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STUDIES IN AUSTRALIAN MURIDAE: REVIEW OF *MASTACOMYS FUSCUS,* AND DESCRIPTION OF A NEW SUBSPECIES OF *PSEUDOMYS HIGGINSI*

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Abstract

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Data are presented of cranial and dental characters of series of *Mastacomys* from extant populations and from fossil deposits of Holocene and of late Pleistocene ages. It is considered that *Mastacomys* is a monotypic genus, that the species, *M. fuscus* Thomas, comprises two subspecies—*M. f. fuscus* of Tasmania and *M. f. mordicus* Thomas of the Australian mainland —and that *M. f. brazenori* Ride and *M. wombeyensis* Ride are synonyms of *M. f. mordicus*. *Pseudomys higginsi* (Trouessart) is recorded from the Australian mainland, from fossil material of late Pleistocene age. The Australian population is distinguished from the nominate Tasmanian race and is described as *P. higginsi australiensis*, a new subspecies. *P. h. australiensis* is compared with *P. oralis* (Thomas) and *P. australis* Gray.

Introduction

This paper is adapted from part of the taxonomic section of a document (Wakefield 1969) summarizing an investigation of mammal fossils from SE. Australian caves. Other sections of the document, dealing with palaeo-ecology and age of the fossils, have been incorporated in a separate paper (Wakefield, in press). Another part of the taxonomic section of the document, dealing with subspecific grouping of populations of *Rattus*, is currently being extended by further study.

Dimensions used in this paper, and their abbreviations, are as follows:

BL. Basal length of skull, from anterior margin of foramen magnum to anterior ends of premaxillae.

IC. Interorbital constriction: least width.

PL. Palatal length, along mid-line.

ZPH. Zygomatic plate height, from anteriormost alveolus of M^1 to junction of plate with zygomatic arch.

ZPL. Zygomatic plate length: Minimum antero-posterior length of plate.

FL. Foramen length: Mean length of incisive foramina.

FW. Foramen width: Maximum lateral extent of the two incisive foramina.

DL. Dentary length, from posterior end of condylar process to anterior end of dentary.

RD. Ramus depth: Minimum dorso-ventral depth of ramus in vicinity of M_3.

M^{1-3}L, M_{1-3}L. Antero-posterior length of upper and lower molar row, respectively, at alveolar level.

M^1W, M_1W. Maximum crown width of the tooth specified, irrespective of which cusps are involved.

I^1W, I_1W. Width of upper and lower incisor, respectively, at anterior edge of alveolus.

Measurements were made correct to 0·1 mm, using Helios dial calipers or cross-over vernier calipers.

Proportions such as ZPL/ZPH, I_1W/DL and RD/DL were computed, and these are expressed as percentages in this paper.

The Student's t test was used for most statistical comparisons, with probability values computed correct to the third decimal place. In some other cases the t test was applied, and less precise assessments of probability obtained. In certain cases involving small series, the Mann-Whitney U test was used, as in Siegel (1956).

The following abbreviations are used for institutions:

AM. Australian Museum, Sydney.

BM. British Museum (Natural History), London.

FM. Field Museum of Natural History, Chicago.

FWD. Fisheries and Wildlife Department, Melbourne.

QVM. Queen Victoria Museum, Launceston.

TM. Tasmanian Museum, Hobart.

WRD. Wildlife Research Division, CSIRO, Canberra.

The Pyramids Cave deposit referred to in this paper was an accumulation of bones of small animals, essentially the prey of owls, located four miles NNE. of Buchan, E. Vict. Material from the deposit was divided, according to texture and colour of the bones, into two fractions which are referred to as Holocene and Pleistocene respectively. Age of the Holocene fraction has not been assessed, and the Pleistocene fraction is considered to have accumulated mainly during the recession of the main Würm glaciation. (Wakefield, in press).

The bulk of the Pyramids Cave collection is to be placed in the National Museum of Victoria. Specimen numbers prefixed with P, in this paper, refer to registrations in the palaeontological department of that museum. The sources of other specimens are set out in Appendix 2 of this paper; locality data are provided in Appendix 3.

Delimitation of subspecies

Concerning subspecies taxonomy, the following principles have been observed in the present studies:

When the geographic range of a species is found to comprise major subdivisions, and the populations of these subdivisions are found to differ significantly from each other in one or more morphological features (at or beyond a probability level of 0·05), then each of these populations should be identified as a subspecies and recognized taxonomically by a distinguishing trinomen.

The geographic subdivisions should represent primary subdivisions of the gene pool of the species. Thus, as a taxon, subspecies should be meaningful biologically, and should have genetic, zoogeographic and evolutionary significance. Minor, or secondary, subdivisions of a species population should not be recognized as subspecies, because the significance of the primary subdivisions would then be obscured and the taxon become less meaningful biologically.

This subspecies concept is essentially that defined and discussed by Mayr (1969) except that, surprisingly, Mayr denies evolutionary significance of the taxon.

In these studies, it has not been accepted that populations which have attained a particular degree of morphological differentiation must necessarily be classified as different subspecies. This course is demanded by the gross dissimilarities in patterns and degrees of morphological divergence found in different species which have closely similar patterns of distribution and subdivision of population and therefore, presumably, analogous zoogeographic histories.

Problems inherent in the statistical approach to taxonomy are demonstrated by the following data concerning species of *Rattus* (Muridae) and *Antechinus* (Dasyuridae):

Horner and Taylor (1965) demonstrated by interbreeding experiment, that population groups, which on the evidence of general morphology had been classified as distinct species (Troughton 1941, Tate 1951), were in fact subspecies of the one species—*Rattus fuscipes.* Further, on the evidence of sympatric occurrence, they concluded that *R. lutreolus* was correctly classified as a species distinct from *R. fuscipes.*

Cranial and dental morphology of the three major population groups of *R. fuscipes* and of two groups of *R. lutreolus* have been compared, using 18 linear dimensions and 8 proportions. No character was found for which mean differences between specifically distinct populations were consistently greater than those between conspecific populations. The degree of difference, in cranial and dental morphology, between major population aggregates (i.e., subspecies) of *R. fuscipes*, was found to be of the same order as that between the nominate subspecies of *R. fuscipes* and the subspecies *velutinus* of *R. lutreolus.* (Wakefield 1969).

Unpublished data from an extension of this study of *Rattus* show that there are a number of small local populations of *R. fuscipes greyii* in the Central Division of S. Aust., which differ significantly from each other in cranial and dental morphology.

A different situation pertains with certain species of *Antechinus*.

A. minimus and *A. swainsonii* are distinguishable only on minor morphological characters, but sympatric occurrence demonstrates that these two are in fact distinct species (Wakefield and Warneke 1963). Likewise, *A. flavipes* and *A. stuartii* are specifically distinct though closely similar morphologically (Wakefield and Warneke 1967). Depending on morphology, Thomas (1888) and Troughton (1941) regarded *stuartii* and *flavipes* as conspecific. Finlayson (1958) did likewise and in addition named the S. Australian population of *A. minimus* as a subspecies of *A. swainsonii*.

The dental and cranial differences which distinguish *Antechinus swainsonii* from *A. minimus*, and *A. stuartii* from *A. flavipes*, are of the order of those which distinguish subspecies within *Rattus fuscipes* and *R. lutreolus*. The order of morphological divergence found between primary population subdivisions of *Antechinus flavipes, A. swainsonii* and *A. minimus*, is less than that found between adjacent local populations of *R. fuscipes greyii*. The application of an arbitary statistical subspecies formula to these species of *Rattus* and *Antechinus* would produce an artificial classification with very little biological significance.

