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A shark turns into an undetermined crocodylian: the case of *Acanthias bicarinatus* Sismonda, 1849

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KEY WORDS - Crocodylia, Italy, Miocene, palaeobiogeography, Torino Hill.

ABSTRACT - The holotype and only specimen referred to the Early Miocene shark Acanthias bicarinatus *Sismonda, 1849 is housed in the collections of the Museo di Geologia e Paleontologia dell'Università degli Studi di Torino and was collected from the serpentinite sandstone of the middle-late Burdigalian Termofourà Formation of the Torino Hill. The specimen, formerly interpreted as a fragment of a squalid dorsal-fin spine, is reinterpreted herein as an isolated crocodylian tooth. The validity of the species* Acanthias bicarinatus *is therefore reconsidered and referred to as a nomen dubium. The tooth, replaced while the crocodylian was alive, was deposited in a near-shore marine environment at a time when modern crocodylian lineages were already widespread along the northern sector of the Mediterranean area.*

INTRODUCTION

Since the beginning of the XIX century, several fossil reptiles were described as fishes due to the limited knowledge and understanding of the vertebrate osteology at that time. Some well-known examples include the early descriptions of extinct marine reptiles, such as ichthyosaurs and plesiosaurs, which were sometimes initially misinterpreted as fishes because of their depositional environment and superficial similarities to those organisms due to their aquatic lifestyle (e.g., Home, 1814; Evans, 2010). As the field of Palaeontology evolved, gaining a better understanding of osteology and comparative anatomy, scientists were able to correctly identify and classify these marine reptiles.

In the present contribution, we focus on the revision of the holotype of the putative shark *Acanthias bicarinatus* Sismonda, 1849 from the Miocene serpentinite sandstone ("arenaria serpentinosa") of the Torino Hill (Piedmont, NW Italy). Sismonda (1849) provided the first description of the specimen, an isolated tooth now housed in the collections of the Museo di Geologia e Paleontologia dell'Università degli Studi di Torino (MGPT) and described it as a dorsal-fin spine of a new dogfish species. He assigned the specimen to a new species of the genus *Acanthias* Risso, 1827, with the new name *A. bicarinatus*. A common practice followed by many other 19th century authors was to refer many fossil and recent shark species to the waste basket genus *Acanthias*. The species was later mentioned by Sismonda himself in a table summarising the fossil fish and crustaceans of Piedmont (1861) and subsequently by De Alessandri (1897), who commented that the spine identified by Sismonda as *Acanthias bicarinata* (sic), because of its truncated conical shape and the compactness of its tissue, could represent a "saurian" tooth rather than a fish spine. However, the Database of Fossil Elasmobranch Teeth (Pollerspöck & Straube, 2023) includes *Acanthias bicarinatus* Sismonda, 1849 with the synonym of *Squalus bicarinatus* (Sismonda, 1849). The aim of this contribution is to update the knowledge of this taxon and clarify its validity.

SYSTEMATIC PALAEONTOLOGY

Order Crocodylomorpha Hay, 1930
Sub-order Crocodylia Gmelin, 1789
Crocodylia incertae sedis

1849 *Acanthias bicarinatus* Sismonda, p. 28-29, Tav. 2, figs 42-43.
1861 *Acanthias bicarinatus* Sismonda 1849 - Sismonda, p. 22.
1897 *Acanthias bicarinata* Sismonda 1849 - De Alessandri, p. 29.

Material - MGPT-PU 11096: an isolated tooth (Fig. 1).

Locality and Age - Termofourà Formation, Torino Hill (Piedmont, NW Italy); middle-late Burdigalian, Miocene (see Festa et al., 2009; Zunino & Pavia, 2009). Sismonda (1849, p. 29) indicated that the fossil has a Miocene age and was collected in the serpentinite sandstone ("arenaria serpentinosa") of the Torino Hill. This description fits very well with the serpentinite sandstone layers and conglomerates intercalated in the silty marls and siltstones of the Termofourà Formation, which dates back to the middle-late Burdigalian (Festa et al., 2009; Zunino & Pavia, 2009). These re-sedimented terrigenous levels are well known since the early XIX century for their very abundant palaeontological content, mostly represented

