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Structural Composition and Dental Variations in the Murids of the Broom Cave Fauna, late Pleistocene, Wombeyan Caves Area, N.S.W., Australia

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This study is based on materials procured by William D. Turnbull and E. L. Lundelius Jr (University of Texas) and prepared by the authors with National Science Foundation assistance (Grants GB975 and GB3729)

Plates 1-3. Figures 1-5. Manuscript received, 20th July, 1967.

INTRODUCTION

Robert Broom (1895 a & b, 1896) described several marsupials from a Late Pleistocene bone breccia of the Wombeyan Caves area near Taralga, New South Wales, Australia. W. D. L. Ride (1956 a & b, 1960) treated Broom's fauna more completely. He described a new species of the murid genus *Mastacomys*, recorded two other rodents, and analysed the faunal constitution of the breccia based on a sample of "nine large pieces" of this formation from the Broom collection in the Anatomical Museum at Edinburgh. He designated the fossils from this locality the Broom Cave Fauna.

In 1964, one of us (W.D.T.) arranged with H. O. Fletcher (Deputy Director, Australian Museum) for the loan of an unprepared collection of 189 pieces of this Wombeyan Cave bone breccia. This collection was made by Mr Fletcher several years ago and he kindly offered to share any specimens obtained from these blocks with the Field Museum, if we, in turn, would prepare and study the material. For the past 2 years we have done this. We wish to thank Mr Fletcher and the Australian Museum for generously making these materials available.

Acid treatment of the first 44 of these blocks has produced sufficient material for an analysis of the murid element of this fauna. Nearly 300 specimens of maxillae, rami, and individual cheek teeth were obtained, containing a total of 372 teeth.

There are four rodent taxa in the sample: *Pseudomys oralis*, *Gyomys glaucus*, *Mastacomys wombeyensis*, all recorded by Ride, and *Rattus* sp., a new record. Age distributions and estimations of numbers of individuals present in the sample along with variations in dental characters are noted.

This report is the first of a planned series that will be presented as the preparation and study of the Fletcher collection continues. Only the murid species are considered in this paper.

METHODS AND PROCEDURES

Preparation Methods

The breccia pieces, ranging in weight from a few ounces to about 4 pounds, were broken down with 10 per cent acetic acid to free the contained bones and teeth. This acid concentration was found to be ideal, for at this strength the bone is least affected and the matrix is readily attacked. Stronger concentrations hazard the bone to a far greater extent, and require much more effort in periodically impregnating the newly exposed bone with an impervious plastic to prevent its destruction along with the matrix. A detailed discussion of the preparation methods was given by Ride (1956a). Even after this weak acid treatment the small, loose, individual bones and teeth are very fragile. A thin solution of methyl methacrylate ("plexiglass" or "perspex") dissolved in ethylene dichloride (Ride, 1956a) was used to impregnate and strengthen them for pin-mounting within gelatine capsules for protection and ease of handling.

Initially each matrix block was lettered for identification. As the acid treatment progressed, frequent examinations were made to note articulations and/or associations of elements as they appeared. All materials from a single block of breccia were segregated, recorded, and distinguished according to the block of origin so that undetected associations might be made later.

Ride (1960, pp. 76–77) concluded that the Broom Cave Fauna was largely the result of an owl pellet accumulation. We concur in this and, in addition to the sort of evidence set forth by Ride, we have also observed, as acid treatment progressed, many pellet-like aggregations of bones. Since recent owl pellets are typically very fragile objects, such intact pellet-like structures suggest that there was only a limited amount of sorting and redeposition prior to cementation of the breccia. Accordingly, in a few instances, we stopped the acid treatment and set aside examples of these aggregations for the record and future study.

Study Methods and Procedures

The methods of study require some detailed comment.

First, since we are working with fragmentary materials (mostly, but not entirely, with isolated teeth and bones), care has been taken to distinguish between numbers of teeth, numbers of specimens, and estimates of numbers of individuals. In so doing cognizance is taken of known correlations and/or positive associations. In most instances this involves correlations within molar quadrants. In the case of *Mastacomys*, in which we have two essentially complete palates, it also involves correlations between quadrants.

Second, an attempt has been made to separate clearly three related kinds of statements: (1) those pertaining to our sample and its associated statistics; (2) those that draw inferences from this sample concerning the peculiar nature of the burial assemblage that it was drawn from (an owl pellet accumulation); and (3) those that in turn make inferences about the original population.

In dealing with the sample, we encounter a problem which frequently plagues paleontologists and archaeologists. Most neozoological samples are drawn *directly* from a fauna, and hence the sample is of a *known* size, i.e., a definite number of individuals (N). With fragmentary fossil materials, however, the actual size of a sample, i.e., the number of individuals the sample represents, is often quite uncertain. In such cases, for purposes of comparisons within the fauna the absolute minimum number of individuals that could have contributed to the sample is often used because it is easy to derive. But it is difficult to compare directly modern samples of a known N and those fossil samples for which only the absolute minimum of specimens is available, although relative comparisons may have meaning.

Assessment of the absolute minimum number of individuals comprising a sample is usually based on the largest number of specimens of any single element contained in the sample such as L.$M^{\underline{1}}$ or R.$M_{\overline{3}}$, or if more than dental and cranial elements are being considered, L. calcanea, or R. femora, etc. This is done by taking the element represented by the greatest number of specimens to indicate the very least number of individuals present. If, for example, a collection contained specimens as follows: 15 R.$M^{\underline{1}}$, 13 R.$M^{\underline{2}}$, 20 L.$M^{\underline{3}}$, 17 R.$M_{\overline{3}}$, and 14 L.$M_{\overline{1}}$ of "species X", then this collection must represent at least 20 individuals. When dental remains are involved, it is often possible to refine the assessment of the minimum number by taking account of the age spread of the sample as is indicated by tooth wear. In our samples, to do this the five age grades used by Ride (1956a, p. 433) were employed: "(a) distinct cusps on all molars, (b) wear beginning to unite cusps into laminae, (c) all cusps united transversley but cusps still discernible, (d) cusps no longer discernible, (e) laminae themselves disappearing". If all the teeth are arranged tabularly (appendix) and numbers of teeth in each age group are noted, then the most frequently represented tooth in an age category gives the minimum number of individuals at that age stage. For example (appendix table 1) in *Gyomys glaucus* the most frequently represented tooth at wear stage "a" is the R.$M^{\underline{1}}$ with two teeth; for wear stage "b" it is the L.$M_{\overline{2}}$ with eight; for "c" it is R.$M^{\underline{1}}$ (or $M^{\underline{2}}$) with eleven; etc. The total of these most frequently represented teeth from all age categories (shown in next to the bottom row of the table) gives the "age spread" minimum number of individuals in the sample. In this example we obtain 32 individuals as opposed to 23 as assessed by the traditional method. This age spread method is basically identical with the traditional method, except that the sample is first broken into age groups.

In order to arrive at an estimate of the actual size of a sample that is comprised largely (or entirely) of very fragmentary materials, a means of confining and restricting the spread between the assessments of maximum and minimum numbers of individuals must be found (see fig. 1). The age spread minimum number appears to be an adequate restricting parameter for the low end of the scale, but the upper end has usually been more troublesome to deal with. Before a more realistic estimate of sample size can be achieved, a similar means of restricting the maximum must be found.

It is easy to assess the absolute maximum number of individuals that could be represented by a sample on the assumption that each uncorrelated tooth represents a different individual. (For this sample of *G. glaucus* we get 166 individuals.) This is not very helpful, for it provides only an outside, and not very narrowly restricting value for the upper end of the scale. Also, under many depositional situations relating to the burial assemblage from which a sample might be drawn, one would expect some overlap of the isolated teeth whereby some would be from individuals already represented by other teeth. Thus, unfortunately, there does not appear to be a universal means of judging the reasonableness of the basic assumption in most instances. An owl pellet accumulation offers a notable exception, however—and as a general rule the less disturbed the accumulation, the more striking is the exception. Regurgitated pellets contain, in addition to (and among) the hair and other indigestibles, more or less associated skeletal remains of the victims of each separate feeding by the owl. Most of the minor separation of elements that were originally contained within the pellet (i.e., that which occurs subsequent to regurgitation and initial deposition) must result from natural organic breakdown and mixing from such causes as drying, bacterial action, and the activity of invertebrate scavengers. This type of activity more easily moves small objects such as individual teeth, than larger ones such as jaw rami, maxillaries or whole skulls. If intact pellets are present (as appears to be the case for the Broom Cave) then the possibility of larger scale redeposition is ruled out. Thus in this sort of deposit we can be reasonably certain of a high degree of inter-correlation among specimens with respect to numbers of individuals—so high as to favour the use of an estimate based upon the assumption of almost full correlation. This we call the "minimal estimate" of the maximum number of individuals which could be represented in the sample.

The method of obtaining this minimal estimate of the maximum number involves age spreading, as with the age spread minimum. Here, however, the number of *specimens* in the largest suite of teeth likely to have been preserved as a unit is employed, instead of individual teeth. This suite is taken to be a molar row; left or right, upper or lower. The number of specimens represented by four molar quadrants is thus determined instead of dealing with the numbers of twelve different teeth as in the minimum number assessment.

The tables in the appendix record by age group both numbers of teeth (first column) and numbers of specimens for the molar quadrants (second column). For example, in *G. glaucus* the 31 teeth in the right upper molar quadrant at wear stage "c" (11, 11, and 9), are in 25 specimens. These 25 specimens could represent as many as 25 individuals if no correlations among the teeth exist other than those that were observed, or as few as eleven if full correlation were the case.

