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LATE PLEISTOCENE MAMMALS FROM THE "KEILOR CRANIUM SITE", SOUTHERN VICTORIA, AUSTRALIA

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Abstract

Two late Pleistocene mammal faunas have been recorded from the "Keilor Cranium Site", southern Victoria, Australia. The older late Pleistocene Dry Creek Local Fauna from the "D Clay" includes *Sarcophilus laniarius, Thylacinus cynocephalus, Perameles nasuta, Vombatus ursinus, Thylacoleo carnifex, Protemnodon anak, P. brehus, Macropus rufogriseus, M. agilis, M. titan, M.* cf. *ferragus*, and *Zygomaturus trilobus*. Disconformably overlying the "D Clay" is the slightly younger Doutta Galla Silt with a basal age of 18,000 yr B.P. The Maribyrnong Local Fauna of the Doutta Galla Silt is represented by *Vombatus ursinus, Megaleia rufa, Macropus giganteus, Mastacomys fuscus, Pseudomys* cf. *australis* and *Pseudomys* cf. *gracilicaudatus*. Late-Pleistocene dwarfing is demonstrated in four species in the Dry Creek Local Fauna and two species in the Maribyrnong Local Fauna, with one species common to both. Late Pleistocene extinctions and late-Pleistocene dwarfing were probably caused by a common factor. The term megafauna is defined to include (1) species now extinct, and (2) species which have undergone late-Pleistocene dwarfing.

Introduction

For nearly two decades fossil mammals have been known from the Doutta Galla Silt in southern Victoria, Australia; these include *Rattus* cf. *assimilis*, and species of kangaroos, wallabies, wombats and native cats similar to those living today (Gill 1955a,b). A C_{14} date of 18,000 ± 500 yr B.P. (NZ-207), obtained on a charcoal sample from the base of the Doutta Galla Silt, indicates that the fauna is of latest Pleistocene age (10,000 yr B.P. is accepted here as the Pleistocene-Holocene boundary).

Disconformably underlying the Doutta Galla Silt at the Keilor Cranium Site is an unnamed dark unit referred to by Gallus (1971) as the "D Clay", from which are recorded species of *Diprotodon* and *Thylacoleo* (Gill 1967).

Over the past eight years Dr. A. Gallus and a team of workers from the Archaeological Society of Victoria have made a large collection of fossil mammals from the Keilor Cranium Site, both from the Doutta Galla Silt and "D Clay". These faunas are described here as the Maribyrnong Local Fauna and Dry Creek Local Fauna respectively.

Locality

"1940 Cranium Site" of Bowler (1970, p. 17, fig. 1). One mile N. of Keilor at confluence of Dry Creek and Maribyrnong River, S. Vict., Australia. Grid ref. 881495 on Sunbury Military Map.

Methodology

Linear tooth dimensions were measured with a pair of vernier calipers to the nearest 0·1 mm when possible. All measurements are in millimetres unless indicated otherwise.

The following abbreviations are used:

- a—approximate measurement
- AW—anterior width (protoloph and protolophid width)
- DB—distal breadth
- DD—distal depth
- DP—deciduous premolar
- L—length
- M—molar
- MW—maximum width
- P—premolar
- PB—proximal breadth
- PD—proximal depth
- PW—posterior width (metaloph and hypolophid width)

The specimens described here were deposited in the fossil collections of the National Museum of Victoria (NMV), Melbourne, Australia. The roman numerals following the specimen numbers in the tables refer to the level from where that specimen was collected. A complete list of the identifiable specimens from each level of the "D Clay" is given in Appendix 1. The specimens from the Doutta Galla Silt are listed in Appendix 2. The higher taxonomic categories are of Ride (1964).

1. "D Clay" (Dry Creek Local Fauna)

Because there are no detailed studies of the complex stratigraphy at the Keilor Cranium Site, I will restrict my comments to the general relationships between the fossil bearing units.

Three basic mapable units are recognizable at the Keilor Cranium Site: (1) the Arundel Formation, (2) an unnamed intermediate unit, and (3) the Doutta Galla Silt, from oldest to youngest (formational names follow Gill 1962). All three of these units are separated by disconformities. The relationship of the Arundel Formation and Doutta Galla Silt are discussed by Bowler (1970). The intermediate unnamed unit has been referred to as the "D Clay" by Gallus (1971), although it has not been formally named. The age of the "D Clay" has yet to be established, although it is certainly late Pleistocene in age and probably in the order of 25,000-40,000 yr B.P. (J. M. Bowler, pers. comm.). The material described here as the Dry Creek Local Fauna was collected from the "D Clay".

During initial excavation of the fossil materials from the Doutta Galla Silt, Gallus organized his collections on the basis of their relationship of one to the other (local concentrations) and on superpositional relationships where this was clearly defined. Differences in the lithology of the sediment were also taken into account. For the most part the collection is organized into specific collection sites (layers or levels as sometimes used by Gallus) and the relationships of these sites to each other have not been firmly established. In the interest of convenience and clarity I have given "level" numbers to each of Gallus's collection sites (Appendix 1). These levels (I-XI) are roughly organized such that level I probably represents the oldest and level XI probably represents the youngest, although this is only an approximation and needs further clarification. Until the stratigraphic and time relationships of these levels are worked out in detail it is not possible to discuss differences in faunal composition within the different levels in any meaningful context.

The Fauna

The Dry Creek Local Fauna consists of 12 species of marsupials representing three orders and seven families. Two of these families, Diprotodontidae and Thylacoleonidae, are now extinct; the other five families, Thylacinidae, Dasyuridae, Peramelidae, Vombatidae, and Macropodidae, are represented by extant species. Table 1 lists the minimum number of individuals of each species necessary to account for all of the specimens recovered from each level (based on both dental and postcranial remains).

Macropods are the dominant group, comprising 76% of the total minimum number of individuals and are represented by at least five, and possibly as many as six, species (*Protemnodon anak*, *P. brehus*, *Marcopus rufogriseus*, *M. agilis*, *M. titan*, *M.* cf. *ferragus*). *Macropus titan* is the most abundant species in most of the levels, followed by *M. rufogriseus* and *M. agilis* which appear in about equal numbers. The other species appear rather sporadically throughout and are not abundant in any particular level. The ratio of carnivores (*Sarcophilus laniarius*, *Thylacinus cynocephalus*, *Thylacoleo carnifex*) to herbivores (all other species) is approximately 1 : 10.

The species in the fauna can be placed into three basic groups: (1) species represented by living forms indistinguishable from specimens in the fauna (*Perameles nasuta*, *Vombatus ursinus*, *Macropus rufogriseus*); (2) the larger Pleistocene forms of living species (*Sarcophilus laniarius*, *Thylacinus cynocephalus*, *Macropus agilis*, *M. titan*), and (3) species now extinct (*Thylacoleo carnifex*, *Protemnodon anak*, *P. brehus*, *Macropus* cf. *ferragus*, and *Zygomaturus trilobus*).

TABLE 1

Under "levels" I-XI from the "D Clay" are listed the minimum number of individuals necessary to account for the specimens recovered from each "level" based on both dentitions and postcranial remains. The minimum number of individuals of each species in the total fauna based solely on dentitions is given in the right-hand column.

Species Level	I	II	III	IV	V	VI	VII	VIII	IX	X	XI	Total
Sarcophilus laniarius	-	-	-	1	1	1	-	-	-	-	-	1
Thylacinus cynocephalus	-	-	-	-	-	1	-	-	-	-	-	1
Perameles nasuta	-	-	1	-	-	-	-	-	-	-	-	1
Vombatus ursinus	-	-	2	1	-	-	-	-	-	-	-	2
Thylacoleo carnifex	-	-	-	-	-	-	-	-	-	-	1	1
Protemnodon anak	-	-	-	-	1	-	-	-	-	-	1	2
Protemnodon brehus	-	-	1	-	-	-	-	-	1	-	-	1
Protemnodon sp.	-	-	1	-	-	1	-	-	1	1	-	-
Macropus rufogriseus	-	-	-	1	1	1	1	-	-	-	1	3
Macropus agilis	-	-	-	3	1	1	1	-	-	-	-	5
Macropus titan	-	1	3	2	2	3	3	2	1	1	3	13
Macropus cf. *ferragus*	-	-	1	-	-	-	-	-	-	-	-	1
macropodid	-	2	1	2	2	1	-	1	1	1	1	-
Zygomaturus trilobus	1	1	-	-	-	-	-	-	-	-	-	2
diprotodontid	-	-	-	-	-	-	-	1	-	-	1	-
Total	1	4	10	10	8	9	5	4	4	3	8	33

Dry Creek Local Fauna

Class Mammalia
  Infraclass Metatheria
    Superorder Marsupialia
      Order Marsupicarnivora
        Family Dasyuridae
          Sarcophilus laniarius
        Family Thylacinidae
          Thylacinus cynocephalus
      Order Peramelina
        Family Peramelidae
          Perameles nasuta
      Order Diprotodonta
        Family Vombatidae
          Vombatus ursinus
        Family Thylacoleonidae
          Thylacoleo carnifex
        Family Macropodidae
          Protemnodon anak
          Protemnodon brehus
          Macropus rufogriseus
          Macropus agilis
          Macropus titan
          Macropus cf. *ferragus*
        Family Diprotodontidae
          Zygomaturus trilobus

Palaeoecology

The probable habitat preferences of the species in the Dry Creek Local Fauna (Table 2) are based on those of extant populations. It is assumed that the larger late Pleistocene forms (*Sarcophilus laniarius, Macropus titan*) had habitat requirements similar to their living descendants (*S. harrisii* and *M. giganteus* respectively). These data show that the region in the Dry Creek area in late Pleistocene time was most probably covered by sclerophyll forest. It is possible that mesophytes lined the river valleys which dissected the open rolling bushlands and grasslands much as occurs in the area today.

