THE MIDDLE PLEISTOCENE HERPETOFAUNA OF VALDEMINO CAVE (LIGURIA, NORTH-WESTERN ITALY)

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The herpetofauna from the Middle Pleistocene cave deposit of Valdemino (Borgio Verezzi, Liguria, north-western Italy) is represented by the following taxa: Triturus sp., Speleomantes sp., Pelodytes punctatus, Bufo bufo, Hyla gr. H. arborea, Rana dalmatina, Testudo hermanni, Tarentola cf. T. mauritanica, Anguis fragilis, Lacerta gr. L. viridis, Lacertidae indet., Coronella cf. C. austriaca, Elaphe sp., Hierophis viridiflavus, Malpolon monspessulanus, Colubrines indet., Natrix natrix and Vipera aspis. The most striking characteristic of the Valdemino assemblage is its modernity: all the identified taxa are members of the modern herpetofauna of western Liguria, including Pelodytes and Malpolon (identified for the first time in the Italian fossil record), that nowadays differentiate the western Ligurian herpetofauna from that of all the neighbouring Italian regions. The modernity of the herpetofauna sharply contrasts with the associated mammal fauna that still hosts, among others, Barbary ape, elephant, rhinoceros, leopard and sabre-toothed tiger. The assemblage testifies that the Ligurian herpetofauna was already established in the Middle Pleistocene and that it is not the result of post Würmian dispersal, although cyclical immigrations (from Iberian or French refugia) during warm stages, followed by extinctions during the cold ones, cannot be ruled out.

Key words: amphibians, Malpolon, Pelodytes, reptiles, Speleomantes

INTRODUCTION

The Quaternary history of the Ligurian herpetofauna is almost unknown: the only attempts to depict its evolutionary history have been made by Arillo et al. (1974) and Sindaco (1998) who expressed some considerations based almost exclusively on the modern distribution of taxa. So far, the fossil record of the Ligurian herpetofauna has been of little help, in being rather scarce and limited to a few remains found in the renowned prehistoric localities of "Arene Candide" (Morelli, 1891a; Sorrentino, 1995, 1999) and "Balzi Rossi" (Brocchi, 1879; Brocchi & Rivière, 1886; Boule, 1906, 1919), or in caves such as those of Pietra Ligure (Morelli, 1891b; Issel, 1892; Delfino, 2002), Borgio Verezzi (Issel, 1892) and Bergeggi (Morelli, 1891a). Nearly all the remains have been referred to the genus Bufo or to chelonians belonging to the genera Emys and Testudo, but since they have not been usually described or illustrated, a revision is necessary. The same can be said for reports of "Zamenis viridiflavus" and Lacerta viridis (Boule, 1906), and particularly Timon lepidus and Varanus (Morelli, 1891a, b); the Varanus dentary is unfortunately no longer available and even though it has been described by Morelli, it is not possible to refer it with confidence to any saurian (Delfino, 2002).

The only Ligurian site excavated with modern and stratigraphic criteria is the Valdemino cave, a fossiliferous locality in Borgio Verezzi (Savona Province), whose faunal list published by Tozzi (1969) comprises also a small herpetofauna represented by

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Bufo bufo, Testudo hermanni, Lacerta sp. and "Ophidia" indeterminate.

The present paper deals with the new and abundant amphibian and reptile remains of the Valdemino Cave that have been partly studied by Delfino (2002).

MATERIALS AND METHODS

The Valdemino Cave is located in the Borgio village (Borgio Verezzi Commune), its entrance is 25 m above the sea level and its position can be summarized as follows: I.G.M. sheet of Albenga, tablet of Loano, F° 92 II NW, Lat. 44,1633°N, Long. 12,4523°E (Tozzi, 1969; Fornasiero, 1989).

The fossil herpetofauna here described comes from three different stratigraphic units here called the Ancient, the Middle and the Recent Units. The Ancient fossil assemblage (units from 20 to 24) have been referred to the Middle Pleistocene and more in particular to the "Isernia Faunal Unit" (700,000 years before present approximately) that corresponds to the Galerian Mammal Age (for large mammal students) and to the beginning of the Toringian (for small mammal students; see Sala, 1992, and Gliozzi et al., 1997). The Recent assemblage (units 26 and 27) is relatively younger: it precedes the last glacial phase (Würmian) and therefore an early Late Pleistocene age cannot be ruled out; a precise chronological allocation is still not available and, according to Nocchi & Sala (1997), it is here considered as post-Galerian. The Middle Unit (25) is nearly sterile and its age could be similar to one of the others, or inter-

The remains here described have been collected during the 1989 fieldwork (Fornasiero, 1989) and are stored in the palaeontological collections of the "Museo

Civico" of Finale Ligure with the collection numbers VAL MF 1-1549.

No distinction has been made in the section "Referred material" between perfectly preserved or fragmentary remains. The number between square brackets, that follows the section "Referred material", represents the total number of remains assigned to a given taxon.

The chelonian material is represented by few skeletal fragments and not by shell remains although abundant bony plates are stored in the same collection.

The remains are relatively well preserved and are totally disarticulated but not always completely free of the matrix, that sometimes covers the bones with a thin crust.

SYSTEMATIC STUDY

AMPHIBIA LINNAEUS, 1758

Nearly one sixth (267 remains) of the herpetofauna remains is represented by amphibians. Anurans are much more common than caudates. Altogether, six taxa (two caudates and four anurans) have been identified.

CAUDATA SCOPOLI, 1777

Caudates are very rare: only six remains belong to this order. Family Salamandridae and Plethodontidae are represented.

SALAMANDRIDAE GOLDFUSS, 1820

Triturus Rafinesque, 1815 Triturus sp. (Fig. 1)

Referred material. Ancient unit: trunk vertebra: 1. [total 1]

Vertebra. A single fragmentary vertebra (VAL MF 1) shows the following characteristics: opisthocoelous body, hint of a postcondilar constriction, prezygapophyseal facets oval-shaped and antero-laterally oriented, double rib-bearers caudally directed and linked by a bony plate, deeply concave anterior margin of the neural arch, neural spine present but (at least anteriorly) very low, subcentral foramina present although different in size and development (the left one being much wider), ventral connections between lower rib-bearer and the vertebral body not much developed on both sides. The vertebra lacks right rib-bearers, the tip of the left prezygapophyses and the posterior area of the neural arch (postzygapophyses included). The cotyle rim is partially eroded. The total centrum length can be estimated in 3.3 mm.

The morphology and the size of the vertebra match well with a caudate of the genus *Triturus* (among others: Haller-Probst & Schleich, 1994) and of *T. carnifex* (Laurenti, 1768) in particular (which lives few tens of kilometres north of the site; Raineri in Doria & Salvidio, 1994) because of the concavity of the anterior margin of the neural spine; the material is however too scarce and fragmented to allow a reliable identification at specific rank.

PLETHODONTIDAE GRAY, 1850

Speleomantes Dubois, 1984 Speleomantes sp. (Fig. 1)

Referred material. Ancient unit: trunk vertebra: 4. [total 4]

Vertebra. Four vertebrae found in the same stratigraphic unit (V90 27 B/5) share the presence of a biconvex-amphicoelous centrum and only one pair of rib-bearers on each side (only one vertebra seems to show traces of a second pair of rib-bearers). In dorsal view: neural arch with a distinct interzygapophyseal constriction; anterior margin widely concave and posterior one with median concavity delimited by two pointed convexities (shorter than the posterior margins of the postzygapophyses); rib-bearers slightly bent and posteriorly directed; prezygapophyseal facets ovalshaped and antero-laterally directed. In ventral view: vertebral body hour-glass-shaped being laterally delimited by a deep furrow medially constricted; rib-bearers posteriorly connected to the vertebral body by a small lamina; prezygapophyseal facets with the same shape of the prezygapophyseal ones. In lateral view: vertebral body with a marked ventral concavity (the vertebral body is hour-glass-shaped); distinct roundish foramen located posteriorly to the rib-bearers; neural spine hardly visible although a little more pronounced in the anterior

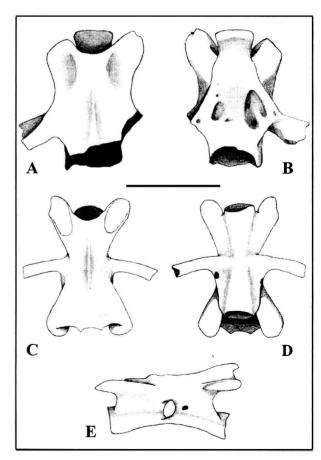


FIG. 1 *Triturus* sp., A, B: trunk vertebra (VAL MF 1), dorsal and ventral views. *Speleomantes* sp., C, D, E: trunk vertebra (VAL MF 2), dorsal, ventral and left lateral view. Scale = 2 mm

section. In cranial view: cotyle roundish; neural canal relatively wide; prezygapophyses nearly horizontal. In caudal view: cotyle and neural canal opening similar to the anterior ones; neural arch moderately vaulted.

The total centrum length of the best-preserved vertebra (VAL MF 2) is approximately 2.3 mm.

