Palaeogeography, Palaeoclimatology, Palaeoecology 691 (2026) 113727

Contents lists available at ScienceDirect

Palaeogeography, Palaeoclimatology, Palaeoecology

journal homepage: www.elsevier.com/locate/palaeo

Regional body-mass dynamics and long-term mixed feeding diet in the Pleistocene *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae) from Western Europe☆

Antigone Uzunidis[a,*], Luca Pandolfi[b]

[a] LAMPEA, UMR 7269 CNRS, Aix Marseille Université, Ministère de la Culture, Aix-en-Provence, France
[b] Università di Pisa, Dipartimento di Scienze della Terra, via S. Maria 53, 56126 Pisa, Italy

ARTICLE INFO

Keywords:
Weight
Gracility index
Dental mesowear
Dental microwear
Mediterranean area
Northern area
Refuge zone

ABSTRACT

We synthesize body mass, limb gracility, and diet in *Stephanorhinus hemitoechus* from 57 western European cohorts (MIS12–MIS3) using body mass-estimation equations, metapodial gracility indices, dental mesowear, and microwear. Two region-specific dynamics emerge: 1) in Northern Europe, cohorts are consistently heavier than Mediterranean contemporaries but remain broadly stable through time; 2) in the Mediterranean core range, body masses are stable from MIS 12 to MIS 7, rise in MIS 6, and then plateau through MIS 3. Gracility indices show little variations through time. Mesowear and microwear indicate a durable mixed-feeding strategy across the species' range, with northern populations incorporating slightly more grass. In specimens with paired estimated body mass and mesowear ($n = 14$), we found that higher grass intake relates to lower body mass, suggesting that diet modulates, but does not drive, size variation. These results support a distinction between core-range cohorts and peripheral interglacial incursions: in the North, climatic deterioration likely led to local extirpation rather than in situ size adjustment, as instead observed in the Mediterranean area. Near the last occurrences (MIS 4–3), several assemblages (Axlor, El Castillo) depart from year-round mixed feeding and show seasonal specialization toward grazing or browsing, consistent with colder, floristically simplified landscapes and heightened competition. We propose that this late loss of year-round dietary flexibility, coupled with the prior Mediterranean body-mass increase, increased vulnerability and may have contributed to extinction.

1. Introduction

Stephanorhinus hemitoechus (Falconer *in* Gaudin, 1859) is one of the rhinoceros species that inhabited Western Europe during the Middle and Late Pleistocene. It is first documented in Campagna Romana (Italy) in deposits dated around 500 ka during MIS13 (Pandolfi et al., 2013), and its last known occurrence is located at Gruta da Figueira Brava (Portugal), spanning from 24 ka to 30–31 ka (Antunes and Cardoso, 2000; Cardoso, 1993; Stuart, 2005). Its geographical range roughly covered Europe (Guérin, 1980), the Near East (Pokines et al., 2019), and North Africa (Antoine et al., 2025). This species is mostly known from Mediterranean areas, with occasional extensions of its range into northern Europe during interglacial periods (Pandolfi and Tagliacozzo, 2015).

Across the Middle and Late Pleistocene, glacial–interglacial oscillations repeatedly reorganized temperature–moisture regimes, but vegetation responses were strongly regional, producing habitat mosaics rather than a fixed ‘steppe vs forest’ dichotomy. Long pollen sequences and refugia syntheses highlight state-dependent shifts in openness, contractions into southern/cryptic refugia, and latitudinal gradients in expansion potential (Schmitt and Varga, 2012; Stewart et al., 2010; Tzedakis, 1994). Large-mammal communities and herbivore guild structure tracked these changes through time. Regionally structured turnover and redistribution in large mammals, and community-scale tooth-wear study shows higher dietary trait diversity during interglacials and geographic gradients in abrasiveness, linking local assemblages to both habitat heterogeneity and species turnover (Puzachenko et al., 2021; Rivals et al., 2009). How *S. hemitoechus* tracked changing habitats through the Middle–Late Pleistocene remains poorly understood. Available dietary reconstructions point to a general

☆ This article is part of a Special issue entitled: ‘dental microwear’ published in Palaeogeography, Palaeoclimatology, Palaeoecology.

* Corresponding author.
E-mail address: antigone.uzunidis@univ-amu.fr (A. Uzunidis).

https://doi.org/10.1016/j.palaeo.2026.113727
Received 8 November 2025; Received in revised form 8 March 2026; Accepted 17 March 2026
Available online 23 March 2026

flexible mixed-feeding strategy, with substantial overlap with other large herbivores depending on local habitat diversity (Rivals and Lister, 2016; van Asperen and Kahlke, 2015).

Although described in the 19th century, this species is still poorly known. Despite several attempts to characterize *S. hemitoechus* (Fortelius et al., 1993; Guérin, 1973, 1980; Lacombat, 2003, 2009; Pandolfi and Tagliacozzo, 2015; van der Made, 2010), only recently has a new study proposed a revision of the lectotype of the species (Pandolfi et al., 2025). Drawing on Italian and UK specimens, Azzaroli (1962) distinguished two size-based sub-species: the gracile *Rhinoceros hemitoechus falconeri* from the Middle Pleistocene, and the robust *Rhinoceros hemitoechus aretinus* from the Late Pleistocene (Anfossi and Cantaluppi, 1987; Azzaroli, 1962). The hypothesis of two chronostratigraphic forms was later extended to other European cohorts (Fortelius et al., 1993; Guérin, 1982). However, these sub-species, together with a third erected in the 1980s (*Dicerorhinus hemitoechus intermedius*; Anfossi and Cantaluppi, 1987), have recently been invalidated (Pandolfi et al., 2025). Numerous attempts have also been made to describe and understand *S. hemitoechus* evolutionary trends through time. Previous works have observed either a stability (Saarinen et al., 2016) in its body mass or highlighted size variations. *Stephanorhinus hemitoechus* size would have been large during MIS12, decreasing between MIS11 and MIS8 and increasing again from MIS7 to MIS3 (Lacombat, 2009). Another scenario indicates that *S. hemitoechus* would have always been more gracile in the Iberian Peninsula, with a continuous size increase from the Middle to the Late Pleistocene (Cerdeño, 1990), while Italian specimens are suggested to have remained robust through time (Pandolfi and Tagliacozzo, 2015). This anatomical variability in *S. hemitoechus* may be explained, at least in part, by its equally variable diet. Although most studies characterized the species as a mixed-feeder with a grazing tendency (Rivals et al., 2022b; Rivals and Lister, 2016; Saarinen and Lister, 2016; van Asperen and Kahlke, 2015), no attempts to measure the relationship between the diet and anatomy have yet been undertaken.

In this work, we focus on Western Europe from northern regions (UK, Germany) to the Mediterranean area (France, Monaco, Italy, Spain, Portugal) in order to describe both the body mass and the ecological adaptations of *S. hemitoechus* to its habitats. This study aims to 1) estimate and describe *S. hemitoechus* body mass evolution from MIS12 to MIS3, 2) analyze its diet at two time scales, last years (dental mesowear) and last days (dental microwear), and 3) assess the putative connection between body mass and diet. Ultimately, we aim to provide a comprehensive picture of *S. hemitoechus* ecological requirements.

2. Material and methods

2.1. *Stephanorhinus hemitoechus* sample

In order to understand the body mass and ecological diversity of *S. hemitoechus* in western Europe during the Pleistocene, we have gathered original and previously published data. In total, 57 cohorts from the UK, Germany, France, Monaco, Italy, Spain, and Portugal, ranging from MIS12 to MIS3, were selected (Table 1; Fig. 1). *Stephanorhinus hemitoechus* assemblages are often scarce and associated with incomplete skeletal documentation; therefore, not all the analyses were feasible for each cohort. Thirty-six were used to reconstruct the body mass of the rhinoceros, 12 to analyze changes in their gracility, 15 to analyze dental mesowear, and 17 for dental microwear.

The raw data are available at the following URL: https://zenodo.org/records/17550583

2.2. Reconstruction of body weight and diet of *S. hemitoechus*

Teeth and bone measurements as well as dental meso- and microwear analyses were based on original and on previously published datasets. In order to limit the inter-observers' variation, we included published data only when measurement protocols were similar to ours. Regarding dental wear analyses, we included studies authored by Florent Rivals and collaborators, whose methods closely match those used by the author of the dental wear studies (AU) (Uzunidis et al., 2021, 2024a, 2024b).

All the statistical analyses were performed using RStudio (RStudio Team, 2018).

2.2.1. Body mass and conformation analyses

The weight of the *S. hemitoechus* was estimated from measurements taken at the neck of the upper second (M2) and third (M3) molars as well as the first lower molar (m1) with a digital caliper. Measurements at the neck were selected to include teeth from individuals of all age and to minimize the influence of crown height on the estimates. For the body mass estimates based on upper molars, we used the length at the neck, expressed in millimeters, and the equations published by Fortelius and Kappelman (1993). For the body mass estimation based on the lower first molar, we used the length and the width at the neck, in millimeters, and the equation by Legendre (1989). To increase the number of cohorts included in this part of the study by incorporating Lunel-Viel and La Fage, we combined body mass estimates derived from tooth measurements with estimates based on the transverse width between the medial and lateral trochlear ridges of the tibial trochlea of the talus (Tsubamoto, 2014), a method previously applied successfully to rhinocerotids (Antoine, 2025; Antoine et al., 2022). At the three sites where both approaches were available (Radice, Monte Sacro, and Ilford), the latter was also used as an independent estimator to evaluate the consistency of the tooth-based estimates. Nevertheless, to avoid overrepresenting a single individual, only the tooth-based estimates were retained in subsequent analyses for these three sites.The role of the forelimb and hindlimb differ in quadrupedal mammal locomotion, the former being related to weight support and the latter to propulsion (Heglund et al., 1982). In rhinoceroses, the morphology of the zeugopodial fore- and hindlimb bones correlates with brachypody, body mass, and phylogenetic history (Mallet et al., 2022). In another perissodactyl representative, *Equus* sp., the degree of gracility of the metapodial bones has also been linked to environmental parameters, and especially humidity (Boulbes and van Asperen, 2019; Eisenmann, 1984; Gromova, 1949; Uzunidis, 2021; van Asperen, 2010). Here we test whether small differences in *S. hemitoechus* metapodial gracility can be linked to changes in environmental parameters and, therefore, used as indicators of them. Gracility was estimated using gracility indices (transversal diameter of the diaphysis/maximal length of the bone*100) on both the third metacarpal and metatarsal.

2.2.2. Diet reconstruction

Dietary patterns were reconstructed using two complementary approaches: dental mesowear and microwear analyses (Fortelius and Solounias, 2000; Solounias and Semprebon, 2002). These two proxies track dietary signals at distinct temporal scales within an individual's life. Dental mesowear records dietary abrasiveness over several years, often the terminal year of life, whereas dental microwear records dietary habits from the last few days to weeks before death. Combined together, they provide a multi-scale view of dietary information. Mesowear captures long-term averages of dietary abrasiveness and provides insight into the regional vegetation composition, while microwear reflects short-term, often seasonal, dietary shifts linked to the local feeding conditions (Sánchez-Hernández et al., 2016; Uzunidis and Rivals, 2023).

Both methods support a three-category framework: browsers, mixed-feeders, and grazers. Browsers consume mainly dicotyledonous plants, including woody species and forbs; grazers feed predominantly on monocotyledonous grasses; and mixed-feeders alternate between these sources. For instance, in Kruger National Park (South Africa), browsers include 0–15% grass in their diet, grazers 84–100%, and mixed-feeders 4–76% (Codron et al., 2007).

Table 1
Inventory of the *Stephanorhinus hemitoechus* cohorts used in this study, with their age and their geographical location. The type of analysis (weight estimation, gracility index, dental mesowear, dental microwear) performed on each cohort is given, as all as the references of the original data. In the site column, the numbers in brackets correspond to the site identifications shown in Fig. 1 In the last column, osteometry refers to the measurements used for weight estimation and gracility analysis, whereas dental wear refers to the quantitative and qualitative data collected for mesowear and microwear analyses.

