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Metrical and non-metrical skull traits of the common shrew *Sorex araneus* and their use in population studies

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This paper describes in detail dozens of metrical and non-metrical (epigenetic) skull traits of the common shrew that have been found useful in ecological and other biological studies. Cleaning of the bone material for morphometrical studies is described with some practical hints. A new method of taking metrical measurements of the lower jaw from digitized outlines of the bone is described. The technique may be adapted to other bones as well. We describe thirty non-metrical traits, mostly minor foramina, of the skull and the lower jaw. The distributions of different variants of these traits are described, and differences between sexes, age groups and years in one set of material are analysed. The use of bilateral traits in the study of fluctuating asymmetry is discussed, with examples.

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1. Introduction

Phenotypic variation within and between populations of mammals is usually characterized with measurements of the skull. In large species of mammals, metrical measurements can be taken with a sliding caliper, while in smaller species a dissecting microscope with an ocular micrometer is commonly used. Apart from the metrical measurements, non-metrical or "epigenetic" traits have been scored in some species, especially in rodents (for a review see Bachau 1988). Non-metrical variation is often considered to reflect underlying genetical variation in natural populations (e.g. Berry 1963, Berry et al. 1978, Bachau 1988). In shrews, non-metrical variation has been examined by Hanski (1986) and Hanski & Kuitunen (1986).

The purpose of this study is to describe in detail the metrical and non-metrical traits which we have found useful in studies of morphological variation of the common shrew *Sorex araneus* L. Cleaning of the skull of the shrew poses special problems because of its small size. We present here a rapid and easy cleaning method suitable for small mammals. Taking manual measurements of small bones is time-consuming and requires some training. We describe a measurement system based on the digitized outline of the bone, which avoids these problems and reduces measurement error. We apply this approach to the lower jaw (mandible), but it is adaptable to other relatively flat bones. The metrical and non-metrical traits described in this paper are used in our studies of population differentiation (Hanski & Kuitunen 1986), developmental stability (Zakharov et al. unpubl.) and dispersal (Hanski & Peltonen unpubl.). For the purposes of demonstration we use here a sample of 180 common shrews from South Finland.

2. Material and methods

2.1. Trapping and dissecting of shrews

The sample of shrews which we use in this paper to illustrate the various morphological traits was caught with pitfall traps in Lohja, Jalassaari, southern Finland in 1975–80 (Pankakoski 1979, Pankakoski & Tähkä 1982). The length of the shrew was measured with a ruler to the nearest mm, and the animal was weighed with a "Pesola" spring-scale (capacities of 10 or 30 g)

to the nearest 0.1 g. After preservation in 80% alcohol for several years, random samples of about 30 juvenile (year-born) shrews caught in late summer in 1975–80 were selected for further study. The sample consisted of equal numbers of the two sexes. A sample of 10 adult (overwintered) males caught in the early summer of 1980 was included for a comparison of age groups.

2.2. Cleaning of skulls

The skulls were cleaned enzymatically with papain (Searle 1954, Hanski & Kuitunen 1986). The recommended procedure is as follows. The head of the animal is skinned, removed, boiled for 5 minutes and placed in a solution of papain (about 60 mg of papain in 100 ml of 0.9% NaCl solution). The heads are kept individually in plastic tubes at 38°C for 2–3 days, and the tubes shaken once a day. The skull and the lower jaws are then washed in water and allowed to dry on blotting paper.

Prolonged exposure of the skulls to papain may soften or fracture the bone. If the skulls are cleaned for foramen counts, it is preferable to keep them for less than 3 days in the enzyme solution, and to clean the residual soft tissues under the dissecting binocular microscope. Manual cleaning is best done in water, using a small brush with the hairs cut short; this is the best method of cleaning the palate and the largest openings of the skull. The removal of the brain is also possible at this stage, but it is not essential. If mandibles only are needed, manual cleaning with the brush can be replaced by longer exposure to the enzyme, which may, however, cause loss of the teeth, and the joints between the bones of the braincase may open, making measurements of the braincase impossible. Enzymatic cleaning of the entire carcass is also possible, even with specimens preserved in alcohol (Hanski & Kuitunen 1986), though deep-freezing is a preferable method for preservation. The alcohol solution must not be too strong (preferably about 70%).

3. Non-metrical traits

3.1. Scoring of foramina: principles

The numbers of foramina (openings for nerves and small blood vessels) in the cleaned skulls are counted under a dissecting binocular microscope (in our case Wild M5, magnification 25×, ocular 10×). We have scored 30 foramen areas on both sides of the skull (Fig. 1). Two of the areas (nos 10 and 11) actually represent the roots of teeth, which usually become loosened during enzymatic cleaning, but these are also called "foramina" below.

The smallest foramina are often difficult to see and score. If the foramen is not visible as a dark opening in the bone, it is not taken into count. Because there is a continuum in the size of foramina, the presence of the smallest foramina is confirmed by using a lower magnification (12×): the foramen is included if it is still visible. During the scoring the investigator must turn the skull under the microscope, so that foramina that are slanting in position will be recognized. Occasionally it is impossible to reliably tell to which of two adjacent foramen areas a foramen should be included (for example, areas 5 and 6). In studies of asymmetry one must take care not to increase asymmetry artificially by placing the borderline between the two foramen areas in different places on different sides of the skull (for example, foramen 5: 0–1, foramen 6: 1–0). This point will be further discussed in Section 3.4.

