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Shark-toothed dolphin remains (Mammalia, Cetacea, Squalodontidae) from the Early Miocene of Greece

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(With 4 Plates)

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Abstract

We describe here the remains of an Early Miocene shark-toothed dolphin (Squalodontidae) from Anargyroi, Tsotilion (West Macedonia, Greece). The tooth-bearing partial skull and other bone fragments of the same individual are recognized as *Squalodon* cf. *bellunensis* DAL PIAZ, 1900. The evolution of the dentition of early odontocetes is discussed and the dental characters in the Squalodontidae are reviewed.

Key words: Mammalia, Cetacea, Odontoceti, Squalodontidae, *Squalodon*, Early Miocene, Greece.

Zusammenfassung

Die Reste eines Squalodontiden (Cetacea: Squalodontidae) aus dem unteren Miozän von Anargyroi, Tsotilion (Westmazedonien, Griechenland) werden hier beschrieben. Das zahortragende Schädelbruchstück und andere Knochenfragmente des gleichen Individuums werden als Angehörige der Art *Squalodon* cf. *bellunensis* DAL PIAZ, 1900 angesehen. Die Evolution des Gebisses der frühen Zahnwale wird diskutiert und eine Übersicht über die Zahnmerkmale der Squalodontidae wird erstellt gegeben.

Stichworte: Mammalia, Cetacea, Odontoceti, Squalodontidae, *Squalodon*, Untermiozän, Griechenland.

Introduction

The fossil remains described here were collected in 1951 and remained undescribed until 2001, when the third author of the present paper discovered these in the collection of the Athens Museum of Palaeontology and Geology. The fossils were accompanied by a hand-written label with the information: "Locality Tsotilion, W. Macedonia, 20/6/51; inside grey marls of marine origin; close to the village Anargyroi, north of Tsotilion". The presence of fossil cetaceans, close to the village Anargyroi, is first mentioned by BRUNN (1956: 185-186): "J'en ai rapporté également les fragments d'un dauphin récolté près du village d'Anarghyro (N de Tsotilion), sur les indications du Pope de ce village. Ces restes ont été examinés par M. l'abbé Lavocat, mais n'ont pu être déterminés spécifiquement". After personal communication with Prof. Jan Brunn, we have been informed that these fossils were sent to the Athens Museum.

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The tooth bearing cranial and mandibular fragments and some postcranial elements of a single individual represent a shark-toothed dolphin of the extinct family Squalodontidae.

Squalodontids appeared early in the history of toothed whales (Odontoceti). Their fossil record starts in the Late Oligocene and the family became widespread during the Miocene (KELLOGG 1923). The remains of squalodontid dolphins are well known from all around the world: from North and South America, Europe, Asia including Japan, Australia and New Zealand (e.g. ALLEN 1887, KELLOGG 1923, CABRERA 1926, MCHEDLIDZE 1976, OKAZAKI 1982, FORDYCE 1985). In Europe, several forms have been described or identified (e.g. BRANDT 1873, DAL PIAZ 1904, DAL PIAZ 1916, ROTHAUSEN 1968, CIGALA-FULGOSI & PILLERI 1985), mostly from the Late Oligocene and Early Miocene of the Mediterranean and the Northeast Atlantic Ocean.

The Squalodontidae were traditionally regarded as an archaic group ancestral to modern odontocetes (e.g. BARNES et al. 1985). More recently, MUIZON (1990, 1994) recognized that the Squalodontidae are in some respects more specialized than most later groups of odontocetes. Based on synapomorphies of the scapula he grouped the Squalodontidae along with some other extinct families and the Platanistidae into the platanistoid superfamily (MUIZON 1990).

The aim of the present paper is to describe the remains of the shark-toothed dolphin collected in West Macedonia (Greece) and to review the European occurrences of the genus *Squalodon*.

Abbreviation of Institutions – **AMPG**, Athens Museum of Palaeontology and Geology, Greece; **IRScNB**, Institut Royal des Sciences Naturelles de Belgique, Bruxelles, Belgium; **NHMW**, Naturhistorisches Museum Wien, Austria; **OL**, Oberösterreichisches Landesmuseum, Linz/Donau, Austria; **USNM**, National Museum of Natural History, Smithsonian Institution, Washington D.C., USA; **MGUP**, Museo Geologico della Università di Palermo, Sicily, Italy.

