# The effect of selection for body weight on the skeletal variation of the mouse 

By GILLIAN M. TRUSLOVE<br>Department of Human Genetics and Biometry, University College London, Wolfson House, 4, Stephenson Way, London NW1 2HE

(Received 24 February 1975)


#### Abstract

SUMMARY The incidence of many minor skeletal variants in the inbred mouse strain C57BL can be influenced by the diet on which the parents live: in many cases, the effect is mediated by a correlation with body size. This also seems to be true in Falconer's (1973) Q-strain in which body size has been increased or decreased by selection. However, there was so much heterogeneity between replicates within selection lines that variants influenced by body size could be detected as a group, but not identified individually.


## 1. INTRODUCTION

Minor variants of the skeleton have been studied in considerable detail in the mouse (for a general review see Grüneberg, 1963). Their incidence differs greatly between inbred strains (Howe \& Parsons, 1967; Wickramaratne, 1974) which is clear evidence that part, at least, of this interstrain variation is under genetical control. Within a given inbred strain, a small part of the variance is due to tangible causes such as sex, maternal age and parity, but intangible non-genetic factors accounted for over $80 \%$ of the variance in three-quarters of the characters studied by Searle ( $1954 a$ ). In an attempt to identify other causes of this large amount of 'chance' variation, Searle (1954c) kept mice of the C57BL inbred strain on an unbalanced (oats) diet; the young borne of parents on that diet showed striking changes in the frequency of many minor variants, some frequencies going up and others down. These findings were confirmed by Deol \& Truslove (1957) with a variety of unbalanced cereal diets (oats, wheat, barley and buckwheat). These authors made the additional discovery that the incidence of about half of those variants which responded to diet were correlated with body size. The frequency of variants which tended to occur in large mice went down whereas those which occurred in small mice went up, in both cases because on these unbalanced diets the average size of the young was reduced. This raised the question whether a similar effect on minor skeletal variants could be demonstrated when the size of the mouse was increased or decreased genetically as in selection experiments. An opportunity to test this question arose in the replicated selection experiments for
body weight of Falconer (1973). Professor Falconer generously placed animals from these experiments at my disposal and the findings are reported here.

## 2. MATERIAL AND METHODS

The details of the Q-strain experiment are given by Falconer (1973) and will only be summarized here. A random-bred strain of mice was divided into six replicates (labelled A-F inclusive) and each of them was selected for large and small body-size at six weeks with an unselected control (designated Large, Small

Table 1. Number of skeletons collected, mean ages and 6-week weights in the replicates with the selection and control means

| Line | No. of <br> skeletons | Mean age <br> (days) | Mean 6.week <br> No. weighed |  |
| :--- | :---: | :---: | :---: | :---: |
| weight (g) |  |  |  |  |

and Control). Each line was maintained by minimal inbreeding from eight singlepair matings. For the first ten generations the overall mean responses were linear and very regular both up and down. But, 'over the first ten generations the six replicates gave widely divergent estimates of the realised heritability and of the asymmetry of the response'. After generation 10 the upward regression decreased but the downward regression increased, and the regressions were no longer clearly linear (Falconer, 1973).

About 50 ठ ${ }^{\top}$ and 50 아 were collected from each of the 18 replicates at generations $13+14$ (Table 1) and after preparing the skeletons by the papain maceration method they were classified for an array of 52 minor variants (Tables 2, 5). For a description of the skeletal characters see Deol (1955) and Berry \& Searle
(1963) and for turned-up nose, size of p.s. of ThI and pink caudal vertebrae see Appendix. Falconer also supplied data such as age at killing and 6-week weight (where this was known; litters other than the first were not always weighed as they did not usually contribute to the next generation). The collection of some 1900 animals occupied a considerable time and inevitably included mice from several generations, although the bulk of them came from generations 13 and 14. Care was taken to avoid bias in classification and the results were recorded on printed, cards, coded and punched on data cards. The sexes were at first treated separately, but

## Table 2. Mean percentage incidence of 37 minor skeletal variants in the $Q$-strain, based on the data given in Appendix, Table 5

