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NEW SERIES, NO. 17

The Mammalian Fauna of Madura Cave, Western Australia Part VII: Macropodidae: Sthenurinae, Macropodinae, with a Review of the Marsupial Portion of the Fauna

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References should be typed in the following form:

Croat, T. B. 1978. Flora of Barro Colorado Island. Stanford University Press, Stanford, Calif., 943 pp.

Grubb, P. J., J. R. Lloyd, and T. D. Pennington. 1963. A comparison of montane and lowland rain forest in Ecuador. I. The forest structure, physiognomy, and floristics. Journal of Ecology, **51**: 567–601.

Langdon, E. J. M. 1979. Yagé among the Siona: Cultural patterns in visions, pp. 63–80. *In* Browman, D. L., and R. A. Schwarz, eds., Spirits, Shamans, and Stars. Mouton Publishers, The Hague, Netherlands.

Murra, J. 1946. The historic tribes of Ecuador, pp. 785–821. *In* Steward, J. H., ed., Handbook of South American Indians. Vol. 2, The Andean Civilizations. Bulletin 143, Bureau of American Ethnology, Smithsonian Institution, Washington, D.C.

Stolze, R. G. 1981. Ferns and fern allies of Guatemala. Part II. Polypodiaceae. Fieldiana: Botany, n.s., **6**: 1–522.

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The Mammalian Fauna of Madura Cave, Western Australia Part VII: Macropodidae: Sthenurinae, Macropodinae, with a Review of the Marsupial Portion of the Fauna

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The Mammalian Fauna of Madura Cave, Western Australia Part VII: Macropodidae: Sthenurinae, Macropodinae, with a Review of the Marsupial Portion of the Fauna

Abstract

The Sthenurinae and Macropodinae from Madura Cave consist of *Sthenurus* (*Simosthenurus*) near *S. oreas* and *S. gilli*, *Lagorchestes hirsutus*, *Lagostrophus fasciatus*, *Onychogalea lunata*, *Protemnodon* near *P. brehus* and *P. roechus*, *Petrogale* sp., *Macropus fuliginosus*, *Macropus titan*, and *Macropus robustus*. With the exception of *Macropus robustus* and *M. fuliginosus*, which occur only in Units 2–7, all the extant species are found in all units of the deposit.

The marsupial fauna from the Pleistocene Units 2–7 is more diverse than that of the Holocene Unit 1, and contains species that are found today in more mesic areas to the east and west of the Nullarbor Plain. These Pleistocene units also contain numerous disharmonious pairs of species that indicate a more equable climate than that of the present. The assemblage from Unit 1 more closely approximates the present fauna of the region, but retains a few taxa now found to the east and west.

Introduction

This section of the study of the Madura Cave mammalian fauna covers Sthenurinae and Macropodinae and concludes the systematic treatment of the marsupials. It also gives a brief analysis of the marsupial fauna as discussed here and in the previous sections (Lundelius & Turnbull, 1973, 1975, 1978, 1981, 1982, 1984) and its relationships to other major Pleistocene marsupial faunas of Australia. Scales for the drawings are indicated adjacent each object; all are in centimeters except for Figures 12 and 13, where some are in centimeters, others, in millimeters. Scales shown along the edges of Figures 16 and 18 are in millimeters. Values given in Tables 1–20 are in millimeters.

Measurements, abbreviations, and statistical and dental terminology are either those in standard use, or they have been given in the previous sections of this report, or they are defined where used. The study was completed before the dental terminology of Archer (1978) became widely accepted; hence, the older standard of Thomas (1888) was followed.

MACROPODIDAE 1839

Sthenurinae Glauert, 1926

Sthenurus Owen, 1873 (*nomen nudum*), 1874
(***Simosthenurus***) Tedford, 1966
***Sthenurus* (*Simosthenurus*) sp.** near *S. oreas* DeVis, 1895, and *S. gilli* Merrilees, 1965

MATERIAL

Trench 2, Unit 2, 2½ ft
- PM 4356, right P_4 (*Sthenurus* sp., Lundelius; 1963, *S. ?gilli*, Merrilees, 1965; *S.* cf. *oreas*, Tedford, 1966) (fig. 1A)

Trench 4, Unit 2, Level 1
- PM 38998, anterior third, left P_4 or P_3 (fig. 1B)

Trench 4, Unit 2, Level 2
- PM 38996, partial crown, right upper molar (fig. 1D)
- PM 38997, molar fragment

Trench 4, Units 4–5
- TMM 41106-3500, crown, left upper molar (fig. 1C)

COMPARATIVE MATERIAL

Sthenurus andersoni

Weetalibah (Binnia Creek), New South Wales
- PM 4516, symphysis and rami with left I–M_2, right I–M_1 (fig. 1F)

Sthenurus atlas

Wellington Caves, New South Wales
- PM 1571, right maxillary fragment with M^{1-3} (fig. 1E)

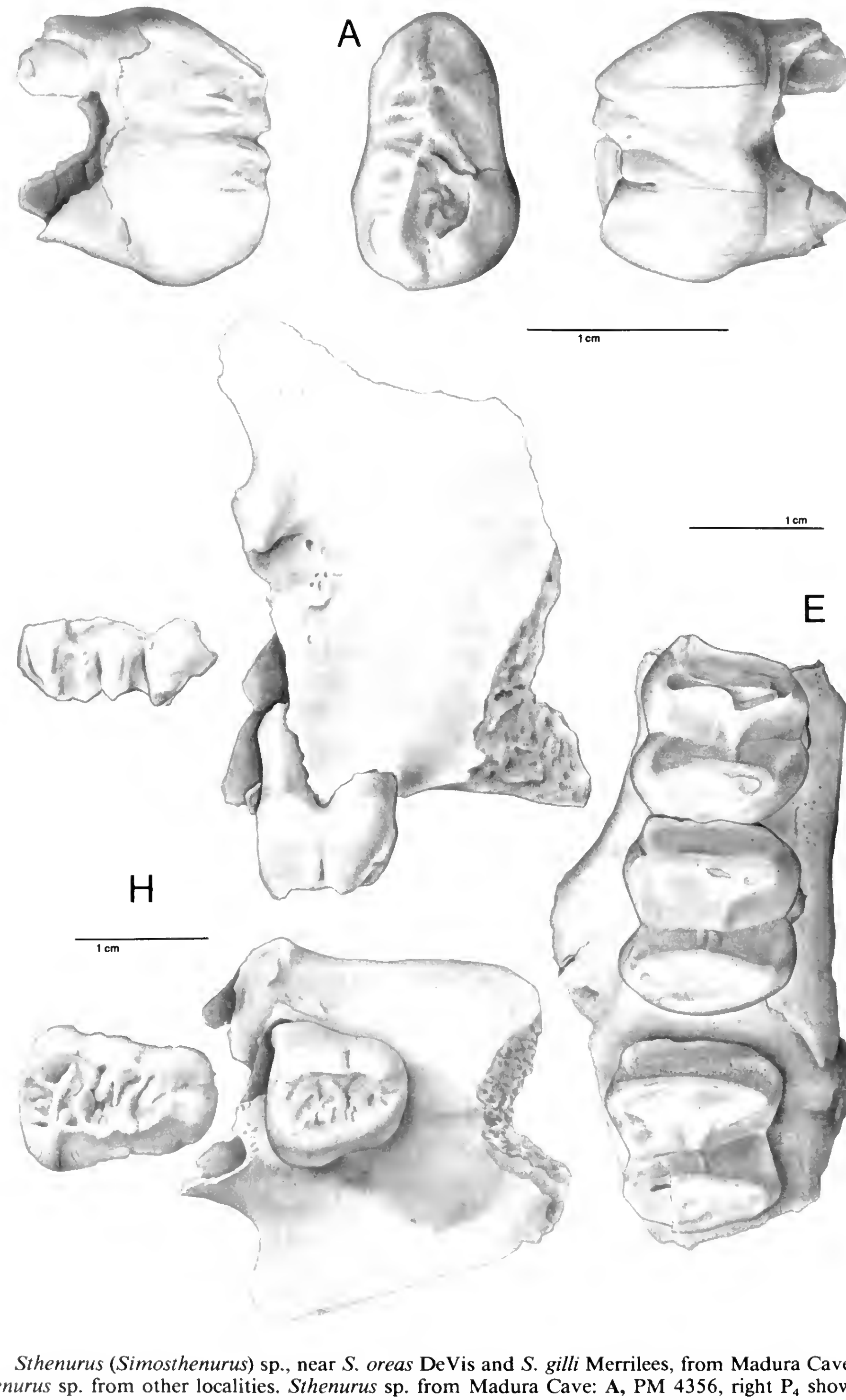
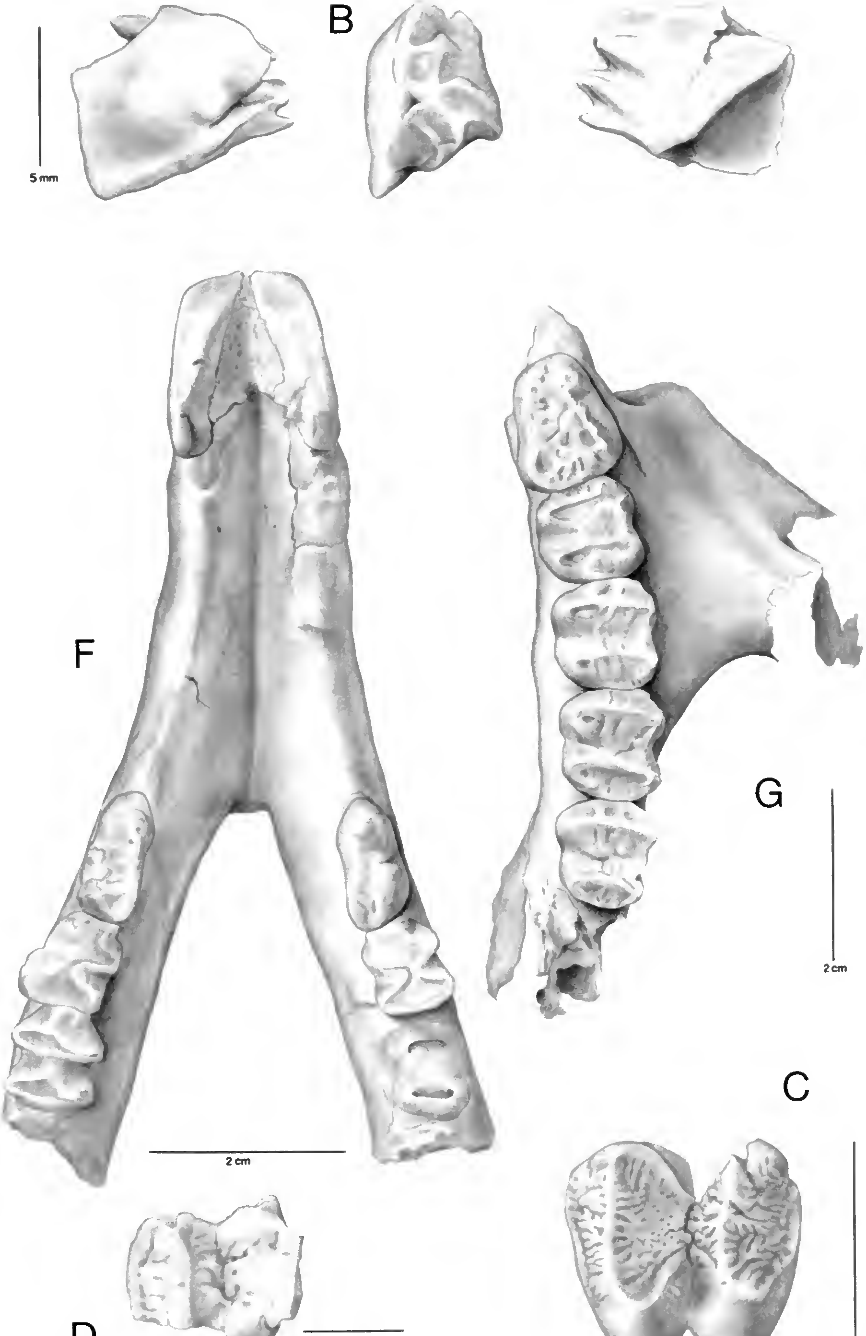


FIG. 1. *Sthenurus* (*Simosthenurus*) sp., near *S. oreas* DeVis and *S. gilli* Merrilees, from Madura Cave compared with *Sthenurus* sp. from other localities. *Sthenurus* sp. from Madura Cave: **A,** PM 4356, right P_4 shown in labial (right), lingual, and crown views; **B,** PM 38998, partial left P_4 or P_3 shown in labial (left), lingual, and crown views; **C,** TMM 41106-3500, left upper molar crown shown in crown view; **D,** PM 38996, partial right upper molar shown



in crown view. *Sthenurus atlas* from Wellington Caves, New South Wales: **E**, PM 1571, right maxillary fragment with M^{1-3} shown in crown view. *Sthenurus andersoni* from Weetalibah (Binnia Creek), New South Wales: **F**, PM 4516, symphysis and part of both rami with left I–M_2 and right I–M_1 shown in crown view. *Sthenurus brownei* from Mammoth Cave, Western Australia: **G**, PM 4414, left maxilla with P^4–M^4 shown in crown view; **H**, PM 7981, right maxillary fragment with P^3 and P^4 (removed from crypt) shown in crown and labial views.

PM 39065, left P^4
PM 6776, P^3 (or P_3)
PM 6777, right P^4

Sthenurus brownei

Mammoth Cave, Western Australia
PM 4414, left maxillary with P^4–M^4 (fig. 1G)
PM 7891, right maxillary fragment with P^3 and P^4 removed from crypt (fig. 1H)

Sthenurus tindalei

Lake Menindee, New South Wales
PM 4529 (cast of SAM P13820), palatal portion of skull with adult dentition

Descriptions

The P_4 is a two-crested tooth (fig. 1A). Its main crest begins near the anterior end of the crown at the anterior cusp. The crest soon incorporates a second laterally compressed, in-line cusp before dividing just anterior to the midpoint of the crown. From there the main crest is notched and continues as the lingual crest. It first runs diagonally posterolingually to within the posterior quarter of the crown and then turns back toward the midline and abruptly tapers down to the crown base at the posterior edge of the tooth. This lingual crest is comprised of three narrow cusps, the anterior one (which lies just behind the notch) being the most distinct. From the dividing point at the notch a lower but distinct labial crest rapidly descends, at first running transversely, then turning posteriorly and reaching its lowest point before beginning a steady rise as it continues posteriorly. Nearly at the rear of the tooth, where it is again nearly as high as the main crest, it arcs lingually across the labial half of the tooth, descends, and swings slightly forward as it enters the median valley. This forms a backward-opening posterior central basin between the two crests. Anteriorly within the basin, a low, sharp ridge connects the labial crest to the anterior end of the lingual portion of the main crest. This ridge is nearly parallel to the anterior, curved portion of the labial crest. At least two other crenulations swing off from the labial crest into the shallow posterolabial side of the basin. Measurements in millimeters of the tooth are: length 14.65, anterior width 6.63, posterior width 8.47, posterior basin length 8.15, and width 3.17. The fragment of a P_4 (or P_3) blade (fig. 1B) corresponds roughly to the anterior cusp of the main crest in the complete tooth, but differs in having more pronounced relief in its grooves and ridges.

The two upper molars (fig. 1C–D) are similar in size and major morphological features, but differ in detail. Both are brachyodont with lophs that are slightly convex anteriorly. The anterior cingulum of TMM 41106-3500 is small, but extends across the entire anterior face of the tooth. The posterior cingulum of both molars is very low and thin. The two teeth differ markedly in the density and coarseness of the crenulations on the faces of the lophs. In PM 38996 the crenulations are less dense and coarser than in TMM 41106-3500. In addition, the posterior crest of the paracone of PM 38996 is more prominent than that of TMM 41106-3500, and it closes the median valley labially. Low extensions of the midlink can be seen on the faces of the lophs in PM 38996, but not in TMM 41106-3500. In TMM 41106-3500 both faces of both lophs and the median valley are covered with fine crenulations that tend to be oriented at right angles to the crests and lophs. The longer crenulations are slightly curved, and many bifurcate away from the main crests and lophs. TMM 41106-3500 is less worn than the other tooth and further wear would undoubtedly simplify the ornamentation, but probably not to the extent seen in PM 38996.

Discussion

The dimensions of the Madura Cave specimens have been compared with measurements for various species of *Sthenurus* given by Bartholomai (1963), Tedford (1966), Merrilees (1965, 1968a), and Marcus (1962, 1976), and with an additional specimen of *S. andersoni* from Weetalibah, N.S.W. (PM 4516: P_4 length 14.65 mm, anterior width 6.40, posterior width 7.50) (fig. 2). This comparison shows that the P_4 from Madura Cave is too short to be assigned to *S. occidentalis*, *S. orientalis*, *S. antiquus*, *S. pales*, *S. tindalei*, *S. atlas*, or *S. notabilis*. It is too wide to be assigned to *S. andersoni* and slightly too narrow to be readily assigned to *S. brownei*. Its proportions are closest to those of *S. gilli* and *S. oreas*, which agrees with the Merrilees (1965) and Tedford (1966) assignments. It is also close to both of these species in the size of the posterior basin and in the absence from the basin of a ridge from the anterior cusp such as is shown by Tedford (1966) in *S. pales*.

Comparisons of the two molars from Madura Cave with those from other localities is difficult because of the uncertainty of their positions in the tooth row. Their small size (measurements, ob-

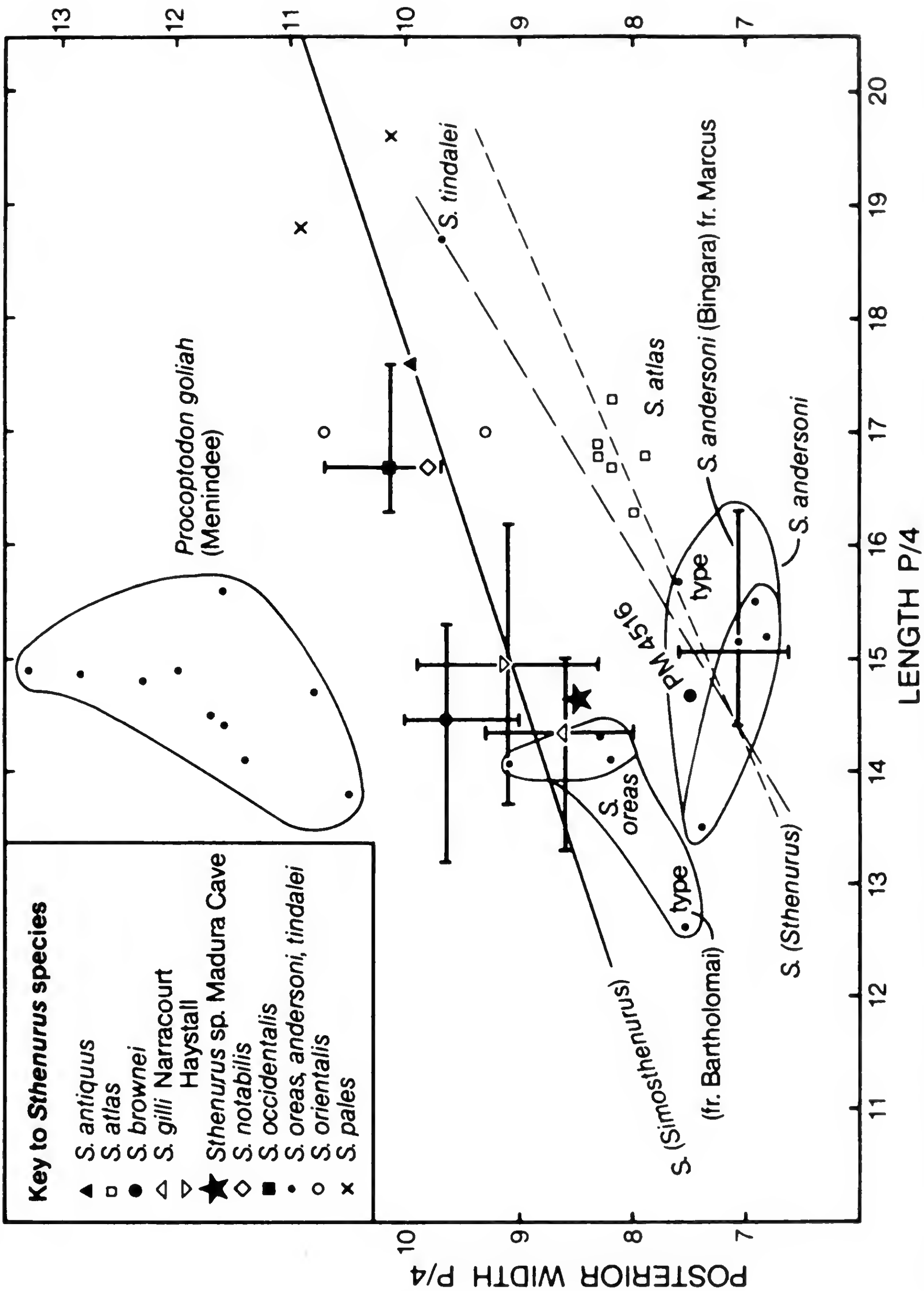


FIG. 2. Bivariate graph with length of P_4 plotted against posterior width of P_4 for samples of the various species of *Sthenurus*. Crude trend lines appear to distinguish the two subgenera. For comparison the *Procoptodon goliah* sample from Menindee is also shown.

tainable only from TMM 41106-3500, are: length 11.5 mm, anterior width 10.3 mm, posterior width 10.5 mm) excludes them from *Sthenurus pales*, *S. tindalei*, *S. atlas*, *S. andersoni* (except for the M^1), probably from *S. notabilis* and *S. antiquus*, and possibly from *S. oreas*. They are within the size range of one or more of the upper molars of *S. gilli*, *S. brownei*, and *S. occidentalis*. The weak development of the forelink and the presence of a buccal ridge closing the median valley in PM 38996 are features cited by Merrilees (1968a) as characteristic of *S. brownei*. Extensive fine crenulations are also cited by Merrilees (1968a) as characteristic of *S. brownei*, but his Figures 4 and 6 are not clear enough to allow detailed comparisons with TMM 41106-3500. Comparison of the upper molars from Madura Cave with those of *S. oreas* is uncertain because of the lack of upper teeth which have been unequivocally assigned to that species. Material from Queensland referred to *S. oreas* by Bartholomai (1963) is reported by him to have coarse ornamentation. Bartholomai's Figure 5 indicates coarser ornamentation than is seen in TMM 41106-3500, but is not unlike that of PM 38996.

It is not possible to make a positive assignment to species on the basis of the available material. The Madura Cave specimens are not necessarily all from the same taxon, but not enough is known about intraspecific variation of minor morphological features to rule out their assignment to the same taxon. Flannery (pers. comm., 1983) states that the difference in ornamentation between the two molars is greater than the range of variation in known samples of *Sthenurus*. Milham and Thompson (1976) reported *Sthenurus* teeth from the south passage of Madura Cave, referring them to two species, *S. gilli* and an unnamed larger form, but no figures or descriptions of the specimens are given. More material is needed from Madura Cave to determine the number and identity of the species of *Sthenurus* from this locality.

Macropodinae Thomas, 1888

Lagorchestes hirsutus Gould, 1844

MATERIAL

Surface
- TMM 41106-679, skull and left ramus (figs. 4A–D, 5A)

Trench 1, top 1 ft
- PM 4784, left ramus fragment with M_{1-3}, alveoli for P_4 and M_4
- PM 25540, right ramus fragment with M_3, alveoli of M_2 and M_4

Trench 2, 2½ ft below surface
- PM 25221, left ramus with dP_4, M_1, part of M_2, part of crypt for P_4 (fig. 7B).

Trench 3, Unit 2, Level ?
- PM 39038, right P_4
- PM 39039, left P_4

Trench 4, Unit 1, Level 1
- PM 39047, right I^1

Trench 4, Unit 1, top 1 ft
- TMM 41106-5130, left P_4
- PM 39003, skull and mandible (figs. 5B, 6A–C)

Trench 4, Unit 2, Level 1
- TMM 41106-5087, right I^1
- PM 38916, P^3

Trench ? (probably 4), Unit 2, Level ?
- PM 38914, left maxillary fragment with P^3 (fig. 7C)

Trench 4, Unit 2, Level 2
- PM 38947, right M^4

Trench 4, Unit 2, Level 4
- TMM 41106-150, left P^4

cf. ***Lagorchestes hirsutus***

Trench 3, Unit 2, Level 1
- TMM 41106-5044, left M_3 (or M_2 or M_4)
- TMM 41106-5045, right M_4 or M_3
- TMM 41106-5049, left M_1
- PM 38922, left M_3 or M_2
- PM 39035, left M^4 or M^3
- PM 39041, right M_1

Trench 3, Unit 2, Level 2
- TMM 41106-140, left ramus fragment with M_{3-4}

Trench 4, Unit 1, top 1 ft
- TMM 41106-5059, left M_4 or M_3
- TMM 41106-5082, right M_2 or M_3
- PM 38892, left M_3 or M_4
- PM 38893, left M_4
- PM 38898, left P^4
- PM 38901, right M^3 or M^4

Trench 4, Unit 2, Level 1
- PM 38942–38944, three left M^4s

Trench 4, Units 4–5
- PM 36981, right I^3

COMPARATIVE MATERIAL

Bernier Island, Western Australia
- AMNH 155106 (fig. 3)

Webb's Cave (surface), Mundrabilla Station, Western Australia
- TMM 41209-528

TMM 41209-891
TMM 41209-892 (fig. 7A)

Descriptions

SKULL—The skull has the normal macropodid shape with the braincase relatively more inflated and the rostrum relatively narrower than in the large species of *Macropus*. The muzzle is wider than that of most *Lagostrophus* or *Onychogalea* of comparable size (*O. unguifera* being one exception). In dorsal view the rostrum narrows abruptly immediately anterior to the orbits. The sides of the zygomatic arches and the interorbital area are straight and parallel.

The nasals taper anteriorly and extend only slightly anterior to the dorsal ends of the premaxillae. They extend posteriorly as far as the lacrimals and are square or gently rounded posteriorly. The frontals extend approximately one-half the distance from the posterior end of the nasals to the nuchal crest. The posterior end of each is gently rounded. The frontals expand anterolaterally to contact the maxillary and lacrimal bones. Between the orbits, where the lateral edges of the frontals are parallel to each other, they are sharply angled at the junction of the median wall of the orbit and the dorsal surface of the skull. In contrast, the modern comparative specimens of *Lagostrophus* and *Onychogalea* exhibit several different frontal shapes. The frontals of *Lagostrophus fasciatus* are narrower and taper posteriorly nearly to a point, those of *Onychogalea frenata* bow outward from a narrowest point just behind the flange for the lacrimal and then taper roundly posteriorly, and those of *O. unguifera* are wide and more closely resemble those of *Lagorchestes* than those of *O. frenata*.

The parietals make up approximately two-thirds of the dorsal part of the braincase. They extend anteriorly, lateral to the frontals, as far as the posterior end of the interorbital constriction. A small triangular interparietal is present in front of the supraoccipital, at the junction of the sagittal and occipital crests. The modern comparative specimen also has the interparietal, as do specimens of *Onychogalea frenata* and *O. unguifera*; specimens of *Lagostrophus fasciatus* lack it. The dorsal border of the temporal fossa is marked by a weak ridge which extends from the posterior end of the interorbital constriction diagonally across the dorsal surface of the braincase to join its mate, forming a short sagittal crest just anterior to the interparietal. In a modern specimen from Bernier Island (AMNH 155106, fig. 3), the ridges converge but do not join to form a sagittal crest. Each lacrimal has a small flange that projects into the anterodorsal part of the orbit.

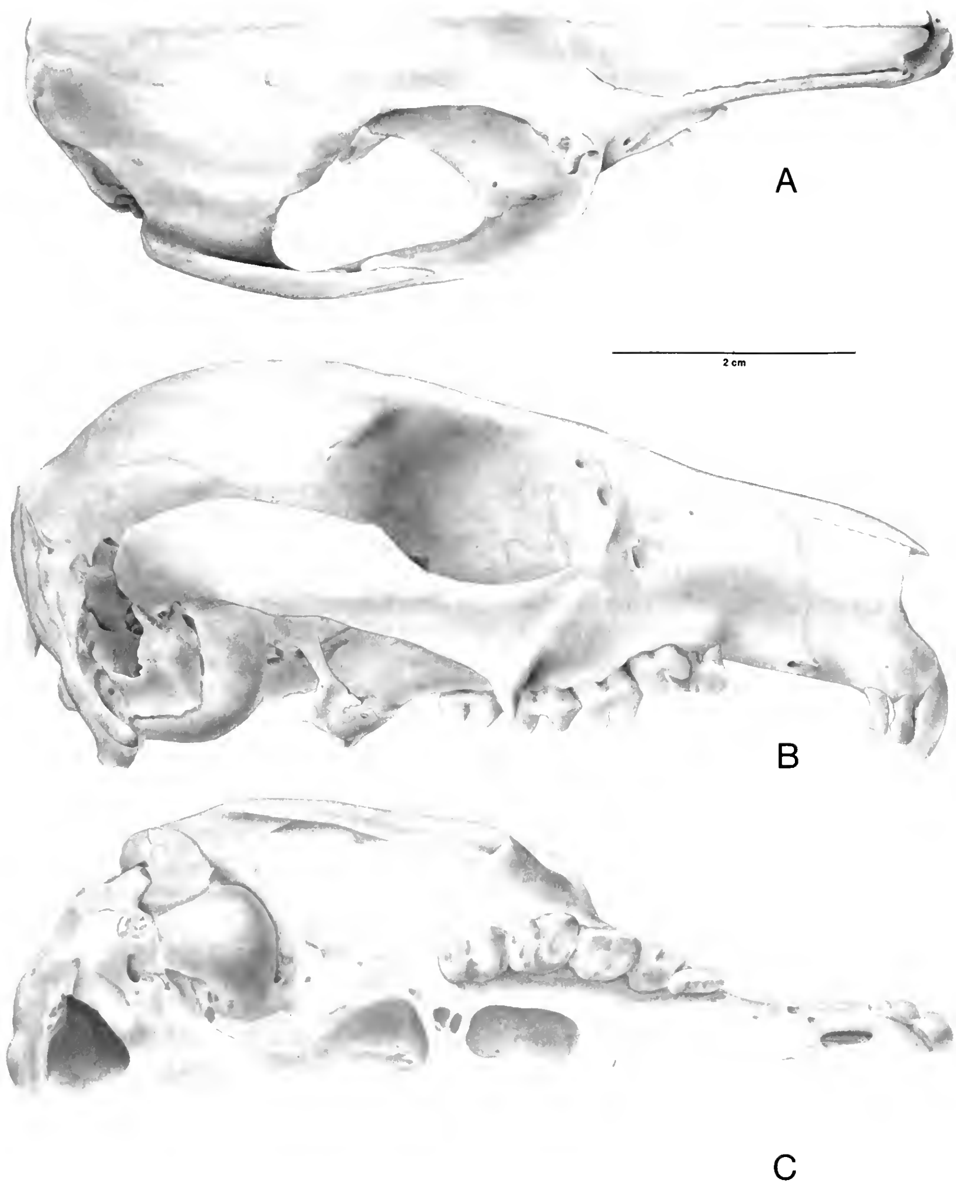
In lateral view the premaxilla with its incisors projects below the plane of the molars. The dorsal profile of the skull is straight from just ahead of the frontoparietal suture to the anterior end of the nasal. This profile resembles that of the modern *Lagostrophus fasciatus*, but differs from *Onychogalea frenata* and *O. unguifera*, which have a more rounded and undulating profile. The muzzle is deep, with sides that are almost flat. This is also true of the modern specimen and of specimens of *Lagostrophus fasciatus*. There is no prominent depression on the lower part of the lateral surface of the maxilla ahead of P^4, such as is seen in modern *Onychogalea*. The anterior opening of the infraorbital foramen is small (~ 1 mm), as in the modern specimen and in *Lagostrophus fasciatus* and *Onychogalea unguifera*; in *O. frenata* it varies between ~ 1 mm and ~ 3 mm. In the Madura Cave specimens the foramen is located immediately ahead of the orbit, about halfway between the tooth row and the dorsal surface of the skull. In *Lagostrophus* and *Onychogalea* the anterior opening of the infraorbital foramen is located nearer the tooth row.

The descending process of the zygomatic arch extends to the level of the occlusal surface of the molars, as in *Lagostrophus*. In *Onychogalea* the descending process is smaller and shorter.

In ventral view the tooth rows are bowed outward slightly, with the maximum width at the position of the descending process of the zygomatic arch.

The palate shows little narrowing anterior to P^4; this differs from both *Onychogalea* and *Lagostrophus*. The modern specimen from Bernier Island (AMNH 155106) shows more taper than the Madura Cave specimens (figs. 3A,C, 4A,C, 6A,C). The incisive foramina are elongate ovals which extend from the level of the midpoint of I^3 to the suture between the premaxilla and maxilla. They are larger than those of modern *Lagostrophus*, approaching the size of those of modern *Onychogalea*.

