



## TALPA MASINII N. SP., A NEW FOSSIL MOLE SPECIES FROM THE LATE VILLANYIAN FAUNA OF RIVOLI VERONESE (NORTH-EASTERN ITALY) IN THE CONTEXT OF THE EUROPEAN FOSSIL RECORD OF GENUS TALPA

MARCO MARCHETTI

Via Casaline 39, 37014 Castelnuovo del Garda (VR), Italy; e-mail: marcopaleo@hotmail.com.

Marchetti, M. (2024): *Talpa masinii* n. sp., a new fossil mole species from the late Villanyian fauna of Rivoli Veronese (north-eastern Italy) in the context of the European fossil record of genus *Talpa*. – Fossil Imprint, 80(2): 285–311, Praha. ISSN 2533-4050 (print), ISSN 2533-4069 (online).

**Abstract:** Rivoli Veronese (Verona, north-eastern Italy) is a karst fissure filling that yielded an Early Pleistocene fauna, including many remains belonging to the genus *Talpa*, assigned to the late Villanyian rodent age. Some of these remains, characterized by tiny size and primitive features, were already in the past suggested to represent a new mole species. To better characterize this mole, a re-analysis of the most representative fossil and living populations of the genus *Talpa* was performed. This allowed confirmation that it represents a new species, which was named *Talpa masinii* n. sp., to infer that this species existed in earlier periods in Central Europe too, and to better define the taxonomy and biochronology of the fossil *Talpa* populations.

**Key words:** *Talpa*, taxonomy, biochronology, Early Pleistocene, Europe

Received: June 15, 2024 | Accepted: November 12, 2024 | Issued: December 20, 2024

Zoobank: <http://zoobank.org/pub:3EFB5661-0729-4226-BBC1-5FB570C0FF89>

### Introduction

Today, the genus *Talpa* includes several species widespread in Europe and north-western Asia, and only one in Central Siberia (Loy et al. 2005, Colangelo et al. 2010, The IUCN Red List of Threatened Species. Version 2021-2. <https://www.iucnredlist.org>). It is one of the most fossorial representatives of the family Talpidae (Piras et al. 2012). The adaptation to the fossorial style of life triggered a strong specialization of the postcranial elements, while the cranium retained primitive characteristics, so much that elements such as teeth did not evolve enough to generate important morphological differences among species to be useful in distinguishing between species, with some exceptions. Because the genus *Talpa* is rather conservative, the specific identification on skeletal remains is often difficult and is usually based merely on morphometric and few morphological features (Fanfani 1999).

The earliest recorded species is the fairly small *T. tenuidentata* ZIEGLER, 1990, a species still not fully adapted to a fossorial lifestyle, and somewhat intermediate in morphology between Talpini and Scalopini (Hoek Ostende and Fejfar 2006, Klietmann et al. 2015), which lived during the Early Miocene, from MN 2 (Ziegler 1990) to MN 3 (Hoek Ostende and Fejfar 2006) (the adopted biochronologic and chronostratigraphic subdivisions are

specified in the Material and Methods section). Since MN 3, if not already in MN 2, the long-lasting (up to MN 11) tiny *T. minuta* BLANVILLE, 1838, already fully adapted to digging, became a common species (Ziegler 2003, 2006, Klietmann et al. 2015). Larger unnamed forms appeared occasionally during the Early Miocene, since MN 3 (Klietmann et al. 2015). However, they became more common only from the Middle to Late Miocene, from MN 7+8 to MN 12, first with *T. vallesensis* VILLALTA et CRUSAFONT, 1944, and later with *T. gilothi* STORCH, 1978 and *T. aff. gilothi* (Storch 1978, Fejfar and Sabol 2005, Hoek Ostende and Furió 2005, Ziegler 2006, Ménouret and Mein 2008, Rzebik-Kowalska and Rekovets 2015). New species emerged around the Miocene/Pliocene boundary (MN 13/14; Doukas et al. 1995), and with even larger representatives, during the Pleistocene (MN 17 to MQ 2).

Especially the Plio-Pleistocene *Talpa* species were emphasized to be recognizable primarily on morphometric criteria, and accordingly grouped into three size groups: small, middle and large (Niethammer 1990, Fanfani 1999, Cleef-Roders and Hoek Ostende 2001). *T. minor* KORMOS, 1930 (senior synonym of *T. gracilis* KORMOS, 1937 according to the majority of the authors; see discussion in Cleef-Roders and Hoek Ostende 2001) and *T. neagui* RĂDULESCU et SAMSON, 1989 are assigned to the small category; *T. fossilis* PETÉNYI, 1864 (senior synonym of *T. praeglacialis* KORMOS, 1930

and *T. europaea* var. *major* FREUDENBERG, 1914 according to the majority of the authors; Kretzoi 1938, Heller 1958, Koenigswald 1970, Rzebik-Kowalska 2013) to the middle category; and *T. episcopalis* KORMOS, 1930 and *T. romana* THOMAS, 1902 to the large category. *T. csarnotana* KRETZOI, 1959 was initially placed alternately into the small (Kretzoi 1959) or middle (Sulimski 1962) category but, since Storch (1978) gave its measurements, it has been placed into the middle category. The Würmian *T. magna* WOLDRICH, 1893 would fit in the large category. However, it is interpreted as an expression of the high size variability of *T. europaea*, in the absence of any morphological difference, being only slightly larger than the recent populations of the latter species (Stein 1955, Koenigswald 1985).

According to many authors, such as Doukas et al. (1995), Cleef-Rodgers and Hoek Ostende (2001), Angelone et al. (2011), and López-García et al. (2024), the taxonomy of the fossil representatives of the genus *Talpa* is still confused and needs revision, with significantly varying opinions among authors (see for example Cleef-Rodgers and Hoek Ostende (2001) versus Sansalone et al. (2015) about *T. fossilis* and *T. europaea* synonymy). It suffers from important deficiencies as well. For example, usually the type population of *T. fossilis* from Beremend 1 (early Villanyian – MN 16a) is notably absent, or merely mentioned in later works. The cause is that the given description and measurements in the rather old work (Petényi 1864) are outdated, hardly comparable to those of the other fossil *Talpa* populations studied later. Actually, the morphological traits and morphometric landmarks that are currently regarded as important for species discrimination were not defined in that work. Furthermore, Petényi's use of archaic language and ancient units of measurement complicates easy comparison with the remains described by later authors. In fact, later authors assigned to *T. fossilis* some remains they studied solely on the basis that they were observed to be of comparable size with recent *T. europaea*, like the type population was emphasised by Petényi to be, without making a direct morphometric comparison between these remains and those of the type population. That way of reasoning represents an oversimplified and potentially problematic approach to species identification. Therefore, the type population is omitted also in this work, because of the above-mentioned not fully reliable data in Petényi's paper, and needs a total revision that is beyond the scope of the present work. The consequence is that, for the time being, the specific attribution to *T. fossilis* of all the other fossil populations later assigned to that species remains ambiguous and provisional.

In summary, the above-mentioned confusion is due to: the poor morphological variation and strong overlapping in size among *Talpa* species; the scantiness and fragmentary nature of remains in the fossil faunas – the reason why many fossil species were established only on poor remains, mainly or only represented by the robust humeri; the lack of any report of diagnostic morphometric measurements and morphological features of some mole populations in older and sometimes also in modern literature; the absence in some papers of the used protocol of measurements, especially in those older than the paper of Hutchison (1974), which is since then used as the source for measuring methods on talpids; the general comparison of fossil species with recent

ones; the nearly complete absence in later works of a critical revision of old literature; and, finally, the poor interest in the study of *Talpa* genus, because that genus was depicted to be useless for biochronological purpose.

Hutchison (1974), Fanfani (1999), and authors cited in the latter paper proved that some humerus linear measurements and ratios (length, diaphysis width, distal width, length vs. diaphysis width ratio, and index of flattening), the femur and radius length, the height of the mandible below m2, and the length of the lower molar row are all morphometrical characteristics useful to distinguish among the different species. Moreover, from a morphological point of view, they showed that the shape and position of the pectoral tubercle in the humerus and the number of mental foramina are useful for the taxonomical purpose as well. Conversely, for example, teeth morphology is less useful to discriminate between *Talpa* species.

Because of the above-mentioned lacunas, the re-analysis of the Plio-Pleistocene remains, by means of the above-mentioned measurements, ratios, and features, is made to try to adjust the taxonomy of the fossil populations of that period, and to get it into the proper biochronological context.

The tiny *Talpa* from Rivoli Veronese site is analyzed in the above-mentioned background. Rivoli Veronese is a karst fissure filling, exposed in a limestone quarry 18 km NW from Verona (north-eastern Italy), containing a late Villanyian – MN 17 (chronologically corresponding to the first half of the Early Pleistocene, i.e., to the Gelasian Stage) small mammal fauna retrieved from a 2 m-high portion of the lower fissure infilling. The absence of a stratified sequence together with a coherent fauna suggested that the fissure infilling was a rapid and single event (Berto et al. 2022). The mole remains from Rivoli Veronese were already partly studied by Fanfani and Masini (1997) and Fanfani (1999). They recognised only two mole species: one, characterised by a tiny size, was assigned to *Talpa* sp., although it was assumed to probably represent a new mole species; the other was assigned to the small *T. minor*. Berto et al. (2022), who made the revision of the fauna, recorded a third mole species, the middle-sized *T. cf. fossilis*, within the remains previously assigned to *T. minor*, and confirmed that the tiny specimens represent a new species of *Talpa*, but did not name it, leaving the matter to the present study.

The above-mentioned re-analysis demonstrates, despite all its limitations, both intrinsic (poor morphological variation and strong overlapping in size among *Talpa* species) and extrinsic (lack of revision on modern grounds of the type populations of some fossil species), that the taxonomy of many fossil remains of *Talpa* can be fixed, that the genus can be useful for biochronological discussion, and that the new tiny species from Rivoli Veronese, here described and named, is recognised in other fossil populations as well.

## Material and methods

To better define the taxonomy of the new species, the mole remains from the most representative fossil and living mole populations were re-analysed. This comparison was made gathering from literature (Tab. 1, App. Tab. A1) the most significant morphometrical and morphological



**Table 1. List of localities containing analysed *Talpa* populations with published and revised determinations. Publications refer to published determination and stratigraphy. Symbols refer to those used in Text-figs 3–9. u.l. – upper level, l.l. – lower level.**

Locality (acronyms for Text-fig. 3 in parentheses)	Published determination	References	Symbols used in Text-figs	Determination used in this study	Biochronological position (see Text-fig. 2 for details)
Italy – (IT)	<i>T. romana</i>	Niethammer 1990	●	<i>T. romana</i>	RECENT
Greece – (GR)	<i>T. stankovici</i>	Niethammer 1990	⊗	<i>T. stankovici</i>	RECENT
Kleinalm/Niedere Tauern (Austria), Ramsau/Dachstein and Rheinland (Germany) – (KRR)	<i>T. europaea</i>	Niethammer 1990	■	<i>T. europaea</i>	RECENT
Poland – (PL)	<i>T. europaea</i>	Rzebiak-Kowalska 2006	■	<i>T. europaea</i>	RECENT
Bergen op Zoom and Oude Mirrum (The Netherlands) – (B&O)	<i>T. europaea</i>	Cleef-Rodgers and Hoek Ostende 2001	■	<i>T. europaea</i>	RECENT
Colli Berici - recent (Italy)	<i>T. europaea</i>	Bartolomei 1964	■	<i>T. europaea</i>	RECENT
Southeastern Bulgaria – (BG)	<i>T. europaea</i>	Popov 2004a	■	<i>T. europaea</i>	RECENT
	<i>T. martinorum</i> , <i>T. levantis</i>	Kryštufek et al. 2018, Popov 2004a	◆	<i>T. martinorum</i>	
Spain – (ES)	<i>T. occidentalis</i>	Niethammer 1990	×	<i>T. occidentalis</i>	RECENT
Andalusia (Spain)	<i>T. occidentalis</i>	Cleef-Rodgers and Hoek Ostende 2001	×	<i>T. occidentalis</i>	RECENT
Abetone, Osiglia, Monesi, and San Benedetto In Alpe (Italy), Tessin (Switzerland), Pelister (Macedonia) – (ISM)	<i>T. caeca</i>	Niethammer 1990	▲	<i>T. caeca</i>	RECENT
Erkenbrechtsweiler, Biederman'scher Stbr. S1, Villa Seckendorff, Hohlenstein, Ochtenburg, Eurwang C, Dietfurt 12a (Germany) – (ERK)	<i>T. europaea</i>	Koenigswald 1985	■	<i>T. europaea</i>	MQ 2/1 + MQ 2/2 + HOLOCENE
Krucza Skala Rock Shelter (Poland) – (KSRS)	<i>T. europaea</i>	Rzebiak-Kowalska 2006	■	<i>T. europaea</i>	MQ 2/2 + HOLOCENE
	<i>T. cf. minor</i>		+	<i>T. aff. minor</i>	
Genkingen 2+3 (Germany) – (Gen2+3)	<i>T. europaea</i>	Ziegler 1995	■	<i>T. europaea</i>	MQ 2/2 + HOLOCENE
Kleine Scheuer (Germany)	<i>T. magna</i>	Niethammer 1990	■	<i>T. europaea</i>	MQ 2/2
Michelberg (Germany)	<i>T. magna</i>	Niethammer 1990	■	<i>T. europaea</i>	MQ 2/2
Kettig (Germany) – (Ket)	<i>T. magna</i>	Kalthoff 1998	■	<i>T. europaea</i>	MQ 2/2
Komarowa Cave (Poland) – (KC)	<i>T. europaea</i>	Rzebiak-Kowalska 2006	■	<i>T. europaea</i>	MQ 2/2
	<i>T. cf. minor</i>		+	<i>T. aff. minor</i>	
Castelcivita (Italy) – (CC)	<i>T. romana</i>	Fanfani 1999	●	<i>T. romana</i>	MQ 2/2
	<i>T. minor-caeca</i>		▲	<i>T. caeca</i>	
Santenay (France) – (Stn)	<i>T. europaea</i>	Giacobini et al. 1980	■	<i>T. europaea</i>	MQ 2/2
Belvédère 5 (The Netherlands)	<i>T. europaea</i>	Kolfschoten 1985	■	<i>T. europaea</i>	MQ 2/2
Pottenstein C-E (Germany)	<i>T. europaea</i> / <i>T. europaea</i> + <i>T. episcopalis</i>	Brunner 1951, Fanfani 1999	■	<i>T. europaea</i>	MQ 2/1 + MQ 2/2
Pottenstein D8 (Germany)	<i>T. n. sp. 1</i> (small)	Brunner 1951	+	<i>T. aff. minor sp. 1</i> (small)	MQ 2/2
Pottenstein D7 (Germany)	<i>T. n. sp. 2</i> (small)		+	<i>T. aff. minor sp. 2</i> (small)	
Belvédère 3+4 (The Netherlands) – (Bel3+4)	<i>T. europaea</i>	Kolfschoten 1985	■	<i>T. europaea</i>	MQ 2/1
	<i>T. romana</i>		●	<i>T. romana</i>	
Grotta Cola (Italy)	<i>T. caeca</i>	Di Canzio and Petronio 2001	▲	<i>T. caeca</i>	MQ 2/1
	<i>T. cf. europaea</i>		■	<i>T. cf. europaea</i>	
Aven I des Abîmes de la Fage (France) – (AAF)	<i>T. cf. europaea</i>	Jammot 1973	■	<i>T. cf. europaea</i>	MQ 2/1
Colli Berici - Middle Pleistocene (Zovencedo, Loara, Spessa III, Sossano 2, S. Agostino l.l.) (Italy)	<i>T. europaea</i>	Bartolomei 1964	■	<i>T. europaea</i>	MQ 2/1
	<i>T. romana</i>		●	<i>T. romana</i>	
Viatelle (Italy) – (Via)	<i>T. fossilis-europaea</i> + <i>T.</i> <i>romana</i>	Fanfani 1999	■	<i>T. cf. europaea</i>	MQ 2/1
	<i>T. europaea</i>		■	<i>T. europaea</i>	
Spessa II (Italy)	<i>T. caeca</i>	Bartolomei 1964	▲	<i>T. caeca</i>	MQ 2/1
	<i>T. europaea</i>		■	<i>T. europaea</i>	
Boscocchiesanuova (Italy) – (BC)	<i>T. europaea</i> ; <i>T. fossilis-</i> <i>europaea</i>	Bartolomei and Pasa 1970, Fanfani 1999	■	<i>T. cf. europaea</i>	MQ 2/1
	<i>T. caeca</i> ; <i>T. minor-caeca</i>		▲	<i>T. caeca</i>	
Moravitsa Cave (Bulgaria) – (MC)	<i>T. cf. europaea</i>	Popov 1989	■	<i>T. cf. europaea</i>	MQ 2/1
Westbury-Sub-Mendip Bed 10 (England)	<i>T. europaea</i>	Bishop 1982	■	<i>T. europaea</i>	MQ 2/1
	<i>T. minor</i>		△	<i>T. minor</i>	
Breitenberghöhle (Germany)	<i>T. episcopalis</i>	Brunner 1958	◆	<i>T. episcopalis</i>	MQ 2/1
	<i>T. minor</i>		△	<i>T. minor</i>	
Petersbuch 1 (Germany) – (Pet1)	<i>T. europaea</i>	Koenigswald 1970	■	<i>T. europaea</i>	MQ 2/1
	<i>T. minor</i>		△	<i>T. minor</i>	
Valdemino (Italy) – (Vd)	<i>T. fossilis-europaea</i>	Fanfani 1999	■	<i>T. europaea</i>	MQ 2/1
	<i>T. minor-caeca</i>		▲	<i>T. caeca</i>	
Erpfingen 3 (Germany)	<i>T. cf. episcopalis</i>	Heller 1958	■	<i>T. cf. europaea</i>	MQ 2/1
	<i>T. gracilis</i> + <i>T. gracilis</i> or <i>T.</i> <i>praeglacialis</i>		△	<i>T. minor</i>	
Monte del Cros (Italy)	<i>T. minor</i>	Giacobini et al. 1980	▲	<i>T. cf. caeca</i>	MQ 2/1
Visogliano (Italy) – (Vis)	<i>T. romana</i>	Fanfani 1999	●	<i>T. romana</i>	MQ 2/1
	<i>T. fossilis-europaea</i>		□	<i>T. fossilis</i>	
Boxgrove (England)	<i>T. minor-caeca</i>	Maul and Parfitt 2010	▲	<i>T. cf. caeca</i>	MQ 2/1
	<i>T. europaea</i>		□	<i>T. cf. fossilis</i>	
Sudmer-Berg 2 (Germany) – (SB2)	<i>T. minor</i>	Fanfani 1999	△	<i>T. minor</i>	MQ 2/1
	<i>T. minor</i>		△	<i>T. minor</i>	
Husarenhof 4 (Germany)	<i>T. minor</i>	Koenigswald 1973	△	<i>T. minor</i>	MQ 2/1

