



**The shark-toothed dolphin *Squalodon* (Cetacea: Odontoceti)
from the remarkable Montagna della Majella
marine vertebrate assemblage (Bolognano Formation, central Italy)**

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Abstract: The extinct family Squalodontidae consists of heterodont, medium-sized odontocetes, featuring a long rostrum that houses large, procumbent incisors and heavily ornamented postcanine teeth carrying accessory denticles, hence their vernacular name, "shark-toothed dolphins". These longirostrine toothed whales are often seen as bridging the anatomical gap between archaic Oligocene odontocetes and their late Miocene to Holocene relatives. Possibly among the major marine predators of their time, the shark-toothed dolphins are important components of several lower Miocene marine-mammal assemblages from the North Atlantic and Mediterranean/Paratethysian realms. In the present work, a partial skull of Squalodontidae is described from the strata of the Bolognano Formation cropping out in the northeastern sector of the Montagna della Majella massif (Abruzzo, central Italy), which has previously yielded a rich lower Miocene marine-vertebrate assemblage, including eleven taxa of elasmobranchs as well as subordinate teleosts and very fragmentary remains of marine reptiles and mammals. The specimen consists of the anterodorsal portion of a rostrum, preserving parts of both premaxillae and left maxilla, and the anteriormost seven upper left teeth. This partial skull is here identified as belonging to the genus *Squalodon*, whose presence in the Montagna della Majella vertebrate assemblage had already been tentatively proposed on the basis of two fragmentary teeth. The paleontological significance of this find is discussed in the broader framework of the Euromediterranean record of *Squalodon*.

Key-words:

- Burdigalian;
- lower Miocene;
- Mediterranean Basin;
- Neoceti;
- paleobiogeography;
- paleoecology;
- Squalodontidae;
- toothed whales

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Résumé : Le dauphin à dents de requin *Squalodon* (Cetacea: Odontoceti) du remarquable assemblage de vertébrés marins de Montagna della Majella (Formation de Bolognano, Italie centrale). - La famille éteinte des Squalodontidae comprend des odontocètes de taille moyenne, hétérodontes, présentant un long rostre qui abrite de grandes dents incisives procombantes et de post-canines très ornées comportant des denticules accessoires, d'où leur nom vernaculaire "dauphins à dents de requin". Ces odontocètes longirostres sont souvent perçus comme des formes intermédiaires comblant le fossé anatomique entre les odontocètes oligocènes archaïques et leurs parents du Miocène tardif jusqu'à l'Holocène. Probablement parmi les principaux prédateurs marins de leur époque, les dauphins à dents de requin sont d'importants éléments au sein de plusieurs assemblages de mammifères marins du Miocène inférieur des domaines nord-atlantique et méditerranéen/para-téthysien. Dans le présent travail, un crâne partiel de Squalodontidae est décrit dans les couches de la Formation de Bolognano affleurant dans le secteur nord-est du massif de Montagna della Majella (Abruzzes, Italie centrale), qui a livré par le passé un riche assemblage de vertébrés marins du Miocène inférieur, comprenant onze taxons d'élasmodontes, ainsi que des téléostéens moins nombreux et des restes très fragmentaires de reptiles et de mammifères marins. Ce spécimen comprend la partie antéro-dorsale du rostre, comportant des parties des deux prémaxillaires et du maxillaire gauche, et les sept dents supérieures gauches les plus antérieures. Ce crâne partiel est identifié ici comme appartenant au genre *Squalodon*, dont la présence dans l'assemblage de vertébrés de Montagna della Majella avait déjà été proposée provisoirement sur la base de deux dents fragmentaires. La signification paléontologique de cette découverte est discutée dans le contexte plus large du registre euro-méditerranéen du genre *Squalodon*.

Mots-clefs :

- Burdigalien ;
- Miocène inférieur ;
- bassin méditerranéen ;
- Neoceti ;
- paléobiogéographie ;
- paléoécologie ;
- Squalodontidae ;
- odontocètes