| Variant | Large $\pm$ S.E. | Control $\pm$ S.E. | Small $\pm$ S.E. |
| :---: | :---: | :---: | :---: |
| 1. Bent nose | $0.5 \pm 0.3$ | $1 \cdot 7 \pm 1 \cdot 2$ | $3 \cdot 8 \pm 1 \cdot 9$ |
| 2. Turned-up nose | $0 \cdot 3 \pm 0.3$ | $0 \cdot 6 \pm 0 \cdot 3$ | $3 \cdot 9 \pm 1.7$ |
| 3. Maxillary-turbinal fusion | $16 \cdot 5 \pm 2 \cdot 5$ | $18 \cdot 7 \pm 3 \cdot 6$ | $13 \cdot 1 \pm 1 \cdot 8$ |
| 4. Nasals fused | $0 \cdot 3 \pm 0 \cdot 2$ | $0 \cdot 3 \pm 0 \cdot 3$ | $2 \cdot 9 \pm 1 \cdot 8$ |
| 5. Fused frontals | $22 \cdot 3 \pm 4 \cdot 9$ | $19 \cdot 6 \pm 6 \cdot 3$ | $10 \cdot 2 \pm 3 \cdot 3$ |
| 6. Interfrontal absent | $\mathbf{9} \cdot \mathbf{3} \pm 4 \cdot 1$ | $10 \cdot 3 \pm 4 \cdot 5$ | $10 \cdot 2 \pm 2 \cdot 4$ |
| 7. Interfrontal-frontal fusion | $5 \cdot 6 \pm 2 \cdot 9$ | $3 \cdot 0 \pm 1 \cdot 0$ | $2 \cdot 5 \pm 1 \cdot 0$ |
| 8. Parted frontals | $77 \cdot 4 \pm 10 \cdot 8$ | $91.9 \pm 3 \cdot 2$ | $89 \cdot 1 \pm 8 \cdot 7$ |
| 9. Frontal fontanelle | $0 \cdot 8 \pm 0.3$ | $4 \cdot 3 \pm 2 \cdot 3$ | $12 \cdot 6 \pm 7 \cdot 7$ |
| 10. Frontal foramen double | $5 \cdot 4 \pm 0 \cdot 8$ | $2 \cdot 8 \pm 0 \cdot 5$ | $3 \cdot 1 \pm 0 \cdot 6$ |
| 11. Preoptic sutures | 35.0 $\pm 10 \cdot 6$ | $26 \cdot 9 \pm 5 \cdot 4$ | $43 \cdot 8 \pm 7 \cdot 8$ |
| 12. Metoptic roots abnormal | $18 \cdot 9 \pm 4 \cdot 7$ | $25 \cdot 7 \pm 6 \cdot 9$ | $34 \cdot 5 \pm 10 \cdot 1$ |
| 13. Basisphenoid-presphenoid fusion | $10 \cdot 4 \pm 2 \cdot 6$ | $5 \cdot 2 \pm 1 \cdot 2$ | $8 \cdot 2 \pm 3 \cdot 1$ |
| 14. Basisphenoid-basioccipital fusion | $13 \cdot 5 \pm 3 \cdot 8$ | $2 \cdot 7 \pm 1 \cdot 6$ | $2 \cdot 3 \pm 1 \cdot 0$ |
| 15. Preorbital foramen double | $14 \cdot 1 \pm 1 \cdot 8$ | $17 \cdot 5 \pm 1 \cdot 9$ | $20 \cdot 6 \pm 2 \cdot 0$ |
| 16. Accessory maxillary foramen | $5 \cdot 7 \pm 1 \cdot 2$ | $6 \cdot 7 \pm 1 \cdot 3$ | $3 \cdot 6 \pm 0 \cdot 8$ |
| 17. Foramen palatinum majus double | $11 \cdot 3 \pm 1 \cdot 7$ | $6.7 \pm 0.6$ | $\mathbf{7} \cdot 9 \pm \mathbf{2 \cdot 4}$ |
| 18. Foramen ovale single | $17 \cdot 1 \pm 2 \cdot 6$ | $25 \cdot 6 \pm 6 \cdot 5$ | $32 \cdot 7 \pm 6 \cdot 4$ |
| 19. Foramen sphenoidale medium | $79 \cdot 1 \pm 3 \cdot 1$ | $77 \cdot 9 \pm 3 \cdot 2$ | $75 \cdot 8 \pm 5 \cdot 6$ |
| 20. Absent processus pterygoideus | $3 \cdot 8 \pm 1 \cdot 2$ | $12 \cdot 7 \pm 5 \cdot 3$ | $16.4 \pm 3 \cdot 2$ |
| 21. Interparietal-occipital fusion | $2 \cdot 0 \pm 1 \cdot 3$ | $1.0 \pm 0.5$ | $1.4 \pm 0.6$ |
| 22. Occipital-periotic fusion | $3 \cdot 6 \pm 1 \cdot 5$ | $1 \cdot 9 \pm 1 \cdot 0$ | $1 \cdot 8 \pm 1 \cdot 8$ |
| 23. Foramen hypoglossi double | $76 \cdot 3 \pm 1 \cdot 5$ | $64 \cdot 9 \pm 5 \cdot 9$ | $62 \cdot 6 \pm 4 \cdot 0$ |
| 24. Absent fenestra flocculi | $5 \cdot 2 \pm 1 \cdot 5$ | $3 \cdot 7 \pm 1 \cdot 6$ | $5 \cdot 0 \pm 2 \cdot 8$ |
| 25. Accessory mental foramen | $9 \cdot 7 \pm 1 \cdot 3$ | $17 \cdot 3 \pm 3 \cdot 0$ | $17 \cdot 3 \pm 3 \cdot 9$ |
| 26. Lower third molar missing | $0 \cdot 4 \pm 0 \cdot 2$ | 0.0 | $0 \cdot 9 \pm 0 \cdot 4$ |
| 27. Dyssymphysis posterior CII | $3 \cdot 0 \pm 1 \cdot 0$ | $1 \cdot 1 \pm 0 \cdot 8$ | $0 \cdot 5 \pm 0.5$ |
| 28. Absent arch foramina CIII | $2 \cdot 0 \pm 0 \cdot 4$ | $3 \cdot 0 \pm 0.9$ | $2 \cdot 2 \pm 0 \cdot 3$ |
| 29. Foramen transversarium on CVII | $4 \cdot 4 \pm 2 \cdot 2$ | $2 \cdot 3 \pm 0 \cdot 8$ | $2 \cdot 2 \pm 1 \cdot 1$ |
| 30. Size processus spinosus ThI | $17 \cdot 4 \pm 5 \cdot 6$ | $9 \cdot 5 \pm 4 \cdot 1$ | $2 \cdot 0 \pm 1 \cdot 1$ |
| 31. Absent processus ThII | $4 \cdot 8 \pm 2 \cdot 4$ | $4 \cdot 8 \pm 1 \cdot 8$ | $10 \cdot 0 \pm 4 \cdot 5$ |
| 32. Arch foramina ThV | $26 \cdot 1 \pm 4 \cdot 8$ | $23 \cdot 7 \pm 3 \cdot 5$ | $25 \cdot 7 \pm 4 \cdot 0$ |
| 33. LVI sacralized | $6.9 \pm 3 \cdot 9$ | $2 \cdot 5 \pm 0.9$ | $2.6 \pm 0.8$ |
| 34. Sacral fusions | $30 \cdot 4 \pm 5 \cdot 1$ | $32 \cdot 3 \pm 3 \cdot 5$ | $19 \cdot 0 \pm 4 \cdot 2$ |
| 35. Pink caudal vertebrae | $6 \cdot 0 \pm 1 \cdot 4$ | $2 \cdot 4 \pm 0 \cdot 8$ | $0 \cdot 6 \pm 0 \cdot 4$ |
| 36. Fossa olecrani perforata | $9 \cdot 7 \pm 1 \cdot 3$ | $4 \cdot 6 \pm 1 \cdot 6$ | $0 \cdot 9 \pm 0.2$ |
| 37. Foramen acetabuli perforans | $0 \cdot 6 \pm 0 \cdot 3$ | $0 \cdot 3 \pm 0.2$ | $0 \cdot 2 \pm 0 \cdot 1$ |

