GENETICAL STUDIES ON THE SKELETON OF THE MOUSE

III. SKELETAL VARIATION IN WILD POPULATIONS

By W. WEBER, *Veterinär-Anatomisches Institut der Universität, Bern, Switzerland*

(With Five Text-figures)

Introduction

In the first paper of this series, Grüneberg (1950*a*) has described a considerable polymorphism of the skeleton of the mouse which is under genetical control. The most variable part of the skeleton seems to be the cervical and upper thoracic region of the vertebral column. It seemed of interest to discover whether this polymorphism is a property of the tame mouse or whether similar variations also occur in wild populations.

For this purpose, six wild populations have been sampled, four in London, one in Edinburgh and one in Bern. Some of the samples are smaller than had been intended. The animals were either poisoned or trapped alive in special traps so as to obtain undamaged skeletons. Maceration of the skeletons was carried out by digestion with the proteolytic enzyme papain; the bones collected included the vertebrae, scapula, clavicula, humerus, radius, ulna, os innominatum, femur, tibia + fibula and the mandible. The total number of skeletons examined is 218, derived from the following localities.

Three populations were obtained from the London Zoological Gardens; they came from the Small Bird House (S.B.H.; 76 mice), the Tropical Bird House (T.B.H.; 56 mice) and the Parrot House (P.H.; 16 mice) respectively. The Small Bird House and the Tropical Bird House stand side by side, but do not communicate with each other; it will be shown below that the respective mouse populations of these houses differ appreciably from each other. The Parrot House is several hundred yards away from the other two houses and separated from them both by open ground and by other animal houses. The populations of these animal houses are presumably relatively isolated from each other and rather inbred.

The fourth population, of fourteen mice only, came from the London Docks. The animals were taken in several widely separated localities and presumably are not related to each other at all closely.

A fifth population of eighteen mice was trapped near Edinburgh (Redside Farm, Carrington, East Lothian).

Finally, thirty-eight mice were trapped in the animal house of the Frauenspital in Bern. Some tame albino mice are kept in that animal house, but it is believed that none have escaped during the past two or three years; before that time, occasional escapes seem to have happened. The possibility must therefore be borne in mind that this group is not entirely 'wild', but may have some admixture of tame blood.

Foramina transversaria imperfecta (f.t.i.)

Ventrally open foramina transversaria have been encountered in five of the six populations examined. The anatomical situation tallies precisely with that described by Grüneberg (1950*a*) for tame mice; three typical specimens are shown in Fig. 1. The third cervical vertebra (C III) was not affected in any of the animals examined; the distribution of the anomalies by population and vertebra (C IV to C VI) and side of body is summarized in

Table 1. Although f.t.i. occurs in all but one of the populations sampled, its incidence varies strikingly from population to population. For instance, the two bird houses in the London Zoo, standing in close proximity to each other, have a significantly differing incidence of f.t.i. as seen from the following fourfold table:

	Normal	Abnormal	Total
S.B.H.	63	13	76
T.B.H.	54	2	56
Total	117	15	132

which, treated by Fisher's 'exact' method, gives $P = 0{\cdot}0131$. The highest incidence of the anomaly, not much short of a third of the whole sample, occurs in the Bern population. As in the tame mice, the anomaly is essentially symmetrical, the slight preponderance of the left side not being significant. A curious feature is the fact that in the Bern population, C IV is involved at least as frequently as the two following vertebrae, while all British populations behave like the tame mice, C IV being much less affected than C V and C VI. It seems probable that this difference is due to a different genetic background in the Bernese mice, in a similar way to that in which the manifestation of f.t.i. on C VI is increased in the presence of the *undulated* gene (Grüneberg, 1950*b*).

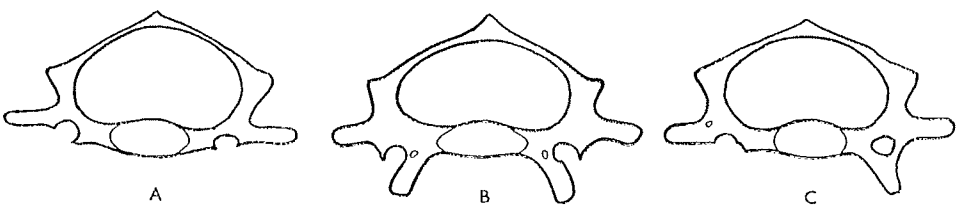

Fig. 1. Foramina transversaria imperfecta. A, a C V from a male from Bern; B, a C VI from a female from the London Docks; in this animal, there are two little accessory foramina which may remain independent or join the canalis transversarius. C is a C VI from a female from the S.B.H. with absence of the tuberculum anterius on the left and a small supernumerary foramen on the base of the arcus. Camera lucida drawings, caudal views.