1. Introduction

The extinct family Squalodontidae consists of heterodont, medium-sized odontocetes, featuring a long rostrum that houses large, procumbent incisors and heavily ornamented postcanine teeth provided with accessory denticles, hence their vernacular name "shark-toothed dolphins" (MARX *et al.*, 2016, and references therein). Known from a rather rich fossil record which ranges from the upper Oligocene (Chattian) to the upper middle Miocene (Serravallian), squalodontids are important components of several lower Miocene marine-mammal assemblages from the North Atlantic and Mediterranean/Paratethysian realms (*e.g.*, DOOLEY, 1998). Possibly among the major marine predators of their time, squalodontids are often seen as bridging the anatomical gap between the archaic Oligocene odontocetes and their late Miocene to Holocene relatives (GODFREY, 2013; MARX *et al.*, 2016). For a long time, these longirostine toothed whales have been regarded as members of the crown Odontoceti clade, in the superfamily Platanistoidea, which also includes the South Asian river dolphin *Platanista gangetica* (*e.g.*, MUIZON, 1991, 1994; FORDYCE, 1994; FORDYCE & MUIZON, 2001; TANAKA & FORDYCE, 2016); now however, many phylogenetic analyses recover squalodontids as late-branching stem odontocetes (*e.g.*, GEISLER & SANDERS 2003; TANAKA & FORDYCE, 2014; CHURCHILL *et al.*, 2016; BIANUCCI *et al.*, 2018a). The current lack of consensus upon the phylogenetic position of the squalodontids is highlighted by the observation that several recent papers dealing with the affinities of the heterodont long-snouted toothed whales present both the aforementioned solutions as plausible (*e.g.*,

TANAKA & FORDYCE, 2015a, 2015b; LAMBERT *et al.*, 2018; MUIZON *et al.*, 2018; VIGLINO *et al.*, 2018).

The type genus of Squalodontidae, *i.e.*, *Squalodon*, has been identified from several lower-middle Miocene deposits of the North Atlantic (including the southern North Sea), the Mediterranean (including some Italian sites), and the Paratethys (*e.g.*, BIANUCCI & LANDINI, 2002; DOOLEY, 2003; SYMEONIDIS *et al.*, 2004; MARSILI *et al.*, 2007). In the remarkable lower Miocene marine-vertebrate assemblage of the Bolognano Formation (Montagna della Majella massif, central Apennines, central Italy), *Squalodon* was tentatively identified on the basis of two isolated partial teeth whose preservation state fails to permit a definitive and unambiguous genus-level assignment (MARSILI *et al.*, 2007). In the present paper, we report on a partial squalodontid rostrum, exhibiting seven articulated teeth, from the Bolognano strata exposed close to the village of Pretoro, in the northeastern sector of the massif. This fossil specimen is here referred to *Squalodon* sp. and its paleontological significance is briefly discussed in the broader framework of the Euro-mediterranean record of this genus.

2. Geological and paleontological framework

The Montagna della Majella, from which the fossil specimen described here comes, is a wide massif located in the central Apennines (Abruzzo region, central Italy). The massif (Fig. 1) is largely underlain by a thick package of upper Jurassic to upper Miocene carbonates developed on the northern margin of the Apulian platform and forming an east-verging, box-shaped anticline. From



the Santonian, the Mesozoic-Cenozoic succession of the Montagna della Majella testifies to open-shelf and carbonate-ramp depositional environments (BALLY, 1954; CRESCENTI *et al.*, 1969; CATE-
NACCI, 1974; ACCARIE, 1988; VECSEI *et al.*, 1998; GHISETTI & VEZZANI, 2002; SCISCIANI *et al.*, 2002; RUSTICHELLI *et al.*, 2012, 2013; BRANDANO *et al.*, 2013). The youngest lithostratigraphic unit in the succession is the upper Oligocene to upper Mio-
cene Bolognano Formation, a sedimentary wedge composed of three stacked warm-water carbona-
te-ramp depositional systems (MUTTI *et al.*, 1997; VECSEI & SANDERS, 1999; DANESE, 1999; MARSILI *et al.*, 2007). The middle portion of the Bolognano Formation, which has been referred to the lower Burdigalian SBZ 25 zone of CAHUZAC and POIGNANT (1997), has yielded a rich marine-vertebrate assemblage, including eleven taxa of elasmo-
branchs (*Carcharias acutissima*, *Carcharias cuspi-
data*, *Carcharocles chubutensis*, *Cosmopolitodus hastalis*, *Isurus oxyrinchus*, "*Isurus*" sp., *Hemi-
pristis serra*, *Galeocerdo aduncus*, *Negaprion* cf. *eurybathrodon*, *Parotodus benedeni*, and *Physo-
galeus contortus*), eight taxa of teleosts (*Chilo-
myxterus* sp., *Diplodus* sp. and two indeterminate sparids, *Diodon* sp., *Labrodon* sp., *Sphyræna* sp., and *Trigonodon jugleri*), an indeterminate croco-
dile, and two taxa of odontocetes (an indetermi-
nate kentriodontid and a squalodontid-like taxon tentatively identified as *Squalodon*). On the whole, this fossil vertebrate assemblage depicts a warm-water, food-rich paleoenvironment located close to the coast (MARSILI *et al.*, 2007); more-
over, its taxonomic composition (including an elasmobranch taxon, *C. chubutensis*, which is only known from lower Miocene deposits; CARRILLO-
BRICEÑO *et al.*, 2019) supports the estimated Burdigalian age for the middle portion of the Bolognano Formation.

