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SKULL AND TOOTH VARIATION IN THE GENUS *PERAMELES*

Part 3: Metrical Features of *P. gunnii* and *P. bougainville*

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Plates 32-34. Manuscript received, 10th January, 1966.

This paper is concerned with the intraspecific variation of the metrical features of the skull and teeth in the long-nosed bandicoot species *Perameles gunnii* and *Perameles bougainville*. Part 1 of the study (Freedman, 1967) listed the numbers of specimens and the source and localities of the material used and reviewed the taxonomy of the genus. A description of the anatomy of the skull and teeth of *P. nasuta* was also given and some of the anatomical differences found in *P. gunnii* and *P. bougainville* were discussed. Part 2 (Freedman and Joffe, 1967) described the system of measurements and ageing and sexing criteria used in the study and analysed the sex and locality variations in the metrical features of the skull and teeth of *Perameles nasuta*.

MATERIALS AND METHODS

Of the species *P. gunnii*, 51 specimens were available for study: 14 males and 9 females from south-western Victoria (possibly overlapping into south-eastern South Australia) and 12 males and 16 females from various parts of Tasmania. The *P. bougainville* material (43 specimens) consisted of: (i) *P. bougainville notina*—13 specimens from south-western South Australia and 4 from the adjacent south-eastern Western Australia, (ii) *P. bougainville bougainville*—5 specimens from Dorre and Bernier Islands in Shark Bay off the central part of the west coast of Western Australia, and (iii) 5 specimens widely scattered through the central western part of the continent, some or all of which come from an area in which *Perameles eremiana* is said to occur. In addition there was a group of 16 specimens (4 adult and 12 immature or juvenile) for which no localities were available, but which metrically and anatomically seemed clearly to belong in the *P. bougainville notina* group. The above material was all described more fully in Part 1 and the localities of the various specimens were plotted on a map. The definitions of the measurements taken, criteria for sex and age and other aspects of methods and technique were discussed in detail in Part 2.

ANALYSIS

1. *P. gunnii* (plate 32).

(a) Metrical characteristics and sexual dimorphism.

In Tables 1 and 2 the numbers of specimens used and the mean values and standard deviations of the 77 skull and tooth measurements of the males and females of the pooled *P. gunnii* specimens from Victoria and Tasmania are tabulated. In addition, the results of F tests, for comparison of the variances of the 2 sexes, and Aspin-Welch tests (Pearson and Hartley, 1954), for comparing the male and female mean values, are listed.

The comparisons of the male and female variances of the skull measurements have yielded significant F test values at the 1 per cent level, in the nasal length and maximum length and height at M_2 of the mandible; in the teeth, the measurements significant at this level are, $\underline{C}$—M^4, M^3 labial length, $\overline{C}$—M_4 and $\overline{C}$ length. At the 5 per cent level, maximum, basal, condylo-basal, and anterior to I^1 lengths, bizygomatic breadth and cranial height are significant in the skull; whilst in the tooth measurements I^1—M^4, $\underline{C}$ height, I_1—M_4 and M_4 distal breadth are significant. Because of these results and the fact that, in general, the differences between the variances were not proportional to the equivalent differences between the mean values, the Aspin-Welch test was employed instead of the t-test for comparing the mean values of the 2 sexes.

Examination of the male and female mean values for the skull measurements shows that, except for the breadth measurements of the cranium, the male mean values are larger than those of the females in almost every case (19/21) and in the remaining 2 they are equal. In the breadth measurements the females are larger in 4/6 measurements. However, when these differences are examined by Aspin-Welch tests, only the maximum length of the mandible is significant at the 2 per cent level and the palatal and nasal lengths and the alisphenoid bulla breadth at the 10 per cent level.

In the tooth measurements, the mean values for the canine teeth measurements of the 2 sexes are all significantly different by Aspin-Welch tests at the 2 per cent level; the male mean value being larger in each case. In the tooth row measurements, Aspin-Welch tests of the mean values for the 2 sexes of $\underline{C}$—M^4, I_1—M_4 and $\overline{C}$—M_4 are significantly different at the 2 per cent level and I^1—M^4 and I^1—I^4 are significantly different at the 10 per cent level, the male mean value being larger in each case. In the remaining tooth measurements, the male or female measurement is equally frequently larger (male larger in 17/36 and 2 equal to female). Amongst these remaining tooth measurements, the breadths of P^1, P^2, M^1 and M^2 differ significantly by Aspin-Welch tests at the 2 per cent level and M^4 buccal length, P_2 breadth, and P_3 breadth and M_2 length are significantly different at the 10 per cent level, the male mean being the larger in all except 2 instances (M^1 and M^2 breadths).

(b) Locality differences.

Because of the significant differences found in the sexual dimorphism analysis, males and females were compared separately to determine whether there were significant differences between the Victorian and Tasmanian samples of the species.

Examination of the mean values for the 27 skull measurements for the 2 localities showed that there appeared to be a size difference between the 2 populations. The Tasmanian sample was larger in 19/27 of the male mean measurements and in 22/27 of the female mean measurements. In Table 3, the mean values for males and females of Victoria and Tasmania are listed for the 10 measurements chosen for the *P. nasuta* intraspecific analysis in Part 2 and also for 2 alisphenoid bulla measurements (discussed later). When the various male and female pairs of values for these 12 measurements were compared by t-tests, only 5/24 differences were found to be significant—in males, frontal length, minimum frontal breadth and alisphenoid bulla breadth at the 5 per cent level; in the females, palatal length and minimum frontal breadth at the 1 per cent level. It was therefore felt that multivariate analysis was necessary to determine whether a significant difference could be established between the 2 populations.

