



**Another thermophilic "Miocene survivor"
from the Italian Pliocene:**

**A geologically young occurrence
of the pelagic eagle ray *Aetobatus*
in the Euro-Mediterranean region**

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Abstract: *Aetobatus* (Myliobatiformes: Aetobatidae) is a living genus of eagle rays that occurs in shallow-marine, tropical and subtropical environments of the Atlantic, Pacific, and Indian Oceans. Nowadays, *Aetobatus* does not inhabit the cool- to warm-temperate European and Mediterranean waters, though it is known from this broad region by virtue of several fossil teeth ranging chronostratigraphically from the lower Palaeogene to the upper Neogene. The present paper reports on a fossil aetobatid tooth discovered in mid-Pliocene (upper Zanclean to lower Piacenzian, 3.82-3.19 Ma) marine deposits exposed in the vicinities of Certaldo (Tuscany, Italy) and identified as belonging to †*Aetobatus* cf. *cappettai*. This specimen comprises the youngest occurrence of *Aetobatus* along the coasts of mainland Europe; furthermore, together with previous finds from roughly coeval deposits of Mallorca (Balearic Islands, Spain), it represents the most recent record of this genus in the whole Euro-Mediterranean region. In light of the environmental preferences of extant *Aetobatus* spp., our discovery suggests palaeoenvironmental conditions favourable to the persistence of tropical/subtropical taxa of "Miocene survivors" along the Pliocene coasts of Tuscany. In addition, it raises the question of whether or not the Messinian Salinity Crisis really resulted in the complete collapse of the Mediterranean marine biota and in the subsequent recolonisation of the Mediterranean Basin from the adjoining Atlantic waters and/or scattered marginal intrabasinal refugia at the beginning of the Pliocene. The possibility of *Aetobatus* recolonising the Mediterranean Sea through the Suez Canal in the near future is discussed.

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**Key-words:**

- Aetobatidae;
- climate change;
- conservation palaeobiology;
- Myliobatiformes;
- palaeobiogeography;
- palaeoecology;
- palaeoichthyology;
- Tuscany

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Résumé : Un autre "survivant miocène" thermophile du Pliocène italien : Une occurrence précoce de l'aigle de mer pélagique *Aetobatus* dans la région euro-méditerranéenne.-

Le genre *Aetobatus* (Myliobatiformes : Aetobatidae) est un genre actuel de raies aigles vivant dans les environnements tropicaux et subtropicaux marins peu profonds des océans Atlantique, Pacifique et Indien. De nos jours, *Aetobatus* n'habite plus les eaux tempérées de l'Europe et de la Méditerranée, bien qu'il soit connu dans cette vaste région par le recensement de plusieurs dents fossiles dont la distribution chronostratigraphique s'étale du Paléogène inférieur au Néogène supérieur. Le présent article décrit une dent fossile d'Aetobatidae, identifiée comme appartenant à †*Aetobatus* cf. *cappettai*, découverte dans les dépôts marins du Pliocène moyen (3,82-3,19 Ma, Zancéen supérieur - Piacenzien inférieur) affleurant dans les environs de Certaldo (Toscane, Italie). Ce spécimen représente l'occurrence la plus récente d'*Aetobatus* le long des côtes d'Europe continentale ; en outre, avec les découvertes antérieures de gisements plus ou moins contemporains de Majorque (Baléares, Espagne), il représente l'enregistrement fossile le plus récent de ce genre dans toute la région euro-méditerranéenne. Compte tenu des préférences environnementales des espèces actuelles d'*Aetobatus*, notre découverte évoque des conditions paléo-environnementales favorables à la persistance de taxons "survivants miocènes" à affinités tropicales/subtropicales le long des côtes du Pliocène de la Toscane. En outre, cela soulève la question de savoir si la crise de salinité messinienne a abouti ou non à l'effondrement complet du biote marin méditerranéen et à la recolonisation ultérieure de ce bassin à partir des eaux atlantiques voisines et/ou des refuges intra-bassinaux marginaux dispersés au début du Pliocène. La possibilité de recoloniser la mer Méditerranée à travers le canal de Suez dans un futur proche est enfin discutée pour ce qui concerne le genre *Aetobatus*.

Mots-clefs :

- Aetobatidae ;
- changement climatique ;
- paléobiologie de la conservation ;
- Myliobatiformes ;
- paléo-biogéographie ;
- paléoécologie ;
- paléo-ichtyologie ;
- Toscane

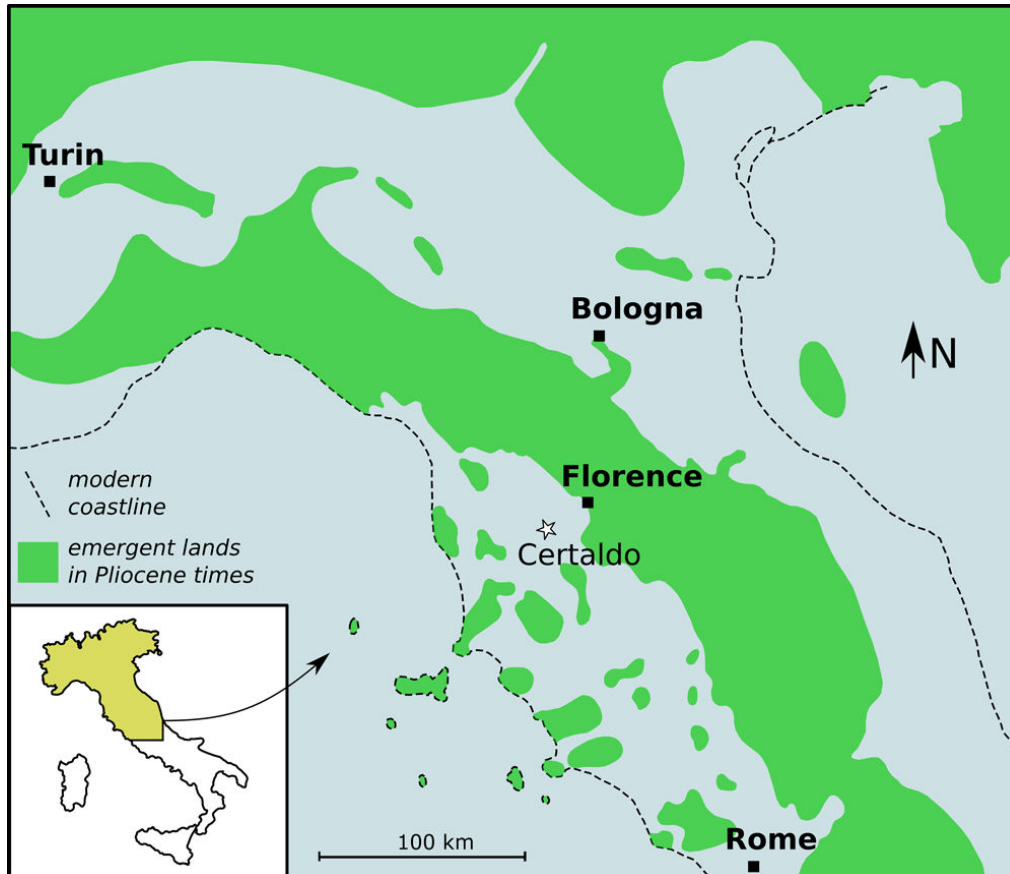
1. Introduction

Among extant stingrays (Myliobatiformes: Myliobatoidei), those assigned to the pelagic eagle ray genus *Aetobatus* occur in shallow tropical and subtropical waters of the Atlantic, Pacific, and Indian Oceans (WEIGMANN, 2016; LAST *et al.*, 2016). *Aetobatus* mainly differs from the allied genera *Aetomylaeus* and *Myliobatis* in having a deeply notched internasal flap, spiracles that are placed on the dorsolateral region of the head, pectoral fins that join the head at the level of the eyes, broadly rounded free rear tips of the pectoral fins, and a single median dental file on each jaw at all growth stages (CAPAPÉ & QUIGNARD, 1975; COMPAGNO & LAST, 1999; CAPPETTA, 2012; WHITE & MOORE, 2013; WHITE, 2014; WHITE & NAYLOR, 2016). Long regarded as belonging to the eagle ray family Myliobatidae, *Aetobatus* is now placed in its own family, the currently monotypic Aetobatidae (WHITE & NAYLOR, 2016).