characteristics of these remains. No direct comparison was possible with other collections, because hundreds of Plio-Pleistocene fossil mole remains (including hundreds of humeri) are scattered in collections all over various European

institutions. There, they are tentatively labelled under several different names, awaiting definitive identification. However, because few insectivore genera are as badly in need of revision as the genus *Talpa*, a basis, represented by

Table 1. continued

Locality (acronyms for Text-fig. 3 in parentheses)	Published determination	References	Symbols used in Text-figs	Determination used in this study	Biochronological position (see Text-fig. 2 for details)
Cengelle 1 (Italy) – (Cen)	<i>T. romana</i>	Fanfani 1999	●	<i>T. romana</i>	MQ 2/1
	<i>T. europaea-fossilis</i>		■	<i>T. cf. fossilis</i>	
Hundsheim (Austria) – (HH)	<i>T. cf. episcopalis</i>	Kormos 1937	◆	<i>T. cf. episcopalis</i>	MQ 2/1
	<i>T. europaea major</i> / <i>T. europaea</i>	Freudenberg 1914, Rabeder 1972	□	<i>T. cf. fossilis</i>	
	<i>T. minor</i> n. sp.		△	<i>T. minor</i>	
Hohensülzen (Germany)	<i>T. fossilis</i>	Storch et al. 1973	□	<i>T. fossilis</i>	MQ 1/3
	<i>T. minor</i>		△	<i>T. minor</i>	
Sackdilling (Germany)	<i>T. praeglacialis</i>	Brunner 1934	□	<i>T. fossilis</i>	MQ 1/3
	<i>T. gracilis</i>		△	<i>T. minor</i>	
West Runton Upper Freshwater Bed (England)	<i>T. fossilis</i>	Maul and Parfitt 2010	□	<i>T. fossilis</i>	MQ 1/3
	<i>T. minor</i>		△	<i>T. minor</i>	
Voigstedt (Germany)	<i>T. fossilis</i>	Maul and Parfitt 2010	□	<i>T. fossilis</i>	MQ 1/3
	<i>T. minor</i>		△	<i>T. minor</i>	
Betfia VII/3a+VII/3c+VII/4 (Romania) – (BeVII)	<i>T. fossilis</i>	Rzebik-Kowalska 2000	□	<i>T. fossilis</i>	MQ 1/3
Köversvárad (Hungary)	<i>T. fossilis</i>	Jánossy 1963	□	<i>T. fossilis</i>	MQ 1/3
	<i>T. minor</i>		△	<i>T. minor</i>	
Varbeshnitsa (Bulgaria) – (Vrb)	<i>Talpa</i> sp.	Popov 1988	□	<i>T. cf. fossilis</i>	MQ 1/3
Futjova Cave Layer 4c (Bulgaria)	<i>T. europaea</i>	Popov 2017	□	<i>T. cf. fossilis</i>	MQ 1/2
Tatinja draga (Croatia) – (TD)	<i>T. cf. europaea</i>	Paunovic and Rabeder 1996	■	<i>T. cf. europaea</i>	MQ 1/2
	<i>T. minor</i>		▲	<i>T. cf. caeca</i>	
Untermassfeld (Germany)	<i>T. europaea</i>	Maul 2001, 2022	□	<i>T. cf. fossilis</i>	MQ 1/2
	<i>T. minor</i>		△	<i>T. minor</i>	
Betfia V (Romania)	<i>T. cf. episcopalis</i>	Rzebik-Kowalska 2000	◇	<i>T. cf. episcopalis</i>	MQ 1/2
	<i>T. fossilis</i>		□	<i>T. fossilis</i>	
Podumci 1 (Croatia) – (Pdm)	<i>T. cf. minor</i>	Kowalski 1958a, Malez and Rabeder 1984	△	<i>T. cf. minor</i>	MQ 1/2
Razvodje (Croatia)	<i>T. minor</i>	Paunovic and Rabeder 1996	▲	<i>T. cf. caeca</i>	MQ 1/2
Les Valerots (France) – (LV)	<i>T. minor</i>	Giacobini et al. 1980	△	<i>T. minor</i>	MQ 1/2
Monte Peglia A+B (Italy) – (MP)	<i>T. fossilis</i>	Meulen 1973, Petronio et al. 2020	▲	<i>T. cf. caeca</i>	MQ 1/2
Püspökfürdő (= Betfia 2) (Romania)	<i>T. episcopalis</i> n. sp.	Kormos 1930	◇	<i>T. episcopalis</i>	MQ 1/1
	<i>T. praeglacialis</i> n. sp.		□	<i>T. fossilis</i>	
	<i>T. gracilis</i> n. sp.		△	<i>T. minor</i>	
Pirro Nord (Italy) – (PN)	<i>T. minor-caeca</i>	Fanfani 1999	△	<i>T. cf. minor</i>	MQ 1/1
Monte Argentario (Italy)	<i>T. cf. fossilis</i>	Siori et al. 2014	△	<i>T. cf. fossilis</i>	MQ 1/1
	<i>T. cf. fossilis</i>		□	<i>T. cf. minor</i>	
Betfia IX u.I. (Romania) – BelX	<i>T. cf. episcopalis</i>	Rzebik-Kowalska 2000	◇	<i>T. cf. episcopalis</i>	MQ 1/1
Betfia XI+X+IX u.I.+VIII/1b-e (Romania) – (BeXI-IX)	<i>T. fossilis</i>		□	<i>T. fossilis</i>	
	<i>T. minor</i>		△	<i>T. minor</i>	
Soave Cava Sud (Italy) – (SCS)	<i>T. minor-caeca</i>	Fanfani 1999	△	<i>T. cf. minor</i>	MQ 1/1
Monte La Mesa (Italy)	<i>T. minor</i>	Marchetti et al. 2000	□	<i>T. cf. fossilis</i>	MQ 1/1
	<i>T. minor</i>		△	<i>T. minor</i>	
Beremend 16 (Hungary)	<i>T. cf. fossilis</i>	Jánossy 1996	□	<i>T. cf. fossilis</i>	MQ 1/1
Żabia Cave (Poland) – (ZC)	<i>T. fossilis</i>	Rzebik-Kowalska 2013	□	<i>T. fossilis</i>	MN 17/2
	<i>T. minor</i>		△	<i>T. minor</i>	
Betfia XIII (Romania)	<i>T. cf. episcopalis</i>	Rzebik-Kowalska 2000	◇	<i>T. cf. episcopalis</i>	MN 17/2
	<i>T. fossilis</i>		□	<i>T. fossilis</i>	
Kamyk (Poland)	<i>Talpa</i> sp.	Kowalski 1960b	◇	<i>T. cf. episcopalis</i>	MN 17/2
	<i>Talpa</i> sp.		□	<i>T. cf. fossilis</i>	
Schernfeld (Austria)	<i>T. fossilis</i>	Dehm 1962	□	<i>T. fossilis</i>	MN 17/2
	<i>T. minor</i>		△	<i>T. minor</i>	
Montagnola Senese 1 (Italy)	<i>T. fossilis</i>	Fondi 1972	□	<i>T. fossilis</i>	MN 17/1
	<i>T. fossilis</i>		△	<i>T. minor</i>	
Kadzelnia 1 (Poland) – (KD1)	<i>T. fossilis</i> + <i>T. minor</i> pro parte	Kowalski 1958b	□	<i>T. fossilis</i>	MN 17/1
	<i>T. minor</i>		△	<i>T. minor</i>	
Tegelen (The Netherlands)	<i>T. minor</i>	Fanfani 1999	△-□	<i>T. minor</i> and/or only <i>T. cf. fossilis</i>	MN 17/1
Casablanca 1 (Spain)	<i>T. cf. fossilis</i>	Furió Bruno 2007	□	<i>T. cf. fossilis</i>	MN 17/1
Coste San Giacomo (Italy)	<i>Talpa</i> sp. and <i>T. minor</i>	Bona et al. 2015	□	<i>T. cf. fossilis</i>	MN 17/1
	<i>Talpa</i> sp. and <i>T. minor</i>		△	<i>T. cf. minor</i>	
	<i>Talpa minor</i>		*	<i>T. cf. masinii</i>	
Gundersheim 2 (Germany)	<i>T. gracilis</i>	Heller 1936	△	<i>T. minor</i>	MN 17/1
Rivoli Veronese (Italy) – (RV)	<i>T. minor</i> / <i>T. minor</i> / <i>T. cf. fossilis</i>	Fanfani and Masini 1997, Fanfani 1999, Berto et al. 2022, pers. obs.	□	<i>T. cf. fossilis</i>	MN 17/1
	<i>T. minor</i>		△	<i>T. minor</i>	
	<i>Talpa</i> sp. / <i>Talpa</i> sp. / <i>Talpa</i> n. sp.		*	<i>T. masinii</i> n. sp.	
Pedreira del Corral d'en Bruach (Spain)	<i>T. cf. fossilis</i>	López-García et al. 2024	□	<i>T. cf. fossilis</i>	MN 17/1
Varshets (Bulgaria) – (Var)	<i>T. martinorum</i> / <i>T. levantis</i>	Kryštufek et al. 2018, Popov 2004a	◆	<i>T. martinorum</i>	MN 17/1

the present work, was needed as a starting point to study in the future these collections one by one, by anyone who can access them.

The findings containing only a few dental elements with no mandibles and humeri hamper precise identification of

talpid assemblages. Therefore, they were omitted from the re-analysis.

*T. vallesensis* and *T. tenuidentata* were not considered, because the combination of their size, proportions, and age excludes them from the purpose of this work. *T. tyrrenica*

Table 1. continued

Locality (acronyms for Text-fig. 3 in parentheses)	Published determination	References	Symbols used in Text-figs	Determination used in this study	Biochronological position (see Text-fig. 2 for details)
Saint-Vallier (France)	<i>T. fossilis</i>	Martín Suárez and Mein 2004	□	<i>T. fossilis</i>	MN 17/1
Beremend 15 (Hungary)	<i>T. fossilis</i>	Jánossy 1987	□	<i>T. fossilis</i>	MN 16b/2
Rebيلية Królewskie (= Rebيلية Królewskie 1A) (Poland) – (RK1A)	<i>T. cf. fossilis</i>	Kowalski 1960a	□	<i>T. cf. fossilis</i>	MN 16b/1
	<i>T. minor</i>		△	<i>T. minor</i>	
Hajnáčka I (Slovakia)	<i>T. fossilis</i> + <i>Talpa</i> sp.	Sabol 2004	□	<i>T. cf. fossilis</i>	MN 16a
	<i>T. cf. minor</i>		✱	<i>T. cf. masinii</i>	
Csarnóta 2 I.I. (Hungary) – (Csa2)	<i>T. csarnotana</i> n. sp.	Storch 1978	□	<i>T. cf. fossilis</i>	MN 15b/2
Gundersheim 4) (Germany) – (Gun4)	<i>T. minor</i>	Dahlmann and Storch 1996	✱	<i>Talpa</i> cf. <i>masinii</i>	MN 15b/2
Wölfersheim (Germany) – (Wöl)	<i>T. gilothi</i>	Dahlmann 2001	○	<i>T. cf. neagui</i>	MN 15b/2
	<i>T. minor</i>		✱	<i>Talpa</i> cf. <i>masinii</i>	
Weże 1 (Poland) – (WE1)	<i>T. fossilis</i>	Sulimski 1959,	□	<i>T. fossilis</i>	MN 15b/1
	<i>T. minor</i> / <i>T. neagui</i>	Rădulescu and Samson 1989	○	<i>T. neagui</i>	
	<i>T. minor</i> young individuals	Sulimski 1962	✱	<i>T. cf. masinii</i>	
Muselievo (Bulgaria)	<i>T. minor</i>	Popov 2004b	□	<i>T. cf. fossilis</i>	MN 15b/1
Mălușteni (Romania) – (Mal)	<i>T. neagui</i>	Rădulescu and Samson 1989	○	<i>T. neagui</i>	
Berești (Romania)	<i>T. neagui</i> n. sp.	Rădulescu and Samson 1989	○	<i>T. neagui</i>	MN 14a
Podlesice (Poland) – (Pdl)	<i>T. minor</i>	Kowalski 1956	○	<i>T. cf. neagui</i>	
Maramena (Greece)	<i>T. fossilis</i>	Doukas et al. 1995	□	<i>T. fossilis</i>	MN 13/14
Kohfidisch (Austria) – (Kfd)	<i>T. gilothi</i> - <i>T. aff. gilothi</i>	Storch 1978, Ziegler 2006	■	<i>T. aff. gilothi</i>	MN 11
Dom-Dürkheim 1 (Germany) – (DD1)	<i>T. gilothi</i> n. sp.	Storch 1978	■	<i>T. gilothi</i>	MN 11
Soblay (France)	<i>T. gilothi</i>	Ménouret and Mein 2008	■	<i>T. gilothi</i>	MN 10
Can Llobateres (Spain) – (CL)	<i>T. gilothi</i>	Storch 1978	■	<i>T. gilothi</i>	MN 10
Rudabánya (Hungary)	<i>Talpa</i> sp.	Ziegler 2004	-	<i>Talpa</i> sp.	MN 9
Petersbuch 6, 10, 18, 31, 48 (Germany) – (Pet Mio)	<i>T. minuta</i>	Ziegler 2003	◆	<i>T. minuta</i>	MN 7+8
Sansan (France) – (San)	<i>T. minuta</i> n. sp.	Ziegler 2003	◆	<i>T. minuta</i>	MN 6

BATE, 1945, a Middle to Late Pleistocene insular endemism of Corsica and Sardinia (Pereira et al. 2001, Palombo 2006), probably descending from a still unrecognized Miocene species that migrated there during the Messinian salinity crisis (Made 1999), or less convincingly, from a form similar to *T. minor* that migrated there during the sea regression during the “Middle Pliocene – late Ruscian – late MN15” (Palombo 2006) / “Early/Middle Pliocene” (Furió and Angelone 2010) (Early/Late Pliocene according to the here adopted chronostratigraphic scheme), was excluded as well. *T. stromeri* BRUNNER, 1950, a species of indefinite age, Pliocene according to Fanfani (1999), Biharian (late Early or early Middle Pleistocene) according to Reumer (1995), poorly studied, and of ill-defined systematic position, needs revision and was also excluded from the present work.

