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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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Manuscripts

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3 1 **Ecogeographical patterns of morphological variation in pygmy shrews *Sorex minutus***  
4  
5 2 **(Soricomorpha: Soricinae) within a phylogeographic and continental-and-island**  
6  
7 3 **framework**  
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10 4  
11  
12 5 RODRIGO VEGA<sup>1,2,3\*</sup>, ALLAN D. MCDEVITT<sup>4</sup>, BORIS KRYŠTUFEK<sup>5,6</sup> and JEREMY B.  
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2  
3 **23 ABSTRACT**  
4

5 24 Ecogeographical patterns of morphological variation were studied in the Eurasian pygmy shrew  
6  
7 25 *Sorex minutus* to understand the species' morphological diversity in a continental and island  
8  
9 26 setting, and within the context of previous detailed phylogeographic studies. In total, 568  
10  
11 27 mandibles and 377 skulls of *S. minutus* from continental and island populations from Europe  
12  
13 28 and Atlantic islands were examined using a geometric morphometrics approach, and the  
14  
15 29 general relationships of mandible and skull size and shape with geographical and environmental  
16  
17 30 variables was studied. Samples were then pooled into predefined geographical groups to  
18  
19 31 evaluate the morphological differences among them using analyses of variance, to contrast the  
20  
21 32 morphological and genetic relationships based on morphological and genetic distances and  
22  
23 33 ancestral state reconstructions, and to assess the correlations of morphological, genetic and  
24  
25 34 geographic distances with Mantel tests. We found significant relationships of mandible size with  
26  
27 35 geographic and environmental variables, fitting the converse Bergmann's rule; however, for  
28  
29 36 skull size this was less evident. Continental groups of *S. minutus* could not readily be  
30  
31 37 differentiated from each other by shape. Most island groups of *S. minutus* were easily  
32  
33 38 discriminated from the continental groups by being larger, indicative of an island effect.  
34  
35 39 Moreover, morphological and genetic distances differed substantially, and again island groups  
36  
37 40 were distinctive morphologically. Morphological and geographical distances were significantly  
38  
39 41 correlated, but not so the morphological and genetic distances indicating that morphological  
40  
41 42 variation does not reflect genetic subdivision in *S. minutus*. Our analyses showed that  
42  
43 43 environmental variables and insularity had important effects on the morphological differentiation  
44  
45 44 of *S. minutus*.  
46  
47 45

53 46 **ADDITIONAL KEYWORDS:** Bergmann's rule – environmental correlates – geometric  
54  
55 47 morphometrics – island rule – morphological evolution – resource rule – small mammal.  
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## 48 INTRODUCTION

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

53 Two of the best-known ecogeographical rules are Bergmann's rule and the island rule. In its  
54 original form, Bergmann's rule states that warm-blooded vertebrate species (or races or  
55 populations within a species) from cooler climates tend to be larger than congeners from  
56 warmer climates (Bergmann, 1847; Blackburn, Gaston & Loder, 1999). This vaguely defined  
57 rule, later reformulated to refer to populations within species or to species in a monophyletic  
58 higher taxon, describes a positive relationship between body size and latitude (Mayr, 1963;  
59 Blackburn *et al.*, 1999; Meiri, 2011). The island rule predicts an increase of body size for small  
60 mammals (gigantism) and a decrease of body size for large mammals (dwarfism) in island  
61 populations compared to mainland populations (Van Valen, 1973). Although it has been argued  
62 that Bergmann's rule is a valid generalisation (Ashton, Tracy & Queiroz, 2000; Meiri & Dayan,  
63 2003), there are species data showing the opposite trend (the converse Bergmann's rule) and a  
64 lack of support (non-significant results) from a large number of species [see Ashton *et al.* (2000)  
65 and Meiri & Dayan (2003)]. Likewise, the validity of the island rule has been questioned  
66 because most studies have used poor size indices, very large islands or mainland populations  
67 only distantly related to the island populations (Lomolino, 2005; Meiri, Dayan & Simberloff,  
68 2006; Meiri, Cooper & Purvis, 2008), and because there is a large number of studies that show  
69 evidence against it (Raia & Meiri, 2006; Meiri *et al.*, 2008; Meiri, Raia & Phillimore, 2011).  
70 Furthermore, McNab (2010) argued that geographic patterns in size variation should not be  
71 subdivided into different ecological rules, but rather considered as aspects of the same  
72 phenomenon concerning the differential allocation of energy and physiological responses to  
73 resource availability.

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2  
3 74 Considering the controversy associated with these ecogeographical patterns, more  
4  
5 75 comprehensive intra- and interspecific studies are needed to determine their validity and basis  
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7 76 (Lawlor, 1982; Lomolino, 2005; Gaston *et al.*, 2008; Meiri *et al.*, 2008). This includes careful  
8  
9 77 attention to anomalous findings because they may reflect distinctive features that point to causal  
10  
11 78 explanations, or the use of combined approaches important for developing an integrative  
12  
13 79 understanding of biogeographic patterns and generation of hypotheses (Lomolino *et al.*, 2006).

16 80 In this study, we use the Eurasian pygmy shrew *Sorex minutus* (Linnaeus, 1766;  
17  
18 81 Soricomorpha: Soricinae) as a model species for investigating different ecogeographical  
19  
20 82 patterns along geographic, climatic and environmental gradients in continental and insular  
21  
22 83 settings, and in a phylogeographic context. *S. minutus* has a broad geographic distribution in  
23  
24 84 continental Eurasia, from Lake Baikal in Siberia to Southern, Central and Northern Europe, and  
25  
26 85 in the British Isles (Mitchell-Jones *et al.*, 1999). It is found in very different habitats such as  
27  
28 86 alpine and northern tundra, forests, shrub lands, swamps, heaths and grasslands (Hutterer,  
29  
30 87 1990). The phylogeographic history has been thoroughly studied. Six mitochondrial (mt) DNA  
31  
32 88 lineages with discrete geographic distributions have been described (Mascheretti *et al.*, 2003,  
33  
34 89 McDevitt *et al.*, 2010, 2011; Vega *et al.*, 2010a,b), with support from Y-chromosome markers  
35  
36 90 (McDevitt *et al.*, 2010, 2011): four Southern European lineages distributed within the three  
37  
38 91 European Mediterranean peninsulas, namely the 'Iberian', 'Italian', 'South Italian' and 'Balkan'; a  
39  
40 92 'Northern' clade distributed from Lake Baikal to Central and Northern Europe, and also found in  
41  
42 93 Britain; and a 'Western' clade found in the Pyrenees, Northern Spain (Cantabria Mountain  
43  
44 94 Range), Western France, Ireland and in the periphery of Britain and islands off the western and  
45  
46 95 northern coast of Britain forming a 'Celtic fringe' (Searle *et al.*, 2009; McDevitt *et al.*, 2011). The  
47  
48 96 Northern and Western lineages colonised Britain sometime after the Last Glacial Maximum over  
49  
50 97 the land bridge with continental Europe (Vega *et al.*, 2010a; McDevitt *et al.*, 2011), and the  
51  
52 98 Western lineage colonised Ireland within the last 10,000 years via a human-mediated  
53  
54 99 introduction (McDevitt *et al.*, 2009, 2011).

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2  
3 100 We explored the following questions: 1) What is the morphological diversity of *S.*  
4  
5 101 *minutus* throughout its European range; in particular, are there geographic, climatic and/or  
6  
7 102 environmental patterns in continental Europe and/or relating to island occupancy in the British  
8  
9 103 Isles? 2) To what extent does the morphological diversity in continental Europe and the British  
10  
11 104 Isles resemble the phylogeographic pattern detected with molecular markers? To study these  
12  
13 105 questions, we used a geometric morphometric approach (Rohlf & Marcus, 1993) combined with  
14  
15 106 environmental and phylogeographic information to investigate the biogeography of *S. minutus*,  
16  
17 107 one of the many small mammals that are widespread in Europe but for which there has been  
18  
19 108 remarkably little effort to document or understand their non-molecular geographic variation  
20  
21 109 using modern methodologies.  
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23

24  
25 110 Geometric morphometrics is a method for the study of form (the shape and size of an  
26  
27 111 object) based on Cartesian landmark coordinates, where the geometry of the configuration of  
28  
29 112 landmarks is preserved throughout the analysis (Zelditch *et al.*, 2004; Mitteroecker & Gunz,  
30  
31 113 2009). Combined with genetic, ecological, environmental and taxonomical information,  
32  
33 114 geometric morphometrics is an exceptionally powerful tool for studying intraspecific variation  
34  
35 115 (Loy, 1996; Zelditch *et al.*, 2004; Nogueira, Peracchi & Monteiro, 2009; Vega *et al.*, 2010b) and  
36  
37 116 has great potential for our understanding of ecogeographical patterns.  
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## 42 118 **MATERIALS AND METHODS**

### 43 119 **COLLECTION AND DIGITISATION OF SAMPLES**

44  
45  
46 120 We acquired *S. minutus* specimens from our own fieldwork ethically collected (Sikes *et al.*  
47  
48 121 2011), from owl pellets and from museum and private collections (Appendix S1, Table S1). In  
49  
50 122 total, we analysed 568 mandibles and 377 skulls from continental and island sites in Europe  
51  
52 123 (Fig. 1). Photographic images of the external side of left hemi-mandibles and the left half of the  
53  
54 124 ventral side of skulls were taken using a digital camera at a fixed distance. Mandibles were  
55  
56 125 placed flat under the camera lens. Skull samples were placed on a purpose-built polystyrene  
57  
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1  
2  
3 126 and Plasticine cradle leaving the ventral side parallel to the lens, judged by eye. A small piece of  
4  
5 127 graph paper was included as a scale in each photograph and the sample was placed in the  
6  
7 128 middle of the image area to avoid parallax.  
8  
9

10 129 Morphological analyses on the mandible and skull data sets were carried out using the  
11  
12 130 'tps-Series' software (by F.J. Rohlf, available at <http://life.bio.sunysb.edu/morph/>). Eighteen  
13  
14 131 landmarks were placed on the external side of left hemi-mandibles and 19 landmarks were  
15  
16 132 placed on the left half of the ventral side of skulls using tpsDig2 (Appendix S1, Fig. S1). The  
17  
18 133 selected landmarks provided a comprehensive sampling of the morphology of the biological  
19  
20 134 structures under study (Zelditch *et al.*, 2004).  
21  
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23

## 24 136 **MORPHOMETRIC ANALYSIS OF MANDIBLES AND SKULLS**

25  
26  
27 137 The size of each mandible and skull was estimated as the Centroid Size (CS) obtained with  
28  
29 138 tpsRelw and was transformed with natural logarithms. CS is a convenient estimator for size  
30  
31 139 used commonly in geometric morphometric studies (Bookstein, 1996; Slice *et al.*, 1996; Frost *et*  
32  
33 140 *al.*, 2003); it is uncorrelated with shape in the absence of allometry (Zelditch *et al.*, 2004) and it  
34  
35 141 is often highly correlated with body mass (Frost *et al.*, 2003). The landmark configurations were  
36  
37 142 aligned, translated, rotated and scaled to unit CS using Generalised Procrustes Analysis (GPA),  
38  
39 143 and the Procrustes coordinates and average landmark configuration were obtained (Rohlf &  
40  
41 144 Slice, 1990). The Procrustes distances to the average configuration and pairwise Procrustes  
42  
43 145 distances among samples (Zelditch *et al.*, 2004) were computed, approximated to a Euclidean  
44  
45 146 space using an orthogonal projection and used as a measurement of morphometric distances.  
46  
47

48  
49 147 **The significance of allometry (change in shape associated with size differences) was**  
50  
51 148 **tested for the continental and island groups separately for mandibles and skulls with multivariate**  
52  
53 149 **regressions using MorphoJ (Klingenberg, 2011). Allometry was significant in continental and**  
54  
55 150 **island groups for mandibles and skulls; therefore, the regression slopes between groups were**  
56  
57 151 **then compared with MANCOVA in tpsRegr and were not statistically significant (data not shown)**  
58  
59  
60



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3 152 (Viscosi & Cardini, 2011). To control for allometric effects on mandible and skull shape  
4  
5 153 variables, we performed multivariate regressions using MorphoJ and kept the residuals as  
6  
7 154 allometry-free shape variables for further analysis. We performed a Principal Components  
8  
9 155 Analysis (PCA) in JMP version 10 (SAS Institute, Cary, NC, USA) on the shape variables and  
10  
11 156 kept 16 and 17 PCs for mandibles and skulls, respectively, which explained  $\geq 1\%$  of total shape  
12  
13 157 variation. We also carried out a variety of other preliminary analyses including landmark  
14  
15 158 placement repeatability, sexual dimorphism and a test for phylogenetic signal (see Supporting  
16  
17 159 Information for details).  
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19  
20  
21 160

