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INDEPENDENT WATER VOLE (*MIMOMYS SAVINI, ARVICOLA*: RODENTIA, MAMMALIA) LINEAGES IN ITALY AND CENTRAL EUROPE

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Abstract: Water voles are important key fossils of the Quaternary. Given their wide distribution, regional differences were expected to exist in different areas. Early hints on possible independent evolutionary trends of water voles in Italy came from palaeontology and specifically from the comparison of enamel differentiation (SDQ value) of the first lower molars between specimens from Italy and Germany. The data available at that time indicated that in the early Middle Pleistocene there were only minor enamel differences between first lower molars of water voles from these two geographical regions, whereas from the late Middle Pleistocene onwards, two lineages were clearly distinguished. Examination of mitochondrial DNA of extant *Arvicola* populations from across Europe by Wust-Saucy led to a similar conclusion that *Arvicola* populations from the Italian Peninsula had undergone independent evolution during the last 0.2 million years.

The inclusion of new fossil and extant *Arvicola* samples from Italy and Central Europe, together with the examination of additional morphological parameters of the occlusal surface (so-called van der Meulen indexes), have provided further support for the proposed evolutionary pattern. The combined analysis of length, SDQ and A/L index reveal a certain degree of inter-correlation and indicate an essentially continuous evolutionary trend. However, variations are discernible, related to the age and geographical origins of the samples, and become more clearly seen at least since the beginning of the Late Pleistocene. Italian samples have a characteristic tendency to grow larger, elongate the anteroconid, and have less derived SDQ. This corroborates the suggestion that Italian water voles underwent an evolutionary history distinct from that of their Central European counterparts. The differences in morphology may be related to a combination of etho-/ecological (aquatic or terrestrial habits) and palaeo-biogeographical factors.

Key words: water voles, first molars, Europe, evolution, Pleistocene, morphometrics

Introduction

Extant water voles are members of the genus *Arvicola*, which includes four species: *Arvicola amphibius* (Linnaeus, 1758) (= *A. terrestris* (Linnaeus, 1758), as it was commonly known a few years ago, was recognised to be a junior synonym – see Wilson and Reeder 2005), which includes European, Siberian, and Anatolian lineages (Kryštufek 2017a), *A. italicus* Savi, 1838 (on the Italian Peninsula; Castiglia et al. 2016), *A. monticola* de Sélys-Longchamps, 1838 (in northern Spain and NW Alp mountains; Kryštufek 2017b), and *A. sapidus* Miller, 1908 (Spain and France;

Kryštufek 2017c). The genus is geographically distributed over most of the Palaearctic, ranging as far west as the Iberian Peninsula to as far east as the Lake Baikal, and as far north as the Polar Sea to as far south as Israel and Iran. The term "water vole" may be somewhat misleading: most *Arvicola* actually inhabit water bodies (rivers, streams, ponds etc.), but some are fossorial and live far from water. *A. sapidus* is strictly aquatic, whereas *A. monticola* is fossorial, and *Arvicola amphibius* and *A. italicus* include both aquatic and fossorial morphotypes (Kryštufek et al. 2015).

The fairly rich fossil record has provided sufficient evidence to analyse many aspects of the evolution of water

voles in great detail. These animals are largely represented by molars which occur in hundreds in Eurasian fossil sites. Their very rapid dental evolution, most studied especially through the taxonomically diagnostic first lower molar (m1) makes them key terrestrial taxa with very high stratigraphic value.

Arvicola has rootless molars. Similarly to other Arvicolinae with arhizodont (= rootless) cheek teeth (*Microtus* s. l., *Lemmus* or *Lagurus*), the loss of roots in *Arvicola* is a secondary adaptation achieved through an evolutionary trend of increasing growth rates of the teeth from an ancestral condition of rooted molars. In many European and Asian regions, the ancestor seems to have been *Mimomys savini* HINTON, 1910. The molars are assumed to have grown so high to leave no space in the jawbone for both crown and roots, thereby causing the suppression of the latter (the root formation was postponed beyond the life span of the animal, see Koenigswald 1982; for a discussion on possible feedback processes see Maul 2001). This evolutionary process is rather common within the mammalian clade.

M. savini and the oldest *Arvicola*, *A. mosbachensis* (SCHMIDTGEN, 1911) (= *A. cantianus* (HINTON, 1910) = *A. cantiana* (HINTON, 1910) = *A. terrestris cantiana* (HINTON, 1910)) (for a discussion on the taxonomy see Maul et al. 2000) possess m1s with similar occlusal patterns, but the tooth is rooted in *Mimomys* and rootless in *Arvicola*. An ancestor-successor relationship between the latest *M. savini* and the earliest *Arvicola* could be supported by the stratigraphic records and areal distribution of the two taxa.

The transition would have occurred in Central Europe presumably between Marine Isotope Stage (MIS) 17 and 15 (Koenigswald and Van Kolfschoten 1996).

The evolution from the primitive *Arvicola mosbachensis* to the extant *A. amphibius* can be traced by a change in the thickness of the enamel. The evolutionary differentiation of the enamel was first observed by Heller in fossil remains of *Arvicola* from Mosbach (Heller 1933: 109; "… in the molars of the recent species, the enamel band on the concave side of the salient angles is always thicker than on the convex, and in the teeth of the fossil remains the opposite is usually the case"); similar changes were later observed in the material from Erpfingen (Heller 1958: 58), Süßenborn (Fejfar 1969: 763), and Petersbuch (Koenigswald 1970: 418). Eventually Heinrich (1978) introduced the SDQ (Schmelzband-Differenzierungs-Quotient) ratio to quantify the degree of enamel change (see section "Compared parameters" for details). This index is a measure of the relative thickness of the enamel walls in the dental triangles of molars, and accounts for a very general evolutionary trend not only in *Arvicola* but also in other clades of the subfamily Arvicolinae (Hinton 1926, Heinrich 1978, Koenigswald 1980, Heinrich 1982, 1987, 1990b, Van Kolfschoten 1992, Lippi et al. 1998, Martin and Tesakov 1998). Martin (1987: 271–272) introduced the terms "positive differentiation" when concave enamel edges (anterior in lower molars, posterior in upper ones) are thicker than the convex edges (posterior in lower molars, anterior in upper ones), and "negative differentiation" in the opposite case of enamel thickness.
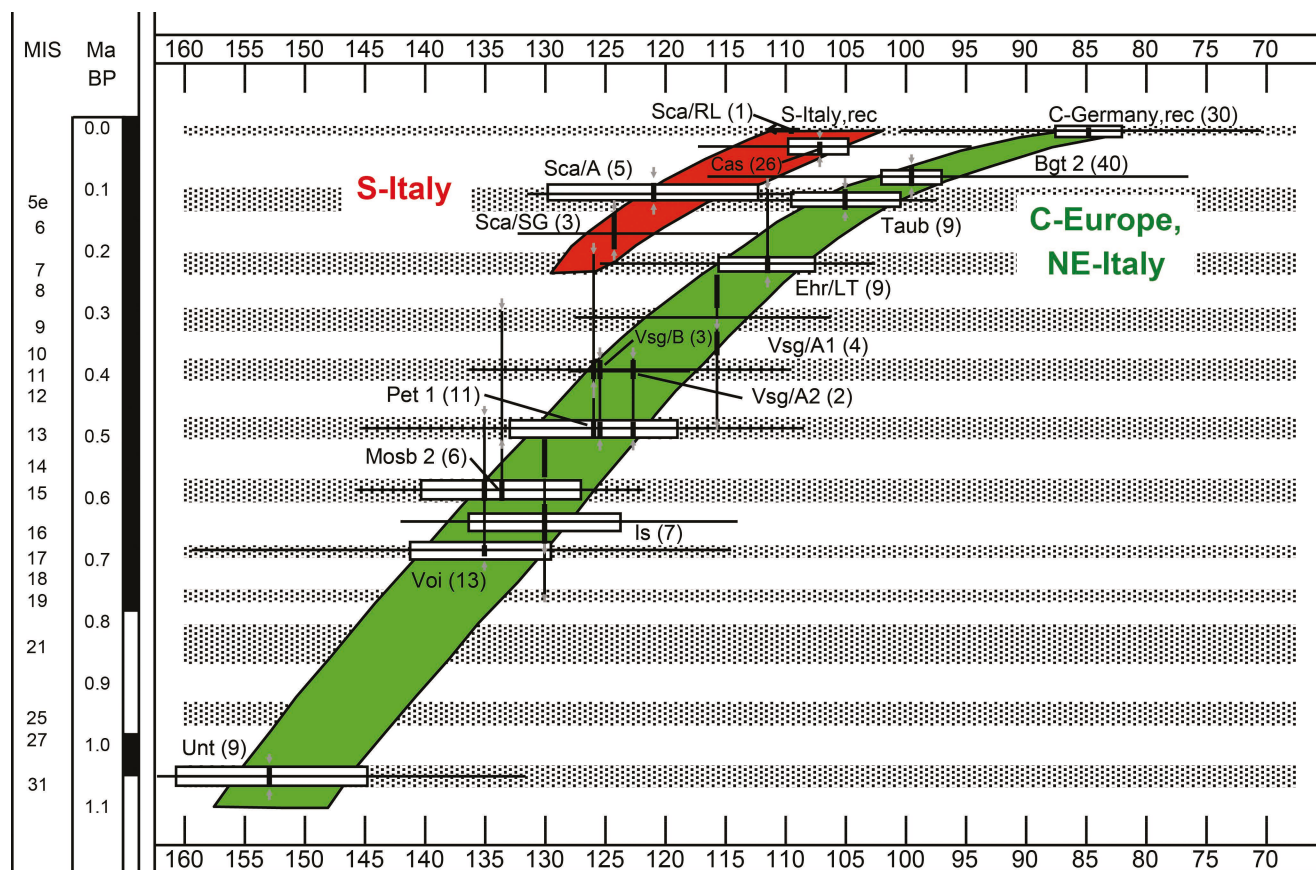
Text-fig. 1. SDQ vs stratigraphic time in samples of *Mimomys savini* and *Arvicola* from various Italian and German localities (in brackets: sample size), showing a parallel trend starting from ca. 200 ka. From Maul et al. (1998b: fig. 4), modified.
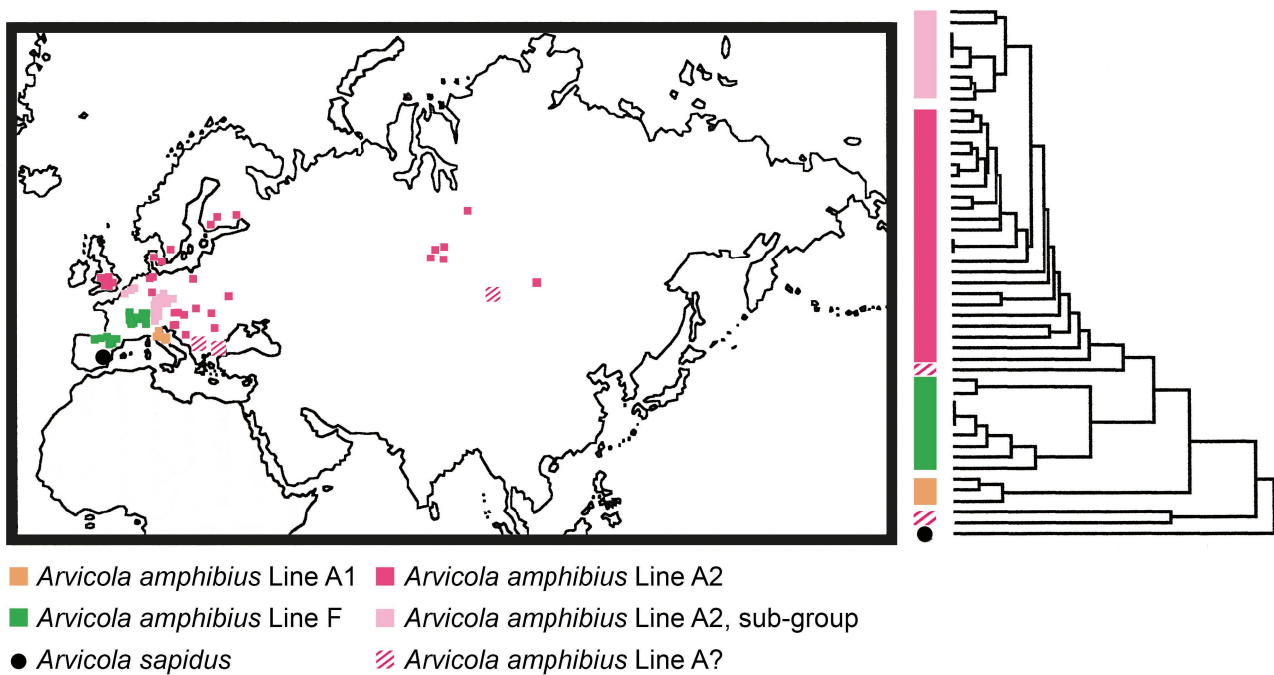
Text-fig. 2. Phylogeography based on mitochondrial phylogeny showing several evolutionary lineages of *Arvicola* and the separation of the Italian lineage of *Arvicola*, currently *A. italicus* (lineage A1), from European and Euro-Asiatic groups. From Wust-Saucy (1998: fig. 27), modified.

SDQ values grow lower through time: they range from 150–160 in *Mimomys savini* to about 80–70 in extant *Arvicola amphibius*. The lowest values are reached in advanced and most recent species. The transition between *A. mosbachensis* and *A. amphibius* is revealed by the SDQ values (*A. mosbachensis* > 100, *A. amphibius* < 100) and occurred in Central Europe during MIS 5 (Heinrich 1978, 1982, 1987, Koenigswald and Heinrich 1999).

The first who found regional and altitudinal influences on the relatively high SDQ values observed in Spanish and Swiss extant populations of *Arvicola* was Kratochvíl (1981). Röttger (1986, 1987) calculated this ratio (measurement method slightly modified from Heinrich 1978) in extant European and western Asian populations of *Arvicola* and found relatively high SDQs in the populations living in Spain, Turkey and western Iran.

