

# A salamandrid from the middle Pleistocene of northern Latium (Fosso di San Martino, Rome, Italy)

# Simone D'Orazi Porchetti, Riccardo Manni & Gianluca Sottili

- S. D'Orazi Porchetti, Via Centuroni 27, I-02100 Rieti, Italy; simone.dorazi.porchetti@gmail.com
- R. Manni, Dipartimento di Scienze della Terra, Sapienza Università di Roma, P.le Aldo Moro 5, I- 00185 Roma, Italy; riccardo.manni@uniroma1.it
- G. Sottili, Dipartimento di Scienze della Terra, Sapienza Università di Roma, P.le Aldo Moro 5, I- 00185 Roma, Italy; Istituto di Geologia Ambientale e Geoingegneria-CNR, Roma, Italy; gianluca.sottili@uniroma1.it

KEY WORDS - Amphibia, Salamandridae, middle Pleistocene, diatomite basins, central Italy.

ABSTRACT - An almost complete salamandrid specimen has recently been discovered from diatomite deposits in the Sabatini Volcanic District, at the Fosso di San Martino locality, about 45 km north of Rome (Rignano Flamino, Latium, central Italy). The age of the fossilbearing level is constrained between 488±2 and 457±4 ka based on the presence of well-dated volcanic ash layers at the top and at the bed of the diatomite level where the specimen was embedded. The fossil record of Caudata from the Pleistocene of central Italy is scarce, and this new find adds important data on the presence of the taxon in this area. The specimen, although comprised of a fairly complete and articulated skeleton, shows a sub-optimal preservation of single bony elements, to such an extent that a definite taxonomic assignment is not feasible. Moreover, it probably represents a juvenile individual in somatic terms at the time of the death. The specimen is tentatively referred to Triturus sp.

RIASSUNTO - [Un salamandride dal Pleistocene medio del Lazio settentrionale (Fosso di San Martino, Roma, Italia)] - Un esemplare quasi completo di Salamandridae è stato recentemente scoperto nei depositi diatomitici del Distretto Vulcanico Sabatino, presso la località Fosso di San Martino, circa 45 km a nord di Roma (Rignano Flaminio, Lazio, Italia centrale). La presenza di livelli vulcanici al tetto e al letto del livello diatomitico da cui proviene il nuovo esemplare, già datati con metodo 40 Ar/89 Ar in precedenti lavori, ha permesso di restringere l'intervallo temporale tra i 488±2 e i 457±4 mila anni fa. Il registro fossile pleistocenico relativo ai Caudata è scarso per l'Italia centrale ed in generale per tutto il territorio italiano. Il ritrovamento di un nuovo esemplare aggiunge quindi dati utili circa la distribuzione degli anfibi in questa area geografica. L'esemplare, benché sufficientemente completo, presenta tuttavia uno stato di conservazione sub-ottimale, in quanto in gran parte preservato come sottile pellicola organica o come modello esterno dello scheletro originale. Il particolare stato di conservazione ha limitato le possibilità di una attribuzione tassonomica a livello di specie. Inoltre, l'esemplare potrebbe non aver raggiunto la maturità somatica al momento della morte. In base ai dati morfometrici derivati dall'analisi dell'esemplare, quest'ultimo è provvisoriamente attribuito al genere Triturus.

## INTRODUCTION

The industrial exploitation of Pleistocene diatomite deposits in the neighboring of Rome has provided scientists with a large amount of fossils, sometimes in a remarkable state of preservation. Extremely detailed palaeobotanical and palynological studies have been produced since the mid of the last century and allowed researchers to outline a palaeoenvironmental reconstruction of this area during the middle and upper Pleistocene (Follieri, 1958, 1962; Follieri & Magri, 1998; Follieri et al., 1998). Vertebrate macrofossils and especially large-bodied mammals have been recovered from diatomitic basins in the Riano area (Accordi & Maccagno, 1962; Maccagno, 1962; Caloi et al., 1998) and a large number of smaller taxa, such as invertebrates and small vertebrates, namely fishes, amphibians, reptiles, mammals is known as well (Mastrorilli, 1965; Bottali, 1975). Indeed, the amphibian record was limited so far to a couple of localities, with only two Caudata taxa, namely Lissotriton vulgaris cf. meridionalis from the middle Pleistocene of Riano Flaminio (Rome) (Mastrorilli, 1965) and a late Pleistocene Triturus carnifex from Baccano (Rome) (Kotsakis et al., 2011). The discovery of an almost complete salamandrid specimen is therefore relevant as it adds new data to the urodelian fossil record of the Italian peninsula.

