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Ecogeographical patterns of morphological variation in pygmy shrews *Sorex minutus* (Soricomorpha: Soricinae) within a phylogeographic and continental-and-island framework

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Ecogeographical patterns in pygmy shrews

ABSTRACT

Ecogeographical patterns of morphological variation were studied in the Eurasian pygmy shrew *Sorex minutus* to understand the species' morphological diversity in a continental and island setting, and within the context of previous detailed phylogeographic studies. In total, 568 mandibles and 377 skulls of *S. minutus* from continental and island populations from Europe and Atlantic islands were examined using a geometric morphometrics approach, and the general relationships of mandible and skull size and shape with geographical and environmental variables was studied. Samples were then pooled into predefined geographical groups to evaluate the morphological differences among them using analyses of variance, to contrast the morphological and genetic relationships based on morphological and genetic distances and ancestral state reconstructions, and to assess the correlations of morphological, genetic and geographic distances with Mantel tests. We found significant relationships of mandible size with geographic and environmental variables, fitting the converse Bergmann's rule; however, for skull size this was less evident. Continental groups of *S. minutus* could not readily be differentiated from each other by shape. Most island groups of *S. minutus* were easily discriminated from the continental groups by being larger, indicative of an island effect. Moreover, morphological and genetic distances differed substantially, and again island groups were distinctive morphologically. Morphological and geographical distances were significantly correlated, but not so the morphological and genetic distances indicating that morphological variation does not reflect genetic subdivision in *S. minutus*. Our analyses showed that environmental variables and insularity had important effects on the morphological differentiation of *S. minutus*.

ADDITIONAL KEYWORDS: Bergmann's rule – environmental correlates – geometric morphometrics – island rule – morphological evolution – resource rule – small mammal.

INTRODUCTION

Ecogeographical 'rules' describe general trends in morphology and related traits along geographical gradients. Recently, there has been a renewed interest in developing a more comprehensive and integrative understanding of the generality of these trends and the mechanisms that cause them (Lomolino *et al*., 2006; McNab, 2010).

Two of the best-known ecogeographical rules are Bergmann's rule and the island rule. In its original form, Bergmann's rule states that warm-blooded vertebrate species (or races or populations within a species) from cooler climates tend to be larger than congeners from warmer climates (Bergmann, 1847; Blackburn, Gaston & Loder, 1999). This vaguely defined rule, later reformulated to refer to populations within species or to species in a monophyletic higher taxon, describes a positive relationship between body size and latitude (Mayr, 1963; Blackburn *et al*., 1999; Meiri, 2011). The island rule predicts an increase of body size for small mammals (gigantism) and a decrease of body size for large mammals (dwarfism) in island populations compared to mainland populations (Van Valen, 1973). Although it has been argued that Bergmann's rule is a valid generalisation (Ashton, Tracy & Queiroz, 2000; Meiri & Dayan, 2003), there are species data showing the opposite trend (the converse Bergmann's rule) and a lack of support (non-significant results) from a large number of species [see Ashton *et al*. (2000) and Meiri & Dayan (2003)]. Likewise, the validity of the island rule has been questioned because most studies have used poor size indices, very large islands or mainland populations only distantly related to the island populations (Lomolino, 2005; Meiri, Dayan & Simberloff, 2006; Meiri, Cooper & Purvis, 2008), and because there is a large number of studies that show evidence against it (Raia & Meiri, 2006; Meiri *et al*., 2008; Meiri, Raia & Phillimore, 2011). Furthermore, McNab (2010) argued that geographic patterns in size variation should not be subdivided into different ecological rules, but rather considered as aspects of the same phenomenon concerning the differential allocation of energy and physiological responses to resource availability.

Considering the controversy associated with these ecogeographical patterns, more comprehensive intra- and interspecific studies are needed to determine their validity and basis (Lawlor, 1982; Lomolino, 2005; Gaston *et al*., 2008; Meiri *et al*., 2008). This includes careful attention to anomalous findings because they may reflect distinctive features that point to causal explanations, or the use of combined approaches important for developing an integrative understanding of biogeographic patterns and generation of hypotheses (Lomolino *et al*., 2006).

In this study, we use the Eurasian pygmy shrew *Sorex minutus* (Linnaeus, 1766; Soricomorpha: Soricinae) as a model species for investigating different ecogeographical patterns along geographic, climatic and environmental gradients in continental and insular settings, and in a phylogeographic context. *S. minutus* has a broad geographic distribution in continental Eurasia, from Lake Baikal in Siberia to Southern, Central and Northern Europe, and in the British Isles (Mitchell-Jones *et al*., 1999). It is found in very different habitats such as alpine and northern tundra, forests, shrub lands, swamps, heaths and grasslands (Hutterer, 1990). The phylogeographic history has been thoroughly studied. Six mitochondrial (mt) DNA lineages with discrete geographic distributions have been described (Mascheretti *et al*., 2003, McDevitt *et al*., 2010, 2011; Vega *et al*., 2010a,b), with support from Y-chromosome markers (McDevitt *et al*., 2010, 2011): four Southern European lineages distributed within the three European Mediterranean peninsulas, namely the 'Iberian', 'Italian', 'South Italian' and 'Balkan'; a 'Northern' clade distributed from Lake Baikal to Central and Northern Europe, and also found in Britain; and a 'Western' clade found in the Pyrenees, Northern Spain (Cantabria Mountain Range), Western France, Ireland and in the periphery of Britain and islands off the western and northern coast of Britain forming a 'Celtic fringe' (Searle *et al*., 2009; McDevitt *et al*., 2011). The Northern and Western lineages colonised Britain sometime after the Last Glacial Maximum over the land bridge with continental Europe (Vega *et al*., 2010a; McDevitt *et al*., 2011), and the Western lineage colonised Ireland within the last 10,000 years via a human-mediated introduction (McDevitt *et al*., 2009, 2011).

We explored the following questions: 1) What is the morphological diversity of *S. minutus* throughout its European range; in particular, are there geographic, climatic and/or environmental patterns in continental Europe and/or relating to island occupancy in the British Isles? 2) To what extent does the morphological diversity in continental Europe and the British Isles resemble the phylogeographic pattern detected with molecular markers? To study these questions, we used a geometric morphometric approach (Rohlf & Marcus, 1993) combined with environmental and phylogeographic information to investigate the biogeography of *S. minutus*, one of the many small mammals that are widespread in Europe but for which there has been remarkably little effort to document or understand their non-molecular geographic variation using modern methodologies.

Geometric morphometrics is a method for the study of form (the shape and size of an object) based on Cartesian landmark coordinates, where the geometry of the configuration of landmarks is preserved throughout the analysis (Zelditch *et al*., 2004; Mitteroecker & Gunz, 2009). Combined with genetic, ecological, environmental and taxonomical information, geometric morphometrics is an exceptionally powerful tool for studying intraspecific variation (Loy, 1996; Zelditch *et al*., 2004; Nogueira, Peracchi & Monteiro, 2009; Vega *et al*., 2010b) and has great potential for our understanding of ecogeographical patterns.

MATERIALS AND METHODS

COLLECTION AND DIGITISATION OF SAMPLES

We acquired *S. minutus* specimens from our own fieldwork ethically collected (Sikes *et al.* 2011), from owl pellets and from museum and private collections (Appendix S1, Table S1). In total, we analysed 568 mandibles and 377 skulls from continental and island sites in Europe (Fig. 1). Photographic images of the external side of left hemi-mandibles and the left half of the ventral side of skulls were taken using a digital camera at a fixed distance. Mandibles were placed flat under the camera lens. Skull samples were placed on a purpose-built polystyrene and Plasticine cradle leaving the ventral side parallel to the lens, judged by eye. A small piece of graph paper was included as a scale in each photograph and the sample was placed in the middle of the image area to avoid parallax.

Morphological analyses on the mandible and skull data sets were carried out using the ‘tps-Series’ software (by F.J. Rohlf, available at http://life.bio.sunysb.edu/morph/). Eighteen landmarks were placed on the external side of left hemi-mandibles and 19 landmarks were placed on the left half of the ventral side of skulls using tpsDig2 (Appendix S1, Fig. S1). The selected landmarks provided a comprehensive sampling of the morphology of the biological structures under study (Zelditch *et al*., 2004).

MORPHOMETRIC ANALYSIS OF MANDIBLES AND SKULLS

The size of each mandible and skull was estimated as the Centroid Size (CS) obtained with tpsRelw and was transformed with natural logarithms. CS is a convenient estimator for size used commonly in geometric morphometric studies (Bookstein, 1996; Slice *et al*., 1996; Frost *et al*., 2003); it is uncorrelated with shape in the absence of allometry (Zelditch *et al*., 2004) and it is often highly correlated with body mass (Frost *et al*., 2003). The landmark configurations were aligned, translated, rotated and scaled to unit CS using Generalised Procrustes Analysis (GPA), and the Procrustes coordinates and average landmark configuration were obtained (Rohlf & Slice, 1990). The Procrustes distances to the average configuration and pairwise Procrustes distances among samples (Zelditch *et al*., 2004) were computed, approximated to a Euclidean space using an orthogonal projection and used as a measurement of morphometric distances.

The significance of allometry (change in shape associated with size differences) was tested for the continental and island groups separately for mandibles and skulls with multivariate regressions using MorphoJ (Klingenberg, 2011). Allometry was significant in continental and island groups for mandibles and skulls; therefore, the regression slopes between groups were then compared with MANCOVA in tpsRegr and were not statistically significant (data not shown)

(Viscosi & Cardini, 2011). To control for allometric effects on mandible and skull shape variables, we performed multivariate regressions using MorphoJ and kept the residuals as allometry-free shape variables for further analysis. We performed a Principal Components Analysis (PCA) in JMP version 10 (SAS Institute, Cary, NC, USA) on the shape variables and kept 16 and 17 PCs for mandibles and skulls, respectively, which explained ≥ 1% of total shape variation. We also carried out a variety of other preliminary analyses including landmark placement repeatability, sexual dimorphism and a test for phylogenetic signal (see Supporting Information for details).

GENERAL ECOGEOGRAPHICAL PATTERNS

For each specimen we determined geographical data including latitudinal and longitudinal coordinates from fieldwork and museum records, and digital elevation data from the Consortium for Spatial Information at a 90 arc-minute resolution (available at http://srtm.csi.cgiar.org). Data for climatic variables (taken from the 1950-2000 period) were obtained from WorldClim (available at http://www.worldclim.org/) at a 2.5 arc-minute resolution using DIVA-GIS version 7.4.0.1 (available at http://www.diva-gis.org/), including annual trends variables and extreme or limiting environmental variables: annual mean temperature (BIO1), maximum temperature of the warmest period (BIO5), minimum temperature of the coldest period (BIO6), annual precipitation (BIO12), precipitation of the wettest period (BIO13), precipitation of the driest period (BIO14), precipitation of the warmest quarter (BIO18) and precipitation of the coldest quarter (BIO19). Seasonal variables (annual range in temperature and precipitation) were excluded because they are composite climatic variables [e.g. BIO7 = temperature annual range (BIO5-BIO6)] and would only complicate the interpretation of the results. We also obtained terrestrial net primary production (NPP) values from MODIS GPP/NPP (MOD17) at 1 km resolution from 2000 through 2009 (Zhao & Running, 2010). NPP is an environmental variable that quantifies the amount of atmospheric carbon fixed by plants and accumulated as biomass. In total, we obtained data for

12 geographic, climatic and environmental variables, and for simplicity they are called ‘environmental variables’ throughout.

Because combinations of the 12 environmental variables showed correlations with each other, we performed a PCA using JMP on these variables and kept the first three environmental PCs for further analysis. PC1, PC2 and PC3 had eigenvalues ≥ 1.0 and together explained more than 80% of the variation for the environmental data sets (Appendix S1, Tables S2 and S3). The eigenvector matrices showed that: 1) PC1 was loaded with positive eigenvectors for all precipitation variables; low values indicate low precipitation mostly found in the central regions of the Iberian peninsula, eastern parts of the Balkan peninsula but also in central-northern regions in Europe, while high values indicate high precipitation mostly found in the western coast of Ireland and in some areas of the Alps. 2) PC2 was loaded with a combination of negative eigenvectors for latitude and minimum temperature of the coldest period, and positive eigenvectors for longitude and altitude; low values indicate high latitude, low altitude and moderate temperatures during winter mostly found in central and western regions of continental Europe and in the Atlantic islands, while high values indicate high altitude, low latitude, high longitude and relatively low temperatures during winter mostly found in central and eastern regions like in the Balkan peninsula and in mountain areas of the Italian peninsula. 3) PC3 was loaded with a combination of negative eigenvectors for latitude and positive eigenvectors for annual mean temperature, maximum temperature of the warmest period and NPP; low values indicate colder climate and moderate productivity from high latitudes, while high values indicate warmer climate and higher productivity mostly found in central latitudes.

