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The first recognition of the enigmatic fossil shark genus *Megalolamna* (Lamniformes, Otodontidae) from the lower Miocene of Europe and *M. serotinus* (Probst, 1879) as the newly designated type species for the genus

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Abstract

Megalolamna is an elusive extinct shark genus (Lamniformes: Otodontidae) previously known from the upper Oligocene–Miocene of the USA, Colombia, Ecuador, Peru, and Japan. Here, we document the first occurrence of *Megalolamna* from Miocene marine deposits in Europe, specifically from Austria, France, Germany, and Italy. Although the taxon is regarded as a monospecific genus, this study reveals that the species name *serotinus* has the priority over any previously used names for the taxon and thus redescribes it as *Megalolamna serotinus* (Probst), **comb. nov.** This study is also significant because it demonstrates the existence of *Megalolamna* in the Mediterranean and Paratethys seas during the Miocene. *Megalolamna* inhabited the tropical–mid-latitudinal zones with spotty but wide geographic distribution.

Keywords

Austria, Elasmobranchii, France, Germany, Italy, Neogene, taxonomy

Introduction

Megalolamna is a lamniform shark genus known from the upper Oligocene–Miocene marine deposits by a single species, *M. paradoxodon* (Carrillo-Briceño et al. 2016, 2020; Shimada et al. 2017, in press). *Megalolamna* is regarded as enigmatic because of its sparse but geographically wide distributions with an uncertain phylogenetic position within the otodontid clade (Shimada et al. 2017, in press). The genus has so far been reported from the upper Oligocene Chandler Bridge Formation in South Carolina, USA, as well as the following eight Miocene localities: the Calvert Formation of Maryland, USA; Pungo River Formation of North Carolina, USA; Jewett Sand in California, USA; Uitpa Formation in Colombia; Dos Bocas Formation of Ecuador; Chilcatay Formation of Peru; Oi Formation in Mie Prefecture, Japan; and O'oshimojo Formation in Nagano Prefecture, Japan (Shimada et al. in press, and references therein).

In this study, we report the first occurrence of *Megalolamna* in Miocene marine deposits in four different countries in Europe (i.e., Austria, France, Germany, and Italy). Because the previous occurrences of the taxon are confined to the Pacific Rim and the western Atlantic Ocean (Shimada et al. in press, and references therein), the occurrences reported here significantly expand the geographic range of the genus. In addition, the recognition also includes cases of previously described specimens under two different species, one of which must be regarded as the senior synonym for the monospecific genus. Therefore, the aim of this paper is two-fold: (1) to describe the new specimens and revise the species-level taxonomy for *Megalolamna*; and (2) to document the significantly extended known geographic range for *Megalolamna*.

Geologic setting

Upper Marine Molasse Baltringen, Walbertsweiler, Baden-Württemberg, Germany

The North Alpine Foreland Basin or "Molasse Basin" is part of the Paratethys realm and was formed during the early Oligocene to late Miocene by the Alpine Orogeny (Lemcke 1988; Hofmayer et al. 2019). The sediments of the Molasse Basin are divided into marine, brackish and freshwater Molasse units, which were formed as a result of two transgressive-regressive megacycles. The first megacycle includes the Lower Marine Molasse, the Lower Brackish Molasse and the Lower Freshwater Molasse, whereas the second megacycle comprises the Upper Marine Molasse, the Upper Brackish Molasse and the Upper Freshwater Molasse (Janssen et al. 2018; Hofmayer et al. 2019). In the Ottnangian, the marine transgression of the western Paratethys started from the Southwest. In Baden-Württemberg, the sediments of the Upper Marine Molasse consist of approximately 50 m thick glauconitic sands of the Heidenlöcher Beds (Doppler et al. 2005), which are overlain by 20 to 70 m thick sediments of the Kalkofen Formation. The Kalkofen Formation consists of glauconitic sands and marls (Heckeberg et al. 2010) and is overlain by the Baltringen Formation and the fossil-rich Baltringer Horizon (Fig. 1).

The syntype of *Otodus serotinus* described by Probst (1879) was found at the site of the now closed Kodelsberg quarry east of Baltringen (near Mietingen, district of Biberach, 48.176593, 9.895192; Baltringen Formation, middle Ottnangian, middle Burdigalian) (Pollerspöck and Unger in press).