#### GEOLOGICAL SETTING

The new specimen has been discovered at Fosso di San Martino, about 45 km north of Rome. The stratigraphic succession of Fosso di San Martino crops out in the eastern sector of the Sabatini Volcanic District (SVD), Latium, central Italy (0.8-0.1 Ma) (Fig. 1) and consists of a ca. 60 m-thick sedimentary succession with alternating diatomrich silts and sandy silts, and diatomites. Several primary pyroclastic layers from the ultrapotassic Quaternary volcanism of the Roman Province interfinger with the diatomitic deposits.

The fossiliferous diatomites rest on top of a pyroclastic flow deposit erupted during the ancient SVD volcanic activity (*Tufo Giallo di Prima Porta* unit, radiometric <sup>40</sup>Ar/<sup>39</sup>Ar age 514±3 ka; Karner et al., 2001) and are overlain by a pyroclastic flow deposit from the early SVD volcanic activity (*Tufo Rosso a Scorie Nere* unit, radiometric <sup>40</sup>Ar/<sup>39</sup>Ar age 449±1 ka; Karner et al., 2001; Sottili et al., 2004). More specifically, the new specimen was found in the middle portion of the diatomites succession, which have been deposited in a lacustrine environment after the emplacement of a ca. 30 cm-thick pumice fall deposit (hereafter Lower Volcanic Unit, LVU; Fig. 2). A ca. 20 cm-thick, well-sorted, ash-poor, scoria fall deposit overlies the fossiliferous diatomitic horizon (hereafter

ISSN 0375-7633 doi:10.4435/BSPI.2012.02

Upper Volcanic Unit, UVU). Lithostratigraphy, integrated by field observations of distinctive mineralogical and petrographic features, and distinctive composition and variation profiles provide an unequivocal characterisation of the LVU and UVU as stratigraphic markers for the middle Pleistocene successions of central Italy.

In particular, LVU is correlated to *Fall B* eruption, a widespread plinian fall deposit from the early SVD activity (40Ar/39Ar age 488±2 ka; Karner et al., 2001; Sottili et al., 2004). Dispersal area and distinctive mineralogical and petrographic features (Freda et al., 2011), allow us to correlate the UVU to the *Pozzolane Rosse* eruption (40Ar/39Ar age 457±4 ka; Karner et al., 2001) from the Colli Albani volcanic district, central Italy.

From a biostratigraphic point of view, this fossil belongs to MIS 13 (see Fig. 2) and may be included in the Fontana Ranuccio Faunal Unit (Gliozzi et al., 1997).

#### **METHODS**

The specimen is preserved on two separate slabs of diatomite, which have been recovered by one of the authors (G. S.) during fieldwork on the volcanic deposits

in the Sabatini area. The specimen has been prepared by removing the embedding matrix, having special care in not exceeding with mechanical treatment because of the softness of the enclosing material and the fragility of the specimen. The slabs have been successively soaked in high-diluted vinyl glue to prevent exfoliation of the surfaces.

#### SYSTEMATIC PALAEONTOLOGY

Order Caudata Scopoli, 1777 Family Salamandridae Goldfuss, 1820

Genus Triturus Rafinesque, 1815

Triturus sp.

*Material* - The specimen is stored at the Museo di Paleontologia of the Sapienza Università di Roma under the accession numbers MPUR-NS 156.1 and MPUR-NS 156.2 (Figs 3A-B). Slab MPUR-NS 156.1 yields the skull and the post-cranial skeleton up to the rear limbs, whereas the pelvic girdle and the tail are preserved on