Abbreviation of anatomical terms – **b, B**, buccal (postcanine) tooth; **c, C**, dens caninus; **fm_x**, maxillary foramen; **i, I**, dens incisivus; **ID**, index denticulorum; **mx**, maxilla; **pm_x**, premaxilla.

Material and methods

The material consists of some cranial and postcranial elements of a single specimen (see Systematic palaeontology).

Direct comparisons with the following specimens were made by the second author: *Patriocetus ehrlichi* [OL Cet. 18, holotype; OL Cet. 4, paratype; NHMW SK 192 a, in situ mandibular, and b-c, isolated upper buccal teeth], *Squalodon calvertensis* [USNM 10484, holotype], *Squalodon antwerpiensis* [IRScNB Ct.M. 503, 504, cotype]; *Squalodon* "a" [IRScNB Ct.M. 505]; *Neosqualodon assenzae* [MGUP]. Comparisons with other specimens were based on the illustrations of the original descriptions. Measurements were made with a digital calliper.

In the descriptive terminology for dental morphology and in the definition of the dental indices we have followed ROTHAUSEN (1968). All postcanine teeth are termed buccal teeth (following ROTHAUSEN 1968 and DUBROVO & SANDERS 2000). Upper buccal teeth are indicated by uppercase letters, whereas mandibular buccal teeth by lowercase letters.