The tooth described by Barthelt et al. (1991) comes from the Walbertsweiler sand pit (between the towns of Meßkirch and Pfullendorf, district of Sigmaringen, 47.95145, 9.1572; Kalkofen Formation, Lower Ottnangian, Middle Burdigalian: Fig. 1), which is no longer accessible and has been recultivated. Organic debris and bedding planes with ripple marks indicate a nearshore, interior neritic to shallow marine environment. The water depth is estimated to be less than 50 m based on the abundance of shallow water foraminifera (Barthelt et al. 1991; Heckeberg et al. 2010; Pippèrr et al. 2011). The former coastline was located to the north, less than 25 km away.

Upper Marine Molasse, Plesching, Upper Austria

In the former sand pits near Plesching, the deposits of the "Linzer Sande" (Egerian) and the phosphorite sands (Ottnangian) were exposed. The "Linzer Sande" of the Linz-Melk-Formation overlie the gneiss of the Bohemian Massif. The sand is whitish-grey in colour. While bivalves and gastropods are mostly distributed in the sand, a concentrated occurrence of oysters can be found at the base of the so-called oyster bank. The "Linzer Sande", which dip at about 20° to the NNE, are unconformably overlain by the phosphorite sands of the Plesching Formation. A hiatus created by a transgression in this part of the Molasse Sea comprises the complete Eggenburgian. The coarse to fine-grained phosphorite sands are green-brownish in color due to the glauconite and phosphorite content. Beach block heaps indicate a steep rocky coast (Reiter and Berning 2012). The sands were intensively collected, especially due to the relatively frequent occurrence of shark teeth (Schultz 1968). The previously undescribed tooth was found around 1985 by Dietmar Stadlhuber (Engerwitzdorf/Mittertreffling, Austria) in the phosphorite sands near Plesching (Plesching Formation, middle Ottnangian, 48.324547, 14.342461; Fig. 1).

Mazan, Mormoiron Basin (Vaucluse), Southeastern France

The Mazan site is located in Provence (Southeastern France, 44.029044, 5.157797), the southern part of the Mormoiron Basin (Vaucluse), which is part of a succession of basins that subsided between the rising Alps and the Rhodian trough. The Malemort-du-Comtat quarry, still in operation today where gypsum (Blauvac Complex Formation, Eocene) is quarried comprises sediments dating from the Miocene to the Eocene (Besson 2005; Vialle et al. 2011; Maridet et al. 2013). While the Paleogene sediments have been lithostratigraphically studied (Blauvac Complex Formation, Patis Formation, *Brotia laurae* and *Tympanotonos labyrinthus* Formation; Triat et al. 1971), the Neogene sediments lack such studies. Vialle et al. (2011) described a species-rich selachian fauna from the younger sandstone layers of the middle Miocene with predominantly deep-sea-dwelling species. The tooth found here comes from a layer that was deposited directly above the clearly recognisable Paleogene-Neogene boundary (Fig. 1). This layer can be dated to the lowest Burdigalian.

Pietra da Cantoni, Eastern Monferrato, Italy

The Monferrato succession can be considered the north-western end of the Appenninic chain. It is composed of a predominantly terrigenous sequence of Eocene and Miocene age, deposited in complex internal basins (Mancin et al. 2003) and resting unconformably on the Upper Cretaceous–Eocene Ligurian Flysch. According to recent stratigraphic and structural studies, the Monferrato area consists of two stratigraphic successions that emerge in the western and eastern parts, respectively. The western sequence of the Monferrato, that consists of coarse Oligocene to Early Miocene terrigenous sediments deposited