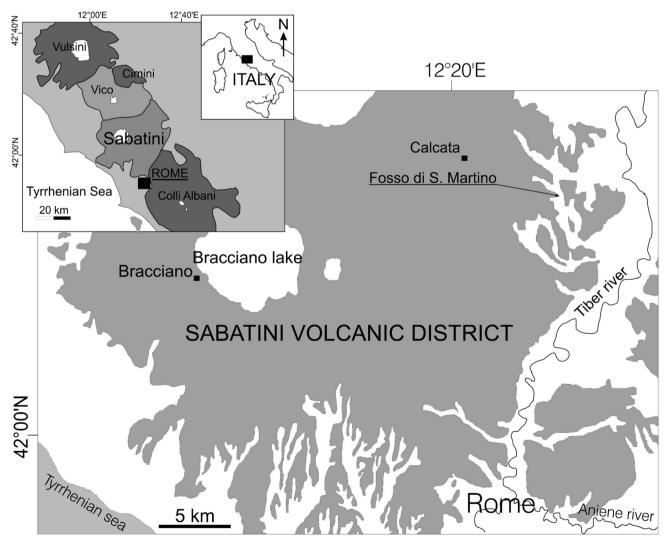


Fig. 1 - Geological sketch map of the Sabatini Volcanic District (SVD), showing the location of the new finding. Top left inset: the SVD within the Quaternary Potassic Roman Province of central Italy.

slab MPUR-NS 156.2. Slab MPUR-NS 156.1 is the counterpart of MPUR-NS 156.2, and the separate portions of the specimen partly overlap in the region of the pelvic girdle of the specimen. A composite reconstruction of the specimen is given in Fig. 4.

# Description -

Cranial skeleton - Diagenetic processes hampered the preservation of the original shape of the skull and most of the cranial bones are deformed and crushed to such an extent that single elements are hardly distinguishable. Nonetheless, some elements such as the squamosal, quadrate and dentary bones are relatively well preserved. The skull (approximately 10 mm long) is longer than wide, elongated along the main axis of the body. The cranial roof is virtually lost, and neither dermal nor neural bones are recognizable. Preserved portions of the skull consist of a subtle brownish organic layer, with a noticeable accumulation of pigmented material in correspondence with the ocular region. The dentaries bear a row of small conical teeth.

Post-cranial skeleton - The postcranial skeleton consists of a fairly complete vertebral column, a complete set of ribs, a portion of the front girdle, front and rear limbs, and an almost complete tail. As a whole, the pre-sacral section of the vertebral column (ca. 17 mm long) is preserved as a tridimensional mould, but the original shape of the vertebrae is not exactly discernible on the specimen. Only small and uninformative bone fragments. useless for taxonomic purposes, are preserved. Up to 14 vertebrae can be counted in the pre-sacral region (the atlas plus 13 trunk vertebrae). Twelve couples of ribs can be observed, which are short, proximally bicapitate and distally truncated (not pointed). The four anterior sets of ribs bear dorsally projecting spines at their mid-shaft. Rib dimensions decrease caudally and the shape becomes splint-like from the ninth vertebra on. The tail (ca. 15 mm long) is distally truncated, and preserves 19 vertebrae, whose shape increasingly blurs distally. The tail is twisted about 90° in respect to its axis.

The left arm is mostly preserved as moulds of the original bones. The autopodium lacks the carpalia and preserves metacarpalia I-IV. Phalanges are preserved as moulds, with the following formula: 2-2-3-2. Ulna and radius are partly preserved as actual bone along their shaft (3/4 of the ulna, only a small fragment of the radius), and show clear gaps in correspondence with the epiphyses. The humerus is preserved as a mould, except for a small distal bony portion. The proximal section of the humerus lies over the vertebral column. The scapulocoracoid has been identified close to the proximal end of the humerus.

The right arm is well exposed on slab MPUR-NS 156.1, although the distal portion of the manus is hidden by sediment. The manus shows four delicate metacarpal elements (I-IV) but lacks all carpalia. Ulna and radius are preserved as moulds, and both lack epiphyses. The humerus is delicate and only partially preserved as actual bone distally. A portion of the scapulocoracoid lies close to the proximal end of the humerus.