The Pliocene transitional and marine deposits of Tuscany (central Italy) have been the setting

of remarkable discoveries of vertebrate fossils for several centuries (COLLARETA *et al.*, 2020b, and references therein). Vertebrate finds from these Tuscan Pliocene successions include marine mammals (both odontocete and mysticete cetaceans as well as sea cows and rarer pinnipeds), sea turtles, bony and cartilaginous fishes, and even terrestrial forms (*e.g.*, DOMINICI *et al.*, 2018, and references therein). In spite of a long history of palaeontological research, discoveries of new taxa or somewhat "exotic" vertebrate specimens are still relatively frequent from the Tuscan Pliocene marine and paralic sediments (*e.g.*, SPADINI & MANGANELLI, 2015; COLLARETA *et al.*, 2017a, 2017b, 2018, 2020a, 2020c, 2020d, 2021; BIANUCCI *et al.*, 2019; MANGANELLI & SPADINI, 2019).

Here, we report on the discovery of a fossil eagle ray tooth attributed to *Aetobatus* from mid-Pliocene marine deposits of Tuscany and briefly discuss its relevance with respect to palaeoecology, palaeobiogeography and conservation palaeobiology.



◀ **Figure 1:** Schematic palaeogeographic map of central and northern Italy in Pliocene times, showing the location of the site where the aetobatid tooth described herein was found. Palaeogeographical reconstruction redrawn and modified after VAI (1989).

2. Geological and palaeontological framework

The myliobatoid fossil tooth described herein was discovered by two of the authors (S.C. and A.D.C.) at an outcrop in the vicinity of Certaldo village (Florence Province, Tuscany), in the Valdelsa Basin (Fig. 1). The Universal Transverse Mercator (=UTM) geographic coordinates of the finding site are: 32N 668021 4826620 (note that this outcrop is located ca. 4 km east of that investigated by COLLARETA *et al.*, 2020d, 2021, and therein indicated as the "Certaldo quarry").

The succession cropping out at this locality belongs to the S3 Synthem recognised in the upper Miocene to lower Pleistocene Valdelsa succession by BENVENUTI *et al.* (2014). S3 is a large-scale depositional sequence that mostly consists of an alternation of sands and mudstones, interpreted as deltaic, overlain by shelf mudstones (BENVENUTI *et al.*, 2014). According to BENVENUTI *et al.* (2014), the planktonic foraminiferal assemblages from the S3 mudstones belong to Mediterranean Pliocene (MPI) zone 4 of CITA (1975), whose bounding bioevents have been calibrated to 3.98 and 3.19 Ma (VIOLANTI, 2012). Furthermore, the calcareous nannofossil

assemblages from the same strata are indicative of Calcareous Nannofossil Plio-Quaternary (CNPL) zone 4 of the more recent Neogene biozonation scheme of BACKMAN *et al.* (2012), whose bounding bioevents have been calibrated to 3.82 and 2.76 Ma (BENVENUTI *et al.*, 2014). In light of these considerations, the deposits cropping out at the finding site are referable to the 3.82-3.19 Ma interval, which is consistent with a late Zanclean to early Piacenzian time span.

At the study site, strata belonging to S3 crop out along an artificial cliff. These deposits consist of interbedded sands and clayey sands. Vertebrate fossils are concentrated in a few decimeter-thick horizons that feature abundant remains of bivalves (including veneroids, ostreids and pectinids), gastropods, echinids and barnacles. Besides the aetobatid specimen described herein, vertebrate fossils from the discovery site include several teeth and dermal elements of bony and cartilaginous fishes, including *Carcharhinus brachyurus*, *Carcharhinus cf. falciformis*, *Carcharias taurus*, †*Cosmopolitodus cf. plicatilis*, *Dasyatidae* indet., †*Megascyliorhinus mio-caenicus*, *Myliobatis* sp., *Rhizoprionodon* sp., *Sparidae* indet., *Squatina* sp. and *Trichiuridae* indet. (Fig. 2), as well as some indeterminate otoliths.



3. Systematics

ELASMOBRANCHII BONAPARTE, 1838

BATOMORPHII CAPPETTA, 1980

MYLIOBATIFORMES COMPAGNO, 1973

MYLIOBATOIDEI COMPAGNO, 1973

AETOBATIDAE AGASSIZ, 1858

***Aetobatus* BLAINVILLE, 1816**

†*Aetobatus cappettai*

ANTUNES & BALBINO, 2006

†*Aetobatus* cf. *cappettai*

(Fig. 3)

Referred material. One incomplete upper tooth, currently stored at Badia a Settimo (Scandicci, Italy), in the permanent exhibition of "Gruppo AVIS Mineralogia e Paleontologia Scandicci" (=GAMPS), under accession number GAMPS-00967.

Occurrence. Mid-Pliocene (3.82-3.19 Ma) marine deposits exposed in the vicinities of Certaldo, Tuscany, central Italy (see Section 2 above).

Remarks. GAMPS-00967 measures 15.2 mm in maximum preserved width, 4.3 mm in maximum preserved length, and 5.7 mm in maximum preserved height. Based on comparisons with fossil and Recent teeth of *Aetobatus*, it is here identified as comprising the leftmost third or quarter of an upper tooth, including the well-preserved left lateral margin. The occlusal (Fig. 3.d) and lingual (Fig. 3.a) faces of GAMPS-00967 are mostly pristine, whereas the basal (Fig. 3.c) and labial (Fig. 3.b) faces are locally damaged and the latter is slightly abraded. The well-preserved lingual crown face of this specimen is vertical and gently ornamented by means of weak costulae. These costulae are short, irregular and subhorizontal in the vicinity of the inner ledge for tooth interlocking that marks the crown base, whereas they appear as longer and more erect close to the occlusal face (Fig. 3.a). Such an ornamentation pattern strongly recalls that observed on the labial crown face of upper teeth of extant members of *Aetobatus* (HERMAN *et al.*, 2000, Pl. 26; A.C., personal observation on uncatalogued materials kept at Università di Pisa) while differing from the stronger ornamentation (consisting of pustules, pits or wrinkles) that is found on the lingual crown face of most members of the allied myliobatoid genera *Myliobatis*, *Aetomylaeus* (including species that have previously been assigned to *Pteromylaeus*; WHITE, 2014), and *Rhinoptera* (HERMAN *et al.*, 2000; PURDY *et al.*, 2001; CAPPETTA, 2012; HOVESTADT & HOVESTADT-EULER, 2013).

ANTUNES & BALBINO (2006, p. 44) diagnosed †*Aetobatus cappettai* as follows:

"Upper teeth narrow, long, slightly convex; crown low, thickened in the central part; lateral extremities prominent; root higher than crown, decreasing in height from the centre to the edges; blades on the labial face are almost smooth, lacking marked grooves; grooves on the lingual face very marked, they persist almost to the crown; basal surface of the root with narrow, deep grooves as well as blades, all of the same width; lower teeth arched and labially convex, extremely flat; basal angle ca 30°, with very oblique basal face; root high, thinning from the central part to the lateral edges; blades wide and separated by deep, wide grooves."

The same authors (*op. cit.*, p. 44) characterised the upper teeth of †*A. cappettai* in these terms:

"The upper teeth are narrow, long and slightly convex. The crown is low and thicker in its central part. Lateral extremities are prominent; in occlusal view, the lateral extremities constitute a lateral border that is not affected by abrasion. The vertical, lingual face of the crown is separated from the root by a thin edge. The root is thicker than the crown; the thickness regularly decreases from the central part towards the borders (in lateral view). The basal surface presents alternating (narrow and shallow) grooves and blades. Width is the same in all blades, whose basal surface is flat. The tooth's labio-lingual section is nearly straight."

