FIELDIANA
Geology

Published by Field Museum of Natural History

Volume 38

THE MAMMALIAN FAUNA OF MADURA CAVE, WESTERN AUSTRALIA

PART III

ERNEST L. LUNDELIUS, JR.
and
WILLIAM D. TURNBULL

December 28, 1978

FIELDIANA: GEOLOGY

A Continuation of the

GEOLOGICAL SERIES

of

FIELD MUSEUM OF NATURAL HISTORY

VOLUME 38

FIELD MUSEUM OF NATURAL HISTORY
CHICAGO, U.S.A.

THE MAMMALIAN FAUNA OF MADURA CAVE, WESTERN AUSTRALIA

PART III

FIELDIANA
Geology

Published by Field Museum of Natural History

Volume 38

THE MAMMALIAN FAUNA OF MADURA CAVE, WESTERN AUSTRALIA

PART III

ERNEST L. LUNDELIUS, JR.
Professor of Geological Sciences
University of Texas at Austin
and
Research Associate
Field Museum of Natural History

and

WILLIAM D. TURNBULL
Curator, Fossil Mammals
Field Museum of Natural History
and
Research Associate
Texas Memorial Museum

December 28, 1978

Publication 1290

Library of Congress Catalog Card No.: 72-97564

ISSN 0096-2651

PRINTED IN THE UNITED STATES OF AMERICA

TABLE OF CONTENTS

INTRODUCTION

This part of the report on the fauna of the Madura Cave completes the systematic sections of the Order Marsupicarnivora begun in Parts I and II (Lundelius and Turnbull, 1973, 1975). The following taxa are considered: *Antechinus flavipes*, *Phascogale calura*, *P. tapoatafa*, *Parantechinus apicalis*, *Dasycercus cristicauda*, *Dasyuroides byrnei*, *Dasyurus geoffroyi*, *Sarcophilus harrisi*, *Thylacinus cynocephalus*, and *Myrmecobius fasciatus*. The carnivorously specialized *Thylacoleo carnifex*, usually classified in the Order Diprotodonta, is included here as *incertae sedis* within the Cohort Marsupiata. For each taxon there is a brief discussion of the morphology and zoogeography. A final section deals with zoogeography and environmental interpretations.

Measurements, abbreviations, and dental terminology are either those in standard use or those outlined in Parts I and II except for the following: 1) Anterior width (AW) measurement of the lower molars. The new measurement (with noted exception) has been taken along the epicristid in all specimens whether or not it corresponds to the width normal to the long axis of the tooth. It seems most reasonable to measure this functional crest. The measure is designated as anterior width along the epicristid (AW-E) to distinguish it from the standard anterior width measure. AW and AW-E are the same only when the epicristid is transverse to the long axis of the tooth. 2) United States National Museum is abbreviated as USNM; and British Museum (Natural History) is abbreviated as BMNH.

SYSTEMATICS

Class Mammalia

Subclass Theria

Infraclass Eutheria (Sensu VandeBroek, 1961, 1964)

Cohort Marsupiata (Sensu Turnbull, 1971; = Metatheria)

Order Marsupicarnivora (Ride, 1964)

Dasyuridae Waterhouse, 1838, 1841 (restricted)

Phascogalinae Gill, 1872

Antechinus Macleay, 1841

Antechinus flavipes (Waterhouse), 1838. Tables 1-4; Figures 1, 2, 3A, 4, 5A.

Material. –

Lower Dentitions

Trench 3, Unit 2

PM 25787, right ramus fragment with M_{3-4}

Trench 3, Unit 3

TMM 41106-734, left ramus with M_{1-4} (fig. 2A, B)
PM 26134, left ramus with P_4-M_2, alveoli for other teeth (fig. 2C, D)
PM 26135, right ramus with M_2
PM 26136, left ramus with M_4
WAM 74.9.8, right ramus fragment with M_4

Trench 4, Unit 2, level 2

TMM 41106-7, right ramus with M_{2-4}, alveoli for incisors, C, P_2M_1
WAM 74.9.9, left ramus with M_{2-4}
PM 29907, left ramus fragment with M_4
PM 29908, right ramus fragment with M_4

PM 29909, left ramus fragment with P_3, alveoli for other teeth

Trench 4, Units 4-5

TMM 41106-704, left ramus fragment with $M_{2 \text{ or } 3}$
TMM 41106-785, right ramus with M_4
PM 25609, right ramus with M_3
PM 25610, right ramus with P_4-M_4
PM 25611, right ramus with M_2
PM 25612, right ramus with M_1
PM 29432, right ramus with M_3

Unit 7
PM 25631, right ramus with $M_{2\text{-}3}$, roots of M_4

Upper Dentitions

Trench 3
Unit 2, level 2
TMM 41106-737, left maxillary fragment with M^3 (fig. 2E, F,G)

Trench 4

Units 4-5
WAM 74.9.10, left maxillary fragment with M^3

Description. — This phascogale is uncommon in the Madura Cave deposits, being represented by 19 specimens. It was not recovered in the earlier work at Madura Cave (Lundelius, 1963).

These specimens are similar to a Recent specimen (FM 18889, fig. 1) of *Antechinus flavipes leucogaster* from Western Australia. The mandible of one of the best of the Madura Cave specimens (TMM 41106-734, fig. 2A, B) is slightly deeper and has teeth that are moderately worn. In another Madura specimen (TMM 41106-7) the mandible is shallow and the teeth are only slightly worn, while in PM 26135 a worn molar sits in an equally shallow ramus. Apparently, the depth of the jaws is variable. This is true of the Recent specimens of *A. stuartii adusta* (FM 60955-60960)[1] — most are deep and relatively heavy-jawed, but two (FM 60959 and 60960) are delicately built. In both Recent specimens representing the two subspecies, *A. f. flavipes* (FM 35337) and *A. f.*

[1]We follow the taxonomic arrangement of Wakefield and Warneke (1967) with respect to the species of *Antechinus*, but retain the name *A. f. rufogaster* for convenience in referring to the South Australian population.

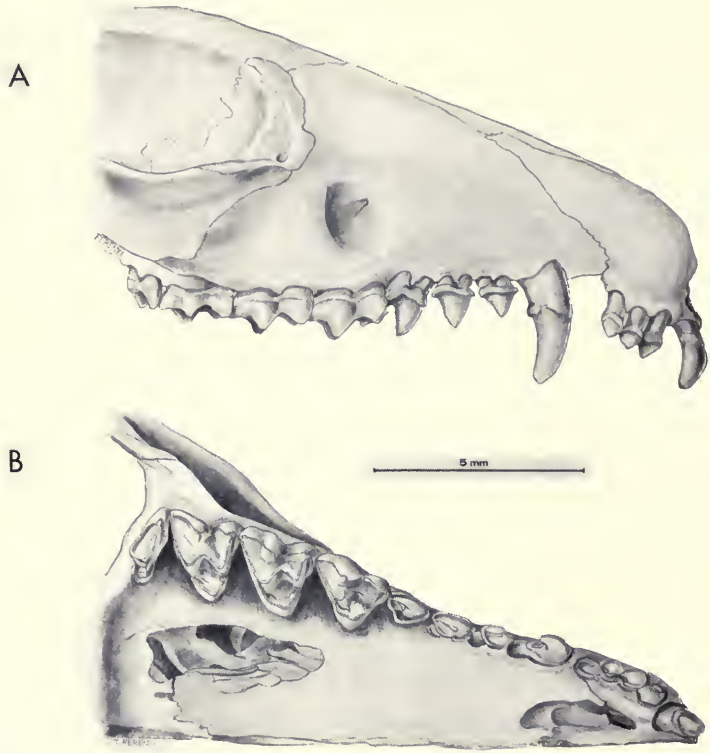


FIG. 1. *Antechinus flavipes leucogaster*, FM 18889. **A, B,** Rostrum with right upper dentition shown in labial and crown views.

rufogaster (FM 104787), the mandible is delicately built as in the most slender of the Madura fossils. Mental foramina in the Madura Cave specimens vary both in number and position. The posterior one(s) opens under M_1, or P_4 and M_1. The anterior one(s) opens under P_2 or P_3.

No incisors or anterior premolars are preserved, but two specimens have alveoli for all of the antemolar teeth (PM 26134, fig. 2C, D; TMM 41106-7). The incisor alveoli are arranged in a triangle and show that the teeth were procumbent. The canine alveoli indicate that the canines were upright, and the alveoli of the premolars show that these teeth were double-rooted and nearly in line. The anterior root of P_2 is situated somewhat more labially than the others, but the premolars do not appear to have been tightly crowded. The P_4 is preserved in only two specimens, PM 25610 and PM 26134. The latter is the basis of the following description: P_4 is relatively narrow with one principal cusp in the

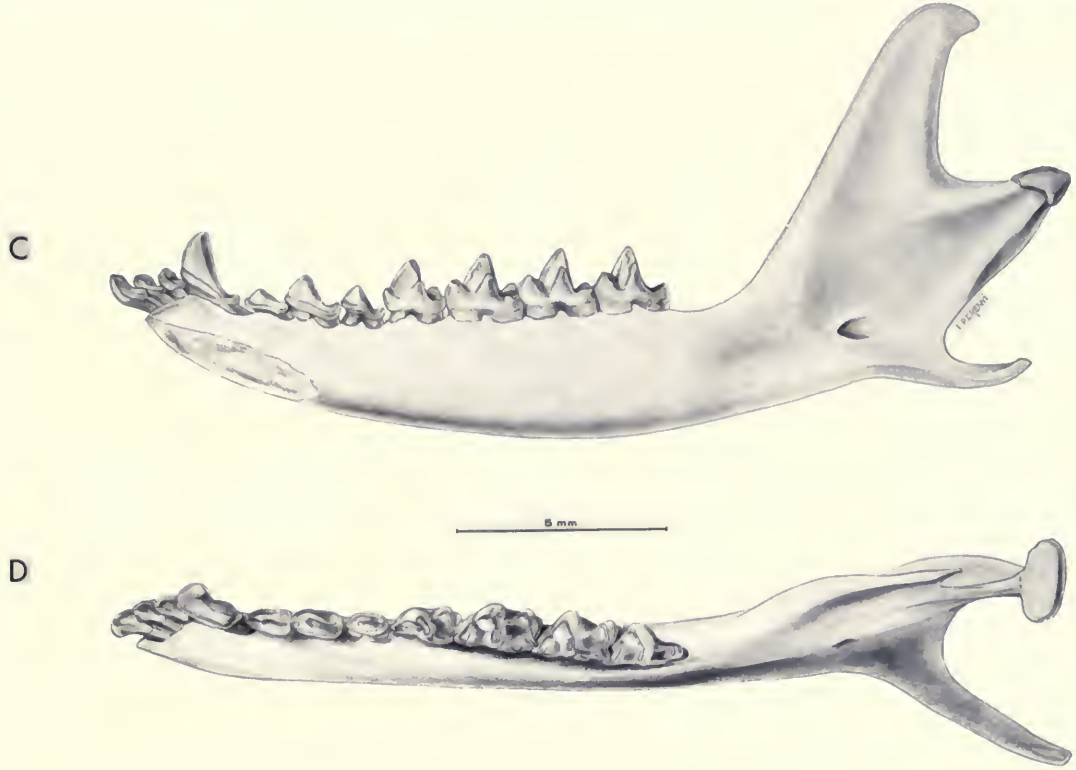


FIG. 1. **C, D.** Right ramus with lower dentition shown in lingual and crown views.

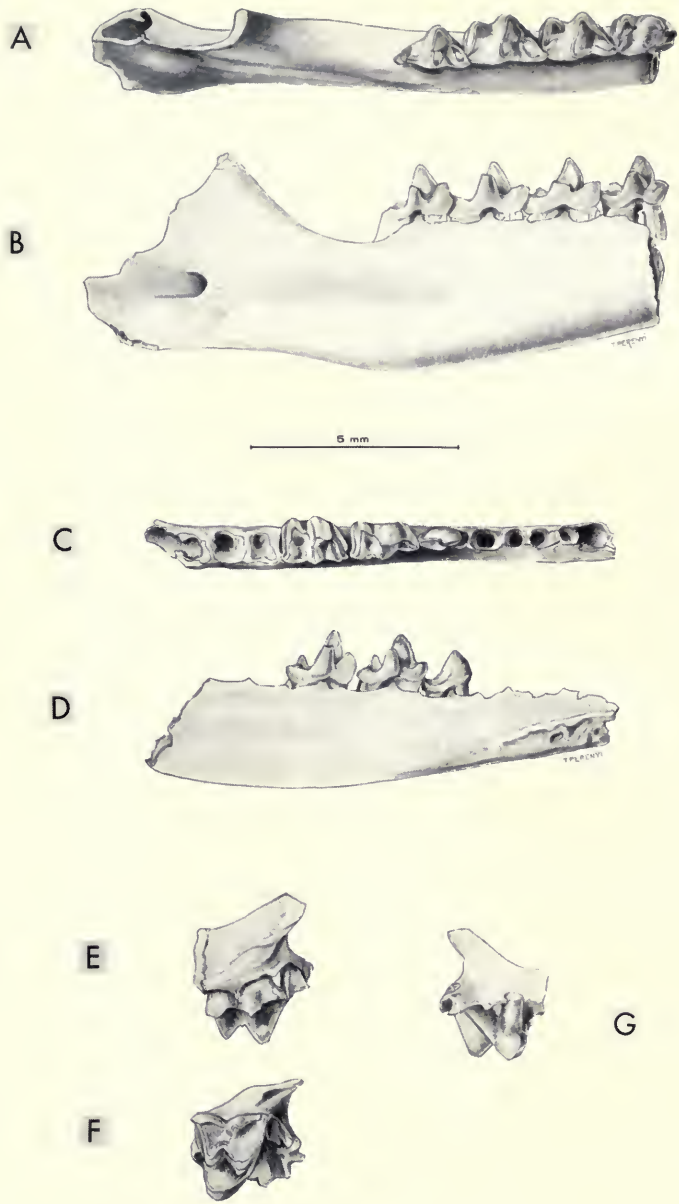


FIG 2. *Antechinus flavipes* from Madura Cave. **A, B,** TMM 41106-734, left ramus with M_{1-4}, shown in crown and lingual views. **C, D,** PM 26134, left ramus with P_4-M_2 and the alveoli of two (or three) incisors, C, P_{2-3}, M_3, and part of M_4, shown in crown and ligual views. **E-G,** TMM 41106-737, left maxillary fragment with M^3, shown in labial, crown, and posterior views.

anterior third of the tooth over the anterior root. The posterior edge of the cusp is ridged; the ridge connects it with a cuspule at the posterior end of the tooth. The anteroposterior axis of the tooth parallels that of the ramus. However, in PM 26136 the alveoli show that the tooth was angled in this specimen. A cingulum is present on the back side of the tooth. It is better developed lingually than labially, but does not reach midway forward on either side. The Recent specimen of *A. f. leucogaster* also has a narrow P_4, but the tooth is oriented at a slight angle to the long axis of the tooth row. A specimen of *A. f. rufogaster* (FM 104787) shows a relatively thicker P_4 with a lower principal cusp and better developed cingula.

The molars are sufficiently similar so that the description of the best specimen (TMM 41106-734, fig. 2A, B) will suffice with a few noted exceptions. The protoconid is much the largest of the trigonid cusps. The metaconid is the next largest, followed by the paraconid in $M_{1\text{-}3}$. The paraconid in M_1 is reduced, but not to the extent that it is in FM 104787 (*A. f. rufogaster*). In M_4 the fused paraconid-parastylid and the metaconid are subequal, but the metaconid is slightly thinner and taller. There is a parastylid on $M_{2\text{-}4}$, but although this area of the M_1 is extremely worn, it does not appear to have had a parastylid. The M_1 of the Recent specimen, which is less worn, also lacks the parastylid. There is a slight difference in the trigonid of the M_1, the fossil form having the protoconid and metaconid slightly closer together, possibly because the metaconid is slightly larger in the fossil. The protoconid and metaconid are located more nearly on a line transverse to the long axis of the tooth than in the Recent specimen.

The talonid is basined in $M_{1\text{-}3}$ and is lower than the trigonid. The hypoconid is the largest talonid cusp. The back of the talonid is broken in M_4 so that little can be discerned concerning details of its form, but it resembles the Recent specimen in possessing a narrow basin. In the Recent specimen there are vaguely defined hypoconulid and entoconid cuspules in addition to the hypoconid.

In $M_{1\text{-}3}$ of the fossils the hypoconulids protrude posteriorly and fit into the notch between the cingulum and the parastylid of the tooth behind. They have a weak diagonal ridge that extends toward the talonid basin, the result of wear on the back side of the postmetacristid (I″). Entoconids are present on $M_{1\text{-}3}$ but are very minute, laterally-compressed cusps. They are smaller than those of the Recent specimen of *A. f. leucogaster* or those of the sub-

Recent sample of A. *flavipes* from Wedge's Cave, Western Australia. In comparison, the entoconids of the M_{1-3} of the Recent specimen of *A. f. rufogaster* are larger.

In the Madura specimens there is a distinct anterolabial cingulum on M_{1-4} that extends from the base of the protoconid almost to the parastylid. On M_{2-4}, between the end of this cingulum and the parastylid (which is a weak crest on the anterior edge of the paraconid), there is a small notch into which the hypoconulid of the tooth ahead protrudes. An equally well-defined posterior cingulum extends from the base of the hypoconid to the tip of the hypoconulid on M_{1-3}, and there is a slight cingular bulge between the protoconid and hypoconid on M_3. In the Recent specimen, this bulge is present on M_{1-3} and is more pronounced.

The only maxillary fragments assignable to *A. flavipes* are specimens TMM 41106-737 (fig. 2E, F, G) and WAM 74.9.10. Each is only a small fragment that bears but one tooth — an M^3. In TMM 41106-737, in addition to the M^3, the alveoli, a chip of M^4, and just enough of the anterior buttress of the zygomatic arch are preserved to permit an assessment of maxillary proportions. This fragment appears to be similar to the Recent *A. flavipes* and to be a bit more delicately built than is the comparable region in the Recent *Phascogale calura*.

On M^3 the metacone is the largest and highest cusp. The protocone is low and massive; the paracone high and slender. The eocrista is prominent, from parastyle-stylocone to paracone, to metacone, and on to metastyle. The stylar shelf is broad and, in addition to the styles, bears a prominent stylar cusp C (Turnbull, 1970, pp. 160-161 for cusp terminology). In TMM 41106-737 the protocone is crested and somewhat crescentic as a result of wear. In the less worn specimen, WAM 74.9.10, it is slightly more angular. Both protoconule and metaconule are present but weakly developed. They are located on the anterior and posterior crests of the protocone respectively — crests which continue their course labially from the conules as cingulae. The anterior of these is stout and expanded toward the parastyle. The posterior one is more reduced, but it continues for well over two-thirds of the distance across the posterior face of the tooth.

Discussion. — Recent populations of *Antechinus flavipes* show a geographic cline in size with the largest specimens from Queensland and the smallest from southwestern Australia with a

slight reversal of this trend in South Australia (Wakefield and Warneke, 1967). The two Recent specimens available to us fit this cline (tables 1, 2). The size of the entoconids of the lower molars also shows geographic variation but does not follow the size variation completely. The largest entoconids are found in the molars of *A. f. flavipes* followed by those found in *A. f. rufogaster* and *A. f. leucogaster*. The Recent samples upon which these statements are based consist of only one specimen of each species. The specimen of *A. f. leucogaster* (FM 18889) is believed to be representative of the Western Australian population because of the close correspondence of several measures to the means of those of a sample of *A. f. leucogaster* in the Western Australian Museum measured earlier (table 3).

The Madura Cave sample (table 4) is most similar to the Western Australian samples. However, although it holds a geographic position intermediate between the western and eastern Australian samples, it is not intermediate in size or morphology. It is smaller and has entoconids that are much smaller than the specimens of *A. f. rufogaster* and slightly smaller than the western *A. f. leucogaster* (the Recent specimen, or the sample of fossils from Wedge's Cave). The paraconids of the M_1's of the Madura Cave sample are most like those of the specimen of *A. f. flavipes*; they are larger and better developed than those of either the Western Australian sample or the specimen of *A. f. rufogaster*.

The Madura Cave *Antechinus* can be distinguished from the similar *Phascogale calura* by its smaller size (tables 5-9; fig. 4) the much smaller entoconids, and the higher main cusp on the P^4.

Antechinus flavipes has not been recorded in the Recent fauna of the Nullarbor Plain nor from the sub-Recent deposits of other caves in this region. Its Recent distribution is not known to extend east of Ravensthorp in Western Australia or west of Adelaide in South Australia (Wakefield and Warneke, 1967).

There is some difference of opinion concerning the habitat of this species in eastern Australia. Marlow (1958) states that its preferred habitat is rainforest and sclerophyll forest, while Calaby (1966) states that it occurs in woodland and dry forests from Queensland to Victoria. According to Wakefield and Warneke (1967) and Ride (1970), *A. flavipes* is found in rainforest, sclerophyll forest, and woodland. In Western Australia it occurs mainly in Jarrah (*Eucalyptus marginata*) and Tuart (*E. gom-*

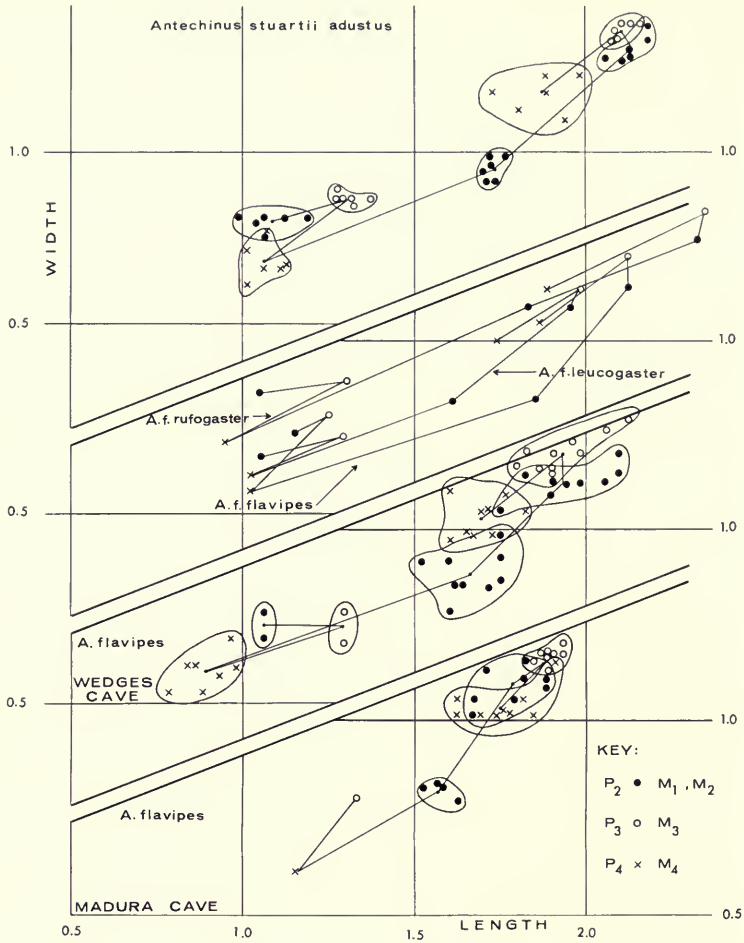


FIG. 3. **A**, Bivariate graphs comparing proportions of the lower cheek teeth of Recent *Antechinus stuartii adustus* and *A. flavipes* subspecies with samples of fossils of *A. flavipes* from Madura and Wedge's Caves.

phocephala) from Perth to Albany (Wakefield and Warneke, 1967). It is clear that it is restricted to forests and woodland and probably does not occur in areas with less than 15 in. of rain per year.

Its presence in Units 2 through 7 implies that conditions more humid than present prevailed at the times of deposition and that its subsequent absence is due to the present aridity of the region. Its absence from Unit 1 may indicate that this unit was deposited after the onset of the climatic change to more arid conditions.

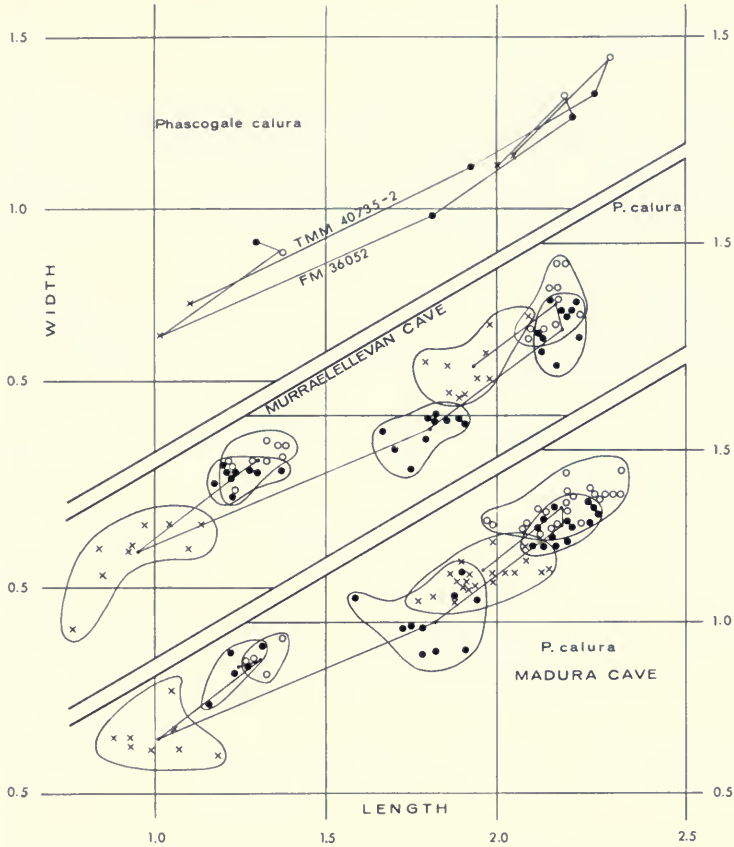


FIG. 3. **B**, Bivariate graphs for Recent *Phascogale calura* and for samples of fossils of *P. calura* from Madura and Murraelellevan Caves. The lines connect the means of each sample. The key is the same for **A** and **B**; scale units in millimeters.

Phascogale Temminck, 1824 (restricted)

Phascogale calura Gould, 1844. Tables 5-9; Figures 3B, 4, 5A, 6-8.

Material. –

LOWER DENTITIONS

Trench 1

Top first foot (possibly Unit 1)

PM 4798, right ramus with P_2-M_4; alveoli for other teeth

PM 4799, left ramus with P_2, P_4-M_1, $M_{3\text{-}4}$; alveoli for other teeth

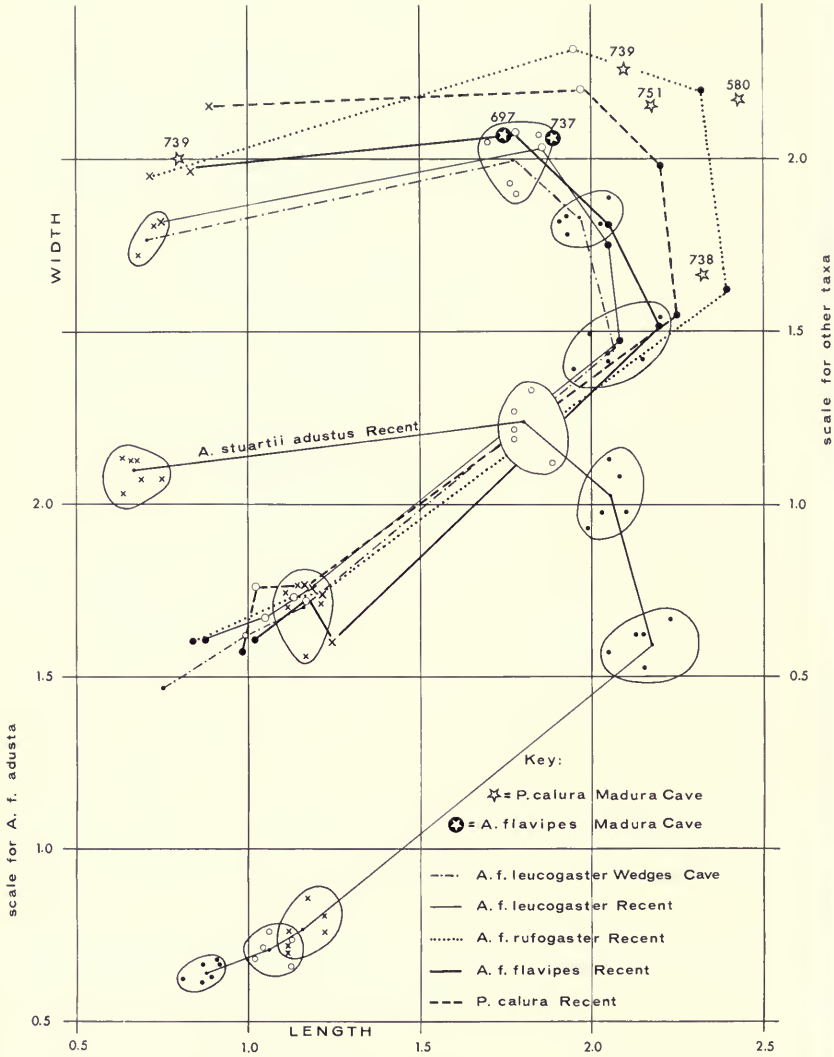


FIG. 4. Bivariate graphs comparing proportions of the upper cheek teeth of Recent *Antechinus stuartii adustus* and *A. flavipes* subspecies with fossil *A. flavipes* from Madura and Wedge's Cave, and Recent *Phascogale calura* with fossil *P. calura* from Madura and Murraelellevan Caves. Key is given in Figure 3. The Madura Cave *A. flavipes* 697 and 737 are M^3's; and the *P. calura* 739's are M^3 and M^4, 580 is an M^2, 738 is an M^1, and 751 (= WAM 74.9.16) is an M^3.

