THE GIANT RAT-KANGAROO PROPLEOPUS OSCILLANS (DE VIS), (POTOROIDAE: MARSUPILIA) IN SOUTH AUSTRALIA

BY N. S. PLEDGE

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Isolated teeth referable to one juvenile Propleopus oscillans have been found scattered in a cave deposit at Naracoorte. They have been interpreted as a lower premolar (rP_3); four upper molars : rM^1 (described for the first time), rM^2, two of rM^3 or ^{4}; a lower incisor ($1I_1$) and four lower molars : $1M_2$, rM_3 or $_4$, $1M_5$, rM_5. The 'deciduous" molar M^1 is rectangular and quadritubercular, showing greater similarity to the M^1 of Bettongia spp. than to Hypsiprymnodon. The form of the incisor indicates that this tooth had a period of continued 'rootless' growth until maturity. A large humerus is referred tentatively to P. oscillans and body proportions are calculated. P. oscillans was an animal of about the same bulk as an Eastern Grey Kangaroo (Macropus giganteus), but much stockier and with longer legs. Apparently it inhabited dense scrub, living on a diet of herbaceous vegetation, occasional carrion and small animals.

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Isolated teeth referable to one juvenile *Propleopus oscillans* have been found scattered in a cave deposit at Naracoorte. They have been interpreted as a lower premolar (rP_3); four upper molars : rM^1 (described for the first time), rM^2, two of rM^3 or ^{4}; a lower incisor (lI_1) and four lower molars : lM_2, rM_3 or $_4$, lM_5, rM_5. The "deciduous" molar M^1 is rectangular and quadritubercular, showing greater similarity to the M^1 of *Bettongia* spp. than to *Hypsiprymnodon*. The form of the incisor indicates that this tooth had a period of continued 'rootless' growth until maturity. A large humerus is referred tentatively to *P. oscillans* and body proportions are calculated. *P. oscillans* was an animal of about the same bulk as an Eastern Grey Kangaroo (*Macropus giganteus*), but much stockier and with longer legs. Apparently it inhabited dense scrub, living on a diet of herbaceous vegetation, occasional carrion and small animals.

Introduction

The kangaroos, wallabies and their allies (the Macropodoidea), contains many species, living and fossil; some are quite common and others exceedingly rare. Modern taxonomists (e.g. Archer & Bartholomai 1978) split this large group into two families: the kangaroos and wallabies in the family Macropodidae, and the rat kangaroos (potoroos, bettongs, etc.) in the family Potoroidae. The latter family is divided into the subfamily Potoroinae, containing potoroos and bettongs, and the subfamily Hypsiprymnodontinae, containing the living Musky Rat-kangaroo *Hypsiprymnodon moschatus* Ramsay and the extinct *Propleopus* species.

Modern *H. moschatus* is a small, rat-like animal living in restricted areas of rain forest in northern Queensland. It is distinguished from other kangaroos by a combination of several primitive characters (Ride 1961, 1964), such as a simple alimentary canal, the presence of the hallux on the inner side of the foot, the presence of an upper canine and a second lower incisor, and relatively simple bunodont molars. These features are combined with a number of specializations. The most striking of these are the large 'plagiaulacoid' premolars, i.e. secant (bladed) premolars, which are larger than the adjacent molars, with a curved and serrated cutting edge, and faces strengthened with a number of parallel, vertical ridges corresponding to the points of the serrations. Such premolars are, in fact, most distinctive teeth (Woods 1960).

The fossil species of *Propleopus* are believed to be the closest known relatives of *Hypsiprymnodon*. All have large secant premolars, although in *Propleopus* these are more than three times the size of the modern teeth. The molars are also similar. The Mountain Pigmy Possum, *Burramys parvus* has similar premolars but a different molar structure and a jaw structure that precludes macropodoid affinities (Ride 1956, 1964). Despite the relatively large size and robustness of the fossil teeth and jaws, however, *P. oscillans* is known from only a handful of specimens. By comparison, kangaroos of similar size from the same deposits often are represented by hundreds of specimens. Nevertheless, occurrences of *Propleopus* are widespread. Woods (1960) listed two specimens, a fragmentary incisor and a near-complete lower jaw, and Bartholomai (1972) described a partial maxilla, from the Eastern Darling Downs.

