

AN OVERVIEW OF THE LATE MIOCENE VERTEBRATES FROM THE FISSURE FILLINGS OF MONTICINO QUARRY (BRISIGHELLA, ITALY), WITH NEW DATA ON NON-MAMMALIAN TAXA

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To cite this article: Villa A., Carnevale G., Pavia M., Rook L., Sami M., Szyndlar Z. & Delfino M. (2021) - An overview of the late Miocene vertebrates from the fissure fillings of Monticino Quarry (Brisighella, Italy), with new data on non-mammalian taxa. *Riv. It. Paleontol. Strat.*, 127(2): 297-354.

Keywords: Fish; Amphibians; Reptiles; Birds; Messinian.

Abstract. The latest Messinian Monticino Quarry fissure fillings, near Brisighella in Italy, are well known for their diverse mammal fauna. Conversely, little is known about other vertebrates from this rich site. Beside presenting an overview of the mammals, here we describe fish, amphibian, reptile, and bird remains, identifying three, eight, at least 18, and five taxa, respectively. Some of these represent the oldest occurrences either worldwide (an erycine snake related to *Eryx jaculus*, *Malpolon*, and otidids birds) or locally (common toads in the Apennine Peninsula and eremiadine lacertids in Europe, the latter being also the only known occurrence of these lizards in Italy). Altogether, the vertebrate fauna from Monticino Quarry is indicative of a complex palaeoenvironment, which was warm and somehow dry. Water bodies were indeed present though, as well as a patchy set of habitats with loose or sandy soils, rocky outcrops, open biotopes, and (even though maybe to a lesser extent) wooded areas. Furthermore, estuarine or lagoonal conditions were likely present near the depositional site.

From a palaeobiogeographical point of view, the non-mammal vertebrate assemblage from Monticino Quarry shows considerable Afro-Asian affinities at least for some components. In the context of the Italian late Miocene continental vertebrate assemblages, that of Monticino is remarkably similar to those from the Piedmont Basin, especially if compared with the Tusco-Sardinian area, Apulian Platform, Calabrian Arc and Sicily. This is consistent with the palaeobiogeographic scenario defined by mammal assemblages, with northcentral Italy, Tuscany and Sardinia, Apulian Platform, and Calabria and Sicily representing separated bioprovinces.

INTRODUCTION

Costa et al. (1986) first reported the occurrence of a latest Miocene (Messinian) fossil vertebrate fauna from karst fillings affecting the Messin-

ian gypsum in a quarry near Brisighella in Emilia Romagna, Central Italy (the so called Monticino gypsum Quarry; Fig. 1). The strict local and regional geological constraints (Marabini & Vai 1989; Vai 1989) allowed a correlation of the vertebrate assemblage with the latest Messinian and with the European Land Mammal Age MN 13.

Received: June 16, 2020; accepted: March 12, 2021

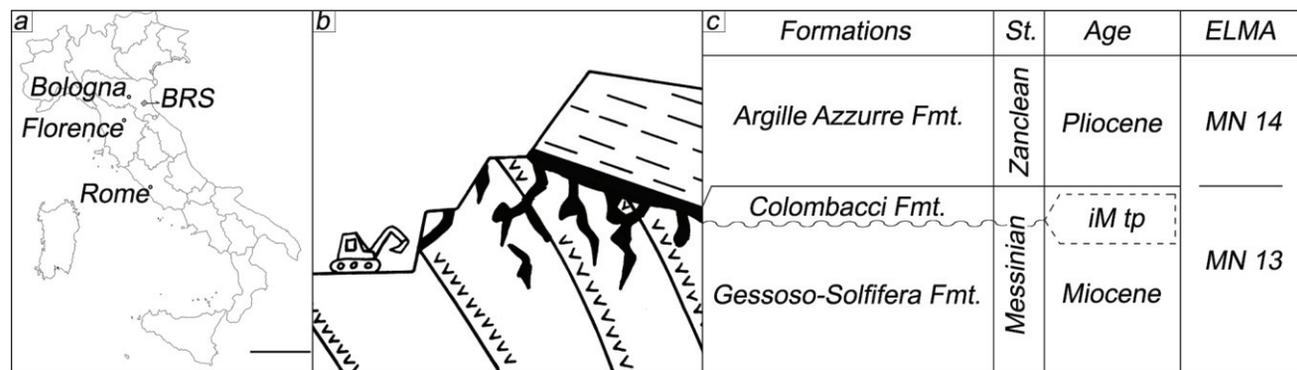


Fig. 1 - Location and geological context of the Monticino Quarry - a) Map of Italy, showing the position of Brisighella, where the Monticino Quarry is located. b) Schematic geological section of the Monticino gypsum quarry. c) Formal geological units and chronological setting of the sediments exposed in the quarry. Abbreviations: BRS, Brisighella; ELMA, European Land Mammal Ages; iM tp, intra-Messinian tectonic phase; St., stage. Scale bar in a = 200 km. Modified after Rook & Bernor (2013).

The study of the abundant vertebrate fauna from the fissure fillings exposed in the Monticino Quarry has been mostly focused on mammals (De Giuli 1989; Ferretti 2008; Kotsakis & Masini 1989; Masini & Thomas 1989; Torre 1989; Rook et al. 1991; Rook 1992; Masini & Rook 1993; Rook & Masini 1994; Gallai & Rook 2011; Rook & Bernor 2013; Pandolfi & Rook, 2017). No detailed information on the other vertebrates is available, except for a preliminary note on the amphibians and reptiles that was published by Kotsakis (1989). In this note, devoid of figures and descriptions and not reporting collections numbers, the following taxa were listed: *Rana* sp., *Trionyx* sp., Emydidae indet., (?) Testudinidae indet., Gekkonidae indet., *Lacerta* (s.l.) sp., *Anguis* sp., *Ophisaurus* cf. *pannonicus*, Varanidae indet., cf. *Eryx* sp., Colubrinae indet., and Natricinae indet.

Later on, Delfino (2002) included some of the amphibian and reptile remains from Monticino Quarry in his PhD thesis and based on these identifications, the amphibians and reptiles were mentioned and partly figured in a popular scientific paper (Rook & Delfino 2003) and two book chapters published in Italian (Rook & Delfino 2007; Rook et al. 2015).

The present contribution to the knowledge of the vertebrates from the karst fissures of Monticino Quarry is focused on the thorough description of the whole non-mammal vertebrate fauna but provides also an overview on the mammal taxa described so far. Therefore, besides focusing for the first time on fishes and birds, it deals with all the amphibian and reptile remains currently available in the collections of the Museo Civico di Scienze Na-

turali di Faenza and those of the Dipartimento di Scienze della Terra of the Università degli Studi di Firenze that were recently expanded thanks to the screen washing and selection of unprepared fossiliferous sediments collected in the 1980s.

GEOLOGICAL SETTING

The exposed succession within the Monticino gypsum Quarry consists of middle Messinian evaporitic (gypsum) succession (the so-called Gessoso-Solfifera Formation). Due to emersion and tectonization (tilting), the gypsum has been eroded and affected by karstic dissolution. The deposits that infill the fissures intersecting the gypsum and the depressions on the upper surface of the gypsum sequence consist of marly-clays, fine grained conglomerates and sand lenses belonging to the latest Messinian Colombacci Formation. They contain partially articulated and fragmented vertebrate fossils (mostly microvertebrate remains). Several fossiliferous collecting points have been identified along the Monticino gypsum Quarry outcrop. The succession is capped by up to 20 m of early Pliocene marine gray marly clays (Argille Azzurre Formation), the base of which falls in the *Sphaeroidinellopsis* Zone, and which overlie the Colombacci Formation. Dismissed in the early 1990s, the Monticino Quarry was then subject to environmental recovery and, because of its geological and palaeontological values, in 2006 it was converted into an open geological museum and included in the regional park “Parco regionale della Vena del Gesso” (Sami 2007). We refer the reader to Vai (1989) for a more complete discussion of the geological setting of the

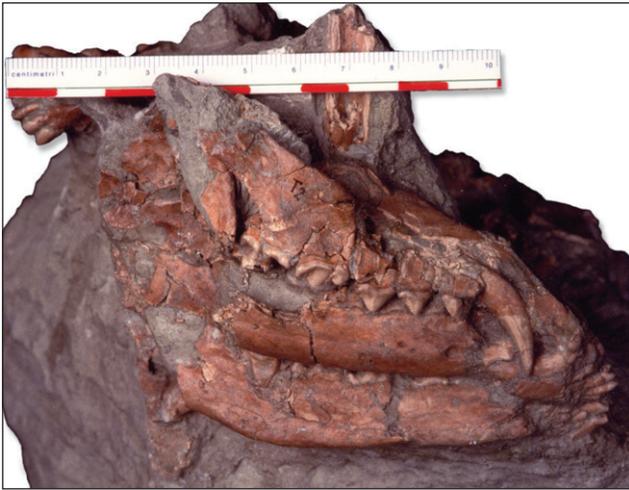


Fig. 2 - Partially articulated skull of *Plioverropros faventinus* from Monticino Quarry.

Romagna Apennine and to Marabini & Vai (1989) for further details on the geology of the Monticino gypsum Quarry.

TAPHONOMY

In the Monticino Quarry, most of the deposits yielding fossil vertebrate remains were found inside the cavities of a complex karst network developed on the evaporites (gypsum) of the Gesso-Solfifera Formation and filled with lithotypes of the overlying Colombacci Formation. Small vertebrate remains constitute the vast majority of the faunal assemblage, by far dominated by murids. In some cases, the fossiliferous sediments are extremely rich, due to a very high concentration of bones and teeth. This peculiarity (not unusual in the case of karst fissure fillings) could be at least in part attributed to the accumulation of pellets produced by birds of prey that used perches placed within the karst area. Such an interpretation (proposed by e.g., Rook et al. 2015) may be in agreement with the fact that no substantial differences were observed in the presence of both left and right molars and in the number of first and second molars; moreover, some bone findings showed a particular type of wear comparable to that produced by the gastric juices of the stomachs of some predatory birds (De Giuli et al. 1988). Fossil remains of medium-large sized vertebrates are mainly present as skeletal portions that have been transported and, in any case, in a much lower percentage in comparison to the microfauna.

The relative scarcity of large animals makes the Monticino faunal assemblage not fully representative of the mammal communities of the time. For example, among herbivores the proboscideans are represented by only two fragments, just as very few remains represent rhinos, equids, and large bovids. One of the factors responsible for this underrepresentation of large animals can be identified in the “size” of the tectonic-karst fissure network, characterized in almost all cases by small fissures/cracks. In some cases (especially in the largest fissures or in the doline-like morphologies on the top of the gypsum succession), the occurrence of skeletal portions in anatomical articulation (Fig. 2) suggests that some karst cavities may also have functioned as either natural “traps” or as dens in which the animals remained trapped. This hypothesis (again, proposed by e.g., Rook et al., 2015) is also confirmed by the unusual overabundance of carnivorous remains in the same cracks.

An alternative hypothesis to explain the taphonomy and the accumulation of the macrofaunal remains inside the fissures affecting the gypsum has been suggested by some authors (Costa et al. 1986), according to which the filling of the cracks/fissures studied would have occurred as consequence of the phenomenon known as “Neptunian dykes”: the deposits of the Colombacci Formation would have been injected downwards following the opening of cracks in the gypsum due to a tectonic phase that occurred after the deposition of fossil sediments at the base of the same unit.

MATERIAL & METHODS

As reported above, fossils of non-mammalian vertebrates from Monticino Quarry are stored either at the Dipartimento di Scienze della Terra, Università degli Studi di Firenze (Florence, Italy) or at the Museo Civico di Scienze Naturali di Faenza (Faenza, Italy). They were identified using data from the literature and by direct comparisons with prepared skeletons of extant taxa (Marco Pavia Ornithological Collection MPOC and Massimo Delfino Herpetological Collection MDHC, both housed in the Dipartimento di Scienze della Terra, Università degli Studi di Torino for birds and the herpetofauna respectively). Online resources from the digital repository MorphoSource (<https://www.morphosource.org/>) were also consulted for some taxa. Consulted specimens from MorphoSource are: *Alytes obstetricans* cas:sua:21691; *Pipa parva* uf:herp:37924; *Xenopus borealis* cas:herp:152778; *Xenopus clivii* uf:herp:92074; *Rhinophrynus dorsalis* cas:herp:71766; *Barbourula busuangensis* uf:herp:70546; *Bombina maxima* uf:herp:96648; and *Pelobates varaldii* cas:herp:92371. Pictures of selected specimens were taken with a Leica M205 microscope equipped with the Leica application suite v4.10 at the Università degli

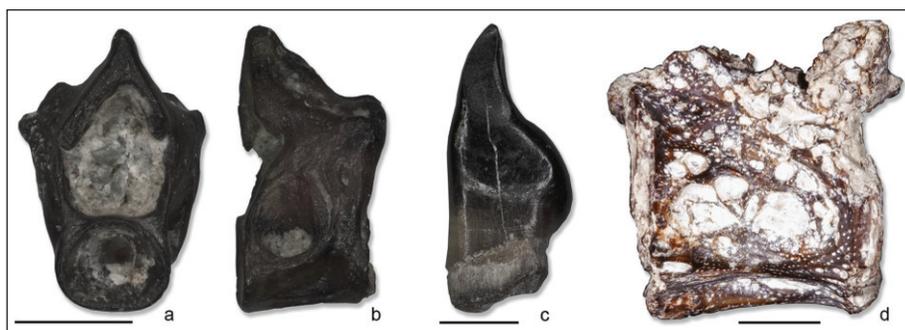


Fig. 3 - Fish from Monticino Quarry - *Aphanius crassicaudus*: abdominal vertebra (BRS2/F/1) in anterior (a) and right lateral (b) views. ?Cichlidae indet.: isolated tooth (BRS19/F/1) in lateral view (c). ?Sciaenidae indet.: abdominal vertebra (BRS19/F/2) in right lateral view (d). Scale bars = 0.5 mm (a, b); 1 mm (c); 5 mm (d).

Studi di Torino and with a Canon 5DII 100 mm and 50 mm macro lenses. Drawings were made with a camera lucida. The anatomical terminology follows Ratnikov & Litvinchuk (2007) for urodeles, Sanchez (1998) for anurans, Zangerl (1969) for turtles, Villa & Delfino (2019a) for lizards, Szyndlar (1984) for snakes, and Baumel & Witmer (1993) for birds. Snake taxonomy in this paper follows the recent work by Zaher et al. (2019). A complete list of the non-mammalian remains from Monticino presented in this study, separated according to the fissures in which they were recovered, is given in the Supplementary Information.

Acronyms

BRS: Brisighella collection hosted at the Dipartimento di Scienze della Terra of the Università di Firenze; the acronym of the locality is followed by the number of the fissure, then by a letter indicating the group (Av = Aves; H = herpetofauna, F = Fish) and a progressive number; MSF: Museo Civico di Scienze Naturali di Faenza (RA), Italy.

SYSTEMATIC PALAEOLOGY

Infraclass TELEOSTEI Müller, 1845

Family Cyprinodontidae Gill, 1865

Genus *Aphanius* Nardo, 1827

Aphanius crassicaudus (Agassiz, 1832)

Fig. 3a-b

Referred material: One abdominal vertebra (BRS2/F/1).

Description. The vertebral centrum is amphicoelous, thickened, cylindrical and nearly rectangular in lateral view. A well-developed rounded parapophysis is present along the lateral surface of the centrum (Fig. 3b). The neural arch and spine are hypertrophied. The neural spine is conical and obliquely oriented forming an angle of approximately 45° with the main axis of the vertebral centrum (Fig. 3b). There is a prominent neural prezygapophysis at the base of the neural spine.

Remarks. The overall morphology of the vertebra, and especially the structure and configuration of the neural arch and spine, are consistent

with those of the cyprinodontid *Aphanius crassicaudus* (see Gaudant, 1979), a species very common in the Messinian paralic and coastal biotopes throughout the Mediterranean (see Carnevale et al. 2006b, 2018, 2019; Reichenbacher & Kowalke 2009; Colombero et al. 2014).

Family ?Cichlidae Rafinesque, 1818

?Cichlidae indet.

Fig. 3c

Referred material: One isolated tooth (BRS19/F/1).

Description. The tooth is incisiform, slender and laterally compressed. The crown has a lingual bulbous structure and is supported by a well-developed pedicel with a nearly rounded cross section.

Remarks. The configuration of this incisiform tooth is in many ways consistent with that of several members of the family Cichlidae (e.g., Greenwood 1974; Trewavas 1983), to which it is tentatively referred. Tilapiine cichlids are known based on articulated skeletal remains in the Messinian deposits of the northern Apennines, including the euxinic layers of the basal evaporite cycles of the Gessoso-Solfifera Formation (Carnevale et al. 2003).

Family ?Sciaenidae Cuvier, 1829

?Sciaenidae indet.

Fig. 3d

Referred material: One partially complete abdominal vertebra (BRS19/F/2).

Description. The vertebra consists of an almost complete amphicoelous centrum bearing a partially preserved left neural prezygapophysis. The neural arches and spine are not preserved at all. In lateral view, the centrum appears massive, subrectangular in outline, longer than high. The anterior face

of the centrum is rather oval, whereas the posterior one is more rounded. The notochordal canal is small, characterized by a rounded profile. The maximum height of the anterior face of the centrum measures 23.7 mm, the maximum width is 24.1 mm, whereas the anteroposterior length measured along the ventral edge of the centrum is 28.8 mm. The dorsal prezygapophysis is stout and obliquely oriented, forming an angle of about 45° with the main axis of the centrum. The lateral surface of the centrum is extensively ornamented with delicate striae and ridges and deep pits of different size and shape (Fig. 3d). What appears to be a moderately large articular facet (or fossa) for rib articulation can be observed anteroventrally on the lateral side of the centrum. A deep groove is present along the ventral surface of the centrum.

Remarks. The overall morphology of the centrum, the absence of parapophyses, and the peculiar ornamentation are reminiscent of those of many “percoid” percomorphs, especially those of certain croakers (Sciaenidae), jacks (Carangidae), and groupers (Serranidae). The complete absence of parapophyses and the presence of what appears to be an articular facet for a rib concur to suggest that the abdominal vertebra described herein can be interpreted as an anterior trunk element, most likely the third element of the abdominal series. The lack of unambiguous distinctive features do not allow to provide an unquestionable taxonomic assignment for the vertebra described above. However, the abundance of croaker otoliths (e.g., *Leptosciaena caputoi*, *Trewasciaena kokeni*) in the deposits of the Colombacci Formation (Carnevale et al. 2006a; 2018; 2019; Bannikov et al. 2018) may support a tentative assignment to the family Sciaenidae.

Class AMPHIBIA Linnaeus, 1758

Order **Urodela** Duméril, 1806

Family Salamandridae Goldfuss, 1820

Genus *Lissotriton* Bell, 1839

***Lissotriton* sp.**

Fig. 4a-f

Referred material: One trunk vertebra (BRS25/H/243).

Description. The trunk vertebra is very small (centrum length is less than 1.5 mm) and rather poorly preserved. The opisthocoelous centrum has

a well-developed neck, which separates the main body from a flat and subvertical anterior condyle. Ventral crest are mostly broken away (Fig. 4f), but they were most likely well-developed in origin. Few subcentral foramina are preserved on the left side. The transverse processes are missing. The neural arch is also mostly missing, but the preserved anterior half appears moderately high and rather flat (most likely rising to some degree posteriorly). A neural spine was present, even though it is broken. The spine almost reaches the anterior margin. The margin is straight in dorsal view (Fig. 4a) and is located close to the anterior margin (roughly by the end of the anterior fourth) of the only prezygapophysis preserved, which is the left one. The latter is elliptical. The anterior zygapophyseal crests are moderately developed. In anterior view, the neural canal is subelliptical in cross section and slightly larger than the anterior condyle (Fig. 4b).

Remarks. The opisthocoelous trunk vertebra of a small salamandrid is present in the fossil material from Brisighella. The combination of subvertical condyle, moderately high neural arch, well-developed ventral crest, and anterior margin of the neural arch straight and located by the anterior fourth of the prezygapophyseal facets hints for the referral of this specimen to the genus *Lissotriton* (Ratnikov & Litvinchuk 2007). The very small size would suggest its belonging to a small representatives of the genus, such as the extant *Lissotriton vulgaris* and *Lissotriton helveticus* or the extinct *Lissotriton robrsi* (Herre 1955). However, the poor preservational status and the very short length of the vertebra even compared to the ranges reported for the above-mentioned small species hints for a more cautious identification limited to the genus level.

Urodela indet.

Fig. 4g-n

Referred material: One caudal vertebra (BRS2/H/6); one radius (BRS25/H/244); three ilia (BRS1bis/H/4; BRS25/H/67, 209).

Description

Caudal vertebra. The caudal vertebra (Fig. 4g-l) is small, with a centrum length of 2 mm. The centrum is opisthocoelous, with a well-developed neck anteriorly. The anterior surface of the condyle is eroded, but it appears flat and slightly inclined ventrally. The neural canal is subtriangular in ante-

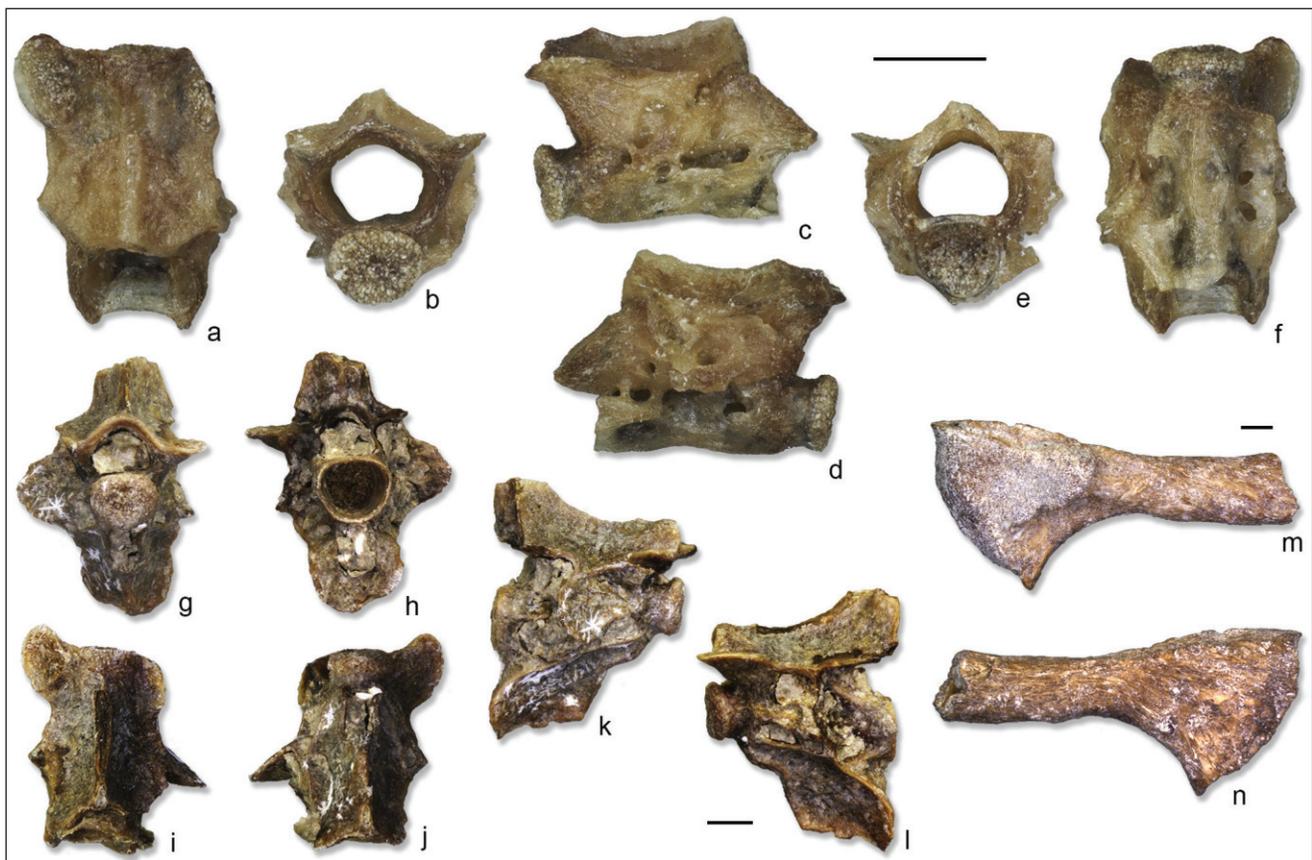


Fig. 4 - Urodeles from Monticino Quarry - *Lissotriton* sp.: trunk vertebra (BRS25/H/243) in dorsal (a), anterior (b), left lateral (c), right lateral (d), posterior (e) and ventral (f) views. Urodela indet.: caudal vertebra (BRS2/H/6) in anterior (g), posterior (h), dorsal (i), ventral (j), right lateral (k) and left lateral (l) views; right ilium (BRS25/H/67) in lateral (m) and medial (n) views. Scale bars = 0.5 mm.

rior view and about the same size of the condyle (Fig. 4g). The prezygapophyses are horizontal in anterior view. The postzygapophyses are missing. The neural arch has a straight anterior margin that is located slightly anteriorly to the midlength of the prezygapophyses (Fig. 4i). The neural spine is completely broken away, but its anterior end was located quite far from the anterior margin of the neural arch (roughly at the level of the posterior end of the prezygapophyses). In lateral view, the neural arch is quite low anteriorly, but it rises steeply posteriorly (Fig. 4k-l). A rather wide and moderately deep posterior notch is present (Fig. 4i). The neural spine contacts the notch. The zygapophyseal crests are rather well developed. The ventral crests, on the other hand, are less developed (Fig. 4j). The lateral processes of the vertebra are either missing (the left one; Fig. 4l) or poorly preserved (the right one; Fig. 4k). Ventrally, a well-developed hemal arch is present.

Radius. The radius is rather small and slender.

Ilia. The ilia (Fig. 4m-n) are medium-sized (ex-

cept for BRS1bis/H/4, which is small). They have an anterior rod-like portion and expands posteriorly. The acetabulum is rather wide (Fig. 4m), with a distinctly raised anterior margin.

Remarks. These remains clearly pertain to urodeles. The caudal vertebra is comparable with the one above referred to *Lissotriton* in terms of size, but few morphological differences are present. These are the slightly lower anterior portion of the neural arch and the slightly more posteriorly located anterior margin of the neural arch. It is not clear whether these differences might be interpreted as taxonomically significant or they are just individual and/or columnar variation. Because of this, the caudal vertebra is only referred to an indeterminate urodele here. There is no known diagnostic feature for the ilia and radia of urodeles, which are therefore identified only at order level here. They might pertain to the already recognised *Lissotriton* as well, but the presence of slightly larger specimens (e.g., some of the ilia) could also be evidence of the presence of other, larger urodeles in Monticino.

Order **Anura** Fischer, 1813
 Superfamily Discoglossoidea Günther, 1858
 Family Alytidae Fitzinger, 1843
 Subfamily Discoglossinae Günther, 1858
 Genus *Latonia* v. Meyer, 1843

?*Latonia* sp.

Fig. 5a

Referred material: Two urostyles (BRS1bis/H/3; BRS25/H/205).

Description. The urostyle BRS25/H/205 (Fig. 5a) is small. It has two anterior cotyles, which are clearly separated in the middle. Due to poor preservation, their exact shape in anterior view cannot be stated with confidence. The neural arch bears no crista dorsalis, but it has two transverse processes located near the anterior end. The processes are broken on both sides, but they clearly have a rather enlarged base and narrow distally. In spite of being more damaged than the left one, the right process clearly displays a long posterior laminar extension, which is less developed on the left side of the urostyle. The neural arch is dorsally closed only by its anterior end, being still open posteriorly. Just posterior to the closed part, the left margin of the aperture is broken, thus resulting in a moderately large space. More posteriorly, the aperture is represented by a narrow space. In anterior view, the neural canal is suboval. The other urostyle, BRS1bis/H/3 is less preserved, but it shares a comparable morphology. In this specimen, the cotyles retain their original shape, being subcircular but slightly mediolaterally elongated.

