

GROWTH OF THE MOUSE COAT

VI. DISTRIBUTION AND NUMBER OF VIBRISSAE IN THE HOUSE MOUSE

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Summary

The vibrissae of 1-day-old mice were classified into major and minor groupings. The presence of many poorly developed vibrissae in the major groups made counting difficult. The minor groups were small isolated collections of large vibrissae. They were easily counted by the naked eye in 4- to 8-day-old mice.

The variation in the number of vibrissae in the minor groups of 3000 mice were investigated. The mice were from inbred and random-bred stocks showing normal coat development. Several discrete variations were found associated with the supra-orbital group. These abnormalities were not observed in the inbred lines. The number of inter-ramal vibrissae showed variation in all stocks except the inbred lines Aw101 and CBA. The other minor groups showed approximately one abnormality per 500 groups counted, with the exception of the postorbital vibrissa which was invariably present.

I. INTRODUCTION

The distribution of certain of the facial vibrissae in the mouse has been described by Danforth (1925) and Figure 1, which shows the tactile hair arrangement on the head and fore limbs, is partly derived from his illustration. His observations were confirmed, in general, by Grüneberg (1943) although he describes the mystacial group as consisting of five horizontal rows and makes no mention of the vertical row E-F-G-H described by Danforth (1925). Davidson and Hardy (1952) examined the mystacial group and their findings support those of Danforth (1925). None of these authors mention the ulnar-carpal vibrissae (Beddard 1902) which occur on the fore limbs of the mouse.

Variation in the number of vibrissae was examined by Danforth (1925) using approximately 200 adult mice. He found no variation in the vertical row and the most posterior three vibrissae in the horizontal rows of the mystacial group. He noted one doubtful case in which a postorbital vibrissa appeared to be absent. The supra-orbital and postoral groups were slightly more variable showing 1 and 3 per cent. of aberrant scores respectively. Vibrissae were not counted at the inter-ramal and ulnar-carpal sites. The invariant nature of vibrissa number is particularly striking when consideration is given to the age of the mice which Danforth scored. Because of the cyclic activity of hair follicles, scores for vibrissa number in older mice could be falsely reduced by the shedding of fibres.

Grüneberg (1943) recorded the invariable presence of the postorbital vibrissa follicle in 140 normal mouse embryos. He also examined the postoral group and recorded the presence of two and, rarely, three follicles. He did not record specific observations on the remaining vibrissae.

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Davidson and Hardy (1952) described the number of vibrissae in the mystacial group but details of mice examined were not stated. Rows I and II each had four large vibrissae. Row III had five vibrissae while there were always at least six and eight vibrissae in rows IV and V respectively. Hardy (personal communication, 1956) indicated that in counts on approximately 100 young mice there was agreement with the earlier counts of Danforth (1925). In addition, the ulnar-carpal group showed 2 per cent. aberrant scores while the inter-ramals were highly variable (27 per cent. of groups with 2, 72 per cent. with 3, and 1 per cent. with 4 vibrissae).

Although the scoring methods used by these workers were varied and the number of mice examined was small, there is good agreement of results. In particular only one doubtful case of a missing postorbital vibrissa was observed. All other vibrissae showed a small amount of variation, the exception being the inter-ramals which were shown to be highly variable by Hardy.

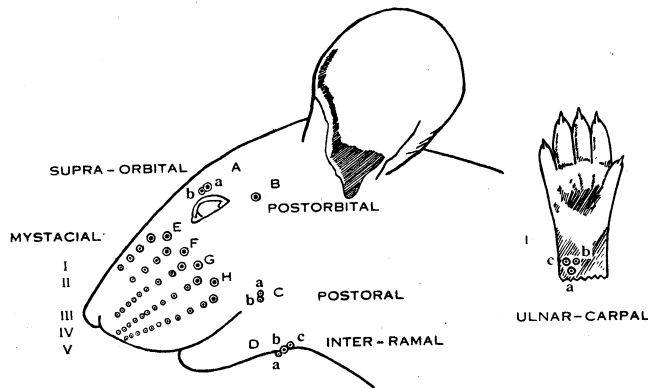


Fig. 1.—Head and distal part of right fore limb of the mouse showing distribution of vibrissae.