A further specimen has been reported from Wellington Caves, N.S.W. (Woods 1960) and another from L. Menindee (Tedford 1955, 1967). A second Pleistocene species *P. chillagoensis* has been found in cave deposits at Chillagoe, north Queensland (Archer *et al.* 1978). Archer & Bartholomai (1978) mention a specimen from a Pliocene deposit in northern N.S.W. This dentary may be conspecific with a single isolated molar (Gill 1953, 1957; Ride 1964) from a sub-basaltic Pliocene deposit near Hamilton, Vic., dated at 4.3 million years.

* South Australian Museum, North Terrace, Adelaide, S. Aust. 5000.

Williams (1980) lists two additional specimens of *P. oscillans*, found recently in South Australia at Hookina Creek (P22425) and near Mt Gambier (Green Waterhole, P20815). These have been inspected, but are under study elsewhere so only the cheek-tooth measurements will be given in this paper.

Tooth nomenclature follows the system of Archer (1978): the total dental formula for *Propleopus* would probably be $dI\frac{3}{2}$, $I\frac{3}{2}$, $dC\frac{1}{1}$, $C\frac{1}{1}$ $P\frac{2-3}{2-3}$ $M\frac{1-5}{1-5}$. The first molar M1 and premolar P2 are replaced by the erupting P3.

New South Australian occurrence

Rich Pleistocene bone deposits are currently being excavated in caves at Naracoorte. These deposits have produced large and varied fossil faunas of mammals, together with associated amphibians, reptiles and birds (Williams 1980). One of these deposits partially filled and sealed a small cave, the Henschke Fossil Cave, that was discovered by quarry operations on the edge of Naracoorte township in 1969. Excavations of the deposit were undertaken by me and continue to yield an abundance of fossil bones. Associated charcoal has been collected, and preliminary radiocarbon results give the deposit an age of around 35 000 years for the upper metre or so of sediment. (SUA-140, depth 105-120 cm, > 35 000 years BP, δC^{14}—997.7±4.0; SUA 243, 30-75 cm, 33 800 $^{+2400}_{-1800}$ years BP, δC^{14} —985.1 ± 3.9).

Macropodoids constitute more than half of the Henschke Fossil Cave assemblage, and potoroids are well represented. Amongst these specimens are several isolated teeth, found over a period of eight years, that may be referred confidently to *P. oscillans*. This small sample comprises one lower premolar (rP_3) and seven molars, one of which I consider to be a deciduous molar (m^1). An unusual lower incisor, by elimination from all other taxa in the assemblage, also appears to be *P. oscillans*. Most of the specimens consist of enamel crowns only. They show little or no wear, indicating a juvenile age for the individual(s) represented. There is no evidence in the form of duplication to suggest more than one individual, but the preservation and spatial distribution of the teeth might indicate otherwise (Fig. 1). The teeth with their inferred serial position, area of occurrence, and dimensions are listed in Table 1.

TABLE 1. *Measurements of P. oscillans teeth, Henschke Fossil Cave.*

Tooth	Specimen No.	Excavation area/level	length	ant. width	post. width
rM^1	P22736	A7/9	8.9	7.4	7.4
rM^2	P22734	A7/9	10.1	8.9	8.6
rM^3 or 4	P22815	A6/11	12.1	10.3	9.2
rM^3 or 4	P22826	A11 x /14±†	10.7	9.3	8.7
lI_1	P22816	A11 x /14±†	36	n.a.	5.5
rP_3	P22733	A6/10	14.2	*7.9	
lM_2	P17692	X3/3+	10.0	8.2	8.2
rM_3 or 4	P22814	A7/11	11.1	9.2	9.2
lM_5	P22735	A7/9	11.2	9.5	8.7
rM_5	P22813	A10/12	11.1	9.3	8.4

Measurements in mm. * approximate. † Specimen found during cleanup of slumped sediment from a large area centred on A11, previously excavated to level 17. Levels excavated were 15 cm thick except in this instance.