Remarks. Following the diagnostic key provided by Bailon (1999), the combination of bicotylylar sacrourostyle articulation, presence of transverse processes, and absence of a crista dorsalis identifies urostyles of *Alytes* and *Discoglossus*. The same morphology is also found in *Latonia* (Roček 1994; Biton et al. 2016), being therefore probably diagnostic for Alytidae as a whole. The dorsal fissure is found in both members of the subfamily Discoglossinae, *Discoglossus* and *Latonia* (Roček 1994; Biton et al. 2016), but not in *Alytes*. These urostyles are therefore evidence for the presence of a small discoglossine anuran in the herein-studied material. Biton et al. (2016) stated that *Discoglossus* lacks horizontal laminae related to the transverse processes, which are on the other hand present sometimes in

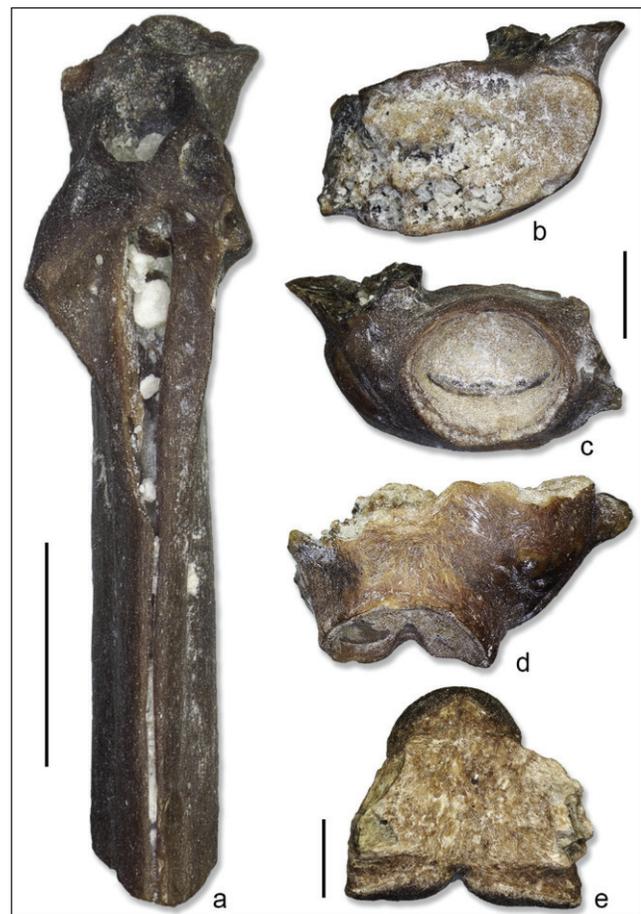


Fig. 5 - Discoglossoid anurans from Monticino Quarry - ?*Latonia* sp.: urostyle (BRS25/H/205) in dorsal view (a). ?Discoglossoidae indet.: atlas (BRS25/H/203) in anterior (b), posterior (c) and ventral (d) views; sacral vertebra (BRS25/H/207) in dorsal view (e). Scale bars = 1.5 mm.

Latonia. Moreover, these laminae can even be asymmetrically developed on the two sides in some cases (Hossini 1993; Rage & Hossini 2000). A certain affinity of these two specimens with *Latonia* can therefore be suggested, even though the absence of other, more taxonomically significant bones in the material hinders a completely confident attribution.

?Discoglossoidae indet.

Fig. 5b-e

Referred material: One atlas (BRS25/H/203); one sacral vertebra (BRS25/H/207).

Description

Atlas. BRS25/H/203 is a fragment of a rather large, opisthocelous atlas (Fig. 5b-d). Anteroposteriorly, the centrum is short (Fig. 5d). Only part of the left anterior cotyle is preserved (Fig. 5b) and it is not possible to observe whether it coalesced with the right one or not. The posterior cotyle is circular

(Fig. 5c). There is no sign of a notochordal canal. On the ventral surface of the atlas, there is no keel (Fig. 5d). The rest of the vertebra is missing.

Sacral vertebra. The sacral vertebra (Fig. 5e) is moderately large, preserving only the centrum. It has a subelliptical anterior condyle and two medio-laterally elongated posterior condyles.

Remarks. Among anurans reported as either fossils or living in Laurasia, opisthocoelous vertebrae are found in some members of the superfamilies Discoglossoidea and Pipoidea (Roček 2013). The only pipoid family that is known to have occurred in Europe, the extinct Palaeobatrachidae, had procoelous vertebrae, whereas opisthocoelous ones are found in the Afroamerican Pipidae and the American Rhinophrynidae. Vertebrae of pipids have a strongly dorsoventrally compressed centrum, which contrast with the uncompressed, posteriorly circular one of the herein-described atlas. *Rhinophrynus*, the only extant rhinophrynid, has hour-glass shaped vertebrae, which might be more comparable with the Monticino atlas. However, these vertebrae are notochordal (Walker 1938), unlike the latter. The morphology of the atlas from Monticino is more similar to at least some of the opisthocoelous discoglossoids. It clearly differs from Bombinatoridae because of the wider, shorter and less compressed centrum, which also does not display a flattened ventral surface. The large and circular centrum is more comparable with alytids, even though differences are evident also when BRS25/H/203 is compared with genera included within this group. It does not show horizontal and elongated anterior cotyles as in *Alytes* (Bailon 1999), whereas it differs from both *Discoglossus* and *Latonia* because of the absence of a ventral keel (Roček 1994; Bailon 1999). The identification of BRS25/H/203 appears therefore rather complicated. Affinities with discoglossoids seems more plausible than with pipoids, but all the above-mentioned differences hinder a confident referral to any of the group included in this superfamily. Even though alytids seem to be the most similar group in term of atlas morphology, we here refrain to push the identification that far and prefer to tentatively assign the atlas to an indeterminate discoglossoid taxon. The future recovery of other fossil material may help to better understand the nature of this large anuran. The sacral vertebra is here referred to the same taxon because of the similar size and the anterior condyle, indicating a probable

opisthocoelous nature of the vertebrae. Ranids also have sacral vertebrae with an anterior condyle, but they display subcircular posterior condyles.

Superfamily Hyloidea Stannius, 1856

Family Bufonidae Gray, 1825

Genus *Bufo* Laurenti, 1768

cf. *Bufo* gr. *bufo* (Linnaeus, 1758)

Fig. 6a-c

Referred material: One humerus (BRS25/H/214); one ilium (BRSNoNumber/H/12); two femurs (BRS25/H/208, 248).

Description

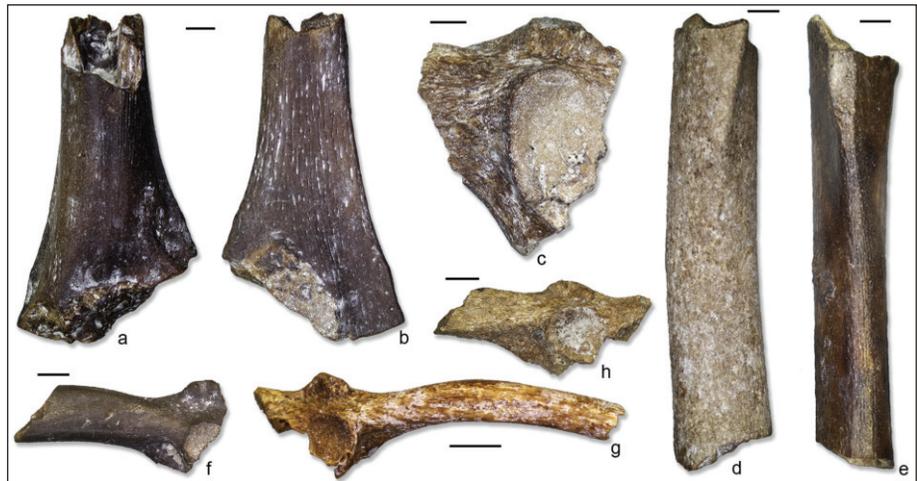
Humerus. BRS25/H/214 is a large and robust humerus (Fig. 6a-b). The proximal half of the shaft is missing, as well as most of the distal end of the bone. The eminentia capitata is not preserved, but judging from the position of the olecranon scar (Fig. 6b), it was shifted laterally compared to the main axis of the bone. The preserved part of the scar appears rather wide. The dorsal surface of the humerus is flat. Ventrally, a deep fossa cubitalis ventralis is present (Fig. 6a). The cristae medialis and lateralis are marked, but not strongly developed.

Ilium. This large and robust ilium (Fig. 6c) is poorly preserved. The preserved portion of the shaft shows no dorsal crest. The dorsal tubercle is dorsally rounded and shows some irregularities dorsally. There is no preacetabular fossa. The posterior half of the body of the bone is missing.

Femurs. The femurs are large and robust. They bear a well-developed crista femoris. In BRS25/H/208 (Fig. 6d), the crista is sharp and does not clearly split into a triangular structure proximally. However, the absence of the triangle could be due to the preservation of the bone, given that the most proximal part is missing and a certain degree of erosion of the bone surface is recognisable. This might be confirmed by BRS25/H/248 (Fig. 6e), which seems to display the starting of the split (represented by a clear thickening of the crista) by the proximalmost preserved portion of the bone.

Remarks. The presence of a large bufonid is testified by few bones, all displaying a comparable size. The dorsally rounded dorsal tubercle, the absence of a preacetabular fossa, and the apparent split of the crista femoris support a referral to the *Bufo bufo* species complex (Bailon 1999). However, the poor preservational status of these elements

Fig. 6 - Bufonids from Monticino Quarry - cf. *Bufo* gr. *bufo*: right humerus (BRS25/H/214) in ventral (a) and dorsal (b) views; left ilium (BRSNoNumber/H/12) in lateral view (c); right femur (BRS25/H/208) in medial view (d); left femur (BRS25/H/248) in medial view (e). *Bufo* gr. *viridis*: left ilium (BRS15/H/9) in medial view (f); right ilium (BRS25/H/174) in medial view (g); left ilium (BRS25/H/206) in medial view (h). Scale bars = 1 mm.



does not allow a completely confident assignment and so we treat this identification as tentative here.

Genus *Bufo* Rafinesque, 1814

Bufo gr. *viridis* (Laurenti, 1768)

Fig. 6f-h

Referred material: Two scapulae (BRS1bis/H/5; BRS3/H/5); nine ilia (BRS5tg2/H/43; BRS15/H/9; BRS19/H/30-31; BRS24/H/28; BRS25/H/174, 206; BRSNoNumber/H/24); seven femurs (BRS5tg2/H/41; BRS18/H/8; BRS19/H/29; BRS25/H/212, 216, 223).

Description

Scapula. BRS3/H/5 is a small and poorly preserved scapula that clearly display a small supraglenoidal fossa. There is no crista anterior along the anterior margin. Both ends of the bone are almost completely missing, but the fossa glenoidalis is clearly posteroventrally directed. BRS1bis/H/5 is also small, but better preserved. It is rather slender and display a ventrally directed fossa glenoidalis. It also has no crista anterior and is provided with a small supraglenoidal fossa. Both the pars acromialis and glenoidalis are rather robustly built, in proportion.

Ilia. These ilia (Fig. 6f-h) have a shaft with no dorsal crest and a deep preacetabular fossa. The dorsal tubercle is well developed and displays a small accessory lobe anteriorly (except maybe for BRS25/H/206, but its absence there could be a preservational artifact; Fig. 6h). The posterior portion of the body of the bone is usually missing, but in BRS25/H/174 (Fig. 6g) and BRS25/H/206 (Fig. 6h) it preserves a rather short dorsal acetabular expansion.

Femurs. Few small femurs have a sharp and well-developed crista femoris, which clearly does not split anteriorly. BRS25/H/212 is very small, whereas the others are distinctly larger (even though still not as large as the femur above referred to cf. *Bufo* gr. *bufo*).

Remarks. A second, smaller bufonid is also present. It displays features of the *Bufo viridis* species complex, such as the deep preacetabular fossa, the bilobed dorsal tubercle, and the not clearly undivided crista femoris (Bailon 1999). The supraglenoidal fossa is also present in *Epidalea calamita* (Bailon 1999), but the similar size and the absence of other remains clearly referable to the natterjack toad allows to favor an attribution of the scapulae to the green toads as well.

Bufonidae indet.

Referred material: Two trunk vertebrae (BRS5bis/H/27; BRS25/H/27); one sacral vertebra (BRS25/H/92); two urostyles (BRS18/H/9; BRS?/H/20); seven humeri (BRS4/H/28; BRS9/H/20; BRS25/H/179; BRS?/H/19).

Description

Trunk vertebra. BRS25/H/27 is a well-preserved trunk vertebra, whereas BRS5bis/H/27 is fragmentary and preserves only part of the vertebral centrum and part of the left half of the neural arch. The vertebrae are robustly built and small- (BRS25/H/27) or medium-sized (BRS5bis/H/27). The centrum is procoelous and well developed. The base of the transverse processes is located posteriorly to the prezygapophysis.

Sacral vertebra. The sacral vertebra is small. It has a wide and elliptical anterior cotyle and two subcircular posterior condyles, which appear slightly mediolaterally elongated. The vertebra misses both transverse

processes. Dorsally, it displays a well distinct carina neuralis on the dorsal surface of the neural arch.

Urostyles. The small urostyles have two well-distinct articular cotyles anteriorly, which appear mediolaterally elongate despite being partly damaged. Posteriorly, these bones have a moderately high crista dorsalis, which bears no transverse processes. The neural canal is subtriangular in anterior view.

Humeri. Few small humeri have a poorly ossified eminentia capitata, a deep fossa cubitalis ventralis, a wide and rather short olecranon scar and a rather flat dorsal surface. The cristae flanking the eminentia are not developed. The proximal half of the bone is always missing.

Remarks. These remains can be referred to indeterminate bufonids following the diagnostic key of Bailon (1999). A more precise identification cannot be provided, either because the bones represented do not bear significant diagnostic features or because the preservation is too poor. The small size of all these elements may suggest that they pertain to the smaller *Bufo* gr. *viridis*, but their belonging to juvenile individuals of the larger cf. *Bufo* gr. *bufo* should also be taken into account as a possibility.

Family Hylidae Rafinesque, 1815

Genus *Hyla* Laurenti, 1768

cf. *Hyla* sp.

Fig. 7a-b

Referred material: One ilium (BRS25/H/15).

Description. This very poorly preserved ilium bears only a small portion of the shaft, which clearly lacks a dorsal crest. The dorsal tubercle is present, but it is very poorly preserved. Anteroventrally to the acetabulum, the ilium is expanded and shows no preacetabular fossa. The medial surface of the preserved portion of the body of the ilium is rather flat.

Remarks. Despite the very poor preservation, this ilium still displays some features that are useful for its identification. Following Bailon's (1999) key, it shares affinities with *Hyla*, as highlighted by the following combination of features: absence of dorsal crest; presence of dorsal tubercle; anteroventral expansion of the body of the bone. Because of these, but also adopting a cautious approach due to the preservation, we here tentatively identify this fossil as cf. *Hyla* sp.

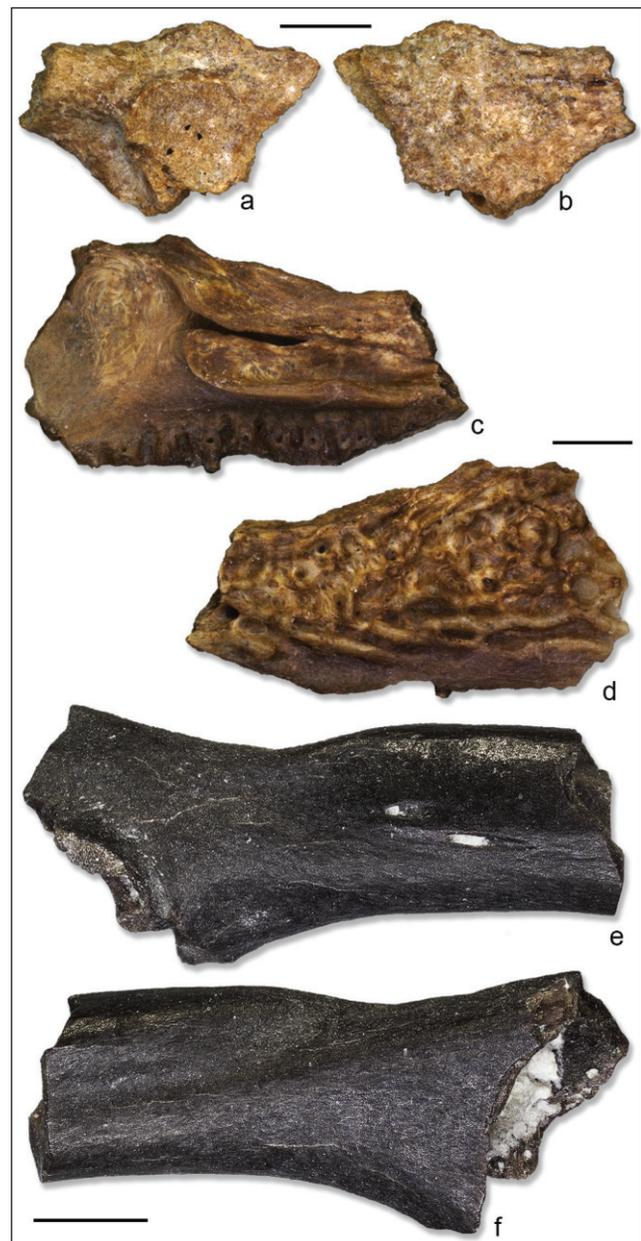


Fig. 7 - Hylids and pelobatids from Monticino Quarry - cf. *Hyla* sp.: left ilium (BRS25/H/15) in lateral (a) and medial (b) views. *Pelobates* sp.: left maxilla (BRS25/H/8) in medial (c) and lateral (d) views. ?*Pelobates* sp.: right ilium (BRS25/H/71) in lateral (e) and medial (f) views. Scale bars = 1 mm.

Superfamily Pelobatoidea Bonaparte, 1850

Family Pelobatidae Bonaparte, 1850

Genus *Pelobates* Wagler, 1830

Pelobates sp.

Fig. 7c-d

Referred material: Six maxillae (BRS5tg2/H/44; BRS25/H/8, 16, 141, 213; BRS?/H/7).

Description. All maxillae preserve only the posterior portion, except for BRS5tg2/H/44 and BRS25/H/141. In those preserving the posterior part, the lateral surface is almost completely covered by a dense dermal ornamentation (Fig. 7d), which is firmly attached to the bone (i.e., not connected to it by a trabecular layer as in species of *Latonia* with ornamented maxillae; Roček 1994; Syromyatnikova et al. 2019). This ornamentation is composed by tubercles and ridges. In BRS25/H/8, the best-preserved specimen, tubercles are mostly found in the middle of the surface, whereas ridges are mostly located towards the margins. In BRS25/H/16, on the other hand, the tubercles are connected by ridges also in the middle of the surface. From what can be observed on the preserved portion, the dorsal margin of the bone is strongly concave. Medially (Fig. 7c), a narrow lamina horizontalis is visible. There is no processus pterygoideus. The alveolar border, provided with at least 20 closely spaced tooth positions in BRS25/H/8, extends far beyond the posterior end of the lamina horizontalis. Dorsally to the lamina, a large, posteriorly-directed cavity is visible. The cavity of BRS25/H/8 is enclosed by two osseous laminae, which however do not contact, leaving a narrow slit visible in medial view (Fig. 7c). Anteriorly, this slit is still visible, even though the two laminae contact and fuse. BRS5tg2/H/44 and BRS25/H/141 preserve a more anterior portion of the bone (even if not the anterior end). These specimens also present dermal ornamentation on the lateral surface similar to the former ones, but this is less developed in BRS25/H/141. The lamina horizontalis is less narrow in medial view and is grooved dorsally. At least 21 and 18 tooth positions are preserved or partially preserved in BRS5tg2/H/44 and BRS25/H/141 respectively, some of them still hosting complete pleurodont and cylindrical teeth in the latter.

Remarks. The dermal ornamentation firmly attached to the lateral surface of these maxillae allows their attribution to a pelobatid (Bailon 1999; Roček 2013). An ornamentation composed by tubercles and ridges is found in *Pelobates*, contra the pit-and-ridge ornamentation that characterizes *Eopelobates* (Roček 2013; Syromyatnikova 2017, 2019). Some Oligo-Miocene species of *Pelobates* also have a pit-and-ridge ornamentation (Venczel 2004; Syromyatnikova 2017, 2019), thus excluding affinities between these forms and the taxon from Montici-

no. The tubercular (pustular) ornamentation is, on the other hand, typical of the Pliocene-Recent species (see Venczel 2004), even though its presence is already attested since at least the late Miocene (MN 11) of Northern Caucasus (Syromyatnikova 2017). The maxillae from Monticino differ from *Pelobates fuscus* in the strongly concave dorsal margin and in the dense ornamentation, appearing in this sense more closely comparable with *Pelobates cultripes* and *Pelobates syriacus* (Bailon 1999; Blain et al. 2016). Maxillae attributed to *Pelobates* aff. *praefuscus* from the late Miocene of Northern Caucasus (Syromyatnikova 2019) also have a strongly concave dorsal margin, but they display a less dense ornamentation. *Pelobates varaldii*, on the other hand, share with the Monticino specimens a dense ornamentation, but it seems to have a rather less concave dorsal margin. Taking all of this into consideration, these maxillae are here referred only as *Pelobates* sp., even though we can highlight their affinities with the youngest group of *Pelobates* species.

?*Pelobates* sp.

Fig. 7e-f

Referred material: Three ilia (BRS25/H/71, 105, 282).

Description. All ilia are poorly preserved. The main body is almost entirely missing. The shaft bear no dorsal crest and, judging from the preserved portion of the bone, the dorsal tubercle is also missing. Most of the shaft is missing and therefore it is not possible to state whether it was straight or more curved. There is no preacetabular fossa.

Remarks. The absence of both a dorsal crest and of a dorsal tubercle is diagnostic of *Pelodytes* and *Pelobates* according to Bailon (1999). Following the diagnostic key proposed by the same author, the discrimination between ilia of these two genera is based on structures that are not preserved in the specimen described above. However, we tentatively assign them to *Pelobates* with doubt given that no clear remains of *Pelodytes* are known from Monticino Quarry, whereas the former genus is testified also by other elements.

Superfamily Ranoidea Rafinesque, 1814

Family Ranidae Rafinesque, 1814

Genus *Pelophylax* Fitzinger, 1843

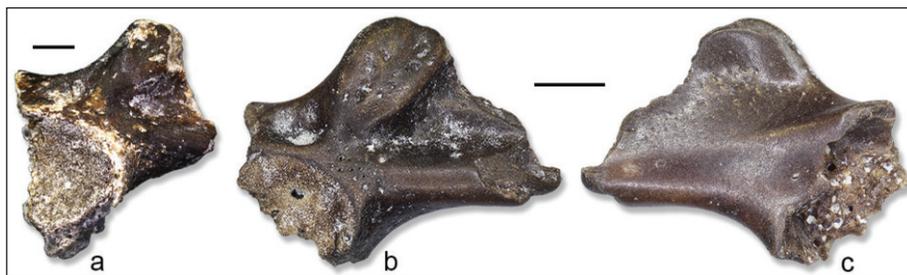


Fig. 8 - Ranids from Monticino Quarry - *Pelophylax* sp.: right ilium (BRS3/H/3) in lateral view (a); right ilium (BRS6/H/23) in lateral (b) and medial (c) views. Scale bars = 1 mm.

Pelophylax sp.

Fig. 8

Referred material: Three ilia (BRS3/H/3-4; BRS6/H/23).

Description. These three ilia preserve only part of the body of the bone and the base of the shaft. Their preservational status is, on the whole, rather poor. The dorsal crest was present in origin, even though now it is broken in all specimens. It started from an elongated and well distinct dorsal tubercle. In BRS3/H/3, which preserves a small dorsal acetabular expansion, an angle close to 90° between the latter and the tubercle is recognisable (Fig. 8a). A similar angle can be inferred for BRS6/H/23 (Fig. 8b-c), even though its dorsal expansion is less preserved.

Remarks. These three ilia can be referred to *Pelophylax* based on the following combination of characters (Bailon 1999): presence of a dorsal crest; well-distinct dorsal tubercle; angle between the tubercle and the dorsal acetabular expansion close to 90°. Blain et al. (2015) demonstrated that precise identification of *Pelophylax* species is impossible with a small number of ilia.

Anura indet.

Remarks. See the Supplementary Information for a complete list of remains of indeterminate anurans. Two specimens are particularly interesting and deserve further comments. BRSNoNumber/H/8 is a very large humerus preserving only the spherical eminentia capitata. It has a rather elongated olecranon scar. These features suggest that this bone does not pertain to a bufonid. It might belong to the large indeterminate possible discoglossoid recognised in the material, but this cannot be supported by any clear evidence at the moment. BRS25/H/181 is the procoelous centrum of a large vertebra, which is dorsoventrally compressed and slightly ventrally concave in lateral

view. This morphology may somehow recall that of a bufonid (a large taxon, such as cf. *Bufo* gr. *bufo*), but the poor preservational status does not allow to be more confident with this identification.

Class REPTILIA Laurenti, 1768

Order **Testudines** Batsch, 1788

Family Testudinidae Batsch, 1788

Genus *Testudo* Linnaeus, 1758

Testudo s.l.

Fig. 9a-k

Referred material: Two nuchals (MFS.551; BRS25/H/254); two neurals (BRS25/H/255); two undetermined peripherals (MFS.550,2; MFS.550,3); one left peripheral 7 sutured to the peripheral 8 (MFS.550,4); two bridge peripherals 3 or 7 (MFS.537; BRS?/H/26); one suprapygal (BRS?/H/25); two pygals (MFS.549; BRS?/H/27); one entoplastron (BRS?/H/24); one left hyoplastron (MSF.553,2); one right hypoplastron (MSF.553,1); one tibia (BRS25/H/274); 29 limb osteoderms (BRS25/H/3,13, 64, 98, 225, 256, 265, 272, 273; BRS28/H/5).