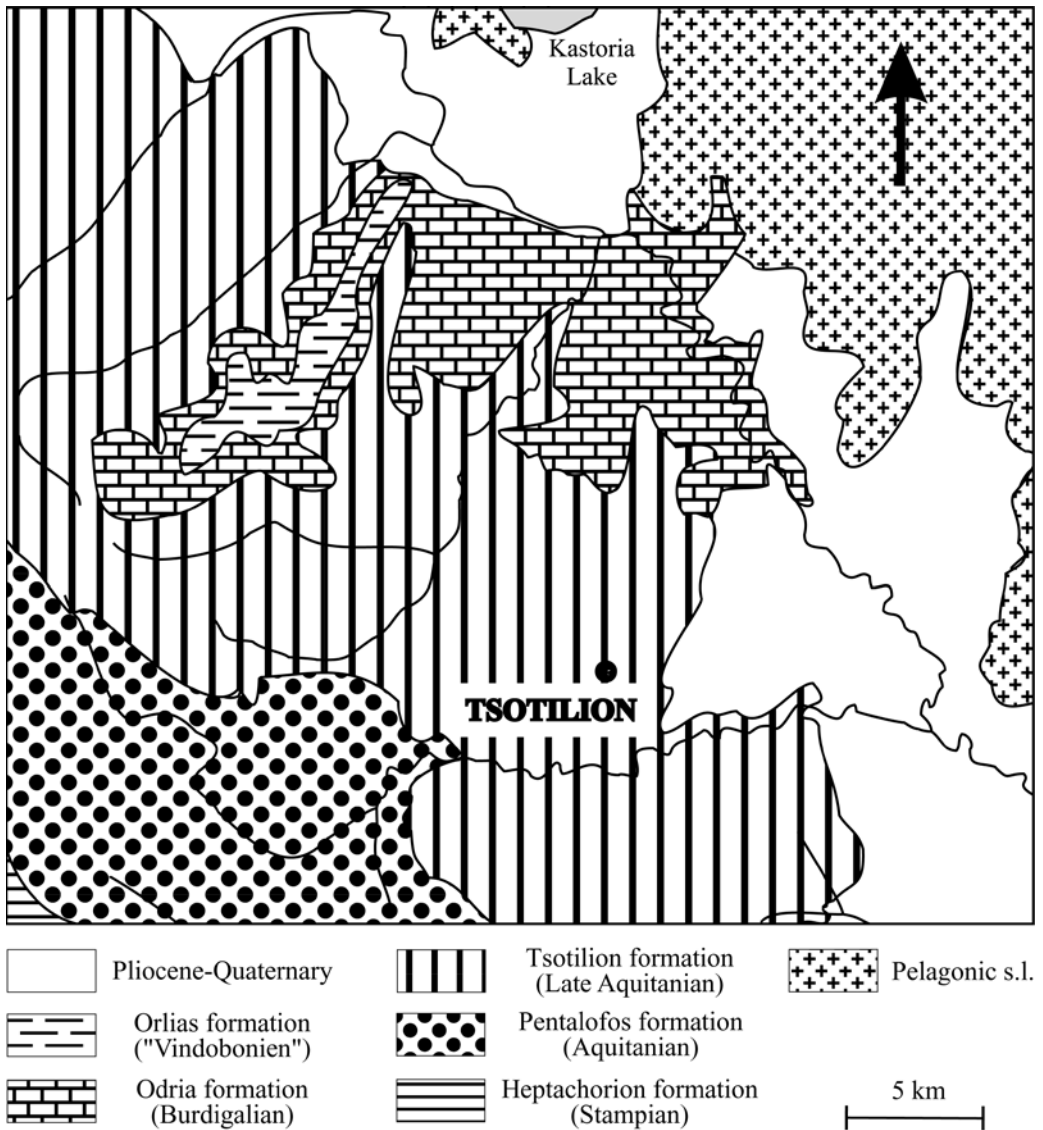


Fig. 1: Geological map of the Tsotilion area showing the most important geological formations (after BRUNN 1956; simplified).

Geology of the site

The material of the present study comes from the Anargyroi locality, close to Tsotilion. Tsotilion village is in the Mesohellenic trough (Fig. 1), which is an elongated depression of NW-SE direction along the axis of the Hellenides, extending from Albany to the Thessalic plain. The Mesohellenic basin is Late Eocene-Middle Miocene in age and is a typical molasse (BRUNN 1956, DERMITZAKIS & PAPANIKOLAOU 1981). It has been inter-

preted as a back-arc basin, evolved mainly during Oligocene-Early Miocene times behind the island arc of the Pindos and Western Thessaly tectonic units, and the ophiolites of Northern Pindos (PAPANIKOLAOU et al. 1988). The litho-stratigraphic sequence of the Mesohellenic trough has been studied by BRUNN (1956), and its formations are the Krania formation, the Heptachorion formation, the Pentalofofos formation, the Tsotilion formation, the Odria formation and the Orlias formation.

The fossil cetaceans described here originate from the Tsotilion formation, which consists mainly of grey marls and sandstones. The age of this formation has been considered Late Aquitanian (BRUNN 1956) or Aquitanian-Early Burdigalian (BRUNN & DESPRAIRIES 1965).

Systematic palaeontology

Cetacea BRISSON, 1762

Odontoceti FLOWER, 1867

Platanistoidea GRAY, 1846

Squalodontidae BRANDT, 1873

Squalodon GRATELOUP, 1840

Squalodon cf. bellunensis DAL PIAZ, 1900

Material: – Cranial fragment with teeth, teeth-bearing mandibular fragment including the symphyseal portion and the anterior tip, a fragment of the posterior portion of the right mandibular ramus, 13 isolated teeth, two thoracic vertebrae, two isolated vertebral epiphyses, numerous fragments of ribs and a large number of unidentifiable dental, cranial, vertebral and costal fragments; collected in 1951 [AMPG no TS 1].

All the material is stored in the Geolog.-Paläontolog. Abteilung of the Naturhistorisches Museum in Vienna: NHMW 2003z0024/0001-0014.

Locality: – Near the village Anargyroi, North of Tsotilion, West Macedonia, Greece.

Age and stratigraphy: – Marine marl of the village Anargyroi, Tsotilion formation, Early Miocene.

Description: – C r a n i a l f r a g m e n t (Fig. 2, Pl. 1) – This is a 378 mm long (as preserved) rostrum fragment bearing fragments of B4 through B10 and the alveolus of B11 of the left tooth row; fragments of B4 through B8 of the right tooth row. The anterior tip of the rostrum anterior to B4s is missing. The left side is more complete: this side of the rostrum is preserved posteriorly to the level of the posterior margin of B11, whereas the right side of the rostrum is preserved posteriorly to the level of B8.

The bone is massive and dense. Posterior to the anterior margin of B10 the palatal surface is strongly arched. Anterior to the anterior margin of B6 the ventral surface of the rostrum is double arched in cross section: each maxilla is slightly convex while the intermaxillary region forms a shallow groove. Between these regions, which is, posterior to B6s and anterior to B10s the ventral surface of the rostrum is horizontal and neither arched nor grooved. The vomer is exposed between the maxillaries as a narrow strip at the level of B5 and B6 at least 110 mm long. The posterior termination of the exposed

