Small vertebrates from the Late Pleistocene of Avetrana (Apulia, southern Italy) karst filling

Pequeños vertebrados del relleno kárstico del Pleistoceno Superior de Avetrana (Apulia, Sur de Italia)

T. Kotsakis[1], L. Pandolfi[2,*], L. Maiorino[1], C. Petronio[3], G. Sansalone[1,4], L. Salari[3]

[1] Dipartimento di Scienze, Università Roma Tre, Largo San Leonardo Murialdo 1, 00146 Roma, Italy. ORCID ID: https://orcid.org/0000-0002-1142-1332; https://orcid.org/0000-0002-7267-2557; http://orcid.org/0000-0003-3680-8418

[2] Dipartimento di Scienze della Terra, Università degli Studi di Firenze, Via G. La Pira 4, 50121 Firenze, Italy. Email: luca.pandolfi@unifi.it; ORCID ID: https://orcid.org/0000-0002-4186-4126

[3] Dipartimento di Scienze della Terra, Università "La Sapienza" di Roma, Piazzale Aldo Moro 5, 00185 Roma, Italy. ORCID ID: https://orcid.org/0000-0003-2020-5495; https://orcid.org/0000-0002-1670-530X

[4] Form, Evolution and Anatomy Research Laboratory, Zoology, School of Environmental and Rural Sciences, University of New England, Armidale, NSW 2351, Australia.

* Corresponding author

ABSTRACT

The fossiliferous deposit (karst cavity) in La Grave, a locality near the small town of Avetrana (Taranto, southern Italy), has yielded numerous fossils of vertebrates. The remains of large mammals have been the subject of several studies. This paper examines the remains of small vertebrates and identifies four taxa of amphibians (*Bufo bufo*, *Bufotes* gr. *B. viridis*, *Hyla* gr. *H. arborea* and *Rana* (s.l.) sp.), four taxa of reptiles (*Testudo hermanni*, *Podarcis* sp., *Zamenis* gr. *Z. longissimus*, *Natrix natrix*), and nine taxa of small mammals (*Erinaceus europaeus*, *Crocidura suaveolens*, *Arvicola italicus*, *Microtus (Terricola) savii*, *Microtus (Microtus) arvalis*, *Apodemus* gr. *A. sylvaticus - A. flavicollis*, *Hystrix (Acanthion) vinogradovi*, *Oryctolagus cuniculus* and *Lepus corsicanus*). From a biochronological point of view, the data on small and large vertebrates indicate an age between the beginning of the Late Pleistocene (MIS 5e) and the central part of MIS 3. The most recent fossiliferous layer (bed 8) is likely to have been deposited during a cooler period when compared to the previous layers.The data from small fossil vertebrates combined with those emerging from the large mammals and birds evidence the presence, near the karstic cavity, of open spaces (prairies) with pools of water, bordered by wooded areas and, not far, the presence of a rocky coastline.

Keywords: Systematics; Biochronology; Palaeoenvironment.

RESUMEN

El depósito (cavidad kárstica) de La Grave, localidad cercana a la pequeña ciudad de Avetrana (Tarento, Italia meridional), ha dado lugar a numerosos fósiles de vertebrados. Los restos de grandes mamíferos han sido objeto de varios estudios. En este trabajo se examinan los restos de pequeños vertebrados y se identifican cuatro taxones de anfibios (*Bufo bufo*, *Bufotes* gr. *B. viridis*, *Hyla* gr. *H. arborea* and *Rana* (s.l.) sp.), cuatro de reptiles (*Testudo hermanni*, *Podarcis* sp., *Zamenis* gr. *Z. longissimus*, *Natrix natrix*), y nueve de pequeños mamíferos

(*Erinaceus europaeus*, *Crocidura suaveolens*, *Arvicola italicus*, *Microtus (Terricola) savii*, *Microtus (Microtus) arvalis*, *Apodemus* gr. *A. sylvaticus - A. flavicollis*, *Hystrix (Acanthion) vinogradovi*, *Oryctolagus cuniculus* and *Lepus corsicanus*). Desde un punto de vista biocronológico, los datos sobre los vertebrados pequeños y grandes indican una edad entre el comienzo del Pleistoceno tardío (MIS 5e) y la parte central del MIS 3. Es probable que el estrato fosilífero más reciente (nivel 8) se haya depositado durante un período más frío en comparación con las capas anteriores. Los datos de pequeños vertebrados fósiles combinados con los que proceden de los grandes mamíferos y aves evidencian la presencia, cerca de la cavidad kárstica, de espacios abiertos (praderas) con charcos de agua, bordeados por zonas boscosas y, no muy lejos, la presencia de una costa rocosa.

Palabras clave*: Sistemática; Biocronología; Paleoambientes.

Introduction

The fossiliferous deposit found at locality La Grave near Avetrana (Taranto, southern Italy) (Fig. 1) has been the subject of an intensive campaign of excavation (october 2003) carried out by "Sapienza" University of Rome, in agreement with the "Soprintendenza per i Beni Archeologici" of Apulia and with the collaboration of researchers of "Museo delle Civiltà preclassiche della Murgia meridionale" of Ostuni (Brindisi), and of Turin University (Sardella *et al*., 2005; Petronio *et al*., 2008; Salari & Sardella, 2009). Numerous subsequent investigations and collections of fossil remains, carried out by "Sapienza" University of Rome, have progressively involved the researchers of "Roma Tre" University (Pandolfio & Petronio, 2011; Pandolfi *et al*., 2011, 2013; Bertè & Pandolfi, 2014).

The mammal assemblage has been referred to early Late Pleistocene (Petronio *et al*., 2008; Pandolfi *et al*., 2013). As described by Sardella *et al*. (2005) and Petronio *et al*. (2008), the fossiliferous deposit is found in an open-air karst cavity within Early Pleistocene limestone (called "Calcareniti di Gravina"). The cavity infilling is constituted by abundant remains of mammals, other vertebrates, and fine sediments. According to Petronio *et al*. (2008) and Pandolfi *et al*. (2013), different layers or beds, are recognized in the site of Avetrana (Fig. 2), which were probably deposited rapidly during a short time span (from a geological point of view) by exceptional events, resulting in the rapid incorporation of carcasses and isolated vertebrate remains in the karst cavity. In particular, beds 2, 5 and 7 were deposited over a very short time and probably each represent a single depositional event; by contrast, beds 3, 4, 6 and 8, which are characterized by sparse fossil remains and abundant clayey-sandy matrix, have been probably deposited over a longer time span.

Aurochs, fallow deers and red deers have provided useful information about the season of death and consequently the probable time span of the aggradations. In beds 5 and 7, the estimated season of death of these three species has suggested probable catastrophic deposition between the autumn and the winter (Pandolfi *et al*., 2013).

When compared to the others, bed 8 shows some peculiar features. In this bed the percentage of damaged bones and bones covered with concretions is relatively high. Furthermore, bed 8 is characterized by a very high percentage of carnivore remains, in particular wolf (Bertè & Pandolfi, 2014; Mecozzi & Bartolini Lucenti, 2018). Despite these peculiarities of bed 8 have been pointed out by Pandolfi *et al*. (2013), they have not been adequately investigated.

During the recent investigations at the site of Avetrana (2012 and 2013), new fossil remains were recovered and new insightful observations about stratigraphy and taphonomy have been performed.

The aim of this additional work on the fossil deposit of Avetrana is therefore to describe in detail the small vertebrates found in all levels (some remains of large-sized rodent *Hystrix vinogradovi* have alredy been studied by Salari & Sardella, 2009, 2011). The study of small vertebrates offers considerable possibilities for the biochronological, palaeoecological and palaeoclimatical analysis of the faunal assemblage of the studied site, integrating the data with those obtained from the study of large mammals. The usefulness of the use of small vertebrates for this type of analysis is demonstrated by the constantly increasing number of publications concerning this topic (see for the Late Pleistocene of the Italian peninsula: Bona *et al*., 2009; Bona, 2011; López-García *et al*., 2014, 2015, 2017, 2018; Berto *et al*., 2016, 2017, 2018, 2019; Gatta *et al*., 2019, among others)
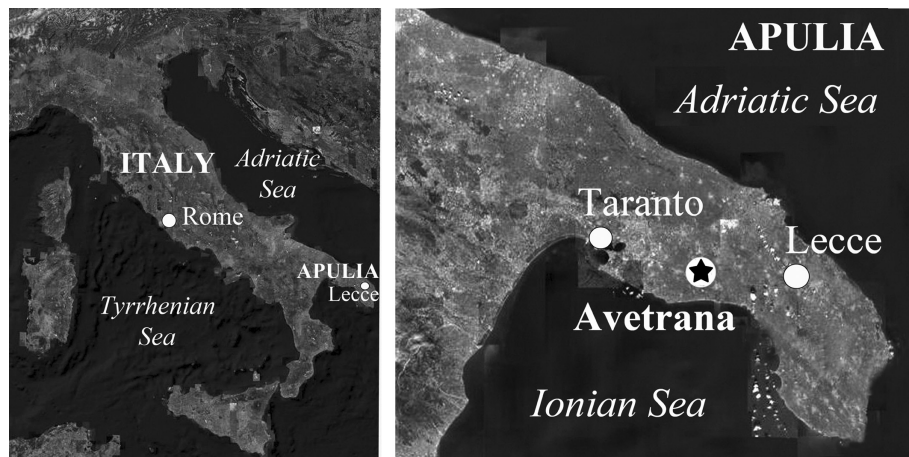
Figure 1.—Location of the fossiliferous site of La Grave (modified from Pandolfi et al., 2013).
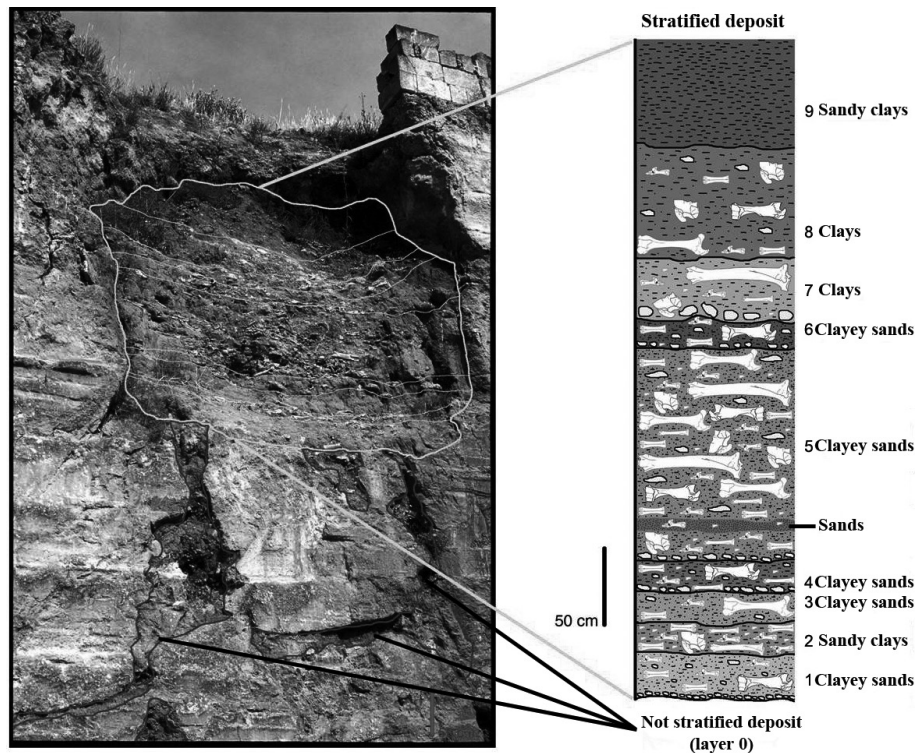

Figure 2.—Avetrana (Apulia, Southern Italy), Late Pleistocene: Stratigraphy of the La Grave karst filling (modified from Pandolfi et al., 2011 and Pandolfi et al., 2013).

The Avetrana karst filling and the fossil vertebrates

The karst cavity of Avetrana (Fig. 2), as already reported by Petronio *et al.* (2008), presents two thin fissures at the base (named bed 0 in the previous works) filled with non-bedded yellow-orange sandy clays and small vertebrate remains (Tab. 1).

On top of bed 0 there are eight levels containing abundant large mammal bones and teeth in an excellent state of preservation among which *Bos primigenius* clearly prevails (up to 60% of the fossil remains),

Table 1.—Distribution of taxa for each layer.

Taxa	Bed 8	Bed 7	Bed 6	Bed 5	Bed 4	Bed 3	Bed 2	Bed 1	Bed 0
AMPHIBIA									
Bufo bufo	X								
Bufotes gr. *B. viridis*	X			X					
Hyla gr. *H. arborea*	X								
Rana (s.l.) sp.				X					
REPTILIA									
Testudo hermanni	X								
Podarcis sp.	X								
Zamenis gr. *Z. longissimus*				X					
Natrix natrix				X					
Serpentes indet.	X								
AVES									
Perdix perdix									X
Otis tarda							X		
Columba livia	X	X	X	X	X	X	X		X
Columba sp.	X								
Aquila sp.	X						X		
Athene noctua									X
Pyrrhocorax pyrrhocorax	X						X		
Pyrrhocorax graculus	X						X		X
MAMMALIA									
Erinaceus europaeus	X			X				X	X
Crocidura suaveolens	X			X					
Microtus (Terricola) savii			X	X				X	X
Microtus (Microtus) arvalis	X								
Microtus sp.	X		X	X				X	X
Arvicola italicus	X			X					
Apodemus gr. *A. sylvaticus - A. flavicollis*				X					
Hystrix vinogradovi	X	X		X				X	X
Oryctolagus cuniculus	X	X	X	X	X	X			X
Lepus corsicanus	X			X		X			X
Leporidae indet.	X	X	X	X	X	X	X		X
Vulpes vulpes	X	X	X	X	X	X	X		
Canis lupus	X	X	X	X	X	X	X		
Meles meles	X			X		X	X		
Martes sp.	X								
Mustela putorius	X								
Crocuta crocuta	X	X		X			X		
Felis silvestris	X								X
Lynx lynx				X			X		

Continued

Table 1.—Continued

Taxa	Bed 8	Bed 7	Bed 6	Bed 5	Bed 4	Bed 3	Bed 2	Bed 1	Bed 0
Lynx sp.	X								
Panthera spelaea	X								
Stephanorhinus hemitoechus	X	X	X				X		
Hippopotamus amphibius			X	X			X		
Sus scrofa	X		X	X			X		
Capreolus capreolus				X					
Dama dama	X	X	X	X	X	X	X		
Cervus elaphus	X	X	X	X	X	X	X		
Bos primigenius	X	X	X	X	X	X	X	X	

and several small vertebrate remains. The covering deposit, at the top of the sequence, consists of a clayey soil with rare decalcified bones.

Bed 1 is composed of an uninterrupted stratum of calcareous pebbles, overlain by a thin deposit (30 cm) of argillaceous sand containing rare clayey pebbles (which are visibly altered) and a few fossil remains (Tab. 1).

In all the subsequent beds, the bones are generally chaotically disposed, with isolated long bones lying mainly parallel to the stratigraphic surface but without a clear orientation pattern.

Bed 2 comprises a thin (20 cm) deposit of sandy clay including numerous bone remains (Tab. 1). The majority of the remains of the large mammals (about 83%) are very well preserved; a modest number of remains (about 12%) are slightly damaged through crushing or pressure and occasional bones have calcareous concretions (about 3%). Bed 3 consists of 20 cm of argillaceous sand with only a few bones (Tab. 1). Bed 4, again around 20 cm thick, contains calcareous pebbles and fragmentary fossil remains (Tab. 1).

