Multiproxy approach to reconstruct the climate and environment of a new late Middle Pleistocene vertebrate site in northwestern Italy

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ABSTRACT

The Moleto site (Ottiglio, AL, Piemonte, Italy) was discovered in the 1990s in an abandoned quarry carved into a Burdigalian–Langhian carbonate succession called Pietra da Cantoni. Sediment collection in three closely spaced fissures provided a rich vertebrate association whose age can be constrained to the late Middle Pleistocene on the basis of the presence of the extinct water vole *Arvicola mosbachensis* and its enamel characteristics (SDQ values ranging from 100 to 130). The very similar faunal content, evidenced by the common presence of *Arvicola mosbachensis* and its similar SDQ values, is indicative of a coeval deposition of the fillings of the three fissures. The vertebrate assemblage is represented by 30 taxa, including amphibians, squamate reptiles, birds, and mammals. Interestingly, a diverse fish assemblage from the embedded sediments of the Miocene Pietra da Cantoni has been found in the fissure fillings. We present here a multi-method approach using the small vertebrate assemblages (rodents, insectivores, amphibians, and squamate reptiles) from Moleto to characterise the environment and climate of the site. In order to reconstruct the palaeoenvironmental and palaeoclimatic conditions, we applied the Mutual Ecogeographic Range using UDA-ODA technique, the Bioclimatic Model, the Habitat Weightings, and the Quantified Ecology methods. The results revealed a landscape dominated by woodland habitats with presence of open humid meadows, under temperate and moist climatic conditions, although somewhat colder and drier than today. According to all evidence, the associations from Moleto would correspond to the interglacial MIS 7.

Keywords: vertebrate assemblage; Mutual Ecogeographic Range; Bioclimatic Model; Quantified Ecology; Habitat Weightings; Marine Isotope Stage 7.

1. Introduction

The late Middle Pleistocene and the early Late Pleistocene represent periods of significant climatic variability. They could be included into the Marine Isotope Stages (MIS) 7 to 5, culturally characterised by the Mousterian which is a Middle Palaeolithic ensemble of Neanderthal-related techno-complexes in Europe. Climatic oscillations affected small mammal faunas, as well as hominid groups, mainly through availability of resources (Dennell et al., 2011). Studies on the Middle/Late Pleistocene fauna are essential to provide a sound biochronology and to reconstruct palaeoenvironmental shifts involving hominid migrations, population size changes and species turnover (Berto et al., 2021).

Small vertebrates are particularly suited for biochronology and palaeoenvironmental reconstructions. In the late Middle Pleistocene, at the boundary between the early and late Toringian, a critical transition in the rodent fauna took place, when *Arvicola mosbachensis* was replaced by *Arvicola amphibius* (Fejfar and Heinrich, 1988; Maul et al., 2000; Kalthoff et al., 2007; Berto et al., 2021).

The MIS 7 corresponds to the late Middle Pleistocene, being dated to ca. 246–186 ka. It is characterised by a marked alternation of three warm (MIS 7e, MIS 7c, and MIS 7a) and two cold episodes (MIS 7d and MIS 7b) (Desprat et al., 2006; Roucoux et al., 2006, 2008; Railsback et al., 2015). It seems that during MIS 7, the Middle Palaeolithic culture was established in Italy (Torre in Pietra site; Villa et al., 2016). In the Italian Peninsula, terrestrial records based on small vertebrate studies from the late Middle Pleistocene are limited to Torre in Pietra 2 in Latium (Caloi and Palombo, 1978), and three localities in Berici Hills (Vicenza): the lower layers of Grotta del Broion (Sala, 1980; Colamussi, 2002), the lower units (Units VIII-VII) of Grotta Maggiore di San

Bernardino (López-García et al., 2017) and probably Sossano 2 (Bartolomei, 1980; Bon et al., 1991).

The MIS 6 (ca. 185–135 ka) corresponds to the penultimate glacial period and to the late Saalian glaciation in Europe (Ehlers et al., 2011). According to pollen data, the early part of MIS 6 in Europe was marked by a moderately severe climate with fluctuating tree abundances. This phase was followed by more extreme conditions characterised by a mainly treeless environment at the end of the penultimate glacial (Roucoux et al., 2011). However, there are very few palaeontological sites in southern Mediterranean Europe documenting terrestrial faunas of the MIS 6 (Blain et al., 2017; López-García et al., 2021), with one of them, Poggetti Vecchi (Benvenuti et al., 2017), located in Italy.

The MIS 5, dated to ca. 130 to 75 ka (early Late Pleistocene), represents a stage of minimum ice volume. It includes three warm phases (MIS 5e, MIS 5c, and MIS 5a) alternating with two cold phases (MIS 5d and MIS 5b) (Kukla et al., 2002; Sánchez-Goñi et al., 2012; among others). Again, the continental record with small vertebrate surveys for MIS 5 in Italy is scarce, being limited to Ciota Ciara cave in Borgosesia (Berto et al., 2016), upper layers of Caverna degli Orsi in Trieste (Berto and Rubinato, 2013), and Unit V of Grotta Maggiore di San Bernardino (López-García et al., 2017).

Here, the vertebrate assemblage from the site of Moleto (northwestern Italy) is presented in order to help to expand our knowledge on the faunistic context of the late Middle to early Late Pleistocene in northern Italy. Considering the small mammal assemblage, a chronological approach of the sites has been performed, putting it in relation to a broad context. In addition, an environmental and climatic reconstruction of Moleto has been carried out using a set of methods applied to small mammals and herpetofauna to shed light on the landscape and climate prevailing in the studied region at the end of the Middle Pleistocene.

2. Site

The Moleto site is formed by a set of fissures filled by sediments of Middle/Late Pleistocene age. It is located near the small town of Moleto (Ottiglio Monferrato, Piedmont region, Northwest Italy; Fig. 1A), at an altitude between 187 and 207 m.a.s.l. The location coordinates are 45° 1' 42" N, 8° 13' 12" E. The Monferrato area (southeastern Piedmont) is part of the Tertiary Piedmont Basin, a marine sedimentary basin formed during the Cenozoic (late Eocene–Late Miocene), and is characterised by two separate stratigraphic successions cropping out in western and eastern sections, respectively. The eastern Monferrato sequence (Oligocene–Late Miocene) is made up of terrigenous deposits of variable thickness, overlain by shallow-water shelf carbonates (Mancin et al., 2003). These include different units, among which the Pietra da Cantoni Formation occupies the uppermost portion (Tosetto et al., 2023). The Moleto site was discovered in the 1990s in an abandoned quarry carved into a Burdigalian–Langhian carbonate succession of the Pietra da Cantoni Formation (Bonsignore et al., 1969; Clari et al., 1994; Roggero, 2003).

Remarkably, a diverse fish assemblage including squalomorph and galeomorph sharks, batoids, and percomorph bony fishes reworked from the embedded sediments of the Miocene Pietra da Cantoni, and indicative of shallow to deep shelf marine biotopes, has been found in the fissure fillings (see supplementary material 1).

The Moleto site hosts three closely spaced fissures with palaeontological content: Moleto 0, Moleto 1, and Moleto 2. All the deposits filling the three fissures have the same sedimentary source. In addition, their very similar faunal content, evidenced by the common presence of *Arvicola mosbachensis* and its similar SDQ values (as discussed below), is indicative of a coeval sediment deposition of the three localities, which are considered as a single assemblage in the following analyses.

Moleto 0 is 1.5 m wide and 0.2 to 0.4 m thick (Fig. 1C) and consists of a conglomerate with centimetric to pluricentimetric pebbles of Pietra da Cantoni carbonates in a reddish-brown sandy clay matrix with well-thickened Mn and Fe oxides. Small vertebrate remains are relatively abundant. This fissure has also yielded some large mammal remains.

Moleto 1 is 1.3 m thick and up to 0.85 m wide (Fig. 1B). The fissure is rich in small vertebrates, but limited in large mammals. It can be subdivided from the base to the top into six levels of variable thickness: Level 6 (10–15 cm), Level 5 (15–20 cm), Level 4 (10–15 cm), Level 3 (20–25 cm), Level 2 (~30 cm), and Level 1 (30–35 cm). Level 6 consists of reddish silty sands, with some pebbles and abundant carbonaceous residues and oxides of Mn and Fe, with the base more conglomeratic, including centimetric, moderately rounded pebbles of Pietra da Cantoni carbonates. Microvertebrates are abundant. Level 5 is formed by slightly pebbly silty sands, with dark green clays and oxides of Mn and Fe. It has yielded microvertebrates remains. Level 4 consists of silt with red-brown sands, lacking lamination. Fossils are absent. Level 3 is composed of yellow ochraceous silts, slightly sandy and densely laminated. There are pockets of sandy, reddish-brown sediment with microvertebrates. Level 2 consists of reddish-brown sandy silts, with pockets of dark brown sandy sediment. Fossils are present. The non-fossiliferous Level 1 is formed by slightly clayey sandy silts, lacking lamination.

Moleto 2 is 2.5 m wide and 0.4 to 0.5 m thick (Fig. 1D). The fissure is infilled by a yellow ochraceous sandy clay sediment with scarce small and large vertebrate remains.

