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Trapped in a roman well: amphibians and reptiles from Tenuta Zuccarello near Marcon, Venice, Italy

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ABSTRACT

The Roman well US 100, located in the Tenuta Zuccarello near Venice, has yielded a large number of different animals remains, dated back to 2000 ± 40 years BP. Amphibians and reptiles are represented by at least 11 taxa: two caudates (*Lissotriton* gr. *L. vulgaris*, *Triturus* gr. *T. cristatus*), three anurans (*Bombina* sp., *Bufo bufo*, *Rana dalmatina* vel *R. latastei*), one turtle (*Emys orbicularis*), at least two lizards (*Anguis* gr. *A. fragilis*, *Lacerta* gr. *L. viridis*), and three snakes (*Natrix natrix*, cf. *Coronella* sp., *Hierophis viridiflavus*). Based on this assemblage, an ecotonal environment with water bodies, open and humid areas, as well as dry and sunny areas, is here suggested for the surroundings of the well when the sediments deposited.

Most of the identified taxa were found in other Venetian sites since the Pleistocene, suggesting a certain continuity in the amphibians and reptiles population in Veneto during the Quaternary. The only taxon that is absent from the Venetian Lagoon today is *Bombina*. Its presence in a 2000-years-old archaeological site proves that the disappearance of suitable environments for the genus is a recent phenomenon near the Lagoon. This may support future reintroduction projects in suitable areas, following a conservation palaeobiology perspective.

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Introduction

Fossil remains found inside fillings of geomorphological structures such as stream gullies or karstic fissures are very frequent (e.g. Freudenthal et al. 1976; Sala et al. 1994; Bonfiglio et al. 1997; Delfino and Bailon 2000; Abbazzi et al. 2004; Fraser and Wells 2006; Arzarello et al. 2007; Delfino and Atzori 2013; Rook et al. 2015; Rage 2016; Savorelli A and Masini 2016; Savorelli et al. 2016; Villa et al. 2016, 2018). These natural structures can act either as traps in which living animals fall and then die or as gatherers of sediments and remains washed away from the nearby area. From the Holocene onwards, artificial structures built by modern humans have flanked the natural ones in originating a similar system of fossil or subfossil accumulation. One of such artificial structure is the well.

Being basically vertical cavities in the ground, wells are structurally similar to natural fissures and may equally accumulate sediments inside. These sediments might include plant remains, invertebrate and vertebrate remains, as well as tools used by the people living around the well (e.g. Arobba et al. 2013). Of course, the accumulation might originate from direct filling by people, who may actively throw remains and tools inside the well. However, falls of animals in the well or washing of remains inside it are also possible.

This paper is based on remains coming from a similar accumulation originated in a Roman well discovered in July 2000 during an excavation campaign directed by the Soprintendenza Archeologica per il Veneto – Museo

Archeologico Nazionale di Altino. The well, located in the Tenuta Zuccarello near Marcon (province of Venice, Italy; Figure 1), was named US 100. It was part of a wide agricultural area located between the Zero and Dese Rivers, including cultivated fields and other agricultural structures such as small drainage canals. The well has an average diameter of 80 cm and was filled by clayey-silty and clayey-sandy sediments. Two different filling sequences were recognised, but they are considered approximately coeval. A rather large number of faunal remains were found in the well, representing both invertebrates (molluscs) and vertebrates (amphibians, reptiles, birds, and small mammals). A preliminary list of the taxa recovered in the well is given by Bon et al. (2010), but a very brief account is also reported here.

Molluscs include mainly terrestrial species, but some freshwater taxa and even few marine elements are also present. As far as bird remains are concerned, nearly complete skeletons of two individuals of *Athene noctua* and of a *Sturnus vulgaris* were found, together with other unidentifiable remains. Most of the remains found in the well consist of bones of small mammals (insectivores and rodents; see Bon et al. 2010, for a complete list of the 13 species identified). These indicate a humid and somewhat forested landscape, without a strong manmade influence. Domestic animals are represented by three bones only (all pertaining to medium- or large-sized mammals; Bon et al. 2010), suggesting that the well never acted extensively as a dump. Fragments of pottery artefacts are rare in the fillings rich with faunal remains.

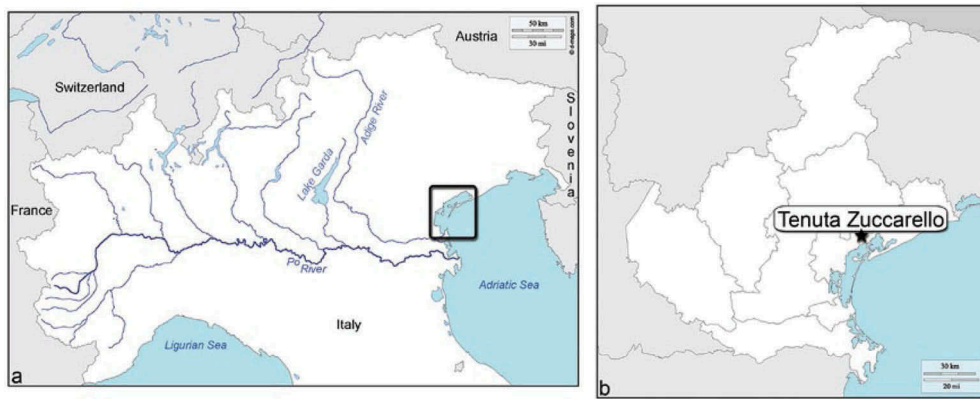


Figure 1. Maps. Map of Northern Italy (a) showing the position of the Venetian Lagoon (black rectangle) and map of Veneto (b) showing the position of Tenuta Zuccarello.

The faunal remains are very well preserved and have been radiocarbon dated at 2000 ± 40 years BP (Bon et al. 2010). Bon et al. (2010) considered the assemblage to be originated because of the well acting as a trap, based on the good preservation of the remains, the absence of signs of transport, digestion and predatory activities, and the dominance of wild species. However, the alternative possibility of remains of animals that died in the nearby and were later washed into the well should also be taken into account, considering that some kind of superficial water body was most likely in direct contact with the well (as suggested by the presence of some of the freshwater molluscs; Bon et al. 2010). This second explanation might better agree with the fact that some vertebrate taxa are represented only by few remains and not by a number of skeletal elements congruent with complete, or roughly complete, individuals as one would expect in case of animals falling into the well and then being subject to little or no disturbance.

In this paper we focus on the analysis of the amphibians and reptiles, in order to better characterize the herpetofauna recorded in the two fillings (Figure 2–4). This is part of a wider study on the late Quaternary herpetofaunas from Veneto (Delfino et al. 2008) aimed at the understanding of the evolution of the modern amphibians and reptiles communities in the region.

Materials and methods

We studied 8315 remains of amphibians and reptiles coming from US 100 at Tenuta Zuccarello. The identifications are based on diagnostic features found in the literature as well as on direct comparisons with disarticulated skeletons stored in the Massimo Delfino Herpetological Collection (MDHC), housed in the Department of Earth Sciences of the University of Torino. The anatomical terminology follows Ratnikov and Litvinchuk (2007) for caudates, Sanchiz (1998) and Bailon (1999) for anurans, Młynarski (1976) and Hervet (2000) for chelonians, Barahona and Barbardillo (1997) and Klembara et al. (2010) for lizards and Szyndlar (1984) for snakes. The most significant specimens were photographed with a Leica M205 microscope equipped with the Leica application suite V 3.3.0 in the University of Torino. The remains

are stored in the collections of the Natural History Museum of Venezia (MSNVE).

Abbreviations – cl, minimum centrum length; CL, maximum centrum length; pr-po = minimum distance between anterior margin of prezygapophyses and posterior margin of postzygapophyses; PR-PO = maximum distance between anterior margin of prezygapophyses and posterior margin of postzygapophyses.

Systematic palaeontology

Amphibia Linnaeus, 1758
 Caudata Scopoli, 1777
 Salamandridae Goldfuss, 1820
Lissotriton Bell, 1839
Lissotriton gr. *L. vulgaris* (Linnaeus, 1758)
 (Figure 2A–E)

Referred material

- I filling: 8 trunk vertebrae (MSNVE-23360/1–2); 1 humerus (MSNVE-23360/3); 1 femur (MSNVE-23360/4).

Description

Trunk vertebrae are small and opisthocelous (cl: 1.1 mm; CL: 2 mm; pr-po: 1.4 mm; PR-PO: 2.2 mm), with a well-developed neck, well-developed anterior ventral crests, moderately or well-developed posterior ventral and zygapophyseal crests and large subcentral foramina (sometimes replaced by a various number of smaller foramina). The anterior surface of the condyle is flat and roughly vertical or inclined in antero-ventral direction. The high neural arch shows a very high neurapophysis with a horizontal dorsal margin and a roughly vertical or anteriorly sloping anterior margin, running from the anterior fourth of the arch to its posterior margin. In dorsal view, the anterior margin of the arch is straight and is located near the anterior margin of the prezygapophyses or by their anterior third, whereas the posterior one is placed slightly anteriorly to the posterior margin of the postzygapophyses and shows a large