Our interest in mouse vibrissae has arisen firstly from their low variability in normal mice, and secondly from the reduction in vibrissae which is produced by the pleiotropic genes crinkled (*cr*) (autosomal) (Falconer, Fraser, and King 1951), its sex-linked mimic tabby (*Ta*) (Falconer 1953), and ragged (*Ra*) (Carter and Phillips 1954). Waddington (1952) has shown that an invariant character, e.g. wing venation in *Drosophila melanogaster*, can be caused to vary by suitable treatment. Selection on such variability can be used to build up genetic effects which eventually make themselves felt in the absence of the treatment. We wished to see whether the variation introduced into the expression of a character by a major gene could be used in selection to change an invariant character eventually even in the absence of the gene.

A selection experiment was therefore planned, the aim being to influence vibrissa number by selection of genes which are unmasked by inclusion of the tabby gene in the selection stock. If these genes are identical or partially identical with the polygenic combinations which are responsible for the strongly buffered vibrissa development, such selection would eventually lead to a breakdown in the homeostatic mechanism. Before the results of such an experiment could be evaluated, the normal variation in vibrissae would have to be known with greater accuracy than is possible

from an examination of the literature. This paper describes the examination of large numbers of mice in an attempt to measure the variation in vibrissa number between and within mouse strains. In addition, an examination was made of the entire vibrissa complement of the mouse in order to find the groups which could be most easily and accurately counted.

II. MATERIALS AND METHODS

When making complete vibrissa counts, 1-day-old mice were fixed in formol-saline and examined with a dissection microscope. An ocular micrometer was used for measurement of vibrissa length. Mice for this part of the observations were produced by crossing inbred line CBA with an albino stock.

TABLE 1
NUMBER OF VIBRISSAE IN MYSTACIAL ROWS III, IV, AND V

	Row III	Row IV	Row V
Number of rows counted	306	306	306
Mean number of vibrissae	9.88	10.61	11.44
Standard deviation	0.719	0.653	0.595

The smaller groups of vibrissae can be accurately counted by naked eye under a strong light. An extensive examination was therefore made of the variation in these groups, using mice between 4 and 8 days of age. Mice examined were from the normally coated stocks maintained at the Animal Genetics Section, C.S.I.R.O. All mice born over the period March to August 1956 were examined and scored. Mice were from the following stocks:

(i) *Inbred Lines*—Aw101; CBA; C₃H; C₅₇; A. These lines are all 30 or more generations inbred by full sib mating.

(ii) *Selection Lines on Oestrogen Sensitivity*.—WI/OS and BI/OS are the original high and low selection lines. They were selected from a heterogeneous albino stock



and have been separated for about 10 generations. WG/OS and WR/OS and BG/OS and BR/OS are sublines of WI/OS and BI/OS respectively. They have been separated from their parent lines for four generations. There are 40 matings in each line and inbreeding has been minimized.

(iii) *WOS*.—This is a general laboratory stock of albinos formed from BI/OS and A strain inbreds.

(iv) *LB*.—This stock has several segregating genes including pied and dilute.

III. RESULTS AND DISCUSSION

The distribution of vibrissae in the mouse is illustrated in Figures 1 and 2. Size of dots is an indication of vibrissa size. Comparative lengths of vibrissae are presented in Figure 3. Observations are recorded below under group headings.

The pattern is of curved rows radiating from a point on the mid line ventral to the lower lip. The rows are symmetrical with the exception of three centrally placed vibrissae. Commencing from the mid line, row I has four to five vibrissae of which the second most posterior is large and conspicuous. Row II has two to three vibrissae. Row III extends laterally with six to seven vibrissae, the posterior vibrissa being very large. Above this row, several further rows, each of four to six small vibrissae can be seen.

Like the ventral rows of mystacial, the submental vibrissae are variable in number and difficult to count. The only vibrissae from the major groups which would be of value for an invariant selection score are mystacial rows I and II.

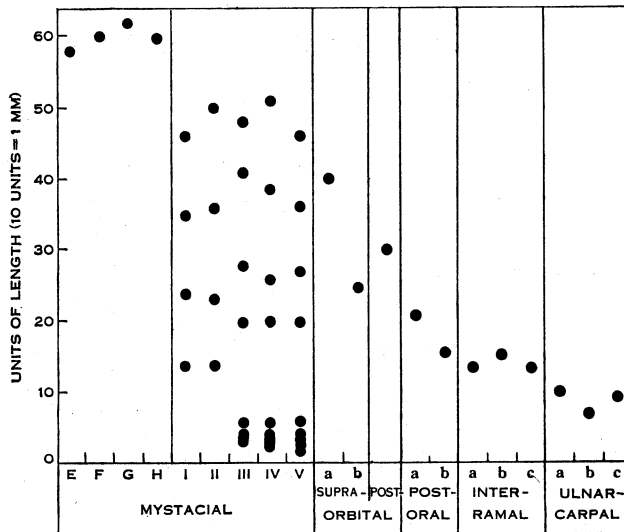


Fig. 3.—Comparative length of mouse vibrissae at 5 days of age.