Table 1. *Foramina transversaria imperfecta*

R = right, L = left, RL = both sides affected.

			Vertebrae affected per abnormal mouse			C IV			C V			C VI			F.t.i. per abnormal mouse
	n	Abnormals	1	2	3	R	L	RL	R	L	RL	R	L	RL	
S.B.H.	76	13	6	6	1	—	—	—	1	3	1	3	5*	4	1·7
P.H.	16	1	1	—	—	—	—	—	1	—	—	—	—	—	1
T.B.H.	56	2	1	1	—	—	1	—	1	—	—	1†	—	—	1·5
Docks	14	2	—	2	—	—	—	—	—	2	—	—	—	2	3
Edin.	18	—	—	—	—	—	—	—	—	—	—	—	—	—	—
Bern	38	12	5	4	3	3	3	3	2	5	3	1	1	1	2·4
Total	218	30	13	13	4	3	4	3	5	10	4	5	6	7	

* Tuberculum anterius missing in three of these animals.
† Tuberculum anterius missing in this animal.

Other anomalies of the cervical region

The shape of the vertebral foramen (canalis vertebralis) may vary considerably. In animals of the same size, a very wide or a comparatively narrow foramen may be found. Sometimes a remarkably short dorsoventral diameter is combined with a rather large horizontal diameter so that the foramen becomes a compressed oval. The contrary is also found, the foramen being roundish. The extent to which these variations are genetically determined is uncertain.

No anomalies were found in the atlas. In a few very young mice the foramen transversarium was not yet closed, but this was almost certainly a sign of immaturity. The tuberculum anterius atlantis is sometimes more or less deeply split, resembling an inverted ⅄; this was observed in 30·4% of all the mice examined. In one case the tuberculum was bent towards the left, in two further cases towards the right. Fusions of the atlas with the occiput or with the axis (epistropheus) did not occur.

A single mouse showed a condition resembling dyssymphysis posterior of the axis described by Grüneberg (1950*a*); no major anomalies have been observed in C III. Sometimes a small accessory foramen of pin-point size occurs medial (rarely lateral) to the foramen transversarium; this leads into a canal which either remains independent or ultimately joins the canalis transversarius; similar foramina also occur in other cervical vertebrae.

The C III in the mouse has paired foramina on the dorsal side of the arcus which either lead by a short canal into the canalis vertebralis, or by a longer canal into the canalis transversarius. The foramina were double on the left side in 5% and on the right side in

Fig. 2.

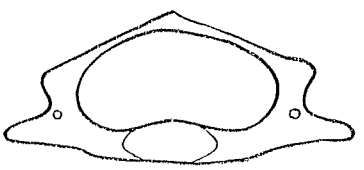

Fig. 3.

Fig. 2. Dorsal view of fused C IV and C V. The right arcus of C IV is fused with the intact arcus of C V. Female, T.B.H.

Fig. 3. C VII with accessory foramina. Female, P.H.

Table 2. *Accessory foramen of C VII*

Population	Accessory foramen: Left	Right	Both sides	Total	Foramen absent	Percentage with foramen
S.B.H.	6	5	33	44	32	57·8
P.H.	2	2	9	13	3	81·2
T.B.H.	5	3	11	19	37	34·7
Docks	2	1	2	5	9	35·7
Edinburgh	3	2	0	5	13	27·8
Bern	5	2	3	10	28	26·3
Total	23	15	58	96	122	44·0

3% of the vertebrae examined; bilateral duplication was not observed. Once the foramen was absent on the right side only to reappear on C IV; the latter vertebra may have similar but smaller foramina; they were present in 6% on the left, in 8% on the right and in 2·5% on both sides.

Fusions between C IV and C V occurred once in the T.B.H. and once in the Bern population. One case is shown in Fig. 2; fusion is by means of the laminae in each case, the bodies of the vertebrae not being joined.

In C VII a small foramen often occurs in the position indicated in Fig. 3. It has nothing to do with a foramen transversarium which that vertebra usually lacks. This can be seen readily in C VI and C V in which the same foramen occasionally occurs side by side with a foramen transversarium. This accessory foramen occurred in all wild populations sampled, but the frequency differs considerably from population to population. The data given in Table 2 are based on well-developed foramina only, pin-point foramina having

been disregarded. A homogeneity test gives $\chi^2 = 24{\cdot}045$; $n = 5$; $P < 0{\cdot}001$. There being thus clear evidence of heterogeneity, it seems the most likely assumption to ascribe the divergence between populations to genetical differences.