The cetacean fossil described here comes from the Bolognano strata exposed at a quarry close to the village of Pretoro (approximate geographic coordinates: 42°13'N, 14°08'E), in the north-
eastern portion of the Montagna della Majella (Fig. 1). The specimen was collected several de-
cades ago by a local quarryman and its exact stratigraphic position is unknown. Nevertheless, the fossiliferous lower Miocene beds of the Bolog-
nano Formation are well exposed in the north-
eastern portion of the Montagna della Majella, southeast of Lettomanoppello (MARSILI *et al.*, 2007). Considering that all other discoveries of marine vertebrates (including odontocete re-
mains) from this area of the massif come from the middle portion of the Bolognano Formation, an early Miocene age can be confidently proposed for the fossil specimen described in the present paper.

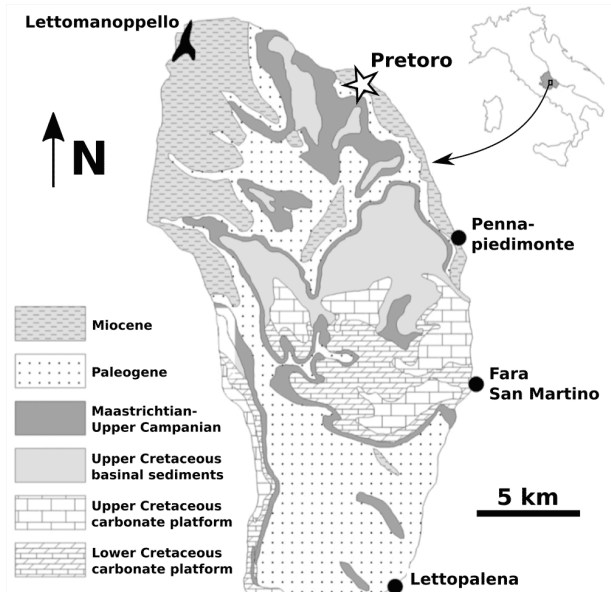


Figure 1: Location of the site where the fossil cetacean specimen MSNUP I-16944 was found (Pretoro, black star) and schematic regional geological map. Modified after MARSILI *et al.* (2007).

3. Systematic paleontology

CETACEA BRISSON, 1762

PELAGICETI UHEN, 2008

NEOCETI FORDYCE & MUIZON, 2001

ODONTOCETI FLOWER, 1867

SQUALODONTIDAE BRANDT, 1873

***Squalodon* GRATELOUP, 1840**

***Squalodon* sp.**

Figs. 2 -3

Material and repository. An incomplete rostrum, featuring seven articulated teeth, enclosed in a limestone block kept at Museo di Storia Naturale dell'Università di Pisa (=MSNUP) with accession number MSNUP I-16944.

Occurrence. MSNUP I-16944 was collected at a quarry close to the village of Pretoro (approximate geographic coordinates: 42°13'N, 14°08'E), in the northeastern portion of the Montagna della Majella massif (central Apennines, central Italy), where the lower Miocene strata of the Oligo-Miocene Bolognano Formation are exposed (Fig. 1).

Description, comparisons, and remarks. MSNUP I-16944 consists of the anterodorsal portion of the rostrum of an odontocete, preserving parts of both premaxillae and left maxilla, as well as the anteriormost seven upper left teeth. This