3. Material and methods

3.1. Vertebrate sorting and taxonomic study

The large mammal specimens and most of the small vertebrate material documented herein were collected from the Moleto site during the 2009 sampling campaign conducted by the Università degli Studi di Torino, in addition to the material recovered during a survey carried out in Moleto 0 in the 1990s. Raw sediment retrieved on site in Moleto 1 and 2 was systematically water-screened using superimposed 2 and 0.8 mm mesh sieves. The 0.8 mm mesh sieve was not used during the screening of the Moleto 0 sediment, leading to a bias in the smaller specimens, as is the case for murids and *Muscardinus*, groups expected to occur but apparently absent. The resulting Moleto small vertebrate collection includes 209 identified small mammal teeth, mandibles, and maxillae (plus two humeri of a talpid) corresponding to 13 different taxa, and 167 disarticulated cranial and postcranial bones of amphibians and squamate reptiles comprising at least 8 taxa. 14 large mammal teeth and bones belonging to eight taxa have also been recovered, together with two avian bones representing a single taxon (see supplementary material 2). These fossils are part of the collections of the Museo di Geologia e Paleontologia, Università degli Studi di Torino (MGPT-PU) and are housed at the Dipartimento di Scienze della Terra, Università degli Studi di Torino (Torino, Italy).

All the measurements are expressed in millimetres and were taken with the software DinoCapture 2.0, using photographs from the Digital Microscope AM4115TL Dino-Lite Edge. Small vertebrate remains are illustrated by means of digital photographs taken with the same device. The upper teeth are marked with capital letters and the lower teeth by lowercase letters. Taxonomy follows Speybroeck et al. (2020) for herpetofaunal taxa. Osteological terminology follows Macaluso et al. (2023) for urodeles; Sanchiz (1998), Bailon (1999), and Gómez and Turazzini (2016) for anurans; Villa and Delfino (2019) and Čerňanský et al. (2019) for lizards; and Szyndlar (1984) for snakes. The terminology and measuring methods employed in the descriptions of the arvicolid teeth (only m1 have

been considered) are those of Van der Meulen (1973), modified by Petruso et al. (2011) for *Microtus* (*Terricola*), and by Nadachowski (1984) and Cuenca-Bescós and Laplana (1995) for *Microtus* gr. *arvalis-agrestis*. For *Arvicola*, we have calculated the SDQ index (enamel differentiation index; Heinrich, 1978), which quantifies the difference in enamel thickness between the anterior and the posterior wall of each triangle of arvicolid molars. The index was calculated using complete m1 samples (SDQ7) following the formula: SDQ = [Σ (teet × 100/leet)] / N, where N is the number of dentine fields of the studied tooth, teet (trailing edge enamel thickness) refers to the maximum thickness of the posterior enamel band, and leet (leading edge enamel thickness) is the maximum thickness of the anterior enamel band of each dentine field (Heinrich, 1978, 1987; von Koenigswald and van Kolfschoten, 1996; Cuenca-Bescós et al., 2010; Lozano-Fernández et al., 2013). In describing and measuring the glirid teeth, we have followed the nomenclature and methods proposed by Daams (1981) and Freudenthal (2004), respectively. Van de Weerd (1976) was followed when we describe murid teeth, and length and width have been measured as defined by Martín-Suárez and Freudenthal (1993). For the nomenclature and measurements of sciurids, we have followed Sinitsa and Pogodina (2019) and Van de Weerd (1976), respectively. The terminology and measurements used to describe lagomorphs remains follow Angelone and Sesé (2009). We used the terminology and methods of Furió et al. (2015) for the Erinaceidae, of Reumer (1984) for the Soricidae family, and of Hutchison (1974) for the Talpidae.

3.2. Palaeoclimatic reconstructions

Palaeoclimatic reconstructions were carried out following the Bioclimatic Model (BM) on small mammal assemblages, and the Quantified Ecology (QE) and Mutual Ecogeographic Range (MER) on the herpetofaunal assemblages.

193 The qualitative Bioclimatic Method was established by Hernández-Fernández
194 (2001a, 2001b) and updated by Royer et al. (2020). This analysis is based on the
195 hypothesis of a significant correlation between climate and mammal community
196 composition, applying multivariate discriminant analysis to modern mammal faunas and
197 climates throughout the world (Hernández-Fernández and Peláez-Campomanes, 2003).
198 The approach to the past climatic conditions at Moleto was based on the bioclimatic
199 components from the rodent and insectivore fauna (Hernández-Fernández and Peláez-
200 Campomanes, 2005; Royer et al., 2020). The bioclimatic characterisation of the living
201 and extinct species from Moleto that was required for calculation of the bioclimatic
202 spectra was taken from Hernández-Fernández (2001a, 2001b) and Hernández-Fernández
203 et al. (2007). According to this method, mammal assemblages can be assigned to ten
204 climate types, five of which are represented by the rodent assemblage in Moleto: IV -
205 subtropical with winter rains and summer droughts, VI - typical temperate, VII - arid
206 temperate, VIII - cold-temperate (boreal), and IX - polar. After obtaining this distribution,
207 we calculated the Bioclimatic Component, from which a mathematical model was
208 elaborated using a multiple linear regression (Hernández-Fernández and Peláez-
209 Campomanes, 2005). By means of a series of functions, this allows the estimation of
210 various climatic parameters, such as mean annual temperature (MAT) and mean annual
211 precipitation (MAP).

212 The Quantified Ecology method (Jeannet, 2010, 2018) is based on assigning
213 climato-ecological values, stemming from randomly collected geographic and climatic
214 data provided by remote climatic stations over 30 years, to each species in relation to their
215 climatic and ecological potentialities (Jeannet, 2010). For each species, the climatic data
216 provided by remote stations and averages thereof are associated with those of other
217 species of the same level. The values obtained for each parameter are given in Jeannet

(2010). The mean of all the species represented in a site and/or a level permits estimation of various climatic parameters, such as the MAT, MAP, mean temperature of the warmest month (MTW), and mean temperature of the coldest month (MTC). In cases of higher taxa categories, the mean between the climate parameters of the different referred species has been done. However, the somewhat important differences observed between the weighting (according to Jeannet, 2010) of *Rana dalmatina* vs. *Rana temporaria* concerning temperature (with the exception of MTW) and % of forested areas and of *Natrix* gr. *natrix* vs. *Natrix tesselata* concerning temperature, rainfall, and % of forested areas prevented proposal of any reasonable mean and have been disregarded here.

The Mutual Ecogeographic Range method (MER; Blain et al., 2009, 2016) was used to identify the common current geographical range of the extant herpetofaunal species present in the studied levels. The MER method is based on presence/absence (and not abundance) and therefore is not particularly affected by taphonomic biases and/or over-representation of some species in the fossil sites (Blain et al., 2016). This method assumes that each species' and genus' ecological niche is preserved, so that extinct populations of extant species have the same climatic tolerances and preferences as their living representatives (Jackson and Overpeck, 2000; Jackson and Williams, 2004). To determine the current spatial distributions of European amphibians and reptiles, we used the data from Sillero et al. (2014) represented in a geographic coordinate system (datum WGS 84) with a 50 × 50 km grid. In the cases where species-level identification was not achieved (i.e. *Rana* sp. and *Vipera* gr. *aspis*), all the extant species belonging to the genus or taxonomical group were taken into consideration (see Table S1 in supplementary material 3). Once the common overlapping areas of the species from the assemblages were obtained, in order to achieve a more precise common species distribution areas, the fundamentals of the UDA-ODA discrimination technique were applied (Fagoaga et al.,

2019a; Marquina-Blasco et al., 2022). This recent procedure, partially derived from the MER method, identifies the Occupied Distribution Area (ODA), which denotes realistic occupied areas where the species may be present, and the UDA (Uncertain Distribution Area) where the species may be absent. The technique sharpens each species distribution using the species environmental requirements, creating the real ODA that were used to determine the current analogue association from where climatic parameters will be extrapolated to past fossil assemblages. In this case, the upper elevation limit has been used to obtain more precise areas within the overlapping area in which all the species of the three intersections analysed could coincide. The upper limit of elevation at which all species in the assemblages could coincide has been established at 2000 m (based on *Hierophis viridiflavus*; Vogrin et al., 2009).

Annual (MAT, MAP) and monthly climatic parameters (MTW, MTC) were extracted from the final overlapping areas from climate layers belonging to WorldClim 2.1 with a 30 arcseconds resolution grid (Fick and Hijmans 2017). The same climatic parameters were calculated for the recent vicinity of Ottiglio (1970–2001, with a 154 km^2 area). Data sets were processed using the ArcGIS 10.3 application (ESRI 2014). The mean and standard deviation were calculated using the statistical program IBM SPSS Statistics 22 (IBM Corp. Released 2013).

3.3. Palaeoenvironmental reconstruction

In order to reconstruct the ecological conditions that prevailed in the area of Moleto during the late Middle Pleistocene, we used the method of Habitat Weightings on small mammals and herpetofauna (Evans et al., 1981; Andrews, 2006) and the Quantified Ecology and MER methods on herpetofauna. These methods have not been applied to large mammals and birds due to scarcity of material.