Bed 5, around 140 cm thick, is composed by argillaceous sand containing very abundant bones and rare calcareous pebbles. In this bed, the majority of the remains (Tab. 1) are in a very good state of preservation (about 88%) and several bones are still articulated; about 11% of the remains are slightly crushed. The following bed 6 is formed by about 20 cm of argillaceous sandy matrix and yielded several mammal remains. The bones (Tab. 1), in a good state of preservation

(about 73%), are fewer than in the previous bed, whereas there is an increase in the percentage of damaged and concreted bones. A single Mousterian lithic artifact was also discovered in this layer. In bed 7, around 40 cm thick, the abundance of fossil remains of large mammals is similar to that in bed 5 (Tab. 1). The percentage of well preserved bones is relatively low (about 35%) and there is an increase in the percentage of damaged bones, although some are in anatomical connection.

Bed 8 is formed by about 75 cm of argillaceous sandy sediments with calcareous pebbles and scattered fossil remains of several species (Tab. 1). A large number of undetermined remains belonging to Anura was also collected. Well preserved remains are very scarce in comparison with older beds and represent about 13% of the total assemblage from this horizon. Remains covered with concretions are abundant (about 60%), and there are damaged remains (about 20%). All the filling is surmounted by humus (bed 9 in Fig. 2).

Materials and methods

One of the targets of the December 2013 campaign in Avetrana was the systematic collection of small vertebrates. The field work of the previous campaigns had led to the collection of a few remains of small mammals and much more abundant fossils belonging to large size rodents and especially lagomorphs (*Hystrix, Oryctolagus, Lepus*). The remains of a few small mammals were recovered from bed 0 and bed 8 (Pandolfi *et al.* 2013).

During the 2013 campaign we tried to sample all the layers in search of small vertebrates, sifting a few tens

of kg for each bed. The two pockets named bed 0 were completely emptied. Bed 1 delivered a few remains of small vertebrates and an extremely worn tooth of *Hystrix*. The beds 2, 3 and 4 have provided only fragments of arvicoline molars. Bed 5 turned out relatively rich. A few specimens of small mammals were collected in level 6. Bed 7 resulted sterile as for small vertebrates, except for an incisive of *Hystrix*. Bed 8 yielded abundant remains of small vertebrates, unfortunately, most of them extremely fragmented. In the latter level, which closes the deposit of Avetrana, the vast majority of the remains belongs to anurans. However, the condition of the amphibian fossils hampers a more precise systematic attribution for a large portion of these specimens. In addition of fossils collected during 2013, a few specimens picked-up in a rapid field-trip in October 2017 were studied.

The fossil remains were compared with osteological material, both fossil and recent, curated in the Department of Sciences of "Roma Tre" University. The measurements and photos of microvertebrates were obtained with a Leica MZ6 microscope and a Leica Application Suite software version 2.6.0 R1. The material is stored temporarily in the Department of Sciences of "Roma Tre" University, pending the decision of Soprintendenza Archeologica di Taranto for the final collocation. The inventory numbers are provisional.

Abbreviations: dx = right; sx = left; L = Length; W = Width; Pn = Provisional number.

Systematic Palaeontology

Amphibia

Bufo bufo (LINNAEUS, 1758)

Specimen: The ventral part of a very large vertebra (Pn. 001/1) (bed 8).

The common toad is represented by a fragment of a large dorsal procoelus vertebra, with a very flat condyle. Dimensionally and morphologically it is identical with the dorsal vertebrae of females of the extant species *Bufo bufo* (LINNAEUS, 1758). The common European toad is found in many Neogene and Quaternary deposits in mainland Italy and in Sicily. The oldest report goes back to the late Miocene, but the majority of the findings are younger, i.e. of Late Pleistocene age (Holman, 1998; Delfino, 2002 with bibliography, 2004; Curcio *et al*., 2007; Bartolini *et al*., 2014; Villa *et al*., 2018a, 2018b; Gatta *et al*., 2019). The common toad currently has a wide distribution in Italy and Sicily. It is present in a wide range of environments, ingluding semiarid (Böhme *et al*., 2007)

A   **B**

Figure 3.—Two urostyles of *Bufotes* gr. *B. viridis* from bed 5: A) "Normal" urostyle (Pn 002/7); B) Teratological urostyle (Pn 002/8). L = 14.4 mm (A), 14.2 mm (B).

Bufotes **gr. B. viridis** (LAURENTI, 1768)
(Fig. 3)

Specimens: Two humeri dx, one ilium sx, one ilium dx and four urostyles (Pn. 002/1-8) (bed 5); two trunk vertebrae, one ilium sx, one urostyle (Pn. 003/1-4) (bed 8).

The two humeri collected in bed 5 are slightly different in size but morphologically identical. The ilia are devoid of the thin bone crest and have the tuberosity well developed, typical of *"Bufo" viridis* LAURENTI, 1768 (cfr. Böhme, 1977). The urostyles have two facet joints in the proximal part and a quite long ridge, well-preserved in the specimen found in the bed 8. The ridge is broken in the specimens collected from bed 5. The systematics of the "*B.*" *viridis* group has been much debated in recent times. In particular for Italy instead of the single species *B. viridis* reported until a few years ago, today three distinct species are accepted as valid: *"Bufo" viridis* in the North-East, *"Bufo" balearicus* BOETTGER, 1880 in the remaining peninsular area, Sardinia, and the North-East of Sicily and *"Bufo" siculus* STÖCK, SICILIA, BELFIORE, BUCKLEY, LO BRUTTO, LO VALVO & ARCULEO, 2008 in the rest of Sicily (Balletto *et al*., 2007; Stöck *et al*., 2008). According Balletto *et al*. (2007) the specific name *"Bufo" lineatus* NINNI, 1879 would have priority over *B. balearicus*. Moreover, the attribution of the group of "*B.*" *viridis* to the genus *Bufo* is questioned. *Bufotes*, *Epidalea* and *Pseudepidalea* have been proposed as generic or subgeneric names for members of the group of green toads (Frost *et al*., 2006; Dubois & Bour, 2010). However, regardless of the nomenclatorial problems, there are no osteological

studies that could allow a clear distinction between the three species. The fossils come from Avetrana, a town located within the present distribution area of *B. balearicus* (= *B. lineatus*) and it is tempting to ascribe to this species the remains belonging to a green toad. However, given the lack of distinguishing features between the different species we prefer to assign the fossils of Avetrana to *Bufotes* gr. *B. viridis*. The presence of *Bufotes* gr. *B. viridis*, usually reported in the literature as *Bufo viridis*, goes back in the Italian mainland to the late Miocene (Delfino, 2002; Colombero *et al*., 2017). Green toads are reported in many sites of Plio-Pleistocene age of the Italian peninsula, Sardinia and Sicily (Holman, 1998; Delfino, 2002, with bibliography; Abbazzi *et al*., 2004; Curcio *et al*., 2007; Delfino *et al*., 2011; Cossu *et al*., 2018; Villa *et al*., 2018c; Gatta *et al*., 2019). The green toads of mainland Italy are thermophilous animals that live mostly in open environments (Balletto *et al*., 2007 - in reference to *B. lineatus*).

An urostyle collected from bed 5 is characterized by a very distinctive morphology. The proximal part of the ridge that overlooks the well-developed dorsal channel features on the left side a clear expansion forming a transverse "wing" while on the right side an irregular structure is present (Fig. 3). Lateral expansions are typical for *Discoglossus, Alytes, Bombina* and *Latonia* (including only extant and/or fossil taxa reported from Italy). However the genera *Alytes* and *Bombina* do not present a dorsal ridge (Rage, 1974). On the other hand, the Plio-Pleistocene representatives of *Latonia* are much larger compared to the specimen of Avetrana (Delfino, 2002). This leaves *Discoglossus* as a possibility but this genus shows a very low dorsal ridge. In one of the fossil urostyles of *Discoglossus pictus* OTTH, 1837 from Spinagallo (Sicily, early Middle Pleistocene, Kotsakis, 1977), there is a large asymmetry between the two processes and the same can be observed in an urostyle of a specimen of the extant *Discoglossus sardus* TSCHUDI in OTTH, 1837 figured by Púgener & Maglia (1997 - Fig. 3D). However the presence of a rather irregular bone structure at the proximal right side of the urostyle leads us to hypothesize a teratological situation. Rage (1974) observe the frequent presence of specimens (belonging to genera with urostyles without lateral expansions) with expansions or other anomalies in the anterior part of the urostyle. Moreover, one of the vertebrae presents an anomaly as it is amphicoelus, with concavities on both (posterior and anterior) sides. This type of pathology is common in the vertebrae of the anurans (Rage, 1974). Since the morphology of the articular part of this urostyle with the last vertebra and its size are identical with those of *Bufotes* present in the the fossiliferous site, these fossil is also assigned to *Bufotes* gr. *B. viridis*.

Hyla* gr. *H. arborea (LINNAEUS, 1758)
Specimen: One humerus dx (Pn. 004/1) (bed 8).

A small fragment of a right humerus is characterized by the *eminentia capitata* displaced from the axis of the diaphysis. The same morphology is present in the humeri of the extant European tree frogs. Five species of *Hyla* have been described for the extant fauna of Italy: *H. arborea* (LINNAEUS, 1758) in the easternmost area of Italy near the political border with Slovenia; *H. intermedia* BOULENGER, 1882 in the central and southern part the Italian mainland and in Sicily; *H. perrini* DUFRESNES *et al*., 2018 in the northern part of Italy; *H. meridionalis* BOETTGER, 1874 in Liguria (north-western Italy); and *H. sarda* (DE BETA, 1857), endemic of Sardinia, Corsica and some islands of the Tuscany Archipelago (Lanza *et al*., 2007; Dufresnes *et al*., 2018). The genus is reported as fossil (late Miocene – Holocene) from a limited number of localities from mainland Italy, Sicily and Sardinia (Holman, 1998; Delfino, 2002 with bibliography, 2004; Delfino *et al*., 2011; Colombero *et al*., 2017; Villa *et al*., 2018a). Almost all of these fossils are ascribed to *Hyla* gr. *H. arborea* or to *Hyla* sp. The close phylogenetic affinities of *H. arborea*, *H. intermedia, H. perrini*, and *H. sarda* are clear, whilst *H. meridionalis* is considered more distant (Stöck *et al*., 2012). After Holman (1998) it is possible to distinguish *H. arborea* from *H. meridionalis* on the basis of the structure of the *tuber superior* of the ilium. The scanty material from Avetrana does not include ilia. In southern Italy the extant species is, as we mentioned, *H. intermedia*. Therefore, it is very probable that the fossil could belong to this species. However the absence of specific characters in the single specimen assigned to this genus recommend to classify it as *Hyla* gr. *Hyla arborea*. All the Italian species of the genus *Hyla* have arboreal habits in the proximity of water (Lanza *et al*., 2007)

***Rana* (s.l.) sp.**
Specimen: One humerus dx (Pn. 005/1) (bed 5).
A single right humerus collected from bed 5 belongs to a member of the family Ranidae. The diaphysis of this fossil is straight in ventral and dorsal views and the condyle is placed in the axis of the bone. After Delfino (2002), the development of the mesial crest of humerus in males of "water frogs" and "brown frogs" allows a distinction between these two supraspecific groups of frogs, that is, between the genus *Pelophylax* and the genus *Rana*. Unfortunately, the specimen of Avetrana does not have the mesial crest of the humerus because clearly belongs to a female. We classify this fossil as *Rana* (s.l.) sp. "*sensu lato*", in this case, indicates the possibility that the fossil either belongs to a medium-sized form of the genus

Pelophylax or of the genus *Rana*. In Italy, fossils belonging to the genus *Rana* (without distinction between the above mentioned genera) are reported from a good number of fossiliferous localities (especially of Pleistocene age) since the late Miocene (Holman, 1998; Delfino, 2002 with bibliography, 2004; Curcio *et al*., 2007; Kotsakis *et al*., 2011; Bartolini *et al*., 2014; Villa *et al*., 2018a; Gatta *et al*., 2019).

Reptilia

Testudo hermanni GMELIN, 1789

Specimen: Peripheral fragment of the second costal plate of the carapace (Pn 006/1) (bed 8).

A single fragment of the carapace of a tortoise was collected from bed 8. The fragment corresponds to the peripheral part of the second right costal bone of *Testudo hermanni* GMELIN, 1789, with the boundary between the first and the second pleural scute impressed on the rugose surface. The length of the fragment along the peripheral boundary (23 mm) corresponds to a specimen of about 16.0 cm long. The fragment lacks diagnostic characters but corresponds perfectly to the same plate of the common European tortoise. *Testudo hermanni* is common in the Pleistocene fossiliferous sites of Italy (Delfino, 2002 with bibliography, 2004; Villa *et al*., 2018c). Several Italian fossils of Pleistocene age reported as *Testudo* sp. likely belong to the same species (see Delfino, 2002 for an exhaustive list). *Testudo hermanni* occupies a wide variety of open and wooded habitats, especially coastal areas with thermo- and meso-Mediterranean climate (Cheylan *et al*., 2011).

Podarcis sp.

Specimen: fragment of the central part of a right dentary (Pn. 007/1) (bed 8).

A single fragment of a right dentary bearing three bicuspid teeth and the space for another one between them, has been found in bed 8. The morphology is indicative of a member of the family Lacertidae. In comparison with the extant lacertids of the Italian herpetofauna (Corti *et al*., 2011), the dimensions of the fragment (2 mm) exclude the attribution to a large species as *Lacerta viridis* (LAURENTI, 1768), *L. trilineata* BEDRIAGA, 1866 or *Timon lepidus* (DAUDIN, 1802). Biogeographical reasons exclude also the attribution to the genera *Algyroides*, *Archaeolacerta, Iberolacerta, Zootoca, Psammodromus*, to the endemic insular members of the genus *Podarcis* and to *Lacerta agilis* LINNAEUS, 1758. On the other hand, the dentaries of *Podarcis muralis* (LAURENTI, 1768) seem slightly smaller. The fossil from Avetrana corresponds very well in dimension to the dentaries of *Podarcis siculus* (RAFINESQUE-SCHMALTZ, 1810), a species now living in the area of the fossiliferous site. However, since the fossil

is represented by a single fragment we classify this lacertid as *Podarcis* sp. Fossils assigned to the genus *Podarcis* (and in rare cases classified to species level) have been collected in a few sites of Pleistocene or Holocene age in mainland Italy, Sicily or Sardinia (Delfino, 2002 with bibliography; Kotsakis *et al*., 2011; Gatta *et al*., 2019). No ecological indications are possible without a species attribution.

Zamenis **gr.** *Z. longissimus* (LAURENTI, 1768)

Specimens: Three precloacal vertebrae (Pn. 008/1-3) (bed 5).

