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EARLY PLEISTOCENE HERPETOFAUNA FROM CAVA DELL'ERBA AND CAVA PIRRO (APULIA, SOUTHERN ITALY)

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The Early Pleistocene fissure fillings of Cava Dell'Erba and Cava Pirro (Apricena, Apulia, Southern Italy) have yielded abundant fossil vertebrate remains. The study of more than 14 000 amphibian and reptile remains revealed the presence of the following 18 taxa (6 amphibians and 12 Reptiles): *Triturus* cf. *T. alpestris, T. vulgaris* group, *Bufo bufo, Bufo viridis, Hyla arborea* group, *Rana* cf. *R. ridibunda* vel *Rana* kl. *R. esculenta, Testudo hermanni* group, *Emys orbicularis, Mauremys* sp., *Pseudopus* sp., *Podarcis* sp., *Lacerta* sp., *Blanus* sp., *Hierophis viridiflavus, Elaphe longissima, Coronella* cf. *C. austriaca, Natrix natrix, Vipera aspis* group. Some of the materials referred to "Colubrines" indet. could represent taxa different from those listed above. The high taxonomic diversity, good preservation and abundance of the material place this herpetofauna amongst the most informative ever recovered in the European Quaternary. Some of the identified taxa are reported for the first time in Italy. Others are of particular interest as they help to fill present or past gaps in E-W disjunct ranges. The ecological requirements of the amphibians and reptiles suggest the presence of a typical Mediterranean landscape: a relatively dry environment with water bodies of temporary nature (at least those closer to the sites) surrounded by scattered trees or/and bushes.

Key words: amphibians, reptiles, palaeontology, early Pleistocene, late Villafranchian, Italy

INTRODUCTION

The fossiliferous localities known as Cava Dell'Erba and Cava Pirro are situated near Apricena (Foggia province, Apulia, southern Italy) on the north-western slopes of the Gargano promontory. The presence of fossil remains in the area had been signalled at the beginning of the 1970s by Freudenthal (1971). During the following decades, systematic field research led by Florence University in collaboration with Camerino University and the Museo Civico of San Severo, established a wide collection of Neogene and Quaternary vertebrate remains. The Pleistocene fossil assemblage to which the materials here described belong consists of several mammals, birds, reptiles, amphibians and rare fishes coming from the sand-clay fillings of a karst network developed along the contact between a Mesozoic and a Pliocene succession. The fossil remains have been sampled from different karst fissures of two adjacent quarries. As there is evidence that the fissures were filled over a short time period, all the material has been considered as contemporary in geological terms (Abbazzi *et al.*, 1996).

Mammals have been the most extensively studied group from both a taxonomic and chronological point of view: about 40 different taxa of small and large mammals have been described up to now (De Giuli & Torre, 1984; De Giuli, Masini & Torre, 1987; Santini, 1989; Masini & Santini, 1991; Colucci, 1993; Rook, 1994; Fanfani, 1995, 1999; Rook & Torre, 1996; Abbazzi & Masini, 1997; Lippi, 1997). An interesting feature of the mammal fauna is the contemporaneous presence of taxa typical of the Faunal Unit Farneta (Masini, Ficcarelli & Torre, 1994; Gliozzi *et al.*, 1997), as well as new forms. Remarkable is, among others, the presence of the ancient bison *Eobison degiulii* - an ovibovine related to the musk ox group - the horse *Equus altidens*, an advanced form of the fallow deer *Pseudodama*, a deer close to *Megaceroides solilhacus*, the wolf *Canis* aff. *C. arnensis* (advanced form) and the arvicolid *Microtus* cf. *M.* (*Allophaiomys*) *ruffoi*.

The late Villafranchian elements of the mammal fauna suggest a late early Pleistocene age probably preceding the Jaramillo sub-magnetochrone as is also evidenced by the sediments geomagnetic polarity (Masini, Ficcarelli & Torre, 1994). Therefore the fossil assemblage is considered to be one of the last Italian faunas of the late Villafranchian and Cava Pirro has been designated as the type locality of the Pirro Faunal Unit (Gliozzi *et al.*, 1997).

Works devoted to the remaining groups of vertebrates chronologically follow those of the mammals. An analysis of the herpetofauna has been undertaken only recently in a degree thesis (Delfino, 1996), and

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reports of a "large size" *Lacerta* (Delfino, 1995) and of amphisbaenians (Delfino, 1997). The present paper represents a summary and a revision of previous works.

MATERIALS AND METHODS

The materials analysed here are currently stored at the Department of Earth Science, University of Florence, and were excavated from Cava Pirro (PN) between 1983 and 1986, and from Cava Dell'Erba (DE) between 1991 and 1993. During the initial field research, each fissure was sampled without recording any stratigraphic detail, but in the more recent work each level of a single fissure was sampled independently.

These fissure fillings have been described by Abbazzi *et al.* (1996) and referred to the local lithostratigraphic unit number 8. Each sampled karst fissure bears a code (quarry-fissure-level; DE = Cava Dell'Erba, PN = Cava Pirro); the materials considered in this work come from 25 different fissures whose codes are listed in Table 1. At present the remains do not bear collection numbers.

SYSTEMATIC STUDY

AMPHIBIA LINNAEUS, 1758

Amphibians are well represented: 5048 remains (35.3% of all the material) have been referred to six taxa belonging to caudates and anurans.

CAUDATA SCOPOLI, 1777

The presence of caudates is demonstrated by a relatively small number of vertebrae and few other skeletal elements (174 altogether). All the remains, coming exclusively from the Cava Dell'Erba fissures, are from the family Salamandridae.

SALAMANDRIDAE GOLDFUSS, 1820

Triturus vulgaris Linnaeus, 1758
Triturus vulgaris group (Fig. 1).
Referred material: trunk vertebra: 4.
Triturus cf. T. alpestris (Laurenti, 1768) (Fig. 1).
Referred material: trunk vertebra: 7.

Trunk vertebrae are assigned to the genus *Triturus* on the basis of the following characters: opisthocoelous; round condyle well distinct from the centrum; ventral vertical crests absent; rib-bearers well developed and connected to each other with a bony plate; neural arch unflattened and with neural spine (Gonzales & Sanchiz, 1986).

Four trunk vertebrae are characterized by a very small size (total length 1.8 mm); high neural spine flattened at the back and without dermal ossifications; well developed plates between centrum and dorsal rib-bearers; ventral foramina wide; and centrum connections having ventral rib-bearers with a developed arched anterior edge. These features clearly identify the

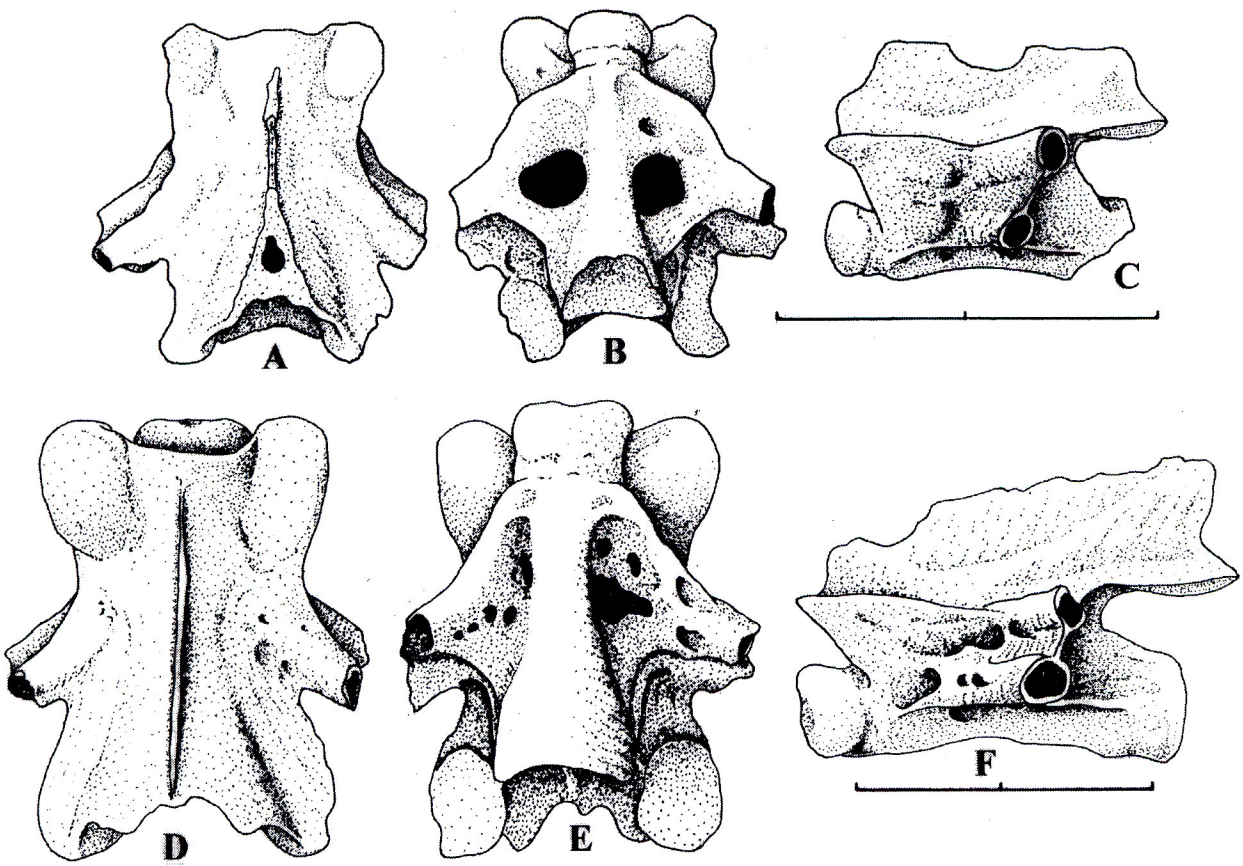

FIG. 1. *Triturus vulgaris* group, A, B, C: trunk vertebra, dorsal, ventral and left lateral views. *Triturus* cf. *T. alpestris*, D, E, F: trunk vertebra, dorsal, ventral and left lateral views. Scale = 2 mm.