While there may be little similarity between patterns of divergence in species of unrelated genera such as *Rattus* and *Antechinus*, degrees of morphological variation within species of the Muridae have been found to be generally similar (Wakefield 1969). Further analogy has been assumed within the Muridae in connection with interpretation of certain data in the present paper. In this connection, patterns within *Rattus fuscipes* are considered to be very relevant, in view of the biological relationships established by the work of Horner and Taylor (*loc. cit.*).

A. Review of *Mastacomys fuscus* Thomas

Materials and Method

The following specimens of *Mastacomys* are included in the study:

(a) SE. Aust. series. 34 skulls of modern museum specimens: 12 from Whites River, Kosciusko State Park, S. N.S.W.; 13 from Otway Ranges, W. central Vict., including holotype of *M. fuscus brazenori*; 5 from Loch Valley, E. central Vict.; 4 from other Victorian localities. (See Appendix 2).

(b) Tasm. series. 27 skulls of modern museum specimens: 11 from Waratah, 9 from Mt. Kate, 7 from other Tasmanian localities (See Appendix 2).

(c) Pleist. Pyramids series. 21 right maxillae and 57 right dentaries, each with complete molar row, selected from Pleistocene fraction of Pyramids Cave deposit. (P20674-751).

(d) Holocene Pyramids series. 67 cranial specimens each with right molar row and zygomatic plate, and 59 right dentaries each with molar row, selected from Holocene fraction of Pyramids Cave deposit. (P20752-877).

(e) Fern Cave series. 12 cranial specimens, and 12 right dentaries, from Fern Cave, near Portland, SW. Vict. (P20985-21008).

(f) Holotype of *M. wombeyensis* (AM, F47322).

(g) Holotype of *M. mordicus* (BM, 22. 10. 1. 3). The specimen was not seen but measurements were communicated by J. E. Hill (letter, 12 March 1965), and photographs were seen.

(h) Carrieton series (see Appendix 2).

Each series was sorted into subseries according to tooth-wear, using the system of Ride (1956):

Subseries A.	With distinct cusps on all molars.
Subseries B.	With wear beginning to unite cusps into laminae.
Subseries C.	With cusps united into transverse laminae but still discernible.
Subseries D.	With cusps no longer discernible.

General data of the series were determined by combining data of subseries B and subseries C in each case, thus eliminating all or most specimens of very immature animals and of aged animals. Such restricted data of the main series studied, and similarly restricted data of series from specific localities, are set out in Tables 1 and 2. Data of subseries A and B of certain of the main series are set out in Table 3.

This system of tooth-wear categories has been used in the present paper in connection with *Mastacomys* so that relevant comparisons could be made with data documented by Ride and others who adopted the system. However, in the series of *Mastacomys* which have been studied, tooth-wear is more advanced in certain small skulls than it is in certain larger and presumably older skulls. Moreover, tooth-wear is usually much more advanced on third molars than it is on first molars of the same specimen. In these circumstances degree of tooth-wear is not regarded as a wholly reliable key to age-grouping.

RESULTS AND DISCUSSION: It is assumed that the Tasm. series represents the *Mastacomys fuscus* of Thomas (1882) and thus the nominate race, *M. fuscus fuscus*. Compared with this series, the SE. Aust. series has these features:

Size (indicated by BL and DL) similar.

I^1W 10 percent greater, I_1W 13 percent greater, I_1W/DL greater (p= 0·003, 0·000, 0·000).

RD 3 percent greater, RD/DL greater (p = 0·022, 0·001).

Comparisons of the Tasm. series with the two Pyramids series, the Fern Cave series, and the Carrieton series, show that all the mainland Australian series which have been studied differ similarly from the Tasm. in having incisors 10-13 percent wider, ramus 3-5 percent deeper, and the proportions I_1W/DL and RD/DL greater. In all cases the differences are significant. Tasmanian specimens differ further from those of the mainland in having the posterior portions of the incisive foramina comparatively broad and obtuse (Plate 3, figs. 2-3).

Fig. 1 illustrates the relationship of I_1W and DL, in both the Tasmanian and the mainland Australian populations of *Mastacomys*.

Brazenor (1934) stated that tail length averaged 64 percent of head-body length in Tasmanian specimens. However, Green (1968) found that this proportion averaged 70·8 percent for 20 adult males and 72·0 percent for 17 adult females of the nominate Tasmanian race, and he observed that these figures were very similar to the 74 percent and 71 percent noted by Calaby and Wimbush (1964) for series from Loch Valley, Vict., and Whites River, N.S.W., respectively.

Significant differences occur between the two main local populations represented in the Tasm. series, and between two of the three main local populations of the SE. Aust. series, according to the data shown in Table 2.

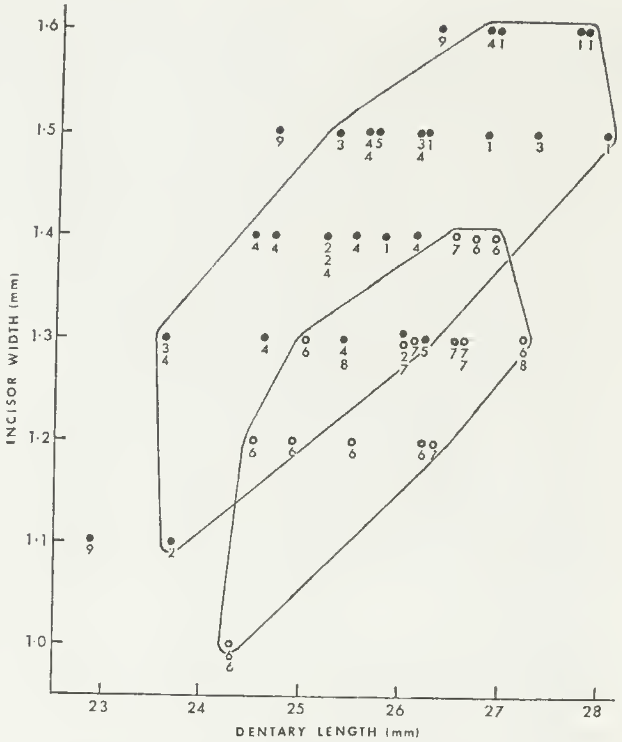

FIGURE 1

Relationship of I_1W and DL in subspecies of *Mastacomys fuscus*. The data apply to specimens of the restricted series, comprising tooth-wear categories B and C only.

● *M. f. mordicus* ○ *M. f. fuscus*

The boundary shown for *M. f. mordicus* applies to all modern and Holocene series studied. Points for the 59 specimens of the Holocene Pyramids series are not shown, but all would fall within the boundary.

Each plotted point shows dimensions of one or more specimens (as indicated by the number of figures beneath each plot). The figures refer to the source of each specimen, as follows:

1. Whites River
2. Otway Ranges
3. Loch Valley
4. Fern Cave
5. Other Vict. localities
6. Waratah
7. Mt. Kate
8. Other Tasm. localities

The figure 9 indicates dimensions of three exceptional specimens of the Pleistocene Pyramids series. The points for the other eight specimens of this series would fall within the boundary indicated for *M. f. mordicus*.

Compared with the Mt. Kate series, the Waratah series differs as follows:

ZPL 10 percent less, and ZPL/ZPH less.

FW 8 percent greater but FL 7 percent less, so FW/FL greater.

RD/DL greater.
($0{\cdot}01 < p < 0{\cdot}05$, in each case).