Several statistical analyses were done on size and shape variables for the mandible and skull data sets. Using a Standard Least Squares approach in JMP, we performed multiple regressions of size on latitude, altitude and annual mean temperature (typical variables used to study Bergmann’s rule) for the mandible and skull data sets. Because Bergmann’s rule and the island rule may be better explored using biologically relevant environmental variables, we performed multiple regressions of size and shape on the three environmental PC for the mandible and skull data sets. This approach was used to see the effects of each variable on size but controlling for the effects of the other variables. The significance of the models and of each variable was obtained with ANOVAs comparing the fitted model to a simple mean model. Moreover, size differences between continental and island samples for the mandible and skull data sets were estimated with ANCOVA in JMP using the three environmental PCs as covariates after testing for homogeneity of slopes.

To evaluate the environmental effects on mandible and skull shape, and to estimate how well the variation in shape can be predicted by environmental variables, we did multivariate multiple regression analysis of shape variables on the three environmental PCs using JMP. Two-Block Partial Least Squares analysis was conducted in JMP to describe the covariation between the geographical (latitude, longitude, altitude), climatic (WorldClim) and NPP variables with the variation in shape (Appendix S1, Tables S4 and S5). In Two-Block Partial Least Squares analysis linear combinations of the predictors are extracted with the objective of explaining as much of the variation in each response variable as possible, but accounting for variation in the predictors.

The mandible and skull photographs, landmark coordinates (in TPS format) and the environmental variables for all samples are available from DRYAD (doi: upon acceptance).

GENETIC ANALYSES

A total of 519 cyt *b* sequences of *S. minutus* were obtained from GenBank (AB175132, AJ535393-AJ535457, GQ494305-GQ494305, GQ272492-GQ272518, JF510321-JF510376). A sequence of *S. volnuchini* (AJ535458) from Anatolia was used as the outgroup (Fumagalli *et al*., 1999). DNA sequences were edited in BioEdit version 7.0.9.0 (Hall, 1999) and aligned by eye. The phylogenetic relationships within *S. minutus* were inferred by Bayesian analysis as in Vega *et al.* (2010a). The lineages found were the same as in previous phylogeographic studies (*e.g.*

Mascheretti *et al.*, 2003; McDevitt *et al.*, 2010, 2011; Vega *et al.*, 2010a, b) and were used as phylogroups for further analysis.

With DnaSP version 5.10 (Librado & Rozas, 2009), we calculated the corrected net number of nucleotide substitutions between pairs of phylogroups (Da), which represent the proportional sequence divergence among them (Nei, 1987). The pairwise divergence values (Da) among previously identified phylogroups were used for statistical comparison with the morphometric data. We used the matrix of pairwise Da values to construct a Neighbour-Joining (NJ) tree with MEGA version 4 (Tamura *et al.*, 2007) to depict the evolutionary distances and relationships between the phylogroups.

ECOGEOGRAPHICAL PATTERNS IN GEOGRAPHICAL GROUPS

To analyse size and shape differences in *S. minutus* among regions in a phylogeographic context, we pooled the mandible and skull samples into 12 and 11 mutually exclusive geographical groups, respectively, according to their cyt *b* phylogroup membership (if DNA data were available from samples used in other studies) or to their known geographical origin (Fig. 1). The groups were designated as: 'Iberian', 'Italian', 'South Italian', 'Balkan', 'Northern' and 'Western'. Island groups were identified separately as 'Ireland', 'Orkney Mainland', 'Orkney Westray', 'Orkney South Ronaldsay', 'Belle Île' (not available for skulls) and 'Britain'.

We performed multiple regressions of size on the three environmental PCs using a Standard Least Squares approach in JMP to determine the differences among the geographical groups while controlling for the effects of each predictor variable. Mandible and skull size differences among the groups were evaluated by ANCOVA followed by Tukey–Kramer post-hoc tests as it allows for unequal sample size (Sokal & Rohlf, 1995).

Mandible and skull shape differences among the groups were evaluated with MANOVAs on the allometry-free shape variables (16 for mandibles and 17 for skulls), followed by Hotelling T^2 tests for multivariate comparisons performed in PAST version 2.17 (Hammer, Harper & Ryan, 2001). Shape changes were visualised as thin-plate spline transformation grids (Zelditch *et al*., 2004) computed with tpsSplin. Canonical Variate Analyses (CVA) using the shape variables as predictors were performed in JMP to differentiate among the groups for the mandible and skull data sets. The first two CVs were used to graph the samples separated by group membership (Appendix S1, Table S6). Discriminant Function Analyses (DFA) were performed in JMP to estimate group membership of the mandible and skull data sets using linear combinations of the predictor variables that best discriminate between the groups. The leave-one-out (jackknife) with cross-validation approach was used to validate the DFA (Cardini *et al*., 2009). Results were averaged among three runs using a random subset of 70% of the samples from each group for training the model and 30% for testing. The number of discriminant functions used for analysis equalled the number of groups (K = 12 or K = 11) minus 1.

The Procrustes distances among the average configurations of the groups (including the outgroup), for the mandible and skull data sets, were computed with tpsSmall and entered into PAST to produce distance matrices and distance trees using the NJ method to evaluate the morphological relationships. The geographic midpoints for the groups were calculated with the Geographic Midpoint Calculator (available at http://www.geomidpoint.com/), and were used to obtain the pairwise geographic distances among them with the Geographic Distance Matrix Calculator version 1.2.3 (by P.J. Ersts, available at http://biodiversityinformatics.amnh.org/open_source/gdmg). Mantel tests were performed in PAST on pairwise Procrustes and geographic distances among the groups, and on pairwise Procrustes distances among the groups and pairwise genetic divergence (Da) values of the cyt *b* phylogroups. In addition, we did a partial Mantel test of Procrustes distances and geographic distances, but controlling for genetic distance. The significance of the tests was obtained by a permutation procedure with 10,000 bootstraps. Mandible and skull CS and Procrustes distances were mapped onto the NJ tree of cyt *b* phylogroups using squared-change parsimony in

Mesquite 2.75 (Maddison & Maddison 2011) to show size and shape evolution using eight categorical bins.

RESULTS

GENERAL ECOGEOGRAPHICAL PATTERNS

The results from multiple regressions of size on latitude, altitude and annual mean temperature), or on environmental variables (PC1, PC2 and PC3) are summarised in Table 1 (see also Appendix S1, Table S3). Typical Bergmann's rule variables statistically predicted mandible size, but the data contains a high amount of unexplained variability ($F_{4,\,563}$ = 5.274, P < 0.001, R^2 = 0.036). Latitude was negatively related with size, and annual mean temperature did not contribute significantly to the model. Environmental variables statistically predicted mandible size also with a high amount of unexplained variability ($F_{4,\,563}$ = 4.179, P = 0.02, R^2 = 0.029). All variables were positively related with size and contributed significantly to the model. On average, continental samples showed significantly larger mandible size than island samples (F = 6.204, P = 0.013) mostly driven by the larger mandible size of southern samples from continental Europe. Typical Bergmann's rule variables statistically predicted skull size, and the model explained more variability than in the mandible data set ($F_{4,\,372}$ = 31.155, P < 0.001, R^2 = 0.251). Annual mean temperature did not contribute significantly to the model and latitude only marginally so. Environmental variables statistically predicted skull size with a high amount of unexplained variability ($F_{4,\,372}$ = 4.1, P = 0.03, R^2 = 0.042), and only PC1 contributed significantly to the model. On average, island samples showed marginally significant larger skull size than continental samples (F = 4.661, P = 0.031).

Environmental variables had small but significant effects on allometry-free shape of mandibles and skulls, and together accounted for 5.1% and 11.9% of mandible and skull shape variation, respectively (Table 2). PC3 explained the highest percentage of shape variation in both data sets. With the Two-Block Partial Least Squares analysis, 10 and 9 factors were extracted which explained 13.6% and 18.4% of mandible and skull shape variation, respectively (Appendix S1, Tables S4 and S5).

GENETIC ANALYSES

There were 303 cyt *b* haplotypes for *S. minutus* that clustered into six main phylogroups (Mascheretti *et al*., 2003; McDevitt *et al*., 2010, 2011; Vega *et al*., 2010a, b). We distinguished the following continental phylogroups for comparison with the morphological data (Fig. 3): 'Northern' (n = 101), which included samples from Central and Northern Europe to Lake Baikal in Siberia. 'Italian' (n = 26), mostly restricted to the northern and central parts of the Italian peninsula. 'Western' (n = 15), which included samples from the Cantabrian Mountains, the Pyrenees and Western France. 'South Italian' (n = 4), geographically restricted to La Sila Mountain, Calabria in Southern Italy. 'Iberian' (n = 3), geographically restricted to the Iberian peninsula. 'Balkan' (n = 4), which included samples from Macedonia and Turkish Thrace in the Balkan peninsula. We also distinguished the following island groups (Fig. 3): 'Ireland' (n = 94), 'Orkney Mainland' (n = 44), 'Orkney Westray' (n = 33), 'Orkney South Ronaldsay' (n = 40) and 'Belle Île' (n = 5) which clustered within the Western clade, and 'Britain' (n = 91) which clustered within the Northern clade. Other samples (n = 59) clustered in the Western clade in the molecular studies but were not used here because they belong to islands in the periphery of Britain from where there were no morphological samples for comparison. Pairwise divergence (Da) values among the phylogroups are shown in Appendix S2, Tables S7 and S8. The South Italian, Iberian and Balkan groups and the outgroup showed the highest pairwise Da values, whilst pairwise Da values among the Western, Irish and Orkney islands groups were the lowest.

ECOGEOGRAPHICAL PATTERNS IN GEOGRAPHICAL GROUPS

While controlling for environmental factors, we found significant size differences among groups for the mandible and skull data sets (mandibles: $F_{11, 556}$ = 24.186, P < 0.001; skulls: $F_{10, 366}$ = 8.658, P < 0.001; Appendix S3, Table S9).

For mandible and skull size, there were latitudinal trends converse to Bergmann's rule among the continental groups, and island effects for the island groups (Fig. 2A, B). The South Italian, Iberian and Balkan groups, belonging to the southernmost latitudes, had the largest mandibles among the continental groups. The Northern group had the smallest mandible of all continental groups, and it was significantly different from all other continental groups, but not significantly different from some island groups. The Orkney Mainland group, although at a high latitude, had the largest mandible of all island groups, but only significantly different from Orkney South Ronaldsay. All other island groups had comparable mandible sizes to those found in continental groups, but larger than expected by latitude. The skull data set showed less variation in size among the groups than the mandible data set, but also had a decreasing size tendency with increasing latitude. The Iberian group had the largest skulls of the continental samples. The Northern group had the smallest skulls on average, as in the mandible data set, but this group was only significantly different in size from the Iberian and Orkney Westray groups. Notably, the skulls from the Orkney islands were as large as the ones from the southern groups and larger than the ones from the northern group, indicative of an island effect even controlling for the latitudinal effect. The results relating to South Italy and Britain should be taken with caution because of low sample size, but they are still indicative of the size trends in these two areas.

The MANOVAs on allometry-free shape variables of mandibles and skulls showed significant differences among the groups (mandibles: Wilks' λ = 0.1954, $F_{176, 4959}$ = 5.521, P < 0.001; skulls: Wilks' λ = 0.0415, $F_{170, 3056}$ = 5.319, P < 0.001; Appendix S3, Tables S10 and S11). Based on thin-plate splines (Fig. 3A, B), shape variation was small and mostly evident between the southern groups and the Orkney islands. In southern latitudes and in larger mandibles there was a relative forward movement of the landmarks on the lower part of the mandible (landmarks 1 and 16 – 18) in relation to the landmarks between teeth alveoli (landmarks 3 – 8), and a relative forward shift of the coronoid process (Fig. 3A). The three groups from the Orkney islands had notable backward shifts of the coronoid process in comparison to other groups, with Westray also showing pronounced variation in the frontal part of the mandible, whereas in the Iberian and Balkan groups the coronoid process moved slightly forward (Fig. 3A). In southern latitudes and in larger skulls, there was an outward movement of landmarks 2 and 7 in relation to other landmarks between teeth alveoli (landmarks 3 – 6, 8 and 9), and opposite movements of landmarks 16 and 17 (Fig. 3B). This generally resulted in a wider separation of the upper premolars, less pointed snouts, and smaller foramen magnum compared to skulls from northern latitudes (Fig. 3B).

The first two CVs explained 69.6% and 62.2% of total shape variation among groups in the mandible and skull data sets, respectively (Appendix S1, Table S6). For purposes of visualisation, scatter plots of the first two CVs are presented with group memberships for mandibles (Fig. 4A) and skulls (Fig. 4B). In both data sets, the shape distribution of the continental groups mostly overlapped, while Ireland and the Orkney islands could be discriminated. Westray was the island group most easily discriminated, in accordance with the large Procrustes distances and shape variation found in the mandible and skull data sets. Belle Île (mandible data set only) and Britain (mandibles and skull data sets) could not be differentiated from the continental samples. With the DFA, we classified correctly on average 44.9% and 54.6% of the individuals to their predefined group of mandibles and skulls, respectively; however, this was mostly due to low classification scores for the continental groups. The classification scores in the mandible and skull data sets were high the Orkney islands groups in agreement with its notable shape differences.