As suggested above, the chance of post-regurgitation movements of small individual teeth either into or out of the immediate area of a pellet is quite good, and is very much more likely than a comparable shifting of larger objects such as rami or maxillae (molar quadrants). Hence, correlation of loose teeth should be low while that of molar quadrants should be high. Since we are searching for a minimal estimate of the *maximum number* of individuals we assume we found most of the correlations for the loose teeth and that the estimate of the maximum number of 25 individuals is reasonably realistic for those 25 specimens comprising 31 teeth. To make the estimate *minimal* for this maximum number, we next assumed nearly full correlation between the specimens (quadrants) represented. The bottom row of the table gives the tally for the maximum number of specimens by molar quadrant for the age groups, which total is our minimal estimate of the maximum number of individuals represented in the sample—in this case 53.

These estimates serve to place limits on the size of the sample (fig. 1). For instance, for *G. glaucus*, which is represented in this sample by 209 teeth in 166 specimens, the absolute maximum and minimum limits on numbers of individuals are 166 and 32 respectively. As has been explained, 53, the minimal estimate of the maximum number of individuals represented, is *probably* a fairly close assessment of the actual number of individuals comprising the sample in this special case.

Teeth were measured either with an ocular micrometer or vernier caliper. Where justified, mean, standard deviation, and coefficient of variation were calculated. Observations on the gross morphologic variations in cusp pattern and arrangement were made. Abbreviations used for specimens are as follows: F — Australian Museum; AMEU — Anatomical Museum of Edinburgh University; BM — British Museum (Nat. Hist.); and PM, which is a prefix for some of the fossil mammal collections of the Field Museum; unprefixed number refers to a specimen in the recent mammal collection of the Field Museum. A specimen listing of all materials of the Broom Cave fauna used in this work is given in the appendix.

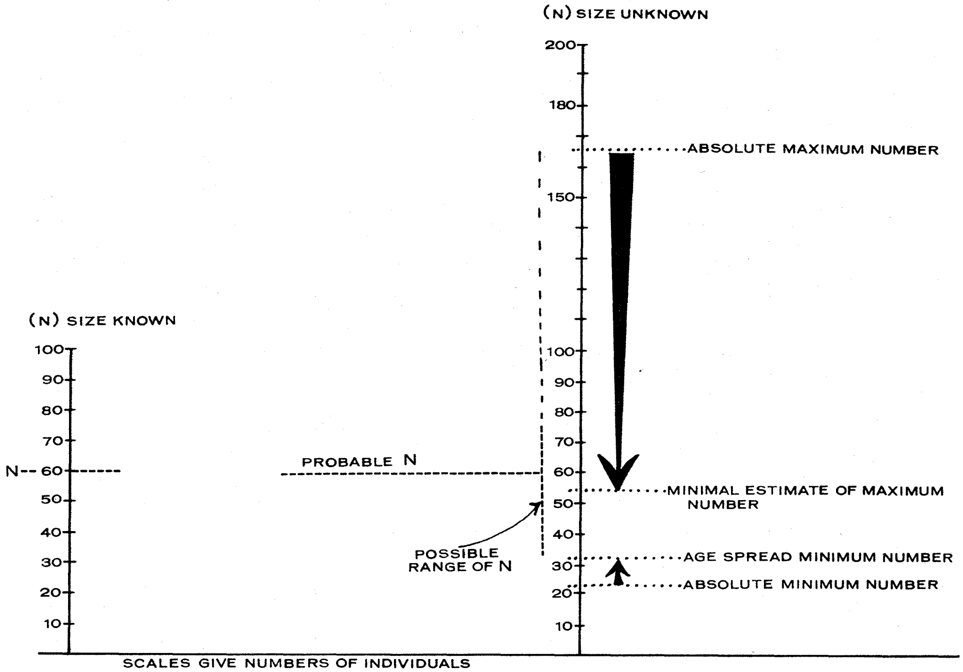

Figure 1.—Comparisons of a standard modern biological sample (left) with a sample comprised of fragmentary fossils (right). In the standard sample, which is usually drawn directly from a living population, sample size (N) is an exact, known number of individuals. For a sample of fragmentary fossils drawn from a burial assemblage, and not directly from a living population, N is usually unknown. The absolute maximum and minimum numbers of individuals that could comprise the sample can be determined, but such limits to the possible range of sample size are usually not restrictive enough to make the samples comparable to standard samples. Variations in wear of teeth often provide a better means of determining the minimum number of individuals (age-spread min.), but no satisfactory means of further restricting the upper end of the scale has existed (arrows). With undisturbed owl pellet accumulations, where theoretically the minimal estimate of the maximum number of individuals should approximate the true N closely (see text), we do have a means of achieving a restriction of the possible range of estimates. Data for this example are for *Gyomys glaucus* from text table 1 and appendix table 1, for which a value for N of about 60 appears probable.

RESULTS AND DISCUSSION

The relative abundance of each murid in the sample according to various estimates discussed above, is set forth in table 1. By any of these standards *Pseudomys oralis* and *Gyomys glaucus* are seen to have been the common rodents and *Mastacomys wombeyensis* and *Rattus* sp. were scarce. It is therefore not surprising that the earlier, smaller samplings of the fauna did not turn up a single *Rattus* tooth, and only yielded one specimen of *M. wombeyensis*.

The bivariate scatter diagrams for the M^2's of the Broom Cave murids (fig. 2) reflects this relative abundance, and shows other features such as size, proportions, and variability for *P. oralis* (table 4) and *G. glaucus* (table 5) for which there are fair-sized samples. For *Rattus* sp. and *M. wombeyensis*, the materials are still too inadequate to do more than give crude approximations of these features.

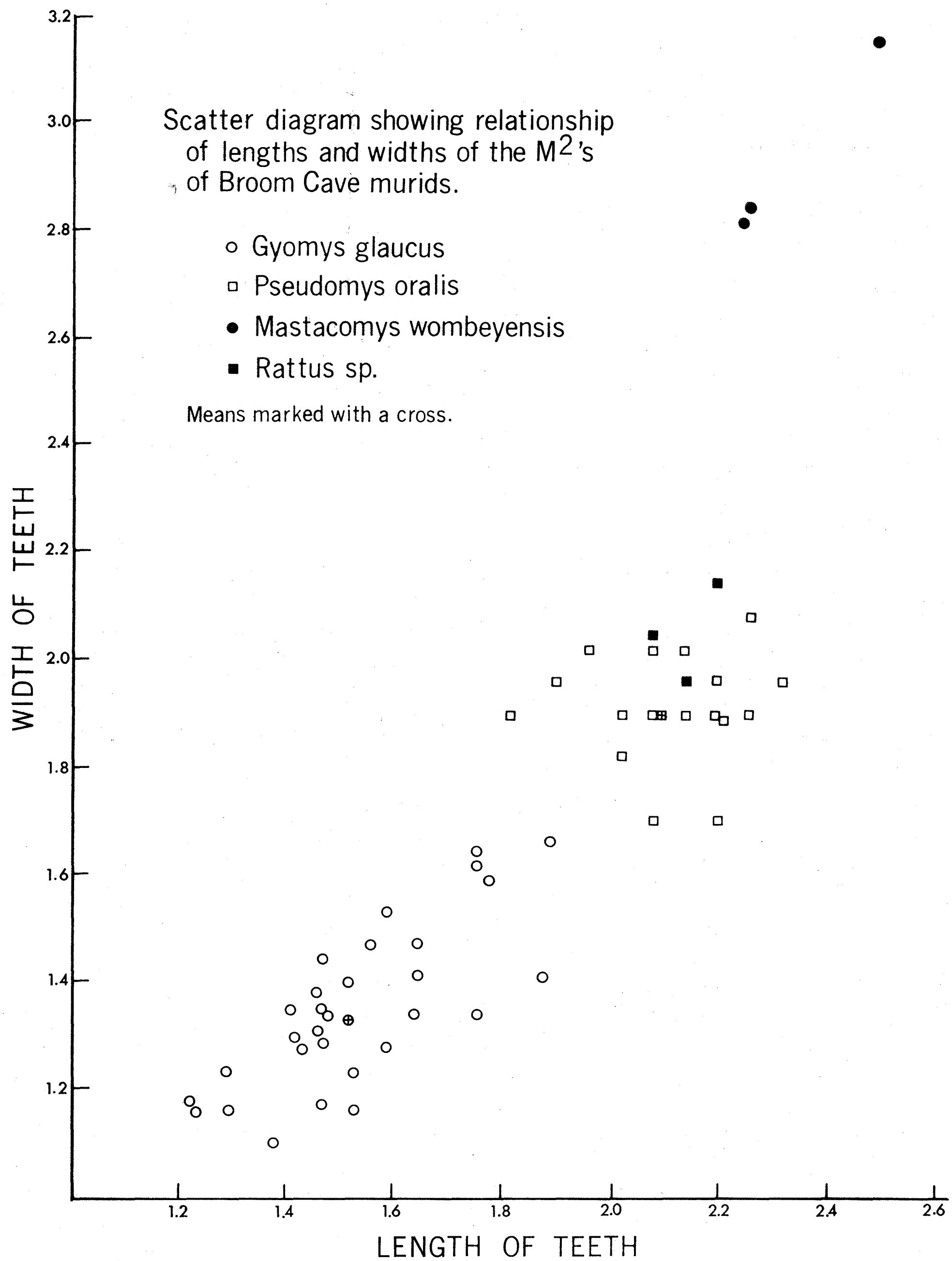

Figure 2

TABLE 1. Relative abundance of murids in the sample of the Broom Cave fauna

Species	Number of teeth	Minimum number individuals		Estimates of maximum numbers of individuals	
		Traditional	Age spread	Minimal estimate	Absolute maximum number (number of specs)
Mastacomys wombeyensis Ride ..	23	4	5	6	12
Pseudomys oralis Thomas ..	130	18	24	40	97
Gyomys glaucus Thomas	209	23	32	53	166
Rattus sp.	6	2	4	4	5

Age distributions of the specimens upon which table 1 was based are given in figure 3. In each case a bell-shaped curve is seen, regardless of the method of population estimation used. If owls are approximately indiscriminate in capturing rodents, the expected distributions should be some sort of survivorship curves, perhaps more like those expressed by the combination curves made up of the dotted lines and the right sides of the bell curves. The deficiencies in numbers of young animals must result from their being in the nest, where they are largely freed from owl predation. The bell curve is then a picture of the part of the population that is actually roaming about when and where the owls could capture them.