3.2. Foramina scored

We have scored the following foramina (Fig. 1; modified from the system of Peter King 1985, in a letter). Nos 1–9: foramina on the sides of the snout in the upper jaw; nos 10–16: foramina on the sides of the middle and posterior part of the skull; nos 17–25: foramina in the underside of the cranium; nos 26–30: foramina in the mandibles.

Foramen areas 1–9 (foramina on the sides of the snout in the upper jaw):

The foramina were counted on both sides of the snout, excluding the upper part, above the hatched line in Fig. 1a. Foramen areas can be separated as follows (Fig. 1a):

1: Area above the teeth, posterior to the front tooth to halfway of the 2nd unicuspid. The number of foramina may be large, up to 10 or more in this area.

2 and 3: Area above the teeth from the halfway of the 2nd unicuspid to the border between the 3rd and 4th unicuspids. This area contains almost always at least one big foramen (no 3). The small foramina that are usually situated near the teeth include no 2. The exceptional small foramina close to the large one (no 3) are counted as belonging to it.

4: Area above the teeth from the border of the 3rd and 4th unicuspids to the border of the 5th unicuspid and the 1st molar (M^1).

5 and 6: Areas situated above M^1, some distance above it, anteriorly to the large opening (I in Fig. 1a). Area 5 is usually situated on the ridge formed by the anterior root of M^1, area 6 is located somewhat more posteriorly. The large openings which are often present on the upper end of the anterior root of M^1 are included in area 5. Area 6 does not include the foramina inside the large opening I.

7: Area is situated above the second molar (M^2) below the posterior end of opening I and the anterior

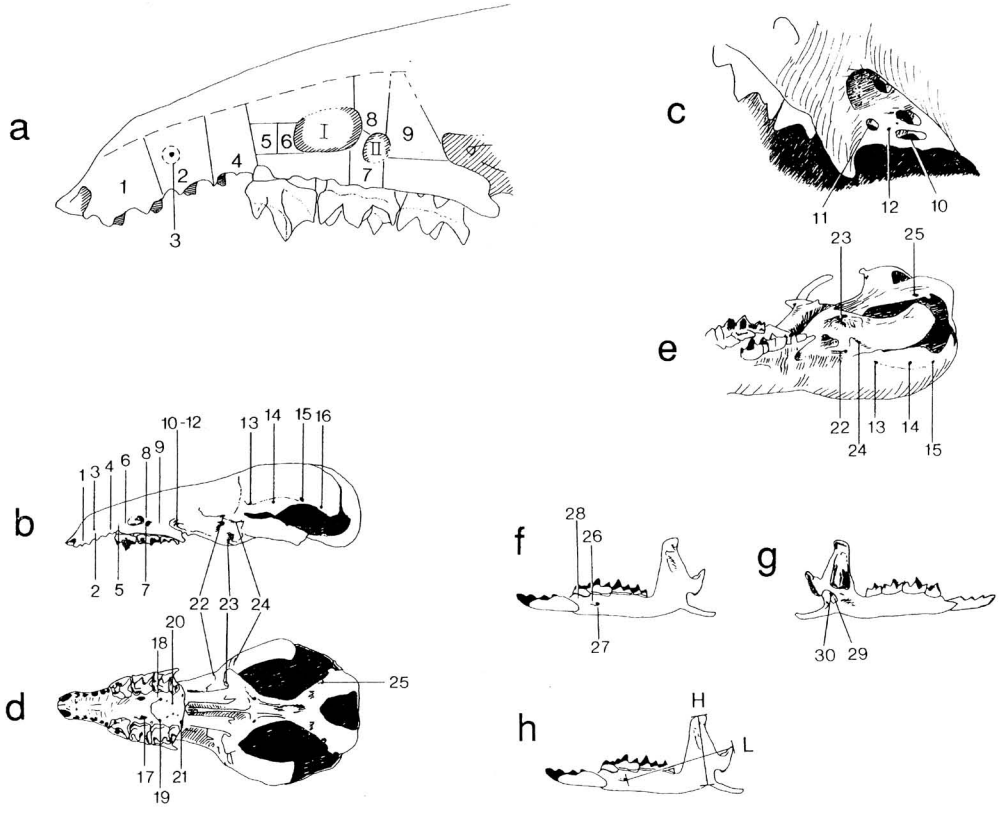

Fig. 1. The foramina scored and the two metrical measurements taken under the dissecting binocular microscope. For details, see text.

end of opening II (Fig. 1a); occasionally foramina can also be found just inside opening II. The foramina in this area are usually of medium to large size, but can be slanted and therefore difficult to see.

8: Area is situated above the previous one, posteriorly to opening I and above opening II (Fig. 1a). Foramina may also be present on the posterior edge of opening I.

9: Area is situated posteriorly to area 8, at about the same height as the latter, at some distance above the teeth.

Foramen areas 10–16 (foramina on the sides of the middle and posterior part of the skull; Fig. 1b,c):

Foramina 10–12 are scored by looking at the region of the 4th upper molar from above (Fig. 1c).