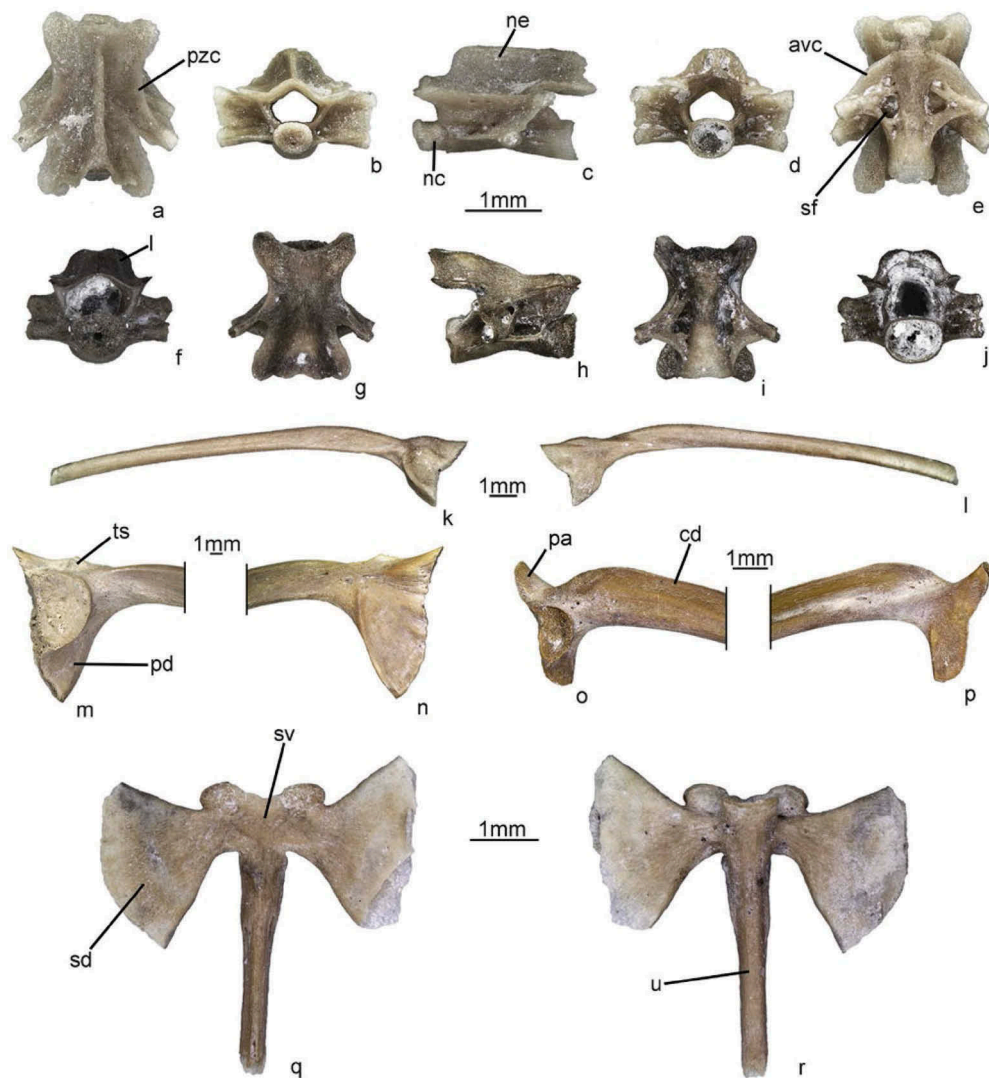


Figure 2. Amphibians from the I filling. *Lissotriton* gr. *L. vulgaris*: trunk vertebra (MSNVE-23360/1) in dorsal (a), anterior (b), left lateral (c), posterior (d) and ventral (e) views. *Triturus* gr. *T. cristatus*: trunk vertebra (MSNVE-23361) in anterior (f), dorsal (g), right lateral (h), ventral (i) and posterior (j) views. *Bombina* sp.: left ilium (MSNVE-23362/10) in lateral (k) and medial (l) views. *Bufo bufo*: right ilium (MSNVE-23363/24) in lateral (m) and medial (n) views. *Rana dalmatina* vel *R. latastei*: right ilium (MSNVE-23364/39) in lateral (o) and medial (p) views. Anura indet.: sacral vertebra fused with the urostyle (MSNVE-23365/15) in dorsal (q) and ventral (r) views. avc, anterior ventral crest; cd, crista dorsalis; l, lamina; nc, neck; ne, neuropophysis; pa, pars ascendens; pd, pars descendens; pzc, prezygapophyseal crest; sd, sacral diapophysis; sf, subcentral foramen; sv, sacral vertebra; ts, tuber superior; u, urostyle.

and deep notch in the middle. Laminae are flat or slightly concave in anterior view.

The humerus is 4.6 mm long. It has a thin shaft and a crista ventralis strongly inclined in anterior view compared to the proximal end of the bone.

The femur is 4.8 mm long and has a moderately thin shaft. The area between the caput femoris and the trochanter is moderately elongated and the distal margin of the bone is only slightly convex.

Triturus Rafinesque, 1815

Triturus gr. *T. cristatus* (Laurenti, 1768)

(Figure 2F-J)

Referred material

- I filling: 1 trunk vertebra (MSNVE-23361).

Description

MSNVE-23361 is a small opisthocoelous trunk vertebra (centrum length: 1.7 mm; distance between anterior margin of prezygapophyses and posterior margin of postzygapophyses: 2 mm), with a weakly developed neck, moderately developed ventral and zygapophyseal crests and large subcentral foramina. The anterior surface of the condyle is flat and vertical in lateral view. No clearly developed neuropophysis is present on the moderately high neural arch: only a hint of it is visible in the middle of its dorsal surface. The anterior margin of the arch is concave and its bottom is located by the anterior third of the prezygapophyses, whereas the posterior one is wavy, presents a small notch in the middle and extends slightly beyond the posterior margin of the postzygapophyses. Laminae are slightly convex in anterior view.

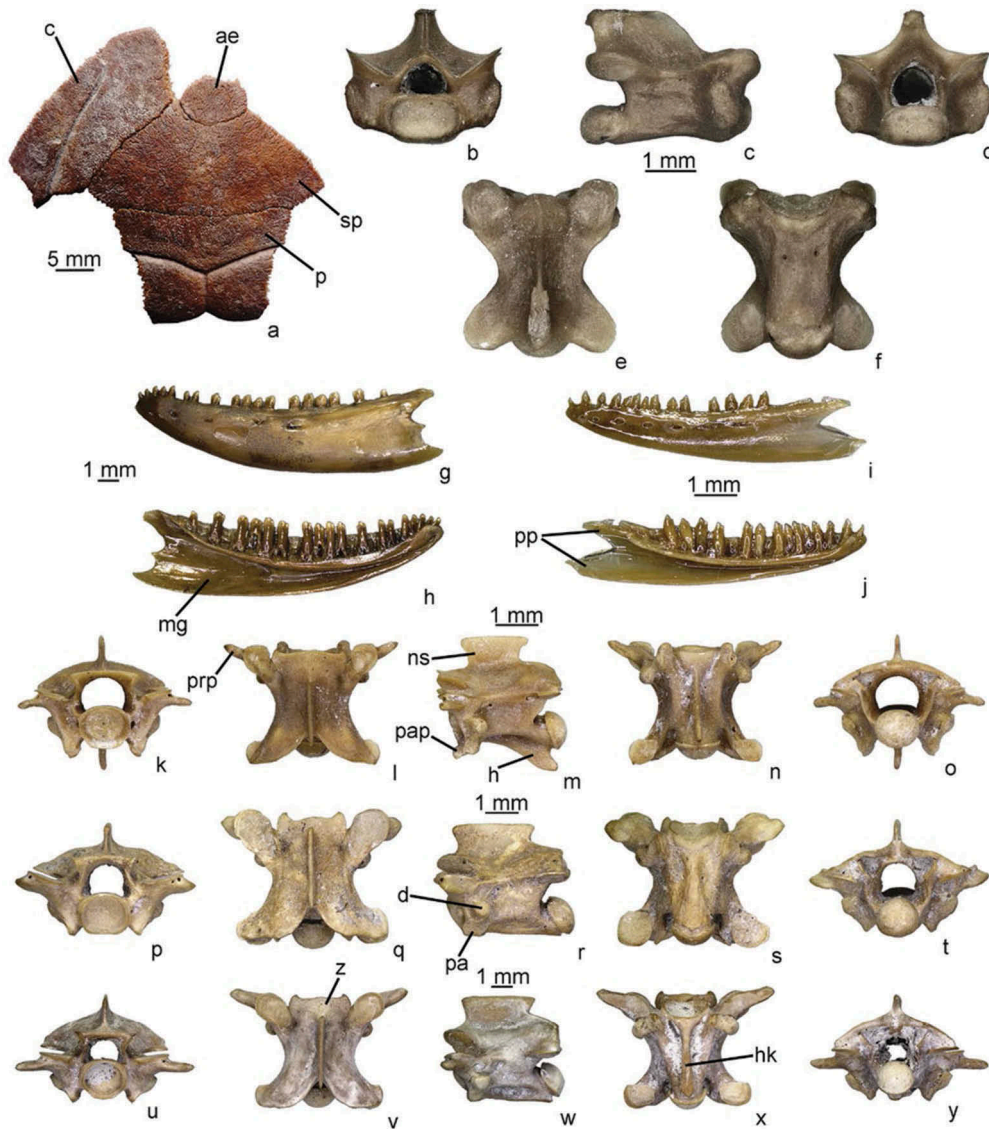


Figure 3. Reptiles from the I filling. *Emys orbicularis*: accessory element, suprapygals 2, pygal and left costal 8 (MSNVE-23373/1) in dorsal (a) view. *Anguis* gr. *A. fragilis*: trunk vertebra (MSNVE-23368/16) in anterior (b), right lateral (c), posterior (d), dorsal (e) and ventral (f) views. *Lacerta* gr. *L. viridis*: left dentary (MSNVE-23366/1) in lateral (g) and medial (h) views. Lacertidae indet.: left dentary (MSNVE-23367/3) in lateral (i) and medial (j) views. *Natrix natrix*: trunk vertebra (MSNVE-23369/1) in anterior (k), dorsal (l), left lateral (m), ventral (n) and posterior (o) views. cf. *Coronella* sp.: trunk vertebra (MSNVE-23370/1) in anterior (p), dorsal (q), left lateral (r), ventral (s) and posterior (t) views. *Hierophis viridiflavus*: trunk vertebra (MSNVE-23371/1) in anterior (u), dorsal (v), left lateral (w), ventral (x) and posterior (y) views. ae, accessory element; c, costal; d, diapophysis; h, hypapophysis; hk, hemal keel; mg, Meckel's groove; ns, neural spine; p, pygal; pa, parapophysis; pap, parapophyseal process; pp, posterior projection; prp, prezygapophyseal process; sp, suprapygals; z, zygosphenes.

Identification

The opisthocoelous centrum, the presence of subcentral foramina, the moderately or well-developed ventral and zygapophyseal crests and the notch on the posterior margin of the neural arch are diagnostic features of the trunk vertebrae of salamandrids (Ratnikov and Litvinchuk 2007). The different morphologies of MSNVE-23360/1 and 2 and MSNVE-23361 clearly suggest the presence of two different taxa. The almost-lacking neurapophysis, the concave anterior margin of the neural arch, the small posterior medial notch and the convex laminae allow the attribution of the latter to the genus *Triturus* (Ratnikov and Litvinchuk 2007) and therefore to the species complex *Triturus* gr. *T. cristatus* (including all central and eastern European *Triturus* species: *T. arntzeni*, *T. carnifex*, *T. cristatus*, *T. dobrogicus*, *T. karelinii* and *T. macedonicus*; Sillero

et al. 2014). It should be noticed, however, that MSNVE-23361 differs from trunk vertebrae of *T. dobrogicus* and *T. karelinii* because of the moderately developed posterior ventral crests and of the very low developed neurapophysis respectively (Ratnikov and Litvinchuk 2007). Moreover, its very small size can suggest that it belonged to a juvenile. The other vertebrae can be assigned to *Lissotriton* because of very high neurapophysis, horizontal dorsal margin of the latter, straight anterior margin of the neural arch, well-developed posterior medial notch and flat or slightly concave laminae (Ratnikov and Litvinchuk 2007). Trunk vertebrae of *Ichthyosaura* and *Ommatotriton* are morphologically similar to those of *Lissotriton*, but MSNVE-23360/1 and 2 cannot be referred to those genera since the anterior margin of their neural arch is not located posteriorly to the anterior third of the



Figure 4. Amphibians and reptiles from the II filling. *Bombina* sp.: left ilium (MSNVE-23374/3) in lateral (a) and medial (b) views. *Bufo bufo*: right humerus (MSNVE-23375/4) in medial (c), dorsal (d), ventral (e) and lateral (f) views. *Rana dalmatina* vel *R. latastei*: right ilium (MSNVE-23376/22) in lateral (g) and medial (h) views. *Anguis* gr. *A. fragilis*: right dentary (MSNVE-23379/6) in lateral (i) and medial (j) views. *Lacerta* gr. *L. viridis*: caudal vertebra (MSNVE-23378/1) in dorsal (k), anterior (l), ventral (m) and posterior (n) views. *Hierophis viridiflavus*: right compound bone (MSNVE-23380) in lateral (o) and medial (p) views. apr, angular process; cd, crista dorsalis; cl, crista lateralis; cp, crista paraventralis; cpr, coronoid process; cv, crista ventralis; dc, dorsal crest; ec, eminentia capitata; fcv, fossa cubitalis ventralis; lfl, lateral flange; mf, mandibular fossa; mfl, medial flange; os, olecranon scar; pa, pars ascendens; pd, pars descendens; rp, retroarticular process; sc, supraangular crest; ts, tuber superior.

prezygapophyses and the anterior margin of their neuropophysis can be vertical (Ratnikov and Litvinchuk 2007); moreover, the largest vertebrae herein described are much smaller than the maximum size reached by trunk vertebrae of those two genera: CL: 3.1 mm and PR-PO: 3.6 mm for *Ichthyosaura* and CL: 4.4 mm and PR-PO: 5.0 mm for *Ommatotriton* (Ratnikov and Litvinchuk 2007). The maximum size of the vertebrae from Tenuta Zuccarello is also smaller than that of *L. montandoni* (CL: 3.4 mm and PR-PO: 3.8 mm) and comparable with that of *L. vulgaris* (CL: 2.5 mm and PR-PO: 2.9 mm) as reported by Ratnikov and Litvinchuk (2007), but since trunk vertebrae of such species are strongly similar, we simply referred MSNVE-23360/1 and 2 to the species complex *Lissotriton* gr. *L. vulgaris*. We include at least *L. vulgaris* and *L. italicus* in this complex, but the comparative osteology of *Lissotriton* species in general is poorly known and therefore other species cannot be excluded a priori. MSNVE-23360/3 and 4 have been assigned to the same species complex because of the small size and the thin shaft, but also because of the strongly inclined crista ventralis of the humerus, the elongated area between caput femoris and trochanter and the slightly convex distal margin of the femur (Holman 1998).