MIS	Country	Site	Weight estimation analysis	Gracility analysis	Dental mesowear analysis	Dental microwear analysis	Author
MIS12	France	Arago [1]	Yes				Lacombat, 2003
MIS11	UK Germany	Clacton-on-sea [2]	Yes	Yes	Yes	Yes	Osteometry: This work Dental wear: Rivals and Lister, 2016
		Heppenloch [3]			Yes	Yes	Rivals and Ziegler, 2018
		Steinheim [4]			Yes	Yes	Rivals and Ziegler, 2018
	France	Terra Amata [5]	Yes				Lacombat, 2003
MIS10	Italy	Monte Sacro [6]	Yes				Pandolfi and Marra, 2015
		Monte Verde [7]	Yes				Pandolfi and Marra, 2015
MIS9	UK	Grays Thurrock [8]		Yes	Yes	Yes	Osteometry: Pandolfi and Tagliacozzo, 2015 Dental wear: Rivals and Lister, 2016
	France	Orgnac III [9]	Yes	Yes			Lacombat, 2003
	Italy	Torre del Pagliacetto lower level [10]		Yes			Caloi and Palombo, 1978, 1994
MIS8	Italy	Vigna San Carlo [11]	Yes				Pandolfi and Marra, 2015
MIS7	UK	Ilford [12]	Yes	Yes	Yes	Yes	Osteometry: This work Dental wear: Rivals and Lister, 2016
		Crayford [13]			Yes		Rivals and Lister, 2016
	Germany	Ehringsdorf [14]	Yes				Kahlke, 1975
		Neumark-Nord [15]	Yes				van der Made, 2010
	France	Payre G [16]				Yes	Uzunidis-Boutillier, 2017; this work
		Payre F [16]	Yes		Yes	Yes	Uzunidis-Boutillier, 2017; this work
		La Fage [17]	Yes	Yes			Guérin, 1973
		Lunel-Viel [18]	Yes	Yes		Yes	Uzunidis-Boutillier, 2017; this work
	Italy	Passo Corese [19]	Yes				This work
MIS6	France	Payre D [16]	Yes		Yes	Yes	Uzunidis-Boutillier, 2017; this work
		Rigabe [20]	Yes		Yes	Yes	Uzunidis-Boutillier, 2017; this work
		Grotte de Mars [21]	Yes	Yes			Lacombat, 2003
	Italy	Maspino [22]	Yes				This work
MIS5	UK	Joint Minor Cave [23]		Yes	Yes	Yes	Rivals and Lister, 2016
	Germany	Burgtonna [24]	Yes				Kahlke, 1978
	Italy	Acque Albule [25]	Yes				This work
		Melpignano [26]	Yes				This work
		San Colombano [27]	Yes				Cantaluppi, 1969; this work
		Ugento [28]	Yes				This work
		Parignana [29]			Yes	Yes	This work
		Cucigliana [30]			Yes	Yes	This work
	Spain	Pinilla-del-Valle [31]		Yes			Cerdeño, 1990
		Lezetxiki [32]		Yes			Cerdeño, 1990
MIS4	Monaco	Grotte du Prince [33]	Yes				Lacombat, 2003
	Italy	Barma Grande [34]	Yes				Lacombat, 2003
		Romanelli [35]	Yes				This work
	Spain	El Castillo l. Mousterian-Beta [36]	Yes		Yes	Yes	This work
		Axlor l.D [37]	Yes			Yes	Uzunidis et al., 2025; this work
		Cova del Gegant [38]		Yes			Pandolfi and Tagliacozzo, 2015
MIS4/3	Italy	Valle Radice [39]	Yes				Pandolfi and Tagliacozzo, 2015
	Gibraltar	Genista cave [40]		Yes			Busk, 1879
	Monaco	Observatoire [46]		Yes			Lacombat, 2003
MS3	Spain	Cueva Millan [41]	Yes				Cerdeño, 1990; This work
		Cueva del Conde [42]	Yes				Cerdeño, 1990; This work
		El Castillo l. Mousterian-Alfa [36]	Yes		Yes	Yes	This work
		El Castillo l. Aurignacian-Delta [36]	Yes		Yes	Yes	This work
		Cueva Morin [43]	Yes				Altuna, 1971
		Cueva Buho [44]	Yes				Iñigo, 1995
	Portugal	Lorga de Dine [45]	Yes				Cardoso, 1993

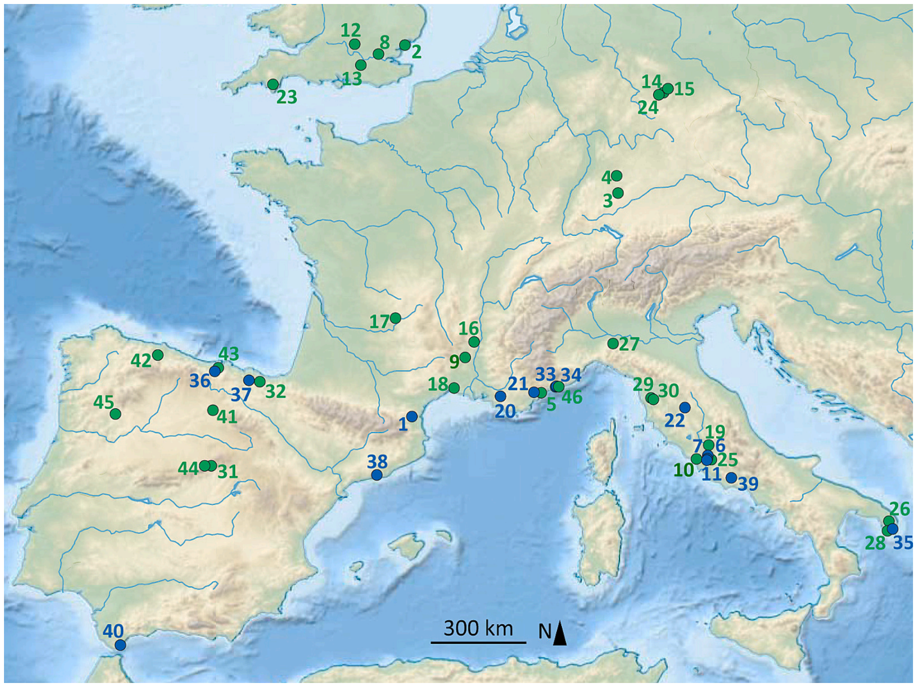

Fig. 1. Geographical position of the sites used in this study. 1: Arago, 2: Clacton-on-sea, 3: Heppenloch, 4: Steinheim, 5: Terra Amata, 6: Monte Sacro, 7: Monte Verde, 8: Grays Thurrock, 9: Orgnac III, 10: Torre del Pagliacetto lower level, 11: Vigna San Carlo, 12: Ilford, 13: Crayford, 14: Ehringsdorf, 15: Neumark-Nord, 16: Payre, 17: La Fage, 18: Lunel-Viel, 19: Passo Corese, 20: Rigabe, 21: Grotte de Mars, 22: Maspino, 23: Joint Minor Cave, 24: Burgtonna, 25: Acque Albule, 26: Melpignano, 27: San Colombano, 28: Ugento, 29: Parignana, 30: Cucigliana, 31: Pinilla-del-Valle, 32: Lezetxiki, 33: Grotte du Prince, 34: Barma Grande, 35: Romanelli, 36: El Castillo, 37: Axlor, 38: Cova del Gegant, 39: Valle Radice, 40: Genista Cave, 41: Cueva Millan, 42: Cueva del Conde, 43: Cueva Morin, 44: Cueva Buho, 45: Lorga de Dine, 46: Observatoire. In green: deposits from interglacial periods; in blue: deposits from glacial periods. Creative Commons Attribution-Share Alike 3.0 Unported license. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

2.2.2.1. Dental mesowear. Dental mesowear analysis assesses macroscopic wear patterns on tooth cusps that reflect the physical properties of ingested food (Fortelius and Solounias, 2000). While exogenous particles such as dust or grit can contribute to wear (Kaiser et al., 2009), the dominant abrasive agents are generally phytoliths contained in grasses, directly linking mesowear patterns to dietary behavior (Kaiser et al., 2013; Saarinen and Lister, 2016).

Sharp, high cusps are associated with attrition (tooth-on-tooth wear) and indicate low-abrasion diets, whereas rounded or blunt cusps result from abrasion (tooth-on-food contact) and reflect high-abrasion diets. The mesowear signal represents an undefined cumulative record of diet over an extended period. It could represent a lifetime accumulation (Ackermans et al., 2020) or reflect dietary habits from several years before the animal's death (Louys et al., 2011; Ulbricht et al., 2015; Uzunidis et al., 2023).

Following the protocol of Fortelius and Solounias (2000), the paracone of the upper second molar was preferentially selected from well-preserved specimens. Teeth exhibiting taphonomic alteration or extreme wear were excluded. Cusp shape and relief were evaluated using the "ruler method" of Mihlbachler et al. (2011) and modified by Rivals et al. (2013) and classified into seven categories: 0 = high and sharp cusp; 1 = high, narrow-angled, slightly rounded cusp; 2 = high, wide-angled, rounded cusp; 3 = medium-high, very rounded cusp; 4 = low, rounded cusp; 5 = nearly flat cusp; 6 = blunt cusp with no relief.

The average mesowear value per assemblage was expressed as a Mesowear Score (MWS). Typical values range between 0-2 for browsers, 1–2.5 for mixed-feeders, and 2–5.5 for grazers.

2.2.2.2. Dental microwear. Dental microwear analysis focuses on microscopic wear features formed on enamel surfaces during chewing (Walker et al., 1978). These microtraces primarily reflect the physical properties of consumed food, especially the presence of phytoliths (Rivals et al., 2015; Walker et al., 1978), although exogenous particles such as dust and grit may also contribute (Gallego-Valle et al., 2020; Rivals and Semprebon, 2017; Schulz-Kornas et al., 2020). Dental microwear provides a short-term dietary snapshot, typically representing the last few days to a month of an animal's life (Hoffman et al., 2015; Teaford, 1988; Winkler et al., 2020).

The analysis followed the procedures established by Semprebon et al. (2004) and Solounias and Semprebon (2002). Occlusal surfaces were cleaned with 96% ethanol, and impressions were taken using high-resolution vinylpolysiloxane. Transparent epoxy resin casts were examined under a stereomicroscope at 35× magnification using a maneuverable light. Observations were restricted to a standardized 0.16 mm^2 area using an ocular reticule. They were performed on two locations, preferentially on the metacone of the occlusal surface and the results were averaged.

Microwear features were classified into pits (small and large), scratches (fine, coarse, and hypercoarse), and gouges. Pits are rounded to subrounded depressions: small pits are shallow and bright, while large pits are deeper, darker, and irregular. Scratches are elongated parallel features: fine scratches are narrow, shallow, and faintly refractive; coarse scratches are wide, deep, and highly refractive. Each specimen was assigned a Scratch Width Score (SWS): 0 = predominantly fine scratches; 1 = mixed fine and coarse scratches; 2 = predominantly coarse scratches.

Second premolars and second deciduous teeth were excluded, as they do not record the same occlusal signal as other cheek teeth (Kaiser and Fortelius, 2003; Xafis et al., 2017). Other deciduous teeth were, however, included in the analysis since they display a microwear signal similar to that of permanent teeth (Rivals et al., 2022a; Smith and DeSantis, 2018). Teeth showing taphonomical damage or poorly preserved enamel were also removed following established criteria (King et al., 1999; Micó et al., 2024a, 2024b; Uzunidis et al., 2021).

Since dental microwear is impacted by seasonal alternation, reconstruction of the duration of mortality events is critical to differentiate multi-seasonal and seasonal signals. Microwear scratch density variability is indicative of the duration of an herbivore cohort accumulation. It was quantified using standard deviation (SD) and coefficient of variation (CV), following Rivals et al. (2015). Since microwear reflects seasonal dietary changes, SD and CV values provide a proxy for the temporal span of death assemblages. Combining both parameters allows classification into three categories: (A) Low SD and CV = short-term or single-season events; (B) Moderate SD and CV = accumulations spanning multiple contiguous seasons; (C) High SD and CV = accumulations from non-contiguous seasons.

Although the exact season cannot be determined, these variability measures provide a relative estimate of accumulation duration. For small samples, a bootstrap resampling procedure ($n = 500$, with replacement) was applied to generate robust SD–CV estimates, following Domínguez-Rodrigo et al. (2019). Results were visualized using a heatmap, where a grayscale gradient (white to black) indicates the probability of each cohort's position relative to these temporal categories.

3. Results

3.1. Evolution of body mass and gracility in S. hemitoechus in western Europe

Body mass was estimated for 36 *S. hemitoechus* cohorts from Northern and Mediterranean Europe spanning from MIS12 to MIS3. Body mass was estimated using both tooth- and talus-based approaches. At the sites where both methods could be applied (Monte Sacro, Ilford, and Radice), they produced comparable results. Values range from 914 kg (Payre l.F, France, MIS 7) to 2975 kg (Neumark-Nord, MIS 7, Germany) (Table 2; Supplementary data 1), with substantial among-site variation. A preliminary comparison indicates that Northern cohorts (UK, Germany) are heavier (mean ± SD: 1850 ± 584 kg) than Mediterranean cohorts (France, Italy, Monaco, Spain, Portugal) (mean ± SD: 1739 ± 445 kg); however, this difference is not significant (Wilcoxon, $p = 0.8432$) when all northern sites are compared with all Mediterranean sites (Fig. 2).

Considering all 34 *S. hemitoechus* cohorts, modest body mass differences can be observed with respect to both geographical position and

Table 2
Summary of the estimated weight and of the gracility indices of western European *Stephanorhinus hemitoechus* according to their age (in MIS) and location (country). The gracility indices are given for the third metacarpal (MTC3) and the third metatarsal (MTT3). The number of bones and teeth used to reconstruct the weight is given, as well as the mean, standard deviation, minimum (Min), and maximum (Max). The average body masses with an asterisk (*) are the ones estimated using talus-based estimator. In the site column, the numbers in brackets correspond to the site identifications shown in Fig. 1.