Site:	*T. vulgaris* group	*T.* cf. *T. alpestris*	*Triturus* sp.	*B. viridis*	*B. bufo*	*Bufo* sp.	*R. esculenta/ridib.*	*Rana* sp.	*H.* gr. *H. arborea*	Anura indet.	*T.* gr. *T. hermanni*	*E. orbicularis*	*Mauremys* sp.	Emydidae indet.	Testudines indet.	*Podarcis* sp.	*Lacerta* sp.	*Pseudopus* sp.	Lacertilia indet.	*Blanus* sp.	*H. viridiflavus*	*E. longissima*	*C.* cf. *C. austriaca*	Colubrines indet.	*N. natrix*	*V. aspis* group	Serpentes indet.
DE 2D	0	0	X	X	X	X	0	X	X	X	/	/	/	/	/	X	X	0	X	X	X	X	X	X	X	0	X
DE 6.2-2A	0	0	0	X	0	X	X	X	X	X	0	0	0	0	X	X	0	0	X	X	0	X	X	X	X	0	X
DE 6.2-2B	0	0	X	X	0	X	0	X	X	X	0	0	0	0	X	X	0	0	X	X	0	0	X	X	X	X	X
DE 6.2-3	0	0	X	X	X	X	0	X	0	X	0	0	0	0	0	X	0	0	X	0	0	0	X	X	X	0	X
DE 6.2-4	0	0	X	X	X	X	0	X	0	X	X	X	0	0	X	X	X	0	0	X	X	X	0	X	X	0	X
DE 6.2-4+5	0	0	0	0	0	X	0	X	0	X	X	0	0	0	X	X	0	0	X	0	X	X	0	X	0	0	X
DE 6.2B-1	0	0	0	X	0	0	X	X	0	X	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	X
DE 6.2B-3+4	0	0	0	X	0	X	0	X	X	X	X	X	X	0	X	X	X	0	X	X	X	0	0	X	0	0	X
DE 6.2B-5	X	X	X	X	X	X	X	X	X	X	X	X	0	0	X	X	X	0	X	X	X	X	0	X	X	0	X
DE 6.6 r	0	0	0	X	0	X	X	X	0	X	X	0	0	0	X	X	X	0	X	X	0	X	0	X	X	0	X
DE 6.6-1A	0	0	0	X	0	X	X	X	0	X	0	0	0	0	0	X	0	0	X	0	0	0	0	0	0	0	X
DE 6.6-1A cp	0	0	0	X	0	X	0	0	0	X	0	0	0	0	0	X	0	0	X	0	0	0	0	X	X	0	X
DE 6.6-1B	0	0	0	X	0	X	0	X	0	X	0	0	0	0	0	X	0	0	X	0	0	0	X	X	X	0	X
DE 6.6-2	0	X	0	X	0	X	0	X	0	X	0	0	0	0	X	X	X	0	X	0	0	0	X	X	X	0	X
DE 6.6-3	0	0	0	0	0	0	0	X	0	X	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	X
DE 6.6-4	X	X	X	X	0	X	X	X	X	X	0	X	0	0	X	X	X	0	X	X	0	X	0	X	X	0	X
DE 6.6-5	0	0	X	X	0	X	X	X	X	X	0	0	0	X	X	X	X	0	X	X	X	0	0	X	X	0	X
DE 11.1-2	0	0	0	0	0	X	0	0	0	0	/	/	/	/	/	0	0	0	0	0	0	0	0	0	0	0	0
DE 11.1-3	0	0	0	0	0	X	X	X	X	X	/	/	/	/	/	X	0	X	0	X	X	0	0	0	0	0	X
DE 11.1-4A	0	0	X	0	X	X	X	X	X	X	/	/	/	/	/	X	0	0	X	0	0	0	0	X	X	0	X
DE 11.1-6A	0	0	0	X	0	X	X	X	0	X	/	/	/	/	/	X	0	0	X	0	0	0	0	X	0	0	X
DE 11.1-7	0	0	X	0	0	0	0	X	0	X	/	/	/	/	/	0	0	0	0	0	0	0	0	0	0	0	X
DE 11.1-9	0	0	0	0	0	0	0	0	0	0	/	/	/	/	/	0	0	0	0	0	0	0	0	X	0	0	X
DE 11.1-9A	0	0	0	X	0	X	0	X	0	X	/	/	/	/	/	0	0	0	0	0	0	0	0	X	0	0	X
DE 12.1-1A	0	0	X	X	0	X	0	X	0	X	/	/	/	/	/	X	0	0	0	0	0	0	X	0	0	0	X
DE 12.1-2A b	X	0	X	X	X	X	X	X	X	X	/	/	/	/	/	X	0	0	0	0	0	0	X	X	0	0	X
DE 12.1-2A c	0	0	0	X	0	X	0	X	X	X	/	/	/	/	/	X	0	0	X	0	X	0	X	X	X	X	X
DE 12.1-2A t	0	0	X	X	0	X	0	X	X	X	/	/	/	/	/	X	0	0	X	0	0	0	X	X	X	0	X
DE 12.1-3A	0	0	X	X	0	X	0	X	X	X	/	/	/	/	/	X	0	0	X	0	0	0	X	X	X	0	X
DE 12.1-4A	0	0	X	X	0	X	0	X	X	X	/	/	/	/	/	X	X	0	X	0	0	0	X	X	0	0	X
PN 1	0	0	0	X	X	X	X	X	X	X	X	X	0	X	X	X	X	0	X	0	X	0	0	X	X	0	X
PN 2	0	0	0	0	0	X	0	X	0	0	X	X	X	X	X	X	X	0	X	0	0	0	0	0	0	0	X
PN 5	0	0	0	0	0	0	0	0	0	0	X	X	0	0	X	X	0	0	X	0	X	X	0	X	X	0	X
PN 5 b	0	0	0	0	X	0	0	X	0	0	X	0	0	X	X	X	X	0	X	0	0	X	0	0	X	0	0
PN 6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	X	0	0	0	0	0	0	0	0
PN 9	0	0	0	0	X	X	X	X	0	X	X	0	0	X	X	X	X	0	X	0	X	X	X	0	X	0	X
PN 11	0	0	0	0	X	X	0	0	X	0	X	0	X	X	X	X	X	0	X	0	0	X	0	X	0	0	X
PN 11 spb	0	0	0	0	0	X	0	0	0	0	0	0	X	X	0	0	0	0	0	0	0	0	0	X	0	0	X
PN 12	0	0	0	X	0	0	0	0	0	0	X	0	0	0	0	X	X	0	X	0	0	0	0	0	0	0	0
PN 15	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	X	0	0	0	0	0	0	0	0	0	0
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PN 17	0	0	0	0	X	0	0	X	0	0	X	0	0	X	X	X	X	0	X	0	X	0	0	X	X	0	X
PN 18	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	X	0	0	0
PN 22 err.	0	0	0	0	0	0	0	X	0	0	X	X	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X
PN 22 sacca	0	0	0	0	0	0	0	0	0	0	X	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0
PN 22 in posto	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0	0	0	X	0	X
PN 22 b	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0
PN 24	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	0	0
PN 24 b	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0
PN 25	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	X	X	0	0	0	0	0	0	X	0	0	X
PN 26	0	0	0	0	0	0	0	0	0	0	X	X	0	X	X	X	X	0	X	0	0	0	0	0	0	0	X
PN 30	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	X	0	0	0	0	0	0	0	0
PN 32	0	0	0	0	0	0	0	0	0	0	X	X	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
PN 34 err.	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	0	X	0	0	0	0	0	0	0	0
PN 34 a	0	0	0	0	0	0	0	X	0	0	X	0	0	0	X	X	0	0	X	0	0	0	0	0	0	0	X
PN 34 c	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	X	0	X	0	0	0	0	0	0	0	X
PN 34 d	0	0	0	0	0	X	0	0	0	0	0	0	0	0	0	X	X	0	0	0	0	0	0	0	0	0	0
PN 35	0	0	0	0	0	0	0	0	0	0	X	0	0	X	X	X	0	0	0	0	0	0	0	0	0	0	0

TABLE 1. Presence (X) or absence (0) of the taxa identified in the level and fissures analysed in this work. The chelonian remains of some fissures (/) have not been studied.

subgenus *Paleotriton* or "*vulgaris* group" that is represented in southern Italy by *T. vulgaris* and *T. italicus* only. A distinction between these species, considered possible by some authors (Holman, Stuart & Clayden, 1990; Holman & Stuart, 1991), but in some cases difficult by others (Sanchiz & Szyndlar, 1984), has not been attempted and the material is referred to the species group.