as they generally did not differ from each other in the frequencies of the variants examined, the data were subsequently pooled. The sorting of the data was done by computer which was programmed to produce tables with the number of skeletons affected in each replicate and the percentages of affected animals. Only the first 37 of the original 52 variants were used in this analysis (Tables 2, 5). The remaining variants occurred in so few animals in this material that they contributed virtually no information and were therefore disregarded.

## 3. RESULTS

The statistical treatment of the data has proved difficult and controversial; the full data have therefore been given in the Appendix (Table 5) so that the reader may carry out his own tests. The mean percentage incidence of 37 minor skeletal variants and their standard errors are given in Table 2, and this shows that in many cases the replicates differ widely from each other. Considering the variants jointly as a group, if the Large, Control and Small mice are designated $1,2,3$ respectively, then if there is a correlation between variant and body size, one would expect the respective means to be either in the order $1,2,3$ or $3,2,1$

Table 3. Analysis of variance of percentage incidence of five variants with significant $F$ values

| Character | Mean sq. between L, C and S | $F_{2,10}$ | Mean sq. between replicates | $F_{510}$ | Mean sq. residual |
| :---: | :---: | :---: | :---: | :---: | :---: |
| 2. Turned-up nose | $25 \cdot 8$ | $5 \cdot 0$ | $7 \cdot 2$ | $1 \cdot 4$ | $5 \cdot 2$ |
| 10. Frontal foramen double | $12 \cdot 7$ | $4 \cdot 4$ | $1 \cdot 5$ | 0.5 | $2 \cdot 9$ |
| 14. Basisphenoidbasioccipital fusion | 233.9 | 12•8* | $70 \cdot 8$ | $3 \cdot 9$ | $18 \cdot 2$ |
| 35. Pink caudal vertebrae | $44 \cdot 4$ | 11•1* | $8 \cdot 6$ | $2 \cdot 2$ | $4 \cdot 0$ |
| 36. Fossa olecrani perforata | $115 \cdot 7$ | 18•* | $13 \cdot 2$ | $2 \cdot 1$ | $6 \cdot 2$ |

(i.e. in ascending or descending order as in variants 5 and 1 in Table 2). The other four possible orders would not constitute a prima facie case for correlation. In the absence of correlation with body size, the six possible orders are equally likely, with 1, 2, 3 and 3, 2, 1 combined expected to form one third of the total. A significant excess of these two classes over that expectation would constitute evidence that the group as a whole includes variants whose manifestation is correlated with body size.