These descriptive notes are also largely applicable to the morphology of the incomplete tooth GAMPS-00967. In particular, the latter resembles the upper teeth of †*A. cappettai* in displaying: i) a gentle posterior bending (Fig. 3.c-d); ii) an apico-basally low crown (Fig. 3.a-b); iii) a distinct thickening of the crown close to the lateral margin of the tooth (Fig. 3.a-b); iv) a lateral border of the crown that is well-defined, not significantly abraded, nor laterally pointed (Fig. 3.c-d); v) a root whose apicobasal thickness decreases progressively towards the lateral margin of the tooth (Fig. 3.a-b). Strong similarities are observed particularly between GAMPS-00967 and the specimens depicted by ANTUNES & BALBINO (2006) in their figures 1 and 2, the latter featuring the holotype of †*A. cappettai* [we note here that the identifications of the lingual and labial sides provided by ANTUNES and BALBINO (2006) for these teeth may not be correct].

In light of the above considerations, GAMPS-00967 is here assigned to the genus *Aetobatus*. Owing to the incomplete nature of the specimen and the scarcity of species-diagnostic characters in the teeth of myliobatoids in general (HOVESTADT & HOVESTADT-EULER, 2013) and aetobatids in particular (BOR *et al.*, 2012), it is here placed in open nomenclature as belonging to †*Aetobatus* cf. *cappettai*.

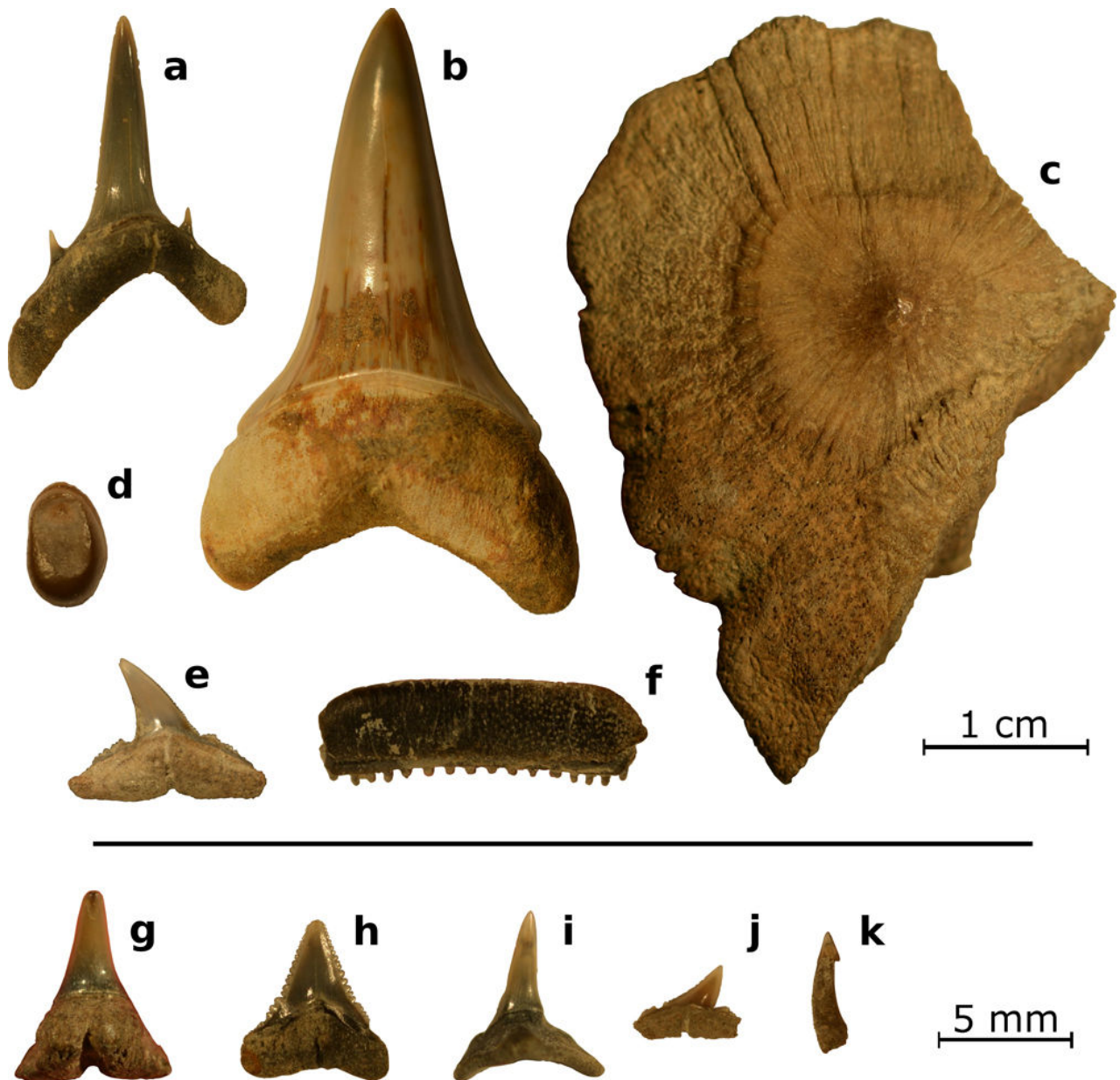


Figure 2: Selection of fossil fish remains (dental and dermal elements) associated with the aetobatid specimen GAMPS-00967 from the Pliocene locality of Certaldo (Tuscany, central Italy). **a**, *Carcharias taurus*, **b**, †*Cosmopolitodus* cf. *plicatilis*, **c**, Dasyatidae indet., **d**, Sparidae indet., **e**, *Carcharhinus brachyurus*, **f**, *Myliobatis* sp., **g**, †*Megascyliorhinus miocaenicus*, **h**, *Carcharhinus* cf. *falciformis*, **i**, *Squatina* sp., **j**, *Rhizoprionodon* sp., **k**, Trichiuridae sp. Specimens a, b, e, g, h, i and j are depicted in lingual view, specimens c, d, and f are depicted in apical view, specimen k is depicted in profile view. All the figured specimens are currently stored at the GAMPS.

Recently, REINECKE *et al.* (2011), BOR *et al.* (2012), CAPPETTA (2012) and FIALHO *et al.* (2019) have confirmed the validity of †*A. cappettai*. However, a deeper understanding of the alpha-diversity of living aetobatids, as well as a better knowledge of their dental morphology and variability, is nonetheless needed for reassessing the taxonomic status of several nominal species that are based on isolated fossil teeth whose morphology is closely comparable to the general dental design of extant *Aetobatus*, including †*A. cappettai*

(HOVESTADT & HOVESTADT-EULER, 2013).

HOVESTADT and HOVESTADT-EULER (2013) highlighted several morphological similarities between the teeth of †*A. cappettai* and those of juveniles of extant *A. narinari*. GAMPS-00967 is alike in this regard. A juvenile status for GAMPS-00967 might be supported by its relatively small size, distinct from the larger dimensions of adult teeth of extant members of *Aetobatus* (A.C., personal observation on uncatalogued materials kept at Università di Pisa).