Three precloacal vertebrae of a middle sized snake (L= 4.8 mm) belongs to the family Colubridae, subfamily Colubrinae (sensu Lawson *et al*., 2005). The presence of a prominent slightly spatulate haemal keeland a not acutepro-zygapophyseal processes, indicates affinities with the group *Zamenis longissimus* (LAURENTI, 1768) (Szyndlar, 1984, 1991a; Delfino 2002 - at that time *Elaphe longissima*). The genus *Zamenis* includes three species of the extant Italian herpetofauna. *Zamenis situla* (LINNAEUS, 1758) is a rather small snake with not pronounced haemal keel in the precloacal vertebrae (Szyndlar, 1984). The other two species, *Z. longissimus* and *Z. lineatus* (CAMERANO, 1891) are similar and for a long time the later species was considered as subspecies of the first one. The formal resurrection of *Z. lineatus* as a valid species was proposed by Lenk & Wüster (1999). Salvi *et al*. (2018) consider the two species as sister species. *Zamenis lineatus* is endemic of southern Italy and Sicily. The northern limit of its geographical range is in the Province of Caserta in the West and the Province of Foggia in the East. It is absent from the Salentine Peninsula. To the North of this "line" its vicariant form, *Z. longissimus is* present (in limited areas both species coexist) (Venchi & Luiselli, 2011a, b). The remains of Avetrana should belong to *Z. lineatus*. However, the lack of material and the absence of diagnostic characters recommend the attribution to *Z.* gr. *Z. longissimus*. Remains of *Z.* gr. *Z. longissmus* (or *Z. longissimus*) are reported from a few fossiliferous localities (Early Pleistocene-Holocene) of the Italian peninsula (Delfino & Bailon, 2000; Delfino, 2002 with bibliography as *E. longissima*; Villa *et al*., 2018a). The two species of *Zamenis* seem to share many behavioral and ecological characteristics. They are found in a wide range of environments as in mixed forests of oak, in coastal pine forests, in Mediterranean *macchia*, in coastal wetlands (Venchi & Luiselli, 2011a, b).

Natrix natrix LINNAEUS, 1758

Specimens: One precloacal vertebra (Pn. 009/1) (bed 5)

A single small precloacal vertebra with a distally obtused hypapophysis has been collected from bed 5. This is a characteristic of the natricine genus *Natrix* and in particular of the species *Natrix natrix* (LINNAEUS, 1758) (Szyndlar,

1984, 1991b) (comparisons limited to European Plio-Pleistocene and extant species). The grass snake is present in several fossiliferous sites of mainland Italy and also in Sardinia since the Early Pleistocene (Delfino, 2002 with bibliography; Delfino, 2004; Delfino & Atzori, 2013; Gatta *et al*., 2019). Much more fossil remains have been classified as *Natrix* sp. (Delfino, 2002 with bibliography). *Natrix natrix* inhabits various environments, preferably wet with standing water (lakes, ponds, swamps) (Scali *et al*., 2011).

Serpentes indet

Specimen: One fragment of a precloacal vertebra (Pn. 010/1) (bed 8).

A fragment of a vertebra belonging to a snake is present in the bed 8. Any attempt of classification is impossible.

Mammalia

Erinaceus europaeus LINNAEUS, 1758.
(Fig. 4A)

Specimens: Fragment of maxillary dx bearing P^4 (L = 3.85 mm; W = 5.95 mm) and M^1 (L = 5.63 mm;

W = 6.62 mm) (Pn. 011) (bed 0); M_2 sx (L = 5.34 + mm; W = 3.59 mm) (Pn. 012) (bed 1); M_2 dx (L = 5.54; W = 3.95 mm) (Pn. 013) (bed 5); distal fragment of a sx tibia (Pn. 061) (bed 8).

Remains of hedgehog are reported by Pandolfi *et al.* (2013) from bed 0. The species is present also in bed 1 and bed 5. The genus is currently represented in Europe by two species, *Erinaceus europaeus* LINNAEUS, 1758, the western hedgehog and *Erinaceus roumanicus* BARRETT-HAMILTON, 1910, the eastern hedgehog. Both are well known in the fossil record (since the Middle Pleistocene). The second species often reported as *Erinaceus concolor*, MARTIN 1938, an Anatolian-Middle East species with which it was confused until recently. Five extinct European Plio-Pleistocene species were also described: *Erinaceus samsonowiczi* SULIMSKI, 1959 (late Miocene - Pliocene), *Erinaceus lechei* KORMOS 1934, (late Pliocene - Early Pleistocene) *Erinaceus ostramosi* JANOSSY 1972 (Early Pleistocene) *Erinaceus praeglacialis* BRUNNER, 1933, (Early and Middle Pleistocene), and *Erinaceus davidi* JAMMOT 1973 (Middle Pleistocene). The species distinction is based largely on size differences: *E. samsonowiczi*,
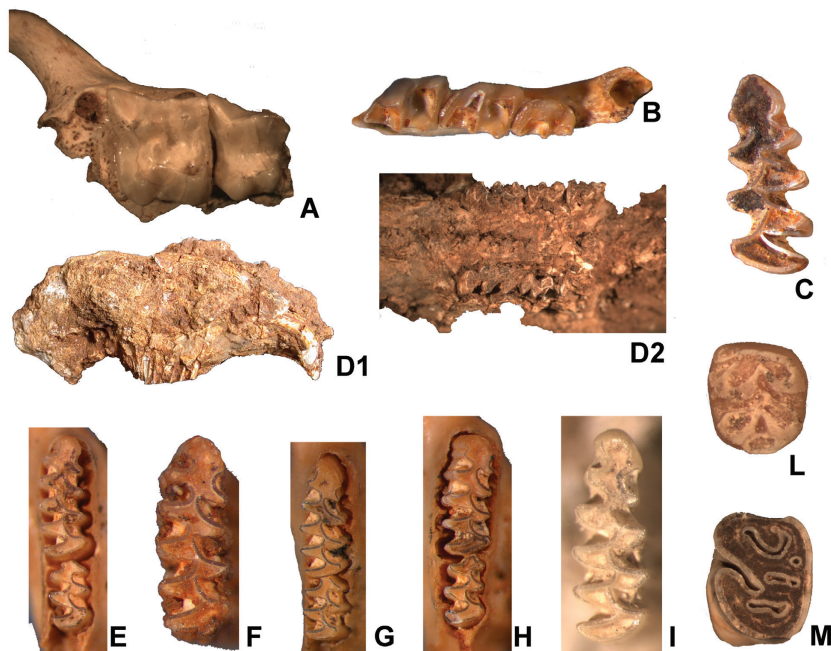

Figure 4.—A) *Erinaceus europaeus*, fragment of maxillary dx bearing P^4 (L = 3.85 mm; W = 5.95 mm) and M^1 (L = 5.63 mm; W = 6.62 mm) (Pn. 011) (bed 0), occlusal view; B) *Crocidura suaveolens*, mandibular fragment dx bearing M_1-M_3 (L = 3.57 mm)(LM_1 = 1.56 mm; LM_2 = 1.42 mm; LM_3 = 1.03 mm) (Pn. 014) (bed 5), occlusal view; C) *Arvicola italicus*, M_1 six (L = 4.51 mm) (Pn. 018) (bed 8), occlusal view; D) *Arvicola italicus*, encrusted skull (total skull L = 40.62 mm; L M^1-M^3 sx = 10.20 mm) (Pn 065) (bed 8), in lateral dx (D1) and ventral (D2) view; E) *Microtus (Terricola) savii*, M_1(L = 2.76 mm)-M_2 dx (Pn. 020/5) (bed 0), occlusal view; F) *Microtus (Terricola) savii*, M_1(L = 2.76 mm) dx (Pn. 021) (bed 1), occlusal view; G) *Microtus (Terricola) savii*, M_1(L = 2.53 mm)-M_2 dx (Pn. 022/1) (bed 5), occlusal view; H) *Microtus (Terricola) savii*, M_1(L = 2.69 mm)-M_2 dx (Pn. 023) (bed 6), occlusal view; I) *Microtus (Microtus) arvalis*, M_1(L = 2.96 mm) dx (Pn. 024/2) (bed 8), occlusal view; L) *Apodemus* gr. *A. sylvaticus-A. flavicollis*, M_2 dx (L = 1.26 mm) (Pn. 026) (bed 5), occlusal view; M) *Hystrix (Acanthion) vinogradovi*, M_1 dx (L = 7.49 mm) (Pn. 027/1) (bed 1), occlusal view.

E. leachei and *E. ostramosi* are smaller than *E. europaeus* (Janossy, 1972; Doukas, *et al.* 1995; Popov, 2004), while *E. praeglacialis* and *E. davidi* are larger (Jammot, 1973; Furió *et al.*, 2015). The size of our specimens does not allow the attribution to these species (but see critical observations in Reumer & Hordijk, 1999 and Furio, 2007). In particular, the Late Pleistocene remains collected in Melpignano (Lecce, Apulia) and assigned to *E.* cf. *E. praeglacialis* by Fanfani (2000, plate V.5) are very large with swollen cusps. In the fossils of Avetrana there is no visible swelling in the teeth. The Melpignano remain is the only indication of the presence of *E. praeglacialis* during Late Pleistocene in Europe. The distinction between the two extant species *E. europaeus* and *E. roumanicus* is based on the values of the maxillary index (Niethammer & Krapp, 1990) and on some differences in the morphology of the lingual side of the posterior part of mandible (Holz & Niethammer, 1990). Unfortunately, the fragment of the maxillary with P^4 and M^1 collected in bed 0 of Avetrana does not allow to measure the total length and height of this bone, while there are no mandibular fragments between the fossil remains of this site. However, both the size and the morphology of the remains of the hedgehog from Avetrana correspond perfectly to those of *E. europaeus* from the Late Pleistocene site of Castelcivita (Salerno, Campania) illustrated by Fanfani (2000, plate IV.5). Moreover, the length of metacrista of M^1 (see discussion in Furio *et al.*, 2015) is identical to the extant *E. europaeus* one. For this reason, these remains are classified as *E. europaeus*, the species currently present in the area. *Erinaceus europaeus* is reported as fossil in many Middle and Late Pleistocene Italian sites (Rustioni *et al.*, 1994, 2003; Fanfani, 2000; Kotsakis *et al.*, 2003; Tang & Kotsakis, 2008; Berto *et al.*, 2017, 2018, 2019; López García *et al.*, 2017; Pandolfi *et al.*, 2017a;). *Erinaceus roumanicus* appears in Northeastern Italy during the Holocene (Sala & Marchetti, 2006). The European hedgehog is present in a large variety of environments, both open and forested (Reggiani & Filippucci, 2008).

Crocidura suaveolens (PALLAS, 1811).
(Fig. 4B)
Specimens: Mandibular fragment dx bearing M_1-M_3 (L = 3.57 mm)(LM_1 = 1.56 mm; LM_2 = 1.42 mm; LM_3 = 1.03 mm) (Pn. 014) (bed 5); one M^1 or M^2 dx (L = 1.32 mm; W = 1.73 mm) (Pn. 015) (bed 8).
The presence of a soricid is attested inboth beds 5 and 8. The absence of red pigment on the cusps of the teeth indicates that the remains belong to the subfamily Crocidurinae. The dimensions of the fossils make possible to exclude their assignment to the two larger species

present in Italy during the Late Pleistocene (Fanfani, 2000): the extant *Crocidura leucodon* (HERMANN, 1780), and the extinct *Crocidura zorzii* PASA, 1942. Dimensions and morphology are identical with those of the extant lesser white-toothed shrew *Crocidura suaveolens* (PALLAS, 1811) (Fanfani, 2000). The presence of this species is tentatively reported in Italy during the Middle Pleistocene (Anzidei *et al.*, 1993, as *C.* cf. *C. suaveolens*). However, many remains of *Crocidura* from this period are reported as *Crocidura* sp. (see Kotsakis *et al.*, 2003). The lesser white-toothed shrew is quite common, from the North to the South of the Peninsula, during the Late Pleistocene (Fanfani, 2000 with references; Kotsakis *et al.*, 2003 with references; Curcio *et al.*, 2007; Kotsakis, 2008; Ronchitelli *et al.*, 2011; De Curtis, 2012; Berto *et al.*, 2016; Bona & Savoldi, 2016) and the Holocene (Berto & Rubinato, 1913; Salari & Silvestri, 2015). In a phylogeographic study carried out on *C. suaveolens* populations of central and southern Italy, Castiglia *et al.* (2017) indicated a strong affinity of the Italian populations of the species with those of the Balkan peninsula and indicate as a cloning period a time interval between 149 and 60 ka. This hypothesis coincides with the data emerging from the study of the fossil assemblages. *Crocidura suaveolens* is an ubiquitous species present both in open environments where it is more frequent, and in environments with wooded cover. In southern Italy the species is more common in humid environments rather than in arid ones (Sarà, 2008).

Arvicola italicus (SAVI, 1832).
(Figs. 4C, 4D1, 4D2)
Specimens: One mandible dx bearing M_1-M_3 (M_1 L = 3.82 mm) and a few teeth (not M_1) (Pn. 016-017) (bed 5); a skull encrusted (Total L skull = 40.62 mm; L M^1-M^3 sx = 10.20 mm) (Pn 065), one M_1 sx (L = 4.51 mm) (Pn. 018) (bed 8). Several other teeth (not M_1) belong to the genus *Arvicola* and most likely to the same species (Pn. 019) (bed 8).
A considerable number of teeth of a large arvicoline have been collected frombed 8 and others, less numerous, from bed 5. These remains belong to a species of the genus *Arvicola*. Unfortunately, among the collected fossil material, there are only two M_1, the element that presents the diagnostic characters that allow a specific attribution. We are obliged, therefore, to base our classification on the dimensions and the SDQ (= Schmelzbanddifferenzierungs-quotient = enamel differentiation ratio, after Heinrich, 1978) of these two specimens. The SDQ ratio of the studied specimens was measured according to the scheme indicated by Heinrich (1982) and Maul *et al.* (1998, Fig. 1a) on the labial anticlines Al4, Al3, Al2, and on the buccal anticlines Ab2 and

Ab2. The SDQ ratio for the first specimen (Pn. 016, bed 5) is 115.21 and it perfectly matches the SDQ ratio indicated by Maul *et al*. (1998) for Italy's southern populations of the early Late Pleistocene. For the second specimen (Pn. 018), collected in bed 8, SDQ is equal to 111.20, in good agreement with the values reported by Maul *et al*. (1998) for the Italian populations of the Late Pleistocene *Arvicola*. However, these are two single specimens for two of the beds of the karst cavity filling, and the value of the measurements is only indicative.

Both the nomenclature and the systematics of the genus *Arvicola* have undergone various vicissitudes during the recent decades. Traditionally, the three extant European species of *Arvicola* were classified as *Arvicola terrestris* (LINNAEUS, 1758), *Arvicola sherman* (SHAW, 1801) and *Arvicola sapidus* MILLER, 1908. According to Corbet (1978), the name *Arvicola amphibius* (LINNAEUS, 1758) (name often used in the past instead of *A. terrestris*) has priority over *A. terrestris*. The observation, reaffirmed by many scholars (Musser & Carleton, 2005 with references) has been accepted by the scientific community, and the name *A. amphinius* is currently used for the water vole. *Arvicola terrestris* is now considered as the Scandinavian subspecies of *A. amphibius*, *A. amphibius terrestris* (see Musser & Carleton, 2005). Also for the fossil members of the genus have been nomenclatorial problems. *Arvicola cantianus* (HINTON, 1910) has been used as a specific name to indicate the species considered by palaeontologists as the ancestor of the extant *A. amphibius*. Maul *et al*. (2000) have observed that the species established by Hinton (1910) is based on only four teeth and among them two fragmentary M_1they proposed to use this name to indicate only the few fossil remains from the type locality, and instead use the name *Arvicola mosbachensis* (SCHMIDTGEN, 1911) for all specimens previously attributed to *A. cantianus*.

