

The extinct catshark *Pachyscyllium distans* (PROBST, 1879) (Elasmobranchii: Carcharhiniformes) in the Pliocene of the Mediterranean Sea

Alberto Collareta, Marco Merella, Frederik H. Mollen, Simone Casati, and Andrea Di Cencio

With 4 figures and 1 table

Abstract: Sharks assigned to the carcharhiniform family Scyliorhinidae account for about 160 extant species placed in 18 genera. Most living scyliorhinids are small- to medium-sized ground sharks provided with cat-like eyes and nasal barbels similar to whiskers; hence their vernacular name, “catsharks”. Living catsharks mostly inhabit deep or rather deep waters of the warm and temperate seas worldwide, foraging on small fishes and invertebrates. In the present paper, we report on a lateral tooth of Scyliorhinidae collected from a clay pit at Certaldo (central Italy), where marine mudstones belonging to the famously fossiliferous Pliocene successions of Tuscany are exposed. This catshark specimen represents the second bona fide record of the extinct premontereine species *Pachyscyllium distans* in the Pliocene of the Mediterranean Sea, as well as the geologically youngest confirmed occurrence of this species worldwide. In the Mediterranean Pliocene, *P. distans* thus coexisted with the similar but distinct species *Pachyscyllium dachiardii*. After having been widespread in Northern Atlantic, Paratethyan, and Mediterranean waters in Miocene times, *P. distans* became confined to the Mediterranean Sea during the Pliocene. Therefore, similar to what has recently been suggested for *P. dachiardii*, we hypothesise that the range of *P. distans* contracted southward as colder conditions took hold in the Northern Hemisphere. The eventual extinction of *P. distans* might be related to the first cooling episode that significantly affected the Mediterranean biota around 3 Ma.

Key words: Chondrichthyes, Scyliorhinidae, Premontreinae, Valdelsa Basin, blue clays, Tuscany, climate change, palaeobiogeography, palaeoichthyology.

1. Introduction

The carcharhiniform family Scyliorhinidae includes around 160 living species placed in 18 genera (WEIGMANN 2016; WHITE *et al.* 2019); as such, it represents one of the largest living families of sharks. Most extant scyliorhinids are small- to medium-sized (i.e., less than 1.5 m in total length) ground sharks that exhibit lengthened, cat-like eyes and, sometimes, whisker-like nasal barbels (COMPAGNO 1984; CAPPETTA 2012); hence their vernacular name, “catsharks”. They inhabit seabottoms in tropical and temperate seas all over the world, ranging from very shallow, marginal-marine areas to depths of more than 2000 m (COMPAGNO 1984). That said, most of the Recent scyliorhinids live in

deep or rather deep waters (CAPPETTA 2012). Extant catsharks feed mostly on invertebrates and small fishes; however, the life histories of several living scyliorhinid species are still very poorly known (COMPAGNO 1984).

For almost two centuries, the Pliocene marine successions of Tuscany (central Italy) have been the location of important finds of fossil remains of elasmobranchs (e.g., LAWLEY 1876), mostly shark teeth and batoid dental plates and dermal spines (MARSILI 2006, and references therein). These fossils were collected to form important palaeontological collections, such as the famous “Lawley collection” (MANGANELLI *et al.* 2006), which was studied (in the past) by illustrious naturalists (e.g., BASSANI 1901; DE STEFANO 1909).

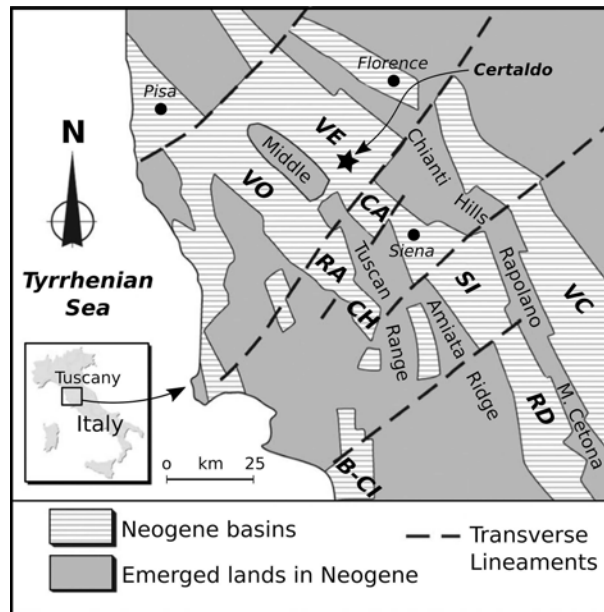


Fig. 1. Location of Certaldo, the locality where the fossil scyliorhinid tooth GAMPS-00924 was found (black star), and schematic regional geological map. B-CI = Baccinello-Cinigiano Basin; CA = Casino Basin; RD = Radicofani Basin; SI = Siena Basin; VC = Val di Chiana Basin; VE = Valdelsa Basin; VO-RA-CH = Volterra-Radicondoli-Chiusdino basins. Modified after MARTINI et al. (2013) and SPADINI & MANGANELLI (2015).

Following the emergence of modern palaeontological research standards, however, these historical collections have lost some of their scientific importance due to widespread uncertainties regarding their geographical and stratigraphic context (LANDINI 1977; CIGALA FULGOSI et al. 2009; COLLARETA et al. 2016). Now however, the recent reports of rare and elusive elasmobranch taxa from the Pliocene deposits of Tuscany (SPADINI & MANGANELLI 2015; COLLARETA et al. 2017a; COLLARETA et al. 2017b; COLLARETA et al. 2018; MANGANELLI & SPADINI 2019), as well as the discovery of new fossil localities that are rich in shark and ray teeth (BIANUCCI et al. 2019), are contributing to shed new light on the late Neogene cartilaginous fish faunas of the Mediterranean Sea.

In the present paper, on the basis of a single lateral tooth collected from Pliocene marine mudstones exposed at the locality of Certaldo (Tuscany), we provide the second unambiguous record of the extinct catshark species *Pachyscyllium distans* (Scyliorhinidae: Premonstreinae) from the Pliocene of the Mediterranean Sea and briefly discuss its palaeobiogeographical significance.

2. Stratigraphic framework

The scyliorhinid fossil tooth described herein was discovered by one of the authors (S.C.) at an abandoned quarry at the periphery of the Certaldo village (Florence Province, Tuscany, central Italy) (Fig. 1). The GPS geographic coordinates of our find are the following: 43° 34' 08" N; 11° 01' 51" E.