Description. Two large, partially preserved nuchals (MFS.551, Fig. 9a, and BRS25/H/254) share the presence of a relatively narrow cervical and a vertebral sulcus with an arched, deeply convex anterior profile. The convexity of the vertebral makes the cervical very short on the dorsal surface but it is long (nearly the double in BRS25/H/254) on the inner surface. There are no signs of pleural overlapping on the nuchal. The two neurals BRS25/H/255 are quadrangular and crossed by an intervertebral sulcus. The best preserved peripherals as MFS.550,2 (Fig. 9b) and MFS.550,3 show that the pleuro-marginal sulcus overlaps the costo-peripheral suture or is very close to it. The elliptic suprapygal BRS?/H/25 is markedly convex dorsally but only weakly ventrally. It hosts the vertebro-marginal sulcus very close to, but separated from, the suprapygal-pygal suture. The two pygals are both rather flat and trapezoidal in shape. BRS?/H/27 (Fig. 9c-d) is slightly wider than long and shows a sagittal intermarginal sulcus on its external surface

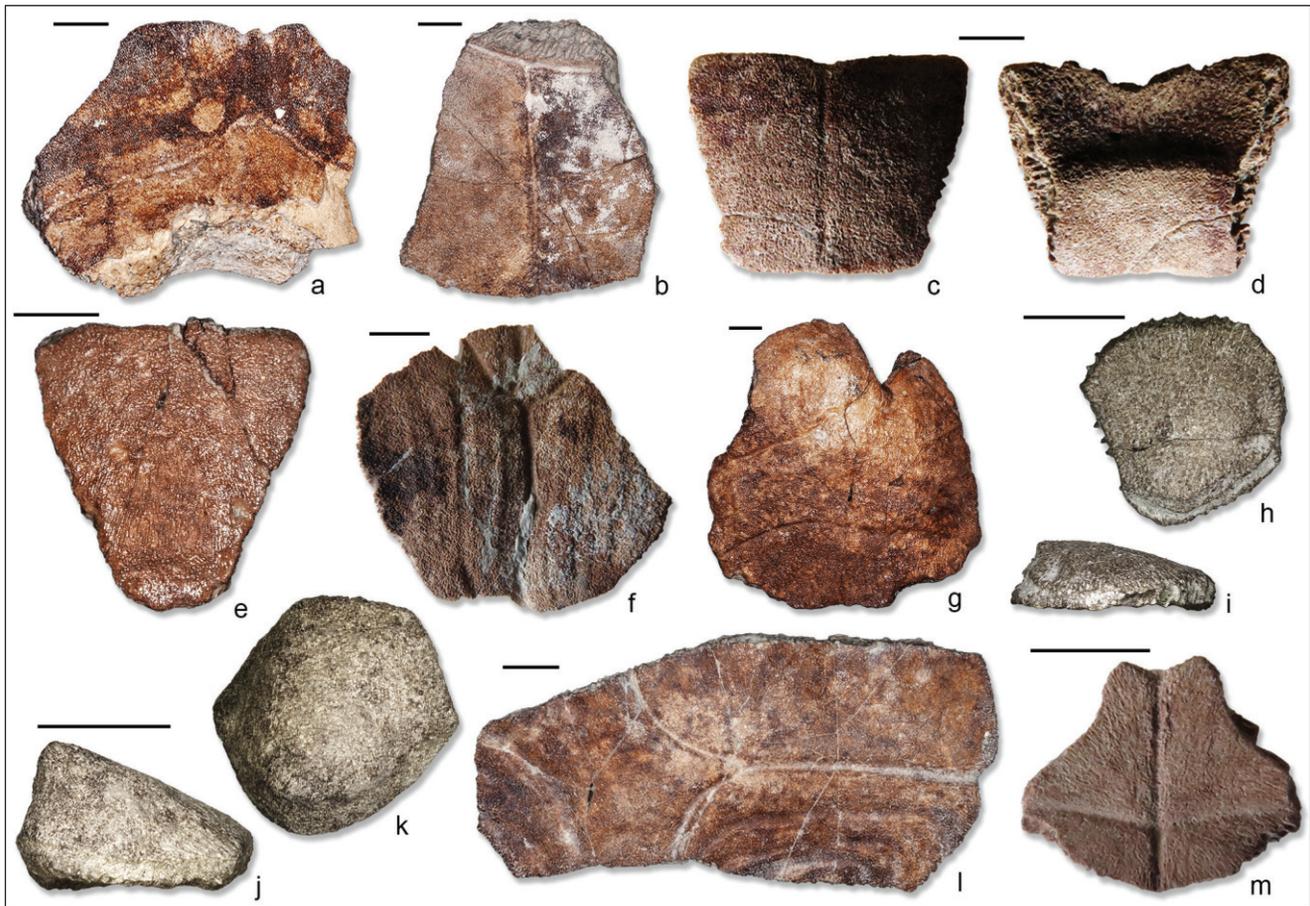


Fig. 9 - Chelonians from Monticino Quarry - *Testudo* s.l.: nuchal (MFS.551) in external view (a); peripheral (MFS.550,2) in external view (b); pygal (BRS?/H/27) in external (c) and internal (d) views; pygal (MFS.459) in external view (e); entoplastron (BRS?/H/24) in external view (f); left hyoplastron (MSF.553,2) in external view (g); flat osteoderm (BRS25/H/272) in external (h) and lateral (i) views; conical osteoderm (BRS25/H/273) in lateral (j) and external (k) views. *Mauremys* sp.: costal (MSF.70) in external view (l); entoplastron (BRS25/H/257) in external view (m). Scale bar = 5 mm.

only; its dorsal (anterior) edge is slightly concave, whereas the ventral (posterior) edge is straight. MFS.459 (Fig. 9e) is about as long as wide and has no sagittal (intermarginal) sulcus. The incomplete entoplastron BRS?/H/24 (Fig. 9f) is nearly circular in ventral view. It is modestly overlapped by the gulars anteriorly, but in the posterior area it does not host the humero-pectoral sulci. The ventral surface is slightly concave in the anterior area; the humeral surfaces show longitudinal growth marks. The visceral surface is totally altered. The left hyoplastron MSF.553,2 (Fig. 9g) is compatible with the entoplastron BRS?/H/24 because of the position of the humero-pectoral sulcus that is located posteriorly to the ento-hyoplastron suture. The partially preserved right hyoplastron MSF.553,1 hosts the markedly arched lateral end of the abdomino-femoral sulcus. Because of the incompleteness of this element, it is not possible to assess the presence of

an hypo-xiphial suture or a hinge. The several limb osteoderms have a general morphology that varies from nearly flat to distinctly conical. The flat ones (Fig. 9h-i) are generally smaller than the conical ones (Fig. 9j-k) that can be up to 10 mm long and 5 mm tall. Most of them show a sort of base, in some cases partly encircled by a sulcus parallel to the margin, and have a tip that can project outside the base or elevate on it. The position of tip is therefore eccentric in all cases. The elliptic base can be concave.

Remarks. The morphology of the shell elements described in this section is broadly congruent with that of a group of Miocene to Holocene tortoises from the western Palearctic traditionally referred to the genus *Testudo* (Lapparent et al. 2006a,b), but the phylogenetic relationships of which have been only partly explored and resolved. Since the extinct taxa do not constitute a monophy-

letic group along with the extant ones (among others, Corsini et al. 2014; Vlachos & Rabi 2018), the material herein described is generically referred to a *Testudo*-like taxon. Worth mentioning is that the late Miocene species from Tuscany (Italy) *Testudo amiatae* Pantanelli, 1893 has never been formally described, nor its phylogenetic relationships were evaluated in a modern context. The presence or absence of an intermarginal sulcus on the pygal is a character, among others, generally used to distinguish *Testudo hermanni* Gmelin, 1789 from *Testudo graeca* Linnaeus, 1758, but there is also a certain degree of intraspecific variation (Lapparent et al. 2006a,b) and therefore MFS.459 and BRS?/H/27 could perhaps belong to the same taxon (but the difference in terms of general shape should also be taken into consideration). The limb osteoderms have been tentatively referred to *Testudo* s.l. because of their overall resemblance with those of extant species of this genus.

Family Geoemydidae Theobald, 1868
Genus *Mauremys* Gray, 1869

***Mauremys* sp.**

Fig. 9l-m

Referred material: One neural (BRS25/H/258); one costal 6 (MSF.70); one entoplastron (BRS25/H/257).

Description. The incomplete, very small neural BRS25/H/258 is characterized by a sulcus crossing transversally its anterior portion and by a marked constriction posterior to it. The external surface of the constricted portion has a broad keel. The costal MSF.70 (Fig. 9l) is rather complete and curved (likely being a right sixth element). Its external surface hosts the Y-shaped sulci left by the vertebral shield and by the two pleurals. The lateral sides of the vertebral shield are markedly concave and therefore the lateral corner of the vertebral has an acute angle. The triple junction of the sulci is located approximately in the middle of the element. The small entoplastron BRS25/H/257 (Fig. 9m) is anteriorly incomplete. It is crossed by nearly straight humero-pectoral sulci in its posterior area (but far from the posterior edge of the entoplastron). Careful inspection with a microscope indicated that the anterior breakage followed the gulo-humeral sulci that therefore likely crossed the anterior most portion of the entoplastron.

Remarks. The most diagnostic element, the entoplastron BRS25/H/257 clearly indicates the presence of a second turtle taxon in the Monticino assemblage. The position of the sulci (the humero-pectoral sulci crossing the entoplastron in particular) is congruent with the morphology of *Mauremys* spp. (Hervet 2000; Chesi et al. 2009; Vlachos et al. 2019). The peculiar arrangement of the sulci on the costal MSF.70 is somewhat reminiscent of *Mauremys aristotelica* Vlachos et al., 2019 recently described for the late Miocene-Pliocene of Northern Greece (Vlachos et al. 2019) that is characterized by very broad vertebral shields. The broadness of the vertebral shield and the degree of concavity of the vertebral lateral edges in MSF.70 seems to be intermediate between the one of *M. aristotelica* and that of *Mauremys campani* (Ristori, 1891) (see Chesi et al. 2009) hindering a specific identification of the geoemydid from Monticino Quarry that is therefore simply assigned at genus level. The small neural BRS25/H/258 is tentatively referred to the same taxon on the basis of its broad dorsal keel.

Testudines indet.

Remarks. See the Supplementary Information for a list of the remains identified only as Testudines indet.

Order **Crocodylia** Gmelin, 1789
Crocodylia indet.

Fig. 10

Referred material: Two teeth (BRS3/H/2; BRS6/H/6).

Description. The two isolated, conical teeth BRS3/H/2 and BRS6/H/6 are both characterized by being represented by the crown only and by having a conical depression at their base. BRS6/H/6 (Fig. 10a) is slightly taller than BRS3/H/2 (10.5 and 8.5 mm respectively) and has a larger base (8.1 and 5.2 mm respectively). The major breakage shows several overlapping inner layers. The outer surface of BRS6/H/6 is significantly damaged and in the only preserved area it shows few shallow, longitudinal groves separating small ridges. Two evident mesiodistal carinae separate the lingual and the labial surfaces. BRS3/H/2 (Fig. 10b-c) is slender and more curved than the previous teeth. Its surface is also better preserved and shows more ridges and

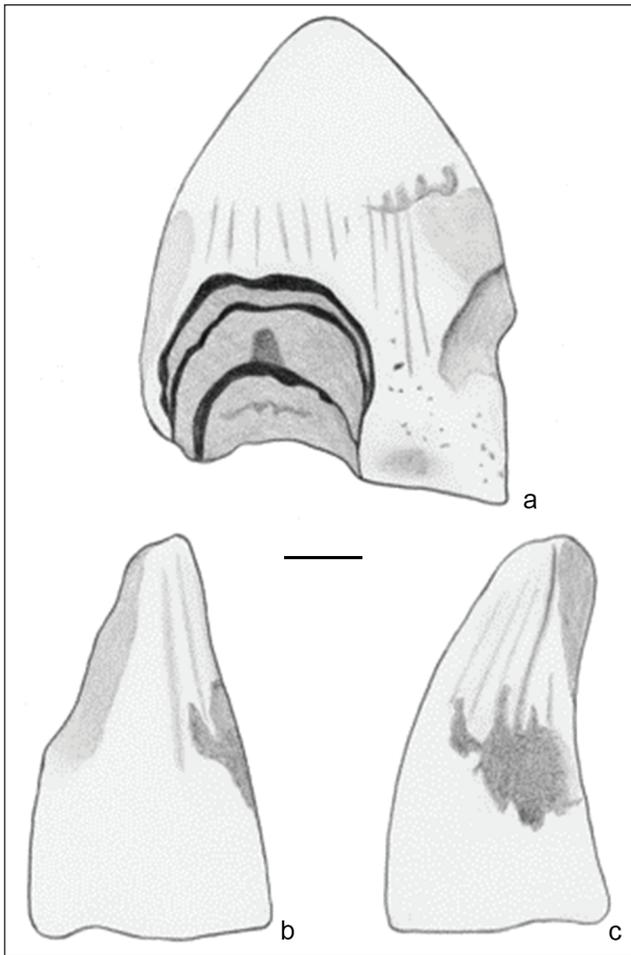


Fig. 10 - Crocodylians from Monticino Quarry - *Crocodylia* indet.: isolated tooth (BRS6/H/6) in labial view (a); isolated tooth (BRS3/H/2) in labial (b) and mesial (c) views. Scale bar = 2 mm.

grooves than that of the previous one. The lingual surface, slightly concave, hosts a larger number of ridges than the nearly smooth labial surface. Only one of the mesiodistal carine is preserved.

Remarks. The two isolated teeth BRS3/H/2 and BRS6/H/6 clearly show a reabsorbed root indicating that they were lost before the death of their owner. Since isolated crocodylian teeth are, with very few exceptions, not diagnostic even at family level, the remains from Monticino Quarry are simply referred at Order level despite they likely belong to *Crocodylus* Laurenti, 1768, the only crocodylian with similar teeth so far identified in the central Mediterranean sector during the late Miocene (Delfino et al. 2007; Delfino & Rook 2008; Delfino & Rossi 2013). Young long snouted crocodylians belonging to *Tomistoma* Müller, 1846 have teeth that are usually more slender than those from Monticino Quarry, whereas later in ontogeny at least some of the

teeth are significantly larger and more massive (for an overview on its presence in the Mediterranean area see Piras et al. 2007). During the late Miocene, crocodylians were rather common in the Mediterranean area of what is now Europe, but they are often represented by isolated teeth (among others, Georgalis et al. 2016b; Colombero et al. 2017; Zoboli et al. 2019) and therefore they were rarely identified at genus level.

Order **Squamata** Oppel, 1811

Family **Agamidae** Spix, 1825

Subfamily **Agaminae** Spix, 1825

Agaminae indet.

Fig. 11

Referred material: Two fragmentary maxillae (BRS25/H/4, 5); one dentary (MSF 67).

Description

Maxillae. The fragmentary maxillae are robust and very poorly preserved. Both specimens carry acrodont teeth, the number of which is two in BRS25/H/4 and five in BRS25/H/5 (Fig. 11a-b). The teeth are triangular and closely spaced. Despite the wearing, a very small cusp is visible in some of them, both anteriorly and posteriorly to the main tip. The tooth base is expanded towards the medial surface of the alveolar border, rather than being located on its edge (Fig. 11a). The size of the teeth increases towards one of the end of both bones, which is probably the posterior one. In lateral view, there are no interdental grooves (Fig. 11b).

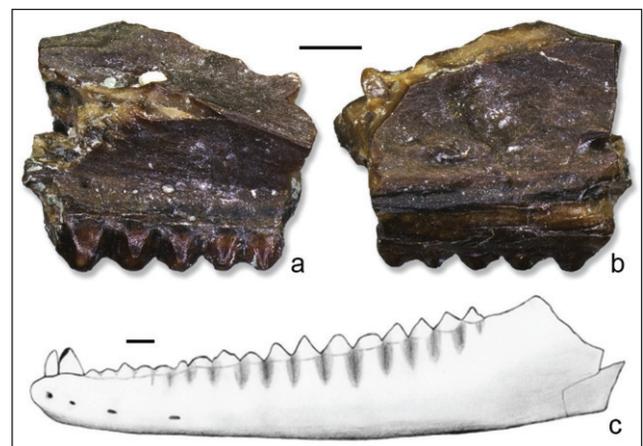


Fig. 11 - Agamids from Monticino Quarry - *Agaminae* indet.: left maxilla (BRS25/H/5) in medial (a) and lateral (b) views; left dentary (MSF 67) in lateral view (c). Scale bars = 1 mm.

Dentary. The dentary (Fig. 11c) is almost complete, but still plunged in a block of sediment. Only the smooth lateral surface is visible, showing four mental foramina. The tooth row is roughly 17 mm long and carries 19 teeth. The two anterior-most ones are subpleurodont, conical and pointed, whereas all other teeth are acrodont, closely spaced and subtriangular. Distinct interdental grooves are recognisable. The ventral margin of the bone is straight. The posterior end is broken off.

Remarks. In spite of the possible presence of variability in the main characters used to separate the two families (see Rage & Bailon 2011), fragmentary tooth-bearing bones of Agamidae are usually distinguished from those of Chamaeleonidae because of the closely spaced acrodont teeth extending onto the lingual side of the alveolar border (Evans et al. 2002; Delfino et al. 2008; Villa & Delfino 2019a). The presence of an agamid in the late Miocene of Monticino is further supported by the isolated dentary MSF 67, which carries both pleurodont and acrodont teeth (Delfino et al. 2008; Blain et al. 2014; Villa & Delfino 2019a). The number of subpleurodont teeth suggests that MSF 67 belongs to a member of the subfamily Agaminae (Maul et al. 2011).

Family Lacertidae Batsch, 1788
Subfamily Lacertinae Oppel, 1811
Tribe Eremiadini Shcherbak, 1975
Eremiadini indet.

Fig. 12a-f

Referred material: Eight pairs of fused frontals (BRS4/H/23; BRS5bis/H/11; BRS5tg2/H/2; BRS6/H/3; BRS24/H/22; BRS25/H/87; BRSNoNumber/H/14; BRS?/H/14).

Description. Each specimen represents a pair of fused frontals. The anterior end is always missing, whereas the posterior one is preserved partially in BRS4/H/23 (which misses the posterior margin and the posterolateral processes; Fig. 12a-c), BRS5bis/H/11 (Fig. 12d-f), and BRS6/H/3 (which both lack the right posterolateral process and the tip of the left one). In ventral view, no suture line is visible in the middle (Fig. 12b, f). Two low and moderately robust cristae cranii run along the lateral margins. The cristae are more sharpened and slightly more developed in the anterior portion of BRS5bis/H/11, BRS5tg2/H/2, BRS6/H/3, BRS24/H/22, and BRS?/H/14, which preserve a

larger part of the anterior half of the bone. In spite of the anterior portion being always absent, a middle constriction seems to be recognizable in dorsal view. The dorsal surface is covered by a dermal ornamentation made up of a crust covered by small pits and low ridges (Fig. 12a, e). Three grooves are visible on it, separating the frontal shield from the frontoparietal ones and the latter from one another. In BRS6/H/3, however, a small and triangular area (the vertex is directed posteriorly) is visible in the middle of the posterior end of the bone, between the frontoparietal shields. Moreover, the ornamentation is slightly less developed in this same specimen. The ornamentation is more developed on the frontoparietal shields, whereas it is poorly defined on the frontal one. The grooves separating frontal and frontoparietal shields are located posteriorly to the middle constriction. By the posterior margins of the preserved portion of the specimens, the anterior end of the articulation surfaces with the postfrontals are visible (Fig. 12c-d). A portion of those with the prefrontals is visible by the anterior end of the preserved portion of BRS5bis/H/11 (Fig. 12d), BRS6/H/3, BRS24/H/22, and BRS?/H/14. The two articulation surfaces are far from each other. The length of the specimens is 2 mm in BRS5tg2/H/2 (which, however, is only a very small fragment), 3 mm in BRS24/H/22, 4 mm in BRS6/H/3 and BRS?/H/14, 5.3 mm in BRSNoNumber/H/14, 5.5 mm in BRS4/H/23, and reaches 6 mm in BRS5bis/H/11. BRS25/H/87 is represented only by a fragment of the anterior portion, but its morphology and its size are similar to those of the other specimens.

Remarks. Among lacertids, fused frontals lacking a longitudinal suture line in ventral view (meaning that they fused in an early stage of the ontogeny) are found only in some members of the tribe Eremiadini (Arnold 1989; Arnold et al. 2007; Villa & Delfino 2019a). Following Arnold (1989) and Hipsley & Müller (2017), fused frontals with a strong middle constriction are related to adaptation to arid environments in lacertids. The poor preservation of the specimens from Monticino, the absence of other taxonomically significant elements clearly referable to this tribe of lacertids and the fact that no other Eremiadini-like frontals to which the herein considered remains could be compared are known from Miocene localities in Europe prevent a more precise identification.

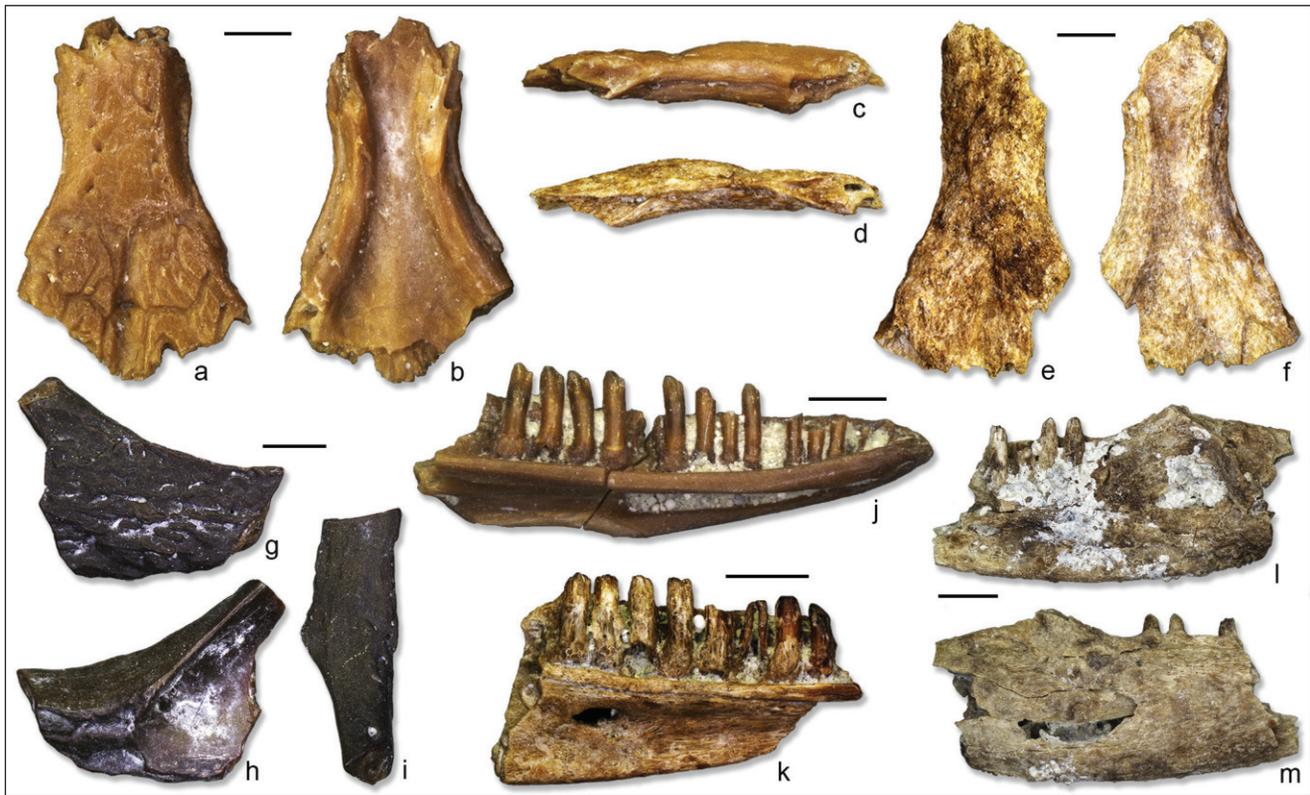


Fig. 12 - Lacertids from Monticino Quarry - Eremiadini indet.: fused frontals (BRS4/H/23) in dorsal (a), ventral (b) and right lateral (c) views; fused frontals (BRS5bis/H/11) in left lateral (d), dorsal (e) and ventral (f) views. Lacertidae indet.: right jugal (BRS25/H/187) in lateral (g), medial (h) and dorsal (i) views; left dentary (BRS4/H/21) in medial view (j); left dentary articulated with the splenial (BRS25/H/148) in medial view (k); right lower jaw (BRS25/H/251) in medial (l) and lateral (m) views. Scale bars = 1 mm.

Lacertidae indet.

Fig. 12g-m

Referred material: Four fragmentary maxillae (BRS4?/H/5; BrS24/H/17; BRS28/H/17); one jugal (BRS25/H/187); two dentaries (BRS4/H/21; BRS?/H/13); 22 fragmentary dentaries (BRS4/H/20; BRS5tg2/H/16; BRS8/H/1; BRS18/H/6; BRS19/H/11; BRS24/H/18, 21, 35; BRS25/H/184; BRS27/H/12; BRS28/H/18); four fragmentary dentaries articulated with the splenial (BRS5tg2/H/18; BRS25/H/11, 12, 148); 71 fragments of tooth-bearing bones (BRS4/H/19; BRS4?/H/6; BRS5bis/H/10; BRS5tg2/H/17; BRS8/H/2; BRS15/H/6; BRS16/H/4; BRS18/H/5; BRS19/H/10, 12; BRS24/H/19; BRS25/H/10, 47, 84, 147, 183; BRS27/H/13); two teeth (BRS5tg2/H/1; BRS25/H/48); one fragmentary lower jaw (BRS25/H/251).

Description. All specimens are very fragmentary, poorly preserved and small- or medium-sized.

Jugal. The medium-sized jugal, BRS25/H/187 (Fig. 12g-i), preserves only the middle portion, where the anterior and the posterodorsal processes meet. Both processes seem to be moderately robust and the base of a well-developed quadratojugal process is present, though its tip is missing. The palatal process is also well developed and seems to origi-

nate a very short medial process (Fig. 12i). A large foramen opens on the posteromedial surface of the bone, ventral to this latter process. The lateral surface is completely covered by a light but distinct vermicular ornamentation (Fig. 12g).

Tooth-bearing bones. The tooth-bearing bones bear cylindrical, slender and pleurodont teeth, among which the best preserved ones show a mono-, bi- or tricuspid crown. The best preserved specimens, BRS4/H/21 (Fig. 12j) and BRS?/H/13, are dentaries, with preserved portions reaching about 6.5 mm in length and carrying 18 and 17 tooth positions respectively; the posterior portion, however, is missing in both of them. The lateral surface of both maxillae and dentaries is smooth and the one of BRS28/H/17, a maxilla, is also distinctly concave. Moreover, on the dorsal surface of the palatal shelf of the maxillae, there is a wide and posteriorly directed superior dental foramen, continuing posteriorly in a wide groove. When preserved, the mandibular symphysis of the dentaries is narrow and subhorizontal, whereas the Meckelian fossa is wide and medially opened. In BRS24/H/21

and BRS[?]/H/13, a convex ventral margin is also recognizable. In BRS5tg2/H/18, BRS25/H/11, BRS25/H/12, and BRS25/H/148, the fragment of dentary is still articulated with a fragment of the splenial. Though poorly preserved, the splenial is wide and narrows towards the anterior end. In BRS25/H/148 (Fig. 12k), a large anterior inferior foramen (dorsally) and a very small anterior mylohyoid foramen (ventrally) are visible in the middle of the bone in medial view.

Lower jaw. BRS25/H/251 preserves only part of the middle portion of the articulated right lower jaw (Fig. 12l-m). Its preservational status is very poor and it is partially covered by matrix. The total length of the specimen is 6.5 mm. Anteriorly, the posterior portion of the dentary is preserved. It has a wide and medially opened (but covered by the splenial) Meckelian fossa and bears four pleurodont, cylindrical and closely-spaced teeth. The tooth crowns are eroded, but a bicuspid condition is recognisable in the two posteriormost teeth. The lateral surface of the dentary is smooth and its ventral margin appears convex. The posterior processes are not recognisable. The splenial has a strongly concave medial surface, the concavity of which is maybe enhanced as a taphonomic artifact. On the anterior preserved part of this bone, a large anterior inferior foramen is present, flanked ventrally by the small anterior mylohyoid foramen. The posterior half of the specimen is composed by the anterior end of both the compound bone and the free angular, but the preservational status hinders recognition of main morphological features of these bones. Dorsally, part of the coronoid is visible. It has a moderately short and pointed labial process. Medially, the anteromedial process is largely covered by dentary and splenial, whereas the posteromedial process displays a well-developed coronoid ridge. The coronoid process is not preserved.

Remarks. The tooth morphology of the above-described tooth-bearing bones, as well as the convex ventral margin of BRS24/H/21, BRS25/H/251, and BRS[?]/H/13, are clear evidence of them being attributable to the family Lacertidae (Delfino et al. 2011; Villa & Delfino 2019a). The jugal, on the other hand, can be assigned to lacertids because of the vermicular ornamentation and the overall morphology not as slender as in scincids and anguids (Villa & Delfino 2019a). It is not clear whether these specimens belong to the previously

recognised indeterminate member of the tribe Eremiadini or they represent a second lacertid taxon. Nevertheless, it has to be noted that in all extant European Eremiadini the palatal process of the jugal is poorly developed (Villa & Delfino 2019a), in contrast with the condition seen in BRS25/H/187.

Scincidae Gray, 1825

Scincidae indet.

Fig. 13a

Referred material: One fragmentary dentary (BRS25/H/142).