The systematics of the genus *Arvicola* has also been discussed and reviewed. Maul *et al*. (1998) pointed out that the morphology of the M_1 from the southern Italy *Arvicola* populations would not belong to the same evolutionary line of the transalpine populations, a thesis reiterated by Masini *et al*. (2003). Molecular studies (Taberlet *et al*., 1998; Piertney *et al*., 2005; Kryštufek *et al*., 2015) revealed that the evolutionary history of the genus *Arvicola* is more complicated than the previously proposed models (see cladograms in Taberlet *et al*., 1998 and Pirtney *et al*., 2005, combined in Marcolini *et al*., 2011 and Piras *et al*., 2012). Recently, Castiglia *et al*. (2016) demonstrated the existence of a divergent mtDNA lineage for the populations of *Arvicola amphibius* (s.l.) in Italy and resurrected the specific name *Arvicola italicus* (SAVI, 1838) for this taxon (alredy proposed by

Gippoliti, 2012). We follow this attribution and, taking into account the observations of Maul *et al*. (1998) on the extinct populations of southern Italy, we classify our specimens as *A. italicus*.

Arvicola italicus (= Italian records of *A. amphibius*) appears in Italy at the beginning of the Late Pleistocene (Kotsakis *et al*., 2003 with references; Sala & Masini, 2007) and is present in almost all Late Pleistocene and Holocene fossiliferous sites of mainland Italy (among others Di Canzio & Petronio, 2001; Kotsakis *et al*., 2003 with references, 2011; Tang & Kotsakis, 2008; Bona *et al*., 2009; Bona, 2011; Berto & Rubinato, 2013; Salari, 2014; López García *et al*., 2014, 2015, 2018; Berto *et al*., 2016, 2017, 2018, 2019; Benvenuti *et al*., 2017; Gatta *et al*., 2019), reported as *A. amphibius* or *A. terrestris*. In the Grotta di San Bernardino Maggiore site (Veneto, northern Italy) the species is present in the upper levels whilst in the lower part of the sequence its putative ancestor, *A. mosbachensis*is present (López-García *et al*., 2017). The Italian semi-aquatic members of *Arvicola* are typical of humid plains or valleys and banks of rivers, ditches, ponds, swamps and lakes with rich vegetation (Cagnin, 2008 as *A. amphibius*).

Microtus (Terricola) savii (DE SÉLYS-LONGCHAMPS, 1838).
(Figs. 4E, 4F, 4G, 4H)
Specimens: Three M_1 dx and three M_1 sx (L = 2.55, 2.69, 2.73, 2.76, 2.78, 2.85 mm) (Pn. 020/1-6) (bed 0); one M_1 dx (L = 2.62 mm) (Pn. 021) (bed 1); one M_1 dx and three M_1 sx (L = 2.53, 2.67, 2.70, 2.71 mm) (Pn. 022/1-4) (bed 5); one M_1 dx (L = 2.69 mm) (Pn. 023) (bed 6).

The most common (or less rare) arvicoline at Avetrana is a member of the subgenus *Terricola* as indicated by the presence of a pitymyan rhombus in M_1. The morphology of the anterior cap and of the pitymyan rhombus of this tooth corresponds perfectly to the M_1 of the Savi's pine vole, *Microtus (Terricola) savii* (DE SÉLYS-LONGCHAMPS, 1838) (Piras *et al,.* 2009, 2010; Petruso *et al*., 2011). Arvicoline teeth with characters very similar to those of the extant *M. (T.) savii* are known from deposits dating back to the middle part of the early Toringian. Teeth with similar characters are known in Italy since the middle part of early Toringian, classified as *M. (T.) gr. savii* (Bon *et al*., 1991; Marcolini *et al*., 2003). The species is abundant during the warmer periods of the late Middle and Late Pleistocene in many fossiliferous sites of central-southern Italy (Kotsakis *et al*., 2003 with references, 2011; Curcio *et al*., 2005, 2007; Sala & Masini, 2007; Kotsakis, 2008; Tang & Kotsakis, 2008; Petruso *et al*., 2011; Ronchitelli *et al*., 2011; López-García *et al*., 2014; Bona & Savoldi, 2016; Berto *et al*., 2017; Gatta *et al*., 2019). The Savii's

pine vole is a very common element of the Holocene fossil mammalian assemblages of Italian peninsula (Salari, 2014) and at present is the most common arvicoline in peninsular Italy and in particular in its central and southern areas (Contoli *et al.*, 2008). *Microtus (T.) savii* prefers rather open areas and its distribution is limited primarily by edaphic factors (Contoli *et al.*, 2008).

Recent biomolecular studies (Bezerra *et al.*, 2016; Amori & Castiglia, 2018) have led to the conclusion that in Italy there are three distinct species of the *M. (T.) savii* group: The nominal species in the center-North of the Peninsula, *M. (T.) brachycercus* (von LEHMANN, 1961), not only restricted to Calabria but present in the entire center-South of the mainland Italy, and *M. (T.) nebrodensis* (MINÀ-PALUMBO, 1868) endemic to Sicily. At this point, a study involving a large number of fossils from different sites is necessary to solve the problems of the systematic attribution of *M. (T.)* gr. *savii*, a target clearly beyond the purpose of this work.

Microtus (Microtus) arvalis (PALLAS, 1778).
(Fig. 4I)

Specimen: Two M_1 dx (L = 2.94, 2.96 mm) (Pn. 024/1-2) (bed 8).

The morphology of the M_1 is characterized by five closed, rather symmetrical triangles and a rounded anterior cap, typical of this species (Nappi, 2001). Currently *Microtus (Microtus) arvalis* (PALLAS, 1778) is found only in northern Italy, where it is abundant in the fossil record (Bona *et al*. 2008, 2009; Bona, 2011; Berto & Rubinato, 2013; López García *et al.*, 2015, 2017; Berto *et al.*, 2016, 2018, 2019). However, since the late Middle Pleistocene it has been recorded also in central and southern Italy, only being absent during MIS 5 and the Late Holocene (Kotsakis *et al.*, 2003 with references, 2011; Tang & Kotsakis, 2008; López García *et al.*, 2014, 2018; Salari, 2014; Berto *et al.*, 2017; Pandolfi *et al.*, 2017a; Gatta *et al.*, 2019). The species is typical of open environments and rather cool climate (Paolucci & Amori, 2008).

Microtus sp.
Specimens: Several molars not diagnostic at species level from beds 0, 1, and 5. Three molars (M_2 and M_3) not diagnostic at species level from bed 6. Two molars not diagnostic at species level from bed 8 (Pn 025).

Several arhizodont molars (M^2, M_2, and one M_3) have been collected from beds 0, 1, 5, 6, and 8. It is impossible to assign these fossils to a particular species.

Apodemus gr. *A. sylvaticus* (LINNAEUS, 1758) - *A. flavicollis* (MELCHIOR, 1834)
(Fig. 4L)

Specimen: One M_2 dx (L = 1.26 mm) (Pn. 026) (bed 5).

The only specimen belonging to murids is a lower right M_2 which has a stretched and compressed t E and some tiny tubercles (c1, c2 and a third one) along the labial border (for the nomenclature of the tubercles see Michaux, 1971). The general morphology of the tooth excludes the attribution to the genera *Micromys*, *Mus*, and *Rattus*, being identical to that of the genus *Apodemus* (cf. Niethammer & Krapp, 1978). Unfortunately, the lower M_2 does not present diagnostic characters that could allow a specific attribution. The size falls within the variability of *Apodemus sylvaticus* (LINNAEUS, 1758) and, even if very close to the lower limit, also in that of *Apodemus flavicollis* (MELCHIOR, 1834), both extant species known from the fossil record in Italy (Pasquier, 1974; Argenti, 1999). Accordingly, this fossil is classified as *Apodemus* gr. *A. sylvaticus - A. flavicollis*. With this attribution, or as *Apodemus* sp., are reported fossil *Apodemus* from several Italian fossil assemblages (Kotsakis *et al.*, 2003 with references; Masini *et al.*, 2005; López-García *et al.*, 2017; Berto *et al.*, 2019; Gatta *et al.*, 2019; among others). Both species are known in Italy since the middle part of early Biharian (Siori *et al.*, 2014). *Apodemus sylvaticus* and *A. flavicollis* prefer wooded areas (Capizzi & Filippucci, 2008a, 2008b).

Hystrix (*Acanthion*) *vinogradovi* ARGYROPULO, 1941.
(Fig. 4M)

Specimens: Two M_1 dx (L = 7. 49, 7.12 mm) (Pn. 027/1-2) (bed 5), one extremely worn ?M3 (Pn. 028) (bed 1) and a fragment of a sx upper incisive (Pn. 063) (bed 7) (in addition of the material described by Salari & Sardella (2009) from bed 0 (three specimens) and bed 8 (one specimen).

Two right lower M1s belonging to a hystricid have been collected in bed 5. Their dimensions are similar to those reported for *Hystrix vinogradovi* ARGYROPULO, 1941 by Weers (1994) and Salari & Sardella (2011). They match very well with the specimens collected in the same fossiliferous site and described by Salari & Sardella (2009). These authors (Salari & Sardella, 2009, 2011) discussed the systematic problems and the geographic distribution of the Eurasian porcupine of the subgenus *Acanthion*. We agree with the expressed opinions, based on morphometric analyzes performed on the skulls of *H. vinogradovi* and *H. brachyura* by Barishnikov(2003), and report two publications which added new fossiliferous sites where *H. vinogradovi* (in both reported as *Hystrix brachyura vinogradovi*, but see discussion in Salari & Sardella, 2011) is present: Covacha de los Zarpazos (Atapuerca, Spain) (Galindo-Pellicena *et al.*, 2011), and several caves in the Urals and the Altai mountains (Kuzmin *et al.*, 2017).

Oryctolagus cuniculus (LINNAEUS, 1758)
(Figs. 5F, 5G, 5H)

Specimens: Two premaxillaries, one dx (Pn. 28/1) and one sx (Pn. 28/2), very probably belonging to the same animal, bearing I^1-I^2, two I^1, one dx (Pn. 29/1) and one sx (Pn. 29/2) (bed 0); fragment of skull bearing two teeth rows, dx complete P^2-M^3 (L = 13.04 mm), sx with P^2-M^2 (Pn. 30), two mandibular fragments bearing P_3-M_2 (sx, Pn. 31/1) (P_3: L = 2.51, W = 2.19 mm), and P_3-M_1 (dx Pn. 31/2) (P_3: L = 2.91, W = 2.89 mm) respectively, a proximal fragment of femur dx (Pn. 32) (bed 3); a distal fragment of a humerus dx (Pn 33) (bed 4); one dx mandibular ramus bearing P_3-M_2 (P_3: L = 2.73, W = 2.70 mm) (Pn. 34), one I^1 sx (Pn. 35), a proximal fragment of a juvenile femur sx (Pn. 36), a distal part of a tibia sx (Pn 37) (bed 5); one P_3 sx (L = 2.63, W = 2.68 mm) (Pn 38) (bed 6); a fragment of a mandibular ramus dx with P_3 (L = 2.87, W = 2.58 mm) and two or three more teeth completely covered by incrustations (Pn 39), a P_3 sx (L = 2.80, W = 2.47 mm) (Pn. 40) (bed 7); one P_3 dx (L = 2.62, W = 2.53) (Pn. 62) (bed 8).

For the attribution of the various remains of lagomorphs, the morphological criteria indicated by Callou (1997) and Nocchi & Sala (1997a) were followed. In the fossils of Avetrana, I^1(Pn. 28/1-2, 29/1-2, 35) present the mesial lobe (for the nomenclature of the teeth see López Martínez, 1989) more rounded than the hares. The P_3 (Pn. 31/1-3, 34, 38, 39, 40) have almost identical lingual and vestibular anteroconids and the aspect is subquadrangular. The palatal fragment (Pn. 30) features the opening of the nasal choanae narrow, while the mandibular fragments (Pn. 31/1-3, 34) have the mental foramen near the anterior border of the teeth row. The distal part of the humerus (Pn. 33) presents a very pronounced medial epicondyle. The femur (Pn. 32, 36) is characterized by a very short neck and by the presence of an intertrochanteric crest; the foramen opens at the distal end of the small trochanter.

Villafranchian (= Villanyian and early Biharian) representatives of the genus *Oryctolagus* in Italy, for a long time classified as *Oryctolagus lacosti* (POMEL, 1853), have recently been attributed by Angelone & Rook (2012) to *Oryctolagus valdarnensis* (WEITHOFER, 1889). It is a large-sized species with labial anteroconid of P_3 more massive of the vestibular one. Two species of rabbits have been described from post-Villafranchian assemblages of the Italian peninsula, *Oryctolagus burgi* NOCCHI & SALA, 1997 from the middle Galerian of Valdemino (Liguria) and probably from Casal Selce (Latium) (Nocchi & Sala, 1997a, 1997b; Kotsakis & Barisone, 2008), and the extant *O. cuniculus* (LINNAEUS, 1758), present in Aurelian assemblages (Kotsakis *et al.*, 2003).
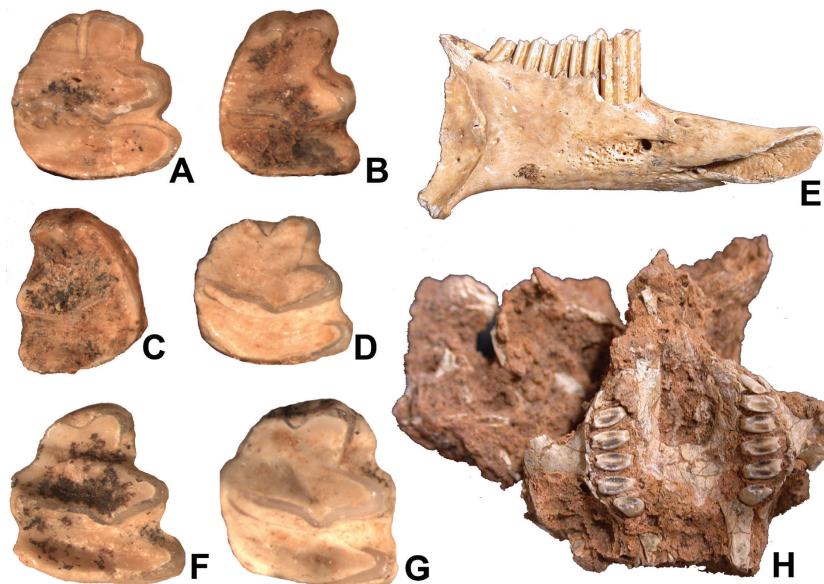

Figure 5.—A) *Lepus corsicanus*, P_3 dx (L = 3.71, W = 3.78 mm) (Pn. 041) (bed 0), occlusal view; B) *Lepus corsicanus*, P_3 dx (L = 3.43, W = 3.21 mm) (Pn. 044/2) (bed 5), occlusal view; C) *Lepus corsicanus*, P_3 sx (L = 3.64, W = 3.27 mm) (Pn. 053) (bed 8), occlusal view; D) *Lepus corsicanus*, P_3 dx (L = 3.07, W = 3.10 mm) (Pn. 31/2) (bed 3), occlusal view; E) *Lepus corsicanus*, mandibular ramus dx bearing P_3-M_3 (L = 17.26 mm) (P_3 illustrated in A) (Pn 41) (bed 0), labial view; F) *Oryctolagus cuniculus*, P_3 dx (L = 2.91, W = 2.89 mm) (Pn. 031/2) (bed 3), occlusal view; G) *Oryctolagus cuniculus*, P_3 dx (L = 2.73, W = 2.70 mm) (Pn. 034) (bed 5), occlusal view; H) *Oryctolagus cuniculus*, incrusted fragment of skull bearing two teeth rows, dx complete P^2-M^3 (L = 13.04 mm), sx with P^2-M^2 (Pn. 030) (bed 3), ventral view.

