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The Mammalian Fauna of Madura Cave, Western Australia

Part I

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INTRODUCTION

This is the first of several planned reports of the second investigation of the stratified deposits of Madura Cave, one of the few caves in the Eucla Basin known to contain such deposits. As such, it is important for the establishment of a sequence. Much material was obtained during this investigation and the collections of the earlier investigation have also been used in the preparation of the present report.

The deposits of Madura Cave were investigated in 1955 by Lundelius. A brief description of the cave, its sediments and contained fossils, and their importance in the determination of the faunal history of the region was published (Lundelius, 1963). This established that the deposits were stratified and that extinct marsupial remains (*Sthenurus*) present in the lower of the two stratigraphic units then recognized demonstrated a Pleistocene age for that unit. Thus it indicated a potential for gaining a longer and more complete record of late Pleistocene faunal elements and changes if a more extensive study and excavation could be made.

Madura Cave is located in the Eucla Basin, which occupies a large (nearly 170,000 sq. km. or 70,000 sq. miles) area in southern Australia bordering on the Great Australian Bight (fig. 1). The basin is vaguely crescent-shaped, bounded on the south for over 500

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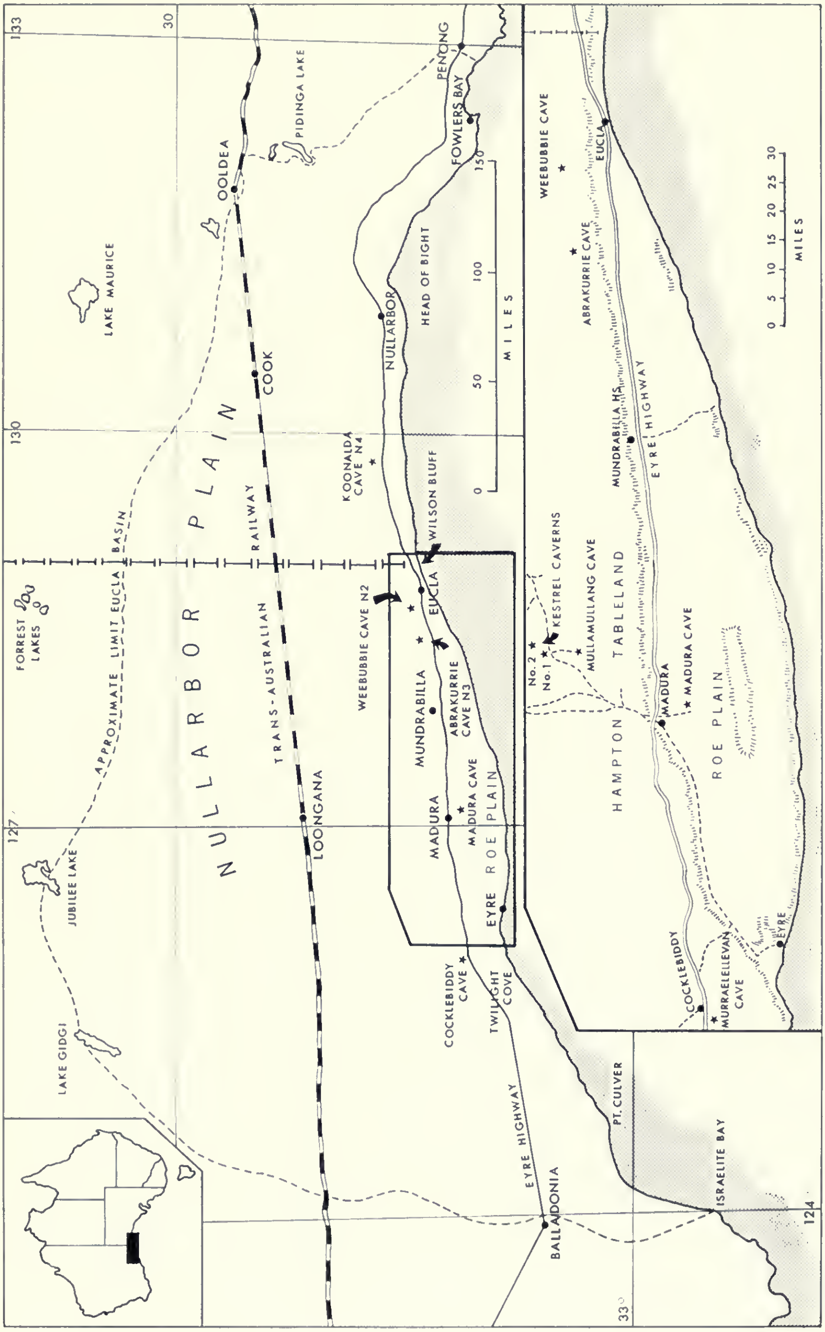
miles by the Southern Ocean from near Penong on Fowlers Bay in the east to Israelite Bay in the west. Inland its border reaches north from Penong to Lakes Pidinga and Ifould, then to Ooldea where it makes a decided bend westward, in a great sinuous swing that takes it past Lakes Jubilee and Gidgi. From this point it takes a southerly course to Balladonia and Israelite Bay. Thus about two-thirds of the Eucla Basin lies within Western Australia, and one-third within South Australia.

The basement complex of the basin is reported to be composed of granitic or high grade metamorphic rocks (Ludbrook, 1958a, b). The basin is a broad, shallow embayment that is filled with onlapped Cretaceous marine conglomerates and shales and by Cenozoic marine limestones. The latter (the Eucla group for the most part, which is widespread and over 900 ft. thick at Madura) have a youthful karst development with numerous caves and dolines. Hence this constitutes one of the world's largest karst regions (Jennings, 1963). The Eucla group is comprised of the lower and thicker Wilson's Bluff Limestone and the upper and thinner (100 ft. or less) Nullarbor Limestone (Singleton, 1954).

Physiographically it is an area of extremely low relief broken only by the Hampton Scarp which extends from near Eucla on the east (where it forms a sea cliff—the Bunda Cliff) for approximately 150 miles west near Eyre where it again runs along the Southern Ocean. This scarp divides the region into the low-lying Roe, or Eyre, Plain (about 100 ft. above sea level) to the south and the far larger Bunda Plateau, or Hampton Tableland, (about 250 to 600 ft. or more above sea level) to the north. The first geologic, biologic, and physiographic reports of the region were made by Tate (1879). The large central portion of the Hampton Tableland constitutes the true Nullarbor Plain, although this term is sometimes loosely used for the whole region of the Eucla Basin.

There has been speculation and some controversy as to the nature of the Hampton Scarp. Frost (1958) and others before him (Woolnough, 1933; David & Browne, 1950, v. 1, p. 538; v. 2, p. 548) have considered it to be a fault scarp. Ludbrook (1958a) concluded on the basis of paleontological correlations and Pleistocene depositional evidence that the Nullarbor Limestone was missing from the seaward

Fig. 1. Map of region of the Nullarbor Plain in Western Australia and South Australia, with detail map of Madura Cave area showing location of the cave, the Hampton scarp, and other caves nearby on the Hampton tableland.



NULLARBOR PLAIN
TRANS-AUSTRALIAN RAILWAY
APPROXIMATE LIMIT EUCLA BASIN
FORREST LAKES
JUBILEE LAKE
LAKE GIDGI
LAKE MAURICE
PIDINGA LAKE
OOLDEA
COOK
LOONGANA
NULLARBOR
HEAD OF BIGHT
FOWLERS BAY
PENONG
KOONALDA CAVE N4
WILSON BLUFF
WEEBUBBIE CAVE N2
EUCLA
MUNDRABILLA
ABRAKURRIE CAVE N3
MADURA
MADURA CAVE
ROE PLAIN
EYRE
COCKLEBIDDY CAVE
TWILIGHT COVE
EYRE HIGHWAY
BALLADONIA
PT. CULVER
ISRAELITE BAY
MILES
0
50
100
150
133
130
127
124
30
33
WEEBUBBIE CAVE
ABRAKURRIE CAVE
MUNDRABILLA HS
EYRE HIGHWAY
No. 2
No. 1
KESTREL CAVERNS
MULLAMULLANG CAVE
HAMPTON TABLELAND
MADURA CAVE
COCKLEBIDDY
MURRAELELLEVAN CAVE
0 5 10 15 20 25 30

side of the scarp as a result of marine erosion, being replaced unconformably by thin shelly Pleistocene marine deposits. Frost's interpretation was based on joint patterns and lithic correlations from the Madura Bores (number 1 below the scarp and numbers 2 and 3 above). Prior fault scarp postulates were only based on physiographic evidence. Jennings (1963) has thoroughly reviewed the various arguments, concluding that, "Further stratigraphical evidence may be necessary before this issue can be finally decided; one thing seems certain, however, namely that the Hampton Range [Scarp] has been subjected to marine erosion and is no longer a simple fault scarp. Air photographs show that the western part of the Hampton Range takes the form of a series of shallow, smooth curves in plan, best interpreted as the wavecut bays of a former sea cliff."

The Eucla Basin is the southern part of the central arid region of Australia. Most of this area receives less than 10 in. of rain per year and is subjected to high evaporation rates. The climate of most of this area falls into the BSh category of the Koppen and the E B'd of the Thornthwaite classifications of climate (Trewartha, 1954).

This area is interesting from the standpoint of paleo-biogeography because it is situated between the more humid coastal areas of southeastern and southwestern Australia, and its aridity is a barrier to the free exchange of faunal elements of the two humid regions. The floral zonation is directly controlled by climatic zonation. A number of studies of speciation patterns of various groups of Recent and fossil vertebrates in southwestern and southeastern Australia have shown that these two regions have exchanged faunal elements across this area at one or more times in the past (Serventy, 1951, 1953; Main et al., 1958; Gentilli, 1961; and others). The living fauna is a desert adapted one. Most of these cited studies agree that the Nullarbor Plain was the probable route of this exchange, and that the exchange or exchanges took place when the climate was more humid than it is today. Most also correlate the humid periods with glacial stages of the Pleistocene. There is, however, disagreement on the time of the most recent exchange.

The fossil record, which can provide the basis for the reconstruction of the faunal and climatic history, is poorly known for the Nullarbor Plain. It is confined at present to several pond deposits near Balladonia on the western edge and to cave deposits in many places. The former contain remains of a number of extinct marsupials which are widely distributed in Pleistocene deposits in Australia, (Glauert, 1912; Merrilees, 1968). The latter contain remains of both extant and extinct forms (Lundelius, 1957, 1963). While the assemblages mentioned above demonstrate a more humid climate in the past, there is little or no data that permit the construction of a sequence of faunas or the correlation of the known assemblages with those in other places. Merrilees (1968) has recently reviewed various interpretations of the evidence relating to the Pleistocene and post-Plesitocene climates of the continent in comparison with those of the rest of the world.