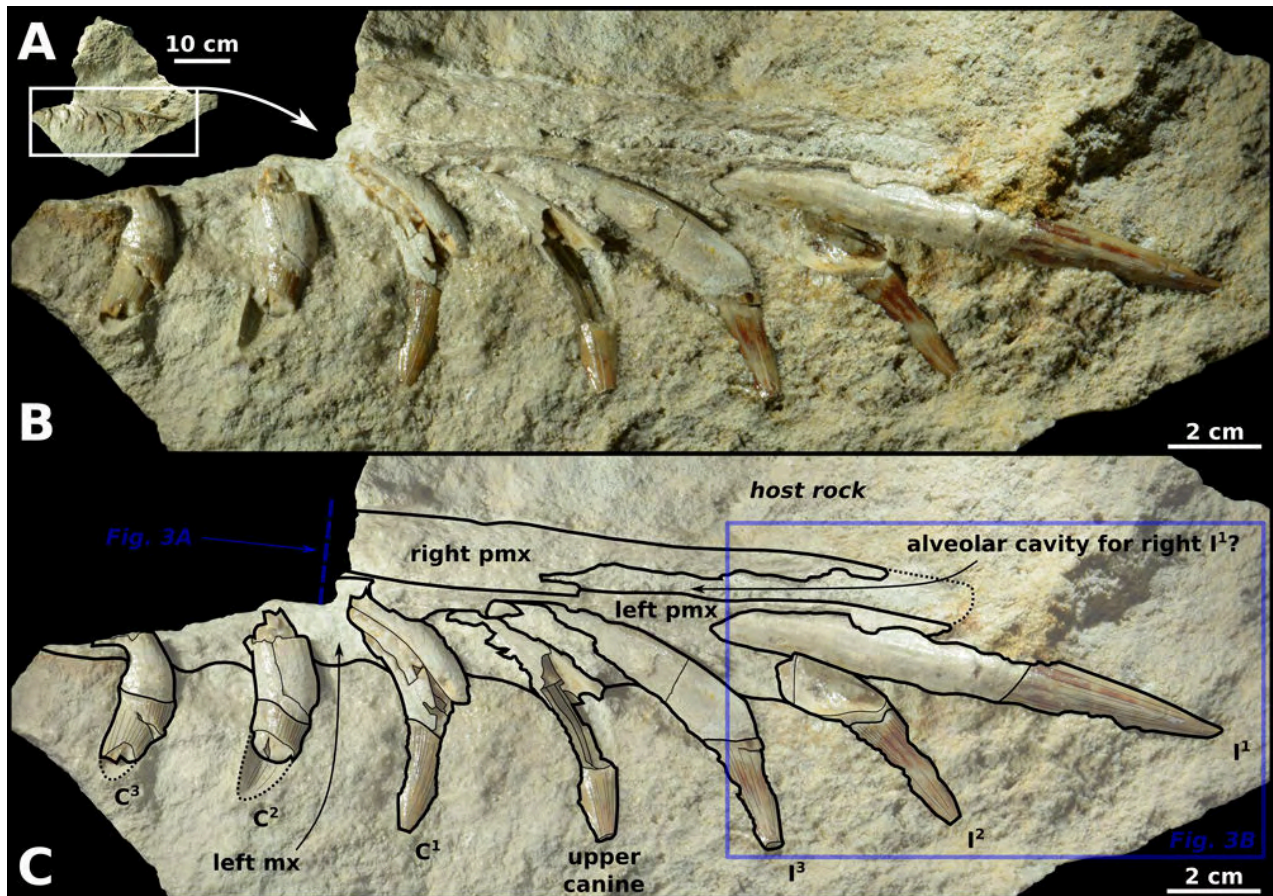


Figure 2: MSNUP I-16944, partial skull of *Squalodon* sp., enclosed in a limestone block from the Bolognano Formation of central Italy. A) General view of the fossil-bearing block. B) Incomplete rostrum in right-ventrolateral view and C) corresponding line drawing (note that the teeth are displayed in lingual view).

fragment of rostrum is about 20 cm long (not including the length of the first incisor) and is preserved within a hard limestone block that could not be prepared mechanically without damaging the cetacean fossil; as such, only the right ventrolateral aspect (Fig. 2) and a transverse section (Fig. 3.A) of the rostrum can be observed and described. In the exposed right ventrolateral view, the premaxillae and right maxilla appear as strongly abraded. The lateral margins of the preserved anterior portion of the rostrum are almost straight and roughly parallel to each other, recalling the condition observed in various early Neogene groups of heterodont odontocetes, including Squalodontidae. An anteroposteriorly elongated opening that occurs at the anterior termination of the left premaxilla is here interpreted as representing the alveolar cavity of the missing first upper right incisor (Fig. 2). At the level of the posterior preserved end of the rostrum, the transversely sectioned mesorostral groove is roughly oval (*i.e.*, slightly higher than wide) and open upwards (Fig. 3.A).

