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SKULL AND TOOTH VARIATION IN THE GENUS *PERAMELES*

Part 2: Metrical Features of *P. nasuta*

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Plates 28-31. Fig. 1. Manuscript received, 10th January, 1966.

This paper deals with an analysis of the sex and locality differences in the metrical features of the skull and teeth of the species *P. nasuta*. It is the second part of an overall study dealing with the variation in the skull and teeth of bandicoots of the marsupial genus *Perameles*. Part 1 (Freedman, 1967) included an anatomical description of the skull and teeth of *P. nasuta*, followed by a discussion of the anatomical variations in certain of these features in the different species of the genus.

MATERIALS AND METHODS

For the present study, a total of 111 specimens of *P. nasuta* were examined, 54 males and 57 females. The localities of these specimens were given in Part 1 and the material was described there as coming from 3 regions east of the Great Dividing Range (Queensland, New South Wales and Victoria) along the east coast of Australia. For the present analysis, the Queensland group was initially further subdivided into a northern and a southern sub-group. This was done partly to make 4 approximately equal geographical areas but also because the most northern Queensland specimens (from Ravenshoe, Cairns district) have been described (e.g., Iredale and Troughton, 1934) as representing a separate sub-species (*P. nasuta pallescens*). However, it can be seen from Table 1, in which the various groups studied are listed by sex and locality, that the numbers of specimens, especially of the females, are very small in the North and South Queensland groups. Because of this, after being used in the tests for the assessment of sexual dimorphism, these two groups had to be combined again for the multivariate analysis tests used to investigate possible locality differences.

A number of features of the skull and teeth were assessed non-metrically for use in the ageing and sexing of the material and also for the description of skull and tooth anatomy. These include: the degree of development of the temporal, sagittal and lambdoid crests; whether the posterior palatine vacuities were single or double; the presence and size of additional vacuities (i.e., additional to the usual anterior and posterior pairs); the degree of synostosis between (i) the 4 parts of the occipital bone, (ii) the 2 frontal bones and (iii) the basi-occipital and basi-sphenoid bones; and finally, the state of eruption and the amount of attrition of the teeth, especially of the canines, last premolar teeth and all of the molars. Relevant data on these features are given in various parts of the whole study.

Specimens in which the full dentition was not yet present (i.e. juvenile or "immature" specimens) were only used for measurements of those teeth which were fully erupted. No skull dimensions or tooth row measurements of these specimens were included in the main metrical studies. Specimens with all teeth fully erupted were termed "mature" and, on tooth wear (of the molars, mainly M3), were classed as young adult, adult or old adult. Although analysis of the point was not practical in the present study, it is clear from work by other authors (discussed in Part I) that some relatively small size increase does occur after the last tooth has fully erupted.

Sexing (when not recorded) was done on the basis of canine structure and size. These differences are quite clear in *P. nasuta*, but become progressively less so in *Perameles gunnii* and the smaller species of the genus (see Part 1 and also Table 3 below).

The 27 skull and 50 tooth measurements used in this study were devised specifically for the project on the basis of those most commonly used in mammalian studies (e.g., Cockrum, 1957). Some additional measurements were added because of previous work (Kingsmill, 1962) and certain others because of the special anatomical features of the group. The 77 measurements used are defined in Appendix 1, which should be read in conjunction with Plates 28-31, which illustrate the main features of the skull and teeth of *P. nasuta*. As a number of the specimens used in the study were partially damaged, not all of the measurements could be taken on every specimen.

Most of the measurements were made with a dial caliper reading to 0.05 mm and readings were recorded to the nearest 0.1 mm. Certain awkward dimensions of the teeth were measured under a dissecting microscope with a calibrated eyepiece. The latter dimensions include: length of the last upper and lower premolars, buccal length of each upper molar and greatest length of each lower molar. These measurements were also recorded to the nearest 0.1 mm.

Because of the anatomical form of the various individual teeth, wear had to be considerable before its effects on the measurements taken were marked. Where this was the case, the relevant measurements were omitted. The effects of attrition were, as a rule, most marked on the molars, the upper teeth usually being affected before their lower equivalents and, in each, the length dimensions considerably before the breadths. Further, in the upper molars, the buccal length was affected before the lingual and, in the lower molars, the distal breadth before the mesial.

ANALYSIS

The skull and tooth data of *P. nasuta* were analysed to determine, firstly, whether sexual dimorphism was present and, secondly, whether groups of specimens from certain localities differed significantly in any particular measurements, or in the overall pattern of measurements.

(1) *Sex differences*

Sexual dimorphism in the metrical features of a species may take the form of differences between the male and the female variances, means, or both. Tables 2 (skull) and 3 (A-upper teeth, B-lower teeth) list the numbers of specimens, mean values and standard deviations for each of the 77 skull and tooth measurements of all of the males and of all of the females of *P. nasuta* studied. The standard deviations given in these Tables were found by regarding all of the males and all of the females as each forming a single, separate population.