The Habitat Weightings method is based on the distribution of each small vertebrate taxon in the habitat(s) where they are found today (for extant species) or where they are assumed to have lived in the past (for extinct species). Habitats are divided into six types: open dry meadows, open humid meadows, rocky areas, open woodland, woodland and woodland-margin areas, and areas surrounding water (Cuenca-Bescós et al., 2005, 2009; Blain et al., 2008; López-García et al., 2010, 2014; Piñero et al., 2016). Each taxon was rated to a maximum score of 1.00, which was divided proportionally to its habitat preferences if the species dwelled in more than one habitat type. To implement the Habitat Weightings method, it was necessary to calculate the proportions of each taxon in the assemblage using the minimum number of individuals (MNI).

In addition to the climatic parameters, Jeannet (2010) proposed some quantification for environmental parameters. The Quantified Ecology method avoids the use of the MNI, as it is judged to not always be representative of the environment (Jeannet, 2010). It thus proposes to weight the preference of each species for forested environments, with mean values representing a proxy for the extension of wooded (% of forested) environments around the archaeo-palaeontological localities.

4. Faunal content

The vertebrate assemblage from Moleto includes up to 30 different taxa (see Table 1). Amphibians are represented by *Salamandra salamandra*, *Bufo* gr. *bufo*, and *Rana* sp.; squamate reptiles by *Anguis* gr. *fragilis*, Lacertidae indet., *Hierophis* sp., *Natrix* sp., and *Vipera* gr. *aspis* (Fig. 2). Among birds, only Passeriformes indet. has been identified (Fig. 2I). The small mammal association comprises *Erinaceus europaeus*, *Talpa europaea*, *Sorex* sp., *Arvicola mosbachensis*, *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, *Microtus* (*Agricola*) cf. *agrestis*, *Microtus* (*Microtus*) cf. *arvalis*, *Apodemus* gr.

sylvaticus-flavicollis, *Sciurus* sp., *Glis glis*, *Muscardinus avellanarius*, *Clethrionomys glareolus*, and Lagomorpha indet. (Fig. 3). The large mammal association includes *Mustela putorius*, Carnivora indet., *Stephanorhinus* sp., *Sus* cf. *scrofa*, *Dama* cf. *dama*, *Cervus elaphus*, *Capreolus capreolus*, Bovidae indet. (Fig. 4). Detailed taxonomic descriptions and remarks for each taxon can be found in supplementary material 2. Tables with measurements and additional digital photographs of rodent and insectivore remains are provided in supplementary material 3.

5. Remarks on the small mammal taphonomy

The study of small mammal taphonomy employs a descriptive and systematic approach, analysing alterations resulting from predation (Andrews, 1990; Fernandez-Jalvo et al., 2016). In this preliminary study, we specifically observed and described the modifications caused by digestion in the first lower molars of arvicoline rodent species, as stated in Andrews (1990) and Fernandez-Jalvo et al. (2016). This enables us to recognise the action of predators responsible for the accumulation of small mammal remains.

Among the 49 analysed molars, 39% show evidence of light digestion, characterised by the progressive reduction of enamel on the teeth. This suggests the involvement of predators in the accumulations. The limited remains recovered from Moleto 2 (two m1s) does not allow for a taphonomic interpretation. In Moleto 0, 38% of arvicoline first lower molars are affected by light digestion, while in Moleto 1, the percentage of lightly digested molars reaches 46%. The relatively low degree of alteration in the Moleto sample, detected in less than 50%, indicates that the agent responsible for the accumulation is likely a strigiform, such as *Athene noctua* or *Strix aluco* (according to Andrews, 1990; Fernandez-Jalvo et al. 2016). Most authors consider that small

mammal remains in karstic sites are accumulated by the action of nocturnal avian predators through the rejection of pellets rich in skeletal material after digestion (Dauphin et al., 1996; Saavedra and Simonetti, 1998; Terry, 2004; Piñero et al. 2016).

The material from Moleto does not reveal any discernible pattern of prey consumption, as described by Andrews (1990) and Fernandez-Jalvo et al. (2016). Consequently, the palaeoecological interpretations based on the relative abundances of small mammal taxa reliably indicate the habitat where predators consumed their prey.

6. Chronological remarks

Based on the rodent assemblage it is possible to estimate the chronology of Moleto. European Plio-Pleistocene deposits are usually rich in arvicolids (voles), rodents particularly suited for the dating of continental sediments of this time interval. The high evolutionary rates and rapid diversification of this successful group, its unusually adequate fossil record, and its cosmopolitanism make it an excellent tool for biochronological correlations (Maul et al., 1998; Maul and Markova, 2007; Piñero et al., 2018, 2020, 2022; Piñero and Agustí, 2019; among others). The arvicolid assemblage from Moleto includes *Clethrionomys glareolus*, *Microtus* (*Terricola*) gr. *multiplex-subterraneus*, *Microtus* (*Microtus*) cf. *arvalis*, *Microtus* (*Agricola*) cf. *agrestis* and *Arvicola mosbachensis*. Among them, *Arvicola mosbachensis* is the most significant biochronological element.

The oldest specimens of the living *Clethrionomys glareolus* date back to the late Biharian (late Early Pleistocene; Glazek et al., 1976). This species has been documented from several Middle and Late Pleistocene sites, becoming dominant in small mammal assemblages between the Late Pleistocene and the Holocene (Nadachowski, 1982, 1989; Kowalski, 2001; Krokhmal et al., 2022). The first occurrence of the extant *Microtus*

arvalis and *Microtus agrestis* is still under debate due to problems of identification of both species. However, the earliest remains of *Microtus* gr. *arvalis-agrestis* (or *Microtus* aff. *arvalis-agrestis*) date back to the Early-Middle Pleistocene boundary (Maul and Markova, 2007). On the other hand, *Microtus* (*Terricola*) is strictly related to the subgenus *Microtus* (*Allophaiomys*), which originated at the end of the Early Pleistocene. In Italy, the oldest records of *Microtus* (*Terricola*) sp. are found in early Toringian sites (Kowalski, 2001).

The genus *Arvicola* is one of the best time markers for Middle and Late Pleistocene assemblages (Socha, 2014). Changes in its enamel thickness are used to establish chronological schemes. *Arvicola mosbachensis* (=*A. cantianus*) is considered the ancestor of *Arvicola amphibius* (=*A. terrestris*) in the lineage *Mimomys savini-Arvicola mosbachensis-Arvicola amphibius*. This lineage is based on the late Biharian-Toringian small mammal biozones (Fejfar and Heinrich, 1988; Maul and Markova, 2007; Sala and Masini, 2007; Berto et al., 2021). The transition between the early Toringian (Middle Pleistocene) and the late Toringian small mammal age (Late Pleistocene) is marked by the progressive replacement of *Arvicola mosbachensis* by *Arvicola amphibius* with modern morphology (López-García et al., 2017). The distinction between these two species is based on the SDQ index, with a threshold ascertained at 100 (Heinrich, 1978).

Arvicola members with SDQ index around 100 are characteristic of the Middle/Late Pleistocene boundary in western Europe (Rekovets, 1990, 1994; Rekovets and Nadachowski, 1995; Markova, 2004, 2006). A pattern of progressive decline over time in this index has been recognised (Berto et al., 2021). While *Arvicola* representatives with SDQ exceeding 100 are generally considered to be characteristic of the Middle Pleistocene, values close to or smaller than 100 are typical of the Late Pleistocene (Socha, 2014, and references therein). It should be noted that when samples from different

364 geographical areas are compared in detail, regional variations of SDQ values may be
365 observed. Such is the case for Italian water voles and their Central European counterparts,
366 but these variations are more evident in *A. amphibius* since the beginning of the Late
367 Pleistocene, while the *A. mosbachensis* of northern Italy presents the same characteristic
368 as the Central European ones (Masini et al. 2020).

369 The transition between *A. mosbachensis* and *A. amphibius* is not abrupt, having
370 been affected by morphological and geographical variability (Maul et al., 1998; Masini
371 et al., 2003; Paunescu et al., 2004). However, the first appearance of *A. amphibius* in Italy
372 precedes the end of the Eemian interglacial, MIS 5e (Sala and Masini, 2007; López-
373 García et al., 2017). In Moleto, all the SDQ values of *Arvicola* exceeds 100 (see Table S2
374 in supplementary material 3). These results suggest that the deposition of the three
375 fissures took place during the latest Middle Pleistocene (older than the Eemian
376 interglacial), when the mean SDQ values exceed 100, being within the range of variation
377 of SDQ for European representatives of *Arvicola* of that period (Fig. 5) (von
378 Koenigswald, 1973, 1980; Heinrich, 1978, 1982, 1987, 1990; van Kolfschoten, 1990;
379 Rekovets and Nadachowski, 1995; von Koenigswald and van Kolfschoten, 1996;
380 Desclaux et al., 2000; Maul et al., 2000; Kalthoff et al., 2007; Nadachowski et al., 2009;
381 Socha, 2014; Valde-Nowak and Nadachowski, 2014; Berto et al., 2021).