SDQ values plotted against the estimated ages of Italian and German specimens of water voles show that Italian populations of *Arvicola*, at least during the last 0.2 Ma, maintained relatively less advanced (higher) SDQ values than coeval water voles from Germany (Maul et al. 1998a, b). The Italian water vole can thus be assumed to have undergone geographical differentiation and independent evolution during the late Middle Pleistocene and Late Pleistocene, a time period roughly including the two latest glacial cycles (from Saalian to Holocene) (Text-fig. 1).

Also, Wust-Saucy (1998; reported also in Taberlet et al. 1998), on the basis of molecular phylogenetical-phylogeographical studies on extant *Arvicola* populations, observed that Italian *Arvicola* populations had evolved independently from Central European *A. amphibius*. Wust-Saucy (1998) conducted an extensive analysis of Mitochondrial DNA (cytochrome b gene) of recent *Arvicola* populations scattered over the entire geographical range of the genus (particularly from large parts of Europe and

Siberia) (see Text-fig. 2). The results of this analysis (Text-fig. 2) showed that *Arvicola sapidus* from Spain and southern-western France had originally separated from an *Arvicola amphibius* (= *terrestris*) clade inhabiting the other geographical regions of distribution of water voles. Worth noting, however, is that the study revealed the occurrence of three distinct evolutionary lineages within this broad *A. amphibius* group, originally reported as *A. terrestris terrestris*, *A. terrestris scherman* and *A. terrestris italicus* in Taberlet et al. (1998). The Italian *Arvicola* populations (initially indicated as "South of Alps" by Wust-Saucy 1998) would form a distinct, well-characterised lineage, apparently the first to split from the hypothetical common ancestor of the *A. amphibius* group (Taberlet et al. 1998: fig. 2).

The consistency between the molecular phylogenetic results and the fossil record prompted a morphological-stratigraphical study of Italian *Arvicola*. In the present study, a brief survey of the fossil record of Italian water voles is followed by the presentation of morphometric data of new recent and fossil samples of *Arvicola*. To better explore the peculiarities of the Italian lineage, it is compared with samples from Central Europe and France. The analysis has also been extended considering further indexes, besides the SDQ already investigated by Maul et al. (1998a, b). This study is an extended version of a poster communicated in 2007 (Masini et al. 2007). It intends to provide a more accurate analysis of the morphological trends of the Italian water vole lineage with the ultimate aim of gaining improved knowledge of the evolutionary patterns of these rodents. In most cases the Italian Late Pleistocene/Holocene specimens will be referred to as "*Arvicola amphibius* group" pending a clear-cut morphological discrimination from the extant *A. italicus*.

Gerhard Storch – to whom this article is dedicated – was a true multitalented expert on both extant and fossil small mammals. He wrote several "now-by-everybody-cited" basic

papers on Pleistocene mice (see the G. Storch's bibliography in the introduction of volume 1 of this memorial). He was always very interested and open to discussions on these topics, and was, among others, senior author of the paper in which *Arvicola mosbachensis* from its type locality was studied in detail (Maul et al. 2000). We are confident that he would have enjoyed discussing with us the topic of the present article.

Water vole record of Italy

Mimomys savini

Mimomys savini is known only from Palaearctic Biharian sites. The Biharian biochronological unit is based on the co-occurrence of the genera *Microtus* and *Mimomys*; it therefore extends from the first occurrence of *Microtus* (represented by *Allophaiomys*, which includes primitive members of the genus *Microtus*) to the disappearance of *Mimomys* (represented by *M. savini*) (Fejfar et al. 1998). *Allophaiomys* and *M. savini* appear roughly at the same time in Eurasia, around 2 Ma.

In Europe, and more specifically in Italy, *M. savini* characterises both the early Biharian (defined by the co-occurrence of *M. savini* and *M. pusillus* and correlated with the Calabrian Age, early Early Pleistocene) and the late Biharian (time interval when *M. savini* was not associated with *M. pusillus*), which corresponds approximately to the first part of the early Middle Pleistocene. Readers are kindly referred to Gliozzi et al. (1997), Sala and Masini (2007) and Masini and Sala (2007) for correlations between Fejfar et al.'s (1998) standard biochronological scale based on small mammals and Azzaroli's (1977) Italian Mammal Ages, on the one hand, and the International Chronostratigraphic Scale, on the other.

Mimomys savini is first recorded in Italy based on a few remains from the localities Le Strette and Bosco Chiesa Nuova, in Upper Valdarno, where also large mammal remains of the Tasso Faunal Unit were found (Bosco 1898, 1899, Torre 1985, Sala and Masini 2007). These Lower Pleistocene deposits are magnetostratigraphically correlated with the base of the Calabrian Stage and biochronologically with the early part of the early Biharian; they therefore date to around 1.6–1.8 Ma (Torre et al. 1996, Azzaroli 1998, Masini and Sala 2007, Sala and Masini 2007, Rook and Martínez-Navarro 2010). Breda and Marchetti (2007) correlated the *M.* cf. *savini* bearing levels of Leffe (Stehlin 1930, Masini et al. 1996) with the transition between the Early Pleistocene Tasso and Farneta Faunal units and therefore with the early Biharian. Scoppito (L'Aquila Basin) is yet another early Biharian site that yielded *Mimomys savini* (Masini et al. 1996, Kotsakis et al. 2003). A younger age is assumed for the fossiliferous site of Soave/Cava Sud (*Mimomys* cf. *savini*) (Pasa 1947, Bartolomei 1980, Masini and Santini 1991), and further Italian early Biharian sites with *M. savini* are Monte Peglia (Van der Meulen 1973, Masini et al. 1998), and Castagnone/Pontrestura I (Northern Monferrato, Piedmont, NW Italy) (Siori and Sala 2007). In the latter site fossils come from both the basal levels of the local sedimentary succession (1st Alluvial Unit, fluviatile deposits and soils) and from the Alluvial Unit, at the (pedogenetic) top of the sequence. At least the basal levels are late Early Pleistocene (late early Biharian) in age

because *M. savini* co-occurs with evolved representatives of *Microtus* (*Allophaiomys*) cf. *nutiensis*, *Mimomys pusillus*, and *Ungaromys* cf. *nanus* (Giraudi et al. 2003, Sala and Masini 2007, Siori and Sala 2007). The fossil bearing stratigraphical sequence yielded a positive magnetization referred to the Jaramillo by Giraudi et al. (2003).

Late Biharian faunas with *M. savini* were found at Soave/Monte Tenda (Bon et al. 1991, Masini et al. 1996), and Slivia (Ambrosetti et al. 1979, Bon et al. 1991, Gliozzi et al. 1997). Scant, late Biharian remains of *M. savini*, somewhat more recent than the specimens from Soave/Monte Tenda, also come from Rifreddo in Sant'Arcangelo Basin (Basilicata), which yielded *Microtus* (*Terricola*) *arvalidens*, *Microtus* (*Iberomys*) ex gr. *huescarensis-brecciensis*, *Macroneomys* cf. *brachygnathus* and which show normal magnetisation of the early part of the Brunhes magnetochron (Fanfani 2000, Masini et al. 2000, 2005).

Arvicola mosbachensis

The oldest Italian *Arvicola* is from Isernia La Pineta. Although its age and taxonomic position have been debated (e.g., Koenigswald and Van Kolfschoten 1996, Maul et al. 2000) it is a very primitive *A. mosbachensis* still with incipient roots in some upper molars (see also Sala and Masini 2007). The fossil-bearing layers are ^{40}Ar/^{39}Ar dated to about 600 ka (Coltorti et al. 2005). *A. mosbachensis* is not very abundant in Middle Pleistocene localities, but its stratigraphic distribution is fairly continuous. The most significant localities where it was found are Venosa Notarchirico (Basilicata) (Sala 1999) and Visogliano Shelter (inner and outer deposits) (Cattani et al. 1991, Abbazzi et al. 2000). It was also found in recently discovered localities, such as Campani Quarry (Marcolini et al. 2000, 2003, Marcolini 2002), Cretone (Latium) (Di Canzio et al. 2003) and Campitello Quarry (Upper Valdarno, Tuscany) (Mazza et al. 2006) where an "evolved form" is quoted. *A.* cf. *mosbachensis* is reported from Fontana Marella Cave (Lombardian pre-Alps Varese Northern Italy); its remains were found in a layer sealed by a flowstone dated to 350 ka (Bona et al. 2008). Cretone is referred to the "Torre in Pietra" Faunal Unit of the Italian biochronological scale (Gliozzi et al. 1997) and correlated with MIS 10–9 (Milli and Palombo 2005). A number of finds, referred to as *A. mosbachensis* and *Arvicola* sp., and considered early Toringian in age, come from karst deposits in Verona and Friuli-Venezia Giulia (a more detailed report on these finds see in Pasa 1947, Bon et al. 1991, Kotsakis et al. 2003). Unfortunately, almost all the finds of this species have received scarce attention so far, and morphometric and morphologic descriptions are lacking.

Arvicola amphibius group

Arvicola amphibius (resp. cited as *A. terrestris*) is reported from the majority of Last Glacial Italian sites (Kotsakis et al. 2003). Its first occurrence apparently precedes the Last Interglacial. *A. amphibius* and *Arvicola* sp. were found in several pre-Eemian localities of Italy (Kotsakis et al. 2003, Sala and Masini 2007). Fossil finds of *A. amphibius* are reported from all over the peninsula, with the exception of southern Apulia. *A. amphibius* is absent from Sardinia and is reported only from the early-mid Holocene in Sicily (Tagliacozzo 1993, Catalisano and Sarà 1995, Agnesi et al.

2000, López-García et al. 2013). The latter authors gave a ^{14}C dating of $3,950 \pm 35$ years to the youngest occurrence of *Arvicola* at Vallone Inferno, Northern Sicily. The morphology of *A. amphibius* is imperfectly known like that of *Arvicola mosbachensis*, since only a very few samples are properly figured and described (Maul et al. 1998b), whereas almost all the other occurrences are simple quotations in faunal lists. The recently published finds of water vole from Cava Muracci in Latium (dated at MIS 3) are referred to *A. italicus* by Gatta et al. (1998) who, however, do not report information on SDQ of these specimens.

Extant *Arvicola* in Italy

Over the last thirty years *Arvicola amphibius* (= *terrestris*) was commonly thought to be Italy's only water vole. In his careful report on the Italian fauna, Toschi (1965) considered two valid subspecies: *A. terrestris italicus*, allegedly distributed in northern and central Italy, but also present in southern Switzerland as well as in the north-west of the Balkan Peninsula, and *A. terrestris musignani*, from central to southern Italy. The distributions of two subspecies were thought to partially overlap. According to Toschi (1965) the two subspecies were adapted to both fossorial and aquatic ways of life, similarly to the Alpine representatives and *A. sapidus*, respectively. Toschi (1965) reported the possible occurrence of a "more aquatic" population, geographically isolated on the Sila Mountains (Calabria). Eventually, Lapini and Paolucci (1994) suggest that in north-eastern Italy there are two subspecies, one, the fossorial *A. terrestris scherman*, distributed in mountainous areas (Carnic Alps) and the other, *A. terrestris italicus*, typical of the valley bottoms and of low altitude flatlands.

According to Castiglia et al. (2016), the current taxonomy includes two endemic taxa (Gippoliti 2012) considered as subspecies (Cagnin 2008): *A. amphibius italicus* Savi, 1839, restricted to central-northern Italy, and *A. amphibius musignani* DE Sélys Longchamps, 1839, thought to be distributed in central-southern Italy.

Castiglia et al. (2016) revised Wust-Saucy's (1998) and Taberlet's (1998) studies and claimed significant differences discriminating the two "Italian clades, one with north western distribution and the other with central southern distribution", from the "western European clade" and a large group indicated as "Euro-Asiatic clade". They proposed to use the name *A. italicus* for the Italian water voles and ignored *A. scherman* (Castiglia et al. 2016).

Wust-Saucy's (1998) and Taberlet's (1998) molecular-based phylogeny and dispersals changed significantly the taxonomy of European and Italian water voles. The taxonomic-phylogenetic revision revealed a more complex evolution of *Arvicola* than previously assumed, and yet many taxonomic aspects still remain unclear.

Quantitative comparisons of m1 from Italy and selected areas of Europe

Material and methods

Material

Two samples of *Mimomys savini* and 58 both fossil and extant samples of various *Arvicola* populations are considered in the analysis (Tab. 1). Several samples have been measured directly, while data from the literature have been used for others (Tab. 1, Text-fig. 4). The list of the locations and short descriptions of the examined sites are to be found in Appendix A.

Compared parameters

Three parameters of the lower first molar m1 have been used (Text-fig. 3): (1) the total length L, (2) the relative length of the Anteroconid complex (ACC), index A/L (= [Anteroconid length A / total length L] × 100) ratio, introduced by Van der Meulen (1973) for *Microtus* molars, (3) the SDQ (Enamel Differentiation Quotient = ratio of thickness of the posterior to the anterior enamel edges of all salient angles in m1) ratio, introduced by Heinrich (1978).

