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REVIEW

Holocene biogeography of the southwestern European white-toothed shrew (*Crocidura iculisma*, Eulipotyphla) through its fossil record

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ABSTRACT

1. *Crocidura iculisma* (=*C. suaveolens*) is a shrew (Soricidae, Eulipotyphla) showing a fragmented distribution limited to the Iberian Peninsula, southern and western France and northwestern Italy. Although it has been in the Iberian Peninsula since the Middle Pleistocene, its biogeographical history remains poorly known.
2. Here, we provide new data on *Crocidura iculisma* from the Castillejo del Bonete site (southern Spain) dated as 3.8–3.6 cal kyr BP. At the same time, we analyse changes in its geographic distribution based on its palaeontological record.
3. We have reviewed thoroughly the Holocene record of *Crocidura iculisma* in southwestern Europe, considering independently the three time intervals according to the stages defined for this geological time series (Greenlandian,

Northgrippian and Meghalayan). Whenever found together in fossil sites, the relative abundance of the two sympatric shrews of the genus *Crocidura* (*Crocidura russula* and *Crocidura iculisma*) was analysed. The data obtained concerning past distribution range and relative abundance were compared with the current status of the species in Iberia to interpret changes through time.

4. The distribution range of the southwestern European white-toothed shrew in the Iberian Peninsula has notably reduced over time until today. The occurrence at Castillejo del Bonete and other palaeontological records located beyond its current distribution range show that it was distributed in several areas of the eastern part and southern interior of Iberia, at least until the second half of the Meghalayan. Relative abundance patterns observed in the fossil assemblages suggest that competitive exclusion by *Crocidura russula* and climatic changes played a crucial role in driving the extirpation of *Crocidura iculisma* from a substantial portion of the Iberian Peninsula.

INTRODUCTION

From a palaeontological standpoint, the study of the Holocene small mammal record in southwestern Europe allows the reconstruction of recent biogeographic processes influenced by climatic evolution, ecological interactions or human impacts (Auffray et al. 1990, Poitevin et al. 1990, Vigne 1992, Cuenca-Bescós et al. 2009, Laplana & Sevilla 2013, Domínguez García et al. 2019, Álvarez-Vena et al. 2023). Particularly for shrews (Soricidae), some research has been done (e.g. Rzebik-Kowalska 1998, Furió 2007, Rofes & Cuenca-Bescós 2011, Moya-Costa & Cuenca-Bescós 2021, Moya-Costa et al. 2023), although few studies have focused on their Holocene palaeobiogeography (Rofes et al. 2018, Domínguez García et al. 2020).

Under the name of the lesser white-toothed shrew, *Crocidura suaveolens* s.l., a species group of tiny shrews, inhabits a wide geographic range in Eurasia, extending continuously from Central Europe to Asia (Palomo et al. 2016). In Western Europe, they are less abundant, particularly in the Iberian Peninsula, where a single species is represented with a small distribution since it is found mainly restricted to areas of Atlantic influence (Rey 2007, Bencatel et al. 2017).

The systematics and taxonomic status of the *Crocidura suavolens* s.l. group has been considered one of the most problematic within the genus (Hutterer 2005). Mitochondrial DNA studies have found that the white-toothed shrews of Europe belong to two clearly differentiated clades (Dubey et al. 2006, Biedma et al. 2018): one from central Europe, corresponding to the subspecies *Crocidura suaveolens mimula*, and another from the extreme southwest, corresponding to the subspecies *Crocidura suaveolens iculisma*. The latter shows a wide divergence and is placed in a more basal position than other clades and is clearly differentiated from the other European clade (Dubey et al. 2006, 2007). In parallel, Bannikova et al. (2006), in a study with mitochondrial DNA which did not include individuals from the southwestern European clade, concluded that *Crocidura s. mimula* should be considered a valid species and named *Crocidura mimula*, which is in agreement with the results obtained by Dubey et al. (2006), who suggested that the status of many taxa should be re-evaluated. Recent studies (Wilson & Mittermeier 2018, Burgin et al. 2020) have proposed, as a preliminary solution and in the absence of nDNA analysis, that populations from western and central Europe, Mediterranean islands and southwestern Asia should be classified as *Crocidura gueldenstaedtii*, while *Crocidura suaveolens* should be retained for populations from eastern Europe and Asia. This proposal has also been recently adopted by the IUCN Red List of Threatened Species (Kryštufek & Gazzard 2023). However, the most recent studies, using mitogenomes and nDNA, have concluded that both *Crocidura mimula* and *Crocidura iculisma* are valid species (Gritsyshin et al. 2023, İbiş et al. 2023). Therefore, here we will use *Crocidura iculisma* to refer to the populations of lesser white-toothed shrews of the Iberian Peninsula and Mediterranean France, as this is in agreement with the most recent knowledge. Under this denomination, we have included all previous mentions of *Crocidura suaveolens* or *Crocidura gueldenstaedtii* from the Iberian Peninsula or France.

Fossils assigned to *Crocidura iculisma* have been described in the Iberian Peninsula since the Middle Pleistocene, probably as a descendant of *Crocidura kornfeldi* (Rofes & Cuenca-Bescós 2011), although fossil occurrences are not abundant (Sesé & Sevilla 1996, Arribas 2004, Moya-Costa 2020). During the Pleistocene glacial periods, the southern European peninsulas such as Iberia, Italy and the Balkans operated as refugia for temperate species (Hewitt 1996, Taberlet et al. 1998, Sommer & Nadachowski 2006). Previous works have recognised a post-glacial diversification and dispersal process of *Crocidura iculisma* from its Iberian refuge to the north fringe of Europe (Biedma et al. 2018, Rofes et al. 2018). Particularly, the Western European populations show a current geographic distribution that is fragmented in various areas due to the evolution of three main lineages in separate glacial sub-refugia during the Quaternary (Biedma et al. 2018). In addition, some authors have also suggested that the use of resource competition with the congeneric species *Crocidura russula* has been a key factor in its biogeographic history, showing the influence of competitive exclusion of *Crocidura iculisma* by *Crocidura russula* in large areas of Europe (Niethammer 1979, Poitevin et al. 1987, Kraft 1998, Biedma et al. 2018, 2020, Bellocq et al. 2023).