Variants 4, 25 and 31 (Table 2) cannot be used for this test as two of the three means are identical. Among the remaining 34 variants, there are 19 which occur in the order $1,2,3$ or $3,2,1$ (chance expectation in the absence of correlation $=$ $11.33)$. The difference is significant at the 0.01 level $\left(\chi_{1}^{2}=7.79\right)$ and hence the
conclusion seems justified that the array of 34 variants includes a group whose manifestation is correlated with body size.

An analysis of variance of percentages of each of the 37 variants revealed five with significant $F$ values (Table 3). Even though the usual assumptions of analysis of variance are not altogether met, these seem reasonably trustworthy. For pink caudal vertebrae (no. 35 of Table 2) and fossa olecrani perforata (36) there was a significant difference between the means of the selections and the controls. In turned-up nose (2) the mean for Small mice was significantly different from both the other two means, which were not significantly different from each other. For frontal foramen double (10) and basisphenoid-basioccipital fusion (14) Large

Table 4. Q-strain (generation 10) : birth weights, 3-week weights and 6-week weights of Large ( $L$ ) and of Small ( $S$ ) mice; L/S values

|  | Birth weights | 3 -week <br> weights | 6 -week <br> weights |
| :--- | :---: | :---: | :---: |
| A | 1.153 | 1.787 | 1.766 |
| B | 1.087 | 1.334 | 1.746 |
| C | 1.172 | 1.004 | 1.411 |
| D | 1.159 | 1.353 | 1.768 |
| E | 1.093 | 1.358 | 1.691 |
| F | 1.371 | 1.378 | 1.896 |
| Mean | 1.173 | 1.369 | 1.713 |

mice were significantly different from the other two groups which, again, were not significantly different from each other. In each of these cases (except for frontal foramen double) the means are in ascending or descending order (see above) and therefore constitute evidence for correlation with size. Frontal foramen double, which is a bilateral character, affected very few animals symmetrically and is not a particularly common variant in this material. However, the variant was present in Large mice almost twice as frequently as in the Control and Small mice, although this does not constitute evidence for correlation with size.

Selection in Falconer's Q-strain was based on 6 -week weights. The majority of the minor skeletal variants arise in pre-natal life. Hence, if the genes selected mostly affect post-natal growth, they would not be expected to influence the manifestation of variants which arise before birth. For generation 10 (and this will differ little from generations 13-14), Professor Falconer has kindly supplied birth- and 3 -week weights of Large, Control and Small mice; the 6-week weights were read off Falconer's (1973) graphs in Fig. 7. Values of L/S for the six replicates are given in Table 4. At birth, $L$ already exceeds $S$ by about $17 \%$ in weight, and it may be presumed that this difference arose early enough in pre-natal life to have influenced the manifestation of some of the 34 variants; later the difference increases to $37 \%$ at 3 weeks and to $71 \%$ at 6 weeks. The high degree of heterogeneity between replicates is noteworthy. The correlation between birth weights and 60day weights could be demonstrated from other sources but, coming from different
(and inbred) strains, it would have been less direct, and in any case the data of Table 4 are sufficient for our purpose.

## 4. DISCUSSION

As shown above, there is good evidence that a group of skeletal variants in the Q-strain include some characters which are correlated with body size. It would be of interest to compare them with the similar group of variants identified in the diet experiment of Deol \& Truslove (1957). Unfortunately, this is fraught with difficulty. The C57BL strain is noted for the richness of its skeletal variation. The Qstrain mice, by contrast, are rather disappointingly uniform in this respect, and many of the features studied in C57BL are either completely absent or so rare as to give virtually no information either way. Moreover, the four variants for which there is evidence for correlation with size have not been classified in C57BL. It therefore seems unprofitable to discuss these variants in detail. The most that can be said is that the present data do not seem to be at variance with those found in the C57BL experiment.

All the replicates in the $Q$-strain have unique skeletal profiles so far as the minor skeletal variants are concerned, and this is presumably mainly, if not entirely, the result of genetic drift (Falconer, personal communication). On the other hand, the skeletons of Large and Small mice have characteristic bones (i.e. size, shape, density, etc.) which presumably are the direct or indirect result of selection. The study of these differences is outside the scope of the present investigation, but they may well turn out to be of considerable interest.

I am indebted to Professor D. S. Falconer and to Miss H. I. Macrae (for providing the mice), to Miss Jacky Cox (for help with classification), to Professor C. A. B. Smith (for statistical advice), to Dr G. A. de S. Wickramaratne (for help with the calculations) and to Professor H. Grüneberg for his help and encouragement.