Compared with the Otway Ranges series, the Whites River series has the incisors broader by 12-18 percent, dentaries longer by 8 percent, and the proportion I_1W/DL greater ($0{\cdot}01 < p < 0{\cdot}05$, in each case).

Some of the above differences observed between local populations may be due to age bias in these small samples. (See tooth-wear groupings in Appendix 2). In any case, these differences are of the same order as those found between local populations of *Rattus greyii* (See comments in Introduction).

Compared with data of the composite SE. Aust. series (Table 1), the $M^{1-3}L$ is 3 percent less in the Holocene Pyramids series and 5 percent less in the Pleist. Pyramids series ($p = 0{\cdot}014$, $0{\cdot}002$). Except for the differences in molar sizes, means of the dimension and proportions for each of the Pyramids series are very similar to those of the SE. Aust. series.

The Fern Cave series differs significantly from the SE. Aust. series only in the shorter incisive foramina and the proportion FW/FL. It does not differ significantly in any observed character from either of the Pyramids series.

The holotype of *M. mordicus* is a maxilla with molar row, originating from the Mount Gambier area, S. Aust. Thomas (1922) designated it a distinct species on the evidence of the very short crown length of the molar row and the small zygomatic plate. The specimen belongs to tooth-wear category A, and the supposed diagnostic characters are due to its immaturity.

The geological age of the *mordicus* holotype is not known, but it is most likely to have originated from a Holocene deposit. There are numerous Holocene deposits, in which *Mastacomys* is represented, about the lower Glenelg River in the Mount Gambier area (Wakefield, unpublished data), and the Fern Cave deposit (Wakefield 1963) is typical of these.

In the holotype of *mordicus*, $M^{1-3}L$ (alveolar) is 9·0 mm, which is not significantly different from the mean for any of the series discussed above. With ZPL 3·1, ZPH 5·6, and ZPL/ZPH 55·4, the holotype of *mordicus* is comparable with a similarly immature specimen (NMV, C5539) from the Otway Ranges, Vict., which has ZPL 3·3, ZPH 5·9, and ZPL/ZPH 55·9. Moreover, the 55·4 of the holotype is identical with the mean ZPL/ZPH for subseries A of the Holocene Pyramids series, and very close to the means for subseries A of the Tasm., SE. Aust. and Pleist. Pyramids series (Table 3).

The evidence which has been outlined indicates that the extant SE. Australian population of *Mastacomys fuscus*, and the populations represented by the Fern Cave series, the Holocene Pyramids series, and the Pleist. Pyramids series, collectively represent a subspecies distinct from the Tasmanian *M. fuscus fuscus*. As pointed out by Troughton (1941), the valid name for this mainland subspecies is *M. fuscus mordicus*. Geographically, the holotype of *mordicus* belongs to the mainland subdivision of the species, and morphologically it is not separable from the mainland series which have been studied.

Ride (1956) suggested that 'the name *M. fuscus mordicus* should be restricted to the ?Pleistocene S. Australian populations of *M. fuscus*', and he proposed the name *M. fuscus brazenori* for the extant mainland population, depending on the supposed difference in tail length to distinguish it from the nominate race. The holotype of *brazenori* (NMV, C199, Beech Forest, Otway Ranges, Vict.) is a badly broken specimen, but details available ($M^{1-3}L$ 9·6 mm, ZPH 8·9 mm, ZPL 4·4 mm, $M_{1-3}L$ 8·7 mm, ZPL/ZPH 49·4) distinguish it in no way from the extant mainland race (Table 1). With the application of the name *M. fuscus mordicus* to this race, the name *brazenori* becomes a subjective synonym of *mordicus*.

Tate (1951) treated the Carrieton specimens as topotypical of *M. mordicus*, but as pointed out by Ride (1956), this is not so. Carrieton is 610 km. from Mt. Gambier, and *Mastacomys* has not been recorded between these two localities.

In depth of ramus and width of incisors, as well as in the proportions examined, the Carrieton series is not separable from the SE. Aust. series. Mean lengths of molar rows are 6 percent less in the Carrieton series than in the SE. Aust. series (significantly, with $p = 0{\cdot}000$, 0·012). The smaller tooth-size probably represents the lower limit of a clinal gradient occurring when wetter climatic conditions provided tolerable habitat for *Mastacomys* as far inland as Carrieton. On present evidence, the Carrieton series is included in *M. fuscus mordicus*.

The holotype of *M. wombeyensis* is a maxilla with molar row. In describing the specimen, Ride (1956) assessed the tooth-wear in his category B. The M^{1-3}L (8·9 mm) is smaller by 5-9 percent than the means for the series of *M. fuscus* under review (Table 1), but in no case is the difference significant ($0\cdot17 > p > 0\cdot05$, in each case). Minimum observed values of M^{1-3}L are 8·6 mm for P20788 of the Holocene Pyramids series, 8·7 mm for NMV no. C200 of the Tasm. series, and 8·8 mm for P20675 and P20689 of the Pleist. Pyramids series.

The ZPH of the holotype of *wombeyensis* (8·3 mm) is close to the mean for each of the series studied (Table 1). However, the ZPL (5·0 mm) is 15-23 percent greater than means of ZPL for those series, though the difference is in no case significant ($0\cdot12 > p > 0\cdot05$, in each case). The 5·0 is 19-27 percent greater than the means for the subseries B of those series (see Table 3), the differences being barely significant for the comparisons with the Tasm. and the Holocene Pyramids series ($p = 0\cdot045, 0\cdot040$) and not significant for the comparisons with the SE. Aust. and the Pleistocene Pyramids series ($p = 0\cdot08, 0\cdot12$).

The proportion ZPL/ZPH (60·2) in the *wombeyensis* holotype is greater than the mean for each of the principal series studied (Table 1), not significantly in the case of the Pleist. Pyramids series, the SE. Aust. series or the Tasm. series ($p = 0\cdot168, 0\cdot079, 0\cdot111$), and barely significantly in the cases of the Holocene Pyramids and Carrieton series ($p = 0\cdot036, 0\cdot047$). The 60·2 is not significantly greater than the mean for subseries B of any of these series (Table 3), all probability values lying between 0·1 and 0·3. High individual values for this proportion occur as follows: 60·5 for P20708 in subseries C of the Pleist. Pyramids series, 60·9 for a specimen in subseries A of the Carrieton series, 62·5 for P20761 in subseries A of the Holocene Pyramids series, and 63·6 for QVM 1963.1.306 in subseries B of the Tasm. series.

The holotype of *wombeyensis* possesses 'a small additional cusp on the third molar, internal to and lying between the innermost cusp of the last two rows' (Ride 1956). An additional cusp occurs in the same position in QVM 1963.1.262 of the Tasm. series (on left M^3 only), in FWD R2954 (on right M^3 only) and NMV C134 (on both M^3s) of the SE. Aust. series, and in P20778 (right maxillary piece) of the Holocene Pyramids series (Pl. 3, fig. 1). Additional cusps of similar size occur in other positions on various molars, in some specimens on each of two opposite teeth but in other specimens on one tooth only. For example, the additional cusp on M^1, as illustrated in Pl. 3, fig. 2, occurs occasionally in *M. fuscus fuscus* and in *M. fuscus mordicus*, and an additional cusp on the mid-posterior of M^3 has been observed in several specimens of *M. f. mordicus* but not in *M. f. fuscus*.