## 161 GENERAL ECOGEOGRAPHICAL PATTERNS

22  
23 162 For each specimen we determined geographical data including latitudinal and longitudinal  
24  
25 163 coordinates from fieldwork and museum records, and digital elevation data from the Consortium  
26  
27 164 for Spatial Information at a 90 arc-minute resolution (available at <http://srtm.csi.cgiar.org>). Data  
28  
29 165 for climatic variables (taken from the 1950-2000 period) were obtained from WorldClim  
30  
31 166 (available at <http://www.worldclim.org/>) at a 2.5 arc-minute resolution using DIVA-GIS version  
32  
33 167 7.4.0.1 (available at <http://www.diva-gis.org/>), including annual trends variables and extreme or  
34  
35 168 limiting environmental variables: annual mean temperature (BIO1), maximum temperature of the  
36  
37 169 warmest period (BIO5), minimum temperature of the coldest period (BIO6), annual precipitation  
38  
39 170 (BIO12), precipitation of the wettest period (BIO13), precipitation of the driest period (BIO14),  
40  
41 171 precipitation of the warmest quarter (BIO18) and precipitation of the coldest quarter (BIO19).  
42  
43 172 Seasonal variables (annual range in temperature and precipitation) were excluded because they  
44  
45 173 are composite climatic variables [e.g. BIO7 = temperature annual range (BIO5-BIO6)] and  
46  
47 174 would only complicate the interpretation of the results. We also obtained terrestrial net primary  
48  
49 175 production (NPP) values from MODIS GPP/NPP (MOD17) at 1 km resolution from 2000 through  
50  
51 176 2009 (Zhao & Running, 2010). NPP is an environmental variable that quantifies the amount of  
52  
53 177 atmospheric carbon fixed by plants and accumulated as biomass. In total, we obtained data for  
54  
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1  
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3 178 12 geographic, climatic and environmental variables, and for simplicity they are called  
4  
5 179 'environmental variables' throughout.  
6

7  
8 180 Because combinations of the 12 environmental variables showed correlations with each  
9  
10 181 other, we performed a PCA using JMP on these variables and kept the first three environmental  
11  
12 182 PCs for further analysis. PC1, PC2 and PC3 had eigenvalues  $\geq 1.0$  and together explained  
13  
14 183 more than 80% of the variation for the environmental data sets (Appendix S1, Tables S2 and  
15  
16 184 S3). The eigenvector matrices showed that: 1) PC1 was loaded with positive eigenvectors for all  
17  
18 185 precipitation variables; low values indicate low precipitation mostly found in the central regions  
19  
20 186 of the Iberian peninsula, eastern parts of the Balkan peninsula but also in central-northern  
21  
22 187 regions in Europe, while high values indicate high precipitation mostly found in the western  
23  
24 188 coast of Ireland and in some areas of the Alps. 2) PC2 was loaded with a combination of  
25  
26 189 negative eigenvectors for latitude and minimum temperature of the coldest period, and positive  
27  
28 190 eigenvectors for longitude and altitude; low values indicate high latitude, low altitude and  
29  
30 191 moderate temperatures during winter mostly found in central and western regions of continental  
31  
32 192 Europe and in the Atlantic islands, while high values indicate high altitude, low latitude, high  
33  
34 193 longitude and relatively low temperatures during winter mostly found in central and eastern  
35  
36 194 regions like in the Balkan peninsula and in mountain areas of the Italian peninsula. 3) PC3 was  
37  
38 195 loaded with a combination of negative eigenvectors for latitude and positive eigenvectors for  
39  
40 196 annual mean temperature, maximum temperature of the warmest period and NPP; low values  
41  
42 197 indicate colder climate and moderate productivity from high latitudes, while high values indicate  
43  
44 198 warmer climate and higher productivity mostly found in central latitudes.  
45  
46  
47

48  
49 199 Several statistical analyses were done on size and shape variables for the mandible and  
50  
51 200 skull data sets. Using a Standard Least Squares approach in JMP, we performed multiple  
52  
53 201 regressions of size on latitude, altitude and annual mean temperature (typical variables used to  
54  
55 202 study Bergmann's rule) for the mandible and skull data sets. Because Bergmann's rule and the  
56  
57 203 island rule may be better explored using biologically relevant environmental variables, we  
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3 204 performed multiple regressions of size and shape on the three environmental PC for the  
4  
5 205 mandible and skull data sets. This approach was used to see the effects of each variable on  
6  
7 206 size but controlling for the effects of the other variables. The significance of the models and of  
8  
9 207 each variable was obtained with ANOVAs comparing the fitted model to a simple mean model.  
10  
11 208 Moreover, size differences between continental and island samples for the mandible and skull  
12  
13 209 data sets were estimated with ANCOVA in JMP using the three environmental PCs as  
14  
15 210 covariates after testing for homogeneity of slopes.  
16  
17

18 211 To evaluate the environmental effects on mandible and skull shape, and to estimate how  
19  
20 212 well the variation in shape can be predicted by environmental variables, we did multivariate  
21  
22 213 multiple regression analysis of shape variables on the three environmental PCs using JMP.  
23  
24 214 Two-Block Partial Least Squares analysis was conducted in JMP to describe the covariation  
25  
26 215 between the geographical (latitude, longitude, altitude), climatic (WorldClim) and NPP variables  
27  
28 216 with the variation in shape (Appendix S1, Tables S4 and S5). In Two-Block Partial Least  
29  
30 217 Squares analysis linear combinations of the predictors are extracted with the objective of  
31  
32 218 explaining as much of the variation in each response variable as possible, but accounting for  
33  
34 219 variation in the predictors.  
35  
36

37  
38 220 The mandible and skull photographs, landmark coordinates (in TPS format) and the  
39  
40 221 environmental variables for all samples are available from DRYAD ([doi: upon acceptance](#)).  
41  
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## 45 223 GENETIC ANALYSES

46 224 A total of 519 *cyt b* sequences of *S. minutus* were obtained from GenBank (AB175132,  
47  
48 225 AJ535393-AJ535457, GQ494305-GQ494305, GQ272492-GQ272518, JF510321-JF510376). A  
49  
50 226 sequence of *S. volnuchini* (AJ535458) from Anatolia was used as the outgroup (Fumagalli *et al.*,  
51  
52 227 1999). DNA sequences were edited in BioEdit version 7.0.9.0 (Hall, 1999) and aligned by eye.  
53  
54 228 The phylogenetic relationships within *S. minutus* were inferred by Bayesian analysis as in Vega  
55  
56 229 *et al.* (2010a). The lineages found were the same as in previous phylogeographic studies (*e.g.*  
57  
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60

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2  
3 230 Mascheretti *et al.*, 2003; McDevitt *et al.*, 2010, 2011; Vega *et al.*, 2010a, b) and were used as  
4  
5 231 phylogroups for further analysis.  
6

7  
8 232 With DnaSP version 5.10 (Librado & Rozas, 2009), we calculated the corrected net  
9  
10 233 number of nucleotide substitutions between pairs of phylogroups (Da), which represent the  
11  
12 234 proportional sequence divergence among them (Nei, 1987). The pairwise divergence values  
13  
14 235 (Da) among previously identified phylogroups were used for statistical comparison with the  
15  
16 236 morphometric data. We used the matrix of pairwise Da values to construct a Neighbour-Joining  
17  
18 237 (NJ) tree with MEGA version 4 (Tamura *et al.*, 2007) to depict the evolutionary distances and  
19  
20 238 relationships between the phylogroups.  
21

22  
23 239

## 24 240 **ECOGEOGRAPHICAL PATTERNS IN GEOGRAPHICAL GROUPS**

25  
26  
27 241 To analyse size and shape differences in *S. minutus* among regions in a phylogeographic  
28  
29 242 context, we pooled the mandible and skull samples into 12 and 11 mutually exclusive  
30  
31 243 geographical groups, respectively, according to their *cyt b* phylogroup membership (if DNA data  
32  
33 244 were available from samples used in other studies) or to their known geographical origin (Fig.  
34  
35 245 1). The groups were designated as: 'Iberian', 'Italian', 'South Italian', 'Balkan', 'Northern' and  
36  
37 246 'Western'. Island groups were identified separately as 'Ireland', 'Orkney Mainland', 'Orkney  
38  
39 247 Westray', 'Orkney South Ronaldsay', 'Belle Île' (not available for skulls) and 'Britain'.  
40  
41

42 248 We performed multiple regressions of size on the three environmental PCs using a  
43  
44 249 Standard Least Squares approach in JMP to determine the differences among the geographical  
45  
46 250 groups while controlling for the effects of each predictor variable. Mandible and skull size  
47  
48 251 differences among the groups were evaluated by ANCOVA followed by Tukey–Kramer post-hoc  
49  
50 252 tests as it allows for unequal sample size (Sokal & Rohlf, 1995).  
51

52  
53 253 Mandible and skull shape differences among the groups were evaluated with MANOVAs  
54  
55 254 on the allometry-free shape variables (16 for mandibles and 17 for skulls), followed by Hotelling  
56  
57 255  $T^2$  tests for multivariate comparisons performed in PAST version 2.17 (Hammer, Harper & Ryan,  
58  
59  
60

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2  
3 256 2001). Shape changes were visualised as thin-plate spline transformation grids (Zelditch *et al.*,  
4  
5 257 2004) computed with tpsSpln. Canonical Variate Analyses (CVA) using the shape variables as  
6  
7 258 predictors were performed in JMP to differentiate among the groups for the mandible and skull  
8  
9  
10 259 data sets. The first two CVs were used to graph the samples separated by group membership  
11  
12 260 (Appendix S1, Table S6). Discriminant Function Analyses (DFA) were performed in JMP to  
13  
14 261 estimate group membership of the mandible and skull data sets using linear combinations of the  
15  
16 262 predictor variables that best discriminate between the groups. The leave-one-out (jackknife) with  
17  
18 263 cross-validation approach was used to validate the DFA (Cardini *et al.*, 2009). Results were  
19  
20 264 averaged among three runs using a random subset of 70% of the samples from each group for  
21  
22 265 training the model and 30% for testing. The number of discriminant functions used for analysis  
23  
24 266 equalled the number of groups ( $K = 12$  or  $K = 11$ ) minus 1.

27 267 The Procrustes distances among the average configurations of the groups (including the  
28  
29 268 outgroup), for the mandible and skull data sets, were computed with tpsSmall and entered into  
30  
31 269 PAST to produce distance matrices and distance trees using the NJ method to evaluate the  
32  
33 270 morphological relationships. The geographic midpoints for the groups were calculated with the  
34  
35 271 Geographic Midpoint Calculator (available at <http://www.geomidpoint.com/>), and were used to  
36  
37 272 obtain the pairwise geographic distances among them with the Geographic Distance Matrix  
38  
39 273 Calculator version 1.2.3 (by P.J. Ersts, available at  
40  
41 274 [http://biodiversityinformatics.amnh.org/open\\_source/gdmg](http://biodiversityinformatics.amnh.org/open_source/gdmg)). Mantel tests were performed in  
42  
43 275 PAST on pairwise Procrustes and geographic distances among the groups, and on pairwise  
44  
45 276 Procrustes distances among the groups and pairwise genetic divergence ( $D_a$ ) values of the *cyt*  
46  
47 277 *b* phylogroups. In addition, we did a partial Mantel test of Procrustes distances and geographic  
48  
49 278 distances, but controlling for genetic distance. The significance of the tests was obtained by a  
50  
51 279 permutation procedure with 10,000 bootstraps. Mandible and skull CS and Procrustes distances  
52  
53 280 were mapped onto the NJ tree of *cyt b* phylogroups using squared-change parsimony in  
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3 281 Mesquite 2.75 (Maddison & Maddison 2011) to show size and shape evolution using eight  
4  
5 282 categorical bins.  
6  
7  
8 283

## 9 284 RESULTS

### 10 285 GENERAL ECOGEOGRAPHICAL PATTERNS

11  
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13  
14 286 The results from multiple regressions of size on latitude, altitude and annual mean temperature),  
15  
16 287 or on environmental variables (PC1, PC2 and PC3) are summarised in Table 1 (see also  
17  
18 288 Appendix S1, Table S3). Typical Bergmann's rule variables statistically predicted mandible size,  
19  
20 289 but the data contains a high amount of unexplained variability ( $F_{4, 563} = 5.274$ ,  $P < 0.001$ ,  $R^2 =$   
21  
22 290 0.036). Latitude was negatively related with size, and annual mean temperature did not  
23  
24 291 contribute significantly to the model. Environmental variables statistically predicted mandible  
25  
26 292 size also with a high amount of unexplained variability ( $F_{4, 563} = 4.179$ ,  $P = 0.02$ ,  $R^2 = 0.029$ ). All  
27  
28 293 variables were positively related with size and contributed significantly to the model. On  
29  
30 294 average, continental samples showed significantly larger mandible size than island samples ( $F$   
31  
32 295 = 6.204,  $P = 0.013$ ) mostly driven by the larger mandible size of southern samples from  
33  
34 296 continental Europe. Typical Bergmann's rule variables statistically predicted skull size, and the  
35  
36 297 model explained more variability than in the mandible data set ( $F_{4, 372} = 31.155$ ,  $P < 0.001$ ,  $R^2 =$   
37  
38 298 0.251). Annual mean temperature did not contribute significantly to the model and latitude only  
39  
40 299 marginally so. Environmental variables statistically predicted skull size with a high amount of  
41  
42 300 unexplained variability ( $F_{4, 372} = 4.1$ ,  $P = 0.03$ ,  $R^2 = 0.042$ ), and only PC1 contributed significantly  
43  
44 301 to the model. On average, island samples showed marginally significant larger skull size than  
45  
46 302 continental samples ( $F = 4.661$ ,  $P = 0.031$ ).