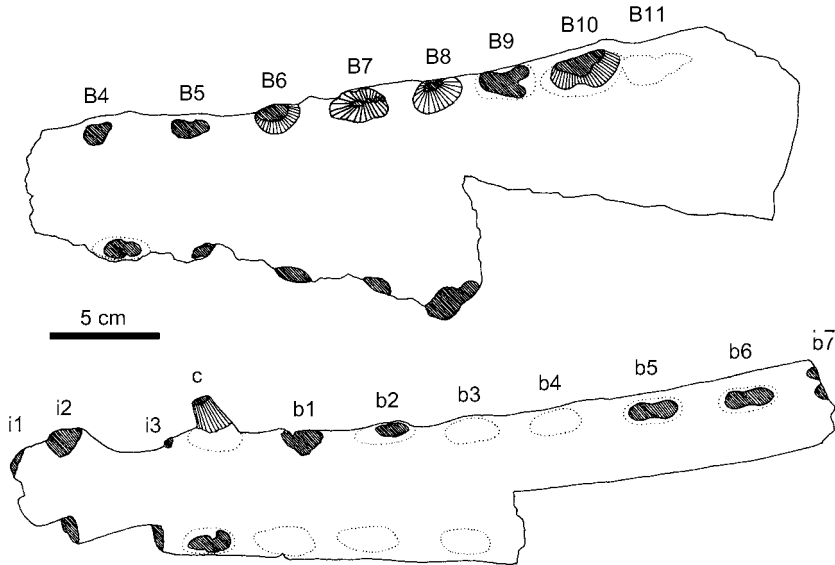


Fig. 2: Ventral view of the cranial fragment (above) and dorsal view of the mandibular fragment (below) of *Squalodon* cf. *bellunensis* from Tsofilon, Greece. Hatched areas delineate cross-sections or poorly preserved fragments of in situ teeth. Abbreviations defined in the Introduction.

area is unknown. Posterior to the level of the anterior margin of B5 the lateral margins of the maxillae diverge. Anterior to this point, the lateral margins of the maxillae and the tooth rows run parallel. All of the preserved in situ teeth are lodged in the maxillae.

The rostrum fragment (including the missing portion of the right tooth row posterior to B8) is roughly triangular in dorsal view. The posterior end of the fragment represents the base of the rostrum immediately anterior to the antorbital notch. This has been concluded from the presence of a maxillary rim at the posterolateral portion of the better-preserved left side of the fragment. This rim starts in the level of B10 and extends posteriorly. A small maxillary foramen opens on the dorsal surface of the maxilla at the level of the diastema between B10 and B11. The premaxillae are not preserved. In the present state, the mesorostral gutter forms an open ditch widely separating both maxillae. The maxillae are closest together at the preserved anterior end of the fragment, where they are ca. 18 mm apart. From this point, they gradually converge posteriorly. At the level of the posterior termination of the right premaxillary fragment (level of B8), they are 33 mm apart. At this point, the V-shaped cross-section of the vomer is exposed due to the breakage of the bone.

M a n d i b l e s (Fig. 2, Pl. 2) – The preserved part of the mandibles is 394 mm long. This is the symphyseal part of both rami including the anterior tip, and a post-symphyseal portion of the right ramus. None of the tooth rows are complete. The last tooth of the left row is b3, that of the right row is the anterior fragment of b7. An isolated bone fragment with remnant of a double-rooted tooth most probably originates from the posterior part of the right mandibular ramus. There is no trace of an alveolus posterior to this tooth, indicating that this tooth was the last one in the lower dental series. The fragment is mediolaterally flattened and it bears a marked coronoid crest dorsally.

The anterior tip of the mandibles is dorsoventrally flattened, whereas they become more vertically oriented and mediolaterally constricted posteriorly. The anterior portion of the mandibles is narrow in dorsal view, as is typical of the genus *Squalodon*. The posterior cross-section of the right ramus is elliptical, its depth measures 49.1 mm, its width 35.6 mm. Mental foramina are not observed on the lateral surface. The symphysis was 342 mm long, as concluded from the depression on the medial surface of the right ramus corresponding to the attached surface of the left ramus. The two rami were plausibly fused in the anteriormost ca. 5-7 cm of the symphyseal part.

D e n t i t i o n (Figs. 2 & 3, Pl. 3) – Fragments of the anteriormost mandibular teeth indicate the presence of three incisors on each side. This was followed by one caninus in each tooth row. Presumably 11 upper and at least seven (eight if the isolated mandibular fragment was correctly identified) lower buccal teeth followed. Posterior to the remnant of the left B11 there is no trace of an alveolus, indicating that there were no more than 11 buccal (postcanine) teeth in the upper dental series. Thus, the dental formula can be given as follows: I3C1B11/i3c1b10(?11).