DESCRIPTION OF MADURA CAVE

Madura Cave is located on the Roe Plain, six miles south of the settlement of Madura, 110 miles west of Eucla (fig. 1). It is one of the few known caves on the Roe Plain and is the only cave south of the Hampton Scarp investigated by us. The cave system consists of a shallow doline, an oval depression whose long axis is oriented NW-SE, with two tunnels extending outward from its margins (fig. 2, and see Frost, 1958). The oval depression quite clearly is the product of a collapse of the roof of a cave. Frost believed the cave to be formed in the Nullarbor ls., but if the Ludbrook (1958a, b) assessments are correct, it is developed in the Wilson Bluff ls. One tunnel extends southwestward from the doline's southern end, the other northwestward from its northern end. The southern tunnel is open for 160 ft. It is 40 ft. wide and 7 ft. high at the opening. Its floor consists of loose gray sand and is at the same level as the bottom of the central depression. No excavations were carried out in this tunnel.

The northern tunnel is much larger. It extends northwestward for 275 ft. where it divides into two, one branch trending southwestward, the other north-northwest. Each of these subdivide again into smaller tunnels which gradually shrink until they cannot be entered. The main part of this tunnel is about 20 ft. wide with little variation (fig. 2). A small tunnel leaves the main tunnel to the southeast 140 ft. from the entrance.

The floor of the main tunnel is 8–10 ft. lower than the surface of the depression. It has a gentle gradient toward the back of the cave. The floor has a small meandering channel cut into it to a depth of one to two feet. This channel sends a small distributary branch into the small southeast trending passage at the halfway point of the main tunnel. The main channel continues on to the branching of the main

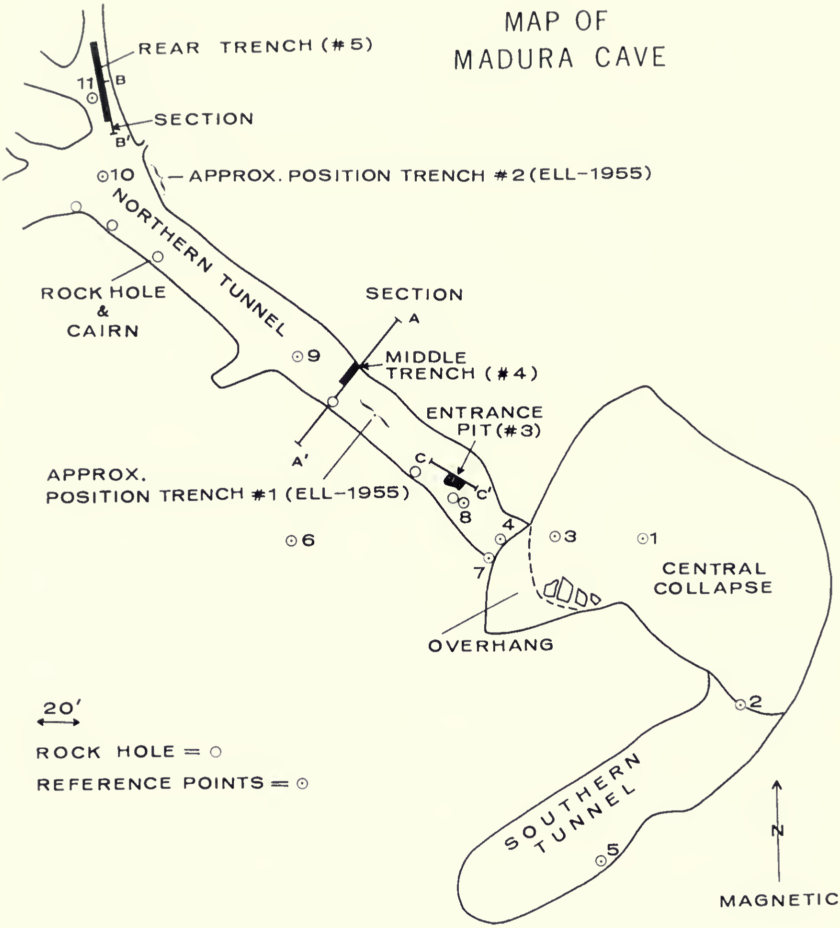


FIG. 2. Map of cave.

tunnel where it follows the larger southwest-trending branch. This channel clearly carries water from the surface depression during heavy rains.

STRATIGRAPHY

In 1955 Lundelius dug two test trenches in the main tunnel of Madura Cave, numbered Trenches 1 and 2. In 1964 we added three more trenches (fig. 2), numbers 3–5. These are precisely located with respect to the cave entrance and to one another, as well as to various

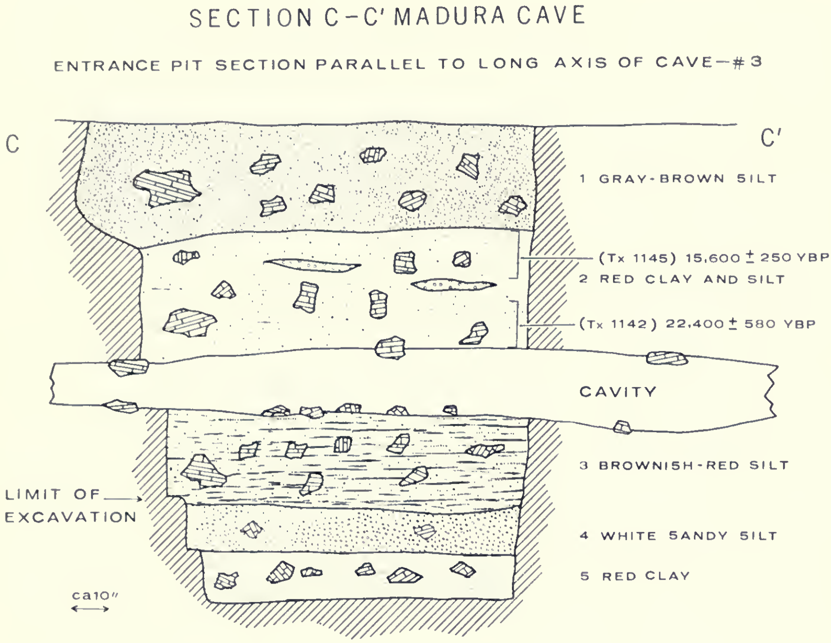


FIG. 3. Section C-C′, Entrance Trench, 3.

other landmarks within the cave. The exact locations of Trenches 1 and 2 were not recorded and we were unable to relocate them precisely in 1964. Trench 1 lay about 80 ft. in from the entrance, near Trench 4, and Trench 2 lay about E of Instrument Station 10 (fig. 2), near Trench 5. Trench No. 3, the Entrance Pit, is located 40 ft. from the entrance in approximately the center of the cave. Trench 4, the Middle Trench, is 110 ft. from the entrance and extends out from the northeast wall to the midline of the cave. Trench 5, the Rear Trench, is located in the northern branch and is oriented parallel to the axis of the branch.

The sequence in the northeast wall of Trench 3 (Sec. C-C′; fig. 3) from top to bottom is as follows:

1. Loose, gray-brown silt with many limestone fragments and boulders up to 4 in. in diameter and abundant small bones and organic materials. This unit forms the floor of the main passage of the cave. Its surface is irregular because of the incised drainage channel which is filled with limestone boulders. This unit is 2 ft. thick.

2. Loose, red clayey silt with lenses of gravel and bones and numerous limestone boulders. This unit is 2 ft. thick at this place.

Two C-14 dates[1] based on bone are available from this unit. One (Tx 1145) from the upper one foot is 15,600 ± 250 years B.P. The other (Tx 1142) from the lower one foot is 22,400 ± 580 years B.P.

The bottom of this unit forms the roof of an extensive void or opening, a "tunnel" 12 to 18 in. high. This tunnel which is formed completely in the cave fill has an arched roof and a floor which slopes gently toward the present entrance. The floor of the "tunnel" is covered with limestone cobbles in a matrix of gray-brown clay and silt. This grades downward rapidly into the more reddish-colored material typical of unit 3.

3. Very loose, brownish-red silt with many limestone cobbles and some bones. This unit is 23 in. thick.

4. Loose, almost white, sandy silt with a few cobbles and some very fragile bones. Many of the cobbles are composed of limestone fragments cemented together. This unit is 7 in. thick.

5. Friable, red clay with limestone cobbles and sparse bones. There were ten inches exposed.

The sequence in the southeast wall of Trench 4, the main trench, (Sec. A-A′; fig. 4) from top to bottom is as follows:

1. Loose gray-brown silt with numerous limestone cobbles and boulders. The contact of this unit with unit two is irregular and is marked by a 1–2 in. zone of relatively clean gravel. The top has apparently been eroded off by the present drainage. As a result of these irregularities, the thickness varies from 42 in. near the wall to 12 in. in the center of the cave. A C-14 date (Tx 1146) of 7,470 ± 120 B.P. was obtained from bone from the top one foot of this unit.

2. Loose, red to orange-red clay and silt with numerous cobbles and boulders and abundant bones. Thickness is 24 in. Two C-14 dates based on bone are available for this unit. One (Tx 1140) from the upper 6 in. is 18,990 ± 220 years. The other (Tx 1141) from 6 to 12 in. below the top of this unit is 20,000 ± 430 years.

3. Loose to tight, yellow orange sand with few cobbles. Bones are not abundant. It is composed mostly of fine limestone fragments and dust. It is tightly cemented in place and incorporates cobbles and pebbles of the underlying unit where the cemented areas are in contact with it. This unit dips slightly toward the center of the cave

[1] All C-14 dates reported here were obtained from bone samples by the method developed by Haynes (1968). They are based on the calcium carbonate contained in the structure of the apatite crystallites of the bone.

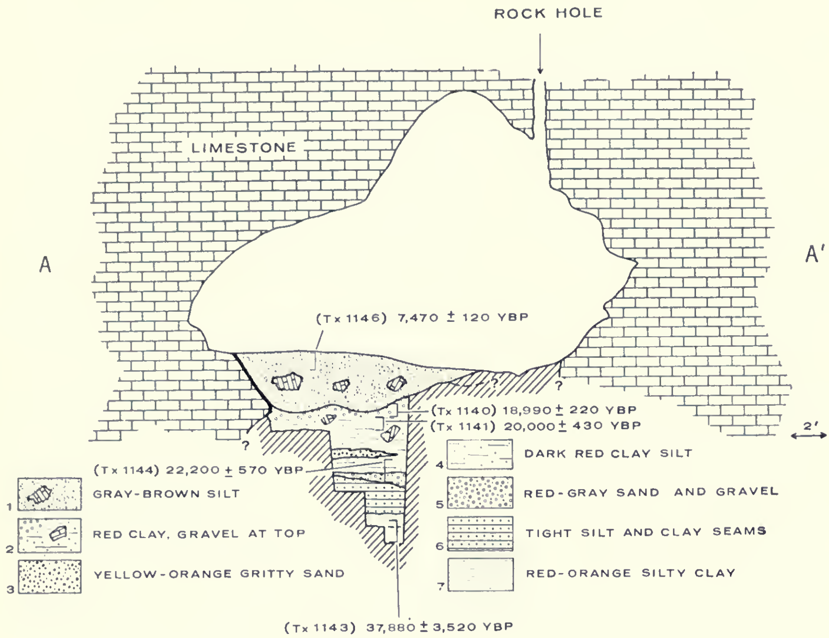


FIG. 4. Section A-A′, Middle Trench, 4.

and the thickness varies from 6 to 8 in. near the wall to 0 in. near the middle of the cave.

