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Andrew C Kitchener[1] & John M Lynch[2]

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A morphometric comparison of the skulls of fossil British and extant European beavers, *Castor fiber*

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SUMMARY

1. The Eurasian beaver, *Castor fiber*, became extinct in Scotland in the 16th century, mainly due to hunting and habitat loss. Scottish Natural Heritage, as part of its Species Action Programme, is investigating the feasibility of re-introducing the European beaver to Scotland. This is being assessed against World Conservation Union (IUCN) guidelines.

2. One re-introduction criterion requires that the taxonomically closest extant population is used for a re-introduction. Eurasian beavers are found today in several distinct populations, which have been through severe population bottlenecks in the last 300 years. These isolated populations are the basis for several sub-species that are recognised today.

3. A morphometric study of 21 measurements from 388 beaver skulls and mandibles was carried out using bivariate and multivariate statistical techniques. This allows comparison of fossil British beavers with those from the three geographically closest extant populations (Germany, France and Scandinavia), whose ancestors may have colonised Britain at the end of the last ice age. A molecular study was not feasible given the limitations of current techniques.

4, These analyses showed that fossil British beavers are morphologically closest to extant Scandinavian populations. There were insufficient Scottish fossils to allow a separate determination.

5, It is recommended that Scandinavian beavers be used for any re-introduction to Scotland. Although Scandinavian beavers display low genetic variability, they have shown a remarkable capacity to recolonise former habitats and have increased dramatically in numbers during the 20th century.

1. INTRODUCTION

1.1 Background

In 1995 Scottish Natural Heritage announced its intention to carry out a feasibility study on the possibility of re-introducing the Eurasian beaver, *Castor fiber*, to Scotland as part of its Species Action Programme (Scottish Natural Heritage, 1995). Any re-introduction of the beaver to Scotland would follow World Conservation Union guidelines (IUCN, 1995); one of these requires that, as far as is possible, the taxonomically closest population should be used for that re-introduction. Clearly, any re-introduced animals should have the co-adapted gene complexes and other adaptations that are appropriate to the habitats and climate, into which they are placed.

One problem for any beaver re-introduction programme is to decide which population should be used as a donor. The nearest geographically neighbouring population could be used (i.e. Scandinavia), but this may not take into account colonisation routes by different ancestral populations at the end of the last ice age, c. 10,000 years BP. Therefore, central European beaver populations might be taxonomically closer to former British populations than Scandinavian beavers.

1.2 Aim

The aim of this study was to identify which extant population of Eurasian beavers should be used for a re-introduction to Scotland. The study was done by comparing fossil skeletal specimens with those from contemporary populations in Europe.

1.3 The approach: genetics or morphometrics?

One approach would be to compare genetically any fossil material with extant European populations. The use of ancient DNA to solve palaeontological, archaeological and taxonomic problems has increased in recent years (e.g. Hagelberg *et al.*, 1994), but large quantities of bone are still required to offer only the possibility of a successful DNA extraction (E. Barratt, pers. comm.). In Scotland fossil beavers are known from 12 locations and only six skeletal specimens are known to survive in museums (Kitchener & Conroy, 1997). It would not be acceptable to use these specimens for molecular analysis, since this would require their complete or partial destruction, and the successful extraction of useable DNA cannot be guaranteed.

An alternative solution is to compare the skull morphometrics of fossil Scottish beaver skulls with those from extant European populations. The basic assumption in using this approach is that beavers with skulls of similar sizes and shapes are most likely to be genetically similar. This technique is relatively fast, inexpensive and non-destructive. It also provides hypotheses which may be tested using genetic techniques, but in this case this will have to wait until such tests require only small amounts of bone. Skull morphometrics have been used widely to examine geographical variation in beavers, *Castor* spp. (Frahnert, 1993; Frahnert & Heidecke, 1992; Lavrov, 1979, 1983; Véron, 1992a).

1.4 Multivariate morphometrics

Morphometrics have been defined as a formal treatment of our ideas about the dissimilarity of geometrical form between biological objects; in this case, skulls (Bookstein, 1991). If large morphological data sets are available, how should the data be analysed: univariately, bivariately or multivariately?

The answer depends on how we view morphological adaptation and evolution. Sokal & Rinkel (1963) favour a multivariate perspective and believe that geographical variation is not likely to be due to adaptation of a few characters to a single environmental variable, but is more likely to be a multi-dimensional process involving the adaptation of many characters to a variety of inter-dependent environmental factors. A correct understanding of morphological variation is, therefore, multivariate (Gould & Johnston, 1972) and we should strive to examine the patterns of variance and covariance among characters using multivariate statistics (Winians, 1987).

Therefore, while there has been some debate as to the relative suitability of univariate and multivariate methodology in morphometrics studies, it has been generally realised that multivariate methods offer many advantages to the researcher (Neff & Marcus, 1980).

A useful introduction to multivariate statistical techniques can be found in Manly (1994).

1.5 A morphometric study of beaver skulls - potential problems

Two potential problems face any morphometric (or genetic) studies. First, sample sizes may be too low for conclusive results to be drawn. For example, there are only three reasonably complete Scottish beaver skulls, whereas a minimum sample size of 20 per sex would be desirable. To overcome this, fossil beavers from throughout Britain were measured to provide a much larger sample, even though clinal differences in size with latitude might be expected (see below). This is reasonable given that Scotland would have been colonised from the south or east via England and all these specimens are known to be from the Holocene or were found in contexts which suggest that they date to this period (i.e. since the end of the last ice age, c. 10,000 BP).

Secondly, sexual dimorphism should be taken into account in morphometric studies, but it may not be possible to sex fossil specimens unless dimorphism is great. Hill (1982) and Hoffmeister (1986) gave no information on sexual dimorphism (beyond body weight) in North American beavers, while Nowak (1991, p. 634) noted that the "sexes are approximately the same size". Lastly, Lavrov (1979), Frahnert & Heidecke (1992) and Senotier (pers. comm.) all pooled sexes for craniometrical analyses across populations (although Frahnert & Heidecke (1992) do document dimorphism). We follow these authors and ignore the effects of sex. It was thus assumed that the degree of sexual dimorphism was similar across all samples (if not negligible).

Thirdly, populations of beavers in Europe may have undergone changes over time since the fossils were preserved. For example, reduction in body size is commonly seen in Holocene mammals (Kurtén, 1968) and all European beaver populations have undergone severe population bottlenecks during the last 300 years (Wilson, 1858; Véron, 1992b), so that today's isolated populations may not be representative of the formerly contiguous beaver populations of Europe. In order to overcome this, a multivariate analysis of beaver skull measurements was carried out which included and excluded size components.

1.6 Taxonomy of the Eurasian beaver

The Eurasian beaver displays geographical variation throughout its European range (Freye, 1960; Heidecke, 1986; Véron, 1992a). For example, in Scandinavia there is a cline of declining body size with increasing latitude (Hartman, 1992; Macdonald & Barrett, 1993). The various relict populations in Europe which survived hunting pressure and habitat loss (Wilson, 1858; Véron, 1992b; Kitchener & Conroy, 1997) are considered to be so different that this has resulted in the recognition of several sub-species (Table 1; Figure 1), although when described sample sizes are often inadequate (mostly n=1) or not controlled sufficiently for age and sex. For example, on the basis of three specimens, Matschie (1907) described the Elbe beaver as a new species, *Castor albicus*, distinct from the Scandinavian beaver, *C. fiber*, because of its apparently distinctive dentition and the shape of its nasal bones. However, Lönnberg (1909) showed that these features were either age-related or due to individual variation so that both populations shared these characteristics. On the basis of skull measurements Lavrov (1979) revived *C. albicus* (including French beavers), although Corbet (1984) regarded this study as being unconvincing.

The most recent revision of sub-species taxonomy of *Castor fiber* recognised eight sub-species (Heidecke, 1986), although it was not clear how these were diagnosed (Table 1). We follow this classification for convenience and regard the sub-specific status as tentative.

Therefore, there appear to be four morphologically distinctive populations in mainland Europe (Table 1), which have been recognised as separate sub-species or even species. The ancestors of one or more of these populations could have colonised Britain after the last ice age (c. 10,000 years BP) and before the English Channel and North Sea were created by rising sea levels about 8,000 years BP. The beaver did not apparently colonise Ireland during the Holocene (Barrett-Hamilton & Hinton, 1910-1921; Véron, 1992b; N. Monaghan, pers. comm.).

In this study we compare the skull morphometrics of fossil beavers from Scotland and England with contemporary samples from the geographically-closest populations, namely Scandinavia (putative sub-species *fiber*), France (*galliae*) and Germany (*albicus*). Measurements from the skulls of beavers from other putative sub-species are included where available from the literature.

Table 1. The taxonomy of Eurasian beavers following Heidecke (1986).