Oryctolagus burgi is characterized by a P^2 with three well developed flexes (Nocchi & Sala, 1997b), whilst in the fossils of Avetrana the lateral flexes (mesoflexus and hypoflexus) are shallow, similar to *O. cuniculus*. The P_3 of Avetrana specimens present a rather shallow anteroflexid similar to *O. cuniculus*. For these reasons we assign the Avetrana specimens to the common rabbit, *O. cuniculus*.

The species makes its appearance in the Iberian peninsula during the Middle Pleistocene (López-Martínez, 1989, 2008) and expands its range in France and Italy during the most recent part of the Middle Pleistocene. It is well known in the Italian peninsula since Torre in Pietra FU (Early Aurelian, late Middle Pleistocene) and especially in Apulia (south-eastern Italy) (Kotsakis *et al.*, 2003; Pandolfi *et al*, 2017a). However, there is a debate whether the rabbit was present in the last phases of the Late Pleistocene or has become extinct (see Angelici & Spagnesi, 2008a; Kotsakis, 2008). In this latter case, the presence of *O. cuniculus* in Italy during the Holocene would be the result of a new colonization perhaps due to anthropic intervention. A review of all the fossil lagomorphs of the Late Pleistocene of the Italian peninsula would be necessary to solve this problem.

The wild rabbit currently lives in plains and hills with preference for dry and well-drained soils, rich in low bushes. However, it manages to adapt to many environments (Angelici & Spagnesi, 2008a).

Lepus corsicanus DE WINTON, 1898.
(Figs. 5A, 5B, 5C, 5D, 5E)

Specimens: One mandibular ramus dx bearing P_3-M_3 (L = 17.26 mm) (P_3: L = 3.71, W = 3.78 mm) (Pn 41), one P_3 sx (L = 3.22, W = 2.93 mm) (Pn. 42), one I^1 sx (Pn. 43) (bed 0); one mandibular ramus dx bearing P_3-M_2 (P_3: L = 3.07, W = 3.10 mm) (Pn 064) (bed 3); two fragments of mandibular rami dx bearing P_3-M_1 (Pn. 44/1)(P_3: L = 3.43, W = 3.21 mm) and P_3-M_3 (Pn. 44/2) (P_3: W = 3.68 mm), two I^1 one sx (Pn. 45/1) and one dx (Pn. 45/2), two P_3 sx (L = 3.05, W = 2.94 mm; L = 3.10, W = 3.11 mm) (Pn. 46/1-2), two articular fragments of scapulae sx (Pn. 47/1-2), one juvenile humerus dx, and a distal fragment of a humerus sx (Pn. 48/1-2), the distal half of a radius sx (Pn. 49), a proximal part of an ulna dx (Pn 50), three proximal (two sx (Pn. 51/1-2), one dx (Pn. 51/3)) and two distal parts (both dx) of femur (Pn 51/4-5), a tibia sx lacking the distal part (Pn. 52/1), and distal fragment of a tibia dx (Pn. 52/2) (bed 5); a fragment of mandibular ramus sx bearing P_3-M_3 (L = 17.34 mm) (P_3: L = 3.64, W = 3.27 mm) (Pn 53), a distal fragment of a humerus dx (Pn 54), two proximal fragments of femurs (one dx (Pn. 55/1) and one sx (Pn. 55/2)) (bed 8).

As for *O. cuniculus*, the criteria proposed by Callou (1997) are used to distinguish the genera *Oryctolagus* and *Lepus*. For the systematic attribution of dental remains, the criteria used by Callou (1997) and Vismara (2012) were utilized.

The fossil remains assigned to *Lepus* present the I^1 (Pn 43, 45/1-2) with the mesial lobe less rounded than those attributed to *Oryctolagus*. In P_3 (Pn. 41, 42, 44/1-2, 46/1-2, 53) the lingual and vestibular anteroconids are asymmetric, inclined towards the labial part with the profile of this tooth becoming semicircular. The mandible (Pn 41, 44/1-2, 53) has a long diastema and the mental foramen is spaced from the front edge of P_3. The articular surface of the scapula has a flat surface between the glenoid cavity, the supraglenoid tubercle and the coracoid process. In the humerus (Pn. 48/1) the deltoid crest gradually attenuates and, in the distal part (Pn. 48/2, 54), the medial epicondyle is short. In the distal part of the radius (Pn. 49) the ridges present in the anterior part are extremely tenuous and, in the ulna (Pn. 50), the ridges present on the olecranon tuberosity are of equal size. In the femur (Pn 51/1-3, 55/1-2), the neck has a straight proximal border, the foramen is well beyond the distal part of the small trochanter, the intertrochanteric crest is absent (except for the specimen Pn. 55/2). The tibia (Pn. 52/1) presents the two highly developed tubercles of intercondylar eminence.

In Italy, fossils of the genus *Lepus* are attributed to an extinct species, *Lepus terraerubrae* KRETZOI, 1956 and to four extant species, *Lepus europaeus* PALLAS, 1778, *Lepus corsicanus* DE WINTON, 1898, *Lepus timidus* LINNAEUS, 1758 and *Lepus capensis* LINNAEUS, 1758. *Lepus terraerubrae* is reported, with only one tooth, in Monte Peglia (Umbria) (Van der Meulen, 1973). Such fossil unfortunately seems to be lost. *Lepus capensis*, a species of wide African distribution, is found in Italy only in Sardinia, where it was introduced by man in Holocene times (Angelici *et al.*, 2008). *Lepus timidus*, now present in Italy in the Alps, is reported in some deposits of the recent Late Pleistocene and Holocene of northern, and central, and even southern Italy (Cassoli & Tagliacozzo, 1974; Di Stefano *et al.*, 1992; Minieri *et al.*, 1995; Farina, 2014). However, many of these reports should be reviewed. The mountain hare or variable hare is characterized by square I^1 and a P_3 with highly developed anteroflexid, angular entoconid and poorly-developed protoconid (Callou, 1997). The fossils of Avetrana present rectangular I^1 with the lateral width much more developed than the anteroposterior axis, and P_3 with medium-developed anteroflexid, non-prominent entoconid and massive protoconid. The lingual termination of the hypoflexid is in most cases symmetric and the edge of the hypoflexid slightly or not

crenulated at all. These characteristics exclude an attribution to *L. timidus*. Compared to *L. europaeus*, present throughout the Italian peninsula (introduced for hunting reasons in its central-southern part) (Angelici & Spagnesi, 2008b), the fossils of Avetrana present a P_3 without the centroflexid in the anterior edge of the hypoflexid, the hypoconid without crenulations and the antero-lingual edge of the tooth without paraflexid. This morphology coincides perfectly with that of *L. corsicanus*.

Lepus corsicanus populates the central-southern region of the Italian peninsula (Angelici & Spagnesi, 2008c) and was introduced by man in Corsica (Vigne, 1992). The endemic Italian hare was considered as a subspecies of *L. europaeus* by Miller (1912) and was raised again at a specific level by Palacios (1996). As a consequence all the fossil remains collected in Italy and described before 2000 have been attributed without distinction to *L. europaeus*. In fact it is very probable that most or all the remains coming from southern Italy belong to *L. corsicanus*, as proven by a few revisions of material in museum collections (Riga *et al*., 2003; Trocchi & Riga, 2005; Vismara, 2012) and by the systematic study of new material collected in recent excavations (Salari *et al*., 2011; Vismara, 2012; Pandolfi *et al*., 2017a). The presence of *L. corsicanus* in the fossiliferous site of Visogliano (Friuli-Venezia Giulia - Middle Pleistocene - late Galerian) (Abbazzi *et al*., 2000; Falguères *et al*., 2008), well outside its current distribution area, allowed Vismara (2012) to hypothesize a first hare colonization of the Italian peninsula from a group (*L. castroviejoi* - *L. corsicanus* – see Alves *et al*., 2008) to which also the Italic hare belongs. Eventually, the arrival of *L. europaeus* would have restricted the area of *L. corsicanus* to the center-South (Vismara, 2012; Vismara *et al*., 2014). Also for the genus *Lepus*, a revision of all the Italian fossil material is necessary. The Italic hare populates open spaces with bushes like *L. europaeus* but, unlike the latter species, it also populates the deciduous forest. It occurs from the plains at sea level up to over 2000 m altitude (Angelici & Spagnesi, 2008c).

Leporidae indet.

Specimens: Fragment of a mandibular ramus sx bearing P_4-M_1 of very small dimensions, fragment of maxillary dx bearing P_4-M_1, several isolated molars (Pn. 56/1-9) (bed 0); two isolated molars (Pn. 57/1-2) (bed 2); three maxillary fragments (two dx, one sx) bearing P^3-M^3, P^3-M^1, P^3-M^2 respectively, some isolated molars (Pn. 58/1-7) (bed 3); a proximal fragment of femur of large dimensions, and some metapodials belonging to the same limb, several postcranial fragments (Pn. 59/1-6) (bed 5); a fragment of maxillary dx bearing P^2-P^4, fragments of molars (Pn. 60/1-3) (bed 8).

Various remains classified as Leporidae indet. are present in all the layers of the sequence with the exception of bed 1. It can reasonably be excluded that these remains belong to different species than *O. cuniculus* or *L. corsicanus*.

Discussion and Conclusions

At the bottom of the filling (bed 0), *Microtus (Terricola) savii* with a morphology of the M_1 identical to those of the extant populations is present. Remains belonging to *M. (T.)* gr. *savii* are known in Italy since the Middle Pleistocene (Bartolomei, 1977; Marcolini *et al*., 2003). However, specimens of this arvicoline with advanced morphology unquestionably belonging to the extant species, are known since the beginning of Late Pleistocene (Kotsakis *et al*., 2003). From bed 5, two other elements were collected, *Crocidura suaveolens* and *Arvicola italicus*, that only appear in Late Pleistocene (see discussion in the previous chapter). Fallow deer and red deer are both represented by specimens with morphology identical to the extant *Dama dama* and *Cervus elaphus* respectively (Petronio *et al*., 2008; Pandolfi *et al*., 2013; Di Stefano *et al*., 2015). The advanced subspecies of these cervids appear at the beginning of Late Pleistocene (Petronio *et al*., 2007). Among the large mammals, *Stephanorhinus hemitoechus* disappears in Italy during MIS 3 (Gliozzi *et al*., 1997; Pandolfi & Tagliacozzo, 2015; Pandolfi *et al*., 2017b). Since this rhinocerotid is also present at bed 8 the entire filling must be deposited between MIS 5e, beginning of Late Pleistocene, and the middle part of MIS 3. Another large mammal, *Hippopotamus amphibius*, is present up to bed 6. According to Gliozzi *et al*. (1997) the hippopotamus disappears in Italy at the beginning of MIS 4. However, the presence of remains of this species in the level G of Grotta Romanelli (Apulia, southern Italy) would at least witness a survival in southern Italy until the beginning of MIS 3 (Pandolfi & Petronio, 2015).

Inside the deposit, the presence of *Microtus (Microtus) arvalis* is reported only from bed 8. In southern Italy the species is currently absent and has never been found in the numerous fossil assemblages of Apulia assigned to MIS 5 (De Giuli, 1983; Kotsakis *et al*., 2003; Pandolfi *et al*., 2017a). It is present in more recent assemblages (Kotsakis *et al*., 2003;

Berto *et al*., 2017). It could therefore be assumed that most of the infilling (bed 0 - bed 7) was deposited during one or more phases of MIS 5, whereas bed 8 was deposited during MIS 4 or the first phases of MIS 3. However, given the scarcity of the findings of small vertebrates (a good number of species, but few remains for each one) and taking into account that the absence of discovery of a given species certainly does not mean absence of this species from the area, the proposal can be considered the most probable working hypothesis.

The number of small vertebrates is not sufficient to present statistical diagrams to highlight any environmental change. However, some qualitative considerations can be made. From an environmental point of view, some species of small vertebrates are ubiquitous. However, some of them would indicate an open environment (*Bufotes* gr. *B. viridis*, *M. (T.) savii*, *Oryctolagus cuniculus* for bed 0-bed 7 and *M. (M.) arvalis* for bed 8) and other species indicate a humid one *(Bufotes, Rana, Natrix, C. suaveolens, A. italicus)*. This indication is confirmed by the birds *Perdix perdix*, *Otis tarda*, and by *Pyrrhocorax pyrrhocorax*, a mountain species that in western Europe prefers the rocky coasts in proximity to coastal meadows (Kerbiriou *et al*., 2006). *Pyrrhocorax graculus* is normally found in the high mountains, even higher than *P. pyrrhocorax*. However, in Corsica it goes down to sea-cliffs (Louchart, 2002). Also *Columba livia* prefers rocky environments and sea-cliffs (Gibbs *et al*., 2001). Among the large mammals, the ubiquitous elements predominate but there are also some elements related to the forest such as *Lynx lynx* and *Capreolus capreolus*. The presence of *H. amphibius* and *Sus scrofa* confirms the presence of areas rich in water nearby. The appearance of *M. (M.) arvalis* in bed 8 would indicate a cooler climate compared to the previous situation dominated by *M. (T.) savii*.

The environment should be that of a coastal plain with marshes bordered by wooded areas and with rocky coastal areas nearby. The study of small vertebrates confirmed the hypothesis advanced by Petronio *et al*. (2008).

ACKNOWLEDGMENTS

References

Abbazzi, L.; Angelone, C.; Arca, M.; Barisone, G.; Bedetti, C.; Delfino, M.; Kotsakis, T.; Marcolini, F.; Palombo, M.R.; Pavia, M.; Piras, P.; Rook, L.; Torre, D.; Tuveri, C.; Valli, A. & Wilkens, B. (2004). Plio-Pleistocene fossil vertebrates of Monte Tuttavista (Orosei, E. Sardinia, Italy), an overview. Rivista Italiana di Paleontologia e Stratigrafia, 110: 681–706.

Abbazzi, L.; Fanfani, F.; Ferretti, M.P.; Rook, L.; Cattani, L.; Masini, F.; Mallegni, F.; Negrino, F. & Tozzi, C. (2000). New human remains of archaic *Homo sapiens* and Lower Palaeolithic industries from Visogliano (Duino Aurisina, Trieste, Italy). Journal of Archaeological Science, 27: 1173–1186. https://doi.org/10.1006/jasc.1999.0541

Alves, P.C.; Melo-Ferreira, J.; Branco, M.; Suchentrunk, F.; Ferrand, N. & Harris, D.J. (2008). Evidence for genetic similarity of two allopatric European hares (*Lepus corsicanus* and *L. castroviejoi*) inferred from nuclear DNA sequences. Molecular Phylogenetics and Evolution, 46: 1191–1197. https://doi.org/10.1016/j.ympev.2007.11.010

Amori, G. & Castiglia, R. (2018). Mammal endemism in Italy: A review. Biogeographia, The Journal of Integrative Biogeography, 33: 19–31. https://doi.org/10.21426/B633035335

Angelici, F.M. & Spagnesi, M. (2008a). *Oryctolagus cuniculus* (Linnaeus; 1758). In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 292–302.

Angelici, F.M. & Spagnesi, M. (2008b). *Lepus europaeus* Pallas; 1778. In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 267–282.