Anura Fischer Von Waldheim, 1813
 Bombinatoridae Gray, 1831
Bombina Oken, 1816
Bombina sp.
 (Figures 2K-L, 4(A,B))

Referred material

- I filling: 3 parasphenoids (MSNVE-23362/1); 3 atlasses (MSNVE-23362/2); 8 trunk vertebrae (MSNVE-23362/3; 16); 2 sacral vertebrae (MSNVE-23362/4); 1 urostyle (MSNVE-23362/5); 9 humeri (MSNVE-23362/6–7); 4 ilia (MSNVE-23362/8–10); 5 femurs (MSNVE-23362/11–12, 17); 6 tibiofibulae (MSNVE-23362/13–15).
- II filling: 3 trunk vertebrae (MSNVE-23374/1); 1 urostyle (MSNVE-23374/2); 4 humeri (MSNVE-23374/5–6); 1 ilium (MSNVE-23374/3); 1 femur (MSNVE-23374/4).

Description

Parasphenoids are cross-shaped. Pars medialis and partes laterales have a wide end and the former is almost twice as

large and roughly twice as long as the latter. A large, triangular processus posterior is present posteriorly. No prominent ridges are present on the ventral surface.

Atlases are opisthocoelous. Their anterior cotyles are dorso-ventrally inclined and separated medially by a moderately wide spatium interglendoidale. Both ventral surface of the centrum and dorsal surface of the neural arch are smooth, without ventral keel and carina neuralis.

Trunk vertebrae are opisthocoelous and have a dorso-ventrally compressed centrum. Transverse processes are cylindrical and placed posteriorly to the prezygapophyses. The neural arch is moderately long and shows a pseudo-zygosphene on the anterior margin. There is no developed carina neuralis, but a small posterior point is present in the middle of the posterior margin of the dorsal surface of the arch. MSNVE-23362/16 differs from this morphology in having both an anterior and a posterior condyle, no posterior point and strongly dorso-ventrally compressed transverse processes. Moreover, its left process is bifurcated.

Sacral vertebrae have both an anterior and a posterior condyle. The dorsal surface of their neural arch shows a pseudo-zygosphene anteriorly and no carina neuralis. The sacral diapophyses are well developed antero-posteriorly.

Urostyles have an anterior cotyle and two small transverse apophyses near the anterior end. In MSNVE-23362/5, the left apophysis is moderately large by its base and has a pointed end curving in postero-lateral direction, whereas the right one is truncated and does not curve posteriorly. There is no crista dorsalis.

Humeri are moderately thin and have a straight diaphysis in ventral view. The eminentia capitata is spherical and shifted laterally. The crista ventralis is well developed, but there is no crista paraventralis. The crista lateralis is moderately developed, whereas the crista medialis varies from moderately developed to well developed. The fossa cubitalis ventralis is not developed and the olecranon scar is well marked.

There is no crista dorsalis on the thin shaft of the ilia (Figures 2K-L, 4(A,B)) and only a very small hint of tuber superior is visible on the dorsal surface of their body. The pars descendens is not developed, whereas the pars ascendens is moderately developed.

Femurs are thin. In dorsal view, their distal epiphysis is slightly larger than the proximal one. A low crista femoris is present on the medial surface, near the proximal epiphysis.

Tibiofibulae are small, thin and straight. Their epiphyses are strongly larger than the diaphysis.

Bufonidae Gray, 1825

Bufo Garsault, 1764

Bufo bufo (Linnaeus, 1758)

(Figures 2M-N, 4C-F)

Referred material

- I filling: 4 sphenetmoids (MSNVE-23363/1, 34); 3 parasphenoids (MSNVE-23363/2; 7); 3 prootics fused with the occipital (MSNVE-23363/3-4); 3 pterygoids (MSNVE-23363/

5-6); 2 squamosals (MSNVE-23363/8); 4 atlases (MSNVE-23363/35-36); 27 trunk vertebrae (MSNVE-23363/9); 6 sacral vertebrae (MSNVE-23363/10); 1 clavicle (MSNVE-23363/11); 6 coracoids (MSNVE-23363/12-13); 14 scapulae (MSNVE-23363/15-16); 2 suprascapulae (MSNVE-23363/14); 15 humeri (MSNVE-23363/17-20, 32, 33); 5 radioulnae (MSNVE-23363/21-23); 12 ilia (MSNVE-23363/24-26); 13 femurs (MSNVE-23363/27-28); 11 tibiofibulae (MSNVE-23363/29-31).

- II filling: 4 trunk vertebrae (MSNVE-23375/3); 2 humeri (MSNVE-23375/4-5); 4 tibiofibulae (MSNVE-23375/1-2).

Description

The well-ossified sphenetmoids are roughly as long as they are large. They have a very short anterior process and moderately developed lateral processes, which are little individualized in ventral view. The incisura semielliptica is large. In anterior view, a moderately developed sella amplificans is visible in each antrum olfactorium of MSNVE-23363/1, but its roof is not indented.

Parasphenoids are cross-shaped, with partes laterales almost as long as the pars medialis. The end of the former is pointed, whereas that of the latter is more rounded. A small and triangular processus posterior is present. A ridge runs on the ventral surface of partes laterales, starting from an osseous swelling located at their meeting point. In MSNVE-23363/7, the ridges and the swelling are very well developed and another ridge runs anteriorly from the middle of the latter to the base of pars medialis.

The large prootics are almost completely fused with the occipitals. They have a large and robust prootic process and an occipital condyle that is subrectangular-shaped in posterior view. The ridges on the dorsal surface are very well developed and thick.

Pterygoids do not show an alary dilatation. The long ramus maxillaris is strongly curved medially. The other two rami (posterior and interior) are shorter than the former and are almost equally long. The width of the three branches is roughly the same. The middle part of the tympanic border is gutter-shaped in ventral view.

Squamosals show a moderately developed lamina along the transverse branch, whose lateral surface is not ornamented. Both anterior and posterior portion of the transverse branch are short.

Atlases are large and robust and have a posterior dorso-ventrally compressed condyle and a short neural arch. The neural canal has an ogival section. Except for MSNVE-23363/35, the atlases show a moderately developed osseous expansion under each postzygapophysis.

Trunk vertebrae are large, robust and procoelous. They have a large centrum, short lateral walls, a short neural arch and laterally-, antero-laterally- or postero-laterally-directed transverse processes located posteriorly to the prezygapophyses.

Sacral vertebrae are procoelous and have two well-separated, circular condyles posteriorly. Sacral diapophyses are moderately expanded antero-posteriorly and do not show a fossa by their base. A well-developed carina neuralis is present on the dorsal surface of the neural arch.

The clavicle is large, moderately robust and straight.

Coracoids are robust and their ends are similar in width.

Scapulae are robust and longer than they are large. On the margo anterior, only a very small hint of crista anterior is present near the pars acromialis. The cavitas glenoidalis is well visible in ventral view. There is no supraglenoidal fossa.

Suprascapulae are large and L-shaped. Their margins are regular and the two branches of the L create an angle of 90°. The anterior margin is folded in ventral direction.

Humeri (Figure 4C-F) are moderately robust and straight (MSNVE-23363/18, 19, 32 and 33) or moderately curved laterally (MSNVE-23363/17 and 20; MSNVE-23375/4 and 5) in ventral view. They have a laterally shifted eminentia capitata. The crista ventralis is very well developed, whereas the crista paraventralis, if present (in MSNVE-23363/17–20 and MSNVE-23375/4), is only a hint. A moderately deep fossa cubitalis ventralis is present. The distal epiphysis is distally eroded and both epicondyles and crista lateralis are moderately developed. The crista medialis is very slightly developed. The olecranon scar is large and very well marked.

Radioulnae are robust. The two portions of the distal epiphysis are almost equally large and slightly compressed in distal view. Only in MSNVE-23363/21, the radial portion is subcircular and larger than the ulnar one.

Ilia (Figure 2M-N) have no crista dorsalis. A dorsally rounded tuber superior is present. There are neither a lamina calamita on the shaft nor a preacetabular fossa on the body. The pars ascendens is short, whereas the pars descendens is well developed.

Femurs are robust and show a well-developed crista femoris, which splits proximally forming a triangular structure.

Tibiofibulae are robust and stocky. The two portions of the proximal epiphysis are roughly subelliptical and roughly parallel, whereas those of the distal one are roughly subcircular. On both epiphyses, the lateral portion is larger than the medial one. MSNVE-23363/31 shows a roughly cylindrical osseous proliferation developed in medio-distal direction on the medial side of the diaphysis.

Ranidae Rafinesque, 1814

Rana Linnaeus, 1758

Rana dalmatina Fitzinger in Bonaparte, 1839 vel *Rana latastei* Boulenger, 1879

(Figures 2O-P, 4G-H)

Referred material

- I filling: 7 premaxillae (MSNVE-23364/9–10); 137 maxillae (MSNVE-23364/1–2); 10 frontoparietals (MSNVE-23364/5–6); 1 frontoparietal fused with prootic and exoccipital (MSNVE-23364/7); 26 sphenetmoids (MSNVE-23364/3); 86 parasphenoids (MSNVE-23364/4); 6 prootics fused with the exoccipital (MSNVE-23364/8, 55–57); 5 squamosals (MSNVE-23364/23–24); 3 pterygoids (MSNVE-23364/53–54); 66 angulars (MSNVE-23364/11–12); 50 atlas (MSNVE-23364/13–14); 532 trunk vertebrae (MSNVE-23364/16–17); 3 atlas fused with the first trunk vertebra

(MSNVE-23364/15); 1 7th trunk vertebra fused with 8th one (MSNVE-23364/18); 74 sacral vertebrae (MSNVE-23364/19); 2 sacral vertebrae fused with the 8th trunk vertebra (MSNVE-23364/20, 22); 75 urostyles (MSNVE-23364/21); 101 coracoids (MSNVE-23364/27–28); 1 clavicle (MSNVE-23364/50); 116 scapulae (MSNVE-23364/25–26); 1 right scapula fused with the clavicle (MSNVE-23364/49); 106 humeri (MSNVE-23364/29–35, 51–52); 178 radioulnae (MSNVE-23364/36–38); 236 ilia (MSNVE-23364/39–41); 363 femurs (MSNVE-23364/42–44); 394 tibiofibulae (MSNVE-23364/45–48).

