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Broom Cave *Cercartetus:* With Observations on Pygmy Possum Dental Morphology, Variation, and Taxonomy*

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INTRODUCTION

The murids of the Broom Cave Fauna were dealt with in the first of a series of reports planned to cover the mammals of this Late Pleistocene deposit in the Wombeyan Caves area of New South Wales (Schram & Turnbull, 1970). The fauna is contained in a breccia derived in large part from an accumulation of regurgitated owl pellets. Continuing this series, we now consider the two pygmy possums in the Broom fauna: *Cercartetus nanus* and *Cercartetus lepidus*. Study of these species has involved us with the definition of the genus *Cercartetus* as advanced by Wakefield (1963). Consequently we put forth some observations relating to this delineation along with an analysis of certain dental patterns of the members of this group.

METHODS AND PROCEDURES

Most of the preparation and study techniques we employed are discussed in detail in Schram & Turnbull (1970). We have now completed the preparation of the Fletcher material and therefore this and subsequent studies are based on the complete collection.

We have continued to employ the previously described methods for arriving at an estimate of the maximum and minimum numbers of individuals represented by each sample, viz., the age-spread minimum and the minimal estimate of the maximum. Four age categories were used for the pygmy possums: (a) cusps very sharp and clear, little or no wear; (b) wear of enamel beginning, cusps slightly round, wear facets appearing; (c) wear of enamel well advanced, cusps clearly worn down; (d) tips of cusps almost gone, with dentine exposed and beginning to wear.

All measurements of teeth were made with an ocular micrometer, which with the optics used, permitted direct reading to .038 or .051 mm, with ready interpolation to half of these values per unit. Mean, standard deviation and coefficients of variation were calculated using the IBM 360 computer at Eastern Illinois University.

Extensive examination of Recent material was necessitated in attempting to arrive at an understanding of modern pygmy possum taxonomy. Abbreviations for specimens used in this study are as follows:

AMNH   American Museum of Natural History.
MU   Monash University recent mammal collection.
QVM   Queen Victoria Museum, Launceston, Tasmania.
F   Prefix for fossil collections of Australian Museum.
PM   Some of fossil mammal collections of Field Museum.
FM   Recent mammal collections of Field Museum.
UT   Fossil collections of University of Texas, Austin.

DESCRIPTIONS

(A complete listing of specimens is given in Appendix A.)

Cercartetus nanus

Upper dentition

A single specimen, PM7424, (Plate 26, fig. B) with I^1 and I^3 is all we have of the premaxillary bone and dentition. The premaxillary had a high lateral wall. I^1 is an elongate tooth with a tapering slightly recurved crown that is nearly elliptical in cross-section. It is worn at the tip so that its apex is gone, and the long axis of its elliptical root is parallel to the lateral edge of the bone. I^3 is triangular in occlusal outline, the anterior and medial sides being vertical and terminating in crests that meet at nearly a right angle. The lateral side is gently curved in both its occlusal outline and in the vertical plane as that side of the crown merges with the other two sides along the two crests.

Nine specimens contribute to our knowledge of the canine and anterior premolar region (F52671, F52720, F52723, F52724, PM6162, PM7426, PM7446, PM7618 and PM17196)—and between them they show a variety of conditions (fig. 1). In no case do we have the canine or anteriormost premolar (P^1 or P^2*) preserved, but the alveolus of the canine root is large and oval. Behind this there is always a sizable, diastema before the alveolus (or alveolae) of the anterior of the premolars

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* There is some disagreement as to which of the anterior two of the four primitive premolars is lost. Since the identity of the anterior-most premolars are debated (P^1_1 or P^2_2) we shall herein refer to the premolars as P^1_1, P^3_3, P^4_4 without intending to take sides in this controversy.

C

DIASTEMA

P^1 or ^{2}

P^3

P^4

M^1

M^2

M^3

439

F 52724   PM.17196   PM 7618   F 52671   PM 6162   F 52723

F 52720   PM 7426

PM 7446

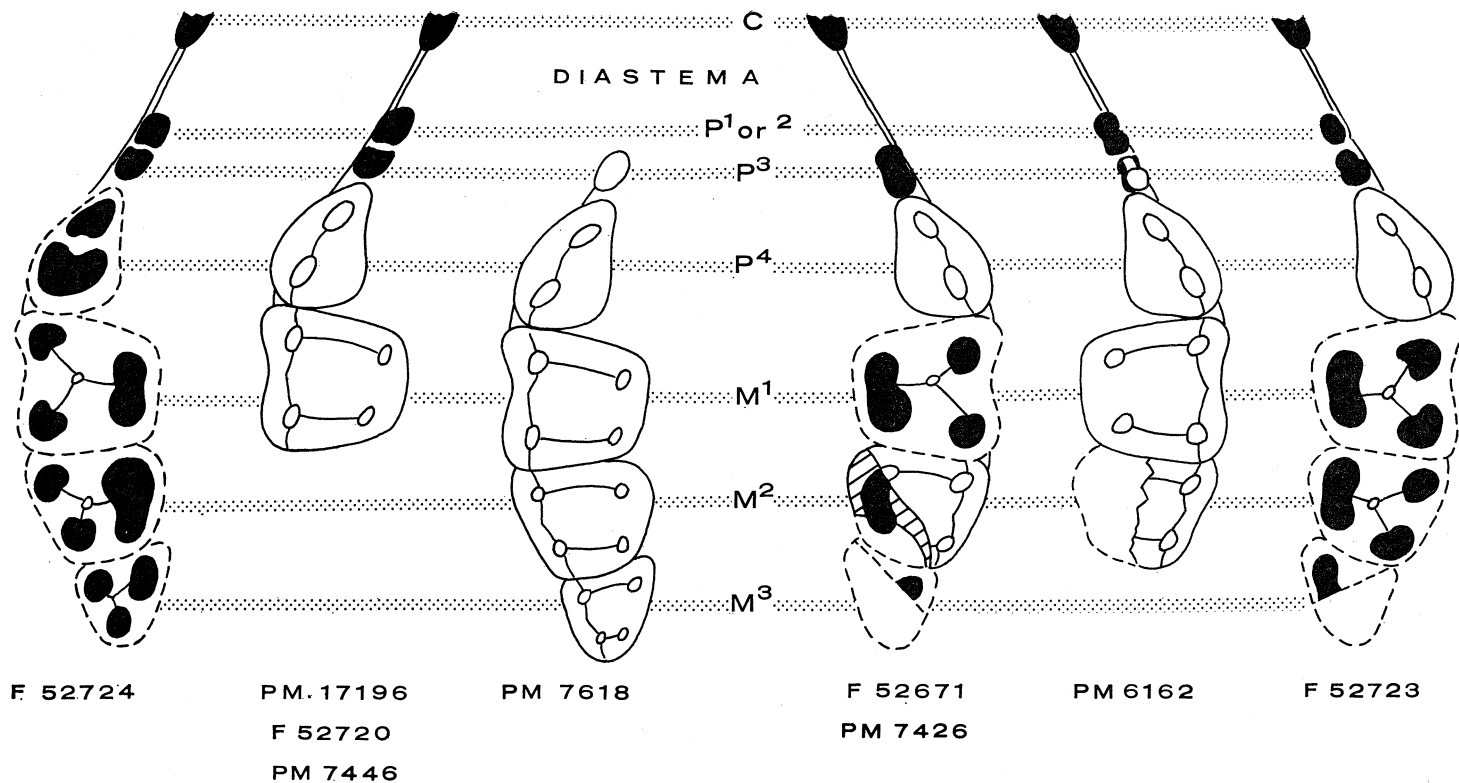Figure 1.   Schematic outline views of the cheek teeth and/or their alveolae (black), showing the variability found in the Broom Cave specimens of *C. nanus*, especially in the anterior premolar region.   For tooth crowns, circles and lines represent cusps and crests.   For alveolar specimens, circles and lines represent ridges and protuberances of the maxillary bone between the roots beneath the crowns of the teeth.

is encountered. In PM17196 and F52724 there are two large alveolae presumably for two single-rooted teeth comparable to the single-rooted P^3 of PM7618. PM6162 however, has a double-rooted P^3 and the alveolus for its P^1 is bilobed which suggests that this tooth was double-rooted too. In F52671 there is a single hour-glass shaped alveolus anterior to P^4 which might indicate either a double-rooted, large P^3 or two very closely appressed teeth (P^1 and P^3). PM7426 has two large alveoli with a high spire of bone between them not unlike the bone buttress which occurs on two rooted teeth indicating perhaps a relatively large double-rooted P^3 and no P^1.

PM7618 (Pl. 26, fig. A), preserves the most complete tooth row (P^3–M^3). The P^3 is a small oval tooth in occlusal view. Its crown is expanded anteriorly over an even smaller single, peg-like root. The tooth is not as extremely reduced as its counterpart on QVM 1963 : 1 : 14 in which both of the anterior premolars are very tiny single-rooted pegs (Pl. 28, fig. B). The occlusal outline of P^4 has a slightly constricted oval shape. There is a small cuspule immediately behind this constriction on the lingual side near the base of the crown, and sometimes there may be a similar small cuspule behind the constriction on the labial side (PM7446). In addition on PM7426 and PM7446 there is another cuspule at the postero-labial corner of the P^4.

The M^1 is a nearly square, low crowned tooth composed of the four major cusps. The paracone and metacone are larger and stand higher than the protocone and hypocone which are low and somewhat crescentic. The paracone and metacone are crested antero-posteriorly on all the upper molars. These crests abut one another so that there is a continuous arc from the anterior edge of P^4 to the posterior edge of M^3. Three weak labial cingula are developed antero-lateral to the paracone, postero-lateral to the metacone, and lateral to the crest connecting the two cusps. Occasionally a broad lateral cingular shelf may develop as in PM17196 (Pl. 26, fig. D). The distance between the paracone and metacone is greater than that between the protocone and hypocone but a line between the labial cusps is roughly parallel to one between the two lingual cusps. In addition, the labial length of the tooth crown is somewhat greater than the lingual length.

The M^2 is wider anteriorly than posteriorly and the distance between the protocone and paracone is greater than that between the hypocone and metacone. The protocone is the largest cusp in occlusal view, but it is not as high as the paracone and metacone which are about subequal. The hypocone is the smallest cusp. The distinct anterior cingulum is best developed near the paracone at the antero-labial corner of the tooth. It is continuous with an antero-labially directed ridge from the protocone. There is a posterior cingular shelf on the rear of the tooth between the metacone and hypocone. In both M^1 and M^2 there are weakly and somewhat variably, developed transverse lophs (protoloph and metaloph). These lophs usually are stronger on M^2 (F52670) than on M^1 (Pl. 26, fig. E).

The M^3 is triangular in shape. It is broad across the anterior edge where it contacts the M^2. The metacone and hypocone are very reduced and lie close to each other. The protocone is the largest of the cusps in occlusal view but the paracone is the highest. Between the main cusps there is an elongate oval basin whose axis lies lateral to the center of the tooth.

The anterior buttress of the zygomatic arch comes off from an area lateral to the posterior third of M^1 and the anterior third of M^2, and diverges posteriorly at about 45°. The infraorbital foramen lies approximately over the posterior root of the P^4.

Lower dentition

There are a number of specimens which preserve a considerable portion of the mandible but no ramus is complete. Several specimens preserve the coronoid process and two preserve the angle. No one specimen has an entire tooth row, nor do any have a complete condyle.

The elongate, procumbent $I_{\overline{1}}$ is elliptical in cross-section at the point where it protrudes from its alveolus. It tends to flatten at its tip and is slightly twisted, but in none of these specimens is the $I_{\overline{1}}$ spatulate. The weak cresting on the ventral edge of the medial surface of this incisor tends to be eliminated with wear. Wear on this tooth seems to be excessive and peculiar: F52619 (Pl. 27, fig. C) had the enamel breached all along its length (though the tip is broken off) and PM16981 has its pulp cavity exposed at the tip (Pl. 26, fig. F). No $I_{\overline{2}}$ is preserved in our material. But five out of seven specimens in which this region of the jaw is preserved indicate it was a small, single-rooted tooth procumbent on the larger incisor. The $P_{\overline{1}}$ and $P_{\overline{3}}$ are small and about the same size. They are cuspless and double-rooted with low, oval, pillow-like crowns that protrude in all directions over the roots. PM16981 shows these premolars and the alveolus of the $I_{\overline{2}}$ to the best advantage (Pl. 26, fig. F).

The double-rooted $P_{\overline{4}}$ is a large tooth with a single, central, high cusp. It is nearer in size to the molars than to the tiny premolars (Pl. 26, figs. F & G; Pl. 27, figs. B, C, D & E). There is a weak anterior crest from the apex of the cusp to the anterior edge of the base of the crown. There is a slightly stronger posterior crest that proceeds from the apex of the cusp nearly to the back edge of the crown where it curves lingually. The central cusp is usually perpendicular, but may be slightly bent anteriorly or posteriorly. In occlusal view a $P_{\overline{4}}$ is typically broadly rounded anteriorly while posteriorly the oval form is blunted at a slight angle on the postero-lingual corner. It is usually longer than wide but occasionally may be as broad posteriorly as it is long.

