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)

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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, Bufoes 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 y Rana (s.l.) sp.), cuatro de reptiles (Testudo hermanni, Podarcis sp., Zamenis gr. Z. longissimus, Natrix natrix), y nueve de pequeños mamíferos...


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 (Pandolfi & 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.

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 already 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).
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     |       |       |       |       |       |       |       |       |
| *Bufoes 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     | X     |
| *Columba sp.*       | X     |       |       |       |       |       |       |       |       |
| *Aquila sp.*        | X     |       |       |       |       |       |       | X     |       |
| *Athene noctua*     |       |       |       |       |       |       |       |      | X     |
| *Pyrhocorax pyrrhocorax* | X   |       |       |       |       |       |       |       |       |
| *Pyrhocorax graculus* | X   |       |       |       |       |       |       | X     | X     |
| MAMMALIA            |       |       |       |       |       |       |       |       |       |
| *Erinaceus europaeus* | X   |       |       |       |       |       |       | X     | X     |
| *Crocidura suaveolens* | X   |       |       |       |       |       |       | X     | X     |
| *Microtus (Terricola) savii* |       | X   | X     | X     | X     |       |       |       |       |
| *Microtus (Microtus) arvalis* | X   |       |       |       |       |       |       |       |       |
| *Microtus sp.*      | X     | X     | X     | X     | X     |       |       |       |       |
| *Arvicola italicus* | X     |       |       |       |       |       |       | X     | X     |
| *Apodemus gr. A. sylvaticus - A. flavicollis* | X |       |       |       |       |       |       |       |       |
| *Hystrix vinogradovi* | X   | X     | X     | X     | X     | X     | X     | X     |       |
| *Oryctolagus cuniculus* | X   | X     | X     | X     | X     | X     | X     | X     |       |
| *Lepus corsicanus*  | X     |       |       | X     | X     | X     | X     | X     |       |
| *Leporidae indet.*  | X     | X     | X     | X     | X     | X     | X     | X     | X     |
| *Vulpes vulpes*     | X     | X     | X     | X     | X     | X     | X     | X     |       |
| *Canis lupus*       | X     | X     | 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     | X     | X     | X     | X     |       |
| *Felis silvestris*  | X     |       |       |       |       |       |       | X     |       |
| *Lynx lynx*         |       | 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 (Hystric, 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, including semi-arid (Böhme et al., 2007).

![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).](image)

*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 nomenclatural 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. bali-
arcus* (= *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 Pügener & 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. *H. 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, Psammoborus, 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 keel and a not acutezypaphyseal 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. longissimus (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 small single 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,
Small vertebrates from the Late Pleistocene of A vetrana (Apulia, southern Italy) karst filling

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), 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_6 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_1 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.

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 ostramoci* JANOSZY 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_6 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_1 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. daviidi** 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 Furió, 2007). In particular, the Late Pleistocene remains collected in Melpignano (Leccce, Apulia) and assigned to **E. cf. E. praeglacialis** by Fanfani (2000, plate V5) 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 P4 and M1 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 species. 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 meta- crist of M1 (see discussion in Furió 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 roumanicus** 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; Pandolfini 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 M1-M3 (L = 3.82 mm) and a few teeth (not M3) (Pn. 016-017) (bed 5); a skull encrusted (Total L skull = 40.62 mm; L M1-M3 sx = 10.20 mm) (Pn 065), one M1 sx (L = 4.51 mm) (Pn. 018) (bed 8). Several other teeth (not M1) 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 from bed 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 M1, 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 (= Schmelzbanddifferenziungs-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 antcines Al4, Al3, Al2, and on the buccal antcines Ab2 and

**Arvicola italicus** (SAVI, 1832).

(Figs. 4C, 4D1, 4D2)

Specimens: One mandible dx bearing M1-M3 (L = 3.82 mm) and a few teeth (not M1) (Pn. 016-017) (bed 5); a skull encrusted (Total L skull = 40.62 mm; L M1-M3 sx = 10.20 mm) (Pn 065), one M1 sx (L = 4.51 mm) (Pn. 018) (bed 8). Several other teeth (not M1) belong to the genus **Arvicola** and most likely to the same species (Pn. 019) (bed 8).
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 considered 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 (Messer & Carleton, 2005 with references) has been accepted by the scientific community, and the name A. amphibius is currently used for the water vole. Arvicola terrestris is now considered as the Scandinavian subspecies of A. amphibius, A. amphibius terrestris (see Messer & 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 M1, they 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 M1, 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; Pirtney 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 (already 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 M1, dx and three M1, sx (L = 2.55, 2.69, 2.73, 2.76, 2.78, 2.85 mm) (Pn. 020/1-6) (bed 0); one M1, dx (L = 2.62 mm) (Pn. 021) (bed 1); one M1, dx and three M1, sx (L = 2.53, 2.67, 2.70, 2.71 mm) (Pn. 022/1-4) (bed 5); one M1, 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 M1. The morphology of the anterior cap and of the pitymyan rhombus of this tooth corresponds perfectly to the M1 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-Garcia et al., 2014; Bona & Savoldi, 2016; Berto et al., 2017; Gatta et al., 2019). The Savi’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.) nebrodenis* (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 M₁ dx (L = 2.94, 2.96 mm) (Pn. 024/1-2) (bed 8).