Description. This specimen is a poorly preserved fragment of a small dentary, carrying pleurodont, cylindrical and slender teeth. Only two teeth are preserved, but they are in good preservational conditions. The crowns are bicuspid, with parallel lingual and labial cusps, and appear pointed in medial view. The tip curves slightly in posteromedial direction and light striae are visible only on the lingual surface of the tooth crowns.

Remarks. BRS25/H/142 is referred to Scincidae because of the pleurodont, bicuspid teeth provided with parallel labial and lingual cusps, a slightly bending crown and striae on the lingual surface (Townsend et al. 1999; Caputo 2004; Villa & Delfino 2019a), but the very poor preservational status prevent a more precise attribution.

?Scincidae indet.

Fig. 13b-c

Referred material: One fragment of tooth-bearing bone (BRS27/H/15).

Description. BRS27/H/15 is a small fragment of tooth-bearing bone carrying four pleurodont, cylindrical and slender teeth. Teeth are well preserved and show a bicuspid crown, with parallel lingual and labial cusps. The cusps are only slightly distinguishable, but this could be due to erosion. The tip of the crown is strongly curved in posteromedial direction and distinct striae are clearly visible on both the labial and lingual surfaces.

Remarks. The tooth morphology of BRS27/H/15 recalls the one of scincids (see above), but the strongly curved crown and the striae on the labial surface distinguish this specimen from the one attributed above to this latter family,

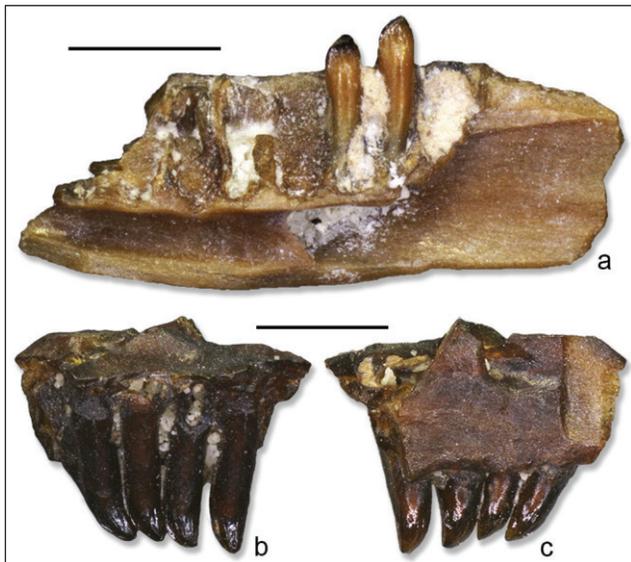


Fig. 13 - Scincids from Monticino Quarry - Scincidae indet.: right dentary (BRS25/H/142) in medial view. ?Scincidae indet.: fragment of tooth bearing bone (BRS27/H/15) in medial (b) and lateral (c) views. Scale bars = 1 mm.

BRS25/H/142. According to Kosma (2004), the parallel cusps and the distinct lingual striation are also present in the dentition of Cordylidae, but teeth of this family are usually more robust and lack striae on the labial surface. BRS27/H/15 is here tentatively attributed to an indeterminate scincid (maybe different from BRS25/H/142), but the possibility that it belongs to a different taxon cannot be totally ruled out.

Family Anguillidae Gray, 1825
Subfamily Anguinae Gray, 1825
Genus *Ophisaurus* Daudin, 1803

Ophisaurus sp.

Fig. 14

Referred material: One frontal (BRS25/H/160); one parietal (BRS25/H/119); one fragmentary parietal (BRS25/H/121); one fragmentary maxilla (BRS5tg2/H/7); two dentaries (BRS25/H/7, 135); seven fragments of tooth-bearing bone (BRS4/H/22; BRS4?/H/4; BRS5tg2/H/6; BRS25/H/6, 137; BRS27/H/14); 12 teeth (BRS5tg2/H/4; BRS24/H/10; BRS25/H/136, 271); two trunk vertebrae (BRS5bis/H/35; BRS28/H/15).

Description

Frontal. BRS25/H/160 (Fig. 14a-c) is a medium-sized and well-preserved frontal (length = 9 mm), missing only the tip of the medial process and the anterior part of the crista cranii. In dorsal view (Fig. 14b), the anterior end is roughly half as wide

as the posterior one and there is no lateral process. The articular surface with the nasal is clearly distinguishable by the anterior end. Moreover, the frontal is not constricted in the middle and its lateral margin is straight. The posterolateral process is short, moderately wide and roughly pointed. The posterior margin is straight, but slightly irregular. In lateral view, both the articulation surfaces with the prefrontal and the postfrontal are visible (Fig. 14a). The former is very wide and surpasses the middle of the length of the bone, whereas the latter is smaller and covers only the posterior fifth of the lateral margin. The two surfaces are distinctly separated from one another. A wide crista cranii is visible on the ventral surface: it is low in its posterior half, but becomes more ventrally developed anteriorly. The ventral portion of its anterior half, however, is missing. A well-developed dermal ornamentation is present on the dorsal surface, but the orbital margin remains smooth (Fig. 14b). The frontal shield covers almost entirely the bone, but the small areas covered by the frontoparietal (laterally) and the interfrontal (medially) shields are visible by its posterior end. The ornamentation is less developed on these latter shields and the grooves separating them from the frontal one are recognisable.

Parietal. BRS25/H/119 is a fragmentary parietal (Fig. 14d-e), preserving only the right part of the shelf. A short, rounded and slightly laterally developed anterolateral process is present by the anterolateral corner. There are no distinct interdigitations on the anterior margin. The dorsal surface is covered by a strong dermal ornamentation (Fig. 14d), which does not reach the lateral margin. The ornamentation is made up of very low ridges and pits. A smooth area levis is also present posteriorly. The right lateral, interparietal, and occipital shields are recognizable, whereas the right frontoparietal one is absent since the lateral one reaches the anterior margin. The occipital shield is small, whereas the interparietal one is very large. Anteriorly, the latter occupies a wide portion of the anterior margin, without reaching the anterolateral corner though. The lateral margin of the lateral shield is straight. The parietal foramen is large and circular and it is located anteriorly to the middle of the shelf. The ventral surface is smooth (Fig. 14e), except for a robust and well-developed anterolateral ventral crest running along the lateral margin. There is no facies muscularis (sensu Klembara et al. 2010) laterally to

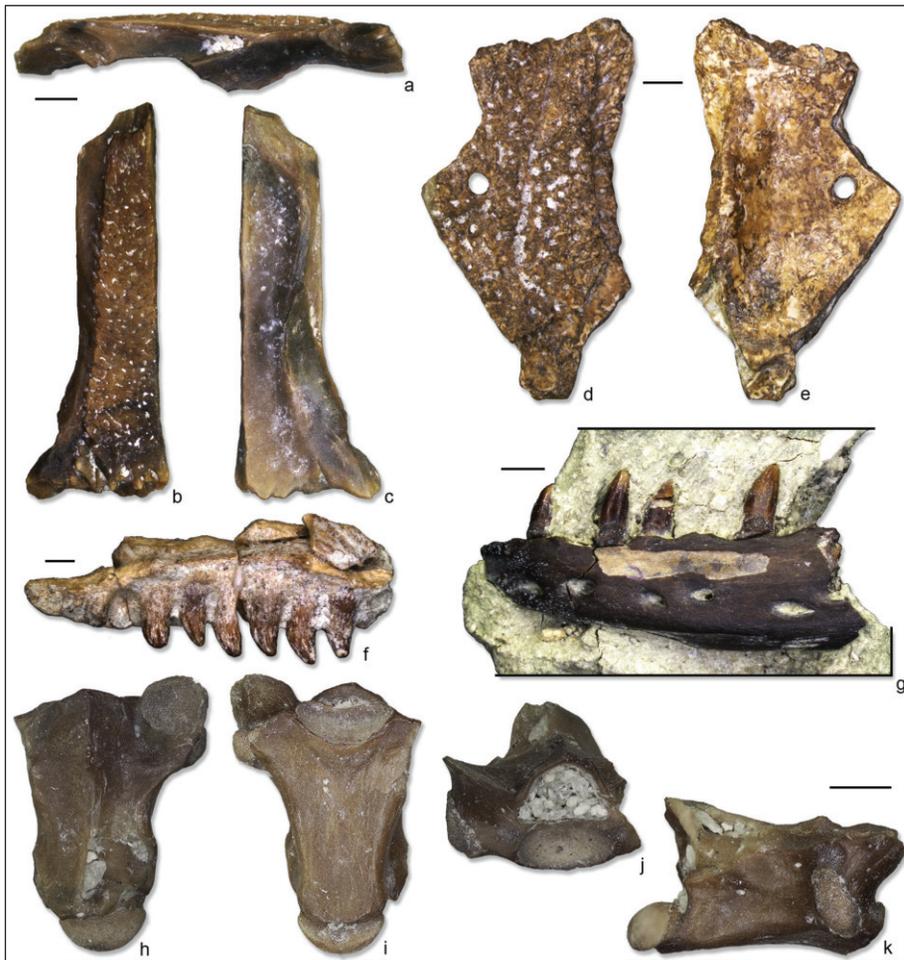


Fig. 14 - *Ophisaurus* from Monticino Quarry - *Ophisaurus* sp.: left frontal (BRS25/H/160) in lateral (a), dorsal (b) and ventral (c) views; parietal (BRS25/H/119) in dorsal (d) and ventral (e) views; right maxilla (BRS5tg2/H/7) in medial view (f); left dentary (BRS25/H/135) in lateral view (g); trunk vertebra (BRS28/H/15) in dorsal (h), ventral (i), anterior (j) and right lateral (k) views. Scale bars = 1 mm.

the crest. The specimen is large-sized, being 9.5 mm in length. BRS25/H/121 is a fragment of a robust and large-sized parietal, representing only the left anterolateral corner of the shelf. A poorly developed anterolateral process is recognizable and very little developed interdigitations are present along the anterior margin. The ventral surface shows the anterior end of the left anterolateral ventral crest, whereas the dorsal one bears a strong dermal ornamentation. A portion of the interparietal and of the left lateral shields are recognisable, since they are separated by a distinct groove. The latter shield reaches the anterior margin and so the left frontoparietal shield is not visible.

Maxilla. BRS5tg2/H/7 is a very fragmentary maxilla (Fig. 14f), preserving only part of the tooth row. The posterior process is completely missing, whereas only the anterolateral portion of the anterior premaxillary one is preserved. The anterolateral process is long, pointed in dorsal view and rather rounded in lateral view. The lateral surface is smooth and the ventrolateral foramina are not recognizable because of the poor preservation-

al status. The specimen is moderately robust and 12.5 mm in length. It carries at least 10 tooth positions. The teeth are large, subpleurodont, closely spaced and canine-like, provided with a slightly posteromedially bending tip. No distinct striae are visible neither on the lingual, nor on the labial surface of the teeth. Two distinct cutting edges run along both the anterior and posterior margins of the crown, with the anterior one being strongly more developed than the posterior one.

Dentaries. BRS25/H/135 preserves only the anterior half of a left dentary, still plunged in the sediment (Fig. 14g). Only the external surface of the bone and the dorsal portions of four teeth are visible. Five labial foramina are visible on the lateral surface and a sixth one is cut by the posterior breakage. The teeth are conical, slender and slightly posteromedially bending by their pointed tip. There are no striae on their exposed surface. The second dentary, BRS25/H/7, includes the posterior half, even if the angular process and the ventral margin are missing. Teeth are morphologically similar to those of BRS5tg2/H/7 and a total

of eight tooth positions is present. A small and pointed splenial spine is present by the fifth tooth position from the end of the tooth row. The opening of the alveolar canal is visible, in ventral view, under the third posteriormost tooth position. Because of the absence of the ventral half of the posterior end, it is not possible to see whether a free posterior projection of the intramandibular septum was present or not. The superior posterior process is made up by two projections: the dorsal one (the coronoid process) is pointed and distinctly longer than the more rounded ventral one (the surangular process). Because of this, the notch between the two projections, the coronoid incisure, is very shallow in lateral view. The lateral surface is smooth, showing only two mental foramina.

Tooth-bearing bones and isolated teeth. BRS4?/H/4, composed by two separated portions, was part of a large-sized tooth-bearing bone. It shows four tooth positions, bearing subpleurodont teeth. Two of the four teeth are well preserved, whereas only the base remains of the other two. The well-preserved teeth are morphologically similar to those of BRS5tg2/H/7. The lateral surface of the tooth-bearing bone appears rough and four foramina are visible on it, roughly anteroposteriorly aligned. The isolated teeth and the teeth carried by most of the other fragments of tooth-bearing bones are similar in morphology to those of BRS4?/H/4 and BRS5tg2/H/7, even if BRS25/H/136 differs from them in the absence of the cutting edges. BRS25/H/137, on the other hand, shows teeth similar to those of the dentary BRS25/H/135. In BRS25/H/137, the cutting edges are present, whereas they are not clearly visible in BRS25/H/135 because of this specimen being plunged in the matrix.

Trunk vertebrae. The two vertebrae are medium sized and rather lightly built. The procoelous centrum is 4 mm long in BRS28/H/15 (Fig. 14h-k) and exceeds 6 mm in BRS5bis/H/35; it is distinctly dorsoventrally compressed. In ventral view, the centrum is subtriangular, with oblique and distinctly concave lateral margins and a flat ventral surface (Fig. 14i). There is no precondylar constriction. Only the right synapophysis of BRS28/H/15 is preserved (Fig. 14k): it is clearly dorsoventrally elongated. The neural arch is poorly preserved, but it appears low. In both specimens, there is one single zygapophysis preserved, the right prezygapo-

physis. It is wide, subelliptical and dorsally inclined of about 45°. In anterior view, the neural canal is higher than the cotyle (Fig. 14j).

Remarks. The tooth morphology of the above described tooth-bearing bones recalls that of *Ophisaurus* (Klembara et al. 2014). Despite being very fragmentary, BRS25/H/119 is clearly not attributable to *Pseudopus* (the only other anguid identified in the remains from Monticino; see below) because of the absence of a facies muscularis (Klembara 1986; Klembara et al. 2017). Moreover, parietals of both *Anguis* and *Pseudopus* usually display small frontoparietal ornamented shields by the anterolateral corners of the shelf preventing the lateral shields to reach the anterior margin of the bone (Villa & Delfino 2019a). This appears not to be true for at least some *Ophisaurus* species (see e.g., *Ophisaurus boleci* in Klembara 2015). It seems possible, therefore, to assign the herein described parietals to *Ophisaurus*. The frontal from BRS 25 is also not attributable to *Pseudopus* because of the completely smooth lateral margin (Klembara 2015; Klembara et al. 2017; Villa & Delfino 2019a). This is also a feature present in *Anguis* frontals, but in the latter genus this bone displays a contact between the articular surfaces for the postfrontal and the postorbital and a not clearly distinguishable articular surface with the nasal (Villa & Delfino 2019a). Given that, the above mentioned frontal is also assigned to *Ophisaurus*. The trunk vertebrae are attributed to the same genus because of the subtriangular vertebral centrum with concave lateral margins and the neural canal higher than the cotyle in anterior view (Klembara 1981; Čerňanský et al., 2019). Most of the *Ophisaurus* species known from European Neogene localities are described based on parietals, but because of the very fragmentary nature of the parietals from Monticino, it is here preferred to identify them (and all other *Ophisaurus* remains) only at generic level. It has to be noted, however, that the anterior margin of the interparietal shield not reaching the anterolateral corner (i.e., the anterior end of the sulcus between it and the lateral shield is located far from the corner) is a feature of *O. boleci*, in contrast with an interparietal shield more laterally expanded or even contacting the anterolateral corner in the other species for which the parietal is known (Klembara 2015; Klembara & Rummel 2018): *Ophisaurus fejfari*, *Ophisaurus spinari*, and *Ophisaurus robustus*.

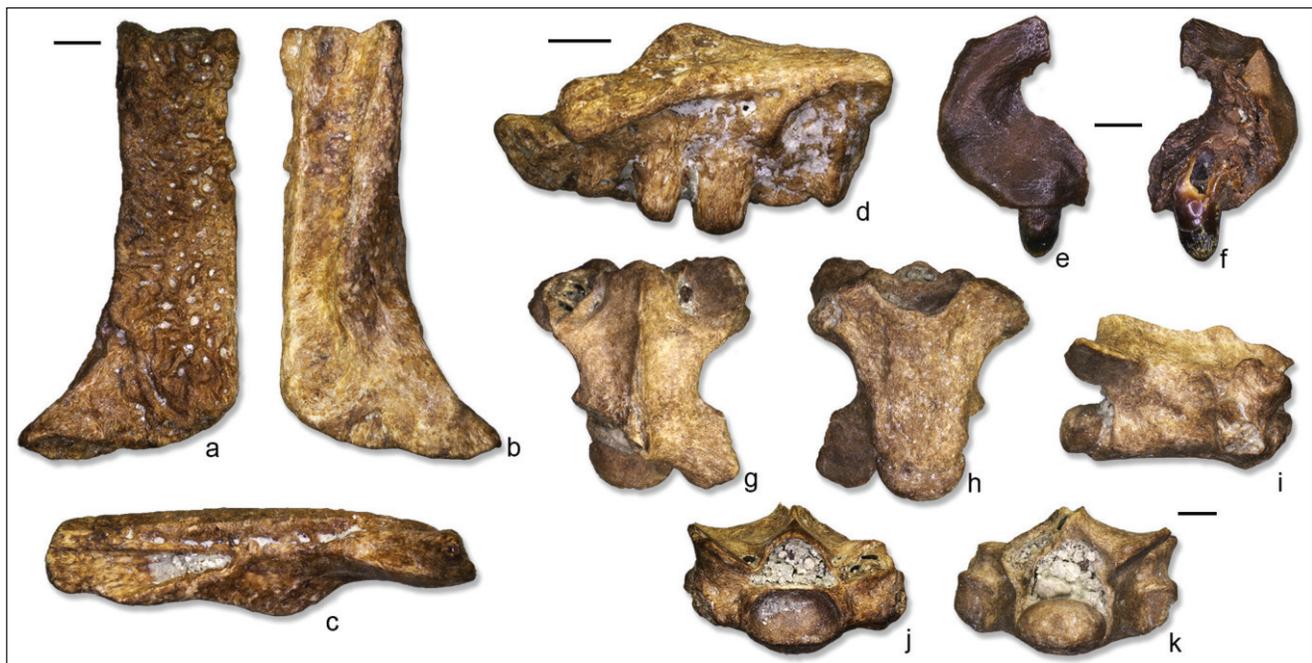


Fig. 15 - *Pseudopus* from Monticino Quarry - *Pseudopus* sp.: left frontal (BRS25/H/117) in dorsal (a), ventral (b) and lateral (c) views; right maxilla (BRS25/H/182) in medial view (d); fragment of tooth-bearing bone (BRS25/H/122) in lateral (e) and medial (f) views; trunk vertebra (BRS28/H/4) in dorsal (g), ventral (h), right lateral (i), anterior (j) and posterior (k) views. Scale bars = 1 mm.

Genus *Pseudopus* Merrem, 1820

Pseudopus sp.

Fig. 15

Referred material: Two frontals (BRS25/H/117-118); one fragmentary maxilla (BRS25/H/182); one fragment of tooth-bearing bone (BRS25/H/122); three trunk vertebrae (BRS24/H/9; BRS25/H/166; BRS28/H/4).

Description

Frontal. BRS25/H/117 is a well-preserved left frontal (Fig. 15a-c), lacking only the anterior end. It is roughly 8.5 mm long. In dorsal view, there is no constriction at midlength and both the lateral and medial margins are straight and roughly parallel (Fig. 15a). In lateral view, the articulation surface with the prefrontal is moderately wide and long, reaching midlength, whereas the one with the postfrontal is smaller and shorter (Fig. 15c). The two surfaces are not in contact, but they are not far from one another. The posterolateral process is wide, pointed and moderately long. A poorly developed lappet is present on its ventral surface. A small and triangular articulation surface is visible ventrally, medially to the lappet. Though broken, the crista cranii is clearly robust and well developed. A strong dermal ornamentation covers almost completely the dorsal surface of the bone (Fig. 15a), except for the posterolateral

process. The ornamentation reaches the lateral margin and is made up of low ridges and pits. Because of the smooth surface of the posterolateral process, the frontoparietal shield cannot be recognized, but the oblique groove between it and the frontal shield is distinguishable. The margin of the frontal shield marked by this groove, its posterolateral margin, is distinctly longer than its posteromedial margin. Moreover, the frontal shield reaches the posterior margin, excluding therefore the interfrontal shield from the dermal cover of the frontal. The second frontal, BRS25/H/118, is more poorly preserved, being represented only by a moderately eroded posterior half. However, its morphology recalls that of BRS25/H/117, except for the presence of a moderately developed dermal cover on the posterolateral process also. BRS25/H/118 is roughly 5.3 mm in length.

Maxilla. BRS25/H/182 is a fragmentary and very poorly preserved maxilla (Fig. 15d), representing the anterior portion of the bone. The anterior premaxillary process is clearly composed by an anterolateral and an anteromedial processes, of which the former is twice as robust as the latter. Both processes are strongly eroded and the anteromedial one also misses its anterior end. They are separated by a roughly U-shaped notch. The anterior concavity in which the vomeronasal foramen opens is bordered

both laterally and medially by low ridges, but the foramen is not clearly distinguishable because it is covered by matrix. The medial ridge continues on the dorsal surface of the anteromedial process in a moderately low lappet. The lateral surface of the specimen is smooth, carrying only four ventrolateral foramina. Four tooth positions are visible and three teeth are still present, though eroded. The teeth are subpleurodont, cylindrical and distinctly robust; their crown is blunt and rounded. It seems that some striae are present on both the lingual and the labial surface of the teeth, but this cannot be ascertained because of the erosion. The size of the teeth increases posteriorly.

Tooth-bearing bone. BRS25/H/122 is a very poorly preserved fragment of an indeterminate robust and large-sized tooth-bearing bone (Fig. 15e-f). The bone carries a single, well-preserved tooth, which is subpleurodont, robust, cylindrical and monocuspid. Its crown is rather rounded and bears distinct striae on both the labial and lingual surfaces.

Trunk vertebrae. BRS24/H/9, BRS25/H/166, and BRS28/H/4 (Fig. 15g-k) have a medium size (centrum length goes from 4 mm to 6 mm), a robustly-built aspect, and a dorsoventrally compressed, procoelous centrum, provided with a smooth and flattened ventral surface and lacking a precondylar constriction. In ventral view, the centrum is subtriangular, since its lateral margins converge posteriorly (Fig. 15h). Such margins are straight, with the only exception of BRS24/H/9, in which they appear slightly concave in ventral view. The neural arch is low, with a neural canal that is lower in height than the anterior cotyle in anterior view (Fig. 15j). The neural spine was present, but it is broken in all specimens. When preserved, the zygapophyses are suboval in dorsal view and dorsally tilted at an angle of about 45°.

Remarks. These specimens are clearly referable to *Pseudopus* because of the dermal ornamentation reaching the lateral margin of the frontals, the cylindrical and robust teeth with a blunt crown, the subtriangular vertebral centrum with straight or slightly concave lateral margins, and the neural canal smaller than the cotyle (Klembara 1981, 2015; Klembara et al. 2014, 2017; Čerňanský et al. 2019; Villa & Delfino 2019a). The specific identification, on the other hand, is more complex, because of a number of features or combination of features that seems to distinguish the *Pseudopus* remains

found in Monticino from the other Neogene *Pseudopus* species. First, both the ornamentation reaching the lateral margin for the entire length and the very long posterolateral margin of the frontal shield compared to its posteromedial margin separate the frontals BRS25/H/117 and 118 from *Pseudopus abnikoviensis* and *Pseudopus laurillardii*, in which the ornamented cover touches the lateral margin only near the anterior end and the posterolateral margin of the frontal shield is either as long as (in *P. abnikoviensis*) or slightly longer (in *P. laurillardii*) than the posteromedial one (Klembara et al. 2010; Klembara 2012; Klembara & Rummel 2018). *Pseudopus abnikoviensis* differs from the herein described remains also because it does not show striae on the dentition (Klembara 2012; Klembara & Rummel 2018). The interfrontal shield, absent in the two frontals from Monticino, is on the other hand present and distinctly large in all *Pseudopus* species, except for *Pseudopus apodus* and *Pseudopus confertus*, in which it can be either absent or narrow (Klembara et al. 2010, 2017; Klembara 2012, 2015; Klembara & Rummel 2018; Villa & Delfino 2019a). The frontal referred to *P. confertus* (= *Pseudopus rugosus*) by Klembara (2015) displays a dermal ornamentation which is distinctly different from the one of BRS25/H/117 and 118. Therefore, the *Pseudopus* from the late Miocene of Monticino seems to be somehow different from all other species of the genus found in European Neogene localities. Nonetheless, given the scarce amount of remains and the absence of other taxonomically important skeletal elements (i.e., parietals), either a possible identification as a new taxon or a tentative attribution to one of the known species are here avoided and the fossils are attributed only to *Pseudopus* sp.

non-*Anguis* Anguinae indet.

Fig. 16

Referred material: Two fragmentary maxillae (BRS5tg2/H/8; BRS24/H/13); two pterygoids (BRS5tg2/H/3, 22); one ectopterygoid (BRS5tg2/H/23); six fragments of tooth-bearing bones (BRS5tg2/H/5; BRS6/H/2; BRS25/H/140); 65 fragments of trunk vertebrae (BRS4/H/5; BRS5bis/H/2; BRS5tg2/H/20; BRS9/H/2; BRS15/H/5; BRS16/H/2; BRS19/H/7; BRS24/H/11; BRS25/H/1, 45, 111, 170-171; BRSNoNumber/H/16); 58 caudal vertebrae (BRS4/H/6; BRS5bis/H/3; BRS5tg2/H/21; BRS16/H/3; BRS19/H/8; BRS24/H/12, 37; BRS25/H/46, 112-114, 127, 139, 168, 172, 270, 285; BRSNoNumber/H/15); 2737 osteoderms (BRS1bis/H/1; BRS3/H/1; BRS4/H/1-4; BRS5bis/H/1; BRS5tg2/H/27; BRS6/H/1; BRS8/H/5; BRS9/H/1; BRS15/H/4; BRS16/H/1; BRS18/H/1; BRS19/H/6, 9; BRS24/H/8, 23-24;

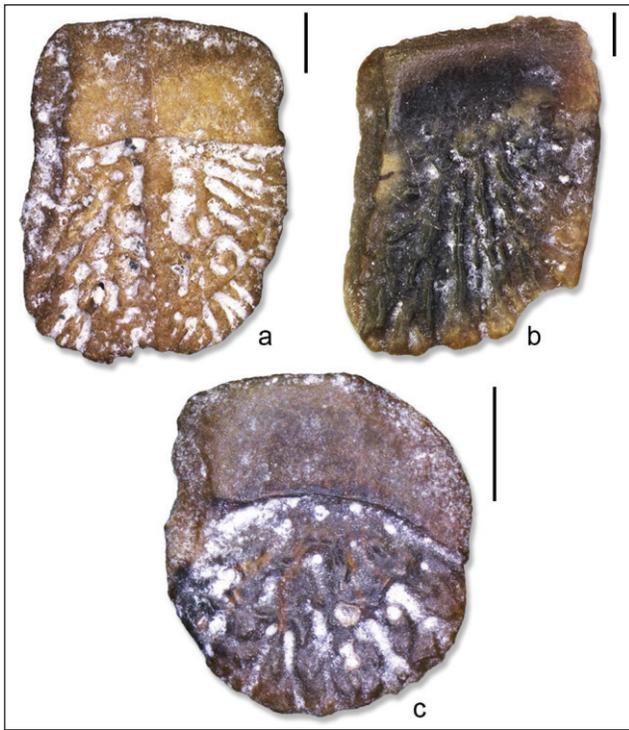


Fig. 16 - Osteoderms of non-*Anguis Anguinae* indet. from Monticino Quarry - Osteoderm (BRS19/H/9) in external view (a). Osteoderm (BRS25/H/185) in external view (b). Osteoderm (BRS27/H/2) in external view (c). Scale bars = 1 mm.