The fossil specimen was collected from deposits belonging to the Argille Azzurre Formation, a lithostratigraphic unit that largely consists of mostly massive, shelf mudstones (hence their formational name, meaning 'blue clays'), whose deposition in this area is referred to the Pliocene (COSTANTINI et al. 2004). According to BENVENUTI et al. (2014), in the Valdelsa Basin, an intraformational unconformity divides the Argille Azzurre Formation into 'lower' and 'upper' blue clays, dated to the basalmost Zanclean and upper Zanclean – lower Piacenzian, respectively. The succession exposed at Certaldo belongs to the upper blue clays (= 'upper Argille Azzurre' of NALIN et al. 2016) and can be referred to the S3 Syntem recognised in the Valdelsa Basin by BENVENUTI et al. (2014). The S3



Fig. 2. The Pliocene deposits exposed at the abandoned Certaldo quarry. **A** – General view of the outcrop. **B** – Collection of fossil invertebrate and vertebrate remains at the base of the partly revegetated artificial cliff (white arrow). **C** – Close-up view on a fossil-rich horizon cropping out a couple of meters below the top of the cliff.

Synthem is a large-scale depositional sequence that consists of a coarse-grained, deepening-upward delta front stratal package, overlain by a fine-grained division from an open shelf setting (DOMINICI *et al.* 2018). The latter comprises a rather monotonous mudstone succession that, in the study area, features several *Ostrea*- and *Serpulorbis*-rich shell beds (DOMINICI *et al.* 2018).

According to BENVENUTI *et al.* (2014), the mudstones belonging to the S3 Synthem bear planktonic foraminifer assemblages indicative of the Mediterranean Pliocene (MPL) zone 4 of CITA (1975) and SPROVIERI (1992), whose bounding bioevents (i.e., the last common occurrence of *Globorotalia margaritae* and the last appearance datum of *Sphaeroidinello-*

sis spp.) have been calibrated to 3.98 and 3.19 Ma, respectively (VIOLANTI 2012).

At the study site, strata belonging to the Argille Azzurre Formation crop out along a partly revegetated artificial cliff (Fig. 2A). The succession exposed at the Certaldo quarry is mostly comprised of substantially structureless, greyish-bluish mudstones that host common remains of macro-invertebrates and erode in a badland-like fashion (Fig. 2B). Fossils concentrate in a ca. 25-cm-thick horizon (Fig. 2C) that also feature rare invertebrate vertical burrows; this interval runs subhorizontally a couple of meters below the top of the cliff. The invertebrate assemblage detected at the study site includes several species of bivalve and gastropod molluscs (*Bathytoma cataphracta*, *Calcarata calcara-*

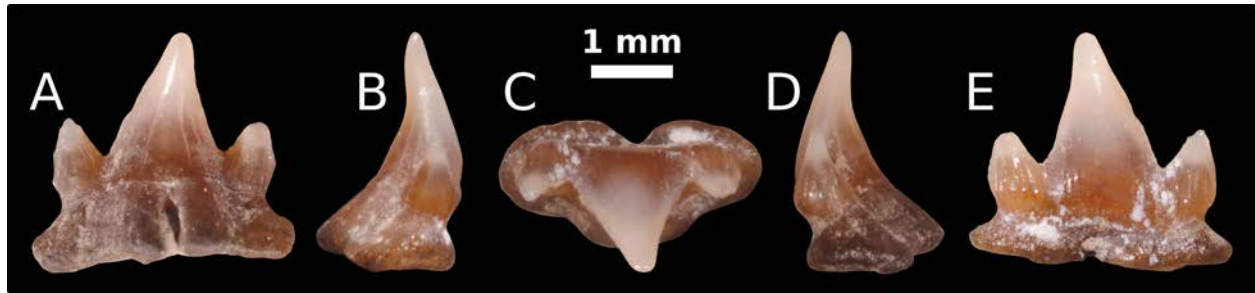


Fig. 3. GAMPS-00924, lateral tooth of *Pachyscyllium distans* (PROBST, 1879) from Certaldo (Tuscany, central Italy). **A** – Lingual view; **B** – distal view; **C** – apical view; **D** – mesial view; **E** – labial view.

ta, *Pelecypora brocchii*, *Petalococonchus intortus*, *Tenagodus obtusus*, and *Thylacodes arenarius*, among others) and a single species of acorn barnacle (*Concavus concavus*). Vertebrate fossils from the Certaldo quarry include the scyliorhinid specimen studied herein, as well as a few other teeth of elasmobranchs (assigned to *Megascyliorhinus miocaenicus* and *Rostroraja* sp.) and indeterminate otoliths. Most of these remains, including the specimen described herein, lack a precise stratigraphic position; they rolled down from the easily erodible cliff to accumulate at its base (Fig. 2B).

3. Systematic palaeontology

Class Chondrichthyes HUXLEY, 1880
 Subclass Elasmobranchii BONAPARTE, 1838
 Order Carcharhiniformes COMPAGNO, 1973
 Family Scyliorhinidae GILL, 1862
 Subfamily Premontreinae CAPPETTA, 1992
 Genus *Pachyscyllium* REINECKE, MOTHS, GRANT & BREITKREUTZ, 2005