MIS	Country	Site	Weight estimation			MTC3 gracility			MTT3 gracility		
			n	Mean (in kg)	Min-Max	n	Mean	Min-Max	n	Mean	Min-Max
MIS12	France	Arago [1]	2	1634 ± 155	1524–1743						
MIS11	UK	Clacton-on-sea [2]	2	1555 ± 318	1330–1779	1	24.7				
	France	Terra Amata [5]	1	1324							
MIS10	Italy	Monte Sacro [6]	1	1897 (1836*)							
		Monte Verde [7]	1	1532							
MIS9	Italy	Torre del Pagliacetto lower level [10]				1	28.4				
	France	Orgnac III [9]	1	1297					1	26.2	
	UK	Grays Thurrock [8]							2	25 ± 1.1	24.2–25.8
MIS8	Italy	Vigna San Carlo [11]	1	1471							
MIS7	UK	Ilford [12]	3	2032 ± 746 (1889*)	1318–2807	1	27.3		3	26.8 ± 0.7	26–27.4
	Germany	Ehringsdorf [14]	2	1316 ± 13.1	1307–1325						
		Neumark-Nord [15]	9	1971 ± 689	1395–2975						
	France	Payre F [16]	1	915							
		Lunel-Viel [18]	1	1288*					1	25.6	
		La Fage [17]	1	1257*					1	26.8	
	Italy	Passo Corese [19]	1	1311							
MIS6	France	Payre D [16]	1	1633							
		Rigabe [20]	2	2192 ± 36.2	2166–2218						
		Mars [21]	1	2101					1	25.9	
	Italy	Maspino [22]	2	1485 ± 671	1010–1959						
MIS5	UK	Joint Minor Cave [23]				1	28.3				
	Germany	Burgtonna [24]	3	1857 ± 273	1665–2170						
	Italy	Acque Albule [25]	5	1618 ± 127	1472–1752						
		Melpignano (26]	1	1267							
		San Colombano [27]	2	1883 ± 127.9	978.2–2788						
		Ugento [28]	1	1603							
	Spain	Pinilla del Valle [31]				1	26.1		1	23.9	
MIS4	Monaco	Grotte du Prince [33]	1	1790							
	Italy	Barma Grande [34]	1	1870							
		Romanelli [35]	2	1503 ± 253	1324–1682						
		Valle Radice [39]	1	1698 (1685*)							
	Spain	El Castillo l. Mousterian-Beta [36]	8	2011 ± 397	1652–2747						
		Axlor l.D [37]	1	2336							
		Cova del Gegant [38]				1	25.5				
MIS4/3	Gibraltar	Genista Cave [40]							1	25.8	
MS3	Italy	Valle Radice [39]				2	27.9 ± 0.99	27.3–28.7	1	26	
	Monaco	Observatoire [46]				1	28.9				
	Spain	Cueva Millan [41]	1	2924							
		Cueva del Conde [42]	1	1558							
		El Castillo l. Mousterian-Alfa [36]	24	1800 ± 442	952–2856						
		El Castillo l. Aurignacian-Delta [36]	2	1311 ± 356	1059–1563						
		Cueva Morin [43]	1	1529							
		Cueva Buho [44]	1	1721							
	Portugal	Lorga de Dine [45]	1	1775							

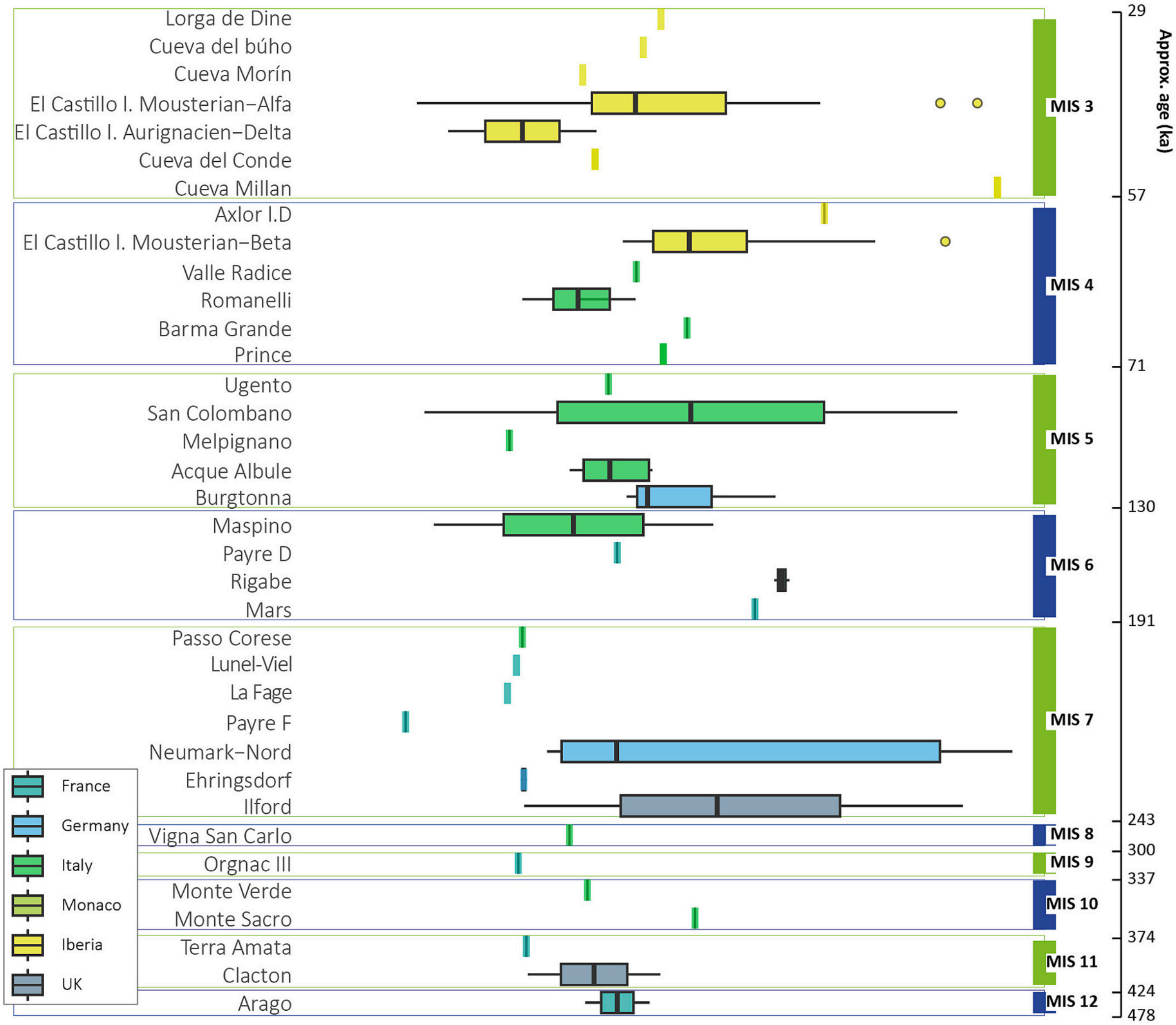

Fig. 2. Boxplot showing the evolution of the weight of *Stephanorhinus hemitoechus* through time from bottom to top and according to their geographical location.

geological age. We grouped cohorts into two regional groups: northern specimens (UK, Germany) and Mediterranean ones (France, Monaco, Italy, Spain, Portugal). Within this framework, northern *S. hemitoechus* are larger than contemporaneous Mediterranean specimens during at least MIS11, MIS7, and MIS5 (Fig. 3). Owing to uneven sample sizes across time spans and regions (MIS11-Mediterranean, $n = 1$; MIS11-Northern, $n = 2$; MIS7-Mediterranean, $n = 4$; MIS7-Northern, $n = 14$; MIS5-Mediterranean, $n = 9$; MIS5-Northern, $n = 3$) (Table 2), no statistical analyses were performed.

Different evolutionary trends are observed between Northern and Mediterranean cohorts. In Northern Europe, the median body mass is relatively constant, with only a small and non-significant increase during MIS5 (Wilcoxon, $p = 0.4$). In Mediterranean Europe, body mass is stable from MIS12 to MIS7 and then increases from MIS6, and remains stable from MIS6 to MIS3. Here the chronological difference is significant (Wilcoxon, $p = 0.00304$).

Gracility indices were calculated for 12 *S. hemitoechus* cohorts using third metacarpals and metatarsals (Table 2). Results should be interpreted with caution given the small sample sizes, which further preclude statistical tests.

For the third metacarpal, the mean gracility index is 27.2 ± 1.5 and for the third metatarsal is 25 ± 2.4. Overall, the gracility indices are approximately constant across cohorts (Fig. 3). Some specimens display lower values, namely the oldest northern specimens from MIS11 and MIS9 (Clacton-on-Sea and Grays Thurrock) and Mediterranean specimens from MIS5 and MIS4 (Pinilla del Valle, Lezetxiki, and Cova del Gegant). This indicates more elongated distal limbs compared with the rest of the sample.

3.2. Evolution of the diet of *S. hemitoechus* in western Europe

Mesowear score (MWS) values for *S. hemitoechus* mostly fall between 2 and 4, indicating a mixed diet that included both dicots and monocots (Table 3; Fig. 4). Occasional shifts toward a more browser-like diet, with medians equal to 1, are observed at Grays Thurrock in northern Europe and at El Castillo l. Mousterian Beta, in the Mediterranean area. These results, however, are based on very small samples ($n = 3$ and $n = 1$, respectively) and should therefore be treated with caution.

In northern Europe, MWS values are typically between 3 and 4 across MIS spans, placing *S. hemitoechus* among grazers or mixed-feeders with a grazing tendency. In Mediterranean Europe, MWS values are slightly lower, mostly ranging between 3 and 2. Although still within the variability of mixed-feeders, they indicate a somewhat reduced monocot intake compared to northern cohorts.

Cold stage cohorts are scarce: three individuals for MIS6 (Payre, level D, and Rigabe) and one for MIS4 (El Castillo l. Mousterian Beta). Their MWS values lie within the range of mixed-feeders with a browsing tendency, suggesting lower grass incorporation during these periods.

At the microwear scale, herbivore diet is impacted by seasonal alternation. Their diet can, therefore, reflect seasonal plant availability

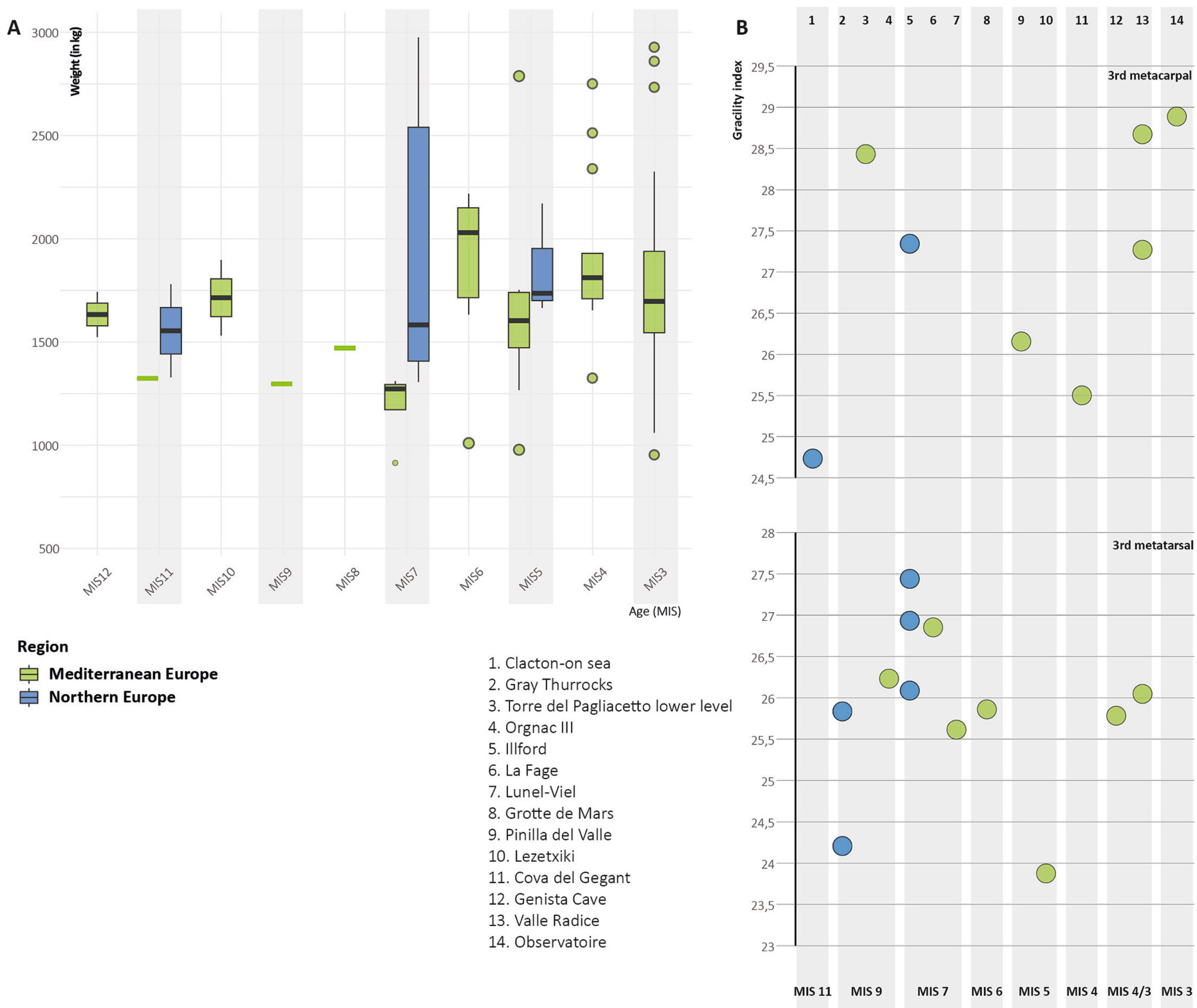

Fig. 3. A: Boxplot showing the evolution of the weight of *Stephanorhinus hemitoechus* from Northern Europe (UK, Germany) and Mediterranean Europe (France, Monaco, Italy, Spain, Portugal) through time. B: Values of the gracility indices of 12 *Stephanorhinus hemitoechus* cohorts from Northern and Mediterranean Europe and according to their age (in MIS), based on third metacarpal and metatarsal measurements. Time runs from left to right.

(Uzunidis and Rivals, 2023). To assess whether microwear patterns in western European *S. hemitoechus* cohorts represent one or multiple seasons, we analyzed dietary diversity. Most cohorts included in the analysis show low standard deviation and coefficient of variation, plotting in region A of Fig. 5; among them, Heppenloch, Steinheim, Grays Thurrock, Crayford, Ilford, Lunel-Viel, El Castillo l. Mousterian-Beta and El Castillo l. Aurignacian-Delta. This pattern is consistent with a short mortality event encompassed within an undefined single season (Rivals et al., 2015). In contrast, Joint Minor Cave exhibits higher dispersion (SD and CV), mapping to region B of the heatmap and indicating a long-term accumulation spanning several consecutive seasons. The positions of Clacton-on-sea, Payre l.F, and El Castillo l. Mousterian-Alpha remain uninformative due to the high error associated with their position.