The main objective of this study is to reconstruct the Holocene biogeographic history of *Crocidura iculisma*, analyse its changes compared to the present and infer the causes behind these changes. To achieve this goal: 1) we present a new record of *Crocidura iculisma* coming from Castillejo del Bonete site in southeastern Spain; 2) we compiled all known records of the species from Holocene archaeological and palaeontological sites in southwestern Europe; and 3) we conducted a comparative analysis of the relative abundances of *Crocidura iculisma* and *Crocidura russula* between past and modern assemblages.

METHODS

New data on the presence of *Crocidura iculisma*

The shrew remains studied in this work come from Castillejo del Bonete site (Terrinches, Ciudad Real, Spain), one of the most outstanding archaeo-palaeontological sites for studying Holocene small mammals in the Iberian Peninsula. It is a burial mound complex from the Chalcolithic and Bronze Age built on a cave (Benítez de Lugo et al. 2014, 2015, Benítez de Lugo 2018). The sediments of the underlying cave have yielded an exceptionally large and diverse microvertebrate record, providing new valuable data to reconstruct the biogeographical history of some species in Western Europe (Domínguez García et al. 2019, Benítez de Lugo et al. 2020).

Crocidura spp. cranial remains from the cave of Castillejo del Bonete were picked from the fossiliferous sediments excavated during the fieldwork campaign in 2012. The specimens studied here come from the west test pit of Gallery 2 (SWG2, layers UE 26018, UE 26019 and UE 26020), its small mammal assemblage previously described by Domínguez García et al. (2019), who identified a minimum number of 81 individuals (MNI) corresponding to *Crocidura russula*. For a more detailed description of the site and the collecting and sorting methodology for the recovery of the microvertebrate remains, see Domínguez García et al. (2019) and Benítez de Lugo et al. (2015, 2020).

Concerning the age of this microvertebrate assemblage, the material from SWG2 has been dated as 3,819–3,615 cal years BP (Domínguez García et al. 2019, Benítez de Lugo et al. 2020), thus evidencing that the remains were accumulated during the early Meghalayan (Late Holocene).

Taxonomic identifications were made based on the morphology of diagnostic elements (upper fourth premolar – P4, and second lower molar – m2) following the criteria broadly recognised to discriminate dental remains of *Crocidura iculisma* from those of *Crocidura russula* (Rey & Landin 1973, Saint-Girons et al. 1979, Poitevin et al. 1986, Calzada & Román 2017) and also genetically validated by Biedma et al. (2018). To characterise the size of the *Crocidura* remains here analysed, length and width measurements of the P4 were taken following Reumer (1984). Comparisons were made with specimens from modern localities and Holocene sites from Spain and Mediterranean France. Measurements of the modern referential material were taken on the samples from the collections of the Museum National d'Histoire Naturelle (MNHN, Paris, France) and the Estación Biológica de Doñana (EBD-CSIC, Sevilla, Spain) (Appendix S1).

Review of Holocene record

To reconstruct the biogeographical history of *Crocidura iculisma*, a review of published Holocene records in the Iberian Peninsula and Mediterranean France was conducted. An updated database was built for this purpose, considering the taxonomic and/or chronological precision of each case. Previous publications reviewing the record of Iberian Quaternary fossil mammals (Arribas 2004, López-García 2011) were considered.

All fossil occurrences of *Crocidura iculisma* were compiled in the database and arranged in three intervals according to the stages/subepochs of the Holocene following Walker et al. (2018): Greenlandian/Early Holocene (11.7–8.2 ka), Northgrippian/Middle Holocene (8.2–4.2 ka) and Meghalayan/Late Holocene (4.2 ka till present). The geographic location of these records was compared to the current distribution range of the species (Rey 2007, Palomo et al. 2016, Bencatel et al. 2017) to identify changes that may have during the Holocene in southwestern Europe.

Abundance ratio analysis

We compiled published fossil assemblages in which *Crocidura iculisma* and *Crocidura russula* co-occurred

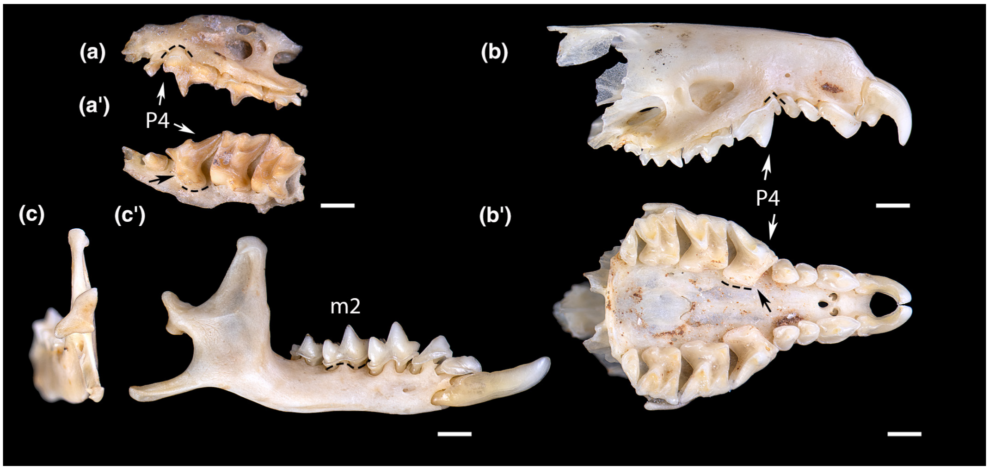

Fig. 1. Selected fossil specimens from Castillejo del Bonete. *Crocidura iculisma*: left maxilla with A3-M2 in labial (a) and occlusal (a′) views (BO12_SWG2_26018_018); *Crocidura russula*: skull with complete dentition in labial (b) and occlusal (b′) views (BO18_S2.2G2_229_020), right mandible with complete dentition in posterior (c) and labial (c′) views (BO18_S2.2G2_229_014). Arrows indicate the position of P4 in the maxilla. Dashed lines indicate morphological diagnostic features. Scale bars 1 mm.

and the abundance data provided by authors (Asquerino & Woloszyn 1991, Poitevin & Sénégas 1999, Poitevin et al. 2005, Valenzuela et al. 2009, Guillem Calatayud 2011, Álvarez-Vena et al. 2023, Cernadas-Garrido et al. 2023). Taphonomic information related to the origins of each assemblage was considered, whenever available, to make abundance values with modern assemblages comparable.