Comparisons based on indexes B/W and C/W of the occlusal surface (cf. Van der Meulen 1973) did not show significant patterns, and are thus not included in this report. L and A/L display evolutionary trends towards increasing values (Fejfar 1972, Van der Meulen 1973), whereas the opposite is observed with SDQ (Heinrich 1978). A list of basic statistics of each measurement or index for almost each locality, is given in Appendix B.
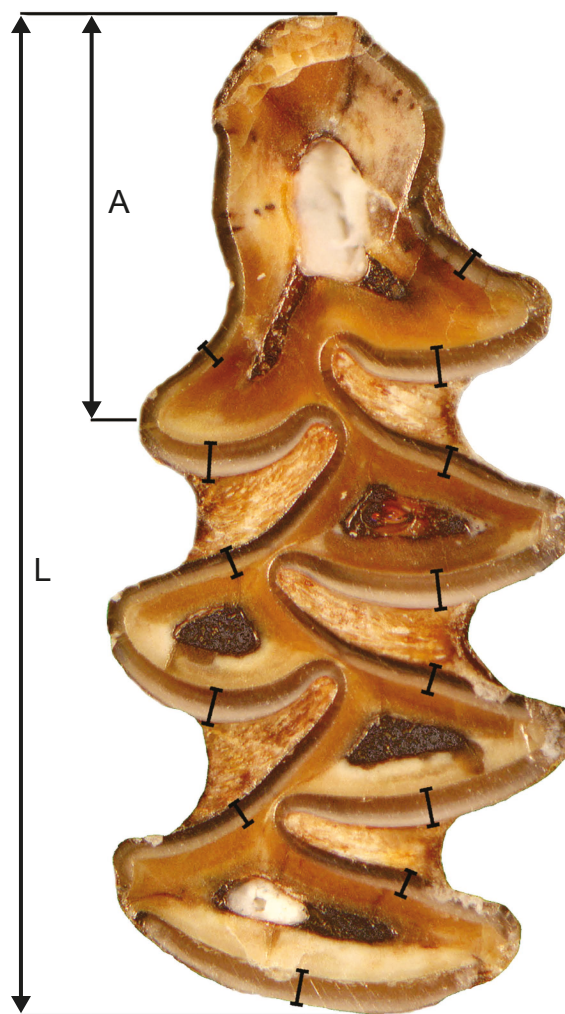
Text-fig. 3. Scheme of measurement of the first molar of *Mimomys* and *Arvicola* adopted in the present work. L – maximal length, A – anteroconid length.

Table 1. Compilation of L, A/L, and SDQ values for all examined samples. Reported values are those used in the plots. Symbols are used the same as in Text-fig. 4.

Taxon	Geographic Location	Locality / Site Stratigraphic horizon	L	SDQ	A/L	n	Age	Time slice	Source	Symbol
A. sapidus	Spain	Madrid	4.35	122.96	40.80	16	Rec	1	This paper	◯
A. amphibius	Austria	Graz. Rabwitz	3.86	99.28	42.07	10	Rec	1	This paper	
A. amphibius	Germany	Eisfeld	3.79	84.91		30	Rec	1	Frahnert 1991	
A. amphibius	Germany	Langen	3.69	89.96	43.42	7	Rec	1	Maul et al. 1998	
A. amphibius	Italy North	Delta Po	3.85	112.97	43.58	17	Rec	1	This paper	◯
A. amphibius	Italy North	Rovigo	3.83	116.47	43.76	6	Rec	1	This paper	
A. amphibius	Italy North	Ferrara	4.03	114.67	44.97	7	Rec	1	This paper	
A. amphibius	Italy South	Calabria	3.98	103.85	44.58	12	Rec	1	This paper	
A. amphibius	Italy N. East	Caverna degli Orsi-Holocene	3.82	107.22	41.98	8	MIS 1	2	This paper	
A. ex gr. amphibius	Italy N. West	Arma delle Manie 7-3	4.00	99.84		25	MIS 4	3	Desclaux et al. 2000	△
A. ex gr. amphibius	Italy N. West	Riparo Mochi 1	4.06	100.75		11	MIS 3	3	Desclaux et al. 2000	
A. ex gr. amphibius	Italy N. West	Riparo Mochi 2	3.96	98.20		29	MIS 3	3	Desclaux et al. 2000	
A. ex gr. amphibius	Italy South	Grotta di Castelcivita	4.02	108.12	43.10	26	MIS 3	3	Maul et al. 1998	
A. ex gr. amphibius	Italy South	Grotta della Serratura	4.11	113.58	42.60	28	MIS 2	3	This paper	
A. ex gr. amphibius	Italy South	Grotta del Romito	4.05	110.06	43.10	19	MIS 2	3	This paper	
A. ex gr. amphibius	Italy South	Scario Grotta Grande - sector A	4.08	116.61	42.64	5	MIS 5	4	Maul et al. 1998	
A. ex gr. amphibius	Italy Central	Grotta di Cucigliana	4.14	110.99	41.11	4	MIS 5	4	This paper	
A. ex gr. amphibius	Italy South	Scario Grotta Grande - sector SG	4.07	121.39	43.44	3	MIS 6	5	Maul et al. 1998	
A. ex gr. amphibius	Ialy Central	Upper Valdarno Campitello	3.95	114.17	42.00	2	MIS 6?	5	This paper	
A. mosbachensis	Italy N. East	Riparo di Visogliano ext. breccia	3.39	123.42	39.14	13	M-Pleist	6	This paper	
A. mosbachensis	Italy N. East	Riparo di Visogliano A L. levels	3.47	122.77	39.19	2	M-Pleist	6	This paper	
A. mosbachensis	Italy N. East	Riparo di Visogliano A U. level 2	3.43	122.89	40.30	18	M-Pleist	6	This paper	
A. mosbachensis	Italy N. East	Riparo di Visogliano A U. level 1	3.38	116.43	38.51	17	M-Pleist	6	This paper	
A. mosbachensis	Italy South	Isernia la Pineta	3.48	134.08	40.66	8	M-Pleist	6	Maul et al. 1998	
A. ex gr. amphibius	France East	Baume Gigny 6	4.07	78.40		30	MIS 2	3	Desclaux et al. 2000	△
A. ex gr. amphibius	France East	Baume Gigny 10	3.89	87.50		34	MIS 3	3	Desclaux et al. 2000	
A. ex gr. amphibius	France S. East	Baume Moula Guercy 8-4	3.90	81.00		5	MIS 4	3	Desclaux et al. 2000	
A. ex gr. amphibius	France S. West	Grotte de l'Eglise II	4.02	83.59		31	MIS 4?	3	Desclaux et al. 2000	
A. ex gr. amphibius	France S. West	Grotte-abri Suard	4.00	91.59		32	Würmian-early	3	Desclaux et al. 2000	
A. ex gr. amphibius	France East	Baume Gigny-19a	3.76	96.40		18	MIS 5a	4	Desclaux et al. 2000	
A. ex gr. amphibius	France S. West	Grotte d'Artenac-c10	3.73	99.96		21	MIS 5	4	Desclaux et al. 2000	
A. ex gr. amphibius	France S. West	Grotte d'Artenac-c8	3.73	93.85		14	MIS 5d-a	4	Desclaux et al. 2000	△
A. ex gr. amphibius	France East	Baume Gigny 20-19c	3.74	93.68		41	MIS 5d-c	4	Desclaux et al. 2000	
A. ex gr. amphibius	France S. East	Pié Lombard	3.71	101.02		4	MIS 5d-c	4	Desclaux et al. 2000	
A. ex gr. amphibius	France S. East	Baume Moula Guercy 15-14	3.83	100.53		15	MIS 5e	4	Desclaux et al. 2000	
A. ex gr. amphibius	France S. West	Abri Vaufrey-8	3.87	94.19		31	Riss-late	5	Desclaux et al. 2000	
A. ex gr. amphibius	France S. East	Baume Moula Guercy 19-18	3.82	87.41		31	Riss-late	5	Desclaux et al. 2000	
A. ex gr. amphibius	France East	Baume Gigny 22-19	4.21	94.00		65	Riss	5	Desclaux et al. 2000	
A. ex gr. amphibius	France S. East	Grotte du Lazaret	3.85	107.90		47	Riss	5	Desclaux et al. 2000	
Arvicola sp.	France S. West	Abri Gaudry	3.89	113.90		64	MIS 8?	5	Desclaux et al. 2000	
A. amphibius	Germany	Pisede	4.05	80.17		144	Holocene	2	Heinrich and Maul 1983	△
A. ex gr. amphibius	Germany	Euerwanger Bühl	4.09	83.03		27	Weichselian	3	Heinrich 1982	
A. ex gr. amphibius	Germany	Kemathenhöhle	4.05	89.23		11	Weichselian	3	Heinrich 1982	
A. ex gr. amphibius	Germany	Krockstein (Rübeland 1)	4.04	89.08		40	Weichselian	3	Heinrich 1982	
A. ex gr. amphibius	Germany	Burgtonna 2	3.76	99.65		41	Würmian-early	3	Heinrich 1982	
A. ex gr. amphibius	Germany	Burgtonna Cm	3.82	78.91		11	Eemian	4	This paper	
A. ex gr. amphibius	Germany	Burgtonna Hy	3.88	103.66	41.64	10	Eemian	4	This paper	
A. ex gr. amphibius	Germany	Parkhöhle (Weimar)	3.90	109.62		3	Eemian	4	Heinrich 1982	△
A. ex gr. amphibius	Germany	Stuttgart-Untertürkheim	3.81	101.19		37	Eemian	4	Heinrich 1987	
A. ex gr. amphibius	Germany	Taubach	3.95	105.15		11	Eemian	4	Heinrich 1982	
A. ex gr. amphibius	Germany	Ehringsdorf	3.70	112.30		8	Saalian-early	5	Heinrich 1982	
A. ex gr. amphibius	Germany	Plaidter-Hummerich	3.80	82.17		5	Saalian	5	Van Kolfschoten 1990	
A. mosbachensis	Germany	Mosbach 2	3.23	133.34	39.93	44	M-Pleist	6	Maul et al. 2000	
A. mosbachensis	Germany	Petersbuch 1	3.65	126.16		10	M-Pleist	6	Maul et al. 2000	
A. mosbachensis	Germany	Bilzingsleben 2	3.58	132.10		9	M-Pleist	6	Maul et al. 2000	
A. mosbachensis	Germany	Miesenheim 1	3.48	140.62		9	M-Pleist	6	Maul et al. 2000	
M. savini	Germany	Voigtstedt	3.53	139.09		108	M-Pleist	7	Maul et al. 2014	
M. savini	Germany	Untermassfeld	3.14	153.20		9	E-Pleist	8	Maul 2001	
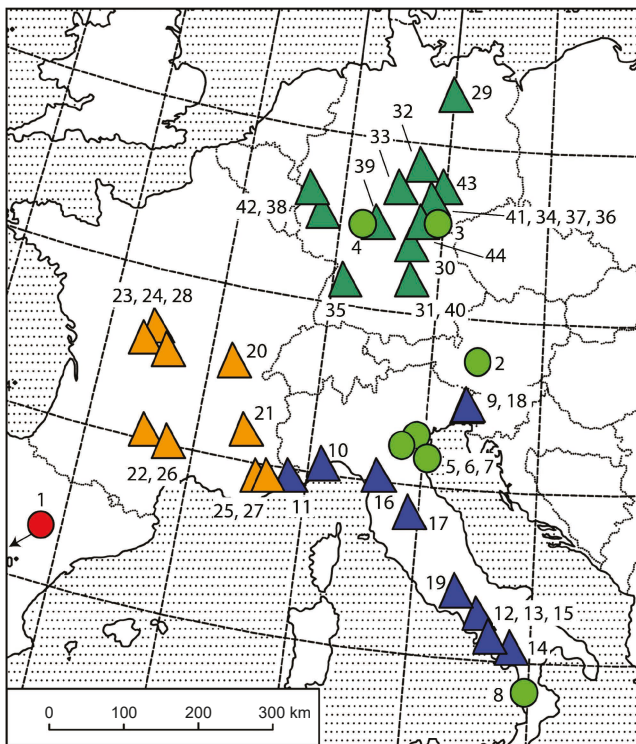
Text-fig. 4. Location Map of the examined water vole localities. From Masini et al. (2007), modified. 1: Madrid, surroundings, 2: Graz, 3: Eisfeld, 4: Langen, 5: Delta Po, 6: Rovigo, 7: Ferrara, 8: Calabria, 9: Caverna degli Orsi, 10: Arma delle Manie, 11: Riparo Mochi, 12: Grotta di Castelcivita, 13: Grotta della Serratura, 14: Grotta del Romito, 15: Scario Grotta Grande, 16: Grotta di Cucigliana, 17: Upper Valdarno Campitello, 18: Riparo di Visogliano, 19: Isernia La Pineta, 20: Baume Gigny, 21: Baume Moula Guercy, 22: Grotte de L'Eglise, 23: Grotte-Abri Suard, 24: Grotte d'Artenac, 25: Pié Lombard, 26: Abri Vaufrey, 27: Grotte du Lazaret, 28: Abri Gaudry, 29: Pisede, 30: Euerwanger Bühl, 31: Kemathenhöhle, 32: Krockstein (Rübeland 1), 33: Burgtonna, 34: Parkhöhle (Weimar), 35: Stuttgart-Untertürkheim, 36: Taubach, 37: Ehringsdorf, 38: Plaidter-Hummerich, 39: Mosbach, 40: Petersbuch 1, 41: Bilzingsleben, 42: Miesenheim 1, 43: Voigtstedt, 44: Untermassfeld. See Table 1 for symbol explanations.

Chronological frame

The sites under consideration are dated in different ways (either radiometrically, or climate-stratigraphically and/or biochronologically), and are thus not "homogeneous". For this reason, they have been grouped in eight "time slices" (see Tab. 1). The number and duration of these time slices has been chosen in a way to maximise the number of localities within given time slices and to obtain reasonably reliable stratigraphic resolution. The time slices are the following:

(1) Recent

(2) Holocene (absolute age: 10 to 0 ka)

(3) Würmian/Weichselian (pro parte): MIS 4–2 including the Late Glacial (absolute age: ca. 75 to 10 ka)

(4) Eemian + early Würmian/Weichselian: penultimate interglacial and the following climatic oscillations that precede the onset of first cold phase (MIS 4) of the last glaciation: MIS 5e (Eemian), MIS 5d, b (cold oscillations) and 5c, a (warm oscillations) (absolute age: ca. 125–75 ka)

(5) Pre-Eemian: Rissian/Saalian Glaciation; MIS 6, MIS 7 (absolute age: ca. 250 to 125 ka), Middle Pleistocene

(6) Time of occurrence of older *Arvicola* samples (absolute age: ca. 600 to 250 ka)

(7) Time of occurrence of younger *Mimomys savini* faunas (absolute age: ca. 800 to 600 ka)

(8) Time of occurrence of older *Mimomys savini* faunas (absolute age: ca. 1 Ma to 800 ka).