Tarsals are completely lacking on the left hind-limb, whereas metatarsals I-IV and V are faintly preserved as

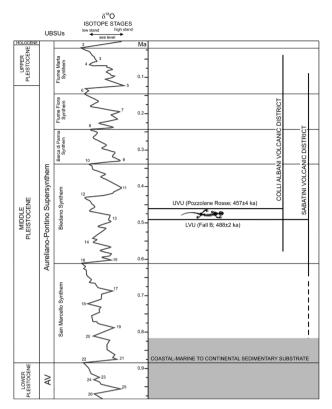


Fig. 2 - Stratigraphic frame of the investigated succession and chronostratigraphic context of the new finding. The Upper Volcanic Unit (UVU; *Pozzolane Rosse*, 457±4 ka) from the Colli Albani Volcanic District and the Lower Volcanic Unit (LVU; *Fall B*, 488±2 ka) from the Sabatini Volcanic District provide an age constraint for the fossil-bearing horizon. Main activity periods for the Colli Albani and Sabatini volcanic districts are also reported. Major unconformity-bounded stratigraphic units (UBSUs), as defined for the central Italy area, are correlated to oxygen isotope stages which correspond to climatic variations ( $\delta^{18}$ O curve after Shackleton et al., 1990; Shackleton, 1995). AV-Acquatraversa supersynthem. Stratigraphic units nomenclature and geochronological data after Karner et al. (2001); Sottili et al. (2004); Palladino et al. (2010); Sottili et al. (2010).

moulds of the original bones. A single proximal phalanx is recognizable on digit I and two phalanges on the II, three phalangeal elements are preserved on digit III, and IV. Phalangeal elements are lacking on digit V. The phalangeal formula of the left pes is therefore: ?.2.3.3.?. Tibia and fibula are preserved as moulds, and epiphyses are lacking, as in other long bones.

The right hind-limb is mostly preserved as a mould of the original bones, except for a short portion (1/3 of the total length) of the femur diaphysis. Epiphyses are completely lacking and the shape of the shaft is cilindrical, lacking any distinctive taxonomic features. The limb is about 8 mm long, the autopodium being the longest element. Tarsalia are missing, metatarsals I, II, III and V are preserved, whereas metatarsal IV is lacking. Digit I and V lack phalangeal elements, whereas digits II and III preserve the first phalangeal element. Digit IV is complete and shows three phalanges. A small bony element, which lies close to the proximal end of the right femur, may be tentatively interpreted as a portion of the ilium.

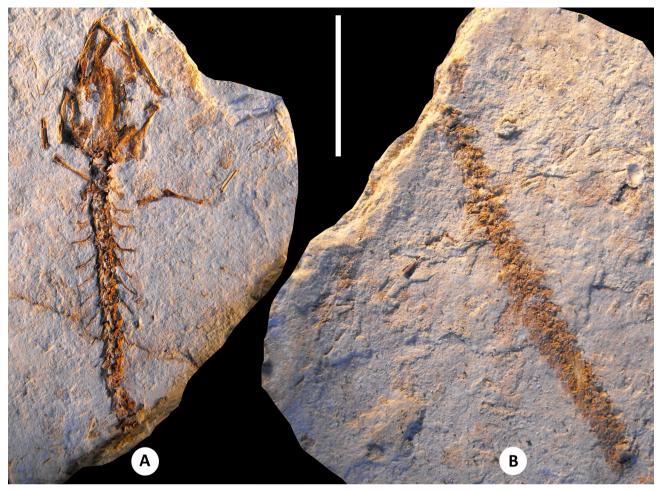


Fig. 3 - Triturus sp. from Fosso di San Martino. A) slab MPUR-NS 156.1; B) slab MPUR-NS 156.2. Scale bar 1 cm.

# DISCUSSION AND REMARKS

Although the specimen may be considered as almost complete (total length 42 mm), the preservation of single bones differs depending on the sector of the body. The specimen mainly consists of a thin brownish organic layer, and few portions of the skeleton are preserved tridimensionally, as for some sectors of the dentary bone. The preservation pattern could be ascribed to an incomplete mineralization of bony elements, as a primary cause, or alternatively, to the effects of taphonomic and diagenetic processes (dissolution or mechanic loss of mineralized bones). The absence of epiphyses in long bones, as well as the lack of carpalia and tarsalia, suggests however an overall low degree of skeletal mineralization. Assuming a very low taphonomic bias on the relative position of skeletal elements, we evaluated the amount of cartilage on a selected limb (left arm), expressed as percentage against the total length of the limb. About 22% of the front-limb skeleton was non-mineralized at the time of death. Roček (1996) suggested that the degree of ossification of the skeleton may be evidence for somatic maturity, highlighting however that some taxa (i.e., Andrias) lack ossified basipodials even in adult stage. Somatic immaturity of the specimen is further evidenced by relative proportions of the body, with a clear positive polarity of the front-limbs respect to the rearlimbs (Epperlein & Junginger, 1982; Fox, 1984; Watson & Russell, 2000; Nye et al., 2003). Linear measurements reveal a head/trunk ratio around 0.6, a substantial equal length of the front limb and the skull, and a 1.25 ratio between the front- and the rear-limbs. Manus length compared to the overall length of the front-limb has a ratio of 0.7.