4. Loose, dark red clayey silt with less rock than overlying unit. Thickness varies from 6 in. near the wall to 3 in. near the center of cave.

5. Loose, reddish gray sand and gravel with a minor amount of limestone dust and abundant bones. This unit has a "speckled" appearance because of the presence of well-rounded particles of dark carbonaceous limestone. The thickness varies from 6 in. near the wall to 16 in. toward the center of the cave. A C-14 date (Tx 1144) of 22,220 ± 570 years B.P. was obtained on bone from units 4 and 5, most of it from near the contact of these units or at the interface.

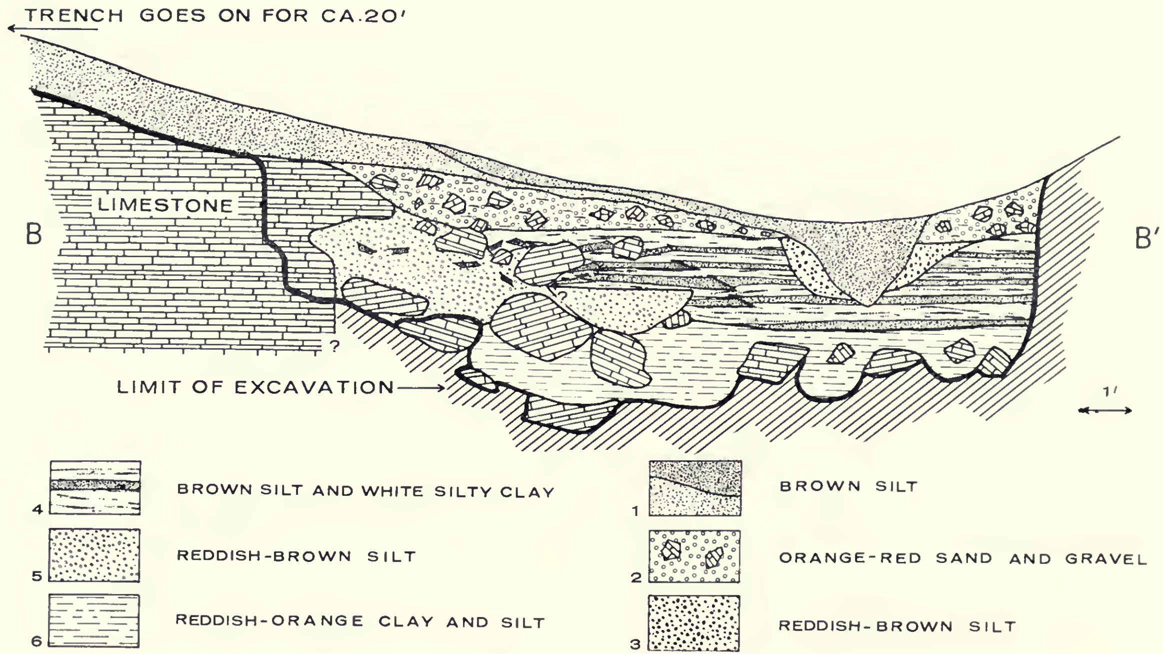
6. Soft, white limestone powder with thin seams of orange clay. Bones absent. Thickness varies from 27 in. near the wall to 15 in. near the center of the cave.

7. Tight, reddish-orange, silty to sandy clay with few large rocks. Fifteen inches were exposed. A C-14 date (Tx 1143) of 37,880 ± 3,520 years B.P. was obtained from bone from the lower one foot of this unit.

SECTION B–B′ MADURA CAVE

SHOWING 20 FEET OF EAST WALL OF REAR TRENCH—#5

(SCALE APPROXIMATE)



In the east wall of Trench 5 (Sec. B-B′; fig. 5), parallel to the long axis of the passageway, the following sequence is exposed:

1. Loose, brownish-gray sandy silt with limestone cobbles and boulders. This is lenticular and appears to be the filling of a channel which was cut 30 in. into the underlying sediments. To the north, it forms the surface of the cave floor, thickens to approximately 2 ft. and acquires thin layers of rock dust which thin and disappear southward.

2. Loose, light orange to reddish-orange sand and gravel with a minor amount of silt and many limestone fragments. It is about 1 ft. thick. To the north it ends against large limestone boulders.

3. Loose, reddish-brown silt with no cobbles. This is a channel fill which has been cut through by a subsequent channel of unit 1, leaving this unit preserved only on the sides of the channel it fills.

4. Alternating layers of brown silt and white rock dust. The strata in the upper part are up to 6 in. thick with lenses of coarser material and bones. The lower layers are 1–2 in. thick. The relationship of unit 5 to this one may indicate that unit 4 is compound. Unit 5 appears to be emplaced into the lower part of unit. 4. No evidence of any change was seen in unit 4, aside from the change in the thickness of the layers of silt and rock dust.

To the north this unit becomes coarser and ends among large limestone boulders. The upper part overlaps these boulders and a few of the individual layers extend into the silts characteristic of unit 5, suggesting that the upper parts of units 4 and 5 interdigitate in this area. The bedding in the parts of both units 4 and 5 that underlie the boulders is disturbed in a way that suggests that the boulders fell from the roof of the cave into the sediments.

5. Loose, reddish-brown silt with few rocks. It is similar to unit 3. This unit rests largely on large limestone boulders.

6. Large limestone boulders in a matrix of reddish-orange clayey silt. The base of the unit was not reached in the excavations.

Multiple channelings and other disturbances of the sedimentary regime, so clearly seen in the walls of Trench 5, indicate a very complex genesis of the sequence of beds in the rear of the cave. This appears to be in contrast to the simpler-looking sequences in Trenches 3 and 4. These are somewhat deceptive because the evidences of disturbances in deposition (cavity, lenses, and channels), being near

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FIG. 5. Section B-B′, Rear Trench, 5.

horizontal and low-angled features, are less apparent. All such evidences of a complex depositional history argue for extreme caution when attempting to correlate strata between trenches. Hence no correlation will be made for Trench 5 beyond noting that the brown silt (unit 1, the uppermost channel) is similar to that of the top unit in Trenches 1, 3, and 4: presumably unit 1 in each of these trenches is approximately equivalent.

It is possible to make some limited correlations of stratigraphic units between Trenches 3 and 4 on the basis of the C-14 dates. It is probable that the uppermost brown silt exposed in both is the same age. It is similar in both trenches and is very different from the underlying material. The C-14 date of 7,470 $\pm$ 120 years B.P. was obtained from bone adjacent to Trench 4. No C-14 date on this unit from Trench 3 is available. The red clay and silt, designated unit 2 in Trenches 3 and 4 is similar in both places and is probably equivalent to the red soil reported for Trench 1 (Lundelius, 1963). In general, the C-14 dates support a correlation based on lithology.

The discrepancies concern the top and bottom of the red clay and silt, designated unit 2 in both trenches, and units 4–5 of Trench 4. The difference in the age of the top of unit 2 is readily explicable in terms of the erosion surface that separates the upper brown silt from the underlying red clay and silt. The discrepancies in the ages of the unit 2 lower boundaries are interpreted as the result of different ages for the onset of deposition of unit 2 material in the two areas of the cave. In Trench 4 we have no C-14 dates for the lowermost foot of unit 2, but the date for units 4–5 indicates that the bottom of unit 2 in this trench is younger than the bottom of this unit in Trench 3. Different materials are being deposited in different parts of the cave today. Light-colored, fine-grained, granular material similar to that of unit 6 of Trench 4 is accumulating, apparently by spalation from the walls, along the sides of the cave in some cases. This is different from the brown silt and clay that is being deposited by runoff from the surface.

Correlations with the units exposed in the other trenches seem impossible at present with the exception of the upper brown silt and the uppermost 6 in. of the underlying red clay in Trench 1 reported by Lundelius (1963). They are probably the same as units 1 and units 2 in Trenches 3 and 4. No correlations can be made for units below unit 2 of Trenches 3 and 4.

The fact that all of the deposits in the northern tunnel are topographically lower than the material in the central doline raises the possibility that material in the northern tunnel may be in part reworked. This is not believed to be a serious problem because stratigraphy and C-14 date chronology are consistent. Reworking may have happened with an occasional specimen, however.

An analysis of the salts in the dry screen concentrates has been carried out for us by Mr. Gordon F. U. Baker (personal communication, 1965). The brown silt of unit 1 contained .26 per cent chlorides and 2 per cent sulfates; the concentrates from unit 2 contained .05 per cent chlorides. Although these results were obtained from dry screen concentrates and may not be completely accurate indicators of the salt content of the two materials, they are highly suggestive of significant climatic differences at the times of deposition of the two units. This will be discussed in more detail in a later publication on environmental interpretation in our series.

METHODS

Material was removed from Trenches 3–5 in approximately 6 in. intervals within each stratigraphic unit, with one exception (unit 1) for which a sample of the top 1 ft. was taken adjacent to Trench 4. All matrix was dry sieved in the field and all concentrate larger than 1/50 in. was kept. The better specimens were picked in the field and treated with shellac to minimize breakage and loss of teeth.

The map of the cave (fig. 2) was made with a Brunton compass and tape and an open-sight alidade.

Tooth measurements were made as shown in Figure 6 using either micrometer calipers graduated to .01 mm. or a microscope ocular micrometer graduated into 100 units, which, with the optics usually used, permitted direct reading to either .038 mm. or .051 mm. Interpolation permitted accurate readings to half of these values per unit. Other measurements were made with vernier calipers graduated to .1 mm. and capable of interpolation to about .01 with the vernier scale.

The dental nomenclature in general follows the familiar Cope-Osborne terminology with additions taken from Hershkovitz's (1971) summary of terms used by a great number of authors. The first use of a term is followed by the Hershkovitz numerical designation given in parenthesis.