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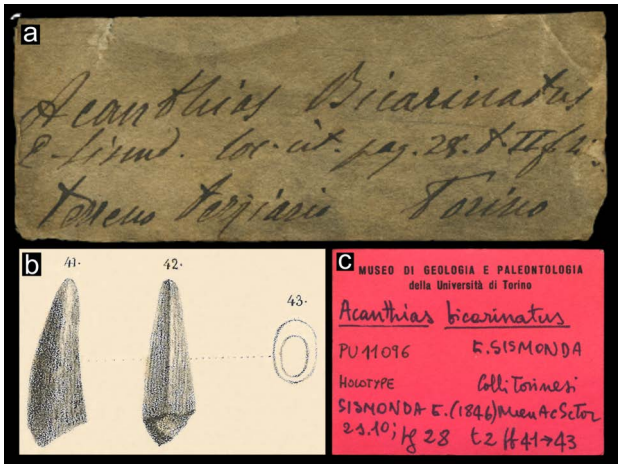

Fig. 1 - (color online) Collection labels and illustration of *Acanthias bicarinatus* Sismonda, 1849 (MGPT-PU 11096). a) Original label by Sismonda. b) Illustration of MGPT-PU 11096 by Sismonda (1849, tav. 2, figs 42-43). c) Current label of MGPT-PU 11096.

by marine molluscs, which have been extensively investigated for more than a century (see Zunino & Pavia, 2009 and references therein).

Description - The tooth MGPT-PU 11096 (Fig. 2) has the shape of an elongated, slightly curved cone with a blunt apex and a concave base. It is 22.0 mm high and nearly circular at the base, showing a diameter varying from 7.7 to 7.9 mm. The apex is clearly worn because it is devoid of the external enamel layer (Fig. 2a3). The base is deeply concave, and its rim is irregular due to inadequate preservation. It is not clear if the asymmetry in the thickness of the wall of the base is only due to the preservation. The tooth is characterized by two moderately developed, not serrated mesiodistal carinae (Fig. 2a5). The carinae show, on both sides, regularly spaced depressions that do not give rise to serrations (Fig. 2a6-a7). They reach the base of the tooth that as a consequence does not preserve the neck and the root but only the crown. The lingual surface is slightly less broad than the labial one (Fig. 2a4). In distal and medial view, the outline of the lingual surface shows a shallow angle at around two thirds of its dorsal height, making the apex point mediodorsally (Fig. 2a1-a2). Both these surfaces are rather smooth and devoid of evident ridges but host very fine wrinkles.

DISCUSSION

Comparative remarks and status of the name Acanthias bicarinatus *Sismonda, 1849*

Shark dorsal-fin spines are specialized dermal denticles that lie on the anterior edge of the dorsal fins of the extant families Heterodontidae, Squalidae and Echinorhinidae, and the extint ctenacanth and hybodont sharks (e.g., Maisey, 1979; Cappetta, 2012). Sismonda (1849) erroneously referred MGPT-PU 11096 to an anterior dorsal-fin spine of the squalid genus *Acanthias* Risso, 1827 (currently considered as junior synonym of *Squalus* Linnaeus, 1758), on the basis of very few uninformative characters, including the presence of longitudinal furrows along the entire crown, which appears to be massive with a little pronounced curvature, although also admitting its tooth-like appearance. The presence of the two mesiodistal carinae was used as the main feature to diagnose a new dogfish shark species, *A. bicarinatus.*

The gross morphology and the external features of the dorsal-fin spines of dogfish sharks of the family Squalidae (Fig. 3) have been described in detail by Maisey (1979). The morphological analysis of MGPT-PU 11096 has revealed the presence of a number of characters that strongly argues against its attribution to a squalid dorsal-fin spine, including: 1) a sharp and stubby trunk not very elongated (shark fin spines are instead sharp, elongated in the vertical axis and have a graceful curvature; Maisey, 1979), 2) a nearly circular transverse cross section (fin spine are subtriangular or pear-shaped in cross section, with a posterior concave depression producing a sulcus