At the microwear scale, all *S. hemitoechus* cohorts, except El Castillo l. Moustrien-Alpha and Beta and Axlor l.D, show moderate numbers of pits and scratches, falling within the range of variation of mixed-feeders (Table 3; Figs. 4 and 6). This suggests that they incorporated both dicots and monocots into their diet, consistent with mesowear inferences. Specimens from El Castillo l.Moustrien-Alpha and Beta display fewer scratches, plotting among browsers, whereas the cohort from Axlor l.D shows higher scratch counts, indicative of grazing.

The recurrence of large pits is highly variable among cohorts: they are absent at Grays Thurrock, Crayford, Payre l.G and D, Parignana, Cucigliana and Axlor l.D, systematic at Rigabe, El Castillo l.Aurignacian-Delta and intermediate at Clacton-on-sea, Heppenloch, Steinheim, Ilford, Payre l.F, Lunel-Viel, Joint Minor Cave, El Castillo l. Mousterian-Beta and Mousterian-Alpha. Large pits are compatible with a mixed-feeding or grazing diet (Semprebon et al., 2011). Most cohorts also display mixed scratch textures, likewise indicative of mixed or grazing diets. Gouges and hyper-coarse scratches are only common in the three cohorts from El Castillo, suggesting ingestion of grit in food (Semprebon et al., 2011).

Cohorts from the UK are characterized, within equivalent MIS stages, by significantly higher pit counts than their southern counterparts (Wilcoxon, $p = 0.001$), including those from Germany (Table 3; Fig. 4). On average, individuals from Grays Thurrock show more pits than those from Heppenloch and Steinheim during MIS11. Crayford and Ilford

Table 3
Summary of dental meso- and microwear data for *Stephanorhinus hemitoechus* from western Europe ranging between MIS11 and MIS3.

MIS	Country	Site		Mesowear		Microwear							
				n	MWS	n	NP	NS	%LP	%G	SWS	%HC	%XS
MIS11	UK	Clacton-on-sea [2]	m	5	3.6	11	16.95	15	54.5	9	1.27	0	27.3
			s		1.14		3.5	3.2					
	Germany	Heppenloch [3]	m	19	2.21	16	13.59	19.25	43.75	12.5	0.94		0
			s		1.11		2.12	2.36					
		Steinheim [4]	m	7	4.14	7	12.93	19.71	71.43	28.57	1.3		100
			s		0.9		3.07	1.22					
MIS9	UK	Grays Thurrock [8]	m	3	1.33	4	23.25	19.25	0	0	1	0	100
			s		0.58		4.21	2.72					
MIS7	UK	Ilford [12]	m	3	3.67	9	28.28	18.78	22.22	11.11	1.11	0	100
			s		1.53		3.73	2.28					
		Crayford [13]	m	4	2.83	5	20.9	18	0	0	1	0	80
			s		2		4.14	2.29					
	France	Payre l.G [16]	N°G5-M5–1174			1	9	20	0	0	1	0	100
		Payre l.F [16]	m	2	2.5	3	10.5	17.5	33.33	0	0.5	0	100
			s		0.7		3.5	6.14					
		Lunel-Viel [18]	m			7	15.14	19	28.57	0	0	0	100
			s				1.65	2.38					
MIS6	France	Payre l.D [16]	N°D-N8–2		2		10	13.5	0	0	1	0	100
		Rigabe [20]	N°V-?-82		2		19.5	16	100	0	1	0	1
MIS5	UK	Joint Minor Cave [23]	m	6	3.33	9	16.67	22.22	22.22	0	1	0	44.44
			s		1.21		3.27	4.87					
	Italy	Parignana [29]	m	3	1.41	2	8.5	17.5	0	0	0.5	0	0
			s		2		0.7	0.7					
		Cucigliana [30]	N°I14380	2	2.5		6	17	0	0	2	0	100
					2.12								
MIS4	Spain	Axlor l.D [37]	N°K15–3–12-26				5	24	0	0	1	0	100
		El Castillo	m	1	1	4	24.62	10.87	75	100	0.75	100	0
		l. Mousterian-Beta [36]	s				5.34	2.09					
MIS3	Spain	El Castillo	m	7	3.43	16	17	11.72	81.25	93.75	0.94	93.75	0
		l. Mousterian-Alpha [36]	s		1.39		3.36	2.25					
		El Castillo	m	1	4	3	25.67	18.67	100	100	1	100	0.33
		l. Aurignacian-Delta [36]	s				7.1	1.53					

Abbreviations: # = identifier of the teeth; n = Number of specimens; MWS = Mesowear score; NP = Mean number of pits; NS = Mean number of scratches; %LP = Percentage of specimens with large pits; %G = Percentage of specimens with gouges; SWS = scratch width score; %HC = Percentage of specimens with hypercoarse scratches; %XS = Percentage of specimens with cross scratches; m = Mean; s = Standard deviation. The authors of the analysis are also given. In the site column, the numbers in brackets correspond to the site identifications shown in Fig. 1.

exceed Payre (levels G and F) and Lunel-Viel during MIS7, and Joint Minor Cave exceeds Parignana and Cucigliana during MIS5. This pattern suggests that UK cohorts systematically ingested more dust than central and Mediterranean European ones (Rivals and Semprebon, 2017).

In Mediterranean Europe (France, Italy, and Spain), modest dietary variation in *S. hemitoechus* is evident when considering four microwear features (mean pits, mean scratches, mean number of large pits, SWS) (Fig. 7). A PCA of these variables explains 64.2% of total variance: PC1 (35.9% of total variance) is mostly built on the opposition between the quantity of pits and scratches, while PC2 (28.3% of total variance) represents the importance of the SWS and of the quantity of large pits. The three French MIS7 cohorts share features with Italian MIS5 cohorts. They generally display numerous scratches, few pits, and moderate SWS, pointing to a mixed diet with a majority of monocots. During MIS6, French cohorts are similar but show slightly fewer scratches, suggesting reduced monocot intake while remaining within mixed-feeder variability. The two Spanish MIS4 cohorts show opposite profiles: El Castillo (Mousterian–Beta) exhibits many pits and few scratches (browsing), whereas Axlor l. D shows few pits and many scratches (grazing). During MIS3, the two Spanish cohorts from El Castillo (l. Mousterian-Alpha and Aurignacian-Delta) display low scratch counts and high pit frequency, again consistent with browsing.

4. Discussion

4.1. Body weight and gracility evolutionary trends of S. hemitoechus in Western Europe

Limb robustness in *S. hemitoechus* is broadly similar across cohorts and time spans, with only slightly more gracile specimens in MIS11, MIS5, and MIS4. In agreement with Pandolfi et al. (2025) and Pandolfi and Tagliacozzo (2015), our data do not support earlier claims from Azzaroli (1962), Guérin (1982), Fortelius et al. (1993) and van der Made (2010) of a Western European succession of two forms: from an older robust form to a younger gracile one. Variations in metapodial gracility indices are limited, and sufficiently complete bones are too scarce to infer reliable trends during MIS11, MIS5, and MIS4 or to assess individual variability.

Only four assemblages provide both a long-term dietary proxy (dental mesowear) and limb gracility based on metapodial proportions (Clacton-on-Sea, Grays Thurrock, Ilford, and Joint Minor Cave). Given this limited overlap, it is not currently possible to formally test for a relationship between gracility and long-term dietary abrasiveness. Nevertheless, we can observe that Grays Thurrock, showing one of the lowest gracility indices measured on the third metatarsal (MTT3; mean GI = 25), is also associated with a particularly low-abrasion mesowear signal (MWS = 1.33). This pattern is best viewed as an exploratory lead that will require additional paired assemblages to evaluate robustly. Accordingly, the present data allow us to outline a possible trend, but not to demonstrate it.

In our sample, *S. hemitoechus* body mass ranges from 914 to 2975 kg and varies across Western Europe between MIS12 and MIS3 (Fig. 2). At the regional scale (Fig. 3), during interglacial periods, *S. hemitoechus* expanded into northern latitudes, and northern cohorts (UK, Germany) were larger-bodied than contemporaneous Mediterranean cohorts. Moreover, two distinct temporal patterns can be observed between the two areas: 1) during warm interglacial stages, when *S. hemitoechus* populations expanded into northern latitudes (UK and Germany in our

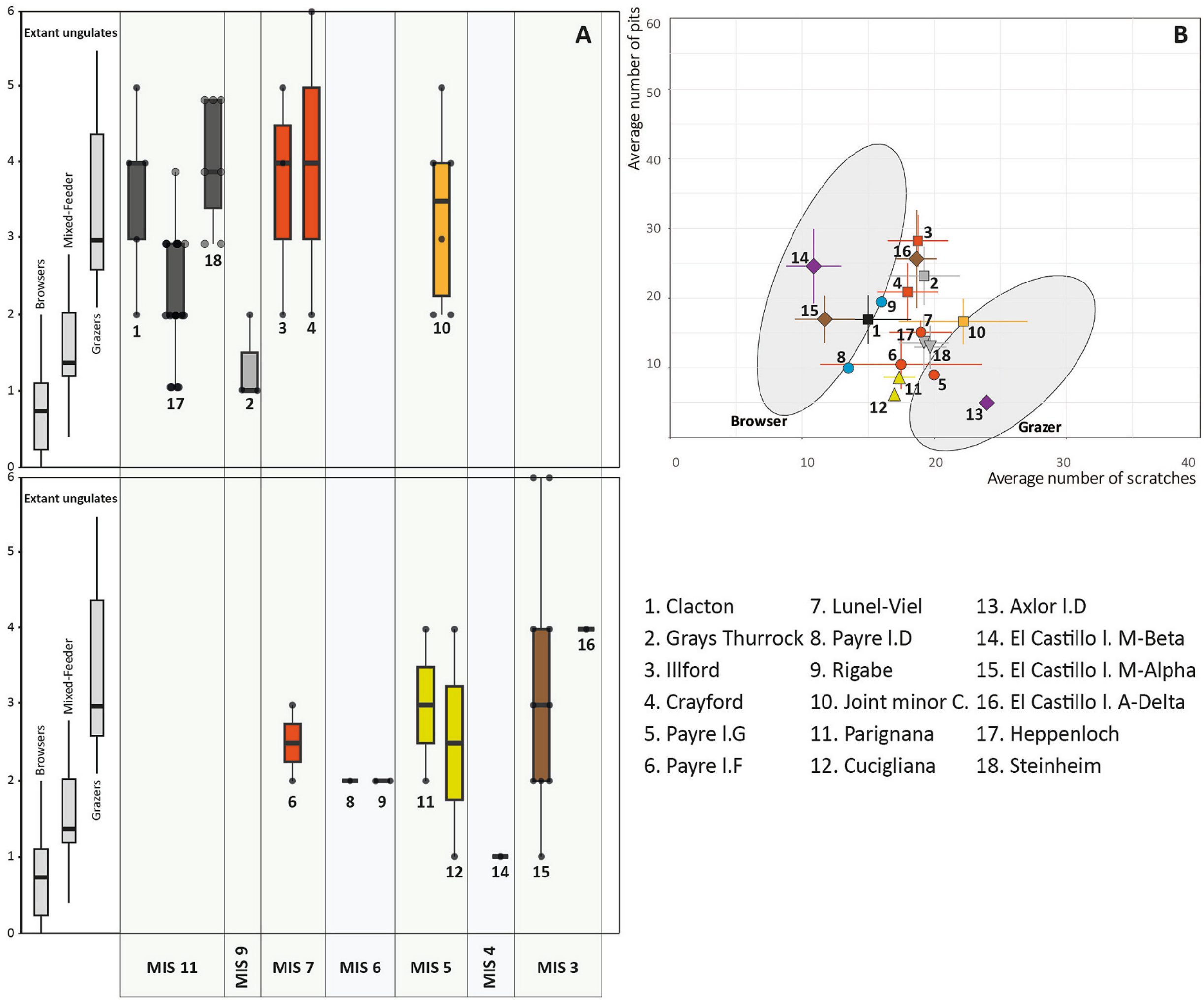

Fig. 4. A: Mesowear scores (MWS) of the *Stephanorhinus hemitoechus* from Northern and Mediterranean Europe from MIS11 to MIS3 compared to the values of recent ungulates published by (Fortelius and Solounias, 2000; Rivals et al., 2010, 2014). B: Bivariate plot of the mean number of pits and scratches of the *Stephanorhinus hemitoechus* from Northern and Mediterranean Europe from MIS11 to MIS3. Black: MIS11, Gray: MIS9, Orange: MIS7, Blue: MIS6, Yellow: MIS5, Purple: MIS4, Brown: MIS3. Square: UK, Triangle head-down: Germany, Circle: France, Triangle head-up: Italy, lozenge: Spain. Time runs from left to right. The error bars correspond to the standard deviation (±1 SD). The ellipses correspond to the Gaussian confidence ellipse (p. = 0.95) around the centroids of current grazers and browsers published by Solounias and Semprebon (2002). (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

sample), the species tended to be larger-bodied than its contemporaneous Mediterranean counterparts. Within Northern Europe, body masses are relatively stable through time, with a possible minor, non-significant uptick in MIS5. Accordingly, there is no significant long-term trend; 2) in contrast, populations in Southern Europe (which was probably the core, continuous habitat for the species) show a stable body mass from MIS12 to MIS7, a notable increase in MIS6, and then remains approximately constant from MIS6 to MIS3. We cannot, however, exclude a modest influence of sexual dimorphism (or shifting sex–age composition) on this pattern, although our sample size makes it likely that both males and females are represented.