On the average, additional cusps have been found in approximately 4 percent of the specimens of each of the larger samples of *Mastacomys* which have been studied. Some are distinct and functional, with the apex worn, while others are merely small non-functional lobes fused to the side of a normal cusp. The occurrence of such additional cusps appears to be due to comparatively uncommon alleles distributed widely amongst the various major populations, and they thus appear to be of no taxonomic significance.

Schram and Turnbull (1970) provide data of two further cranial specimens of *Mastacomys* obtained from the Wombeyan Caves bone breccia. The following details are included:

FM, PM5861—M^{1-3}, alveolar length, 9·3 mm; M^1W 3·2 mm.

AM, F52303—M^{1-3}, alveolar length, 8·3 mm; M^1W 2·8 mm; ZPL 4·1 and 4·2 mm; IC 3·4 mm; PL 16·2 mm.

The two measurements for PM5861 are not significantly different from means for the various series studied (Tables 1-3).

Schram and Turnbull placed F52303 in tooth-wear category B, but their photograph of it shows very little tooth-wear and indicates a much younger state than that of the holotype of *wombeyensis*. The measurements given for F52303 may be compared with data of subseries A and B in Table 3. The teeth measurements, IC and PL, of F52303, are significantly less than means observed for the respective features in the subseries tabulated, but ZPL is greater than the observed means in all but one case. This indicates that, as in the holotype of *wombeyensis*, the ZPL in F52303 is proportionately great.

F52303 and PM5861 each has the additional cusp on M^3, as in the holotype of *wombeyensis*. In F52303 it is of medium development on the right M^3 and is less developed on the left, and in PM5861 it is partially fused to the hypocone on the one M^3 present (Schram and Turnbull Pl. 1).

The three Wombeyan specimens of *Mastacomys* appear to represent a population with comparatively small teeth, proportionately long zygomatic plate, and a comparatively high incidence of the additional cusp on M^3. Ride (1960) considered the Wombeyan deposit to be essentially an owl pellet accumulation, and he suggested 'an age somewhat later that the last pluvial period of the Pleistocene'. Subsequent work (Wakefield, in press) supports both contentions and indicates that all components of the Wombeyan faunal assemblage are identifiable with modern species.

The diagnostic characters of *M. fuscus mordicus*, being present in the Pleist. Pyramids series, were established at least as long ago as the main Würm glaciation. As certain forest species such as *Petaurus breviceps* and *Rattus fuscipes* were plentiful in the Pleistocene fraction of the Pyramids Cave deposit (Wakefield, in press) but are not indigenous in Tasmania, conditions on the Bass Strait land bridge during the main Würm glaciation evidently did not favour the crossing of it by forest animals, so it is highly unlikely that there was intercommunication at that time between Tasmanian and Australian mainland populations of *Mastacomys fuscus*.

Whilst the Pleist. Pyramids and the Carrieton series differ little from the Holocene and modern *M. fuscus mordicus*, there is suggestion of greater differentiation in the case of the Wombeyan group. Even if confirmed by study of further specimens, such differentiation is what might be expected within a primary population subdivision of a murid species. Therefore, on present knowledge, the Wombeyan *Mastacomys* cannot justifiably be classified other than in *M. fuscus mordicus*.

In summary, this study indicates the following taxonomy of *Mastacomys fuscus:*

(a) **Mastacomys fuscus fuscus**

(*Mastacomys fuscus* Thomas, 1882; Tasmania)
Tasmania. Holocene.

(b) **Mastacomys fuscus mordicus**

(*Mastacomys mordicus* Thomas, 1922; Mt. Gambier district, S. Aust.; subfossil).
Central and E. Vict., SE. N.S.W. (subfossil or fossil in SE. Aust., SW. Vict., E. N.S.W.). Pleistocene to Holocene. Subjective synonyms: *Mastacomys wombeyensis* Ride, 1956; Wombeyan Caves, E. N.S.W.; fossil. *Mastacomys fuscus brazenori* Ride, 1956; Beech Forest, W. central Victoria.

B. *Pseudomys higginsi australiensis*, **new subspecies**

Diagnosis

A population of *Pseudomys*, presumably extinct, represented by fragmentary subfossil specimens of late Pleistocene age, from Pyramids Cave (lat. 37°27′, long. 148°13′) near Buchan, E. Vict., identified at species level as *P. higginsi* (Trouessart) and distinguished from the nominate Tasmanian race by smaller mean tooth-size and the zygomatic plate generally of less height and greater length.

Holotype

NMV, P20903—a right maxilla with M^{1-3} (Pl. 3, fig. 9).

M^{1-3}L 6·0 mm, M^1W 2·0 mm, ZPH 7·0 mm, ZPL 3·7 mm.

The M^1 has a small auxiliary cusp anterior to the anterolingual conule, and a very slight anteromedian cingular ridge.

Upper anterior edge of zygomatic plate is pointed; posterior end of incisive foramen is level with middle of anteriormost root of M^1.

Paratypes

P20878-902, P20904-13—right maxillary specimens with teeth; used, together with holotype, for measurement and estimation of population parameters.

P20914—edentulous right maxilla with alveoli of molars.

P20915—incomplete right dentary with incisor, M^{1-2}, and the coronoid process entire.

P20916-83—right dentary specimens, used for measurement and estimation of population parameters.

P20984—incomplete right dentary, with condylar and angular processes entire.

General data

The holotype and paratypes were selected from 230 maxillary and 330 dentary specimens of the subspecies, found in the Pleistocene fraction of the Pyramids Cave deposit. Series of these specimens were identified originally (Wakefield 1960) as *'Pseudomys oralis'*, and later (Wakefield 1967) as *'Pseudomys* sp.'.

Data of the 36 maxillary specimens (P20878-913) and the 68 dentary specimens (P20916-83), which were used for measurement and estimation of parameters, are set out in Table 4. This series constitutes all available right-hand specimens in which the three molars were present. Such specimens are mature in dentition, all molars being fully developed in both crown and roots. (In immature specimens the M^3, and often the M^2 also, become detached owing to incomplete formation of their roots).

Photographs of the holotype and of five of the paratypes comprise figs. 7-12 of Pl. 3.

In the Pyramids Cave deposit, *P. higginsi australiensis* was associated with wet forest species such as *Burramys parvus, Gymnobelideus leadbeateri* and *Schoinobates volans*. It was absent from the dry sclerophyll forest and woodlands faunal assemblage of the Holocene fraction of the deposit. Its habitat tolerance appears to have been limited to wet forests of the kind which occur today in E. central Victoria where mean annual rainfall is 100 cm or more (Wakefield, in press).

P. higginsi australiensis has not been found in any Holocene fossil deposit. Evidently it became extinct several thousand years ago.

Comparison with P. higginsi higginsi

A series of 49 skulls of *Pseudomys higginsi* from Tasm. (Appendix 2) was taken to represent the nominate race. Only mature specimens (with BL > 27 mm) were included. Data of this series are set out in Table 4. Compared with those of this series, means for *P. higginsi australiensis* differ as follows:

M^{1-3}L 8 percent greater, M^1W 12 percent greater, M_{1-3}L 8 percent greater, M_1W 8 percent greater ($p = 0{\cdot}000$ in each case).

ZPH 5 percent less and ZPL 12 percent greater, so ZPL/ZPH much greater ($p = 0{\cdot}000$ in each case).

