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Original Article

Insular evolution from an archaeological perspective: a case study of Orkney house mouse

Andrzej A. Romaniuk^{1,*}, Sabrina Renaud², Robin Bendrey^{3,**}, Jeremy B. Searle⁴,
Olwyn Owen⁵ and Jeremy Herman⁶

¹Institute for Advanced Studies in the Humanities, The University of Edinburgh, Hope Park Square, Edinburgh EH8 9NW, UK

²Laboratoire de Biométrie et Biologie Evolutive, UMR 5558, CNRS, Université Lyon 1, Université de Lyon, 69100 Villeurbanne Cedex, France

³School of History, Classics and Archaeology, The University of Edinburgh, Teviot Place, Edinburgh EH8 9AG, UK

⁴Department of Ecology & Evolutionary Biology, Corson Hall, Cornell University, Ithaca, NY 14853, USA

⁵Institute of Archaeology, University of the Highlands and Islands, Orkney College, East Road, Kirkwall, Orkney KW15 1LX, UK

⁶Department of Natural Sciences, National Museums Scotland, Chambers Street, Edinburgh EH1 1JF, UK

*Corresponding author. Institute for Advanced Studies in the Humanities, The University of Edinburgh, Hope Park Square, Edinburgh EH8 9NW, UK.

E-mail: andrzej.romaniuk@ed.ac.uk

**Secondary corresponding author. School of History, Classics and Archaeology, The University of Edinburgh, Teviot Place, Edinburgh EH8 9AG, UK.

E-mail: robin.bendrey@ed.ac.uk

ABSTRACT

Archaeological material adds a temporal dimension to evolutionary studies that is valuable for elucidating long-term population stability and evolutionary shifts for species closely associated with humans. Here, a two-dimensional geometric morphometrics approach on first upper molars was applied to modern and archaeological samples to assess the evolution of house mice in Orkney, an archipelago north of Scotland. Modern populations included localities in Orkney, north Scotland, and France. Two archaeological sites in Orkney represented the Norse period: Birsay Beachview (Mainland) and Tuquoy (Westray) (10th–14th/15th centuries AD). The archaeological specimens were larger than modern specimens from similar settings, suggesting processes leading to a recent decline in the size of Orkney house mice. Molar morphology and associated non-metric traits distinct to the Orkney lineage were already established in the Norse period, as indicated by morphological similarity of the Birsay samples to modern Orkney and north Scotland populations. Stability of human settlement is likely to influence morphological evolution in house mice. The Birsay site, located in Birsay village, which has been inhabited since Norse times, might represent the ancestral house mouse population in Orkney. Tuquoy, a settlement abandoned by the end of the medieval period, provided samples different from modern house mouse populations in Westray and neighbouring isles.

Keywords: Birsay; body size; commensalism; evolution; geometric morphometrics; insular environment; *Mus musculus*; Orkney; population stability; Tuquoy

INTRODUCTION

The inclusion of archaeological or palaeontological samples in evolutionary studies on modern species can contribute to our understanding of the complexity of individual population histories. In the case of the water vole (*Arvicola amphibius*) population in Britain, for example, only the consideration of ancient DNA samples from multiple sampling locations, alongside modern DNA evidence, enabled two major introduction events to be distinguished effectively, with a second wave leading to replacement of the original population in England (Brace *et al.* 2016). Well-preserved fossil molar teeth can also

be a valuable source of information on the past, being helpful in understanding how early populations were established and to decipher their subsequent history [e.g. dispersion of the house mouse, *Mus musculus*, from the Near East (Cucchi *et al.* 2020) and colonization of islands by house mice (Michaux *et al.* 2007) and spiny mice, *Acomys cahirinus* (Renaud *et al.* 2020)] or to investigate specific morphological changes between time periods [e.g. size of house mice (Cassaing *et al.* (2011) or Japanese field mice, *Apodemus speciosus* (Millien and Damuth 2004)]. Over longer time scales, evolutionary research can rely predominantly on palaeontological samples, for example to test the relationship

between evolution and climate change in related species (Renaud *et al.* 2005).

The well-studied house mouse (Berry *et al.* 2008) has its recent evolution associated with its ability to take advantage of the ecological niches created by human populations moving to a sedentary lifestyle in the late Upper Palaeolithic (Weissbrod *et al.* 2017). The early adoption of the commensal lifestyle and behaviour (Ganem 2012, Hulme-Beaman *et al.* 2016) resulted in introductions of house mice, alongside human migrations and trade, beyond their natural range and their current presence throughout the majority of Eurasia, the Americas, Australia, and a significant portion of Africa (Auffray *et al.* 1990, Cucchi *et al.* 2005, 2020, Berry *et al.* 2008, Jones *et al.* 2013, Suzuki *et al.* 2013). In particular, insular populations of western subspecies of the house mouse (*Mus musculus domesticus* Schwarz & Schwarz, 1943) have received much attention from archaeologists and evolutionary biologists. On certain islands, multiple introductions have resulted in high levels of genetic diversity (e.g. Cyprus; García-Rodríguez *et al.* 2018). However, long-term isolation and distinct environments apparently drove differentiation in many other insular populations.

Such a case of insular evolution is found in Orkney, an archipelago located off the north coast of Scotland, UK. The introduction of house mice to the isles most probably happened during the intensification of Atlantic trade in the Norse period (9th–12th centuries AD; Booth and Booth 2005, Searle *et al.* 2009), which was later followed by a period of stagnation and subsequent societal decline alongside a shift towards inland farming (13th–15th centuries AD; Griffiths *et al.* 2019: 309–24) and long-term relative isolation (Berry 2000: 198–219). The research on modern samples in the 1970s–1990s using a variety of approaches (cytogenetics, morphometrics, allozymes, and Y-chromosome and mitochondrial DNA typing; reviewed by Searle 1991), more recent mitochondrial DNA studies (Searle *et al.* 2009), and subsequent studies combining mitochondrial and microsatellite data with morphometrics (Chevret *et al.* 2021) have all pointed to a distinct ‘Orkney’ population. The so-called ‘Orkney lineage’ is currently present both in the archipelago and in the two northernmost counties of mainland Scotland, Caithness and Sutherland. The most recent morphometric studies of Chevret *et al.* (2021) were based on the upper first molar and, in addition to confirming an ‘Orkney’ population, they demonstrated differentiation between the isles composing the Orkney archipelago, with a significant contributory factor being genetic drift rather than adaptation. A pattern of accessory cusps located frontally on the main second cusp, specific to insular populations (Renaud *et al.* 2011) and probably related to tooth elongation (Ledevin *et al.* 2016, Hayden *et al.* 2020), has also been found in the archipelago (Renaud *et al.* 2018), alongside the presence of accessory cusps on other parts of the molar.

In this paper, we extend this earlier morphometric work on modern samples by including archaeological material, investigating the relationship between modern continental, Orkney, and north Scotland (Caithness and Sutherland) house mouse populations and two archaeological populations from the period when house mice were introduced to the Orkney isles. Teeth are usually the most durable representation of micromammals in sieved archaeological contexts (e.g. Romaniuk *et al.* 2023), and their morphological variation mirrors the

genetic differentiation of house mice even on small spatial scales (Chevret *et al.* 2021). Therefore, geometric morphometrics of the first upper molar was applied to compare modern and archaeological samples, together with the record of accessory cusps potentially specific to Orkney populations. Investigation of molar shape over time using archaeological and modern specimens allows inferences to be made about selection pressures and related evolutionary changes, both of which are influenced by the changing environment. Modern continental populations of house mice from France were used as a reference to study the modern and archaeological Orkney populations.

Three research questions were asked based on our morphological analysis. First, is there a size difference between modern and archaeological house mice in Orkney, and if yes, what might explain the trends observed? Second, was the idiosyncrasy of the Orcadian population already established in the Norse period when they were introduced? Third, how morphologically stable was the Orkney population over the long term?

MATERIALS AND METHODS

Material

Archaeological first upper molars included in this study came from two localities, both being settlement sites dated to the Norse/medieval period (10th–14th/15th centuries AD; for location, see Fig. 1; for details, see Table 1). One represents Mainland, the largest island and the socio-economic centre of Orkney, and the other Westray, a mid-sized island in the northern part of the archipelago. Recent research on micromammal assemblages from these sites (Romaniuk 2022, Romaniuk *et al.* 2023) provided evidence for the presence of a population of house mice during the period of construction of the sites, their utilization and later abandonment, with data obtained providing evidence for likely residence of this species within or nearby to identified enclosures.

Mainland is represented by the site of Birsay Beachview (also referenced as Birsay Bay), a group of three excavation areas in the vicinity of the modern Birsay village, investigated between 1978 and 1980 and radiocarbon dated to between AD 980 and 1210 (Cook 1996). Area 1 (Beachview Studio; see Morris 1996: 1–8 and 76–160) was the largest trench excavated and produced structural remains and midden-like contexts reflecting a period of construction, utilization, and abandonment of a building and its peripheries. Areas 2 and 3 (Beachview Burnside; see Morris 1996: 1–8 and 52–74) provided evidence associated with open-space activity, such as refuse dumping and minor stone structures, overlain by natural sand accumulation. Sampling and sieving (through meshes of 2, 0.895, and 0.5 mm) encompassed a substantial part of area 1, with key in-enclosure sections having contexts sieved in full, whereas in areas 2 and 3, four specific 1 m × 1 m squares were sieved fully.

