Leporillus (Rodentia: Muridae) from Madura Cave, W.A.

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Two species of the genus *Leporillus* are represented in the Pleistocene-Holocene sediments of Madura Cave. *Leporillus conditor* is abundant and ranges from the surface to the deepest level (38,000 BP). *L. apicalis* is less abundant and appears to be restricted to levels dating from 7,500 to 22,400 BP.

Most of the specimens are dissociated because they are derived from owl pellets and thus specific identification is difficult. Many of the dimensions of the teeth of the two species overlap and there are few diagnostic features that separate them. Watts and Aslin gave criteria for the genus based on modern material. We have attempted to evaluate features that would separate the species on the basis of incomplete cranial and dental materials.

We describe a few of the better specimens, discuss their morphologic features and historic distributions. From this work we are able to document the time span of their presence on the Roe Plain, that part of the Nullarbor Plain south of the Hampton Scarp. The species do not show any significant evolutionary changes during these intervals.

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KEYWORDS: Australia, dentition, Holocene, *Leporillus apicalis*, *Leporillus conditor*, Muridae, Nullarbor Plain, Pleistocene, Rodentia.

INTRODUCTION

This report is abstracted from an ongoing study of the rodents from Madura Cave, Part VIII of THE MAMMALIAN FAUNA OF MADURA CAVE. Here we report the presence of both species of the murid rodent genus *Leporillus*; *L. conditor*, the greater sticknest rat, or Walpilkara, and *L. apicalis*, the lesser sticknest rat, or Tchujalpi, Turulpa, Tweealpi and show their chronologic distributions within the cave deposits. There are well over 1,700 specimens of *L. conditor* ranging from the surface, all units between Unit 1, dated at 7,500 BP, to the bottom unit of the deepest trench, Unit 7, dated at 38,000 BP. *L. apicalis* is much less abundant; 59 specimens were recovered, none from the surface, most (38) from Unit 1 and 21 from the upper part of Unit 2. (15,600 to 22,400 BP).

Madura Cave is located on the Roe Plain, the area on the southern edge of the Nullarbor Plain, six miles south of Madura, 110 miles west of Eucla. A fuller description of the cave is given in Lundelius and Turnbull (1973). The earlier illustrations of the cave map and trench sections are repeated here (Figs. 1–4) to give the reader convenient access to the stratigraphy encountered in each trench.

AGE OF DEPOSITS

Five radiocarbon dates from Trench 4 span a 30,000 year period between 7,470 ± 129 BP (TX 1146) and 37,880 ± 3,500 BP (TX 1143). Two radiocarbon dates from Trench 3 are 15,600 ± 250 BP (TX 1145) from the top of the second unit (red clay) and

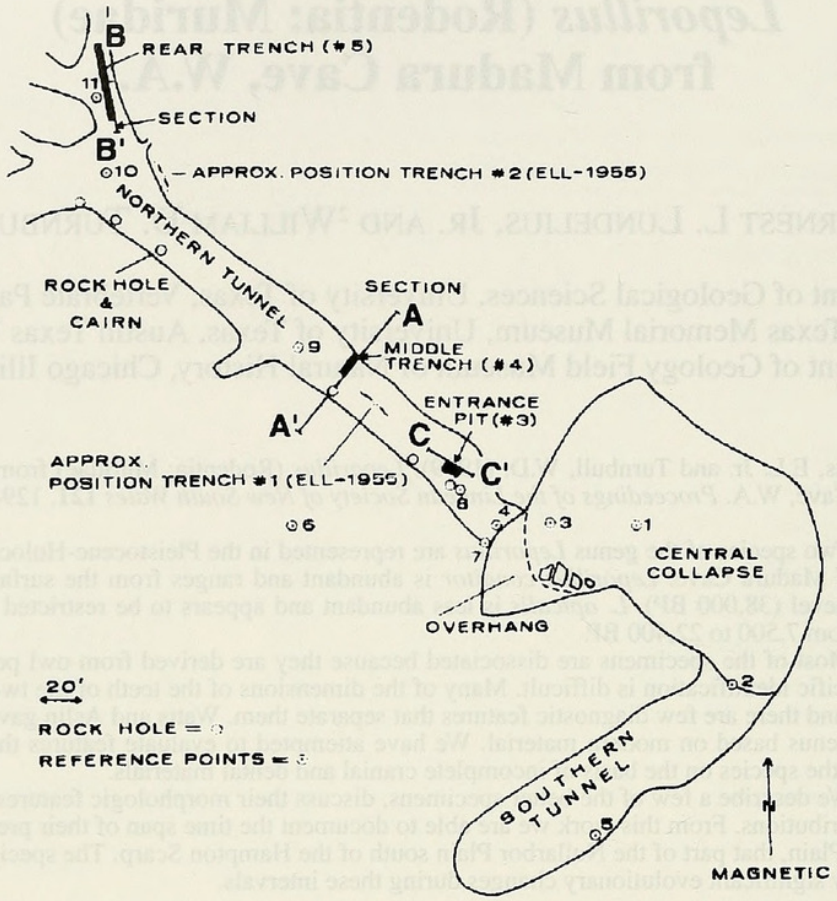


Figure 1. Map of Madura Cave showing the central doline, the northern and southern tunnels, and the positions of the excavations.

