize it, *P. oscillans* would have been adept at capturing and consuming small to medium-sized vertebrate prey and scavenging on cadavers of larger animals. It would also have been equipped for opportunistic feeding such as on arthropods, fruits, etc. which the fox in arid Australia demonstrates can be so important to such a predator. It seems not to have been capable of rapidly running down large cursorial vertebrate prey, although it may have had some capacity for wearing down such forms through a slower more extended chase.

## SUMMARY

**1.** *P. oscillans*, as indicated by the few cranial and dental structures preserved and discovered to date, is clearly a long faced animal with a well-developed capacity to grasp, pierce and hold items to be ingested that are themselves liable to dislocate the grasper.
**2.** The items ingested contain both structurally resistant material through which cracks may be propagated by puncture-crushing as well as soft and tough material that may be processed by all of shearing, milling, and crushing. The material contained a quantity of irregular fragments harder than enamel capable of making abrasion grooves on surfaces of teeth, such as those usually attributed in carnivores to grit inclusions in the fur of prey; however, the distribution of shearing surfaces continuously along the molar row indicates that the material ingested was also fibrous requiring shearing – not only crushing.
**3.** The molar structure is not that required for shearing materials with fibre bundles such as those of grasses and leaves with characteristics outlined by Sanson (1989). Moreover, in the micro-grooving present in the enamel, there is no indication of the uniform features produced by opaline phytoliths characteristic of the teeth of grazers (Walker et al. 1978).
**4.** The most extensive puncture crushing, apart from incidental damage at sharp cusps, is concentrated in a relatively few areas of the premolars and along the molar rows. Indicating that brittle resistant parts of the items ingested could be located deliberately at particular points within the tooth row as is done by Canidae.
**5.** The condylar position relative to the tooth row and the cylindrical form of the condyle are typical of carnivorous mammals and not of herbivores or omnivores.
**6.** The view that *P. oscillans* is necessarily less carnivorous and more herbivorous than

other Propleopinae with larger premolars and reduced molars is not supported. Instead, if *P. oscillans* is a carnivore, as the evidence presented here suggests, it can equally well be interpreted as indicating the existance of a branch of long-faced carnivores among diprotodont marsupials with wide gape and with shearing distributed along an unreduced molar row comparable with the Thylacinidae, but having the additional capability of premolar shear.

**7.** The partial humerus described by Pledge (1981) and a second less complete one described here are attributed to *P. oscillans* on the dual basis that they cannot be attributed to any other taxa known from Henschke's Fossil Cave and that they are very similar in a great many respects to the equivalent bone in *H. moschatus*.

**8.** The humeri attributed to *P. oscillans* share features with those of *H. moschatus* which set both forms apart from bipedal macropodiform marsupials and suggest that the fossil form was consistently quadrupedal during normal terrestrial locomotion.

**9.** Although the humeri attributed to *P. oscillans* exhibit some similarity in form to those of certain atypical arboreal mammals (upright postured primates and sloths), certain features of morphology argue against the fossil having been arboreal.

**10.** Similarities of form between the humeri of *P. oscillans* and those of cursors suggest that the former may have been a capable runner. However, these similarities, and the development of muscles indicated by them, are suggestive of moderate speed endurance running rather than high speed sprinting capabilities.

## ACKNOWLEDGEMENTS

We thank staff at the CSIRO Division of Wildlife and Ecology in Canberra, the South Australian Museum, the Queensland Museum and the National Museum of Australia for allowing us access to material in their care. Particular thanks are due to Neville Pledge, Ralph Molnar and Jim McNamara for permission to subject precious material to SEM examination and to Tom Rich (National Museum of Victoria) who made a humerus referable to *Protemnodon anak* available to us for examination. Joan Dixon and Lina Frigo of the Museum of Victoria provided photographs of the limb bones of *Acinonyx* and *Dolichotis* and John Kirsch and E. Elizabeth Pillaert (University of Wisconsin) and Sharon Jansa (University of Michigan) provided illustrations and measurements of humeri of *Gulo*. Linda Gibson (Australian Museum) provided information on the skeleton of *Dorcopsulus vanheurni*. Lyn Queale of the South Australian Museum provided measurements of macropodid humeri. We thank Colin Groves for providing access to primate and *Choloepus* post-cranial material in his care and Peter Johnson and Graeme George, respectively, for information on the locomotor behaviour of *Hypsiprymnodon* and *Dorcopsulus vanheurni*. Chris Tassell (Queen Victoria Museum, Launceston) attempted to locate the two humeri referred to *P. anak* by Scott and Lord (1923). We are gratefull to Gordon Sanson for reviewing the manuscript and making many valuable suggestions. Steve Wroe generously made copies of his manuscripts on *Propleopus* and *Ekaltadeta* available to us. Uli Troitzsch translated relevant sections of Carlsson (1914, 1915). The Division of Botany and Zoology at ANU provided access to skeletal material and facilities for dissecting a road-killed specimen of *M. rufogriseus* which was collected under NSW National Parks and Wildlife permit A1125 to WDLR. The contributions of Wal Ambrose of the Division of Archaeology and Natural History ANU and David Fredke at Flinders University Medical School, who prepared the radiographs used in this study, and the support of Sally Stowe of the ANU Electron Microscopy Unit, are gratefully acknowledged.