Westray is represented by Tuquoy, an eroding settlement site located adjacent to, and associated with, the 12th century AD chapel of Cross Kirk (Owen 1993, 2023, Romaniuk *et al.* 2023). Rescue excavations, in 1982–83, 1988, and 1993, revealed two major Norse structures, termed by their excavators as a Norse ‘hall’ and a ‘workshop’, while a substantial pit on the beach in the immediate vicinity produced rich waterlogged deposits, very rare in an Orkney context. The majority of human activity identified

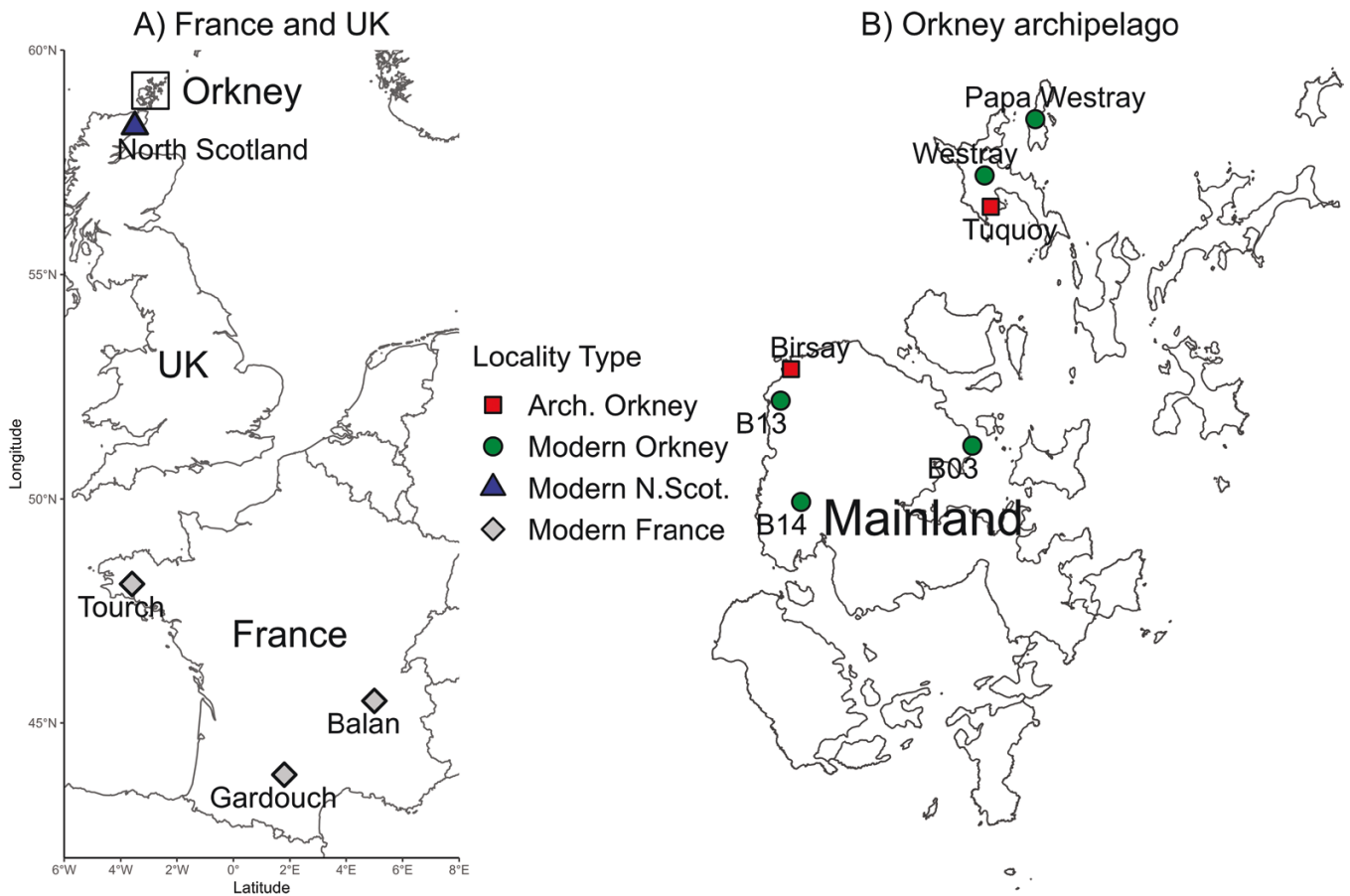


Figure 1. Map showing sampled localities in Orkney, north Scotland, and France. A, localization of the sampling sites in France and UK. B, enlarged view of Orkney.

on the site can be attributed to the 11th–14th centuries AD, with occupation ceasing probably in the 15th century AD, as indicated by an intensive radiocarbon dating programme (Anthony Krus in [Owen forthcoming](#)). Sampling was carried out during the first excavation season, with many soil contexts having >10 L of their content sieved by 1 mm mesh. The second excavation season resulted in the majority of contexts being sieved in full through 4 mm followed by 0.5 mm meshes.

For Birsay, sampling encompassed areas 1 and 2. For area 1, molars were predominantly taken from period 9 internal deposits within the main or kiln structure, when those structures were gradually filled with refuse, clay, sand, ash, and organic material while still in use. Two key contexts from this period, 182 and 198, were radiocarbon dated, the former to AD 1000–1220 and the latter to AD 1134–1280. Other material came from earlier periods 5 and 8, from in-structure contexts representing earlier site utilization, below period 9, or later periods 13–15 overlaying the same area. For area 2, an open-area accumulation contemporary to area 1 (context 11 dated to AD 1030–1280 and context 12 to AD 1020–1280), all unbroken upper molars were sampled.

For Tuquoy, the suitable samples came from three key phases: phase 3 (construction, occupation, and refurbishment of the hall) and phase 4 (construction and use of the workshop, including early, middle, and late phases), followed by phase 5 (gradual abandonment of the site). More than half of the sampled molars

came from deposits within structures; at Tuquoy, these related to hall and workshop floor deposits. Additional samples were found in stone wall infills, while several contexts represented adjacent deposits outside the main buildings or paved areas. A total of 39 radiocarbon dates were obtained for Tuquoy (Krus in [Owen forthcoming](#)), but only two molars came from contexts that have been radiocarbon dated: an artefact-rich midden, context 181, from phase 4 was dated to cal AD 1030–1280 (95% confidence); and context 234, a floor deposit in the middle workshop, also phase 4, was dated to cal AD 1150–1270. Context 181 also provided skeletal remains of a domestic cat.

After the initial check, 172 upper molars were sampled from these sites, photographed, and later incorporated into the study (general overview in [Table 1](#)). All contexts considered were fully sealed under later depositions, with no evidence of invasive burrowing. A brief description and location of each context, including associated radiocarbon dates where available, is provided in [Supporting Information, Table S1](#) (for Birsay, ¹⁴C data are based on [Cook 1996](#); for Tuquoy, ¹⁴C data are taken from Krus, in [Owen forthcoming](#)). A Keyence Digital Microscope VHX-7000/7100 was used to obtain 2160 pixel × 2880 pixel (72 dpi) photographs of the archaeological first upper molars, under ×100 magnification.

Modern molars incorporated in this research have been published previously in studies devoted to Orkney and French house mice ([Renaud et al. 2017](#), [Chevret et al. 2021](#)). To avoid

Table 1. Summary of sampling for this study, including the division into regions and populations, the number of measured molars, and established dating (for archaeological sites) or the year of trapping (for modern localities). For more details, see the [Supporting Information \(Table S1\)](#).

Region	Population	Phase, locality, or province/county	Dating or year sampled	<i>n</i>
Archaeological Orkney	Birsay	Area 1: periods 5 and 8	~980–1210 AD	6
		Area 1: period 9		114
		Area 1: periods 13–15		6
	Tuquoy	Area 2		14
		Phase 3	12 th century AD	6
Phase 4		12–14 th centuries AD	15	
Modern Orkney	Mainland	Phase 5	14–15 th centuries AD	11
		B03	2012	18
		B13	2012	8
	Papa Westray	B14	2012	20
			1992	10
			2012	11
		Westray	1992	9
North Scotland	Brora	Sutherland	1992	9
	Brough	Caithness	1992	3
	Dunnet	Caithness	1992	2
	John o' Groats	Caithness	1992	6
	Lybster	Caithness	1992	4
France	Balan	Auvergne–Rhône–Alpes	2015	10
	Gardouch	Occitania	2003–2004	30
	Tourch	Brittany	2011–2002	30

any effect related to the operator or outline acquisition software, these molars were outlined again according to the same protocol as the archaeological ones. No new sampling or sacrifice took place for the present research.