Faunal Correlation

Lake Colongulac (= *Lake Timboon*)

The Dry Creek Local Fauna compares well with the late Pleistocene fauna from Lake Colongulac, N. of Camperdown, S. Victoria. The following species are represented in the Lake Colongulac Local Fauna:

Class Mammalia
  Superorder Marsupialia
    Order Marsupicarnivora

TABLE 2

Basic habitat preferences of species in the Dry Creek Local Fauna based on living populations of these species (x indicates preferred habitat).

Species	Rain-forest	Sclerophyll forest	Woodland	Plains
Sarcophilus laniarius* (as S. harrisii)		x		
Thylacinus cynocephalus*		x	x	
Perameles nasuta+	x	x	x	
Vombatus ursinus+		x		
Macropus titan+ (as M. giganteus)		x	x	x
Macropus agilis*		x	x	x
Macropus rufogriseus+		x	x	

+ from Marlow (1958)   * from Ride (1970)

Family Dasyuridae
Sarcophilus laniarius (P30218)
Family Thylacinidae
Thylacinus rostralis (see DeVis 1899)
Order Diprotodonta
Family Vombatidae
Lasiorhinus sp.?
Vombatus ursinus (P30785)
Family Thylacoleonidae
Thylacoleo carnifex (P24000) (Type locality)
Family Macropodidae
Sthenurus sp. (P29488)
Procoptodon rapha (P26901)
Thylogale billardierii (P23996)
Protemnodon anak (P30207)
Protemnodon brehus (P30214)
Macropus rufogriseus (P30217)
Macropus agilis (*M. siva*?) (P30215)
Macropus titan (P28549)
Family Diprotodontidae
Diprotodon optatum (P15902)

A large collection of fossil mammals from Lake Colongulac and the surrounding lake region (generally referred to as the Camperdown District) is in the National Museum of Victoria; but unfortunately this important fauna has not been adequately described. The diversity of this fauna is considerably greater than previously recognized as is seen in comparing the faunal list given by Gill (1953b, p. 35) with the revised and expanded list given above. The fauna from Lake Colongulac and that from Dry Creek are similar in age and share a close geographical proximity; differences between these faunas are probably due to sampling.

Murray River Basin

Late Pleistocene local faunas from the Lower Murray River Basin have been recovered from Lake Menindee (Tedford 1967), Lake Tandou (Merrilees 1973), and Lake Victoria (Marshall 1973). These faunas are typified by an abundance of grazers (*Macropus ferragus*, *M. titan*) and browser-grazers (*Sthenurus tindalei*, *S. andersoni*, *S. atlas*, *Protemnodon brehus*, *P. anak*, *Osphranter cooperi*) and dominated by the large browsing macropod *Procoptodon goliah*.

The Lake Victoria Local Fauna (which is typical of the Murray River Basin faunas) is considerably different from that of the Dry Creek Local Fauna. Five of the twelve species in the Dry Creek Local Fauna (*Perameles nasuta*, *Vombatus ursinus*, *Macropus agilis*, *M. rufogriseus*, and *Zygomaturus trilobus*) are absent from the Lake Victoria Local Fauna whereas *Perameles gunnii*, *Lasiorhinus Krefftii*, *Lagorchestes leporides*, *Onychogalea fraenata* and *Diprotodon optatum* occur in the Lake Victoria Local Fauna and not in the Dry Creek Local Fauna. These faunal differences are probably the result of the presence of an open woodland-savannah-grassland in the Murray River Basin during late Pleistocene time.

The Collection

The major part of the fossil materials were collected *in situ* as isolated specimens. A few associated left and right rami were obtained, although these finds are certainly exceptions. Most of the postcranial material was broken except for podial and metapodial bones. Because of the dearth of associations it is difficult to assign postcranial elements to respective dentitions with complete certainty. In the case of *Protemnodon*, all podial elements are referred to *Protomnodon* sp. as there were no feet of *P. anak* or *P. brehus* available for comparison. All of the postcranial elements of a large species of *Macropus* are referred to *M. titan*. Although associated rami (P30716) are referred to *M.* cf. *ferragus*, the presence of this species in the fauna cannot be established with complete certainty (see below). The postcranial remains of smaller species of *Macropus* are potentially referable to *M. agilis* or *M. rufogriseus* and some may even be referable to females? of *M. titan*; these are all listed collectively under the heading macropodid. The postcranial remains of a diprotodontid are probably referable to *Zygomaturus trilobus*. Except for basing the identification of *Thylacinus cynocephalus* on a humerus, the identifications of all other species in the fauna are based on teeth. Nearly one third of the total bone sample consists of postcranials which are too fragmented to permit reasonably accurate identification. These specimens are not discussed in this study although their presence is recorded for completion.

Systematics Review

Class Mammalia
Infraclass Metatheria
Superorder Marsupialia
Order Marsupicarnivora
Family Dasyuridae
Sarcophilus laniarius (Owen, 1838)

Specimens of *Sarcophilus laniarius* were collected from levels IV, V, and VI. As there is no duplication in the elements represented they may in theory be attributed to a single individual (Table 3).

The relationship of L M^2 and MW M^2 of P29587 from Dry Creek is compared in Fig. 1 with an extant sample of *Sarcophilus harrisii* from Tasmania and a sample of *S. laniarius* from late Pleistocene deposits in Strathdownie Cave, Victoria (Merrilees 1965). The Dry Creek specimen falls well within the range of the *S. laniarius* sample.

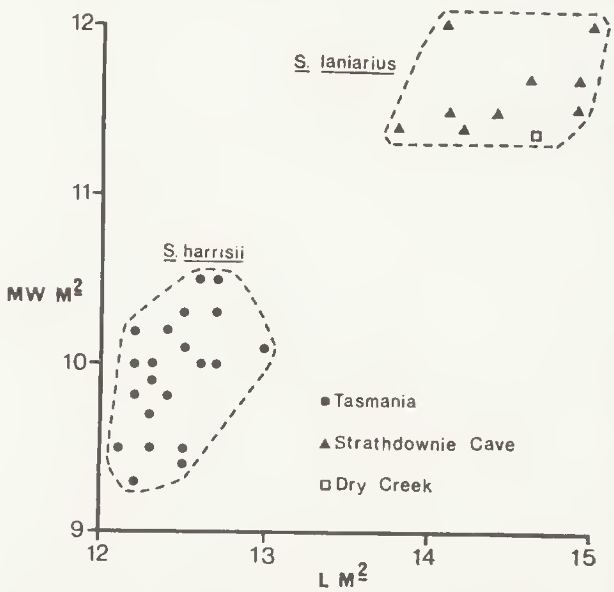

Fig. 1—Scatter diagram showing relationship of L M^2 and MW M^2 of a living sample of *Sarcophilus harrisii* from Tasmania, a fossil sample of *S. laniarius* from late Pleistocene deposits in Victoria, and a specimen (P29587) referable to *S. laniarius* from the Dry Creek Local Fauna.

No morphological differences were observed in the dentitions of the *S. laniarius* or *S. harrisii* samples studied, and except for the superior size of the former (approximately 15% based on tooth measurements) separation of the dentitions of these species was difficult. *S. laniarius* is typically found in deposits of late Pleistocene age in direct association with extinct megafaunal species of *Procoptodon*, *Protemnodon*, *Sthenurus*, and *Zygomaturus*, to name just a few. *S. harrisii*, on the other hand, occurs in slightly younger deposits always in association with a typically modern fauna (for example see Thorne 1972). Although the association of specimens of *S. harrisii* with extinct megafaunal species are reported (Owen 1877) the contemporaneity of these species is highly questionable (Frank 1971). The direct association and temporal overlap of these species have not been substantiated. This evidence suggests that *S. laniarius* represents a larger, ancestral, late Pleistocene form of *S. harrisii*; a relationship first recognized by Lydekker (1887).

TABLE 3

Dimensions of the cheek teeth of *Sarcophilus laniarius*

Specimen	P^2		M^1		M^2		M^3	M^4	
	L	MW	L	MW	L	MW	L	L	MW
P29587 (VI)	-	-	12.2	9.7	14.6	11.3	13.7	9.2	4.7
P29631 (V)	6.8	6.0	-	10.0	-	-	-	-	-

Family Thylacinidae

Thylacinus cynocephalus (Harris, 1808)

A single left humerus (P29588) collected from level VI is the only element referable to this species.

Ride (1964) reviewed the status of the five proposed species of *Thylacinus* (*T. major* Owen 1877, *T. breviceps* Krefft 1871, *T. spelaeus* Owen 1845, *T. cynocephalus* Harris 1808, and *T. rostralis* DeVis 1894). Ride's study of dental and cranial characters of a living sample of *Thylacinus* from Tasmania, and fossil samples from cave deposits in W. and E. Australia "do not support separation [of these samples] even at a subspecific level at the present time". Ride recognized that these samples represent a single variable species, *T. cynocephalus*, which includes *T. breviceps* and *T. spelaeus* as junior synonyms (see footnote of Ride 1964, p. 105 concerning the identity of *T. major*). Ride further noted, "although recognition by name is not justified there is no doubt that in the Pleistocene of W. Australia there existed a population of *Thylacinus cynocephalus* which on an average contained smaller individuals than the modern form (and by inference its eastern Pleistocene representative)". *T. rostralis* from the late Pleistocene fluviatile deposits of the E. Darling Downs, SE. Queensland was shown to be larger than the specimens referred to *T. cynocephalus* by Ride. Ride recommended that *T. rostralis* retain its specific identity, at least for the time being.