Table 4 gives the results of Mahalanobis' D^2 (Rao, 1952) applied to the first 10 measurements listed in Table 3. The results for both males and females are not significant at the 5 per cent level. The test was then re-applied but this time substituting alisphenoid bulla length and breadth (Table 3) for posterior palatal vacuity length and breadth. This substitution was made because of the importance of alisphenoid bulla size in other species of the genus (e.g. *P. bougainville*). For this test, the D^2 value is significant for males at the 5 per cent level (Table 4). Relative to the number of observations, the use of 10 characters results in comparatively few degrees of freedom in the denominator of the F statistic used for testing significance of the D^2 value. Consequently a further D^2 analysis was carried out using only 5 measurements: maximum cranial length, cranial breadth, occipital height, mandibular ramus length and mandibular height. The D^2 values obtained in this analysis are not significant at the 5 per cent level (Table 4). Finally, investigation of the size difference between the 2 populations of *P. gunnii*, using maximum cranial length, cranial breadth and occipital height (as was done in *P. nasuta*), gave a non-significant result.

When the mean values of the 50 tooth measurements of *P. gunnii* for Victoria and Tasmania were compared, it was found that, in the males, 25/50 were larger in the Tasmanian sample and 3 equal in the 2 samples; in the females, 34/50 were larger in the Tasmanian group and 3 again equal. There appeared to be no clear pattern in these results, although all of the mean tooth row measurements were larger in the Tasmanian sample in both males and females, but it was felt that this mainly reflected the greater palatal length in that group. Because of these findings, and the negative results for the skull measurements, no multivariate analysis of tooth measurements in the two examples was made.

2. *P. bougainville* and the central group (plates 33 and 34).

In these specimens, because of the paucity of material, only one sample, *P. bougainville notina* was examined for sexual dimorphism. In Table 5, the results of t-tests on the canine teeth of males and females of this group are listed. The male mean values are larger in 5/6 instances, but only one of the 6 comparisons is significant at the 5 per cent level. It would seem from these results that the 2 sexes differ very little in the measurements of these teeth, which in the previously examined species of the genus differed significantly. For this reason, and because of the small numbers of specimens available, the 2 sexes were considered together in the rest of the analysis.

The samples of *P.b. notina* and *P.b. bougainville* were next compared. Tables 6 and 7 list the numbers of specimens and mean values for the skull and tooth measurements of these 2 samples. Because of the small number of *P.b. bougainville* specimens available, only a pooled standard deviation for each measurement in the 2 samples has been included in the Tables and these values have been used for calculating the t-test values listed. In the skull measurements (Table 6), the *P.b. notina* mean value is larger than that for *P.b. bougainville* in 21/27 instances, but only 4 of these are significant by t-tests at the 1 per cent level and a further 5 at the 5 per cent level. Of interest are the facts that the alisphenoid bulla length and breadth measurements are both significantly different at the 1 per cent level and 3/6 cranial breadth and 2/4 cranial height measurements are also significantly different at either the 1 per cent or 5 per cent level. All of these mean measurements are larger in *P.b. notina.*

In the teeth (Tables 7A and B), the *P.b. notina* mean measurements are larger in 29/51 instances. However, of the 7 measurements which differ significantly by t-tests in the 2 samples at the 1 per cent level, only 4 are larger in *P.b. notina* and of the 4 which differ at the 5 per cent level, 3 are larger in that species. The single striking difference between the 2 groups highlighted by the t-tests of the tooth measurements is the longer length of I^5 in *P.b. bougainville*, which is significantly different in the 2 groups at the 1 per cent level.

The juvenile/immature group of 12 specimens from uncertain localities, the adult group of 4 specimens also from uncertain localities, and the central group of 5 specimens, were next compared with *P.b. notina* and *P.b. bougainville.* Inspection of the mean values for the tooth measurements of the juvenile/immature group, and the skull and tooth mean values of the uncertain adult group and the central group, suggested that, in the first 2 cases there was a close similarity to *P.b. notina,* while in the 3rd this was not clear cut. Because of their immaturity, the skull measurements of the juvenile/immature group could not be used, but study of the individual alisphenoid bullae of the group indicated that, although not yet at maximum size, they were similar in size to those of *P.b. notina.*

A one-way analysis of variance was next performed on the five populations for each of 6 selected measurements. (See Table 8 for the numbers of specimens and mean values of the 3 additional groups.) Pairwise comparisons of the means were then carried out by Scheffe's S method of multiple comparisons (Scheffe, 1959) and the results are given in Table 9. When comparing *P.b. notina* and *P.b. bougainville* by this method there is a significant difference at the 1 per cent level for alisphenoid bulla length and breadth and the length of I^5. The remaining comparisons are not significant. It should be pointed out that the residual variances from the analyses of variance were all larger than the corresponding variances as estimated in Tables 6 and 7 and this indicates that the additional data were more heterogeneous than that of *P.b. notina* and *P.b. bougainville.* It also explains why the occipital height difference between *P.b. notina* and *P.b. bougainville* is significant in terms of the t-test (Table 6), but is not significant in the multiple comparison table (Table 9).