Methods

On photographs of the occlusal surface, the outline was traced in TPSDIG2 software (Rohlf 2015, previously used by Cucchi *et al.* 2020), starting from the anterior-most point of the frontal cusp. The resulting curve was down-sampled to 64 evenly spaced points, following a standard procedure for the study of murine (-like) molars (e.g. Renaud *et al.* 2018, 2020, Cucchi *et al.* 2020). Following Cucchi *et al.* (2020) and Chevret *et al.* (2021), these points were considered as semi-landmarks during the Procrustes superimposition standardizing for size, position, and orientation of the configurations [generalized Procrustes analysis (GPA); Rohlf and Slice 1990]. According to this procedure, semi-landmarks were allowed to slide along their tangent vectors until their positions minimized the difference in shape between specimens, the criterion being bending energy. Given that for the first upper molars, the first point is defined only as a maximum of curvature, some slight offset might occur between specimens. It was therefore considered as a semi-landmark and allowed to slide between the last and second point (Renaud *et al.* 2020, Chevret *et al.* 2021).

Two GPAs were performed, one including all first upper molars and one focused on Orkney and the neighbouring north Scotland regions of Caithness and Sutherland. Alongside the GPA, the centroid size (*c*-size), defined as the square root of the

sum of the squared distances between each point and the centroid of the configuration, was calculated. The GPA and all subsequent analyses, in addition to visualizations, were coded and executed in R (v.4.2.2, RSTUDIO v.2022.07.2), using R functions available in *geomorph* (Adams *et al.*, 2022), *Morpho* (Schlager, 2017), and *ggplot2* (Wickham 2016) packages.

The maximum length of each molar was also measured in TPSDIG2 from the anterior-most point of the anterior cusp to the posterior-most point. Accessory cusps were scored as present or absent for three locations: between cusps t1 and t4, between cusps t6 and t9, and in front of cusp t2. For this last accessory cusp, variation in its location was also noted by an additional scoring (frontally, on buccal side), with an option of positive score in both cases. For details and examples, see Figure 2.

Between-group differences in univariate data (*c*-size and maximum length) were tested using non-parametric ANOVA (Kruskal–Wallis test) complemented by pairwise Wilcoxon signed-rank test and associated descriptive statistics: median and interquartile range. The correlation between *c*-size and maximum length was investigated using a Pearson correlation and linear regression. Regarding multivariate data (molar shape), between-group differences were tested using Procrustes ANOVA with 10 000 permutations, complemented by pairwise tests based on Procrustes (Euclidean) distances between groups. Parametric and non-parametric ANOVA considered several levels of hierarchical geographical groupings (regions, populations, and localities; see Table 1) before moving to post hoc tests. Given the large number of tests, the significance threshold

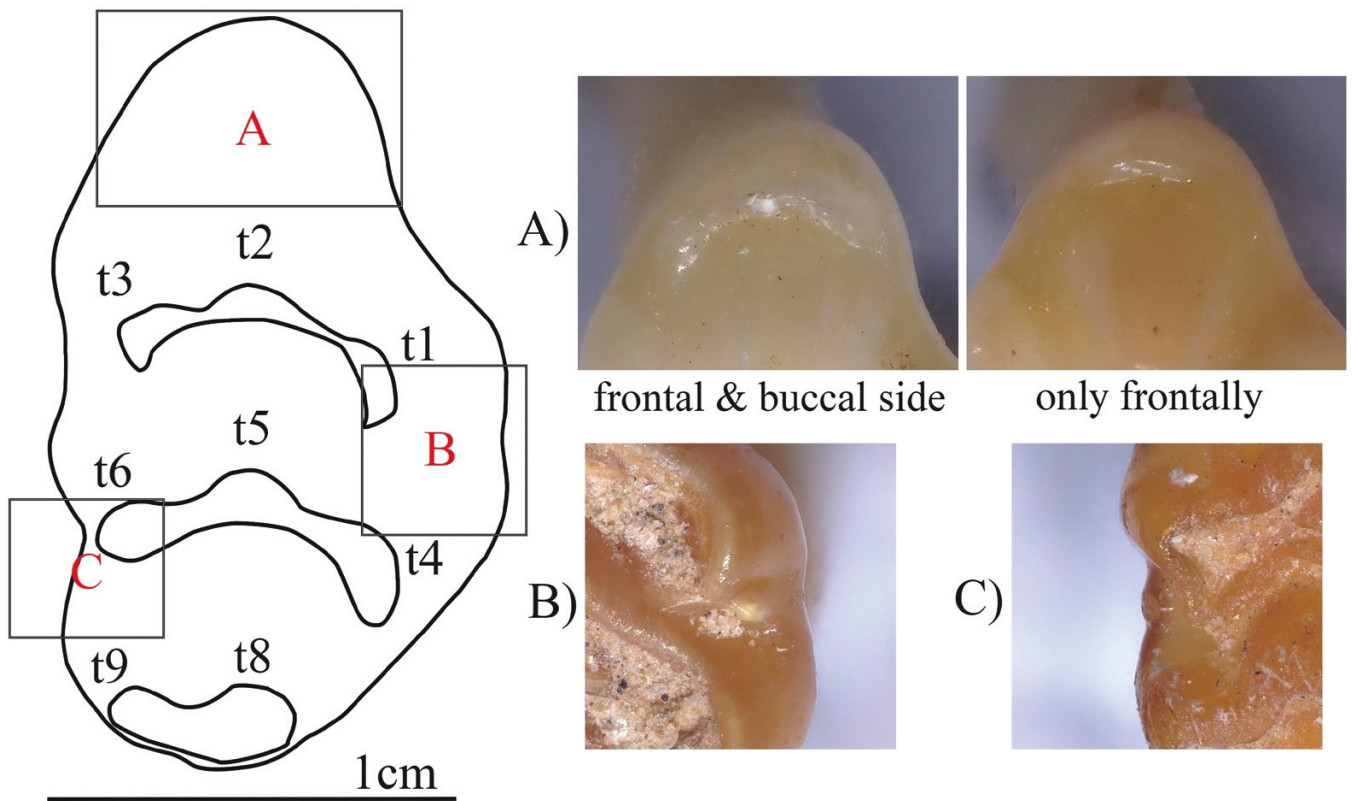


Figure 2. Locations scored for the presence of accessory cusps (A–C), with examples from the archaeological sample included. Regular cusps are shown as t1–t9. For location A, an additional two subscores were created (frontal and buccal side), because the accessory cusps could create a ridge going from the frontal side to the buccal side of t2 (A, left example) or could be visible as a single cusp frontally (A, right example).

in both univariate and multivariate data was considered as corresponding to P -values $< .01$.

Between-group differences in molar shape were visualized using a canonical variate analysis (CVA). Such analysis is prone to an ‘over-fitting’ problem when too many variables are included in comparison to the number of specimens (Kovarovic *et al.* 2011, Mitteroecker and Bookstein 2011). A procedure of dimensionality reduction was therefore applied, retaining in the CVA only a subset of axes of the principal component analysis on the aligned coordinates. The number of axes to be retained was determined as maximizing the cross-validation performance of the CVA (Evin *et al.* 2013). Best performance when using the complete dataset was obtained for either 41 or 42 axes, and in the case of the Scotland-only dataset for 35 or 39 axes. The lower number of axes was used (41 for all data; 35 for Scotland-only data) for the CVAs.

Given knowledge about genetic and morphological differences today (Chevret *et al.* 2021), modern Orkney populations used in the main analysis were divided into individual sampling localities from Mainland (B03, B13, and B14) and years of sampling for Papa Westray (1992 and 2012), whereas the north Scotland localities (Brora, Brough, Dunnet, John o’ Groats, and Lybster) were treated jointly. Westray was considered as the whole island.

RESULTS

Size

Centroid size shows almost perfect linear regression with molar length in millimetres ($P < .001$ and $R^2 = .924$), confirming

that it acts as an overall molar size estimator in our samples of house mice. An overall decrease in c -size occurs between archaeological (median, 5.94; interquartile range, 5.86–6.04) and modern (5.76; 5.63–5.94) Orkney populations, with specimens from modern north Scotland (5.66; 5.51–5.77) and France (5.42; 5.31–5.54) being noticeably smaller (Fig. 3). Kruskal–Wallis test results confirm the difference (Table 2).