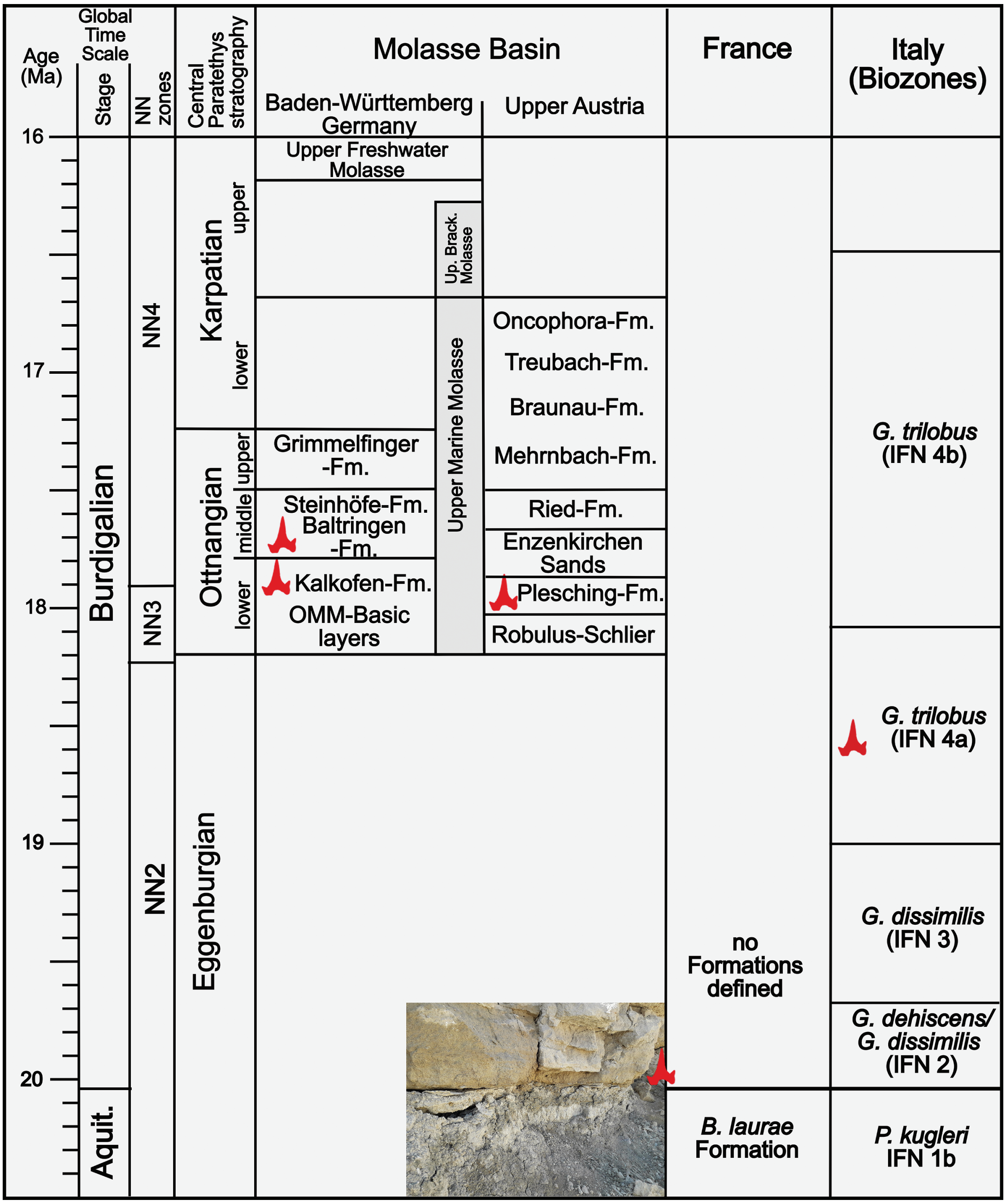

Figure 1. Stratigraphic positions of European specimens of *Megalolamna* according to their country of discovery described in this paper.

both in strongly subsiding basins and on adjacent structural uplifts, includes (from base to top): the Ranzano Sandstones, the Antognola Marls and finally the Pteropod Marls and their lateral equivalents. The eastern succession of the Monferrato, which consists of Oligocene to Early Miocene terrigenous deposits of different depths (Clari et al. 1987) and is followed by unconformable carbonates of the shelf, comprises (from bottom to top): the "Cardona Unit", the Antognola Marls and finally the "Pietra da Cantoni Group" (Mancin et al. 2003). The tooth described by Alessandri (1897) and two other specimens are housed in the Collection of the Earth Sciences Department of the University of Turin, Italy. All come from Rosignano (La Colma), which are assigned to the Pietra da Cantoni Group (*Globigerinoides trilobus* zone, INF 4a, lower Burdigalian, Fig. 1).

Results

Class Chondrichthyes Huxley, 1880
Subclass Elasmobranchii Bonaparte, 1838
Cohort Euselachii Hay, 1902
Subcohort Neoselachii Compagno, 1977
Order Lamniformes Berg, 1958
Family Otodontidae Glikman, 1964

Genus *Megalolamna* Shimada, Chandler, Lam, Tanaka & Ward, 2017

Type species. *Otodus serotinus* Probst, 1879, Kodelsberg (E Baltringen), Baden-Württemberg (Germany).