Seven vertebrae are slightly larger in size (total length up to 4 mm). They are characterized by a high neural spine that is narrow over the entire length of the vertebra; neural arch high in posterior view; well developed plates between centrum and dorsal rib-bearers. In ventral view, the anterior centrum connections with the ventral rib-bearers are slightly sigmoidal in shape and distinctly less developed than in the material referred to the *Triturus vulgaris* group. The ventral foramina are generally numerous and variable in size. These features fit well with those of *T. alpestris*. In the absence of more representative material, the fossil remains are referred to as *T.* cf. *T. alpestris.*

Triturus sp.

Referred material: maxilla: 2; parasphenoid: 1; humerus: 5; femur: 18; fibula: 1; rib: 1; scapulocoracoid: 3; ilium: 2; cervical vertebra: 8; trunk vertebra: 86; sacral vertebra: 7; caudal vertebra: 17; undetermined vertebra: 12.

Several vertebrae have been attributed only to the genus as they are partially damaged. Although according to Holman & Stuart (1991) it is possible to discriminate between the femora and humeri of *T. cristatus* and those of the group *T. vulgaris*/*T. helveticus*, in this work they have been referred to as *Triturus* sp. along with other skeletal elements of low diagnostic value. There is no reason to suppose the presence of a species (or a species group) different from those described above.

The larger cervical vertebrae, femora and humeri are characterized by strong crests for muscular insertion.

ANURA RAFINESQUE, 1815

Anuran remains are very common in the fissures of the two sites (4874 remains). In total 1633 fossil remains (carpals, metacarpal and metatarsal elements, phalanxes and other fragmentary elements) have been referred only to the order.

Three families are present: Bufonidae, Hylidae and Ranidae.

BUFONIDAE GRAY, 1825

Bufo bufo Linnaeus, 1758 (Fig. 2).

Referred material: sphenethmoid: 1; parasphenoid: 1; humerus: 3; radio-ulna: 3; scapula: 4; tibio-fibula: 1; ilium: 7; "atlas": 2; vert. 2-8: 8; sacrum: 2; urostyle: 2.

Bufo viridis Laurenti, 1768 (Fig. 2).

Referred material: sphenethmoid: 23; exoccipital + prootic: 9; prootic: 3; squamosal: 6; frontoparietal: 17; parasphenoid: 21; humerus: 132; radio-ulna: 170; scapula: 131; femur: 78; tibiofibula: 68; ilium: 241; "atlas": 12; vert. 2-8: 9; sacrum: 108; urostyle: 96.

The osteology of *Bufo* has been discussed in detail by several authors (Sanchiz, 1977; Böhme, 1977; Bailon, 1999; Bailon & Hossini, 1990). The following discussion is limited to the most representative elements.

Sphenethmoid. Following Böhme (1977) the distinction between *B. bufo* and *B. viridis* based on this element is quite simple. It is wider than long in the former and approximately as long as wide in the latter. Only in *B. viridis* is the *sella amplificans* highly developed.

Vertebrae. All vertebrae of the genus *Bufo* are procoelous. *B. bufo* has dorsal vertebrae with condyles more robust and less broad that *B. viridis*. The sacral vertebra of *B. viridis* is characterized by the presence of anteroposteriorly wide sacral apophyses; a W-shaped neurapophysis and a deep notch, laterally opened, at the base of each sacral apophyses. In *B. bufo* the sacral apophyses are less wide and the neurapophysis has the shape of an inverted Y. The notch lateral to the neurapophysis is less developed (Sanchiz, 1977) or absent (Bailon, 1991).

Scapula. That of *B. viridis* is shorter and stockier than that of *B. bufo*; in the former it frequently displays a supraglenoidal *fossa.*

Humerus. The genus is characterized by a shaft that is rectilinear in males and more or less curved in females; the condyle is laterally (radially) shifted. In male *B. viridis*, the *crista medialis* is dorsally curved and long whereas it is approximately flat and restricted to the distal part of the epiphysis in *B. bufo.*

Ilium. Bufo is characterized by the presence of a dorsal prominence (= *tuber superior*) and the absence of an ilial crest (= *crista dorsalis*). In *B. bufo* the dorsal prominence is low and rounded, whereas in *B. viridis* it is slightly higher and frequently provided with a secondary anterior tubercle. In the latter species a deep notch (= *fossa preacetabularis)* is present.

Femur. It usually has a low ridge (deltoid crest) proximally flattened and forming a triangle in *B. bufo*; the ridge is higher, sharper and characteristically bifurcated in *B. viridis* (Sanchiz, 1977; Bailon, 1999).

All the skeletal elements referred to *B. bufo* are particularly large, robust and with well-marked crests.

Bufo sp.

Referred material: premaxilla: 2; maxilla: 3; angulosplenial: 68; sphenethmoid: 7; exoccipital: 1; exoccipital + prootic: 1; squamosal: 14; frontoparietal: 9; humerus: 60; radio-ulna: 71; carpal 2-4: 15; scapula: 91; coracoid: 56; clavicle: 7; femur: 117; tibiofibula: 90; ilium: 9; ischium: 13; "atlas": 16; vert. 2-8: 502; sacrum: 8; undet. vert.: 33; urostyle: 2.

Due to its poor conservation or low diagnostic value, it has not been possible to assign the reported material to the species of *Bufo* found at the site.

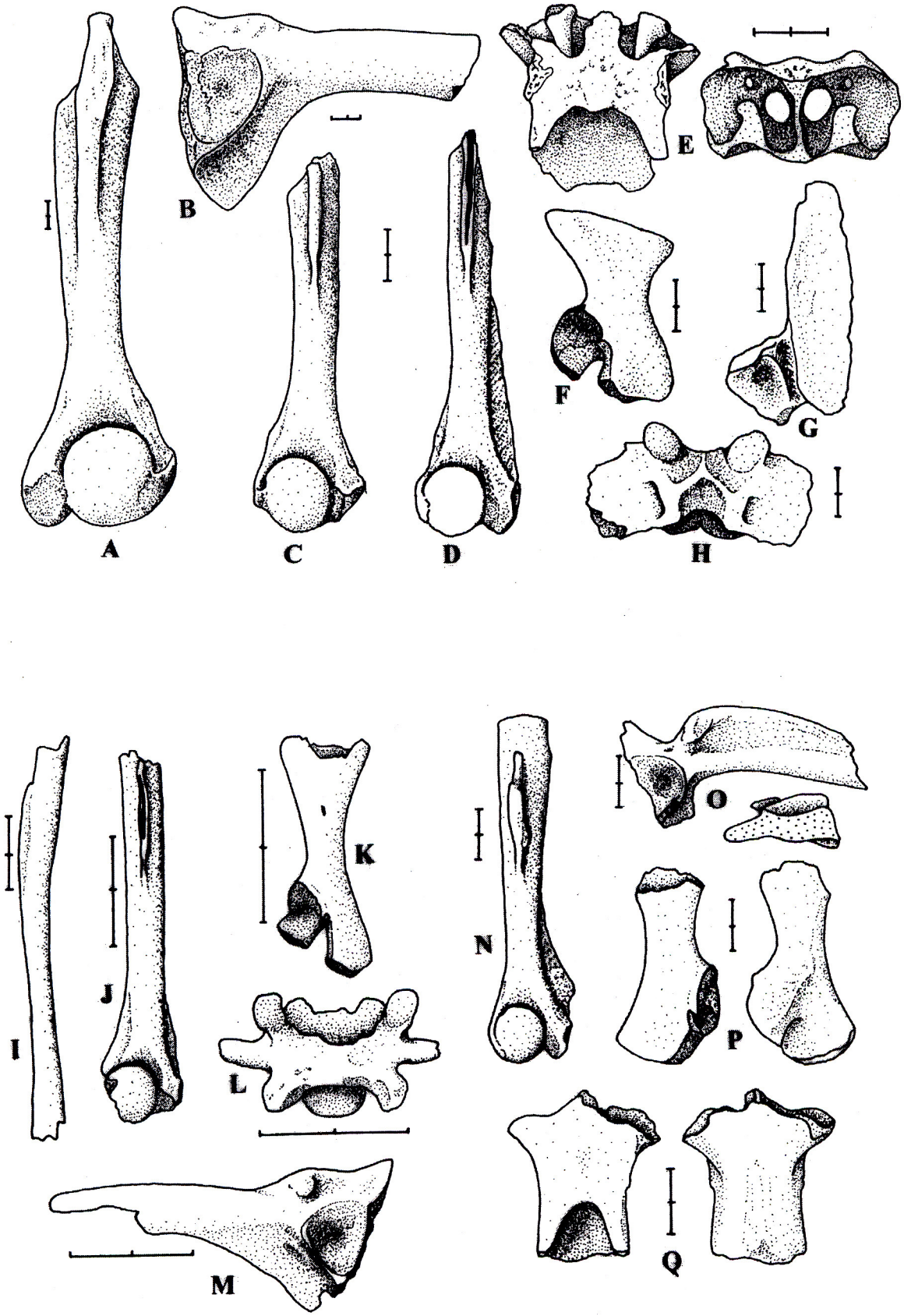

FIG. 2. *Bufo bufo*, A: left female humerus, ventral view; B: right ilium, lateral view. *Bufo viridis*, C: right female humerus, ventral view; D: right male humerus, ventral view; E: sphenethmoid, dorsal and anterior views; F: right scapula, external view; G: left frontoparietal-prootique-exoccipital, dorsal view; H: sacral vertebra, dorsal view. *Hyla arborea* group, I: femur, lateral view; J: right male humerus, ventral view; K: right sacapula, external view; L: trunk vertebra, dorsal view; M: left ilium, lateral view. *Rana* cf. *R. ridibunda* vel *R. esculenta*, N: right male humerus, ventral view, O: right ilium, lateral and posterior views; P: left scapula, external and internal views; Q: sphenethmoid, dorsal and ventral views. Scale = 2 mm.

