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# Craniological differentiation between European wildcats (*Felis silvestris silvestris*), African wildcats (*F. s. lybica*) and Asian wildcats (*F. s. ornata*): implications for their evolution and conservation

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Intraspecific diversification of the wildcat (*Felis silvestris*), including the European wildcat (*F. s. silvestris*), the Asian wildcat (*F. s. ornata*) and the African wildcat (*F. s. lybica*), was examined based on 39 cranial morphology variables. The samples of free-ranging cats originated from Britain, Europe, Central Asia and southern Africa, consisting of both nominal wildcat specimens (referred to henceforth as 'wildcats') and nominal non-wildcat specimens ('non-wildcats') based on museum labels. The skull morphology of 'wildcats' from Britain and Europe is clearly different from that of 'wildcats' of Central Asia and southern Africa. The latter are characterized especially by their proportionately larger cheek teeth. On the basis of principal component, discriminant function and canonical variate analyses, the skull morphology of British 'non-wildcats' is less distinct than is that of British 'wildcats' from the skull morphologies of 'wildcats' of Central Asia and southern Africa. On the other hand, the skull morphology of southern African 'non-wildcats' is as distinct from those of 'wildcats' of Britain and Europe as is that of southern African 'wildcats'. We suggest that the evolution of the modern wildcat probably consisted of at least three different distribution expansions punctuated by two differentiation events: the exodus from Europe during the late Pleistocene, coinciding with the emergence of the steppe wildcat lineage (phenotype of Asian–African wildcat), followed by its rapid range expansion in the Old World. The second differentiation event was the emergence of the domestic cat followed by its subsequent colonization of the entire world with human assistance. Considering the recent evolutionary history of, and morphological divergence in, the wildcat, preventing hybridization between the European wildcat and the domestic cat is a high conservation priority.  *Biological Journal of the Linnean Society*, 2004, **83**, 47–63.

ADDITIONAL KEYWORDS: Felidae – *Felis lunensis* – *F. lybica* – *F. ornata* – *F. silvestris* – forest cat – hybridization – morphology – Pleistocene – steppe cat.

## INTRODUCTION

The wildcat (*Felis silvestris* Schreber, 1777) is distributed widely throughout Europe, Africa and Asia (Nowell & Jackson, 1996). The existence of distinguishable phenotypes across this wide distribution, along with apparently considerable local variation (Pocock, 1951; Haltenorth, 1953), has left wildcat taxonomy in a state of confusion for many years (Guggisberg, 1975). It has become customary to consider a single species of the wildcat with three main morphological types: the European wildcat (*F. s. silvestris*), the African wildcat (*F. s. lybica* Forster, 1780) and the Asian wildcat (*F. s. ornata* Gray, 1830) (Guggisberg, 1975; Hemmer, 1978; Kitchener, 1991; Nowell & Jackson, 1996).

According to earlier morphological studies (Pocock, 1951; Roberts, 1951; Haltenorth, 1953; Heptner &

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Sludskii, 1972; Guggisberg, 1975), the three wildcat groups possess external characteristics that are fairly distinct from each other and ubiquitous within each group. The European wildcat has been characterized by its bushy tail, which ends as a broadly rounded black tip, and long soft fur with relatively conspicuous stripes, and is distributed in Britain, Europe including some Mediterranean islands, and part of south-western Asia (Fig. 1). The African wildcat is widely distributed in Africa, the Arabian Peninsula, part of south-western Asia and other Mediterranean islands. It has a tapering tail, a reddish or rusty-brown tint to the back of the ears and inconspicuous body stripes compared with the European wildcat. The domestic cat [*F. s. catus* Linnaeus, 1758: concerning the use of different scientific names for the wildcat and the domestic cat see Opinion 2027 (Case 3010) (International Commission on Zoological Nomenclature, 2003)] is widely believed to have descended from the African wildcat (and perhaps some Asian wildcat populations) and historical records suggest that the domestic cat first appeared in Egypt approximately 4000 years ago. The Asian wildcat is the least known and inhabits Eurasia from the Middle East to western India, through Central Asia to Mongolia and north-western China. It is similar to the African wildcat, but is distinguishable by its coat pattern, which consists mainly of distinct dark spots instead of stripes.

In the last 20 years, advances in biomolecular techniques and the accessibility of powerful statistical analyses have yielded several important results regarding the phylogeny of the wildcat. Such studies have focused mainly on taxonomy-related conservation problems of the wildcat concerning hybridization between its local populations and free-ranging domestic cats in Scotland (French, Corbett & Easterbee, 1988; Daniels *et al*., 1998; Beaumont *et al*., 2001; Daniels *et al*., 2001; Reig, Daniels & Macdonald, 2001), continental Europe (Randi & Ragni, 1986, 1991; Randi *et al*., 2001; Pierpaoli *et al*., 2003), or

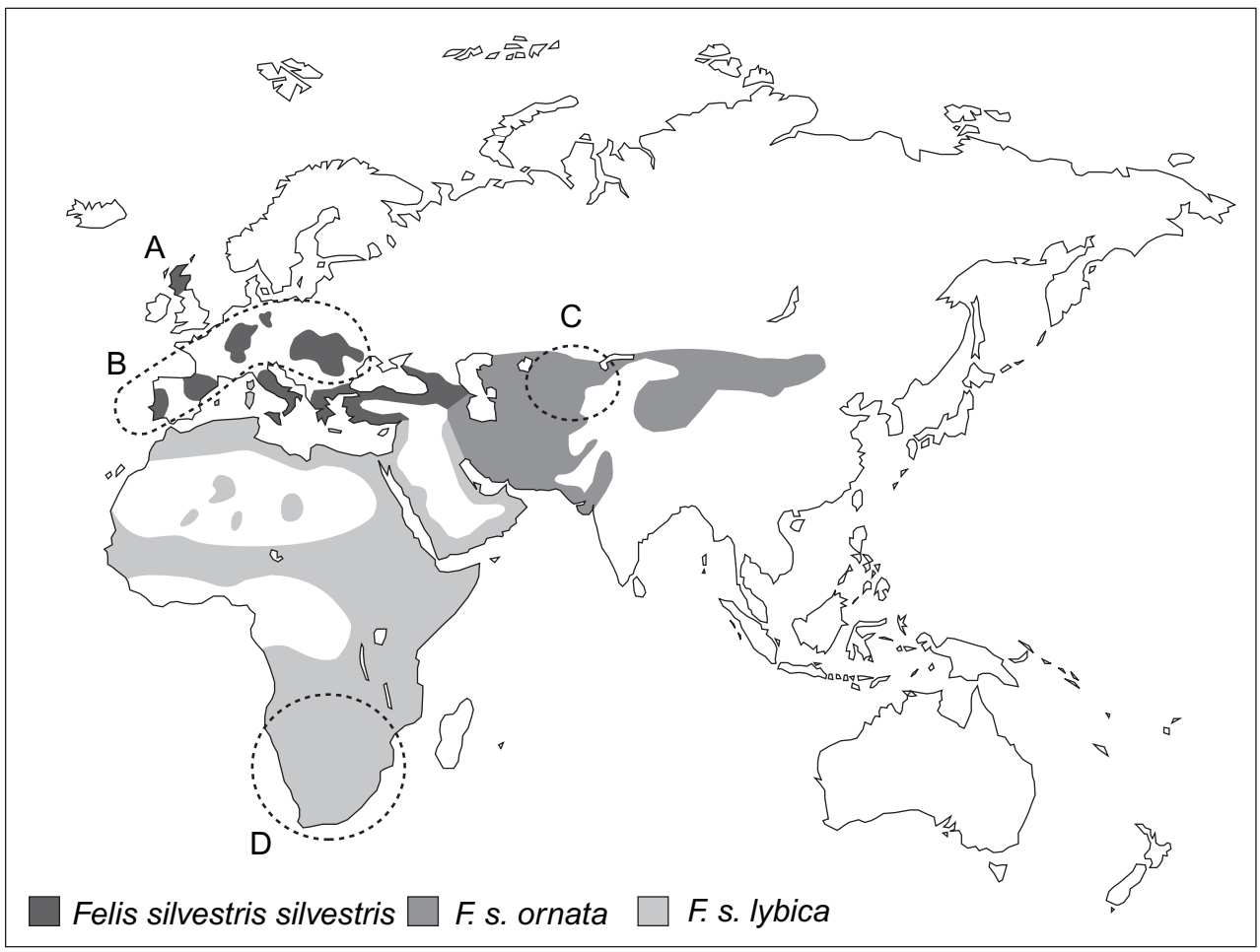


**Figure 1.** Distribution of the wildcat. Skulls used for this study originated from four geographically separate regions consisting of Britain (A), Europe (B), Central Asia (C) and southern Africa (D).

southern Africa (Wiseman, O'Ryan & Harley, 2000). These recent studies have also suggested, largely independently of the earlier taxonomic work, that European wildcats, African wildcats and domestic cats are phylogenetically very close, such that they belong to a single polytypic species. These data suggest that the European and African wildcats may have diverged from each other as recently as 20 000 years ago, and that the domestic cat is phylogenetically closer to the African than it is to the European wildcat (Collier & O'Brien, 1985; Randi & Ragni, 1986, 1991; Johnson & O'Brien, 1997). However, because most of these studies are based on regional populations either in Scotland or in Italy, there has been no elucidation of the intraspecific phylogeny of the wildcat, especially concerning the position of the Asian wildcat, which until now has escaped study owing to the paucity of data on many quantitative parameters. Furthermore, a biologically coherent approach to the conservation of extant wildcats necessitates understanding their evolutionary history, especially when current taxonomic distinctions, whether based on traditional morphology or molecular biology, are proving elusive (French *et al*., 1988; Kitchener, 1998; Daniels *et al*., 2001).