Mean ZPL/ZPH is 45·9 for the *P. higginsi higginsi* series, and 53·4 for the *P. higginsi australiensis* series; but this divergence does not deny conspecificity. Greater divergence is observed with this proportion in *Rattus fuscipes:* 53·5 for a series of *R. f.greyii* from SW. Vict., and 61·7 for a series of *R. f. assimilis* from the Pleistocene fraction of the Pyramids Cave deposit (Wakefield 1969).

Mean DL is the same for each series of *P. higginsi*, indicating closely similar skull size for each population. In both series the coronoid process is well developed (fig. 10), the upper anterior edge of the zygomatic plate is pointed (figs. 6, 8-9), and the posterior ends of the incisive foramina are level, on the average, with the middle of the anteriormost root of the M^1 (figs. 5-9).

Occasionally in *P. higginsi higginsi*, the M^1 has a well developed low cusp or cingular ridge extending from the anterior face of the anterolingual conule to the anteromedian end of the tooth; for example, in TM nos. 0191 and 0816. Such well developed cusp or ridge was not observed in any of the Pyramids series of *P. higginsi australiensis*, though four of the paratypes (P20879, P20883, P20893, P20908) show what appears to be a modification of the feature in the form of a small auxiliary cusp anterior to the anterolingual conule, and the holotype (P20903) has both the auxiliary cusp and a slight cingular ridge.

All known occurrences of *P. higginsi higginsi* have been in or near rainforest, in areas with mean annual rainfall from about 125 to over 250 cm. (Green 1968). This habitat is generally similar to that which *P. higginsi australiensis* is believed to have occupied.

Comparison with P. oralis

To represent the Pyramids Cave *Pseudomys oralis*, 97 cranial specimens (P21009-21105) and 84 dentary specimens (P21106-21189) were selected. The selection was limited to those having the right-side molar row complete. Data of the series are summarized in Table 4. In this series the means of DL, $M^{1-3}L$ and $M_{1-3}L$ are each approximately 10 percent greater, and mean I_1W 26 percent greater, than in *P. higginsi australiensis*.

P. oralis is absolutely distinguished from *P. higginsi* by the rounded upper anterior edge of the zygomatic plate, and the much smaller (obsolete) coronoid process. It is distinguished further by the lesser posterior extent of the incisive foramina, the ends of which are, on the average, level with the anterior edge of the anteriormost root of M^1.

P. oralis occurred in the Holocene fraction of the Pyramids Cave deposit and was absent from the Pleistocene fraction, so it and *P. higginsi australiensis* were not associated in either faunal assemblage.

Comparison with P. australis

Two series of *Pseudomys australis* were used:

(a) A series of 21 specimens (P21190-21210) from Fern Cave, SW. Vict., comprising 12 right-side maxillary pieces each with complete molar row and zygomatic plate, and nine right-side dentary specimens each with complete molar row.

(b) A series of six cranial specimens from central Australian localities (Appendix 2).

In comparison with these series of *P. australis*, the *P. higginsi australiensis* series differs as follows:

Size, as evidenced by DL, ZPH and lengths of molar rows, is approximately 6 per cent less than for the Fern Cave series and 8 percent greater than for the central Australian series.

ZPL/ZPH is greater than in either series of *P. australis* ($p. < 0.001$ in each case).

No anteromedial cingular ridge has been observed on M^1 in any specimen of *P. australis*, though occasionally there is a small auxiliary cusp anterior to the anteromedian style.

The incisive foramina do not extend as far posteriorly as in either series of *P. australis*. This is the key morphological feature upon which the identification of the Pyramids Cave series as *P. higginsi*, rather than as *P. australis*, depends.

This identification is supported by the fact that *P. australis* is a species of habitats much drier than that of the faunal assemblage in which the Pyramids Cave population, now identified as *P. higginsi australiensis*, occurred. See Appendix 1 for relevant details of morphology and habitat of *P. australis*.

Occurrence at Wombeyan Caves

Ride (1960) reported a small series of *Pseudomys oralis* from bone breccia obtained at Wombeyan Caves, E. N.S.W. Three of these specimens were examined during the present study. One (Ride's B 58/6), with $M^{1-3}L$ and M^1W 7·4 and 2·3 mm respectively, and a second (B 58/C), with M_1W 1·8 mm, are correctly identified as *P. oralis*. The third (B8/g) is a dentary with teeth dimensions ($M_{1-3}L$ 6·0 mm, M_1W 1·7 mm, and I_1W 0·8 mm) and other features typical of *P. higginsi australiensis*.

Schram and Turnbull (1970) identified as *P. oralis* a series of specimens which they extracted from Wombeyan Caves breccia. The mean which they report for M^1W (2·10 mm), and the presence of 'a clearly defined antero-medial style' on the M^1 of some specimens, indicates that at least part of this series is *P. higginsi* rather than *P. oralis*.

The faunal assemblage represented in the Wombeyan Caves breccia includes *Burramys parvus, Gymnobelideus leadbeateri* and *Schoinobates volans*; it was a wet forest fauna very similar to, and most probably contemporaneous with, the fauna represented in the Pleistocene fraction of the Pyramids Cave deposit (Wakefield 1969). Therefore it must be expected that the Wombeyan specimens which are similar to *P. higginsi* are in fact this species rather than *P. australis*. Furthermore, as Wombeyan Caves and the Pyramid Cave are both in the highland region of SE. Aust., it must be expected that the specimens in question should be *P. higginsi australiensis*.

Addendum

While this paper was in press, *Mastacomys* and *Pseudomys* material was examined from a cave deposit ('Wombeyan Quarry') located approximately 1·6 km. W. of Broom's Wombeyan Caves site and at the same elevation. The deposit includes remains of extinct animals such as *Sthenurus* and *Thylacoleo*, indicating that it is of Pleistocene origin. Absence of arboreal mammals suggests that the vegetation was montane shrubbery associated with colder climatic conditions than at present. Remains of *Burramys* were present.

The specimens examined include 20 left maxillae and 20 incomplete left dentaries of *Mastacomys*, and four maxillae (two left, two right) of *Pseudomys* cf. *higginsi*. This material has not yet been allocated to a museum but is part of a collection being studied by Dr Jeannette Hope, Department of Prehistory, Australian National University. I am indebted to Dr Hope for the loan of the murid specimens and for information about the quarry site.

Of the *Mastacomys* maxillae, two were of tooth-wear category B and 15 of category C, and of the dentaries, six were of category B and 13 of category C. Data of these specimens are as follows, the three figures in each case being number of observations, mean value, and standard deviation:

$M^{1-3}L$—17, 9·45 mm, 0·23
ZPH—17, 8·06 mm, 0·56
ZPL—16, 4·48 mm, 0·33
ZPL/ZPH—16, 56·0 percent, 4·18
I_1W—16, 1·38 mm, 0·09
RD—19, 6·44 mm, 0·18

Of the 20 *Mastacomys* maxillae, the small auxiliary cusp of *M. wombeyensis* was present in two specimens and absent in 16. Teeth in the other two specimens were too worn for the occurrence of the cusp to be assessed. These details, in a series of late Pleistocene *Mastacomys* from the Wombeyan area, tend to confirm the suggestion in this paper that presence of the auxiliary cusp is not of taxonomic significance.

Mean incisor width in the Wombeyan Quarry *Mastacomys* is 10 percent greater than in the Tasmanian *M. fuscus fuscus* (significantly with $p < 0·02$) but not significantly different from means for the mainland Australian *M. f. mordicus* (Table 1). In size (as evidenced by $M^{1-3}L$, ZPH and RD) the Wombeyan Quarry *Mastacomys* is essentially similar to the other major series studied. These details lead to the identification of the Wombeyan Quarry series as *M. fuscus mordicus*, and this supports the same identification for the Wombeyan Caves specimens otherwise classified as *Mastacomys wombeyensis*.