PM 4800, left ramus with C, P_2-M_4, alveoli for incisors

Trench 2

2½ ft. below surface (possibly Unit 2)

PM 6248, left ramus with P_2, M_{2-4}; alveoli for other teeth
PM 25266, right ramus with P_4-M_2; alveoli for other teeth
PM 25267, left ramus fragment with M_{2-4}

Trench 3

Unit 2

TMM 41106-132, left ramus with P_2-M_4, alveolus for C
PM 25582, right ramus with M_2, M_4, alveoli for C, other cheek teeth
PM 25587, left ramus fragment with M_{3-4}
WAM 74.9.11, left ramus fragment with M_1

Unit 3

PM 26138, right ramus with M_{2-4}

Trench 4

Unit 1, level 1

TMM 41106-522, right ramus fragment with M_{3-4}
PM 29436, left ramus fragment with M_{3-4}

Unit 2, level 1

PM 25593, left ramus fragment with M_{2-4}, condyle
PM 25594, left ramus fragment with M_{1-2}; alveoli for two incisors, C, P_{2-4}
WAM 74.9.12, left ramus fragment with M_{2-4}

Unit 2, level 2

TMM 41106-11, right ramus fragment with M_{3-4}
PM 25546, right ramus fragment with broken M_{2-4}; alveoli for C, P_4, M_1
PM 25708, right ramus fragment with M_3

Units 4-5

PM 25542, left ramus with M_{3-4}
PM 25543, left ramus with P_4-M_4; alveoli for C-P_3
PM 25548, right ramus with P_3-M_4; condyle; alveoli for C-P_2
PM 25554, left ramus fragment with M_3, broken M_4, angular process
PM 25556, left ramus with C, P_4-M_4; alveoli for 1_{1-3}, P_{2-3}
PM 25595, left ramus fragment with M_4
PM 29433, right ramus fragment with M_1; alveoli for C, P_{2-4}, M_2

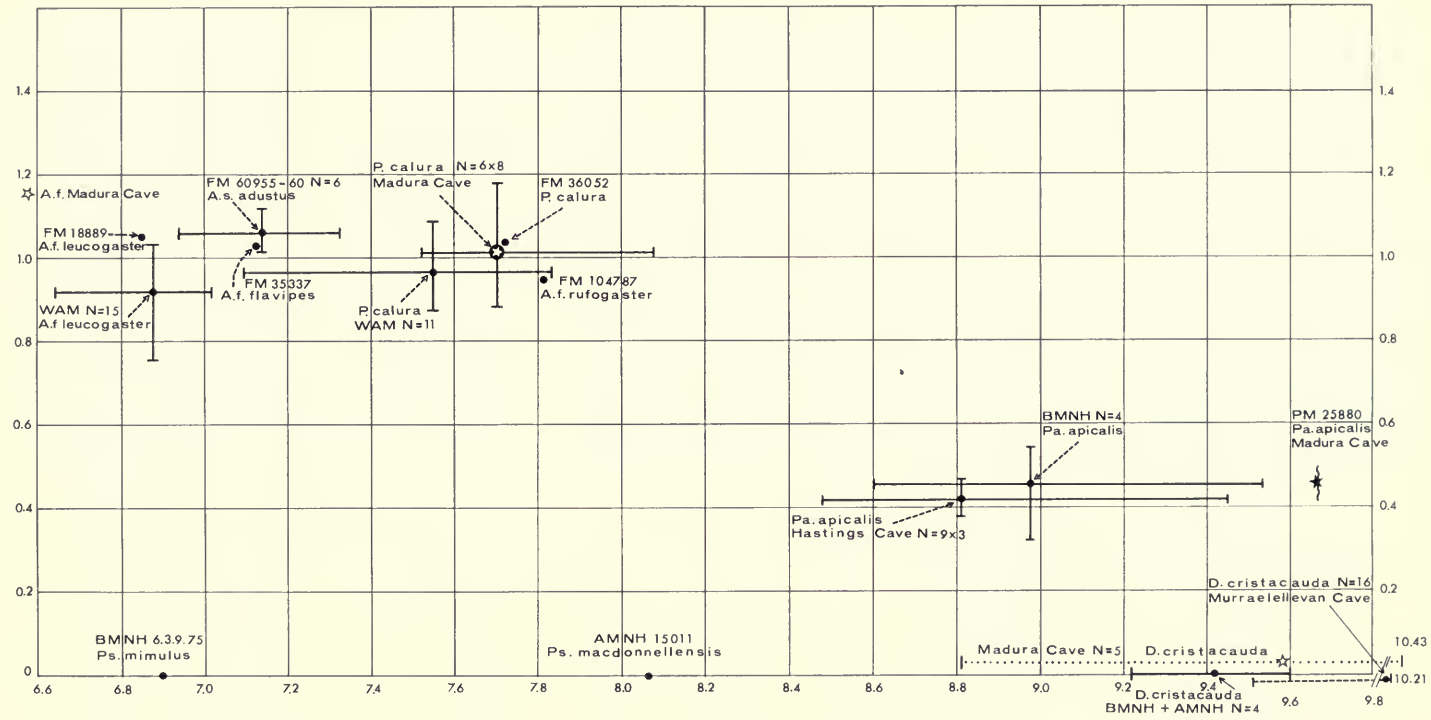
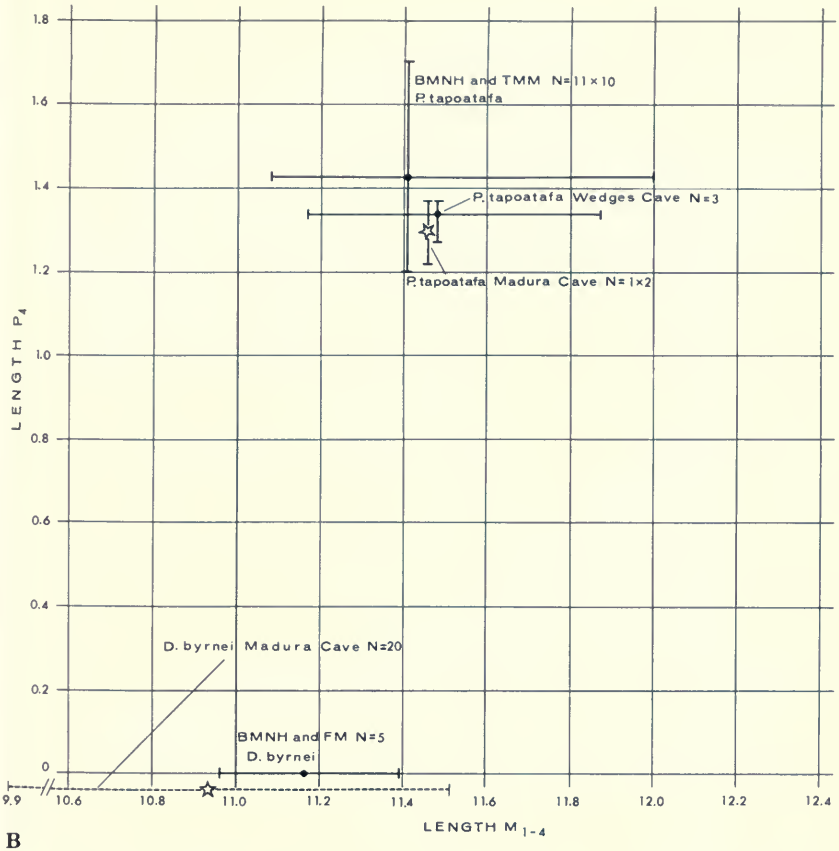

A.f. Madura Cave
FM 18889
A.f. leucogaster
WAM N=15
A.f leucogaster
FM 60955-60 N=6
A.s. adustus
FM 35337
A.f. flavipes
P. calura N=6x8
Madura Cave
FM 36052
P. calura
P. calura
WAM N=11
FM 104787
A.f. rufogaster
BMNH N=4
Pa. apicalis
Pa. apicalis
Hastings Cave N=9x3
PM 25880
Pa. apicalis
Madura Cave
D. cristacauda N=16
Murraelellevan Cave
BMNH 6.3.9.75
Ps. mimulus
AMNH 15011
Ps. macdonnellensis
Madura Cave N=5
D. cristacauda
D. cristacauda
BMNH + AMNH N=4
10.43
10.21
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0
6.6
6.8
7.0
7.2
7.4
7.6
7.8
8.0
8.2
8.4
8.6
8.8
9.0
9.2
9.4
9.6
9.8

FIG. 5. A.



B

FIG. 5. Bivariate graphs of length of lower molar series *vs*. length P_4 for various taxa of dasyurids showing relative size of the P_4's. This graph is an extension of Figure 13 of Part I, and Figure 2 of Part II.

Shown in **A** are:
Antechinus stuartii adustus
Antechinus flavipes
Phascogale calura
Pseudantechinus mimulus and *Ps. macdonnellensis*
Parantechinus apicalis
Dasycercus cristicauda

Shown in **B** are:
Dasyuroides byrnei
Phascogale tapoatafa

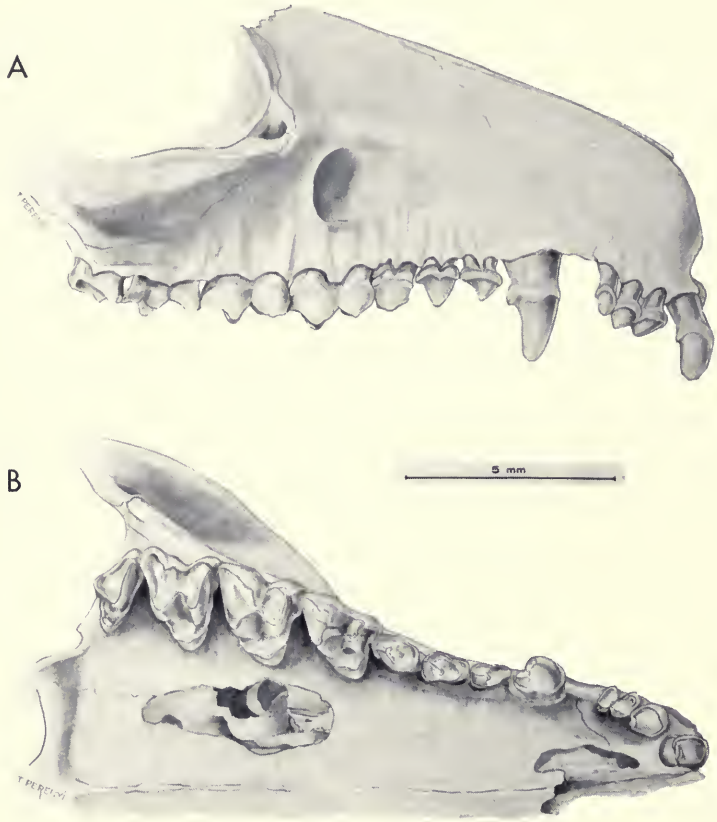


FIG. 6. *Phascogale calura* FM 36052. **A, B**, Rostrum with right upper dentition shown in labial and crown views.

WAM 74.9.13, right ramus fragment with $M_{2 \text{ or } 3}$, alveolus for $M_{3 \text{ or } 4}$

WAM 74.9.14, right ramus, edentulous, with alveoli for P_4-M_4

WAM 74.9.15, left ramus fragment with $M_{3\text{-}4}$

Unit 7, level 2

TMM 41106-733, right ramus fragment with $M_{2\text{-}3}$, alveoli for C, $P_{3\text{-}4}$, M_1, M_4 (fig. 7A, B)

Trench 5

Unit 3

PM 29431, right $M_{2 \text{ or } 3}$

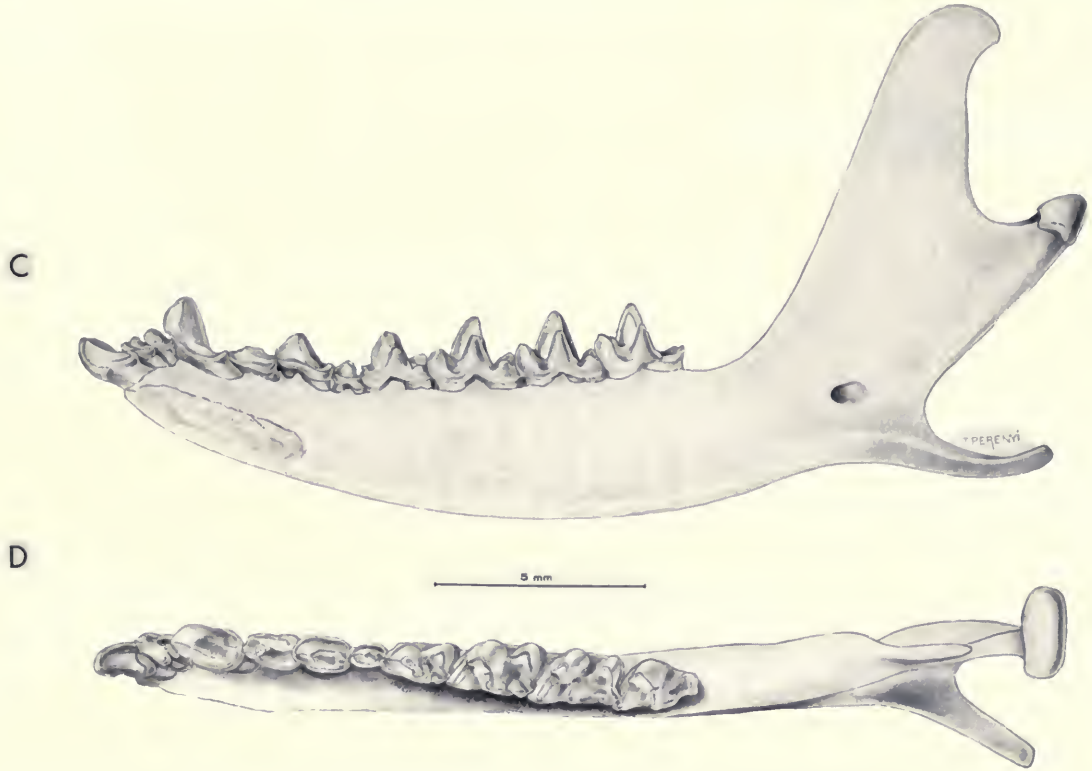


FIG. 6. **C, D**. Right ramus with lower dentition shown in lingual and crown views.

Upper Dentitions

Trench 3

Unit 2

WAM 74.9.16, right maxillary fragment with M^3; alveoli for M^2, M^4

Trench 4

Unit 1, level 1

TMM 41106-739, left maxillary fragment with M^{3-4}; alveoli for M^{1-2} (fig. 8D, E, F)

Unit 2, level 1

PM 25580, left maxillary fragment with M^2; alveoli for other molars, P^4 (fig. 8G, H, I)

Unit 2, level 2

TMM 41106-738, left maxillary fragment with M^1; alveoli for P^4, M^2 (fig. 8A, B, C)

Description.—**Mandibles:** The jaws are slightly more massive than in *Antechinus flavipes,* and they each have a masseteric fossa with prominent surrounding ridges and an upward- and backward-flaring configuration, more like that of *Sminthopsis crassicaudata* than that of *Antechinomys spenceri*. The condyle lies slightly above the dental occlusal plane; when viewed from the side it is seen as being nearer to the tip of the coronoid process than to the tip of the inflected angular process. A large mental foramen opens either beneath the posterior root of M_1 or between M_1 and M_2. A smaller anterior one may be single or divided into two openings located beneath P_2 or P_3, or, if split, with one foramen under the front of M_1. Occasionally, a smaller additional one is found behind the large posterior foramen.

Lower Dentitions: The lower premolars are best seen in PM 4798-4800, PM 25266, and TMM 41106-132. They are double-rooted, broad at the base, with well-developed lateral and posterior cingula. There are small cingular cuspules on the posterior ends of the premolars, and their principal cusps are relatively low. A crest extends from the principal cusp of each premolar to its posterior cingular cuspule. This ridge is located slightly labial to the midline in each tooth, and a slight furrow is present lingual to the ridge. The furrow is best developed in the P_4. There is a notch at the posterior end of the furrow in P_2 and P_3 (best developed in P_2) into which the anterior end of the following tooth

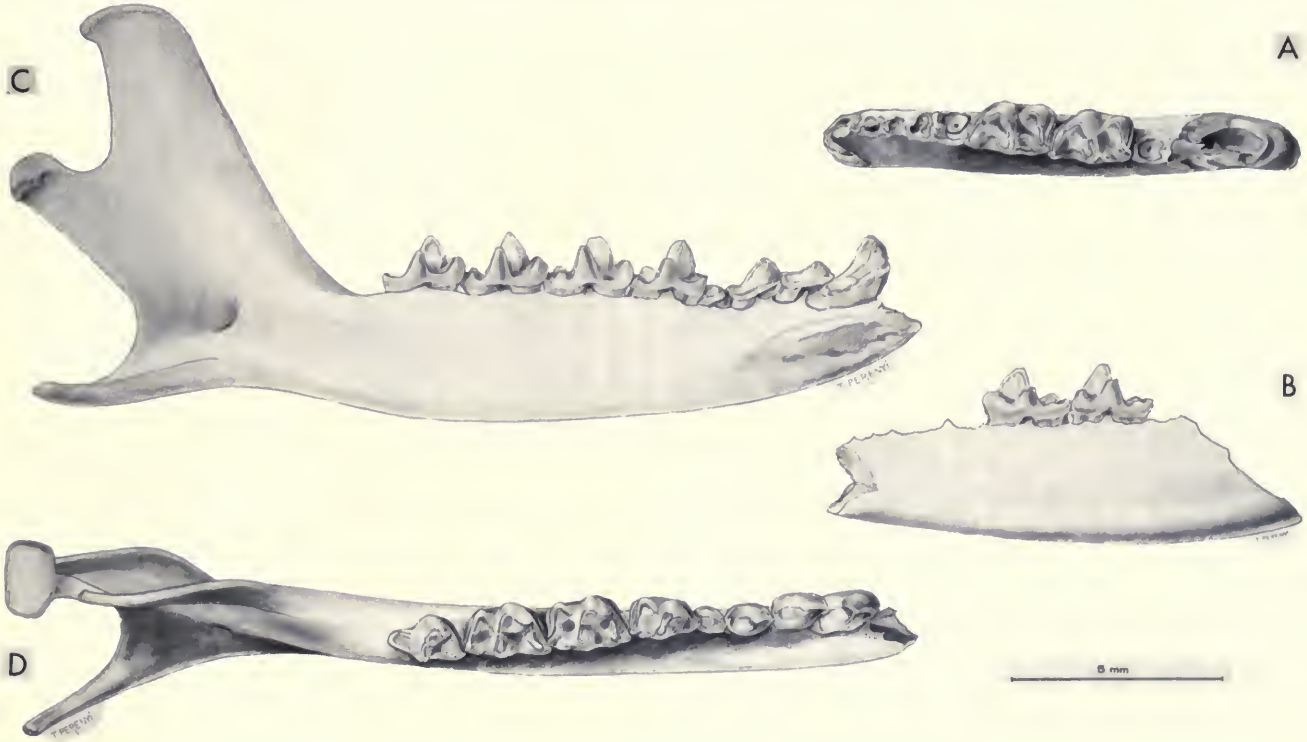


FIG. 7. *Phascogale calura* from Madura Cave. **A, B**, TMM 41106-733, a right ramus with M_{2-3} and alveoli of C, P_{3-4} and M_4 shown in crown and lingual views. **C, D**, PM 4800, a left ramus with C, P_2-M_4, and alveoli for incisors shown in lingual and crown views.

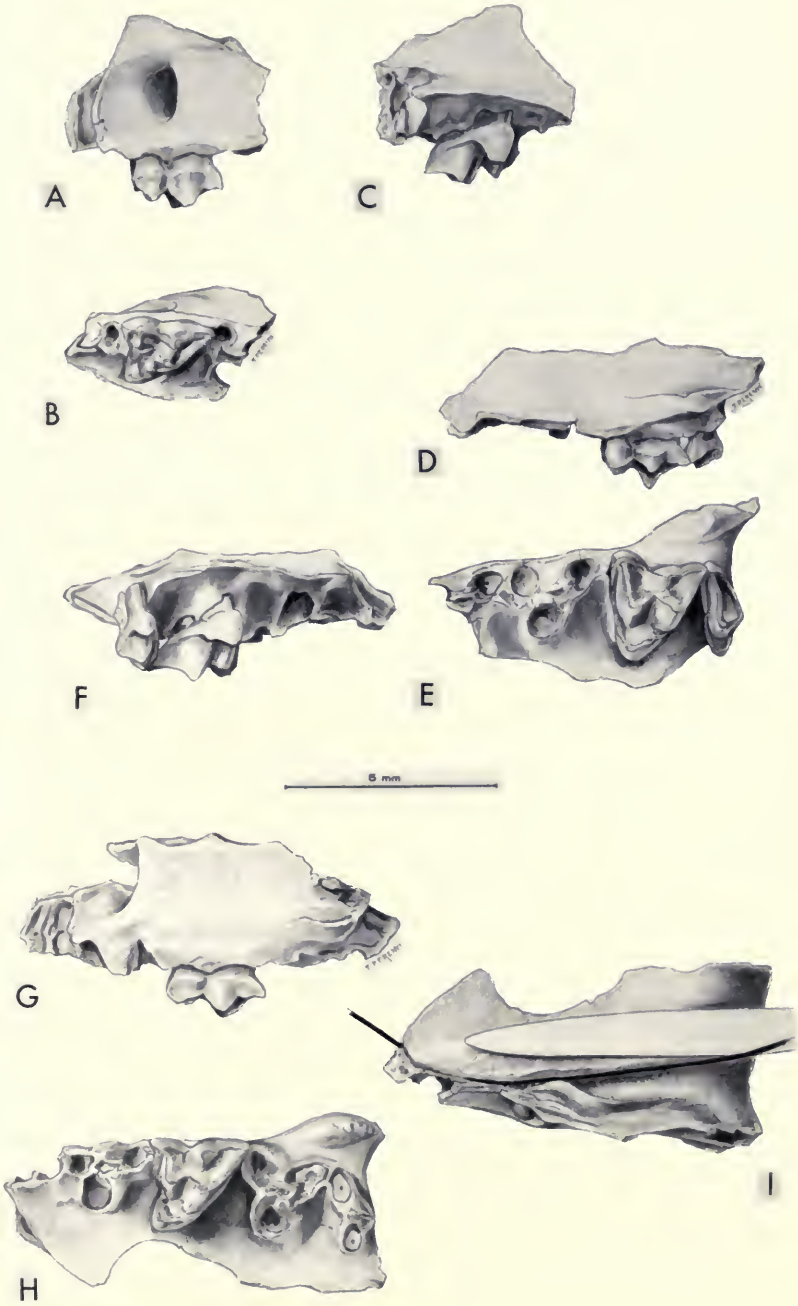
fits. Wear progressively truncates the crest and produces a flattened or broadly convex surface on the posterior half of P_2 and P_3. The P_3 is the largest premolar, followed by P_2 and P_4. The P_4 is usually oriented at a noticeable angle (10°-40°) to the long axis of the tooth row. Its posterior end lies labial to the anterior end of the M_1.

The lower molars have the normal dasyurid structure. Seven specimens have complete, or nearly complete, lower series (TMM 41106-132, PM 4798-4800, PM 25548, and PM 25556). In each, the protoconid is the largest cusp, followed by the metaconid and paraconid. The talonid is basined. The hypoconid is joined to the hypoconulid by the postcristid. The labial border of the talonid is formed by the cristid obliqua. This ridge joins the protolophid at the center of the protoconid in M_1. The junction is located progressively farther lingually in the posterior molars until, in M_4, it is located at the center of the protolophid. The entoconid is usually a prominent cusp, is higher than the hypoconulid, and is located on the lingual border of the talonid slightly closer to the hypoconulid than to the metaconid. It is oval to almost circular in cross-section. The entoconid is small on M_4 and variably developed on M_3. The labial side of each lower molar tooth has a well-developed cingulum that joins the pre- and post-cingula. Usually there is some cingular development in the valley between the paraconid and metaconid, but its extent is varied.

Another specimen, PM 25542, shows some variations. It has a somewhat larger-than-average $M_{3\text{-}4}$, and the M_3 has a better developed entoconid — even more developed than in the Recent specimen. This specimen preserves the alveoli of C-M_2. These show that the P_2 and P_4 were both set at an angle to the tooth row, since the anterior alveolus of P_2 is labial to that of the canine and the posterior alveolus of P_4 is anterolabial to the anterior alveolus of the M_1.

Opposite:

FIG. 8. *Phascogale calura* from Madura Cave. **A-C**, TMM 41106-738, a left maxillary fragment with M^1 and alveoli of P^4 and M^2 shown in labial, crown, and lingual views. **D-F**, TMM 41106-739, a left maxillary fragment with $M_{3\text{-}4}$ and alveoli of $M_{1\text{-}2}$ shown in labial, crown, and lingual views. **G-I**, PM 25580, a left maxillary fragment with M^2 and alveoli of P^4 and the other molars shown in labial, crown, and dorsal views. The black fiber marks the path of a canal for a branch of the infraorbital artery.


A
C
B
D
F
E
5 mm
G
I
H

Upper dentitions: The largest maxillary fragments are PM 25580 and TMM 41106-739 and between them they preserve the alveoli of P^4 and all of the upper molars. The former also preserves part of the infraorbital foramen and palate, as does TMM 41106-738, the fragment with M^1. Specimen PM 25580 shows a divergent canal branching off from the infraorbital foramen (fig. 8I) which extends forward and medially into the interior of the palatal portion of the maxillary bone. The P^4 was double-rooted with the roots aligned with the edge of bone.

In crown view the molars are all triangular in outline and have the usual dasyurid morphology with a well-developed stylar shelf and strong eocrista. The protocone is low and crescentic in all of the molars. In M^{1-3} the metacone is taller and larger than the other cusps and the paracone is the smallest. In M^4, as would be expected, the paracone is near normal size while the metacone is very reduced. In M^1 the stylocone is quite distinct, as is the parastyle, while in the other molars they are fused. A stylar cuspule (C_2) is present in M^{1-3}, situated just anterior to the metastyle and behind stylar cusp C of Bensley (1903). The anterior ridge from the protocone runs to a protoconule which is developed in M^1. There is a metaconule in M^{1-3} and, in addition, either a low ridge or a cuspule between the metaconule and the base of the metacone. A posterior cingulum runs well labiad in M^{1-3}, extending farthest on M^1.

Discussion. — The lower teeth of *Phascogale calura* (tables 5-9) are readily distinguishable from those of *P. tapoatafa* (tables 10-12) by their substantially smaller size. *P. calura* is somewhat larger than *Antechinus flavipes leucogaster*, its premolars are slightly broader and more massive, and the entoconids tend to be relatively better developed.

The mandibles and lower dentitions of *P. calura* from Madura Cave cannot be distinguished from those from Hasting's Cave and Wedge's Cave, Western Australia, and comparisons with a Recent specimen (FM 36052, fig. 6) show a close similarity.

Most of the lower dentition of *Phascogale calura*, both fossil and Recent, is so similar in size and proportions to that of a Recent specimen of *Antechinus flavipes rufogaster* that they could be easily confused. There are differences that appear to be valid. A comparison of the Recent specimens shows the lower canine of *P. calura* to be larger and more massive than that of *A. f. rufogaster*; the I_1 of *P. calura* is larger than that of *A. f. rufogaster*. Specimens PM 4798-4800 from Madura Cave all have alveoli for large I_1's.

The P_2 of *Phascogale calura* from Madura Cave is longer than that of Recent specimens of *Antechinus flavipes rufogaster* and *A. f. leucogaster* (fig. 3A, B; tables 1, 5, 6). The principal cusp of the P_4 of *A. f. rufogaster* when viewed from the labial side is relatively higher, and is slightly more extensive anteroposteriorly than that of the Recent *P. calura*. The Madura Cave fossils conform to the *P. calura* pattern. Also, the labial cingulum of the P_4 dips lower over the posterior root in both fossil and Recent specimens than it does in *A. f. rufogaster* and the paraconid of the M_1 is larger in both the Recent and Madura Cave specimens of *P. calura* than it is in *A. f. rufogaster*.

This taxon is represented by samples from three statigraphic levels within trench 4 (units 1, 2, and 4-5) and equivalent units from trenches 1, 2, 3, and 5 that are large enough to allow a check on possible size change through time. An examination of Tables 5-7 shows that there was no significant change, although mean values of some measures show a decrease from older to younger units.

Comparison of the upper dentitions with the Recent specimen (FM 36052) shows that the M^1 of the fossil has a slightly developed stylar cusp behind cusp D which is lacking in the Recent specimen. There are no other differences in morphology or size in the upper dentition worthy of mention (tables 8, 9).

This species has not been recorded living from the Nullarbor Plain, but the presence of its remains throughout the entire known sequence in Madura Cave and surface deposits in other caves on the Nullarbor Plain (Lundelius, 1963) indicates that it was an element of the Pleistocene and sub-Recent fauna that has only recently disappeared from this region. Its current distribution is in more humid parts of southwestern Australia, in the Adelaide area, and in isolated refugia near Alice Springs and the junction of the Murray and Darling Rivers (Jones, 1923; Marlow, 1962). According to Ride (1970), it is an inhabitant of sclerophyll forest and woodland. This distribution pattern plus its recent disappearance from the Nullarbor Plain suggests that the species was very widespread until fairly recently and that the environment has continued to deteriorate since the end of the Pleistocene.

?Phascogale calura

Material. —

Trench 4

Unit 2, level 1
PM 25581, left ramus fragment with P_4, M_1; alveoli for C, P_{2-3}, anterior root M_2

Description. — This specimen has a P_4 that is oval, with the principal cusp located in the anterior half of the tooth and a well-developed cingulum all around the tooth. The long axis is oriented 45° off the axis of the tooth row, and the M_1 overlaps the posterior half of the P_4 lingually.

The M_1 has a trigonid with the protoconid as the largest cusp, followed by the metaconid and paraconid. The talonid has a small entoconid which has been eliminated by wear.

Discussion. — This specimen resembles the Madura Cave *Phascogale calura* in every character except the larger overall size of the M_1 and the greater development of the anterior part of the trigonid. The larger size is primarily in the anteroposterior length. It is probable that this specimen is a larger example of *Phascogale calura*, but we are calling attention to it on the chance that it represents another taxon.

Phascogale tapoatafa (Meyer), 1793. Tables 10-12; Figures 5B, 9, 10A-B, 15

Material. —

LOWER DENTITIONS

Trench 4
Unit 1, level 1
PM 29437, left M_3
PM 29438, left ramus fragment with M_4

Unit 2, level 2
PM 30580, left ramus fragment with broken M_1; M_2; alveoli for C, P_{2-4}, M_3

Units 4-5
PM 29901, right ramus fragment, edentulous, alveoli for M_{2-4}
PM 29902, right ramus, edentulous, alveoli for C-M_4
PM 29903, left ramus fragment with P_4, partial M_1; alveoli for I_1-P_3, M_2
PM 29904, right ramus with C-M_4, alveoli for I_{1-2} (fig. 10A, B)
PM 29905, right ramus with M_{3-4}, alveolus for M_2

WAM 74.9.17, right ramus fragment with M_{1-2}, anterior part M_3, alveoli for C-P_4

Description. — *Phascogale tapoatafa*, the largest of the phascogalines, is not well represented in the Madura Cave material. Only nine specimens with teeth have been recovered, and none from the 1954 excavation (Lundelius, 1963). We have had only one Recent specimen (TMM M-838; fig. 9) and four fossil specimens (PM 30438-PM 30441) from Western Australia for comparison.

P. tapoatafa is easily distinguished from its congener, *P. calura*, by its much greater size (tables 5-12). It usually can be distinguished from the comparably-sized dasyurines, *Dasycercus* and *Dasyuroides*, by the presence of double-rooted P^4's. The P^4 of *P. tapoatafa* is approximately the size of the P^3, while the P_4 is much smaller than the P_3. In *Dasycercus* the P^4's are usually much reduced or absent, but occasionally the P_4's approach the size of those of *P. tapoatafa*. In *Dasyuroides* the P_4 is absent or represented by a small vestige of a tooth, while the P^4 is variable — most often double-rooted and somewhat smaller than the P^2 or P^3, but sometimes reduced to a single-rooted peg. Our one Recent specimen of *Dasyuroides* (FMNH 104786) has a single-rooted RP^4; however, the LP^4 is not present.

Mandibles: The mandibular ramus has no features that are strongly divergent from those of other comparably-sized phascogalines. There is some variation in the depth of the horizontal ramus in the Madura Cave specimens which is related to the different ages of the individuals at death. The anterior border of the ascending ramus is more horizontally inclined than that of *Sminthopsis*, *Dasycercus*, or *Dasyuroides*, but is less inclined than in *Antechinomys*. The masseteric fossa is deep and is bordered both dorsally and ventrally by well defined ridges. The lower of these ridges is the larger and is flared to a distinct, laterally projecting shelf between the base of the angular process and the condyle. The coronoid process in lateral view is broad anteroposteriorly at its apex and has a small, slightly posteroventrally directed point.

The condyle is located slightly above the tooth row, closer to the coronoid than to the angular process. Its articular surface is oval and convex upward as in the one Recent specimen that is available for comparison. The dental canal opens immediately above the base of the angular process. There are two or three

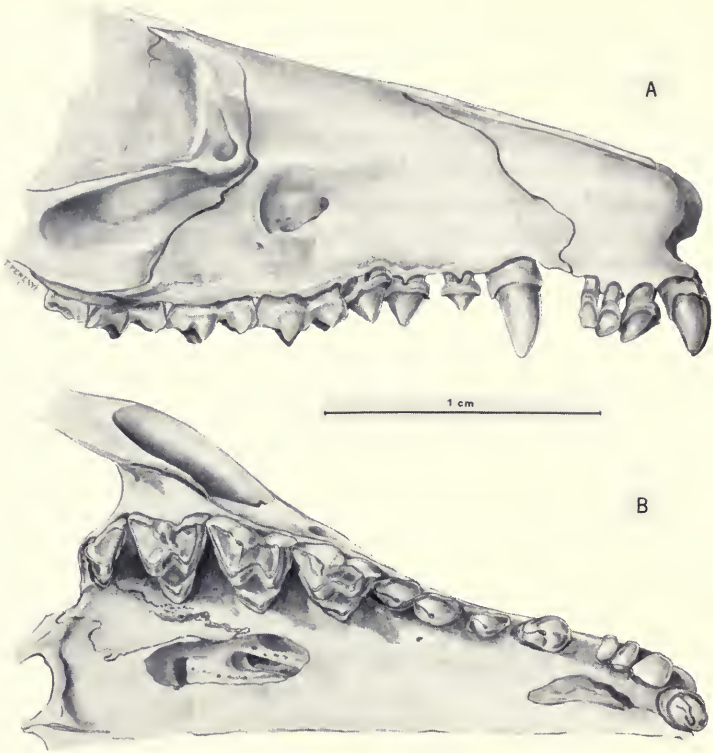


FIG. 9. *Phascogale tapoatafa*. TMM M 838. **A, B,** Rostrum with right upper dentition shown in labial and crown views.

mental foramina. The posterior one(s) open beneath the M_1 in all the Madura Cave specimens and in the Recent specimen. The anterior one opens beneath either the P_2 or P_3 in the fossils. In the Recent specimen the anterior foramina opens beneath P_3 on the right side, and beneath P_4 on the left.

Lower Dentitions: None of the fossil *P. tapoatafa* from Madura Cave preserve the lower incisors, but two specimens, PM 29903 and PM 29904, have alveoli for the incisors. The alveoli provide some information about these teeth. The alveoli show that there were three lower incisors, that I_1 was much larger than the other two, and that all three were procumbent. This is also the situation in the Recent specimen.