Morphology

Our materials are adequate for some detailed considerations of tooth morphology. The dental terminology of Hershkovitz (1962) is used rather than simple numbering of cusps and styles such as that used by Ellerman (1941) or Ride (1960), (see figure 4). Tables 2 through 6 give measurements for the Australian Museum and Field Museum specimens and repeat certain measurements from other sources.

Mastacomys wombeyensis Ride 1956

We have no basis for judging the value of one of Ride's diagnostic characters, zygomatic plate width (actually zygomatic plate length), but merely give its measurement for F52303. The M^3 carries the other diagnostic character of this species, the lateral accessory cusp noted by Ride. It is located between the second and third laminae on the lingual side. We designate this structure an enterostyle (plate 1, e and f). All the upper molars have a characteristic great width in this genus. As is generally the case with the older endemic Australian murids (see p. 13), the labial elements of M^1, i.e., the anterolabial style and the mesostyle, show atrophy. There is no indication of the anteromedian style which is sometimes present in the *Pseudomys* group of murids. The diagnostic enterostylar character appears to be a valid one, relieving somewhat Ride's (and our) reservations. Out of 12 specimens assignable to this species only three M^3's are present but all three show a developed enterostyle.

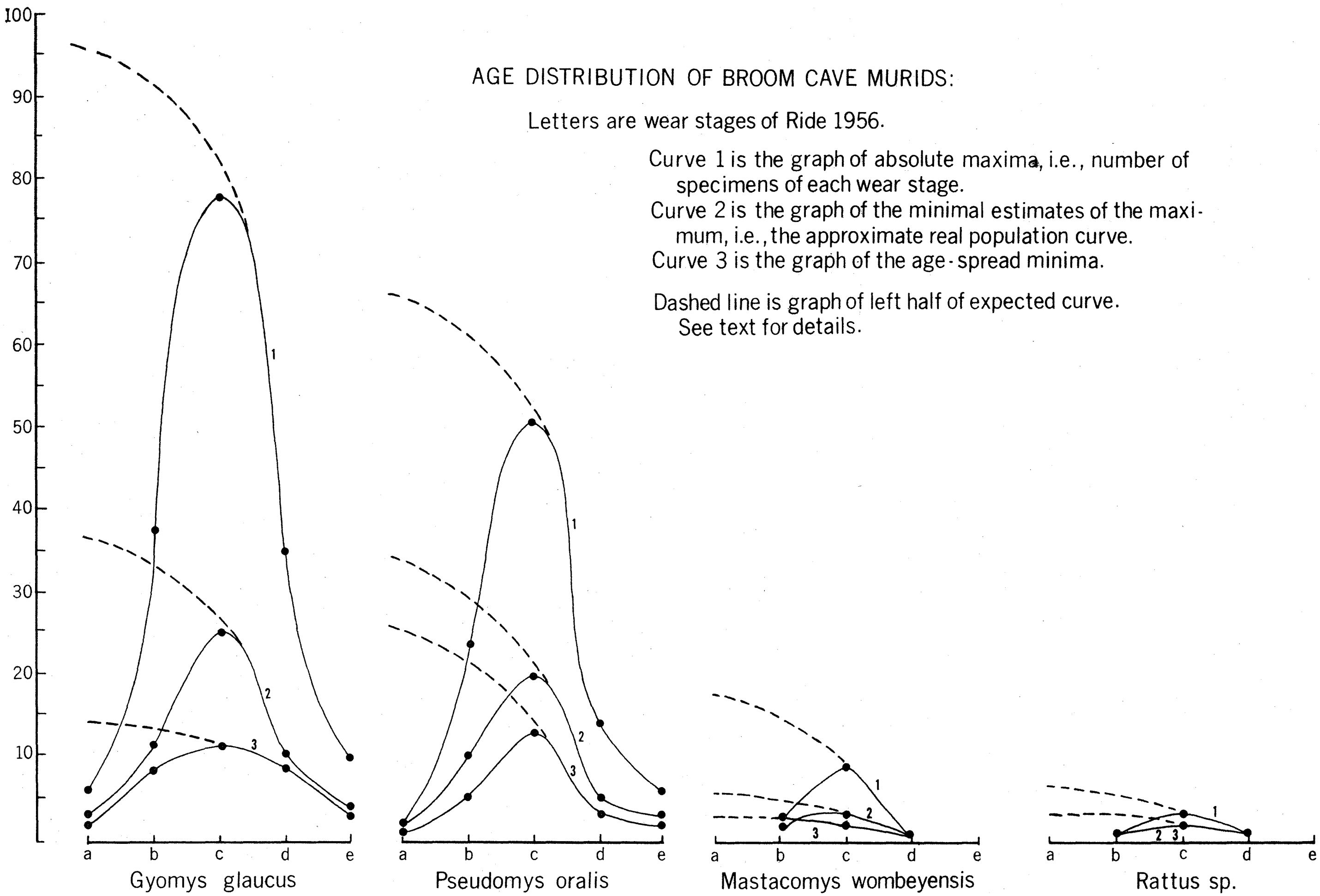
AGE DISTRIBUTION OF BROOM CAVE MURIDS:
Letters are wear stages of Ride 1956.
Curve 1 is the graph of absolute maxima, i.e., number of specimens of each wear stage.
Curve 2 is the graph of the minimal estimates of the maximum, i.e., the approximate real population curve.
Curve 3 is the graph of the age-spread minima.
Dashed line is graph of left half of expected curve. See text for details.
100
90
80
70
60
50
40
30
20
10
a
b
c
d
e
Gyomys glaucus
Pseudomys oralis
Mastacomys wombeyensis
Rattus sp.
1
2
3

Figure 3

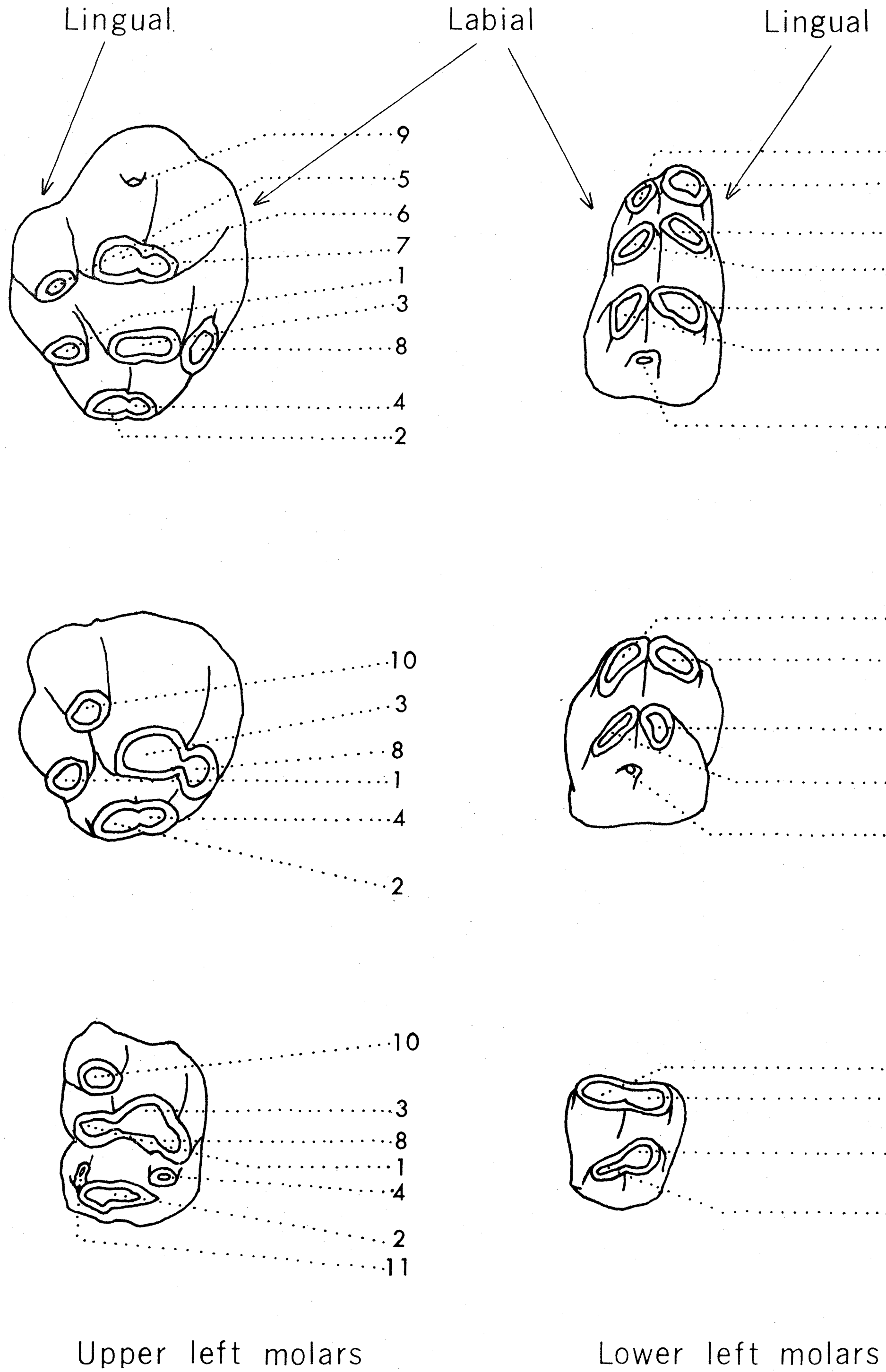

Figure 4 (for explanation see bottom of next page)

TABLE 2. Measurements of skull and upper molars of *Mastacomys wombeyensis* specimens, in mm.