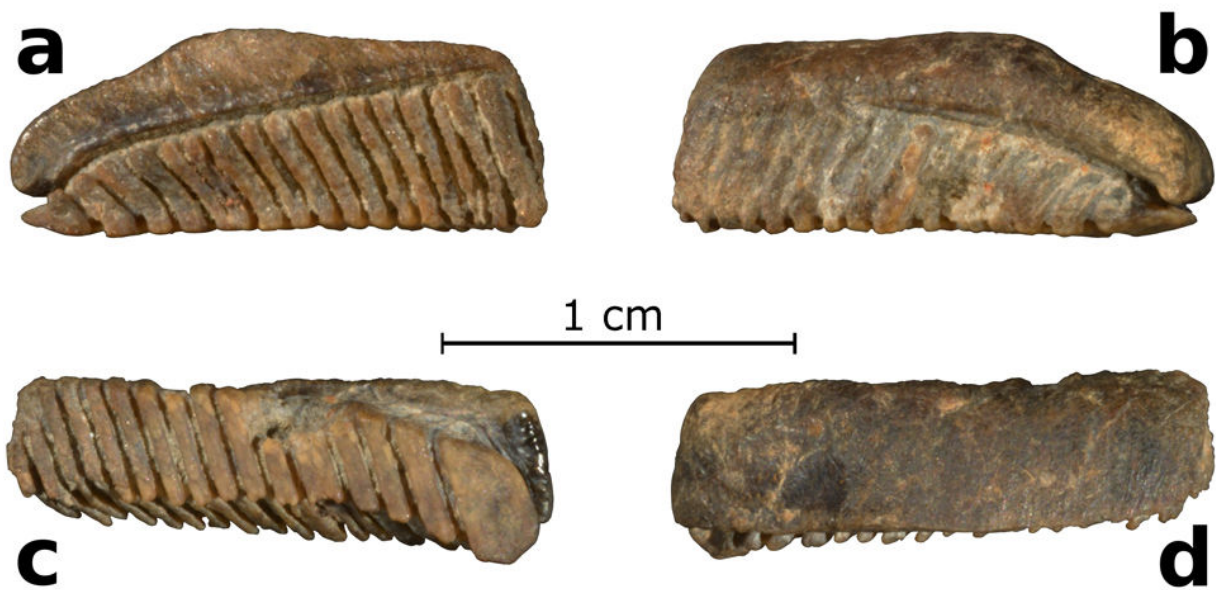


Figure 3: †*Aetobatus* cf. *cappettai* (GAMPS-00967), incomplete upper tooth from the Pliocene locality of Certaldo (Tuscany, central Italy). **a**, lingual view; **b**, labial view; **c**, basal view; **d**, apical view.

4. General discussion

The eagle rays of the genus *Aetobatus* do not currently inhabit the cool- to warm-temperate European and Mediterranean waters (SERENA, 2005) (Fig. 4). However, *Aetobatus* has a long and relatively conspicuous palaeontological record in the Euro-Mediterranean region, its earliest fossils including occurrences from early and middle Eocene deposits of England, Belgium, Morocco and Egypt (proto-Mediterranean area) (MARRAMÀ *et al.*, 2018, and references therein). During the Miocene, this genus was widespread in the North Sea Basin (*e.g.*, BOR *et al.*, 2012), western Paratethys (*e.g.*, HÖLTKE *et al.*, 2020), central Paratethys (*e.g.*, VILLAFANA *et al.*, 2020), Atlantic western Europe (*e.g.*, JONET, 1968), and Mediterranean Sea (*e.g.*, MENESINI, 1969), though it declined in the European high latitudes starting from the middle Miocene, possibly because of decreasing seawater temperatures (REINECKE *et al.*, 2011). As regards the upper Neogene fossil record of Europe and the Mediterranean Basin, *Aetobatus* is a rare genus, reported only from the Tortonian of continental Spain (MARÍN, 1992), the Tortonian-Messinian of The Netherlands (MOLLEN, 2010), the Messinian of Portugal (ANTUNES & BALBINO, 2006), the basal Pliocene of Libya (PAWELLEK *et al.*, 2012), the Pliocene of continental Spain (MORA MOROTE, 1997), and the upper Pliocene of the Spanish island of Mallorca (MAS, 2010) (Fig. 4). The Libyan Pliocene occurrence, from near Al Khums and identified in open nomenclature as belonging to *Aetobatus* sp., is found in a transgressive lag on top of an erosional unconformity that is regarded as representing the Messinian event (PAWELLEK *et al.*, 2012). The shark and ray assemblage studied by PAWELLEK *et al.* (2012) is

unique in featuring a high abundance of tropical elements (including the lemon shark *Negaprion* and the snaggletooth shark *Hemipristis*, neither of which is known from any other Plio-Quaternary site of the Mediterranean Basin) as well as the coexistence of the large- to mega-toothed mackerel sharks †*Carcharocles*, *Carcharodon* and †*Cosmopolitodus* (PAWELLEK *et al.*, 2012). On the other hand, it is worth noting that the taxonomic composition of this Libyan fossil fauna is reminiscent of the purportedly Pliocene Angolan shark and ray assemblages studied by ANTUNES (1977, 1978). Teeth of †*Aetobatus* cf. *arcuatus* (AGASSIZ, 1843) were described by MORA MOROTE (1997) from the Pliocene of Guardamar del Segura, near Alicante, southern Spain. These teeth are part of a diverse elasmobranch assemblage (see MORA MOROTE, 1996) that likely originated in the ~5.3–4.19 Ma time span, corresponding to the lower to mid-Zanclean (see Discussion in COLLARETA *et al.*, 2020d). A third record of *Aetobatus* from the Mediterranean Pliocene was provided by MAS (2010) and consists of some teeth of *Aetobatus* sp. from calcarenite deposits regarded as representative of the basal portion of the Sant Jordi Formation exposed in Mallorca, Balearic Islands, Spain (*e.g.*, CAPÓ & GARCIA, 2019). A Piacenzian depositional age has been inferred for this unit on the sole basis of the detection of Zanclean microfossils in the underlying Son Mir Formation, whose upper strata pass gradually into the lowermost horizons of the Sant Jordi Formation (POMAR *et al.*, 1983). This means that a Piacenzian age estimate is at best tentative for the elasmobranch assemblage studied by MAS (2010). Given also that the fossil-bearing deposits directly overlie finer sediments assigned to the Zanclean (MAS, 2010), the finds of *Aetobatus* from the Pliocene of Mallorca are



possibly not younger than early Piacenzian, and as such, indistinguishable in age from the better chronostratigraphically constrained Italian fossil studied herein. In light of these considerations, GAMPS-00967 comprises the youngest occurrence of *Aetobatus* along the coast of mainland Europe as well as in the central Mediterranean Basin. Furthermore, together with the Mallorcan finds described by MAS (2010), it represents the most recent record of this genus in the whole Euro-Mediterranean region. Differing from previous palaeofaunistic analyses (e.g., MARSILI, 2008), our find corroborates the presence of the family Aetobatidae in the Mediterranean Sea during the Pliocene, thus improving our knowledge of the late Neogene Mediterranean biodiversity.

At present, *Aetobatus* accounts for five or six living species that are distributed in the warm waters of the Atlantic, Pacific and Indian Oceans (WHITE *et al.*, 2013; LAST *et al.*, 2016; WEIGMANN, 2016; SALES *et al.*, 2019). In the Atlantic Ocean (including the Caribbean and Gulf of Mexico), *Aetobatus* is represented by the spotted eagle ray *Aetobatus narinari* and, possibly, by *Aetobatus latirostris* (a species whose validity is currently regarded as dubious; WHITE & NAYLOR, 2016; SALES *et al.*, 2019). Along the eastern Atlantic coast, *A. narinari* does not extend northwards of Cabo Verde and Senegal, ca. 19°N (KYNE *et al.*, 2006; SALES *et al.*, 2019). Interestingly, south of 20–22°N, the coast of western Africa is currently home to some mollusc species [e.g., *Gastrana lacunosa* (CHEMNITZ, 1782) and *Tugonia anatina* (GMELIN, 1791)] that inhabited the Mediterranean Sea until ca. 3 Ma, when they were extirpated from this basin following a major interval of climate cooling (MONEGATTI & RAFFI, 2001). Considering the thermophilic nature of *Aetobatus*, its presence in the S3 deposits of Certaldo indicates tropical or subtropical affinities for the north-western Mediterranean Sea during the mid-Pliocene, ca. 3.8–3.2 Ma. This is also suggested by the recent discovery of rostral spines of the knifetooth sawfish *Anoxypristis* from shelf mudstones, belonging to the same synthem, exposed at the nearby locality of Tegoliccio (COLLARETA *et al.*, 2017a). Recent palaeothermometric estimates for the Mediterranean Sea during the Zanclean and early Piacenzian support surface seawater temperatures ca. 2–3°C higher than today (e.g., PRISTA *et al.*, 2015; RAGAINI *et al.*, 2019; COLETTI *et al.*, 2021), that is, in line with the environmental preferences of the extant species *A. narinari* (FROESE & PAULY, 2019). The eventual extirpation of *Aetobatus* from the Mediterranean Sea is likely to have occurred during some late Pliocene or early Pleistocene episode of climate change, as hypothesised for other thermophilic marine vertebrates (including *Anoxypristis*) that inhabited the Mediterranean Basin during the first part of the Pliocene and disappeared afterward (e.g., SORBI *et al.*, 2012; COLLARETA *et al.*, 2017a).