The Dry Creek specimen agrees well in morphology with the living specimens of *T. cynocephalus* from Tasmania (NMV C5742, C5746, C5753) with which it was compared, although the Tasmanian specimens are slightly smaller. No specimens of postcranial material referable to *T. rostralis* were available for study and it may be that the Dry Creek specimen is referable to this species. DeVis (1899) reported *T. rostralis* from Lake Colongulac in S. Victoria. I was unable to relocate the specimen(s) upon which this identification was based.

The Dry Creek specimen agrees well in size and morphology with a nearly complete skeleton of *T. cynocephalus* (P26573) from late Pleistocene deposits at Lake Victoria, N.S.W. The cranial dimensions of P26573 fall well within the range of males of *T. cynocephalus* studied by Ride (1964).

Order Peramelina

Family Peramelidae

Perameles nasuta Geoffroy, 1804

A right ramus fragment with P_1-M_3 and an associated fragment of a left maxillary with M^{2-3} (P29634) of this species were found in level III (Table 4).

The upper molars of species of *Isoodon* possess a well developed hypocone which is subequal in size to the protocone. In species of *Perameles* a hypocone is absent or only incipiently developed. The Dry Creek specimen has only an incipiently developed hypocone and is readily referred to a species of *Perameles*. The dentitions of *Macrotis*, *Chaeropus* and *Echimiptera* are sufficiently distinct from *Perameles* and *Isoodon* to dispense with a detailed comparison with the Dry Creek specimen.

The L M_3 and AW M_3 of living samples of *Perameles bougainville* (including *P. fasciata*, *P. myosura*, *P. arenaria*; see Tate 1948, pp. 324-325), *P. gunnii*, and *P. nasuta* are compared with the Dry Creek specimen in Fig. 2. Values of the dental parameters of *P. bougainville* are significantly smaller than those of the other two species. Freedman (1967) reported that the teeth of *P. gunnii* and *P. nasuta* "are of approximately similar size" although those of *P. gunnii* were shown to be slightly smaller. He noted that the dentitions of these species could be separated by differences in the morphology of the upper incisors and canine. Unfortunately, these teeth are not represented in the collection from Dry Creek. I was unable to find morphological differences in the molar teeth of these species which would allow them

TABLE 4

Dimensions of the cheek teeth of Perameles nasuta

Specimen	P1		P2		M1			M2			M3		
	L	MW	L	MW	L	AW/MW	PW	L	AW/MW	PW	L	AW/MW	PW
Upper													
P29634 (III)	-	-	-	-	-	-	-	4.0	4.0	-	3.8	3.9	-
Lower													
P29634 (III)	2.9	0.9	3.3	1.3	3.9	2.2	2.6	4.1	2.6	3.0	4.2	2.5	2.7

to be distinguished. As seen in Fig. 2, *P. gunnii* is slightly smaller than *P. nasuta*. The Dry Creek specimen falls within the range of the *P. nasuta* sample and outside of the *P. gunnii* sample. The Dry Creek specimen is tentatively referred to *P. nasuta* based on this (admittedly minor) size difference.

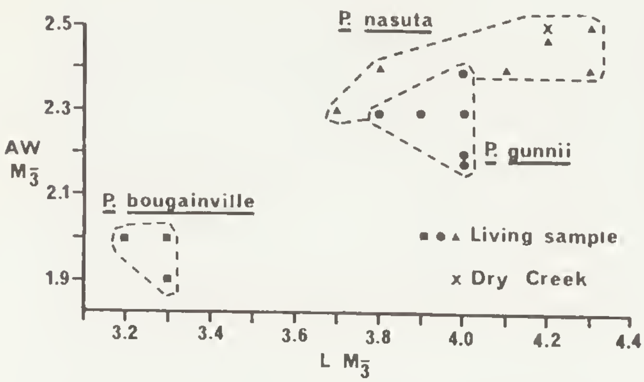

Fig. 2—Scatter diagram showing relationship of L M_3 and AW M_3 for living samples of *Perameles bougainville*, *P. gunnii*, and *P. nasuta*, and a fossil specimen of *Perameles* from the Dry Creek Local Fauna.

Order Diprotodonta

Family Vombatidae

Vombatus ursinus (Shaw, 1800)

A minimum of two individuals of *Vombatus ursinus* are represented by two rami (P23026, P29519) and a fragment of a left ilium (P29548), collected from levels III and IV respectively. Remains of this species are commonly found in late Pleistocene deposits throughout Victoria, E. New South Wales and S. Queensland.

The molars of *V. ursinus* typically have W-shaped lobes and sharp interlobe valleys as opposed to the more U-shaped or rounded lobes and more open interlobe valleys of *Lasiorhinus* (Merrilees 1967, p. 407).

Family Thylacoleonidae

Thylacoleo carnifex Owen, 1858

A single fragment from level XI of a right maxillary (P29545) with the lower edge of the orbit and the anterior root of P^3 is all that is known of this species.

At the present time one late Pleistocene species, *T. carnifex*, is recognized and is virtually pan-Australian in distribution. Merrilees (1968) reports *Thylacoleo* sp. not *T. carnifex* from Mammoth Cave in SW. W. Aust. This specimen(s) has not been described and I do not know how it differs from *T. carnifex*.

Mylodon australis Krefft 1870, *Thylacoleo oweni* McCoy 1876, and *Thylacopardus australis* Owen 1888 are presently recognized as junior synonyms of *T. carnifex* (Anderson 1929). A concise description of the cranium and dentition of this species is given by Woods (1956) and the species distribution is outlined by Gill (1954).

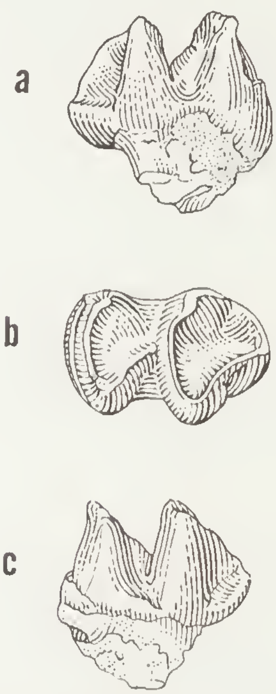

Fig. 3—*Protemnodon anak*, right M_3, NMV P29555, level V; a, lingual; b, occlusal; and c, labial views; all x 1½.

Family Macropodidae

Protemnodon anak Owen, 1873

Dentitions of *Protemnodon anak* were found in levels V (P29554, P29555) and XI (P29604), representing a minimum of two individuals (Table 5). Postcranial remains from levels III, VI, IX and X may be referable to this species (Table 9). These specimens agree in all respects with the holotype (BMNH M1895) figured by Stirton (1963, p. 136, fig. 13a,b) (Fig. 3).

TABLE 5

Dimensions of the cheek teeth of *Protemnodon anak* and *P. brehus*

Specimen	P3		M3			M4		
	L	PW	L	AW	PW	L	AW	PW
P. brehus								
Upper								
P29522 (III)	-	-	-	-	13.1	19.2a	-	12.8
Lower								
P29628 (IX)	-	-	16.5	11.5	11.5	17.7	-	
P. anak								
Lower								
P29604 (XI) (left)	-	-	13.7	-	-	15 6	-	9.8
P29604 (XI) (right)	15.0	5.5	13.5a	-	-	15.7	-	10.0

Protemnodon brehus (Owen, 1874)

Dentitions of this species were found in levels III (P29522) and IX (P29628). An isolated right lower incisor (P29586) from level VI is probably referable to this species. These specimens represent the first record of *P. brehus* in Victoria.

P29522 agrees in all respects with the holotype (BMNH 43303a) figured by Stirton (1963, p. 140, fig. 15b). The lower molars of *P. brehus*, as represented by P29628, differ from those of *P. anak* (P29601) in being larger and relatively broader (Table 5). Both species have weakly developed cingula on the lower molars.

Macripus rufogriseus (Desmarest, 1817)

Dentitions of this species were found in levels IV-VII and XI, and represent a minimum of three individuals (Table 6). Some of the postcranials from levels II-VI, VIII-XI listed under macropodid may be referable to this species.

In Fig. 4 the Dry Creek specimens are compared with specimens of *M. rufogriseus* from an extant population. There is complete overlap in the range of the two samples. *M. rufogriseus* is found as a living species in the Dry Creek area; the living firms are indistinguishable in size and tooth morphology from the specimens in the Dry Creek Local Fauna.

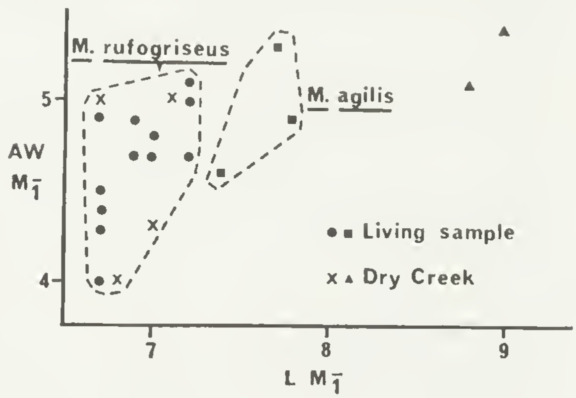

Fig. 4—Scatter diagram showing relationship of L M_1 and AW M_1 of a living sample of *Macropus agilis* (squares) and *M. rufogriseus* (circle) and specimens referable to *M. agilis* (triangles) and *M. rufogriseus* (x) from the Dry Creek Local Fauna.