By the presence of amphicoelous vertebral bodies, lateral *foramina* for the intravertebral exit of spinal nerves and rib-bearers not connected to the body by wide body plates, it is possible to ascribe these vertebrae to the genus *Speleomantes*, the only European member of the family Plethodontidae (Deiana & Serra, 1978; Estes, 1981).

The taxonomy of this genus has been thoroughly discussed by Lanza et al. (1995) who considered seven species valid, widespread in south-western France, mainland Italy and Sardinia, that are "more differentiated at a genetic rather than morphological level" and whose "identification can be carried out also on the basis of the geographical provenience".

Unfortunately, none of the detailed osteological characters described by these authors can be applied to isolated bones or fossils. Moreover, the allocation of fossil material at specific rank based only on geographical provenience, usually inadvisable, is particularly tenuous in the case of several species with close and restricted modern ranges. The material is therefore referred at genus rank even if the only species living at present in the area is *S. strinatii* Aellen, 1958 (Salvidio in Doria & Salvidio, 1994; Lanza *et al.*, 1995).

CAUDATA INDET.

Referred material. Ancient unit: femur: 1. [total 1]

A single caudate femur does not show features that allow it to be referred to the taxa identified above. It is therefore referred to Caudata indeterminate; since it could reasonably belong to these taxa, Caudata indet. will be not reported in the faunal list.

ANURA RAFINESQUE, 1815

The majority of the amphibian fossils are anurans (261 remains; 98% of the amphibians) referable to the families Pelodytidae, Bufonidae, Hylidae and Ranidae. A relatively high number of meaningless fragments (123) has been allocated simply at order level.

PELODYTIDAE BONAPARTE, 1850

Pelodytes Fitzinger in Bonaparte, 1838 Pelodytes punctatus (Daudin, 1802) (Fig. 2)

Referred material. Ancient unit: ilium: 2. [total 2] Ilium. Two small ilia (the total length of the best preserved, almost complete, fragment is nearly 11 mm -VAL MF 3; the other is more fragmentary but should have belonged to a larger specimen -VAL MF 4) are characterized by the absence of ilial crest, preacetabular and supracetabular fossae, the presence of well developed dorsal and ventral acetabular expansion and of a

distinct groove that separates the dorsal acetabular expansion from the ilial shaft.

All these characteristics are shared by the genera *Pelobates* and *Pelodytes*, but the weak development of the interiliac articulation (the postero-medial surface is rather smooth and not striated) and the presence of a small tubercle perceptible on the dorsal margin of the dorsal acetabular expansion, refers them to the genus *Pelodytes* (Böhme, 1977; Bailon, 1991, 1999).

Moreover, the lateral surface of the dorsal acetabular expansion laterally protrudes in caudal view as in *Pelodytes* (it does not protrude in the comparison material of *Pelobates*; compare Tab. 19 F with 19 G, H in Bailon, 1999: 36, and also Tab. 10 F, M with 10 E, L in Böhme, 1977: 296) and even though this character is not explicitly reported in literature, it could have some taxonomic weight.

The fossil material is referred to *Pelodytes* punctatus, the only modern and Quaternary European representative of the genus (not considering the Trans-Caucasian species; Kuzmin in Gasc et al., 1997; Guyétant in Gasc et al., 1997).

Nowadays *Pelodytes punctatus* has the eastern edge of its range in the Apennines between Liguria and Piedmont; due to its punctuated distribution (perhaps underestimated because of its secretive habits) and high human pressure, it is one of the Italian amphibians most endangered with extinction. Some small populations,

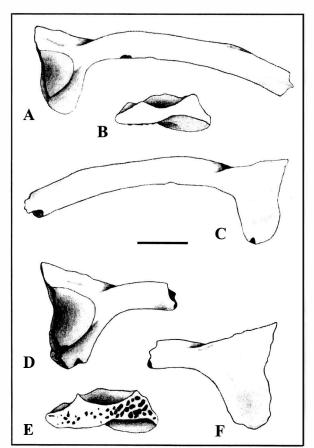


FIG. 2. Pelodytes punctatus, A, B, C: right ilium (VAL MF 3), lateral, caudal and medial views; D, E, F: right ilium (VAL MF 4), lateral, caudal and medial view. Scale = 2 mm.

living only few kilometers far from the site, are known (Sindaco in Doria & Salvidio, 1994).

BUFONIDAE GRAY, 1825

Bufo Laurenti, 1768 Bufo bufo Linnaeus, 1758 (Fig. 3)

Referred material. Recent unit: sphenethmoid: 1; parasphenoid: 1; humerus: 3; scapula: 1; femur: 5; tibio-fibula: 6; ilium: 8; "atlas": 1; trunk vertebra: 5; sacrum: 1; urostyle: 1. Middle unit: radio-ulna: 1. Ancient unit: humerus: 1; radio-ulna: 2; femur: 2; tibio-fibula: 5; ilium: 1; trunk vertebra: 2; urostyle: 2; indet.: 1. [total 50]

Sphenethmoid. One sphenethmoid (VAL MF 6) is relatively large and wider than long (length: 11.5 mm; width: 9.1 mm). Anthrum pro lobo olfactorio wide but not much deep and sella amplificans only slightly developed.

Ilium. Several ilia, some of which are very large, are devoid of either preacetabular and supracetabular *fossae* and have cylindrical ilial shafts (lacking ilial crest) and pronounced dorsal prominences (= tuber superior) without distinct tubercles.

Femur. The crista femoris is usually low and flattened proximally.

The described features unequivocally characterize the species *Bufo bufo* (Böhme, 1977; Sanchiz, 1977; Bailon, 1999). The bulk of the remains referred to this taxon are large and robust and some of them would have belonged to very large specimens: 44 mm is the maximum length for the humeri, 31.6 mm for radio-ulnae and 39.6 mm for tibio-fibulae (they all lack the articular surfaces); *B. bufo* is by far the largest Middle Pleistocene anuran of Europe. This species is at present widespread across Liguria (see map of Schiavo in Doria & Salvidio, 1994) and could be the commonest anuran.

HYLIDAE GRAY, 1825

Hyla Laurenti, 1768 Hyla gr. H. arborea (Linnaeus, 1758) (Fig. 3)

Referred material. Ancient unit: ilium: 1; trunk vertebra: 1. [total 2]

Alium. A small ilium (VAL MF 7) coming from the ancient unit differs from the rest of the ilia in having a one lobed tuber superior (distinct but not particularly raised) and ventral acetabular expansion developed in a relatively wide lamina. The preacetabular and supracetabular fossae and the ilial crest are lacking.

Vertebra. In the same stratigraphic unit there is a trunk vertebra (VAL MF 8) as small as the ilium; it is procoelous and devoid of neural crest, with a wide neural canal, short neural arch (in a cranio-caudal sense) showing a deep anterior concavity, condyle and cotyle roundish and characteristically small with respect to the vertebral body.

These two remains are referred to the genus *Hyla* to which the morphology fully agrees (Böhme, 1977; Bailon, 1999). Due to the poor knowledge of the osteology of the five species of Mediterranean tree frogs that are recognized at present, it is advisable not to identify fragmentary fossil remains at species rank (Delfino & Bailon, 2000); therefore the described material is referred to the *Hyla arborea* group.

Following Emanueli (in Doria & Salvidio, 1994), two species of this genus live at present in W. Liguria, *H. intermedia* Boulenger, 1882 (still included in *H. arborea* in the quoted papers) and *H. meridionalis* Boettger, 1874 but only the latter is found at present in the surroundings of the Valdemino cave and in the Mediterranean vegetational belt of Western Liguria.

RANIDAE GRAY, 1825

Rana Linnaeus, 1758
Rana dalmatina Fitzinger in Bonaparte, 1838 (Fig. 4)

Referred material. Recent unit: maxilla: 11; parasphenoid: 1; scapula: 6; coracoid: 4; humerus: 11; radioulna: 4; ilium: 9; femur: 1; tibio-fibula: 21; trunk vertebra: 3; sacrum: 3; urostyle: 4. Middle unit: scapula: 1. Ancient unit: humerus: 1; radio-ulna: 1; ilium: 2; trunk vertebra: 1. [total 84]

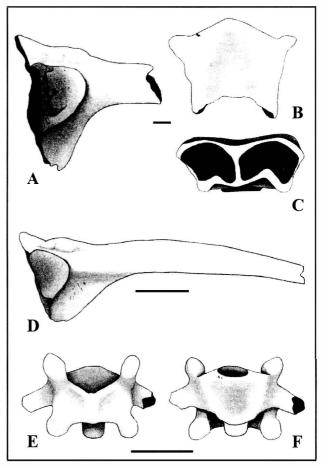


FIG. 3. Bufo bufo, A: right ilium (VAL MF 5), lateral view; B, C: sphenethmoid (VAL MF 6), dorsal and cranial view. Hyla gr. H. arborea, D: right ilium (VAL MF 7), lateral view; E, F: trunk vertebra (VAL MF 8), dorsal and ventral view. Scale = 2 mm.

Ilium. Several ilia show the characteristic morphology of the genus Rana: very well developed and proximally vertical ilial crest; supracetabular fossa generally present, preacetabular one lacking; ventral acetabular expansion relatively wide; slender junctura; dorsal prominence well developed and particularly elongated, forming with the dorsal acetabular expansion an angle wider than 90°, and with dorsal margin gently sloping to the ilial crest (with no sign of a step).