BRS25/H/2, 19, 110, 120, 123-126, 167, 185-186, 233, 237, 246, 275, 293; BRS27/H/1-3; BRS28/H/1-2, 16; BRSNoNumber/H/17; BRS?/H/8-12).

Description

Pterygoids. Pterygoids are medium-sized and moderately robust. Both specimens are very fragmentary, preserving only the base of the quadrate process and part of the anterior half of the bone (part of the palatine process in BRS5tg2/H/3 and part of the pterygoid flange in BRS5tg2/H/22). The palatine process shows a large number of pterygoid teeth on the ventral surface, whereas a well-developed ridge runs along the lateral margin on the ventral surface of the pterygoid flange. The preserved portion of the quadrate process presents a wide and flattened basipterygoid fossa, which is marked ventrally by a distinctly developed and roughly thumb-like basisphenoid process (sensu Klembara et al. 2010). Part of a deep fossa columellae is visible dorsally in BRS5tg2/H/22.

Ectopterygoid. BRS5tg2/H/23 is a fragmentary, but very robust and large-sized ectopterygoid, which lacks almost completely the anterior end and the posteriormost portions of the posterior one. The bone has a medially concave shape and

presents a dorsomedially expanded posterior portion, the lateral surface of which bears a wide and deep articulation surface for the pterygoid flange of the pterygoid. The anterior half of the lateral surface, on the other hand, is covered by the very narrow articulation surface with the posterior process of the maxilla. The two articular surfaces contact each other. A small and anterolaterally directed flange marks ventrally the anterior articulation surface. The medial surface of the specimen is smooth.

Tooth-bearing bones. The fragments of tooth-bearing bones, BRS5tg2/H/8 included, are very poorly preserved. Each of them carries subpleurodont, large-sized and moderately preserved teeth. The preserved teeth seem to narrow dorsally, suggesting a possible conical shape, but, since they lack the crown, it is not possible to say whether the tip was pointed or not. No striae are visible on the preserved portion of the teeth, but in BRS5tg2/H/8 and BRS24/H/13, they show the anterior and posterior cutting edges visible in the above described *Ophisaurus* sp. BRS5tg2/H/8 is particularly robust and is 8 mm in length.

Fragments of trunk vertebrae. Though the specimens are very poorly preserved, the preserved portions of the fragments of trunk vertebrae are morphologically similar to those described above as pertaining to either *Ophisaurus* or *Pseudopus*. However, their poor preservation hinders a confident recognition of the diagnostic features. Some of the fragmentary vertebrae are very large-sized (e.g., the centrum of BRS25/H/171 is 10 mm long) and robustly built.

Caudal vertebrae. The caudal vertebrae present a dorsoventrally compressed centrum and the bases of broken hemapophyses on the ventral surface. Some of the best-preserved specimens are robust and very large (the centrum length reaches 11 mm in BRS25/H/114 and 172), whereas the other ones are smaller. When preserved, the neural arch and the zygapophyses are similar to those of the above described trunk vertebrae. The autotomy plane is clearly lacking, except for BRS25/H/113.

Osteoderms. Osteoderms (Fig. 16), the preservational status of which varies from complete to very fragmentary, are mainly large- to very-large-sized and robust, even if there are also smaller specimens. They usually have a subrectangular shape (Fig. 16a-b), but some more subtrapezoi-

dal or more suboval specimen is also present (e.g., BRS27/H/2; Fig. 16c). A vermicular ornamentation is always present on the external surface (except for the smooth anterior gliding surface), whereas the inner one is smooth. The rectangular osteoderms bear also a distinct longitudinal keel in the middle of the external surface.

Remarks. Numerous vertebral fragments and osteoderms are assigned to indeterminate non-*Anguis* Anguinae. As far as the vertebrae are concerned, this is because of the large size and overall similarity with those assigned to the two anguines already identified in the locality. Identification of the osteoderms, on the other hand, is based on the large size, rectangular shape, and the external keel (Holman 1998; Delfino et al. 2011). Both the pterygoids and the ectopterygoid display anguid features (e.g., osseous expansion marking ventrally the basiptyergoid fossa, articular surface with the maxilla limited to the lateral surface of the anterior half of the ectopterygoid; Villa & Delfino 2019a). The large size suggests that they can be attributed to a non-*Anguis* taxon, like the other similar-sized specimens from Monticino, but since these skeletal elements are not clearly known for the Neogene anguid species, they are not assigned neither to *Pseudopus* nor to *Ophisaurus*. The dentition of the fragmentary tooth-bearing bones is also comparable with that of a non-*Anguis* anguine (teeth not as spaced and curved as in *Anguis*; Klembara et al. 2014; Villa & Delfino 2019a), but due to their poor preservation, it is not possible to confidently assign them to a particular taxon. The only exceptions might be BRS5tg2/H/8 and BRS24/H/13, the teeth of which are more similar to those of the specimens attributed to *Ophisaurus*.

Family Varanidae Gray, 1827 (sensu Estes et al., 1988)

Genus *Varanus* Merrem, 1820

***Varanus* sp.**

Fig. 17

Referred material: Two teeth (BRS5bis/H/13; BRS6/H/7); two trunk vertebrae (BRS6/H/4; BRS25/H/138); two fragments of trunk vertebrae (BRS25/H/85, 129); two caudal vertebrae (BRS25/H/130; BRS27/H/4); four fragments of vertebrae (BRS6/H/5; BRSNoNumber/H/1-2); one humerus (BRS25/H/128).

Description

Teeth. Both teeth are medium-sized and lack their tip (Fig. 17a-d). BRS6/H/7 is also slightly eroded. They are canine-like in shape and distinctly posteriorly curved. The implantation was subpleurodont and the tooth base shows a labially directed area made of spongy tissue (Fig. 17a, c). BRS5bis/H/13 is still connected to part of the original tooth-bearing bone (Fig. 17a). The teeth are medio-laterally compressed and present sharpened anterior and posterior margins, on which a light milling is still visible in spite of the erosion. Both the lingual and the labial surfaces of BRS5bis/H/13 show a number of dorsoventrally directed striae near the tooth base (Fig. 17a-b). In BRS6/H/7, such striae are not visible on the labial surface (Fig. 17c), but this could be due to the preservational status.

Trunk vertebrae. The trunk vertebrae (Fig. 17e-l) are procoelous, robust and large-sized (the centrum length of the best preserved one, BRS25/H/138, is 10 mm). BRS25/H/138 (Fig. 17g-l) is almost complete and roughly as long as it is large. It has a wide and dorsoventrally compressed centrum, provided with a smooth and flattened ventral surface, strongly posteriorly convergent lateral margins (giving it a triangular shape in ventral view) and a distinct precondylar constriction (Fig. 17k). The neural arch has a subtrapezoidal section in anterior view and carries a neural spine, which is, however, broken. Dorsally, there is no pseudozygosphene (Fig. 17g-h). Both the zygapophyses and the synapophyses are missing. In BRS6/H/4, only the anterior end of the centrum and part of its prezygapophyses are preserved. Size, robustness and general morphology of this specimen is similar to the other trunk vertebra. The prezygapophyses are slightly eroded, but they appear dorsoventrally inclined at about 45° in anterior view. The vertebral fragments are very poorly preserved, but they are very large and robust. The size and the robustness of the specimens is comparable with those of the other remains attributable to *Varanus*, but some of them are even larger (e.g., BRS25/H/85; Fig. 17e). BRS25/H/85, 129, and BRSNoNumber/H/1 show a wide and dorsoventrally compressed posterior condyle, preceded by a strong precondylar constriction (Fig. 17e-f).

Caudal vertebrae. BRS25/H/130 is the posterior portion of a moderately large-sized caudal vertebra, provided with a dorsoventrally compressed

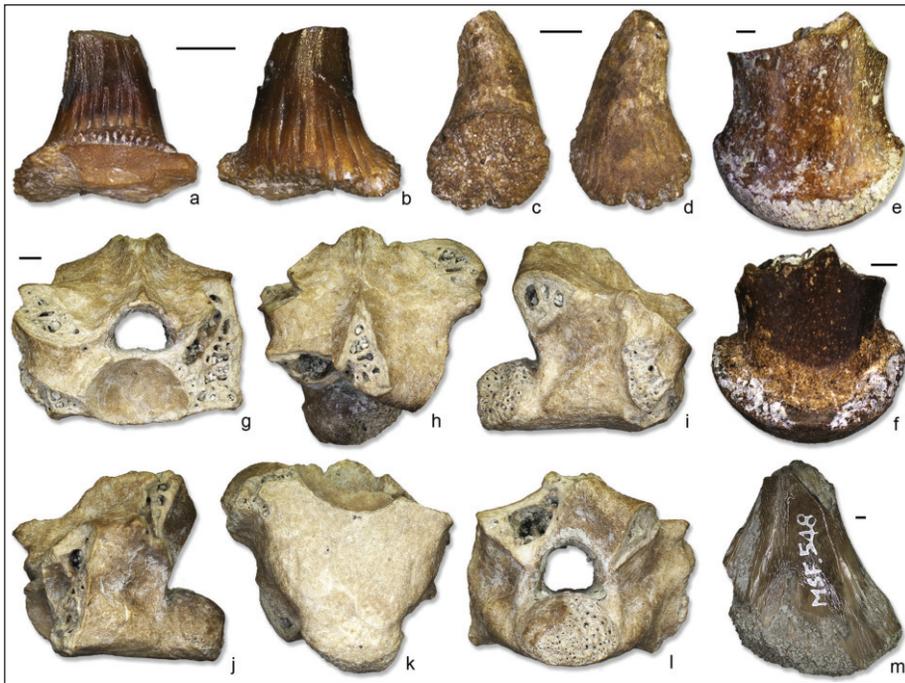


Fig. 17 - Varanids from Monticino Quarry - *Varanus* sp.: isolated tooth (BRS5bis/H/13) in lateral (a) and medial (b) views; isolated tooth (BRS6/H/7) in lateral (c) and medial (d) views; fragment of trunk vertebra (BRS25/H/85) in ventral view (e); fragment of trunk vertebra (BRS25/H/129) in ventral view (f); trunk vertebra (BRS25/H/138) in anterior (g), dorsal (h), right lateral (i), left lateral (j), ventral (k) and posterior (l) views; right humerus (BRS25/H/128) in anterior view (m). Scale bars = 1 mm.

centrum and a wide posterior cotyle. A precondylar constriction is present and the pedestals for the chevron bone are visible on the ventral surface, near the cotyle. The postzygapophyses are suboval and dorsally tilted at 45°. A broken, but strongly dorsally projecting neural spine is present. The autotomy plane is recognizable anteriorly. BRS27/H/4 is less preserved, but has a comparable size and a similar morphology, in particular for what the pedestals are concerned. This specimen is also split into two portions, but it is not clear if the separation plane between them is a real autotomy plane or just the result of breakage.

Humerus. BRS25/H/128 is the poorly preserved distal epiphysis of a very large-sized and very robust humerus (Fig. 17m).

Remarks. Together, the precondylar constriction and the absence of the pseudozygosphene are distinctive features of the trunk vertebrae of *Varanus* (Hoffstetter 1943; Estes 1983; Bailon 1991). Caudal vertebrae and teeth also display varanid features, such as the precondylar constriction in the former and the presence of long basal striae and spongy tissue (suggesting the presence of plicidentine) in the latter (Estes 1983; Bailon 1991; Pianka et al. 2004; Kearney & Rieppel 2006). Because of the comparable size and the fact that, among Varanidae, only *Varanus* has been reported from the European Neogene so far (Delfino et al. 2013; Georgalis et al. 2017a; Villa & Delfino 2019b), both

caudal vertebrae and teeth can be confidently attributed to this taxon too. The humerus is assigned to *Varanus* because of its very large size, which is comparable only with *Varanus* among all limbed lizards identified in Monticino. The robustness of this bone agrees with the hypothesis of robust-limbed varanids living in Europe during the Neogene suggested by Georgalis et al. (2018), as also supported by the only Neogene European varanid species for which the limbs are known, *Varanus marathonsensis* (based on the almost complete specimen described by Villa et al., 2018). Teeth with a milling are not common among European *Varanus*. They are known in few middle and late Miocene sites in central and eastern Europe (see Georgalis et al. 2019), but not in material referred to *Varanus mokrensis* Ivanov et al., 2018. Contra Villa et al. (2018) and Georgalis et al. (2019), *V. marathonsensis* indeed has serrated teeth, at least in the almost complete individual described by Villa et al. (2018) from Cerro de los Batallones (A.V., pers. obs.). The taxonomic significance of this feature is still unknown. However, new observations on the Batallones specimen seem to suggest that it is strongly influenced by taphonomic processes and that it could be even variable in different teeth of a single individual.

Suborder **Amphisbaenia** Gray, 1844
Amphisbaenia indet.

Fig. 18

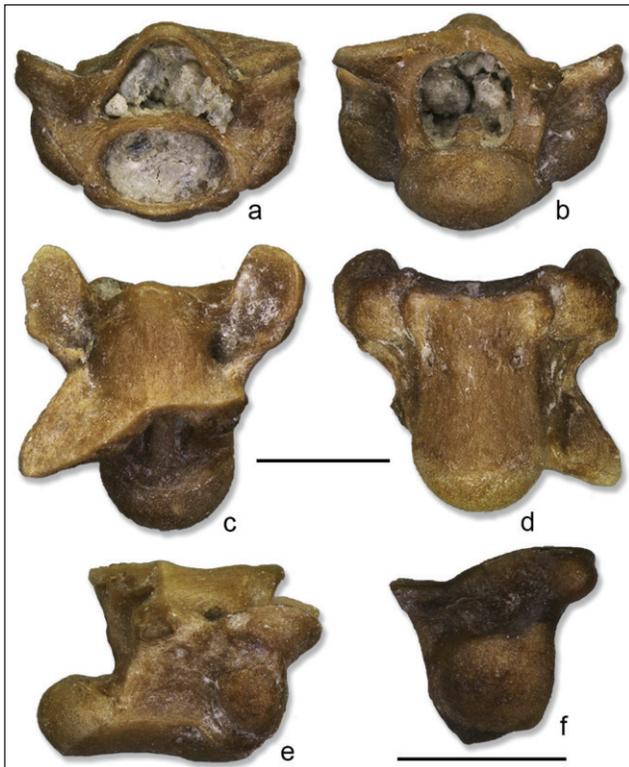


Fig. 18 - Amphisbaenians from Monticino Quarry - *Amphisbaenia* indet.: trunk vertebra (BRS19/H/1) in anterior (a), posterior (b), dorsal (c), ventral (d) and right lateral (e) views; fragment of trunk vertebra (BRS25/H/18) in right lateral view (f). Scale bars = 1 mm.

Referred material: Four trunk vertebrae (BR19/H/1, 2; BRS25/H/17, 86); one fragment of trunk vertebra (BRS25/H/18).

Description. The trunk vertebrae are very small, with the centrum length of the best preserved ones that is 2 mm in BR19/H/1, 2.2 mm in BRS25/H/86, and 2.4 mm in BR19/H/2. BR19/H/1 (Fig. 18a-e) is almost complete, lacking only the posterior portion of the neural arch, whereas the other specimens are more fragmentary. The vertebral centrum is procoelous, dorsoventrally compressed and has a flattened ventral surface. Its lateral margins are very slightly concave and roughly parallel in ventral view (Fig. 18d). The synapophyses are bulbous and massive (Fig. 18e-f). The prezygapophyses are suboval in dorsal view and dorsally tilted at roughly 30° in anterior view. In BR19/H/1 and BRS25/H/17, the dorsal surface of the neural arch is smooth and there is no trace of a neural spine in its preserved portion (Fig. 18c). A very small and rounded prezygapophyseal process is visible in BRS25/H/18 (Fig. 18f) and 86, but it is almost indistinct in other specimens preserving the prezygapophyses (i.e., BR19/H/1 and 2).

Remarks. Small trunk vertebrae without zygosphenes and neural spine and provided with a dorsoventrally compressed centrum with a flattened ventral surface and subparallel lateral margins can be referred to indeterminate amphisbaenians (Estes 1983; Delfino 2003), but a more precise identification is not possible.

Suborder **Serpentes** Linnaeus, 1758

Superfamily Booidea Gray, 1825

Family Boidae Gray, 1825

Subfamily Erycinae Bonaparte, 1831

Genus *Eryx* Daudin, 1803

Eryx cf. *jaculus* (Linnaeus, 1758)

Fig. 19

Referred material: One cervical vertebra (BRS25/H/153); 35 trunk vertebrae (BRS2/H/4; BRS4/H/33; BRS5bis/H/15; BRS5tg2/H/26; BRS6/H/9; BRS9/H/10; BRS15/H/3; BRS19/H/4; BRS25/H/151, 156, 198; BRS27/H/17); two articulated trunk vertebrae (BRS25/H/252); 40 caudal vertebrae (BRS4/H/34; BRS4?/H/2; BRS5bis/H/16; BRS5tg2/H/24; BRS6/H/8, 10-11; BRS9/H/8-9; BRS24/H/1; BRS25/H/131, 143, 155, 157-159; BRS28/H/3); two articulated caudal vertebrae (BRS5tg2/H/25); one fragment of vertebra (BRS25/H/152).

Description

Trunk vertebrae. All trunk vertebrae (Fig. 19a-b) are massively built. The centrum is distinctly wider than long, with a very broad (but indistinct) haemal keel (Fig. 19b). The prezygapophyseal processes, acute in shape, are very short but well visible in dorsal view. The paradiapophyses are weakly divided into para- and diapophyseal portions. The paracotylar foramina are absent. The basic measurements of the largest vertebra are as following: centrum length is 2.9 mm, whereas centrum width is 4.2 mm.

Caudal vertebrae. Most caudal vertebrae (Fig. 19c-h) come from the posterior part of the caudal portion of the column. The vertebrae are provided with a number of additional apophyses, among others pterapophyses, posterior extensions of prezygapophyses, posterior extensions of pleurapophyses, and postzygapophyseal wings (the latter structures are mostly broken off).

Remarks. The complex morphology of the caudal vertebrae is characteristic of the boid subfamily Erycinae and is not observed in any other groups of snakes (Szyndlar 1991a). Trunk vertebrae with a wider than long centrum and short prezygapophyseal processes are also assigned to this subfam-

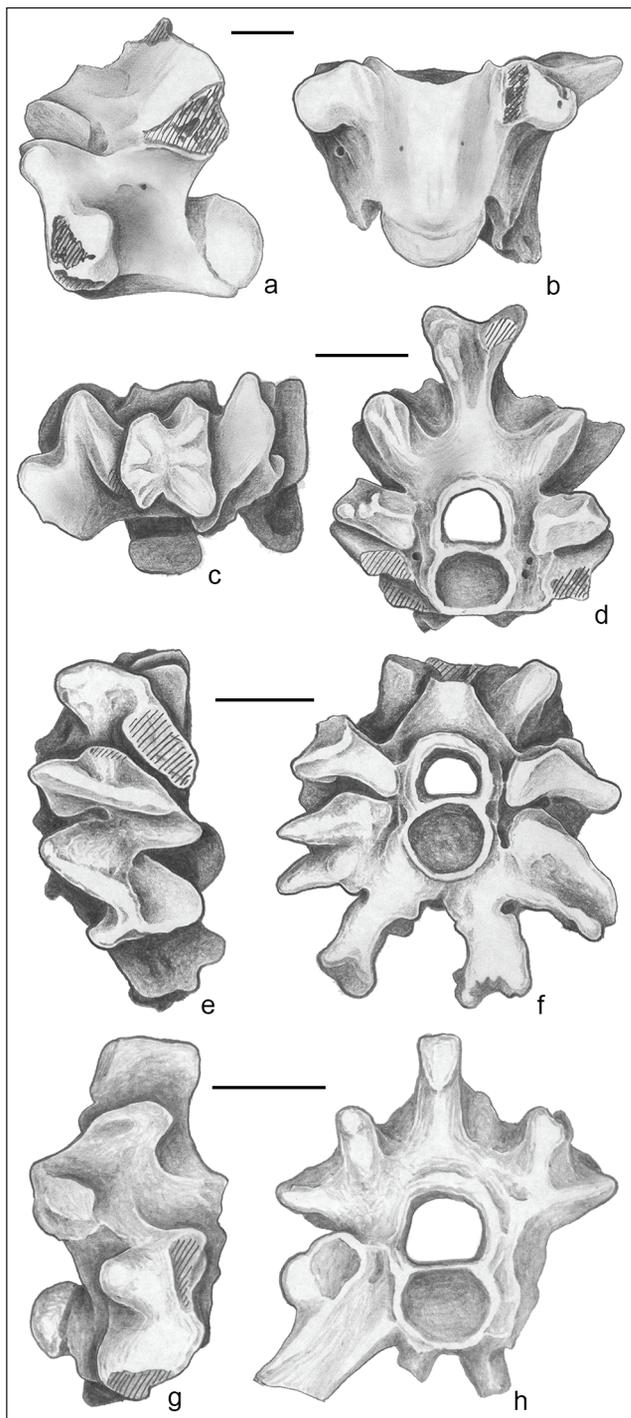


Fig. 19 - Erycinae from Monticino Quarry - *Eryx* cf. *jaculus*: trunk vertebra (BRS25/H/156) in left lateral (a) and ventral (b) views; caudal vertebra (BRS6/H/11) in dorsal (c) and anterior (d) views; caudal vertebra (BRS25/H/158) in left lateral (e) and anterior (f) views; caudal vertebra (BRS25/H/155) in right lateral (g) and anterior (h) views. Scale bars = 1 mm

ily (Szyndlar 1991a). All these vertebrae, especially those from the caudal portion of the column, are referable to the living European snake *E. jaculus* or a closely related extinct species. Contrary to other members of the genus, in the posterior caudal ver-

tebrae of *E. jaculus* the postzygapophyseal wings are not fused anteriorly with the prezygapophyses (Szyndlar & Schleich 1994). The latter condition is also well visible in the herein-described vertebrae (despite the lack of distal portions of the wings).

Taxon **Colubroides** Zaher et al., 2009
Family Colubridae Oppel, 1811
Genus *Platyiceps* Blyth, 1860

Platyiceps planicarinatus (Bachmayer & Szyndlar, 1985)

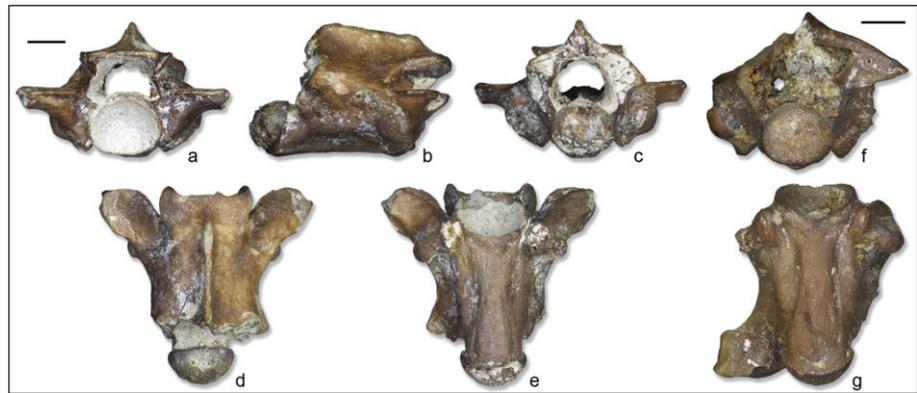
Fig. 20

Referred material: Three trunk vertebrae (BRS?/H/3, 17-18).

Description. These vertebrae are elongated and reach a centrum length of about 4.5 mm in the largest specimen. They are moderately preserved. The centrum bears a wide and very low hemal keel (Fig. 20e, g), which is marked laterally by very shallow (almost indistinguishable in the largest vertebrae) subcentral grooves. The grooves are little more developed in the smallest specimen. The posterior end of the keel is almost indistinct, but it is clearly separated from the posterior condyle. On the lateral surface of the neural arch, the parapophyses are longer than the diapophyses (Fig. 20b). However, there is no parapophyseal process. In anterior view, the neural canal is smaller than the cotyle in the largest specimen, but as large as or even larger than it in smaller ones. When preserved, the zygapophyses go from slightly tilted dorsally to subhorizontal, with a gradient toward more horizontal facets with increasing size. The prezygapophyseal processes are never preserved. The zygosphene has a straight or almost straight anterior margin, with two small lateral lobes (Fig. 20d). The neural spine is always broken. In posterior view, the neural arch is distinctly dorsoventrally depressed (Fig. 20f).

Remarks. The morphology of these trunk vertebrae perfectly recalls that of *Nanus planicarinatus* Bachmayer & Szyndlar, 1985 in having (Bachmayer & Szyndlar 1985; Szyndlar 1991a): small size; wide and low hemal keel; very shallow subcentral grooves; absence of parapophyseal processes and thus not strongly developed paradiapophyses; and straight to almost straight anterior margin of the zygosphene, flanked by two small lateral lobes. They

Fig. 20 - Colubrids from Monticino Quarry - *Platyceps planicarinatus*: trunk vertebra (BRS2/H/17) in anterior (a), right lateral (b), posterior (c), dorsal (d) and ventral (e) views; trunk vertebra (BRS2/H/18) in posterior (f) and ventral (g) views. Scale bars = 1 mm.



are therefore attributed to this species. *Nanus planicarinatus* was later moved to *Coluber* by Bachmayer & Szyndlar (1987) following the referral of a basiparasphenoid from the type locality, which was virtually identical to the same bone in snakes of the *Coluber najadum/rubriceps* group. In modern taxonomy, however, the genus *Coluber* is restricted to a single species living in Central and North America, the eastern racer *Coluber constrictor* Linnaeus, 1758, and the *Coluber najadum/rubriceps* group is now part of the genus *Platyceps*. Considering this, and pending a real revision of the extinct species also including a vertebral comparison with other colubroid snakes, we here follow Wallach et al. (2014) in referring it to *Platyceps* as *P. planicarinatus* in order to reflect Bachmayer & Szyndlar's (1987) original intentions.

Family Dipsadidae Bonaparte, 1838
Genus *Paleoheterodon* Holman, 1964

cf. *Paleoheterodon arcuatus* Rage & Holman,
1984

Fig. 21

Referred material: One trunk vertebra (BRS25/H/9); one fragment of trunk vertebra (BRS25/H/191).

Description. BRS25/H/9 is an elongated trunk vertebra, which is rather poorly preserved. It has a procoelous centrum provided with a very robust hemal keel (Fig. 21d). The keel is wide in ventral view and even slightly wider in its posterior half. The same portion is also ventrally flat. The posterior tip of the keel is somehow pointed and it is located distinctly away from the posterior condyle of the vertebra. Shallow but distinct subcentral grooves mark the keel laterally. Low subcentral ridges are also visible. In anterior view, the neural canal appears not much wider than the cotyle (Fig.