47  
48  
49  
50 303 Environmental variables had small but significant effects on allometry-free shape of  
51  
52 304 mandibles and skulls, and together accounted for 5.1% and 11.9% of mandible and skull shape  
53  
54 305 variation, respectively (Table 2). PC3 explained the highest percentage of shape variation in  
55  
56 306 both data sets. With the Two-Block Partial Least Squares analysis, 10 and 9 factors were  
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1  
2  
3 307 extracted which explained 13.6% and 18.4% of mandible and skull shape variation, respectively  
4  
5 308 (Appendix S1, Tables S4 and S5).  
6

7  
8 309

## 9 310 **GENETIC ANALYSES**

11 311 There were 303 *cyt b* haplotypes for *S. minutus* that clustered into six main phylogroups  
12  
13 312 (Mascheretti *et al.*, 2003; McDevitt *et al.*, 2010, 2011; Vega *et al.*, 2010a, b). We distinguished  
14  
15 313 the following continental phylogroups for comparison with the morphological data (Fig. 3):  
16  
17 314 'Northern' (n = 101), which included samples from Central and Northern Europe to Lake Baikal  
18  
19 315 in Siberia. 'Italian' (n = 26), mostly restricted to the northern and central parts of the Italian  
20  
21 316 peninsula. 'Western' (n = 15), which included samples from the Cantabrian Mountains, the  
22  
23 317 Pyrenees and Western France. 'South Italian' (n = 4), geographically restricted to La Sila  
24  
25 318 Mountain, Calabria in Southern Italy. 'Iberian' (n = 3), geographically restricted to the Iberian  
26  
27 319 peninsula. 'Balkan' (n = 4), which included samples from Macedonia and Turkish Thrace in the  
28  
29 320 Balkan peninsula. We also distinguished the following island groups (Fig. 3): 'Ireland' (n = 94),  
30  
31 321 'Orkney Mainland' (n = 44), 'Orkney Westray' (n = 33), 'Orkney South Ronaldsay' (n = 40) and  
32  
33 322 'Belle Île' (n = 5) which clustered within the Western clade, and 'Britain' (n = 91) which clustered  
34  
35 323 within the Northern clade. Other samples (n = 59) clustered in the Western clade in the  
36  
37 324 molecular studies but were not used here because they belong to islands in the periphery of  
38  
39 325 Britain from where there were no morphological samples for comparison. Pairwise divergence  
40  
41 326 (*Da*) values among the phylogroups are shown in Appendix S2, Tables S7 and S8. The South  
42  
43 327 Italian, Iberian and Balkan groups and the outgroup showed the highest pairwise *Da* values,  
44  
45 328 whilst pairwise *Da* values among the Western, Irish and Orkney islands groups were the lowest.  
46  
47  
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51 329

## 52 330 **ECOGEOGRAPHICAL PATTERNS IN GEOGRAPHICAL GROUPS**



1  
2  
3 331 While controlling for environmental factors, we found significant size differences among groups  
4  
5 332 for the mandible and skull data sets (mandibles:  $F_{11, 556} = 24.186$ ,  $P < 0.001$ ; skulls:  $F_{10, 366} =$   
6  
7 333  $8.658$ ,  $P < 0.001$ ; Appendix S3, Table S9).

9  
10 334 For mandible and skull size, there were latitudinal trends converse to Bergmann's rule  
11  
12 335 among the continental groups, and island effects for the island groups (Fig. 2A, B). The South  
13  
14 336 Italian, Iberian and Balkan groups, belonging to the southernmost latitudes, had the largest  
15  
16 337 mandibles among the continental groups. The Northern group had the smallest mandible of all  
17  
18 338 continental groups, and it was significantly different from all other continental groups, but not  
19  
20 339 significantly different from some island groups. The Orkney Mainland group, although at a high  
21  
22 340 latitude, had the largest mandible of all island groups, but only significantly different from Orkney  
23  
24 341 South Ronaldsay. All other island groups had comparable mandible sizes to those found in  
25  
26 342 continental groups, but larger than expected by latitude. The skull data set showed less  
27  
28 343 variation in size among the groups than the mandible data set, but also had a decreasing size  
29  
30 344 tendency with increasing latitude. The Iberian group had the largest skulls of the continental  
31  
32 345 samples. The Northern group had the smallest skulls on average, as in the mandible data set,  
33  
34 346 but this group was only significantly different in size from the Iberian and Orkney Westray  
35  
36 347 groups. Notably, the skulls from the Orkney islands were as large as the ones from the southern  
37  
38 348 groups and larger than the ones from the northern group, indicative of an island effect even  
39  
40 349 controlling for the latitudinal effect. The results relating to South Italy and Britain should be taken  
41  
42 350 with caution because of low sample size, but they are still indicative of the size trends in these  
43  
44 351 two areas.

45  
46 352 The MANOVAs on allometry-free shape variables of mandibles and skulls showed  
47  
48 353 significant differences among the groups (mandibles: Wilks'  $\lambda = 0.1954$ ,  $F_{176, 4959} = 5.521$ ,  $P <$   
49  
50 354  $0.001$ ; skulls: Wilks'  $\lambda = 0.0415$ ,  $F_{170, 3056} = 5.319$ ,  $P < 0.001$ ; Appendix S3, Tables S10 and  
51  
52 355 S11). Based on thin-plate splines (Fig. 3A, B), shape variation was small and mostly evident  
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1  
2  
3 356 between the southern groups and the Orkney islands. In southern latitudes and in larger  
4  
5 357 mandibles there was a relative forward movement of the landmarks on the lower part of the  
6  
7 358 mandible (landmarks 1 and 16 – 18) in relation to the landmarks between teeth alveoli  
8  
9  
10 359 (landmarks 3 – 8), and a relative forward shift of the coronoid process (Fig. 3A). The three  
11  
12 360 groups from the Orkney islands had notable backward shifts of the coronoid process in  
13  
14 361 comparison to other groups, with Westray also showing pronounced variation in the frontal part  
15  
16 362 of the mandible, whereas in the Iberian and Balkan groups the coronoid process moved slightly  
17  
18 363 forward (Fig. 3A). In southern latitudes and in larger skulls, there was an outward movement of  
19  
20 364 landmarks 2 and 7 in relation to other landmarks between teeth alveoli (landmarks 3 – 6, 8 and  
21  
22 365 9), and opposite movements of landmarks 16 and 17 (Fig. 3B). This generally resulted in a  
23  
24 366 wider separation of the upper premolars, less pointed snouts, and smaller foramen magnum  
25  
26 367 compared to skulls from northern latitudes (Fig. 3B).

27  
28  
29 368 The first two CVs explained 69.6% and 62.2% of total shape variation among groups in  
30  
31 369 the mandible and skull data sets, respectively (Appendix S1, Table S6). For purposes of  
32  
33 370 visualisation, scatter plots of the first two CVs are presented with group memberships for  
34  
35 371 mandibles (Fig. 4A) and skulls (Fig. 4B). In both data sets, the shape distribution of the  
36  
37 372 continental groups mostly overlapped, while Ireland and the Orkney islands could be  
38  
39 373 discriminated. Westray was the island group most easily discriminated, in accordance with the  
40  
41 374 large Procrustes distances and shape variation found in the mandible and skull data sets. Belle  
42  
43 375 Île (mandible data set only) and Britain (mandibles and skull data sets) could not be  
44  
45 376 differentiated from the continental samples. With the DFA, we classified correctly on average  
46  
47 377 44.9% and 54.6% of the individuals to their predefined group of mandibles and skulls,  
48  
49 378 respectively; however, this was mostly due to low classification scores for the continental  
50  
51 379 groups. The classification scores in the mandible and skull data sets were high the Orkney  
52  
53 380 islands groups in agreement with its notable shape differences.  
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1  
2  
3 381 There were different topologies among the phylogenetic tree and the Procrustes  
4  
5 382 distances trees of mandibles and skulls (Fig. 5). For mandible and skull shape, the South Italian  
6  
7 383 group is the first to split from the rest, and Orkney Westray shows the highest shape distance of  
8  
9 384 all groups (Fig. 5A, B). Intraspecific variation in size and shape, mapped using squared change  
10  
11 385 parsimony and visualized on the NJ tree of phylogroups (based on Da), showed no apparent  
12  
13 386 relationship of size and shape with phylogenetic history of *S. minutus* (Fig. 5C-F). The Mantel  
14  
15 387 tests revealed that there were significant positive correlations between Procrustes and  
16  
17 388 geographic distances of mandible ( $R = 0.2653$ ,  $P = 0.0471$ ) and skull groups ( $R = 0.6019$ ,  $P =$   
18  
19 389  $0.0004$ ). However, the correlations between Procrustes and genetic distances were not  
20  
21 390 significant for mandible ( $R = -0.0827$ ,  $P = 0.5978$ ) and skull groups ( $R = -0.2189$ ,  $P = 0.8869$ ).  
22  
23 391 While controlling for genetic distances, partial Mantel tests also revealed significant correlations  
24  
25 392 among Procrustes and geographic distances for mandible ( $R = 0.2935$ ,  $P = 0.0360$ ) and skull  
26  
27 393 groups ( $R = 0.6818$ ,  $P < 0.0001$ ). Pairwise geographic and Procrustes distances among  
28  
29 394 mandible and skull groups are shown in Appendix S2, Tables S7 and S8.  
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## 396 DISCUSSION

### 397 CONTINENTAL DIFFERENTIATION IN *SOREX MINUTUS*

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

403 For *S. minutus*, the significant negative relationship of mandible size with latitude, and  
404 the larger mandible and skull size in southern than in northern continental groups indicate a  
405 pattern converse to Bergmann's rule. Using PC of geographical and environmental variables  
406 shows a more complex basis to the size trends in *S. minutus* than purely an impact of latitude,

1  
2  
3 407 altitude or temperature. PC1, PC2 and PC3, loaded with various combinations of latitude,  
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5 408 longitude, temperature and precipitation variables and NPP consistently showed a positive  
6  
7 409 relationship with mandible size, but only PC1 showed a positive relationship with skull size. We  
8  
9 410 concur with McNab (2010) that an emphasis in relation to Bergmann's rule may be unhelpful,  
10  
11 411 and that the size trends relate to the availability of resources in a broad sense, which in turn  
12  
13 412 relates to various underlying environmental factors.

14  
15  
16 413 The converse Bergmann's rule has frequently been reported in shrews and may be a  
17  
18 414 common trend within Soricidae [for exceptions see White & Searle (2007) who found  
19  
20 415 Bergmann's rule in *S. araneus* from British islands, and Ochocińska & Taylor (2003) who  
21  
22 416 showed non-significant relationships of size with latitude for *S. isodon* and *S. tundrensis*].  
23  
24  
25 417 Accordingly, the condylobasal skull lengths of *S. araneus*, *S. caecutiens* and *S. minutus* from  
26  
27 418 the Palearctic region relate negatively to latitude (Ochocińska & Taylor, 2003). Three mainland  
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29 419 populations of *S. trowbridgii* from Western USA have decreasing cranial and mandibular  
30  
31 420 dimensions with increasing latitude (Carraway & Verts, 2005) and variation in body size of *S.*  
32  
33 421 *cinereus* in Alaska contradicts Bergmann's rule (Yom-Tov & Yom-Tov, 2005). Morphological  
34  
35 422 measurements of *Neomys anomalus* from Eastern Europe and the Balkans also relate  
36  
37 423 negatively to latitude but show evidence of character displacement when in sympatry with *N.*  
38  
39 424 *fodiens* (Kryštufek & Quadracci, 2008). The northern short-tailed shrew (*Blarina brevicauda*) has  
40  
41 425 a negative albeit non-significant relationship of size with latitude (Ashton *et al.*, 2000).  
42  
43  
44 426 Consistent with converse Bergmann's rule, size in *N. anomalus* and *N. fodiens* from Poland was  
45  
46 427 the smallest in the north and largest in the south when in sympatry, but when in allopatry both  
47  
48 428 species were larger at northern latitudes, showing the opposite pattern (Rychlik, Ramalhinho &  
49  
50 429 Polly, 2006).

51  
52  
53 430 Regarding shape patterns, environmental variables (reflected in the first three PCs)  
54  
55 431 explained small percentages of total shape variation (5.1% and 11.9% for mandibles and skulls,  
56  
57 432 respectively). It is not surprising that so much shape variation remained unexplained because  
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2  
3 433 other exogenous and endogenous factors may be playing important roles. Based on the CVA,  
4  
5 434 evolution on islands maybe a contributing factor. In a similar ecogeographical study on the  
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7 435 primate *Cercopithecus aethiops* from sub-Saharan Africa, the response of skulls to climatic  
8  
9 436 variables was stronger for size than for shape despite the evident intraspecific geographical  
10  
11 437 differences, and approximately 80% of shape variance remained unexplained (Cardini, Jansson  
12  
13 438 & Elton, 2007). Morphology can also be influenced in a complex way by climatic and  
14  
15 439 phylogenetic factors, and in *Microtus savii* both sets of factors contribute to shape variation of  
16  
17 440 the first lower molars, while tooth size is not affected by climatic conditions (Piras *et al.*, 2010).  
18  
19 441 However, we did not detect a significant phylogenetic signal and the mapping of size and shape  
20  
21 442 on the phylogeny showed no apparent relationships. Although Mantel tests showed no  
22  
23 443 relationships of shape and genetic distances, the results have to be taken with caution because  
24  
25 444 Mantel test has lower power in comparison with other tests (Legendre & Fortin, 2010); however,  
26  
27 445 Mantel test has been traditionally used in morphological, ecological and genetic studies, it is  
28  
29 446 useful when data can be expressed as distances, and the Mantel test results are coherent with  
30  
31 447 other results presented here.