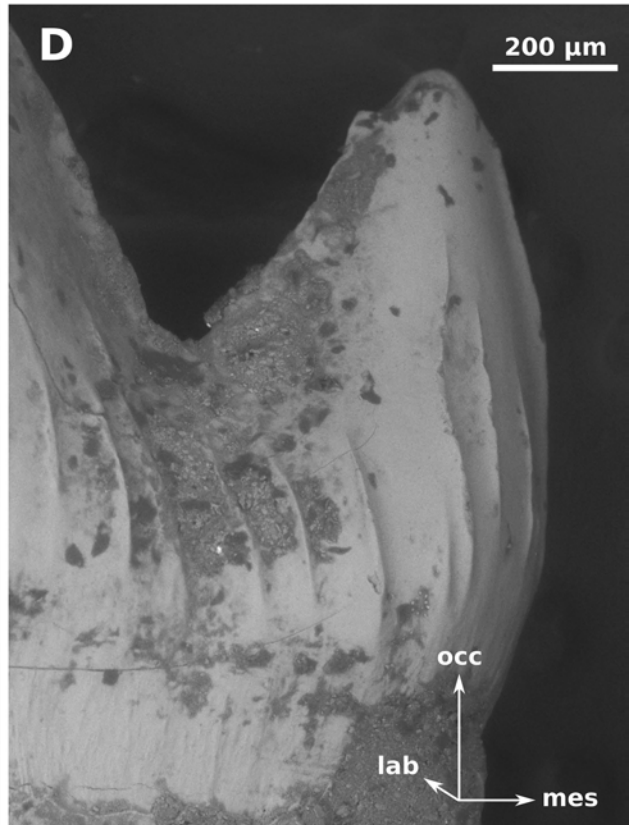
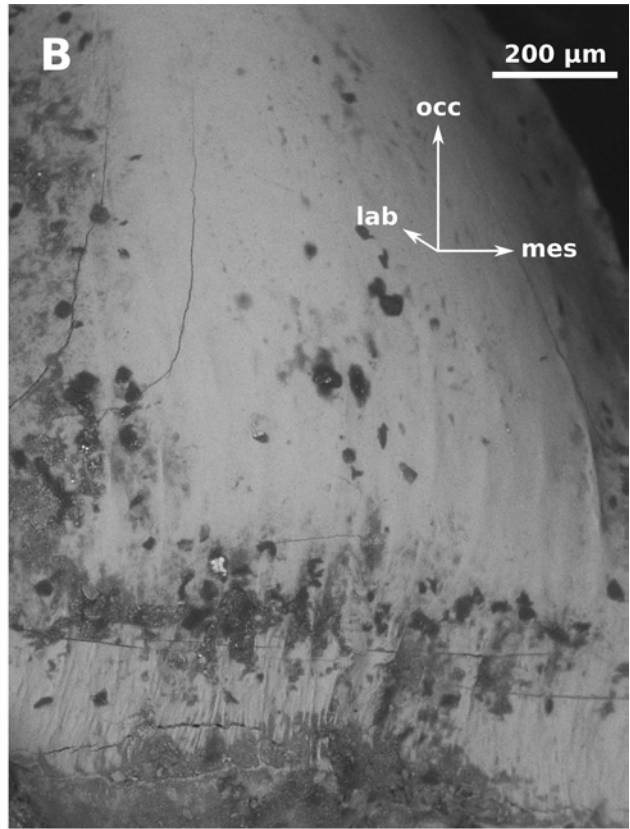
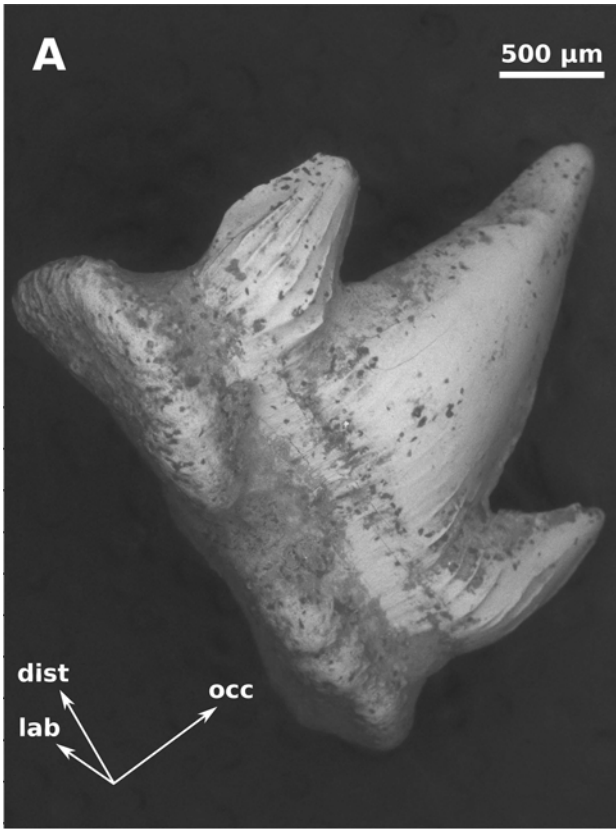
Type species: *Pachyscyllium albigensis* REINECKE, MOTHS, GRANT & BREITKREUTZ, 2005.

Pachyscyllium distans (PROBST, 1879)
 Figs. 3, 4

Synonymy: See REINECKE et al. (2011: 52), where this species is referred to as *Premontreia (Oxyscyllium) distans* (PROBST, 1879); for an updated list of synonyms and other selected references, include also:

- ?1949 *Scyliorhinus guttatum* PROBST, 1879. – BAUZÁ RULLÁN, p. 208, pl. 15, figs. 1, 2.
- 1953 *Scylliorhinus* (= *Scyllium*) sp. – BAUZÁ RULLÁN, p. 5 (in part), figs. 7–14.
- 1976 *Scyliorhinus distans* (PROBST, 1879) – DE CEUSTER, p. 136, pl. 5, figs. 13, 14.
- ?1992 *Scylliorhinus distans* (PROBST, 1879). – MARÍN, p. 12, pl. 1, figs. 6, 7.
- 1996 *Scyliorhinus distans* PROBST, 1879. – MORA MOROTE, p. 109, pl. 7, figs. 1–2, 4, 5.
- 2009 *Pachyscyllium dachiardi* (LAWLEY, 1876) – BRISSEWALTER, p. 32 (in part; personal observation by F.H.M., Elasmobranch Research Belgium collections – Cabrières d’Aigues), table 3a.
- 2011 *Pachyscyllium* aff. *dachiardii* (LAWLEY, 1876). – VIALLE et al., p. 250 (in part), figs. ?3.8, 3.9.
- 2012 *Premontreia distans* (PROBST, 1879). – BOR et al., p. 41, pl. 22.
- 2014 *Pachyscyllium distans* (PROBST, 1879). – REINECKE, p. 7.
- 2019 *Pachyscyllium distans* (PROBST, 1879). – EVERAERT et al., table 1, pl. 3, figs. 1, 2.

Fig. 4. GAMPS-00924, lateral tooth of *Pachyscyllium distans* (PROBST, 1879) from Certaldo (Tuscany, central Italy). **A** – General view of the labial aspect of the tooth; **B–D** – four details of the labial aspect of the crown, with a focus on the longitudinal labial ridges that are found at the crown base. Note that the longitudinal labial ridges ornamenting the lateral cusplets (panels C and D) are more salient than those located at the base of the main cusp (panel B). Scanning Electron Microscope (SEM) images by KAREN GARIBOLDI, taken at the Dipartimento di Scienze della Terra dell’Università di Pisa (Pisa, Italy) using a Hitachi TM3030Plus Tabletop Microscope operating in the back-scattered electron mode.



Taxonomic caveat: *Pachyscyllium distans* has a somewhat troubled taxonomic history. As several other extinct scyliorhinids, it was originally described by PROBST (1879) as a member of *Scyllium*; the latter is a junior synonym of the living genus *Scyliorhinus*, to which *Scyllium distans* was transferred by CAPPETTA et al. (1967). Later, CAPPETTA (2006; see also preliminary comments in CAPPETTA 1992) reassigned *Scyliorhinus distans* to the extinct genus and subgenus *Premontreia (Oxyscyllium)*, hence the new combination *Premontreia (Oxyscyllium) distans*. Finally, REINECKE (2014) transferred PROBST's species to the fossil premonstreine genus *Pachyscyllium*, a view that is followed here.