Among elasmobranchs, and along with pristids, the aetobatids represent some of the most recently (re)discovered lineages of "Miocene survivors" in the Mediterranean Pliocene. Similar cases have also been pointed out among thermophilic invertebrates that were thought to have disappeared from the Mediterranean Sea at the end of the Miocene (e.g., the lingulid brachiopods; DI CENCIO *et al.*, 2021). This raises the question of whether or not the latest Miocene Messinian Salinity Crisis did in fact result in the collapse of the Mediterranean marine biota and in the subsequent recolonisation of the Mediterranean Basin from the adjoining Atlantic waters and/or scattered marginal intrabasinal refugia at the beginning of the Pliocene. Research focused on the bony fish record has recently questioned the reliability of such a reconstruction, revealing instead a remarkable degree of ecological homogeneity throughout the Messinian Salinity Crisis, with a nearly continuous presence of marine stenohaline and euryhaline taxa (CARNEVALE *et al.*, 2006, 2008, 2018, 2019). Although data on the cartilaginous fishes are more fragmentary, and very few data exist regarding the Mediterranean elasmobranch fauna during the Messinian (e.g., ARAMBOURG, 1927), major discontinuities are unlikely to emerge between the late Miocene and early to mid-Pliocene shark and ray assemblages of the Mediterranean Sea. More research and new sampling campaigns at stratigraphically constrained, elasmobranch-rich horizons from the upper Miocene and lower Pliocene of the Mediterranean region are definitely needed to shed further light on this palaeontological *vexata quaestio*.

As a possible consequence of current anthropogenic global warming, many thermophilic marine organisms are expanding their range towards the higher latitudes of both hemispheres (e.g., CARLTON, 2000). This might ultimately lead pelagic eagle rays to re-enter the Mediterranean Basin. Indeed, the occurrence of *A. narinari* off remote islands such as Bermuda have led to speculation that this fish is capable of extensive journeys (BIGELOW & SCHROEDER, 1953), and the extant white-spotted eagle rays living along the western coast of Florida are known to move over large distances along shallow-marine, nearshore migratory corridors to meet their environmental (mostly thermal) preferences (DEGROOT *et al.*, 2021). Rather than via the Gibraltar Strait, which is quite far from the northernmost border of the modern range of *Aetobatus* along the western coast of Africa, the pelagic eagle rays might re-enter the Mediterranean Basin from the Red Sea (which is inhabited by various aetobatid species; KYNE *et al.*, 2006, 2016; WHITE, 2006), through the Suez Canal, in the frame of the so-called "Ilessepsian migration" (e.g., POR, 1978) that also accounts for the occurrence of the dasytid myliobatoid *Himantura uarnak* in the eastern Mediterranean Sea (BAŞUSTA *et al.*, 1998). By displaying values

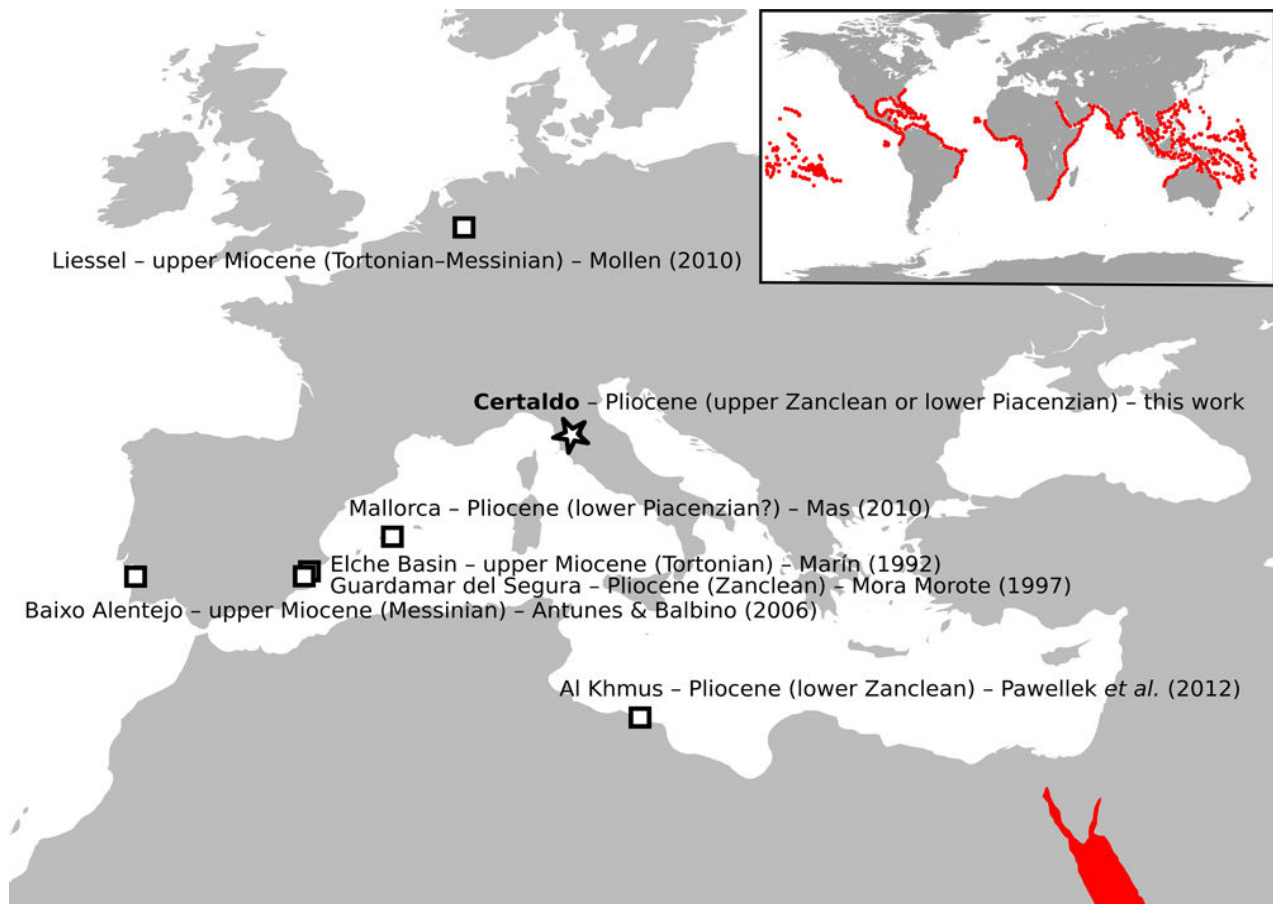


Figure 4: Distribution of fossil remains of *Aetobatus* in the upper Miocene and Pliocene of the Euro-Mediterranean region. Red shading indicates the modern range of *Aetobatus* in the Red Sea (main map) and worldwide (top right panel) as reported by KYNE *et al.* (2006). See the main text for further information.

of seawater temperature that are likely even slightly higher than those associated with the northwestern Mediterranean during the early and mid-Pliocene (LANGER *et al.*, 2012; COLETTI *et al.*, 2021), the present-day eastern Mediterranean would indeed prove climatically suitable for the dispersal of *Aetobatus*. However, most living elasmobranchs are increasingly imperilled due to overfishing, habitat loss, and other typologies of human-induced pressure, and *Aetobatus* is no exception in this respect (SALES *et al.*, 2019), its worldwide population being currently estimated as declining (KYNE *et al.*, 2006, 2016; WHITE, 2006). Considering also that several elasmobranch fisheries of the Red Sea are at present unsustainable (SPAET & BERUMEN, 2015), a recolonisation of the Mediterranean Sea by the pelagic eagle rays is here regarded as possible but not very likely.