For examining the metrical sex differences in *P. nasuta*, the male and female data were each treated as comprising separate samples from 4 localities (North Queensland, South Queensland, New South Wales and Victoria) in view of possible locality differences. For each measurement estimates of the overall male and the overall female variances were obtained by pooling the estimates from each of the 4 localities. When these pooled male and female variances were compared by an F test, significant results were obtained at the 1 per cent level in a considerable number of instances, but mainly in the skull measurements (Tables 2 and 3). Thus, in the skull, males and females of *P. nasuta* differ in their variances in 14/27 measurements at the 1 per cent level and in another 3 measurements at the 5 per cent level; in the teeth, the two sexes differ in 8/50 at the 1 per cent level and in a further 3 measurements at the 5 per cent level.

Examination of the differences between the variances of the 8 populations showed that, particularly in the case of the skull measurements, they were not in general proportional to the differences between the equivalent mean values. A simple transformation for stabilizing the variances was thus not available. Because of this (and the significant F test findings), the "t" test was not applicable for comparing the mean values of males and females of this species. The standard Aspin-Welch test (Pearson and Hartley, 1954) was thus modified to take account of the fact that each of the two means (male and female) was itself the average of 4 means based on varying numbers of observations. By this test, significant results were found at the 2 per cent level in 23/27 skull measurements and in 40/50 of the tooth measurements; at the 10 per cent level, a further 1 measurement was significant in the skull and 4 in the teeth. Males and females thus differ considerably in their mean values for measurements of both the skull and the teeth. Further, inspection of Tables 2 and 3 shows that in all 77 measurements, the male mean figure is greater than that for the female.

(2) *Locality differences*

The significant sex differences found clearly indicated that separate analysis of the two sexes was necessary for the study of possible locality differences. An examination of the data for the 4 male and the 4 female populations showed that the locality differences are not as marked as the sex differences. This can be seen in Tables 4 and 5 which include the mean values for 10 skull and 10 dental dimensions for males and females separately from the 4 localities. It was consequently apparent that some form of multivariate analysis was necessary in order to compare material of *P. nasuta* from different localities.

Ten dimensions were selected from the skull measurements and 10 from the dental measurements (Tables 4 and 5). These particular dimensions were chosen (a) for their representation of different parts and different types of measurements of the skull and teeth, (b) because inspection of the full table of basic data suggested that certain features might be of particular interest with regard to their distribution over the 4 localities and (c) for the technical requirement of obtaining completeness of data on a maximum number of specimens.

Using 4 localities, the numbers of specimens in each of the 8 populations which included either all of the 10 skull measurements or all of the 10 dental dimensions, were clearly too small to make comparisons meaningful. For the first set of multivariate tests, it was therefore decided to re-arrange the relevant material of each sex into 2 groups to obtain reasonable numbers of specimens for each comparison. North and South Queensland were added together to form a northern group and New South Wales and Victoria were combined to make a southern group. For each sex, the resulting 2 populations were then compared separately for the 10 skull and the 10 tooth measurements by Mahalanobis' D^2 (Rao, 1952). The results of the tests are listed in Table 6 and were all found to be significant at the 1 per cent level. The differences indicated by the D^2 values are greater in the males than in the females and, within each sex, are greater in the skull features than in those of the teeth.

As the above D^2 values were so clearly significant, the data were re-arranged into 3 groups (Queensland (Q)—in the north, New South Wales (N.S.W.)—central and Victoria (V)—in the south) and, using the same 2 sets of characters, the various D^2 values were calculated. The results of this examination (Table 7 and Fig. 1) are far less clear than those using 2 localities. From the female comparison, in both the skull and the teeth, it appears that there is a greater difference between N.S.W. and V than between Q and N.S.W.; the difference between Q and V is clearly the greatest in both cases. In the male comparison, in both the skull and the teeth, N.S.W. and V differ by less than Q and N.S.W.; in the teeth the Q and V comparison is only just the largest, whilst in the skull, the Q and V figure lies between those of the other two tests. Because of the small numbers involved, significance tests were not applied to these results.

Because of the nature of the foregoing results, there seemed little point in attempting a 4 locality multivariate comparison. Instead, as the question of a possible north-south clinal change in size was of interest, and inspection of the relevant data suggested that the northern specimens were very frequently larger than the southern, especially in the skull (e.g. Tables 4 and 5), an attempt was made to assess the size difference between the northern and southern specimens.

For this test, males and females of the north-south population subdivision were used and 3 measurements were selected (maximum length, cranial breadth and occipital height) which could be considered as illustrating overall cranial size. Standardized mean values were subtracted (north minus south) for each of the 3 characters in males and females separately and the sum of the differences was found to be positive for each sex. These sums of differences are proportional to the square roots of the size measurement (C^2_Q) of Penrose (1954). On being tested for significance by an appropriate "t" test which allows for intercorrelations, the male figure ($t = 2.16$, with 26 d.f.) was found to be significant at the 5 per cent level; the female figure ($t = 1.28$, with 28 d.f.) was not significant.

DISCUSSION

The F and Aspin Welch tests have clearly shown the degree of sexual dimorphism in the species *P. nasuta*. In their variances, the significant metrical differences are mainly restricted to certain of the measurements of the skull, tooth rows and canine teeth, but in their mean values, males were found to be significantly larger than females in almost all of the measurements of both the skull and teeth (Tables 2 and 3).

The D^2 comparisons between the northern and southern subdivisions of the species, revealed a clear, significant difference between the selected skull and tooth measurements in both the males and females. Differences are greater in the males than in the females and more marked in the skull measurements than in those of the teeth.