Because the dental morphology of many of the taxa of Australian mammals is poorly known, we have figured dentitions of Recent species in cases in which this aids the identification and description of

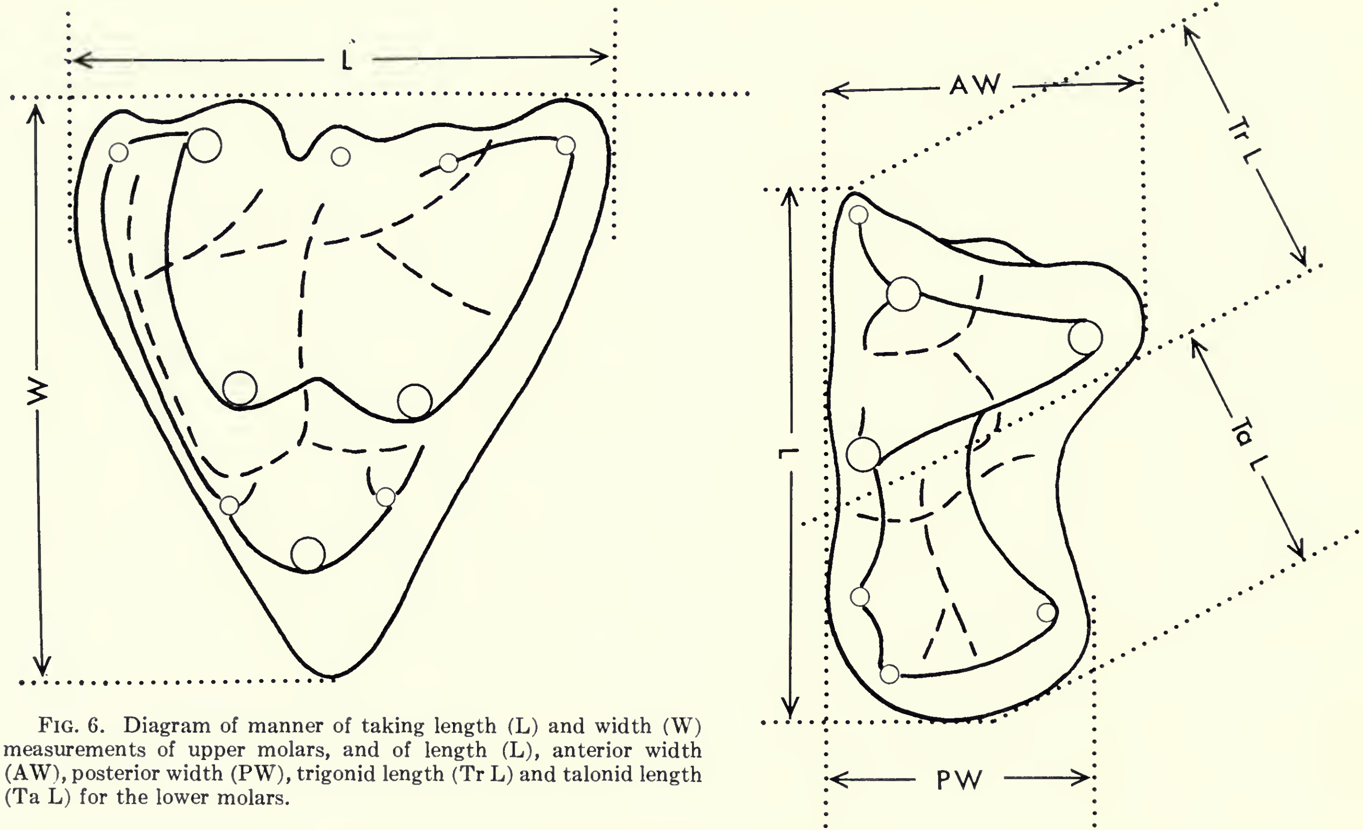


FIG. 6. Diagram of manner of taking length (L) and width (W) measurements of upper molars, and of length (L), anterior width (AW), posterior width (PW), trigonid length (Tr L) and talonid length (Ta L) for the lower molars.

the fossil material. The drawings were made by Dr. Tibor Parenyi from camera lucida drawings of the specimens. They are accurate as to scale, dimensions, and proportions, and are shaded to show details of surface texture and appearance, and to de-emphasize distracting cracks, breaks, or other artifacts.

The bivariate scatter diagrams are plotted to the same scale for each group of organisms to facilitate comparisons (see figs. 12, 13, for examples).

ABBREVIATIONS

Abbreviations used are as follows: FMNH or FM—Field Museum of Natural History, Recent Mammal Collection; PM—Field Museum fossil mammal collection; MVZ—Museum of Vertebrate Zoology, University of California, Berkeley; TMM or UT—Texas Memorial Museum, University of Texas at Austin[1]; WAM—Western Australian Museum; L—length; W—width; AW—anterior width; PW—posterior width; Tr. L—trigonid length; Tal. L—talonid length. Other abbreviations are either in common use or are defined where used in the text.

SYSTEMATICS

Class Mammalia

Subclass Theria

Infraclass Eutheria (Sensu VandeBroek, 1961, 1964)

Cohort Marsupiata (Sensu Turnbull, 1971; = Metatheria)

Order Marsupicarnivora (Ride, 1964)

Dasyuridae

Phascogalinae

Genus and species indet.

The fauna contains this indeterminate taxon, a pigmy antechinus, which is close to *Planigale ingrami* and *Antechinus maculatus* in size and most of its dental morphology, but which differs from both in several ways that prevent an assignment to either genus.

[1] Fossil vertebrates at Austin were formerly in the collections of the Bureau of Economic Geology and (in earlier reports) bore the prefix BEG. They have been transferred to the Texas Memorial Museum and will henceforth bear the prefix TMM. An integral part of every TMM catalogue number is the five-digit locality designation. That for Madura Cave is 41106-. In addition, recent mammals in the UT or TMM collection have an M prefix designation.

Material.—

Entrance Pit (Trench 3), Lower red unit, under collapse (unit 3)

- TMM 41106-660, right mandible with $M_{\overline{1}}$.

Middle Pit (Trench 4), unit 2, level 2

- TMM 44106-661, -662, edentulous left mandibles with alveoli for $M_{\overline{2}-\overline{4}}$
- TMM 41106-663, right mandible with $M_{\overline{2}-\overline{3}}$ and alveoli for rest of cheek teeth and C.
- WAM 72.3.6, right mandible with $M_{\overline{1}-\overline{2}}$ and alveoli for other cheek teeth and C.
- TMM 41106-667, -668, edentulous mandibular fragments with alveoli of last tooth or two.
- TMM 41106-741, left $M^{\underline{2}}$ (fig. 8)
- TMM 41106-742, left $M_{\overline{1}}$
- TMM 41106-743, right $M_{\overline{2}}$ or $_{\overline{3}}$
- TMM 41106-744, right ramus fragment with $M_{\overline{4}}$
- TMM 41106-745-6, two edentulous right ramus fragments
- PM 25596, right ramus with $M_{\overline{3}}$ and alveoli for $M_{\overline{2}}$ and $M_{\overline{4}}$
- PM 25597, right ramus with $M_{\overline{3}-\overline{4}}$ (fig. 9B)
- PM 25710, right ramus fragment with $M_{\overline{3}}$
- PM 25713, right ramus fragment with $M_{\overline{1}}$ or $M_{\overline{2}}$
- WAM 72.3.7, left mandible with $M_{\overline{2}-\overline{3}}$ and alveoli for $P_{\overline{4}}$ and other molars
- PM 26189, edentulous right ramus with alveoli for $M_{\overline{2}-\overline{4}}$
- PM 26193, left $M_{\overline{1}}$
- PM 26194, -5, a right ramus fragment with alveoli for four teeth and a left with alveoli for three, respectively.
- PM 26268, left $M_{\overline{1}}$
- PM 26269, right $M_{\overline{2}}$ or $_{\overline{3}}$
- PM 26270-1, two edentulous right ramus fragments.

Units 4–5

- WAM 72.3.3, right maxillary with $M^{\underline{3}}$ and alveoli for other molars
- TMM 41106-696, left ramus with $P_{\overline{4}}$–$M_{\overline{3}}$ and alveoli for other cheek teeth (fig. 9A)
- TMM 41106-699, left mandible with $M_{\overline{2}-\overline{3}}$ and alveoli for rest of cheek teeth through C.

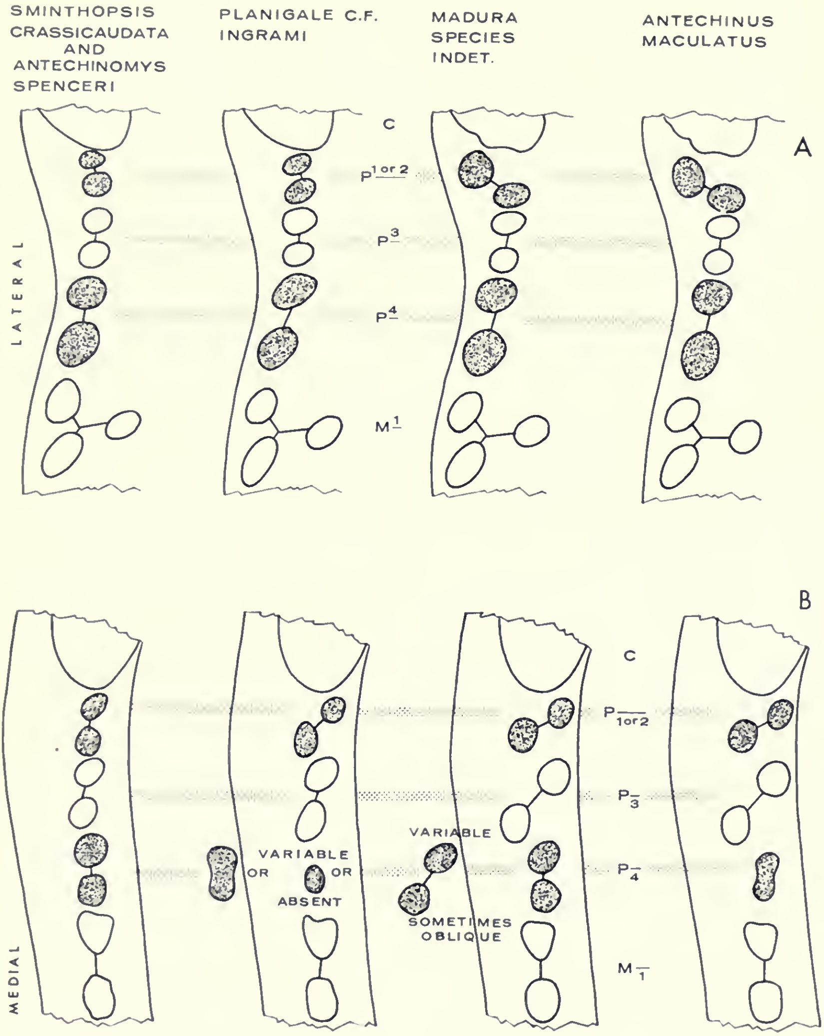


FIG. 7. Diagram of condition of crowding of premolars of certain phascogales as reflected in their alveolar patterns. Shown are the Madura *Planigale*-like form and several other small phascogales which are compared to it.

TMM 41106-740, left $M^{\underline{1}}$ (fig. 8)

WAM 72.3.1, edentulous right max.