Referred material: One isolated tooth, currently kept at Badia a Settimo (Scandicci, Italy) in the permanent exhibition of “Gruppo AVIS Mineralogia e Paleontologia Scandicci” (GAMPS) under accession number GAMPS-00924.

Occurrence: Pliocene (3.98–3.19 Ma) open shelf mudstones exposed at Certaldo, Florence Province, Tuscany, central Italy.

Description: The crown of this tooth has a main central cusp flanked up by a pair of lateral cusplets. In labial view, the stout main cusp is distinctly triangular and moderately projects distally; in lateral view, it exhibits a weakly sigmoidal profile as its tip moderately bends labially. The labial surface of the main cusp is slightly convex transversely, although its limit appears as concave in occlusal view; in turn, the lingual face is invariantly strongly convex. Whereas the lingual surface of the main cusp is substantially smooth, the basal part of the labial surface displays obvious vertical ridges; the latter are closely spaced and parallel to each other. The labial base of the main cusp moderately overhangs the labial face of the root. Both the mesial and the distal cutting edges of the main cusp are unserrated and complete; the mesial cutting edge is gently convex, whereas the distal cutting edge is very weakly concave. The lateral cusplets are continuous with (although well-set apart from) the main cusp; they are robust, relatively high, and similar to each other, being shaped as onion domes. The lateral cusplets weakly diverge from each other and the main cusp by projecting respectively apicomediaally (the mesial cusplet) and apicodistally (the distal cusplet). Both the mesial and the distal cutting edges of the main cusp prosecute through the lateral cusps to reach the tooth root, thus forming a sharp, continuous, mediolateral crown contour. Strong, salient, carina-like longitudinal ridges, distinctly stronger than those observed at the labial base of the main cusp, mark the labial and labiolateral surfaces of both the lateral cusplets. The root is rather robust and holaulacorhize; it is comprised of two lobes that flare laterobasally and are separated from each other by a relatively narrow but well-marked furrow. The basal surface of the root is remarkably flat and somewhat heart-shaped. On the lingual face of the root, a deep, longitudinal, nutrient groove bisects a rather prominent, horizontally elongated lingual bulge.

GAMPS-00924 is recognised as a lateral tooth based on the observation of a rather stout crown whose main cusp is distinctly bent distally (REINECKE et al. 2011; CAPPETTA 2012). According to REINECKE et al. (2011) and BOR et al. (2012), the observation of a gently convex (rather than straight) mesial cutting edge might be related to a low degree of dognathic heterodonty.

Table 1. Measurements of GAMPS-00924, lateral tooth of *Pachyscyllium distans* (PROBST, 1879) from the Pliocene of Certaldo (Tuscany, central Italy). All measurements are reported in millimetres.

	GAMPS-00924
Apicobasal tooth height	2.8
Mediolateral tooth width	3.2
Labiolingual tooth thickness	1.7

Measurements: Measurements of GAMPS-00924 are reported in Table 1.

Remarks on the species-level attribution: Some authors (e.g., CAPPETTA 2006; CAPPETTA 2012) consider *P. distans* as a junior synonym of *Pachyscyllium dachiardii* (= *Scyllium D'Achiardii*) – a view first proposed by LANDINI (1977). *Scyllium D'Achiardii* was erected by LAWLEY (1876) on the basis of eleven fossil teeth from the Pliocene deposits of Tuscany; unfortunately, the original description of this extinct species was not accompanied by any figure depicting the type series. LAWLEY (1876: 36) described the teeth of *P. dachiardii* (often misspelled as “*dachiardi*” in later publications) as follows:

“Alcuni denti tricuspidati, privi di qualunque seghettatura, molto rigonfi alla base e che vanno terminando in punta, la quale si rivolta dalla parte interna, portando un piccolo dentino per lato similmente rigonfio e appuntato senza traccia in qualunque parte della base di solchi longitudinali, con radice bassa e piana [...]”

A translation of LAWLEY's text is here proposed:

“Some tricuspidate teeth, devoid of any serrations, strongly bulging at their basis and tapering towards their apexes, which are buccally recurved; [teeth] bearing a similarly bulging and pointed small denticle at each side, without any trace of longitudinal sulci on any part of the basis, with low and flat root [...]”

Unfortunately, only one out of the eleven LAWLEY's specimens of *P. dachiardii* is currently known from the palaeontological collections of the Museo di Storia Naturale dell'Università di Pisa (LANDINI 1977). This specimen, which was first figured by LANDINI (1977), conforms well to the description provided by LAWLEY (1876) and, crucially, exhibits a smooth labiobasal margin of the crown. By reading LAWLEY's original description, it is clear that all the eleven teeth comprising the type series of *P. dachiardii* showed the same character, which LAWLEY (1876) regarded as crucial for distinguishing this species from *Scyllium pauluccii* (a junior synonym of the living Mediterranean species *Scyliorhinus stellaris* according to BASSANI 1901). In turn, one of the most striking features of the sole diagnostic syntype of *Pachyscyllium distans* (REINECKE et al. 2011: text-fig. 17) relies in the presence of well-distinct longitudinal labial ridges at the crown base. Personal observations by the present authors on an unpublished tooth set of *Pachyscyllium* from some Pliocene localities of Tuscany (including the lower Pliocene vertebrate-bearing site of Arcille; BIANUCCI et al. 2019) revealed that the presence of a smooth labiobasal margin of the crown represents a stable dental character of LAWLEY's species, GAMPS-00924 being indeed the sole

examined Tuscan Pliocene *Pachyscyllium* tooth that bears “*distans*-like” longitudinal labial ridges at the crown base. Consequently, we agree with REINECKE *et al.* (2011) in regarding *P. distans* as a valid, separate species that significantly differs from *P. dachiardii* (and not just a result of sexual dimorphism or any other form of intraspecific heterodonty).

4. General discussion and conclusions

A scrutiny of the palaeoichthyological literature reveals that teeth of *Pachyscyllium distans* have been reported from several Neogene sites of the Mediterranean, Paratethys, and the Northeastern Atlantic (palaeo-North Sea and Portugal). *Pachyscyllium distans* has also been recorded from lowermost Miocene (Aquitanian) deposits of the Northwestern Atlantic (Eastern coast of the USA) (see CASE 1980), but these strata (i.e., the Trent Marl Formation at River Bend Plantation, Craven County), are here considered to be of Oligocene age (see WARD 1978), and thus not dealt with in this study. The same applies for other Oligocene records of *Pachyscyllium* aff. *distans* from Europe (see e.g. REINECKE *et al.* 2014).