Biogeographical frame

Remarks on the biogeographical situation

The Italian territory is not homogeneous biogeographically. For our purpose, at least two areas should be distinguished.

During the Pleistocene and Holocene north-eastern Italy can be separated biogeographically and climatically from the Tyrrhenian regions; also a north-south clinal variation occurs (Sala 1990, 2003, Sala and Marchetti 2004, 2006, Sala and Masini 2007). Particularly, the faunal composition of the Po Valley, north-eastern regions of Veneto Friuli and down south along the Adriatic side of the peninsula, had (and partly still have) affinities with the Balkan province. During cold-arid, glacial climatic phases, "steppe" taxa, like pikas, hamsters, the voles *Microtus gregalis* and *M. oeconomus* spread into this north-eastern part of the country (e.g., Sala 1990, 2003, Sala and Marchetti 2004). For example, a vole that was distributed in both the Balkan province and north-eastern Italy, is the Balkan snow vole *Dinaromys*, a genus today endemic to the Balkans. It was present also in north-east Italy since the Late Pliocene and very widespread at the base of the Alpine Arch at least till the early part of the Late Pleistocene.

A similar situation, albeit less commonly reported, existed between the western, Tyrrhenian side of the peninsula and southern France. One of the most notable examples is that of members of the subgenus *Microtus* (*Iberomys*), a vole typical of Spain and southern France, which spread from the north western border throughout Italy during the Middle Pleistocene (López-García et al. 2015).

The history of past and extant specimens of Italian *Arvicola* should reasonably be expected to be influenced by exchanges between populations from neighbouring bioprovinces, but also to show a tendency to undergo endemic evolution.

To highlight the peculiarities of Italian water vole samples, morphometric comparisons were made with their counterparts distributed in Germany, which is situated north of the Alps, is included in the continental biogeographical zone, and experienced directly the effects of glacial ice sheets that extended both from the north (Scandinavian glaciation) and the south (Alpine glaciation). Other specimens included in the analysis come from south-east France and Spain, which are areas of the Mediterranean zone, and from central-eastern France, which is also part of the continental zone.

Results of the quantitative comparison

Length, A/L and SDQ versus time slices

The chronological distribution of L, A/L, and SDQ values reveals the evolutionary patterns and rates of morphologic change of the vole teeth considered in this
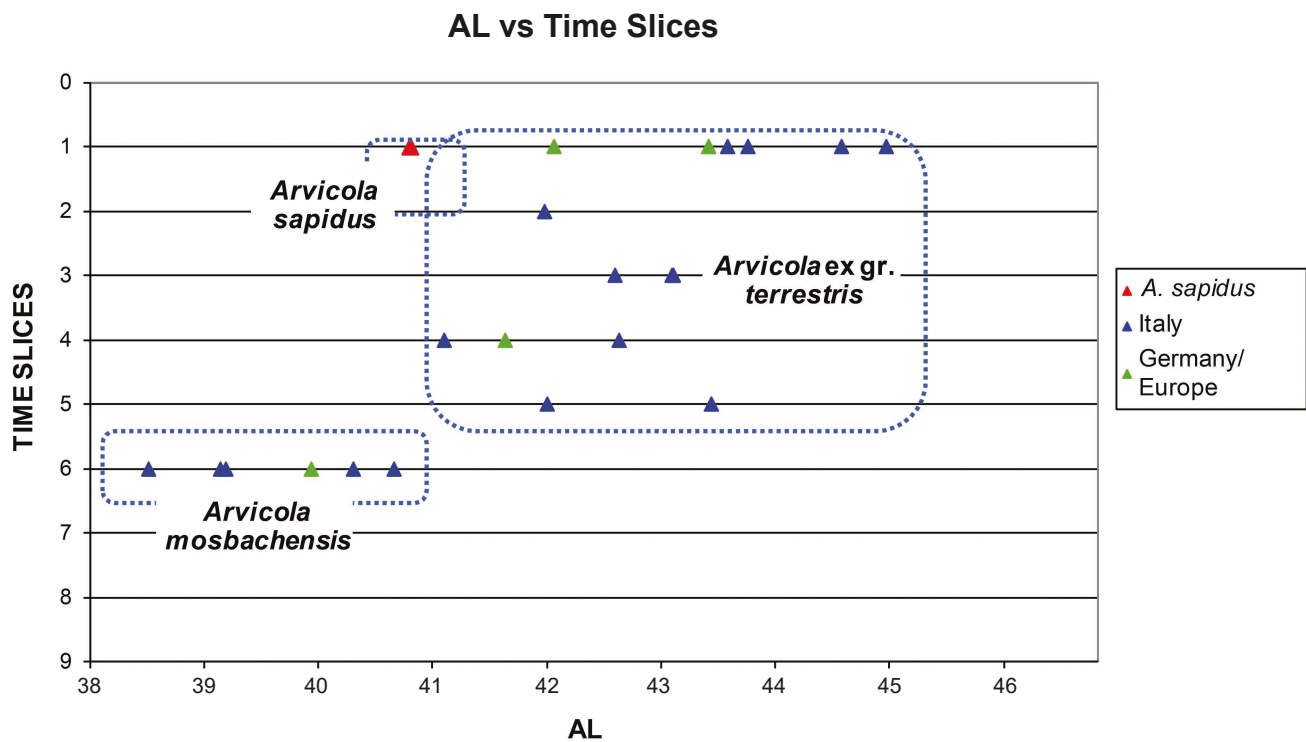
AL vs Time Slices

Text-fig. 5. Diagram showing the variation of Anteroconid length (index A/L) vs Time slices in m1s of *M. savini* and *Arvicola* from different geographical provenances.

study (Text-figs 5–7). These values exhibit a certain degree of correlation and strong directional and correlated increment from the most primitive taxon (*Mimomys savini*) to the primitive *Arvicola* (*A. mosbachensis*) and then to the fossil and recent samples of the *A. amphibius* group (which likely includes also representatives of *A. italicus*). However, age and geographical differences are visible.

M. savini displays the smallest values of L and the greatest of SDQ, with minimum overlap with *A. mosbachensis*. *A. mosbachensis* and the *A. amphibius* group are clearly separated in the development of the anteroconid complex (A/L), whereas there is an overlap in SDQ between *A. mosbachensis* and the minimum values of *A. amphibius*. The size of *A. mosbachensis* is relatively small and overlaps
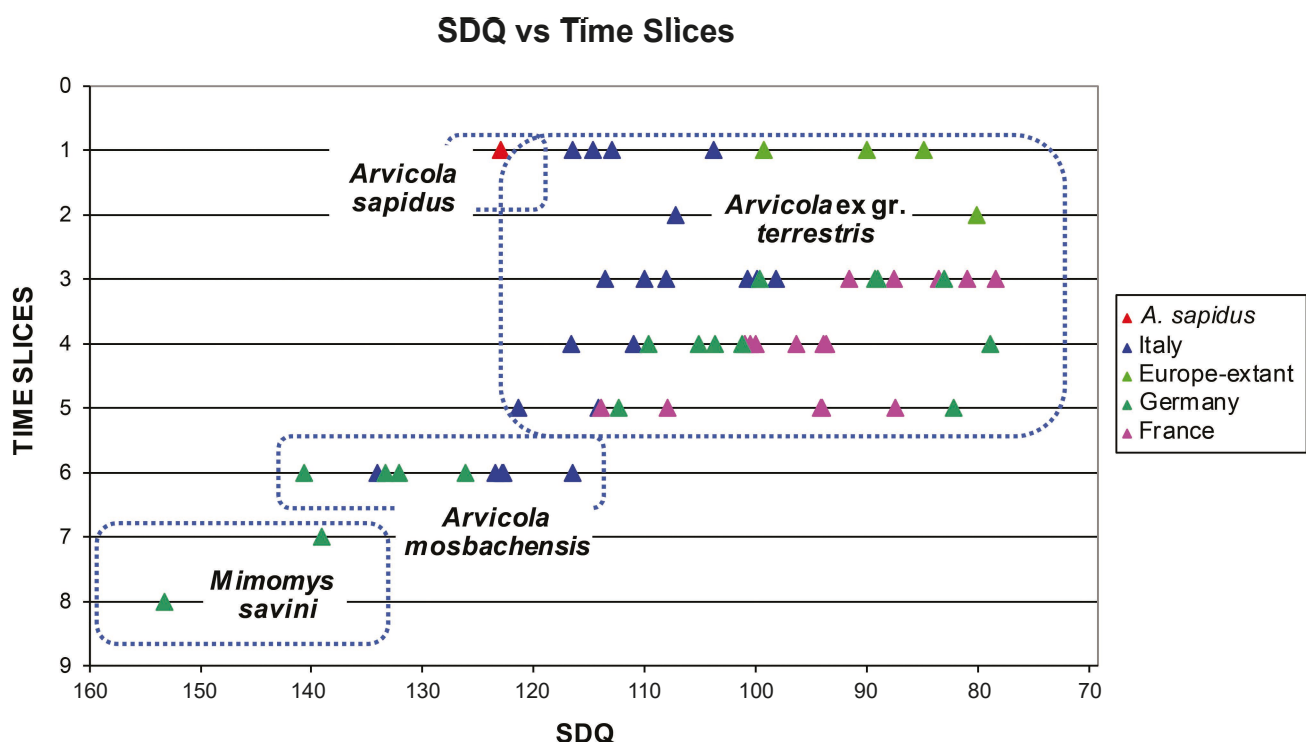
SDQ vs Time Slices

Text-fig. 6. Diagram showing the variation of the enamel pattern (index SDQ) vs Time slices in m1s of *M. savini* and *Arvicola* from different geographical provenances.
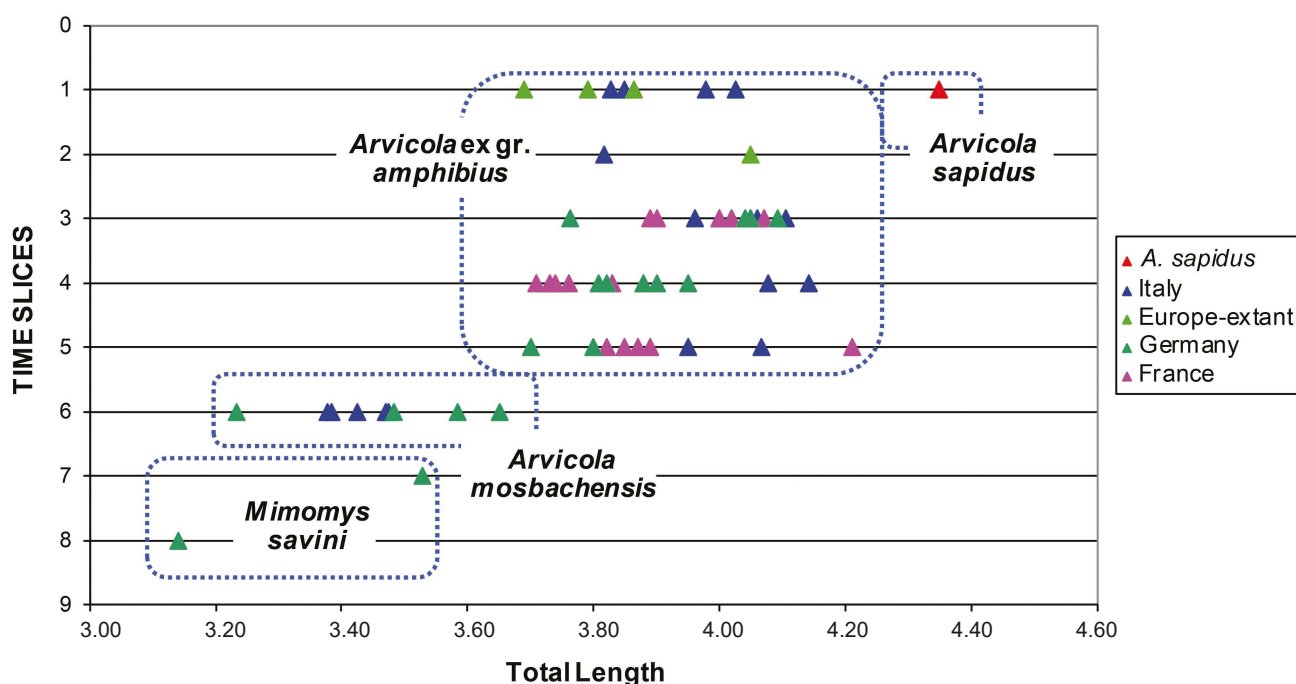
Text-fig. 7. Diagram showing the variation of the size (L) vs Time slices in m1s of *M. savini* and *Arvicola* from different geographical provenances.

with the medium- and large-sized specimens of *M. savini* samples. Notable is that the A/L values of the Spanish *A. sapidus* are very close to the minimum values of the *A. amphibius* group; *A. sapidus* also has large SDQ values, although exhibiting the largest size.

A/L vs SDQ (0.6 Ma to Recent)

The A/L vs SDQ diagram (Text-fig. 8) confirms the clear separation between the stratigraphically older *Arvicola mosbachensis* and the *A. amphibius* group. The latter are larger sized, have more elongated ACC and lower SDQ values. Therefore, the enamel wall in the teeth of the *A. amphibius* group tends to be thinner on the posterior edges than anterior ones. Extant *A. sapidus* maintains SDQ and A/L values typical of primitive members compared to the *A. amphibius* group.

The SDQ vs L plot diagram (Text-fig. 9) confirms the separation of *A. mosbachensis* from the *A. amphibius* group, and shows the clear separation of *A. sapidus* from both species. The *A. amphibius* group displays rather scattered, overlapping areas.