Taxon	Authority	Distribution
Castor fiber fiber	Linnaeus, 1758	Scandinavia, Russia, Latvia, Germany, Switzerland, Austria
Castor fiber belarusicus	Lavrov, 1974	Belarus, Ukraine, Russia
Castor fiber osteuropaeus	Lavrov, 1974	E. Russia, Belarus, Poland, Germany
Castor fiber pohlei	Serebrennikov, 1929	W. Siberia, Urals, W. Russia
Castor fiber birulai	Serebrennikov, 1929	W. Mongolia, China, Altai
Castor fiber tuvinicus	Lavrov, 1969	Azas R., Upper Yenesei, Siberia
Castor fiber albicus	Matschie, 1907	Germany (Elbe), Poland
Castor fiber galliae	Geoffroy, 1803	France (Rhone), Switzerland, Germany

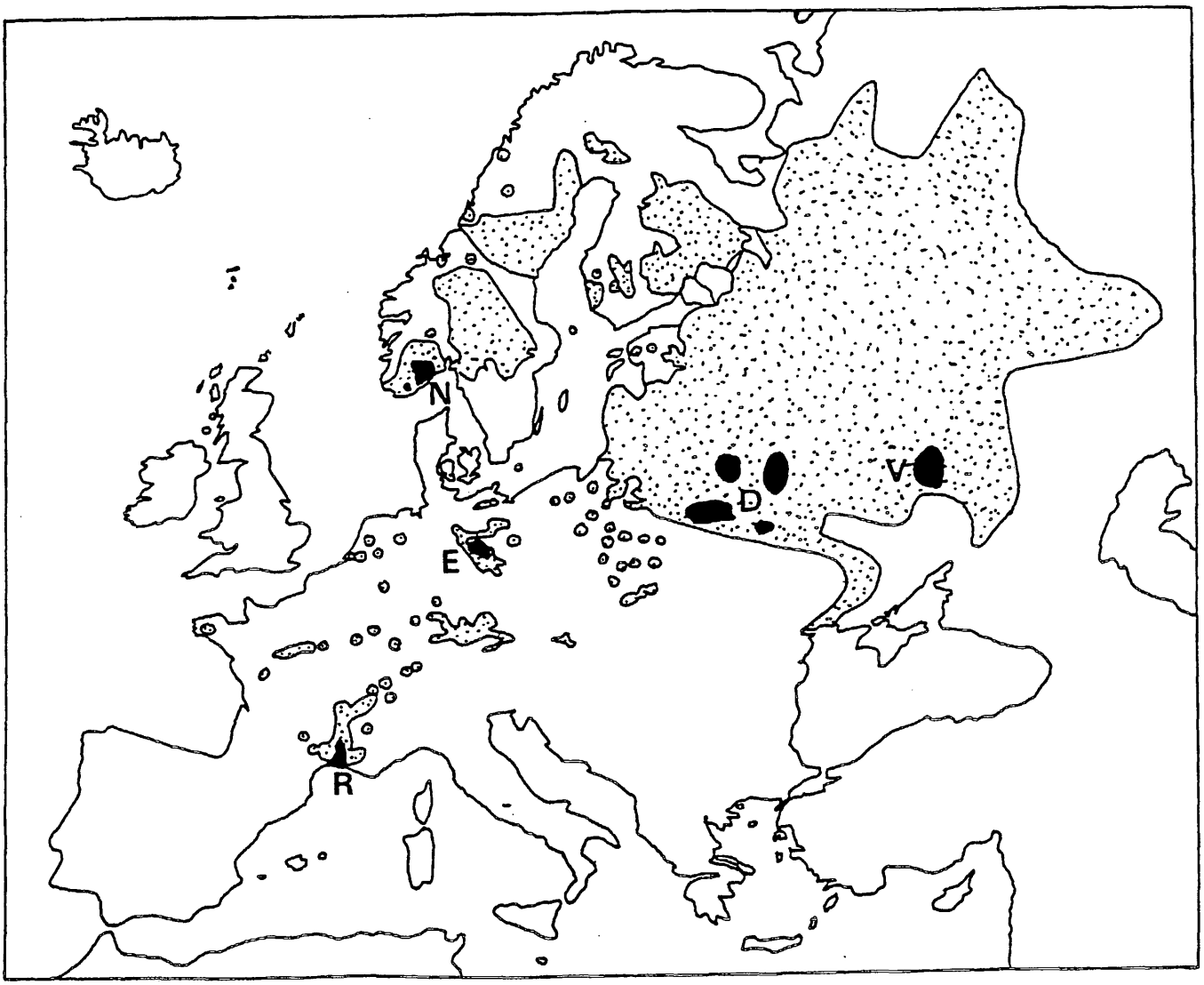

Figure 1. Current distribution of the Eurasian beaver, *Castor fiber*, in Europe (stippled) (after Nolet, 1997). The following relict populations are shown as they were at the beginning of the 20th century (black): R - Rhône (France), E - Elbe (Germany), N - Scandinavia, D - Dnepr Basin, V - Voronezh.

2. MATERIALS AND METHODS

2.1 Specimens

Measurements were available from a total of 388 beaver specimens (Table 2).

2.1.1 Fossil beavers

Only three Scottish fossil beaver skulls were available for measurement (Table 2) (Kitchener & Conroy, 1997). However, a larger sample of fossil beavers, mostly from the Cambridge Fens, was also available from the Zoology and Sedgwick Museums, Cambridge University and the Natural History Museum, London (Table 2).

Table 2. Beaver specimens used in this study

	Total	Crania	Mandibles	Sources
1. Scotland	3	3	1	NMS, PMAG
2. England	105	43	73	CZ, CS, BMNH, Véron
3. France	34	33	12	Véron, Senotier, BMNH, Ognev (1963)
4. France	3	3	2	Véron (fossil)
5. Germany	68	68	61	Frahnert, Véron, BMNH, Ognev (1963), Lönnberg (1909)
6. Switzerland	3	3	0	Senotier
7. Scandinavia	57	57	48	UU, BMNH, NMS, Lönnberg (1909)
8. Russia	20	20	0	Ognev (1963)
9. Mongolia	7	7	7	Stubbe & Dawaa (1983)
10. North America	78	78	47	Véron, BMNH
11. No data	10	9	8	Véron
Totals	388	324	259	

Key:

BMNH	Natural History Museum, London
CS	Sedgwick Museum, Cambridge
CZ	Zoology Museum, Cambridge
NMS	National Museums of Scotland
PMAG	Perth Museum and Art Gallery
UU	Uppsala University

2.1.2 Extant beavers

There are insufficient samples of European beaver skulls in UK museum collections for a complete analysis. The largest sample of adult skulls is at the Natural History Museum (n=11; Table 2), but there were insufficient skulls for each distinct population and/or putative sub-species to be characterised. Therefore, researchers and museums in Europe were contacted for either the loan of skulls or for the use of existing data sets of measurements made by these researchers. The advantage of this approach was the relatively rapid accumulation of data, but the disadvantage was that several different individuals had taken measurements, so that there was the

possibility of measurement errors between recorders. However, in a previous study on badgers, *Meles meles*, Lynch *et al.* (1997) have shown that although there may be differences in the way in which measurements are taken by different individuals, these are consistent and not significant. We hope to test for measurement errors between individuals recorders in the future, but this was beyond the scope of this study. The other problem of this approach is that not all researchers had taken the same set of measurements, which limited the number of variables and specimens that could be used in the subsequent analyses.

In addition, measurements were taken from the literature, including Lönnberg (1909), Miller (1912), Ognev (1963) and Stubbe & Dawaa (1983).

Measurements from some North American beavers, *C. canadensis*, were included in order to assess the degree of variation between populations of *C. fiber* with respect to this separate species.

2.2 Methods

2.2.1 Measurements and bivariate analyses

The 25 measurements that were made on beaver skulls following Lavrov (1979), Véron (1992a) and J.-L. Senotier (pers. comm.) are shown in Fig. 2 and Table 3. In part these were selected where authors had previously used bivariate or multivariate relationships (see below) to distinguish between beavers from different populations (e.g. Lavrov, 1979), and these were also based on what measurements were recorded in the literature by a variety of authors (e.g. Ognev, 1963; Lavrov, 1979; Stubbe & Dawaa, 1983; Heidecke, 1986; Véron, 1992a; Frahnert, 1993). The measurements were taken using dial callipers to 0.01 mm accuracy, except where these exceeded 150 mm, when measurement accuracy was to 0.5 mm.

Lavrov (1979) used four bivariate relationships to distinguish between the three species (*C. fiber, C. albicus* and *C. canadensis*) that he recognised:

- greatest length of skull (GL) and inter-orbital breadth (IOB),
- occipital height (OH) and mastoid breadth (MB),
- nasal length (NL) and nasal width (NW), and
- occipital height (OH) and cranial length (CRL) (super-orbital process to the occipital crest)

As a first stage analysis, these relationships were tested for the British fossil beavers to see if they could be assigned to one of the three taxa recognised by Lavrov (1979). All bivariate analyses were carried out using Excel 5.0 for Windows. J.-L. Senotier (pers. comm.) had already shown that French beavers could be readily distinguished from Elbe beavers using these relationships, although Lavrov (1979) included French beavers within *C. albicus*.