The canine (PM 29904) is large, procumbent, and somewhat incisiform, and it is long and broad at the base. The lingually

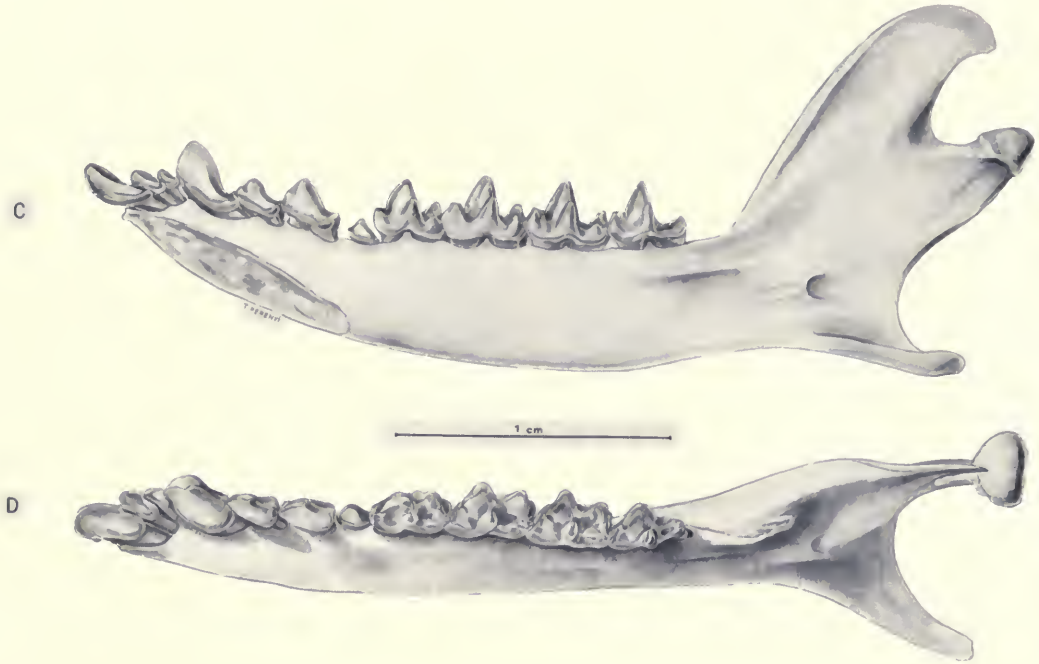


FIG. 9. **C, D**, Right ramus with lower dentition shown in lingual and crown views.

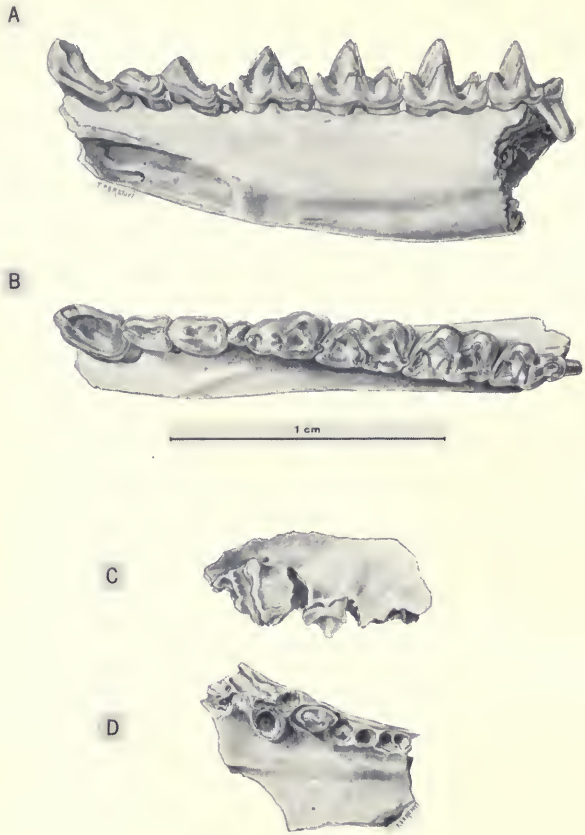


FIG. 10. **A, B**, *Phascogale tapoatafa* from Madura Cave, PM 29904. Right ramus with canine through M_4 shown in lingual and crown views. **C, D**, *Dasyuroides byrnei*, PM 30437 from Madura Cave. Right maxillary fragment with P^4 alveoli of P^{2-3} and M^1 shown in labial and crown views. Originally identified as ?*Phascogale tapoatafa*, assignment revised on basis of Figure 15E.

recurved main cusp has a longitudinal ridge that climbs its anterior edge to the apex and runs down the posterior side of the cusp to the center of the posterior cingulum; the posterior half of this ridge is very weak. A strong cingulum extends from the anterolingual corner posteriorly and ventrally around the posterior end of the tooth to the posterolabial corner. At the posterior end of the tooth there is a small cingular cuspule. Wear takes place on the posterolingual side of the main cusp. The canine shows no structural differences from the Recent specimen.

There are three premolars, all of which are double-rooted. The P_2 and P_3 are subequal, similar in morphology, and are nearly twice the length of the P_4. The first two are elongate with their long axes in line and parallel to the long axis of the tooth row. They are bluntly pointed anteriorly, and the squared posterior edge of each has a weak groove near its midpoint into which the adjoining tooth fits. The P_3 may even overlap P_2 slightly. The principal cusp of each is located in the anterior one-third of the tooth. The posterior edge is a ridge that extends backward across a talonid-like area to the posterolabial corner of the tooth where it joins a small cingular cusp. The posterior occlusal surfaces of both P_2 and P_3 are flattened. This feature becomes emphasized with wear. The first two premolars each have a cingulum that is large on the sides and posterior end and is weaker anteriorly. The P_4 is oval in shape and about half the length of the anterior premolars. It is oriented *en echelon* to the other teeth, with more than half of its length located labial to the anterior end of M_1. It has one main cusp, which is located anterior to the midpoint of the tooth and which is joined to cingular cusps anteriorly and posteriorly by ridges. A cingulum encircles the tooth. The premolars of the known *P. tapoatafa* fossil specimens show no differences in structure from those of the Recent specimen; however, they are larger in the fossil (tables 10-12) and are more crowded in the jaw.

The lower molars have the usual dasyurid structure of a high trigonid and a low talonid. The M_1 is distinctive, is narrower anteriorly than the other molars, and retains a functional paraconid. The paraconid is well formed but is much smaller relative to the protoconid and metaconid than it is in the posterior molars; the paraconid is located almost directly anterior to the protoconid. This condition pertains in the three Madura Cave specimens (PM 29904, WAM 74.9.17, PM 30580), as well as in the one Recent specimen available (TMM M-838) and in the three specimens from Wedge's Cave (PM 30439, 30440, 30441). This results in an anteroposterior orientation of the paracristid (I′). Despite this reduction, there is a distinct, well-developed (though small) carnassial notch in the paracristid. The protoconid is taller and about twice the size of the metaconid. They are joined by a short but well-formed epicristid (II′, III′) with a distinct carnassial notch. The epicristid is oriented approximately 45° to the long axis of the tooth. In crown view the talonid is strongly basined and broad, almost as broad as in $M_{2\text{-}3}$. The hypoconid is by far the

largest cusp of the talonid. It is joined to the base of the protoconid by the cristid obliqua, which has a small notch close to the protoconid. The hypoconulid is the smallest and the posteriormost cusp of the talonid. It is joined to the hypoconid by the postmetacristid (I′). It protrudes backward into a notch in the front edge of the adjacent tooth. The entoconid is larger than the hypoconulid, stands nearly as high as the paraconid, and forms the internal border of the talonid basin. It is laterally compressed at its base but becomes conical toward the apex. A ridge, the entocristid (V), joins it to the metaconid. The entocristid, like the cristid obliqua, has a small but distinct notch close to the epicristid. The entoconid and hypoconulid are separated by an open groove. The floor of the talonid basin is smooth and featureless. Well-developed cingula extend posteriorly on both sides of the tooth from the paraconid. The labial cingulum is part of the main cingulum of the tooth. The lingual cingulum disappears abruptly anterior to the base of the metaconid. This produces a distinct lingual bulge anterior to the metaconid.

The M_2 and M_3 are similar in size and morphology. The trigonids of $M_{2\text{-}4}$ are almost identical. In each the protoconid is the largest cusp, followed by the metaconid and the paraconid. The protoconid is joined to the paraconid by the paracristid and to the metaconid by the epicristid. Both of these cristids have prominent carnassial notches as in the other dasyurids. All three teeth have blade-like parastylids that project forward and lie linguad of the hypoconulid of the preceding tooth. The paraconid and metaconid are separated by an open valley. The talonids of $M_{2\text{-}3}$ are deeply basined and much alike and, except for their slightly larger size relative to the entire tooth, resemble the talonid of M_1.

The talonid of M_4 is reduced in *Phascogale tapoatafa* as in all dasyurids. The Madura Cave sample shows some variation in the size of this structure. All three cusps of the talonid are present on the two M_4s that are available, although they are much reduced in size. The talonids of both teeth have distinct basins.

All the lower molars have cingula on their labial, anterior and posterior borders. The cingulum is weak where it skirts the protoconids and hypoconids and absent on the posterior side of M_4. The anterior cingulum is prominent on $M_{2\text{-}4}$ and ends at a notch that receives the hypoconulid of the preceding tooth. The posterior cingulum is prominent on $M_{1\text{-}3}$ and joins the hypoconulid.

Discussion. — The lower dentition of *Phascogale tapoatafa* can be readily distinguished from other similar-sized forms (*Dasycercus* and *Dasyuroides*) on the basis of the presence of a P_4, the structure of the trigonid of M_1, and the well-developed basin of the M_4. Neither of these other genera has the well-developed paraconid and expanded anterior end of the M_1 or the broadly basined talonid on M_4. In both *Dasycercus* and *Dasyuroides*, the anterior ends of M_1 are highly compressed laterally, and the paraconids are reduced. The metaconids are relatively much smaller than the protoconids and are located more posteriorly than in *P. tapoatafa*. The talonids of the M_4's in *Dasycercus* and *Dasyuroides* are much reduced, and if they are basined, they are much narrower. *P. tapoatafa* can also be distinguished from *Dasycercus* by its larger size and the large size of the entoconids of the lower molars. The entoconids in *Dasycercus* are low and in cross-section are narrowly elliptical. Unfortunately, these last two characters will not reliably separate *P. tapoatafa* from *Dasyuroides*.

Phascogale tapoatafa is known to occur as a living animal in the coastal area of southern Queensland, New South Wales, and Victoria; in the area of Adelaide, South Australia; in extreme southwestern Australia; in the Kimberly District; and from northeast of Kalgoorlie, Western Australia eastward to the border (Marlow, 1962; Ride, 1970). This would place it immediately north of the Nullarbor Plain, if not on it. It appears that this species has long been a resident of the Nullarbor Plain. Its absence from stratigraphic units other than Units 1, 2, and 4-5 is probably the result of sampling accidents.

Subfamily Dasyurinae Gill, 1872

cf. **Parantechinus** Tate, 1947

cf. **Parantechinus apicalis** (Gray), 1842. Tables 13-14; Figures 5A, 11, 15.

Material. —

Trench 1

Top first foot (possibly Unit 1)

PM 25330, right ramus fragment with M_1, anterior half M_2, M_4; alveoli for I_{1-3}, C, P_{2-4}, posterior alveolus for M_2, alveolus for M_3 (fig. 11)

Description. — We have no Recent comparative materials of

this taxon. Our comparisons are based on a few Holocene fossils (PM 7268-7270) collected from Hasting's Cave, Western Australia, in 1954 and compared directly with Recent specimens in the collections of the Western Australian Museum at that time.

The horizontal ramus is shallow and slender and has the normal dasyurid form, with a convex ventral margin. The ascending ramus is incomplete but appears to have had a wide masseteric fossa with the anterior margin steeply inclined with respect to the tooth row. There are three mental foramina — a posterior one located under the M_1 and two anterior ones located under P_3 and P_2, respectively.

The alveoli for the P_2 and P_3 are oriented slightly *en echelon* to the tooth row, and the alveolus for the anterior root of P_2 opens into that of the canine. Between the posterior alveolus for the P_3 and the M_1 is a small circular alveolus 0.5 mm. in diameter for a single-rooted P_4.

The M_1 is deeply worn, and part of the anterior end is broken. As a result, little can be said about the trigonid. The metaconid is in the same position relative to the protoconid as in the M_1 of specimens of *Parantechinus apicalis* from Hasting's Cave, Western Australia. The talonid has a well-developed hypoconid and a posteriorly projecting hypoconulid, as in the Hasting's Cave specimens. The presence or absence of an entoconid cannot be determined because of the worn condition of the tooth. The postcingulum is large and extends around the base of the hypoconid to the base of the protoconid. The development of this cingulum is variable in the Hasting's Cave sample, but the degree of development of the Madura Cave specimen is matched by specimen PM 7268.

The M_2 is so incomplete that little can be learned from it. A broad anterior cingulum that does not reach the parastylid is present.

The M_4 has a well-developed trigonid. The protoconid is the largest cusp. The metaconid and paraconid are subequal in size, but breakage of the former renders a precise determination of relative size impossible. The metaconid appears to have been higher than the paraconid, which is more massive. The paracristid and protocristid have well-developed carnassial notches. The talonid is narrow and basined with a small but distinct hypoconid with a weak cristid obliqua. No entoconid is discernable. The anterior cingulum is broad but does not reach the blade-like parastylid.

Discussion. — In all these characters except size (tables 13,

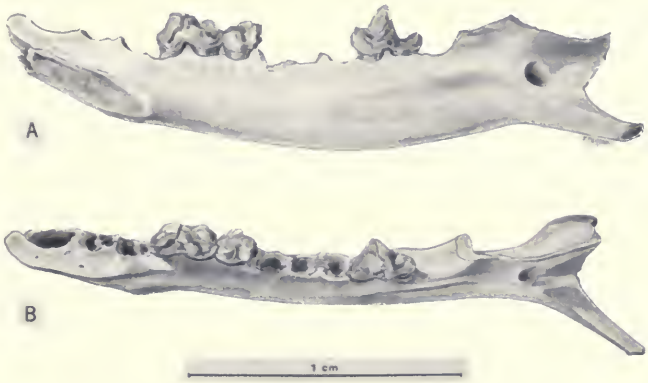


FIG. 11. *Parantechinus apicalis* from Madura Cave. PM 25330 right ramus with M_1, M_2 broken, M_4 and alveoli for canine, premolars, posterior root of M_2 and M_3, shown in (**A**) lingual and (**B**) crown views.

14; fig. 11) this specimen resembles the Recent sample and the sample of *Parantechinus apicalis* from Hasting's Cave. In tooth size this specimen is larger than the Hasting's Cave specimens and is much more comparable to *Dasycercus cristicauda*, but the depth of the horizontal ramus is less than in *D. cristicauda* and is similar to that of *P. apicalis*. The trigonids of M_1 and M_4 are narrower and less massive than those of *D. cristicauda* (fig. 15A, B, C). These features, plus the presence of the P_4, lead to the identification as *P. apicalis*.

Dasycercus Peters, 1875

Dasycercus cristicauda (Krefft), 1867. Tables 15-18; Figures 5A, 12-15.

Material. —

LOWER DENTITIONS

Trench 1

Top first foot (possibly Unit 1)

PM 6070, right ramus with C-M_4, alveoli for incisors
PM 6071, right ramus with C-M_2, M_4; alveoli for incisors, M_3
PM 6072, left ramus with P_2-M_4, alveoli for incisors, C
PM 6073, left ramus with C-M_2, alveoli for incisors, M_{3-4}
PM 6074, right ramus with C-M_4, alveoli for incisors
PM 6075, left ramus with C, P_3, M_{3-4}; alveoli for incisors, P_2, M_{1-2}
PM 25331, left ramus with C, P_2, alveoli for other teeth

Trench 2

2½ ft. below surface (possibly Unit 2)

PM 6233, left ramus with M_{1-4}; alveoli for incisors, C, P_{2-3}

PM 25264, left ramus, edentulous, with ascending ramus, angular process

PM 25265, right ramus fragment with M_4

Trench 3

Unit 2

TMM 41106-127, right ramus, edentulous

PM 25586, left ramus, edentulous

PM 25588, right ramus fragment with M_{2-4}

WAM 74.9.19, left ramus fragment with M_{2-3}; alveoli for two incisors C-M_1

Unit 3

PM 29383, right ramus fragment with M_{2-3}; alveoli for C, P_{2-3}, M_1, M_4

PM 29390, left ramus fragment with M_3; alveoli for M_2, M_4

PM 29391, right ramus fragment with M_3, broken M_4

Trench 4

Unit 1, level 1

TMM 41106-517, right ramus with M_1; alveoli for P_{2-3}, M_{2-4}

PM 29911, left ramus fragment with M_2, part M_3

PM 29912, left ramus fragment with M_3 (or M_2)

Unit 2

PM 30443, left ramus fragment with P_{2-3}, broken M_1; alveoli for one incisor, C

Unit 2, level 1

WAM 74.9.20, right ramus fragment with M_{1-3}

PM 29430, right ramus fragment with M_2; alveoli for P_{2-3}, M_1, M_3

Unit 2, level 2

TMM 41106-16, left ramus fragment with P_3, M_{1-2}

PM 30444, left ramus fragment with M_3, alveolus for M_2 (or M_2, alveolus for M_1)

PM 30445, left ramus fragment with M_2; alveoli for M_{3-4}

Units 4-5

PM 25553, right ramus fragment with broken M_3; alveoli for one incisor, C, P_{2-3}, rest of molars

PM 29426, left ramus fragment with M_4; alveoli for M_{2-3}
PM 29446, right ramus with M_{1-4}; alveoli for P_{2-3} (fig. 13C,D)
PM 29447, left ramus fragment with M_{1-3}, broken M_4, alveolus for P_3
PM 29448. right ramus fragment with M_3; alveoli for M_2, M_4
PM 29449, left ramus fragment with M_2; alveoli for P_2-M_1, M_3
PM 29450, right ramus fragment with M_{2-3}; alveoli for C, P_{2-3}, M_1
PM 29451, left ramus fragment with M_3; alveoli for M_{1-2}, M_4
PM 29452, left ramus fragment with M_3; alveoli for M_2, M_4
PM 29453, left ramus fragment with M_3; alveoli for M_2, M_4
PM 29454, right ramus fragment with M_2; alveoli for P_{2-3}, M_1, M_3
PM 29455, right ramus fragment with M_{1-2}, alveolus for P_3
WAM 74.9.21, left ramus fragment with M_1, alveoli for P_{2-3}, M_2
PM 30446, right M_4
PM 30447, left M_4 (or M_3) broken

Unit 5
WAM 74.9.22, right ramus fragment with M_4, alveolus for M_3
PM 29418, right ramus fragment with M_2; alveoli for M_1, M_3
PM 29419, left ramus fragment with M_4
PM 29420, right ramus fragment with M_{2-4}
PM 29421, right ramus fragment with M_4; alveoli for M_{2-3}
PM 29422, left ramus fragment with M_{1-3}; alveoli for C-P_3, M_4
WAM 74.9.23, right M_2

Unit 7, level 1
PM 29415, right ramus fragment with M_4

Trench 5

Unit 4
PM 29427, right ramus with M_3; alveoli for P_2-M_2

Unit 5
PM 29428, right M_3
PM 30448, right ramus fragment with M_4; alveoli for M_{2-3}

Upper Dentitions

Trench 1

Top first foot (possibly Unit 1)
PM 6067, right maxillary with P^2, M^{1-4}; alveoli for C, P^{3-4}
PM 6068, right maxillary with P^{2-4}, M^{1-4}, alveolus for C, (fig. 14A, B)

PM 6069, left maxillary with M^{1-4}; alveoli for C-P^3

Trench 3

Unit 2

PM 25589, left maxillary fragment with M^3, roots for M^4

Unit 2, level 2

PM 29368, left maxillary fragment with M^{2-4}

WAM 74.9.24, left maxillary fragment with M^{2-4}

Trench 4

Unit 2, level 1

PM 25591, left maxillary fragment with M^{3-4}

PM 25592, left maxillary fragment with M^{2-3}

Unit 2, level 2

WAM 74.9.25, right maxillary fragment with M^2

Units 4-5

PM 29439, right maxillary fragment with M^{2-3}; alveoli for C, P^{2-3}, M^1, M^4

PM 29440, left maxillary fragment with M^3; alveoli for M^2, M^4

PM 29441, right maxillary fragment with M^1; alveoli for C, P^{2-3}, M^2

PM 29442, right maxillary fragment with M^3; alveoli for M^2, M^4

PM 29443, left maxillary fragment with M^3; alveoli for M^2, M^4

PM 29444, right maxillary fragment with M^3; alveoli for M^2, M^4

WAM 74.9.26, right maxillary fragment with M^3; alveoli for M^2, M^4

PM 29461, right M^3

Trench 5

Unit 5

PM 29429, right M^3 (or M^2)

Description. — **Mandibles**: The mandible is robust, and the horizontal ramus is relatively deep. The ascending ramus is broad with the condyle widely separated from the coronoid process. The anterior edge is inclined at a steep angle to the tooth row. The coronoid process is short, broad, and only slightly turned posteriorly. The central part of the ventral edge of the masseteric

fossa is expanded laterally to form a broad shelf. The condyle is high above the level of the tooth row. Its articular surface is elliptical in shape and is gently convex anteroposteriorly. Despite the robustness of the mandible, there are no rugosities for muscle attachments on the medial surface of the ascending ramus except that for the deep portion of the *M. temporalis*. On one specimen, PM 6072, there is a mylohyoid groove that extends anterior from just below the mandibular foramen.

The mandibular symphysis is ligamentous and extends from the anterior end of the mandible posteriorly to the position of the anterior end of M_1. A prominent foramen is present near the center of the symphyseal surface. There are two mental foramina, an anterior one opening under P_2 and a posterior one under M_1.

Lower Dentitions: The lower dentition of *Dasycercus* is characteristic of the more advanced dasyurids (e.g., *Dasyuroides*, *Dasyurus*, *Sarcophilus*) in the absence of the P_4. Although none of the Madura Cave specimens have the incisors preserved, the alveoli of some specimens (PM 6072-6075, TMM 41106-407) show that three were present, as in the Recent population.

The canine is prominent and stands almost vertically in the jaw. It is recurved posteriorly and slightly inwardly. There is a basal cingulum which is weak externally and strong internally. The cingulum rises on the tooth anteriorly and joins a low, longitudinally oriented ridge on the anterior face of the tooth, best seen on an unworn specimen (PM 6073). In these characters the canines of *Dasycercus* differ from those of *Phascogale tapoatafa* in which they are strongly procumbent with a well-developed posterior shelf.

The P_2 and P_3 are both oval to subquadrate in shape. Each has a principal cusp located in the anterior half of the tooth, which is connected to anterior and posterior cingular cuspules by low crests. A cingulum encircles each tooth. The posterior border of P_2 has a concavity into which the anterior end of P_3 fits. The apex of the principal cusp of P_3, when unworn, turns lingually.

The M_1 is narrow and tapers anteriorly. The trigonid is highly compressed laterally with a large, centrally-placed protoconid and with a much smaller metaconid located very close to the protoconid. The paraconid is reduced to a small cingular cuspule on the anterior end of the tooth. The talonid is basined in the unworn state but becomes flat as wear reduces the bordering cusps. The hypoconid is approximately as tall as the metaconid when

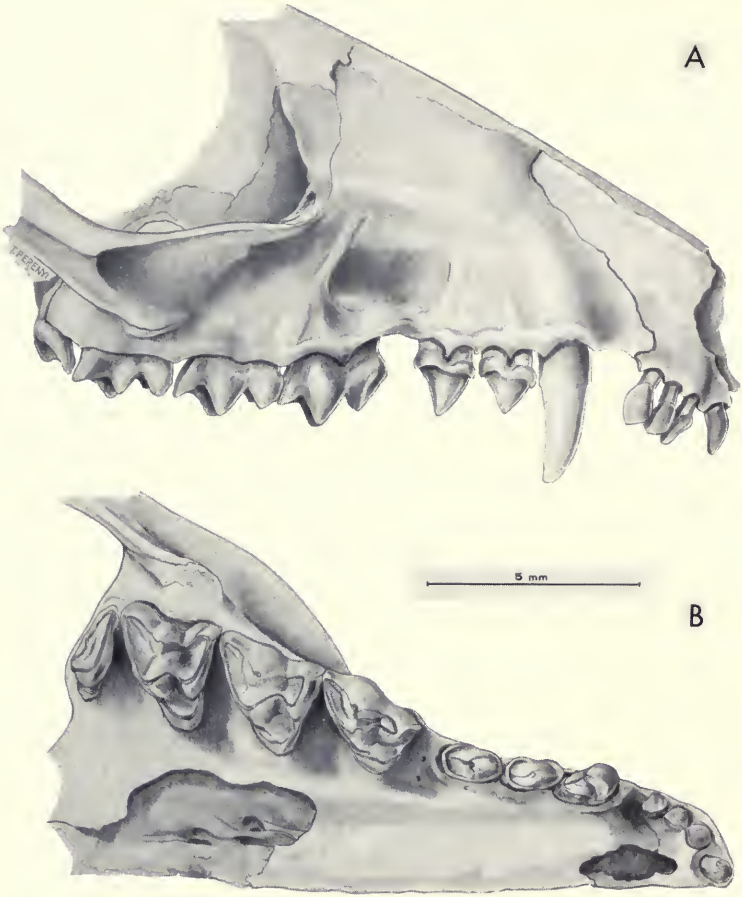


FIG. 12. *Dasycercus cristicauda* AMNH 15009. **A, B,** Rostrum with right upper dentition shown in labial and occlusal views.

unworn. The premetacristid from the hypoconid and the postparacristid from the protoconid almost meet on the labial side of the talonid to form a narrow slit that is similar to the carnassial notches in the paracristid and epicristid. The lingual border of the talonid has a small entoconid whose shape in cross-section is that of an elongate ellipse. The hypoconulid is located at the posterior end of the tooth only slightly lingual to the midline of the tooth. The postmetacristid joining the hypoconid and hypoconulid is oriented more anteroposteriorly, especially the posterior part, than it is in M_2 and M_3. A cingulum extends from the vestigial paraconid around the labial side of the tooth to the hypoconulid.

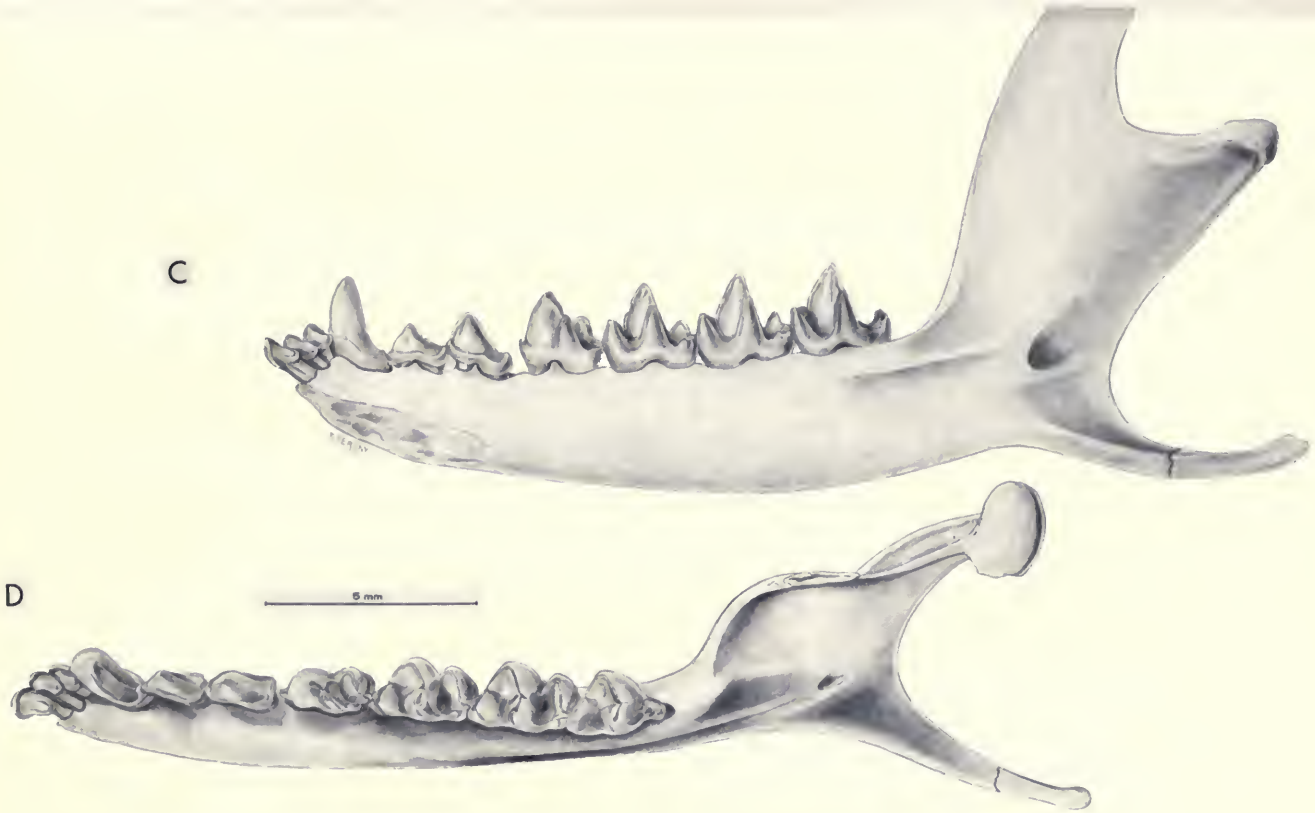


FIG. 12. **C, D**, Right ramus with lower dentition shown in lingual and occlusal views.

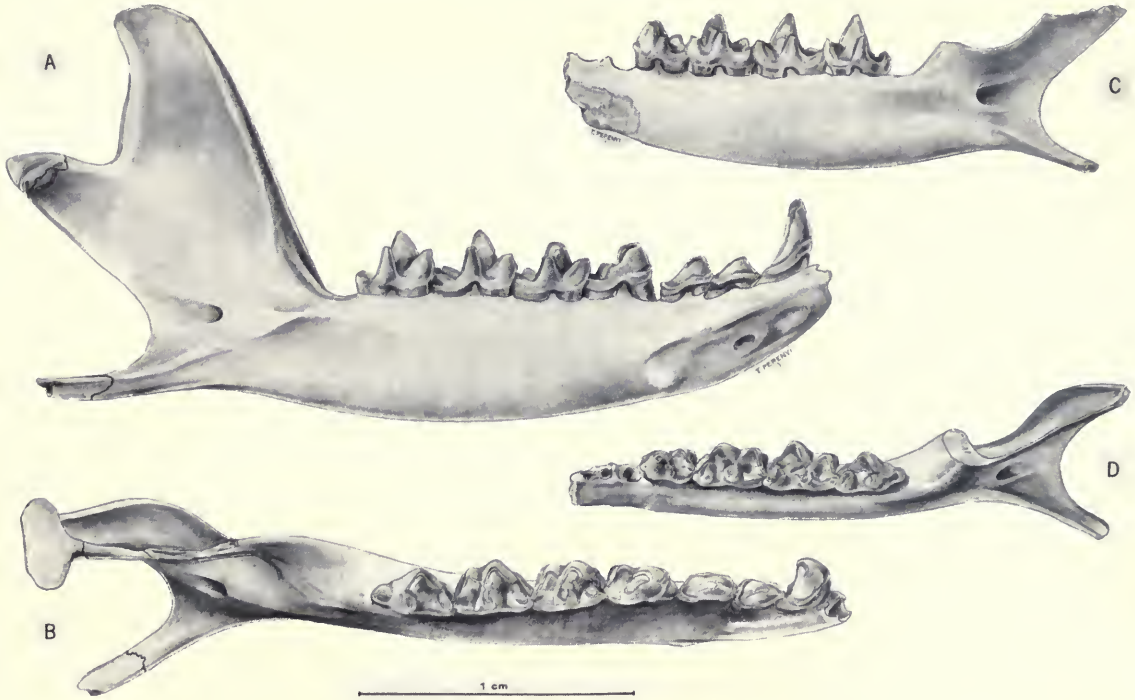


FIG. 13. *Dasycercus cristicauda* from Madura Cave. **A, B**, PM 6072. Left ramus with canine through M_4 and incisor alveoli shown in lingual and crown views. Condyle, angular process, and canine restored from PM 6075. **C, D**, PM 29446. Right ramus with M_{1-4}, alveoli for P_{3-4} shown in lingual and crown views.

The M_2 and M_3 are similar in size and morphology. The trigonid has no features that distinguish it from those of other dasyurids of comparable size. The talonid is basined when unworn. When worn it becomes shallower and flatter. It is bordered labially by the hypoconid which, in contrast to the condition in the M_1, is not as high as the metaconid. As in the M_1, the premetacristid and postparacristid meet and form a tight notch on the labial side of the talonid. The talonid is bordered lingually by the entoconid which is somewhat variable in size but usually is low and elongate. The hypoconulid is the posteriormost part of the tooth. A broad cingulum is present on the anterior and posterior ends of the tooth. It is not present around the bases of the protoconid and hypoconid and does not reach the parastylid because of the notch for the hypoconulid of the next anterior tooth.

The M_4 has a trigonid that differs from those of the M_2 and M_3 only in its slightly smaller size (tables 15-16). The talonid is reduced and may or may not be basined. In those specimens in which it is basined, a vestigial hypoconid can be identified, but no entoconid is discernable.

Maxillaries and Upper Dentitions: The identified skull material of this taxon from Madura Cave is limited to maxillary fragments. These show that the infraorbital foramen is large and opens above the M^1. A subsidiary canal leaves the main canal and extends into the parietal part of the maxillary. The infraorbital canal usually opens into a well-defined fossa on the lateral surface of the maxillary, but occasionally no fossa is developed. No incisors or canines are preserved. Alveoli for the canines are preserved in some specimens which show that the size of the canine in the fossils was comparable to that of the Recent specimen and to a sample of Recent to sub-Recent specimens from Murraelelleven Cave.