This study would not have taken place had it not been for the enthusiastic support, hospitality, and generosity of John and Julie Barrie for which we are most grateful. We gratefully acknowledge that part of the study by WDLR was supported by a grant from the Australian Research Council to W.D.L. Ride and G. Taylor for research on the fossil mammal-bearing deposits of the eastern highlands.

## ENDNOTES

[1] Specimen numbers which do not include an institutional name refer to the collection of the South Australian Museum. Material from other collections is abbreviated as follows: ANU DBZ = Australian National University, Division of Botany and Zoology; ANU PL = Australian National University, Palaeontology Laboratory (Dept. Geology); ANWC = Australian National Wildlife Collection (Division of Wildlife and Ecology, CSIRO); NMA IAC = National Museum of Australia, Institute of Anatomy Collection; NMV = Museum of Victoria; Qd Mus. = Queensland Museum; UWZS = University of Wisconsin Zoological Museum.

[2] At this stage of knowledge of dental development, it is a matter of preference as to whether the small tooth found in some species immediately after the large lower incisor is designated a canine or an incisor. Currently it seems probable that the large procumbent incisor of macropodiforms is not $I_1$. But the evidence which suggests that it is $I_3$ or $I_4$ requires re-evaluation (see Ride 1962, Luckett 1993). If it is $I_4$ it is the last of the incisor series and the small tooth following cannot be an incisor. Here, following Flower (1868), we call the small tooth a canine and, following custom, continue to designate the procumbent tooth $I_1$.

[3] This is the designation used on South Australian Museum labels, but we use the shortened locality name Henschke's Fossil Cave throughout this work except where information is taken directly from such labels.

[4] The palatal fissure (associated with Jacobson's Organ) and the anterior palatal foramen (which transmits a branch of the Vth cranial nerve) have a common opening in *Propleopus*. Because the two are separate in some mammals (e.g. in *Aepyprymnus*), following Hildebrand (1988, fig. 8.21) the term palatal fissure is preferred, it being the larger of the two confluent components. Besides which, the term 'fissure' avoids confusion with the different anterior palatine foramen in the horizontal plate of the palatine bone.

[5] The terms attrition and abrasion are used here to describe wear features as follows: attrition is fine polished wear, usually planar and presumably the result of tooth-on-tooth contact, although soft and tough material between closely opposed surfaces will produce a similar effect; abrasion is irregular wear not resulting in planar features, it consists of pits, gouges and grooves (and even fine polish) and is presumably the result of ingested materials containing abrasive items such as grit, bone fragments, phytoliths, or by the polishing action of soft materials, being forced along or across the tooth surface during the power stroke of mastication. Abrasion features overlie planar attrition facets.

[6] Ride (1962, p. 302 footnote) has argued that the widespread occurence of a character within a related group of organisms can be used to determine the antiquity of the chararacter within the group.

[7] Thegosis or tooth sharpening is a process by which mammals use tooth-on-tooth attrition to maintain sharpness or edges (including angle of contact). There is debate about the mechanics of the process and its extent, but there is no doubt that it occurs in some mammal teeth such as the lower incisors of rodents and the canines of baboons (Kay and Hiiemae 1974 p. 254). In *P. oscillans* the occurence of incisor wear facets in newly erupted teeth close behind the enamel tipped crowns seems to justify the conclusion that incisor thegosis occurred in this species and that it probably commenced in the pouch.

[8] Sanson 1989, pp. 154-57, in a most valuable review of his own and other studies clarifying relationships between principles of tooth design, function and food materials with respect to different forms of herbivory, redefines the terms cutting, shearing, crushing, and grinding. In addition, he distinguishes between the different processes high amplitude shearing and fine shearing (distinguishing the latter from grinding). His definitions and terminology are adopted here with the addition of the terms puncture crushing (see Hiiemae and Crompton 1985, p. 281) to describe the process whereby crack propagation in hard brittle food takes place from a blunt cusp or edge without shearing blades being brought into play, and point shearing and point crushing to describe occurrences of high amplitude shearing and puncture crushing at a particular place in the tooth row.

[9] The separate names given to the components of the adductor muscle mass are used here to simplify description and do not imply that these are discrete muscles. In *Didelphis* and *Macropus* the divisions between the elements are not clear (Hiiemae and Crompton 1985; Ride 1959) but different components of the mass function in a coordinated manner. Hiiemae and Jenkins (1969, pp. 4-6) discuss the anatomy of the mass and alternative terminologies for its components.