Macropus agilis (Gould, 1842)

Macropus agilis is the second most abundant species in the fauna and is represented by a minimum of five individuals (Table 7, Figs. 5, 6). *M. agilis*, like *M. rufogriseus*, is repre-

TABLE 6

Dimensions of the cheek teeth of *Macropus rufogriseus*

Specimen	DP3	P3			M1			M2			M3		M4	
	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	PW	L	AW
Upper														
P29578 (V)	-	-	-	-	-	-	-	-	6.9	6.9	8.3	-	9.0	7.0a
Lower														
P29577 (IV)	-	4.3	-	-	7.1	5.0	-	7.9	-	-	-	-	-	-
P29574 (XI)	-	4.1	1.6	1.8	6.7	5.0	5.4	7.6	5.4	5.4	8.6	5.5	-	-
P30905 (VII)	4.2	-	-	-	7.0	4.3	4.7	7.6	5.3	5.3	-	-	-	-
P30725 (IV)	-	-	-	-	6.8	4.0	-	-	-	-	-	-	-	-

sented by dental remains in levels IV-VII, although is not present in level XI. Some of the postcranials from levels II-VI, VIII-XI may well prove to be referable to this species.

DeVis (1895) erected *M. siva* on the basis of a partial ramus collected from the late Pleistocene fluviatile deposits of the E. Darling Downs in SE. Queensland (see Bartholomai 1966, pp. 118-119). Specimens referable to *M. siva* have subsequently been recorded from late Pleistocene deposits in Mount Hamilton Cave, Victoria (Wakefield 1963, p. 326; as *M.* cf. *M. siva*), the Frenchman's Creek Local Fauna in SW. New South Wales, and Wellington Caves, N.S.W. (Marshall 1973).

Specimens recognized as *M. siva* are typically larger than *M. agilis*, but except for this small size difference the dentitions of these species are indistinguishable. *M. siva* is reported only from deposits of late Pleistocene age. The most logical explanation regarding the relationship of these two species is that *M. siva* probably represents a slightly larger late Pleistocene form of *M. agilis*. No large samples of *M. siva* have been described and what materials have been referred to this species consist either of isolated specimens or small samples. Thus the precise size difference between populations of *M. siva* and *M. agilis* has yet to be established; I would estimate it to be in the order of 10-15%. A detailed study may show these species to be conspecific.

In Fig. 4 the dimensions of the Dry Creek specimens are compared with three specimens of *M. agilis* from a living population and show that the late Pleistocene Dry Creek specimens are larger. The sample sizes are admittedly small and for this reason it is unwise to place too much emphasis on these differences. The dimensions of the Dry Creek specimens do, however, fall within the range of the large sample of *M. agilis* from Queensland described by Bartholomai (1971, p. 11). For this reason I refer the Dry Creek specimens to the living species *M. agilis*.

The relative abundance of *M. agilis* in the Dry Creek Local Fauna indicates that a large population of this species was present in

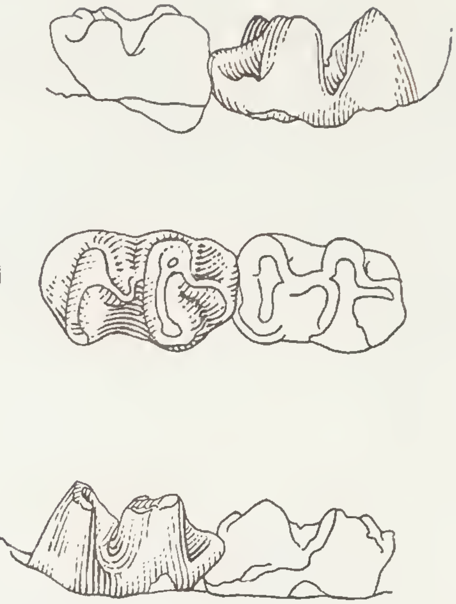

Fig. 5—*Macropus agilis*, left M_{3-4} of NMV P29550a, level IV; a, labial; b, occlusal; and c, lingual views; all x 2.

TABLE 7

Dimensions of the cheek teeth of *Macropus agilis*

Specimen	P2		DP3			P3			M1			M2			M3			M4		
	L	MW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
Upper																				
P29579 (VI)	-	-	-	-	-	9.8	4.0	5.0	-	-	-	9.8	7.7	7.7	-	-	-	-	-	-
Lower																				
P29549 (IV)		-	-	-	-	-	-	-	-	-	-	9.7	-	6.2	10.5	6.7	6.7	-	-	-
P29550 (IV) (left)		-	-	-	-	-	-	-	-	-	-	-	-	6.6	10.6	6.8a	6.8	11.3	6.8	6.1
P29550 (IV) (right)		-	-	-	-	7.8	2.5	3.4	-	-	5.6	-	6.0	6.4	-	6.7	-	-	-	-
P29575 (V)	-	-	-	-	-	-	-	-	9.0	5.4	6.1	9.8	6.0	6.4	-	-	-	-	-	-
P29576 (V)	6.6	3.5	7.8	4.2	4.7	-	-	-	8.8	5.1	5.4	-	-	-	-	-	-	-	-	-
P29603 (VII)	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	-	10.6	6.7	6.4

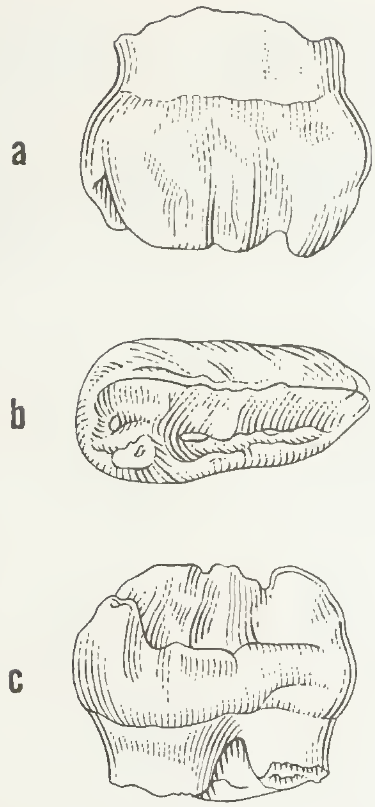

Fig. 6—*Macropus agilis*, right P^3, NMV P29579, level VI; a, labial; b, occlusal; and c, lingual views; all x 3.

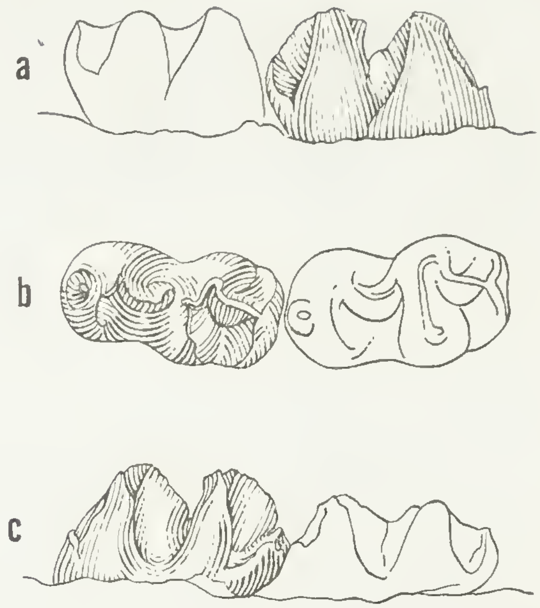

Fig. 7—*Macropus titan*, left M_{3-4} of NMV P29524, level III; a, labial; b, occlusal; and c, lingual views; all x 1½.

southern Victoria in late Pleistocene time. The absence of this species in Victoria today presents a problem because other macropods in the Dry Creek Local Fauna which are represented by living forms (*M. rufogriseus* and *M. titan*) are the dominant macropods in the Dry Creek area today. The factor(s) responsible for the post-Pleistocene change in distribution of *M. agilis* is presently unknown.

Macropus titan Owen, 1838

Macropus titan, the most abundant species in the fauna, is represented by a minimum of 13 individuals, accounting for 40% of the individuals in the fauna (Table 8). Dentitions of this species were recovered at all levels except level I (Fig. 7).

In Fig. 9 Dry Creek specimens are compared with a sample of *M. titan* from Lake Colongulac, Vict., showing that there is nearly complete overlap in the range of the two samples. In linear dimensions of M_3, *M. titan* is intermediate in size between the smaller living species *M. giganteus* and the larger extinct late Pleistocene species *M. ferragus*.

Of the four complete metatarsal IVs listed in Table 9, two (P29534, P29535) are similar in size and are significantly smaller than the other two (P29556, P29589). I attribute these differences to sexual dimorphism with the smaller specimens representing females and the larger the males (Fig. 8).

Macropus faunus DeVis 1895 and *Macropus magister* DeVis 1895 are recognized as junior synonyms of *M. titan* (Tedford 1967). The specimen figured by Tedford (1967, Fig. 27a) and referred to *Macropus birdselli* is also referable to *M. titan*.