Two of the specimens, PM 6067-8, have the upper premolars preserved, and specimens PM 6069, PM 29441, and PM 29439 have the alveoli for P^{2-3}. These show that P^2 and P^3 are double-rooted and about the same size as those of the Recent specimen. Two specimens, PM 6068, which has a P^4, and PM 6069, which has an alveolus for P^4, indicate that the tooth was single-rooted as in the Recent specimen. In PM 6067 the P^4 which has been broken off or shed was smaller than that of PM 6068. The absence of the alveolus in the other two specimens is consistent with a sample of 29 specimens (18 left, 20 right) from post-Pleistocene deposits in Murraelellevan Cave in which the tooth is missing on

one or both sides in 30-33 per cent of the sample. When present, the tooth shows considerable variation but almost always is a single-rooted peg. One specimen (PM 4880) from Murraelellevan Cave has premolars that raise a question as to the identity of the peg-like tooth usually termed the P^4. This is discussed in the section dealing with *Dasyuroides byrnei*.

The M^1 is triangular and asymmetrical, with the protocone located as far anterior as the paracone. The stylocone and paracone are apparently fused. The parastyle is an anteriorly projecting process. It is connected to an anterior cingulum that extends only half way across the base of the paracone. The metacone and stylar cusp C are approximately equal in size and are close together but distinct. The protocone is triangular with convex sides. A distinct protoconule is located at the lingual edge of the base of the paracone. The posterior margin of the protocone extends posteriorly around the base of the metacone in varying degrees. There is no posterior cingulum.

The M^2 is triangular and slightly asymmetrical. The labial edges of the major stylar cusps are almost in line, resulting in a nearly straight edge for the stylar shelf. There is a moderate embayment in the labial edge of the stylar shelf between cusp C and the metastyle. The metacone is the tallest cusp, followed in order of decreasing size by cusp C, the stylocone, and the paracone. A short cingulum is present from the parastyle to the midpoint of the base of the paracone. The sides of the protocone are straight to convex. A well-defined protoconule is present at or immediately anterior to the lingual edge of the paracone. The posterior border of the protocone may extend onto the posterior side of the metacone. There is no posterior cingulum. A small cusp D is located on the edge of the stylar shelf just anterior to the metastyle.

M^3 is a triangular, symmetrical tooth with the protocone located at the apex of the triangle. Stylar cusp C is located lingual to a line that connects the stylocone and the metastyle. The metacone is the tallest cusp, followed closely by cusp C, then the stylocone, paracone, and metastyle. Small, ridge-like stylar cusps B_1 and D are present. The protocone is triangular with straight to convex margins. A protoconule is present anterolingual to the base of the paracone, and a metaconule is present posterolingual to the base of the metacone. The edges of the protocone do not extend around the paracone or metacone.

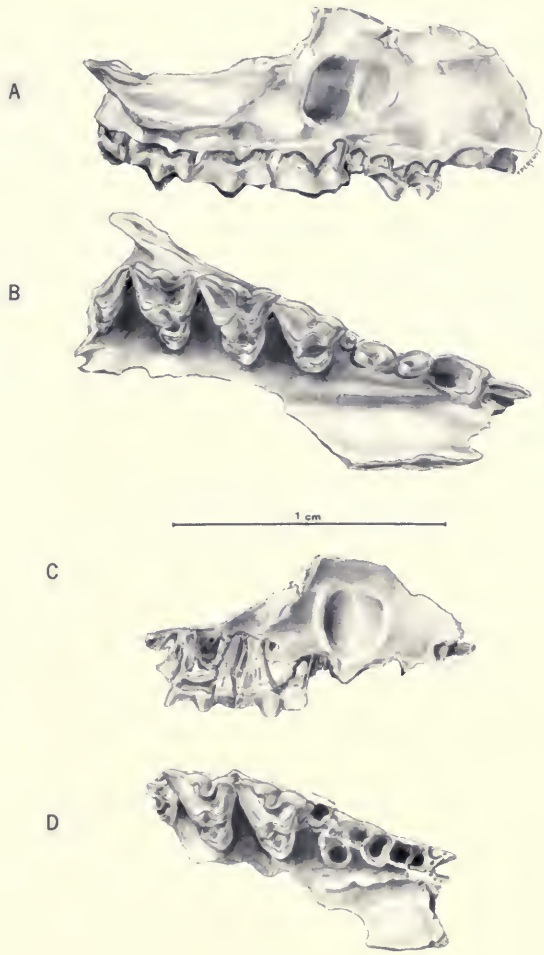


FIG. 14. *Dasycercus cristicauda* from Madura Cave. **A, B**, PM 6068. Right maxillary with P^2 - M^4, alveoli for canine shown in labial and crown views. **C, D**, PM 29439. Right maxillary fragment with M^{2-3}, alveoli for P^3 - M^1, M^4 shown in labial and crown views.

M^4 is much reduced posteriorly. The stylocone and paracone — the largest cusps — are widely separated and are joined by a slightly sinuous paracrista which is oriented transverse to the tooth row. The metacone is small and poorly separated from the paracone. The stylar shelf is a narrow, posteriorly sloping surface with no cusps. The protocone is a small, lingually rounded cusp

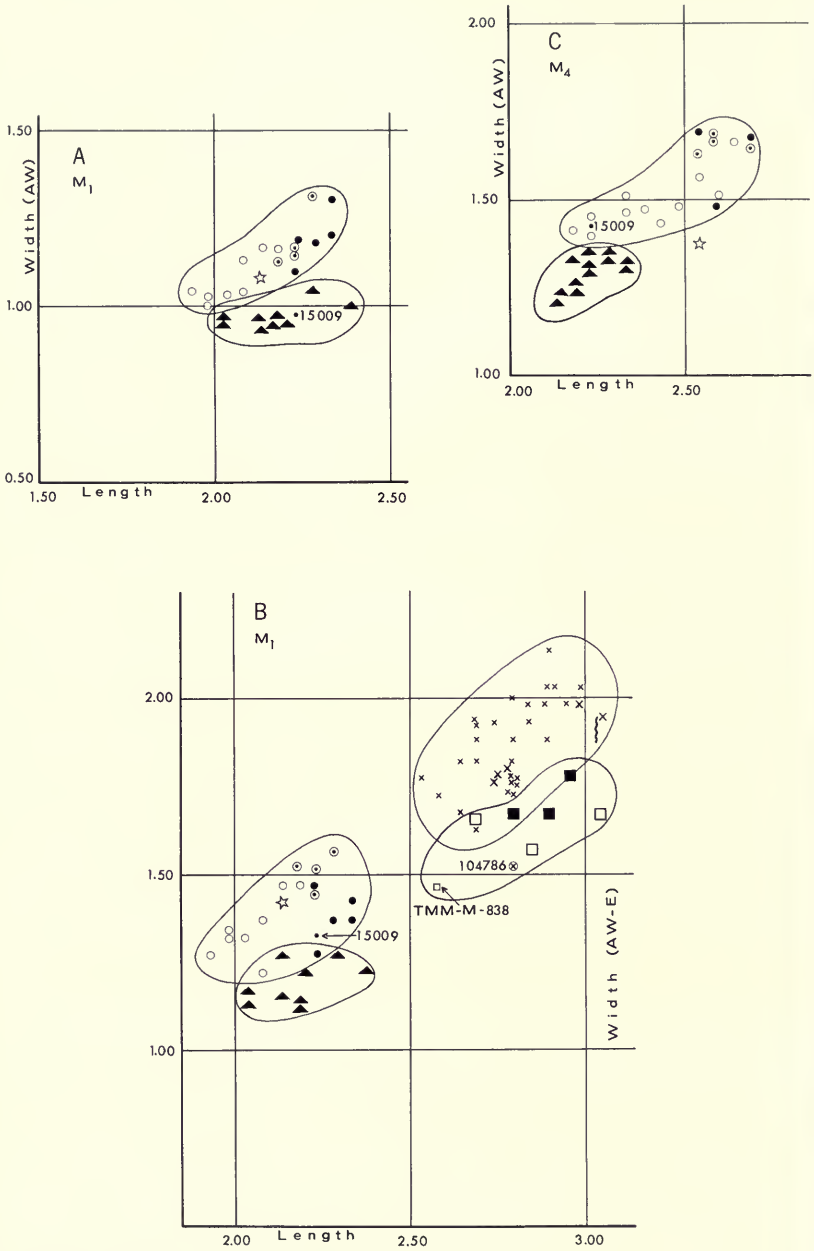
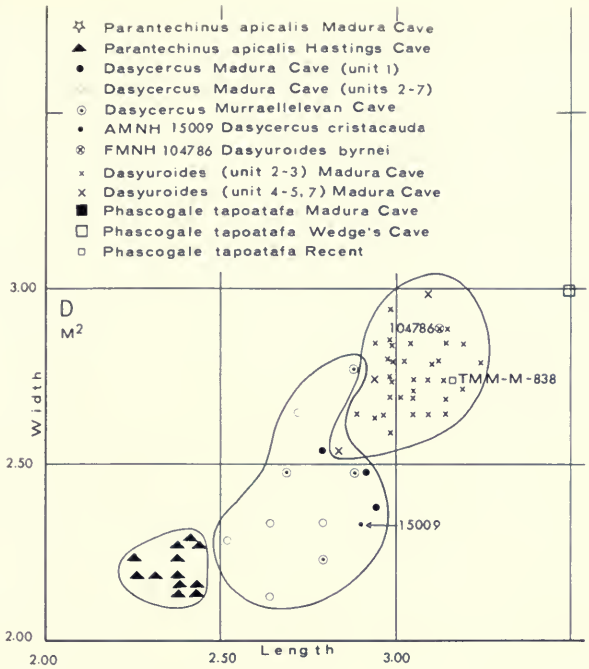


FIG. 15. Bivariate graphs comparing various dental measures of *Parantechinus apicalis*, *Dasycercus cristicauda*, *Dasyuroides byrnei*, and *Phascogale tapoatafa*.


Parantechinus apicalis Madura Cave
Parantechinus apicalis Hastings Cave
Dasycercus Madura Cave (unit 1)
Dasycercus Madura Cave (units 2-7)
Dasycercus Murraellelevan Cave
AMNH 15009 Dasycercus cristacauda
FMNH 104786 Dasyuroides byrnei
Dasyuroides (unit 2-3) Madura Cave
Dasyuroides (unit 4-5, 7) Madura Cave
Phascogale tapoatafa Madura Cave
Phascogale tapoatafa Wedge's Cave
Phascogale tapoatafa Recent
D
M2
Width
Length
3.00
2.50
2.00
2.00
2.50
3.00
104786
TMM-M-838
15009

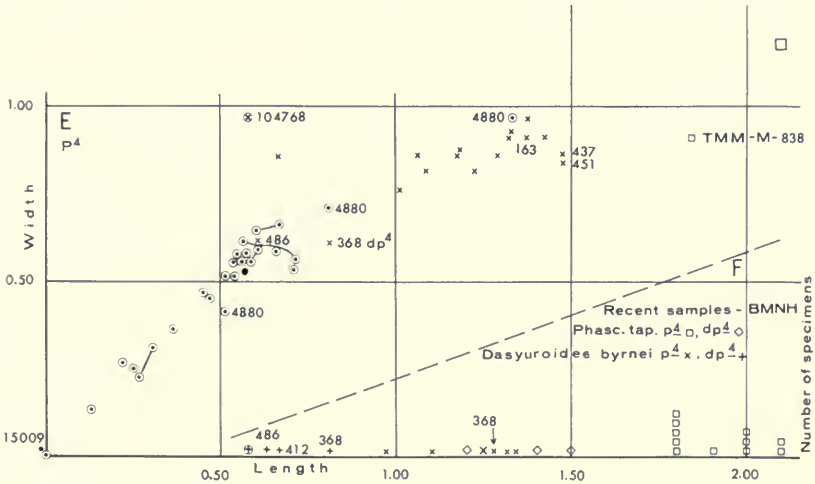

E
P4
Width
Length
1.00
0.50
15009
0.50
1.00
1.50
2.00
104768
4880
163
437
451
TMM-M-838
4880
486
368 dp4
F
4880
Recent samples - BMNH
Phasc. tap. p4 □, dp4 ◇
Dasyuroides byrnei p4 x, dp4 +
368
486
412
368
Number of specimens

FIG. 15

located lingual to the paracone. Its margins extend around the base of the paracone. An anterior cingulum is present from the stylocone to the midpoint of the paracrista.

Discussion. — Two species of *Dasycercus* have been described: *D. cristicauda* from the Nullarbor Plain and central Australia and *D. blythi* from northwestern Australia. They are distinguished on the basis of the lack of a P^4 in the latter species; Ride (1970) indicates that they may be conspecific. More information on the nature of the zone of contact between the two populations is needed to establish the validity of the two species. The Madura Cave material is assigned to *D. cristicauda* on the basis of the presence of the P^4.

Criteria for distinguishing the lower dentition of *Dasycercus cristicauda* from that of *Phascogale tapoatafa* have been discussed in the section dealing with the latter taxon. It can be distinguished from that of *Dasyuroides byrnei* on the basis of the slightly smaller size of most of the molar teeth (tables 15-16, 19-23; figs. 5, 15), the form of the M_1, and the size of the entoconids on M_1 through M_3. The M_1 of *Dasycercus cristicauda* has a smaller paraconid and smaller anterior cingulum than *Dasyuroides byrnei*. The entoconids are smaller and more ridge-like on all lower teeth of *Dasycercus cristicauda*. The entoconids of the M_2 and M_3 of *Dasyuroides byrnei* are almost as high as the hypoconids and are almost circular in cross-section at their apices. The lower canine of *Dasycercus cristicauda* is straighter, with a less well-developed base than that of *Dasyuroides byrnei*.

The upper dentition of *Dasycercus cristicauda* differs from that of *Dasyuroides byrnei* in its generally smaller size and less massive form. This is usually reflected in the more robustly developed metacone and the consequent greater anteroposterior length of the M^4 in the latter taxon (tables 17, 23; figs. 12A, B; 14A, B; 16A B; 17A, B). The P^4 of *Dasycercus cristicauda* is a single-rooted tooth, while in *Dasyuroides byrnei* it is double-rooted and usually has a more complex crown.

The presence of *Dasycercus cristicauda* in the Madura Cave deposits is not unexpected in view of its presence in the Recent fauna. This species is widely distributed in desert areas in the central part of Australia where it occupies sandridge, stony desert, and spinifex grassland situations (Ride, 1970). Its presence in the lower units of Madura Cave indicates that it inhabited more humid areas in the past.

An examination of Tables 15-17 and Figure 15A, B, C suggests that the species underwent a size increase between the time of deposition of unit 2 and unit 1. The differences between various dental measures of the two samples were tested for statistical significance by means of the Mann-Whitney U test (Siegel, 1956, pp. 116-126). The results are summarized in Table 18.

The measures that show statistically significant differences at $P \lesssim .05$ are those of the molars, primarily the lengths. This trend toward larger size is contrary to that shown by most mammals through the Pleistocene-Recent transition, but it is not unknown. Kurtén (1965) has shown that the red fox (*Vulpes fulva*) in the Palestinian cave sequence increased in size through this time. Such changes may reflect some improvement of a limiting environmental requirement.

Dasyuroides Spencer, 1896

Dasyuroides byrnei Spencer, 1896. Tables 19-24; Figures 5B, 15-17.

Material. —

LOWER DENTITIONS

Trench 3

Unit 2

WAM 74.9.27, left ramus with broken M_2, M_{3-4}, alveoli for P_{2-3}

TMM 41106-369, right ramus with M_{2-4}; alveoli for other teeth

TMM 41106-370, right ramus with P_3, M_{2-3}; alveoli for P_2, M_1, M_4

TMM 41106-371, right ramus fragment with M_{2-4}

TMM 41106-372, left ramus fragment with M_{1-4}; alveoli for P_{2-3}

TMM 41106-373, right ramus with P_3, M_{1-4}; alveoli for other teeth

TMM 41106-374, right ramus with dP_4 or P_4, M_{1-4}; alveoli for incisors, C, P_{2-3}, ?dP_3. (fig. 17E, F.)

WAM 74.9.28, left ramus fragment with P_2, broken P_3, M_{1-4}

TMM 41106-376, left ramus with P_3-M_4, alveoli for other teeth

TMM 41106-377, right ramus fragment with M_{1-4}; alveoli for P_3, dP_4, or P_4

TMM 41106-378, right ramus with M_{1-4}; alveoli for C-P_3

TMM 41106-379, left ramus with P_3-M_4; alveoli for other teeth
TMM 41106-380, right ramus with P_3, M_{2-4}; alveoli for C, P_2, M_1
WAM 74.9.29, right ramus with P_3-M_4; alveoli for other teeth
WAM 74.9.30, right ramus fragment with M_{1-3}; alveoli for C, P_{2-3}, M_4
TMM 41106-383, right ramus with P_{2-3}, M_{1-3}; alveoli for other teeth
TMM 41106-384, right ramus fragment with P_3-M_4, alveolus for P_2
TMM 41106-385, left ramus fragment with M_2; alveoli for P_3, M_1, M_{3-4}
TMM 41106-386, left ramus, edentulous, with alveoli for all teeth
TMM 41106-387, left ramus fragment with M_{2-3}; alveoli for incisors, C, P_2-M_1
TMM 41106-388, right ramus with M_{1-4}; alveoli for other teeth
TMM 41106-389, left ramus fragment with M_{2-3}; alveoli for C, P_{2-3}, M_1, M_4
TMM 41106-390, right ramus fragment with M_{2-4}
TMM 41106-391, right ramus fragment with M_{2-4}, alveoli for M_1
TMM 41106-392, right ramus fragment with M_{2-4}, alveoli for M_1
TMM 41106-393, right ramus fragment with broken P_3, M_{1-3}; alveoli for C, P_2
TMM 41106-394, left ramus fragment with M_{3-4}, alveoli for M_2
TMM 41106-395, left ramus fragment with P_3, M_{2-3}; alveoli for C, P_2, M_1
TMM 41106-396, left ramus fragment with M_3, alveoli for M_4
TMM 41106-397, left ramus fragment with M_{3-4}
TMM 41106-398, right ramus fragment with M_{1-3}; alveoli for incisors, C, P_{2-3}
PM 25583, left ramus fragment with P_3, alveoli for M_1
PM 28360, left ramus fragment with M_2; alveoli for C, P_{2-3}, M_1
PM 28361, right ramus fragment with M_4
PM 29356, right ramus fragment with M_3; alveoli for M_{1-2}, M_4
PM 29357, left ramus fragment with M_1; alveoli for C, P_{2-3}
PM 29359, right ramus fragment with P_3-M_1; alveoli for incisors, C, P_2, M_2

PM 29362, right ramus fragment with M_{2-4}
PM 29363, right ramus fragment with M_{1-3}; alveoli for C, P_{2-3}
PM 29364, left ramus fragment with M_4
PM 29365, left ramus, edentulous, (juv.)
PM 29366, left ramus fragment with M_{2-4}
PM 29367, right ramus fragment with P_3-M_4; alveoli for C, P_2
PM 30506, right ramus fragment with M_{2-4}

Unit 2, level 2

TMM 41106-138, right ramus, edentulous, with alveoli for all teeth
TMM 41106-401, left ramus with P_{2-3}, M_{1-4}
TMM 41106-403, right ramus with M_{1-4}; alveoli for incisors, C, P_{2-4}
TMM 41106-404, left ramus fragment with M_{3-4}, alveoli for M_2
TMM 41106-406, right ramus with P_3-M_4; alveoli for C, P_2
TMM 41106-407, left ramus with M_{1-3}, broken M_4; alveoli for other teeth
TMM 41106-409, right ramus fragment with M_3; alveoli for M_{1-2}, M_4
TMM 41106-410, left ramus fragment with M_3; alveoli for M_2, M_4
PM 29370, right ramus fragment with M_4

Unit 3

TMM 41106-48, right ramus with M_{2-4}; alveoli for C-M_1
TMM 41106-49, left ramus with M_{2-4}; alveoli for C-M_1
TMM 41106-50, right ramus with M_{2-4}, alveoli for M_1
PM 29384, right $M_{2 \text{ or } 3}$
PM 29385, left ramus fragment with M_4, alveoli for M_3
PM 29386, right ramus fragment with M_{3-4}, alveoli for M_2
PM 29387, right ramus fragment with M_2; alveoli for M_1, M_{3-4}
PM 29388, right ramus fragment with M_4; alveoli for M_{2-3}
PM 29389, left ramus fragment with M_4
PM 30563, right ramus fragment, edentulous, with alveoli for M_{3-4}

Trench 4

Unit 1, level 1

PM 30507, left ramus fragment with M_3, alveolus for M_4
PM 30508, left ramus fragment with broken M_1; alveoli for P_3, M_{2-3}
PM 30509, right ramus fragment with M_{2-3}

Unit 2, level 1

PM 30459, right ramus with M_{1-4}; alveoli for other teeth
PM 30460, right ramus with M_{1-4}; alveoli for C, P_{2-3}
PM 30461, right ramus with P_3-M_4; alveoli for other teeth
PM 30462, right ramus fragment with M_{2-4}
PM 30463, right ramus with M_{3-4}; alveoli for other teeth
PM 30464, right ramus fragment with M_{3-4}
PM 30465, right ramus fragment with M_{2-4}
PM 30466, left ramus fragment with M_4, alveolus for M_3
PM 30467, left ramus with C, P_{2-3}, M_{2-4}; alveoli for incisors, M_1
PM 30510, right ramus fragment with $M_{2 \text{ or } 3}$
PM 30511, right ramus fragment with M_{2-3}; alveoli for incisors, C, P_{2-3}, M_1
WAM 74.9.31, right ramus fragment with M_{2-3}; alveoli for M_1, M_4
WAM 74.9.32, right ramus fragment with M_3; alveoli for M_{1-2}

Unit 2, level 2

PM 30482, left ramus with M_{2-4}; alveoli for P_3, M_1
PM 30483, left ramus fragment with M_3, broken M_4
PM 30484, left ramus fragment with M_{3-4}
PM 30485, left ramus fragment with $M_{2 \text{ or } 3}$, alveolus for $M_{3 \text{ or } 4}$
PM 30491, right ramus fragment with M_{3-4}
WAM 74.9.33, right ramus with P_{2-3}, M_{1-4}; alveoli for incisors, C. (fig. 17G, H)
WAM 74.9.34, right ramus fragment with M_4
PM 30494, right ramus with M_{2-4}; alveoli for other teeth
PM 30495, right ramus with P_3-M_4; alveoli for other teeth
PM 30496, right ramus fragment with M_{2-3}; alveoli for M_4
PM 30497, left ramus with M_{2-4}; alveoli for other teeth
PM 30498, left ramus fragment with M_3, broken M_4
PM 30499, left ramus fragment with M_4
PM 30500, left ramus fragment with M_{1-2}, roots of M_3

Units 4-5

PM 29457, left ramus fragment with M_4
PM 30514, left ramus fragment with M_{3-4}
PM 30515, left ramus fragment with $M_{2 \text{ or } 3}$
PM 30516, right ramus fragment with M_4, alveolus for M_3
PM 30517, right ramus with M_{2-4}; alveoli for C-M_1 including P_4 or dP_4
PM 30518, right ramus fragment with M_1; alveoli for incisors, C, P_{2-3}, M_2

PM 30519, right ramus fragment with M_4

Unit 5

PM 29423, right ramus fragment with M_4; alveoli for M_{2-3}
PM 29424, left ramus fragment with M_3; alveoli for M_2, M_4

Unit 7 (or possibly Unit 5)

PM 30472, right ramus with P_{2-3}; M_{1-3}; alveoli for incisors, C, M_4
PM 30473, right ramus fragment with M_{2-3}; alveoli for P_3, M_1, M_4
PM 30474, right ramus fragment with M_{2-4}
PM 30475, right ramus with M_{2-4}; alveoli for C-M_1
PM 30476, right ramus with M_{2-4}; alveoli for C-M_1
PM 30477, right ramus fragment with P_3; alveoli for incisors, C, P_2-M_{1-2}
PM 30478, right ramus fragment with M_3; alveoli for M_{1-2}; M_4
PM 30479, right ramus fragment with M_4
PM 30480, right ramus fragment with M_{2-4}
PM 30481, left ramus fragment with broken M_2, M_{3-4}; alveoli for M_1

Unit 7, level 2

PM 29392, left ramus fragment with M_3; alveoli for M_2, M_4
PM 29393, right ramus with M_{3-4}; alveoli for P_2-M_2
PM 29394, right ramus fragment with M_3 (or $_2$); alveoli for $M_{2 \text{ and } 4}$ (or $M_{1 \text{ and } 3}$)
PM 29395, left ramus fragment with M_{2-3}; alveoli for P_{2-3}, M_1
PM 29396, right ramus fragment with M_1; alveoli for P_3, M_2
PM 29397, right ramus fragment with P_{2-3}, M_2; alveoli for C, M_1, M_3
PM 29398, right ramus fragment with M_{3-4}, alveoli for M_2
PM 29399, left ramus fragment with M_{2-4}, alveoli for M_1
PM 29400, right ramus fragment with M_2; alveoli for C, P_{2-3}, M_1
PM 29401, left ramus fragment with M_4; alveoli for M_{1-3}
PM 29402, right ramus fragment with M_{3-4}; alveoli for M_{1-2}
PM 29403, right ramus fragment with M_1; alveoli for C, P_{2-3}, M_{2-4}, also minute pits possibly for P_4 or dP_4

Trench 5

Unit 5 or 6

PM 30501, left ramus fragment with M_1; alveoli for C, P_{2-4}, M_2

Upper Dentitions

Trench 3

Unit 2

TMM 41106-364, right maxillary with P^{3-4}, M^{1-4}, alveoli for C, P^2 (fig. 17A, B)

TMM 41106-365, right maxillary with M^{1-4}, alveoli for C, P^{2-4}

TMM 41106-368, left maxillary with dP^4, unerupted P^4, M^{1-2}; alveoli for C, P^{2-3}, M^3, (fig. 17C, D)

PM 29348, right maxillary with P^4, roots of dP^4, M^{1-3}; alveoli for C, P^{2-3}, M^4

PM 29349, right maxillary fragment with M^{2-3}, alveolus for M^4

PM 29350, right maxillary with M^{1-3}, alveoli for C, P^{2-4}, M^4

PM 29351, right maxillary fragment with M^{2-4}

PM 29353, right maxillary with M^{1-2}; alveoli for P^{2-4}, M^{3-4}

WAM 74.9.35, right maxillary fragment with M^1; alveoli for C, P^{2-4}

WAM 74.9.36, left maxillary fragment with P^{2-3}; alveoli for C, P^4, M^1

Unit 2, level 4

PM 26163, right maxillary fragment with P^4; alveoli for C, P^{2-3}, M^1

Unit 3

TMM 41106-51, left maxillary fragment with M^{2-3}, alveolus for M^4

PM 29379, right maxillary with P^4-M^2; alveoli for C, P^{2-3}, M^{3-4}

PM 29380, left maxillary with P^4-M^4; alveoli for P^{2-3}

PM 29381, right maxillary fragment with M^{2-3}; alveoli for M^1, M^4

PM 29382, left maxillary fragment with M^1; alveoli for M^{2-4}

Unit 3, level 2

TMM 41106-323, left maxillary fragment with P^4-M^3, alveolus for M^4

TMM 41106-324, right maxillary with M^{1-3}; alveoli for C, P^{2-4}, M^4

TMM 41106-325, left maxillary with M^{1-4}; alveoli for P^{2-4}

TMM 41106-411, left maxillary with M^{1-2}, broken M^3; alveoli for C, P^{3-4}, M^4

TMM 41106-412, right maxillary with M^{1-2}; alveoli for C, ?dP^4, M^3

TMM 41106-413, left maxillary fragment with P^{2-4}, M^1, alveolus for C

WAM 74.9.37, left maxillary fragment with M^2, broken M^3, M^4, alveolus for M^1
PM 29371, left maxillary fragment with M^3; alveoli for M^2, M^4
PM 29372, left maxillary fragment with M^1, roots of dP^4 (nearly resorbed), crypt for P^4, alveolus for M^2
PM 29373, left maxillary fragment with M^1
PM 29374, left maxillary fragment with M^{1-2}
PM 29375, left M^3
PM 29376, right maxillary fragment with $M^{2 \text{ or } 3}$
PM 29377, left maxillary fragment with M^3; alveoli for M^2, M^4
PM 29378, right maxillary fragment with M^{3-4}

Trench 4

Unit 1, level 1
TMM 41106-511, right maxillary fragment with M^{1-4}; alveoli for P^{2-4}

Unit 2, level 1
WAM 74.9.38, left maxillary with P^4-M^3; alveoli for P^{2-3}, M^4
PM 30469, left maxillary fragment with M^1; alveoli for C-P^4
PM 30470, right maxillary fragment with M^{1-4}; alveoli for P^{3-4}
PM 30471, right maxillary fragment with M^{1-2}, alveolus for M^3
PM 30486, right maxillary with P^{3-4}, M^{1-4}; alveoli for C, P^2
PM 30487, right maxillary fragment with M^{1-3}, alveolus for M^4
PM 30488, right maxillary fragment with P^{3-4}, M^1, alveolus for P^2
WAM 74.9.39, right maxillary fragment with M^3; alveoli for M^2, M^4
WAM 74.9.40, right maxillary with P^4-M^2; alveoli for C, P^{2-3}, M^3

Unit 2, level 2
PM 29407, right maxillary with P^4-M^4, alveolus for P^3
PM 29408, right maxillary fragment with M^2; alveoli for M^{3-4}
PM 29409, left maxillary fragment with M^{2-3}, alveolus for M^1
PM 29410, right maxillary fragment with M^2
PM 29411, right maxillary fragment with M^2, alveolus for M^1
PM 29412, right maxillary with M^1, broken M^2, M^{3-4}; alveoli for C-P^4
PM 30449, left maxillary fragment with M^3; alveoli for M^2, M^4
PM 30450, right maxillary fragment with M^3; alveoli for M^{1-2}; M^4

WAM 74.9.18, right maxillary fragment with P^4; alveoli for C, P^{2-3}, M^1
PM 30452, right maxillary fragment with M^3; alveoli for M^2, M^4
PM 30453, left maxillary fragment with broken M^3; alveoli for M^2, M^4
PM 30454, left maxillary fragment with M^1; alveoli for C, P^{2-4}
PM 30455, right maxillary fragment with M^{1-2}, alveolus for M^3
PM 30456, right maxillary fragment with P^4, M^1
PM 30457, left maxillary fragment with M^2; alveoli for M^1, M^3
PM 30458, right maxillary fragment with P^4, M^1; alveoli for C, P^{2-3}

Units 4-5
PM 30504, left maxillary fragment with $M^{2 \text{ or } 3}$
PM 30505, right maxillary fragment with M^3; alveoli for M^{1-2}, M^4

Unit 7, level 1
PM 29414, left maxillary fragment with M^3; alveoli for M^2, M^4
WAM 74.9.41, left maxillary fragment with M^2; alveoli for M^{3-4}

Unit 7, level 2
PM 29404, left maxillary fragment with M^3; alveoli for M^2, M^4
PM 29405, left maxillary fragment with M^3; alveolus for M^4
PM 29406, ?left M^3

Trench 5

Unit 5
PM 30437, right maxillary fragment with P^4; alveoli for P^{2-3}, M^1 (fig. 10C, D)

Unit 5 or 6
PM 30502, right maxillary fragment with M^3, alveolus for M^4
PM 30503, left $M^{2 \text{ or } 3}$

Description. — **Mandibles**: The mandible of *Dasyuroides byrnei* is similar to that of *Dasycercus cristicauda*. The horizontal ramus is convex ventrally and has two mental foramina, one under the M_1 and one under the posterior end of P_2. The anterior border of the ascending ramus rises steeply above the tooth row; the masseteric fossa is wide.

Lower Dentitions: No specimen has the lower incisors preserved, but a number have alveoli indicating that three lower in-

cisors were present, as in the Recent specimen, and that the teeth were arranged in the same way with the root of the I_1 extending under the roots of the two lateral incisors at depth.

The canine is preserved in only one specimen of *Dasyuroides byrnei* (PM 30467). It is a prominent tooth, recurved posteriorly and lingually. Its base is expanded posteriorly. A lightly defined cingulum extends from the edges of this base anteriorly and upward on each side of the tooth and joins on the anterior edge. The lower part of the posterior edge has a small wear facet where it comes in contact with the upper canine.

The two lower premolars, P_2 and P_3, are similar in size and shape and will be described together. Both are oval in occlusal view and each has one principal cusp located in the anterior half of the tooth. The principal cusp of each has anterior and posterior ridges that extend to cingular cuspules on each end of the tooth. The posterior cuspule is the larger in each premolar. Each is encircled by a cingulum that is more developed posteriorly. The posterior border of P_2 is convex rather than concave as in many phascogalines. The degree of crowding of the premolars is variable. In those specimens in which the premolars are arranged *en echelon*, the posterior end of each tooth is lingual to the anterior end of the following tooth.