[10] It should be noted that in both of these species, in the last upper molar the posterior, non-occluding, moity is reduced. In the lower tooth rows, the complete last lower molar is retained (and enlarged). In *Thylacinus* the crushing elements are reduced – it is said to be a specialized soft-parts feeder (like the cheetah) while in *Sarcophilus*, that eats both flesh and bone (apparently without discriminating), the crushing elements are exaggerated, as well as shearing elements being maintained.

## REFERENCES

Alexander, R.M., Jayes, A.S., Maloiy, G.M.O. and Wathut, E.M. (1979). Allometry of the limb bones of mammals from shrews (*Sorex*) to elephant (*Loxodonta*). *Journal of Zoology, London* **189**, 305-314.

Andrews, P., and Groves, C.P. (1975). Gibbons and brachiation. In 'Gibbon and siamang. Vol. 4' (Ed. D.M. Rumbaugh) pp. 167-218. (Karger: Basel).

Archer, M. (1987). A wolf in kangaroo's clothing. In 'The antipodean ark' (Eds S. Hand and M. Archer) pp. 70-72. (Angus & Robertson: North Ryde).

Archer, M., Bartholomai, A. and Marshall, L.G. (1978). *Propleopus chillagoensis*, a new north Queensland species of extinct giant rat-kangaroo (Macropodidae: Potoroinae). *Memoirs of the National Museum of Victoria* **39**, 55-60.

Archer, M. and Flannery, T.F. (1985). Revision of the extinct gigantic rat kangaroos (Potoroidae: Marsupialia), with description of a new Miocene genus and species and a new Pleistocene species of *Propleopus*. *Journal of Paleontology* **59**, 1331-1349.

Archer, M., Hand, S.J. and Godthelp, H. (1991). 'Riversleigh, the story of animals in ancient rainforests of inland Australia' (Reed Books: Chatswood).

Ardran, G.M., Kemp, F.H. and Ride, W.D.L. (1958). A radiographic analysis of mastication and swallowing in the domestic rabbit: *Oryctolagus cuniculus* (L). *Proceedings of the Zoological Society of London* **130**, 257-274.

Balme, J.M. and Hope, J.H. (1990). Radiocarbon dates from midden sites in the lower Darling River area of western New South Wales. *Archaeology in Oceania* **25**, 85-101.

Barbour, R.A. (1963). The musculature and limb plexuses of *Trichosurus vulpecula. Australian Journal of Zoology* **1**, 488-610.

Barrie, J. (1990). Skull elements and additional remains of the Pleistocene boid snake *Wonambi naracoortensis. Memoirs of the Queensland Museum* **28**, 139-151.

Bartholomai, A. (1972). Some upper cheek teeth in *Propleopus oscillans* (de Vis). *Memoirs of the Queensland Museum* **16**, 211-213.

Bartholomai, A. (1973). The genus *Protemnodon* Owen (Marsupialia: Macropodidae) in the Upper Cainozoic deposits of Queensland. *Memoirs of the Queensland Museum* **16**, 309-323.

Bayley, C.P. (1978). A comparison of the diets of the red fox and the feral cat in an arid environment. *South Australian Naturalist* **53**, 20-28.

Beddard, F. (1958). 'The Cambridge natural history Vol. 10. Mammalia' (Wheldon and Wesley: Codicate).

Bennett, A.F. and Baxter, B.J. (1989). Diet of the long-nosed potoroo, *Potorous tridactylus* (Marsupialia: Potoroidae), in Southwestern Victoria. *Australian Wildlife Research* **16**, 263-271.

Biewener, A.A. (1983). Allometry of quadrupedal locomotion: the scaling of duty factor, bone curvature and limb orientation to body size. *Journal of Experimental Biology* **105**, 147-171.

Boardman, W. (1941). On the anatomy and functional adaptation of the thorax and pectoral girdle in the wallaroo (*Macropus robustus*). *Proceedings of the Linnean Society of New South Wales* **66**, 349-387.

Boyde, A. (1984). Dependence of rate of physical erosion on orientation and density in mineralised tissues. *Anatomy and Embryology* **170**, 57-62.

Boyde, A. and Lester, K.S. (1967). The structure and development of marsupial enamel tubules. *Zeitschrift für Zellforschung* **82**, 558-576.

Buchmann, O.L.K. and Guiler, E.R. (1974). Locomotion of the potoroo. *Journal of Mammalogy* 55, 203-206.

Carlsson, A. (1914). *Über Dendrolagus dorianus. Zoologische Jahrbücher Abteilung für Systematik, Geographie und Biologie der Tiere* **36**, 547-617.

Carlsson, A. (1915). Zur morphologie des *Hypsiprymnodon moschatus. Kunglinga Svenska vetenskapsakademiens Handlingar* **52**, 1-48.

Catling, P.C. (1988). Similarities and contrasts in the diets of foxes, *Vulpes vulpes*, and cats, *Felis catus*, relative to fluctuating prey populations and drought. *Australian Wildlife Research* **15**, 307-315.