Heterochrony, which leads to sexual maturity without attaining an adult phenotype, may affect caudates. Neoteny (Kollman, 1885) is the term adopted to define sexual maturity when it is attained at premetamorphic stage, whereas progenesis (Gould, 1977) involves a sexual maturity with a postmetamorphic juvenile phenotype. In order to distinguish between these two types of heterocronic processes in fossil amphibians, it is essential to define the stage of development of the hyobranchial skeleton (Roček, 1995, 1996). Unfortunately, the new specimen lacks any evidence of the branchial skeleton and any further definition of potential heterocronic processes is therefore hampered.

The taxonomic assignment of MPUR-NS 156.1/2 proved to be extremely difficult owing to various reasons. The most relevant one is related to the anatomical features (skull bones, vertebrae), which are either deformed, lost or too poorly preserved to provide fine morphological information useful for taxonomy. Additionally, the specimen is probably not fully grown in somatic terms.

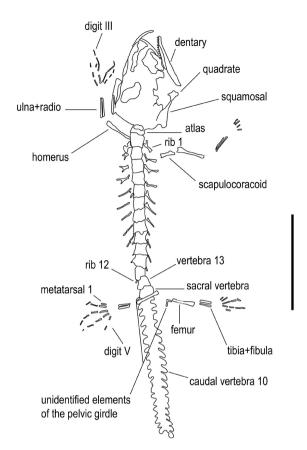


Fig. 4 - Triturus sp. from Fosso di San Martino. Schematic reconstruction of the specimen, scale bar 1 cm. The poor preservation of the specimen hinders the detection of fine morphological details.

Nonetheless, we investigated all evidence useful to restrict the field of potential identifications.

Among the caudate families distributed in the central Mediterranean region of Europe by the middle Pleistocene, we restricted a priori our comparison to Salamandridae, Plethodontidae, and Albanerpetontidae (Delfino, 2006; Delfino & Sala, 2007). This latter family can be easily excluded on the basis of gross anatomic features. The phalangeal formula, as deduced from the new specimen (2-2-3-2 for the front-limbs and ?.2.3.3.? for the rear-limbs), is widespread among Caudata, and is by no mean exclusive of selected groups within the clade. Moreover this character is further flawed by the fact that intraspecific variation in the number of digits has been noticed in several taxa (Alberch & Gale, 1985; Pacces Zaffaroni et al., 1992; Shubin et al., 1995). Some authors (Vanni et al., 2007) pointed out that extremely slender and long digits are a distinctive feature for field identification of *Triturus carnifex* larvae. This feature is of limited help in this case, owing to its qualitative nature and due to the unknown stage of growth of our specimen. In a recent work, Lanza et al. (2010) take into account the number of trunk vertebrae to define average patterns for several extant taxa of western Palearctic Caudata. In this regard, the vertebral count of the trunk region of the MPUR-NS 156.1/2 (13) falls within the range of several genera (Chioglossa, Euproctus, Lissotriton, Mesotriton, Neurergus, Ommatotriton, Salamandrina, Pleurodeles,

Speleomantes). All these taxa belong to Salamandridae except for Speleomantes (Plethodontidae) and both families were established in Europe long before the middle Pleistocene (Delfino et al., 2005). We can infer from our specimen an aquatic lifestyle for at least a portion of its life cycle, but this feature is unlikely for Speleomantes. Moreover, the shape of the ribs is highly unlikely for Plethodontidae. When the number of rib-bearing vertebrae (12) is considered, the field of potential attribution can be further restrained. Rib counts are considered as a reliable method for taxonomic attribution, at least within the "crested newt group" (Arntzen & Wallis, 1994, 1999). MPUR-NS 156.1/2 (13 trunk vertebrae and 12 rib-bearing vertebrae) falls inside the Triturus marmoratus range (Vallée, 1959; Arntzen & Wallis, 1994, 1999; Crnobrnja-Isailoviç et al., 1997).