The slenderness of the *junctura* and the shape of the dorsal prominence allow to refer the material to *R. dalmatina* and to exclude *R. temporaria* Linnaeus, 1758 (Böhme, 1977; Bailon, 1999), the only other brown frog that inhabits W Liguria at present (Barbieri in Doria & Salvidio, 1994).

To the same taxon are tentatively referred all the Rana remains – although they are not diagnostic to species level, there is no evidence of the presence of different species. All the male humeri have a thin diaphysis and show a mesial crest (crista medialis) proximally extended and dorsally bent in a fashion that is exclusive of brown frogs (Bailon, 1991, 1999); the same can be said about the development toward the pars suprascapularis of the internal crest of the scapula.

ANURA INDET.

Referred material. Recent unit: humerus: 2; femur: 1; tibio-fibula: 15; ilium: 1; ischium: 1; urostyle: 1; indet.:

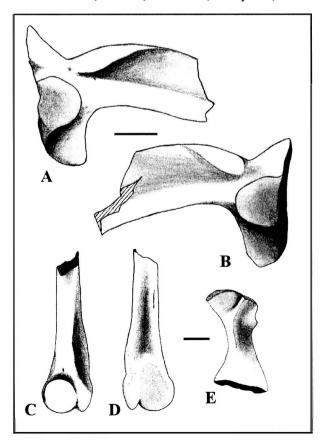


FIG. 4. Rana dalmatina, A: right ilium (VAL MF 9), lateral view; B: left ilium (VAL MF 10), lateral view; C, D: right male humerus (VAL MF 11), ventral and dorsal view; E: left scapula (VAL MF 12), internal view. Scale = 2 mm.

57; Middle unit: indet: 1; Ancient unit: scapula: 1; humerus: 1; radio-ulna: 4; tibio-fibula: 9; trunk vertebra: 11; indet: 18. [total 123]

Part of the anuran material has been referred to order level since it is represented by unidentifiable fragments or non-diagnostic elements. A short and stout scapula (V89 20 A) shows a developed *margo anterior* as in *Pelodytes* but it is too fragmentary to identify it with confidence. The taxon Anura indet. is not reported in the faunal list since all the undetermined material could well belong to the identified species.

REPTILIA LAURENTI, 1768

Reptiles are much more common than amphibians being represented by 1282 remains. Chelonians, lizards and snakes belonging respectively to 1, 4 and 7 taxa have been identified.

CHELONII BRONGNIART, 1800

Chelonians are very well represented at Valdemino and abundant are the shell fragments. The few non-shell remains here studied do not properly exemplify the chelonian abundance. Only the family Testudinidae has been identified.

TESTUDINIDAE BATSCH, 1788

Testudo Linnaeus, 1758 Testudo hermanni Gmelin, 1789

Referred material. Middle unit: scapula/acromion: 1. Ancient unit: dentary: 1; coracoid: 3; caudal vertebra: 10. [total 15]

The few chelonian remains here studied are referred to *Testudo hermanni* accordingly to Tozzi (1969) who first quoted its presence in the site. Although not diagnostic as shell elements, the remains here listed show a morphology that fits well with land tortoises (i.e. the coracoid widens caudally forming a triangle).

At present, *Testudo hermanni* can be considered as probably extinct in Liguria because of overcollection and habitat alteration or destruction; all the specimens found in the region seem to be allochthonous (Jesu in Doria & Salvidio, 1994).

LACERTILIA OWEN, 1842

Altogether, 261 remains have been referred to saurians; they belong to three families: Gekkonidae, Anguidae and Lacertidae.

GEKKONIDAE GRAY, 1825

Tarentola Gray, 1825

Tarentola cf. T. mauritanica (Linnaeus, 1759) (Fig. 5)

Referred material. Recent unit: dentary: 2; maxilla: 1; frontal: 1. [total 4]

Maxilla. A left maxilla (VALMF 13) is 6.7 mm long and nearly complete (only the prefrontal process is

partly eroded): 31 are the teeth positions; all but one retain teeth that are pleurodont, isodont, long, slender, cylindrical with conical and smooth apices devoid of crests and accessory cusps; some of the apices of the first teeth are caudally oriented; reabsorption pits variably sized developed at the base of many teeth; external surface of the prefrontal process with seven roundish foramina (nearly aligned at its base) but smooth and devoid of any ornamentation; a small hole pierces the process at mid height in correspondence of the third lower foramen.

Dentary. Two fragmentary dentaries are characterized by a high number of teeth whose morphology is similar to that of the maxillary ones. The Meckel's groove is partially covered by the dentary and therefore it opens in a posterior position.

Frontal. A frontal (VAL MF 14) made by the complete median fusion of the two paired frontals (the suture is not visible) is associated with the described maxilla. It is characterized by: lateral margins (descending processes), ventrally folded, meet and fuse medially delimiting a relatively wide canal; dorsal surface slightly concave medially without traces of dermal ornamentations and furrows between scales; middle region of the bone with a marked interorbital constriction if seen in dorsal view.

The described tooth morphology and the unpaired (fused) and dorsally smooth frontal, as well as the size

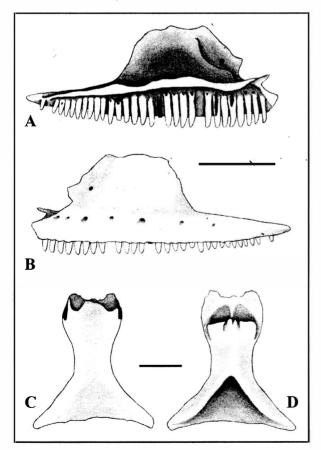


FIG. 5. Tarentola cf. T. mauritanica, A, B: left maxilla (VAL MF 13), internal and external view; C, D: frontal (VAL MF 14), dorsal and ventral view. Scale = 2 mm.

itself of the elements, clearly indicate the presence of a member of the family Gekkonidae (see summaries and literature in Estes, 1983; Bailon, 1991) of a size comparable to that of T. mauritanica or (of a large) H. turcicus. Following Bailon (1991) the degree of robustness and position of the inner premaxillary permit discrimination between T. mauritanica and H. turcicus: this process is relatively more robust and less inclined in the former species than in the second. Moreover, when observed in dorsal view, the sub-orbital region of the horizontal lamina is wider and more robust in T. mauritanica than in H. turcicus, and the prefrontal process is so dorsomedially bent in T. mauritanica that the zygomatic process is partially covered (more straight and not so covering in H. turcicus). The fossil maxilla agrees with the description of T. mauritanica but since the comparison material shows some variability, the fossil remains are tentatively referred to T. mauritanica.

This species is the only representative of the genus in Europe and the commonest gecko of Liguria where it is presently widespread in nearly all the Mediterranean belt of the region (see map in Jesu in Doria & Salvidio, 1994).

ANGUIDAE GRAY, 1825

Anguis Linnaeus, 1758 Anguis fragilis Linnaeus, 1758 (Fig. 6)

Referred material. Recent unit: dentary: 7; maxilla: 2; trunk vertebra: 3; caudal vertebra: 5. Ancient unit: trunk vertebra: 11; caudal vertebra: 1. [total 29]

Dentary. One of the most informative elements is a small left dentary (7.1 mm; VAL MF 15) that is nearly complete even if almost totally devoid of teeth and the angular process is broken off. In internal view: intramandibular septum visible inside the Meckel's groove; the latter is relatively wide in the posterior area of the dentary but very small more anteriorly (where it runs ventrally) and slightly enlarged again in the symphysary area; symphysis well defined and posteromedially directed; horizontal lamina medially inclined, showing a concave profile; it develops a small splenial spine under the ninth tooth; anterior-inferior alveolar foramen opens near the spine; most likely 10 teeth position are present (horizontal lamina has an irregular surface); three retain teeth that are subpleurodont and conical; the apices are worn or broken; the seventh and eighth teeth are strongly bent backward (and slightly lingually); the coronoid process is nearly as long as the supra-angular one but a little smaller; both have a rounded tip. In lateral view: four foramina open at mid height on the external surface of the dentary; the anterior one is the biggest.

Another left dentary (VAL MF 16) is nearly as long as the previous (7.2 mm) but more damaged in the posterior region: the angular process is broken off and the horizontal lamina is partially damaged. Its morphology is comparable to that already described with the difference that supra-angular process seems to be a little

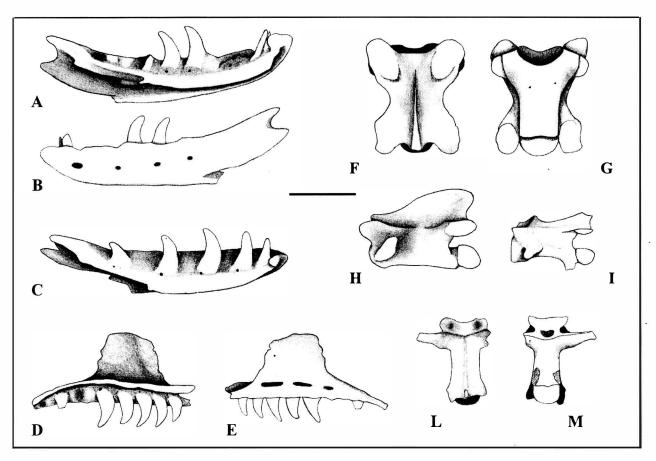


FIG. 6. Anguis fragilis, A, B: left dentary (VAL MF 15), internal and external view; C: left dentary (VAL MF 16), internal view; D, E: left maxilla (VAL MF 17), internal and external view; F, G, H: trunk vertebra (VAL MF 18), dorsal, ventral and left lateral view; I, L, M: caudal vertebra (VAL MF 19), dorsal, ventral and left lateral view. Scale = 2 mm.

longer that the coronoid one. The total number of teeth position is 10, while five are the preserved teeth.