(b) *Distribution of Vibrissae—Minor Groups*

(i) *Supra-orbital*.—A, a and b (Fig. 1). These two vibrissae arise from a single tubercle placed above the eye. The large vibrissa a is postero-medially placed to its smaller companion b.

(ii) *Postorbital*.—B (Fig. 1). This is a single large vibrissa placed posterior to the eye.

(iii) *Postoral*.—C, a and b (Fig. 1). This group consists of two vibrissae, a (dorsal) and b (ventral), arising from a single tubercle which is found posterior to the lip commissures.

(iv) *Inter-ramal*.—D, a, b, and c (Fig. 1). The usual arrangement is a transverse row of three vibrissae centrally placed between the rami of the lower jaw.

(v) *Ulnar-carpal*.—I, a, b, and c (Fig. 1). These vibrissae arise from a single large tubercle on the lateral volar surface of the forearm just above the carpus. The

vibrissae are arranged at the corners of an equilateral triangle, the apex being proximal on the limb. Designation is *a*, proximal, *b*, medial distal, and *c*, lateral distal.

(c) *Variation in the Number of Vibrissae in the Minor Groups*

(i) *Inbred Lines*.—Results are summarized in Table 2 and Figure 4. With the exception of the inter-ramals, group size is remarkably constant. Incidence of vibrissa deletions was of the order of one in 500 groups examined, the postorbital vibrissa being an exception in that it was invariably present. Apart from the inter-ramals, the only increased count was seen in a DBA mouse with a group of three post-oral vibrissae.

TABLE 2

FREQUENCY DISTRIBUTION OF THE NUMBER OF VIBRISSAE IN SIX INBRED STRAINS OF MICE

Strain	Supra-orbital		Post-orbital		Postoral			Inter-ramal				Ulnar-carpal	
	No. of Vibrissae in Group												
	1	2	1	1	2	3	1	2	3	4	2	3	
Aw101	1	459	460	1	459	—	—	—	230	—	—	460	
CBA	—	496	496	—	496	—	—	3	245	—	—	496	
C ₃ H	—	403	408	1	407	—	—	8	194	2	1	407	
C ₅₇	—	324	324	—	324	—	1	22	137	2	—	324	
DBA	—	308	308	—	307	1	—	56	98	—	—	308	
A	1	231	232	1	231	—	1	62	47	6	9	223	
Total	2	2226	2228	3	2224	1	2	151	951	10	10	2218	
Incidence (%)	0.09	99.91	100.00	0.13	99.82	0.05	0.18	13.55	85.37	0.90	0.45	99.55	

Figure 4 shows differences between inbred lines with respect to count variation in the inter-ramal group. No mice were detected in Aw101 with other than three inter-ramal vibrissae. The incidence of variation increased through CBA, C₃H, C₅₇, and DBA to a peak in A strain, where a score of three is seen in a minority of groups and possible counts range from one to four vibrissae.

Concomitant with the increase in inter-ramal variation, there is a marked drop in fertility. The bracketed numbers after the strain names in Figure 4 are the numbers of mice scored and as there are approximately equal numbers of matings in each line, this figure is a good index of fertility. The negative correlation between inter-ramal variation and fertility is clearly shown.

(ii) *Non-inbred Stocks*.—In these mice, both the supra-orbital and inter-ramal vibrissae show marked variation. Observations on these two groups are recorded in Table 3 and Figure 5. The postorbital vibrissa was again invariant while the post-orals and ulnar-carpals showed about one reduced group per 500 scored.

Supra-orbital score.—Examination of Table 3 and Figure 5 reveals a very marked difference between BI/OS and WI/OS strains with regard to supra-orbital group size, the former showing a high incidence of groups with three vibrissae. The arrangement is shown as type *A* in Figure 6. The extra vibrissa was of a similar size to the shorter of the two normal vibrissae and was situated antero-medially on the same tubercle. In 36 per cent. of cases, groups were bilaterally affected. Two-thirds of the remaining mice show the “trio” grouping only on the right side.

Four mice were found in the line BG/OS where three vibrissae occurred above the eye, the arrangement differing in that the extra vibrissa was on a separate tubercle placed posterior to a normal supra-orbital group (Fig. 6, *B*).