The first and second incisors of the mandibles (i1 and i2) lie almost horizontally: they were oriented anteriorly and slightly dorsolaterally. The cross-section of the preserved root fragment of the left i1 is almost circular: it is 14.7 mm deep and 16.6 mm wide. Its root is oriented horizontally and expands into the dentale at least 78 mm long. (The posterior portion of the root is exposed through a damage on the dorsal surface of the mandible). The crown of this tooth is entirely missing. The second incisors are as robust as the preceding ones. The cross-section of the right i2 is cylindrical (depth: 16.8 mm, width: 14.6 mm). Both i3s are missing, their presence is indicated by the remnants of their roots. The canines have crowns with cylindrical cross-sections: the length of the right c1 is 19.2 mm, its width measures 11.6 mm. The in situ preserved right lower caninus has a high crown, the tip of which is broken off. Its estimated height is 30 mm. The anterior and posterior margins are keeled. The enamel has fine longitudinal clefts. The isolated fragments of eight teeth appear to be either upper or lower incisivi, canines or anterior postcanines. All are single-rooted and all have similar crown morphology to the right c1. One well-preserved isolated tooth crown, possibly an anterior postcaninus, differs from the previous ones in that its anterior and posterior margins are not only keeled but finely serrated (Pl. 3: fig. 2). The enamel of the buccal side shows fine clefts, whereas on the lingual surface there are elongate, vertically sculptured ornaments termed *cristae rugosae* by ROTHAUSEN (1968). The apex of this tooth was worn away during life.

In the mandible the first and second buccal teeth are single-rooted and b5 is double-rooted. It is unknown whether b3 and b4 are single- or double-rooted. In the upper row, B4 is single-rooted. The root of B5 shows a slight depression possibly corresponding to bifurcation, whereas B6, B7 and B8 are double-rooted. Presence of a third root on the posteriormost upper teeth is likely. A slight lingual swelling, possibly corresponding to a third root, can be observed with the left B9 and B10 (and plausibly with the left B11, as concluded from the enlarged width of the medial part of the remnant of this tooth). The roots of the double-rooted buccal teeth are slightly depressed below the crown base.

The preserved crowns of the posterior buccal teeth are triangular, laterally compressed, and relatively high; the crown height/crown length ratio of the left B7 is 1,125. The

basal index (crown length at base/crown width at base) varies between the buccal teeth, ranging from 38% (estimation, right b6) through 50% (estimation, left B7) and 52% (left B6). The crowns of all buccal teeth are inclined posteriorly.

The number of the anterior and posterior accessory denticles of the posterior buccal teeth is uncertain because none of the buccal tooth crowns have complete anterior and posterior margins. The anterior margin is best preserved (albeit hidden by the attached B7) on the left b8. Here, two small denticles sit very close together near the crown base, and a third is slightly larger and positioned more apically but still ventrad from the mid-height of the crown. The preserved portion of this tooth apparently does not have posterior denticles. The right b8, which is attached to the skull between the right B7 and B8, exhibits one basal posterior accessory denticle but the rest of the crown is fragmentary.

Of the upper tooth row, the preserved basal portion of the anterior margin of the left B6 is serrated and has no accessory denticles. Two posterior denticles are preserved of the same tooth but originally it may have had more (probably three). The left B7 has three well-developed posterior denticles spaced ca. equally along the posterior margin of the crown. The main (apical) denticle is considerably larger than the accessory denticles. All three denticles have strongly worn apices. Likewise, an isolated tooth crown fragment (possibly that of the left B9 or B10, Pl. 3: fig. 6) shows three presumably posterior accessory denticles. Two of them are situated close together and near the enamelocementum boundary, while the third one is situated more apically. The posterior margin of the crown is finely serrated between the denticles. The apices of all denticles were worn away by use. The main denticle is worn to the greatest extent; the worn facet has the form of a deltoid. The cingulum is weakly developed on both sides of this tooth. (The cingulum of the other teeth can not be observed due to their preservation states.)

Cristae rugosae are present in the crowns of all preserved buccal teeth, their number approximating ten per 5 mm. Papillae are present on the buccal (labial) sides of the crowns but they are neither numerous nor strongly developed.