We attempted calculating the Wolterstorff index (WI), which is a useful tool for species identification among crested newts (Wolterstorff, 1923) on the basis of body proportions. Operatively, the WI is a ratio obtained by dividing the fore-arm length by the interlimb distance, multiplied by a factor of 100 (Arntzen & Wallis, 1994).

This method is usually restricted to *in vivo* specimens or at least on fleshy preserved ones, and our attempt must be considered as tentative. The value we obtained (71.72) is outside the common range for European crested newts with a closer score with *Triturus marmoratus* mean value 64.0 (Arntzen & Wallis, 1999). Interestingly the maximum value for *T. marmoratus* is 72.2 (Arntzen & Wallis, 1999), which is extremely close to the one calculated on our specimen. It is worth noting that the new specimen is probably not an adult, whereas the WI dataset for comparison is based on measurements taken exclusively on adult forms.

Further somatic stage constraints may be based on the shape of the teeth. In *Triturus* larvae teeth are monocuspidate, whereas they become bicuspidate after metamorphosis (Greven, 1989; Accordi & Mazzarani, 1992). Unfortunately, the preservation of the teeth in MPUR-NS 156.1/2 is extremely poor, and this feature is currently not discernible.

In conclusion, the new specimen is considered as an immature salamandrid, and it seems reasonably that it is close to the European crested newts. The material is however too poorly preserved to permit a reliable identification at species rank, and the identification at the genus level is not based on unambiguous characters. In conclusion, we propose a tentative attribution to *Triturus* sp. Further better preserved material from the same locality may add details to the taxonomic assignment.

## **CONCLUSIONS**

The taphonomy of the site in which the specimen has been found (a small lake or pond) with calm water, the inferred juvenile age of the specimen and anatomical features such as the long and slender digits in addition to well-developed neural and haemal arcs of the tail vertebrae (potentially related to a caudal fin), suggest a water lifestyle for the specimen, at least in its early stage of life.

The taxonomic assignment of the new specimen is based on available quantitative and qualitative anatomical features and is in accordance with the palaeobiogeographic distribution at family and genus level. Further refining of the taxonomic identification is actually hampered by inconsistency of characters at specific level. Future work on the outcrop will help defining better its palaeoenvironment.

#### **ACKNOWLEDGMENTS**

M. Delfino (Università di Torino) is kindly acknowledged for constant and helpful advice, M.L. Kalezić and A. Caurosević (Univerzitet u Beogradu) provided us with bibliographic help. We thank the reviewers A. Kotsakis (Università degli Studi Roma Tre) and F. Accordi (Sapienza Università di Roma) and the assistant editor J. Pignatti (Sapienza Università di Roma) who helped to increase the quality of this paper with their comments and suggestions.