HYLIDAE GRAY, 1825

Hyla arborea Linnaeus, 1758 (Fig. 2).

Hyla arborea group

Referred material: angulosplenial: 2; squamosal: 14; humerus: 13; radio-ulna: 4; scapula: 8; coracoid: 13; femur: 7; tibiofibula: 4; ilium: 54; "atlas": 1; vert. 2-8: 25; sacrum: 10; urostyle: 3.

Vertebra. Dorsal vertebrae are characterized by a short neural arch, a reduced neural spine, and condyle and cotyle small in relation to the vertebral body; the sacral vertebra displays moderately anteroposteriorly wide apophyses.

Humerus. The diaphysis is straight and the condyle is laterally shifted in a characteristic manner.

Ilium. Hyla may be distinguished from the other European anurans by the round, laterally oriented and one-lobed *tuber superior*, the *pars descendens ilii* ventrally expanded and the absence of an ilial crest (Sanchiz & Mlynarski, 1979).

Femur. Few elements, slender and with a small but evident and sharp proximal crest, have been attributed to *Hyla*.

Sanchiz & Mlynarski (1979), Sanchiz & Sanz (1980) and Sanchiz (1981) considered the specific allocation of fossil ilia belonging to the European *Hyla* as being impossible. More recently Holman (1992) stated that *H. arborea* and *H. meridionalis* can be identified by the morphology of the ilium. Since the taxonomic landscape of the European tree frogs is more complex than that considered by Holman for Britain (in the Mediterranean Basin: *H. arborea*, *H. intermedia*, *H. meridionalis*, *H. sarda*, *H. savignyi* and probably others- Lanza & Vanni, 1987; Dubois, 1995) the fossil material has been simply attributed to *Hyla arborea* group.

RANIDAE GRAY, 1825

Rana cf. *R. ridibunda* Pallas, 1771

vel *R.* kl. *R. esculenta* Linnaeus, 1758 (Fig. 2).

Referred material: sphenethmoid: 1; humerus: 5; ilium: 58.

Ilium. The presence of a high ilial crest, the *corpus ossis ilii* relatively thick and stout (if observed on the *junctura*) and a well-developed *tuber superior* clearly indicate the presence of green frogs. The material has been referred to the group *R. ridibunda* vel *R.* kl. *R. esculenta* because the *tuber superior* is laterally flattened and anterior to the anterior margin of the *acetabulum*. In the other green frog, *R. lessonae*, the *tuber* is laterally prominent, steeper and lies over the anterior margin of the *acetabulum* (Böhme & Günther, 1979).

Sphenethmoid: in green frogs, the lateral processes are more individualized and the posterior chamber is, in ventral view, narrower that in brown frogs

Humerus: the genus *Rana* has straight diaphyses with the condyle located on the main axis at its base. The *crista medialis* is dorsally oriented only in male brown frogs.

Scapula: in dorsal view, the glenoid apophysis is partially hidden by the acromial apophysis. The internal crest is generally more developed in green frogs.

Rana sp.

Referred material: premaxilla: 9; maxilla fragments: 106; angulosplenial: 40; exoccipital: 2; squamosal: 2; frontoparietal: 4; humerus: 51; radio-ulna: 34; scapula: 64; coracoid: 18; metasternum: 2; omosternum: 10; femur: 11; tibiofibula: 39; fibulare: 3; ilium: 122; ischium: 13; "atlas": 9; vert. 2-8: 79; sacrum: 37; undet. vert.: 7; urostyle: 4.

The reported material has been referred only to genus level. All the remains of this genus are relatively small sized suggesting the presence of specimens smaller than the modern adult green frog.

REPTILIA LAURENTI, 1768

Reptilia are represented by turtles, saurians, amphisbaenians and ophidians. Altogether 9264 remains (64.7% of all the material) have been referred to 13 taxa.

CHELONII BRONGNIART, 1800

Overall, 1143 turtle remains have been identified. The determinations have been based on the general bone morphology of the shell elements and on the pattern resulting from the impression of the epidermal shields. The nomenclature of the shell epidermal shields and dermal bones follows Loveridge & Williams (1957).

In the present work, the genus *Mauremys* has been considered as a member of the family Emydidae and not Bataguridae as reported by David (1994). The *Testudo hermanni* group is a working taxon here considered as composed of *T. hermanni* and its supposed ancestor *T. globosa,* that is to say the Pleistocene members of this genus with two supracaudal horny shields (= two 12th marginals).

Both terrestrial (Testudinidae) and aquatic forms (Emydidae) are present.

Several skeletal elements (665), devoid of diagnostic value or too fragmentary to allow an accurate identification, have been attributed at order level.

EMYDIDAE GRAY, 1825

Emys orbicularis Linnaeus, 1758 (Fig. 3).

Referred material: nuchal: 3; neural: 6; pleural: 22; peripheral: 35; epiplastron: 6; entoplastron: 2; hyoplastron: 4; hypoplastron: 7; xiphiplastron: 7.

Mauremys sp. Gray, 1869. (Fig. 3).

Referred material: peripheral: 5; suprapygal: 3; pygal: 1; epiplastron: 1; hyoplastron: 2; xiphiplastron: 4.

TESTUDINIDAE GRAY, 1825

Testudo hermanni Gmelin, 1789

Testudo hermanni group (Fig. 3).

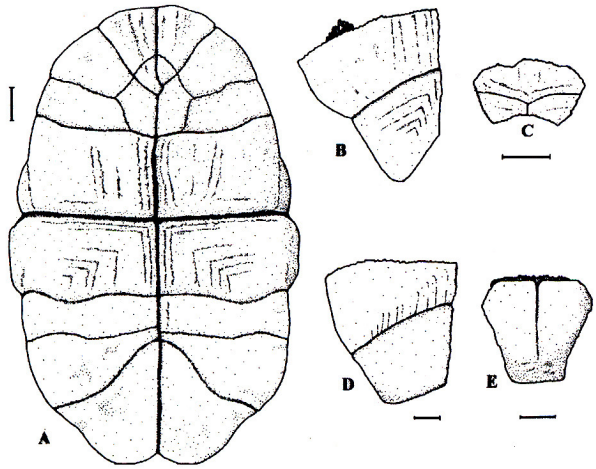

FIG. 3. *Emys orbicularis*, A: plastron, ventral view. *Mauremys* sp., B: right xiphiplastron, ventral view, C: suprapygal, dorsal view. *Testudo hermanni* group, D: right female xiphiplastron, ventral view, E: pygal, dorsal view. Scale = 10 mm.

Referred material: nuchal: 12; neural: 8; pleural: 48; peripheral: 120; suprapygal: 4; pygal: 10; epiplastron: 14; entoplastron: 5; hyoplastron: 29; hypoplastron: 15; xiphiplastron: 27; humerus: 25; radius: 5; ulna: 5; scapulocoracoid/acromion: 6; coracoid: 7; femur: 3; ilium: 4; ischium: 1; cervical vert.: 1.

Nuchal. In the three European genera *Testudo*, *Emys* and *Mauremys*, the nuchal bone is highly characteristic. The genus *Testudo* is characterized by thick nuchals in which the furrow between the first vertebral shield and the first marginal generally crosses the point at which the nuchal, the first peripheral and the first costal bone join.

Holman (1995) pointing out the diagnostic value of the shell bones in *E. orbicularis* and *M. leprosa* (there considered as a subspecies of *M. caspica*) emphasizes that in *E. orbicularis* the nuchal bone is "wider than long, anteriorly truncated, and has a cervical scute impression that is less than one-third the length of the bone", whereas it is "about as wide as long, not anteriorly truncated, and has a cervical scute impression that is more than one-third the length of the bone" in *Mauremys leprosa.* These characters have been taken into account but they seem to be somewhat variable in the modern and fossil material observed.

Pygal and suprapygal. The furrow between the 5th vertebral and the supracaudal horny shield/s approximately coincides with the suture between the suprapygal (= metaneural) and the pygal in *Testudo*, while it crosses the pygal in *Emys* and the suprapygal in *Mauremys*. This character easily allows identification of the pygal and the suprapygal in the three genera.