In addition, we collected published data on the abundance of the two shrew species from modern populations obtained from owl pellet analyses (Nores 1989, Biedma et al. 2019) and live trapping (Biedma et al. 2020). We also included unpublished data obtained from barn owl pellets recovered at 12 modern localities showing the co-occurrence of both *Crocidura* species. The biogeographical region (Eurosiberian or Mediterranean) in which each site and modern locality are located was also considered.

To test the possible dominance pattern between the two *Crocidura* species, the relative abundance (% MNI) of each was calculated for all the Holocene fossil assemblages in which they were found together, and the resulting values were compared with the relative proportion in which they are represented in modern localities. To check if there are differences between fossil sites and modern localities, a statistical analysis was conducted using the Clopper–Pearson method (Clopper & Pearson 1934) with PAST 4.01 software (Hammer et al. 2001). We calculated multiple-proportion 95% confidence intervals (CI) for the relative abundance of each species in every site and modern population. Following Suchéras-Marx et al. (2019), variations were considered statistically significant when CI values for each species did not overlap between fossil and modern assemblages. Since both *Crocidura* shrews are potentially found in the same habitats and exhibit similar morphology and behaviour, it is reasonable to assume equal catchability by predators (Biedma et al. 2019). Therefore, ecological factors other than selective predation can be argued to explain differences in abundance values between assemblages.

RESULTS AND DISCUSSION

Castillejo del Bonete record

This study adds a new Holocene occurrence of the southwestern European white-toothed shrew in Spain, belonging to the west test pit in Gallery 2 (SWG2) of the cave of Castillejo del Bonete site. A maxilla from this assemblage assigned in a previous paper (Domínguez García et al. 2019) to *Crocidura russula* was found to display the features that are characteristic of *Crocidura iculisma* and have been consequently included in the present study (Fig. 1a).

The morphological traits that allow assigning material to *Crocidura iculisma* according to Rey and Landin (1973), Saint-Girons et al. (1979), Poitevin et al. (1986) and Calzada and Román (2017) are the rounded outline in the upper edge of the parastyle on the fourth upper premolar (P4) in labial view, being well developed behind the paracone and with a thick cingulum (Fig. 1a) and the position in occlusal view of its protocone which stands at a distance from the lingual edge of the tooth (Fig. 1a′). On the other hand, in the P4 of *Crocidura russula*, the parastyle has an angular outline in labial view (Fig. 1b) and the protocone in occlusal view is found at the lingual border (Fig. 1b′); in the lower dentition, the m2 of *Crocidura russula* on labial view displays a distinct constriction in its labial cingulum (Fig. 1c′). Although this constriction is less pronounced in certain remains, no morphotypes of *Crocidura iculisma* showing a straight labial cingulum have been found.

Additionally, the biometrical study supports the taxonomic assignations of the material from Castillejo del Bonete (Fig. 2, Appendix S1). Overall, the P4 in *Crocidura iculisma* is smaller than *Crocidura russula*, except in Punta Lucero III. This is in accordance with the size gradient pattern observed today in the Iberian Peninsula, which reveals that *Crocidura* spp. populations of the Basque Country are considerably larger than in other more southern localities (Rey & Landin 1973, Zabala 1985). The specimen from Castillejo del Bonete assigned to *Crocidura iculisma* clearly falls within the range of variability of this species, being closer to the smaller values obtained in the Cueva del Caballo (6) and Postes Cave (9) samples. In the same way, the size of *Crocidura russula* from Castillejo del Bonete (1) is closer to the smaller values within the range displayed by the species in the Cueva del Estrecho sample (10).

Biogeography

The review of the Holocene record of *Crocidura iculisma* in the Iberian Peninsula and southern France has provided 21 records, to which the new occurrence from Castillejo del Bonete has now been added. Eleven of these records come from sites that are geographically placed out of the current distribution range of the species, mainly in eastern and southern Spain (Fig. 3, Table 1).

A few of these records may be considered to not be fully reliable, either because the age of the site is imprecise or because no descriptions or figures supporting the taxonomic assignation are given. This is the case of Cueva de Ardales (1), for which a wide temporal range between Late Pleistocene and Late Holocene is assigned to the single remains of *Crocidura iculisma* (Rofes 2023) found in the site. Similarly,