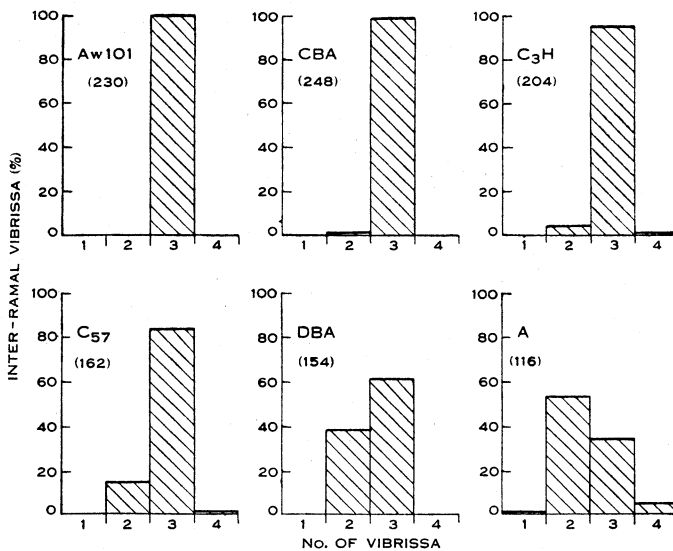


Fig. 4.—Frequency distribution of inter-ramal vibrissa count in six inbred mouse strains. Number of mice examined is shown in parenthesis for each strain.

Inter-ramal score.—Most stocks showed approximately 20 per cent. of groups with two vibrissae. The exception on the high variability extreme was LB, where the majority of inter-ramal groups had two vibrissae and there was almost as many with one as three vibrissae. BG/OS showed low variation with only 4 per cent. of reduced scores. Another point of interest was the frequent increase in inter-ramal group size in WI/OS and related strains. In WR/OS this was particularly well marked, two counts of five vibrissae being recorded.

Before concluding it is interesting to consider possible genetic models for the differences observed in the supra-orbital and inter-ramal groups. Considering the supra-orbital variants first, Table 4 shows parent-offspring comparison from BI/OS on the presence of trio groups (Type *A*, Fig. 6). The very large χ^2 value indicates that this arrangement is highly heritable, possibly through a single gene showing 30–50 per

cent. penetrance when homozygous. Strong supporting evidence for this hypothesis is the complete absence of the trio group in the inbred lines and high frequency only in those lines directly derived from BI/OS. Because the effect of environment and modifiers is strong, it is not possible to test for the presence of a major gene until a stock selected for high penetrance is available. The inheritance of the BG/OS type *B* arrangement is probably also governed by a major gene plus modifiers. The problem of test matings is even more acute in this case because penetrance is only 10 per cent. in matings between individuals showing the abnormality.

TABLE 3
FREQUENCY DISTRIBUTION OF THE NUMBER OF SUPRA-ORBITAL AND INTER-RAMAL VIBRISSAE IN
NON-INBRED STRAINS OF MICE

Strain	Supra-orbital				Inter-ramal				
	No. of Vibrissae in Group								
	0	1	2	3	1	2	3	4	5
WI/OS	—	8	1636	2	1	157	660	5	—
WG/OS	—	1	438	1	—	46	172	2	—
WR/OS	—	2	458	2	—	49	170	10	2
BI/OS	—	6	1323	251	—	140	649	1	—
BG/OS	1	4	402	23	—	10	204	1	—
BR/OS	—	4	347	23	—	19	168	—	—
WOS	—	1	318	59	—	30	159	—	—
LB	—	1	105	—	9	31	13	—	—
Total	1	27	5027	361	10	482	2195	19	2
Incidence (%)	0.02	0.50	92.81	6.67	0.37	17.80	81.06	0.70	0.07

The inter-ramal variation is not easily explained. From examination of inbred line results, it was originally postulated that the inter-ramals were more sensitive to environmental fluctuation than the other vibrissae. In this case, the range of variation through the inbred lines could have been due to decreasing homeostasis. This hypothesis was supported by the association between increasing inter-ramal variation and decreasing fertility.

No further support has been found for this hypothesis and a preferable explanation is provided by one of the forms of quasi-continuous inheritance listed by Grüneberg (1952). Experimental support was produced by crossing inbred lines, an intermediate level of inter-ramal count being obtained in the F_1 . Selection high and low on inter-ramal vibrissa number was undertaken with mice from WR/OS. Selection changes have been marked in both directions indicating a high heritability. No fertility differences have been noted between the selection lines.