Emended diagnosis. Lamniform differing from all known species of otodontids by the following combination of characters: tooth consisting of a sharply-pointed, relatively tall, triangular main cusp, in anterior or anterio-lateral teeth one prominent pair of triangular lateral cusplets, in posterior teeth sometimes a second pair of small, secondary cusplets and strongly bilobed root; main cusp erect, in anterior teeth slightly inclined distally, or gently curved distally, in posterior teeth clearly inclined distally; lingual crown face very convex without ornamentation; labial crown face flat or subtly convex except center of base with weak depression; height and width of each lateral cusplet nearly equal with tendency to point outward; both mesial and distal cutting edges of main cusp and lateral cusplets smooth and razor-like, and continuous from apex to base; main cusp and lateral cusplets nearly erect to gently curved lingually; concave crown base and distinct, chevron-shaped tooth neck on lingual face characterized as a bourlette covered with thin enameloid layer; prominent tooth neck also on labial face in tall teeth, forming rounded ledge with thin enameloid layer that grades into enameloid of main cusp and lateral cusplets; bilobed root with rounded basal tips and moderately tight basal concavity in between; root overall robust but particularly at lingual protuberance that generally exhibits one or two prominent and a few smaller nutritive foramina; root width slightly wider than total crown width; osteodentine tooth histology (Shimada et al. in press; this study).

Megalolamna serotinus (Probst, 1879), comb. nov.

Figs 2, 3

Lamna bassanii – Alessandri 1897: 38–39, pl. 1, figs 16–16a.
Otodus sp. – Hasegawa and Uyeno 1967: 116, pl. 21, fig. 1a–c.
Odontaspis taurus obliqua – Caretto 1972: 29, pl. 4, figs 1a–c, 2a–c.
Lamna sp. – Barthelt et al. 1991: 200, pl. 2, fig. 8.
Lamna sp. – Renz 2009: 158.
Lamnidae gen. et sp. indet. – Tanaka 2013: 99, pl. 12, fig. 11a–c.
Brachycarcharias sp.? – Chandler and Young 2015: 49.
Lamniformes gen. et sp. indet. – Carrillo-Briceño et al. 2016: 86, fig. 4.16–17.
Megalolamna paradoxodon – Shimada et al. 2017: 706, fig. 2.
Megalolamna paradoxodon – Landini et al. 2019: 257, fig. 3S–U.
Megalolamna paradoxodon – Carrillo-Briceño et al. 2020: 13, fig. 5U–X.
Megalolamna paradoxodon – Shimada et al. in press: 8, fig. 2a–h.
Megalolamna paradoxodon – Pollerspöck and Unger in press.

Material. One isolated tooth (GPIT-PV-31738, as *Otodus serotinus* sp. nov. in Probst (1879): pl. 2, fig. 84) from the Baltringen-Formation (Baltringen Horizon) in Kodelsberg (east of Baltringen), Baden-Württemberg, Germany, housed in Collection of the Institute and Museum of Geology and Palaeontology of the University of Tübingen, Germany (Fig. 2A–C); one isolated tooth (SNSB-BSPG 1984 X 21, as *Lamna* sp. in Barthelt et al. (1991), pl. 2, fig. 8) from the Kalkofen Formation in Walbertsweiler, Baden-Württemberg, Germany, housed in Bavarian State Collection for Palaeontology and Geology, Munich, Germany (Fig. 3A); one isolated tooth (2022/46) from the Plesching Formation in Plesching, Austria, housed in Oberösterreichische Landes-Kultur GmbH, Geosciences collections, Leonding, Austria (Fig. 3B–E); two isolated teeth (Illustration originals, uncat.: Caretto (1972) pl. 4, figs 1a–c, 2a–c) from the lower part of the “Pietra da canton” formation, Monferrato region, Italy (lower Miocene) housed in the collections of the Museo Civico di Storia Naturale di Milano, Italy (Fig. 3F–K); three isolated teeth (syntype: Alessandri (1897) pl. 1, fig. 16b: MGPT-PU 11196; additional two specimens: MGPT uncat.) from the Pietra da Cantoni Rosignano (La Colma) housed in the collections of the Earth Sciences Department of the University of Turin, Italy (Fig. 3L–Q); one isolated tooth (UM MAZ 38)

Figure 2. Tooth of *Megalolamna serotinus* comb. nov. (GPIT-PV-31738) from the Upper Marine Molasse Baltringen, Walbertsweiler, Baden-Württemberg, Germany, that was originally described as *Otodus serotinus* by Probst (1879, pl. 2, fig. 84). (**A**) lingual, (**B**) profile, and (**C**) labial views. Scale bar: 5 mm.