The re-analysis allowed adjustment in the taxonomy of some poorly representative fossil populations (represented by scanty remains or by sketchy description) that were misinterpreted in the past, because of being compared against only a partial set of the mole record. In fact, I made new species assignments for these populations (Tab. 1, App. Tab. A1) on the basis of size comparisons and reasoning similar to what past authors did when they assigned those remains to particular species, but comparing them with a broader mole record.

The characteristics, cited in the Introduction section and established by past authors to be of diagnostic importance for discrimination among fossil moles were respectively measured on and described for the Rivoli Veronese remains, too. For this purpose, measuring methods and terminology employed in the text were those used by Hutchison (1974) for postcranial bones, and by Reumer (1984) for mandibles and teeth, because their methodology is widely adopted by the majority of authors who study fossil talpids. By checking all the literature here analysed, the measuring methodology of earlier authors was seen to not differ much from that used by Reumer and Hutchison. Therefore, it was inferred

that most of the measurements taken by past authors were obtained with the same or, in the worst case, with a similar protocol, with a few possible exceptions in the earliest works. This should not have introduced too much bias into the current re-analysis.

Measurements, in millimetres, taken on Rivoli Veronese mole remains were determined using a Parker Hannifin M4000DM Series Digital Micrometer. They are shown partially in Appendix, Table A1 (for comparison purpose with the other European *Talpa* populations) and fully in Table 2. The pictures (Text-fig. 10) were taken with a Leica EZ4HD microscope and processed with ImageJ software.

The biochronologic subdivisions, adopted in this work (Text-figs 1, 2) to cover the long period from the Early Miocene to the present, are built on those of Fejfar et al. (1998), and supplemented following the works of Rabeder (1981), Jánossy (1986), Fejfar et al. (1997), Horáček and Ložek (1988), Kordos (1991), Steininger et al. (1996), Tesakov (1998, 2004), Fejfar (2001), Koufos et al. (2005), Tesakov et al. (2007, 2017), and Mayhew (2015). The chronostratigraphic subdivisions of the same time period are those of Cohen et al. (2013).

## Systematic palaeontology

Morphometrical and morphological characteristics of the examined mole record are graphically summarized and compared in Text-figs 3–9. They show why some species assignments changed, mostly between couples overlapping in size to a certain degree, such as *T. caeca* and *T. minor*, *T. minor* and *T. fossilis*, *T. europaea* and *T. fossilis*, and *T. fossilis* and *T. episcopalis*, that is, mainly for size reasons. Notably, I consider *T. csarnotana* a synonym of *T. fossilis*, because neither the original vague description (without a diagnosis, illustration, or even type-designation) provided by Kretzoi (1959), nor the measurements, which were



Table 2. Measurements of *Talpa* remains from Rivoli Veronese (\* – alveolar length).

Anatomic element	Measurements	<i>Talpa masinii</i> n. sp.			<i>Talpa minor</i>			<i>Talpa</i> cf. <i>fossilis</i>		
		min	mean	max	min	mean	max	min	mean	max
Humerus	L2	3.93	4.17	4.27	6.41	3.08	6.60	3.33	3.40	3.52
	L4	6.32	6.36	6.36	3.06	3.10	3.10	10.69	8.90	11.13
	L5	6.07	6.72	6.72	13.07	2.06	13.15	13.94	13.97	14.00
	L6	9.07	9.44	9.80	1.51	5.48*	1.10	2.19	2.25	2.37
	L7		6.50	7.00						
	W7	6.90	5.31	5.56						
	W8	4.95	2.37	2.43						
	W9	2.26	8.87	0.07						
Radius	W13									
Femur	L									
Mandible	H m1/m2									
	L m1–m3									
p1	L		4.1*	1.57						
p3	L		0.53					1.31	1.34	
p4	L		1.74*					1.93	2.25	
m1	L							1.20	1.46	
m2	W							2.46	2.56	
m3	L		1.62					2.00	2.01	
C1	L		1.56*					1.05	1.06	
M2	W							2.19	2.27	
	L							2.49	2.53	
	W									

specified by Storch (1978) only many years after the species was erected, of the type population display differences from the latter species. Other adjustments in taxonomy are cited in the text.

Text-figs 3–9 also show that the smallest remains from Rivoli Veronese are distinctively smaller than and morphologically different from any so far recognized tiny to small mole species.

The whole re-analysis permitted better definition and summarization of the characteristics among the tiny to middle-sized *Talpa* species as well, allowing better differentiation among those species (Tab. 3).

Past works (Fanfani 1999, Berto et al. 2022), together with this re-analysis showed that, among the 68 mole remains from Rivoli Veronese, 12 of them belong to the new species.

**Class Mammalia LINNAEUS, 1758**  
**Order Eulipotyphla WADDELL, CAO, HAUF et**  
**HASEGAWA, 1999**  
**Family Talpidae FISCHER, 1814**

**Genus *Talpa* LINNAEUS, 1758**

***Talpa masinii* n. sp.**

Text-fig. 10

<http://zoobank.org:act:E32BC2FE-8E69-4B6F-9E24-6654BC14682F>

- 1962 *T. minor* young individuals; Sulimski, tab. 4, pl. I, figs 5–7. [Weże 1]
- 1996 *T. minor*; Dahlmann and Storch, tab. 5, pl. 1, fig. 17. [Gundersheim 4]
- 1997 *Talpa* sp.; Fanfani and Masini, p. 371, pl. 1 figs 7–9. [Rivoli Veronese]
- 1999 *Talpa* sp.; Fanfani, pl. 1.7, figs f–h. [Rivoli Veronese]
- 2001 *T. minor*; Dahlmann, tab. 8, fig. 7.2–3, pl. 7 figs 4–5. [Wölfersheim]
- 2004 *T. cf. minor*; Sabol, tab. 7.1 + 7.2, figs 7.1.1, 7.1.2. [Hajnáčka 1]
- 2015 *T. minor*; Bona et al., tab. 7, pl. 2, fig. 2 (CSG 24). [Coste San Giacomo]
- 2022 *Talpa* n. sp.; Berto et al., tab. 3, fig. 2. [Rivoli Veronese]

**H o l o t y p e.** Right humerus (inv. no. RV374, Museo di Paleontologia e Preistoria Piero Leonardi of the University of Ferrara; Text-fig. 10a).

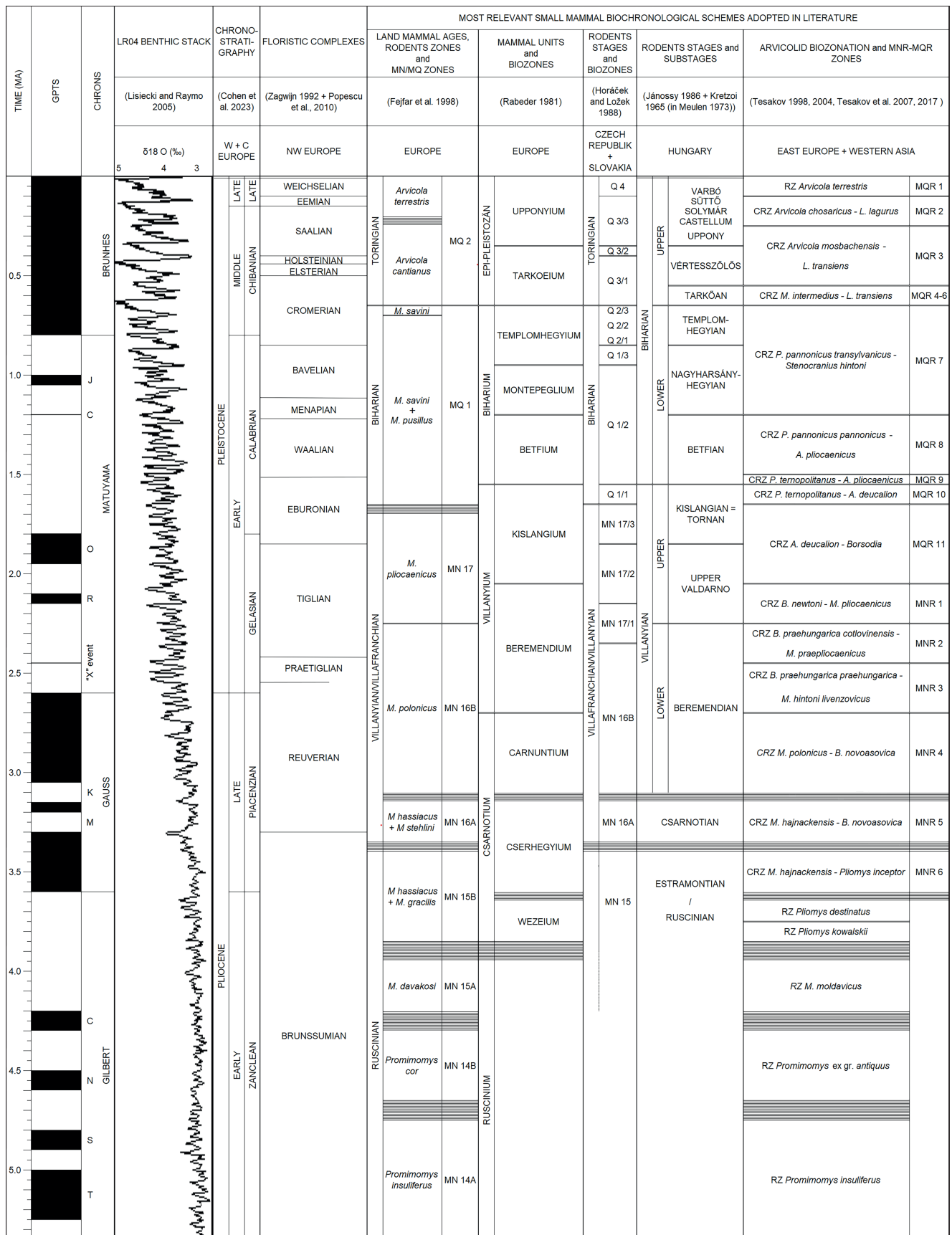
**P a r a t y p e s.** 1 toothless left mandible (RV386), 1 right mandible with p3 and m2 (RV385), 1 sternum (RV330), 3 left humeri (from RV375 to RV377), 1 right humerus (RV374), 1 right distal humerus (RV373), 1 left radius (RV381), 1 left distal femur (RV358), 1 right distal femur (RV383), 1 right proximal tibia (RV382).

**E t y m o l o g y.** In honour of Prof. Federico Masini of the Faculty of Mathematical, Physical, and Natural Sciences of the University of Palermo, who first acknowledged that the remains of this tiny mole probably belonged to a new species.

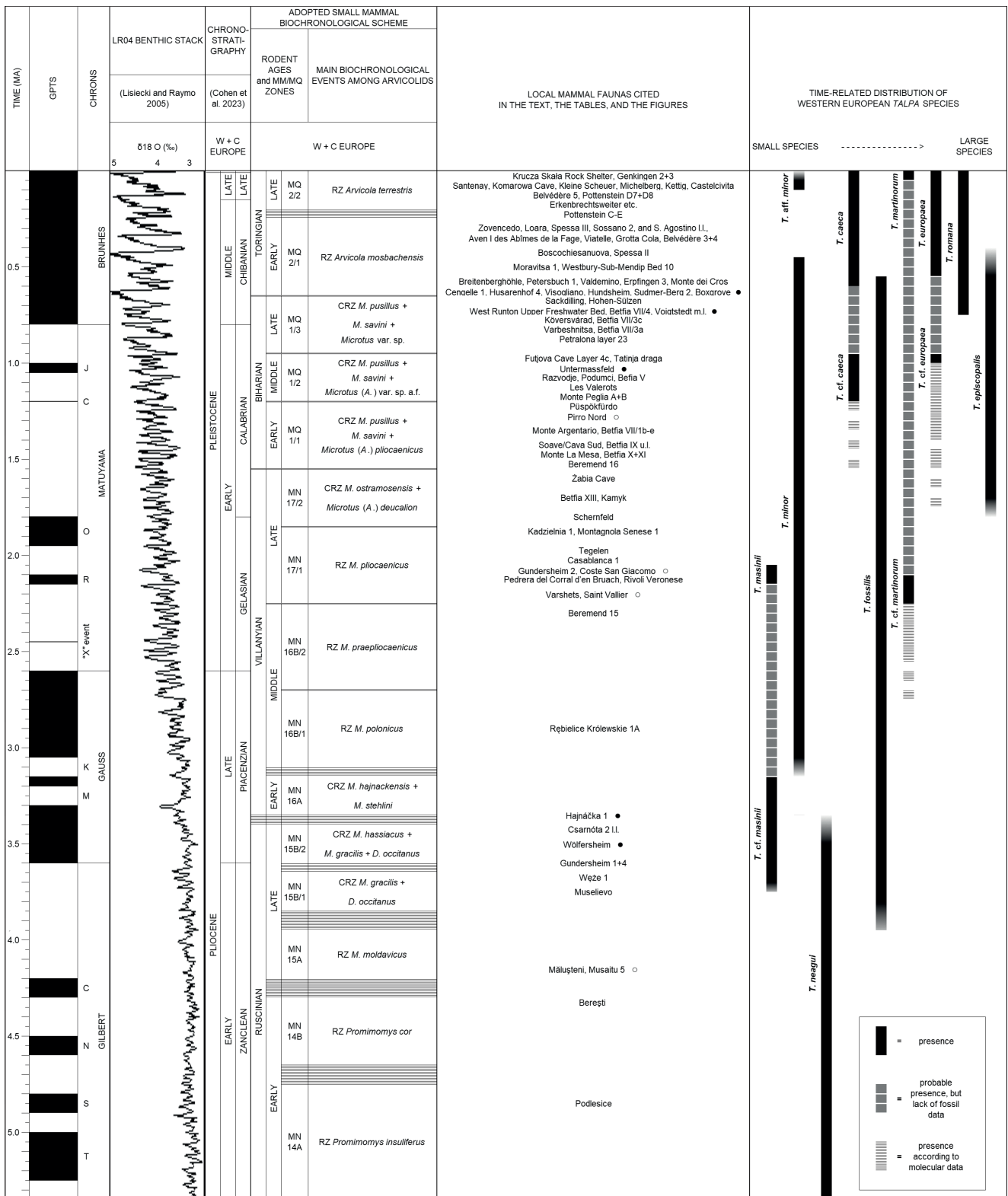
**T y p e l o c a l i t y.** Rivoli Veronese (Verona, north-eastern Italy). Late Villanyian – MN17/1.

**M e a s u r e m e n t s.** See Table 2.

**D i a g n o s i s.** *Talpa* species much smaller than any Ruscinian to modern *Talpa* species in both cranial and



Text-fig. 1. Time-related chart of Plio-Pleistocene chronostratigraphic and former biochronological subdivisions (Legend: ○, ● – respectively negative and positive palaeomagnetic polarity of sediments bearing local mammal fauna. RZ – range zone; CRZ – concurrent range zone. A. – *Allophaiomys*, B. – *Borsodia*, D. – *Dolomys*, L. – *Lagurus*, M. – *Mimomys*, P. – *Prolagurus*).