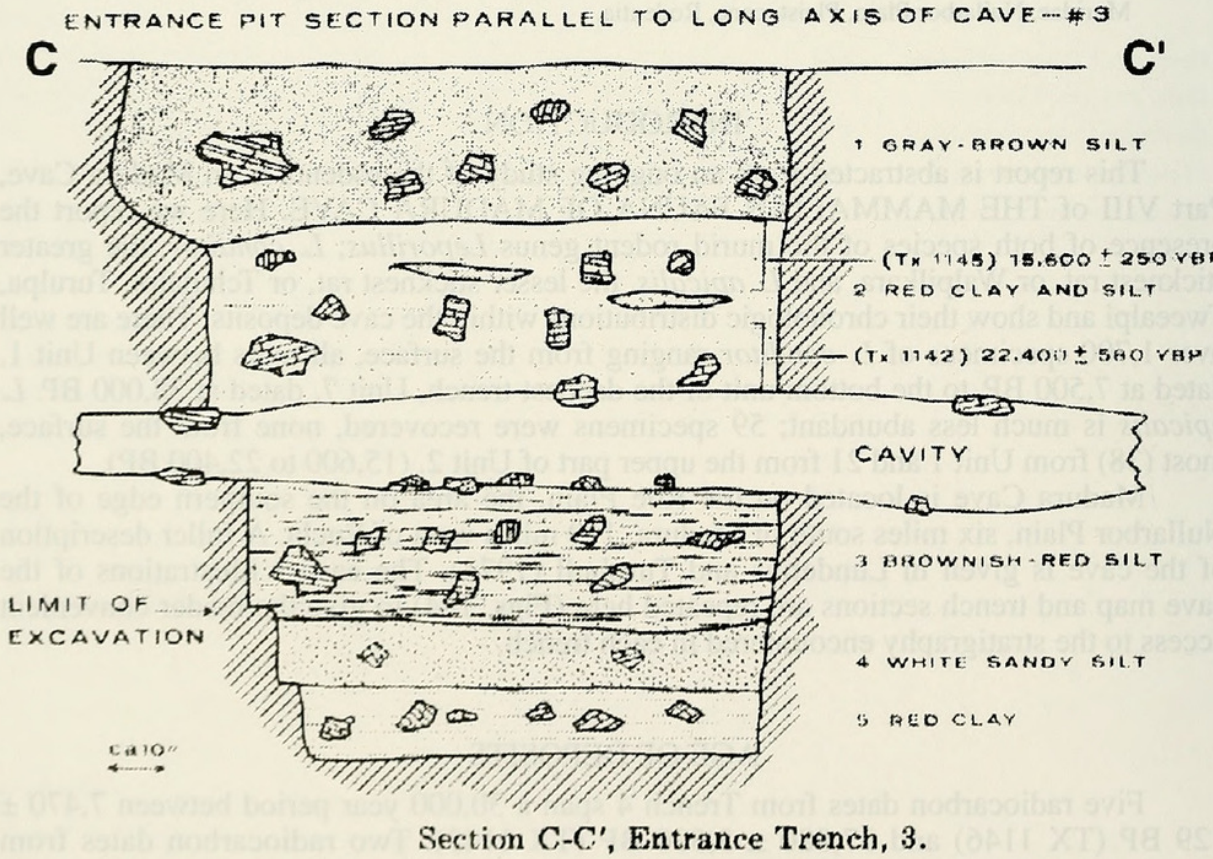
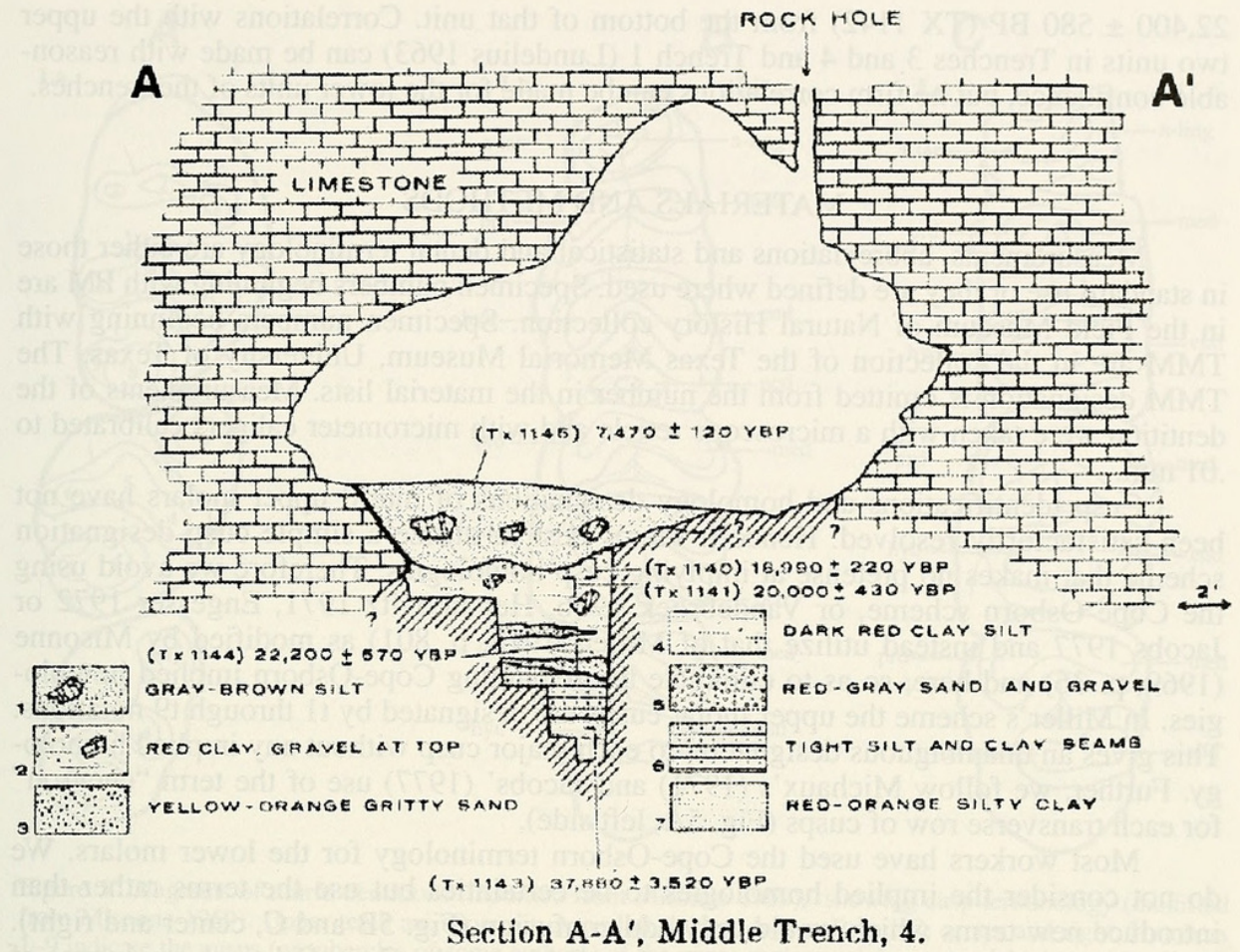


Figure 2. Stratigraphic section exposed in Trench #3.



Section A-A', Middle Trench, 4.

Figure 3. Stratigraphic section exposed in Trench #4.