In this paper, we aim to explore and discuss the phylogenetic relationships amongst European, African and Asian wildcats based on their skull morphology, against a backdrop of the probable recent evolutionary history of these taxa. All samples studied here originated from populations separated either by sea or by great geographical distances, so that we consider there has not been recent regular gene flow, which may result in similar phenotypes, between any combination of the sampled populations. Thus, we have eliminated the potential confounding effects concerning possible recent population mixtures and isolations, of which there is currently only a poor understanding.

## MATERIAL AND METHODS

### Specimens

The morphological investigation was undertaken using 218 skulls of free-ranging cats from Britain and Europe (originating from Germany, France, Spain, Italy, Hungary, Austria, Switzerland, Slovenia and Romania), 145 from southern Africa (South Africa, Namibia, Botswana, Zimbabwe, Malawi, Mozambique and Zambia), and 103 from Central Asia (Uzbekistan, Kazakhstan and Kyrgyzstan) (Fig. 1) from museum collections. The skulls of the European cats were examined by two of the authors (N.Y. & J.M.W.) and the others by one author (N.Y.). Only adult and subadult skulls, assessed from the fusion of skull sutures (Daniels *et al*., 1998), were included in the analyses. Although the very existence of pristine wildcats and possible identification of their characteristics have been the subject of extensive debate (Daniels *et al*., 1998; Kitchener, 1998; Daniels *et al*., 2001; Reig *et al*., 2001; Yamaguchi *et al.*, in press), cats were nominally classified as either 'wildcat' or 'non-wildcat' based on museum labels. Being mindful of the debate over what really constitutes a true wildcat (Yamaguchi *et al.*, in press), we are careful throughout the text, to use quotation marks, such as 'wildcat', when we refer to the nominal categories labelled in the museum collections. Because these specimens were identified at various times throughout a period of more than 100 years, it is impossible to know exactly on what basis these distinctions were made; however, they were likely determined from external morphology, especially pelage (e.g. Pocock, 1951; Haltenorth, 1953; Heptner & Sludskii, 1972; Smithers, 1983; Kitchener, 1998).

Pooling all regional free-ranging cats, which very probably include ubiquitous domestic cats and their hybrids, may mask any morphological differences between wildcats from different geographical regions. Although defining a wildcat based purely on external morphology may be problematic, morphological diversity appears to reflect distinct gene pools both in British and European (Beaumont *et al*., 2001; Randi *et al*., 2001) and in southern African (Wiseman *et al*., 2000) populations. For example, strict possession of the coat coloration and markings classically taken to characterize wildcats appears to be sufficient to place an individual in the non-domestic genetic group in the Scottish population (Beaumont *et al*., 2001). Therefore, we assumed that, to a certain extent, basing analyses on nominal 'wildcats' alone should reduce the possibility of regional morphological differences being masked.

### Skull parameters

The following five skull characteristics, which have been traditionally used to distinguish European wildcats from domestic cats (Pocock, 1951; Kitchener, 1995), were scored (1–3) for each specimen (Fig. 2):

1. shape of the anterior end of the nasals;
2. extent of a pit at the posterior end of the nasals;
3. shape of the parietal suture;
4. length of the nasals relative to the maxillae;
5. whether the mandibles tip over on a horizontal surface.

The scores of two observers using ten randomly selected skulls agreed totally for characters –3 and –5, disagreed by a score of 1 in one case each for characters –1 and –4 and in two cases for character –2; they never disagreed by a score of 2 for any character. All five scores were summed as the total skull score and used in analyses.

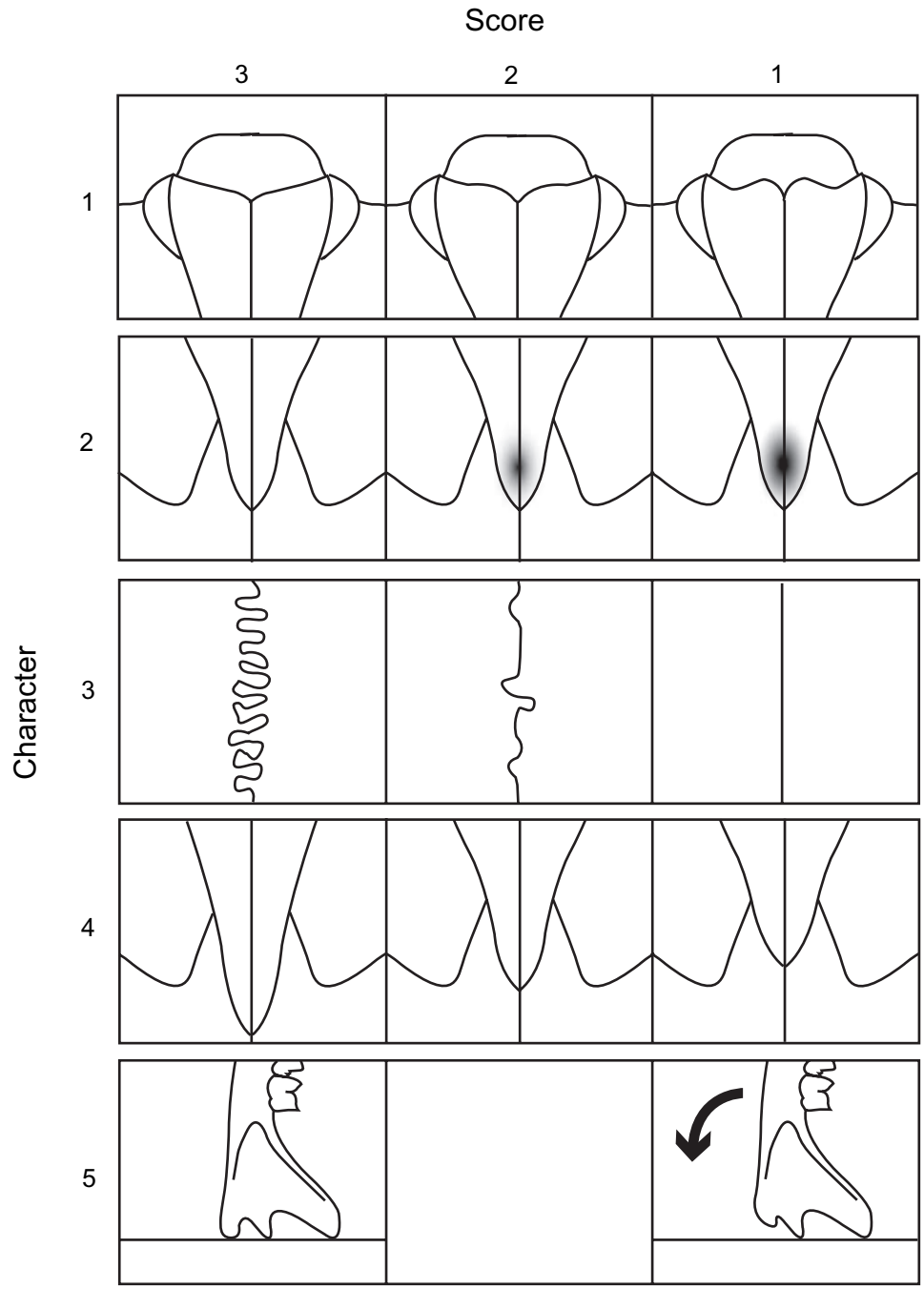


**Figure 2.** Diagram indicating how to score the five skull characteristics.

Forty-four numerical measurements (modified from French *et al*., 1988) of the cranium and mandible were taken. The cranial volume was measured using either steel shot approximately 1 mm in diameter or glass beads approximately 2 mm in diameter. The volume measured with the smaller steel shot was consistently very slightly greater than that measured with the glass beads. Therefore, we converted the former to the latter using the equation:

$$\text{volume (glass beads)} = 1.017 \times \text{volume (steel shot)} - 1.214,$$

based on regression coefficients calculated for volumetric measurements for both methods on ten randomly selected skulls ($R^2 = 0.998$, $t = 70.63$,

$P < 0.0001$). All other parameters were measured to the nearest 0.02 mm using metal calipers. To test for measurement errors both by an individual observer and between observers, six skulls were randomly selected and each measurement was taken six times on each skull. The coefficient of variation for each variable was calculated (Lynch *et al*., 1996). Variables with a mean coefficient of variation of more than 2% were excluded from further analyses. As a result 31 numerical variables were retained for analysis (Fig. 3 and Appendix 1). There were significant differences between the two observers in the maximum length of the nasals (paired *t*-test, $N = 6$ skulls, d.f. = 5, $t = 3.57$, $P = 0.016$) and the depth of the mandible behind $M_1$ ($t = -2.71$, $P = 0.042$) although much less consistently compared with that in the cranial volume, so these were also removed from further analyses.