M. titan is the most widely distributed of the late Pleistocene macropod species and occurs in almost every late Pleistocene deposit studied. It is typically the most abundant species in late Pleistocene deposits in Vict. (Lake Colongulac), E. N.S.W. (Wellington Caves), and SE. Qd. (E. Darling Downs). At Lake Victoria in SW. N.S.W., however, *M. titan* is less abundant than the larger grazing macropod *M. ferragus* (Marshall 1973). *M. titan* was

TABLE 8

Dimensions of cheek teeth of *Macropus titan*

Specimen	P3			M1			M2			M3			M4		
	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
Upper															
P29537 (IV)	-	-	-	14.2	-	-	15.5	12.0	10.3	-	-	-	-	-	-
P29538 (XI)	-	-	-	-	-	-	14.6	-	12.8	16.4	13.5	13.5	17.3	13.8	13.2
P29606 (VII)	10.1	3.6	5.0	12.3	9.7	-	-	-	-	-	-	-	-	-	-
P29611 (VIII)	-	-	-	-	-	-	-	-	-	-	-	-	17.0	14.8	13.7
P29626 (IX)	-	-	-	-	-	-	15.3	-	-	16.8	13.5	13.3	17.4	14.7	14.1
Lower															
P29524 (III)	-	-	-	-	-	-	15.7	-	10.2	17.4	11.4	10.5	18.0	10.0	-
P29525 (III)	8.0	3.5	4.2	-	-	-	16.0	-	10.3	17.1	11.2	10.4	-	-	-
P29528 (XI)	-	-	-	-	-	-	-	-	-	-	-	-	17.6	-	-
P29529 (XI)	-	-	-	-	-	-	-	-	-	-	-	-	19.0	11.6	-
P29531 (II)	-	-	-	-	-	-	-	-	-	16.4	9.9	9.2	17.2	9.9	9.5
P29552 (V)	-	-	-	-	-	-	-	-	-	-	-	-	17.0	10.3	9.3
P29553 (V)	-	-	-	-	-	-	-	-	-	15.5	9.5	9.4	17.1	9.9	9.3
P29580 (VI)	-	-	-	-	-	-	13.8	-	9.5	16.9	10.7	10.7	-	-	-
P29581 (VI) (right)	-	-	-	-	-	-	-	-	-	17.0	-	-	18.9	-	11.2
P29581 (VI) (left)	-	-	-	-	-	-	-	-	-	-	-	-	18.7	-	-
P29582 (VI)	-	-	-	-	-	-	-	-	-	17.0	9.7	9.3	-	-	-
P29583 (VI)	-	-	-	13.2	7.7	8.2	15.3	9.1	-	-	-	-	-	-	-
P29584 (VI)	8.6	3.1	4.2	14.0	8.0	8.3	-	8.0	-	-	-	-	-	-	-
P29600 (VII)	-	-	-	-	-	-	-	-	-	17.0	11.6	11.0	17.6	11.5	10.7
P29602 (VII)	-	-	-	13.0	-	8.7	15.4	9.7	9.8	-	-	-	-	-	-
P29609 (VIII)	-	-	-	-	-	-	-	-	-	17.0	11.3	10.8	17.5	11.6	10.7
P29610 (VIII)	-	-	-	-	-	-	-	-	-	-	-	-	18.4	10.6	10.5
P29624 (IX)	-	-	-	-	-	-	-	-	-	-	-	-	18.2	11.0	-
P30714 (III)	-	-	-	-	-	-	16.0	-	10.4	-	-	-	-	-	-

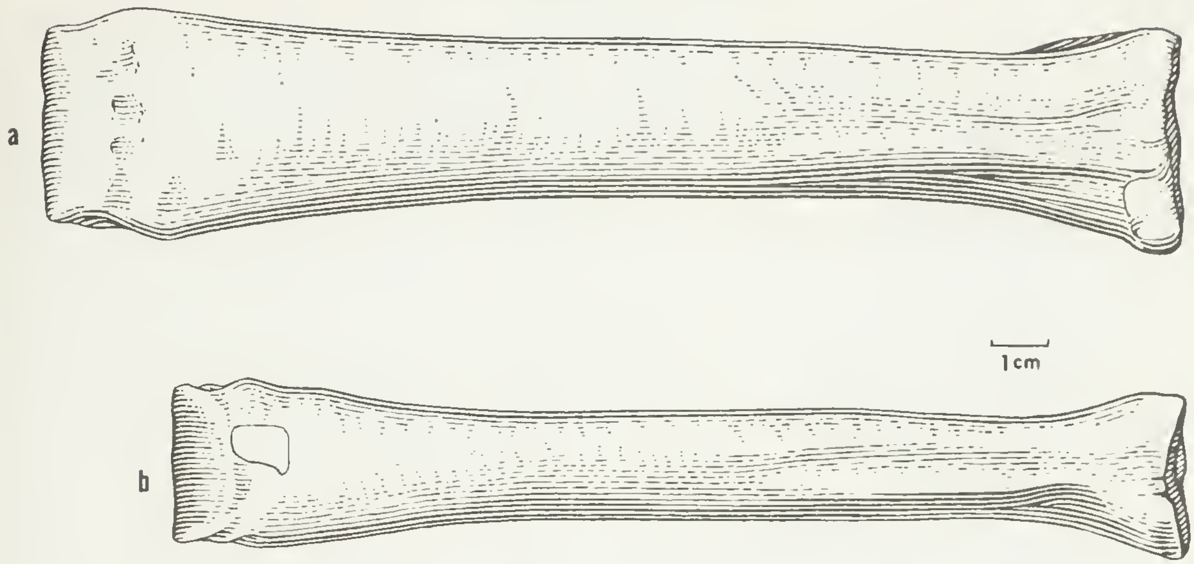

Fig. 8—*Macropus titan*, a, left metatarsal IV (male?), NMV P29556, level V, dorsal view; b, left metatarsal IV (female?), NMV P29534, level IV, dorsal view.

probably a woodland-savannah species and occupied a niche which was probably identical to that of *M. giganteus* today (see below).

M. titan appears to represent a 30% larger late Pleistocene form of *M. giganteus*. The only consistent difference between these species is in the superior size of the former. *M. titan* occurs in deposits of late Pleistocene age and older, typically in association with extinct megafaunal species of *Thylacoleo*, *Diprotodon*, *Sthenurus*, *Procoptodon*, and *Protemnodon*, to name just a few. *M. giganteus* is found in younger late Pleistocene deposits ($< 20{,}000$ yr B.P.) and never occurs in direct association with extinct megafaunal species or with *M. titan*. There is also no evidence of temporal overlap in the occurrence of these species. It thus appears most logical to regard *M. titan* as the larger late Pleistocene ancestor of *M. giganteus*. This lineage represents the fourth example of late-Pleistocene dwarfing in the fauna (see Discussion).

A large number of postcranials belonging to a large species of *Macropus* are represented in the Dry Creek collection. Except for the single questionable specimen referred to *M.* cf. *ferragus* from level III (P30716) (see below) there is no other evidence that this species is present in the fauna. For this reason the post-

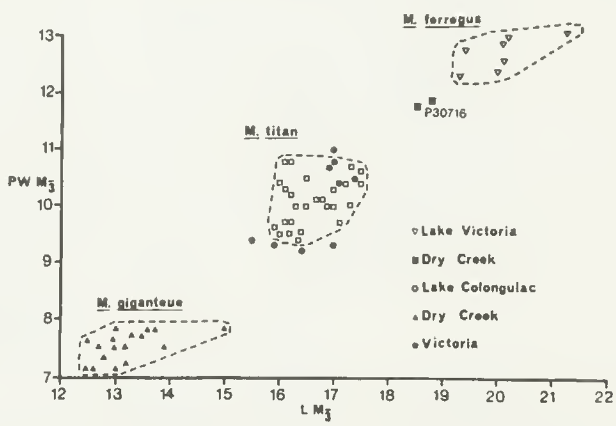

Fig. 9—Scatter diagram showing relationship of L M_3 and PW M_3 of a living sample of *Macropus giganteus* from Victoria, a fossil sample of *M. titan* from Lake Colongulac, Vict., a fossil sample of *M. ferragus* from Lake Victoria, N.S.W., and specimens referable to *M. titan* and *M.* cf. *ferragus* from Dry Creek.

cranials are assigned with relative certainty to *M. titan*.

Macropus cf. *ferragus* Owen, 1874

An associated left and right ramus (P30716) from level III may be referable to this species (Table 10). The Dry Creek specimen is compared in Fig. 9 with a sample of *M. ferragus* from Lake Victoria, N.S.W., *M. titan* from

TABLE 9

Dimensions of macropodid metatarsals and phalanges

Specimen	L	PB	PD	DB	DD
		Macropus titan			
Metatarsal IV					
P29533 (XI)	-	35.0	32.5	-	-
P29534 (IV)	177.0	29.8	26.3	29.5	21.8
P29535(IV)	178.0	30.6	27.5	31.0	23.2
P29556 (V)	198.0	40.4	32.4	39.2	26.8
P29558 (IV)	-	31.3	28.5	-	-
P29589 (VI)	207.0	39.0	28.0	39.6	28.3
P29591 (VI)	-	31.0a	26.0	-	-
P29633 (X)	-	33.0	27.8	-	-
Proximal Phalanx Digit IV					
P29518 (III)	29.7	29.5	25.2	26.5	17.0
P29560 (V)	-	-	-	20.1	13.1
Medial Phalanx Digit IV					
P29520 (III)	42.4	26.4	20.4	21.5a	13.0a
P29612 (VIII)	41.4	27.6	19.3	-	13.6
Metatarsal V					
P29557 (V)	156.0	14.8	18.4	18.6	18.7
P29605 (VII)	187.0	21.4	29.5	22.5	23.7
P29633 (X)	-	17.6	20.9	-	-
		Macropodid			
Proximal Phalanx Digit IV					
P29539 (IV)	38.3	18.4	13.7	14.6	10.3
Metatarsal IV					
P29618 (VIII)	80.0	13.6	12.0	13.1	10.0
P30722 (IV)	132.4	22.5	19.2	20.8	14.4
Metatarsal V					
P29544 (IV)	117.5	11.3	14.0	14.6	13.2
P29569 (V)	-	-	-	13.4	13.0
P29618 (VIII)	71.0	7.6	9.3	9.7	11.0
		Protemnodon sp.			
Metatarsal IV					
P29527 (III)	136.5	35.8	30.8	40.2	24.0
P29625 (IX)	118.0	-	31.2	-	-
P29632 (X)	-	37.0	32.5	-	-

Lake Colongulac, Vict., and an extant sample of *M. giganteus* from Victoria. In size of M_3, P30716 is closest to the *M. ferragus* sample, falls well outside the range of the *M. titan* sample and is considerably larger than *M. giganteus*. In addition to size, P30716 agrees best with the *M. ferragus* specimens in tooth morphology. As in *M. ferragus* there is a large pit on the posterior face of the hypolophid. The lower molars of specimens referable to *M. titan* typically have a small pit in this same area which is consistently present but never large or developed to the degreee found in *M. ferragus*. The possibility of P30716 representing a variant individual of *M. titan* is not dismissed. The problem of assigning P30716 to *M. titan* or *M. ferragus* with certainty reflects the close similarity in molar tooth morphology of these species. P30716 possibly represents the first reported occurrence of *M. ferragus* in Victoria.