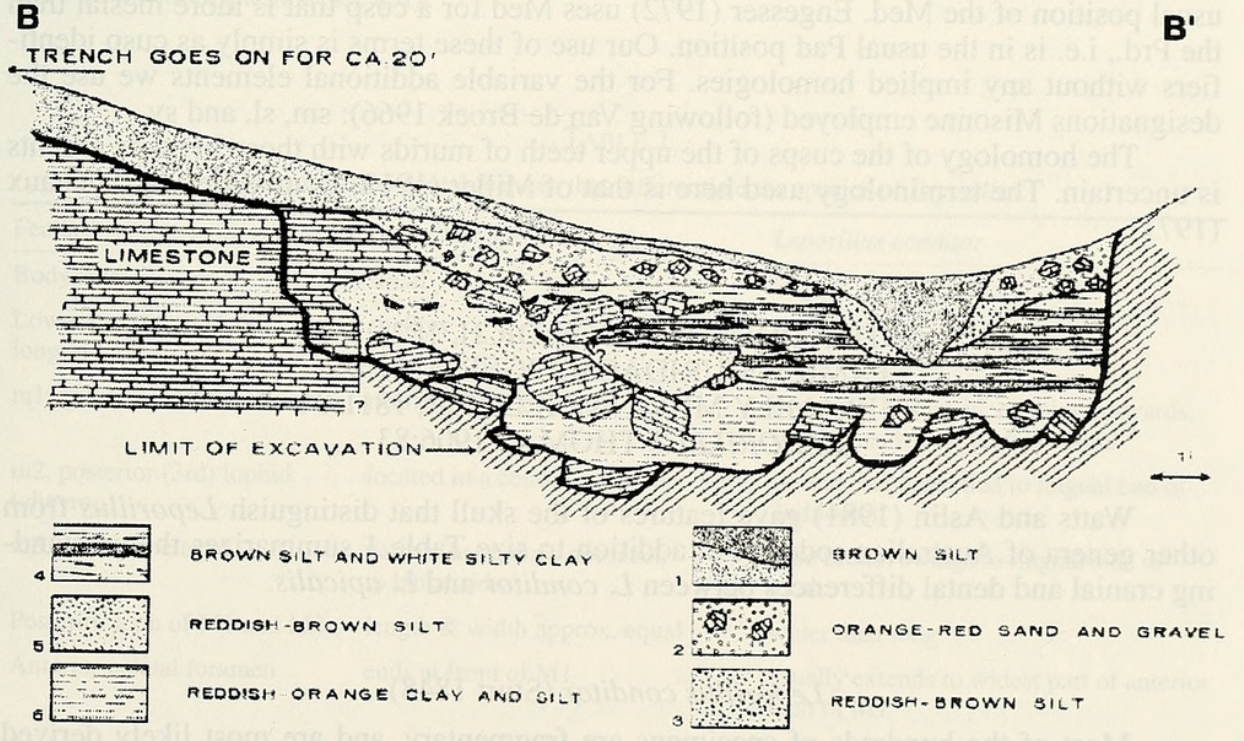


Figure 4. Cross section of northern tunnel at Trench #5 showing the stratigraphic section exposed in this trench.

22,400 ± 580 BP (TX 1142) from the bottom of that unit. Correlations with the upper two units in Trenches 3 and 4 and Trench 1 (Lundelius 1963) can be made with reasonable confidence, but no firm correlations can be made for the lower units of the trenches.

MATERIALS AND METHODS

Measurements, abbreviations and statistical and dental terminology are either those in standard use or they are defined where used. Specimen numbers beginning with PM are in the Field Museum of Natural History collection. Specimen numbers beginning with TMM are in the collection of the Texas Memorial Museum, University of Texas. The TMM designation is omitted from the number in the material lists. Measurements of the dentition were taken with a microscope reticle and with micrometer calipers calibrated to .01 mm.

Cusp identifications and homology designations of murid upper molars have not been satisfactorily resolved. Hence it seems best to utilize a simple cusp designation scheme that makes no pretense at implying cusp homologies. Therefore we avoid using the Cope-Osborn scheme, or Vandebroek 1966, Hershkovitz 1971, Engesser 1972 or Jacobs 1977 and instead utilize that of Miller (1912, p. 801) as modified by Misonne (1969, p. 36) and here, so as to eliminate the remaining Cope-Osborn implied homologies. In Miller's scheme the upper molar cusps are designated by t1 through t9 notations. This gives an unambiguous designation to each major cusp without any implied homology. Further, we follow Michaux's (1971) and Jacobs' (1977) use of the term "chevron" for each transverse row of cusps (Fig. 5A, left side).

Most workers have used the Cope-Osborn terminology for the lower molars. We do not consider the implied homologies to be certainties but use the terms rather than introduce new terms which would only add confusion (Fig. 5B and C, center and right). The cusps labeled Prd, Hyd, End and Hyld probably are the Cope-Osborn homologues of protoconid, hypoconid, entoconid and hypoconulid respectively. The homologies of those labeled Pad (paraconid) and Med (metaconid) however are dubious. For example, Misonne used Pad, which he states is more distal than the Prd. However that is the more usual position of the Med. Engesser (1972) uses Med for a cusp that is more mesial than the Prd., i.e. is in the usual Pad position. Our use of these terms is simply as cusp identifiers without any implied homologies. For the variable additional elements we use the designations Misonne employed (following Van de Broek 1966): sm, sl, and sv.

The homology of the cusps of the upper teeth of murids with those of other rodents is uncertain. The terminology used here is that of Miller (1912) as modified by Michaux (1971).

ORDER RODENTIA BOWDICH, 1821:7, 51
FAMILY MURIDAE ILLIGER, 1811:84
SUBFAMILY MURINAE ILLIGER, 1811:84
LEPORILLUS THOMAS 1906:83

Watts and Aslin (1981) gave features of the skull that distinguish *Leporillus* from other genera of Australian rodents. In addition to size Table 1 summarizes the outstanding cranial and dental differences between *L. conditor* and *L. apicalis*.

Leporillus conditor (Sturt 1848)

Most of the hundreds of specimens are fragmentary, and are most likely derived from owl pellets.

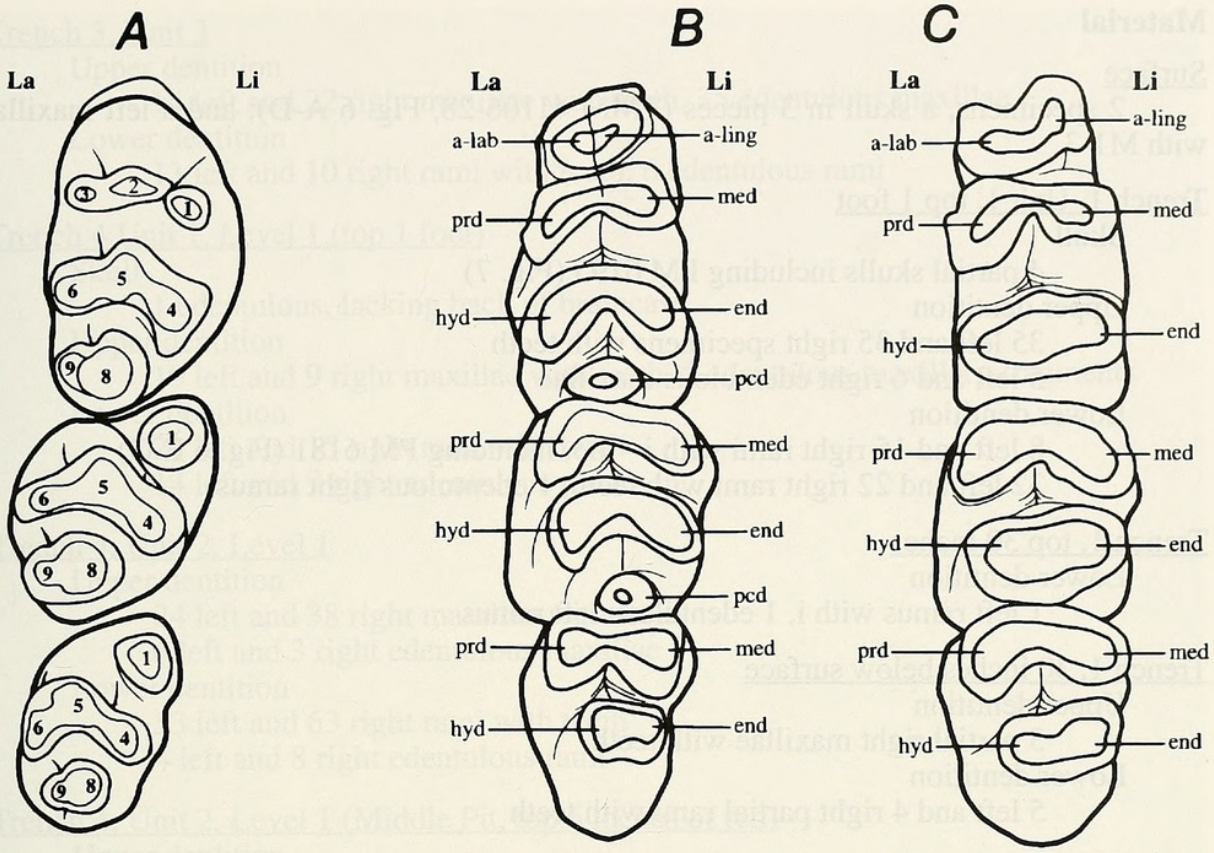


Figure 5. Diagrams of murid dentitions (modified from Misonne 1969), showing cusp terminology (modified from Misonne 1969). Upper teeth are shown in A on left, lower teeth in B and C, center and right. Numbers 1–9 indicate the cusps (or tubercles of some authors) of the upper molars, a-lab = anterolabial cuspid, a-ling = anterolingual cuspid, end = entoconid, hyd = hypoconid, med = metaconid, pcd = postcingulid, and prd = protoconid. For the lower teeth we show different age/wear stages. In B, the younger of the two, a post-cingulid cuspid is present (pcd of m1, m2), and in C those cuspids have worn away so that their bases are fused with the posterior lophids. For lower teeth, Misonne followed Vandebroek (1966) adding the Cope-Osborne equivalents, a few of which we question (see text).