- II filling: 8 maxillae (MSNVE-23376/3–4); 1 sphenetmoid (MSNVE-23376/9); 3 angulars (MSNVE-23376/6–7); 13 trunk vertebrae (MSNVE-23376/17–18); 3 sacral vertebrae (MSNVE-23376/5); 3 urostyles (MSNVE-23376/14); 4 coracoids (MSNVE-23376/15–16); 1 scapula (MSNVE-23376/8); 6 humeri (MSNVE-23376/19–21); 6 ilia (MSNVE-23376/1–2, 22); 12 femurs (MSNVE-23376/12–13); 11 tibiofibulae (MSNVE-23376/10–11).

Description

Premaxillae bear teeth and show two well-developed posterior processes by the lateral and medial sides of the pars dentalis, whose posterior margin is therefore concave in dorsal view.

Maxillae are large-sized and elongated. They bear teeth and are devoid of ornamentation on the lateral surface. There is no processus palatinus. In lateral view, the frontal process is rectangular or subrectangular and the lamina anterior is low.

The paired frontoparietals are straight and rectangular in dorsal view. The dorsal surface is flat and smooth, except for two very low ridges starting from the parietal eminence (canthus postero-lateralis): the medial ridge, running anteriorly and forked in its anterior half, and the very low developed occipital ridge, running postero-medially. The parietal eminence is shifted laterally, by the beginning of the well-developed processus lateralis. A shallow occipital canal is present laterally to the eminence. On the ventral surface, the incrassatio frontoparietalis is double, with a circular posterior portion. One of the frontoparietals, MSNVE-23364/7, is fused with a prootic/exoccipital complex. In such specimen, the complex is completely fused. The prootic process tends to narrow distally and the occipital condyle is roughly subelliptical in posterior view.

The well-ossified sphenetmoids are slightly longer than they are large. Anterior and lateral processes are moderately developed and the latter are moderately to well individualized in ventral view. The incisura semielliptica is moderately deep. No sella amplificans is visible in anterior view. In ventral view, the posterior portion of the bone does not shrink.

Parasphenoids are slender. They have an anteriorly pointed pars medialis, which is twice as long as the lobe-shaped partes laterales. The width of the three partes is similar. A moderately small and triangular-shaped processus posterior is present, whereas there are no ridges on the ventral surface.

Prootics fused with exoccipitals are morphologically similar to those of MSNVE-23364/7, except for MSNVE-23364/57 in which the fusion is not complete.

Squamosals are T-shaped. They do not develop a lamina along the transverse branch and their lateral surface is smooth. Anterior and posterior portions of the transverse branch are equally long, except for MSNVE-23364/23 (the largest one) in which the posterior part is shorter. The distal end of the descending branch is distinctly lobed. A moderately developed internal ridge runs along the medial surface of the descending branch.

Pterygoids do not show expansions on the margo maxillaris. Their ramus interior is strongly shorter than the ramus posterior.

Angulars are large and moderately slender, with a well-developed, vertical processus coronoideus.

Atlases have a moderately small and dorso-ventrally compressed posterior condyle. Their centrum is little individualized. The neural arch is short and have thin lateral walls and a moderately developed carina neuralis, which continues posteriorly in a short posterior point. MSNVE-23364/14 is partially burned.

Trunk vertebrae are procoelous (MSNVE-23364/16 and MSNVE-23376/17) or amphicoelous (MSNVE-23364/17 and MSNVE-23376/18) and slender. They have a small, dorso-ventrally compressed and little individualized centrum and a short neural arch with thin lateral walls. A very low or moderately developed carina neuralis is present on the dorsal surface of the arch; it continues posteriorly in a very little- to well-developed posterior point. Transverse processes are located posteriorly to the prezygapophyses and are directed laterally, antero-laterally or postero-laterally.

Three atlases (MSNVE-23364/15) are fused with the first trunk vertebra, whereas MSNVE-23364/18 consists of two fused trunk vertebrae, the posterior one of which has a posterior cotyle (and could be identified, therefore, as the amphicoelous eight vertebra).

Sacral vertebrae have an anterior condyle and two circular posterior condyles. Their sacral diapophyses are cylindrical and postero-laterally directed.

Two sacral vertebrae (MSNVE-23364/20 and 22) are fused with the eight trunk vertebra. In MSNVE-23364/20, the left postzygapophysis of the trunk vertebra and the left prezygapophysis of the sacral vertebra are lacking.

Urostyles have two circular anterior condyles and a high crista dorsalis. The neural arch is narrow or moderately narrow in anterior view and there are no transverse processes.

Coracoids have a moderately thin body and a pars epicoracoidalis which is strongly larger than the pars glenoidalis.

MSNVE-23364/50 is a thin, straight and elongated clavicle.

Scapulae are longer than they are large and have no crista anterior. The pars acromialis hides partially the cavitas glenoidalis in ventral view, but does not participate in the articulation with the humerus. A low- to well-developed internal ridge is visible on the dorsal surface of the pars glenoidalis and of the body of the bone. One of the scapulae, MSNVE-23364/49, is fused with a thin and straight clavicle.

Humeri are moderately thin and straight in ventral view. They do not have a crista paraventralis, whereas the crista

ventralis is well developed. The spherical eminentia capitata is aligned with the diaphysis. Cristae medialis and lateralis go from not developed (MSNVE-23364/29–31 and 51; MSNVE-23376/20 and 21) to low developed (MSNVE-23364/32, 33 and 52) and well developed (MSNVE-23364/34 and 35; MSNVE-23376/19); in the latter case, the crista medialis runs up to the middle of the diaphysis and slightly bends in dorsal direction. A deep fossa cubitalis ventralis is present and the olecranon scar is narrow and elongated. MSNVE-23364/31 shows a ventrally developed and rounded spur located proximally to the medial epicondyle.

Radioulnae are slender. The radial portion of their distal epiphysis is subcircular in distal view, whereas the ulnar one is slightly compressed. A distally developed, subcylindrical osseous proliferation can be seen on the ventro-lateral surface of the radial portion of the distal epiphysis of MSNVE-23364/38.

Ilia (Figure. 2O-P, 4G-H) have a high crista dorsalis, not distinctly bending in medial direction. The tuber superior is present, but it is not strongly individualized and does not exceed the height of the crista. Both partes ascendens and descendens are well developed and neither interiliac tubercle nor groove are present. The angle between tuber and pars ascendens is slightly greater than 90°.

Femurs are long and thin and do not have a crista femoris.

Tibiofibulae are slender. The portions of the proximal epiphysis are roughly subelliptical and roughly parallel, whereas those of the distal one are roughly subcircular. On both epiphyses, the lateral portion is slightly larger than the medial one. MSNVE-23364/46 and 47 show a stocky osseous swelling near the distal and the proximal epiphyses respectively.

Anura indet.

Referred material

- I filling: 6 sphenetmoids (MSNVE-23365/14); 1 prootic (MSNVE-23365/13); 3 exoccipitals (MSNVE-23365/11–12); 1 sacral vertebra fused with the urostyle (MSNVE-23365/15); 25 sternal elements (MSNVE-23365/2); 3 coracoids (MSNVE-23365/4, 6); 1 scapula (MSNVE-23365/8); 120 humeri (MSNVE-23365/9–10); 16 ischia (MSNVE-23365/3); 6 femurs (MSNVE-23365/5); 1 tibiofibula (MSNVE-23365/7); 955 indeterminate elements (MSNVE-23365/1).
- II filling: 1 humerus (MSNVE-23377/2); 9 radioulnae (MSNVE-23377/3–4); 1 tibiofibula (MSNVE-23377/1); 34 indeterminate elements (MSNVE-23377/5).

Description

MSNVE-23365/15 (Figure 2Q-R) is a small sacral vertebra fused with a rod-shaped urostyle. It has an anterior cotyle and strongly antero-posteriorly developed sacral diapophyses. Prezygapophyses are well differentiated from the rest of the sacral vertebra and the anterior end of the urostyle does not show expansions contacting the diapophyses.

MSNVE-23365/7 is broken by the middle of the diaphysis and shows an anomalous development of the bone tissue by the breakage.

Identification

Anurans remains have been identified using diagnostic features reported by Bailon (1999). Ilii are particularly informative and allow the distinction of three different taxa. The ones with a high and vertical (that is, not bending) crista dorsalis, a not strongly individualized tuber superior and an angle of more than 90° between tuber and pars ascendens can be referred to the genus *Rana* and in particular to *R. dalmatina* because of the crista being higher than the tuber. However, Bailon does not consider in his key *Rana latastei*, which is also currently present in the area of Tenuta Zuccarello (Sillero et al. 2014). Given that clear osteological features distinguishing *R. dalmatina* from *R. latastei* are currently unknown, we here decided to assign all ilia showing the *Rana* morphology to *R. dalmatina* vel *R. latastei*. Ilii devoid of crista dorsalis can be further distinguished based on the morphology of the tuber superior and of the posterior portion of the body: a well-developed tuber and a short pars ascendens are features of the genus *Bufo*, whereas poorly developed tuber and pars descendens identify *Bombina*. The absence of lamina calamita and preacetabular fossa on the ilia of *Bufo* rules out *Bufo calamita* and *Bufo viridis*, whereas the dorsally rounded tuber superior allows their assignment to *B. bufo*. The other skeletal elements have been attributed to one of the three taxa following the key of Bailon (1999); elements that could be identified only at the generic level of *Rana* and *Bufo* have been tentatively referred to the previously recognized species. A number of fragmented or uninformative elements are referred only to indeterminate anurans. MSNVE-23365/15 could resemble a sacral vertebra of a juvenile of *Pelobates fuscus* because of the fused urostyle and the cotyle (Bailon 1999), but it is different from a similar-sized specimen stored in the collection of the University of Torino (MDHC 181) in the well-differentiated prezygapophyses, the absence of a contact between diapophyses and urostyle and the rod-like shape of the latter. Diapophyses are morphologically similar to those of *Bombina*, in which the fusion between the sacral vertebra and the urostyle is possible (Madej 1965). However, sacral vertebrae of *Bombina* have an anterior condyle (Bailon 1999) and so we decided not to assign MSNVE-23365/15 to this taxon, identifying it only as an indeterminate anuran. Nevertheless, it could represent a pathological condition of *Bombina*. It has to be noted that other pathological specimens have been found both among the material attributed to *Bombina* and among the one assigned to the other taxa (e.g. MSNVE-23362/16, MSNVE-23363/31, MSNVE-23364/38 and MSNVE-23365/7). Among the humeri of *B. bufo* and *R. dalmatina* vel *R. latastei*, MSNVE-23363/18, 19, 32 and 33 (9 humeri), MSNVE-23364/34 and 35 (18 humeri) and MSNVE-23376/19 (2 humeri) belonged to male individuals, whereas MSNVE-23363/17 and 20 (6 humeri), MSNVE-23375/4 and 5 (2 humeri), MSNVE-23364/29–33, 51 and 52 (88 humeri) and MSNVE-23376/20 and 21 (4 humeri) belonged to females (Bailon 1999).