The seven anteriormost upper left teeth are preserved *in situ*, *i.e.*, partly embedded in the left premaxilla and maxilla, the labial face of these teeth being hidden by the hard host rock (Fig. 2). The preserved teeth are the three incisors (I^1 to I^3), the canine, and the three anteriormost post-

canines (*i.e.*, the cheek teeth C^1 to C^3). All of these teeth are single-rooted and have similar (*i.e.*, roughly conical) crown morphologies. Mesial/distal carinae (*i.e.*, keels) appear to be present at least on the crowns of I^1 , C^2 , and C^3 , providing them with slightly ogival transverse sections. The crown of the incisors is considerably shorter than the root and strongly procumbent. The anteriormost incisor (I^1) is almost horizontal, and is dorsal to I^2 ; in turn, I^2 and I^3 are moderately curved and have a more ventrolateral orientation (Figs. 2, 3.B). The roots of I^2 and I^3 exhibit distinct bulges close to the root-crown passage. The canine is badly damaged but seems to be more strongly curved than the adjoining incisor, with a proportionally shorter root. The morphology of the three preserved anteriormost postcanine teeth recalls that of the canine, from which they mainly differ by their stronger curvature and shorter crowns that are more posteriorly oriented. No accessory denticles could be observed along the crowns of C^1 , C^2 , and C^3 . Enamel ornamentation is present on the crown of all the preserved teeth but particularly evident on C^2 and C^3 ; it consists of delicate, slightly undulatory, closely spaced apicobasal ridges (Figs. 2, 3.B). Dental wear is ubiquitous in form of apical wear facets, here interpreted as attritional.