There were different topologies among the phylogenetic tree and the Procrustes distances trees of mandibles and skulls (Fig. 5). For mandible and skull shape, the South Italian group is the first to split from the rest, and Orkney Westray shows the highest shape distance of all groups (Fig. 5A, B). Intraspecific variation in size and shape, mapped using squared change parsimony and visualized on the NJ tree of phylogroups (based on Da), showed no apparent relationship of size and shape with phylogenetic history of *S. minutus* (Fig. 5C-F). The Mantel tests revealed that there were significant positive correlations between Procrustes and geographic distances of mandible (R = 0.2653, P = 0.0471) and skull groups (R = 0.6019, P = 0.0004). However, the correlations between Procrustes and genetic distances were not significant for mandible (R = – 0.0827, P = 0.5978) and skull groups (R = – 0.2189, P = 0.8869). While controlling for genetic distances, partial Mantel tests also revealed significant correlations among Procrustes and geographic distances for mandible (R = 0.2935, P = 0.0360) and skull groups (R = 0.6818, P < 0.0001). Pairwise geographic and Procrustes distances among mandible and skull groups are shown in Appendix S2, Tables S7 and S8.

DISCUSSION

CONTINENTAL DIFFERENTIATION IN *SOREX MINUTUS*

Bergmann's rule has traditionally been studied in terms of latitude, altitude and temperature (Meiri & Dayan, 2003; Meiri, 2011) and we explored this in *S. minutus*. However, because Bergmann's rule may relate to a combination or an interaction of environmental factors, we also explored the morphological variation in *S. minutus* in relation to a whole range of geographic, climatic and NPP variables within a phylogeographic and continental-and-island framework.

For *S. minutus*, the significant negative relationship of mandible size with latitude, and the larger mandible and skull size in southern than in northern continental groups indicate a pattern converse to Bergmann's rule. Using PC of geographical and environmental variables shows a more complex basis to the size trends in *S. minutus* than purely an impact of latitude, altitude or temperature. PC1, PC2 and PC3, loaded with various combinations of latitude, longitude, temperature and precipitation variables and NPP consistently showed a positive relationship with mandible size, but only PC1 showed a positive relationship with skull size. We concur with McNab (2010) that an emphasis in relation to Bergmann's rule may be unhelpful, and that the size trends relate to the availability of resources in a broad sense, which in turn relates to various underlying environmental factors.

The converse Bergmann's rule has frequently been reported in shrews and may be a common trend within Soricidae [for exceptions see White & Searle (2007) who found Bergmann's rule in *S. araneus* from British islands, and Ochocińska & Taylor (2003) who showed non-significant relationships of size with latitude for *S. isodon* and *S. tundrensis*]. Accordingly, the condylobasal skull lengths of *S. araneus*, *S. caecutiens* and *S. minutus* from the Palearctic region relate negatively to latitude (Ochocińska & Taylor, 2003). Three mainland populations of *S. trowbridgii* from Western USA have decreasing cranial and mandibular dimensions with increasing latitude (Carraway & Verts, 2005) and variation in body size of *S. cinereus* in Alaska contradicts Bergmann's rule (Yom-Tov & Yom-Tov, 2005). Morphological measurements of *Neomys anomalus* from Eastern Europe and the Balkans also relate negatively to latitude but show evidence of character displacement when in sympatry with *N. fodiens* (Kryštufek & Quadracci, 2008). The northern short-tailed shrew (*Blarina brevicauda*) has a negative albeit non-significant relationship of size with latitude (Ashton *et al*., 2000). Consistent with converse Bergmann's rule, size in *N. anomalus* and *N. fodiens* from Poland was the smallest in the north and largest in the south when in sympatry, but when in allopatry both species were larger at northern latitudes, showing the opposite pattern (Rychlik, Ramalhinho & Polly, 2006).

Regarding shape patterns, environmental variables (reflected in the first three PCs) explained small percentages of total shape variation (5.1% and 11.9% for mandibles and skulls, respectively). It is not surprising that so much shape variation remained unexplained because other exogenous and endogenous factors may be playing important roles. Based on the CVA, evolution on islands maybe a contributing factor. In a similar ecogeographical study on the primate *Cercopithecus aethiops* from sub-Saharan Africa, the response of skulls to climatic variables was stronger for size than for shape despite the evident intraspecific geographical differences, and approximately 80% of shape variance remained unexplained (Cardini, Jansson & Elton, 2007). Morphology can also be influenced in a complex way by climatic and phylogenetic factors, and in *Microtus savii* both sets of factors contribute to shape variation of the first lower molars, while tooth size is not affected by climatic conditions (Piras *et al*., 2010). However, we did not detect a significant phylogenetic signal and the mapping of size and shape on the phylogeny showed no apparent relationships. Although Mantel tests showed no relationships of shape and genetic distances, the results have to be taken with caution because Mantel test has lower power in comparison with other tests (Legendre & Fortin, 2010); however, Mantel test has been traditionally used in morphological, ecological and genetic studies, it is useful when data can be expressed as distances, and the Mantel test results are coherent with other results presented here.

Why is the pygmy shrew generally smaller in northern latitudes than in southern latitudes? There is some dispute about the mechanisms involved for Bergmann's rule or its converse (Blackburn *et al*., 1999; Meiri, 2011). However, the lower food availability in northern, colder or less productive habitats is likely to be a selective factor acting on small mammals, combined with lower absolute food requirements for smaller vs. larger species of small mammals in less productive habitats (Ochocińska & Taylor, 2003). This may explain the small size of shrews of the northern group of *S. minutus* which evolved in and expanded from northern glacial refugial areas (Vega *et al*., 2010a). Populations of *S. araneus* in Finland are up to 13% smaller inland than in the coast, where the main differences are lower winter temperatures and less snow cover at inland sites, factors associated with lower habitat productivity, which could selectively favour smaller shrews (Frafjord, 2008). In *S. cinereus* it has been suggested that the increase in size during the second half of the twentieth century is related to increasing winter temperatures and higher food availability in winter due to improved weather conditions for its prey (Yom-Tov & Yom-Tov, 2005).

Dehnel’s phenomenon (*i.e.* reduction of body size and mass of organs of soricine shrews from northern temperate regions during winter) has been interpreted as an adaptation to reduced prey abundance permitting a reduction in absolute food requirements in a group of species that do not hibernate. However, recent findings indicate that prey numbers and biomass available for shrews (which do not hibernate) do not decrease during winter, but soil invertebrates do change their vertical distribution, apparently requiring shrews to have a modified more energetically costly foraging behaviour for consumption of energetically less favourable prey (Churchfield, Rychlik & Taylor, 2012). In our study, a Dehnel effect is unlikely to play a role because < 5% of our samples were collected during winter (those few individuals that were collected in winter were from Switzerland where we have a good sample size, and from Central Spain where results indicate large mandible and skull size). It should be noted that phenotypic plasticity (the ability of a single genotype to produce more than one alternative form of morphology, physiological state or behaviour in response to changes in environmental conditions) cannot be ruled out as a possible explanation until proper experimental studies are undertaken with shrews (Husby, Hille & Visser, 2011).

Size and shape variation of the mandible can affect the biomechanics of mastication by modifying the sites of attachment of mandible muscles (Monteiro, Duarte & dos Reis, 2003). Larger and morphologically distinctive mandibles could reflect stronger bite force or higher mechanical potential for mastication, which could be an adaptation or a plastic response to more arid conditions, to exploit a wider size-range of prey and prey with harder exoskeletons, and/or character release in the absence of competitors (Strait, 1993; Carraway & Verts, 2005; Monteiro *et al*., 2003). The association of diet and skull shape can be strong because muscles used for mastication are tightly linked to bone structure; for example, diet may explain up to

25% of skull shape variance in marmots (Caumul & Polly, 2005). In *S. minutus*, a stronger bite force was estimated for South Italian than for north European populations in relation to the positioning of the coronoid process and horizontal ramus length (Vega *et al.*, 2010b), and the morphological patterns described in that study were similar to those found here.

ISLAND DIFFERENTIATION IN *SOREX MINUTUS*

Under the island rule, it is expected that small mammals on islands will have a larger body mass than mainland conspecifics (Van Valen, 1973). Our results indicate that there is a strong island effect operating on the size of mandibles and skulls of *S. minutus* from Ireland and the Orkney islands. Moreover, these island groups were distinctive from continental groups in terms of shape variation, and samples were assigned correctly to their island of origin. There was a lack of correspondence between Procrustes distances and cyt *b* tree terminal branches. Overall, it appears that environmental factors and insularity have stronger effects on morphology, perhaps through local adaptation, genetic bottlenecks and/or plastic responses, than provided by phylogenetic relationships. Therefore, *S. minutus* from Ireland and the Orkney islands shows morphological differentiation from continental groups through island effects, while cyt *b* reveals the close phylogenetic relationship of these island groups with continental Western Europe (McDevitt *et al.*, 2011).

Other shrew species on islands share similar trends. For example, *S. trowbridgii* from Destruction Island (Washington State, USA) has greater average skull-breadth and mandibular dimensions than the mainland counterpart (Carraway & Verts, 2005). *S. araneus* from several Scottish islands are significantly larger than populations in mainland Britain and show larger body size on islands in relation to distance to the mainland (White & Searle, 2007). *Crocidura russula* from several French islands also show divergence in mandible shape in relation to distance from the mainland and island size (Cornette *et al.*, 2012). *C. suaveolens* from Corsica is larger and has a smaller litter size than mainland populations in Southern France (Fons *et al.*, 1997), indicating an island effect (Adler & Levins, 1994). Studies of other small mammals have also shown morphological divergence of recently colonised island populations (e.g. Michaux *et al*., 2007; Renaud & Michaux, 2007; Cucchi *et al*., 2014). Similar to our study, the mandible and skull shape of *Marmota vancouverensis* from Vancouver Island is highly divergent from the mainland counterpart *M. caligata*, despite small mtDNA sequence divergence (Cardini, 2003; Cardini & O'Higgins, 2004). Previous morphological studies on *S. minutus* from islands around Britain relate to presence/absence of *S. araneus* (Malmquist, 1985) but are difficult to interpret because of anomalies in the reporting of sympatric and allopatric status of *S. minutus* on these islands.

It may be possible that morphological traits in mammals evolve quickly on islands in a matter of a few decades after colonisation (Pergams & Ashley, 2001; Millien, 2006; Cucchi *et al*., 2014; but see also Meiri *et al*., 2006, 2008; Raia & Meiri, 2006, 2011). Given that *S. minutus* is the only shrew species in the Orkney islands and, until recently, it was the only shrew species in Ireland, larger body mass (reflected in larger mandibles and skulls) could have evolved on these islands driven by competitive release, the absence of predators and availability of resources (McDevitt *et al*., 2014). Additionally, geographic isolation from continental populations for several thousand years, genetic bottlenecks after colonisations from a low number of migrants and low genetic diversity (very few cyt *b* haplotypes were observed in the Orkney islands despite the large sample size) could lead to deviation in morphology of island populations of *S. minutus* compared with the mainland (Cornette *et al*., 2012). Contrastingly, specimens of *S. minutus* in Belle Île and Britain have higher cyt *b* diversity (McDevitt *et al*., 2011) and are similar in terms of mandible shape to continental samples. Additionally, Belle Île and mainland Britain are occupied by other species of shrews.

Morphological differences may actually represent phenotypic plasticity expressed in insular environments; however, this hypothesis has rarely been tested. Although, with our results in *S. minutus* we cannot rule out phenotypic plasticity as a possible explanation, at least for *C. suaveolens*, differences in body size and litter size between island and mainland populations were persistent over three generations in laboratory breeding conditions, thus supporting the hypothesis that these differences are genetically determined rather than phenotypic plasticity (Fons *et al*., 1997). The evolution of different size and shape in island populations of *S. minutus* may thus be an adaptive response to changed availability of resources, the 'resource rule' *sensu* McNab (2010), acting together with demographic and historical factors.

CONCLUSIONS

In this study we explored the morphological variation of mandibles and skulls of *S. minutus* across Europe using a geometric morphometric approach. We found notable ecogeographical variation in mandible and skull size related to environmental variables and insularity, which may suggest that the converse Bergmann's rule and the island rule operate in *S. minutus*. We believe, however, that these ecogeographical patterns could be more reasonably explained as a response to resource availability, possibly reflecting adaptation or a phenotypically plastic response to different habitats and environmental conditions, differential allocation of energy and physiological responses, differential food availability and presence/absence of competitors. Correlative studies such as this are an important source for identifying patterns that require further investigation by in-depth studies measuring the strength of selection or the experimental link between performance, morphology, and ecology generating local adaptations (Calsbeek & Irschick, 2007).

Considering variation in morphological shape rather than size, the most divergent populations among those examined in *S. minutus* were those from the Atlantic islands, although distinctive features could also be identified for populations in southern Europe (*e.g.* with thin-plate spline transformation grids). Interestingly, with respect to both size and shape, the morphological variation observed here does not follow previous genetic subdivisions within the species, and indicate a complex role for different evolutionary and/or environmental processes in determining geographical variation in *S. minutus*.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Sample information and dimensionality reduction results.