TABLE 1.

Size, cranial and dental features that differentiate the species of *Leporillus*.

Feature	*Leporillus apicalis*	*Leporillus conditor*
Body size	small	large
Lower molars, median longitudinal groove	shallow	deep
m1, anterior lophid	nearly evenly rounded	decidedly V-shaped, opening forwards, sometimes with a central cuspid
m2, posterior (3rd) lophid (chevron)	located in a central position	central, but more tied to lingual end of 2nd lophid
m3, posterior cuspid	narrow base; does not reach to labial side	base broad; swings to lingual side of tooth
Posterior loph of M1 and M2	length & width approx. equal	wider than long
Anterior palatal foramen	ends at front of M1	usually extends to widest part of anterior loph of M1
Position of mental foramen	Just at front of masseteric tubercle	well anterior to masseteric tubercle

Material

Surface

2 specimens, a skull in 3 pieces (TMM 41106-28, Fig. 6 A-D); and a left maxilla with M1-3

Trench 1, Unit 1, top 1 foot

Skull

4 partial skulls including PM 6195 (Fig. 7)

Upper dentition

35 left and 35 right specimens with teeth

5 left and 6 right edentulous maxillae

Lower dentition

8 left and 15 right rami with i - m3, including PM 6181 (Fig. 6 E-G)

32 left and 22 right rami with teeth, 1 edentulous right ramus

Trench 1, top 30 inches

Lower dentition

1 left ramus with i, 1 edentulous left ramus

Trench 1, 30 inches below surface

Upper dentition

3 partial right maxillae with teeth

Lower dentition

5 left and 4 right partial rami with teeth

Trench 2, Unit 1, Level 1

Upper dentition

1 right maxilla with M1-3

Lower dentition

1 left and 2 right partial rami with teeth

Trench 2, 2 1/2 feet below surface

Upper dentition

3 right maxillae with teeth, 1 edentulous right maxilla

Lower dentition

2 left and 5 right rami with teeth, 1 edentulous right ramus

Trench 3, Unit unknown

Upper dentition

1 left maxilla with M1

Trench 3, Unit 2, Level unknown

Skull

1 with left and right M1-3, 1 with right M2-3

Upper dentition

94 left and 108 right specimens with teeth, 6 isolated molars

Lower dentition

134 left and 129 right rami with teeth

16 left and 16 right edentulous rami

Trench 3, Unit 2, Level 2

Upper dentition

33 left and 33 right maxillae with teeth, 1 right I

15 left and 12 right edentulous maxillae

Lower dentition

6 left and 19 right rami with teeth, 2 left and 7 right edentulous rami

Trench 3, Unit 3
- Upper dentition
  - 14 left and 22 right maxillae with teeth, 35 edentulous maxillae
- Lower dentition
  - 13 left and 10 right rami with teeth, 6 edentulous rami

Trench 4 Unit 1, Level 1 (top 1 foot)
- Skull
  - 1 edentulous, lacking back of braincase
- Upper dentition
  - 10 left and 9 right maxillae with teeth, 5 edentulous maxillary fragments
- Lower dentition
  - 21 left and 15 right rami with teeth
  - 14 left and 9 right edentulous rami

Trench 4, Unit 2, Level 1
- Upper dentition
  - 24 left and 38 right maxillae with teeth
  - 6 left and 3 right edentulous maxillae
- Lower dentition
  - 53 left and 63 right rami with teeth
  - 4 left and 8 right edentulous rami

Trench 4, Unit 2, Level 1 (Middle Pit, top 6 inches of red)
- Upper dentition
  - 4 left and 2 right maxillae with teeth, and 2 edentulous left maxillae
- Lower dentition
  - 8 left and 8 right rami with teeth, 3 edentulous rami

Trench 4, Unit 2, Level 2
- Upper dentition
  - 22 left and 25 right maxillae with teeth
  - 10 left and 14 right edentulous maxillae
- Lower dentition
  - 79 left and 56 right rami with teeth
  - 12 left and 13 right edentulous rami

Trench 4, Unit 2, Level 3
- Upper dentition
  - 1 left and 1 right maxillae with teeth, 2 edentulous maxillary fragments
- Lower dentition
  - 1 left and 8 right rami with teeth, 2 left and 4 right edentulous rami

Trench 4 Unit 4–5
- Upper dentition
  - 9 left and 16 right maxillae with teeth, 24 edentulous maxillary fragments
- Lower dentition
  - 6 left and 11 right rami with teeth
  - 12 left and 11 right edentulous rami

Trench 4, Unit 7, Level 1
- Upper dentition
  - 2 left and 3 right maxillae with teeth, 1 edentulous maxillary fragment
- Lower dentition
  - 2 left and 1 right rami with teeth

