

AUSTRALIAN MUSEUM SCIENTIFIC PUBLICATIONS

Freedman, L., 1967. Skull and tooth variation in the genus *Perameles*. Part I: anatomical features. *Records of the Australian Museum* 27(6): 147–165, plates 16–23. [14 July 1967].

doi:10.3853/j.0067-1975.27.1967.441

ISSN 0067-1975

Published by the Australian Museum, Sydney

nature culture **discover**

Australian Museum science is freely accessible online at
www.australianmuseum.net.au/publications/
6 College Street, Sydney NSW 2010, Australia



SKULL AND TOOTH VARIATION IN THE GENUS *PERAMELES*

Part I: Anatomical Features

By L. FREEDMAN

Department of Anthropology, University of Wisconsin, Madison, Wisconsin, U.S.A.,
and formerly of the Department of Anatomy, University of Sydney, Australia

Plates 16-23. Figs 1-7.

Manuscript received, 30th March, 1965

This study of the anatomical and metrical features of the skull and teeth of bandicoots of the genus *Perameles* was undertaken in order to analyse age, sex, and locality variations and trends. It is hoped that the results of the study will assist in the assessment of intra- and inter-specific taxonomic, phylogenetic and ecological relationships, enable the various subgeneric taxa to be more clearly defined, and facilitate the identification of subfossil and fossil fragments and isolated teeth.

The present section of the study, Part I, outlines the taxonomy of the genus *Perameles* and describes generally the material used in the whole study. It also includes an illustrated, anatomical description of the skull and teeth of *Perameles nasuta* and a discussion of the anatomical variations of these features in other members of the genus *Perameles*.

TAXONOMY

With regard to the taxonomy of the long-nosed bandicoots, most of the early studies, such as that by Waterhouse (1846), included rather superficial accounts of a number of not very clearly defined species. However, in 1888 Thomas gave comprehensive descriptions and reliable keys to most of the species still currently recognised. In this study, Thomas recognised three genera (*Perameles*, *Peragale*, and *Chaeropus*) in the family Peramelidae. In the most recent studies, Simpson (1945) divides this family into five genera: *Perameles* (which includes *Peroryctes*), *Echymipera*, *Thylacomys* (syn. *Macrotis*, *Paragalia*), *Chaeropus*, and *Thylaxis* (= *Isoödon*); whilst Tate (1948) describes eight genera of bandicoots: *Perameles*, *Isoödon*, *Macrotis*, *Echymipera*, *Peroryctes*, *Chaeropus*, *Rhynchomeles*, and *Microperoryctes*. The genus *Perameles* in the present study is taken to include the long-nosed bandicoots of Australia only, i.e., the genus as defined by Tate.

At the specific level, Iredale and Troughton (1934) classified the long-nosed bandicoots as follows:

Genus: **Perameles** Geoffroy, 1803

Long-nosed bandicoot

Perameles nasuta nasuta Geoffroy, 1804. N.S.W., Victoria, South Queensland.

Perameles nasuta pallescens Thomas, 1923. North Queensland.

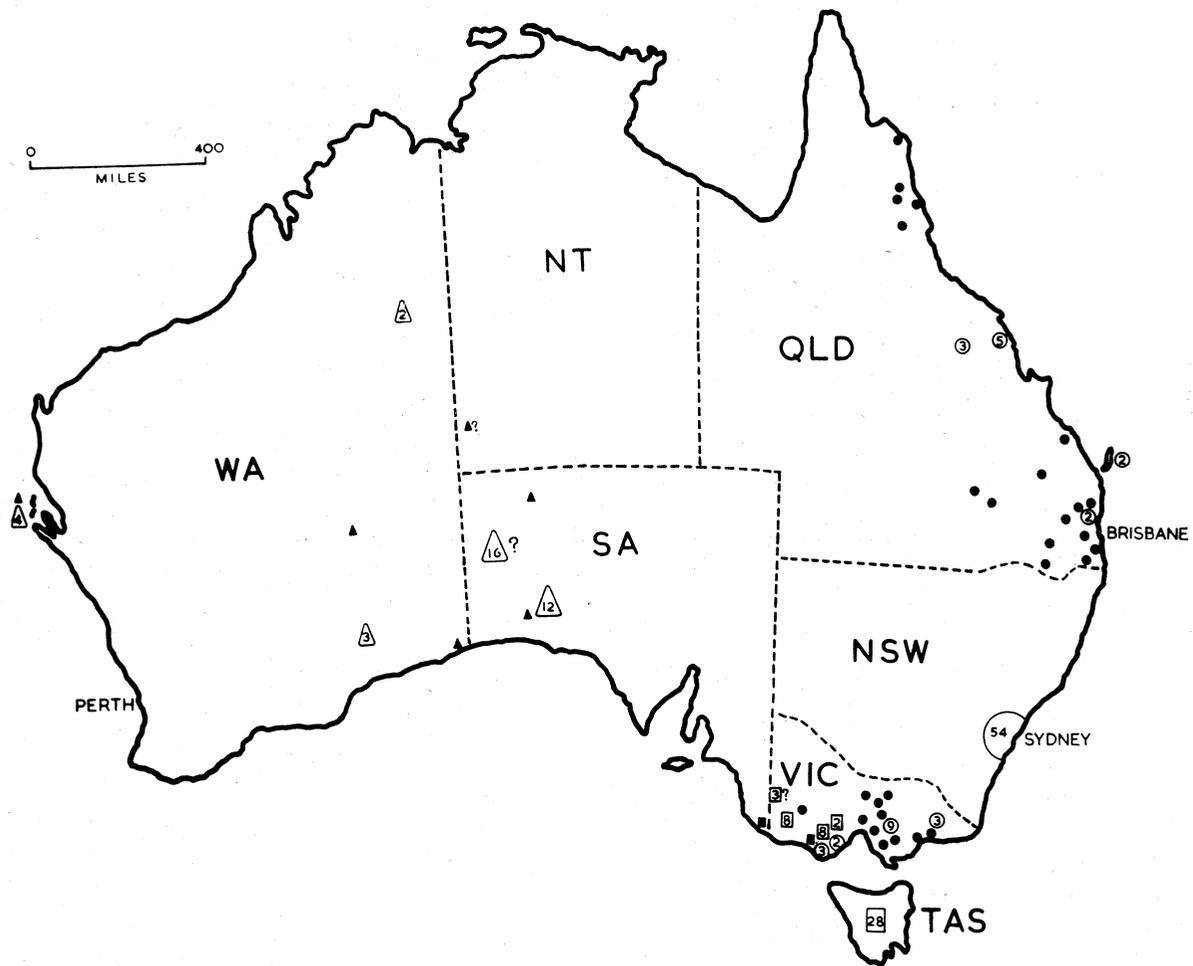


Fig. 1.—Map of Australia, including State boundaries, to show the distribution of *Perameles* material examined. Circles, *P. nasuta*; squares, *P. gunnii*; triangles, *P. bougainville* group; blacked-out, one specimen; numbered, number of specimens; ?, locality uncertain.

Orange-backed bandicoot

Perameles eremiana Spencer, 1897. Central Australia.

Eastern barred bandicoot

Perameles fasciata Gray, 1841. N.S.W., Victoria.

Tasmanian barred bandicoot

Perameles gunnii Gray, 1838. Tasmania.

Marl, or western barred bandicoot

Perameles myosura myosura Wagner, 1841. South-western Australia.

Perameles myosura notina Thomas, 1922. South Australia.

Little marl

Perameles bougainville Quoy and Gaimard, 1824. Mid western Australia and Islands of Shark Bay.

In a more recent taxonomic review of the genus *Perameles*, Tate (1948) made the following comments: He expressed doubts as to whether the differences between the northern and southern *P. nasuta* specimens should be maintained and he felt that *P. myosura* was "at best a race of *bougainvillei*". His final suggestions were that "the small bandicoots *P. bougainvillei*, *fasciata*, *notina*, and *eremiana* may be local races of a single widespread southern species, or, if this is not so, that they may be members of a single species-group, as opposed to the larger northeastern *Perameles nasuta*. To this species-group I would add the much larger *gunnii* as a full species".

Discussing *Perameles* in 1962, Marlow retained the two subspecies of *P. nasuta*, the full species *P. gunni*, *eremiana*, *fasciata*, and *bougainvillei*, but dropped *P. myosura myosura* and made *P. myosura notina* a subspecies of *P. bougainvillei* (*P. b. notina*). His distributions for the various species follow those of Iredale and Troughton (1934) fairly closely, although, in general, his distributions are rather more restricted. However, the range of *P. gunni* is extended to include the southern part of Victoria.

From the foregoing taxonomic resumé, it would appear that the species *P. nasuta* and *P. gunnii* are clearly valid, whilst there is some doubt about the status of the smaller species of *Perameles* which have been described under the names *fasciata*, *eremiana*, *myosura*, and *bougainville*. Consequently, for the purpose of the present study, it was decided initially to consider the available material in three groups, (a) *P. nasuta*, (b) *P. gunnii*, and (c) *P. bougainville*—the latter to include the four smaller species. The present paper will consider anatomical features and variations of the skull and teeth within and between these three groups; succeeding papers will deal with metrical aspects.

(Note: There has been confusion in the published literature about the correct spelling of the names of *P. gunnii* and *P. bougainville*, as can be seen from the above outline of past taxonomy, where the spelling used by the respective authors has been retained. The spelling, as given by the original authors, is *P. gunnii* (Gray, 1838) and *P. bougainville* (Quoy and Gaimard, 1824). The name *P. bougainville* has been tentatively used for group (c) as it was the first described species of the group and thus has priority.)