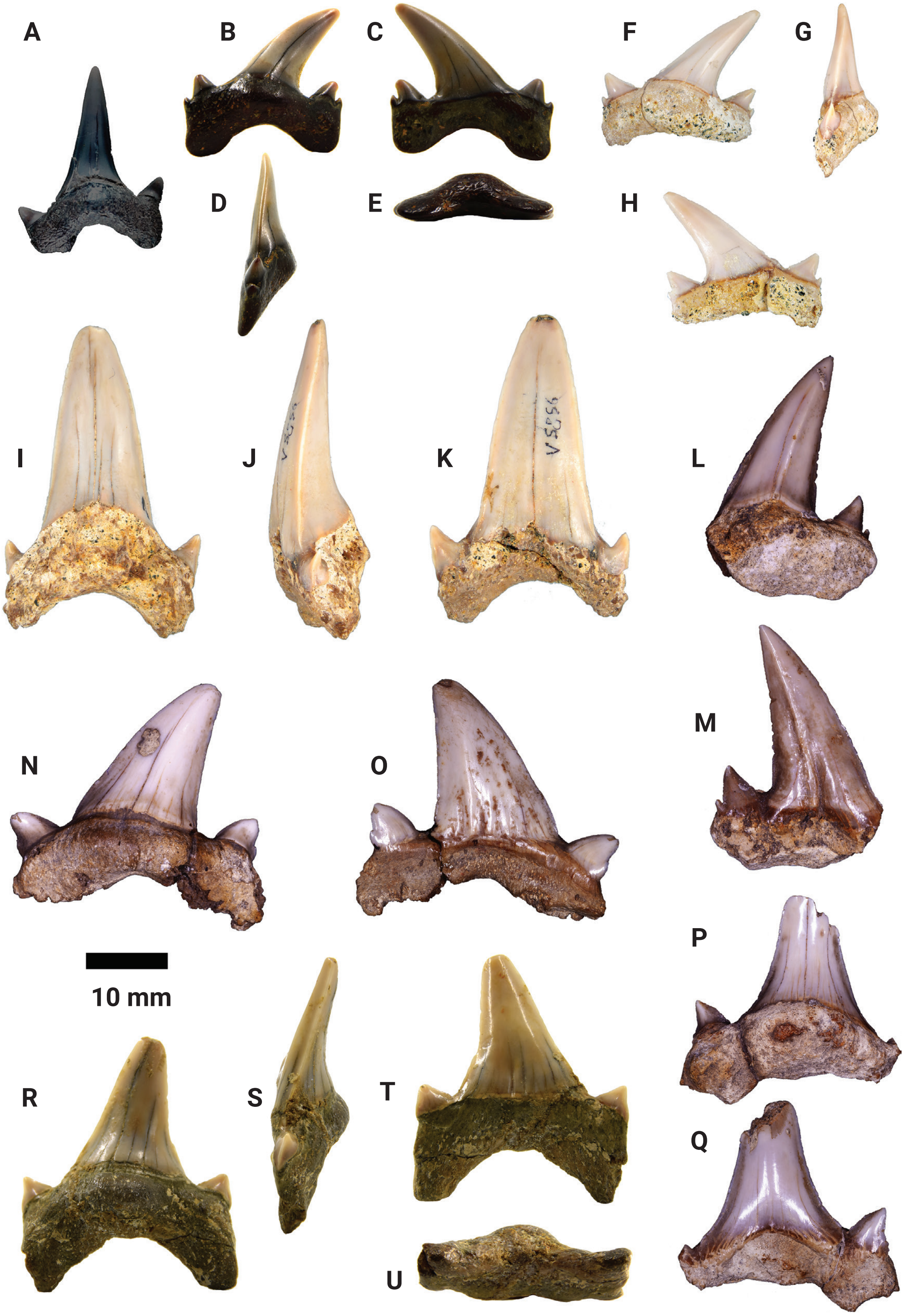

Figure 3. Additional teeth of *Megalolamna serotinus* comb. nov. from Miocene deposits of Europe described in this paper. **A:** SNSB-BSPG 1984 X 21 from the Upper Marine Molasse Baltringen, Walbertsweiler, Baden-Württemberg, Germany, in lingual view; **B–E:** Oberösterreichische Landes-Kultur GmbH Coll. no. 2022/46 from the Upper Marine Molasse, Plesching, Austria, in (**B**) lingual, (**C**) labial, (**D**) profile, and (**E**) basal views; **F–K:** Museo Civico di Storia Naturale di Milano Coll. no. V5858 and 5856 from the lower part of the “Pietra da canton” formation, Monferrato region, Italy, in (**F, I**) lingual, (**G, J**) profile, and (**H, K**) labial views; **L–Q:** Three teeth from Pietra da Cantoni, eastern Monferrato, Italy, the collection of the Earth Sciences Department of the University of Turin: MGPT uncat. in (**L**) lingual and (**M**) labial views; MGPT-PU 11196 in (**N**) lingual and (**O**) labial views; and MGPT uncat. in (**P**) lingual and (**Q**) labial views; **R–U:** UM MAZ 38 from Mazan, Mormoiron Basin, Vaucluse, France, in (**R**) lingual, (**S**) profile, (**T**) labial, and (**U**) basal views. Scale bar: 10 mm.

from the Burdigalian sediments of the Gypsum quarry "la Plâtrière" of the company Syniat, (France) housed in Institut des Sciences de l'Evolution de Montpellier, Montpellier, France (Fig. 3R–U).

Description. GPIT-PV-31738 (Fig. 2(A)–(C)) is an almost complete tooth, missing only a small portion of the mesial root lobe. It measures approximately 8.2 mm in total tooth height and 8.2 mm in total tooth width. The thickness at the crown base is about 2.3 mm, the distal lateral cusplet is slightly narrower at the base than the mesial one (1.2 mm *vs*. 1.4 mm). Its crown consists of a distally inclined main cusp with a pair of low lateral cusplets, the total crown height and width being about 5.8 mm and 8.1 mm, respectively. A small piece of the crown apex is broken off. The mesial and distal cutting edges of the main cusp are sigmoidally curved, very sharp, straight or slightly convex mesially and strongly concave distally, and their basal side continues to become the cutting edges of the lateral cusplets with practically no clear demarcation. The lingual crown base is essentially concave and slightly wavy. A thin and