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A historical overview of the reptile fauna from the Eocene Bolca Fossil-Lagerstätte (Italy)

Simone Matteo SEGHETTI*, Georgios L. GEORGALIS, Emanuel TSCHOPP & Massimo DELFINO

S.M. Seghetti, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; seghe.simon@gmail.com **corresponding author*

G.L. Georgalis, Institute of Systematics and Evolution of Animals, Polish Academy of Sciences, Sławkowska 17, 31-016 Kraków, Poland; georgalis@isez.pan.krakow.pl

E. Tschopp, Fachbereich Biologie, Universität Hamburg, Martin-Luther-King-Platz 3, 20146 Hamburg, Germany; American Museum of Natural History, Division of Paleontology, Central Park West at 79th Street, 10024-5192 New York, USA; etschopp@amnh.org

M. Delfino, Dipartimento di Scienze della Terra, Università degli Studi di Torino, Via Valperga Caluso 35, I-10125 Torino, Italy; Institut Català de Paleontologia Miquel Crusafont, Universitat Autònoma de Barcelona, Edifici ICTA-ICP, c/ Columnes s/n, Campus de la UAB, 08193 Cerdanyola del Vallés, Barcelona, Spain; massimo.delfino@unito.it

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ABSTRACT - The Eocene fossil reptiles from the Bolca Fossil-Lagerstätte (Verona, Italy) have been known in the literature since at least the 1850' and were the subject of many studies during the second half of the XIX century and the first decades of the XX century. However, with the exception of a few papers, only rare works have been published on the Monte Bolca herpetofauna in recent years, and in many cases knowledge of the anatomy, taxonomy, and proper nomenclature of the Bolca reptiles still remains uncertain. Herein, we reassess the history of the discoveries, the earlier taxonomy and revisions of the crocodilians, turtles, and snakes from Bolca. To date, a total of 13 crocodilian specimens have been described in the literature or are housed in museum collections and remain unpublished. Two of the crocodilian specimens formerly cited and/or described are currently lost. All the fossil crocodilian specimens had originally been referred to two species, Crocodilus vicetinus *Lioy, 1865, and* Crocodilus bolcensis *Sacco, 1895. In this study these identifications are considered invalid, and some specimens are referred to the genera* Asiatosuchus*,* Boverisuchus*,* Diplocynodon *and* Hassiacosuchus *while assignment at species level is still debatable. The turtles are represented by multiple specimens, which had been referred in the past to several different taxa of pleurodires and trionychids. However, only two species of turtles from Monte Bolca are currently accepted as being valid, both with species epithets dedicated to the renowned Italian palaeontologist Giovanni Capellini (1833-1922): the pleurodire* Neochelys capellinii *(de Zigno, 1890), which is the type species of its genus, and the trionychid "*Trionyx*"* capellinii *Negri, 1892. Both the crocodilians and the turtles had been collected at the Purga di Bolca locality. Only three snake specimens have been described from the Bolca area, representing also the oldest Cenozoic snakes from Italy:* Coluber ombonii *de Zigno, 1889 from Purga, and the archaeophiine* Archaeophis proavus *Massalongo, 1859 and anomalophiid* Anomalophis bolcensis *(Massalongo, 1859) from the Pesciara locality. The affinities of* C. ombonii *are still not clear, whereas* A. proavus *and* A. bolcensis *are considered valid and represent the type species of their genera but also are among the very few representatives of Archaeophiinae and Anomalophiidae respectively. The fossil reptiles from Bolca are housed in public collections in Italy (Turin, Verona, Padua, Rome, Pavia), the United Kingdom (London), USA (Pittsburgh, Cambridge), Germany (Darmstadt, Berlin) and Austria (Vienna).*

INTRODUCTION

Bolca (Verona, NE Italy) is one of the most iconic Fossil-Lagerstätten worldwide. It is an Eocene complex of five main localities, with some other, smaller, satellite sites (Fig. 1a) of different age and different depositional settings (among others, Fabiani, 1914, 1915; Barbieri & Medizza, 1969; Medizza, 1980; Sorbini, 1980, 2007; Sorbini Frigo & Sorbini, 1999; Schwark et al., 2009; Carnevale et al., 2014; Dominici, 2014; Giusberti et al., 2014a, b; Papazzoni et al., 2014a, b, c, d; Roghi et al., 2014; Wilde et al., 2014): the Pesciara and the Monte Postale localities form together the core of Bolca; Purga di Bolca and Vegroni are part of a volcanic complex with fossils of terrestrial organisms; and at Spilecco, fossils are found in the oldest Paleogene fossiliferous carbonates in the Veneto Region (Papazzoni et al., 2014c). The smaller fossiliferous sites include: Brusaferri, Loschi, La Possette, Pratricini, Valecco-Zovo and some small scattered outcrops (Blot, 1986; Papazzoni et al., 2014c). The most studied and known locality is the Pesciara, which preserves a shallow marine environment dated from the Ypresian to the Lutetian (Papazzoni et al., 2014a). The lithology suggests an anoxic environment, which promoted the preservation of organisms. Among them, the exceptionally preserved fossil fishes are especially well-known, but there are also algae, molluscs, jellyfishes, and worms (Papazzoni & Trevisani, 2006; Papazzoni et al., 2014b). A few tetrapod remains were also found in the Pesciara, including bird feathers and two species of snakes (Carnevale et al., 2014). The Monte Postale site is close to the Pesciara and displays a comparable lithology and fossiliferous content (Papazzoni et al., 2014b). The Spilecco site is dated from the Thanetian to the Ypresian, and was used by Fabiani (1912), who erected the stage "Spilecciano", to fill the gap between the Cretaceous Scaglia Rossa and the middle Eocene Calcari Nummulitici (Papazzoni et al., 2014d). It is a shallow water deposit with fossils of large foraminifera, algae, crinoids, brachiopods, shark teeth, and an isolated crocodilian tooth (Papazzoni et al., 2014d). The Purga di Bolca and the Vegroni sites are considered as more recent than the Pesciara and Monte Postale. Most of the fossils of terrestrial organisms come from these two sites, which were part of a volcanic cone,

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first described by Nicolis (1884) and later by Fabiani (1915) and Malaroda (1954). Barbieri & Medizza (1969) figured the stratigraphic section (see Geological Setting below for details). The digs were mainly due to the extraction of the lignites for commercial purposes, which eventually led to the discovery of the aforementioned fossils (Sorbini Frigo & Sorbini, 1999; Zorzin et al., 2017). In the vertebrate fauna of the lignite beds of the Purga di Bolca, chelonian remains are the most abundant, but it also includes crocodilians, an ophidian, and bird feathers (see Giusberti et al., 2014b for a review of the fossils from the Purga di Bolca-Vegroni site). Blot (1969, p. 19, fig. 2; see Fig. 1a of this work), in the legend for the map of the fossiliferous sites of Bolca, reports the presence of fossil crocodilians and chelonians also in the localities of Loschi, La Possette, Zovo, and Valecco, without providing details on the fossils he stated to be present. However, these sites completely lack any stratigraphic or chronological study, so no precise correlation with the Purga di Bolca and Vegroni localities is known. The

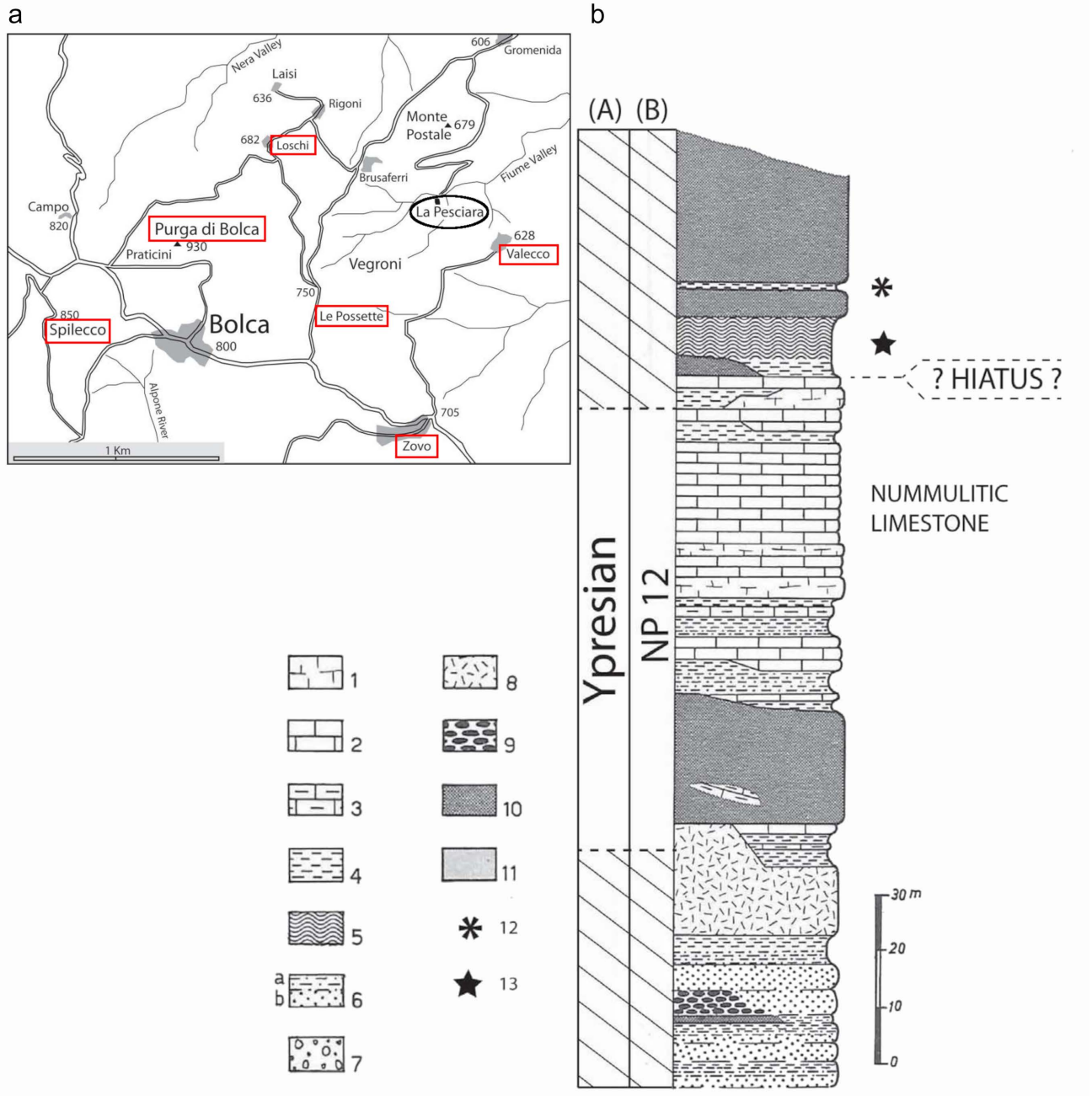

Fig. 1 - a) Map of the sites in the surroundings of Bolca. The rectangles mark the crocodilian- and chelonian-bearing sites. The oval marks the Pesciara site, in which *Archaeophis* and *Anomalophis* were found. The exact locality of the holotype of *Coluber ombonii* is unknown, so we did not indicate it here. b) Stratigraphy of Purga di Bolca according to Barbieri & Medizza (1969). 1: reefal limestone with algae; 2: nummulitic limestone; 3: marls and marly limestone with nummulites; 4: clayey marls and volcanic clays; 5: clays, silt and lignites; 6: chaotic volcanoclastic rocks; 7: chaotic, extra diametric explosive breccias; 8: chaotic hyaloclastites; 9: basaltic pillow lavas; 10: subaqueous basaltic lavas flows; 11: sub-aerial basaltic lavas flows; 12: vertebrate remains; 13: plant remains; (A): chronostratigraphy; (B): Calcareous Nannofossils Zonation of Martini (1971). Modified from Giusberti et al. (2014a).

Catalogue number	Locality	Current location	First reference	Original identification	Relevant revisions	Current identification	Material
MGP-PD 27568 (Fig. 2)	Purga di Bolca	MGP-PD	Lioy, 1865	*Crocodilus vicetinus*	Berg, 1966; Vasse, 1992	*Asiatosuchus* cf. *depressifrons*	Skeleton; cast of the holotype of *C. vicentinus*
MGPT PU 17329 (Fig. 4 and Fig. S2)	Purga di Bolca	MGPT	Sacco,1895	*C. vicetinus*	Berg, 1966	*Hassiacosuchus* cf. *haupti*	Skeleton
CM 96616 (Fig. 5a and Fig. S3b)	Purga di Bolca	CM	Sacco, 1895	*C. vicetinus*	none	none	Skeleton
None (Fig. S3a)	Purga di Bolca	Unknown	Sacco, 1895	*C. vicetinus*	none	none	Skeleton
NHMUK 2789 (Fig. 5b and Fig. S4)	Monteviale (not Monte Bolca as originally published)	NHMUK	Sacco, 1895	*Crocodilus* cf. *vicetinus*	Macaluso et al., 2019	*Diplocynodon* sp.	Partial skeleton
MCSNV V.7097 (Fig. 7)	Purga di Bolca	MCSNV	Medizza, 1980	*C. vicetinus*	Berg, 1966; Vasse, 1992	*A.* cf. *depressifrons*	Skeleton
MCSNV V.12621 (Fig. 8)	Bolca (unspecified locality)	MCSNV	None	None	None	None	Isolated tooth
Lignit von Bolca, Geol. Samml. Wiener Hochschule?	Purga di Bolca	Unknown	Nicolis, 1884	*C. vicetinus*	Berg, 1966	*H.* cf. *haupti*	Mandible
MGPT PU 17328 (Fig. 3 and Fig. S1)	Purga di Bolca	MRSN	Sacco, 1895	*Crocodilus bolcensis*	Berg, 1966; Brochu, 2013	*Boverisuchus* sp.	Skeleton; holotype of *C. bolcensis*
MGP-PD 2 (Fig. 6)	Purga di Bolca	MGP-PD	Lioy, 1896	*C. bolcensis*	Rossmann, 1998; Brochu, 2013	*Boverisuchus* sp.	Skeleton
CM 85825 (Fig. 9a)	Bolca (unspecified locality)	CM	none	none	none	none	Partial skull and mandible
CM 96617 (Fig. 9b)	Bolca (unspecified locality)	CM	none	none	none	none	Skeleton
MCSNV V 1028 (Fig. S5)	Spilecco	MCSNV	Nicolis, 1907	Mosasaurid	Medizza, 1980; Papazzoni et al., 2014d	Crocodylia indet.	Tooth and partial dentary

Tab. 1 - List of the crocodilian specimens from Bolca (with referred chapter and figure in this work).

history of the palaeontological interest for the fossils of Bolca starts in the XVI century (Roghi et al., 2014b) and has been carried on to the modern days. Fishes and other marine fossils were the most studied organisms (see a summary in Carnevale et al., 2014), but also the reptiles, mainly found at the Purga di Bolca site, have received some attention. To date, 13 specimens of crocodilians, 21 turtles, and four snakes have been discovered.