Tab. 1: Lengths of teeth (upper rows) and lengths of diastemata between neighboring teeth (lower rows). All measurements in mm. + minimum value, e estimated value, ? missing data, – lack of diastema.

left	C	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11
tooth	?	?	?	?	15.8	20.9	22.8	23.9+	24.9	26.0	28.0	33.4e
diastema	?	?	?	29.5+	30.5	22.5	20.1	15.4	7.1	11.6	–	
right	C	B1	B2	B3	B4	B5	B6	B7	B8	B9	B10	B11
tooth	?	?	?	?	19.2	20.6	22.5	24.7	25.0	?	?	?
diastema	?	?	35.4+	27.3	20.3	20.2	11.8e	?	?	?	?	?
left	c	b1	b2	b3	b4	b5	b6	b7	b8	b9	b10	?
tooth	19.2	?	?	?	?	?	?	?	?	?	?	?
diastema	?	?	?	?	?	?	?	?	?	?	?	?
right	c	b1	b2	b3	b4	b5	b6	b7	b8	b9	b10	?
tooth	15.3	15.1	15.2	?	?	21.1	23.8	?	?	23.0	?	?
diastema	15.5	23.7	?	?	?	22.6	19.1	?	?	?	?	?

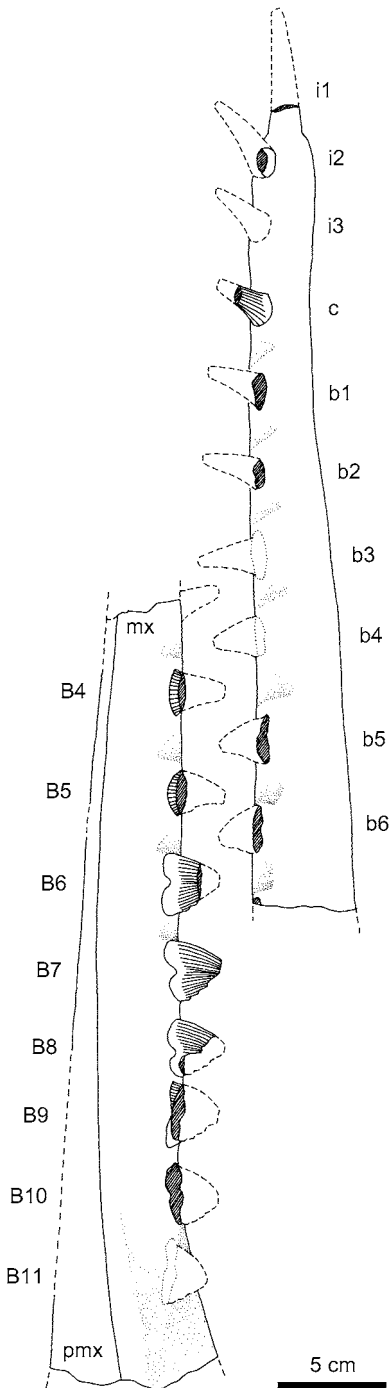


Fig. 3: Partial restoration of the rostrum and mandible of *Squalodon* cf. *bellumensis* from Tsotilion, Greece, in lateral view, showing tooth crown marks of the antagonistic jaw.

There are wide diastemata between the teeth posterior to *i3* of the mandible and anterior to *B8* of the upper jaw (for measurements, see Table 1). There is no diastema between *B10* and *B11*. The tooth crowns of the lower jaw not only occupy the gaps between the neighboring teeth of the maxilla and vice versa but they reach farther. The tight bite of the animal caused the impressions of tooth crowns on the lateral surfaces of the maxilla and the mandibles (Fig. 3).

V e r t e b r a e – Two incomplete thoracic vertebrae are preserved, one from the anterior, the other from a more posterior position in the series, as concluded from the smaller (30.0 mm) and greater (34.0 mm) length of their centra. Both vertebrae have epiphyses fused to the centra. Parapophyses (termed preapophyses and katapophyses by SLIJPER 1936) are not preserved on either of the vertebrae. The base for the diapophysis and the neural arch are preserved on the more posterior vertebra (Pl. 4: fig. 1). It is set anteriorly on the centrum and is directed outward and slightly forward. The neural canal is wide. The dorsal surface of the centrum forming the ventral side of the neural canal is dorsally arched and has a faint longitudinal medial keel. The depth of the centrum of the posterior thoracic vertebra is 51.0 mm, its width measures 64.0 mm.

Two additional, isolated epiphyses belong with the specimen. Their sides facing the vertebral centra are finely ornamented, similar in appearance to vertebral epiphyses of *S. calvertensis* (KELLOGG 1923: Pl. 15).

R i b s – The number of pairs of ribs possessed by the specimen can not be determined. The material includes the fragments of at least five, possibly of 10-15 ribs. The description here will be limited to the best preserved four ribs that probably correspond to the first, second, fourth? and fifth? ribs.