## REFERENCES

Berry, R.J. \& Searle, A. G. (1963). Epigenetic polymorphism of the rodent skeleton. Proceedings of the Zoological Society of London 140, 577-615.
Deos, M. S. (1955). Genetical studies on the skeleton of the mouse. XIV. Minor variations of the skull. Journal of Genetics 53, 498-514.
Deol, M. S. \& Troslove, G. M. (1957). Genetical studies on the skeleton of the mouse. XX. Maternal physiology and variation in the skeleton of C57BL mice. Journal of Genetics 55, 288-312.
Falconer, D. S. (1973). Replicated selection for body weight in mice. Genetical Research 22, 291-321.
Grüneberg, H. (1950). Genetical studies on the skeleton of the mouse. I. Minor variations of the vertebral column. Journal of Genetics 50, 112-141.
Grüneberg, H. (1963). The Pathology of Development. Oxford: Blackwell Scientific Publications.
Howe, W. L. \& Parsons, P. A. (1967). Genotype and environment in the determination of minor skeletal variants and body weight in mice. Journal of Embryology and Experimental Morphology 17, 283-292.

Levin, E. Y. \& Flyger, V. (1971). Uroporphyrinogen III cosynthetase activity in the fox squirrel (Sciurus niger). Science 174, 59-60.
Searle, A. G. ( $1954 a)$. Genetical studies on the skeleton of the mouse. IX. Causes of skeletal variation within pure lines. Journal of Genetics 52, 68-102.
Searle, A. G. (1954b). Genetical studies on the skeleton of the mouse. X. Rarer variants in the A and C57BL pure lines. Journal of Genetics 52, 103-110.
Searie, A. G. (1954c). Genetical studies on the skeleton of the mouse. XI. The influence of diet on variation within pure lines. Journal of Genetics 52, 413-424.
Wickramaratne, G. A. de S. (1974). The 'skeletal profile' and dentition of some inbred strains of mice. Journal of Anatomy 117, 565-573.

## APPENDIX

The full data are given in Table 5, below. The variants not previously described are as follows:
(i) Variant 2: turned-up nose

Turned-up nose, unlike bent-nose (Searle, 1954b), only involves the anterior border of the nasals. These bones instead of being almost flat dorsally have the anterior quarter tilted dorsally. There may also be shortening of the underlying jaw bones. This variant tends to be a particular feature of Small mice.
(ii) Variant 30: size of processus spinosus on ThI

In $17 \%$ of the Large mice there was an abnormally large processus spinosus on the neural arch of the first thoracic vertebra. This was not associated with a dystopia of a large spine from the second thoracic vertebra. In fact this latter condition was extremely rare ( 4 mice in QLE, 2 in QLF and 1 in QCB), while the size of the spine on ThI was increased irrespective of the size of that on ThII. This is in marked contrast to the position in C57BL, where dystopia is the most usual cause of an increase in the size of the processus spinosus on ThI (Grüneberg, 1950).

## (iii) Variant 35: pink caudal vertebrae

This is a new entity which was noticed as the skeletons were processed and after they had passed through hydrogen peroxide and through acetone. Some of the proximal caudal vertebrae in certain skeletons seemed to be stained pale pink and further investigation revealed that this was usually confined to the larger animals (Table 2, no. 35). On the other hand there were some skeletons where the proximal caudal vertebrae were yellowish or brown. These may have started off as pink vertebrae, but faded in the light. If the skeletons were classified for coloured caudal vertebrae (pink, yellow or brown) then there are $57 \%$ in $\mathrm{L}, \mathbf{3 6 \%}$ in C and $36 \%$ in S . Males are more often affected than females (L, $59 \%{ }^{\mathbf{o}} \mathbf{\delta} \mathbf{\delta}, 55 \%$ 아;


The substance causing the coloration has not been identified, but it is not soluble in acetone and it does not fluoresce in u.v. light. Levin \& Flyger (1971) report an increase in the amount of uroporphyrin I in fox squirrels (Sciurus niger) owing to the lower activity of uroporphyrinogen III cosynthetase in tissue extracts compared with similar extracts from grey squirrels (Sciurus carolinensis). In the
former animals the bones are pink, but the authors do not say in what state the bones are, as all of them always look pink in freshly killed animals. The authors claim that this provides a small animal model for studies of erythropoietic porphyria, an hereditary disease of man and cattle which is associated with a similar partial deficiency of uroporphyrinogen III cosynthetase. It looks as though there may perhaps be a similar condition in the mouse, even though the only bones that are coloured are the first few caudal vertebrae.