well-defined enameloid coating is missing due to the poor preservation of the root. However, a clear ridge is recognisable, particularly under the base of the mesial lateral cusplet, which indicates the original presence of this enameloid coating on the tooth neck. The labial base of the crown is almost straight, with some of the enameloid missing due to the state of preservation. Despite the damage to the mesial side of the root, it is recognisable that the root lobes are asymmetrical and the mesial root lobe is slightly wider than the distal root lobe. The lingual root surface is gently rounded. Large foramina or a lingual basal furrow are absent. Due to the small size and the strongly distally inclined crown, the tooth likely represents a latero-posterior tooth from a small individual.

A detailed description of the other records shown in Fig. 3 ((A)–(Q)) is not given here, as some of the material has already been published and illustrated or corresponds to the previous species diagnosis.

Discussion

Taxonomic remarks

The monospecific genus *Megalolamna* with the species *paradoxodon* was described by Shimada et al. (2017) based on Miocene teeth from the USA, Japan and Peru. However, the present study reveals that there were already two cases of historical findings of this species that have so far remained unnoticed or unrecognized in the literature. The first case is represented by the work of Probst (1879), who described the species *Otodus serotinus* from the Baltringen Formation (lower Miocene, Burdigalian, regional stage Ottnangian) on the basis of four specimens that represent the syntypes of the species (Probst 1879: pl. 2 fig. 82–85). During a recent revision of the fossil shark fauna described by Probst (1879) it was determined that the syntype under fig. 84 is conspecific and belongs to *Megalolamna paradoxodon* Shimada, Chandler, Lam, Tanaka & Ward, 2017 (Pollerspöck and Unger in press). The second case is represented by the study of Alessandri (1897), who described the species *Lamna bassanii* from Pietra da Cantoni, Eastern Monferrato (Miocene, Burdigalian, *G. trilobus* Zone (INF 4) and illustrated two teeth (pl. 1, fig. 16, 16a). Based on the description and illustration by Alessandri (1897) and the visible morphological characters, these two teeth also belong to the genus *Megalolamna*.