The first crocodilian specimen was discovered in 1860 by Attilio Cerato (the main Bolca fossil collector of that time) and described by Paolo Lioy (1865), who erected the species *Crocodilus vicetinus* Lioy, 1865 (currently the accepted spelling of the genus is *Crocodilus*). In 1865, Edoardo Suess found an isolated mandible. In 1895, Federico Sacco described five new, more informative, crocodilian specimens: one of them was referred to the new species *Crocodilus bolcensis* Sacco, 1895, whereas the other four were referred to *C. vicetinus*. Additional specimens were still found later. In total, nine specimens were described and officially referred to *C. vicetinus* and *C. bolcensis* (Lioy, 1865; Nicolis, 1882, 1884; Sacco, 1895; Fabiani, 1912, 1915). One of these, the tooth from Spilecco, was only cited and not described and is currently referred to Crocodylia indet. (Papazzoni et al., 2014d). Three additional specimens are still unpublished, but according to the Institutions that host them, they come from the Bolca area (see Tab. 1 for a summary of the citations and descriptions of the specimens).

As far as the chelonians are concerned, the first specimen from Bolca was described in 1889 by Achille de Zigno, who referred a carapace to his new species *Emys capellinii* de Zigno, 1889. Subsequently, in his preliminary reports, Bergounioux (1953a, b) recognized the pleurodire affinities of this taxon and assigned it to the genus *Elochelys*, and also identified a second pleurodire from Bolca, which he called *Platyarkia bolcensis*. One year later, in his large monograph, the same author established the new genus *Neochelys* Bergounioux, 1954 in order to accommodate these two Bolca pleurodires as *Neochelys capellinii* and *Neochelys bolcensis*, respectively (Bergounioux, 1954; see below for details). Two additional fossil pleurodire specimens were briefly described by Broin (1977). Besides the pleurodires, a number of trionychid specimens, some of which fairly well preserved, were described by Arturo Negri (1892) and Federico Sacco (1894), who referred them to different taxa of the genus *Trionyx* Geoffroy Saint-Hilaire, 1809.

De Zigno (1889) established a new ophidian species, *Coluber ombonii* de Zigno, 1889, from Purga di Bolca. Nevertheless, the most important snakes from the

Bolca Fossil-Lagerstätte had been already described several decades earlier from the Pesciara: *Archaeophis proavus* Massalongo, 1859 and *Anomalophis bolcensis* (Massalongo, 1859).

Some of these reptile fossils are crucial for the study of Paleogene herpetofaunas, as they actually represent the holotypes of the type species of their genera (*Neochelys*, *Archaeophis* Massalongo, 1859 and *Anomalophis* Auffenberg, 1959). The taxonomy of the crocodilians is still much confused. Since the original descriptions, only one study reassessed some of them in detail (Berg, 1966), whereas subsequent works mentioned the crocodilians of Bolca without providing updated descriptions and accepting, in some cases, the historical identifications (Sorbini, 1972; Steel, 1973; Medizza, 1980; Pinna, 1989; Vasse, 1992; Roccaforte et al., 1994; Rauhe & Rossmann, 1995; Del Favero, 1999; Kotsakis et al., 2004; Brochu, 2013; Macaluso et al., 2019). With the goal of providing a basis for future revisions, we summarize the history of the discoveries, the whereabouts of the fossil specimens, and the historical and modern nomenclature, with comments on the state of the preservation of the fossils and on the future perspectives of research.

Institutional abbreviations

CDL: Museo Civico C. Dal Lago, Valdagno, Vicenza, Italy; CM: Carnegie Museum of Natural History, Pittsburgh, Pennsylvania, USA; HDML: Hessisches Landesmuseum, Darmstadt, Germany; MCSNV: Museo Civico di Storia Naturale di Verona, Italy; MCZ: Museum of Comparative Zoology, Harvard University, Cambridge, Massachusetts, USA; MFB: Museum of Fossils of Bolca, Verona, Italy; MGP-PD: Museo di Geologia e Paleontologia dell'Università di Padova, Italy; MPURLS: Museo di Paleontologia dell'Università di Roma La Sapienza, Roma, Italy (formerly the acronym of the collection was M.P.U.R/R.); MGPT PU: Museo di Geologia e Paleontologia dell'Università degli Studi di Torino, Italy; MNAV: Museum of Nature and Archaeology of Vicenza, Italy; MRSN: Museo Regionale di Scienze Naturali, Torino, Italy; MSNPV: Museo di Storia Naturale dell'Università di Pavia, Italy; NHMUK: Natural History Museum, London, United Kingdom; MNB: Museum für Naturkunde, Berlin, Germany; NHMW: Naturhistorisches Museum Wien, Vienna, Austria.

GEOLOGICAL SETTING

The Purga di Bolca and Vegroni localities are part of a volcanic cone whose base was dated to the Ypresian (early Eocene; Fabiani, 1915; Barbieri & Medizza, 1969; Medizza, 1980; Del Favero, 1999; Kotsakis et al., 2004; Giusberti et al., 2014b). It is covered by layers of clays, silts and lignite with fossils of vertebrates and molluscs, followed by tuffaceous layers with palms (Fig. 1b). This succession is interrupted by layers of basalts. The presence of freshwater and brackish sediments indicates an ephemeral emersion of islands caused by intense volcanism during the early and middle Eocene (Barbieri & Medizza, 1969; Antonelli et al., 1990; Giusberti et al., 2014b). Although the age of the base was dated to the Ypresian using calcareous nannofossils (Giusberti et al., 2014b), the precise age of the fossiliferous layers is still debated. Fabiani (1915) proposed the Bartonian, whereas Malaroda (1954) proposed the Lutetian. Then, Barbieri & Medizza (1969) proposed the Ypresian (still called Cuisian at the time). However, the palm-bearing beds of Vegroni were dated to the early Oligocene after correlations with the outcrops found in various localities in the Vicenza province (Massalongo, 1858a, b; Molon, 1867; Nicolis, 1884; Barbieri & Medizza, 1969; Medizza, 1980; Giusberti et al., 2014b). An ongoing revision of the geology of this site (Roghi & Zorzin, 2021) confirms a Bartonian age (38.73 Ma) for the basaltic level. Another basaltic layer, in the locality Il Termine (between Bolca and Zovo; Roghi & Zorzin, 2021) is dated to the middle Lutetian (45.21 Ma). As for the Pesciara (for a detailed geology see the summary of Papazzoni et al., 2014b), the sedimentology of its limestone levels is compatible with that of a shallow marine deposit. The richness of the fish fauna led many authors to consider the layers of the Pesciara to be a heterogenous tropical coastal region associated to a coral reef (see Carnevale et al., 2014). Most of the vertebrate fossils (mostly fishes, but snakes too) were found in the micritic limestone levels.

REPTILE SPECIMENS FROM BOLCA: HISTORY AND EARLY SYSTEMATICS

The area of Bolca yielded several reptile specimens that have a convoluted history and a complex taxonomy, in most cases complicated by poor preservation and even by the loss of specimens. In order to provide a comprehensive overview of all the specimens reported from Bolca in the literature, we arranged the materials in chapters and subchapters, each focusing on a particular fossil or group of fossils.

CROCODILIANS

Holotype of Crocodilus vicetinus

The first crocodilian from Bolca to be described was the holotype of *Crocodilus vicetinus* (Lioy, 1865; Sacco, 1895, tab. 1, fig. 1; Fabiani, 1912, fig. 1; Fig. 2a-b), misspelled as *Crocodilus Vicentinus* (with the first letter of the specific name in capital) in Lioy (1896). The fossil consists of a slab with a near-complete, but compressed, dorsally exposed skeleton. It was referred to the genus *Crocodilus* (note the common spelling of the genus with "i" in many 19th century works, unlike its current valid spelling, *Crocodilus*) based on the triangular shape of the snout and because of the fact that the fourth dentary tooth was visible with the jaw in occlusion (characters often used in older literature to distinguish crocodiles from alligators; see comments in Brochu, 2000, 2003). The holotype was discovered in 1860, purchased by the MNAV and subsequently lost during a fire in 1945 (Giusberti et al., 2014b; Roghi & Zorzin, 2021). Replicas are currently stored at MGP-PD, MFB, and MNAV (Giusberti et al., 2014b). The first is accessioned under the number MGP-PD 27568, whereas the latter two are both not catalogued. The fossil is a large specimen of 2.19 m in total length, with

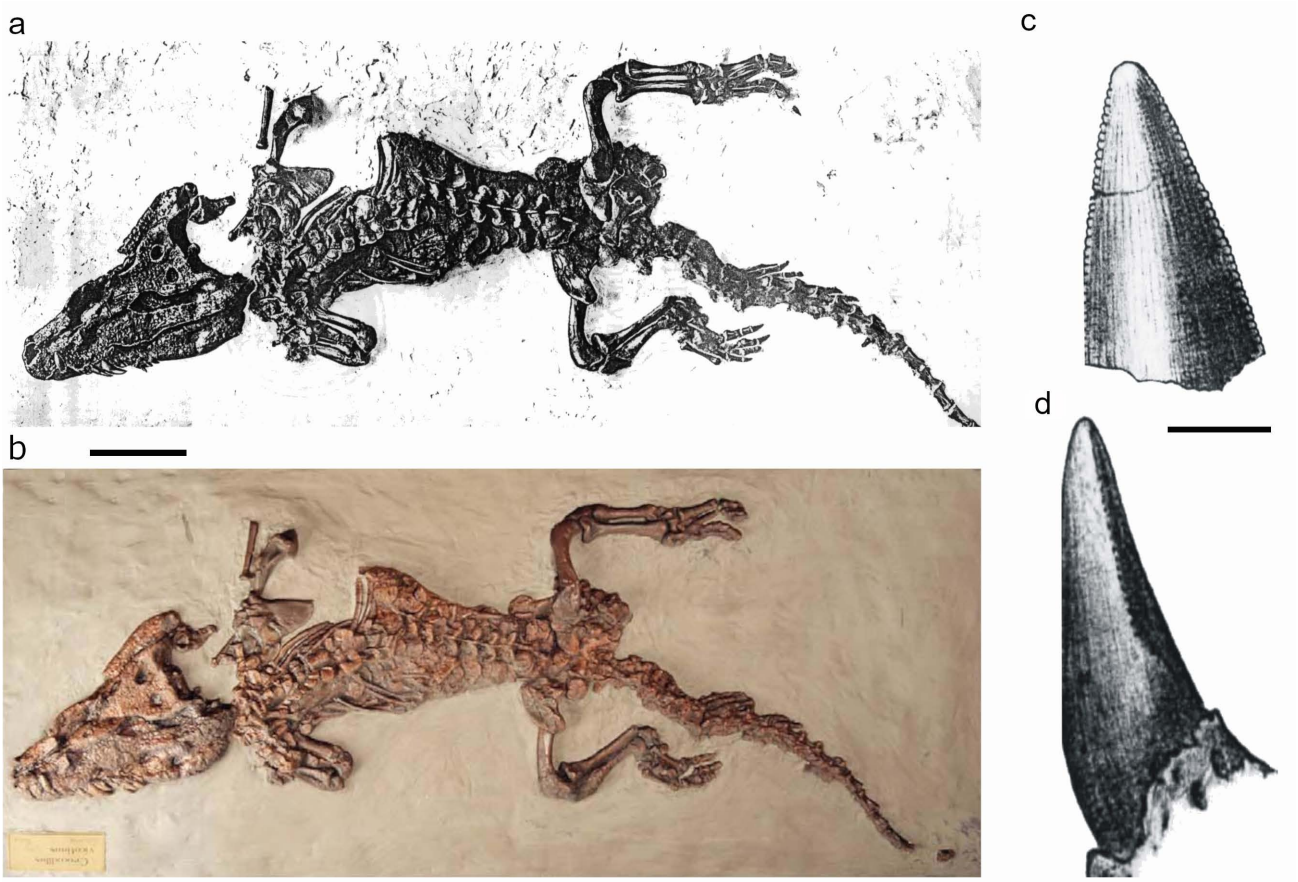

Fig. 2 - *Crocodilus vicetinus* Lioy, 1865 (holotype). a) Photo of the original fossil, modified from Fabiani (1912). b) MGP-PD 27568, the replica currently exhibited in the MGP-PD, modified from Giusberti et al. 2014a. c-d) Two teeth as in the original drawings of Fabiani (1912). Scale bar in (a-b) equals 15 cm; scale bar in (c-d) equals 0.5 cm.

a complete skull, dorsal and caudal vertebrae, girdles, the left forelimb, and both the hind limbs. According to Fabiani (1912), who described this specimen with more detail than Lioy & Sacco, the skull has a triangular, *Crocodilus*-like shape, truncated distal tips of the nasals, medio-laterally compressed and "serrated" anterior teeth (Fabiani, 1912, figs 2-4; Fig. 2c-d), and sub-conical or slightly blunt posterior teeth, a notch between the maxilla and the premaxilla for the fourth dentary tooth, and caudal vertebrae with dorsoventrally high neural spines. Also, Fabiani (1912) recognized an affinity between *C. vicetinus* and *Crocodilus* (*Asiatosuchus*) *depressifrons* Blainville, 1855, reporting only few differences in the proportions of the skull (in the latter the skull is shorter and more triangular-shaped). This species is currently considered a nomen dubium, and the type specimen of *Crocodilus vicetinus* is regarded to belong to the genus *Asiatosuchus* Mook, 1940 (Berg, 1966; Kotsakis et al., 2004), a basal crocodyloid represented by many Late Cretaceous to early Oligocene fossils from Asia, Europe and North America (Delfino et al., 2017). At least six species of *Asiatosuchus* are considered valid (for a review, see Delfino et al., 2017). Some of the synapomorphies for *Asiatosuchus* are, among others, the presence of a single, enlarged fifth maxillary tooth, the lack of the preorbital ridge, the medially shifted foramen aërum, and a long mandibular symphysis extending at least to the sixth dentary alveolus (Delfino & Smith, 2009). Berg (1966) was the first to refer the holotype of *C. vicetinus* to *Asiatosuchus* comparing the shape of its teeth with that of the abundant material of *Asiatosuchus germanicus* Berg, 1966, from the Eocene Messel Pit. In his work, Berg also noticed that, strictly speaking, these species did not have serrated teeth. Indeed, *Asiatosuchus* is considered to be a false-ziphodont (Prasad & Broin, 2002; Andrade & Bertini, 2008). Later, Vasse (1992) and Rauhe & Rossmann (1995) referred *C. vicetinus* to *C. depressifrons*, assuming that only a single species of *Asiatosuchus* existed in Europe (Vasse, 1992; Kotsakis et al., 2004). On the other hand, both *A. germanicus* and *C. depressifrons* were considered valid by Brochu (2003). *Crocodylus depressifrons* is now referred to *Asiatosuchus* (see Delfino et al., 2017). However, according to some works (e.g., Brochu, 2003, 2013; Delfino & Smith, 2009, 2017; Brochu & Storrs, 2012; Jouve, 2016; Wang et al., 2016), *Asiatosuchus* is polyphyletic. Hence, the generic taxonomic status of the holotype of *C. vicetinus* remains questionable, having been referred both to the "false" *Asiatosuchus* species *A. germanicus* (Berg, 1966) and to the "true" *Asiatosuchus* species *A. depressifrons* (Vasse, 1992). Ongoing revisions of the *Asiatosuchus*-like taxa are shedding light on the phylogeny of these crocodilians, but the condition of the holotype of *C. vicetinus*, in which none of the key-features of *A. depressifrons* or *A. germanicus* are confidently visible on the available cast, renders its identification difficult.