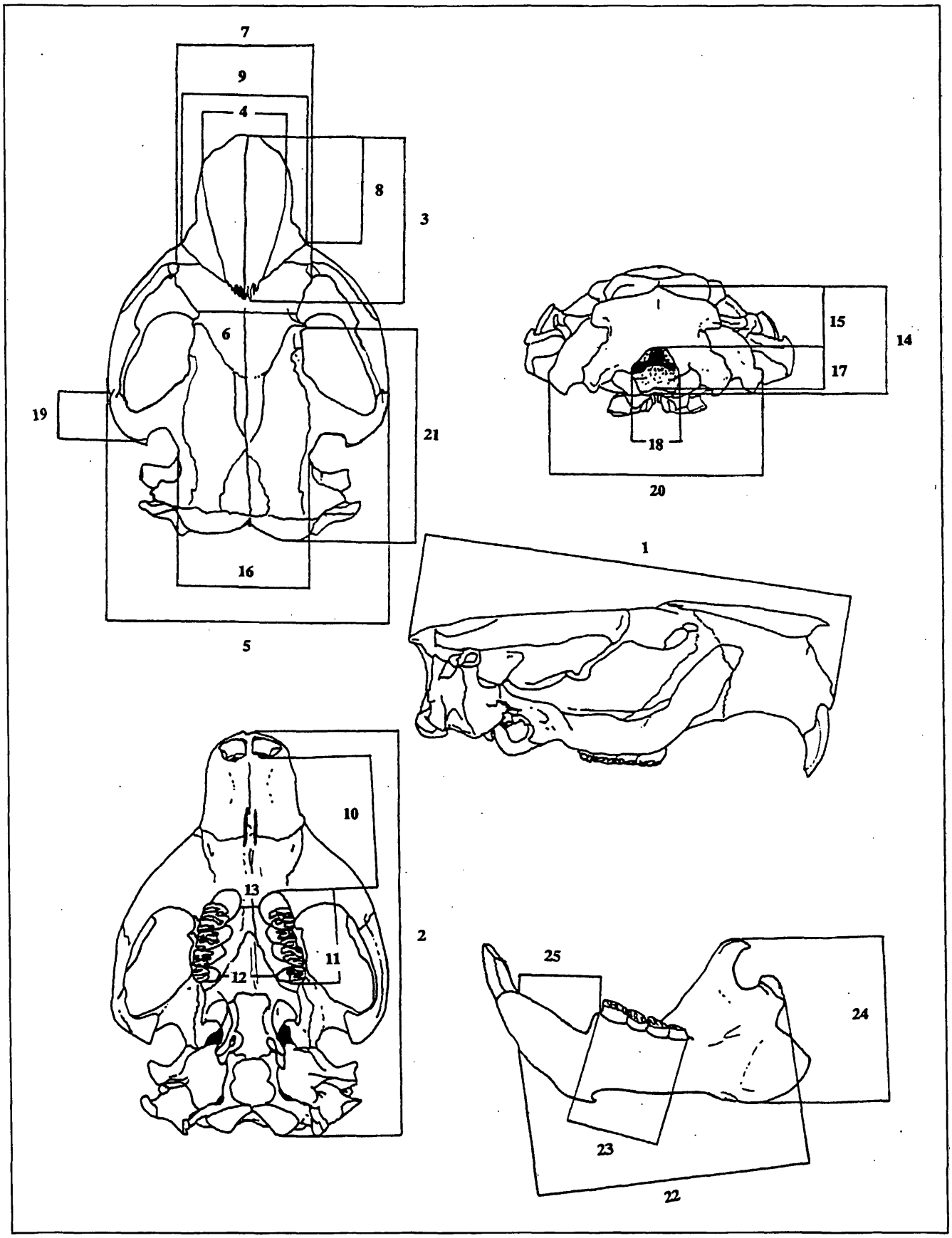

Figure 2. Measurements taken from beaver skulls in this study. See Table 3 for descriptions and abbreviations (after Frahnert, 1993).

Table 3. Measurements of skulls and their abbreviations as shown in Figure 1 (after Lavrov, 1979; Véron, 1992a; Frahnert, 1993; J.-J. Senotier, pers. comm.). All measurements were in mm.

1.	Greatest length of skull (GL)
2.	Condylobasal length (CL)
3.	Length of nasals (NSL)
4.	Width of nasals (NSW)
5.	Zygomatic width (ZW)
6.	Interorbital width (IOW)
7.	Width across frontals (IOF)
8.	Length from junction of nasals to junction of premaxilla and maxilla (NIM)
9.	Breadth of premaxillae at the junction with the maxillae (IMW)
10.	Length of upper diastema (UPDL)
11.	Length of upper molar toothrow (UML)
12.	Width at third upper molars (M3W)
13.	Width at premolars (PMW): N.B. Width at first upper molars (M1W) was taken mistakenly owing to incorrect labelling in Senotier (pers. comm.)
14.	Cranial height (CH)
15.	Occipital height (OH)
16.	Cranial width (CW)
17.	Foramen magnum height (FMH)
18.	Foramen magnum width (FMW)
19.	Length of temporal/zygomatic suture (TZL)
20.	Mastoid width (MW)
21.	Cranial length (POOL): Length from postorbital process to the occipital crest.
22.	Length of mandible (LM).
23.	Mandibular molar tooth-row length (LTL)
24.	Coronoid height (COH).
25.	Length of mandibular diastema (LDL)

2.2.2 *Multivariate analyses: data screening*

Data were screened for outliers[1] (often errors in data input or measurement) using standard univariate procedures (descriptive statistics, histograms, probability plots and bivariate plots). Outlying data were either corrected or the individual measurement removed depending on the nature of the outlier.

[1] An outlier is an individual measurement that does not follow the trend within a population. For example, a value for condylobasal length of 100 mm would be an outlier if all other values for the population ranged between 30 mm and 50 mm. In this case, it is unlikely to be a data entry error (as a value of 10 mm would still be an outlier), and the individual measurement would be removed. If an individual specimen was an outlier for a number of measurements, the specimen would be removed. This did not happen in this study.

2.2.3 *Estimation of missing data*

A large proportion of the specimens were missing some measurements. Indeed, only 38 specimens had all measurements taken. A multiple regression approach was used to estimate some of the missing values. Table 4 shows the increase in sample sizes for each measurement following this procedure (abbreviations are given in Table 3).

Regression analysis is a common technique for the estimation of missing values in a multivariate context (e.g. Reig, 1992; Lynch, 1996). In this situation, nine of the most prevalent measurements (marked '(a)' in the third column of Table 4) were chosen, and stepwise multiple regression was used to predict any missing values for an individual measurement. For example, this allowed the number of specimens with values for greatest length (GL), to rise from 188 to 195 (Table 4). It proved impossible to estimate values of M3W (width at 3rd upper molars), PMW (width at premolars), CW (cranial width), FMH (Foramen magnum height) and FMW (foramen magnum width) using this technique as the resulting regression equations had low values for r^2 (less than 0.60). In other words they were so poorly correlated with other variables, that it would have been unreliable to estimate missing values in this way.

2.2.4 *Multivariate analyses*

Principal component analyses (PCAs) were carried out separately on four mandibular and 17 cranial measurements (see Appendix 1 for details of justification for and the use of this methodology). In summary, principal component analysis allows us to reduce the number of variables (i.e. measurements) to indices which are just linear combinations of those variables which provide the maximum differentiation between groups, in this case, different beaver populations. Obviously, there are many measurements which could be taken from a skull, but we do not know which ones separate groups best until we carry out this analysis.

Discriminant function analyses (DFAs) were also carried out to assess size and shape variation separately (see Appendix 1). In summary, discriminant function analysis allows us to see whether it is possible to separate different groups on the basis of the available measurements. Like PCA, DFA produces linear combinations of variables, which can also be used to predict the likelihood of a particular individual belonging to those groups. Manly (1994) provides an introduction to the use of these techniques.

Table 4. The effect of multiple regression on the sample sizes of measurements used in the multivariate statistical analysis of beaver skulls. See Table 3 for abbreviations.

Measurement	Before regression	After regression
GL	188	195
CL	272	272 (a)
NSL	277	277 (a)
NSW	287	287 (a)
ZW	260	277
IOW	243	243 (a)
IOF	122	142
NIM	109	143
IMW	116	116
UPDL	210	210 (a)
UML	276	276 (a)
M3W	113	113 (b)
M1W	94	94 (b)
PMW	103	103 (b)
CH	107	208
OH	125	141
CW	109	109 (b)
FMH	228	228 (b)
FMW	224	224 (b)
TZL	106	282
MW	190	190 (a)
POOL	86	116
ML	230	235
LTL	216	216 (a)
LDL	206	206 (a)

Note: (a) These measurements were used in the regression estimation;
(b) It proved impossible to estimate missing values for these measurements (see main text).