Specimen	AMEU No. B59/a	PM 6170‡	F 52303		PM 5861		PM 7333	F 52304	PM 7556
Character	Left	Left	Left	Right	Left	Right	Right	Left	Left
Length of cheek tooth row (occlusual aspect)	9.0	..	8.2	8.4	e9.9	†	..	..	..
Length of wear surface for cheek tooth row	7.8	..	6.8	7.1	e8.4	†	..	..	..
Alveolar length, cheek tooth row	8.9	7.1	†	8.3	9.3	e9.3	..	..	..
M^1 .. Length .. Tooth base	..	..	3.05	3.05	3.34	e3.4	e3.1	†	†
Occl. surf	..	..	2.5	2.6	3.1	†	e3.0	†	†
Width	..	..	2.82	2.80	3.20	e3.2	†	†	†
M^2 .. Length .. Tooth base	..	..	2.26	2.25	2.50	†	..	..	..
Occl. surf	..	..	2.1	2.3	e2.4	†	..	..	..
Width*	3.0*	..	2.90*	2.9*	e3.20*	†	..	..	..
	..	..	2.84	2.82	3.10	†	..	..	..
M^3 .. Length .. Tooth base	..	..	2.60	2.65	e2.4	†	..	..	..
Occl. surf	..	..	2.0	2.1	e2.3	†	..	..	..
Width	..	..	2.15	2.05	†	..	..	..	..
Least zygomatic plate length (Ride's least width)	5.0	4.1	4.1	4.2	..	..	..	..	..
Length pterygoid fossa	..	..	7.5		..	..	..	..	..
Length diastema	..	..	8.7		..	..	..	..	..
Width of rostrum	..	..	5.0		..	..	..	..	..
Least interorbital width	..	..	3.4		..	..	..	..	..
Midfrontal width	..	..	4.0		..	..	..	..	..
Palatal bridge width	..	..	6.2		..	..	..	..	..
Palatal length	..	..	16.2		..	..	..	..	..

* From anterolingual style to mesostyle.

e — estimate.

† — element present, but not measurable.

‡ An edentulous jaw questionably referred to *M. wombeyensis.* Its zygomatic plate lacks a pronounced anterior prong. This and the similarly noted specimen in table 3 do not figure in the dental (tooth row) specimen counts.

EXPLANATION OF FIGURE 4 (PREVIOUS PAGE)

Generalized composite cusp and style patterns of Broom Cave murids

Upper left molars

1. Protocone.
2. Hypocone.
3. Paracone.
4. Metacone.
5. Anterolingual conule.
6. Anterolabial conule.
7. Anterolabial style.
8. Mesostyle.
9. Anteromedian style.
10. Anterolingual style.
11. Mesostyle.
12. Enterostyle.

Lower left molars

1. Protoconid.
2. Hypoconid.
3. Metaconid.
4. Entoconid.
5. Anterolabial conulid.
6. Anterolingual conulid.
7. Posterolophid.

Terminology based on Hershkovitz (1962)

On F52303, an almost complete skull, the enterostyle is larger on the right side than on the left (plate 1, e). PM 5861 (plate 1, f) is a palate bearing most of the teeth. These teeth are in a more advanced stage of wear, Ride's "age c", than those in F52303 but the enterostyle on the right M^{2} is still distinguishable though somewhat fused into the hypocone at this stage.

TABLE 3. Measurements in mm for lower molars of *M. wombeyensis*. All are maximum dimensions at crown base

Specimen	M_1		M_2		M_3	
	Length	Width	Length	Width	Length	Width
PM 6174 ..	3·58	2·40	..	..	..	..
F 52306	3·50	2·04	..	..	..	..
F 52305	†	†	2·05	1·96	1·75	1·49
F 52308	..	..	2·40	†	..	..
PM 6175 ..	..	..	1·97	1·83	..	..
F 52307	†	2·00	..	..	..	..
PM 6178 ..	3·43	2·04	..	..	..	..
PM 6172* ..	†	†	..	..	..	..

* An edentulous specimen. Neither it nor the similarly marked edentulous maxilla shown in table 2 figure in the dental (tooth row) specimen counts.

† Element present, but not measurable.

Some specimens of lower molars, identifiable mainly on size and general morphology, are placed in this species. They are chipped and fragmented to varying degrees. Though not quite as wide as the uppers, they are certainly more massive in character than any other lower molars found in this sample. However, since the type lacks lower molars we cannot be certain. It may be that some of these are very large specimens of *Pseudomys oralis*, though the general character of the teeth and their average size would seem to exclude this.

Pseudomys oralis and *Gyomus glaucus*

A large number of specimens of these species were obtained, and from them estimates of morphological variation have been made (tables 4 and 5). Our measurements represent maximum dimensions at the crown base. Those of the types of *P. oralis* and *G. glaucus* are from Tate (1951). It should be kept in mind that they probably are not exactly comparable since Tate did not specify how he took his measurements. They probably represent dimensions of the occlusal surface, and are therefore apt to be bigger than ours.

TABLE 4. Statistical data for tooth measures of *Pseudomys oralis* from Broom Cave

	N	$\bar{x}$	s	V	Observed range	Tate 1951 B.M. No. 92.8.7.2
Length M^1 ..	25	2.92 ± .034	.17	5.86	3.16—2.74	3.5
Width M^1 ..	24	2.10 ± .021	.10	5.00	2.26—1.93	2.1
Length M^2 ..	18	2.09 ± .036	.16	7.41	2.32—1.76	1.7
Width M^2 ..	18	1.90 ± .029	.12	6.57	2.08—1.64	2.0
Length M^3 ..	14	1.58 ± .025	.09	5.88	1.70—1.40	1.4
Width M^3 ..	14	1.45 ± .028	.10	7.24	1.64—1.34	1.6
Length M_1 ..	26	2.84 ± .030	.15	5.35	3.22—2.56	..
Width M_1 ..	27	1.81 ± .024	.13	7.40	2.14—1.64	..
Length M_2 ..	24	1.87 ± .029	.14	7.49	2.26—1.64	..
Width M_2 ..	26	1.83 ± .027	.14	7.69	1.08—1.52	..
Length M_3 ..	19	1.59 ± .022	.10	6.11	1.74—1.34	..
Width M_3 ..	19	1.45 ± .034	.15	10.2	1.64—1.10	..

Pseudomys oralis Thomas 1921

The variation in the $M^{\underline{1}}$ is marked. F52264 (plate 2a) displays the maximum development of the cusps. A clearly defined anteromedian style is present in some specimens. Lundelius (1964, p. 70) pointed out that this feature is by no means restricted to *Thetomys* as Tate (1951, p. 240) and others have said. The other elements of the procingulum are well developed including a distinct anterolabial style. The mesostyle is well separated from the paracone but the metacone shows incipient fusion into the hypocone. The general trend towards degeneration of the labial elements is shown in a fine series in these specimens. PM 7634 (plate 2b) has the anterolabial style somewhat fused into the anterolabial conule and the metacone has completely merged into the hypocone F52262 (plate 2c) shows similar loss of elements but has also lost the little accessory anteromedian style. The typical cusp pattern is displayed by PM 5878 (plate 2d) where only the anterolabial and anterolingual conules remain of the procingulum.

In $M^{\underline{2}}$ the variation is not nearly as marked as in $M^{\underline{1}}$. The standard pattern has a first lamina comprised of only an anterolingual style, a second lamina of protocone, paracone, and mesostyle, and a third lamina of only the hypocone. Slight variations of the hypocone occur. There may be a grooving on the usually smooth anterior face which is all that remains of a formerly double cusped row, i.e., an advance state of fusion of the metacone with the hypocone (PM 7328, pl. 2e). The hypocone may also bear a slight lingual bulge (F 52270, pl. 2f), the cusp wearing so as to form a comma-shaped lake, or it may wear as two "wings" directed laterally (PM 5885, pl. 2g). All these variations are quite minor and seem to be fairly common throughout the specimens present.

$M^{\underline{3}}$ varies little from the typical pattern expressed for $M^{\underline{2}}$. PM 7636 (pl. 2h) provides an outstanding exception. It bears a clearly defined metacone, completely separated from the hypocone. This is a very rare instance of such a marked development of this primitive condition.

The lower molars show only very little variation. In the $M_{\bar{1}}$ changes in the chevron-like angulation of the second and third laminae occur. In some the central angle between the cusps (arms of the chevron) is less than 90° (F 52281, pl. 2i) and in others it is greater than 90° (PM 5866, pl. 2j). The posterolophid may be missing occasionally.

On $M_{\bar{2}}$ the posterolophid may be quite distinct and apparently functional enough to show wear (F 52284, pl. 2k). More usually (PM 7319, pl. 2l), it is reduced and fused to the base of the hypoconid.

$M_{\bar{3}}$ reveals a tendency to fuse the protoconid and metaconid into a ridge. The entoconid is accentuated with the hypoconid fused into it (PM 7321, pl. 2m). F 52302 (pl. 2n) illustrates a less common condition in which the cusps in the first row are distinct and the hypoconid, though reduced, is also distinct. Variation in size and proportion of the lower molars of *P. oralis* is shown in the scatter diagram (fig. 5).