Individual populations also differ significantly from each other, with size variation occurring among localities within the same regions (Tables 2 and 3). Samples collected in 1992 from Papa Westray are significantly larger than all other modern and archaeological samples, in terms of both the median and interquartile range (6.18; 6.14–6.25). The difference is most pronounced for comparisons with modern samples, with essentially no overlap present besides other samples from Papa Westray (Fig. 3). For archaeological specimens, Papa Westray samples overlap within the upper end of both site size ranges. However, mice from the same island collected in 2012 display teeth that are similar in size to those from the Birsay site, the nearby island of Westray, and two of the localities from Mainland Orkney (B13 and B14; see Table 3). The remaining Orkney populations are similar to each other and are not substantially different from the north Scotland samples. Differences among regions in France relate exclusively to the Gardouch population being the smallest (5.27; 5.20–5.40). In contrast, the archaeological group seems relatively homogeneous regarding molar size. Tuquoy specimens are slightly larger on average (median 6.02 vs. 5.93 noted for Birsay), with the third quartile also higher (6.14 vs. 6.02). However, the Wilcoxon test P -value between Birsay and Tuquoy

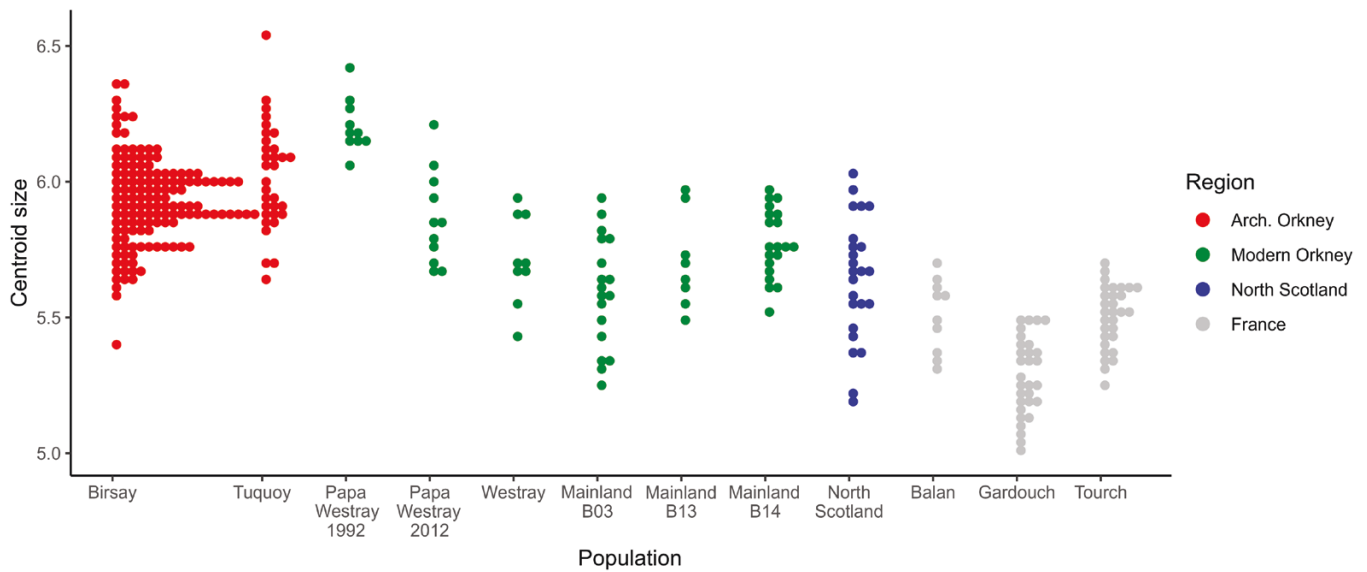


Figure 3. First upper molar centroid size in the different populations.

Table 2. Results of non-parametric Kruskal–Wallis test on centroid size and parametric Procrustes ANOVA on shape data, depending on data and hierarchy level used. Regions and populations are defined as in Table 1. The Scotland dataset combines the Orkney and north Scotland data. *P*-values lower than the adopted significance level of .01 are in bold.

Data	Groups considered	Size (Kruskal–Wallis, whole dataset)			Shape (ANOVA)							
		d.f.	χ^2	<i>P</i> -value	Whole dataset		Scotland dataset					
					d.f. 1	d.f. 2	<i>F</i>	<i>P</i> -value	d.f. 1	d.f. 2	<i>F</i>	<i>P</i> -value
All data	Regions	3	178.35	<.001	3	338	25.9	<.001	2	269	8.96	<.001
All data	Populations	11	219.69	<.001	11	330	11.95	<.001	8	263	7.24	<.001
Modern Orkney	Mainland (B03, B13, and B14), Papa Westray (1992 and 2012), Westray	5	35.28	<.001	5	70	4.66	<.001			4.74	<.001
North Scotland	Brora, Brough, Dunnet, John o' Groats, and Lybster	4	11.82	.019	4	19	0.98	.477			0.97	.486
France	Balan, Gardouch, and Touch	2	29.81	<.001	2	67	3.98	<.001				
Birsay	Periods 5 and 8, period 9, and period 13–15, area 2	3	4.98	.173	3	136	0.97	.481			1	.436
Tuquoy	Phase 3, phase 4, and phase 5	2	2.63	.268	2	29	1.1	.343			1.19	.288

was relatively low ($P = .020$), although higher than the adopted significance level of .01.

Shape

The results of a CVA following a procedure of dimensionality reduction and including all the samples revealed three major groups (Fig. 4): the French populations, Mainland Orkney/north Scotland and nearby archaeological samples, and the northern Orkney isles (Westray and Papa Westray). Among the French populations, Gardouch and Balan are the most extreme towards negative canonical variate 1 (CV1) scores. In contrast, all Scottish populations plot towards positive CV1 values. Orkney populations from the northern isles (Papa Westray and Westray) are differentiated from other Scottish populations towards negative canonical variate 2 (CV2) values. A cluster including Mainland Orkney populations and Birsay plots towards positive CV2 values. Tuquoy and north Scotland appears

as intermediate between this cluster and the other populations from the northern Orkney isles.

Another CVA, focused on Orkney and north Scotland samples (Fig. 5), further enlightens the relative position of the archaeological populations compared with modern ones. North Scotland, Mainland Orkney, and Westray appear in a relatively central position, with Papa Westray being extreme towards positive CV1 values, Birsay towards negative CV1 values, and Tuquoy extreme along the CV2 axis. The separation of Tuquoy samples from the rest of the Orkney molars is especially clear, with only a limited overlap in the morphospace.

These patterns of differentiation are supported by Procrustes ANOVA results and later post hoc tests (Tables 2 and 4). Procrustes ANOVA (Table 2) confirms significant differences in both whole dataset and Scotland sample pools, for whole regions and individual populations (all $P < .001$). However, there is no evidence for significant differences in shape between major

Table 3. Centroid size (median and interquartile range) and *P*-values for Wilcoxon signed-rank test comparisons between population pairs. *P*-values lower than the adopted significance level of .01 are in bold.

Population	Median	Interquartile range	Birsay	Tuquoy	Papa Westray 1992	Papa Westray 2012	Westray	Mainland B03	Mainland B13	Mainland B14	North Scotland	Balan	Gardouch
Birsay	5.93	5.85	6.02										
Tuquoy	6.02	5.89	6.14	.020									
Papa Westray 1992	6.18	6.14	6.25	<.001	.002								
Papa Westray 2012	5.85	5.73	5.97	.143	.014	<.001							
Westray	5.70	5.66	5.87	.001	<.001	<.001	.175						
Mainland B03	5.60	5.45	5.77	<.001	<.001	<.001	.002	.145					
Mainland B13	5.66	5.60	5.79	.001	<.001	<.001	.051	.888	.261				
Mainland B14	5.77	5.69	5.87	<.001	<.001	<.001	.244	.390	.005	.218			
North Scotland	5.66	5.51	5.77	<.001	<.001	<.001	.008	.437	.521	.564	.034		
Balan	5.53	5.40	5.61	<.001	<.001	<.001	<.001	.010	.308	.034	<.001	.066	
Gardouch	5.27	5.20	5.40	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001
Tourch	5.52	5.42	5.60	<.001	<.001	<.001	<.001	.001	.129	.003	<.001	.006	.963 <.001

periods and phases in Birsay or Tuquoy. Regarding the post hoc test results (Table 4), the Tuquoy and Tourch populations were found to be significantly different from the others with the highest *P*-value of .003. The majority of non-significant *P*-values were recorded between Mainland Orkney localities and their comparison to Westray and north Scotland, with two others between Westray and sampling years on Papa Westray. For Birsay, the only non-significant results are related to Mainland locality B13 and north Scotland.

The tree visualizing distances between the mean molar shape for populations (Fig. 6) also supports the dichotomy between the specimens from France and Scotland, at the same time emphasizing the distinctiveness of Tuquoy in comparison to the rest of the populations from Orkney. All modern Orkney populations are clustered together and with north Scotland. Within this cluster, Birsay is most closely associated with north Scotland.

Accessory cusps

Two of the three molar locations scored for the presence of accessory cusps show the presence of the traits only in archaeological and modern Orkney and north Scotland populations (Fig. 7). An accessory cusp in front of and/or to the side of the t2 is present only in Orkney and north Scotland populations. It is documented in almost half of Mainland Orkney molars (45% of B14 teeth) and ~41% of Birsay molars. However, only one molar from Tuquoy exhibits this trait. Accessory cusps on the lingual side, between t1 and t4, are almost exclusive to Papa Westray molars, with only a single case found elsewhere. Samples from both Scotland and France show the occasional presence of an accessory cusp between cusps t6 and t9.