10 and 11: The roots of the two last upper molars are visible through large openings in dorsal view. The teeth easily become loosened during enzymatic cleaning, so that usually only the openings can be seen. One opening of the 3rd upper molar and three of the 4th upper molar is a common count (no 10). Some of the root openings are small. The number of these small openings represents no 11. Notice that these small openings are thus included in the numbers of both nos 10 and 11.

12: Foramen 12 is the number of small foramina bounded by the triangle of the three root openings of the 4th upper molar.

13–16: Foramina 13–16 are situated on the side of the braincase (Fig. 1b). Foramina 13 and 15 in particular are generally relatively large openings in the

bone. No 14 is situated below the ridge of the bone connecting the areas of nos 13 and 15. No 15 may sometimes be expressed as a narrow slip. No 16 is situated at the posterior end of a thin bone projection.

Foramen areas 17–25 (foramina in the underside of the cranium; Fig. 1d):

17: A large opening approximately in the middle of the hard palate, near the posterior side of the 2nd upper molar.

18 and 19: The hard palate has a U-shaped suture in the bone, the pointed ends projecting backwards. No 19 is the number of relatively large openings (usually 1 or 2) in this suture or "inside" it. No 18 is situated anteriorly to this suture ("outside" it) between nos 17 and 19. No 18 is rare.

20: Area posterior to the U-shaped suture, near the 3rd and 4th upper molars. There are frequently several foramina in this area, which is rather wide and sometimes difficult to separate from no 21.

21: These foramina are usually longitudinal openings in the posterior ridge of the palate.

Foramina 22–24 are situated approximately in the middle of the skull. The numbers of foramina are small or they may be absent (Fig. 1b,d,e).

22: The foramina in the groove anterior to the relatively large, round opening towards the brain. In some cases another groove and nerve opening can be found below this area. All the openings, the large ones included, comprise no 22.

23: Area down and backwards from the previous area. The number of foramina on the sides of the large cavity or "tunnel" projecting towards the brain. To score these foramina the skull should be in an anterior-dorsal position (as in Fig. 1e).

24: The oval depression, which is the place in which the mandible is joined to the cranium.

25: Under the braincase, near the Foramen magnum there is always a reasonably large foramen. The number of smaller foramina adjacent to it is counted.

Foramen areas 26–30 (foramina in the mandibles; Fig. 1f,g):

There is always a large foramen (Foramen mentale) on the outer (buccal) side of the mandible. It is projected forwards and there is a groove in front of it.

26 and 27: Small foramina in the groove anterior to Foramen mentale (26), or below it, not in the groove (27).

28: Area is situated anterior to the previous foramina near the front teeth on the outer side of the mandible.

29 and 30: On the inner (lingual) side of the coronoid process (Fig. 1g) there is a large depression, into which at least one large opening usually opens from below (no 30). Small foramina near the large one represent no 29.

Table 1. Statistics for skull foramen counts of juvenile shrews (Lohja 1975–80). The values given are the means for the two sides, except the range, in which extreme values on either side are presented. The foramina are divided into three groups based on standard deviations (*SD*): Group I: $SD < 0.45$; Group II: $SD = 0.45 - 0.95$; Group III: $SD = > 0.95$.

Foramen	Mean	*SD*	Median	max	min	*N*	Group
1	4.74	2.36	4.5	18	0	170	III
2	1.13	0.95	1.0	5	0	170	III
3	1.55	0.50	1.5	3	0	170	II
4	2.78	1.82	2.5	9	0	170	III
5	0.39	0.52	0.0	2	0	170	II
6	0.28	0.49	0.0	3	0	170	II
7	1.17	1.01	1.0	8	0	169	I
8	0.51	0.57	0.5	3	0	168	II
9	0.32	0.61	0.0	5	0	170	II
10	4.04	0.26	4.0	6	3	152	I
11	0.17	0.40	0.0	2	0	152	I
12	2.71	1.08	2.5	8	0	151	I
13	1.12	0.38	1.0	6	0	170	I
14	1.20	0.70	1.0	5	0	168	II
15	1.04	0.15	1.0	3	1	170	I
16	0.77	0.58	1.0	4	0	170	II
17	1.08	0.22	1.0	3	1	163	I
18	0.16	0.28	0.0	1	0	164	I
19	1.14	0.41	1.0	3	0	164	I
20	3.89	0.98	4.0	8	2	164	III
21	1.60	0.48	1.5	4	1	170	II
22	1.13	0.30	1.0	3	1	170	I
23	0.36	0.45	0.0	2	0	170	II
24	0.20	0.44	0.0	3	0	170	I
25	0.80	0.64	1.0	4	0	170	II
26	0.18	0.35	0.0	2	0	170	I
27	0.01	0.01	0.0	1	0	170	I
28	0.47	0.63	0.0	4	0	170	II
29	0.74	0.75	0.5	4	0	170	II
30	1.09	0.44	1.0	3	0	170	I

3.3. Numbers of foramina

Table 1 gives the mean foramen counts, calculated as the average of the two sides of the skull, for a sample from South Finland. By far the greatest range of variants was observed for foramen 1. In most traits, the average number of foramina is not significantly correlated with body size, whether the latter is measured by body weight and length or by the height and

Table 2. Correlations (r) between size and the foramen counts in juvenile shrews (N=170).