Of the juvenile/immature group, only I^5 length could be compared to the other 4 groups by Scheffe's S method. In these comparisons (Table 9), a significant difference to the *P.b. bougainville* group is found at the 1 per cent level and the other comparisons are all not significant. For the uncertain adult group, all of the 6 selected means could be compared pairwise by Scheffe's S method. Table 9 shows that this group differs significantly from the *P.b. bougainville* group in 3 measurements (alisphenoid bulla length at the 1 per cent level; alisphenoid bulla breadth and occipital height at the 5 per cent level; I^5 length falls just below the 5 per cent level) and only differs from the *P.b. notina* group in one measurement (occipital height) at the 5 per cent level. Despite the apparent affinity of both of these uncertain groups to the *P.b. notina* sample, it was felt advisable not to include them with that group in the statistical analyses.

Still using Scheffe's S method, the group of 5 specimens from the western part of Central Australia is found only to differ from the *P.b. notina* group in maximum cranial length at the 5 per cent level and not to differ significantly in any of the 6 measurements to the uncertain adult group; compared to the *P.b. bougainville* sample, the central group differs in alisphenoid bulla length and breadth at the 1 per cent level and also in occipital height at the 5 per cent level (Table 9). The affinity of this group thus appears to be greater to the *P.b. notina* than to the *P.b. bougainville* group. However, the probable heterogeneity of the group was mooted in Part 1 and for this reason the individual measurements of 3 of the 5 specimens for the 6 features discussed are listed in Table 10. M. 2630 and M. 1575 are juveniles and only a few tooth measurements are known (M. 1575: I^5 length = 0·9 mm). The possible affinities and implications of these specimens will be taken up in the discussion.

DISCUSSION

Comparisons between the male and female skull and teeth measurements of *P. gunnii* have revealed mean size differences in the skull, tooth row, and canine teeth measurements. The male mean measurements were found to be the larger in the majority of cases, but in some, mainly in the breadth measurements of the cranium, the female mean measurements were larger. In the remaining measurements of the teeth, the male or female mean dimension was larger with about equal frequency. However, few of the above differences (4 in the skull and 19 in the teeth) were significant by the Aspin-Welch test, only the tooth rows and canine teeth showing consistent sexual dimorphism. These results contrast with those found in Part 2 for *P. nasuta*, where almost every male mean value was higher than the female equivalent and where, further, most of the differences were significant by the Aspin-Welch test at the 2 per cent level. In their variances, 9 differences in the skull and 8 in the teeth were significantly different between the sexes of *P. gunnii* by F tests. The equivalent figures for *P. nasuta* were 17 for the skull and 11 for the teeth. Thus, in mean values and variances, considerably less difference was found between the sexes in *P. gunnii* than in *P. nasuta*.

Separate comparisons of *P. gunnii* males and females from Tasmania and Victoria showed the Tasmanian samples to have the larger mean values in the majority of skull measurements. However, of 24 skull differences (12 male and 12 female) examined by t-tests, only 5 gave significant t-values. In the tooth measurements the 2 samples have larger mean values with about equal frequency. Multivariate analysis of various groupings of skull measurements only gave a significant D^2 value in one male comparison. It was suggested above that the lack of significance in the multivariate analyses might in part be due to the relatively few degrees of freedom in the denominator of the F statistic used for testing the D^2 value, but it is never the less clear that the mainland and island populations do not differ greatly, certainly not as much as the northern and southern subdivisions of *P. nasuta* studied in Part 2. It is doubtful whether the northern and southern *P. nasuta* populations merit taxonomic subdivision and there would thus seem to be no support from the present study for making a subspecific distinction between the Tasmanian and Victorian *P. gunnii* populations, despite the geographical isolation in the latter case.

Sexual dimorphism in the skull and tooth measurements of *P. bougainville* is probably of a very low order and in the small samples available was scarcely detectable. It is of interest to note the decrease in sexual dimorphism in the genus from *P. nasuta* to *P. gunnii* to *P. bougainville* which parallels a general size decrease.

In the comparisons of the skull measurements of *P.b. notina* with those of *P.b. bougainville* the situation appears similar to that found when comparing the Victorian and Tasmanian samples of *P. gunnii*. Whilst the *P.b. notina* mean measurements are mostly larger than those of *P.b. bougainville*, relatively few of the differences are significant by the t-test. In the tooth measurements, only the I^5 length appears to be of interest. The differences found between the 2 groups become of taxonomic importance when their pattern and magnitude are examined. The larger alisphenoid bulla measurements and the shorter length of I^5 in *P.b. notina* are significantly different from those of *P.b. bougainville* at the 1 per cent level and the magnitude of these differences is such that on the alisphenoid bulla alone one can separate virtually every one of specimens included in these 2 samples. Further, these differences are re-inforced by a number of significant differences in the cranial breadth and height measurements. This degree of difference is clearly adequate to justify subspecific separation of the 2 groups, as the 75 per cent rule is generally considered stringent enough for subspecific differentiation (Mayr, Linsley, and Usinger, 1953). Specific differentiation of the 2 groups might even be supported, particularly if differences in features other than the skull and teeth are suitably documented. Examination of such features and samples from intervening regions are, however, required before deciding on the most satisfactory taxonomic status for the 2 populations—especially as no mainland specimens of *P.b. bougainville* were available for study.

The juvenile/immature and adult groups of specimens of uncertain localities, anatomically and metrically appear to belong in the *P.b. notina* group. Further, certain scraps of information about locality and taxonomy which accompany some of them, suggest that they probably came from South Australia. However, particularly in view of the similarity found between the central group of specimens and the *P.b. notina* group, it would seem that this material cannot be utilized further at this stage in discussions of the taxonomy of the long-nosed bandicoots.