Christensen, P.E.S. (1980). The biology of *Bettongia penicillata* Gray 1937, and *Macropus eugenii* (Desmarest, 1818) in relation to fire. *Forests Department of Western Australia Bulletin* No. 91.

Claridge, A.W., Tanton, M.T. and Cunningham, R.B. (1993). Hypogeal fungi in the diet of the long-nosed potoroo (*Potorous tridactylus*) in mixed-species and regrowth eucalypt forest stands in south-eastern Australia. *Wildlife Research* **20**, 321-337.

Cunningham, D.J. (1882). Report on some points of anatomy of the thylacine (*Thylacinus cynocephalus*), cuscus (*Phalanger maculata*) and phascogale (*Phascogale calura*) collected during the voyage of H.M.S. Challenger in the years 1873-1876; with an account of the intrinsic muscles and nerves of the mammalian pes. *Voyage of H.M.S. Challenger, Zoology* **5** (16), 1-192.

De Blase, A.F. and Martin, R.E. (1981). 'A manual of mammalogy' (W.C. Brown Co.: Dubuque).

Demes, B., Jungers, W.L. and Selpien, K., 1991. - Body size, locomotion, and long bone cross-sectional geometry in indriid primates. *American Journal of Physical Anthropology* **86**, 537-547.

Dennis, A.J. and Johnson, P.M. (1995). Musky Rat-kangaroo *Hypsiprymnodon moschatus*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 282-284. (Reed Books: Chatswood).

De Vis, C.W. (1888). On an extinct genus of the marsupials allied to *Hypsiprymnodon. Proceedings of the Linnean Society of New South Wales* **3**, 5-8.

Evans, F.G. and Krahl, V.E. (1945). The torsion of the humerus: a phylogenetic survey from fish to man.

*American Journal of Anatomy* **76**, 303-337.

Finch, M.I. (1982). *Thylacoleo carnifex* Owen an Australian fossil phalangerid marsupial: taxonomy, functional morphology, feeding and locomotory habits. PhD thesis, University of Western Australia, Perth.

Flannery, T.F. (1985). *Propleopus oscillans* (De Vis, 1888) The giant rat kangaroo. In 'Kadimakara extinct vertebrates of Australia' (Eds P.V. Rich and G.F. van Tets) pp. 245-248. (Pioneer Design Studio Pty Ltd: Lilydale).

Flannery, T.F. (1989). Phylogeny of the Macropodoidea; a study in convergence. In 'Kangaroos, wallabies and rat kangaroos' (Eds G. Grigg, P. Jarman and I. Hume) pp. 1-46. (Surrey Beatty and Sons: New South Wales).

Flannery, T.F. and Archer, M. (1985). *Palorchestes* Owen, 1874 Large and small palorchestids. In 'Kadimakara extinct vertebrates of Australia' (Eds P.V. Rich and G.F. van Tets) pp. 234-239. (Pioneer Design Studio Pty Ltd: Lilydale).

Flannery, T.F. and Archer, M. (1987). *Hypsiprymnodon bartholomaii* (Potoroidae: Marsupialia), a new species from the Miocene Dwornamor Local Fauna and a reassessment of the phylogenetic position of *H. moschatus*. In 'Possums and opossums: studies in evolution 2' (Ed. M. Archer) pp. 749-758. (Surrey Beatty and Sons Pty Ltd and the Royal Zoological Society of New South Wales: Mossman).

Flannery, T.F., Rich, T.H., Turnbull, W.D. and Lundelius, E.L., JR (1992). The Macropodoidea (Marsupialia) of the Early Pliocene Hamilton Local fauna, Victoria, Australia. *Fieldiana Geology* N.S. 25: 1-37.

Flower, W.H. (1868). On the development and succession of the teeth in the Marsupialia. *Philosophical Transactions of the Royal Society of London* **157**, 631-641.

Frith, H.J. and Calaby, J. (1969). 'Kangaroos' (F.W. Cheshire: Melbourne).

Freundenberger, D.O., Wallis, I.R. and Hume, I.D. (1989). Digestive adaptations in of kangaroos, wallabies and rat-kangaroos. In 'Kangaroos, wallabies and rat kangaroos' (Eds G. Grigg, P. Jarman and I. Hume) pp. 179-187. (Surrey Beatty and Sons: New South Wales).

Gambaryan, P.P. (1974). 'How mammals run: anatomical adaptations' (Wiley: New York).

Gans, C. (1988). Muscle insertions do not insure mechanical advantage. *Acta Zoologica Cracovensis* **31**, 615-624.

Gans, C. and De Vree, F. (1987). Functional bases of fiber length and angulation in muscles. *Journal of Morphology* **192**, 63-85.

Garland, T., JR (1983). The relation between maximal running speed and body mass in terrestrial mammals. *Journal of Zoology, London* **199**, 157-170.