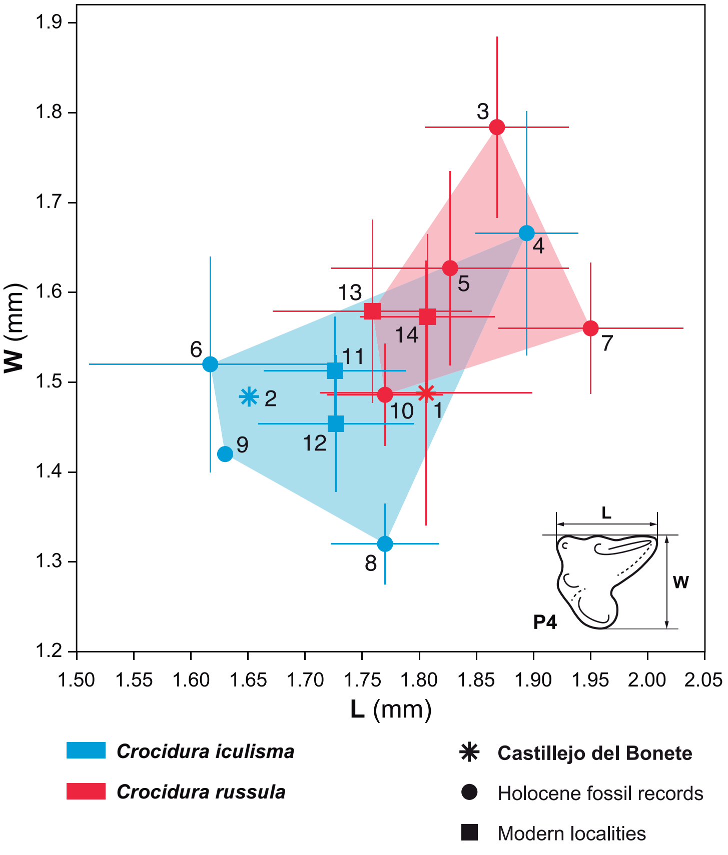

Fig. 2. Bivariate plot comparing the length and width of the P4 (mean ± SD values). 1–2: Castillejo del Bonete; 3–4: Punta Lucero III; 5–6: Cueva del Caballo; 7–8: Cueva de los Mármoles; 9: Postes Cave, 10: Cueva del Estrecho; 11: Mediterranean France; 12, 14: Doñana/Cádiz; and 13: Doñana/Almonte. 1–6: This work (Appendix S1); 7–8: (Asquerino & Woloszyn 1991); 9: (Domínguez-García et al. 2023); and 10–14: this work (Appendix S1).

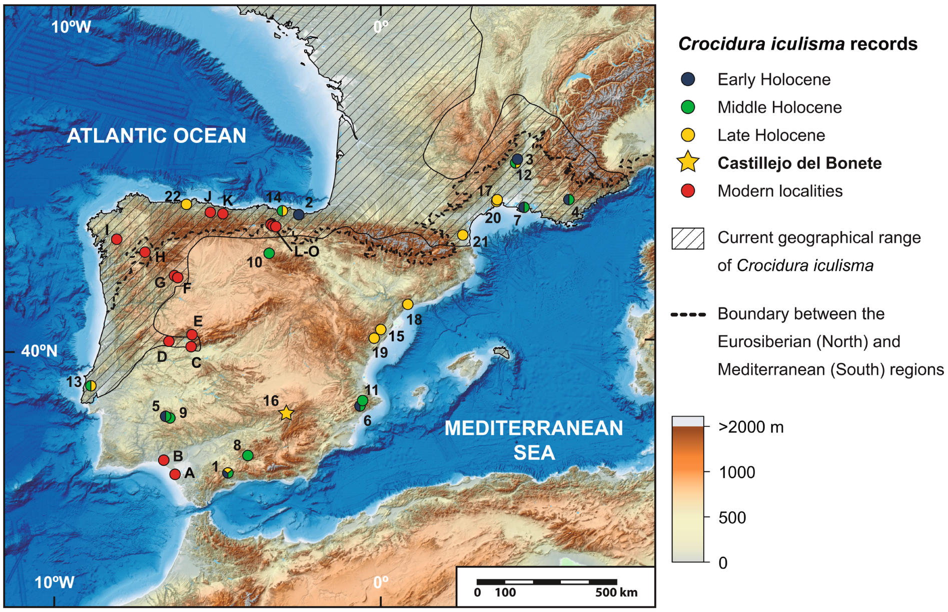

Fig. 3. Map showing the *Crocidura iculisma* records in southwestern Europe considered in this work. Letters and numbers (ID, Table 1) indicate modern localities and Holocene fossil sites respectively. Fossil occurrences spanning multiple time intervals are denoted by points of various colours following the legend. The current geographic distribution of the species is based on Palomo et al. (2016). Map modified from the GEBCO_2021 Grid (GEBCO Bathymetric Compilation Group 2021).

no radiocarbon date is provided for Cueva de los Mármoles (8), where *Crocidura iculisma* was found in a context linked to the Middle Neolithic based on its archaeological content (Asquerino & Woloszyn 1991). Other sites (2, 3, 4, 7, 12) lack descriptions or figures describing the material (Poitevin et al. 1990, Pemán 1994, Jeannet & Vital 2009) preventing verification of the taxonomic assignation. Apart from these, the remaining records can be considered both taxonomically and chronologically reliable.

The presence of *Crocidura iculisma* in Mesolithic levels of Postes Cave (5), in the Neolithic–Chalcolithic of Cueva de los Mármoles (8), Cueva del Caballo (9) and Portalón (10), and finally, in the Bronze Age of Castillejo del Bonete (16) shows its persistence in the southern interior regions of the Iberian Peninsula, at least until the first half of Meghalayan. At the same time, the site of Castro do Zambujal (13) has yielded a record of *Crocidura iculisma* right at the southernmost limit of its current distribution in Portugal. Concerning the records of eastern Spain, most of them belong to sites located in the easternmost mountain ranges of the Iberian and Baetic mountainous systems (6, 11, 15, 19), showing that *Crocidura iculisma* survived there until at least the Iron Age and Roman Period, according to its record in *c.* 2000 years ago in Alorda Park (18) and Estrets-Racó de Rata (19). For the Eurosiberian region, where the species is still found today, three occurrences have been published, belonging to the sites of Laminak (2), Punta Lucero III (14) and level 0 of Cueva del Hueso (22).

Relative abundance

A total of nine archaeological and palaeontological sites where *Crocidura iculisma* and *Crocidura russula* co-occurred were compiled, with Castillejo del Bonete included in the abundance ratio analysis (Table 2, Fig. 4).