In the 3 population multivariate analysis, the D^2 values obtained did not suggest as clear cut inter-relationships (Fig. 1). Of the 3 populations, geographically the most northerly is Queensland (Q) and the most southerly Victoria (V), with New South Wales (N.S.W.) lying between the two. In the females, the Q-V value is greater than that of either of the other 2 comparisons in both the skull and the teeth and further, the N.S.W.-V values are greater than the Q-N.S.W. values in both cases. In the males, however, the Q-V value is slightly greater than either of the other 2 values in the tooth comparison, but in the skull comparison, it is less than the Q-N.S.W. value. Also, in this sex the Q-N.S.W. value is considerably greater than the N.S.W.-V value in both the skull and the tooth comparisons, which is the opposite of what was found in the females. Thus no general meaningful clinal pattern appears to emerge from the 3 population comparisons—quite possibly because of the small numbers of specimens available, particularly from Victoria (V). Because of these results and the similarily small numbers of specimens available from North Queensland, it was felt that the possibility of a metrical difference in that region did not merit further investigation on the present data.

In the comparison of overall cranial size between north and south based on 3 characters, it was found that the northern males and females were larger than their southern counterparts, but only in the case of the males was the difference found to be significant at the 5 per cent level. Although the observed female difference was less than the corresponding male figure, it is felt that this female difference is real and that the non-significant result obtained could have arisen from the relatively small numbers of specimens involved, particularly in the northern group (7). If this is so, it is of interest to note than an increase in size for *P. nasuta* from the cooler south to the subtropical north runs contrary to "Bergmann's Rule", which states that, within a warm-blooded vertebrate species, there should be a size decrease in a warmer climate. A number of exceptions to the "rule" have, however, been recorded (Rensch, 1959: pg. 43).

Examination of the full data for the 27 skull measurements for the north-south subdivision of the species supports an hypothesis that, in most instances skull dimensions are larger in the north than in the south in both sexes. However, study of equivalent data for the 50 tooth measurements, seems to indicate that, in both males and females, these measurements vary randomly with respect to whether the northern or the southern mean values are larger.

It therefore seems reasonable to conclude that the significant difference found for the 10 skull character comparison between northern and southern males of *P. nasuta* depends, at least in part, on a south to north size increase. It is felt that there is a similar size increase in the female skull measurements, but this has not been established conclusively. On the other hand, in the corresponding tooth comparisons, the significant differences found between north and south in both the males and the females would not appear to be attributable to a size increase in either direction.

SUMMARY

(1) The metrical features of the skulls and teeth of 111 specimens of *P. nasuta* from various localities on the east coast of Australia have been studied.

(2) In their mean values, males were found to be significantly larger than females for most of the 27 skull and 50 tooth measurements analysed, but, in their variances, the 2 sexes only differed in certain of the skull, tooth row and canine teeth dimensions.

(3) In a north-south subdivision of the species, significant differences were found, in both males and females, by multivariate analysis of selected groups of skull and tooth measurements. In a 3-fold subdivision of the species, no clinal pattern was apparent.

(4) The significant north-south difference in the skull measurements is, at least in the case of the males, partially the result of a size increase from south to north. The corresponding significant differences in the tooth measurements of both sexes do not appear to be attributable to a systematic, regional size increase.

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APPENDIX 1: MEASUREMENTS OF THE SKULL AND TEETH (PLATES 28-31)

In general, all of the measurements are maxima—length measurements being antero-posterior, breadths bilateral and heights dorso-ventral—but modified by the points and planes given in the various definitions. Where measurements are unilateral the left side was used, unless it was damaged. The special terms used below to facilitate the description of the measurements are modified from anthropological usage (Martin and Saller, 1957).

Cranium

(a) Length—

Maximum (Max.): Most anterior point on premaxillae (prosthion) to most posterior point of cranium (on lambdoid crest or occipital bone).

Basal (Bas.): Prosthion to most anterior point on foramen magnum (basion).

Condylo-basal (Cond.-Bas.): Prosthion to most posterior part of condyles.

Palatal (Pal.): Prosthion to most anterior point of posterior border of palate (on palatine bone).

Nasal (Nas.): Most anterior point on nasal bones to naso-frontal suture in dorsal midline (nasion).

Frontal (Fr.): Nasion to fronto-parietal suture in midline (bregma).

Parietal (Par.): Bregma to parieto-occipital suture in midline (lambda).

Premaxilla anterior to I^1 (Ant. to I^1): Prosthion to most posterior point on I^1 alveolus. (Taken to enable basal and palatal to be converted to basilar and palatar).

(b) Breadth—

Muzzle anterior to $\underline{C}$ (Ant. to $\underline{C}$): Between sides of muzzle, just anterior to $\underline{C}$ teeth.

Muzzle at M^2 (At M^2): Between the external alveolar margins of maxillae, at midpoints of M^2 teeth.

Interorbital (Int.-Orb.): Between the lacrimal margins of the orbits, just above the malar bones.

Minimum frontal (Min. Fr.): Minimum post-orbital constriction of cranial roof, on frontal bones.

Bizygomatic (Bizyg.): Between most lateral parts of outer surfaces of zygomatic arches.