Regarding the exact location of accessory cusps on t2, Birsay molars more commonly exhibit them only frontally, as

a single protrusion, with less than half of molars showing a longer ridge extending to the buccal side or as two separate cusps. A frontal-only location is also noted exclusively for samples from north Scotland and Westray, contrasting with other populations showing predominantly two accessory cusps or a larger ridge between both areas. Mainland Orkney locality B14 is the only place where side-only cusps are frequent.

DISCUSSION

Revisiting the three research questions

The analysis of molar centroid size points towards the presence of two separate decreasing trends, from modern Orkney/north Scotland samples to continental France, and from archaeological to modern specimens (research question 1). Depending on the context, molar size can be considered as an indicator of body size. Within populations, molar and body sizes are unrelated, because molar size does not vary after eruption; hence, it does not document growth of the animal with age (e.g. Lister and Hall 2014, Renaud *et al.* 2017). However, between populations, an increase in molar size is often coupled with an increase in body size (e.g. Renaud *et al.* 2011), with some exceptions, such as cases of macrodontism in Corsican mice (Vigne *et al.* 1993). In the case of Orkney mice, the large molar size appears to be coupled with large body size in comparison to continental mice (see Gray *et al.* 2015). Therefore, differences in molar size noted in this study are likely to reflect changes in body size when making comparisons between regions and time periods or between individual islands and can be investigated as such. The first research question is addressed further in the second section of the Discussion.

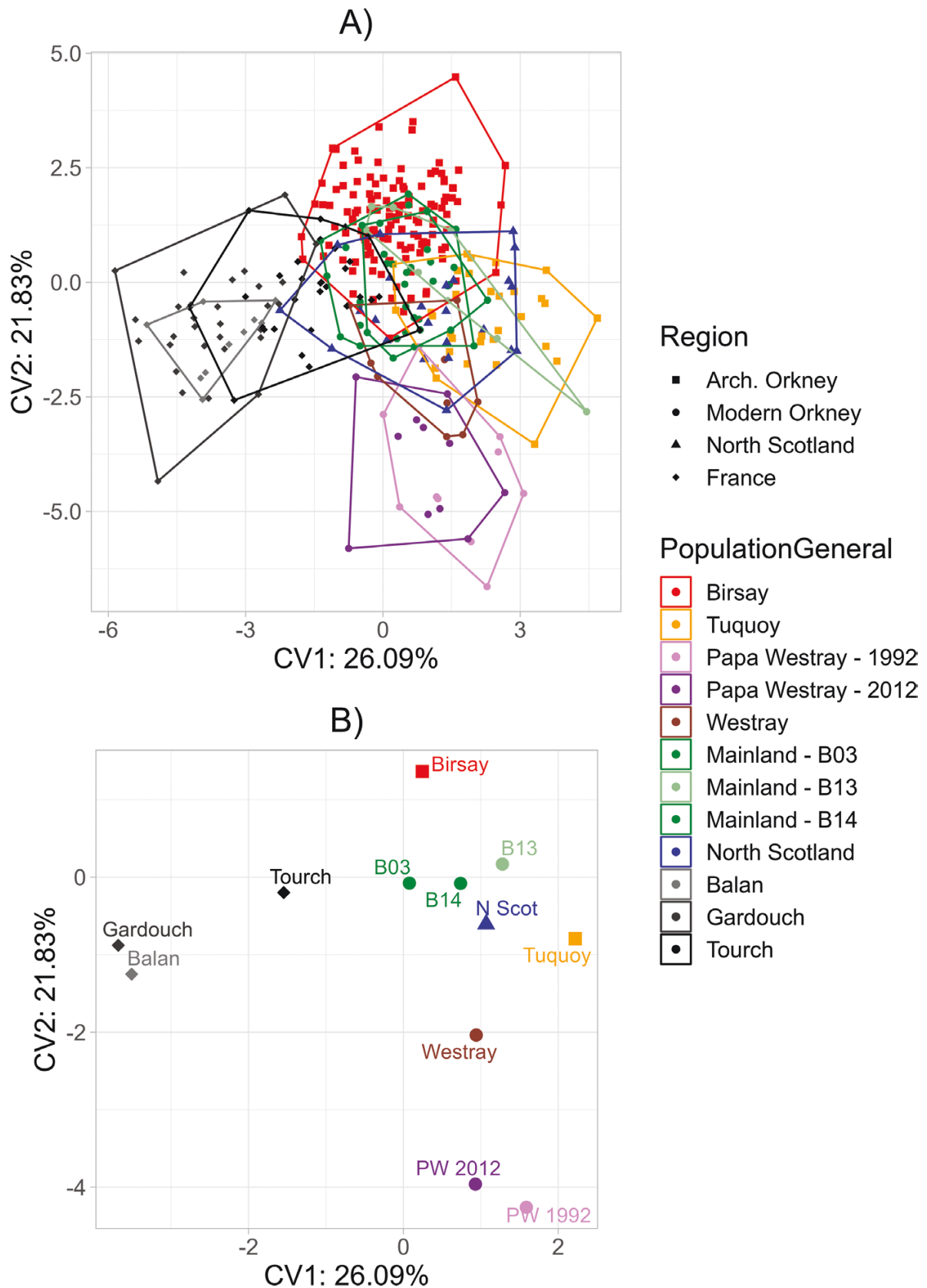


Figure 4. Differentiation of molar shape among populations, based on a canonical variate (CV) analysis on principal component analysis axes on the aligned coordinates, according to a dimension reduction procedure. A, morphospace for the whole dataset (Orkney, north Scotland, and France). Each symbol represents one specimen. B, same morphospace as in A, but each symbol represents a population mean. Abbreviation: PW, Papa Westray.

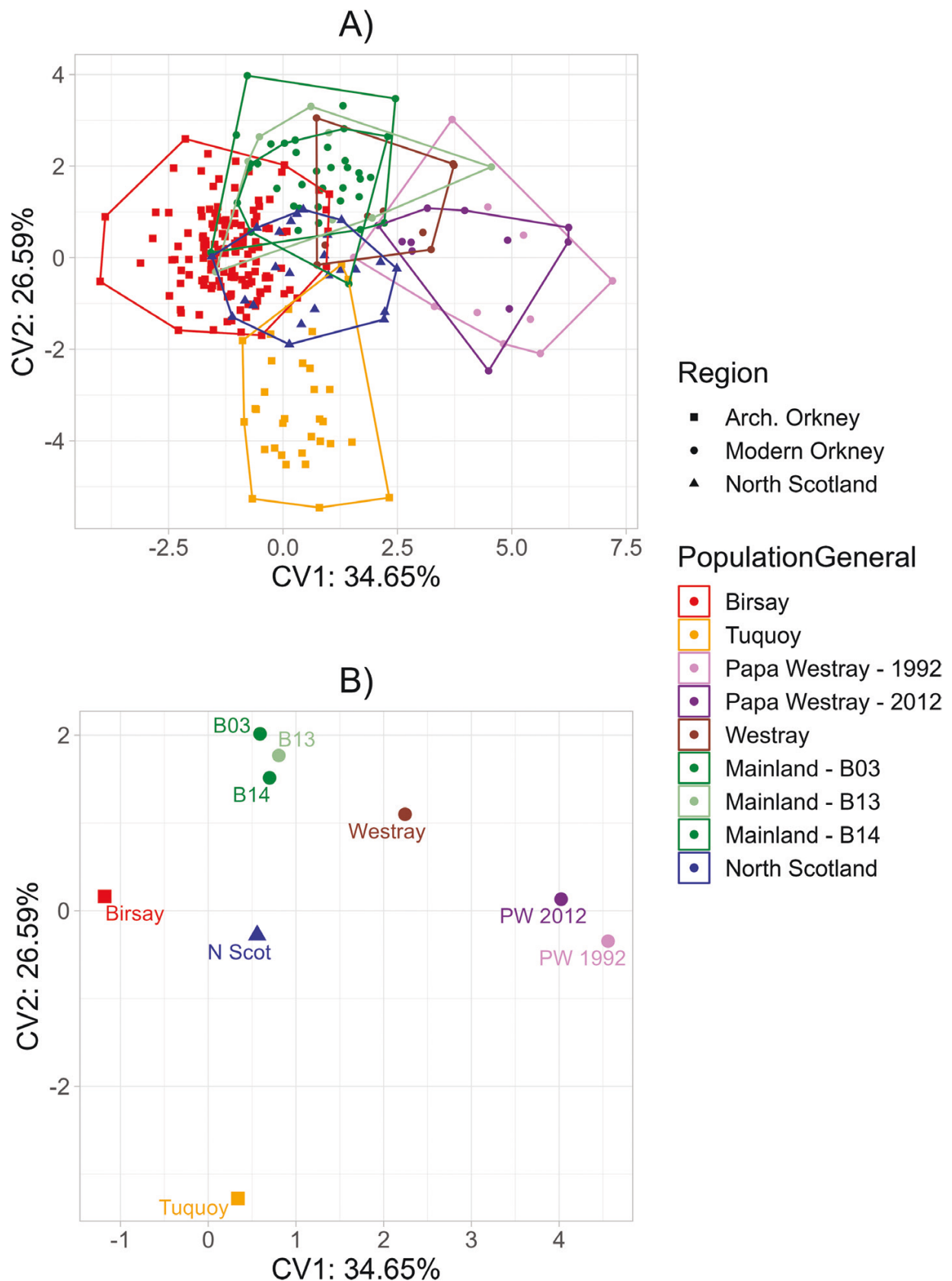


Figure 5. Differentiation of molar shape among populations, based on a canonical variate (CV) analysis on principal component analysis axes on the aligned coordinates, according to a dimension reduction procedure. A, morphospace for the Orkney and north Scotland dataset. Each symbol represents one specimen. B, same morphospace as in A, but each symbol represents a population mean. Abbreviation: PW, Papa Westray.