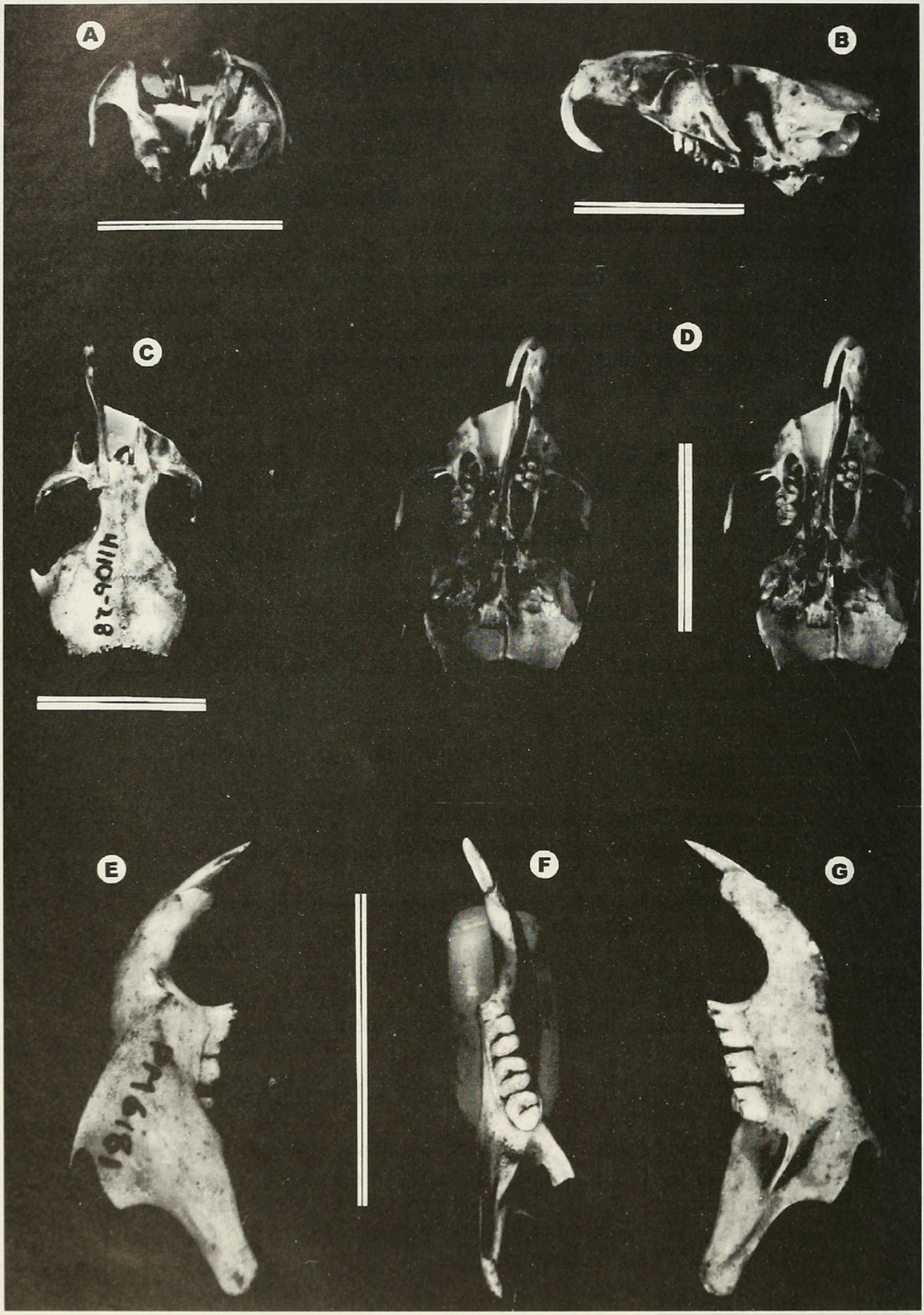


Figure 6. *Leporillus conditor*. A–D, TMM 41106-28, a nearly complete skull shown in A, anterior; B, left lateral; C, dorsal; and D, ventral stereo views; E–G, PM 6181, left mandibular ramus with I, m1-3 shown in E, left lateral; F, occlusal; and G, lingual views. Scale bars are 2 cm. long. FMNH negative numbers are G 85962-85967.

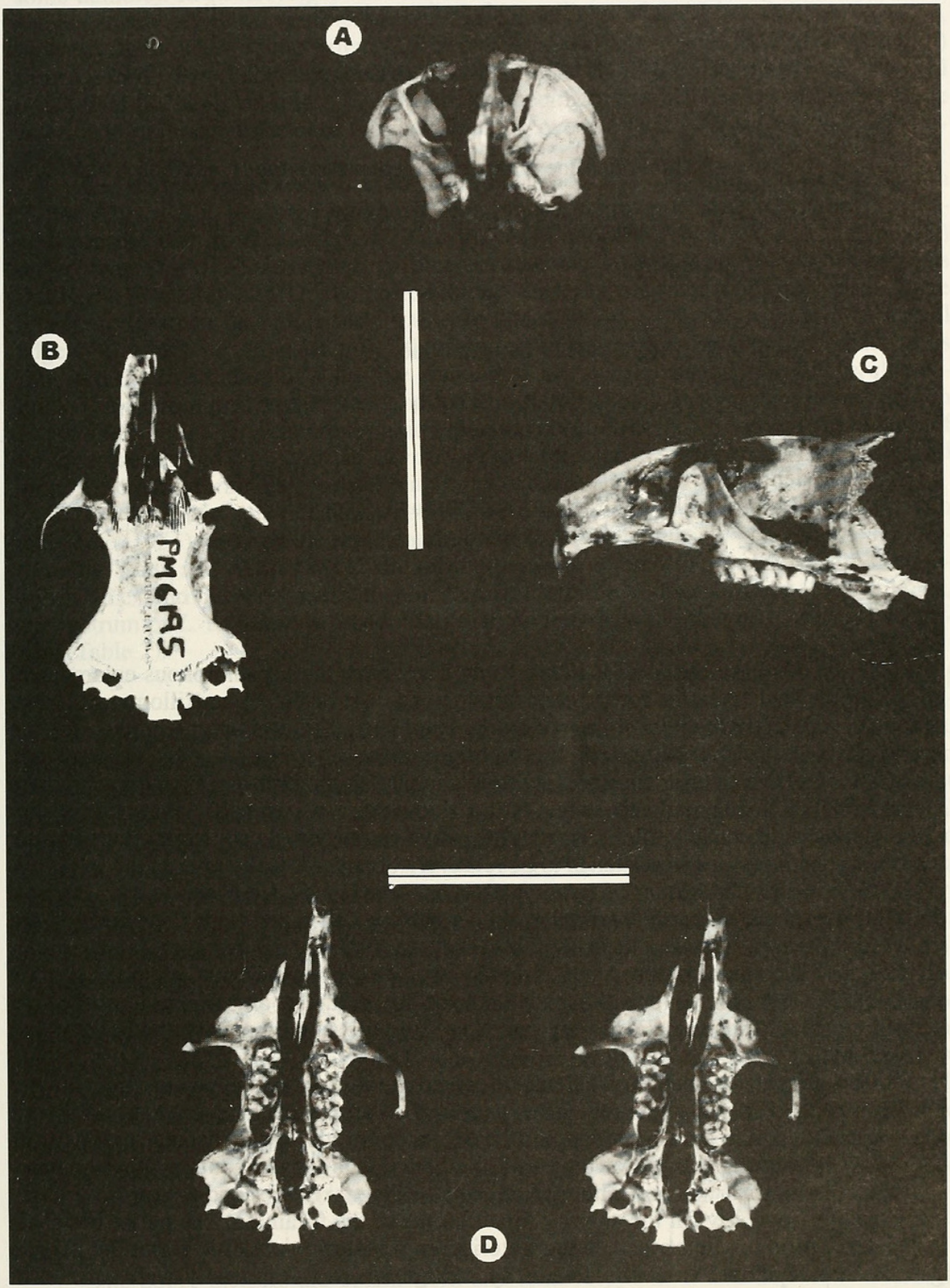


Figure 7. *Leporillus conditor*. A–D, PM 6195, a nearly complete skull shown in A, anterior; B, dorsal; C, left lateral; and D, ventral stereo views. Scale bars are 2 cm. long. FMNH negative numbers are G 85954-85958.