Reptilia Laurenti, 1768
Testudines Linnaeus, 1758
Emydidae Rafinesque, 1815
Emys Duméril, 1805
Emys orbicularis (Linnaeus, 1758)
(Figure 3A)

Referred material

- I filling: 1 fragmented carapace (MSNVE-23373/1); 3 vertebrae (MSNVE-23373/4–6); 1 fragment of rib (MSNVE-23373/2); 1 right femur (MSNVE-23373/3).

Description

MSNVE-23373/1 is a partial fragmented carapace including nuchal, neurals 1–6, suprapygal 2, pygal, right costals 1–8, right peripherals 1–10, left costals 2–5 and 7–8, left peripherals 1, 3–5 and 7–10. Due to its irregular shape, the small bone located anteriorly to the suprapygal 2 (Figure 3A) is tentatively considered an accessory element and not the suprapygal 1. The dorsal surface is smooth, with moderately shallow grooves for the horny shields. Although broken, the carapace is rather flat. No change in declivity occurs at the contact between suprapygal 2 and the pygal. The grooves marking the contact between pleurals and marginals are located strongly laterally in respect to the sutures between costals and peripherals.

The nuchal is hexagonal and larger than it is long. The postero-lateral margins are slightly longer than the antero-lateral ones and the posterior margin is short. On its dorsal surface, are clearly evident the grooves marking the contacts between cervical and the first marginals, cervical and the first vertebral, the first marginals and the first vertebral, the first vertebral and the first pleurals.

Neurals are hexagonal and slightly larger than they are long, except for the first one, which is subrectangular and longer than it is large. Both anterior and posterior margins of neural 1 are convex, whereas its lateral margins are only slightly rounded. The other neurals have a slightly concave anterior margin and a slightly convex posterior one; their antero-lateral margins are very short. Neurals 1, 3 and 5 show the grooves between vertebrae on the dorsal surface (between vertebral 1 and 2, 2 and 3 and 3 and 4 respectively). All the grooves are located in the posterior half of the plates.

Suprapygal 2 (Figure 3A) has 6 sides and is roughly trapezoidal in shape. Its width is distinctly smaller than that of vertebral 5. There are no grooves on its dorsal surface.

The pygal (Figure 3A) is slightly trapezoidal and larger than it is long. The grooves between left and right marginals 12 and between them and vertebral 5 can be seen on its dorsal surface. A shallow notch is present on the posterior margin of the plate, between the marginals.

All costals show a short postero-medial side at their proximal end: in costal 1–7 this side is very short, whereas in costal 8 it is longer than the antero-medial one (Figure 3A). The first costal is the longest one. The groove marking the contact between vertebrae and pleurals passes through the dorsal surface of all costals; costals 1, 3, 5 and 7 also show the contact between consecutive vertebrae, whereas on 2, 4 and 6

there are the grooves between consecutive pleurals. The contact between vertebral 1 and pleural 1 passes through the middle of the suture between nuchal and costal 1, whereas the contact between vertebral 4 and 5 is located almost by the suture between costal 7 and 8. The free portion of the ribs is well developed and inserts in the peripherals.

Peripherals 4–7 show ventrally the surface for the ligamentous contact with the plastron. The lateral border of the fourth, fifth and sixth ones is folded in ventral direction, whereas the eighth, ninth and tenth ones are horizontally raised in their lateral portion. Width and length are similar in peripherals 8–10, whereas peripherals 1 and 2 are very slightly larger than they are long and peripherals 3–7 are longer than they are large.

The cervical horny element was very narrow and shorter than the first third of the nuchal. Its posterior margin was straight, without indentation for the first vertebral.

Vertebrae 1–4 were hexagonal and larger than they were long; their lateral margins were wavy. Vertebral 1 covered also a very small part of peripheral 1, but not the lateral extremities of the nuchal. Vertebral 5 was heptagonal, roughly trapezoidal and larger than it was long; it covered the anterior half of the pygal.

All pleurals but the fourth one were larger than vertebrae. The first one was the largest, whereas the fourth one was the smallest. Width and length were similar in pleural 1 and 4, whereas pleural 2 and 3 were larger than they were long. The grooves between consecutive pleurals do not continue in those between consecutive marginals.

Marginals were distinctly longer than they were large. Grooves between them are never located by the sutures between peripherals. Right and left marginals 12 were separated.

The femur is slender, elongated and strongly curved. The head of the bone is moderately large, whereas tuberositas internus and trochanter are similar in size.

Identification

According to Hervet (2000), all the morphological characters of MSNVE-23373/1 listed above identify the carapace of *E. orbicularis*, even though the contact between vertebral 4 and 5 located on costal 7 near the suture with costal 8 is a feature of *Mauremys leprosa*. Since this is the only relevant exception, we referred MSNVE-23373/1 to the former species, together with the other chelonian remains.

Squamata Oppel, 1811

Lacertilia Owen, 1842

Anguidae Gray, 1825

Anguis Linnaeus, 1758

Anguis gr. *A. fragilis* Linnaeus, 1758

(Figures 3B–F, 4(I,J))

Referred material

- I filling: 1 premaxilla (MSNVE-23368/1); 13 maxillae (MSNVE-23368/2–3); 1 frontal (MSNVE-23368/12); 3 parietals (MSNVE-23368/6–7, 14); 1 quadrate (MSNVE-23368/26); 39 dentaries (MSNVE-23368/4–5); 1 coronoid (MSNVE-23368/27); 6 compound bones (MSNVE-23368/28–29); 3 axes (MSNVE-23368/25); 92

cervical vertebrae (MSNVE-23368/8); 1732 trunk vertebrae (MSNVE-23368/16–17, 24); 63 cloacal vertebrae (MSNVE-23368/9–10, 15, 18); 1296 caudal vertebrae (MSNVE-23368/19–23); 4 osteoderms (MSNVE-23368/11, 13).

- II filling: 1 maxilla (MSNVE-23379/4); 2 dentaries (MSNVE-23379/5–6); 1 cloacal vertebra (MSNVE-23379/3); 44 caudal vertebrae (MSNVE-23379/1–2).

Description

The small, unpaired premaxilla has a large and arrow-shaped nasal process. It bears five conical, monocuspid teeth, provided with a slightly posteriorly curved and non-striated tip.

Maxillae are small and bear large, conical, monocuspid teeth, strongly curving posteriorly at the tip. Teeth are well spaced from each other and do not show striae. Their number goes from 4 to 7.

MSNVE-23368/12 is a small, paired frontal with a moderately ornamented dorsal surface and a well-developed crista cranii frontalis. In dorsal view, it is triangular and antero-posteriorly elongated. A well-developed posterolateral process is visible by the postero-lateral corner of the bone. In lateral view, the articulation surface with the prefrontal covers two thirds of the length of the bone and no ventral process of the crista cranii is recognizable.

The small, unpaired parietals show a moderately developed ornamentation on the dorsal surface and a large parietal foramen in the middle of the parietal table (although partially obliterated in MSNVE-23368/6). A small and smooth area levis is present between the dorsal ornamentation and the posterior margin of the bone, whose center is marked by a deep parietal notch. A long and slender supratemporal process runs postero-ventrally from each postero-lateral corner of the bone. In ventral view, one can see the very small fossa parietalis, strongly smaller than the parietal notch.

The quadrate and the coronoid are small-sized.

Dentaries (Figure 4I–J) are small and distinctly curved dorsally in the posterior portion. They bear teeth similar to those of the maxillae, whose number goes from 4 to 9. In lateral view, the dorsal crest covers less than a half of the length of the teeth. The intramandibular septum ends by the last tooth position or slightly anteriorly. No surangular spine can be seen on the posterior margin of the bone and the posterior end of the angular process is located strongly anteriorly to that of the coronoid process.

Compound bones are small and have a short and quadrangular retroarticular process.

All vertebrae (Figure 3B–F) are small-sized and slightly antero-posteriorly elongated. They have a dorso-ventrally compressed centrum with parallel lateral margins in the posterior half. No keel is present on the ventral surface of the centrum of trunk and cloacal vertebrae, whereas the caudal ones show a well-developed hemal arch fused with the centrum. The autotomy plane can be either present (MSNVE-23368/20 and MSNVE-23379/2) or absent (MSNVE-23368/19 and MSNVE-23379/1). The left lateral apophysis of MSNVE-23368/10 presents a thick osseous swelling near its base, whereas the lateral

one of MSNVE-23368/18 is lacking (probably not because of breakage). A number of caudals show a pathological osseous proliferation posteriorly (MSNVE-23368/21 and 22: 13 vertebrae) or anteriorly (MSNVE-23368/23: 1 vertebra); some of them (MSNVE-23368/22: 11 vertebrae) are fused with a consecutive anomalously ossified vertebra.

Osteoderms are very small and very thin. They are suboval in shape and have no ridges on the external surface.

Lacertidae Batsch, 1788

Lacerta Linnaeus, 1758

Lacerta gr. *L. viridis* (Laurenti, 1768)

(Figures 3G-H, 4K-N)

Referred material

- I filling: 5 premaxillae (MSNVE-23366/12); 28 maxillae (MSNVE-23366/2-5); 3 jugals (MSNVE-23366/34); 3 frontals (MSNVE-23366/6-7); 1 postorbital (MSNVE-23366/15); 5 pterygoids (MSNVE-23366/8-9); 6 quadrates (MSNVE-23366/16-17); 4 otooccipital regions (MSNVE-23366/10); 1 sphenoid (MSNVE-23366/11); 26 dentaries (MSNVE-23366/1, 30-31); 1 splenial (MSNVE-23366/29); 1 coronoid (MSNVE-23366/36); 1 angular (MSNVE-23366/37); 3 articulars fused with surangulars (MSNVE-23366/20); 1 surangular (MSNVE-23366/35); 6 axes (MSNVE-23366/41); 228 presacral vertebrae (MSNVE-23366/40); 14 cloacal vertebrae (MSNVE-23366/45); 1 pair of fused cloacal vertebrae (MSNVE-23366/46); 69 caudal vertebrae (MSNVE-23366/42-43); 1 chevron (MSNVE-23366/44); 1 rib (MSNVE-23366/47); 5 clavicles (MSNVE-23366/32-33); 20 humeri (MSNVE-23366/25-26); 4 ilia (MSNVE-23366/23-24); 8 ischia (MSNVE-23366/18-19); 5 pubes (MSNVE-23366/27-28); 18 pelvic girdles (MSNVE-23366/38-39); 24 femurs (MSNVE-23366/21-22); 23 tibiae (MSNVE-23366/13-14).
- II filling: 2 caudal vertebrae (MSNVE-23378/1-2).

Description

Premaxillae have a leaf-shaped posterodorsal process and show 9 to 11 tooth positions. The maximum width of their shelf reaches 3.8 mm.

Maxillae are very large and present 16 to 20 tooth positions. Their maxillary shelf reaches a maximum length of 11.5 mm. The anterior projection of the dorsal process and the lappet on the anterior process are well developed (except for the lappet of MSNVE-23366/2 and 4, which is poorly developed). The posterior process shows a clear step near its end.

Jugals are large and are provided with a well-developed quadratojugal process. There is no medial process on the palatal shelf. In lateral view, the exposed portion of the anterior part is very small.

The unfused frontals reach 13 mm in length. They are not constricted in the medial region and show a strongly interdigitated posterior margin. In dorsal view, the articulation surface with the dorsal process of the maxilla is very small.

The postorbital is large and not fused with the postfrontal. The anteromedial process is present and well developed.

Pterygoids are very large, reaching 16 mm in length. They present a strong pterygoid recess and a large number of pterygoid teeth on the ventral surface.