Table 4. Pairwise post-hoc test on Procrustes (Euclidean) distances; *P*-values are provided for all pairs when comparing data from the whole dataset (A) and from the Scotland-only dataset (B). *P*-values lower than adopted significance level of .01 are in bold.

(A)											
Population	Birsay	Tuquoy	Papa Westray 1992	Papa Westray 2012	Westray	Mainland B03	Mainland B13	Mainland B14	North Scotland	Balan	Gardouch
Tuquoy	<.001										
Papa Westray 1992	<.001	<.001									
Papa Westray 2012	.002	.001	.078								
Westray	<.001	<.001	.045	.001							
Mainland B03	<.001	<.001	.001	<.001	.249						
Mainland B13	.212	.001	.001	.008	.029	.187					
Mainland B14	.007	<.001	<.001	<.001	.019	.084	.947				
North Scotland	.075	<.001	.003	.005	.003	.004	.215	.027			
Balan	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001		
Gardouch	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	.064	
Tourch	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	<.001	.001	.003

(B)											
Population	Birsay	Tuquoy	Papa Westray 1992	Papa Westray 2012	Westray	Mainland B03	Mainland B13	Mainland B14			
Tuquoy	<.001										
Papa Westray 1992	<.001	<.001									
Papa Westray 2012	<.001	<.001	.038								
Westray	<.001	<.001	.017	<.001							
Mainland B03	<.001	<.001	<.001	<.001	.152						
Mainland B13	.138	.001	.001	.003	.011	.117					
Mainland B14	.003	<.001	<.001	<.001	.006	.034	.924				
North Scotland	.028	<.001	<.001	<.001	.001	.001	.129	.010			

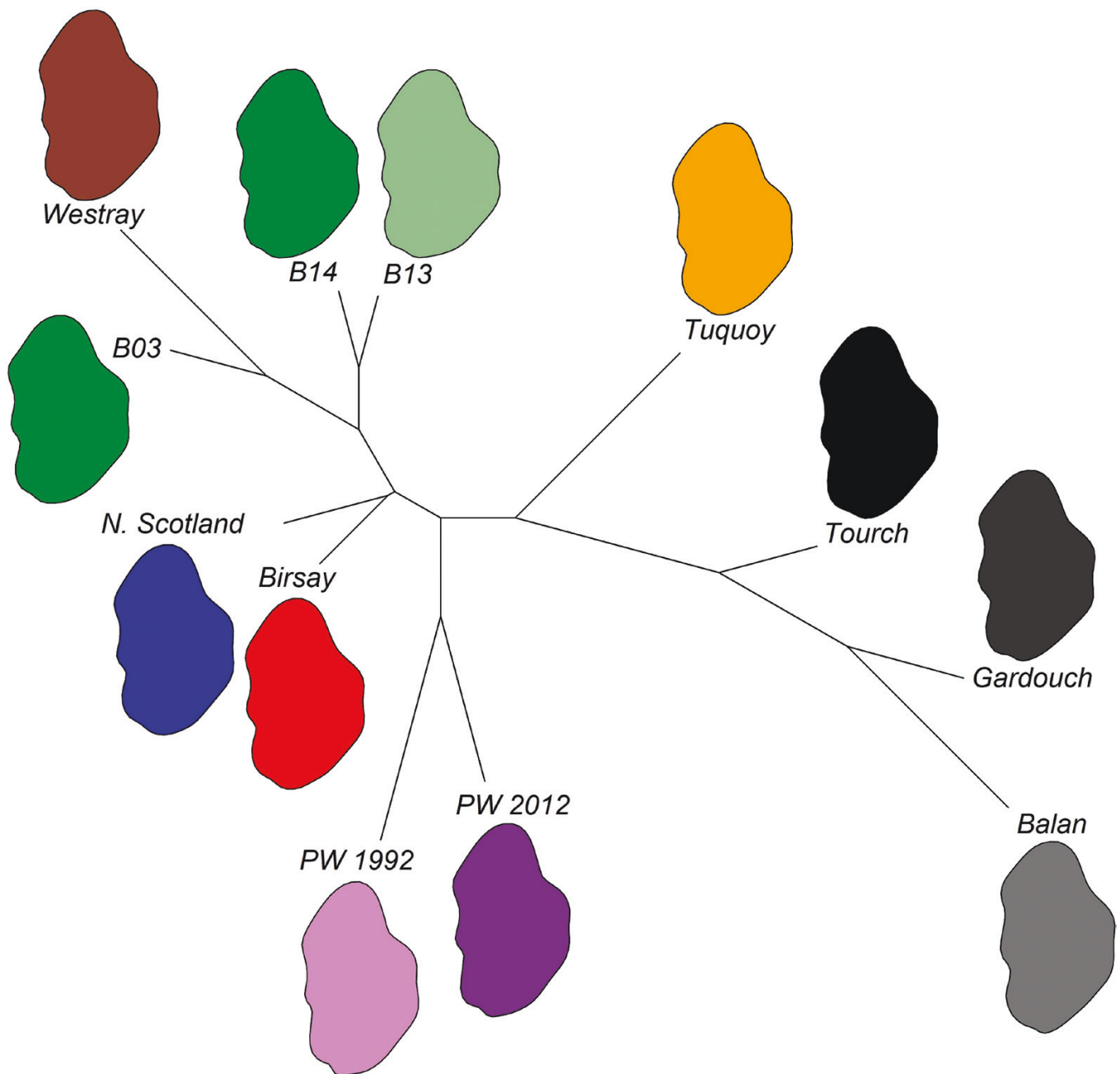


Figure 6. Procrustes distances visualized as a neighbour-joining tree, with the mean shape for each population presented. See [Figure 1](#) for population details. Abbreviation: PW, Papa Westray.

The analysis of size, shape, and non-metric traits points towards the ‘Orkney lineage’ appearing relatively early in the Norse period (research question 2). When plotted, the archaeological populations of Birsay and Tuquoy clearly cluster with Orkney and north Scotland when compared with French continental populations and highlight the presence of accessory cusps on t_2 , a trait specific to insular or otherwise isolated populations, including Orkney (Renaud *et al.* 2011, 2018). Additionally, archaeological molars are about the same size, suggesting similar factors affecting the body size, although resulting in larger specimens than modern ones. Both sites, despite providing samples deposited over several centuries, showed no marked difference in size and shape between sampled stratigraphy. Thus, the

second research question can be answered positively. Following dating established for each site, in both cases the population was already established by ~11th–12th century AD on their respective island. It can be inferred that a set of morphological and non-metric traits specific to Orkney is likely to have evolved between ~9th and 10th century AD, in the early Norse period.

However, differences are noticeable between the Birsay and Tuquoy samples, especially in their relationship to modern Orcadian populations (research question 3). Birsay shape data highlight similarities with several modern localities in Orkney Mainland and north Scotland, with a large proportion of molars exhibiting accessory cusps on t_2 . In contrast to Birsay, Tuquoy house mice align well with the Orkney morphological signature