TMM 41106-748, edentulous left max.

TMM 41106-749, -750, edentulous right mandible fragments

TMM 41106-751, -752, 753, edentulous left mandible fragments

TMM 41106-754, right $M_{\overline{1}}$

PM 25621, left maxillary fragment with $P^{\underline{3-4}}$ and alveoli for C, $P^{\underline{2}}$ and $M^{\underline{1}}$ (fig. 8)

PM 26190, left maxillary with $M^{\underline{3}}$ and alveoli for $M^{\underline{2}}$ and $M^{\underline{4}}$ (fig. 8)

PM 26191, right ramus fragment with $M_{\overline{1}}$ and alveoli for $P_{\overline{3-4}}$ and $M_{\overline{2-3}}$

PM 26192, right ramus fragment with $M_{\overline{2}}$ and part of $M_{\overline{3}}$ and alveoli for $M_{\overline{1}}$

PM 26216, left $M^{\underline{1}}$

PM 26272, edentulous left max. with alveoli for C-$M^{\underline{2}}$

PM 26273, -274, -275, -276, edentulous left ramus fragments

WAM 72.3.4 and WAM 72.3.5, edentulous right ramus fragments

WAM 72.3.2, right $M^{\underline{1}}$

Unit 7, level 2

TMM 41106-659, right mandible with $P_{\overline{4}}$, $M_{\overline{1}}$

Descriptions.—This is the smallest and one of the rarest dasyurids represented in the Madura collection. Only ten fragments were recovered that preserve any part of the maxillary bone or upper dentition and, fortunately, one of them (PM 25621) shows the condition of the root pattern of the upper premolars. The pattern corresponds to that of *A. maculatus*, with $P^{\underline{1}}$* being crowded out of alignment, rather than with that of *Planigale* c.f. *ingrami* in which the premolars are all aligned (fig. 7A).

The $P^{\underline{3}}$ and $P^{\underline{4}}$ are each elliptical in outline with a single prominent central cusp that is rounded anteriorly and ridged posteriorly (and worn in PM 25621, fig. 8B). The posterior ridge runs to a prominent cingular cuspule and a weak cingulum surrounds each tooth.

The $M^{\underline{1}}$'s (TMM 41106-740 and PM 26216) are triangular in outline, with very small paracones. In both, the metacone is much the

* P^1 or P^2. The first of the premolar teeth, whatever its true homology is.

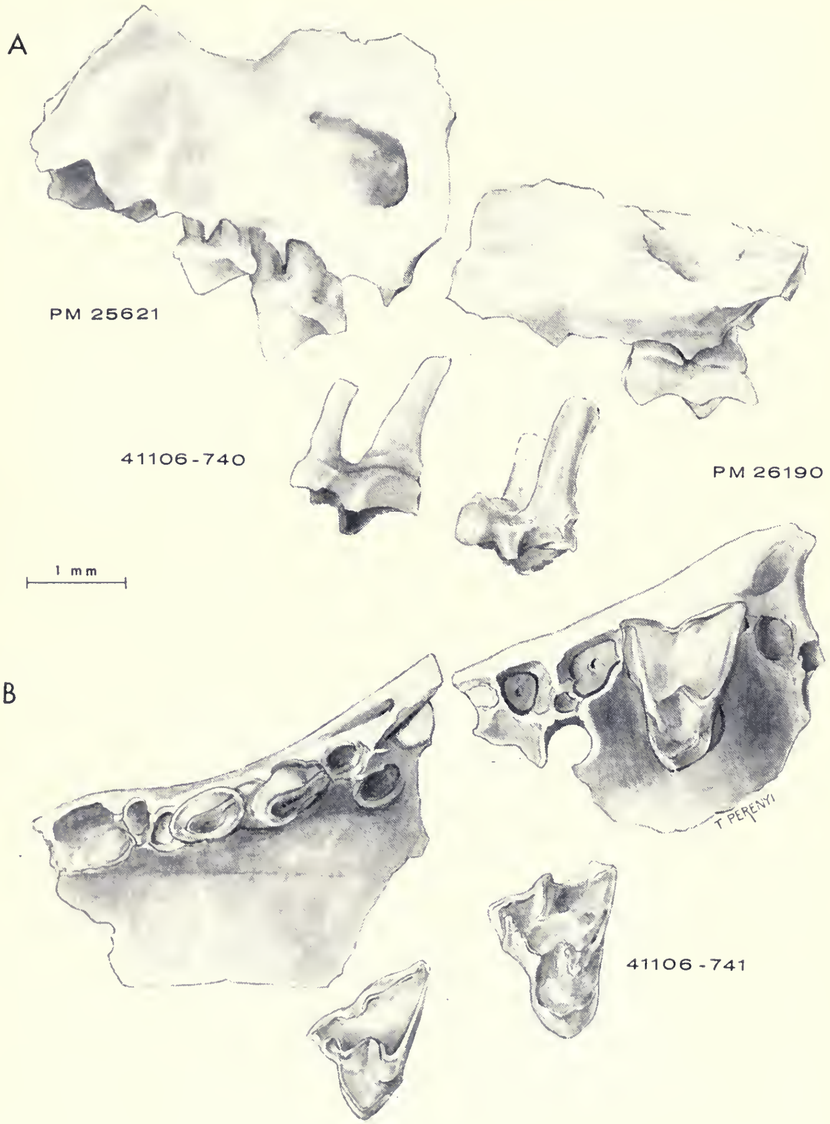


FIG. 8. The Madura *Planigale*-like form. The right upper dentition in buccal (A) and occlusal (B) views, based upon four of the fragmentary specimens that contribute the most to knowledge of the maxillary and its dentition. Shown, left to right are PM 25621 and PM 26190, the maxillary fragments with P^{3-4} and M^3 and TMM 41106-740 and -741, isolated M^1 and M^2.

largest primary cusp, and the protocone is low and intermediate in size (fig. 8). The paracone-stylocone crest (stylocrista) portion of the eocrista is very short, as in most phascogales, due to the very narrow anterior part of the stylar shelf. The posterior half of the stylar shelf is high and posterolaterally expanded. There is a well-formed anterior cingulum which ties the protocone to the parastyle at the posterior edge of that cuspule. No distinct conule is present, but this anterior cingulum is inflected near the base of the paracone in a manner suggestive of a vestigial protoconule. The posterior cingulum also ties to the protocone, but shortly after leaving that cusp it becomes very weak and continues in that manner past the base of the metacone almost to the posterolateral corner of the tooth. In this it is like both *A. maculatus* and *P. ingrami* (figs. 10, 11) and differs from most *Sminthopsis crassicaudata* and *S. murina* in which it rarely reaches as far as the posterior side of the metacone.

The $M^{\underline{2}}$ (TMM 41106-741) is a deeply worn tooth that is closer in its overall shape to that of the $M^{\underline{3}}$ than to that of the $M^{\underline{1}}$ (fig. 8). It is intermediate in the degree of development of the parastylar shelf.

The $M^{\underline{3}}$ in both specimens (TMM 41106-680 and PM 26190) is worn and the relative development of the secondary cusps cannot be determined with certainty. The tooth has the normal dasyurid triangular shape but the protocone is smaller relative to the remainder of the cusps than is the case in other dasyurids and it lacks the posterior bulge seen in many dasyurids (fig. 8). The paracone is smaller and lower than the metacone. The mesostyle (stylar cusp C of Bensley, 1903) is the only stylar cusp preserved. It is about the same size relative to the whole tooth as in other small dasyurids (*Planigale* and *Antechinus*), but is less pronounced than in *Sminthopsis* and *Antechinomys spenceri* (AMNH 15012). The labial (ectoloph) margin is notably straighter with the pre-mesostyle notch shallower than in *Planigale* cf. *ingrami* (AMNH 160308) or *Sminthopsis crassicaudata* (UT M-839). In this it is more like *A. maculatus*. There is a small procingulum in the region of the anteroexternal root that extends lingually from the parastyle down to the base of the tooth where it is weakly joined to the anterior crest from the protocone.

The lower jaws and dentition are represented by more and better, though also fragmentary, materials. Specimen TMM 41106-696 is the most complete of the lot (fig. 9A). In no case are incisor or canine teeth preserved and, of the premolars, only the last ($P_{\overline{4}}$) is

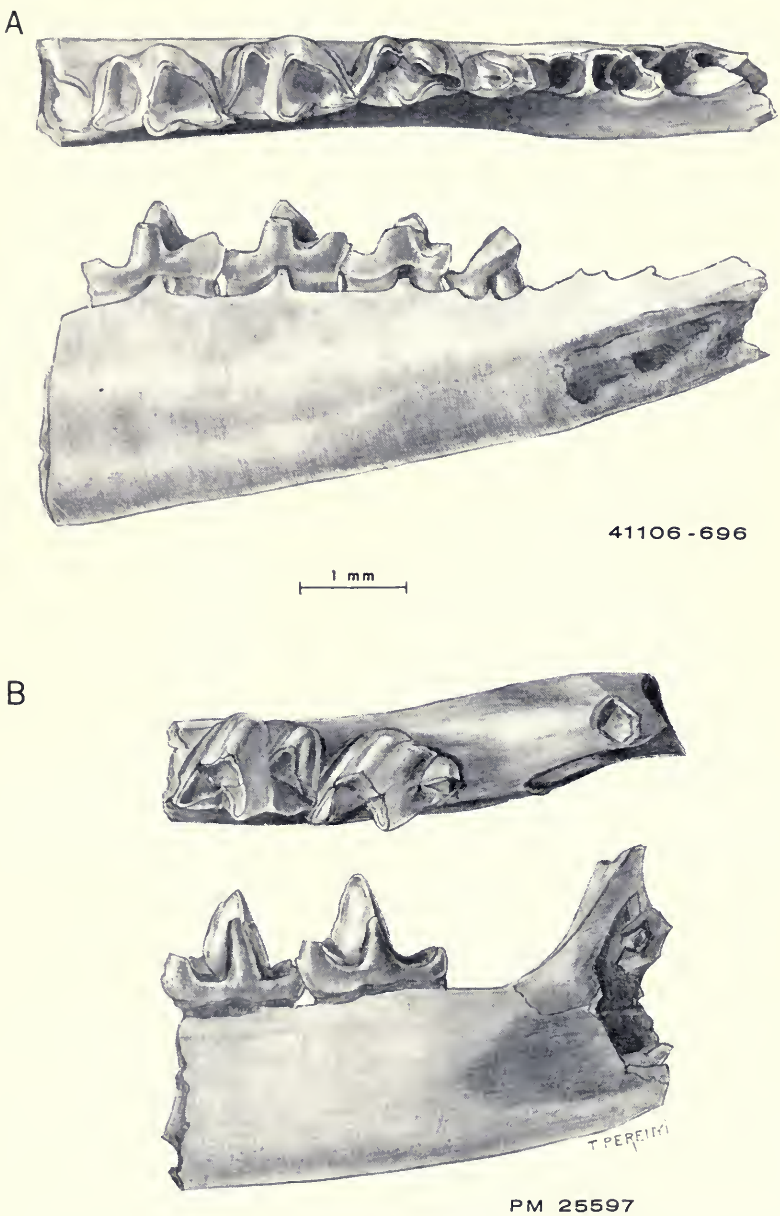


FIG. 9. The lower dentition of the Madura *Planigale*-like form, seen in occlusal and lingual views. A. Left mandibular fragment with $P_{\overline{4}}$ through $M_{\overline{3}}$, TMM 41106-696. B. Right mandibular fragment, PM 25597, with $M_{\overline{3}-\overline{4}}$.