Finally there remains the group of 5 specimens from the western part of central Australia. This material is clearly inadequate for any definitive assessment of *P. eremiana* or other population(s) linking the 2 samples, *P.b. notina* and *P.b. bougainville*, discussed above, but even the few specimens available indicate certain possibilities. The most northern of these specimens, M. 2630 and its mother M. 2629 (from Well 35, Canning Stock Route, Western Australia) and also C. 213 (labelled "Central Australia"), in their general dimensions and on I^5 length and alisphenoid bulla length and breadth could readily be referred to *P.b. notina*. Of the remaining 2 specimens, M. 1575 is an immature specimen from Gahanda, Western Australia. It has a short I^5 tooth, similar to that of *P.b. notina*, but its alisphenoid bulla, although not yet fully developed, appears to be of the small variety, as seen in *P.b. bougainville*. The last specimen (S. 1753), for which there is some doubt about exact locality, is larger even than the *P.b. notina* specimens in the majority of its measurements. In addition, it has an I^5 length similar to that of *P.b. bougainville* and an alisphenoid bulla comparable in size to that of *P.b. notina*. These latter 2 specimens thus suggest the possible presence of one or more populations in central Australia, which differ from both *P.b. notina* and *P.b. bougainville*.

SUMMARY

(1) 51 male and female specimens of *P. gunnii* from Victoria and Tasmania have been studied for metrical features of the skull and teeth.

(2) Sexual dimorphism in *P. gunnii* is present in the skull, tooth row, and canine teeth measurements, but not in the other teeth. However, only in the tooth rows and canine teeth are the differences consistently significant.

(3) The Tasmanian sample of *P. gunnii* is larger than the Victorian sample in most of the mean skull measurements, but few of these differences reach a level of significance. Subspecific differentiation of the 2 samples is not merited on this data.

(4) 43 male and female specimens of *P. bougainville* (including 5 specimens which came from *P. eremiana* localities) were also examined for metrical features of the skull and teeth.

(5) The sexed material of *P. bougainville* was very limited, but there appears to be little sexual dimorphism in the skull and tooth measurements.

(6) The *P.b. notina* sample from South Australia differed from the *P.b. bougainville* sample from the islands off the central coast of Western Australia in their generally larger mean measurements. The significantly different alisphenoid bulla and I^5 length, the former being larger and the latter smaller in the *P.b. notina* group, warrant at least a subspecific separation of this sample from the *P.b. bougainville* specimens.

(7) The need for further material, especially from central and western Australia, is indicated by a few scattered specimens from these areas which suggest possibly extensive limits for the range of *P.b. notina* and perhaps the presence of one or more other population(s).

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Table 1.—Comparison of *P. gunnii* male and female skull measurements (in mm)

Measurement	Males			Females			F test	A-W test
	N	$\overline{X}$	SD	N	$\overline{X}$	SD		
Cranium—								
(a) length—								
Max.	19	77·12	3·77	16	75·59	2·39	*	ns
Bas.	18	69·82	3·69	16	68·70	2·25	*	ns
Cond.-Bas.	18	74·05	3·65	16	72·86	2·25	*	ns
Pal.	18	48·23	2·31	15	47·02	1·83	ns	*
Nas.	17	35·76	2·43	18	34·78	1·34	**	*
Fr.	19	24·90	1·76	18	24·68	1·26	ns	ns
Par.	19	13·06	0·65	17	13·00	0·56	ns	ns
Ant. to I^1	19	2·50	0·27	18	2·44	0·18	*	ns
(b) breadth—								
Ant. to $\underline{C}$	18	8·02	0·55	18	8·03	0·47	ns	ns
At M^2	18	18·76	0·86	18	18·92	0·74	ns	ns
Int.-Orb.	18	26·02	1·22	18	26·18	1·00	ns	ns
Min. Fr.	19	14·75	0·64	18	14·97	0·67	ns	ns
Bizyg.	16	31·37	1·50	16	31·30	0·83	*	ns
Cran.	18	23·16	0·86	16	22·91	0·69	ns	ns
(c) height—								
Ant. to $\underline{C}$	17	6·15	0·46	17	6·13	0·31	ns	ns
Post. to M^4	18	16·91	0·66	19	16·60	0·76	ns	ns
Cran.	18	23·07	1·07	16	22·84	0·63	*	ns
Occip.	18	16·93	0·80	16	16·77	0·56	ns	ns
(d) bulla—								
L	19	5·81	0·48	18	5·63	0·33	ns	ns
B	19	6·54	0·34	18	6·38	0·22	ns	*
(e) vacuities—								
A.P. Vac. L.	17	9·75	0·85	18	9·53	0·82	ns	ns
P.P. Vac. L.	18	9·55	0·72	17	9·14	0·82	ns	ns
P.P. Vac. Br.	17	9·94	0·86	17	9·94	0·98	ns	ns
Mandible—								
Max. L.	21	61·48	3·41	19	59·58	1·74	**	**
Ramus L.	21	6·41	0·44	19	6·27	0·30	ns	ns
Br. at M_2	21	2·82	0·22	20	2·82	0·17	ns	ns
Ht. at M_2	21	6·01	0·73	20	5·75	0·36	**	ns

Significance level: F test ** 1 per cent, * = 5 per cent, ns = not significant;
A-W test ** 2 per cent, * = 10 per cent, ns = not significant.