Appendix S2. Pairwise distances for mandible and skull data sets.

Appendix S3. Post-hoc results for analyses of variance of size and shape variables.

FIGURE LEGENDS

Figure 1. Sampling localities of *Sorex minutus* for morphological analysis. (A) Mandible data set and (B) skull data set. The symbols distinguish the geographical groups defined by previous genetic studies or by geographic isolation on islands (see text).

Figure 2. Boxplots of (A) mandible and (B) skull Centroid Size (transformed with natural logarithms; LnCS) after Standard Least Squares analysis of geographical groups of *Sorex minutus*. Symbols correspond to sampling localities shown in Fig. 1. Groups are arranged by increasing latitude and by continental and island origin. The outgroup (*S. volnuchini*) was not included in the analysis but is shown for comparison purposes. Letters A-D show pairwise significance.

Figure 3. Shape changes from the average configuration of (A) mandibles and (B) skulls of *Sorex minutus* represented using thin-plate spline transformation grids (3X scale factor to highlight shape changes). Arrows denote shape changes discussed in text. Symbols correspond to sampling localities shown in Fig. 1. Groups are arranged by increasing latitude.

Figure 4. Canonical Variate Analysis (CVA) of shape variables for (A) mandibles and (B) skulls of *Sorex minutus* showing differences among geographical groups. All continental samples are shown with the same symbol for simplicity.

Figure 5. Rooted Neighbour-Joining (NJ) trees of pairwise Procrustes distances for (A) mandible and (B) skull groups of *Sorex minutus*. Rooted NJ trees of cyt *b* genetic distances (Da) among phylogroups of *S. minutus* (detected here and in previous studies) showing intraspecific variation in Centroid Size (CS) and shape (Procrustes distances, PD) for mandible (C, D) and

skull groups (E, F) mapped onto the phylogeny using squared change parsimony. Symbols correspond to sampling localities shown in Fig. 1. Asterisks indicate bootstrap support (≥ 50%).

TABLES

Table 1. Multiple regressions between size and predictor variables for the mandible and skull data sets

Traditional Bergmann's rule variables				Geographical and environmental variables			
Mandibles (n = 568)							
Factor	Coefficient[a]	*t* value[b]	*P* value	Factor	Coefficient	*t* value	*P* value
Latitude	-0.002	-6.723	< 0.001	PC1	0.008	9.211	< 0.001
Altitude	0.000	7.022	< 0.001	PC2	0.003	2.501	0.013
AMT	0.001	1.427	0.154	PC3	0.005	3.959	< 0.001
Skulls (n = 377)							
Factor	Coefficient	*t* value	*P* value	Factor	Coefficient	*t* value	*P* value
Latitude	0.000	-1.975	0.049	PC1	0.002	3.303	0.001
Altitude	0.000	3.066	0.002	PC2	-0.001	-1.617	0.107
AMT	0.001	1.379	0.169	PC3	0.000	-0.266	0.790

[a]Unstandardised coefficients.

[b]Test for the statistical significance of each independent variable.

Table 2. Multivariate multiple regressions between shape and environmental Principal Components (PCs) for mandibles and skulls

Mandibles	All factors	PC1	PC2	PC3
Wilk's λ	0.240	0.792	0.653	0.613
F ratio	7.139	4.387	8.895	10.556
DF1	128	32	32	32
DF2	2119	535	535	535
P value	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Percentage explained	5.1%	0.9%	1.7%	2.4%
Skulls	**All factors**	**PC1**	**PC2**	**PC3**
Wilk's λ	0.1583	0.7748	0.5284	0.5697
F ratio	5.8560	2.9230	8.9760	7.5960
DF1	136	34	34	34
DF2	1352	342	342	342
P value	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Percentage explained	11.9%	0.92%	4.8%	6.2%

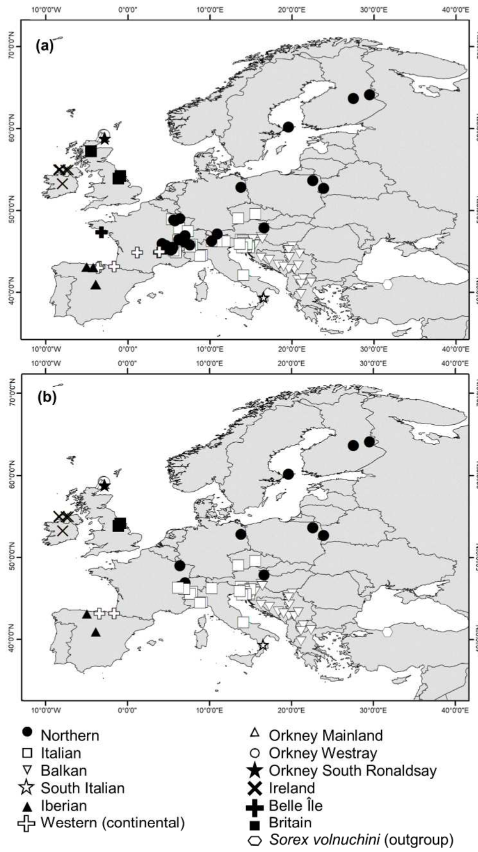

Figure 1. Sampling localities of Sorex minutus for morphological analysis. (A) Mandible data set and (B) skull data set. The symbols distinguish the geographical groups defined by previous genetic studies or by geographic isolation on islands (see text).
215x279mm (300 x 300 DPI)

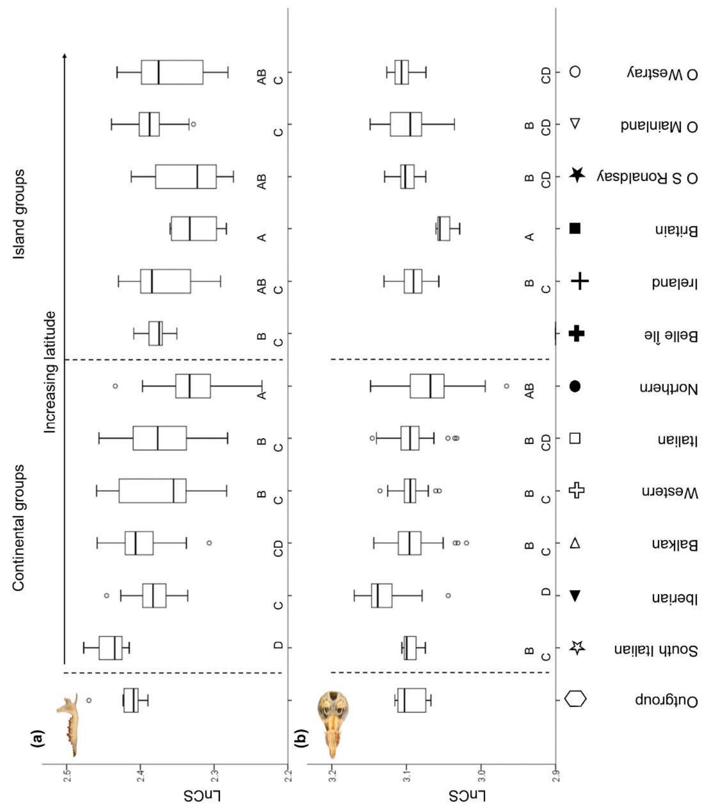

Figure 2. Boxplots of (A) mandible and (B) skull Centroid Size (transformed with natural logarithms; LnCS) after Standard Least Squares analysis of geographical groups of Sorex minutus. Symbols correspond to sampling localities shown in Fig. 1. Groups are arranged by increasing latitude and by continental and island origin. The outgroup (S. volnuchini) was not included in the analysis but is shown for comparison purposes. Letters A-D show pairwise significance.
215x279mm (300 x 300 DPI)

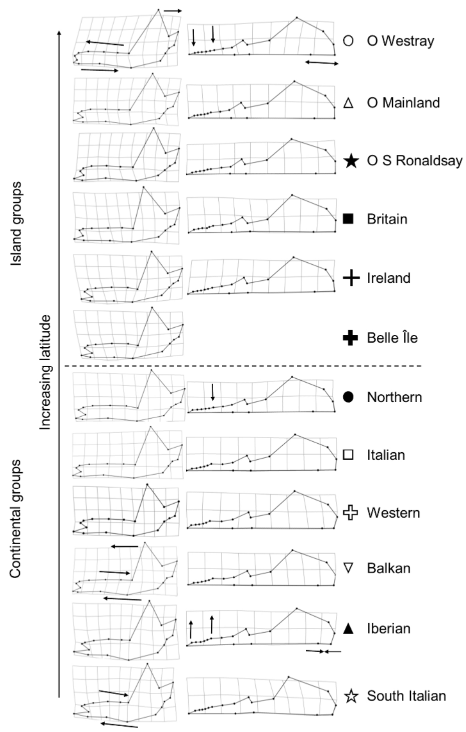

Figure 3. Shape changes from the average configuration of (A) mandibles and (B) skulls of Sorex minutus represented using thin-plate spline transformation grids (3X scale factor to highlight shape changes). Arrows denote shape changes discussed in text. Symbols correspond to sampling localities shown in Fig. 1. Groups are arranged by increasing latitude.
209x296mm (300 x 300 DPI)

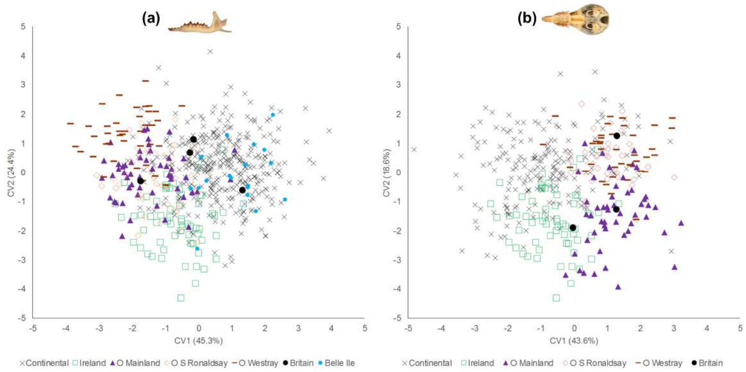

Figure 4. Canonical Variate Analysis (CVA) of shape variables for (A) mandibles and (B) skulls of Sorex minutus showing differences among geographical groups. All continental samples are shown with the same symbol for simplicity.
215x279mm (300 x 300 DPI)

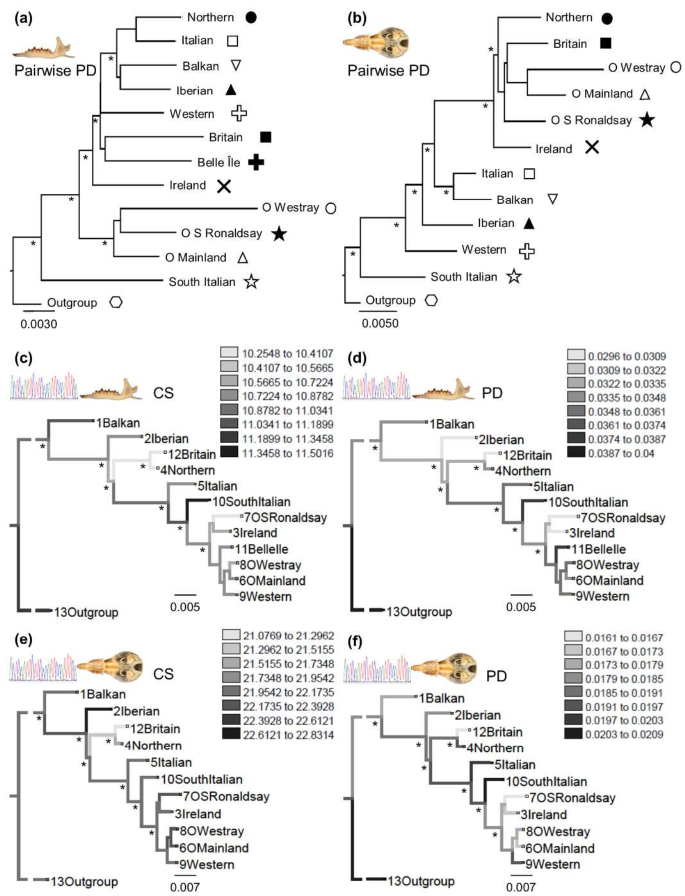

Figure 5. Rooted Neighbour-Joining (NJ) trees of pairwise Procrustes distances for (A) mandible and (B) skull groups of Sorex minutus. Rooted NJ trees of cyt b genetic distances (Da) among phylogroups of S. minutus (detected here and in previous studies) showing intraspecific variation in Centroid Size (CS) and shape (Procrustes distances, PD) for mandible (C, D) and skull groups (E, F) mapped onto the phylogeny using squared change parsimony. Symbols correspond to sampling localities shown in Fig. 1. Asterisks indicate bootstrap support (≥ 50%).
215x279mm (300 x 300 DPI)

SUPPORTING INFORMATION

Ecogeographical patterns of morphological variation in pygmy shrews *Sorex minutus* (Soricomorpha: Soricinae) within a phylogeographic and continental-and-island framework

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Running title:

Ecogeographical patterns in pygmy shrews

SUPPORTING INFORMATION

LANDMARKS

A description of landmarks (Fig. S1): mandibles: 1) inferior end of the alveolus of the incisor, 2) inferior margin of the alveolus of the incisor, 3-8) posterior ends of the alveoli of the mandibular teeth, 9) superior margin of the coronoid process, 10) inferior point of the saddle between the condylar and coronoid processes,11) lateral end of the superior surface of the condyle, 12) posterior end of the inferior surface of the condyle, 13) medial end of the inferior surface of the condyle, 14) superior side of the junction of the angular process to the body of the mandible, 15) inferior side of the junction of the angular process to the body of the mandible, 16) inferior-most point of the posterior convex saddle of the body of the mandible, 17) superior-most point of the concave saddle of the body of the mandible, and 18) inferior-most point of the anterior convex saddle of the body of the mandible; skulls: 1) anterior point of the midline suture between the premaxillae, 2-10) medial side of the point at which adjacent teeth meet, from the incisor through the third molar, 11) intersection between the lateral margin of the pterygoid plates and the posterior margin of the palate, 12) anterior margin of the glenoid fossa, 13) mastoid process, 14) lateral end of the posterior margin of the occipital condyle, 15) medial end of the posterior margin of the occipital condyle, 16) midline of the posterior margin of the foramen magnum, 17) midline of the anterior margin of the foramen magnum, 18) midline of the posterior margin of the palate, and 19) midline of the sutures between the palatine and maxilla.