The $M_{\overline{1}}$ is quite distinctive, being nearly rectangular in occlusal view (Pl. 26, fig. G). It is slightly narrower in front than behind in the fossils, but the Recent specimen (QVM 1963 : 1 : 14) has an $M_{\overline{1}}$ which is more subtriangular in occlusal view (Pl. 28, fig. A). The $M_{\overline{1}}$ has three triangularly placed cusps; the anterior one is presumably a metaconid, the posterior pair are the hypoconid and entoconid. The three cusps are connected by ridges so that an elongate triangular basin is formed in the center of the tooth. The posterior ridge of the metaconid and the anterior ridge of the entoconid meet at the lingual edge of the valley between these cusps. There is a strong crest extending forward from the metaconid. This is aligned with the crest of the $P_{\overline{4}}$ with which it forms a nearly continuous blade. The hypoconid is broadly crescentic as a result of its cresting. Its anterior crest progressively diminishes as it runs antero-lingually and approaches the metaconid. The posterior crest proceeds postero-lingually and joins the posterior crest of the entoconid at the postero-labial corner of the tooth. In some specimens there is a slight bulge or inflection along the posterior crest from the metaconid which may be interpreted as a vestige of a metastylid. Similarly on the anterior crest of the metaconid there is occasionally an irregularity which could be interpreted as a vestige of a paraconid. The region where a protoconid would lie is a broad, steeply inclined, curving surface without indication of a cusp, (so, in some respects, the trigonid region of the Broom Cave fossils is more primitive than that of the recent specimen (QVM 1963 : 1 : 14) which does not have this protoconid bulge or the other features mentioned above).

There is little cingular development; what there is lies along the anterior edge of the tooth on both its lingual and labial sides. There cingula rise steeply to terminate at the anteriormost point of the anterior crest of the metaconid. There is typically a weak embayment on the anterior face of the tooth to accommodate the posterior face of the $P_{\overline{4}}$.

$M_{\overline{2}}$ and $M_{\overline{3}}$ are nearly rectangular, elongate teeth, each with a similar dental morphology. The most notable difference is size, $M_{\overline{3}}$ being slightly smaller (Pl. 27, figs. D & E). In both teeth the protoconid and hypoconid are low cusps. In each the protoconid is ridged anteriorly and posteriorly from its apex, the anterior ridge running to the antero-labial edge of the tooth and the posterior ridge proceeding posteriorly and somewhat lingually, meeting the anterior crest of the hypoconid. Each hypoconid has a nearly lingually directed posterior crest which lies along the back edge of the tooth to join the posterior crest of the entoconid. The metaconids and entoconids have apices which lie far to the lingual sides of the teeth. A crest runs from the apex of each of these cusps towards the other to meet in the valley between them. A second metaconid crest, the anterior one, does not always reach the apex of that cusp. It extends to the antero-lingual corner of the tooth and becomes contiguous with the anterior cingulum crossing the front of the tooth to join with the anterior crest of the protoconid. The crests of all these cusps thus delimit a rather sinuous central basin whose undulating form is enhanced by subsiding crests that lead inward for a short distance from each cusp. There is considerable variability in the length/width ratios of these teeth: $M_{\overline{3}}$ is always longer than wide and slightly wider in front than behind; $M_{\overline{2}}$ is usually longer than wide and parallel sided, but can occasionally be almost square. An antero-labial cingulum rises to meet the anterior crest of the protoconid where that crest joins the main cingulum across the front of the tooth. There is no $M_{\overline{4}}$.

The masseteric fossa is variably developed. It is usually quite deep and the surrounding crests are pronounced (Pl. 27, figs. A, B, & E), especially that leading to the tip of the coronoid process. The angulation of the antero-ventral corner of the fossa and the extent to which it extends onto the ramus is variable (PM16980 and F52618). The angular process is stout, tapering, weakly inflected, bluntly rounded in front, flattened on its ventro-lateral surface, and concave on its dorso-medial surface behind the ridged anterior edge. The inferior dental foramen (mental foramen) is single and usually lies beneath the anterior root of $P_{\overline{4}}$ but may be situated slightly anterior to this. Nearby and in front of it are a few small nutrient foramina which are variable in their occurrence.

If the single Recent specimen we have studied is indeed typical, then it is our impression that the Broom Cave *Cercartetus nanus* is somewhat different. It is undoubtedly still the same species, but the variations noted above in the $M_{\overline{1}}$ and the upper premolar series could be considered indicative of primitiveness, while most other variations argue neither for a more primitive nor a more advanced condition.

Cercartetus lepidus

Upper dentition

The two edentulous maxillary fragments of *C. lepidus* preserve approximately the same structures. In both, the anterior buttress of the zygomatic arch extends from the area lateral to $M^{\underline{1}}$ and $M^{\underline{2}}$. Specimen F52768 has the greatest number of alveoli, preserving about half of that of the canine and those of all the cheek

teeth (Pl. 30, fig. C). Behind the canine there is a diastema posterior to which lie four aligned equal alveoli for the paired roots of the first two premolars, followed by two large alveoli for the $P^{\underline{4}}$. The triangularly placed alveoli of $M^{\underline{1}}$ through $M^{\underline{3}}$ form a rather uniform decreasing size gradient. Alveoli of $M^{\underline{4}}$ are variable: in F52768 the labial ones are very reduced and combine with the lingual one, whereas in PM17244, the alveoli are all distinct though reduced (Pl. 30, fig. A).

The $P^{\underline{4}}$ has two subequal fused cusps which are merged for at least $\frac{2}{3}$ of their height. They appear as distinct entities only at their apices. In PM7578 the posterior one is slightly larger than its twin. The $P^{\underline{4}}$s are broad posteriorly and narrow anteriorly with a weak axial crest. In PM 17246 the anterior root is exceptional in that it extends forward quite markedly (Pl. 25, fig. B).

The $M^{\underline{1}}$ is longer on the labial side than on the lingual. The paracone and metacone are relatively large cusps connected by a ridge that runs the full length of the labial side. The protocone and hypocone are connected by a weak crest. They are subequal but are much smaller cusps, and are closer together than are paracone and metacone (Pl. 30, fig. B). There are additional crests from the protocone (running antero-labially) and from the hypocone (running postero-labially). Both these laterally directed crests extend as cingular ridges to the longitudinal crest of the labial cusps. There is a weak suggestion of a connection between the hypocone and metacone but basically the cusps sit on the perimeter of the crowns and are separated by a broad open valley. There is no distinct parastyle or metastyle but there is a weak bulging in the appropriate position for each.

The $M^{\underline{2}}$ is decidedly wider anteriorly than posteriorly. The paracone is the highest and largest cusp, followed in size by the protocone, metacone and hypocone. The cresting of these cusps is essentially as in $M^{\underline{1}}$. Usually there is no stylar shelf development beyond a weak cingular bulge at the base of the crown (Eg. F52777; Pl. 30, fig. D), but occasionally a rather decided cingular shelf is developed. This shelf is greatest on F52769 (Pl. 30, fig. F). A comparable situation exists in the AMNH series of *C. caudatus;* here too this may be a matter of individual variation.

The $M^{\underline{3}}$ is essentially a smaller version of the $M^{\underline{2}}$ with the exception of having a less decided hypocone which is little more than a cingular bulge (Pl. 30, fig. E). We found none of the tiny $M^{\underline{4}}$s of this species in our sample, however, as noted above, the edentulous maxillae do have alveoli for the $M^{\underline{4}}$.

Lower dentition

As is the case with the maxillary fragments, specimens of the mandibles have lost most, if not all of their teeth (Pl. 30, fig. G; Pl. 31, fig. A). The alveolus for the $I_{\overline{3}}$ is single and larger than any of the four alveoli of the first two premolars that follow it. The alveoli for $P_{\overline{4}}$ through $M_{\overline{2}}$ are large, those of $M_{\overline{3}}$ are noticably smaller, and those of $M_{\overline{4}}$ are minute. The condyle is flat and spatulate, the masseteric fossa is broad, and the coronoid process is weak (Pl. 31, fig. A). The angular process is well developed and inflected.

The $I_{\overline{1}}$ (F52767) is gently curved and tapered with a ventro-median ridge (Pl. 31, fig. B). It is not very spatulate but retains a subtriangular cross section throughout its length. The broken incisor in F52780 is less ridged than F52767.

The $P_{\overline{4}}$ in jaw PM6163 (one of the few with a tooth in place) is blade-like with two high compressed cusps with very little space between them, (Pl. 30, fig. G). The tooth is broader posteriorly than anteriorly. There is an incipient cuspule on the posterior ridge of the posterior main cusp. A more typical condition, however, has the $P_{\overline{4}}$ with a less blade-like condition and no incipient cuspule behind the posterior cusp.

The $M_{\overline{1}}$ has an elongate, triangular outline in occlusal view, with the widest portion across the talonid (Pl. 31, fig. C). Its protoconid, metaconid, hypoconid and entoconid are well developed. The protoconid and metaconid are well separated, the latter is crested on its posterior side. The protoconid and hypoconid have strong, oblique anterior crests and weaker posterior crests. The posterior crests proceed in a postero-lingual direction, that from the hypoconid arcs across the posterior face of the tooth as a cingulum. There is merely the faintest suggestion of an anterior cingulum antero-labial to the protoconid. A stronger cingular ridge runs along the anterior face of the tooth to join the anterior crest from the metaconid at approximately the position that the weak labial cingulum joins the crest. It is possible that this junction represents a vestige of the paraconid. The hypoconid is the largest of the cusps. The protoconid and entoconid are about equal and slightly larger than the metaconid. The talonid has an elongate open valley.

The $M_{\overline{2}}$ and $M_{\overline{3}}$ have essentially the same form. They are rectangular teeth in occlusal view though slightly constricted across the middle (Pl. 31, figs. D & E). In both these teeth, the hypoconid is the largest cusp, the protoconid and entoconid are subequal, and the metaconid is the smallest. Each of the cusps tends to be concave on the side toward the center of the tooth, so that an extensive elongate valley runs the length of the tooth. It is broader and more developed in the talonid than in the trigonid, yet both areas form a connected, open basin. The labial cusps carry anterior and posterior crests as they did in $M_{\overline{1}}$. The $M_{\overline{2}}$ is slightly wider posteriorly while the $M_{\overline{3}}$ is wider anteriorly (Pl. 31, fig. F). There are no $M_{\overline{4}}$s in our sample though there are alveoli for this tooth in all the mandibles.

The morphology of the fossils of *C. lepidus* compares favorably with that observed in the small series of Recent individuals from the Queen Victoria Museum. Stereo-photos of the upper and lower teeth of a Recent specimen from that series (QVM 1964 : 1 : 249) are offered for comparison in Plate 29, figures A–B.

Statistical data for both species of Broom Cave *Cercartetus* are given in Tables 1 and 2.

RESULTS AND DISCUSSION

Relative abundance

The pygmy possums *Cercartetus nanus* and *Cercartetus lepidus*, were both noted by Ride (1960). His relative abundances were based on a very limited sample. He found *C. nanus* specimens to be five times more abundant than *C. lepidus*, and in number of individuals the ratio was 3 : 1. We find the ratios in our much larger sample to be 10 : 1 when comparing total numbers of teeth, 6 : 1 with minimum number of individuals, and 7 : 1 with the more realistic mode of assessing population (see Table 3 and Appendix B). Based on our experience, it appears that Ride was extremely lucky in getting enough *C. lepidus* to get the small ratios he got. *Cercartetus nanus* is the most common of all marsupials in the fauna while *Cercartetus lepidus* is relatively rare. The apparent scarcity of *C. lepidus* may be due in part to the small and fragile nature of the material. Practically no teeth were found in jaws or maxillaries, having fallen out either during the diagenesis of the deposit or (undoubtedly) during our acid preparation of the breccia.