Specimens described by Sacco, 1895: holotype of Crocodilus bolcensis *and specimens of* Crocodilus vicetinus

Thirty years after the first description of *Crocodilus vicetinus*, five additional specimens from Bolca were described by Sacco (1895), who referred one of them to a new species, *Crocodilus bolcensis* Sacco, 1895 (*Crocodilus Bolcensis* in Lioy [1896], with the first letter of the specific name in capital), and the other four to *C. vicetinus* (see below). The holotype of *C. bolcensis* (Sacco, 1985, pl. 1, fig. 5a-b; Fig. 3; Supplementary Online Material, SOM, Fig. S1) was found by the Cerato family and donated to the National Exposition of Turin (Esposizione Nazionale di Torino) in 1884. It was cited in a brief note by Nicolis (1884) with the name of *Crocodrylus* cfr. *Vicetinus* (note the misspelled genus name). This specimen, catalogued as MGPT PU 17328, is currently housed at MRSN. It consists of a slab with a nearly complete skeleton, approximately two meters in total length, exposed in dorsal view and dorsoventrally compressed. The skull is complete, with a longirostrine snout, large posterior teeth, with one of them visibly compressed labiolingually (on the left dentary; Fig. 3a3), and smaller, rounded anterior teeth. The entire postcranial skeleton is present, but the cervical and dorsal vertebrae are too damaged to provide any morphological data. Sacco (1895) claimed that *C. bolcensis* was surely not a specimen of *C. vicetinus*, nor a true *Crocodilus*; however, he included MGPT PU 17328 in this genus because Boulenger (1889) referred the taxon now called *Mecistops cataphractus* Cuvier, 1825, which was used by Sacco for the main comparison for the identification of MGPT PU 17328, to *Crocodilus*. The taxonomic history of *C. bolcensis* is equally complex as the history of *C. vicetinus*. Arambourg (1934, 1952), on the basis of some unspecified features (but also considering some unreported differences) suggested a close affinity

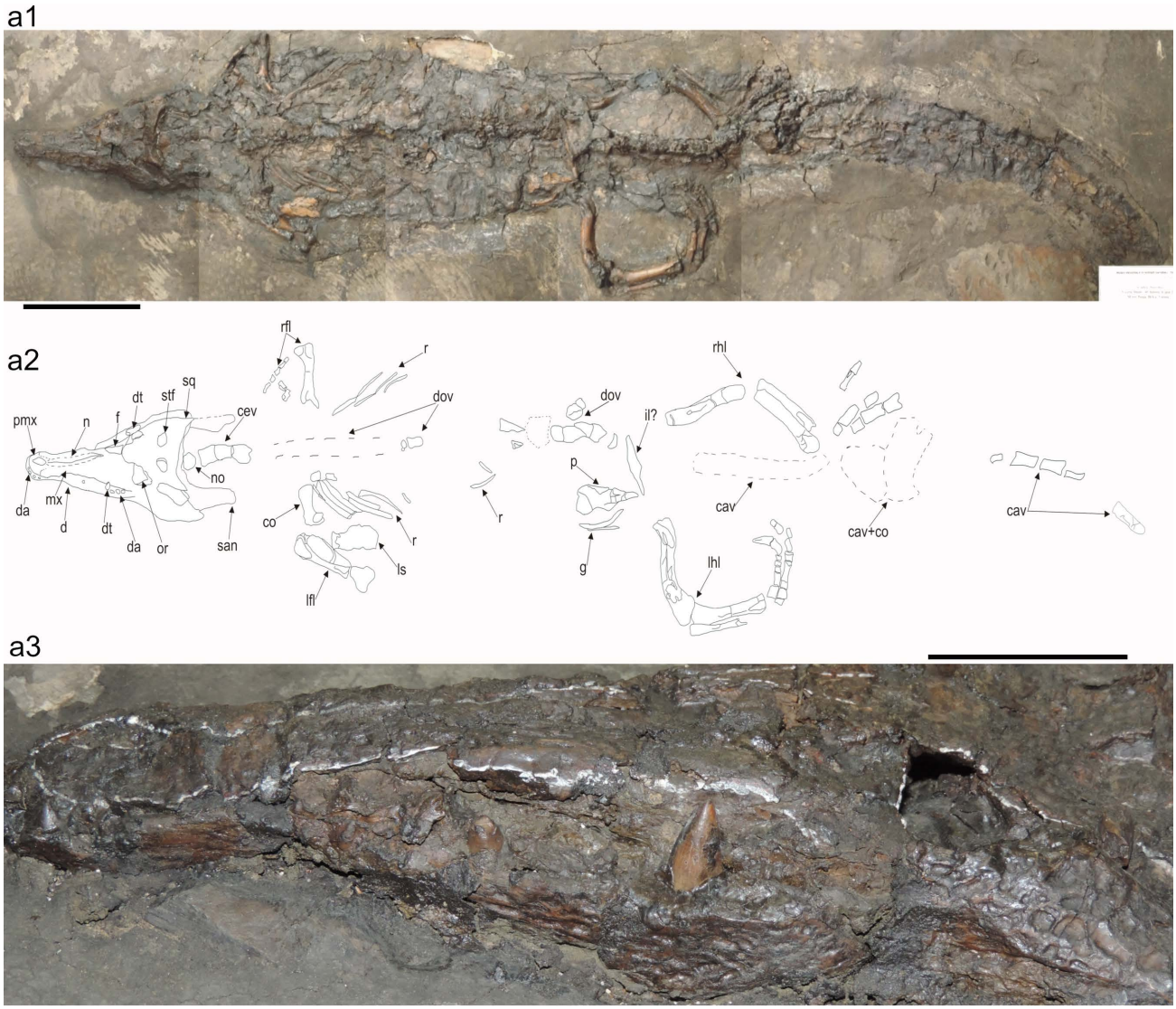

Fig. 3 - *Crocodilus bolcensis* Sacco, 1895 (holotype MGPT PU 17328). a1) Composition of photographs displaying the current state of preservation. a2) Interpretative drawing. a3) Close up of part of the skull and the left mandible showing the poor preservation of the skeletal elements and one well-visible posterior tooth. Scale bar in (a1) equals 20 cm; scale bar in (a3) equals 5 cm. Cav: caudal vertebrae; cav+co: caudal vertebrae and caudal osteoderms; cev: cervical vertebrae; co: coracoid; d: dentary; da: dentary alveolus; dov: dorsal vertebrae; dt: dentary tooth; f: frontal; g: gastralia; il?; ilium?; lfl: left forelimb; lhl: left hind limb; ls: left scapula; mx: maxilla; n: nasal; no: nuchal osteoderm; or: orbit; p: pubis; pmx: premaxilla; r: rib; rfl: right forelimb; rhl: right hind limb; san: surangular; sq: squamosal; stf: supratemporal fenestra.

with some fossils from Morocco, which are currently referred to the tomistomine *Moroccosuchus zenarroi* Jonet & Wouters, 1977 (see also Jouve et al., 2014). Later, Berg (1966) referred the holotype of *C. bolcensis* to the genus *Pristichampsus* Gervais, 1853, after a comparison with its type species *Pristichampsus rollinati* (Gray, 1831) from Argenton (France; Gray, 1831). Fossils of *P. rollinati* were also found in other European localities (Caraven-Cachin, 1880; Astre, 1931; Weitzel, 1938; Berg, 1966; Lapparent de Broin et al., 1993; Windolf, 1994; Rossmann, 1998; Kotsakis et al., 2004; Brochu, 2013). However, the name *P. rollinati* was once used to identify almost every ziphodont, hoofed crocodilian from Europe and Asia (Rauhe & Rossmann, 1995; Rossmann, 1998; Brochu, 2013). In fact, the type material of *P. rollinati* is very fragmentary (Rossmann, 2000) and lacks diagnostic features (Langston, 1975; Brochu, 2013). As a consequence, Brochu (2013) considered *Pristichampsus* to be a nomen dubium and proposed to replace it with *Boverisuchus* Kuhn, 1938. According to Brochu (2013), MGPT PU 17328, the holotype of *C. bolcensis*, has a similar cranial shape as the planocraniid specimens from Messel and Geiseltal referred to *Boverisuchus magnifrons* Kuhn, 1938. All these fossils are approximately coeval with those from Argenton, Messel, and Geiseltal, so it is likely that they are all conspecific. If correct, the name *C. bolcensis* has priority over *B. magnifrons*, so Brochu (2013) proposed the new combination "*Boverisuchus bolcensis*", a view which was later followed by Iijima et al. (2018). However, it is worth mentioning that some features observed in the skull of the holotype of *C. bolcensis* are shared with the tomistomine *Megadontosuchus arduini* (de Zigno, 1880) (SMS, pers. ob.) from the middle Eocene of Monte Duello (Verona, Italy), such as the large supratemporal fenestrae relative to the orbits, the long and elliptical external naris, the slender but robust snout, and large posterior teeth (Piras et al., 2007). Future revisions will be needed to confirm or reject this hypothesis.

The other four specimens described by Sacco (1895) were all referred to *Crocodilus vicetinus.* Three of them are currently housed in Turin (Italy; MGPT PU 17329), Pittsburgh (USA; CM 96616), and London (UK; NHMUK PV R 2789), whereas one is currently lost.

The Turin specimen, MGPT PU 17329 (Sacco, 1895, tab.1, fig. 3a-b; Fig. 4 and Fig. S2) is a nearly complete, but strongly damaged skeleton on a slab. It was discovered by Attilio Cerato and purchased by Bartolomeo Gastaldi for the School of Application for Engineers of Turin, and later given to the MGPT, where it is still housed. The specimen, about 73 cm in total length, preserves the skull, cervical, dorsal, and caudal vertebrae, parts of the forelimbs, both hind limbs, and some osteoderms. The pelvis was initially present but is now lost as a consequence of pyrite oxidation. The skull has a short triangular shape, large orbits, pointed distal tips of the nasals, which form a short projection into the external nostril, a wavy dentary, pointed anterior teeth and blunt posterior teeth (Seghetti, 2014; Seghetti et al., 2014). Based on these characters and given the small size of the specimen, MGPT PU 17329 was considered to be a young specimen of *C. vicetinus* by Sacco (1895). This specimen was also revised by Berg (1966), who referred it to *Allognathosuchus* Mook, 1921, based on the affinities between the Bolca specimen and *Allognathosuchus haupti* (Weitzel, 1935) from the Messel Pit (now accepted as *Hassiacosuchus haupti* Weitzel, 1935). The main features that allow this identification were the wavy dentary and the posterior blunt teeth, along with other similar skull features. *Allognathosuchus* is a genus of alligatorids found mainly in North America and Europe (Mook, 1921; Case, 1925; Simpson, 1930; Weitzel, 1935; Berg, 1966; Buffetaut, 1985). The genus was once used as a waste-basket taxon that included all specimens with a wavy dentary and specialized dentition, from the Eocene to the Oligocene (see Brochu, 2004 for a review). At some point, fifteen species were referred to this genus (Brochu, 2004), until cladistic analysis proved that *Allognathosuchus* is polyphyletic (Brochu, 1997, 1999, 2004). This means that the most iconic features of *Allognathosuchus* (the wavy dentary and the blunt teeth) have appeared multiple times within Alligatoridae (Brochu, 2004). In fact, according to Brochu (1999, 2004), the most relevant characters for the phylogeny of *Allognathosuchus*-like taxa are the prefrontal-lacrimal length ratio, the shape of the mid-line osteoderms, the length of the premaxillary process and the projection of the anterior tip of the nasal into the external naris. After these considerations, Brochu (2004) resurrected *Hassiacosuchus* Weitzel, 1935, which is considered an Alligatorinae (Brochu, 2004; Massonne et al., 2019; Godoy et al., 2020). As for the Bolca specimen MGPT PU 17329, preliminary revisions seem to confirm a relationship with *H. haupti*, although some key features (such as the prefrontal-lacrimal length ratio) are difficult to assess. Alternatively, Rauhe, in a note associated with the specimen MGPT PU 17329 in the collections, suggested that the specimen could represent a new species ("*Allognathosuchus longimetatarsus*"), probably based on the very long metatarsus of MGPT PU 17329 compared to other "allognathosuchid" specimens. Very little has been done on the postcranial skeleton of the *Allognathosuchus*-like alligatorids, which is mostly because there are few fossils preserving postcranial elements (among others, there is an unpublished thesis of Rauhe, 1993 on the postcranial elements of *H. haupti*). Future studies on the variability of metatarsus length in these taxa would surely help to confirm or reject the hypothesis of a new *Hassiacosuchus* species in Bolca.

In addition to the specimens described by Sacco (1895), Dal Lago (1901) and Squinabol (1902) reported further crocodilian fossils from Cornedo Vicentino (VI), about 25 km East of Bolca. Dal Lago (1901) cited some fossils (hypothetically referred to *C. vicetinus*) comprising teeth, bones, coprolites and a skeleton that was not collected and was lost. Squinabol (1902) referred yet another crocodilian fossil, CDL 600, to *Crocodilus* cfr. *vicetinus* because of its similarity with MGPT PU 17329. So it could be considered an additional specimen of *Hassiacosuchus*, but it is not sure if it belongs to the same faunal assemblage of Bolca or not. Fabiani (1914) noticed that the sites of Cornedo were probably coeval with those of Bolca. Indeed, there are geological affinities (Beschin et al., 2012), but in the absence of a general revision any consideration is speculative. Currently, CDL 600 is in a poor state of conservation; the analysis of D'Anastasio et al. (2014) confirms the presence of pyrite oxidation. The specimen was restored in 2006 (Pallozzi, pers. comm. to