21a). The zygospine is well preserved. In dorsal view, it is wavy, with a well-developed median lobe and two narrower lateral lobes (Fig. 21c). The rest of the vertebra is too damaged to be satisfactorily

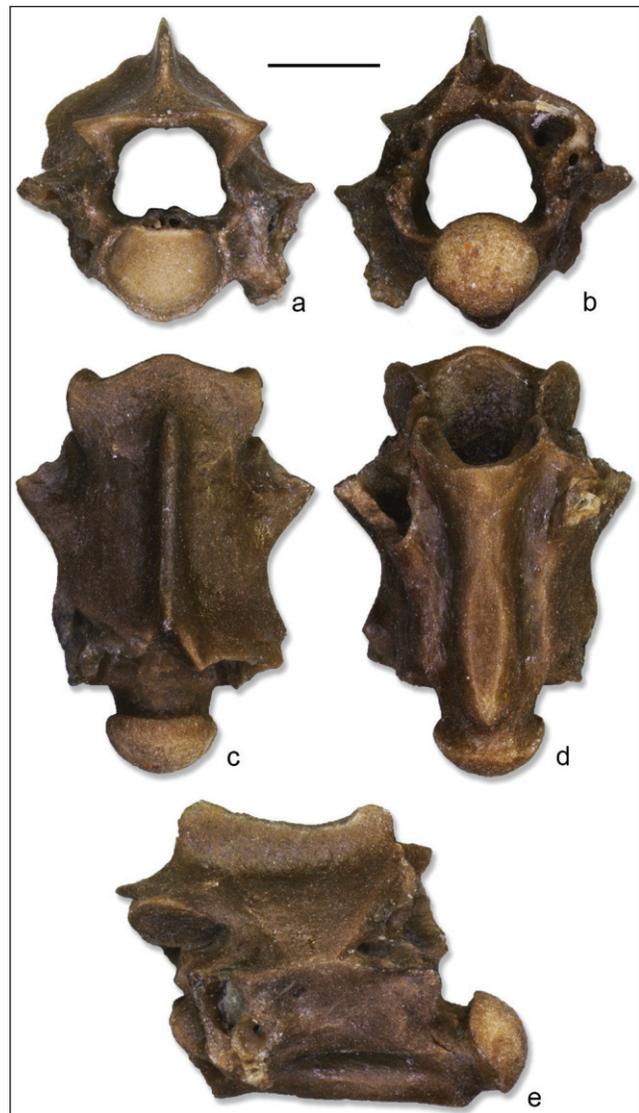


Fig. 21 - Dipsadids from Monticino Quarry - cf. *Paleoheterodon arcuatus*: trunk vertebra (BRS25/H/9) in anterior (a), posterior (b), dorsal (c), ventral (d) and left lateral (e) views. Scale bar = 1 mm.

described, but the neural arch appears moderately depressed in posterior view in spite of the bad preservation status (Fig. 21b). The centrum length is 3 mm. One other fragment of vertebra shares with BRS25/H/9 a similar hemal keel.

Remarks. This small snake displays a rather peculiar vertebral morphology, which appears rather similar to the one of the holotype trunk vertebra of *P. arcuatus* from the Miocene of France (Rage & Holman 1984; Szyndlar 2012). Significant affinities between the Italian and the French fossils are found in: the small size; the elongated centrum; the wide hemal keel flanked by shallow subcentral grooves; the low subcentral ridges; the trilobed zygosphene; and the moderate depression of the neural arch in posterior view. Based on Rage & Holman's (1984: fig. 3c) original figure, the holotype of *P. arcuatus* also shows a light widening of the posterior half of the keel and a separation between the tip of the latter and the condyle. These are features present in the Italian material as well, thus possibly supporting our attribution. Nevertheless, we here considered this identification as tentative due to the few remains available.

Family Natricidae Bonaparte, 1838
Genus *Natrix* Laurenti, 1768

Natrix sp.

Fig. 22

Referred material: One trunk vertebra (BRS15/H/1).

Description. This very small and rather damaged trunk vertebra is procoelous, anteroposteriorly elongated, and lightly built. The centrum is subcylindrical, with an anterior cotyle which appears slightly wider than the neural canal in anterior view (Fig. 22a). A well-developed hypapophysis is present on the ventral surface, but its distal portion is broken off. It does not develop a keel anteriorly. The preserved portion of the neural arch does not appear compressed in posterior view. The neural spine is well preserved, being moderately high and overhanging both anteriorly and posteriorly (Fig. 22e). Other important morphological structures are either missing or poorly preserved.

Remarks. The vertebra, although strongly damaged, displays features characteristic of natricid (Natricinae sensu Szyndlar 1991b) snakes (i.e., pres-

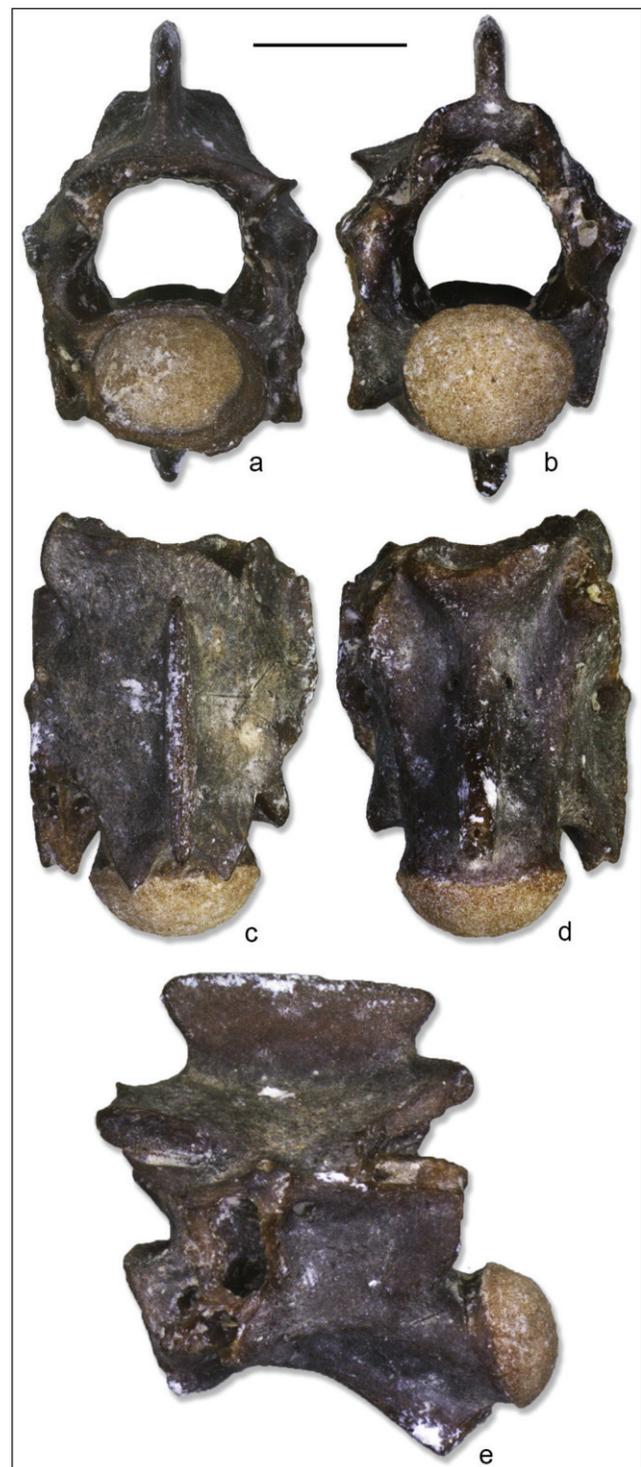
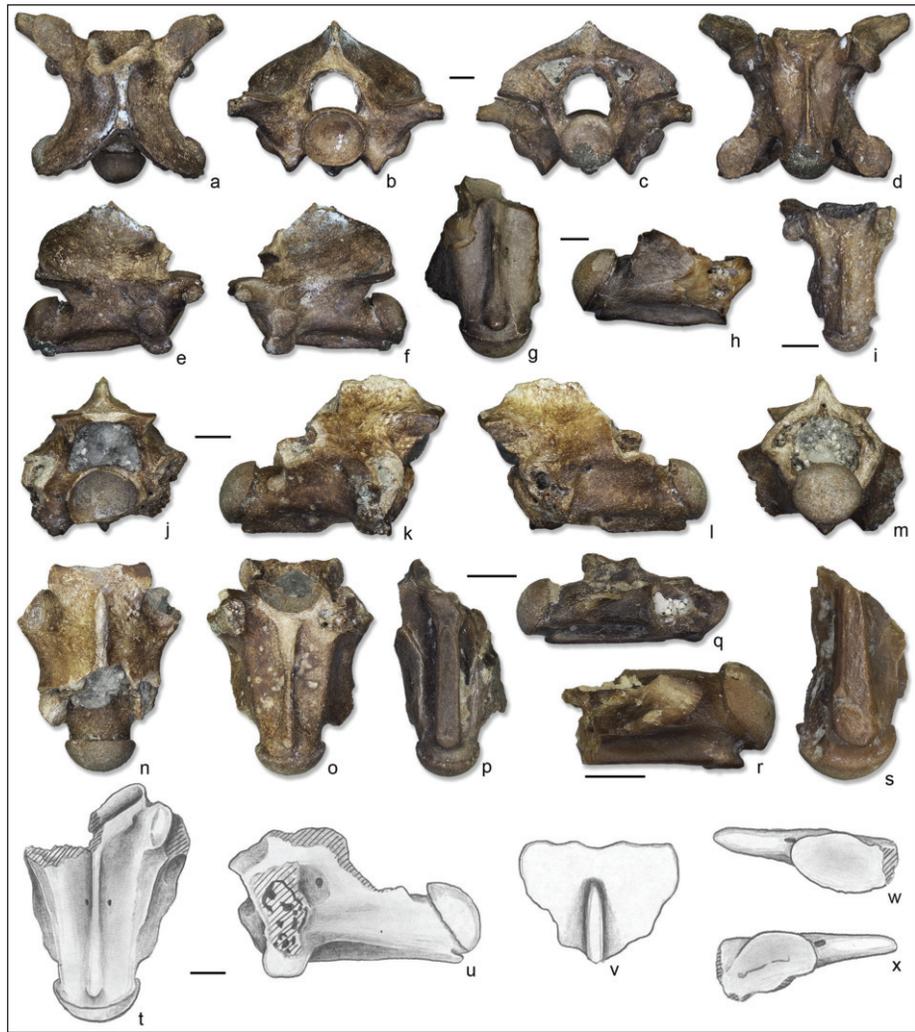


Fig. 22 - Natricines from Monticino Quarry - *Natrix* sp.: trunk vertebra (BRS15/H/1) in anterior (a), posterior (b), dorsal (c), ventral (d) and left lateral (e) views. Scale bar = 1 mm.

ence of hypapophysis, neural arch not compressed posteriorly, and neural spine overhanging anteriorly; Szyndlar 1984, 1991b). Based on the shape of its neural spine, which is rather high and provided with prominent anterior and posterior overhangs, the vertebra is referable to the modern genus *Natrix*

Fig. 23 - Psammophiids from Monticino Quarry - *Malpolon* sp.: anterior trunk vertebra (BRS19/H/18) in dorsal (a), anterior (b), posterior (c), ventral (d), right lateral (e), and left lateral (f) views; anterior trunk vertebra (BRS25/H/194) in ventral (g) and right lateral (h) views; anterior trunk vertebra (BRS25/H/188) in ventral view (i); anterior trunk vertebra (BRS25/H/193) in anterior (j), right lateral (k), left lateral (l), posterior (m), dorsal (n), and ventral (o) views; posterior trunk vertebra (BRS25/H/189) in ventral (p) and right lateral (q) views; posterior trunk vertebra (BRS4/H/35) in left lateral (r) and ventral (s) views; anterior trunk vertebra (BRS5bis/H/18) in ventral (t) and left lateral (u) views; fragment of trunk vertebra (BRS5bis/H/21) in dorsal view (v); fragment of trunk vertebra (BRS5bis/H/19) in dorsal view (w); fragment of trunk vertebra (BRS5bis/H/20) in dorsal view (x). Scale bars = 1 mm.



(Szyndlar 1991b; Szyndlar & Schleich 1993; Augé & Rage 2000). A specific identification is not attempted here due to the poor overall preservation of the specimen.

Family Psammophiidae Dowling, 1967
Genus *Malpolon* Fitzinger, 1826

***Malpolon* sp.**

Fig. 23

Referred material: One hundred forty anterior trunk vertebrae (BRS1bis/H/8; BRS3/H/10; BRS4/H/32; BRS5bis/H/17, 31; BRS5tg2/H/28, 35; BRS6/H/12-13, 17; BRS9/H/11, 15; BRS15/H/14; BRS16/H/8; BRS18/H/13; BRS19/H/17-18, 21; BRS25/H/52, 88, 144, 150, 188, 192-194, 196, 222, 229, 231, 288; BRS28/H/6; BRS28?/H/6; BRSNoNumber/H/6, 20); nine posterior trunk vertebrae (BRS4/H/35; BRS6/H/18; BRS25/H/29, 189, 195, 197; BRS28/H/19); five fragments of indeterminate trunk vertebra (BRS5bis/H/18-21; BRS25/H/291).

Description. Most of these vertebrae are represented by fragments or incompletely pre-

served specimens, most of which preserving only the centrum. Both anterior and posterior trunk vertebrae are represented. The largest ones reach a centrum length of about 7.5 mm. These vertebrae have a distinct ventral keel, the morphology of which is variable probably in relation with the position of the vertebra along the column. In those that can be interpreted as anterior trunk vertebrae (Fig. 23a-o, t-u), the keel is narrow, tall and sharp. It expands to various degrees at the posterior end. In the posterior portion of the trunk (Fig. 23p-s), on the other hand, the keel is rather wide and distinctly flattened, with a rather constant width. Among vertebrae interpreted as coming from this portion of the column, only BRS4/H/35 possesses a keel that expands towards the posterior end (Fig. 23s). The distance between the posterior end of the keel and the condyle is also subject to a certain variation. Some vertebrae possess very large subcotylar tubercles, which are poorly developed in others (e.g., BRS25/H/222). Subcentral grooves are poor-

ly marked in anterior trunk vertebrae (Fig. 23d, g, i, o, t), but deeper in posterior ones (Fig. 23p, s). Some specimens preserve the paradiapophyses. These are well developed and the parapophyseal portion is roughly similar to the diapophyseal portion in size. There is no parapophyseal process. Prezygapophyseal processes are preserved only in few fragments (e.g., BRS5bis/H/19-20; Fig. 23w-x) represented by the prezygapophyseal area, with BRS19/H/18 as the only exception preserving their base (Fig. 23a-d). When complete the processes are slender, very long (approximately as long as the facet) and pointed. BRS19/H/18 preserves a strongly vaulted neural arch in posterior view (Fig. 23c).

Remarks. These vertebrae are herein referred to *Malpolon* because of the large size and the long, slender and pointed prezygapophyseal processes (Szyndlar 1984, 1991a). A thin and sharp (i.e., unflattened) hemal keel was also considered diagnostic for the genus by Szyndlar (1984, 1991a), but our own observations on comparative material at our disposal confirmed that variation is present in this feature, with vertebrae coming from the posterior portion of the trunk that carry a flatter and wider keel. The extant *Malpolon monspessulanus* (Hermann, 1804) seems not to show the strongly developed subcotylar tubercles visible in at least some of the vertebrae from Monticino Quarry. This suggests that the late Miocene taxon might belong to a different species. Vertebrae of the extinct *Malpolon laurenti* (Depéret, 1890) are very similar, or even identical, to those of *M. monspessulanus* according to Hoffstetter (1939), thus hinting at a similarly different taxonomic identity. However, the largest vertebra described and figured by Depéret (1890), which is from the cloacal area, has a shorter appearance than the *Malpolon* from Monticino, even though we only have trunk vertebrae at our disposal. Moreover, the French species seems to have shorter prezygapophyseal processes and a lower hemal keel according to Depéret's (1890) descriptions. *Malpolon mlynarskii* Szyndlar, 1988 may possess developed subcotylar tubercles (see Szyndlar 1988: fig. 2.3), but the neural arch has straight sides in posterior view, not as convex as in the Monticino vertebra for which this feature is known. The specific identity of the *Malpolon* from Monticino Quarry is therefore uncertain and we here refrain from identify it more precisely than at genus level, also considering the general poor preservation of most of the vertebrae.

Family Viperidae Oppel, 1811

Genus *Vipera* Laurenti, 1768

Vipera s.l. ("Oriental vipers" group)

Fig. 24a-d

Referred material: Thirty-nine trunk vertebrae (BRS5bis/H/14; BRS6/H/19; BRS9/H/16; BRS15/H/2; BRS18/H/10; BRS19/H/3, 22; BRS25/H/220-221, 228, 249); eight fragments of trunk vertebra (BRS25/H/50, 76, 97, 284).

Description. BRS19/H/3 is a very large vertebra (Fig. 24a-b), with a centrum length of about 9.5 mm. It is procoelous, elongated but rather short, and robustly built. On the ventral surface of the centrum, a distinct hypapophysis is present. Only its basis is preserved. Anteriorly, the hypapophysis is represented by a sharp keel, flanked by very shallow subcentral grooves. The subcentral ridges are low and robust. The right side of the anterior portion of the vertebra is broken off and so only the small left paracotylar foramen is still visible (Fig. 24b). Part of the anterior cotyle is also missing, but it was clearly larger than the neural canal in origin. On the left side, para- and diapophysis have roughly the same size (Fig. 24a). A short and slender parapophyseal process is present. Both pre- and postzygapophyses are missing. Even though the right portion is missing, the overall morphology of the zygosphenes is still recognisable. It has a very slightly wavy anterior margin, with a very small central lobe. On the left side, a small lateral lobe is visible. The neural spine is broken, as well as the entire posterior portion of the neural arch. The other vertebrae are less preserved, but share with BRS19/H/3 similar morphology, robustness, and size range. Some fragmentary vertebrae preserve a larger portion of the hypapophysis (Fig. 24c-d), which is robust and appears straight and well developed.

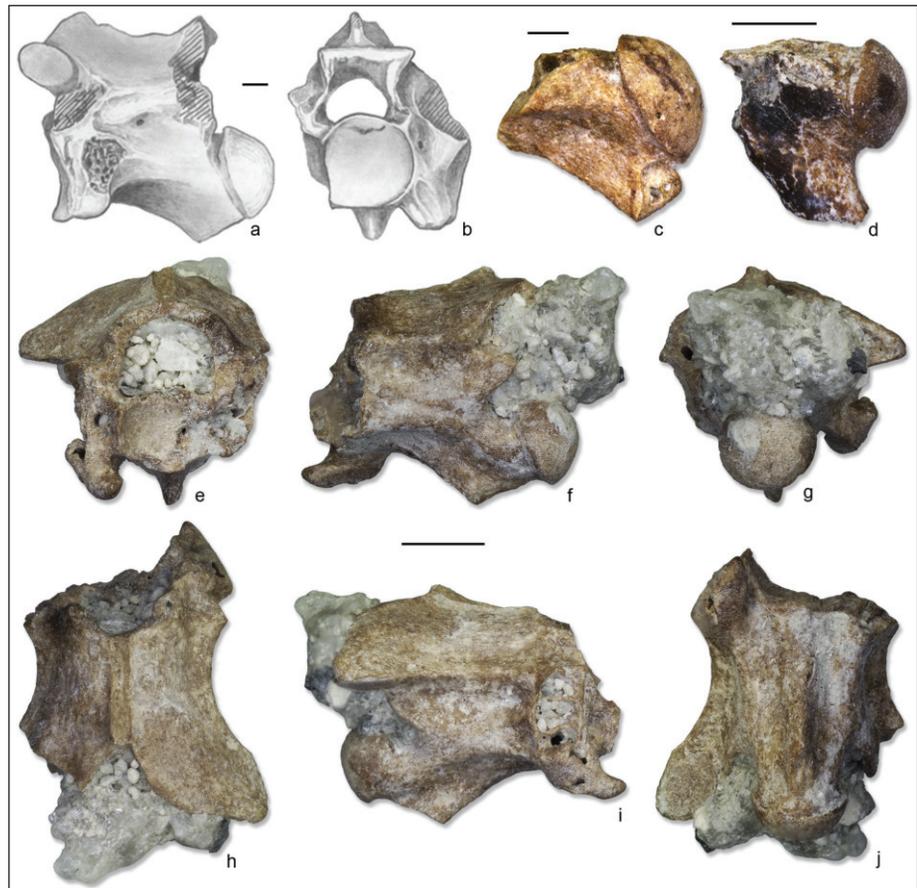
Remarks. The presence of a possibly straight hypapophysis, rather short centrum, overall robust morphology and very large size, and large cotyle and condyle allow attribution of these vertebrae to a member of the oriental vipers species complex (Szyndlar 1991b; Szyndlar & Rage 1999; Bailon et al. 2010).

Vipera sp. 2

Fig. 24e-j

Referred material: One trunk vertebra (BRS25/H/232).

Fig. 24 - Viperids from Monticino Quarry - *Vipera* s.l. ("Oriental vipers" group): trunk vertebra (BRS19/H/3) in left lateral (a) and anterior (b) views; fragment of trunk vertebra (BRS25/H/50) in left lateral view (c); fragment of trunk vertebra (BRS25/H/97) in left lateral view (d). *Vipera* sp. 2: trunk vertebra (BRS25/H/232) in anterior (e), left lateral (f), posterior (g), dorsal (h), right lateral (i) and ventral (j) views. Scale bars = 1 mm.



Description. BRS25/H/232 is a poorly preserved, small trunk vertebra, missing most of the anterior end of the bone (except for a small part of the anterior cotyle and the right parapophyseal process), most of the hypapophysis, the neural spine and the left posterolateral corner of the neural arch. The overall shape of the vertebra is anteroposteriorly elongated, with a lightly-built construction. Ventrally, the base of the hypapophysis is preserved and it is possible to infer that the latter was well developed. Laterally, the subcentral grooves are shallow and the subcentral ridges are lowly prominent. Based on what remains of the anterior end of the vertebra, it is possible to state that the neural canal was either as large as or maybe even narrower than the anterior cotyle. The preserved parapophyseal process is moderately slender and pointed (Fig.24i). The interzygapophyseal ridges are well developed. The single zygapophysis preserved, the right postzygapophysis, is subhorizontal. In posterior view, the neural arch is distinctly roof-shaped (Fig. 24e, g).

Remarks. A second viperid species is represented by this small and lightly built vertebra, provided with hypapophysis and roof-shaped neural

arch (Szyndlar 1984, 1991b). The small size and the low robustness hints for attribution to a small species and not to the large and robust oriental vipers. Distinction between small species of European viperids (namely, the *Vipera aspis* and *Vipera berus* complexes; Szyndlar 1991b; Bailon et al. 2010) is, however, difficult based on such a few and poorly preserved record. Because of this, this specimen is here attributed only to a second, smaller viper.

Colubroides indet.

Fig. 25

Referred material: Seven trunk vertebrae (BRS25/H/133-134, 289; BRS27/H/11).

Description. These few trunk vertebrae are too poorly preserved to be significantly described. They are elongated and provided with an hemal keel. Some more information could be provided for BRS25/H/134 (Fig. 25). This very large and robustly-built trunk vertebra is moderately preserved, but it displays a strong degree of wearing caused by an indeterminate agent. This hinders a confident recognition of the original morphology of most

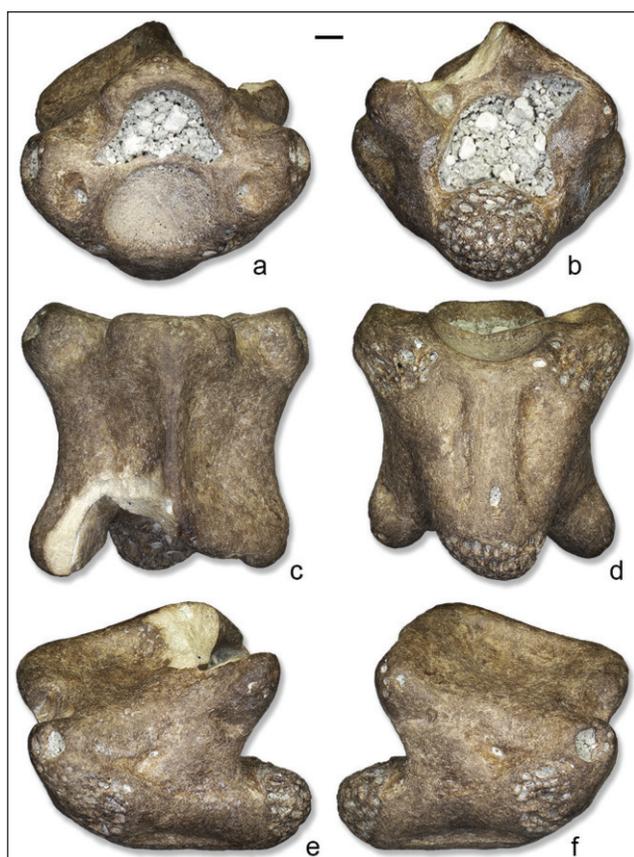


Fig. 25 - Indeterminate Colubroides from Monticino Quarry - Colubroides indet.: trunk vertebra (BRS25/H/134) in anterior (a), posterior (b), dorsal (c), ventral (d), left lateral (e) and right lateral (f) views. Scale bar = 1 mm.

of its structures, because it is not clear how much the preserved morphology is influenced by the wearing. Nevertheless, it clearly has an elongated procoelous centrum, with a wide hemal keel (Fig. 25d). The hemal keel appears moderately distinct and flanked by rather shallow subcentral grooves, even though, as mentioned before, this might be a result of the wearing as well.

Remarks. Elongated trunk vertebrae with a hemal keel are a feature of “Colubrines” according to Szyndlar (1984, 1991a), but this taxon included snakes that are currently referred to different families. Because of their poor preservation, these vertebrae cannot be identified more precisely than as indeterminate Colubroides, even though the absence of an hypapophysis prevents assignment to both natricids and viperids. The very large and robust morphology of BRS25/H/134 and its wide hemal keel, a combination of feature that is not seen in any other snake already recognised in Mon-



Fig. 26 - Possible indeterminate snake from Monticino Quarry - ?Serpentes indet.: tooth-bearing bone (BRS9/H/17) in medial (a) and lateral (b) views. Scale bar = 1 mm.

ticino, suggest that another large colubroid snake was present in the assemblage, even though it is currently not possible to identify it.

Serpentes indet.

Remarks. See the Supplementary Information for a list of the remains identified only as Serpentes indet.

?Serpentes indet.

Fig. 26

Referred material: One tooth-bearing bone (BRS9/H/17).

Remarks. A small fragment of tooth-bearing bone could pertain to a snake. It is elongated and carries three partial teeth, plus an empty space that is as wide as a tooth and could therefore have hosted a fourth one even though no sign of such a tooth is present. Teeth were most likely conical, but the tip is always missing and thus this cannot be confirmed. They are fused with the tooth-bearing bone in a subpleurodont way.

(Non-snake) Squamata indet.

Remarks. See the Supplementary Information for a list of the remains identified only as indeterminate lizards.

Class **AVES** Linnaeus 1758
 Order **Galliformes** Temminck, 1820
 Family Phasianidae Vigors, 1825
 Phasianidae indet.

Fig. 27a-b

Referred material: One proximal fragment of left scapula (BRS24/Av/3); one proximal left coracoid (BRS24/Av/1); one shaft of right coracoid (BRS25/Av/6); one distal right humerus (BRS19/Av/2); one distal left ulna (BRS86/Av/1); one proximal right ulna (BRS24/Av/2); one fragment of proximal left carpometacarpus (BRS4/Av/1); one proximal right carpometacarpus (BRS15/Av/1); two complete left wing phalanges (BRS4/Av/2; BRS5b/Av/2).

Description. All the remains are extremely fragmented, with the exception of the distal right humerus BRS19/Av/1 (Fig. 27b) and the proximal left coracoid BRS24/Av/1 (Fig. 27a). Despite the preservation status, in all the remains it is possible to detect at least one morphological character of the Phasianidae, as described by Göhlich & Mourer-Chauviré (2005).

Remarks. The fossil remains from Monticino belong to a middle species of Phasianidae, similar in size to the extinct *Palaeortyx gallica* Milne-Edwards, 1869 or *Palaeocryptonyx donnezani* Depéret, 1892. The first species has been reported from several Oligocene and Miocene European localities (Göhlich & Mourer-Chauviré 2005); moreover, it has been also tentatively identified from the almost coeval site of Moncuoco Torinese (Colombero et al. 2017). *Palaeocryptonyx donnezani* is commonly found in Pliocene and Early Pleistocene sites in Mediterranean Europe (Pavia et al. 2012; Bedetti & Pavia 2013). The fragmentary status of the specimens described herein prevents any further taxonomical attribution, since the osteological differences among the various middle-sized Phasianidae can be detected, in some cases with uncertainty, only with complete bones, as pointed out by Göhlich & Mourer-Chauviré (2005) and Louchart (2011).