MATERIAL

The *Perameles* material described in this study was loaned to me by the following Institutions: The Queensland Museum, Brisbane; The Australian Museum, Sydney; The Macleay Museum, Sydney; The National Museum of Victoria, Melbourne; The Fisheries and Wildlife Department, Melbourne; The Queen Victoria Museum and Art Gallery, Launceston; The Tasmanian Museum and Art Gallery, Hobart; The South Australian Museum, Adelaide; and The Western Australia Museum, Perth. My sincere thanks are due to the Directors and relevant Staff Members for their courtesy and co-operation.

In addition to the above material, Dr A. G. Lyne, C.S.I.R.O., Prospect, N.S.W., lent me some particularly useful *P. gunnii* specimens, and twenty-one *P. nasuta* specimens from Sydney, N.S.W., were specially collected and prepared for this study by Mr A. B. Bailey, Department of Anatomy, University of Sydney, Sydney, N.S.W.

The total number of skulls examined was 205: (a) *P. nasuta*—111; (b) *P. gunnii*—51; and (c) *P. bougainville* group—43. The distribution of this material is shown in Fig. 1. Of *P. nasuta*, the Queensland specimens (20 males and 9 females) are sparsely scattered, mainly along the coastal strip, from Cooktown in the north to Tambourine in the south; the New South Wales specimens (19 males and 35 females), except for one specimen which comes from further afield, were all collected within a radius of 50 miles of Sydney; the Victorian specimens (15 males and 13 females) are, bar one from the south-west, all from the south-eastern half of that State. Of *P. gunnii*, 14 males and 9 females come from the south-western corner of Victoria, with possibly some slight overlap into south-eastern South Australia; 12 males and 16 females come from various localities in Tasmania. The *P. bougainville* group can initially be considered in 3 subsections (Fig. 1): (i) south-western South Australia (12 plus 1) and south-eastern Western Australia (3 plus 1); (ii) 5 specimens from Dorre and Bernier Islands in Shark Bay off the central west coast of Western Australia; and (iii) 5 specimens scattered through the western part of central Australia, i.e., eastern Western Australia (2 plus 1), south-western Northern Territory (1) and north-western South Australia (1). The 16 (?) specimens included in Fig. 1, as will be discussed later, fit on size and anatomy in subsection (i). No specimens from south-western Western Australia (*P. myosura myosura*) or from western New South Wales and Victoria (*P. fasciata*) were found in the available material in Australia. Certain specimens labelled *P. fasciata* (National Museum of Victoria) are clearly *P. gunnii*. The sex distribution of the *P. bougainville* material has not been included above, as few specimens are of known sex and, as will be shown later, sexual dimorphism is not clearly apparent in the skulls and teeth of these specimens.

The material used in this study has been collected over a considerable period of time, some dating into the latter part of the last century, and some being collected in the past year. Because of this, the distribution of the genus, as shown in Fig. 1, may not necessarily represent the present distribution, as the ranges have been steadily shrinking over the years with the fuller utilisation of the land for settlement and agriculture. (Similarly, it should be noted that many areas have clearly not been sampled and absence does certainly not imply that the genus is not present.) Temporal differences may occur in the material, but the sample was inadequate for any tests of the possibility.

As will be discussed below, the sexing of *P. nasuta* skulls by the anatomy and size of the canine teeth is fairly simple and it is similarly possible, although sometimes more difficult, to sex *P. gunnii* skulls by this method. In the *P. bougainville* group sex dimorphism in the non-metrical features is not apparent.

With regard to the age of the individual specimens, a skull was considered to have come from an adult when all of the teeth were fully erupted and in use. However, it is clear that some skull growth occurs subsequent to this stage. On the basis of a very small sample (partial records from 6 specimens) it appears from Lyne (1964) that the rate of growth in head length in *P. nasuta* is very rapid up to 100 days, slows quite markedly between 100 and 200 days and then drops to a very slow rate which, however, continues at least until about 375 days, when the records cease. On even more limited material, it appears from Kingsmill (1962) that the last tooth (P₃) emerges some time between 137 and 361 days. From this admittedly very inadequate data (and for practical necessity) it would appear that the full emergence of P₃ (and the canine, particularly in the male) are the most suitable available criteria for calling a specimen adult, despite the fact that some slight further growth of the skull undoubtedly occurs.

THE ANATOMY OF THE SKULL AND TEETH OF *P. NASUTA*

The main features of the cranium and mandible of *P. nasuta* are described by a series of notes dealing with points of particular taxonomic value, by four labelled drawings, (figs 2-5) and by three photographs (plates 16, 21, and 22). (In addition, a number of photographs of standard views of *P. nasuta* will be included in Part II of this study.) The anatomy of the cranium and mandible of the American marsupial, *Caenolestes*, which is very similar to that of *P. nasuta*, has been described in considerable detail by Osgood (1921). Reference should be made to that study for aspects of cranial anatomy not considered here, such as internal structure and the names of foramina.

With regard to the dentition of *P. nasuta*, a full, illustrated account of dental anatomy, eruption sequence, occlusion, and attrition is included. Terminology for the teeth basically follows that of Gregory (1922).

Sexual dimorphism (except in size) is not apparent in the cranium or mandible of *P. nasuta*, but in the teeth, the canines of the two sexes differ considerably in both size and anatomical details. Thus, except for the canine teeth, the descriptions which follow (for *P. nasuta* and for the other *Perameles* species) are applicable to both males and females.

(a) *Cranium*: The following features of the cranium are of particular interest (see figs 2-5, plate 16 and plates 21 and 22):

(1) The muzzle is very considerably elongated by the forward growth of the maxilla, premaxilla and nasal bones. The cartilagenous nasal septum extends forward about another 6 mm beyond the premaxillae and nasals. The prolongation of the premaxilla anterior to the incisors is an unusual feature and is probably correlated with the habit of burrowing small holes with the tip of the muzzle in the search for insects in the ground.

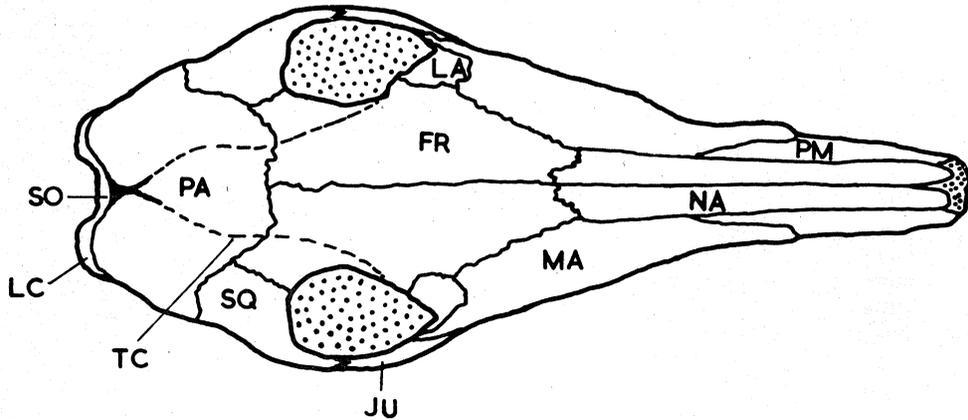


Fig. 2.—Drawing of dorsal view of *P. nasuta* cranium. Key to labelling Figures 2 to 5: AB alisphenoid bulla, APV anterior palatine vacuity, AS alisphenoid, BO basioccipital, BS basisphenoid, CO condyle, EO exoccipital, FM foramen magnum, FR frontal, JU jugal, LA lacrimal, LC lambda, MA maxilla, MS mastoid, NA nasal, PA parietal, PL palatine, PM premaxilla, PO periotic, PPV posterior palatine vacuity, PS presphenoid, PT pterygoid, SO supraoccipital, SQ squamosal, TC temporal crest (line), TY tympanic.

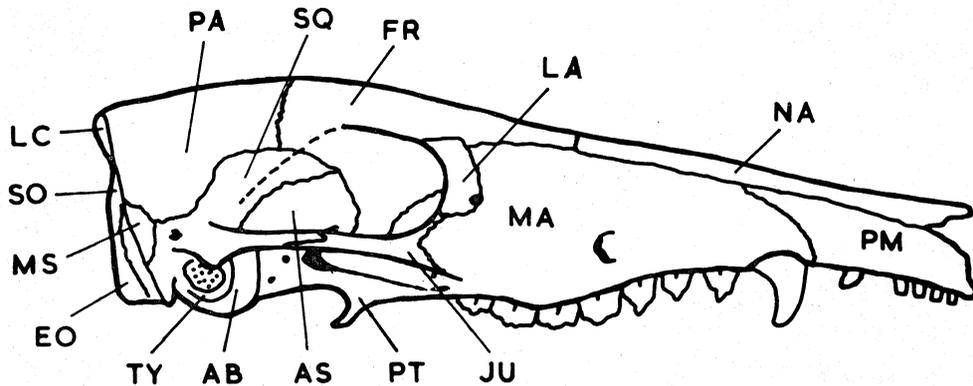


Fig. 3.—Drawing of lateral view of *P. nasuta* cranium (male)