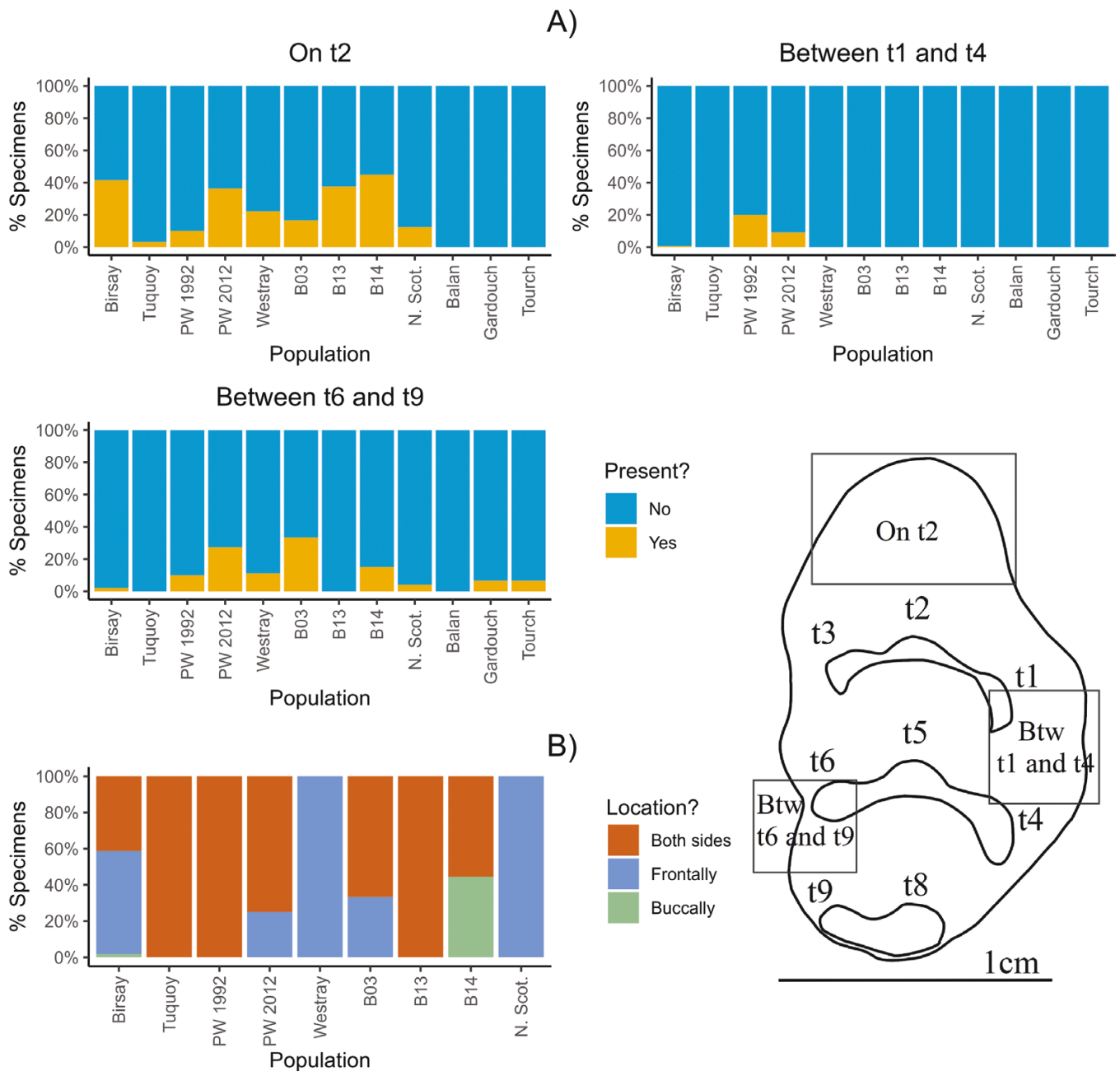


Figure 7. Proportion of the accessory cusps in each population. A, scoring for main accessory cusps. B, results of location subscore for the accessory cusp on t2. To the side, schematic molar surface with regions considered in squares. For population details, see [Figure 1](#); and for the accessory cusp scoring summary statistics, see the [Supporting Information \(Table S2\)](#). Abbreviation: PW, Papa Westray.

when compared with France, but within the Orkney lineage they appear clearly differentiated from the other archaeological and all modern samples, including the modern Westray population. Moreover, only one tooth out of 32 showed an accessory cusp on t2. Owing to those differences, the answer to the third research question varies between the sites and is considered in the last two sections of the Discussion.

Decrease in molar size between archaeological and modern populations

The size difference between Orkney house mice and reference populations in France can be related to the well-known trend

of small mammals to become larger in insular environments ('Foster's rule'; [Van Valen 1973](#)). The change in selective pressures between source areas and the islands in which they are introduced promotes the adjustment of body size to be more optimal for the insular environment ([Lomolino 2005](#)). Previous research has especially highlighted lower predation and competition pressures on islands as driving factors for enlargement ([Van Valen 1973](#), [Case 1978](#), [Lomolino 2005](#)). However, Orkney appears not to differ significantly from continental Europe or Mainland Britain regarding such pressures on typically commensal species. The population of field mice, *Apodemus sylvaticus*, a generalist species often competing with house mice ([Tattersall](#)

et al. 1997, Flowerdew and Tattersall 2008), was established in Mainland Orkney as early as the fourth–third millennia BC (Romaniuk *et al.* 2016). All the major Orkney islands seem currently to be inhabited by both house and field mice (Berry 2000: 142–3). Domestic cats were introduced to the Orkney isles at the same time as house mice, with evidence for this from several Mainland Orkney archaeological sites (e.g. Howe and Earls Bu; O'Connor 2007), including Birsay (Morris 1996: 150 table 14; Rackham 1996). As new species introductions to continental Europe eventually found their way to Mainland Britain, followed by Orkney, predation and competition pressure observed on the continent and the islands most probably remained comparable until modern times. A good example would be black rat (*Rattus rattus*) or later brown rat (*Rattus norvegicus*) introductions, although the former species is currently considered extinct in the majority of the Orkney isles (Booth and Booth 2005: 84).

A climatic component might be involved in the observed difference in size between the populations in Orkney and France, corresponding to body size enlargement of endotherms in colder environments (Bergmann's rule, see Bergmann 1847) and documented in modern house mice (Ballinger and Nachman 2022). In both archaeological and modern house mouse samples, Bergmann's rule has been documented as a decrease in size from western continental Europe to the Mediterranean region (Cassaing *et al.* 2011). Although Bergmann's rule has traditionally been associated with temperature as a key factor, at the level of taxonomic order, rodent body mass is best related to precipitation, especially precipitation connected to primary plant productivity and thus likely food availability (Alhajeri and Steppan 2016). However, perhaps reflecting unique adaptations in different rodents, at the individual species level several different factors have been noted, with general body size being heritable, but intergenerational plasticity possible (Millen *et al.* 2006, Ballinger and Nachman 2022). In the case of another small mammal in Scotland, the common shrew (*Sorex araneus*) populations inhabiting western Scotland and nearby isles (the Inner Hebrides and Clyde Islands), various relationships were demonstrated. The most significant correlations found were between body size and annual temperature, island size, and the presence of pygmy shrews, *Sorex minutus* (White & Searle 2007). For commensal species, various factors can, to some extent, be moderated by human presence, but variation in the size of house mice still seems to be related to climate, given the previously observed patterns (Cassaing *et al.* 2011, Ballinger and Nachman 2022). House mice are susceptible to low temperatures, especially in outdoor environments (e.g. Skokholm Island in the work of Berry 1968). The temperature in Orkney is relatively low throughout the year (~4°C in winter and ~13°C during summer). Additionally, temperatures experienced can be lower owing to a typically hyperoceanic climate, with strong winds and high precipitation (Berry 2000: table 1.1).

The second trend noted is the reduction in molar size between archaeological and modern specimens. The temporal gradient is congruent with observations made using archaeological finds of house mice (Vigne *et al.* 1993, Cassaing *et al.* 2011) and other murid species (e.g. Algerian mouse, *Mus spretus*; Stoetzel *et al.* 2013) within western Europe and north-western Africa, respectively. A decrease in molar size with time was also noted separately for Orkney and France in the case of common voles

(Cucchi *et al.* 2014). These latter results from a different species make an interesting comparison with the house mice, being a similar human-mediated introduction to the Orkney isles, with population idiosyncrasy established early and with molar gigantism appearing without any known transitional forms.

The introduction of brown rats (*Rattus norvegicus*) to Britain in the 18th century AD could have driven a decrease in the size of house mice there, as a result of competition or even predation, although it is unlikely in the case of Orkney. Indeed, their introduction could be of relevance only for Mainland Orkney populations. Brown rats have never settled in some islands (Westray), whereas in other islands the rats became extinct alongside a decrease in human population (20th century in Papa Westray; Booth and Booth 2005: 84). Thus, the introduction of brown rats does not explain the decrease in the size of mice between archaeological Tuquoy and modern Westray.

The decrease in molar size between archaeological and modern times might be related to both shifts in human activity and long-term climate changes. The end of Norse rule over the Orkney isles is visible as the abandonment and destruction of many Norse period structures or, in some instances, their re-use (Griffiths *et al.* 2019: 309–24). However, there was continuity of human settlement on Mainland and other major islands after the Norse period. The most significant socio-economic shift in Orkney occurred during the agricultural intensification and population growth in the 19th and 20th centuries, resulting in a sudden increase in human population and the alteration of most available land to some degree (Berry 2000: 198–219). Modern anthropogenic factors, especially large-scale farming, intensification of cultivation, and population fragmentation are proposed as factors causing the decrease in size of non-commensal species (e.g. Algerian mice in the study by Stoetzel *et al.* 2013). The same has been proposed for common voles in Orkney (Cucchi *et al.* 2014). Anthropogenic changes visible in Orkney also relate to the wider trend visible globally from the 19th century onwards of increasing human impact on long-term climatic trends. The decrease in size of house mice can thus be related to the necessity to adapt to human-driven factors, such as changing human population density, economy, land usage, and introductions of new species.

The contemporary decrease in molar size observed in Papa Westray between 1992 and 2012 supports the notion of size being impacted by human activity. A recent human population increase (National Records of Scotland 2013: appendix 2), part of a larger resettlement and revitalization programme, resulted in a larger island area being redeveloped and put in active use, with regular connections to nearby Westray and other islands (Papay Development Trust 1999). Although not documented, the expansion in numbers of local domestic fauna, including livestock, pets, and other commensal species, is also a possibility.