Mean ZPL/ZPH is significantly greater for the Wombeyan Quarry series than for the SE. Australian series and the Holocene Pyramids series ($p < 0·001$ in each case), but is closely similar to that of the Pleistocene Pyramids series. This supports the suggestion that the Wombeyan *Mastacomys fuscus* had a proportionately long zygomatic plate, and the similar character of the older Pyramids series suggests that the long zygomatic plate may have been general in late Pleistocene populations of the species in SE. Australia.

Data of the series of *Pseudomys* cf. *higginsi* (giving number, mean and standard deviation) are:

$M^{1-3}L$—4, 5·95 mm, 0·18
ZPH—4, 6·24 mm, 0·16
ZPL—3, 3·30 mm, 0·10
ZPL/ZPH—3, 52·5 percent, 1·87

The posterior end of the incisive foramen is level with the anterior edge of the anteriormost root of the M^1 in two of the specimens, and with the middle of the same root in the other two. This distinguishes these specimens from *P. australis*. The distinction is supported by the evidence indicating that the Wombeyan Quarry fauna belonged to a cold montane habitat.

The upper anterior edge of the zygomatic plate is pointed in the two specimens which have this feature unbroken. This, together with the linear dimensions, distinguishes the series from *P. oralis* (Table 4).

The proportion ZPL/ZPH in the Wombeyan Quarry sample is significantly greater than in the Tasmanian *P. higginsi higginsi* ($p < 0·02$) but is closely similar to that of the Pleistocene Pyramids series.

The foregoing details indicate that the Wombeyan Quarry *Pseudomys* is taxonomically the same as the *P. higginsi australiensis* of the Pleistocene fraction of the Pyramids Cave deposit.

APPENDIX 1: Data of *Pseudomys australis*

Incisive foramina

Thomas (1921) included the following comment in his original description of *Pseudomys australis oralis* (now *Pseudomys oralis*):

'Palatal foramina proportionately shorter, not or scarcely penetrating between the molars, while in *australis* they reach to the level of the middle of m^1'.

Proportionately long and narrow incisive foramina comprise a diagnostic character which distinguishes *P. australis* from other species, including *P. higginsi*. For example, the central Australian series of *P. australis* (see Appendix 1) and the Tasmanian series of *P. higginsi* (see Appendix 1) compare as follows:

In *P. australis*, mean FL/BL is 24·9 percent ($n = 5$, $SD = 0{\cdot}6$), and mean FW/FL is 23·3 percent ($n = 6$, $SD = 2{\cdot}0$).

In *P. higginsi*, mean FL/BL is 23·5 percent ($n = 47$, $SD = 1{\cdot}1$), and mean FW/FL is 28·4 percent ($n = 49$, $SD = 3{\cdot}0$).

In these proportions, the differences between the two series are highly significant, with $p = 0{\cdot}008$ in the case of FL/BL and 0·000 in the case of FW/FL.

The greater proportionate length of the foramina of *P. australis* results in their extending farther posteriorly than in *P. higginsi*. In *P. australis*, the posterior end of each foramen is level, on the average, with the anterior edge of the middle (internal) root of the adjacent M^1. This feature is diagnostic in maxillary specimens, such as those in the Fern Cave series of *P. australis*, in which the foramina are incomplete.

Habitat

Data on the habitat of *Pseudomys australis* are noted by Gould (1863) as follows:

Under the synonym *Hapalotis murinus* (Gould's Pl. 7)—'Plains bordering Namoi and Gwydir', NE. N.S.W., and 'on edge of dry salt water lagoon of Plains' near Lake Albert, S. Aust.

Under the synonym *Mus lineolatus* (Gould's Pl. 18)—Darling Downs, SE. Qd., on 'all open parts of the grassy plains'.

Further distributional and habitat data of *P. australis* are provided by Troughton (1941), under the synonym *Pseudomys minnie*. These include the occurrence at Minnie Downs, NE. S. Aust., and 'on well-timbered sand ridges', 220 km. S. of Longreach, Qd.

P. australis has been recorded (in some cases under the synonym *Pseudomys auratus*) from several Holocene subfossil deposits in W. Vict. (Wakefield 1964). In one case (at Mount Hamilton) some of the remains appeared to be quite modern, but in all other cases the specimens were of unknown age.

The foregoing data indicate that *P. australis* was an animal of comparatively dry habitats, in which the range of mean annual rainfall was from 15 cm. (at Minnie Downs) to 60 or 75 cm. (in SE. Qd. and W. Vict.).

P. australis did not occur either in the dry forest and woodland faunal assemblage of the Holocene fraction of the Pyramids Cave deposit (Wakefield 1967) or in other Holocene deposits in the same district (Wakefield 1960). The habitat data of *P. australis*, together with the fact that *P. higginsi australiensis* also was absent from the Holocene fraction of the Pyramids Cave deposit, demonstrate that these two *Pseudomys* were separated by a habitat tolerance gap of substantial width.

APPENDIX 2: Data of series of *Mustacomys* and *Pseudomys*

Mastacomys fuscus

Whites River, Kosciusko Park, SE. N.S.W.

Subseries A—WRD: CM408, CM595, CM-608.

Subseries B—WRD: CM405-6, CM409, CM411.

Subseries C—WRD: CM402, CM404, CM-607. AM: M7170.

Subseries D—WRD: CM622.

Otway Ranges, SW. Vict.

Subseries A—NMV: C849-50, C903 (Beech Forest); C5539 (Lavers Hill).

Subseries B—NMV: C848, C893, C896, C900 (Beech Forest); C5540 (Lavers Hill).
Subseries C—NMV: C199 (Beech Forest).
Subseries D—NMV: C842, C902 (Beech Forest); C5541 (Lavers Hill).

Loch Valley, EC. Vict.

Subseries B—FWD: R2220-2.
Subseries C—FWD: R2693.
Subseries D—FWD: R2219.

Other Vict. specimens

Subseries B—FWD: R2954 (Kalorama).
Subseries C—NMV: C134-5 (no precise locality); C8146 (Leongatha).

Waratah, NW. Tasm.

Subseries B—QVM: 1963:1:116, 121-2, 130-1, 133, 140.
Subseries C—QVM: 1963:1:135, 145, 160, 173.

Mt. Kate, NW. Tasm.

Subseries B—QVM: 1963:1:82, 88, 262-4.
Subseries C—QVM: 1963:1:256, 259-60, 270.

Other Tasm. specimens

Subseries A—QVM: 1963:1:71, 78-9, 309 (Cradle Mt.).
Subseries B—QVM: 1963:1:306 (Cradle Mt.).
Subseries C—QVM: 1963:1:74 (Cradle Mt.). NMV: C200 (Swan Id.).

Carrieton, S. Aust.

Subseries A—1 maxillary specimen.
Subseries B—2 max., 2 dentary specimens.
Subseries C—3 max., 8 dent. specimens.
Subseries D—2 max. specimens.
These 18 specimens, each with molar row complete, were selected from 93 fragments which comprised collectively, MCZ no. 7049.

Pseudomys higginsi (Tasm. series)

QVM: 63:1:251-2, 254-5; 64:1:257-9, 300, 314; 65:1:23 (Mt. Kate). 63:1:159, 181-6, 231; 64:1:29, 226, 230; 65:1:87, 128-9, 229 (Waratah). 65:1:251-2 (Golden Valley). 65:1:38-9, 48, 55, 130-2 (Renison Bell). 65:1:74 (Corinna).
TM: A76, A78 (Florentine Valley); A479-81 (St. Valentine Peak); A79 (Junee).