The morphology of the M₁ 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 Garcia 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 Garcia 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 (M₁ and M₂) not diagnostic at species level from bed 6. Two molars not diagnostic at species level from bed 8 (Pn. 025).

Several arhizodont molars (M₂, M₃, and one M₄) 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 M₂ dx (L = 1.26 mm) (Pn. 026) (bed 5). The only specimen belonging to murids is a lower right M₁ which has a stretched and compressed 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 M₁ 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 M₁ 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 analyses 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 Zarzapos (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 I1-I2, two I1, one dx (Pn. 29/1) and one sx (Pn. 29/2) (bed 0); fragment of skull bearing two teeth rows, dx complete P2-M3 (L = 13.04 mm), sx with P2-M2 (Pn. 30), two mandibular fragments bearing P1-M2 (Pn. 31/1) (P1: L = 2.51, W = 2.19 mm), and P1-M1 (dx Pn. 31/2) (P1: 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 P3-M2 (P3: L = 2.73, W = 2.70 mm) (Pn. 34), one I1 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 P3 sx (L = 2.63, W = 2.68 mm) (Pn 38) (bed 6); a fragment of a mandibular ramus dx with P3 (L = 2.87, W = 2.58 mm) and two or three more teeth completely covered by incrustations (Pn 39), a P3 sx (L = 2.80, W = 2.47 mm) (Pn 40) (bed 7); one P3 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, I1 (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 P3 (Pn. 31/1-3, 34, 38, 39, 40) have almost identical lingual and vestibular anteroconids and the aspect is sub-quadrangular. 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 epi-condyle. 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 P3 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, P3 dx (L = 3.71, W = 3.78 mm) (Pn. 041) (bed 0), occlusal view; B) Lepus corsicanus, P3 dx (L = 3.43, W = 3.21 mm) (Pn. 044/2) (bed 5), occlusal view; C) Lepus corsicanus, P3 sx (L = 3.64, W = 3.27 mm) (Pn. 053) (bed 8), occlusal view; D) Lepus corsicanus, P3 dx (L = 3.07, W = 3.10 mm) (Pn. 31/2) (bed 3), occlusal view; E) Lepus corsicanus, mandibular ramus dx bearing P3-M2 (L = 17.26 mm) (P3 illustrated in A) (Pn 41) (bed 0), labial view; F) Oryctolagus cuniculus, P3 dx (L = 2.91, W = 2.89 mm) (Pn. 031/2) (bed 3), occlusal view; G) Oryctolagus cuniculus, P3 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 P2-M3 (L = 13.04 mm), sx with P2-M2 (Pn. 030) (bed 3), ventral view.
Orvctolagus burgi is characterized by a $P_2^2$ 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 $P_2$-$M_3$ ($L = 17.26$ mm) ($P_2$: $L = 3.71$, $W = 3.78$ 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 $P_2$-$M_2$ ($P_2$: $L = 3.07$, $W = 3.10$ mm) (Pn 064) (bed 3); two fragments of mandibular rami dx bearing $P_1$-$M_1$ (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 $P_j$ 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), aibia sx lacking the distal part (Pn 52/1), and distal fragment of aibia dx (Pn 52/2) (bed 5); a fragment of mandibular ramus sx bearing $P_2$-$M_3$ ($L = 17.34$ mm) ($P_2$: $L = 3.64$, $W = 3.27$ 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 Orvctolagus 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 Orvctolagus. 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 $P_2$ 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 antero-posterior axis, and $P_2$ 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
Small vertebrates from the Late Pleistocene of Avetrana (Apulia, southern Italy) karst filling

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 P₁ 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*.

*L. 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; Falguéres 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 Italian 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 Italian 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 P₃-M₁ of very small dimensions, fragment of maxillary dx bearing P₃-M₄, several isolated molars (P₆/1-9) (bed 0); two isolated molars (P₅/1-2) (bed 2); three maxillary fragments (two dx, one sx) bearing P₁-M₁, P₃-M₃, P₃-M₅ respectively, some isolated molars (P₅/8-1-7) (bed 3); a proximal fragment of femur of large dimensions, and some metapodials belonging to the same limb, several postcranial fragments (P₅/9-1-6) (bed 5); a fragment of maxillary dx bearing P₂-P₄, fragments of molars (P₆/60-1-3) (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 M₁ 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).

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