Table 2A.—Comparison of *P. gunnii* 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		19	43·53	1·90	18	42·63	1·22	*	*
I^1—I^4		19	6·17	0·26	19	6·03	0·25	ns	*
$\underline{C}$—M^4		19	31·80	1·26	19	31·02	0·61	**	**
M^1—M^4		19	14·55	0·40	21	14·47	0·45	ns	ns
$\underline{C}$	L	19	2·76	0·35	20	2·30	0·26	ns	**
	B	19	1·06	0·07	20	0·88	0·08	ns	**
	H	19	3·08	0·49	20	2·55	0·31	*	**
P^1	L	23	2·80	0·14	25	2·78	0·11	ns	ns
	B	23	0·96	0·05	25	0·94	0·06	ns	**
P^2	L	24	2·82	0·15	25	2·85	0·12	ns	ns
	B	24	1·44	0·11	25	1·40	0·10	ns	**
P^3	L	18	3·36	0·24	22	3·33	0·30	ns	ns
	B	20	2·13	0·15	20	2·13	0·12	ns	ns
M^1	B	21	2·92	0·09	25	3·00	0·08	ns	**
	LB	24	4·56	0·22	24	4·60	0·19	ns	ns
	LL	23	2·64	0·14	24	2·67	0·14	ns	ns
M^2	B	22	3·39	0·10	25	3·47	0·09	ns	**
	LB	24	4·04	0·14	24	4·01	0·15	ns	ns
	LL	24	2·63	0·12	25	2·65	0·66	ns	ns
M^3	B	20	3·79	0·11	23	3·82	0·11	ns	ns
	LB	22	3·80	0·26	24	3·66	0·84	ns	ns
	LL	21	2·46	0·19	24	2·52	0·15	**	ns
M^4	B	20	2·79	0·24	22	2·71	0·24	ns	ns
	LB	21	3·13	0·22	22	3·05	0·19	ns	*
	LL	21	1·43	0·12	22	1·45	0·13	ns	ns

Significance level: F test ** = 1 per cent, * = 5 per cent, ns = not significant;
A-W test ** = 2 per cent, * = 10 per cent, ns = not significant.

Table 2B.—Comparison of *P. gunnii* 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	19	42·04	1·84	20	41·25	1·40	*	**
$\underline{I_1}$ —I_3	22	5·10	0·27	24	5·10	0·24	ns	ns
$\overline{C}$ —M_4	20	33·03	1·28	20	32·28	0·84	**	**
M_1—M_4	21	15·38	0·37	23	15·33	0·48	ns	ns
$\overline{C}$ L	20	2·30	0·36	20	1·95	0·19	**	**
B	20	0·95	0·09	20	0·84	0·09	ns	**
H	19	2·14	0·26	20	1·92	0·22	ns	**
P_1 L	26	2·76	0·11	25	2·73	0·12	ns	ns
B	26	0·90	0·04	25	0·89	0·06	ns	ns
P_2 L	26	3·23	0·11	25	3·28	0·14	ns	ns
B	26	1·15	0·05	25	1·12	0·07	ns	*
P_3 L	21	3·63	0·36	20	3·67	0·26	ns	ns
B	21	1·45	0·08	22	1·40	0·09	ns	*
M_1 BM..	24	2·02	0·07	25	2·01	0·05	ns	ns
BD	24	2·45	0·10	25	2·47	0·09	ns	ns
L	23	3·71	0·11	25	3·67	0·15	ns	ns
M_2 BM..	25	2·38	0·09	25	2·38	0·08	ns	ns
BD	24	2·77	0·12	25	2·78	0·11	ns	ns
L	23	4·16	0·13	25	4·11	0·17	ns	*
M_3 BM..	26	2·40	0·07	25	2·39	0·07	ns	ns
BD	25	2·52	0·09	24	2·56	0·12	ns	ns
L	24	4·14	0·14	25	4·12	0·13	ns	ns
M_4 BM..	22	2·15	0·10	24	2·16	0·10	ns	ns
BD	22	1·50	0·15	24	1·52	0·10	*	ns
L	21	3·99	0·16	24	4·02	0·18	ns	ns

Significance level: F test ** = 1 per cent, * = 5 per cent, ns = not significant;
A-W test ** = 2 per cent, * = 10 per cent, ns = not significant.

Table 3.—Mean values (in mm) of 12 selected skull measurements in 2 populations of *P. gunnii*

Measurement	Males		Females	
	Victoria N = 7	Tasmania N = 10	Victoria N = 6	Tasmania N = 10
Max. L.	75·31	78·17	74·48	76·46
Pal. L.	46·99	48·76	45·67	47·92
Fr. L.	23·93	25·74	24·12	25·11
Min. Fr. Br.	14·30	14·97	14·43	15·41
Cran. Br.	23·01	23·26	22·70	23·04
Occip. Ht.	16·86	16·98	16·50	16·93
Mand. Ram. L.	6·46	6·24	6·27	6·45
Mand. Ht.	6·11	5·85	5·87	5·84
P.P. Vac. L.	9·73	9·31	8·92	9·43
P.P. Vac. Br.	9·87	9·89	10·15	9·96
Bulla L.	5·81	5·81	5·65	5·61
Bulla B.	6·40	6·72	6·27	6·40

Table 4.—D^2 values for skull measurements of *P. gunnii* males and females, using samples from Victoria and Tasmania

Measurements	Males N = Vict.—7; Tasm.—10	Females N = Vict.—6; Tasm.—10
10 measurements, incl. vacuity ..	16·6	19·1
10 measurements, incl. bulla ..	54·6*	23·2
5 measurements	3·4	1·2

* Significant at 5 per cent level.