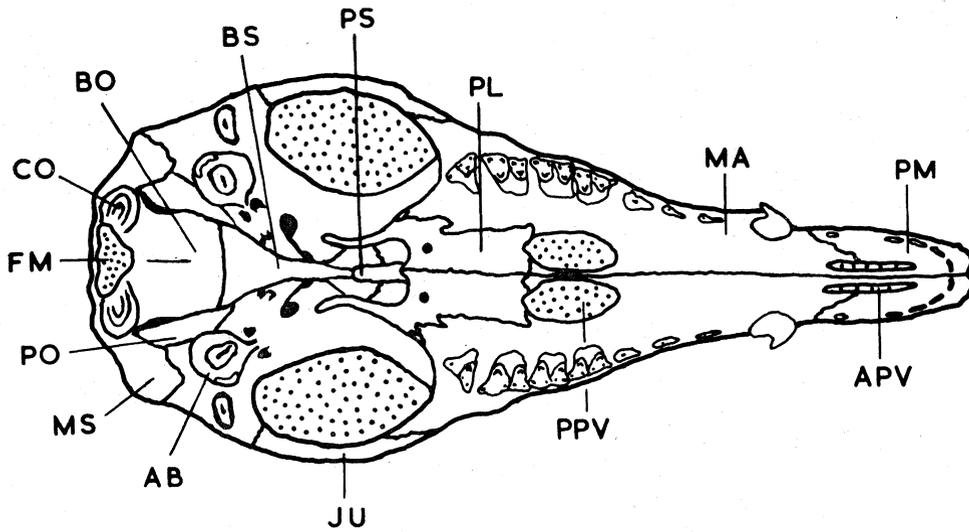


Fig. 4.—Drawing of ventral view of *P. nasuta* cranium (male)

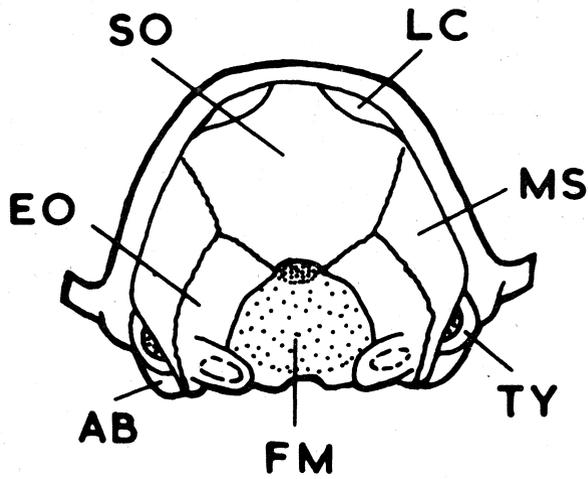


Fig. 5.—Drawing of posterior view of *P. nasuta* cranium

(2) The temporal lines on the dorsal surface of the calvaria are usually not very prominent. The lines of the two sides generally join posteriorly to form a short, weak sagittal crest.

(3) The occipital or lambdoid crests are well developed, particularly superiorly where they form large, posterolaterally-projecting protuberances on either side of the midline.

(4) The palate is very long and narrows markedly from the premolars forward. The paired anterior palatal vacuities are long and thin, whilst the posterior pair have usually lost their thin median partition and together form a single, very large opening. At the level of M³ and M⁴ the palate is very thin, but only occasionally (usually posterior to M⁴) are there any other palatal vacuities and these are generally few, small, and asymmetrical.

(5) The alisphenoid bullae are not markedly inflated; the tympanic bone is crescent-shaped and is not fused onto the alisphenoid.

(6) The zygomatic arches are very slender and arched laterally.

(7) The foramen magnum is large and the two condyles lie on either side of the ventral margin. There is a large characteristic notch in the middle of the dorsal margin of the foramen magnum. The notch separates the two exoccipital bones and is situated in the position where Kerkring's centre of ossification may be found during the development of the human cranium.

(8) A considerable part of each lacrimal bone extends onto the dorsolateral surface of the muzzle adjacent to the orbit. The foramen for the lacrimal duct is found in this part of the lacrimal bone.

(9) The infraorbital foramen, which lies on the lateral side of the muzzle, just above M¹, is very large.

(10) The sutures of the cranial vault and base (including the sutures between the supra-, ex- and basi-occipitals and also the one between the basioccipital and the basisphenoid) usually remain patent, or at least are clearly visible, throughout the animal's life. An exception is the interparietal suture which is obliterated almost completely in all except one of the specimens examined. This suture closes, as a rule, at about the time the last teeth are erupting.

(11) With advancing age, the crania in both sexes become more rugged. This applies particularly to the amount of development of the temporal, sagittal, and lambdoid crests. There is also a strong suggestion that overall size continues to increase well after the last tooth has erupted and is in use.

(b) *Mandible* (plate 16):

(1) The coronoid process is very high and marked off from the condyle by a deep notch.

(2) The gonial angle is very obtuse; the angular process is well developed.

(3) The masseteric fossa is large and fairly deep.

(4) The two halves of the mandible do not synostose at the symphysis.

(c) *Dentition:*

(i) *Deciduous:* In *P. nasuta*, as in most marsupials, there is only a single deciduous tooth in each quadrant of the jaws. The tooth is generally designated as the last premolar, dp₃ (Wilson and Hill, 1897). In both jaws the tooth is similar, relatively simple in structure and minute in size. In the unworn state, the mesial end of the tooth is considerably higher than the rest of the tooth and forms a prominent cusp; at the distal end, there is a suggestion of a much smaller, lower cusp. Unworn, the mesiodistal diameter is usually the greater, but, in a worn tooth, the buccolingual measurement may on occasions be larger. The occlusal surface of the crown of a worn tooth eventually forms a homogeneous concavity, circular or oval in outline. In both jaws dp₃ is replaced by the last permanent premolar.

(ii) *Permanent:* The adult dental formula is: $\frac{5 \cdot 1 \cdot 3 \cdot 4}{3 \cdot 1 \cdot 3 \cdot 4}$. In occlusal view, the sides of the upper dental arcade lie close together anteriorly and are almost parallel up to the canines. The buccal surfaces of the two sides then broaden out in the region of the premolars and M¹ and finally converge very slightly at M⁴ (plate 17). Because of the considerable inward projection of the large molars, this broadening out is not as marked when the lingual surfaces of the teeth are followed. The two sides of the lower dental arcade (plate 19) diverge evenly from anterior to posterior when the lingual surfaces are considered, but the broad molars bulge outwards when the buccal surfaces are viewed. From the side (plate 16), the occlusal surfaces of the upper teeth form a sinuous curve, concave downwards from the mesial incisor to the last premolar, and convex downwards from there to the distal end of the toothrow. The occlusal surfaces of the lower teeth form a weaker reciprocally curved profile (plate 16); but in both jaws, the line is interrupted (particularly in the male) by the large canine teeth. The three premolars in *Perameles* have been designated P₁, P₂, and P₃ (Wilson and Hill, 1897 and Bensley, 1903), but their homologies are considered uncertain. Sexual dimorphism is only found in the canines. The term "crown" has been used to denote that portion of the tooth which normally lies above the alveolar margin.

(1) *Upper teeth* (plates 16 and 17): The first four upper incisors of each side are small teeth, buccolingually (labiolingually) flattened and relatively long mesiodistally. I¹ is considerably smaller than I², I³, and I⁴, which are subequal. I¹ leans slightly lingually and the mesial part of I² may also lean inwards slightly. The left and right I¹ are separated by a small diastema, but the other adjacent teeth of this group either touch or almost touch. I¹–I⁴ of the two sides form a parabolic arch on the premaxilla. I⁵ is similar in size to I²–I⁴ in its mesiodistal and buccolingual dimensions, although in the former measurement, it is usually slightly shorter. In the height dimension, this tooth is considerably larger than any of the other incisors. In shape, I⁵ is distinctly caniniform with a clearly pointed tip; viewed from the side, it is directed slightly backwards, i.e., posteriorly. I⁵ is separated from both I⁴ and the C by a diastema, each of which measures about 3.5 mm. Only the incisal half of the crown of each of the incisors is enamel-covered, i.e., only the incisal half of the tooth above the alveolus.

The C tooth has a large root which, particularly in the male, forms a prominent eminence on the external surface of the maxilla. Within its alveolus, starting from the apex, the root first runs anteriorly and then curves sharply ventrally just before it emerges from the alveolus. The tooth is almost invariably much smaller in the

female than in the male (see Part II) and, in addition, also differs anatomically (plate 18). The male \underline{C} tooth is very large, particularly in mesiodistal length, as it leaves its alveolus. The crown portion is of considerable height and tapers evenly and gradually as it curves towards its tip. Only about the incisal $1/3$ of the crown is enamel-covered. In the female, the crown of the \underline{C} is not nearly as high as in the male. The sides of the basal half of the crown are parallel, but thereafter the crown tapers rapidly to a point, the mesial edge being convex and the distal edge concave. Only the incisal, tapered portion is enamel-covered in this sex and it is marked off from the basal part by very small mesial and distal cuspules. In both males and females the \underline{C} is considerably flattened buccolingually. Although the \underline{C} teeth are so different in the mesiodistal length in the two sexes, the diastemata separating these teeth from I^5 and P^1 respectively, are of similar length in the two sexes.

Of the upper premolars, P^2 is slightly larger than P^1 , and P^3 is considerably larger than P^2 (plate 16). In shape, P^1 and P^2 are very similar. They are buccolingually flattened teeth with a large central cusp and very small mesial and distal cuspules. Seen from the occlusal surface (plate 17), P^3 is somewhat triangular in outline, with the buccal surface forming the base and the apex being situated slightly distal to the centre of the tooth, on the lingual side. On the buccal side of the tooth, there is a large central cusp, a very small mesial cuspule and a fairly prominent distal cuspule. In addition, there is a moderate sized cuspule on the lingual side, which may be separated from the large central cusp on the buccal side by a small furrow or fovea. Each premolar has a mesial and a distal root; the roots of P^3 (particularly the distal one) being the largest in cross-sectional area. The two roots of each being premolar, especially P^1 and P^2 , join the crown well below (i.e., ventral to) the general level of the palate. Bony downgrowths from the alveolar margin of the maxilla project over the buccal and lingual sides of each of the premolars and cover their central portions (i.e., mainly the region where the roots join). In life, the basal portions of the premolars (and also of the molars) are covered by the very thick, mucous membrane which lines the mouth.