Maxilla. The best-preserved maxilla (VAL MF 17) is 4.8 mm long: the prefrontal process seems to be slightly eroded; internal premaxillary process and the zygomatic one are partly broken; eight (or maybe nine) teeth positions are visible; six teeth are preserved; they are subpleurodont, conical, caudo-laterally bent, not striated; apices pointed (if not eroded or broken); each tooth has a small foramen at the base; lateral surface of the prefrontal process without any sign of dermal ossification or furrow; three wide (elongated and deep) foramina aligned at the base of the process.

Vertebra. A few trunk vertebrae share the following characteristics: vertebral body procoelous, moderately elongated, ventral surface flattened and with parallel margins (in the posterior section); condyle and cotyle moderately depressed; two small subcentral foramina usually present; prezygapophyses antero-laterally directed, dorsally tilted and devoid of processes; neural spine usually well developed and sometimes relatively high; distinct interzygapophyseal constriction in dorsal view.

Some caudal vertebrae display haemapophyses fused to the posterior ventral surface of the vertebral body, long transverse processes flattened and laterally directed, and autotomic line that separates the cotylar region from the rest of the vertebra (it runs in the anterior area of the transverse processes).

All the described characteristics are typical of the family Anguidae and of the genus Anguis in particular, the sole that shares with the fossil material the number and shape of dentary and maxillary teeth as well as the shape of the vertebrae (Klembara, 1979, 1981, 1986; Bailon, 1991). All the anguid material is referred to Anguis fragilis, the only species known in the European Quaternary because Anguis stammeri Brunner, 1954 (Middle Pleistocene of Germany) has been recently considered a large sized form of A. fragilis (Bailon, 1991; Holman, 1998). Anguis cephallonicus Werner, 1894, a living species recently revalidated (Cabela in Gasc et al., 1997), has not been taken into consideration since it is endemic to the Peloponnese and to the southern Ionian Islands and, moreover, its comparative osteology is still unknown.

A. fragilis is widespread and common in Liguria at the present time (Schiavo in Doria & Salvidio, 1994).

LACERTIDAE BONAPARTE, 1831

Lacerta Linnaeus, 1758 Lacerta gr. L. viridis (Laurenti, 1768) (Fig. 7)

Referred material. Recent unit: dentary: 19; maxilla: 6; teeth bearing bone: 1; trunk vertebra: 2; caudal vertebra: 3. Ancient unit: dentary: 6; premaxilla: 2; maxilla: 5; teeth bearing bone: 1; parietal: 1; articular: 1; humerus: 2; coxal: 1; femur: 1; trunk vertebra: 37; sacral vertebra: 3; caudal vertebra: 19. [total 110]

Dentary and maxilla. The presence of pleurodont and cylindrical teeth distinguishes some dentaries and maxillae. The teeth show usually two cusps (a very small anterior cusp and a bigger posterior one) but the anteriormost teeth are monocuspidate while the posteriormost can have three cusps. Although none of the dentaries is perfectly preserved, it is possible to state that the Meckel's groove is wide along the entire length of the dentary. The largest dentaries have a dental lamina of 10.5 and 11.5 mm.

Parietal. A fragmentary parietal (VAL MF 21) of medium size $(8.3 \times 6.6 \text{ mm})$ shows a dorsal surface with an evident crusta calcarea and the imprints of the boundaries among the frontoparietals, parietals and interparietal scales; the pineal foramen opens in the middle of the interparietal scale area, the shape of which is slightly irregular; it is not clear wether its asymmetric posterior prolongation represents a narrow occipital scale (without a marked interparietal-occipital boundary) or not.

Vertebra. Some trunk vertebrae show a procoelous vertebral body, moderately elongated, ventrally convex, with condyle and cotyle slightly oval or subcircular; prezygapophyses dorsally tilted (without processes) and with oval facets; neural spine high and running along almost all the neural arch (only the area between prezygapophyses is free); a sort of haemal keel well defined at least anteriorly; no traces of zygosphene-zygantrum articulations; the largest vertebra has a centrum 4.2 mm long.

By the tooth morphology (pleurodont, cylindrical, bicuspid teeth) of several teeth bearing bones it is possible to identify the family Lacertidae. The size itself of the remains allow to exclude the smallest member of the

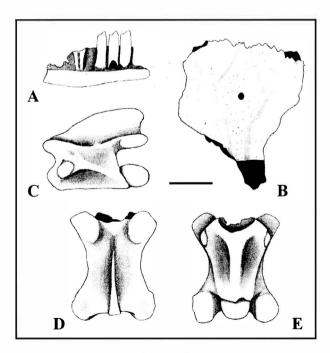


FIG. 7. Lacerta gr. L. viridis, A: right dentary fragment (VAL MF 20), internal view; B: parietal (VAL MF 21), dorsal view; C, D, E: trunk vertebra (VAL MF 22), left lateral, dorsal and ventral view. Scale = 2 mm.

family (up to the size of a big *Podarcis*) and hypothesize the presence of a medium-sized member of the genus Lacerta. The length of the dental lamina, as well as the length and width of the parietal, fall in the ranges of both L. viridis (complex) and Timon lepidus (Daudin, 1802) reported by Barahona & Barbadillo (1997; respectively bigger than 8.4 mm, 6 mm and 5.7 mm) but the centrum length of the trunk vertebrae (4.2 mm maximum) allows referral of the material to L. viridis (in the sample studied by Barbadillo & Sanz, 1983, this length is never higher than 4.38 mm in L. viridis). The allocation at species rank of these remains is therefore based on their size: unfortunately the posterior area of the parietal is damaged and it is not possible to see the occipital scale whose shape is a diagnostic morphological character (Barahona & Barbadillo, 1997).

Since the modern *L. viridis* populations have been split into two species, *L. viridis* and *L. bilineata* Daudin, 1802 (Rykena, 1991; Amann *et al.*, 1997), whose comparative osteology has not been described, the fossil material is simply referred to the *L. viridis* group that includes both.

Nowadays, *L. bilineata* is quite a common lizard in Liguria (Schiavo in Doria & Salvidio, 1994).

LACERTIDAE INDET.

Referred material. Recent unit: dentary: 18; premaxilla: 1; maxilla: 7; teeth bearing bone: 4. Ancient unit: dentary: 52; premaxilla: 1; maxilla: 23; teeth bearing bone: 5; parietal: 1; humerus: 1; ilium: 1; cervical vertebra: 1; caudal vertebra: 2. [total 117]

Several lacertid remains of small size are simply referred to family rank since it is not possible to identify a genus with confidence. They could either belong to full-grown *Podarcis* or to juvenile *Lacerta* specimens as well as to different taxa. The taxon Lacertidae indet. is therefore reported in the faunal list.

SAURIA INDET.

Referred material. Ancient unit: dentary: 1. [total 1] A dentary fragments devoid of teeth cannot be allocated at a rank lower than the order.

SERPENTES LINNAEUS, 1758

Snake vertebrae are by far the most common elements of the herpetofauna and therefore this order is the best-represented (1006 remains). Seven taxa belonging to two families, Colubridae and Viperidae, have been recognised.

COLUBRIDAE OPPEL, 1811

Coronella Laurenti, 1768 Coronella cf. C. austriaca Laurenti, 1768 (Fig. 8)

Referred material. Ancient unit: trunk vertebra: 31. [total 31]

Vertebra. Some of the smallest vertebrae (2.6 mm is the centrum length of the figured one; VAL MF 23) are

characterized by: depressed neural arch whose posterior margins are sometimes nearly straight sometimes slightly curved (if seen in caudal view); condyles and cotyles slightly oval; haemal keel narrow, long and non-well defined; prezygapophyseal facets invariably damaged but should have been oval and at least two times longer than the processes; the latter are short, pointed and with a wide and robust base; parapophyses slightly bigger than the diapophyses; anterior margin of the zygosphene is nearly straight; neural spine low and reaching anteriorly the middle of the zygosphene.

The small size of the vertebra, along with the shape of the prezygapophyseal processes and, overall, the shape of the posterior end of the neural arch, permit the material to be referred to the genus *Coronella* and more precisely to *C. austriaca* (Szyndlar, 1984). Due to the variability of these structures in the modern species (Szyndlar, 1991a), it is not possible to allocate this material with confidence and therefore the taxonomic particle "cf." has been introduced.