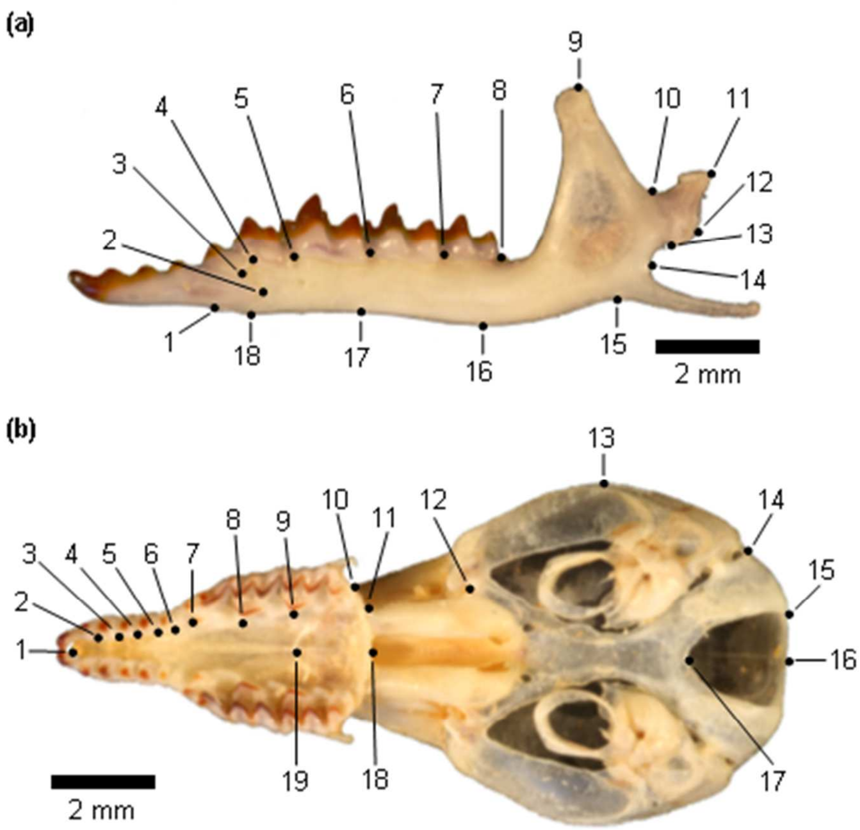

Figure S1. Landmarks placed on (A) mandibles and (B) skulls of *Sorex minutus*. A description of landmarks is shown in Supporting Information.

PRELIMINARY MORPHOMETRIC ANALYSES

To check for landmark placement repeatability we photographed 23 mandibles and 28 skulls five times each. The size of mandibles and skulls among photographs were subjected to Analysis of Variance (ANOVA) and the shape variables among photographs were analysed with Multivariate Analysis of Variance (MANOVA). To check for sexual dimorphism male and female samples were compared by ANOVA for size and by MANOVA for shape variables. There were 130 known males and 127 known females for mandibles, and there were 133 known males and 126 known females for skulls. To establish whether the mandible and skull data sets contain a phylogenetic signal (*i.e.* closely related individuals are phenotypically more similar to one another than expected by chance), we performed a Phylogenetic Independent Contrast in MorphoJ version 1.05a between the cytochrome *b* (cyt *b*) NJ tree and the size and shape of the average configurations of the mandible and skull data sets divided into groups. This test simulates the null hypothesis of the absence of phylogenetic signal by randomly permuting the size and shape data among the terminal taxa of a known phylogeny in the analysis (20,000 iterations for the permutation tests) (Klingenberg & Gidaszewski, 2010).

RESULTS OF PRELIMINARY MORPHOMETRIC ANALYSES

Preliminary analyses supported landmark placement repeatability, no sexual dimorphism for size and shape and negligible phylogenetic signal in the morphological dataset. There were no significant differences with respect to size or shape among the five repeated photographs of mandibles (size: $F_{4, 110} = 0.0053$, $P = 0.9999$; shape: Wilks' $\lambda = 0.8861$, $F_{64, 374.2} = 0.1835$, $P = 0.9999$) and skulls (size: $F_{4, 135} = 0.0726$, $P = 0.9903$; shape: Wilks' $\lambda = 0.8688$, $F_{68, 469.3} = 0.2518$, $P = 0.9999$); therefore, landmarks can be considered to have been placed accurately.

There were no significant differences between male and female mandibles for size ($F_{1, 255} = 0.0235$, $P = 0.8782$) and shape (Wilks' $\lambda = 0.9419$, $F_{16, 240} = 0.9256$, $P = 0.5404$). Similarly, there were no significant differences between male and female skulls for size ($F_{1, 257} = 0.0352$, $P = 0.8513$) and shape (Wilks' $\lambda = 0.9507$, $F_{17, 241} = 0.7345$, $P = 0.7658$). Moreover, comparisons of male and female samples within groups and within large regional samples showed no significant differences (data not shown). All subsequent analyses on mandibles and skulls were performed pooling all samples irrespective of sex.

The null hypothesis (absence of a phylogenetic signal) was not rejected when mapping the phenotypic data of the average configurations of the groups for the mandible ($P_{size} = 0.7448$, $P_{shape} = 0.1247$) and skull data sets ($P_{size} = 0.0748$, $P_{shape} = 0.6867$) onto the cyt *b* NJ tree; therefore, we concluded that the phylogenetic signal in our data sets is negligible.

86 **SUPPORTING INFORMATION**

87 **Appendix S1.** Sample information and dimensionality reduction results for Principal

88 Components Analysis and for Partial Least Squares Analysis.

89

Table S1. *Sorex minutus* and *S. volnuchini* samples for the mandible and skull data sets

Sample ID	Group	Cont/Island	Source	LongDec	LatDec	Data set
ATDo1611	Balkan	Continent	Trapping	16.641250	47.895703	mand/skull
BAKu2517	Balkan	Continent	Trapping	17.320656	44.002197	mand/skull
BAOs5670	Balkan	Continent	Trapping	16.288742	44.239742	mand/skull
BAZe4239	Balkan	Continent	Trapping	18.388903	43.394850	mand/skull
GREp6406	Balkan	Continent	Trapping	21.169192	39.770506	mand/skull
MEBj381	Balkan	Continent	Trapping	19.701092	42.865747	mand/skull
MEBj382	Balkan	Continent	Trapping	19.701092	42.865747	mand/skull
MEBj383	Balkan	Continent	Trapping	19.701092	42.865747	mand/skull
MEDu3403	Balkan	Continent	Trapping	19.041186	43.145475	mand/skull
MEDu3430	Balkan	Continent	Trapping	19.041186	43.145475	mand/skull
MKBi2450	Balkan	Continent	Trapping	20.768839	41.516908	mand
MKJa9212	Balkan	Continent	Trapping	21.418861	41.689061	mand/skull
MKJa9222	Balkan	Continent	Trapping	21.418861	41.689061	mand
MKJa9223	Balkan	Continent	Trapping	21.418861	41.689061	mand/skull
MKKo194	Balkan	Continent	Trapping	22.394211	41.154392	mand/skull
MKKo195	Balkan	Continent	Trapping	22.394211	41.154392	mand/skull
MKPe3834	Balkan	Continent	Trapping	21.167500	41.008939	mand
MKPe3835	Balkan	Continent	Trapping	21.167500	41.008939	mand/skull
MKPe3836	Balkan	Continent	Trapping	21.167500	41.008939	skull
MKPe3896	Balkan	Continent	Trapping	21.167500	41.008939	mand/skull
MKPe9494	Balkan	Continent	Trapping	21.167500	41.008939	mand/skull
MKPe9505	Balkan	Continent	Trapping	21.167500	41.008939	mand/skull
MKPe9645	Balkan	Continent	Trapping	21.167500	41.008939	mand/skull
RSBe178	Balkan	Continent	Trapping	20.080025	45.614672	mand/skull
RSKo40169	Balkan	Continent	Museum	20.998061	44.729006	mand
RSMF53266	Balkan	Continent	Museum	19.662544	45.170711	mand/skull
RSMF566	Balkan	Continent	Trapping	19.662544	45.170711	mand/skull
RSMK10066	Balkan	Continent	Museum	20.810628	43.296739	mand/skull
RSMK1078	Balkan	Continent	Trapping	20.810628	43.296739	mand/skull
RSMK1276	Balkan	Continent	Trapping	20.810628	43.296739	mand/skull
RSMK17377	Balkan	Continent	Museum	20.810628	43.296739	mand/skull
RSMK2449	Balkan	Continent	Trapping	20.810628	43.296739	mand/skull
RSMK578	Balkan	Continent	Trapping	20.810628	43.296739	mand/skull
RSMK678	Balkan	Continent	Trapping	20.810628	43.296739	mand/skull
RSMP35866	Balkan	Continent	Museum	20.361897	42.839728	mand

RSMP35966	Balkan	Continent	Museum	20.361897	42.839728	mand/skull
RSVa7841	Balkan	Continent	Trapping	19.736253	44.314847	mand/skull
RSVa7842	Balkan	Continent	Trapping	19.736253	44.314847	mand/skull
RSVa7855	Balkan	Continent	Trapping	19.736253	44.314847	mand/skull
SIGo2042	Balkan	Continent	Trapping	15.561217	45.857758	mand/skull
SIHo15910	Balkan	Continent	Museum	16.329503	46.811033	mand/skull
SIKr14709	Balkan	Continent	Museum	15.476147	45.895617	mand/skull
SILe1145	Balkan	Continent	Trapping	16.457517	46.551106	mand/skull
SILe1146	Balkan	Continent	Trapping	16.457517	46.551106	mand/skull
SILe1147	Balkan	Continent	Trapping	16.457517	46.551106	mand/skull
SILe1163	Balkan	Continent	Trapping	16.457517	46.551106	mand/skull
SIPh3126	Balkan	Continent	Trapping	15.256711	46.519253	mand/skull
SIPh3131	Balkan	Continent	Trapping	15.256711	46.519253	mand/skull
SIPh3489	Balkan	Continent	Trapping	15.256711	46.519253	mand/skull
SIRa16104	Balkan	Continent	Museum	15.340292	45.685878	mand/skull
SISe16100	Balkan	Continent	Museum	15.234997	45.507833	mand
SISe16101	Balkan	Continent	Museum	15.234997	45.507833	mand/skull
FRBI100	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI101	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI102	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI103	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI104	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI105	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI106	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI107	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI108	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI109	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI110	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI111	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI93	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI94	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI95	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI96	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI97	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI98	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
FRBI99	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
GBCa1	Britain	Britain	Trapping	-0.892633	53.964711	mand/skull
GBCH1	Britain	Britain	Trapping	-0.910433	54.120878	mand/skull
GBDrG140	Britain	Britain	Trapping	-4.489267	57.308992	mand
GBHe1	Britain	Britain	Trapping	-1.057706	53.943211	mand/skull
ESArE135	Iberian	Continent	Trapping	-4.200000	43.033300	mand
ESPE47	Iberian	Continent	Trapping	-4.999678	43.104939	mand/skull
ESPE57	Iberian	Continent	Trapping	-4.999678	43.104939	mand/skull
ESRa0640	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
ESRa2653	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull

ESRa3443	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
ESRa3444	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
ESRa3445	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
ESRa3446	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
ESRa3447	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
ESRa3448	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
ESRa3449	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
ESRa3451	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
IECL1	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL10	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL11	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL12	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL13	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL14	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL15	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL16	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL17	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL18	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL19	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL2	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL20	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL3	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL4	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL5	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL6	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL7	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL8	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IECL9	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
IEDY1	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY10	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY11	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY12	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY13	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY14	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY15	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY16	Ireland	Ireland	Trapping	-7.250000	55.000000	mand
IEDY17	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY18	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY19	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY2	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY20	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY3	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY4	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY5	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY6	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull

IEDY7	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY8	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
IEDY9	Ireland	Ireland	Trapping	-7.250000	55.000000	mand
IEE1RV	Ireland	Ireland	Trapping	-8.350450	54.950261	mand/skull
IEE2RV	Ireland	Ireland	Trapping	-7.515247	54.975419	mand/skull
IEE3RV	Ireland	Ireland	Trapping	-7.515247	54.975419	mand/skull
IEE4RV	Ireland	Ireland	Trapping	-7.515247	54.975419	mand/skull
IEGw1	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw17	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw1RV	Ireland	Ireland	Trapping	-8.383333	55.050000	mand/skull
IEGw26	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw3	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw4	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw43	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw46	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw5	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw51	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw51A	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw51B	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw51C	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw55	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw55B	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw5b	Ireland	Ireland	Trapping	-8.230000	55.050000	mand
IEGw5C	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGw64	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
IEGwTILES	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
CHVI4746	Italian	Continent	Museum	6.892742	46.204300	mand/skull
CHVI4748	Italian	Continent	Museum	6.892742	46.204300	mand/skull
CZHa9166	Italian	Continent	Museum	15.560653	49.604761	mand/skull
CZSS4767	Italian	Continent	Trapping	13.475481	49.065617	mand/skull
CZSS4838	Italian	Continent	Trapping	13.475481	49.065617	mand/skull
FRDi3003	Italian	Continent	Trapping	6.143175	46.356817	mand/skull
FRHa59	Italian	Continent	Owl pellet	6.284722	47.843611	mand
FRHa60	Italian	Continent	Owl pellet	6.284722	47.843611	mand
FRHa61	Italian	Continent	Owl pellet	6.284722	47.843611	mand
FRHa62	Italian	Continent	Owl pellet	6.284722	47.843611	mand
FRHa63	Italian	Continent	Owl pellet	6.284722	47.843611	mand
FRHa64	Italian	Continent	Owl pellet	6.284722	47.843611	mand
FRHa65	Italian	Continent	Owl pellet	6.284722	47.843611	mand
FRLa87	Italian	Continent	Owl pellet	5.410833	48.939722	mand
FRLa88	Italian	Continent	Owl pellet	5.410833	48.939722	mand
FRLa89	Italian	Continent	Owl pellet	5.410833	48.939722	mand
FRLG003A	Italian	Continent	Trapping	5.903056	45.091944	mand
FRLG003B	Italian	Continent	Trapping	5.903056	45.091944	mand
FRLG003C	Italian	Continent	Trapping	5.903056	45.091944	mand

FRLV27	Italian	Continent	Owl pellet	5.589069	45.127964	mand
FROR15	Italian	Continent	Owl pellet	5.870556	44.921944	mand
FRSo091A	Italian	Continent	Trapping	7.336111	47.483889	mand
FRSo091B	Italian	Continent	Trapping	7.336111	47.483889	mand
FRSo90	Italian	Continent	Trapping	7.336111	47.483889	mand
FRSo92	Italian	Continent	Trapping	7.336111	47.483889	mand
ITAn23	Italian	Continent	Museum	7.696569	45.822425	mand
ITCh16	Italian	Continent	Museum	7.622858	45.621664	mand
ITCh17	Italian	Continent	Museum	7.622858	45.621664	mand/skull
ITCh18	Italian	Continent	Museum	7.622858	45.621664	mand
ITGa33	Italian	Continent	Museum	7.848183	45.851881	skull
ITGa36	Italian	Continent	Museum	7.848183	45.851881	mand/skull
ITGa38	Italian	Continent	Museum	7.848183	45.851881	mand/skull
ITMa9815	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
ITMa9830	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
ITMa9832	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
ITMa9833	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
ITMa9834	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
ITMa9835	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
ITMa9849	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
ITMa9850	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
ITMC32500	Italian	Continent	Museum	10.836031	46.238711	mand
ITPr0001	Italian	Continent	Trapping	10.248014	46.286975	mand/skull
ITSC54303	Italian	Continent	Museum	8.832010	44.477300	mand/skull
ITTg47	Italian	Continent	Museum	7.571240	45.807200	mand/skull
ITTg48	Italian	Continent	Museum	7.571240	45.807200	mand/skull
ITTr17692	Italian	Continent	Museum	11.833333	46.250000	mand
ITVB54317	Italian	Continent	Museum	9.064750	44.555300	mand/skull
SICe142	Italian	Continent	Trapping	14.945650	46.172950	skull
SIDo2040	Italian	Continent	Trapping	14.797406	45.501464	mand/skull
SIDo2041	Italian	Continent	Trapping	14.797406	45.501464	skull
SIDr2778	Italian	Continent	Trapping	14.029192	46.358772	mand/skull
SIDr2779	Italian	Continent	Trapping	14.029192	46.358772	mand/skull
SIGr973	Italian	Continent	Trapping	14.132525	46.105453	mand/skull
SIGr974	Italian	Continent	Trapping	14.132525	46.105453	mand/skull
SIIg1563	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
SIIg1564	Italian	Continent	Trapping	14.542856	45.946967	mand
SIIg1565	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
SIIg1628	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
SIIg1648	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
SIIg1766	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
SIIg1773	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
SIIg1847	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
SIIg2143	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
SIKn6167	Italian	Continent	Trapping	13.784367	46.469472	mand/skull

SIKn6380	Italian	Continent	Trapping	13.784367	46.469472	mand/skull
SIKo6781	Italian	Continent	Trapping	14.820278	45.656956	mand
SIKo6782	Italian	Continent	Trapping	14.820278	45.656956	mand/skull
SIKo6827	Italian	Continent	Trapping	14.820278	45.656956	mand/skull
SIKo6845	Italian	Continent	Trapping	14.820278	45.656956	mand/skull
SIKr1042	Italian	Continent	Trapping	14.247114	45.821514	mand/skull
SING54318	Italian	Continent	Museum	13.657053	45.944656	mand/skull
SING54320	Italian	Continent	Museum	13.657053	45.944656	mand/skull
SIPd1045	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
SIPd1372	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
SIPd1374	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
SIPk16394	Italian	Continent	Museum	14.029192	46.358772	mand/skull
SISl1378	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
SISl1380	Italian	Continent	Trapping	13.940200	45.512914	mand
SISl1381	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
SISl1382	Italian	Continent	Trapping	13.940200	45.512914	skull
SISl1383	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
SISl1384	Italian	Continent	Trapping	13.940200	45.512914	skull
SISn1043	Italian	Continent	Trapping	14.401383	45.573331	mand/skull
SISn1044	Italian	Continent	Trapping	14.401383	45.573331	mand/skull
ATDo1612	Northern	Continent	Trapping	16.641250	47.895703	mand/skull
ATUmA139	Northern	Continent	Trapping	10.927683	47.136119	mand
CHBa0441	Northern	Continent	Museum	6.231061	46.462789	mand/skull
CHBa1816	Northern	Continent	Museum	6.231061	46.462789	mand/skull
CHBa1817	Northern	Continent	Museum	6.231061	46.462789	mand/skull
CHBa1818	Northern	Continent	Museum	6.231061	46.462789	mand/skull
CHBa1819	Northern	Continent	Museum	6.231061	46.462789	mand/skull
CHBa1820	Northern	Continent	Museum	6.231061	46.462789	mand/skull
CHBa1821	Northern	Continent	Museum	6.231061	46.462789	mand/skull
CHBa3002	Northern	Continent	Museum	6.231061	46.462789	mand/skull
CHCh7622	Northern	Continent	Museum	6.997358	46.932742	mand/skull
CHPo7628	Northern	Continent	Museum	6.997358	46.932742	mand/skull
CHVI4747	Northern	Continent	Museum	6.892742	46.204300	mand/skull
DEEb3996	Northern	Continent	Museum	13.810889	52.833108	mand/skull
FIAE1747	Northern	Continent	Museum	19.611839	60.203744	mand/skull
FIAE1760	Northern	Continent	Museum	19.611839	60.203744	mand/skull
FIKu2071	Northern	Continent	Museum	29.495703	64.125364	mand/skull
FISo1773	Northern	Continent	Museum	27.529589	63.669514	mand/skull
FISo1779	Northern	Continent	Museum	27.529589	63.669514	mand/skull
FISo1783	Northern	Continent	Museum	27.529589	63.669514	mand/skull
FISo1785	Northern	Continent	Museum	27.529589	63.669514	mand/skull
FRAF174	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF175	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF176	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF179	Northern	Continent	Owl pellet	5.639722	48.856111	mand

FRAF180	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF181	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF182	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF183	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF184	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF185	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF186	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF187	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF188	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF189	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF190	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF192	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF193	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF194	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF195	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF196A	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF196B	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF197	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRAF198	Northern	Continent	Owl pellet	5.639722	48.856111	mand
FRBe19	Northern	Continent	Owl pellet	5.265556	45.203333	mand
FRBe20	Northern	Continent	Owl pellet	5.265556	45.203333	mand
FRBe21	Northern	Continent	Owl pellet	5.265556	45.203333	mand
FRBo141	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo142	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo143	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo144	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo145	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo146	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo147	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo148	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo149	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo150	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo151	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo152	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo153	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo154	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo155	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo156	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo157	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo158	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo159	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo160	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo161	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo162	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo163	Northern	Continent	Owl pellet	5.762222	48.747500	mand

FRBo164	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo165	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRBo166	Northern	Continent	Owl pellet	5.762222	48.747500	mand
FRCh043A	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh38	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh39	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh40	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh41	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh42	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh44	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh45	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh46	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh48	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh49	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh50	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh51	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh52	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh54	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh55	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh56	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCh58	Northern	Continent	Owl pellet	5.431667	45.444722	mand
FRCM1	Northern	Continent	Owl pellet	4.727500	45.384722	mand
FRFS24	Northern	Continent	Owl pellet	4.692778	45.297500	mand
FRFS25	Northern	Continent	Owl pellet	4.692778	45.297500	mand
FRFS26	Northern	Continent	Owl pellet	4.692778	45.297500	mand
FRFT12	Northern	Continent	Owl pellet	5.524444	45.527500	mand
FRGL035A	Northern	Continent	Owl pellet	5.420556	45.399167	mand
FRGL33	Northern	Continent	Owl pellet	5.420556	45.399167	mand
FRGL34	Northern	Continent	Owl pellet	5.420556	45.399167	mand
FRLe37	Northern	Continent	Owl pellet	5.114167	45.300000	mand
FRLo13	Northern	Continent	Owl pellet	5.348333	45.419722	mand
FRLo14	Northern	Continent	Owl pellet	5.348333	45.419722	mand
FRMu16	Northern	Continent	Owl pellet	5.315833	45.213889	mand
FRMu36	Northern	Continent	Owl pellet	5.315833	45.213889	mand
FRPD3082	Northern	Continent	Owl pellet	6.381797	49.007092	mand/skull
FRSJ030A	Northern	Continent	Owl pellet	5.138611	45.503056	mand
FRSJ030B	Northern	Continent	Owl pellet	5.138611	45.503056	mand
FRSJ030C	Northern	Continent	Owl pellet	5.138611	45.503056	mand
FRSJ10	Northern	Continent	Owl pellet	5.138611	45.503056	mand
FRSJ11	Northern	Continent	Owl pellet	5.138611	45.503056	mand
FRSJ28	Northern	Continent	Owl pellet	5.138611	45.503056	mand
FRSJ31	Northern	Continent	Owl pellet	5.138611	45.503056	mand
FRSJ32	Northern	Continent	Owl pellet	5.138611	45.503056	mand
FRSJ9	Northern	Continent	Owl pellet	5.138611	45.503056	mand
FRSS3	Northern	Continent	Owl pellet	4.212500	45.948611	mand