Size variable	Range	Positive values	Negative values	Deviation from 1:1
Body length	–0.13 – +0.18	10	20	ns
Body weight	–0.17 – +0.16	15	15	ns
Mandible height	–0.13 – +0.14	7	23	*
Mandible length	–0.13 – +0.15	7	23	*

the length of the mandible (these mandibular measurements were taken under the binocular microscope using an ocular scale; Fig. 1h). Although the absolute values of the correlation coefficients are low, there is a significant tendency towards negative correlations between the numbers of foramina and the dimensions of the mandible (Table 2). In other words, unexpectedly, foramen numbers are higher in individuals with smaller mandibles.

Females tend to have higher foramen counts than males. Univariate comparisons gave significant results for foramina 12 and 28 only, but Friedman's test over all the foramina gave a significant result (Table 3). Males belonging to the same cohort were compared before and after overwintering. The age groups did not differ in foramen counts, excepting foramina 10, 13 and 19 (higher values in juveniles; Table 3).

Univariate comparisons of foramen counts with the Kruskal-Wallis test show significant differences between the six years in several traits (Table 3). The foramina were classified into three groups according to the observed level of variation (Table 1). The sums of the two groups with most variable foramina show significant variation between the years (Sum-II and Sum-III; Table 3). These traits tended to have low foramen counts in 1975–1976, high counts in 1978, and intermediate counts in 1977 and 1979–80. Friedman's test over all the foramina and years also gave a highly significant result (Table 3).

Table 3. Comparison of foramen counts between sexes, age groups and years. Individual foramina and foramina in groups I to III (see Table 1) were tested with the Mann-Whitney and Kruskal-Wallis tests. Differences in foramen counts were also compared using Friedman's test based on the means of all foramina ("All foramina"). The age comparison was made between 15 juvenile and 10 adult males from the same cohort. The significant differences in sex and age are due to higher medians in females and juveniles, respectively. Foramina with no significant results have been omitted. Significance is indicated with asterisks: ns = not significant; o = P<0.1; * = P<0.05; ** = P<0.01; *** = P<0.001.

Foramen	Sex	Age	Years
1	ns	ns	*
2	ns	ns	o
5	ns	ns	*
7	o	ns	*
8	o	ns	ns
9	ns	ns	o
10	ns	*	ns
11	o	o	ns
12	*	o	*
13	ns	*	*
15	ns	ns	*
18	ns	ns	*
19	ns	**	ns
22	o	ns	ns
25	ns	ns	**
26	o	ns	ns
28	*	ns	ns
Sum-I	ns	ns	ns
Sum-II	ns	ns	**
Sum-III	ns	ns	*
All foramina	*	ns	***

3.4. Objective mapping of foramina

The positions of foramina on the side of the snout, below the hatched line in Fig. 2a, were mapped as accurately as possible with black dots on a line drawing of the skull (paper size 210 × 297 mm; Fig. 2a). Foramen size was roughly indicated by the size of the dot, ranging from 2 to 7 mm in diameter (usually ca 3 mm). Foramina were mapped for the two sides of 170 juveniles.

The drawings with dots were digitized with the following system. The digitizer used was "MicroScale I" (Digithurst Ltd.), with a 256 × 256 pixel image scanner (256 grey levels). The digitizer was con-

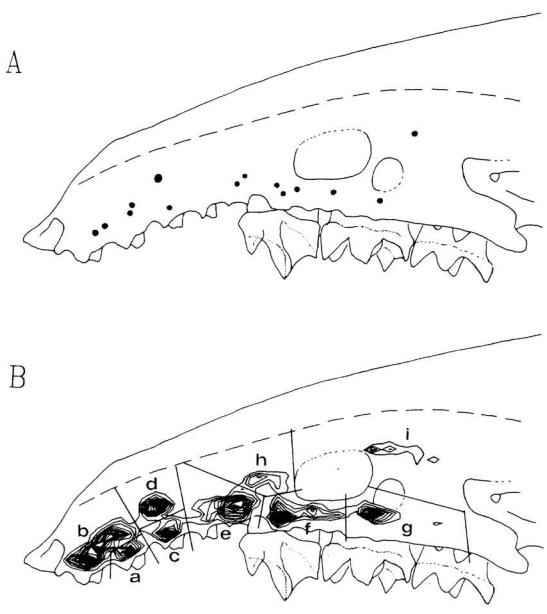

Fig. 2. Mapping of foramina of the snout on paper. A. An example of position and size of foramina when marked with black dots of different size on a line drawing. B. The distribution of the mean points of the coordinates of foramina for the 170 juvenile shrews. The new division of foramen areas is indicated by letters (a to i; cf. Fig. 1a).

nected to a videocamera and a microcomputer. We used a macro lens on the camera to obtain maximum resolution, and powerful sources of light to create a good contrast. The data was analyzed with a Pascal program written by IH.

The coordinates and the size of each foramen were calculated. Fig. 2b gives the distribution of the mean points of the foramina for the 170 shrews. Concentrations of foramina on certain areas is apparent, giving rise to a new division of these into nine foramen areas (a to i in Fig. 2b). The original delimitation of foramen areas (Fig. 1a) is generally supported, with the following exceptions: the original foramen area 1 may be divided into two areas (a and b; see below, however); the distinctions between the original foramen areas 5 and 6 (h) and 8 and 9 (i) appear not to be justified; while a new foramen area (f) might be introduced (Fig. 2b).