Table 5.—Comparison by t-tests of male and female canine teeth measurements in *P. bougainville notina*

Measurement		t-value	d.f.
$\underline{C}$	L	0·90	7
	B	1·73	8
	H	0·95	7
$\overline{C}$	L	3·28*	7
	B	0·41	8
	H	0·09	7

* Significant at 5 per cent level.

Table 6.—Comparison of *P.b. notina* and *P.b. bougainville* skull measurements (in mm)

Measurement	*P.b. notina* N	*P.b. notina* $\overline{X}$	*P.b. bougainville* N	*P.b. bougainville* $\overline{X}$	Pooled SD	t test
Cranium—						
(a) length—						
Max.	9	58·82	1	56·60	1·22	ns
Bas.	10	52·98	1	50·80	1·06	ns
Cond.-Bas. ..	10	56·11	1	54·30	1·11	ns
Pal.	7	31·57	2	33·65	0·88	ns
Nas.	9	24·39	2	23·55	0·82	ns
Fr.	11	19·57	2	18·40	0·62	*
Par.	10	12·50	2	12·95	0·94	ns
Ant. to I¹	11	2·28	2	2·25	0·16	ns
(b) breadth—						
Ant. to C ..	11	5·58	2	5·55	0·62	ns
At. M²	10	14·12	2	14·15	0·32	ns
Int.-Orb.	7	21·24	2	19·50	0·50	**
Min. Fr.	11	13·14	2	11·70	0·64	*
Bizyg.	8	24·70	2	24·00	0·31	*
Cran.	10	19·14	2	18·00	0·69	ns
(c) height—						
Ant. to C ..	10	4·35	2	4·30	0·13	ns
Post. to M⁴ ..	11	13·50	2	13·00	0·25	*
Cran.	10	19·57	1	19·00	0·80	ns
Occip. ..	10	14·28	1	13·40	0·19	**
(d) bulla—						
L	11	8·05	2	5·40	0·39	**
B	11	6·96	2	5·75	0·27	**
(e) vacuities—						
A.P. Vac. L. ..	6	6·53	2	5·80	0·31	*
P.P. Vac. L. ..	7	8·17	1	7·20	0·39	ns
P.P. Vac. Br. ..	7	7·21	2	7·25	0·54	ns
Mandible—						
Max. L.	11	44·50	2	44·05	1·19	ns
Ramus L.	11	4·51	2	4·70	0·22	ns
Br. at M_2	11	2·10	2	2·00	0·16	ns
Ht. at M_2	11	3·98	2	4·10	0·19	ns

Significance level: t-test ** = 1 per cent, * = 5 per cent, ns = not significant.

Table 7A.—Comparison of *P.b. notina* and *P.b. bougainville* upper tooth measurements (in mm)

Measurement		*P.b. notina* N	*P.b. notina* X̄	*P.b. bougainville* N	*P.b. bougainville* X̄	Pooled SD	t test
I¹—M⁴		12	31·38	2	31·10	0·92	ns
I¹—I⁴		13	4·43	5	4·36	0·16	ns
C—M⁴		12	23·14	2	23·15	0·70	ns
M¹—M⁴		13	10·80	2	10·10	0·30	**
C	L	13	1·27	2	1·45	0·16	ns
	B	16	0·73	5	0·74	0·05	ns
	H	13	1·61	2	1·80	0·16	ns
P¹	L	16	2·35	5	2·30	0·10	ns
	B	16	0·86	5	0·90	0·05	ns
P²	L	16	2·37	5	2·42	0·09	ns
	B	16	1·04	5	1·14	0·06	**
P³	L	12	2·63	2	2·60	0·15	ns
	B	13	1·62	2	1·60	0·10	ns
M¹	B	16	2·42	5	2·44	0·08	ns
	LB	17	3·31	5	3·28	0·15	ns
	LL	16	2·04	5	2·00	0·10	ns
M²	B	16	2·74	5	2·92	0·11	**
	LB	16	3·13	5	2·88	0·09	**
	LL	16	2·03	5	1·98	0·08	ns
M³	B	13	3·01	2	3·20	0·12	ns
	LB	13	2·88	2	2·65	0·16	ns
	LL	13	1·92	2	1·70	0·10	*
M⁴	B	12	1·79	2	1·90	0·20	ns
	LB	13	2·48	2	2·20	0·21	ns
	LL	12	1·08	2	1·10	0·06	ns
I⁵	L	14	0·93	5	1·20	0·08	**

Significance level: t-test ** = 1 per cent, * = 5 per cent, ns = not significant.

Table 7B.—Comparison of *P.b. notina* and *P.b. bougainville* lower tooth measurements (in mm)

Measurement		*P.b. notina* N	*P.b. notina* $\bar{X}$	*P.b. bougainville* N	*P.b. bougainville* $\bar{X}$	Pooled SD	t test
I_1 —M_4	.. .. ..	13	30·47	2	30·40	0·89	ns
I_1 —I_3	.. .. ..	16	3·78	5	3·70	0·14	ns
$\bar{C}$ —M_4	.. .. ..	13	24·33	2	24·20	0·66	ns
M_1—M_4	.. .. ..	13	11·70	2	11·15	0·31	*
$\bar{C}$	L	14	1·62	2	1·80	0·13	ns
	B	16	0·68	5	0·64	0·05	ns
	H	14	1·47	2	1·65	0·11	*
P_1	L	15	2·61	5	2·64	0·11	ns
	B	16	0·79	5	0·84	0·06	ns
P_2	L	15	2·93	5	2·86	0·08	ns
	B	16	1·01	5	1·06	0·07	ns
P_3	L	11	2·67	2	2·70	0·21	ns
	B	12	1·11	2	1·10	0·09	ns
M_1	BM	15	1·53	5	1·54	0·05	ns
	BD	15	1·90	5	1·76	0·05	**
	L	15	2·91	5	2·72	0·12	**
M_2	BM	16	1·84	5	1·80	0·08	ns
	BD	16	2·08	5	2·02	0·05	*
	L	16	3·06	5	3·00	0·11	ns
M_3	BM	16	1·88	5	1·86	0·06	ns
	BD	16	1·94	5	1·92	0·08	ns
	L	16	3·04	5	3·08	0·10	ns
M_4	BM	13	1·65	2	1·60	0·10	ns
	BD	13	1·15	2	1·20	0·08	ns
	L	13	3·09	2	2·85	0·13	ns