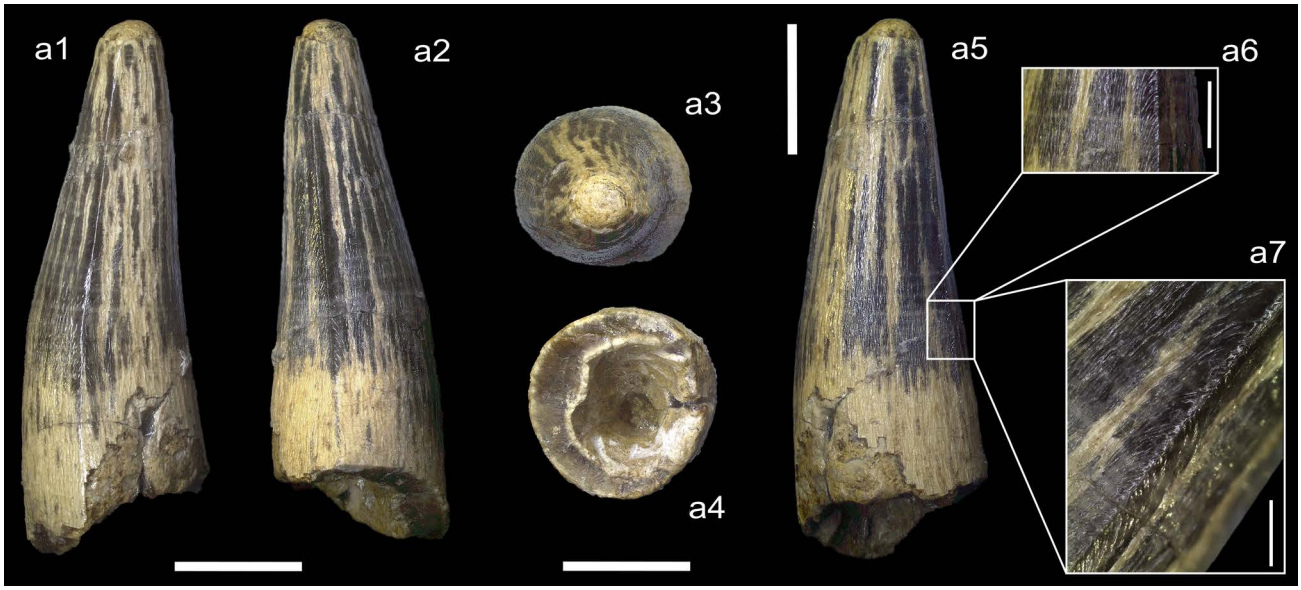

Fig. 2 - (color online) Alternative illustrations of MGPT-PU 11096 in mesial (a1), distal (a2), apical (a3), ventral (a4) and linguo-distal (a5) views. a6-7) Close-ups of the distal carina. Scale bars equal to 5 mm for a1-5, 2 mm for a6, and 1 mm for a7.

Fig. 3 - (color online) Isolated dorsal-fin spine of *Squalus* sp. (NRM-PZ P16000) from the Priabonian of La Meseta Formation, Seymour Island, Antarctica (see Kriwet et al., 2016) in left lateral (a1), right lateral (a2), anterior (a3) and basal (a4) views. Scale bars equal to 5 mm. Photos courtesy of Jürgen Kriwet (University of Vienna).

which in life is occupied by a glandular epithelium; Fig. 3a4; e.g., Maisey, 1979; Cappetta, 2012), and 3) an enamel cap with very fine wrinkles covering the whole surface (the enameloid cap of shark fin spines may be smooth anteriorly, or may possess a restricted development of enamelled ribs anteriorly and posterolaterally; Maisey, 1979; Cappetta, 2012). In this context, there are no reasons to recognize MGPT-PU 11096 as a dogfish shark dorsal-fin spine.

Regarding the attribution to a crocodylian genus, no unquestionable diagnostic characters are known from crocodylian teeth only, making the identification of MGPT-PU 11096 at the genus level unreliable. Exceptions exist but represent at best attributions to familial taxonomic level (e.g., planocraniids; see Brochu, 2013) or single taxa (as *Eosuchus lerichei* Dollo, 1907; Delfino et al., 2005), based on distinct peculiar morphologies very different from those exhibited by the specimen described herein. MGPT-PU 11096 instead closely resembles isolated crocodylian teeth reported from the Sardinian localities of Laerru (Sassari Province) (fig. 2C in Zoboli et al., 2019) or Bingia Fargeri (Cagliari Province) (Del Vecchio, 1921; fig. 2K-L in Zoboli et al., 2019). Considering the age of the specimen and coeval crocodylian taxa diversity, MGPT-PU 11096 can only be reasonably referred to an undetermined crocodylian. The name *Acanthias bicarinatus* should therefore be considered as a nomen dubium because there is no available evidence to permit the recognition of a species, and the option of considering it a nomen vanum, on the basis of the absence of diagnostic characters, is discarded because this name is not included in the International Code of Zoological Nomenclature (Mones, 1989; Sanchiz, 1998; ICZN, 1999).