382 The Late Pleistocene site of De Nadale Cave (northeastern Italy), correlated to near
383 the onset of MIS 4 (71–57 ka), has some elements in common with Moleto such as
384 *Microtus* (*Terricola*) *multiplex-subterraneus, Clethrionomys glareolus, Microtus arvalis,*
385 *Microtus agrestis,* and *Apodemus* gr. *sylvaticus-flavicollis* (López-García et al., 2018).
386 However, De Nadale Cave includes *Arvicola amphibius*, descendant of *Arvicola*
387 *mosbachensis*, suggesting a younger age than Moleto. Similarly, the Late Pleistocene
388 sequence of Fumane Cave (MIS 3 to MIS 2), in northeastern Italy, shares with Moleto

389 the presence of the rodents *Microtus* (*Terricola*) *multiplex-subterraneus, Clethrionomys*
390 *glareolus, Microtus arvalis, Microtus agrestis, Apodemus* gr. *sylvaticus-flavicollis, Glis*
391 *glis*, and *Muscardinus avellanarius* (López-García et al., 2015). Nevertheless, the
392 occurrence of *Arvicola amphibius* in Fumane Cave indicates that Moleto is somewhat
393 older. This is also the case for the MIS 5 layers of Caverna degli Orsi (northeastern Italy;
394 Berto and Rubinato, 2013), and the MIS 5 locality of Ciota Ciara (Piedmont region; Berto
395 et al., 2016), which record some species also found in Moleto, but they include *Arvicola*
396 *amphibious* or *A.* cf. *amphibious* with SDQ values lower than those of Moleto, suggesting
397 a somewhat younger age than the studied site.

398 The rodent assemblage from the lower levels of Grotta Maggiore di San Bernardino
399 (northeastern Italy), dated to MIS 7 (López-García et al., 2017), is very similar to that of
400 Moleto. Similar taxa have been recognised in units VIII-VII such as *Arvicola*
401 *mosbachensis, Microtus* (*Terricola*) *multiplex-subterraneus, Clethrionomys glareolus,*
402 *Microtus arvalis, Microtus agrestis,* and *Apodemus* gr. *sylvaticus-flavicollis*, *Sciurus* sp.,
403 and *Glis glis*, suggesting that they have a very close age (Fig. 6). The younger units IV-
404 V (MIS 5) and III-II (MIS 3) already include a modern form of *Arvicola* (*A. amphibius*).

405 According to all of these evidences, the assemblages from Moleto likely date back
406 to the late Middle Pleistocene, older than MIS 5e (MIS 8–6, probably interglacial MIS 7
407 as discussed in the next section). However, we cannot exclude that Moleto 0, 1, and 2
408 were deposited at the boundary of the Middle and Late Pleistocene. Although the SDQ
409 values for all deposits exceeded 100, the paucity of data makes it difficult to interpret the
410 results unambiguously.

411 **7. Environmental approach**

412 Small mammals, amphibians, and reptiles have been widely used as palaeoclimatic
413 and palaeoecological indicators, allowing to reconstruct past environmental and climatic
414 conditions (e.g. Blain et al., 2009; Piñero et al., 2016; Lozano-Fernández et al., 2019;
415 López-García et al., 2021; Sánchez-Bandera et al., 2023). Here, we attempt to analyse the
416 environment and climate in the area of Moleto at the time of the deposition of the
417 fossiliferous sediments.

418 The Habitat Weightings method applied to the small mammal assemblage of the
419 Moleto site reveals an environment dominated by woodland and open woodland habitats
420 (66.7%), represented mainly by the species *Glis glis*, *Apodemus* gr. *sylvaticus-flavicollis*,
421 and *Clethrionomys glareolus*. There was also an important presence of water streams
422 (8.3%) and open humid meadows (18.8%), indicated by the relative abundance of
423 *Arvicola mosbachensis* and *Microtus* (*Terricola*) gr. *multiplex-subterraneus* (Table 2).
424 The presence of open dry areas was limited to 6.3%.

425 The results obtained from the Habitat Weightings method using the amphibian and
426 squamate reptile assemblages (Table 2) again suggest the dominance of woodland and
427 open woodland areas (48.6%), with presence of water streams (10.7%), and a high
428 representation of open moist areas (33.6%). Open dry meadows are poorly represented
429 (7.1%). The percentage of forest is somewhat higher in data provided by the small
430 mammal assemblage, but the overall palaeoenvironmental results are very close. It is
431 usual that reconstructions based exclusively on small mammals (e.g. Fagoaga et al.,
432 2019b) provide higher forest values than those based on herpetofauna (Marquina-Blasco
433 et al., 2017, 2021).

434 The percentage of wooded areas obtained with the small mammal assemblage
435 agrees well with the palaeonvironmental results obtained from Quantified Ecology
436 (Jeannet, 2010) on the amphibian and squamate reptile assemblages from Moleto, which

437 indicate 64% of forest cover (Table 3). Similarly, according to the data obtained from
438 Mutual Ecogeographic Range, the extension of wooded environments in Moleto reached
439 51.8%, 7% higher than that of today.

440 Overall, the small mammal and herpetofaunal assemblages suggest the prevalence
441 of a landscape dominated mainly by woodland and open-woodland areas, with presence
442 of open herbaceous areas and development of water courses in the vicinity of Moleto
443 during the formation of the site (Fig. 7). The predominance of forested environments at
444 Moleto is supported by the appearance of browsing herbivores, such as the red deer
445 (*Cervus elaphus*), roe deer (*Capreolus capreolus*), and fallow deer (*Dama dama*). In
446 addition, the preferred habitats by wild boars (*Sus scrofa*) and European polecats (*Mustela*
447 *putorius*), present at Moleto, are mixed forests under humid conditions (Petronio et al.,
448 2011). The existence of open environments and open woodlands around Moleto is
449 consistent with the occurrence of a large bovid (such as *Bison* or *Bos*) and the rhinoceros
450 *Stephanorhinus* sp. (Petronio et al., 2011).

451 **8. Palaeoclimatic reconstruction**

452 The present-day climate in Moleto is characterized by a mean annual precipitation
453 (MAP) of 1137 mm, and a mean annual temperature (MAT) of 12.7 ºC. The thermal
454 gradient ranges approximately from 23.8 ºC (mean temperature of warmest month,
455 MTW) to 1.7 ºC (mean temperature of coldest month, MTC) (Climate-data.org).

456 The palaeoclimatic results obtained from Quantified Ecology (Jeannet, 2010)
457 applied to the herpetofaunal assemblages (Table 4) point to a slightly cooler climate with
458 relatively lower rainfall than today (Fig. 7). The MAT was 2.3 ºC lower, and the MAP
459 402 mm lower than present-day values. The MTC was 1 ºC, and the MTW was 20.8 ºC,
460 a thermal gradient close to the current one. Likewise, the results attained from Mutual

461 Ecogeographic Range (MER) using UDA/ODA technique on the herpetofauna
462 assemblages (Table 5; Fig. S6) suggest somewhat colder temperatures than today (MAT
463 = 10.7 ºC, MTC = 2.4 ºC, MTW = 19 ºC). The MER reconstructed rainfall suggests,
464 however, MAP closer to current data (MAP = 880 mm).

465 The data obtained by the Bioclimatic Model (BM) on small mammals suggest MAT
466 2.8 ºC lower than nowadays in the area of Moleto, but standard deviation with ±6.9 ºC
467 overlaps with the current ones. Similar to the herpetofaunal assemblages, the small
468 mammals from Moleto suggests mild summers, with MTW = 20.8 ±5.5 ºC, and relatively
469 cold winters, with MTC = -0.8 ±15.9 ºC. This thermal gradient is similar to the current
470 one in the area (Table 6). The BM reconstructed rainfall also indicates a drier climate
471 (ΔMAP = -551.1 mm) (Fig. 7). The bioclimatic components are dominated by the climate
472 VI (43%) (typical temperate, related with a temperate deciduous forest), indicating winter
473 rain and summer drought. It is followed by climate VIII (23.6%) (cold-temperate, related
474 to a boreal coniferous forest-taiga), denoting cold-temperate conditions (Royer et al.,
475 2020) (Table 7).

476 The climatic parameters reconstructed using the herpetofauna and those
477 reconstructed with small mammals are coherent (Fig. 7). The results of all the
478 palaeoclimate methods suggest that the small vertebrate assemblage from Moleto was
479 probably related to temperate and moist climatic conditions. This is consistent with
480 deposition during an interglacial event, thus discarding the late Middle Pleistocene cold
481 MIS 8 and MIS 6 periods.

482 When comparing the palaeoclimatic data of Moleto with those of the nearby MIS 6
483 site of Lazaret (Nice, France) (López-García et al., 2021), located around 160 km
484 southwest of Moleto, we observe that the MAT reconstructed at Lazaret (~8.8 ºC) is lower
485 than that of Moleto (~10 ºC). Most remarkable is the marked contrast between the current

MAT at Nice (15 ºC) and that of Lazaret (ΔMAT = -6.2 ºC), representing a significantly more pronounced difference than in Moleto (<3 ºC). In addition, the percentage of forest at Lazaret cave (ca. 35%) is lower than that of Moleto. These data support the dismissal of the correlation of Moleto with the glacial MIS 6.

According to the chronological data presented above, the interglacial stage of Moleto would correspond to MIS 7. Considering that the reconstructed MAT is somewhat cooler than today, Moleto may have been deposited during a cold episode within MIS 7 such as MIS 7d (the cold substage 7b is less severe). Alternatively, the site could represent a transition between MIS 7 and MIS 6 (Fig. 7). Nevertheless, more solid chronological data are essential to reach a firm conclusion on this regard.