While in Northern Europe, the weight of *S. hemitoechus* was already described as stable (Saarinen et al., 2016), for Mediterranean Europe different scenarios have been suggested. Based largely on French sites, Lacombat (2009) proposed a framework with large individuals in MIS12, smaller ones in MIS11-MIS8, and larger ones again in MIS7-MIS3. Differences between this model and our pattern reflect revised chronologies of certain sites, particularly Lunel-Viel, which no longer corresponds to MIS11 (Lacombat, 2009) but to MIS7 instead (Falguères et al., 2024), and the mixing of northern European cohorts. Consistent with Pandolfi and Tagliacozzo (2015), Italian cohorts show broadly similar gracility indices through time, indicating generally robust specimens (Fig. 3). In Spain, Cerdeño (1990) recorded a general size increase from the late Middle Pleistocene to the Late Pleistocene, which is also apparent here. In contrast, she also noted a small-sized form from the Iberian Peninsula that is not recovered by our tooth-based mass estimates. Notably, the most gracile metapodials in our dataset occur in the Iberian Peninsula (Fig. 3), potentially indicating taller, slenderer animals comparable in mass to other Mediterranean contemporaries; a hypothesis that requires additional material to test.

In summary, what previously appeared as a Europe-wide size pattern resolves into a regional-specific dynamic, suggesting relative stasis at the northern periphery versus a step-increase and subsequent stabilization in the Mediterranean core.

In the subset with paired data, 14 teeth provided sufficient information to reconstruct both general diet, based on dental mesowear, and body mass; body mass showed a modest but statistically significant association with diet. (Spearman's correlation, $p = 0.048$) (Fig. 8): mass decreases as grass intake increases, whereas heavier individuals tend to be more browsing-oriented. The weakness of the Spearman rho (−0.54) underlines, however, that diet would modulate but not drive body-mass variation. Additional factors (e.g., thermoregulation, locomotion,

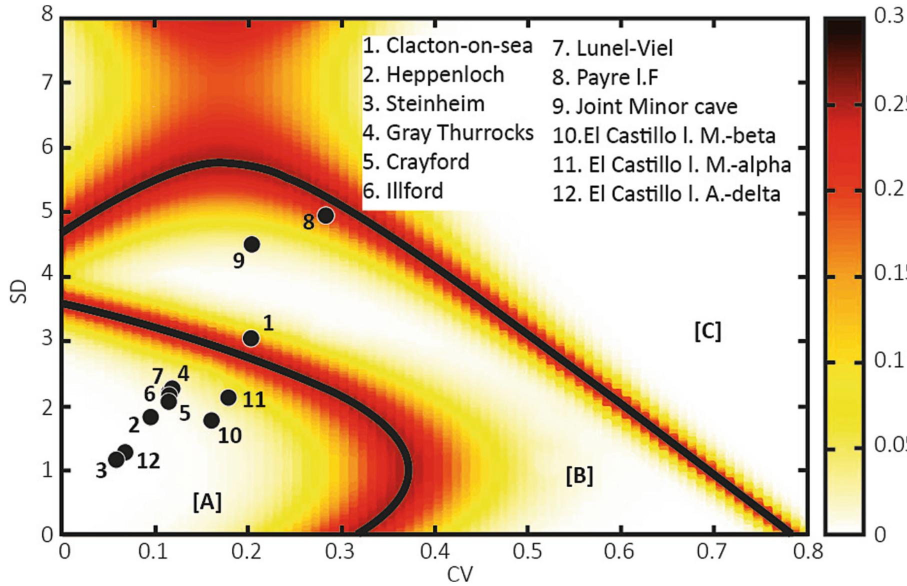

Fig. 5. Boundary lines with the error probability (heat map) based on standard deviations (SD) and coefficient of variation (CV) values of microwear data used for the classification of several Pleistocene Western European *Stephanorhinus hemitoechus* cohorts of more than 4 individuals into short events (region A), long-term events (region B) or two separate short events (region C).

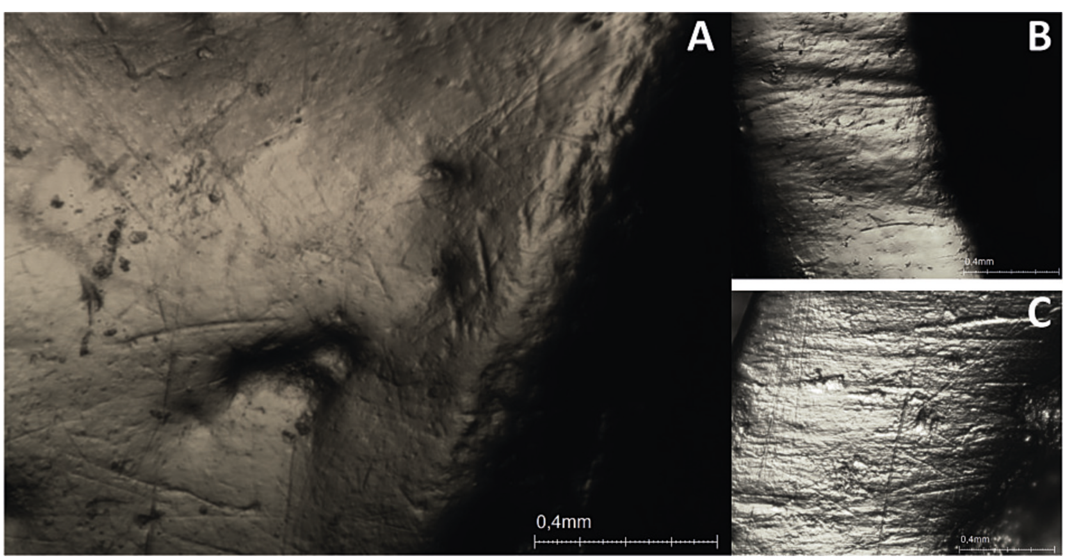

Fig. 6. Photomicrographs of the occlusal surface of A: a mixed-feeder *Stephanorhinus hemitoechus* from Lunel-Viel (MNP-LVI-5248) compare to B: a browser, the bovid *Bos primigenius* (MNP-LVI-3970) and C: a grazer, the equid, *Equus mosbachensins palustris* (MNP-LVI-15671) of the same site. Magnification x35, scales: 0,4 mm.

demographic structure) likely contribute to the observed pattern, considering that even heavy individuals can still be characterized as grazing-orientated.

Therefore, body mass variability in *S. hemitoechus* reflects the interplay of several factors, among them: regional setting, chronological span, and long-term dietary tendency.

The species followed different trajectories in relation to the environmental contexts of Northern and Mediterranean Europe, suggesting region-specific patterns. Its continuous occupation of the Mediterranean area probably exposed populations to environmental constraints that culminated in a body mass increase at the end of the Middle Pleistocene. By contrast, *S. hemitoechus* expansions into northern Europe only occurred during the most temperate MIS stages (Pandolfi and Tagliacozzo, 2015). In this region, the arrival of climatic deterioration likely led simply to local disappearance rather than *in situ* adaptations. Comparable dynamics are already documented in other herbivore species such as the equid *Equus hydruntinus* (Uzunidis et al., 2024c), the elephantid *Palaeoloxodon antiquus* (Roditi et al., 2024), or cervids (Meiri et al., 2018; Uzunidis et al., 2022; Vasiljevic et al., 2022). In contrast, other perissodactyls, such as *Equus ferus*, persisted in both Northern and Mediterranean Europe throughout the Pleistocene and thus underwent marked body-size adaptations in relation to environmental constraints (Eisenmann, 1984; Gromova, 1949; Uzunidis, 2021; van Asperen, 2010). Accordingly, analyses of *S. hemitoechus* evolutionary trends should explicitly distinguish between its core range (Mediterranean) and its peripheral expansions (North), as ecological responses differ. Within the Mediterranean, body mass variation in *S. hemitoechus* likely reflects multi-causal adaptations, including diet and climatic conditions, none of which appears dominant.

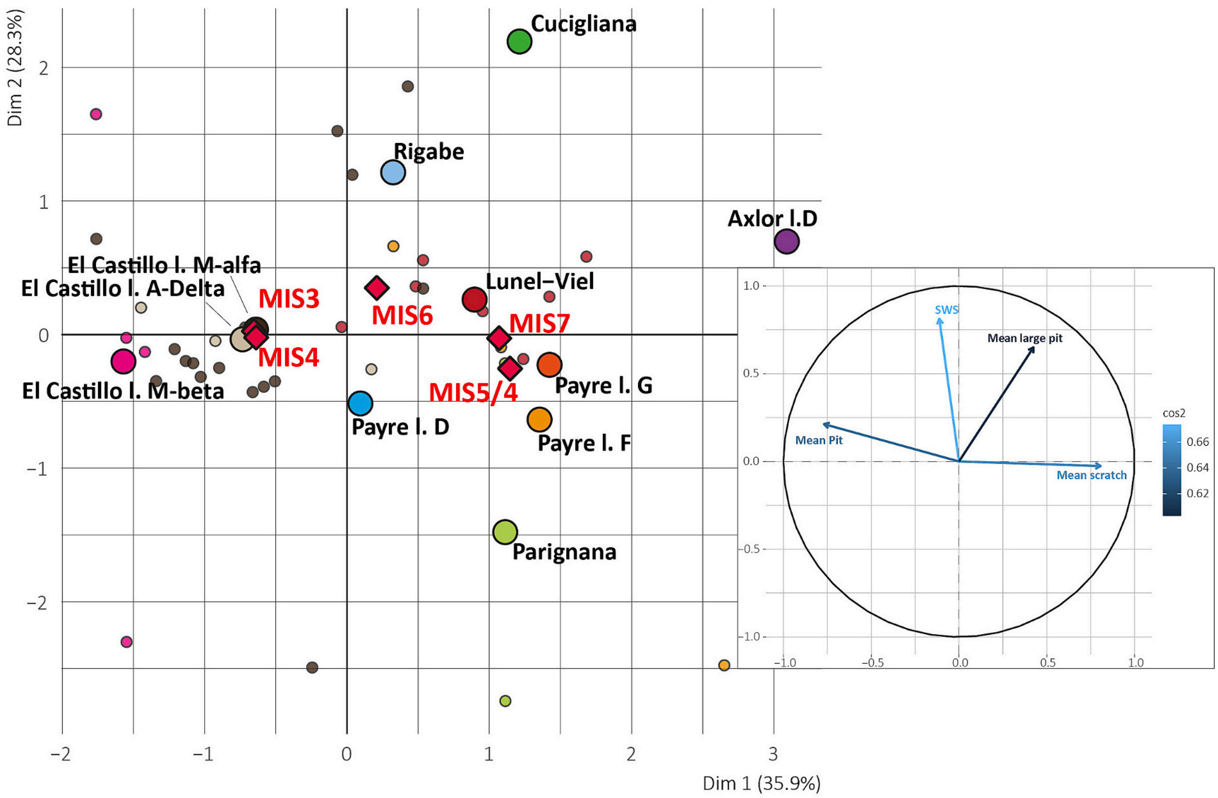

Fig. 7. Principal components (PC) scatterplot between PC1 (35.9%) and PC2 (28.3%) performed on four features of the microwear data (mean pits, mean scratches, mean number of large pits, SWS) of Mediterranean cohorts of *Stephanorhinus hemitoechus*. The large circle represents the centroid for each cohort and the large lozenge represents the centroid for each isotopic stage (MIS).

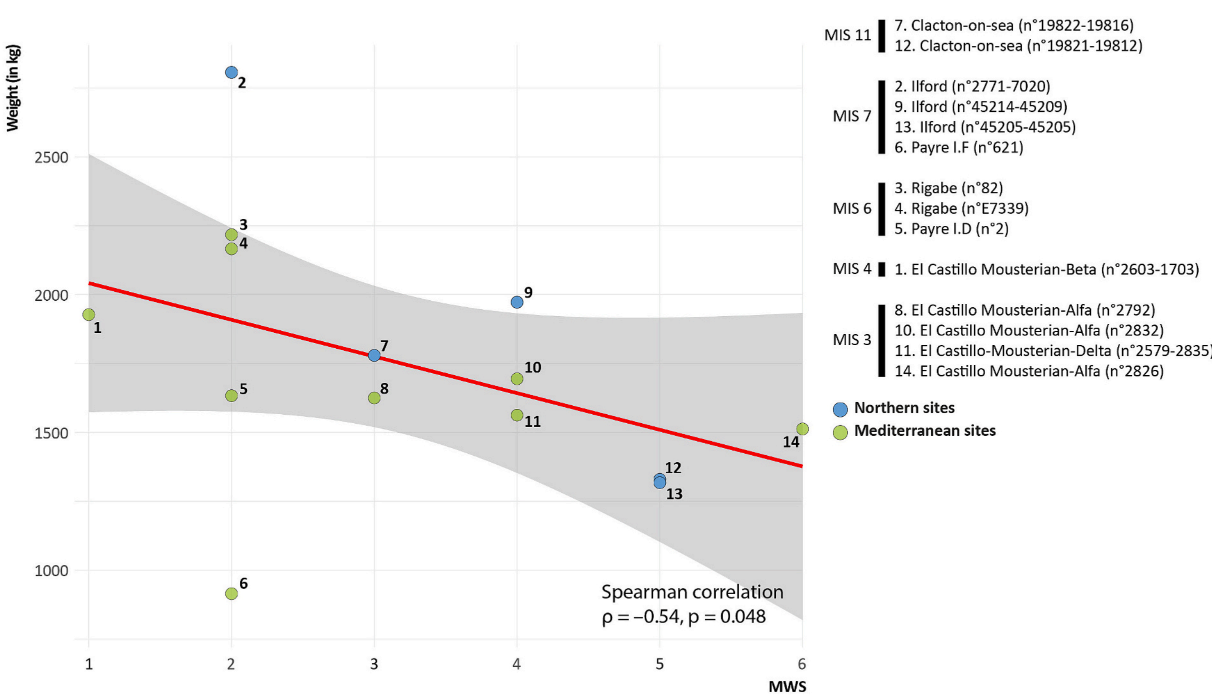

Fig. 8. Biplot comparing the estimated weight in kilograms and the mesowear scores of 14 *Stephanorhinus hemitoechus* teeth. Each dot represents an individual specimen from either Northern (blue) or Mediterranean (green) European sites. The red line shows the loess regression with a 95% confidence interval. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Dietary evolutionary trends in *S. hemitoechus* from Western Europe

Dental mesowear in *S. hemitoechus* indicates highly persistent mixed-feeding, with all 15 cohorts analyzed falling within the mixed-feeder range (Fig. 4). Minor differences exist between Northern and Mediterranean Europe, with northern cohorts incorporating slightly more grass than southern ones. Dental microwear, sensitive to seasonal plant availability (Uzunidis and Rivals, 2023), shows that at least 15 of 17 cohorts (Heppenloch, Steinheim, Grays Thurrock, Crayford, Ilford, Lunel-Viel, El Castillo l. Mousterian-Beta and El Castillo l. Aurignacian-Delta, Alxor l.D, Payre l.G and D, Rigabe, and Cucigliana) are uni-seasonal accumulations. Except at El Castillo and Axlor, this pattern implies that *S. hemitoechus* regularly incorporated both dicots and monocots all year long and did not switch from browser to grazer according to seasonal plant availability.