To calculate differences between the two sides the signs of the coordinates on the right side were reversed, and the two sides were centered according to the mean values of the foramen coordinates. Signed differences between right and left sides ($D_i = r_i - l_i$) on the nine new foramen areas were then calculated. These differences should not be correlated between adjacent, "natural" foramen areas. However, significant negative correlations were found between a and b ($P<0.001$), a and d ($P<0.05$), b and c ($P<0.05$), c and d ($P<0.05$), which are all situated adjacent to each other. Significant positive correlations were found between b and i ($P<0.05$), g and h ($P<0.05$), which are not situated adjacent to each other. The negative correlations may indicate that the borderline between the two areas is artifical. The level of asymmetry is erroneously increased if a relatively homogeneous area is divided into two subareas, especially if the borderline between the subareas is difficult to localize in exactly the same way on the two sides. In any case, the largest negative correlation between a and b suggests that these areas should not be separated (Fig. 2b).

3.5. Phenodeviants

In most foramina, one (or two) variant(s) was clearly most dominant, the "norm" of the trait. Other variants can then be considered as "phenodeviants" (Table 4). For the traits and the sample studied here, it was not feasible to find the "norm" for six foramina out of 30. There were no differences between the sexes or age groups (Table 5) but the numbers of phenodeviants varied significantly between the years (Table 6).

3.6. Fluctuating asymmetry of bilateral traits

Methodological questions

Most bilateral traits show some degree of asymmetry or divergence of the values on the right and the left side. There are three kinds of asymmetry, which, in the order of decreasing frequency in populations are termed fluctuating asymmetry, directional asymmetry and antisymmetry (Van Valen 1962). In fluctuating asymmetry the difference between the two sides in some measurable trait is normally distributed around the mean of zero. In directional asymmetry the value of one particular side is systematically greater than the value of the other side. In antisymmetry there is a substantial difference between the two sides, but it cannot be predicted which side will have the greater value (Van Valen 1962, Soulé 1967). Several traits, such as the size of paired formations, numbers of

Table 4. List of the phenodeviants of 24 foramina in the material from South Finland (N=170). The norm could not be identified for six traits (1, 2, 4, 8, 12 and 20). % norm = percentage of individuals with a norm on both sides of the skull.

Foramen	Norm	Phenodeviants	% norm
3	1,2	0,3,4	87.1
5	0	1,2	55.3
6	0	1–3	69.4
7	0,1	2–8	53.9
9	0	1–5	67.7
10	4	3,5,6	85.5
11	0	1,2	79.6
13	1	0,2–6	82.4
14	1	0,2–5	39.3
15	1	2,3	92.4
16	0,1	2–4	82.4
17	1	2,3	86.5
18	0	1	73.8
19	1	0,2,3	58.5
21	1,2	3,4	88.2
22	1	2,3	81.2
23	0	1,2	55.3
24	0	1,2,3	78.2
25	0,1	2–4	72.9
26	0	1,2	77.1
27	0	1	97.7
28	0,1	2–4	89.4
29	0,1	2–4	71.8
30	1	0,2,3	60.0

Table 5. Comparison between the sexes and age groups in asymmetry, number of asymmetric traits and number of phenodeviants (Friedman's test (χ^2) over the variances or ANOVA (F) over the number of traits per individual). For comparison of the age groups samples of the same male cohort were studied before and after overwintering. Sample size in parentheses. For statistical significances, see Table 3.

	Asymmetry (unscaled)	Asymmetry (scaled)	Asymmetric traits	Phenodeviants
	Median	Median	Mean	Mean
Sex				
Females (80)	0.449	0.159	10.75	6.19
Males (90)	0.335	0.116	9.40	5.70
	χ^2=1.20 ns	χ^2=2.13 ns	F=8.01 **	F=1.45 ns
Age groups				
Juveniles (15)	0.210	0.069	8.25	4.92
Adults (10)	0.280	0.115	11.14	6.29
	χ^2=6.53 *	χ^2=5.63 *	F=4.22 o	F=2.80 ns

scales or chaetae, wing venation in insects and formation of dentition have been used in studies of fluctuating asymmetry (e.g. Zakharov 1981).

According to Palmer & Strobeck (1986), the best index of fluctuating asymmetry is the variance of the difference between the two sides, either as such (unscaled, formula 4 in Palmer & Strobeck 1986) or divided by the mean (scaled, formula 6):

unscaled: $\mathrm{var}(r_i - l_i)$

scaled: $var\left[\dfrac{r_i - l_i}{(r_i + l_i)/2}\right]$

where r_i = value of the trait on the right side, and l_i = value of the trait on the left side. Both formulae have been used in the present study to measure fluctuating asymmetry. The level of asymmetry was also measured by counting the number of asymmetric traits per individual (Leary et al. 1983). For this purpose the traits were dichotomized into two classes, those with and those without asymmetry.

Palmer & Strobeck (1986) recommend that prior to estimating asymmetry in population studies, one should check asymmetry for directional asymmetry and for possible correlations between the average value of the trait.