Trench 4, Unit 7, Level 2

Upper dentition

5 left and 14 right maxillae with teeth, 6 edentulous maxillary fragments

Lower dentition

11 left and 8 right rami with teeth, 9 left and 8 right edentulous rami

Trench 4, Unit 7

Upper dentition

2 left and 3 right maxillae with teeth, 6 edentulous right maxillae

Lower dentition

6 left and 3 right rami with teeth, 9 left and 4 right edentulous rami

Trench 5, Lower Red Unit

Upper dentition

5 left and 5 right maxillae with teeth

15 left and 21 right edentulous maxillae

Lower dentition

2 left and 3 right rami with teeth, 9 left and 10 right edentulous rami

Trench 5, Laminated Unit

Upper dentition

1 right maxilla with M1-3, 1 edentulous left maxilla

1 right M1, and 1 left M2

Descriptions

Skull

The skulls have the normal murid form. They have the myomorphous enlargement of the infraorbital foramina for the transmission of a part of the M. maxillomandibularis. It is more oval, less circular than in *Rattus norvegicus*. There is an enlargement of the anterior face of the zygomatic arch for the origin of the anterior part of the M. masseter, pars profunda. The anterior edge of the zygomatic plate is straight. At its ventral end there is a small tubercle that marks the origin of the M. masseter, pars superficialis and probably also the M. masseter, pars reflexa. There is no spine on the dorsal end. In anterior view the zygomatic plate of *L. conditor* tends to be relatively broader dorsally rather than in *L. apicalis*. The anterior part of the zygomatic arch is not broadened as in *Notomys*.

In dorsal view the interorbital width is narrow compared with the width of the braincase which is expanded laterally. This is true for both species but is more extreme in *L. conditor*. There are no raised supraorbital ridges on the frontal bone, although it turns ventrally very abruptly to form the medial side of the orbit. The dorsal margin of the area of origin of the M. temporalis closely corresponds to the suture between the parietal and squamosal.

The incisive foramen is large and is located at the front of the palate, immediately posterior to the upper incisors. The anterior palatal foramina are long, extending forward from just posterior to the anterior end of the M1 three fourths of the distance to the upper incisors. They have the shape of long ovals and are about equally contained by the maxillary and premaxillary bones. The median parts of the maxillaries and the premaxillaries are expanded to nearly fill the anterior three fourths of the foramina. The palate has shallow lateral grooves that connect the anterior and posterior palatine foramina. These grooves are separated from the alveoli by a ridge which is especially well defined in younger individuals. The posterior palatal foramina are oval in shape and are located opposite the M2. The post palatine spine is larger than that of *Rattus norvegicus*.

The cranial foramina are similar in their arrangement to those of *Rattus norvegicus*. The foramen ovale is about the same size in *L. conditor* as in *R. norvegicus*

and is located low on the outer edge of the ectopterygoid fossa (entire pterygoid fossa of some authors). In *R. norvegicus* the foramen ovale is more inclined upwards anteriorly and is entirely above the ectopterygoid fossa. Further, in *R. norvegicus* there is variation, probably age related, in the extent of its ventral exposure. Musser (1981, p. 235, Fig. 5) shows it to be partly hidden and partly confluent with the median lacerate foramen based on AMNH 207554, while in a Field Museum specimen, FMNH 154733, it is seen to lie anterior to the median lacerate foramen, bridged over and partly obscured by the pterygoid ridge.

The ectopterygoid fossa is triangular and shallow but is broader and deeper than in *R. norvegicus*. It is bordered internally by a more prominent descending internal pterygoid process than in *R. norvegicus*. This process (entopterygoid crest of some authors) differs from that of *R. norvegicus* in its larger size and in its sinus development which is lacking in *R. norvegicus*. On the posterolateral corner of the fossa in *R. norvegicus* there is a large foramen that joins the foramen ovale dorsally, but in *L. conditor* the lateral edge of the fossa is anterolateral to the foramen ovale so that the foramen ovale opens first into the fossa, then in a slit-like opening to the anterior lateral face of the alisphenoid. The anterior part of the pterygoid fossa in *R. norvegicus* is more fenestrated than in *L. conditor*, with a large interpterygoid (sphenopterygoid) foramen located at the base of the internal pterygoid process. In *L. conditor* this foramen is small. In the more extended work the cranial foramina are dealt with more extensively.

The optic and sphenopalatine foramina are larger than in *Rattus* and about equal in size. Tate (1951) reported the same condition in *L. jonesi* (now synonomized with *L. conditor* by Watts and Aslin 1981). The orbital portions of both the maxillary and the presphenoid extend farther dorsally than in *Rattus*. From the Watts and Aslin (1981) figures, the rostrum of *L. conditor* is broad relative to its length, while that of *L. apicalis* is narrow (Table 2).

Mandible

No mandibles were found articulated with skulls in the Madura Cave deposits. Mandibles were assigned to *L. conditor* on the basis of size, morphology and comparison with other more complete material from other localities . The mandible is shallowest under m2 and is much deeper posteriorly to the end of the angular process. The ventral border is slightly irregularly concave beneath the molars. The ascending ramus and the angular process are in essentially the same plane. The coronoid process is reduced to a small spine on the anterior edge of the ascending ramus. The condyle is rounded in lateral view and is laterally compressed. There is a low rounded ridge on the lateral surface of the ascending ramus that extends from the condyle into the masseteric fossa where it disappears. The expanded angular process is smoothly rounded ventrally. The posterior margin of the mandible is a smoothly rounded re-entrant extending from the posterior end of the angular process to the condyle. The masseteric ridge extends along the ventral edge of the angular process and ends in a tubercle on the lateral edge of the jaw below the m1 and just posterior to the mental foramen. The small mandibular foramen is well posterior to the m3 just dorsal to a prominent thin ridge that extends posteriorly and upwards from the alveolus of m3 towards the condyle and forms the dorsal edge of the pterygoid fossa. The diastema is about equal in length to that of the lower molar row. The mental foramen lies just anterior to the masseteric tubercle and to the m1.

Dentition

The upper incisors are opisthodont and relatively narrow for the size of the skull (Fig. 6). They are so narrow that it is difficult if not impossible to assign isolated incisors to this species or to *L. apicalis*. The cutting edges are straight and oriented with the lateral end slightly posterior to the medial. The upper incisors of *L. conditor* are narrower than those of *L. apicalis* (Table 2).

TABLE 2.

Measurements of skull and upper teeth of *Leporillus* (mm).

	Leporillus conditor Madura Cave	*Leporillus apicalis* Webb's Cave
Width of rostrum		
sample size	3	5
mean	5.47	4.75
range	5.15–5.85	4.45–4.90
Width zygomatic plate		
sample size	4	5
mean	8.86	6.96
range	8.63–8.98	6.80–7.12
Length M1-3		
sample size	3	5
mean	8.14	6.88
range	8.03–8.18	6.79–7.14
Width upper incisor		
sample size	4	5
mean	.848	1.00
range	.783–.957	.986–1.015

The upper molars have three antero-posterior rows of cusps with the buccal row significantly smaller than the other two. The teeth are high crowned. The M1 is made up of three transverse rows of cusps termed chevrons by Michaux (1971) and Jacobs (1977). The first chevron is made up of three cusps, with the largest being t2, followed by t3 and t1. The t1 and t3 are located slightly behind the t2. The three cusps of the second chevron are close to the same size. The t4 is located farther posterior to the t5 and is better separated from it than is the t6. The posterior end of the tooth has two cusps, a large centrally located cusp (t8) and a much smaller cusp, the t9, located buccally to it. With wear the buccal cusps join the central cusps before the lingual cusps (Fig. 5A).