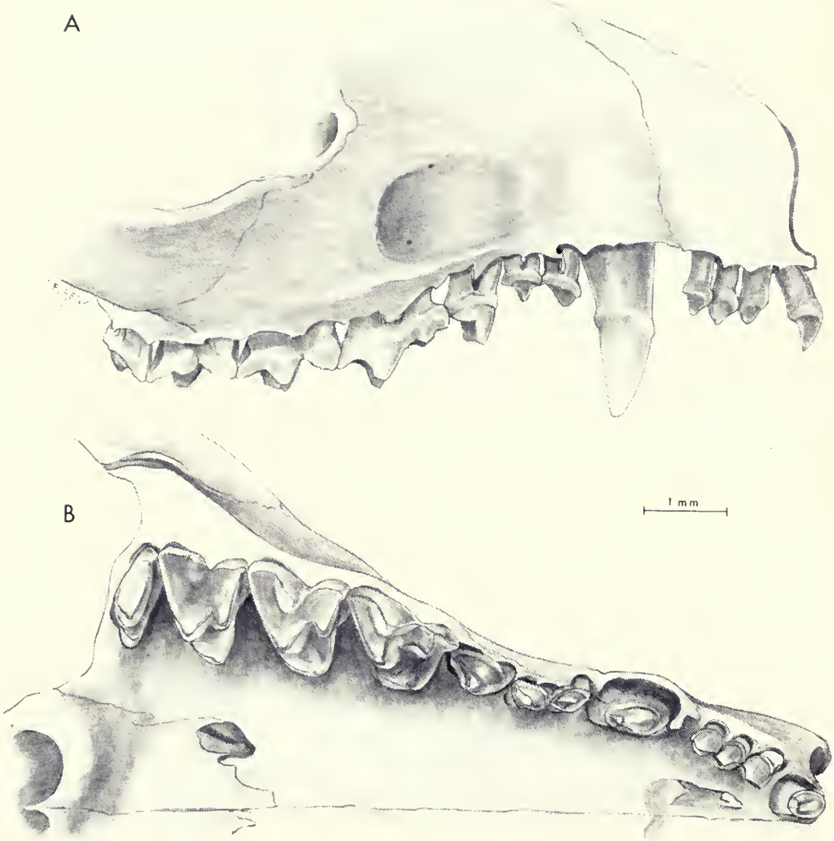


FIG. 10. *Antechinus maculatus*, FM 64350. **A, B.** Buccal and occlusal views of right maxillary and its dentition.

known in any of the specimens. In all specimens in which the evidence of premolar condition is preserved by teeth or alveoli (TMM 41106-663, PM 26188, TMM 41106-666, TMM 41106-696, TMM 41106-699, and PM 26191 and TMM 41106-659) there is crowding in this region. But unlike the condition of crowding in Recent *Planigale ingrami,* in which $P_{\overline{4}}$ is consistently crowded out of line and is reduced considerably, here it is the anterior-most premolar that is consistently out of line while the $P_{\overline{4}}$ is usually aligned or just slightly out of line in some specimens. Figure 7B diagrams these conditions for *P. ingrami, A. maculatus,* the Madura specimens discussed here, and other small phascogales. The depth of the horizontal ramus is

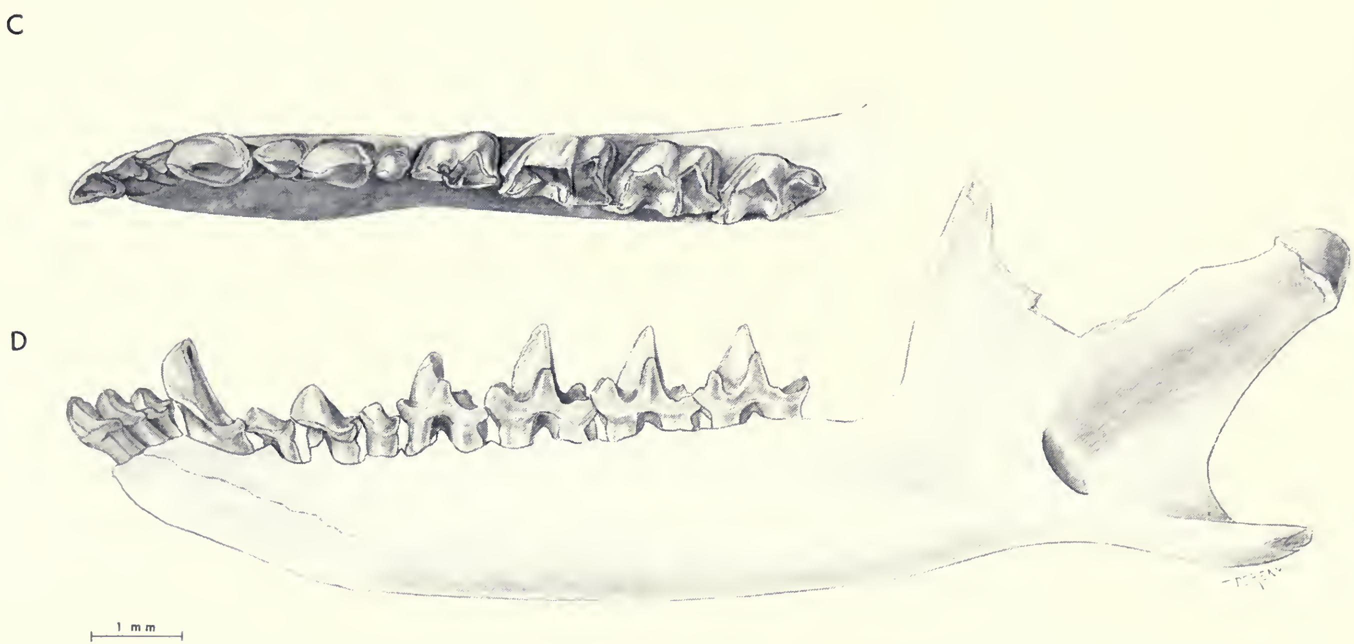


FIG. 10. C, D. *Antechinus maculatus*, FM 64350. Occlusal and lingual views of right jaw and the lower dentition.

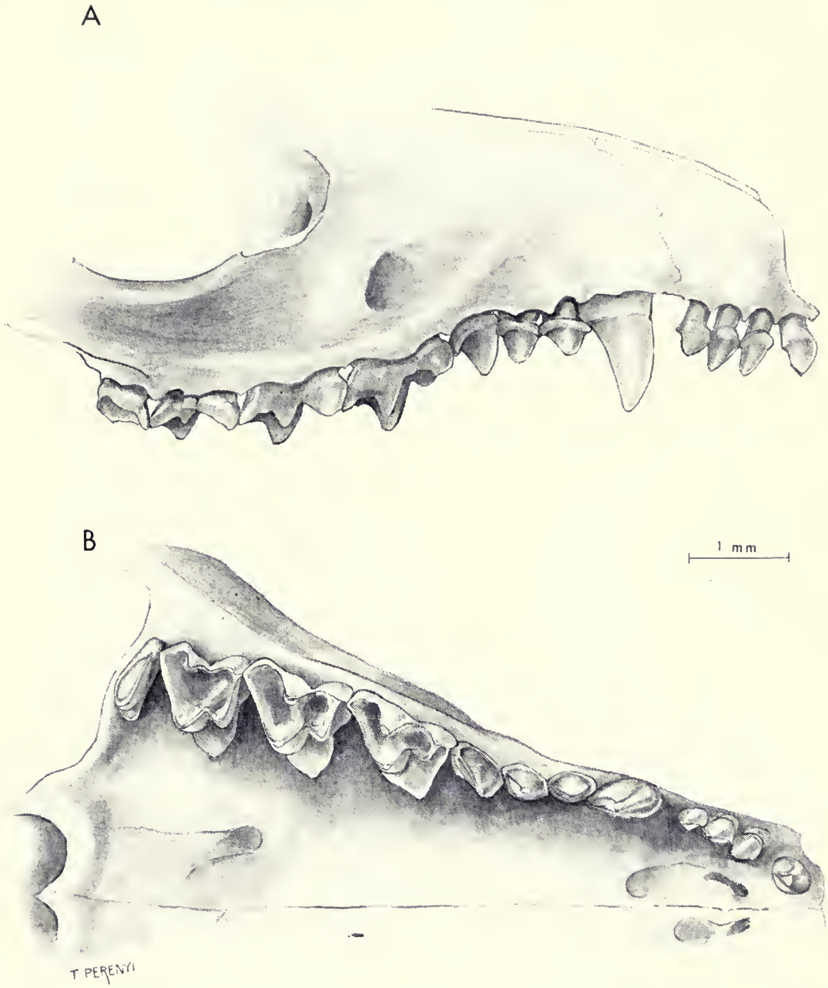


FIG. 11. *Planigale ingrami*, AMNH 160308. **A, B.** Buccal and occlusal views of the right maxillary and upper dentition.

variable, but never very deep. The inferior dental canal is usually divided so that the anterior foramen is at the level of $P_{\overline{3}}$ (or this may be further divided as in PM 26191, with reduced openings in the region of $P_{\overline{2}-\overline{3}}$ and $P_{\overline{3}-\overline{4}}$) and the posterior foramen is beneath $M_{\overline{1}-\overline{2}}$, often under the posterior root of $M_{\overline{1}}$.