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Bibliographic references

- AGASSIZ L. (1833-1843).- Recherches sur les poissons fossiles, vol. 3.- Petitpierre, Neuchâtel, 392 p.
- AGASSIZ L. (1858).- [A new species of skate from the Sandwich islands].- *Proceedings of the Boston Society of Natural History*, vol. 6, p. 385.
- ANTUNES M.T. (1977).- Late Neogene fish faunas from Angola, their age and significance.- *Journal of the Palaeontological Society of India*, Lucknow, vol. 20, p. 224-229.
- ANTUNES M.T. (1978).- Faunes ichthyologiques du Néogène supérieur d'Angola, leur âge, remarques sur le Pliocène marin en Afrique australe.- *Ciências da Terra (UNL)*, Lisbon, vol. 4, p. 59-90.
- ANTUNES M.T. & BALBINO A.C. (2006).- Latest Miocene myliobatids (Batoidei, Selachii) from the Alvalade Basin, Portugal.- *Cainozoic Research*, Leiden, vol. 4, p. 41-49.
- ARAMBOURG C. (1927).- Les poissons fossiles d'Oran.- *Matériaux pour la Carte Géologique de l'Algérie (1re série)*, Paléontologie (sér. 1), Alger, vol. 6, 298 p.
- BACKMAN J., RAFFI I., RIO D., FORNACIARI E. & PÄLIKE H. (2012).- Biozonation and biochronology of Miocene through Pleistocene calcareous nannofossils from low and middle latitudes.-



- Newsletters on Stratigraphy*, Stuttgart, vol. 45, p. 221-244.
- BAŞUSTA N., ERDEM U. & KURLU M. (1998).- Two new fish records for the Turkish seas: Round stingray *Taeniura grabata* and skate stingray *Himantura uarnak* (Dasyatidae).- *Israel Journal of Zoology*, Tel Aviv, vol. 44, p. 65-66.
- BENVENUTI M., DEL CONTE S., SCARSELLI N. & DOMINICI S. (2014).- Hinterland basin development and infilling through tectonic and eustatic processes: Latest Messinian-Gelasian Valdelsa Basin, northern Apennines, Italy.- *Basin Research*, vol. 26, p. 387-402.
- BIANUCCI G., PESCI F., COLLARETA A. & TINELLI C. (2019).- A new Monodontidae (Cetacea, Delphinoidea) from the lower Pliocene of Italy supports a warm-water origin for narwhals and white whales.- *Journal of Vertebrate Paleontology*, vol. 39, article #e1645148.
- BIGELOW H.B. & SCHROEDER W.C. (1953).- Sawfishes, guitarfishes, skates and rays. Part 2. Fisheries of the Western North Atlantic.- *Memoirs of the Sears Memorial Foundation for Marine Research*, vol. 1, 514 p.
- BLAINVILLE H.M.D. de (1816).- Prodrome d'une nouvelle distribution systématique du règne animal.- *Bulletin de la Société Philomathique de Paris*, vol. 8, p. 105-112, 121-124.
- BONAPARTE C.L.J.L. (1838).- Selachorum tabula analytica.- *Nuovi Annali delle Scienze Naturali*, Bologna, vol. 1, p. 195-214.
- BOR T., REINECKE T. & VERSCHUEREN S. (2012).- Miocene Chondrichthyes from Winterswijk-Miste, The Netherlands.- *Palaeontos*, vol. 21, 136 p.
- CAPAPÉ C. & QUIGNARD J.P. (1975).- Contribution à la systématique et à la biologie de *Pteromylaeus bovinus* (GEOFFROY SAINT-HILAIRE, 1817), (Pisces, Myliobatidae) des côtes tunisiennes.- *Bulletin du Muséum National d'Histoire Naturelle de Paris, Zoologie* (sér. 3), no. 338, p. 1329-1347.
- CAPÓ A. & GARCIA C. (2019).- Basin filling evolution of the central basins of Mallorca since the Pliocene.- *Basin Research*, vol. 31, p. 948-966.
- CAPPETTA H. (1980).- Les séliaciens du Crétacé supérieur du Liban. II. Batoïdes.- *Palaeontographica Abteilung A, Paläozoologie-Stratigraphie*, Stuttgart, vol. 168, p. 149-229.
- CAPPETTA H. (2012).- Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii. Teeth. In: SCHULTZE H.P. (ed.), *Handbook of Paleichthyology*, vol. 3E.- Dr. Pfeil Verlag, Munich, 512 p.
- CARLTON J.T. (2000).- Global change and biological invasions in the oceans. In: MOONEY H.A. & HOBBS R.J. (eds.), *Invasive Species in a Changing World*.- Island Press, Covelo, p. 31-53.
- CARNEVALE G., CAPUTO D. & LANDINI W. (2006).- Late Miocene fish otoliths from the Colombacci Formation (Northern Apennines, Italy): Implications for the Messinian 'Lago-mare' event.- *Geological Journal*, London, vol. 41, p. 537-555.
- CARNEVALE G., DELA PIERRE F., NATALICCHIO M. & LANDINI W. (2018).- Fossil marine fishes and the 'Lago Mare' event: Has the Mediterranean ever transformed into a brackish lake?- *Newsletters on Stratigraphy*, Stuttgart, vol. 51, p. 57-72.
- CARNEVALE G., GENNARI R., LOZAR F., NATALICCHIO M., PELLEGRINO L. & DELA PIERRE F. (2019).- Living in a deep desiccated Mediterranean Sea: An overview of the Italian fossil record of the Messinian salinity crisis.- *Bolletino della Società Paleontologica Italiana*, Modena, vol. 58, p. 109-140.
- CARNEVALE G., LONGINELLI A., CAPUTO D., BARBIERI M. & LANDINI W. (2008).- Did the Mediterranean marine reflooding precede the Mio-Pliocene boundary? Paleontological and geochemical evidence from upper Messinian sequences of Tuscany, Italy.- *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 257, p. 81-105.
- CHEMNITZ J.H. (1782).- Neues Systematischen Conchylien Cabinet, vol. 6.- Gabriel Nicolaus Raspe, Nürnberg, 375 p.
- CITA M.B. (1975).- Studi sul Pliocene e gli strati di passaggio dal Miocene al Pliocene. VII. Planktonic foraminiferal biozonation of the Mediterranean Pliocene deep-sea record. A revision.- *Rivista Italiana di Paleontologia e Stratigrafia*, Milan, vol. 81, p. 527-544.
- COLETTI G., BOSIO G. & COLLARETA A. (2021).- Lower Pliocene barnacle facies of western Liguria (NW Italy): A peek into a warm past and a glimpse of our incoming future.- *Rivista Italiana di Paleontologia e Stratigrafia (Research in Paleontology and Stratigraphy)*, Milan, vol. 127, p. 103-131.
- COLLARETA A., CASATI S., CATANZARITI R. & DI CENCIO A. (2017b).- First record of the knifetooth sawfish *Anoxypristis* (Elasmobranchii: Rhinopristiformes) from the Pliocene of Tuscany (central Italy).- *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, Stuttgart, vol. 284, p. 289-297.
- COLLARETA A., CASATI S. & DI CENCIO A. (2017a).- A pristid sawfish from the lower Pliocene of Luciolabella (Radicofani basin, Tuscany, central Italy).- *Atti della Società Toscana di Scienze Naturali, Memorie* (ser. A), Pisa, vol. 124, p. 49-55.
- COLLARETA A., CASATI S. & DI CENCIO A. (2018).- The porbeagle shark, *Lamna nasus* (Elasmobranchii: Lamniformes), from the late Pliocene of the central Mediterranean Basin.- *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, Stuttgart, vol. 287, p. 307-316.
- COLLARETA A., CASATI S., ZUFFI M.A.L. & DI CENCIO A. (2020a).- First authentic record of the freshwater turtle *Mauremys* from the upper Pliocene of Italy, with a new occurrence of the rarely reported ichnotaxon *Thathtelithichnus holmani*.- *Carnets Geol.*, Madrid, vol. 20, no.