A common pattern emerges from the archaeological and palaeontological assemblages regarding abundance ratios. Whereas *Crocidura russula* showed notably higher abundances than *Crocidura iculisma* in all mentioned sites, at Punta Lucero III level F (Table 2, Fig. 4) this ratio reversed. This indicates that in the areas surrounding the archaeological and palaeontological sites where *Crocidura iculisma* has been found, the species was less common than *Crocidura russula*. This relative abundance pattern coincides with what is observed in current sympatric populations in the Mediterranean and Eurosiberian regions, except for the population studied through live trapping within the Odiel Marshes Natural Reserve (B – Biedma et al. 2020), where *Crocidura iculisma* was found and clearly dominated the tidal marsh environment. The authors of this research interpreted this result as an evolutionary response of *Crocidura iculisma*, indicating its

Table 1. Holocene palaeontological sites and modern localities with *Crocidura iculisma* records in southwestern Europe. The ID refers to Fig. 3. Abbreviations: ES = Spain, FR = France, PT = Portugal

Time interval	ID	Site/Locality	Levels	Age	Reference
Late Pleistocene-Meghalayan/Late Holocene	1	Cueva de Ardales (ES)	Zone 2 – Layers 16–14	29–3.8 cal kyr BP	Rofes (2023)
Late Pleistocene-Greenlandian/Early Holocene	2	Laminak II (ES)	L. I (1–2)	12.5–11.7 cal kyr BP	Pemán (1994)
Greenlandian/Early Holocene	3	Chauve Souris (FR)	BA	±9.9 kyr BP	Jeannet and Vital (2009)
Greenlandian-Northgrippian/Early-Mid Holocene	4	Fontbrégoua (FR)	71–54; 53–31	8.6–8.2 cal kyr BP 6.8–6.2 cal kyr BP	Poitevin et al. (1986, 1990)
	5	Cueva de los Postes (ES)	Stage 3	8.4–7.4 cal kyr BP	Domínguez-García et al. (2023)
	6	Abric de la Falguera (ES)	Phases VIII-VI	8.4–6.3 cal kyr BP	Guillem Calatayud (2006)
	7	L'Abri de la Font-des Pigeons (FR)	L. 19-10	8.6–8.2 cal kyr BP 6.9–6 cal kyr BP	Poitevin et al. (1986, 1990)
Northgrippian/Middle Holocene	8	Cueva de los Mármoles (ES)	Surface, SW, F, SC	–	Asquerino and Woloszyn (1991)
	9	Cueva del Caballo (ES)	UE 16	5.6–5.7 cal kyr BP	Domínguez García (2021)
	10	Portalón (ES)	Funerary – Habitat/Stabling	5.3–4.2 cal kyr BP	Rofes et al. (2021)
	11	Abric de la Falguera (ES)	Phases V-IV	5.1–4.4 cal kyr BP	Guillem Calatayud (2006)
Northgrippian-Meghalayan/ Mid-Late Holocene/ Meghalayan/Late Holocene	12	Chauve Souris (FR)	15-6C	4.9–2.3 kyr BP	Jeannet and Vital (2009)
	13	Castro do Zambujal (PT)	–	4.8–3.9 ca kyr BP	Storch and Uerpmann (1976)
	14	Punta Lucero III (ES)	F	4.4–4.1 cal kyr BP	Álvarez-Vena et al. (2023)
	15	Cova de les Tàbegues (ES)	–	4–3 kyr BP	Guillem Calatayud (2002)
	16	Castillejo del Bonete (ES)	UE 26020-26018 SWG2	3.8–3.6 cal kyr BP	This work, Domínguez García et al. (2019)
	17	Lattara (FR)	–	2.4–2.2 BP	Poitevin and Sénégas (1999)
	18	Alorda Park (ES)	–	2.3–2.1 cal kyr BP	Valenzuela et al. (2009), Rofes et al. (2018)
	19	Estrets-Racó de Rata (ES)	2004–2005	2.3–2.1 kyr BP	Guillem Calatayud (2011)
	20	Puits de Lattara (FR)	–	2.1–1.8 kyr BP	Poitevin et al. (2005)
	21	Canet 59 (FR)	–	2 cal kyr BP	Callou and Vigne (2013), Rofes et al. (2018)
	22	Cueva del Hueso (ES)	0	–	Cernadas-Garrido et al. (2023)
Modern	A	Guadalquivir marshes (ES)	–	–	Biedma et al. (2019)
	B	Odiel marshes (ES)	–	–	Biedma et al. (2020)
	C	Cuacos de Yuste (ES)	–	–	This work
	D	Gata (ES)	–	–	This work
	E	Candelario (ES)	–	–	This work
	F	Torres de Aliste (ES)	–	–	This work
	G	Figueruela de Arriba (ES)	–	–	This work
	H	Castro Candelas (ES)	–	–	This work
	I	Forcarei (ES)	–	–	This work
	J	Infiesto (ES)	–	–	Nores (1989)
	K	Avín (ES)	–	–	This work
	L	Partearroyo (ES)	–	–	This work
	M	Carniego (ES)	–	–	This work
	N	Ungo (ES)	–	–	This work
	O	Encima Angulo (ES)	–	–	This work

specialisation to tidal marsh habitats to avoid direct competition with *Crocidura russula*. Relative abundance patterns in the areas where both species co-occur may explain the result of highly asymmetric interspecific competition, with *Crocidura russula* being the dominant species. This dominance may have led to the gradual displacement of *Crocidura iculisma* from large areas, pushing it into the most humid and forested habitats, as seen in its current distribution and, in a more extreme way, to the tidal marshes in the Gulf of Cádiz (Niethammer 1979, Poitevin et al. 1987, Román & Ruiz 2003, Biedma et al. 2018, 2019, 2020).