Stephanorhinus hemitoechus is widely regarded as a life-trend mixed-feeder, sometimes with a grazing tendency (Rivals et al., 2022b; Rivals and Lister, 2016; Saarinen et al., 2016; van Asperen and Kahlke, 2015). Our results refine this hypothesis by showing that mixed feeding was maintained across seasons, not only across lifespans. In many herbivores, mixed-feeding allows seasonal switching from one type of plant to another according to availability (Abraham et al., 2022; Belovsky, 1986; van der Merwe and Marshal, 2014). This is notably the case for extant rhinoceros species such as the greater one-horned rhinoceros *Rhinoceros unicornis*, largely a grazer that browses more in the cold dry season (Gagnon and Chew, 2000; Hullot et al., 2019; Laurie, 1982; Laurie et al., 1983), or the black rhinoceros *Diceros bicornis*, a browser (Hullot et al., 2019) can shift toward mixed-feeding under competition with elephants (Landman et al., 2013). Other taxa maintain year-round flexibility, such as most of the *S. hemitoechus* cohorts. The springbok, *Antidorcas marsupialis* remains mixed-feeding throughout the year (Lehmann et al., 2013; Sewell et al., 2019), likely to maximize nutriment intake in semi-arid environments (Stapelberg, 2007). The nilgai *Boselaphus tragocamelus*, in more temperate climates, maintains a mixed-feeding diet, intermediary between the browser New World cervid *Odocoileus virginianus* and the grazer domestic cattle, to mitigate direct competition (Sheffield, 1983). In high density communities, large herbivores may adopt a broader resource range to avoid niche overlap with smaller and more specialized species (Gordon and Illius, 1996; de Iongh et al., 2011). Thus, rather than a hazardous plant consumption to maintain its optimal grazing diet (van Asperen and Kahlke, 2015), mixed-feeding likely represents the preferred ecological position of *S. hemitoechus* within the herbivory guild.

Stephanorhinus hemitoechus goes extinct during MIS3, with its latest known occurrence in Gruta da Figueira Brava (Portugal) spanning from 24 ka to 30–31 ka (Antunes and Cardoso, 2000; Cardoso, 1993; Stuart, 2005). It is also described at the Merle Cave (France) in Epigravettian levels that were not directly dated (Valensi et al., 2025). The most recent cohorts in our sample, Axlor l.D (MIS4), El Castillo l. Mousterian-Beta and El Castillo l. Mousterian-Alpha (MIS3), are the only ones showing seasonal shifts toward browsing (El Castillo) or grazing (Axlor). In these late stages, *S. hemitoechus* was seemingly unable to sustain year-round mixed feeding, instead focusing seasonally on one plant category. During MIS4-MIS3, climatic conditions in the north-western part of the Mediterranean basin became colder, with less diverse open landscapes (Fletcher et al., 2010; Fourcade et al., 2024; Sánchez Goñi, 2022; Sánchez Goñi et al., 2020). Such climatic conditions likely increased competitive pressure on the locally scarcer plant category, browse or grass. Generalist mixed-feeders are adapted to exploit a broad range of plant resources, but their ability to process the most "difficult" plants (mechanically challenging, hard to access…) remains limited (Shipley et al., 2009) and they may exhibit lower short-term plasticity than specialized taxa during limited-resource periods (Lehmann et al., 2013). We propose that increased competition with more specialized herbivores and reduced plant diversity during MIS4-MIS3 forced seasonal specialization in *S. hemitoechus* toward the more available plants and nutritionally critical resources, potentially contributing to the species'decline.

5. Conclusion

Across its Western European record (MIS12–MIS3), the steppe rhinoceros *Stephanorhinus hemitoechus* shows substantial anatomical and ecological variation, but not a single continent-wide trajectory. Two region-specific dynamics emerge: in Northern Europe, where the species only expanded during interglacial periods, body masses are consistently higher than in contemporaneous Mediterranean cohorts, yet remain broadly stable through time, with at most a minor uptick in MIS5; in the Mediterranean core range, occupied continuously, body masses are stable from MIS12 to MIS7, they increase sharply in MIS6, and then plateau through MIS3. Given the lack of a single dominant driver for body mass or gracility, the scarcity and unequal distribution of remains, and the capacity of rhinoceroses for rapid local adaptations (Groves, 1967), any simple "two-trend" narrative likely oversimplifies finer, locality-specific responses.

Dietary evidence is strikingly consistent: mesowear and microwear together indicate a durable mixed-feeding strategy, with regular incorporation of both monocots and dicots across regions and seasons for most of the species' occurrence. Near the end of its range (MIS4–3), however, several assemblages deviate from this pattern and show seasonal specialization toward either browsing or grazing, consistent with colder, floristically simplified landscapes and more drastic interspecific competition. We suggest that the loss of year-round dietary flexibility, coinciding with a prior increase in body mass in the Mediterranean, may have increased vulnerability and contributed to the species' eventual disappearance.

CRediT authorship contribution statement

Antigone Uzunidis: Writing – review & editing, Writing – original draft, Validation, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Luca Pandolfi:** Writing – review & editing, Writing – original draft, Investigation, Data curation.

Declaration of competing interest

The authors have nothing to declare.

Acknowledgements

The authors would like to thanks Camille Daujeard (MNHN, Paris) and the project RINO (Emergence Sorbonne Université & MNHN), Marie-Hélène Moncel (MNHN, Paris), Jesus González-Urquijo (IIIPC, Cantabria), and Talía Lazuen (IIIPC, Cantabria). We are also very grateful to all the curators and staff who helped and assisted the authors during the collection visits. LP was supported by the SYNTHESYS Project http://www.synthesys.info/ (AT-TAF-2550, DE-TAF-3049, GB-TAF-2825, HU-TAF-3593, HU-TAF-5477, ES-TAF-2997), by the SYNTHESYS+ (HU-TAF 2021, 2022), which was financed by the European Community Research Infrastructure Action under the FP7 'Capacities' Programme, and by the University of Pisa (Fondi di Ateneo 2024, no. 579999).

The authors would like to thank Dr. Pierre-Olivier Antoine and the anonymous reviewer for their valuable comments, which greatly improved the quality of the manuscript.

Appendix A. Supplementary data

https://zenodo.org/records/17550583

Data availability

The authors confirm that all data necessary for supporting the scientific findings of this paper have been provided.

References

Abraham, J.O., Hempson, G.P., Faith, J.T., Staver, A.C., 2022. Seasonal strategies differ between tropical and extratropical herbivores. J. Anim. Ecol. 91, 681–692. https://doi.org/10.1111/1365-2656.13651.

Ackermans, N.L., Martin, L.F., Codron, D., Hummel, J., Kircher, P.R., Richter, H., Kaiser, T.M., Clauss, M., Hatt, J.-M., 2020. Mesowear represents a lifetime signal in sheep (*Ovis aries*) within a long-term feeding experiment. Palaeogeogr. Palaeoclimatol. Palaeoecol. 553, 109793. https://doi.org/10.1016/j.palaeo.2020.109793.

Altuna, J., 1971. Los mamíferos del yacimiento prehistórico de Morín. In: Gonzalez Echegaray, J., Freeman, L.G. (Eds.), Cueva Morín: Excavaciones 1966–1968. Patronato de las Cuevas Prehistóricas, Santander, pp. 369–398.

Anfossi, G., Cantaluppi, G., 1987. Rinvenimento di un cranio di rinoceronte nelle alluvioni quaternarie pavesi. Atti Tic. Sci. Terra 31, 263–468.

Antoine, P.-O., 2025. Rhinocerotids from the Siwalik Record. In: Badgley, C., Morgan, M. E., Pilbeam, D. (Eds.), At the Foot of the Himalayas: Paleontology and Ecosystem Dynamics of the Siwalik Record. Johns Hopkins University Press, pp. 281–294.

Antoine, P.-O., Reyes, M.C., Amano, N., Bautista, A.P., Chang, C.-H., Claude, J., De Vos, J., Ingicco, T., 2022. A new rhinoceros clade from the Pleistocene of Asia sheds light on mammal dispersals to the Philippines. Zool. J. Linnean Soc. 194, 416–430. https://doi.org/10.1093/zoolinnean/zlab009.

Antoine, P.-O., Becker, D., Pandolfi, L., Geraads, D., 2025. Evolution and fossil record of old world rhinocerotidae. In: Melletti, M., Talukdar, B., Balfour, D. (Eds.), Rhinos of the World: Ecology, Conservation and Management. Springer Nature Switzerland, Cham, pp. 31–48. https://doi.org/10.1007/978-3-031-67169-2_2.

Antunes, M.T., Cardoso, J.L., 2000. Gruta Nova da Columbeira, Gruta das Salemas and Gruta da Figueira Brava: stratigraphy, and chronology of the pleistocene deposits. In: Últimos Neandertais Em Portugal – Evidência, Odontológica e Outra, Memórias Da Academia Das Ciências de Lisboa, Classe de Ciências. Academia das Ciências de Lisboa, Lisboa, pp. 23–67.

Azzaroli, A., 1962. Validità della specie *Rhinoceros hemitoechus* Falconer. Palaeontogr. Ital. 57, 1–34.

Belovsky, G., 1986. Generalist herbivore foraging and its role in competitive interactions. Am. Zool. 26, 51–69. https://doi.org/10.1093/icb/26.1.51.

Boulbes, N., van Asperen, E.N., 2019. Biostratigraphy and palaeoecology of European *Equus*. Front. Ecol. Evol. 7. https://doi.org/10.3389/fevo.2019.00301.

Busk, G., 1879. On the ancient or quaternary fauna of Gibraltar, as exemplified in the mammalian remains of the ossiferous breccia. Trans. Zool. Soc. Lond. 10, 53–131. https://doi.org/10.1144/GSL.JGS.1865.021.01-02.35.

Caloi, L., Palombo, M.R., 1978. Anfibi, rettili e mammiferi di Torre del Pagliaccetto (Torre in Pietra, Roma). Quaternaria 20, 315–428.

Caloi, L., Palombo, M.R., 1994. Functional aspects and ecological implications in Pleistocene endemic herbivores of Mediterranean Islands. Hist. Biol. 8, 151–172. https://doi.org/10.1080/10292389409380475.

Cantaluppi, G., 1969. Il rinoceronte di S. Colombano al Lambro. Atti dell'Ist. Geol. dell'Univ. Pavia 20, 67–81.

Cardoso, J.L., 1993. Contribuição para o conhecimento dos grandes mamíferos do plistocenico superior de Portugal. Ph.D. thesis. Universidade Nova de Lisboa, Câmara Municipal de Oeiras, Portugal.

Cerdeño, E., 1990. *Stephanorhinus hemitoechus* (Falc.) (Rhinocerotidae, Mammalia) del Pleistoceno medio y superior de España. Estud. Geol. 46, 465–479. https://doi.org/10.3989/egeol.90465-6475.

Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., De Ruiter, D., Sealy, J., Grant, R., Fourie, N., 2007. Diets of savanna ungulates from stable carbon isotope composition of faeces. J. Zool. 273, 21–29. https://doi.org/10.1111/j.1469-7998.2007.00292.x.

de Iongh, H.H., de Jong, C.B., van Goethem, J., Klop, E., Brunsting, A.M.H., Loth, P.E., Prins, H.H.T., 2011. Resource partitioning among African savanna herbivores in North Cameroon: the importance of diet composition, food quality and body mass. J. Trop. Ecol. 27, 503–513. https://doi.org/10.1017/S0266467411000307.

Domínguez-Rodrigo, M., Sánchez-Flores, A.J., Baquedano, E., Carmen Arriaza, M., Aramendi, J., Cobo-Sánchez, L., Organista, E., Barba, R., 2019. Constraining time and ecology on the Zinj paleolandscape: microwear and mesowear analyses of the archaeofaunal remains of FLK Zinj and DS (Bed I), compared to FLK North (Bed I) and BK (Bed II) at Olduvai Gorge (Tanzania). Quat. Int. 526, 4–14. https://doi.org/10.1016/j.quaint.2019.05.041.