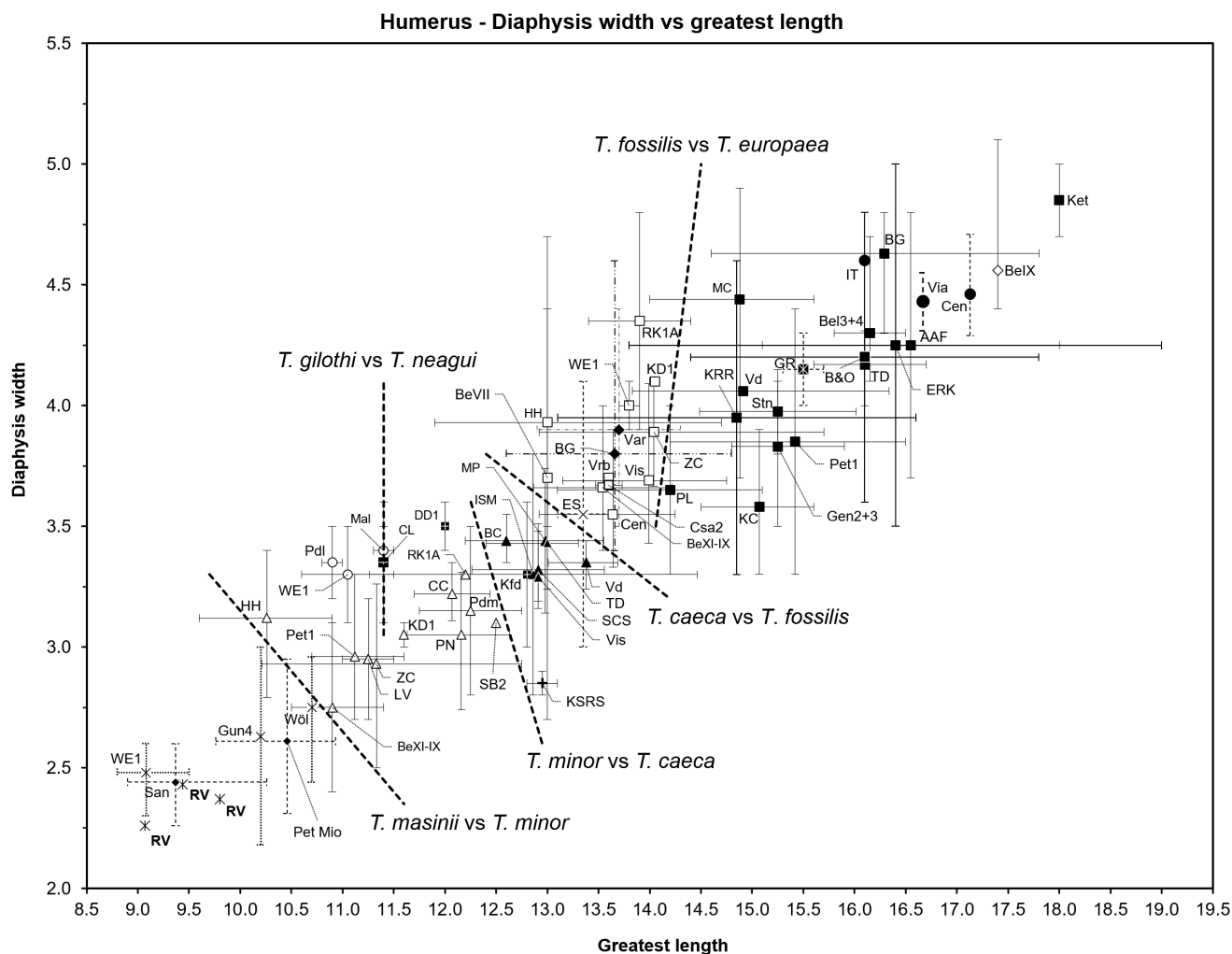
**Text-fig. 2.** Time-related chart of Plio-Pleistocene biochronological subdivisions adopted here, with time-related distribution of local mammal faunas and of *Talpa* species cited in present work. Presence according to molecular data taken from Colangelo et al. (2010), Bannikova et al. (2015), and Feuda et al. (2015) (div. sp. – various species).

postcranial elements, bearing at least up to three mental foramina and the pectoral tubercle of the humerus positioned in a rather variable position (central in some specimens, lateral in others).

**Differential diagnosis.** It differs from the similarly-sized *T. minuta* BLAINVILLE, 1840, as described

by Hutchison (1974) and Ziegler (2003, 2006), because the only teeth available for comparison (p3 and m2) are distinctively smaller than those of *T. minuta*, while the Lm1 is, conversely, somewhat larger (even more so, because derived from alveolar length); furthermore, in *T. masinii* n. sp. the pectoral tubercle is in a central to lateral position,





Text-fig. 3. Diagram of diaphysis width vs. maximum length of humerus in fossil and recent *Talpa* (acronyms of localities in Tab. 1).

while in *T. minuta* it is always centrally placed; additionally, the former mole, though this observation is based on one individual, bears three mandibular foramina, whereas the latter mole consistently exhibits only two mandibular foramina.

The small species, *T. neagui* and *T. minor*, are found respectively during the Ruscinian – MN 14–15 and since the early Villanyian – MN 16 to Toringian – MQ 2. Reference populations of the former species are those from Berești (type locality), Mălușteni, Weże 1, and Podlesice (Rădulescu and Samson 1989), all well described and rich in number of remains. Reference populations for the latter species are mainly those from Erpfingen 3 (Heller 1958), Petersbuch 1 (Koenigswald 1970), Hundsheim (type locality) (Rabeder 1972), Betfia (Rzebik-Kowalska 2000), Żabia Cave (Rzebik-Kowalska 2013), and Rivoli Veronese (Berto et al. 2022). The smallest remains from Rivoli Veronese differ noticeably from the two above-mentioned species in their unambiguously smaller size. Only exceptionally, in few cranial and postcranial elements, they reach the size of the smallest specimens of *T. neagui* and *T. minor*. However, when the proportions of the corresponding elements are considered, they totally differ from those of the latter two species. Moreover, the pectoral tubercle of the humerus is positioned in a central to lateral position, while it is always

in a central position in *T. neagui*, and conversely, in a lateral position in *T. minor*.

Because the remains of this tiny mole differ from the other fossil and recent mole species, and are represented by cranial and postcranial remains with a high systematic value among talpids, such as mandibles, and especially, some well-preserved humeri, this definitely supported the past idea that they represented a new species.

**Description.** All the cranial and postcranial elements are tiny, although they belong to adult individuals. Even those postcranial elements, such as sternum, radius, femurs, and tibia, that basically have no morphological features useful to discriminate among *Talpa* species, can nevertheless be assigned to the new species. In fact, they are distinctively smaller than those from Rivoli Veronese assigned to *T. minor*, or those from the collection of the Museo di Paleontologia e Preistoria Piero Leonardi of the University of Ferrara belonging to *T. caeca*, a species slightly larger than *T. minor*, collected near Tarvisio (Friuli-Venezia Giulia Region, north-eastern Italian Alps) and in Grotta della Serratuta (near Marina di Camerota, Salerno, Campania Region, southern Italy), in strata of latest Pleistocene to sub-recent age.

**Mandibles.** Based on scanty remains, three mental foramina, one below the original emplacement of m1, between the two alveoli, one below the distal end of the

**Table 3. Comparison of characteristics between *T. masinii* n. sp. and other analysed tiny- to middle-sized *Talpa* species. Filling in dark grey: total correspondence of feature with that possessed by *T. masinii* n. sp.; filling in light grey: partial correspondence of feature with that possessed by *T. masinii* n. sp.; no filling: no correspondence of feature with that possessed by *T. masinii* n. sp.; characteristics in bold type: feature representative for the species, because observed in many remains or populations; characteristics not in bold type: features poorly representative for the species, because observed on scanty remains or in few populations.**

Features Mole species	Humerus size	Radius length	Pectoral tubercle position	Size graduation of teeth of lower molar row	Number of mental foramina
<i>T. caeca</i>	small	short	lateral	Lm2>Lm1=Lm3	2
<i>T. europaea</i>	medium to large	medium to large	lateral	Lm2>Lm1≥Lm3	2 (3 uncommon)
<i>T. fossilis</i>	small to medium	medium	lateral	Lm2>Lm1=Lm3	2–3 (4 uncommon)
<i>T. minor</i>	tiny to small	short	lateral	Lm2>Lm1=Lm3	2 (3 uncommon)
<i>T. masinii</i>	tiny	very short	central to lateral	Lm1>Lm2=Lm3	2–3
<i>T. neagui</i>	small	–	central	Lm1>Lm2>Lm3	2–(3?)
<i>T. aff. gilothi</i>	small	–	central	–	–
<i>T. gilothi</i>	small	–	lateral	–	2
<i>T. minuta</i>	tiny	very short	central	Lm2≥Lm3≥Lm1	2

emplacement of p3, one below the original emplacement of p1 and p2, at the boundary of their alveoli.

**Teeth.** m2 and p3 are badly preserved, so no morphological features can be described.

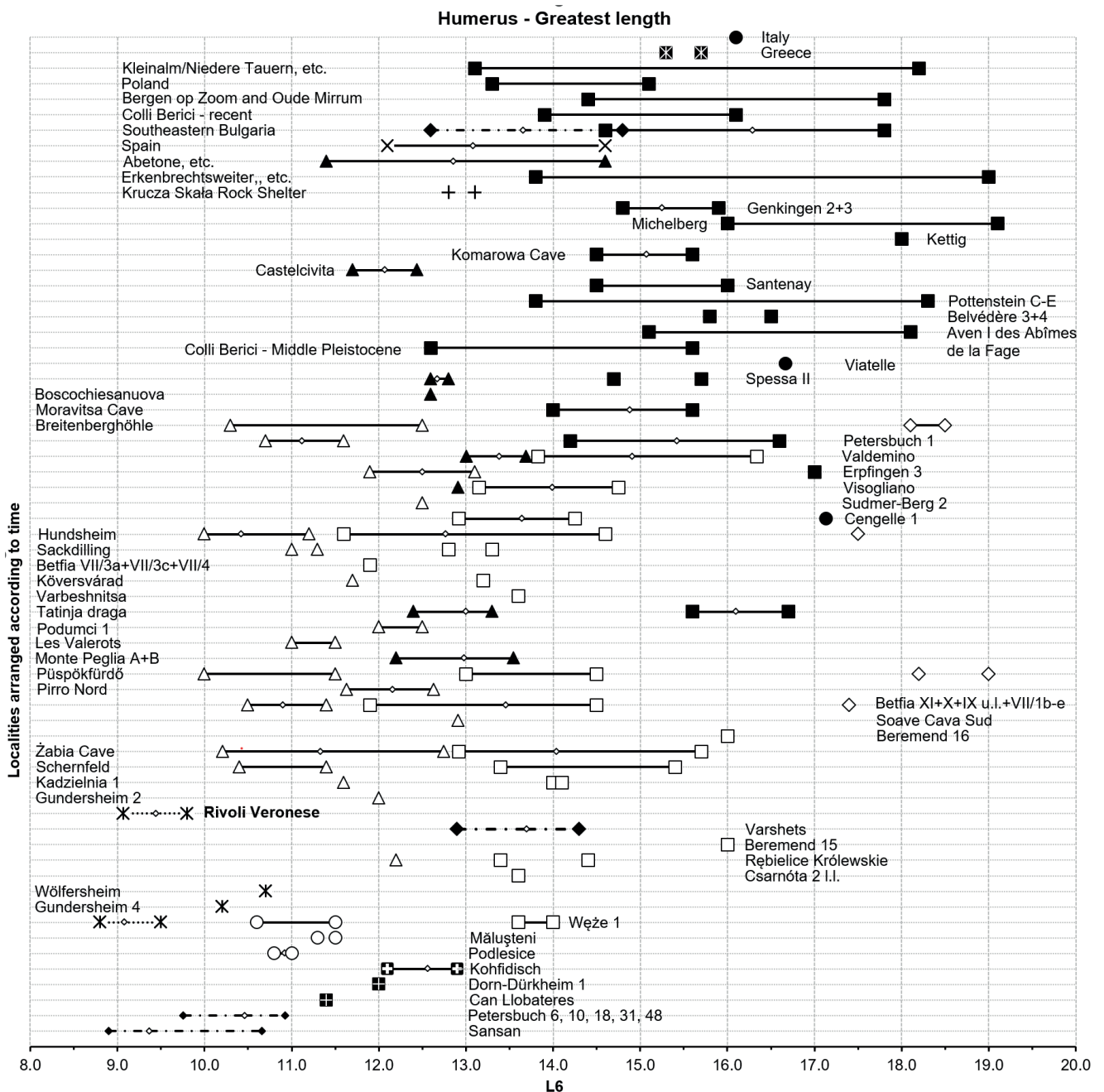
**Humeri.** V-shaped delto-pectoral ridge; rather variable pectoral tubercle both in outline and position, respectively triangular and in a central position (RV374; Text-fig. 10a), or tongue-shaped and in a lateral position (RV376) (Text-fig. 10c), depending on the specimens; head situated rather laterally; axis of the head subparallel to the long axis from the base to the proximal end.

**Related forms.** Fanfani (1999) observed on the humeri of the Italian *Talpa* populations an increase of size and robustness, and conversely, a decrease of the index of flattening over time. On the basis of these observations, he showed that the tiny mole from Rivoli Veronese is at the most primitive stage of evolution. An additional primitive characteristic noticeable in some remains from Rivoli Veronese can be considered the central position of the pectoral tubercle, given that this feature is found only in some of the earlier species (Tab. 3). Therefore, I inferred that this tiny mole cannot represent an offspring of any penecontemporaneous species, and thus is not merely an isolated occurrence in the history of moles. Instead, given its primitiveness, it is likely evolutionarily related to earlier populations.

Tiny mole remains were previously found in Central European late Ruscian – MN 15 to early Villanyian – MN 16 faunas of Węże 1 (Sulimski 1962), Wölfersheim and Gundersheim 4 (Dahlmann 2001), and Hajnáčka 1 (Sabol 2004) as well. Nevertheless, they were assigned to *T. minor*. For example, Sulimski (1962) believed that the smallest humeri and teeth he described from Węże 1 belonged to young individuals of the population of *T. minor*, already recorded by Sulimski (1959) at the site, and later assigned to *T. neagui* by Rădulescu and Samson (1989). Fanfani and Masini (1997) and Fanfani (1999) implicitly rejected this assumption. According to the pictures and the text, even if some humeri seem in fact to belong to young individuals, some others of these supposed young individuals display

the same structure as those stated to represent adults. In that circumstance, individuals with an intermediate size between the supposed young individuals and the adults would have been expected. In any case, no size difference in teeth can exist between young and adult individuals, because in *Talpa*, tooth-succession occurs before birth or, at least, before the time when fur grows upon the young creatures' backs, and milk teeth differ notably from the permanent functional teeth, being rudimental and useless as organs of mastication (Spence Bate 1867, Bolk 1923). Instead, according to the text, the teeth assigned to young individuals are permanent functional teeth while being sharply smaller than those assigned to adult individuals.

As I observed a sharp size difference between the above-mentioned Central European late Ruscian to early Villanyian moles and the other moles of same age assigned to *T. neagui* and *T. minor* (Text-figs 3–9), I inferred that these tiny moles might represent a new species. Hence, I assumed that they belong to *T. masinii* n. sp., because of the absence of any clear dimensional and morphological difference with the tiny mole from Rivoli Veronese. The large age difference between the above-mentioned faunas and that from Rivoli Veronese cannot be used to reject a specific similarity. In fact, the absence of *T. masinii* n. sp. for such a long time can be explained by the scantiness of *Talpa* remains in faunas of intermediate age, and by the scantiness itself of small mammal faunas from that intermediate time period (Text-fig. 2). Its absence from faunas of intermediate age could also imply that, in later periods, it survived only locally as a Pliocene relict species, like other taxa collected in Rivoli Veronese (*Rhagapodemus* and *Pliopetaurista*; Berto et al. 2022) and in other late Villanyian European faunas (for example, *Blarinoides mariae*, *Sulimskia kretzoi*, and *Deinsdorfia hibbardi* in Poland (Nadachowski 1998), and *Dolomys milleri* in Hungary (Pazonyi et al. 2016)). Finally, I assumed that the smallest humerus (Text-fig. 6) collected at Coste San Giacomo (Bona et al. 2015) might represent an additional late Villanyian record of *T. masinii* n. sp., and thus its southernmost record. As a result, by taking into consideration all the populations here assigned to *T. masinii*



Text-fig. 4. Diagram of greatest length of humerus in fossil and recent *Talpa*.

n. sp., the lower molar row, even if represented by scanty remains, appears to be graded in size with  $Lm1 > Lm2$  and possibly with  $Lm2 = Lm3$ .

**Phylogenetic links.** Because *T. masinii* n. sp. shows both similarities and differences in morphology and size compared to both earlier and later tiny to small species *T. minuta*, *T. gilothi*, *T. aff. gilothi*, *T. neagui*, and *T. minor*, with a mixture of features without any apparent ancestor-descendant relationship, this pushed me to exclude a phylogenetic link between *T. masinii* n. sp. and those five species, although *T. neagui* appears to be the species with the greatest similarities, particularly with regard to the size graduation of lower molars (Tab. 3). However, this is a preliminary observation, as the comparison is, in some circumstances, of limited value, due to the scarcity or lack of data regarding some features of these species.

**Biochronological range of the new species.** From late Ruscinian – MN 15b to late Villanyian – MN 17/1 Rodent Ages (chronologically corresponding to the latest Early Pliocene to early Early Pleistocene Subepoch – latest Zanclean to Gelasian Ages).