The palatal fenestrae are irregularly oval and lie across the maxillary-palatine suture, opposite M^{3-4} or M^{2-3}. Additional fenestration of the palatines is not extensive. The fenestrae of the Madura Cave specimens are smaller than those of the modern specimen, and much smaller than those


A
2 cm
B
C

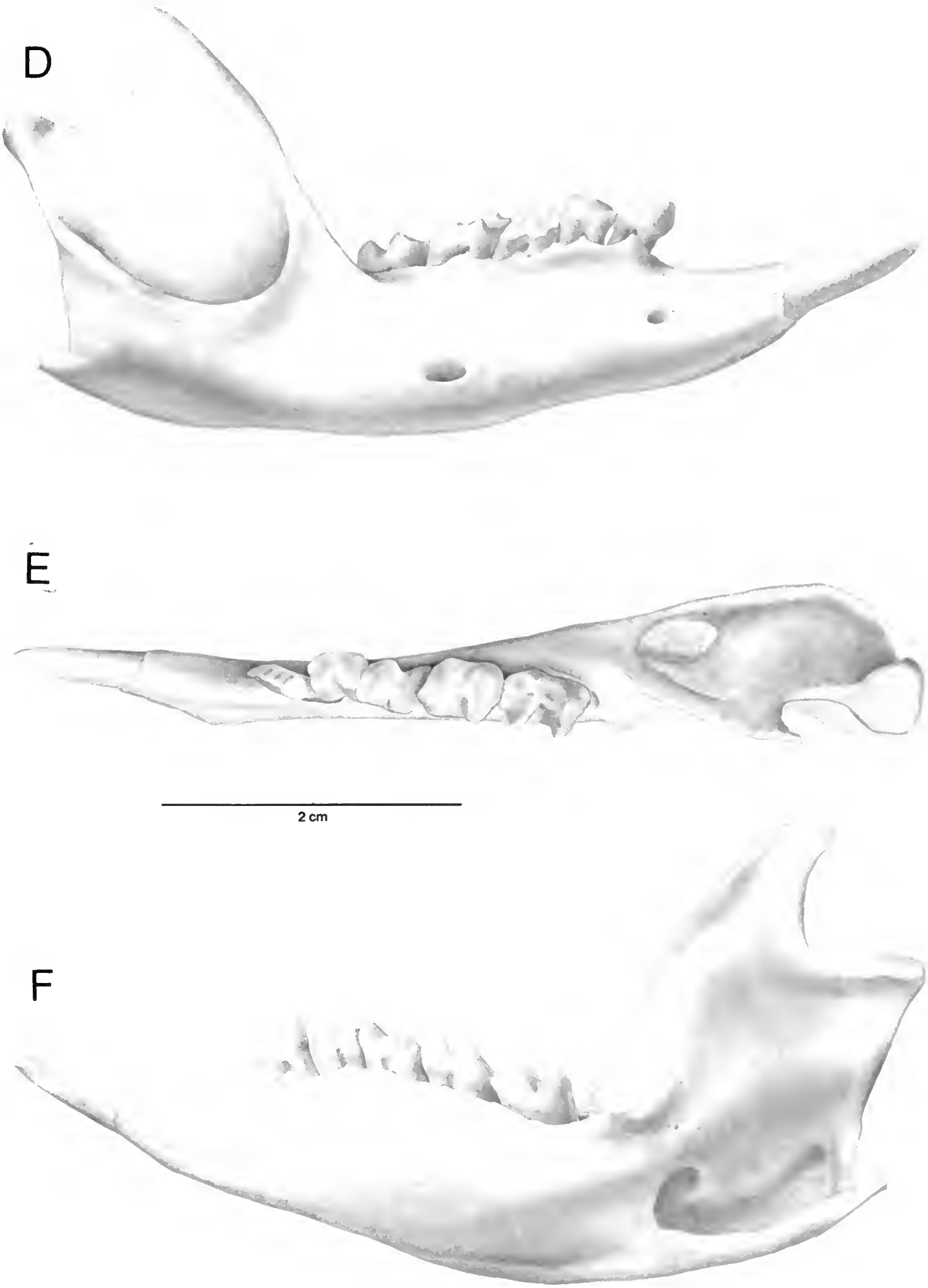


FIG. 3. Drawing of the skull and right mandible of the modern *Lagorchestes hirsutus*, AMNH 155106, from Bernier Island, Western Australia. Views of skull: **A**, dorsal; **B**, right lateral; **C**, ventral. Views of jaw: **D**, lateral; **E**, dorsal; **F**, mesial.

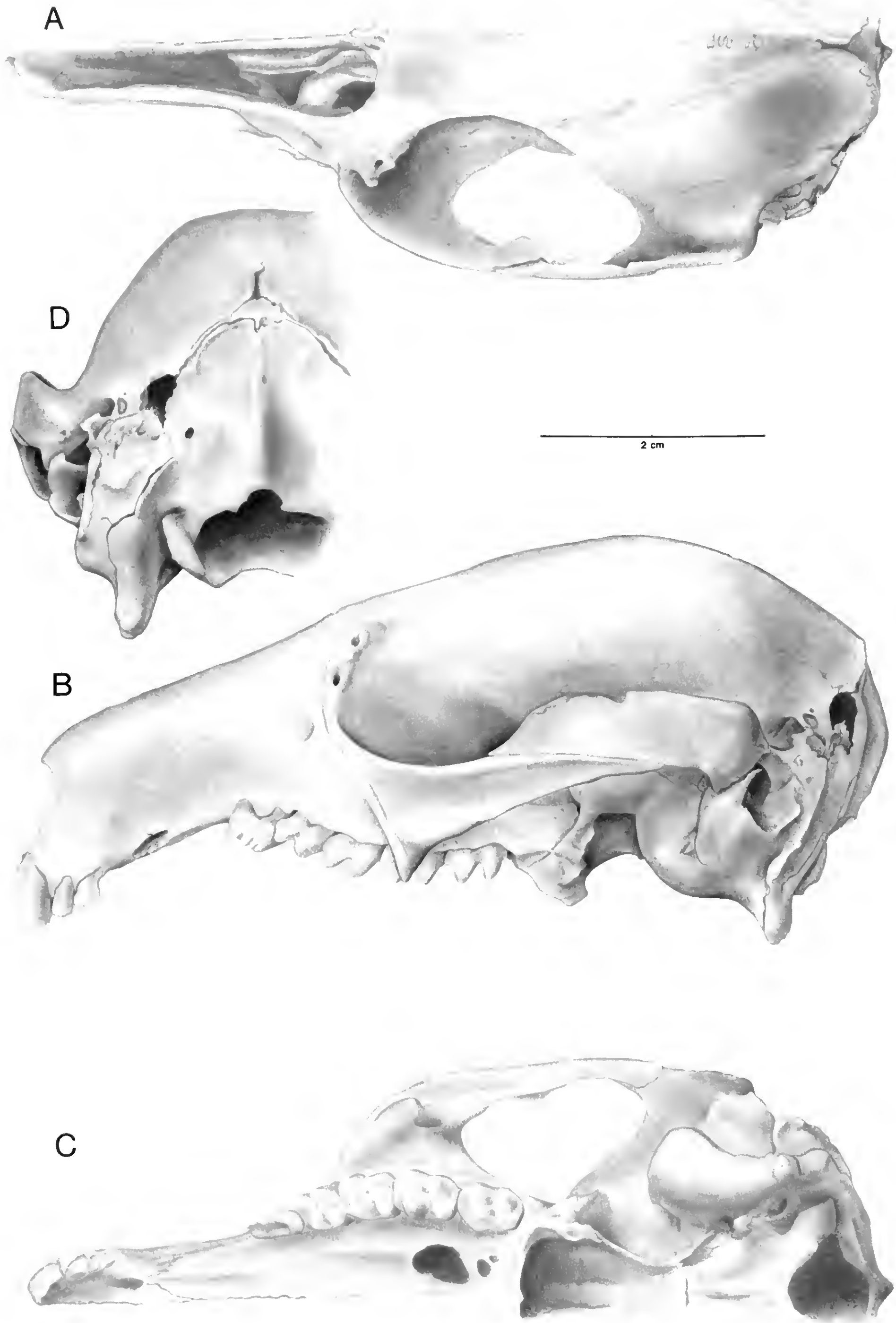


FIG. 4. Four views of a skull of *Lagorchestes hirsutus*, TMM 41106-679, from the surface of Madura Cave: **A,** dorsal; **B,** left lateral; **C,** ventral; **D,** posterior.

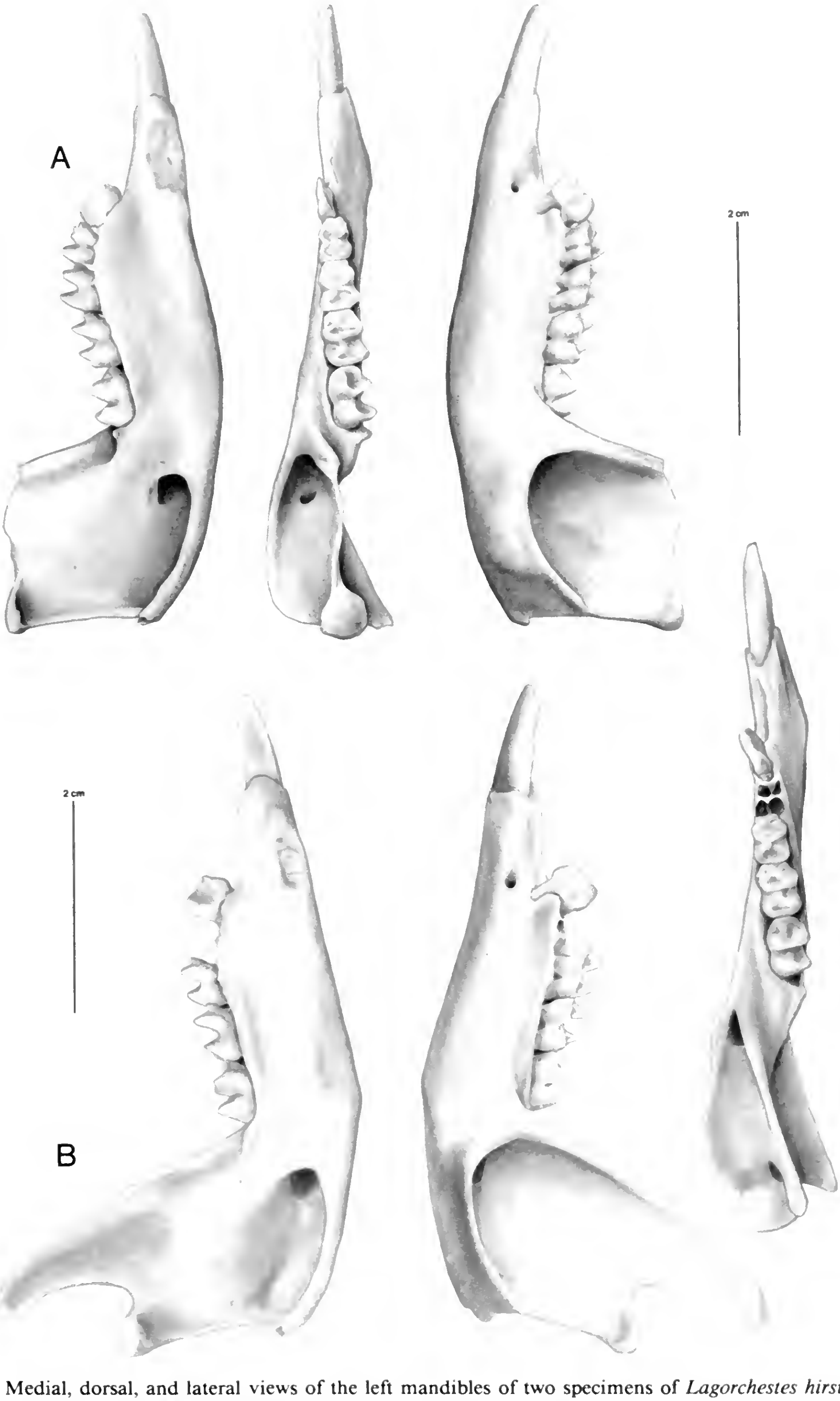


FIG. 5. Medial, dorsal, and lateral views of the left mandibles of two specimens of *Lagorchestes hirsutus* from the surface of Madura Cave: **A**, TMM 41106-679 (jaw belongs to skull shown in fig. 4); **B**, PM 39003 (jaw belongs to skull shown in fig. 6).

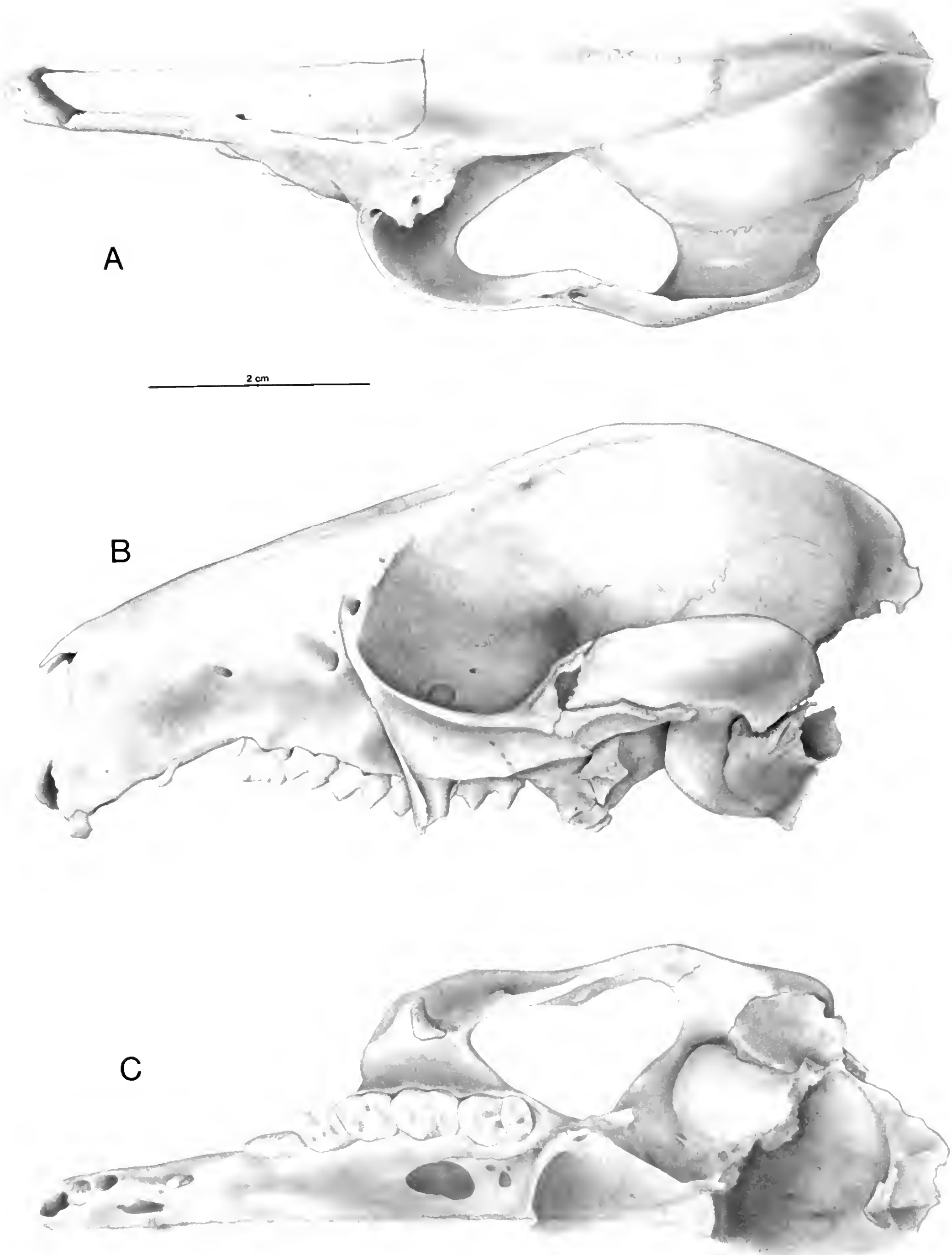


FIG. 6. Three views of a skull of *Lagorchestes hirsutus*, PM 39003, from the surface of Madura Cave: **A**, dorsal; **B**, left lateral; **C**, ventral. (Jaw of this specimen is shown in fig. 5B.)

of modern *Lagostrophus fasciatus* and *Onychogalea frenata*, where they extend farther forward into the maxilla. The very young modern *O. unguifera* specimen has no true palatal fenestrae; instead, a small perforation pierces each maxilla at or near the suture with the palatine, and both maxilla and palatine are riddled with a dozen similar perforations, plus so many minute perforations that the bone resembles lacework.

The auditory bullae are inflated to a greater degree than in *Lagostrophus* or *Petrogale* and to about the same degree as in *Onychogalea*, but not to the extent seen in *Bettongia*. The bullae of *Lagorchestes* are more elongate than those of *Onychogalea*. The mastoid process protrudes farther ventrally and laterally, but is not bent forward to lap around the side of the tympanic as it is in *Onychogalea*. The tympanic in each of these taxa is expanded laterally to form a considerable meatal tube.

Upper Dentition—The upper incisors are arranged in a smooth, broadly U-shaped arch in the fossil and modern *Lagorchestes*, like modern *Onychogalea* (ROM 91.11.1.190; USNM 122614, 237643), and in contrast to the V-shape of this arch in *Lagostrophus* (AMNH 155104). The I^1 is the largest incisor. It is almost oval in cross section, with a flat area on the medial side and a shallow indentation posteriorly for the I^2. In *Lagostrophus* the I^1 is smaller than I^2 and I^3 and is triangular in cross section. In *Onychogalea* the I^1 is larger than I^2 or I^3 and has a more flattened oval cross section than that of *Lagorchestes*.

The I^2 and I^3 are approximately equal in size, but are different in shape. The I^2 is oval in cross section except for a flattening on the outside and a broad, shallow depression posteriorly for the anterior edge of I^3. A small posterior lobe is present but is not seen in worn teeth. The I^2 of *Onychogalea* is slightly larger and has a better developed posterior lobe. The I^2 of *Lagostrophus* is much larger and more elongate than that of either *Lagorchestes* or *Onychogalea*, and is divided into two lobes by a diagonal anterior-interior groove along the occlusal surface.

The I^3 is an elongate tooth that is divided into two lobes, a rounded antero-external (labial) one and a sigmoidal lingual one that extends to the posterior end of the tooth. The two lobes are joined at the anterior end of the tooth. The I^3 of *Onychogalea* is somewhat wider anteriorly and has a less continuous lingual sigmoidal ridge. The I^3 of *Lagostrophus* has a straight lingual lobe that is not connected to the labial lobe anteriorly.

A small (1 mm diameter) canine is located at the anterior end of the maxilla, separated from the I^3 and the P^4 by diastemas.

Two bladelike teeth (PM 38914, 38916) are tentatively identified as P^3 of this species. Their structure is similar to that of the P^4, but they are slightly smaller and their main ridges have only three cusps; those of the P^4 have four. The lingual shelf of each is weaker than that of the P^4 and the posterolingual cusp is continuous with the posterior cusp of the main ridge. Marshall (1973a) found that the basic cusp number in *Lagorchestes leporides* was the same for P^3 as for P^4, but in *L. hirsutus*, if these identifications are correct, these two teeth differ. Their dimensions are similar to those of two modern specimens (WAM 685 from Dorre Island, M1471 from Canning Stock Route, tables 1–2). A positively identified dP^4 is not present in the Madura Cave sample.

The P^4 is an elongate blade with four cusps aligned along its ridge. There is a low lingual ledge that varies somewhat in its development from specimen to specimen. It may be represented by one or more separate cuspules, or there may be a low ridge incorporating them. Wear on these structures is also variable; in PM 39003, in which the left M_1 has been shed, the P_4 has worn a distinct abrasion facet on the central cuspule of the lingual ledge of P^4. The main ridge bends sharply lingually at its posterior end to join a large posterolingual cusp which lies in line with the lingual ledge. This last cusp is usually separated from the lingual ledge by an open valley, but they may be connected. The anterior cusp of the main ridge is the same size as the posterior one. It forms a continuation of the main longitudinal crest of the blade. The anterior cusp lacks a distinct labial ridge. A weak labial cingulum is present.

The upper molars are slightly longer than wide. In the specimens from Madura Cave and in the modern specimens, mesial drift has pushed the M^1 against the posterior end of P^4 and interdental wear has removed most of the procingulum. Remnants of the procingulum of the M^1 of PM 39003 indicate that it was about as extensive originally as those on M^{2-4}. The molars increase in size from M^1 to M^4. In M^1 the protoloph is slightly shorter than the metaloph, in M^2 the two lophs are nearly equal, and in M^3 and M^4 the metalophs are progressively shorter than the protolophs. Unworn lophs are thin and bowed forward in the middle. Worn lophs are straight. Low crests on the paracone and metacone become exaggerated by wear to give the appearance of a labial link. The midlinks are formed

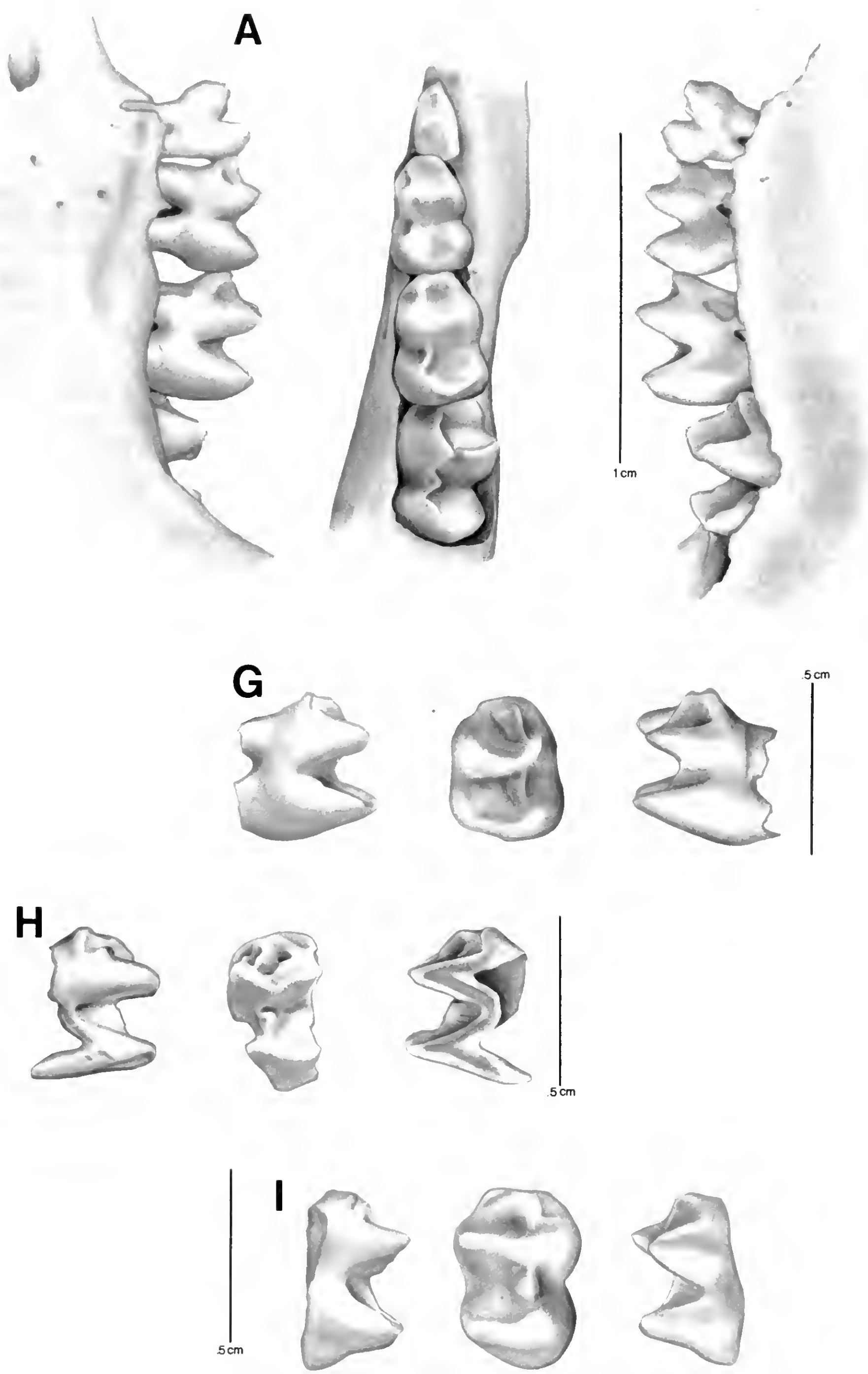
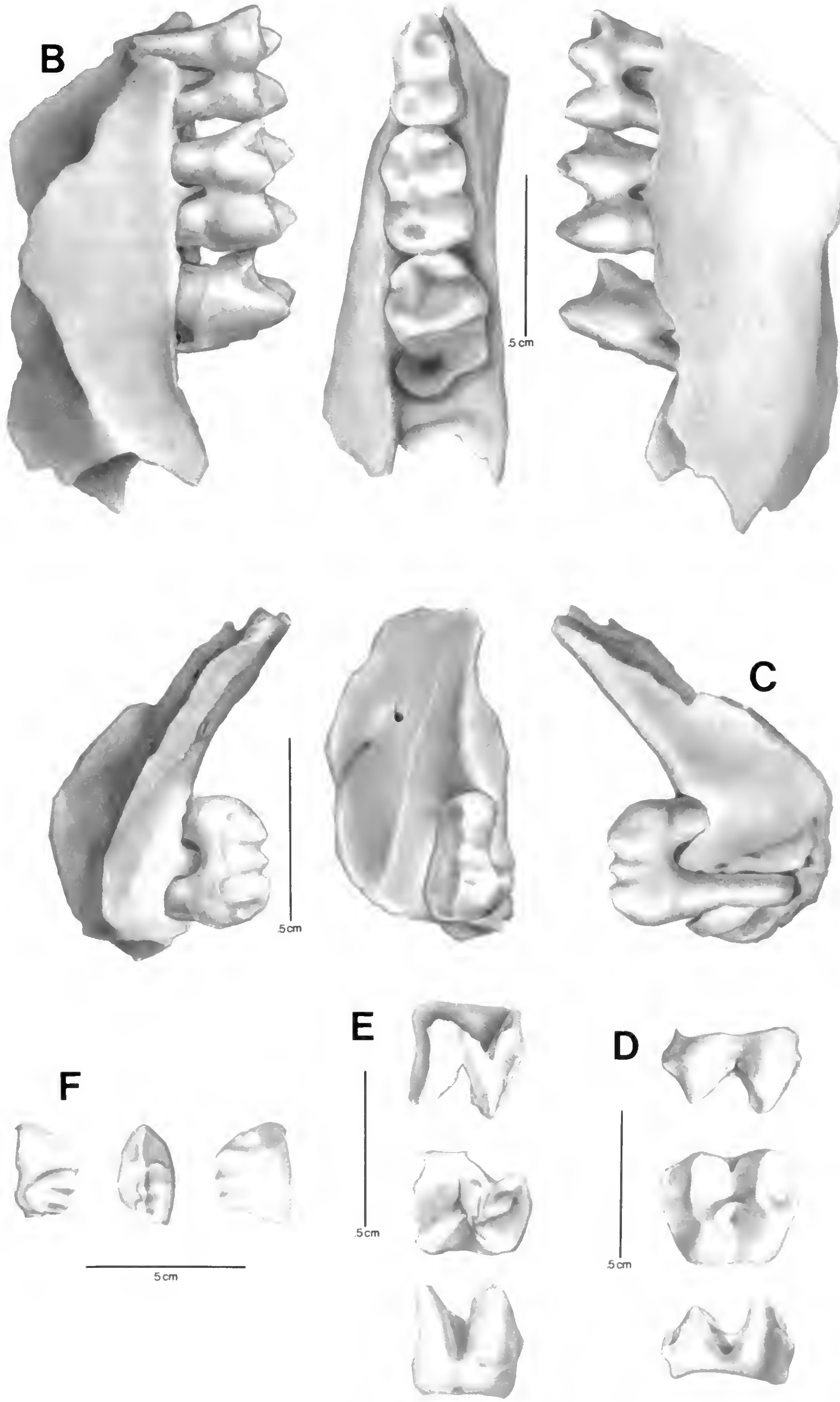


FIG. 7. *Lagorchestes hirsutus* and *Lagostrophus fasciatus* from Madura Cave compared with *Lagorchestes hirsutus* from Webb's Cave, Mundrabilla Station, Western Australia. *Lagorchestes hirsutus*: **A,** TMM 41209-892, Recent specimen from the surface of Webb's Cave, left ramus with P_3 and dP_4–M_2 in lateral (left), dorsal, and medial views; **B,** PM 25221, from Madura Cave, left ramus with dP_4, M_1, part of M_2, and a part of the crypt for P_4 in lateral (left), dorsal, and medial views; **C,** PM 38914, from Madura Cave, left maxillary fragment with P^3 shown in lateral (left), dorsal, and medial views. *Lagostrophus fasciatus* from Madura Cave: **D,** PM 38979, left M^1 shown in labial (top),



crown, and lingual views; **E,** PM 38909, left upper molar shown in labial (top), crown, and lingual views; **F,** PM 39054, right P^4 shown in labial (right), crown, and lingual views; **G,** TMM 41106-580, right M_1 shown in lingual (left), crown, and labial views; **H,** TMM 41106-5067, partial left M_1 or M_2 shown in labial (left), crown, and lingual views; **I,** TMM 41106-5084, right M_2 or M_3 shown in lingual (left), crown, and labial views.

TABLE 1. Numerical data on upper dentitions of *Lagorchestes hirsutus* from Madura Cave.

		N	OR	Mean
I^3	L	2	3.94–4.08	4.01
	AW	2	1.72–1.82	1.77
	PW	2	2.32–2.34	2.33
P^4	L	2	4.81–5.30	5.06
	AW	2	1.68–1.80	1.74
	PW	2	2.10–2.25	2.18
M^1	L	2	3.80–4.07	3.94
	AW	2	3.40–3.55	3.48
	PW	2	3.82–3.83	3.83
M^2	L	2	5.12–5.22	5.17
	AW	2	4.09–4.17	4.13
	PW	2	3.93–3.95	3.94
M^3	L	2	5.65–5.96	5.81
	AW	2	4.09–4.36	4.23
	PW	2	3.55–3.67	3.61
M^4	L	2	5.54–6.05	5.80
	AW	2	3.97–4.04	4.01
	PW	2	3.45–3.65	3.55
M^{1-2}	L	2	8.34–8.76	8.55
M^{2-3}	L	2	10.25–10.49	10.37
M^{1-3}	L	2	13.72–14.37	14.05
M^{1-4}	L	2	19.29–19.45	19.37

by spurs of unequal size that join in the central valley. The protolophs make up the larger part of the midlinks, in the form of a posterior crest of the protocone that turns sharply to meet the spur from the metaloph.

MANDIBLE—The mandible has the normal macropodid form. The horizontal ramus has about the same depth from M_1 through M_4. The proportions of the horizontal ramus are similar for *Lagorchestes hirsutus* from Madura Cave, Webb's Cave (TMM 41209-891), the modern specimen from Bernier Island, a modern specimen of *Lagostrophus fasciatus*, and material of *Onychogalea lunata* from Webb's Cave on the Nullarbor Plain. However, modern specimens of *Onychogalea frenata* from Queensland and New South Wales and of *O. unguifera* from Western Australia have a more slender and elongate ramus, possibly because of their immaturity (each has the P_3 and dP_4 in place). The profile of the tooth row in the modern specimens is slightly arched in the region occupied by P_4 and M_1, apparently as the result of some forward molar progression. The P_4 in both Madura Cave specimens and in the modern specimens from Bernier Island is rotated forward and downward. The diastema is relatively shorter than in *Onychogalea* and about the same length as in *Lagostrophus*. A mental foramen is located just anterior to the P_4 and about halfway between the upper and lower edges of the mandible.

The ascending ramus and masseteric fossa show few distinctive features. The ventral border of the masseteric fossa is located higher above the ventral margin of the jaw and the posteroventral margin of the masseteric fossa is more rounded than in *Lagostrophus*. The foramen into the dental canal is located lower than in *Onychogalea*.

The condyle of the jaw is oval in *Lagorchestes* and the articular surface is gently convex anteroposteriorly. In *Lagostrophus* the condyle is more elongate transversely and in *Onychogalea* it is almost round and smaller than in *Lagorchestes*. In the modern *Lagostrophus* and all three species of *Onychogalea* a small bony spur projects forward from the medial side of the condyle; this has not been seen in *Lagorchestes*.

LOWER DENTITION—The lower incisors are slender, procumbent, lancelike teeth. Enamel is present all along the ventrolateral surface. In the Madura Cave specimens the anterior ends are truncated by a prominent wear surface oriented at an angle of about 45° to the long axis of the tooth. *Onychogalea frenata* has a similarly oriented wear surface, but in *Lagostrophus fasciatus* the wear surface is almost parallel to the long axis of the tooth, giving the tooth a sharply pointed end. This difference in the wear of the lower incisors is related to the difference in the upper incisors in these taxa. The I^1 and I^2 of *Lagorchestes* and *Onychogalea* are large and occlude primarily with the ends of the lower incisors, producing wear surfaces only at the ends of the lower incisors. In *Lagostrophus* the I^1 is small relative to the I^2 and I^3, which are elongate teeth that occlude with a considerable length of the upper edge of the lower incisors, producing wear surfaces along the upper edges of the lower incisors. The ventromedial edge of the lower incisors shows a wear facet produced by wear between the two lower incisors. This facet is better developed in *Lagostrophus* than in *Lagorchestes*.

The P_3s have not been identified in the Madura Cave material. The dP_4 of *Lagorchestes* is known from only one specimen, PM 25221. It is assigned to *Lagorchestes* on the basis of its association in a mandible with an M_1 and M_2 which lack the complex procingula characteristic of *Lagostrophus*, and of the presence under the dP_4 of a crypt for an unerupted P_4 larger than that of *Onychogalea*. The dP_4 is an elongate molariform tooth that is wider across the hypolophid than across the

TABLE 2. Numerical data on upper dentitions of Holocene samples of *Lagorchestes hirsutus* from Western Australia.