In addition to these variables, five derived variables were calculated: (1) cranial index by dividing the greatest length of the skull by cranial volume (Schauenberg, 1969); (2) broadness of the nuzzle by dividing the distance between the infraorbital foramena by lateral length of snout; (3) ratio of palatal breadth to $Pm^2$-$M^1$; (4) ratio of postorbital constriction to interorbital breadth; (5) ratio of the distance

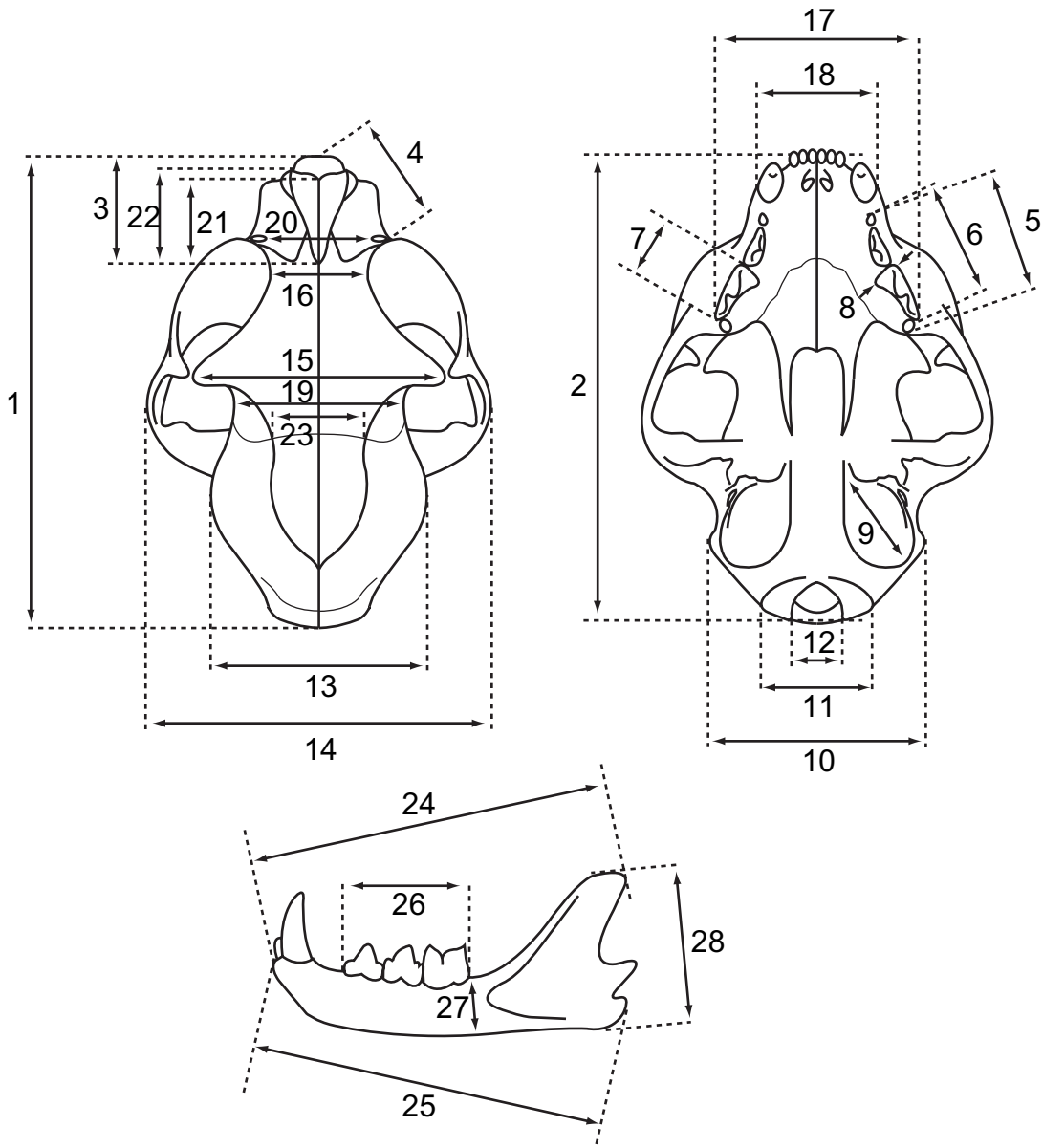


**Figure 3.** Skull variables measured during the study. The numbers correspond to those in the text.

between pogonion and coronoid process to that between pogonion and angular process.

### Statistical analyses

All statistical analyses were carried out using the Statistica statistics package (Statsoft, Tulsa, USA). A principal component analysis (PCA) was carried out using all free-ranging cats together mainly to reduce the numbers of variables for the subsequent analyses. Specimens with any missing value were removed from the analysis, and hence from the subsequent analyses too, reducing the sample size to 80 British cats (39 'wildcats' and 41 'non-wildcats'), 22 European cats (19, 3), 58 Central Asian cats (57, 1) and 89 southern African cats (80, 9). Because of the resultant small sample sizes for both European and Central Asian 'non-wildcats', these were excluded from the later analyses. Discriminant function and canonical variate analyses were carried out to investigate if the four geographically separated groups could be distinguished based on skull morphology using all principal components with eigenvalues greater than 1 (Tabachnick & Fidell, 2001). The four groups a priori consisted of cats originating in Britain, Europe, Central Asia and southern Africa. Furthermore, to enable future use of standard measurements for the classification of skulls, each variable for 'wildcats' originating from the four geographical areas was also analysed and statistically significant differences were detected using Kruskal–Wallis tests and ANOVAs.

## RESULTS

A PCA based on total skull score, 29 measured variables and five derived variables resulted in six principal components (Table 1). The first component (PC1) was probably related to the overall size of the skull along the anteroposterior axis, PC2 to overall breadth of the skull along the mediolateral axis, PC3 to cranial capacity, PC4 to characteristics concerning the middle part of the skull, including teeth, along the anteroposterior axis, PC5 to characteristics concerning the middle part of the skull along the mediolateral axis, and PC6 to the anterior part of the skull. The PCA quite clearly separated British and European 'wildcats' from those originating from Central Asia and southern Africa without any attempt to discriminate those groups (Fig. 4). However, the range of PC scores for British 'non-wildcats' spread well beyond those of British 'wildcats' and overlapped with those of Central Asian and southern African 'wildcats' (Fig. 4). In contrast, the range of PC scores for southern African 'non-wildcats' overlapped extensively with those of southern African 'wildcats' (Fig. 4).

**Table 1.** Results of principal component analysis based on 35 variables with 251 valid cases

| Principal component | Eigenvalue | % explained | % cumulative |
|---|---|---|---|
| 1 | 16.25 | 46.43 | 46.43 |
| 2 | 4.48 | 12.81 | 59.24 |
| 3 | 4.07 | 11.62 | 70.86 |
| 4 | 1.71 | 4.70 | 75.76 |
| 5 | 1.36 | 3.87 | 79.63 |
| 6 | 1.09 | 3.13 | 82.76 |

A discriminant function analysis (DFA) successfully classified most (*c.* 91%) 'wildcat' skulls into one of the four geographical groups from which each skull originated, on the basis of the six PCs (Table 2). The canonical variate analysis (CVA), which produced three canonical variates, showed good separation between the skulls of British and European 'wildcats' and those from Central Asia and southern Africa (Fig. 5). A summary of the overall similarity relationships amongst the four groups was obtained from the squared Mahalanobis distance ($D^2$) between the centroid of each group on the basis of the three canonical variates extracted in the analysis. The UPGMA (unweighted pair-group method using arithmetic average) tree built from the pairwise $D^2$ similarity matrix placed British and European 'wildcats' closest together whereas Central Asian and southern African 'wildcats' were closest to each other (Fig. 6A).

The separation between the four geographically separated populations became less clear when 'wildcats' and 'non-wildcats' were pooled (Table 3). Also, a CVA which extracted three CVs did not show a clear separation between the two larger geographical groups compared with the result using only 'wildcats' (Fig. 7). Furthermore, when free-ranging cats were pooled, the mean $D^2$ between British–European and Central Asian–southern African cats became less compared with those based only on 'wildcats' (Fig. 6B). When southern African 'non-wildcats' were analysed with 'wildcats' from Britain, Europe and Central Asia, the tree was relatively similar to that of 'wildcats' only (Fig. 6C). However, when British 'non-wildcats' were analysed in the same way, the shape of the tree changed dramatically and the average $D^2$ between the two larger groups became smaller (Fig. 6D).

The most highly significant differences between the four groups of 'wildcats' were nasal shape, relative nasal length, total skull score, distance between infra-orbital foramena divided by lateral snout, palatal breadth divided by $Pm^2$-$Pm^4$, $Pm^2$-$M^1$, $Pm^2$-$Pm^4$, auditory bulla length, mandibular $Pm_3$-$M_1$ and man-