In medial view, quadrates have a rounded anterior outline. Their anterior platform is flat and they reach a maximum length of 6 mm.

Bones composing the otooccipital regions are very large. The sphenoid shows an undepressed ventral surface and strongly laterally expanded basiptyergoid processes. Its ventrolateral crests form the anterior wall of the sphenoccipital tubercles. Prootics have a very well developed alar process and a very distinct posterior process. The paroccipital process of the otooccipital is very long. The anterolateral margins of the supraoccipital are distinctly convergent and the processus ascendens is largely ossified.

Dentaries (Figure 3G-H) have a large and medially opened Meckel's groove. They are very large, with a dental shelf reaching 14 mm in length. The posterior projections are almost equal in size. Number of tooth positions goes from 21 to 27.

Articulars are large and straight in medial view. They are fused with surangulars.

The teeth on maxillae and dentaries are pleurodont, cylindrical and mono-, bi- or tricuspid. In the premaxillae, only mono- and bicuspid morphologies are present.

Vertebrae are large and antero-posteriorly elongated. Their centrum is circular in posterior view, with a well-developed keel on the ventral surface (only in the cloacal ones the keel is less developed). The maximum centrum length of presacral vertebrae is 4.8 mm. Caudal vertebrae (Figure 4K-N) do not present fused hemapophyses. Autotomy plane can be present (MSNVE-23366/42) or absent (MSNVE-23366/43 and MSNVE-23378/1-2). MSNVE-23366/46 is a pair of fused cloacal vertebrae.

All other bones are large-sized.

Lacertidae indet

(Figure 3I-J)

Referred material

- I filling: 19 maxillae (MSNVE-23367/1-2); 2 postorbital (MSNVE-23367/31); 2 pterygoids (MSNVE-23367/21); 1 quadrate (MSNVE-23367/32); 23 otooccipital regions (MSNVE-23367/27); 3 sphenoids (MSNVE-23367/29); 1 basioccipital (MSNVE-23367/28); 1 otooccipital (MSNVE-23367/30); 17 dentaries (MSNVE-23367/3-6, 8); 12 axes (MSNVE-23367/7); 41 presacral vertebrae (MSNVE-23367/9, 11); 2 pairs of fused cloacal vertebrae (MSNVE-23367/14-15); 87 caudal vertebrae (MSNVE-23367/10, 12); 1 chevron (MSNVE-23367/13); 5 interclavicles (MSNVE-23367/19); 7 humeri (MSNVE-23367/16, 22-23); 14 femurs (MSNVE-23367/17-18, 23-24); 2 tibiae (MSNVE-23367/26); 12 indeterminate elements (MSNVE-23367/20).

Description

Remains assigned to indeterminate lacertids are morphologically similar to those referred to *Lacerta* gr. *L. viridis*, but much smaller. The maximum length of the shelf of the maxillae is

6 mm and they bear 13 to 17 tooth positions. Pterygoids reach a maximum length of 9 mm and have no pterygoid teeth. The maximum length of the quadrate is 3.4 mm. As for the dentaries, the maximum length is 7 mm and the number of tooth positions goes from 16 to 23. In MSNVE-23367/5, the ventral projection is longer than the dorsal one. Otooccipital regions are not completely fused. Alar and posterior processes of the prootics, paroccipital processes of the otooccipitals and the processus ascendens of the supraoccipital are less developed than the same structures in remains referred to *Lacerta* gr. *L. viridis*. Maximum centrum length of presacral vertebrae is 2.3 mm. Autotomy plane is absent in caudal vertebra MSNVE-23367/10 and present in MSNVE-23367/12. Both MSNVE-23367/14 and 15 are represented by two fused cloacal vertebrae each. Interclavicles are small and cross-shaped.

Identification

The presence of a small-sized species of anguid is testified by the small vertebrae with a dorso-ventrally compressed centrum (Delfino et al. 2011). Anguid remains can be referred to *Anguis* gr. *A. fragilis* (including *A. cephalonica*, *A. colchica*, *A. fragilis*, *A. graeca* and *A. veronensis*; Gvoždík et al. 2013) because of: large, conical, moncuspid and strongly posteriorly curved teeth without striae on the tip; strongly reduced fossa parietalis; dorsal crest covering less than a half of teeth on the dentary; end of the intramandibular septum located by or nearly to the last tooth position; posterior portion of dentaries dorsally curved; no surangular spine; short retroarticular process; elongation of vertebrae; parallel margins in the posterior half of the centrum; small size, thinness and rounded shape of the osteoderms; absence of ridges on the latter (Holman 1998; Delfino 2002; Delfino et al. 2011; Klembara et al. 2014). Maxillae and dentaries bearing pleurodont, cylindrical, mono-, bi- or tricuspid teeth are, on the other hand, a feature of the family Lacertidae (Bailon 1991; Delfino 2002; Delfino et al. 2011). Following Barahona and Barbardillo (1997), the largest remains can be assigned to *Lacerta* gr. *L. viridis*, a species complex comprising middle-sized European lacertids of the genus *Lacerta*. Assignment of the remains to *Timon lepidus*, the largest lacertid currently living in Europe, is prevented by frontals not constricted, stepped posterior process of the maxillae, flat anterior platform of the quadrates, strong pterygoid recess and sphenoids with an undepressed ventral surface (Barahona and Barbardillo 1997). Smaller remains of lacertids, whose identification is notoriously tricky (Villa et al. 2017), have been attributed only to indeterminate members of the family. They could represent another smaller species, but also juveniles of *Lacerta* gr. *L. viridis*. The length of the posterior projections of MSNVE-23367/5 seems to confirm the second hypothesis (Barahona and Barbardillo 1997).

Serpentes Linnaeus, 1758
Colubridae Opperl, 1811
'Natrix' sensu Szyndlar, 1991b
Natrix Laurenti, 1768
Natrix natrix (Linnaeus, 1758)
(Figure 3K-O)

Referred material

- I filling: 67 trunk vertebrae (MSNVE-23369/1-2).

Description

Trunk vertebrae have an elongated vertebral centrum, a sigmoid-shaped and obtuse hypapophysis and a neural spine whose antero-dorsal corner is moderately to well developed anteriorly. The distal end of the prezygapophyseal processes is obtuse and the parapophyseal processes are obtuse and moderately thin. In posterior view, the neural arch is vaulted.

'Colubrines' sensu Szyndlar, 1991a
Coronella Laurenti, 1768
cf. *Coronella* sp.
(Figure 3P-T)

Referred material

- I filling: 2 trunk vertebrae (MSNVE-23370/1-2).

Description

Trunk vertebrae have an elongated centrum (centrum length is 3 mm in both specimens) and are provided with a moderately low neural spine. The anterior margin of the zygosphenes shows a very little developed median convexity. Instead of a developed hypapophysis, they have a weakly defined hemal keel, which broadens posteriorly. Prezygapophyseal processes are very short and stocky and the proximal portion of the prezygapophyses is thick. Parapophyses are longer than diapophyses. In posterior view, the neural arch is depressed.

Hierophis Fitzinger, 1843
Hierophis viridiflavus (Lacepède, 1789)
(Figures 3U-Y, 4(O,P))

Referred material

- I filling: 1 compound bone (MSNVE-23371/5); 89 trunk vertebrae (MSNVE-23371/1-4).
- II filling: 1 compound bone (MSNVE-23380).

Description

Compound bones are large and have a moderately deep (MSNVE-23380) or deep (MSNVE-23371/5) mandibular fossa. In lateral view, the medial flange is dorsally rounded and strongly higher than the lateral one. The posterior end of the bone is preserved only in MSNVE-23380 (Figure 4O-P); in this specimen, a thick supraangular crest is present ventrally to the articulation surface with the quadrate and the retroarticular process is short and straight.

Trunk vertebrae (Figure 3U-Y) are provided with an elongated centrum (CL: 6 mm) and with a neural spine, which is longer than it is high. A well-developed hemal keel is present on the ventral surface of their centrum; its posterior portion is flat and larger than the anterior one. The anterior margin of

the zygosphene is almost straight, but in some small specimen (MSNVE-23371/4: 35 vertebrae) it can present a very little developed median convexity. Prezygapophyseal processes are long and the neural arch is vaulted in posterior view.

Serpentes indet.

Referred material

- I filling: 1 right pterygoid (MSNVE-23372/4); 23 cervical vertebrae (MSNVE-23372/1); 1 trunk vertebra (MSNVE-23372/5); 3 cloacal vertebrae (MSNVE-23372/3); 10 caudal vertebrae (MSNVE-23372/2).

Description

MSNVE-23372/5 is a trunk vertebra provided with an anomalous hemal keel. It is well developed, but splits into two flanked portions by its posterior end. The vertebra has an elongated centrum, a little developed neural spine, a straight anterior margin of the zygosphene with a small V-shaped notch in the middle, long prezygapophyseal processes and a vaulted neural arch in posterior view.

Identification

Trunk vertebrae can be referred to the operative taxa ‘natricines’ or ‘colubrines’ based on the presence or absence of the hypapophysis, whereas the presence of a neural spine and the elongated centrum rule out Scolecophidia and Boidae respectively (Szyndlar 1984, 1991a, 1991b). In addition, trunk vertebrae provided with hypapophysis are not referable to Viperidae because of the sigmoid shape of the latter, the vaulted neural arch, the anteriorly developed antero-dorsal corner of the neural spine and the obtuse prezygapophyseal processes (Szyndlar 1984). Among ‘natricines’, obtuse ends of both hypapophysis and parapophyseal processes are features of *Natrix natrix* (Szyndlar 1984, 1991b). Vertebrae devoid of hypapophysis can be further separated into two different morphologies: on the one hand, there are vertebrae with a weakly developed and not flat hemal keel and on the other hand vertebrae whose keel is well developed and flat. The former morphology, together with the small size (CL < 5 mm), the short prezygapophyseal process, the poorly developed neural spine and the depressed neural arch, is distinctive of the genus *Coronella* (Szyndlar 1984, 1991a). Szyndlar (1984, 1991a) reports the robustness of the proximal portion of the prezygapophyses and parapophyses longer than diapophyses as diagnostic features of *Coronella austriaca*, but these informations were based on few comparative material and the same author (Szyndlar 1991a) notes that vertebrae of this species are strongly similar to those of *Coronella girondica*. Even though only *C. austriaca* is currently reported in the Laguna Veneta (Sillero et al. 2014), localities where both species occur are present not so far from there in the Po Plain and therefore we decided not to rule out *C. girondica* based on biogeography. MSNVE-23370/1 and 2 are thus identified only at a generic level. On the other hand, vertebrae with a flattened and posteriorly wider hemal keel, an almost straight anterior margin of the zygosphene, long prezygapophyseal processes, an elongated neural spine and a

centrum exceeding 5 mm in length can be referred to *Hierophis viridiflavus* (Szyndlar 1984, 1991a). According to Szunyoghy (1932) and Szyndlar (1984, 1987), a well-developed supraangular crest is found only in compound bones of *H. viridiflavus* among European ‘colubrines’. The Pliocene species *Coluber robertmentensi* also showed this feature (Szyndlar 1984), but it was later synonymized with *H. viridiflavus* (Szyndlar 1991a). A pathological trunk vertebra and a number of other skeletal elements are attributed to indeterminate snakes.