The Phasianidae are among the most common avian taxa in the Paleogene and Neogene fossil record, with a large number of described fossil taxa, the relationships among which are not always clarified (Mlíkovský 2002, Göhlich & Mourer-Chauviré 2005). The oldest representatives of the crown group Phasianidae dates back to the early Oligocene of France (Mayr 2017). After the early Oligocene, they became much more common in the Old World fossil record (Mayr 2017), sometimes representing the dominant group in the bird assemblages.

Order **Otidiformes** Wagler 1830
 Family Otididae Rafinesque, 1815
 Otididae indet.

Fig. 27c

Referred material: One distal fragment of a left tibiotarsus (BRS5b/Av/1).

Description. BRS5b/Av/1 is a portion of a distal tibiotarsus with the condylus medialis, sulcus extensorius, pons supratendineus, and a short portion of shaft well preserved. The condylus lateralis is missing and the incisura intercondylaris is preserved only in its medial part. A tuberculum on the lateral distal side of the pons supratendineus is clearly visible and well preserved. The distal edge of the pons supratendineus is characterized by a ridge that runs for the abovementioned tuberculum to the proximal side of the condylus medialis.

Remarks. The tibiotarsus, even if incomplete, shows the general features of Otididae, especially the presence of the tuberculum and the ridge on the distal edge of the pons supratendineus, which allow to recognize them from the other Gruiformes.

This incomplete tibiotarsus belongs to a small species of Otididae, similar in size to the recent *Tetrax tetrax* Linnaeus, 1758. The fragmentary status of the specimen does not allow to further clarify its taxonomic attribution, even at a tentative level. Nevertheless, the presence of a shaft portion allows to exclude its attribution to the similar-in-size genus *Gryzaja* Zubareva, 1939, which shows a very peculiar blade-shaped shaft of the tibiotarsus (Olson 1985a; Mlíkovský 2002; Mayr 2017).

Bustards have not been recorded before the Miocene and the late Miocene fossils are quite fragmentary and of doubtful affinities (Boev et al. 2013; Mayr 2017). The earliest true Otididae dates back to the Pliocene of Eurasia and North Africa (Mlíkovský 2002; Mourer-Chauviré & Geraads 2010), thereby implying that the record from Monticino Quarry represents the oldest Otididae known so far.

Order **Strigiformes** Wagler, 1830
 Strigiformes indet.

Referred material: One ungual phalanx with broken tip (BRS25/Av/2).



Fig. 27 - Birds from Monticino Quarry - Phasianidae indet.: proximal left coracoid (BRS24/Av/1) in dorsal view (a); distal right humerus (BRS19/Av/2) in cranial view (b). Otidae indet.: distal left tibiotarsus (BRS5b/Av/1) in cranial view (c). Accipitridae indet.: complete ungueal phalanx (BRS5/Av/1), side view (d). Scale bars = 2 mm.

Description. The ungueal phalanx shows a rounded shape of the claw and a rounded and not well-protruding shape of the processus flexorius.

Remarks. The abovementioned characters allow to refer this phalanx to the Strigiformes rather than to the Accipitridae or to any other bird of prey. The inadequate preservation of the specimen and the extreme similarities between the Tytonidae and the Strigidae prevent a more detailed identification.

The fossil record of Strigiformes dates back to the Paleocene (Mayr 2017) and became very rich from the Eocene onward, with the extant genera well established during the late Cenozoic.

Order **Accipitriformes** Vieillot 1816

Family **Accipitridae** Vigors, 1824

Accipitridae indet.

Fig. 27d

Referred material: One complete ungueal phalanx (BRS5/Av/1); two ungueal phalanges with broken tip (BRS25/Av/1; BRS85/Av/1).

Description. The three ungueal phalanges referred to the Accipitridae show a not-rounded shape of the claw and an edged and plantarely well-protruding processus flexorius.

Remarks. The characters described above allow to refer these ungueal phalanges to the Accipitridae. The two phalanges from BRS 25 and BRS 85 belong to a small-sized form, comparable in size to the recent *Accipiter nisus* (Linnaeus, 1758), whereas that from BRS 5 belongs to a middle-sized form, such as the recent *Buteo buteo* Linnaeus, 1758. The fossil record of Accipitridae dates back to the Oligocene, although some middle Eocene specimens have been tentatively referred to this family. Unfortunately, the scarce number and fragmentary status of the remains and their scattered distribution made the phylogenetic affinities of the various fossil forms and their relationships with the crown group poorly constrained.

Order **Passeriformes** Linnaeus 1758

Passeriformes indet.

Referred material: One distal left humerus (BRS85/Av/2); two proximal left ulnae (BRS25/Av/3; BRS25/Av/4); one proximal right carpometacarpus (BRS25/Av/5); one distal right tarsometatarsus (BRS9/Av/1).

Description and remarks. Although the specimens show all the morphological characters of the Passeriformes and allow to exclude other small-

sized bird groups commonly reported in Miocene deposits, such as the Coliidae (Colombero et al. 2017), their poor preservation prevent any further considerations on their relationships within the passerines. During the late Miocene, the Passeriformes already showed a considerable diversity and widespread global distribution, after their first appearance outside Australia during the Oligocene (Mayr 2017).

Class MAMMALIA Linnaeus, 1758

The Monticino Quarry site yielded a diverse mammalian assemblage (39 species are represented at the site). Most of the mammal fauna was described in detail in a series of papers and, for this reason, herein we provide a synthesis of the mammalian taxa identified to date at the site.

Primates are represented by the colobine monkey *Mesopithecus* cf. *pentelicus*, documented by a very limited number of remains. *Mesopithecus* is relatively common in the late Miocene to Pliocene of Eurasia, and, albeit rare, occurs in a number of latest Miocene sites in Italy (Rook 1999; Alba et al. 2014). Two fragmentary enamel fragments (a splinter of a tusk and a molar fragment) are the only remains documenting proboscidean occurrence. Albeit the impossibility to attribute them to a specific taxon, the molar fragment would suggest the presence of a gomphotherid mastodont (Ferretti 2008). At Monticino, Carnivora are recorded by five species, belonging to four families. *Eucyon monticinensis* (Rook 1992, 2009) is a small primitive dog, well represented at Monticino, among the oldest European representatives of the family Canidae. The genus *Eucyon* is the earliest advanced member of the tribe Canini, first occurring in the Clarendonian (late Miocene; 12-9 Ma) of North America and expanding its geographic range into the Old World by the end of the Miocene (Rook 2009). A single mandibular ramus is assigned to *Mellivora benfieldi* (Rook et al. 1991); this large mustelid represents the only occurrence of the taxon outside the African continent, where it is a relatively common carnivore in late Miocene to Pliocene sites (Haile Selassie & Howell 2009). The Hyaenidae family is represented by two different species. A fragmentary skull and a few dental and postcranial remains represent *Thalassictis* (*Lycyaena*) ex gr. *chaerethis-macrostoma*, a large bone-cracking

hyaena well represented during the late Miocene across the Eurasiatic continent from Pakistan to Greece (Rook et al. 1991). The most abundant carnivore at Monticino is the small hyaenid *Plioviverrops faventinus* (Torre 1989) (Fig. 2). *Plioviverrops* is a mongoose-like, carnivorous/insectivorous/omnivorous type (Werdelin & Solounias 1996), with a specialized dentition characterized by the increasing cusps height in molars and premolars. *Plioviverrops faventinus* is one of the most advanced and specialized species within the evolutionary lineage of the genus. The carnivore guild is completed by the occurrence of a small Felidae belonging to “*Felis*” ex gr. *attica-christolli*. This group of felids is documented in a number of localities across the Mio-Pliocene boundary in the Old World (Rook et al. 1991). One of the rarest mammals documented within the rich mammals assemblage is the aardvark (Tubulidentata) *Orycteropus* cf. *gaudryi*. Albeit relatively uncommon, the genus *Orycteropus* is documented across a wide geographic range during Mio-Pliocene time at Mediterranean latitudes. The Monticino fossils represent the westernmost occurrence of *Orycteropus* in the Miocene of Eurasia (Rook & Masini 1994). Perissodactyla are represented by few remains of rhinoceros and hipparionines. Rhinoceros specimens have been assigned to “*Dibopius*” *megarhinus*, a species traditionally considered as a typical Pliocene taxon but recently recorded in several late Miocene (MN 12 and MN 13) mammal assemblages of eastern Europe (Pandolfi et al. 2015). The occurrence of “*D.*” *megarhinus* in the latest Messinian of Italy (in addition to Monticino, the species is recorded also at Baccinello V3 and Moncucco Torinese) confirms the presence of this species during the late Miocene in Europe and suggests a dispersal of eastern European taxa in western Europe and Italy during the latest Miocene (Pandolfi & Rook 2017). The small horse sample is attributable to a single species of hipparionine horse (Rook & Bernor 2013) and is referred to *Hippotherium malpassii*, a species named based on the rich hipparionine remains from the late Messinian of Baccinello V3 in southern Tuscany (Bernor et al. 2011). Arctiodactyla (like Perissodactyla) are also underrepresented at Monticino with respect to coeval European sites. The best represented bovid from the site, and among the most common taxa in the assemblage, is the caprine antelope *Oioceros occidentalis* (Pandolfi et al. 2021c). The species stands as the recentmost representative of an evolutionary

lineage that originated in late Vallesian and Turolian of Greece and Turkey (Masini & Thomas 1989). The species has been recently recorded in other late Miocene Italian localities (Pandolfi et al. 2021c) such as Verduno in Piedmont (Colombero et al. 2014) and Borro Strolla in Tuscany (Abbazzi et al., 2008a). Other scanty Bovidae remains allow the identification of four other bovids at Monticino: Antilopinae indet. (medium size), Bovidae indet. (small-size), cf. Boselaphini, and cf. *Parabos* (Pandolfi et al. 2021c). A large sized Suidae is represented in the assemblage and referred to as *Propotamochoerus provincialis*, a species with a wide distribution in the late Miocene of Europe (Gallai & Rook 2011). Finally, a small number of brachydont teeth as well as a horn fragment testify the occurrence of small deers belonging to *Pliocervus* sp. and to *Procapreolus* cf. *loczyi*, two quite widespread taxa in late Miocene sites across western Europe, including other latest Miocene Italian sites (Pandolfi et al. 2021b).

Small mammals are actually the best represented taxa at Monticino, due to the concentration of mostly dental remains resulting from taphonomic concentration. Rodents represent the most abundant taxa among the assemblage (12 species documented by thousands of dental remains). Murids are the most abundant family, represented by five species (De Giuli 1989): *Stephanomys debruijnii* (a species belonging to a genus that spread in the late Miocene and early Pliocene); *Centralomys benericettii*, a second murid described as a new species on the basis of material from Monticino (De Giuli 1989) and later on identified also in other Italian sites such as Verduno in Piedmont (Colombero et al. 2014); *Paraethomys anomalus*; *Occitanomys* sp.; and *Apodemus* cf. *gudrunae*. Two species belong to the family Cricetidae (*Cricetus* cf. *barrierei* and *Ruscinomys* cf. *lasallei*), two to Sciuridae (*Atlantoxerus* cf. *rhodius* and *Hylomyscus* sp.), and two to the Gliridae (*Myomimus* sp. and *Muscardinus* sp.). The largest rodent present in the fauna is the porcupine (Masini & Rook 1993) identified as *Hystrix depereti* (Weers & Rook 2003). Lagomorphs are relatively abundant, with the leporid *Trischizolagus* sp. (Angelone et al. 2020) and the ochotonid *Prolagus sorbinii* (Masini 1989; Angelone et al. 2020). Among insectivorans (Eulipotyphla), relatively common is the large-sized erinaceid *Parasorex depereti* (Masini et al. 2019), whereas other insectivorans occurring in the assemblage are the small erinaceid *Mioechinus* sp. and the soricids *Neomiosorex*

sp. and cf. *Miosorex pusilliformis* (De Giuli 1989). Finally, Chiroptera are relatively diverse in the assemblage, with six different species (Kotsakis & Masini 1989): the megadermid *Megaderma* cf. *mediterraneum*; the two rhinolophids *Rhinolophus* cf. *kowalskii* and *Rhinolophus* sp.; the vespertilionid *Myotis* cf. *boyeri*; and the two hipposiderids *Hipposideros* (*Syndesmotis*) cf. *vetus* and *Asellia* cf. *mariaetheresae*.

DISCUSSION

Diversity and palaeoenvironmental implications of the Monticino non-Mammal vertebrates

A remarkable diversity for the Monticino fissures palaeofauna was already pointed out for its mammalian component (Rook et al. 2015; see also above). Our detailed study of the non-mammalian remains highlighted a high diversity also in the palaeoherpetological assemblage, with at least 26 (27 if the two fossils attributed to either indeterminate scincids or possible scincids indeed belong to different species) taxa identified (Tab. 1). Birds and especially fish are, on the other hand, much less diverse, with just five and three taxa recognised respectively. In the Monticino herpetofauna, reptiles are far more diversified than amphibians: 18 (or 19) taxa versus only eight. This might be related to a certain degree of aridity that characterized the palaeoenvironment in the area when the sediments accumulated in the fissures. This somehow dry environment is suggested by the presence of reptile taxa such as the agamines, eremiadine lacertids, and sand boas of the genus *Eryx* (Speybroeck et al. 2016), but also by otidid and phasianid birds. Water bodies were nevertheless present, as documented by fishes and supported by the fact that all amphibians and some of the identified reptiles (*Mauremys*, the crocodylians, *Natrix*) are strictly linked to the availability of water. Remains of green toads (*Bufo* gr. *viridis*) suggest that at least some of these water bodies might have been temporary. The other information given by the Monticino Quarry fossil fauna hints for a complex environment surrounding the fissures (most of the ecological data for the taxa reported in the following part of the text are from Rook et al., 2015, and Speybroeck et al., 2016). *Pelobates*, eremiadine lacertids, amphisbaenians, and *Eryx* indicate loose/sandy soils, but the same *Eryx*

	Ibis	Itris	2	3	4	4?	5	5bis	5tg2	6	8	9	15	16	18	19	24	25	27	28	28?	85	86	No Number	?	
Fish																										
<i>Aphanius crassicaudus</i>			X																							
Cichlidae indet.																?										
Sciaenidae indet.																?										
Amphibians																										
<i>Lissotriton</i> sp.																		X								
Urodela indet.	X		X															X								
<i>Latonia</i> sp.	?																	?								
Discoglossioidea indet.																		?								
<i>Bufo</i> gr. <i>bufo</i>																		cf.						cf.		
<i>Bufo</i> gr. <i>viridis</i>	X			X					X				X		X	X	X	X						X		
Bufoidea indet.				X				X				X			X			X								X
<i>Hyla</i> sp.																		cf.								
<i>Pelobates</i> sp.									X									X								X
<i>Pelophylax</i> sp.				X						X																
Anura indet.	X		X	X	X	X		X	X	X		X			X	X	X	X	X	X	X				X	
Reptiles																										
<i>Testudo</i> s.l.																		X		X						X
<i>Mauremys</i> sp.																		X								
Testudines indet.		X						X	X	X	X							X		X				X		X
Crocodylia indet.				X						X																
Agaminae indet.																		X								
Eremiadini indet.				X				X	X	X								X	X					X		X
Lacertidae indet.				X	X			X	X		X		X	X	X	X	X	X	X	X	X					X
Scincidae indet.																		X	?							
<i>Ophisaurus</i> sp.				X	X			X	X									X	X	X	X					
<i>Pseudopus</i> sp.																		X	X		X					
non-Anguis Anguinidae indet.	X			X	X			X	X	X	X	X	X	X	X	X	X	X	X	X	X				X	X
<i>Varanus</i> sp.								X		X								X	X					X		
Amphisbaenia indet.																		X	X							
<i>Eryx</i> cf. <i>jaculus</i>			X	X	X			X	X	X	X	X				X	X	X	X	X	X					
<i>Platyceps planicarinatus</i>																										X
cf. <i>Paleoheterodon arcuatus</i>																					X					
<i>Natrix</i> sp.													X													
<i>Malpolon</i> sp.	X			X	X			X	X	X		X	X	X	X	X		X		X	X				X	
<i>Vipera</i> s.l. ("Oriental vipers" group)								X		X	X	X			X	X		X								
<i>Vipera</i> sp. 2																		X								
Colubroides indet.																		X	X							
Serpentes indet.	X		X	X	X	X		X	X	X	X	X	X	X	X	X	X	X	X	X	X				X	X
(non-snake) Squamata indet.			X		X			X	X		X	X	X	X	X	X	X	X			X	X			X	X
Birds																										
Phasianidae indet.				X				X					X			X	X	X						X		
Otididae indet.								X																		
Strigiformes indet.																		X								
Accipitridae indet.							X											X					X			
Passeriformes indet.												X						X					X			

Tab. 1 - Distribution of the identified taxa in the different Monticino Quarry fissures.

and the agamines support the presence of rocky habitats as well. Similarly, taxa related to open habitats were found (Eremiadini, *Eryx*, Otididae, Phasianidae, and *Orycteropus* among the mammals), but the tentative identification of a tree frog, if correct, may suggest that bushy areas were not completely absent from the surroundings. Presence of woody environments could be supported by the very few

primate remains found in the site (Rook et al. 2015). A more vegetated (and more humid) environment dominated by ferns was also suggested by palynological data (Bertolani Marchetti & Marzi 1988; Rook et al. 2015), based on sediments that are however slightly younger than those in which the fossil faunas were collected. Adding to this, crocodylians and *Varanus* support a warm climate, which was al-

ready reported for Monticino based on the recovery of bats of the genus *Megaderma* (Rook et al. 2015).

Together with the previously mentioned taxa with specific ecological requirements and other taxa the ecology of which is too wide to be significant for the palaeoenvironmental reconstruction (either because they are generalist like *Bufo gr. bufo* or *Pelophylax* or because the identification was possible only at a high taxonomic level), there are a few extinct taxa in the Monticino non-mammalian fossil assemblage that are worth discussing. First of all, the Monticino *Malpolon* sp. displays features that are not known in the extant *Malpolon* (i.e., the developed subcotylar tubercles in at least some vertebrae) and might therefore represent an extinct species of this genus. Living European representatives of *Malpolon* are found in Mediterranean habitats, with a complex of different environmental features such as maquis, sand dunes, humid areas, and rocky outcrops (Speybroeck et al. 2016). The Afroasiatic *Malpolon moilensis* (Reuss, 1834), on the other hand, seems to be related to even more arid habitats (Trape & Mané 2006; Oudjani et al. 2016). Extinct members of the genus may have had different ecological requirements of course, but its occurrence in Monticino Quarry may suggest that at least the taxon inhabiting this area during the Miocene shared a similar environment with living European congeners. It has to be noted, however, that this may not hold true for other extinct *Malpolon* as well; for example, the palaeoenvironment of Layna, the Pliocene type locality of *M. mlynarskii*, is thought to have been more wooded, with only occasional savanna and desertic areas (Domingo et al. 2013). Definition of specific ecological requirements is even more difficult for *P. planicarinatus* and *P. arcuatus*. The latter has no living close relatives to which its environmental preferences could be correlated, whereas affinities of the former with the genus *Platyceps* still has to be thoroughly confirmed through a real phylogenetic analysis. Thus, possible ecological data can be only presumed for both based on the palaeoenvironment reconstructed for the localities where they were found, which involve just Monticino Quarry, their respective type localities, and, only for *P. arcuatus*, an additional locality. According to Bachmayer & Szyndlar (1985) and Tempfer (2005), *P. planicarinatus* lived in a warm, Mediterranean climate with relatively dry conditions, but with available woods and water bodies in Kohfidisch. The palaeoenviron-

ment was therefore similar in the Austrian locality and Monticino Quarry, even though the latter could have been less vegetated. Closer affinities to dry woodlands could maybe explain the higher abundance of *P. planicarinatus* remains in Kohfidisch. As far as *P. arcuatus* is concerned, this other species is reported from La Grive-Saint-Alban and Sansan (Rage & Holman 1984), adding to the new occurrence in Monticino. Based on the avian assemblage, Cheneval (2000) reconstructed a wooded environment for Sansan, an hypothesis later supported also by Pavia (2014). Woods were likely present at La Grive as well, given that the locality yielded fossils of primates (Mein & Ginsburg 2002). Therefore, *P. arcuatus* might have been either more linked to wooded environments (thus possibly explaining the low number of remains identified in Monticino) or less specialized in terms of ecological requirements.

Aphanius crassicaudus, in the end, lived in a wide spectrum of different waters, from brackish to hyperaline (Gaudant 1979; Gaudant et al. 1988; Caputo et al. 2009). Together with the rest of the ichthyofauna, this indicates that estuarine or lagoonal conditions were represented not far from the area where the Monticino karstic fissures originated. Still, the fact that only very few remains of fish were found in the fissures suggests that main water bodies were not in direct contact with them. Fish remains may have been brought into the Monticino Quarry fissures by flooding events, as is also the case for some remains of large mammals showing erosion signs due to water transportation (Rook et al. 2015). The same floods could also have buried animals that either used the fissures as dens or were trapped in them. Articulated remains of animals that died in the fissures and were not subsequently disturbed by scavengers or other factors are indeed present (Rook et al. 2015). On the other hand, the accumulation of the very abundant small vertebrate remains, particularly those of the small mammals, has been interpreted as the result of the accumulation of prey remains by birds of prey (De Giuli et al., 1988; Rook et al., 2015). In contrast with what stated in previous studies (De Giuli et al. 1988; Rook et al. 2015), the presence of mostly isolated mammal teeth and heavily fragmented postcranial elements, both with extensive digestion tracks and polished surfaces, suggests that the main accumulation agent was not a bird of prey, either nocturnal or diurnal, but more likely a mammalian predator (An-

drews 1990) of small or middle size, extremely specialized in small ground vertebrates (thus including amphibians and reptiles as well), rather than a more generalist species. Such hypothesis is in agreement with the dietary habit of the most abundant predator of the Monticino assemblage, the small hyaenid *Plioiverrops* (cfr. Werdelin & Solounias 1996) as well as with the recent dietary evaluation of the small canid *Eucyon* (Bartolini Lucenti & Rook 2020). Herpetofaunal remains with possible signs of digestions are also present. This hypothesis is also supported by the virtual absence of bird remains, less than 20 specimens among the several thousands of bones and teeth of the other taxa, which is at odds with other fissure-filling sites with bones accumulated by birds of prey (Ballmann 1969, 1973, 1976; Andrews 1990; Abbazzi et al. 2004; Pavia 2004; Pavia & Mourer-Chauviré 2011; Bedetti & Pavia 2013), where birds are always present, sometimes in large numbers, including the predators responsible of the bone accumulation.

Palaeobiogeographical insights

Miocene European continental faunas were strongly affected by immigration from both Asia and Africa, with the latter which came in contact with Europe as soon as the early Miocene (MN 3; Rögl 1999; Koufos et al. 2005). During the whole Epoch, new animals entered the continent following different dispersal waves (among others, Rage & Roček 2003; Koufos et al. 2005; Rage 2013; Georgalis et al. 2016a, and reference therein). For amphibians and reptiles, this led to a modernization of the fauna, following the extinction of peculiar Paleogene taxa at the Oligocene/Miocene boundary or shortly after (e.g., amblyodont lacertid lizards; Villa & Delfino 2019b) and with the appearance of close relatives of modern groups (e.g., relatives of extant urodeles and anurans, green lizards; Bailon et al. 1988; Čerňanský 2010; Villa & Delfino 2019b). It is therefore not surprising to find taxa with Afro-Asian affinities in the late Miocene fauna from the Monticino Quarry fissures, as well as taxa linked with extant groups in its herpetological component. This is the case, for example, for the toads, as both the green toads and, even if only tentatively identified at Monticino Quarry, the common toads belong to groups that are still present in Europe. Bufonids were reported in the European Paleogene herpetofauna preceding the Eocene, but then they

went extirpated and reappeared in the continent in the MN 4 (Rage & Roček 2003). Both European green toads, which are the first to appear in Miocene Europe (MN 4/5 of Spain and France; Alférez Delgado & Brea López 1981; Bailon & Hossini 1990; Rage & Roček 2003), and common toads may have an Asian origin (Stöck et al. 2006; Garcia-Porta et al. 2012; Syromyatnikova 2015). Bufonids were already known in the European Messinian, even from localities very far from each other such as in Spain and Hungary. In Italy, late Messinian fossil green toads were recently reported from Piedmont (Colombero et al. 2014, 2017), but the common toad remains from Monticino Quarry represent the oldest known occurrence of this bufonid group in the Apennine Peninsula. Sanchiz & Roček (1996) considered *Hyla* as a possible Miocene Asian immigrant as well, even though at least some of the extant European populations are the result of more recent dispersal events from Africa likely mediated at least in part by human introduction (Recuero et al. 2007). Other anurans found at Monticino Quarry such as *Latonia*, *Pelobates*, and *Pelophylax* were persistent inhabitant of Europe since Paleogene times (Roček 1994; Rage & Roček 2003; Vasilyan 2018). At the moment, it is impossible to hypothesize the palaeobiogeographical affinities for the indeterminate possible discoglossoid found in fissure BRS 25. The urodele *Lissotriton* is widely distributed in Europe during the Miocene, following a first appearance in the late Oligocene (Böhme 2008). This first occurrence is referred to the species *Lissotriton rohrsi* (*Triturus rohrsi* in the original identification by Böhme, 2008), which was referred to *Ommatotriton* by Martín et al. (2012) but recently considered as better allocated to *Lissotriton* by Georgalis et al. (2019). In any case, clear geographical affinities for this late Paleogene/early Neogene *Lissotriton* populations in Europe are not well understood.

Among the reptiles, one of the most interesting taxa in palaeobiogeographical terms is the member of the Eremiadini tribe. Currently, representatives of this lacertid tribe are largely distributed in arid habitats in Africa, but they are also found in Asia and even in Europe (Sindaco & Jeremčenko 2008; Sillero et al. 2014; Speybroeck et al. 2016; Uetz et al. 2019). According to Arnold et al. (2007), Eremiadini originated probably in the middle Miocene (around 16 Ma), in association with colonization of Africa by lacertids passing through Arabia.

A similar, but slightly younger divergence time for the split between Eremiadini and Lacertini was also found by Guo et al. (2011). In contrast with this, Hipsley et al. (2009) obtained an Eocene split for the two tribes, thus pushing back their origin and consequently the possible colonization of Africa. Unfortunately, this controversy cannot be solved by the fossil record at the moment, given that there are no undisputed stem or crown Eremiadini remains from either the Paleogene or the first half of the Miocene. *Succinilacerta succinea* (Boulenger, 1917) from the Baltic amber was originally referred to the Eremiadini genus *Nucras*, but real affinities with this and/or other African lacertids should be thoroughly assessed with new analyses of this taxon possibly including study of its osteology using CT-scans. The oldest fossil occurrence of Eremiadini is then that attributed to *Eremias* sp. by Rage (1976) from the Serravallian (around 13 Ma) of Beni Mellal, in Morocco. Later, *Eremias* was also reported from the Zanclean of Kazakhstan (Vasilyan et al. 2017). *Eremias* remains from the late Miocene of Mongolia (Böhme 2007) were recently reallocated to indeterminate Eremiadini (Čerňanský & Augé 2019). Not considering the Monticino Quarry occurrence, the oldest (and only pre-Quaternary) Eremiadini report in Europe is possibly a still unpublished and unverified *Acanthodactylus* sp. mentioned by Böhme & Ilg (2003) from the Zanclean of La Gloria 4, in Spain (Villa & Delfino 2019b). As far as the extant European populations are concerned, molecular data hint at a recolonization of the continent either from Asia or Africa, rather than at a derivation from an ancient European stock. As a matter of fact, the European *Acanthodactylus erythrurus* (Schinz, 1833) entered Europe from Africa and separated from its African relatives likely around the Miocene/Pliocene boundary (Fonseca et al. 2009). Origin of *Eremias arguta* (Pallas, 1773) is also likely dated to a comparable time (Guo et al. 2011; Poyarkov et al. 2014), but it probably occurred in western Asia; northwestern populations of this species (i.e., those reaching Europe) show a low genetic differentiation, thus suggesting a recent expansion (Poyarkov et al. 2014). *Ophisops elegans* Ménétries, 1832, in the end, originated earlier in the late Miocene, probably around the Tortonian/Messinian boundary, and colonized eastern Aegean islands (the only part of the European territory where it is found today) from Asia, maybe being unable to move further west due

to the presence of the Mid-Aegean Trench (Kyriazi et al. 2008). Geographical barriers and recent colonization appear therefore to exclude relationships between the Monticino Eremiadini and both extant European *Eremias* and *Ophisops*. Affinities with the *Acanthodactylus* lineage that originated the extant European populations of this genus cannot be ruled out on the same bases, on the other hand. Fonseca et al. (2009) gave a confidence interval comprised between 8.2 and 2.9 Ma for the split of the European lineage, which is not in contrast with a possible diffusion of these lizards towards the Apennine Peninsula resulting in their presence in Monticino in the late Messinian. Nevertheless, this cannot be confirmed at the moment, due to the absence of other Miocene Eremiadini remains in Europe and the impossibility to further identify the fossils studied by us, and therefore other scenarios, such as a different colonization event still occurring in the late Miocene or even earlier from either Asia or Africa or the persistence of a still unknown European lineage, should be considered equally probable at the moment. Thus, the Monticino Eremiadini are of poor help in assessing the palaeobiogeographical affinities of the Monticino fauna. Nevertheless, they represent the only occurrence of this lacertid tribe known so far in the Italian territory, both considering the fossil record (Villa & Delfino 2019b) and the current herpetofauna (Sindaco et al. 2005; Sillero et al. 2014; Speybroeck et al. 2016). They might therefore have been part of a short-living offshoot of the tribe in the area.