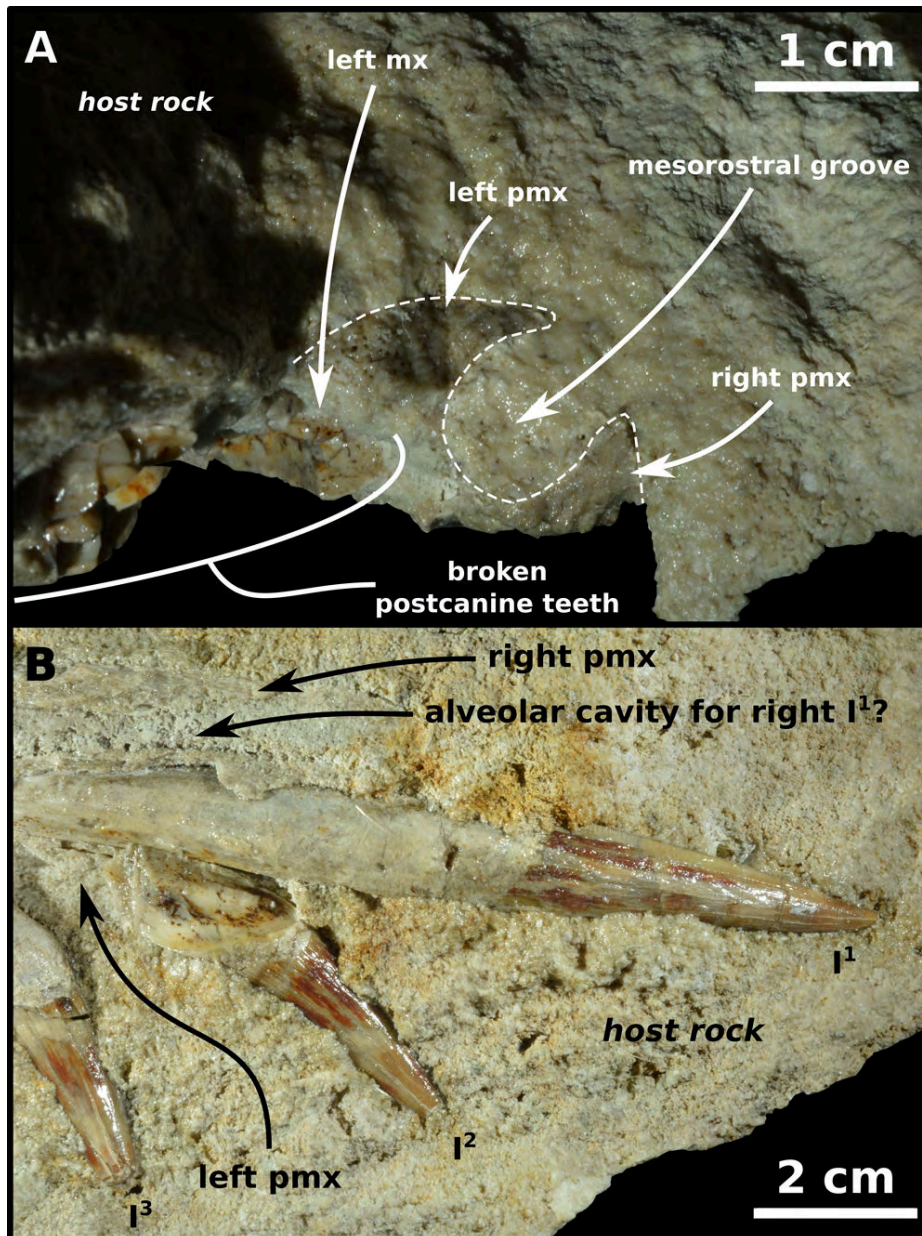


Figure 3: MSNUP I-169 44, partial skull of *Squalodon* sp., enclosed in a limestone block from the Bolognano Formation of central Italy. A) Detail of the transverse section of the rostrum at the level of the root of the first upper postcanine (C^1) left tooth; note the dorsally open mesorostral groove (the dashed white line denotes the extent of the bone). B) Detail of the upper left incisors in lingual view; note the root of I^1 situated dorsal to that of I^2 , the strong protrusion of the teeth, and the gentle longitudinal fluting of the tooth crowns.

MSNUP I-16944 is attributed to Squalodontidae owing to the observation of large, procumbent incisors, whose crowns display gentle longitudinal fluting of the dental enamel, with the root of I^1 being placed dorsal to that of I^2 (e.g., DOOLEY, 1998; MARX *et al.*, 2016; MUIZON *et al.*, 2018; VIGLINO *et al.*, 2018). Four genera of Squalodontidae are currently represented by diagnostic material: *Squalodon*, *Eosqualodon*, *Phoberodon*, and *Kelloggia* (a possible junior synonym of *Squalodon*; FORDYCE and MUIZON, 2001) (MARX *et al.*, 2016; MUIZON *et al.*, 2018); recently, however, *Phoberodon* has been recognized as a stem odontocete or an early-diverging platanistoid not closely related to the squalodontids (VIGLINO *et al.*, 2018). Whereas the mesorostral groove of MSNUP I-16944 is widely open dorsally at the level of the root of the first upper postcanine left

tooth, the mesorostral groove of the European form *Eosqualodon* is almost completely roofed by the medial portion of the premaxillae from the apex of the rostrum to a much more posterior level (personal observation on *Eosqualodon langewieschei*). *Eosqualodon* further differs from MSNUP I-16944 in its pattern of dental ornamentation, which consists of stronger and less closely spaced ridges and sulci. MSNUP I-16944 also clearly differs from the South American form *Phoberodon*, in which the third upper incisor is curved lingually (with the apex pointing medially) and the upper canine and anteriormost cheek teeth exhibit widely separated enamel striations (VIGLINO *et al.*, 2018). By contrast, MSNUP I-16944 closely matches the morphology of *Squalodon*, which is known from several specimens of the Euromediterranean region (Fig. 4).