2.2.5 *Interpretation of results*

The aim of our analyses was to examine whether size and shape variation existed within the data examined for the different populations. It was not intended to describe this variation, as this would have proved impossible given the nature of the dataset. Therefore, we were unable to interpret variation in relation to any ecological or biomechanical factors affecting individual specimens. This would require a further and much different study. Instead, we simply answer the question 'Which extant population of Eurasian beavers resembles the extinct British population the most?'

3. RESULTS

3.1 Bivariate analyses

The bivariate analyses showed no clear distinction between Lavrov's (1979) putative taxa (i.e. *fiber*, *albicus* and *canadensis*) (Figs. 3-6), although they did show three main partially overlapping groups: 1. Germany (Elbe), 2. North America and 3. the rest of Europe (Scandinavia, France, England and Scotland). In some cases, the relationships showed clinal variation in size throughout Europe with German beavers being the largest (e.g. Figs. 3 and 4). In other cases, there were proportional differences in the skull (e.g. Figs. 5 and 6), so that German beavers had relatively higher occiputs for their cranial lengths and relatively wider nasals for their nasal lengths compared with those of other European beavers. However, these groups were not consistent and this had consequences for Scottish fossil beavers. For example, Scottish beavers appear more like German ones (Fig. 6; occipital height and cranial length), one Scottish beaver appears to be borderline with North American and European beavers (Fig. 5; nasal width and length), one is borderline between German and European beavers, and the third one is most like the remaining European beavers.

3.2 Multivariate analysis of mandibular measurements

Three measurements (LM: mandibular length, LTL: length of the mandibular tooth row, and LDL: Length of the mandibular diastema) provide a simple index of mandibular size and shape. It was thus decided to analyze these data separately from the cranial dataset (particularly as a large number of sub-fossil mandibles survive without cranial material).

A principal component analysis (PCA[2]) of the three measurements, resulted in three principal components (henceforth, PC1, PC2 and PC3). Means and standard deviations for all principal components are given in Table 5.

3.2.1 Principal Component 1 (PC1)

Principal component 1 accounted for 70.4% of the variation within the sample and was taken to be an overall measure of mandibular 'size' and allometric shape variation (i.e. change in shape with size), as all of the three measurements had high, positive loadings, i.e.

$$PC1 = +0.91\ LM + 0.77\ LTL + 0.84\ LDL$$

An analysis of variance (ANOVA) for principal component 1 revealed highly significant variation ($F_{3,157} = 48.18$, $P < 0.00001$), with the German material being characterized as having significantly higher principal component 1 scores (and thus mandibular 'size') than all other groups. A least-significant-difference test revealed that the Scandinavian and French specimens had similar 'size' scores, as did English and French.

[2] See Appendix

Mandibular 'size' can thus be seen to vary according to

Scandinavian < French < English < German.

The North American specimens (though not statistically tested due to small sample size), were characterised as having very small mandibles, while the Mongolian specimens had larger mandibles than the English specimens, but smaller than the German (Table 5).

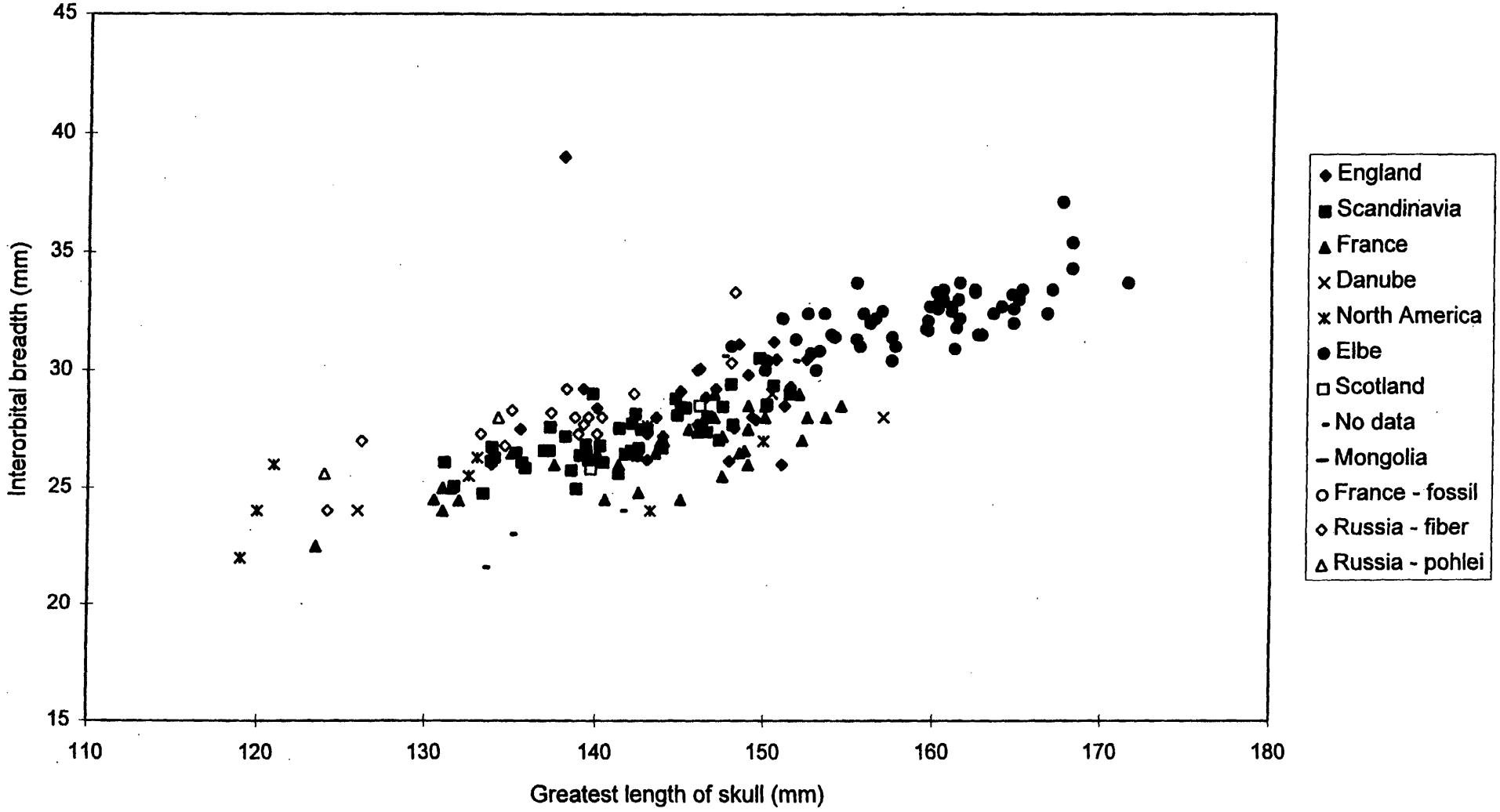

Figure 3: The relationship between interorbital breadth and greatest length of skull in beavers