All the plots show a clear separation between *A. ßmosbachensis* and the *A. amphibius* group (Text-figs 10–13). The former is smaller-sized (mean values of m1 Length range from 3.23 to 3.65 mm in Mosbach 2 and Petersbuch 1, respectively), has shorter ACC (mean values for the considered populations range from 38.53 to 40.66 mm) and higher (more primitive) SDQ values than the latter (Text-figs 5–7, Tab. 1) (values range from 140.6 in Miesenheim 1, to 116.5 in the Upper Levels of Visogliano A). *M. savini* from Voigtstedt (an advanced population, close in age to the oldest *A. mosbachensis*) has size and SDQ values that fall in

the field of variation of *A. mosbachensis*, which confirms the phyletic relationship between the two taxa.

Another interesting result is that obtained with the recent population of *A. sapidus*. Also, this water vole plots away from *A. mosbachensis* and the *A. amphibius* group for its much larger size (length of m1 greater than 4.3 mm in the considered population), moderately developed ACC (A/L = 40.8) and primitive enamel differentiation (SDQ value of 122.10). It is evident that the species evolved independently both phylogeographically and morphologically.

The *Arvicola amphibius* group exhibits the greatest degree of variation. This reflects the fact that the group actually includes the majority of the fossil and non-fossil specimens used for this study and also that the non-fossil teeth come from very different geographical areas (Italy, France, Austria, and Germany).

The A/L vs SDQ bivariate plot is based on a limited number of observations. The A/L parameter is available only for *A. mosbachensis*, *A. sapidus* and for fossil and recent specimens of the *A. amphibius* group from the Italian Peninsula and from a small number of European populations (see also Appendix B).

In Text-fig. 8 past and living populations of the *A. amphibius* group appear to be characterised by elongated ACC, and by relatively low values of the enamel quotient, in line with the general evolutionary tendency of genus *Arvicola* outlined above. In this limited subset of data, the Italian specimens, especially the fossil ones from the central southern peninsula, are characterised by a higher enamel quotient (i.e., more primitive enamel pattern) than the recent European populations used for comparison. Recent Italian specimens also show a tendency to have slightly longer ACC.

All Samples – 0.6 Ma to Recent
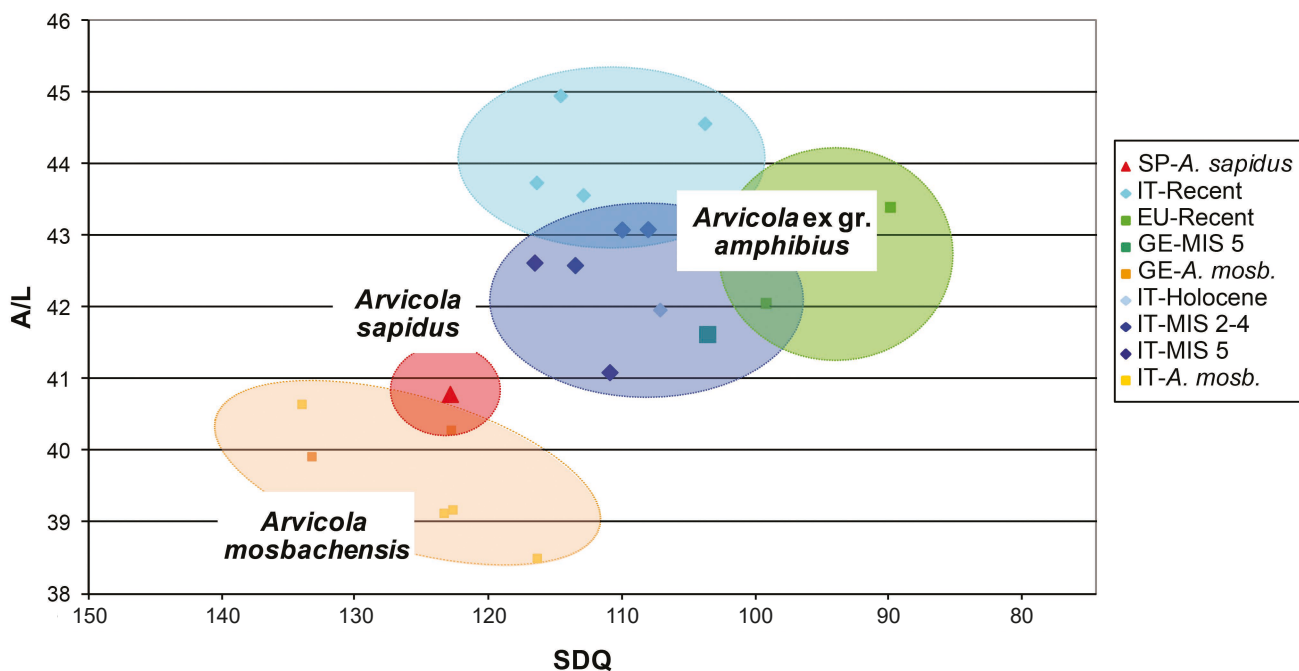
Text-fig. 8. Scatter diagram of SDQ vs A/L *M. savini* and *Arvicola* from different geographical provenances and ages.

SDQ vs L (0.6 Ma to Recent)

The diagram of the quotient of enamel thickness versus the length of m1 is particularly interesting. It includes the greatest number of observations and permits an exhaustive evaluation of the inter-population variation (Text-fig. 9).

The diagram contains a considerable amount of information (both geographical and stratigraphical). It has therefore been analysed step-wise, starting from the recent population and then progressively passing to older specimens (Würmian/Weichselian – Eemian – Rissian/Saalian).

All Samples – 0.6 Ma to Recent
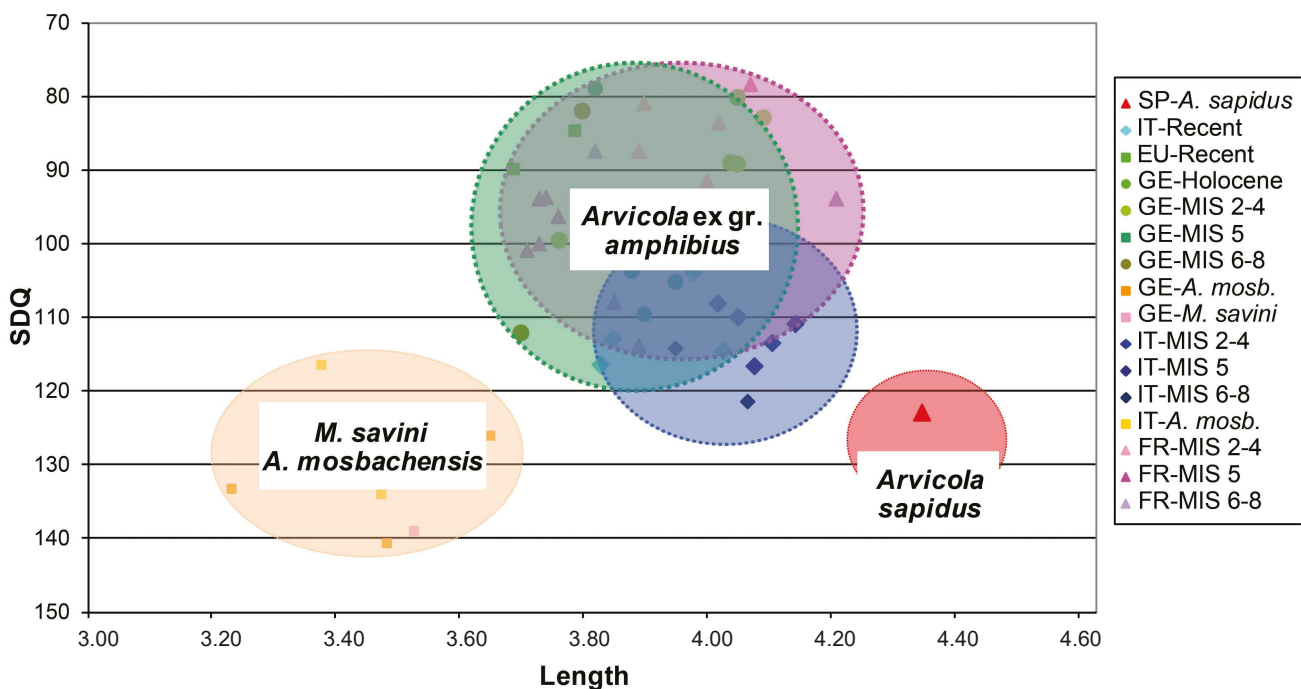
Text-fig. 9. Scatter diagram of m1 length vs SDQ for *M. savini* and *Arvicola* from different geographical provenances and ages.

Recent – Holocene
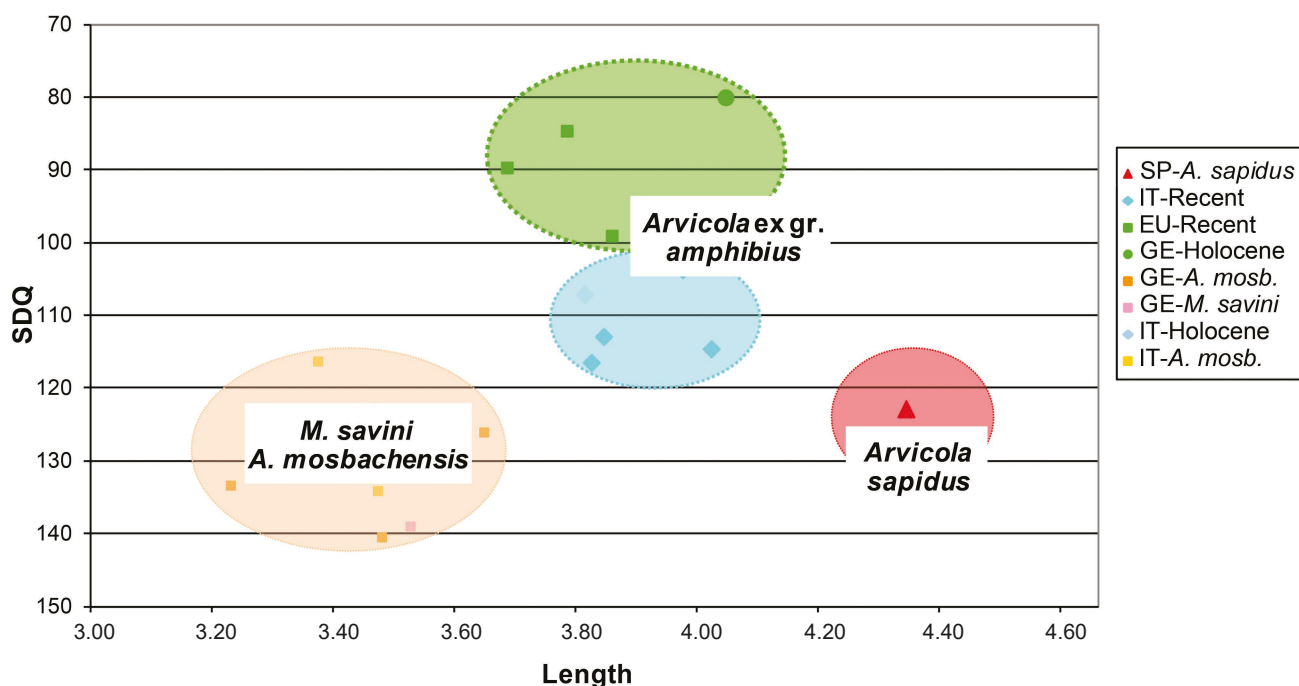
Text-fig. 10. Scatter diagram of m1 length vs SDQ for Extant (time slice 1 and 2) *Arvicola* samples of different geographical provenances compared with *M. savini-A. mosbachensis*. Abbreviations: EU – Europe, GE – Germany, IT – Italy, SP – Spain.

Recent and Holocene specimens

As already noted, the recent population of Italy forms a "cloud" characterised with slightly higher SDQ values than those of the western and central European group of *A. amphibius* (Text-fig. 10). Most of the teeth gave negative to undifferentiated values ($120 \geq SDQ \geq 100$). In contrast, the group of European populations provided lower SDQ values ($100 \geq SDQ \geq 80$), which indicates that they possess a more advanced enamel pattern. The molars of the two groups do not differ markedly in size.

Würmian/Weichselian specimens

Fossil molars of Würmian/Weichselian age come from Italy, Germany and France (data from Heinrich 1982, 1990a, Van Kolfschoten 1990, Desclaux et al. 2000). The French and the German Würmian/Weichselian sample clusters overlap; in contrast, the Italian group is more isolated, with only partial overlap with previous two (Text-fig. 11). The peninsular and the north-westernmost Italian (Ligurian) molars are large-sized ($3.90 \leq L \leq 4.15$) and have negative or undifferentiated enamel pattern ($113 > SDQ > 98$). A sort of morpho-geographical cline can be observed from the central-southern peninsula to the Liguria region; the latter specimens have more advanced enamel quotient ($100 > SDQ > 98$ vs $113.5 > SDQ > 108$, respectively). The central-southern Italian Würmian/Weichselian molars have SDQ values comparable to those of recent specimens, whereas the Ligurian specimens have more derived SDQ values, close or lower than those with undifferentiated pattern.

The French and German Würmian/Weichselian groups include molars with similar enamel characteristics: $99.96 \geq$ SDQ ≥ 78.4 and $101.2 \geq SDQ \geq 83.1$ for French and German samples respectively. Also, the sizes are comparable, although an individual sample from Germany is significantly smaller (Burgtonna 2). There is partial overlap between the Würmian/Weichselian fossils from Germany and France and the composite group of recent "European" taxa (i.e., recent populations from Germany and Austria), but the former are larger sized and have somewhat more advanced enamel pattern.

Eemian and early Würmian/Weichselian specimens

This plot (Text-fig. 12) includes *Arvicola* from Eemian levels (MIS 5e) and from the other MIS 5 sub-stages that record the effects of the cool-warm fluctuations that preceded the first stadial of the MIS 4 glacial episode.