TABLE 10

Dimensions of the cheek teeth of *Macropus* cf. *ferragus*

Specimen	M3		M4		
	L	PW	L	AW	PW
P30716 (III) (left)	18.8	11.9	18.7	12.4	10.6
P30716 (III) (right)	18.6	11.8	18.8	12.8	10.5

The type locality of *M. ferragus* is the late Pleistocene fluviatile deposits of the E. Darling Downs, SE. Qd. *Macropus gracilis*, also from the E. Darling Downs, is recognized as a junior synonym of *M. ferragus* (Tedford 1967). As in the Dry Creek Local Fauna *M. titan* is the most abundant macropod in the E. Darling Downs collections whereas *M. ferragus* is uncommon. Remains of *M. ferragus* are abundant at Lake Menindee (Tedford 1967) and Lake Victoria (Marshall 1973) in SW. N.S.W. At Lake Victoria *M. ferragus* is more abundant than *M. titan*. *M. ferragus* was predominately a savannah-grassland species and is the largest grazing species of macropod known.

TABLE 11

Dimensions of the cheek teeth of *Zygomaturus trilobus*

Specimen	P_3			M_1			M_2			M_3			M_4		
	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW	L	AW	PW
P29514 (I) (left)	19.9	15.0	17.0	30.0	23.0	24.3	-	-	-	-	-	33.1	-	-	-
P29514 (I) (right)	19.4	14.1	15.8	31.0	24.8	24.6	36.7	28.9	28.7	43.0	35.5	33.2	47.6	37.6	32.3
P29515 (II)	-	-	-	-	-	-	-	28.1	29.7	-	-	-	-	-	-

Family Diprotodontidae

Zygomaturus trilobus Macleay, 1857

A well preserved mandible (P29514) found in level I and an isolated M_2 (P29515) from level II, represent a minimum of two individuals (Table 11). Postcranials of a diprotodontid were found in levels VIII and XI (Table 12). There is no duplication among these elements suggesting that they may all have come from a single individual.

The podial elements were compared with those of *Diprotodon optatum* figured by Stirling and Zietz (1899), and it is evident that they are not referable to that species. They are probably referable to *Zygomaturus trilobus*, the only diprotodontid so far known with certainty from the fauna. Gill's (1967) record of *Diprotodon* remains in this fauna was based on these specimens.

TABLE 12

Dimensions of metatarsals of *Zygomaturus trilobus*

Specimen	L	PB	PD	DB	DD
P29619 (VIII)	90.0	37.0	41.0	39.5	32.9
P29620 (VIII)	90.5	28.3	45.2	30.8	33.6

2. Doutta Galla Silt (Maribyrnong Local Fauna)

Geology

Disconformably overlying the "D Clay" containing the Dry Creek Local Fauna at the Keilor Cranium Site is the Doutta Galla Silt. The Doutta Galla Silt consists of "basal gravels three to four feet thick (basalt, sandstone, quartz, and mudstone) passed up through two to three feet of medium to fine quartz sands to 20 feet of yellowish-brown to dark grey, very fine sands and silts which form the main body of the terrace" (Bowler 1970, p. 19). "Gill (1953a, 1957) has equated the sediments of the Braybrook terrace with those of the Keilor Terrace . . . The sediments of these terraces have been formally defined as the Doutta Galla Silt, for which the type locality is located at the Dry Creek section (Gill 1962)" (Bowler *ibid*, p. 18). The fauna from the Doutta Galla Silt from the Keilor Cranium Site, Braybrook, and Green Gully is collectively described here as the Maribyrnong Local Fauna (see Appendix 2).

Age

Bowler (1970, p. 43) noted that "deposition of the Keilor Terrace silts [began] at approximately 18,000 yr B.P. This situation is similar to that reported from the excavations of A. Gallus at the cranium site . . . The independent radiocarbon dates from other sites confirm the validity of the chronological sequence outlined above". An 18,000 yr B.P. date is accepted here as the basal age of the Doutta Galla Silt.

The Fauna

Six species of mammals are represented in the fauna: *Vombatus ursinus*, *Macropus giganteus*, *Megaleia rufa*, *Mastacomys fuscus*, *Pseudomys* cf. *gracilicaudatus*, and *Pseudomys* cf. *australis*, all represented by living populations. The fauna is modern in all respects.

Systematics Review

Family Vombatidae

Vombatus ursinus (Shaw, 1800)

Vombatus ursinus is represented by a single mandible (P30724). This species has been discussed above under the Dry Creek Local Fauna.

Family Macropodidae

Megaleia rufa (Desmarest, 1822)

This species is represented by a minimum of four individuals and is the most abundant species in the fauna (Table 13). The L M_3 and PW M_3 of the Dry Creek specimens are compared in Fig. 11 with an extant sample of *Megaleia rufa*, *Osphranter robustus*, and *Macropus giganteus*. In size, the Dry Creek specimen falls well within the range of the *M. rufa* sample.

On lower molars of *M. rufa* the posterior face of the hypolophid is plain and the entoconid is set more posteriad from the metaconid than the hypoconid is from the protoconid (Fig. 10). In *O. robustus* a faint diagonal groove is present on the posterior face of the hypolophid, whereas *M. giganteus* typically has a well developed (although usually small) vertical groove on the hypolophid which appears as a well defined pit on the occlusal surface in worn teeth. In both *O. robustus* and *M. giganteus* the hypolophid and protolophid are subparallel (Tedford 1967, pp. 113-114).

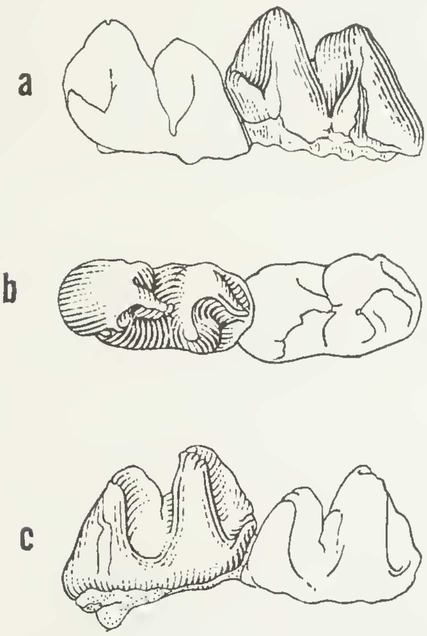

Fig. 10—*Megaleia rufa*, left M_{3-4}, NMV P30750a, Doutta Galla Silt; a, labial, b, occlusal, and c, lingual views; all x 1½.

Fossil remains of *M. rufa* have been recorded in Victoria from the outlet of Lake Gnapurt to Lake Corangamite. A C_{14} date of 4,550 ±120 (GaK-2518) yr B.P. was obtained from associated *Coxiella* shells (Gill 1971). There is also a specimen of *M. rufa* (P30216) from a bone bed on the E. shore of Lake Werranganuck. Gill (1971, p. 76) reports that a C_{14} date of 25,300±1,200 (GaK-986) yr B.P. was obtained on *Coxiella* shells from this bone bed making the *M. rufa* specimen (P30216) late Pleistocene in age and roughly equating this deposit with the "D Clay". P30216 is compared in Fig. 11 with an extant sample of *M. rufa* and specimens referable to *M. rufa* from the Maribyrnong Local Fauna. The larger size of the Lake Werranganuck specimen suggests that larger forms of *M. rufa* lived in late Pleistocene time. This species apparently underwent a late Pleistocene dimunition in body size similar to that occurring in the *Macropus titan-M. giganteus* lineage. Average individuals in living populations of *M. rufa* are about 25-30% smaller than individuals in the late Pleistocene, i.e. >20,000 yr B.P.

As a living species *M. rufa* has been recorded in Victoria from Benetook and Ned's Corner in the NW. corner of the State (Wakefield 1966, p. 632).

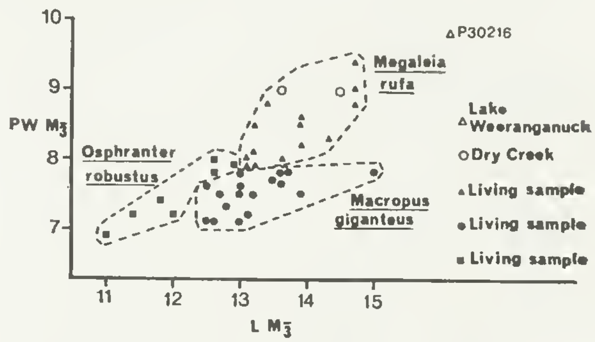

Fig. 11—Scatter diagram showing relationship of L M_3 and PW M_3 of living samples of *Megaleia rufa*, *Osphranter robustus*, and *Macropus giganteus*, a fossil sample of *Megaleia rufa* from the Doutta Galla Silt, and a fossil specimen of *M. rufa* from Lake Weeranganuck, W. Victoria.