		Canning Stock Route*			Dorre Island†			Bernier Island AMNH 155106	
		N	OR	Mean	N	OR	Mean		
P^3	L	1	3.7	3.7	1	3.9	3.9	...	...
	AW	1	1.5	1.5	1	1.8	1.8	...	...
	PW	1	2.1	2.1	1	2.0	2.0	...	...
dP^4	L	1	3.7	3.7	1	4.1	4.1	...	...
	AW	1	3.1	3.1	1	3.0	3.0	...	...
	PW	1	3.4	3.4	1	3.2	3.2	...	...
P^4	L	2	5.0–5.3	5.15	4	4.8–5.1	4.95	1	4.7
	AW	2	1.8–2.2	2.00	4	1.9–2.0	1.93	1	1.8
	PW	2	2.1–2.3	2.20	4	1.9–2.3	2.18	1	2.1
M^1	L	3	3.5–4.0	3.73	5	3.5–4.7	4.22	1	3.2
	AW	3	3.6–3.8	3.73	5	3.7–3.9	3.86	1	3.4
	PW	3	3.5–4.1	3.80	5	3.7–4.1	4.00	1	3.9
M^2	L	3	5.0–5.4	5.17	5	5.0–5.6	5.42	1	5.0
	AW	3	4.2–4.5	4.40	5	4.0–4.8	4.38	1	4.3
	PW	3	4.0–4.6	4.37	5	3.9–4.8	4.30	1	4.2
M^3	L	2	5.9–6.0	5.95	4	6.0–6.2	6.08	1	5.2
	AW	2	4.9–5.0	4.95	4	4.2–4.6	4.33	1	4.4
	PW	2	4.0–4.5	4.25	4	3.7–4.1	3.88	1	4.1
M^4	L	...	...	...	1	6.3	6.3	1	5.8
	AW	1	4.6	4.6	1	4.3	4.3	1	3.8
	PW	...	...	...	1	3.8	3.8	1	3.5
M^{1-2}	L	...	...	...	...	...	...	1	7.5
M^{2-3}	L	...	...	...	...	...	...	1	10.2
M^{1-3}	L	...	...	...	...	...	...	1	13.2
M^{1-4}	L	...	...	...	1	20.5	20.5	1	18.1

* Sample from Canning Stock Route in The Western Australian Museum (M1464, M1465, M1471).
† Sample from Dorre Island in The Western Australian Museum (WAM 685, 10565, 10567, 10624, 10625).

protolophid. The procingulum projects forward and is narrower than in any of the molars. The metaconid and entoconid have anterior and posterior crests. The anterior crest of the metaconid does not join the procingulum as it does in the molars, but instead turns into the cingular basin. The forelink extends in a sigmoid curve to the anterior point of the tooth. Labial to the forelink, the cingulum is very weak. The P_4 is a simple blade made up of a long, compressed cusp on either end and two lower and smaller, indistinct cusps between. The anterior cusp is smooth labially and has a variably developed ridge on its lingual side. The posterior cusp is bent lingually. There is no external cingulum and only a hint of an internal cingulum. The Madura Cave specimens agree with the descriptions of P_4 of *Lagorchestes leporides* from Lake Victoria (Marshall, 1973a).

The lower molars increase in size posteriorly (table 3). The hypolophid is wider than the protolophid in M_1, about equal in M_2, and narrower in M_3 and M_4. There are no accessory ridges in the midlink area. The forelink tends to have a lingual bow, as is pointed out by Marshall (1973a) for *Lagorchestes leporides* from Lake Victoria.

Mesial Drift

Mesial (anterior) drift of the cheek teeth of *Lagorchestes* is apparent in the crowding of the M^1 against the P^4 in the upper dentition and in the rotation of P_4 forward and downward in the mandible. Other indications are the tendency of the lower tooth row to be arched and for the anterior molars to show heavy wear while the posterior ones show little or none. Sanson (1983) has pointed out that mesial drift is at a maximum in those taxa in which the premolars are either reduced in size or are quickly shed; *Peradorcas* is the most extreme example.

TABLE 3. Numerical data on lower dentitions of *Lagorchestes hirsutus* from Madura Cave.

		N	OR	Mean
dP_4	L	1	3.72	3.72
	AW	1	2.04	2.04
	PW	1	2.14	2.14
P_4	L	5	4.4–4.8	4.60
	AW	6	1.5–1.8	1.65
	PW	5	1.5–1.9	1.78
M_1	L	4	3.8–4.1	3.90
	AW	4	2.7–3.0	2.82
	PW	4	2.8–3.4	3.10
M_2	L	3	4.5–4.7	4.62
	AW	4	3.2–3.6	3.33
	PW	3	3.3–3.7	3.56
M_3	L	4	5.0–6.0	5.47
	AW	4	3.1–4.3	3.82
	PW	4	3.3–4.3	3.75
M_4	L	3	5.5–5.6	5.54
	AW	3	3.6–4.7	4.05
	PW	3	3.1–3.8	3.37
M_{1-2}	L	2	8.5–8.7	8.60
M_{2-3}	L	2	9.7–10.8	10.13
M_{1-3}	L	2	13.6–14.3	13.94
M_{1-4}	L	2	19.3–19.6	19.46

In *Lagorchestes*, P_4 appears to drift more readily than P^4. After drifting over the hump in the jaw, the P_4 becomes the most steeply inclined of all the teeth. The P^4 appears to have a firmer anchorage to the bone than P_4, and its lesser drift results in a slightly different mechanism of accommodation in the upper molar dentition. Here the drift is accomplished by extreme interdental wear so that M^1 soon loses the lingual two thirds of its procingulum and a very appreciable portion of the protoconal and hypoconal areas of the crown itself. The result is that the tooth occupies a space only about one half that of its original length, and comes to overlap the labial side of P^4. The P^4 erupts progressively, so that the level of its occlusal surface remains below that of M^1, causing a break in the curved surface of the functional occlusal plane. This helps it to maintain its occlusal relationship with P_4 and M_1.

Another striking indication of mesial drift is the remarkable way that the most heavily stressed of the upper molar roots are eroded and resorbed, and apparently remodeled in the area between the crown base and the alveolar surface. This results in molar roots that curve posteriorly toward their tips. This phenomenon is best seen in the hypoconal region of the anterior molars (TMM 41106-679, PM 39003, AMNH 155106). As far as we can tell it is most pronounced in *Lagorchestes*, intermediate in *Onychogalea*, and absent in *Lagostrophus*, which shows less mesial drift. The reasons for these differences are not known, but one could speculate that in *Onychogalea*, in which mesial drift is fully comparable to that in *Lagorchestes*, P^4 is a very reduced tooth which offers very little resistance to drift. Perhaps without much resistance the alveoli have never had time to become as extensively ossified and alveolar remodeling is all that is necessary to permit drift to occur. Conversely, in *Lagorchestes*, where a larger blade resists the drift more effectively, a more complete ossification may result; in this case the remodeling, which involves both the alveolar bone and the tooth base and roots, may depend to a greater extent on tooth root changes.

Discussion

Mean values of dental measures of the Madura Cave sample of *Lagorchestes hirsutus* average slightly larger than those of Recent samples given by Tedford (1967) and Marshall (1973a), but in most cases there is extensive overlap. There also is extensive overlap in dental dimensions between the Madura Cave sample and Recent samples from the Canning Stock Route and Dorre and Bernier Islands, Western Australia (tables 1–4). The lengths of P^4_4 are greater in the Madura Cave sample than in Tedford's and Marshall's samples, and there is no overlap in the lengths of the P_4. The lengths of M^1_1 are lower in the Madura Cave sample, with no overlap, probably because the Madura Cave sample is made up of older individuals in which both occlusal and interdental wear would act to reduce the length. As pointed out by Marshall (1973a), measures of *L. hirsutus* and *L. leporides* overlap. Tedford (1967, fig. 2) separated *L. leporides* and *L. hirsutus* by plotting length of P_4 against maximum width of M^1. This separation is actually the result of the non-overlapping values of the length of P_4, which is shown in Tedford's Table 30. The Madura Cave sample extends the range of lengths of P_4 upward to 5.30 mm (table 1), which is below the lowest value (5.4 mm) for the combined Recent samples of *L. leporides* of Tedford (1967) and Marshall (1973a). On the basis of their smaller size all Madura Cave P_4s are assigned to *L. hirsutus*.

Lagorchestes hirsutus is known from a wide area in the interior of Western Australia and from Bernier and Dorre islands, in Shark Bay, northwestern Australia (Ride & Tyndale-Biscoe, 1959; Finlay-

TABLE 4. Numerical data on lower dentitions of *Lagorchestes hirsutus* from Western Australia.

		Canning Stock Route*			Dorre Island†			Bernier Island AMNH 155106	
		N	OR	Mean	N	OR	Mean		
P_3	L	1	3.5	3.5	1	3.0	3.0	...	...
	AW	1	1.4	1.4	1	1.6	1.6	...	...
	PW	1	1.7	1.7	1	1.9	1.9	...	...
dP_4	L	1	3.5	3.5	1	3.8	3.8	...	...
	AW	1	2.3	2.3	1	1.8	1.8	...	...
	PW	1	2.7	2.7	1	2.6	2.6	...	...
P_4	L	1	4.6	4.6	4	4.4–4.6	4.48	1	3.8
	AW	1	1.8	1.8	4	1.6–1.9	1.75	1	1.6
	PW	1	1.8	1.8	4	1.7–1.9	1.83	1	1.6
M_1	L	3	3.5–4.0	3.70	4	4.0–4.5	4.28	1	3.5
	AW	2	2.9	2.9	4	2.7–2.9	2.80	1	2.5
	PW	3	2.9–3.2	3.10	4	2.9–3.2	3.03	1	2.8
M_2	L	3	4.0–5.4	4.70	5	4.3–5.0	4.86	1	4.2
	AW	3	3.4–3.5	3.43	5	3.3–3.6	3.46	1	3.0
	PW	2	3.0–3.4	3.20	5	3.4–3.7	3.50	1	3.2
M_3	L	2	5.7–5.9	5.80	4	5.7–6.0	5.83	1	4.8
	AW	2	3.7–3.9	3.80	4	3.7–4.0	3.83	1	3.7
	PW	2	3.6–3.9	3.75	4	3.4–3.8	3.53	1	3.6
M_4	L	2	5.9–6.0	5.95	2	5.7–6.3	6.00	1	5.5
	AW	2	3.7–3.9	3.80	2	3.9–4.0	3.95	1	3.2
	PW	...	...	...	1	3.3	3.3	1	2.9
M_{1-2}	L	1	19.5	19.5	...	...	...	1	7.2
M_{2-3}	L	...	...	...	...	...	...	1	9.6
M_{1-3}	L	...	...	...	...	...	...	1	12.9
M_{1-4}	L	...	...	...	...	...	...	1	16.5

* Sample from Canning Stock Route in The Western Australian Museum (M1464, M1465, M1471).
† Sample from Dorre Island in The Western Australian Museum (WAM 685, 10565, 10567, 10624, 10625).

son, 1936; Glauert, 1933). Since it has previously been reported from Horseshoe Cave on the Nullarbor Plain (although without stratigraphic context; Archer, 1972, 1974), its presence in the Madura Cave fauna is not unexpected. Like many other species, it had a wider distribution in the past. It has been reported from deposits dated between 30,000 and 35,000 B.P. in Devil's Lair, in the southwestern corner of Western Australia (Dortch & Merrilees, 1972; Baynes et al., 1975; Balme et al., 1978; Merrilees, 1979). Tedford (1967) reported a specimen, probably of Holocene age, from the lower Cooper's Creek 40 mi (61 km) east of Lake Eyre in South Australia. *Lagorchestes hirsutus* is said to have been an inhabitant of the open plains.

Lagostrophus Thomas, 1887
Lagostrophus fasciatus (Peron & Lesueur), 1807

MATERIAL

Trench 4, Unit 1, Level 1
TMM 41106-5067, left M_1 or M_2 (fig. 7H)
TMM 41106-5068, right M_2 or M_3
PM 38909, left upper molar (fig. 7E)
PM 38911, left M_2

Trench 4, Unit 1, top 1 ft
TMM 41106-580, right M_1 (fig. 7G)
TMM 41106-5084, right M_2 or M_3 (fig. 7I)
PM 39054, right P^4 (fig. 7F)

Trench 4, Unit 2, Level 4
PM 38979, left M^1 (fig. 7D)

COMPARATIVE MATERIAL

Lagostrophus f. fasciatus

Bernier Island, Western Australia
AMNH 155104 (fig. 8)
Dorre Island, Western Australia
USNM 218467

Descriptions

UPPER DENTITION—The P^4 is represented by the anterior half of an unrooted tooth, which preserves

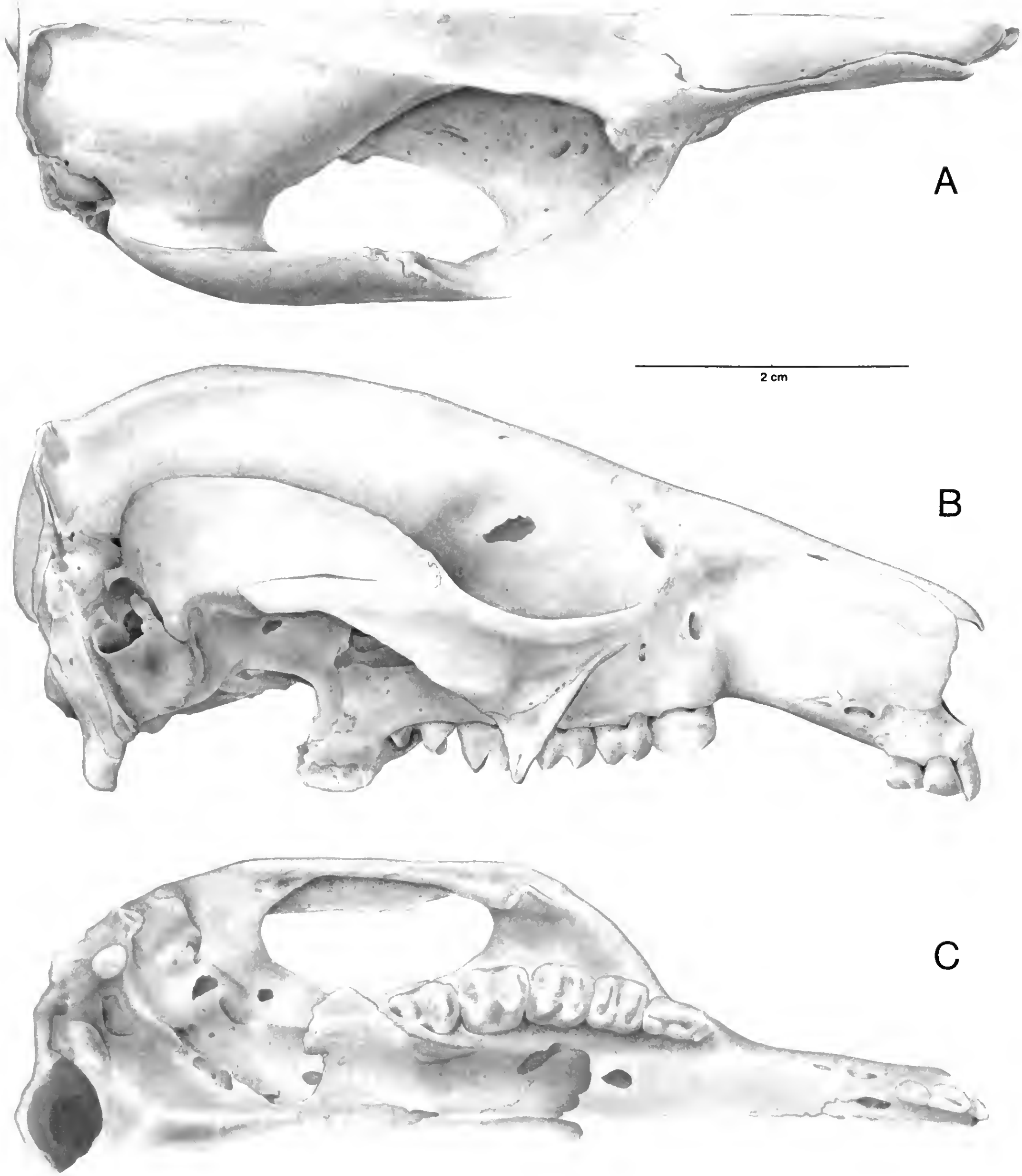
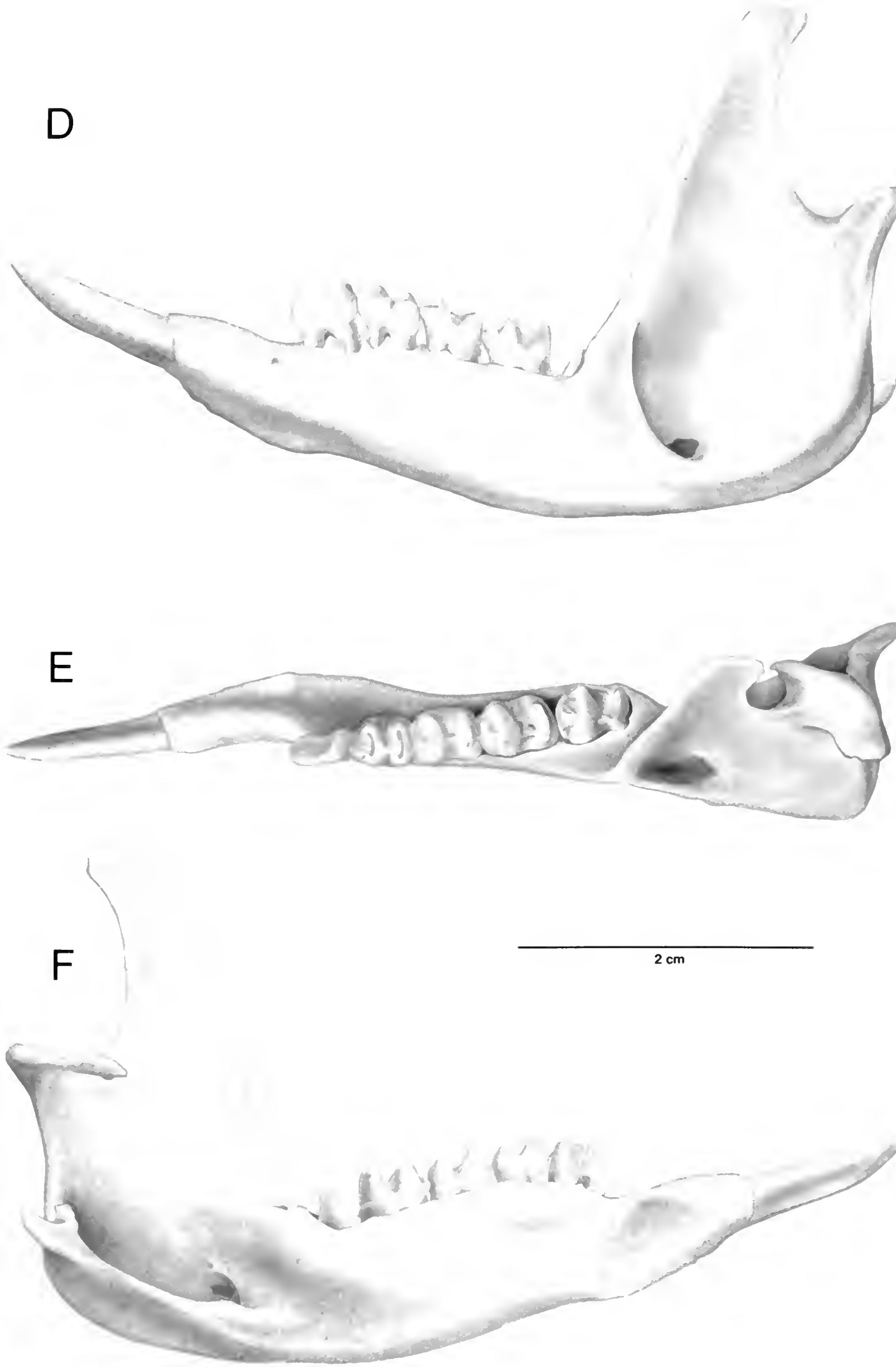


FIG. 8. Skull and left mandible of *Lagostrophus f. fasciatus*, AMNH 155104, from Bernier Island, Western Australia. Views of skull: **A**, dorsal; **B**, right lateral; **C**, ventral. Views of mandible: **D**, lateral; **E**, dorsal; **F**, medial.


D
E
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2 cm

TABLE 5. Measurements of upper dentitions of *Lagostrophus fasciatus.*

		Madura Cave		Recent	
		PM 38979	PM 38909	AMNH 155104	USNM 218467
P^3	L	...	...	...	4.5
	AW	...	...	...	2.6
	PW	...	...	...	2.6
dP^4	L	...	...	...	4.1
	AW	...	...	...	3.6
	PW	...	...	...	3.3e
P^4	L	...	...	5.4	...
	AW	...	...	2.6	...
	PW	...	...	2.8	...
M^1	L	4.2	...	4.2	4.2
	AW	3.4	...	3.8	3.8
	PW	3.6	...	4.1	3.7
M^2	L	...	...	4.7	4.6
	AW	...	...	4.5	4.0
	PW	...	...	4.3	3.8
M^3	L	...	...	5.1	4.9
	AW	...	...	4.5	4.5e
	PW	...	...	4.5	3.9e
M^4	L	...	...	5.7e	...
	AW	...	...	...	...
	PW	...	...	...	...
Molariform tooth	L	...	...	...	...
	AW	...	...	...	...
	PW	...	3.3	...	...

e = Estimate.

the anterior three of the usual 5+ cusps (fig. 7F). The tooth is bladelike, with the axial ridge continuing onto the front of the anteriormost cusp. That cusp also has labial and lingual ridges that ascend posteriorly toward the tooth base. The lingual ridge joins a weak lingual cingulum; the labial ridge joins the outward-bulged side of the tooth about halfway toward the base of the crown.

The M^1 is an unworn, unrooted tooth (fig. 7D). The crown is rectangular, nearly as wide as long, and has only a weak constriction between its two parts. There is a distinct but unexpanded procingulum across the front of the tooth from the anterior crest of the paracone to the anteromedial corner of the base of the protocone. A weak forelink connects the base of the protoloph with the midpoint of the cingulum. Both lophs are bowed forward slightly, and the paracone and metacone have longitudinal anterior and posterior crests along their labial borders, which lie nearly in line. The midlink is a thin, simple, arcuate ridge that curves off from the protocone to join the anterior side of the metaloph at about midheight. The posterior basin is open, and its medial and lateral margins are symmetrical. The distinctive second "postlink" is thin but pronounced. This structure is not the true postlink of Tedford (1966), which is also present. We call the tooth an M^1 because it compares well in size with the M^1 of the American Museum specimen (fig. 8; table 5). In that specimen the other molars have a very similar morphology but are each successively slightly larger, suggesting that size is the best means of distinguishing one tooth from another.

The other upper molar is a partial tooth lacking the anterior side of the protoloph and the posterolabial corner (fig. 7E). It also appears to have been unerupted and unrooted. It has a well developed "postlink." Its only unusual feature is an anterior double wrinkle in the metaloph which is the metaloph contribution to the midlink. Otherwise it agrees with the description of the M^1.

LOWER DENTITION—The lower molars conform to a standard pattern (fig. 7G–I). In the modern specimen used for comparison (fig. 8), all are elongate and rectangular with simple posteriorly bowed cross lophs, and there is a uniform gradual increase in size from M_1 to M_4 (table 6). All lower molars of *L. fasciatus* have a distinctive forelink-procingulum pattern in which the link stands off from the cingulum, rather than merging with it as it does in most other wallabies. The hypolophid makes the greatest contribution to the midlink. The contribution of the protolophid to the link is variable, and sometimes absent. Other variable features are low, rounded bulges that sometimes occur on the anterior faces of the lophids medial to their midpoints. The Madura Cave teeth all conform to this pattern, and one or more exhibit each of the minor variables seen in the modern specimen. Estimates of their positions in the series are based on size.

In spite of the small number of specimens of this taxon, the close agreement of morphological detail between the Madura Cave specimens and the modern comparative materials permits confident assignment of the Madura Cave material to *Lagostrophus fasciatus*.

Discussion

Lagostrophus fasciatus was found over much of southwestern Australia during the early period of European settlement (Shortridge, 1909; Calaby, 1971). It may be extinct now on the mainland, but it survives on Bernier and Dorre islands in Shark Bay (Ride & Tyndale-Biscoe, 1959). It has been

TABLE 6. Measurements of lower dentitions of *Lagostrophus fasciatus*.

		Madura Cave				Recent	
		TMM 41106-5067	TMM 41106-5068	TMM 41106-580	TMM 41106-5084	AMNH 155104	USNM 218467
P_3	L	...	...	...	...	...	4.0
	AW	...	...	...	...	...	1.8
	PW	...	...	...	...	...	2.1
dP_4	L	...	...	...	...	...	4.0
	AW	...	...	...	...	...	3.2
	PW	...	...	...	...	...	3.4
P_4	L	...	...	...	...	4.7	...
	AW	...	...	...	...	2.0	...
	PW	...	...	...	...	2.3	...
M_1	L	4.4	...	4.3	...	4.2	4.5
	AW	...	...	3.1	...	3.2	3.4
	PW	...	...	3.3	...	3.4	3.4
M_2	L	...	...	...	5.2	4.5	4.8
	AW	...	3.2	...	3.7	3.6	3.6
	PW	...	...	...	3.3	3.7	3.5
M_3	L	...	...	...	...	4.9	...
	AW	...	...	...	...	3.8	...
	PW	...	...	...	...	3.8	...
M_4	L	...	...	...	...	5.2e	...
	AW	...	...	...	...	4.9e	...
	PW	...	...	...	...	...	...

e = Estimate.

reported previously with no stratigraphic context from Horseshoe Cave on the Nullarbor Plain (Archer, 1972, 1974). The Nullarbor Plain records, some of which are of Holocene age (including most of the Madura Cave materials), together with its presence in archaeological sites of Holocene age along the lower Murray River in South Australia (Wakefield, 1964), indicate a former distribution throughout South Australia. It has not been reported from Pleistocene faunas at Lake Menindee (Tedford, 1967) or Lake Victoria (Marshall, 1973a).

Onychogalea Gray, 1841
Onychogalea lunata (Gould), 1840

MATERIAL

Trench 1, Unit 1, top 1 ft
- PM 4783, left maxilla with P^4–M^4 (fig. 12B)
- PM 4785, left ramus with I_1–M_4 (fig. 12A)
- PM 25538, right maxillary fragment with P^3, dP^4, P^4 removed from crypt (fig. 12C)
- PM 25539, right ramus fragment with P_4 removed from crypt, M_1, alveoli for P_3 and dP_4, M_{2-3} in crypt (fig. 12D)
- PM 25541, left ramus with M_{2-4}, alveoli for P_4–M_1

Trench 2, 2½ ft below surface
- PM 25222, right ramus with part of M_4

Trench 3, Unit 2, Level ? (presumably 1)
- TMM 41106-183, right ramus with M_{1-2}, P_4 removed from crypt, M_3 in crypt, alveoli for P_3 and dP_4 (fig. 13A)
- TMM 41106-184, right maxilla with P^3, dP^4, P^4 removed from crypt, M^{1-2} (fig. 13B)
- TMM 41106-5061, left maxillary fragment with P^3, dP^4, P^4 removed from crypt, alveoli for M^1 (fig. 13C)
- TMM 41106-5088, right ramus fragment with dP_4, P_4 removed from crypt, alveoli for M_1, crypt for M_{2-3} (fig. 13D)
- PM 34469, left maxillary fragment with P^4
- PM 38918, left ramus fragment with M_1 or dP_4
- PM 38926, left M_1 or dP_4
- PM 38927, trigonid, left M_2 or M_3
- PM 39005, right maxillary fragment with P^4–M^1 (fig. 13E)
- PM 39007, right premaxillary fragment with I^1 (fig. 13F)
- PM 39049, right maxilla with M^{1-2}, alveoli for dP^4, crypt for P^4
- PM 39050, left maxilla with M^{1-2}
- PM 39052, right maxillary fragment with M^{3-4}

Trench 3, Unit 2, Level 2
TMM 41106-141, left maxilla with unworn dP^4, alveoli for P^3 and M^1, crypt for P^4 (opened but tooth lost) (fig. 13G)
TMM 41106-142, left maxillary fragment with dP^4, alveoli for P^3, P^4 removed from crypt (in two pieces)
Trench 3, Unit 2, Level 4
PM 38919, left P^4
Trench 4, Unit 1, top 1 ft
TMM 41106-494, left maxillary fragment with M^{1-2}, crypt for P^4
TMM 41106-495, right maxillary fragment with M^{1-2}
TMM 41106-5063, edentulous right premaxilla (fig. 13H)
PM 38884, left premaxilla with I^2 (fig. 13I)
PM 38894, right P^4
PM 38899, left M^1
PM 38900, right M^3 or M^2
PM 38902, left P^4
PM 38915, left dP_4 or M_1
PM 39046, left maxillary fragment with P^3
Trench 4, Unit 2, Level 1
TMM 41106-315, left ramus with M_3, alveoli for P_4–M_2 and M_4
TMM 41106-316, right maxillary fragment with dP^4, P^4 removed from crypt, alveoli for P^3, M^1
PM 38775, right dP^4
PM 38940, left P^4 or P^3
PM 38941, left dP^4
PM 38995, left M_4

cf. ***Onychogalea lunata***

Trench 3, Unit 2, Level 1
TMM 41106-5039, right M^4 or M^3
TMM 41106-5040, right M^3 or M^4
TMM 41106-5047, right M^3 or M^2
PM 39033, right M_4 or M_3
Trench 3, Unit 2, Level 4
PM 39016, left M^1
PM 39017, left dP^4
Trench 4, Unit 1, top 1 ft
TMM 41106-492, left ramus fragment with M_2 or M_3
TMM 41106-493, right M_3 or M_2
TMM 41106-542, left ramus fragment with M_{3-4}
TMM 41106-543, left ramus fragment with M_{3-4}
TMM 41106-579, left dP_4 or M_1
TMM 41106-581, left M_3
TMM 41106-594, broken right M^1
TMM 41106-625, right dP_4
TMM 41106-627, right M_1 or M_2
TMM 41106-2833, right M_1
TMM 41106-2834, right dP^4
TMM 41106-5069, left upper molar, probably M^1 or M^2
TMM 41106-5072, right upper molar, probably M^2 or M^3, possibly M^4
TMM 41106-5075, worn left dP_4
TMM 41106-5076, right M_1 or dP_4
TMM 41106-5078, right M_4
TMM 41106-5079, left M^3 or M^4
TMM 41106-5080, left M_3
TMM 41106-5151, left dP_4
PM 38903, left M_4
Trench 4, Unit 2, Level 1
PM 38925, right ramus fragment with M_{2-3}
PM 38980, right M_2 or M_3 or M_4
PM 38982, right M_1
PM 38984, right M^3 or M^4
PM 38986, right M^1
PM 38987, left M^3 or M^2
PM 38988, left M^3 or M^2
PM 38989, left M^2 or M^3
PM 38991, right M^4
PM 38993, left M_1
Trench 4, Unit 2, Level 2
PM 38931, right dP_4
PM 38932, left M^1

Comparative Material

Onychogalea frenata

Warwick, Queensland
ROM 91.11.1.190 (fig. 9C)
New South Wales via National Zoological Park
USNM 122614, male (fig. 9A–B)
National Zoological Park
USNM 219299, male (diseased and abnormal)

Onychogalea unguifera

Derby, Western Australia
USNM 237643 (fig. 10A–B)

Onychogalea lunata

Weeke's Cave (surface), South Australia
PM 38776, subadult (fig. 10C)
PM 38777, subadult (fig. 11C)
Weebubbie Cave (surface), Western Australia
TMM 41107-334, juvenile
TMM 41107-335, juvenile
Jenning's Cave (surface), Western Australia
TMM 42121-1, juvenile
Snake Pit Cave (surface), Western Australia
TMM M-937 (fig. 11A–B)

Descriptions

Upper Dentition—An I^1 and an I^2, both in premaxillary fragments, are the only upper incisors from Madura Cave assigned to *Onychogalea.* The I^1 (fig. 13F) is curved along its long axis and has a flattened oval cross section. The occlusal surface makes an acute angle with the mesial surface of the tooth. The morphology is like that of modern *O. frenata,* but the size is smaller. The I^2 (fig. 13I) is almost square in cross section. It too is slightly smaller than the I^2 of modern *O. frenata,* and is more deeply worn than the I^2 of the modern Queensland specimen, as a result lacking the posterior lobe seen in that specimen. The occlusal surface is oriented at an angle of about 45° to the long axis of the tooth. The morphology of the incisors clearly marks them as *Onychogalea.* Their assignment to *O. lunata* is based on their small size (Marshall, 1973a) and the presence of other specimens clearly assignable to that species.

The P^3 is a variable tooth (figs. 12C, 13B–C,G). Most specimens are triangular, with two large crested cusps on the labial edge separated by a valley. A third smaller cusp is located lingual to the main posterior one and is connected to it by a weak ridge. One specimen (PM 25538; fig. 12C) has an elongate molariform P^3 with four cusps and incipient transverse lophs. This tooth is narrower across the anterior loph than across the posterior loph. None of the P^3s has a lingual cingulum.

The dP^4 is a molariform tooth that differs from M^1 in its slightly smaller size, more elongate rectangular form, and greater development of the parastylar crest (figs. 12C, 13B–C,G). The protoloph is variably developed. Most specimens, such as TMM 41106-5061 (fig. 13C), have a well-defined protoloph, but one (TMM 41106-316) lacks a protoloph, the protocone and paracone being separated by a V-shaped valley. The procingulum is more asymmetrical than it is in the molars because of the strong development of the parastylar area. The midlink is low and extends straight from the protocone to the center of the metaloph. There is only a hint of a forelink.

The P^4 is smaller than the P^3. Its morphology is variable (figs. 12B–C, 13B–C,E), but less so than that of the P^3. All available specimens are triangular with three cusps, two large ones on the labial side of the tooth separated by a deep valley, and a smaller cusp lingual to the large posterior cusp and connected to it by a ridge. One specimen (PM 38919) has a small cuspule in the valley between the two labial cusps, and an incipient lingual cingulum.

The upper molars increase in size posteriorly (table 7; figs. 12B, 13B,E). The protoloph is narrower than the metaloph in M^1, about the same width in M^2, and wider in M^3 and M^4. The paracone and metacone are crested when unworn. The protoloph and metaloph are strongly bowed anteriorly, particularly in unworn teeth. The midlinks consist of an anterior part that extends from the protocone to the center of the interloph valley, and a posterior part that extends from the center of the metaloph. Small accessory ridges are present on the midlink at the point where the two halves meet; these ridges are particularly noticeable on unworn teeth. There usually are other accessory ridges in the interloph valleys, those on the lingual side developed from the base of the tooth between the protocone and the hypocone. The procingulum is prominent, and reaches almost all the way across the front of the tooth. The anterior edge of the procingulum is joined to the paracone by a ridge. There is no forelink, but a swelling is present on the cingulum in the position usually occupied by the forelink. The postlink isolates a small pit at the back of each tooth.