Significance level: t-test ** = 1 per cent, * = 5 per cent, ns = not significant.

Table 8.—6 measurements (in mm) of 2 samples of *P. bougainville* and the Central group

Measurement	Juvenile/ Immature N	Juvenile/ Immature $\bar{X}$	Uncertain Localities N	Uncertain Localities $\bar{X}$	Central Group N	Central Group $\bar{X}$
Max. L.	..	..	4	62·22	2	64·50
Cran. Br.	..	..	4	19·40	3	19·33
Occ. Ht.	..	..	4	15·05	3	14·83
Bulla L.	..	..	4	7·38	3	7·70
Bulla Br.	..	..	4	6·65	3	6·97
I^5 L.	12	0·89	3	0·97	4	1·03

Table 9.—Paired comparisons by Scheffe's S method of 4 samples of *P. bougainville* and the Central group using 6 measurements

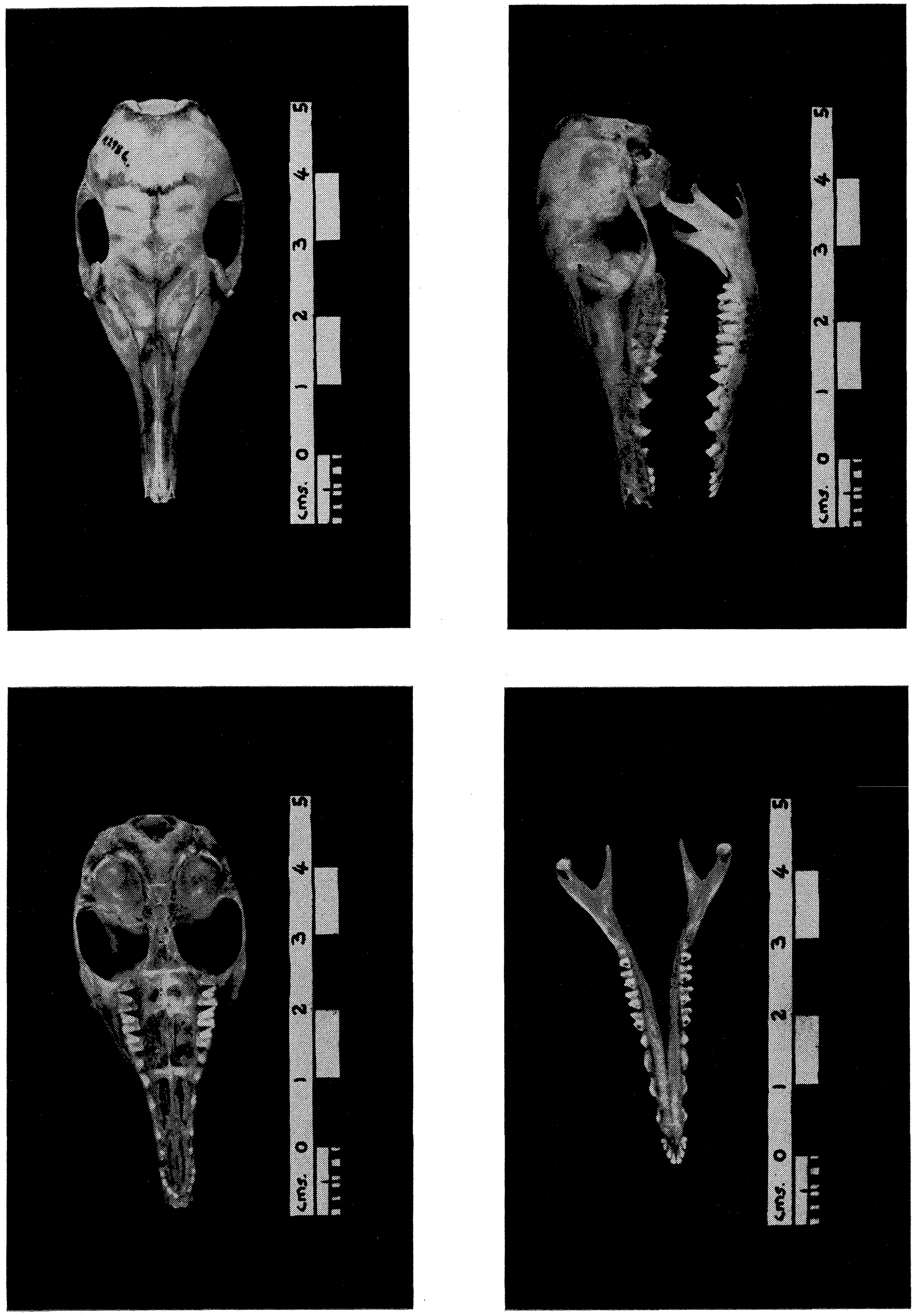
Measurement	I-II	I-III	I-IV	I-V	II-III	II-IV	II-V	III-IV	III-V	IV-V	Pooled SD	d.f.
Max. L.	ns	..	ns	*	..	ns	ns	..	..	ns	2·18	12
Cran. Br.	ns	..	ns	ns	..	ns	ns	..	..	ns	0·81	15
Occ. Ht.	ns	..	*	ns	..	*	*	..	..	ns	0·38	14
Bulla L.	**	..	ns	ns	..	**	**	..	..	ns	0·45	16
Bulla Br.	**	..	ns	ns	..	*	**	..	..	ns	0·32	16
I^5 L.	**	ns	ns	ns	**	ns	ns	ns	ns	ns	0·10	33