Macropus giganteus (Shaw, 1790)

Two specimens represent a minimum of one individual of this species (Table 13). The relationship of *M. giganteus* to *M. titan* was discussed under the Dry Creek Local Fauna. The Keilor specimens of *M. giganteus* are indistinguishable in size and tooth morphology from extant specimens.

As a living species *M. giganteus* is abundant in sclerophyll forest, common in woodland and rare in plains habitat (Marlow 1958). That the species is presently found in such diverse habitats reduces its usefulness as an indicator of paleohabitats.

Order Rodentia

Family Muridae

Mastocomys fuscus Thomas, 1882

This species is represented by a single specimen (P30906) consisting of the greater part of a skull and associated fragment of the left ramus with M_{1-2} (Table 14).

Approximately 4% of the specimens of *M. fuscus* studied by Wakefield (1972) had supernumerary cusps on the lingual side of the upper molars. There is no trace of these cusps in P30906. P30906 is the specimen recorded by Gill (1955a,b) as *Rattus* cf. *assimilis.*

At lower altitudes on the Australian mainland this species lives in "wet sclerophyll forest with dense undergrowth containing ferns, shrubs, and grasses" (Ride 1970, p. 152).

TABLE 13

Dimensions of the lower cheek teeth of *Macropus giganteus* and *Megaleia rufa* from the Doutta Galla Silt

Specimen	DP_3			M_1			M_3		M_4		
	L	AW	PW	L	AW	PW	L	PW	L	AW	PW
Macropus giganteus											
P30750b	-	-	-	-	-	-	-	-	15.8	9.7	8.6
Megaleia rufa											
P30750a	-	-	-	-	-	-	13.6	9.0	-	-	-
P30730	-	-	-	-	-	-	14.5	9.0	-	-	-
P30751	9.0	4.7	5.7	11.2	6.5	6.9	-	-	-	-	-

TABLE 14

Cheek teeth dimensions of the rodents from the Doutta Galla Silt

Specimen	M1		M2		M3		M1-3
	L	MW	L	MW	L	MW	L
Upper cheek teeth							
Mastacomys fuscus							
P30906 (left)	3.8	3.2	2.6	3.1	2.9	2.4	9.9
P30906 (right)	3.8	3.3	2.6	3.1	2.9	2.4	9.8
Pseudomys cf. australis							
P15773 (left)	2.7	2.0	1.8	1.8	1.4	1.3	5.9
P15773 (right)	2.7	2.0	1.7	1.8	1.4	1.4	5.9
Lower cheek teeth							
Mastacomys fuscus							
P30906 (left)	3.9	2.8	2.6	2.7	-	-	-
Pseudomys cf. gracilicaudata							
P30907	2.3	1.7	1.8	1.7	1.3	1.2	5.5
P30908	2.5	1.7	1.9	1.7	-	-	-
Pseudomys cf. australis							
P15773 (left)	2.8	1.7	1.7	1.8	1.2	1.4	5.9

That this animal was considered to be extinct only four decades ago (Wood-Jones 1923-25) indicates that there is still much to be learned about its biology before palaeontologists can use it in palaeoecological considerations.

Pseudomys cf. *australis* Gray, 1832

and

Pseudomys cf. *gracilicaudatus* (Gould, 1845)

The genus *Pseudomys* is represented by three specimens, representing two species (Table 14). These have been identified by Mr. J. A. Mahoney as *Pseudomys* cf. *gracilicaudatus* (P30907, P30908) and *P.* cf. *australis* (P15773).

"Native cats"

Gill (1955a,b) reported the presence of "native cats" in the Doutta Galla Silt, but I have not been able to relocate the specimens upon which this was based. "Native cat" is the colloquial name generally applied to one of the four species of *Dasyurus* (*D. hallucatus*, *D. geoffroyi*, *D. maculatus*, *D. viverrinus*) which live today on the Australian mainland and Tasmania. *D. maculatus* and *D. viverrinus* occur in the Dry Creek area today and are abundant in Holocene and late Pleistocene deposits in S. Victoria. The presence of either or both of these species in the Maribyrnong Local Fauna would not be unexpected.

Discussion

The major reservation which must be immediately recognized in comparing the Dry Creek Local Fauna with the Maribyrnong Local Fauna is that the sample size from the latter is extremely small. For this reason larger sample sizes from the Doutta Galla Silt will surely result in expansion of the present study; the basic theme of late Pleistocene faunal succession as outlined below should, however, remain unchanged.

In the time interval between deposition of the "D Clay" and the Doutta Galla Silt two major faunal changes occurred: (1) many of the megafaunal species became extinct (i.e. *Thylacoleo carnifex*, *Protemnodon anak*, *P. brehus*, *Macropus ferragus* and *Zygomaturus trilobus*), and (2) some megafaunal species associated with the now extinct megafaunal species underwent a reduction in body size giving rise to smaller living forms. Some of these smaller living forms are presently recognized as distinct species (i.e. *Macropus giganteus* represents a smaller living form of *M. titan*; *Sarcophilus harrisii* represents a smaller living form of *S. laniarius*).

It is a well established fact that many living species of both carnivorous and herbivorous mammals are represented in late Pleistocene deposits by populations which are on the whole larger in absolute body size. This reduction in body size has been discussed by various workers under the heading of "post-Pleistocene dwarfing" and has been shown to occur on a world wide scale (Hooijer 1950, Kurten 1959, Wen-Chung 1963). Hooijer (1950) has referred to this dwarfing as "a sort of general evolutionary trend that is going on in the Quaternary". Kurten (1959, 1968 and references) has established the present of post-Pleistocene dwarfing in many European and Asian mammals with many of the lineages showing a 25-30% reduction in body size. As seen in the present study this dimunition in body size is not restricted to post-Pleistocene time but occurs also in the late Pleistocene. I have, therefore, used the term "late-Pleistocene dwarfing" throughout the text in reference to this phenomena in the Australian marsupials.

The presence of late-Pleistocene dwarfing has not been well established for Australian marsupials although I have found it to occur in a large number of species. These include the following species or lineages as the case may be (where the late Pleistocene forms are recognized as distinct species they are listed first): *Macropus titan-M. giganteus*, *Macropus siva-M. agilis* (probably), *Megaleia rufa*, *Osphranter cooperi-O. robustus*, *Wallabia vishnu-W. bicolor*, *Thylacinus cynocephalus*, *Sarcophilus laniarius- S. harrisii*, and possibly *Dasyurus maculatus*. *Macropus rufogriseus* has remained unchanged in size and tooth morphology from the late Pleistocene to the present. *M. rufogriseus* is also the smallest macropod species in the Dry Creek Local Fauna and it is interesting and probably significant that larger macropod species experienced either a late-Pleistocene dimunition in body size (probably in the lineage *M. siva-M. agilis* and definitely in the lineage *M. titan-M. giganteus*), while still larger body species became extinct (i.e. *Protemnodon anak*, *P. brehus*, *Macropus ferragus*). It would thus appear that the late-Pleistocene fate of a species was determined to a large extent by its absolute body size, as reflected in tooth dimensions.

The immediate problem arising from recognition of late-Pleistocene dwarfing is how to treat the populations of each species through time. Are the larger late Pleistocene forms specifically distinct, subspecifically distinct, or taxonomically indistinct from the smaller living forms? Some of the lineages show size differences of 5%, others 30%. Can all of these lineages be treated collectively or is it best to treat each lineage separately depending upon the amount of dwarfing involved? An attempt to answer these questions must be based on more extensive collections and larger sample sizes than those constituting the faunas described here.

Kurten (1959) considered the populations he studied which showed post-Pleistocene dwarfing to be distinct at the subspecific level. These species differed by a magnitude equal to the differences which occur in the Australian species. If Kurten's example is followed then such late Pleistocene species as *Macropus titan* would be regarded as subspecies of the living *M. giganteus* (i.e. *Macropus giganteus titan*). Such taxonomic changes are not proposed here although the option is made available for future studies.

The term megafauna as used in this study includes those large body sized species of mammal which occur in late Pleistocene deposits >20,000 yr B.P. As shown above, the megafauna is composed of two very distinct groups: (1) species now extinct, and (2) species which have undergone a late-Pleistocene dimunition in body size. It is thus necessary to indicate which of these groups is being considered when using the term megafauna; if no distinction is made it must be assumed that both groups are being considered collectively.

In late Pleistocene faunas >20,000 yr B.P. and represented by large sample sizes, both megafaunal groups occur together. There are no faunas to my knowledge which are composed of only one of these groups. Based on this evidence it may be induced that where extinct megafaunal species are found there will also be found larger forms of living species; where living species occur which are of their present size there will be no extinct megafaunal species found. I know of no exceptions to this generalization although it must be kept in mind that within the time interval between extinction of part of the megafauna and dwarfing of part of the megafauna these groups may not show complete overlap. Deposits showing this transition are presently unknown.

At Lake Menindee, N.S.W., a C_{14} date of 26,300 ± 1,500 yr B.P. was obtained on charcoal from an Aboriginal oven associated with the remains of the extinct macropod *Macropus ferragus* (Tedford 1967). At Lake Victoria, N.S.W., an 18,000 yr B.P. date is tentatively recognized as representing a possible terminal date for extinction of late Pleistocene megafaunal species (Marshall 1973). These studies complement the age and faunal composition of the Dry Creek and Maribyrnong Local Faunas respectively.