While both species names, '*O. serotinus*' and '*L. bassanii*', were published under the conditions of Article 10 of the International Code of Zoological Nomenclature (ICZN 1999) and are available, the taxonomic position, as described in Systematic Paleontology above, must be clarified, in particular, which species name is valid on the basis of the ICZN Article 23 (Principle of Priority).

ICZN Article 23 provides that "the valid name of a taxon is the oldest available name applied to it, unless that name has been invalidated or another name is given precedence by any provision of the Code or by any ruling of the Commission". Exceptions to this principle are only possible under the conditions of Article 23.9 (Reversal of precedence). In this case, both of the following two conditions must be cumulatively fulfilled:

1. the senior synonym or homonym has not been used as a valid name after 1899 (Article 23.9.1.1.), and
2. the junior synonym or homonym has been used for a particular taxon, as its presumed valid name, in at least 25 works, published by at least 10 authors in the immediately preceding 50 years and encompassing a span of not less than 10 years (Article 23.9.1.2.)

An extensive literature search revealed that the species names *O. serotinus* and/or *L. bassanii* were used as valid names after 1899 in the following works: Joleaud (1907: *Lamna serotina* p. 172); D'Erasmo (1924: *Lamna bassanii*, p. 24); Fowler (1966: *Otodus serotina*, p.135; *Lamna bassanii*, p. 131); Cappetta (2006: ?*Cretolamna bassanii*, p. 31). It follows that the species names *bassanii* and *paradoxodon* are to be regarded here as junior synonyms of *O. serotinus*, representing the only known species within the genus *Megalolamna*.

Geographic remarks

Prior to this study, the genus *Megalolamna* was known from the upper Oligocene–Miocene deposits (but mostly Miocene) in only the following five countries: USA, Colombia, Ecuador, Peru, and Japan (Shimada et al. in press, and references therein). Therefore, the specimens reported in this paper nearly doubles the known occurrences of the genus by country, which now also include Austria, France, Germany, and Italy (a total of