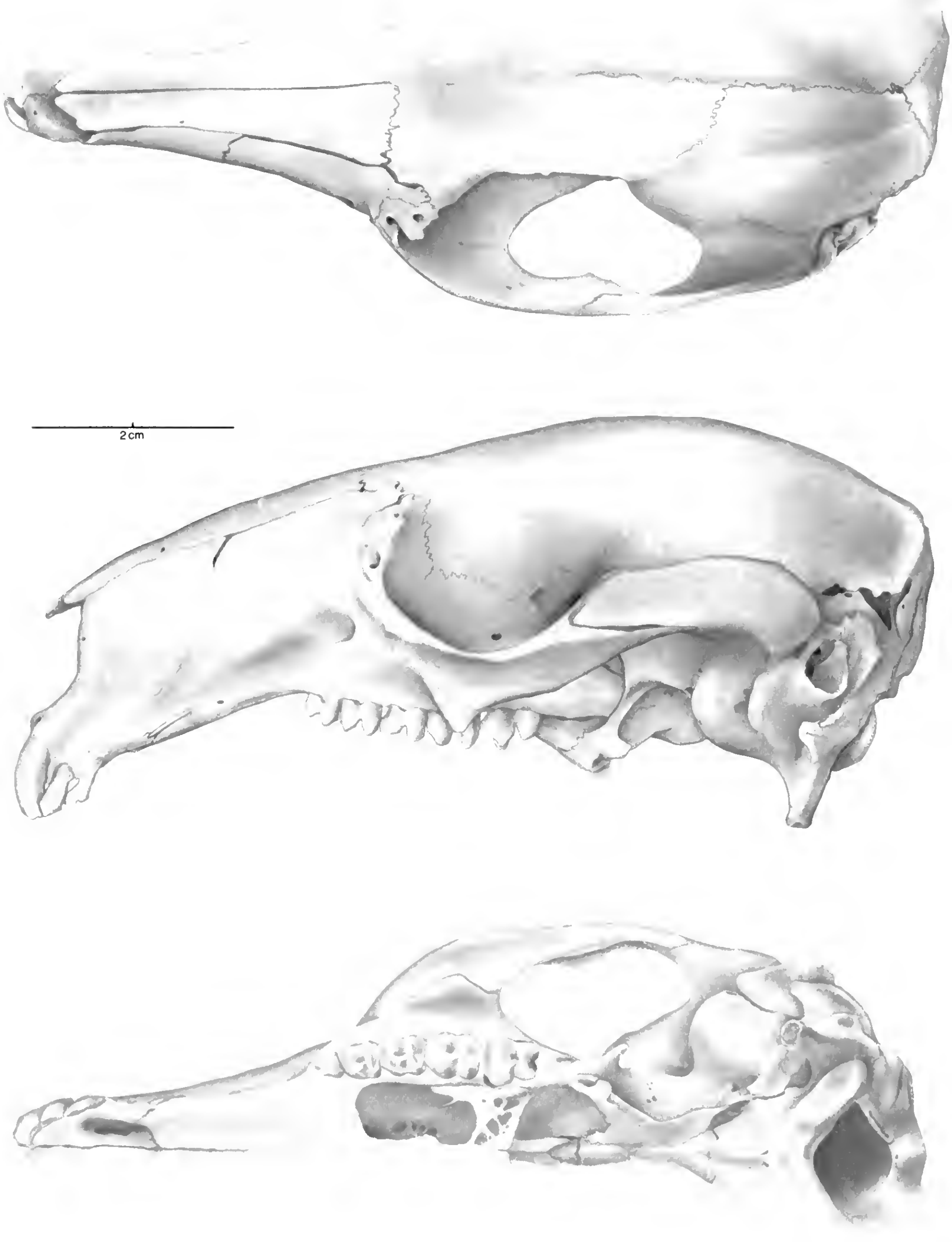
MANDIBLE—The mandible of *Onychogalea lunata* from Madura Cave is similar to that of *Lagorchestes hirsutus,* but is slightly smaller and more delicate (figs. 12A,D, 13A,D). It also is slightly smaller than the modern comparative mandible of *O. frenata.* The horizontal ramus has upper and lower borders which are parallel in adults, but in one juvenile (PM 25539; fig. 12D) the horizontal ramus is deeper under the alveolus for the dP_4. In profile, the tooth row is arched, with the apex of the arch located at dP_4 in PM 25539, at P_4–M_1 in PM 4785 (fig. 12A), and at M_2 in PM 25541. This change in the position of the teeth with respect to the apex of the arch, together with the more anterior position of the M_4 relative to the ascending ramus in older individuals, indicates the existence of mesial drift in *Onychogalea lunata,* as in *Lagorchestes hirsutus.* A prominent rugosity is located on the side of the jaw below the ventral margin of the temporal fossa. This is not present in *Lagorchestes* or *Lagostrophus,* but is present in the modern specimens of *Onychogalea frenata.* A mental foramen is located just anterior to P_4.

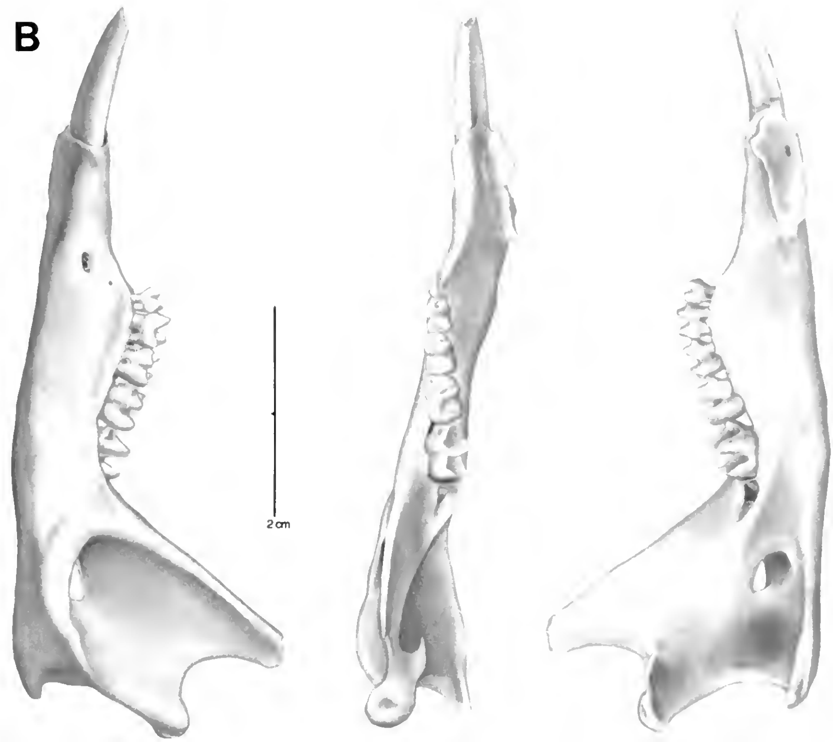
LOWER DENTITION—Only one of the specimens (PM 4785; fig. 12A) that can be reliably assigned to *Onychogalea* has a lower incisor. The end is broken, but the small part of the wear surface that remains is oriented at an angle of about 45° to the long axis of the tooth. This is similar to the orientation of the wear surface in *Lagorchestes* (see the section on that taxon) and different from the wear surface on the lower incisor of *Lagostrophus,* in which it is oriented at a very low angle to the long axis of the tooth.

No P_3 has been recognized from the Madura Cave material.

Only TMM 41106-5088 (fig. 13D) has a dP_4 in

A





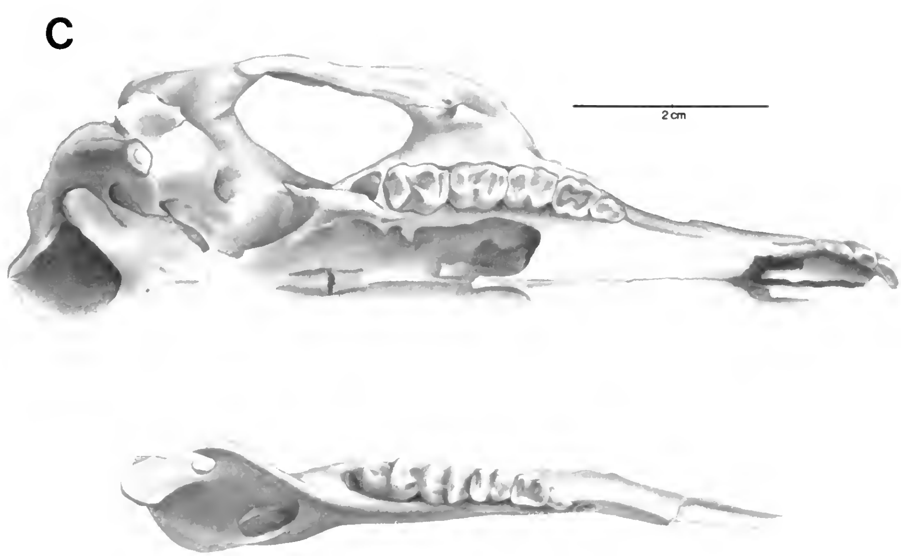


FIG. 9. *Onychogalea frenata*, USNM 122614, from New South Wales (via National Zoological Park): **A**, skull shown in dorsal, left lateral, and ventral views; **B**, left mandible shown in lateral (left), dorsal, and medial views. *Onychogalea frenata*, ROM 91.11.1.190, from Warwick, Queensland: **C**, right maxilla and mandibular dentitions shown in occlusal views.

A

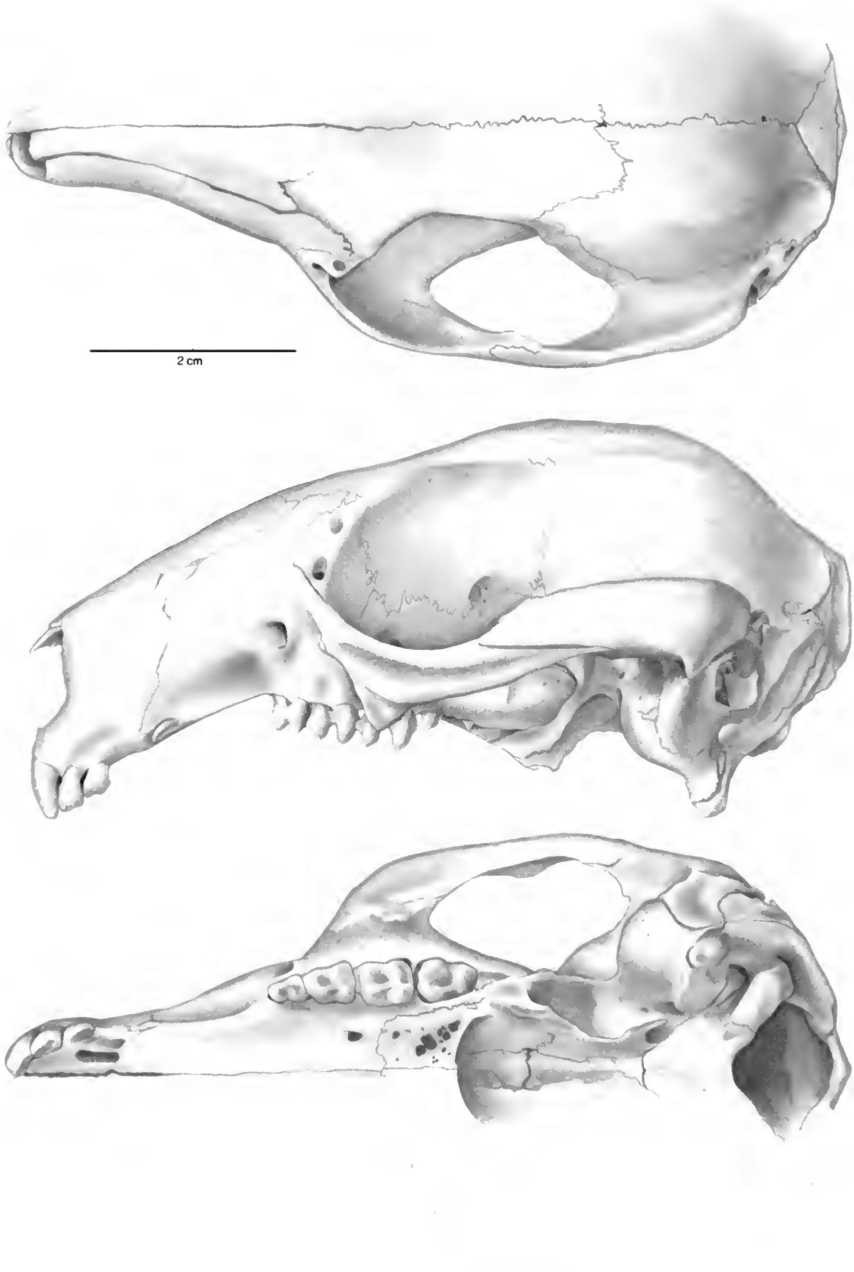
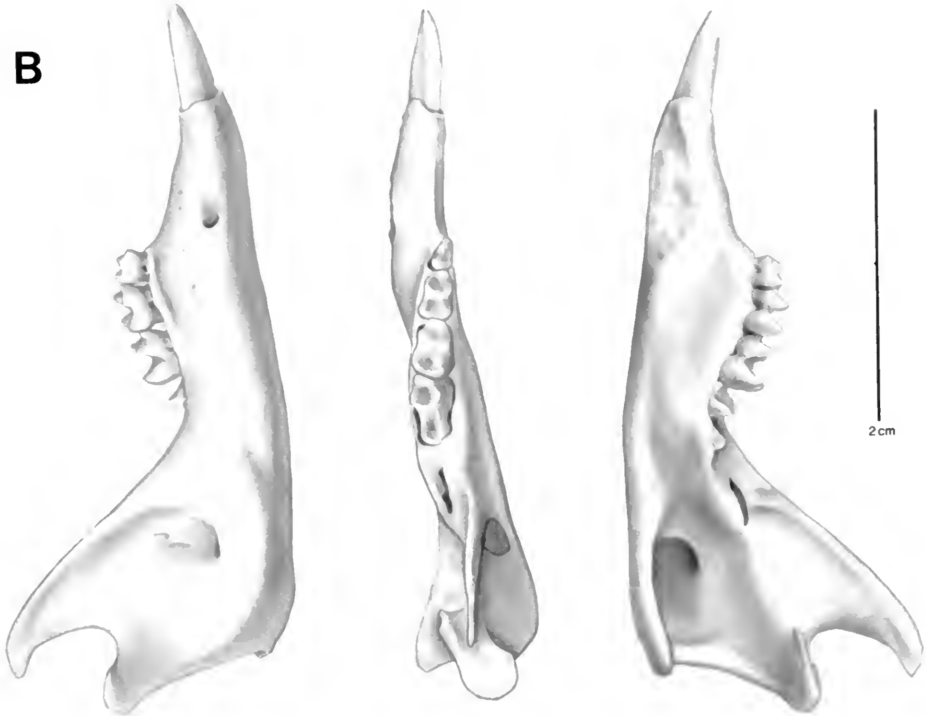
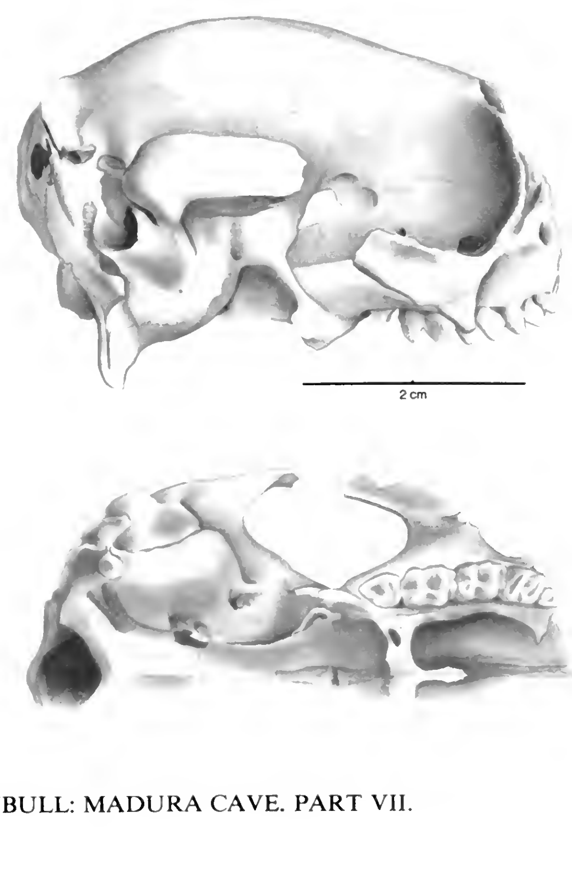


FIG. 10. *Onychogalea unguifera*, USNM 237643, from Derby, Western Australia: **A,** skull shown in top dorsal, left lateral, and ventral views; **B,** right mandible shown in lateral (left), dorsal, and medial views. *Onychogalea lunata*, PM 38776, from Weeke's Cave, South Australia: **C,** partial skull shown in right lateral and ventral views.

B



C



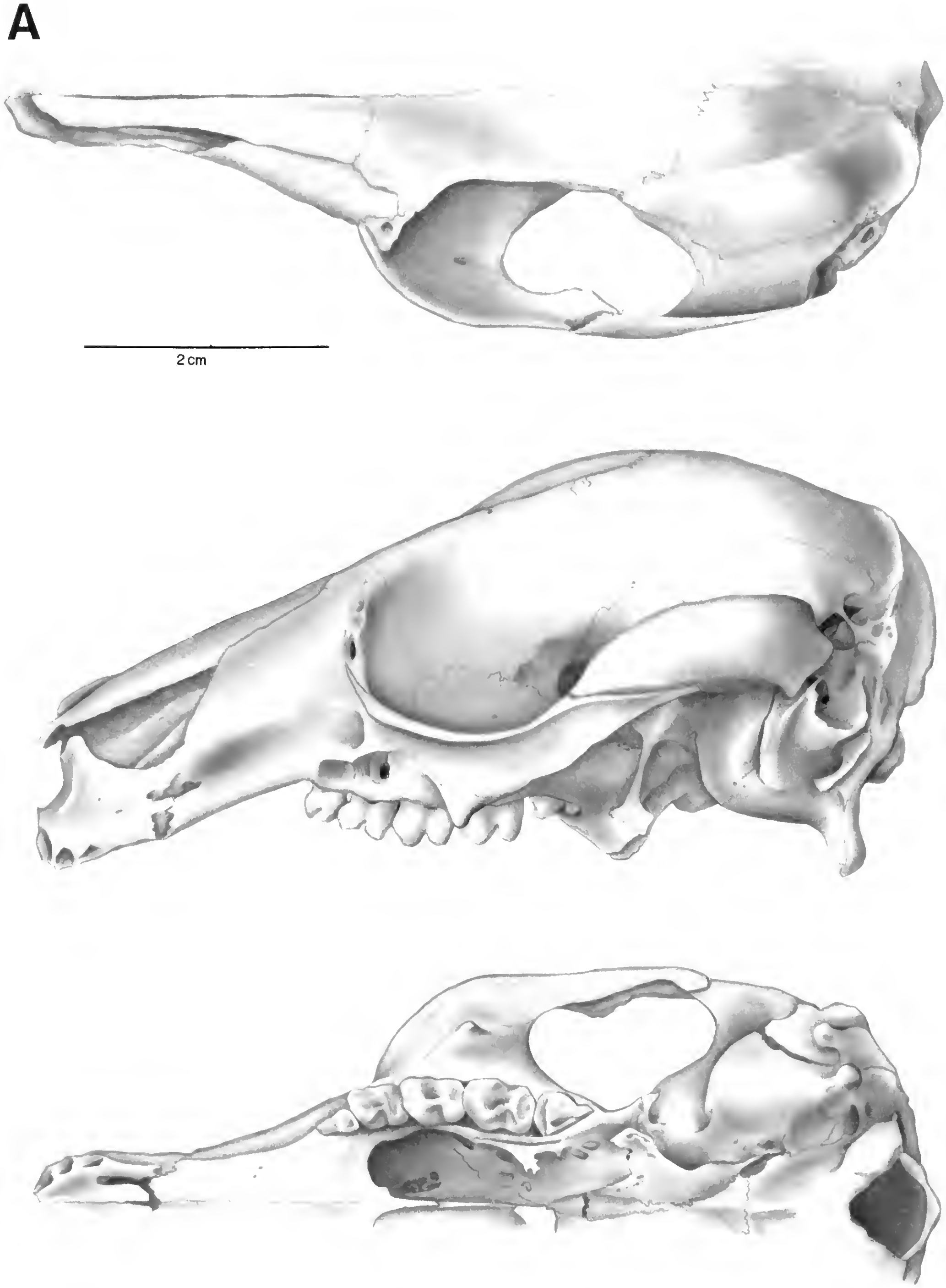
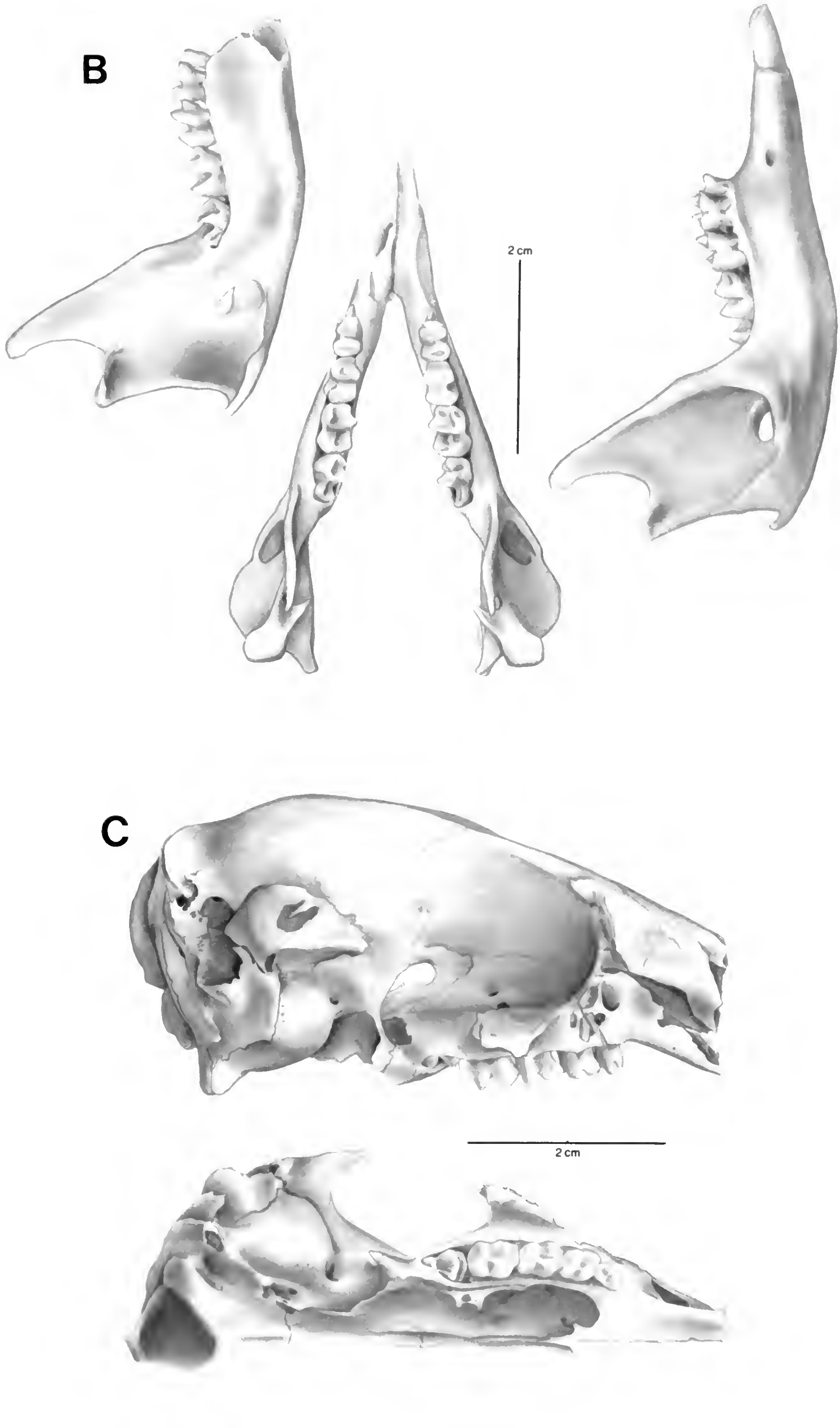


FIG. 11. *Onychogalea lunata*, TMM M-937, from Snake Pit Cave, Western Australia: **A,** skull shown in dorsal, left lateral, and ventral views; **B,** lower jaws shown in dorsal view, with medial view of left ramus and lateral view of right ramus. *Onychogalea lunata*, PM 38777, from Weeke's Cave, South Australia: **C,** partial skull shown in right lateral and ventral views.


B
2 cm
C
2 cm

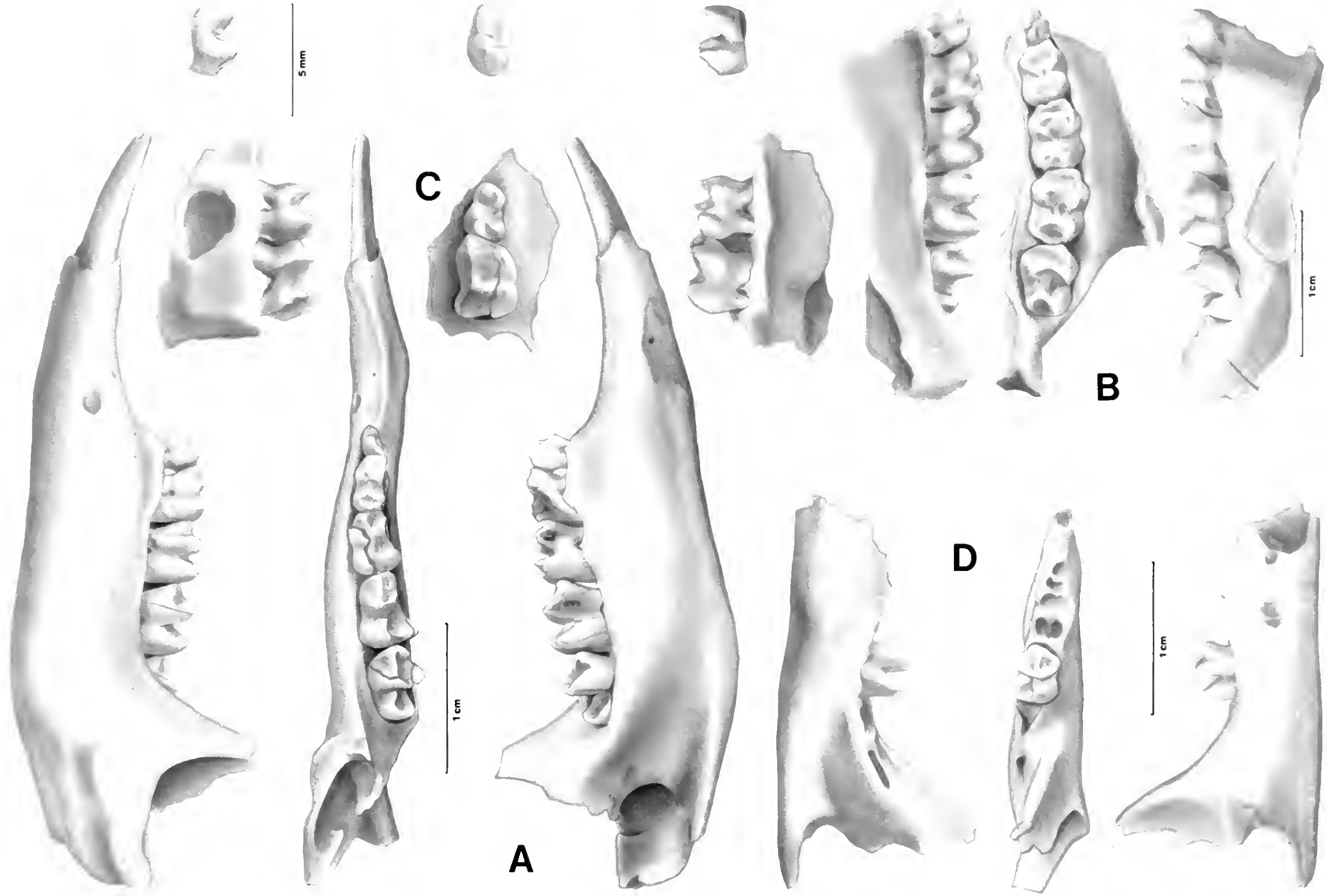


FIG. 12. *Onychogalea lunata* from Madura Cave. **A,** PM 4785, left ramus with I_1–M_4 shown in lateral (left), dorsal, and medial views. **B,** PM 4783, left maxilla with P^4–M^4 shown in medial (left), crown, and lateral views. **C,** PM 25538, right maxillary fragment with P^3, dP^4, and P^4 removed from its crypt shown in lateral (left), crown, and medial views. **D,** PM 25539, right ramus fragment with P_4 removed from its crypt, and M_1 and alveoli of P_3 and dP_4 shown in medial (left), dorsal, and lateral views; M_{2-3} are in their crypts.

place. This tooth is elongate and molariform, differing from the molars in being slightly smaller and relatively narrower across the protolophid. The protolophid and hypolophid are slightly bowed posteriorly. The midlink extends in a straight line from the hypoconid to a point labial to the center of the protolophid. There are no accessory ridges in the interloph valley. The procingulum is an arcuate ridge that connects the forelink with a crest on the anterior side of the metaconid to enclose an almost circular cingular basin. Two of the isolated teeth have the morphology of dP_4s. However, they are slightly wider across the protolophids than is the dP_4 of the one specimen which has that tooth in place (TMM 41106-5088), so it is uncertain whether they are dP_4s or M_1s with narrower than normal protolophids.

The P_4 apparently is highly variable. Two specimens show its well-developed form—a two-cusped tooth which is widest posteriorly. The cusps are in line with the long axis of the tooth. The anterior cusp is the smaller of the two, and may be either a simple cone (as in PM 4785; fig. 12A) or flattened from side to side and thus more bladelike (as in TMM 41106-183; fig. 13A); in PM 4785, this cusp has another much smaller cusplet adhering to its labial side. The posterior cusp has a posterolingual bladelike crest, and may have other weaker crests or bulges. In two other specimens (TMM 41106-5088, fig. 13D; PM 25539), this tooth is only a single cusp in a crypt, at a very early developmental stage. Each is a minute cone, about 1 mm high and less than 1 mm in diameter, and one shows a small posterior crest. A modern young adult specimen from the surface of another Nullarbor cave, Snake Pit Cave (TMM M-937; fig. 11B), has the tooth fully erupted and shows that it may sometimes be much smaller and have a far simpler morphology, consisting of a single high cusp and a low talonid bulge. The crown of this tooth is supported by two in-line fused roots.

The lower molars differ from each other only in minor details (figs. 12A,D, 13A). The size gradient is $M_1 < M_2 < M_3 \cong M_4$ (table 8). The protolophids and hypolophids are slightly bowed posteriorly. In M_1 to M_3 the widths of both lophs are very nearly the same, but in M_4 the protolophid is noticeably wider than the hypolophid. The anterior crest of the hypoconid makes a smooth, slightly sigmoid sweep, first medially, then anteriorly, to join the protolophid just labiad to its midpoint. At this junction the link reaches to midheight on the nearly vertical posterior side of the protolophid. The protolophid contribution to the midlink is very weak. There tends to be a bulge or cusplet on the lingual side of the procingulum. This feature is distinct from the bulge of the edge of the cingulum itself and varies in its expression. It is commonest on M_3, often found on M_4, and rarely present on the anterior molars.

Discussion

Onychogalea lunata has been recorded as a living species from southwestern Western Australia, inland across southern Australia to the region of the junction of the Murray and Darling rivers in western New South Wales or Victoria, and within the southern part of the Northern Territory. The Elder Expedition reported it in the Everard Range of South Australia, and the Horn Expedition collected it at Alice Springs (Shortridge, 1909; Glauert, 1933; Jones, 1923–1925). Tedford (1967) gives measures for a juvenile from Rawlinna, on the Nullarbor Plain in Western Australia. This record supports the belief of Shortridge (1909) that this animal was distributed across the Nullarbor Plain in the recent past. The easternmost record from the junction of the Murray and Darling rivers is based on specimens collected by the Blandowski Expedition (Wakefield, 1966). In eastern Australia it is known from Holocene deposits in an archaeological site at Fromm's Landing on the lower Murray River (Wakefield, 1964), and from Pleistocene deposits at Lake Menindee and Lake Victoria in western New South Wales (Tedford, 1967; Marshall, 1973a). In Western Australia it is known from undated deposits in Horseshoe Cave (Archer, 1972, 1974). It is present in both Holocene and Pleistocene deposits in Madura Cave.

Comparison of dental measurements of specimens from different stratigraphic levels in Madura Cave (tables 7–8), from Lake Menindee (Tedford, 1967, tables 33–34), and from Lake Victoria (tables 9–10) shows extensive overlap in all cases. To test for differences between the samples from Unit 2 and Unit 1, Mann-Whitney tests were run on lengths, anterior widths, and posterior widths of dP^4, P^4, M^1, dP_4, and M_1. No significant differences ($P > .05$) were found. All samples currently available are too small to demonstrate any significant geographic or chronological differences.

***Incertae Sedis* within the Small Wallabies**

MATERIAL

Probably *Onychogalea lunata*

Trench 3, Unit 2, Level ?