A lost tooth

Contra Sismonda (1849), the holotype MGPT-PU 11096 of *Acanthias bicarinatus* is here interpreted as a replaced crocodylian tooth. In crocodylians, the replacement tooth absorbs the root of the preceding element during growth, until the isolated crown is shed due to the lack of structural attachment in the alveolus (Poole, 1961). This process may explain the thinner lingual wall: as the replacement tooth grows in a dorsolateral direction, the lingual surface of the replaced tooth would be absorbed first. Typically, the teeth lack a root, with a strict cross section at the base of the crown (Frey & Monninger, 2010). The simultaneous occurrence of latter features in MGPT-PU 11096 supports our interpretation of a crocodylian tooth, replaced while the animal was still living.

Italian fossil reptile misidentifications

The case of reptile remains misidentified and designed as type of a taxon referred to another vertebrate group, as the one documented herein of a crocodylian tooth formerly referred to as the type of a shark species, is much rarer in the history of Italian palaeontology than the opposite case, a fish or a mammal remain misidentified and designed as the type of reptile taxon. Worth of being briefly mentioned here are the following three cases that have been pending for several decades or even for much more than a century. The real identity of the snake *Paleopython sardus* Portis, 1901 from the Middle Miocene of Monte Albu (Sardinia) has been disentangled thanks to the retrieval of the type specimen MDLCA 14402 in the collections of the Museo Sardo di Geologia e Paleontologia "Domenico Lovisato" (Cagliari) and its identification as an undetermined acanthomorph fish premaxilla (Delfino et al., 2014). The type material of the new crocodylian genus and species *Rhytisodon tuberculatus* Costa, 1854 from the Miocene of the Lecce area is currently lost, but, thanks to the description and the figures published by the author, it has been later referred to an undetermined squalodontid cetacean mammal (Fordyce & De Muizon, 2001; Delfino, 2002). The cervical vertebra that has been originally referred to the new crocodylian genus and species *Eridanosaurus brambillae* Balsamo-Crivelli (1864) from the Quaternary gravels of the Po River (between Portalbera and Arena Po) is also currently lost, but a cast has been detected at the beginning of this century in the Collezioni di Geologia of the Museo Giovanni Capellini in Bologna (MGGC 8862; formerly misidentified as *Lariosaurus balsami* Curioni, 1847; Delfino, 2002). As already proposed by Boni (1943) it is a rhinoceros cervical vertebra and not a crocodylian.

Faunal context of Miocene crocodylians in Italy

European crocodylian faunas included several genera in the Miocene, such as crocodylids, tomistomines and the basal alligatoroid *Diplocynodon* (Rio & Mannion, 2021). The Italian Peninsula did not differ from the rest of the continent, as the crocodylian record from Miocene localities is represented by an extensive number of disarticulated material and isolated teeth referred to either crocodylids or tomistomines (Del Vecchio, 1921; Kotsakis et al., 2004; Zoboli et al., 2019). While the presence of tomistomines in the Mediterranean arch of Europe is known since the Paleogene (Piras et al., 2007; Nicholl et al., 2020), the biogeographic radiation of crocodylids (namely *Crocodylus* spp.) is restricted to the Late Miocene and subsequent periods: the earliest fossil occurrences in Europe date back to the Messinian (Delfino et al., 2007; Delfino & Rook, 2008; Brochu & Storrs, 2012). The endemic European *Diplocynodon*, conversely, became extinct in the Middle Miocene, as attested by the fossils recovered from the Early to Middle Miocene of European mainland and Iberian Peninsula (Martin & Gross, 2011; Aráez et al., 2017; Lujàn et al., 2019; Chroust et al., 2021;