Examination of the graphs of the age group assignments of the Broom Cave pygmy possums shows an array of distorted bell-shaped curves (Fig. 2, left and middle). These curves are reminiscent of those representing the population distribution of the murids of this fauna. The rat distribution conformed fairly closely to a normal curve, there being a marked shortage of individuals at the young half of the array. In the murid case it was suggested that if, as presumed, the owls
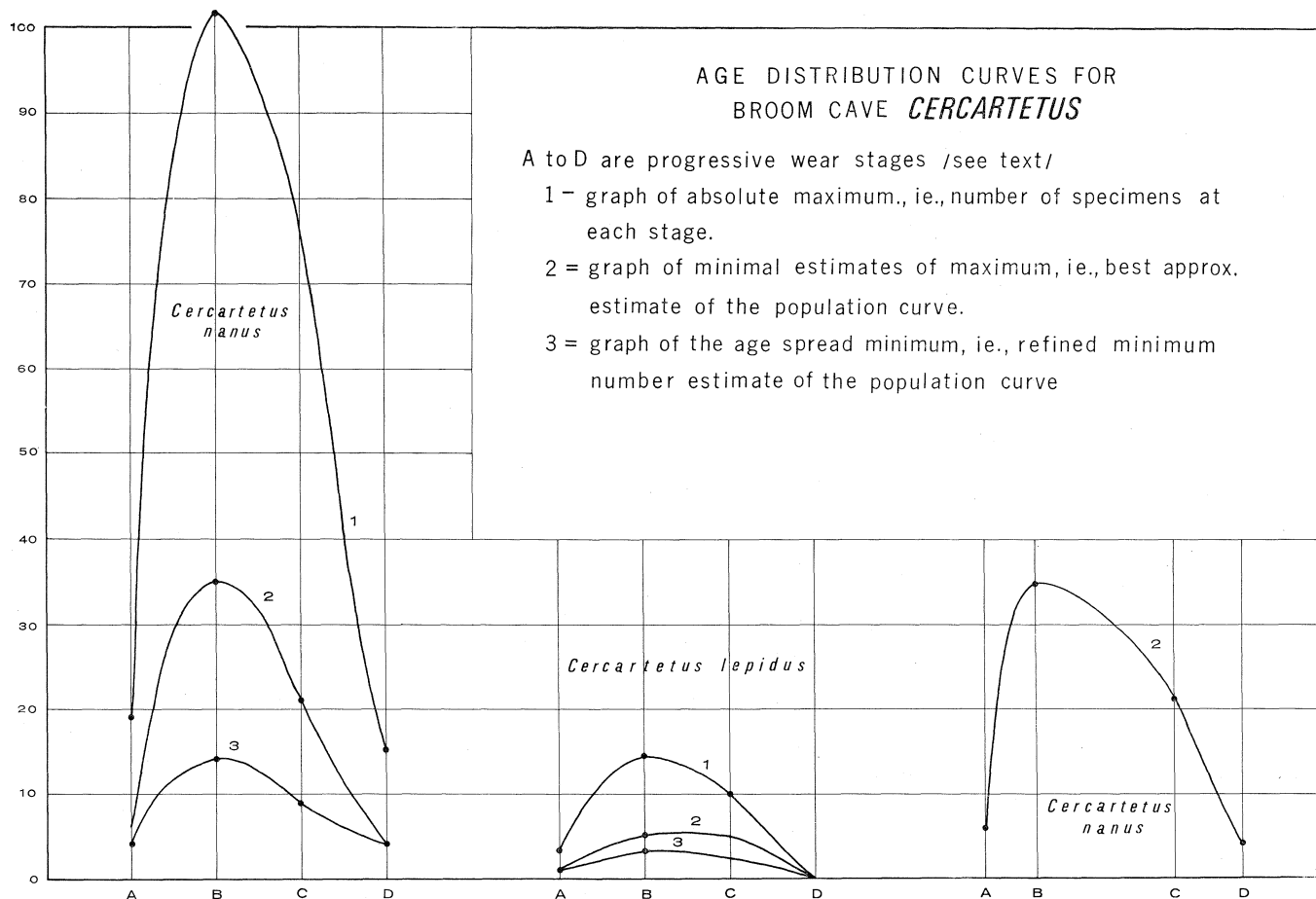

AGE DISTRIBUTION CURVES FOR
BROOM CAVE *CERCARTETUS*

A to D are progressive wear stages /see text/
1 − graph of absolute maximum., ie., number of specimens at each stage.
2 = graph of minimal estimates of maximum, ie., best approx. estimate of the population curve.
3 = graph of the age spread minimum, ie., refined minimum number estimate of the population curve

Cercartetus nanus

Cercartetus lepidus

Cercartetus nanus

Figure 2. Curves of the age distribution of the Broom Cave *Cercartetus* species. The two sets shown left and center are plotted against four equally spaced lines that represent progressive wear stages A through D. The right curve for *C. nanus* (No. 2) is plotted against the same wear stages. But here the spacing between the stages is varied so as to be more in accord with the time needed to achieve the degree of wear appropriate to each wear stage.

were essentially indiscriminate in their predation, one would expect a distribution more like a survivorship curve than a bell curve. The pygmy possum curves, are however, different from the murid curves. The pygmy possum distribution is definitely skewed toward the younger forms. Indeed the major portion of the curve is basically one of survivorship. Only the very youngest stage as defined by us is low. In the murids, the numerical deficiency of young rodents was explained by assuming many of the young rats were protected from predation in the nest. But since marsupial mothers carry their young with them, the apparent low number of young is initially puzzling. Clearly the explanation applied to the murids cannot be extended to the pygmy possums. Where then have all the young pygmy possums gone?

A possible solution to this problem may lie in the life style and breeding habits of the pygmy possums. These animals live in bush and forest situations. In such confined environments they would tend to be protected from owl predation. Troughton (1957) says that pygmy possums *C. concinnus* (and presumably the other species of pygmy possums) breed twice a year, summer and winter. Those young born in winter would be protected for the rest of that season and upon emerging from hibernation with their mother would be at an advanced age. Those born in the summer and not having fallen prey would then hibernate and emerge at a more advanced age. In addition, the males might tend to be more far ranging in foraging habits, females possibly staying close to the nest. The males would be more likely then to be captured. The curves would then represent a sample subject to seasonal influxes of pygmy possums into the environment and perhaps with more males than females.

The discrepancy in the numbers of young individuals may in part also be an artifact due to our age assignments based on tooth wear. It is sometimes difficult to decide on an age for a specific tooth. Ages A and B are probably not too far separated in time in the animals life cycle. There are all sorts of gradations between ages B and C. Consequently, instead of drawing a curve based on four equally spaced points, the first two points (ages A and B) should be perhaps rather closely aligned, the second and third points (ages B and C) should be quite far apart since they represent a substantial portion of the life cycle, and the fourth point (age D) should follow soon on the third (Fig. 2, right).

Dental patterns and taxonomy

Iredale and Troughton (1934) and Troughton (1957) recognized two genera of pygmy possums: *Cercartetus*, with two species, *C. nanus* and *C. concinnus;* and *Eudromicia*, with three species, *E. caudata*, *E. lepida* and *E. macrura*. Wakefield (1963) reviewed the taxonomy of these animals and placed all species in *Cercartetus* and made *macrura* a subspecies of *caudata* (which on the basis of dental morphology and measurements appears to be correct). He claimed the differences among the species were insufficient to warrant their separation into separate genera. We have re-examined in detail all the species in question paying especial attention to dental characteristics. Our conclusions, at variance with Wakefield, illustrate a continuing palaeozoological problem; attempting to reconcile taxonomic conclusions based on gross external observations with detailed dental and/or skeletal studies.

We have undertaken an examination of the species in question utilizing any materials we could borrow and study, both fossil and Recent. The material (including items from the collections of the Field Museum and specimens borrowed from the Archbold Collection of the American Museum, The University of Texas, The Australian Museum, Sydney, and the Queen Victoria Museum in Launceton, Tasmania) was limited but we believe sufficient to give us a very clear idea as to the dental variation which occurs in the pygmy possums.

Figure 3. Figures 3–6 are each bivariate graphs resulting from plotting length (abscissa) and width (ordinate) measurements of upper cheek teeth for each of the species of *Cercartetus*. With the molars, anterior width was always used, while with premolars, where often the crown is not bilobate or rectangular, either maximum width or anterior width was used according to which measure was appropriate. In each case the resulting cluster of points is contained within a hand-drawn cloud, and the means for each tooth are connected in sequence by a line to provide the distinctive pattern of each species. Figure 3 is below. Figures 4, 5, and 6 are on the next three pages.
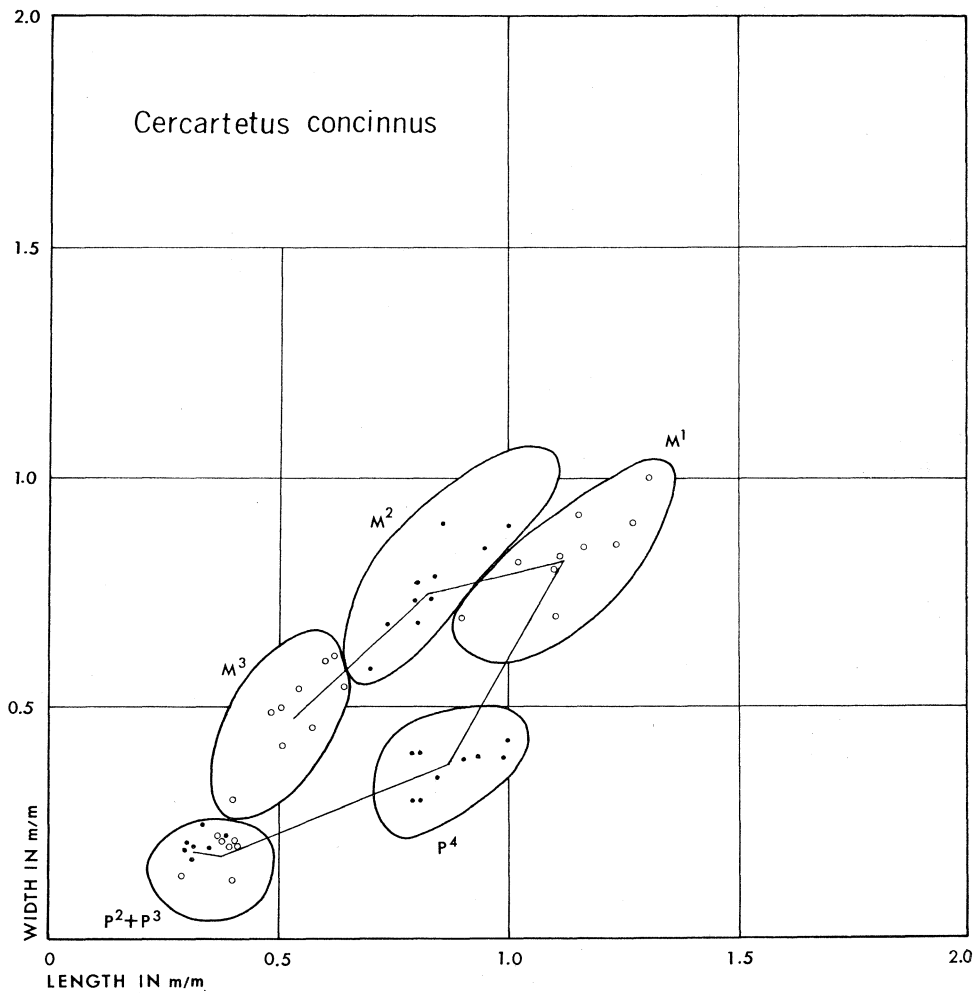
One of the lines of investigation we found most useful was comparative analysis of tooth size patterns resulting from bivariant plots of cheek teeth series. This involves plotting lengths and widths of teeth and observing changes in relative sizes from tooth to tooth along a series, within and between species.