32  
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34  
35 448 Why is the pygmy shrew generally smaller in northern latitudes than in southern  
36  
37 449 latitudes? There is some dispute about the mechanisms involved for Bergmann's rule or its  
38  
39 450 converse (Blackburn *et al.*, 1999; Meiri, 2011). However, the lower food availability in northern,  
40  
41 451 colder or less productive habitats is likely to be a selective factor acting on small mammals,  
42  
43 452 combined with lower absolute food requirements for smaller vs. larger species of small  
44  
45 453 mammals in less productive habitats (Ochocińska & Taylor, 2003). This may explain the small  
46  
47 454 size of shrews of the northern group of *S. minutus* which evolved in and expanded from  
48  
49 455 northern glacial refugial areas (Vega *et al.*, 2010a). Populations of *S. araneus* in Finland are up  
50  
51 456 to 13% smaller inland than in the coast, where the main differences are lower winter  
52  
53 457 temperatures and less snow cover at inland sites, factors associated with lower habitat  
54  
55 458 productivity, which could selectively favour smaller shrews (Frafjord, 2008). In *S. cinereus* it has  
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3 459 been suggested that the increase in size during the second half of the twentieth century is  
4  
5 460 related to increasing winter temperatures and higher food availability in winter due to improved  
6  
7 461 weather conditions for its prey (Yom-Tov & Yom-Tov, 2005).  
8  
9

10 462 Dehnel's phenomenon (*i.e.* reduction of body size and mass of organs of soricine  
11  
12 463 shrews from northern temperate regions during winter) has been interpreted as an adaptation to  
13  
14 464 reduced prey abundance permitting a reduction in absolute food requirements in a group of  
15  
16 465 species that do not hibernate. However, recent findings indicate that prey numbers and biomass  
17  
18 466 available for shrews (which do not hibernate) do not decrease during winter, but soil  
19  
20 467 invertebrates do change their vertical distribution, apparently requiring shrews to have a  
21  
22 468 modified more energetically costly foraging behaviour for consumption of energetically less  
23  
24 469 favourable prey (Churchfield, Rychlik & Taylor, 2012). In our study, a Dehnel effect is unlikely to  
25  
26 470 play a role because < 5% of our samples were collected during winter (those few individuals  
27  
28 471 that were collected in winter were from Switzerland where we have a good sample size, and  
29  
30 472 from Central Spain where results indicate large mandible and skull size). It should be noted that  
31  
32 473 phenotypic plasticity (the ability of a single genotype to produce more than one alternative form  
33  
34 474 of morphology, physiological state or behaviour in response to changes in environmental  
35  
36 475 conditions) cannot be ruled out as a possible explanation until proper experimental studies are  
37  
38 476 undertaken with shrews (Husby, Hille & Visser, 2011).  
39  
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42 477 Size and shape variation of the mandible can affect the biomechanics of mastication by  
43  
44 478 modifying the sites of attachment of mandible muscles (Monteiro, Duarte & dos Reis, 2003).  
45  
46 479 Larger and morphologically distinctive mandibles could reflect stronger bite force or higher  
47  
48 480 mechanical potential for mastication, which could be an adaptation or a plastic response to  
49  
50 481 more arid conditions, to exploit a wider size-range of prey and prey with harder exoskeletons,  
51  
52 482 and/or character release in the absence of competitors (Strait, 1993; Carraway & Verts, 2005;  
53  
54 483 Monteiro *et al.*, 2003). The association of diet and skull shape can be strong because muscles  
55  
56 484 used for mastication are tightly linked to bone structure; for example, diet may explain up to  
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1  
2  
3 485 25% of skull shape variance in marmots (Caumul & Polly, 2005). In *S. minutus*, a stronger bite  
4  
5 486 force was estimated for South Italian than for north European populations in relation to the  
6  
7 487 positioning of the coronoid process and horizontal ramus length (Vega *et al.*, 2010b), and the  
8  
9 488 morphological patterns described in that study were similar to those found here.  
10  
11

12 489

### 14 490 **ISLAND DIFFERENTIATION IN *SOEX MINUTUS***

15  
16 491 Under the island rule, it is expected that small mammals on islands will have a larger body mass  
17  
18 492 than mainland conspecifics (Van Valen, 1973). Our results indicate that there is a strong island  
19  
20 493 effect operating on the size of mandibles and skulls of *S. minutus* from Ireland and the Orkney  
21  
22 494 islands. Moreover, these island groups were distinctive from continental groups in terms of  
23  
24 495 shape variation, and samples were assigned correctly to their island of origin. **There was a lack**  
25  
26  
27 496 **of correspondence between Procrustes distances and *cyt b* tree terminal branches.** Overall, it  
28  
29 497 appears that environmental factors and insularity have stronger effects on morphology, perhaps  
30  
31 498 through local adaptation, genetic bottlenecks and/or plastic responses, than provided by  
32  
33 499 phylogenetic relationships. Therefore, *S. minutus* from Ireland and the Orkney islands shows  
34  
35 500 morphological differentiation from continental groups through island effects, while *cyt b* reveals  
36  
37 501 the close phylogenetic relationship of these island groups with continental Western Europe  
38  
39 502 (McDevitt *et al.*, 2011).  
40  
41

42 503 Other shrew species on islands share similar trends. For example, *S. trowbridgii* from  
43  
44 504 Destruction Island (Washington State, USA) has greater average skull-breadth and mandibular  
45  
46 505 dimensions than the mainland counterpart (Carraway & Verts, 2005). *S. araneus* from several  
47  
48 506 Scottish islands are significantly larger than populations in mainland Britain and show larger  
49  
50 507 body size on islands in relation to distance to the mainland (White & Searle, 2007). *Crocidura*  
51  
52 508 *russula* from several French islands also show divergence in mandible shape in relation to  
53  
54 509 distance from the mainland and island size (Cornette *et al.*, 2012). *C. suaveolens* from Corsica  
55  
56 510 is larger and has a smaller litter size than mainland populations in Southern France (Fons *et al.*,  
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2  
3 511 1997), indicating an island effect (Adler & Levins, 1994). Studies of other small mammals have  
4  
5 512 also shown morphological divergence of recently colonised island populations (e.g. Michaux *et*  
6  
7 513 *al.*, 2007; Renaud & Michaux, 2007; Cucchi *et al.*, 2014). Similar to our study, the mandible and  
8  
9 514 skull shape of *Marmota vancouverensis* from Vancouver Island is highly divergent from the  
10  
11 515 mainland counterpart *M. caligata*, despite small mtDNA sequence divergence (Cardini, 2003;  
12  
13 516 Cardini & O'Higgins, 2004). Previous morphological studies on *S. minutus* from islands around  
14  
15 517 Britain relate to presence/absence of *S. araneus* (Malmquist, 1985) but are difficult to interpret  
16  
17 518 because of anomalies in the reporting of sympatric and allopatric status of *S. minutus* on these  
18  
19 519 islands.  
20  
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22  
23 520 It may be possible that morphological traits in mammals evolve quickly on islands in a  
24  
25 521 matter of a few decades after colonisation (Pergams & Ashley, 2001; Millien, 2006; Cucchi *et*  
26  
27 522 *al.*, 2014; but see also Meiri *et al.*, 2006, 2008; Raia & Meiri, 2006, 2011). Given that *S. minutus*  
28  
29 523 is the only shrew species in the Orkney islands and, until recently, it was the only shrew species  
30  
31 524 in Ireland, larger body mass (reflected in larger mandibles and skulls) could have evolved on  
32  
33 525 these islands driven by competitive release, the absence of predators and availability of  
34  
35 526 resources (McDevitt *et al.*, 2014). Additionally, geographic isolation from continental populations  
36  
37 527 for several thousand years, genetic bottlenecks after colonisations from a low number of  
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39 528 migrants and low genetic diversity (very few *cyt b* haplotypes were observed in the Orkney  
40  
41 529 islands despite the large sample size) could lead to deviation in morphology of island  
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43 530 populations of *S. minutus* compared with the mainland (Cornette *et al.*, 2012). Contrastingly,  
44  
45 531 specimens of *S. minutus* in Belle Île and Britain have higher *cyt b* diversity (McDevitt *et al.*,  
46  
47 532 2011) and are similar in terms of mandible shape to continental samples. Additionally, Belle Île  
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49 533 and mainland Britain are occupied by other species of shrews.  
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52  
53 534 Morphological differences may actually represent phenotypic plasticity expressed in  
54  
55 535 insular environments; however, this hypothesis has rarely been tested. Although, with our  
56  
57 536 results in *S. minutus* we cannot rule out phenotypic plasticity as a possible explanation, at least  
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3 537 for *C. suaveolens*, differences in body size and litter size between island and mainland  
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5 538 populations were persistent over three generations in laboratory breeding conditions, thus  
6  
7 539 supporting the hypothesis that these differences are genetically determined rather than  
8  
9 540 phenotypic plasticity (Fons *et al.*, 1997). The evolution of different size and shape in island  
10  
11 541 populations of *S. minutus* may thus be an adaptive response to changed availability of  
12  
13 542 resources, the 'resource rule' *sensu* McNab (2010), acting together with demographic and  
14  
15 543 historical factors.  
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## 20 545 **CONCLUSIONS**

21  
22 546 In this study we explored the morphological variation of mandibles and skulls of *S. minutus*  
23  
24 547 across Europe using a geometric morphometric approach. We found notable ecogeographical  
25  
26 548 variation in mandible and skull size related to environmental variables and insularity, which may  
27  
28 549 suggest that the converse Bergmann's rule and the island rule operate in *S. minutus*. We  
29  
30 550 believe, however, that these ecogeographical patterns could be more reasonably explained as a  
31  
32 551 response to resource availability, possibly reflecting adaptation or a phenotypically plastic  
33  
34 552 response to different habitats and environmental conditions, differential allocation of energy and  
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36 553 physiological responses, differential food availability and presence/absence of competitors.  
37  
38 554 Correlative studies such as this are an important source for identifying patterns that require  
39  
40 555 further investigation by in-depth studies measuring the strength of selection or the experimental  
41  
42 556 link between performance, morphology, and ecology generating local adaptations (Calsbeek &  
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44 557 Irschick, 2007).  
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49 558         Considering variation in morphological shape rather than size, the most divergent  
50  
51 559 populations among those examined in *S. minutus* were those from the Atlantic islands, although  
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53 560 distinctive features could also be identified for populations in southern Europe (*e.g.* with thin-  
54  
55 561 plate spline transformation grids). Interestingly, with respect to both size and shape, the  
56  
57 562 morphological variation observed here does not follow previous genetic subdivisions within the  
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3 563 species, and indicate a complex role for different evolutionary and/or environmental processes  
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5 564 in determining geographical variation in *S. minutus*.  
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18 775 **SUPPORTING INFORMATION**

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20 776 Additional Supporting Information may be found in the online version of this article at the  
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22 publisher's web-site:  
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25 778 **Appendix S1.** Sample information and dimensionality reduction results.

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27 779 **Appendix S2.** Pairwise distances for mandible and skull data sets.

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29 780 **Appendix S3.** Post-hoc results for analyses of variance of size and shape variables.  
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783 **FIGURE LEGENDS**

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

787  
788 **Figure 2.** Boxplots of (A) mandible and (B) skull Centroid Size (transformed with natural  
789 logarithms; LnCS) after Standard Least Squares analysis of geographical groups of *Sorex*  
790 *minutus*. Symbols correspond to sampling localities shown in Fig. 1. Groups are arranged by  
791 increasing latitude and by continental and island origin. The outgroup (*S. volnuchini*) was not  
792 included in the analysis but is shown for comparison purposes. Letters A-D show pairwise  
793 significance.

794  
795 **Figure 3.** Shape changes from the average configuration of (A) mandibles and (B) skulls of  
796 *Sorex minutus* represented using thin-plate spline transformation grids (3X scale factor to  
797 highlight shape changes). Arrows denote shape changes discussed in text. Symbols correspond  
798 to sampling localities shown in Fig. 1. Groups are arranged by increasing latitude.

799  
800 **Figure 4.** Canonical Variate Analysis (CVA) of shape variables for (A) mandibles and (B) skulls  
801 of *Sorex minutus* showing differences among geographical groups. All continental samples are  
802 shown with the same symbol for simplicity.

803  
804 **Figure 5.** Rooted Neighbour-Joining (NJ) trees of pairwise Procrustes distances for (A)  
805 mandible and (B) skull groups of *Sorex minutus*. Rooted NJ trees of *cyt b* genetic distances (Da)  
806 among phylogroups of *S. minutus* (detected here and in previous studies) showing intraspecific  
807 variation in Centroid Size (CS) and shape (Procrustes distances, PD) for mandible (C, D) and

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

For Peer Review

810 **TABLES**

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**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 <sup>a</sup>	<i>t</i> value <sup>b</sup>	<i>P</i> value	Factor	Coefficient	<i>t</i> value	<i>P</i> 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	<i>t</i> value	<i>P</i> value	Factor	Coefficient	<i>t</i> value	<i>P</i> 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

<sup>a</sup>Unstandardised coefficients.<sup>b</sup>Test for the statistical significance of each independent variable.