With respect to the Mediterranean and Paratethyan regions, *Pachyscyllium distans* has frequently been collected from Miocene strata. In particular, as regards the Paratethyan sectors, *P. distans* has commonly been reported from the upper lower Miocene (i.e., Burdigalian) of southern Germany, Switzerland, and Austria, as well as from the middle Miocene of Austria and Poland, whereas the Mediterranean records are mostly from deposits of Aquitanian to Langhian age of France [REINECKE *et al.* 2011, and references therein, but see BAUZÁ RULLÁN (1953) for a reliable occurrence of *P. distans* from supposedly lower upper Miocene (i.e., Tortonian) strata of Mallorca, Balearic Islands, Spain]. Under various names [i.e., *Scyliorhinus distans*, *Pachyscyllium dachiardi* (error pro *dachiardii*), and *Pachyscyllium* aff. *dachiardii*], CAPPETTA (1970: e.g. pl. 9, fig. 4), BRISWALTER (2009), and VIALLE *et al.* (2011: e.g. fig. 3.9) described and figured material of *P. distans* from the middle Miocene of the Montpellier region, the Luberon Massif, and Mazan, respectively; overall, these records from southeastern France testify to the presence of *P. distans* in the southern Rhodanian Basin, a narrow seaway that might have connected the Mediterranean Sea to the western Paratethys (e.g., REYNAUD & JAMES 2012). To our knowledge, besides the present study, there are only three possible records

of *P. distans* from the Mediterranean Pliocene, all of which are from Spanish localities and were published on magazines of natural sciences that are not widely distributed outside Spain. The first of these records was provided by BAUZÁ RULLÁN (1949), who reported on one tooth identified as belonging to *Scyliorhinus guttatum* (currently recognised as a junior synonym of *Chaenogaleus affinis*; REINECKE *et al.* 2011) from supposedly Pliocene deposits of Son Talapí, Mallorca, Balearic Islands. This tooth seemingly displays a typically premontreine outline (BAUZÁ RULLÁN 1949: figs. 1, 2) and was described as exhibiting small vertical folds at the crown base; as such, it likely represents a specimen of *P. distans*. That said, the stratigraphic whereabouts of this find are somewhat uncertain, as demonstrated by some inconsistencies in later works by the same author [e.g., BAUZÁ RULLÁN 1955, in which both the terms “Plaisanciense” (= Piacenzian) and “Plioceno inferior” (= lower Pliocene, corresponding to the Zanclean stage) are applied to the *Scyliorhinus guttatum* locality]. A second possible record of *P. distans* from the Mediterranean Pliocene was provided by MARÍN (1992), who reported on teeth of *Scyliorhinus* [sic] *distans* from presumably lower Pliocene (Zanclean) deposits of Butano, near Elche, Alicante Province. MARÍN (1992) did not describe these teeth, and the poor quality of his illustrations (MARÍN 1992: pl. 1, figs. 6, 7) does not allow a positive identification of these specimens as belonging either to *P. distans* or to *P. dachiardii*, which in turn is well-known from various Mediterranean Pliocene localities (LAWLEY 1876; BAUZÁ RULLÁN 1953: figs. 1–6; LANDINI 1977; BELLOCCHIO *et al.* 1991; MAÑE *et al.* 1996; CAPPETTA & CAVALLO 2006; MARSILI 2008). Finally, MORA MOROTE (1996) described and illustrated teeth of *Scyliorhinus distans* from the Pliocene of Guardamar del Segura, near Alicante, southern Spain. The dental characters of these specimens, as reported by MORA MOROTE (1996), compare favourably with those of *Pachyscyllium distans*, and include allegedly diagnostic traits such as the presence of longitudinal labial ridges at the crown base. As regards the provenance of these teeth, ADNET *et al.* (2010) reported that the material studied by MORA MOROTE (1996) comes from the Rojales Sandstone Formation, whose geologically youngest marine strata (belonging to the P2 system of SORIA *et al.* 2005) bear intercalations of palustrine marls that host rodent fossils dating into the Mammal Neogene 14 zone; the latter has recently been calibrated by MINWER-BARAKAT *et al.* (2012) at the ~5.3–4.19 Ma time span. Therefore, considering also

the uncertainties associated with the taxonomic identification and the geological age of the specimens mentioned by BAUZÁ RULLÁN (1949) and MARÍN (1992), GAMPS-00924 represents the second bona fide record of *P. distans* from the Pliocene of the Mediterranean Sea. Therefore, our discovery contributes to our knowledge on the late Neogene central Mediterranean biodiversity and encourages to pursue the quest for fossil elasmobranchs over the entire Tuscan Pliocene marine succession.

Outside the Mediterranean/Paratethyan realm, *P. distans* has been recorded from various upper lower Miocene (Burdigalian) to ?upper Miocene (?Tortonian) localities of Portugal (ANTUNES & JONET 1970; JONET 1978; ANTUNES et al. 1981). *Pachyscyllium distans* is also known as a common component of the Miocene elasmobranch assemblages of the North Sea Basin, where it ranges chronostratigraphically between the Aquitanian and the Langhian (REINECKE et al. 2011; BOR et al. 2012; EVERAERT et al. 2019, and references therein). Teeth of *P. distans* reported by DE CEUSTER (1976) from basal Pliocene deposits exposed at Rumst (near Antwerp, Belgium) are most likely reworked from the lower to middle Miocene strata of the Berchem Formation, as most of the fossil material from that horizon (REINECKE et al. 2011; personal observation by F.H.M.). In the light of these distributional data, and considering also the aforementioned age estimates regarding the *P. distans* specimens described by MORA MOROTE (1996), GAMPS-00924 represents the geologically youngest confirmed occurrence of *P. distans* worldwide. Furthermore, it appears that *P. distans* was extirpated from the North Sea Basin at the end of the Langhian, whereas it persisted along the coasts of Portugal till the Serravallian or Tortonian, and eventually survived into the Pliocene in the Mediterranean Sea only. This southward trend of Neogene regional extinctions might suggest that, somewhat similar to what has been hypothesised for the congeneric and largely sympatric species *P. dachiardii* (REINECKE et al. 2011), *P. distans* was a thermophilic catshark, whose range contracted southward as colder conditions progressively took hold in the Northeastern Atlantic by effect of a progressively cooling global climate and following the onset of the Northern Hemisphere glaciation (e.g., HERBERT et al. 2016). If this interpretation is correct, it seems reasonable to hypothesise that *P. distans* went definitively extinct around 3 Ma, when the Mediterranean region experienced a pulse of severe climate degradation (PRISTA et al. 2015, and references therein) that likely led to the extirpation of several taxa

of thermophilic marine vertebrates (e.g., SORBI et al. 2012; PRISTA et al. 2013; COLLARETA et al. 2017b). However, other events, such as the disruption of the psychrospheric ecosystems (and related deep-water trophic webs) of the Mediterranean Sea (CIGALA FULGOSI 1996; MARSILI 2007; CIGALA FULGOSI et al. 2009; COLLARETA et al. 2019) might also explain the eventual extirpation of *P. distans* and other elasmobranch taxa from this satellite basin of the North Atlantic. Hopefully, the collection of new specimens of *P. distans* from chronostratigraphically framed localities of the Tuscan Pliocene will contribute to further shed light on this issue and, more generally, on the palaeoecological and palaeobiogeographic dynamics of the late Neogene elasmobranch faunas of the Mediterranean Sea.