Pseudomys australis (C. Aust. series)

NMV: C4883-5 (Mulka, S. Aust.); C157, C161 (Charlotte Waters, C. Aust.); C4885-6 (Brighton Downs, Qd.).

Appendix 3: Locality Data

Locality	Latitude (S)	Longitude (E)
Brighton Downs	23°30′	141°30′
Buchan	37°30′	148°10′
Carrieton	32°26′	138°32′
Charlotte Waters	25°55′	135°46′
Corinna	41°40′	145°06′
Cradle Mt.	41°40′	145°56′
Darling Downs*	28°	150°
Fern Cave	38°04′	141°10′
Florentine Valley	42°40′	146°28′
Glenelg River (lower)*	38°	141°
Golden Valley	41°38′	146°43′
Gwydir River*	29°30′	150°
Junee	42°45′	146°39′
Kalorama	37°48′	145°22′
Lake Albert	35°42′	139°10′
Lavers Hill	38°40′	143°24′
Leongatha	38°29′	145°57′
Loch Valley	37°47′	146°01′
Longreach	23°26′	144°15′
Minnie Downs	26°30′	140°
Mount Gambier	37°50′	140°46′
Mount Hamilton	37°47′	143°00′
Mount Kate	41°37′	145°55′
Mulka	28°18′	138°38′
Namoi River*	30°30′	150°
Pyramids Cave	37°27′	148°13′
Renison Bell	41°48′	145°26′
St. Valentine Peak	41°20′	143°48′
Swan Island	40°45′	148°07′
Waratah	41°27′	145°32′
Whites River	36°18′	148°23′
Wombeyan Caves	34°19′	149°59′

* The position indicated is at about the middle of the feature.

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Plate 3

Details of *Mastacomys* and *Pseudomys*

Fig. 1. P20778. *Mastacomys fuscus mordicus*, with additional cusp of M^3 indicated by arrow.

Fig. 2. P20799. *M. f. mordicus*, with additional cusps of molars indicated by arrows. Note posteriorly narrow incisive foramina.

Fig. 3. NMV, C200. *M. f. fuscus*, illustrating posteriorly broad incisive foramina.

Fig. 4. NMV, C4884. *Pseudomys australis*, illustrating posterior extent of incisive foramina.

Fig. 5. NMV, C7884. *P. higginsi higginsi*, illustrating posterior extent of incisive foramina.

Figs. 6-8. P20914, P20908, P20880 respectively. Maxillary paratypes of *P. higginsi australiensis*. Arrow indicates an additional cusp on M^1.

Fig. 9. P20903. Holotype of *P. higginsi australiensis*.

Figs. 10-12. P20915, P20940, P20984 respectively. Dentary paratypes of *P. higginsi australiensis*.

Enlargements: Figs. 1-2 × 5, figs. 3-5, 10-12 × 3, figs. 6-9 × 4.

TABLE 1

Data of series of *Mastacomys*

Each group comprises from top to bottom, number of observations, mean, and standard deviation.

Series	Tasm.	S.E. Aust.	Fern Cave	Holocene Pyramids	Pleist. Pyramids	Carrieton
$M^{1-3}L$	23 9·49 0·37	22 9·78 0·41	12 9·58 0·29	37 9·52 0·34	12 9·34 0·26	5 9·26 0·20
M^1W	23 3·33 0·10	21 3·25 0·16	12 3·33 0·12	36 3·36 0·13	12 3·23 0·14	5 3·14 0·06
I^1W	23 1·37 0·12	21 1·50 0·15	12 1·43 0·10	15 1·41 0·16		
ZPH	23 8·08 0·60	22 8·32 0·76	12 8·26 0·62	37 8·22 0·89	12 8·10 0·48	5 8·26 0·51
ZPL	23 4·13 0·42	22 4·14 0·44	12 4·33 0·51	37 4·23 0·47	12 4·33 0·34	4 4·05 0·51
FL	21 7·80 0·50	21 8·12 0·61	12 7·28 0·69	19 7·55 0·73		
FW	21 1·74 0·17	21 1·90 0·16	12 1·94 0·32	19 1·92 0·20		
BL	14 34·66 1·45	17 34·82 2·25		5 35·74 1·02		
DL	19 25·90 0·91	19 25·86 1·54	12 25·31 0·86	59 25·62 1·02	22 25·31 0·69	
RD	22 6·22 0·21	21 6·43 0·36	12 6·45 0·31	59 6·51 0·19	57 6·40 0·26	10 6·41 0·20
$M_{1-3}L$	22 8·71 0·20	22 8·96 0·28	12 8·81 0·26	59 8·87 0·27	57 8·60 0·28	10 8·40 0·25
L_1W	22 1·26 0·12	21 1·42 0·16	12 1·42 0·09	59 1·41 0·10	18 1·39 0·07	7 1·37 0·11
ZPL/ZPH	23 51·2 5·3	22 50·0 5·4	12 52·7 6·2	37 51·6 3·9	12 53·6 4·3	4 47·8 3·4
FW/FL	21 22·4 2·6	21 23·5 2·9	12 26·9 3·5	19 25·6 3·4		
I_1W/DL	19 4·9 0·3	19 5·5 0·4	12 5·6 0·3	59 5·5 0·3	11 5·5 0·3	
RD/DL	19 23·9 1·0	19 25·1 1·1	12 25·6 1·0	59 25·4 1·1	22 25·2 1·3	

TABLE 2

Data of local populations of *Mastacomys*

Each group comprises, from top to bottom, number of observations, mean, and standard deviation.

	Tasmania		Australian Mainland		
	Mt. Kate	Waratah	Otway Ranges	Loch Valley	Whites River
$M^{1-3}L$	9 9·66 0·27	11 9·36 0·33	5 9·76 0·23	4 9·85 0·54	7 9·81 0·35
$M^{1}W$	9 3·37 0·10	11 3·31 0·08	4 3·30 0·00	4 3·35 0·10	7 3·26 0·08
$I^{1}W$	9 1·38 0·08	11 1·33 0·14	4 1·43 0·22	4 1·48 0·10	7 1·60 0·06
ZPH	9 8·13 0·42	11 8·00 0·75	5 8·00 0·76	4 8·65 0·51	7 8·64 0·51
ZPL	9 4·29 0·21	11 3·87 0·41	5 4·18 0·40	4 4·33 0·55	7 4·17 0·50
FL	9 8·04 0·46	9 7·52 0·40	4 8·38 0·21	4 8·15 0·52	7 8·04 0·61
FW	9 1·64 0·05	9 1·78 0·17	4 1·83 0·22	4 1·98 0·26	7 1·93 0·17
BL	7 35·30 0·68	5 33·68 1·99	2 33·60 2·26	3 35·07 2·25	7 36·07 1·10
DL	7 26·37 0·24	10 25·55 1·12	4 25·00 1·00	4 25·58 1·55	7 27·03 0·84
RD	9 6·21 0·22	11 6·23 0·22	4 6·33 0·25	4 6·55 0·37	7 6·61 0·24
$M_{1-3}L$	9 8·76 0·18	11 8·67 0·23	5 8·92 0·19	4 9·00 0·40	7 9·03 0·14
$I_{1}W$	9 1·26 0·10	11 1·24 0·14	4 1·30 0·14	4 1·45 0·10	7 1·53 0·08
ZPL/ZPH	9 52·8 3·3	11 48·6 5·0	5 52·4 5·0	4 50·7 4·9	7 48·3 5·8
FW/FL	9 21·4 1·7	8 23·5 2·5	4 21·8 2·5	4 24·3 2·0	7 24·0 1·9
$I_{1}W/DL$	7 4·9 0·2	10 4·8 0·4	4 5·2 0·5	4 5·7 0·2	7 5·7 0·3
RD/DL	7 23·2 0·7	10 24·3 0·2	4 25·5 1·5	4 25·6 1·0	7 24·5 1·6

TABLE 3

Data of subseries of *Mastacomys*

Each group comprises, from top to bottom, number of observations, mean, and standard deviation.