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

Mandibles	All factors	PC1	PC2	PC3
Wilk's $\lambda$	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
<i>P</i> 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 $\lambda$	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
<i>P</i> value	< 0.0001	< 0.0001	< 0.0001	< 0.0001
Percentage explained	11.9%	0.92%	4.8%	6.2%

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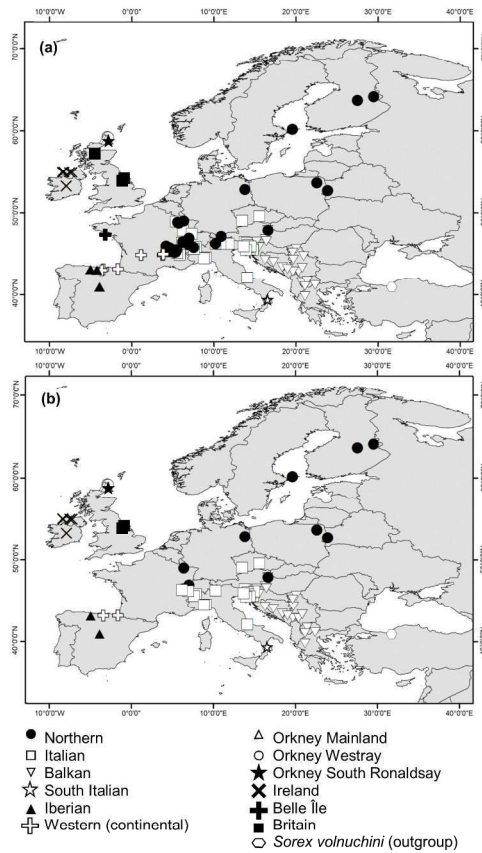


Figure 1. Sampling localities of *Sorex minutus* for morphological analysis. (A) Mandible data set and (B) skull data set. The symbols distinguish the geographical groups defined by previous genetic studies or by geographic isolation on islands (see text).  
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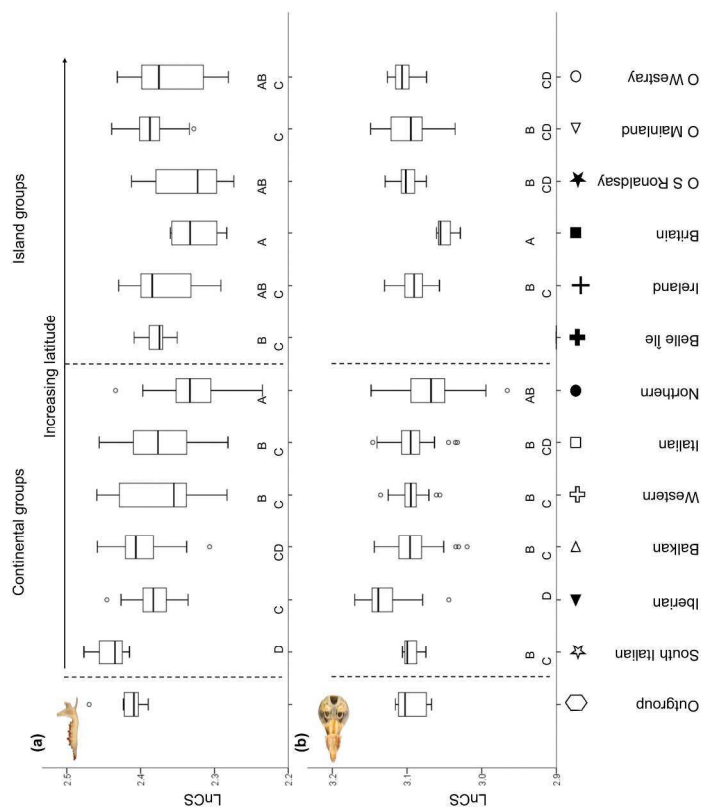


Figure 2. Boxplots of (A) mandible and (B) skull Centroid Size (transformed with natural logarithms; LnCS) after Standard Least Squares analysis of geographical groups of *Sorex minutus*. Symbols correspond to sampling localities shown in Fig. 1. Groups are arranged by increasing latitude and by continental 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.  
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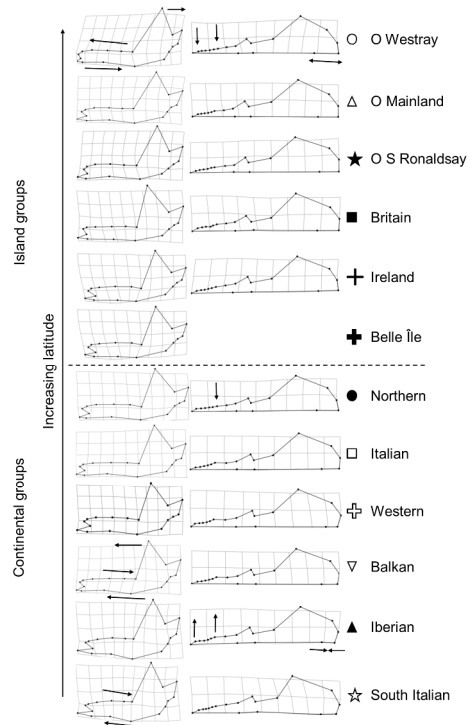


Figure 3. Shape changes from the average configuration of (A) mandibles and (B) skulls of *Sorex minutus* represented using thin-plate spline transformation grids (3X scale factor to highlight shape changes). Arrows denote shape changes discussed in text. Symbols correspond to sampling localities shown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

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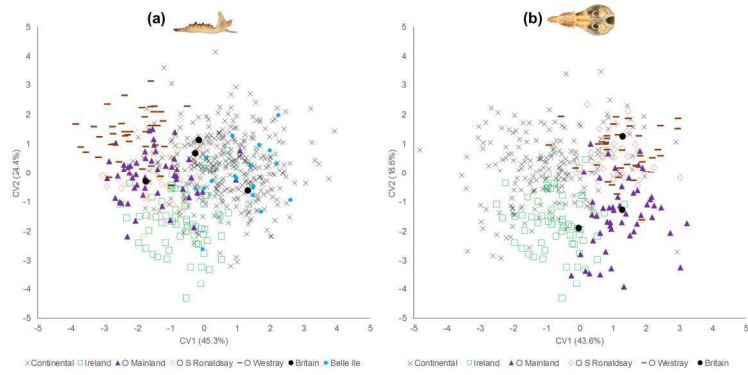


Figure 4. Canonical Variate Analysis (CVA) of shape variables for (A) mandibles and (B) skulls of *Sorex minutus* showing differences among geographical groups. All continental samples are shown with the same symbol for simplicity.  
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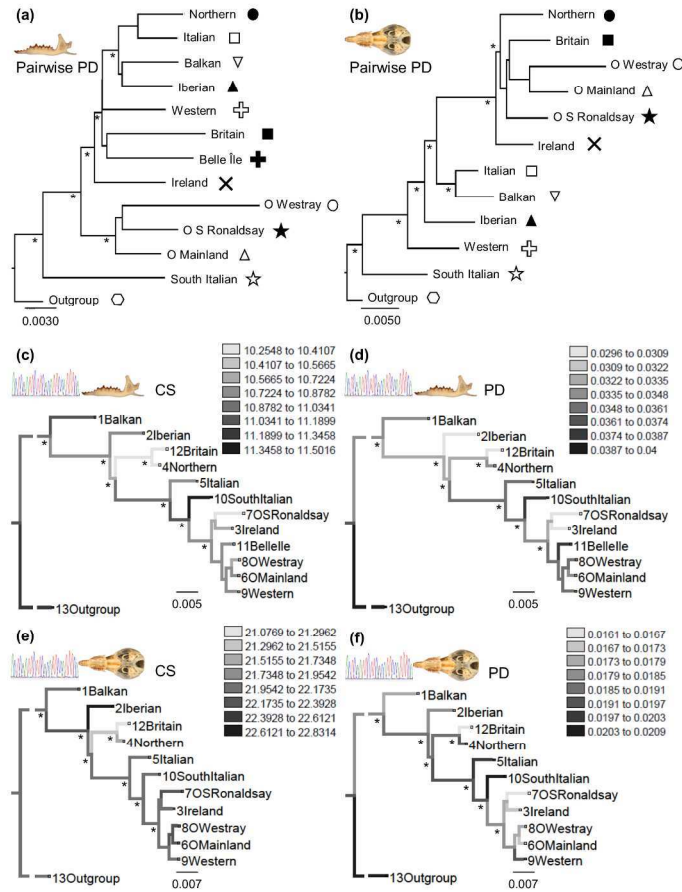


Figure 5. Rooted Neighbour-Joining (NJ) trees of pairwise Procrustes distances for (A) mandible and (B) skull groups of *Sorex minutus*. Rooted NJ trees of cyt b genetic distances (Da) among phylogroups of *S. minutus* (detected here and in previous studies) showing intraspecific variation in Centroid 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 ( $\geq 50\%$ ).  
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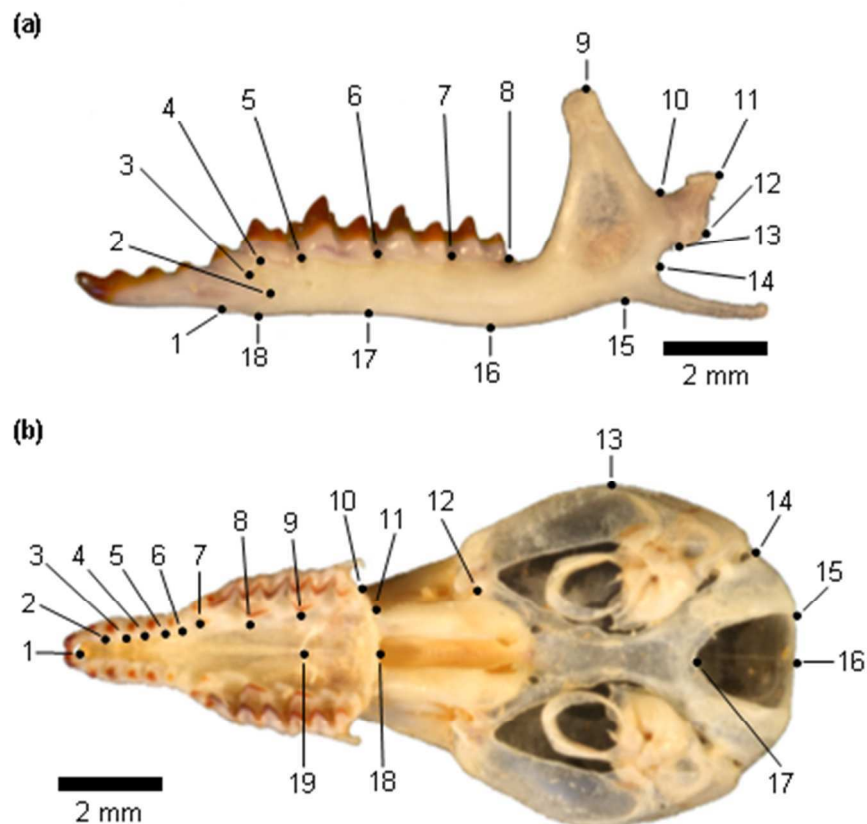
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3 1 **SUPPORTING INFORMATION**  
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7 3 **Ecogeographical patterns of morphological variation in pygmy shrews *Sorex minutus***  
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9 4 **(Soricomorpha: Soricinae) within a phylogeographic and continental-and-island**  
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11 5 **framework**  
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13 614  
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16 7 RODRIGO VEGA<sup>1,2,3\*</sup>, ALLAN D. MCDEVITT<sup>4</sup>, BORIS KRYŠTUFEK<sup>5,6</sup> and JEREMY B.  
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3031 14 <sup>3</sup>*Department of Ecology and Evolutionary Biology, Cornell University, Ithaca NY 14853, USA*  
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3 27 **SUPPORTING INFORMATION**  
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5 28 **LANDMARKS**  
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7 29 A description of landmarks (Fig. S1): mandibles: 1) inferior end of the alveolus of the incisor, 2)  
8 30 inferior margin of the alveolus of the incisor, 3-8) posterior ends of the alveoli of the mandibular  
9 31 teeth, 9) superior margin of the coronoid process, 10) inferior point of the saddle between the  
10 32 condylar and coronoid processes, 11) lateral end of the superior surface of the condyle, 12)  
11 33 posterior end of the inferior surface of the condyle, 13) medial end of the inferior surface of the  
12 34 condyle, 14) superior side of the junction of the angular process to the body of the mandible, 15)  
13 35 inferior side of the junction of the angular process to the body of the mandible, 16) inferior-most  
14 36 point of the posterior convex saddle of the body of the mandible, 17) superior-most point of the  
15 37 concave saddle of the body of the mandible, and 18) inferior-most point of the anterior convex  
16 38 saddle of the body of the mandible; skulls: 1) anterior point of the midline suture between the  
17 39 premaxillae, 2-10) medial side of the point at which adjacent teeth meet, from the incisor  
18 40 through the third molar, 11) intersection between the lateral margin of the pterygoid plates and  
19 41 the posterior margin of the palate, 12) anterior margin of the glenoid fossa, 13) mastoid process,  
20 42 14) lateral end of the posterior margin of the occipital condyle, 15) medial end of the posterior  
21 43 margin of the occipital condyle, 16) midline of the posterior margin of the foramen magnum, 17)  
22 44 midline of the anterior margin of the foramen magnum, 18) midline of the posterior margin of the  
23 45 palate, and 19) midline of the sutures between the palatine and maxilla.  
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**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

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3 61 another than expected by chance), we performed a Phylogenetic Independent Contrast in  
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5 62 MorphoJ version 1.05a between the cytochrome *b* (*cyt b*) NJ tree and the size and shape of the  
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7 63 average configurations of the mandible and skull data sets divided into groups. This test  
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9 64 simulates the null hypothesis of the absence of phylogenetic signal by randomly permuting the  
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11 65 size and shape data among the terminal taxa of a known phylogeny in the analysis (20,000  
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13 66 iterations for the permutation tests) (Klingenberg & Gidaszewski, 2010).  
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## 19 68 **RESULTS OF PRELIMINARY MORPHOMETRIC ANALYSES**