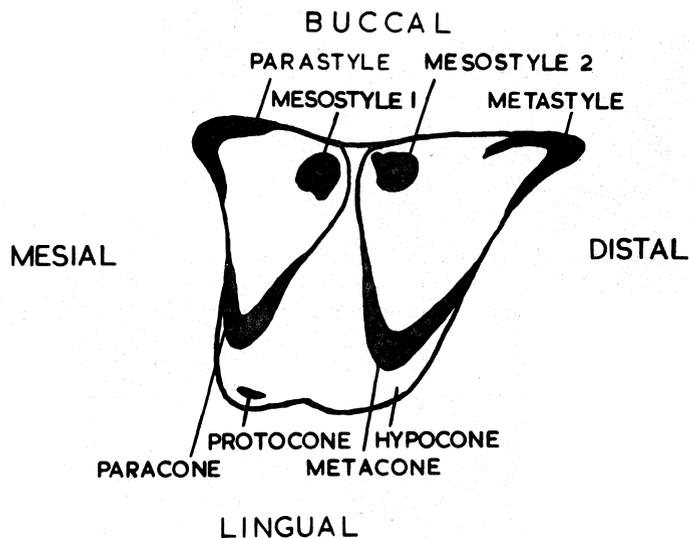
The diastemata between the teeth were not measured for the metrical study of *P. nasuta* (Part II), but some measurements of most were taken to give an approximate indication of their relative sizes.

In a small series of male and female crania, the approximate size of the diastema between \underline{C} and P^1 was found to be 2.75 mm, between P^1 and P^2 —1.90 mm, between P^2 and P^3 —0.35 mm; P^3 lies close up against M^1 . The lengths of these diastemata vary quite considerably (\underline{C} to P^1 , 2.2–3.5 mm; P^1 to P^2 , 1.2–2.8 mm; P^2 to P^3 , 0.1–0.5 mm), but \underline{C} to P^1 is always greater than P^1 to P^2 , and P^2 to P^3 is invariably the smallest by far in each of the individuals examined. The differences between male and female diastemata in this small series did not appear to be significant.

The anterior three upper molars all follow the same basic pattern (plate 17). Each consists of four main cusps situated on the lingual half of the tooth and four buccal cusps derived from the external cingulum. The names of these cusps (following the terminology of Gregory, 1922) are (fig. 6):—

Four main cusps: mesiolingual, protocone; distolingual, hypocone; mesiocentral, paracone; disto-central, metacone.

Fig. 6.—Diagram of the cusp arrangement in a typical *P. nasuta* upper molar (left M³).



(Gregory suggests that the "hypocone" may be a true hypocone as derived in placentals, or an extension of the metaconule).

Four buccal cingulum cusps: (from mesial to distal) parastyle, mesostyle 1, mesostyle 2, metastyle.

(In his drawings on page 72, Gregory has labelled the posterior four teeth of *Perameles* as P₄, M₁, M₂, and M₃, instead of M₁ to M₄). In shape, the first three upper molars are roughly trapezoidal, with the mesiodistal dimension longer buccally than lingually and the lingual and buccal surfaces more or less parallel. The buccal part of the occlusal surface of each molar projects ventrally more than the lingual part, but, as the alveolar margin projects ventrally far more on the buccal than on the lingual side, it is the lingual part of each molar which is the more hypsodont. M¹, M², and M³ each show two raised triangular areas, the bases of which lie along the buccal border of the tooth and the apices of which point lingually. The bases are thus formed by the cingulum cusps and the apices by the large V-shaped paracones and metacones. Each mesial triangle consists of the paracone lingually and the parastyle and mesostyle 1 at the mesial and distal ends of the base on the buccal side; each distal triangle is formed by the metacone lingually and mesostyle 2 and the metastyle at the mesial and distal ends of the base on the buccal side. The metacone is larger than the paracone and, in general, the cusps of the distal triangle are larger than those of the mesial triangle. Compared with the distal triangle, the mesial triangle is particularly small in M¹, relatively less so in M² and the difference is still less marked in M³. On the lingual side of each molar, there is a narrow platform, well below the level of the tips of the paracone and metacone. On the lingual edge of this platform, the weakly developed protocone (mesially) and the still weaker developed hypocone (distally) are situated. This lingual platform is extended buccally to fill the gap between the mesial and distal triangles of each molar. M⁴ is built on the same basic pattern as M¹–M³, but it is considerably reduced, mainly distally. The mesial triangle of the tooth is intact and has a particularly large paracone, but mesostyle 1 is rather small; of the distal triangle, only a single cusp remains. Bensley (1903) working on *P. doreyana* (= *Echymipera doryana*) suggests that the reduction of the distal part is due to the lack of development of the metacone. If this is so, the remaining distal cusps would be mesostyle 2 or the metastyle, but it would seem that

the homology of this cusp is best considered uncertain. Of the two lingual cusps of M^4 , the protocone is present and well developed, but the hypocone appears to be consistently absent. All four of the upper molars have three roots, two situated buccally and a larger, single, lingual root. The adjacent surfaces of M^1 - M^4 are in close contact with one another buccally, but lingually they are well separated. There is thus a triangular gap (base lingually) between the adjacent mesial and distal ends of the upper molars (plate 17).

(2) *Lower teeth*: The lower incisors, are all fairly large teeth and, especially the mesial two pairs, markedly procumbent (plate 19). The buccal (labial) surface of the crown of I_1 and I_2 are high, thickly enamel-covered and have sharp incisal edges. In I_3 , the buccal surface is also enamel-covered, but the incisal edge, and in fact the whole of the incisal half of the crown, is bifid, the mesial portion being about double the size of the distal. There is a small diastema between the mesial incisors, but the other adjacent surfaces of the incisors lie close together or touch. Viewed from the occlusal surface, the mesial and distal surfaces of each of the three incisors converge lingually from the incisal edge towards the base of the crown. Because of the marked procumbency of the teeth, a small amount of what should probably be termed root is then usually also seen on I_1 and I_2 before these teeth enter their alveoli. All of the incisors have extremely long roots which run back posteroventrally from the crown into the mandible. On the external surface of the mandible, a substantial portion of the roots of the incisors are generally exposed, due to the thin, outer, bony walls of the alveoli having been resorbed or lost.

The male and female \bar{C} teeth are each similar in structure and size to their upper equivalents. The base of the crown of the male \bar{C} is large, mainly due to its considerable mesiodistal length. The crown is generally buccolingually flattened and the mesial and distal edges curve gradually and evenly up from the base until they meet at the incisal tip. Approximately the incisal $1/3$ of the tooth is enamel-covered, on both the buccal and lingual surfaces. As it emerges from its alveolus, the female \bar{C} is far smaller than the male equivalent (see Part II), but, like the male \bar{C} , it is also buccolingually flattened. From the base upwards, the mesial and distal edges run roughly parallel for a short distance, but they then converge rapidly to a point, a small distal cuspule marking the junction of the two portions. In the female, the incisal half of the tooth is enamel-covered, both lingually and buccally. In both sexes, the \bar{C} teeth lean buccally to the extent of about 45° from the vertical. The \bar{C} is separated in both sexes by large diastemata from I_3 and P_1 ; the size of the former diastema is about 4.75 mm, and the latter about 3.5 mm.

The three lower premolars (plate 19) are very similar in structure to their upper equivalents, except that P_3 is similar to P_1 and P_2 and does not have the extra development found on P^3 . The lower premolars are all buccolingually flattened and have a large central cusp and small mesial and distal cuspules. However, in all of these teeth the distal cuspule and associated part of the tooth is considerably larger than the mesial (plate 16). In size, $P_1 < P_2 < P_3$. P_1 is separated from P_2 by a diastema of about 1.25 mm, on average; P_2 lies close to P_3 , but a very small gap can usually be seen; P_3 lies close to, and often actually abuts against, M_1 . Each lower premolar has subequal, buccolingually-flattened mesial and distal roots. The bony processes described between the roots of the individual and adjacent upper premolars are also present between the lower premolars.

The four lower molars are each relatively more elongated than their upper equivalents in the mesiodistal direction and do not have any cingulum cusps such as are found in the upper molars (plate 19). In addition, the lower molars are hypsodont teeth both lingually and buccally. All four lower molars have a similar cusp arrangement, but in M_4 the distal portion of the tooth is considerably reduced, although not relatively as much as M^4 . The names of the cusps of the lower molars, again following Gregory (1922) are (fig. 7):—

Buccal (mesial to distal): protoconid, hypoconid.

Lingual (mesial to distal): paraconid, metaconid, entoconid, hypoconulid.

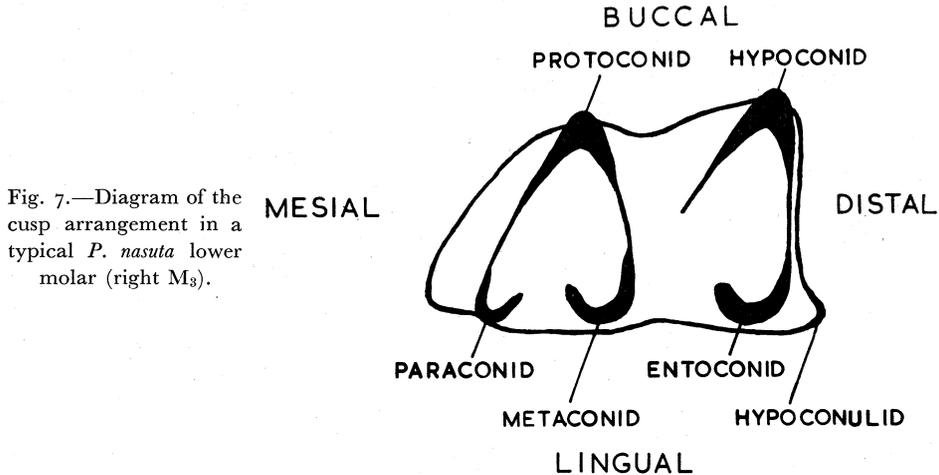


Fig. 7.—Diagram of the cusp arrangement in a typical *P. nasuta* lower molar (right M_3).