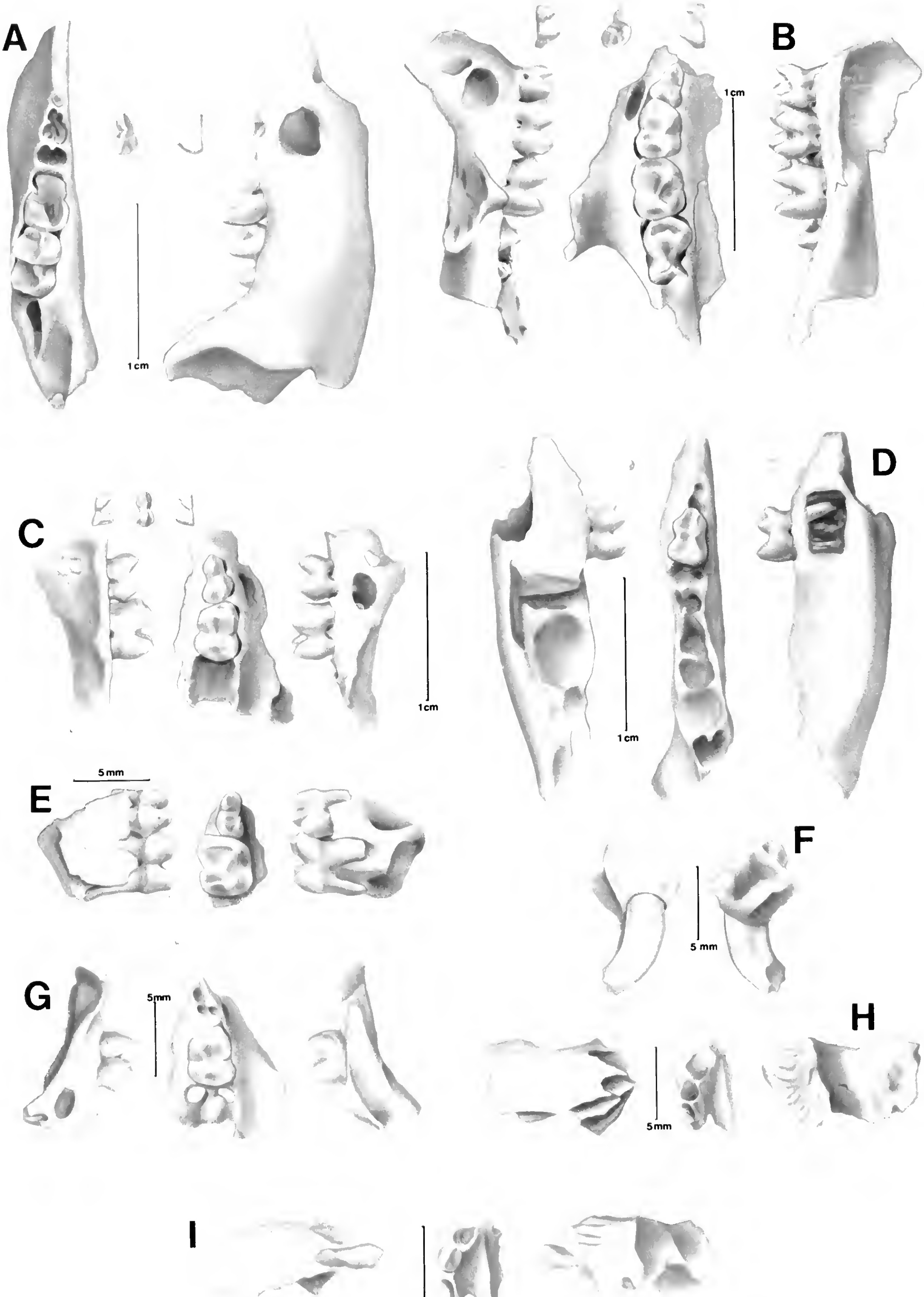

A
1 cm
B
1 cm
C
1 cm
D
1 cm
E
5 mm
F
5 mm
G
5mm
H
5mm
I
5mm

TABLE 7. Numerical data on upper dentitions of *Onychogalea lunata* from Madura Cave.

		Unit 1			Unit 2		
		N	OR	Mean	N	OR	Mean
P^3	L	2	2.6–2.9	2.75	2	2.7–3.0	2.85
	AW	2	1.3–1.4	1.35	2	1.3–1.4	1.35
	PW	2	2.0	2.0	2	2.0	2.0
dP^4	L	1	3.5	3.5	7	3.7–4.3	3.93
	AW	1	2.7	2.7	7	2.6–3.1	2.89
	PW	1	2.8	2.8	7	2.9–3.5	3.15
P^4	L	3	2.7–3.1	2.86	5	2.9–3.3	3.02
	AW	3	1.2–1.4	1.31	5	1.2–1.7	1.45
	PW	4	1.6–2.3	1.84	5	1.9–2.4	2.05
M^1	L	4	3.7–4.2	3.87	4	3.4–4.0	3.76
	AW	4	3.2–3.4	3.25	4	3.0–3.2	3.12
	PW	4	3.3–3.5	3.38	4	3.1–3.3	3.20
M^2	L	3	4.5–4.6	4.54	2	4.0–4.5	4.25
	AW	3	3.6–3.7	3.62	2	3.4–3.7	3.55
	PW	3	3.5–3.6	3.55	2	3.3–3.6	3.45
M^3	L	1	5.1	5.1	1	4.7	4.7
	AW	1	3.8	3.8	1	3.6	3.6
	PW	1	3.5	3.5	1	3.3	3.3
M^4	L	1	5.3	5.3	1	4.8	4.8
	AW	1	3.9	3.9	1	3.6	3.6
	PW	1	3.0e	3.0e	1	2.8	2.8
M^{1-2}	L	1	8.3	8.3	2	7.8–8.5	8.15
M^{2-3}	L	1	9.5	9.5	...	...	...
M^{1-3}	L	1	13.1	13.1	...	...	...
M^{1-4}	L	1	18.1	18.1	...	...	...

e = Estimate.

TMM 41106-55, left M_1
TMM 41106-5041, right M^1
PM 39034, left M_3 or M_2
Trench 4, Unit 1, top 1 ft
TMM 41106-544, left M_2 or M_3
TMM 41106-2835, right M^1
TMM 41106-2836, left M_1
TMM 41106-5073, right M^1 or M^2
TMM 41106-5074, right M^1 or M^2
TMM 41106-5083, right M_4 or M_3
Trench 4, Unit 2, Level 1
PM 38901, right M^3 or M^4
PM 38977, left M^1 or dP^4
PM 38978, right M_3 or M_2
Trench 5, Unit 6
PM 38885, right M_2

Probably *Lagorchestes hirsutus*

Trench 4, Unit 1, top 1 ft
TMM 41106-5081, left M_2 or M_3
PM 38891, right M_2

Probably *Lagorchestes hirsutus* or *Onychogalea lunata*

Opposite Page:

FIG. 13. *Onychogalea lunata* from Madura Cave. **A**, TMM 41106-183, right ramus fragment with P_4 removed from crypt, M_{1-2}, M_3 in crypt, and alveoli of P_3 and dP_4 shown in dorsal and lateral views. **B**, TMM 41106-184, right maxilla with P^3–M^2 shown in lateral (left), occlusal, and medial views. **C**, TMM 41106-5061, left maxillary fragment with P^3, dP^4, P^4 (removed from its crypt), and alveoli of M^1 shown in medial (left), crown, and lateral views. **D**, TMM 41106-5088, right ramus fragment with dP_4, P_4 (only partly formed and removed from its crypt), alveoli of M_1, and crypts for M_{2-3} shown in lateral (left), dorsal, and medial views. **E**, PM 39005, right maxillary fragment with P^4–M^1 shown in lateral (left), crown, and medial views. **F**, PM 39007, right premaxillary fragment with I^1 shown in lateral (left) and medial views. **G**, TMM 41106-141, left maxilla with dP^4 and alveoli of P^3 and M^1 shown in medial (left), crown, and lateral views. **H**, TMM 41106-5063, edentulous right premaxilla shown in lateral (left), ventral, and medial views. **I**, PM 38884, left premaxilla with I^2 shown in lateral (left), ventral, and medial views.

TABLE 8. Numerical data on lower dentitions of *Onychogalea lunata* from Madura Cave.

		Unit 1			Unit 2		
		N	OR	Mean	N	OR	Mean
dP_4	L	...	...	...	1	3.5	3.5
	AW	1	2.2	2.2	1	2.0	2.0
	PW	1	2.4	2.4	1	2.4	2.4
P_4	L	1	2.6	2.6	1	2.7	2.7
	AW	1	1.1	1.1	1	1.0	1.0
	PW	1	1.3	1.3	1	1.6	1.6
M_1	L	2	3.7–3.9	3.80	2	3.6–3.7	3.65
	AW	1	2.6	2.6	2	2.2–2.4	2.30
	PW	1	2.8	2.8	3	2.4–2.8	2.57
M_2	L	1	4.2	4.2	1	4.5	4.5
	AW	...	...	...	1	3.1	3.1
	PW	1	3.1	3.1	2	2.9–3.1	3.00
M_3	L	1	4.9	4.9	1	4.9	4.9
	AW	...	...	...	1	3.2	3.2
	PW	1	3.4	3.4	1	3.2	3.2
M_4	L	2	4.8–5.0	4.90	...	...	...
	AW	1	3.3	3.3	...	...	...
	PW	2	2.7	2.7	1	2.8	2.8
M_{1-2}	L	1	7.8	7.8	...	...	...
M_{2-3}	L	1	9.1	9.1	...	...	...
M_{1-3}	L	1	12.7	12.7	...	...	...
M_{1-4}	L	1	17.2	17.2	...	...	...

Trench 3, Unit 2, Level ?
TMM 41106-5043, left dP_4
TMM 41106-5046, right M_3
TMM 41106-5086, right ramus fragment with M_{1-3} or M_{2-4}
Trench 4, Unit 1, top 1 ft
TMM 41106-5058, right M_2 or M_3
TMM 41106-5077, left dP_4 or M_1

Undetermined

Trench 3, Unit 2, Level ?, probably level 1
TMM 41106-2838, right P_4
TMM 41106-5029, left I_1
TMM 41106-5030, right I_1
TMM 41106-5031, right I_1
TMM 41106-5032, left I_1
TMM 41106-5033, incisor or canine
TMM 41106-5034, badly eroded left lower molar
TMM 41106-5035, left M_1 or M_2
TMM 41106-5036, broken right M_4
TMM 41106-5037, broken left M_3 or M_4
TMM 41106-5042, broken left M_4
TMM 41106-5048, broken left M_3 or M_4
TMM 41106-5050, right M_1 or M_2
TMM 41106-5051, worn out upper molar
TMM 41106-5052, right M_2 or M_3
TMM 41106-5053, broken right M_3 or M_4
TMM 41106-5054, worn out upper molar
TMM 41106-5055, broken right M_3 or M_4
TMM 41106-5056, broken left M^2 or M^3
PM 38923, right I_1
PM 39008, right ramus with alveolus for dP_4–M_1, crypts for P_4 and M_{2-3}
PM 39009, right ramus fragment with alveolus for one molar, crypt for one molar
PM 39010, maxillary fragment with two worn and broken molars
PM 39036, broken right M_3 or M_4
PM 39037, worn out molar fragment
PM 39042–39044, three right I_1s
PM 39045, left I_1
PM 39051, left M_1
PM 39053, right maxillary fragment with alveolus for two molars
Trench 3, Unit 2, Level 2
TMM 41106-5121, broken left M_2 or M_3
Trench 3, Unit 2, Level 4
PM 38920, broken and eroded right M_1 or dP_4
PM 39011, worn left I_1
PM 39012, right I_1

TABLE 9. Dimensions of upper dentitions of *Onychogalea* from various sources.

		O. lunata					***O. unguifera***	***O. frenata***		
		Lake Victoria, N.S.W.*		**Weeke's Cave, S.A., and Snake Pit Cave, W.A., surface**			**Derby, W.A.**			
		NMV P 28573	**NMV P 28830**	**PM 38777**	**PM 38776**	**TMM M-937**	**USNM 237643**	**USNM 219299**	**USNM 122614**	**ROM 91.11.1.190**
P^3	L	...	...	...	...	...	3.5	...	3.7	3.5
	AW	...	...	...	...	...	2.0	...	2.0	1.8
	PW	...	...	...	...	...	2.7	...	2.5	2.8
dP^4	L	...	3.7	...	...	...	4.8	...	3.9	4.0w
	AW	...	2.8	...	...	...	3.6	...	3.2	3.7
	PW	...	3.0	...	...	...	4.0	...	3.5	3.8
P^4	L	...	...	3.3	2.5	3.3	...	3.8	...	...
	AW	...	...	1.6	1.4	1.2	...	2.3	...	...
	PW	...	...	2.1	1.8	2.1	...	2.8	...	...
M^1	L	...	4.0	3.7	3.6	4.3	5.6	4.8	4.5	4.7
	AW	...	3.2	3.1	3.1	3.5	4.3	4.1	3.8	4.1
	PW	...	3.3	3.1	3.2	3.5	4.4	4.2	3.8	4.2
M^2	L	...	...	4.2	4.3	4.9	...	5.7	5.3	5.6
	AW	...	...	3.5	3.6	3.8	...	4.5	4.2	4.4
	PW	...	3.5	3.4	3.7	3.6	...	4.5	4.2	4.4
M^3	L	5.0	...	4.9	5.0	5.6	...	6.7	5.8e	6.4
	AW	...	...	3.8	3.7	4.0	...	4.9	4.6	4.8
	PW	3.6	...	3.6	3.4	3.7	...	4.6	...	4.3e
M^4	L	4.9	...	...	...	...	...	...	...	...
	AW	3.9	...	...	...	...	...	...	...	...
	PW	3.4	...	...	...	...	...	...	...	...
M^{1-2}	L	...	...	7.9	7.7	8.9	...	...	10.4	9.9
M^{2-3}	L	...	...	9.3	9.1	10.4	...	...	12.5	11.9
M^{1-3}	L	...	...	12.7	12.4	14.2	...	...	16.8	16.3

* Data from Marshall (1973a, table 45). w = Worn; e = estimate.

PM 39015, broken right upper molar
PM 39019, broken left upper molar

Trench 3, Unit 3, Level ?
TMM 41106-37, left ramus fragment with alveolus for M_{2-4}

Trench 4, Unit 1, Level ?, probably level 1
TMM 41106-2837, broken premolar fragment
PM 39137, right upper I^1
PM 39142, terminal phalange

Trench 4, Unit 1, Level 1
TMM 41106-552, broken right lower molar
TMM 41106-5064, maxillary fragment with alveolus for two molars
TMM 41106-5065, left upper molar
TMM 41106-5066, eroded and broken M_1 or dP_4
TMM 41106-5148, broken left I_1
PM 38896, broken molar fragment
PM 38908, incompletely formed left I^1
PM 39109, anterior half, upper molar

Trench 4, Unit 1, top 1 ft
TMM 41106-624, broken lower molar
TMM 41106-626, broken upper molar
TMM 41106-5070–5071, two broken right upper molars
PM 38897, ramus fragment
PM 38904, worn out M_1
PM 38905, worn right I_1
PM 38910, broken left M_4
PM 38913, right ramus fragment
PM 39132, right upper I
PM 39133, right upper molar

Trench 4, Unit 2, Level 1
PM 7986–7987, right lower I and left M_1, respectively
PM 38936, left premaxilla with I^2

TABLE 10. Dimensions of lower dentitions of *Onychogalea* from various sources.

		O. lunata					*O. frenata*		
		Weebubbie Cave, surface		Jenning's Cave, surface	Snake Pit Cave, surface	*O. unguifera* Derby, W.A.	National Zoological Park	New South Wales (via National Zoological Park)	Warwick, Queensland
		TMM 41107-335	TMM 41107-334	TMM 42141-1	TMM M-937	USNM 237643	USNM 219299	USNM 122614	ROM 91.11.1.190
P_3	L	2.5	2.4	...	...	3.5	...	3.7	3.5
	AW	1.3	1.3	...	...	1.7	...	2.0	1.8
	PW	1.4	1.4	...	...	2.2	...	2.5	2.8
dP_4	L	3.5	3.5	3.2	...	4.7	...	3.9	4.0w
	AW	2.1	2.3	2.0	...	2.7	...	3.2	3.7
	PW	2.5	2.4	2.3	...	3.1	...	3.5	3.8
P_4	L	...	...	...	1.8	...	3.8	...	...
	AW	...	...	...	1.1	...	2.3	...	...
	PW	...	...	...	...	...	2.8	...	...
M_1	L	3.8	3.7	3.6	4.1	5.7	4.8	4.5	4.7
	AW	2.6	2.7	2.4	2.6	3.4	4.1	3.8	4.1
	PW	2.6	2.7	2.6	2.9	3.8	4.2	3.8	4.2
M_2	L	...	...	...	5.0	...	5.9	5.3	5.6
	AW	...	...	...	3.1	...	4.5	4.2	4.4
	PW	...	...	...	3.3	...	4.5	4.2	4.4
M_3	L	...	...	...	5.5	...	6.7	5.8e	6.4
	AW	...	...	...	3.3	...	4.9	4.6	4.8
	PW	...	...	...	3.3	...	4.7	...	4.3e
M_4	L	...	...	...	5.2e	...	...	...	...
	AW	...	...	...	3.3	...	...	...	...
	PW	...	...	...	2.6e	...	...	...	...
M_{1-2}	L	...	...	...	8.9	...	10.4	9.7	9.9
M_{2-3}	L	...	...	...	10.2	...	12.5	11.0	11.9
M_{1-3}	L	...	...	...	14.0	...	16.8	15.4	16.3
M_{1-4}	L	...	...	...	19.2e	...	...	...	...

* w = Worn; e = estimate.

PM 38975, worn out lower molar
PM 38976, right M^2 or M^3
PM 38981, right M_1 or M_2
PM 38983, broken upper molar
PM 38985, broken lower molar
PM 38990, broken left M_2 or M_3
PM 38992, broken left M_2 or M_3
PM 38994, broken right lower molar
PM 39119–39121, three terminal phalanges
PM 39122–39123, two subterminal phalanges
PM 39146, 39148, two anterior halves, upper molars
PM 39150, posterior half, left upper molar
PM 39151, posterior half, left lower molar

Trench 4, Unit 2, Level 2
PM 38933, left M^2
PM 38934, left M^3
PM 38948, right I_1
PM 38954, broken left upper molar
PM 39072, anterior half, left upper molar
PM 39077, partial upper incisor

Trench 4, Unit 2, Level 3
TMM 41106-4A–B, right I_1s

Trench 4, Units 4–5
PM 38876, left I_1
PM 38877–38878, two maxillary fragments
PM 39080, partial left upper molar
PM 39090, half, molar
PM 39096, anterior half, left lower molar

Trench 4, Unit 7, Level ?
PM 38928, right ramus fragment with alveolus for M_{2-3}, crypt for M_4
PM 38929, right ramus fragment with alveolus for M_{1-3}, crypt for M_4

Trench 4, Unit 7, Level 2
PM 38882, left maxillary fragment with broken P^4, alveolus for M^1
PM 38930, broken left M^1
Trench 5, Unit 5
PM 38887, left I^2 or I^3
Trench 5, Unit 5 or 6(?)
PM 39126, molar fragment
Trench 5, Unit 6
TMM 41106-641, broken left lower molar
PM 38886A–B, two upper incisors
PM 39125, left I^1

Protemnodon Owen, 1873 (*nomen nudum*), 1874
***Protemnodon* sp.** near *P. brehus* (Owen) and *P. roechus* Owen

MATERIAL

Trench 2, 2½ ft
PM 53920, ventral side, left I_1
Trench 4, Unit 2, Level 1
PM 39063, left ramus with broken P_4, M_{1-3}, roots of M_4 (fig. 14A)
Trench 4, Unit 2, Level 2
PM 39089, posterior one-third, left P^4 (fig. 14B)
TMM 41106-2832, anterior half, left upper M^3 or M^4 (fig. 14C)

COMPARATIVE MATERIAL

Protemnodon anak
Wellington Caves, New South Wales
PM 1553, left ramus with broken I, P_4–M_4 (fig. 14D)

cf. *Protemnodon brehus*
Wellington Caves, New South Wales
PM 1534, left ramus with I, dP_4, P_4 in crypt (fig. 15A)
PM 1541, right ramus with P_3, dP_4, and P_4 and M_3 in crypts (fig. 15B)
PM 1543, right ramus with dP_4–M_1, broken P_4 in crypt (fig. 15C)
PM 1544, left ramus with M_{1-3} (fig. 15D)
PM 1551, right ramus with P_3, dP_4, P_4 in crypt
PM 1557, left ramus with P_3, dP_4–M_2
PM 1560, right mandible with P_4 exposed in crypt, M_{1-3}, M_4 in crypt (fig. 15E)

cf. *Protemnodon roechus*
Wellington Caves, New South Wales
PM 1570, right maxilla with P^3, dP^4–M^2, P^4 in crypt (fig. 15F)
PM 1583–1584, left maxilla in two fragments with P^3, dP^4–M^2, P^4 and M^3 in crypt (fig. 15G)
PM 39064, right P^3 (fig. 15H)
PM 39066, right P^4

Descriptions

The horizontal ramus (fig. 14A) is moderately shallow and thick (depth at M_1–M_2 = 34.2 mm, thickness = 16.35 mm; depth at M_2–M_3 = 33.2 mm, thickness = 17.9 mm). From P_4 to M_3, it shows little change in depth, but thickens appreciably. The base of the symphysis rises at a low angle from the plane of the ventral edge of the horizontal ramus. Only the posterior part of the symphysis is preserved, so its shape and length cannot be determined. The shape of the preserved portion suggests that it was shallow, but it is deeper than that of a specimen of *Protemnodon anak* from Wellington (PM 1553; fig. 14D). The symphysis is rugose, but not ankylosed. The geniohyal pit is shallow and located at the posterior end of the symphysis. The mental foramen is located about 11 mm anterior to P_4 and about 4 mm below the dorsal edge of the diastema. The lateral groove is shallow and is located 7 mm below the edge of the alveolus; it extends from the premolar at least to the posterior root of M_2.

The posterior part of the P_4 is broken away. The outline of this tooth is an elongate oval. The labial surface bears an irregular wear facet for most of its length, which covers from one-third (in rear) to one-half (in front) of the crown below the crest of the occlusal surface. The anterior part of this wear surface has a broad groove across it, setting off a triangular ridge. The anterior part of the unworn lingual surface is gently convex.

The lower molars are rectangular in occlusal view with a slight constriction at the interloph valley, which is mostly confined to the labial side of the teeth. The relative sizes of the molars are: $M_1 < M_2 < M_3$. The protolophid is slightly narrower than the hypolophid in M_1 and about equal to it in M_2 and M_3 (table 11). The lophids are weakly convex posteriorly when unworn but are straight when worn. Forelinks are moderately well developed, extending from the protoconid anterolingually and then anteriorly to join the procingulum just labiad the center line of the tooth. The procingulum is prominent but narrow. It descends labially from its junction with the forelink to the

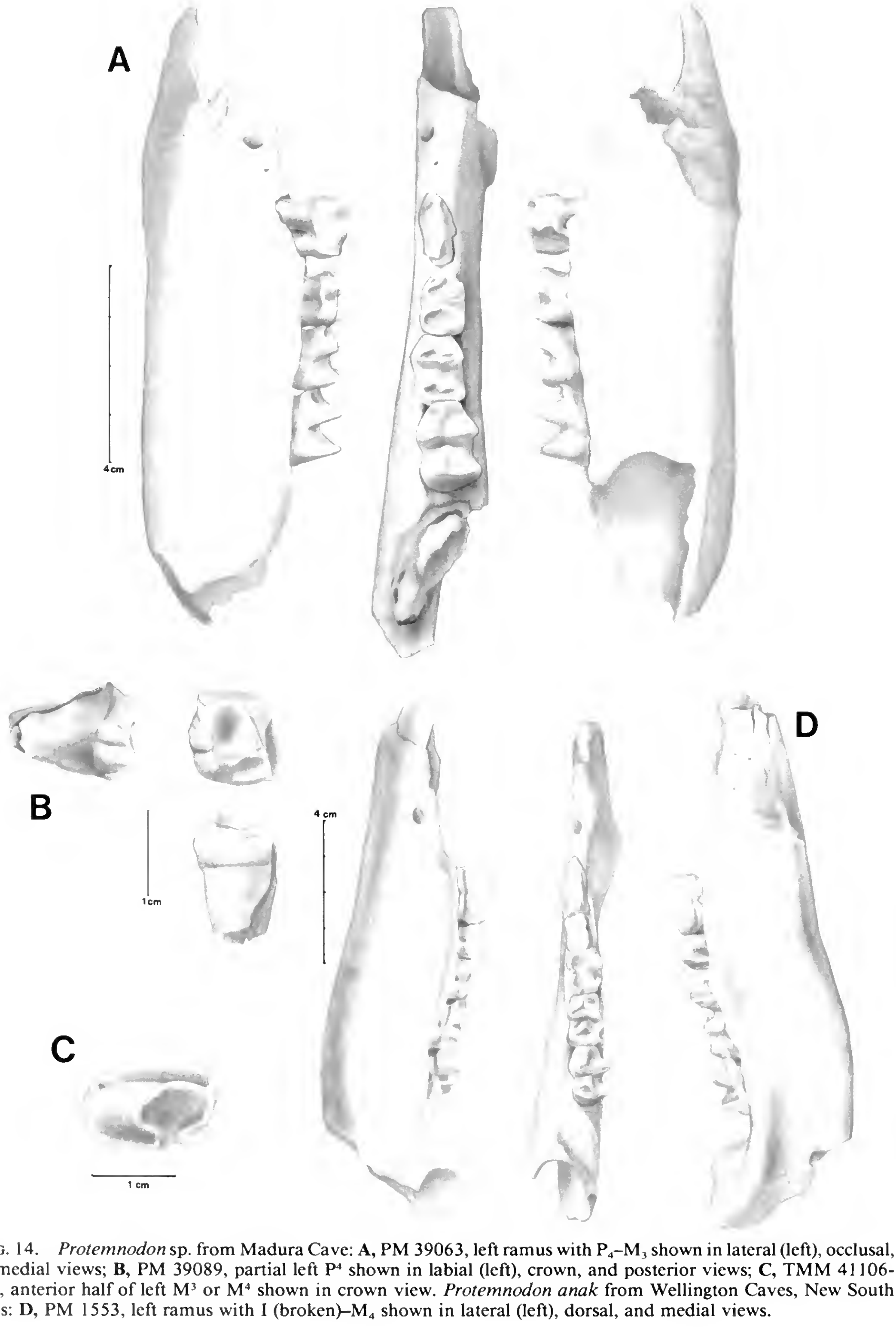


FIG. 14. *Protemnodon* sp. from Madura Cave: **A,** PM 39063, left ramus with P_4–M_3 shown in lateral (left), occlusal, and medial views; **B,** PM 39089, partial left P^4 shown in labial (left), crown, and posterior views; **C,** TMM 41106-2832, anterior half of left M^3 or M^4 shown in crown view. *Protemnodon anak* from Wellington Caves, New South Wales: **D,** PM 1553, left ramus with I (broken)–M_4 shown in lateral (left), dorsal, and medial views.

base of the protoconid, forming an anterolabial pit. The anterolingual area of the procingulum is nearly flat. The midlink descends anterolingually from the hypoconid and then turns anteriorly to join the protolophid near its base at the midline of the tooth. The labial side of the interloph valley slopes away from the midlink more steeply than does the lingual side. Low, indistinct lingual ridges descend from the metaconid and entoconid toward the interloph valley. The postcingulum is very small or absent. There is no bulge at the base of the crown.

The P^4 is represented by the posterior third of the crown and most of the posterior root (fig. 14B). The outer blade is missing, but the posterior basin formed by the posterior cingulum, the posterolingual cusp, and the rear of the labial crest is well preserved, as is the posterior part of the lingual trough. The ridgelike posterolingual cusp is joined to the main crest and to the lingual crest. There is a vertical groove on the lingual surface where it joins the lingual crest. The Madura Cave specimen is similar in size and morphology to a specimen from Lake Menindee figured by Tedford (1967, fig. 25C), which he referred to *Protemnodon brehus*.

Because of its large size (width across protoloph = 15.1 mm), the anterior half of the upper molar (TMM 41106-2832) probably is an M^3 or M^4. Its anterior width falls within the limits of the ranges of M^2, M^3, and M^4 of Bartholomai's (1973) Darling Downs, Queensland, sample of *Protemnodon roechus*, and just within the range of M^3 of his Queensland sample of *P. brehus*, and of M^4 of his Bingara, New South Wales sample. It also falls within the range of M^3 of Marshall's (1973a) Lake Victoria, New South Wales, sample. There is no forelink, and the stout procingulum has a low angle of inclination. The protoloph is bowed anteriorly in its middle. There is a delicate but distinct protoconal spur. A similarly developed labial crest and spur extend from the posterolabial edge of the paracone. Both of these spurs lead into the interloph valley. The tooth is slightly larger than that recorded by Stirton (1963, pp. 152–153) for the type and most of the other specimens of *P. brehus*, as well as any of the specimens of other species measured by him.

Discussion

Six species of *Protemnodon* were named by Owen (1874, 1877) on the basis of material from Pleistocene deposits in Australia: *P. anak*, *P. og*, *P. minutus*, *P. brehus*, *P. antaeus*, and *P. roechus*. Stirton's review of the genus (1963) made a start at determining the relationships of these species by unraveling several taxonomic problems, but presented no definitive discussion of the validity of each species. Bartholomai's review of the genus (1973) synonymized *P. og* into *P. anak*, *P. mimas* into *P. brehus*, and *P. antaeus* into *P. roechus*, and split off *P. chinchillaensis* and *P. devisi*, both Pliocene in age, from *P. anak*.

The characters which have been used to differentiate these species show considerable intrasample variability, the extent of which has been poorly understood until recently. This has made specific identification of *Protemnodon* specimens difficult, especially in the case of isolated specimens. Bartholomai (1973) analyzed large samples of *Protemnodon* from Queensland, which provided some information on intraspecific variation for material from that area. Marcus (1976) has done the same for material from Bingara.

We have doubts about the usefulness of the qualitative characters suggested by Bartholomai (1973) as distinguishing *Protemnodon brehus* from *P. roechus*. The tuberculation on the lingual side of the interloph valley of the upper molars is variable in the two comparative specimens from Wellington Cave. Furthermore, one of Bartholomai's figures (1973, pl. 13) shows a specimen of *P. brehus* (which is supposed to lack this feature) to have a weakly developed tuberculation on M^1 and M^3. The degree of labial concavity of the labial crest of P^4 in *P. roechus*, as shown in Bartholomai's figures (1973, fig. 7, nos. 5–8), appears to be variable. The extent of the expansion of the bases of the lower molars also is variable. In view of these doubts and of the extensive overlap in the size ranges of virtually all metric characters (see Bartholomai, 1973, tables 6, 10, fig. 9), we have doubts, as did Flower (1884), Lydekker (1887), and Marshall (1973a), that the two species are distinct. Nonetheless, since we lack the comparative material to investigate this question, we will consider these to be two separate species in the following discussion.

The width of the protoloph of the upper molar fragment from Madura Cave exceeds the upper limit of the observed range for all upper molars of *Protemnodon anak* given by Bartholomai (1973), but is within the observed range for M^3 and M^4 of *P. brehus* and M^{2-4} of *P. roechus* (table 12). No qualitative character, such as the tuberculation seen by Bartholomai (1973) on the labial side of the

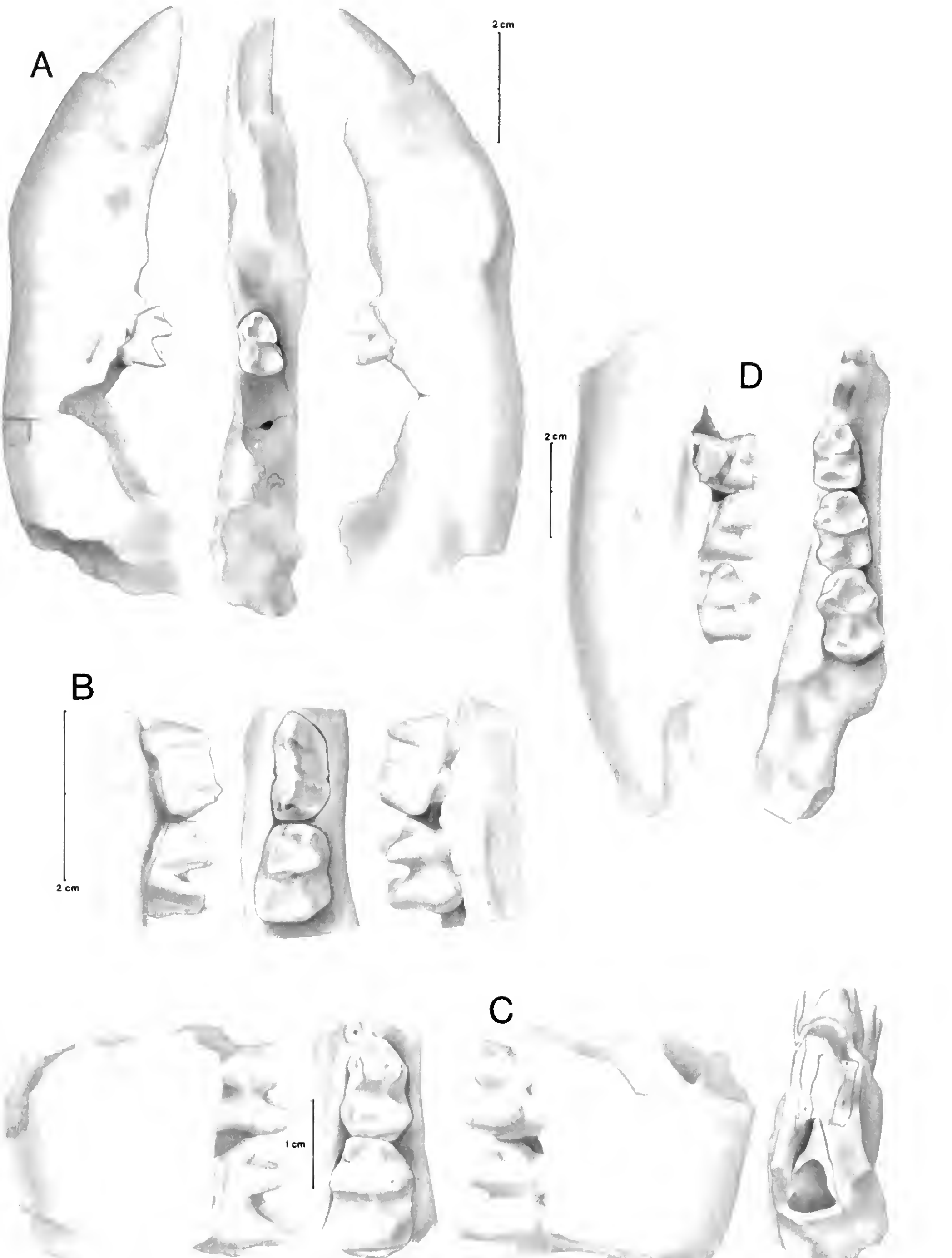
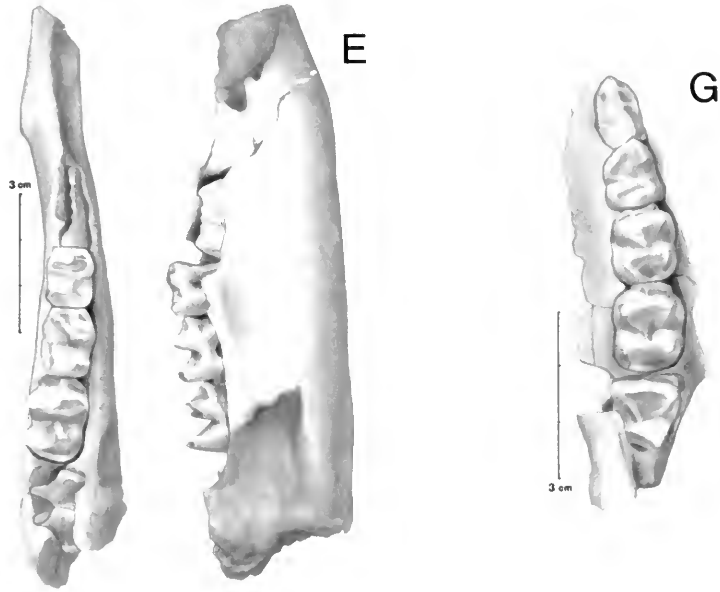
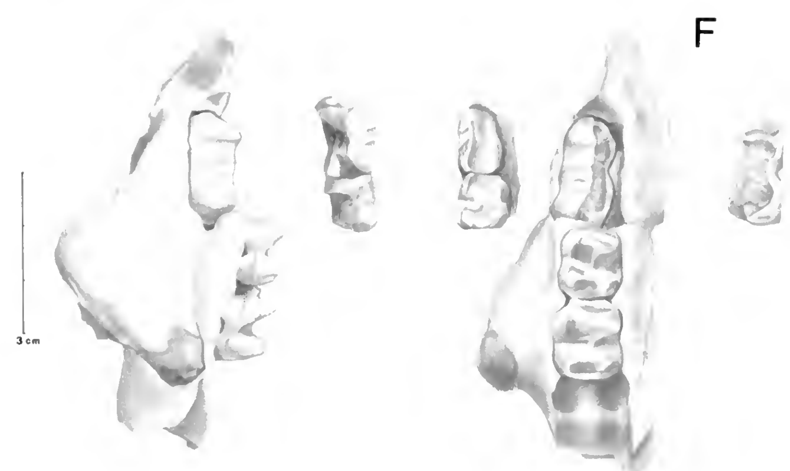


FIG. 15. *Protemnodon* sp. from Wellington Caves, New South Wales, for comparison. *Protemnodon brehus*: **A,** PM 1534, left ramus with I, dP_4, and P_4 in crypt shown in lateral (left), dorsal, and medial views; **B,** PM 1541, right ramus with P_3 and dP_4 shown in lingual (left), crown, and labial views; **C,** PM 1543, right ramus with posterior roots of P_3, broken P_4, and dP_4–M_1 shown in medial (left), dorsal, lateral, and anterior views; **D,** PM 1544, left ramus with





M_{1-3} shown in lateral and crown views; **E,** PM 1560, right mandible with P_4–M_4 shown in dorsal and lateral views. *Protemnodon roechus*: **F,** PM 1570, right maxilla with P^3–M^2 shown in lateral and ventral views, and P^4 exposed in crypt shown in lateral, ventral, and lingual views; **G,** PM 1583–1584, adjoining maxillary fragments with P^3–M^3 shown in crown view; **H,** PM 39064, right P^3 shown in labial (left), crown, and lingual views.