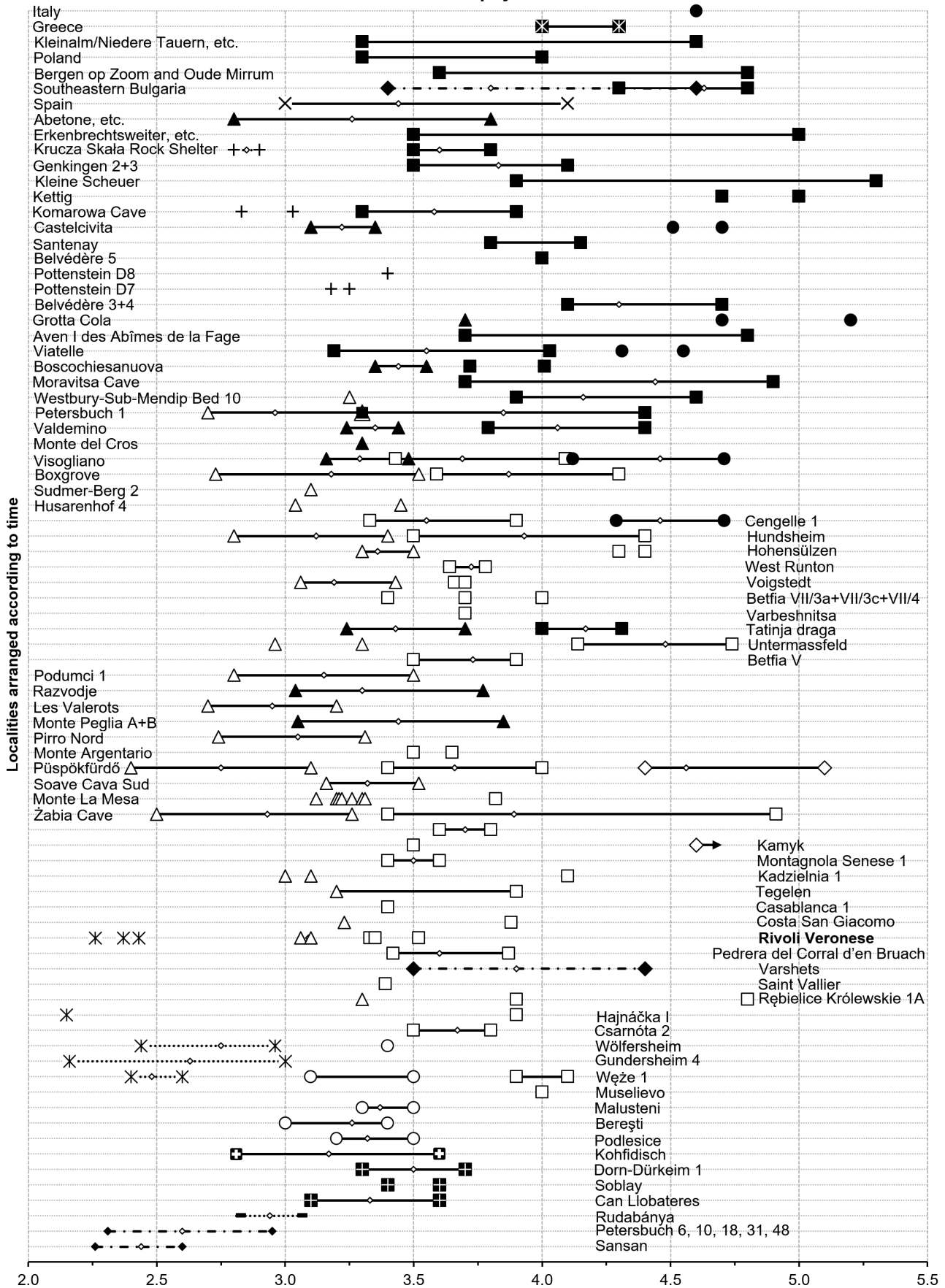
**Palaeobiogeographical range of the new species.** Central Europe and Italy.

## Discussion

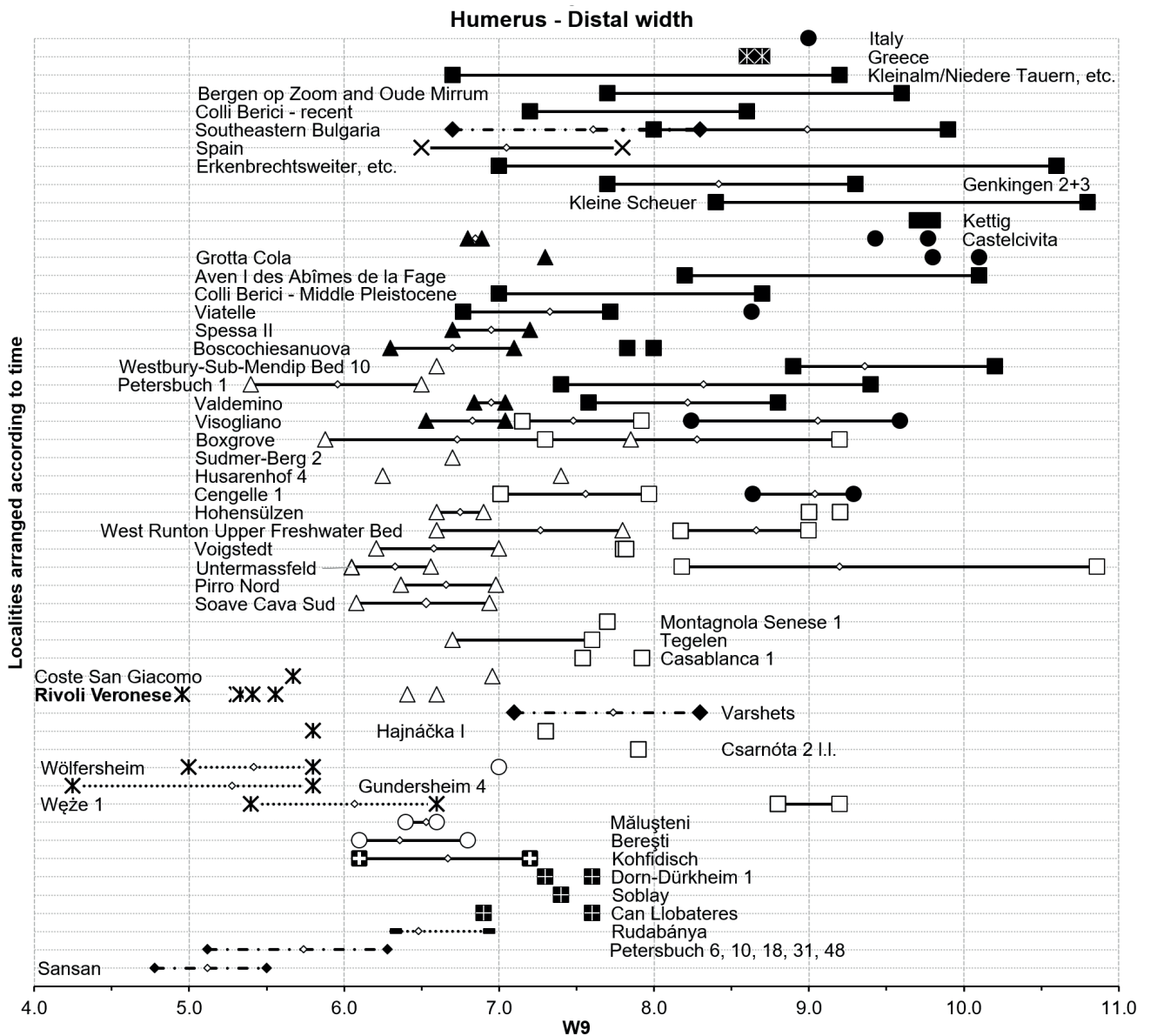
The mole remains fitting in the tiny size category from Central Europe and here assigned to *T. masinii* n. sp. were sometimes found associated with those fitting in the small size category that were ascribed to *T. gilothi* in Wölfersheim (Dahlmann 2001) (a species originally described by Storch



### Humerus - Diaphysis width



Text-fig. 5. Diagram of diaphysis width of humerus in fossil and recent *Talpa*.

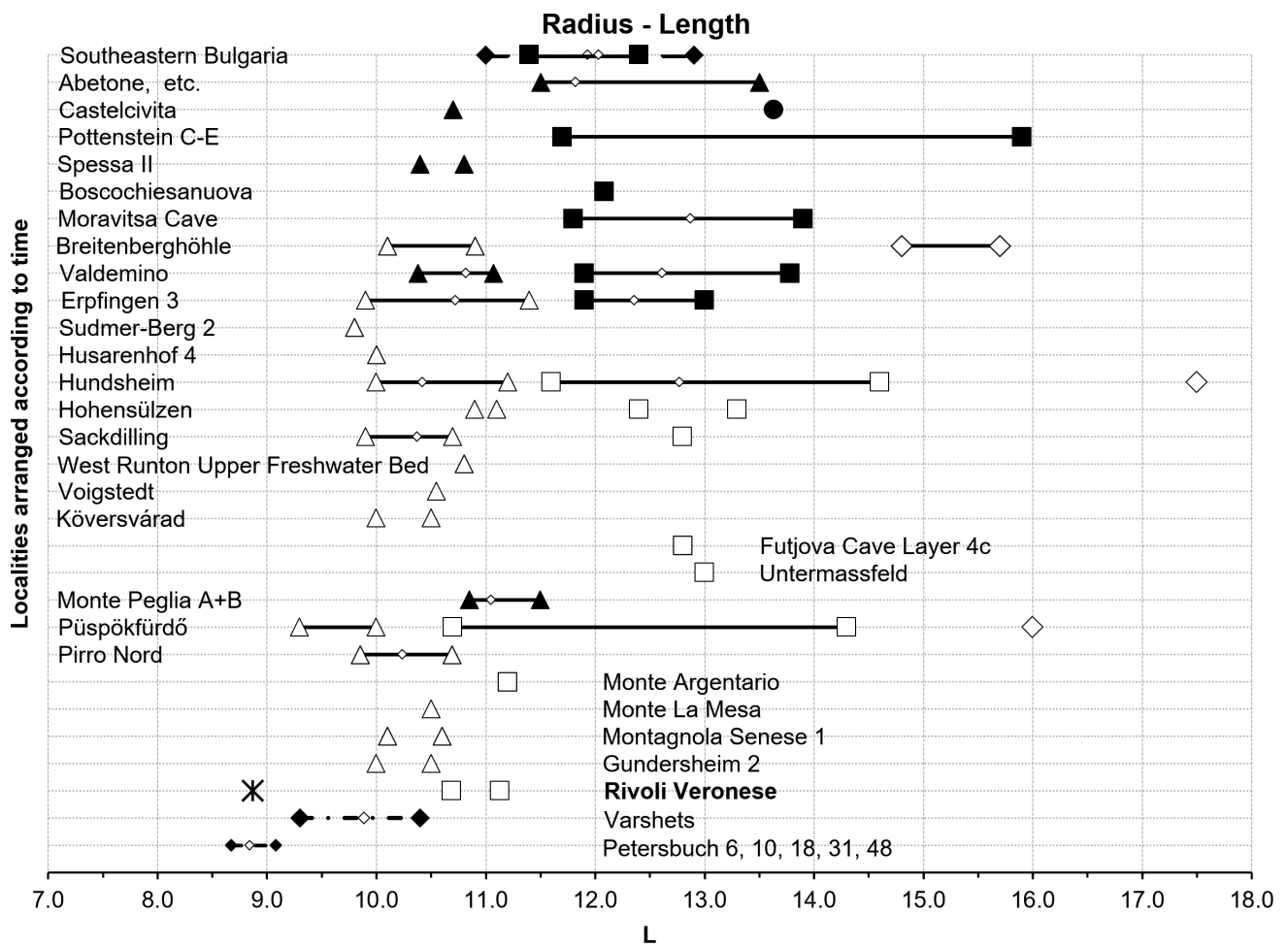


Text-fig. 6. Diagram of distal width of humerus in fossil and recent *Talpa*.

(1978) from the early Turolian Dorn-Dürkheim 1 fauna), and to *T. neagui* in Weže 1 (Rădulescu and Samson 1989). Rădulescu and Samson (1989) observed that *T. neagui* was common and widespread during the Ruscinian, as it was recorded in Berești, Podlesice, Mălușteni, and, possibly, in Musaid (= Musaitu 5) too. It differs from the similarly small Villanyian to early Toringian *T. minor*. In fact, when compared to the latter, it bears: on average, a more robust humerus (L4 in the range of *T. minor*, whereas W1 and W2 in the range between the largest remains of *T. minor* and the smallest remains of *T. fossilis*); a pectoral tubercle with a rather central position (instead of being lateral); and a more gracile mandible with lower molars that, even if based on scanty remains, appears to be graded in size with  $Lm1 > Lm2 > Lm3$ , instead of being graded in size with  $Lm2 > Lm1 = Lm3$  (Text-fig. 9). Meanwhile, *T. gilothi* and *T. neagui*, besides differing distinctively in age (MN 10–12 and MN 14–15, respectively), are clearly different from each other in proportions of the humerus and position of the pectoral tubercle (Rădulescu and Samson 1989) (Tab. 3). The humeri from Wölfersheim

equal in size those of *T. neagui* too, and no reason is found to differentiate the remains of Wölfersheim from the latter species. Therefore, all the small remains of Ruscinian age assigned in the past to *T. gilothi* or to *T. minor* should belong to *T. neagui*. The mole remains found in Moncucco Torinese ascribed to *T. minor* by Colombero et al. (2017) may belong to *T. neagui* as well. In fact, although no dimensional data were given by the authors, these remains were described to be smaller than those of *T. gilothi* and *T. vallesensis*, and similar to those of *T. minor* described by Sulimski (1959) from the Pliocene of Poland, the latter remains being merely those from Weže 1, which I here assigned to *T. neagui*, according to the humerus size and proportions. This could imply that the latter species already existed in MN 13.

*T. minuta*, as an extra note because it is similar in size to *T. masinii* n. sp., is exceptionally mentioned outside the Miocene in the Middle Pleistocene layer 23 of Petralona Cave (Kretzoi and Poulianos 1981). The authors did not give any measurements, but only asserted that it was probably referable to the Middle Pleistocene species *T. minuta* FREUDENBERG.



Text-fig. 7. Diagram of greatest length of radius in fossil and recent *Talpa*.

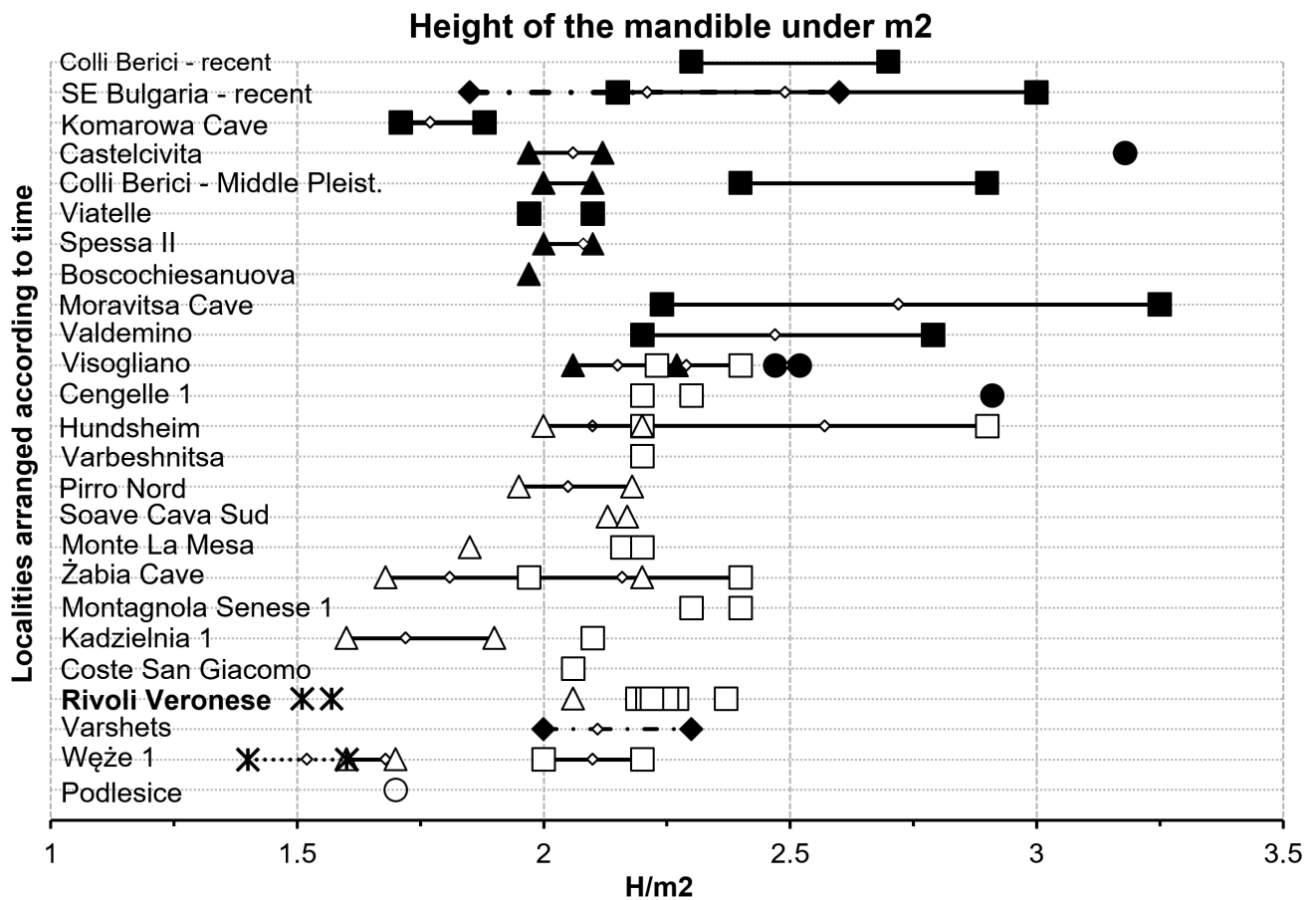
Because Freudenberg was the author who erected the species *T. minor*, whereas *T. minuta* was erected by Blainville, and *T. minor* type population is of Middle Pleistocene age, whereas *T. minuta* lived during the Miocene, I inferred that, in truth, Kretzoi and Poulianos intended to refer it to *T. minor*.