- 16, p. 301-313.
- COLLARETA A., COLLARETA M., BERTA A. & BIANUCCI G. (2020b).- On LEONARDO and a fossil whale: A reappraisal with implications for the early history of palaeontology.- *Historical Biology*, London, <https://doi.org/10.1080/08912963.2020.1787403>
- COLLARETA A., MERELLA M., CASATI S. & DI CENCIO A. (2020c).- Did titanic stingrays wander the Pliocene Mediterranean Sea? Some notes on a giant-sized myliobatoid stinger from the Piacenzian of Italy.- *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, Stuttgart, vol. 298, p. 155-164.
- COLLARETA A., MERELLA M., MOLLEN F.H., CASATI S. & DI CENCIO A. (2020d).- The extinct catshark *Pachyscyllium distans* (PROBST, 1879) (Elasmobranchii: Carcharhiniformes) in the Pliocene of the Mediterranean Sea.- *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, Stuttgart, vol. 295, p. 129-139.
- COLLARETA A., MOLLEN F.H., MERELLA M., CASATI S. & DI CENCIO A. (2021).- Remarkable multicuspid teeth in a new elusive skate (Chondrichthyes, Rajiformes) from the Mediterranean Pliocene.- *Paläontologische Zeitschrift*, Stuttgart, vol. 95, p. 117-128.
- COMPAGNO L.J.V. (1973).- Interrelationships of living elasmobranchs. In: GREENWOOD P.H., MILES R.S. & PATTERSON C. (eds.), *Interrelationships of fishes*.- *Zoological Journal of the Linnean Society*, London, vol. 53, suppl. 1, p. 15-61.
- COMPAGNO L.J.V. & LAST P.R. (1999).- Order Myliobatiformes. In: CARPENTER K.E. & NIEM V.H. (eds.), *FAO species identification guide for fisheries purposes. The living marine resources of the western central Pacific. Volume 3. Batoid fishes, chimaeras and bony fishes. Part 1 (Elopidae to Linophrynidae)*.- FAO, Rome, p. 1467-1529.
- DEGROOT B.C., BASSOS-HULL K., WILKINSON K.A., LOWERRE-BARBIERI S., POULAKIS G.R. & AJEMIAN M.J. (2021).- Variable migration patterns of whitespotted eagle rays *Aetobatus narinari* along Florida's coastlines.- *Marine Biology*, vol. 168, p. 1-21.
- DI CENCIO A., DULAI A., CATANZARITI R., CASATI S. & COLLARETA A. (2021).- First record of the brachiopod *Lingula*? from the Pliocene of Tuscany (Italy): The youngest occurrence of lingulides in the Mediterranean Basin.- *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, Stuttgart, vol. 299, p. 237-249.
- DOMINICI S., DANISE S. & BENVENUTI M. (2018).- Pliocene stratigraphic paleobiology in Tuscany and the fossil record of marine megafauna.- *Earth-Science Reviews*, vol. 176, p. 277-310.
- FIALHO P., BALBINO A. & ANTUNES M.T. (2019).- Langhian rays (Chondrichthyes, Batomorphii) from Brielas, Lower Tagus Basin, Portugal.- *Geologica Acta*, Barcelona, vol. 17, p. 1-16.
- FROESE R. & PAULY D., eds. (2020).- FishBase. World Wide Web electronic publication (version 12/2020).- Accessed on 21 January 2021. <https://www.fishbase.org>
- GMELIN J.F. (1791).- Vermes. In: GMELIN J.F. (ed.), *Caroli a Linnaei Systema Naturae per Regna Tria Naturae*, Ed. 13, tome 1(6).- G.E. Beer, Leipzig, p. 3021-3910.
- HERMAN J., HOVESTADT-EULER M., HOVESTADT D.C. & STEHMANN M. (2000).- Part B: Batomorphii 4c: Order Rajiformes - Suborder Myliobatoidei - Superfamily Dasyatoidea - Family Dasyatidae - Subfamily Dasyatinae - Genus: *Urobatis*, Subfamily Potamotrygoninae - Genus: *Paratrygon*, Superfamily Plesiobatoidea - Family Plesiobatidae - Genus: *Plesiobatis*, Superfamily Myliobatoidea - Family Myliobatidae - Subfamily Myliobatinae - Genera: *Aetobatus*, *Aetomylaeus*, *Myliobatis* and *Pteromylaeus*, Subfamily Rhinopterinae - Genus: *Rhinoptera* and Subfamily Mobulinae - Genera: *Manta* and *Mobula*. Addendum 1 to 4a: erratum to Genus *Pteroplatytrygon*. In: STEHMANN M. (ed.), *Contributions to the study of the comparative morphology of teeth and other relevant ichthyodurulites in living supraspecific taxa of Chondrichthyan fishes*.- *Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie*, Brussels, vol. 70, p. 5-67.
- HÖLTKE O., UNGER E., POLLERSPÖCK J. & RASSER M.W. (2020).- The elasmobranch fauna from the Upper Marine Molasse (lower Miocene, Burdigalian) of Ursendorf (SW-Germany).- *Palaeontos*, Antwerp, vol. 33, p. 3-55.
- HOVESTADT D.C. & HOVESTADT-EULER M. (2013).- Generic assessment and reallocation of Cenozoic Myliobatinae based on new information of tooth, tooth plate and caudal spine morphology of extant taxa.- *Palaeontos*, Antwerp, vol. 24, p. 1-66.
- JONET S. (1968).- Notes d'ichthyologie miocène portugaise. V. - Quelques batoides.- *Revista da Faculdade de Ciências da Universidade de Lisboa*, Lisbon, vol. 15, p. 233-258.
- KYNE P.M., DUDGEON C.L., ISHIHARA H., DUDLEY S.F.J. & WHITE W.T. (2016).- *Aetobatus ocellatus*.- *The IUCN Red List of Threatened Species*, article #e.T42566169A42566212.- Accessed on 21 January 2021. <http://dx.doi.org/10.2305/IUCN.UK.2016-1.RLTS.T42566169A42566212.en>
- KYNE P.M., ISHIHARA H., DUDLEY S.F.J. & WHITE W.T. (2006).- *Aetobatus narinari*.- *The IUCN Red List of Threatened Species*, article #e.T39415A10231645.- Accessed on 21 January 2021. <https://dx.doi.org/10.2305/IUCN.UK.2006.RLT.S.T39415A10231645.en>
- LANGER M.R., WEINMANN A.E., LÖTTERS S. & RÖDDER D. (2012).- "Strangers" in paradise: Modeling the biogeographic range expansion of the foraminifera *Amphistegina* in the Mediterranean Sea.- *Journal of Foraminiferal Research*, Lawrence, vol. 42, p. 234-244.
- LAST P.R., WHITE W.T., CARVALHO M.R. de, SÉRET B., STEHMANN M.F.W. & NAYLOR G.J.P. (2016).- *Rays of the World*.- CSIRO Publishing, Melbourne, 800 p.