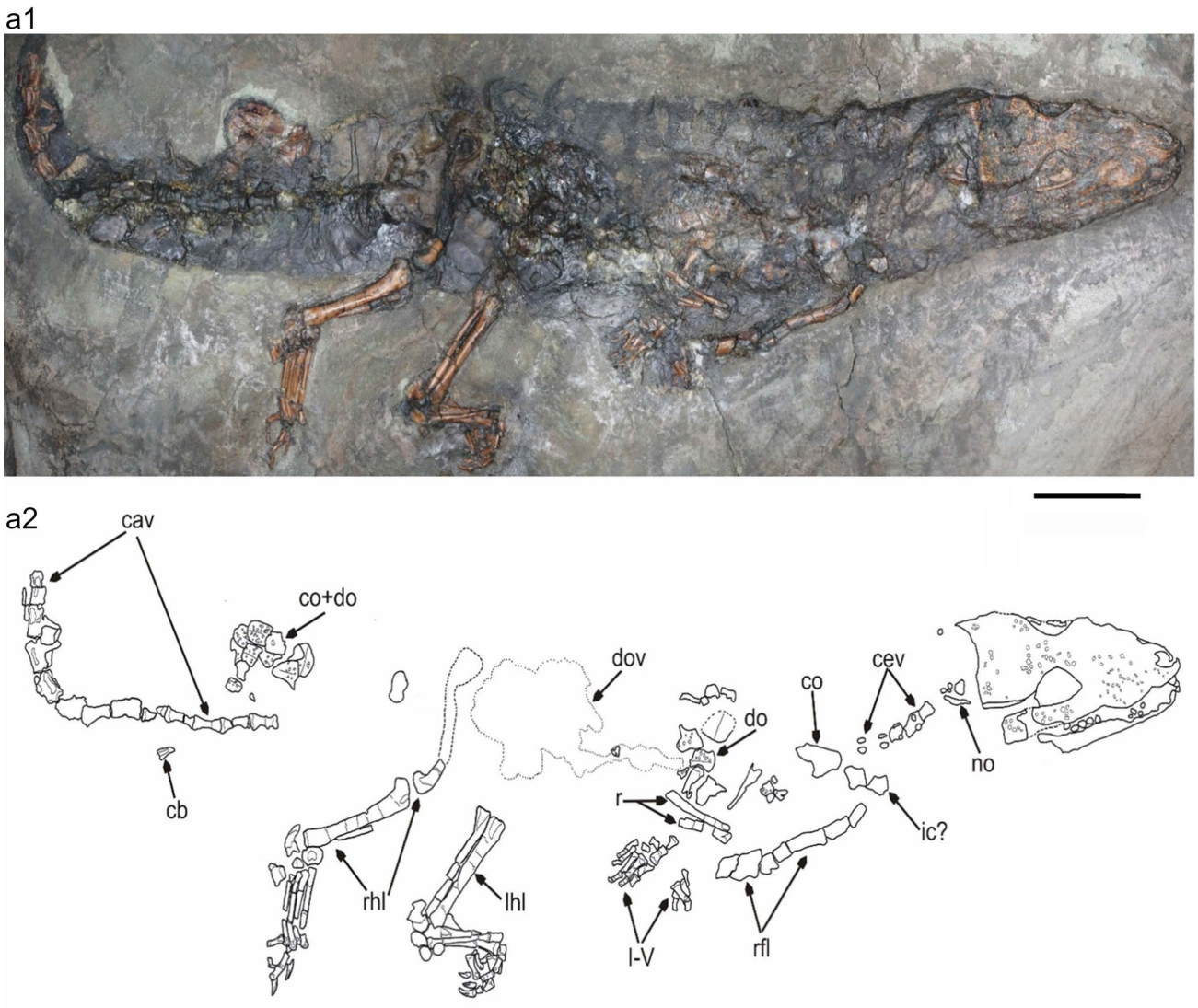

Fig. 4 - *Hassiacosuchus* sp., formerly *Crocodilus vicetinus* Lioy, 1865 (MGPT PU 17329). a1) Current state of preservation. a2) Interpretative drawing. Scale bar equals 10 cm. Cav: caudal vertebrae; cb: chevron; cev: cervical vertebrae; co: coracoid; co+do: caudal and dorsal osteoderms; do: dorsal osteoderms; dov: dorsal vertebra; ic: interclavicle; lhl: left hind limb; no: nuchal osteoderm; r: rib; rhl: right hind limb; rfl: right forelimb; I-V: phalanges from digits 1-5.

SMS, 2020) and has since been housed in a controlled environment to prevent further oxidation.

Two of the specimens figured and described by Sacco (1895) (Fig. S3) were later purchased by Baron Ernest Bayet (or de Bayet) of Brussels (as mentioned in Lioy, 1896), a fossil collector who bought a large number of fossils from Bolca. In 1903, he sold at least parts of his collection to the Carnegie Museum of Natural History, Pittsburgh (Friedman & Carnevale, 2018; for further information on the Bayet Collection of the Carnegie Museum see the official site of the Museum at https://carnegiemnh.org/monte-bolca-fish/). One of the specimens bought by Bayet (Sacco, 1895, tab. 1; Fig. S3a), which is currently lost, was mounted on plate and preserved in ventral view, but it was in an advanced state of degradation, and Sacco was not able to provide a detailed description. This specimen was 1.60 m in total length, with "sub-acute maxillary teeth". The other specimen, CM 96616 (Sacco, 1895, pl. 1, fig. 2; Fig. 5a and Fig. S3b), is a large specimen of 1.80 m in total length, exposed in dorsal view and embedded as usual in a slab. It displays an approximately triangular, crocodylid skull, pointed distal tips of the nasals, large anterior teeth and smaller and rounded posterior teeth. This specimen is currently stored in the Bayet Collection at CM and it is in a relatively good state of preservation.

The last crocodilian specimen originally considered to be from Bolca and described by Sacco (1895) is NHMUK PV R 2789 (Sacco, 1895, pl. 1, fig. 6; Fig. 5b and Fig. S4). The partial skeleton has a length of 35 cm and preserves the dorsal osteoderms and the limbs. Sacco (1895) identified it as a juvenile individual. The absence of the skull made the proper identification impossible, but Sacco considered it to be likely a member of *C. vicetinus*, so he proposed the name *Crocodilus* cf. *vicetinus*. As reported by Macaluso et al. (2019), the strontium isotope ratio of this specimen actually indicates that NHMUK PV R 2789 more likely originates from the Oligocene of Monteviale than from Bolca and might be referred to *Diplocynodon*. It is possible that the

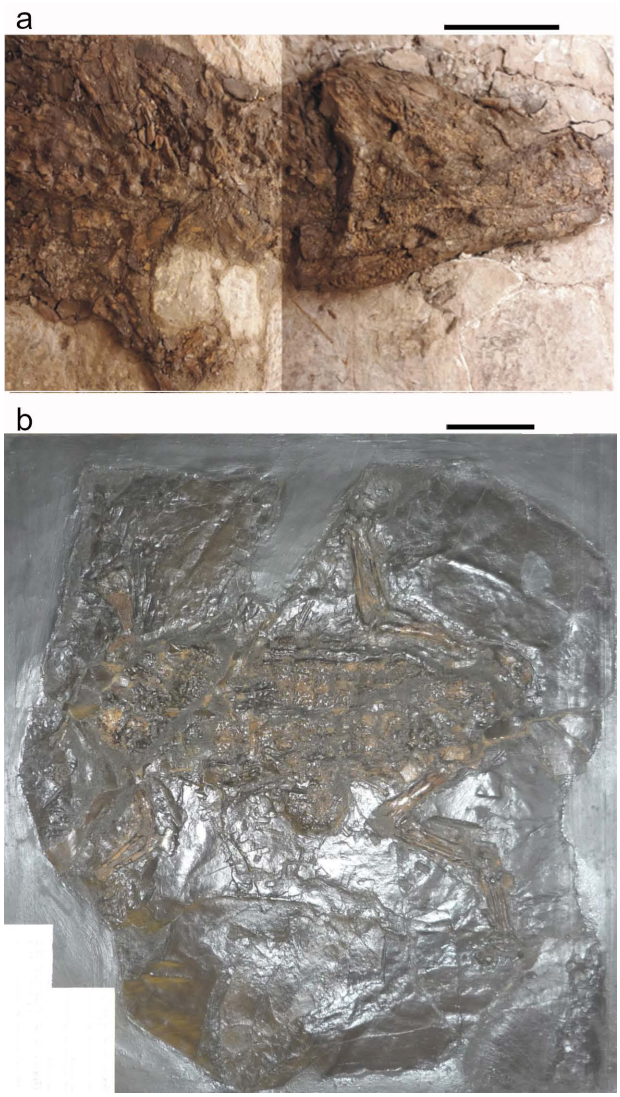

Fig. 5 - a) *Crocodilus vicetinus* Lioy, 1865 (CM 96616, one of the specimens bought by Ernest Bayet). Composition of photographs showing the current state of the anterior region. b) *Diplocynodon* sp., formerly assigned to *Crocodilus* cf. *vicetinus* Lioy, 1865 (NHMUK PV R 2789). It was originally described as coming from Bolca but is more probably from the Oligocene of Monteviale. Photograph (a) of courtesy of A. Henrici (CM). Scale bar in (a) equals 15 cm; scale bar in (b) equals 5 cm.

misunderstanding could be related to the vaguely similar name between "Monte Bolca", the traditional Italian name of the Bolca Fossil-Lagerstätte, and Monteviale (Macaluso et al., 2019), but it is known that fossils from other localities were sometimes sold as if they were from Bolca.

Briefly described and cited crocodilian specimens from the Bolca area

In addition to the specimens described by Lioy (1865) and Sacco (1895), other crocodilian specimens were only mentioned and referred to a genus or species even without a formal description.

One of the first specimens discovered in Bolca preserves an isolated wavy mandible. It was found by Suess in 1865 and mentioned by Nicolis (1884) and Lioy (1896), who referred it to *C. vicetinus* (see the introduction). According to Nicolis (1884) and Lioy (1896), this specimen was preserved in the Paläontologisches Universitäts-Museum in Vienna (Austria). However, we cannot confirm its current location. According to Berg (1966) it should be catalogued as "Lignit von Bolca, Geol. Samml. Wiener Hochschule, 1864/5 X. 5". However, "Geologische Sammlung, Wiener Hochschule", is the historic name for the geological collection of the Technical University of Vienna (Göhlich, pers. comm. to SMS, 2022). The palaeontological items of this collection were spread among other Institutions. Some of them are in the NHMW (Göhlich, pers. comm. to SMS, 2022), in the Institute of Geotechnics of Vienna (Wieser, pers. comm. to SMS, 2022) and maybe in the Department of Geology of the University of Vienna (Wagreich, pers. comm. to SMS, 2022). However, none of these Institutions houses this specimen, so we should consider it as currently lost. This specimen is neither described nor figured. Only Berg (1966) briefly mentions it, stating an affinity with *Allognathosuchus*, to which he also referred it.

MGP-PD 27567 is a small, nearly complete skeleton on a slab (Brochu, 2013, fig. 8 a-b; Fig. 6), exposed in ventral view. It was mentioned by Lioy (1896), who did not refer it to any species but identified it as a juvenile individual without providing any evidence for this statement. Giovanni Omboni purchased it from Attilio Cerato in 1876 (Fornasiero, pers. comm. to SMS, 2020), for the geological collection of the University of Padua (Lioy, 1896) where it is still housed. According to Rossmann (1998) and Brochu (2013), it may be referred to *C. bolcensis*. This specimen lacks a complete description. However, further revisions are difficult because this specimen, in addition to its damaged state, is partially covered by a brownish paint (Fornasiero, pers. comm. to SMS, 2020). This specimen was referred to *Pristichampsus* by Rossmann (1998; but see difficulties with this taxon above). Later, Brochu (2013) briefly described it and tentatively identified it to *Boverisuchus bolcensis*, although reporting the absence of some features typical of

Fig. 6 - *Crocodilus bolcensis* Sacco, 1895 (MGP-PD 27567). a1) Current state of preservation. a2) Detail of the proximal part of the caudal region displaying the brown paint covering the specimen. Photographs of S. Castelli, courtesy of M. Fornasiero, MGP-PD. Scale bar in (a1) equals 15 cm; scale bar in (a2) equals 5 cm.

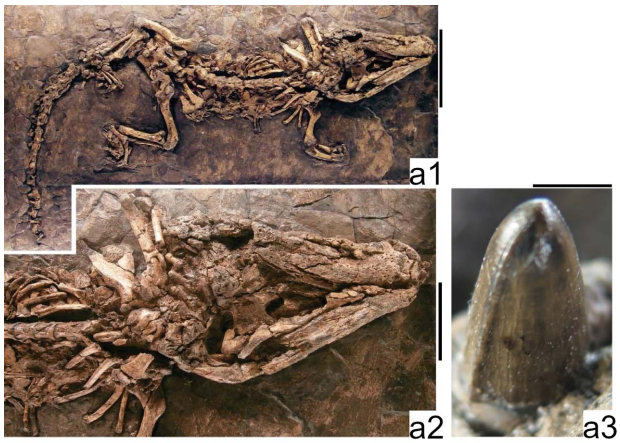

Fig. 7 - *Asiatosuchus* cf. *depressifrons* (MCSNV V.7097). a1) The complete skeleton. a2) Close-up of the skull. a3) Detail of a sharp-carinated tooth. (a1) and (a2) modified from Giusberti et al. (2014a). Scale bar in (a1-a2) equals 30 cm; scale bar in (a3) equals 0.5 cm.

Boverisuchus (the unserrated teeth, a craniocaudally shorter and mediolaterally wider mandibular symphysis, probable absence of ventral armour). Thus, this identification cannot be considered definitive. A revision of this specimen would be useful, even if its poor state of preservation hinders an accurate evaluation of diagnostic morphological characters.

Another specimen stored in the Museum of Vicenza is MCSNV V.1028 (figured in Papazzoni et al., 2014d; Fig. S5), a tooth and partial dentary found in Spilecco. Initially, it was identified as a mosasaurid (Nicolis, 1907), but it was later referred to an indeterminate crocodilian due the Paleogene age of the site (Medizza, 1980; Kotsakis et al., 2004; Papazzoni et al., 2014d). Currently, this fossil lacks any description and a proper identification.

A well-preserved specimen is MCSNV V.7097 (Medizza, 1980, unnumbered fig. on p. 147; Fig. 7), also preserved in the collection of the MCSNV. It was found by the Cerato family in 1946 in the lignite mine called Miniera della Purghetta (Zorzin, pers. comm. to SMS, 2021; see Cerato, 1981; Zorzin, 2017) and consists of a well-preserved, near-complete skeleton on a slab. It was restored soon after the discovery because the slab was broken during the extraction. Another restoration was done in 2002 using Paraloid as consolidating agent (Zorzin, pers. comm. to SMS, 2021; see also Zorzin, 2017, page 37 for photographs of the restoration of this specimen). Although cited and figured several times (De Zanche & Mietto, 1977; Medizza, 1980; Sorbini Frigo & Sorbini, 1999; Vihol, 2008; Giusberti et al., 2014b; Zorzin et al., 2017), this specimen was only briefly described, and not figured, by Berg (1966) in his comprehensive work on some Eocene taxa from Germany. MCSNV V.7097 was referred to *Asiatosuchus* by Berg (1966) for the long mandibular symphysis, and subsequently (after the considerations of Vasse, 1992), the specimen was referred to *A. depressifrons* due to its similarity with the holotype of *C. vicetinus* (Kotsakis et al., 2004). This specimen is currently under revision, with the aim to solve the issue.

Unreported specimens

Few specimens that presumably originate from Bolca have never been reported in literature. One of these is MCSNV V.12621 (Fig. 8), an isolated tooth from an unspecified locality (and unreported year) that still lacks a proper description (Vaccari, pers. comm. to SMS, 2013; and Zorzin, pers. comm. to SMS, 2021). It is a conical, smooth tooth of about three cm in length.

Two other specimens were bought by Bayet and, as most other fossils from the Bayet Collection, these are currently housed in the CM. One of them is CM 85825 (Fig. 9a), a partial skull and mandible, preserved in ventral view, with some well visible maxillary teeth. The other specimen is CM 96617 (Fig. 9b), a nearly complete, well-preserved skeleton, which is also prepared in ventral view. It is currently stored in a wooden case with glass cover (probably an old exhibit; Henrici, pers. comm. to SMS, 2020).

Berg (1966) claimed the presence of *Diplocynodon* in Bolca based on an unspecified specimen. Del Favero (1999) identified that specimen as MGP-PD 27403 based on a note written by Berg and attached to it. Del Favero (1999) and Kotsakis et al. (2004) questioned the inferred geological age of this fossil, suggesting that it is more recent than the specimens from Bolca. Macaluso et al. (2019) confirmed that this *Diplocynodon* specimen comes from the Oligocene of Monteviale, so the presence of *Diplocynodon* in Bolca is currently unsupported. This absence is remarkable, because *Diplocynodon* is a common fossil crocodilian in Europe, and it was also found along with *Asiatosuchus* in the Eocene deposits at Messel and Geiseltal (Brochu, 2003; Reid et al., 2018),

Fig. 8 - Crocodylia indet. (MCSNV V.12621). Scale bar equals 0.5 cm. Archive of the MCSNV, photograph courtesy of R. Zorzin.