The *Arvicola* from the Italian localities (Scario A, Campania and Cucigliana, Tuscany) and the southern Italian populations of the last glacial cycle cluster close to one another and share similar size and SDQ values. The morphological similarity may reflect substantial continuity of the Eemian and Würmian/Weichselian *Arvicola* populations of the peninsula.

In contrast, the Eemian molars from Germany and France differ from their Würmian/Weichselian counterparts, by having less advanced enamel pattern and smaller size. The clusters overlap, but the French specimens have somewhat smaller SDQ values and size. The two groups, however, tend to form a rather homogenous cluster characterised at its extremes by SDQ and L values ($109.6 \geq SDQ \geq 93.7$ and $3.73 \leq L \leq 3.95$, respectively), clearly distinct from those of the Italian Peninsular specimens. A single sample from
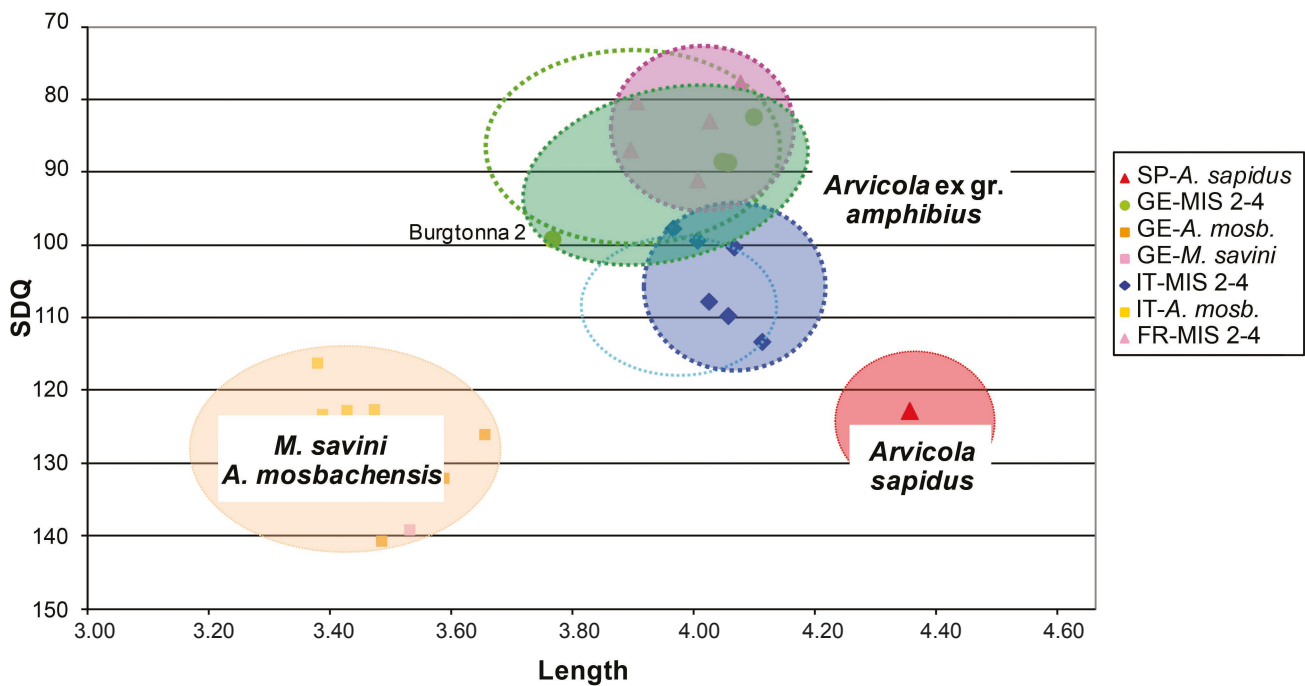
Text-fig. 11. Scatter diagram of m1 length vs SDQ for Würmian/Weichselian (time slice 3) *Arvicola* samples from different geographical provenances compared with *M. savini-A. mosbachensis* and extant *Arvicola sapidus*. Empty dotted ovals indicate the range of extant *Arvicola* ex gr. *amphibius* samples from Italy (cyan) and from the other European locations (green) Abbreviations: FR – France, GE – Germany, IT – Italy, SP – Spain.

Germany, (Burgtonna/Cm level), is distinctly separated from the others because of its very advanced enamel pattern (SDQ = 78.9).

Pre-Eemian (Saalian/Rissian sensu lato) specimens

The ages of these specimens are more varied than the previous ones. This may be responsible of the greater morphological variation observable in the graph (Text-fig. 13).

The two pre-Eemian molars from southern (Scario SG pit) and central (Campitello) Italy partially overlap (or are close to) the lower limits of the range of variability of the German and French water voles. They plot very close to the younger (Eemian and Würmian) Italian specimens. The result reinforces the hypothesis of continuity of the *Arvicola* lineage in this sub-region.

Nonetheless, the German and French clusters have rather heterogeneous size and enamel pattern. In particular, the two groups include molars with rather primitive and very advanced enamel quotient (113.9 ≥ SDQ ≥ 107.9 and 94.2 ≥ SDQ ≥ 82.2, respectively), whereas the size ranges from 3.7 to 4.21 mm.

Interpretation of the morpho-stratigraphical pattern

Starting from the recent specimens, the results show that the so called *Arvicola italicus* lineage is morphologically fairly distinct from other European representatives (*A. amphibius* lineage). A similar situation is observed during the Würmian/Weichselian time slice, but with interesting differences. Compared to molars of living representatives,

those of Würmian/Weichselian *Arvicola* are in general larger-sized and the specimens from Germany and France apparently tend to have a somewhat more advanced enamel pattern. In contrast, the Würmian/Weichselian teeth from southern Italy show the same range of enamel variation as the molars of living representatives. The Ligurian molars stand out by having more advanced SDQ values, close or overlapping those of the French and German specimens.

The situation is very different in the Eemian. The European *A. amphibius* water voles of this time period were smaller, on average, and had more primitive enamel pattern than the Würmian/Weichselian members. Representatives of the Italian Peninsula were already very large sized and had proportionally less advanced enamel differentiation. This data indicates that perhaps at least the *A. italicus* already existed during the Eemian warm period as a separated lineage, independent from that of *A. amphibius*. The latter group contains an outlier with rather advanced enamel quotient, represented by the water vole from the Burgtonna/ Cm level (Germany).

During the pre-Eemian Rissian/Saalian (s. l.) time slice, French and German *Arvicola* specimens show rather varied sizes and enamel quotients. The outlying value of the Eemian vole from Burgtonna/Cm falls in the field of the highest values of the "Rissian/Saalian" European water voles. Despite its stratigraphic age, the Burgtonna/ Cm specimen could actually be a sort of holdover of the advanced "Rissian/Saalian" *amphibius*-like *Arvicola* in this central northern region of Europe. The two specimens from the Italian Peninsula (Campitello and Scario SG), on
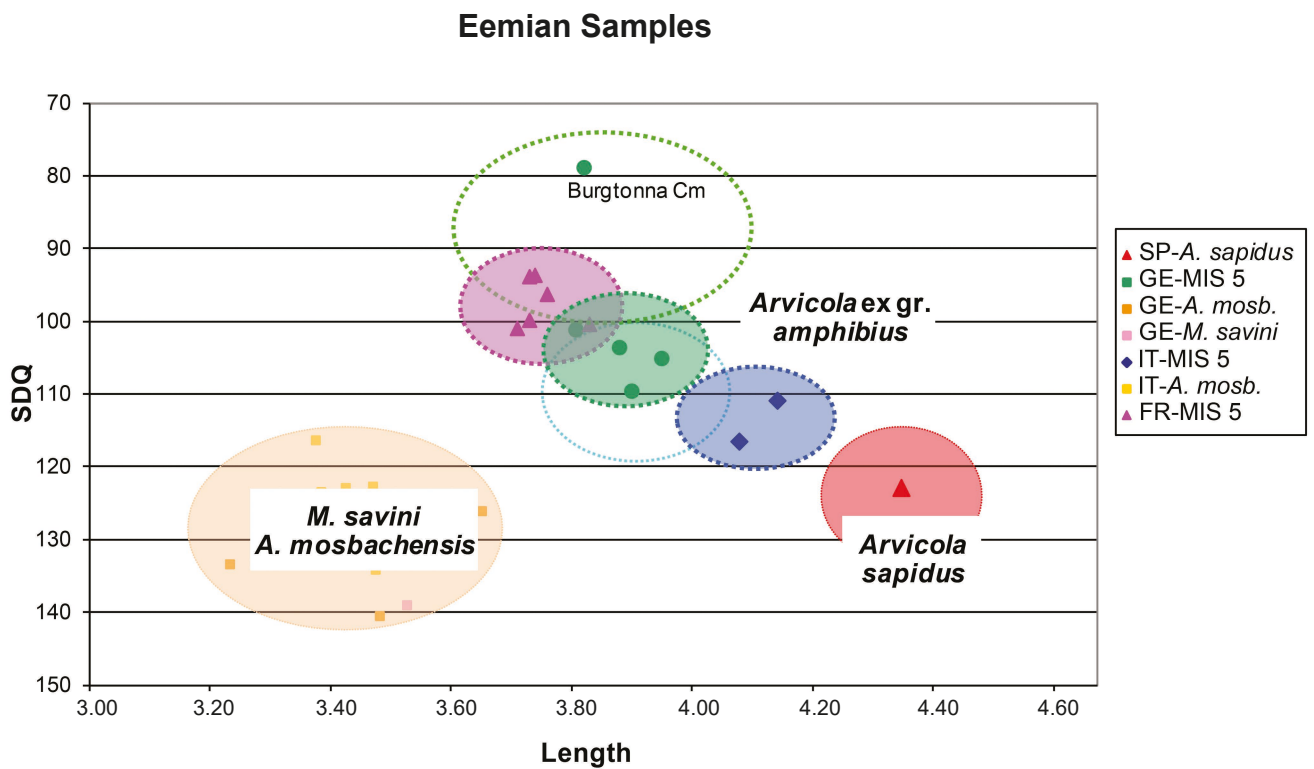
Text-fig. 12. Scatter diagram of m1 length vs SDQ for Eemian (time slice 4) *Arvicola* samples from different geographical provenances compared with *M. savini-A. mosbachensis* and *Arvicola sapidus*. Empty dotted ovals indicate the range of extant *Arvicola* ex gr. *amphibius* samples from Italy (cyan) and from the other European locations (green) Abbreviations: FR – France, GE – Germany, IT – Italy, SP – Spain.
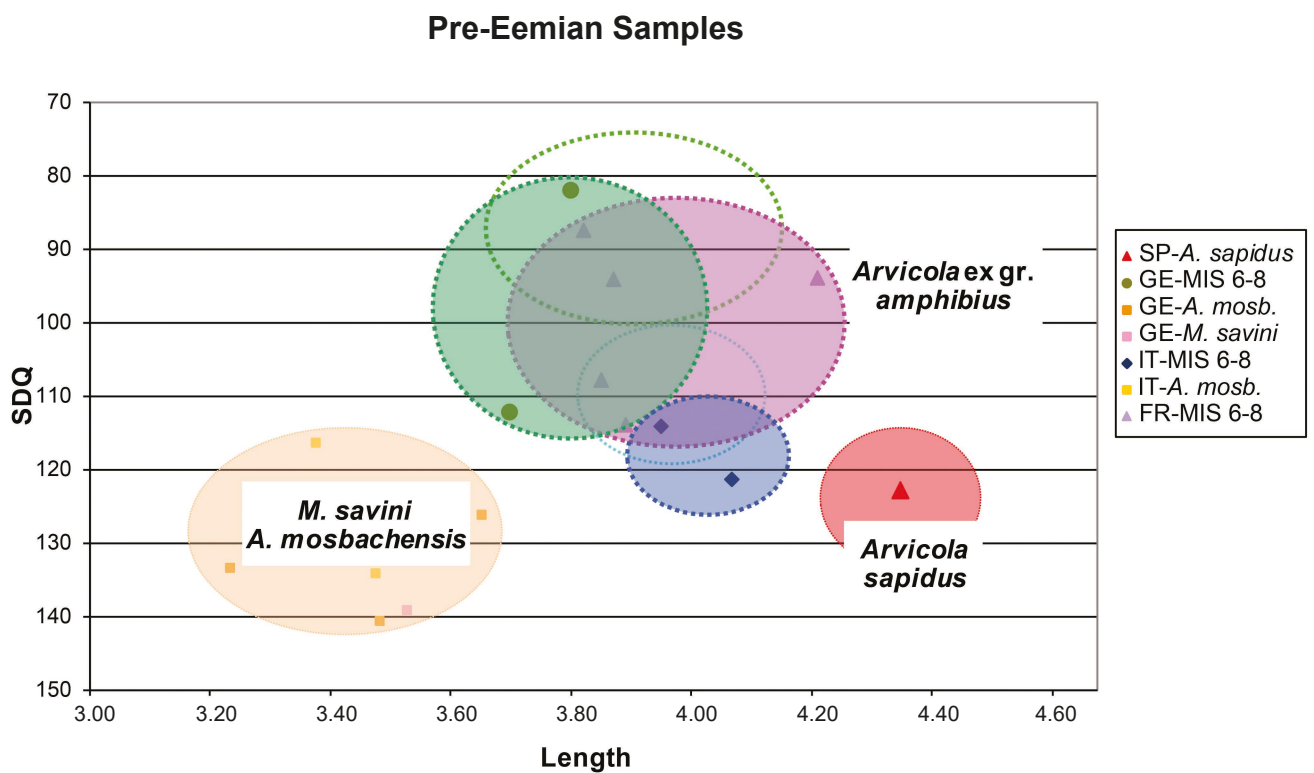
Text-fig. 13. Scatter diagram of m1 length vs SDQ for pre-Eemian (time slice 5) *Arvicola* samples from different geographical provenances compared with *M. savini-A. mosbachensis* and *Arvicola sapidus*. Empty dotted ovals indicate the range of extant *Arvicola* ex gr. *amphibius* samples from Italy (cyan) and from the other European locations (green) Abbreviations: FR – France, GE – Germany, IT – Italy, SP – Spain.

the other hand, plot close to the range of variation of the "Eemian" Italian samples and tend to overlap the fields of the less advanced European voles. This morphological stability suggests phyletic continuity of the *A. italicus* lineage. Although less clear than that of the voles analysed so far, the status of the Rissian/Saalian *Arvicola* suggests that during the penultimate glacial cycle, some "proto-*amphibius*" *Arvicola* population had already acquired an advanced enamel pattern analogous to that of the Würmian *A. amphibius*; the less advanced populations are in fact of older age (e.g., Ehringsdorf in Germany and Abri Gaudry in France). Alternatively, the advanced populations can be assumed to result from dispersal from North Eastern regions, where *Arvicola* had already achieved an advanced morphology.