The pygal is sexually dimorphic in *Testudo,* being typically curved in males. This element is particularly meaningful in discriminating between living *T. hermanni* and other living European species: only the former (with few exceptions, Cheylan, 1981) shows a furrow corresponding to the boundary between the two supracaudal horny shields (the caudal shield is divided in two parts). All the fossil pygals of *Testudo* from Cava Dell'Erba and Cava Pirro display a median furrow.

Hypoplastron. The border between the abdominal and the femoral shields forms an inverted 'U' in *Testudo*, whereas it is more rectilinear in *Emys* and *Mauremys*. The inguinal shield and consequently the furrow produced by its margins, is present only in the latter genus.

Xiphiplastron. The xiphiplastral notch is deeper in *Mauremys* than in *Emys* (Holman, 1995). Moreover the general morphology and the shape of the furrow between the femoral and anal shields are typical. This furrow is vaguely sigmoidal in *Emys,* but more rectilinear in *Mauremys* and in *Testudo*. The *Mauremys* fossil xiphiplastra are characterized by a lobed outer margin with a deep notch where the furrow between the femoral and the anal shields meets the border.

The xiphiplastron is highly characteristic and sexually dimorphic in *Testudo*: it is cranio-caudally compressed in *T. hermanni* (Cheylan, 1981) and particularly in males. The fossil xiphiplastra show the furrow between the femoral and anal shield with the shape typical of *T. hermanni* (see Cheylan, 1981).

All the *Emys* remains (some of them belong to one single specimen that has been partly reconstructed) are assigned to the only living species: *E. orbicularis*. The *Mauremys* fossil material is not allocated to specific level as we are not acquainted with any osteological differences between *M. caspica*, *M. leprosa* and *M. rivulata.*

More complex is the specific allocation of the *Testudo* remains. The presence of a median furrow on the pygal bone (as well as several other "*hermanni*-like" features) restricts the choice to the living species *T. hermanni* and its close fossil relative *T. globosa* Portis, 1890. The latter has been defined by Kotsakis (1980) as member of the genus *Testudo* with a pygal bone showing a median furrow and characterized by a carapax larger in its rear region, a long suprapygal, a short "*saillie gulaire*", xiphiplastra very wide at the back and shell bones thicker than those of *T. hermanni.* In the comparative material all these features - except the thickness - seem to vary considerably. It is noteworthy that the short "*saillie gulaire*" (= *bourrelet epiplastral* not much cranio-caudally developed) is characteristic of *T. hermanni* (and not of *T. graeca*; Cheylan, 1981) whereas a wide posterior carapax and xiphiplastra are typical of males (surprisingly, in the original description by Portis in 1890 of *T. globosa* there is a detailed list of male characteristics without referring them to sexual dimorphism). Moreover, Guyot & Devaux (1997) have recently reported that male *T. hermanni boettgeri* from Greece are characterized by a posterior shell broadening. Unfortunately, it has not been possible to establish the affinity of the analysed fossils to either of the two modern subspecies by the pectoral/femoral ratio as no plastron is complete.

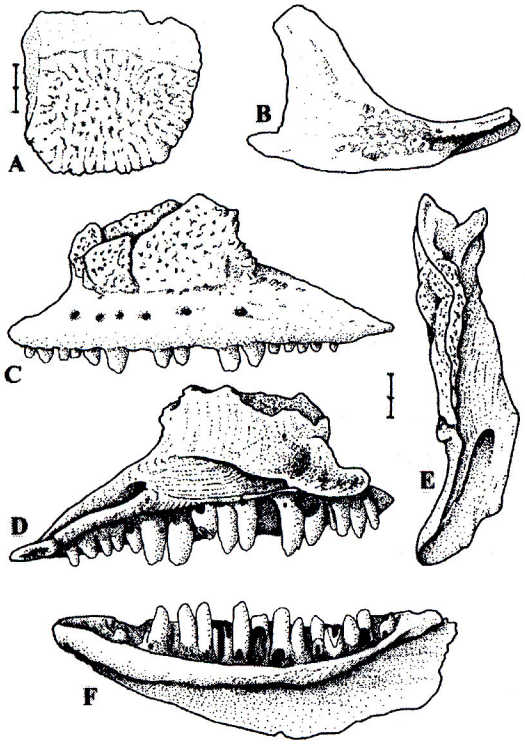

FIG. 4. *Pseudopus* sp., A: osteoderm. *Lacerta* sp., B: right jugal, lateral view; C, D, E: left maxilla, lateral, medial and dorsal views; F: right dentary, medial view. Scale = 2 mm.

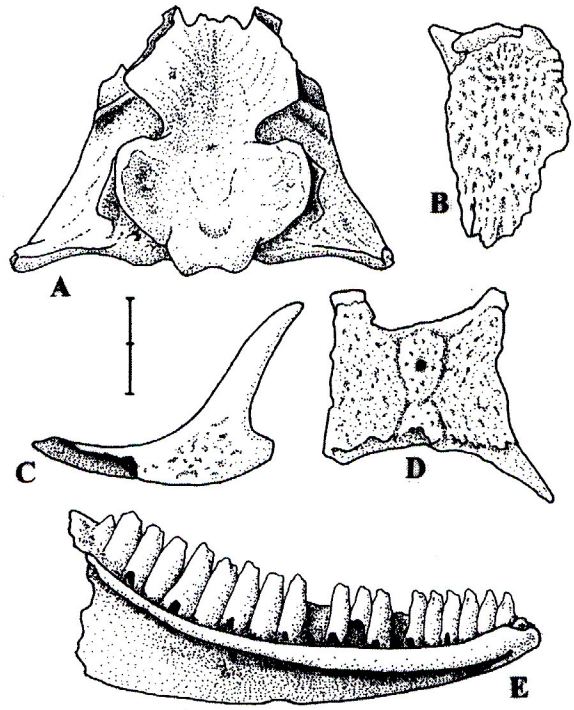

FIG. 5. *Podarcis* sp., A: basicranium, ventral view; B: postfrontal and postorbital, dorsal view; C: left jugal, lateral view; D: parietal, dorsal view; E: left dentary, medial view. Scale = 2 mm.

A simple comparison between the remains from Cava Dell'Erba and Cava Pirro with those of *Testudo globosa* (the holotype and all the material preserved in the Geology and Palaeontology Museum, University of Florence) reveals that the remains here described are at least as thick as those of the fossil species.

It is worth mentioning that the meaning of the shell thickness is still an open problem: has it a taxonomic value or does it simply characterize an ecotype? On this subject, Cheylan (1981) has previously underlined that the greater thickness of the Villafranchian *Testudo hermanni* could be related to the optimal environmental conditions.

Since, according to Das (1997), "a larger size (and, to us, a greater thickness) may not by itself conclusively demonstrate a specific status", all the fossil material is referred to the group constituted by *T. globosa* and *T. hermanni*, here named after the living species as *T. hermanni* group.

EMYDIDAE INDET.

Referred material: neural: 1; pleural: 5; peripheral: 3; humerus: 3; coracoid: 5; femur: 1; cervical vert.: 3.

The listed materials (except the shell bones when well preserved) do not allow a distinction between *Emys* and *Mauremys*.

LACERTILIA OWEN, 1842

The bulk of the fossil material belongs to the order Lacertilia (6556 remains). Highly damaged elements have been assigned only to order level (459 remains). Two families, Anguidae and Lacertidae, have been identified. Surprisingly, the former is represented by one item of remains only.

ANGUIDAE GRAY, 1825

Pseudopus sp. (Fig. 4).

Referred material: latero-dorsal osteoderm: 1.

One single osteoderm is referred to an unknown species belonging to the genus *Pseudopus*.

It is a left latero-dorsal osteoderm, roughly rectangular in shape, slightly wider than long (6.8 mm long and 7.9 mm wide). On the external side, a smooth surface is restricted to the cranial gliding area and to a small stripe on the left border whereas the remaining surface shows a vermicular pattern. There is no medial keel.

The general morphology and size of the osteoderm clearly indicates the presence of a member of *Pseudopus* and not of *Anguis*, the only other Pleistocene European member of the family Anguidae.

In the early Pleistocene Europe was inhabited by two species of *Pseudopus* (*sensu* Klembara, 1979): *P. apodus* and *P. pannonicus* (see references in Bailon, 1991). Following Estes (1983) and Holman (1998) *P. pannonicus* could be a larger form of *P. apodus* differing only for some minor traits.

The material described here, although larger in size than the modern comparative material of *P. apodus*, is assigned to *Pseudopus* sp., as it is too scarce to allow more detailed consideration.

LACERTIDAE BONAPARTE, 1831

The taxonomic allocations of lacertid remains are almost entirely based on the morphology of teeth and teeth bearing bones. The dentition is characterized by the presence of pleurodont teeth - usually bicuspid, but sometimes tricuspid or canine-like (the few anterior maxillary teeth and those on the premaxilla) and approximately cylindrical. The number of teeth and the number of foramina in the lateral wall of dentaries and maxillae have not been taken into account for taxonomic allocation because they are related to the age and size of the animal (Rocek, 1980; Mateo, 1988; Mateo & Lopez-Jurado, 1997). The B or C caudal pattern *sensu* Arnold (1973) has not been evaluated as all the autotomic vertebrae are disarticulated or badly preserved.

Two forms of different size have been identified.