Table 2. List of sites and modern localities included in the abundance relationship analysis. ID referred to Figs 3 and 4. MNI = Minimum number of individuals, *C. i* = *Crocidura iculisma*, *C. r* = *Crocidura russula*

Biogeographic region	ID	Site/locality	MNI *C. i*	MNI *C. r*	Total MNI	%MNI *C. i*	%MNI *C. r*	Origin of the assemblage
Palaeontological sites								
Mediterranean	8	Cueva de los Mármoles	29	44	73	39.73	60.27	Indeterminate
	16	Castillejo del Bonete	1	78	79	1.27	98.73	Generalist carnivore predation
	17	Lattara	5	13	18	27.78	72.22	Probably barn owl pellets
	18	Alorda Park	12	352	364	3.3	96.7	Barn owl pellets
	19	Estrets-Racó de Rata	5	27	32	15.63	84.38	Barn owl pellets
	20	Puits de Lattara	3	63	66	4.55	95.45	Barn owl pellets
Eurosiberian	14-F	Punta Lucero III - F	49	9	58	84.48	15.52	Accidental falling and/or nocturnal birds of prey pellets
	14-C-B	Punta Lucero III - C-B	0	130	130	0	100	Accidental falling and/or nocturnal birds of prey pellets
	22	Cueva del Hueso	11	60	71	15.49	84.51	Nocturnal birds of prey pellets
Modern localities								
Mediterranean	A	Guadalquivir marshes	32	341	373	8.58	91.42	Barn owl pellets
	B*	Odiel marshes	0	17	17	0.00	100	Live trapping
	A-Tm	Guadalquivir marshes Tidal marshes <220 m	68	256	324	20.99	79.01	Barn owl pellets
	B-Tm*	Odiel marshes Tidal marshes	355	27	382	92.93	7.07	Live trapping
	C	Cuacos de Yuste	66	2729	2795	2.36	97.64	Barn owl pellets
	D	Gata	13	510	523	2.49	97.51	Barn owl pellets
	E	Candelario	38	230	268	14.18	85.82	Barn owl pellets
	F	Torres de Aliste	5	173	178	2.81	97.19	Barn owl pellets
	G	Figueruela de Arriba	4	176	180	2.22	97.78	Barn owl pellets
Eurosiberian	H	Castro Candelas	5	237	242	2.07	97.93	Barn owl pellets
	I	Forcarei	44	105	149	29.53	70.47	Barn owl pellets
	J	Infiesto	35	255	290	12.07	87.93	Barn owl pellets
	K	Avín	9	105	114	7.89	92.11	Barn owl pellets
	L	Partearroyo	6	174	180	3.33	96.67	Barn owl pellets
	M	Carniego	6	375	381	1.57	98.43	Barn owl pellets
	N	Ungo	5	297	302	1.66	98.34	Barn owl pellets
	O	Encima Angulo	2	191	193	1.04	98.96	Barn owl pellets

The statistical test conducted using the 95% confidence intervals (CI) for the relative abundance of each species does not reveal statistically significant overall differences among fossil sites, nor when compared to modern localities from the Mediterranean and the Eurosiberian regions (Fig. 4). Fossil samples with reduced sizes (*Crocidura* spp. MNI < 35) display wider CIs, overlapping regardless of their biogeographic region between them and with certain modern localities. Excluding these samples, the Cueva de los Mármoles (8) shows a high relative abundance of *Crocidura iculisma*, with CI values indicating significant differences from the rest of the fossil sites, and overlapping only with the sample from Forcarei in Galicia (I), which is under a strong Atlantic influence. This situation could be a consequence of the Middle Holocene age of this assemblage, which is the oldest considered for this analysis. Climate and environment were then distinctly more humid than in later periods in the Mediterranean region of Iberia, under a clear trend of aridification since the Middle Holocene onwards (Jalut et al. 2009; Carrión et al., 2010; Ilvonen et al. 2022). Consequently, humid habitats would have been more prevalent during this period, favouring the presence of *Crocidura iculisma*. Nevertheless, the precise age and agents involved in the accumulation of this assemblage are unclear, and in need of further chronological and taphonomic analyses to consider this result relevant.

A particularly noteworthy case is that of Punta Lucero III at level F (14-F), as it is the only sample displaying differences among all fossil sites, with CI values only overlapping with those from the Odiel Marshes Natural Reserve obtained by live trapping in tidal marshes (B-Tm*). In the stratigraphic sequence of the site, no *Crocidura iculisma* was found at younger levels C and B, where *Crocidura russula* was represented alone (14-C-B). This has been interpreted as an example of displacement of *Crocidura iculisma* by *Crocidura russula*, linked to the progressively drier and anthropised environments (Álvarez-Vena et al. 2023).

The cases of Castillejo del Bonete (16), Alorda Park (18) and Puits de Lattara (20) are also noteworthy for their reduced CI due to their high sample sizes, absence