The cusps on the lower molars (plate 19) show a similar arrangement to that seen in the upper molars in that they are also arranged to form mesial and distal triangles on each tooth, but in the lower molars, the bases are on the lingual instead of the buccal sides of each tooth and, in addition, there are certain other differences. The apex of the mesial triangle is formed buccally by the large, V-shaped protoconid; lingually, the small paraconid (mesially) and the large metaconid (distally) form the base. The apex of the distal triangle is formed by the large V-shaped hypoconid on the buccal side. On the lingual side, the fairly large entoconid lies almost directly lingual to the hypoconid and forms the distolingual corner of the base, but there is no cusp to complete the mesiolingual corner of the triangle. A very small additional cusp, the hypoconulid, is found on the extreme distolingual corner of M_1 – M_3 . It forms a small backward extension of the distolingual corner of the tooth, but does not take part in the formation of the distal triangle. In M_1 to M_3 the distal triangle is the larger, but as one proceeds from M_1 to M_3 the mesial triangle becomes more nearly equal to the distal triangle in each tooth. In M_4 the distal triangle is very greatly reduced and is only a small fraction of the size of the triangles in any of the other lower molars. In M_1 – M_3 there is only a trace of the flat platform described between the mesial and distal triangles of the upper molars; in M_4 the platform is better developed because of the great reduction of the distal triangle. On the mesial ends of M_2 , M_3 and M_4 a fairly prominent shelf is developed from the cingulum. The shelf gets progressively larger from M_2 to M_4 where it is particularly well developed. Each lower molar has a mesial and a distal root, each of considerable length and subequal in size.

(3) *Eruption sequence*: Material available from the present study only allows assessment of the relative eruption times of the last four teeth—the last premolar and the last three molars. In the youngest specimens available, the incisors, canines, P₁, P₂, dp₃, and M₁ are all present. The canines are only about half erupted, but the other teeth are all fully out. M₂ is the next tooth to erupt and it is followed by M₃. Finally M₄ erupts and, at about the same time, P₃ replaces dp₃. The canines, particularly in the males, may not be fully erupted, even after P₃ and M₄ are fully out. The lower teeth all appear to erupt in advance of their upper equivalents. The incisors, canines, and premolars lie close together when they first erupt and the various diastemata described above open up as the cranium and mandible elongate.

From the material studied by Wilson and Hill (1897) it is clear that the first tooth to erupt in *P. nasuta* is dp₃, lower tooth first. The incisors follow (again lower teeth first); the canines, P₁, P₂, and M₁ follow closely behind the incisors and may even start erupting at about the same time as those teeth.

Kingsmill (1962) gives some indications as to the age at which the various teeth erupt. At 48 days, the age of the youngest specimen examined, dp₃, the incisors, canines, P₁, P₂, M₁, M₂, and M₃ project above the bone. At 61 days, dp₃ can be seen above the gum and these teeth are not shed before 137–361 days. Most of the permanent teeth are visible above the gum in the period between 48 and 61 days, but M₃ and M₄ do not appear until 61–126 days and M₄ not until about 137 days. P₃ appears above the alveolar margin at 61 to 126 days, but was “still embedded in the gum” till 137–361 days. These figures were based on only five specimens, but they do give some rough indication of eruption times.

(4) *Occlusion and attrition*: The dentition of *P. nasuta* is adapted to an omnivorous, mainly insectivorous, type of diet, but, to quote Gregory (1922), with “incipient adaptation towards a grinding type of molars”. When the fully closed jaws are examined in a prepared skull (plate 20), or a formalin preserved whole specimen, four most significant features of occlusion can be seen:

(a) The lower incisors lie considerably lingual to, and do not directly occlude with, the upper incisors. Although this is the case when the jaws are in the fully closed position, during biting or chewing, a slight amount of unilateral movement at the mandibular condyles would allow the upper incisors (I²–I⁴) of the left or right side to bite into the occlusal surfaces of the lower incisors (I₁–I₃) of the same side. This slight amount of movement should be possible at the condyles although, according to Abbie (1939), the temporo-mandibular joint of *Perameles* does not include an intra-articular disc. Examination of the occlusal surfaces of the lower incisors shows mesiodistally oriented facets which could be the result of attrition by the incisal edges of I²–I⁴. The worn shape of the incisal edges of the upper incisors appear to confirm this type of usage. Each takes the form of a blunt point, with a very long mesio-ventrally directed portion which would occlude with the occlusal surface of the lower incisors, followed by a short, distoventrally directed section, possibly the result of wear by the incisal edges of the lower incisors in passing buccally or lingually in the unilateral movement postulated above.

(b) I⁵, the upper and lower canines and all of the premolars, alternate (starting mesially with I⁵, and lower and upper teeth then alternating). Together, these teeth form a very efficient grasping and holding mechanism.

(c) The upper molars overhang the lower considerably buccally. As a result, the buccal cingulum cusps of the upper molars do not directly occlude with any part of the lower molars in the resting position. In any lateral chewing movements, with the jaws slightly open, they do however offer an increased grinding surface for the lower molars to work on.

(d) The mesial and the distal triangles of the upper and lower molars interdigitate, the distal triangle of the lower molar occluding between the mesial and distal triangles of its upper equivalent. The mesial triangle of M_1 occludes between the mesial triangle of M^1 and the distal part of P^3 . This arrangement would function particularly well in a chopping type of action.

With regard to attrition, the deciduous premolars develop an occlusal concavity, with the mesial portion higher than the distal. This wear must be caused indirectly by food (probably including some sand), as the upper and lower deciduous premolars cease to occlude at a very early age whilst the animal is still suckling.

Wear of the incisors was dealt with above, under occlusion; wear on the canines is in almost all cases only slight and generalised. Viewed from the lateral surface, the premolars form an efficient, interlocking series of triangles and the distal edges of the lower premolars wear against the mesial edges of the upper. Reciprocally shaped facets, usually approximately straight, are worn.

In the upper molars, the mesial triangle shows signs of wear before the distal triangle and the lingual part of each tooth wears before the buccal portion. Correspondingly in the lower molars, the distal triangle and the buccal half of the tooth show wear sooner. Very little wear at all occurs on the buccal cingulum cusps of the upper molars. The relative amount of wear on each molar in the tooththrow of an individual follows the eruption sequence M_1 to M_4 . Resorption of alveolar bone was noted in a number of older specimens in the premolar-molar region. In these individuals, the coronal halves of the roots of the premolars and molars were often exposed above the resorbed alveolar margin and the remaining portions of the sockets were eroded, often to twice their natural diameter.

THE ANATOMY OF THE SKULL AND TEETH OF *P. GUNNII*

The anatomy of the skull and teeth of *P. gunnii* is very similar to that of *P. nasuta*. However, in general, the skull of *P. gunnii* is smaller and more delicately built than that of *P. nasuta* and, in addition, there are a few features in which there are clear-cut anatomical differences between the two species.

(a) *Cranium* (Plates 21 and 22).

(1) The temporal lines in *P. gunnii* are quite well developed, but they remain widely separated (6 to 9 mm apart) right up to the lambdoid crests and thus do not form a sagittal crest posteriorly.

(2) The lambdoid crests are much smaller and less rugged than in *P. nasuta*.

(3) Partly as a result of (1) and (2) above, the posterior part of the dorsal surface of the calvaria is flattened, low, and rounded in *P. gunnii*. Also, the most posteriorly projecting region of the cranium in *P. gunnii* is the central portion of the occipital bone, and not the lambdoid crests as in *P. nasuta*.

(4) Viewed from above, the minimum diameter of the cranium between the orbits is considerably greater in *P. gunnii* than in *P. nasuta*.

(5) The alisphenoid bullae and the tympanic bones of *P. gunnii* are larger than those in *P. nasuta*.

(6) The height of the foramen magnum of *P. gunnii* is relatively slightly less than in *P. nasuta* and hence the foramen is generally more oval-shaped.

(7) In addition to anterior and posterior palatal vacuities, similar to those seen in *P. nasuta*, certain additional areas of the palate are typically missing in *P. gunnii*. (i) One or two anteroposteriorly elongated pairs of vacuities are found between the anterior and posterior palatal vacuities; and (ii) random fenestration occurs in most of the palate posterior to the posterior palatal vacuities. The posterior palatal vacuities are generally larger in *P. gunnii* than in *P. nasuta* and almost invariably lack a median partition.

(b) *Mandible*: The mandible of *P. gunnii* is considerably more slender than that of *P. nasuta* and the relative narrowness of the anteroposterior dimension of its ascending ramus is particularly striking. Compared to *P. nasuta*, the coronoid process of *P. gunnii* is usually relatively higher, anteroposteriorly shorter, and its tip tends to be directed posteriorly more frequently. The mandibular notch is relatively deeper in *P. gunnii* than in *P. nasuta*.

(c) *Dentition* (plates 21 and 22): There are two major differences between the dentitions of *P. gunnii* and *P. nasuta*:

(1) The crown of I³ in *P. gunnii* (plate 23) is mesiodistally long, buccolingually flattened and bears more resemblance to a small *Perameles* premolar than to the caniniform-shaped I⁵ of *P. nasuta*. In addition, this tooth is two-rooted in *P. gunnii*, whereas the equivalent tooth in *P. nasuta* has only a single root.

(2) In *P. gunnii* the male canine is only slightly larger than that of the female, and much smaller than the equivalent tooth in *P. nasuta*. The same anatomical differences are present between the male and female canines in *P. gunnii* as were described for *P. nasuta*, but they are not as clearcut in *P. gunnii* and, on occasions, sexing by means of the canines only can be extremely difficult.