Dependence of asymmetry on the mean for the trait. The unsigned difference $D_i = /r_i - l_i/$ between the two sides was not correlated with the size of the shrew: only two correlation coefficients out of 120 were significant at the 5% level. In contrast, the value of D_i clearly depends on the average number of foramina ($r_i + l_i$); correlation coefficients were positive and statistically significant in all 30 foramina. The D_i-values divided by the mean were not generally correlated with the average number of foramina (13 positive and 17 negative coefficients, all smaller in value than the ones obtained with unscaled values).

Directional asymmetry. We found a systematic difference between the right and the left side (directional asymmetry) in only one trait, foramen no 19, in which the left side had a significantly greater mean (P=0.003). In the 30 traits, the right side value was greater, on average, in 17 cases and the left side in 13 cases, further supporting the conclusion that foramen counts show no directional asymmetry.

Table 6. Comparison between the years in asymmetry, calculated over 30 foramina. Annual differences in unscaled and scaled asymmetry were compared with Friedman's tests, and the number of asymmetric traits or phenodeviants per individual by ANOVA. The annual rank sums of Friedman's test (R_i) or mean values as well as the rank order of the years are presented. For phenodeviants the number of traits is 24 (see Table 4).

	Asymmetry (unscaled)		Asymmetry (scaled)		Asymmetric traits		Pheno-deviants	
Year	R_i	rank	R_i	rank	Mean	rank	Mean	rank
1975	110.5	3.	110.5	4.	9.0	2.	4.7	2.
1976	72.0	1.	78.0	1.	8.4	1.	4.5	1.
1977	112.0	4.	100.0	3.	10.4	4.	6.0	4.
1978	138.0	6.	129.5	6.	11.7	6.	7.4	6.
1979	83.5	2.	94.5	2.	9.7	3.	5.7	3.
1980	114.0	5.	117.5	5.	10.6	5.	6.8	5.
	χ^2= 26.67 ***		χ^2= 15.72 **		F=4.31 ***		F=5.68 ***	

Differences between sexes, age groups and years in asymmetry

Females tend to have higher levels of asymmetry than males (significant difference in the number of asymmetric traits/ind.; Table 5). Somewhat surprisingly, adults were more asymmetric than juveniles of the same cohort (Table 5). In the material from South Finland, there is significant variation between the years in asymmetry, regardless of how it was measured (Table 6). The rank order of the years is almost similar in all measures of asymmetry (lowest values in 1976, highest in 1978; Table 6).

4. Metrical traits

The video digitizer-microcomputer system described in Section 3.4 was used to take metrical measurements of the mandible. Both mandibles were measured. The program used to process the video image first located the outline of the bone, which was stored as a vector of coordinates of consecutive pixels.

Eighteen mandibular measurements were taken, which are here given in the actual measurement units (pixels). The 18 measurements arise from three sets of distance measurements taken along the outline of the mandible. The first set with 10 measurements are based on the point 1 in Fig. 3a, which was determined as the point along the convex outline of the lower part of the mandible with the sharpest angle between two lines 30 pixels long, drawn from the focal point in opposite directions along the outline (Fig. 3a). All the remaining points shown in Fig. 3a were determined as the end points of maximum or minimum distances to the opposite stretch of the outline (maxima: from 1 to 2, from 3 to 2, from 3 to 4, from 5 to 4, from 5 to 6, from 7 to 6; minima: from 1 to 3, from 1 to 7, from 3 to 5). The 10 distance measurements were taken as indicated in the figure. Unfortunately, there is substantial measurement error in determining point 1, which is reflected in relatively large measurement errors in many of the 10 distance measures (Table 7). Only four of the 10 measures (A1–A10) have reasonably small (less than 3%) measurement error and were used in this study: A4, A7, A8 and A9 (Table 7).

The second set of 4 measurements (B1–B4) are simply absolute minima or maxima between two stretches of the outline, as shown in Fig. 3b. The measurement was found by exhaustively searching for the minimum or the maximum distance between two points along the opposing stretches of the outline, within such limits that the true value could not have been missed. The measurement error is minimal for these measurements, usually less than 2% (Table 7). Such absolute minimum or maximum measurements are preferable, but unfortunately, not many such measurements can be taken from the mandible of the common shrew.

The third set of measurements was taken as explained in Fig. 3c. The height of the mandible was measured as the maximum from the end point of B1 (from Fig. 3b) or from the point 1 (in Fig. 3a). C3 is the minimum from the end point of B1. C4 is the area

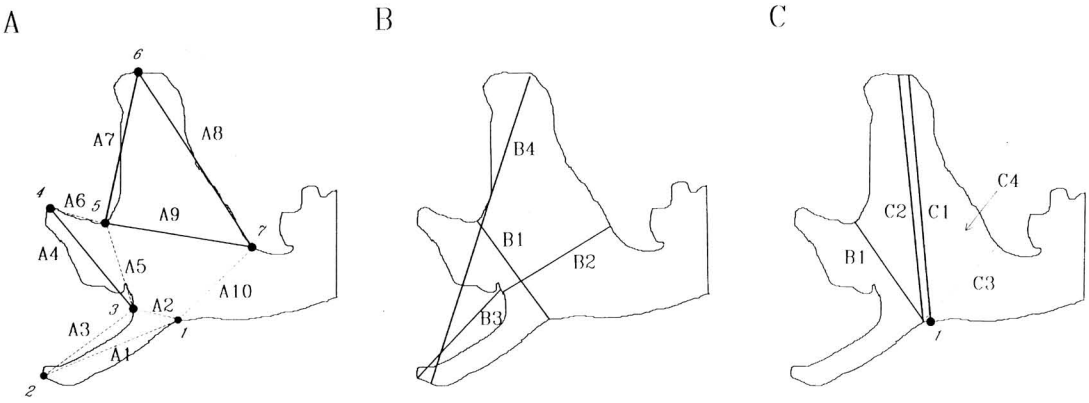

Fig. 3. Video measurements of the mandible. The measurements shown as solid lines have the lowest measurement errors (Table 7). Note that C4 is an area (defined by B1 and C3). For further explanation see the text.