A genuine foramen transversarium of C VII (Fig. 4) has been found in three animals of the Bern population, each of them on the right side. In two cases the size was normal, in the third about half normal. Usually the arteria vertebralis passes ventral to the processus transversus of C VII where, in 3 % of the specimens examined, it produced a gutter.

As is well known, the processus transversus of the cervical vertebrae includes a rib element which is usually incorporated so completely as to be unrecognizable as a separate entity. Sometimes a line marks the position of the fusion; a continuous fissure, with or without an aperture, on C VII as shown in Fig. 5 occurred seven times among the 218 mice. The oblique position of the processus transversus, as shown on the left side of Fig. 5, was found but four times in all the mice examined.

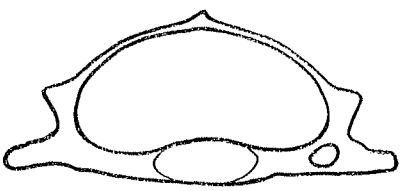

Fig. 4.

Fig. 5.

Fig. 4. C VII with foramen transversarium on the right. Male, Bern. Camera lucida drawing, caudal view.
Fig. 5. C VII with incomplete fusion (dyssymphysis) of the rib element on the right and oblique processus transversus on the left. Male, London Docks. Camera lucida drawing, caudal view.

Remainder of the vertebral column

Small accessory foramina, like those described on C VII, were found seven times on Th I (three times on the left, twice on the right, and twice bilaterally).

The variations of the vertebra prominens (Th II) observed in the wild populations were similar to those described by Grüneberg (1950*a*) for tame mice. Complete absence of the processus spinosus was observed only twice in the whole material, once in the S.B.H. and once in a London Docks mouse; the latter specimen has fourteen thoracic vertebrae.

Two cases of incomplete dystopia of the processus spinosus were observed. In one mouse from Bern, a processus spinosus occurred both on Th I and Th II, both of them being smaller than the one normally present on Th II; the situation is thus like that not rarely found in the C 57 B stock (Grüneberg, 1950*a*). The second case was a caudal dystopia in a fully grown mouse from the London Docks which had a rather short processus spinosus both on Th II and on Th III, somewhat reminiscent of a solitary case observed in the X stock by Grüneberg (1950*a*).

The short processus spinosus of the Th X was absent in 9 % of the skeletons examined. It was frequently only rudimentary and often flat and atypical. In three adult specimens of the S.B.H. group the arcus dorsalis was not closed (spina bifida).

No significant variations of the lumbar vertebrae have been observed except for variations on the lumbo-sacral border which are also common in many strains of tame mice.

No variations were found in the sacral vertebrae. In particular, the large processus spinosus of S I was always present and of normal size. The caudal vertebrae have not been studied in detail.

Variations in other parts of the skeleton

No significant variations were observed in the following bones: the mandible, scapula, clavicula, ulna, radius, femur, and tibia + fibula.

In the humerus, the thin lamina of bone which separates the fossa radii and the fossa coronoidea in front from the fossa olecrani behind is sometimes pierced by a foramen supratrochleare. Such a foramen occurred in fifty-four out of 207 mice bilaterally, in seven on the left and in eighteen on the right side (38·2% altogether). There seemed to be no significant differences between the various populations as regards the incidence of this foramen. The foramen, if present, seems to develop early in life; it was seen in three out of ten Strong CBA mice which were examined at the age of 15–19 days.

In the pelvis, the acetabulum has ventrally a deep incisura acetabuli which is bridged by a ligamentum transversum acetabuli. The latter can ossify to a greater or lesser extent. Variations of that kind encountered were probably merely an expression of age differences.

Four times, a hole in the bottom of the acetabulum was observed at the point where the three bones forming the pelvis meet; apparently the bones had failed to join up completely.

Discussion

The variations of the vertebral column observed in wild mice are of the same general kind as those encountered in tame strains. All the variants described in this paper also occur in tame strains, though some of them have not yet been analysed in detail. The differences between populations cannot be explained as environmental, but must be regarded as genetical like those between tame strains of mice.

None of the variations observed seems to lower the fitness of the mouse to an appreciable extent. This probably explains why these variations have not been eliminated by natural selection.

Variations like those described may be used as a tool in ecological studies. Differences between neighbouring populations with regard to these internal polymorphic characters may give an indication as to whether and to what extent they are isolated breeding units.

Summary

Skeletal variations observed in six wild populations of mice are of a similar kind to those found in tame strains. The incidence of individual anomalies may vary greatly from population to population and is probably determined genetically.

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