Both *C. austriaca* and *C. girondica* (Daudin, 1803) are present nowadays in Liguria (and in the area of the palaeontological site as well) but the latter is much more common in the region (Doria in Doria & Salvidio, 1994).

Elaphe Fitzinger, 1833 Elaphe sp. (Fig. 8)

Referred material. Recent unit: trunk vertebra: 1 [to-tal 1]

Vertebra. A trunk vertebra (VAL MF 24) is quite different from the others because it is more cranio-caudally

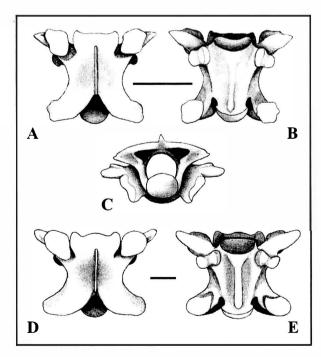


FIG. 8. Coronella cf. C. austriaca, A, B, C: trunk vertebra (VAL MF 23), dorsal, ventral and caudal view. Elaphe sp., D, E: trunk vertebra (VAL MF 24), dorsal and ventral view. Scale = 2 mm.

compressed and shows small prezygapophyseal processes. In dorsal view: the vertebra is "x" shaped; zygosphene crenate; prezygapophyseal facets oval (but with an anterior roundish profile); prezygapophyseal processes relatively small and with rounded tips. In ventral view: haemal keel narrow with well-defined margins, not ventrally flattened and not posteriorly widened; diapophyses bigger than the parapophyses. In cranial view: prezygapophyses nearly horizontal and zygosphene slightly convex. In caudal view: neural arch not particularly high and with straight and not vaulted dorsal margins. In lateral view: neural spine not high and overhanging posteriorly only. The centrum length is 4.4 mm.

This description fits with the morphology of the genus Elaphe (see among others, Szyndlar, 1991a; Bailon, 1991) and all the mentioned characteristics fall into the variability of either E. longissima (Laurenti, 1768) [inclusive of E. lineata (Camerano, 1891)] or E. scalaris (Schinz, 1822). Following Bailon (1991) it is possible to discriminate between these two species on the basis of the more square shape of the vertebral body of E. scalaris whose CL/NAW ratio is proximate to 1 (1.05). This ratio has a mean value of 1.15 in fossil or 1.4 in living E. longissima studied by Szyndlar (1991a). Although the ratio of the Valdemino vertebra is 1.19 (CL 4.4 mm / NAW 3.7 mm) and therefore it falls in the range of E. longissima, the material is too scarce to exclude the presence of E. scalaris, a species whose morphology and variability are largely unknown. Investigations recently carried out by Helfenberger (2001) and Utiger et al. (2002) suggest the latter species should be separated from Elaphe and included in Rhinechis Michahelles (in Wagler), 1833; such a proposal has not been taken into consideration in this work.

The Western Liguria hosts both E. longissima and E. scalaris at present, but while the former is relatively common (Poggi in Doria & Salvidio, 1994), the latter has been found only once and very close to the border with France (Ferri in Doria & Salvidio, 1994).

Hierophis Fitzinger, 1843 Hierophis viridiflavus (Lacépède, 1789) (Fig. 9)

Referred material. Recent unit: maxilla: 1; trunk vertebra: 1. Ancient unit: parabasisphenoid: 1; compound bone: 1; trunk vertebra: 19. [total 23]

Maxilla. An edentulous right maxilla (VAL MF 25) is broken at both extremities. Assuming that the first tooth position is missing, the maxilla should have had 13 teeth positions followed by a short diastema (as long as one tooth position) followed in its turn by two last positions; the prefrontal process should correspond to the 6-8 positions and the ectopterygoid process to the diastema. Dorsally to the latter process, a distinct constriction is well delimited anteriorly but weakly posteriorly.

Basiparasphenoid. Although not complete (the parasphenoid process is broken off), a basiparasphenoid

(VAL MF 26) is quite informative because its surface, ridges included, is perfectly preserved.

In external view: evident pterygoid crests, sigmoid in shape, originate from well-developed basipterygoid processes and nearly meet medially, delimiting a small central area; postpterygoid area broad and showing a very weak basisphenoid crest; wide common *foramina* (resulting from union of the posterior orifice of Vidian canal with the cerebral *foramen*) give rise to a shallow furrow postero-laterally directed; anterior orifices of the Vidian canal open anteriorly to the pterygoid crest and are much smaller than the previous; posterior margin of the bone with two lateral lobes and a median, more pronounced, one. In internal view: the foramina for the *abducens* nerve open laterally and posteriorly to a wide pituitary fossa; only the base of the frontal crest is preserved.

Vertebra. Several trunk vertebrae are robust and relatively large in size: their centrum length generally exceeds 5 mm and one reaches 6.3 mm.

In dorsal view: prezygapophyseal facets usually ovalshaped (but sometimes nearly rectangular), prezygapophyseal processes long (a little less than the facets) and pointed; anterior margin of the zygosphene straight or concave. In ventral view: the parapophyses are usually well separated from the diapophyses, the haemal keel is always well delimited, high, ventrally

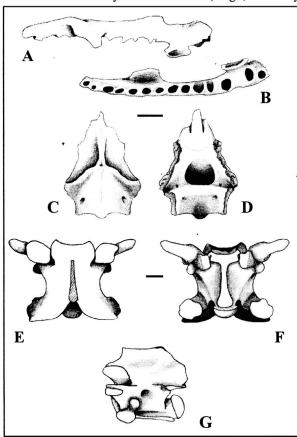


FIG. 9. Hierophis viridiflavus, A, B: right maxilla (VAL MF 25), medial and ventral view; C, D: basiparasphenoid (VAL MF 26), ventral and dorsal view; E, F, G: trunk vertebra (VAL MF 27), dorsal, ventral and left lateral view. Scale = 2 mm.

flattened and posteriorly expanded in a characteristic way. In cranial view: prezygapophyses approximately horizontal; dorsal margin of the zygosphene usually straight. In caudal view: neural arch high and vaulted. In lateral view: neural spine appears to be high and robust.

Some of the largest vertebrae (as the one figured) show a deeply concave zygosphene, evident epizygapophyseal spines an paracotylar tubercles, parapophyses distinctly larger than diapophyses and wide lateral foramina.

The morphology of the prezygapophyseal processes, haemal keel and posterior margin of the neural arch permits identification of *Hierophis viridiflavus* (cf. description and literature quoted in Szyndlar, 1984, 1991a; Bailon, 1991). Also the fossil maxilla matches well with the comparison material of this species in teeth positions numbers, presence and position of the frontal and ectopterygoid processes as well as of a short diastema. A slight difference concerns the dorsal constriction that is not so well delimited posteriorly (cf. Delfino & Bailon, 2000). The basiparasphenoid displays crests developed and located similarly to *H. viridiflavus* (cf. Bailon, 1991).

Today, *H. viridiflavus* is a very common snake in Liguria being present in all the suitable habitats (Cortesogno in Doria & Salvidio, 1994).

Malpolon Fitzinger, 1826 Malpolon monspessulanus (Hermann, 1804) (Fig. 10)

Referred material. Recent unit: trunk vertebra: 2. [to-tal 2]

Vertebra. Two large vertebrae (VAL MF 28 and 34) of the Recent unit (V91A 20B) can be grouped together on the basis of the following features. In dorsal view: zygosphene straight or slightly concave; prezygapophyseal facets oval-shaped (but the original morphology could have been different since they are eroded); the only preserved prezygapophyseal process is robust, long, apically rounded and antero-laterally directed in a characteristic fashion. In ventral view: vertebral body distinctly elongated, well delimited laterally by evident subcentral ridges; subcentral grooves well marked; haemal keel high, narrow, well delimited and, though not flattened, tends to progressively widen toward its caudal end; para- and diapophyses almost totally eroded. In cranial view: zygosphene convex and prezygapophyses horizontal. In caudal view: neural arch particularly high and with dorsal margin nearly straight (not vaulted). In lateral view: neural spine seems not to be high and overhanging on both sides (partially preserved in one vertebra only). The centrum length of the vertebrae is 6.4 and 6.5 mm (NAW is 5.1 and 5.0 respectively; CL/NAW is about 1.3 for both).

The material can be referred to *Malpolon monspessulanus* on the basis of the length and orientation of the prezygapophyseal processes, the elongation of the vertebral body, the shape of the haemal keel and of the posterior edge of the neural arch (Szyndlar, 1984, 1988; 1991*a*; Bailon, 1991).

Remarkable is the apparent absence of epizygapophyseal spines, structures regularly present in the modern comparison material ("le plus souvent presentes" following Bailon, 1991): since the vertebrae are slightly eroded and some edges smoothed, it is not know if these structures were originally present or not; even if they were absent, a proper taxonomic allocation of the two vertebrae is granted by several other reliable characters. Although it is advisable not to identify taxa on the basis of scarce and fragmentary fossil remains, as is the case of the two vertebrae here described, the morphology of this species is so characteristic that it is easily recognisable even if the material is relatively poor.

The modern range of *M. monspessulanus* includes W. Liguria, where the nominal subspecies reaches its eastern range limit (Ferri in Doria & Salvidio, 1994).