Cranial (Cran.): At base of cranium, on subsquamosal foramina i.e. just posterior to zygomatic arches and anterior to lambdoid crests.

(c) Height—

Anterior to $\underline{C}$ (Ant. to $\underline{C}$): Alveolar margin anterior to $\underline{C}$ (below) to internasal suture (above), at right angles to dorsal muzzle profile.

Posterior to M^4 (Post. to M^4): Alveolar margin posterior to M^4 (below) to interfrontal suture (above), at right angles to dorsal muzzle profile.

Cranial (Cran.): Basion to bregma.

Occipital (Occip.): Basion to lambda (on occipital, above).

(d) Alisphenoid bulla (bulla)—

Length (L): Length axis runs anteromedially from external auditory meatus. (Measurement does not include otic bone).

Breadth (B): At right angles to length axis.

(e) Palatal vacuities (vacuities)—

Anterior palatal vacuity length (A.P.Vac.L.): Anteroposterior measurement of the longer of the pair.

Posterior palatal vacuity length (P.P.Vac.L.): As A.P.Vac.L.

Posterior palatal vacuity breadth (P.P.Vac.B.): Between lateral margins of the two vacuities.

Mandible

Maximum length (Max. L.): Most posterior part of one condyle to most anterior point of same half of mandible.

Length of Ramus (Ramus L.): Between the anterior and posterior borders of the ramus, from midpoint of posterior border and at right angles to ramus midline.

Breadth at M_2 (Br. at M_2): Thickness of body below M_2.

Height at M_2 (Ht. at M_2): Alveolar margin at middle of M_2 (above) to inferior border of mandible (below), at right angles to the alveolar margin.

Teeth

(a) Rows—

I1–M4—

Upper: More anterior labial surface of I^1 to distal surfaces of both M^4 teeth, all at level of alveolar margin.

Lower: Mesiolabial part of incisal tip of I_1 to distal surface of M_4 at alveolar margin.

Incisors—

Upper: Along incisal edge, from most mesiolabial point of I^1 to most distal point of I^4.

Lower: Along incisal edge, from most mesiolabial point of I_1 to most distal point of I_3.

C–M4—

Mesial surface of C to distal surface of M4, both at level of alveolar margin.

M–1 M4—

Most mesial part of M1 to most distal part of M4, both on enamel-covered crown.

(b) Canines—

Length (L): Mesiodistal measurement at alveolar margin.

Breadth (B): Labiolingual measurement at alveolar margin.

Height (H): Mesial edge at alveolar margin to incisal tip.

(c) Premolars—

Length (L)—

P1 and P2: Maximum mesiodistal measurement on enamel-covered crown.

P3: Most mesial point of tooth at alveolar margin to most distal point.

Breadth (B)—

Maximum buccolingual.

(d) Molars (All taken on enamel-covered crown)—

Upper—

Breadth (B): Maximum buccolingual.

Length, buccal (LB): Maximum mesiodistal on buccal half of tooth.

Length, lingual (LL): Maximum mesiodistal on lingual half of tooth.

Lower—

Breadth, mesial (BM): Maximum buccolingual of mesial triangle.

Breadth, distal (BD): Maximum buccolingual of distal triangle.

Length (L): Maximum mesiodistal.

Table 1

Numbers of specimens of *P. nasuta* studied, listed by sex and locality

	Males	Females	Total
N.Q.	8	5	13
S.Q.	12	4	16
N.S.W.	19	35	54
VICT.	15	13	28
TOTAL	54	57	111

Table 2

Comparison of *P. nasuta* male and female skull measurements (in mm)

Measurement	Males N	Males $\overline{X}$	Males SD	Females N	Females $\overline{X}$	Females SD	F Test	A-W Test
Cranium—								
(a) length—								
Max.	32	88.80	6.26	32	80.61	3.10	**	**
Bas.	30	80.97	5.34	30	73.12	2.80	**	**
Cond.-Bas.	32	85.02	5.64	30	77.17	2.78	**	**
Pal.	31	54.29	3.04	31	50.03	1.60	**	**
Nas.	34	39.68	2.45	30	36.00	1.56	*	**
Fr.	37	27.02	2.03	34	24.85	1.41	ns	**
Par.	36	16.08	1.84	34	14.53	1.00	**	**
Ant. to I^1	30	3.22	0.31	30	3.00	0.22	ns	**
(b) breadth—								
Ant. to C	34	9.17	0.70	34	8.03	0.50	ns	**
At M^2	36	21.21	1.13	33	19.36	0.79	*	**
Int.-Orb.	35	25.47	1.19	32	23.76	1.02	ns	**
Min. Fr.	37	14.17	0.45	34	13.90	0.49	ns	*
Bizyg.	32	34.79	2.36	30	30.97	1.22	**	**
Cran.	34	25.48	1.64	32	23.40	0.95	**	**
(c) height—								
Ant. to C	32	7.31	0.59	32	6.31	0.40	*	**
Post. to M^4	36	18.58	0.73	32	17.30	0.54	ns	**
Cran.	33	25.46	1.58	32	23.33	0.94	**	**
Occip.	33	19.87	1.56	32	17.93	0.83	**	**
(d) bulla—								
L	34	5.39	0.60	30	4.98	0.30	**	**
B	34	6.03	0.30	31	5.99	0.21	ns	ns
(e) vacuities—								
A.P. Vac. L.	32	9.19	0.87	32	8.25	0.46	**	**
P.P. Vac. L.	34	8.30	1.03	31	7.88	0.97	ns	ns
P.P. Vac. Br.	35	9.02	2.06	30	8.44	0.69	**	ns
Mandible—								
Max. L.	35	68.41	4.25	34	62.59	2.36	**	**
Ramus L.	35	9.53	0.98	34	8.03	0.73	ns	**
Br. at M_2	36	3.84	0.46	35	3.23	0.28	**	**
Ht. at M_2	36	7.23	0.75	35	6.15	0.70	ns	**