Studies of small vertebrates from late Middle Pleistocene sites in Italy are limited. Three of these sites are Torre in Pietra 2 (Latium) (Caloi and Palombo, 1978), Sossano 2 (Berici Hills, Vicenza) (Bon et al., 1991), and lower units (VIII-VII) of Grotta Maggiore di San Bernardino (Berici Hills, Vicenza) (López-García et al., 2017). Among them, only Grotta Maggiore di San Bernardino has a palaeoenvironmental and palaeoclimatic study comparable to that of Moleto. According to López-García et al. (2017, 2019), the lower units of the nearby Grotta Maggiore di San Bernardino site are characterized by the dominance of forest species such as *A.* gr. *Sylvaticus-flavicollis*, *G. glis*, and *C. glareolus*. The presence of water streams (mainly suggested by the abundance of *A. mosbachensis*) and open humid meadows (indicated by the relative abundance of *M. agrestis* or *Talpa* cf. *europaea*) is also important in units VIII-VII of Grotta Maggiore di San Bernardino. Thus, as in Moleto, these MIS 7 levels are characterized by the predominance of woodland formations and temperate and moist climatic conditions (López-García et al., 2017, 2019).

9. Conclusions

The vertebrate assemblage from Moleto is represented by amphibians (*Salamandra salamandra*, *Bufo* gr. *Bufo*, *Rana* sp.), squamate reptiles (*Anguis* gr. *Fragilis*, Lacertidae indet., *Hierophis* sp., *Natrix* sp., *Vipera* gr. *Aspis*), birds (Passeriformes indet.), and mammals (*Erinaceus europaeus*, *Talpa europaea*, *Sorex* sp., *Arvicola mosbachensis*, *Microtus* (*Terricola*) gr. *Multiplex-subterraneus*, *Microtus* (*Agricola*) cf. *agrestis*, *Microtus* (*Microtus*) cf. *arvalis*, *Clethrionomys glareolus*, *Apodemus* gr. *Sylvaticus-flavicollis*, *Sciurus* sp., *Glis glis*, *Muscardinus avellanarius*, Lagomorpha indet., *Mustela putorius*, Carnivora indet., *Stephanorhinus* sp., *Sus* cf. *scrofa*, *Dama* cf. *dama*, *Cervus elaphus*, *Capreolus capreolus*, Bovidae indet.). The overall assemblage composition is typical of a warm phase and such elements are not present in assemblages dated later than MIS 5. The enamel characteristics of the rodent *Arvicola mosbachensis* indicates a latest Middle Pleistocene age. A multi-method approach using the small mammal and herpetofaunal assemblages point to the dominance of forested environments in Moleto during the deposition of the site, with development of open grassy areas and water courses. The palaeoclimatic data suggest temperate and moist climatic conditions, with slightly cooler temperatures and lower rainfall than today. According to the age of the site and palaeoclimatic results, the accumulation of remains may have occurred during the interglacial MIS 7. The Moleto site thus joins other European localities from the latest Middle Pleistocene, contributing to improve the knowledge of vertebrate communities, climate and environment in northern Italy during the Middle–Late Pleistocene boundary.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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562 **Appendix A. Supplementary data**

563 Supplementary data to this article can be found online at https://doi.org/xxxxx

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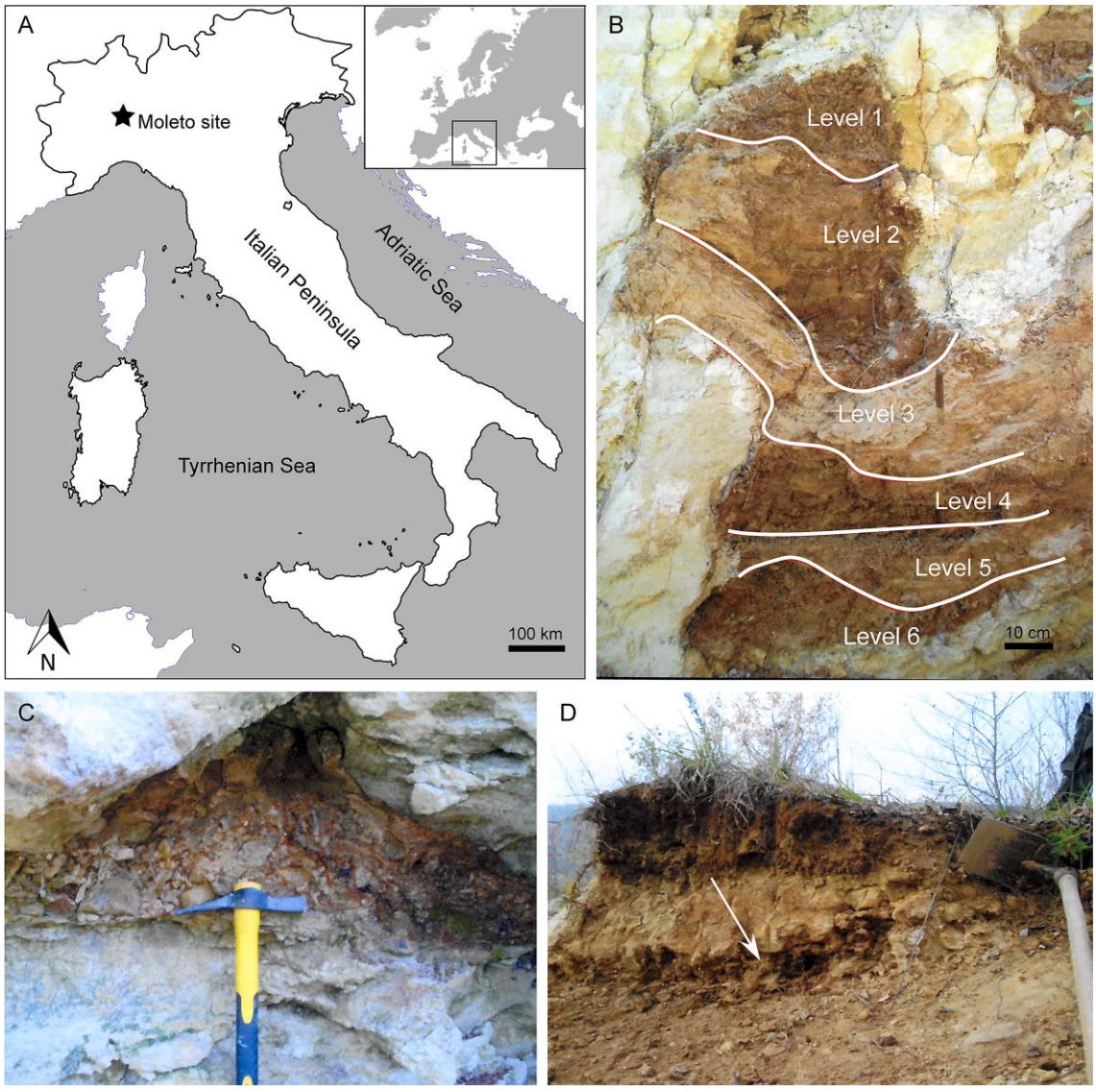
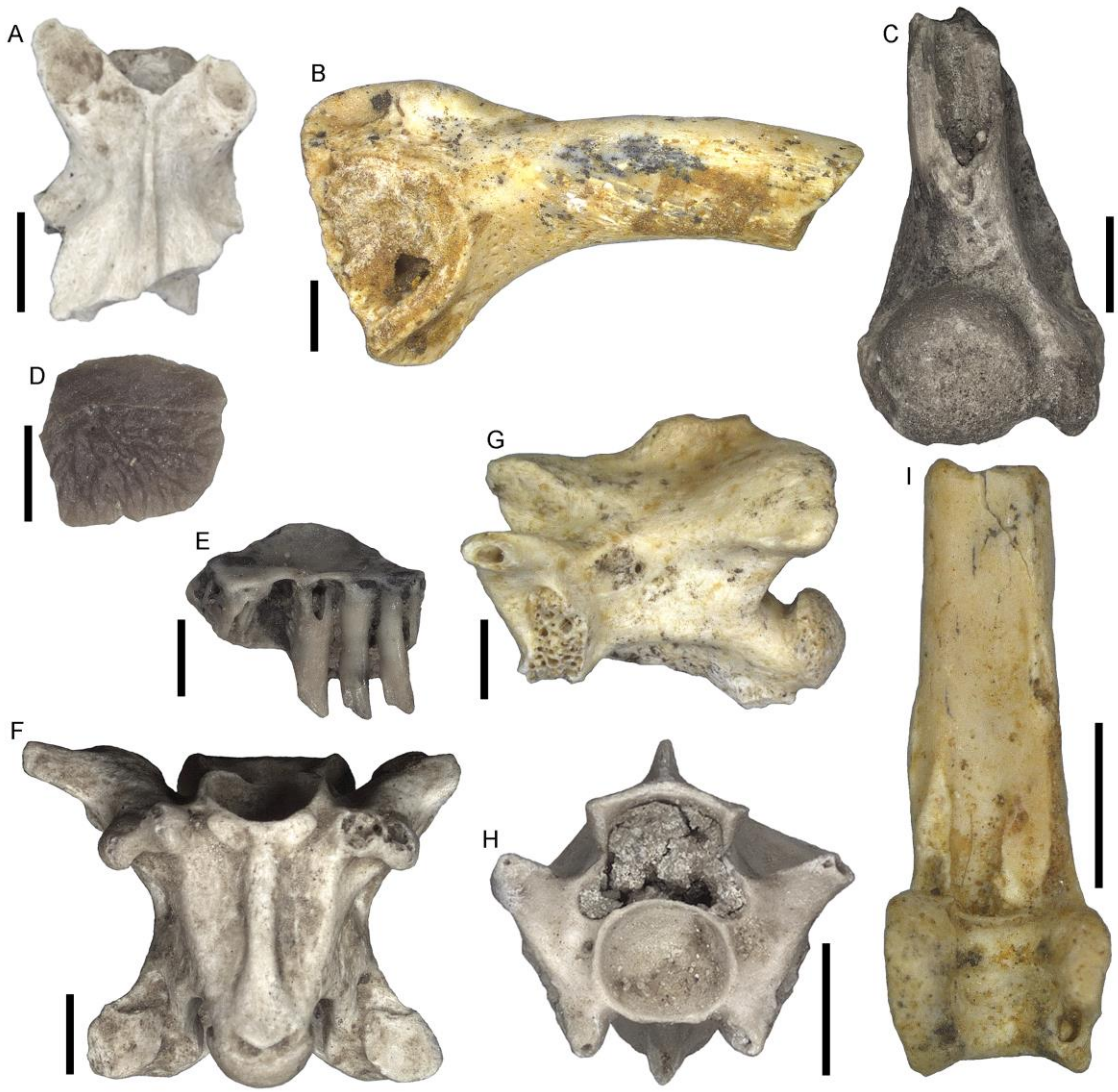
965 **Figures**