Eisenmann, V., 1984. Sur quelques caractères adaptatifs du squelette d'*Equus* et leurs implications paléoécologiques. Bull. Muséum d'Histoire Nat. 6, 185–195.

Falguères, C., Lahaye, C., Tombret, O., Garbé, L., Lebrun, B., Bahain, J.-J., Frerebeau, N., Giuliani, C., Brugal, J.-P., 2024. ESR/U-series and pIR-IR290 dating of the Middle Pleistocene site of Lunel-Viel (LV I), Hérault, Southern France. Quat. Geochronol. 81, 101516. https://doi.org/10.1016/j.quageo.2024.101516.

Fletcher, W.J., Sánchez Goñi, M.F., Allen, J.R.M., Cheddadi, R., Combourieu-Nebout, N., Huntley, B., Lawson, I., Londeix, L., Magri, D., Margari, V., Müller, U.C., Naughton, F., Novenko, E., Roucoux, K., Tzedakis, P.C., 2010. Millennial-scale variability during the last glacial in vegetation records from Europe. Quat. Sci. Rev. 29, 2839–2864. https://doi.org/10.1016/j.quascirev.2009.11.015.

Fortelius, M., Kappelman, J., 1993. The largest land mammal ever imagined. Zool. J. Linnean Soc. 107, 85–101. https://doi.org/10.1111/j.1096-3642.1993.tb01503.x.

Fortelius, M., Solounias, N., 2000. Functional characterization of ungulate molars using the abrasion-attrition wear gradient: a new method for reconstructing paleodiets. Am. Mus. Novit. 3301, 1–36.

Fortelius, M., Mazza, P.P.A., Sala, B., 1993. *Stephanorhinus* (Mammalia: Rhinocerotidae) of the western European Pleistocene, with a revision of *S. etruscus* (Falconer, 1868). Palaeontogr. Ital. 80, 63–115.

Fourcade, T., Sánchez Goñi, M.F., Lesven, J., Lahaye, C., Philippe, A., 2024. Vegetation response in NW Mediterranean borderlands to the millennial-scale climate variability of the last glacial period. Quat. Sci. Rev. 334, 108722. https://doi.org/10.1016/j.quascirev.2024.108722.

Gagnon, M., Chew, A.E., 2000. Dietary preferences in extant african Bovidae. J. Mammal. 81, 490–511.

Gallego-Valle, A., Colominas, L., Burguet-Coca, A., Aguilera, M., Palet, J.-M., Tornero, C., 2020. What is on the menu today? Creating a microwear reference collection through a controlled-food trial to study feeding management systems of ancient agropastoral societies. Quat. Int. 557, 3–11. https://doi.org/10.1016/j.quaint.2020.02.020.

Gaudin, C.-T., 1859. Modifications apportées par Mr Falconer à la faune de Val d'Arno. Bull. Soc. Vaudoise Sci. Nat. 6, 130–131. https://doi.org/10.5169/SEALS-252619.

Gordon, I.J., Illius, A.W., 1996. The nutritional ecology of African ruminants: a reinterpretation. J. Anim. Ecol. 65, 18–28. https://doi.org/10.2307/5696.

Gromova, V., 1949. Le Genre "*Equus*", Premiere partie: revue et description des formes, Trad. Pietresson de Saint-Aubin. Ann. Cent. Etud. Doc. Paleontol. 1955 (13) (Travaux Inst. Paléontol. Acad. Sci. URSS).

Groves, C.P., 1967. On the rhinoceroses of South-East Asia. Saugetierkd. Mitt. 15, 221–237.

Guérin, C., 1973. Les trois espèces de rhinocéros (Mammalia, Perissodactyla) du gisement pléistocène moyen des Abîmes de La Fage à Nouailles (Corrèze). Nouv. Arch. Mus. Hist. Nat. Lyon 11, 55–84.

Guérin, C., 1980. Les Rhinocéros (Mammalia, Perissodactyla) du Miocène terminal au Pleistocène superieur en Europe occidentale. Comparaison avec les espèces actuelles. Ph.D. thesis.. Université Claude Bernard, Département des Sciences de la Terre, Lyon.

Guérin, C., 1982. Les Rhinocerotidae (Mammalia, Perissodactyla) du Miocène terminal au Pleistoène supérieur d'Europe Occidentale comparés aux espèces actuelles: Tendances évolutives et relations phylogénétiques. Géobios 15, 599–605.

Heglund, N.C., Cavagna, G.A., Taylor, C.R., 1982. Energetics and mechanics of terrestrial locomotion. III. Energy changes of the Centre of mass as a function of speed and body size in birds and mammals. J. Exp. Biol. 97, 41–56. https://doi.org/10.1242/jeb.97.1.41.

Hoffman, J.M., Fraser, D., Clementz, M.T., 2015. Controlled feeding trials with ungulates: a new application of in vivo dental molding to assess the abrasive factors of microwear. J. Exp. Biol. 218, 1538–1547. https://doi.org/10.1242/jeb.118406.

Hullot, M., Antoine, P.-O., Ballatore, M., Merceron, G., 2019. Dental microwear textures and dietary preferences of extant rhinoceroses (Perissodactyla, Mammalia). Mammal. Res. 64, 397–409. https://doi.org/10.1007/s13364-019-00427-4.

Iñigo, C., 1995. El rinoceronte del Pleistoceno Superior de la Cueva del Buho (Segovia). Bol. Geol. Min. 106, 107–110.

Kahlke, H.D., 1975. Die Rhinocerotiden-Reste aus den Travertinen von Weimar-Ehringsdorf. Paläontol. Abhandlungen 23, 337–397.

Kahlke, H.D., 1978. Die Rhinocerotiden-Reste aus den Travertinen von Burgtonna in Thüringen. Quartärpaläontologie 3, 129–135.

Kaiser, T.M., Fortelius, M., 2003. Differential mesowear in occluding upper and lower molars: opening mesowear analysis for lower molars and premolars in hypsodont horses. J. Morphol. 258, 67–83. https://doi.org/10.1002/jmor.10125.

Kaiser, T.M., Brasch, J., Castell, J.C., Schulz, E., Clauss, M., 2009. Tooth wear in captive wild ruminant species differs from that of free-ranging conspecifics. Mamm. Biol. 74, 425–437. https://doi.org/10.1016/j.mambio.2008.09.003.

Kaiser, T.M., Müller, D.W.H., Fortelius, M., Schulz, E., Codron, D., Clauss, M., 2013. Hypsodonty and tooth facet development in relation to diet and habitat in herbivorous ungulates: implications for understanding tooth wear. Mammal Rev. 43, 34–46. https://doi.org/10.1111/j.1365-2907.2011.00203.x.

King, T., Andrews, P., Boz, B., 1999. Effect of taphonomic processes on dental microwear. Am. J. Phys. Anthropol. 108, 359–373. https://doi.org/10.1002/(SICI)1096-8644(199903)108:3%253C359::AID-AJPA10%253E3.0.CO;2-9.

Lacombat, F., 2003. Étude des rhinocéros du Pléistocène de l'Europe méditerranéenne et du Massif Central. Paléontologie, phylogénie et biostratigraphie. Ph.D. thesis. Muséum national d'Histoire naturelle, Paris.

Lacombat, F., 2009. Biochronologie et grands mammifères au Pléistocène moyen et supérieur en Europe occidentale: l'apport des Rhinocerotidae (genre *Stephanorhinus*). Quaternaire 52, 429–435.

Landman, M., Schoeman, D.S., Kerley, G.I.H., 2013. Shift in Black Rhinoceros Diet in the Presence of Elephant: evidence for competition? PLoS One 8, e69771. https://doi.org/10.1371/journal.pone.0069771.

Laurie, A., 1982. Behavioural ecology of the Greater one-horned rhinoceros (*Rhinoceros unicornis*). J. Zool. 196, 307–341. https://doi.org/10.1111/j.1469-7998.1982.tb03506.x.

Laurie, A., Lang, E.M., Groves, C.P., 1983. Rhinoceros unicornis. Mamm. Species 211, 1–6. https://doi.org/10.2307/3504002.

Legendre, S., 1989. Les communautés de mammifères du Paléogène (Eocène supérieur et Oligocène) d'Europe occidentale: structures, milieux et évolution. Münchner geowissenschaftliche Abhandlungen.

Lehmann, D., Mfune, J.K.E., Gewers, E., Cloete, J., Brain, C., Voigt, C.C., 2013. Dietary plasticity of generalist and specialist ungulates in the Namibian Desert: a stable isotopes approach. PLoS One 8, e72190. https://doi.org/10.1371/journal.pone.0072190.

Louys, J., Meloro, C., Elton, S., Ditchfield, P., Bishop, L., 2011. Mesowear as a means of determining diets in African antelopes. J. Archaeol. Sci. 38, 1485–1495. https://doi.org/10.1016/j.jas.2011.02.011.

Mallet, C., Billet, G., Cornette, R., Alexandra Houssaye, A., 2022. Adaptation to graviportality in Rhinocerotoidea? An investigation through the long bone shape variation in their hindlimb. Zool. J. Linnean Soc. 196, 1235–1271. https://doi.org/10.1093/zoolinnean/zlac007.

Meiri, M., Kosintsev, P., Conroy, K., Meiri, S., Barnes, I., Lister, A., 2018. Subspecies dynamics in space and time: a study of the red deer complex using ancient and modern DNA and morphology. J. Biogeogr. 45, 367–380. https://doi.org/10.1111/jbi.13124.

Micó, C., Blasco, R., Muñoz Del Pozo, A., Jiménez-García, B., Rosell, J., Rivals, F., 2024a. Differentiating taphonomic features from trampling and dietary microwear, an experimental approach. Hist. Biol. 36, 760–782. https://doi.org/10.1080/08912963.2023.2184690.

Micó, C., Blasco, R., Rivals, F., 2024b. Simulating taphonomic processes on teeth: the impact of sediment pressure and thermal alteration on dental microwear. Quat. Sci. Adv. 14, 100195. https://doi.org/10.1016/j.qsa.2024.100195.

Mihlbachler, M.C., Rivals, F., Solounias, N., Semprebon, G., 2011. Dietary change and evolution of horses in North America. Science 331, 1178–1181. https://doi.org/10.1126/science.1196166.

Pandolfi, L., Marra, F., 2015. Rhinocerotidae (Mammalia, Perissodactyla) from the chrono-stratigraphically constrained Pleistocene deposits of the urban area of Rome (Central Italy). Geobios 48, 147–167. https://doi.org/10.1016/j.geobios.2015.02.003.

Pandolfi, L., Tagliacozzo, A., 2015. *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae) from the Late Pleistocene of Valle Radice (Sora, Central Italy) and re-evaluation of the morphometric variability of the species in Europe. Geobios 48, 169–191. https://doi.org/10.1016/j.geobios.2015.02.002.

Pandolfi, L., Gaeta, M., Petronio, C., 2013. The skull of *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae) from the Middle Pleistocene of Campagna Romana (Rome, central Italy): biochronological and paleobiogeographic implications. Bull. Geosci. 88, 51–62. https://doi.org/10.3140/bull.geosci.1331.

Pandolfi, L., Cerdeño, E., Antoine, P.-O., 2025. Cranial variability in *Stephanorhinus hemitoechus* (Mammalia, Rhinocerotidae): a revision of Azzaroli's subspecies and the systematics of Middle-late Pleistocene European rhinoceroses. Boll. Soc. Paleontol. Ital. 64, 227–244.

Pokines, J.T., Lister, A.M., Ames, C.J.H., Nowell, A., Cordova, C.E., 2019. Faunal remains from recent excavations at Shishan Marsh 1 (SM1), a Late Lower Paleolithic open-air site in the Azraq Basin, Jordan. Quat. Res. 91, 768–791. https://doi.org/10.1017/qua.2018.113.

Puzachenko, A.Yu., Titov, V.V., Kosintsev, P.A., 2021. Evolution of the European regional large mammals assemblages in the end of the Middle Pleistocene – the first half of the Late Pleistocene (MIS 6–MIS 4). Quat. Int. 605–606, 155–191. https://doi.org/10.1016/j.quaint.2020.08.038.

Rivals, F., Lister, A.M., 2016. Dietary flexibility and niche partitioning of large herbivores through the Pleistocene of Britain. Quat. Sci. Rev. 146, 116–133. https://doi.org/10.1016/j.quascirev.2016.06.007.

Rivals, F., Semprebon, G., 2017. Latitude matters: an examination of behavioural plasticity in dietary traits amongst extant and Pleistocene Rangifer tarandus. Boreas 46, 254–263. https://doi.org/10.1111/bor.12205.

Rivals, F., Ziegler, R., 2018. High-resolution paleoenvironmental context for human occupations during the Middle Pleistocene in Europe (MIS 11, Germany). Quat. Sci. Rev. 188, 136–142. https://doi.org/10.1016/j.quascirev.2018.03.026.

Rivals, F., Schulz, E., Kaiser, T.M., 2009. Late and middle Pleistocene ungulates dietary diversity in Western Europe indicate variations of Neanderthal paleoenvironments through time and space. Quat. Sci. Rev. 28, 3388–3400. https://doi.org/10.1016/j.quascirev.2009.09.004.

Rivals, F., Mihlbachler, M.C., Solounias, N., Mol, D., Semprebon, G., de Vos, J., Kalthoff, D.C., 2010. Palaeoecology of the Mammoth Steppe fauna from the late Pleistocene of the North Sea and Alaska: separating species preferences from geographic influence in paleoecological dental wear analysis. Palaeogeogr. Palaeoclimatol. Palaeoecol. 286, 42–54. https://doi.org/10.1016/j.palaeo.2009.12.002.