Significance level:

F Test ** = 1%, * = 5%, ns = not significant;

A-W Test ** = 2%, * = 10%, ns = not significant.

Table 3A

Comparison of *P. nasuta* male and female upper tooth measurements (in mm)

Measurement		Males			Females			F Test	A-W Test
		N	$\overline{X}$	SD	N	$\overline{X}$	SD		
I^1 —	M^4	32	48.19	2.34	31	44.43	1.02	**	**
I^1 —	I^4	39	5.97	0.26	42	5.87	0.32	ns	ns
C —	M^4	35	34.29	1.65	33	31.39	0.66	**	**
M^1 —	M^4	41	15.08	0.54	42	14.54	0.52	ns	**
C	L	32	4.19	0.58	33	2.32	0.28	**	**
	B	32	2.07	0.37	34	1.09	0.08	ns	**
	H	31	6.28	1.49	32	3.24	0.41	ns	**
P^1	L	47	2.87	0.15	53	2.78	0.12	ns	**
	B	53	1.13	0.07	55	1.06	0.07	ns	**
P^2	L	50	2.89	0.11	54	2.82	0.14	ns	**
	B	51	1.50	0.10	55	1.45	0.12	ns	*
P^3	L	32	3.98	0.37	33	3.52	0.28	ns	**
	B	40	2.18	0.17	41	2.03	0.18	ns	**
M^1	B	50	3.06	0.13	53	2.94	0.10	ns	**
	LB	43	4.26	0.16	52	4.12	0.15	ns	**
	LL	47	2.86	0.21	53	2.79	0.17	ns	ns
M^2	B	48	3.40	0.16	55	3.29	0.12	ns	**
	LB	45	4.20	0.13	53	4.10	0.16	*	**
	LL	48	2.82	0.17	54	2.76	0.15	ns	*
M^3	B	44	3.85	0.17	45	3.75	0.13	ns	**
	LB	46	4.47	0.17	44	4.42	0.15	ns	**
	LL	44	2.65	0.13	44	2.63	0.15	ns	ns
M^4	B	41	2.71	0.20	40	2.70	0.24	ns	ns
	LB	39	3.77	0.21	42	3.50	0.32	ns	**
	LL	41	1.54	0.14	41	1.52	0.14	ns	ns

Significance levels:

F Test ** = 1%, * = 5%, ns = not significant;

A-W Test ** = 2%, * = 10%, ns = not significant.

Table 3B

Comparison of *P. nasuta* male and female lower tooth measurements (in mm)

Measurement		Males			Females		F Test	A-W Test
		N	$\overline{X}$	SD	N	$\overline{X}$	SD		
I_1 — M_4		30	46.55	1.75	30	43.16	0.89	**	**
I_1 — I_3		46	4.94	0.30	46	4.84	0.25	ns	ns
C — M_4		33	36.73	1.85	34	33.39	0.78	**	**
M_1 — M_4		41	16.02	0.52	42	15.52	0.58	ns	**
C	L	31	4.11	0.68	35	2.42	0.29	**	**
	B	31	1.77	0.33	35	0.98	0.06	**	**
	H	31	4.27	0.93	35	2.60	0.31	**	**
P_1	L	49	2.93	0.13	51	2.80	0.13	ns	**
	B	52	1.03	0.06	53	0.96	0.06	ns	**
P_2	L	47	3.29	0.13	54	3.20	0.13	ns	**
	B	52	1.30	0.08	55	1.24	0.09	ns	**
P_3	L	35	4.10	0.37	36	3.66	0.34	ns	**
	B	40	1.52	0.12	42	1.42	0.10	ns	**
M_1	BM	49	2.03	0.09	53	1.96	0.07	ns	**
	BD	46	2.43	0.12	53	2.31	0.09	ns	**
	L	45	3.54	0.17	50	3.46	0.16	ns	*
M_2	BM	51	2.35	0.09	54	2.29	0.09	ns	**
	BD	49	2.63	0.13	54	2.55	0.09	*	**
	L	47	4.12	0.13	51	3.99	0.19	ns	**
M_3	BM	51	2.48	0.08	54	2.42	0.08	ns	**
	BD	49	2.58	0.14	51	2.47	0.11	ns	**
	L	47	4.30	0.14	53	4.17	0.17	ns	**
M_4	BM	46	2.38	0.11	45	2.35	0.10	ns	*
	BD	41	1.63	0.13	45	1.58	0.13	ns	**
	L	41	4.72	0.30	44	4.57	0.23	*	**

Significance levels:

F Test ** = 1%, * = 5%, ns = not significant;

A-W Test ** = 2%, * = 10%, ns = not significant.