966

967 **Figure 1**. Geographic and stratigraphic context. A, Location of the Moleto site (source:
968 Google Earth Pro). B, Section of Moleto 1 showing six different levels. C, Fissure of
969 Moleto 0. D, Moleto 2 with the arrow pointing to the fossiliferous deposit. [2-column]



970

971 **Figure 2**. Digital images of amphibians, squamate reptiles, and birds from Moleto.
972 *Salamandra salamandra*: A, trunk vertebra in dorsal view, MGPT-PU 142439. *Bufo* gr.
973 *bufo*: B, right ilium in lateral view, MGPT-PU 142447. *Rana* sp.: C, right humerus in
974 ventral view, MGPT-PU 142448. *Anguis* gr. *fragilis*: D, osteoderm in external view,
975 MGPT-PU 142445. Lacertidae indet.: E, fragment of right maxilla in medial view,
976 MGPT-PU 142442. *Hierophis* sp.: F, trunk vertebra in ventral view, MGPT-PU 142443.
977 *Natrix* sp.: G, trunk vertebra in left lateral view, MGPT-PU 142525. *Vipera* gr. *aspis*: H,
978 trunk vertebra in anterior view, MGPT-PU 142449. Passeriformes indet.: I, right
979 tibiotarsus in cranial view, MGPT-PU 130648. Scale bars equal 1 mm (A–C and F–I) or
980 0.5 mm (D and E). [2-column]

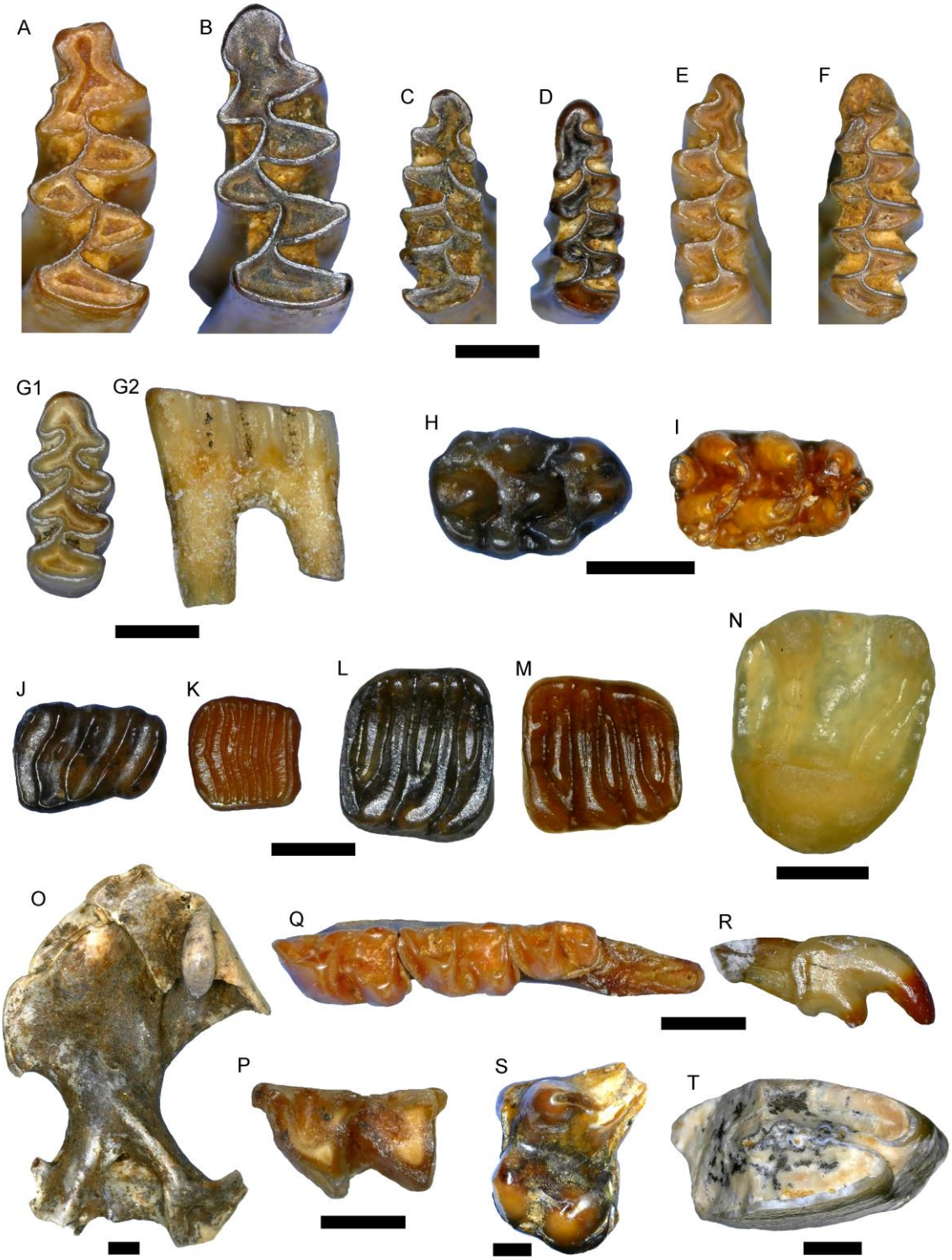


Figure 3. Digital images of small mammals from Moleto. *Arvicola mosbachensis*: A, left m1 from Moleto 0, MGPT-PU 129539; B, left m1 from Moleto 0, MGPT-PU 129538. *Microtus* (*Terricola*) gr. *multiplex-subterraneus*: C, right m1 from Moleto 0, MGPT-PU 129543; D, left m1 from Moleto 1, MGPT-PU 129604. *Microtus* (*Agricola*) cf. *agrestis*:

E, right m1 from Moleto 0, MGPT-PU 129544. *Microtus* (*Microtus*) cf. *arvalis*: F, left m1 from Moleto 0, MGPT-PU 129545. *Clethrionomys glareolus*: G, left m1 from Moleto 1, in occlusal (1) and lateral (2) views. *Apodemus* gr. *sylvaticus-flavicollis*: H, right M1 from Moleto 1, MGPT-PU 129627; I, right m1 from Moleto 1, MGPT-PU 129650. *Muscardinus avellanarius*: J, right M1 from Moleto 1, MGPT-PU 129583; K, right M2 from Moleto 1, MGPT-PU 129597. *Glis glis*: M, right M2 from Moleto 2, MGPT-PU 129665; N, right m1 from Moleto 2, MGPT-PU 129664. *Sciurus* sp.: O, left M1/2 from Moleto 1, MGPT-PU 129568. *Talpa europaea*: P, right humerus from Moleto 0, MGPT-PU 129504; Q, left m2 from Moleto 2, MGPT-PU 129663. *Sorex* sp.: R, left mandible with m1, m2 and m3 from Moleto 0, MGPT-PU 129503; S, right I1 from Moleto 0, MGPT-PU 129502. *Erinaceus europaeus*: T, right P4 from Moleto 0, MGPT-PU 129500. Lagomorpha indet: M, left P3 from Moleto 0, MGPT-PU 129505. Scale bars equal 1 mm. [2-column]