Both observable trends, large initial size and later decrease in modern times, could also relate to more global reaction to climate change. Research on modern and fossil large Japanese field mouse, *Apodemus speciosus*, pointed towards a uniform evolutionary response, a decrease in size, to climate warming since the Last Glacial Maximum, with the insular environment only inhibiting the pace of this response (Millien and Damuth 2004). A similar trend of size decrease since the Last Glacial Maximum was also noted for Orkney common voles, with the decrease

being more pronounced for continental specimens (Cucchi *et al.* 2014). Additionally, the impact of climate change has already been noted for many animal and plant species, with size reduction over the last 100–200 years being observed most commonly (Sheridan and Bickford 2011). House mice in Orkney might initially have experienced a longer period of relative climate stability owing to the previously mentioned hyperoceanic climate, with the latest anthropogenic influences speeding up the process of size reduction.

Long-term morphological stability on Mainland Orkney

Given the similarity in shape and the presence of multiple specimens with accessory cusps on t2, the archaeological population represented by Birsay is likely to be a direct ancestor to modern house mice in Mainland Orkney and north Scotland. Frequent contact between north Scotland and south-western Orkney house mouse populations has also been suggested based on mitochondrial DNA (Searle *et al.* 2009). Even today there are regular ferry contacts between Orkney and port towns on the northern shore of Caithness (Scrabster, John o' Groats, and Gills Bay), with multiple minor seasonal ferry lines across the rest of Caithness and further away.

The long-term stability of key human settlements in western Mainland Orkney might have allowed direct ancestry between archaeological and modern house mice. The archaeological site of Birsay Beachview is located on the outskirts of the long-inhabited village of Birsay. The Brough of Birsay, a tidal island occupied during the Pictish (6th–9th centuries AD) and Norse (9th–12th centuries AD) periods, is located to the northwest of the village and Birsay Bay (Curle 1982, Morris 1996: 209–255). The village itself contains structures built over a long time span, including the 17th century St. Magnus Church, itself built on the site of an even earlier church dating back probably to the 11th century, and the ruins of the Earl's Palace from the 16th century AD (Morris 1996: 4–13, 22–3 and 193). Archaeologically and historically, within the broader region, it seems there was no significant hiatus in human habitation, at least from the Pictish period onwards. Continuous human presence in Birsay is therefore likely to have contributed to the survivability of the house mouse population, with the Norse decline and subsequent isolation period perhaps contributing to the observed congruence of mitochondrial DNA, microsatellite, and morphometric data, with any differences attributable to genetic drift (Chevret *et al.* 2021). Birsay parish could be the origin of many later introductions and reintroductions over the Orkney archipelago and northern Scotland. Both the Brough of Birsay, a seat of power for the Norse rulers of Orkney, and the Earl's Palace show the ongoing political importance of the settlement/region at least until the 16th century AD (Morris 1996: 203–8 and 250–5), most probably resulting in frequent sea contacts with the rest of the Orkney archipelago and beyond, and with that, the possibility of stowaway mice.

Complex dynamics of morphological evolution in Westray

The reason behind the Tuquoy population differing from modern Orkney mice might lie in the site being a relatively short-lived settlement, with archaeological samples representing a currently extinct population and the modern Westray population being related to later reintroductions. The period

of gradual site abandonment started as early as the 13th century AD and continued into the 15th century AD, when Norse rule over the Orkney Isles ended (Owen 1993). The fine Romanesque chapel immediately adjacent denoted the high status of the settlement during its floruit in the 12th century, but it is the only structure that survived in use beyond the Norse period (Owen 1993). The gradual abandonment probably affected all commensal and semi-commensal species living in or nearby the settlement. Without the support stemming from human presence, house mice most probably had to search for food sources in the wild. However, this would mean competition with better-adapted field mice, also found among the rubble deposits within the site (Romaniuk *et al.* 2023). Westray (47.13 km²) is also a substantially smaller island than Orkney Mainland (523.25 km²), with noticeably fewer settlements to support a house mouse population. Such competition on smaller islands can lead to total population extinction, as noted for St. Kilda house mice (Boyd 1956, Berry and Tricker 1969). Westray has been at the crossroads of maritime trade for a long time, with incoming waves of stowaway mice from other Orkney islands either reintroducing the species after local extinction or contributing to a gradual morphological shift in a previously diminished population. This is supported by the fact that Westray mice display a relatively high genetic diversity when compared with other Orkney isles (Chevret *et al.* 2021), suggesting multiple introductions from the surrounding isles. In a similar way but at a larger scale, Cyprus, as a long-standing hotspot of human activity, experienced multiple introductions of house mice, also leading to high genetic diversity (García-Rodríguez *et al.* 2018).

The presence of several house mouse bones in modern contexts, overlaying archaeological Tuquoy in addition to later agricultural layers from the 18th and early 19th centuries AD (Romaniuk *et al.* 2023), might point towards mouse populations returning to the area alongside human activity in the 19th and early 20th centuries. The remains identified were highly incomplete and scattered across the site (Romaniuk *et al.* 2023), pointing towards a displacement of archaeological material in younger layers, as is common in the case of agriculturally active regions, or other forms of post-mortem material dispersal (Lyman 1994: 150–88). However, this could also be attributable to low-level human activity in the area centuries later, with the chapel remaining in use probably until around AD 1775, and with later evidence of agriculture and kelp burning. The presence in modern samples could be a sign of house mice resettling the area alongside people.

CONCLUSIONS

There is a noticeable difference in size between archaeological and modern house mice in Orkney, with the archaeological population consisting of notably larger individuals at both sites analysed (based on molar size). Given the presence of other size differences between Orkney/north Scotland and the continental European population, probably reflecting climatic factors, in addition to the recent history of substantial environmental alteration in Orkney by humans, the size decline from archaeological to modern times is likely to reflect anthropogenic impact on the commensal niche of house mice.

Our results point towards the house mouse population in Orkney being established early in the Norse period. The morphometric analysis of the first upper molar, by allowing integration in a single morphospace of archaeological and modern samples, provides a temporal aspect to assess the evolution of Orkney house mice. Accepting that house mice were introduced during the Norse period, as indicated by their archaeological presence in the Norse-period sites (Morris 1996, Romaniuk *et al.* 2023) and supported by the genetic research results (Searle *et al.* 2009, Chevret *et al.* 2021), our study shows that the initial adaptation occurred rapidly, probably in the 9th and 10th centuries AD, resulting in specific features of Orkney mice already present in the archaeological samples, including the insular-style accessory cusps common in modern Orkney populations.

The most interesting result, however, is the likely relationship between long-term population stability of house mice with stability of human settlement in Orkney. Human populations driving the evolutionary history of house mice, already suggested by modern morphometrics and microsatellite data (Chevret *et al.* 2021), was confirmed here by morphological proximity between archaeological and modern mouse teeth in areas characterized by a continuous human occupation since the Norse period. In contrast, in areas where human occupation ceased before recent times, a difference between archaeological and modern samples suggests a discontinuity in the mouse populations as well.

Our results can form the basis for further research, challenging a better integration between biological and archaeological approaches. Incorporation of new archaeological material can provide further answers regarding the relationship between the evolution of house mice and human population dynamics (Jones *et al.* 2013), beyond the already established impact of human migrations on introductions of house mice and the relationship between human population stability and house mouse long-term stability demonstrated here.

SUPPLEMENTARY DATA

Supplementary data is available at *Biological Journal of the Linnean Society* online.

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AUTHOR CONTRIBUTIONS

Andrzej A. Romaniuk (Conceptualization, Data curation, Formal analysis, Funding acquisition, Investigation, Methodology, Project administration, Resources, Software, Supervision, Validation, Visualization, Writing – original draft, Writing – review & editing), Sabrina Renaud (Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Validation, Resources, Software, Supervision, Writing – review & editing), Robin Bendrey (Conceptualization, Funding acquisition, Methodology, Supervision, Writing – review & editing), Jeremy B. Searle (Conceptualization, Methodology, Supervision, Validation, Writing – review & editing), Olwyn Owen (Data curation, Resources, Writing – review & editing), Jeremy Herman (Conceptualization, Methodology, Supervision, Resources, Validation, Writing – review & editing).

CONFLICT OF INTEREST

The authors have no competing financial interests.

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DATA AVAILABILITY

All data are available as Supplementary Tables. **Supporting Information, Table S1** contains sampling information, including region and locality/population, side, stratigraphic and radiocarbon dating, in addition to context number, description, and location (for archaeological samples), scoring of accessory cusp scores, measured size (length and c-size), and canonical variate scores from canonical variate analysis. **Supporting Information, Table S2** provides summary statistics for accessory cusps, related to **Figure 7**. **Supporting Information, Table S3** contains generalized Procrustes analysis coordinates of all data formatted as an array. **Supporting Information, Table S4** contains generalized Procrustes analysis coordinates of Scottish data only. All procedures were performed in RSTUDIO with libraries stated in the Materials and methods.

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