Table 7. Measurement errors (%) in the metrical mesurements. Results are based on 70 individuals measured twice (a sample from Ilomantsi, East Finland). The recommended measurements are marked with "+".

Trait	Measurement error		Trait	Measurement error	
A1	23.63		B1	1.58	+
A2	21.21		B2	1.08	+
A3	6.78		B3	2.60	+
A4	2.62	+	B4	1.79	+
A5	5.39				
A6	5.97		C1	2.39	+
A7	2.02	+	C2	1.81	+
A8	1.66	+	C3	11.22	
A9	1.87	+	C4	2.19	+
A10	16.14				

limited by the lines B1 and C3, and the outline of the bone (Fig. 3c).

Two of the video measurements (C1 and C2) describe approximately the same dimension of mandible height as was measured manually by microscope using an ocular micrometer (Fig. 1h). This makes comparison of the two methods possible. The correlations between the two video measurements and the one microscope measurement are all very high (R^2=0.964 and 0.951 for comparisons of the microscope measurement with C1 and C2, respectively). Asymmetry in the same measurements (as calculated by differences between the two sides) also correlate significantly, but the coefficients of determination are lower (R^2=0.404 and 0.257). Variability is of about the same level in all three measurements, the coefficient of variation (CV =100 SD/mean) ranging from 2.53 to 2.63 (including both measurement error and variation in the bones).

We demonstrate the value of these mandibular measurements with material from Ilomantsi, eastern Finland, where Hanski and Peltonen (unpubl.) have trapped shrews for 5 years on small islets on a lake and on the mainland. The islets are so small that no shrews can overwinter or breed there, hence all young shrews caught from the islets in late summer are certain natal dispersers (Hanski and Peltonen 1988).

The islet and mainland samples were significantly different in several mandibular measurements in one or more years (Table 8): A8, A9, B1, B2, C1 and C4. In 1986 the shrews from the islets were smaller in all these measurements, while in 1982 and 1985 there were no differences between the islet and mainland shrews. In 1983 and 1984 the islet shrews had lower values in some but not all measurements, indicating that there were some differences in the shape of the mandible between the dispersers and the mainland shrews. The rate of dispersal to islets was clearly higher in 1982 and 1985 than in the remaining years (Hanski and Peltonen unpubl.). These results therefore suggest that dispersal in the common shrew is selective (social subordinates disperse) when the rate of dispersal is relatively low, while when the rate of natal dispersal is high, dispersal is not selective, many or most shrews having a tendency to disperse regardless of their social position, assumed to be related to size (Hanski and Peltonen unpubl.).

Table 8. Comparison of 6 mandibular measurements in young common shrews caught from the islets and the mainland. The 4 figures for each character and year are: the mean ($\bar{x}$) and the standard deviation (*SD*) in the mainland sample, the difference between the mainland mean and the islet mean in units of the mainland standard deviation (*d*), and the significance of this deviation (*P*). The sample sizes are (islet, mainland): 1982 (6,63), 1983 (14,14), 1984 (6,85), 1985 (17,75) and 1986 (11,185).

Year		B1	B2	A8	A9	C1	C4*)
1982	$\bar{x}$	84.50	87.47	146.60	103.80	185.40	104.50
	SD	3.13	3.06	5.53	2.62	4.32	5.09
	d	0.67	0.78	–0.30	0.76	0.07	0.43
	P	0.11	0.06	0.61	0.20	0.89	0.47
1983	$\bar{x}$	86.78	89.51	147.00	106.00	186.50	105.10
	SD	1.75	2.63	3.50	2.04	4.04	3.53
	d	0.93	0.87	0.31	1.32	0.17	0.88
	P	0.08	0.01	0.48	0.00	0.51	0.06
1984	$\bar{x}$	85.71	88.84	145.40	104.80	185.80	105.30
	SD	2.86	3.07	5.02	2.64	4.32	5.04
	d	0.71	0.97	0.48	0.80	0.25	0.36
	P	0.08	0.02	0.26	0.05	0.53	0.39
1985	$\bar{x}$	85.30	87.82	145.90	104.90	184.60	105.20
	SD	3.14	3.25	4.18	2.87	4.17	4.68
	d	0.12	–0.06	–0.05	0.00	0.00	–0.11
	P	0.65	0.81	0.78	0.89	0.94	0.73
1986	$\bar{x}$	86.32	89.08	147.50	105.00	188.00	107.70
	SD	2.81	2.93	4.60	2.44	4.61	5.10
	d	0.86	0.73	0.89	0.74	0.98	0.84
	P	0.00	0.01	0.00	0.02	0.00	0.01

*) Note that C4 is an area (Fig. 3).