"COLUBRINES" INDET.

Referred material. Recent unit: trunk vertebra: 12. Ancient unit: trunk vertebra: 327. [total 339]

Vertebra. All the colubrid vertebrae, possessing haemal keel and not hypapophyses, but strongly damaged or showing mixed set of characters have been referred to the working taxon "Colubrines" indet. (sensu Szyndlar, 1984; Szyndlar, 1991a). Since they could belong to either the identified taxa or others, the taxon Colubrines indet. is reported in the faunal list.

Natrix (Laurenti, 1768) Natrix natrix (Linnaeus, 1758) (Fig. 11)

Referred material. Recent unit: maxilla: 1; compound bone: 1; trunk vertebra: 3. Ancient unit: compound bone: 3; trunk vertebra: 191. [total 199]

Maxilla. A right maxilla (VALMF 29) lacks the area anterior to the prefrontal process and therefore it is not possible to estimate the teeth positions original number: 15 are those preserved, only four still host teeth (robust

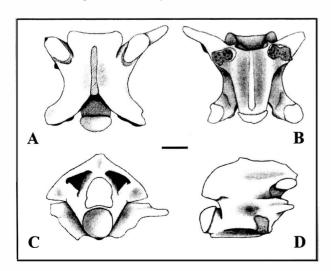


FIG. 10. Malpolon monspessulanus, A, B, C, D: trunk vertebra (VAL MF 28), dorsal, ventral, caudal and right lateral view. Scale = 2 mm.

and posteriorly curved); the size of the tooth sockets suggests that the last four teeth were particularly large (much larger than the preceding); both processes preserved, robust and mesio-ventrally projecting; area posterior to the ectopterygoid process dorsally bent. Maxilla "X" shaped in ventral view.

Compound bone. At least four compound bones share the following characters: medial flange hardly higher that the lateral flange (the mandibular fossa is therefore relatively shallow); retroarticular process robust and mesio-ventrally directed; supraangular foramen located far from anterior margin of the mandibular fossa; supraangular crest not present.

Vertebra. The morphology of many hypapophysisbearing vertebrae is rather similar.

In dorsal view: general appearance of the vertebra peculiarly elongated; anterior margin of the zygosphene slightly variable from concave to convex; prezygapophyseal processes long, particularly large, with rounded tips and often with a small anterior concavity; prezygapophyseal facets oval in shape; epizygapophyseal spines usually present. In ventral view: parapophyses well distinct (and more developed) from the diapophyses. In cranial view: prezygapophyses regularly horizontal (the ventral inclination is negligible); dorsal margin of the zygosphene variably shaped.

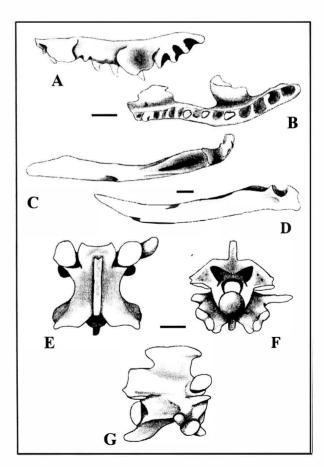


Fig. 11. Natrix natrix, A, B: right maxilla (VAL MF 29), medial and ventral view; C, D: left compound bone (VAL MF 30), dorsal and lateral view; E, F, G: trunk vertebra (VAL MF 31), dorsal, caudal and left lateral view. Scale = 2 mm.

In caudal view: neural arch distinctly vaulted (sometimes with an angle). In lateral view: neural spine always high and overhanging anteriorly and posteriorly; sometimes (mainly in large specimens) its dorsal edge is thickened; parapophyseal processes long, apically rounded and anteriorly directed; hypapophyses long, robust, sigmoid shaped and usually apically rounded (although pointed tips are not uncommon). Some of the vertebrae are very large: their centrum length is about 7 mm

All of this material can be referred to the genus *Natrix* on the basis of the opisthomegadont maxilla, scarce depth of the mandibular fossa and the position of the supraangular foramen of the compound bone, and by several characteristics of the vertebrae (i.e. presence and shape of the hypapophyses as well as prezygapophyses and neural arch shape). It is possible to identify with reasonable confidence the presence of *N. natrix* on the basis of the roundish tips of the parapophyseal processes and hypapophyses (Szyndlar, 1984; 1991b, Holman, 1991; Ivanov, 1999a) although they show some variability in the fossil and modern comparative material.

All the three European species of the genus *Natrix* inhabit Liguria at present but only *N. natrix* and *N. maura* (Linnaeus, 1758) have been quoted in the area of the palaeontological site (Andreotti in Doria & Salvidio, 1994; Raineri in Doria & Salvidio, 1994; Salvidio in Doria & Salvidio, 1994).

VIPERIDAE LAURENTI, 1768

Vipera Laurenti, 1768 Vipera aspis (Linnaeus, 1758) (Fig. 12)

Referred material. Recent unit: trunk vertebra: 23. Ancient unit: maxilla: 1; trunk vertebra: 40. [total 64]

Maxilla. A right maxilla (VAL MF 32) is relatively well preserved: only the tip of the fang is broken off. The morphology of the fang base is masked by matrix. The prefrontal process is tall, highly developed and widens a bit apically, where it bends laterally. On the posterior surface (between the fang and the process) there is a relatively deep fossa delimited cranially by a small crest but "opened" on the sides. The fang is hollow, slender and its anterior surface shows a proximal orifice (the orifice for the venom duct) giving rise to a median line that marks the fang for its entire length. The total length of the maxilla (fang included) is 8.9 mm.

Vertebra. A peculiar set of characters allows some vertebrae to be grouped together. In dorsal view: clear interzygapophyseal constriction; prezygapophyseal facets oval and antero-laterally directed; prezygapophyseal processes very short and acute shaped; zygosphene anterior margin strongly crenate. In ventral view: parapophyses and diapophyses well separated; subcentral grooves usually more marked in the anterior area of the vertebral body. In cranial view: cotyle large and slightly depressed; paracotylar foramina present and well visible; parapophyseal processes exceeding the ventral margin of the cotyle; prezygapophyses dorsally

tilted; dorsal margin of the zygosphene usually straight. In caudal view: the condyle wide and robust; the neural arch depressed and with straight dorsal margins. In lateral view: neural spine generally high (lower in posteriormost trunk vertebrae) and overhanging posteriorly only; parapophyseal processes anteroventrally directed (acute or rounded); hypapophysis usually long, robust and exceeding the condyle posteriorly. The largest vertebra is 4.2 mm long (CL).

The general morphology of the maxilla (i.e. its shortness and the presence of an hollow fang) and that of the trunk vertebrae (i.e. presence of hypapophyses, dorsally prezygapophyses, ventrally parapophyseal processes, depressed and straight neural arch) indicates the family Viperidae, while the absence of a labial pit in the maxilla (that hosts the thermoreceptive organ) excludes the presence of the subfamily Crotalinae (Ivanov, 1999b). The general proportions of the vertebrae (among others, not particularly elongated - cf. Szyndlar & Rage, 1999) agrees with the V. aspis group, and although a distinction between adult V. aspis and subadult V. ammodytes (Linnaeus, 1758) (the two members of the group that can be reasonably taken into consideration) can be difficult, the material is abundant enough to identify with confidence the presence of V. aspis.

This species is the only viper that lives in Liguria at present (Borgo in Doria & Salvidio, 1994).

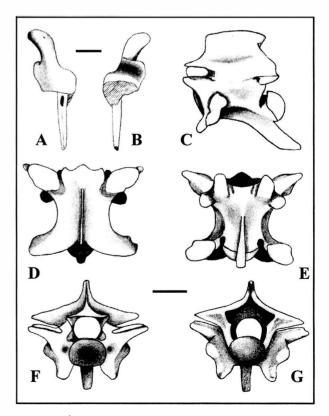


FIG. 12. Vipera aspis, A, B: right maxilla (VAL MF 32), antero-ventral and postero-dorsal view; C, D, E, F, G: trunk vertebra (VAL MF 33), left lateral, dorsal, ventral, cranial and caudal view. Scale = 2 mm.

SERPENTES INDET.

Referred material. Recent unit: dentary: 6; pterygoid: 2; teeth bearing bone: 5; trunk vertebra: 2; cloacal vertebra: 1; caudal vertebra: 8. Ancient unit: dentary: 6; maxilla: 4; teeth bearing bone: 1; compound bone: 9; vertebra: 155; cloacal vertebra: 1; caudal vertebra: 147. [total 347]

Several remains devoid of relevant structures because of extreme fragmentation, as well as some uninformative elements, such as caudal vertebrae, have been simply referred to order rank.

DISCUSSION

The Valdemino Cave yielded 1549 herpetofaunal remains referable to the following 18 taxa (six amphibians and 12 reptiles): Triturus sp., Speleomantes sp., Pelodytes punctatus, Bufo bufo, Hyla gr. H. arborea, Rana dalmatina, Testudo hermanni, Tarentola cf. T. mauritanica, Anguis fragilis, Lacerta gr. L. viridis, Lacertidae indet., Coronella cf. C. austriaca, Elaphe sp., Hierophis viridiflavus, Malpolon monspessulanus, Colubrines indet., Natrix natrix and Vipera aspis. This study confirms and enriches the list of the taxa identified by Tozzi (1969) and Delfino (2002): a more detailed analysis allowed the identification of Elaphe sp. and Malpolon monspessulanus, improving the allocation of some of the remains that have been previously referred to "Colubrines" by the latter author.