## Table 5. Incidence of minor skeletal variants in the six replicates $(A-F)$ of Large ( $L$ ), Control (C) and Small (S) mice of the Q-strain

(For central characters the numbers refer to individuals and for bilateral characters to sides of individuals)

| Variant |  | A | B | C | D | E | F |
| :--- | ---: | ---: | ---: | ---: | ---: | ---: | ---: |
|  | L | $0 / 110$ | $2 / 107$ | $0 / 101$ | $0 / 105$ | $0 / 105$ | $1 / 108$ |
| 1. Bent nose | C | $0 / 104$ | $0 / 100$ | $8 / 104$ | $0 / 104$ | $1 / 109$ | $2 / 111$ |
|  | S | $0 / 102$ | $10 / 103$ | $0 / 136$ | $4 / 103$ | $0 / 105$ | $9 / 100$ |
| 2. Turned-up nose | L | $0 / 110$ | $0 / 107$ | $0 / 101$ | $0 / 105$ | $0 / 105$ | $2 / 108$ |
|  | C | $0 / 104$ | $0 / 100$ | $1 / 104$ | $0 / 104$ | $2 / 109$ | $1 / 111$ |
| 3. Maxillary-turbinal fusion | S | $0 / 102$ | $8 / 103$ | $1 / 136$ | $4 / 103$ | $2 / 105$ | $10 / 100$ |
|  | L | $42 / 220$ | $21 / 214$ | $28 / 202$ | $33 / 210$ | $57 / 210$ | $29 / 216$ |
|  | C | $38 / 208$ | $11 / 200$ | $63 / 208$ | $30 / 208$ | $56 / 218$ | $38 / 222$ |
|  | S | $21 / 204$ | $20 / 206$ | $23 / 272$ | $31 / 206$ | $38 / 210$ | $37 / 200$ |
| 4. Nasals fused | L | $1 / 110$ | $0 / 107$ | $0 / 100$ | $0 / 105$ | $0 / 105$ | $1 / 108$ |
|  | C | $0 / 103$ | $0 / 100$ | $0 / 104$ | $0 / 103$ | $2 / 109$ | $0 / 111$ |
|  | S | $0 / 102$ | $6 / 103$ | $1 / 133$ | $1 / 102$ | $0 / 105$ | $11 / 100$ |
| 5. Fused frontals | L | $13 / 110$ | $9 / 107$ | $34 / 101$ | $24 / 105$ | $41 / 105$ | $21 / 108$ |
|  | C | $52 / 104$ | $13 / 100$ | $23 / 104$ | $10 / 104$ | $15 / 109$ | $11 / 111$ |
|  | S | $6 / 102$ | $27 / 103$ | $8 / 136$ | $11 / 103$ | $9 / 105$ | $5 / 100$ |
| 6. Interfrontal absent | L | $13 / 110$ | $5 / 107$ | $29 / 101$ | $4 / 105$ | $6 / 105$ | $2 / 108$ |
|  | C | $7 / 104$ | $27 / 100$ | $23 / 104$ | $3 / 104$ | $3 / 109$ | $2 / 111$ |
|  | S | $9 / 102$ | $2 / 103$ | $27 / 136$ | $9 / 103$ | $9 / 105$ | $10 / 100$ |
| 7. Interfrontal-frontal fusion | L | $4 / 194$ | $2 / 202$ | $12 / 132$ | $7 / 200$ | $37 / 198$ | $2 / 212$ |
|  | C | $15 / 192$ | $4 / 144$ | $2 / 158$ | $5 / 198$ | $4 / 210$ | $3 / 214$ |
|  | S | $1 / 180$ | $12 / 202$ | $1 / 206$ | $3 / 174$ | $10 / 190$ | $1 / 172$ |
|  | L | $95 / 110$ | $88 / 107$ | $96 / 101$ | $102 / 105$ | $27 / 105$ | $84 / 108$ |
| 8. Parted frontals | C | $83 / 104$ | $98 / 100$ | $94 / 104$ | $103 / 104$ | $94 / 109$ | $109 / 111$ |
|  | S | $102 / 102$ | $47 / 103$ | $130 / 136$ | $101 / 103$ | $98 / 105$ | $100 / 100$ |
|  | L | $1 / 110$ | $0 / 107$ | $1 / 101$ | $2 / 105$ | $1 / 105$ | $0 / 108$ |
| 9. Frontal fontanelle | C | $0 / 104$ | $15 / 100$ | $0 / 104$ | $5 / 104$ | $5 / 109$ | $2 / 111$ |
|  | S | $24 / 102$ | $1 / 103$ | $0 / 136$ | $49 / 103$ | $2 / 105$ | $6 / 100$ |
|  | L | $12 / 220$ | $10 / 214$ | $5 / 202$ | $14 / 210$ | $17 / 210$ | $11 / 216$ |
| 10. Frontal foramen double | C | $6 / 208$ | $5 / 200$ | $8 / 208$ | $2 / 208$ | $10 / 218$ | $4 / 222$ |
|  | S | $8 / 204$ | $5 / 206$ | $8 / 272$ | $11 / 206$ | $3 / 210$ | $5 / 200$ |
| 11. Preoptic sutures | L | $51 / 220$ | $131 / 214$ | $34 / 202$ | $15 / 210$ | $58 / 210$ | $156 / 216$ |
|  | C | $38 / 208$ | $96 / 198$ | $46 / 208$ | $79 / 208$ | $49 / 218$ | $32 / 222$ |
| 12. Metoptic roots abnormal | S | $84 / 204$ | $120 / 206$ | $79 / 270$ | $156 / 206$ | $76 / 210$ | $52 / 200$ |
|  | $14 / 220$ | $62 / 214$ | $29 / 202$ | $30 / 210$ | $78 / 210$ | $27 / 216$ |  |
|  | C | $86 / 208$ | $15 / 198$ | $23 / 208$ | $80 / 208$ | $26 / 218$ | $94 / 222$ |
|  | S | $20 / 204$ | $26 / 206$ | $47 / 270$ | $135 / 206$ | $117 / 210$ | $102 / 200$ |
|  |  |  |  |  |  |  |  |