Lacerta sp. (Fig. 4).

Referred material: premaxilla: 16; maxilla: 41; dentary: 23; pterygoid: 9; splenial: 2; jugal: 3; sovraocular osteoderm: 2; frontal: 2; postfrontal: 2; postorbital: 2; quadrate: 5; basicranium: 2; humerus: 7; scapulocoracoid: 2; femur: 6; tibia: 3; pelvis: 8; ilium: 5; dorsal vertebra: 46; sacral vert.: 6; anterior autotomic caudal vert.: 13; posterior aut. caudal vert.: 14; caudal vert.: 21.

Podarcis sp. (Fig. 5).

Referred material: premaxilla: 62; maxilla: 402; dentary: 609; pterygoid: 116; undet. teeth bearing bones: 390; splenial: 64; coronoid: 99; angular: 30; articular: 8; jugal: 124; supraocular osteoderm: 28; prefrontal: 60; frontal: 221; postfrontal: 22; postorbital: 12; parietal: 165; quadrate: 134; basicranium: 17; humerus: 298; ulna: 15; scapulocoracoid: 56; clavicle: 1; femur: 292; tibia: 120; pelvis: 340; ilium: 78; axis: 32; dorsal vertebrae: 1246; sacral vert.: 142; anterior autotomic caudal vert.: 63; posterior aut. caudal vert.: 53; caudal vert.: 557.

A small number of remains (238) is represented by large specimens. Maxillae have a relatively reduced number of teeth: between 16 and 17. At least 6 of the 7 best preserved maxillae display tooth-morphologic differentiation corresponding to that described by Mateo (1988) for the south-eastern population of *L. lepida*. The rear region of the fossils is characterized by some markedly reduced teeth whose number varies between 3 and 5. A careful examination with optical or scanning electron microscope (SEM) shows the presence of 2 or 3 tiny cusps on the crown of the posterior undamaged teeth. In dorsal view, the posterior process is laterally curved and the foramen for the *nerves alveolar superior* is placed in the posterior third of the dental lamina.The free region between the insertion of the ectopterygoid and that of the palatine is prominent and with a straight medial edge. The prefrontal process shows a massive *crusta calcarea* and the furrows between the postnasal, the two loreals, the frontonasal and the prefrontal scales are clearly visible. Six labial foramina are present. The 7th maxilla is characterized by its smaller size, a regular dentition and a posterior process less curved.

The large sized dentaries show the typical lacertid morphology. The tooth morphology is less heterogeneous than in the maxillae: in 3 of the 4 best preserved dentaries, 3 to 5 of the posterior teeth are slightly smaller.

The presence of a "heterodont" dentition recalls the fossil taxon *L. siculimelitensis* from the Middle and Upper Pleistocene of Sicily and Malta. Böhme & Zammit-Maempel (1982) attributed to this species a *Lacerta* dentary (Late Pleistocene, Malta) characterised by 5 little posterior teeth of conical shape. The same authors recognized as conspecific, some remains recovered from the Early Middle Pleistocene of Spinagallo (Sicily; then thought to be Late Pleistocene) and previously considered by Kotsakis (1977) as *Lacerta* sp.

Subsequently, Kotsakis has also reported this species from the Middle Pleistocene site of Poggio Schinaldo (only postcranials, Sicily; Esu *et al.*, 1986) and the Middle/Late Pleistocene site of Contrada Fusco (dentaries, not figured; Sicily; Kotsakis, 1996).

Estes (1983) synthesized the diagnosis of *L. siculimelitensis* in this way: "A large *Lacerta* (total length ca. 700-750 mm) with expanded molariform teeth and last few dentary teeth much reduced in size." Moreover, Holman (1998) quoted *L. siculimelitensis* as the "only *Lacerta* in which tooth expansion occurs" and considered it as an "unquestionably valid extinct Pleistocene species".

On the other hand, Mateo (1988) underlined the wide range of dental morphology variability between the living populations of *L. lepida*. He suggested that the diagnostic characters of *L. siculimelitensis* might fall within the range of variability of the living species and therefore cannot be used to support a specific allocation. Of the same opinion are Barahona & Barbadillo (1997).

The dental morphology of the large sized lacertids from Cava Pirro and Cava Dell'Erba seems to share some characters with the fossil species *L. siculimelitensis* and with some living populations of *L. lepida*. The morphology of the other skeletal remains does not provide any further taxonomic information. The size of some elements fits well with that of adult *L. lepida* whereas others suggest the presence of adult *L. viridis* group or subadult *L. lepida*. From the size and morphology we cannot exclude the presence of two different species. Therefore, all the material is referred only to genus level.

Most of the remains (5856) display a size comparable to that of a "big" *Podarcis* (e.g. *P. sicula* with a snout-vent length up to approximately 90 mm) and have been referred to *Podarcis* sp. on the basis of the jugal bone: the lower border of the lateral face is markedly stepped (Arnold, 1989).

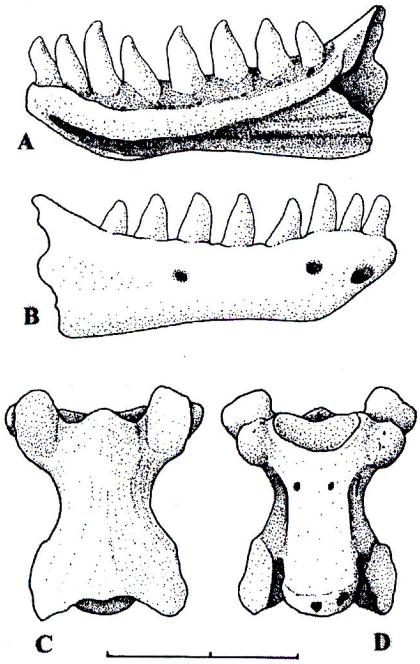

FIG. 6. *Blanus* sp., A, B: right dentary, medial and lateral views; C, D: trunk vertebrae, dorsal and ventral views. Scale = 2 mm.

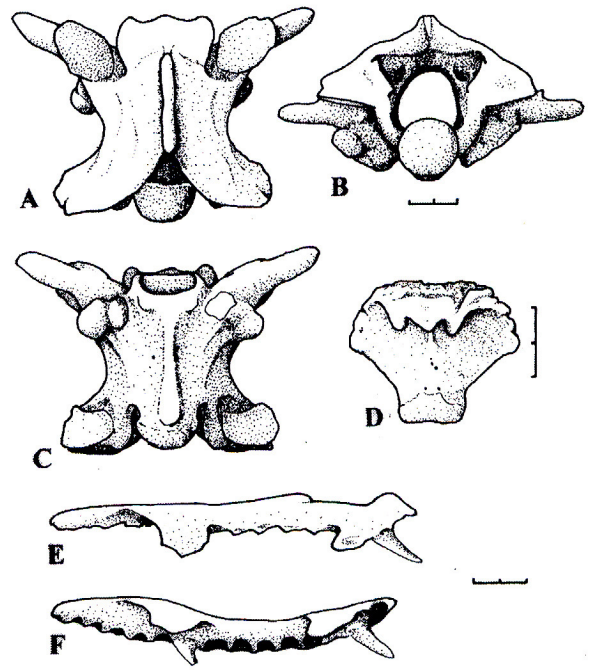

FIG. 7. *Hierophis viridiflavus*, A, B, C: trunk vertebra, dorsal, posterior and ventral views; D: basioccipital, ventral view; E, F: right maxilla, dorso-medial and medio-occlusal views. Scale = 2 mm.

Moreover, the postfrontal and postorbital bones do not show the furrow left by the parietal scale. The first character points to *Podarcis* - *L. agilis* group while the second allows discrimination of the two (Arnold, 1989: characters no. 17 and 39 respectively). Other characters perceivable on the fossil material are: maxilla with stepped posterior process; separate frontals (with few exceptions) with medial region constricted; occipital scale impression on the parietal; parietal with posterior edge straight, and with anterolateral crests and posterolateral crests just touching; osteoderm of the parietal reaches the posterior edge; jugal with evident quadratojugal process; anterior outline of the quadratum rounded; alar process of the prootic developed. Following Barahona & Barbadillo (1997), the abovementioned set of characters are present in *Podarcis*. The fossils differ from the skeletons of recent *P. muralis* and *P. sicula* (the only two species living in peninsular Italy at present) as follows: neurocranium lateral margins more anteroposteriorly divergent; basipterygoid processes closer to basioccipital; more robust dentary; more convex dentary crest and presence of teeth on the pterygoids (not observed in the modern comparative material). The dentaries exhibit up to 22-23 (max. 25) robust teeth, sometimes regularly arranged and rather close to each other. Meckel's groove is generally wider than in any modern *Podarcis* or *Lacerta* observed. The maxillae show 18-19 teeth with the same characteristics. The lateral vertical wall is covered by the *crusta calcarea* but the furrows left by the horny scales are not visible.

The taxonomic allocation has been restricted to genus level as all these features are generally considered not diagnostic.

AMPHISBAENIA GRAY, 1844

The 124 amphisbaenian remains are assigned to one genus only on the basis of the morphology of the dentaries and maxillae. It is possible to reasonably consider all the vertebrae as belonging to the same taxon, although they are not diagnostic at genus level (Estes, 1983).