Acknowledgements

We are very grateful to MARK BOSSELAERS, BERT GIJSEN, KRISTIAAN HOEDEMAKERS, JÜRGEN POLLERSPÖCK, and THOMAS REINECKE, who provided precious comparative material and bibliographic support. THOMAS REINECKE is also warmly thanked for fruitful discussions over the issues dealt with in the present paper. Thanks are also due to KAREN GARIBOLDI, for having led the SEM analysis of GAMPS-00924, and to GIULIA BOSIO, for her field support. Last but not least, we are sincerely indebted to GIORGIO CARNEVALE, an anonymous reviewer, and GÜNTER SCHWEIGERT, whose thorough reviews greatly contributed to improve an early draft of this paper.

References

- ADNET, S., BALBINO, A. C., ANTUNES, M.T. & MARÍN-FERRER, J.M. (2010): New fossil teeth of the White Shark (*Carcharodon carcharias*) from the Early Pliocene of Spain. Implication for its paleoecology in the Mediterranean. – Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, **256** (1): 7–16. doi: [10.1127/0077-7749/2009/0029](https://doi.org/10.1127/0077-7749/2009/0029)
- ANTUNES, M.T. & JONET, S. (1970): Requins de l'Helvétien supérieur et du Tortonien de Lisbonne. – Revista da Faculdade de Ciências da Universidade de Lisboa, C-Ciências naturais, (2), **16** (1): 119–280.
- ANTUNES, M.T., JONET, S. & NASCIMENTO, A. (1981): Vertébrés (crocodiliens, poissons) du Miocène marin de l'Algarve occidentale. – Ciências da Terra (UNL), **6**: 9–38
- BASSANI, F. (1901): Su alcuni avanzi di pesci del Pliocene toscano. – Monitore Zoologico Italiano, **12** (7): 189–191.
- BAUZÁ RULLÁN, J. (1949): Contribuciones al conocimiento de la fauna ictiológica fósil de Mallorca. – Boletín

- de la Real Sociedad Española de Historia Natural, **47**: 203–217.
- BAUZÁ RULLÁN, J. (1953): Contribuciones al conocimiento de la ictiología fósil de Cataluña y Baleares. – Memorias y comunicaciones del Instituto Geológico Provincial, **10**: 5–10.
- BAUZÁ RULLÁN, J. (1955): Contribuciones al conocimiento de la fauna ictiológica fósil de España. Otolitos fósiles de Mallorca. – Bolletí de la Societat d'Història Natural de les Balears, **1955** (1–3): 71–79.
- BELLOCCHIO, G., CARBONI, M.G., NAMI, M. & PALLINI, G. (1991): Fauna ad ittiodontoliti del Pliocene di Allerona (Terni, Umbria). – Bollettino della Società dei Naturalisti in Napoli, **100**: 41–73.
- 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, **26** (3): 387–402. doi: [10.1111/bre.12031](https://doi.org/10.1111/bre.12031)
- 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, **39** (3): article #e1645148. doi: [10.1080/02724634.2019.1645148](https://doi.org/10.1080/02724634.2019.1645148)
- BONAPARTE, C.L. (1838): Selachorum tabula analytica. – Nuovi Annali delle Scienze Naturali, **1** (2): 195–214.
- BOR, T., REINECKE, T. & VERSCHUEREN, S. (2012): Miocene Chondrichthyes from Winterswijk-Miste, The Netherlands. – Palaeontos, **21**: 1–136.
- BRISWALTER, G. (2009): Inventaire des Élasmobranches (requins, raies, chimères) des dépôts molassiques du Sud-Luberon (Miocène supérieur), Cabrières d'Aigues (Vaucluse) France. – Courriers scientifiques du Parc naturel Régional du Lubéron, Hors Série: 1–100.
- CAPPETTA, H. (1970): Les sélaciens du Miocène de la région de Montpellier. – Palaeovertebrata, Mémoire extraordinaire, **1970**: 1–139.
- CAPPETTA, H. (1992): Carcharhiniformes nouveaux (Chondrichthyes, Neoselachii) de l'Yprésien du Bassin de Paris. – Geobios, **25** (5): 639–646. doi: [10.1016/0016-6995\(92\)80103-K](https://doi.org/10.1016/0016-6995(92)80103-K)
- CAPPETTA, H. (2006): Elasmobranchii Post-Triadici (Index specierum et generum). – In: RIEGRAF, W. (ed.): Fossilium Catalogus I: Animalia, **142**: 472 pp.; Leiden (Backhuys).
- CAPPETTA, H. (2012): Chondrichthyes. Mesozoic and Cenozoic Elasmobranchii: Teeth. – In: SCHULTZE, H.-P. (ed.): Handbook of Paleichthyology, **3E**: 512 pp.; Munich (Pfeil).
- CAPPETTA, H. & CAVALLO, O. (2006): Les Sélaciens du Pliocène de la région d'Alba (Piémont, Italie Nord-Ouest). – Rivista Piemontese di Storia Naturale, **27**: 33–76.
- CAPPETTA, H., GRANIER, J. & LEDOUX, J.-C. (1967): Deux faunes de sélaciens du Miocène méditerranéen de France et leur signification bathymétrique. – Compte Rendu sommaire des Séances de la Société Géologique de France, **7**: 292–294.
- CASE, G.R. (1980): A selachian fauna from the Trent Formation, Lower Miocene (Aquitanian) of Eastern North Carolina. – Palaeontographica, (A), **171**: 75–103.
- CIGALA FULGOSI, F. (1996): Rare oceanic deep water squaloid sharks from the Lower Pliocene of the Northern Apennines (Parma province, Italy). – Bollettino della Società Paleontologica Italiana, **34** (3): 301–322.
- CIGALA FULGOSI, F., CASATI, S., ORLANDINI, A. & PERSICO, D. (2009): A small fossil fish fauna, rich in *Chlamydoselachus* teeth, from the Late Pliocene of Tuscany (Siena, central Italy). – Cenozoic Research, **6** (1–2): 3–23.
- 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, **81** (4): 527–544.
- COLLARETA, A., BOSSELAERS, M. & BIANUCCI, G. (2016): Jumping from turtles to whales: a Pliocene fossil record depicts an ancient dispersal of *Chelonibia* on mysticetes. – Rivista Italiana di Paleontologia e Stratigrafia, **122** (2): 35–44.
- COLLARETA, A., CASATI, S. & DI CENCIO, A. (2017a): A pristid sawfish from the lower Pliocene of Lucciolabella (Radiconfani Basin, Tuscany, central Italy). – Atti della Società Toscana di Scienze Naturali, Memorie, (A), **124**: 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, **287** (3): 307–316. doi: [10.1127/njgpa/2018/0718](https://doi.org/10.1127/njgpa/2018/0718)
- 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, **284** (3): 289–297. doi: [10.1127/njgpa/2017/0663](https://doi.org/10.1127/njgpa/2017/0663)
- COLLARETA, A., CIGALA FULGOSI, F. & BIANUCCI, G. (2019): A new kogiid sperm whale from northern Italy supports psychrospheric conditions in the early Pliocene Mediterranean Sea. – Acta Palaeontologica Polonica, **64** (3): 609–626. doi: [10.4202/app.00578.2018](https://doi.org/10.4202/app.00578.2018)
- 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, **53** (1), Supplement: 15–61.
- COMPAGNO, L.J.V. (1984): FAO species catalogue. Vol 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. – FAO Fisheries Synopsis, **125**: 251–655.
- COSTANTINI, A., LAZZAROTTO, A., MAZZANTI, R., MAZZEI, R., SALVATORINI, G. & SANDRELLI, F. (2004): Note illustrative della Carta Geologica d'Italia alla scala 1:50.000. Foglio 285 Volterra. – 153 pp.; Roma (Servizio Geologico d'Italia).
- DE CEUSTER, J. (1976): Stratigrafische interpretatie van jongcenozoische afzettingen bij Rumst (België, provincie Antwerpen) en beschrijving van de in een post-Mioceen basisgrind aangetroffen vissefauna, II. Systematische