Table 5 (cont.)

| Variant |  | A | B | C | D | E | F |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 13. Basisphenoid-presphenoid fusion | L | 15/110 | 10/107 | 2/101 | 7/105 | 22/105 | 10/108 |
|  | C | 2/104 | 6/100 | 6/104 | 3/104 | 11/109 | 5/111 |
|  | S | 2/102 | 6/103 | 3/136 | 6/103 | 15/105 | 21/100 |
| 14. Basisphenoid-basioccipital fusion | L | 29/110 | 20/107 | 2/101 | 4/105 | 13/105 | 18/108 |
|  | C | 10/104 | 5/100 | 0/104 | 0/104 | 1/109 | 1/111 |
|  | S | 5/102 | 6/103 | 3/136 | 0/103 | 1/105 | 0/100 |
| 15. Preorbital foramen double | L | 48/220 | 31/214 | 25/202 | 32/210 | 19/210 | 24/214 |
|  | C | 37/208 | 46/200 | 44/208 | 40/208 | 29/218 | 25/222 |
|  | S | 33/204 | 39/206 | 42/272 | 51/206 | 58/208 | 44/200 |
| 16. Accessory maxillary foramen | L | 13/220 | 10/214 | 22/202 | 13/210 | 8/210 | 6/216 |
|  | C | 9/208 | 22/200 | 10/208 | 16/208 | 20/218 | 7/222 |
|  | S | 5/204 | 5/206 | 16/272 | 2/206 | 10/210 | 9/200 |
| 17. Foramen palatinum majus double | L | 19/220 | 28/214 | 29/202 | 33/210 | 10/210 | 25/216 |
|  | C | 12/208 | 12/200 | 19/208 | 14/208 | 16/218 | 11/222 |
|  | S | 8/204 | 11/206 | 52/272 | 11/206 | 13/210 | 7/200 |
| 18. Foramen ovale single | L | 43/220 | 18/214 | 35/202 | 35/210 | 57/210 | 29/216 |
|  | C | 76/208 | 94/200 | 36/208 | 31/208 | 11/218 | 75/222 |
|  | S | 63/204 | 81/206 | 87/272 | 121/206 | 27/210 | 46/200 |
| 19. Foramen sphenoidale medium | L | 22/110 | 24/107 | 23/101 | 35/105 | 17/105 | 12/108 |
|  | C | 85/104 | 71/100 | 93/104 | 80/104 | 74/109 | 89/111 |
|  | S | 88/102 | 76/103 | 122/136 | 74/103 | 81/105 | 51/100 |
| 20. Absent processus pterygoideus | L | 19/220 | 9/214 | 3/202 | 2/210 | 11/210 | 4/216 |
|  | C | 10/208 | 12/200 | 1/208 | 76/208 | 37/218 | 24/222 |
|  | S | 11/204 | 25/206 | 76/272 | 36/206 | 41/210 | 24/200 |
| 21. Interparietal-occipital fusion | L | $0 / 110$ | 1/107 | 0/101 | 9/105 | 2/105 | 1/108 |
|  | C | 0/104 | 1/100 | 2/102 | 0/104 | 0/109 | 3/111 |
|  | S | 0/102 | 2/103 | 5/136 | 2/103 | 0/105 | 0/100 |
| 22. Occipital-periotic fusion | L | 4/220 | 8/214 | 3/202 | 3/210 | 5/210 | 23/216 |
|  | C | 12/208 | 1/200 | 2/208 | 9/208 | 0/218 | 0/222 |
|  | S | 0/204 | 22/206 | 0/272 | 1/206 | 0/210 | 0/200 |
| 23. Foramen hypoglossi double | L | 159/220 | 171/214 | 149/202 | 153/210 | 165/210 | 174/216 |
|  | C | 143/208 | 161/198 | 97/208 | 98/206 | 157/218 | 162/222 |
|  | S | 155/204 | 139/206 | 155/272 | 129/206 | $140 / 210$ | 95/200 |
| 24. Absent fenestra flocculi | L | 6/220 | 8/214 | 3/202 | 16/210 | 8/208 | 25/216 |
|  | C | 5/208 | 3/200 | 21/208 | 14/206 | 0/218 | 3/222 |
|  | S | 2/204 | 37/206 | 5/272 | 2/204 | 2/210 | 17/200 |
| 25. Accessory mental foramen | L | 23/220 | 31/214 | 23/202 | 12/210 | 15/210 | 19/216 |
|  | C | 32/208 | 41/200 | 36/208 | 61/208 | 34/218 | 15/222 |
|  | S | 52/204 | 68/206 | 41/272 | 23/206 | 19/210 | 22/220 |
| 26. Lower third molar missing | L | 1/220 | 0/214 | 1/202 | 0/210 | 3/210 | 0/216 |
|  | C | 0/208 | 0/200 | 0/208 | 0/208 | 0/218 | 0/222 |
|  | S | 3/204 | 0/206 | 3/272 | 1/206 | 0/210 | 5/200 |
| 27. Dyssymphysis posterior CII | L | 0/110 | 1/107 | 5/101 | 7/105 | 3/105 | 3/108 |
|  | C | 1/102 | 1/100 | 0/104 | 5/104 | 0/109 | 0/111 |
|  | S | 3/101 | 0/103 | 0/136 | 0/103 | 0/105 | $0 / 100$ |
| 28. Absent arch foramina CIII | L | 1/220 | 4/214 | 5/202 | 3/208 | 6/210 | 6/214 |
|  | C | 1/208 | 13/198 | 3/208 | 8/208 | 6/216 | 6/218 |
|  | S | 5/204 | 6/206 | 8/272 | 3/204 | 4/210 | 2/200 |