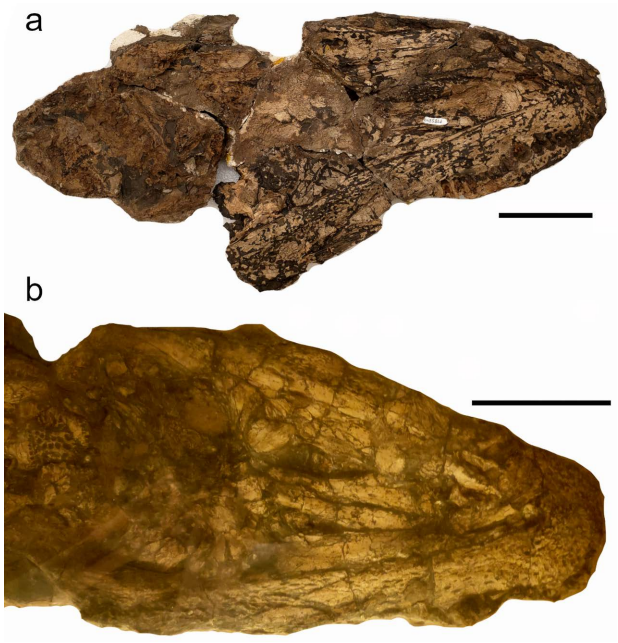

Fig. 9 - Crocodylia indet. Specimens presumably from Bolca in the Bayet Collection of the CM. a) CM 85825. b) CM 96617. Photographs courtesy of A. Henrici, CM. Scale bars equal 5 cm.

which share geological, chronological and fossiliferous affinities with some of the localities of the Bolca area.

In summary, of the 13 specimens originally referred to *C. vicetinus* and *C. bolcensis*, 12 presumably come from the Bolca area (Purga di Bolca, Spilecco and minor sites). Of these, nine were at least partly described, whereas the others lack any description (one of these was only briefly mentioned). One of the specimens described by Sacco (1985) actually originates from Monteviale (Oligocene; Macaluso et al., 2019), which makes necessary not only a taxonomic revision of the specimens, but a stratigraphic one as well. Currently, three crocodilian genera are considered to be present in the Bolca area: *Asiatosuchus*, *Boverisuchus*, and *Hassiacosuchus*. In addition, more material of crocodilians was mentioned from other, minor localities (Loschi, La Possette, and Valecco-Zovo), but these fossils are still unstudied. A detailed understanding of the stratigraphy of these localities could be useful to clarify the origin of some undescribed crocodilian specimens that presumably originate from Bolca. See Tab. 1 for a summary.

TURTLES

Despite a large array of beautifully preserved specimens and a number of named taxa established during the late 19th and 20th centuries, only two turtle species from the Bolca area are currently considered valid: the pleurodire *Neochelys capellinii* (de Zigno, 1889) and the trionychid "*Trionyx*" *capellinii* Negri, 1892. Worth mentioning is that Sorbini (1999) reports a carapace of a terrestrial turtle found in the Pesciara, probably implying the presence of a testudinid tortoise. However, this specimen is neither figured nor described in any paper (just cited in Carnevale et al., 2014) and apparently not hosted in any collection, so we cannot confirm this identification. The revised specimens are currently housed in the collections of MCSNV, MGP-PD, MGPT, MPURLS, MSNPV (housed in the Kosmos Museum), and NHMUK.

The Bolca pleurodires

Pleurodires represent a nowadays predominantly Southern Hemisphere turtle group (Rhodin et al., 2021), which in the past had a much higher diversity and broader distribution, encompassing also Europe (Gaffney et al., 2011; Joyce et al., 2021). In the latter continent, pleurodires flourished particularly during the Eocene (Kotsakis, 1978; Lapparent de Broin, 2001; Pérez-García & Lapparent de Broin, 2013, 2015), with the group becoming ultimately extinct in Europe during the Miocene (Georgalis & Kear, 2013; Georgalis et al., 2013). Among them, the podocnemidid genus *Neochelys* Bergounioux, 1954 represents an abundant and important faunal component in many Eocene localities of Europe (Kotsakis, 1978; Lapparent de Broin, 2001; Pérez-García & Lapparent de Broin, 2013; Cadena, 2015; see Pérez-Garcìa & Lapparent de Broin, 2015 for a diagnosis of *Neochelys*). The type species of this genus is *Neochelys capellinii* (de Zigno, 1889) (Bergounioux, 1954; Kotsakis, 1978; Chesi, 2009; Gaffney et al., 2011; Pérez-García & Lapparent de Broin, 2015; Georgalis et al., 2020b) originally established from Purga di Bolca and witnessing a rather perplexing taxonomic and nomenclatural history.

Achille de Zigno (1889) established *Emys capellinii* on the basis of a single carapace from Purga di Bolca. As it was a relatively common practice of this time, de Zigno (1889) originally referred his new species to the then wastebasket genus *Emys* Duméril, 1805. The holotype (pl. III of de Zigno, 1889; Fig. 10) of *Emys capellinii* was a compressed carapace, about 25 cm long and 21 cm wide. Whereas the original fossil specimen is currently lost (Broin, 1977), replicas are housed at MGP-PD (MGP-PD 6810Z; termed as "calcotype" by Broin, 1977) and in the Kosmos Museum of Pavia. De Zigno (1889) considered that the Italian shell possessed enough features that could differentiate it from other European taxa and therefore established his new species *Emys capellinii* de Zigno, 1889, honoring Giovanni Capellini, who had described the first Venetian Mesozoic chelonian, *Protosphargis veronensis* Capellini, 1884 (Capellini, 1884; de Zigno, 1889).

Subsequent studies by Bergounioux (1934, 1953a, b, 1954) revealed the pleurodire affinities of *Emys capellinii* but also created a nomenclatural chaos. In particular, Bergounioux (1953a, b) in his preliminary reports proposed to recombine *Emys capellinii* into *Elochelys* Nopcsa, 1931, and mentioned also the presence of a second, sympatric pleurodire in Bolca, for which he proposed the name *Platyarkia bolcensis* (species epithet misspelled as "*bolkensis*" in Bergounioux, 1953b). Nevertheless, in these two 1953 preliminary reports, the French author provided no descriptions or figures, and thus, *Platyarkia bolcensis* Bergounioux, 1953a has been considered a nomen nudum (see e.g., Broin, 1977; Georgalis et al., 2020b). In any case, in his large monograph the following year, Bergounioux (1954) formally introduced the binomen *Neochelys capellinii*, which, however, he curiously treated as a new genus and species and not as simply as a new generic combination

Catalogue number	Locality	Current location	First reference	Original identification	Relevant revisions	Current identification	Material
MGP-PD 6810Z (Fig. 10)	Purga di Bolca	MGP-PD	de Zigno, 1889	*Emys capellinii*	Bergounioux, 1954	*Neochelys capellinii*	Cast of carapace; holotype of *Neochelys capellinii* and syntype of *Neochelys bolcensis*
MGP-PD 26558 (Fig. 11)	Purga di Bolca	MGP-PD	Bergounioux, 1954	*Neochelys capellinii*	Kotsakis, 1978	*Neochelys capellinii*	Carapace
MCSNV V.2353 (Fig. 12a)	Purga di Bolca	MCSNV	Broin, 1977	*N. capellinii*	Chesi, 2009	*Neochelys capellinii*	Carapace
MCSNV V.2354 (Fig. 12b)	Purga di Bolca	MCSNV	Broin, 1977	*N. capellinii*	Chesi, 2009	*Neochelys capellinii*	Plastron
MCSNV V.2352 (Fig. 12c-d)	Valecco	MCSNV	Broin, 1977	*N. capellinii*	None	*Neochelys capellinii*	Articulated carapace and plastron
MCSNV V.2356	Purga di Bolca	MCSNV	Broin, 1977	*N. capellinii*	None	*Neochelys capellinii*	Carapace and limb
MGP-PD 5157 (Fig. 14)	Purga di Bolca	MGP-PD	Negri, 1892	*Trionyx gemmellaroi*		"*Trionyx*" *capellinii*	Skeleton with skull; holotype of *Trionyx gemmellaroi*
MGP-PD 12883 (Fig. 13a and Fig. S6a)	Purga di Bolca	MGP-PD	Negri, 1892	*Trionyx capellinii*	Bergounioux, 1954; Kotsakis, 1977; Georgalis & Joyce, 2017	"*Trionyx*" *capellinii*	Carapace and skull's elements; syntype of "*Trionyx*" *capellinii*
MGP-PD 12882 (Fig. 13b and Fig. S6b)	Purga di Bolca	MGP-PD	Negri, 1892	*T. capellinii*		"*Trionyx*" *capellinii*	Carapace; syntype of "*Trionyx*" *capellinii*
MGP-PD 12806 (Fig. 13c and Fig. S6c)	Purga di Bolca	MGP-PD	Negri, 1892	*Trionyx affinis*	Bergounioux, 1954; Kotsakis, 1977; Georgalis & Joyce, 2017	"*Trionyx*" *capellinii*	Carapace; holotype of *Trionyx affinis*
MGPT PU 17281 (Fig. 15a and Fig. S7)	Purga di Bolca	MGPT	Sacco, 1894	*Trionyx capellinii conjungens*	Bergounioux, 1954; Georgalis & Joyce, 2017	"*Trionyx*" *capellinii*	Carapace; syntype of *Trionyx capellinii conjungens*
MGPT PU 17282 (Fig. 15b and Fig. S8)	Purga di Bolca	MGPT	Sacco, 1894	*T. capellinii conjungens*	Bergounioux, 1954; Georgalis & Joyce, 2017	"*Trionyx*" *capellinii*	Carapace; syntype of *Trionyx capellinii conjugens*
MGPT PU 17283 (Fig. 15d and Fig. S10)	Purga di Bolca	MGPT	Sacco, 1894	*T. capellinii conjungens*	Bergounioux, 1954; Georgalis & Joyce, 2017	"*Trionyx*"*capellinii*	Carapace and appendicular element; syntype of *Trionyx capellinii conjugens*
MGPT PU 17284 (Fig. 15c and Fig. S9b)	Purga di Bolca	MGPT	Sacco, 1894	*Trionyx* cf. *capellinii*	Bergounioux, 1954; Georgalis & Joyce, 2017	"*Trionyx*" *capellinii*	Carapace
None (Fig. S9a)	Purga di Bolca	Unknown	Sacco, 1894	*T.* cf. *capellinii*	Bergounioux, 1954; Georgalis & Joyce, 2017	"*Trionyx*" *capellinii*	Carapace
MGP-PD 12814 (Fig. 16)	Purga di Bolca	MGP-PD	Bergounioux, 1954	*Trionyx intermedius*	Kotsakis, 1977; Georgalis & Joyce, 2017	"*Trionyx*" *capellinii*	Carapace; holotype of *Trionyx intermedius*
MPURLS 21 (Fig. S11)	Purga di Bolca	MPURLS	Kotsakis, 1977	*T. capellinii*	None	"*Trionyx*" *capellinii*	Carapace
MPURLS 22	Purga di Bolca	MPURLS	Kotsakis, 1977	*T. capellinii*	None	"*Trionyx*" *capellinii*	Carapace
MCSNV V.2357 (Fig. 17a)	-	MCSNV	this paper	-	-	"*Trionyx*" *capellinii*	A shell
NHMUK PV R 2787 (Fig. 17b)	-	NHMUK	this paper	-	-	"*Trionyx*" *capellinii*	A shell
NHMUK PV R 2788 (Fig. 17c)	-	NHMUK	this paper	-	-	"*Trionyx*" *capellinii*	A shell
MNB 1902.1357 (Fig. 18)	Pesciara	MNB	Massalongo, 1859	*Archaeophis proavus*	Janensch, 1906; Rage, 1984; Smith & Georgalis, 2022	*Archaeophis proavus*	Almost complete skeleton with skull; holotype of *Archaeophis proavus*

Tab. 2 - List of the turtle and snake specimens from Bolca (with referred chapter and figure in this work).

Catalogue number	Locality	Current location	First reference	Original identification	Relevant revisions	Current identification	Material
MCZ-VP 1001, 1002, 1003 (Fig. 19; Fig. S12)	Pesciara	MCZ	Massalongo, 1859	*Arch. bolcensis*	Auffenberg, 1959; Rage, 1984; Smith & Georgalis, 2022	*Anomalophis bolcensis*	Three slabs with portions of the vertebral column; holotype of *Anomalophis bolcensis*
MGP-PD 8360 (Fig. 20; Fig. S13)	Purga di Bolca	MGP-PD	de Zigno, 1890	*Coluber ombonii*	Rage, 1988	Serpentes indet.	Portion of the vertebral column; holotype of *Coluber ombonii*
IG.VR. 69589	Pesciara	MCSNV	Zorzin, 2017	?Serpentes	None	None	Skin print on slab

Tab. 2 - Continuation.

of de Zigno's (1889) species. Moreover, Bergounioux (1954) explicitly stated that the holotype of *Neochelys capellinii* was a carapace that he figured in his plate V (which corresponds to the actual specimen MGP-PD 26558; Fig. 11) and not the carapace previously described and figured by de Zigno (1889) (which corresponds to the actual specimen MGP-PD 6810Z [which is a "calcotype", i.e., cast]). At the same time, Bergounioux (1954) established another congeneric species from Bolca, *Neochelys bolcensis* on the basis of a carapace and a plastron, which he figured in his plate VI, claiming that these two specimens had been designated under the name "*Emys bolcensis* Zigno", but had so far remained nomina nuda as they had not been described. Apparently, *N. bolcensis* corresponds to the nomen nudum *Platyarkia bolcensis* which that author had introduced the previous year (Bergounioux, 1953a) but he apparently changed his opinion and eventually treated it as congeneric with *N. capellinii* (Bergounioux, 1954). However, what makes this case even more perplexing is that the (syntype) carapace of *Neochelys bolcensis* is actually the same specimen upon which de Zigno (1889) had previously established *Emys capellinii* (specimen MGP-PD 6810Z - note that the collection number "6810" was also used in Bergounioux, 1954, p. 46). This bizarre case was highlighted by Broin (1977) and Kotsakis (1978) and it is further confirmed here by our first-hand observation (GLG) of the MGP-PD collection, where MGP-PD 26558 is labelled as the "tipo" of "*Elochelys capellinii* Bergounioux" and MGP-PD 6810Z is labelled as the "tipo" of "*Platyarkia bolcensis* Bergounioux".