The $P_{\overline{4}}$ has a sub-elliptical outline in crown view. It is made up of a primary cusp that lies somewhat anterior to the center of the tooth. A ridge leads anteriorly from its apex to its base where it

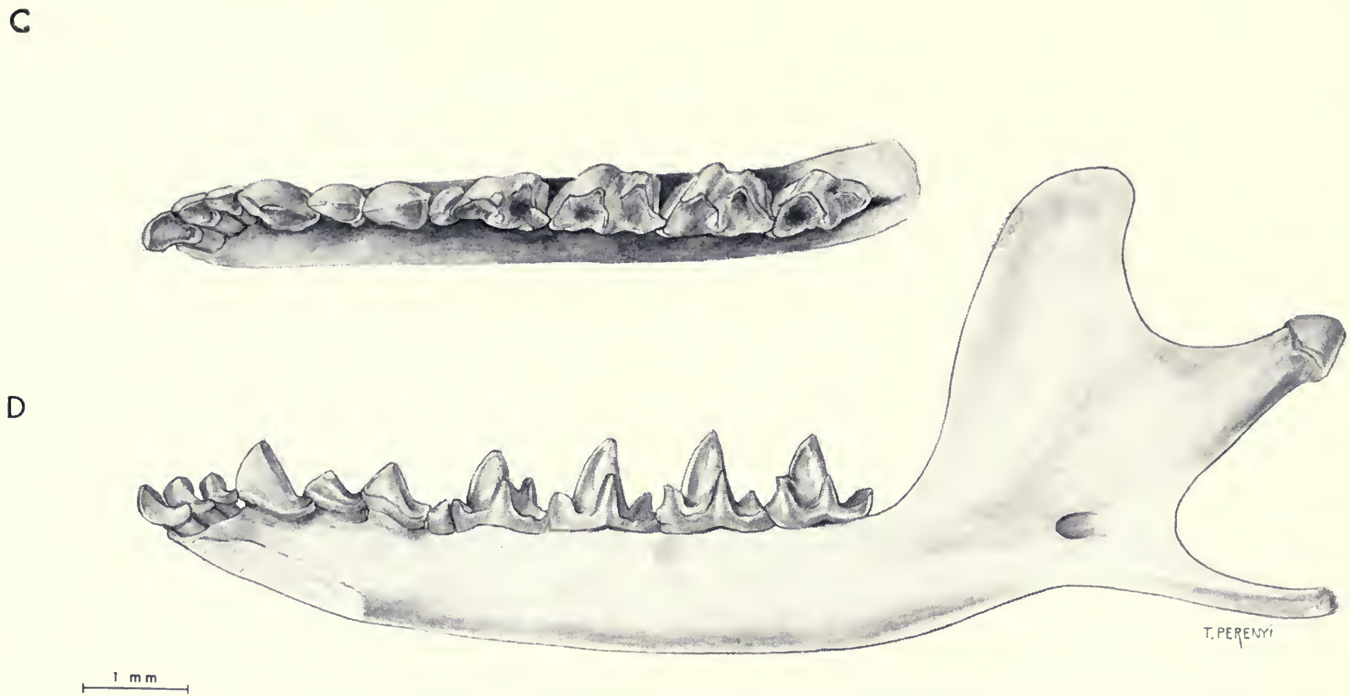


FIG. 11. C, D. *Planigale ingrami*, AMNH 160308. Occlusal and lingual views of right jaw and the lower dentition.

joins the cingulum. Posterior to the apex there is a similar crest that descends to the broadened cingular shelf with its cuspule. Wear rapidly produces a flat surface on this crest, a surface that broadens with increased attrition. The cingulum completely surrounds the tooth at its base. It is weak anteriorly, and pronounced posteriorly, especially postero-labially.

The $M_{\overline{1}}$ is a triangular tooth with the protoconid and metaconid about equal in height and placed very close together. The paraconid is very much smaller and forms the anterior end of the tooth. The talonid is basined. It is bordered labially by the hypoconid, which is about one-half the height of the protoconid. It is bordered lingually by a low, rounded ridge which joins the metaconid and the hypoconulid. The posterior margin of the talonid is concave and broadly "V"-shaped. The hypoconulid is a low cusp in TMM 41106-666 located at the posterolingual corner of the talonid. It is the posterior-most cusp of the tooth. The hypoconid and the hypoconulid are joined in TMM 41106-666 by a ridge that forms the posterior margin of the talonid basin. The hypoconulid in TMM 41106-660 is a slightly elongate blunt cusp. It is not joined to the hypoconid. The talonid basin is thus open posteriorly. There is no entoconid in either TMM 41106-666 or TMM 41106-660. A postcingulum extends from the base of the hypoconid up the posterior face of the tooth and merges with the hypoconulid.

The $M_{\overline{2}}$ and $M_{\overline{3}}$ have the normal dasyurid structure. The trigonid is well developed. There is a deep, narrow cleft developed in the paracristid (I′) ridge that connects the paraconid and protoconid. The talonid is basined and is wider than long. As in the $M_{\overline{1}}$ there is no entoconid. The talonid is proportionately shorter than in most other dasyurids. Its posterior edge is straight and parallel to the posterior edge of the trigonid except at the posterolingual corner where it turns abruptly posteriorly to join the hypoconulid. The anterior cingulum extends upward from the antero-labial side of the base of the protoconid but does not reach the anterior edge of the paraconid. It ends abruptly where the postero-lingual corner of the preceeding tooth is in contact with the paraconid. The posterior cingulum extends upward along the posterior face of the talonid and joins the hypoconulid.

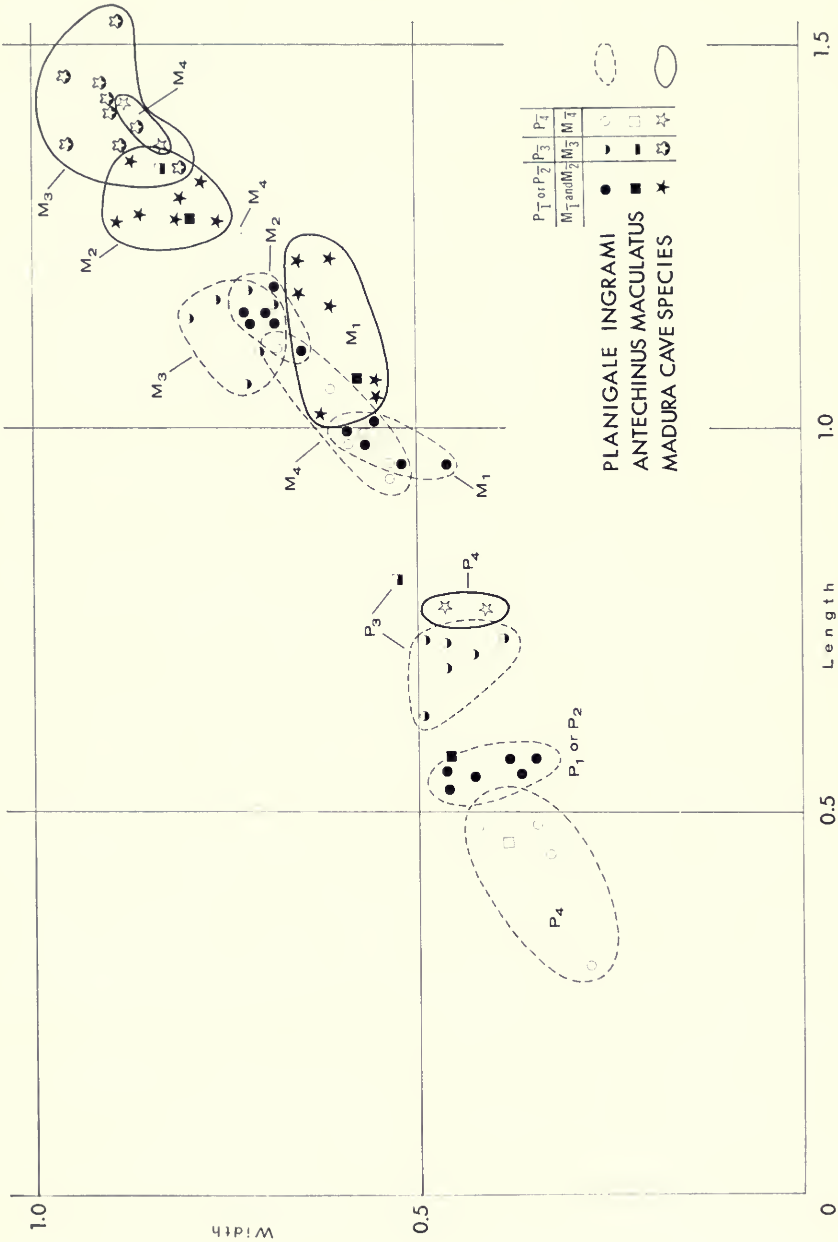
The only $M_{\overline{4}}$ is in PM 25597. It has a trigonid that is nearly the same as that of $M_{\overline{3}}$ in its proportions (fig. 9B), being only slightly smaller and more compressed laterally. The protoconid is much the largest cusp in both height and bulk. It is followed by the metaconid which is rather columnar and stands nearly two-thirds as high as the protoconid. The paraconid has a broad base but it barely reaches to two-thirds the height of the metaconid in its worn state. Since this cusp shows more wear than the others, it probably was nearly as high as the metaconid in the unworn tooth. Both crests, paracristid (I′) and the combined epicristid-centrocristid (II′ and Ia‴), have a carnassial notch and groove. The posterior part of the centrocristid (Ib‴) joins this main crest of the epicristid at its base, medial to the groove. The talonid is laterally compressed, progressively toward the rear. It has a well-developed hypoconid. Antero-lingual to the hypoconid there is an elongated shallow basin delimited by hypoconid, centrocristid, metaconid, and a low cingular crest, apparently equivalent to the combined postmetacristid, disto-cristid, and entocristid (I″, VI, and V in the Hershkovitz symbolism) There is no entoconid or hypoconulid. The anterior cingulum is well developed with a good parastylid and another more labial stylid, the two surrounding the hypoconulid of the $M_{\overline{3}}$.

Discussion.—Pigmy antechinuses are the smallest of the dasyurids and are among the smallest-sized mammals. They are not well-represented in collections and are poorly known as to their dental morphology, their ecology, and their taxonomy.

A comparison of the Madura Cave specimens with those of Recent species shows many similarities, such as size and the tendency to crowd the premolars. Comparison also reveals a number of differences that indicate that the Madura Cave form is different from the described Recent species. In general, the cheek teeth of the Madura Cave form are slightly larger than their counterparts in Recent *Planigale ingrami*, especially $P_{\overline{4}}$ and $M_{\overline{2}-\overline{4}}$ (figs. 12, 13; tables 1, 2). Comparison with $M_{\overline{1}-\overline{3}}$ of *Antechinus maculatus* is very close (fig. 12). However, $P_{\overline{4}}$ is much longer in the Madura Cave form than it is in either *Planigale ingrami* or *Antechinus maculatus*. The $M_{\overline{4}}$ is also larger than that of *Antechinus maculatus* but the difference is not as great as with *Planigale ingrami*.

It is clear that the Madura Cave material cannot be referred to any of the described species of pygmy antechinuses. In addition, it is clear, as stated by Ride (1970), that the generic grouping of the species of pygmy antechinuses is still in doubt. For these reasons we are not assigning the Madura Cave material to a genus or species.