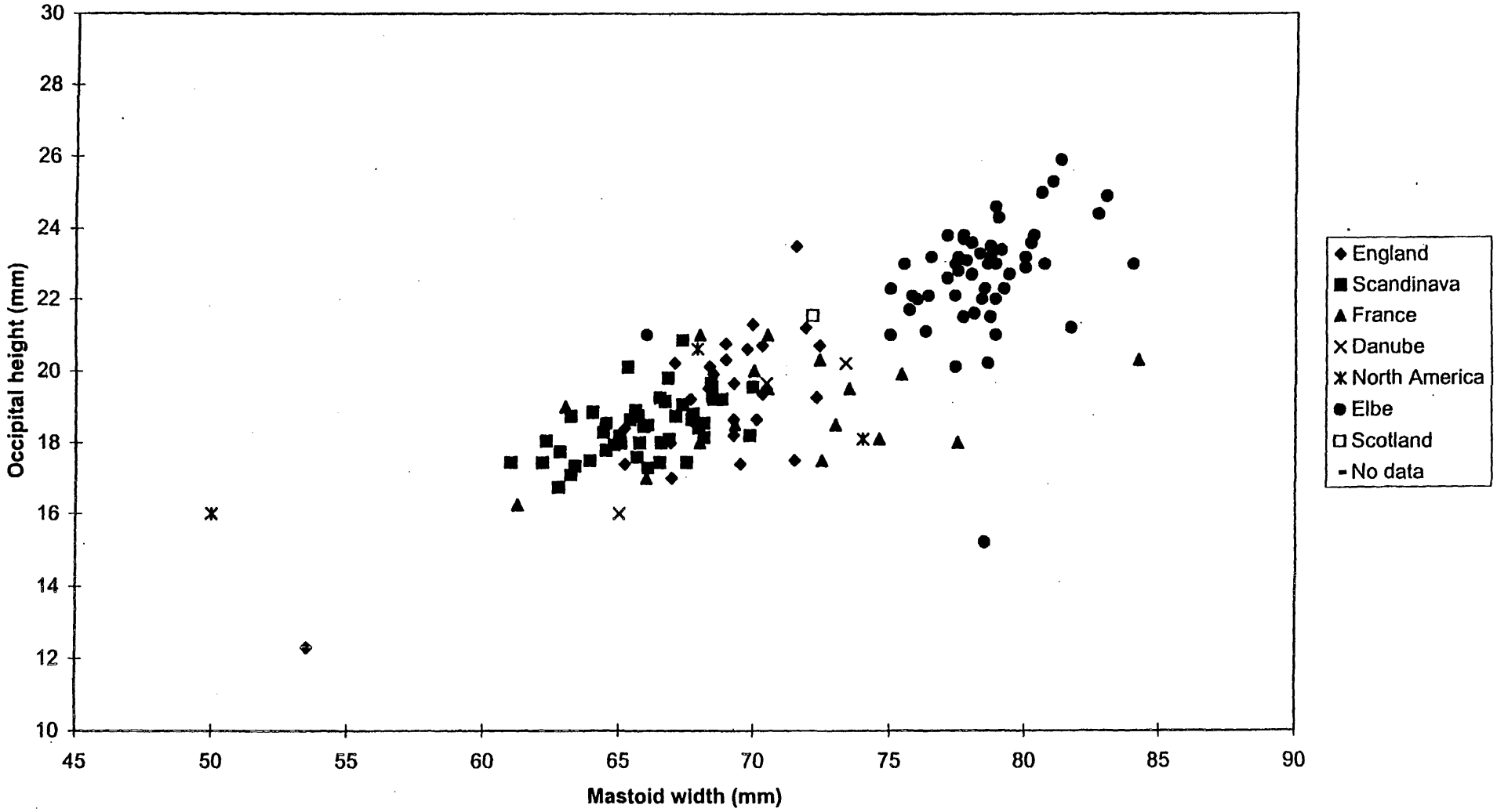

Figure 4: The relationship between occipital height and mastoid length in beavers

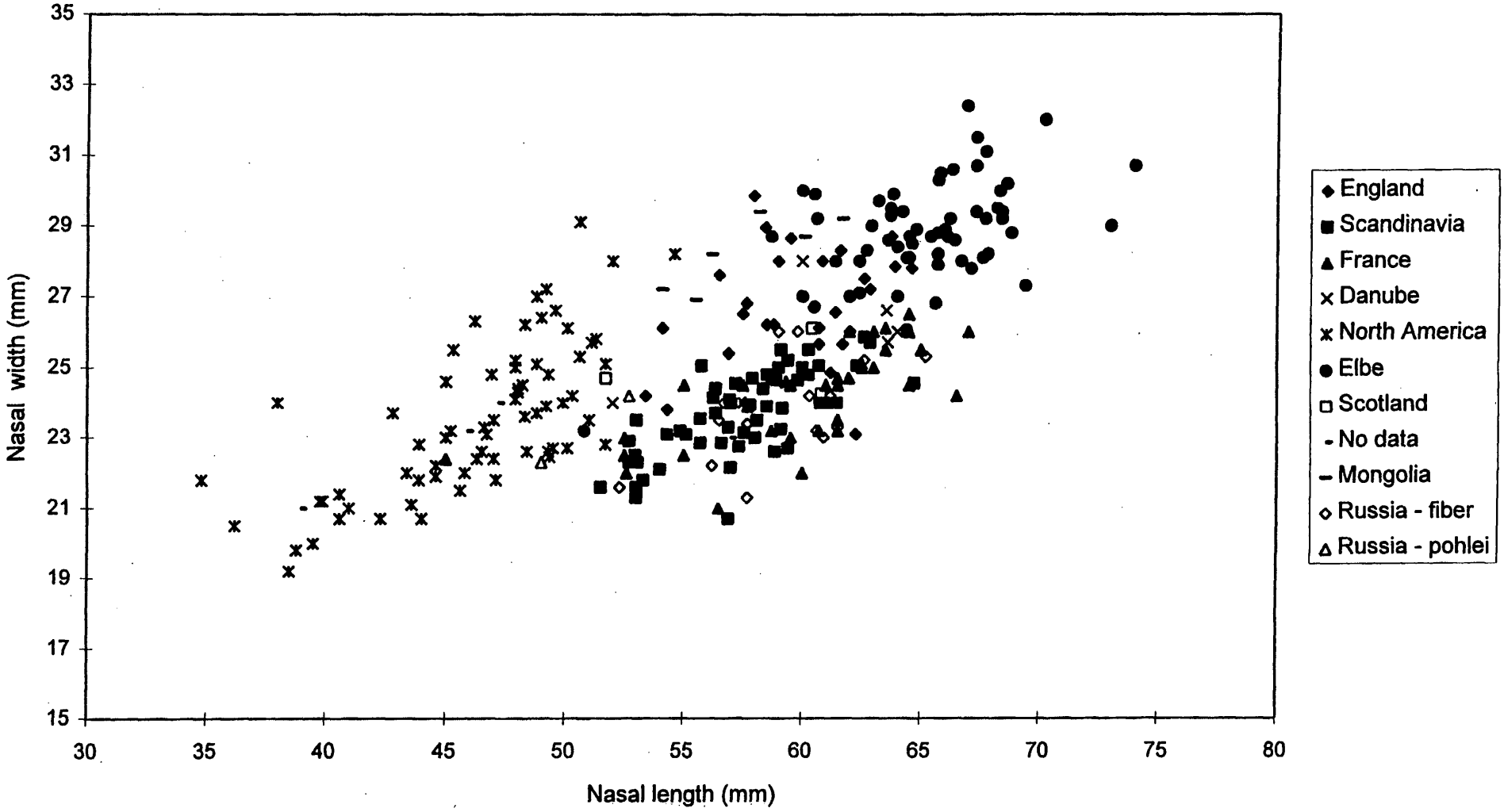

Figure 5: The relationship between the width and length of nasals in beavers

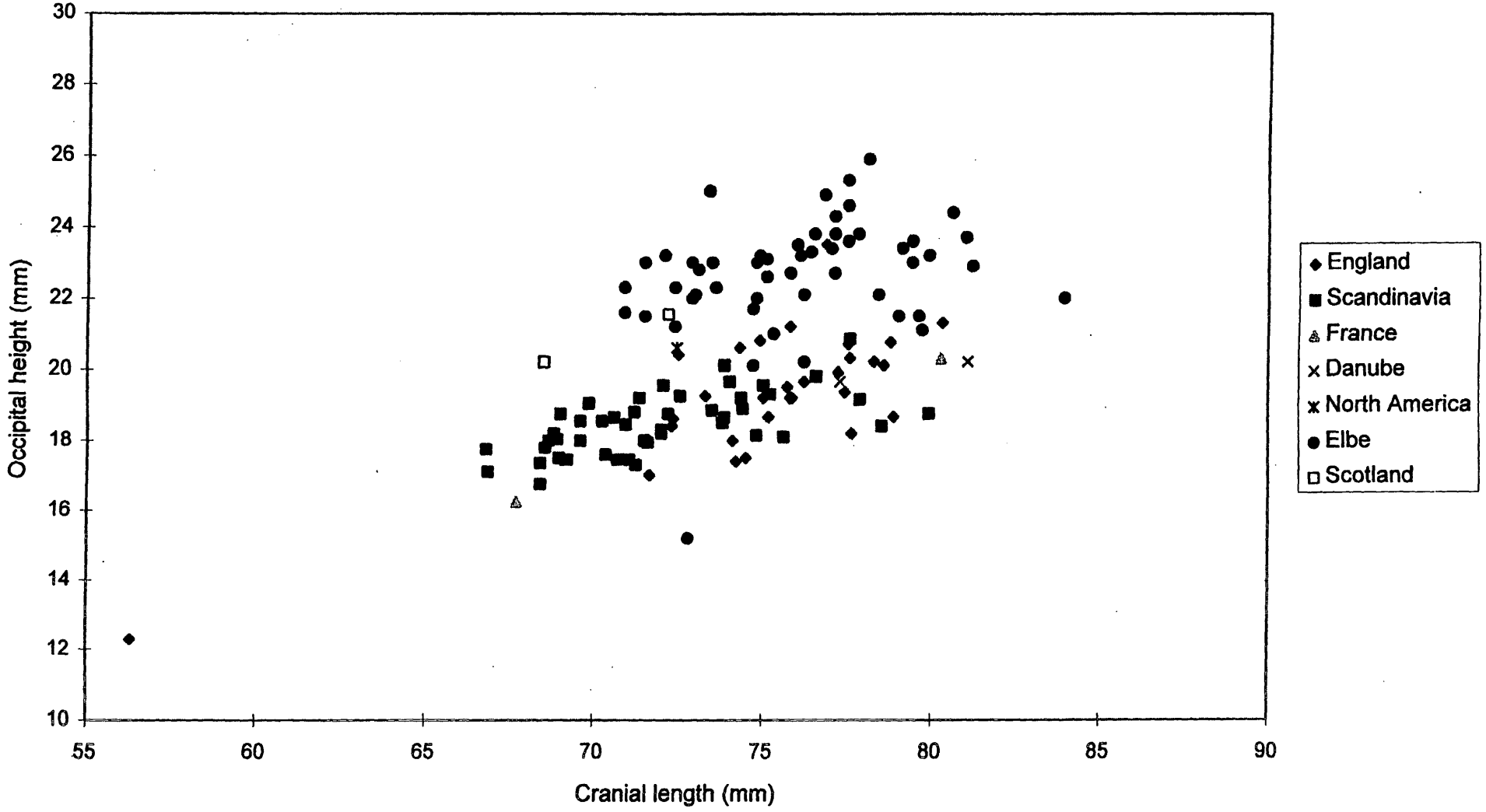

Figure 6: The relationship between occipital height and cranial length in beavers

3.2.2 *Principal Component 2 (PC2)*

Principle component 2 accounted for 20.1% of the within-sample variation, and was taken to be a measure of increasing tooth-row length according to:

$$PC2 = -0.10\ LM + 0.62\ LTL - 0.46\ LDL$$

Analysis of variance again revealed highly significant variation ($F_{3,157} = 16.31$, $P < 0.00001$) with a least-significant-difference test differentiating three groupings: French, German and Scandinavian, and English. Thus, French specimens are characterised as having a relatively short mandibular tooth-row for their mandible size, particularly in comparison to the English specimens.