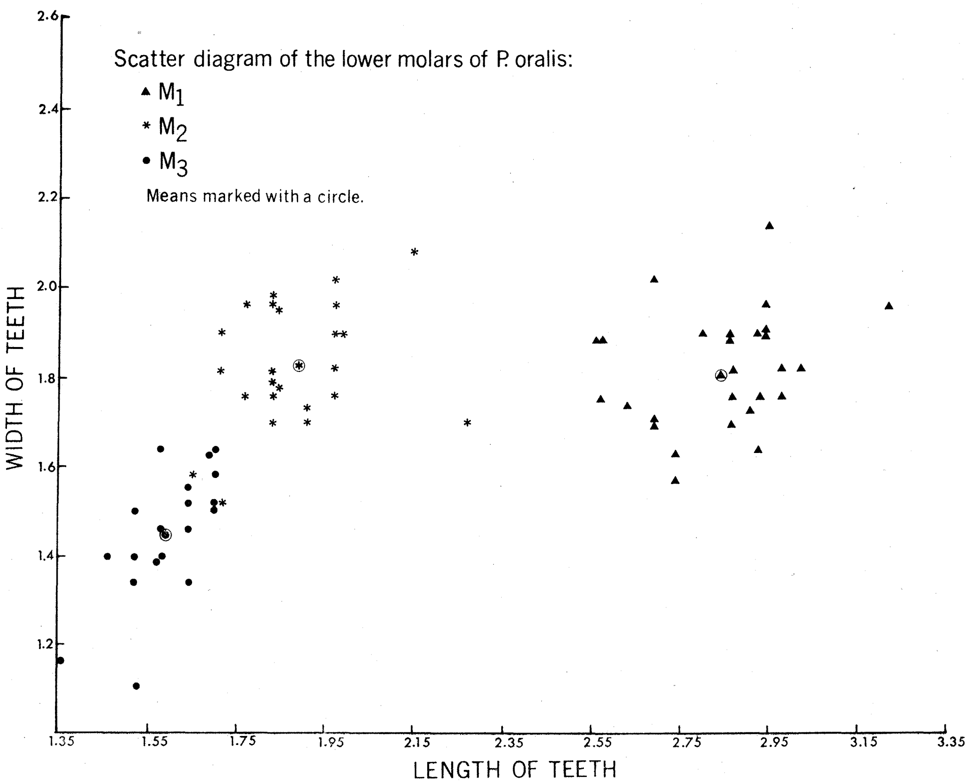

Figure 5

Gyomys glaucus Thomas 1910

This species shows less variation in cusp and style development than does *P. oralis.* $M^{\underline{1}}$ usually does not carry an anterolabial style. A few specimens have it (PM 7605, PM 5922, pl. 3b and a), but in these it is degenerate and partly fused into the anterolabial conule. Few cases of the accessory anteromedian style have been seen, PM 6179 (pl. 3c) in which it is marked, and F 52192 (pl. 3d) in which it is reduced. It may be significant that the variants of anteromedian style and anterolabial style have not been observed together on a specimen. M^2 is also less varied than that of *P. oralis* except for one specimen (F 52185, pl. 3g), which has the second lamina bent back at an angle towards the hypocone instead of running in a gentle arc across the whole width of the tooth. M^3 presents only minor variations in cusp union with the onset of age.

The lower molars of *G. glaucus* are even more uniform in style and cusp development than the uppers and show none of the minor variations (fusions) that are evident in *P. oralis*.

TABLE 5. Statistical data for tooth measures of *Gyomys glaucus* from Broom Cave

	N	$\bar{x}$	s	V	Observed	Tate 1951 BM No. 92.8.7.2
Length M^1 ..	35	2.15 ± .017	.10	4.79	2.32—1.90	2.0
Width M^1 ..	37	1.52 ± .019	.12	8.15	1.78—1.23	1.4
Length M^2 ..	31	1.52 ± .030	.17	11.0	1.89—1.23	1.2
Width M^2 ..	33	1.35 ± .025	.14	10.7	1.66—1.10	1.3
Length M^3 ..	22	1.10 ± .024	.11	10.1	1.29—0.92	0.9
Width M^3 ..	22	1.00 ± .026	.12	12.3	1.16—0.80	1.0
Length M_1 ..	33	2.07 ± .023	.13	6.37	2.32—1.84	..
Width M_1 ..	33	1.19 ± .019	.11	9.49	1.44—1.01	..
Length M_2 ..	35	1.40 ± .017	.10	7.35	1.59—1.16	..
Width M_2 ..	35	1.29 ± .036	.22	16.7	1.58—1.04	..
Length M_3 ..	32	1.14 ± .016	.10	8.77	1.34—0.86	..
Width M_3 ..	32	1.01 ± .015	.09	9.10	1.16—0.74	..

In contrast to the slight degree of variation in cusp and style development in *G. glaucus*, some of the coefficients of variation (V's) of certain tooth measures for this species offer a different picture (tables 4 and 5). The value of V is consistently high for upper M^2 and M^3, whereas most values for the other teeth are more in line with what might be expected. Such high values usually indicate a mixed sample. Conceivably there may be other taxa included in the series, but because of the overall morphological consistency of form and lack of variation of detail in cusp and style development, we think this is not the case. Nor do all of the V's suggest a mixed sample. It is most unlikely that age variations in the measured teeth could account for the high V's, for all the measurements were taken at the crown bases in order to eliminate wear as a factor. This was done in order to utilize all specimens. Hence the measurements at all age classes are essentially comparable to maximum length and width of teeth at Ride's class "e" age. We can offer no conclusive explanation for the high V's, but a possible one is that teeth are inherently more variable than the others. This may be true for the entire population, or perhaps this is a secondary sexual variation, which might be ascertained if the specimens could be sexed.

The striking differences in variability in *G. glaucus* between the relatively stable cusp and loph form and arrangement on one hand, and the highly varied dimensions of some teeth on the other, may be related to small size for it is quite likely that selective advantages in grinding efficiency can accrue in a variety of ways. Probably two such ways are by (1) a relative increase in tooth size without an accompanying structural change, and (2) by a relative increase in occlusual surface complexity without any significant size change. If this is the case, the smaller *G. glaucus* may be thought of as following the second alternative, and the larger *P. oralis* the first one. If size is indeed the critical factor, a check should be possible for parallels to this situation should then be found elsewhere within other groups of small rodents.

TABLE 6. Measurements of the teeth of the *Rattus* sp. specimens in the Broom Cave fauna. Dimensions are given in mm, and represent maximum measures taken at the base of the crown

Specimens	M^1		M^2		M_2	
	Length	Width	Length	Width	Length	Width
PM 7337 ..	..	..	2.14	1.96	..	..
F 52310	..	..	2.08	2.14	..	..
PM 16184 ..	3.62	2.51	..	..	..	..
F 52309	3.25	2.08	1.96	2.02	..	..
PM 16183 ..	..	..	..	..	2.08	1.96

Rattus sp.

The genus *Rattus* is reported to have a typical root pattern by Wood Jones (1922) and Ride (1960). On the basis of the general *Rattus*-like crown morphology and this peculiar (typical) root pattern we have assigned five of our specimens to the genus (pl. 1a, b, c, d). No species determination has been attempted for them. The Murines are extremely difficult to classify on the basis of dental characters and we lack the comparative materials that would permit one to distinguish between isolated teeth of animals of Ride's (1960, p. 75) Groups I, II or the *Uromys*-branch of his Group III. Ride delineates these as follows: "Australian Murinae may be divided into three groups (see Tate 1951) which are: Group I, "Modern introductions", e.g., *Rattus rattus*, *R. norvegicus*, *Mus musculus*; Group II, "Young endemics", e.g., species of *Rattus* which have probably evolved in Australia, including the *R. assimilis* and *R. lutreolus* species groups; Group III, "old endemics", i.e., Murinae of genera peculiar to Australia and the adjacent islands".

From what can be seen on the Broom Cave specimens, we at first felt certain of an assignment to the genus *Rattus* (pl. 1a, b), but examination of root patterns of a few recent specimens of the *Uromys*-branch (*Melomys platyops fuscus* 54181) makes this now seem less certain (pl. 1i). Further investigation of the root pattern and its variation for a variety of Australian species of *Rattus*, *Uromys* and especially *Melomys*, which though similar to *Rattus* seems to have more roots than *Rattus*, is in order if a firm assignment of such isolated teeth is to result. It nevertheless is clear that the fauna does contain either a *Rattus* or a near relative of *Rattus*.

Ride (1960) commented on the absence from the fauna as known to him of a representative of any "modern introduced" *Rattus* or *Mus*, "young endemic" *Rattus*, or of a *Uromys*-branch "old endemic". Tate (1951, p. 318-320) has recognized four, possibly five, major divisions of the genus *Rattus* for the Australia-New Guinea region.

Two of these presumably would have been in Australia at the time of the operative Broom Cave: the members of the *Rattus assimilis* division (*R. assimilis*, *R. ruber*, *R. leucops*, and *R. niobe* groups) generally rainforest inhabitants, and those of the *Rattus lutreolus* division (*R. lutreolus*, *R. youngi*, *R. sordidus*, and *R. gestri* groups) typically are found in an open forest environment.

The presence of a *Rattus* in the fauna now raises some new alternatives with regard to the former observations about this assemblage. (1) The fauna may be younger than has been thought. The *Rattus* (sensu stricto) invasion of the Australian mainland is usually thought to have been a relatively recent occurrence in relation to the overall history of the murids on the continent. (2) *Rattus* actually may have arrived in Australia somewhat earlier than had been thought. The Broom Cave *Rattus* would then be the expression of this very early invasion. At present there seems to be no basis for making a choice between these alternatives.

SUMMARY

The largest sample yet reported of the murid element of the Broom Cave fauna, Late Pleistocene, New South Wales, Australia, has been examined. Included is a small series of specimens of *Mastacomys wombeyensis* Ride, a species previously known only from its type. Variations in dental morphology are described and statistical data are set down for series of *Pseudomys oralis* and *Gyomus glaucus.* In addition to these three species which had been previously reported, a new record, *Rattus* sp., is registered. Some observations on age distributions and an age-spread determination of the absolute minimum numbers of individuals represented are made. A method is advanced for making a conservative estimate of the maximum number of individuals represented, which in the case of undisturbed owl pellet deposits closely approximate the actual number of individuals in the sample.

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APPENDIX

LIST OF MATERIALS STUDIED

Gyomys glaucus

L. Maxillae, wear stage—
- B: PM 5922 with $M^{\underline{1-2}}$.
- C: F 52171 with $M^{\underline{1-2}}$; F 52172 with $M^{\underline{1-3}}$.
- E: PM 5921 with $M^{\underline{1-2}}$.

L $M^{\underline{1}}$, wear stage—
- B: F 52173, F 52174, PM 16141.
- C: F 52175, F 52176, F 52177, PM 16140, PM 16146, PM 16147.
- D: F 52178, F 52179, PM 7660.