Giebel, C.G. and Leche, W. (1874-1900). *H.G. Bronn's Klassen und Ordungen des Thier-Reichs wissenschaftlich dargestelltin wort und Bild. Sechster Band. V. Abtheilung. Säugethiere: Mammalia. 1* (C.F. Winter'sche Verlangshandlung: Leipzig).

Gilkeson, C.F. and Lester, K.S. (1989). Ultrastructural variation in enamel of Australian marsupials. *Scanning Microscopy* **3**, 177-191.

Gillespie, R., Horton, D.R., Ladd, P., Macumber, P.G., Rich, T.H., Thorne, R. and Wright, R.V.S. (1978). Lancefield Swamp and the extinction of the Australian megafauna. *Science* **200**, 1044-1048.

Gregory, W.K. (1910). The orders of mammals. *Bulletin of the American Museum of Natural History* **27**, 1-524.

Gregory, W.K. (1912). Notes on the principles of quadrupedal locomotion and on the mechanism of the limbs in hoofed animals. *Annals of the New York Academy of Sciences* **22**, 267-292.

Gregory, W.K. (1951). 'Evolution emerging. Vol. 2' (Macmillan Co.: New York).

Griffiths, M., Wells, R.T. and Barrie, D.J. (1991). Observations on the skulls of fossil and extant echidnas (Monotremata: Tachyglossidae). *Australian Mammalogy* **14**, 87-101.

Heighway, F.R. (1939). The anatomy of *Hypsiprymnodon moschatus*. MD thesis, University of Sydney, Sydney.

Hiiemae, K.M. and Ardran, G.M. (1968). A cinefluorographic study of mandibular movement during feeding in the rat *Rattus norvegicus*. *Journal of Zoology, London* **154**, 139-154.

Hiiemae, K.M. and Crompton, A.W. (1970). Molar occlusion and mandibular movements during occlusion in the American opossum, *Didelphis marsupialis* L. *Zoological Journal of the Linnean Society, London* **48**, 21-47.

Hiiemae, K.M. and Crompton, A.W. (1985). Mastication, food transport, and swallowing. In 'Functional vertebrate morphology' (Eds M. Hildebrand, D.M. Bramble, K.F. Liem, and D.B. Wake) pp. 262-290. (Belknap Press: Cambridge).

Hiiemae, K. and Jenkins, F.A., JR (1969). The anatomy and internal architecture of the muscles of mastication in *Didelphis marsupialis*. *Postilla* **140**, 1-49.

Hildebrand, M. (1974). 'Analysis of vertebrate structure' (John Wiley & Sons: New York).

Hildebrand, M. (1985a). Walking and running. In 'Functional vertebrate morphology' (Eds M. Hildebrand, D.M. Bramble, K.F. Liem and D.B. Wake) pp. 38-57. (Belknap Press: Cambridge).

Hildebrand, M. (1985b). Digging of quadrupeds. In 'Functional vertebrate morphology' (Eds M. Hildebrand, D.M. Bramble, K.F. Liem and D.B. Wake) pp. 89-109. (Belknap Press: Cambridge).

Hildebrand, M. (1988). 'Analysis of vertebrate structure' 2nd Edition. (John Wiley & Sons: New York).

Hill, W.C.O. (1953). 'Primate comparative anatomy and taxonomy. I – Strepsirhini. (Edinburgh University Press: Edinburgh).

Hopwood, A.T. (1936). Contribution to the study of some African mammals. I. The humerus and femur of certain East African antelopes. *Journal of the Linnean Society of London Zoology* **40**, 71-92.

Hopwood, A.T. (1947). Contribution to the study of some African mammals. III. Adaptations in the bones of the fore limb of the lion, leopard and cheetah. *Journal of the Linnean Society of London Zoology* **41**, 259-271.

Hopwood, P.R. (1974). The intrinsic musculature of the pectoral limb of the Eastern Grey Kangaroo (*Macropus major* (Shaw) *Macropus giganteus* (Zimm)). *Journal of Anatomy* **118**, 445-468.

Howell, A.B. (1944). 'Speed in animals' (University Press of Chicago: Chicago).

Jenkins, F.A., JR and Weijs, W.A. (1979). The functional anatomy of the shoulder in the Virginia opossum (*Didelphis virginiana*). *Journal of Zoology, London* **188**, 379-410.

Johnson, P.M. and Strahan, R. (1982). A further description of the Musky Rat-kangaroo, *Hypsiprymnodon moschatus* Ramsay, 1876 (Marsupialia, Potoroidae), with notes on its biology. *Australian Zoologist* **21**, 27-46.

Jones, F.W. (1949). The study of a generalized marsupial (*Dasycercus cristicauda* Krefft). *Transactions of the Zoological Society of London* **26**, 409-501.

Kay, R.F. and Hiiemae, K.M. (1974). Jaw movement and tooth use in Recent and fossil primates. *American Journal of Physical Anthropology* **40**, 227-256.

Koenigswald, W.V. and Clemens, W.A. (1992). Levels of complexity in the microstructure of mammalian enamel and their application in studies of systematics. *Scanning Microscopy* **6**, 195-218.