There is normally no P_4 present, but three specimens (TMM 41106-373, -374, -377) have either small teeth or alveoli for small teeth that are probably the dP_4 and/or the P_4. The first specimen has a remnant of a tooth root between the P_3 and M_1. TMM 41106-374 has one alveolus for P_2 immediately behind that of the canine, and it is separated from that for the anterior root of the P_3 by a small diastema with a pitted alveolar surface suggesting that the posterior part of P_2 may have been broken away during life, and the alveolus occluded by bone. The alveoli for P_3 appear to be normal sized for *Dasyuroides* but are located slightly more labially than usual. Lingual to the anterior alveolus of P_3 are two tooth fragments which appear to be either the remnants of two small single-rooted teeth, or of a somewhat larger double-rooted tooth. The anterior of these two tooth stubs shares an enlarged alveolus with an unerupted tooth. Lingual to the posterior alveolus of P_3 is a double-rooted tooth with an expanded base and single conical cusp (dimensions: l = .95 mm., w = .65 mm.). TMM 41106-377 has a single rooted P_4 .38 mm. in diameter.

The M_1 is a distinctive tooth. The trigonid is laterally com-

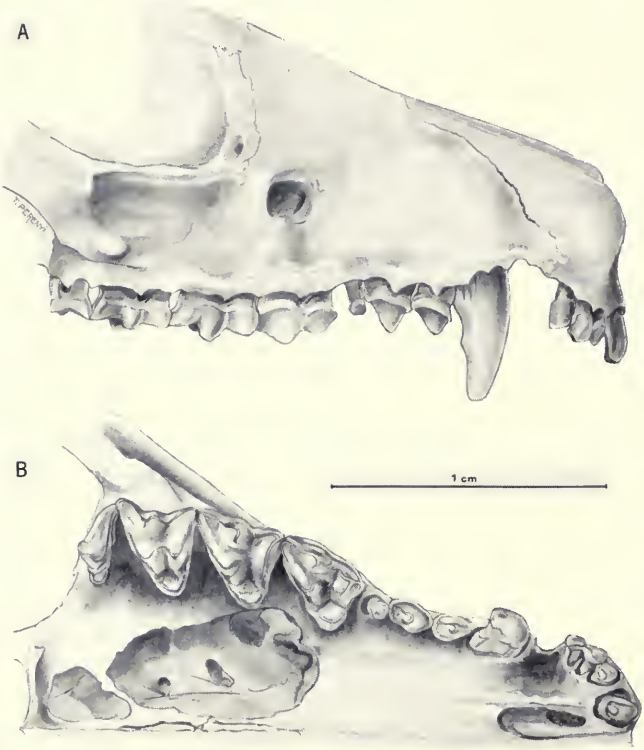


FIG. 16. *Dasyuroides byrnei* FM 104786. **A, B**, Rostrum with right upper dentition shown in labial and crown views, I^4 restored from left side. P^4 not present on left side.

pressed, especially its anterior part. The protoconid is the largest cusp, is located centrally in the anterior part of the tooth, and is elongated anteroposteriorly. The metaconid is much smaller and is located on the posterolingual flank of the protoconid. The paraconid is reduced to a small cingular cuspule on the anterior end of the tooth. The anterior cingulum disappears on the lingual side of the tooth over the anterior root of the tooth. Labially the cingulum is continuous from the anterior end of the tooth to the hypoconulid. In occlusal view the anterolabial corner of the tooth is a right angle. The hypoconid is the largest cusp of the talonid. It is almost as tall as the metaconid and is more massive. The premetacristid (from the hypoconid) is separated from the postparacristid (from the metaconid) by a narrow notch. The hypoconid is connected to the hypoconulid at the posterior end of the tooth by a

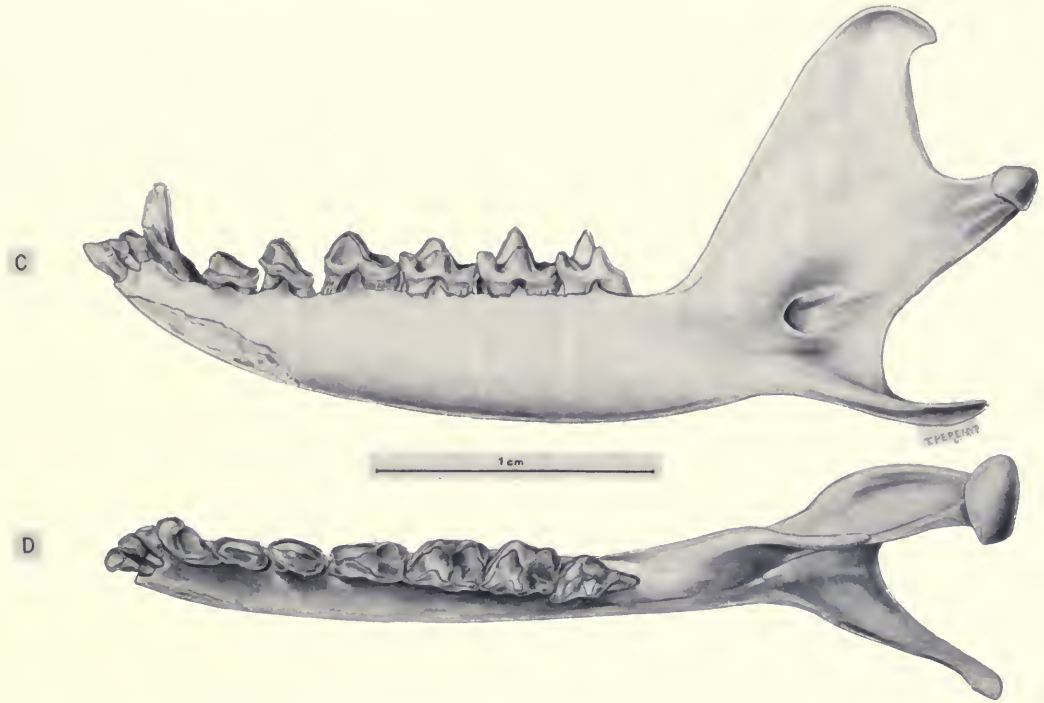


FIG. 16. **C, D**. Right ramus and lower dentition shown in labial and crown views.

continuous postmetacristid that is oriented approximately 30° from the transverse axis of the tooth for most of its length. It turns abruptly posteriorly just as it joins the hypoconulid. The entoconid is somewhat variable in size but is a distinct and well-formed conical cusp on most specimens. It may or may not be joined to the metaconid by a low entocristid. It is joined by a low crest to the postmetacristid at the point where it turns posteriorly to join the hypoconulid. The talonid basin is oval with its long axis extending from the base of the protoconid to the entoconid. The margin formed by the metaconid is noticeably steeper than that formed by the hypoconid.

The M_2 and M_3 are similar in size and morphology and will be described together. The trigonid shows no features that distinguish it from other dasyurids of comparable size. The anterior and posterior cingula are very broad. In occlusal view, the anterior cingulum makes a right angle as it joins the much weaker cingulum on the labial side of the protoconid. The cingulum is variably developed on the labial side of the tooth. In some specimens it is absent on the sides of the protoconid and hypoconid. The talonid basin is square and smooth. The hypoconid is the largest cusp of the talonid. A premetacristid extends anteriorly from the hypoconid and is separated by a narrow cleft from the postparacristid, which runs posteriorly from the protoconid. The entoconid is large in most specimens; in some specimens it stands almost as high as the hypoconid. In a few specimens the entoconid is relatively low and elliptical on one or two of the molars. In one specimen (PM 30467) the entoconids are low and elliptical on all the molars. In its typical form, the entoconid is broadly oval at its base and circular near its apex. The entoconid may be joined to the metaconid by a low entocristid but is separated from the hypoconulid by an open groove. A small cuspule is present on the postmetacristid of most specimens where it turns posteriorly to join the hypoconulid. This cuspule is removed early by wear.

The M_4 differs from the M_2 and M_3 only in the small size of its talonid. The talonid is highly variable in size, but is usually basined and has a hypoconid. A small entoconid is sometimes present. No distinctive hypoconulid is present on the M_4 of any of the Madura Cave specimens, although most have a terminal cingular bulge in this position behind the hypoconid.

Maxillaries and upper dentitions: Skull material of *Dasyuroides byrnei* is limited to maxillary fragments with teeth.

The infraorbital foramen is large and opens over M^1 as in the Recent specimen. Anterior to the upper canine in specimen TMM 41106-413 is the posterior part of the pit into which the lower canine fits when the jaws are occluded.

No incisors or canines are represented in the Madura Cave sample, but alveoli in a number of specimens show that size of the canine tooth in the fossils was comparable to that in the Recent specimen.

The P^2 and P^3 are similar in shape, but the P^2 is markedly smaller than the P^3. They are each oval in shape with a principal cusp located just anterior to the midpoint of the tooth. Each is encircled by a cingulum that is weak, or sometimes absent, lingually. There may be other small interruptions in the cingulum that give an irregular appearance to the edge of the tooth in occlusal view. There are usually cingular cuspules, one at each end of the tooth. The ridge connecting the principal cusp with the posterior cingulum is usually the better defined of the two.

One specimen (TMM 41106-368) has the dP^4 in place and above it a developing P^4 in the crypt (fig. 17C, D). The dP^4 is single-rooted, peg-like oval in crown outline with its long axis oriented obliquely to the tooth row. Its crown consists of a pointed central cusp with tiny anterior, posterior, and labial cingular tubercles.

In the Madura Cave sample the P^4 is variable in size. In most specimens it is small, oval, or triangular in occlusal view. It usually has a distinct central cusp and an encircling cingulum. It may have one or two roots. The larger P^4's (such as PM 30437) may have posterior and labial cingular cuspules. One specimen (PM 30486) has a single-rooted, peg-like tooth in the P^4 position. This tooth is similar to the dP^4 of TMM 41106-368 in size, but unlike that specimen there is no developing P^4 to be found in the maxillary above it. The situation in the Recent materials appears to be similar. The one Recent specimen we have available for comparison (FM 104786) has a peg-like tooth in the P^4 position on the right side, and no tooth on the left. Tate (1947, p. 153) gives length measures of 1.1 and 1.25 mm. for the P^4's of two Recent specimens from central Australia. Our measurements of a small series in the BMNH are 1.09, 1.34, 1.32, and 0.97 mm. These measurements are within the range of size of the undoubted P^4's of the Madura Cave sample (fig. 15E). The resemblance of the small teeth in the Recent specimen and PM 30486 to the un-

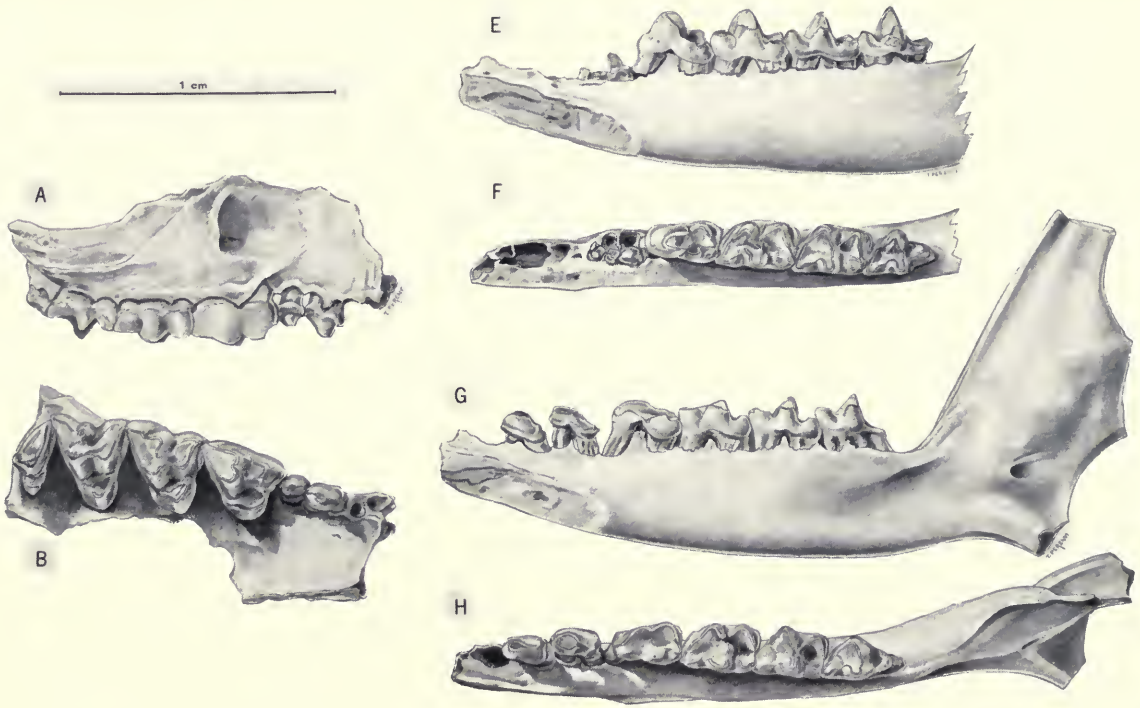


FIG. 17. *Dasyuroides byrnei* from Madura Cave. **A, B**, TMM 41106-364. Right maxillary with P^3 - M^4, alveoli for P^2 shown in labial and crown views. **E, F**, TMM 41106-374. Right ramus with M_{1-4}, anomalous pre-molars and alveoli, alveoli for I_{1-3} and canine shown in lingual and crown views. **G, H**, WAM 74.9.33. Right ramus with P_2 - M_4, alveoli and I_{1-3}, and canine shown in lingual and crown views.

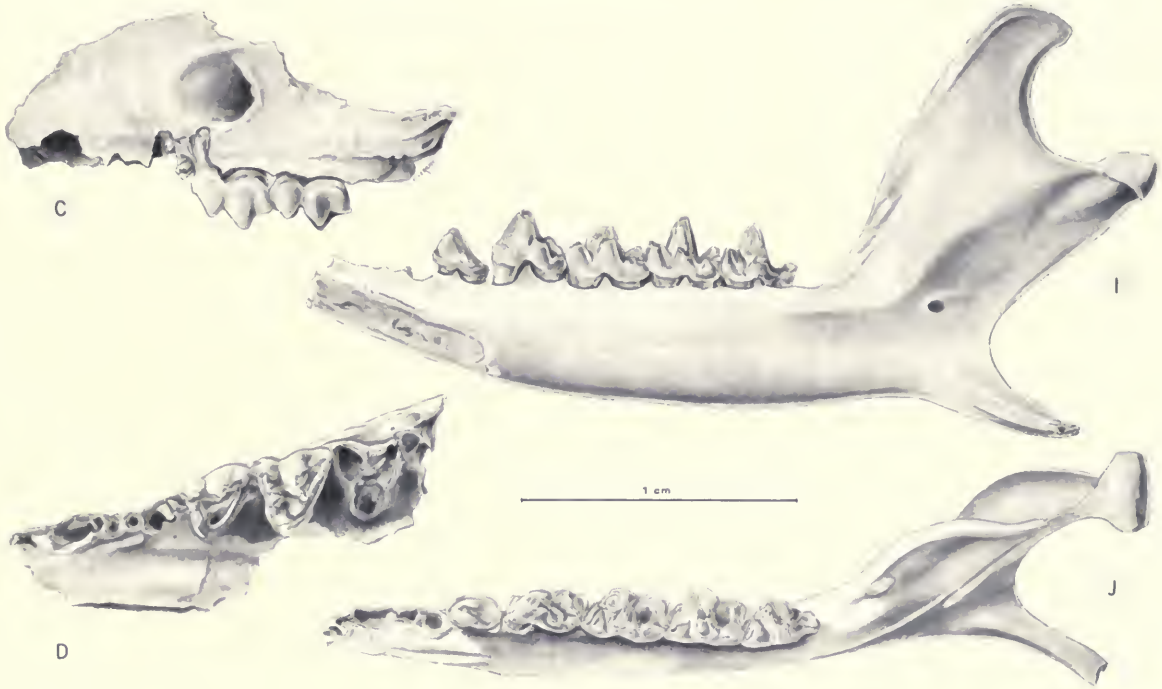


FIG. 17. **C, D**, TMM 41106-368. Left maxillary with DP^4, P^4 - M^2, alveoli for canine — P^3, M^{3-4} shown in labial and crown views. P^4 unerupted. **I, J**, PM 30461. Right ramus with P_3 - M_3, alveoli for I_{1-3} canine and P_2 shown in lingual and crown views.

doubted dP^4 of TMM 41106-368 suggests that the dP^4 is variably retained and in some individuals is not replaced by a P^4.

The peg-like dP^4 of *Dasyuroides byrnei* is similar in size and morphology to the tooth that usually occupies the P^4 position in *Dasycercus cristicauda* (fig. 14A, B; table 17). One specimen in the Murraelellevan sample (PM 4880) has a tooth on its left side that resembles the P^4 of *Dasyuroides byrnei* both in size (fig. 15E) and morphology. On its right side it has two teeth, one resembling the P^4 of *Dasyuroides byrnei* in morphology but not in size and one resembling the usual single-rooted peg seen in the remainder of the *Dasycercus cristicauda* sample. The abnormal situation seen in this specimen, plus the undoubted replacement of a simple dP^4 by a more complex P^4 in *Dasyuroides byrnei* suggest that the usual single-rooted tooth in the P^4 position in *Dasycercus cristicauda* is also a dP^4.

The M^1 has the asymmetrical shape typical of the M^1's of other dasyurids. The metacone is the highest cusp, followed in order by the stylar cusp C, paracone, and protocone. The metacone and stylar cusp C are close together but separated by a deep groove. The stylocone is fused with the paracone, and a distinct parastyle with a short cingulum is present. The protocone is long anteroposteriorly; crests from it extend anteriorly around the metacone. A small protoconule is present. A very indistinct stylar cusp D can be seen close to the metastyle on unworn teeth.

The M^2 is triangular and slightly asymmetrical. The metacone is the tallest cusp, with stylar cusp C only slightly shorter, followed by the stylocone, paracone, and protocone. The labial edges of the major stylar cusps are almost in line, resulting in a nearly straight edge to the stylar shelf.

The M^3 is triangular with stylar cusp C located far lingual to a line that connects the stylocone and the metastyle. The metacone is the tallest cusp, followed by cusps C, the paracone, stylocone, and protocone. The parastyle is joined to an anterior cingulum that reaches lingually to the base of the midpoint of the paracone. There is no posterior cingulum. The protocone is less massive than in M^1 or M^2. Protoconule and metaconule are present just anterolingual and posterolingual to the bases of paracone and metacone respectively. The stylar shelf bears a small cusp C, and a cusp D is located near the metastyle.

The M^4 is reduced posteriorly. The stylocone and paracone are the largest cusps. They are widely separated and joined by a slightly sinuous paracrista. The metacone is joined to the paracone by a short, straight centrocrista. The protocone is a small, lingually rounded cusp located lingual to and lower than the paracone; its margins extend around the base of the paracone. An anterior cingulum is present from the stylocone to the midpoint of the paracrista. The stylar shelf is a posteriorly sloping surface with no cusps.

Discussion. — The two dasyurids that are most similar to *Dasyuroides byrnei* are *Phascogale tapoatafa* and *Dasycercus cristicauda:* The distinctions between the upper dentitions of *Dasyuroides byrnei* and *Dasycercus cristicauda* have been discussed in detail in the section dealing with the latter taxon.

The upper dentition of *Phascogale tapoatafa* differs from that of *Dasyuroides byrnei* primarily in the larger size of the P^4 and the M^4. The other molars are much the same size. The P^4 is always present in *P. tapoatafa* and is sometimes absent in *Dasyuroides byrnei.* The P^4 of *Dasyuroides byrnei,* when present, is shorter, lower crowned, and relatively less compressed laterally. The dP^4 of *P. tapoatafa* is longer than that of *Dasyuroides byrnei* (fig. 15E). The M^4 of *P. tapoatafa* is longer anteroposteriorly as a result of the greater development of the stylar area.

The lower dentition of *Dasyuroides byrnei* can be distinguished from that of *Phascogale tapoatafa* by the more reduced and laterally compressed trigonid of its M_1. This has been described in detail in the *P. tapoatafa* section. *Dasyuroides byrnei* can be distinguished from *Dasycercus cristicauda* by the relatively longer protoconid and larger paraconid of the M_1 and a trend toward larger and more conical entoconids on M_1 through M_3. The lower canine of *Dasyuroides byrnei* differs from that of *Dasycercus cristicauda* in being relatively shorter, more procumbent and recurved, with a greater expansion at its base.

Dasyuroides byrnei is known as a living animal only from the area where Queensland, South Australia, and the Northern Territory come together. It is an occupant of desert grassland or desert steppe (Spencer, 1896; Marlow, 1962; Ride, 1970). Finlayson (1961) has reported it from Charlotte Waters, Killalpaninna, and Birdsville. Its presence at Madura Cave demonstrates that it

had a much wider distribution in the past. Remains of this species are rare in the upper stratigraphic unit (Unit 1). It apparently was disappearing from this region at the time of the climatic change that is implied by the change in the character of the sediments between units 1 and 2 (Lundelius and Turnbull, 1973).

The waning number of *Dasyuroides byrnei* coincides with a small increase in size of *Dasycercus cristicauda*. These two species are quite similar in size and structure and, although no information is known to us about their competitive relationships where they occur together today, it is possible that the reduction in numbers of *Dasyuroides byrnei* somewhat lessened the restrictions on *Dasycercus cristicauda* and permitted an increase in size.

INCERTAE SEDIS

Dasycercus cristicauda or *Dasyuroides byrnei*

Material. —

Trench 3

Unit 2

PM 29352, left maxillary fragment with M^1; alveoli for C, P^{2-3}, dP^4, or P^4

Description and Discussion. — This specimen cannot be unequivocally assigned to either taxon. It is intermediate in size, and the one tooth has no morphological features that allow an assignment.

Additional uncatalogued, edentulous ramus and maxillary fragments or isolated teeth which probably belong to one or the other of these taxa are:

Trench 4, Unit 2, level 2

One maxillary, five ramus fragments, and approximately 50 isolated teeth.

Trench 4, Unit 2, level 3

Four ramus fragments.

Trench 4, Units 4-5

Two ramus fragments.

Trench 4, Unit 7, level 1

One maxillary, nine ramus fragments, and one isolated lower molar.

Trench 4, Unit 7, level 2

Five maxillary and 17 ramus fragments.

Trench 5, Unit 5
One ramus fragment and approximately 25 isolated teeth.

Dasyurus Geoffroy, 1796

Dasyurus (Dasyurinus) geoffroyi Gould, 1841. Tables 25-27; Figures 18-19.

Material. —

LOWER DENTITIONS

Trench 3
Unit 2
WAM 74.9.42, right ramus fragment, edentulous, with alveoli for M_{3-4}, (fig. 18A2, B2)

Unit 3
TMM 41106-44, right ramus fragment, edentulous, with alveoli for M_{3-4}

Trench 4
Unit 1
TMM 41106-477, left ramus fragment with alveoli for C-M_2; M_2 that may belong to the jaw. (fig. 18A3, A4, B3, B4)
TMM 41106-519, right M_3
TMM 41106-554, right lower C (fig. 18B7)

Unit 2, level 1
PM 30525, left M_2 (probably goes with PM 30526) (fig. 18 A5, B5)
PM 30526, left M_3 (probably goes with PM 30525) (fig. 18 A6, B6)

Unit 2, level 2
PM 30528, right M_1 (fig. 18B8)
PM 30529, broken left $M_?$
PM 30530, left M_2
PM 30531, left M_2
WAM 74.9.43, left M_2

Units 4-5
WAM 74.9.44, right M_2
PM 30541, left $M_{2 \text{ or } 3}$
PM 30542, left M_2
PM 30545, right M_1
PM 30546, right M_2

Unit 7, level 1
PM 30555, left M_2

Unit 7, level 2
PM 30556, left M_3
WAM 74.9.45, right M_1

Trench 5

Unit 5 or 6
PM 30562, left M_3

UPPER DENTITIONS

Trench 3

Unit 2
TMM 41106-68, left M^1
TMM 41106-69, right maxillary with M^1; alveoli for C-P^3, M^{2-3}, (fig. 19A2, B2)
PM 30520, left M^1

Unit 3
PM 30521, right M^1

Trench 4

Unit 1
PM 30522, broken right M^1
PM 30523, left M^3

Unit 2, level 1
PM 30524, left maxillary with M^1; alveoli for P^3, M^{2-3}
PM 30527, right M^3 (fig. 19A5, B5)

Units 4-5
PM 30533, broken right M^1
PM 30534, left M^1
PM 30535, left M^1
WAM 74.9.46, right M^1
WAM 74.9.47, broken right M^2
PM 30538, right M^2
PM 30540, right P^3 (fig. 19A3, B3)
PM 30543, right M^1
PM 30544, right M^2 (fig. 19A4, B4)
PM 30547, left M^1
PM 30548, left M^1

Unit 7, level 1
PM 30553, right M^1
PM 30554, right M^2

Unit 7, level 2
PM 30557, right M^2

Trench 5
Unit 5
PM 30559, right M^3
PM 30560, right M^3
WAM 74.9.48, right M^3

Description. — **Mandibles**: The fossil mandibular material closely resembles a Recent specimen of *Dasyurus geoffroyi* from southwestern Australia (FMNH 35329, fig. 18A1, B1; 19A1, B1) in all morphological characters, but is slightly smaller. Specimen TMM 41106-477 (fig. 18A3, B3), having alveoli for the canine P_2, P_3, and M_1, particularly demonstrates the similarity in size and arrangement of these teeth. A large mental foramen opens under M_1. The characters of the posterior end of the mandible are shown by specimen WAM 74.9.42 (fig. 18A2, B2). The anterior edge of the ascending ramus rises about 60° from the line of the tooth row, the angle of the masseteric fossa is approximately 45°, and the ventral border of the masseteric fossa curves dorsally in a posterior direction. The articular face of the condyle is oval and convex anteroposteriorly. The angular process has a ridge on the dorsal surface. The specimen is that of a young adult as shown by the position of the posterior alveolus of the M_4 lingual to the anterior border of the ascending ramus. This probably accounts for some of the size difference between the Madura Cave specimen and the Recent specimen.

Lower Dentitions: No lower incisors of this taxon have been recognized. The lower canine is a simple curved tooth (TMM 41106-554, fig. 18B7). It is oval in cross-section for most of its length and is twisted medially toward the apex. The root constitutes more than half of the length of the tooth and is expanded just below the base of the crown. The medial surface at this point has a broad, shallow, concave groove. The posterior edge of the crown has a thin ridge from apex to base. A faint basal cingulum is present lingually; it extends anteriorly and downward to join a poorly defined ridge on the anterior edge of the tooth at a cingular cuspule. The flattened lingual surface of the crown is continuous with that of the root.

The M_1 is a laterally compressed tooth with a reduced trigonid (PM 30528, fig. 18B8). The protoconid, by far the largest cusp of the trigonid, is laterally compressed with sharp ridges on both the

anterior and posterior edges. The anterior ridge connects the apex with a minute cingular cuspule and usually there is no paraconid. The anterior cuspule is variable in its size and relationship to other structures. In PM 30528 there is a small but distinct paraconid and a definite carnassial notch on the anterior ridge of the protoconid. In PM 30558 there is another small cingular cuspule in the position of the missing paraconid, but it is situated just lingual to the ridge. The posterior ridge of the protoconid connects the apex with the metaconid. The anterior cingulum is large but does not extend onto the base of the protoconid. The metaconid is variable. In WAM 74.9.45 and PM 30528, the metaconid is a small but discrete cusp, round in cross-section, that is located on the posterolingual flank of the protoconid. In PM 30545 the metaconid is reduced to a small rounded cuspule in the same position. The talonid basin is oval with its long axis extending from the posterolabial corner of the protoconid to the groove between the entoconid and hypoconulid. The hypoconid is the largest cusp of the talonid, followed by the entoconid and hypoconulid. The hypoconid is connected with the hypoconulid by a postmetacristid that turns abruptly posterior just anterior to the hypoconulid. A well-defined carnassial notch separates the premetacristid from the postparacristid on the labial side of the tooth. The postparacristid is a prominent ridge on the posterior side of the protoconid. The entoconid is large, oval to round in cross-section, and separated from all other cusps by rounded grooves. The posterior cingulum does not have the usual ridge structure but is reduced to a smooth bulge and cuspule on the posterolabial corner of the tooth.

The M_2 and M_3 are similar in size and morphology and will be described together (fig. 18A4, A5, A6; B4, B5, B6). The major difference between these two teeth is the greater lateral compression of the trigonid of the M_2 and its smaller paraconid and metaconid relative to the protoconid. In both the M_2 and M_3 the trigonid is well developed. The protoconid is the largest trigonid cusp, followed by the paraconid and metaconid. The lingual surface of the protoconid has a broad, rounded ridge from apex to base. The paracristid and epicristid have strong carnassial notches. The parastyle is weak on most teeth and is separated from the anterior cingulum by a notch into which fits the hypoconulid of the tooth in front. The talonid basin is round. The largest talonid cusp is the hypoconid, followed by the entoconid and hypoconulid. A strong carnassial notch separates the postparacristid from the premetacristid. As in the M_1, the postpara-

FIG. 18. *Dasyurus geoffroyi* lower dentitions. Recent specimen FM 35329 (**1**) is shown for comparison with the Madura Cave specimens as follows: (**2**) WAM 74.9.42 a right ramus fragment with alveoli of M_{3-4}; (**3**) TMM 41106-477 a left ramus fragment with alveoli of C - M_2 and part of the symphysis. Also an isolated M_2 that may belong to the ramus (**4**). (**5**) PM 30525 and (**6**) PM 30526 are left M_2 and M_3 respectively that probably came from the same mouth. All are shown in crown view (**A**), and in medial view (**B**). Also shown in B are TMM 41106-554 (**7**) and PM 30528 (**8**).

cristid is a prominent ridge on the posterior face of the protoconid. The entoconid is large, oval in cross-section at its base, round at its apex. It is not joined to any other cusps by ridges. The hypoconulid is the posterior extremity of the tooth. It is not joined to the posterior cingulum. The anterior cingulum is broad but is not joined to the parastylid and does not extend onto the labial surface of the tooth. The posterior cingulum is variable in its form; it may be ridge-like or it may be a rounded bulge, with or without a cuspule. It does not reach the hypoconulid or extend onto the labial surface of the hypoconid.

There are no M_4's in the Madura Cave material.

Maxillaries and upper dentitions: The only identifiable skull material of *Dasyurus geoffroyi* from Madura Cave are parts of two left maxillaries. One specimen (TMM 41106-69, fig. 19A2, B2) has an M^1 and alveoli for C-P^3 and M^{2-3}. The other (PM 30524) has an M^1 and alveoli for P^3 and M^{2-3}. These two specimens show the infraorbital foramen to be large and situated over the M^1. There is no well-defined fossa on the lateral surface of the maxillary into which the foramen opens as in *Dasycercus*.

No upper incisors, canines, or P^2's have been identified for this taxon. One right P^3 (PM 30540, fig. 19A3, B3) is present. It is a double-rooted tooth with a large cusp on its anterior half. Its greatest width is posterior to the apex of the main cusp where the cingular area is expanded on the lingual side. A cingulum is present on each side of the tooth, from the base of the main cusp to the posterior end of the tooth. A small cuspule marks the junction of this posterior cingulum with a ridge on the posterior edge of the main cusp. An anterior cingulum is present that does not join the posterior one. This is similar to the P^3 in the Recent specimen of *Dasyurus geoffroyi*.