Analysis of the four species (of Wakefield) reveals distinct differences among all of them as well as certain similarities (Figs. 3–6). We confine our discussion here to the upper tooth series for which the differences are most striking. *C. concinnus* has the anterior two premolars peglike and small. P^4 is small and elongate with a typical primitive premolar pattern of two roots and a crown with a single central cusp. M^1 is somewhat elongate and small; M^2 is smaller than M^1 and nearly square; M^3 is quite small and square; M^4 is absent.
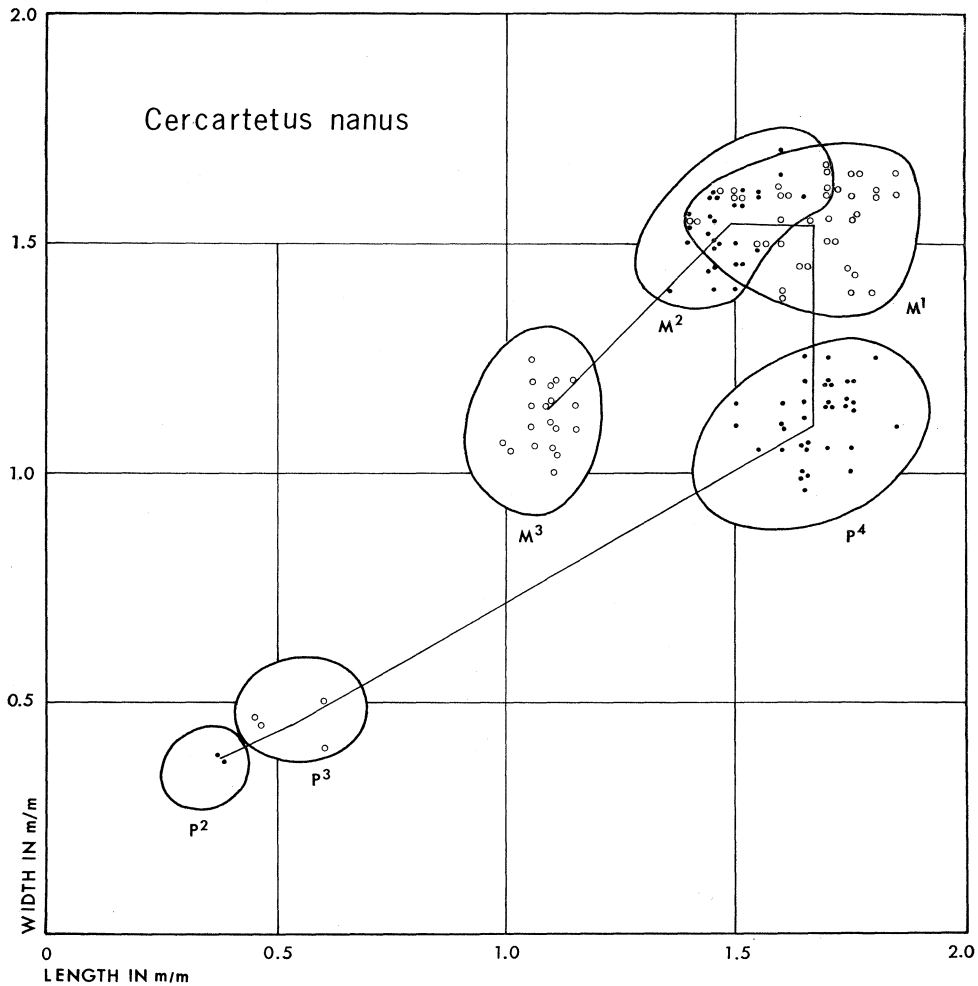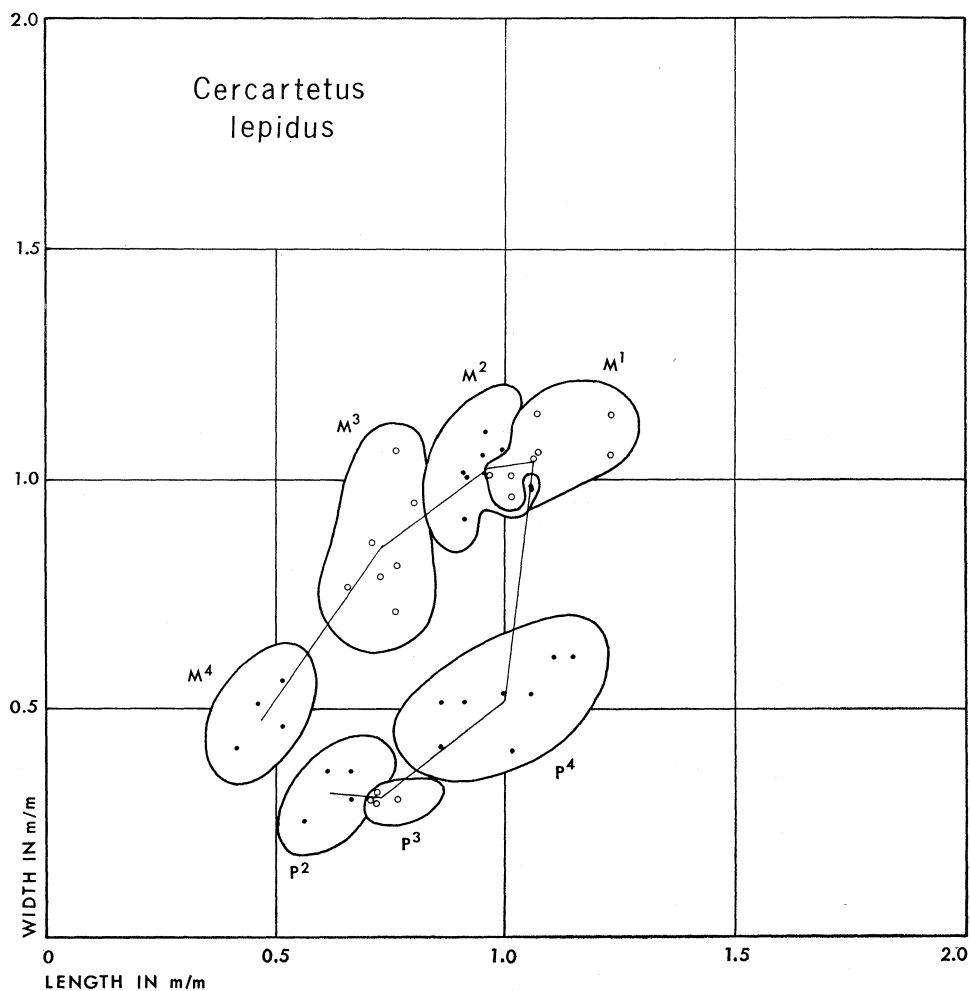

Figure 4

Figure 5

C. *nanus* has two very small peglike anterior premolars, and P^4 is quite large both in length and width (nearly the size of M^1) with two prominent distinct cusps. M^1 is a large square tooth, M^2 proportioned nearly as M^1, except somewhat shorter. M^3 is smaller than M^1 or M^2 and its length and width dimensions are nearly equal. M^4 is absent.

C. *lepidus* also has the anterior two premolars peglike and small. P^4 is small and elongate with a small set of twinned cusps. M^1 and M^2 are small, square and nearly the same size. M^3 is similarly proportioned but smaller yet and M^4 is very reduced (shorter than any of the premolars).
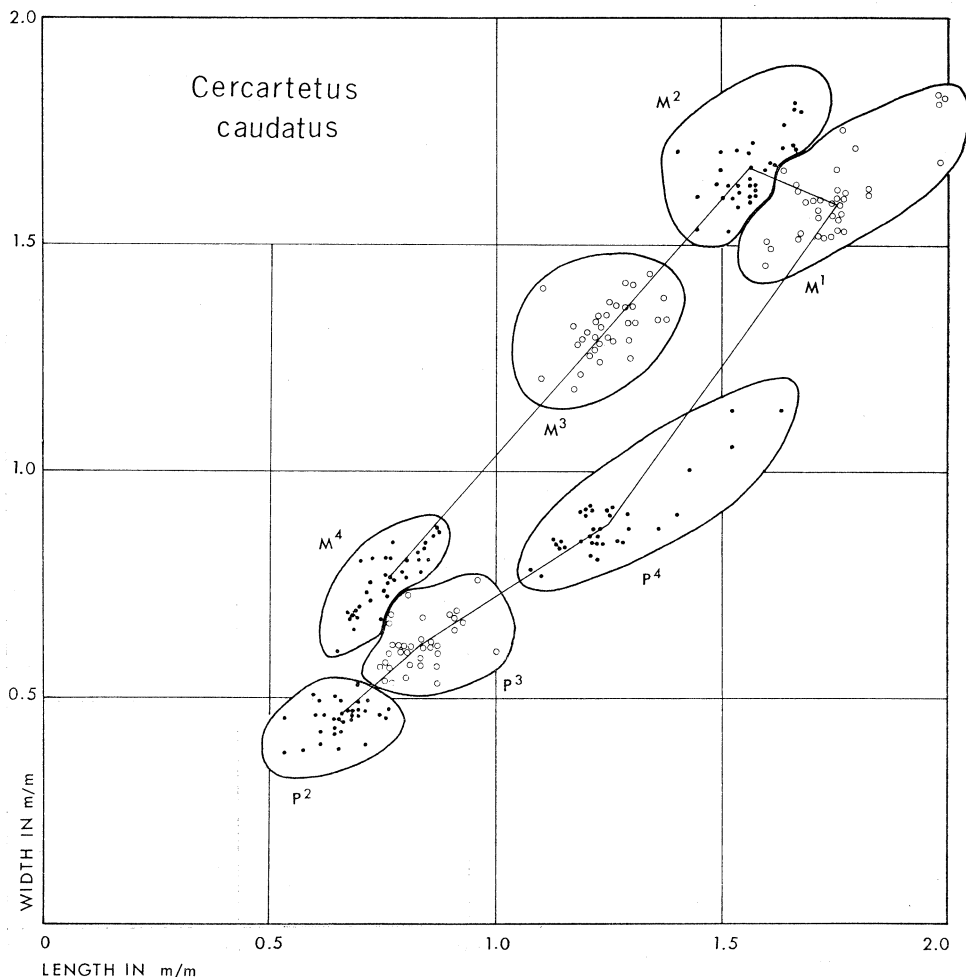
Figure 6

In *C. caudatus* the anterior two premolars are small, single-rooted but elongate. P^4 is elongate, but is much shorter and narrower than any of the first three molars and has a large single cusp that shows an incipient clefting of its tip. M^1 and M^2 are large with nearly equal length and width measurements, M^1 being slightly elongate. M^3 is proportioned quite like M^2 but is somewhat smaller and M^4 is very reduced.

Figure 7 summarizes the upper cheek tooth proportions for each of these species and presents a vignette of the characteristic P^{4}s. The latter shows the wide range of differences in the nature of that tooth from single cusped in *C. concinnus* and *C. caudatus* to definitely double-cusped in *C. lepidus* and *C. nanus*. Unworn specimens of *C. caudatus* show a tendency toward a clefting of the stout cusp, but all traces of this incipient division are readily erased by wear.
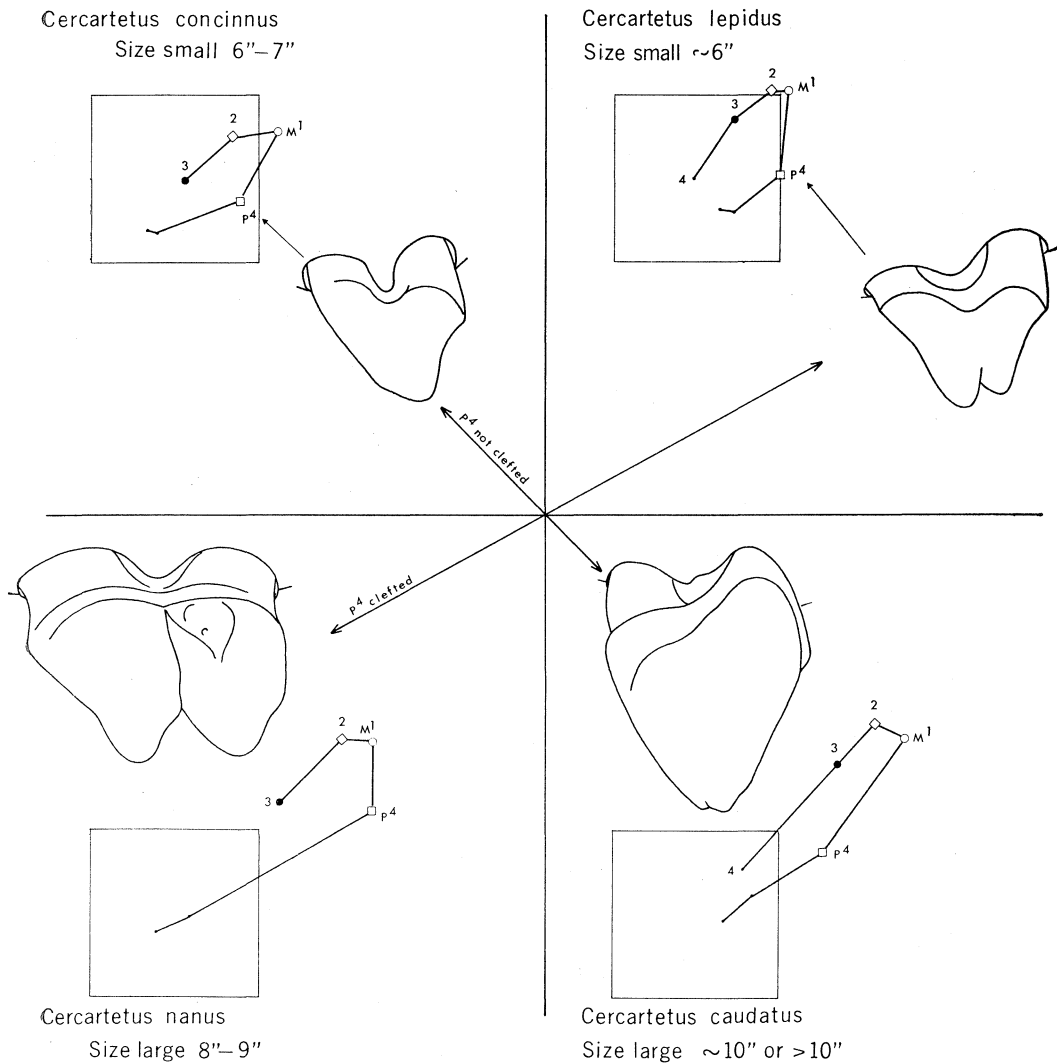
Figure 7. Comparisons of the patterns of the serially connected means of the bivariant tooth plots from Figs 3–6, along with a vignette of the $P^{\underline{4}}$ of each species. Note that body size does not correlate with either clefting of $P^{\underline{4}}$, or presence of $M^{\underline{4}}_{\overline{4}}$. Nor do these features correlate with one another, or with the Iredale & Troughton generic assignments to *Cercartetus* (left pair) and *Eudromicia* (right pair).

Note in figure 7 that size does not correlate with either premolar form or with presence or absence of the M^4, the chief dental feature correlated with the Iredale and Troughton genera, *Cercartetus* and *Eudromicia*.

It would appear to us that these four species, *C. nanus*, *C. lepidus*, *C. concinnus* and *C. caudatus* are all distinctly different based on dental characters. The actual taxonomic history of these animals has been quite peripatetic and confusing. Desmarest (1817) described the species *Phalangista nana* which stood until Gray (1841) erected a separate genus *Dromicia* for this species. This was the common generic name in use for some years until it was discovered that Gloger (1841) had priority over Gray by several months with his genus *Cercartetus*. In 1845, Gould described the species *D. concinna* and in 1877, Milne-Edwards recognized the species *D. caudata*. Thomas (1888) in re-examining material of so-called "young" *D. nana* erected the separate species *D. lepida* based on the distinctive premolar differences. Mjöberg (1916) erected a new genus *Eudromicia*, to accommodate his new species *E. macrura* from New Guinea and placed in this genus *E. lepida* and *E. caudata*. Matschie (1916) preferred to delineate these forms still more and on the basis of pelage, ear shape, tail shape, molar number and size placed *D. lepida* in a separate subgenus *Dromiciola*, and *D. concinna* in the new subgenus, *Dromiciella*. Iredale and Troughton (1934) pointed out the priority of Gloger's *Cercartetus* and recognized only two genera: *Cercartetus* with *C. nanus* and *C. concinnus*, and *Eudromicia* with *E. caudata*, *E. macrura*, and *E. lepidus*. Finally, Wakefield (1963) synonymized *E. macrura* with *E. caudata* and somewhat arbitrarily minimized the cranial, dental and biological characters employed by previous authors and recognized only one genus, *Cercartetus*.