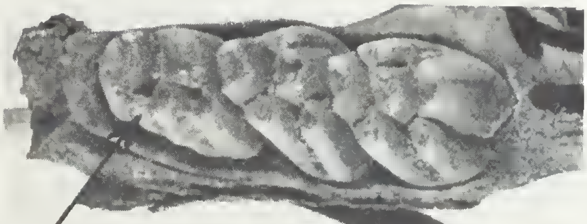
	Series	Tasmania	S.E. Aust.	Holocene Pyramids	Pleist. Pyramids	Carrieton
Subseries A	$M^{1-3}L$	4 9·60 0·25	7 9·50 0·43	14 9·31 0·30	4 8·97 0·17	1 8·80 —
	M^1W	4 3·40 0·16	7 3·31 0·07	13 3·36 0·10	4 3·22 0·05	1 3·20 —
	IC	4 4·20 0·28	7 4·19 0·18	4 4·57 0·71		
	PL	4 20·95 0·95	7 20·71 1·15	4 20·57 0·84		
	ZPH	4 7·35 0·72	7 6·83 0·62	14 6·56 0·57	4 7·35 0·66	1 6·40 —
	ZPL	4 4·00 0·29	7 3·69 0·27	14 3·64 0·45	4 3·95 0·24	1 3·90 —
	ZPL/ZPH	4 54·6 2·8	7 54·1 2·8	14 55·4 3·7	4 53·9 2·3	1 60·9 —
Subseries B	$M^{1-3}L$	13 9·42 0·38	13 9·72 0·48	15 9·49 0·38	4 9·35 0·31	2 9·05 0·07
	M^1W	13 3·35 0·08	13 3·31 0·09	15 3·37 0·12	4 3·30 0·14	2 3·15 0·07
	IC	11 4·09 0·18	13 4·12 0·24	7 4·33 0·29		
	PL	11 21·93 0·79	13 22·45 1·48	6 21·50 1·42		
	ZPH	13 7·75 0·49	13 8·05 0·82	15 7·47 0·90	4 7·90 0·70	2 7·55 0·07
	ZPL	13 3·98 0·42	13 4·06 0·47	15 3·92 0·46	4 4·20 0·34	1 3·30 —
	ZPL/ZPH	13 51·4 5·4	13 50·7 5·6	15 52·7 4·2	4 53·4 5·1	1 43·4 —

TABLE 4

Data of series of *Pseudomys*

Each group comprises, from top to bottom, number of observations, mean, and standard deviation.

	P. oralis	*P. higginsi australiensis*	*P. higginsi higginsi*	*P. australis* (Fern Cave)	*P. australis* (C. Aust.)
$M^{1-3}L$	97 6·88 0·19	36 6·19 0·17	49 5·73 0·24	12 6·49 0·19	6 5·84 0·34
$M^{1}W$	97 2·24 0·09	36 1·93 0·08	49 1·73 0·06	12 2·08 0·05	6 1·92 0·09
ZPH	96 7·38 0·48	29 6·50 0·37	49 6·84 0·35	11 6·91 0·16	6 6·03 0·48
ZPL	95 3·86 0·27	25 3·49 0·16	49 3·13 0·26	12 3·64 0·20	6 2·93 0·25
DL	83 22·88 0·68	8 20·54 0·64	48 20·54 0·66	5 21·42 1·16	6 18·88 1·29
RD	82 5·14 0·13	60 4·70 0·19	49 4·60 0·20	9 4·76 0·18	6 4·28 0·25
$M_{1-3}L$	84 6·58 0·18	59 5·94 0·19	49 5·61 0·20	9 6·67 0·17	6 5·56 0·32
$M_{1}W$	84 1·79 0·08	66 1·66 0·07	49 1·54 0·07	9 1·76 0·05	6 1·73 0·05
$I_{1}W$	83 1·06 0·06	14 0·84 0·06	49 0·84 0·06	8 0·90 0·03	6 0·83 0·08
ZPL/ZPH	94 52·5 3·7	24 53·4 2·5	49 45·9 4·4	12 48·3 3·7	6 48·6 2·2
$I_{1}W$/DL	82 4·7 0·3	2 4·2 0·5	48 4·1 0·2	4 4·3 0·2	6 4·4 0·5
RD/DL	81 22·5 0·7	7 23·3 0·7	48 22·4 1·0	5 22·2 1·7	6 22·7 1·0



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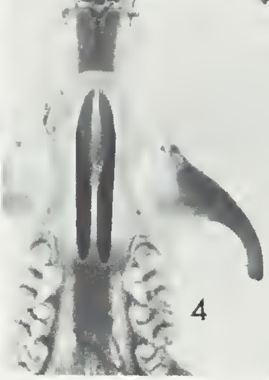

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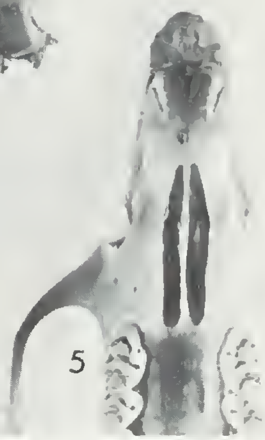

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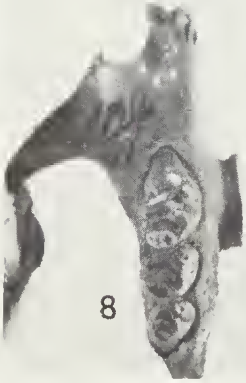

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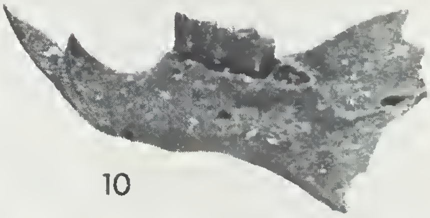

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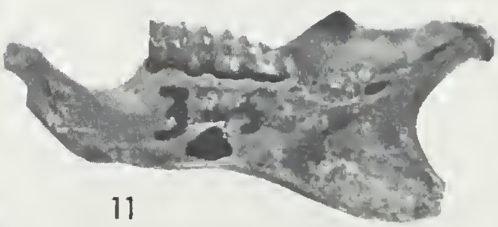

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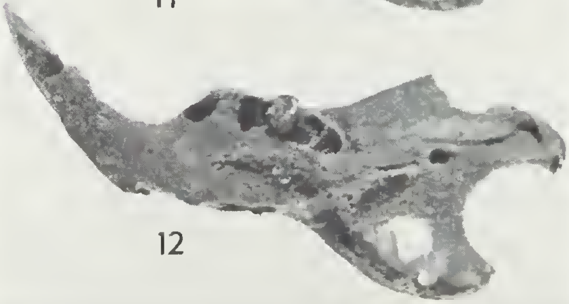

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