The first rib is relatively thin, broad and flattened, more so in its proximal part (Pl. 4: fig. 2). The preserved portion is slightly arched. The neck region is not preserved. Likewise, the proximal portion of the

second rib is thin, broad and flattened, but it becomes abruptly constricted distally (Pl. 4: fig. 3). The fourth? rib is more noticeably curved than the first and second ribs (Pl. 4: fig. 4). It is neither thin nor flattened. A slight broadening occurs at its curvature. The fifth? rib is best preserved (Pl. 4: fig. 5). The tubercle is present but poorly defined. Immediately distal to the tubercle the body of the rib becomes slightly constricted. The curvature of this rib is moderate.

Comparisons – The new specimen differs from members of the genus *Patriocetus* ABEL, 1913 in the larger relative size of the main denticle of the buccal teeth; in the larger number of cristae rugosae per 5 mm; and in having higher buccal tooth crowns with a narrower base. The upper left postcanines of the Greek whale differ from the only known buccal tooth of *Agorophius pygmaeus* (MÜLLER, 1849) (upper left mid cheek-tooth, FORDYCE 1981) in their more heavily wrinkled enamel; in the presence of cristae rugosae on their buccal sides; and in the smaller size of the basal accessory denticles of their posterior margins. The new find differs from *Prosqualodon* LYDEKKER, 1894 and *Phoberodon* CABRERA, 1926 in having a longer rostrum. It differs from *Kelloggia* MCHEDLIDZE, 1976 in the smaller number of upper teeth that have only few accessory denticles (if any) whereas *Kelloggia* has five to seven (MCHEDLIDZE 1976). The small accessory denticles of the new find are in contrast with the large, blade-like accessory cusps of the cheek-teeth of *Neosqualodon* DAL PIAZ, 1904 and *Metasqualodon symmetricus* OKAZAKI, 1982.

The new find differs from *Eosqualodon latirostris* (CAPELLINI, 1903) in having a broader rostrum base. The posterior buccal teeth of the Greek specimen generally have higher crowns, a larger number of cristae rugosae, less accessory denticles and relatively larger main denticles than the single known cheek-tooth of the holotype of *E. latirostris*. Likewise, the posterior teeth of the new material exhibit higher crowns and more cristae rugosae, less papillae than the holotype teeth of *E. langewieschei* ROTHAUSEN, 1968. The mandibles of the new find have a morphology typical of squalodontids and are clearly different from the unique mandible morphology of *Squalodon kelloggi* ROTHAUSEN, 1968. The Greek squalodontid differs from *S. bariensis* (JOURDAN, 1861) in having larger diastemata between the neighboring teeth, in having smaller ID values (which is, smaller accessory denticles), larger apical angles and a more pronounced system of cristae rugosae of the buccal teeth. It differs from *S. catulli* MOLIN, 1859 in having only three posterior denticles of the upper molars whereas *S. catulli* has five to six. The new specimen differs from *S. calvertensis* KELLOGG, 1923 in having 11 buccal teeth that are more widely spaced. The Greek specimen shares a number of characters with *S. bellunensis* DAL PIAZ, 1900. E.g. both have 11 buccal teeth in the upper tooth row (unknown with the holotype), both have buccal tooth crowns with a large density of cristae rugosae, with two to three small posterior but no anterior accessory denticles.

Based on the preserved material, the Greek squalodontid remains could not be reasonably compared with *S. dalpiazii* FABIANI, 1949, *S. antwerpiensis* VAN BENEDEN, 1861, *S. peregrinus* DAL PIAZ, 1971 and some other European named species referred to the genus *Squalodon*. Among the investigated taxa, the Greek specimen shows marked similarities with *S. bellunensis* DAL PIAZ, 1900. Nevertheless, the incompleteness of the new material prevents a definite allocation.

Discussion

The phylogenetic relationships among the Late Oligocene to Early Miocene odontocetes traditionally classified within the Squalodontidae (e.g. KELLOGG 1923, SIMPSON 1945) are unresolved. MUIZON (1990) defined the family with an apomorphic lengthening of the rostrum, with the reduction of the lateral lamina of the pterygoid hamulus, and with the enlarged, horizontally oriented large medial incisors. The fossil material from the Early Miocene of W. Macedonia (Greece) clearly shows the presence of such incisors and should, therefore be regarded as a member of the Squalodontidae sensu MUIZON (1990). According to MUIZON (1990), *Eosqualodon*, *Squalodon*, *Kelloggia*, *Phoberodon* and perhaps *Neosqualodon* belong in the Squalodontidae. The comparison of the Greek odontocete with these genera revealed that it shows marked similarities with members of the genera *Eosqualodon* and *Squalodon*. Nevertheless, the new material lacks diagnostically important cranial features and could be best compared to previously described species of *Eosqualodon* and *Squalodon* on the basis of its dentition and tooth morphology. Thus, a brief summary of the main tendencies in the evolution of the cetacean dentition seems necessary.