CONCLUSIONS

We feel that, at least dentally, these animals are not closely similar at all, and consequently they probably should not be placed within the same genus. But we also recognize the fact that our conclusions are based almost exclusively on dental anatomy, and that such one system based taxonomies are risky, and in this case unnecessary. Furthermore there is still uncertainty as to the level of confidence that one can place on inferences drawn from the sort of bivariate dental plots that we have used. As yet too few such graphic attempts have been made to provide an adequate basis for sound comparative judgements, although these that have appeared to date do seem to characterize both genera and species remarkably well.

Turnbull and Lundelius (1970) when seeking a meaningful comparative way to express graphically sets of observed dental proportions developed this technique. They showed (in their graphs F through I) that in the macropodids sampled, the species patterns were much alike within a genus and that allied genera differed in varying degrees—much as the species of *Cercartetus* differ from one another. In their graph E, in which various species groups of pseudocheirines were compared, the size range varied considerably, but the kinds of patterns observed conformed to established subgeneric and generic groupings. Here taxonomic interpretation is somewhat ambiguous: it suggests perhaps, that the genus *Pseudocheirus* (sensu lato) should be split (as Thomas, Troughton and Marlow have indeed done). The situation in *Cercartetus* is quite comparable as far as the dental graphs go, and it shows discrete, gross differences as to the form of the P^4s, and the presence or absence of the M^4s. Additionally, ongoing work by Lundelius and Turnbull (in press and MS), in which dentitions of the small phascogales are similarly treated, shows the genera *Planigale*, *Antechinus*, *Sminthopsis*, *Antechinomys* to have patterns far more alike

than do those of the species of *Cercartetus*. In fact the graphic patterns for some of these genera are so alike that they do not always provide an easy means of distinguishing between them. Also the few such plots that one of us (WDT) has made for some of the other phalangerid genera appear to be of two sorts. At one extreme are *Acrobates*, *Distochoerus* and *Dactylopsila* where the differences are similar to those between the species of *Cercartetus*. At the other extreme *Petaurus* and *Gymnobelideus* are scarcely distinguishable. Therefore, on these comparative grounds, *Cercartetus* as presently constituted appears to encompass the sort of diversity of bivariant dental patterns within its four species that is usually found between several genera. Wakefield pointed out that variations in the tympanic bulla and squamosal inflation are also not consistent among the species. From what we have seen we would tend to agree, and this adds support to our contention that more than one genus is represented.

We feel that a more extensive and detailed examination of the biology of the four species of *Cercartetus* is in order and should precede any proposed taxonomic changes. Such a study would test the conclusions drawn from the dental evidence presented here. The dental differences are great enough to suggest strongly the recognition of four monotypic genera with the following species:

> *Cercartetus nanus* (Desmarest) 1818.
>
> *Eudromicia caudata* (Milne-Edwards) 1877.
>
> *Dromiciola lepida* (Thomas) 1888.
>
> *Dromiciella concinna* (Gould) 1845.

Pending the extensive restudy indicated above, we very reluctantly adhere to the arrangement of Wakefield. A partial synonymy of the genus *Cercartetus* and its included species following the Wakefield arrangement, listing the major systematic and nomenclatural changes for the pygmy possums, is given in Appendix C.

Other conclusions are that the Broom Cave specimens of *Cercartetus* differ in only minor ways from the Recent representatives of their species; the specific identities are thus confirmed. The rare *C. lepidus* of the fauna is now known from a small suite of materials. *C. nanus* turns out to be the most abundant marsupial in the fauna, approaching the murid taxa* in numbers of individuals within the sample.

SUMMARY

The largest sample to date of members of the genus *Cercartetus* from the Broom Cave fauna, Late Pleistocene, New South Wales, Australia, has been studied and discussed. Interspecific differences among *all* living species of *Cercartetus* are examined as well as morphologic variations within the Broom Cave material. Very strong evidence that the four living species of *Cercartetus* belong in separate monotypic genera is presented.

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* Referred to by us (Schram & Turnbull, 1970) following earlier authors as *Pseudomys oralis* and *Gyomys glaucus* but Wakefield (pers. comm.) believes the former also includes *P. higginsi* and that the latter is a mixed sample of mostly *P. fumeus* and some *P. novaehollandiae*.

ACKNOWLEDGMENTS

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APPENDIX A

Materials listing of Broom Cave CERCARTETUS

Cercartetus nanus

Fragments from a palate, with L. M^1, R. P^4 and broken R. M^1, PM7425, wear stage B.

L. Edentulous maxillary F52745.

L. Maxillae, wear stage—
    A: PM6162 with P^3–M^2, PM7431 with M^2.
    B: PM7426 with P^4, PM7446 with P^4, PM17197 with P^4–M^2, F52671 with P^4 and part of M^2, F52723 with P^4.
    C: F52670 with M^2.

L. P^4 wear stage—
    A: PM17224, F52717.
    B: PM7445, PM17219, PM17223, F52721.
    C: PM7444, PM17222, F52710, F52718, F52719.
    D: PM17221.

L. M^1 wear stage—
    A: PM7428, F52707.
    B: PM17209, PM17211, PM17212, PM17213, PM17214, F52700, F52702, F52703, F52705, F52706.
    C: PM17207, PM17208, F52695, F52697, F52699.
    D: F52696.

L. M^2, wear stage—
    B: PM7427, PM17204, PM17206, F52683, F52684, F52686, F52701.
    C: PM7580, PM7581, F52682.
    D: PM7429, PM7430.

L. M^3, wear stage—
    B: PM7433, F52677.
    C: PM7583, PM7629, PM17199, PM17201, F52673, F52675, F52676.

R. Premaxillary with I^1 and I^3, PM7424.

R. Edentulous maxillary, F52724.

R. Maxillae, wear stage—
    B: PM17195 with P^4–M^1, PM17196 with P^4–M^1, F52720 with P^4.
    C: PM7618 with P^3–M^3, F52669 with M^1 (broken) –M^2.
    D: F52668 with P^4, M^2 and M^3.

R. P^4, wear stage—
    B: PM7673, PM17217, PM17218, PM17220, F52713, F52714, F52715, F52716, F52722.
    C: PM7443, PM17215, PM17216, F52711, F52712.
    D: F52709.

R. M^1, wear stage—
    A: PM7442, F52693, F52694.
    B: PM7438, PM7441, PM17210, PM17225, F52687, F52688, F52690, F52691, F52692, F52704, F52708.
    C: PM7437, F52689.

R. M^2, wear stage—
    A: F52728.
    B: PM7439, PM7440, PM17202, PM17205, F52679, F52680, F52681, F52685.
    C: PM17203, F52678.

R. M^3, wear stage—
    B: PM7584, PM17200, F52674.
    C: PM17198, F52672.
    D: PM7672.

L. Edentulous mandible PM17226.

L. Mandibles, wear stage—

    A: PM6161 with $P_{\bar{3}}$–$M_{\bar{3}}$, F52620 with $P_{\bar{4}}$–$M_{\bar{1}}$.
    B: PM7405 with $P_{\bar{4}}$–$M_{\bar{3}}$, PM16981 with $I_{\bar{1}}$, $P_{\bar{3}}$–$P_{\bar{4}}$, F52617 with $M_{\bar{1}}$–$M_{\bar{3}}$, F52618 with $P_{\bar{4}}$–$M_{\bar{3}}$.
    C: PM7404 with $I_{\bar{1}}$, $P_{\bar{3}}$–$M_{\bar{1}}$, F52616 with $M_{\bar{1}}$–$M_{\bar{3}}$.
    D: PM16980 with $P_{\bar{4}}$–$M_{\bar{3}}$.

L. $P_{\bar{4}}$, wear stage—

    B: PM7420, PM7582, PM17191, F52663, F52667.
    C: F52666.

L. $M_{\bar{1}}$, wear stage—

    A: PM7423, F52661.
    B: PM7422, PM17188, F52659, F52660.
    C: PM7421, F52657, F52658.

L. $M_{\bar{2}}$, wear stage—

    B: PM7417, PM7418, PM17182, F52636, F52644, F52645, F52646, F52652.
    C: PM7416, PM7419, PM17000, PM17181, F52639, F52640, F52641, F52643.
    D: PM16998, PM16999, F52637.

L. $M_{\bar{3}}$, wear stage—

    B: PM7670, PM16989, PM16990, F52628, F52630.
    C: PM16987, PM16988, F52626, F52627.

R. Edentulous mandibles PM7390, PM7403, PM16979A, PM26371, F52725, F52727.

R. Mandibles, wear stage—

    A: F52615 with $P_{\bar{4}}$–$M_{\bar{3}}$, F52619 with $I_{\bar{1}}$ and $P_{\bar{4}}$.
    C: PM16978 with $P_{\bar{4}}$–$M_{\bar{3}}$.

R. $P_{\bar{4}}$, wear stage—

    A: PM17193.
    B: PM17192, F52664.
    C: PM17189.
    D: F52662.

R. $M_{\bar{1}}$, wear stage—

    B: PM7413, F52653, F52654.
    C: PM7411, PM7414, PM17183, PM17187, F52649, F52651.
    D: PM7412, F52647.

R. $M_{\bar{2}}$, wear stage—

    A: PM7410.
    B: PM16984, PM16996, PM16997.
    C: PM7409, PM16991, PM16994, F52631, F52632, F52633, F52634, F52635.
    D: PM7407.

R. $M_{\bar{3}}$, wear stage—

    A: F52629.
    B: PM7402, PM7406, PM16984, F52623, F52624.
    C: PM16982, PM16983, F52621, F52622.

Cercartetus lepidus

    R. $P^{\underline{4}}$

        PM7578, F52771, F52772, F52773.

    L. $P^{\underline{4}}$

        PM7620, PM17246.

L. $M^{\underline{1}}$, wear stage—
    A: PM7400.
    B: F52774.
    C: PM7401, F52775.

R. $M^{\underline{2}}$, wear stage—
    C: F52769.

L. $M^{\underline{2}}$, wear stage—
    B: F52776, F52777.
    C: PM17247, PM17248.

R. $M^{\underline{3}}$, wear stage—
    B: F52770.

L. $M^{\underline{3}}$, wear stage—
    C: PM17245.

    Edentulous R. maxillae
        PM17244, F52768.

L. $I_{\overline{1}}$
        F52767.

R. $P_{\overline{4}}$
        PM7394, F52782.

L. $P_{\overline{4}}$
        PM7619, F52783.

L. $M_{\overline{1}}$, wear stage—
    B: PM17249.
        F52784 (fragment).

L. $M_{\overline{2}}$, wear stage—
    A: PM7398.
    C: PM7399, PM17250.

L. $M_{\overline{3}}$, wear stage—
    C: PM7393.

L. Mandible with $P_{\overline{4}}$, PM6163.

L. Mandible with $I_{\overline{1}}$, F52780.

L. Edentulous mandibles
        PM7389, F52781.

R. Edentulous mandibles
        PM7391, PM7392, F52778, F52779.

C. lepidus?
        PM7395, PM7396, F52765, F52766.

APPENDIX B

Age group assignments of the teeth of the Broom Cave *Cercartetus nanus* and *C. lepidus*, using the wear stages A through D. These are as follows:

(A) Cusps very sharp and clear, little or no wear.
(B) Wear of enamel beginning, cusp slightly round, wear facets appearing.
(C) Wear of enamel well advanced, cusps clearly worn down.
(D) Tips of cusps almost gone, with dentine exposed and beginning to wear.

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.

Cercartetus nanus

	A Teeth	A Spec.	B Teeth	B Spec.	C Teeth	C Spec.	D Teeth	D Spec.	Totals Teeth	Totals Spec.
L. P⁴	3		9		5		1		18	
L. M¹	3	6	12		5	21	1	4	21	60
L. M²	2		9	29	4		2		17	
L. M³	0		2		7		0		9	114
				63						
R. P⁴	0		13		6		2		21	
R. M¹	3	4	14	35	4	13	0	3	21	55
R. M²	1		8		4		1		14	
R. M³	0		3		3		2		8	
L. P⁴	2		8		2		1		13	
L. M¹	4	4	7	26	5	18	1	4	17	52
L. M²	1		11		9		4		*25	
L. M³	1		6		5		1		13	94
				39						
R. P⁴	3		2		2		1		8	
R. M¹	1	5	3	13	7	20	2	4	13	42
R. M²	2		3		9		1		15	
R. M³	2		5		5		0		12	
Total number of teeth	28	..	115	..	82	..	20	..	245	..
Total number of specimens	..	19	..	102	..	72	..	15	..	208****
Most frequently represented tooth	4	..	14	..	9	..	4	..	**31	..
No. of specimens in largest suite	..	6	..	35	..	21	..	4	..	66***

* 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.