Discussion

The time of *Mimomys savini-Arvicola mosbachensis* transition in Italy

The transition from rooted (*M. savini*) to rootless voles (*Arvicola*) is the so-called *Mimomys*/*Arvicola* boundary (Koenigswald and Van Kolfschoten 1996). The transition occurs in three stages: (1) Late populations of *Mimomys savini*, characterised by molars with clearly separated roots and with rootless teeth possessed only by juvenile individuals. Examples come from Voigtstedt, Süßenborn (both Germany) and West Runton (UK) (Kretzoi 1965, Fejfar 1969, Maul and Parfitt 2010). (2) The appearance of incipient roots (clear closure of the crown base) among predominantly rootless molars marks the advent of an ancient *Arvicola* (or transitional) population. However, distinctly separated roots have never been observed in transitional populations, such as Isernia, Mosbach, and Mauer (Koenigswald and Van Kolfschoten 1996, Maul et al. 2000). (3) Populations with exclusively rootless molars, undoubtedly typical of *Arvicola*.

The Italian site of Isernia was the first site where a very primitive *Arvicola* (stage 2) could be directly dated, yielding an Ar/Ar age of ca. 605 ka (Coltorti et al. 2005). Later on, also the German site of Mauer was palaeontologically dated ca. 600 ka (Wagner et al. 2011). Both sites therefore correlate with the MIS 15 interglacial.

Is this transition synchronous throughout Europe? A recent careful compilation by Mahmoudi et al. (2019) and Maul (2019) indicates that the transition from *Mimomys savini* to *Arvicola* occurred roughly at the same time in most places of Europe (except parts of Spain where *Arvicola jacobaeus* was distributed); dated finds of ancient *Arvicola* are reported from MIS 13. An unresolved issue is whether this is evidence of synchronous evolution (multiregional anagenetic process) or of a single evolutionary event followed by subsequent multiple immigrations.

General and punctual inferences

The pattern of morphological variation through time, seen so far in the molars analysed for this study, enables interesting inferences to the evolution of European water voles. With the large number of observations considered in this study, we can exclude that the enamel pattern of *Arvicola* evolved synchronously along a single, linear trend over the entire geographical range of the genus. Results show that there were at least two lineages of *Arvicola* in the European regions considered for this investigation: one in the Italian Peninsula and at least another one spread throughout Central and Western Europe.

It was Van Kolfschoten (1992), who first assumed that the evolutionary pattern of *Arvicola* is more intricate than it at first seemed, and that older populations of *Arvicola* (e.g., those of the time of the Rissian/Saalian glaciation, the ones from Ariendorf 2, Plaidter Humerich 1) have already acquired a more advanced enamel pattern than the Eemian ones. He explained this apparent evolutionary "reversal" with the re-immigration of more "primitive" *Arvicola* populations during warmer interglacials from their southern refuge areas. An unresolved issue is if and/or where, the evolved population survived during interglacials. The results of the present study indicate the presence of patchy, isolated, more advanced populations during the Eemian interglacial, possibly belonging to a third lineage, but the evidence is still largely circumstantial and inconclusive. In any case, these observations indicate that water voles underwent a complex history during the last two glaciations.

The results also hint that water vole populations/species may have been driven by climate-related changes. The possible influences of climatic drivers were analysed by Piras et al. (2012) using geometrical morphometrics on the shape and size of m1. The authors reached the conclusion that climate is just one of the factors that affect the morphology of the *Arvicola* dentition ("interspecific variation in shape is mostly correlated with climate" – Piras et al. 2012: 342). The results of the present study demonstrate that there are connections between the morphological variations in *Arvicola* and glacial/interglacial cycling; morphological variations are particularly strong during glacials. Climate perhaps acts on the dental morphology of water voles in a twofold manner. On the one hand, climate changes may trigger adaptive responses, such as, for instance, the variations in the enamel pattern, thus producing in situ evolutionary changes. The spread of arid steppes over large parts of Europe during glacial episodes, and the subsequent adaptation of water voles to the new landscapes, is a consequence of climatic deterioration. On the other hand, glacial cycles also force populations to migrate or, at least, to change their distribution ranges; allochthonous populations thus mix with resident ones and different morphologies forcefully coexist in the same geographical region.

Regions north of the Alpine chain are more exposed to severe climatic stress as well as to biotic influences from eastern and north-eastern regions; in fact, several "cold" mammalian taxa (both small and large mammals) spread to France and Germany during phases of climatic deterioration. The areal distribution of *Arvicola* extends considerably eastward, and it is likely that some populations migrated into central-western Europe during stadial phases, or at least that high rates of inbreeding were favoured between resident and immigrant populations. Noteworthy is that the populations of the Italian Peninsula were less exposed to these phenomena. Faunal influences from the other Eurasian regions are less

intense in the Italian Peninsula; they are only observed in northeastern areas and in areas restricted to the north-west boundary. Conversely, both in the Italian Peninsula and in central and western Europe, more stable environmental conditions of interglacial cycles may be related to periods of reduced variability in the water vole populations. During interglacials, however, entire species, or populations more adapted to warm-temperate climates are expected to spread from their refuge areas.

The rather homogeneous features of *Arvicola* from the Italian Peninsula, which can be traced back to at least the "Rissian/Saalian" glaciation indicates that this water vole evolved in rather isolated conditions during the last two glacial cycles. The occurrence of the "primitive" *A. italicus* lineage is consistent with the model of the refuge areas, played by Mediterranean peninsulas – such as Italy (*A. italicus*) and Spain (*A. sapidus*), for temperate taxa. Morphological evidence excludes that the "*A. italicus*" water vole can be a potential re-colonizer during the last interglacial, because it is fairly different from the other members of the genus *Arvicola* also during the Eemian time slice.

The results of dental-morphological studies are substantially consistent with the phylogenetic-phylogeographic pattern inferred by Wust-Saucy (1998) and by Castiglia et al. (2016). These authors found the endemic species *A. italicus* distributed over almost the whole Italian Peninsula. The present work permits to trace the Italian lineage at least back to the penultimate glaciation. Older *Arvicola* specimens from the north-easternmost areas of the Italian territory do show all the features of *A. mosbachensis*; they show no trace of morpho-phyletic change leading to *A. italicus*. In our opinion they represent "true" *A. mosbachensis*. If the molecular clock indicates that the *A. italicus* lineage emerged earlier than the penultimate glaciation, it should have taken place in the peninsular territory and not in the north east of Italy. The present investigation did not find any evidence of the occurrence of *A.* "*scherman*" nor of *A. monticola* in the examined locations.

Interpretation of the morphometric changes

Arvicola shows morphometric changes in size. The *A. amphibious-A. italicus* species became increasingly larger, elongated the ACC, and reduced the relative thickness of convex enamel edges in upper and lower teeth.

Size is especially related to ecological preferences as well as to lifestyle habits (i.e., mountain dwelling species are smaller). Fossorial water voles are actually smaller than aquatic ones (see Cubo et al. 2006).

The relative thickness of enamel is a more complex question. Enamel differentiation seems not to be susceptible to evolutionary reversals. Trends observed in different regions can be the result of several "interferences", e.g., migrations from various regions of populations with different enamel quotient, altitude or dietary effects, different life histories. We still ignore if the trends evolved in response to adaptive needs. In his pioneering work Rensberger (1975) interpreted the development of asymmetric enamel wall thickness in the molars of fossorial rodents as an adaptation to chewing hard food. Maul et al. (2014) suggested that a switch to a fossorial habit, which involves chewing soil particles, could trigger

the evolution of asymmetric enamel ratio in arvicolines. The question, however, is far from being settled.

Unlike *Microtus*, *Arvicola* shows minimum variation in the relative length of the ACC. Nonetheless, recent species/populations tend to develop somewhat longer ACC. This was never observed before in water voles and requires further investigation to be confirmed. The elongation and increased complexity of ACC in m1, in M3 and the decrease of SDQ values in several species of *Microtus* seem to be correlated phenomena (Lippi et al. 1998). The significance of this trend is still not fully understood. Reduced thickness of trailing edges is related to thickened and hardened leading edges, which became more rapidly broken and abraded. One can speculate that a longer tooth with a greater number of protruding leading edges is more efficient in chewing hard food than a shorter molar with less protruding couples of edges in each dental triangle.

Conclusions

The morphometric-stratigraphical approach used to compare the records of extant and past Italian *Arvicola* with those from selected western and central European regions gave significant results. During the last two glaciations there were already at least two lineages of *Arvicola* in the geographical area selected for this study: a lineage of large-sized peninsular Italian water voles with primitive SDQ values and at least a "North of the Alps" lineage possessing molars with a more advanced enamel pattern. During the Eemian and early Würmian/Weichselian the peninsular lineage is less well-defined and during the last glacial period, in north western Italy lived water voles with more advanced dental morphotypes. What all this delineates is a clinal variation, or a faunal exchange with the neighbouring French region.

The results of the morphological analysis conducted for this study are substantially in line with the phylogenetic-phylogeographic pattern inferred by Wust-Saucy (1998) and by Castiglia et al. (2016) using molecular methods; according to the results obtained by these authors an endemic species, *A. italicus*, distinct from counterparts in other European areas, is distributed throughout almost all Italian Peninsula. In sum, the conclusions of the present analysis corroborate the results obtained by Maul et al. (1998b) and Masini et al. (2007).

Some reflections on the taxonomy and evolution of the genus *Arvicola* can be offered. The occurrence of directional trends in both *Arvicola* and *M. savini* indicate that channelled, parallel morphological changes play a significant role in the evolution of this clade of Arvicolinae. This mode of evolution has an unexpected bearing on our conception of phylogeny and taxonomy. Some authors (Cuenca-Bescós et al. 2010) included in genus *Arvicola* the species *A. jacobaeus* as possible sister group of all other *Arvicola* species. *A. jacobaeus*, however, is much older than the oldest *Arvicola* species, and had already developed rootless molars. Under this perspective, in a younger time period, the ancestral *M. savini* would originate independently *A. mosbachensis* and also other species of *Arvicola*. The resulting phylogenetic pattern would be polyphyletic and the stemming of several chrono-species from the same ancestor, with very complex relationships. Also, the apparently synchronic origin of the

rootless *Arvicola* from *M. savini* in different geographical places would delineate an anagenetic mode of evolution; this would be in stark contrast to dichotomous cladogenetic models, which are the fundament of current taxonomy and systematics. The evolution of *Arvicola* has the potential for significant systematic theoretical developments.

A few words need to be said about the three chronospecies included in the lineage that leads to modern *A. amphibius*. Koenigswald and Van Kolfschoten (1996) focused on the variations in the enamel pattern of m1 and proposed the following criteria to set specific boundaries between the various species: *A. mosbachensis* (SDQ > 120), *A. mosbachensis/amphibius* (120 < SDQ < 95) and *A. amphibius* (SDQ < 95). These distinctions are valid if *Arvicola* is assumed to form a single lineage. The varying SDQ values in other lineages of *Arvicola* argues against Koenigswald and Van Kolfschoten's (1996) criteria and calls for other standards to be defined to distinguish the different lineages.

This is even more important in the light of the results of the present study, which revealed also great morpho-dental variability in the molars of "north to the Alps" voles. Based on this it can be assumed that another advanced species in more northern and eastern regions of Eurasia dispersed episodically (during glacials) into central and western Europe, but without reaching the peninsular region of Italy.

This work shows how important it is to have a more complete geographic-stratigraphic-morphological picture of water voles. The scenario presented here certainly needs to be extended and completed, for instance extending our observations to *A. monticola*, the fourth species of European *Arvicola*, which was not included in the present analysis. Our knowledge of *Arvicola* populations from the Balkan Peninsula, now still quite imperfect, should also be improved. A careful study of the past and extant Balkan water vole *Dinaromys*, which is distributed both in the Balkans and in northern Italy, would be helpful for future comparative analyses.

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Appendix A

This appendix contains a list in which each locality is mentioned in its stratigraphical-chronological frame and – if necessary – shortly discussed.

Fossil record

The *Mimomys savini* samples came from two deposits of different ages: Untermassfeld is a late Early Pleistocene site, dated at about 1.0 Ma (Wiegank 1997), whereas Voigtstedt is a Middle Pleistocene locality dated at about 0.7 Ma, containing a very hypsodont population of *M. savini* (Maul and Parfitt 2010).

The *Arvicola mosbachensis* set includes eight Middle Pleistocene samples from different geographical locations. The material from Isernia La Pineta (Sala 1996) has been shortly discussed in section "*Arvicola mosbachensis*": it represents one of the oldest *Arvicola mosbachensis* finds (dated at about 0.6 Ma) so far known. As shown in map (Text-fig. 4: no. 19), Isernia is located within the Apennine chain and is the southernmost *A. mosbachensis* site considered here. The site of Visogliano is located in north-eastern Italy, near the town of Trieste. The documentation of the extensive small mammal material recovered during archaeological excavations is carried out by the Pisa University (Abbazzi et al. 2000, Falguères et al. 2008). It includes several taxa, which are indicative of the eastern and central European affinity of the fauna. The three samples considered are from different stratigraphic levels, spanning from about 0.5 to 0.25 Ma. Details on stratigraphy and on mammalian fauna are reported in Abbazzi et al. (2000) and Maul et al. (1998).