Among the three different units, the Ancient one shows the highest number of remains (1205) and therefore of taxa, followed by the Recent (340) and then by the Middle (four remains). The analysed samples represent two different warm stages of the Pleistocene whose herpetofaunas share some elements but differ for others. As shown in Table 1, the Ancient Unit (Galerian) hosts all the identified taxa with the exception of *Tarentola*, *Elaphe* and *Malpolon* that have been found in the Recent Unit (post-Galerian in age) only.

Altogether, the Valdemino assemblage is surprisingly rich because it contains the same number of taxa of the Gargano sites (Apulia, Early Pleistocene; Delfino & Bailon, 2000) even if the number of remains of the former is nearly one tenth of the latter; due to their high diversity, these two herpetofaunas are by far the most interesting ever found in the Italian Pleistocene. The Valdemino herpetofauna is the only one in Italy that hosts fossils of *Pelodytes* and *Malpolon*. Moreover, although relatively rare and not referred at species rank, the remains of *Speleomantes* are the only sign so far published of the ancient presence in continental Europe of this biogeographically enigmatic family.

The assemblage does not show any relevant discrepancy from the present "Ligurian Riviera" association as defined by Sindaco (1998). With the exception of *Testudo hermanni*, all the identified taxa are widespread in western Liguria at present although some of them do not live in the surroundings of the site (cf. maps in Doria & Salvidio, 1994). The Region is devoid of autoch-

thonous population of land tortoises at present, but the fossil remains of Valdemino corroborate, along with those reported by Hervet (2000), the hypothesis (Jesu in Doria & Salvidio, 1994) that this species had a past continuous distribution between Catalunya and Southern Italy.

One of the most striking characteristics of the Valdemino assemblage is the sharp contrast between a mammal fauna that still hosts extinct taxa (among others, Barbary apes, elephants, rhinoceros, leopards and sabre-toothed tigers) and a modern herpetofauna that is entirely represented by modern taxa that nowadays are typical of a Mediterranean environment. A datum that supports, once again, the idea that the herpetofauna experienced an extraordinary evolutionary stasis during the Quaternary (cf. Holman, 1998).

Another relevant topic raised by this fossil herpetofauna is the presence of M. monspessulanus and its apparent sympatry with H. viridiflavus. The former has been considered as the only Palaearctic reptile whose distribution matches well with the average range of the Mediterranean reptiles (Saint Girons, 1982); the only exception is represented by the Italian peninsula that it inhabits only along the narrow littoral strip of the western coast of Liguria, corresponding to the meso-Mediterranean bioclimatic-zone (Salvidio et al., 1996). The two vertebrae of Valdemino referred to M. monspessulanus represent the first fossil record for this species in Italy but since they fall in the modern range of the species, they add only little information to the evolutionary history of its distribution. Its regular absence from all the Neogene and Quaternary Italian sites that yielded herpetofaunal remains (more than 300 localities so far studied), although not definitely proving its absence, seems to strongly support the fact that this large and easily recognisable snake (this is true for the fossil material also) never colonized Italy. An absence that is rather surprising since other taxa with similar modern ranges (East-West disjunct distribution are shown by the genera Mauremys and Blanus) have been recovered in Italy as fossils.

The biogeographic analysis of the north-western Italian herpetofauna carried out by Sindaco (1998) with the aid of affinity indexes based on a presence/absence matrix, showed that the Ligurian Provinces cluster together (Provinces of Savona, Genova and La Spezia) or with the French southern Departments (Provinces of Imperia), and are therefore markedly diverse from the neighbouring Piedmontese Provinces that are separated by moderately high mountain chains. The presence in the Valdemino herpetofauna of taxa as *Pelodytes* (rare and localised in Piedmont at present), *Testudo* and *Malpolon* seems to testify that such a diversification could potentially have existed during the Middle Pleistocene already.

Moreover, Sindaco (1998), discussing the origin of the herpetofauna of north-western Italy, suggested that some taxa, as *P. punctatus*, could have reached Italy

	Triturus sp.	Speleomantes sp.	Caudata indet.	P. punctatus	B. bufo	H. gr. H. arborea	R. dalmatina	Anura indet.	T. gr. T. hermanni	T. cf. T. mauritanica	A. fragilis	Lacerta gr.L. viridis	Lacertidae indet.	Sauria indet.	C. cf. C. austriaca	Elaphe sp.	H. viridiflavus	M. monspessuianus	Colubrines indet.	N. natrix	V. aspis	Serpentes indet.
Recent Unit (340 remains)							•	•		•		•									•	•
Middle Unit (4 remains)					•		•	•	•													
Ancient Unit (1205 remains)	•	•	•	•	•	•	•	•	•		•	•		•			•		•		•	•

TABLE 1. The distribution of the taxa within the stratigraphic units.

from Iberian or North African refugia after the Würmian cold phase (Late Pleistocene), but the Valdemino fossils pre-date its arrival in the area, although they do not exclude recurrent extinctions and recolonizations of western Liguria respectively during and after the Pleistocene climatic worsening.

At least in the late Neogene and Quaternary, the area corresponding to the present western Liguria should have been a privileged "biotic corridor" due to its physiography: a narrow E-W oriented strip of land delimited by the sea on one side, and by a mountain chain on the other. During stadial and glacial marine lowstand, the strip should have been relatively broader at least locally (because the slopes of the Maritime Alps are generally rather steep). For reasons that can probably vary for different taxa, and still need to be identified, this way of dispersal has been a "dead end" corridor indeed: none of the taxa that characterise at present the area (Hyla meridionalis, Chalcides striatus, Timon lepidus, Elaphe scalaris and Malpolon monspessulanus), are know as fossils in the rest of the peninsula even if the herpetofauna of Valdemino testify a relatively ancient presence of some of them in Liguria.

ACKNOWLEDGEMENTS

The study of this material has been possible thanks to the courtesy of Giuseppe Vicino (Museo Civico di Finale Ligure) and Benedetto Sala (Ferrara). Benedetto Sala, Sebastiano Salvidio (Genova), Roberto Sindaco (Torino) and Wolfgang Wüster (Bangor) critically revised the manuscript and provided helpful literature. Chris Gleed-Owen (Bournemouth) kindly improved the language of the manuscript.

REFERENCES

- Amann, T., Rykena, S., Joger, U., Nettmann, H. K. & Veith, M. (1997). Zur artlichen trennung von *Lacerta bilineata* Daudin, 1802 und *L. viridis* (Laurenti, 1768). *Salamandra* 33, 255-268.
- Arillo, A., Balletto, E. & Spanò, S. (1974). Origine e costituzione della fauna terrestre del Promontorio di Portofino. In Atti del Convegno "Il Monte di Portofino. Una presa di coscienza e un fermo impegno per il suo futuro", 72-76. Genova: Provincia di Genova.

- Bailon, S. (1991). Amphibiens et reptiles du Pliocène et du Quaternaire de France et d'Espagne: mise en place et évolution des faunes. Paris: doctoral thesis., Univ. Paris VII.
- Bailon, S. (1999). Différenciation ostéologique des anoures (Amphibia, Anura) de France. In Fiches d'ostéologie animale pour l'Archéologie. Série C:
 Varia. N° 1, 1-41. J. Desse and N. Desse-Berset (Eds).
 Valbonne: Centre de Recherches Archéologiques-CNRS.
- Barahona, F. & Barbadillo, L. J. (1997). Identification of some Iberian lacertids using skull characters. *Revista Española de Herpetologia* 11, 47-62.
- Barbadillo, L. J. & Sanz, J. L. (1983). Análisis Osteométrico de las Regiones Sacra y Presacra de la Columna Vertebral en los Lagartos Ibéricos Lacerta viridis Laurenti, Lacerta lepida Daudin y Lacerta schreiberi Bedriaga. Amphibia-Reptilia 4, 215-239.
- Böhme, G. (1977). Zur Bestimmung quartärer Anuren Europas an Hand von Skelettelementen. Wissenschaftliche Zeitschrift der Humboldt-Universität zu Berlin, Mathematisch-Naturwissenschaftliche Reihe 26, 283-300.
- Boule, M. (1906). Les Grottes de Grimaldi (Baoussé-Roussé). Géologie et Paléontologie. Tome I, Fascicule II. Monaco: Imprimerie de Monaco.
- Boule, M. (1919). Les Grottes de Grimaldi (Baoussé-Roussé). Géologie et Paléontologie (fin). Tome I, Fascicule IV. Monaco: Imprimerie de Monaco.
- Brocchi, P. (1879). Note sur des ossements de Batraciens recueillis par M. Rivière dans les grottes de Menton. Bulletin de la Société Philomathique de Paris, (ser.7) 3, 223-226.
- Brocchi, P. & Rivière, E. (1886). Des reptiles et des poissons trouvés dans les grottes de Menton, Italie. Comptes Rendus des Séances Hebdomadaires de l'Académie des Sciences de Paris 103, 1211-1213.
- Deiana, A. M. & Serra, G. P. (1978). Anatomia comparata della colonna vertebrale in *Hydromantes genei* Schleg. e *Hydromantes brunus* Gorm. (Anfibi Urodeli Pletodontidi). *Rendiconti del Seminario della Facoltà di Scienze dell'Università di Cagliari* 48 (suppl.), 193-197.
- Delfino, M. (2002). Erpetofaune italiane del Neogene e del Quaternario. Modena: doctoral thesis, Modena & Reggio Emilia University.