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21 69 Preliminary analyses supported landmark placement repeatability, no sexual dimorphism for  
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23 70 size and shape and negligible phylogenetic signal in the morphological dataset. There were no  
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25 71 significant differences with respect to size or shape among the five repeated photographs of  
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27 72 mandibles (size:  $F_{4, 110} = 0.0053$ ,  $P = 0.9999$ ; shape: Wilks'  $\lambda = 0.8861$ ,  $F_{64, 374.2} = 0.1835$ ,  $P =$   
28  
29 73  $0.9999$ ) and skulls (size:  $F_{4, 135} = 0.0726$ ,  $P = 0.9903$ ; shape: Wilks'  $\lambda = 0.8688$ ,  $F_{68, 469.3} =$   
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31 74  $0.2518$ ,  $P = 0.9999$ ); therefore, landmarks can be considered to have been placed accurately.  
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34 75 There were no significant differences between male and female mandibles for size ( $F_{1,}$   
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36 76  $_{255} = 0.0235$ ,  $P = 0.8782$ ) and shape (Wilks'  $\lambda = 0.9419$ ,  $F_{16, 240} = 0.9256$ ,  $P = 0.5404$ ). Similarly,  
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38 77 there were no significant differences between male and female skulls for size ( $F_{1, 257} = 0.0352$ ,  $P$   
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40 78  $= 0.8513$ ) and shape (Wilks'  $\lambda = 0.9507$ ,  $F_{17, 241} = 0.7345$ ,  $P = 0.7658$ ). Moreover, comparisons  
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42 79 of male and female samples within groups and within large regional samples showed no  
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44 80 significant differences (data not shown). All subsequent analyses on mandibles and skulls were  
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46 81 performed pooling all samples irrespective of sex.  
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49 82 The null hypothesis (absence of a phylogenetic signal) was not rejected when mapping  
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51 83 the phenotypic data of the average configurations of the groups for the mandible ( $P_{\text{size}} = 0.7448$ ,  
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53 84  $P_{\text{shape}} = 0.1247$ ) and skull data sets ( $P_{\text{size}} = 0.0748$ ,  $P_{\text{shape}} = 0.6867$ ) onto the *cyt b* NJ tree;  
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55 85 therefore, we concluded that the phylogenetic signal in our data sets is negligible.  
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86 **SUPPORTING INFORMATION**87 **Appendix S1.** Sample information and dimensionality reduction results for Principal

88 Components Analysis and for Partial Least Squares Analysis.

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**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