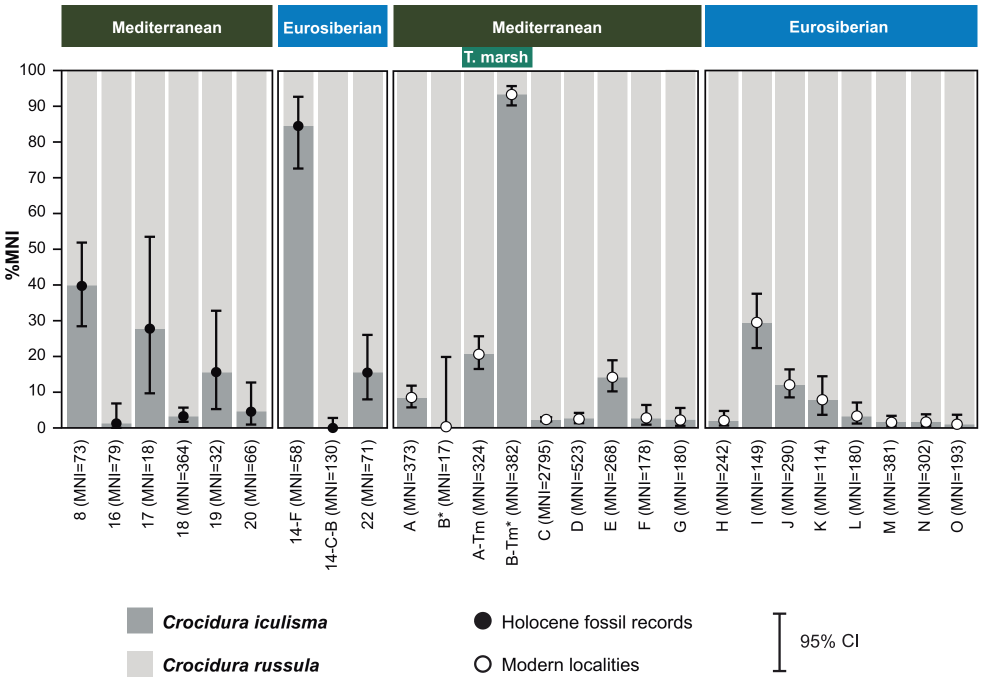

Fig. 4. Abundance ratio (%MNI) among *Crocidura iculisma* and *Crocidura russula* in fossil sites and modern localities is listed in Table 2. (*) Indicates live-trapping method. *T. marsh* (tidal marshes) refers to samples obtained from owl roosts located less than 220 m away from the tidal marshes, as well as the sample obtained by live trapping within the tidal marshes. MNI, Minimum number of individuals of *Crocidura* spp. CI, Multiple-proportion 95% confidence intervals for the %MNI obtained using the Clopper–Pearson method (Clopper & Pearson 1934).

of significant differences between them or with most of the modern localities in the Mediterranean and the Eurosiberian regions. The assemblage from Cueva del Hueso (22) displays a similar pattern, showing higher abundance of *Crocidura iculisma* with CI values overlapping with Puits of Lattara but displaying significant differences with Castillejo del Bonete and Alorda Park values. Compared to modern referential data, it overlaps with the relatively closer modern populations in Asturias (J, K) and Galicia (I) under the Atlantic climatic influence, and with the samples from Candelario (E) and the Guadalquivir marshes (A, A-Tm). These results are not influenced by differences in sample size nor by their taphonomic origin, given that the accumulation of microvertebrate remains is known to be the result of the accumulation of barn owl pellets, except at Castillejo del Bonete (Table 2). Even though the latter assemblage comes from the activity of generalist carnivore predators (Domínguez García et al. 2019), it has had no influence on the abundance relationship between these two shrew species.

Holocene retraction of the geographic range of *Crocidura iculisma*

Our review shows that the southwestern European white-toothed shrew underwent a significant reduction in its geographic range during the Holocene. Although fossil occurrences of *Crocidura iculisma* are relatively uncommon, they are enough to show that it still had several populations in the Mediterranean biogeographical region of Spain, even in the Late Holocene. In Mediterranean France, the species has records dating since the Early Holocene and is still extant in the region (Fig. 3). According to our analysis, this biogeographic process could be explained by the combined action of the competitive exclusion with the greater white-toothed shrew and habitat change linked to climatic evolution.

In this sense, since *Crocidura iculisma* has been able to withstand the competitive pressure of *Crocidura russula* in the Mediterranean biogeographic region only in relatively wetter habitats (Poitevin et al. 1987, Román & Ruiz 2003, Biedma et al. 2018, 2019, 2020), it seems reasonable to infer more humid climatic conditions than at present as the conditions in which the Mediterranean fossil assemblages included in this study were formed.

The current Mediterranean climate is characterised by rainy winters and dry summers; the differences between these two seasons being more pronounced in the southern areas and eastern coasts of Iberia (Fick & Hijmans 2017). Throughout the Holocene, the climate in the western Mediterranean realm has been modulated by a series of long-term trends with superimposed short and less intense drought events (Sánchez Goñi et al. 2008, Jalut et al. 2009, Cacho et al. 2010, Pérez-Obiol et al. 2011, Schirrmacher et al. 2020, Ilvonen et al. 2022). These studies show overall, the existence during the Early and Middle Holocene of an initial relatively humid phase, between 8000 and 6000 years, during which the highest Holocene values of precipitation were reached, known as the Holocene climatic optimum. Posteriorly, after a transitional phase, the increasing aridity trend of the Late Holocene initiated extending until today, being particularly perceptible in the southern regions of Iberia. This provides the scenario in which the wetter conditions of the first half of the Holocene allowed the survival of some *Crocidura iculisma* populations in the eastern and interior areas of the Iberian Peninsula, which persisted at least until the Iron Age–Roman Period transition (Alorda Park and Estrets-Racó de Rata).

Focusing on the statistically significant results of %MNI of *Crocidura* spp., excluding samples influenced by reduced sizes or uncertainties associated with the age of the assemblages mentioned above, *Crocidura iculisma* represents in the fossil samples from the Mediterranean region between 1.27 and 4.55 %MNI (16, 18, 20), similar to those from most modern samples (Table 2, Fig. 4). This suggests that the species was under competitive pressure from *Crocidura russula* in the area around the sites already in the Bronze Age and Iron Age – Roman Period in the Meghalayan. At the same time in Mediterranean France, the southwestern European white-toothed shrew has survived until today, probably because of milder Mediterranean climate and the availability of suitable habitats, while in southern and eastern Iberia, the increasing aridification of climate may have caused the final extirpation of the species, since it is less adapted to face warmer and drier conditions.

Previous studies have already hypothesised that past interspecific competition between the two *Crocidura* species determined their current geographic distribution and recent population dynamics (Poitevin et al. 1987, Biedma et al. 2018, 2019, 2020). Here, we provide for the first time data supporting that this ecological process could have been at work since at least the Meghalayan/Late Holocene in the populations of these two species occupying southwestern Europe.