Table 5 (cont.)

| Variant |  | A | B | C | D | E | F |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| 29. Foramen transversarium on CVII | L | 0/218 | 3/214 | 28/198 | 6/208 | 16/210 | 2/214 |
|  | C | 1/208 | 2/198 | 5/206 | 11/208 | 1/218 | 9/222 |
|  | S | 14/202 | 9/204 | 0/272 | 3/206 | 1/210 | 2/200 |
| 30. Size of processus spinosus ThI | L | 17/110 | 13/106 | 18/100 | 5/104 | 10/105 | 47/107 |
|  | C | 0/103 | 6/100 | 24/104 | 4/104 | 23/109 | 3/110 |
|  | S | 0/102 | 3/103 | 1/136 | 1/103 | 1/105 | 7/99 |
| 31. Absent processus ThII | L | 13/110 | 1/106 | 1/100 | 0/104 | 13/104 | 2/107 |
|  | C | 8/103 | 3/99 | 2/104 | 13/103 | 1/108 | 3/107 |
|  | S | 28/100 | 8/101 | 2/133 | 5/100 | 20/104 | 0/91 |
| 32. Arch foramina ThV | L | 33/220 | 32/214 | 44/202 | 94/208 | 56/210 | 73/216 |
|  | C | 51/208 | 31/200 | 41/208 | 81/208 | 37/218 | 59/222 |
|  | S | 55/204 | 38/206 | 34/272 | 79/206 | 74/210 | 53/200 |
| 33. LVI sacralized | L | 2/220 | 1/212 | 0/202 | 6/210 | 30/210 | 49/214 |
|  | C | 13/208 | 1/200 | 6/208 | 0/208 | 8/218 | 4/222 |
|  | S | 5/204 | 13/206 | 5/272 | 2/204 | $6 / 210$ | 2/200 |
| 34. Sacral fusions | L | 42/110 | 16/107 | 18/101 | 34/105 | 31/105 | 52/108 |
|  | C | 39/104 | 46/100 | 28/104 | 28/104 | 38/109 | 25/111 |
|  | S | 17/102 | 27/103 | 23/136 | 5/103 | 16/105 | 35/100 |
| 35. Pink caudal vertebrae | L | 1/110 | 9/107 | 6/101 | 3/105 | 10/105 | 9/108 |
|  | C | 0/104 | 2/100 | 2/104 | 1/104 | 4/109 | 6/111 |
|  | S | 2/102 | 0/103 | 0/136 | 0/103 | 0/105 | 2/100 |
| 36. Fossa olecrani perforata | L | 18/220 | 34/214 | 18/202 | 19/210 | 13/210 | 21/216 |
|  | C | 19/208 | 19/200 | 1/208 | 4/208 | 6/218 | 9/222 |
|  | $\mathbf{S}$ | 0/204 | 3/206 | 4/272 | 2/206 | $2 / 210$ | 1/200 |
| 37. Foramen acetabuli perforans | L | 4/220 | 0/214 | 0,202 | 2/210 | $0 / 210$ | 1/216 |
|  | C | 0/208 | 1/198 | 2/208 | 0/208 | 0/218 | 1/222 |
|  | S | 0/204 | 0/206 | 1/272 | 0/206 | 0/210 | 1/200 |