Significance level: ** = 1 per cent, * = 5 per cent, ns = not significant. Key: I = *P.b. notina*, II = *P.b. bougainville*, III = Juvenile/ Immature, IV = Uncertain Localities, V = Central Group.

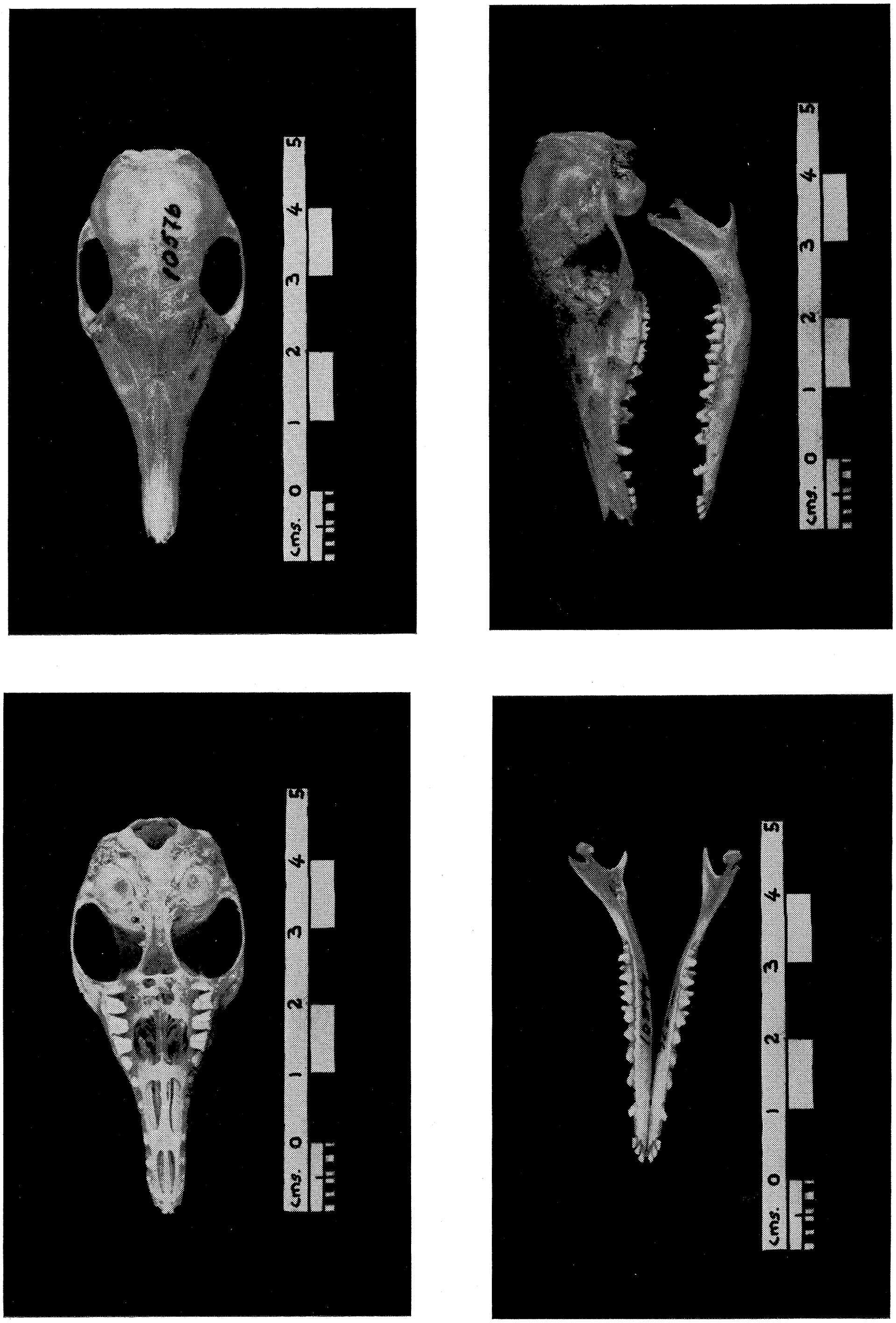
Table 10.—6 measurements (in mm) of 3 Central group specimens

Measurement	S.1753	C.213	M.2629
Max. L.	68·3	60·7	..
Cran. Br.	20·8	18·4	18·8
Occ. Ht.	15·6	14·1	14·8
Bulla L.	7·6	8·3	7·2
Bulla Br.	7·1	7·0	6·8
I^5 L.	1·3	0·9	1·0

Cranium and mandible of *P. gunnii*, male (X.428)



Cranium and mandible of *P.b. notina*, sex unknown (M.2986)



Cranium and mandible of *P.b. bougainville*, male (10576)