TABLE 11. Numerical data on mandibles and lower dentitions of *Protemnodon* from Lake Victoria, Wellington Caves, and Madura Cave.

		Protemnodon brehus* Lake Victoria			***Protemnodon* cf. *brehus***				***Protemnodon anak***
					Madura Cave PM	**Wellington Caves**			**Wellington Caves PM**
		N	**OR**	**Mean**	**39063**	**N**	**OR**	**Mean**	**1553**
P_3	L	...	...	...	...	3	11.7–12.3	12.05	...
	AW	...	...	...	...	3	5.5–6.5	5.90	...
	PW	...	...	...	...	3	6.3–6.9	6.60	...
dP_4	L	...	...	...	...	5	10.3–12.5	11.55	...
	AW	...	...	...	...	4	5.9–7.5	6.85	...
	PW	...	...	...	...	5	7.1–8.7	8.04	...
P_4	L	...	...	...	16.4	1	17.5	17.5	17.4
	AW	...	...	...	6.3	...	...	...	5.1
	PW	...	...	...	...	...	...	...	7.3
M_1	L	1	12.2	12.2	11.9	4	12.1–13.9	13.20	10.9
	AW	1	10.0	10.0	8.9	4	8.7–10.2	9.45	6.5
	PW	1	9.7	9.7	9.3	4	8.9–9.9	9.55	7.6
M_2	L	2	15.0–15.2	15.07	13.0	2	15.8–16.7	16.23	12.7
	AW	...	...	...	10.4	2	11.1–11.5	11.30	10.0
	PW	2	11.6–12.3	11.95	10.5	1	11.2	11.2	9.3
M_3	L	6	17.4–18.0	17.68	16.2	2	18.1–19.9	19.00	15.4
	AW	3	12.8–13.9	13.43	11.9	2	12.6–12.7	12.65	...
	PW	3	12.7–13.6	13.10	12.0	2	12.4–12.9	12.65	...
M_4	L	5	18.8–19.5	19.10	...	...	...	...	17.0
	AW	1	13.1	13.1	...	...	...	...	11.1
	PW	2	11.6–12.7	12.15	...	...	...	...	9.7
Mandible below M_{1-2}	Depth	...	...	...	34.2	2	32.0–32.2	32.10	32.3
Mandible below M_{2-3}	Depth	...	...	...	33.2	2	30.9–31.2	31.05	32.8
Mandible at M_{1-2}	Thickness	...	...	...	16.3	2	13.7–14.4	14.05	10.9
Mandible at M_{2-3}	Thickness	...	...	...	17.9	2	15.4–16.2	15.80	11.3

* Data from Marshall (1973a, table 61).

interloph valley in *P. roechus* is preserved. It is not clear whether this molar and the ramus represent the same species. However, since they are similar in size and lack features which might suggest a difference, the most parsimonious assumption is that they do represent the same taxon.

The ramus from Madura Cave differs from others assigned to *Protemnodon anak* in a number of characters which have been cited as diagnostic by Bartholomai (1973) and Marcus (1976). The angle between the base of the symphysis and the ventral margin of the horizontal ramus rises at a steeper angle (10°–20°), and the symphysis is deeper. The geniohyal pit is prominent just behind the symphysis. The horizontal ramus is deeper and thicker, as is the ramus of our comparative specimen from Wellington Cave (PM 1553; table 11, fig. 16A), but matches the dimensions given by Bartholomai for *P. brehus* and *P. roechus* and by Marcus for *P. brehus*.

The dental dimensions of the Madura Cave specimen are larger than those given for *Protemnodon anak*, but within the ranges given for *P. brehus* and *P. roechus* by Bartholomai (1973), Marshall (1973a), and Marcus (1976) (tables 11–12, fig. 16). A comparison of the Madura Cave specimen with the qualitative dental characters given by Bartholomai is less easily made. The anterior cingular areas of the lower molars of the Madura Cave specimen are not as wide relative to the widths of the lophids as is shown in Bartholomai's figures of *P. brehus*, but are wider than is shown for *P. anak*. The Madura Cave specimens also differ from *P. anak* and are similar to *P. brehus* and *P. roechus* in most other characters, but because of the doubts mentioned above it is difficult to be certain to which of these two species they belong. All measurements which could be taken on the Madura Cave specimens fall within the broad area of overlap of the size ranges of these two species (table 11, fig. 16). The qualitative character that suggests the most unequivocal assignment is the degree of expansion of the base of the crown in the lower molars. In *P. roechus* the base of the crown is expanded (Bartholomai, 1973); in *P. brehus* and the Madura Cave specimens the base of the crown is not expanded.

Protemnodon has been reported from other localities on the Nullarbor Plain. Glauert (1912) reported *P. anak* from Balladonia, but Merrilees (1968a) subsequently referred this material to *Sthenurus*. *Protemnodon* cf. *brehus* has been reported by Milham and Thompson (1976) from the south passage of Madura Cave, but they did not figure the material or give the basis for their assignment; *P. brehus* has also been reported from the Mammoth Cave deposits in southwestern Australia (Tedford, 1967).

Petrogale Gray, 1837
Petrogale Species Indeterminate

MATERIAL

Trench 3, Unit 2
PM 39006, left I^1 in a fragment of the premaxilla (fig. 17A)
Trench ? (probably 4), Unit 1, top 1 ft
PM 39130, left I^1 (fig. 17B)
Trench 4, Unit 2, Level 2
PM 39068, left M^4 (fig. 17C)

COMPARATIVE MATERIAL

Petrogale brachyotis

Kimberly District, Western Australia
FM 119823 (fig. 17F)
FM 120577

Petrogale cf. *lateralis*

Northwest Cape, Western Australia (Late Pleistocene or Holocene)
PM 26694
PM 26701
PM 36718
Wedge's Cave, Mimegara (north of Perth), Western Australia (Late Pleistocene or Holocene)
PM 5749 (fig. 17D)
PM 5771
PM 5772
PM 5773

Petrogale inornata

Rockhampton-Atherton area, Queensland
FM 64360
FM 64430 (fig. 17G)

Petrogale venustula

Oenpelli, East Alligator River, Northern Territory
USNM 284068

Petrogale pearsoni

Oenpelli, East Alligator River, Northern Territory
RCS London A.348.51 (fig. 17E)

Descriptions

The left M^4 (PM 39068; fig. 17C) compares well with that of a Holocene specimen of *Petrogale* from Wedge's Cave, Western Australia (PM 5749; fig. 17D) in most morphological characters, although it is slightly smaller. The protoloph and metaloph are convex anteriorly, while the protoloph is noticeably longer than the metaloph. Both lophs contribute to the midlink. A cleft divides the midlink in the median valley. Ridges from the paracone and metacone almost meet on the labial side of the median valley to form a median basin. The procingulum occupies the entire anterior border of the tooth. It is connected to the paracone by a prominent ridge, but is not connected to the metacone, leaving the procingular basin open on the lingual side. The postcingulum is connected to the hypocone by a ridge, forming a posterior cingular basin. According to Merrilees (1979), this is characteristic of M^{2-4}; this agrees with our observations on recent specimens of *Petrogale* from Queensland, Western Australia, and the Northern Territory. This character distinguishes the M^{2-4} of *Petrogale* from those of macropodids such as *Macropus irma* and *M. eugenii* that have dentitions similar to those of *Petrogale*. The Madura Cave specimen differs from the Wedge's Cave specimen principally in its small size and in the form of the procingulum, which does not slope lingually toward the base of the tooth.

The dimensions of PM 39068 are: length 7.50 mm, anterior width 5.00 mm, and posterior width

TABLE 12. Numerical data on upper teeth of *Protemnodon* from Wellington Caves, Lake Victoria, and Bingara, New South Wales, and Queensland in comparison with the broken tooth of *Protemnodon* sp. from Madura Cave.

		P. roechus							***Protemnodon* sp.**	***P. brehus***		
		Wellington Caves, N.S.W.*				**Darling Downs, Qld.†**			**Madura Cave, W.A. TMM 41106-2832**	**Bingara, N.S.W.‡**		
		PM 1570	**PM 1583-84**	**PM 39066**	**Mean**	**N**	**OR**	**Mean**		**N**	**OR**	**Mean**
P^4	L	22.4	...	20.4	21.40	7	18.3–20.7	19.4	...	...	...	...
	AW	10.3	...	10.4	10.35	7	9.2—10.4	9.7	...	...	...	...
	PW	11.3	...	10.5	10.90	...	...	...	...	...	...	...
M^1	L	13.5	13.7	...	13.60	4	12.9–14.0	13.4	...	...	...	...
	AW	11.9	12.1	...	12.00	9	12.2–13.9	12.8	...	...	...	...
	PW	12.0	12.2	...	12.10	...	...	...	...	...	...	...
M^2	L	15.2	15.5	...	15.35	12	15.7–17.7	16.7	...	4	15.4–16.6	16.00
	AW	13.5	12.9	...	13.20	10	13.7–15.4	14.6	15.1	4	13.3–13.9	13.60
	PW	13.0	12.7	...	12.85	...	...	...	...	...	...	...
M^3	L	...	...	...	...	18	17.2–19.9	18.6	...	1	16.7	16.70
	AW	...	(13.6)	...	...	12	14.9–16.2	15.6	15.1	...	...	...
	PW	...	...	...	...	...	...	...	...	...	...	...
M^4	L	...	...	...	...	13	17.7–20.0	19.0	...	2	18.7	18.70
	AW	...	...	...	...	11	14.7–16.5	15.7	15.1	2	14.4–15.2	14.80
	PW	...	...	...	...	...	...	...	...	2	...	...

* FMNH specimens not previously reported. † Data from Bartholomai (1973, table 10). ‡ Data from Bartholomai (1973, table 6). § Data from Marshall (1973a, table 61).

4.35 mm. A comparison of these dimensions with those given by Merrilees (1979) for a series of Pleistocene, Holocene, and modern samples of *Petrogale* from southwestern Western Australia shows that the length of the Madura Cave specimen is within the observed range but the widths, especially the posterior width, are below the observed ranges.

The I^1s (PM 39006, 39130; fig. 17A–B) are strongly curved, with a wear surface developed on the lingual face. There is a shallow groove near the posterior edge of the labial surface of PM 39006, which produces a notch on the cutting edge of the tooth; no trace of this groove can be found on the other specimen. A vertical buttress is present on the posterior part of the lingual surface of the tooth. None of the Madura Cave specimens shows a discrete cuspule arising from this lobe, as reported by Merrilees (1979) for some specimens from southwestern Western Australia.

Discussion

The taxonomy of this genus is confused. Tate (1948) recognizes three species with eight subspecies. Marlow (1962) shows distributions of seven species divided into 17 subspecies, while Ride (1970) recognizes six species. Calaby (1971) has suggested that this is the result of the highly fragmented distribution of the genus today, which has caused a large amount of local variation. The Madura Cave material is inadequate for a specific assignment.

Rock wallabies of the genus *Petrogale* inhabit cliffs, rock piles, and rocky outcrops in most parts of Australia (Calaby, 1971). The genus has not been reported from the Nullarbor Plain. The only parts of this area that appear to provide suitable habitat are the scarp that separates the Roe Plain from the Hampton Tableland, and possibly some of the karst features such as the larger dolines.

Macropus Shaw, 1790

The taxonomy of the genus *Macropus* has long been a problem. There is no general agreement on the boundaries of the genus, although most students now place the red kangaroo in a separate genus, *Megaleia* (Sharman, 1961; Calaby, 1966; Frith & Calaby, 1969; Bartholomai, 1975). More

TABLE 12. *Extended.*

P. brehus					
Queensland Sample‡			Lake Victoria§		
N	OR	Mean	N	OR	Mean
9	18.1–19.8	19.2	...	...	...
10	9.3–10.6	10.0	...	...	...
...	...	...	...	...	...
6	12.7–14.6	13.6	1	14.4	14.4
4	12.0–12.7	12.3	1	12.2	12.2
...	...	...	1	12.6	12.6
14	14.8–17.0	16.3	1	16.4	16.4
6	13.4–14.6	14.0	1	14.8	14.8
...	...	...	1	14.8	14.8
18	16.2–18.1	17.5	2	18.2–18.4	18.30
15	13.7–15.1	14.5	2	15.0–15.2	15.10
...	...	...	1	15.2	15.2
12	17.3–19.1	18.2	2	17.7–17.8	17.75
11	13.7–15.0	14.3	2	14.6–14.7	14.65
...	...	...	...	...	...

recently, Peacock et al. (1981) have suggested that there is little justification for this separation beyond the chromosome number difference. Even with *Megaleia* removed, the genus is particularly troublesome for the paleontologist because so many species have been named on the basis of minor dental characters whose significance is unknown. Although it has now become possible to separate many of the large-sized species of *Macropus* and to separate *Macropus* from *Megaleia* on the basis of dental characters which are usable on paleontological materials (Tedford, 1967; Frith & Calaby, 1969; Bartholomai, 1975; Marcus, 1976), problems remain.

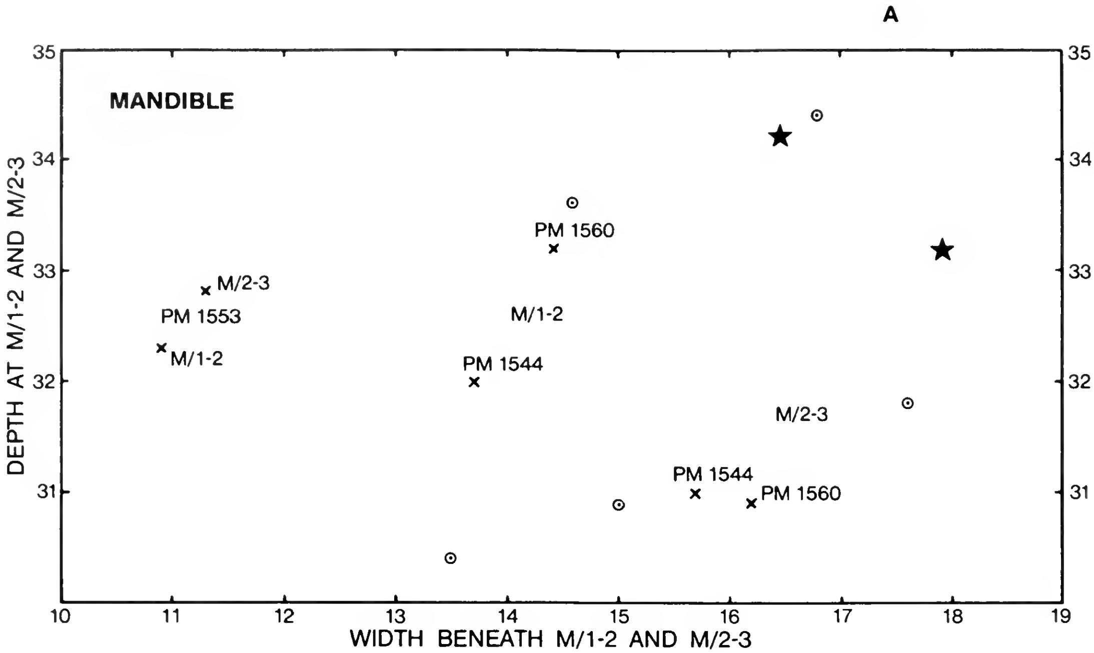
It has been shown by Kirsch and Poole (1967, 1972) on the basis of serological studies and by Peacock et al. (1981) on the basis of DNA sequence studies that the living gray kangaroos are in fact two species, *Macropus giganteus* and *M. fuliginosus*. *Macropus giganteus* is distributed over the eastern part of Queensland, much of New South Wales and Victoria, and northern Tasmania, while *M. fuliginosus* is found in western Victoria, southwestern New South Wales, and the southern parts of South Australia and Western Australia (Shepherd, 1982). The two species overlap without interbreeding in western Victoria and southwestern New South Wales (Shepherd, 1982). In spite of rigorous attempts by Poole et al. (1980) to do so, no dental or skeletal criteria are known that will consistently separate these two species. A third fossil species, *M. titan*, which is morphologically similar to the living species, has been recognized on the basis of significantly larger size (Owen, 1874; Marshall, 1973a; Marshall & Corruccini, 1978).

The deposits in Madura Cave have produced remains that are referable to *Macropus titan* and *M. fuliginosus*. All material that can be confidently assigned to *M. titan* on the basis of both morphology and size comes from Units 2–7, which have radiocarbon dates ranging from 15,600 ± 250 to 37,800 ± 3520 B.P. (Lundelius & Turnbull, 1973). All material that can be assigned to *M. fuliginosus* is from the present surface of the cave or from Unit 1. This unit, which is 2 ft (~60 cm) thick, has an eroded top surface. The top 1 ft (30 cm) of the unit has been radiocarbon-dated at 7470 ± 120 B.P. (Lundelius & Turnbull, 1973). Thus, all of the confidently referred *M. titan* material is of Pleistocene age and the *M. fuliginosus* material is of modern or Holocene age. The tentatively assigned specimens of these taxa seem to follow this same pattern, but those which lack definitive features or are of intermediate size have been assigned to *Macropus* sp.

This stratigraphic and chronological distribution of these two species in the Madura Cave deposits is consistent with their chronological distribution in other parts of Australia as reviewed by Marshall (1973a).

The close morphological resemblance of *M. giganteus-M. fuliginosus* to *M. titan* has been noted by many investigators (Owen, 1874; Lydekker, 1887; Tedford, 1967; Marshall, 1973a; Marshall & Corruccini, 1978) and has been cited by the last two authors as an example of dwarfing in a single lineage at the end of the Pleistocene. The discovery that *M. fuliginosus* and *M. giganteus* are separate species raises questions about the details of the relationship of these three taxa. Furthermore, Marshall (1973a) points out that *M. titan* as it is currently recognized also may have been heterogeneous.

Regardless of the exact phylogenetic relationship between *M. titan* and *M. fuliginosus*, the record at Madura Cave shows that a larger *Macropus* was replaced by a smaller one with similar morphology after 16,000 B.P., about the same time as in other parts of Australia and at the same time as the disappearance of the extinct mammals and the disharmonious assemblages.


A
MANDIBLE
DEPTH AT M/1-2 AND M/2-3
WIDTH BENEATH M/1-2 AND M/2-3
PM 1560
M/2-3
PM 1553
M/1-2
M/1-2
PM 1544
M/2-3
PM 1544
PM 1560
35
34
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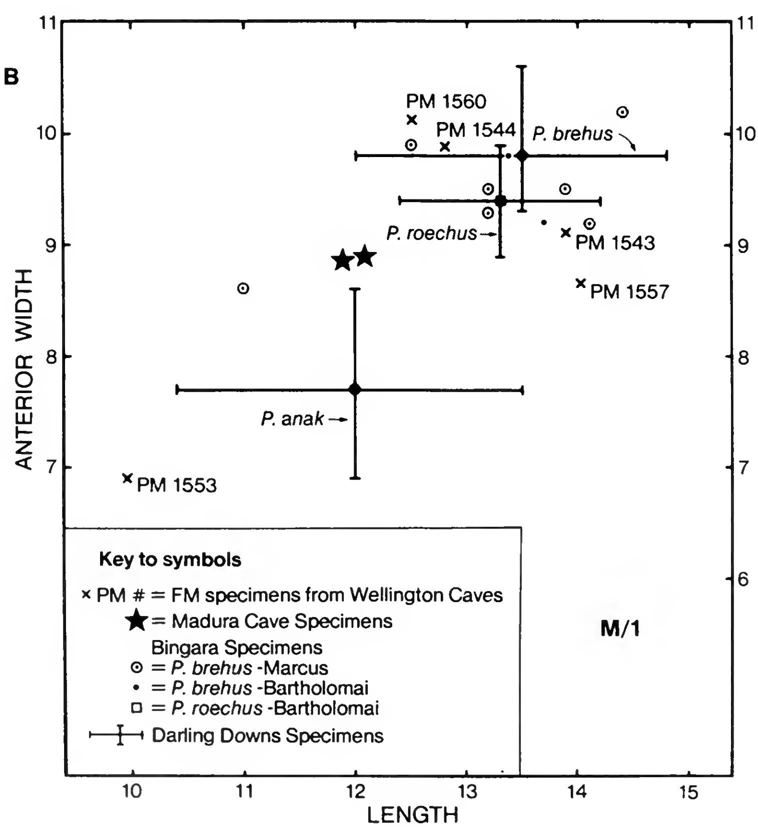
B
PM 1560
PM 1544
P. brehus
P. roechus
PM 1543
PM 1557
P. anak
PM 1553
ANTERIOR WIDTH
LENGTH
M/1
Key to symbols
PM # = FM specimens from Wellington Caves
= Madura Cave Specimens
Bingara Specimens
= P. brehus -Marcus
= P. brehus -Bartholomai
= P. roechus -Bartholomai
Darling Downs Specimens
11
10
9
8
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11
12
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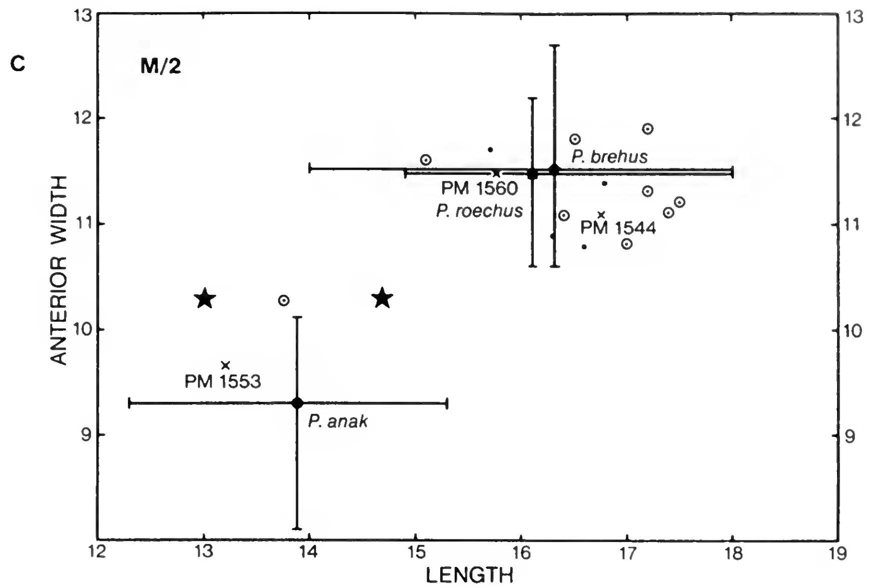


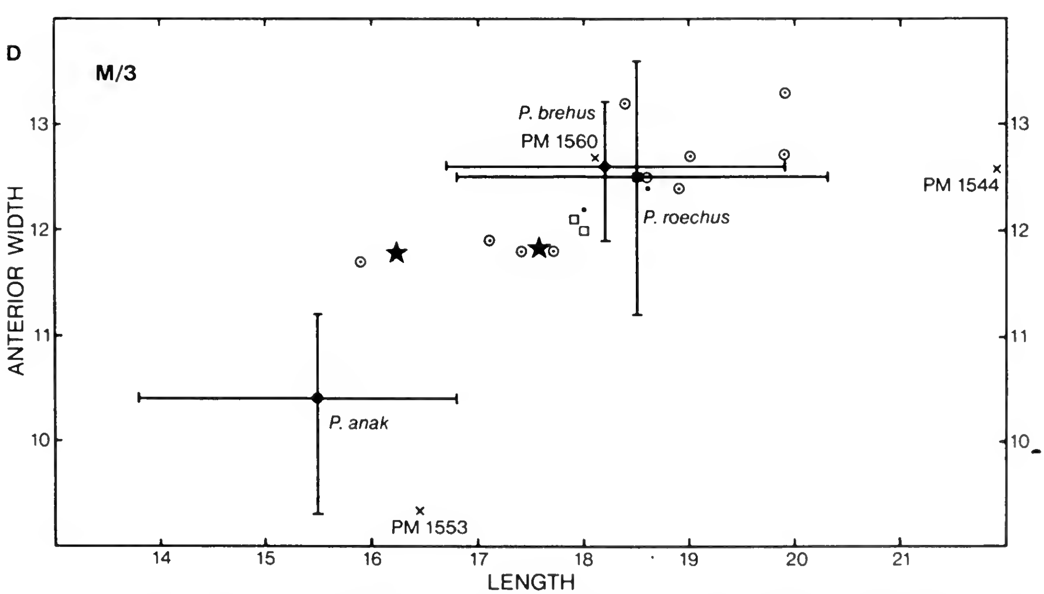


FIG. 16. Bivariate graphs showing the Madura Cave specimens of *Protemnodon* (stars) in comparison with certain Wellington Caves specimens and with samples of *P. brehus* and *P. roechus* from the literature. **Upper left,** mandibular proportions at M_{1-2} and M_{2-3}; **lower left,** length × anterior width of M_1; **upper right,** length × anterior width of M_2; **lower right,** length × anterior width of M_3.

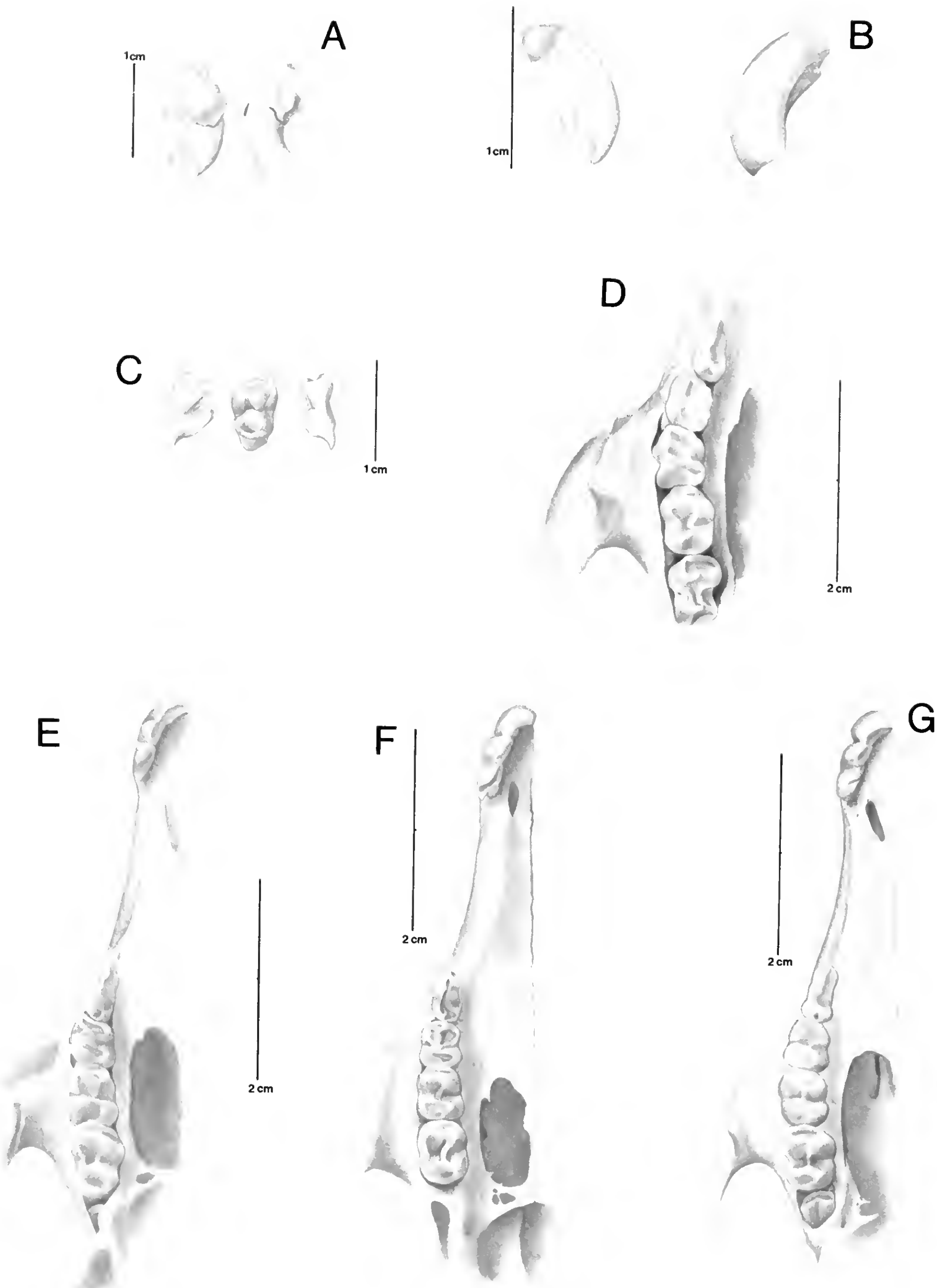


FIG. 17. *Petrogale* sp. from Madura Cave compared with various modern species of the genus. *Petrogale* sp. from Madura Cave: **A**, PM 39006, left I[1] in premaxillary fragment shown in lingual (left) and labial views; **B**, PM 39130, left I[1] shown in lingual (left) and labial views; **C**, PM 39068, left M[4] shown in lingual (left), crown, and labial views. *Petrogale* sp. from Wedge's Cave, Mimegara, Western Australia: **D**, PM 5749, right maxilla shown in ventral view. *Petrogale pearsoni* from Oenpelli, East Alligator River, Northern Territory: **E**, RCS A.348.51, right side of palate shown in ventral view. *Petrogale brachyotis* from Kimberly District, Western Australia: **F**, FM 119823, right side of palate shown in ventral view. *Petrogale inornata* from Rockhampton-Atherton area, Queensland: **G**, FM 64430, right side of palate shown in ventral view.

TABLE 13. Numerical data on upper dentitions of a Recent sample of *Macropus giganteus* from New South Wales.

		N	OR	Mean
P^3	L	2	6.4–6.8	6.60
	AW	2	3.2–3.3	3.25
	PW	2	4.5–4.6	4.55
dP^4	L	2	7.9–8.0	7.95
	AW	2	6.1–6.5	6.30
	PW	2	6.5–6.9	6.70
M^1	L	5	6.9–10.2	9.02
	AW	5	7.2–8.6	7.88
	PW	5	7.5–8.7	8.14
M^2	L	4	9.9–11.2	10.63
	AW	4	8.5–9.5	8.93
	PW	4	8.2–9.5	8.90
M^3	L	3	12.0–13.0	12.47
	AW	3	9.4–10.2	9.77
	PW	3	8.8–10.0	9.33
M^4	L	3	12.8–14.1	13.30
	AW	3	9.9–10.8	10.23
	PW	3	8.9–10.3	9.47
Diastema	L	5	53.0–63.5	58.38
M^{1-4}	L	3	42.2–46.2	43.53

TABLE 14. Numerical data on lower dentitions of a Recent sample of *Macropus giganteus* from New South Wales.