The size of the mole remains from Rivoli Veronese offered new insights into the Plio-Pleistocene mole record regarding size categories. Here three size categories were recognized: one being distinctively smaller than the fossil small size category; one fitting in the fossil small size category; and one fitting in the fossil middle size category. The large size category is missing. Therefore, taking into consideration all the populations assigned in this study to *T. masinii* n. sp., a fourth category existed, the tiny one, not only among the Miocene but also among the Plio-Pleistocene moles.

Rivoli Veronese is thus a site where the coexistence of up to three *Talpa* species is documented within a single fauna. Accordingly to past literature and new species assignments made in this study, three *Talpa* species also co-occurred in Weże 1, Coste San Giacomo, Betfia IX upper level, Püspökfürdő (= Betfia 2), Hundsheim, and Visogliano. Therefore, this is a rare condition, but it is now becoming less unusual in the fossil record. All these faunas were considered assemblages that accumulated over a relatively short period; thus, they are not mixed assemblages. Therefore, this infrequent coexistence rather suggests some form of specialization to avoid competition, particularly considering

that in Europe, sympatry among recent *Talpa* species occurs between a maximum of two species, while syntopy never occurs (Loy et al. 2017). Until now, at least in Italy, the size of mole species has been related to several factors (Fanfani 1999, Loy et al. 2005, Loy 2008), including soil aridity and depth, climate, litter composition, and others; however, no definitive conclusion has been reached. As later discussed by Loy et al. (2017), the reason for the current distribution of European moles is even more complex. Therefore, the coexistence of three *Talpa* species in fossil faunas may have resulted from a mix of factors suitable for each species, either concentrated in one location or, more likely, scattered throughout the catchment area. That area might have been spatially extended both vertically (with the presence of plains, hills, and mountains) and horizontally, encompassing diverse environmental conditions that provided suitable habitats for up to three *Talpa* species. As previously noticed, Fanfani (1999) observed on the humeri of the Italian *Talpa* populations an increase of size, robustness and, conversely, a decrease of the index of flattening over time. This is in line with the trend of increase in size in many mammal species observed by Mazza and Bertini (2012) and Bokma et al. (2016). Additionally, the mole remains from the analysed faunas show a general trend of replacement over time, from Ruscinian to present, of small *Talpa* species with larger ones (Text-fig. 2). Fanfani (1999) suggests that the size, robustness and depth of the humerus in moles indicate an





Text-fig. 8. Diagram of mandible height under m2 in fossil and recent *Talpa*.

evolutionary trend linked to the transition from soft, moist soils, more suitable for small moles, to hard, arid soils, which are better suited for larger moles, resulting from the increasing aridity observed from the Pliocene to the present day. Analysing the cited literature, the aforementioned reasons for geographic distribution appear, in some cases, to contrast with the general trend of evolution, as they are influenced by a complex combination of factors.

For now, the origin of *T. masinii* n. sp. remains unknown, as indicated by the discussion in Phylogenetic links of Systematic Palaeontology section and because the limited records of small *Talpa* species during the long period from MN 12 to MN 14, spanning about four million years, are described either poorly or not at all.

## Conclusions

The Rivoli Veronese fauna filled a gap in our understanding of the history of the genus *Talpa* in Europe as, up to now, the period from the early to late Villanyian yielded only scant faunas containing significant or described mole remains.

Based on the bibliographical analysis of numerous fossil populations, I proposed some changes in the taxonomic attribution of the moles recorded in certain faunas. This permitted:

- to attest that the coexistence of up to three *Talpa* species in a local fauna (with no mixed assemblage) was not an exception in the history of the genus *Talpa*;

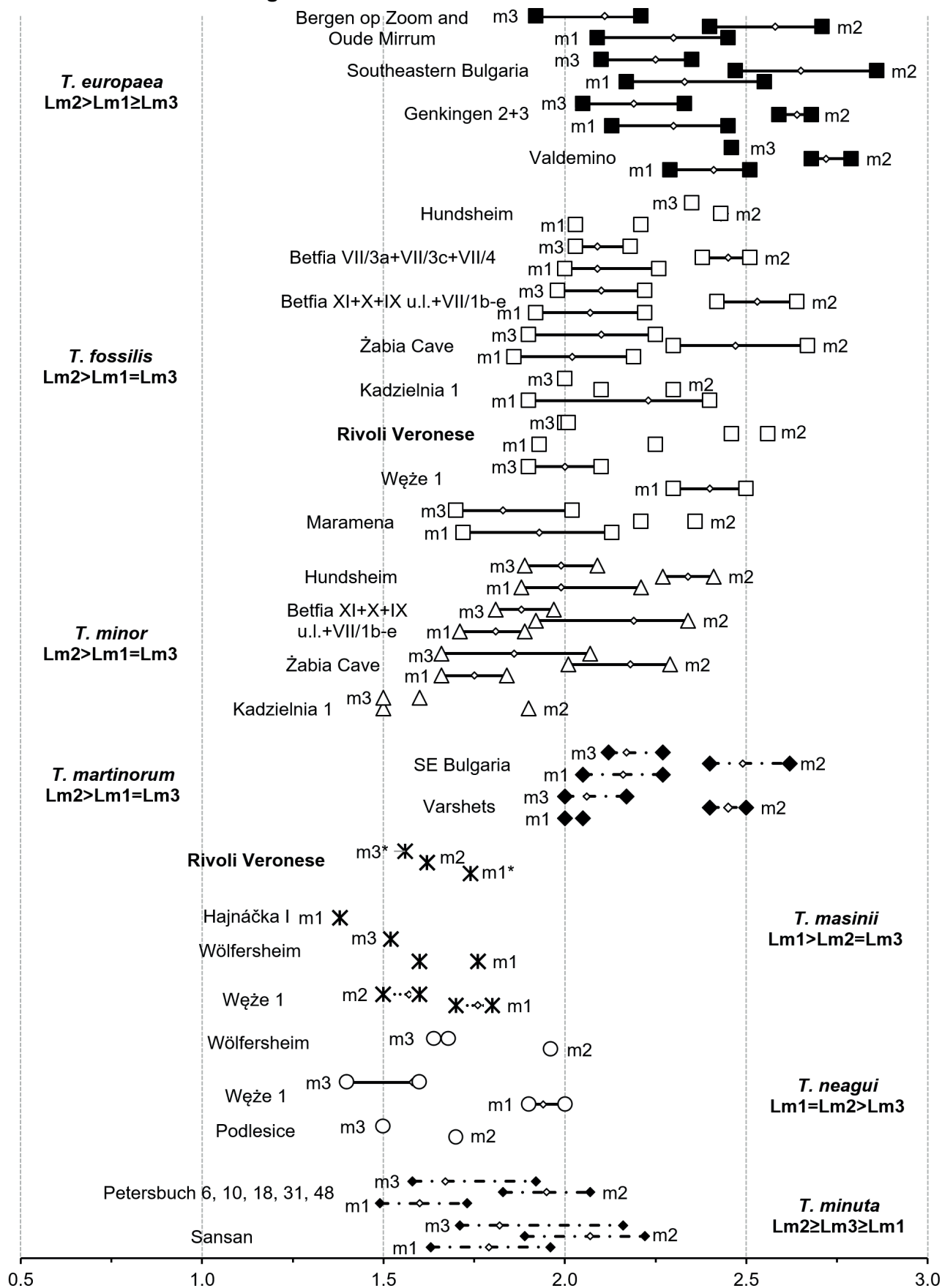
- to extend the existence of tiny moles up to the late Villanyian;
- to stress that the usual dimensional and morphological characteristics, plus some new ones here used, are helpful to some extent to discriminate the species among fossil *Talpa* populations;
- to recognize, by more precisely fixing the taxonomy and the biochronologic age of the examined *Talpa* populations, that the genus *Talpa* is useful for biochronological inferences.

However, the scantiness of fossils remains, and the summary descriptions existing in literature prevent, in some circumstances, solid conclusions, unless a direct revision of the old collections is carried out, in particular those of the type species populations. Thus, the objective to give a comprehensive picture of the evolution of the genus *Talpa* is far from being achieved, also because the present considerations covered mainly those species and populations of interest for the present work. More specific inferences on single species that might be or have been derived from the exposed data need further discussion. All this requires further study.

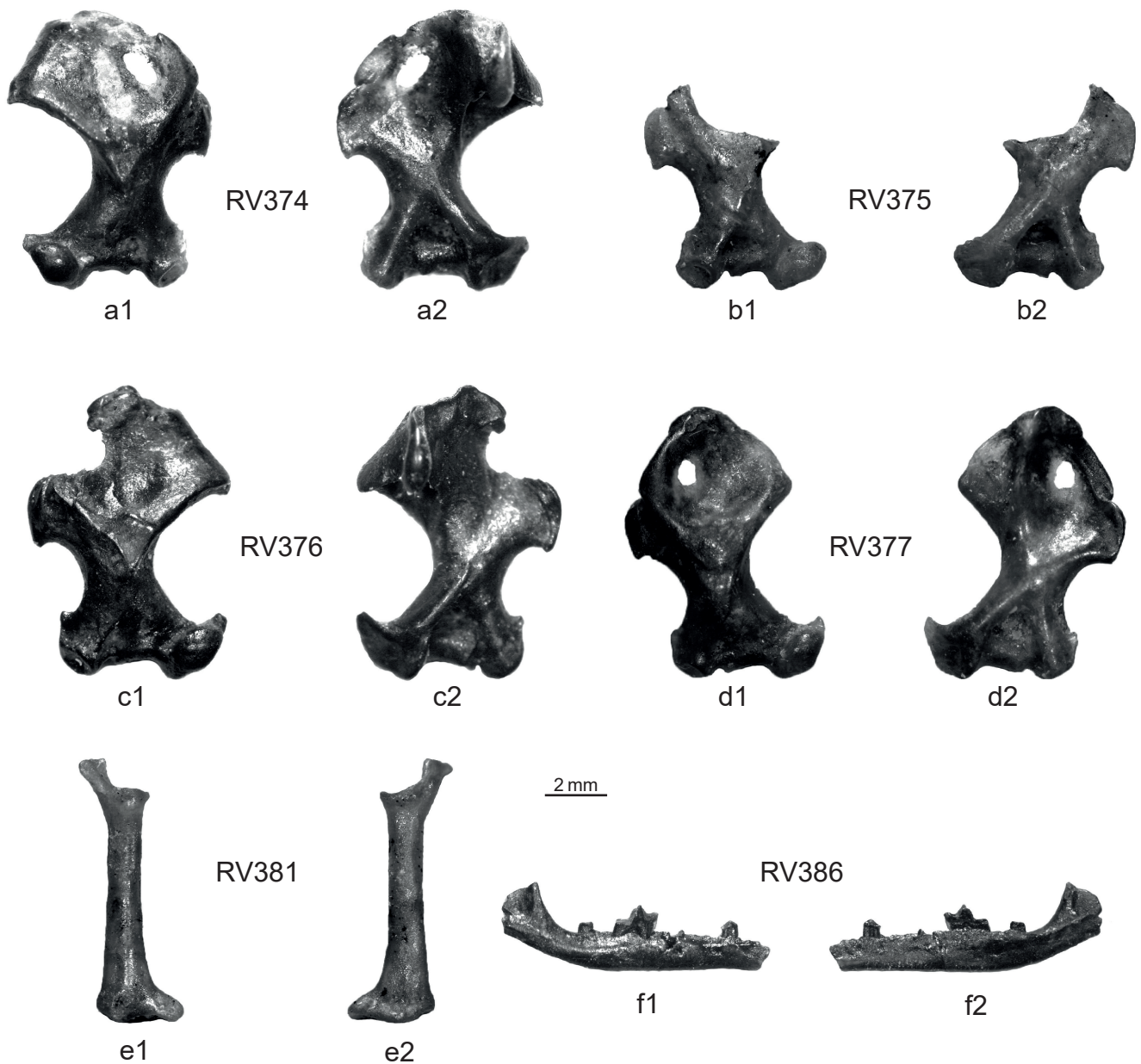
## Acknowledgements

I am deeply grateful to Prof. Benedetto Sala of the Museo di Paleontologia e Preistoria Piero Leonardi of the University of Ferrara for allowing me to study the Rivoli Veronese collection, and for providing access to his extensive

### Size graduation of teeth of the lower molar row



Text-fig. 9. Diagram of length of three lower molars in most representative populations in fossil and recent *Talpa*.



**Text-fig. 10.** *T. masinii* nov. sp. a: R humerus; 1 – anterior view, 2 – posterior view (RV374). b: L humerus; 1 – anterior view, 2 – posterior view (RV375). c: L humerus; 1 – anterior view, 2 – posterior view (RV376). d: L humerus; 1 – anterior view, 2 – posterior view (RV377). e: L radius; 1 – external view, 2 – internal view (RV381). f: R mandible with p3 and m2; 1 – labial view, 2 – lingual view (RV385).

bibliographic collection, as well as for his invaluable teachings. I also thank Dr. Marzia Breda for her valuable feedback on the English and the text. My appreciation extends to the staff at the Library of the Natural Science Museum of Brescia for providing essential bibliographic material.