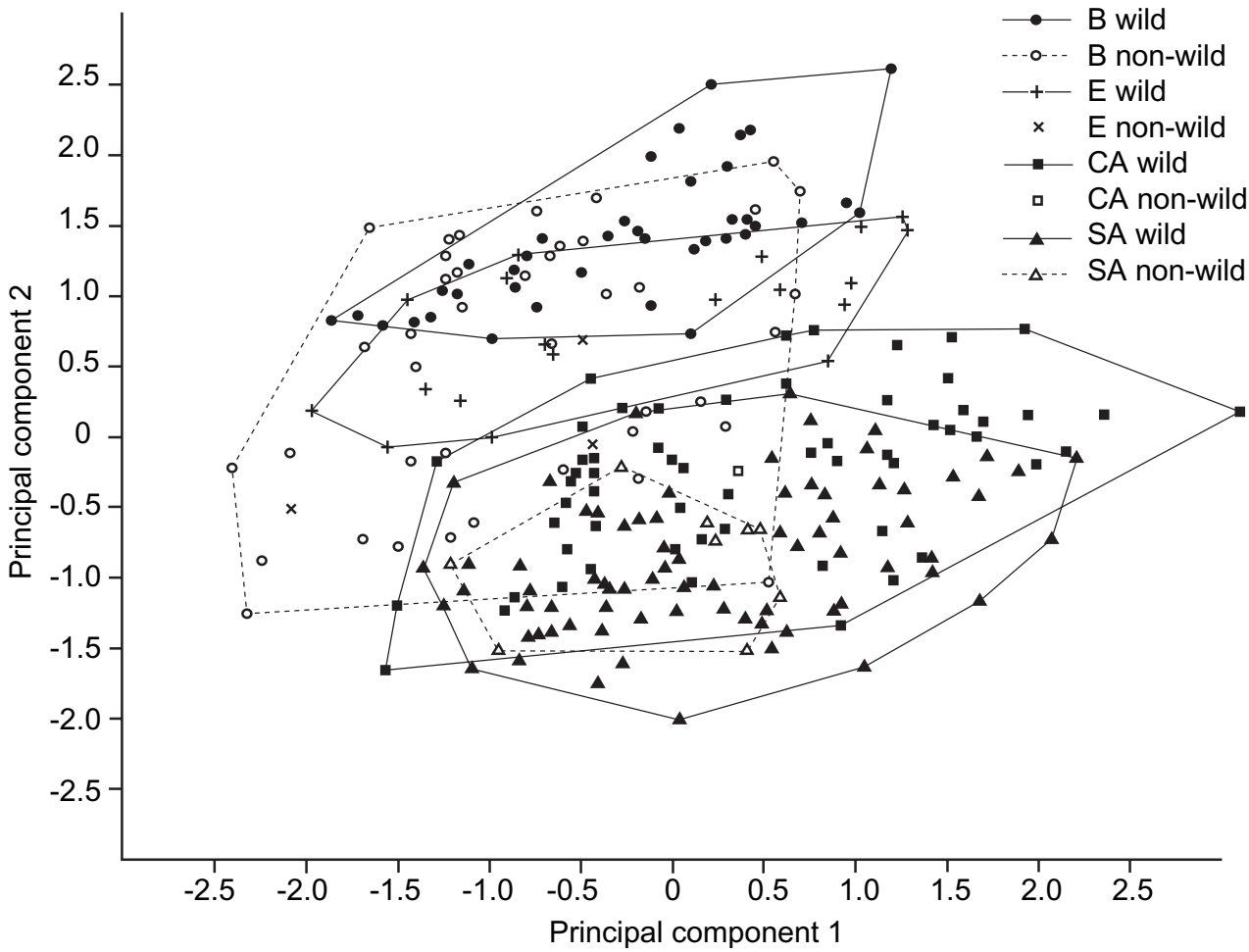


**Figure 4.** Bivariate plot of the first two principal components of each free-ranging cat, which account for 46.4% and 12.8%, respectively, of the variance, based on the 35 skull variables. B, Britain; E, Europe; CA, Central Asia and SA, southern Africa.

**Table 2.** Classification matrix obtained by discriminant function analysis, based on the six extracted principal components, concerning the probabilities of classifying each cat correctly into one of the four geographically separate populations; only 'wildcats' were included in the analysis

| | Predicted classification | | | |
|---|---|---|---|---|
| Observed classification | British | European | Central Asian | Southern African |
| British | 39 | 0 | 0 | 0 |
| European | 4 | 15 | 0 | 0 |
| Central Asian | 0 | 0 | 51 | 6 |
| Southern African | 0 | 0 | 8 | 72 |

dibular $Pm_4$ breadth (Appendices 2 and 3). In general, British and European 'wildcats' were characterized by proportionately shorter cheek tooth rows with smaller teeth and a proportionally broader muzzle compared with Central Asian and southern African 'wildcats'. These groupings were based on the raw variables that showed the most highly significant differences between the four groups and were consistent with the results obtained by PCA, DFA and CVA.

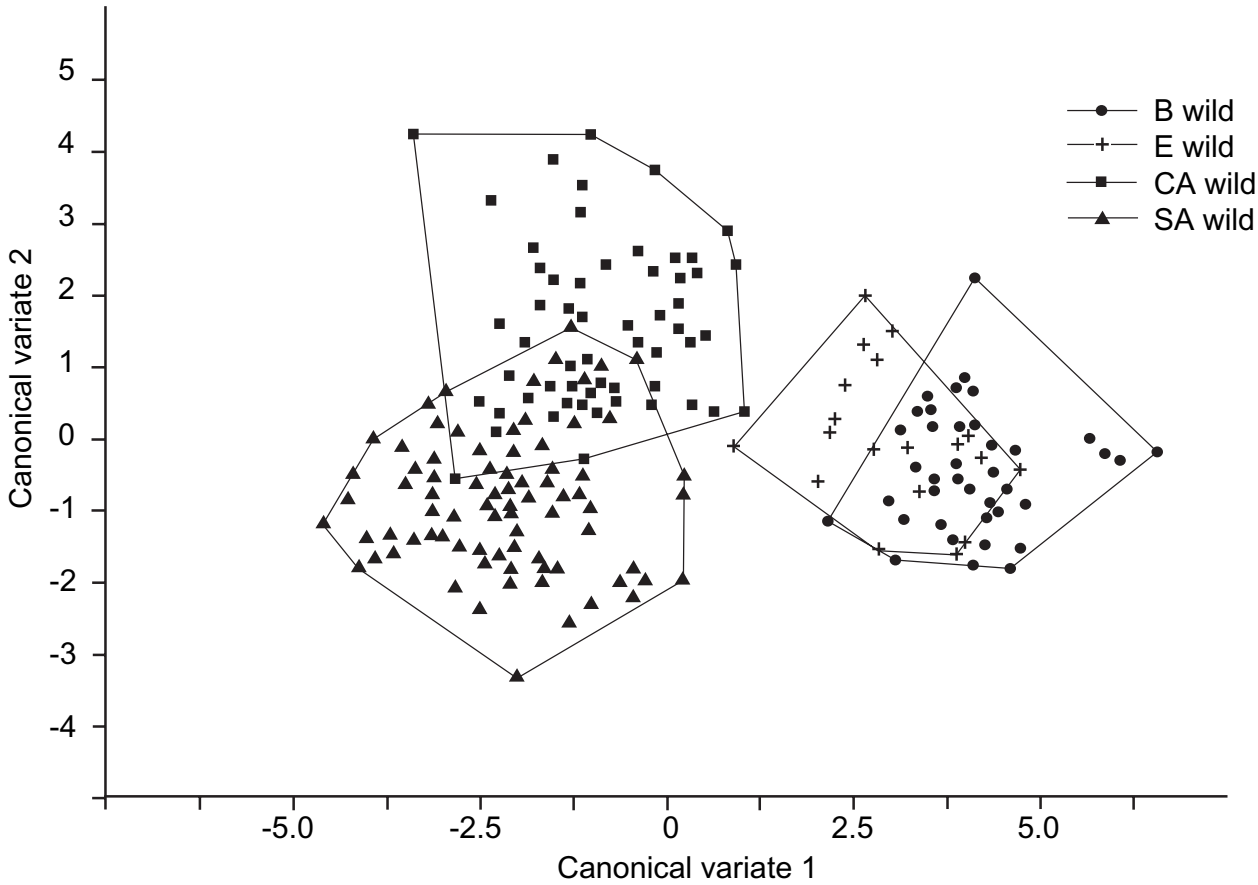


**Figure 5.** Bivariate plot of the first two canonical variates, which explain 82.7% and 9.7%, respectively, of all discriminatory power, based on the six principal components. This plot shows overall morphological similarities amongst the 'wild' cat skulls originating in the four geographically separate areas. B, Britain; E, Europe; CA, Central Asia and SA, southern Africa.

## DISCUSSION

### MORPHOLOGICAL SIMILARITIES AMONGST THE FOUR GROUPS

DFA is designed to develop classification functions to best classify each specimen by following a priori groupings, so that it will usually result in fairly good discrimination between the groups. However, the results of PCA and raw data comparisons, both of which were not influenced by a priori groupings, were consistent with those obtained by the DFA, suggesting that the results are not merely due to a priori groupings.

The results suggest that consistent similarities and differences exist amongst the four geographically separated 'wildcat' populations. All analyses placed the skulls of British and European 'wildcats' closest together, and distinct from those of the Central Asian and southern African 'wildcats', which were also similar to each other. The $D^2$ between the centroid of each group suggest that the extent of morphological similarity between Central Asian and southern African 'wildcats' is comparable to that between British and European 'wildcats' (Fig. 6). The geographical distances over land are *c*. 6500 km between European and Central Asian populations, and *c*. 12 000 km between Central Asian and southern African ones and between European and southern African ones. In addition, Britain has been separated from the European continent for the last *c*. 9500–7500 years based on the estimated worldwide rise in sea-levels as documented by $^{14}$C-dated borings of corals in the Bahamas, Tahiti and New Guinea (Yalden, 1999). We have to underline the fact that there will always be a risk of misinterpretation when phenotypic characteristics are used to reconstruct an intraspecific phylogeny. Nevertheless, the results may suggest that the Central Asian 'wildcat' population has had a stronger connection with the southern African 'wildcat' population than it has with the geographically closer European one. Similarly, in spite of more than 7000 years of