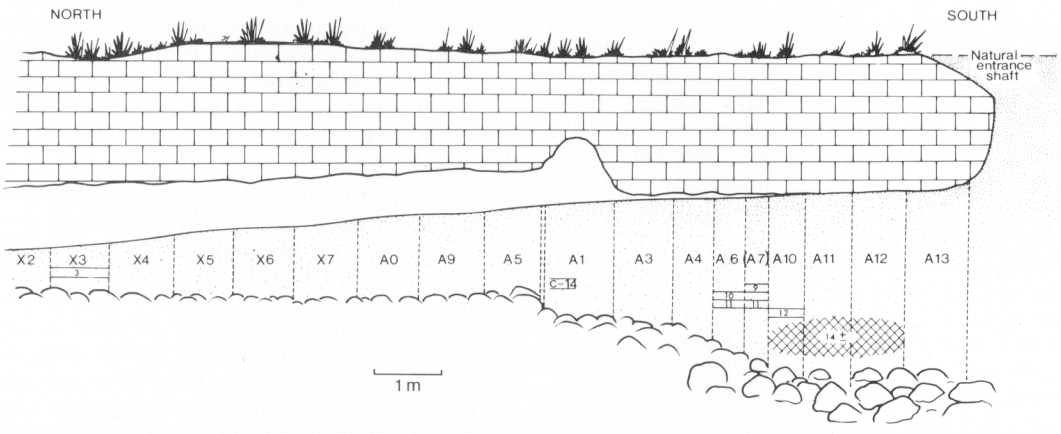

Fig. 1. Cross-section of deposit, Henschke Fossil Cave, Naracorte, showing distribution of fossil *Propleopus* teeth. (Table 2.) C-14 in A1 indicates projected position of dated charcoal sample SUA-140 (>35 000 years B.P. δC^{14} —997. ± 4.0).

The cheek-teeth of *Propleopus* have been described adequately by Woods (1960), Bartholomai (1972) and Archer *et al.* (1978), and will be discussed here only in general terms. One of the notable features about the teeth is the very slight difference in characters that distinguish upper from lower, and indeed left from right, molars. They have roughly the same proportions in both upper and lower molars, and differ only in minute features such as a small lingual ridge coming forwards from the hypocone and a broad anterior cingulum on upper teeth, both absent on lower molars. These teeth bear a superficial resemblance to the deciduous molar M^1 of some short-faced kangaroos, *Sthenurus* spp. (sensu lato), in which the lophs are not as well-developed as in M^{2-5}. However, they are distinguished by different development of the midlink (mainly on the protoloph in *Sthenurus*) and of the crest joining the paracone and metacone (straight and more vertical in *P. oscillans*). The M^1 of *Sthenurus* is also less rectangular than are the molars of *P. oscillans*.

One tooth (P22736) is considered here to represent an M^1 of *Propleopus*. This tooth is quadritubercular, almost rectangular and slightly longer than wide. It resembles the other molars in general form, but is smaller and relatively shorter, and cannot be matched with any described tooth. To some extent it also resembles upper molars (e.g. M^2 and M^3) of the Koala, *Phascolarctos cinereus*, which differ in being selenodont and less rectangular.

While the molar teeth of *P. oscillans* are all similar (Fig. 2), it has been possible to identify two of them with some certainty as last lower molars (M_5) by the reduced size of the talonid, the posterior half of the lower molar (Woods 1960). This is a feature of many marsupials. It was thus possible to check whether this tooth (P22736) was the last upper molar (M^5) of *P. oscillans* by testing the occlusion between it and the lower molars. There was, in fact, no possible match, because of the great size discrepancy. I therefore rule out the possibility that the tooth P22736 is a barely erupted M^5, which tooth is yet unknown.