The other minor groups of vibrissae appear to be independent of the factors causing variation in inter-ramals in that they show no variation in any line, despite

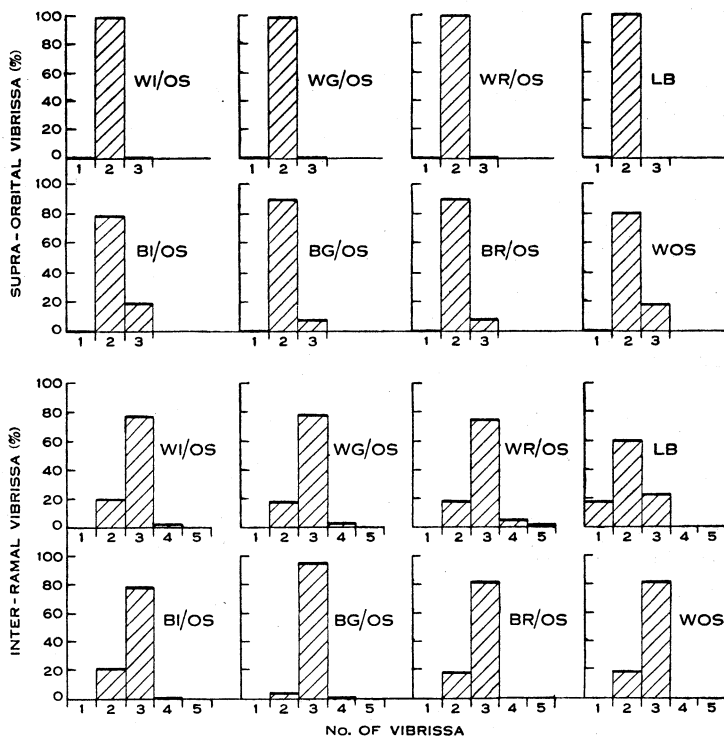


Fig. 5.—Strain differences in vibrissa counts of supra-orbital and inter-ramal groups (non-inbred stocks).

the range of inter-ramal expression. Again in BI/OS, penetrance of the trio supra-orbital group was not correlated with inter-ramal vibrissa count. Further support for

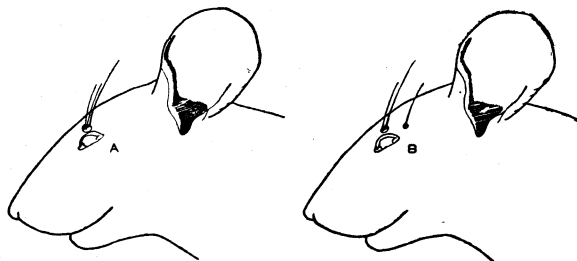


Fig. 6.—A, supra-orbital group with three vibrissae; B, an extra vibrissae behind the normal supra-orbital group.

independence was obtained from the inter-ramal selection experiment, where although the two lines are widely separated on inter-ramal count, there are no correlated changes in the rest of the vibrissa complement.

IV. CONCLUSIONS

Variations in the number of vibrissae in the minor groups of normal mice, were restricted to the following cases:

- (i) Marked variation in the inter-ramal group with counts varying from one to five vibrissae. There were large strain differences which were readily explainable if the variation was governed by polygenic inheritance. Two inbred lines, Aw101 and CBA, were exceptional in that they showed practically no variation at the inter-ramal site.
- (ii) Increase in the supra-orbital count from two to three vibrissae. This change was strain delimited and could be caused by a major gene.
- (iii) Presence of an accessory supra-orbital vibrissa. This was again strain delimited and was probably associated with a major gene.
- (iv) Rare vibrissa deletions occurring in all groups about once in 500 groups scored. The postorbital vibrissa was an exception in that it was invariably present in the 3000 mice examined.

TABLE 4

COMPARISON OF PROGENY FROM MATINGS WITH DIFFERENT SUPRA-ORBITAL SCORE COMBINATIONS
N indicates a normal score of two vibrissae on each side, and T a score of three vibrissae on each side, or three on one side and two on the other. $\chi^2 = 58.86$, d.f. = 3, $P < 0.01$

No. of Supra-orbital Vibrissae	Parent Combinations				Total
	N♂ × N♀	N♂ × T♀	T♂ × N♀	T♂ × T♀	
N	470	29	85	29	613
T	85	25	52	18	180
Total	555	54	137	47	793

Thus the development of mouse vibrissae is very strongly canalized. This is particularly the case in the inbred lines Aw101 and CBA and they would therefore be the best mice to use in the formation of a selection stock for an attempt to break down vibrissa development. In the evaluation of such an experiment, absence of any vibrissae from normal mice would lead one to suspect a change in the basic genotype and, in particular, absence of a postorbital vibrissa would be excellent evidence of such an upset.

V. ACKNOWLEDGMENTS

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