Thorne (1972) described the late Pleistocene fauna from Koonalda Cave, S.A., collected from red, water-laid deposits "which are approximately 20,000 yr B.P. old". All of the species present in the fauna are represented by living forms; no extinct megafaunal species or larger forms of living species are present. The fauna is modern in all respects. Thorne's study upholds the conclusions reached by Jones (1968, p. 203) that "where fauna is found in archaeological sites spanning the last 20,000 yr it is modern".

On the bases of these data it appears that extinction of late Pleistocene megafaunal species and attainment of a fauna of modern aspect occurred in the time interval between 20,000-25,000 yr B.P. In addition, it is concluded that late Pleistocene extinctions and late-Pleistocene dwarfing are correlative and that these phenomena may possibly have been caused by a common, cryptic, factor(s).

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Appendix 1

Dry Creek Local Fauna

Level

I. *Gravel layer 1, D excavation*
   (a) *Zygomaturus trilobus* P29514, mandible.

II. *X clay under L gravel*
   (a) *Zygomaturus trilobus* P29515, isolated M_2.
   (b) *Macropus titan* P29644, left ramus; P29531, right ramus with M_{3-4}.
   (c) macropodid P29516, fragment of right ramus of medium-sized macropod, with roots of M_{2-4}?; P29517, distal end of humerus of large macropod.

III. *D excavation, D clay*
   (a) *Perameles nasuta* P29634, associated right ramus fragment with P_1-M_3 and associated left maxillary fragment with M^{2-3}.
   (b) *Vombatus ursinus* P23026, mandible; P29519, fragment of right ramus.
   (c) *Protemnodon brehus* P29522, fragment of right maxillary with M^{2-4}.
   (d) *Protemnodon* sp. P29527, left metatarsal IV with proximal end of metatarsal III. and left tibia.
   (e) *Macropus titan* P29518, proximal phalanx digit IV; P29520, medial phalanx digit IV; P29521, fragment of right maxillary with M^{2-4}; P29523, right ramus; P29524, left ramus with M_{1-4}; P29525, right ramus with P_3, M_{1-4} (associated with P29524); P29526, tip of right lower incisor; P30904, right ramus; P30714, right ramus; P30719, proximal end of right metatarsal IV; P30720, proximal end of right metatarsal IV.
   (f) *Macropus* cf. *ferragus* P30716, left and right ramus.
   (g) macropodid P30718, distal end of metatarsal IV; P30721, proximal end of left metatarsal IV of medium-sized macropod.

IV. *A clay, level 4*
   (a) *Sarcophilus laniarius* P29547, shaft of left humerus.
   (b) *Vombatus ursinus* P29548, left ilium region of acetabulum.
   (c) *Macropus titan* P29534, left metatarsal IV; P29535, right metatarsal IV; P29537, left maxillary fragment with M^{1-2}; P29541, right astragalus; P29558, proximal end of right metatarsal III and IV; P30715, left ramus; P30726, calcaneum; P29560, proximal phalanx digit IV.
   (d) *Macropus agilis* P29549, left ramus; P29550, associated left and right rami; P29551, fragment of left ramus.
   (e) *Macropus rufogriseus* P30725, left ramus; P29577, right ramus.
   (f) macropodid P29532, distal end of right humerus; P29536, shaft of right humerus; P29539, proximal phalanx of digit IV; P29542, last thoracic or first lumbar vertebra; P29543, left ilium fragment; P29544, left metatarsal V; P29568, right

metatarsal V; P30722, left metatarsal IV; P29563, fragment of right scapula; P29566, fragment of right humerus; P29598, distal end of right femur.

V. *A clay, level 3*
(a) *Sarcophilus laniarius* P29631, right maxillary fragment with P^3-M^1.
(b) *Protemnodon anak* P29554, left ramus with P_3, M_{1-4}; P29555, right M_3.
(c) *Macropus titan* P29552, fragment of right ramus with M_4; P29553, left ramus with M_{3-4}; P29556, left metatarsal IV; P29557, left metatarsal V; P29564, right calcaneum.
(d) *Macropus agilis* P29575, left ramus; P29576, right ramus.
(e) *Macropus rufogriseus* P29578, right maxillary fragment with M^{2-4}.
(f) macropodid P29559, acetabular region of left innominate; P29561, left cuboid; P29562, right scapula fragment; P29567, caudal vertebrae; P29569, distal end of left metatarsal V; P29570, proximal end of right ulna; P29571, distal end of right humerus; P29572, right calcaneum; P29573, left acetabular portion of innominate; P30727, proximal end of left metatarsal IV; P30728, fragment of right innominate.

VI. *A clay, level 2*
(a) *Thylacinus cynocephalus* P29588, left humerus.
(b) *Sarcophilus laniarius* P29587, left maxillary fragment with M^{1-4}.
(c) *Protemnodon* sp. (probably *P. brehus*) P29586, isolated right lower incisor.
(d) *Macropus titan* P29580, left ramus; P29581, right and left ramus; P29582, isolated right M_3; P29583, left ramus; P29584, right ramus; P29589, right metatarsal IV; P29590, left metatarsal V; P29591, left metatarsal IV.
(e) *Macropus agilis* P29579, right P^3, M^{1-2}.
(f) *Marcoput rufogriseus* P29585, series of upper incisors.
(g) macropodid P29592, lumbar vertebra; P29593, vertebra; P29594, caudal vertebra; P29595, left acetabular portion of innominate; P29596, portion of right ilium; P29597, portion of right scapula.

VII. *A clay, level 1*
(a) *Macropus titan* P29600, left ramus; P29602, left ramus; P29605, left metatarsal V; P29606, right maxillary fragment; P29607, left calcaneum; P29608, associated left calcaneum and astragalus.
(b) *Macropus agilis* P29603, left ramus with M_4.
(c) *Macropus rufogriseus* P30905, left ramus.

VIII. *A clay, level 1a*
(a) diprotodontid (probably referable to *Zygomaturus trilobus*) P29619, right metatarsal V; P29620, right metatarsal IV; P29621, right cuboid; P29622, right ectocuneiform; P29623, right navicular.
(b) *Macropus titan* P29609, right ramus; P29610, isolated left M_4; P29611, associated fragments of upper dentition; P29612, medial phalanx of digit IV; P29613, associated left and right innominate.
(c) macropodid P29614, fragment of right scapula; P29615, fragment of right innominate; P29616, caudal vertebra; P29617, right innominate; P29618, right metatarsal IV and V (both large and small species of macropod are included in this group).

IX. *Excavation Y, various levels*
(a) *Protemnodon brehus* P29628, right ramus.
(b) *Protemnodon* sp. P29625, left metatarsal IV.
(c) *Macropus titan* P29624, right ramus; P29626, right maxillary fragment; P29627, left maxillary fragment; P29629, fragment of right tibia.
(d) In addition to the above there are fragments of a large pelvis, a medium-sized pelvis, a medial phalanx of digit IV, and several vertebrae of macropods. These were not catalogued because of their fragmentary condition.

X. *KA Excavation 1963*
(a) *Protemnodon* sp. P29632, right metatarsal IV.
(b) *Macropus titan* P29633, right metatarsal IV and V.
(c) macropodid (small species) P29630, isolated right lower incisor.

XI. *KAA, lowest level*
(a) *Thylacoleo carnifex* P29545, right maxillary fragment with lower edge of orbit, and anterior root of P^3.
(b) *Macropus titan* P29528, right ramus with M_{2-4}; P29529, left ramus with M_{2-3} broken, M_4 complete; P29530, left ramus with M_{3-4}; P29533, proximal end of right metatarsal IV; P29538, left maxillary fragment with M^{1-4}; P29540, right astragalus.
(c) diprotodontid (probably referable to *Zygomaturus trilobus*) P30723, right calcaneum.

KAA, middle level
(a) diprotodontid P29599, shaft of left humerus.
(b) *Macropus rufogriseus* P29574, right ramus.
(c) macropodid P29565, fragment of right humerus.

KAA, highest level
(a) *Protemnodon anak* P29604, associated left and right ramus.
(b) *Macropus titan* P29601, left ramus.

Appendix 2

Maribyrnong Local Fauna

(a) *Vombatus ursinus* P30724, mandible.
(b) *Megaleia rufa* P30730, left maxillary fragment with M^2?; P30749, two lower molar fragments. This specimen was collected as float from the soil quarry in Green Gully downstream from St. Albans Road, Keilor, Victoria. P30749 and

other bones were found washed out of a bulldozed slope in the Doutta Galla Silt where it abuts against the hillside at the southern end of the quarry (slope nearest shed). P30750a, upper molar and lower molar series (left) (M_{2-4}), and isolated left lower molar; P30751, associated with C_{14} date W169, Braybrook.

(c) *Macropus giganteus* P30752, left ramus with broken M_{2-4}; P30750b, isolated lower molar, probably M_4.

(d) *Mastacomys fuscus* P30906, partial skull with left and right M^{1-3}, associated left ramus fragment with M_{1-2}. This specimen was collected by Mr. H. E. Wilkinson, *in situ*, in the soil quarry in Green Gully, downstream from Keilor Terrace-St. Albans Road.

(e) *Pseudomys* cf. *P. australis* P15773, associated skull and postcranial fragments representing a single individual. This specimen was collected by Mr. E. D. Gill seven feet from surface and above diastema in east wall of Keilor cranium quarry.

(f) *Pseudomys* cf. *P. gracilicaudatus* P30907, left ramus with incisor, M_{1-3}; P30908, left ramus with incisor, M_{1-2}. These specimens were collected by Mr. H. E. Wilkinson 13 feet below the surface of high level terrace, in soil pit at mouth of Green Gully, Keilor.

Erratum: Fig. 9, . . . solid triangles represent extant sample of *Macropus giganteus* from Victoria, solid circles represent fossil sample of *Macropus titan* from Dry Creek (opposite as appears in the figure).