AMPHISBAENIDAE GRAY, 1865

Blanus sp. (Fig. 6)

Referred material: dentary: 4; maxilla: 1; cervical vert.: 1; dorsal vert.: 106; caudal vert.: 12.

The taxonomic allocation of the remains referred to the order Amphisbaenia has been treated previously by Delfino (1997) and will be briefly summarized here (note that the remains from the fissure DE 16.2 have been considered in that paper also).

The dentaries display eight pleurodont, conical, pointed and non-striated teeth with a small cavity at the base. The fourth tooth is noticeably shorter. Meckel's groove is almost as long as the dentary and particularly wide under the sixth, seventh and eighth teeth. The only maxilla shows five teeth. The first is very small and supplementary (a small tooth is sometimes present in the first position - Bailon, 1991); the second is the largest. Due to the lack of reliable diagnostic features, all the material is attributed to *Blanus* sp. Holman (1998) erroneously quoted these remains as *Blanus* cf. *B. strauchi*.

SERPENTES LINNAEUS, 1758

The 1443 snake remains are mainly represented by vertebrae (1212; 84%). Although there are nearly twice

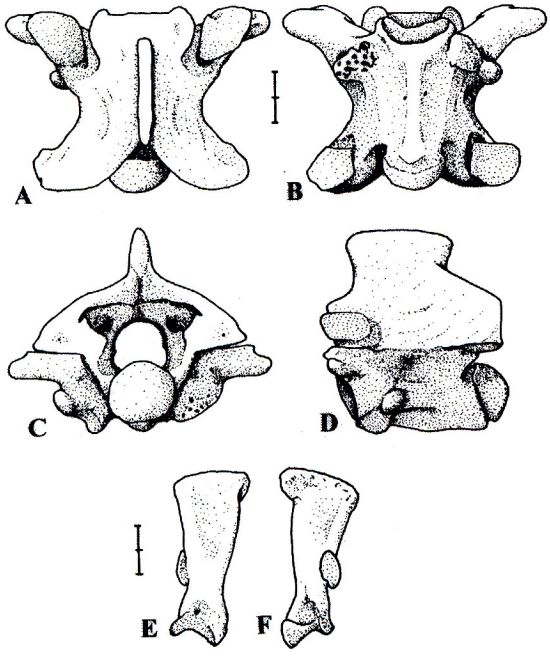

FIG. 8. *Elaphe* cf. *E. longissima*, A, B, C, D: trunk vertebra, dorsal, ventral, posterior and left lateral views; E, F: left quadrate, posterior and anterior views. Scale = 2 mm.

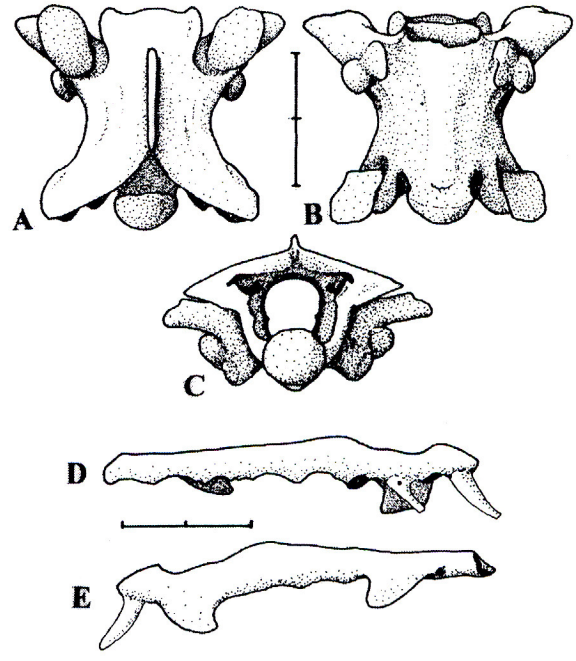

FIG. 9. *Coronella* cf. *C. austriaca*, A, B, C: trunk vertebra, dorsal, ventral and posterior views; D, E: left maxilla, lateral and dorso-medial views. Scale = 2 mm.

as many ribs as there are vertebrae in living snakes, they are underrepresented in the fossil material (181; 12.6%). Moreover, owing to their fragility, the cranial elements constitute only a small part of the sample (50; 3.4%). The taxonomic allocations are mainly based on the detailed descriptions by Szyndlar (1984, 1991*a* and 1991*b*) and Bailon (1991). Members of the families Colubridae and Viperidae have been identified.

COLUBRIDAE OPPEL, 1811

The European fossil members of this family are allocated to the generally accepted working taxa "Colubrines" and "Natricinae" based on the presence of a hypapophysis in the postcervical trunk vertebrae of the latter only (Szyndlar 1984). Although imprecise and sometimes misleading (Szyndlar, 1991*b*) this artificial subdivision has been used in this work.

Hierophis viridiflavus Lacépede, 1789 (formerly *Coluber viridiflavus*) (Fig. 7).

Referred material: maxilla: 1; quadrate: 1; basioccipital: 1; compound bone: 3; dorsal vertebra: 47.

Elaphe cf. *E. longissima* Laurenti, 1768 (Fig. 8).

Referred material: quadrate: 1; dorsal vertebra: 28.

Coronella cf. *C. austriaca* Laurenti, 1768 (Fig. 9)

Referred material: maxilla: 1; supraoccipital: 1; dorsal vertebra: 96.

Natrix natrix Linnaeus, 1758 (Fig. 10)

Referred material: maxilla: 1; parietal: 1; supraoccipital: 1; compound bone: 3; dorsal vertebra: 88.

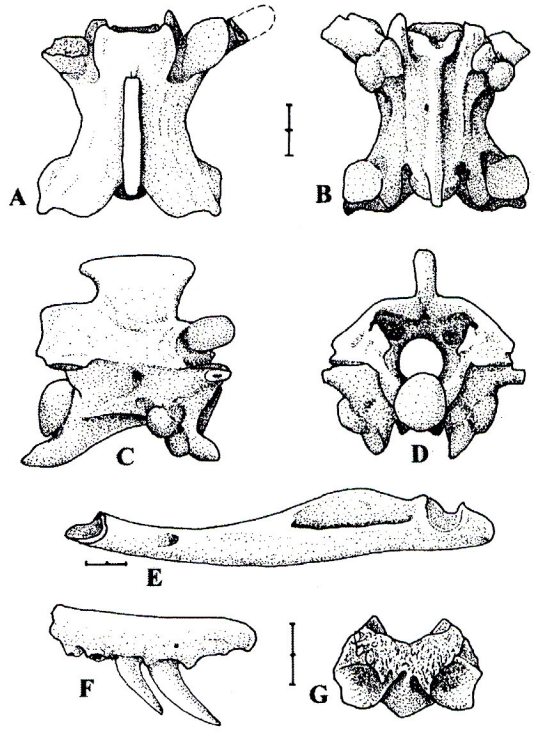

FIG. 10. *Natrix natrix*, A, B, C, D: trunk vertebra, dorsal, ventral, right lateral and posterior views; E: compound bone, lateral view; F: posterior fragment of left maxilla, lateral view; G: supraoccipital, dorsal view. Scale = 2 mm.

A distinction between the members of the genus formerly known as *Coluber* (now split into *Coluber*, *Hierophis* and *Hemorrhois*) and *Elaphe* is generally a difficult task if based on the vertebral morphology. Nevertheless, some fossil vertebrae have been allocated to *Hierophis viridiflavus* on the basis of a flat haemal keel widened at its rear end, and pointed prezygapophyseal processes only a little shorter than the prezygapophyseal facets.

Elaphe longissima vertebrae are characterized by a high and rounded haemal keel that is spatulate at the caudal end. The prezygapophyseal processes are relatively short and show a rounded tip (but slender and pointed in the smaller specimens of the comparison collection). As is usual in large specimens, the zygosphene is generally straight anteriorly (Szyndlar, 1991*a*).

Some small vertebrae have been referred to *Coronella* cf. *C. austriaca* because of the depressed neural arch (when observed in posterior view) and the short prezygapophyseal processes with a strongly constructed base. The haemal keel is generally broad and weakly demarcated; the parapophysis/diapophysis proportions are variable. The taxonomic term "cf." has been introduced in reference to the doubts on the reliability of the diagnostic traits expressed by Szyndlar (1991*a*).

Several hypapophysis-bearing trunk vertebrae belong to *Natrix natrix*. They show a neural arch vaulted when viewed from the back; a relatively high, markedly overhanging cranially and caudally neural spine; both hypapophyses and parapophyseal processes generally have obtuse tips though showing a degree of variability that could be related to the full size of the animal. The presence of these taxa is confirmed and strengthened by a few cranial elements.

Maxilla. One maxilla displays the typical morphology of *H. viridiflavus*: dorsal constriction, allowing the attachment of the maxillary ramus of the ectopterygoid, deep and well delimited anteriorly and posteriorly; prefrontal process blade-like and wider than the ectopterygoid process; tooth row (15 tooth positions) with a short posterior diastema corresponding to the ectopterygoid process.

The dorsal constriction is also present in *Coronella* but the two processes are similarly developed and there is no posterior diastema. *Natrix* does not display dorsal constriction and diastema; moreover the last few teeth are relatively more developed than those of the other species.