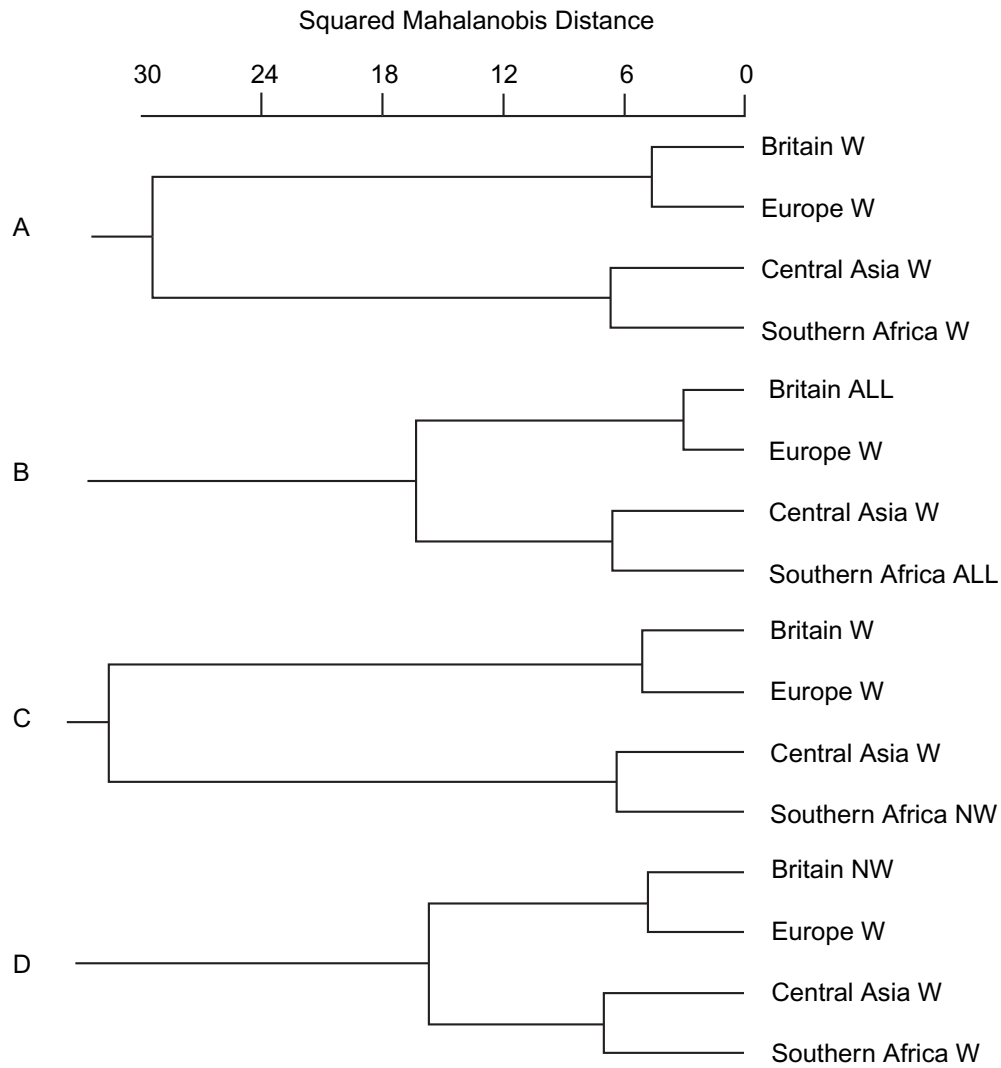


**Figure 6.** UPGMA trees constructed from the matrices of pairwise unbiased squared Mahalanobis distance ($D^2$) between the centroid of each group on the bases of the canonical variates extracted in the analysis. Tree (A) includes only 'wildcats', (B) all free-ranging cats from Britain and southern Africa and 'wildcats' from Europe and Central Asia, (C) southern African 'non-wildcats' and 'wildcats' from the other regions, and (D) British 'non-wildcats' and 'wildcats' from the other regions.

separation, the skull morphology of European 'wildcats' still remains more similar to that of British 'wildcats' than it does to that of Central Asian 'wildcats', despite the potential for gene flow between these two groups via south-west Asia.

We must be cautious in applying results that are based on only four regional populations more widely to the intraspecific phylogeny of the three taxonomic groups of wildcat. Furthermore, we have not addressed the possibility that regionally-specific selection pressures have affected skull morphology. For example, the similarities between Central Asian and southern African wildcats may be due to morphological convergence caused by similar selection pressures, although we cannot test this speculation. Nevertheless, one of the most likely interpretations of our results is that the three groups of wildcat are not equally distinct from each other with respect to their phylogenetic relationships, such that the skulls of European wildcats appear to be very clearly distinct from those of African and Asian wildcats. These results are also in agreement with earlier taxonomic studies, which, although not based on quantitative analyses, have suggested a close taxonomic relationship between African and Asian wildcats (e.g. Pocock, 1951). Regarding diagnostic characters, the European wildcat possesses a proportionally broader anterior part of the skull with a different shape of the nasals compared with the Asian and African wildcats, while the latter two have proportionally and absolutely larger teeth, longer cheek tooth rows and larger auditory bullae.

**Table 3.** Classification matrix obtained by discriminant function analysis, based on the six extracted principal components, concerning the probabilities of classifying each cat correctly into one of the four geographically separate populations; analysis included 'wildcats' from Europe and Central Asia, and both 'wildcats' and 'non-wildcats' from Britain and southern Africa

| | Predicted classification | | | |
|---|---|---|---|---|
| Observed classification | British | European | Central Asian | Southern African |
| British | 75 | 0 | 2 | 3 |
| European | 8 | 9 | 2 | 0 |
| Central Asian | 2 | 0 | 47 | 8 |
| Southern African | 0 | 0 | 10 | 79 |

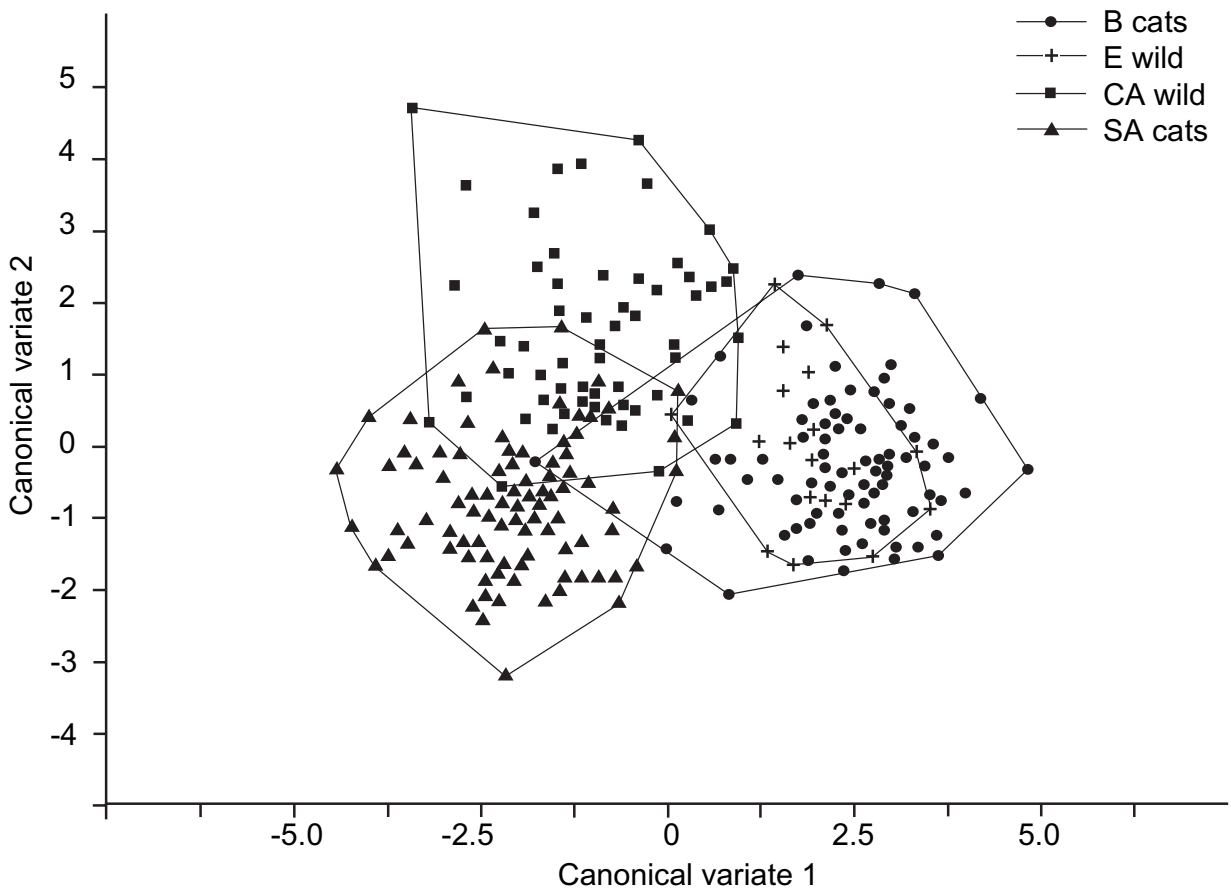


**Figure 7.** Bivariate plot of the first two canonical variates, which explain 78.7% and 9.6%, respectively, of all discriminatory power, based on the six principal components. This plot shows overall morphological similarities amongst the free-ranging cat skulls originating in the four geographically separate areas. B, Britain; E, Europe; CA, Central Asia and SA, southern Africa.

### WILDCATS AND WILD-LIVING CATS

The results demonstrate that the morphological differences between the skulls of all wild-living cats from the four regions are not as clear as are those amongst the different geographical groups of 'wildcats', with or without a priori grouping. Interestingly, this appears to be caused by British 'non-wildcats' but not by those from southern Africa.