Other than on the above two points, the dentitions appear to be very similar, although there is a suggestion that the shapes of the incisal edges of I²-I⁴ may differ slightly in the two species (in *P. gunnii* the distal part seems to be longer than in *P. nasuta* and to end in a minute cuspule) and also that the protocone in the upper molars might be relatively slightly larger in *P. gunnii* than in *P. nasuta*.

THE ANATOMY OF THE SKULL AND TEETH OF THE *P. BOUGAINVILLE* GROUP

The skulls and teeth of *P. nasuta* and *P. gunnii* are of approximately similar size, but readily distinguishable on the anatomical differences discussed under *P. gunnii* above. All of the other *Perameles* skulls studied are of considerably smaller size and have initially been included together in this *P. bougainville* group.

(a) *Cranium* (plates 21 and 22): The *bougainville* group of crania, in addition to being considerably smaller, differs from *P. nasuta* and *P. gunnii* in the following respects:

(1) Viewed from above or below, the muzzle of the *P. bougainville* group appears to taper more sharply from P² forwards; in lateral view, the profile of the dorsal surface of the muzzle shows a slight concavity (mainly at about the region of the fronto-nasal suture). In *P. nasuta* the muzzle profile is flat or even slightly convex; in *P. gunnii* it is usually also flat, but there may occasionally be a very slight concavity.

(2) In the *P. bougainville* group the maxillary fossa, on the lateral side of the maxilla above the posterior molars, appears deeper than in *P. nasuta* or *P. gunnii*, although rarely the fossa may be quite marked in the latter species.

(3) The lacrimal bones in the *P. bougainville* group are prominent and similar in form to those of *P. gunnii*, which stand out slightly more than those of *P. nasuta*.

(4) The palatal vacuities of the *P. bougainville* group are similar to those found in *P. gunnii* and far more extensive than those of *P. nasuta*.

(5) In their weakly developed lambdoid crests and in the absence of sagittal crests, the *P. bougainville* group also resembles *P. gunnii*.

(6) The alisphenoid bulla takes two clearly different forms (plate 22) in the *P. bougainville* group. (i) In the Dorre and Bernier Island specimens, the bulla is of a similar order of size to those of *P. nasuta* and *P. gunnii*, although it is relatively slightly larger than even that of *P. gunnii*. (ii) In all of the rest of the specimens (with one possible exception discussed below) the bullae are all extremely large and more similar in relative size to the bullae found in the genus *Isoödon*.

(b) *Mandible*: No important differences, except size, are apparent in the mandible. The pattern is basically like that of *P. gunnii*.

(c) *Dentition* (plates 21 and 22):

(1) The deciduous premolar is relatively and absolutely larger and generally better developed in the *P. bougainville* group than in either of the two larger species.

(2) The upper molars of the *P. bougainville* group usually appear to have better developed mesiolingual cusps (protocones) than *P. nasuta* and *P. gunnii*.

(3) Sexual dimorphism was not apparent in the canines of this group.

(4) The crown of I⁵ may be either caniniform, as in *P. nasuta*, or it may be elongated mesiodistally and resemble that of *P. gunnii*. In thirty-four out of the thirty-five specimens with caniniform crowns, I⁵ was single-rooted; in three out of the five specimens with mesiodistally elongated crowns, I⁵ was double-rooted. However, because of their small size, the roots are not easy to identify, even when x-rays are used, and the three discordant cases might well be considered uncertain. The long I⁵ is always found in the Dorre and Bernier Island specimens, whilst, with one exception, the rest all have caniniform I⁵ teeth.

DISCUSSION

The anatomical differences in the skull and teeth between *P. nasuta* and *P. gunnii* are straightforward and call for little additional comment. The two species can be readily distinguished on a number of anatomical points, particularly on I⁵, the canines and the palatal vacuities, and hence clearly merit specific separation.

From the foregoing outline of the anatomy of the skull and teeth of the *P. bougainville* group, except for the considerable difference in size, it is apparent that these specimens are very similar to *P. gunnii* in most features examined. The material included in this *P. bougainville* group all come from the western half of Australia, but were listed under "Material" in three subsections. The basis for this subdivision can now be discussed.

The specimens in subsection (1), twelve plus one from south-western South Australia and three plus one from south-eastern Western Australia, all have mesiodistally short (crown length 0.9–1.0 mm), single-rooted I⁵ teeth, and large alisphenoid bullae. These specimens come from an area from which *P. myosura notina* and *P. bougainville notina* were described by Iredale and Troughton (1934) and Marlow (1962) respectively. The sixteen (?) specimens from South Australia have the same characteristics and are anatomically indistinguishable from specimens of subsection (1).

The specimens in subsection (2), the five specimens from Dorre and Bernier Islands, all have mesiodistally long (crown length 1.1–1.3 mm) I⁵ teeth and small alisphenoid bullae. Three out of five of these I⁵ teeth have double roots and the other two are probably single, but mesiodistally long. These specimens come from the localities from which *P. bougainville* and *P. bougainville bougainville* were described by Iredale and Troughton (1934) and Marlow (1962) respectively.

The five specimens in subsection (3) are thinly scattered in the western part of central Australia, the region from which the species *P. eremiana* has been described. I⁵ is absent in one specimen, but three out of the four remaining specimens have small, single-rooted I⁵ teeth, while the fourth specimen has a long, double-rooted I⁵ tooth. Further, in three out of the four specimens in which the relevant feature is undamaged, the alisphenoid bullae are large; the fourth specimen is not fully adult, but the bulla appears to be of the small type. This group of specimens from central Australia is very small, not all are adult, some are damaged and the localities ascribed to most of them are rather vague. It would seem unwise at this stage to use the above information to comment on skull and tooth features of this species.

From the above analysis of the small forms of *Perameles*, it would seem that, at least for the time being, Tate's suggestion (1948) of the close inter-relationship between the small, long-nosed bandicoots should be followed and that, for reasons of priority, Marlow's terminology (1962) of *P. bougainville bougainville* for the Dorre and Bernier Island form and *P. bougainville notina* for the South Australian form should be used. However, the two clearcut differences in the skull and teeth found between these two forms suggest the possibility that, on further investigation, specific separation might be warranted. Material of *P. bougainville myosura* and *P. fasciata*, and features other than the anatomy of the skull and teeth, will clearly have to be considered before the intrageneric taxonomy of *Perameles* can be fully resolved.

SUMMARY

- (1) The anatomy of the skull and teeth of *P. nasuta* has been described.
- (2) Anatomical variations in the skull and teeth between certain species of *Perameles* have been recorded.
- (3) Clear anatomical differences in certain of the above features separate the two large eastern species (*P. nasuta* and *P. gunnii*) and also two of the small western forms (*P. bougainville bougainville* and *P. bougainville notina*).

ACKNOWLEDGEMENTS

I should like to thank Mr P. L. Davies, Department of Anatomy, University of Sydney, and Mr B. J. Marlow, The Australian Museum, Sydney, for discussions on various aspects of this paper. Mr G. L. Williams, Department of Anatomy, University of Sydney, took the photographs which illustrate this paper.

REFERENCES

- Abbie, A. A. (1939). The mandibular meniscus in Monotremes and Marsupials. *Aust. J. Sci.* **2**: 86-8.
- Bensley, B. A. (1903). On the evolution of the Australian Marsupialia; with remarks on the relationships of the Marsupials in general. *Trans. Linn. Soc. Lond. Zool.* (2) **9**: 83-217.
- Gray, J. E. (1838). On a new species of *Perameles*. *Proc. Zool. Soc.* (1838): 1.
- Gregory, W. K. (1922). "The origin and evolution of the human dentition." (Williams and Wilkins Co.: Baltimore).
- Iredale, T. and Troughton, E. le G. (1934). "A check-list of the mammals recorded from Australia." Memoir VI. (The Australian Museum: Sydney.)
- Kingsmill, E. (1962). An investigation of criteria for estimating age in the Marsupials *Trichosurus vulpecula* Kerr and *Perameles nasuta* Geoffroy. *Aust. J. Zool.* **10**: 597-616.
- Lyne, A. G. (1964). Observations on the breeding and growth of the Marsupial *Perameles nasuta* Geoffroy, with notes on other bandicoots. *Aust. J. Zool.* **12**: 322-39.
- Marlow, B. J. (1962). "Marsupials of Australia." (Jacaranda Press: Brisbane.)
- Osgood, W. H. (1921). A monographic study of the American Marsupial, *Caenolestes*. *Fld. Mus. Nat. Hist.* (Chicago) Publ. 207 (Zool.) **14**: 1-162.
- Quoy and Gaimard, P. (1824). Voyage de l'Uranie—Zoologie: 56. In "Voyage Autour du Monde" Ed. by Freycinet, L. D. (Chez Pillet Aine, Imprimeur-Libraire: Paris).
- Simpson, G. G. (1945). The principles of classification and a classification of mammals. *Bull. Amer. Mus. Nat. Hist.* **85**: 1-350.
- Tate, G. H. H. (1948). Results of the Archbold Expeditions. No. 60. Studies in the Peramelidae (Marsupialia). *Bull. Amer. Mus. Nat. Hist.* **92**: art. 6, 313-46.
- Thomas, O. (1888). "Catalogue of the Marsupialia and Monotremata in the collection of the British Museum (Natural History)." (British Museum (Nat. Hist.): London.)
- Waterhouse, G. R. (1846). "Natural History of the Mammalia." Vol. I. Marsupialia. (Bailliere: London.)
- Wilson, J. T. and Hill, J. P. (1897). Observations upon the development and succession of teeth in *Perameles*; together with a contribution to the discussion of the homologies of teeth in marsupial animals. *Quart. J. Micr. Sci.* N.S. **39**: 427-588.