The M1 has three roots of subequal size. One is located at the anterior end of the tooth, one at the posterobuccal corner and one lingually at the midpoint of the tooth. The M2 and M3 also have three roots each. Those of the M3 form the apices of an equilateral triangle with the posterior one located at the posterior end of the tooth.

The M2 has six cusps. The t4, t5 and t6 form a well-defined chevron. The centrally located t5 is slightly larger than the other two cusps which are located posterior to it. A t1 is present on the anterolingual corner of the tooth. It is the same size as the t4 and t6 and is well separated from the t5. An incomplete chevron is formed at the posterior end of the tooth by a large t8 and a very small t9 which is not completely separated from the latter.

The M3 has one well-developed chevron made up of t4, t5 and t6. The t5 is the largest followed by the t4 and the t6. The t4 is more separated from the t5 than is the t6, which merges with it soon after wear starts. A t1 is present on the anterolingual corner of the tooth. It is about the diameter of the t5 and is separate from the other cusps to the base of the tooth. The posterior chevron is elliptical in shape and is made up of the joined t8 and t9.

The lower incisor is narrow with the cutting edge gently rounded and oriented at about 60 degrees in the vertical plane to the long axis of the tooth.

As noted above, we do not consider the homologies of the cusps of the lower teeth to be secure, although they are derived from the cricetid plan. Like the upper molars, the lowers are high crowned. The m1 has six main cuspids that are arranged in two longitudinal rows. The pairs of cuspids (and associated crests) are joined to form chevrons. The

wings of the chevron formed by the anterior pair, the antero-labial and antero-lingual cuspids, project anteriorly. The wings of the other chevrons project posteriorly. A round postcingulid is present between the wings of the posterior chevron. With wear this cuspule merges with the hypoconid and entoconid to form a posterior lophid (Fig. 5B, C).

The m2 has four principal cuspids of about equal size that form two chevrons with backward projecting wings. A circular postcingulid is present between the wings of the posterior chevron. As in the m1, this cuspule merges with the hypoconid and entoconid with wear to form a posterior lophid.

The m3 has two anterior cuspids, the protoconid and 'metaconid', that are joined to form a chevron. The two posterior cuspids, the hypoconid and entoconid, are joined to form an elliptical cusp at the posterior end of the tooth. In both the upper and lower molar series the third molars are equal in width to the first molars, in contrast to *L. apicalis* in which the third molars are narrower than the first molars.

TABLE 3.

Statistical data for the lower teeth of *Leporillus conditor* from Madura Cave (mm).

	STRATIGRAPHIC UNIT		
	Trench 1 Unit 1	Trench 4 Unit 2	Trench 4 Unit 7
m1-3 Length			
Sample size	18	12	—
Mean	8.09	8.19	—
Standard deviation	.417	.319	—
Coeff. variation %	5.15	3.89	—
Range	7.08–8.93	7.65–8.89	—
m1 Length			
Sample size	27	38	14
Mean	3.72	3.71	3.63
Standard deviation	.162	.138	.126
Coeff. variation %	4.35	3.72	3.48
Range	3.43–3.93	3.40–3.98	3.34–3.91
m1 Mid Width			
Sample size	26	39	12
Mean	1.88	1.88	1.89
Standard deviation	.191	.191	.199
Coeff. Variation %	10.12	10.18	10.51
Range	1.48–2.16	1.42–2.20	1.83–2.18
m2 Length			
Sample size	24	28	9
Mean	2.31	2.33	2.31
Standard deviation	.124	.102	.071
Coeff. variation %	5.36	4.38	3.06
Range	2.03–2.58	2.14–2.67	2.18–2.44
m3 Ant. Width			
Sample size	18	14	6
Mean	1.95	1.98	2.05
Standard deviation	.217	.162	.089
Coeff. variation %	11.09	8.198	4.37
Range	1.42–2.29	1.59–2.18	1.89–2.12

Discussion

Data on the historic distribution of this species have been summarized in maps by Robinson in Strahan (1995), Copley (1999), and Baynes (1979). According to Watts and Aslin (1981) it was widely distributed in southern Australia from the lower Darling River of New South Wales through South Australia into the eastern part of the Nullarbor Plain. Its presence on the Nullarbor Plain of South Australia suggests that it probably was present to the west in Western Australia as well. This is supported by its presence in Holocene deposits from the Nullarbor Plain in Western Australia (Lundelius 1957, 1963; Baynes 1987; Archer 1970, 1974). It is also known from Holocene deposits along the west coast of Western Australia from Jurien Bay to Shark Bay (Baynes 1979) and in the Flinders Ranges of South Australia (Smith 1977). The available information indicates that it was distributed along the southern edge of the arid zone (Copley 1999). Its presence throughout the stratigraphic sequence in Madura Cave demonstrates its presence on the Roe Plain for at least the last 38,000 years. Measurements of the midwidth of M1 and length of M3 show no changes in size over the last 38,000 years (Table 3).

Leporillus apicalis (Gould 1853)

Material

Trench 1, Unit 1, Level 1 (top 1 foot)

Upper dentition

3 left, 1 right maxillae with M1-3, including PM 6140, 6146, and 25520 (Fig. 8A-G), 2 left and 1 right maxillae with some teeth

Lower dentition

1 left ramus with i - m3, PM 6185 (Fig. 8H-J), 4 left and 7 right rami with teeth, 1 edentulous ramus fragment

Trench 2, 2 1/2 feet below surface

Lower dentition

3 left, 5 right rami with teeth, 1 incisor

Trench 3, Unit 2, Level ?

Upper dentition

5 left and 1 right maxillae with teeth, 1 right M2, 2 edentulous right maxillae

Lower dentition

2 rami with m1

Trench 4, Unit 1, Level 1, top 1 foot

Upper dentition

1 left and 1 right maxillae with teeth, 2 edentulous left maxillae

Lower dentition

6 left and 8 right rami with teeth

Trench 4, Unit 2, Level 1, top 1 foot)

Upper dentition

1 M2

Descriptions

Skull

The skull of *Leporillus apicalis* differs from that of *Leporillus conditor* mainly in size. Wood Jones (1925) and Watts and Aslin (1981) have stated that the bullae of *Leporillus apicalis* are smaller than those of *Leporillus conditor*. In none of the Madura