The M^1 is a triangular tooth with the protocone extending as far anteriorly as the paracone (fig. 19A2, B2). The metacone is the tallest cusp, followed by cusp C, the paracone, and the protocone. The paracone and stylocone are fused. The parastyle is small and may be either rounded or bladelike. It is connected to the anterior cingulum. The metacone and cusp C are approximately the same size, and, although close together, are separated by a deep, rounded groove. The premetacrista and a parallel crest on the anterior face of cusp C are variably developed. They approach, but do not join, a postparacrista and a stylocrista from the paracone. Stylar cusps B and C may or may not be present. The

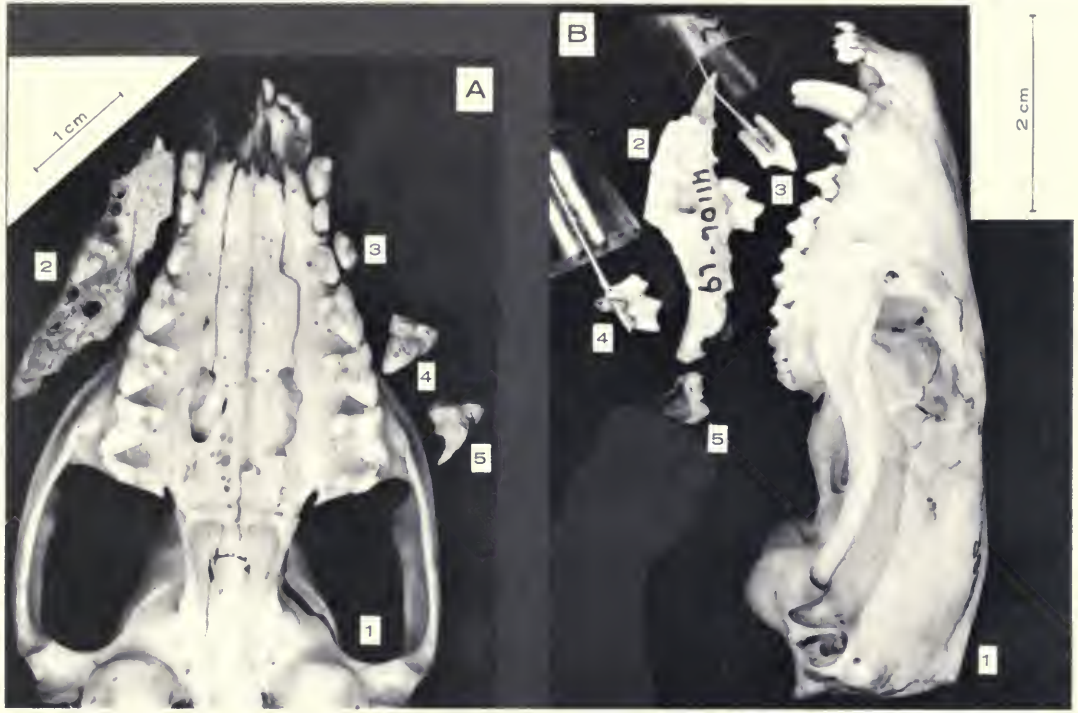


FIG. 19. *Dasyurus geoffroyi* upper dentitions. Recent specimen FM 35329 (**1**) is shown for comparison with the Madura Cave specimens as follows: (**2**) TMM 41106-69 a right maxillary with M^1, alveoli of C - P^3, M^{2-3}; (**3**) PM 30540 right P^3; (**4**) PM 30544 right M^2; (**5**) PM 30527 right M^3. All are shown in crown view (**A**) and in lateral view (**B**).

protocone is long and crescentic. Its posterior crest extends around the base of the metacone, and its anterior crest joins the anterior cingulum. A protoconule and metaconule are usually present. No posterior cingulum is present.

The M^2 is triangular and asymmetrical (fig. 19A4, B4). The metacone is the tallest cusp, followed by cusp C, the paracone, the stylocone, and the metastyle. The lingual faces of the paracone and metacone may be ridged, but the ridges do not join those from the protoconule and metaconule. The parastyle is short but sharply edged. It is joined to an anterior cingulum which may or may not join the anterior crest of the protocone. The protocone is triangular in occlusal view. A posterior cingulum may be present from the posterior crest of the protocone to the middle of the base of the metacone. A small stylar cusp D may be present.

The M^3, in contrast to those of most smaller dasyurids, is not quite symmetrical because of the great length of the posterior segment of the stylar shelf (fig. 19A5, B5). Stylar cusp C lies well lingual to a line connecting the stylocone and the metastyle. The metacone is the tallest cusp, followed by the paracone, cusp C, and the stylocone. The parastyle may or may not have an anteriorly projecting blade. It is connected to an anterior cingulum that is broad labially but narrows markedly lingually. Small stylar cusps C_1 and D may be present. The largest and most noticeable feature of the M^3 is the great length of the posterior stylar shelf. This results in the formation of a very long, slightly curved postmetacrista that is approximately twice the length of each of the other segments of the eocrista. The stylocrista is also long; much longer than in M^2. The Recent specimen shows a rather even gradiant in development of the stylocrista from M^1 where it is nonexistent to M^4 where it occupies over half the width of the tooth. The protocone is relatively small and in occlusal view has the shape of a rounded triangle. A protoconule and metaconule are present. The anterior ridge of the protocone usually continues past the protoconule and joins the anterior cingulum. The posterior ridge usually ends at the metaconule. There is no posterior cingulum. As in the M^2, the lingual edges of the paracone and metacone may have small crests near their bases. These do not join similar ridges from the protoconule and metaconule but are separated from them by narrow clefts.

There are no M^4's in the Madura Cave material.

Discussion. — The material of *Dasyurus geoffroyi* from Ma-

dura Cave is similar in morphology to Recent specimens from southwestern Australia but is slightly smaller (tables 25-27). A comparison with a Recent specimen of *Dasyurus* (*Satanellus*) *hallucatus* (TMM M-705) from northwestern Australia shows the Madura Cave material to be larger (tables 25-27). In addition, the M^3 of *D. hallucatus* does not show the elongation of the posterior part of the stylar shelf seen in *D. geoffroyi*. The lower molars of *D. hallucatus* have posterior cingula that are continuous across the posterior ends of the teeth and join the hypoconulids. Also, the lingual faces of the protoconids are concave rather than convex as in *D. geoffroyi*. In all these characters the Madura Cave material is similar to *D. geoffroyi* and differs from *D. hallucatus*.

Dental measurements of the Madura Cave *Dasyurus* show that it is smaller than *Dasyurus* (*Dasyurops*) *maculatus* and within the size range of *D. geoffroyi* and *D. (Dasyurus) quoll* (tables 25-27). We cannot rule out the possibility that *D. quoll* is represented in the Madura Cave material since the two species overlap broadly in size and no unequivocal dental characters are known that will distinguish them.[1] Although the Recent distribution of *D. quoll* is not known to extend west of the Adelaide area, other species characteristic of the more humid areas of Australia, such as *Antechinus flavipes,* occurred on the Nullarbor Plain during the late Pleistocene.

[1] Thomas (1888) quoted by Tate (1947, pp. 143-144) stated that the M^4 of *D. geoffroyi* is distinctive in its extreme narrowness. This does not hold, as the three FMNH specimens of *D. quoll* all have M^4's as narrow as those of *D. geoffroyi*.

Smith (1972) in a study of fossil remains from Victoria Cave (Naracoorte), South Australia, compared linear dental measurements of the fossil *Dasyurus* teeth with those of Recent specimens of *D. viverrinus* (= *D. quoll*) and *D. geoffroyi* as a means of determining specific identity of the fossils. Smith states, "The teeth of specimens of the two species. . . . are similar in size and morphology . . , and there is overlap in all linear dimensions of individual teeth and of toothrows." A means of separating the two living species was suggested, based upon ratios of protocone-anterior stylar cusp (parastyle) to protocone-posterior stylar cusp (metastyle) distances for M^1 and M^3. We have attempted to check this with some Field Museum specimens without success. Perhaps there is a difference in the manner of measurement of protocone-parastyle and protocone-metastyle distances (we used maximum measures, not cusp tips or centers), or perhaps the differences are real. Our ratio values for two specimens of each species are shown here, tabulated with those given by Smith.

	D. viverrinus (=*D. quoll*)			*D. geoffroyi*		
	(fr. Smith)	FM 34727	FM 81523	(fr. Smith)	FM 34718	FM 35329
M^1	0.525	0.68	0.59	0.570	0.64	0.60
M^3	0.664	0.77	0.65	0.733	0.77	0.80

Dental measures of the material of *D. quoll* (five specimens) and *D. geoffroyi* (three specimens) that we have available for comparison indicate a slightly larger tooth size for the latter. This appears to be at variance with published statements indicating that *D. quoll* has a slightly larger skull length and body size (Jones, 1923; Marlow, 1962); but tooth size and skull and body size need not necessarily be correlated.

Some geographic variation in size of both species is reported in the literature. Specimens of *D. geoffroyi* from the southwestern corner of Australia are larger than those from farther east, while specimens of *D. quoll* from Tasmania and South Australia are smaller than those from the eastern part of its mainland range (Jones, 1923; Tate, 1947). The reversed difference in size shown by our samples could be either the result of sampling errors or the result of a lack of correlation between tooth size and body size. The Madura Cave material is near the upper end of the size range of the combined samples of *D. geoffroyi* and *D. quoll*.

D. geoffroyi has a very wide distribution in the southern half of Australia today (Marlow, 1962).

Sarcophilus Geoffroy and Cuvier, 1837

Sarcophilus harrisii (Boitard), 1841. Table 28; Figures 20-21.

Material. —

LOWER DENTITIONS

Trench 3

Unit 1, level 1
TMM 41106-548, anterolabial edge of left M_1 (fig. 20A4, B4)

Trench ?

Unit 2 or deeper on basis of color
WAM 74.9.49, left ramus, edent., with alveoli for 1_{1-3}, C, P_{2-3}, M_{1-3} (bone appears burned, fig. 20A2, B2)
PM 30566, broken left M_3
WAM 74.9.50, right P_3
PM 30568, right M_3 (fig. 20A8, B8)
PM 30569, right ramus frag. with unerupted C; alveoli for P_{2-3}, M_1 (fig. 20A3, B3)
PM 30571, left P_3 (fig. 20A5, B5)
PM 30572, right C, protoconid of right M_3 (fig. 20A6, B6)

Trench 4

Unit 2, level 3
PM 30574, left I_1 (fig. 20A7, B7)
PM 39575, protoconid of right $M_{3 \text{ or } 4}$

UPPER DENTITIONS

Trench 3

Unit 1, level 1
TMM 41106-498, right I^4, left P^3. (fig. 21A3, A4, B3, B4)

Trench ?

Unit 2 or deeper on basis of color
PM 30565, left C
PM 30570, left M^2 (fig. 21A5, B5)

Trench 3

Unit 2
PM 30578, anterior edge of left M^2

Trench 4

Unit 2, level 2
PM 30573, left C (fig. 21A2, B2)

Description. — **Mandibles**: The largest fragment of this animal represented in the collection is an edentulous left ramus of a young individual (WAM 74.9.49, fig. 20A2, B2), judging by the shallowness of the ramus and the sharp, delicate edge of the lingual alveolar border. It is quite comparable to the condition of a Recent juvenile specimen (FMNH 57801, fig. 20A1, B1). The three incisor alveoli are crowded together exactly as in the Recent specimen, so that seen dorsally, the alveolus for I_2 is the most prominent notch between the canine and the symphysis. The alveoli of I_1 and I_3 are crowded more anteriorly and labially. The alveoli of the two premolars are set at an angle of about 60° to the axis of the ramus, and the anterior alveolus of P_2 has only a thin lamina of bone separating it from that of the canine. There are three pairs of alveoli, all oriented in line, for $M_{1\text{-}3}$. Two mental foramina are present; the larger anterior foramen lies beneath P_3, the smaller, posterior one beneath the posterior root of M_1. The bone appears to have been burned.

A very young individual is represented by PM 30569 (fig. 20A3, B3), a right ramus fragment with an incompletely formed

canine. The tip of the tooth is nearly at the alveolar edge, indicating that the animal was about at the weaning stage when it died: slightly younger than eruption stage 1 (Guiler and Heddle, 1974) which is about 210 days of age. The specimen also has alveolar crypts for P_{2-3} and part of the crypt for M_1. The canine as formed is conical, somewhat recurved and flattened slightly on its medial side. There is a weak ridge from apex to the developing ventral margin of the crown at the anterior junction of the flattened surface anterolingually. Another young individual is represented by the labial half of an unworn right canine (PM 30572, fig. 20A6, B6). This canine is slightly smaller than that of the Recent young specimen and is recurved with a distinct cingular boundary rising posteriorly along the labial side as in the Recent specimen.

Lower Dentitions: One slightly worn left I_1 (PM 30574, fig. 20A7, B7) matches the Recent specimen very closely. It has a triangular outline in occlusal view, with one main anterior cusp, associated lateral and medial crests along the leading edge, and a low cingular heel posteriorly. Its root is half again longer than the crown. Seen from the front, the crown tapers from a maximum width at the cutting edge to about two-thirds that width where it joins the root. It is slightly asymmetrical, with the lateral edge slightly expanded.

The lower premolars are represented by two P_3's (WAM 74.9.50 and PM 30571, fig. 20A5, B5). The former is nearly unworn and is slightly smaller than its Recent counterpart (FMNH 57801) where the wear stage is similar. In older individuals, the primary cusp is worn down to the level of its base and heel. The tooth is roundly triangular in occlusal view, with a single, centrally placed, prominent cusp. This cusp is most pointed anteriorly and squared posteriorly. The anterior root is small in diameter; the posterior root is much broader than long. Crests extend from the apex of the cusp anteriorly and posteriorly. The anterior crest meets the anterior portion of the cingulum which rises to join it from both lingual and labial sides. The posterior crest fades rapidly as it approaches the weak posterior cingulum. The heel is entirely lingual to the posterior ridge and is less well developed in the fossils than in the Recent specimen. The cingulum is best developed on the lingual side of the heel in both the fossils and the Recent specimen. In PM 30571 wear has almost eliminated the main cusp, and the heel is abraded. Comparison with the P_3 of another Recent specimen at a similar wear stage (FMNH 46006)

FIG. 20. *Sarcophilus harrisii* lower dentitions. Recent specimen FM 57801 (**1**) is shown for comparison with the Madura Cave specimens as follows: (**2**) WAM 74.9.49 left ramus fragment with alveoli of I_{1-3}, C; (**3**) PM 30569 right ramus fragment with unerupted canine and alveoli of P_{2-3}; (**4**) TMM 41106-548 part of a left M_1; (**5**) PM 30571 left P_3; (**6**) PM 30572 labial half of a right lower canine; (**7**) PM 30574 left I_1; (**8**) PM 30568 right M_3. All are shown in crown view (**A**) and in dorso-lateral oblique view for the left elements and dorso-medial oblique view for the right (**B**), except that the canine (**6**) is shown in lateral view and the incisor (**7**) is shown in ventral view.

shows the fossil to have a somewhat more discrete facet pattern. (This may be the result of diet — the Recent specimen was captive in a zoo for part of its life.)

The single piece of an M_1 (TMM 41106-548, fig. 20A4, B4) is the anterior half of a left tooth. It is from a young individual and is similar to the M_1 of the Recent FMNH 57801. The break goes through the apex of the protoconid which is high and is situated over the center of the space between the two roots. An anterior crest connects the apex to the anterior cingulum. The cingulum is sharp around the front half of the tooth. As in the Recent specimen, the protoconid is slightly recurved medially, and there is no paraconid.

All other lower molars represent young individuals as the teeth are virtually unworn. The description is based mainly on the complete tooth (PM 30568). The tallest trigonid cusp is the protoconid, followed by the paraconid and metaconid. The apex of the protoconid is high and lies well within the posterior third of the tooth. The anterolabial face of the tooth is high, almost flat, and consists of a sharp, thin crest — the paracristid (I′) which runs forward and down toward the base of the trigonid where it meets a posterolabially directed crest from the lower and prominent paraconid. There is a deep carnassial notch where the two parts of the paracristid meet. The epicristid takes the form of a steep posterior crest from the apex of the protoconid. It runs directly toward the small metaconid at the base of the trigonid but is separated from it by a short cleft. The posterior side of the metaconid joins the cingulum which swings postero-labially, then labially, to meet a posterior cingular cuspule just linguad to the small hypoconid, which it does not join. Instead it sends a minute, but distinct crest anterolabially forward to the base of the protoconid. A tight shallow valley separates this ridge from the hypoconid except at one point midway along its course to the protoconid. A rounded, shallow basin with a small isolated cuspule within it is thus delimited between the metaconid and the hypoconid. The hypoconid is elongated and is also tied to the base of the protoconid by a crest, just labiad the other crest. The hypoconid is notably smaller than its counterpart in the Recent FMNH 57801 (where it is smaller than that of either M_1 or M_2). The cingulum rises slightly at the posterior edge of the tooth near the hypoconid in a cuspule that could be considered a hypoconulid. There is a strong, anteriorly rising cingulum anterolabial to the paraconid. A small notch separates the highest point

of this cingulum from a minute parastylid, but this notch probably served to contact the cingulum of the preceding tooth, for the Recent specimen has M_2's with no trace of a hypoconulid. The posterior cingulum is weakly developed along the lingual side of the base of the protoconid. It extends back and around the posterior edge of the tooth to disappear along the side of the posterior root beneath the junction of the hypoconid and protoconid on the labial side. Behind the carnassial notch of the paracristid and parallel to it there is an elongate shallow groove on the labial surface of the protoconid — a feature that appears to distinguish M_2 and M_3 of *Sarcophilus* from those of *Thylacinus*.

Upper Dentitions: The I^4 (fig. 21A3, B3) has a worn crown, reduced apparently to about half its original height, and a bulbous root expansion typifying advanced age. The crown is rather triangular in occlusal view. A central main cusp has anterior and posterior crests that connect it to the weak cingula. The labial surface is smoothly convex and truncated by wear; the lingual surface is heavily worn in a deep bevel that cuts through the posterolingual cingulum. There is a small but distinct cingular cuspule at the posterior end of the main crest. Aside from differences in wear the fossil material is similar to the Recent specimen used for comparison (FMNH 57801, fig. 21A1, B1).

The upper canines are both heavily worn, and like the I^4 have a bulbous root condition typical of old age. At least half of the crown of both teeth is worn away so that the cusp is truncated below midheight. On PM 30565 the anterior and posterior faces have the enamel worn away as well; on PM 30573 (fig. 21A2, B2) wear on the posterior face did not breach the enamel. The only enamel in PM 30565 is on the labial and lingual sides. On the labial side the enamel retains a weak convexity; on the lingual side it is almost flat. On both canines there is a constricted appearance at the junction of crown and root, apparently the result of the bulbous root condition with some enhancement from wear along the posterior edge just beneath the crown.

The P^3 (fig. 21A4, B4) is an unworn tooth consisting of a blunt, nearly conical main cusp with a surrounding basal cingulum that is heaviest behind. There is a weak crest from the apex of the cusp up its posterolateral side that just reaches the cingulum.

The two left M^2's are similar. PM 30578 consists of only the anterior face of the tooth, including part of the protocone, about half of the paracone, the parastyle, and the anterior cingulum.

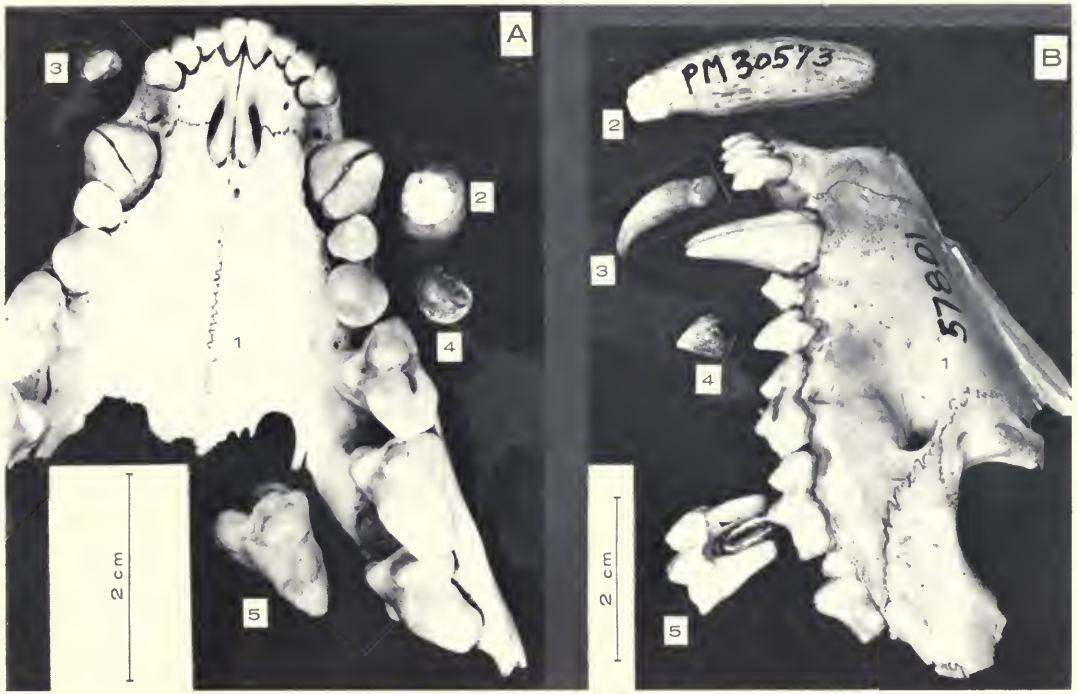


FIG. 21. *Sarcophilus harrisii* upper dentitions. Recent specimen FM 57801 (1) is shown for comparison with the Madura Cave specimens as follows: (2) PM 30573 left upper canine; (3) TMM 41106-498 right I^4, and (4) left P^3; (5) PM 30570 right M^2. All are shown in crown view (**A**) and in lateral view (**B**).

PM 30570 (fig. 21A5, B5) is complete and unworn. All three roots are well formed although not closed off. This tooth is triangular in crown view. The protocone is low, crested, and juts in toward the palate somewhat more than does its counterpart in the Recent specimen (FMNH 57801) so that there is a deeper notch in the anterior margin. The cresting of the protocone is V-shaped, and the anterior crest or protoloph (III′) runs from the tip of the cusp parallel to the front edge of the tooth to the anteromedial edge of the base of the paracone. The posterior crest, plagiocrista, or metaloph (IV′) extends diagonally back and labially to the base of the metacone and then rises abruptly to meet the cingulum. The paracone is high with posterolingual and anterolabial crests. The former crest goes to the base of the metacone; the latter connects the paracone to the stylocone. The metacone is the highest cusp and is also crested. A short crest swings labially from its apex to join immediately the compressed stylar cusp C. The posterior crest from the metacone extends straight back and then posterolaterally to a lightly-defined metastylar corner of the tooth. In the metastylar area a flattened and weakly crested stylar cusp D forms the main feature of the rear part of the stylar shelf between stylar cusp C and the vestigial metastyle. The paracone and metacone, each with its associated stylar cusps and crests, thereby form two shallow basins posterolaterally inclined to their respective cusps. There is an anterior cingulum that descends to a weak parastyle. All of these features agree closely with the M^2 of the Recent specimen.

Discussion. — The material of *Sarcophilus* from Madura Cave is referred to *S. harrisii* on the basis of size and morphology. It is much smaller than that of *S. laniaris* and is either smaller than or equal to the smaller specimens of a Recent sample from Tasmania and late Pleistocene specimens from the west coast area of Australia (table 28).

Sarcophilus is known from three other localities on the Nullarbor Plain, Balladonia (Glauert, 1912; Merrilees, 1968), Webbs Cave (Lundelius, 1963), and Cocklebiddy Cave (Merrilees, 1968). These occurrences are not well dated but are late Pleistocene or post Pleistocene in age. The Madura Cave material is associated with C-14 dates that demonstrate its presence on the Nullarbor Plain from about 20,000 to about 7,500 years before present. Some of the other occurrences are from superficial deposits and may be younger. A discussion of the distribution of this animal on the mainland is given by Calaby and White (1967). The burned

specimen is one of the few evidences uncovered to date that might indicate the presence of man at Madura Cave. Remains of *Sarcophilus* have been found in other localities in circumstances that indicate that it was an aboriginal food item (Gill, 1953; Mulvaney et al., 1964; Calaby and White, 1967; Dortch and Merrilees, 1971).

Thylacinidae Boneparte, 1838

Thylacinus (Temminck, 1824, 1827)

Thylacinus cynocephalus (Harris, 1808). Table 29; Figures 22-23.

Material. —

Trench 3

Unit 2

TMM 41106-59, left P^3 (fig. 23A2, B2)

PM 30576, posterior half of right P^4 (fig. 23A3, B3)

WAM 74.9.51, right M_1 (or M_2), broken (fig. 22A3, B3)

Trench 4

Unit 2, level 1

PM 30579, broken right M_2 or $_3$ (fig. 22A2, B2)

Description. — The material of *Thylacinus* is adequate only to demonstrate its presence in the fauna.

Lower Dentitions: WAM 74.9.51 is the posterolabial face of a right lower molar. It may be considered an M_1 because of the form of the posterior cingulum, the close spacing of the roots, the plunging crown rim over the posterior root, and the flatness of the protoconid. These features resemble the M_1's of the two Recent specimens available (FMNH 81522 and Princeton University, PU Ost 568 — figs. 22A1, B1; 23A1, B1). If it is an M_1, size is the most distinct difference, the fossil being some 15 per cent larger than the Recent specimens. On the other hand, the fossil tooth fragment compares favorably in size with the equivalent parts of M_2 and M_3, the fossil being quite close in size to M_2. The protoconid is gently convex labially, the flat hypoconid about two-thirds the height of the protoconid, and there is a weak posterolabial cingulum.

PM 30579 is the anterior two-thirds of a right M_2 or $_3$. The protoconid is much more massive and stands almost twice as high as the paraconid. There is a heavy, oblique wear facet along the entire paracristid that extends down to the cingulum. The cingulum is truncated by another facet. The anterior root is broad

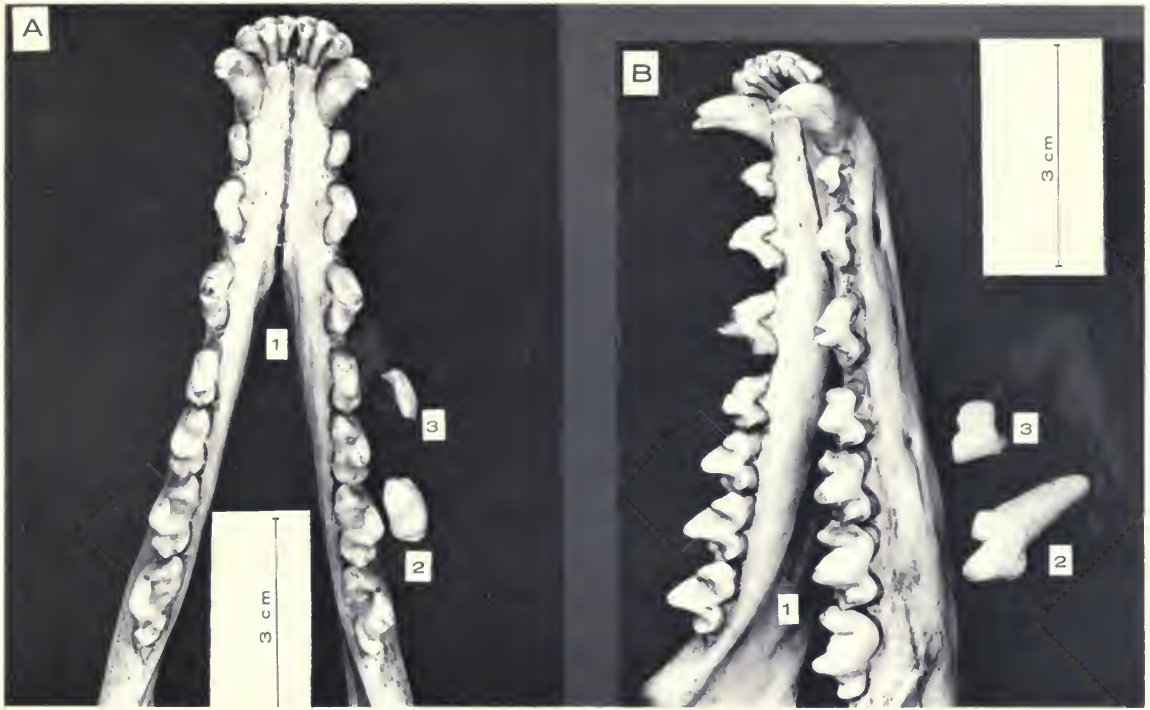


FIG. 22. *Thylacinus cynocephalus* lower dentitions. Recent specimen PU OST 568 (**1**) is shown for comparison with the Madura Cave specimens as follows: (**2**) PM 30579 right M_3; (**3**) WAM 74.9.51 broken right M_2 or M_1. Shown in crown view (**A**) and in dorso-lateral oblique view (**B**).

and grooved behind and narrows somewhat anteriorly. The paraconid appears to have been chipped in life and the broken edges subsequently worn. The carnassial notch is nearly worn away. The fragment represents a tooth that appears to have been slightly more massive than the modern counterpart.

Upper Dentitions: TMM 41106-59 is a complete left P^3 (fig. 23A2, B2). It is elongate and nearly elliptical in crown view, with a single, centrally located, prominent cusp. A weak crest extends forward from the apex of the cusp to an anterior cingular cuspule. A slightly stronger posterior crest runs almost straight from the apex to the base, where it flattens out and extends slightly labially in a backward sweep across the heel to a pronounced posterior cingular cuspule. It is similar to our modern comparative materials as far as wear differences permit comparison.

PM 30576 is the posterior half of a right P^4. It is quite worn but has the rear half of the central cusp with a posterior crest and a rather bulbous posterior cingular cuspule, both heavily worn.

Discussion. — Although only four fragmentary specimens of the thylacine were recovered at Madura Cave, they demonstrate the presence of this taxon in Unit 2. Remains of *Thylacinus* have been reported from several caves on the Nullarbor Plain (Cook, 1963; Lowry and Lowry, 1967; Partridge, 1967; Lowry and Merrilees, 1969; and Archer, 1974).

Ride (1964) compared fossil *Thylacinus* from eastern and western Australia. His data show that the western Australian sample has smaller mean values for most measurements than those for the fossil sample from eastern Australia or the modern sample from Tasmania, although there is extensive overlap between all of the samples.

Ride does not give quantitive data for the two teeth (P^3 and M_3) that are measurable in the Madura Cave sample. A comparison of the size of these two specimens with three Recent specimens and one fossil from Wellington Caves (table 29) shows the same patterns outlined by Ride for other measures on the basis of much larger samples.

Family Myrmecobiidae Jones, 1923

Myrmecobius (Waterhouse, 1836)

Myrmecobius fasciatus (Waterhouse, 1836). Figures 24-25.

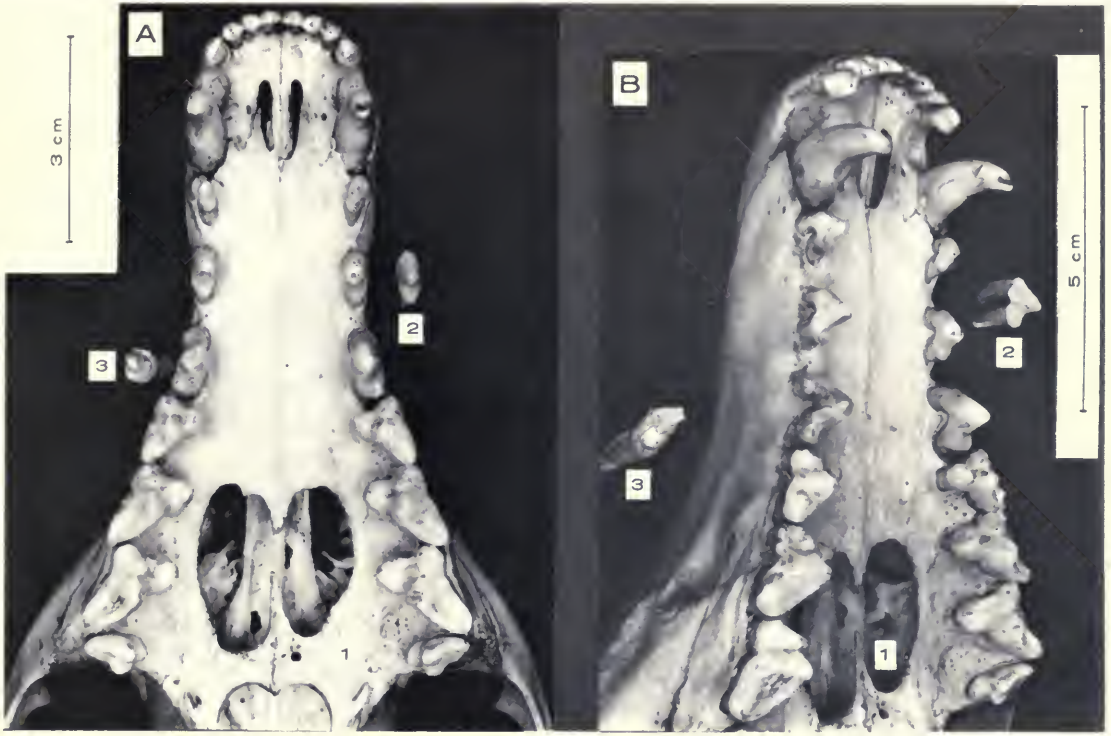


FIG. 23. *Thylacinus cynocephalus* upper dentitions. Recent specimen PU OST 568 (**1**) is shown for comparison with the Madura Cave specimens as follows: (**2**) TMM 41106-59 left P^3; (**3**) PM 30576 posterior half, right P^4. Shown in crown view (**A**), in ventro-medial oblique view for the left teeth and in ventro-lateral oblique view for the right teeth (**B**).