FRSS4	Northern	Continent	Owl pellet	4.212500	45.948611	mand
FRSS5	Northern	Continent	Owl pellet	4.212500	45.948611	mand
FRSS6	Northern	Continent	Owl pellet	4.212500	45.948611	mand
FRVa17	Northern	Continent	Owl pellet	5.411389	45.256944	mand
FRVa18	Northern	Continent	Owl pellet	5.411389	45.256944	mand
FRVe129	Northern	Continent	Owl pellet	4.663333	45.369167	mand
FRVe22	Northern	Continent	Owl pellet	4.663333	45.369167	mand
FRVe23	Northern	Continent	Owl pellet	4.663333	45.369167	mand
FRVy7	Northern	Continent	Owl pellet	4.657222	45.738333	mand
ITPr0004	Northern	Continent	Trapping	10.248014	46.286975	mand/skull
ITTg49	Northern	Continent	Museum	7.571240	45.807200	mand/skull
POBiebrza129355	Northern	Continent	Museum	22.573378	53.643861	mand/skull
POBiebrza129373	Northern	Continent	Museum	22.573378	53.643861	mand/skull
POBiebrza129376	Northern	Continent	Museum	22.573378	53.643861	mand/skull
POBiebrza129377	Northern	Continent	Museum	22.573378	53.643861	mand/skull
POBiebrza129392	Northern	Continent	Museum	22.573378	53.643861	mand/skull
POBiebrza150912	Northern	Continent	Museum	22.573378	53.643861	mand/skull
POBiebrza151115	Northern	Continent	Museum	22.573378	53.643861	mand/skull
POBiebrza151140	Northern	Continent	Museum	22.573378	53.643861	mand
POBiebrza151141	Northern	Continent	Museum	22.573378	53.643861	mand/skull
POBiebrza151151	Northern	Continent	Museum	22.573378	53.643861	mand/skull
POBPN135315	Northern	Continent	Museum	23.900117	52.709481	mand/skull
POBPN135316	Northern	Continent	Museum	23.900117	52.709481	mand/skull
POBPN135318	Northern	Continent	Museum	23.900117	52.709481	mand/skull
POBPN135319	Northern	Continent	Museum	23.900117	52.709481	mand/skull
POBPN135320	Northern	Continent	Museum	23.900117	52.709481	mand/skull
POBPN135345	Northern	Continent	Museum	23.900117	52.709481	mand/skull
POBPN135346	Northern	Continent	Museum	23.900117	52.709481	mand/skull
POBPN135347	Northern	Continent	Museum	23.900117	52.709481	mand/skull
POBPN135402	Northern	Continent	Museum	23.900117	52.709481	mand/skull
POBPN135411	Northern	Continent	Museum	23.900117	52.709481	mand/skull
OMHa10	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
OMHa11	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
OMHa12	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
OMHa3BM	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
OMHa3CM	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
OMHa3M	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
OMHa4	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
OMHa6	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
OMHa9F	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
OMHa9F	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
OMHa9M	OMainland	OMainland	Trapping	-3.190167	59.033728	mand
OMHo15	OMainland	OMainland	Trapping	-3.067628	58.946361	mand/skull
OMSa1	OMainland	OMainland	Trapping	-3.297169	59.048261	mand/skull
OMSa2	OMainland	OMainland	Trapping	-3.297169	59.048261	mand/skull

OMSO1	OMainland	OMainland	Trapping	-2.950003	58.950019	mand
OMSO10F	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO11	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO12	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO13	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO15	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO16	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO17	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO18	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO2	OMainland	OMainland	Trapping	-2.950003	58.950019	mand
OMSO20	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO21	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO24	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO25	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO26	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO28	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO29	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO3	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO30	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO31	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO35	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO36	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO37	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO38	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO4	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO5	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO6M	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO7F	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO8M	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMSO9F	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
OMTa10	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
OMTa2	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
OMTa3	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
OMTa4	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
OMTa5	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
OMTa6	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
OMTa7	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
OMTa8	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
OMTa9	OMainland	OMainland	Trapping	-2.850033	58.950006	skull
OSGr10	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr12	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr14	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr15	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr18	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr20	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull

OSGr23	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr25	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr27	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr28	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr31	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr35	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr39	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr42	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr45	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr49	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr50	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr7	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand
OSGr8	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSGr9	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
OSWW11	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW12	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW13	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW14	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW15	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW16	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand
OSWW17	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW18	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW19	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW20	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW21	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW23	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW24	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW25	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW26	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW28	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW6	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW7	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW8	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
OSWW9	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand
OWLS1	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS112	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS2	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS24	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS25	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS36	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS37	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS38	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS55	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS59	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS6	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull

OWLS60	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS61	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS72	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS73	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS82	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS83	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS84	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS85	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWLS99	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
OWNe102	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe103	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe2	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe26	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe28	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe29	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe30	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe31	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe4	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe41	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe42	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe43	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe47	OWestray	OWestray	Trapping	-2.866747	59.233358	mand
OWNe6	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe62	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe68	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe7	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe75	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe89	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
OWNe90	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
ITSi11	SouthItalian	Continent	Trapping	16.491144	39.352214	mand/skull
ITSi17	SouthItalian	Continent	Trapping	16.491144	39.352214	mand/skull
ITSi21	SouthItalian	Continent	Trapping	16.491144	39.352214	mand/skull
ESCoE138	Western	Continent	Trapping	-3.627161	43.019269	mand
ESEM69	Western	Continent	Trapping	-3.450258	43.142322	mand/skull
ESNa1131	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa1286	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa137	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa1379	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa1576	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa1577	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa1579	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa172	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa1757	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa1758	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa239	Western	Continent	Private	-1.645500	43.175708	skull

ESNa240	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa318	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa399	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa406	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa460	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa461	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa463	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa47	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa509	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa598	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa633	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa739	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa752	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa798	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa803	Western	Continent	Private	-1.645500	43.175708	mand/skull
ESNa861	Western	Continent	Private	-1.645500	43.175708	mand/skull
FRCu136	Western	Continent	Owl pellet	3.885000	44.989444	mand
FRSA079A	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA079B	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA168	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA169	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA171	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA172	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA173	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA68	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA69	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA70	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA71	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA72	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA74	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA75	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA77	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA78	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA81	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA82	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA83	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSA85	Western	Continent	Owl pellet	1.167500	44.886667	mand
FRSN117	Western	Continent	Owl pellet	3.790000	44.891111	mand
FRSN118	Western	Continent	Owl pellet	3.790000	44.891111	mand
FRSN120	Western	Continent	Owl pellet	3.790000	44.891111	mand
FRSN121	Western	Continent	Owl pellet	3.790000	44.891111	mand
FRSN123	Western	Continent	Owl pellet	3.790000	44.891111	mand
FRSN124	Western	Continent	Owl pellet	3.790000	44.891111	mand
FRSN125	Western	Continent	Owl pellet	3.790000	44.891111	mand
FRSN126	Western	Continent	Owl pellet	3.790000	44.891111	mand

FRSN127	Western	Continent	Owl pellet	3.790000	44.891111	mand
Svol10302	Outgroup	Outgroup	Museum	31.723833	40.898814	mand/skull
Svol10303	Outgroup	Outgroup	Museum	31.723833	40.898814	mand/skull
Svol10304	Outgroup	Outgroup	Museum	31.723833	40.898814	mand/skull
Svol11290	Outgroup	Outgroup	Museum	31.723833	40.898814	mand/skull
Svol11312	Outgroup	Outgroup	Museum	31.723833	40.898814	mand/skull
Svol11313	Outgroup	Outgroup	Museum	31.723833	40.898814	mand/skull
Svol11392	Outgroup	Outgroup	Museum	31.723833	40.898814	mand/skull
Svol11393	Outgroup	Outgroup	Museum	31.723833	40.898814	mand/skull

Table S2. Eigenvalues from Principal Components Analysis of geographical and environmental variables for mandible and skull data sets

	Mandibles			Skulls		
Number	Eigenvalue	Percentage explained	Cumulative percentage explained	Eigenvalue	Percentage explained	Cumulative percentage explained
1	4.1837	34.864	34.864	4.3544	36.286	36.286
2	3.2244	26.87	61.735	3.3111	27.593	63.879
3	2.5958	21.632	83.366	2.4222	20.185	84.064
4	0.8096	6.746	90.113	0.8591	7.159	91.223
5	0.5171	4.309	94.422	0.544	4.533	95.756
6	0.3681	3.067	97.489	0.2713	2.261	98.017
7	0.179	1.492	98.981	0.1268	1.057	99.074
8	0.0709	0.591	99.572	0.0696	0.58	99.654
9	0.0334	0.279	99.851	0.0254	0.212	99.866
10	0.0103	0.086	99.936	0.0101	0.084	99.95
11	0.0056	0.046	99.983	0.0043	0.036	99.986
12	0.0021	0.017	100	0.0017	0.014	100

Table S3. Eigenvectors from Principal Components Analysis of geographical and environmental variables

Mandibles	PC1	PC2	PC3
Longitude	-0.1907	**0.4422**	0.0015
Latitude	0.0607	**-0.3332**	**-0.4329**
Altitude	0.0278	**0.4675**	-0.0171
BIO1_AMT	-0.0405	-0.2898	**0.5037**
BIO5_MxTempWarPer	-0.2066	0.1227	**0.5115**
BIO6_MnTempColdPer	0.1452	**-0.4855**	0.1828
BIO12_AnnPrec	**0.4748**	0.0905	0.0842
BIO13_PrecWetPer	**0.4518**	0.0321	0.0526
BIO14_PrecDrPer	**0.4070**	0.2001	0.0888
BIO18_PrecWarQrt	**0.3145**	0.2788	0.0226
BIO19_PrecColdQrt	**0.4462**	-0.1133	0.0706
NPP	-0.0244	0.0196	**0.4903**
Skulls	PC1	PC2	PC3
Longitude	-0.1830	**0.4487**	0.0418
Latitude	-0.0687	**-0.4075**	**-0.3332**
Altitude	0.0114	**0.4541**	-0.0995
BIO1_AMT	0.1235	-0.2309	**0.5340**
BIO5_MxTempWarmPer	-0.0538	0.2154	**0.5541**
BIO6_MnTempColdPer	0.1994	**-0.4515**	0.1799
BIO12_AnnPrec	**0.4686**	0.0869	-0.0650
BIO13_PrecWetPer	**0.4530**	0.0432	-0.0027
BIO14_PrecDrPer	**0.4082**	0.1834	-0.1518
BIO18_PrecWarmQrt	**0.3148**	0.2505	-0.1226
BIO19_PrecColdQrt	**0.4416**	-0.1036	-0.0356
NPP	0.1351	0.0796	**0.4574**

Values in bold indicate the most significant eigenvectors in each principal component.

Table S4. Factors extracted from Partial Least Squares Analysis of shape and geographical and environmental variables

Mandibles

Factor	Percentage explained (Effect)	Cumulative percentage explained (Effect)	Percentage explained (Response)	Cumulative percentage explained (Response)
1	26.8121	26.812	5.0756	5.0756
2	25.089	51.901	2.3507	7.4262
3	31.1802	83.081	0.7513	8.1776
4	4.9684	88.05	1.9711	10.1487
5	5.4054	93.455	0.3503	10.499
6	3.9181	97.373	0.2679	10.7669
7	1.3028	98.676	0.4685	11.2354
8	0.4718	99.148	0.782	12.0174
9	0.6864	99.834	0.4828	12.5003
10	0.0975	99.932	0.6343	13.1346
11	0.0505	99.982	0.2603	13.3948
12	0.0177	100	0.1872	13.582

Skulls

Factor	Percentage explained (Effect)	Cumulative percentage explained (Effect)	Percentage explained (Response)	Cumulative percentage explained (Response)
1	26.1993	26.199	10.1024	10.1024
2	34.1241	60.323	1.5007	11.6031
3	22.4314	82.755	1.198	12.8011
4	7.6432	90.398	1.5977	14.3988

5	5.2877	95.686	0.6531	15.0519
6	2.305	97.991	0.2945	15.3464
7	0.7342	98.725	0.6411	15.9875
8	0.9077	99.633	0.2471	16.2346
9	0.2232	99.856	0.5511	16.7858
10	0.0913	99.947	0.582	17.3677
11	0.0179	99.965	0.7281	18.0959
12	0.0351	100	0.3197	18.4156

Table S5. Variable Importance Plot (VIP) values for Partial Least Squares analysis of geographical and environmental variables

	Mandibles VIP	Skulls VIP
Longitude	**1.1503**	**1.0294**
Latitude	**1.3708**	**1.6241**
Altitude	**1.0498**	**1.1775**
BIO1_AMT	**0.9164**	**0.8505**
BIO5_MxTempWarPer	**1.2166**	**1.3348**
BIO6_MnTempColdPer	**0.9967**	**0.853**
BIO12_AnnPrec	0.6698	0.7057
BIO13_PrecWetPer	**0.9439**	0.6765
BIO14_PrecDrPer	**0.8143**	**0.7348**
BIO18_PrecWarQrt	0.7745	**0.7531**
BIO19_PrecColdQrt	**0.8542**	0.6901
NPP	**1.0248**	**1.0698**

Significant VIP values in bold.