Cercartetus lepidus

	A Teeth	A Spec.	B Teeth	B Spec.	C Teeth	C Spec.	D Teeth	D Spec.	Totals Teeth	Totals Spec.
L. P^{4} ..	.. 0		2		0		0		2	
L. M^{1}	1		1		2		0		*4	
L. M^{2}	0	1	2	5	2	5	0	0	4	11
L. M^{3}	0		0		1		0		1	
L. M^{4}	0		0		0		0		0	
R. P^{4} ..	0		2		1		0		3	
R. M^{1}	0		0		0		0		0	
R. M^{2}	0	0	1	3	0	1	0	0	1	4
R. M^{3}	0		0		0		0		0	
R. M^{4}	0		0		0		0		0	
L. P^{4} ..	0		3		0		0		3	
L. M^{1}	0		1		1		0		2	
L. M^{2}	1	1	0	4	2	4	0	0	3	9
L. M^{3}	0		0		1		0		1	
L. M^{4}	0		0		0		0		0	
R. P^{4} ..	0		2		0		0		2	
R. M^{1}	0		0		0		0		0	
R. M^{2}	0	0	0	2	0	0	0	0	0	2
R. M^{3}	0		0		0		0		0	
R. M^{4}	0		0		0		0		0	
Total number of teeth	1	..	14	..	10	..	0	..	26	..
Total number of specimens ..	..	2	..	14	..	10	..	0	..	****26
Most frequently represented tooth	1	..	3	..	2	..	0	..	**6	..
No. of specimens in largest suite	..	1	..	5	..	5	..	0	..	***11

APPENDIX C

Partial synonymy of the genus *Cercartetus* and its species with the major systematic and nomenclatural sources.

Cercartetus Gloger 1841

1841. *Cercartetus* Gloger, Handb. u. Hilfsb. Nat., p. 85.

1841. *Dromicia* Gray, in Grey, Journ. of Two Expeditions of Discovery in Northwest and Western Australia during the years 1837, '38, and '39. T. and W. Boone. London.

1916. *Eudromicia* Mjöberg, Kungl. Sveska Vetenskapsakademiens Handlingar. **52:** 2, pp. 13–20. January.

1934. *Cercartetus* and *Eudromicia* Iredale and Troughton. Records of the Australian Museum **6:** 1, pp. 22–23.

1963. *Cercartetus* Wakefield. Victorian Naturalist **80:** August, pp. 99–116.

C. nanus (Desmarest) 1818

1818. *Phalangista nana* Desmarest. Nouveau Dictionairie d'Histoire Naturelle, Pas-Pho. Tome XXV, p. 477.

1841. *Cercartetus nanus* Gloger.

1841. *Dromicia nana* Gray (in Grey).

1916. *D. nana*, Mjöberg.

1916. *D. nana*, Matchie.

1934. *Cercartetus nanus*, Iredale and Troughton.

1963. *C. nanus*, Wakefield.

C. caudatus (Milne-Edwards) 1877

1877. *Dromicia caudata* Milne-Edwards. Paris Academie des Science Comptes Rendus. Tome **85:** pp. 1079–1080.

1916. *Eudromicia caudata*, Mjöberg.

1916. *E. macrura* Mjöberg.

1916. *E. caudata*, Matchie.

1916. *E. macrura*, Matchie.

1934. *E. macrura*, Iredale and Troughton.

1963. *Cercartetus caudatus caudatus*, Wakefield.

1963. *C. c. macrurus*, Wakefield.

C. lepidus (Thomas) 1888

1888. *Dromicia lepida*. Catalog of the Marsupials and Monotremes. Brit. Mus. London. pp. 142–143.

1916. *Eudromicia lepida*, Mjöberg.

1916. *E. (Dromiciola) lepida*, Matchie.

1934. *Eudromicia lepida*, Iredale, Troughton.

1963. *Cercartetus lepidus*, Wakefield.

C. concinnus (Gould) 1845

1845. *Dromicia concinnia* Gould. Proc. Zool. Soc. (London) 1845, p. 2.

1916. *D. concinna*, Mjöberg.

1916. *D. (Dromiciella) concinna*, Matchie.

1934. *Cercartetus concinnus*, Iredale and Troughton.

1963. *C. concinnus*, Wakefield.

TABLE 1. Statistical data for tooth measurements of *Cercartetus nanus* from Broom Cave

		N	$\overline{\mathrm{X}}$	S	V	Observed range
L.	P$\frac{4}{}$	34	1.67 ± .01	.08	4.78	1.50–1.85
W.	P$\frac{4}{}$	35	1.14 ± .02	.12	10.24	.96–1.25
L.	M$\frac{1}{}$	42	1.68 ± .02	.10	6.13	1.40–1.85
W.	M$\frac{1}{}$	39	1.56 ± .01	.08	4.89	1.40–1.65
L.	M$\frac{2}{}$	28	1.49 ± .01	.07	4.72	1.34–1.65
W.	M$\frac{2}{}$	27	1.54 ± .02	.08	5.15	1.40–1.70
L.	M$\frac{3}{}$	17	1.09 ± .01	.04	3.71	1.00–1.15
W.	M$\frac{3}{}$	17	1.13 ± .02	.07	6.08	1.00–1.25
L.	P$\frac{}{4}$	20	1.32 ± .04	.16	12.21	1.15–1.85
W.	P$\frac{}{4}$	20	.89 ± .02	.11	12.50	.75–1.10
L.	M$\frac{}{1}$	29	1.57 ± .01	.08	5.01	1.40–1.70
W.	M$\frac{}{1}$	28	1.14 ± .02	.09	8.10	.95–1.35
L.	M$\frac{}{2}$	38	1.61 ± .01	.07	4.34	1.40–1.75
W.	M$\frac{}{2}$	38	1.21 ± .01	.08	7.03	1.00–1.40
L.	M$\frac{}{3}$	21	1.31 ± .02	.09	6.48	1.20–1.55
W.	M$\frac{}{3}$	23	1.02 ± .01	.06	6.23	.90–1.15

TABLE 2. Statistical data for tooth measurements of *Cercartetus lepidus* from Broom Cave

|		N	$\overline{X}$	S	V	Observed range
L.	P^{4}	4	$1.07 \pm .03$	.06	5.96	.99–1.14
W.	P^{4}	5	$.55 \pm .02$	.05	9.69	.49– .61
L.	M^{1}	4	$1.14 \pm .05$	.09	8.10	1.06–1.22
W.	M^{1}	4	$1.10 \pm .02$	.05	4.49	1.05–1.14
L.	M^{2}	5	$1.00 \pm .02$	.05	5.03	.95–1.05
W.	M^{2}	5	$1.04 \pm .02$	.05	4.59	.99–1.10
L.	M^{3}	2	$.78 \pm .02$	.03	3.63	.76– .80
W.	M^{3}	2	$1.00 \pm .05$	.08	7.74	.95–1.06
L.	M^{4}	..	....	..	..	....
W.	M^{4}	..	....	..	..	....
L.	P_{4}	5	$.88 \pm .03$	.06	7.05	.84– .99
W.	P_{4}	5	$.47 \pm .02$	.04	8.66	.42– .53
L.	M_{1}	2	$1.21 \pm .15$	.22	18.04	1.06–1.37
W.	M_{1}	1	.87	..	..	.87
L.	M_{2}	3	$1.00 \pm .03$	.05	5.05	.95–1.05
W.	M_{2}	3	$.71 \pm .05$	.08	11.18	.65– .80
L.	M_{3}	1	.95	..	..	.95
W.	M_{3}	1	.61	..	..	.61
L.	M_{4}	..	....	..	..	....
W.	M_{4}	..	....	..	..	....

TABLE 3. Relative abundance of the pygmy possums of the Broom Cave Fauna. (For explanation of parameters used, see Schram and Turnbull 1970)
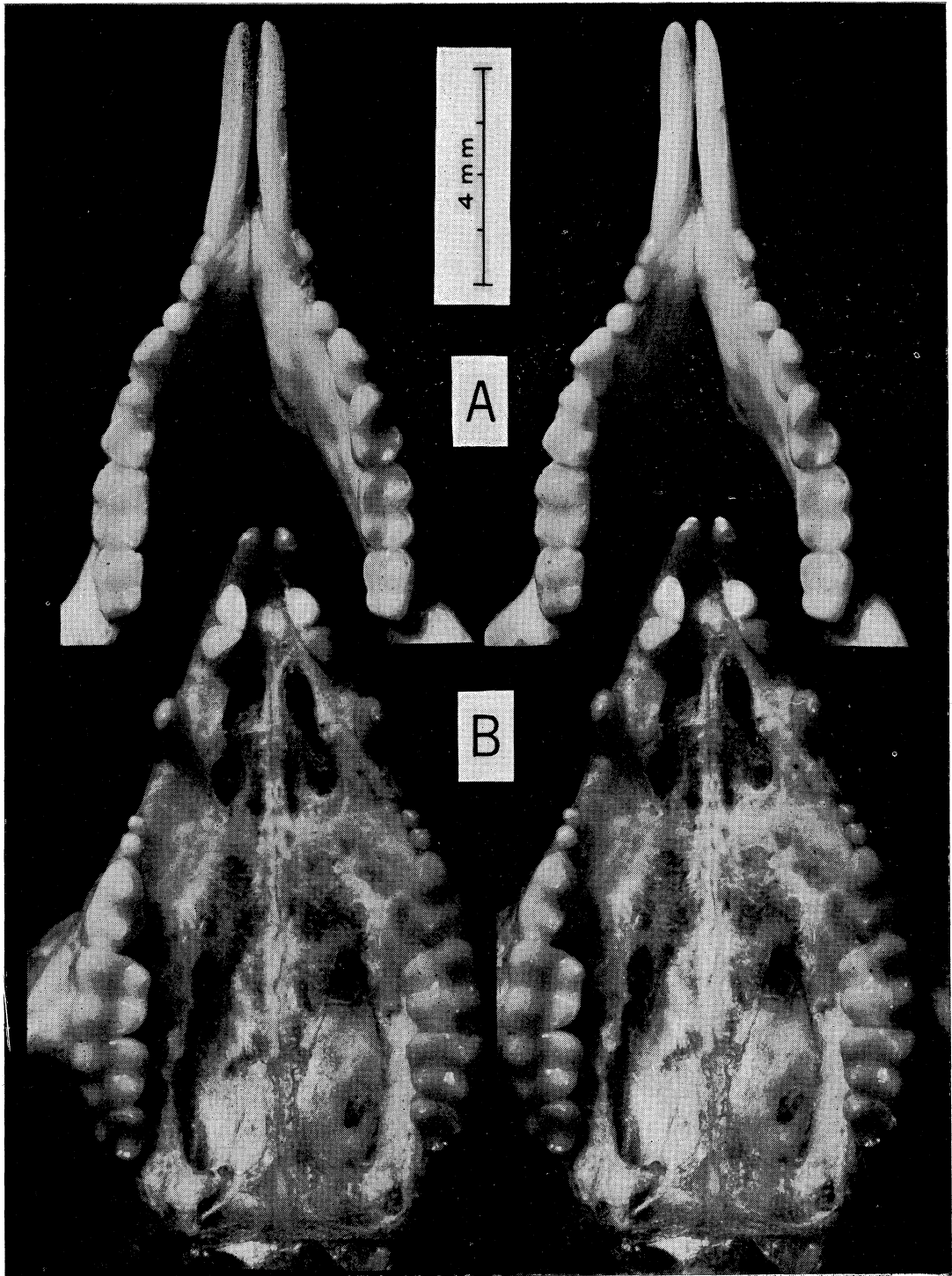
		Various estimates of numbers of individuals			
		Minimum number		Maximum number	
	No. of teeth	Traditional	Age-spread	Minimum est. of maximum	Absolute maximum
Cercartetus nanus ..	245	25	31	66	208
Cercartetus lepidus ..	26	4	6	11	26