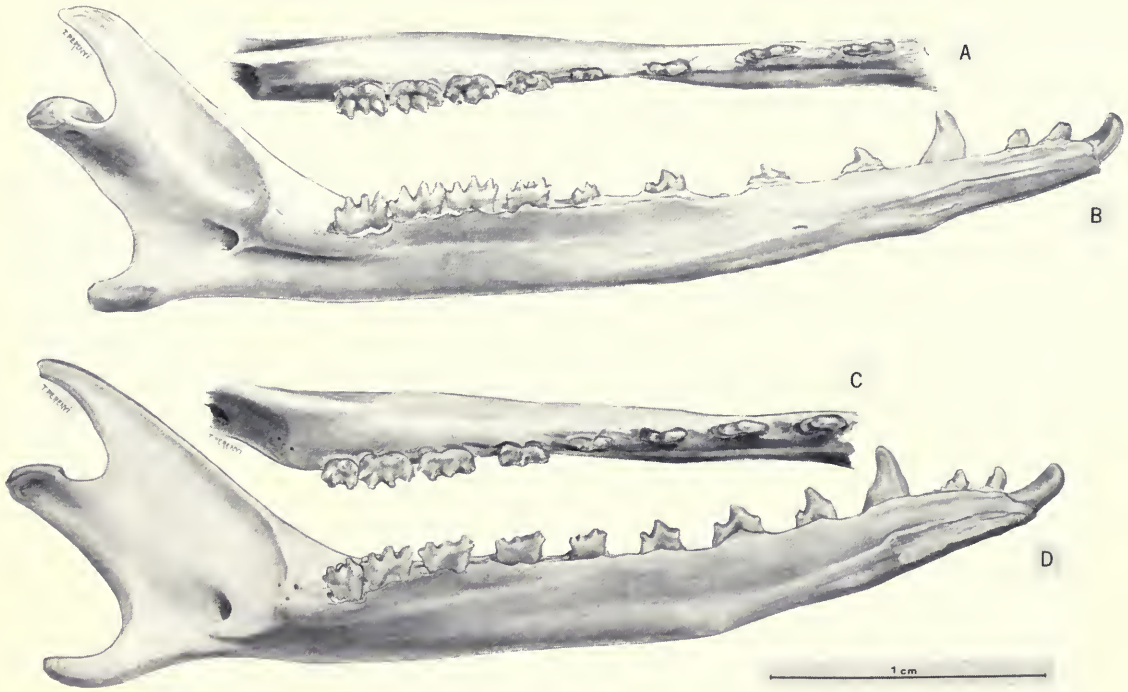


FIG. 24. *Myrmecobius fasciatus*. **A, B**, FM 35259; **C, D**, FM 19982. Left rami and lower dentitions shown in crown and lingual views.

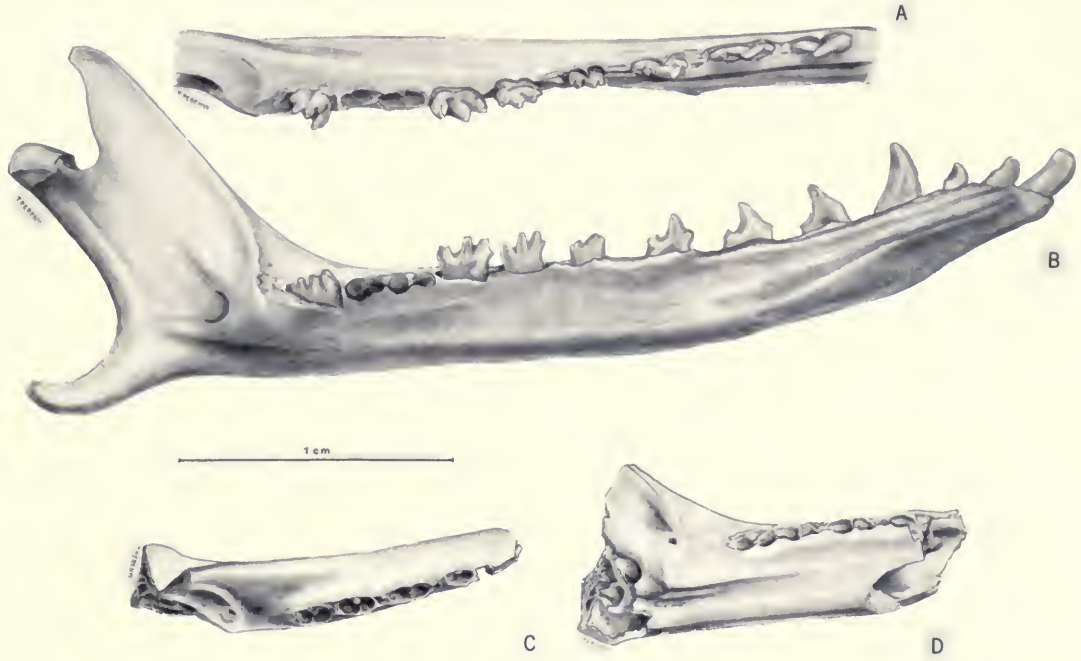


FIG. 25. *Myrmecobius fasciatus*. **A, B**, FM 36049. Left ramus with lower dentition shown in crown and lingual views. **C, D**, TMM 41106-687 from Madura Cave. Left ramus fragment with alveoli for the posterior four teeth shown in crown and lingual views.

Material. —

Trench 4

Top of Unit 1

TMM 41106-687, left ramus, edentulous, with alveoli for posterior four teeth (fig. 25C, D).

Description. — This is the only specimen of this taxon in the Madura Cave deposits. The specimen consists of the posterior part of the mandible with the alveoli of the posterior four teeth, apparently M_{2-5} judging by the three Recent specimens used for comparison. In the Recent specimens (fig. 24A, B, C, D; 25A, B) the variation in the lower tooth formula is as follows:

M. fasciatus fasciatus, FM 35259	$\overline{3}:\overline{1}:\overline{3}:\overline{5}$
M. fasciatus fasciatus, FM 36049	$\overline{3}:\overline{1}:\overline{3}:\overline{5 \text{ or } 6}$
M. fasciatus (?*rufus*), FM 19982	$\overline{3}:\overline{1}:\overline{3}:\overline{4 \text{ or } 5}$

The angular process and most of the ascending ramus are broken away in the fossil. The dorsal and ventral margins of the horizontal ramus are parallel. The small alveoli indicate that each tooth had two roots that were aligned parallel to the long axis of the mandible. There is a broad, rounded groove on the lingual side of the mandible that extends forward from just below the inferior dental foramen. The mandibular foramen is round, about 1 mm. in diameter, and opens posteriorly about 4.5 mm. posterior to and below the last tooth.

The fossil compares well with the Field Museum Recent specimens, but shows the following minor differences:

1. the fossil ramus is slightly thicker and more massive,

2. the fossil specimen has a much larger nutrient foramen located behind the last molar on the lingual crest of the coronoid process, i.e., about half way between the last molar and the mandibular foramen, and

3. in the fossil this crest and those that bound the masseteric fossa are heavier and more distinct.

Discussion. — Modern *Myrmecobius* has a spotty distributional record: the south part of Western Australia, widely separated areas of South Australia, and southwestern-most New South Wales. This pattern indicates that the present populations are remnants of a formerly more continuous distribution across the southern part of Australia. This is the first record of it, fossil

or Recent, on the Nullarbor Plain, and is, as far as we know, the only fossil record to date. Most accounts of its distribution (Marlow, 1962; Troughton, 1962; Ride, 1970) indicate that its occurrence in the more arid parts of Australia is north of the Nullarbor Plain.

Order INCERTAE SEDIS

Thylacoleonidae Gill, 1872

Thylacoleo Owen, 1859

Thylacoleo sp. Figures 26-27.

Material. —

Trench 4, Unit 1

TMM 41106-516, right P_4 (fig. 26A, B, C).

Description. — The right P_4 is the only indication of this species from Madura Cave. The crown of the tooth is complete. The roots, which appear to have been stout, are broken off just below the enamel line. This specimen agrees in every respect except size with the description of Woods (1956). The crown has vertically ridged enamel, especially on the lingual surface. Anteriorly one of these ridges is enlarged to form a prominent, rounded ridge. The anterior edge of the tooth is sharp. There is a narrow wear facet along the labial side of the cutting edge. Another broader wear facet is present on the labial side near the ventral margin of the crown. There is a small interdental facet on the posterior end where it comes in contact with the M_1. The length is 33.8 mm.; anterior width, 10.9 mm.; posterior width, 12.0 mm.

Discussion. — Remains of *Thylacoleo* have been found over a wide area of southern and eastern Australia and from Tasmania (Gill, 1954). No comprehensive study of this animal on a continent-wide basis has been attempted, but size varies geographically (Glauert, 1912) and temporally (Woods, 1956; Bartholomai, 1962). A comparison of the Madura Cave specimen with samples from Wellington, New South Wales, and Kurramulka, South Australia shows it to be considerably smaller than all specimens in either of the other samples (fig. 27). It is also shorter than any of four specimens of *T. crassidentata* from the Chinchilla sand of Queensland, reported by Bartholomai (1962), although it resembles this species in the strong curvature of the cutting edge. The location of the maximum width of the Madura specimen above

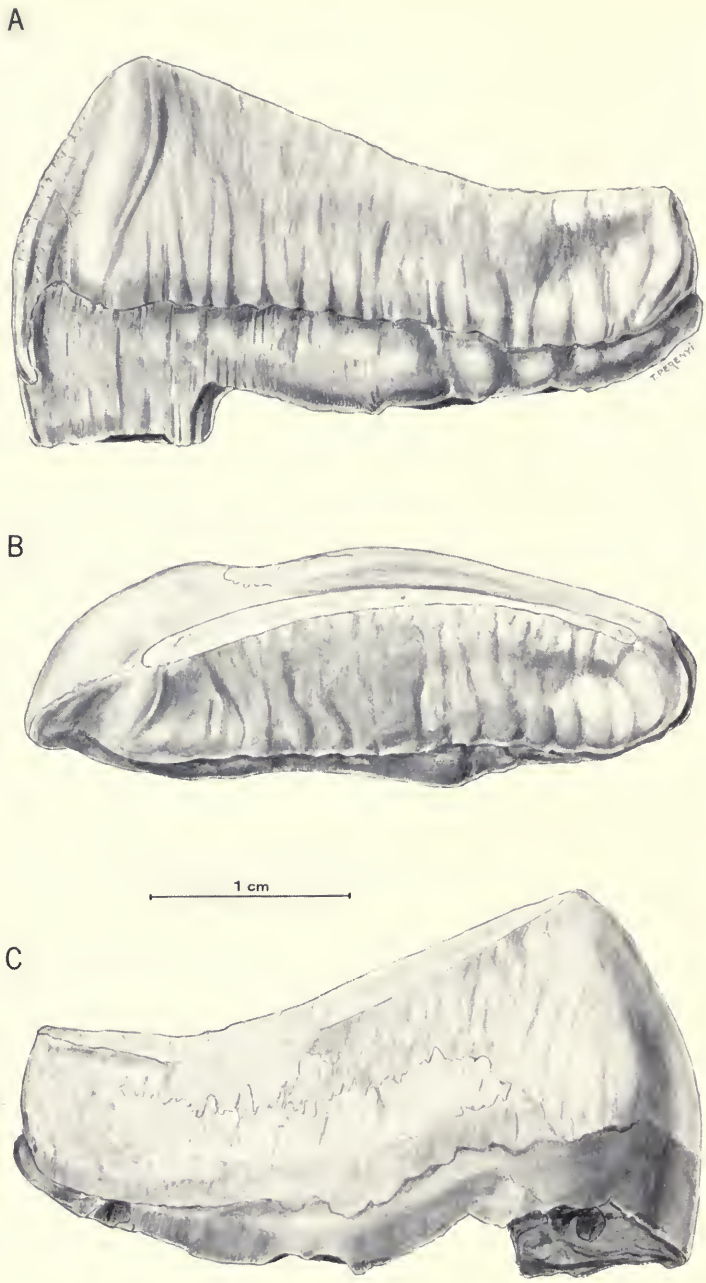
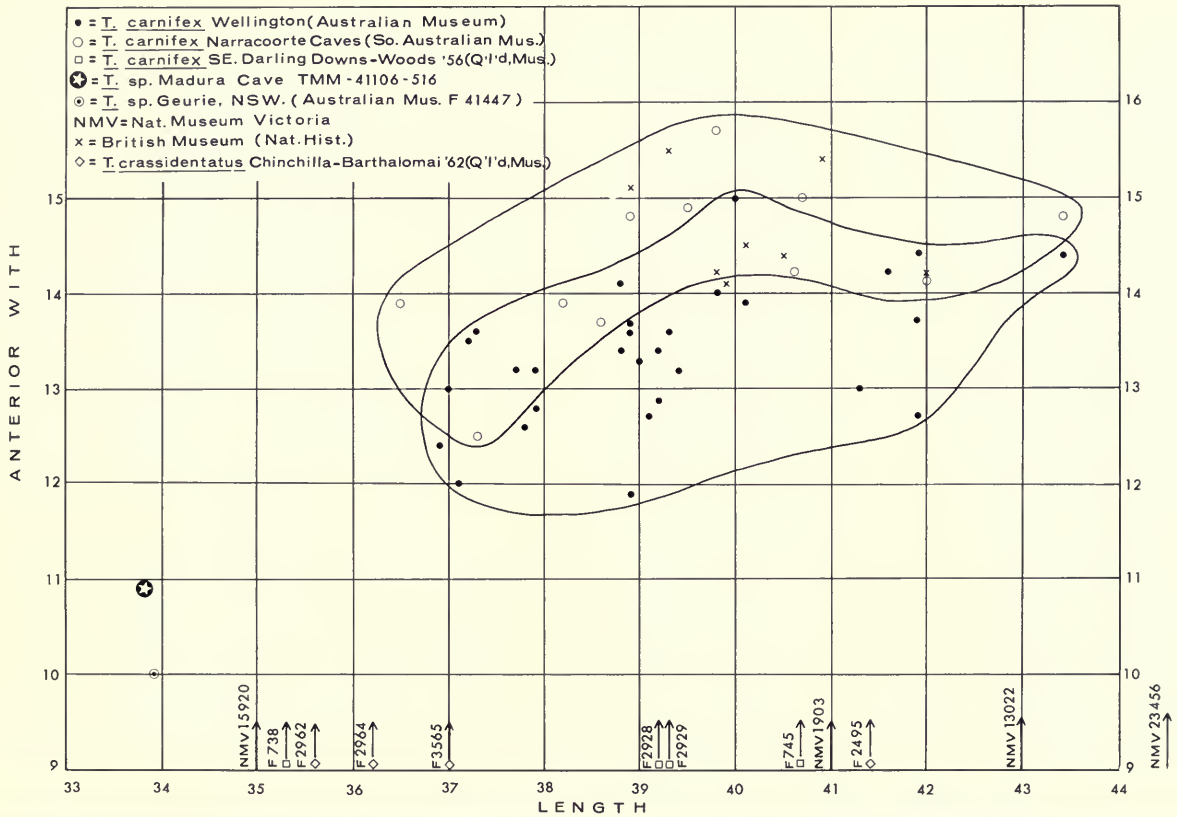


FIG. 26. *Thylacoleo* species indet., from Madura Cave. TMM 41106-516. Right P_4 shown in **A**, lingual, **B**, crown, **C**, labial views.

the anterior part of the posterior root appears to be another point of resemblance to *T. crassidentata*. However, an Australian Museum specimen from Wellington Cave (F 16617) also shows a distinct broadening over the anterior part of the posterior root. In size it resembles the specimen from Balladonia reported by Glauert (1912) to be 72 to 80 per cent of the size of the type. This is close to the difference in size between the Madura Cave specimen and the material from Wellington and Kurramulka caves (fig. 27).

Small examples of *Thylacoleo* are not restricted to Western Australia. A juvenile specimen in the Australian Museum (F 41447) from a cave deposit at Geurie, New South Wales is very close to the size of the Madura Cave specimen (fig. 27). The P_4 of the Geurie specimen is not completely erupted thus preventing a determination of the position of its maximum width. As a comprehensive study based on more complete material is needed to establish the significance of these size differences, the Madura Cave specimen is not assigned to a species.

The presence of this taxon in the Madura Cave deposits is expected from a distributional standpoint, but its association with a relatively recent C-14 date (7,470+120BP, Lundelius and Turnbull, 1973) deserves comment. This is somewhat younger than most terminal dates on extinct genera in Australia (11,000 to 14,000BP, Martin, 1967; 20,000 to 25,000 BP, Marshall, 1974), although a few younger dates have been reported (Martin, 1967). It is possible that the Madura Cave specimen has been eroded from older deposits at the mouth of the cave and redeposited, and one aspect of its preservation (color) suggests this. A C-14 date applicable to *Thylacoleo* of the same general age (6570+100 BP) reported from Lake Menindee, New South Wales by Tindale (1957) is now thought to be too young (Tedford, 1967, pp. 17-18). The Madura Cave date then remains the youngest date on *Thylacoleo*, if its association within Unit 1 is to be trusted. We are reluctant to accept this even though the specimen undoubtedly came from Unit 1, for its red color suggests redeposition from a deeper unit to which the Unit 1 date would not apply.


• = T. carnifex Wellington (Australian Museum)
○ = T. carnifex Narracoorte Caves (So. Australian Mus.)
□ = T. carnifex SE. Darling Downs-Woods '56 (Q'l'd, Mus.)
✪ = T. sp. Madura Cave TMM-41106-516
⊙ = T. sp. Geurie, NSW. (Australian Mus. F 41447)
NMV = Nat. Museum Victoria
× = British Museum (Nat. Hist.)
◇ = T. crassidentatus Chinchilla-Barthalomai '62 (Q'l'd, Mus.)
ANTERIOR WITH
LENGTH
NMV 15920
F 738
F 2962
F 2964
F 3565
F 2928
F 2929
F 745
NMV 1903
F 2495
NMV 13022
NMV 23456

ENVIRONMENTAL INTERPRETATION

The environmental implications of the larger carnivorous marsupials are poorly understood. *Thylacoleo carnifex* is not known as a living animal, and its habitat and other requirements are unknown. *Thylacinus cynocephalus* and *Sarcophilus harrisii* are extant only in Tasmania, but they had a wide distribution in Australia during the Pleistocene and early Recent (Ride, 1964; Calaby and White, 1967). Thus their presence in an assemblage of fossils provides little information on environmental conditions.

The smaller species, all of which are extant, are better environmental indicators. Three species, *Antechinus flavipes*, *Phascogale calura*, and *Parantechinus apicalis*, are not known from the Recent fauna of the Nullarbor Plain but are found today in more humid regions to the east and west. This indicates the presence in this region of more humid conditions in the past, which is in agreement with the interpretations of Main et al. (1958) and Serventy (1951) based on the distribution of living organisms. One species lives today in the area of the junction of South Australia, Queensland, and the Northern Territory where it inhabits desert grassland (Marlow, 1962). The change that lead to its disappearance from the Nullarbor Plain is uncertain.

Opposite:

FIG. 27. Bivariate graph comparing proportions of P_4's of various specimens of *Thylacoleo* with one another and with the Madura Cave specimen. The Wellington Cave sample of *T. carnifex* included the following Australian Museum specimens: MF 21, MF 82-3, MF 116, MF 388, 575, MF 734, F10835, F 16454-5, F 16458-60, F 16606, F 16614, F 16617-9, F 16623-7, F 18659, F 18884, F 19370, F 31035, and F 37691-2. The Naracoorte Caves and other specimens of *T. carnifex* in the South Australian Museum included 11 specimens measured in 1964. Here maximum widths were measured, not necessarily AW, for the following: P50, P89-91, P94, P96-7, P105, P111, and P13719-20. The British Museum specimens are mostly considered to be *T. carnifex*, but it is possible that one or two *T. crassidentatus* are among them. They are: BMNH M39, M2572, M3570, M3665, BMNH 39995, BMNH 42516, BMNH 46835, and one uncatalogued specimen.

The decrease in taxonomic diversity of the insectivorous-carnivorous marsupials indicates the disappearance of some habitats. There are 14 taxa of insectivores and carnivores (13 Marsupicarnivora and one *incertae sedis—Thylacoleo*) represented in the deposits of Madura Cave. If the very specialized, atypical *Myrmecobius* is omitted, the total is 13. This is greater than the number known from the Recent fauna of the Nullarbor Plain (seven) or from the Recent fauna of any area of Australia.

Another difference is the coexistence in the Pleistocene fauna of species that are now allopatric. *Antechinus flavipes*, *Phascogale calura*, and *Parantechinus apicalis* are not found today in the same area with *Dasycercus cristicauda* or *Dasyuroides byrnei*. Similar phenomena have been observed in North America (Hibbard, 1960; Guilday et al., 1964; Dalquest, 1965; Lundelius, 1967; 1974;) and in Europe (Kowalski, 1967). In those areas the disappearance of these associations has been interpreted as indicating a decrease in the equability of the climate. The changes in the carnivorous and insectivorous marsupial fauna from the Nullarbor Plain suggest a change to a lower and less reliable rainfall from the late Pleistocene and Holocene to Recent.

ACKNOWLEDGEMENTS

In addition to those persons and institutions listed in Part I (pp. 32-33) and Part II (pp. 93-94) of this faunal report, we wish to offer our thanks to Dr. Perenyi for the artwork, and to Field Museum and University of Texas Geology Foundation for continuing support. For the loan of specimens, we thank the following institutions: American Museum of Natural History, Australian Museum, British Museum (Natural History), Princeton University Museum, South Australian Museum, United States National Museum, and Western Australian Museum.

REFERENCES

ARCHER, M.

1974. New information about the Quaternary distribution of the thylacine (Marsupialia; Thylacinidae) in Australia. Jour. Roy. Soc. Western Austral., **57**, no. 2, pp. 43-50, figs. 1-2.

BARTHOLOMAI, A.

1962. A new species of *Thylacoleo* and notes on some caudal vertebrae of *Palorchestes azael*. Mem. Queensland Mus., **14**, no. 1, pp. 33-40, figs. 1-4.

BENSLEY, B. A.

1903. On the evolution of the Australian Marsupialia; with remarks on the relationships of marsupials in general. Trans. Linn. Soc., London, Ser. 2, Zool. **9**, pp. 83-216, figs. 1-6, pls. 5-7.

BOITARD, M.

1841, "1842." Pantheon Populaire. Le Jardin des Plantes. G. Barba, Paris; Roe Lockwood and Son, N.Y. 204 pp.

CALABY, J. H.

1966. Mammals of the upper Richmond and Clarence Rivers, New South Wales. Commw. Sci. Industr. Res. Org., Austral. Div. Wildl. Res., Tech. Pap. 10, 55 pp.

CALABY, J. H. and C. WHITE

1967. The Tasmanian devil (*Sarcohilus harrisii*) in Northern Australia in Recent times. Austral. Jour. Sci., **29**, no. 12, pp. 473-475, figs. 1-2.

COOK, D. L.

1963. *Thylacinus* and *Sarcophilus* from the Nullarbor Plain. W. Austral. Nat., **9**, pp. 47-48.

DALQUEST, W. W.

1965. New Pleistocene formation and local fauna from Hardeman County, Texas. Jour. Paleo., **39**, no. 1, pp. 63-79, figs. 1-2.

DORTCH, C. E. and D. MERRILEES

1971. Human occupation of Devil's Lair, Western Australia during the Pleistocene. Archeol. Phys. Anthropol. Oceania, **8**, no. 2, pp. 89-114.

FINLAYSON, H. H.

1961. On central Australian mammals. Part IV. The distribution and status of central Australian species. Rec. S. Austral. Mus., **14**, no. 1, pp. 141-191, fig. 1.

GEOFFROY SAINT-HILAIRE, E.

1796. Mag. Encyclop., ser. 2, **3**, p. 469.

GEOFFROY SAINT-HILAIRE, E. and G. CUVIER

1837. Histoire naturelle des mammiferes, **4**, pt. 60, p. 6.

GILL, E. D.

1953. Distribution of the Tasmanian devil, the Tasmanian wolf, and the dingo in S. E. Australia in Quaternary time. Vict. Nat., **70**, pp. 86-90.

1954. Ecology and distribution of the extinct giant marsupial, *Thylacoleo*. Vict. Nat., **71**, pp. 18-35.

GLAUERT, L.

1912. Fossil marsupial remains from Balladonia in the Eucla division. Rec. W. Austral. Mus., **6**, pp. 47-65, pls. 6-8.

GOULD, J.

1841. Observations on *Dasyurus maugei* and *D. viverrinus* of Geoffroy, and description of a new species. Proc. Zool. Soc., London, **1840**, p. 151.

1844. Exhibition and character of a number of animals transmitted from Australia by Mr. Gilbert. Proc. Zool. Soc., London, **1844**, pp. 103-107.

GRAY, J. E.

1842. A new species of tapering-tailed phascogale in the collections of the British Museum. Ann. Mag. Nat. Hist., ser. 1, **9**, p. 518.

GUILDAY, JOHN E., PAUL S. MARTIN, and ALLEN D. MCCRADY

1964. A Late Pleistocene cave deposit in Bedford County, Pennsylvania. Bull. Nat. Speleo Soc., **26**, no. 4, pp. 121-194.

GUILER, E. R. and R. W. L. HEDDLE

1974. The eruption and growth of teeth in the Tasmanian Devil, *Sarcophilus harrisii* (Marsupialia: Dasyuridae). Pap. Proc. Roy. Soc. Tasmania, **108**, pp. 137-140, 1 fig., 1 pl.

HARRIS, G. P

1808. Description of two new species of *Didelphis* from Van Diemen's Land. Trans. Linnean Soc., London, **9**, no. 11, pp. 174-178, pl. 19.

HIBBARD, CLAUDE W.

1960. An interpretation of Pliocene and Pleistocene climates in North America. Mich. Acad. Arts Sci. Letters, 62nd Ann. Rept. (1959-60), pp. 5-30.

JONES, F. WOOD

1923. The mammals of South Australia. Part 1. The monotremes and the carnivorous marsupials. Handbooks of the Flora and Fauna of South Australia, Adelaide., pp. 1-131, figs. 1-88.

KOWALSKI, K.

1967. The Pleistocene extinction of mammals in Europe, pp. 349-364, 6 text figs. *In* Martin, P. S. and H. E. Wright, Jr., eds., Pleistocene extinctions, The search for a cause, vol. 6, Proc. VII, Congr. Int. Assn. Quaternary Res., Nat. Acad. Sci., Yale Univ. Press, New Haven and London.

KREFFT, G.

1867. On the classification of the small Dasyuridae of Australia, with descriptions of two new genera and one new species. Proc. Zool. Soc., London, 1866, pp. 431-435, pl. 36.

KURTÉN, B.

1965. The Carnivora of the Palestine caves. Acta Zool. Fenn., no. 107, pp. 1-74, 11 figs., 4 pls.

LOWRY, D. C. and J. W. J. LOWRY

1967. Discovery of a Thylacine (Tasmanian Tiger) carcase in a cave near Eucla, Western Australia. Helictite, **5**, pp. 25-29.

LOWRY, J. W. J. and D. MERRILEES

1969. Age of the described carcase of a Thylacine (Marsupialia, Dasyuroidea) from Thylacine Hole, Nullarbor Region, Western Australia. Helictite, **7**, pp. 15-16.

LUNDELIUS, E. L., JR.

1963. Vertebrate remains from the Nullarbor Caves, Western Australia. Jour. Roy. Soc. W. Austral., **46**, part 3, pp. 75-80.

1967. Late-Pleistocene and Holocene faunal history of Central Texas, pp. 287-319, figs. 1-11. *In* Martin, P. S. and H. E. Wright, Jr., eds., Pleistocene extinctions, The search for a cause, vol. 6, Proc. VII, Congr. Int. Assn. Quaternary Res., Nat. Acad. Sci., Yale Univ. Press, New Haven and London.

1974. The last fifteen thousand years of faunal change in North America, pp. 141-160. *In* Black, C. C., ed., History and prehistory of the Lubbock Lake site, Mus. Jour. (Texas Tech. Univ. Lubbock), **15**.

LUNDELIUS, E. L., JR. and W. D. TURNBULL

1973. The mammalian fauna of Madura Cave, Western Australia. Part I. Fieldiana: Geol. **31**, no. 1, pp. 1-35, figs. 1-13, tables 1-2.

1975. The mammalian fauna of Madura Cave, Western Australia. Part II. Fieldiana: Geol. **31**, no. 2, pp. 37-117, figs. 1-21, tables 1-15.

MACLEAY, W. S.

1841. (1842). Notice of a new genus of Mammalia discovered by J. Stuart, esq., in New South Wales. Ann. Mag. Nat. Hist., 8, ser. 1, no. 51, art. XXXIX, pp. 240-243, pl. VII.

MAIN, A. R., A. K. LEE, and M. J. LITTLEJOHN

1958. Evolution in three genera of Australian frogs. Evolution, **12**, pp. 299-304.

MARLOW, B. J.

1958. A survey of the marsupials of New South Wales. Commw. Sci. Industr. Res. Org., Austral., Wildl. Res. **3**, no. 2, pp. 71-114, figs. 1-34.

1962. Marsupials of Australia. Jacaranda Pocket Guides, Jacaranda Press, Brisbane. pp. 1-141.

MARSHALL, L. G.

1974. Late Pleistocene mammals from the "Keilor cranium site," Southern Victoria, Australia. Mem. Nat. Mus. Victoria, **35**, pp. 63-86, 11 figs.

MARTIN, P. S.

1967. Pleistocene overkill, pp. 75-120, figs. 1-4. *In* Martin, P. S. and H. E. Wright, Jr., eds., Pleistocene extinctions, The search for a cause, vol. 6, Proc. VII Congr. Int. Assn. Quaternary Res., Nat. Acad. Sci., Yale Univ. Press, New Haven and London.

MERRILEES, D.

1968. Man the destroyer: late Quaternary changes in the Australian marsupial fauna. Jour. Roy. Soc. W. Austral., **51**, no. 1, pp. 1-24, figs. 1-3.

MEYER [initials not known]

1793. Systematischsummarisch Uebersicht der neusten zoologischen Entdeckugen in Neuholland, pp. 28, 281 (fide Tate, 1947, p. 135).

MULVANEY, D. J., G. H. LAWTON, C. R. TWIDALE; with special reports by N. W. G. MACINTOSH, J. A. MAHONEY, and N. A. WAKEFIELD

1964. Archaeological excavation of Rock Shelter No. 6, Fromm's Landing, South Australia, Proc. Roy. Soc. Vict., **77**, pp. 479-516.

OWEN, R.

1859. XVI. On the fossil mammals of Australia. Part I. Description of a mutilated skull of a large marsupial carnivore (*Thylacoleo carnifex*, Owen), from a calcareous stratum, eighty miles S. W. of Melbourne, Victoria. Phil. Trans. Roy. Soc., **149**, no. 16, part 1, pp. 309-322, pls. 11-15.

PARTRIDGE, J.

1967. A 3,300 year old Thylacine (Marsupialia: Thylacinidae) from the Nullarbor Plain, Western Australia. Jour. Roy. Soc. W. Austral., **50**, pp. 57-59.

PETERS [initials not known]

1875. Sitzber. Gesellsch. Naturf. Fr., Berlin, p. 73, (New Name for *Chaetocercus* Krefft.) (fide Tate 1947, p. 141).

RIDE, W. D. L.

1964. A review of the Australian fossil marsupials. Jour. Roy. Soc. W. Austral., **47**, pt. 4, no. 16, pp. 97-131, figs. 1-13.

1970. A guide to the native mammals of Australia. Oxford Univ. Press, Melbourne, London, Wellington, N.Y. i-xiv, pp. 1-149, figs. 1-62 by Ella Fry.

SERVENTY, D. L.

1951. The evolution of the chestnut-shouldered wrens *Malurus)*. Emu, **51**, pp. 113-120.

SIEGAL, S.

1956. Nonparametric statistics for the behavioral sciences. McGraw Hill, New York, pp. i-xvii, 1-312.

SMITH, M. J.

1972. Small fossil vertebrates from Victoria Cave, Naracoorte, South Australia. II. Peramelidae, Thylacinidae and Dasyuridae (Marsupialia). Trans. Roy. Soc. S. Austral., **96**, Part 3, 125-137, figs. 1-8.

SPENCER, B.

1896. [Preliminary notice of *Dasyuroides byrnei*]. Proc. Roy. Soc., Vic., N.S., **8**, p. 6.

1896. Report on the work of *The Horn* scientific expedition to central Australia, **2**, Zoology, pp. 36-40, pls. 3 and 4 (figs. 1-4).

TATE, G. H. H.

1947. On the anatomy and classification of the Dasyuridae (Marsupialia). Results of the Archbold Expeditions. No. 56. Bull. Amer. Mus. Nat. Hist., **88**, art. 3, pp. 97-156, text-fig. 1.

TEDFORD, R. H.

1967. The fossil Macropodidae from Lake Menindee, New South Wales. Univ. Calif. Pubs., Geol. Sci., **64**, i-v, pp. 1-165, figs. 1-32, plates 1-4.

TEMMINCK, C. J.

1824, 1827. Monographies de Mammalogie, **1**, pp. xxiii, 23, 60, 267 (*Thylacinus*) also xxiii, 23, 56 (*Phascogale*). (fide Tate, 1947 pp. 118, 135).

THOMAS, O.

1888. Catalogue of the Marsupialia and Monotremata in the collection of the British Museum (Nat. Hist.), London. Taylor & Francis, London, I-XIII, 401 pp.

TINDALE, N.

1957. Culture succession in southeastern Australia from late Pleistocene to the present. Rec. S. Austral. Mus., **13**, pp. 1-49.

TROUGHTON, E.

1962. Furred animals of Australia. 7th ed. Angus and Robertson, Sydney, London, Melbourne, Wellington. xxxii pp., 376 pp., pls. I-XXV.

TURNBULL, W. D.

1970. The Trinity therians: their bearing on evolution in marsupials and other therians, chap. 9, pp. 151-179, figs. 1-6. *In* Dahlberg, A. A., ed., Dental morphology and evolution, Univ. of Chicago Press, Chicago, London.