see Massonne & Böhme, 2022, for the correct age of the putative Late Pliocene *Diplocynodon* from Bulgaria). In that context, the reattribution of MGPT-PU 11096 to a crocodylian adds further evidence to the widespread presence of the group in the Miocene of Italy. Isolated crocodylian teeth were already known in the Italian Miocene outcrops thanks to the descriptive works of Del Vecchio (1921), Colombero et al. (2017) (both reporting material from Piedmont), Delfino & Ragazzini (2010) and Villa et al. (2021). The tooth originally described by Sismonda (1849) is however the first and only known evidence of a crocodylian remain in the marine sediments of the Termofourà Formation of the Torino Hill, which is otherwise largely dominated by marine molluscs (Zunino & Pavia, 2009; and references therein).

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REFERENCES

Aráez J.L.D., Delfino M., Luján A.H., Fortuny J., Bernardini F. & Alba D.M. (2017). New remains of *Diplocynodon* (Crocodylia: Diplocynodontidae) from the early Miocene of the Iberian Peninsula. *Comptes Rendus Palevol*, 16: 12-26.

Balsamo-Crivelli G. (1864). Di una vertebra fossile di rettile trovata nelle ghiaje del Po. *Atti Società Italiana Scienze Naturali*, 7: 201-212.

Boni A. (1943). Sull'"*Eridanosaurus brambillae*" Bals. Criv. *Rendiconti della Reale Accademia d'Italia. Classe di Scienze fisiche matematiche e naturali*, 4: 1-10.

Brochu C.A. (2013). Phylogenetic relationships of Palaeogene ziphodont eusuchians and the status of *Pristichampsus* Gervais, 1853. *Earth and Environmental Science Transactions of the Royal Society of Edinburgh*, 103: 521-550.

Brochu C.A. & Storrs G.W. (2012). A giant crocodile from the Plio-Pleistocene of Kenya, the phylogenetic relationships of Neogene African crocodylines, and the antiquity of *Crocodylus* in Africa. *Journal of Vertebrate Paleontology*, 32: 587-602.

Cappetta H. (2012). Handbook of paleoichthyology – Chondrichthyes – Mesozoic and Cenozoic elasmobranchii: Teeth. 512 pp. Verlag Dr. Friedrich Pfeil, Munich, Germany.

Chroust M., Mazuch M., Ivanov M., Ekrt B. & Luján A.H. (2021). First remains of *Diplocynodon* cf. *ratelii* from the early Miocene sites of Ahníkov (Most Basin, Czech Republic). *Bulletin of Geosciences*, 96: 123-138.

Colombero S., Alba D.M., D'Amico C., Delfino M., Esu D., Giuntelli P., Harzhauser M., Mazza P.P.A., Mosca M., Neubauer T.A., Pavia G., Pavia M., Villa A. & Carnevale G. (2017). Late Messinian mollusks and vertebrates from Moncucco Torinese, north-western Italy. Paleoecological and paleoclimatological implications. *Palaeontologia Electronica*, 20.1.10A: 1-66.

Costa O.G. (1854). Paleontologia del Regno di Napoli. Parte III [Paleontology of the Kingdom of Naples. Part III]. *Atti dell'Accademia Pontaniana*, 8: 1-192.

Curioni G. (1847). Cenni sopra un nuovo saurio fossile dei monti di Perledo sul Lario e sul terreno che lo racchiude. *Giornale del Regio Istituto Lombardo di Scienze e Lettere*, 8: 166-167.

De Alessandri G. (1897). La pietra da cantoni di Rosignano e di Vignale (Basso Monferrato). Studi stratigrafici e paleontologici. *Museo Civico di Storia Naturale di Milano*, 6: 1-98.

Del Vecchio C. (1921). Su alcuni denti di Tomistoma (Crocodilia) dell'Oligocene di Visone presso Acqui. *Atti della Società Italiana di Scienze Naturali*, LX: 419-431.

Delfino M. (2002). Erpetofaune Italiane del Neogene e del Quaternario. 382 pp. Ph.D. Thesis, Università degli Studi di Modena e Reggio Emilia, Italy.