General faunal and environmental significance of the presence of this taxon in the Madura Cave deposits will be deferred until the discussion in the final section of our series on the Madura Cave. It


PLANIGALE INGRAMI
ANTECHINUS MACULATUS
MADURA CAVE SPECIES
Length
Width
P1 or P2
P3
P4
M1
M2
M3
M4
0
0.5
1.0
1.5

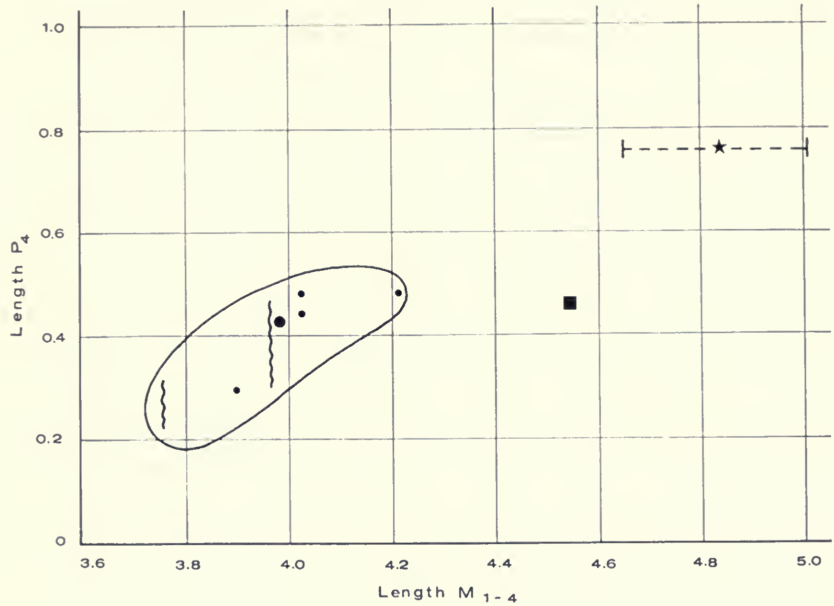


FIG. 13. Bivariate graph comparing *Planigale ingrami* (circle), *Antechinus maculatus* (square), and the Madura Cave *Planigale*-like species (star). Length of lower molar tooth row is plotted against length of $P_{\overline{4}}$ in each case. Individually each of the lower teeth of the Madura form is, or tends to be, slightly larger than its counterpart in the other species. This results in a cumulative difference seen in these plots so as to give complete separation of the taxa. Wavy lines in the *P. ingrami* plot show specimens for which only the $M_{\overline{1}\text{-}\overline{4}}$ length value was available. The dashed line of the Madura species plot is an estimate of the probable limits of the range of the $M_{\overline{1}\text{-}\overline{4}}$ length values. It is based upon the cumulative e ngths of the smallest of each of the molars ($M_{\overline{1}} + M_{\overline{2}}$ etc.) for the shortest limit, and the largest of each for the longest limit. The star is at the position of the mean. In each case a 93 per cent factor was applied to accomodate for the overlapping of the teeth in the series. This factor was chosen because it applied to both of the other taxa shown, and hence gave the best indication of what could be expected in the Madura form. The only $P_{\overline{4}}$'s available are both the same length, so there is no way of estimating the range of variability from the sample in that case.

should be noted that Madura Cave is over 1,000 miles from the closest known occurrence of any living pigmy antechinus as follows: *Antechinus maculatus* in the extreme southeast corner of South Australia; *Planigale ingrami* in north and central Queensland and north of both Western Australia and the Northern Territory; *Plani-*

FIG. 12. Bivariate graph comparing proportions of the lower cheek teeth of *Planigale ingrami, Antechinus maculatus,* and the Madura Cave *Planigale*-like form. Width measurements used are anterior widths of molars and maximum widths of premolars.

TABLE 1. Measurements of upper teeth of the Madura pigmy antechinus near *Planigale ingrami* and *Antechinus maculatus* compared with those of the named species.

Species and Trench, Unit and Level		*Antechinus maculatus*	Madura form, species indet. Trench 4, Units 4–5								*Planigale ingrami*							
Specimen numbers		FMNH 64350	TMM 41106 -680R and -740	PM 25621	PM 26190	TMM 41106 -741	PM 26216	WAM 72.3.2	N	Mean	FMNH 66973	AMNH 160066	AMNH 160307-8		AMNH 160311-2		N	Mean
Side		R	L	L	L	L	L	R						R	R	R		
L. P^1 or $^2 - P^4$		1.69									1.60	1.41	1.56	1.48	1.48	1.75	6	1.55
L. M^{1-3}		3.72									3.31	3.15	3.12	3.19	3.14	3.42	6	3.22
L. M^{1-4}		4.13									3.69	3.53	3.42	3.61	3.57	3.80	6	3.60
P^1 or ^{2}	L.	.49									.39	.34	.42	.49	.46	.48	6	.43
	W.	.32									.34	.34	.30	.34	.36	.34	6	.34
P^3	L.	.49		.84					1	.84	.45	.38	.49	.53	.53	.53	6	.49
	W.	.38		.47					1	.47	.34	.34	.30	.38	.38	.38	6	.35
P^4	L.	.76		1.06					1	1.06	.66	.57	.63	.65	.59	.76	6	.64
	W.	.46		.63					1	.63	.29	.30	.34	.38	.36	.42	6	.35
M^1	L.	1.52	1.37				1.34	1.37	3	1.36	1.25	1.25	1.18	1.24	1.25	1.33	6	1.25
	W.	.87	1.01				1.06	1.01	3	1.03	.72	.76	.72	.76	.80	.87	6	.77
M^2	L.	1.21				1.24			1	1.24	1.10	1.06	1.06	1.10	1.10	1.18	6	1.10
	W.	1.17				1.30			1	1.30	1.05	1.03	.93	1.06	1.14	1.18	6	1.07
M^3	L.	1.06	1.27		1.29				2	1.28	1.03	.87	.91	.91	.87	.95	6	.92
	W.	1.33	1.37		1.44				2	1.41	1.05	1.03	1.03	1.10	1.18	1.29	6	1.11
M^4	L.	.45									.48	.38	.38	.34	.42	.38	6	.40
	W.	1.17									.94	.80	.99	.91	.95	1.10	6	.95

TABLE 2a. Measurements of lower teeth of *Antechinus maculatus* and the Madura fossil pigmy antechinus near *Planigale ingrami* and *A. maculatus* to be compared with those of *P. ingrami* (Table 2b).

			Madura form, species indet.													
			Trench 4, Unit 2, Level 2							Tr. 3, Unit 3	Tr. 4, Units 4–5			Tr. 4, Unit 7		
Species and Trench, Unit and Level Specimen numbers		*Antechinus maculatus* FMNH 64350	TMM 41106 -663	WAM 72.3.6 & PM 25596	PM 25597	TMM 41106 -743R & 744	TMM 25710R & PM 25713R	WAM 72.3.7 & PM 26193	TMM 41106 -754R PM 26269	TMM 41106 -660	TMM 41106 -696	TMM 41106 -699	PM 26191R & PM 26192	TMM 41106 -659		
Side		R	R	R	R	R		L	R	R	L	L	R	R	N	Mean
Distance from front of $P_{\overline{4}}$ to front of $M_{\overline{1}}$		.42									.65			.61	2	.63
L. $M_{\overline{1}-\overline{4}}$		4.55														
$P_{\overline{1}}$ or $_{\overline{2}}$	L.	.57														
	W.	.46														
$P_{\overline{3}}$	L.	.80														
	W.	.53														
$P_{\overline{4}}$	L.	.46									.76			.76	2	.76
	W.	.38									.41			.46	2	.44
$M_{\overline{1}}$	L.	1.06		1.06				1.22	1.15	1.04	1.01		1.22	1.17	7	1.12
	AW.	.57		.56				.66	.61	.56	.63		.61	.66	7	.61
	PW.	.61		.61				.79	.66	.58	.69		.69	.74	7	.69
$M_{\overline{2}}$	L.	1.27	1.27	1.30			*1.37	1.27			1.27	1.28	1.32		6	1.29
	AW.	.80	.76	.81			* .89	.89			.81	.86	.79		6	.82
	PW.	.76	.66	.71			* .71	.86			.74	.76	.74		6	.75
M	L.	1.33	1.34	1.45	1.42	*1.46	1.52	1.37	*1.38		1.37	1.42			7	1.41
	AW.	.84	.81	.91	.91	* .96	.89	.96	* .87		.89	.91			7	.90
	PW.	.72	.63	.71	.76	* .71	.76	.81	* .73		.79	.76			7	.75
$M_{\overline{4}}$	L.	1.25			1.42	1.36									2	1.39
	AW.	.74			.89	.84									2	.87
	PW.	.27			.30	.37									2	.34

*Specimens for which there is some uncertainty as to assignment between $M_{\overline{2}}$ and $M_{\overline{3}}$.
They are omitted from the values of N and Means, but in no case would inclusion change a Mean value by more .01.

TABLE 2b. Measurements of lower teeth of *Planigale ingrami* for comparison with those of *Antechinus maculatus* and the Madura form.

Species and Trench, Unit and Level		*Planigale ingrami*							
		FMNH	AMNH	AMNH		AMNH			
Specimen numbers		66973	160066	160307-8		160311-2		N	Mean
Side		R	R	R	R	R	R		
Distance from front of $P_{\overline{4}}$ to front of $M_{\overline{1}}$		.38	.08		.19			3	.22
L. $M_{\overline{1}-\overline{4}}$		4.03	3.89	3.75	4.03	3.96	4.22	6	3.98
$P_{\overline{1}}$ or $_{\overline{2}}$	L.	.55	.55	.57	.57	.53	.55	6	.55
	W.	.36	.42	.34	.38	.46	.46	6	.40
$P_{\overline{3}}$	L.	.70	.72	.72	.72	.68	.61	6	.69
	W.	.42	.46	.38	.49	.46	.49	6	.45
$P_{\overline{4}}$	L.	.44	.30		.48		.48	4	.43
	W.	.32	.27		.34		.42	4	.34
$M_{\overline{1}}$	L.	.95	.99	.95	1.01	.99	1.03	6	.99
	AW.	.51	.57	.46	.55	.59	—	5	.54
	PW.	.57	.59	.51	.61	.61	.61	6	.58
$M_{\overline{2}}$	L.	1.18	1.14	1.10	1.14	1.14	1.14	6	1.14
	AW.	.68	.68	.65	.68	.72	.72	6	.69
	PW.	.62	.68	.61	.65	.68	.68	6	.65
$M_{\overline{3}}$	L.	1.16	1.10	1.05	1.18	1.14	1.16	6	1.13
	AW.	.68	.70	.72	.72	.80	.76	6	.73
	PW.	.57	.57	.53	.63	.57	.68	6	.59
$M_{\overline{4}}$	L.	.98	.95	.93	1.05	.99	1.10	6	1.00
	AW.	.58	.53	.53	.61	.57	.68	6	.58
	PW.	.27	.17	.23	.25	.19	.23	6	.22

gale tenuirostris in south-central Queensland and northeast New South Wales.

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