- Delfino, M. & Bailon, S. (2000). Early Pleistocene herpetofauna from Cava Dell'Erba and Cava Pirro (Apulia, Southern Italy). *The Herpetological Journal* 10, 95-110.
- Doria, G. & Salvidio, S. (Eds) (1994). Atlante degli Ansibi e Rettili della Liguria. Cataloghi dei Beni Naturali n° 2. Genova: Museo Civico di Storia Naturale "Giacomo Doria" e Regione Liguria.
- Estes, R. (1981). Gymnophiona, Caudata. In *Handbuch* der *Paläoherpetologie*. Part 2. Stuttgart/New York: Fischer Verlag.
- Estes, R. (1983). Sauria terrestria, Amphisbaenia. In *Handbuch der Paläoherpetologie*. Part 10A. Stuttgart/ New York: Fischer Verlag.
- Fornasiero, O. (1989). Cronostratigrafia di due giacimenti quaternari continentali a mammiferi della Liguria. Ferrara: dissertation thesis, Ferrara University.
- Gasc, J.-P., Cabela, A., Crnobrnja-Isailovic, J., Dolmen,
 D., Grossenbacher, K., Haffner, P., Lescure, J.,
 Martens, H., Martinez Rica, J. P., Maurin, H., Oliveira,
 M.E., Sofianidou, T. S., Veith, M. & Zuiderwijk, A.
 (Eds) (1997). Atlas of amphibians and reptiles in Europe. Paris: Societas Europaea Herpetologica & Muséum National d'Histoire Naturelle.
- Gliozzi, E., Abbazzi, L., Argenti, P., Azzaroli, A., Caloi, L., Capasso Barbato, L., Di Stefano, G., Esu, D., Ficcarelli, G., Girotti, O., Kotsakis, T., Masini, F., Mazza, P., Mezzabotta, C., Palombo, M. R., Petronio, C., Rook, L., Sala, B., Sardella, R., Zanalda, E. & Torre, D. (1997). Biochronology of selected mammals, molluscs and ostracods from the Middle Pliocene to the Late Pleistocene in Italy. The state of the art. Rivista Italiana di Paleontologia e Stratigrafia 103, 369-388.
- Haller-Probst, M. & Schleich, H.-H. (1994). Vergleichende osteologische Untersuchungen an einigen Urodelen Eurasiens (Amphibia: Urodela, Salamandridae, Proteidae). Courier Forschungsinstitut Senckenberg 173, 23-77.
- Helfenberger, N. (2001). Phylogenetic relationships of Old World ratsnakes based on visceral organ topography, osteology, and allozyme variation. Russian Journal of Herpetology 8 (suppl.), 1-62.
- Hervet, S. (2000). Tortues du Quaternaire de France: critères de détermination, répartitions chronologique et géographique. *Mésogéé* 58, 3-47.
- Holman, J. A. (1991). Fossil history of the grass snake (*Natrix natrix*) with emphasis on the British fossil record. *British Herpetological Society Bulletin* 36, 8-11.
- Holman, J. A. (1998). Pleistocene amphibians and reptiles
 in Britain and Europe. Oxford Monogr. Geol.
 Geophys. No. 38. New York: Oxford Univ. Press.
- Issel, A. (1892). Liguria geologica e preistorica. Vol. II. Genova: Donath Editore.
- Ivanov, M. (1999a). Quaternary evolution of the grass snake (*Natrix natrix*): new evidence. *Acta Musei Moraviae*, *Scientiae Geologicae* 1999, 153-160.

- Ivanov, M. (1999b). The first European pit viper from the Miocene of Ukraine. *Acta Palaeontologica Polonica* 44, 327-334.
- Klembara, J. (1979). Neue Funde der Gattungen Ophisaurus und Anguis (Squamata, Reptilia) aus dem Untermiozän Westböhmens (CSSR). Vestnik üstøedniho üstavu geologického 54, 163-169.
- Klembara, J. (1981). Beitrag zur Kenntnis der Subfamilie Anguinae (Reptilia, Anguidae). Acta Universitatis Carolinae, Geologica 2, 121-168.
- Klembara, J. (1986). Neue Funde der Gattungen *Pseudopus* und *Anguis* (Reptilia, Anguinae) aus drei Pliopleistozänen Mitteleuropäischen Lokalitäten. *Geologicky Zbornik* 37, 91-106.
- Lanza, B., Caputo, V., Nascetti, G. & Bullini, L. (1995).

 Morphologic and genetic studies of the European
 plethodontid salamanders: taxonomic inferences
 (genus: Hydromantes). Monografie XVI. Torino:
 Museo Regionale di Scienze Naturali, Torino.
- Morelli, N. (1891a). Resti organici rinvenuti nella caverna delle Arene Candide presso Finalmarina. Atti della Società Ligustica di Scienze naturali e geografiche 2, 171-205.
- Morelli, N. (1891b). Di una stazione litica a Pietraligure. Atti della Società Ligustica di Scienze naturali e geografiche 2, 362-386.
- Nocchi, G. & Sala, B. (1997). The fossil rabbit from Valdemino Cave (Borgio Verezzi, Savona) in the context of Western Europe Oryctolagini of Quaternary. *Palaeovertebrata* 23, 167-187.
- Rykena, S. (1991). Hybridization experiments as tests for species boundaries in the genus *Lacerta* sensu strictu. *Mitteilungen aus dem Zoologischen Museum zu Berlin* 67, 55-68.
- Saint Girons, H. (1982). Influence des climats de type méditerranéen sur l'écophysiologie et la répartition des Reptiles. *Ecologia Mediterranea* 8, 254-252.
- Sala, B. (1992). I mammiferi del Quaternario italiano. In I segni del tempo. Memoria delle origini ed icone del primordiale, 209-227. Tugnoli C. (Ed). Trento: Atti del Corso di Aggiornamento per il Personale Docente.
- Salvidio, S., Sindaco, R., Emanueli, L. & Doria, G. (1996).
 Climat mediterraneen et repartition des reptiles dans le Nord-Ouest de l'Italie. In La Méditerranée: variabilités climatiques, environnement et biodiversité, 221-224. Montpellier: Colloque Scientifique International, 6-7 Avril 1995.
- Sanchiz, B. (1977). La familia Bufonidae (Amphibia, Anura) en el Terciario europeo. Trabajos Neógeno-Cuaternarios 8, 75-111.
- Sindaco, R. (1998). Biogeografia. In Erpetologia del Piemonte e della Valle d'Aosta. Atlante degli anfibi e dei rettili, 89-98. Andreone F. & Sindaco R. (Eds). Monografie XXVI. Torino: Museo Regionale di Scienze Naturali.
- Sorrentino, C. (1995). La fauna degli scavi 1972-77 alle "Arene Candide". *Padusa Quaderni* 1, 149-156.
- Sorrentino, C. (1999). Faune terrestri. In *Il Neolitico nella* Caverna delle Arene Candide (scavi 1972-1977), 66-

128

- 108. Tiné S. (Ed). Collezione di Monografie Preistoriche ed Archeologiche X. Bordighera: Istituto Internazionale Studi Liguri.
- Szyndlar, Z. (1984). Fossil snakes from Poland. Acta Zoologica Cracoviensia 28, 1-156.
- Szyndlar, Z. (1988). Two new extinct species of the genera *Malpolon* and *Vipera* (Reptilia, Serpentes) from the Pliocene of Layna (Spain). *Acta Zoologica Cracoviensia* 31, 687-706.
- Szyndlar, Z. (1991a). A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part
 I: Scolecophidia, Boidae, Colubrinae. Estudios Geólogicos 47, 103-126.
- Szyndlar, Z. (1991b). A review of Neogene and Quaternary snakes of Central and Eastern Europe. Part II: Natricinae, Elapidae, Viperidae. Estudios Geológicos 47, 237-266.
- Szyndlar, Z. & Rage, J.-C. (1999). Oldest fossil Vipers (Serpentes: Viperidae) from the Old World. *Kaupia* 8, 9-20.

- Tozzi, C. (1969). Segnalazione di una grotta con fauna fossile a Borgio (Savona). Atti della Società Toscana di Scienze Naturali, Memorie A 76, 195-208.
- Utiger, U., Helfenberger, N., Schätti, B., Schmidt, C., Ruf, M. & Ziswiler, V. (2002). Molecular systematics and phylogeny of Old World and New World ratsnakes, Elaphe auct., and related genera (Reptilia, Squamata, Colubridae). Russian Journal of Herpetology 9, 105-124.

Accepted: 27.5.03