Lessertisseur, J. and Saban, R. (1967). Squelette appendiculaire. 709-1078 In 'Traité de zoologie 16 (1)' (Ed. P. Grassè) pp. 709-1078. (Lesson: Paris).

Le Soeuf, C.F. and Burell, H. (1926). 'The wild animals of Australia' (Harrop: London).

Longman, H.A. (1924). Some Queensland fossil vertebrates. *Memoirs of the Queensland Museum* **8**, 16-24.

Lord, C.E. and Scott, H.H. (1924). 'The vertebrate animals of Tasmania' (Oldham, Beddome and Meredith: Hobart).

Luckett, W.P. (1993). On ontogenetic assessment of dental homologies in therian mammals. In 'Mammal phylogeny' (Eds F.S. Szalay, M.J. Novacek and M.C. McKenna) pp. 182-204. (Springer Verlag: New York).

Lundie-Jenkins, G. (1993). Observations on the behaviour of the rufous hare-wallaby, *Lagorchestes hirsutus* Gould (Macropodidae: Marsupialia) in captivity. *Australian Mammalogy* **16**, 29-34.

Macfadden, B.J. (1986). Fossil horses from "Eohippus" (*Hyracotherium*) to *Equus*: scaling, Cope's Law, and the evolution of body size. *Paleobiology* **12**, 355-369.

Macalister, A. (1872). Further observations on the myology of *Sarcophilus ursinus. The Annals of Natural History* (4th series) **10**, 17-20.

Mansergh, I., Baxter, B., Scotts, D., Brady, T. and Jolley, D. (1990). Diet of the mountain pygmy-possum, *Burramys parvus* (Marsupialia: Burramyidae) and other small mammals in the alpine environment at Mt Higginbotham, Victoria. *Australian Mammalogy* **13**, 167-177.

Martensz, P.N. (1971). Observations on the food of the fox, *Vulpes vulpes* (L.) in an arid environment. *CSIRO Wildlife Research* **16**, 73-75.

Maynard Smith, J. and Savage, R.J.G. (1956). Some locomotory adaptations in mammals. *Journal of the Linnean Society, Zoology* **42**, 603-622.

Maynes, G.M. (1974). Occurrence and field recognition of *Macropus parma. Australian Zoologist* **18**, 72-87.

Megirian, D. (1992). Interpretation of the Miocene Carl Creek Limestone, northwestern Queensland. *The Beagle, Records of the Northern Territory Museum of Arts and Sciences* **9**, 219-248.

Menzies, J., (1991). 'A handbook of New Guinea marsupials & monotremes' (Kristen Pres: Madang).

Merrilees, D. and Porter, J.K. (1979). 'Guide to the identification of teeth and some bones of native land mammals occuring in the extreme south west of Western Australia' (Western Australian Museum: Perth).

Miller, R.A. (1935). Functional adaptations in the forelimb of the sloths. *Journal of Mammalogy* **16**, 38-51.

Morton, S.R. and Burton, T.C. (1973). Observations on the behaviour of the macropodid marsupial *Thylogale billardieri* (Desmarest) in captivity. *Australian Zoologist* **18**, 1-14.

Morton, T. (1981). Mastication in the Potoroinae. Honours thesis, Monash University, Melbourne.

Murray, P. (1991). The Pleistocene megafauna of Australia. In 'Vertebrate palaeontology of Australia' (Eds P. Vickers-Rich, J.M. Monaghan, R.F. Baird and T.H. Rich) pp. 1071-1164. (Pioneer Design Studio Pty Ltd: Lilydale).

Napier. J.R. and Napier, P.H. (1985). 'The natural history of the primates' (British Museum (Natural History): London).

Nowak. R.M. and Paradiso, J.L. (1983). 'Walker's mammals of the world. 4th Edition' (Johns Hopkins University Press: Baltimore).

Osgood, W.H. (1921). A monographic study of the American marsupial, *Caenolestes. Field Museum of Natural History. Zoölogical Series* **14** (1), 1-156.

Owen, R. (1876). On the osteology of the Marsupialia. – (Part V.) *Fam.* Poephaga, *Genus* Macropus. *Transactions of the Zoological Society of London* **9**, 417-446.

Parker, P.J. (1977). Aspects of the biology of *Bettongia penicillata*. PhD thesis, Yale University, New Haven.

Parsons, F.G. (1896). On the anatomy of *Petrogale xanthopus*, compared with that of other kangaroos. *Proceedings of the Zoological Society of London* **1896**, 683-714.

Pledge, N.S. (1981). The giant rat-kangaroo *Propleopus oscillans* (De Vis), (Potoroidae: Marsupialia) in South Australia. *Transactions of the Royal Society of South Australia* **105**, 41-47.

Pledge, N.S. (1990). The upper fossil fauna of the Henschke Fossil Cave, Naracoorte, South Australia.