		N	OR	Mean
P_3	L	2	5.6–6.0	5.8
	AW	2	2.6	2.6
	PW	2	3.4–3.6	3.5
dP_4	L	2	7.8–8.3	8.05
	AW	2	4.4–5.2	4.80
	PW	2	5.3–5.8	5.55
M_1	L	4	7.8–9.7	9.04
	AW	4	5.6–6.1	5.98
	PW	4	6.1–7.4	6.80
M_2	L	5	10.0–11.7	10.86
	AW	5	6.4–8.0	7.20
	PW	5	6.5–8.1	7.24
M_3	L	3	11.5–12.7	12.20
	AW	3	8.2–8.6	8.43
	PW	3	7.6–8.4	8.03
M_4	L	3	12.8–13.4	13.07
	AW	3	8.3–9.2	8.67
	PW	3	7.7–8.6	8.03
Diastema	L	5	43.6–51.0	46.66
M_{1-4}	L	3	36.2–43.0	40.13

Macropus fuliginosus Shaw and Nodder, 1790, part; (Desmarest, 1817) part

MATERIAL

Surface
- TMM 41106-23–24, pair of rami (same individual) with left and right I_1, P_3–dP_4, M_1 in crypt (fig. 19D)

Trench 2, Unit 1, top 1 ft
- PM 6246, right ramus with I, P_4–M_3, M_4 in crypt (fig. 19C)

Trench 4, Surface and Unit 1, top 6 inches
- TMM 41106-510, right maxilla with M^{1-4} (fig. 19A)
- TMM 41106-547, posterior one-third, left dP^4

Trench 4, Unit 1, top 1 ft (presumably level 2)
- PM 39128, left upper molar (fig. 19B)
- PM 39134, right upper molar
- TMM 41106-501, distal half, right metatarsal V (fig. 19F)

Macropus sp. (Probably ***Macropus fuliginosus***)

Trench 1, Unit 1, top 1 ft
- TMM 41106-499, right I^2 or I^1

Trench 4, Surface and Unit 1, top 6 inches
- TMM 41106-551, tooth fragment
- PM 7983, terminal phalanx from one of the syndactylous toes
- PM 7984, terminal phalanx from manus
- PM 39110, anterior half, left dP_4 or M_1
- PM 39113, anterior half, lower molar or dP_4

Trench 4, Unit 1, top 1 ft (presumably level 2)
- TMM 41106-500, left metacarpal II (fig. 19E)
- TMM 41106-502, first phalanx, manus
- TMM 41106-503, terminal phalanx, pes
- TMM 41106-504, terminal phalanx, pes
- PM 39129, left I^3
- PM 39138, right I^3
- PM 39143, terminal phalanx, manus

COMPARATIVE MATERIAL

Macropus sp. (Probably ***Macropus fuliginosus***)

Murraelellevan Cave (surface red clay), Western Australia
- PM 24334, left ramus with M_{1-4}, alveolus of P_4

Hasting's Cave (surface), Western Australia
- PM 50847, skull and mandible with I^3 in crypt, erupted P^3, dP^4, M^1 in crypt; I_1, P_3, dP_4, erupting M_1

Macropus fuliginosus

Jurien Bay, Western Australia
- TMM M-925

West coast north of Perth, Western Australia
- TMM M-927 (fig. 21I)

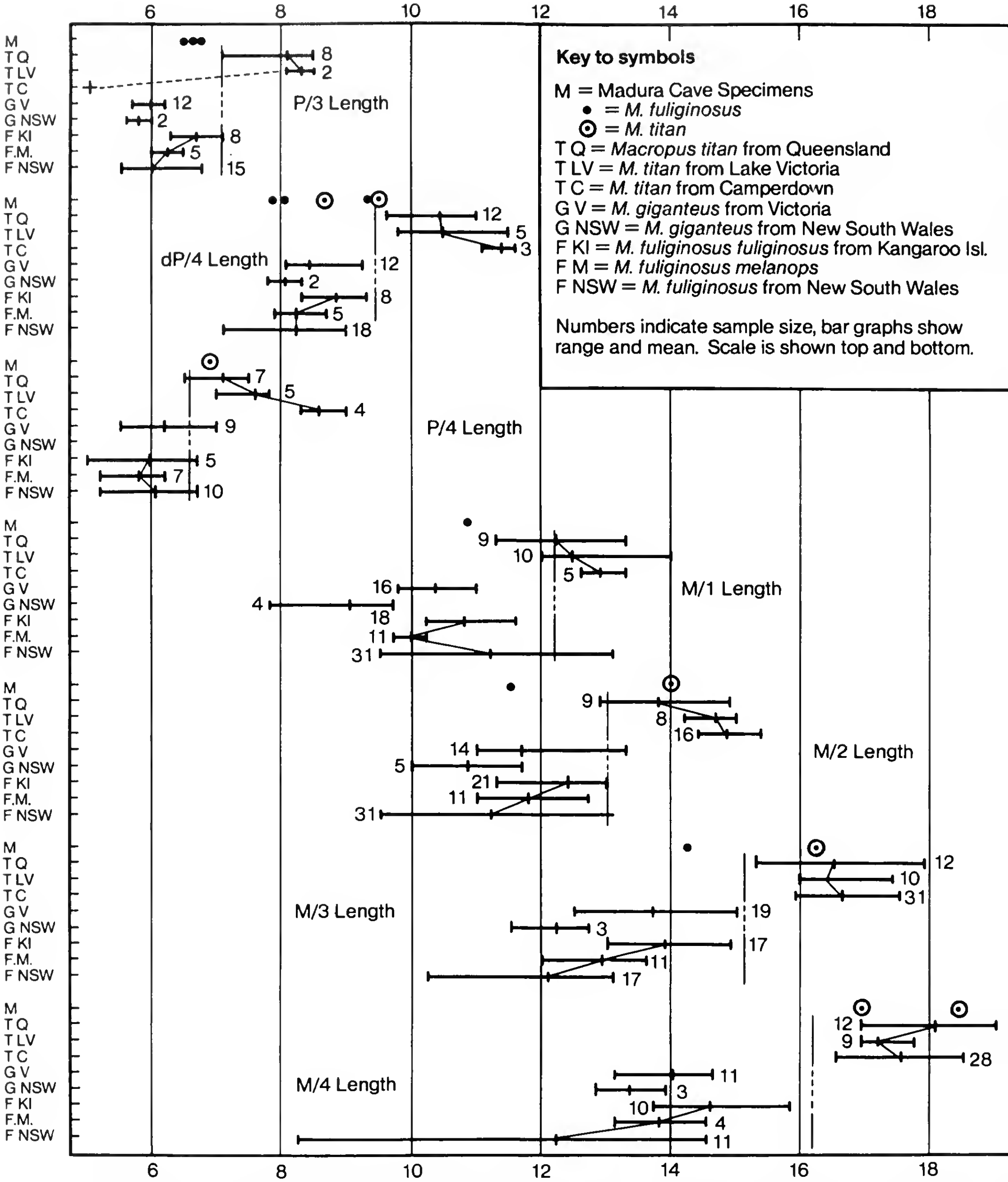
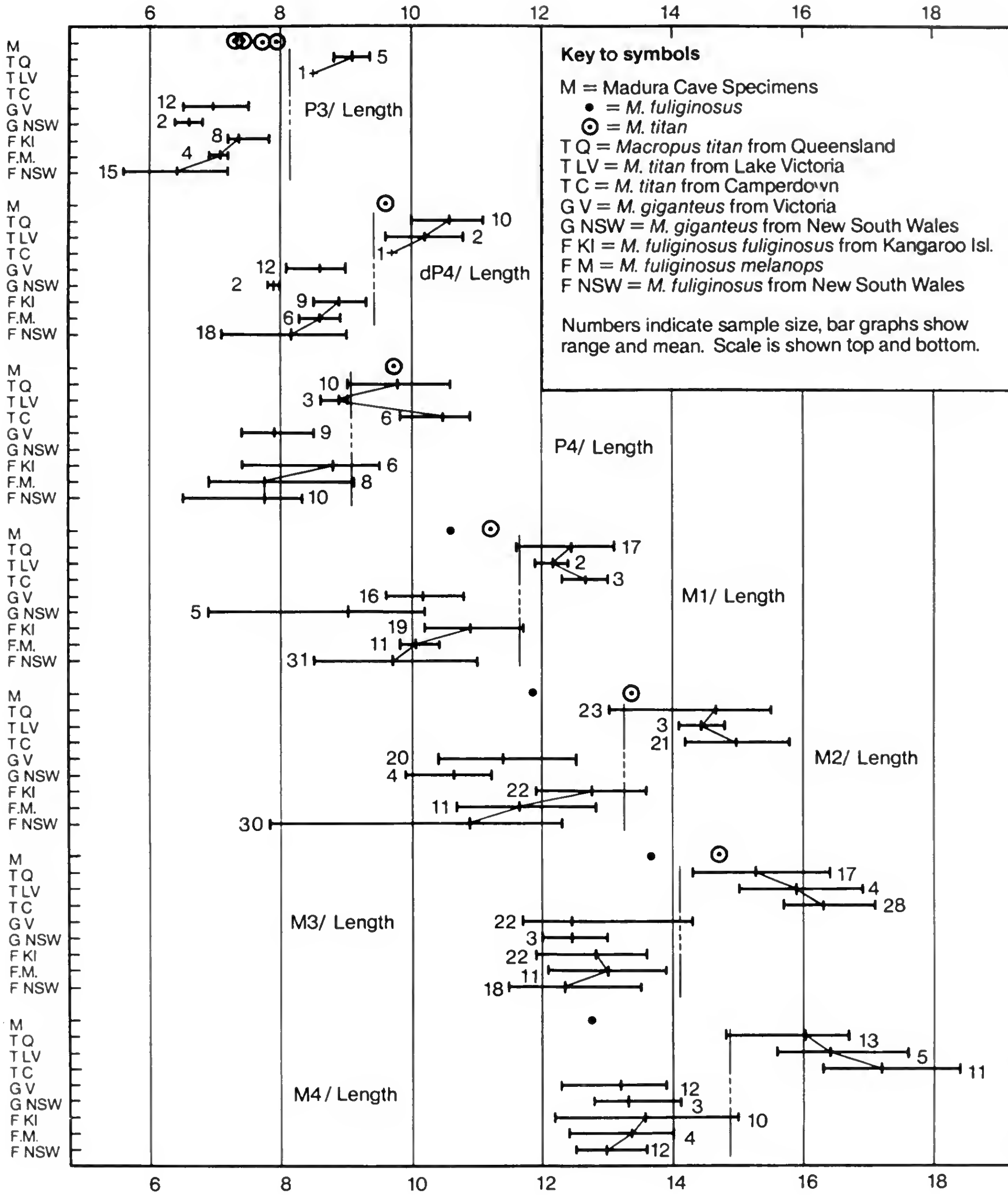


FIG. 18. Graphs showing Madura Cave specimens (M) of *Macropus* sp. in comparison with comparable teeth of *M. titan* (T), *M. giganteus* (G), and *M. fuliginosus* (F) from various localities. **Left,** comparison of lower teeth; **right,** comparison of upper teeth.

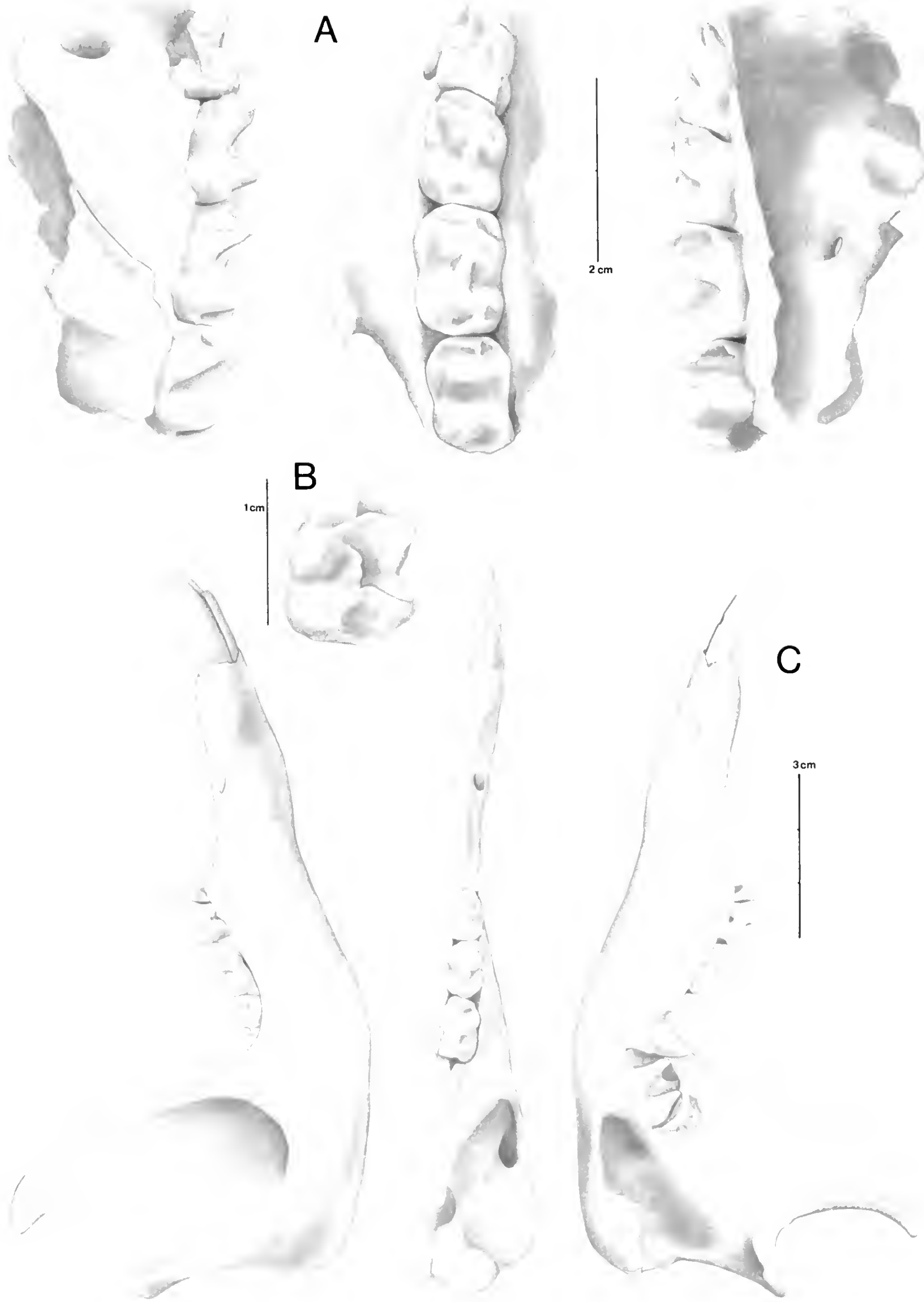
Descriptions

UPPER MOLARS—The lophs of the upper molars (fig. 19A–B) are convex anteriorly when unworn, straight when worn. The anterior cingulum extends across the full width of the tooth, and is tied by a low ridge to the base of the paracone. Lingually, it extends upward to join the protocone close to its base. A low, straight forelink connects the anterior cingulum to the protoloph and divides the cingular basin. In the unworn state, the midlink is lower than the lophs. Both lophs contribute



to the midlink, with their junction point being marked by a cleft. A labially directed spur extends from the metaloph portion at this point. The accessory cuspule on the anterolabial side of the midlink reported by Stirton (1963, p. 121) and Marshall (1973a) in *Macropus titan* is incipient in this specimen. The posterior cingulum is formed by a prominent ridge on the posterior face of the hypocone and a much smaller ridge on the base of the posterior face of the metacone.

Comparison with the upper molars of modern *Megaleia rufa* shows that the Madura Cave specimen differs in having a well-developed forelink and a procingulum which is tied to the paracone.


A
2 cm
B
1cm
C
3cm

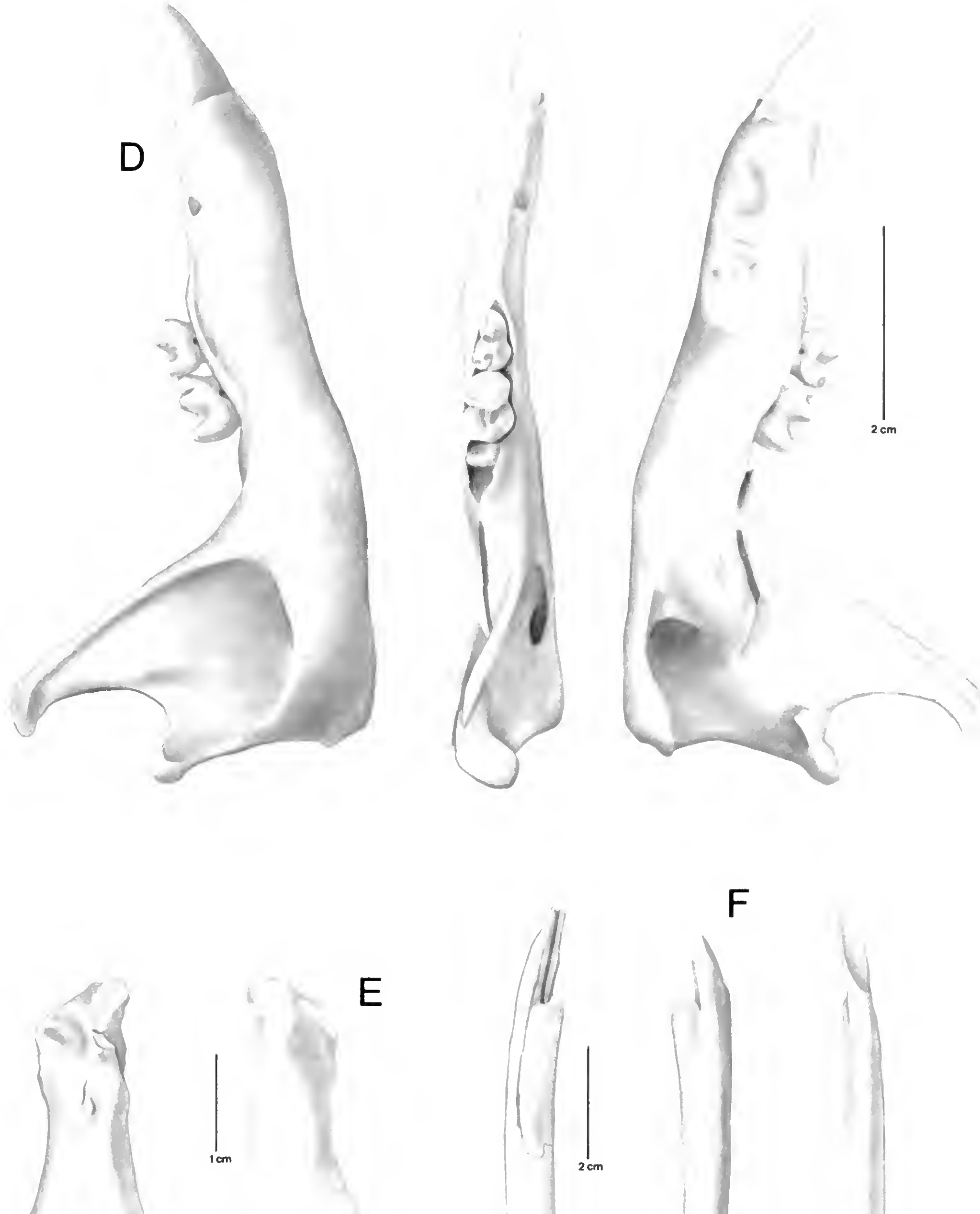


FIG. 19. *Macropus fuliginosus* from Madura Cave. **A,** TMM 41106-510, right maxilla with M^{1-4} shown in lateral (left), ventral, and medial views. **B,** PM 39128, left upper molar shown in crown view. **C,** PM 6246, right jaw ramus with I, P_4–M_3, and M_4 in its crypt shown in lateral (left), dorsal, and medial views. **D,** TMM 41106-24, right jaw ramus with I, P_3–dP_4, and M_1 in crypt shown in lateral (left), dorsal, and medial views. **E,** TMM 41106-500, left metacarpal II, a tentatively referred specimen, shown in left dorsal and ventral views. **F,** TMM 41106-501, distal half of right metatarsal V shown in left ventromedial, lateral, and dorsal views.

TABLE 15. Measurements of upper and lower dentitions of *Macropus fuliginosus* from Madura Cave.

		TMM 41106-510	TMM 41106-547	PM 39128	PM 39134
dP^4	L	...	...	...	...
	AW	...	...	...	...
	PW	...	5.3	...	...
M^1	L	10.6	...	...	...
	AW	8.5b	...	...	...
	PW	8.8b	...	...	...
M^2	L	11.9	...	...	...
	AW	9.6	...	...	...
	PW	9.5	...	...	...
M^3	L	13.6	...	...	...
	AW	10.5	...	...	...
	PW	10.1	...	...	...
M^4	L	12.7	...	...	...
	AW	9.7	...	...	...
	PW	8.2b	...	...	...
Molar	L	...	...	10.1	>9.8
	AW	...	...	7.6	7.8
	PW	...	...	7.8	...

		PM 6246	TMM 41106-23	TMM 41106-24
P_3	L	6.7	6.7	6.6
	AW	3.1	3.1	3.1
	PW	4.4	3.8	3.7
dP_4	L	9.3	8.0	7.9
	AW	5.5	4.9	4.5
	PW	6.7	5.6	5.3
M_1	L	10.8	...	...
	AW	6.8	...	...
	PW	7.4	...	...
M_2	L	11.5	...	...
	AW	7.5	...	...
	PW	6.9?	...	...
M_3	L	14.2	...	...
	AW	...	...	...
	PW	...	...	...

b = broken.

In both of these characters it is similar to modern *Macropus fuliginosus*. The posterior cingular pit is somewhat larger than is seen in specimens of *M. fuliginosus* available for comparison.

LOWER DENTITION—The P_3 (fig. 19D) is elongate with three main cusps and an anterior cuspule. The anterior cusp is laterally compressed, with a low vertical ridge on each side and a sharper ridge connecting its apex with an anterior cuspule and the posterior labial cusp. The two posterior cusps are joined to form a transverse loph.

The dP_4 (fig. 19D) is molariform. The protolophid is distinctly narrower than the hypolophid. The midlink is like that of the molars, but the forelink is incomplete even though the procingulum is large. A shallow vertical groove is present on the posterior face of the hypolophid, as in the molars.

The P_4 of PM 6246 (fig. 19C) is similar to the P_3 in morphology. It is triangular with the large anterior cusp joined to an anterior cuspule by a ridge. It differs from the P_3 in that the posterior ridge of the anterior cusp bifurcates, joining both the posterior cusps to form a posterior basin. The two posterior cusps join to form a posterior lophid. A small ridge extends anteriorly from the middle of the posterior transverse lophid into the posterior basin.

The lower molars are bilophodont and brachyhypsodont. The protolophid and hypolophid are slightly concave anteriorly when unworn and straight when worn. The procingulum projects forward and upward, and where it is joined by the forelink it is almost as high as the protolophid in an unworn tooth.

The forelink arises from the protoconid and turns sharply linguad and then anteriad to join the procingulum. The large midlink is made up of contributions from the protolophid and hypolophid. Their junction is marked by a cleft and some overlap in an unworn tooth. The lophids are parallel, in contrast to *Megaleia rufa* in which the entoconid is located posterior to the hypoconid and the protolophid and hypolophid are not parallel. A vertical groove is present on the posterior face of the hypolophid.

POSTCRANIAL SKELETON—The distal one-third of one right fifth metatarsal (TMM 41106-501; fig. 19F) is present. The distal part of the shaft is strongly curved laterally. The distal articular surface is asymmetrical with the lateral border projecting outward and backward. A median ridge is present ventrally on the posterior part of the articular surface. The transverse diameter of the distal end is 13.0 mm, which is within the size range of two modern specimens of *M. fuliginosus* (TMM M-927, 13.9 mm; TMM M-925, 12.9 mm). The corresponding measurements of two modern specimens of *Megaleia rufa* from Western Australia are 8.7 mm (TMM M-939) and 7.6 mm (TMM M-928). In addition, the distal articular surface in *M. rufa* lacks the median ridge.

A terminal phalanx of digit IV of the pes (TMM 41106-504) is tentatively referred to *M. fuliginosus*. It has the high triangular shape of the artic-

TABLE 16. Numerical data on upper dentitions of a Recent sample of *Macropus fuliginosus* from New South Wales.

		N	OR	Mean
P^3	L	15	5.6–7.2	6.42
	AW	15	3.5–4.2	3.87
	PW	15	4.7–5.7	5.08
dP^4	L	18	7.1–9.0	8.16
	AW	18	6.2–7.2	6.59
	PW	18	6.6–7.7	6.94
P^4	L	10	6.5–8.3	7.23
	AW	10	2.8–4.9	3.26
	PW	10	3.4–5.0	4.25
M^1	L	31	8.5–11.0	9.68
	AW	31	7.2–9.0	7.86
	PW	31	7.3–9.7	8.18
M^2	L	30	7.8–12.3	10.87
	AW	31	7.4–10.4	8.75
	PW	27	8.0–10.6	8.95
M^3	L	18	11.5–13.5	12.32
	AW	19	7.4–11.1	9.42
	PW	18	8.4–10.8	9.48
M^4	L	12	12.5–13.6	12.98
	AW	13	7.7–11.4	9.61
	PW	10	8.6–10.9	9.39
Diastema	L	31	51.0–68.3	57.20
M^{1-4}	L	13	34.3–51.5	42.15

TABLE 17. Numerical data on lower dentitions of a Recent sample of *Macropus fuliginosus* from New South Wales.

		N	OR	Mean
P_3	L	15	5.5–6.8	6.05
	AW	15	2.6–3.3	2.95
	PW	15	3.3–4.3	3.87
dP_4	L	18	7.1–9.0	8.22
	AW	18	4.6–5.5	4.91
	PW	18	5.4–6.3	5.70
P_4	L	10	5.2–6.7	6.06
	AW	10	2.1–3.6	2.67
	PW	10	2.6–3.9	3.26
M_1	L	29	8.4–10.8	9.73
	AW	30	5.4–7.6	6.20
	PW	28	5.6–7.3	6.46
M_2	L	31	9.5–13.1	11.20
	AW	32	6.8–8.4	7.38
	PW	28	6.2–8.2	7.21
M_3	L	17	10.2–13.1	12.08
	AW	17	7.5–9.1	8.13
	PW	17	7.0–8.7	7.70
M_4	L	11	8.2–14.5	12.22
	AW	11	7.4–9.7	8.21
	PW	9	7.0–8.5	7.56
Diastema	L	36	31.6–53.9	44.81
M_{1-4}	L	6	32.6–46.5	40.27

ulation facet and the short, broad protruding ventral base typical of macropodids. It is slightly smaller than modern specimens of *M. fuliginosus* and *Megaleia rufa* (table 18).

Discussion

All of the *Macropus* material that can be confidently assigned to *M. fuliginosus* comes from Unit 1 or from the present surface of the deposits, and thus is either modern or Holocene in age. *M. fuliginosus* is a member of the modern fauna of this region and apparently has been present throughout most of the Holocene.

Macropus titan Owen, 1838

MATERIAL

Trench 2, Unit 2, Level 2½ ft
- PM 6247, right ramus with posterior half, M_3, M_4 (fig. 20A)

Trench 3, Unit 2, Level ?
- TMM 41106-5057, labial side, left P^3

Trench 3, Unit 2, Level 4
- PM 39021, right dP^4

Trench 4, Unit 2, Level 1
- PM 38974, dP^4

Trench 4, Unit 2, Level 2
- PM 7993, right maxillary fragment with M^{1-3} (fig. 20B)
- PM 39070, left dP_4
- PM 39071, left P^3

Trench 4, Units 4–5
- PM 7994, right P^4
- PM 7995, left M_4
- PM 7998, left ramus with dP_4–M_3, P_4 in crypt (fig. 20E)
- PM 39000, left ramus with M_4 (fig. 20D)

Trench 4, Unit 7, Level 4
- PM 7992, right maxillary fragment with P^3, anterior half of dP^4 (fig. 20C)

Macropus sp. (Probably ***Macropus titan***)

Trench 2, Unit 2, Level 2½ ft
- PM 26164, tip, lower incisor
- PM 39102, phalanx

Trench 3, Unit 2, Level ? (probably 1) and Level 1

TABLE 18. Measurements of metatarsals and terminal phalanges of digits IV and V of the pes of Recent and fossil *Macropus*.

	Metatarsal 4				Metatarsal 5	Terminal phalanx, D4, articular facet		Terminal phalanx, D5, articular facet	
	Ant.-post. diam. distal end	Length	Proximal width	Distal width	Distal width	Width	Height	Width	Height
Macropus fuliginosus									
TMM M-925	23.7	171.7	28.7	23.7	...	...	...	...	...
TMM M-927	20.2	166.8	27.2	23.9	...	16.3	16.7	...	...
TMM 41106-501	...	...	...	...	12.9	...	...	...	...
TMM 41106-503	...	...	...	...	...	...	...	9.2	6.2
TMM 41106-504	...	...	...	...	...	12.0	10.8	...	...
Macropus titan									
PM 39002 A	>17.8	173.0	>27.2	>19.7	...	...	...	...	...
PM 39002 B	17.9	...	25.9	23.0	...	...	...	...	...
M. (*Megaleia*) *rufa*									
FM 98914	19.0	165.0	29.0	23.6	...	13.8	13.3	...	...
FM 44274	19.7	158.0	27.5	25.0	8.7	14.7	14.2	...	...
TMM M-928	16.5	160.0	24.6	21.2	7.6	14.0	12.7	5.9	6.2
TMM M-939	...	...	...	...	8.6	12.7	13.3	...	...
Macropus robustus									
FM 104674	15.5	125.0	22.7	20.7	...	...	...	...	...
FM 104813	...	...	...	22.8	...	...	...	...	...
FM 119818	15.7	112.0	21.3	20.0	10.7	...	...	...	...
FM 120574	16.5	134.3	24.5	22.1	11.1	...	...	...	...
TMM 41106-105	...	...	25.6	...	...	...	...	...	...

TMM 41106-103, proximal end, left humerus (fig. 21D)
PM 39060, left upper molar, probably M^4
PM 39061, left upper molar, probably M^4
PM 39062, right I^2 or I^1
PM 39067, left I^1
PM 39083, left upper molar
PM 39084, anterior one-third, lower molar
PM 39085, molar fragment
PM 39086, metaloph, right molar
PM 39149, anterior half, left dP_4 or M_1

Trench 3, Unit 2, Level 4
TMM 41106-144, left upper incisor
TMM 41106-146, thoracic vertebrae, about T-6–9
TMM 41106-147, second phalanx, digit IV, pes

Trench 3, Unit 3, Level ? (probably 1)
TMM 41106-45, tip, left lower incisor

Trench 4, Unit 2, Level 1
PM 7982, fragment, upper incisor
PM 7985, anterior half, right lower molar
PM 7988, terminal phalanx, digit III, manus
PM 7989, terminal phalanx
PM 39124, second phalanx, digit V, pes
PM 39145, molar fragment

Trench 4, Unit 2, Level 2
PM 39055, left I^3
PM 39056, right I^1
PM 39073, broken left upper molar
PM 39074, broken left lower molar
PM 39075, broken molar
PM 39076, molar fragment
PM 39088, terminal phalanx, manus (or possibly of pes of a smaller form)

Trench 4, Unit 2, Level 3
PM 39093, anterior one-fourth, right lower molar

Trench 4, Units 4–5
PM 39001, portion of midshaft, right tibia
PM 39002A–B, two right fourth metatarsals (fig. 21A–C)
PM 39092, anterior half, left lower molar
PM 39097, posterior half, right lower molar

Descriptions

UPPER DENTITION—The P^3 is a triangular tooth with the labial blade interrupted by a shallow notch (fig. 20C). A posterior lingual cusp is joined to the

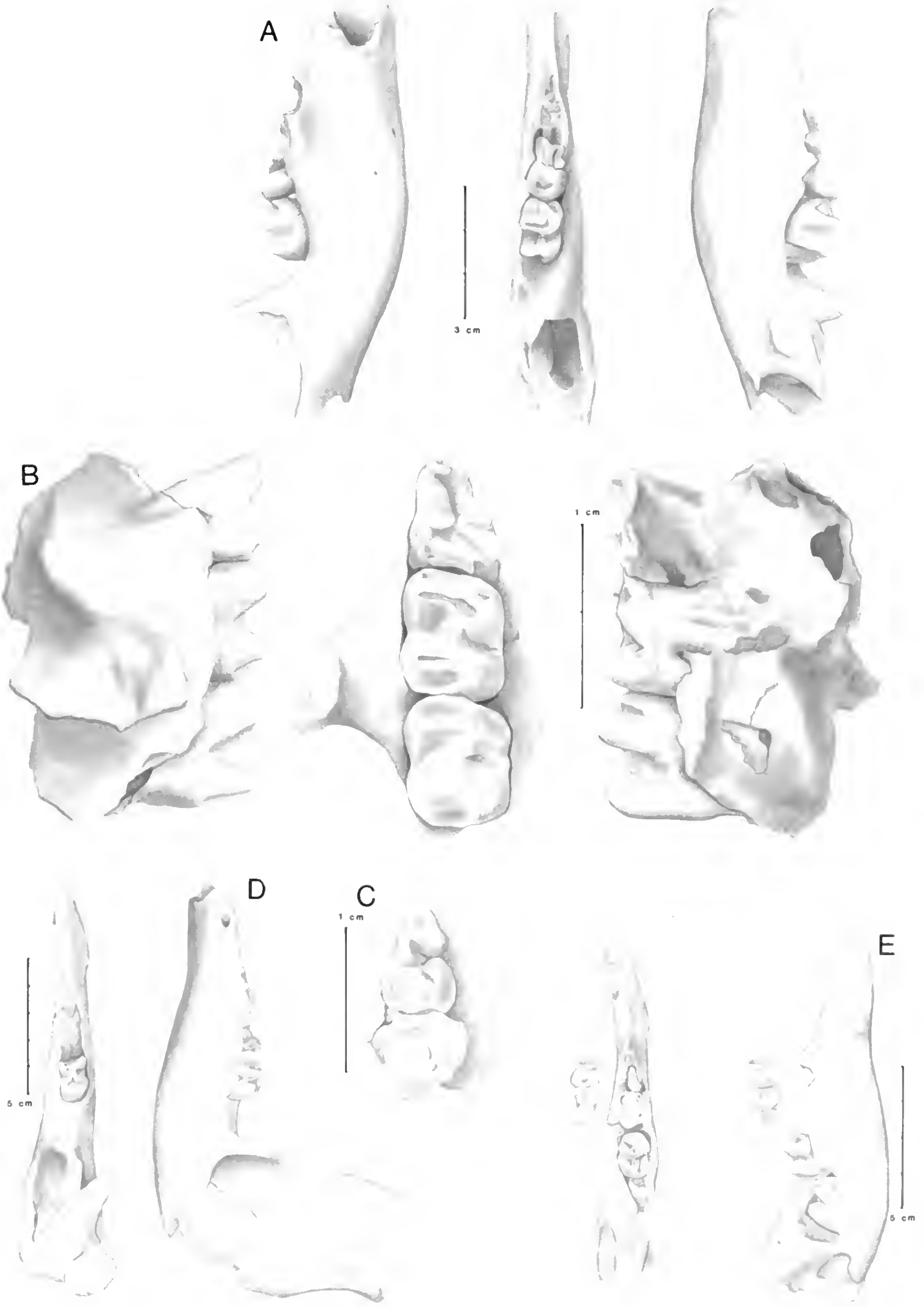


FIG. 20. *Macropus titan* from Madura Cave. **A,** PM 6247, right ramus fragment with part of M_3 and M_4 shown in lateral (left), dorsal, and medial views; **B,** PM 7993, right maxillary fragment with M^{1-3} shown in lateral (left), ventral, and medial views; **C,** PM 7992, right maxillary fragment with P^3 and part of dP^4 shown in ventral view; **D,** PM 39000, left ramus with M_4 shown in dorsal and lateral views; **E,** PM 7998, left ramus with dP_4–M_3 and P_4 in crypt shown in dorsal and medial views.