## References

- Angelone, C., Colombero, S., Esu, D., Giuntelli, P., Marcolini, F., Pavia, M., Trenkwalder, S., Hoek Ostende, L. W. van den, Zunino, M., Pavia, G. (2011): Moncucco Torinese, a new post-evaporitic Messinian fossiliferous site from Piedmont (NW Italy). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen*, 259(1): 89–104. <https://doi.org/10.1127/0077-7749/2010/0108>
- Bannikova, A. A., Zemlemerova, E. D., Colangelo, P., Sözen, M., Sevindik, M., Kidov, A. A., Dzuev, R. I., Kryštufek, B., Lebedev, V. S. (2015): An underground burst of diversity – a new look at the phylogeny and taxonomy of the genus *Talpa* Linnaeus, 1758 (Mammalia: Talpidae) as revealed by nuclear and mitochondrial genes. – *Zoological Journal of the Linnean Society*, 175(4): 1–19. <https://doi.org/10.1111/zoj.12298>
- Bartolomei, G. (1964): Mammiferi di breccie pleistoceniche dei Colli Berici (Vicenza) [Mammals from Pleistocene breccias of the Berici Hills (Vicenza)]. – *Memorie del Museo Civico di Storia Naturale di Verona*, 10 (1962): 233–242. (in Italian)
- Bartolomei, G., Pasa, A. (1970): La breccia ossifera di Boscochiesanuova nei Monti Lessini (Verona): i depositi e la fauna [The ossiferous breccia of Boscochiesanuova in



- the Lessini Mountains (Verona): deposits and fauna]. – *Memorie del Museo Civico di Storia Naturale di Verona*, 17: 475–494. (in Italian)
- Berto, C., Luzi, E., Marchetti, M., Pereswiet-Soltan, A., Sala, B. (2022): Faunal renewals during the Early Pleistocene on the northern Italian Peninsula: Climate and environment reconstructions inferred from the Rivoli Veronese small mammal assemblage (Adige River valley, Verona, Italy). – *Quaternary International*, 633: 134–153. <https://doi.org/10.1016/j.quaint.2021.11.025>
- Bishop, M. J. (1982): The mammal fauna of the early Middle Pleistocene cavern infill site of Westbury-Sub-Mendip. – *Special Papers in Palaeontology*, 28: 1–108.
- Bokma, F., Godinot, M., Maridet, O., Ladevèze, S., Costeur, L., Solé, F., Gheerbrant, E., Peigné, S., Jacques, F., Laurin, M. (2016): Testing for Depéret’s Rule (body size increase) in Mammals using combined extinct and extant data. – *Systematic Biology*, 65(1): 98–108. <https://doi.org/10.1093/sysbio/syv075>
- Bolk, L. (1923): Odontological essays. V. On the relation between reptilian and mammalian dentition. – *Journal of Anatomy*, London, 57: 55–75.
- Bona, F., Bellucci, L., Sardella, R. (2015): The Gelasian (Late Villanyan-MN17) diversified micromammal assemblage with *Miomys pliocaenicus* from Coste San Giacomo (Anagni basin, central Italy), taxonomy and comparison with selected European sites. – *Hystrix, the Italian Journal of Mammalogy*, 26(2): 141–151.
- Brunner, G. (1934): Eine präglaciale Fauna aus dem Windloch bei Sackdilling (Oberpfalz). – *Neues Jahrbuch für Mineralogie*, 71: 303–328.
- Brunner, G. (1951): Die “Kleine Teufelshöhle” bei Pottenstein (Oberfranken). Ein Faunenprofil vom Mindel-Riß-Interglazial bis zum Spätmagdalenien. – *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-naturwissenschaftliche Klasse*, N. F., 60: 1–46.
- Brunner, G. (1958): Die Breitenberg-höhle bei Gossweinstein (Ofr.). – *Neues Jahrbuch für Geologie und Palaeontologie, Monatshefte*, 1958(11): 500–517.
- Cleef-Rodgers, J. T. van, Hoek Ostende, L. W. van den (2001): Dental morphology of *Talpa europaea* and *Talpa occidentalis* (Mammalia: Insectivora) with a discussion of fossil *Talpa* in the Pleistocene of Europe. – *Zoologische Mededelingen*, 75(2): 51–68.
- Cohen, K. M., Finney, S. C., Gibbard, P. L., Fan, J.-X. (2013; updated) The ICS International Chronostratigraphic Chart. – *Episodes*, 36: 199–204. (updated version 2023/09 available online: <http://www.stratigraphy.org/ICSchart/ChronostratChart2023-09.pdf>)
- Colangelo, P., Bannikova, A. A., Kryštufek, B., Lebedev, V. S., Annesi, F., Capanna, E., Loy, A. (2010): Molecular systematics and evolutionary biogeography of the genus *Talpa* (Soricomorpha: Talpidae). – *Molecular Phylogenetics and Evolution*, 55(2): 372–380. <https://doi.org/10.1016/j.ympev.2010.01.038>
- Colombero, S., Alba, D. M., D’Amico, C., Delfino, M., Esu, D., Giuntelli, P., Harzhauser, M., Mazza, P. P. A., Mosca, M., Neubauer, T. A., Pavia, G., Pavia, M., Villa, A., Carnevale, G. (2017): Late Messinian mollusks and vertebrates from Moncuoco Torinese, north-western Italy. Paleoeological and paleoclimatological implications. – *Palaeontologia Electronica*, 20.1.10A: 1–66. <https://doi.org/10.26879/658>
- Dahlmann, T. (2001): Die Kleinsäuger der unter-pliozänen Fundstelle Wölfersheim in der Wetterau (Mammalia: Lipotyphla, Chiroptera, Rodentia). – *Courier Forschungs-institut Senckenberg*, 227: 1–129.
- Dahlmann, T., Storch, G. (1996): Eine pliozäne (ober-russische) Kleinsäugerfauna aus Gundersheim, Rheinhessen – 2. Insektenfresser: Mammalia, Lipotyphla. – *Senckenbergiana lethaea*, 76(1-2): 181–191. <https://doi.org/10.1007/BF03042849>
- Dehm, R. (1962): Altpleistocäne Säuger von Schernfeld bei Eichstätt in Bayern. – *Mitteilungen Bayerische Staatssammlung für Paläontologie und Historische Geologie*, 2: 17–61.
- Di Canzio, E., Petronio, C. (2001): Osservazioni sulla fauna a vertebrati pleistocenici della Grotta Cola (Abruzzo, Aquila) [Observations on the Pleistocene vertebrate fauna of Cola Cave (Abruzzo, Aquila)]. – *Bollettino della Società Paleontologica Italiana*, 40(1): 105–114. (in Italian)
- Doukas, C. S., Hoek Ostende, L. W. van den, Theocharopoulos, C., Reumer, J. W. F. (1995): The vertebrate locality Maramena (Macedonia, Greece) at the Turolian-Ruscian boundary (Neogene). 5. Insectivora (Erinaceidae, Talpidae, Soricidae, Mammalia). – *Münchner Geowissenschaftliche Abhandlungen, A*, 28: 43–64.
- Fanfani, F. (1999): Revisione degli insettivori (Mammalia) tardo Neogenici e Quaternari dell’Italia peninsulare [Review of the Late Neogene and Quaternary Insectivores (Mammalia) of Peninsular Italy]; Ph.D. Thesis. – MS, Università degli Studi di Modena e Reggio Emilia, Modena, Italy, 283 pp. (in Italian) (copy in library of MM)
- Fanfani, F., Masini, F. (1997): Insectivores (Mammalia) from Rivoli Veronese, a Late Villanyian site in Northeastern Italy. – *Bollettino della Società Paleontologica Italiana*, 36(3): 367–380.
- Fejfar, O. (2001): The Arvicolids from Arondelli-Triversa: A new look. – *Bollettino della Società Paleontologica Italiana*, 40(2): 185–193.
- Fejfar, O., Heinrich, W.-D., Pevzner, M. A., Lindsay, E. H. (1998): Updating the Neogene Rodent biochronology in Europe. – *Mededelingen Nederlands instituut voor toegepaste Geowetenschappen TNO*, 60: 533–553.
- Fejfar, O., Heinrich, W.-D., Pevzner, M. A., Vangengeim, E. A. (1997): Late Cenozoic sequences of mammalian sites in Eurasia: An updated correlation. – *Palaeogeography, Palaeoclimatology, Palaeoecology*, 133(3-4): 259–288. [https://doi.org/10.1016/S0031-0182\(97\)00085-0](https://doi.org/10.1016/S0031-0182(97)00085-0)
- Fejfar, O., Sabol, M. (2015): Czech Republic and Slovak Republic. – In: Hoek Ostende, L. W. van den, Doukas, C. S., Reumer, J. W. F. (eds), *The fossil record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia)*, Part I. *Scripta Geologica, Special Issue 5*: 51–60.
- Feuda, R., Bannikova, A. A., Zemlemerova, E. D., Di Febbraro, M., Loy, A., Hutterer, R., Aloise, G., Zykov, A. E., Annesi, F., Colangelo, P. (2015): Tracing the evolutionary history of the mole, *Talpa europaea*, through

- mitochondrial DNA phylogeography and species distribution modelling. – *Biological Journal of the Linnean Society*, 114(3): 495–512.  
<https://doi.org/10.1111/bij.12459>
- Fondi, R. (1972): Fauna cromeriana della Montagnola Senese [Cromerian fauna of Montagnola Senese]. – *Palaeontographia Italica*, 38: 1–27, tabs I–III. (in Italian)
- Freudentberg, W. (1914): Die Säugetiere des älteren Quartärs von Mittel Europa mit besonderer Berücksichtigung der Fauna von Hundsheim und Deutschaltenburg in Niederösterreich. – *Geologie und Paläontologie Abhandlung, N. F.*, 12(4-5): 455–670.
- Furió Bruno, M. (2007): Los Insectívoros (Soricomorpha, Erinaceomorpha, Mammalia) del Neógeno Superior del Levante Ibérico [Insectivores (Soricomorpha, Erinaceomorpha, Mammalia) from the Upper Neogene of the Iberian Levant]; Ph.D. Thesis. – Universitat Autònoma de Barcelona, Barcelona, 299 pp + appendix 1+2. (in Spanish) (available online: <http://www.tdx.cat/TDX-0331109-161745>)
- Furió, M., Angelone, C. (2010): Insectivores (Erinaceidae, Soricidae, Talpidae; Mammalia) from the Pliocene of Capo Mannu D1 (Mandriola, central-western Sardinia, Italy). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlung*, 258(2): 229–242.  
<https://doi.org/10.1127/0077-7749/2010/0100>
- Giacobini, G., Malaroda, R., Biancotti, A., Jeannet, M., Arobba, D. (1980): La breccia ossifera del Monte dei Cros (Andonno, Cuneo) [The ossiferous breccia of Monte dei Cros (Andonno, Cuneo)]. – In: *Quaderni della Soprintendenza archeologica del Piemonte, Studi di Archeologia dedicati a Pietro Barocelli*. Ministero per i beni culturali e ambientali, Torino, pp. 55–71. (in Italian)
- Heller, F. (1936): Eine oberpliozäne Wirbeltierfauna aus Rheinhessen. – *Neues Jahrbuch für Geologie und Paläontologie, Abt. B*, 76: 99–160.
- Heller, F. (1958): Eine neue altquartäre Wirbeltierfauna von Erpfingen (Schwäbische Alb). – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlung*, 118(1): 1–20.
- Hoek Ostende, L. W. van den, Fejfar, O. (2006): Erinaceidae and Talpidae (Erinaceomorpha, Soricomorpha, Mammalia) from the Lower Miocene of Merkur-Nord (Czech Republic, MN 3). – *Beiträge zur Paläontologie*, 30: 175–203.
- Hoek Ostende, L. W. van den, Furió, M. (2005): Spain. – In: Hoek Ostende, L. W. van den, Doukas, C. S., Reumer, J. W. F. (eds), *The fossil record of the Eurasian Neogene Insectivores (Erinaceomorpha, Soricomorpha, Mammalia)*, Part I. *Scripta Geologica, Special Issue 5*: 149–284.
- Horáček, I., Ložek, V. (1988): Palaeozoology and the Mid-European Quaternary past: Scope of the approach and selected results. – *Rozprawy ČSAV, Řada matematických a přírodních věd*, 98(4): 1–102.
- Hutchison, J. H. (1974): Notes on type specimens of European Miocene Talpidae and a tentative classification of Old World Tertiary Talpidae (Insectivora: Mammalia). – *Geobios*, 7(3): 211–256.  
[https://doi.org/10.1016/S0016-6995\(74\)80009-4](https://doi.org/10.1016/S0016-6995(74)80009-4)
- Jamot, D. (1973): Les Insectivores (Mammalia) du gisement pléistocène moyen des Abîmes de la Fage à Noailles (Corrèze). – *Nouvelles archives du Muséum d'histoire naturelle de Lyon*, 11: 41–51.  
<https://doi.org/10.3406/mhnly.1973.1008>
- Jánosy, D. (1963): Die altpleistozäne Wirbeltierfauna von Köversvárad bei Répáshuta (Bükk-Gebirge). – *Annales Historico-Naturales Musei Nationalis Hungarici, Pars Mineralogica et Palaeontologica*, 55: 109–141.
- Jánosy, D. (1986): Pleistocene vertebrate faunas of Hungary (Developments in palaeontology and stratigraphy, no. 8). – Elsevier, Amsterdam, 208 pp.
- Jánosy, D. (1987): Ältestpleistozäne Vertebratenfauna von Beremend 15 (Süd-Ungarn). – *Fragmenta Mineralogica et Palaeontologica*, 13: 89–96.
- Jánosy, D. (1996): Lower Pleistocene vertebrate faunas from the localities 16 and 17 of Beremend (Southern Hungary). – *Fragmenta Mineralogica et Palaeontologica*, 18: 91–102.
- Kalthoff, D. C. (1998): Die Kleinsäuger (Mammalia) der Fundstelle Kettig (Rheinland-Pfalz, Deutschland) im Rahmen der allerödzeitlichen Säugetierfauna Mittel- und Süddeutschlands. – *Paläontologische Zeitschrift*, 72(3-4): 407–424.  
<https://doi.org/10.1007/BF02988369>
- Klietmann, J., Nagel, D., Rummel, M., Hoek Ostende, L. W. van den (2015): A gap in digging: The Talpidae of Petersbuch 28 (Germany, Early Miocene). – *Paläontologische Zeitschrift*, 89(3): 563–592.  
<https://doi.org/10.1007/s12542-014-0228-2>
- Koenigswald, W. von (1970): Mittelpleistozäne Kleinsäugerfauna aus der Spaltenfüllung Petersbuch bei Eichstätt. – *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und historische Geologie*, 10: 407–432.
- Koenigswald, W. von (1973): Husarenhof 4, eine alt- bis mittelpleistozäne Kleinsäugerfauna aus Württemberg mit *Petauria*. – *Neues Jahrbuch für Geologie und Paläontologie, Abhandlung*, 143(1): 23–38.
- Koenigswald, W. von (1985): Die Kleinsäuger aus der *Al-lactaga*-Fauna von der Villa Seckendorf in Stuttgart-Bad Cannstatt aus dem frühen letzten Glazial. – *Stuttgarter Beiträge zur Naturkunde, Ser. B (Geologie und Paläontologie)*, 110: 1–40.
- Kolfschoten, M. (1985): The Middle Pleistocene (Saalian) and Late Pleistocene (Weichselian) mammal faunas from Maastricht-Belvédère, Southern Limburg, The Netherlands. – *Mededelingen Rijks Geologische Dienst*, 39(1): 45–74.
- Kordos, L. (1991): Villányi-hegység, Villány, alsó-pleisztocén ösgerinces lelőhelyek [Lower Pleistocene paleovertebrate localities, Villány, the Villány Mts.]. – *Magyar Állami Földtani Intézet, Magyarország Geológiai Alapszelvényei*, 139: 1–6. (in Hungarian)
- Kormos, T. (1930): Diagnosen neuer Säugetiere aus der oberpliozänen Fauna des Somlyóberges bei Püspökfürdő. – *Annales Historico-Naturales Musei Nationalis Hungarici*, 27: 237–246.
- Kormos, T. (1937): Revision der Kleinsäuger von Hundsheim. – *Földtani Közlöny*, 67: 157–171.
- Koufos, G. D., Kostopoulos, D. S., Vlachou, T. D. (2005): Neogene/Quaternary mammalian migrations in Eastern Mediterranean. – *Belgian Journal of Zoology*, 135(2): 181–190.