*Memoirs of the Queensland Museum* **28**, 247-262.

Ride, W.D.L., (1959). Mastication and taxonomy in the macropodine skull. In 'Function and taxonomic importance' (Ed. A.J. Cain) pp. 33-59. (Systematics Association: London).

Ride, W.D.L., 1961. The cheek-teeth of *Hypsiprymnodon moschatus* Ramsay 1876 (Macropodidae: Marsupialia). *Journal of The Royal Society of Western Australia* **44**, 53-60.

Ride, W.D.L. (1962). On the evolution of Australian marsupials. In 'The evolution of living organisms' (Ed. G.W. Leeper) pp. 281-306. (Melbourne University Press: Melbourne).

Ride, W.D.L (1967). On *Sceparnodon ramsayi* Owen, 1884: the selection of a lectotype, the clarification of its type locality, and on its identity with *Phascolonus gigas* (Owen, 1859). *Records of the South Australian Museum* **15**, 419-425.

Ride, W.D.L. (1993). *Jackmahoneya* gen. nov. and the genesis of the macropodiform molar. *Memoirs of the Association of Australasian Palaeontologists* **15**, 441-459.

Rounsevell, D.E. and Mooney, N. (1995). Thylacine *Thylacinus cynocephalus*. In 'The mammals of Australia' (Ed. R. Strahan) pp. 164-165. (Reed Books, Chatswood).

Sanson, G.D. (1980). The morphology and occlusion of the molariform cheek teeth in some Macropodinae (Marsupialia: Macropodidae). *Australian Journal of Zoology* **28**, 341-365.

Sanson, G.D. (1989). Morphological adaptations of the teeth to diets and feeding in Macropodoidea. In 'Kangaroos, wallabies and rat kangaroos' (Eds G. Grigg, P. Jarman and I. Hume) pp. 151-168. (Surrey Beatty and Sons: New South Wales).

Scott, H.H. and Harrisson, K.M. (1911). On the discovery of a *Nototherium* in Tasmania. Tasmanian Naturalist **2**, 61-70.

Scott, H.H. and Lord, C.E. (1924). Studies in Tasmanian mammals, living and extinct. X. Giant wallaby. *Macropus anak*, Owen. *Papers and Proceedings of the Royal Society of Tasmania* **1923**, 6-8.

Scotts, D.J. and Seebeck, J.H. (1989). Ecology of *Potorous longipes* (Marsupialia: Potoroidae); and preliminary recommendations for management of its habitat in Victoria. *Arthur Rylah Institute for Environmental Research Technical Report* No. 62. Department of Conservation, Forests and Lands, Victoria.

Seebeck, J.H., Bennett, A.F. and Scotts, D.J. (1989). Ecology of the Potoroidae – a review. In 'Kangaroos, wallabies and rat kangaroos' (Eds G. Grigg, P. Jarman and I. Hume) pp. 67-88. (Surrey Beatty and Sons: New South Wales).

Simpson, G.G. (1951). 'Horses' (Oxford University Press: New York).

Smythe, R.H. and Goody, P.C. (1975). 'The horse structure and movement' (J.A. Allen and Co. Ltd: London).

Stirling, E.C. (1900). On the identity of *Phascolonus gigas*, Owen and *Sceparnodon ramsayi*, Owen. *Memoirs of the Royal Society of South Australia* **1**, 127-178.

Stirrat, S.C. (1981). The functional morphology of the plagiaulacoid premolar of *Burramys parvus* Broom. Honours thesis, Monash University, Melbourne.

Stroganov, S.V. (1969). 'Carnivorous mammals of Siberia' (Israel Program for Scientific Translations: Jerusalem).

Swindler, D.R. and Wood, C.D. (1973). 'An atlas of primate gross anatomy' (University of Washington Press: Seattle).

Taylor, R.J. (1992). Seasonal changes in the diet of the Tasmanian bettong (*Bettongia gaimardi*), a mycophagous marsupial. *Journal of Mammalogy* **73**, 408-414.

Teaford, M.F. (1986). Dental microwear and diet in two species of *Colobus*. In 'Primate ecology and conservation Vol. 2' (Eds J.G. Else and P.C. Lee) pp. 63-66. (Cambridge University Press: Cambridge).

Teaford, M.F. (1988a). A review of dental microwear and diet in modern mammals. *Scanning Microscopy* **2**, 1149-1166.

Teaford, M.F. (1988b). Scanning electron microscope diagnosis of wear patterns verses artifacts on fossil teeth. *Scanning Microscopy* **2**, 1167-1175.

Tedford, R. (1955). Report on the extinct mammalian remains at Lake Menindee, New South Wales. *Records of the South Australian Museum* **11**, 299-305.

Tedford, R. (1967). The fossil macropodidae from Lake Menindee, New South Wales. *University of California Publications in Geological Science* **64**, 1-165.

Vallois, H. (1955). Ordre des primates. In 'Traité de zoologie 17' (Ed. P. Grassè) pp. 1854-2206. (Lesson: Paris).