The specimen consists only of the enamel crown of the tooth, and is slightly worn on the cusps and crests. In the Henschke Fossil Cave this sort of preservation is typical of deciduous teeth, and those barely erupted teeth of juvenile individuals where the roots and dentine apparently have not been fully calcified, allowing them to rot away.

I conclude that the tooth is an M^1, despite the fact that it differs so greatly from the M^1 of *Hypsiprymnodon* (Ride 1961), which is a rather irregular three-cusped tooth with a poorly developed hypocone. This may imply a greater systematic separation from *Hypsiprymnodon* than is currently accepted (e.g. Bartholomai 1972). The condition of the tooth is much more like that of M^1 in *Bettongia*, where it is small and somewhat triangular but definitely quadri-tubercular. This agrees with the observations of Bartholomai (1972) on the permanent molars of *Propleopus*.

One of the major problems of "cave palaeontology" is the ever present risk of reworking of the fossils as they are moved piecemeal from the entrance to their final resting place. Some of the dangers are described by Archer (1974). In the present case, despite the considerable lateral and vertical distribution of the specimens, there is no real evidence for more than one individual and, if P22736 is an M^1, the animal was a juvenile. This favours the interpretation that P22816 is a lower incisor of a juvenile *P. oscillans* and explains the difference from the only figured specimen (in QM F3302). Woods (1960) and Bartholomai (1972) have remarked upon the unique pattern of wear of I_1. This is not readily evident in P22816 due to its youth, but a similar wear profile (especially at the tip) may be seen and the enamel pattern corresponds in its ventrolateral distribution to that in *P. oscillans* (Woods 1960). The enamel is broken off short with the tooth, and staining indicates that only half the specimen was exposed in the jaw. These features and the tapering form of the tooth (which is smaller in both diameters than F3302) suggest that it undergoes considerable open-rooted growth during ontogeny.

Dimensions of known specimens of *Propleopus* teeth are given in Table 2. While the Naracoorte teeth (Table 2) are slightly longer and narrower, where comparable, they clearly fit the proportions and description of *P. oscillans* better than *P. chillagoensis*.

The natural history of Propleopus

The teeth, jaw fragments, and associated fossils in the same deposits provide circumstantial evidence for interpretation of aspects of the habitat, as well as the ecological role of the animal within the habitat.

