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Postglacial recolonization and Holocene diversification of *Crocidura suaveolens* (Mammalia, Soricidae) on the north-western fringe of the European continent

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ABSTRACT

Phenotypic variation was characterized in 187 modern and archaeological specimens of the lesser white-toothed shrew (*Crocidura suaveolens*), obtained from both insular and continental European locations. Geometric morphometric methods were used to quantify variation in size and shape of the mandible. The phenotypic distance between populations, and the influence of several eco-geographical factors on the size and shape of the mandible in island populations, were assessed. Based on mandible shape divergence, the populations of *C. suaveolens* were clustered into continental, insular Atlantic and insular Mediterranean groups. Archaeological specimens from Molène Island, more than 3400 years old, display a mandible shape signal closer to that of the continental population than those of modern island populations. Conversely, the continental shape signals of the modern populations from Höedic and Sark suggest that these are relatively recent anthropogenic introductions. The populations of *C. suaveolens* from both the Atlantic and Mediterranean islands (except for Rouzic and Cyprus) show a significant increase in mandible size, compared to those from continental Europe. Significant phenotypic differences support the indigenous condition of *C. suaveolens* on most of the Atlantic islands, suggesting that the species arrived there before the separation of the Scilly Isles and Ushant from the continent due to the post-glacial rise in sea level. This provides an *ante quem* for its colonization of the north-western fringe of continental Europe, notwithstanding its absence from the region in the present day.

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1. Introduction

Over the past two million years, the climate has undergone periodic fluctuations. The advance and retreat of the ice sheets through multiple glacial cycles, most recently the Last Glacial Maximum (LGM) around 23-18 ky BP, had a major impact on the present day distribution of species and this is reflected in their spatial genetic structure (Hewitt, 2000; Stewart et al., 2010; Taberlet et al., 1998). Palaeontological and palynological records, as well as a large body of biogeographical data, suggest that many temperate species persisted through glacial maxima in lower-latitude refugia (Taberlet et al., 1998; Hewitt, 2000) where climatic conditions were less extreme, however some species are also considered to have survived these climatic events in more northerly "cryptic" refugia (Bilton et al., 1998; Provan and Bennett, 2008; Stewart and Lister, 2001).

The efficacy of genetic data for reconstructing historical colonization patterns has been recognized for some time (Hewitt, 2000; Taberlet et al., 1998). However, only recently an improved understanding of molecular clock rates, in particular the time dependence of rates measured over timescales relevant to intraspecific genetic variation (Ho et al., 2005, 2011; Ho and Larson, 2006), has allowed accurate reconstruction of the timing of these processes and an appreciation of the predominant role of the LGM in shaping the colonization patterns and composition of current populations. In some cases genetic data and archaeological evidence have also drawn attention to the role of more recent events than the LGM, for example the Younger Dryas glacial re-advance (Herman and Searle, 2011), or human-mediated introductions to new locations (Jones et al., 2012, 2013; Herman et al., 2016; Pascal et al., 2006), in shaping the present distribution and composition of small mammal populations. Despite its potential value, relatively few phylogeographic studies of small mammals have used "ancient" DNA from zooarchaeological remains (Cucchi et al., 2014; Martínková et al., 2013; Tougard et al., 2008). To our knowledge, none of these have involved members of the Eulipotyphla (shrews, moles, hedgehogs and others), which are in any case often neglected in palaeoenvironmental and bioarchaeological approaches.

The current distribution of the lesser white-toothed shrew, *Crocidura suaveolens* (Mammalia, Soricidae) (Cosson et al., 1996; Poitevin et al., 1986) and previous DNA based phylogeographic studies (Dubey et al., 2006) both point to the Iberian peninsula as the most likely refuge for this species during the LGM. Although *C. suaveolens* is absent nowadays from the north-western part of continental Europe, it is present on several of the small Atlantic islands near to the coasts of France and Britain, including Höedic, Ushant, the Molène Archipelago, Rouzic, Sark and the Scilly Isles. Its status there, whether indigenous or accidentally introduced by humans, is not clear. Previous studies strongly suggest that it originally occupied most of the islands in the English Channel, Iroise Sea and French Atlantic Façade, before it was replaced by its competitor, *C. russula*, which is more anthropophilic and currently present on the islands with the most human contact with the mainland (Cosson et al., 1996; Poitevin et al., 1986). Therefore, it is possible that *C. suaveolens* was distributed from the Scilly Isles to the east of the Channel and the Loire estuary before the post-glacial marine transgression, which began around 14 ky ago.