- MANGANELLI G. & SPADINI V. (2019).- *Megascyliorhinus miocaenicus* (Chondrichthyes, Galeomorphii) from the Zanclean (early Pliocene) of San Quirico d'Orcia, central Italy.- *Bollettino della Società Paleontologica Italiana*, Modena, vol. 58, p. 165-170.
- MARÍN J.M. (1992).- Paleoiictología de algunos yacimientos neógenos de la provincia de Alicante (II).- *Cidaris, Rivista Ilicitana de Paleontología y Mineralogía*, Elche, vol. 1, p. 4-24.
- MARRAMÀ G., CARNEVALE G., ENGELBRECHT A., CLAESON K.M., ZORZIN R., FORNASIERO M. & KRIWET J. (2018).- A synaptic review of the Eocene (Ypresian) cartilaginous fishes (Chondrichthyes: Holocephali, Elasmobranchii) of the Bolca Konservat-Lagerstätte, Italy.- *Paläontologische Zeitschrift*, Stuttgart, vol. 92, p. 283-313.
- MARSILI S. (2008).- Systematic, paleoecologic and paleobiogeographic analysis of the Plio-Pleistocene Mediterranean elasmobranch fauna.- *Atti della Società Toscana di Scienze Naturali, Memorie* (ser. A), Pisa, vol. 113, p. 81-88.
- MAS G. (2010).- Ictiofauna del Pliocè del barranc de sa Talaia (Mallorca, Illes Balears, Mediterrània Occidental). Implicacions paleoambientals.- *Bolletí de la Societat d'Història Natural de les Balears*, Palma de Mallorca, vol. 53, p. 43-70.
- MENESINI E. (1969).- Ittiodontoliti miocenici di Terra d'Otranto.- *Palaeontographia Italica*, vol. 65, p. 1-61.
- MOLLEN F.H. (2010).- A partial rostrum of the porbeagle shark *Lamna nasus* (Lamniformes, Lamnidae) from the Miocene of the North Sea Basin and the taxonomic importance of rostral morphology in extinct sharks.- *Geologica Belgica*, Brussels, vol. 13, p. 61-76.
- MONEGATTI P. & RAFFI S. (2001).- Taxonomic diversity and stratigraphic distribution of Mediterranean Pliocene bivalves.- *Palaeogeography, Palaeoclimatology, Palaeoecology*, vol. 165, p. 171-193.
- MORA MOROTE P. (1996).- Peces Galeomorfos y Squatinomorfos en el Plioceno de Guardamar del Segura (Alicante).- *Cidaris - Rivista Ilicitana de Paleontología y Mineralogía*, Elche, vol. 5, p. 98-124.
- MORA MOROTE P. (1997).- Peces Myliobatiformes y Pristiophoriformes en el Plioceno de Guardamar del Segura (Alicante).- *Cidaris - Rivista Ilicitana de Paleontología y Mineralogía*, Elche, no. 11-12, p. 48-63.
- PAWELLEK T., ADNET S., CAPPETTA H., MÉTAIS E., SALEM M., BRUNET M. & JAEGER J.-J. (2012).- Discovery of an earliest Pliocene relic tropical fish fauna in a newly detected cliff section (Sabratalah Basin, NW Libya).- *Neues Jahrbuch für Geologie und Paläontologie-Abhandlungen*, Stuttgart, vol. 266, p. 93-114.
- POMAR L., MARZO M. & BARÓN A. (1983).- El Terciario de Mallorca. In: POMAR L., OBRADOR O., FORNÓS J.J. & RODRÍGUEZ-PEREA A. (eds.), El Terciario de las Baleares (Mallorca-Menorca). Guía de las Excursiones del X Congreso Nacional de Sedimentología.- Institut d'Estudis Balearics and Universitat de Palma de Mallorca, Palma de Mallorca, p. 21-44.
- POR F.D. (1978).- Lessepsian migrations. The influx of Red Sea biota into the Mediterranean by way of the Suez Canal.- Springer, Heidelberg, 228 p.
- PRISTA G.A., AGOSTINHO R.J. & CACHÃO M.A. (2015).- Observing the past to better understand the future: A synthesis of the Neogene climate in Europe and its perspectives on present climate change.- *Open Geosciences*, Berlin, vol. 7, p. 65-83.
- PURDY R.W., SCHNEIDER V.P., APPLGATE S.P., McLELLAN J.H., MEYER R.L. & SLAUGHTER B.H. (2001).- The Neogene sharks, rays, and bony fishes from Lee Creek Mine, Aurora, North Carolina. In: RAY C.E. & BOHASKA D.J. (eds.), Geology and paleontology of the Lee Creek Mine, North Carolina, vol. III.- *Smithsonian Contributions to Paleobiology*, Washington D.C., vol. 90, p. 71-202.
- RAGAINI L., FICINI F., ZANCHETTA G., REGATTIERI E., PERCHIAZZI N. & DALLAI L. (2019).- Mineralogy and oxygen isotope profile of *Pelecycora gigas* (Veneridae, Bivalvia) from Tuscan Pliocene.- *Alpine and Mediterranean Quaternary*, Rome, vol. 32, p. 5-13.
- REINECKE T., LOUWYE S., HAVEKOST U. & MOTHS H. (2011).- The elasmobranch fauna of the late Burdigalian, Miocene, at Werder-Uesen, Lower Saxony, Germany, and its relationships with early Miocene faunas in the North Atlantic, Central Paratethys and Mediterranean.- *Palaeontos*, Antwerp, vol. 20, 170 p.
- SALES J.B.L., OLIVEIRA C.N. de, SANTOS W.C.R. dos, ROTUNDO M.M., FERREIRA Y., READY J., SAMPAIO I., OLIVEIRA C., CRUZ V.P., LARA-MENDOZA R.E. & SILVA RODRIGUES-FILHO L.F. da (2019).- Phylogeography of eagle rays of the genus *Aetobatus*: *Aetobatus narinari* is restricted to the continental western Atlantic Ocean.- *Hydrobiologia*, The Hague, vol. 836, p. 169-183.
- SERENA F. (2005).- Field identification guide to the sharks and rays of the Mediterranean and Black Sea. In: FAO species identification guide for fishery purposes.- FAO, Rome, 97 p.
- SORBI S., DOMNING D.P., VAIANI S.C. & BIANUCCI G. (2012).- *Metaxytherium subapenninum* (BRUNO, 1839) (Mammalia, Dugongidae), the latest sirenian of the Mediterranean Basin.- *Journal of Vertebrate Paleontology*, Lawrence, vol. 32, p. 686-707.
- SPADINI V. & MANGANELLI G. (2015).- A megachasmid shark tooth (Chondrichthyes, Lamniformes) from the Zanclean (early Pliocene) of San Quirico d'Orcia, central Italy.- *Bollettino della Società Paleontologica Italiana*, Modena, vol. 54, p. 67-70.
- SPAET J.L.Y. & BERUMEN M.L. (2015).- Fish market surveys indicate unsustainable elasmobranch fisheries in the Saudi Arabian Red Sea.- *Fisheries Research*, vol. 161, p. 356-364.



- VAI G.B. (1989).- A field trip guide to the Romagna Apennine geology. The Lamone Valley.- *Bollettino della Società Paleontologica Italiana*, Modena, vol. 28, p. 343-367.
- VILLAFANA J.A., MARRAMÀ G., KLUG S., POLLERSPÖCK J., BALSBERGER M., RIVADENEIRA M. & KRIWET J. (2020).- Sharks, rays and skates (Chondrichthyes, Elasmobranchii) from the Upper Marine Molasse (middle Burdigalian, early Miocene) of the Simssee area (Bavaria, Germany), with comments on palaeogeographic and ecological patterns.- *Paläontologische Zeitschrift*, Stuttgart, vol. 94, p. 725-757.
- VIOLANTI D. (2012).- Pliocene Mediterranean foraminiferal biostratigraphy: A synthesis and application to the paleoenvironmental evolution of northwestern Italy. *In*: ELITOK Ö. (ed.), Stratigraphic analysis of layered deposits.- Intech Open, London, p. 123-160.
- WEIGMANN S. (2016).- Annotated checklist of the living sharks, batoids and chimaeras (Chondrichthyes) of the world, with a focus on biogeographical diversity.- *Journal of Fish Biology*, Oxford, vol. 88, p. 837-1037.
- WHITE W.T. (2006).- *Aetobatus flagellum*.- *The IUCN Red List of Threatened Species*, article #e.T60119A12306888.- Accessed on 21 January 2021. <https://dx.doi.org/10.2305/IUCN.UK.2006.RLTS.T60119A12306888.en>
- WHITE W.T. (2014).- A revised generic arrangement for the eagle ray family Myliobatidae, with definitions for the valid genera.- *Zootaxa*, Auckland, vol. 3860, p. 149-166.
- WHITE W.T., FURUMITSU K. & YAMAGUCHI A. (2013).- A new species of eagle ray *Aetobatus narutobiei* from the northwest Pacific: An example of the critical role taxonomy plays in fisheries and ecological sciences.- *PLOS ONE*, vol. 8, article #e83785.
- WHITE W.T. & MOORE A.B.M. (2013).- Redescription of *Aetobatus flagellum* (BLOCH & SCHNEIDER, 1801), an endangered eagle ray (Myliobatoidea: Myliobatidae) from the Indo-West Pacific.- *Zootaxa*, Auckland, vol. 3752, p. 199-213.
- WHITE W.T. & NAYLOR G.J.P. (2016).- Resurrection of the family Aetobatidae (Myliobatiformes) for the pelagic eagle rays, genus *Aetobatus*.- *Zootaxa*, Auckland, vol. 4139, p. 435-438.