Table 19. Measurements of upper dentitions of *Macropus titan* from Madura Cave.

		TMM 41106-5057	PM 7994	PM 7992	PM 38974	PM 39021	PM 39060	PM 39061	PM 7993	PM 39083
P^3	L	7.7	...	7.3	...	...	...	...	...	...
	AW	...	...	3.5	...	...	...	...	...	...
	PW	...	...	4.9	...	...	...	...	...	...
dP^4	L	...	...	...	8.0	9.6	...	...	...	...
	AW	...	...	5.5	4.1	$\geq$6.1	...	...	...	...
	PW	...	...	...	5.4	7.1	...	...	...	...
P^4	L	...	9.7	...	...	...	...	...	...	...
	AW	...	3.9	...	...	...	...	...	...	...
	PW	...	5.4	...	...	...	...	...	...	...
M^1	L	...	...	...	...	...	...	...	11.2	...
	AW	...	...	...	...	...	...	...	...	...
	PW	...	...	...	...	...	...	...	...	...
M^2	L	...	...	...	...	...	...	...	12.9	...
	AW	...	...	...	...	...	...	...	11.6	...
	PW	...	...	...	...	...	...	...	11.8	...
M^3	L	...	...	...	...	...	...	12.7	14.7	...
	AW	...	...	...	...	...	...	9.5	11.8	...
	PW	...	...	...	...	...	...	9.6	11.6	...
M^4	L	...	...	...	...	...	>11.1	...	...	...
	AW	...	...	...	...	...	>9.0	...	...	...
	PW	...	...	...	...	...	>7.9	...	...	...
Molar	L	...	...	...	...	...	...	...	...	14.7
	AW	...	...	...	...	...	...	...	...	9.6
	PW	...	...	...	...	...	...	...	...	8.9

posterolabial cusp just anterior to its apex by a transverse ridge, and at its posterior end by a low ridge to form a small posterior basin. A small anterior lingual cingular cusp is present, but is not joined to the posterior one.

The dP^4 is a molariform tooth with a prominent procingulum that is connected to the paracone by a sharp ridge. Marshall (1973a) states that this feature, which is not present in the molars, is typical of the dP^4 of *Macropus titan* of the Lake Victoria sample. The small interloph cuspule on the lingual side of the tooth observed by Marshall (1973a) in a Lake Victoria specimen is not present on the Madura Cave specimens.

The upper molars (fig. 20B) are virtually identical to those of *Macropus fuliginosus*. The lophs are high and convex anteriorly when unworn, with sides that are straight but converge toward the crown. The procingulum extends across the complete breadth of the tooth. It is joined to the protoloph by the forelink, which is located slightly lingual to the midline of the tooth, but it is separated from the paracone and protocone by clefts. The midlink is large, with its major part from the protocone and a smaller contribution from the middle part of the metaloph. The midlink does not bow labially, and there are no accessory cuspules associated with the midlink or the posterolabial face of the protoloph, both of which were reported by Marshall (1973a) for some specimens of *M. titan* from Lake Victoria, the Camperdown district of Victoria, and the Darling Downs of Queensland. The bases of the protocone and hypocone of PM 7993 have small cuspules in the lingual side of the median valley. The postcingulum is large and is formed primarily by a ridge from the hypocone. It is joined to the base of the metacone to form a posterior basin. There is no vertical groove on its posterior face.

Lower Dentition—The P_4 is a compressed bladelike tooth with two major cusps and a lower posterolingual cusp joined to the main posterior cusp by a ridge (fig. 20E). This agrees with the description of *M. titan* given by Marshall (1973a).

The lower molars are bilophodont, brachyhypsodont teeth (fig. 20A,E). The lophids are slightly concave anteriorly when unworn and straight when worn. The procingulum projects forward and upward from the base of the tooth. The forelink arises from the protocone, turns sharply linguad, and

TABLE 19. *Extended.*

PM 39084	PM 39086	PM 39092	PM 39097	PM 39071
...	...	...	...	7.3
...	...	...	...	4.4
...	...	...	...	5.4
...	...	...	...	...
...	...	...	...	...
...	...	...	...	...
...	...	...	...	...
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...	...	...	...	...
...	...	...	...	...
...	...	...	...	...
>9.78	...	9.4	...	...
...	8.5	...	7.5	...

then turns anteriad to join the procingulum. In an unworn tooth, the central part of the procingulum where it joins the forelink is as high as the protolophid.

The protolophid and hypolophid contribute to the large midlink, and their junction is marked by a cleft. The protolophid and hypolophid are parallel, in contrast to *Megaleia rufa*, in which the entoconid is located posterior to the hypoconid and the hypolophid and protolophid are not parallel. A vertical groove is located on the posterior surface of the hypolophid.

A cuspule is present in the lingual side of the valley in PM 7998 (fig. 20E), as is reported for *Macropus titan* by Marshall (1973a). In PM 6247 (fig. 20A) and PM 39000 (fig. 20D), the median valley and the lingual part of the procingular valley contain cement.

POSTCRANIAL SKELETON—The proximal part of a left humerus (TMM 41106-103; fig. 21B) from Madura Cave is the same size as the comparable portion of the humeri of modern *Macropus fuliginosus* (TMM M-925, M-927) and *Megaleia rufa* (98914, TMM M-928). The morphology differs only in the shape of the head; the articular surface of the head of the Madura Cave specimen is oval with an extension toward the greater tuberosity, while the articular surfaces of the modern specimens are almost circular.

The fourth metatarsal is represented by a complete specimen (PM 39002A; fig. 21A) and the proximal half and distal articular surface of another (PM 39002B; fig. 21B–C); both are from the left foot. PM 39002A lacks the posterior part of the proximal articular surface. The anterior part of the articular surface is smoothly concave. The proximal articular surface of PM 39002B is also smooth, but is more deeply concave medially. Both specimens have a prominent ridge on the medial side of the anterior surface of the shaft that extends from 2 cm below the proximal end to the middle of the shaft. This feature is present in two modern specimens of *Macropus fuliginosus* (TMM M-925, M-927; fig. 21I) but not on our specimens of *Megaleia rufa* (98914, TMM M-928, M-939; fig. 21J), and is small or absent on specimens of modern *Macropus robustus* (FM 104674, 104813, 119818 [fig. 21K], 120574).

Both of the Madura Cave metatarsals lack the prominent rugose bulge on the proximal part of the posterior face that is seen in *Megaleia rufa*. *Macropus fuliginosus* also lacks this bulge. The condition in *Macropus robustus* is intermediate. The Madura Cave specimens are essentially the same size as modern specimens of *Macropus fuliginosus* (including those from Western Australia) and *Megaleia rufa*, and are 25% larger than modern specimens of *Macropus robustus* (table 18).

Discussion

All previous studies of Pleistocene *Macropus* have concluded that *Macropus titan* is morphologically indistinguishable from *M. giganteus* and *M. fuliginosus* and differs from them only in its 25%–30% larger size (Owen, 1874; Lydekker, 1887; Tedford, 1967; Marshall, 1973a; Marcus, 1976; Bartholomai, 1975; Marshall & Corruccini, 1978). All of the *Macropus* material from Unit 1, which is Holocene in age, can be assigned to *M. fuliginosus* on the basis of both size and morphology. The *Macropus* material from Units 2–7, which is of Pleistocene age, presents a somewhat confused picture. With the exception of a dP_4 (PM 7998), all the lower teeth of *Macropus* from the lower units whose position in the jaw can be determined fall within the size range of samples of *M. titan* from Lake Victoria, the Eastern Darling Downs,

TABLE 20. Measurements of lower dentitions of *Macropus titan* from Madura Cave.

		PM 7998	PM 39070	PM 6247	PM 7995	PM 39092	PM 39084	PM 39074	PM 7985	PM 39075	PM 39093	PM 39097
dP_4	L	9.5	8.7	...	...	...	...	...	...	...	...	...
	AW	>5.8	5.3	...	...	...	...	...	...	...	...	...
	PW	7.4	5.7	...	...	...	...	...	...	...	...	...
P_4	L	6.9	...	...	...	...	...	...	...	...	...	...
	AW	2.3	...	...	...	...	...	...	...	...	...	...
	PW	3.7	...	...	...	...	...	...	...	...	...	...
M_1	L	>10.0	...	...	...	...	...	...	...	...	...	...
	AW	...	...	...	...	...	...	...	...	...	...	...
	PW	...	...	...	...	...	...	...	...	...	...	...
M_2	L	14.0	...	...	...	...	...	...	...	...	...	...
	AW	9.0	...	...	...	...	...	...	...	...	...	...
	PW	8.6	...	...	...	...	...	...	...	...	...	...
M_3	L	16.2	...	...	...	...	...	...	...	...	...	...
	AW	...	...	...	...	...	...	...	...	...	...	...
	PW	...	...	...	...	...	...	...	...	...	...	...
M_4	L	...	...	16.9	18.4	...	...	...	...	...	...	...
	AW	...	...	9.7	10.5	...	...	...	...	...	...	...
	PW	...	...	9.5	9.2	...	...	...	...	...	...	...
Molar	L	...	...	...	...	...	...	...	...	...	...	...
	AW	...	...	...	...	>10.7	>9.8	>9.0	9.3	9.2	9.4	...
	PW	...	...	...	...	...	...	>7.3	...	>8.4	...	7.5

and the Camperdown area of Victoria reported by Marshall (1973a). The dP_4 is slightly below the size range reported by Marshall (1973a), but is larger than the dP_4s of several samples of *M. giganteus* and *M. fuliginosus* from various parts of Australia (fig. 18A). The other dental dimensions are closer to those of *M. titan* than to those of *M. giganteus* and *M. fuliginosus*. With the exception of four P^3s (TMM 41106-5057; PM 38974, 39071, 7992) and an M^1 (PM 50847), those upper teeth from Units 2–7 whose positions in the jaw can be determined fall within, but usually at the lower ends of, the observed size ranges of samples of *M. titan* from Lake Victoria, the Eastern Darling Downs, and the Camperdown area of Victoria reported by Marshall (1973a) and Bartholomai (1975) (fig. 18B). The P^3s are shorter than those of *M. titan* and fall in the upper part of the range of several samples of *M. giganteus* and *M. fuliginosus* (fig. 18B). The postcranial material from Units 2–7 is the same size as that of modern specimens of *M. fuliginosus*.

Marshall (1973a) pointed out that the size of *Macropus titan* increases from Queensland to Victoria parallel to the size change in *M. giganteus* and *M. fuliginosus*. This suggested the possibility of a Bergmann cline, but Marshall believed the data to be inadequate to demonstrate this. The somewhat small size of some of the Madura Cave specimens might cause one to speculate about a possible east-west cline for these taxa across the Nullarbor Plain, which would not be a Bergmann response. Such speculation is premature in any case, for there is inadequate data from the Madura Cave *M. titan* and *M. fuliginosus* samples to show any size trends. In addition, the *M. titan* sample from Units 2–7 in Madura Cave spans a significant period of time and cannot be treated as a single coherent sample; it is also of inadequate size to show change through time.

Macropus robustus Gould, 1840

MATERIAL

Trench 3, Unit 2, Level ? (probably 1)
- PM 39058, left I^3 (fig. 21H, right)
- PM 39057, left I^2 (fig. 21H, left)
- TMM 41106-105, proximal left metatarsal IV (fig. 21E)

Trench 4, Units 4–5
- PM 7991, proximal one-fourth, right ulna, lacking epiphysis of olecranon process and rim of articular facets (fig. 21F)

COMPARATIVE MATERIAL

Macropus robustus cervinus

Cape Range, Western Australia
- FM 104670
- FM 104671
- FM 104674
- FM 104676
- FM 104687
- FM 104690
- FM 104692
- FM 104694
- FM 104701

Macropus robustus

National Zoological Park
- FM 104813

Macropus robustus antilopinus

Kimberly District, Western Australia
- FM 119818 (fig. 21G,K)
- FM 120574

Descriptions

UPPER DENTITION—The left I^3 (PM 39058; fig. 21H) is a long tooth with one groove separating a stout, narrow, anterior lobe from a posteriorly flaring but thinner posterior lobe. This morphology is similar to that of *Macropus robustus* and *Megaleia rufa*, but in the latter the tooth is much smaller. The I^3 of *Macropus fuliginosus* differs from that of the Madura Cave specimen in having two grooves rather than only one.

The I^2 (fig. 21H) resembles that of modern *M. robustus* both in size and in having no groove on its outer face.

POSTCRANIAL SKELETON—The fourth metatarsal fragment (fig. 21D) appears to be referable to *Macropus robustus* on the basis of size (table 18) and morphology. Seen from the front, the articular surface is smoothly concave and the concavity is shallow as in modern *M. robustus*.

The ulna (fig. 21F) is slightly smaller and more delicate than any of our modern comparative specimens (fig. 21G). The frayed edges of the articulation facets make detailed comparison difficult. The olecranon process is small but robust, and the facet for articulation with the radius is very small. The specimen is in the same general size range as the modern specimens of *M. robustus*, and the olecranon process is about 25% shorter than that of the ulna of *Macropus fuliginosus* (fig. 21G) and *Megaleia rufa*.

Discussion

Macropus robustus is widely distributed in Australia where suitable habitats in the form of rocky outcrops occur (Frith & Calaby, 1969). The flat topography of the Nullarbor Plain does not appear to provide suitable habitats for *M. robustus*. However, the scarp that separates the Hampton Tableland from the Roe Plain may have provided small areas of rocky outcrops suitable for *M. robustus*, as well as for *Petrogale*.

Incertae Sedis among the Large Macropodids

Specimens which we cannot identify with certainty, but which probably are referable to one or another of the large macropods are included.

Trench 3, Unit 2, Level 1
- TMM 41106-109–111, one subterminal phalange and two terminal phalanges, probably from the manus of a large species of *Macropus*
- TMM 41106-186, root and labial side, I^1 or I^2, from a large species of *Macropus*
- PM 39156–39157, two terminal phalanges, possibly from the manus of a *Macropus* species (had been associated with TMM 41106-103–111)

Trench 3, Unit 3, Level ?, probably 1
- PM 39082, terminal phalange

Trench 4, Unit 1, Level 1
- PM 39108, molar tooth fragment from between lophs
- PM 39131, macropodid right I^1 or I^2
- PM 39140, macropodid partial right I^2 or I^3

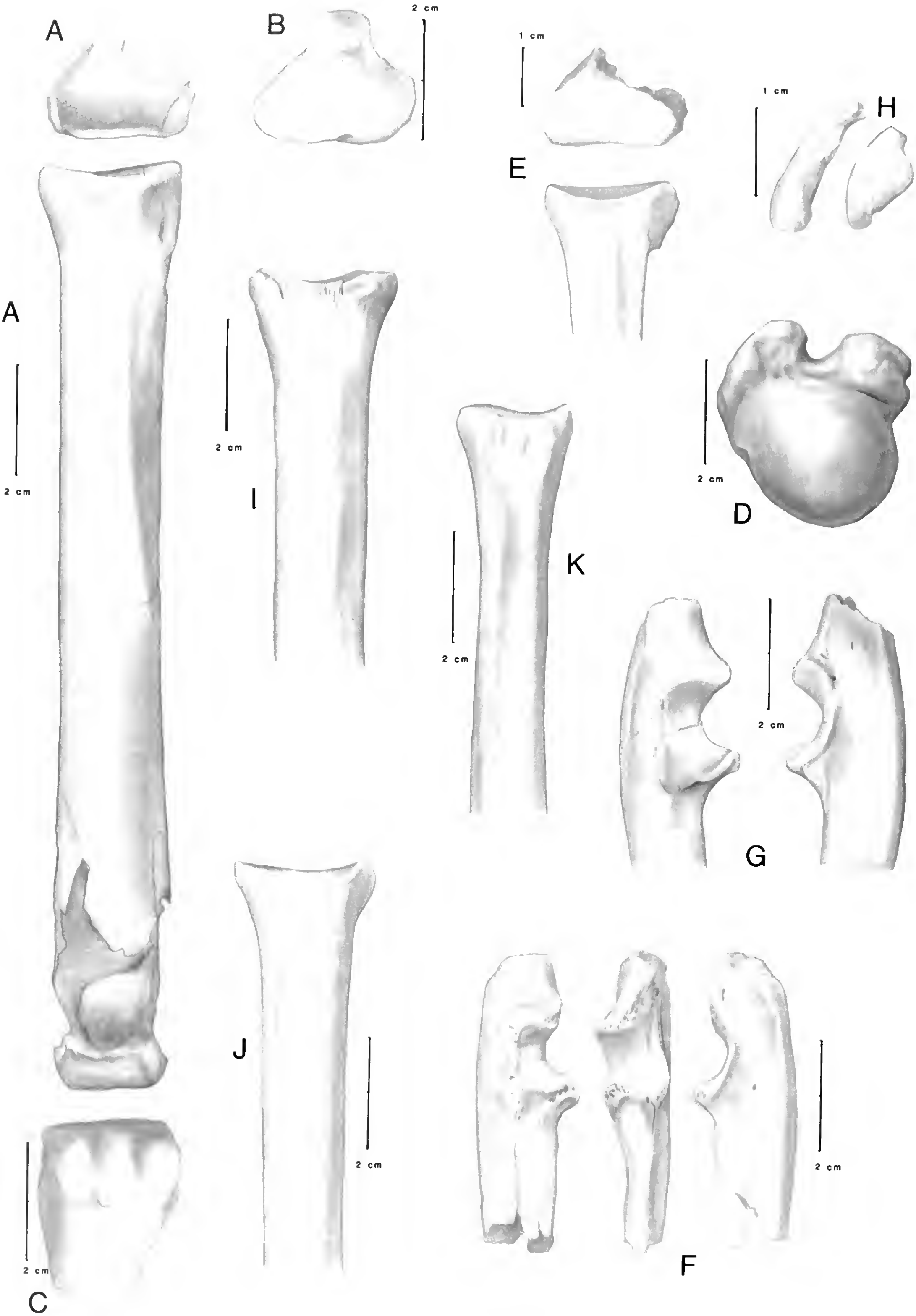
Trench 4, Unit 2, Level 1
- TMM 41106-300–303, four macropodine toe bones
- PM 7990, partial vertebra, either a posterior thoracic or anterior lumbar, consisting of centrum and neural arch

Trench 4, Unit 2, Level 2
- PM 39069, right M^4, similar to that of *Thylogale* and *Macropus irma*
- PM 39087, terminal phalange

Trench 4, Unit 2, Level 3
- PM 7996, distal seven-eighths, large second phalange, digit IV, pes, probably from a large species of *Macropus*

Trench 4, Unit 2, Level 4
- PM 38999, proximal epiphysis, tibia, may be from a large *Protemnodon* or *Macropus*, or possibly a small diprotodont

Trench 4, Units 4–5
- PM 39098, partial right upper molar


A
B
2 cm
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Assessment of the Marsupial Segment of the Fauna

Fossil remains of marsupials from Madura Cave provide a good picture of Australian marsupial faunas during the late Pleistocene and the early Holocene, and the faunal changes that took place through that span of time.

The late Pleistocene fauna shows a higher taxonomic diversity than either that of the early Holocene or the modern historic fauna of the Nullarbor Plain. This diversity is characteristic of Pleistocene faunas in most parts of the world. A total of 37 Pleistocene and 24 early Holocene and modern historic taxa is recorded from the Nullarbor Plain (table 21). Of the 37 Pleistocene taxa, all but one (*Megaleia rufa*) were recovered from Madura Cave. It is more difficult to determine how many species were living on the Nullarbor Plain in historic times because of inadequate surveys of the mammalian fauna prior to the habitat changes brought about by domestic and other introduced animals. Brooker (1977) observed only four species of marsupials during his work in this area, but listed 10 species known to have occurred there prior to 1940. Examination of distribution maps by Shortridge (1909) and Marlow (1962) suggests that there may have been as many as 15 species of marsupials on the Nullarbor Plain prior to the beginning of European influence. The change in diversity between the Pleistocene and historic times is the result not only of extinction of some species (4 completely extinct plus 2 extinct on the mainland), but also of the extirpation of about 16 extant species.

In addition to the increased diversity, the Pleistocene marsupial assemblage from Madura Cave contains a number of species that today are allopatric and seemingly ecologically incompatible. These types of associations, first recognized by Hibbard (1960), and termed "disharmonious" by Semken (1974), are characteristic of late Pleistocene faunas wherever they have been adequately studied. The presence of these disharmonious associations in Australian Pleistocene faunas has been summarized by Lundelius (1983). Seventy-three pairs of species that are now allopatric were found in Units 2–7 of Madura Cave. Examples of such pairs of formerly sympatric, but now allopatric, species are: *Phascolarctos cinereus* and *Dasycercus cristicauda*, *P. c.* and *Dasyuroides byrnei*, *P. c.* and *Caloprymnus campestris*; *Antechinus flavipes* and *Dasycercus cristicauda*, *A. f.* and *Dasyuroides byrnei*. Forty pairs of presently allopatric species were found in Unit 1. It should be pointed out that a substantial number of the disharmonious pairs involve *Sarcophilus harrisi* and *Thylacinus cynocephalus*, whose absence from the historical fauna of the mainland may have more to do with the introduction of the dingo than with the general post-Pleistocene climatic change (Archer, 1974). If the disharmonious pairs involving these two taxa are subtracted the numbers fall to 33 for the older units and 22 for Unit 1.

There is a major change in the marsupial fauna from Unit 2 (dated at 15,600 B.P. at its top) to Unit 1 (dated at 7470 B.P. at its top, but separated from Unit 2 by an erosion surface). Milham and Thompson (1976) give dates of present to ~7000 B.P. for the same unit in the South Tunnel. The faunal changes include the disappearance of most of the extinct taxa, including *Sthenurus*, *Protemnodon*, *Macropus titan*, possibly *Thylacoleo*, and the two extant taxa *Antechinus flavipes* and *Phascolarctos cinereus*.

Milham and Thompson (1976) have reported the presence of *Protemnodon* sp., *Sthenurus* sp., and *Phascolarctos* sp. from the upper unit in the South Tunnel. The results of nitrogen and fluorine analyses on dentine of *Protemnodon* teeth from this unit reported by them suggest that the material of this taxon and probably that of *Sthenurus* and *Phascolarctos* is derived from an older deposit. If this is so, the radiocarbon dates of 3450 to 7880

Opposite Page:

FIG. 21. Various specimens of *Macropus*, some from Madura Cave, some from the modern species from other localities: cf. *Macropus titan* from Madura Cave: **A**, PM 39002A, right metatarsal IV shown in proximal and dorsal (anterior) views; **B**, PM 39002B, proximal half of right metatarsal IV shown in proximal view; **C**, PM 39002B, distal end of right metatarsal IV shown in ventral (posterior) view (fragments in B and C are associated parts of the same bone); **D**, TMM 41106-103, proximal end of left humerus shown in proximal view. *Macropus robustus* from Madura Cave: **E**, TMM 41106-105, portion of metatarsal IV shown in proximal and dorsal (anterior) views; **F**, PM 7991, proximal end of right ulna lacking olecranon epiphysis shown in medial (left), anterior (dorsal), and lateral views; **H**, PM 39057, left I^2 shown in labial view and PM 39058, left I^3 shown in labial view. *Macropus robustus antilopinus* from Kimberly District, Western Australia: **G**, FM 119818, right ulna shown in medial and lateral views; **K**, FM 119818, left metatarsal IV shown in anterior view. Modern *Macropus fuliginosus*: **I**, TMM M-927, right metatarsal IV shown in anterior view. Modern *M.* (*Megaleia*) *rufa*: **J**, TMM M-939, right metatarsal IV shown in anterior view.

Table 21. The marsupial component of the Madura Cave fauna listed by taxon and stratigraphic occurrence, compared with the fauna reported by Milham and Thompson (1976) and the Recent fauna of the Nullarbor as reported by Brooker (1977) and others.

	Modern			Holocene, Madura Cave		Pleistocene, Madura Cave, Lundelius & Turnbull		
Taxon	Brooker 1977	Prior to 1940 (Brooker)	Survey of Literature	Milham & Thompson,* 3400–7900 B.P.	Lundelius & Turnbull, Unit 1, top 1 ft., 7500 B.P.	Units 2–3, 16,000–22,000 B.P.	Units 4–5 22,200 B.P.	Units 6–7, 22,400–38,000 B.P.
cf. *Planigale*	...	...	...	...	...	X	X	x
Sminthopsis crassicaudata	+	...	+	...	X	X	x	x
S. murina	...	...	...	...	X	X	x	x
Antechinomys spenceri	...	+	+	...	x	X	X	x
Antechinus flavipes	...	...	...	...	...	X	X	x
Phascogale calura	...	...	...	...	X	X	X	...
P. tapoatafa	...	...	...	...	x	x	...	...
cf. *Parantechinus apicalis*	...	...	...	...	x	...	...	...
Dasycercus cristacauda	...	...	+	...	X	X	X	x
Dasyuroides byrnei	...	...	...	...	x	X	X	X
Dasyurus geoffroyi	...	+	+	...	x	X	X	X
Sarcophilus harrisi	...	...	...	+	x	X	...	...
Thylacinus cynocephalus	...	...	...	+	...	x	...	...
Myrmecobius fasciatus	...	...	...	...	x	...	...	...
Thylacoleo sp.	...	...	...	...	x†	...	...	...
Perameles bougainvillei	...	+	+	...	X	X	X	X
Isoodon obesulus	...	...	...	...	X	X	X	x
Chaeropus ecaudatus	...	...	...	...	x	x	x	x
Macrotis lagotis	...	+	+	...	X	X	X	X
Lasiorhinus cf. *latifrons*	+	+	+	+	...	X	x	x
Phascolarctos cinereus	...	...	...	+†	...	x	...	...
Trichosurus vulpecula	...	...	?	...	...	x	...	...
Pseudocheirus peregrinus	...	...	?	...	...	x	...	...
Cercartetus concinnus	...	...	+	...	...	X	x	x
Potorous platyops	...	...	?	...	x	X	X	x
Caloprymnus campestris	...	...	?	...	X	X	X	X
Bettongia lesueur	...	+	+	...	X	X	...	X
B. penicillata	...	+	+	...	X	X	X	...
Sthenurus sp.	...	...	...	+† and *S. gilli*	...	x	x	...

TABLE 21. *Continued.*

Taxon	Modern: Brooker 1977	Modern: Prior to 1940 (Brooker)	Modern: Survey of Literature	Holocene, Madura Cave: Milham & Thompson,* 3400–7900 B.P.	Holocene, Madura Cave: Lundelius & Turnbull, Unit 1, top 1 ft., 7500 B.P.	Pleistocene, Madura Cave, Lundelius & Turnbull: Units 2–3, 16,000–22,000 B.P.	Pleistocene, Madura Cave, Lundelius & Turnbull: Units 4–5 22,200 B.P.	Pleistocene, Madura Cave, Lundelius & Turnbull: Units 6–7, 22,400–38,000 B.P.
Lagorchestes hirsutus	. . .	. . .	?+	. . .	X	X	x	. . .
Lagostrophus fasciatus	. . .	. . .	?+	. . .	X	x	. . .	. . .
Onychogalea lunata	. . .	+	+	+	X	X	. . .	. . .
Protemnodon sp.	. . .	. . .	. . .	+†	. . .	x	. . .	. . .
Petrogale sp.	. . .	. . .	?	. . .	x	x	. . .	. . .
Macropus fuliginosus	+	+	+	+	X	. . .	. . .	. . .
M. titan	. . .	. . .	. . .	. . .	. . .	X	X	x
M. robustus	. . .	. . .	?	. . .	. . .	x	x	. . .
Megaleia rufa	+	+	+	+	. . .	. . .	. . .	. . .
Totals	4	10	15 (possibly 21)	10 (+ 22 others)	25	33	22	18

* Milham and Thompson (1976) report the presence of "about forty native species of mammals," but they only list 10 by name. † Specimens appear to be reworked from older units.

. . . = Not recorded; + = recorded; x = recorded by few specimens; X = recorded by many specimens; ? = literature reference uncertain.

B.P. from these deposits do not apply to these taxa. *Thylacoleo* is present in Unit 1. If this specimen was in primary context, then it is the youngest known specimen of this taxon. However, as discussed in Part III (Lundelius & Turnbull, 1978, p. 91), the matrix adhering to the specimen suggests that it may have been eroded from older deposits near the front of the cave and redeposited farther in.

Two other groups of taxa that no longer occur on the Nullarbor Plain are found in Unit 1. One group includes *Parantechinus apicalis, Sminthopsis murina, Phascogale calura, Phascogale tapoatafa*, and *Potorous platyops*, which are found today in association with *Antechinus flavipes* and *Phascolarctos cinereus* in areas of eastern and/or southwestern Australia with climates that are more humid than the present-day climate in the region of Madura Cave. The other group, which consists of *Dasyuroides byrnei, Myrmecobius fasciatus*, and *Caloprymnus campestris*, is found today in areas approximately as arid as that of Madura Cave. The presence of the first group of taxa indicates a climate more humid than the present one. This agrees with information from other parts of Australia. Although the general pattern of climatic change through this period is a shift to drier conditions, the details are not clear. The association in the Pleistocene and early Holocene faunas of members of these two groups of species with seemingly disparate environmental requirements forms the disharmonious associations mentioned above. Disharmonious faunas in North America have been interpreted as indicating more equable climates during the Pleistocene (Hibbard, 1960). The same probably is true for Australia (Lundelius, 1983). The lower number of disharmonious associations in Unit 1 (~40 vs. ~73 in the older units) indicates a change to less equable conditions after approximately 15,000 B.P.

Planigale sp. indet. also disappears at the end of the Pleistocene sequence in Madura Cave. However, we cannot categorize this species as readily as the groups discussed above, for too little is known about its habitat requirements to permit a generalization about its environmental implications. Archer (1976) lists two other occurrences of *Planigale* sp. indet. The closest to Madura Cave is a modern specimen from the eastern edge of the Nullarbor Plain, in much the same sort of arid environment. The other occurrence is from the Hammersly Range in the Pilbara, but habitat data are not given. *Planigale maculata* appears to be limited to wetter climates (Taylor et al., 1982). Andrews and Settle (1982) report that *P. gilesi* is restricted to riverine floodplains and overflows. Denny (1982) states that most planigales are found close to water, but that *P. tenuirostris* can be found in drier habitats. Read (1982) speculated that the drifting home ranges of *P. tenuirostris* are an adaptation to an arid environment.

There are few changes in morphology or size in those taxa that persist into the Holocene or Recent. One change which did occur is the small increase in size of *Dasycercus cristicauda* from Unit 2 to Unit 1. We suggested (Lundelius & Turnbull, 1978, p. 64) that this represents an instance of character release related to the disappearance of the morphologically similar and closely related *Dasyuroides byrnei* after about 16,000 B.P., which may have allowed *Dasycercus cristicauda* to broaden its niche.

The absence of *Megaleia rufa* from the Madura Cave deposits is puzzling, although it is not common anywhere as a fossil. The species is present today on the Nullarbor Plain. It is found in the late Pleistocene fauna from Lake Menindee (Tedford, 1967), where it is associated with many of the same species that occur in the Madura Cave fauna. It is not recorded as having been found in the late Pleistocene fauna of the Lake Victoria region, which has produced many of the same species as Lake Menindee and Madura Cave (Marshall, 1973b). It is present in the late Pleistocene fauna from Unit III of Seton Rock Shelter, Kangaroo Island, South Australia (Hope et al., 1977). Its absence from the Madura Cave fauna may be the result of a sampling accident, since the larger animals are poorly represented. This poor representation of the larger taxa suggests that most of the fossils were accumulated by owls, which could not handle the larger forms. A comparably puzzling situation is the absence of the monotreme *Tachyglossus aculeata*.

Macropus eugenii, M. irma, and *Potorous tridactylus* are also absent from the Pleistocene deposits. These taxa, along with *Vombatus, Phascolarctos*, and *Potorous platyops*, if their Pleistocene records in southwestern and southeastern Australia are considered (Merrilees, 1968b), have disjunct distributions on either side of the Nullarbor Plain, and at some time in the past these populations should have been connected across this area. This expectation has been realized for *Phascolarctos cinereus* (Lundelius & Turnbull, 1982), whose modern distribution is eastern and southeastern Australia, but which is known from Pleistocene deposits in southwestern Australia (Merrilees, 1968b; Balme et al., 1978), and for *Potorous platyops*, known as a living animal in western Australia and as a fossil from eastern Australia (Wakefield, 1964). There are several possible explanations for the absence of these three taxa: (1) They may have been connected across an area north of the Roe Plain, and may not have been present in the vicinity of Madura Cave; (2) the connection or dispersal may have taken place at some time earlier than that represented by the Madura Cave deposits; or (3) their absence may be a sampling accident.

Three species of marsupials, *Parantechinus apicalis*, *Tarsipes spencerae*, and *Setonyx brachyurus*, are restricted to southwestern Australia. Only one of these, *Parantechinus apicalis*, is known from Pleistocene or Holocene faunas of the Nullarbor Plain. If the absence of these taxa from the late Pleistocene fauna of that area is not a sampling accident, then the marsupial fauna from the Pleistocene deposits indicates an environment that was mesic and more equable than the present environment, but which lacked the dense swampy areas preferred by *Setonyx brachyurus*, the thickets preferred by *Macropus eugenii* (Ride, 1970), and the forests preferred by *Vombatus*. A savannah or woodland is indicated.

Acknowledgments

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