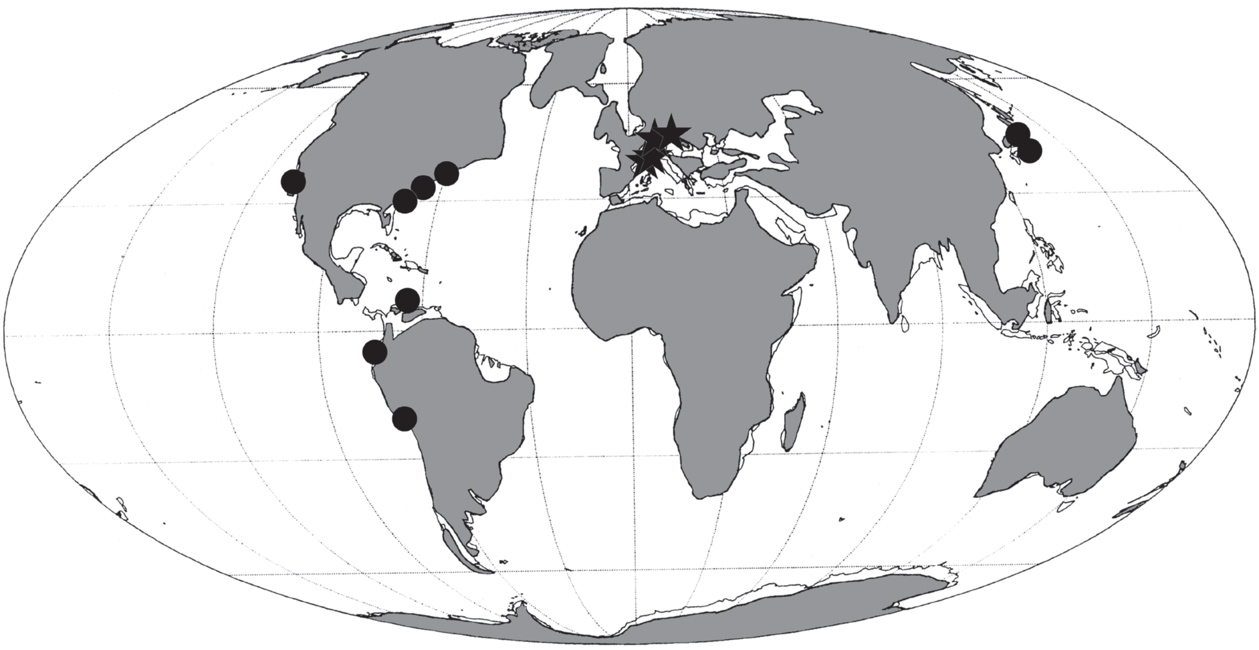

Figure 4. Geographic distribution of previous records (circle) and newly described European records (star) of *Megalolamna* (Carrillo-Briceño et al. 2016, 2020; Shimada et al. 2017, in press) using early Miocene (Aquitanian–Burdigalian) paleogeographic map (after Smith et al. 1994, p. 27).

nine countries: Fig. 4). Ocean-wise, the distribution of *Megalolamna* consists of the eastern and western margins of the Pacific Ocean, western Atlantic Ocean, and the Caribbean Ocean, and the present study adds the Mediterranean and Paratethys seas. Latitudinally, the occurrence of *Megalolamna* is distributed from the tropical to mid-latitudinal zone in both the Northern and Southern hemispheres.

Since the original description in 2017, *Megalolamna* has been characterized as an 'elusive' extinct lamniform shark due to its spotty but geographically widespread occurrences even though its existence was chronologically quite constrained, primarily to the Miocene Epoch (Shimada et al. 2017, in press). The new occurrences from Europe reported here further demonstrates its elusiveness as teeth of *Megalolamna* are never in abundance at any single locality, even though some areas have been heavily exploited palaeontologically, particularly for fossil shark teeth (e.g., Probst 1878, 1879; Schultz 1968; Caretto 1972; Barthelt et al. 1991; Brisswalter 2009; Höltke et al. 2020). In fact, its spotty but geographically widespread occurrences is reminiscent to a few present-day lamniform sharks, such as the goblin shark (*Mitsukurina owstoni*), megamouth shark (*Megachasma pelagios*), and the most elusive of all, the bigeye sandtiger shark (*Odontaspis noronhai*) (Ebert et al. 2021; Ng et al. 2022). Given that these extant taxa are sparsely but broadly distributed, it is quite possible that teeth of *Megalolamna* may be discovered or recognized in the future at other Miocene localities not presently recorded, possibly along the Atlantic coasts of Africa and South America as well as along the Indian Ocean and southwestern Pacific Ocean in the Oceania region.

Conclusions

In this paper, we document the extinct lamniform genus *Megalolamna* from the Miocene marine deposits in Europe for the first time (Figs 1–3). Whereas the genus was traditionally known by a single species *M. paradoxodon* described by Shimada et al. (2017), the new occurrence records include evidence based on specimens previously described under different names: *Otodus serotinus* by Probst (1879, pl. 2 figs 82–85), *Lamna bassanii* by Alessandri (1897, 38–39, pl. 1, figs 16–16a), *Odontaspis taurus obliqua* (Caretto 1972, p. 29, pl. 4, figs 1a–c, 2a–c), and *Lamna* sp. by Barthelt et al. (1991, p. 200, pl. 2, fig. 8.). On the basis of ICZN's Principle of Priority (Article 23), we have determined that the species name *O. serotinus* is a senior synonym to all previously described materials identified to belong to the genus *Megalolamna* – hence, *Megalolamna serotinus* (Probst, 1879), comb. nov.

Based on this study, *Megalolamna* is now known from the USA, Colombia, Ecuador, Peru, and Japan as well as from Austria, France, Germany, and Italy (Fig. 4). More significantly, the new European records demonstrate the presence of *Megalolamna* in the Mediterranean and Paratethys seas during the Miocene. The present distribution of this monospecific genus is characterized as tropical–mid-latitudinal, and its spotty but wide distribution is similar to some of the elusive extant lamniform shark, such as goblin, megamouth, and bigeye sandtiger sharks. Therefore, we contend that *Megalolamna* will possibly be recognized also from other Miocene sites along the Atlantic coasts of Africa and South America as well as along the Indian Ocean and southwestern Pacific Ocean in the future.

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