Rivals, F., Rindel, D., Belardi, J.B., 2013. Dietary ecology of extant guanaco (*Lama guanicoe*) from Southern Patagonia: seasonal leaf browsing and its archaeological implications. J. Archaeol. Sci. 40, 2971–2980. https://doi.org/10.1016/j.jas.2013.03.005.

Rivals, F., Takatsuki, S., Albert, R.M., Macià, L., 2014. Bamboo feeding and tooth wear of three sika deer (*Cervus nippon*) populations from northern Japan. J. Mammal. 95, 1043–1053. https://doi.org/10.1644/14-MAMM-A-097.

Rivals, F., Prignano, L., Semprebon, G., Lozano, S., 2015. A tool for determining duration of mortality events in archaeological assemblages using extant ungulate microwear. Sci. Rep. 5, 17330.

Rivals, F., Baryshnikov, G.F., Prilepskaya, N.E., Belyaev, R.I., 2022a. Diet and ecological niches of the Late Pleistocene hyenas *Crocuta spelaea* and *C. ultima ussurica* based on a study of tooth microwear. Palaeogeogr. Palaeoclimatol. Palaeoecol. 601, 111125. https://doi.org/10.1016/j.palaeo.2022.111125.

Rivals, F., Bocherens, H., Camarós, E., Rosell, J., 2022b. Diet and ecological interactions in the Middle and Late Pleistocene. In: Romagnoli, F., Rivals, F., Benazzi, S. (Eds.), Updating Neanderthals. Academic Press, pp. 39–54. https://doi.org/10.1016/B978-0-12-821428-2.00003-2.

Roditi, E., Bocherens, H., Konidaris, G.E., Athanassiou, A., Tourloukis, V., Karkanas, P., Panagopoulou, E., Harvati, K., 2024. Life-history of *Palaeoloxodon antiquus* reveals Middle Pleistocene glacial refugium in the Megalopolis basin, Greece. Sci. Rep. 14, 1390. https://doi.org/10.1038/s41598-024-51592-9.

RStudio Team, 2018. RStudio: Integrated Development Environment for R. RStudio, Boston, MA.

Saarinen, J., Lister, A.M., 2016. Dental mesowear reflects local vegetation and niche separation in Pleistocene proboscideans from Britain. J. Quat. Sci. 31, 799–808. https://doi.org/10.1002/jqs.2906.

Saarinen, J., Eronen, J., Fortelius, M., Seppä, H., Lister, A.M., 2016. Patterns of diet and body mass of large ungulates from the Pleistocene of Western Europe, and their relation to vegetation. Palaeontol. Electron. 19.3.32A, 1–58.

Sánchez Goñi, M.F., 2022. The climatic and environmental context of the late Pleistocene. In: Romagnoli, F., Rivals, F., Benazzi, S. (Eds.), Updating Neanderthals. Academic Press, pp. 17–38. https://doi.org/10.1016/B978-0-12-821428-2.00017-2.

Sánchez Goñi, M.F., Fourcade, T., Salonen, S., Lesven, J., Frigola, J., Swingedouw, D., Sierro, F.J., 2020. Muted cooling and drying of NW Mediterranean in response to the strongest last glacial North American ice surges. GSA Bull. 133, 451–460. https://doi.org/10.1130/B35736.1.

Sánchez-Hernández, C., Rivals, F., Blasco, R., Rosell, J., 2016. Tale of two timescales: combining tooth wear methods with different temporal resolutions to detect seasonality of Palaeolithic hominin occupational patterns. J. Archaeol. Sci. Rep. 6, 790–797. https://doi.org/10.1016/j.jasrep.2015.09.011.

Schmitt, T., Varga, Z., 2012. Extra-Mediterranean refugia: the rule and not the exception? Front. Zool. 9, 22. https://doi.org/10.1186/1742-9994-9-22.

Schulz-Kornas, E., Winkler, D.E., Clauss, M., Carlsson, J., Ackermans, N.L., Martin, L.F., Hummel, J., Müller, D.W.H., Hatt, J.-M., Kaiser, T.M., 2020. Everything matters: molar microwear texture in goats (*Capra aegagrus hircus*) fed diets of different abrasiveness. Palaeogeogr. Palaeoclimatol. Palaeoecol. 552, 109783. https://doi.org/10.1016/j.palaeo.2020.109783.

Semprebon, G., Godfrey, L.R., Solounias, N., Sutherland, M.R., Jungers, W.L., 2004. Can low-magnification stereomicroscopy reveal diet? J. Hum. Evol. 47, 115–144. https://doi.org/10.1016/j.jhevol.2004.06.004.

Semprebon, G., Sise, P.J., Coombs, M.C., 2011. Potential bark and fruit browsing as revealed by stereomicrowear analysis of the peculiar clawed herbivores known as chalicotheres (Perissodactyla, Chalicotherioidea). J. Mamm. Evol. 18, 33–55. https://doi.org/10.1007/s10914-010-9149-3.

Sewell, L., Merceron, G., Hopley, P.J., Zipfel, B., Reynolds, S.C., 2019. Using springbok (*Antidorcas*) dietary proxies to reconstruct inferred palaeovegetational changes over 2 million years in Southern Africa. J. Archaeol. Sci. Rep. 23, 1014–1028. https://doi.org/10.1016/j.jasrep.2018.02.009.

Sheffield, W.J., 1983. Food habits of nilgai antelope in Texas. J. Range Manag. 36, 316–322.

Shipley, L.A., Forbey, J.S., Moore, B.D., 2009. Revisiting the dietary niche: when is a mammalian herbivore a specialist? Integr. Comp. Biol. 49, 274–290. https://doi.org/10.1093/icb/icp051.

Smith, G.J., DeSantis, L.R.G., 2018. Dietary ecology of Pleistocene mammoths and mastodons as inferred from dental microwear textures. Palaeogeogr. Palaeoclimatol. Palaeoecol. 492, 10–25. https://doi.org/10.1016/j.palaeo.2017.11.024.

Solounias, N., Semprebon, G., 2002. Advances in the reconstruction of ungulate ecomorphology with application to early fossil equids. Am. Mus. Novit. 3366, 1–49. https://doi.org/10.1206/0003-0082(2002)366<0001:AITROU>2.0.CO;2.

Stapelberg, F.H., 2007. Feeding Ecology of the Kalahari Springbok *Antidorcas marsupialis* in the Kgalagadi Transfrontier Park, South Africa. Master's thesis. University of Pretoria, Pretoria.

Stewart, J.R., Lister, A.M., Barnes, I., Dalén, L., 2010. Refugia revisited: individualistic responses of species in space and time. Proc. R. Soc. B Biol. Sci. 277, 661–671. https://doi.org/10.1098/rspb.2009.1272.

Stuart, A.J., 2005. The extinction of woolly mammoth (*Mammuthus primigenius*) and straight-tusked elephant (*Palaeoloxodon antiquus*) in Europe. Quat. Int. 126–128, 171–177. https://doi.org/10.1016/j.quaint.2004.04.021.

Teaford, M.F., 1988. A review of dental microwear and diet in modern mammals. Scanning Microsc. 2, 1149–1166.

Tsubamoto, T., 2014. Estimating body mass from the astragalus in mammals. Acta Palaeontol. Pol. 59, 259–265. https://doi.org/10.4202/app.2011.0067.

Tzedakis, P.C., 1994. Vegetation change through glacial—interglacial cycles: a long pollen sequence perspective. Philos. Trans. R. Soc. B 345, 403–432. https://doi.org/10.1098/rstb.1994.0118.

Ulbricht, A., Maul, L.C., Schulz, E., 2015. Can mesowear analysis be applied to small mammals? A pilot-study on leporines and murines. Mamm. Biol. 80, 14–20. https://doi.org/10.1016/j.mambio.2014.06.004.

Uzunidis, A., 2021. Middle Pleistocene variations in the diet of *Equus* in the South of France and its morphometric adaptations to local environments. Quaternary 4, 23. https://doi.org/10.3390/quat4030023.

Uzunidis, A., Rivals, F., 2023. Where and when? Combining dental wear and death seasons to improve paleoenvironmental reconstruction through ungulate diets. J. Archaeol. Sci. Rep. 52, 104258. https://doi.org/10.1016/j.jasrep.2023.104258.

Uzunidis, A., Pineda, A., Jiménez-Manchón, S., Xafis, A., Ollivier, V., Rivals, F., 2021. The impact of sediment abrasion on tooth microwear analysis: an experimental study. Archaeol. Anthropol. Sci. 13, 134. https://doi.org/10.1007/s12520-021-01382-5.

Uzunidis, A., Rufà, A., Blasco, R., Rosell, J., Brugal, J.-P., Texier, P.-J., Rivals, F., 2022. Speciated mechanism in Quaternary cervids (*Cervus* and *Capreolus*) on both sides of the Pyrenees: a multidisciplinary approach. Sci. Rep. 12, 20200. https://doi.org/10.1038/s41598-022-24684-7.

Uzunidis, A., Mion, L., Boulbes, N., Renaud, A., Gailledrat, E., Gardeisen, A., 2023. War horses and equine herd feeding management at the end of the third century BC: new insights from Pech Maho (Southern France). Environ. Archaeol. 29, 478–497. https://doi.org/10.1080/14614103.2023.2176609.

Uzunidis, A., Blasco, R., Brugal, J.-P., Fourcade, T., Ochando, J., Rosell, J., Roussel, A., Rufà, A., Sánchez Goñi, M.F., Texier, P.-J., Rivals, F., 2024a. Neanderthal hunting grounds: the case of Teixoneres Cave (Spain) and Pié Lombard rockshelter (France). J. Archaeol. Sci. 168, 106007. https://doi.org/10.1016/j.jas.2024.106007.

Uzunidis, A., Brugal, J.-P., Croitor, R., Daura, J., Magniez, P., Panera, J., Rubio-Jara, S., Sanz, M., Yravedra, J., Rivals, F., 2024b. Paleoecology of an extinct Cervidae (*Haploidoceros mediterraneus*) of the Middle-late Pleistocene in Southern Europe. Palaeogeogr. Palaeoclimatol. Palaeoecol. 656, 112565. https://doi.org/10.1016/j.palaeo.2024.112565.

Uzunidis, A., Sanz, M., Daura, J., 2024c. Sub-speciation processes of equids in the Iberian Peninsula: ecological strategies and refuge areas. Quat. Sci. Rev. 325, 108473. https://doi.org/10.1016/j.quascirev.2023.108473.

Uzunidis, A., Roussel, A., González-Urquijo, J., Lazuen, T., 2025. Neandertal predation agenda reveals seasonal strategies during MIS 5–4 transition in Axlor, northatlantic Iberia. Sci. Rep. 15, 24174. https://doi.org/10.1038/s41598-025-08314-6.

Uzunidis-Boutillier, A., 2017. Grands herbivores de la fin du Pléistocène moyen au début du Pléistocène supérieur dans le sud de la France. Implications Anthropologiques pour la lignée néandertalienne. Ph.D. thesis. Université d'Aix-Marseille, Aix-en-Provence.

Valensi, P., El Guennouni, K., Testu, A., Boulbes, N., Michel, V., Onoratini, G., Psathi, E., Moussous, A., Visweswara, S.C., de Lumley, H., 2025. Biostratigraphie et paléoécologie des grands mammifères du Pléistocène moyen et supérieur en Ligurie (Italie) et dans les Alpes-Maritimes (France). L'Anthropologie 129, 103412. https://doi.org/10.1016/j.anthro.2025.103412.

van Asperen, E.N., 2010. Ecomorphological adaptations to climate and substrate in late Middle Pleistocene caballoid horses. Palaeogeogr. Palaeoclimatol. Palaeoecol. 297, 584–596.

van Asperen, E.N., Kahlke, R.-D., 2015. Dietary variation and overlap in Central and Northwest European *Stephanorhinus kirchbergensis* and *S. hemitoechus* (Rhinocerotidae, Mammalia) influenced by habitat diversity: "You'll have to take pot luck!" (proverb). Quat. Sci. Rev. 107, 47–61. https://doi.org/10.1016/j.quascirev.2014.10.001.

van der Made, J., 2010. The rhinos from the Middle Pleistocene of Neumark-Nord (Saxony-Anhalt). Veröff. Land. Archeol. 62, 432–527.

van der Merwe, J., Marshal, J.P., 2014. Grass attributes and seasonal changes in foraging by a preferentially grazing savanna mixed feeder. J. Arid Environ. 102, 34–39. https://doi.org/10.1016/j.jaridenv.2013.11.003.

Vasiljevic, N., Morf, N.V., Senn, J., Pérez-Espona, S., Mattucci, F., Mucci, N., Moore-Jones, G., Pisano, S.R.R., Kratzer, A., Ogden, R., 2022. Phylogeography and population genetic structure of the European roe deer in Switzerland following recent recolonization. Ecol. Evol. 12, e8626. https://doi.org/10.1002/ece3.8626.

Walker, A., Hoeck, H.N., Perez, L., 1978. Microwear of mammalian teeth as an indicator of diet. Science 201, 908–910.

Winkler, D.E., Schulz-Kornas, E., Kaiser, T.M., Codron, D., Leichliter, J., Hummel, J., Martin, L.F., Clauss, M., Tütken, T., 2020. The turnover of dental microwear texture: testing the "last supper" effect in small mammals in a controlled feeding experiment. Palaeogeogr. Palaeoclimatol. Palaeoecol. 557, 109930. https://doi.org/10.1016/j.palaeo.2020.109930.

Xafis, A., Nagel, D., Bastl, K., 2017. Which tooth to sample? A methodological study of the utility of premolar/non-carnassial teeth in the microwear analysis of mammals. Palaeogeogr. Palaeoclimatol. Palaeoecol. 487, 229–240. https://doi.org/10.1016/j.palaeo.2017.09.003.