Currently, there is no uncontroversial definition of a wildcat, either morphological or genetic (Nowell & Jackson, 1996; Daniels *et al*., 1998; Beaumont *et al*.,

2001; Daniels *et al*., 2001; Reig *et al*., 2001), and we discuss this issue fully elsewhere (Yamaguchi *et al.*, in press). However, strict possession of the classical wildcat pelage is sufficient to place an individual in the non-domestic genetic group in the Scottish population, which is unlikely to have very recent domestic cat ancestry (Beaumont *et al*., 2001; Daniels, 2001; Randi *et al*., 2001). Therefore, the 'non-wildcat' category probably contains a larger proportion of cats that are domestic cats or with recent domestic ancestry compared with the 'wildcat' category. Obviously, one cannot assume that each museum possesses an unbiased collection; wild-living cats with obvious domestic coat phenotypes may not have been added to some collections in the first place. Also, as the sample size of southern African 'non-wildcats' was small compared with that of British 'non-wildcats', we need to be careful in making generalizations based on these results. Also, the criteria for defining the non-wildcat group in southern Africa may have been different to those used for the British non-wildcats, which could affect the composition of a priori groups (e.g. museum labels). In other words, the two non-wildcat groups may not be considered to be necessarily equivalent. However, the results do suggest that introgression with domestic cats may have had greater effects on the skull morphology of British wildcats than on that of southern African wildcats. The high degree of morphological similarity between southern African 'wildcats' and 'non-wildcats' is consistent with the suggested origin of the domestic cat. Therefore, one of the possible effects of the supposed worldwide introgression by the domestic cat (Nowell & Jackson, 1996) may be to shift the skull morphology of wild-living cats in Britain and Europe towards that of the more homogeneous widespread African (and probably Asian) wild-living cats.

## Evolution of the wildcat

The modern wildcat (*F. silvestris*) probably descended from Martelli's wild cat (*F. (s.) lunensis* Martelli, 1906) which is known from Europe and may date back to as early as the late Pliocene *c*. 2 Mya (Kurtén, 1965b, 1968; Kitchener, 1991). Fossil remains suggest that the transition from Martelli's wild cat to the modern wildcat may have occurred during the middle Pleistocene, possibly by oxygen isotope stage (OIS) 11 (*c*. 0.45–0.35 Mya) (Kurtén, 1965b; García, Arsuaga & Torres, 1997; Mannion, 1999). In comparison to this long and contiguous fossil record in Europe, wildcat fossils are recorded only from the late Pleistocene onwards (less than *c*. 130 000 years ago) in Africa (both north and south of the Sahara) and the Middle East (Kurtén, 1965a, b; Savage, 1978; Klein, 1986; Kowalski & Rzebik-Kowalska, 1991; García *et al*., 1997), although we are unaware of any published references concerning fossil records of the wildcat from Asia. If we interpret this lack of a fossil record as the absence of the wildcat in both Africa and the Middle East, it is possible that the wildcat may have expanded its range suddenly, rapidly and recently, during the late Pleistocene. Based on the absolute dates of fossil sites in the Palestine region and South Africa (Kurtén, 1965a; Klein, 1986), this rapid expansion may have occurred even as recently as in the last *c*. 50 000 years. This timing of range expansion coincides well, on a geological time scale, with the supposed divergence at *c*. 20 000 years ago between European wildcats and African wildcats, based on allozyme electrophoresis data from animals originating in Italy, Sicily and Sardinia (Randi & Ragni, 1991).

Based on Kurtén (1965b), Klein (1986) and Savage (1978), Randi & Ragni (1991) suggested that throughout Asia and Africa the European wildcat phenotype was replaced by the African wildcat phenotype. Although we do not necessarily reject their hypothesis, especially concerning wildcat colonization in Asia, we could not find evidence suggesting a large wave of character replacement from those original references. We re-analysed the data (mandibular and dental measurements) published in Kurtén (1965a, b), and carefully checked what he suggested in these texts. This re-evaluation of the work of Kurtén (1965a, b) suggested that late Pleistocene Palestine, less than *c*. 50 000 years ago, was inhabited by wildcats characterized by their proportionately larger teeth, compared with present-day wildcats in central and northern Europe and Britain, and possibly late Pleistocene wildcats of these regions as well. The proportionately larger teeth in present-day Central Asian–southern African wildcats (compared with those of European wildcats) may be explained if these two share a common ancestor possessing that character in the geologically recent past. This suggests that Asian and African wildcats are both derived from a large-toothed wildcat such as the one that inhabited Palestine during the late Pleistocene. For the African wildcat this scenario may be even more realistic. The wildcat that had been in Europe could not spread into Africa without crossing the Middle East and then the narrow Sinai Peninsula (or another narrow land bridge which may have existed between the Arabian Peninsula and Africa) even during the late Pleistocene glacial maxima (Stringer, 2000). As a result, it must have experienced a bottleneck (with probable associated genetic and phenotypic consequences) before it colonized the entirety of Africa from the Middle East. However, there may have been more than one migration route between Europe and the Asian steppe. Interestingly, the current Central Asian wildcat is reported to be unable to cope with low temperatures (Heptner & Sludskii, 1972). Its winter coat does not attain the lev-

els of density, length and luxuriance seen in British, central European and Caucasian populations of the European wildcat in spite of severe winter air temperatures as low as –40 °C in the northern part of its distribution (Heptner & Sludskii, 1972; A. C. Kitchener, pers. observ.). This evidence may suggest that the current Central Asian wildcat has recently originated from a warmer region. If so, on the basis of the current distribution of the species (Fig. 1), it may have come from the Middle East, where intergradation occurs today between African and Asian wildcat phenotypes in the northern Arabian Peninsula and south-west Asia (Harrison & Bates, 1991). This hypothesis, colonization through the Middle East, would explain well the high level of similarity in skull morphology between Central Asian and southern African 'wildcats' observed in this study.

Therefore, the evolution of the modern wildcat probably consisted of at least three different range expansions punctuated by two differentiation events. Firstly, during the late Pleistocene (possibly by *c.* 50 000 years ago) it moved out of Europe which had been the centre for wildcat evolution for nearly two million years, and this may have coincided with the emergence of the steppe wildcat phenotype, which colonized the Middle East, i.e. the exodus from Europe. Secondly, the late Pleistocene Middle Eastern wildcat quickly spread eastward to Asia and southward to Africa possibly within the order of a few 10 000 years, i.e. the steppe wildcat wave. However, as Asian and African wildcats possess consistently distinct coat patterns (e.g. Pocock, 1951), this stage may have involved more than one wave of expansion or a series of expansions and contractions possibly affected by the late Pleistocene glacial–interglacial cycles. Thirdly, the domestic cat was derived from one or more Middle Eastern/north African steppe wildcat populations by *c.* 4000 years ago, followed by its colonization of the entire world with human assistance, i.e. the domestic cat wave.

### Implications for conservation

Our results suggest that the wildcat comprises two major lineages, i.e. the steppe wildcat and forest wildcat lineages, as suggested by Heptner & Sludskii (1972). Arguably the most serious current threat to wildcats is introgressive hybridization with sympatric domestic cats (Nowell & Jackson, 1996; Daniels, 2001). The domestic cat colonization wave has resulted mostly from human activities, so that if indigenous wildcat populations are to continue to exist relatively unaffected by human-caused disturbances, this problem must be tackled. However, we may not easily be able to distinguish between steppe wildcats and free-ranging domestic cats surviving in the drier habitats of north-eastern Africa, the Arabian Peninsula and south-west Asia, from where the first domestic cats may have originated. It is even possible that some of the extant populations of the region may derive in large part from early forms of feral domestic cat. The further that steppe wildcat populations occur from the centre of domestication, the more crucial the potential impact of hybridization might become. However, although we can only speculate, the higher degree of similarity in the skull morphology between 'non-wildcats' from southern Africa and 'wildcats' from Central Asia and southern Africa suggests that hybridization with domestic cats would have less marked effects in steppe wildcat populations than it would in forest wildcat populations. Our results, with the re-evaluation of the work by Kurtén (1965a, b), suggest that the steppe wildcat may not have colonized Europe, at least not on a large scale. Instead, it expanded into Africa and Asia. Therefore, bringing domesticated steppe wildcats into Europe and Britain, and allowing them to range freely, has created an interface between the two strands of wildcat evolution for the first time in their evolutionary history. Given its apparently significant impact on the skull morphology of the forest wildcat, minimizing introgressive hybridization between forest wildcats and domestic cats should be regarded as a high conservation priority.

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## APPENDIX 1

Measurements of crania and mandibles. Numbers correspond measurements shown in Figure 3.