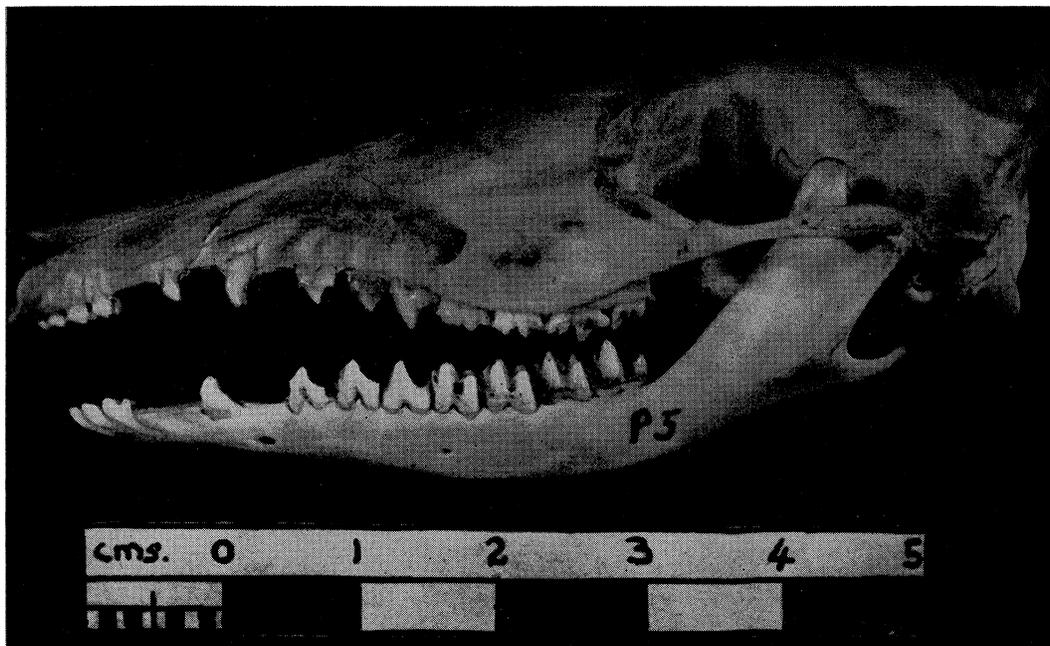
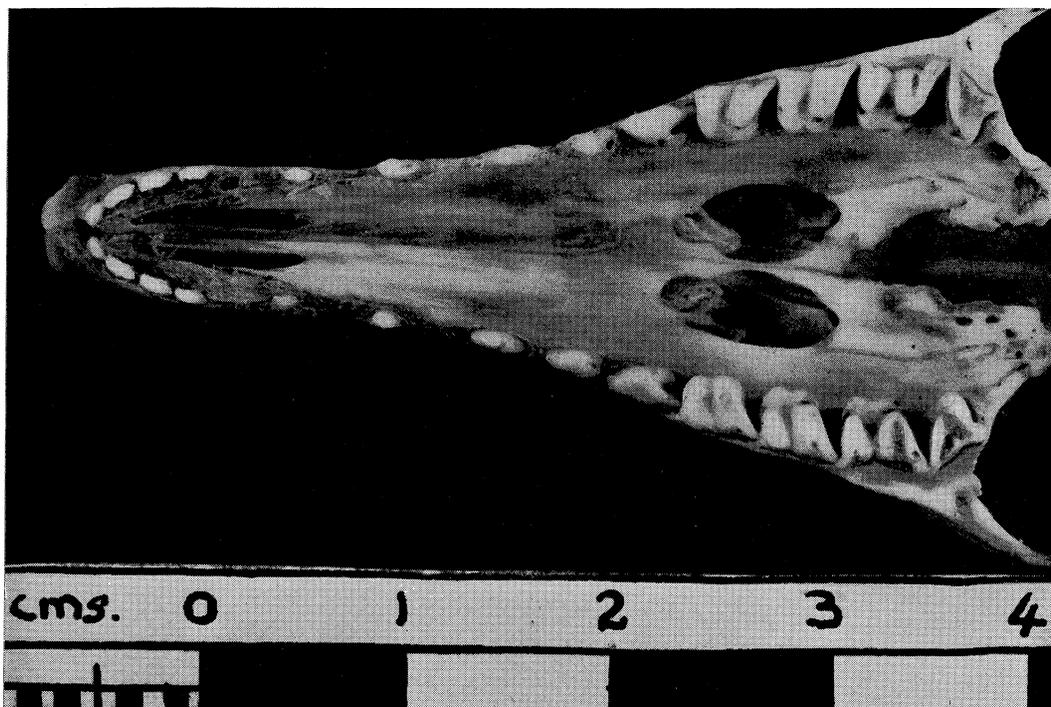
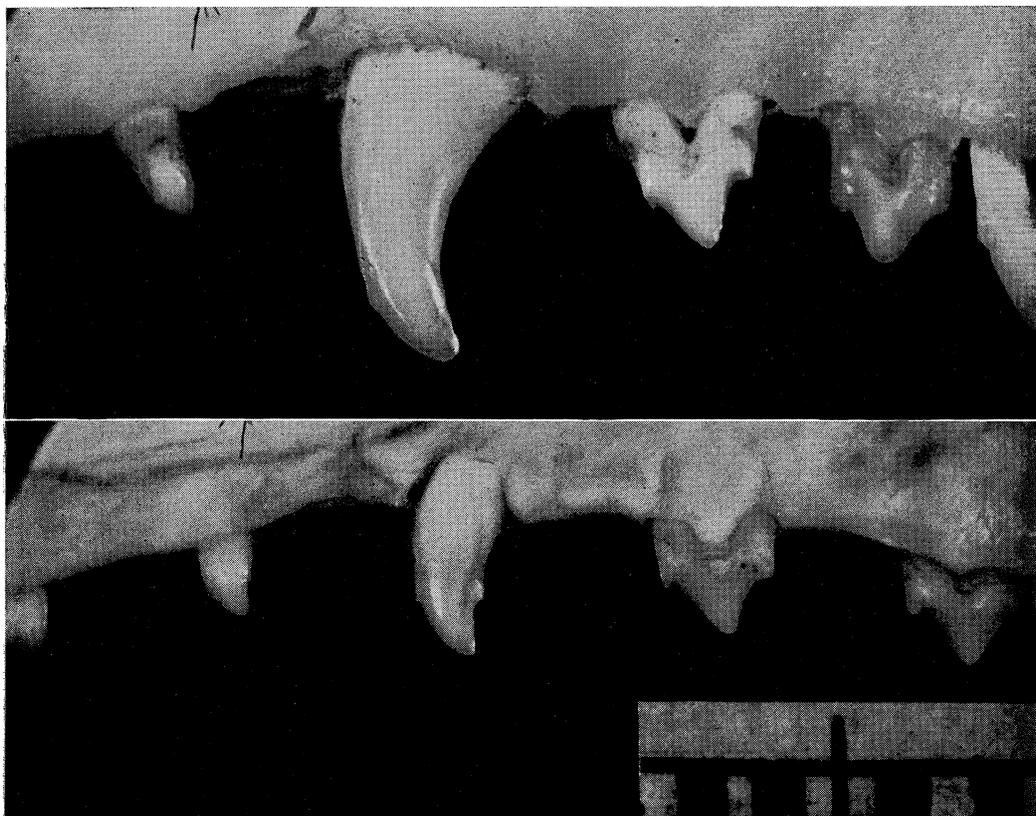


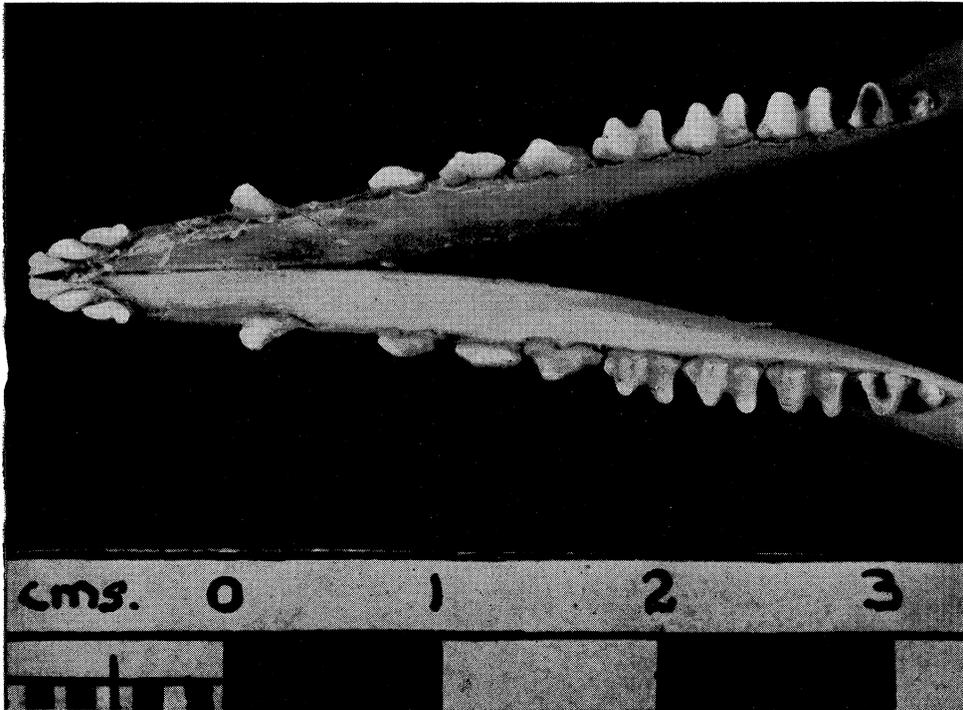
Plate 16 (above): *P. nasuta* female (P.5), lateral view of the skull, teeth and mandible.