Similarly, a few biogeographical information can be retrieved from other reptilian taxa recovered in Monticino Quarry, such as the crocodylians, anguids, most of the lizard taxa identified at suprageneric level, and the amphisbaenians. This is because of the wide distribution these taxa had in Europe in the Neogene and/or the poorly refined taxonomical identification of the herein-studied remains, which hinders a deep understanding of their biogeographical dynamics in the considered times. As far as the crocodylians are concerned, a potential referral to *Crocodylus* could result in another taxon with African affinities in the Monticino fauna. Neogene *Crocodylus* from Europe were considered African immigrants by Kotsakis et al. (2004), mainly on the basis of the old idea that the origins of such genus were related to that continent. More recently, Oaks (2011) demonstrated that *Crocodylus*

originated in Australasia. Nevertheless, Delfino et al. (2007) considered the only confident *Crocodylus* occurrence from Europe, from late Messinian to lowermost Pliocene deposits in southern Italy, to possibly share morphological features with the Libyan *Crocodylus checcchiai* Maccagno, 1947, thus potentially supporting African relationships for the European representatives of the genus. In any case, only (poorly diagnostic) teeth were found in Monticino so far and so the presence of *Crocodylus* (and thus of another Africa-related taxon) in this locality still cannot be ascertained in absence of the discovery of further, more taxonomically-significant fossil material. Asian affinities can, on the other hand, be supposed for *Varanus*, as this is thought to be the case for both European extinct species of the genus currently considered as valid (Ivanov et al. 2018; Villa et al. 2018). *Mauremys* sp. from Monticino has an intermediate morphology of the shell elements between the Italian *M. campanii* and the Greek *M. aristotelica*. These two species were considered as sister taxa by Vlachos et al. (2019), but the Italian species is found in older deposits: thus, a dispersal from Italy towards the Balkans could be a more advisable scenario than the opposite. Chesi et al. (2009) even supported an eastward dispersal of *Mauremys* from central Mediterranean Europe to Arabia and Africa, even though Georgalis et al. (2020) recently proposed a possible alternative (or complementary) way for the passage from Europe to Africa of *Mauremys* through the Sicily-Calabria arch. In this context, it is not clear whether the Monticino Quarry taxon may represent part of a lineage that directly dispersed towards the Balkans (where then it eventually gave origin to *M. aristotelica*) or a descendant of an independent Italian stock deriving from *M. campanii*. Undescribed *Mauremys* remains from the Early Pleistocene of southern Italy (Pirro Nord; Delfino & Bailon 2000; Delfino & Atzori 2013) mentioned by Georgalis et al. (2019) would be significant in better understanding the taxonomy of Apennine *Mauremys*. In contrast with the pattern showed by *Mauremys*, Chesi et al. (2009) reported *Testudo* in Italy only from the Messinian, thus considering it as a later immigrant. However, *Testudo* sp. was recently reported as part of the oldest known assemblage in the late Miocene of Tuscany (Cirilli et al. 2016), even older than assemblages with *Mauremys* from the same area studied by Chesi et al. (2009), and so an earlier appearance of *Testudo* populations in

the Apennine Peninsula is now a fact. Possible affinities with both the middle Miocene *Testudo antiqua* Bronn, 1831 from Germany and the late Miocene *T. amiatae* from Tuscany were highlighted by Cirilli et al. (2016) for the remains studied by them, even though warning that a reevaluation of the latter species is needed. Anyway, considering these affinities, a possible central European origin for the Italian *Testudo* should not be discounted.

The Monticino snake fauna is dominated by descendants of Miocene immigrants. Both oriental vipers and *Eryx* appeared in Europe in the MN 4 (Szyndlar & Rage 1999; Rage 2013), at the same time of the contact of the latter with Africa and Asia. Large viperids are known since the early Miocene in both Asia and Africa (Szyndlar & Rage 1999, 2000). In Asia, they are reported from the Zaisan Basin in Kazakhstan (Chkhikvadze 1985), but these remains were never properly described or figured and so Szyndlar & Rage (2000) warranted caution on them. Rage (2003), on the other hand, published few vertebrae of a large viperid (“Oriental viper” or *Daboia*) from Arrisdrift in Namibia, the age of which is equivalent with either the MN 3 or the MN 4 (Szyndlar & Rage 2000). Based on our current knowledge, therefore, it is not possible to favor either an Asian or an African origin for the Neogene European large viperids, given that the earliest extra-European remains either have uncertain taxonomic affinities (the Asian ones) or their age is more or less comparable with the earliest European fossils (the African ones). The oldest confident occurrences of *Eryx* from both Europe and Asia are rather similar in age: these are from the MN 4-5 of France (Vieux-Collonges; Ivanov 2000) and Kazakhstan (Ayakoz; Malakhov 2005). Possible *Eryx* are reported from older (MN 2-3) sites in Spain and Germany (Szyndlar & Böhme 1993; Murelaga et al. 2002), thus possibly suggesting an older presence in Europe compared to other continents (and maybe also that entrance of this genus in the continent was not related to the connection at MN 4). However, further material with a stronger taxonomical significance is needed before eventually confirming this hypothesis. Nevertheless, *Eryx* does not appear in the African fossil record prior to the Serravallian (Rage 1976; Bailon et al. 2017) and so it is possible that this continent was colonized only later by sand boas. At the species level, the Monticino remains represent the oldest occurrence of a

form morphologically related to the extant *Eryx jaculus*. The same holds true for the Monticino Quarry *Malpolon*, a genus that is otherwise only known from Pliocene to Quaternary remains (Rage 1972; Holman 1998; Bailon 2000; Gleed-Owen 2001; Bailon & Aouraghe 2002; Delfino 2004; Bailon & Blain 2007; Blain et al. 2007, 2008, 2011, 2013; López-García et al. 2008, 2011; Blain 2009, 2015; Jennings et al. 2009; Aouraghe et al. 2010; Pacheco et al. 2011; Laplana et al. 2013; Daura et al. 2015; Bailon et al. 2017; Piñero et al. 2017). Small vipers, belonging to either the *aspis* or the *berus* species complexes, also entered Europe during the Miocene, even though in different moments compared to both oriental vipers and each other. The *Vipera aspis* group is known in Europe since the beginning of the Neogene, whereas *Vipera* gr. *berus* appears in MN 9 (Szyndlar & Rage 1999, 2000; Rage 2013). Moreover, the latter is apparently confined to eastern Europe until MN 17, when a westward spread is finally documented by fossils (Szyndlar & Rage 1999, 2000; Rage 2013). The origins of the Miocene European populations of these two viper groups are not clear, in a similar manner to the oriental viper complex. The *V. aspis* group is known in Africa in the Serravallian (*Vipera maghrebiana* Rage, 1976), thus not really being of help for understanding the origin of the older European occurrences. Chkhikvadze (1985) mentioned the *V. berus* group from the early Miocene of Kazakhstan as well, but, as for the oriental vipers he reported, there are no descriptions or figures and so one should be cautious with this occurrence. The impossibility of assigning the Monticino Quarry vertebra to either of the two small *Vipera* groups further complicates the recognition of biogeographical affinities. Following a stratigraphic rationale, *Vipera* gr. *aspis* could be a more reasonable choice, given the apparent absence of the other complex in this part of Europe at the time. However, morphology should be the first line of evidence when proposing affinities of fossils to specific taxa and so we leave the scenario open here to the alternative possibility of the Monticino *Vipera* sp. 2 being more related to the *V. berus* group, which was already present in eastern Europe when the Monticino Quarry palaeofauna was alive. The other snakes identified in the Monticino Quarry assemblage can give even less palaeobiogeographical information. *Paleoheterodon arcuatus* is known from the French middle Miocene and is

congeneric with a middle to late Miocene North American species, *Paleoheterodon tibeni* Holman, 1964. Considering their similar appearance in the fossil record of both Europe and North America, Rage & Holman (1984) supposed an Asian ancestry for both species, with the two different lineages then spreading towards Europe and North America respectively. *Platyiceps planicarinatus* is additionally known only from central Europe (Bachmayer & Szyndlar 1985, 1987) and the affinities of the indeterminate large Colubroidea represented by the trunk vertebra BRS25/H/134 cannot be tracked. *Natrix*, on the other hand, is widely distributed in the European fossil record, with its first representative found in the Oligocene (*Natrix mlynarskii* Rage, 1988; see also Rage 2013). This wide distribution, both from a geographic and stratigraphic point of view, combined with the impossibility to identify the vertebra recovered in the Monticino Quarry below the genus level, hinders further comments on the affinities of the latter.

When it comes to the other, non-herpetological components of the fauna, the widely-studied Monticino mammals also show the results of dispersals from the East (e.g., presence of *Eucyon*, “*Diboplus*” *megarhinus*; Rook 2009; Pandolfi & Rook 2017) that likely occurred in the latest Miocene, as well as African taxa (*M. benfieldi*, which is solely known in Monticino Quarry outside of Africa; Rook et al. 1991). Issues related to the low precision allowed for taxonomic identification and the wide distribution (and mobility) arise again when considering fish and birds from the quarry from a palaeobiogeographic perspective. This holds particularly true when birds are concerned. As for the fish, *A. crassicaudus* is commonly found in sediments correlated with all the phases of the Messinian Salinity Crisis in the Mediterranean area (e.g., Carnevale et al. 2019). Sciaenids exhibit a wide stratigraphic and geographic distribution during the Neogene (Bannikov et al. 2018). The putative cichlid recognized herein based on a single tooth provides evidence of the African affinity of part of the fish assemblage. As discussed by Carnevale et al. (2003), these and other fish taxa of African origin occupied the northern coasts and rivers of the Mediterranean during the Messinian, with the species *Oreochromis lorenzoi* reported from the Messinian infraevaporitic shales of Gessoso-solfifera Formation. Even if it is not possible to clearly correlate the isolated tooth

form BRS 19 with *O. lorenzoi*, this specimen, even though only tentatively referred to the Cichlidae, suggests the possible persistence of these fishes in the same area even in younger times.

Late Miocene terrestrial vertebrate faunas from Italy

The continental late Miocene of Italy is documented by various sites spread in different parts of the Apennine Peninsula and even the major Italian islands. The best record we have is for the MN 13: sites are located mainly in the north or central north of the Peninsula, but Gravitelli in Sicily is also considered as pertaining to this time span (The NOW Community 2020). Older late Miocene sites are known from Tuscany, but also Sardinia (MN 12) and Calabria (MN 11/12). Age limits from the complex of the deposits in Abruzzo and Apulia (i.e., localities such as Scontrone and the Gargano karstic complex) areas are less clearly defined, but they can be constrained in an interval covering the late Miocene and the early Pliocene (Masini et al. 2010). Altogether, these localities record the presence of three different mammal faunal complexes in Italy during the considered period (Rook et al. 2006). First, in Calabria and Sicily there was a mammalofaunal association showing clear affinities with the African continent (Ferretti et al. 2003; Marra et al. 2011; Marra 2018; Pandolfi et al. 2021a), but also some taxa of European origin (Gallai & Rook 2006; Rook et al. 2006). On the other hand, a strongly endemic insular fauna developed in the Apulian Platform (Freudenthal 1971; Rustioni et al. 1992; Rook et al. 2006; Masini et al. 2010; Savorelli & Masini 2016; Savorelli et al. 2016; Urciuoli et al. 2016; Pavia et al. 2017). Adding to these, a third faunal complex was present in what is now the central north part of the Apennines, even though involving Sardinia as well. This third complex is known as the “*Oreopithecus* Zone Faunas” (OZF) after its most iconic taxon, the hominoid *Oreopithecus bambolii* Gervais, 1872. It is mostly known from Tuscany, in particular the Baccinello-Cinigiano Basin in the province of Grosseto (among others, see Bernor et al. 2001; Rook et al. 2006; Cirilli et al. 2016; Rook 2016), but Fiume Santo in Sardinia also yielded mammals indicative of the complex (Cordy & Ginesu 1994; Cordy et al. 1996; Abbazzi et al. 2008b; Casanovas-Vilar et al. 2011). The OZF record either a large island or a group of smaller islands where endemic

mammals evolved during the first part of the late Miocene (Rook et al. 2006). Immigration events with European incomers in the OZF are also testified during the period of existence of these island, though (Rook et al. 2006). Later, the endemic Tusco-Sardinian mammal assemblage was substituted by a non-endemic assemblage with European affinities in the Messinian (Hürzeler & Engesser 1976; Rook et al. 1999; Abbazzi 2001; Benvenuti et al. 2001; Bernor et al. 2001; Rook et al. 2006), the dispersal of which passed through Piedmont and the Monticino Quarry area (Rook et al. 2006; Colombero et al. 2014).

But what about non-mammalian vertebrates? Do these parallel mammals when it comes to the recognition of different faunal complexes in the Italian late Miocene? Amphibian and reptile assemblages are described from Piedmont (Cavallo et al. 1993; Colombero et al. 2014, 2017), Tuscany (Delfino & Rook 2008; Chesi et al. 2009; Cirilli et al. 2016), Monticino Quarry in Emilia Romagna (Kotsakis 1989; Rook et al. 2015; this paper), Abruzzo (Rustioni et al. 1992; Delfino & Rossi 2013), Sardinia (Abbazzi et al. 2008b; Georgalis et al. 2017b; Zoboli et al. 2019), and Calabria (Georgalis et al. 2020). Except for the crocodylian remains (Delfino et al. 2007), the palaeoherpetofauna from the Gargano “Terre Rosse” is still unpublished, but preliminary comments can be made based on the content of the PhD thesis by Delfino (2002) and our personal observations. A certain affinity is evident between sites in Piedmont (Ciabòt Cagna, Moncucco, and Verduno) and Monticino Quarry. If we consider the Piedmont area as a whole, more than half of the taxa identified there are also present in Monticino. Only allocaudates, *Chelotriton* newts, gekkotans, green lizards, and scolecophidian snakes are missing in the latter site, but present in Piedmont. It has to be noted that the report of a palaeobatrachid in Ciabòt Cagna (Cavallo et al. 1993) is likely erroneous: it is based on a partially preserved synsacrum, the identification of which is rather doubtful due to a subcylindrical vertebral centrum that is not dorsoventrally compressed as in palaeobatrachids (A.V., pers. obs.). Nine taxa (the large discoglossoid, the common toad, the Ereimiadini, scincids, *Pseudopus*, *P. planicarinatus*, cf. *P. arcuatus*, *Natrix*, *Malpolon*, and the small viper) out of 26 (or 27; about one third) of the taxa identified at Monticino Quarry are not known from Piedmont. However, unidentified

“colubrine” snakes are known in both Monticino and Verduno, probably even representing more than a single species (Colombero et al. 2017). Thus, the purported absence in Piedmont of “colubrines” recovered in Monticino Quarry might also be just a matter of missing identification. Almost all the taxa exclusive of Piedmont, on the other hand, were never found in southernmost late Miocene sites in the Apennines, thus probably representing groups the distribution of which did not reach those areas in this time period. The only exception is represented by geckos, which are present in Gargano with a peculiar, maybe endemic, form (Villa & Delfino 2019b). Geckos were reported, without a detailed description and figures, from Monticino Quarry by Kotsakis (1989), but we were unable to confirm this and the original material is not available for study anymore. Anyway, an artifactual absence in our sample of geckos due to a missing preservation of their bones would not be surprising, considering the overall rarity of fossils of these lizards (Daza et al. 2014).

The palaeoherpetofaunal complex characterising the Monticino Quarry and Piedmont area is then somehow different from the pre-Messinian one reported from Fosso della Fittaia by Cirilli et al. (2016) and Tuscany in general by Chesi et al. (2009). In contrast with the younger faunas from Piedmont and Romagna, Fosso della Fittaia yielded a small discoglossine (maybe not referable to the larger *Latonia*, even though this hypothesis is just based on the size of the few remains found and thus should be considered carefully), *Anguis*, and a possible non-*Eryx* erycine snake, together with *Testudo*, non-*Anguis* anguines, indeterminate lizards, and indeterminate “colubrines”. To these, Chesi et al. (2009) added *Trionyx*, which is not present in the assemblage from Piedmont and Romagna, and *M. campanii*, which on the other hand might be somehow related to at least the *Mauremys* from Monticino (see above). Therefore, almost half of the amphibian and reptilian taxa from Tuscany in pre-Messinian late Miocene times are currently unknown in the Messinian of Piedmont and Emilia Romagna. The erycine from Fosso della Fittaia is even more peculiar due to the absence of paracotylar foramina (Cirilli et al. 2016), a feature that distinguishes this taxon from both erycine genera known from the Neogene of Europe (i.e., *Eryx* and *Bransateryx*; Szyndlar & Schleich 1993, 1994). The possible en-

demic nature of this snake, however, as well as a better comprehension of the composition of the herpetofauna of the OZF in Tuscany, need to await for more fossil material to be clearly confirmed and understood. Similar to what written above for the geckos, Kotsakis (1989) also mentioned *Anguis* and *Trionyx* in his note on Monticino Quarry, but again, our data did not confirm their presence. The same holds true for other taxa reported by Kotsakis (1989), such as the emydid turtle. From the Messinian deposits of Tuscany, we only know a few chelonian taxa (Chesi et al. 2009): *M. campanii*, *Testudo*, and *Trionyx* cf. *pliopedemontanus*. Again, *Testudo* is present in Piedmont and Monticino Quarry as well, the *Mauremys* from Monticino Quarry may be related to *M. campanii*, whereas trionychids are currently missing from both Monticino Quarry and the Piedmont localities. Trionychids were also present in Sardinia during the late Miocene (Georgalis et al. 2017b), together with tomistomine crocodylians (Zoboli et al. 2019). Considering all of this, the Tusco-sardinian palaeoherpetological complex could indeed differ from other central north Italian assemblages, but additional fossils are needed prior to have a significant confidence on this, especially for the Messinian levels that are supposedly more likely to share affinities with the latter.

As discussed above, only preliminary comments can be made about the herpetofauna from the Gargano area, as it is still unpublished and the material is still currently under study. Our personal observations and the preliminary data available at the moment points out to a fauna composed of both elements shared with Piedmont and Emilia-Romagna (especially among the anurans, but possibly also some lizards and snakes) and endemic taxa (e.g., the small gecko briefly mentioned by Villa & Delfino, 2019b). At the current status of knowledge, no affinities seem to be shared with Tuscany, on the other hand. The few remains of crocodylians and chelonians from Scontrone (Rustioni et al. 1992) do not add very much to this picture. Similarly, only a few chelonian taxa are known from Cessaniti in Calabria. In addition to a marine turtle, this site yielded *Trionyx pliocenicus* Fucini, 1912 and an indeterminate species of *Mauremys* (Georgalis et al. 2020). In the late Miocene of Italy, other trionychid occurrences are only known from Tuscany, both in the OZF and in Messinian levels. Chesi et al. (2009) reported the OZF trionychid as *Trionyx* unassigned to species and

the Messinian one as *Trionyx* cf. *pliojedemontanus*. *Trionyx pliojedemontana* Sacco, 1889 represents a nomen dubium according to Georgalis & Joyce (2017) and at the moment all the Tuscan late Miocene material can be referred only to interminate trionychines following the same authors. Nevertheless, the species identification of the trionychid from Cessaniti still highlights affinities with Tuscany, given that the lost holotype of *T. pliocenicus* (which is the only specimen known of this species other than the Calabrian remains) came from the Pliocene locality of Mapesi (or Malpessi), near Poggio alle Monache in Tuscany (Georgalis & Joyce 2017). Whether the late Miocene occurrences were conspecific with the Pliocene one (and thus with the Cessaniti specimens) or not is impossible to say. Differently, *Mauremys* is present in Piedmont, Emilia-Romagna, and Tuscany (both in the OZF and the younger Messinian fauna). It is interesting to note that the chelonian fauna from Cessaniti seems not to share clear affinities with the Abruzzo-Apulia area.

Coastal and freshwater fish assemblages in the post-evaporitic Messinian of Italy share numerous affinities throughout the Italian Peninsula (Carnevale et al. 2018, 2019). This is particularly evident between Tuscany and Piedmont, even though it could just result from them being better sampled than other sites (i.e., in Emilia Romagna, Marche, and Abruzzo, for example). Differences are also present, however. Clupeids are known from all above mentioned regions but Piedmont and Emilia Romagna, for example, whereas fossil remains of atherinids, blenniids, mugilids, and sparids were only found in Tuscany. Sciaenids, which are only tentatively identified in the Monticino Quarry fish assemblage, are known from Piedmont, Tuscany, and Marche, but Piedmont and Tuscany do not share sciaenid taxa at the generic level and each one of the only two taxa identified in Marche is shared with only one of the two former regions. Cichlids were not found in any of the Italian late Messinian localities, except for (tentatively) the Monticino Quarry. They occupied the area already during the earliest part of the Messinian Salinity Crisis event (Carnevale et al. 2003). The lack of fossils attributed to this family from other late Miocene sites in Italy may be due to some sort of bias (e.g., sampling- or environmentally-driven).

The bird assemblages also show some degree of similarity, between fossil sites in Piedmont (e.g.,

Moncucco Torinese and Verduno; Colombero et al. 2014, 2017) and Monticino Quarry. Phasianids, accipitrids, and passeriforms were all shared by both areas. Nevertheless, the impossibility to define more precisely the taxonomy of most of the remains found hinders a better understanding of these possible affinities. Otidids, on the other hand, appears only in Monticino, the latter being their oldest occurrence worldwide. A significantly different picture was represented by Gargano, where migratory taxa were flanked by a number of endemic forms (Ballman 1973, 1976; Göhlich & Pavia 2008; Pavia 2013; Pavia et al. 2017).

CONCLUSIONS

In a similar way to the frame depicted previously by the study of mammal remains from the site, the Monticino Quarry proved extremely important also for other vertebrates after a detailed investigation of the non-mammal component of the assemblage. This is certainly true for amphibians and reptiles, given that with 26 (or 27) taxa identified, it represents one of the most diverse herpetofaunas known from the late Miocene. The small amount of fossils recovered that can be attributed to fish or birds hinders a similar achievement for these two groups (only three and five taxa identified, respectively), but important findings are reported for them as well. As a matter of fact and irrespective of the diversity, amphibians, reptiles, and birds from Monticino Quarry include the oldest known occurrences of some taxa. On global terms, this is the case for the snakes *Malpolon* and *Eryx* cf. *jaculus* as well as for otidid birds, whereas common toads represent the oldest known occurrence from the Italian territory and Eremiadini lizards are both the oldest finding of these reptiles in Europe and the only evidence of their presence, either past or present, in Italy. None of the few taxa of fish takes part in this list of oldest occurrences, but the possible cichlid tooth adds to only a few remains of this family in the northern part of the Mediterranean, which furthermore were all found in slightly older levels of few sites in central Italy (including Monticino Quarry).

Overall, the non-mammal vertebrates from Monticino Quarry picture a complex palaeoenvironmental scenario, somehow confirming what

was already suggested by the fossil mammals. According to the ecological data of the newly-identified taxa, the Monticino Quarry area was warm and rather dry when the fossils deposited in the fissures, even though with water bodies and a variegated set of environmental features (such as both sandy soils and rocky outcrops, as well as vegetated areas) in the surroundings. The new data further confirm the hypothesis of a multiple origin of the thanatocoenosis, with flooding events, bones accumulations created by predators, and (only ascertained from mammals, at the moment) animals that died directly inside the fissures.

From a palaeobiogeographic point of view, the Monticino Quarry non-mammal assemblage includes taxa with Afro-Asian affinities that dispersed into Europe during different moments in the Miocene, together with others that already inhabited the European continent. Considered in the context of the Italian late Miocene land vertebrate assemblages, the Monticino Quarry non-mammal vertebrates share affinities mostly with Messinian faunas from Piedmont, even though some differences are indeed present (such as the presence of cichlid fish, some amphibians, some reptiles, and otidid birds). In a more general outline, this agrees with the presence of a faunal complex involving the northern and central part of the Italian Peninsula already recognised based on fossil mammals in the Messinian. Tuscany seems to be part of this Messinian faunal complex as well (again, as suggested by mammals) at least as far as fish are concerned. The absence of sufficient data for the herpetofauna and the avifauna hinders a confirmation of this for these two other group as well. Older herpetofaunas from Tuscany (i.e., those belonging to the OZF) appear to have a clearly stronger endemic nature, compared to those characteristic of the latest Messinian. The Sicilian-Calabrian late Miocene chelonian fauna seems to be somehow similar to Tuscanian ones, but only few data are available at the moment. The Abruzzo-Apulian area, in the end, appears to have an at least partially endemic nature in both the herpetological and avian component of its fauna, even though there are indeed some taxa which are shared with Piedmont and Monticino Quarry. The presence of different faunal complexes in the late Miocene is therefore confirmed for non-mammal vertebrates as well, somehow mirroring the situation depicted

by studies on mammals. Uncertainties and gaps are still present, though, and an increased effort in the studies of these groups is strongly needed in order to gain a better understanding of the Italian non-mammalian vertebrate communities between the end of the Miocene and the beginning of the Pliocene.

Acknowledgements: We would like to acknowledge Antonio Benicetti for the enthusiasm and passion that led him to discover the site and recover an amazing amount of fossil remains. Georgios L. Georgalis (Università degli Studi di Torino, Italy) helped by supplying relevant literature. Fabrizio Coenda (Università degli Studi di Torino, Italy) screenwashed and selected part of the material described in this paper. We further thank Saverio Bartolini Lucenti (Università degli Studi di Firenze, Italy) and Loredana Macaluso (Università degli Studi di Torino, Italy) for useful discussions about palaeoenvironmental implications and the identification of some of the urodele remains respectively, as well as the editor, Silvio Renesto, and the reviewers for useful comments on the manuscript. We also would like to manifest our gratitude for the work done by the team and the contributors of MorphoSource, an online resource without which some of the comparisons we made for this work would have not been possible. This project was supported by grants (ex-60% 2018 and 2019) from the Università degli Studi di Torino and by Fondi di Ateneo dell'Università di Firenze to LR (2017-2019). AV is supported by a Humboldt Research Fellowship provided by the Alexander von Humboldt Foundation. MD acknowledges support from Generalitat de Catalunya (CERCA Program) and Spanish Agencia Estatal de Investigación (CGL2016-76431-P, AEI/FEDER, EU). This is the publication number 355 of the Museo di Geologia e Paleontologia collections at the Università degli Studi di Torino.

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