Supraoccipital. In *Coronella*, the supraoccipital and posterior areas display a similar degree of development whereas in *Natrix* the posterior area is reduced and the insertion area for the parietal is particularly broad.

Basioccipital. Only one basioccipital has been allocated to *H. viridiflavus* on the basis of its developed and three-lobed basioccipital crest.

Quadrate. H. viridiflavus has a triangular quadrate with a long dorsal crest overhanging anteriorly. A single quadrate is tentatively referred to *E. longissima* because it displays a weakly developed quadrate crest, distinct stapedial process and dorsal crest (perpendicular to the main axis of the bone) anteriorly overhanging. The remains described and figured by Szyndlar (1984, fig. 34-11 and 36-10) and the specimens of the comparison collection also show a dorsal crest overhanging at the back.

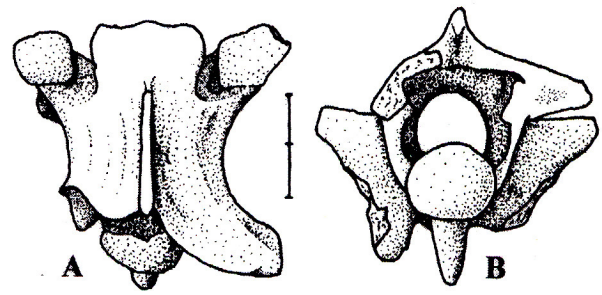

FIG. 11. *Vipera aspis* group. A, B: trunk vertebra, dorsal and posterior views. Scale = 2 mm.

Compound bone (supra-angular + prearticular + articular). H. viridiflavus is characterized mainly by the presence of a supra-angular crest (typical of "*Coluber*" and absent in *Elaphe*; Szyndlar 1991*a*). Other compound bones confirm the presence of *N. natrix* in having a medial flange slightly higher than the lateral flange, a supra-angular foramen typically far from the mandibular fossa and a massive and downwardly curved retroarticular process.

"COLUBRINES" INDET.

Referred material: dorsal vertebra: 318.

Several dorsal vertebrae without hypapophysis have been allocated to this working taxon without more precision as they belong to very young snakes or display features not reliably assigned to the identified taxa. It has not been possible to refer this material to other European snakes but it could well represent taxa different from those described above. In particular, some of them share some characters with *E. quatuorlineata* and *E. situla*. Their small number, the mixed set of characters and the absence of cranial elements do not allow a formal allocation of this material.

VIPERIDAE LAURENTI, 1768

Vipera aspis Linnaeus, 1758

Vipera aspis group (Fig. 11)

Referred material: dorsal vertebra: 2.

Only two dorsal vertebrae can be assigned to this taxon. Their morphology and size are slightly different, but common characters can be summarized as follows: vertebral body convex when observed in cross section; neural arch distinctly depressed with straight posterior border when observed in posterior view; short and pointed prezygapophyseal processes; oval-shaped and dorsally tilted prezygapophyseal facets; parapophyseal processes ventrally oriented; hypapophysis well developed; condyle and cotyle relatively large.

These features clearly identify the genus *Vipera* and the "European Vipers" in particular. The general shape of the vertebral body and hypapophysis indicate the presence of the *V. aspis* group (i.e. *V. aspis*, *V. ammodytes* and *V. latastei*; Szyndlar, 1991*b*). At least one other vertebra (from DE 12.1-2AC) resembles *V. ammodytes* in having a hypapophysis more robust, straight and ventrally directed. A specific allocation based on such poor material is not attempted.

SERPENTES INDET.

Referred material: Maxilla: 3; palatine: 1; pterygoid: 1; prefrontal: 1; frontal: 1; basioccipital: 1; supraoccipital: 1; dentary: 6; compound bone: 6; quadrate: 2; tooth bearing bone: 12; atlas: 2; dorsal vert.: 369; cloacal vert.: 6; caudal vert.: 174; fragmentary vert: 82; rib: 181.

All the remains without characters clearly referable to the above-identified taxa or with juvenile characters (e.g. lightly built skeletal elements, vertebrae with wide neural canal) have been referred to order level only.

DISCUSSION

On the whole, six taxa of amphibians and twelve of reptiles have been identified: their presence in each sampled level and fissure is summarized in Table 1.

Holman (1998) has recently suggested that Pleistocene European herpetofaunas should be considered rich when they contain 10 species, Thus, the high taxonomic diversity, good preservation and abundance of the remains described here place the herpetofauna amongst the most informative ever recovered in the European Quaternary.

The Cava Dell'Erba and Cava Pirro fossil assemblage provides a good opportunity to improve our understanding of the Italian herpetofauna living in the late early Pleistocene. Remains of *Triturus* cf. *T. alpestris*, *Blanus* sp., *Elaphe* cf. *E. longissima*, *Coronella* cf. *C. austriaca*, *Natrix natrix* and *Vipera aspis* group have been recovered for the first time in Italy.

The fauna consists of taxa which are considered to be Mediterranean (*Mauremys, Testudo, Pseudopus, Blanus*), as well as taxa that have a broad latitudinal range today (*Bufo bufo*, *Natrix natrix*, *Coronella austriaca*).

The main peculiarity of the assemblage is the coexistence of taxa still living in the area with a few others that are now restricted to either Iberia, or the Balkans and/or Asia Minor. The European distribution of *Pseudopus* is limited to the Balkans at present, but fossil evidence testifies to its presence in France (Bailon, 1991) and at least north-eastern Italy during the Middle Pleistocene (see references in Bon, Piccoli & Sala, 1991). *Mauremys* and *Blanus* display a disjunct North Mediterranean distribution at present, since they do not occur in the Italian peninsula but are widespread in Iberia and also in the Balkans and/or Asia Minor. Although data from the Balkans are still lacking, the discovery of *Blanus* in Cava Dell'Erba suggests a possible east-west continuous distribution in the past along the northern Mediterranean coasts; the present disjunct range seems to be the result of the post early Pleistocene climatic changes. It is noteworthy that this genus, along with an endemic and peculiar fauna, was formerly present in the Gargano area during the late Miocene/early Pliocene (Cava Rodisano; Delfino, 1997) but the Pleistocene colonization is the result of a new immigration following the late Pliocene submersion of the area. At present *Mauremys* is widespread in all Northern Mediterranean peninsulas except the Italian, but its remains have previously been recovered from some Pleistocene sites in peninsular Italy (Kotsakis, 1980, 1981), and - surprisingly - from the late Pleistocene of Sardinia (Caloi, Kotsakis, Palombo & Petronio, 1981).

The presence of a newt closely related to *Triturus alpestris* fills the gap between the northern main range and the southern relict populations that are still present in southern Italy (Latium & Calabria; Societas Herpetologica Italica, 1996).

All the identified amphibians need water to lay eggs and for larval development, but only the green frogs spend almost all the year in water. Since only five fish vertebrae have been found amongst several tens of thousands of vertebrate remains, it is possible to suppose that there were physical barriers limiting the access of fish to the karst network (otherwise we can assume that fishes were not predated by the birds of prey that might have contributed to the accumulation of the vertebrate fossil assemblage). Moreover, fish can have negative influences on amphibians that leads to the decline and even extinction of the less tolerant amphibian species (e.g. *Triturus* and *Hyla*) due to competition and direct predation (for *Triturus* see Aronsson & Stenson, 1995). It could be that the water bodies (standing or gently flowing) close to the openings of the karst fissures were temporary and consequently unsuitable for fishes. This does not exclude the presence of water turtles as they are able to travel long distances from the permanent water in which they generally live.

The herpetofauna on the whole suggests the presence of a relatively dry environment with water bodies of a temporary nature (at least those closer to the sites) surrounded by scattered trees and bushes and/or very open woodlands. The substrate was probably partially rocky with areas of loose soil allowing amphisbaenians to burrow. This type of landscape corresponds to a typical karst area with scattered vegetation and seasonal shallow pools.

Assuming that their ecological requirements have not changed over time, thermophilous taxa as *Testudo*, *Mauremys*, *Pseudopus* and *Blanus* suggest a July average temperature of at least 23°C (for *Testudo hermanni* see Cheylan, 1981; Saint Girons, 1982). The present absence of *Mauremys*, *Pseudopus* and *Blanus* from the peninsula is probably explained by the lack of suitable

southern refugia there during the post early Pleistocene climatic fluctuations more than by the unsuitability of present-day conditions. Apparently, either the southernmost edge of Iberia and the Balkans were more hospitable than that of Italy during the Pleistocene, or perhaps the peninsulas were recolonized by populations coming from nearby regions (perhaps Turkey for the Balkans). In spite of the fact that a few taxa with wide Pleistocene ranges still survive in some of the southern peninsulas, Europe shows a living herpetofauna (at least at genus level) that is highly impoverished compared to those living in the past. Holman (1998) suggested that this poverty is probably the effect of the presence of some insuperable barriers, such as the Mediterranean Sea to the south and mountain ranges and seas to the east, preventing the recolonization of the area by the taxa that withdrew during the climatic changes since the end of the Miocene. In contrast, the absence of such barriers allowed North American herpetofauna to cyclically recolonize the northern regions and for this reason, it is now richer than the European fauna at the same latitude.

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