Again, the American and Mongolian specimens were not statistically tested, but were both characterized by short tooth-rows in comparison to the English specimens (Table 5).

Table 5. Variation in mandibular size and shape across populations.

		PC 1		PC 2		PC 3	
Population	**N**	**Mean**	**SD**	**Mean**	**SD**	**Mean**	**SD**
Germany	55	+0.969	0.728	+0.068	0.756	-0.585	0.519
France	12	-0.399	0.913	-1.530	0.989	-0.251	1.717
Scandinavia	48	-0.604	0.525	+0.052	0.731	+0.316	0.544
England	46	-0.166	0.772	+0.436	1.070	+0.614	0.947
Mongolia	6	+0.510	0.155	-1.021	0.534	-1.159	0.431
N. America	8	-1.500	1.105	-0.765	0.565	-1.448	0.811

3.2.3 *Principal Component 3 (PC3)*

Although principal component 3 accounted for only 9.5% of the within-sample variation, it still varied significantly between the populations ($F_{3,157} = 21.33$, $P < 0.00001$). It was taken as a measure of increasing tooth-row length and diastema length for decreasing mandibular length, according to:

$$PC3 = -0.41\ LM + 0.15\ LTL + 0.30\ LDL$$

The least-significant-difference test differentiated two groupings: Germany/France and Scandinavia/England, with the German/France group having lower principal Component 3 values and thus relatively large tooth-row and diastema lengths for the mandible length.

The American and Mongolian specimens had the lowest principal component 3 values of all the specimens.

The preceding analysis examined variation in a univariate manner (i.e. considering a single component of size or shape at a time). We can use the technique of

discriminant function analysis (DFA[3]) to examine the relative importance of size and shape in differentiating between the four populations for which we have the most data (i.e. German, French, Scandinavian and English). This will also allow us to examine the similarity of the sole Scottish specimen (with a complete set of mandibular measurements) to these samples.

A discriminant function analysis of these four populations was highly significant (Wilks' $\lambda = 0.234$; $P < 0.00001$). The first two discriminant functions (Fig. 7) accounted for over 99% of the variation in mandibular size and shape[4]. The first discriminant function, accounting for 79.8% of the between-population variation, measures decreasing principal component 1 ('size') versus increasing principal components 2 and 3 ('shape'), whereas the second function (19.5% of the total between-population variation) is largely a measure of principal component 2 (shape'). These loadings are illustrated by the vectors in the top right-hand corner of Fig. 7, and the 95% confidence intervals for the group means for each population are shown as error bars. In other words most of the between-population variation is accounted for by size, but there is an important shape component too involving relative toothrow length.

We can use these two discriminant functions to re-classify the specimens back into groups, and thus get an idea of how separate or differentiated the populations are. If individuals show a low probability of being reclassified in their original group, there is probably no differences between populations. Overall, 75.8% of specimens were re-classified into their correct group of origin (Table 6). Over 95% of the German specimens were correctly re-classified, while the French material was mis-classified 50% of the time (although it should be noted that there were only 12 specimens). While the English and Scandinavian specimens were relatively distinct (70.8% and 63.0% correct re-classification respectively), they were also relatively similar (mirroring their close proximity in Fig. 7).

This same procedure also allows us to classify the Scottish specimen. As is not surprising, given its position in Fig. 7, it had a 73.1% chance of being classified as 'English', with the next greatest probability of it being 'Scandinavian' (26.2%).

If this analysis is run excluding the English material (in order to restrict the analysis to contemporary populations only), 92.2% of the specimens are correctly re-classified (German material was correctly re-classified 96.4%, French again 50%, and Scandinavian 97.9%). This shows also that English beavers were morphologically closest to Scandinavian animals, because Scandinavian individuals are now more likely to be reclassified correctly.

[3] See Appendix

[4] Discriminant function 3 accounted for 0.7% of the between-population variation and was not statistically significant. It will not be considered further.

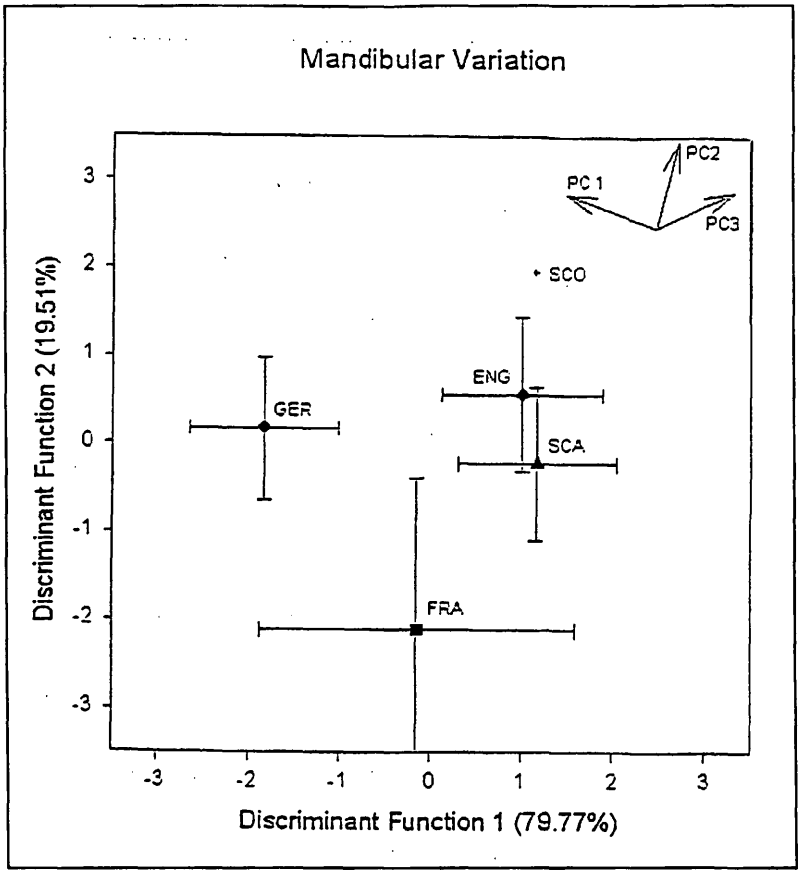

Figure 7. Discriminant function analysis of three mandibular measurements from French (FRA), German (GER), Scandinavian (SCA) and English fossil beavers (ENG). A single Scottish animal (SCO) is shown also. See text for details.

It is necessary to address the issue of how much of this variation is due to size differences. As we saw above, 79.8% of the between-group variation was in PC1 (our measure of size and allometric shape variation). If a discriminant function analysis is run using only PC2 and PC3, a significant separation still occurs (Wilks' $\lambda = 0.501$, $P < 0.0001$), although the separation is not as significant. Overall correct re-allocation drops to 69.6%, with the German specimens remaining the most distinct (89% correct re-allocation). Scandinavian and English populations have a rate of 60.4 and 60.9% respectively, while the French re-allocation rate remains as before. Within this framework, the Scottish specimen remains re-allocated as 'English' (64.9% probability).

Table 6. Re-classification results for the mandibular data.

From \ To	Germany	France	Scandinavia	England	% Correct
Germany	53	1	1		96.4
France	2	6	2	2	50.0
Scandinavia		1	34	13	70.8
England	1	1	15	29	63.0

Summary of mandibular analysis:

1. Significant variation exists in mandibular size and shape across four samples of beaver from Europe.

2. German specimens are characterised as having large mandibles with relatively large tooth-rows.

3. The extinct English populations had a large tooth-row for their mandible size (which was in itself relatively great). Overall, however, these specimens showed the greatest affinity to Scandinavian animals.

4. The single Scottish mandible was re-allocated to the extinct English material. This affinity is independent of size variation.