Delfino M. & Ragazzini S. (2010). Fossil amphibians and reptiles from Abruzzi and Molise: old data and new evidences. *In* Di Tizio L., Di Cerbo A.R., Di Francesco N. & Cameli A. (eds), Atti VIII Congresso Nazionale Societas Herpetologica Italica, Chieti, Settembre 22-26, 2010. Ianieri Edizioni, Pescara: 515-519.

Delfino M. & Rook L. (2008). African crocodylians in the Late Neogene of Europe. A revision of *Crocodylus bambolii* Ristori, 1890. *Journal of Paleontology*, 82: 336-343.

Delfino M., Piras P. & Smith T. (2005). Anatomy and phylogeny of the gavialoid crocodylian *Eosuchus lerichei* from the Paleocene of Europe. *Acta Palaeontologica Polonica*, 50: 565-580.

Delfino M., Böhme M. & Rook L. (2007). First European evidence for transcontinental dispersal of *Crocodylus* (late Neogene of southern Italy). *Zoological Journal of the Linnean Society*, 149: 293-307.

Delfino M., Zoboli D., Carnevale G. & Pillola G.L. (2014). The rediscovered holotype of *Palaeopython sardus* Portis, 1901 from the Miocene of Sardinia belongs to a fish, not a snake. *Bollettino della Società Paleontologica Italiana*, 53: 89-92.

Dollo L. (1907). Nouvelle note sur les reptiles de l'Eocène inférieur de la Belgique et des régions voisines (*Eosuchus lerichei* et *Eosphargis gigas*). *Bulletin de la Société belge de Géologie, Paleontologie et Hydrologie*, 21: 81-85.

Evans M. (2010). The roles played by museums, collections, and collectors in the early history of reptile palaeontology. *In* Moody R., Buffetaut E., Naish D. & Martill D.M. (eds), Dinosaurs and Other Extinct Saurians: A Historical Perspective. *Geological Society of London, Special Publications*, 343: 1-3.

Festa A., Boano P., Irace A., Lucchesi S., Forno M.G., Dela Pierre F., Fioraso G. & Piana F. (2009). Note illustrative alla Carta Geologica d'Italia alla scala 1:50000. Foglio 156 Torino Est. 144 pp. ISPRA, Istituto Superiore per la Protezione e la Ricerca Ambientale, Roma.

Fordyce R.E. & De Muizon C. (2001). Evolutionary history of the cetaceans: a review. *Secondary Adaptations of Tetrapods to Life in the Water*. Verlag Dr. Friedrich Pfeil, Munchen: 169-233.

Frey E. & Monninger S. (2010). Lost in action - the isolated crocodilian teeth from Enspel and their interpretive value. *Palaeobiodiversity and Palaeoenvironments*, 90: 65-81.

Gmelin J.F. (1789). Caroli a Linné, systema naturae per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Editio decima tertia, Tomus 1, Pars 3. 1516 pp. G.E. Beer, Lipsiae.

Hay O.P. (1930). Second bibliography and catalogue of fossil Vertebrata of North America. *Carnegie Institution of Washington Publication*, 390: 1-1077.

Home E. (1814). Some Account of the fossil Remains of an Animal more nearly allied to Fishes than any of the other Classes of Animals. *Philosophical Transactions of the Royal Society of London*, 104: 571-577.

ICZN (1999). International Code of Zoological Nomenclature. Fourth Edition [Incorporating Declaration 44, Amendment of Article 74.7.3, with Effect from 31 December 1999 and the Amendment O]. London: International Trust for Zoological Nomenclature.

Kotsakis T., Delfino M. & Piras P. (2004). Italian Cenozoic crocodilians: taxa, timing and biogeographic implications.

Palaeogeography, Palaeoclimatology, Palaeoecology, 210: 67-87.

Kriwet J., Engelbrecht A., Mörs T., Reguero M. & Pfaff C. (2016). Ultimate Eocene (Priabonian) Chondrichthyans (Holocephali, Elasmobranchii) of Antarctica. *Journal of Vertebrate Paleontology*, 36: e1160911.

Linnaeus C. (1758). Systema naturæ per regna tria naturæ, secundum classes, ordines, genera, species, cum characteribus, differentiis, synonymis, locis. Tomus I. Editio decima, reformata. 824 pp. Laurentii Salvii, Holmia.