In addition to the review conducted for this paper, several studies show that *Crocidura russula* is commonly the only species of the genus represented in Holocene Iberian sites. This holds true for areas with a temperate climate (Pemán 1990, Cuenca-Bescós et al. 2009, López-García et al. 2011, Rofes et al. 2013) as well as a Mediterranean climate (e.g. Cardoso et al. 1996, Guillem-Calatayud 1999, 2010, López-García et al. 2010, Bañuls-Cardona et al. 2017, Pimenta et al. 2017, Daura et al. 2019, Domínguez García et al. 2020) and can be related to the dominance pattern that may have caused the extirpation from most of Iberian territory of *Crocidura iculisma* from up to the present day. However, since *Crocidura iculisma* is much less abundant than *Crocidura russula* both in fossil sites and in the present, and as both species are difficult to distinguish using their fragmentary dental remains, this work exposes the consideration that the western European white-toothed shrew may have often gone unnoticed in fossil assemblages dominated by *Crocidura russula*, generating significant uncertainty about its past distribution. An example of this is given by the maxilla from Castillejo del Bonete included in this work, which was misidentified in a previous study of its small mammal assemblage (Domínguez García et al. 2019).

Some molecular clock studies have estimated that *Crocidura russula* colonised the Iberian Peninsula from Africa during the Late Pleistocene 11–80 kyr (Brändli et al. 2005, Cosson et al. 2005), although an earlier date of arrival is proposed by Biedma et al. (2018), who place this event at the end of Middle Pleistocene (41–200 kyr ~ 126 kyr). When palaeontological data are considered, evidence of an earlier date for its arrival is available, since the oldest Iberian occurrences suggest a minimum age of 300–350 kyr for its presence in Iberia (López Martínez 1980, Sesé & Sevilla 1996, Sesé et al. 2011, 2016, Laplana et al. 2015). However, most of these first records are taxonomically uncertain, since they are based on few fragmentary remains assigned either to *Crocidura* aff. *russula* or *Crocidura* cf. *russula*, and until they are checked there is no solid evidence of the presence of *Crocidura russula* as early as the Middle Pleistocene. On the other hand, several sites from the Middle–Late Pleistocene transition, MIS 5 (Marine Isotope Stage 5), dated 120–80 kyr have yielded more reliable records of *Crocidura russula*, showing the species was widely distributed in the Mediterranean biogeographic region of Iberia (Laplana et al. 2013, López-García et al. 2016, 2022). This latter scenario is more consistent with genetic divergence results and within the maximum age given by Brändli et al. (2005) and Cosson et al. (2005) and the mean date proposed by Biedma et al. (2018).

Despite the new record from Castillejo del Bonete and its importance in the analysis of the biogeography of *Crocidura iculisma* here exposed, our study leaves open some questions. Although our results support the existence of an interspecific competitive relationship between both *Crocidura* species during the Late Holocene, the moment in which it started and how this ecological process might have taken place in the Pleistocene needs to be analysed in more detail. In addition, the morphological and genetic relationships between the modern populations and the fossil specimens are still unknown. The analysis of ancient

DNA (aDNA) in Quaternary small mammals offers valuable information to improve our knowledge of taxonomy, phylogenetic relationships, palaeobiogeographic and palaeoecological studies (Woods et al. 2017, Baca et al. 2020, 2023, Alfaro-Ibáñez et al. 2023, Domínguez-García et al. 2024). This approach could also contribute significantly to advancing this line of research. Indeed, the results presented here leave open further avenues of research, such as extending the temporal range to the Late Pleistocene *Crocidura* records and, including other approaches such as morphometric and molecular analyses, to gather more evidence that might be relevant to clarify the biogeographic history of the *Crocidura iculisma/Crocidura russula* relationship in southwestern Europe.

Finally, given that *Crocidura iculisma* is a rare species showing a highly fragmented distribution range, we find it pertinent to discuss some implications for its conservation status. According to the IUCN Red List of Threatened Species, it is classified as least concern (LC) (*Crocidura gueldenstaedtii* in Kryštufek & Gazzard 2023) due to its wide Eurasian range. However, it is classified as near threatened (NT) in the French Red List (MNHN & OFB, 2003–2023), endangered (EN) in Portugal (Calzada et al. 2023) and data deficient (DD) in Spain (Palomo et al. 2007). In the context of global warming, our results reinforce the idea that the *Crocidura iculisma* populations from the Mediterranean climate areas are vulnerable due to habitat and climate change. Its local potential of extinction is enhanced by competition with *Crocidura russula*, which is better adapted to drier and warmer conditions. Conservation actions concerning the habitat where this species is known to be present should be implemented.

As a final remark, this study shows the relevance of palaeontological data as a continuous source of new valuable data to assess the conservation status and threats influencing the species distribution and abundance. Hopefully, it will encourage researchers to carry out further studies focused on *Crocidura* spp. in other regions of southwestern Europe including its fossil record as a valuable source of information.

CONCLUSIONS

The biogeographic history of *Crocidura iculisma* in southwestern Europe is marked by a significant reduction in its distribution range in the Iberian Peninsula during the Holocene.

Our results support the possibility of a relevant role played by interspecific competition and displacement by *Crocidura russula* in explaining its biogeographic dynamics and habitat specialisation. Climatic factors, characterised by increasing aridity over the last 4,000 years, seem to have been decisive in this process so that the reduction or the disappearance of the humid habitats from the southern and eastern regions of Iberia that once allowed it to withstand competitive pressure with *Crocidura russula* in Mediterranean environments may explain its current low abundance and patchy distribution.

The extent and precision with which palaeontological data contribute to understanding long-term mammal species dynamics are constrained by the nature of these data. Therefore, the similarity in the morphology of both *Crocidura* spp. has put into evidence taxonomic issues regarding the differentiation between both species in fossil small mammal assemblages, restricting the reconstruction of relative abundance ratios and limiting the extent to which their long-term biogeographical history can be reconstructed. Further research complemented with modern techniques will surely help to overcome these issues and achieve a more precise history of these species in the Quaternary of southwestern Europe.

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CONFLICT OF INTEREST STATEMENT

The authors declare that they have no conflict of interest to disclose which could have appeared to influence the work reported in this paper.

DATA AVAILABILITY STATEMENT

Data used for the research described in the article are provided in the main text and Appendix S1 submitted with the paper.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's website.

Appendix S1. Measurements of the upper fourth premolar (P4) employed for the biometric characterization.