PLATE 25

4 mm
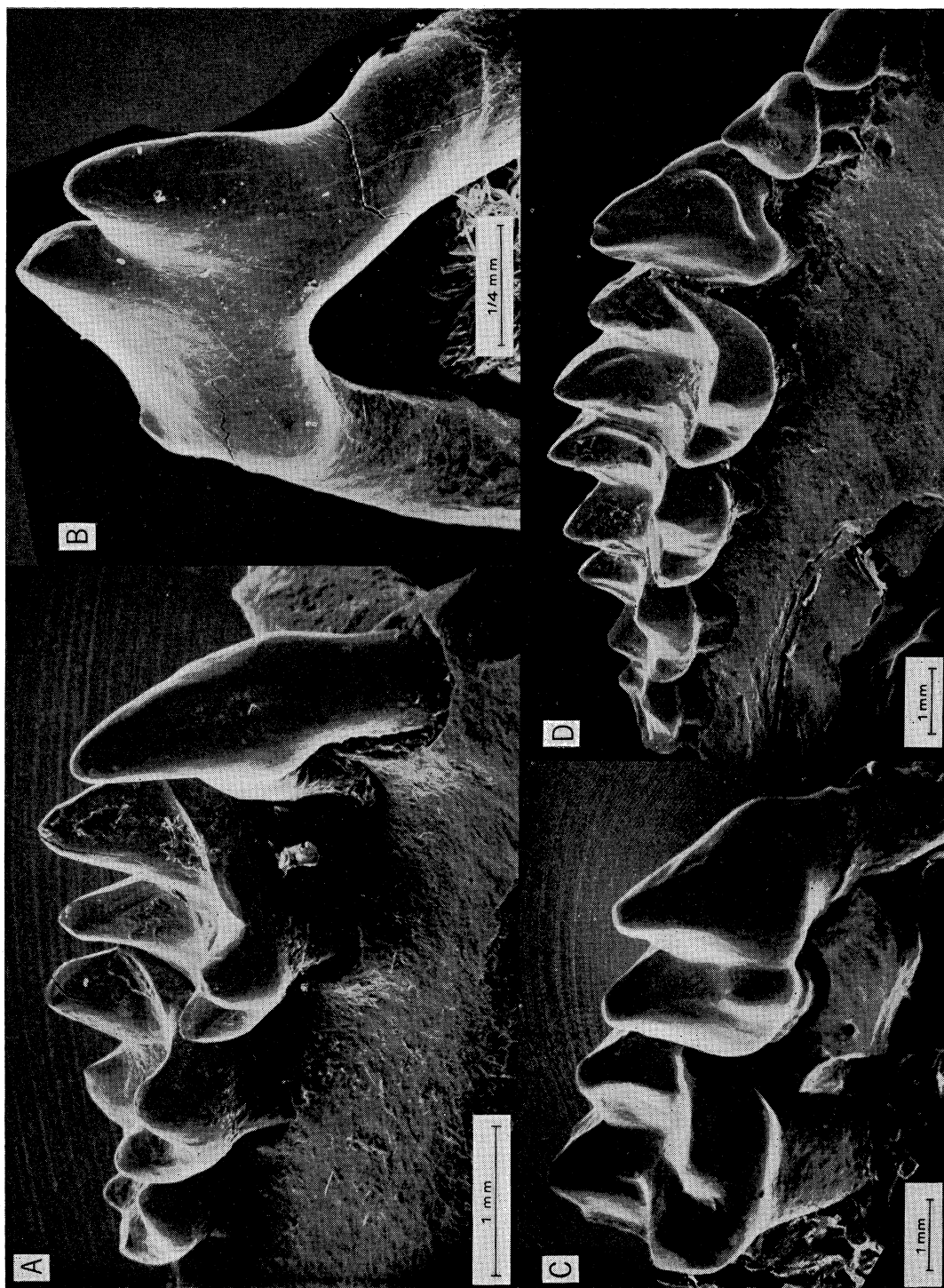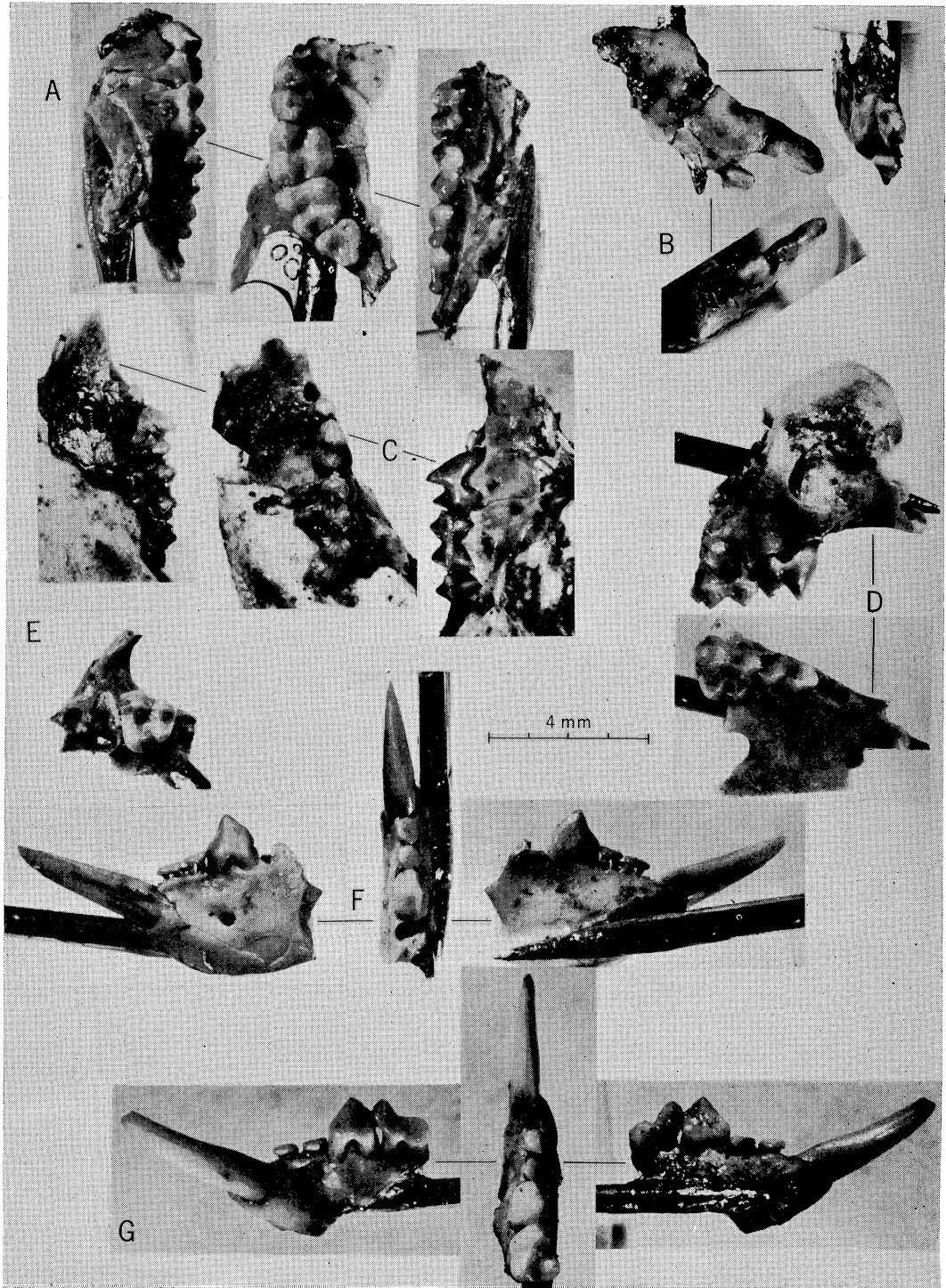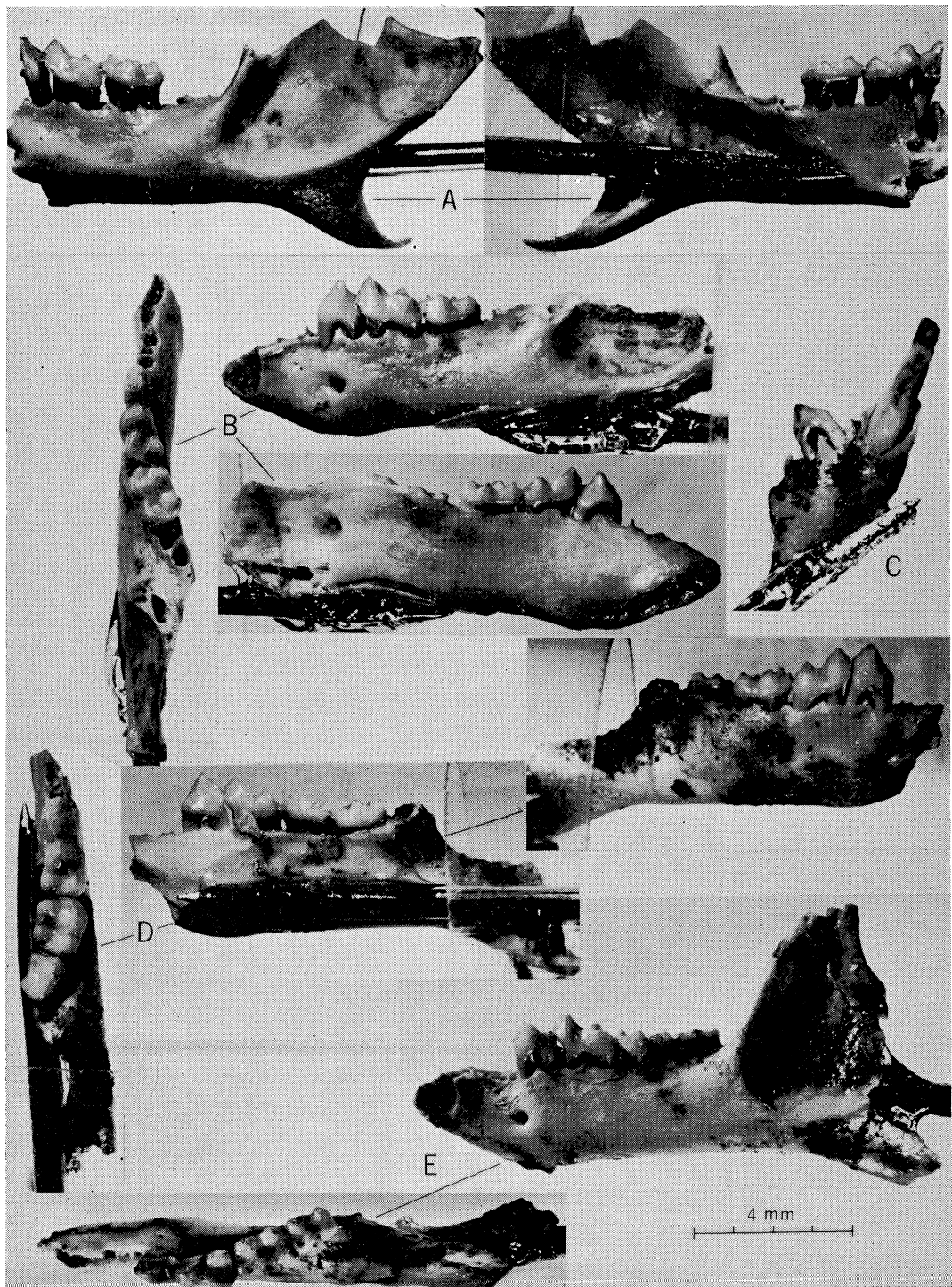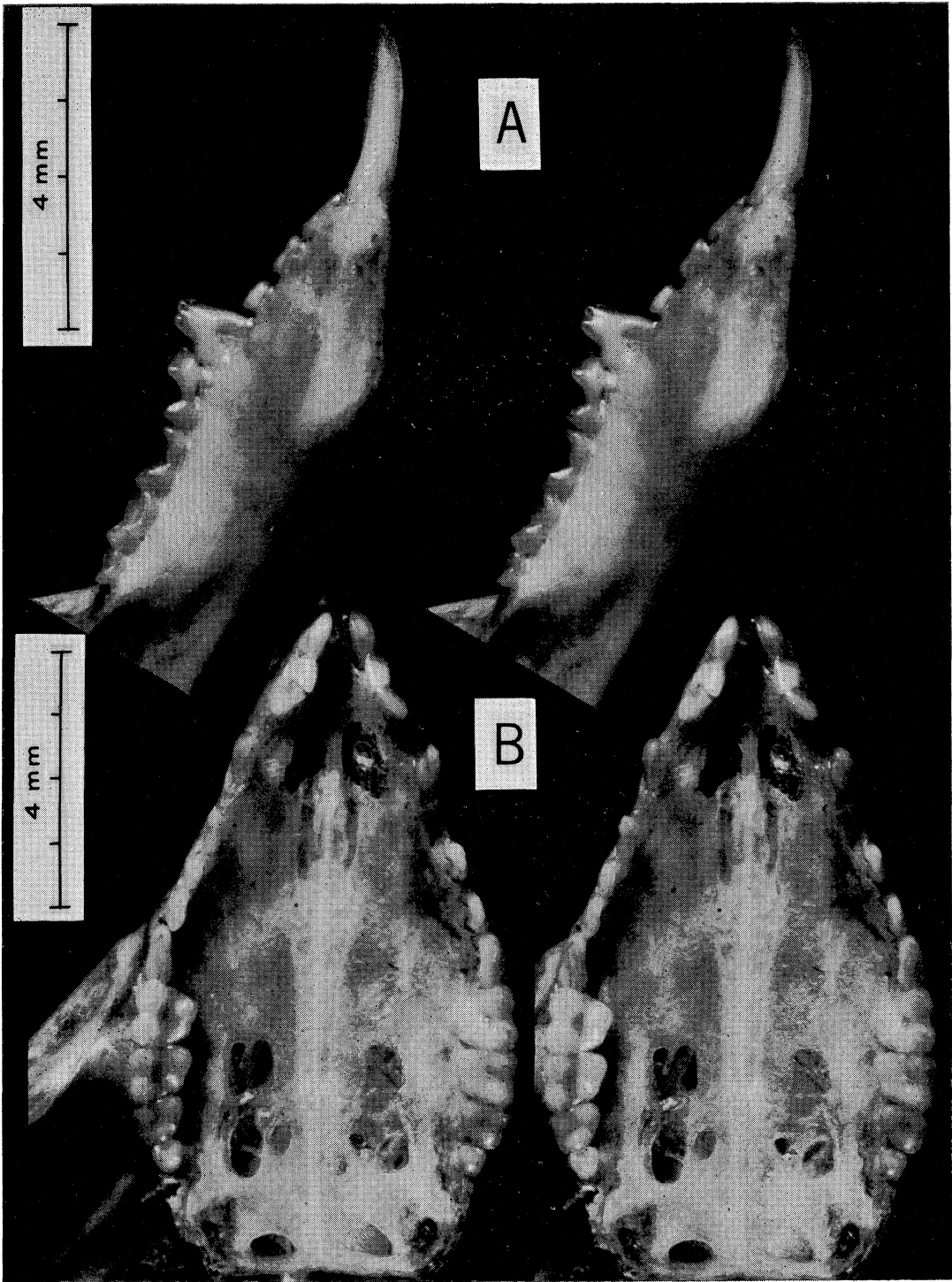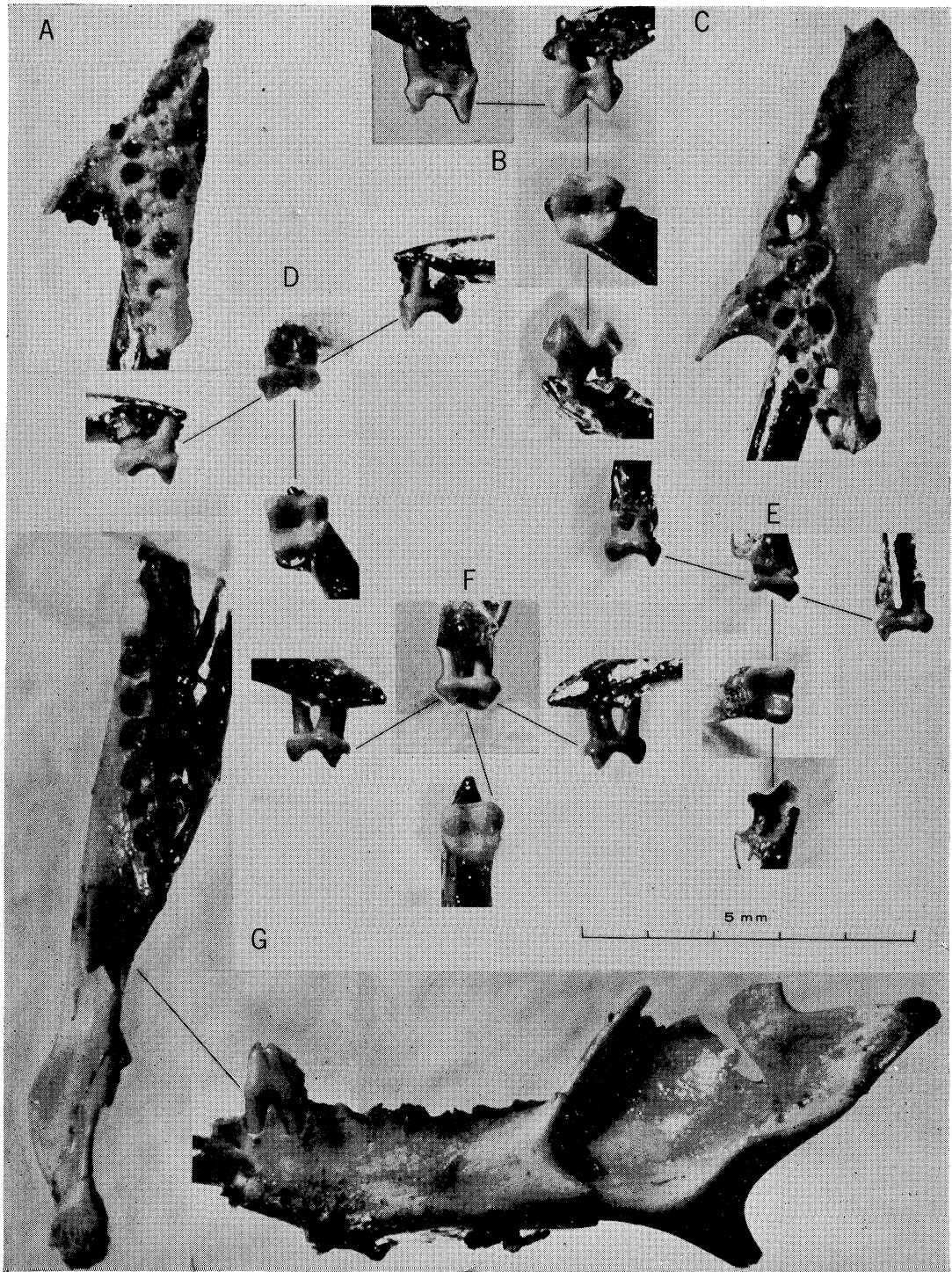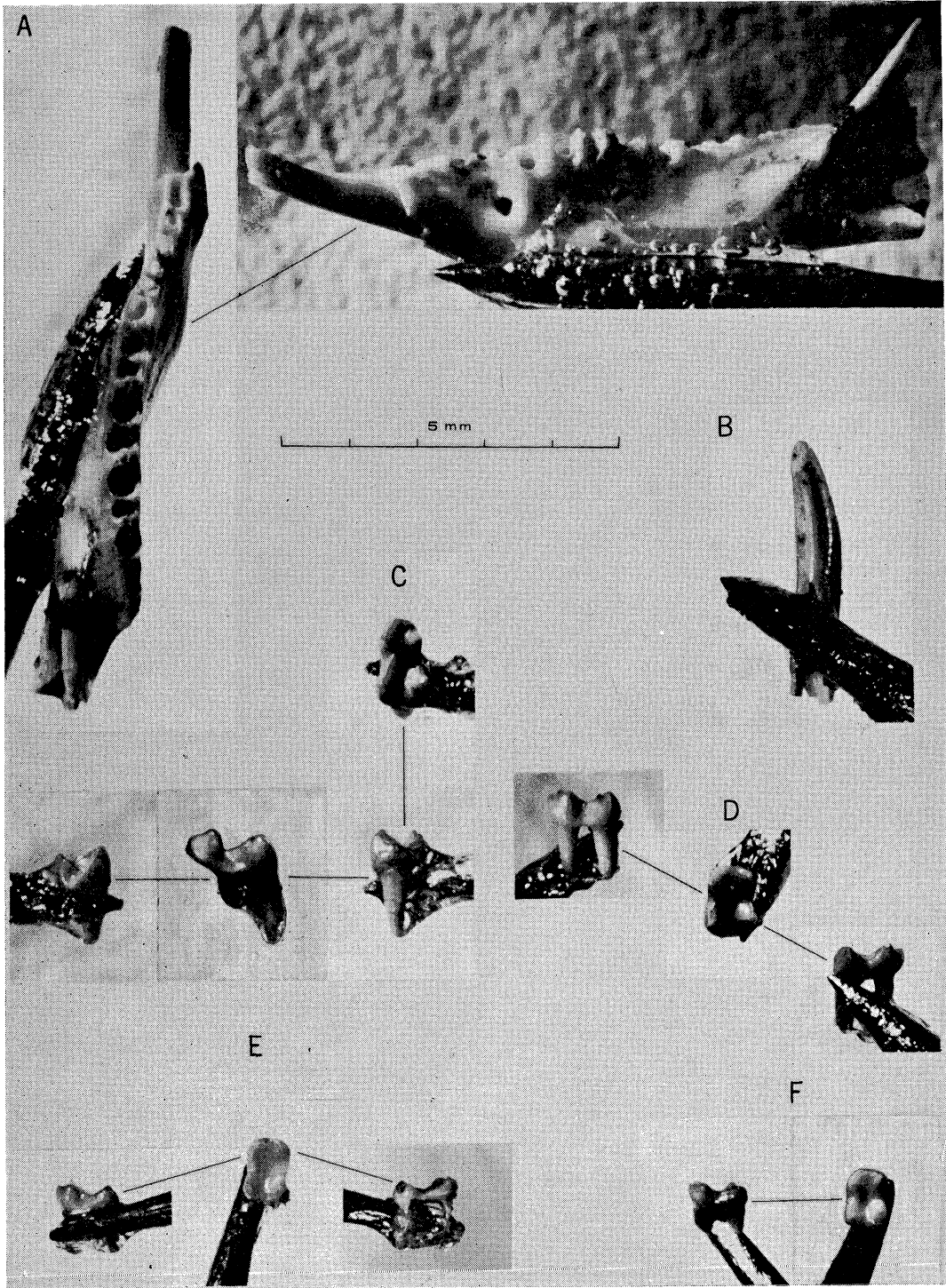
PLATE 28