Table S6. Eigenvalues from Canonical Variates Analysis of shape variables for mandible and skull data sets

	Mandibles			Skulls		
Number	Eigenvalue	Percentage explained	Cumulative percentage explained	Eigenvalue	Percentage explained	Cumulative percentage explained
1	**1.052651**	45.2558	45.2558	**1.277708**	43.6205	43.6205
2	**0.566254**	24.3445	69.6004	**0.543716**	18.5623	62.1828
3	**0.186308**	8.0098	77.6101	**0.351271**	11.9923	74.1751
4	**0.179597**	7.7213	85.3314	**0.308121**	10.5191	84.6942
5	**0.098454**	4.2328	89.5642	**0.197237**	6.7336	91.4278
6	**0.090917**	3.9087	93.4729	**0.126866**	4.3311	95.7589
7	**0.067079**	2.8839	96.3568	0.056318	1.9227	97.6816
8	0.049882	2.1445	98.5013	0.027568	0.9412	98.6228
9	0.017839	0.7669	99.2682	0.024096	0.8226	99.4454
10	0.011404	0.4903	99.7585	0.016246	0.5546	100
11	0.005617	0.2415	100			

Significant eigenvalues in bold.

SUPPORTING INFORMATION

Appendix S2. Pairwise distances for mandible and skull data sets.

Table S7. Pairwise distances for mandible data set

Mandibles													
Procrustes Distances	1	2	3	4	5	6	7	8	9	10	11	12	13
1-Balkan													
2-Iberian	0.0120												
3-Ireland	0.0175	0.0151											
4-Northern	0.0146	0.0151	0.0169										
5-Italian	0.0119	0.0119	0.0160	0.0095									
6-O Mainland	0.0207	0.0201	0.0171	0.0206	0.0172								
7-O S Ronaldsay	0.0225	0.0225	0.0177	0.0211	0.0189	0.0135							
8-O Westray	0.0300	0.0293	0.0299	0.0317	0.0270	0.0203	0.0220						
9-Western	0.0156	0.0170	0.0154	0.0137	0.0164	0.0214	0.0201	0.0336					
10-South Italian	0.0304	0.0310	0.0293	0.0350	0.0341	0.0269	0.0304	0.0363	0.0263				
11-Belle Ile	0.0197	0.0170	0.0204	0.0182	0.0199	0.0203	0.0264	0.0325	0.0179	0.0273			
12-Britain	0.0201	0.0189	0.0213	0.0205	0.0221	0.0249	0.0269	0.0388	0.0185	0.0291	0.0209		
13-Outgroup	0.0213	0.0231	0.0214	0.0262	0.0248	0.0191	0.0219	0.0334	0.0200	0.0201	0.0208	0.0221	
Genetic distances	1	2	3	4	5	6	7	8	9	10	11	12	13
1-Balkan													
2-Iberian	0.0135												
3-Ireland	0.0228	0.0173											
4-Northern	0.0172	0.0109	0.0163										
5-Italian	0.0219	0.0153	0.0114	0.0150									
6-O Mainland	0.0217	0.0143	0.0038	0.0139	0.0092								
7-O S Ronaldsay	0.0246	0.0171	0.0063	0.0172	0.0125	0.0048							
8-O Westray	0.0224	0.0150	0.0035	0.0146	0.0099	0.0003	0.0045						
9-Western	0.0204	0.0138	0.0026	0.0129	0.0083	0.0019	0.0042	0.0016					

	1	2	3	4	5	6	7	8	9	10	11	12	13
10-South Italian	0.0221	0.0150	0.0095	0.0144	0.0102	0.0070	0.0099	0.0077	0.0061				
11-Belle Ile	0.0213	0.0150	0.0048	0.0139	0.0094	0.0035	0.0060	0.0033	0.0017	0.0070			
12-Britain	0.0186	0.0121	0.0176	0.0008	0.0163	0.0152	0.0185	0.0159	0.0142	0.0157	0.0152		
13-Outgroup	0.0548	0.0502	0.0582	0.0490	0.0535	0.0537	0.0595	0.0550	0.0549	0.0559	0.0540	0.0502	
Geographic distances (km)	1	2	3	4	5	6	7	8	9	10	11	12	13
1-Balkan													
2-Iberian	1916.9												
3-Ireland	2277.3	1480.0											
4-Northern	1013.2	1286.8	1265.4										
5-Italian	677.7	1323.4	1641.7	399.0									
6-O Mainland	2264.8	1956.7	582.2	1329.9	1728.2								
7-O S Ronaldsay	2249.1	1936.9	567.7	1311.7	1710.2	20.4							
8-O Westray	2280.3	1988.9	612.3	1351.5	1749.4	32.5	52.0						
9-Western	1577.0	478.4	1184.2	819.9	926.4	1575.5	1555.1	1606.5					
10-South Italian	543.0	1754.4	2477.8	1255.6	856.7	2583.2	2565.4	2603.7	1538.0				
11-Belle Ile	1780.7	663.9	857.4	875.0	1104.6	1295.2	1275.2	1327.2	336.8	1817.5			
12-Britain	1942.5	1505.2	392.6	948.8	1343.5	465.4	445.0	496.1	1110.8	2197.8	841.3		
13-Outgroup	1080.4	2979.2	3269.9	2040.8	1750.8	3139.6	3127.6	3147.7	2657.1	1306.3	2855.2	2902.9	

Table S8. Pairwise distances for skull data set

Skulls												
Procrustes distances	1	2	3	4	5	6	7	8	9	10	11	12
1-Balkan												
2-Iberian	0.0104											
3-Ireland	0.0116	0.0134										
4-Northern	0.0114	0.0157	0.0095									
5-Italian	0.0048	0.0089	0.0095	0.0096								
6-O Mainland	0.0157	0.0167	0.0097	0.0124	0.0141							
7-O S Ronaldsay	0.0127	0.0166	0.0079	0.0095	0.0120	0.0089						
8-O Westray	0.0174	0.0181	0.0135	0.0122	0.0152	0.0112	0.0145					
9-Western	0.0080	0.0103	0.0150	0.0161	0.0088	0.0186	0.0169	0.0217				
10-South Italian	0.0119	0.0170	0.0196	0.0207	0.0153	0.0219	0.0207	0.0242	0.0144			
11-Britain	0.0132	0.0167	0.0095	0.0092	0.0125	0.0098	0.0091	0.0131	0.0180	0.0196		
12-Outgroup	0.0089	0.0166	0.0175	0.0169	0.0123	0.0200	0.0177	0.0217	0.0129	0.0089	0.0165	
Genetic distances	1	2	3	4	5	6	7	8	9	10	11	12
1-Balkan												
2-Iberian	0.0135											
3-Ireland	0.0228	0.0173										
4-Northern	0.0172	0.0109	0.0163									
5-Italian	0.0219	0.0153	0.0114	0.0150								
6-O Mainland	0.0217	0.0143	0.0038	0.0139	0.0092							
7-O S Ronaldsay	0.0246	0.0171	0.0063	0.0172	0.0125	0.0048						
8-O Westray	0.0224	0.0150	0.0035	0.0146	0.0099	0.0003	0.0045					
9-Western	0.0204	0.0138	0.0026	0.0129	0.0083	0.0019	0.0042	0.0016				
10-South Italian	0.0221	0.0150	0.0095	0.0144	0.0102	0.0070	0.0099	0.0077	0.0061			
11-Britain	0.0186	0.0121	0.0176	0.0008	0.0163	0.0152	0.0185	0.0159	0.0142	0.0157		
12-Outgroup	0.0548	0.0502	0.0582	0.0490	0.0535	0.0537	0.0595	0.0550	0.0549	0.0559	0.0502	
Geographic distances (km)	1	2	3	4	5	6	7	8	9	10	11	12
1-Balkan												
2-Iberian	1916.9											

3-Ireland	2277.3	1480.0									
4-Northern	1013.2	1286.8	1265.4								
5-Italian	677.7	1323.4	1641.7	399.0							
6-O Mainland	2264.8	1956.7	582.2	1329.9	1728.2						
7-O S Ronaldsay	2249.1	1936.9	567.7	1311.7	1710.2	20.4					
8-O Westray	2280.3	1988.9	612.3	1351.5	1749.4	32.5	52.0				
9-Western	1577.0	478.4	1184.2	819.9	926.4	1575.5	1555.1	1606.5			
10-South Italian	543.0	1754.4	2477.8	1255.6	856.7	2583.2	2565.4	2603.7	1538.0		
11-Britain	1942.5	1505.2	392.6	948.8	1343.5	465.4	445.0	496.1	1110.8	2197.8	
12-Outgroup	1080.4	2979.2	3269.9	2040.8	1750.8	3139.6	3127.6	3147.7	2657.1	1306.3	2902.9

SUPPORTING INFORMATION

Appendix S3. Post-hoc results for analyses of variance of size and shape variables.

Table S9. Analysis of covariance of size among morphological groups for mandible and skull data sets

Mandibles									
Group	n	Least Squares mean[1]	SE	Lower 95%	Upper 95%	Pairwise significance[2]			
South Italian	3	2.4422	0.0315	0.0182	2.3638				D
Balkan	51	2.4017	0.0313	0.0044	2.3929			C	D
Iberian	13	2.3851	0.0297	0.0082	2.3671			C	
Western	58	2.3785	0.0492	0.0065	2.3656		B	C	
Italian	79	2.3759	0.0419	0.0047	2.3665		B	C	
Northern	146	2.3294	0.0331	0.0027	2.3239	A			
O Mainland	52	2.3856	0.0232	0.0032	2.3791			C	
Belle Île	19	2.3784	0.0143	0.0033	2.3715		B	C	
Ireland	63	2.3703	0.0376	0.0047	2.3608	A	B	C	
O Westray	40	2.3574	0.0449	0.0071	2.3430	A	B	C	
O S Ronaldsay	40	2.3359	0.0404	0.0064	2.3230	A	B		
Britain	4	2.3272	0.0369	0.0185	2.2685	A			
Outgroup	8	2.4160	0.0242	0.0085	2.3958	-	-	-	-

Skulls									
Group	n	Least Squares Mean	SE	Lower 95%	Upper 95%	Pairwise significance*			
Iberian	12	3.1276	0.0351	0.0101	3.1053				D
Italian	57	3.0953	0.0224	0.0030	3.0894		B	C	D
Western	28	3.0947	0.0172	0.0032	3.0880		B	C	
South Italian	3	3.0934	0.0166	0.0096	3.0521		B	C	
Balkan	46	3.0932	0.0274	0.0040	3.0851		B	C	
Northern	42	3.0708	0.0398	0.0061	3.0584	A	B		
O Westray	39	3.1056	0.0134	0.0021	3.1012			C	D
O S Ronaldsay	37	3.0996	0.0128	0.0021	3.0953		B	C	D
O Mainland	50	3.0991	0.0278	0.0039	3.0912		B	C	D
Ireland	60	3.0905	0.0163	0.0021	3.0863		B	C	
Britain	3	3.0481	0.0171	0.0099	3.0057	A			
Outgroup	8	3.0948	0.0199	0.0070	3.0782	-	-	-	-

[1]Groups ordered by mean size in descending order and by continental and island groups.

[2]Groups not connected by letters are significantly different.

Table S10. Post-hoc results for multivariate analyses of variance of shape variables for mandible data set

Group	1	2	3	4	5	6	7	8	9	10	11	12
1-Balkan												
2-Iberian	0.4853											
3-Ireland	0.0023	0.3747										
4-Northern	**<0.001**	0.0079	**<0.001**									
5-Italian	**<0.001**	0.0024	**<0.001**	**<0.001**								
6-O Mainland	**<0.001**	0.1117	**0.0004**	**<0.001**	**0.0004**							
7-O S Ronaldsay	**<0.001**	0.0437	**<0.001**	**<0.001**	**<0.001**	**<0.001**						
8-O Westray	**<0.001**	0.0066	**<0.001**	**<0.001**	**<0.001**	**<0.001**	0.1763					
9-Western	**<0.001**	0.0026	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**0.0003**	0.2481				
10-South Italian	0.0594	1	0.0351	**0.0009**	0.0039	0.0771	0.1364	0.2582	0.0934			
11-Belle Ile	**<0.001**	0.1292	**<0.001**	**<0.001**	**<0.001**	**0.0001**	0.0995	0.2152	0.0079	0.7736		
12-Britain	0.4531	1	0.4569	0.0378	0.1199	0.9099	0.8959	0.9414	0.8867	1	0.9919	

Significant values shown in bold (Bonferroni corrected).

Table S11. Post-hoc results for multivariate analyses of variance of shape variables for skull data set

Group	1	2	3	4	5	6	7	8	9	10	11
1-Balkan											
2-Iberian	0.0279										
3-Ireland	**<0.001**	0.0026									
4-Northern	**<0.001**	0.0059	**<0.001**								
5-Italian	0.9919	0.0058	**<0.001**	**<0.001**							
6-O Mainland	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**						
7-O S Ronaldsay	**<0.001**	**0.0006**	**<0.001**	**<0.001**	**<0.001**	**<0.001**					
8-O Westray	**<0.001**	**0.0002**	**<0.001**	**0.0001**	**<0.001**	**<0.001**	**<0.001**				
9-Western	**0.0009**	0.4016	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**	**<0.001**			
10-South Italian	0.2085	1	0.2016	0.0624	0.1061	0.0818	0.1277	0.0790	0.7271		
11-Britain	0.4506	1	0.8055	0.6768	0.3436	0.8760	0.9244	0.5953	0.5825	1	

Significant values shown in bold.