Van Huet, A.M.S. (1994a). Taphonomy of a late Quaternary site: Lancefield Swamp, Victoria. MSc thesis, Monash University, Melbourne.

Van Huet, A.M.S. (1994b). Lancefield megafauna site, Victoria. (Abstract, CAVEPS) *Records of the South Australian Museum* **27**, 229.

Van Valkenburgh, B. (1996). Feeding behavior in free-ranging, large African carnivores. *Journal of Mammalogy* **77**, 240-254.

Van Valkenurgh, B., Grady, F. and Kurten, B. (1990). The Plio-Pleistocene cheetah-like cat *Miracinonyx inexpectatus* of North America. *Journal of Vertebrate Paleontology* **10**, 434-454.

Van Valkenburgh, B., Teaford, M.F. and Walker, A. (1990). Molar microwear and dit in large carnivores: inferences concerning diet in the sabretooth cat, *Smilodon fatalis*. *Journal of Zoology, London* **222**, 319-340.

Vickers-Rich, P. and Rich, T.H. (1993). 'Wildlife in Gondwana' (Reed Books: Chatswood).

Walker, A., Hoeck, H.N. and Perez, L. (1978). Microwear of mammalian teeth as indicators of diet. *Science* **201**, 908-910.

Walker, W.F. (1980). 'Vertebrate dissection' 6th Edition. (W.B. Saunders Co.: Philadelphia).

Wells, R.T., Horton, D.R. and Rogers, P. (1982). *Thylacoleo carnifex* Owen (Thylacoleonidae, Marsupialia): marsupial carnivore? In 'Carnivorous marsupials' (Ed. M. Archer) pp. 573-586. (Royal Zoological Society of New South Wales: Sydney).

Wells, R.T. and Tedford, R.H. (1995). *Sthenurus* (Macropodidae: Marsupialia) from the Pleistocene of Lake Callabonna, South Australia. *Bulletin of the American Museum of Natural History* **225**, 1-12.

White, J.P. and Flannery, T.F. (1995). Late Pleistocene fauna at Spring Creek, Victoria: a re-evaluation. *Australian Archaeology* No. **40**, 13-17.

Whitelaw, M.J. (1991). Magnetic polarity stratigraphy of Pliocene and Pleistocene fossil vertebrate localities in southeastern Australia. *Geological Society of America Bulletin* **103**, 1493-1503.

Williams, D.L.G. (1980). Catalogue of Pleistocene vertebrate fossils and sites in South Australia. *Transactions of the Royal Society of South Australia* **104**, 101-115.

Windle, B.C.A. (1897). Myology of *Dolichotis patagonica* and *Dasyprocta isthmica. Journal of Anatomy and Physiology* **31**, 343-353.

Windle, B.C.A. and Parsons, F.G. (1897). On the myology of the terrestrial Carnivora. Part I. - Muscles of the head, neck, and fore-limb. *Proceedings of the Zoological Society of London* **1897**, 370-409.

Windle, B.C.A. and Parsons, F.G. (1901). On the muscles of the Ungulata Part I. - Muscles of the head, neck, and fore-limb. *Proceedings of the Zoological Society of London* **1901**, 656-702.

Windsor, D.E. and Dagg, A.I. (1971). The gaits of the Macropodinae (Marsupialia). *Journal of Zoology, London* **163**, 165-175.

Woodburne, M.O., Tedford, R.H., Archer, M., Turnbull, W.D., Plane, M.D. and Lundelius, E.L. (1985). Biochronology of the continental mammal record of Australia and New Guinea. *Special Publications of The South Australian Department of Mines and Energy* **5**, 347-363.

Woods, J.T. (1960). The genera *Propleopus* and *Hypsiprymnodon* and their position in the Macropodidae. *Memoirs of the Queensland Museum* **13**, 199-221.

Wroe, S. (1996). An investigation of phylogeny in the giant rat kangaroo *Ekaltadeta* (Propleopinae: Potoroidae: Marsupialia). *Journal of Paleontology* **70**, 677-686.

Wroe, S. (in press). Stratigraphy and phylogeny in the giant extinct rat kangaroo *Ekaltadeta* (Propleopinae, Hypsiprymnodontidae, Marsupialia). *Memoirs of the Queensland Museum* **41.**

Wroe, S. and Archer, M. (1995). Extraordinary diphyodonty related change in dental function for a tooth of the extinct marsupial *Ekaltadeta ima* (Propleopinae, Hypsiprymnodontidae). *Archives of Oral Biology* **40**, 597-603.

Young, A.H. (1882). The muscular anatomy of the koala (*Phascolarctos cinereus*), with additional notes. *Journal of Anatomy, London* **16**, 217-241.

PROCEEDINGS OF THE LINNEAN SOCIETY OF NEW SOUTH WALE

VOLUME 117

Papers arising from a symposium at Wellington Caves

## CONTENTS