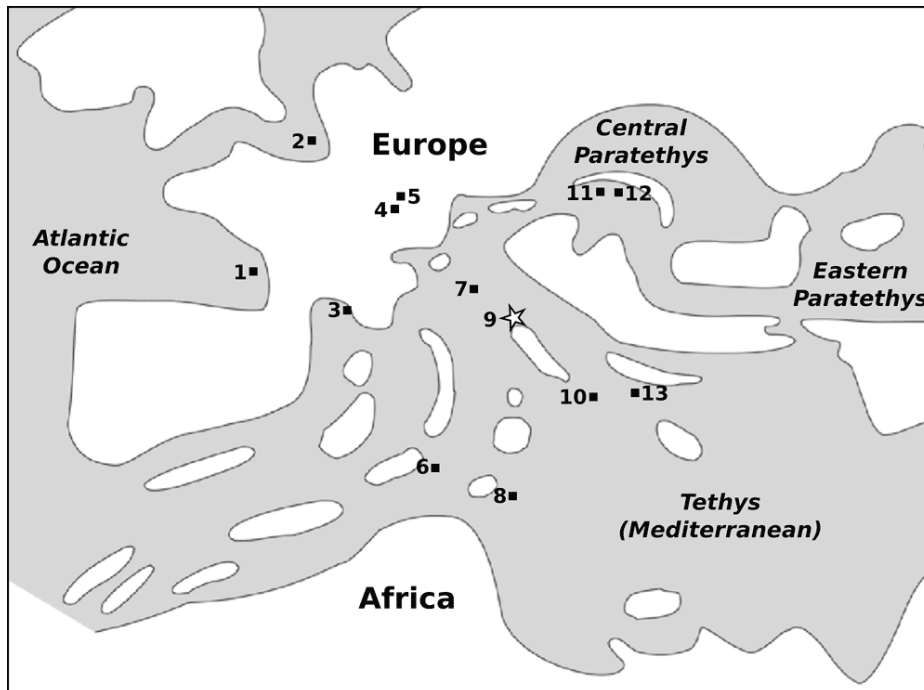


Figure 4: Occurrences of the genus *Squalodon* from lower Miocene deposits of Europe (note that attribution to the early Miocene of the Apulian remains is tentative). 1- Léognan, Bordeaux, southwestern France; 2- Antwerp, northern Belgium; 3- Bari, Saint-Paul-Trois-Châteaux, southern France; 4- Switzerland (various localities); 5- Baltringen, Baden-Württemberg, southwestern Germany; 6- Ragusa, Sicily, southern Italy; 7- Libano and Belluno, Veneto, northern Italy; 8- Malta; 9- Montagna della Majella, Abruzzo, central Italy; 10- Cursi-Melpignano, Apulia, southern Italy; 11- Horné Strháre, Banská Bystrica, southern Slovakia; 12- Mučín, Banská Bystrica, southern Slovakia; 13- Tsotilion, western Macedonia,

Greece. Data after BIANUCCI & LANDINI (2002), SYMEONIDIS *et al.* (2004), and the present study. The paleogeographic reconstruction of the Euromediterranean region in early Miocene times is from RÖGL (1998), modified after SYMEONIDIS *et al.* (2004). The southwestern German and Swiss records are interpreted as reflecting temporary marine transgression over these western Paratethysian sectors.

Species-level attribution of MSNUP I-16944 is challenged by the fragmentary nature of the available material. For example, the Montagna della Majella specimen cannot be compared with the Italian species *Squalodon peregrinus*, for which neither the anterior portion of the rostrum nor the teeth are known (FORNASIERO & DEL FAVERO, 2014). Moreover, an unambiguous species-level determination of these remains would need a detailed revision of several extinct nominal species currently attributed to the genus *Squalodon* (e.g., SYMEONIDIS *et al.*, 2004), which is beyond the scope of this paper. However, the following considerations might lend some support to a tentative referral of MSNUP I-16944 to *Squalodon bellunensis*: 1) no unambiguous dissimilarities in either size or dental morphology distinguish MSNUP I-16944 from specimens of *S. bellunensis* for which the anteriormost portion of the rostrum and the corresponding upper teeth are preserved, e.g., a specimen kept at Museo di Geologia e Paleontologia dell'Università di Padova (=MGPUP) under accession number MGPUP 26131 (Table 1); 2) the type material of *S. bellunensis* comes from a locality that is (and was, in early Miocene times) spatially close to the discovery site of the Montagna della Majella fossil squalodontid; 3) the type horizon of *S. bellunensis* and the fossiliferous portion of the Bolognano Formation are early Miocene in age, and as such, roughly coeval (in particular, they have been referred to the upper Aquitanian-lower Burdigalian and to the lower Burdigalian, respectively). Nevertheless, given the limited diagnostic value of the preserved skull

parts, MSNUP I-16944 is here referred to *Squalodon* sp.

Table 1: Tooth crown height of the upper incisors of *Squalodon* sp. (specimen MSNUP I-16944 from the lower Miocene of the Montagna della Majella massif, central Italy) and *Squalodon bellunensis* (specimen MGPUP 26131 from the lower Miocene of Libano and Belluno, northern Italy). Measurements of MSNUP I-16944 refer to the left tooth row; measurements of MGPUP 26131 refer to the right tooth row. All measurements are expressed in millimeters.

	I ³	I ²	I ¹
MSNUP I-16944	24	33	48
MGPUP 26131	27	30	50

As sometimes observed in the dental remains of juveniles and young adults of extinct odontocetes whose teeth were progressively worn with age due to abrasion or occlusion during feeding (e.g., the stem beaked whale *Messapicetus*; BIANUCCI *et al.*, 2016), apical dental wear is less pronounced in MSNUP I-16944 than in the anteriormost upper teeth of MGPUP 26131 and other full-grown members of *Squalodon*. This difference in the extent of apical dental wear, coupled with the aforementioned overall similarities in size, might indicate that MSNUP I-16944 is a young adult individual.



4. Discussion

The recovery and description of MSNUP I-16944 allows us to confirm the presence of *Squalodon* in the Montagna della Majella marine vertebrate assemblage, thus supporting previous inferences based on much more fragmentary dental material (MARSILI *et al.*, 2007). Moreover, it shows that significant skeletal remains of marine mammals, and not only isolated teeth, might be recovered from the Bolognano Formation. Lending indirect support to this suggestion, DEWAELE *et al.* (2018) have recently proposed that the holotype of the archaic monachine seal *Noriphoca gaudini* collected in the 19th century from the vicinities of Roccamorice (northwestern sector of the Montagna della Majella massif; GUISCARDI, 1870) comes from basal beds of the Bolognano Formation exposed there. These observations encourage the continued search for fossil marine mammals in the Bolognano strata of the Montagna della Majella massif.