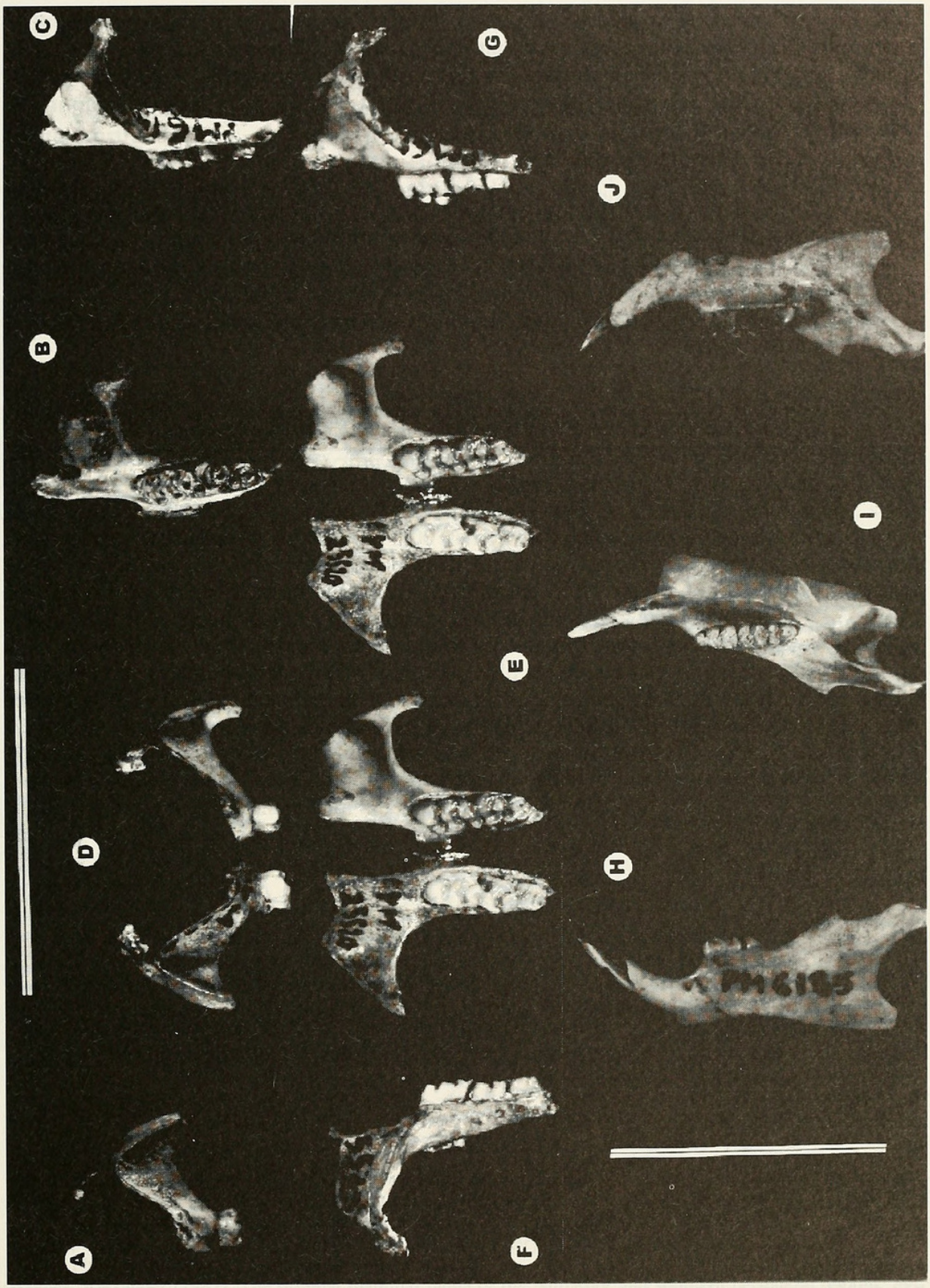


Figure 8. *Leporillus apicalis.* A–C, PM 6146, left maxilla with m1–3 shown in A, anterior; B, occlusal; and C, left lateral views. D and E, show PM 25520 a left maxilla with m1–3, and PM 6140 a right maxilla with m1–3 posed together to simulate the appearance of a partial palate. In D they are shown in anterior view and E stereoscopically in ventral view. F, PM 25520 left lateral view; G, PM 6140 right lateral view. H–J, PM 6185, left mandibular ramus with I, m1–3, H, left lateral; I, occlusal; and J, left lingual views. Scale bar is 2 cm. The FMNH negative numbers are G86189.1–3, G86191.1&.3&.4 for A–G, and G85959-85961 for H–J.

Cave material are these structures preserved, so this feature cannot be determined. The rostrum of *L. apicalis* is narrower than that of *L. conditor*. This is true of the width taken directly over the upper incisor capsules and the width across the tubercles at the base of the zygomatic plate (Table 2). Although the samples are small there is no overlap in the ranges of the two species.

Dentition

As in the skulls, *Leporillus apicalis* and *Leporillus conditor* differ in the size of their dentitions. They also differ in that the lower third molars of *Leporillus apicalis* are narrower than the first (Table 4) whereas in *L. conditor* the m3s are about the same width or slightly wider (Table 3). The incisors of *L. apicalis* are broader than those of the larger *L. conditor* (Table 2).

TABLE 4.

Statistical data for measures of *Leporillus apicalis* from Madura Cave (mm).

	STRATIGRAPHIC LEVEL	
	Trench 1 Unit 1 Level 1	Trench 2 Trench 3 Unit 2
m1–3 Length		
Sample size	5	—
Mean	7.07	—
Standard deviation	.248	—
Coeff. variation %	3.5	—
Range	6.83–7.25	—
m1 Length		
Sample size	12	6
Mean	3.12	3.11
Standard deviation	.103	.135
Coeff. variation %	3.28	4.35
Range	2.95–3.33	2.90–3.24
m1 Mid Width		
Sample size	12	6
Mean	1.80	1.85
Standard deviation	.073	.094
Coeff. variation %	4.03	5.09
Range	1.711–1.943	1.74–1.97
m2 Length		
Sample size	10	—
Mean	2.20	—
Standard deviation	.0947	—
Coeff. variation %	4.29	—
Range	2.088–2.349	—
m3 Ant. Width		
Sample size	5	—
Mean	1.71	—
Standard deviation	.052	—
Coeff. variation %	3.04	—
Range	1.653–1.769	—

Discussion

The distribution of this species prior to European settlement is uncertain. According to maps by Robinson in Strahan (1995), and Copley (1999), wild caught specimens are known from a few localities in western New South Wales, southern Northern Territory and northern South Australia. Nests attributed to this species have been found in the eastern part of Western Australia. It is known from Holocene deposits in a number of caves on the Nullarbor Plain (Lundelius 1957, 1963; Archer 1970, 1974;), the Flinders Ranges in South Australia (Smith 1977; McCarthy et al. 1996) and from cave deposits on the west coast of Western Australia (Baynes 1979, 1987). The record from Madura Cave demonstrates that it was an inhabitant of the area around the cave from 22,400 years ago to 7,500 years ago. Its absence from the lower levels (Unit 7) of Pit 4 is problematical. It is possible that its absence is an accident of sampling as the total amount of material recovered from Unit 7 is small.

SUMMARY AND CONCLUSIONS.

Two species of *Leporillus*, *L. conditor* and *L. apicalis*, are represented in Quaternary deposits in Madura Cave. *Leporillus conditor* is represented by a large amount of material, *L. apicalis* by much less. *Leporillus conditor* is found in all stratigraphic levels, spanning a time interval from 38,000 to 7,500 years before present (and from the surface and top levels of this and other Nullarbor caves). *Leporillus apicalis* is absent from the lowest level and from the surface although it is represented in the top units. Its absence from the lower level may be an accident of sampling as it is much less abundantly represented than *L. conditor* in all units and the total amount of material from the lowest unit (Unit 7) is small in comparison with the higher units. It could be argued that its absence from the surface is also a sampling accident as it is present in surface deposits in caves on the nearby Nullarbor Plain. However a sampling of the surficial deposits of the Nullarbor Region by Baynes (1987) indicates that there are few records from the Roe Plain. In addition, Boscacci et al. (1987) have demonstrated that the Roe Plain has a somewhat different modern mammal assemblage than the Nullarbor Plain proper.

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