The other *Arvicola mosbachensis* samples came from four Middle Pleistocene sites in Germany.

Mosbach 2 (Maul et al. 2000) is the type locality of the species. The site of Mauer contains an *Arvicola* sample, the morphology of which is very similar to the finds of Mosbach, and is dated biochronologically and radiometrically to about 0.6–0.55 Ma (Wagner et al. 2010, 2011). It is thus coeval with Isernia. Also Miesenheim 1 is presumably of the same age (Van Kolfschoten 1990, Koenigswald and Van Kolfschoten 1996), whereas Petersbuch 1 is somewhat younger (Koenigswald 1970, 1973), roughly coeval with the two older stratigraphical levels in Visogliano (Visogliano B and Visogliano A-LL). Bilzingsleben 2 has to be placed to the Holsteinian interglacial/MIS 9 (Mania 1983, 1997, Heinrich 1990, Vlček et al. 2002).

The fossil *Arvicola amphibius* (= *terrestris*) group is represented by 35 samples spanning from the late Middle Pleistocene to the Holocene from different geographical locations in Italy, Germany and France. The samples from the Italian territory can be divided into three geographic sub-groups: Italian Peninsular, Italian north-east and Italian north-west ones. The most conspicuous sub-group is composed by remains from 5 sites located at the western side of the central and southern Peninsula (Campania and Tuscany). The oldest sample are those from the pre-Tyrrhenian (= pre-Eemian) level SG of Scario pit, and from Campitello (Upper Valdarno, identifyied as *A. mosbachensis* "evolved form" by Mazza et al. (2006)). Other two samples are referred to the Eemian – early Würmian/Weichselian: Scario Pit A (Abbazzi and Masini in Ronchitelli 1998, Ronchitelli et

al. 2011) and Cucigliana (near the town of Pisa) (Acconci 1880, Farina 2011). Castelcivita Cave in Campania (Cioni et al. 1980, Masini and Abbazzi 1997, Gambassini 1997) dates to the Würmian inter-pleniglacial (MIS 3, 30–40 kyrs conventional ^{14}C dating), the sample from Serratura Cave layer 18c (Campania) (Bertolini et al. 1996) slightly predates the Late Glacial, whereas the sample from levels D9 to D34 of Grotta del Romito (López-García et al. 2014) dates ca. $12,170 \pm 60$ to $12,970 \pm 150$, ^{14}C yr. To this sub-group also the Holocene sample from Scario/Roman Levels (a single specimen) could be added. All the material is derived from archaeological excavations. The north-eastern sub-group includes *Arvicola* remains from the early Holocene levels at Grotta degli Orsi (Trieste, close to nowadays Slovenian border) (Boschian 1992, Boschian et al. 1996, Boschian and De Santis 2011, Berto and Rubinato 2013, and this paper).

Eventually, the north-western sub-group includes samples from two Cave deposits in Liguria, (Arma delle Manie and Riparo Mochi) which date to the early Würm (MIS 4) and to the Würmian inter-pleniglacial (MIS 3); measurements and age reference are from Desclaux et al. (2000).

The samples from the German sites are more evenly distributed. The remains from Ehringsdorf (Jánossy 1975) and Plaidter-Hummerich 1 (Van Kolfschoten 1990) are the oldest in this group, dated to the Saalian glacial or an intra-Saalian interglacial respectively. Burgtonna/Hy (early Weichselian *Hystrix* horizon), and Burgtonna/Cm (Eemian *Cricetus major* horizon) (Maul 1994), Taubach (Heinrich and Jánossy 1977), Stuttgart-Untertürkheim and Parkhöhle (Weimar) (Heinrich 1981, 1987) represent *Arvicola* samples dated to the Eemian interglacial; samples from the sites Euerwanger Bühl, Kemathenhöhlee, Krockstein (Rübeland 1) (Heinrich 1981, 1987) and Burgtonna level 2 are of Würmian age, while Pisede (Heinrich and Maul 1983) is of Holocene age.

The information about the French samples is compiled from Abbassi and Desclaux (1996) and Desclaux et al. (2000) to whom the reader is addressed for further information.

Eleven samples are considered, coming from excavations (mainly archaeological) in caves and shelters in 8 geographic locations from three geographical regions of the French territory. South-east France sites (Lazaret cave, Pie Lombard) are close to the Mediterranean Sea, and to the Italian border, to eastern France (Gigny Cave and Moula-Guercy Cave) and to western France (Suard Cave, Artenac Cave, Gaudry Cave, Vaufrey Cave, Eglise Cave).

Recent samples of *Arvicola amphibius*/*italicus*

Recent *Arvicola* samples from the Italian Peninsula came from the Po Valley (Delta Po, Rovigo, Ferrara) and from Calabria. Some other sporadic samples (composed by a single specimen) are from Bologna, Osnago (Como) and from the coast of Western Tuscany (locality Massaciuccoli – Pisa).

The recent samples from other European localities include two samples from the German territory (from Eisfeld/Thuringia (Frahnert 1991) and from Langen/Hassia), one for Austria (Rabwitz, close to the town of Graz). Further samples, composed by a single specimen, are from Geneve (Swiss) and from the French region of Isère. Eventually a sample of *Arvicola sapidus* from the surroundings of Madrid (this paper) has been also included in the comparisons.

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Appendix B

A list of basic statistics of measurement ad indexes for selected localities.

Locality	Country	Taxon	L					SDQ					A/L				
			n	min	mean	max	sd	n	min	mean	max	sd	n	min	mean	max	sd
Artenac c10	France	A. ex gr. *amphibius*	21	3.39	3.73	4.09	0.160	21	83.20	99.96	114.40	8.600					
Artenac c8	France	A. ex gr. *amphibius*	14	3.41	3.73	4.32	0.240	14	80.50	93.85	110.80	7.570					
Eglise	France	A. ex gr. *amphibius*	31	3.62	4.02	4.97	0.300	31	68.10	83.59	96.00	6.050					
Gigny 10	France	A. ex gr. *amphibius*	34	3.51	3.89	4.12	0.150	34	78.50	87.50	99.30	4.970					
Gigny 19a	France	A. ex gr. *amphibius*	18	3.59	3.76	4.12	0.170	18	85.60	96.40	106.00	6.510					
Gigny 19c–20	France	A. ex gr. *amphibius*	41	3.53	3.74	4.32	0.190	41	79.20	93.68	108.90	6.960					
Gigny 22	France	A. ex gr. *amphibius*	6	3.67	4.21	4.33	0.250	6	88.70	92.30	97.30	2.910					
Gigny 6	France	A. ex gr. *amphibius*	30	3.66	4.07	4.27	0.170	30	62.50	78.40	90.60	5.870					
Lazaret	France	A. ex gr. *amphibius*	51	3.32	3.85	4.40	0.240	47	90.65	107.90	127.25	8.670					
Moula Guercy VIII–IV	France	A. ex gr. *amphibius*	5	3.65	3.83	4.12	0.180	5	74.10	84.25	102.87	9.590					
Moula Guercy XIX–XVIII	France	A. ex gr. *amphibius*	31	3.40	3.82	4.27	0.210	31	74.50	87.41	106.10	7.470					
Moula Guercy XV–XIV	France	A. ex gr. *amphibius*	15	3.43	3.83	4.20	0.220	15	76.28	100.53	114.29	11.170					
Pié Lombard	France	A. ex gr. *amphibius*	4	3.61	3.71	3.80		4	93.73	101.00		11.82					
Pintaud-Gaudry	France	A. ex gr. *amphibius*	64	3.27	3.89	4.36	0.190	64	98.00	113.90	138.70	8.500					
Abri Suard	France	A. ex gr. *amphibius*	32	3.46	4.00	4.59	0.240	32	79.50	91.59	103.20	5.840					
Vaufrey 8	France	A. ex gr. *amphibius*	31	3.35	3.87	4.24	0.200	31	87.30	104.00	128.97	8.900					
Bilzingsleben	Germany	A. ex gr. *amphibius*	9	3.40	3.58	3.88		10	122.43	134.06	149.52	9.275					
Burgtonna 2	Germany	A. ex gr. *amphibius*	41	3.40	3.76	4.42	0.214	40	76.34	99.65	116.95						
Burgtonna Cm	Germany	A. ex gr. *amphibius*	11	3.52	3.82	4.10	0.17	11	68.76	78.91	86.18	5.23	11	31.51	40.47	45.31	3.50
Burgtonna Hy	Germany	A. ex gr. *amphibius*	10	3.55	3.88	4.12	0.15	10	91.91	103.66	113.74	7.85	10	39.18	41.64	43.51	1.51
C Germany rec.	Germany	A. ex gr. *amphibius*	30	3.45	3.78	4.20		30	70.00	85.00	100.00				41.64		
Eisfeld	Germany	A. ex gr. *amphibius*	30	3.45	3.79	4.18		30	70.96	84.91	100.06						
Euwanger Bühl H	Germany	A. ex gr. *amphibius*	27	3.70	4.09	4.44	0.164	27	74.91	83.03	94.52	4.206					
Kemathenhöhle	Germany	A. ex gr. *amphibius*	11	3.85	4.05	4.40	0.160	11	82.31	89.23	100.51	5.099					
Krockstein/Rübeland	Germany	A. ex gr. *amphibius*	40	3.65	4.04	4.60	0.210	40	72.20	89.08	102.93	6.389					
Miesenheim 1	Germany	*Arvicola mosbachensis*	18	3.21	3.50	3.71		29	126.00	152.03	180.00						
Mosbach 2	Germany	*Arvicola mosbachensis*	44	3.06	3.25	3.50		45	117.60	133.34	159.27						
Parkhöhle (Weimar)	Germany	A. ex gr. *amphibius*	3	3.63	3.90	4.40		3	105.61	109.62	114.17						
Petersbuch 1	Germany	*Arvicola mosbachensis*	10	3.48	3.65	4.00	0.161	11	107.87	126.16	146.40	12.380					
Pisede	Germany	A. ex gr. *amphibius*	144	3.30	4.05	4.80	0.302	10	68.63	80.17	91.83	6.463					
Plaidter-Hummerich 1	Germany	A. ex gr. *amphibius*			3.80			5	66.00	82.17	94.00						
Stuttgart/Unterürkheim	Germany	A. ex gr. *amphibius*	37	3.30	3.81	4.24		37	88.87	101.19	114.63						

Locality	Country	Taxon	L					SDQ					A/L				
			n	min	mean	max	sd	n	min	mean	max	sd	n	min	mean	max	sd
Taubach	Germany	A. ex gr. amphibius	11	3.48	3.95	4.20	0.252	9	97.19	105.15	115.52	6.686					
Untermaßfeld	Germany	Mimomys savini	8	3.15	3.29	3.50		11	129.59	151.00	179.18						
Voigtstedt	Germany	Mimomys savini	115	3.00	3.38	3.80		20	107.14	133.66	159.64						
Riparo Mochi-1	Italy	A. ex gr. amphibius	11		4.06		0.210	8		100.75		5.260					
Riparo Mochi-2	Italy	A. ex gr. amphibius	29		3.96		0.310	25		98.20		6.950					
Arma del Manie	Italy	A. ex gr. amphibius	25	3.67	4.00	4.40	0.170	25	81.80	99.84	119.11	8.400					
Calabria	Italy	A. ex gr. amphibius	6	3.89	3.99	4.09	0.069	6	84.52	102.26	121.43	4.682	12	39.17	44.58	46.64	2.375
Castelcivita	Italy	A. ex gr. amphibius	26	3.72	4.02	4.25	0.165	26	94.00	108.11	132.86	8.011	26	39.49	43.10	45.61	1.616
Serratura	Italy	A. ex gr. amphibius	28	3.65	4.11	4.69	0.261	28	103.64	113.58	128.32	6.183	28	37.53	42.60	46.79	1.816
Romito	Italy	A. ex gr. amphibius	21	3.64	4.05	4.45	0.227	19	90.975	110.06	128.025	7.753	20	37.97	42.10	45.84	2.290
Isernia	Italy	Arvicola mosbachensis	6	3.13	3.47	3.63	0.187	7	113.45	130.28	142.11	14.193	6	36.94	40.66	43.52	2.183
Po Delta	Italy	A. ex gr. amphibius	17	3.57	3.85	4.18	0.254	17	97.15	109.89	121.78	8.670	17	40.33	43.58	46.16	1.601
Rovigo	Italy	A. ex gr. amphibius	6	3.43	3.83	4.41	0.382	6	104.51	111.85	120.42	9.969	6	40.70	43.76	46.24	2.060
Ferrara	Italy	A. ex gr. amphibius	7	3.57	4.03	4.40	0.263	7	105.42	114.67	130.20	8.997	7	42.53	44.97	48.16	1.883
Scario A	Italy	A. ex gr. amphibius	5	3.97	4.08	4.23	0.103	5	108.70	116.61	131.90	9.481	5	38.71	42.64	45.86	3.062
Scario RL	Italy	A. ex gr. amphibius	1		4.03			1		108.76							
Scario S.G.	Italy	A. ex gr. amphibius	3	3.96	4.07	4.13	0.093	3	112.16	124.11	132.50	6.794	3	43.07	43.44	44.07	0.548
Valdarno – Campitello	Italy	A. ex gr. amphibius	2	3.81	3.95	4.09	0.198	2	107.52	114.17	120.81	9.399	2	39.12	42.00	44.88	4.074
Visogliano A-UL-12-13 (upper loess)	Italy	Arvicola mosbachensis	18	3.11	3.38	3.66	0.157	18	91.67	116.43	141.05	12.502	18	34.32	38.51	40.96	1.543
Visogliano A-UL-18-25	Italy	Arvicola mosbachensis	18	3.16	3.43	3.64	0.143	17	108.16	122.89	150.26	13.074	18	37.39	40.30	43.38	1.534
Visogliano A-LL	Italy	Arvicola mosbachensis	2	3.47	3.47	3.47		2	117.80	122.77	127.74	7.029	2	39.19	39.19	39.19	0.000