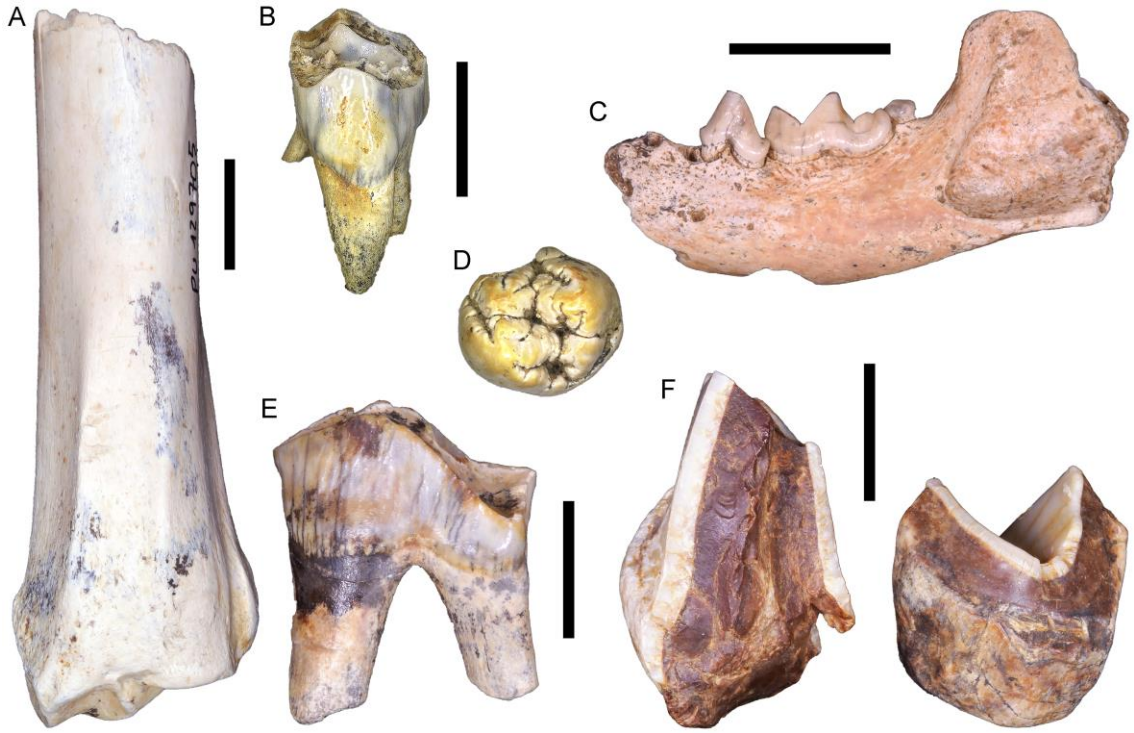


Figure 4. Digital images of large mammals from Moleto. *Capreolus capreolus*: A, left distal radius in dorsal view, MGPT-PU 129705. *Dama* cf. *dama*: B, left P4 in palatal view, MGPT-PU 129694. *Mustela putorius*: C, left hemimandible in labial view, MGPT-PU 129699. *Sus* cf. *scrofa*: D, indeterminate upper molar in occlusal view, MGPT-PU 129696. *Cervus elaphus*: E, left p2 in labial view, MGPT-PU 129695. *Stephanorhinus* sp.: F, fragments of upper molar, MGPT-PU 129698. Scale bars equal 10 mm. [2-column]

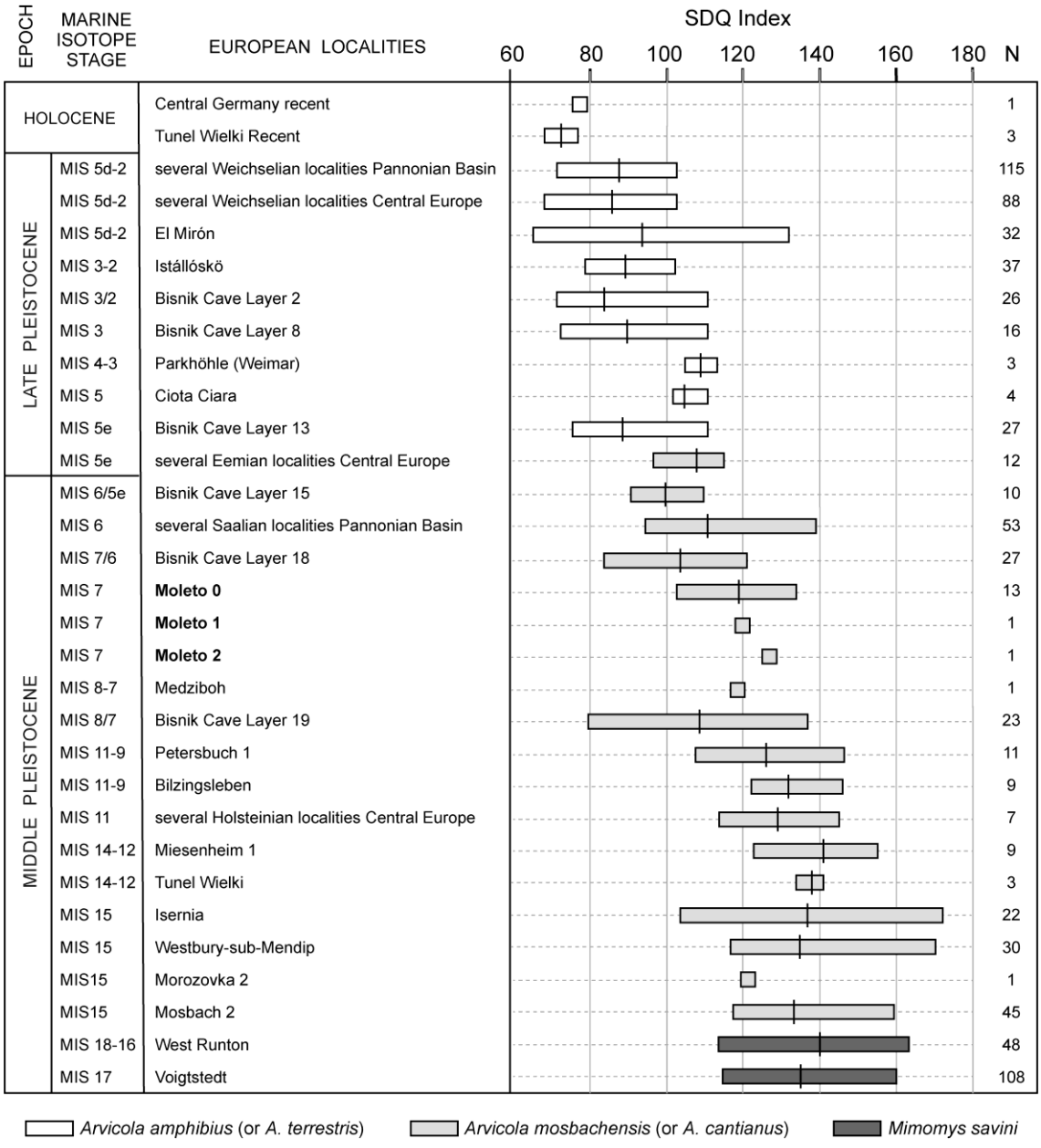


Figure 5. Enamel thickness quotient (SDQ) values of Middle Pleistocene and Late Pleistocene *Mimomys* and *Arvicola* from Europe. A decreasing trend in SDQ can be observed from late populations of *Mimomys savini* to late populations of *Arvicola*. The chronological assignment and the SDQ values have been taken from Heinrich (1982), van Kolfschoten and Turner (1992), Rekovets and Nadachowski (1995), Maul et al. (1998), Maul and Heinrich (2007), Cuenca-Bescós et al. (2010), Maul and Parfitt (2010), Socha (2014), Berto et al. (2016, 2021), Luzi et al. (2019), and this work. N, number of specimens. [2-column]