#### REFERENCES

- Accordi B. & Maccagno A.M. (1962). Researches in the Pleistocene of Riano (Rome). *Geologica Romana*, 1: 25-32.
- Accordi F. & Mazzarani D. (1992). Tooth morphology in *Triturus vulgaris meridionalis* (Amphibia Urodela) during larval development and metamorphosis. *Bolletino di Zoologia*, 59(4): 371-376.
- Alberch P. & Gale E.A. (1985). A developmental analysis of an evolutionary trend: digital reduction in amphibians. *Evolution*, 39: 8-23.
- Arntzen J.W. & Wallis G.P. (1994). The 'Wolterstorff Index' and its value to the taxonomy of the Crested Newt superspecies. *Abhandlungen und Berichte für Naturkunde und Vorgeschichte*, 17: 57-66.
- Arntzen J.W. & Wallis G.P. (1999). Geographic variation and taxonomy of crested newts (*Triturus cristatus* superspecies): morphological and mitochondrial DNA data. *Contributions to Zoology*, 68(3): 180-203.
- Bottali P. (1975). Note su due rari esemplari di Araneidi (Aracnidi) rinvenuti nei depositi diatomitici (Facies lacustre) di Riano Flaminio (Roma). *Fragmenta Entomologica*, 11(2): 169-173.
- Caloi L., Palombo M.R. & Zarlenga F. (1998). Late middle Pleistocene mammal faunas of Latium (Central Italy): stratigraphy and environment. *Quaternary International*, 47-48: 77-86.
- Crnobrnja-Isailoviç J., Dukiç G., Krstiç N. & Kaleziç M.L. (1997). Evolutionary and paleogeographical effects on the distribution of the *Triturus cristatus* superspecies in the central Balkans. *Amphibia-Reptilia*, 18: 321-332.
- Delfino M. (2006). Il registro fossile della moderna erpetofauna italiana. 96-119. In Sindaco R., Doria G., Razzetti E. & Bernini F. (eds), Atlante degli anfibi e rettili d'Italia. Societas Herpetologica Italica, Edizioni Polistampa, Firenze.
- Delfino M., Razzetti E. & Salvidio S. (2005). European plethodontids: palaeontological data and biogeographical considerations. *Atti Museo Civico Storia Naturale Genova*, 97: 45-58.
- Delfino M. & Sala B. (2007). Late Pliocene Albanerpetontid (Lissamphibia) from Italy. *Journal of Vertebrate Paleontology*, 27(3): 716-719.
- Epperlein H.H. & Junginger M. (1982). The normal development of the newt *Triturus alpestris* (Daudin). *Amphibia-Reptilia*, 2: 295-308.
- Follieri M. (1958). La foresta colchica fossile di Riano Romano. I. Studio dei fossili vegetali macroscopici. *Annali di Botanica*, 26: 129-142.
- Follieri M. (1962). La foresta colchica fossile di Riano Romano. II. Analisi polliniche. *Annali di Botanica*, 27: 245-280.

- Follieri M. & Magri D. (1998). Paesaggi vegetali del Quaternario in Italia centrale. *Biogeographia*, 19: 57-68.
- Follieri M., Giardini M., Magri D. & Sadori L. (1998). Palynostratigraphy of the last glacial period in the volcanic region of central Italy. *Quaternary International*, 47/48: 3-20.
- Fox H. (1984). Amphibian Morphogenesis. New Jersey, Humana Press, 301 pp.
- Freda C., Gaeta M., Giaccio B., Marra F., Palladino D.M., Scarlato P. & Sottili G. (2011). CO<sub>2</sub>-driven large mafic explosive eruptions: the Pozzolane Rosse case study from the Colli Albani Volcanic District (Italy). *Bulletin of Volcanology*, 73: 241-256.
- Gliozzi E., Abbazzi L., Argenti P., Azzaroli A., Caloi L., Capasso Barbato L., Di Stefano G., Esu D., Ficcarelli G., Girotti O., Kotsakis T., Masini F., Mazza P., Mezzabotta C., Palombo M.R., Petronio C., Rook L., Sala B., Sardella R., Zanalda E. & Torre D. (1997). Biochronology of selected mammals, molluscs and ostracods from the middle Pliocene to the late Pleistocene in Italy. The state of the art. *Rivista Italiana di Paleontologia e Stratigrafia*, 103: 369-388.
- Goldfuss G.A. (1820). Handbuch der Zoologie. Zweite Abtheilung. Schrag, Nürnberg, 512 pp.
- Gould S.J. (1977). Ontogeny and Phylogeny. Harvard University Press, 501 pp.
- Greven H. (1989). Teeth of extant amphibian: morphology and some implications. Fortschritte der Zoologie, 35: 451-455.
- Karner D.B., Marra F. & Renne P. (2001). The history of the Monti Sabatini and Alban Hills volcanoes: groundwork for assessing volcanic-tectonic hazards for Rome. *Journal of Volcanology* and Geothermal Research, 107: 185-219.
- Kollman J. (1885). Das Ueberwintern von europäischen Frosch- und Triton-larvenund die Umwandlung des meikanischen Axolotl. Verhandlungen der Naturforschenden Gesellschaft in Basel, 7: 387-398.
- Kotsakis T., Marcolini F., De Rita D., Conti M. & Esu D. (2011). Three late Pleistocene small mammal faunas from the Baccano maar (Rome, central Italy). *Bollettino della Società Paleontologica Italiana*, 50(2): 103-110.
- Lanza B., Arntzen J.W. & Gentile E. (2010). Vertebral numbers in the Caudata of the western Palaearctic (Amphibia). *Atti Museo Civico di Storia Naturale di Trieste*, 54: 3-114.
- Maccagno A.M. (1962). Gli elefanti fossili di Riano (Roma). *Geologica Romana*, 1: 33-132.
- Mastrorilli V.I. (1965). I fossili quaternari del bacino diatomitico di Riano presso Roma nella Collezione del Museo Civico di Scienze Naturali "G. Doria" in Genova. Atti dell'Istituto di Geologia del Università di Genova, 3(1): 1-245.
- Nye H.L.D., Cameron J.A., Chernoff E.A.G. & Stocum D.L. (2003). Extending the table of stages of normal development of the Axolotl: limb development. *Developmental Dynamics*, 226: 555-560.
- Pacces Zaffaroni N., Arias E. & Zavanella T. (1992). Natural variation in the limb skeletal pattern of the crested newt, *Triturus carnifex* (Amphibia: Salamandridae). *Journal of Morphology*, 213: 265-273.
- Palladino D.M., Simei S., Sottili G. & Trigila R. (2010). Integrated approach for the reconstruction of stratigraphy and geology of Quaternary volcanic terrains: an application to the Vulsini Volcanoes (central Italy). *In* Groppelli G. & Viereck L. (eds), Stratigraphy and Geology in Volcanic areas. *Geological Society of America, Special Papers*, 464: 66-84.
- Rafinesque C.S. (1815). Analyse de la nature ou Tableau de l'univers et des corps organisés. Palerme, Jean Barravecchia, 124 pp.
- Roček Z. (1995). Heterochrony: response of Amphibia to cooling events. *Geolines*, 3: 55-58.
- Roček Z. (1996). Skull of the neotenic salamandrid amphibian Triturus alpestris and abbreviated development in the Tertiary Salamandridae. Journal of Morphology, 230: 187-197.
- Scopoli I. (1777). Introductio ad Historiam Naturalem, Sistens Genera Lepidium. Plantarum & Animalium. Prague, Gerle, 506 pp.