EXPLANATION OF PLATES

Plate 25

(Scales indicate length of 1 mm in A, C, and D; ¼ mm in B)

Scanning electron microscope photographs showing a part of the upper dentition of each of the four species of *Cercartetus*. In each case the specimen is shown inverted from its normal orientation, and is viewed somewhat antero-medially. The great depth of field and high resolution capabilities of SEM make it an ideal tool for photography of dentitions of small mammals even at these low magnifications.

- A. *Cercartetus concinnus*, PM19462, sub-Recent fossil, from Murraelellevan Cave, W.A., a right maxillary with P^4–M^3.
- B. *C. lepidus*, PM17246, Late Pleistocene, from Broom Cave, Wombeyan Caves area, N.S.W., an isolated right P^4.
- C. *C. nanus*, PM17195, Late Pleistocene, Broom Cave, fragment of a right maxillary with P^4–M^1.
- D. *C. caudatus*, AMNH109807, Recent, 2200m., 18 km North of Lake Habbema, Bele R., Netherlands New Guinea, a right maxillary with the complete cheek tooth series.

Plate 26

(Scale indicates length of 4 mm)

Photographs of a series of specimens (all partial dentitions) selected as representative of the Broom Cave remains of *Cercartetus nanus*. These specimens and those shown in Pls. 27, 30, and 31 were removed from the entombing travertine by dissolution of the matrix with 10 per cent acetic acid.

- A. PM7618, a right maxillary with P^3–M^3 shown in labial, crown and lingual views.
- B. PM7424, a right premaxillary with I^1 and I^3 shown in lateral, occlusal and anterior views.
- C. PM6162, a left maxillary with P^3–M^1 and part of M^2 shown in lingual, crown and labial views.
- D. PM17196, fragment of a right maxillary with P^4–M^1 shown in labial and crown views.
- E. F52670, fragment of a left maxillary with M^2 in crown view.
- F. PM16981, partial left mandible with I_1 and all three premolars shown in labial, crown and lingual views.
- G. PM7404, partial left mandible with I_1, all premolars and M_1 shown in labial, crown and lingual views.

Plate 27

(Scale indicates length of 4 mm)

Continuation of the series of photographs of the Broom Cave *Cercartetus nanus* specimens.

- A. F52618, a left mandible with part of P_4, with M_1–M_2 and preserving most of the masseteric fossa and the condyle, and all of the angular process. Shown in labial and lingual views.
- B. PM7405, a left mandible with P_4–M_2, and alveolae of all other teeth shown in crown, labial and lingual views.
- C. F52619, partial right mandible with I_1 (showing peculiar wear) and P_4 seen in lateral view (slightly antero-ventro-lateral).
- D. F52615, a right mandible with P_4–M_3 shown in crown, lingual and labial views.
- E. PM16980, a left mandible with P_4–M_3 shown in labial and crown views.

Plate 28

(Scale indicates length of 4 mm)

Stereoscopic photo-pairs of the dentition of a Recent specimen of *Cercartetus nanus*, Q.V.M. 1963 : 1 : 14. The mandibles are shown in dorsal view and the palate and upper dentition is shown in ventral (crown) view.

Plate 29

(Scales indicate length of 4 mm., note that upper and lower dentitions are shown at slightly different scales)

Stereoscopic photo-pairs of the dentition of a Recent specimen of *Cercartetus lepidus*, Q.V.M. 1964 : 1 : 249. The left mandible is shown in lingual view; the palate and upper dentition in ventral (crown) view.

Plate 30

(Scale indicates length of 5 mm)

Photographs of series of Broom Cave specimens of *Cercartetus lepidus*.

A. and C., PM17224 and F53768 respectively. Edentulous right maxillaries shown in palatal view. Each preserves alveolae of the full cheek tooth series.

B. PM7400, a left $M^{\underline{1}}$ shown in anterior, labial, crown and lingual views.

D. and F., F52700 and F52869 respectively. Right $M^{\underline{2}}$s shown in labial, anterior, crown and posterior views.

E. F52770, a right $M^{\underline{3}}$, shown in posterior, labial, anterior, crown and lingual views.

G. PM6163, a left ramus with $P_{\overline{4}}$ shown in dorsal (crown) and lateral (labial) views.

Plate 31

(Scale indicates length of 5 mm)

Continuation of the series of specimens of *Cercartetus lepidus* from Broom Cave.

A. F52780, a left ramus with $I_{\overline{1}}$ and alveolae of the rest of the teeth shown in dorsal and lateral views.

B. F52767, a left $I_{\overline{1}}$ and alveolae of the rest of the teeth shown in dorsal and lateral views

C. PM17249, a left $M_{\overline{1}}$ shown in anterior, labial, posterior and crown views.

D. and E., PM17250 and PM7398 respectively. Left $M_{\overline{2}}$s shown in labial, crown and lingual views.

F. PM7393, a left $M_{\overline{3}}$ shown in crown and labial views.