However, according to the archaeological record, the presence of *C. suaveolens* in the Atlantic islands was limited to post-Neolithic contexts, with the earliest evidence found in the mid Bronze Age abandonment levels of Beg ar Loued (Molène island, ~3.5 ky cal. BP), before the terminal episodes of fragmentation of the islands (Pailler et al., 2014). Given the potentially anthropophilic behavior of *C. suaveolens* (Estafiev, 2006), a more recent human-mediated introduction on these islands remains a likely hypothesis which gets some support from the zooarchaeological evidence in the larger Mediterranean islands (Dubey et al., 2007; Vigne, 1999).

To provide new insights into the process of post-glacial recolonization and Holocene diversification of *C. suaveolens* on the north-western fringe of Europe and to examine the potential role of human-mediated dispersal in the colonization of the Atlantic islands, we compared the phenotypic variation of modern and archaeological *C. suaveolens* from both insular and continental locations using the mandible shape as a phenotypic marker (Cornette et al., 2012; Renaud and Michaux, 2007; Renaud et al., 2009; Vega et al., 2016). Shape variation was quantified, analyzed and compared through geometric morphometrics (GMM).

To investigate the patterns and process of diversification in the mandible form of *C. suaveolens* from the north-western fringe of Europe and assess the indigenous or introduced status of the species on the Atlantic islands, we tested three biogeographic questions. Firstly, do insular populations of *C. suaveolens* show an increase in size, with the size of the mandible taken to represent body size (Renaud, 2005; Renaud and Michaux, 2007), as predicted by the island rule (Lomolino, 2005; Lomolino et al., 2012; Van Valen, 1973)? Secondly, can we use shape difference among populations as a biogeographic marker? Lastly, what eco-geographical constraints (i.e. area of the island, distance to mainland, chronology of isolation, latitude and longitude, altitude, average annual temperature and rainfall, number of competitors and predatory species) account for the size and shape divergence among the populations of the different islands?

2. Material and methods

2.1. Modern and ancient samples

A total of 187 *C. suaveolens* mandibles were studied: 111 modern and 76 archaeological. The modern dataset (Table 1; Fig. 1) includes 23 specimens from continental western Europe (France), 6 from eastern Europe (Croatia and Turkey), 15 from Mediterranean islands (Corsica, Karpathos and Cyprus), and 67 from the islands at the north-western fringe of Europe (Atlantic islands) distributed as follows: 6 from Ushant, 30 from the Molène Archipelago (Kemenez, Béniguet, and Balanec), and 31 from the English Channel (Sark, Rouzic, and Saint Mary, the latter belonging to the Scilly archipelago). Specimens were mostly collected from barn owls pellets (*Tyto alba*). Modern specimens from Molène Island were not included in the analysis as on this island *C. suaveolens* has now been completely replaced by *C. russula*.

Table 1
Modern samples of *Crocidura suaveolens*. C, continental samples; I, insular samples; N, number of mandibles included in the morphometric analysis.

Country	Locality	Code	N
France	Camargue [C]	CAM	11
	Charente [C]	CHA	7
	Richelieu [C]	RIC	6
	Ushant [I]	USH	6
	Kemenez [I]	QUE	11
	Béniguet [I]	BEN	11
	Balanec [I]	BAL	8
	Rouzic [I]	ROU	4
	Lano D4, Corsica [I]	LAN4	9
UK	Sark [I]	SAR	8
	St. Mary [I], Scilly	SCI	19
Croatia	Titel [C]	CRO	3
Greece	Karpathos [I]	KAR	3
Cyprus	Profitis ilias [I]	CYP	3
Turkey	Aspendos [C]	TUR	3