Plate 17 (below): *P. nasuta* female (P.5), occlusal view of the upper teeth.





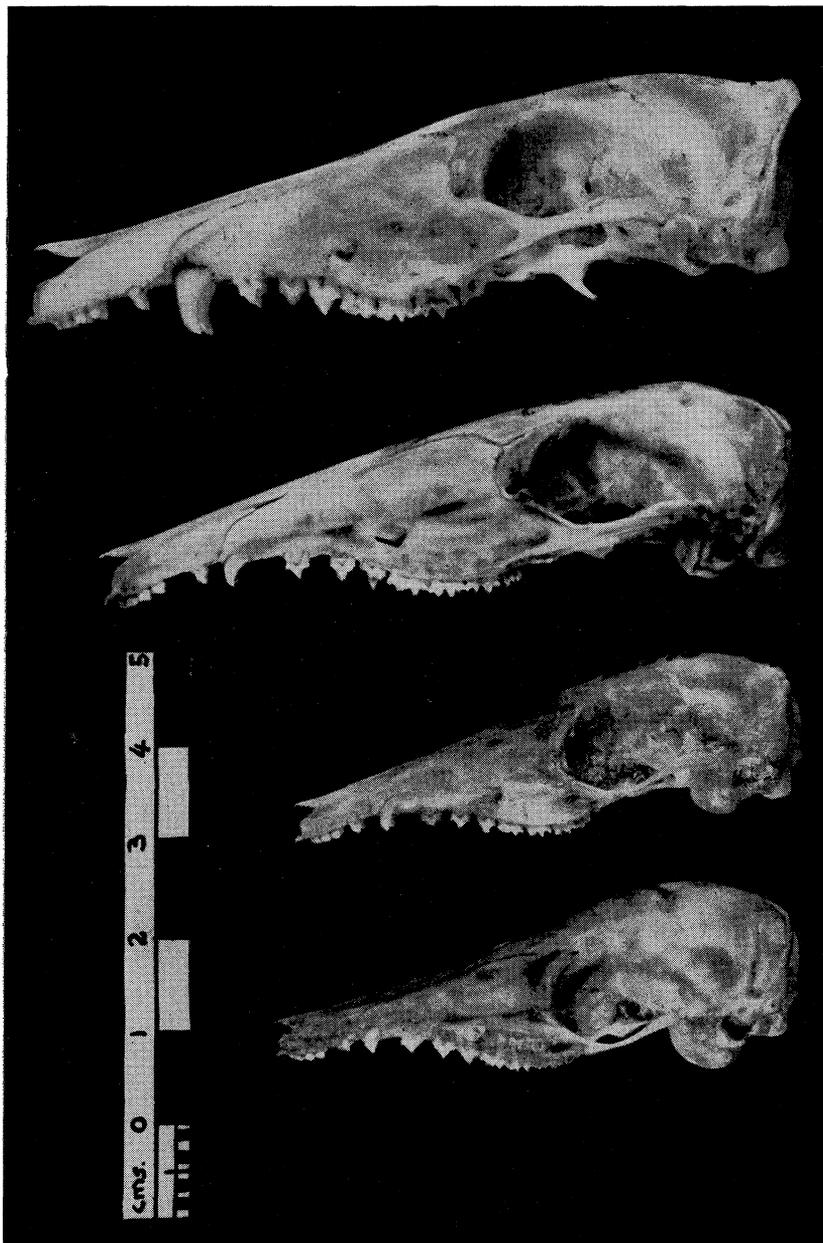
P. nasuta, male (M.8231), above, and female (M.8310), below. Lateral view of I⁵-P².
(C-P¹ diastema unusually small in male).



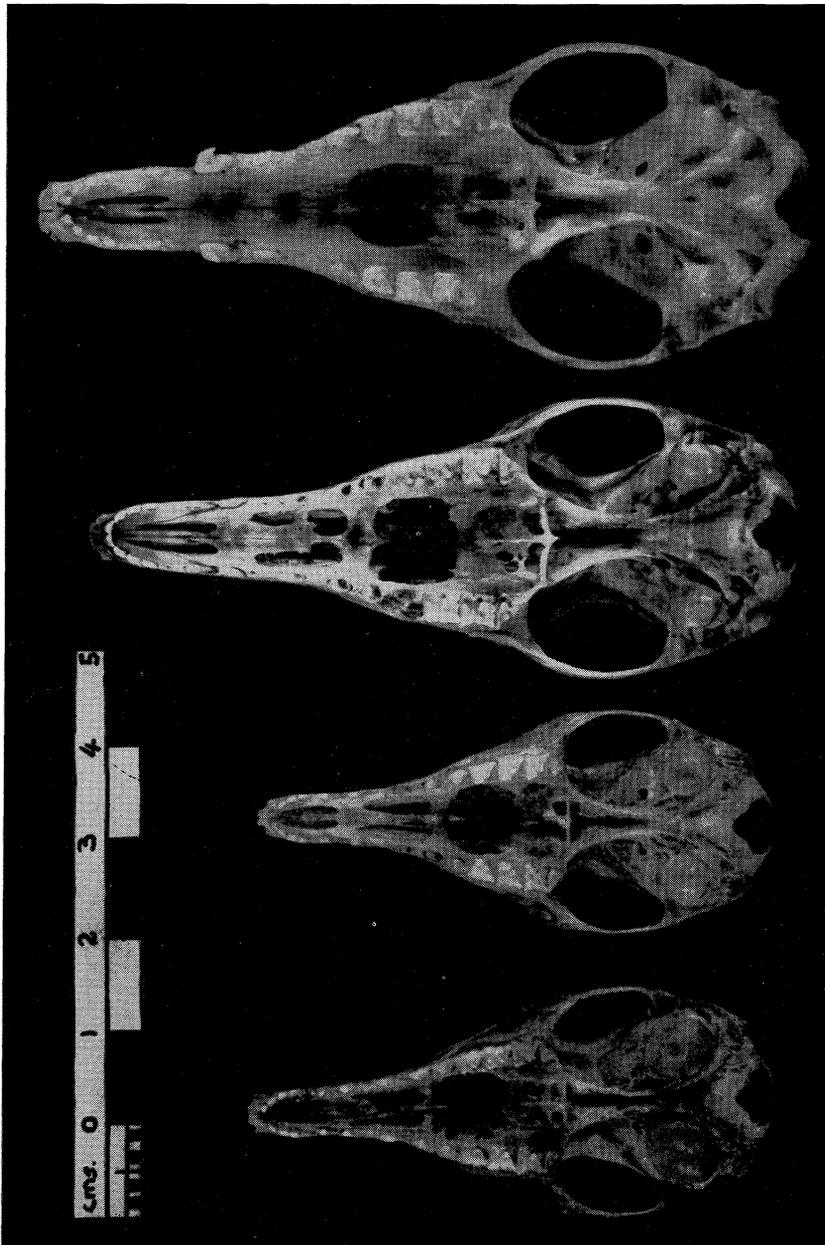
P. nasuta female (P.5), occlusal view of the lower teeth



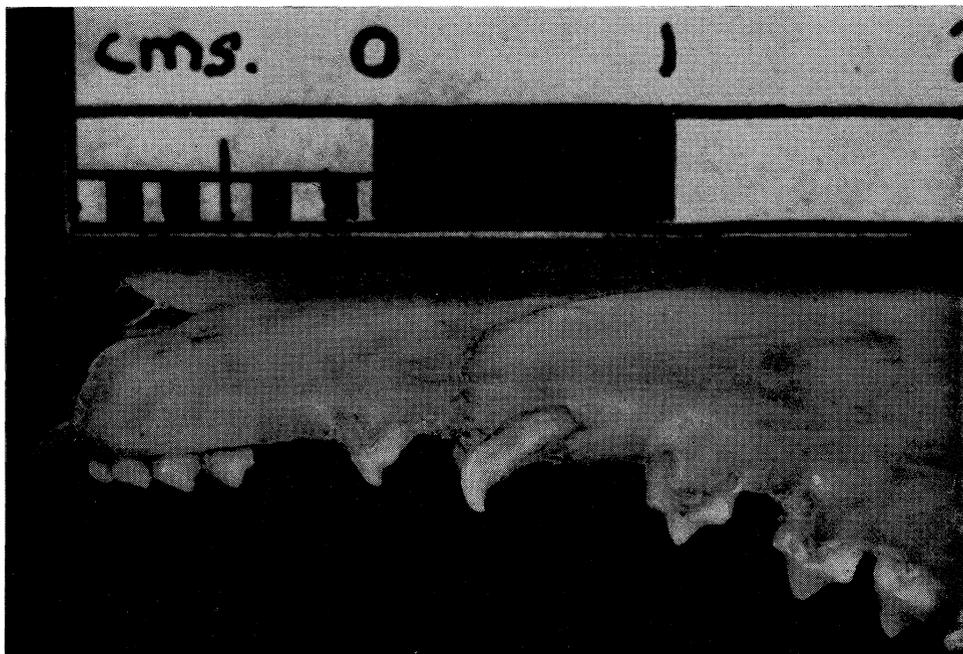
P. nasuta female (P.5), ventrolateral view of the occluded teeth



Crania, lateral views. From above downwards: *P. nasuta* male (M.8231); *P. gunnii* male (X.428); Dorre Island Western Australia, male (10576); Fisher, South Australia, sex unknown (M.2986).



Crania, ventral views. From above downwards: *P. nasuta* male (M.8231); *P. gunnii* male (X.428); Dorre Island, Western Australia, male (10576); Fisher, South Australia, sex unknown (M.2986).



P. gunnii female (MM.2), lateral view of anterior upper teeth