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3	RSMP35966	Balkan	Continent	Museum	20.361897	42.839728	mand/skull
4	RSVa7841	Balkan	Continent	Trapping	19.736253	44.314847	mand/skull
5	RSVa7842	Balkan	Continent	Trapping	19.736253	44.314847	mand/skull
6							
7	RSVa7855	Balkan	Continent	Trapping	19.736253	44.314847	mand/skull
8	SIGo2042	Balkan	Continent	Trapping	15.561217	45.857758	mand/skull
9							
10	SIHo15910	Balkan	Continent	Museum	16.329503	46.811033	mand/skull
11	SIKr14709	Balkan	Continent	Museum	15.476147	45.895617	mand/skull
12	SILe1145	Balkan	Continent	Trapping	16.457517	46.551106	mand/skull
13	SILe1146	Balkan	Continent	Trapping	16.457517	46.551106	mand/skull
14	SILe1147	Balkan	Continent	Trapping	16.457517	46.551106	mand/skull
15	SILe1163	Balkan	Continent	Trapping	16.457517	46.551106	mand/skull
16	SIPh3126	Balkan	Continent	Trapping	15.256711	46.519253	mand/skull
17							
18	SIPh3131	Balkan	Continent	Trapping	15.256711	46.519253	mand/skull
19	SIPh3489	Balkan	Continent	Trapping	15.256711	46.519253	mand/skull
20	SIRa16104	Balkan	Continent	Museum	15.340292	45.685878	mand/skull
21	SISe16100	Balkan	Continent	Museum	15.234997	45.507833	mand
22	SISe16101	Balkan	Continent	Museum	15.234997	45.507833	mand/skull
23							
24	FRBI100	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
25	FRBI101	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
26	FRBI102	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
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28	FRBI103	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
29	FRBI104	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
30	FRBI105	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
31	FRBI106	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
32	FRBI107	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
33							
34	FRBI108	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
35	FRBI109	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
36	FRBI110	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
37							
38	FRBI111	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
39	FRBI93	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
40	FRBI94	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
41	FRBI95	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
42	FRBI96	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
43	FRBI97	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
44	FRBI98	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
45	FRBI99	Belle Ile	Belle Ile	Trapping	-3.195833	47.337500	mand
46							
47	GBCa1	Britain	Britain	Trapping	-0.892633	53.964711	mand/skull
48	GBCH1	Britain	Britain	Trapping	-0.910433	54.120878	mand/skull
49							
50	GBDrG140	Britain	Britain	Trapping	-4.489267	57.308992	mand
51	GBHe1	Britain	Britain	Trapping	-1.057706	53.943211	mand/skull
52							
53	ESArE135	Iberian	Continent	Trapping	-4.200000	43.033300	mand
54	ESPE47	Iberian	Continent	Trapping	-4.999678	43.104939	mand/skull
55	ESPE57	Iberian	Continent	Trapping	-4.999678	43.104939	mand/skull
56	ESRa0640	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
57	ESRa2653	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
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3	ESRa3443	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
4	ESRa3444	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
5	ESRa3445	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
6							
7	ESRa3446	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
8	ESRa3447	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
9							
10	ESRa3448	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
11	ESRa3449	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
12	ESRa3451	Iberian	Continent	Museum	-3.879364	40.903628	mand/skull
13	IECL1	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
14	IECL10	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
15	IECL11	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
16	IECL12	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
17	IECL13	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
18	IECL14	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
19	IECL15	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
20	IECL16	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
21	IECL17	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
22	IECL18	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
23	IECL19	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
24	IECL2	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
25	IECL20	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
26	IECL3	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
27	IECL4	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
28	IECL5	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
29	IECL6	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
30	IECL7	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
31	IECL8	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
32	IECL9	Ireland	Ireland	Trapping	-7.947964	53.267756	mand/skull
33	IEDY1	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
34	IEDY10	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
35	IEDY11	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
36	IEDY12	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
37	IEDY13	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
38	IEDY14	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
39	IEDY15	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
40	IEDY16	Ireland	Ireland	Trapping	-7.250000	55.000000	mand
41	IEDY17	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
42	IEDY18	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
43	IEDY19	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
44	IEDY2	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
45	IEDY20	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
46	IEDY3	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
47	IEDY4	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
48	IEDY5	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
49	IEDY6	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
50							
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3	IEDY7	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
4	IEDY8	Ireland	Ireland	Trapping	-7.250000	55.000000	mand/skull
5	IEDY9	Ireland	Ireland	Trapping	-7.250000	55.000000	mand
6							
7	IEE1RV	Ireland	Ireland	Trapping	-8.350450	54.950261	mand/skull
8	IEE2RV	Ireland	Ireland	Trapping	-7.515247	54.975419	mand/skull
9	IEE3RV	Ireland	Ireland	Trapping	-7.515247	54.975419	mand/skull
10	IEE4RV	Ireland	Ireland	Trapping	-7.515247	54.975419	mand/skull
11	IEGw1	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
12	IEGw17	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
13	IEGw1RV	Ireland	Ireland	Trapping	-8.383333	55.050000	mand/skull
14	IEGw26	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
15	IEGw3	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
16	IEGw4	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
17	IEGw43	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
18	IEGw46	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
19	IEGw5	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
20	IEGw51	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
21	IEGw51A	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
22	IEGw51B	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
23	IEGw51C	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
24	IEGw55	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
25	IEGw55B	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
26	IEGw5b	Ireland	Ireland	Trapping	-8.230000	55.050000	mand
27	IEGw5C	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
28	IEGw64	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
29	IEGwTILES	Ireland	Ireland	Trapping	-8.230000	55.050000	mand/skull
30	CHVI4746	Italian	Continent	Museum	6.892742	46.204300	mand/skull
31	CHVI4748	Italian	Continent	Museum	6.892742	46.204300	mand/skull
32	CZHa9166	Italian	Continent	Museum	15.560653	49.604761	mand/skull
33	CZSS4767	Italian	Continent	Trapping	13.475481	49.065617	mand/skull
34	CZSS4838	Italian	Continent	Trapping	13.475481	49.065617	mand/skull
35	FRDi3003	Italian	Continent	Trapping	6.143175	46.356817	mand/skull
36	FRHa59	Italian	Continent	Owl pellet	6.284722	47.843611	mand
37	FRHa60	Italian	Continent	Owl pellet	6.284722	47.843611	mand
38	FRHa61	Italian	Continent	Owl pellet	6.284722	47.843611	mand
39	FRHa62	Italian	Continent	Owl pellet	6.284722	47.843611	mand
40	FRHa63	Italian	Continent	Owl pellet	6.284722	47.843611	mand
41	FRHa64	Italian	Continent	Owl pellet	6.284722	47.843611	mand
42	FRHa65	Italian	Continent	Owl pellet	6.284722	47.843611	mand
43	FRLa87	Italian	Continent	Owl pellet	5.410833	48.939722	mand
44	FRLa88	Italian	Continent	Owl pellet	5.410833	48.939722	mand
45	FRLa89	Italian	Continent	Owl pellet	5.410833	48.939722	mand
46	FRLG003A	Italian	Continent	Trapping	5.903056	45.091944	mand
47	FRLG003B	Italian	Continent	Trapping	5.903056	45.091944	mand
48	FRLG003C	Italian	Continent	Trapping	5.903056	45.091944	mand
49							
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3	FRLV27	Italian	Continent	Owl pellet	5.589069	45.127964	mand
4	FROR15	Italian	Continent	Owl pellet	5.870556	44.921944	mand
5	FRSo091A	Italian	Continent	Trapping	7.336111	47.483889	mand
6							
7	FRSo091B	Italian	Continent	Trapping	7.336111	47.483889	mand
8	FRSo90	Italian	Continent	Trapping	7.336111	47.483889	mand
9	FRSo92	Italian	Continent	Trapping	7.336111	47.483889	mand
10							
11	ITAn23	Italian	Continent	Museum	7.696569	45.822425	mand
12	ITCh16	Italian	Continent	Museum	7.622858	45.621664	mand
13	ITCh17	Italian	Continent	Museum	7.622858	45.621664	mand/skull
14	ITCh18	Italian	Continent	Museum	7.622858	45.621664	mand
15	ITGa33	Italian	Continent	Museum	7.848183	45.851881	skull
16	ITGa36	Italian	Continent	Museum	7.848183	45.851881	mand/skull
17	ITGa38	Italian	Continent	Museum	7.848183	45.851881	mand/skull
18							
19	ITMa9815	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
20	ITMa9830	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
21	ITMa9832	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
22	ITMa9833	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
23	ITMa9834	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
24	ITMa9835	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
25	ITMa9849	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
26	ITMa9850	Italian	Continent	Trapping	14.115697	42.083411	mand/skull
27							
28	ITMC32500	Italian	Continent	Museum	10.836031	46.238711	mand
29	ITPr0001	Italian	Continent	Trapping	10.248014	46.286975	mand/skull
30	ITSC54303	Italian	Continent	Museum	8.832010	44.477300	mand/skull
31	ITTCg47	Italian	Continent	Museum	7.571240	45.807200	mand/skull
32	ITTCg48	Italian	Continent	Museum	7.571240	45.807200	mand/skull
33	ITTr17692	Italian	Continent	Museum	11.833333	46.250000	mand
34	ITVB54317	Italian	Continent	Museum	9.064750	44.555300	mand/skull
35							
36	SICe142	Italian	Continent	Trapping	14.945650	46.172950	skull
37	SIDo2040	Italian	Continent	Trapping	14.797406	45.501464	mand/skull
38	SIDo2041	Italian	Continent	Trapping	14.797406	45.501464	skull
39	SIDr2778	Italian	Continent	Trapping	14.029192	46.358772	mand/skull
40	SIDr2779	Italian	Continent	Trapping	14.029192	46.358772	mand/skull
41	SIGr973	Italian	Continent	Trapping	14.132525	46.105453	mand/skull
42	SIGr974	Italian	Continent	Trapping	14.132525	46.105453	mand/skull
43	SIIg1563	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
44	SIIg1564	Italian	Continent	Trapping	14.542856	45.946967	mand
45	SIIg1565	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
46	SIIg1628	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
47	SIIg1648	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
48	SIIg1766	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
49	SIIg1773	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
50	SIIg1847	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
51	SIIg2143	Italian	Continent	Trapping	14.542856	45.946967	mand/skull
52	SIKn6167	Italian	Continent	Trapping	13.784367	46.469472	mand/skull
53							
54							
55							
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58							
59							
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3	SIKn6380	Italian	Continent	Trapping	13.784367	46.469472	mand/skull
4	SIKo6781	Italian	Continent	Trapping	14.820278	45.656956	mand
5	SIKo6782	Italian	Continent	Trapping	14.820278	45.656956	mand/skull
6							
7	SIKo6827	Italian	Continent	Trapping	14.820278	45.656956	mand/skull
8	SIKo6845	Italian	Continent	Trapping	14.820278	45.656956	mand/skull
9	SIKr1042	Italian	Continent	Trapping	14.247114	45.821514	mand/skull
10	SING54318	Italian	Continent	Museum	13.657053	45.944656	mand/skull
11	SING54320	Italian	Continent	Museum	13.657053	45.944656	mand/skull
12							
13	SIPd1045	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
14	SIPd1372	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
15	SIPd1374	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
16							
17	SIPk16394	Italian	Continent	Museum	14.029192	46.358772	mand/skull
18	SISl1378	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
19	SISl1380	Italian	Continent	Trapping	13.940200	45.512914	mand
20							
21	SISl1381	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
22	SISl1382	Italian	Continent	Trapping	13.940200	45.512914	skull
23	SISl1383	Italian	Continent	Trapping	13.940200	45.512914	mand/skull
24	SISl1384	Italian	Continent	Trapping	13.940200	45.512914	skull
25	SISn1043	Italian	Continent	Trapping	14.401383	45.573331	mand/skull
26	SISn1044	Italian	Continent	Trapping	14.401383	45.573331	mand/skull
27							
28	ATDo1612	Northern	Continent	Trapping	16.641250	47.895703	mand/skull
29	ATUmA139	Northern	Continent	Trapping	10.927683	47.136119	mand
30							
31	CHBa0441	Northern	Continent	Museum	6.231061	46.462789	mand/skull
32	CHBa1816	Northern	Continent	Museum	6.231061	46.462789	mand/skull
33	CHBa1817	Northern	Continent	Museum	6.231061	46.462789	mand/skull
34	CHBa1818	Northern	Continent	Museum	6.231061	46.462789	mand/skull
35	CHBa1819	Northern	Continent	Museum	6.231061	46.462789	mand/skull
36	CHBa1820	Northern	Continent	Museum	6.231061	46.462789	mand/skull
37	CHBa1821	Northern	Continent	Museum	6.231061	46.462789	mand/skull
38							
39	CHBa3002	Northern	Continent	Museum	6.231061	46.462789	mand/skull
40	CHCh7622	Northern	Continent	Museum	6.997358	46.932742	mand/skull
41	CHPo7628	Northern	Continent	Museum	6.997358	46.932742	mand/skull
42							
43	CHVI4747	Northern	Continent	Museum	6.892742	46.204300	mand/skull
44	DEEb3996	Northern	Continent	Museum	13.810889	52.833108	mand/skull
45	FIAE1747	Northern	Continent	Museum	19.611839	60.203744	mand/skull
46	FIAE1760	Northern	Continent	Museum	19.611839	60.203744	mand/skull
47							
48	FIKu2071	Northern	Continent	Museum	29.495703	64.125364	mand/skull
49	FISo1773	Northern	Continent	Museum	27.529589	63.669514	mand/skull
50	FISo1779	Northern	Continent	Museum	27.529589	63.669514	mand/skull
51	FISo1783	Northern	Continent	Museum	27.529589	63.669514	mand/skull
52	FISo1785	Northern	Continent	Museum	27.529589	63.669514	mand/skull
53							
54	FRAF174	Northern	Continent	Owl pellet	5.639722	48.856111	mand
55	FRAF175	Northern	Continent	Owl pellet	5.639722	48.856111	mand
56	FRAF176	Northern	Continent	Owl pellet	5.639722	48.856111	mand
57	FRAF179	Northern	Continent	Owl pellet	5.639722	48.856111	mand
58							
59							
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3	FRAF180	Northern	Continent	Owl pellet	5.639722	48.856111	mand
4	FRAF181	Northern	Continent	Owl pellet	5.639722	48.856111	mand
5	FRAF182	Northern	Continent	Owl pellet	5.639722	48.856111	mand
6							
7	FRAF183	Northern	Continent	Owl pellet	5.639722	48.856111	mand
8	FRAF184	Northern	Continent	Owl pellet	5.639722	48.856111	mand
9							
10	FRAF185	Northern	Continent	Owl pellet	5.639722	48.856111	mand
11	FRAF186	Northern	Continent	Owl pellet	5.639722	48.856111	mand
12	FRAF187	Northern	Continent	Owl pellet	5.639722	48.856111	mand
13	FRAF188	Northern	Continent	Owl pellet	5.639722	48.856111	mand
14	FRAF189	Northern	Continent	Owl pellet	5.639722	48.856111	mand
15	FRAF190	Northern	Continent	Owl pellet	5.639722	48.856111	mand
16	FRAF192	Northern	Continent	Owl pellet	5.639722	48.856111	mand
17							
18	FRAF193	Northern	Continent	Owl pellet	5.639722	48.856111	mand
19	FRAF194	Northern	Continent	Owl pellet	5.639722	48.856111	mand
20	FRAF195	Northern	Continent	Owl pellet	5.639722	48.856111	mand
21							
22	FRAF196A	Northern	Continent	Owl pellet	5.639722	48.856111	mand
23	FRAF196B	Northern	Continent	Owl pellet	5.639722	48.856111	mand
24	FRAF197	Northern	Continent	Owl pellet	5.639722	48.856111	mand
25	FRAF198	Northern	Continent	Owl pellet	5.639722	48.856111	mand
26							
27	FRBe19	Northern	Continent	Owl pellet	5.265556	45.203333	mand
28	FRBe20	Northern	Continent	Owl pellet	5.265556	45.203333	mand
29	FRBe21	Northern	Continent	Owl pellet	5.265556	45.203333	mand
30							
31	FRBo141	Northern	Continent	Owl pellet	5.762222	48.747500	mand
32	FRBo142	Northern	Continent	Owl pellet	5.762222	48.747500	mand
33	FRBo143	Northern	Continent	Owl pellet	5.762222	48.747500	mand
34	FRBo144	Northern	Continent	Owl pellet	5.762222	48.747500	mand
35	FRBo145	Northern	Continent	Owl pellet	5.762222	48.747500	mand
36	FRBo146	Northern	Continent	Owl pellet	5.762222	48.747500	mand
37							
38	FRBo147	Northern	Continent	Owl pellet	5.762222	48.747500	mand
39	FRBo148	Northern	Continent	Owl pellet	5.762222	48.747500	mand
40	FRBo149	Northern	Continent	Owl pellet	5.762222	48.747500	mand
41	FRBo150	Northern	Continent	Owl pellet	5.762222	48.747500	mand
42							
43	FRBo151	Northern	Continent	Owl pellet	5.762222	48.747500	mand
44	FRBo152	Northern	Continent	Owl pellet	5.762222	48.747500	mand
45	FRBo153	Northern	Continent	Owl pellet	5.762222	48.747500	mand
46	FRBo154	Northern	Continent	Owl pellet	5.762222	48.747500	mand
47	FRBo155	Northern	Continent	Owl pellet	5.762222	48.747500	mand
48	FRBo156	Northern	Continent	Owl pellet	5.762222	48.747500	mand
49	FRBo157	Northern	Continent	Owl pellet	5.762222	48.747500	mand
50	FRBo158	Northern	Continent	Owl pellet	5.762222	48.747500	mand
51	FRBo159	Northern	Continent	Owl pellet	5.762222	48.747500	mand
52	FRBo160	Northern	Continent	Owl pellet	5.762222	48.747500	mand
53	FRBo161	Northern	Continent	Owl pellet	5.762222	48.747500	mand
54	FRBo162	Northern	Continent	Owl pellet	5.762222	48.747500	mand
55	FRBo163	Northern	Continent	Owl pellet	5.762222	48.747500	mand
56							
57							
58							
59							
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3	FRBo164	Northern	Continent	Owl pellet	5.762222	48.747500	mand
4	FRBo165	Northern	Continent	Owl pellet	5.762222	48.747500	mand
5	FRBo166	Northern	Continent	Owl pellet	5.762222	48.747500	mand
6							
7	FRCh043A	Northern	Continent	Owl pellet	5.431667	45.444722	mand
8	FRCh38	Northern	Continent	Owl pellet	5.431667	45.444722	mand
9	FRCh39	Northern	Continent	Owl pellet	5.431667	45.444722	mand
10	FRCh40	Northern	Continent	Owl pellet	5.431667	45.444722	mand
11	FRCh41	Northern	Continent	Owl pellet	5.431667	45.444722	mand
12	FRCh42	Northern	Continent	Owl pellet	5.431667	45.444722	mand
13	FRCh44	Northern	Continent	Owl pellet	5.431667	45.444722	mand
14	FRCh45	Northern	Continent	Owl pellet	5.431667	45.444722	mand
15	FRCh46	Northern	Continent	Owl pellet	5.431667	45.444722	mand
16	FRCh48	Northern	Continent	Owl pellet	5.431667	45.444722	mand
17	FRCh49	Northern	Continent	Owl pellet	5.431667	45.444722	mand
18	FRCh50	Northern	Continent	Owl pellet	5.431667	45.444722	mand
19	FRCh51	Northern	Continent	Owl pellet	5.431667	45.444722	mand
20	FRCh52	Northern	Continent	Owl pellet	5.431667	45.444722	mand
21	FRCh54	Northern	Continent	Owl pellet	5.431667	45.444722	mand
22	FRCh55	Northern	Continent	Owl pellet	5.431667	45.444722	mand
23	FRCh56	Northern	Continent	Owl pellet	5.431667	45.444722	mand
24	FRCh58	Northern	Continent	Owl pellet	5.431667	45.444722	mand
25	FRCM1	Northern	Continent	Owl pellet	4.727500	45.384722	mand
26	FRFS24	Northern	Continent	Owl pellet	4.692778	45.297500	mand
27	FRFS25	Northern	Continent	Owl pellet	4.692778	45.297500	mand
28	FRFS26	Northern	Continent	Owl pellet	4.692778	45.297500	mand
29	FRFT12	Northern	Continent	Owl pellet	5.524444	45.527500	mand
30	FRGL035A	Northern	Continent	Owl pellet	5.420556	45.399167	mand
31	FRGL33	Northern	Continent	Owl pellet	5.420556	45.399167	mand
32	FRGL34	Northern	Continent	Owl pellet	5.420556	45.399167	mand
33	FRLe37	Northern	Continent	Owl pellet	5.114167	45.300000	mand
34	FRLo13	Northern	Continent	Owl pellet	5.348333	45.419722	mand
35	FRLo14	Northern	Continent	Owl pellet	5.348333	45.419722	mand
36	FRMu16	Northern	Continent	Owl pellet	5.315833	45.213889	mand
37	FRMu36	Northern	Continent	Owl pellet	5.315833	45.213889	mand
38	FRPD3082	Northern	Continent	Owl pellet	6.381797	49.007092	mand/skull
39	FRSJ030A	Northern	Continent	Owl pellet	5.138611	45.503056	mand
40	FRSJ030B	Northern	Continent	Owl pellet	5.138611	45.503056	mand
41	FRSJ030C	Northern	Continent	Owl pellet	5.138611	45.503056	mand
42	FRSJ10	Northern	Continent	Owl pellet	5.138611	45.503056	mand
43	FRSJ11	Northern	Continent	Owl pellet	5.138611	45.503056	mand
44	FRSJ28	Northern	Continent	Owl pellet	5.138611	45.503056	mand
45	FRSJ31	Northern	Continent	Owl pellet	5.138611	45.503056	mand
46	FRSJ32	Northern	Continent	Owl pellet	5.138611	45.503056	mand
47	FRSJ9	Northern	Continent	Owl pellet	5.138611	45.503056	mand
48	FRSS3	Northern	Continent	Owl pellet	4.212500	45.948611	mand
49							
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3	FRSS4	Northern	Continent	Owl pellet	4.212500	45.948611	mand
4	FRSS5	Northern	Continent	Owl pellet	4.212500	45.948611	mand
5	FRSS6	Northern	Continent	Owl pellet	4.212500	45.948611	mand
6							
7	FRVa17	Northern	Continent	Owl pellet	5.411389	45.256944	mand
8	FRVa18	Northern	Continent	Owl pellet	5.411389	45.256944	mand
9	FRVe129	Northern	Continent	Owl pellet	4.663333	45.369167	mand
10	FRVe22	Northern	Continent	Owl pellet	4.663333	45.369167	mand
11	FRVe23	Northern	Continent	Owl pellet	4.663333	45.369167	mand
12							
13	FRVy7	Northern	Continent	Owl pellet	4.657222	45.738333	mand
14	ITPr0004	Northern	Continent	Trapping	10.248014	46.286975	mand/skull
15	ITTg49	Northern	Continent	Museum	7.571240	45.807200	mand/skull
16	POBiebrza129355	Northern	Continent	Museum	22.573378	53.643861	mand/skull
17	POBiebrza129373	Northern	Continent	Museum	22.573378	53.643861	mand/skull
18	POBiebrza129376	Northern	Continent	Museum	22.573378	53.643861	mand/skull
19	POBiebrza129377	Northern	Continent	Museum	22.573378	53.643861	mand/skull
20	POBiebrza129392	Northern	Continent	Museum	22.573378	53.643861	mand/skull
21	POBiebrza150912	Northern	Continent	Museum	22.573378	53.643861	mand/skull
22	POBiebrza151115	Northern	Continent	Museum	22.573378	53.643861	mand/skull
23	POBiebrza151140	Northern	Continent	Museum	22.573378	53.643861	mand
24	POBiebrza151141	Northern	Continent	Museum	22.573378	53.643861	mand/skull
25	POBiebrza151151	Northern	Continent	Museum	22.573378	53.643861	mand/skull
26	POBPN135315	Northern	Continent	Museum	23.900117	52.709481	mand/skull
27	POBPN135316	Northern	Continent	Museum	23.900117	52.709481	mand/skull
28	POBPN135318	Northern	Continent	Museum	23.900117	52.709481	mand/skull
29	POBPN135319	Northern	Continent	Museum	23.900117	52.709481	mand/skull
30	POBPN135320	Northern	Continent	Museum	23.900117	52.709481	mand/skull
31	POBPN135345	Northern	Continent	Museum	23.900117	52.709481	mand/skull
32	POBPN135346	Northern	Continent	Museum	23.900117	52.709481	mand/skull
33	POBPN135347	Northern	Continent	Museum	23.900117	52.709481	mand/skull
34	POBPN135402	Northern	Continent	Museum	23.900117	52.709481	mand/skull
35	POBPN135411	Northern	Continent	Museum	23.900117	52.709481	mand/skull
36	OMHa10	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
37	OMHa11	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
38	OMHa12	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
39	OMHa3BM	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
40	OMHa3CM	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
41	OMHa3M	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
42	OMHa4	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
43	OMHa6	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
44	OMHa9F	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
45	OMHa9F	OMainland	OMainland	Trapping	-3.190167	59.033728	mand/skull
46	OMHa9M	OMainland	OMainland	Trapping	-3.190167	59.033728	mand
47	OMHo15	OMainland	OMainland	Trapping	-3.067628	58.946361	mand/skull
48	OMSa1	OMainland	OMainland	Trapping	-3.297169	59.048261	mand/skull
49	OMSa2	OMainland	OMainland	Trapping	-3.297169	59.048261	mand/skull
50							
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2							
3	OMSO1	OMainland	OMainland	Trapping	-2.950003	58.950019	mand
4	OMSO10F	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
5	OMSO11	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
6	OMSO12	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
7	OMSO13	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
8	OMSO15	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
9	OMSO16	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
10	OMSO17	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
11	OMSO18	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
12	OMSO2	OMainland	OMainland	Trapping	-2.950003	58.950019	mand
13	OMSO20	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
14	OMSO21	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
15	OMSO24	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
16	OMSO25	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
17	OMSO26	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
18	OMSO28	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
19	OMSO29	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
20	OMSO3	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
21	OMSO30	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
22	OMSO31	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
23	OMSO35	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
24	OMSO36	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
25	OMSO37	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
26	OMSO38	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
27	OMSO4	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
28	OMSO5	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
29	OMSO6M	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
30	OMSO7F	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
31	OMSO8M	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
32	OMSO9F	OMainland	OMainland	Trapping	-2.950003	58.950019	mand/skull
33	OMTa10	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
34	OMTa2	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
35	OMTa3	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
36	OMTa4	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
37	OMTa5	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
38	OMTa6	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
39	OMTa7	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
40	OMTa8	OMainland	OMainland	Trapping	-2.850033	58.950006	mand/skull
41	OMTa9	OMainland	OMainland	Trapping	-2.850033	58.950006	skull
42	OSGr10	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
43	OSGr12	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
44	OSGr14	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
45	OSGr15	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
46	OSGr18	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
47	OSGr20	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
48							
49							
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3	OSGr23	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
4	OSGr25	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
5	OSGr27	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
6							
7	OSGr28	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
8	OSGr31	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
9							
10	OSGr35	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
11	OSGr39	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
12	OSGr42	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
13	OSGr45	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
14	OSGr49	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
15							
16	OSGr50	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
17	OSGr7	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand
18	OSGr8	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
19	OSGr9	OSRonaldsay	OSRonaldsay	Trapping	-2.916700	58.816678	mand/skull
20							
21	OSWW11	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
22	OSWW12	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
23	OSWW13	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
24	OSWW14	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
25	OSWW15	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
26							
27	OSWW16	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand
28	OSWW17	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
29	OSWW18	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
30	OSWW19	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
31	OSWW20	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
32	OSWW21	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
33	OSWW23	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
34	OSWW24	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
35	OSWW25	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
36	OSWW26	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
37	OSWW28	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
38							
39	OSWW6	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
40	OSWW7	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
41	OSWW8	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand/skull
42	OSWW9	OSRonaldsay	OSRonaldsay	Trapping	-2.940694	58.766808	mand
43							
44	OWLS1	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
45	OWLS112	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
46	OWLS2	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
47	OWLS24	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
48	OWLS25	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
49	OWLS36	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
50	OWLS37	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
51	OWLS38	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
52	OWLS55	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
53	OWLS59	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
54	OWLS6	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
55							
56							
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58							
59							
60							