WAKEFIELD, N. A. and R. M. WARNEKE

1967. Some revision in *Antechinus* (Marsupialia) -2. Vict. Nat., **84**, pp. 69-99, figs. 1-9, pl. 3.

WATERHOUSE, G. R.

1836. Description of a new genus (*Myrmecobius*) of mammiferous animals from New Holland, probably belonging to the marsupial type. Proc. Zool. Soc., London, **1836**, pp. 69, 70, 131 (preliminary description). Trans. Zool. Soc. London, **1841**, pp. 149-154, pls. 27, 28 (extended description).

1838. Characters of some new species of the genera *Mus* and *Phascogale*. Proc. Zool. Soc., London, **1837**, pp. 75-77.

WOODS, J. T.

1956. The skull of *Thylacoleo carnifex*. Mem. Queensland Mus., **13**, pt. 2, pp. 125-140, figs. 1-6.

TABLE 1. Numerical data on lower dentitions of a Recent population of *Antechinus stuartii* and of some specimens of *A. flavipes*.

		Antechinus stuartii adusta FM 60955 - FM 60960			*A.f. flavipes* FM 35337	*A.f. rufogaster* FM 104787	*A.f. leucogaster* FM 18889
Variate	Sample Size	Observed Range	Mean	Standard Deviation			
M_{1-4}	6	6.94-7.32	7.14	.134	7.14	7.81	6.85
L.low.Pm	6	2.98-3.32	3.18	.133	3.18	3.27	3.40
P_2 L	6	.99-1.19	1.08	.069	1.15	1.05	1.05
W	6	.75- .81	.80	.024	.73	.85	.66
P_3 L	6	1.27-1.37	1.30	.039	1.24	1.25	1.29
W	6	.81- .89	.85	.027	.78	.88	.71
P_4 L	6	1.01-1.12	1.06	.049	1.02	.95	1.02
W	6	.61- .76	.68	.052	.56	.71	.61
M_1 L	6	1.70-1.77	1.73	.023	1.85	1.83	1.61
AW-E	6	.91- .99	.95	.036	.83	1.10	.83
PW	6	.94-1.06	1.02	.042	1.02	1.17	.85
M_2 L	6	2.05-2.18	2.13	.050	2.12	2.32	1.95
AW-E	6	1.22-1.37	1.27	.055	1.15	1.29	1.10
PW	6	1.17-1.22	1.21	.022	1.20	1.27	.98
M_3 L	6	2.08-2.15	2.10	.030	2.12	2.34	1.98
AW-E	6	1.06-1.37	1.18	.134	1.24	1.37	1.15
PW	6	1.06-1.17	1.11	.044	1.17	1.20	.98
M_4 L	6	1.72-1.98	1.87	.093	1.85	1.88	1.73
AW-E	6	1.09-1.22	1.17	.052	1.05	1.15	1.00
PW	6	.36- .46	.39	.041	.71	.54	.41

TABLE 2. Numerical data on upper dentitions of Recent specimens of Antechinus flavipes compared with the small sample of A. stuartii adusta, as in Table 1.

	Antechinus stuartii adusta			A.f. flavipes	A.f. rufogaster	A.f. leucogaster
	FM 60955 - FM 60960			FM 35337	FM 104787	FM 18889
Variate	Sample Size	Observed Range	Mean			
M^{1-4}	6	6.39-6.72	6.59	6.48	7.18	6.30
M^{1-3}	5	5.73-5.99	5.83	5.70	6.34	5.63
L.up.Pm	6	2.84-3.17	3.30	3.10	3.08	3.31
p^2 L	6	.81- .91	.87	1.02	.85	.87
W	6	.61- .66	.64	.61	.66	.61
p^3 L	6	1.01-1.12	1.07	1.17	1.10	1.05
W	6	.66- .76	.71	.73	.73	.68
p^4 L	6	1.12-1.22	1.16	1.24	1.22	1.18
W	6	.71- .86	.77	.61	.73	.76
M^1 L	6	2.05-2.23	2.17	2.20	2.39	2.09
W	6	1.52-1.67	1.59	1.51	1.61	1.48
M^2 L	5	2.00-2.10	2.05	2.05	2.32	2.05
W	5	1.93-2.13	2.02	1.81	2.20	1.75
M^3 L	5	1.77-1.88	1.80	1.78	1.95	1.85
W	5	2.13-2.33	2.24	2.07	2.32	2.03
M^4 L	6	.63 .74	.67	.85	.73	.76
W	6	2.03-2.13	2.10	1.98	1.95	1.82

TABLE 3. Numerical data on upper and lower dentitions of Antechinus flavipes leucogaster from Western Australia.

Variate	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
M^{1-4}	15	6.17-6.71	6.37±.030	.149	2.34
M^{1-3}	15	5.32-5.88	5.58±.027	.133	2.38
L.up.Pm	15	2.80-3.61	3.16±.044	.219	6.94
p^3 L	14	1.01-1.33	1.11±.021	.079	7.14
LM_{1-4}	15	6.64-7.20	6.89±.034	.172	2.49
L.low.Pm	14	2.80-3.57	3.22±.057	.213	6.62
P_3 L	14	.75-1.03	.92±.026	.097	10.59

Specimens included are: WAM - M194, M279, M894, M1159, M1334, M1401, M1411, M1695, M1759, M1822, M2037, 7050, 9035, BMNH 41.12.44; and FMNH 18889.

TABLE 4. Numerical data on upper and lower dentitions of *Antechinus flavipes* from Madura Cave.

Variation	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
P_4 L	2	.96-1.16	1.06	--	--
W	3	.56- .71	.63	--	--
M_1 L	4	1.52-1.62	1.57	--	--
AW-E	4	.76- .81	.80	--	--
PW	4	.86- .91	.88	--	--
M_2 L	8	1.67-1.88	1.78 ±.03	.088	4.9
AW-E	8	1.01-1.17	1.096±.02	.052	4.7
PW	8	.99-1.06	1.026±.009	.026	2.5
M_3 L	8	1.83-1.93	1.89 ±.011	.032	1.7
AW-E	8	1.14-1.22	1.18 ±.008	.023	1.9
PW	8	.91-1.01	.98 ±.012	.034	3.4
M_4 L	9	1.62-1.90	1.74 ±.032	.095	5.5
AW-E	9	1.01-1.17	1.04 ±.018	.053	5.1
PW	8	.30- .71	.47 ±.056	.158	33.3
M^3 L	2	1.74-1.88	1.81	--	--
W	2	2.07-2.08	2.08	--	--

TABLE 5. Numerical data on lower dentitions of *Phascogale calura* from Unit 1, Madura Cave.

Variate	Sample Size	Observed Range	Mean
LM_{1-4}	3	7.52-7.66	7.58
L.low.Pm	3	3.36-3.57	3.47
P_2 L	3	1.24-1.32	1.28
W	3	.85- .93	.89
P_3 L	2	1.27-1.29	1.28
W	2	--	.88
P_4 L	3	.88-1.07	.98
W	3	.63- .66	.64
M_1 L	3	1.78-1.88	1.81
AW-E	3	.90-1.07	.98
PW	3	.95-1.00	.98
M_2 L	2	2.15-2.20	2.18
AW-E	2	--	1.24
PW	2	1.15-1.20	1.18
M_3 L	5	2.07-2.32	2.18
AW-E	5	1.27-1.37	1.33
PW	5	1.05-1.20	1.15
M_4 L	5	1.88-1.93	1.90
AW-E	5	1.07-1.17	1.11
PW	5	.49- .57	.52

TABLE 6. Numerical data on lower dentitions of *Phascogale calura* from Units 2 and 3, Madura Cave.

Variate	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
LM_{1-4}	1	--	7.70	--	--
P_2 L	1	--	1.22	--	--
W	1	--	.91	--	--
P_3 L	1	--	1.37	--	--
W	1	--	.95	--	--
P_4 L	2	.93-1.05	.99	--	--
W	2	.66- .80	.73	--	--
M_1 L	4	1.73-1.92	1.83	--	--
AW-E	4	.91-1.14	1.01	--	--
PW	4	.96-1.06	1.00	--	--
M_2 L	7	2.00-2.29	2.17±.039	.102	4.72
AW-E	8	1.22-1.37	1.31±.016	.044	3.38
PW	8	1.15-1.37	1.24±.027	.075	6.06
M_3 L	9	2.08-2.36	2.20±.033	.099	4.48
AW-E	9	1.27-1.44	1.34±.022	.065	4.83
PW	9	1.06-1.24	1.15±.025	.074	6.44
M_4 L	9	1.77-2.13	1.96±.043	.129	6.59
AW	9	1.06-1.22	1.14±.020	.059	5.17
PW	9	.37- .66	.50±.029	.086	16.96

TABLE 7. Numerical data on lower dentitions of *Phascogale calura* from Units 4 and 5, Madura Cave.

Variate	Sample Size	Observed Range	Mean
LM_{1-4}	1	--	8.08
P_3 L	1	--	1.33
W	1	--	.84
P_4 L	3	.93-1.18	1.05
W	3	.61- .68	.64
M_1 L	4	1.59-1.94	1.81
AW-E	4	.91-1.07	1.01
PW	4	.91-1.14	1.07
M_2 L	3	2.16-2.28	2.24
AW-E	3	1.22-1.33	1.28
PW	3	1.14-1.37	1.27
M_3 L	7	1.98-2.34	2.22
AW-E	7	1.26-1.37	1.33
PW	7	1.06-1.28	1.13
M_4 L	6	1.86-2.15	1.99
AW-E	6	1.14-1.22	1.16
PW	6	.44- .61	.51

TABLE 8. Numerical data on dentitions of Recent samples of *Phascogale calura* from Western Australia.[1]

Variate	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
L. upper molars	16	6.74-7.30	7.06±.036	.142	2.01
Length M^{1-3}	17	6.01-6.79	6.27±.044	.183	2.91
P^{2-4} L	16	2.94-3.70	3.28±.056	.224	6.83
P^4 L	16	.95-1.40	1.12±0.28	.111	9.91
M_{1-4} L	17	7.09-8.50	7.69±.078	.321	4.17
P_{2-4} L	16	3.03-3.87	3.46±.058	.230	6.65
P_4 L	15	.87-1.08	.98±.019	.074	7.60

[1]Based on the following specimens: W.A.M. M332, M1246, M2864, M2292, M1277, M866, M2581, M1226, M1262, M1106, M1089, M2532; FMNH 36052; BMNH 83.10.19.11, 35 (or 36).12.5.1, 7.7.18.14.

TABLE 9. Numerical data on upper dentitions of *Phascogale calura* from Madura Cave.

		WAM 74.9.16	TMM 41106-739	TMM 41106-738	PM 25580	PM 36052
M^1	L	--	--	2.32	--	2.27
	W	--	--	1.66	--	1.54
M^2	L	--	--	--	2.43	2.20
	W	--	--	--	2.17	1.98
M^3	L	2.17	2.07	--	--	1.98
	W	2.15	2.27	--	--	2.20
M^4	L	--	.81	--	--	.90
	W	--	2.00	--	--	2.15

TABLE 10. Numerical data on lower dentitions of *Phascogale tapoatafa* from Madura Cave.

Variate	Sample Size	Observed Range	Mean
LM_{1-4}	1	--	11.46
LP_{2-4}	1	--	4.78
P_2 L	1	--	1.93
W	1	--	1.32
P_3 L	1	--	2.18
W	1	--	1.34
P_4 L	2	1.22-1.37	1.30
W	2	.91-1.06	.99
M_1 L	4	2.69-2.94	2.83
AW-E	3	1.67-1.77	1.70
PW	3	1.47-1.57	1.53
M_2 L	3	3.24-3.29	3.27
AW-E	3	1.77-1.93	1.86
PW	3	1.72-1.80	1.76
M_3 L	2	3.14-3.19	3.17
AW-E	2	1.93-2.03	1.98
PW	2	1.77-1.93	1.85
M_4 L	2	2.69-2.84	2.77
AW-E	2	1.67-1.77	1.72
PW	2	.76- .91	.84

TABLE 11. Numerical data on lower dentitions of *Phascogale tapoatafa* from Wedge's Cave.

Variate	Sample Size	Observed Range	Mean
LM_{1-4}	3	11.17-11.87	11.48
LP_{2-4}	1	--	5.52
P_2 L	1	--	2.28
W	1	--	1.72
P_3 L	1	--	2.28
W	1	--	1.62
P_4 L	3	1.27-1.37	1.34
W	3	1.01-1.06	1.03
M_1 L	3	2.69-3.04	2.86
AW-E	3	1.57-1.67	1.64
PW	2	1.52-1.62	1.57
M_2 L	3	3.19-3.42	3.28
AW-E	3	1.85-1.98	1.90
PW	3	1.72-1.88	1.83
M_3 L	3	3.19-3.29	3.22
AW-E	3	1.90-2.03	1.95
PW	3	1.57-1.67	1.64
M_4 L	3	2.58-2.74	2.65
AW-E	3	1.67-1.75	1.71
PW	3	.76- .81	.78

TABLE 12. Numerical data on upper and lower dentitions of a Recent sample of *Phascogale tapoatafa*.[1]

Variate	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
L M^{1-4}	15	9.3-10.9	10.24±.12	.458	4.47
L M^{1-3}	15	8.0-9.6	9.02±.11	.438	4.85
L P^4	15	1.2-2.0	1.77±.05	.202	11.45
L M_{1-4}	15	10.4-12.0	11.27±.12	.474	4.21
L P_4	15	2.0-2.4	2.25±.04	.136	6.02

[1]Based on following specimens: BMNH 7.7.18.13; 44.2.15.19; 46.4.4.89; 42.6.29.5; 41.1240; 53.10.22.18; 42.6.29.4; 54.10.24.20; 41.1239; 44.7.9.8; 46.4.4.63; 43.8.12.27; 53.10.22.17; 4.1.3.101; TMM M-838.

TABLE 13. Numerical data on lower dentitions of *Parantechinus apicalis* from Madura Cave and Hastings Cave.

	Madura Cave		Hastings Cave[1]	
	PM 25330	Sample Size	Observed Range	Mean
Length M_{1-4}	9.68	9	8.48-9.45	8.81
M_1 L	2.13	9	2.03-2.38	2.16
AW	1.09	9	.92-1.04	.97
AW-E	1.42	9	1.12-1.27	1.18
PW	1.22	9	1.01-1.12	1.06
M_4 L	2.54	12	2.13-2.33	2.22
AW	1.37	12	1.20-1.35	1.29
AW-E	1.47	12	1.19-1.37	1.29
PW	.56	12	.48- .61	.53

[1]Based on the following specimens: FM PM 7268-7270; 13329-13337.

TABLE 14. Numerical data on dentitions of a Recent sample of *Parantechinus apicalis* from Western Australia.

Variate	Sample Size	Observed Range	Mean
L.up.Pm	4	3.40-3.65	3.56
L P^4	4	.50- .68	.61
L.up.molar	4	7.57-8.43	7.99
L M^{1-3}	4	6.66-7.47	7.04
L.lw.Pm	4	3.47-4.13	3.65
L P_4	4	.32- .55	.46
L.lw.molar M_{1-4}	4	8.60-9.53	8.98

Based on B.M. 44.9.30.6; 48.1.27.27; 46.4.4.90; 44.6.15.8.

TABLE 15. Numerical data on lower dentitions of *Dasycercus cristicauda* from Unit 1 of Madura Cave.

Variate	Sample Size	Observed Range	Mean
Canine-Ant-Post Diameter	5	1.12-1.57	1.30
Length premolars	4	3.17-3.48	3.30
P_2 L	5	1.52-1.67	1.62
P_2 W	5	0.91-1.06	1.00
P_3 L	5	1.67-2.08	1.84
P_3 W	5	1.01-1.17	1.09
Length molars	2	9.6-10.03	9.82
M_1 L	5	2.23-2.33	2.28
M_1 AW-E	5	1.27-1.47	1.38
M_1 PW	5	1.09-1.32	1.20
M_2 L	6	2.35-2.77	2.64
M_2 AW-E	6	1.32-1.72	1.55
M_2 PW	6	1.27-1.57	1.44
M_3 L	3	2.69-2.89	2.81
M_3 AW-E	3	1.80-1.88	1.83
M_3 PW	3	1.47-1.57	1.53
M_4 L	3	2.59-2.69	2.61
M_4 AW-E	3	1.52-1.72	1.64
M_4 PW	3	0.56-0.66	0.61

TABLE 16. Numerical data on lower dentitions of *Dasycercus cristicauda* from Units 2-7 of Madura Cave.

Variate	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
L.Pm	1	--	3.53	--	--
P_2 L	1	--	1.77	--	--
P_2 W	1	--	0.91	--	--
P_3 L	2	1.42-1.77	1.60	--	--
P_3 W	2	.86-1.06	.96	--	--
M_1 L	4	1.98-2.18	2.07	--	--
M_1 AW-E	4	1.32-1.47	1.37	--	--
M_1 PW	4	1.06-1.37	1.19	--	--
M_2 L	11	2.48-2.59	2.52±.01	.048	1.34
M_2 AW-E	11	1.42-1.72	1.53±.02	.077	5.02
M_2 PW	11	1.32-1.57	1.40±.02	.076	5.44
M_3 L	11	2.53-2.74	2.63±.02	.076	2.95
M_3 AW-E	11	1.62-1.82	1.69±.02	.065	3.84
M_3 PW	11	1.32-1.52	1.39±.02	.062	4.44
M_4 L	8	2.18-2.64	2.38±.05	.145	6.10
M_4 AW-E	8	1.37-1.62	1.48±.03	.073	4.93
M_4 PW	8	0.36-0.56	0.45±.02	.063	13.95

TABLE 17. Numerical data on upper dentitions of *Dasycercus cristicauda* from Madura Cave.

	Unit 1			Units 2-7				
Variate	Sample Size	Observed Range	Mean	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
Length Upper Premolars	1	--	3.28	--	--	--	--	--
P^2 L	2	1.27-1.42	1.35	--	--	--	--	--
P^2 W	2	0.91-0.93	0.92	--	--	--	--	--
P^3 L	1	--	1.57	--	--	--	--	--
P^3 W	1	--	1.06	--	--	--	--	--
P^4 L	1	--	0.56	--	--	--	--	--
P^4 W	1	--	0.53	--	--	--	--	--
LM^{1-4}	2	8.99-9.25	9.12	--	--	--	--	--
LM^{1-3}	2	8.01-8.31	8.16	--	---	--	--	--
M^1 L	3	2.74-2.99	2.86	2	2.80-2.94	2.87	--	--
M^1 W	3	1.93-1.95	1.94	2	1.84-1.98	1.91	--	--
M^2 L	3	2.79-2.94	2.88	5	2.52-2.79	2.66	--	--
M^2 W	3	2.38-2.54	2.47	5	2.12-2.66	2.34	--	--
M^3 L	3	2.64-2.79	2.72	12	2.33-2.64	2.52+.029	.101	4.00
M^3 W	3	2.64-2.74	2.68	12	2.38-2.74	2.53±.030	.103	4.05
M^4 L	3	0.86-0.91	0.88	3	0.81-1.04	0.91	--	--
M^4 W	3	2.33-2.54	2.43	3	2.38-2.44	2.41	--	--

TABLE 18. Results of Mann-Whitney text comparisons of measuremnts of lower and upper dentitions of Dasycercus cristicauda samples from Unit 1 and Units 2-7. (Two tailed tests)

	Mean	Sample Size	U	P
L. lower premolars				
Unit 1	3.30	4	0.0	.4
Units 2-7	3.53	1		
P_2 L Unit 1	1.62	5	0.0	.334
Units 2-7	1.77	1		
P_2 W Unit 1	1	5	0.5	.334-.666
Units 2-7	0.91	1		
P_3 L Unit 1	1.84	5	7.5	>.5
Units 2-7	1.60	2		
P_3 W Unit 1	1.09	5	8.0	>.5
Units 2-7	0.96	2		
M_1 L Unit 1	2.28	5	0.0	.016
Units 2-7	2.07	4		
M_1 AW-E Unit 1	1.38	5	11.5	>.5
Units 2-7	1.37	4		
M_1 PW Unit 1	1.20	5	12.0	>.5
Units 2-7	1.19	4		
M_2 L Unit 1	2.64	6	11.0	<.05
Units 2-7	2.52	11		
M_2 AW-E Unit 1	1.55	6	28.0	>.1
Units 2-7	1.53	11		
M_2 PW Unit 1	1.44	6	26.0	>.1
Units 2-7	1.40	11		
M_3 L Unit 1	2.81	3	3.0	.05
Units 2-7	2.63	11		
M_3 AW-E Unit 1	1.83	3	1.5	.02-.05
Units 2-7	1.69	11		
M_3 PW Unit 1	1.53	3	1.5	.02-.05
Units 2-7	1.39	11		
M_4 L Unit 1	2.61	3	2.0	.048
Units 2-7	2.38	8		
M_4 AW-E Unit 1	1.64	3	1.5	.042-.048
Units 2-7	1.48	8		

TABLE 19. Numerical data on lower dentitions of *Dasyuroides byrnei* from Unit 1 of Madura Cave.

Variate	PM 30504	PM 30507
M_2 L	2.99	--
M_2 AW-E	1.88	--
M_2 PW	1.77	--
M_3 L	2.94	--
M_3 AW-E	1.93	1.98
M_3 PW	1.62	--

TABLE 20. Numerical data on lower dentitions of *Dasyuroides byrnei* from Units 2-3 of Madura Cave.

Variate	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
LM_{1-4}	15	9.99-11.51	10.89±.118	.455	4.17
P_2 L	5	1.52-1.98	1.78±.087	.196	11.01
P_2 W	5	0.91-1.12	1.00±.037	.083	8.32
P_3 L	13	1.88-2.13	1.98±.021	.076	3.82
P_3 W	14	1.04-1.27	1.15±.020	.073	6.38
M_1 L	22	2.48-2.91	2.77±.025	.119	4.31
M_1 AW-E	21	1.67-1.98	1.88±.027	.123	6.55
M_1 PW	22	1.37-1.62	1.49±.015	.069	4.62
M_2 L	39	2.64-3.19	2.99±.019	.116	3.88
M_2 AW-E	39	1.67-1.99	1.82±.012	.073	4.00
M_2 PW	39	1.49-1.93	1.72±.013	.082	4.73
M_3 L	46	2.58-3.19	2.97±.017	.114	3.85
M_3 AW-E	46	1.67-2.03	1.88±.011	.072	3.86
M_3 PW	46	1.47-1.82	1.64±.018	.125	7.61
M_4 L	39	2.38-2.89	2.67±.020	.122	4.56
M_4 AW-E	38	1.57-1.77	1.65±.011	.065	3.96
M_4 PW	39	.41- .81	.59±.014	.089	15.02

TABLE 21. Numerical data on lower dentitions of *Dasyuroides byrnei* from Units 4-5 of Madura Cave.

Variate	Sample Size	Observed Range	Mean
M_3 L	4	2.71-3.04	2.91
M_3 AW-E	4	1.67-1.88	1.81
M_3 PW	4	1.37-1.62	1.55
M_4 L	4	2.43-2.81	2.67
M_4 AW-E	3	1.57-1.77	1.65
M_4 PW	5	0.48-0.91	0.64

TABLE 22. Numerical data on lower dentitions of *Dasyuroides byrnei* from Units 6-7 of Madura Cave.[1]

Variate	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
P_3 L (R)	3	1.88-2.03	1.98	--	--
P_3 W (R)	3	1.12-1.16	1.13	--	--
M_1 L (RL)	4	2.74-3.04	2.89	--	--
M_1 AW-E (RL)	4	1.77-1.98	1.86	--	--
M_1 PW (RL)	4	1.47-1.79	1.58	--	--
M_2 L (R)	7	2.94-3.09	3.03±.025	.067	2.21
M_2 AW-E (R)	8	1.77-1.93	1.82±.021	.058	3.19
M_2 PW (R)	8	1.67-1.82	1.75±.016	.046	2.61
M_3 L (R)	10	2.84-3.19	2.99±.030	.094	3.14
M_3 AW-E (R)	11	1.79-1.98	1.90±.018	.058	3.06
M_3 PW (R)	10	1.52-1.77	1.65±.027	.084	5.10

[1]R based on rights only; RL based on rights and lefts combined.

TABLE 23. Numerical data on upper dentitions of *Dasyuroides byrnei* from Units 2-3 of Madura Cave.

Variate	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
P^2 L	2	--	1.47	--	--
P^2 W	2	0.91-0.96	0.94	--	--
P^3 L	5	1.52-1.69	1.60	--	--
P^3 W	5	0.96-1.08	1.02	--	--
P^4 L	15	1.01-1.47	1.23±.038	.146	11.87
P^4 W	13	0.76	0.87±.015	.054	6.21
M^{1-4}	7	9.62-9.92	9.74	--	--
M^{1-3}	11	8.24-8.92	8.63±.060	.120	2.31
M^1 L	32	2.89-3.40	3.11±.019	.108	3.47
M^1 W	31	2.03-2.28	2.14±.012	.068	3.15
M^2 L	34	2.89-3.24	3.06±.015	.085	2.78
M^2 W	32	2.64-2.94	2.76±.015	.088	3.18
M^3 L	26	2.53-2.89	2.74±.019	.094	3.44
M^3 W	28	2.64-3.09	2.87±.021	.110	3.84
M^4 L	11	0.96-1.16	1.04±.019	.062	5.96
M^4 W	11	2.25-2.56	2.44±.034	.113	4.63

TABLE 24. Numerical data on dentitions of a Recent sample of *Dasyuroides brynei*.

Variate	Sample Size	Observed Range	Mean
M_{1-4} L	6	10.96-11.39	11.13
P_{2-3} L	6	3.76- 4.44	4.14
M^{1-4} L	6	9.76-10.13	9.96
M^{1-3} L	6	8.60- 9.07	8.79
P^{2-4} L	6	3.86- 4.57	4.18
P^4 L	6	0.46- 1.34	0.98

TABLE 25. Numerical data on dentitions of *Dasyurus geoffroyi* from Madura Cave.

Variate	Sample Size	Observed Range	Mean ± Standard Error	Standard Deviation	Coefficient of Variation (%)
M_2 L	9	4.79-5.40	5.12	--	--
M_2 AW	10	2.43-2.96	2.80±.059	.188	6.71
M_2 PW	10	2.43-2.96	2.68±.053	.167	6.24
M_3 L	3	5.24-5.70	5.42	--	--
M_3 AW	4	3.12-3.34	3.19	--	--
M_3 PW	4	2.58-2.93	2.77	--	--
M^1 L	12	4.94-5.85	5.54±.074	.258	4.65
M^1 W	13	3.04-3.66	3.41±.046	.167	4.89
M^2 L	5	5.32-5.93	5.53	--	--
M^2 W	4	3.99-4.33	4.15	--	--
M^3 L	5	5.09-5.78	5.32	--	--
M^3 W	4	4.64-5.12	4.89	--	--

TABLE 26. Numerical data on lower dentitions of Recent samples of various species of *Dasyurus*.

	Dasyurus hallucatus TMM M-705 FM 54234			*Dasyurus quoll* FM 15628, 81523, 42754 34727, 57209			*Dasyurus geoffroyi* FM 35328, 34718 35329			*Dasyurus maculatus* 57803
Variate	Sample Size	Observed Range	Mean	Sample Size	Observed Range	Mean	Sample Size	Observed Range	Mean	
LM_{1-4}	1	--	14.78	5	17.96-19.46	18.61	2	20.76-20.88	20.82	
LP_{2-3}	2	5.87-5.67		5	6.91-8.00	7.37	2	7.80-8.35	14.45	
P_2 L				1	--	3.42	--			
P_2 W				1	--	1.55	--			
P_3 L				1	--	3.57	--			
P_3 W				1	--	1.67	--			
M_1 L	2	3.57-4.10	3.84	5	4.18-4.64	4.40	3	4.48-4.86	4.67	4.71
M_1 AW-E	2	1.82-2.20	2.01	5	2.13-2.43	2.33	3	2.05-2.51	2.28	2.89
M_1 AW	2	1.44-1.98	1.71	5	1.71-2.20	2.00	3	1.82-2.17	2.00	2.43
M_1 PW	2	1.67-2.13	1.90	5	2.28-2.89	2.48	3	2.05-2.43	2.24	2.58
M_2 L	2	4.03-4.71	4.42	5	4.79-5.32	4.96	3	4.98-5.62	5.30	5.55
M_2 AW-E	2	2.13-2.81	2.47	5	2.62-2.96	2.77	3	2.66-2.96	2.81	3.27
M_2 PW	2	2.05-2.51	2.28	5	2.70-3.12	2.86	3	2.43-2.81	2.62	3.12
M_3 L	2	3.88-4.82	4.35	5	4.90-5.47	5.14	3	5.40-6.04	5.72	6.23
M_3 AW-E	2	2.28-2.89	2.59	5	2.89-3.27	3.06	3	3.08-3.34	3.21	3.61
M_3 PW	2	1.86-2.28	3.80	5	2.66-2.93	2.81	3	2.66-2.74	2.70	3.04
M_4 L	1	--	3.80	5	4.64-5.32	4.99	3	5.47-5.78	5.63	6.31
M_4 AW-E	1	--	2.17	5	2.74-3.12	2.93	3	2.89-3.12	3.01	3.57
M_4 PW	1	--	0.91	5	1.39-1.98	1.63	3	1.18-1.44	1.31	1.60

TABLE 27. Numerical data on upper dentitions of Recent samples of various species of Dasyurus (Based on same specimens as Table 26).

	Dasyurus hallucatus TMM M-705 FM 54234			Dasyurus quoll FM 15628, 81523, 42754 34727, 57209			Dasyurus geoffroyi FM 35328, 34718, 35329		
Variate	Sample Size	Observed Range	Mean	Sample Size	Observed Range	Mean	Sample Size	Observed Range	Mean
LM^{1-4}	1	--	13.41	5	16.43-18.11	17.41	2	18.60-18.98	18.79
LM^{1-3}	2	11.78-13.44	12.61	5	14.55-16.35	15.41	2	16.58-17.23	16.91
LP^{2-3}	2	5.84-6.00	5.92	5	6.46-7.59	7.09	2	7.69-8.23	7.96
P^2 L	2	1.98-2.58	2.28	3	2.51-2.74	2.62	2	2.58-3.04	2.61
P^2 W	2	0.84-1.52	1.18	3	--	1.29	2	1.25-1.44	1.35
P^3 L	2	2.81-3.19	3.00	4	3.19-3.57	3.43	3	3.27-3.80	3.60
P^3 W	2	1.22-1.82	1.52	4	1.71-1.90	1.79	3	1.67-1.90	1.82
M^1 L	2	4.33-4.79	4.56	5	4.79-5.70	5.35	3	5.02-6.00	5.60
M^1 W	2	2.92-3.24	3.08	5	3.19-3.69	3.44	3	3.38-3.53	3.47
M^2 L	2	4.03-4.79	4.41	5	4.79-5.40	5.17	3	5.32-5.78	5.55
M^2 W	2	3.50-4.33	3.92	5	4.03-4.56	4.32	3	4.41-4.86	4.71
M^3 L	2	3.71-4.48	4.10	5	4.71-5.47	5.05	3	4.57-5.70	5.17
M^3 W	2	3.88-5.09	4.49	5	4.41-5.24	4.77	3	5.02-5.40	5.20
M^4 L	1	--	1.75	5	1.56-2.47	1.94	2	1.82-2.20	2.01
M^4 W	1	--	3.88	5	4.33-5.02	4.88	2	4.40-5.17	4.79

TABLE 28. Numerical data on selected dental measures of fossil and Recent samples of *Sarcophilus*.

	S. harrisii									*S. laniaris*	
	Recent Tasmania*			Madura Cave PM 30568, 30570, 30571, WAM 74.9.50			Nannup Cave PM 4413, 5249-5252, 5256-5257			Wedge's Cave PM 4353	Wellington Caves PM 4419	PM 6727
	N	O R	$\bar{x}$	N	O R	$\bar{x}$	N	O R	$\bar{x}$			
P_3 length	9	6.77- 7.50	6.93	2	5.75-6.50	6.13	1	--	5.75	5.95	7.50	--
P_3 width	9	5.30- 5.70	5.47	2	4.80-5.15	4.97	1	--	4.75	5.05	6.45	--
M_3 length	9	10.60-12.18	11.57	1	--	10.80	3	11.25-12.80	11.78	11.90	12.85	--
M_3 width	9	6.40- 6.90	6.77	1	--	6.20	2	6.40- 6.50	6.45	8.85	8.85	--
M^2 length	9	11.40-12.35	11.98	1	--	11.60	4	11.20-12.40	11.76	--	--	13.10
M^2 width	9	9.20-10.25	9.70	1	--	9.85	4	9.15-10.0	9.49	--	--	11.80

*Based on the following specimens: FM 46006, 46028, 47166, 47412, 49229, 57638, 57801, 57802, and 81525.

TABLE 29. Numerical data on dentitions of *Thylacinus cynocephalus*

Madura Cave	Length P^3	Width P^3	Width M_3
PM 30579	--	--	6.68
TMM 41106-59	8.10	3.70	--
Recent			
Pu ost 568	7.60	3.77	6.40
USNM 38801	8.26	3.95	6.70
FM 81522	7.60	3.54	6.50
Wellington Caves			
PM 1635	--	--	7.80

Publication 1290