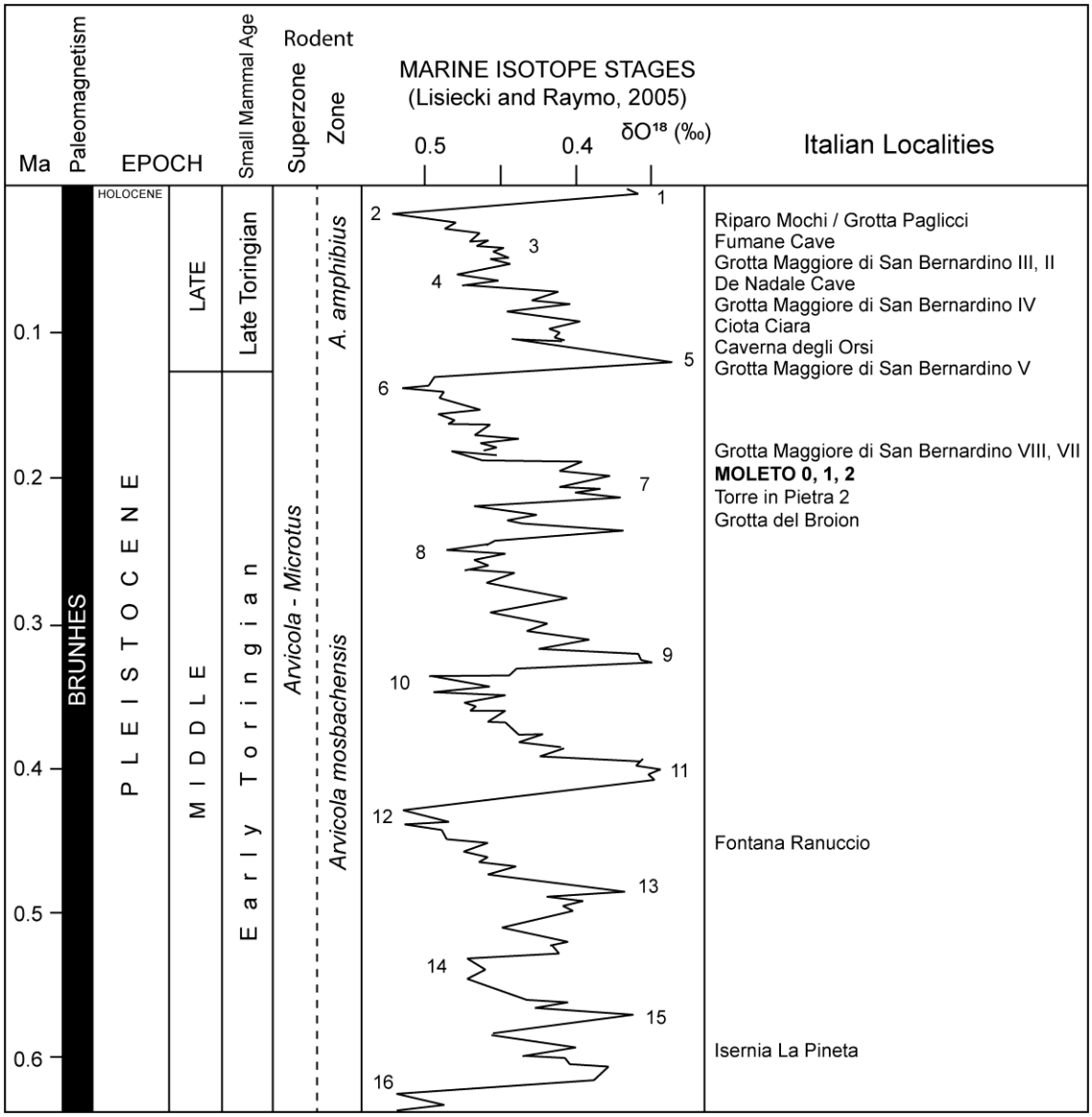
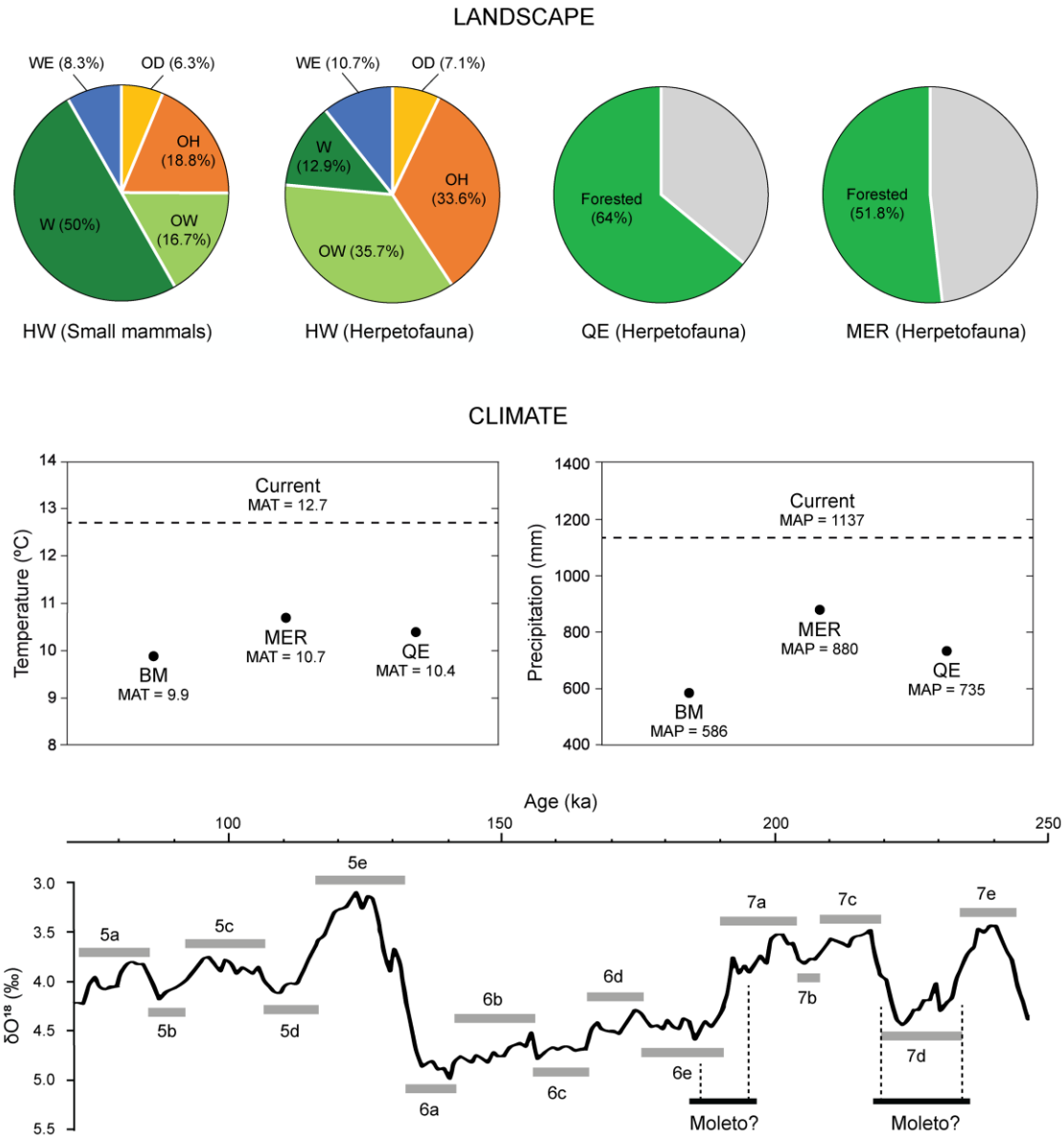


Figure 6. Biostratigraphic position of the Moleto site, placing other Italian localities and their correlation with Marine Isotope Stages (MIS) for comparison (Caloi and Palombo, 1978; Colamussi, 2002; Sala and Mansini, 2007; Berto and Rubinato, 2013; Berto et al., 2016, 2017, 2019; López-García et al., 2015, 2017). [2-column]



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1023 **Figure 7**. Landscape and climate values obtained with the small mammal and
1024 herpetofauna assemblages from Moleto and possible location of the site in the scheme of
1025 marine isotope substages (modified from Railsback et al., 2015). BM, Bioclimatic Model;
1026 QE, Quantified Ecology; HW, Habitat Weightings; MAT, mean annual temperature;
1027 MAP, mean annual precipitation; MER; Mutual Ecogeographic Range; OD: open dry
1028 meadows or shrublands; OH: open humid meadows; OW: open woodland; W: woodland
1029 and woodland-margin areas; WE: water-edges. [2-column]

1030

Table captions

Table 1. Vertebrate faunal list of the site of Moleto.

Table 2. Relative abundances of small mammals (rodents and insectivores) and herpetofauna (amphibians and squamate reptiles) from the late Middle Pleistocene site of Moleto, with the distribution of their potential habitats. W: woodland and woodland-margin areas; OD: open dry meadows or shrublands; OH: open humid meadows; OW: open woodland; WE: water-edges.

Table 3. Palaeoenvironmental results (% forested) obtained from Quantified Ecology (Jeannet, 2010) on the amphibian and squamate reptile assemblages from Moleto. SD: Standard deviation.

Table 4. Palaeoclimatic results obtained from Quantified Ecology (Jeannet, 2010) on the amphibian and squamate reptile assemblages from Moleto. As modern reference, we used the data of climate-data.org giving 12.7 ºC for MAT, 1137 mm for MAP, 1.7 ºC for MTC, and 23.8 ºC for MTW. SD: Standard deviation; Δ: anomaly in relation to present climate.

Table 5. Results obtained from Mutual Ecogeographic Range (Blain et al., 2009, 2016) using UDA-ODA technique (Fagoaga et al., 2019) on the amphibian and squamate reptile assemblages from Moleto. As modern reference, we used the data from WorldClim 2.1 giving 12.1 ºC for MAT and 843.1 mm for MAP (Fick and Hijmans, 2017). SD: Standard deviation; Δ: anomaly in relation to present climate. MAT: mean annual temperature; MAP: mean annual precipitation; MTC: mean temperature of the coldest month; MTW: mean temperature of the warmest month; percentage wood: extension of wooded areas. MAT, MAP, MTC, and MTW are in ºC, whereas percentage wood is expressed in %.

1053 **Table 6**. Climatic parameters for Moleto calculated according to the bioclimatic analysis
1054 based on rodent and insectivore associations proposed by Hernández Fernández (2001),
1055 and present climate data from the area (Climate-data.org). Δ: Difference between results
1056 and current data; MAT: mean annual temperature (in ºC); MTW: mean temperature of
1057 the warmest month (in ºC); MTC: mean temperature of the coldest month (in ºC); MAP:
1058 mean annual precipitation (in mm); SD: standard error for the estimation.

1059 **Table 7**. Distribution of the rodent and insectivore species identified at Moleto according
1060 to their climate preferences, in accordance with Hernández-Fernández (2001) and
1061 Hernández-Fernández et al. (2007). IV, Subtropical with winter rains and summer
1062 droughts; VI, Typical temperate; VII, Arid-temperate; VIII, Cold temperate (boreal) and
1063 IX, Polar. *For *Sciurus* sp. we have used the distribution of *Sciurus vulgaris*.

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