Luján À.H., Chroust M., Čerňanský A., Fortuny J., Mazuch M. & Ivanov M. (2019). First record of *Diplocynodon ratelii* Pomel, 1847 from the early Miocene site of Tušimice (Most Basin, Northwest Bohemia, Czech Republic). *Comptes Rendus Palevol*, 18: 877-889.

Maisey J.G. (1979). Fin spine morphogenesis in squalid and heterodontid sharks. *Zoological Journal of the Linnean Society*, 66: 161-183.

Martin J.E. & Gross M. (2011). Taxonomic clarification of *Diplocynodon* Pomel, 1847 (Crocodilia) from the Miocene of Styria, Austria. *Neues Jahrbuch für Geologie und Paläontologie*, *Abhandlungen*, 261: 177-193.

Massonne T. & Böhme M. (2022). Re-evaluation of the morphology and phylogeny of *Diplocynodon levantinicum* Huene & Nikoloff, 1963 and the stratigraphic age of the West Maritsa coal field (Upper Thrace Basin, Bulgaria). *PeerJ*, 10: e14167.

Mones A. (1989). *Nomen dubium* vs. *nomen vanum*. *Journal of Vertebrate Paleontology*, 9: 232-234.

Nicholl C.S.C., Rio J.P., Mannion P.D. & Delfino M. (2020). A re-examination of the anatomy and systematics of the tomistomine crocodylians from the Miocene of Italy and Malta. *Journal of Systematic Palaeontology*, 18: 1853-1889.

Piras P., Delfino M., Del Favero L. & Kotsakis T. (2007). Phylogenetic position of the crocodylian *Megadontosuchus arduini* (de Zigno, 1880) and tomistomine palaeobiogeography. *Acta Palaeontologica Polonica*, 52: 315-328.

Pollerspöck J. & Straube N. (2023). Database of Fossil Elasmobranch Teeth. *Squalus bicarinatus* (Sismonda, 1849). www.shark-references.com. Version 11/2023.

Poole D.G. (1961). Notes on tooth replacement in the Nile crocodile. *Proceedings of the Zoological Society of London*, 136: 131e140.

Portis A. (1901). Il *Palaeopython sardus* Port. Nuovo pitonide del Miocene medio della Sardegna. *Bollettino della Società Geologica Italiana*, 20: 247-253.

Rio J.P. & Mannion P.D. (2021). Phylogenetic analysis of a new morphological dataset elucidates the evolutionary history of Crocodylia and resolves the long-standing gharial problem. *PeerJ*, 9: e12094.

Risso A. (1827). Histoire naturelle des principales productions de l'Europe Méridionale et particulièrement de celles des environs de Nice et des Alpes Maritimes. Vol. 3. Mammifères. Oiseaux. Poissons. XVI + 480 pp. F.G. Levrault, Paris.

Sanchiz B. (1998). Handbuch der Paläoherpetologie – Encyclopedia of Paleoherpetology. Part 4: Salientia. XII + 275 pp. Verlag Friederich Pfeil, München.

Sismonda E. (1849). Descrizione dei pesci e dei crostacei fossili nel Piemonte. *Memorie della Reale Accademia della Scienze di Torino*, 10: 1-88.

Sismonda E. (1861). Appendice alla descrizione dei pesci e dei crostacei fossili nel Piemonte. *Memorie della Regia Accademia delle Scienze di Torino*, 19: 1-24.

Villa M., Carnevale G., Pavia M., Rook L., Sami M., Szyndlar Z. & Delfino M. (2021). An overview on the late Miocene vertebrates from the fissure fillings of Monticino Quarry (Brisighella, Italy), with new data on non-mammalian taxa. *Rivista Italiana di Paleontologia e Stratigrafia*, 127: 297-354.

Zoboli D., Sanciu L., Pillola G.L. & Delfino M. (2019). An overview of the crocodylian fossil record from Sardinia (Italy). *Annales de Paléontologie*, 105: 123-137.

Zunino M. & Pavia G. (2009). Lower to Middle Miocene mollusc assemblages from the Torino Hills (NW Italy): synthesis of new data and chronostratigraphical arrangement. *Rivista Italiana di Paleontologia e Stratigrafia*, 115: 349-370.

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