Table 4

Mean values (in mm) of 10 selected skull measurements in 4 populations of *P. nasuta*

Measurement	Males				Females			
	N.Q. N = 6	S.Q. N = 6	N.S.W. N = 10	Vict. N = 6	N.Q. N = 3	S.Q. N = 4	N.S.W. N = 19	Vict. N = 4
Max. L.	90.97	92.90	86.05	88.72	79.57	82.90	80.19	79.85
Pal. L.	55.28	55.90	53.12	54.55	49.70	51.02	49.88	49.90
Fr. L.	28.00	28.90	25.74	27.02	25.07	25.85	24.41	25.88
Min. Fr. Br. ..	14.03	13.80	14.23	14.52	13.23	14.15	13.92	14.18
Cran. Br. ..	25.53	26.85	25.32	25.40	23.43	24.25	23.29	23.10
Mand. Ram. L. ..	10.00	10.37	9.36	9.22	8.17	8.35	8.06	7.25
Occip. Ht. ..	19.97	21.53	19.15	19.78	17.73	18.55	17.99	17.58
Mand. Ht. ..	7.85	7.93	6.74	7.22	6.13	6.70	6.05	5.75
P.P. Vac. L. ..	8.62	8.62	8.06	7.77	8.60	8.00	8.04	6.88
P.P. Vac. Br. ..	10.27	10.02	8.90	8.82	9.00	9.02	8.18	8.50

Table 5

Mean values (in mm) of 10 selected tooth measurements in 4 populations of *P. nasuta*

Measurement	Males				Females			
	N.Q. N = 4	S.Q. N = 7	N.S.W. N = 13	Vict. N = 9	N.Q. N = 4	S.Q. N = 4	N.S.W. N = 25	Vict. N = 5
P^1 L	3.00	2.94	2.88	2.84	2.92	2.75	2.81	2.70
P^2 B	1.58	1.57	1.49	1.46	1.65	1.45	1.49	1.34
M^1 LL	2.68	3.04	2.97	2.73	2.90	2.78	2.83	2.56
M^2 LL	2.75	2.96	2.93	2.73	2.82	2.82	2.83	2.58
M^3 B	3.95	3.94	3.80	3.77	3.70	3.78	3.78	3.60
P_1 L	3.08	2.96	2.89	2.79	2.90	2.75	2.81	2.76
M_1 BM	2.08	2.06	2.02	2.00	2.05	1.95	1.97	1.96
M_1 BD	2.42	2.50	2.43	2.42	2.38	2.35	2.32	2.24
M_4 BM	2.35	2.31	2.42	2.48	2.30	2.25	2.36	2.36
M_4 L	4.62	4.54	4.89	4.80	4.62	4.32	4.63	4.44

Table 6

D^2 values for 10 skull and 10 tooth measurements of *P. nasuta* males and females using 2 population subdivisions (north, Queensland; south, New South Wales and Victoria)

	Skull	Teeth
Males	14.9**	9.5**
Females	9.3**	6.5**

** Significant at 1% level.

Table 7

D^2 values for 10 skull and 10 tooth measurements of *P. nasuta* males and females using 3 population subdivisions

SKULL

Males			
	Q.	N.S.W.	Vict.
Q. ..		20.2	13.7
N.S.W. ..	8.8		9.6
Vict. ..	24.2	16.1	
Females			

TEETH

Males			
	Q.	N.S.W.	Vict.
Q. ..		11.2	12.1
N.S.W. ..	6.4		5.0
Vict. ..	35.1	19.9	
Females			