Discussion

At least 11 different taxa have been identified based on the amphibians and reptiles remains coming from the Roman well of Tenuta Zuccarello. These taxa are two caudates (*Lissotriton* gr. *L. vulgaris*, *Triturus* gr. *T. cristatus*), three anurans (*Bombina* sp., *Bufo bufo*, *Rana dalmatina* vel *R. latastei*), one turtle (*Emys orbicularis*), two lizards (*Anguis* gr. *A. fragilis*, *Lacerta* gr. *L. viridis*), and three snakes (*Natrix natrix*, cf. *Coronella* sp. and *Hierophis viridiflavus*). The presence of a third lizard species, representing a small-sized lacertid, cannot be clearly established, given that small lacertid remains identified only at family level might equally pertain to young green lizards. All 11 taxa are recorded in the I filling, which by far has yielded the highest amount of remains, whereas only six of them (the three anurans, the two lizards and *H. viridiflavus*) are present in the II filling. Nevertheless, this might just be due to the distinctly lower amount of remains found in the latter filling, rather than to a real absence of the other taxa at the moment of the deposition. In both fillings, the assemblage is dominated by agile frogs (*Rana dalmatina* vel *R. latastei*). These frogs are usually found in forested environments and in the surrounding meadows (Speybroeck et al. 2016). An ecotonal area with both partially open and humid areas and drier and sunnier areas is suggested for the surroundings of the well by the presence of *Anguis*, *Lacerta* and *Hierophis* (Speybroeck et al. 2016). In any case, the large amounts of amphibians remains, as well as the recovery of *E. orbicularis* and *N. natrix*, are evidence for the presence of water bodies. At least some of the latter could have been ephemeral, as testified by the remains of *Bombina* (Speybroeck et al. 2016).

According to the data reported by Delfino et al. (2008) and Villa et al. (2018), most of the taxa that compose the herpetofaunistic assemblage of Tenuta Zuccarello have a long fossil history in the Quaternary of Veneto. *Lissotriton* gr. *L. vulgaris* is known from the Early Pleistocene of Monte La Mesa. *Bombina* was also found in the same site, as well as in the nearby Early Pleistocene locality of Rivoli Veronese. *Anguis* gr. *A. fragilis* is reported from the Early Pleistocene of Rivoli Veronese and the earliest Middle Pleistocene of Grotta della Fata Nana. *Coronella* is known in the fossil assemblage of Rivoli Veronese and in Breccie di Montorio (Late Pleistocene). Remains of *B. bufo*, *Lacerta* gr. *L. viridis*, *N. natrix* and *H. viridiflavus* were recovered from a number of Venetian sites, spanning from the beginning of the Pleistocene to the Holocene. Agile frogs attributable either to *R. dalmatina* or *R. latastei* are currently known with certainty only from the herein studied site, but representatives of the genus *Rana* that

are not identified at the species level are known in Veneto since the Early Pleistocene and therefore the presence of these frogs in the region in earlier times is possible. Of the 11 taxa, *Triturus* gr. *T. cristatus* is the only one that has never been recovered in any other site in Veneto, whereas *E. orbicularis* was found only in a single other Holocene locality, Lova di Campagna Lupia.

If compared with the amphibians and reptiles currently living near the Venetian Lagoon (see Sindaco et al. 2006; Bonato et al. 2007; and Sillero et al. 2014), the assemblage of the Tenuta Zuccarello well clearly lacks various taxa, notably anurans of the *Bufo* *viridis* complex and the genus *Pelophylax* as well as wall lizards of the genus *Podarcis*. It is not easy to explain the absence of common taxa such as these ones in terms of environmental features of the area in the past, taking also into account the wide range of habitats that they inhabits today. Moreover, it has to be noted that at least some of these taxa has been found in nearby sites of similar age (e.g. green frogs in Lova di Campagna Lupia and Oderzo; Delfino et al. 2008). Their absence from Tenuta Zuccarello is therefore puzzling. Of course, as far as small lacertid lizards like *Podarcis* are concerned, they might be represented, though unrecognised, among the small lacertid remains identified only at family level. On the other hand, almost all of the taxa found in the Roman well are still represented near the Lagoon. The only exception is *Bombina*, which currently lives in most of the Veneto region (*Bombina variegata*; Bonato et al. 2007; Sillero et al. 2014), but not near the Lagoon. The other two fossil occurrences of the genus in Veneto, both Early Pleistocene in age, are located in the Verona province (Delfino et al. 2008; Villa et al. 2018), that is within the current range of *B. variegata*. Tenuta Zuccarello represents therefore the first occurrence of *Bombina* outside its current range.

In addition to giving new information on the past distributional dynamics of this anuran, this occurrence has important implications for conservation sciences also. As a matter of fact, conservation biologists have recently started to use data coming from palaeontological and archaeozoological studies in their works. This even led to the definition of a new science, the conservation palaeobiology, which uses palaeontological/archaeozoological data about past communities of organisms to reconstruct a purported 'undisturbed' (or 'slightly disturbed') condition on which to base studies of human impacts on modern communities (see e.g. Dietl and Flessa 2011; Conservation Paleobiology Workshop 2012; Wood et al. 2012). Nakamura et al. (2009, 2013) gave some examples of the application of this approach to amphibians and reptiles. In the case of Tenuta Zuccarello, the presence of *Bombina* proves that the distribution of the genus extended towards the Venetian Lagoon in the recent past. This suggests that the disappearance of suitable environments for the genus is a rather recent phenomenon and may support future reintroduction projects in suitable areas. Furthermore, it shows that the Roman settlement in Veneto was not the main cause of the local disappearance of this anuran, given that it was still able to live in the agricultural landscape revealed by the excavation activities that also discovered the well at Tenuta

Zuccarello (Bon et al. 2010). However, a complete evaluation of the impact that the Romans had on *Bombina*, as well as the causes of its disappearance from the Lagoon, are still hindered by the absence of remains coming from both older and younger sites in the area.

Conclusions

The Roman well discovered in the Tenuta Zuccarello, named US 100 by its discoverers, has yielded more than 8000 remains of amphibians and reptiles. These remains represent a herpetofaunistic assemblage composed by at least 11 different taxa, including two caudates, three anurans, one turtle, two lizards and three snakes. The assemblage suggests an ecotonal environment with water bodies, open and humid areas, as well as dry and sunny areas. All the taxa are still present in the Veneto region, and most of them were found in other Venetian sites since the beginning of the Pleistocene. This might be an evidence of a certain continuity in the amphibians and reptiles population of the region during the Quaternary.

Nevertheless, *Bombina* is here found for the first time outside of its current range in Veneto, supporting a recent contraction of its distribution and a recent withdrawal from the area surrounding the Venetian Lagoon. It is still not clear whether the Roman settlement had a distinct impact on its presence in the area, but Tenuta Zuccarello provides evidence to reject the hypothesis that its disappearance might have been directly caused by the changes made by the Romans to the environment of the Lagoon. Further findings in other sites in the area are needed in order to get more information on this issue.