- beschrijvingen en conclusies. – Mededelingen van de Werkgroep voor Tertiaire en Kwartaire Geologie, **13** (4): 119–172.
- DE STEFANO, G. (1909): Osservazioni sulla ittiofauna pliocenica di Orciano e San Quirico in Toscana. – Bollettino della Società Geologica Italiana, **28** (3): 539–648.
- DOMINICI, S., DANISE, S. & BENVENUTI, M. (2018): Pliocene stratigraphic paleobiology in Tuscany and the fossil record of marine megafauna. – *Earth-Science Reviews*, **176**: 277–310. doi: [10.1016/j.earscirev.2017.09.018](https://doi.org/10.1016/j.earscirev.2017.09.018)
- EVERAERT, S., DE SCHUTTER, P., MARIËN, G., CLEEMPUT, G., VAN BOECKEL, J., RONDELEZ, D. & BOR, T. (2019): Een vroeg-miocene fauna uit het Zand van Kiel (Formatie van Berchem) bij Post X in Berchem (Antwerpen). – *Afzettingen*, **40** (4): 83–100.
- GILL, T.N. (1862): Analytical synopsis of the order of Squalli; and revision of the nomenclature of the genera. – *Annals of the Lyceum of Natural History of New York*, **7**: 367–408. doi: [10.1111/j.1749-6632.1862.tb00166.x](https://doi.org/10.1111/j.1749-6632.1862.tb00166.x)
- HERBERT, T.D., LAWRENCE, K.T., TZANOVA, A., PETERSON, L.C., CABALLERO-GILL, R. & KELLY, C.S. (2016): Late Miocene global cooling and the rise of modern ecosystems. – *Nature Geoscience*, **9** (11): 843–847. doi: [10.1038/ngeo2813](https://doi.org/10.1038/ngeo2813)
- HUXLEY, T.H. (1880): On the application of the laws of evolution to the arrangement of the Vertebrata, and more particularly of the Mammalia. – *Proceedings of the Zoological Society of London*, **1880**: 649–662.
- JONET, S. (1978): Le Tortonien supérieur (TVII-b) des environs de Fonte da Telha (Peninsule de Setubal) et ses faunes. – *Comunicações dos Serviços Geológicos de Portugal*, **63**: 13–51.
- LANDINI, W. (1977): Revisione degli «Ittiodontoliti pliocenici» della collezione Lawley. – *Palaeontographia Italica*, **70**: 92–134.
- LAWLEY, R. (1876): Nuovi studi sopra ai pesci ed altri vertebrati fossili delle colline Toscane. – 122 pp.; Florence (Tipografia dell'Arte della Stampa).
- MAÑÉ, R., MAGRANS, J. & FERRER, E. (1996): Ictiologia fòssil del Pliocè del Baix Llobregat. II. Selacis pleurotremats. – *Batalleria*, **6**: 19–33.
- 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*, **58** (2): 165–170.
- MANGANELLI, G., BENOCCI, A. & SPADINI, V. (2006): The scientific bibliography of Roberto Lawley (1818–1881) and his contribution to the study of fossil sharks. – *Archives of Natural History*, **33** (2): 267–281. doi: [10.3366/anh.2006.33.2.267](https://doi.org/10.3366/anh.2006.33.2.267)
- MARÍN, J.M. (1992): Paleoiictiologia de algunos yacimientos neógenos de la provincia de Alicante (II). – *Cidaris – Rivista Ilicitana de Paleontología y Mineralogía*, **1** (2): 4–24.
- MARSILI, S. (2006): Analisi sistematica, paleoecologica e paleobiogeografica della selaciofauna Plio-Pleistocenica del Mediterraneo. – Unpublished PhD Thesis in Earth Science, Università di Pisa.
- MARSILI, S. (2007): A new bathyal shark fauna from the Pleistocene sediments of Fiumefreddo (Sicily, Italy). – *Geodiversitas*, **29** (2): 229–247.
- MARSILI, S. (2008): Systematic, paleoecologic and paleobiogeographic analysis of the Plio-Pleistocene Mediterranean elasmobranch fauna. – *Atti della Società Toscana di Scienze Naturali, Memorie*, (A), **113**: 81–88.
- MARTINI, I., ARRAGONI, S., ALDINUCCI, M., FORESI, L.M., BAMBINI, A.M. & SANDRELLI, F. (2013): Detection of detached forced-regressive nearshore wedges: a case study from the central-southern Siena Basin (Northern Apennines, Italy). – *International Journal of Earth Sciences*, **102** (5): 1467–1489. doi: [10.1007/s00531-013-0876-6](https://doi.org/10.1007/s00531-013-0876-6)
- MINWER-BARAKAT, R., GARCÍA-ALIX, A., MARTÍN SUÁREZ, E., FREUDENTHAL, M. & VISERAS, C. (2012): Micromammal biostratigraphy of the Upper Miocene to lowest Pleistocene continental deposits of the Guadix basin, southern Spain. – *Lethaia*, **45** (4): 594–614. doi: [10.1111/j.1502-3931.2012.00324.x](https://doi.org/10.1111/j.1502-3931.2012.00324.x)
- MORA MOROTE, P. (1996): Peces Galeomorfos y Squatinomorfos en el Plioceno de Guadamar del Segura (Alicante). – *Cidaris – Rivista Ilicitana de Paleontología y Mineralogía*, **5** (10): 98–124.
- NALIN, R., GHINASSI, M., FORESI, L.M. & DALLANAVE, E. (2016): Carbonate deposition in restricted basins: a Pliocene case study from the central Mediterranean (Northwestern Apennines), Italy. – *Journal of Sedimentary Research*, **86** (3): 236–267. doi: [10.2110/jsr.2016.14](https://doi.org/10.2110/jsr.2016.14)
- PRISTA, G., AGOSTINHO, R. & CACHÃO, M. (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*, **7** (1): 65–83. doi: [10.1515/geo-2015-0007](https://doi.org/10.1515/geo-2015-0007)
- PRISTA, G., ESTEVENS, M., AGOSTINHO, R. & CACHÃO, M. (2013): The disappearance of the European/North African Sirenia (Mammalia). – *Palaeogeography, Palaeoclimatology, Palaeoecology*, **387**: 1–5. doi: [10.1016/j.palaeo.2013.07.013](https://doi.org/10.1016/j.palaeo.2013.07.013)
- PROBST, J. (1879): Beiträge zur Kenntniss der fossilen Fische aus der Molasse von Baltringen. Hayfische (Selachioidei A. Günther.) (Schluss.). – *Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg*, **35**: 127–191.
- REINECKE, T. (2014): Two new scyliorhinid shark species (Elasmobranchii, Carcharhiniformes, Scyliorhinidae), from the Sülstorf Beds (Chattian, Late Oligocene) of the southeastern North Sea Basin, northern Germany. – *Palaeovertebrata*, **38** (1): 1–8. doi: [10.18563/pv.38.1.e1](https://doi.org/10.18563/pv.38.1.e1)
- REINECKE, T., BALSBERGER, M., BEAURY, B. & POLLERSPÖCK, J. (2014): The elasmobranch fauna of the Thalberg Beds, early Egerian (Chattian, Oligocene), in the Subalpine Molasse Basin near Siegsdorf, Bavaria, Germany. – *Palaeontos*, **26**: 3–129.
- 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*, **20**: 1–170.
- REINECKE, T., MOTHS, H., GRANT, A. & BREITKREUTZ, H. (2005): Die Elasmobranchier des Norddeutschen Chat-