In the lower Miocene of the Mediterranean Basin, *Squalodon* is a relatively common odontocete genus, being known from several deposits of France, Italy, Malta and Greece (Fig. 4). In particular, systematically informative specimens of *Squalodon* come from Bari (near Taulignan), Saint-Paul-Trois-Châteaux, southeastern France (*Squalodon bariensis*: GERVAIS, 1853; MUIZON, 1988, 1991) and Libano and Belluno, Veneto, northern Italy (*Squalodon bariensis*, *Squalodon bellunensis*, and *Squalodon peregrinus*: DAL PIAZ, 1900-1917; ROTHAUSEN, 1968; BIANUCCI *et al.*, 2018b). In addition to the Venetian occurrences, in the vicinity of the discovery site of MSNUP I-16944, the genus *Squalodon* has been reported from Aquitanian (or Langhian) strata of the Pietra Leccese, Apulia, southern Italy (as *Squalodon* sp.: BIANUCCI *et al.*, 1994), the lower Miocene of Ragusa, Sicily, southern Italy (as *Squalodon dalpiazzi*: FABIANI, 1949), the lower Miocene of Malta (BIANUCCI *et al.*, 2012), and the lower Miocene of Tsotilion, western Macedonia, Greece (as *Squalodon* cf. *bellunensis*: SYMEONIDIS *et al.*, 2004). In combination with the observations from the literature cited above, our record of a partial skull of *Squalodon* sp. from central Italy indicates that the epeiric seas of the central Mediterranean basin comprised a high-use area for the *Squalodon* populations during the first part of the Miocene.

The putative closest extant relative of squalodontids, the South Asian river dolphin, is one of the two (or three, if the likely extinct baiji, *Lipotes vexillifer*, is taken into account) living cetacean species strictly restricted to freshwater habitats, besides the Amazon river dolphin *Inia geoffrensis*. The occurrence of *Squalodon* sp. reported herein is in a nearshore but truly marine paleoenvironmental setting, and the same can be said for most of the other *Squalodon* localities shown in Figure 4. The Libano-Belluno assemblage, which includes at least three species of *Squalodon* (BIANUCCI *et al.*, 2018b), is found in sandstones that

testify to a delta-front depositional setting (e.g., CASON *et al.*, 1981; COSTA *et al.*, 1996; GHIBAUDO *et al.*, 1996) - an observation that suggests that *Squalodon* might have inhabited both shelfal environments and estuarine (or even riverine) waters. A similar ability to live in both fresh and marine water is observed in some extant genera of true dolphins (e.g., *Sotalia*, the tucuxi and Guiana dolphins, and *Orcaella*, the Irrawaddy and Australian snubfin dolphins) and might have characterized other odontocete lineages in the past (e.g., some platanistids and lipotids; LAMBERT *et al.*, 2008; BIANUCCI *et al.*, 2013; BOESSENECKER & POUST, 2015). Somewhat akin to these extant odontocetes, squalodontids have been interpreted as nektic or nektobenthic cetaceans that thrived in fluvial and/or neritic environments, feeding near the bottom (LANDINI *et al.*, 2005; BIANUCCI & LANDINI, 2002). Interestingly, as reported above, the genera that are currently assigned to Squalodontidae - *Eosqualodon*, *Squalodon* (possibly including the genus *Kelloggia*) and, perhaps, *Phoberodon* - are only known from the coasts of the Atlantic realm and its northeastern cul-de-sac, the Mediterranean/Paratethysian basins. In spite of their rich and long fossil record, spanning the late Oligocene and most of the Miocene, it seems therefore that the squalodontids did not undergo dispersal to the Indo-Pacific waters, which has instead been recently established for a much lesser known and more elusive group of heterodont long-snouted odontocetes such as Inticetidae, an extinct family that is known from a very few discoveries in the Miocene of Peru, the Atlantic coast of the U.S.A., France and Italy (PERI *et al.*, 2019, and references therein). If Squalodontidae were indeed freshwater-tolerant organisms that thrived in river mouths and marginal-marine settings, a habitat preference for transitional and nearshore environments might explain the relatively restricted paleobiogeographic distribution of this otherwise successful and long-ranging family of longirostrine shark-toothed dolphins.

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