It is unclear how this misunderstanding occurred, but it causes major nomenclatural and typification issues here: if the authorship of both the genus and species *Neochelys capellinii* is attributed to Bergounioux (1954), then the holotype is MGP-PD 26558, whereas if *Neochelys capellinii* of Bergounioux (1954) is merely treated as a new generic combination of *Emys capellinii* de Zigno, 1889, then the holotype is MGP-PD 6810Z (a cast, "calcotype" sensu Broin, 1977), with the latter specimen also serving as a syntype of *Neochelys bolcensis* Bergounioux, 1954. The latter taxonomic treatment is indeed the most common in chelonian literature (e.g., Kuhn, 1964; Broin, 1977; Kotsakis, 1978; Lapparent de Broin, 2001; Pérez-García & Lapparent de Broin, 2013, 2015; Georgalis et al., 2020b). Unfortunately, this is

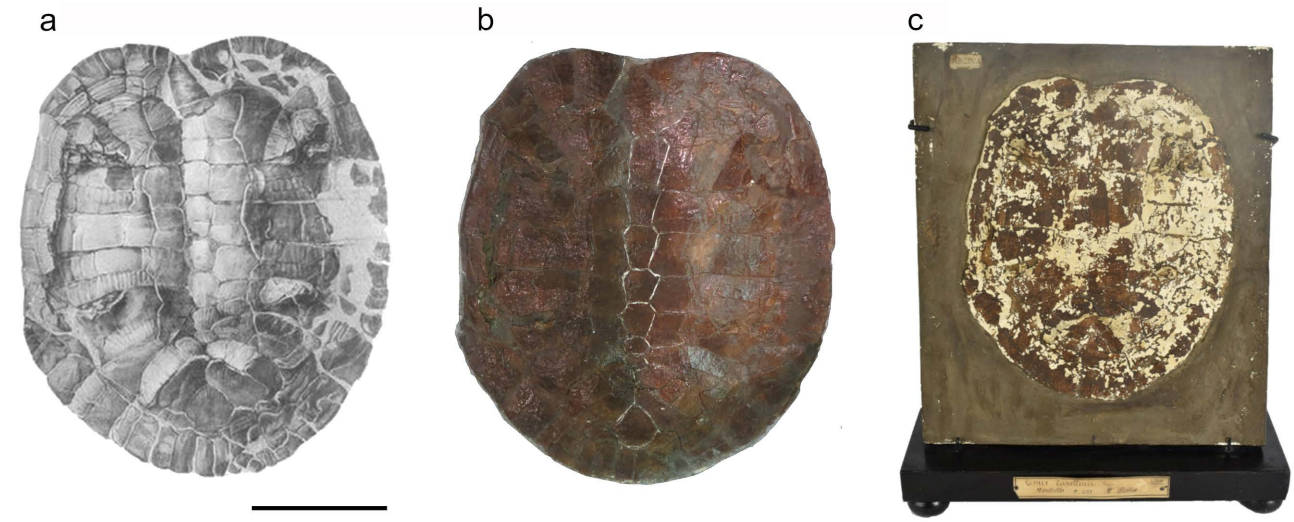

Fig. 10 - *Neochelys capellinii* (de Zigno, 1889), holotype (MGP-PD 6810Z). The same specimen also serves as a syntype of *Neochelys bolcensis* Bergounioux, 1954. a) Original drawing of the specimen from de Zigno (1889), modified from Giusberti et al. (2014a). b) Actual photograph of the specimen in its current state of preservation. c) MSNPV 14659, cast housed in the Kosmos Museum of the specimen, from the Archivio del Museo di Storia Naturale dell'Università di Pavia. Scale bar equals 5 cm.

Fig. 11 - *Neochelys capellinii*, specimen MGP-PD 26558, considered as the holotype of the species by Bergounioux (1954). Scale bar equals 5 cm.

not the first time that such major confusions with fossil turtle typification or nomenclature occur in the works of Bergounioux (see e.g., Joyce, 2016, p. 40).

In any case, it is beyond the scope of this paper to fix this nomenclatural chaos surrounding the taxonomic history of *Neochelys capellinii* but we have to highlight that a revision of the existing material from Bolca should be an essential step that would shed important light on the anatomy and precise affinities of this key taxon of European pleurodires.

Besides the above-mentioned specimens, other pleurodire specimens from Bolca have been briefly described by Broin (1977) and Chesi (2009), all referred to *Neochelys capellinii*. These include a carapace (MCSNV V.2353) and a plastron (MCSNV V.2354) of a single individual found in 1941 by Massimiliano Cerato (Chesi, 2009, fig. 3; Fig. 12a-b), an articulated carapace and plastron found in Valecco by Massimiliano and Giuseppe Cerato in 1915 (MCSNV V.2352; Fig. 12c), and a carapace with right hind limb remains (MCSNV V.2356). Broin (1977) also reported a left chelonian femur "probably" found in Purga di Bolca.

At this point, it is worth mentioning that another species of that genus has also been described from the Eocene of northern Italy, i.e., *Neochelys nicolisii* (de Zigno, 1890), based on a carapace from Avesa (also Verona) (de Zigno, 1890). Similar to the Monte Bolca *Neochelys*, no comprehensive redescription of the material of *N. nicolisii* has been conducted recently; in fact, the taxon has been, almost conveniently, usually simply treated as a junior synonym of the geographically proximate *N. capellinii* (e.g., Kotsakis, 1978; Lapparent de Broin, 2001; Chesi, 2009; Georgalis et al., 2020b), with only a few exceptions that still treated it, at least tentatively, as valid (Kuhn, 1964; Broin, 1977; Kotsakis, 2006; Pérez-García & Lapparent de Broin, 2015).

The Bolca trionychids

Trionychids, commonly known as soft-shelled turtles, represent a charismatic group of chelonians that occur today in Africa, Asia, and North America (Rhodin et al., 2021). Their characteristic sculpturing pattern on their shells and their distinctive skeletal anatomy has facilitated their widespread identification in the fossil record (Vitek & Joyce, 2015; Georgalis & Joyce, 2017). Accordingly, this rich fossil record denotes that, during the Eocene, trionychids literally thrived and were abundant and taxonomically diverse, with their remains being found in Europe, Asia, Australia, the Americas (Georgalis & Joyce, 2017) and recently also in Africa (Georgalis, 2021). Their fossil remains are usually represented by isolated shell fragments, but nevertheless, complete (or almost complete) skeletons are also known, particularly from a few Lagerstätte localities (Georgalis & Joyce, 2017). The latter is the case with Bolca.

Trionychids represent the most abundant and well-preserved chelonians found in Bolca. In fact, the exquisite preservation of the trionychids of Bolca makes them among the most beautiful fossil specimens of this group worldwide, rivalling the respective material from other Lagerstätte localities, such as Messel and Monteviale (see Georgalis & Joyce, 2017). On the other hand, this array of fabulous (although usually crushed) specimens recovered and documented by different workers in the late 19th and 20th centuries, has witnessed a considerable taxonomic confusion surrounded by a plethora of named taxa, often

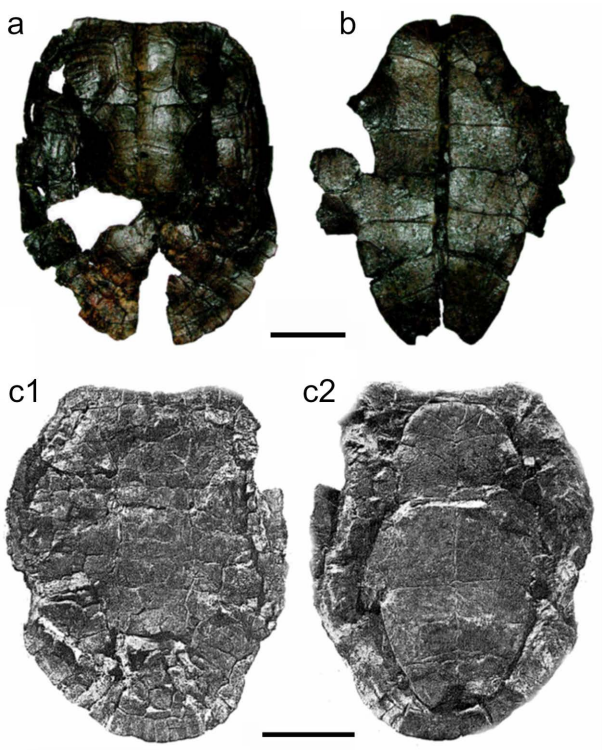

Fig. 12 - *Neochelys capellinii*, specimens described by Broin (1977) and Chesi (2009). a) MCSNV V.2353 (modified from Chesi, 2009, pl. 3). b) MCSNV V.2354 (modified from Chesi, 2009, pl. 3). c) Original photograph of MCSNV V.2352 in dorsal (c1) and ventral (c2) views (modified from Broin, 1977, pl. IV). Scale bars equal 5 cm.

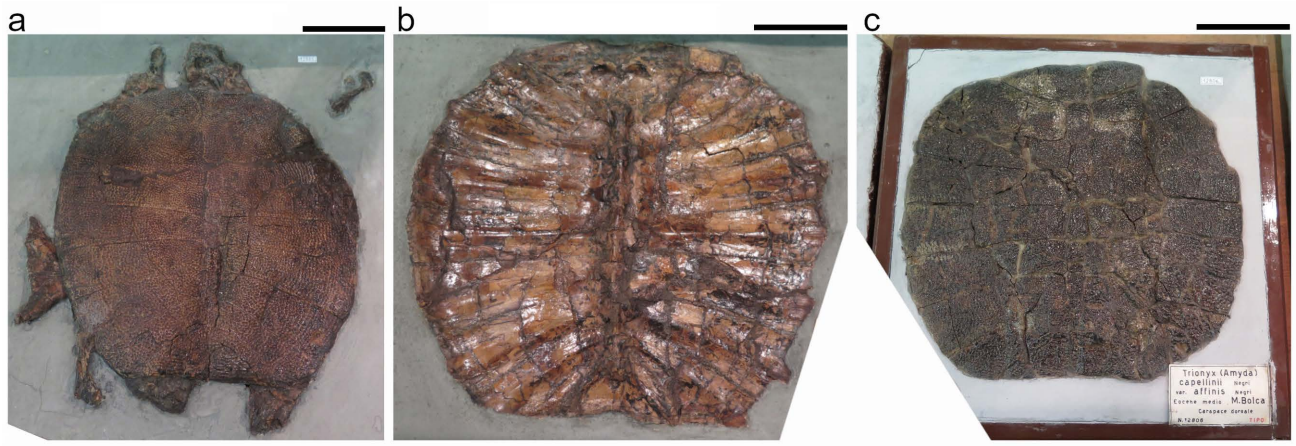

Fig. 13 - "*Trionyx*" *capellinii*, specimens described by Negri (1892). a) Syntype skeleton of *Trionyx capellinii* Negri, 1892 (MGP-PD 12883). b) Syntype shell of *Trionyx capellinii* (MGP-PD 12882). c) Holotype shell of *Trionyx affinis* Negri, 1892 (MGP-PD 12806). Scale bars equal 5 cm.

with little or practically no anatomical differences among each other (see Georgalis & Joyce, 2017).

Arturo Negri was the first to describe the beautiful trionychid specimens from Bolca that were housed in the collection of MGP-PD (Negri, 1892). Upon this material, which comprised crushed but almost articulated skeletons (sometimes also with skull), Negri (1892) established three new species: *Trionyx capellinii* Negri, 1892, *Trionyx gemmellaroi* Negri, 1892, and *Trionyx affinis* Negri, 1892.

Trionyx capellinii was named by Negri (1892) after the prominent palaeontologist Giovanni Capellini, who had already previously described fossil trionychid remains elsewhere from the Italian Peninsula (Capellini, 1878). *Trionyx capellinii* was established on the basis of two well-preserved specimens (Fig. 13a-b and Fig. S6a-b), which had been found in the same levels as the crocodilian *Crocodilus vicetinus*. The most complete specimen is MGP-PD 12883, a partial skeleton consisting of parts of the cranium, the complete carapace in dorsal view, a hyo-hypoplastron, a humerus, and a femur. The other specimen, MGP-PD 12882, is a relatively complete carapace exposed in ventral view. Currently, both these specimens are considered to be the syntypes of the species (Georgalis & Joyce, 2017). *Trionyx gemmellaroi* was established upon one of the most complete turtle specimens ever found from Bolca, MGP-PD 5157, i.e., an almost complete skeleton, including the plastron and carapace, all limb elements, and partial skull and mandible (Fig. 14). It was found, according to Negri (1892), 40 meters below the level of the specimens of *Crocodilus*

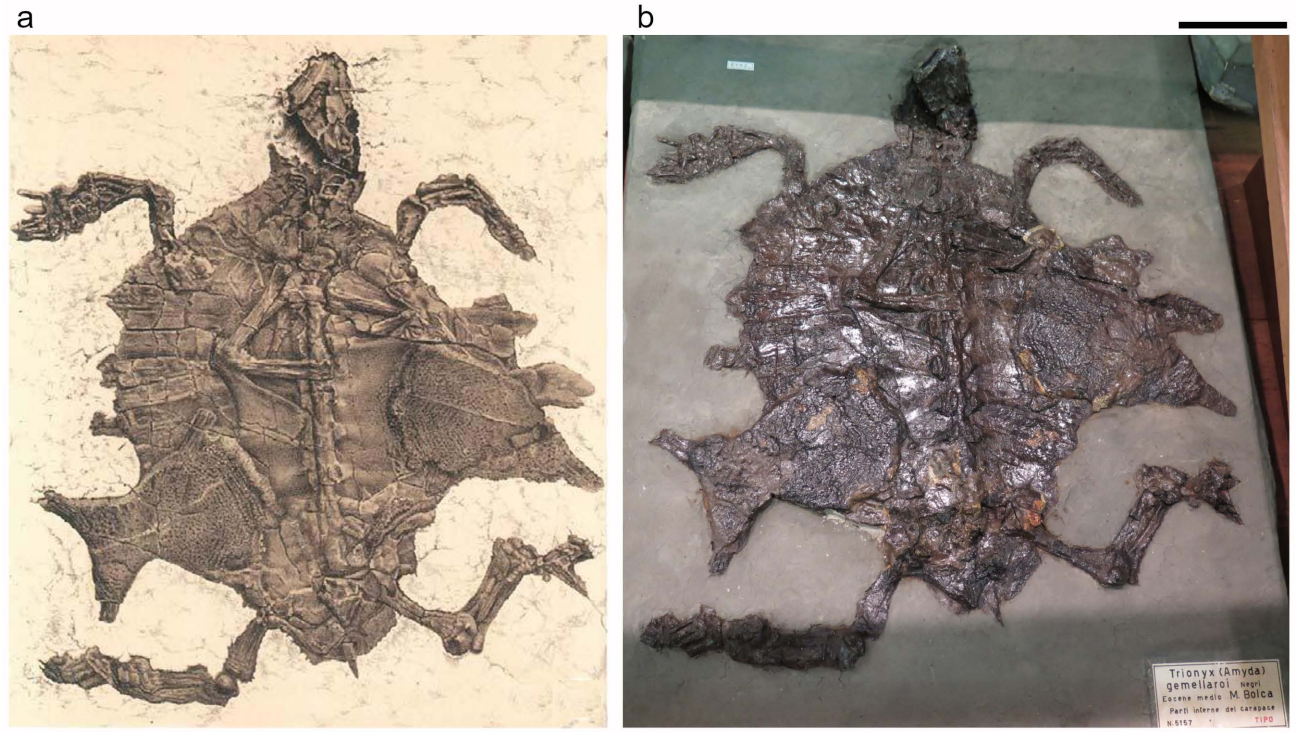

Fig. 14 - "*Trionyx*" *capellinii*, specimen described by Negri (1892). Holotype of *Trionyx gemmellaroi* Negri, 1892 (MGP-PD 5157). a) Original drawing from Negri (1892). b) Current state of the specimen. Scale bar equals 10 cm.