L. $M^{\underline{2}}$, wear stage—
- B: F 52180, F 52181, PM 16144.
- C: F 52182, F 52183, F 52184, F 52185, PM 7562, PM 7564, PM 16142.
- D: F 52186, F 52187, PM 7654, PM 16143.

L. $M^{\underline{3}}$, wear stage—
- B: F 52188.
- C: F 52189, PM 7658.
- D: F 52190, PM 7381, PM 7646.
- E: F 52191.

R. Maxillae, wear stage—
- C: F 52192, PM 5914 with $M^{\underline{1-3}}$; PM 16138 with $M^{\underline{1-2}}$.
- D: F 52193, PM 5913 with $M^{\underline{1-3}}$; PM 5912 with $M.^{\underline{2-3}}$

R. $M^{\underline{1}}$, wear stage—
- A: PM 5917, PM 7676.
- B: F 52194, F 52195, F 52196, PM 6179, PM 7383, PM 7653.
- C: F 52197, F 52198, F 52199, F 52200, PM 5915, PM 5916, PM 7605, PM 7652.
- D: F 52201.

R. $M^{\underline{2}}$, wear stage—
- B: F 52202, PM 7656.
- C: F 52203, F 52204, F 52205, F 52206, PM 7679, PM 7680, PM 7977, PM 7978.
- E: PM 7384.

R. $M^{\underline{3}}$, wear stage—
- C: F 52207, F 52208, F 52209, PM 7387, PM 7567, PM 7980, PM 16137.
- D: F 52210, F 52211, F 52212, PM 7663, PM 7979.
- E: F 52213, F 52214, PM 7388.

L. Mandibles, wear stage—
- B: F 52215 with $M_{\overline{1-3}}$
- C: F 52216 with $M_{\overline{2-3}}$ and PM 5901, PM 7343 with $M._{\overline{1-3}}$
- D: F 52217 and F 52218 with $M_{\overline{1-2}}$; PM 7638 and PM 16159 with $M_{\overline{1-3}}$.
- E: F 52219 with $M_{\overline{1-3}}$.
- Edentulous PM 5890.

L. $M_{\overline{1}}$, wear stage—
- B: PM 7641.
- C: F 52220, F 52221, F 52222, PM 7572, PM 7610, PM 7611, PM 16155.
- D: F 52223, F 52224, PM 7642.

L. $M_{\overline{2}}$, wear stage—
- B: F 52225, F 52226, F52227. PM 7612, PM 7645, PM 16156, PM 16157.
- C: F 52228, F 52229, F 52230, PM 7643, PM 7644, PM 16160.
- D: F 52231.

L. $M_{\overline{3}}$, wear stage—
- A: PM 7575.
- B: F 52232, PM 7358.
- C: F 52233, F 52234, PM 7574, PM 7613.
- D: F 52235, PM 7573.
- E: PM 7356.

R. Mandibles, wear stage—
- C: F 52236 and PM 16154 with $M_{\overline{1-2}}$; F 52237, PM 7346 with $M_{\overline{1-3}}$; PM 7568 with $M_{\overline{2-3}}$.
- D: F 52238 with $M_{\overline{1-3}}$; PM 5892 with $M_{\overline{1-2}}$.
- Endentulous: F 52239, PM 7345, PM 7639.

R. $M_{\overline{1}}$, wear stage—

A: F 52240.
B: F 52241, PM 7361, PM 7609.
C: F 52242, F 52243, F 52244, PM 16148, PM 16149.
D: PM 7608.
E: F 52245.

R. $M_{\overline{2}}$, wear stage—

A: F 52246.
B: F 52247, PM 7365, PM 7570.
C: F 52248, F 52249, PM 16150.
D: PM 7364.

R. $M_{\overline{3}}$, wear stage—

A: F 52250.
B: F 52251, F 52252, PM 7640, PM 16151.
C: F 52253, PM 16152.
D: F 52254, PM 16153.
E: PM 7373.

Pseudomys oralis

L. maxillae, wear stage—

C: F 52255 with $M^{\underline{1-2}}$, PM 5878 with $M^{\underline{1-3}}$.
D: F 52256 with $M^{\underline{1-3}}$; PM 16173 with $M^{\underline{1-2}}$.

L. $M^{\underline{1}}$, wear stage—

B: PM 16169.
C: F 52257, F 52258, PM 16168.

L. $M^{\underline{2}}$, wear stage—

B: PM 7328.
C: F 52259.
D: PM 16171.

L. $M^{\underline{3}}$, wear stage—

B: F 52260.
D: F 52261, PM 7637.

R. maxillae, wear stage—

C: PM 7603, PM 7636, PM 16167 with $M^{\underline{1-3}}$.
D: PM 7559 with $M^{\underline{1-2}}$.

R. $M^{\underline{1}}$, wear stage—

B: F 52262, PM 7634.
C: F 52263, F 52264, F 52265, F 52266, F 52267, PM 7331, PM 7332, PM 7334, PM 7335, PM 16163.
D: F 52268.
E: PM 16164.

R. $M^{\underline{2}}$, wear stage—

B: F 52269, PM 7386.
C: F 52270, F 52271, PM 5885, PM 16165.
E: PM 7338.

R. $M^{\underline{3}}$, wear stage—

B: F 52272.
C: F 52273, F 52274, PM 7662.
D: PM 7635.
E: F 52275.

L. mandibles, wear stages—

B: F 52276, with $M_{\overline{1-2}}$.
C: F 52277, F 52278, PM 7307 with $M_{\overline{2-3}}$, PM 5865, PM 6171 with $M_{\overline{1-3}}$.
E: F 52279 with $M_{\overline{1-3}}$.
Edentulous: PM 7303.

L. $M_{\overline{1}}$, wear stage—

B: F 52280, PM 5812.
C: F 52281, F 52282, PM 5873, PM 7305, PM 7308.
E: F 52283, PM 16178.

L. $M_{\overline{2}}$, wear stage—

A: F 52284.
B: F 52285, F 52286, PM 7318, PM 16180.
C: F 52287, F 52288, PM 7633, PM 16179.

L. $M_{\overline{3}}$, wear stage—

A: PM 7321.
B: F 52289, F 52290, PM 16181.
C: F 52291, PM 7647.
D: PM 5869.

R. mandibles, wear stage—

C: F 52292 with $M_{\overline{1-3}}$; PM 5866 with $M_{\overline{1-2}}$.
D: F 52293 with $M_{\overline{1-2}}$; PM 6180 with $M_{\overline{1-3}}$.
E: F 52294 with $M_{\overline{1-3}}$; PM 16176 with $M_{\overline{2-3}}$.
Edentulous: F 52295, PM 7302.

R. $M_{\overline{1}}$, wear stage—

B: PM 5868.
C: F 52296, F 52297, F 52298, PM 7317, PM 7558, PM 7631.
D: F 52299.

R. $M_{\overline{2}}$, wear stage—

B: F 52300, F 52301, PM 7319.
C: PM 5863.

R. $M_{\overline{3}}$, wear stage—

B: F 52302, PM 7320.

Mastacomys wombeyensis—

Palates and maxillaries, wear stage—

B: F 52303 with L. $M^{\underline{1-3}}$ and R. $M^{\underline{1-3}}$.
C: PM 5861 with L. $M^{\underline{1-3}}$ and R. $M^{\underline{1-2}}$.
Edentulous: PM 6170, a R. maxillary questionably referred.

L. $M^{\underline{1}}$, wear stage—

B: PM 7556.
C: F 52304.

R. $M^{\underline{1}}$, wear stage—

C: PM 7333.

L. mandibles, wear stage—

C: F 52305 with $M_{\overline{1-3}}$.
Edentulous: PM 6172.

L. $M_{\overline{1}}$, wear stage—

C: PM 6178.

R. mandibles, wear stage—

C: F 52306 and PM 6174 both with $M_{\overline{1}}$.

R. $M_{\overline{1}}$, wear stage—

B: F 52307.

R. $M_{\overline{2}}$, wear stage—

C: PM 6175.
D: F 52308.

Rattus sp.

L. maxillary, wear stage—

C: F 52309 with $M^{\underline{1-2}}$.

L. $M^{\underline{2}}$, wear stage—

C: F 52310.

R. $M^{\underline{1}}$, wear stage—

C: PM 16184.

R. $M^{\underline{2}}$, wear stage—

B: PM 7337.

R. $M_{\overline{2}}$, wear stage—

D: PM 16183.

TABLE 1. Age group assignments of teeth of *Gyomys glaucus* from the Broom Cave fauna using Ride's age designation (Ride, 1956a, p. 433). Age group classes are as follows: (a) distinct cusps on all molars, (b) wear beginning to unite cusps into laminae, (c) all cusps united transversley but cusps still discernible, (d) cusps no longer discernible, (e) laminae themselves disappearing. First column under each age group gives numbers of individual teeth. Second columns give the maximum numbers of specimens of that molar quadrant that are represented by the individual teeth of the first columns after all known correlations have been accounted for.

	A		B		C		D		E		Totals	
	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.
L. M^1	0		4		8		3		1		16	
L. M^2	0	0	4	8	9	17	4	*10*	1	2	18	37
L. M^3	0		1		3		3		2		9	
											43	
R. M^1	**2**		6		**11**		4		0		23*	
R. M^2	0	2	2	8	**11**	***25***	3	9	1	*4*	17	48
R. M^3	0		0		9		**8**		**3**		20	
											60	
L. M$_1$	0		2		9		7		1		19	
L. M$_2$	0	1	**8**	***11***	9	21	5	*10*	1	2	23	45
L. M$_3$	1		3		7		4		2		17	
											59	
R. M$_1$	1		3		9		3		1		17	
R. M$_2$	1	*3*	3	10	8	15	3	6	0	2	15	36
R. M$_3$	1		4		6		3		1		15	
											59	
Total number of teeth ..	6	..	40	..	99	..	50	..	14	..	209	..
Total number of specimens ..	..	6	..	37	..	78	..	35	..	10	..	166†
Most frequently represented tooth	**2**	..	**8**	..	**11**	..	**8**	..	**3**	..	32‡	..
No. of specimens in largest suite	..	*3*	..	*11*	..	*25*	..	*10*	..	*4*	..	53¶

* Traditional assessment of minimum number of individuals.