- tiums, insbesondere des Sternberger Gesteins (Eochattium, Oberes Oligozän). – *Palaeontos*, **8**: 1–134.
- REYNAUD, J.-Y. & JAMES, N.P. (2012): The Miocene Sommières basin, SE France: Bioclastic carbonates in a tide-dominated depositional system. – *Sedimentary Geology*, **282**: 360–373. doi: [10.1016/j.sedgeo.2012.10.006](https://doi.org/10.1016/j.sedgeo.2012.10.006)
- 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*, **32** (3): 686–707. doi: [10.1080/02724634.2012.659100](https://doi.org/10.1080/02724634.2012.659100)
- SORIA, J.M., CARACUEL, J.E., YÉBENES, A., FERNÁNDEZ, J. & VISERAS, C. (2005): The stratigraphic record of the Messinian salinity crisis in the northern margin of the Bajo Segura Basin (SE Spain). – *Sedimentary Geology*, **179** (3–4): 225–247. doi: [10.1016/j.sedgeo.2005.05.011](https://doi.org/10.1016/j.sedgeo.2005.05.011)
- 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*, **54** (1): 67–70.
- SPROVIERI, R. (1992): Mediterranean Pliocene biochronology: a high resolution record based on quantitative planktonic foraminifera distribution. – *Rivista Italiana di Paleontologia e Stratigrafia*, **98** (1): 61–100.
- VIALLE, N., ADNET, S. & CAPPETTA, H. (2011): A new shark and ray fauna from the Middle Miocene of Mazan, Vaucluse (southern France) and its importance in interpreting the paleoenvironment of marine deposits in the southern Rhodanian Basin. – *Swiss Journal of Palaeontology*, **130**: 241–258. doi: [10.1007/s13358-011-0025-4](https://doi.org/10.1007/s13358-011-0025-4)
- VIOLANTI, D. (2012): Pliocene Mediterranean foraminiferal biostratigraphy: a synthesis and application to the paleoenvironmental evolution of Northwestern Italy. – In: Eliotok, Ö. (ed.): *Stratigraphic analysis of layered deposits*: 123–160; InTech
- WARD, L.W. (1978): Stratigraphic revision of the middle Eocene, Oligocene, and lower Miocene – Atlantic coastal plain of North Carolina. – *United States Geological Survey Bulletin*, **1457-F**: 1–23.
- 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*, **88** (3): 837–1037. doi: [10.1111/jfb.12874](https://doi.org/10.1111/jfb.12874)
- WHITE, W., FAHMI, F. & WEIGMANN, S. (2019): A new genus and species of catshark (Carcharhiniformes: Scyliorhinidae) from eastern Indonesia. – *Zootaxa*, **4691** (5): 444–460. doi: [10.11646/zootaxa.4691.5.2](https://doi.org/10.11646/zootaxa.4691.5.2)

Manuscript received: January 12nd, 2020.

Revised version accepted by the Stuttgart editor: January 15th, 2020.

Addresses of the authors:

ALBERTO COLLARETA (corresponding author), MARCO MERELLA, Dipartimento di Scienze della Terra, Università di Pisa, via S. Maria 53, Pisa, 56126 Pisa, Italy; e-mails: alberto.collareta@unipi.it; marcomerella1994@gmail.com

FREDERIK H. MOLLEN, Elasmobranch Research, Rehaegenstraat 4, 2820 Bonheiden, Belgium; e-mail: frederik.mollen@gmail.com

SIMONE CASATI, Gruppo Avis Mineralogia e Paleontologia Scandicci, Piazza Vittorio Veneto 1, Badia a Settimo, 50018 Scandicci, Italy; e-mail: simonecasati@alice.it

ANDREA DI CENCIO, Gruppo Avis Mineralogia e Paleontologia Scandicci, Piazza Vittorio Veneto 1, Badia a Settimo, 50018 Scandicci, Italy & Studio Tecnico Geologia e Paleontologia, via Fratelli Rosselli 4, San Casciano Val di Pesa, 50026 Firenze, Italy;

e-mail: andreadicencio@geologiaepaleontologia.eu