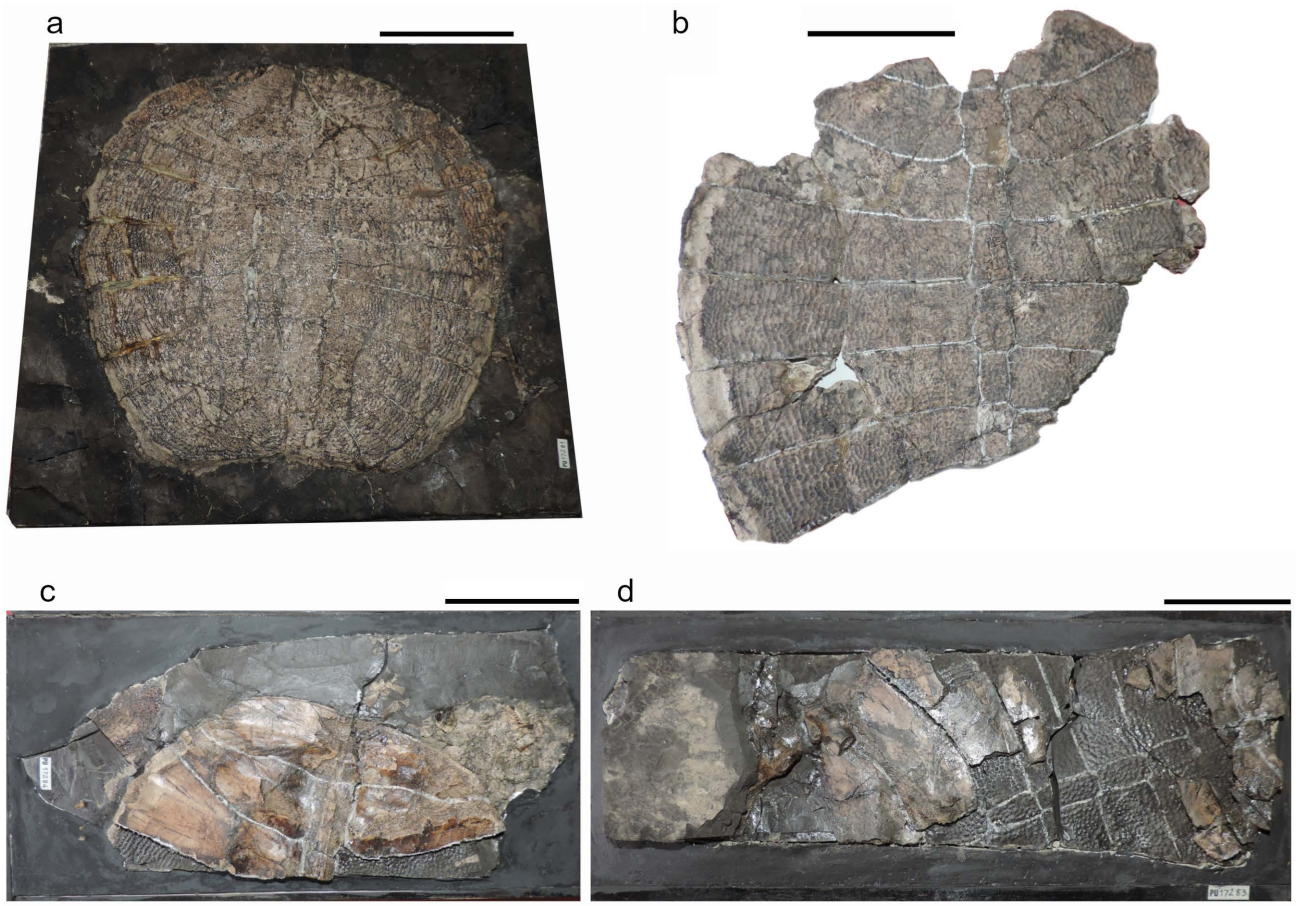

Fig. 15 - "*Trionyx*" *capellinii*, specimens described by Sacco (1894). a) Syntype of *Trionyx capellinii conjungens* Sacco, 1894 (MGPT PU 17281). b) Syntype of *T. c. conjungens* (MGPT PU 17282). c) Unnamed specimen (MGPT PU 17284). d) Syntype of *T. c. conjungens* (MGPT PU 17283). Scale bars equal 5cm.

vicetinus. Negri (1892) considered this specimen as not fully developed ontogenetically due to the large size of the orbits and the (presumably) narrow skull. The third species introduced by Negri (1892), *Trionyx affinis*, is based on an almost complete carapace (MGP-PD 12806; Fig. 13c and Fig. S6c), which was also found in the same level with *Crocodilus vicetinus*. Negri (1892) stated that some bones (the third to seventh right costals and the first two left costals) were artificially attached to this specimen. Although Negri (1892) considered the carapace of *T. affinis* to be different from that of *T. capellinii* in a number of features, he also noticed a few similarities, leading him to consider these two taxa closely related, and for this reason he called the former taxon "affinis" (similar to *T. capellinii*). For all his three species, Negri (1892) paid particular attention to the ornamentation pattern on the carapace and thus based the (supposed) distinction among his three new species based on that feature. However, it is now known that the ornamentation pattern is subject to a large degree of individual variation in trionychids (Vitek & Joyce, 2015; Georgalis & Joyce, 2017). Nevertheless, besides the ornamentation differences, Negri (1892) highlighted also cranial and postcranial differences and similarities among the Bolca trionychids but also with other extinct taxa (particularly those described by Owen & Bell, 1849 from the Eocene of England), as well as with the extant *Trionyx triunguis* (Forskål, 1775).

In 1892, Federico Sacco bought five chelonian remains from Attilio Cerato, for the palaeontological collection of the MGPT, which he eventually described and published two years later (Sacco, 1894). Four of these specimens are still housed at MGPT, whereas one is apparently lost: the best-preserved specimen, MGPT PU 17281 (Fig. 15a and Fig. S7), is a slab with a complete carapace preserved in dorsal view, with a length of about 29.5 cm and a width of about 31 cm. Sacco (1894) recognized shell features which rendered the specimen as reminiscent of *T. capellinii* and *T. affinis* from Bolca, as well as the Monteviale trionychid which was already described by Negri (1892) as *Trionyx capellinii montevialensis* Negri, 1892 (currently synonymized with *Trionyx capellinii*; see Georgalis & Joyce, 2017). Another well-preserved, but not complete, specimen is MGPT PU 17282 (Fig. 15b and Fig. S8). It is the anterior half of a carapace and, according to Sacco (1894), it was similar to *T. capellinii* and *T. affinis*. The third, currently lost specimen (Fig. S9a) was a fragment of a carapace referred by Sacco (1894) to *T. capellinii*. The fourth specimen, MGPT PU 17284 (Fig. 15c and Fig. S9b), is an anterior part of a carapace. Currently it is embedded on a slab inside a wooden box. Sacco (1894) referred it as a young individual of *T. capellinii*. The fifth specimen, MGPT PU 17283 (Fig. 15d and Fig. S10), is represented by a middle portion of a carapace preserved in ventral view and associated to an appendicular element

Fig. 16 - "*Trionyx*" *capellini*, holotype shell (MGP-PD 12814) of *Trionyx intermedius* Bergounioux, 1954 described by Bergounioux (1954). Scale bar equals 5 cm.

(part of a humerus, according to Sacco,1894). The author referred it to *T. capellinii*, despite the presence of some differences. Both elements are currently preserved on a slab in a wooden box. Despite some uncertainties by the author, Sacco (1894) eventually proposed a new subspecies *Tryonix capellinii conjungens* Sacco, 1894 (note the misspelling of the genus name *Trionyx*), to which he referred the first (MGPT PU 17281), the second (MGPT PU 17282), and the fifth (MGPT PU 17283) specimens. The other two specimens were considered by Sacco (1894) as too poorly preserved for a proper identification.

The last taxon to be named among the Bolca trionychids was *Trionyx intermedius* Bergounioux, 1954. Based on a practically complete carapace (MGP-PD 12814; Fig. 16), Bergounioux (1954) established his new species, as he considered that this specimen possessed enough differences from the other Bolca trionychids, in the shape of the carapace, the size and shape of the neurals, and the sculpturing pattern.

Since then, only a few additional trionychid specimens from Bolca have been published. Kotsakis (1977) described two carapaces from Bolca, MPURLS 21 and 22. MPURLS 21 (Fig. S11) is a well-preserved carapace with part of the hypoplastron, part of the right humerus, some scattered bones and a phalange of the right hind limb. Despite the generally good preservational state, some elements are not well visible. MPURLS 22 is a carapace preserving part of the plastron, but in a poor state of preservation. This was mainly due to some interventions of restorations to repair some fractures (some of which had been caused by the bombardments during the WWII in 1944, according to Kotsakis, 1977). Only the costals and part of the sculpturing were reliability visible. Comparing these two specimens with the other specimens from Bolca (and Monteviale), Kotsakis (1977) stated that every character used by previous authors to erect new species and subspecies were in fact due to individual variability, and concluded that almost every soft-shelled turtle in Bolca (including the specimens studied by him) are just specimens of *Trionyx capellinii capellinii* (treated by him at the subspecies level, and, for similar reason, every taxon from Monteviale belonged to *Trionyx capellinii montevialensis*). Besides the aforementioned, some further, undescribed trionychid specimens from Bolca exist in different collections, such as the shells presented here from MCSNV and NHMUK (Fig. 17).

Therefore, in sum, five different taxa have been established from Monte Bolca (*Trionyx affinis*, *Trionyx capellinii*, *Trionyx capellinii conjungens*, *Trionyx gemmellaroi*, and *Trionyx intermedius*). Revisions, overviews, or at least tentative taxonomic rearrangements, coupled occasionally also with novel specimens from Bolca, have been subsequently proposed to evaluate the validity of these named taxa or even their exact affinities or conspecificity with the nearby Oligocene trionychids from Monteviale (Kuhn, 1964; Broin, 1977;

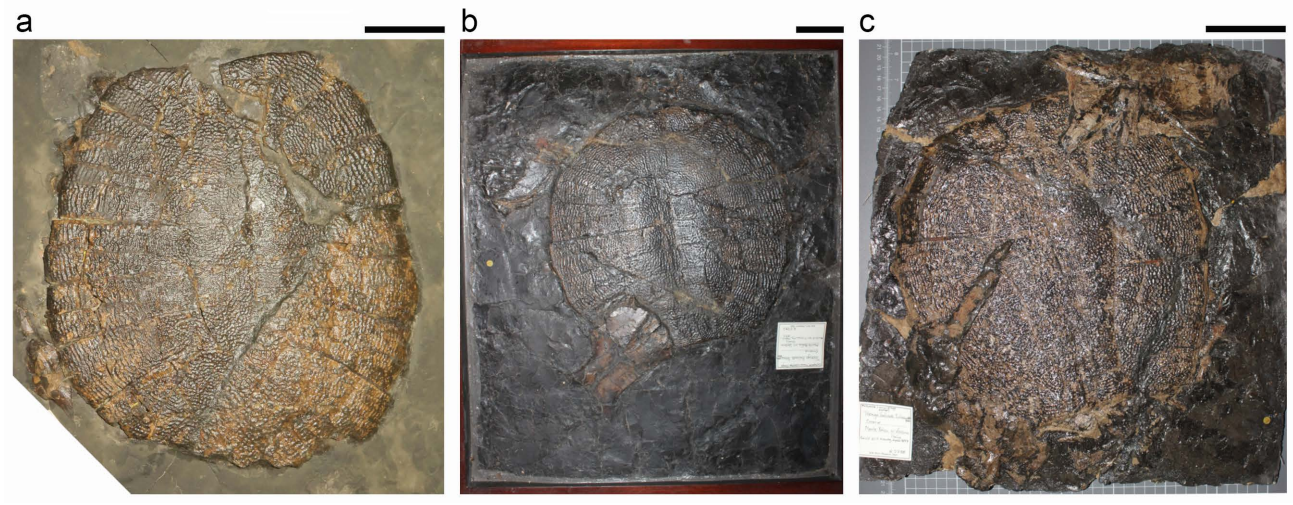

Fig. 17 - "*Trionyx*" *capellinii*; undescribed shells. a) MCSNV V.2357. b) NHMUK PV R 2787. c) NHMUK PV R 2788). Scale bars equal 5 cm.

Kotsakis, 1977, 1985). Currently, the recent revision of all Old World trionychids by Georgalis & Joyce (2017) demonstrated that solely a single valid trionychid species occurs in Bolca, i.e., "*Trionyx*" *capellinii*, and moreover, that this binomen also pertains to the younger (Oligocene) conspecific trionychids from the nearby Lagerstätte of Monteviale. Georgalis & Joyce (2017) further proposed that it is not possible to assess whether the Monte Bolca taxon pertains to *Trionyx* or some other genus and therefore they left the genus level determination as an open question by referring the generic name of "*Trionyx*" *capellinii* into quotation marks. We follow this opinion herein. See Tab. 2 for a summary.

OPHIDIANS

Snakes from Bolca are exceedingly rare when compared to other reptiles, but nevertheless, this scarce record includes some well-to-exceptionally preserved fossils. In fact, only three or four snake specimens are known from Bolca, the type specimens of *Archaeophis proavus* Massalongo, 1859, *Anomalophis bolcensis* (Massalongo, 1859), and *Coluber ombonii* de Zigno, 1889, plus a newly found, but still undescribed, skin remain that potentially pertains to a snake. Contrary to the rest of the reptile fauna from Bolca, only one snake specimen (the holotype of *Coluber ombonii*) was found in the Purga di Bolca site, whereas the specimens of *Archaeophis proavus* and *Anomalophis bolcensis* were found in Pesciara. Despite this limited material, the snake fauna from Bolca presents a drastically different taxonomic composition compared to any other Eocene locality from Europe. Indeed, all European Eocene localities are usually dominated by constrictor snakes (sensu Georgalis & Smith, 2020) in terrestrial environments (Georgalis et al., 2021b) and the giant snake *Palaeophis* Owen, 1841, in aquatic (including marine) ecosystems (Rage, 1983; Smith & Georgalis, 2022), the latter also being the case with the locality of Monte Duello (Georgalis et al., 2020a), nearby to (and slightly younger than) Bolca. To the contrary, Bolca ubiquitously lacks these groups and instead possesses the highly unique archaeophiines and anomalophiids.

Massalongo (1859) established a new genus, *Archaeophis* Massalongo, 1859, in order to accommodate his two new snake species from Bolca: the smaller form as *Ar. proavus* and the larger one as *Ar. bolcensis*. Ever since then, these two taxa formed quintessential components in ophidian palaeontological literature.