3.3 Multivariate analysis of cranial measurements

To increase the sample sizes for cranial analysis, remaining missing values were replaced with their group mean. Principal component analysis of 17 chosen variables revealed a first principal component which accounted for 63% of the total variance. IMW (Breadth of premaxillae at junction with maxillae), M3W (Width at third upper molars), PMW (Width at premolars) and CW (Cranial width) were removed due to large amounts of missing data, resulting in 356 specimens. This component had high, positive loadings (ranging between +0.48 and +0.95, with the majority of loadings approximately +0.85), and was thus taken to be a measure of size and allometric shape. Analysis of variance of this size measure was significant ($F_{3,242} = 73.17$; $P < 0.00001$), with the German material being larger than all other samples (Germany > England > France > Scandinavia). Mandibular and cranial size were highly correlated with each other ($r2 = 0.86$; $P < 0.0001$; $n = 179$).

Beyond interpreting principal component 1 as 'size', no attempt was made to interpret the remaining components (beyond terming them as 'shape'). This decision was due to the large amount of interpolated data, and the general difficulty in interpreting components with large numbers (i.e. 17) of variables.

As could be expected based on the mandibular data, there were significant differences between the samples. A four-group discriminant function analysis (Germany, France, Scandinavia and England) revealed significant variation (Fig. 8; Wilks' $\lambda = 0.0064$; $P < 0.00001$), with three significant functions allowing 97.2% of

specimens to be reallocated to their group of origin (Table 7). All groups remained unique (percentage reallocations varied between 95 & 100%), with little significant confusion between samples.

Table 7. Re-classification results for the cranial data

From \ To	Germany	France	Scandinavia	England	% Correct
Germany	57	1		2	95.0
France		46	1	1	95.8
Scandinavia		1	48		98.0
England			1	88	97.8
(Britain	2	1	1	88	95.7)

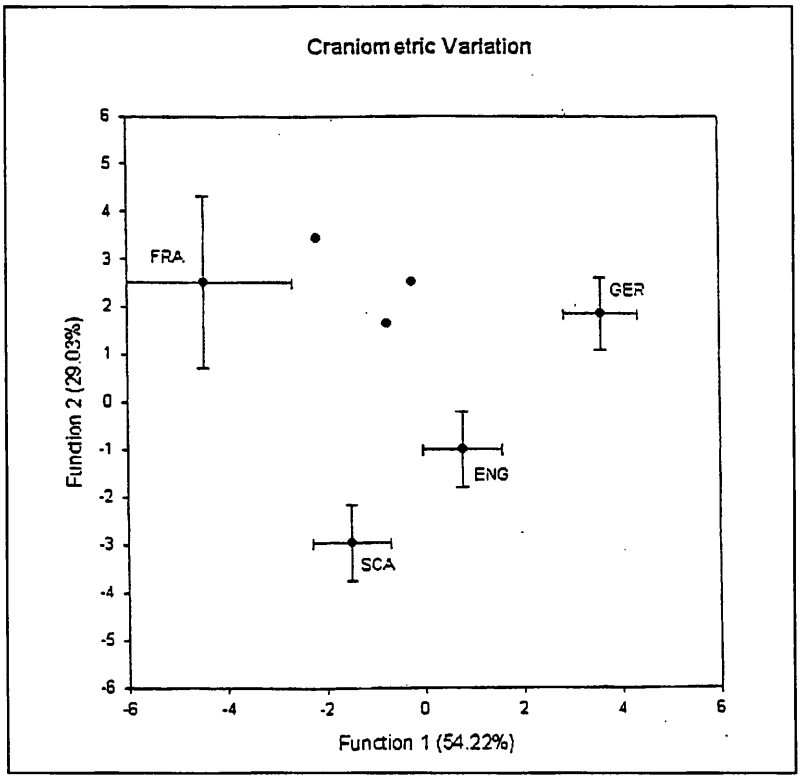

Figure 8. Discriminant function analysis of 17 cranial measurements from French (FRA), German (GER), Scandinavian (SCA) and English fossil beavers (ENG). Three Scottish animals (SCO) are shown also. See text for details.

Given the above, the status of the three Scottish specimens proved a little unclear. Two of the specimens were reallocated as German (with 50% probability), while the remaining specimen was deemed 'French' (with virtually a 100% probability).

If size is 'removed' (by analyzing principal component 2 using 17 variables), significant separation still occurs (Wilks' λ = 0.009; $P < 0.00001$). This analysis allowed 97.6% of the specimens to be correctly reallocated (Table 8). Sample-wise

re-allocation varied between 93 and 100%, with again little significant confusion between samples. Re-allocation of the Scottish specimens continued to be problematic - two specimens were re-classified as 'French' (53 and 99% probability), while the remaining specimen was classified as 'German' (99% probability).

Table 8. Re-classification results for the cranial data ('size' removed).

From \ To	Germany	France	Scandinavia	England	% Correct
Germany	58			2	96.7
France		45		3	93.8
Scandinavia			48		100.0
England	1			88	98.4
(Britain	2	2		88	95.6)

3.3.1 Summary of cranial analysis

1. There is highly significant cranial variation between German, French, Scandinavian and English beavers. This variation is independent of size variation.

2. This analysis confirms that the skulls of British fossil beavers are morphologically closest to those of extant Scandinavian beavers.

3. Further Scottish specimens would be required before any firm conclusions could be made concerning the affinities of this local population. However, no further specimens are currently available. The mis-classification of the Scottish specimens is probably due to sampling from such a small sample.

3.4 Summary and analytical conclusions

There is obviously highly significant craniometric variation within European *Castor fiber*. This variation is largely independent of size variation, with English specimens most resembling those from Scandinavia. There are unfortunately insufficient data to characterise adequately the variation among Scottish specimens. It is unlikely that the addition of further Continental specimens will add further information, unless variation across Eurasia is the goal of the study.

It should be added that it is unlikely that the methods used to interpolate missing data (multiple regression and mean substitution) have caused false differences to appear between groups. In the case of the cranial data, the mean substitution caused groups to appear more separate (by reducing within-group variation), so that the group differences remain real.

4. DISCUSSION

The lack of Scottish fossil beaver specimens means that it is not possible to determine definitively their morphometric relationship to extant beaver populations in Europe. However, the larger sample of English (mostly East Anglian) beavers are morphologically closest to Scandinavian beavers. This is consistent with Lavrov's (1983) *ad hoc* observation of a Fen beaver skull.

Given that Scotland (and England) were re-colonised by beavers after the end of the last ice age (10,000 years BP) and before sea levels rose to cut Britain off from the European mainland (c. 8,000 years BP) (Lambeck, 1995), the ancestors of three extant populations could have colonised Britain from eastern Europe across the North Sea (Scandinavia was still covered by ice during part of this period), from France across the English Channel and from Germany via the southern North Sea (Fig. 9). The multivariate analyses indicate that only one population is likely to have colonised Britain i.e. that ancestral to the Scandinavian one. Recently, beavers have been observed swimming in the Baltic Sea (G. Hartman, pers. comm.), so that colonisation via shallow and narrow seas may have been possible in the early Holocene. Alternatively, French beavers could have colonised Britain and Scandinavia, so that *Castor fiber* should more properly be called the 'Western European beaver' and the Elbe and Mongolian beavers would, therefore, be the 'Eastern beaver' (Lavrov's *C. albicus*). This is consistent with mitochondrial DNA data from brown bears, *Ursos arctos*, which showed that populations from the Pyrenees are identical to those from southern Sweden, but genetically distinct from those of eastern Europe and northern Sweden (Taberlet & Bouvet, 1994).

Postglacial colonisation routes may also be testable using GIS analysis of beaver habitat requirements and the BIOME3 model (Haxeltine, 1986), which predicts habitat distribution at the Last Glacial Maximum (22,000 years BP). A similar approach has been carried out to determine the colonisation routes of tigers, *Panthera tigris*, after the last Ice Age (Kitchener, in prep.), and has led to a re-evaluation of the sub-specific taxonomy of this endangered big cat (Kitchener, in press). It is implausible that German or French beavers could have colonised Scotland before the Fen beaver population was established in England. With such a small sample size (n=3), it was not surprising that the Scottish crania were re-classified anomalously. However, it is impossible to characterise the former Scottish population from such a small sample, so that we must use the larger English sample as a proxy. If the Scottish specimens are included within a British sample, the proportion of mis-classified specimens is still very low (4.3% for analysis including size; 4.4% for analysis excluding size). It is possible that the three Scottish specimens may reflect the greater variation found in beaver populations at that time, because all contemporary populations have been through severe population bottlenecks, which may have limited their morphological and genetical variation through inbreeding and genetic drift.

Therefore, these multivariate analyses of measurements from beaver skulls suggest that the extinct British beaver population from the early Holocene is morphometrically closest to extant populations in Scandinavia. Even if it were shown that these were not genetically the most closely related, these analyses show that the two groups have functionally similar skulls.