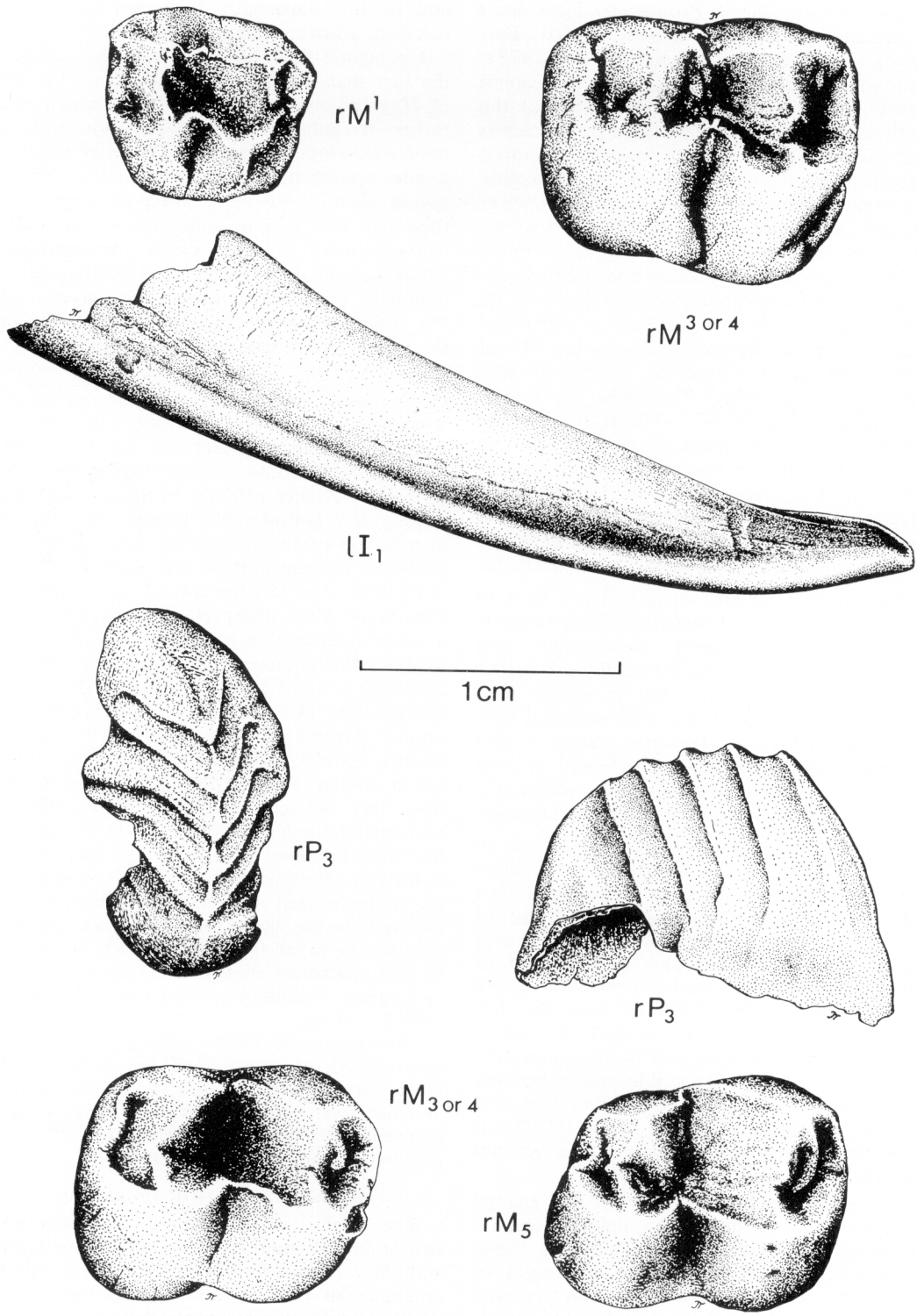

Fig. 2. Isolated teeth of *P. oscillans*, Henschke Fossil Cave, Naracoorte.

TABLE 2. *Propleopus spp. tooth measurements (in mm), length x width (anterior/posterior)*

Tooth	QM F6675 *P. oscillans*	NMV P15917 *P. chillagoensis*
P^3	15.2 x 10.8	21.1 x 13.0
M^2	10.5 x 9.7	9.7 x 12.5/10.9
M^3	11.1 x 10.3	9.7 x 11.0/ 9.6
M^4	—	10.2 x 9.5/ 7.6
M^5	—	9.3 x 7.5

	QM F3302 *P. oscillans*	UCMP 51697 *P. oscillans*	NMV P15919 *P. chillagoensis*	UCMP 45171 *Propleopus* sp.	SAM P20815 *P. oscillans*		SAM P22425 *P. oscillans*
I_1	22.9 x 6.9	—	21.1 x 13.4	—	left	right	—
P_3	13.9 x 9.7	*14 x 10		—	13.8 x 9.8	14.4 x 10.2	14.7 x 7.7
M_2	9.5 x 8.7	* 9 x 9.5		9.6 x 9.7	10.0 x 8.9/ 9.1	9.8 x 9.1/ 9.2	†10.0 x —/8.8
M_3	10.8 x 9.8	*11 x 9.5		10.2 x 10.6	11.1 x 10.3/10.2	11.3 x 10 /10.3	† — x 9.1/—
M_4	11.2 x 10.3	*11 x 10		10.6 x 10.7	12.2 x 11.2/10.4	12.0 x 11.5/10.6	†11.5 x 9.2/8.3
M_5	11.0 x 9.6			10.1 x 9.0	11.2 x 10.1/ 8.5	11.6 x 9.9/ 8.6	† — x 9.7 —

* approximate, measured from Tedford (1967, Fig. 5.).
† approximate, damaged or *in alveolo*. (D. L. G. Williams pers. comm. 1980.)