Angelici, F.M. & Spagnesi, M. (2008c). *Lepus corsicanus* De Winton; 1898. In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 254–266.

Angelici, F.M.; Masseti, M. & Spagnesi, M. (2008). *Lepus capensis* Linnaeus, 1758. Dati paleontologici e archeozoologici. In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 249–250.

Angelone, C. & Rook, L. (2012). Late Neogene and Quaternary lagomorphs from Tuscany: A revision based on specimens in Basel Naturhistorisches Museum and Florence University collections. Swiss Journal

of Palaeontology, 131: 127–145. https://doi.org/10.1007/s13358-011-0035-2

Anzidei, A.P.; Caloi, L.; Giacopini, L.; Mantero, D.; Palombo, M.R.; Sebastiani, R. & Segre, A.G. (1993). Saggi di scavo nei depositi pleistocenici del km. 18.900 della via Aurelia e di Collina Barbattini (Castel di Guido-Roma). Archeologia Laziale, 11: 81–90.

Argenti, P. (1999). La biocronologia dei roditori del Plio-Pleistocene dell'Umbria e l'evoluzione del genere *Apodemus* (Muridae, Rodentia) in Italia. Ph.D. Thesis, Università di Perugia, 277 pp.

Balletto E.; Bologna M.A. & Corti C. (2007). *Bufo viridis* Laurenti, 1768 complex. In: Fauna d'Italia, Amphibia (Lanza, B.; Andreone, F.; Bologna, M.A.; Corti, C. & Razzetti, E., Eds.), Calderini, Bologna, 296–305.

Bartolini, S.; Cioppi, E.; Rook, L. & Delfino, M. (2014). Late Pleistocene fossils and the future distribution of *Rana temporaria* (Amphibia; Anura) along the Apennine Peninsula (Italy). Zoological Studies, 53 (76): 1–10. https://doi.org/10.1186/s40555-014-0076-5

Bartolomei, G. (1977). Breccia ossifera a elefante e micromammiferi presso S. Giovanni di Duino nel Carso di Trieste. Rendiconti dell'Accademia Nazionale dei Lincei, Serie 8, 61 (1976): 274–279.

Baryshnikov, G.F. (2003). Pleistocene small porcupine from the Ural Mountains, Russia, with note on taxonomy of *Hystrix vinogradovi* (Rodentia, Hystricidae). Russian Journal of Theriology, 2: 43–47.

Benvenuti, M.; Bahain, J.-J.; Capalbo, C.; Capretti, C.; Ciani, F.; D'Amico, C.; Esu, D.; Giachi, G.; Giuliani, C.; Gliozzi, E.; Lazzeri, S.; Macchioni, N.; Mariotti Lippi, M.;Masini, F.; Mazza, P.P.A.; Pallecchi, P.; Revedin, A.; Savorelli, A.; Spadi, M.; Sozzi, L.; Vietti, A.; Voltaggio M.; Arangurenh, B. (2017). Paleoenvironmental context of the early Neanderthals of Poggetti Vecchi for the late middle Pleistocene of Central Italy. Quaternary Research, 88: 327–344. https://doi.org/10.1017/qua.2017.51

Bertè, D.F. & Pandolfi, L. (2014). *Canis lupus* (Mammalia, Canidae) from the Late Pleistocene deposit of Avetrana (Taranto, Southern Italy). Rivista Italiana di Paleontologia e Stratigrafia, 120: 367–379.

Berto, C.; Bertè, D.; Luzi, E.; López-García, J.M.; Pereswiet-Soltan, A. & Arzarello, M. (2016). Small and large mammals from the Ciota Ciara cave (Borgosesia, Vercelli, Italy): An Isotope Stage 5 assemblage. Comptes Rendus Palevol, 15: 669–680. https://doi.org/10.1016/j.crpv.2015.05.014

Berto, C.; Boscato, P.; Boschin, F.; Luzi, E. & Ronchitelli, A. (2017). Paleoenvironmental and paleoclimatic context during the Upper Palaeolithic (late Upper Pleistocene) in the Italian Peninsula. The small mammal record from Grotta Paglicci (Rignano Garganico, Foggia, Southern Italy). Quaternary Science Reviews, 168: 30–41. https://doi.org/10.1016/j.quascirev.2017.05.004

Berto, C.; Luzi, E; Montanari Canini, G.; Guerreschi, A. & Fontana, F. (2018). Climate and landscape in Italy during Late Epigravettian. The Late Glacial small mammal sequence of Riparo Tagliente (Stallavena di Grezzana, Verona, Italy). Quaternary Science Reviews, 184; 132–142. https://doi.org/10.1016/j.quascirev.2017.07.022

Berto, C. & Rubinato, G. (2013). The Upper Pleistocene mammal record from Caverna degli Orsi (San Dorligo della Valle e Dolina, Trieste, Italy): A faunal complex between eastern and western Europe. Quaternary International, 284: 7–14. https://doi.org/10.1016/j.quaint.2011.07.025

Berto, C.; Santaniello, F. & Grimaldi, S. (2019). Palaeoenvironment and palaeoclimate in the western Liguria region (northwestern Italy) during the Last Glacial. The small mammal sequence of Riparo Mochi (Balzi Rossi, Ventimiglia). Comptes Rendus Palevol, 18: 13–23. https://doi.org/10.1016/j.crpv.2018.04.007

Bezerra, A.M.R.; Annesi, F.; Aloise, G.; Amori, G.; Giustini, L. & Castiglia, R. (2016). Integrative taxonomy of the Italian pine voles, *Microtus savii* group (Cricetidae, Arvicolinae). Zoologica Scripta, 45: 225–236. https://doi.org/10.1111/zsc.12155

Böhme, G. (1977). Zur Bestimmung quartärer Anuren Europas an Hand von Skelettelementen. Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematische-Naturwissenschaftliche Reihe, 26: 283–300.

Böhme, W.; Paggetti, E.; Razzetti, E. & Vanni, S. (2007). *Bufo bufo* (Linnaeus, 1758). In: Fauna d'Italia, Amphibia (Lanza, B.; Andreone, F.; Bologna, M.A.; Corti, C. & Razzetti, E., Eds.), Calderini, Bologna, 289–296.

Bon, M.; Piccoli, G. & Sala, B. (1991). I giacimenti quaternari di vertebrati fossili nell'Italia nord-orientale. Memorie di Scienze Geologiche, 43: 185–231.

Bona, F. (2011). Upper Pleistocene small mammal fauna from Salnova Quarry (Saltrio-Varese-Northwestern Lombardy): Paleoenvironmental reconstruction and *Chionomys nivalis* population study. Rivista Italiana di Paleontologia e Stratigrafia, 117: 323–330.

Bona, F.; Laurenti, B. & Delfino, M. (2009). Climatic fluctuations during the last glacial in the North-Western Lombardian Prealps: The Upper Pleistocene faunal assemblages of the Caverna Generosa (Como, Italy). Rivista Italiana di Paleontologia e Stratigrafia, 115: 253–267.

Bona, F.; Sala, B. & Tintori, A. (2008). Early Toringian small mammals fauna from Fontana Marella cave (Varese; Lombardy; North Italy). Rivista Italiana di Paleontologia e Stratigrafia, 114: 133–144.

Bona, F. & Savoldi, M. (2016). The first record of birch mouse *Sicista* in the Upper Pleistocene sediments of Caverna Generosa (Como, Italy), with morphometrical, morphological and ecological considerations. Rivista Italiana di Paleontologia e Stratigrafia, 122(2): 1–12.

Cagnin, M. (2008). *Arvicola amphibius* (Linnaeus, 1758). In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 445–458.

Callou, C. (1997). Diagnose différentielle des principaux éléments squelettiques du lapin (genre *Oryctolagus*) et du lièvre (genre *Lepus*), en Europe occidentale. Fiches d'Ostéologie Animale pour l'Archéologie, Série B, Mammifères, 8: 1–21.

Capizzi D. & Filippucci M.G. (2008a). *Apodemus sylvaticus* (Linnaeus, 1758). In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 604–618.

Capizzi, D. & Filippucci, M.G. (2008b). *Apodemus flavicollis* (Melchior, 1834). In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 594–603.

Cassoli, P.F. & Tagliacozzo, A. (1994). I macromammferi dei livelli tardopleistocenici delle Arene Candide (Savona; Italia): considerazioni paleontologiche e archeozoologiche. Quaternaria Nova, 4: 101–262.

Castiglia, R.; Aloise, G.; Amori, G.; Annesi, F.; Bertolino, S.; Capizzi, D.; Mori, E. & Colangelo, P. (2016). The Italian peninsula hosts a divergent mtDNA lineage of the water vole, *Arvicola amphibius* s.l., including fossorial and aquatic ecotypes. Hystrix, the Italian Journal of Mammalogy, 27(2): 1–5.

Castiglia, R.; Annesi, F.; Amori, G.; Solano, E. & Aloise, G. (2017). The phylogeography of *Crocidura suaveolens* from southern Italy reveals the absence of an endemic lineage and supports a Trans-Adriatic connection with the Balkanic refugium. Hystrix, the Italian Journal of Mammalogy, 28: 104–106.

Cheylan, M.; Corti, C.; Carpaneto, G.M.; Mazzotti, S. & Zuffi, M.A.L. (2011). *Testudo hermanni* Gmelin, 1789. In: Fauna d'Italia, Reptilia (Corti, C.; Capula, M.; Luiselli, L; Razzetti, E. & Sindaco, R., Eds.), Calderini, Bologna, 188–199.

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 Moncucco Torinese, north-western Italy. Paleoecological and paleoclimatological implications. Palaeontologia Electronica, 20(1, 10A): 1–66. https://doi.org/10.26879/658

Contoli, L.; Nappi, A. & Castiglia, R. (2008). Caratteri generali dei *Microtus* (*Terricola*) del "gruppo savii". In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 525–535.

Corbet, G.B. (1978). The mammals of the Palaearctic Region: A taxonomic review. Cornell University Press, London & Ithaca, 314 pp.

Corti C.; Sindaco R. & Paggetti E. (2011), Famiglia Lacertidae Oppel, 1811. In: Fauna d'Italia, Reptilia (Corti, C.; Capula, M.; Luiselli, L; Razzetti, E. & Sindaco, R., Eds.), Calderini, Bologna, 328–330.

Cossu, I.M.; Frau, S.; Delfino, M.; Chiodi, A.; Corti, C. & Bellati, A. (2018). First report of *Bufo bufo* (Linnaeus, 1758) from Sardinia (Italy). Acta Herpetologica, 13: 43–49.

Curcio, M.T.; Contoli, L.; Di Canzio, E. & Kotsakis, T. (2005). Preliminary analysis of M1 of Late Pleistocene and Recent populations of Terricola savii from Italy (Arvicolidae; Rodentia). Geo.Alp, 2: 91–98.

Curcio, M.T.; Tata, C.; Kotsakis, T. & Salvini, F. (2007). A Late Pleistocene (MIS 4) vertebrate assemblage from a fluvial terrace of Fiora river (Northern Latium, Central Italy). In: Proceedings of the Giornate di Paleontologia 2005 (Coccioni, R. & Marsili, A., Eds.), Grzybowski Foundation Special Publication, 12: 15–20.

De Curtis, O. (2012). Indicazioni paleoambientali e paleoclimatiche dai reperti di piccoli mammiferi. In: L'insediamento musteriano di Grotta Reali; Rocchetta a Volturno, Molise, Italia (Peretto, C., Ed.), Museologia Scientifica e Naturalistica, 8(2): 19–24.

De Giuli, C. (1983). Le faune pleistoceniche del Salento. 1. La fauna di San Sidero 3. I Quaderni del Museo di Paleontologia di Maglie, 1(1): 45–84.

Delfino, M. (2002). Erpetofaune italiane del Neogene e del Quaternario. Ph.D. Thesis, Università di Modena e Reggio Emilia, 382 pp.

Delfino, M. (2004). The Middle Pleistocene herpetofauna of Valdemino Cave (Liguria; north-western Italy). The Herpetological Journal, 14: 113–128.

Delfino, M. & Atzori, M. (2013). An update on the Early Pleistocene herpetofauna from Pirro Nord. Palaeontographica, Abteilung A, 298: 19–29. https://doi.org/10.1127/pala/298/2013/19

Delfino, M. & Bailon, S. (2000). Early Pleistocene herpetofauna from Cava dell'Erba and Cava Pirro (Apulia; Southern Italy). The Herpetological Journal, 10: 95–110.

Delfino, M.; Bailon, S. & Pitruzzella, G. (2011). The Late Pliocene amphibians and reptiles from 'Capo Mannu D1 Local Fauna' (Mandriola; Sardinia; Italy). Geodiversitas, 33: 357–382. https://doi.org/10.5252/g2011n2a10

Di Canzio, E. & Petronio, C. (2001). Osservazioni sulla fauna a vertebrati pleistocenici della Grotta Cola (Abruzzo; Aquila). Bollettino della Società Paleontologica Italiana, 40: 105–114.

Di Stefano, G.; Peronio, C.; Sardella, R.; Savelloni, V. & Squazzini, E. (1992). Nuove segnalazioni di brecce ossifere nella costa fra Castro Marina e Otranto (Lecce). Il Quaternario, 5: 3–10.

Di Stefano, G., Pandolfi, L., Petronio, C. & Salari, L. (2015). Considerations on the morphometry and the occurrence of *Cervus elaphus* (Mammalia, Cervidae)

from the Late Pleistocene of the Italian Peninsula. Rivista Italiana di Paleontologia e Stratigrafia, 121 (1): 1–18.

Doukas, C.S.; Van den Hoek Ostende, L.W.; Theocharopoulos, C.D. & Reumer, J.W.F. (1995). The vertebrate locality Maramena (Macedonia; Greece) at the Turolian-Ruscinian boundary (Neogene). 5. Insectivora (Erinaceidae; Talpidae; Soricidae; Mammalia). Münchner Geowissenschafliche Abhandlungen, A, 28: 43–64.

Dubois, A. & Bour, R. (2010). The nomenclatural status of the nomina of amphibians and reptiles created by Garsault (1764); with a parsimonious solution to an old nomenclatural problem regarding the genus Bufo (Amphibia; Anura); comments on the taxonomy of this genus; and comments on some nomina created by Laurenti (1768). Zootaxa, 2447: 1–52. https://doi.org/10.11646/zootaxa.2447.1.1

Dufresnes, C.; Mazepa, G.; Rodrigues, N.; Brelsford, A.; Litvinchuk, S.N.; Sermier, R.; Lavanchy, G.; Betto-Colliard, C.; Blaser, O.; Borzée, A.; Cavoto, E.; Fabre, G.; Ghali, G.; Grossen, C.; Horn, A.; Leuenberger, J.; Phillips, B.C.; Saunders, P.A.; Savary, R.; Maddalena, T.; Stöck, M.; Dubey, S.; Canestrelli, D. & Jeffries, D.L. (2018). Genomic evidence for cryptic speciation in tree frogs from the Apennine Peninsula, with description of *Hyla perrini* sp. nov. Frontiers in Ecology and Evolution, 6: 144. https://doi.org/10.3389/fevo.2018.00144

Falguères, C.; Bahain, J.J.; Tozzi, C.; Boschian, G.; Dolo, J.M.; Mercier, N.; Valladas, H.; Yokoyama, Y. (2008). ESR/U series chronology of the Lower Palaeolithic palaeoanthropological site of Visogliano, Trieste, Italy. Quaternary Geochronology, 3: 390–398. https://doi.org/10.1016/j.quageo.2008.01.007

Fanfani, F. (2000). Revisione degli insettivori (Mammalia) tardo neogenici e quaternari dell'Italia peninsulare. Ph.D. Thesis, Università di Modena e Reggio Emilia, 283 pp.