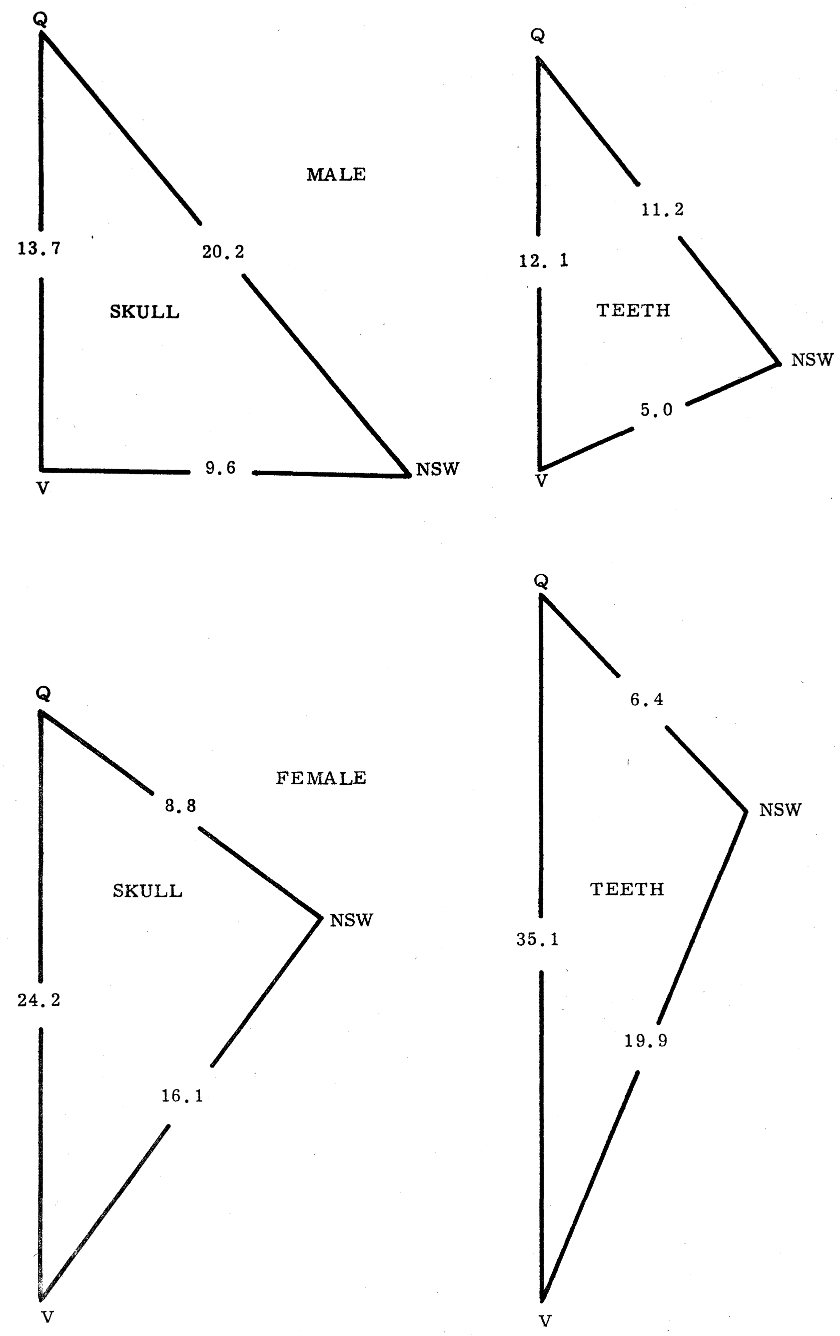


Fig. 1—Diagrams based on D^2 values for 10 skull and 10 tooth measurements of *P. nasuta* males and females using 3 population subdivisions. (Distances plotted are D values).