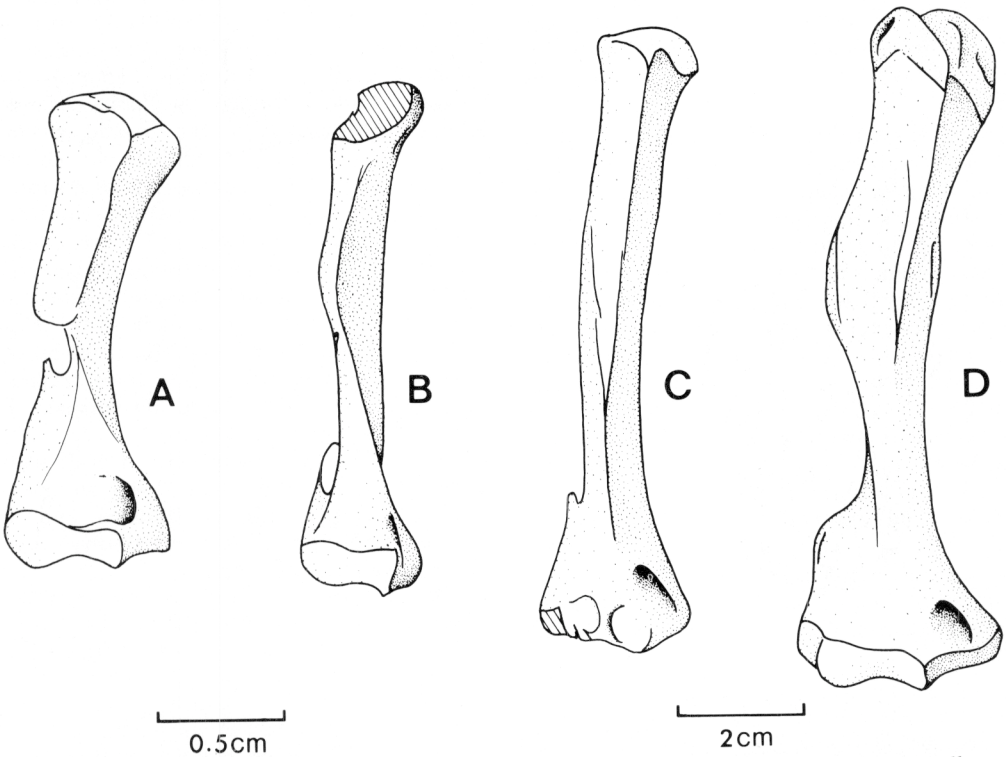

Fig. 3. Comparison of macropodoid right humeri in anterior aspect. A: *Bettongia penicillata,* B: *Hypsiprymnodon moschatus,* C: cf. *Propleopus,* D: *Simosthenurus maddocki.*

1. *Size*: The molar teeth are as large as those of the Eastern Grey and Red Kangaroos, *Macropus giganteus* and *Megaleia rufa.* The only described lower jaw (the holotype) is also as large. I assume that *P. oscillans* had roughly the same bulk as the large kangaroos (Woods 1960). In body proportions and build, however, it differed. The jaw is robust and similar in shape to those of *H. moschatus* and *Bettongia* (Woods 1960) rather than *Potorous.* In view of the apparent close relationship of *Propleopus* with *Hypsiprymnodon,*

we may assume they also had similar body proportions. *H. moschatus* differs from the potoroines in having relatively long forelimbs (Woods 1960), apparently a primitive feature retained because of some advantage in its dense brush habitat. This difference in form from the other rat kangaroos is well shown in Troughton (1973, pl. XI). I calculated the approximate limb-bone ratios for *H. moschatus*, using the specimen QM JM2799, as follows:

humerus : radius : femur : tibia = 1 : 1.17 : 1.57 : 1.72. This compares with 1 : 1.19 : 2.3 : 2.78 for *Bettongia penicillata* Gray, 1837; 1 : 1.33 : 1.9 : 3.07 for the Western Grey Kangaroo *Macropus fuliginosus* (Desmarest); and 1 : 1.24 : 1.48 : 2.09 for the extinct shortfaced kangaroo, *Simosthenurus maddocki* Wells & Murray, 1979, (SAM P17471-82) all of which are, or were, inhabitants of thick scrub. Only *M. fuliginosus* is a grazer, coming out into grassy clearings to feed.

In the Henschke Fossil Cave material there is a large humerus. It is straighter, more slender and more cylindrical than that of the kangaroos and potoroines, and it has markedly reduced deltoid and pectoral ridges and a shorter supinator crest. Of the marsupials compared with it (including species of *Bettongia, Hypsiprymnodon, Macropus, Sthenurus, Thylacinus, Thylacoleo, Phascolarctos*) the fossil bone most closely resembles the humerus of *H. moschatus,* but is even straighter and more cylindrical (Fig 3). The total length of the fossil humerus is estimated at 195 mm. Assuming that it represents *P. oscillans*, and applying the *Hypsiprymnodon* ratios, the radius length is 228 mm, femur 306 mm, and tibia 335 mm: measurements indicating an animal as bulky as a grey kangaroo but with shorter hind legs and much longer fore-legs.

2. *Food*: The teeth are relatively simple in form, quadritubercular and bunodont. These features are also typical of mammals such as Man, pigs and bears, all of which have an omnivorous or browsing vegetarian diet, as in fact have living potoroids. Hume (1978) considered *H. moschatus* to be omnivorous, and Ramsay (1876) recorded that it eats "... insects, worms and tuberous roots ..." and palm berries (*Archontophoenix* (*Ptychosperma*) *alexandrae*). The retention of relatively long forelegs may reflect its method of food gathering, namely turning over scrub debris, and digging like a bandicoot (Troughton 1973). The large secant premolars also seem connected with an omnivorous diet, possibly being used to cut flesh as well as vegetable matter. *P. oscillans* probably lived on soft herbaceous vegetation, carrion, invertebrates, and meat.

3. *Habitat: Hypsiprymnodon* and some of the other potoroids live in dense wet scrub where they can obtain protection against predators. Although so much larger than the living rat-kangaroos, *Propleopus* may have had the same need. Its presumed stocky build would be an advantage in thick brush, just as it seems to be to the stocky Kangaroo Island kangaroo (*M. f. fuliginosus*). The associated fauna adds some support to the idea. Although there are a few fossils species present (such as *Lasiorhinus* sp. and *Procoptodon* sp.) that might suggest a more open environment, the abundance of brush-dwelling animals, such as potoroines, small wallabies (mainly *Macropus rufogriseus*) and bandicoots, indicates the presence of moderately shrubby, open forest in the Naracoorte area during the late Pleistocene. The browsing short-faced kangaroos (*Simosthenurus* spp.) are common and the cow-sized diprotodontid *Zygomaturus trilobus* also is present: these are believed to have inhabited moderately thick scrub. *Diprotodon opatum*, which I consider to be an open scrub or plains animal, is rare: only fragments of three teeth have been recognized. Tortoises (*Chelodina* cf. *longicollis*) were abundant in a nearby swamp. The overall picture given by the fossil fauna is of an area at Naracoorte more thickly forested and with heavier scrub or thicker understory, and a higher rainfall than today.

Thus *Propleopus* may be seen as a large, bulky, relatively short-legged animal, living in dense thickets and scrub, and eating succulent herbaceous vegetation, insects and other small animals and possibly carrion. Its rarity in the fossil record may reflect its strong preference for thick scrub, where remains seldom become fossilized. It may be significant that the fossils reported here represent a juvenile individual, one that was perhaps less cautious than an adult.

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