(1) greatest length of skull
(2) condylobasal length
(3) facial length
(4) lateral length of snout
(5) length between $Pm^2$ and $M^1$
(6) length between $Pm^2$ and $Pm^4$
(7) greatest length of $Pm^4$
(8) greatest breadth of $Pm^4$
(9) anteroposterior diameter of the auditory bulla
(10) mastoid breadth
(11) greatest breadth of the occipital condyles
(12) greatest breadth of the foramen magnum
(13) greatest width of the braincase
(14) zygomatic breadth
(15) frontal breadth
(16) least breadth between the orbits
(17) greatest palatal breadth
(18) rostrum breadth: greatest breadth between the canine alveoli
(19) least breadth of the postorbital constriction
(20) breadth between the infraorbital foramina
(21) minimum length of the nasals
(22) maximum length of the nasals
(23) width of cranial suture
(24) maximum distance between pogonion and coronoid process
(25) maximum distance between pogonion and angular process
(26) length between mandibular $Pm_3$ and $M_1$
(27) depth of the mandible behind $M_1$
(28) height of ramus
(29) maximum width of mandibular condyles (not shown in Fig. 2)
(30) Maximum width of mandibular $Pm_4$ (not shown in Fig. 2)
(31) cranial volume (not shown in Fig. 2)

## APPENDIX 2

Differences in skull characteristic scores amongst the four geographical groups of 'wildcats'. Statistically significant differences were detected by Kruskal–Wallis tests (d.f. = 3 for all tests).

| | Average (Range, number examined) | | | | | |
|---|---|---|---|---|---|---|
| Variables | UK | Europe | Central Asia | Southern Africa | *H* | *P* |
| Nasal shape | 2.6 (1–3, 81) | 2.2 (1–3, 111) | 1.3 (1–3, 101) | 1.9 (1–3, 139) | 133.6 | <0.0001 |
| Nasal pit | 2.8 (2–3, 83) | 2.5 (1–3, 130) | 2.3 (1–3, 102) | 2.4 (1–3, 139) | 23.4 | <0.0001 |
| Parietal suture | 2.9 (2–3, 85) | 2.3 (1–3, 133) | 2.5 (1–3, 87) | 2.2 (1–3, 142) | 56.5 | <0.0001 |
| Nasal length | 2.5 (1–3, 84) | 2.2 (1–3, 132) | 1.7 (1–3, 102) | 1.5 (1–3, 145) | 142.6 | <0.0001 |
| Mandible | 3 (75) | 2.8 (1, 3, 119) | 2.8 (1, 3, 89) | 2.2 (1, 3, 132) | 73.1 | <0.0001 |
| Total | 13.9 (11–15, 71) | 12.3 (5.5–15, 95) | 10.7 (7–13, 74) | 10.1 (5–14, 121) | 175.2 | <0.0001 |

## APPENDIX 3

Differences in skull measurements amongst the four geographical groups of 'wildcats'

| Variable | Mean ± Standard Error (Number examined) | | | | *F* | *P* |
|---|---|---|---|---|---|---|
| | UK | Europe | Central Asia | Southern Africa | | |
| Greatest length | | | | | | |
| Male | 99.54 ± 0.63 (30) | 100.20 ± 0.63 (60) | 105.26 ± 0.58 (63) | 103.55 ± 0.55 (73) | 17.96 | <0.0001 |
| Female | 92.96 ± 0.78 (22) | 91.63 ± 0.58 (15) | 95.86 ± 0.68 (39) | 98.20 ± 0.52 (67) | 16.89 | <0.0001 |
| Condylobasal length | | | | | | |
| Male | 92.58 ± 0.67 (32) | 92.12 ± 0.54 (54) | 99.68 ± 0.50 (63) | 95.93 ± 0.60 (58) | 39.22 | <0.0001 |
| Female | 85.93 ± 0.58 (25) | 84.75 ± 0.57 (15) | 91.20 ± 0.64 (39) | 91.33 ± 0.50 (55) | 25.56 | <0.0001 |
| Facial length | | | | | | |
| Male | 37.13 ± 0.37 (32) | 38.24 ± 0.31 (59) | 39.66 ± 0.32 (62) | 37.98 ± 0.29 (56) | 9.95 | <0.0001 |
| Female | 34.01 ± 0.33 (25) | 34.96 ± 0.40 (16) | 35.67 ± 0.43 (39) | 36.17 ± 0.27 (54) | 6.39 | 0.0005 |
| Lateral snout | | | | | | |
| Male | 24.82 ± 0.21 (33) | 25.17 ± 0.17 (64) | 26.70 ± 0.18 (62) | 25.70 ± 0.20 (57) | 17.49 | <0.0001 |
| Female | 22.69 ± 0.18 (25) | 22.67 ± 0.18 (17) | 24.02 ± 0.24 (39) | 24.37 ± 0.20 (55) | 13.69 | <0.0001 |
| $Pm^2$-$M^1$ | | | | | | |
| Male | 22.08 ± 0.12 (32) | 22.51 ± 0.13 (51) | 24.37 ± 0.16 (58) | 24.82 ± 0.16 (57) | 74.01 | <0.0001 |
| Female | 21.08 ± 0.12 (24) | 21.41 ± 0.19 (16) | 23.03 ± 0.15 (33) | 23.83 ± 0.13 (52) | 72.46 | <0.0001 |
| $Pm^2$-$Pm^4$ | | | | | | |
| Male | 21.10 ± 0.13 (33) | 21.50 ± 0.11 (53) | 23.04 ± 0.16 (58) | 23.76 ± 0.16 (57) | 62.99 | <0.0001 |
| Female | 20.06 ± 0.13 (24) | 20.36 ± 0.24 (16) | 21.81 ± 0.14 (33) | 22.72 ± 0.11 (52) | 75.19 | <0.0001 |
| $Pm^4$ length | | | | | | |
| Male | 11.17 ± 0.07 (34) | 11.36 ± 0.08 (62) | 12.03 ± 0.09 (63) | 11.74 ± 0.08 (58) | 18.41 | <0.0001 |
| Female | 10.47 ± 0.08 (24) | 10.72 ± 0.17 (17) | 11.47 ± 0.09 (39) | 11.32 ± 0.08 (55) | 19.55 | <0.0001 |
| $Pm^4$ breadth | | | | | | |
| Male | 6.01 ± 0.05 (34) | 5.67 ± 0.06 (58) | 6.25 ± 0.07 (63) | 5.97 ± 0.07 (58) | 13.60 | <0.0001 |
| Female | 5.55 ± 0.06 (25) | 5.16 ± 0.09 (16) | 5.91 ± 0.06 (39) | 5.54 ± 0.06 (54) | 15.12 | <0.0001 |
| Auditory bulla | | | | | | |
| Male | 20.86 ± 0.17 (34) | 20.83 ± 0.13 (56) | 22.46 ± 0.15 (62) | 23.28 ± 0.17 (58) | 57.50 | <0.0001 |
| Female | 19.93 ± 0.19 (24) | 19.59 ± 0.23 (17) | 20.75 ± 0.19 (39) | 22.43 ± 0.13 (54) | 52.83 | <0.0001 |
| Mastoid breadth | | | | | | |
| Male | 44.77 ± 0.23 (33) | 44.01 ± 0.23 (53) | 46.32 ± 0.20 (63) | 45.47 ± 0.23 (57) | 20.68 | <0.0001 |
| Female | 42.60 ± 0.25 (25) | 41.10 ± 0.38 (16) | 42.88 ± 0.27 (39) | 43.44 ± 0.23 (54) | 8.84 | 0.0002 |
| Occipital condyles | | | | | | |
| Male | 24.79 ± 0.13 (33) | 23.96 ± 0.17 (55) | 23.96 ± 0.11 (63) | 24.35 ± 0.13 (58) | 6.54 | 0.0003 |
| Female | 23.60 ± 0.14 (25) | 22.98 ± 0.25 (16) | 22.72 ± 0.13 (39) | 23.35 ± 0.13 (55) | 6.33 | 0.0005 |

 