† Absolute maximum number of specimens and individuals (based on all teeth, correlated and uncorrelated).

‡ Age-spread assessment of minimum number of individuals.

¶ Minimal estimate of max. number of individuals.

TABLE 2. Age group assignments for teeth of *Pseudomys oralis* from the Broom Cave fauna. Letters and symbols as in appendix table 1

	A		B		C		D		E		Totals	
	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.
L. M^{1} . . . . L. M^{2} . . . . L. M^{3}	0 0 0	0	1 1 1	3	5 3 1	6	2 **3** **3**	*5*	0 0 0	0	8 7 5 — 20	14
R. M^{1} . . . . R. M^{2} . . . . R. M^{3}	0 0 0	0	2 2 1	5	**13** 7 6	*20*	2 1 1	3	1 1 1	*3*	18* 11 9 — 38	31
L. M_{1} . . . . L. M_{2} . . . . L. M_{3}	0 **1** **1**	*2*	3 **5** 3	*10*	8 9 7	16	2 0 1	3	1 1 1	1	14 16 13 — 43	32
R. M_{1} . . . . R. M_{2} . . . . R. M_{3}	0 0 0	0	1 3 2	6	8 3 1	9	**3** 2 1	3	1 **2** **2**	2	13 10 6 — 29	20
Total number of teeth	2	. .	25	. .	71	. .	21	. .	11	. .	130	. .
Total number of specimens . .	. .	2	. .	24	. .	51	. .	14	. .	6	. .	97†
Most frequently represented tooth	**1**	. .	**5**	. .	**13**	. .	**3**	. .	**2**	. .	24‡	. .
No. of specimens in largest suite	. .	*2*	. .	*10*	. .	*20*	. .	*5*	. .	*3*	. .	40¶

TABLE 3. Age group assignments for teeth of *Mastacomys wombeyensis* from the Broom Cave fauna. Letters and symbols as in appendix table 1

	A		B		C		D		E		Totals	
	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.
L. M^{1}	0	0	**2**	*2*	**2**	2	0	0	0	0	4*	4
L. M^{2}	0		1		1		0		0		2	
L. M^{3}	0		1		1		0		0		2	
				2		3					8	5
R. M^{1}	0	0	1	1	**2**	2	0	0	0	0	3	3
R. M^{2}	0		1		1		0		0		2	
R. M^{3}	0		1		0		0		0		1	
											6	
L. M_{1}	0	0	0	0	**2**	2	0	0	0	0	2	2
L. M_{2}	0		0		1		0		0		2	
L. M_{3}	0		0		1		0		0		1	
				1		5		1			5	7
R. M_{1}	0	0	1	1	**2**	*3*	0	*1*	0	0	3	5
R. M_{2}	0		0		1		**1**		0		2	
R. M_{3}	0		0		0		0		0		0	
											5	
Total number of teeth ..	0	..	8	..	14	..	1	..	0	..	23	..
Total number of specimens ..	..	0	..	3	..	8	..	1	..	0	..	12†
Most frequently represented tooth	**0**	..	**2**	..	**2**	..	**1**	..	0	..	5‡	..
No. of specimens in largest suite	..	0	..	*2*	..	*3*	..	*1*	..	0	..	6¶

TABLE 4. Age group assignments for teeth of *Rattus* sp. from the Broom Cave fauna. Letters and symbols as in appendix table 1

	A		B		C		D		E		Totals	
	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.	teeth	spec.
L. M^1	0		0		1		0		0		1	
L. M^2	0	0	0	0	**2**	*2*	0	0	0	0	2*	2
L. M^3	0		0		0		0		0		0	
											3	
R. M^1	0		0		1		0		0		1	
R. M^2	0	0	**1**	*1*	0	1	0	0	0	0	1	2
R. M^3	0		0		0		0		0		0	
											2	
L. M_1	0		0		0		0		0		0	
L. M_2	0	0	0	0	0	0	0	0	0	0	0	0
L. M_3	0		0		0		0		0		0	
											0	
R. M_1	0		0		0		0		0		0	
R. M_2	0	0	0	0	0	0	**1**	*1*	0	0	1	1
R. M_3	0		0		0		0		0		0	
											1	
Total number of teeth ..	0	..	1	..	4	..	1	..	0	..	6	..
Total number of specimens ..	..	0	..	1	..	3	..	1	..	0	..	5†
Most frequently represented tooth	0	..	**1**	..	**2**	..	**1**	..	0	..	4‡	..
No. of specimens in largest suite	..	0	..	*1*	..	*2*	..	*1*	..	0	..	4¶

EXPLANATION OF PLATES

Plate 1

(Scales indicate length of 2 mm)

Rattus sp.: (a and b), labial and occlusal views of F 52309 L. max. displaying typical *Rattus* root patterns and cusp and style arrangement; (c and d), PM 16183 R. $M_{\overline{2}}$ of wear stage "d" (see text or appendix) showing typical lower root pattern for *Rattus*.

Mastacomys wombeyensis: (e), palatal view of skull, F 52303 showing the diagnostic enterostyles on $M^{\underline{3}}$ indicated with arrows; (f), PM 5861, a palate displaying an enterostyle partially fused into the hypocone; (g), PM 6174, a R. ramus with $M_{\overline{1}}$; (h) F 52308 a R.$M_{\overline{2}}$ of wear stage "c".

Melomys platyops fuscus: (i) 54181, a recent specimen of the Field Museum, displaying the *Rattus*-like cusp and style pattern and the multiplicity of roots characteristic of *Rattus* and near-*Rattus* forms.

Plate 2

(Scale indicates length of 2 mm)

Pseudomys oralis: (a), F 52264 $RM^{\underline{1}}$ displaying maximum development of cusps and styles, a well developed anteromedian style, all conules and style well differentiated on the procingulum, mesostyle well separated and the metacone still distinguishable from the hypocond; (b), PM 7364 $RM^{\underline{1}}$ with the labial elements beginning to atrophy; (c), F 52262 $RM^{\underline{1}}$ showing similar losses as PM 7364 and also lacking an anteromedian style; (d), PM 5878 L. max., an example of the more typical cusp and style pattern of the upper molars; (e), PM 7328 $LM^{\underline{2}}$, with the metacone fusing into the hypocone; (f), F 52270 $RM^{\underline{2}}$, fusion complete, hypocone wearing with a labially directed lake; (g), PM 5885 RM,$^{\underline{2}}$ with the hypocone wearing with two comma-shaped lakes; (h) PM 7636 R. max., with a well developed metacone on the $M_{\overline{3}}$; (i), F 52281 $LM_{\overline{1}}$ having the central angle between the cusps less than 90°; (j), PM 5866, right ramus, the angle between the cusps is greater than 90°; (k), F 52284, $LM_{\overline{2}}$, with the posterolophid as a functional cusp; (l), PM 7319, $RM_{\overline{2}}$, having the posterolophid reduced; (m), PM 7321, $LM_{\overline{3}}$, hypoconid fused into entoconid; (n), F 52302, $RM_{\overline{3}}$, possessing a distinct though reduced hypoconid.

Plate 3

(Scale indicates length of 2 mm)

Gyomys glaucus: (a), PM 5922, L. max., with degenerate anterolabial style fusing into the anterolabial conule; (b), PM 7605 $RM^{\underline{1}}$ showing the same pattern as above; (c), PM 6179, $RM^{\underline{1}}$, having a well developed anteromedian style; (d), F 52192, R. max., see reduced anteromedian style on $M^{\underline{1}}$; (e), F 52177 $LM^{\underline{1}}$ displaying an anteromedian style; (f), PM 5914, R. max., which possesses the typical cusp and style pattern commonly found in the upper molars of this series; (g), F 52185, $LM^{\underline{2}}$, with the second lamina sharply bent back towards the hypocone; (h, i, j), F 52212, F 52209, PM 7387, $RM^{\underline{2}}$'s which show the range of variation found in this tooth; (k), PM 7346, a R. ramus with $M_{\overline{1-3}}$ conforming to the typical pattern for these teeth.