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References

- Abbazzi L, Angelone C, Arca M, Barisone G, Bedetti C, Delfino M, Kotsakis T, Marcolini F, Palombo MR, Pavia M, et al. 2004. Pliopleistocene fossil vertebrates of monte tuttavista (Orosei, Eastern Sardinia, Italy), an overview. *Riv Ital Paleontol S.* 110:681–706.
- Arobba D, Bulgarelli F, Siniscalco C, Caramiello R. 2013. Roman landscape and agriculture on the ligurian coast through macro and micro-remains from a vada sabatia well (Vado Ligure, Italy). *Environ Archaeol.* 18:114–131.
- Arzarello M, Marcolini F, Pavia G, Pavia M, Petronio C, Petrucci M, Rook L, Sardella R, Arechavaleta-Velasco M, Chandra S, et al. 2007. Evidence of earliest human occurrence in Europe: the site of pirro nord (Southern Italy). *Naturwissenschaften.* 94:107–112.
- Bailon S. 1991. Amphibiens et reptiles du pliocène et du quaternaire de France et d'Espagne: mise en place et evolution des faunes [Pliocene and Quaternary amphibians and reptiles of France and Spain] [dissertation]. Paris: Université Paris VII. French.
- Bailon S. 1999. Différenciation ostéologique des anoures (Amphibia, Anura) de France [Osteological differentiation of French anurans (Amphibia, Anura)]. In: Desse J, Desse-Berset N, editors. Fiches d'ostéologie animale pour l'Archéologie, série c: varia, 1 [Notes of animal osteology for archaeology, Series C: varia, 1]. Antibes: APDCA; p. 1–41. French.
- Barahona F, Barbardillo LJ. 1997. Identification of some iberian lacertids using skull characters. *Rev Esp Paleontol.* 11:47–62.
- Batsch GC. 1788. Versuch einer anleitung, zur kenntnis und geschichte der thiere und mineralien [Attempt of a manual, to the knowledge and history of animals and minerals]. Jena: Akademische Buchhandlung. German.
- Bell T. 1839. A history of british reptiles. London: John van Voorst.
- Bon M, Delfino M, Girod A, Trabucco R. 2010. La fauna del pozzo romano di tenuta zuccarello (Marcon, Venezia) [The fauna of the Roman well of Tenuta Zuccarello (Marcon, Venezia)]. In: Tagliacozzo A, Fiore I, Marconi S, Tecchiati U, editors. Atti del V convegno nazionale di archeozoologia [Proceedings of the V National Meeting of Archaeozoology]. Rovereto: Edizioni Osiride; p. 265–268. Italian.
- Bonaparte CLJL. 1839. Iconographia della fauna italica per le quattro classi degli animali vertebrati. tomo II. Amphibi. Fascicolo 26 [Iconography of the Italian Fauna for the Four Classes of the Vertebrate Animals. Book II. Issue 26]. Roma: Salviucci. Italian.
- Bonato L, Fracasso G, Pollo R, Richard J, Semenzato M. 2007. Atlante degli anfibi e dei rettili del veneto [Atlas of the Amphibians and Reptiles of Veneto]. Portogruaro: Associazione Faunisti Veneti, Nuova Dimensione Editrice. Italian.
- Bonfiglio L, Insacco G, Marra AC, Masini F. 1997. Large and small mammals, amphibians and reptiles from a new late pleistocene fissure filling deposit of the hyblean plateau (South Eastern Sicily). *Boll Soc Paleontol I.* 36:97–122.
- Boulenger GA. 1879. Étude sur les grenouilles rouges, *Ranae temporariae* et description d'espèces nouvelles ou méconnues [Study on the red frogs, *Ranae temporariae* and description of new and unknown species]. *B Soc Zool Fr.* 4:158–193. French.
- Conservation Paleobiology Workshop. 2012. Conservation paleobiology: opportunities for the earth sciences. Report to the division of earth sciences, national science foundation. Ithaca (New York): Paleontological Research Institution.
- Delfino M. 2002. Erpetofaune italiane del neogene e del quaternario [Neogene and Quaternary Italian herpetofaunas] [dissertation]. Modena: University of Modena and Reggio Emilia. Italian.
- Delfino M, Atzori M. 2013. An update on the early pleistocene herpetofauna from Pirro Nord. *Palaeontogr Abt A.* 298:19–29.
- Delfino M, Bacciotti M, Bon M, Pitruzzella G, Sala B, Rook L. 2008. A general overview on the plio-quaternary herpetofauna of Veneto. In: Corti C, editor. Herpetologia sardiniae. Latina: Societas Herpetologica Italica/Edizioni Belvedere; p. 196–199.
- Delfino M, Bailon S. 2000. Early pleistocene herpetofauna from cava dell'Erba and cava pirro (Apulia, Southern Italy). *Herpetol J.* 10:95–110.
- Delfino M, Bailon S, Pitruzzella G. 2011. The late pliocene amphibians and reptiles from “capo mannu d1 local fauna” (Mandriola, Sardinia, Italy). *Geodiversitas.* 33:357–382.
- Dietl GP, Flessa KW. 2011. Conservation paleobiology: putting the dead to work. *Trends Ecol Evol.* 26:30–37.
- Duméril AMC. 1805. Zoologie analytique, ou méthode naturelle de classification des animaux, rendue plus facile a l'aide de tableaux synoptiques [Analytic zoology, or natural method of the classification of animals, simplified by the help of synoptic tables]. Paris: Allais. French.
- Fischer Von Waldheim G. 1813. Zoognosia. Tabulis synopticis illustrata, in usum praerlectionum academiae imperialis medico-chirurgicae mosquensis edita [Illustrated Synoptic Tables of Zoology]. 3. Vol. 1. Moscow:Nicolai Sergeidis Vsevolozsky. Latin.
- Fitzinger LJF. 1843. Systema reptilium. fasciculus primus. amblyglossae [Reptile System. Issue one. Amblyglossae]. Wien: Braumüller et Seidel. Latin.
- Fraser RA, Wells RT. 2006. Palaeontological excavation and taphonomic investigation of the late pleistocene fossil deposit in Grant Hall, Victoria Fossil Cave, Naracoorte, South Australia. *Alcheringa Spec Issue.* 1:147–161.
- Freudenthal M, Meijer T, Van Der Meulen AJ. 1976. Preliminary report on a field campaign in the continental pleistocene of tegelen (The Netherlands). *Scr Geol.* 34:1–27.
- Garsault FAP. 1764. Les figures des plantes et animaux d'usage en médecine, décrits dans la matière médicale de Mr. geoffroy médecin, dessinés d'après nature [Figures of plants and animals for the use in medicine, described for the medical subject by Mr. Geoffroy Médecin and drew from Nature]. Paris: Mrs. Defehrt, Prevost, Duflos, Martinet & c. French.
- Goldfuss GA. 1820. Handbuch der zoologie. zweite abtheilung [Handbook of Zoology. Second Part]. Nürnberg: Johann Leonhard Schrag. German.
- Gray JE. 1825. A synopsis of the genera of reptiles and amphibia, with a description of some new species. *Ann Philos.* 10:193–217.
- Gray JE. 1831. Description of two new genera of frogs discovered by John Reeves, Esq. in China. In: Gray JE, editor. Zoological miscellany. London: Treuttel, Wurtz and Co., GB Sowerby, W Wood.
- Gvoždik V, Benkovský N, Crottini A, Bellati A, Moravec J, Romano A, Sacchi R, Jandzik D. 2013. An ancient lineage of slow worms, genus *Anguis* (Squamata: anguidae), survived in the Italian Peninsula. *Mol Phylogenet Evol.* 69:1077–1092.
- Hervet S. 2000. Tortues du quaternaire de France: critères de détermination, répartitions chronologique et géographique [Quaternary turtles from France: determination criteria, chronological and geographical distribution]. *Mésogée.* 58:3–47. French.
- Holman JA. 1998. Pleistocene amphibians and reptiles in Britain and Europe. *Oxford Monographs Geol Geophys.* 38:1–254.
- Klembara J, Böhme M, Rummel M. 2010. Revision of the anguine lizard *pseudopus laurillardii* (Squamata, Anguidae) from the Miocene of Europe, with comments on paleoecology. *J Paleontol.* 84:159–196.
- Klembara J, Hain M, Dobiašová K. 2014. Comparative anatomy of the lower jaw and dentition of *pseudopus apodus* and the interrelationships of species of subfamily anguinae (Anguimorpha, Anguidae). *Anat Rec.* 297:516–544.
- Lacépède BGE. 1789. Histoire naturelle des quadrupèdes ovipares et de serpens [Natural history of the oviparous quadrupeds and snakes]. Vol. 2. Paris:Imprimerie du Roi, Hôtel de Thou. French.
- Laurenti JN. 1768. Specimen medicum, exhibens synopsis reptilium emendatum cum experimentis circa venena et antidota reptilium austriacorum [Medical specimen, presenting a synopsis of the reptiles emended with experiments about poisons and antidotes of the Austrian reptiles]. Wien: Joan Thom nob de Trattnern. Latin.
- Linnaeus C. 1758. Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis [The System of Nature]. Stockholm: Laurentius Salvius. Latin.
- Madej Z. 1965. Variations in the sacral region of the spine in *Bombina bombina* (Linnaeus, 1761) and *Bombina variegata* (Linnaeus, 1758) (Salientia, Discoglossidae). *Acta Bio Cracov.* 3:185–197.
- Młynarski M. 1976. Handbuch der paläoherpetologie 7 [Handbook of Palaeoherpetology 7]. Testudines. Munich: Friedrich Pfeil.

- Nakamura Y, Takahashi A, Ota H. 2009. Evidence for the recent disappearance of the okinawan tree frog *rhacophorus viridis* on yoronjima Island of the Ryukyu Archipelago, Japan. *Curr Herpetol.* 28:29–33.
- Nakamura Y, Takahashi A, Ota H. 2013. Recent cryptic extinction of squamate reptiles on yoronjima Island of the ryukyu archipelago, Japan, inferred from garbage dump remains. *Acta Herpetol.* 8:19–34.
- Oken L. 1816. *Lehrbuch der naturgeschichte.* vol 3. zoologie. abtheilung 2 [Textbook of the natural history. Vol. 3. Zoology. Part 2]. Atlas. Leipzig: Reclam CH. German.
- Oppel M. 1811. Die ordnungen, familien und gattungen der reptilien, als prodrom einer naturgeschichte derselben [The orders, families, and genera of reptiles, as a precursor to their natural history]. Munich: Joseph Lindauer. German.
- Owen R. 1842. Report on british fossil reptiles. Part II. *Rep Br Ass Advmt Sci.* 11:60–204.
- Rafinesque CS. 1814. Fine del prodromo d'erpologia siciliana [End of the prelude to the Sicilian herpetology]. *Specchio Delle Scienze Giornale Enciclopedico Di Sicilia.* 2:102–104. Italian.
- Rafinesque CS. 1815. Analyse de nature, ou tableau de l'universe et des corps organises [Analysis of nature, or tables of the universe and organised bodies]. Palermo: Jean Barravecchia. French.
- Rage JC. 2016. Frogs (amphibia, anura) from the eocene and oligocene of the phosphorites du quercy (France). An overview. *Fossil Imprint.* 72:53–66.
- Ratnikov V, Litvinchuk SN. 2007. Comparative morphology of trunk and sacral vertebrae of tailed amphibians of Russia and adjacent countries. *Russ J Herpetol.* 14:177–190.
- Rook L, Delfino M, Sami M. 2015. I vertebrati fossili della cava del monticino di brisighella: una finestra sui popolamenti continentali del mediterraneo nel miocene superiore [Fossil vertebrates from Cava del Monticino near Brisighella: a window on the continental populations of the Mediterranean in the upper Miocene]. In: Lucci P, Piastra S, editors. *I gessi di brisighella e rontana* [The gypsums of Brisighella and Rontana]. Faenza: CartaBianca Editore. *Memorie dell'Istituto Italiano di Speleologia.* Vol. 28, p. 79–100. Italian.
- Sala B, Masini F, Torre D. 1994. Villanyian arvicolidids from rivoli veronese, a karst fissure in the Adige Valley, Northeastern Italy. *Boll Soc Paleontol I.* 33:3–11.
- Sanchiz B. 1998. *Handbuch der paläoherpetologie 4* [Handbook of Palaeoherpetology 4]. Saliencia. Munich: Friedrich Pfeil.
- Savorelli A, Colombero S, Masini F. 2016. *Apatodemus degiulii* n. gen. et sp. (Rodentia, Muridae), a hitherto undescribed endemite from the Terre Rosse of Gargano (late Miocene, Southeastern Italy). *Palaeontogr Abt A.* 306:25–49.
- Savorelli A, Masini F. 2016. *Mystemys giganteus* n. gen. et sp.: an enigmatic and rare cricetid from the Terre Rosse M013 fissure filling (Gargano, Southeastern Italy). *Palaeontogr Abt A.* 306:1–23.
- Scopoli GA. 1777. *Introductio ad historiam naturalem, sistens genera lapidum, plantarum, et animalium hactenus detecta, caracteribus essentialibus donata, in tribus divisa, subinde ad leges naturae* [Introduction to the natural history]. Prague: Gerle. Latin.
- Sillero N, Campos J, Bonardi A, Corti C, Creemers R, Crochet P-A, Crnobrnja Isailović J, Denoël M, Ficetola GF, Gonçalves J, et al. 2014. Updated distribution and biogeography of amphibians and reptiles of Europe. *Amphibia-Reptilia.* 35:1–31.
- Sindaco R, Doria G, Razzetti E, Bernini F. 2006. *Atlante degli anfibii e dei rettili d'Italia/Atlas of Italian amphibians and reptiles.* Firenze: Societas Herpetologica Italica, Edizioni Polistampa.
- Speybroeck J, Beukema W, Bok B, Van Der Voort J. 2016. *Field guide to the amphibians and reptiles of Britain and Europe.* London: Bloomsbury Publishing.
- Szunyoghy JV. 1932. Beiträge zur vergleichenden formenlehre des colubridenschäels, nebst einer kranialogischen synopsis der fossilen schlangen ungarns mit nomenklatorischen, systematischen und phyletischen bemerkungen [Contributions to the comparative morphology of the Colubridae skull, along with a craniological synopsis of Hungarian fossil snakes with comments on nomenclature, systematics, and phylogenetics]. *Acta Zool-Stockholm.* 13:1–56. German.
- Szyndlar Z. 1984. Fossil snakes from Poland. *Acta Zool Cracov.* 28:1–156.
- Szyndlar Z. 1987. Snakes from the lower miocene locality of dolnice (Czechoslovakia). *J Vertebr Paleontol.* 7:55–71.
- Szyndlar Z. 1991a. A review of neogene and quaternary snakes of central and eastern Europe. Part I: scolecophidia, Boidae, Colubrinae. *Estud Geol Madrid.* 47:103–126.
- Szyndlar Z. 1991b. A review of neogene and quaternary snakes of central and eastern Europe. Part II: natricinae, Elapidae, Viperidae. *Estud Geol Madrid.* 47:237–266.
- Villa A, Blain H-A, Delfino M. 2018. The early pleistocene herpetofauna of rivoli veronese (Northern Italy) as evidence for humid and forested glacial phases in the Gelasian of Southern Alps. *Palaeogeogr Palaeocl.* 490:393–403.
- Villa A, Georgalis GL, Tschopp E, Delfino M. 2017. Osteology, fossil record and palaeodiversity of the European lizards. *Amphibia-Reptilia.* 38:79–88.
- Villa A, Roček Z, Tschopp E, Hoek Ostende LWVD, Delfino M. 2016. *Palaeobatrachus eurydices*, sp. nov. (Amphibia, Anura), the last western European palaeobatrachid. *J Vertebr Paleontol.* 36: e1211664.
- Wood JR, Wilmschurst JM, Worthy TH, Holzapel AS, Cooper A. 2012. A lost link between a flightless parrot and a parasitic plant and the potential role of coprolites in conservation paleobiology. *Conserv Biol.* 26:1091–1099.