- Shackleton N.J. (1995). New data on the evolution of Pliocene climatic variability. 242-248. *In* Vrba E.S., Denton G., Partdrige H.T.C. & Burkle L.H. (eds), Paleoclimate and Evolution, with Emphasis on Human Origins. Yale University Press, New Haven.
- Shackleton N.J., Berger A. & Peltier W.A. (1990). An alternative astronomical calibration of the lower Pleistocene timescale based on ODP Site 677. Transactions of the Royal Society of Edinburgh: Earth Sciences, 81: 251-261.
- Shubin N., Wake D.B. & Crawford A.J. (1995). Morphological variation in the limbs of *Taricha granulosa* (Caudata: Salamandridae): Evolutionary and phylogenetic implications. *Evolution*, 49: 874-884.
- Sottili G., Palladino D.M., Marra F., Jicha B., Karner D.B. & Renne P. (2010). Geochronology of the most recent activity in the Sabatini Volcanic District, Roman Province, central Italy. *Journal of Volcanology and Geothermal Research*, 196: 20-30.
- Sottili G., Palladino D.M. & Zanon V. (2004). Plinian activity during the early eruptive history of the Sabatini Volcanic District, Central Italy. *Journal of Volcanology and Geothermal Research*, 135: 361-379.

- Vallée L. (1959). Recherches sur *Triturus blasii* de l'Isle, hybride naturel de *Triturus cristatus* Laur. x *Triturus marmoratus* Latr. *Mémoires de la Société zoologique de France*, 39: 1-95.
- Vanni S., Andreone F. & Tripepi S. (2007). *Triturus carnifex* (Laurenti, 1786). 265-272. *In* Lanza B., Andreone F., Bologna M.A., Corti C. & Razzetti E. (eds), Fauna d'Italia, vol. XLLII, Amphibia. Edizioni Calderini, Bologna.
- Watson S. & Russell A.P. (2000). A posthatching developmental staging table for the long-toed salamander, *Ambystoma macrodactylum krausei*. *Amphibia-Reptilia*, 21: 143-154.
- Wolterstorff W. (1923). Übersicht der Unterarten und Formen des Triton cristatus Laur. Blätter für Aquarien- und Terrarienkunde, 34: 120-126.

Manuscript received 25 October 2011 Revised manuscript accepted 27 March 2012 Published online 27 June 2012 Editor Johannes Pignatti