5. Discussion

5.1. Cleaning process

Cleaning skeletal material of the soft tissues attached to the bone for the purposes of study or for museum collections is a laborious and complex task. For cleaning large numbers of samples three main methods have been used, namely cleaning by maseration, cleaning with chemicals and cleaning with insects (most often with dermestid beetle larvae; for a review of the methods see Williams et al. 1977). Maseration, in which the sample is kept immersed in water, until all flesh decays is always a slow and odorous process. Due to the disadvantages of maseration, several chemicals have been introduced to minimize the time required and the side effects (Williams et al. 1977, Berland 1985). Papain enzyme is one of them, suggested for the first time by Luther (1949), and used for shrews at least by Searle (1954) and Hanski & Kuitunen (1986). The third method, cleaning by dermestid larvae, is not useful for cleaning small and fragile bones, such as the skull of the shrew, because the insects easily break or dislocate the small bones, which may be lost. Moreover, for foramen counts the degree of cleaning performed by dermestids is not sufficient. Cleaning with papain as used here is an easy and effective method, especially when large numbers of samples are handled. On the other hand, the method clearly has some drawbacks when used for cleaning skeletons of shrews. Due to the frequent opening of the main skull sutures metric measurements of the braincase are difficult or even impossible to take. Loosening of teeth may also be a serious drawback in some studies. Moreover, it has been suggested that the enzymatically cleaned bones are not suitable for long-term preservation, because the enzyme may continue its work in the bone even after cleaning has been completed (Williams et al. 1977).

5.2. Foramen counts

Non-metrical skeletal patterns, such as foramina, have often been considered to characterize populations genetically (Section 1), although the heritability of some non-metrical traits has been shown to be rather low (Thorpe 1981). Environmental factors, such as the condition of the mother during pregnancy (Howe & Parsons 1967) may also affect non-metrical as well as metrical traits (Pankakoski 1985, Pankakoski & Nurmi 1986, Zakharov et al. unpubl.). The appearance of non-metrical traits of the skull depends to some extent on individual size (Hartman 1980, Hanski & Kuitunen 1986). This was also the case in the present study, where the number of foramina tended to be greater in animals with smaller mandibles.

Foramen numbers can possibly tolerate greater variability than adaptively more "important" traits, such as body dimensions associated with locomotion (Bird et al. 1981), feeding (e.g., tooth row dimensions; Barnett 1977, Pankakoski & Nurmi 1986) or the dimensions of the braincase (Pankakoski & Nurmi 1986). It is also possible that foramen counts are more useful in studies of developmental stability than metrical measurements (Zakharov et al. unpubl.)

Because there is a continuum in foramen size in the shrew's skull, the interpretation of foramen counts

is often difficult. Counting foramina is a slow process and, to some extent, involves subjective decisions. The most time-consuming areas to score are the foramen areas 1 to 9, for which reason we have also used restricted sets of traits, for example nos 13 to 25 (Zakharov et al. unpubl.).

The developmental stability of animal populations may be calculated as the asymmetry in the counts of foramina, but also as the number of phenodeviants in foramina (Zakharov 1984, 1987). Phenodeviants cannot be defined for metrical traits, but they are useful in non-metrical traits, if the latter are expressed as one or two typical variants (the norm of the trait). The traits with high ranges and great variability (Group III in Table 1) are unsuitable for this purpose. On the other hand, the non-metrical traits with a high level of variability are most effective in revealing differences between subgroups of samples, both in foramen counts and in asymmetry (Groups II and III in Table 3). Very small ranges that are frequently met in non-metrical traits may also lead to problems in asymmetry studies, as pointed out by Swain (1987).

5.3. Video measurements of the mandible

Variability in the processii of the mandible is extensive in shrews (Schaefer 1975). Mandible dimensions have been shown to be highly heritable (in mouse, Festing 1972, 1973, 1976, Thorpe et al. 1982, in shrews, Hausser & Jammot 1974), to the extent that Thorpe et al. (1982) were able to identify the karyotype of *Mus* from the shape of the mandible. For these reasons, mandible measurements have frequently been used in population studies of shrews. Most investigators have used binocular microscopes and ocular scales to take measurements (e.g., Schaefer 1975, Skarén 1979, van Zyll de Jong 1980,1982,1989, Dötsch 1982, 1983, Catzeflis et al. 1985). An improved method of taking mandibular measurements under the binocular microscope was described by Festing (1972) for the mouse. In Festing's (1972) method, the mandible is placed on an optically reduced mm-graph paper and kept in place by two fixed glass slides (see also Thorpe et al. 1982). This method has been used for insectivores by Searle & Thorpe (1987) and Corti et al. (1985). The video camera-based method described here has several advantages over the traditional ones. Firstly, the method is less time-consuming than the old ones. Secondly, measurement error can be reduced to very low levels (the measurement error primarily depends on the resolution of the video and the digitizer). Thirdly, the results are almost entirely independent of the experience of the investigator. Fourthly, as the results are saved directly in a data file in the computer, any errors in coding the results are avoided. A drawback to this method, however, is that it requires a special computer program that must be adapted by an expert for each kind of bone individually.

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