Archaeophis proavus was erected upon a small slab with an almost complete skeleton, including the skull, teeth and even skin impressions (Massalongo, 1859, pl. III; Janensch, 1906, pls 1-2; Fig. 18) that was found in the Pesciara's limestone (locality Agri Veronensis, in the Calcare Nummulitico). The specimen was originally housed in the collection of Count Ottavio di Canossa but was eventually purchased by the MNB in 1902 from the mineral company Krantz. It is still curated at MNB under the collection number MNB 1902.1357. The surprisingly high vertebral number of this species was already mentioned by Massalongo (1859), who counted 507 vertebrae. Massalongo (1859) also described the scales of the animal as possibly carinated. Some decades later, the German palaeontologist Werner Janensch revised the taxon, initially with a more preliminary work (Janensch, 1904) and later with a thorough, monumental documentation (Janensch, 1906). The complete redescription and figuring of the material by Janensch (1906) elucidated many aspects on the anatomy of *Ar. proavus*, offering valuable clues on its affinities. Janensch (1906) provided an ever higher vertebral count for *Ar. proavus*, mentioning 565 vertebrae. Contrary to Massalongo (1859), who envisaged this taxon as terrestrial, Janensch (1906) concluded that it was instead an aquatic animal. He further proposed important diagnostic features for *Ar. proavus* and felt that this taxon was distinct enough to propose a new family,

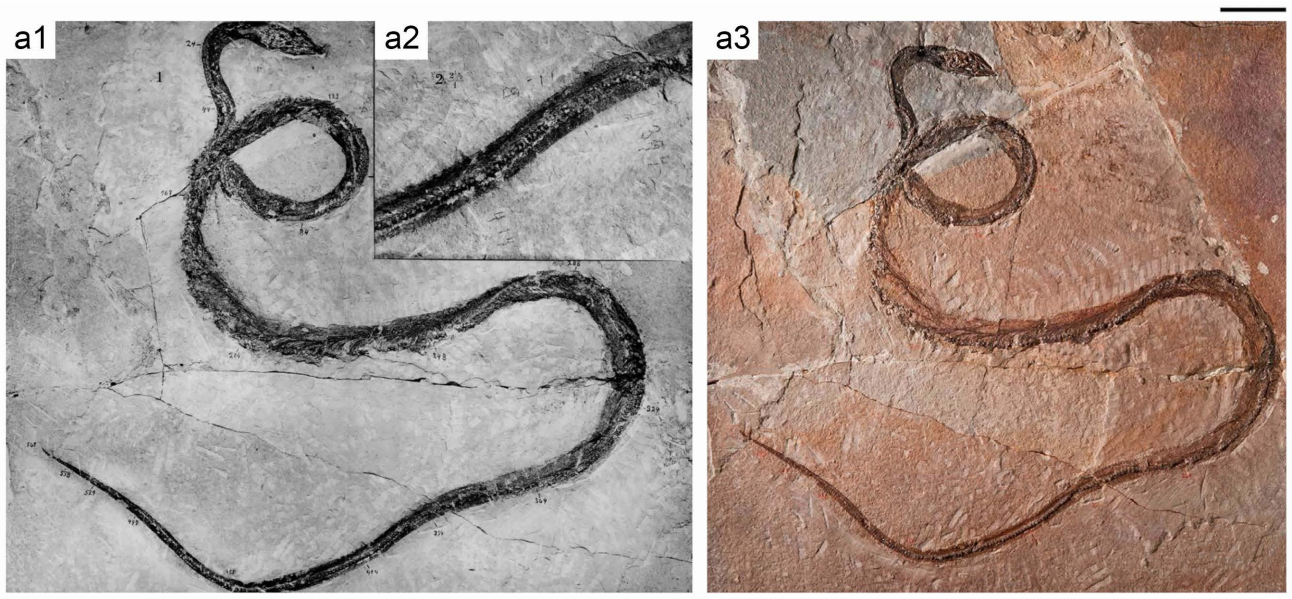

Fig. 18 - *Archaeophis proavus* Massalongo, 1859 (holotype, MNB 1902.1357). a1) Original photograph displaying the whole fossil and a detail of the posterior part of the vertebral column (a2) (modified from Janensch, 1906). a3) Current state of preservation (modified from Carnevale et al., 2014). Scale bar equals 5 cm. Figs (a1) and (a2) not to scale.

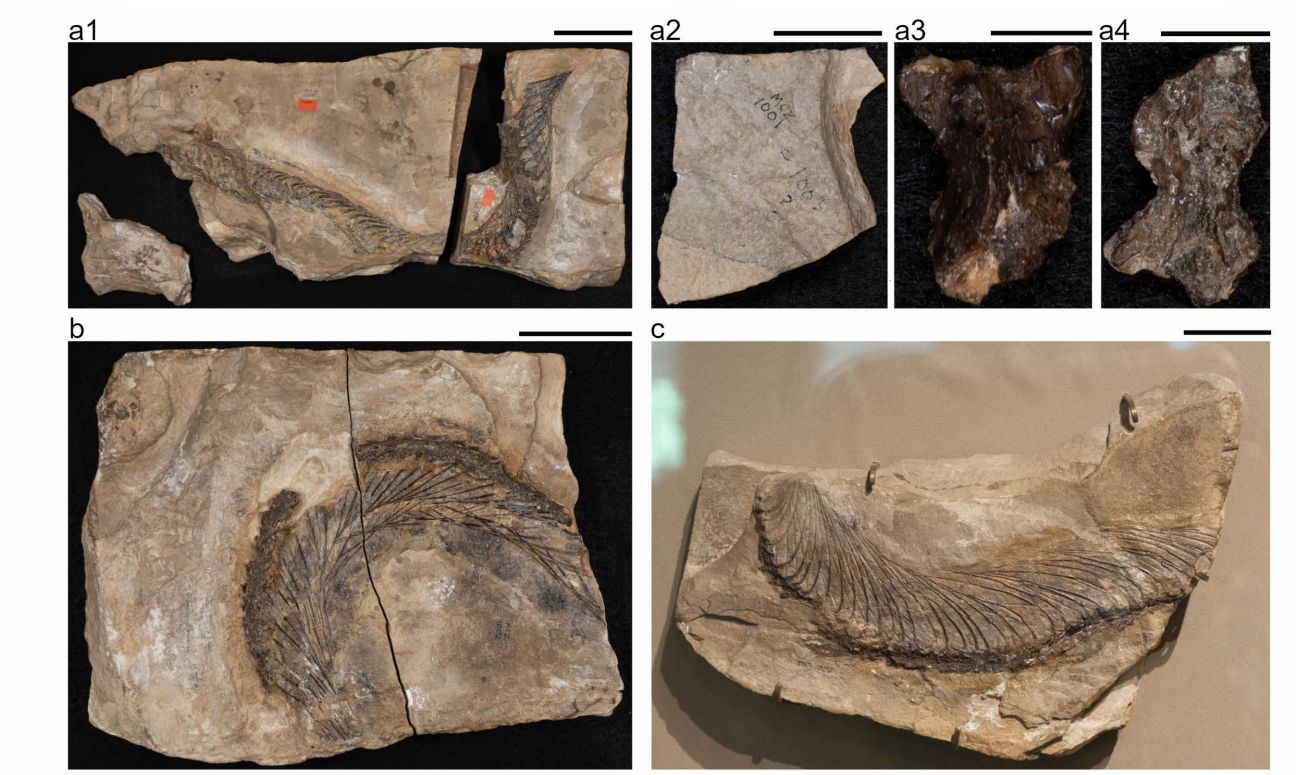

Fig. 19 - *Anomalophis bolcensis* (Massalongo, 1859), portions of skeleton (holotype, MCZ VPRA-1001, MCZ VPRA-1002, and MCZ VPRA-1003). a1) Portion of skeleton MCZ VPRA-1001. a2) Slab from MCZ VPRA-1001. a3-a4) Two isolated vertebrae from MCZ VPRA-1001. b) Portion of skeleton MCZ VPRA-1002. c) Portion of skeleton MCZ VPRA-1003. Scale bars in (a1), (b) and (c) equal 5 cm; scale bar in (a2) equals 2 cm; scale bars in (a3-a4) equal 0.5 cm. Copyrighted material of the Museum of Comparative Zoology, Harvard University, with permission.

Archaeophiidae (spelled as Archaeophidae in Janensch, 1906). Nopcsa (1923a, b) placed *Archaeophis* into his Cholophidia, along with certain Cretaceous hind-limbed snakes and the Paleogene palaeophiids, however, in his later works, the same author excluded *Archaeophis* from that group and instead placed it within alethinophidians (Nopcsa, 1925, 1928). McDowell & Bogert (1954) casted some doubt on the true serpent nature of the Italian taxon, suggesting instead that some anatomical features were indicative of a fish and not a snake. This misconception was later clarified by Auffenberg (1959), who attributed McDowell & Bogert's (1954) opinion to a misinterpretation of Janensch's (1906) drawing, and confirmed the ophidian status of *Ar. proavus*, while also removing *Ar. bolcensis* from *Archaeophis* and placing it in its own genus (see below). Tatarinov (1963, 1988) described a snake from the Eocene of Turkmenistan, which he referred to the Bolca genus (*Archaeophis turkmenicus* Tatarinov, 1963). The congeneric affinities of this Asian taxon with *Ar. bolcensis* have not been widely accepted and it is possible that the former belongs to another genus (Rage, 1984; Rage et al., 2003; Smith & Georgalis, 2022). Subsequently, *Archaeophis* was considered to represent a subfamily of Palaeophiidae (i.e., Archaeophiinae; Rage 1983, 1984; Rage et al., 2003). Still, however, there is no consensus on the alleged palaeophiid affinities of *Archaeophis* (Georgalis et al., 2020a, 2021a; Smith & Georgalis, 2022). In the most recent review of Paleogene snakes by Smith & Georgalis (2022), *Archaeophis proavus* was treated as a valid species, with the authors also highlighting its 565 vertebrae, a record number among all snakes, extinct and extant. The holotype specimen of *Archaeophis proavus* has been reprepared and is currently under revision (Schwarz, pers. comm. to SMS, 2022).

The second snake species presented in Massalongo (1859), *Anomalophis bolcensis* (originally placed in *Archaeophis*) was also found in the Pesciara's limestone (locality Agri Veronensis, in the Calcare Nummulitico) and is as well-known exclusively by its type material. This type material (originally belonging to the Museo dei Marchesi di Canossa in Verona but later purchased by MCZ) consists of three slabs (MCZ VPRA-1001, Fig. 19a1; MCZ VPRA-1002, Fig. 19b; MCZ VPRA-1003, Fig. 19c and Fig. S12) with several vertebrae and ribs, pertaining to the middle and posterior portions of a skeleton of a single individual. In addition, there are two scattered vertebrae that were successfully freed by the matrix of the specimen MCZ 1001 (Auffenberg, 1959), allowing for a description (Fig. 19a3-a4). These three slabs represent the holotype (they were treated as syntypes by Rage, 1984) and only known specimen of *An. bolcensis*; casts of these slabs exist in MGP-PD and MCSNV. The taxon was discussed by Janensch (1906) and McDowell & Bogert (1954), but it was the revision of Auffenberg (1959) which shed important light on its anatomy. Indeed, Auffenberg (1959) highlighted diagnostic features that he felt were distinct enough from other snakes, and therefore, not only he established the new genus *Anomalophis* to accommodate it, but also a new family, Anomalophiidae (spelled as Anomalophidae

Fig. 20 - Serpentes indet. Holotype (MGP-PD 8360) of *Coluber ombonii* de Zigno, 1890. Scale bar equals 2 cm.

in Auffenberg, 1959). Auffenberg (1959) further stated that the body of *An. bolcensis* was more laterally compressed compared to *Ar. proavus*, in a similar fashion as some extant hydrophiines, confirming its marine ecology (as was also suggested previously by Janensch, 1906). Still though, the exact affinities of *Anomalophis* and Anomalophiidae with other snakes remained a mystery and a matter of taxonomical controversy, with different topologies and opinions proposed in the next decades (Hoffstetter, 1962; Kuhn, 1963; Rage, 1983, 1984, 1987; McDowell, 1987; Rieppel, 1988; Rage & Werner, 1999; Smith, 2013; Wallach et al., 2014). More recently, Zaher et al. (2019) considered *Anomalophis* a member of Colubriformes, based on the shape and extent of the neural spine, but its exact placement within that group could not be precisely determined. Similarly, caenophidian affinities for *Anomalophis* were also entertained by Smith & Georgalis (2022).

The third snake specimen from Bolca was described a few decades later. De Zigno (1890) described a new species, *Coluber ombonii*, upon an imprint of the posterior portion of a snake skeleton (MGP-PD 8360), measuring 55 mm of length (de Zigno, 1890, fig. 9; Fig. 20 and Fig. S13), that was found in the Purga di Bolca (note that Rage, 1988 reported it as originating from Pesciara). De Zigno (1890) referred the specimen to the wastebasket genus *Coluber* Linnaeus, 1758. De Zigno (1890) pointed out the shape of the vertebrae, which are almost as wide as long and apparently devoid of a hypapophysis, with the former feature, as stated by Rage (1988), being unusual for a colubrid snake. De Zigno (1890) also noticed some (unspecified) similarity with *Ar. proavus* described a few decades earlier. *Coluber ombonii* was later also accepted as a species of *Coluber* by Kuhn (1963). Subsequently, however, Rage (1974, 1984) casted doubt on the colubrid affinities of this taxon and the same author eventually treated *C. ombonii* to be a nomen dubium (Rage, 1988). In any case, it is obvious that the taxon does not pertain to the genus *Coluber*, which is a New World colubrid genus in modern taxonomies (e.g., Wallach et al., 2014). C*oluber ombonii* is currently under revision and its redescription with the aid of μ-CT scanning will eventually shed light on its validity and affinities.

Finally, more than a century after the last snake find from Bolca, Roberto Zorzin recovered in 2005 in the Pesciara a fossil skin-print IG.VR. 69589, which could belong to a snake (Zorzin et al., 2017). See Tab. 2 for a summary.

CONCLUSIONS

The fossil record of reptiles from the Bolca area includes multiple specimens, pertaining to 13 crocodilians, 21 turtles, and four snakes, coming from three main localities: Purga di Bolca (all turtles, most of the crocodilians, and one snake), Pesciara (two snakes), and Spilecco (one crocodilian).

The first crocodilian was described in 1865, the first turtle in 1889, and the first snake in 1859. Of the 13 crocodilian specimens, six were formally described, four were mentioned or briefly described, and three are still awaiting formal description. Of these, nine were originally referred to *Crocodilus vicetinus* Lioy, 1865, two to *Crocodilus bolcensis* Sacco, 1895 and four have been referred to indeterminate crocodilians. Two specimens are now referred to *Asiatosuchus*, two to *Boverisucus*, and one to *Hassiacosuchus*. For all of these, the species level identification is still debated. One specimen surely does not come from Bolca, and two specimens are currently lost.

Of the several turtle specimens, five are referred to the pleurodiran *Neochelys capellinii* (de Zigno, 1889) and all the rest to the soft-shelled turtle "*Trionyx*" *capellinii* Negri, 1892. One specimen is currently lost among those described by Sacco (1894).

Only three confirmed ophidian specimens are known from Bolca and they all represent type material. *Coluber ombonii* de Zigno, 1890 is the only one found in Purga di Bolca, whereas *Archaeophis proavus* Massalongo, 1859 and *Anomalophis bolcensis* (Massalongo, 1859) were found in Pesciara. A possible fourth snake specimen has been cited (but not figured) in the literature but has still to be described. The snake fauna of Bolca is drastically different than other coeval assemblages and consists of some of the very few representatives of Anomalophiidae and Archaeophiinae.

SUPPLEMENTARY ONLINE MATERIAL

Supplementary data of this work are available on the BSPI website at: https://www.paleoitalia.it/bollettino-spi/bspi-vol-612/

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