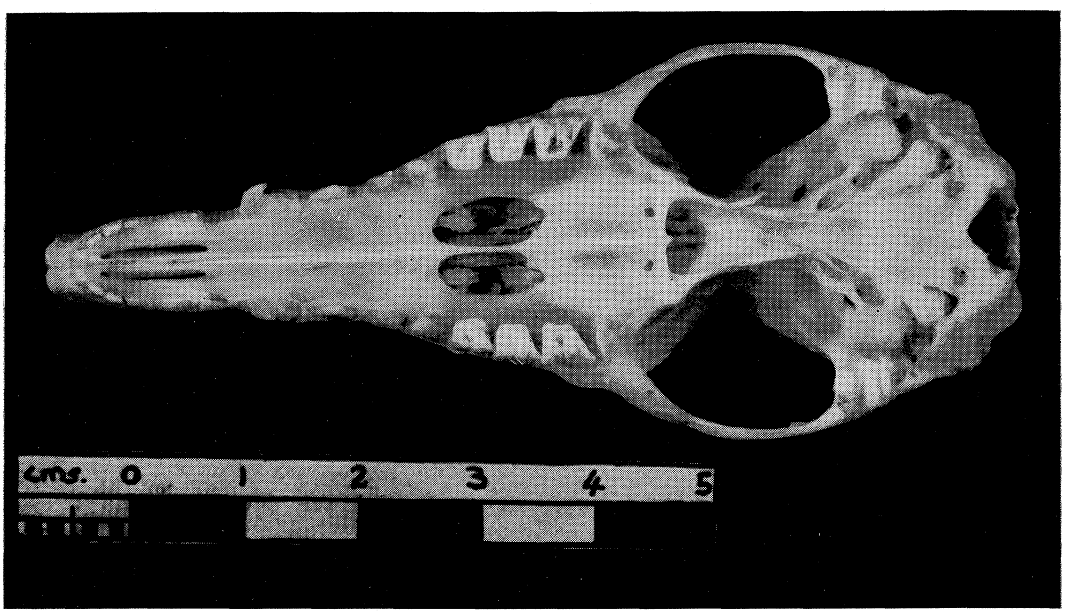
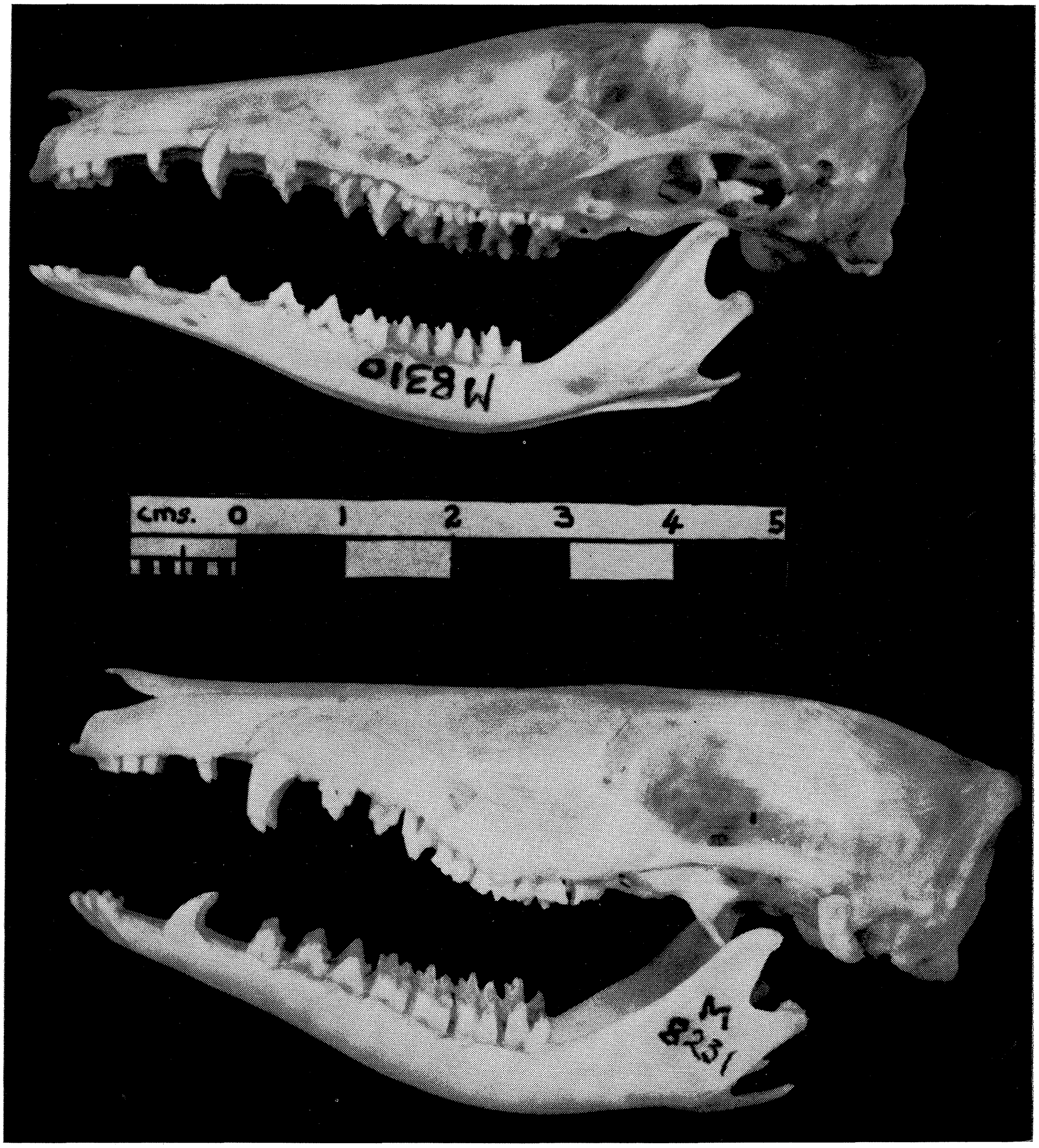
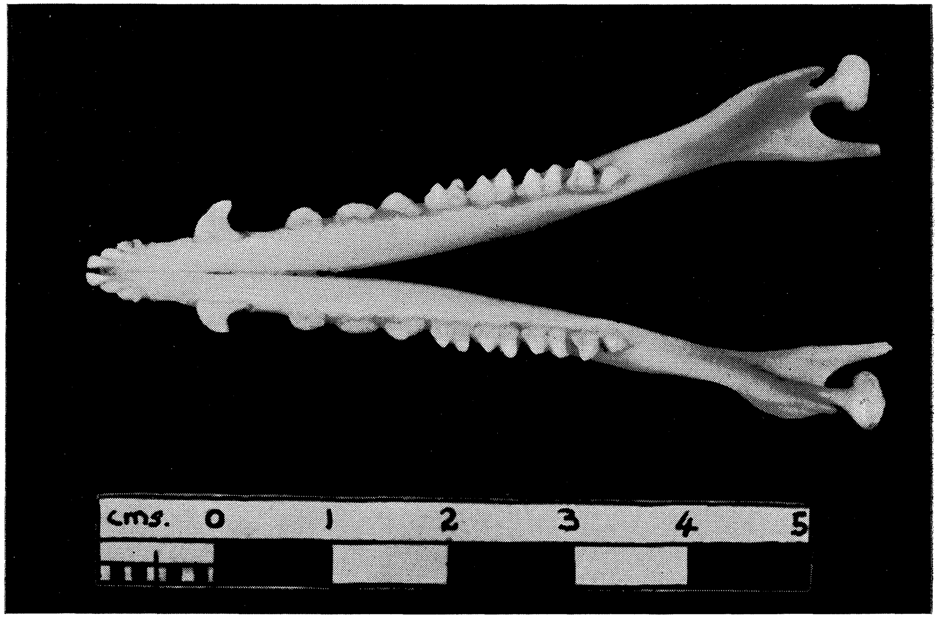


Plate 28 (above).—*P. nasuta*, male (M.8231). Cranium: norma dorsalis.
Plate 29 (below).—*P. nasuta*, male (M.8231). Cranium: norma basalis.



P. nasuta, male (M.8231) and female (M.8310). Skull: norma lateralis.



P. nasuta, male (M.8231). Occlusal view of mandible.

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