- Kowalski, K. (1956): Insectivores, bats and rodents from the Early Pleistocene bone breccia of Podlesice near Kroczyce (Poland). – *Acta Palaeontologica Polonica*, 1(4): 331–394.
- Kowalski, K. (1958a): Altpleistozäne Kleinsäugerfauna von Podumci in Norddalmatien. – *Palaeontologia Jugoslavica*, 2: 4–28.
- Kowalski, K. (1958b): An Early Pleistocene fauna of small mammals from the Kadzielnia Hill in Kielce (Poland). – *Acta Palaeontologica Polonica*, 3(1): 1–47.
- Kowalski, K. (1960a): Pliocene Insectivores and Rodents from Rebielice Królewskie (Poland). – *Acta Zoologica Cracoviensia*, 5(5): 155–201.
- Kowalski, K. (1960b): An Early Pleistocene fauna of small mammals from Kamyk (Poland). – *Folia Quaternaria*, 1: 1–24.
- Kretzoi, M. (1938): Die Raubtiere von Gombaszög nebst einer Übersicht der Gesamtf fauna. – *Annales Historico-Naturales Musei Nationalis Hungarici*, 31: 88–157.
- Kretzoi, M. (1959): Insectivoren, Nagetiere und Lagomorphen der jüngstpliozänen Fauna von Csarnóta im Villányer Gebirge (Südungarn). – *Vertebrata Hungarica*, 1(2): 237–246.
- Kretzoi, M., Poulianos, N. A. (1981): Remarks on the Middle and Lower Pleistocene Vertebrate fauna in the Petralona Cave. – *Anthropos*, 8: 57–72.
- Kryštufek, B., Nedyalkov, N., Astrin, J. J., Hutterer, R. (2018): News from the Balkan refugium: Thrace has an endemic mole species (Mammalia: Talpidae). – *Bonn zoological Bulletin*, 67(1): 41–57.
- Lisiecki, L. E., Raimo, M. E. (2005): A Pliocene-Pleistocene stack of 57 globally distributed benthic  $\delta^{18}\text{O}$  records. – *Paleoceanography*, 20(1): PA1003 (17 pp.). <https://doi.org/10.1029/2004PA001071>
- López-García, J. M., Piñero, P., Agustí, J., Furió, M., Galán, J., Moncunill-Solé, B., Ruiz-Sánchez, F. J., Blain, H.-A., Sanz, M., Daura, J. (2024): Chronological context, species occurrence, and environmental remarks on the Gelasian site Pedrera del Corral d'en Bruach (Barcelona, Spain) based on the small-mammal associations. – *Historical Biology*, 36(3): 657–676. <https://doi.org/10.1080/08912963.2023.2180740>
- Loy, A. (2008): Famiglia Talpidae [Family Talpidae]. – In: Amori, G., Contoli, L., Nappi, A. (eds), *Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia*. Calderini, Bologna, pp. 91–130. (in Italian)
- Loy, A., Cassini, M. H., Colangelo, P., Di Febbraro, M. (2017): Distribution, spatial interaction and niche analysis in three species of European moles (genus *Talpa*, Soricomorpha: Mammalia) in Italy. – *Biological Journal of the Linnean Society*, 122(4): 872–882. <https://doi.org/10.1093/biolinnean/blx085>
- Loy, A., Colangelo, P., Annesi, F., Capanna, E. (2005): Origin and evolution of Western European moles (genus *Talpa*, Insectivora): A multidisciplinary approach. – *Mammal Study*, 30: S13–S17. [https://doi.org/10.3106/1348-6160\(2005\)30\[S13:OAE-OWE\]2.0.CO;2](https://doi.org/10.3106/1348-6160(2005)30[S13:OAE-OWE]2.0.CO;2)
- Made, J. van der (1999): Biogeography and stratigraphy of the Mio-Pleistocene mammals of Sardinia and the description of some fossils. – *DEINSEA*, 7: 337–360.
- Malez, M., Rabeder, G. (1984): Neues Fundmaterial von Kleinsäugetern aus der altpleistozänen Spaltenfüllung Podumci 1 in Norddalmatien (Kroatien, Jugoslawien). – *Beiträge zur Paläontologie von Österreich*, 11: 439–510.
- Marchetti, M., Parolin, K., Sala, B. (2000): The Biharian fauna from Monte La Mesa (Verona, northeastern Italy). – *Acta Zoologica Cracoviensia*, 43(1): 79–105.
- Martín Suárez, E., Mein, P. (2004): The Late Pliocene locality of Saint-Vallier (Drôme, France). Eleven micromammals. – *Geobios*, 37: 115–125. [https://doi.org/10.1016/S0016-6995\(04\)80011-1](https://doi.org/10.1016/S0016-6995(04)80011-1)
- Maul, L. (2001): Die Kleinsäugerreste (Insectivora, Lagomorpha, Rodentia) aus dem Unterpleistozän von Untermassfeld. – In: Kahlke, R.-D. (ed.), *Das Pleistozän von Untermassfeld bei Meiningen (Thüringen)*. Monographien des Römisch-Germanischen Zentralmuseums, 40(3): 783–887.
- Maul, L. (2022): New results on micromammals from the Early Pleistocene site of Untermassfeld. – In: Kahlke, R.-D. (ed.), *The Pleistocene of Untermassfeld near Meiningen (Thüringen, Germany)*. Monographien des Römisch-Germanischen Zentralmuseums Mainz, 40(5): 1567–1603.
- Maul, L., Parfitt, S. A. (2010): Micromammals from the 1995 Mammoth Excavation at West Runton, Norfolk, UK: Morphometric data, biostratigraphy and taxonomic reappraisal. – *Quaternary International*, 228(1-2): 91–115. <https://doi.org/10.1016/j.quaint.2009.01.005>
- Mayhew, D. F. (2015): Revised biostratigraphic scheme for the Early Pleistocene of the UK based on arvicolids (Mammalia, Rodentia). – *Geological Journal*, 50(3): 246–256. <https://doi.org/10.1002/gj.2591>
- Mazza, P. P. A., Bertini, A. (2012): An approach to body size fluctuations in Quaternary continental mammals: the case of hippopotamuses from Western Europe. – *Alpine and Mediterranean Quaternary*, 25(1): 67–74.
- Ménouret, B., Mein, P. (2008): Les vertébrés du Miocène supérieur de Soblay (Ain, France). – *Documents des Laboratoires de Géologie, Lyon*, 165: 3–97.
- Meulen, A. J. van der (1973): Middle Pleistocene smaller mammals from the Monte Peglia (Orvieto, Italy), with special reference to the phylogeny of *Microtus* (Arvicolidae, Rodentia). – *Quaternaria*, 17: 1–144.
- Nadachowski, A. (1998): Faunal succession of small mammal assemblages at the Pliocene-Pleistocene boundary in Poland. – *Mededelingen Nederlands instituut voor toegepaste Geowetenschappen TNO*, 60: 281–286.
- Niethammer, J. (1990): *Talpa*. – In: Niethammer, J., Krapp, F. (eds), *Handbuch der Säugetiere Europas*. Band 3/I, Insektenfresser, Primaten. AULA, Wiesbaden, pp. 93–161.
- Palombo, M. R. (2006): Biochronology of the Plio-Pleistocene terrestrial mammals of Sardinia: the state of the art. – *Hellenic Journal of Geosciences*, 41: 47–66.
- Paunović, M., Rabeder, G. (1996): Die altpleistozänen Kleinsäugerfaunen Razvodje und Tatinja draga in Südkroatien. – *Beiträge zur Paläontologie*, 21: 69–84.
- Pazonyi, P., Mészáros, L., Hír, J., Szentesi, Z. (2016): The lowermost Pleistocene rodent and soricid (Mammalia)



- fauna from Beremend 14 locality (South Hungary) and its biostratigraphical and palaeoecological implications. – *Fragmenta Palaeontologica Hungarica*, 33: 99–134.  
<https://doi.org/10.17111/FragmPalHung.2016.33.99>
- Pereira, E., Ottaviani-Spella, M.-M., Salotti, M. (2001): Punta di Calcina (Conca, South-Corsica): new dating (Middle Pleistocene) elaborated thanks to a discovery of *Talpa tyrrhenica* BATE, 1945 and of *Microtus (Tyrrhenicola) henseli* FORSYTH-MAJOR, 1882 primitive form. – *Geobios*, 34(6): 697–705.  
[https://doi.org/10.1016/S0016-6995\(01\)80031-0](https://doi.org/10.1016/S0016-6995(01)80031-0)
- Petényi, S. J. (1864): A beremendi mészkőbánya természetrajz- és őslénytanilag leírva [The Beremend Limestone quarry: its natural history and palaeontology]. – In: Kubinyi, F. (ed.), Petényi S. Janos hátrahagyott munkái. Pest, Eggenberger, pp. 35–81. (in Hungarian)
- Petronio, C., Angelone, C., Atzori, P., Famiani, F., Kotsakis, T., Salari, L. (2020): Review and new data of the fossil remains from Monte Peglia (late Early Pleistocene, central Italy). – *Rivista Italiana di Paleontologia e Stratigrafia*, 126(3): 791–819.
- Piras, P., Sansalone, G., Teresi, L., Kotsakis, T., Colangelo, P., Loy, A. (2012): Testing convergent and parallel adaptations in talpids humeral mechanical performance by means of geometric morphometrics and finite element analysis. – *Journal of Morphology*, 273(7): 696–711.  
<https://doi.org/10.1002/jmor.20015>
- Popescu, S.-M., Biltekin, D., Winter, H., Suc, J.-P., Melinte-Dobrinescu, M. C., Klotz, S., Rabineau, M., Combourieu-Nebout, N., Clauzon, G., Deaconu, F. (2010): Pliocene and Lower Pleistocene vegetation and climate changes at the European scale: Long pollen records and climatostratigraphy. – *Quaternary International*, 219(1-2): 152–167.  
<https://doi.org/10.1016/j.quaint.2010.03.013>
- Popov, V. V. (1988): Middle Pleistocene small mammals (Mammalia: Insectivora, Lagomorpha, Rodentia) from Varbeshnitsa (Bulgaria). – *Acta Zoologica Cracoviensia*, 31(5): 193–234.
- Popov, V. V. (1989): Middle Pleistocene small mammals (Mammalia: Insectivora, Lagomorpha, Rodentia) from Moravitsa Cave (North Bulgaria). – *Acta Zoologica Cracoviensia*, 32(13): 561–588.
- Popov, V. V. (2004a): Late Pliocene Erinaceidae and Talpidae (Mammalia: Lipotyphla) from Varshets (North Bulgaria). – *Acta Zoologica Cracoviensia*, 47(1-2): 61–80.
- Popov, V. V. (2004b): Pliocene small mammals (Mammalia, Lipotyphla, Chiroptera, Lagomorpha, Rodentia) from Muselievo (North Bulgaria). – *Geodiversitas*, 26(3): 403–491.
- Popov, V. V. (2017): Early Pleistocene small mammals Eulipotyphla, Chiroptera, Lagomorpha and Rodentia) from Futjova Cave, North Bulgaria. – *Acta Zoologica Bulgarica*, 69(2): 263–282.
- Rabeder, G. (1972): Die Insectivoren und Chiropteren (Mammalia) aus dem Altpleistozän von Hundsheim (Niederösterreich). – *Annalen des Naturhistorischen Museums in Wien*, 76: 375–474.
- Rabeder, G. (1981): Die Arvicoliden (Rodentia, Mammalia) aus dem Pliozän und dem älteren Pleistozän von Niederösterreich. – *Beiträge zur Paläontologie*, 8: 1–373.
- Rădulescu, C., Samson, P.-M. (1989): Contributions to the knowledge of the mammalian faunas from Mălușteni and Berești (Romania). – *Travaux de l'Institut de Spéologie "Emile Racovitza"*, 28: 43–56.
- Reumer, J. W. R., (1984): Ruscinian and early Pleistocene Soricidae (Insectivora, Mammalia) from Tegelen (The Netherlands) and Hungary. – *Scripta Geologica*, 73: 1–173.
- Reumer, J. W. R., (1995): Insectivora (Mammalia: Soricidae, Talpidae) from the Late Pliocene of Frechen, Germany. – *Deinsea*, 2(1): 9–15.
- Rzebik-Kowalska, B. (2000): Insectivora (Mammalia) from the Early and early Middle Pleistocene of Betfia in Romania. II Erinaceidae BONAPARTE, 1838 and Talpidae GRAY, 1825. – *Acta Zoologica Cracoviensia*, 43(1-2): 55–77.
- Rzebik-Kowalska, B. (2006): Erinaceomorpha and Soricomorpha (Mammalia) from the Late Pleistocene and Holocene of Krucza Skała Rock Shelter and Komarowa Cave (Poland). – *Acta Zoologica Cracoviensia*, 49(1-2): 83–118.  
<https://doi.org/10.3409/000000006783995481>
- Rzebik-Kowalska, B. (2013): *Sorex bifidus* n. sp. and the rich insectivore mammal fauna from the Early Pleistocene of Żabia Cave in Poland. – *Palaeontologia Electronica*, 16(2): 12A (35 pp.)  
<https://doi.org/10.26879/376>
- Rzebik-Kowalska, B., Rekovets, L. I. (2015): Recapitulation of data on Ukrainian fossil insectivore mammals (Eulipotyphla, Insectivora, Mammalia). – *Acta Zoologica Cracoviensia*, 58(2): 137–171.  
[https://doi.org/10.3409/azc.58\\_2.137](https://doi.org/10.3409/azc.58_2.137)
- Sabol, M. (ed.) (2004): Early Villanyian site of Hajnáčka I (Southern Slovakia). Paleontological research 1996–2000. – Gemer-Malohont Museum in Rimavská Sobota, 143 pp.
- Sansalone, G., Kotsakis, T., Piras, P. (2015): *Talpa fossilis* or *Talpa europaea*? Using geometric morphometrics and allometric trajectories of humeral moles remains from Hungary to answer a taxonomic debate. – *Palaeontologia Electronica*, 18.2.42A: 1–17.  
<https://doi.org/10.26879/560>
- Siori, M. S., Boero, A., Carnevale, G., Colombero, S., Delfino, M., Sardella, R., Pavia, M. (2014): New data on Early Pleistocene vertebrates from Monte Argentario (Central Italy). Paleoeological and biochronological implications. – *Geobios*, 47(6): 403–418.  
<https://doi.org/10.1016/j.geobios.2014.10.001>
- Spence Bate, C. (1867): On the dentition of the common mole (*Talpa europaea*). – *The Annals and Magazine of Natural History*, Ser. 3, 19(114): 377–380.  
<https://doi.org/10.1080/00222936708562693>
- Stein, G. H. W. (1955): Die Kleinsäuger ostdeutscher Ackerflächen. – *Zeitschrift für Säugetierkunde*, 20(1952): 89–113.
- Steininger, F. F., Berggren, W. A., Kent, D. V., Bernor, R. L., Sen, S., Agusti, J. (1996): Circum-Mediterranean Neogene (Miocene and Pliocene) marine continental chronologic correlations of European Mammal Units. – In: Bernor, R. L., Fahlbusch, V., Mittmann, H.-W. (eds), *The evolution of Western Eurasian Neogene mammal faunas*. Columbia University Press, New York, pp. 7–46.
- Storch, G. (1978): Die turolische Wirbeltierfauna von Dorn-Dürkheim, Rheinhessen (SW-Deutschland). 2. Mammalia: Insectivora. – *Senckenbergiana lethaea*, 58(6): 421–449.



- Storch, G., Franzen, J. L., Malec, F. (1973): Die altpleistozäne Säugerfauna (Mammalia) von Hohensülzen bei Worms. – *Senckenbergiana lethaea*, 54(2-4): 311–343.
- Sulimski, A. (1959): Pliocene insectivores from Węże. Study on the Tertiary bone breccia from Węże near Działoszyn in Poland. Part XI. – *Acta Palaeontologica Polonica*, 4(2): 119–173.
- Sulimski, A. (1962): Supplementary studies on the insectivores from Węże 1 (Poland). – *Acta Palaeontologica Polonica*, 7(3-4): 441–496.
- Tesakov, A. S. (1998): Voles of the Tegelen fauna. – *Mededelingen Nederlands Instituut voor Toegepaste Geowetenschappen TNO*, 60: 71–134.
- Tesakov, A. S. (2004): Biostratigrafiya srednego plio-tsena-eopleistotsena vostochnoy Evropy (po melkim mlekipitayushchim) [Biostratigraphy of Middle Pliocene-Eopleistocene of Eastern Europe (based on small mammals)]. – *Trudy Instituta geologicheskikh nauk Akademii nauk SSSR*, 554: 1–247. (in Russian)
- Tesakov, A. S., Vangengeim, E., Pevzner, M. (2007): Arvicolid zonation of continental Pliocene deposits of East Europe. – *Courier Forschungsinstitut Senckenberg*, 259: 227–236.
- Tesakov, A. S., Titov, V. V., Sotnikova, M. V., Bondarev, A. A., Simakova, A. N., Frolov, P. D. (2017): Obnovlennaya biokhronologicheskaya skhema kvartera Vostochnoy Evropy i Zapadnoy Azii [Revised Quaternary biochronological scheme of Eastern Europe and Western Asia]. – In: Lavrushin, Yu. A., Panin, A. V., Zastrozhnov, A. S., Zykin, V. S., Sadchikova, T. A., Tesakov, A. S., Timireva, S. N., Chistyakova, I. A. (eds), *Materialy X Vserossiyskogo soveshchaniya po izucheniyu chetvertichnogo perioda*. GEOS, Moscow, pp. 422–424. (in Russian)
- Zagwijn, W. H. (1992): The beginning of the Ice Age in Europe and its major subdivisions. – *Quaternary Science Reviews*, 11(5): 583–591.  
[https://doi.org/10.1016/0277-3791\(92\)90015-Z](https://doi.org/10.1016/0277-3791(92)90015-Z)
- Ziegler, R. (1990): Talpidae (Insectivora, Mammalia) aus dem Oberoligozän und Untermiozän Süddeutschlands. – *Stuttgarter Beiträge zur Naturkunde, B*, 167: 1–81.
- Ziegler, R. (1995): Pleistozäne Säugetierfaunen von Genkingen bei Reutlingen (Baden-Württemberg). – *Stuttgarter Beiträge zur Naturkunde, B*, 234: 1–43.
- Ziegler, R. (2003): Moles (Talpidae) from the late Middle Miocene of South Germany. – *Acta Palaeontologica Polonica*, 48(4): 617–648.
- Ziegler, R. (2004): The insectivores (Erinaceomorpha and Soricomorpha, Mammalia) from the Late Miocene hominoid locality Rudabánya. – *Palaeontographia Italica*, 90: 53–81.
- Ziegler, R. (2006): Insectivores (Lipotyphla) and bats (Chiroptera) from the Late Miocene of Austria. – *Annalen des Naturhistorischen Museums in Wien, A*, 107: 93–196.