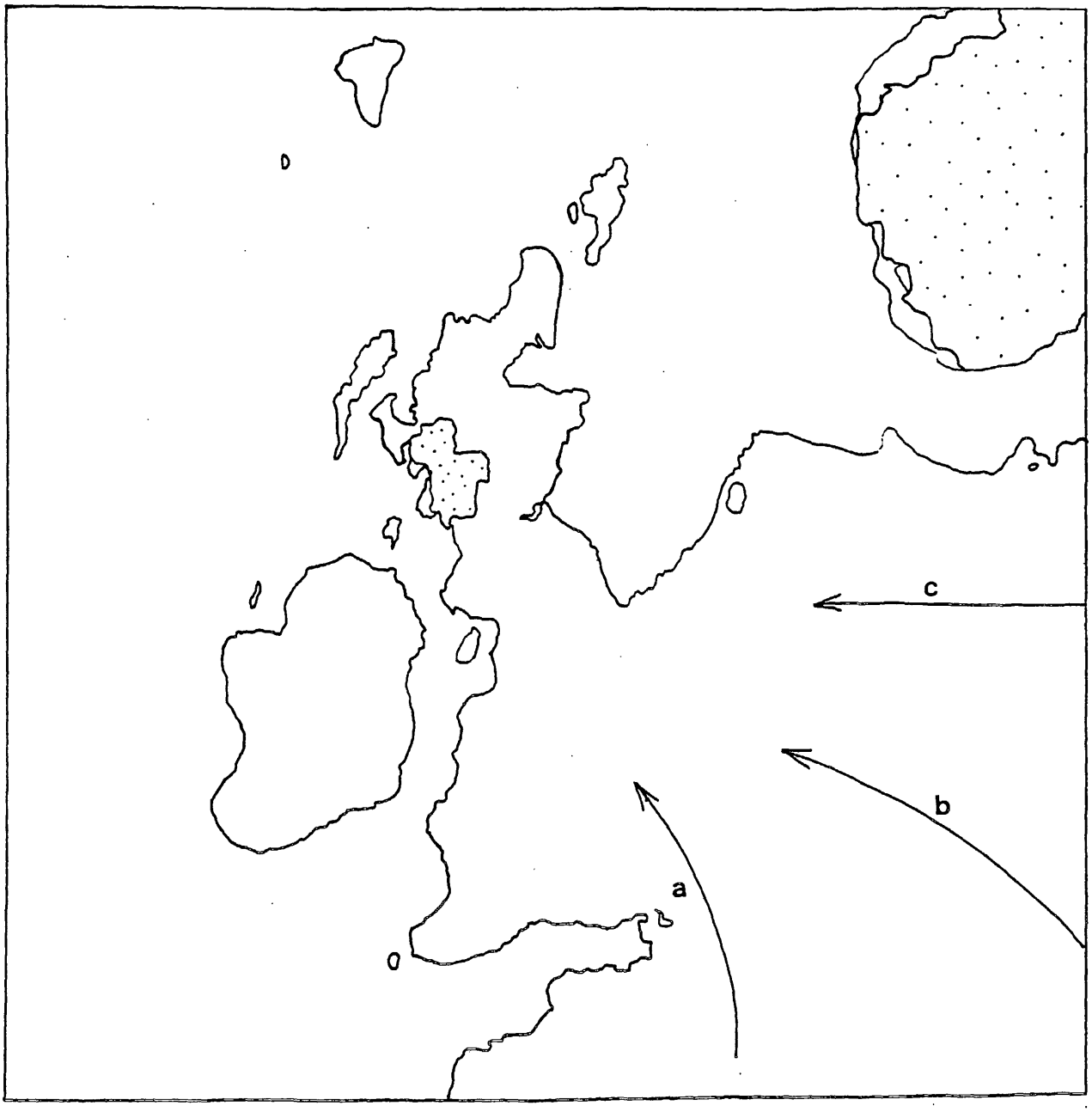

Figure 9. Possible colonisation routes of Britain by beavers in the early Holocene. Shoreline and ice caps (stippled) are as predicted for the end of the last ice age (10,000 years BP) following Lambeck (1995). Potential routes taken by ancestors of (a.) French beavers, (b.) German beavers and (c.) Scandinavian beavers. See text for details.

5. RECOMMENDATIONS

IUCN re-introduction guidelines state that the most closely related population of a former indigenous species should be used for any re-introduction (IUCN, 1995). On the basis of this study we recommend that Eurasian beavers from Scandinavia are used as the source population for any re-introduction to Scotland, because their skulls are the most morphologically similar to those of fossil British beavers.

One concern about using the Scandinavian population for re-introduction is that it is based on few founders and displays very low genetic diversity (Ellegren *et al.*, 1993). This may, in turn, raise concerns that any re-introduced Scottish beavers may become in-bred, or unable to cope with environmental change. However, despite the potential problems of a low founder base, a severe population bottleneck and low genetic variation, Scandinavian beavers have increased dramatically in numbers during the 20th century (Ellegren *et al.*, 1993) (e.g. from a few animals re-introduced in 1922-1939 to about 100,000 in 1993 in Sweden). Moreover, these animals thrive in a wide variety of climatic and environmental conditions (G. Hartman, pers. comm.). Therefore, there is no reason to believe that re-introduction of beavers to Scotland from Scandinavia would be compromised by their low genetic variation. However, it would perhaps be beneficial to select animals which survive in a similar climate with a similar selection of food plants and trees.

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APPENDIX: MULTIVARIATE STATISTICAL TECHNIQUES USED

All analyses were carried out using version 6.0 of SPSS of Windows.

Principal Component Analysis

A common statistical method utilized in the study of within-population variation is principal component analysis (PCA), a technique first developed by Karl Pearson. Indeed, PCA remains the most widely used of the multivariate techniques available to the biometrician. This analysis forms linear combinations of the original variables (termed 'principal components') by extraction of eigenvalues and eigenvectors from the variance-covariance matrix of the variables. The first component that is derived represents a certain proportion of the variance present in the original data and successive components account for decreasing proportions of the variance while remaining uncorrelated with previous components. Thus, a PCA of a N-variable dataset results in N principal components which, by definition, represent uncorrelated patterns of variation within the original sample.

Multivariate analyses of morphometric data sets usually aim to identify size and shape differences among individuals and groups. One of the major uses of PCA been in the separation of within-sample size and shape variation. This separation has been rationalized on the often quoted, and somewhat mistaken, assumption of Jolicoeur & Mossiman (1960) that the size of most organisms is more affected than their shape by fluctuations of the external environment, and that shape tends thus generally to provide a more reliable indication than size of the genetic makeup of organisms. Size has a moderate to high (circa 50%) narrow-sense heritability, so that size and shape variation are of equal importance in morphometric studies.

The exact definition of 'size' and 'shape' has provided fertile ground for discussion since the first appearance of the multivariate generalisation of Huxley's allometric relationship, which characterised change of variables with change in body size. Size and shape are best considered as unmeasured factors, that is, linear combinations of measured variables, rather than single measurements. Jolicoeur (1963) found that the co-efficients of the first principal component can be used to estimate allometric constants. Thus, if size variation is present in the data and the co-efficients of the first principal component are either all positive or all negative, then this component can be said to summarize within-sample size variation. This first component has been termed 'structural size' by some, or 'general size' by others. Shape is thus defined as the remaining n-1 principal components, and quantifies the variation that cannot be explained by size and allometric relationships.

Discriminant Function Analysis

The most commonly used method for the analysis of variation in traits between groups is that of discriminant function analysis (DFA). DFA derives combinations of the original measurements (termed 'discriminant functions') that maximize between-sample variation, while at the same time standardizing the degree of variation within the samples. The analysis is geometrically simple and essentially involves a two-stage principal component analysis. A complete DFA can answer the following;

1. Do the group means differ significantly? The answer is provided by a multivariate analysis of variance (MANOVA) resulting in a statistic analogous to the univariate F-ratio, namely Wilks' λ.

2. How many of the discriminant functions allow separation of the groups? With k groups, there is a maximum of k-1 axes.

3. How are the groups positioned in this transformed canonical space? Group means and confidence intervals can be displayed in two or three dimensions.

4. How well can specimens of unknown provenance be assigned to the groups under study?

Of considerable interest to the study of variation between groups is the examination to what degree size and shape variation (as defined above) contribute to population differentiation. Numerous procedures have been developed to attempt to examine this point. These include 'common principal component analysis', 'multiple group principal component analysis', 'size-constrained principal component analysis', and 'shear analysis'. In this study, it will be sufficient to study the importance of size variation by examining the difference between DFAs run including the 'size' component (PC1) and those run without it.

Scottish Natural Heritage

Scottish Natural Heritage is an independent body established by Parliament in 1992, responsible to the Secretary of State for Scotland.

Our task is to secure the conservation and enhancement of Scotland's unique and precious natural heritage - the wildlife, the habitats, the landscapes and the seascapes - which has evolved through the long partnership between people and nature.

We advise on policies and promote projects that aim to improve the natural heritage and support its sustainable use.

Our aim is to help people to enjoy Scotland's natural heritage responsibly, understand it more fully and use it wisely so that it can be sustained for future generations.