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3	OWLS60	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
4	OWLS61	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
5	OWLS72	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
6							
7	OWLS73	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
8	OWLS82	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
9	OWLS83	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
10	OWLS84	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
11	OWLS85	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
12	OWLS99	OWestray	OWestray	Trapping	-2.933353	59.283347	mand/skull
13	OWNe102	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
14	OWNe103	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
15	OWNe2	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
16	OWNe26	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
17	OWNe28	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
18	OWNe29	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
19	OWNe30	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
20	OWNe31	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
21	OWNe4	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
22	OWNe41	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
23	OWNe42	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
24	OWNe43	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
25	OWNe47	OWestray	OWestray	Trapping	-2.866747	59.233358	mand
26	OWNe6	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
27	OWNe62	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
28	OWNe68	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
29	OWNe7	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
30	OWNe75	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
31	OWNe89	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
32	OWNe90	OWestray	OWestray	Trapping	-2.866747	59.233358	mand/skull
33	ITSi11	SouthItalian	Continent	Trapping	16.491144	39.352214	mand/skull
34	ITSi17	SouthItalian	Continent	Trapping	16.491144	39.352214	mand/skull
35	ITSi21	SouthItalian	Continent	Trapping	16.491144	39.352214	mand/skull
36	ESCoE138	Western	Continent	Trapping	-3.627161	43.019269	mand
37	ESEM69	Western	Continent	Trapping	-3.450258	43.142322	mand/skull
38	ESNa1131	Western	Continent	Private	-1.645500	43.175708	mand/skull
39	ESNa1286	Western	Continent	Private	-1.645500	43.175708	mand/skull
40	ESNa137	Western	Continent	Private	-1.645500	43.175708	mand/skull
41	ESNa1379	Western	Continent	Private	-1.645500	43.175708	mand/skull
42	ESNa1576	Western	Continent	Private	-1.645500	43.175708	mand/skull
43	ESNa1577	Western	Continent	Private	-1.645500	43.175708	mand/skull
44	ESNa1579	Western	Continent	Private	-1.645500	43.175708	mand/skull
45	ESNa172	Western	Continent	Private	-1.645500	43.175708	mand/skull
46	ESNa1757	Western	Continent	Private	-1.645500	43.175708	mand/skull
47	ESNa1758	Western	Continent	Private	-1.645500	43.175708	mand/skull
48	ESNa239	Western	Continent	Private	-1.645500	43.175708	skull
49							
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56							
57							
58							
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2							
3	ESNa240	Western	Continent	Private	-1.645500	43.175708	mand/skull
4	ESNa318	Western	Continent	Private	-1.645500	43.175708	mand/skull
5	ESNa399	Western	Continent	Private	-1.645500	43.175708	mand/skull
6							
7	ESNa406	Western	Continent	Private	-1.645500	43.175708	mand/skull
8	ESNa460	Western	Continent	Private	-1.645500	43.175708	mand/skull
9	ESNa461	Western	Continent	Private	-1.645500	43.175708	mand/skull
10	ESNa463	Western	Continent	Private	-1.645500	43.175708	mand/skull
11	ESNa47	Western	Continent	Private	-1.645500	43.175708	mand/skull
12	ESNa509	Western	Continent	Private	-1.645500	43.175708	mand/skull
13	ESNa598	Western	Continent	Private	-1.645500	43.175708	mand/skull
14	ESNa633	Western	Continent	Private	-1.645500	43.175708	mand/skull
15	ESNa739	Western	Continent	Private	-1.645500	43.175708	mand/skull
16	ESNa752	Western	Continent	Private	-1.645500	43.175708	mand/skull
17	ESNa798	Western	Continent	Private	-1.645500	43.175708	mand/skull
18	ESNa803	Western	Continent	Private	-1.645500	43.175708	mand/skull
19	ESNa861	Western	Continent	Private	-1.645500	43.175708	mand/skull
20	FRCu136	Western	Continent	Owl pellet	3.885000	44.989444	mand
21	FRSA079A	Western	Continent	Owl pellet	1.167500	44.886667	mand
22	FRSA079B	Western	Continent	Owl pellet	1.167500	44.886667	mand
23	FRSA168	Western	Continent	Owl pellet	1.167500	44.886667	mand
24	FRSA169	Western	Continent	Owl pellet	1.167500	44.886667	mand
25	FRSA171	Western	Continent	Owl pellet	1.167500	44.886667	mand
26	FRSA172	Western	Continent	Owl pellet	1.167500	44.886667	mand
27	FRSA173	Western	Continent	Owl pellet	1.167500	44.886667	mand
28	FRSA68	Western	Continent	Owl pellet	1.167500	44.886667	mand
29	FRSA69	Western	Continent	Owl pellet	1.167500	44.886667	mand
30	FRSA70	Western	Continent	Owl pellet	1.167500	44.886667	mand
31	FRSA71	Western	Continent	Owl pellet	1.167500	44.886667	mand
32	FRSA72	Western	Continent	Owl pellet	1.167500	44.886667	mand
33	FRSA74	Western	Continent	Owl pellet	1.167500	44.886667	mand
34	FRSA75	Western	Continent	Owl pellet	1.167500	44.886667	mand
35	FRSA77	Western	Continent	Owl pellet	1.167500	44.886667	mand
36	FRSA78	Western	Continent	Owl pellet	1.167500	44.886667	mand
37	FRSA81	Western	Continent	Owl pellet	1.167500	44.886667	mand
38	FRSA82	Western	Continent	Owl pellet	1.167500	44.886667	mand
39	FRSA83	Western	Continent	Owl pellet	1.167500	44.886667	mand
40	FRSA85	Western	Continent	Owl pellet	1.167500	44.886667	mand
41	FRSN117	Western	Continent	Owl pellet	3.790000	44.891111	mand
42	FRSN118	Western	Continent	Owl pellet	3.790000	44.891111	mand
43	FRSN120	Western	Continent	Owl pellet	3.790000	44.891111	mand
44	FRSN121	Western	Continent	Owl pellet	3.790000	44.891111	mand
45	FRSN123	Western	Continent	Owl pellet	3.790000	44.891111	mand
46	FRSN124	Western	Continent	Owl pellet	3.790000	44.891111	mand
47	FRSN125	Western	Continent	Owl pellet	3.790000	44.891111	mand
48	FRSN126	Western	Continent	Owl pellet	3.790000	44.891111	mand
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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

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

Number	Mandibles			Skulls		
	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

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

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

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

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

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

Significant VIP values in bold.

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

Number	Mandibles			Skulls		
	Eigenvalue	Percentage explained	Cumulative percentage explained	Eigenvalue	Percentage explained	Cumulative percentage explained
1	<b>1.052651</b>	45.2558	45.2558	<b>1.277708</b>	43.6205	43.6205
2	<b>0.566254</b>	24.3445	69.6004	<b>0.543716</b>	18.5623	62.1828
3	<b>0.186308</b>	8.0098	77.6101	<b>0.351271</b>	11.9923	74.1751
4	<b>0.179597</b>	7.7213	85.3314	<b>0.308121</b>	10.5191	84.6942
5	<b>0.098454</b>	4.2328	89.5642	<b>0.197237</b>	6.7336	91.4278
6	<b>0.090917</b>	3.9087	93.4729	<b>0.126866</b>	4.3311	95.7589
7	<b>0.067079</b>	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					

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	

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## 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 <sup>1</sup>	SE	Lower 95%	Upper 95%	Pairwise significance <sup>2</sup>		
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	-	-	-



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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	-	-	-

<sup>1</sup>Groups ordered by mean size in descending order and by continental and island groups.

<sup>2</sup>Groups not connected by letters are significantly different.

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**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	<b>&lt;0.001</b>	0.0079	<b>&lt;0.001</b>									
5-Italian	<b>&lt;0.001</b>	0.0024	<b>&lt;0.001</b>	<b>&lt;0.001</b>								
6-O Mainland	<b>&lt;0.001</b>	0.1117	<b>0.0004</b>	<b>&lt;0.001</b>	<b>0.0004</b>							
7-O S Ronaldsay	<b>&lt;0.001</b>	0.0437	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>						
8-O Westray	<b>&lt;0.001</b>	0.0066	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	0.1763				
9-Western	<b>&lt;0.001</b>	0.0026	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.0003</b>	0.2481				
10-South Italian	0.0594	1	0.0351	<b>0.0009</b>	0.0039	0.0771	0.1364	0.2582	0.0934			
11-Belle Ile	<b>&lt;0.001</b>	0.1292	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>0.0001</b>	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	<b>&lt;0.001</b>	0.0026									
4-Northern	<b>&lt;0.001</b>	0.0059	<b>&lt;0.001</b>								
5-Italian	0.9919	0.0058	<b>&lt;0.001</b>	<b>&lt;0.001</b>							
6-O Mainland	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>						
7-O S Ronaldsay	<b>&lt;0.001</b>	<b>0.0006</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>					
8-O Westray	<b>&lt;0.001</b>	<b>0.0002</b>	<b>&lt;0.001</b>	<b>0.0001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>				
9-Western	<b>0.0009</b>	0.4016	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>	<b>&lt;0.001</b>			
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.