Farina, S. (2014). Catalogue of the Late Pleistocene fossil mammalian collection from "Grotta Parignana" (Natural History Museum, University of Pisa). Atti della Società Toscana di Scienze Naturali Memorie, Serie A, 121: 19–28.

Frost, D.R.; Grant, T.; Faivovich, J.; Bain, R.H.; Haas, A.; Haddad, C.F.B.; de Sá, R.O.; Channing, A.; Wilkinson, M.; Donnellan, S.C.; Raxworthy, C.J.; Campbell, J.A.; Blotto, B.L.; Moler, P.; Drewes, R.C.; Nussbaum, R.A.; Lynch, J.D.; Green, D.M. & Wheeler, W.C. (2006). The amphibian tree of life. Bulletin of the American Museum of Natural History, 297: 1–370. https://doi.org/10.1206/0003-0090(2006)297[0001:TATOL]2.0.CO;2

Furió, M. (2007). Los Insectívoros (Soricomorpha, Erinaceomorpha, Mammalia) del Neógeno Superior del Levante Ibérico. Ph.D. Thesis, Universitat Autònoma de Barcelona, 299 pp.

Furió, M.; Gibert, L.; Ferràndez, C. & Sevilla, P. (2015). The insectivores (Soricidae; Erinaceidae; Eulipotyphla; Mammalia) from Cueva Victoria (Early Pleistocene; Murcia; Spain). Neues Jahrbuch für Geologie und Paläontologie Abhandlungen, 275: 151–161. https://doi.org/10.1127/njgpa/2015/0460

Galindo-Pellicena, M.Á.; Cuenca Bescós, G. & Arsuaga, J.L. (2011). Los micromamíferos (Rodentia; Soricomorpha; Erinaceomorfa; Lagomorpha y Chiroptera) del Pleistoceno Medio de la Covacha de los Zarpazos (Sierra de Atapuerca, Burgos, España). Boletín de la Real Sociedad Española de Historia Natural Sección Geológica, 105: 87–97.

Gatta, M.; Kotsakis, T.; Pandolfi, L.; Petronio, C.; Salari, L.; Achino, K.F.; Silvestri, L.; Rolfo, M.F. (2019). The Late Pleistocene faunal assemblage from Cava Muracci (Latium, Italy): Palaeoenvironmental implications for coastal central Italy during MIS 3. Comptes Rendus Palevol, 18: 51–71. https://doi.org/10.1016/j.crpv.2018.04.006

Gibbs, D.; Barnes, A. & Cox, J. (2001). Pigeons and doves. A guide to the pigeons and doves of the World. Christopher Helm, London, 615 pp. (reprint 2010).

Gippoliti, S. (2012). The name of the Italian water vole *Arvicola* cf. *amphibius* (Linnaeus, 1758). Hystrix, 23: 87–89.

Gliozzi, E.; Abbazzi, L.; Argenti, P.; Azzaroli, A.; Caloi, L.; Capasso Barbato, L.; Di Stefano, G.; Esu, D.; Ficcarelli, G.; Girotti, O.; Kotsakis, T.; Masini, F.; Mazza, P.; Mezzabotta, C.; Palombo, M. R.; Petronio, C.; Rook, L.; Sala, B.; Sardella, R.; Zanalda, E. & Torre, D. (1997). Biochronology of selected mammals; molluscs and ostracods from the middle Pliocene to the late Pleistocene in Italy. The state of the art. Rivista Italiana di Paleontologia e Stratigrafia, 103: 369–388.

Heinrich, W.-D. (1978). Zur biometrischen Erfassung eines Evolutionstrends bei *Arvicola* (Rodentia; Mammalia) aus dem Pleistozän Thüringens. Säugetierkundliche Informationen, 2: 3–21.

Heinrich, W.-D. (1982). Zur Evolution und Biostratigraphie von *Arvicola* (Rodentia; Mammalia) im Pleistozän Europas. Zeitschrift für Geologische Wissenschaften, 10: 683–735.

Hinton, M.A.C. (1910). A preliminary account of the British fossil voles and lemmings; with some remarks on the Pleistocene climate and geography. Proceedings of the Geologist's Association, 21: 489–507. https://doi.org/10.1016/S0016-7878(10)80028-8

Holman, J.A. (1998). Pleistocene amphibians and reptiles in Britain and Europe. Oxford Monographs on Geology and Geophysics, 38. Oxford University Press, Oxford, 254 pp.

Holz, H. & Niethammer, J. (1990). *Erinaceus europaeus* Linnaeus, 1758. In: Handbuch der Säugetiere Europas, 3(1): Insectivora, Primates (Niethammer, J. & Krapp, F., Eds.), AULA Verlag, Wiesbaden, 26–49.

Jammot, D. (1973). Les insectivores (Mammalia) du gisement Pleistocène Moyen des Abîmes de La Fage Nouailles (Corrèze). Nouvelles Archives du Muséum d'Histoire Naturelle de Lyon, 11: 41–51. https://doi.org/10.3406/quate.1974.2129

Janossy, D. (1972). Ein kleiner Hystrix aus dem Altpleistozän der Fundstelle Osztramos 8 (Nordungarn). Vertebrata Hungarica, 13: 163–183.

Kerbiriou, C.; Gourmelon, F.; Jiguet, F.; Le Viol, I.; Bioret, F. & Julliard, R. (2006). Linking territory quality and reproductive success in the red-billed chough *Pyrrhocorax pyrrochorax*: implications for conservation management of an endangered population. Ibis, 148: 352–364. https://doi.org/10.1111/j.1474-919X.2006.00543.x

Kotsakis, T. (1977). I resti di anfibi e rettili pleistocenici della Grotta di Spinagallo (Siracusa, Sicilia). Geologica Romana, 16: 211–229.

Kotsakis, T. (2008). Storia paleontologica di erinaceomorfi; soricomorfi; lagomorfi e roditori attuali d'Italia. In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 1–32.

Kotsakis, T.; Abbazzi, L.; Angelone, C.; Argenti, P.; Barisone, G.; Fanfani, F.; Marcolini, F. & Masini, F. (2003). Plio-Pleistocene biogeography of Italian mainland micromammals. Deinsea, 10: 313–342.

Kotsakis, T. & Barisone, G. (2008). Cenni sui vertebrati fossili di Roma. Memorie Descrittive della Carta Geologica d'Italia, 80: 115–143.

Kotsakis, T.; Marcolini, F.; De Rita, D.; Conti, M. & Esu, D. (2011). Three Late Pleistocene small mammal faunas from the Baccano maar (Rome; central Italy). Bollettino della Società Paleontologica Italiana, 50: 103–110.

Krystufek, B.; Koren, T.; Engelberger, S.; Horvath, G.F.; Arslan, A. & Chisamera, G. (2015). Fossorial morphotype does not make a species in water voles. Mammalia, 79: 293–303. https://doi.org/10.1515/mammalia-2014-0059

Kuzmin, Y.V.; Kosintsev, P.A.; Vasiliev, S.K.; Fadeeva, T.V. & Hodgins, G.W.L. (2017). The northernmost and latest occurrence of the fossil porcupine (*Hystrix brachyura vinogradovi* Argyropulo; 1941) in the Altai Mountains in the Late Pleistocene (ca. 32;000-41;000 cal BP). Quaternary Science Revews, 161: 117–122. https://doi.org/10.1016/j.quascirev.2017.02.010

Lanza, B.; Nistri, A. & Vanni, S. (2007). Genere *Hyla* Laurenti, 1768. In: Fauna d'Italia, Amphibia (Lanza, B.; Andreone, F.; Bologna, M.A.; Corti, C. & Razzetti, E., Eds.), Calderini, Bologna, 326.

Lawson, R.; Slowinski, J.B.; Crother, B.I. & Burbrink, F.T. (2005). Phylogeny of the Colubroidea (Serpentes): New evidence from mitochondrial and nuclear genes. Molecular Phylogenetics and Evolution, 37: 581–601. https://doi.org/10.1016/j.ympev.2005.07.016

Lenk, P. & Wüster, W. (1999). A multivariate approach to the systematics of Italian rat snakes of the *Elaphe longissima* complex (Reptilia; Colubridae): revalidation of Camerano's *Callopeltis longissimus* var. *lineata*. Herpetological Journal, 9: 153–162.

López-García, J.M.; Berto, C.; Colamussi, V.; Dalla Valle, C.; Lo Vetro, D.; Luzi, E.; Malavasi, G.; Martini, F. & Sala, B. (2014). Palaeoenvironmental and palaeoclimatic reconstruction of the latest Pleistocene-Holocene sequence from Grotta del Romito (Calabria; southern Italy) using the small-mammal assemblages. Palaeogeography Palaeoclimatology Palaeoecology, 409: 169–179. https://doi.org/10.1016/j.palaeo.2014.05.017

López-García, J.M.; Dalla Valle, C.; Cremaschi, M. & Peresani, M. (2015). Reconstruction of the Neanderthal and Modern Human landscape and climate from the Fumane cave sequence (Verona, Italy) using small mammal assemblages. Quaternary Science Reviews, 128: 1–13. https://doi.org/10.1016/j.quascirev.2015.09.013

López-García, J.M.; Livraghi, A.; Romandini, R. & Peresani, M. (2018). The De Nadale Cave (Zovencedo, Berici Hills, northeastern Italy): A small-mammal fauna from near the onset of Marine Isotope Stage 4 and its palaeoclimatic implications. Palaeogeography Palaeoclimatology Palaeoecology, 506: 196–201. https://doi.org/10.1016/j.palaeo.2018.06.033

López-García, J.M.; Luzi, E. & Peresani, M. (2017). Middle to Late Pleistocene environmental and climatic reconstruction of the human occurrence at Grotta Maggiore di San Bernardino (Vicenza, Italy) through the small-mammal assemblage. Quaternary Science Reviews, 168: 42–54. https://doi.org/10.1016/j.quascirev.2017.05.005

López Martínez, N. (1989). Revisión sistemática y biostratigráfica de los Lagomorpha (Mammalia) del Terciario y Cuaternario de España. Memorias del Museo Paleontológico de la Universidad de Zaragoza, 3: 1–342.

López Martínez, N. (2008). The lagomorph fossil record and the origin of the European rabbit. In: Lagomorph Biology. Evolution, Ecology, and Conservation (Alves, P.C.; Ferrand, N. & Hackländer, K., Eds.), Springer, Berlin, Heidelberg, New York, 27–46. https://doi.org/10.1007/978-3-540-72446-9_3

Louchart, A. (2002). Les oiseaux du Pléistocène de Corse, et de quelques localités sardes. Écologie, evolution, biogéographie et extinctions. Documents des Laboratoires de Géologie de Lyon, 155: 1–287.

Marcolini, F.; Bigazzi, G.; Bonadonna, F.P.; Centamore, E.; Cioni, R. & Zanchetta, G. (2003). Tephrochronology and tephrostratigraphy of two Pleistocene continental fossiliferous successions from Central Italy. Journal of Quaternary Science, 18: 545–556. https://doi.org/10.1002/jqs.768

Marcolini, F.; Piras, P.; Kotsakis, T.; Claude, J.; Michaux, J.; Ventura, J. & Cubo, J. (2011). Phylogenetic signal and functional significance of incisor enamel microstructure in Arvicola (Rodentia, Arvicolinae). Comptes Rendus Palevol, 10: 479–487. https://doi.org/10.1016/j.crpv.2011.04.007

Masini, F.; Giannini, T.; Abbazzi, L.; Fanfani, F.; Delfino, M.; Maul, L.C. & Torre, D. (2005). A latest Biharian small vertebrate fauna from the lacustrine succession of San Lorenzo (Sant'Arcangelo Basin, Basilicata, Italy). Quaternary International, 131: 79–93. https://doi.org/10.1016/j.quaint.2004.07.008

Masini, F.; Maul, L.C.; Abbazzi, L. & Petruso, D. (2003). Independent Arvicola lineages in Italy and Central Europe? In: IV European Congress on Mammalogy, Abstract Book (Macholan, M.; Bryja, J. & Zima, J., Eds.), Brno, p. 164.

Maul, L.; Masini, F.; Abbazzi, L. & Turner, A. (1998). The use of different morphometric data for absolute age calibration of some South- and Middle European arvicolid populations. Palaeontographia Italica, 85: 111–151.

Maul, L.C.; Rekovets, L.; Heinrich, W.-D.; Keller, T. & Storch, G. (2000). Arvicola mosbachensis (Schmidtgen 1911) of Mosbach 2: A basic sample for the early evolution of the genus and a reference for further biostratigraphical studies. Senckenbergiana Lethaea, 80: 129–147. https://doi.org/10.1007/BF03043667

Mecozzi, B. & Bartolini Lucenti, S. (2018). The Late Pleistocene Canis lupus (Canidae; Mammalia) from Avetrana (Apulia, Italy): Reappraisal and new insights on the European glacial wolves. Italian Journal of Geosciences, 137: 138–150. https://doi.org/10.3301/IJG.2017.22

Michaux, J. (1971). Muridae (Rodentia) néogènes d'Europe sud-occidentale. Evolution et rapports avec les forms actuelles. Paleobiologie Continentale, 2(1): 1–67.

Miller, G.S. (1912). Catalogue of the mammals of Western Europe (Europe exclusive of Russia) in the collections of the British Museum. British Museum (N.H.), London, 1019 p.

Minieri, M.R.; Petronio, C.; Sardella, R. & Scarano, M. (1995). Le faune a mammiferi del Pleistocene superiore dell'Italia peninsulare. Quaderni Padusa, 1: 75–87.

Musser, G.G. & Carleton, M.D. (2005). Superfamily Muroidea. In: Mammal Species of the World, 3rd ed. (Wilson, D.E. & Reeder, D.A.M., Eds.), The John Hopkins University Press, Baltimore, Vol. 2: 894–1531.

Nappi, A. (2001). I micromammiferi d'Italia. Edizioni Simone, Naples, 112 pp.

Niethammer, J. & Krapp, F. (1978). Familie Muridae Gray, 1821. In: Handbuch der Säugetiere Europas, 1(1): Rodentia I (Sciuridae, Castoridae, Gliridae, Muridae) (Niethammer, J. & Krapp, F., Eds.), Akademische Verlagsgesellschaft, Wiesbaden, 281–289.

Niethammer, J. & Krapp, F. (1990). Familie Erinaceidae Bonaparte, 1838. In: Handbuch der Säugetiere Europas, 3(1): Insectivora, Primates (Niethammer, J. & Krapp, F., Eds.), AULA Verlag, Wiesbaden, 20–25.

Nocchi, G. & Sala, B. (1997b). The fossil rabbit from Valdemino Cave (Borgio Verezzi, Savona) in the context of western Europe Oryctolagini of Quaternary. Palaeovertebrata, 26: 167–187.

Nocchi, G. & Sala, B. (1997a). Oryctolagus burgi n. sp. (Mammalia: Lagomorpha) from the Middle Pleistocene levels of Grotta Valdemino (Borgio Verezzi, Savona, north-west Italy). Paleontologia i Evolució, 30/31: 19–38.