APPENDIX 3 *Continued*

| Variable | Mean ± Standard Error (Number examined) | | | | *F* | *P* |
|---|---|---|---|---|---|---|
| | UK | Europe | Central Asia | Southern Africa | | |
| Foramen magnum | | | | | | |
| Male | 15.18 ± 0.10 (33) | 14.97 ± 0.12 (54) | 14.79 ± 0.08 (63) | 15.14 ± 0.09 (58) | 3.23 | 0.023 |
| Female | 14.79 ± 0.12 (25) | 14.60 ± 0.21 (16) | 14.36 ± 0.09 (39) | 14.63 ± 0.09 (55) | 2.42 | 0.069 |
| Brain case | | | | | | |
| Male | 47.12 ± 0.21 (32) | 45.87 ± 0.16 (58) | 46.90 ± 0.14 (63) | 47.36 ± 0.20 (58) | 15.09 | <0.0001 |
| Female | 45.83 ± 0.26 (22) | 44.83 ± 0.35 (16) | 45.40 ± 0.19 (39) | 46.28 ± 0.17 (55) | 7.09 | 0.0002 |
| Zygomatic breadth | | | | | | |
| Male | 70.48 ± 0.57 (34) | 71.26 ± 0.52 (55) | 74.90 ± 0.46 (62) | 72.60 ± 0.51 (54) | 14.13 | <0.0001 |
| Female | 66.42 ± 0.63 (25) | 65.13 ± 0.47 (15) | 67.89 ± 0.62 (39) | 68.37 ± 0.37 (53) | 5.52 | 0.001 |
| Frontal breadth | | | | | | |
| Male | 49.35 ± 0.44 (32) | 52.01 ± 0.38 (55) | 53.89 ± 0.40 (59) | 53.74 ± 0.44 (51) | 20.23 | <0.0001 |
| Female | 48.23 ± 0.49 (24) | 48.89 ± 0.73 (17) | 50.02 ± 0.64 (34) | 51.85 ± 0.37 (51) | 12.33 | <0.0001 |
| Interorbital breadth | | | | | | |
| Male | 19.43 ± 0.25 (33) | 19.32 ± 0.17 (60) | 20.66 ± 0.16 (61) | 19.25 ± 0.20 (57) | 13.96 | <0.0001 |
| Female | 18.42 ± 0.21 (25) | 17.45 ± 0.25 (17) | 18.66 ± 0.18 (39) | 18.18 ± 0.15 (55) | 5.11 | 0.002 |
| Palatal breadth | | | | | | |
| Male | 41.10 ± 0.25 (34) | 40.44 ± 0.25 (59) | 42.65 ± 0.21 (60) | 40.73 ± 0.20 (55) | 20.87 | <0.0001 |
| Female | 38.85 ± 0.27 (25) | 37.80 ± 0.35 (16) | 39.64 ± 0.25 (39) | 38.94 ± 0.21 (54) | 5.90 | 0.0008 |
| Rostrum breadth | | | | | | |
| Male | 24.09 ± 0.18 (34) | 23.78 ± 0.20 (62) | 25.50 ± 0.18 (61) | 24.71 ± 0.17 (57) | 17.55 | <0.0001 |
| Female | 22.31 ± 0.20 (25) | 21.44 ± 0.22 (16) | 23.00 ± 0.24 (39) | 23.13 ± 0.17 (55) | 9.01 | 0.0002 |
| Postorbital constriction | | | | | | |
| Male | 33.52 ± 0.26 (32) | 32.93 ± 0.27 (61) | 33.58 ± 0.21 (63) | 35.18 ± 0.27 (55) | 15.56 | <0.0001 |
| Female | 34.29 ± 0.32 (25) | 32.86 ± 0.57 (17) | 33.81 ± 0.21 (39) | 35.28 ± 0.22 (55) | 11.77 | <0.0001 |
| Between infraorbital foramena | | | | | | |
| Male | 29.22 ± 0.21 (33) | 28.17 ± 0.22 (64) | 28.92 ± 0.20 (61) | 27.96 ± 0.20 (55) | 7.11 | 0.0001 |
| Female | 27.08 ± 0.25 (25) | 25.79 ± 0.57 (17) | 26.55 ± 0.24 (39) | 96.59 ± 0.20 (55) | 2.85 | 0.040 |
| Minimum nasal | | | | | | |
| Male | 22.52 ± 0.32 (30) | 23.24 ± 0.23 (57) | 23.77 ± 0.22 (61) | 21.62 ± 0.23 (54) | 16.43 | <0.0001 |
| Female | 20.83 ± 0.25 (23) | 21.89 ± 0.35 (17) | 22.01 ± 0.34 (39) | 20.81 ± 0.20 (53) | 5.14 | 0.002 |
| Cranial suture | | | | | | |
| Male | 15.86 ± 0.75 (32) | 11.69 ± 0.69 (60) | 10.01 ± 0.67 (63) | 14.85 ± 0.65 (56) | 14.38 | <0.0001 |
| Female | 20.88 ± 0.62 (23) | 17.94 ± 1.40 (15) | 17.67 ± 0.68 (39) | 18.47 ± 0.58 (54) | 2.76 | 0.045 |
| $Pm_3$-$M_1$ (mandible) | | | | | | |
| Male | 21.22 ± 0.14 (32) | 21.78 ± 0.14 (53) | 23.85 ± 0.14 (61) | 23.37 ± 0.15 (54) | 65.60 | <0.0001 |
| Female | 20.33 ± 0.14 (23) | 20.11 ± 0.28 (15) | 22.55 ± 0.15 (38) | 22.43 ± 0.15 (54) | 45.59 | <0.0001 |

| | | | | | | |
|---|---|---|---|---|---|---|
| Ramus (mandible) | | | | | | |
| Male | 30.60 ± 0.40 (32) | 29.36 ± 0.33 (51) | 31.01 ± 0.43 (60) | 30.03 ± 0.30 (55) | 3.89 | 0.010 |
| Female | 27.38 ± 0.40 (23) | 25.57 ± 0.42 (15) | 27.19 ± 0.32 (38) | 27.77 ± 0.24 (54) | 5.63 | 0.001 |
| WMC (mandible) | | | | | | |
| Male | 14.85 ± 0.15 (29) | 15.11 ± 0.19 (53) | 16.40 ± 0.17 (60) | 15.43 ± 0.20 (55) | 13.23 | <0.0001 |
| Female | 13.57 ± 0.18 (20) | 13.40 ± 0.23 (15) | 14.65 ± 0.21 (38) | 13.91 ± 0.14 (55) | 7.44 | 0.0001 |
| $Pm_4$ breadth (mandible) | | | | | | |
| Male | 3.18 ± 0.04 (31) | 3.19 ± 0.03 (52) | 3.86 ± 0.03 (60) | 3.53 ± 0.03 (54) | 98.96 | <0.0001 |
| Female | 3.03 ± 0.03 (23) | 2.97 ± 0.04 (14) | 3.68 ± 0.03 (38) | 3.40 ± 0.03 (55) | 70.21 | <0.0001 |
| Angular process (mandible) | | | | | | |
| Male | 66.29 ± 0.59 (32) | 66.13 ± 0.50 (54) | 70.25 ± 0.48 (61) | 67.22 ± 0.48 (55) | 28.83 | <0.0001 |
| Female | 61.49 ± 0.64 (22) | 59.63 ± 0.72 (15) | 63.03 ± 0.57 (38) | 63.38 ± 0.40 (54) | 21.94 | <0.0001 |
| Coronoid process (mandible) | | | | | | |
| Male | 64.33 ± 0.41 (32) | 66.19 ± 0.47 (50) | 69.83 ± 0.41 (60) | 68.86 ± 0.43 (55) | 15.36 | <0.0001 |
| Female | 60.12 ± 0.57 (23) | 60.56 ± 0.56 (15) | 63.94 ± 0.51 (38) | 65.38 ± 0.43 (53) | 6.80 | 0.0003 |
| Cranial volume (ml) | | | | | | |
| Male | 42.93 ± 0.47 (32) | 44.60 ± 0.89 (33) | 40.69 ± 0.35 (62) | 41.45 ± 0.45 (73) | 9.56 | <0.0001 |
| Female | 41.06 ± 0.69 (21) | 41.85 ± 1.43 (14) | 36.75 ± 0.37 (38) | 38.31 ± 0.43 (65) | 11.89 | <0.0001 |
| *$M_1$ length (mandible) | | | | | | |
| Male | 8.07 ± 0.09 (19) | | 9.51 ± 0.08 (59) | 9.15 ± 0.07 (53) | 47.12 | <0.0001 |
| Female | 7.55 ± 0.11 (14) | | 9.14 ± 0.08 (38) | 8.81 ± 0.08 (55) | 48.73 | <0.0001 |
| **$M_1$ breadth (mandible) | | | | | | |
| Male | 3.73 ± 0.05 (19) | | 4.12 ± 0.03 (59) | 3.98 ± 0.04 (53) | 15.82 | <0.0001 |
| Female | 3.40 ± 0.05 (14) | | 3.94 ± 0.04 (38) | 3.83 ± 0.04 (55) | 24.07 | <0.0001 |
| Derived variables | | | | | | |
| Cranial index | 2.31 ± 0.022 (45) | 2.31 ± 0.046 (60) | 2.61 ± 0.015 (101) | 2.55 ± 0.019 (141) | 33.92 | <0.0001 |
| I.O.F./snout | 1.19 ± 0.005 (61) | 1.12 ± 0.004 (101) | 1.09 ± 0.004 (101) | 1.09 ± 0.004 (112) | 73.33 | <0.0001 |
| Palatal/$Pm^2$-$M^1$ | 1.85 ± 0.008 (58) | 1.79 ± 0.010 (76) | 1.74 ± 0.009 (89) | 1.64 ± 0.007 (109) | 113.44 | <0.0001 |
| POC/IOB | 1.80 ± 0.019 (59) | 1.75 ± 0.016 (92) | 1.70 ± 0.016 (101) | 1.89 ± 0.015 (113) | 27.82 | <0.0001 |
| CP/AP | 0.97 ± 0.003 (55) | 1.01 ± 0.003 (79) | 1.00 ± 0.003 (99) | 1.03 ± 0.002 (111) | 50.25 | <0.0001 |
| Derived variables ($\times 10^{-2}$: ratio to the greatest length of the skull) | | | | | | |
| $Pm^2$-$M^1$ | 22.42 ± 0.12 (51) | 22.69 ± 0.12 (76) | 23.49 ± 0.11 (91) | 24.25 ± 0.07 (111) | 64.68 | <0.0001 |
| $Pm^2$-$Pm^4$ | 21.39 ± 0.12 (51) | 21.65 ± 0.11 (81) | 22.25 ± 0.11 (92) | 23.18 ± 0.08 (111) | 61.49 | <0.0001 |
| Auditory bulla | 21.10 ± 0.14 (52) | 20.99 ± 0.10 (85) | 21.46 ± 0.11 (102) | 22.76 ± 0.10 (115) | 65.34 | <0.0001 |
| $Pm_3$-$M_1$ (mandible) | 21.60 ± 0.13 (52) | 21.82 ± 0.12 (76) | 23.02 ± 0.10 (100) | 22.80 ± 0.09 (110) | 39.50 | <0.0001 |
| $Pm_4$ breadth (mandible) | 3.24 ± 0.02 (52) | 3.21 ± 0.02 (76) | 3.74 ± 0.02 (99) | 3.46 ± 0.02 (111) | 102.40 | <0.0001 |
| *$M_1$ length (mandible) | 8.08 ± 0.08 (33) | | 9.24 ± 0.07 (98) | 8.97 ± 0.05 (110) | 45.81 | <0.0001 |

Statistically significant differences were detected by ANOVA (d.f. = 3 for all tests). Measured variables in mm unless stated.*Measurement was taken by N.Y. only and the coefficient of variation was 0.36% and d.f. = 2. **Measurement was taken by N.Y. only and the coefficient of variation was 0.71% and d.f. = 2. Additional derived variables were calculated by dividing the six measured variables with the highest *F* values by the greatest length of the skull.