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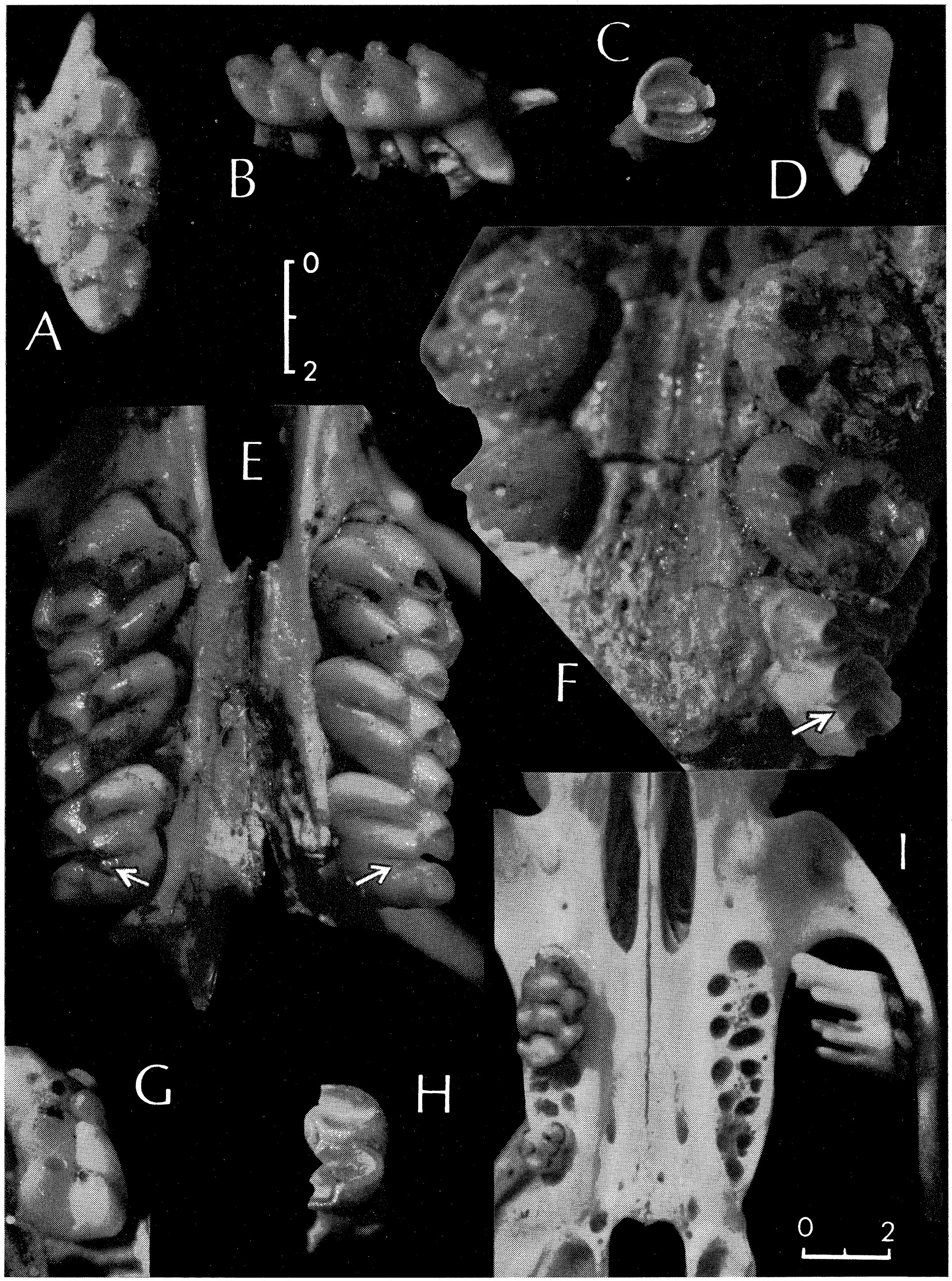
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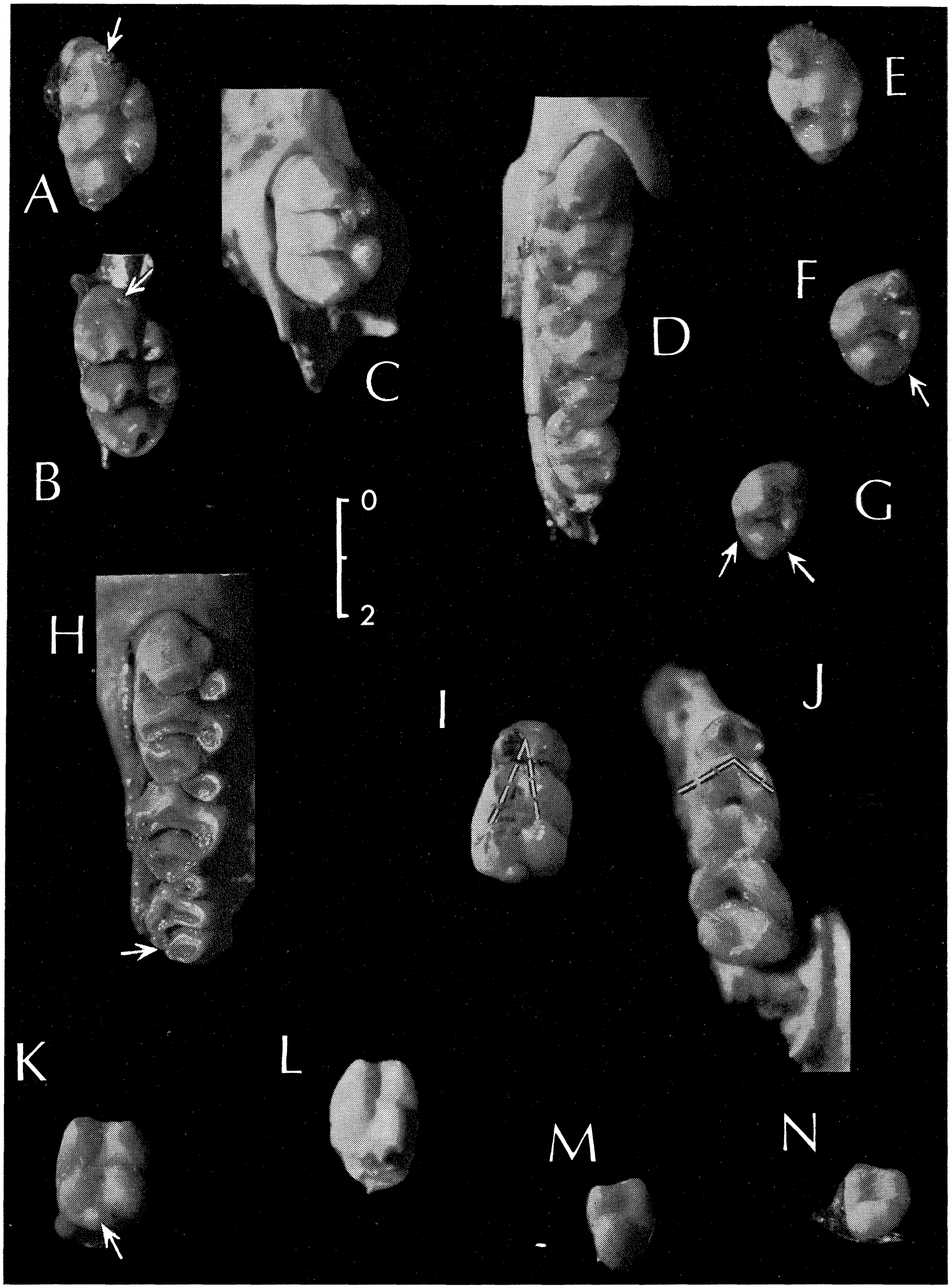
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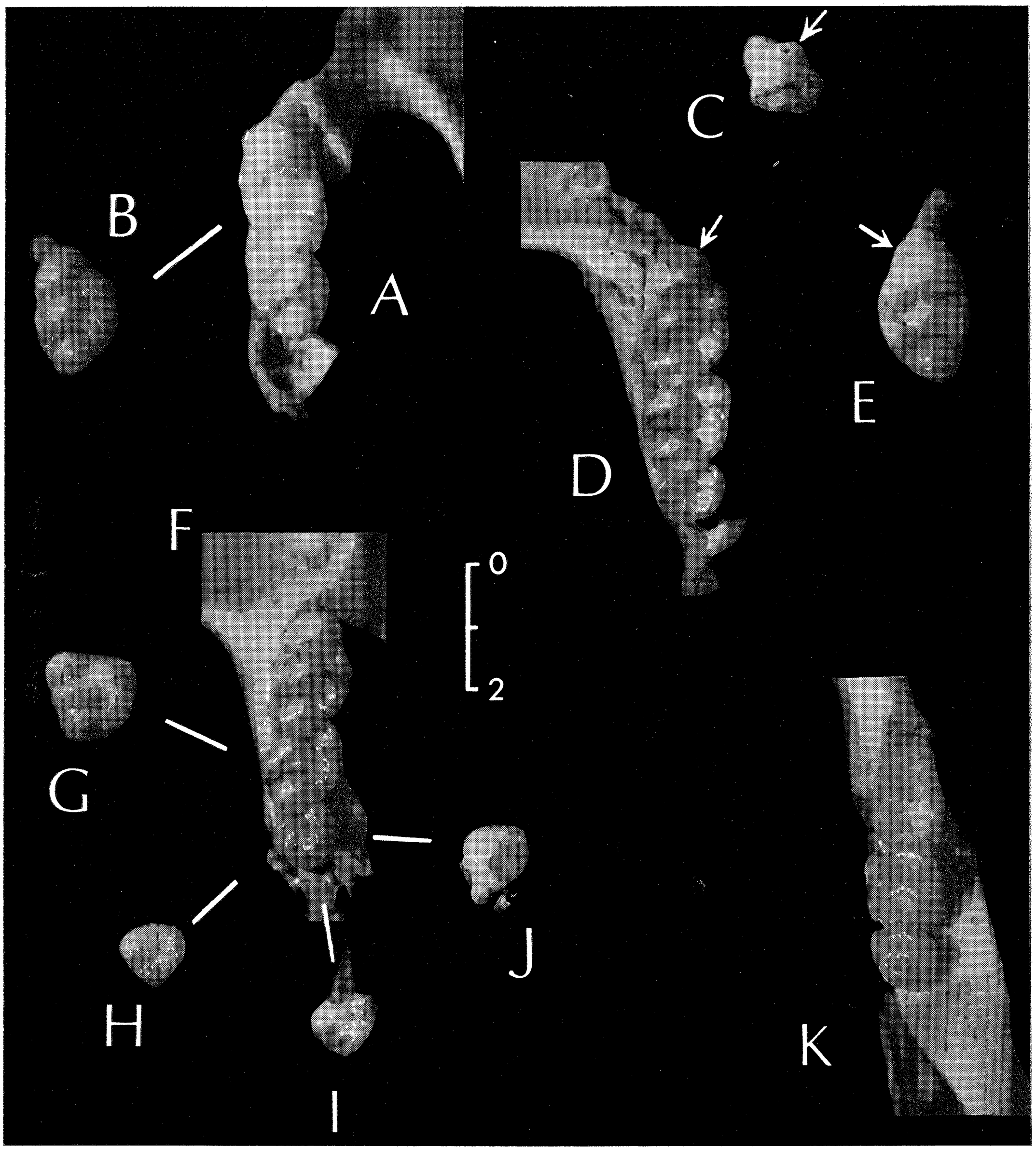

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