Palacios, F. (1996). Systematics of the indigenous hares of Italy traditionally identified as Lepus europaeus Pallas, 1778 (Mammalia: Leporidae). Bonner Zoologische Beiträge, 46: 59–91.

Pandolfi, L.; Boscato, P.; Crezzini, J.; Gatta, M.; Moroni, A.; Rolfo, M. & Tagliacozzo, A. (2017b). Late Pleistocene last occurrences of the narrow-nosed rhinoceros Stephanorhinus hemitoechus (Mammalia; Perissodactyla) in Italy. Rivista Italiana di Paleontologia e Stratigrafia, 123: 177–192.

Pandolfi, L.; Mannino, M.A.; Talamo, S.; Salari, L.; Sanso', P.; Sublimi Saponetti, S.; Vacca, E.; Vicari, D.; Richards, M.P. & Petronio, C. (2017a). A reassessment of the infills and faunal assemblages of karst cavities known as ventarole in Salento (Apulia, Southern Italy): A multidisciplinary investigation on Cava Donno (Corigliano d'Otranto, Lecce). Alpine and Mediterranean Quaternary, 30: 25–40.

Pandolfi, L. & Petronio, C. (2011). The small-sized rhinoceroses from the Late Pleistocene of Apulia (southern Italy). Rivista Italiana di Paleontologia e Stratigrafia, 117 (3): 509–520.

Pandolfi, L. & Tagliacozzo, A. (2015). Stephanorhinus hemitoechus (Mammalia, Rhinocerotidae) from the Late Pleistocene of Valle Radice (Sora, Central Italy) and re-evaluation of the morphometric variability of the species in Europe. Geobios, 48 (2): 169–191. https://doi.org/10.1016/j.geobios.2015.02.002

Pandolfi, L. & Petronio, C. (2015). A brief review of the occurrences of Pleistocene Hippopotamus (Mammalia, Hippopotamidae) in Italy. Geologia Croatica, 68: 313–319. https://doi.org/10.4154/GC.2015.24

Pandolfi, L.; Petronio, C. & Salari, L. (2011). Bos primigenius Bojanus, 1827 from the early Late Pleistocene deposit of Avetrana (Southern Italy) and the variation in size of the species in southern Europe: Preliminary report. Journal of Geological Research, 2011 (ID 245408): 1–11. https://doi.org/10.1155/2011/245408

Pandolfi, L.; Petronio, C. & Salari, L. (2013). Catastrophic death assemblages from the Late Pleistocene of Italy: The case of Avetrana karst filling (Taranto, southern Italy). Rivista Italiana di Paleontologia e Stratigrafia, 119: 109–124.

Paolucci, P. & Amori, G. (2008). *Microtus arvalis* (Pallas, 1778). In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 494–503.

Pasquier, L. (1974). Dynamique évolutive d'un sous-genre de Muridae, *Apodemus* (*Sylvaemus*). Étude biométrique des caractères dentaires de populations fossils et actuelles d'Europe occidentale. Ph.D. Thesis, Université des Sciences et Techniques du Languedoc, Montpellier, 181 pp.

Petronio, C.; Bellardini, F.; Arzarello, M.; Bedetti, C.; Bellucci, L.; Cipullo, A.; Di Stefano, G.; Pandolfi, L.; Pavia, M.; Petrucci, M.; Sardella, R. & Salari, L. (2008). The deposits of the Late Pleistocene from Avetrana (Taranto, southern Italy). Biochronology and palaeoecology. Il Quaternario, 21: 409–422.

Petronio, C.; Di Canzio, E. & Salari, L. (2007). The Late Pleistocene and Holocene mammals in Italy: New biochronological and paleoenvironmental data. Palaeontographica, Abteilung A, 279: 147–157. https://doi.org/10.1127/pala/279/2007/147

Petruso, D.; Locatelli, E.; Surdi, G.; Dalla Valle, C.; Masini, F. & Sala, B. (2011). Phylogeny and biogeography of fossil and extant *Microtus (Terricola)* (Mammalia; Rodentia) of Sicily and the southern Italian peninsula based on current dental morphological data. Quaternary International, 243: 192–203. https://doi.org/10.1016/j.quaint.2011.03.013

Piertney, S.B.; Stewart, W.A.; Lambin, X.; Telfer, S.; Aars, J. & Dallas, J.F. (2005). Phylogeographic structure and postglacial evolutionary history of water voles (*Arvicola terrestris*) in the United Kingdom. Molecular Ecology, 14: 1435–1444. https://doi.org/10.1111/j.1365-294X.2005.02496.x

Piras, P.; Marcolini, F.; Claude, J.; Ventura, J.; Kotsakis, T. & Cubo, J. (2012). Ecological and functional correlates of molar shape variation in European populations of *Arvicola* (Arvicolinae; Rodentia). Zoologischer Anzeiger, 251: 335–343. https://doi.org/10.1016/j.jcz.2011.12.002

Piras, P.; Marcolini, F.; Raia, P.; Curcio, M.T. & Kotsakis, T. (2009). Testing evolutionary stasis and trends in first lower molar shape of extinct Italian populations of *Terricola savii* (Arvicolidae, Rodentia) by means of geometric morphometrics. Journal of Evolutionary Biology, 22: 179–191. https://doi.org/10.1111/j.1420-9101.2008.01632.x

Piras, P.; Marcolini, F.; Raia, P.; Curcio, M.T. & Kotsakis, T. (2010). Ecophenotypic variation and phylogenetic inheritance in first lower molar shape of extant Italian populations of *Microtus* (Terricola) savii (Rodentia). Biological Journal of the Linnean Society, 99: 632–647. https://doi.org/10.1111/j.1095-8312.2009.01379.x

Popov, V.V. (2004). Late Pliocene Erinaceidae and Talpidae (Mammalia: Lipotyphla) from Varshets (North Bulgaria). Acta Zoologica Cracoviensia, 47: 61–80.

Púgener, L.A. & Maglia, A.M. (1997). Osteology and skeletal development of *Discoglossus sardus* (Anura: Discoglossidae). Journal of Morphology, 233: 267–286. https://doi.org/10.1002/(SICI)1097-4687(199709)233:3<267::AID-JMOR6>3.0.CO;2-0

Rage, J.-C. (1974). Les batraciens des gisements quaternaires européens. Détermination ostéologique. Bulletin Mensuel de la Société Linnéenne de Lyon, 43: 276–289. https://doi.org/10.3406/linly.1974.10136

Reggiani, G. & Filippucci, M.G. (2008). *Erinaceus europaeus* Linnaeus, 1758. In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 70–81.

Reumer, J.W. F. & Hordijk, L.W. (1999). Pleistocene Insectivora (Mammalia) from the Zuurland boreholesnear Rotterdam, The Netherlands. Deinsea, 7: 253–281.

Riga, F.; Trocchi, V.; Angelici, F.M.; Randi, E. & Pierpaoli, M. (2003). *Lepus corsicanus* De Winton, 1898 - Apenninenhase. In: Handbuch der Säugetiere Europas, 3(2): Lagomorpha (Niethammer, J. & Krapp, F., Eds.), AULA Verlag, Wiesbaden, 117–135.

Ronchitelli, A.; Boscato, P.; Surdi, G.; Masini, F.; Petruso, D.; Accorsi, C.A. & Torri, P. (2011). The Grotta Grande of Scario (Salerno, Italy): Archaeology and environment during the last interglacial (MIS 5) of the Mediterranean region. Quaternary International, 231: 95–109. https://doi.org/10.1016/j.quaint.2010.07.006

Rustioni, M.; Ferretti, M.P.; Mazza, P.; Pavia, M. & Varola, A. (2003). The vertebrate fauna from Cardamone (Apulia, southern Italy): An example of Mediterranean mammoth fauna. Deinsea, 9: 395–403.

Rustioni, M.; Mazza, P.; Abbazzi, L.; Delfino, M.; Rook, L.; Petrucci, S. & Vianello, F. (1994). The Würmian fauna from Sternatia (Lecce, Apulia, Italy). Bollettino della Società Paleontologica Italiana, 33: 279–288.

Sala, B. & Marchetti, R. (2006). The Po Valley floodplain (northern Italy): A transitional area between two zoogeographical areas during the Late Neogene and Quaternary. Courier Forschungsinstitut Senckenberg, 256: 321–328.

Sala, B. & Masini, F. (2007). Late Pliocene and Pleistocene small mammal chronology in the Italian peninsula. Quaternary International, 160: 4–16. https://doi.org/10.1016/j.quaint.2006.10.002

Salari, L. (2014). Holocene micromammals (Soricomorpha and Rodentia) from some caves of Central Italy. Revue de Paléobiologie, 30: 79–96.

Salari, L.; Passacantando, D. & Rolfo, M.F. (2011). First data on the latest Pleistocene mammals from Mora Cavorso cave (Jenne, Latium, Central Italy). Il Quaternario, 24: 131–140.

Salari, L. & Sardella, R. (2009). The Pleistocene porcupine *Hystrix vinogradovi* Argyropulo, 1941 in Italy. Bollettino della Società Paleontologica Italiana, 48: 123–127.

Salari, L. & Sardella, R. (2011). Il genere *Hystrix* Linnaeus, 1758 in Italia nel Pleistocene. Atti della Società Toscana di Scienze Naturali Memorie, Serie A, 116: 171–178.

Salari, L. & Silvestri, L. (2015). Holocene bats (Mammalia; Chiroptera) from five caves of Central Apennines (Italy). Barbastella, 8: 27–41. https://doi.org/10.14709/BarbJ.8.1.2015.06

Salvi, D.; Mendes, J.; Carranza, S. & Harris, D.J. (2018). Evolution, biogeography and systematics of the western Palaearctic *Zamenis* ratsnakes. Zoologica Scripta, https://doi.org/10.1111/zsc.12295. https://doi.org/10.1111/zsc.12295

Sarà, M. (2008). *Crocidura suaveolens* (Pallas, 1811). In: Fauna d'Italia, Mammalia II. Erinaceomorpha, Soricomorpha, Lagomorpha, Rodentia (Amori, G.; Contoli, L. & Nappi, A., Eds.), Calderini, Milano, 218–225.

Sardella, R.; Bedetti, C.; Bellucci, L.; Conti, N.; Coppola, D.; Di Canzio, E.; Pavia, M.; Petronio, C.; Petrucci, M. & Salari, L. (2005). The Late Pleistocene vertebrate fauna from Avetrana (Taranto, Apulia, Southern Italy): Preliminary report. Geo.Alp, 2: 25–29.

Scali, S.; Gentili, A. & Lanza, B. (2011). *Natrix natrix* (Linnaeus, 1758). In: Fauna d'Italia, Reptilia (Corti, C.; Capula, M.; Luiselli, L; Razzetti, E. & Sindaco, R., Eds.), Calderini, Bologna, 552–562.

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). Paleoecological and biochronological implications. Geobios, 47: 403–418. https://doi.org/10.1016/j.geobios.2014.10.001

Stöck, M.; Dufresnes, C.; Litvinchuk, S.N.; Lymberakis, P.; Biollay, S.; Berroneau, M.; Borzée, A.; Ghali, K.; Ogielska, M. & Perrin, N. (2012). Cryptic diversity among Western Palearctic tree frogs: postglacial range expansion; range limits; and secondary contacts of three European tree frog lineages (*Hyla arborea* group). Molecular Phylogenetics and Evolution, 65: 1–9. https://doi.org/10.1016/j.ympev.2012.05.014

Stöck, M.; Sicilia, A.; Belfiore, N.M.; Buckley, D.; Lo Brutto, S.; Lo Valvo, M. & Arculeo, M. (2008). Post-Messinian evolutionary relationships across the Sicilian channel: Mitochondrial and nuclear markers link a new green toad from Sicily to African relatives. BMC Evolutionary Biology, 8 (56): 1–19. https://doi.org/10.1186/1471-2148-8-56

Szyndlar, Z. (1984). Fossil snakes from Poland. Acta Zoologica Cracoviensia, 28: 1–156.

Szyndlar, Z. (1991a). A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part 1: Scolecophidia, Boidae, Colubrinae. Estudios Geológicos, 47: 103–126. https://doi.org/10.3989/egeol.91473-4422

Szyndlar, Z. (1991b). A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part 2: Natricinae, Elapidae, Viperidae. Estudios Geológicos, 47: 237–266. https://doi.org/10.3989/egeol.91473-4422

Taberlet, P.; Fumagalli, L.; Wust-Saucy, A.G. & Cosson, J.F. (1998). Comparative phylogeographyand postglacial colonization routes in Europe. Molecular Ecology, 7: 453–464. https://doi.org/10.1046/j.1365-294x.1998.00289.x

Tang, Zhuowei & Kotsakis, T. (2008). Tardiglacial micromammals of Riparo Salvini (Latium, Central Italy). Geologica Romana, 41: 125–132.

Trocchi, V. & Riga, F. (2005). I lagomorfi in Italia. Linee guida per la conservazione e gestione. Istituto Nazionale per la Fauna Selvatica, Documenti Tecnici, 25: 1–128.

Van der Meulen A. J. (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.

Venchi, A. & Luiselli, L. (2011a). *Zamenis lineatus* (Camerano, 1891). In: Fauna d'Italia, Reptilia (Corti, C.; Capula, M.; Luiselli, L; Razzetti, E. & Sindaco, R., Eds.), Calderini, Bologna, 584–586.

Venchi, A. & Luiselli, L. (2011b). *Zamenis longissimus* (Laurenti, 1768). In: Fauna d'Italia, Reptilia (Corti, C.; Capula, M.; Luiselli, L; Razzetti, E. & Sindaco, R., Eds.), Calderini, Bologna, 587–590.

Vigne, J.D. (1992). Zooarchaeology and the biogeographical history of the mammals of Corsica and Sardinia since the last ice age. Mammal Review, 22: 87–96. https://doi.org/10.1111/j.1365-2907.1992.tb00124.x

Villa, A.; Blain, H.-A. & Delfino, M. (2018a). The Early Pleistocene herpetofauna of Rivoli Veronese (Northern Italy) as evidence for humid and forested glacial phases in the Gelasian of Southern Alps. Palaeogeography Palaeoclimatology Palaeoecology, 490: 393–403. https://doi.org/10.1016/j.palaeo.2017.11.016

Villa, A.; Bon, M. & Delfino, M. (2018b). Trapped in a roman well: Amphibians and reptiles from Tenuta Zuccarello near Marcon, Venice, Italy. Historical Biology, 2018: 1–16. https://doi.org/10.1080/08912963.2018.1470170

Villa, A.; Boschian, G.; Tozzi, C. & Delfino, M. (2018c). Preliminary report on the amphibians and reptiles from the lower palaeolithic palaeoanthropological site of Visogliano (NE Italy). Abstracts of the XVI Annual Meeting of the European Association of Vertebrate Palaeontologists, Caparica, 195.

Vismara, P. (2012). Il genere *Lepus* in Italia: chiavi diagnostiche morfo-odontologiche e contributi paleobiogeografici. Ph.D. Thesis, Università di Milano, 376 pp.

Vismara, P.; Riga, F.; Sala, B. & Trocchi, V. (2014). Paleobiogeografia di *Lepus corsicanus*. Riassunti del IX Congresso Italiano di Teriologia. Hystrix, the Italian Journal of Mammalogy, 25 (Supplement): 35.

Weers, D.J. van (1994). The porcupine *Hystrix refossa* Gervais, 1852 from the Plio-Pleistocene of Europe, with notes on other fossil and extant species of the genus Hystrix. Scripta Geologica, 106: 35–52.