1. General trends in odontocete dentition and a review of dental characters

The dentition of the squalodont odontocetes represents a transitional form between that of the most primitive archaeocetes and the recent Delphinidae. Modern odontocetes possess a homodont, monophyodont, polydont dentition (sometimes reduced secondarily) that has the exclusive function of capturing the slippery body of prey animals. This highly specialized feeding apparatus is derived from the primitive secodont dentition of the earliest known cetaceans, the Early Eocene land-dwelling pakicetids (THEWISSEN et al. 2001). Their teeth were capable of shearing and grinding, deciduous teeth preceded the permanent teeth and the number of teeth corresponded to the normal eutherian complement (dental formula: 3.1.4.3. / 3.1.4.3.) (GINGERICH & RUSSELL 1990).

Later archaeocetes have high-crowned teeth with serrated profiles. They generally possess large and numerous accessory denticles that are largest in the mid-cheek-teeth and larger on the anterior margins of the crowns (UHEN & GINGERICH 2001). The mandibular and most upper premolars and molars are double-rooted, and the upper third and fourth premolars may be three-rooted (KELLOGG 1936). Fine ornamentation on the enamel might be present or absent. The Middle Eocene dorudontine *Chrysocetus*, the proposed common ancestor of Mysticeti and Odontoceti (UHEN & GINGERICH 2001) possessed premolars with buccolingually compressed tooth crowns. The bilateral compression of the postcanine teeth progressed in the Oligocene Odontoceti. It can be assumed that more advanced forms have more flattened tooth crowns (lower basal index values) at any given position of the tooth row (FORDYCE 1978). Posterior buccal teeth generally have lower values than anterior postcanines (FORDYCE 1978). Although the dentition is clearly heterodont with three incisors and one caninus in each tooth row, a distinction between premolars and molars is no more possible (ROTHAUSEN 1968, FORDYCE 1982). Polydonta probably evolved in the Early Oligocene (FORDYCE 1982). The Oligocene *Patriocetus* possess 10-11 buccal (postcanine) teeth (DUBROVO & SANDERS 2000) and most squalodontids have at least 12 (ROTHAUSEN 1968).

The presence of a third root in the posterior upper buccal teeth is regarded as primitive (ROTHAUSEN 1968). Likewise, the symmetrical tooth crown with an equal number of anterior and posterior accessory denticles is primitive (ROTHAUSEN 1968). The asymmetry of the buccal teeth, seen in more advanced squalodontids, is due to the increase in length of the posterior portion of the crown and/or in the number of posterior denticles (ROTHAUSEN 1968). The high-crowned buccal teeth are thought to be advanced within the Squalodontidae (with exception of the posteriormost ones that are always low-crowned) (ROTHAUSEN 1968, FORDYCE 1978), while some archaeocetes already possessed high-crowned cheek-teeth. Likewise, it is not clear, whether the low or the increased number of accessory denticles should be interpreted as advanced, since archaeocetes generally have a greater number of denticles than early squalodontids (FORDYCE 1978). Primitive squalodontids presumably had three anterior and three posterior denticles, later forms usually have an increased number of denticles (FORDYCE 1978). On the other hand, a reduction of the number of accessory denticles can also be observed in the Miocene Squalodontidae. The loss of some of the accessory denticles is a tendency towards homodonty and should be interpreted as advanced.

In more advanced Squalodontidae, the apical (main) denticle is considerably larger than the anterior and posterior accessory denticles (FORDYCE 1978). During squalodontid evolution, an increase in the number of the cristae rugosae of the enamel can be observed. The low density of cristae rugosae is primitive: Middle and Late Oligocene odontocetes have ca. seven cristae rugosae per 5 mm, Late Oligocene forms 8-10 and Miocene *Squalodon* spp. have ten or more (PLEDGE & ROTHAUSEN 1977).

2. Evolution of the dentition within the Squalodontidae

In the present concept, two main evolutionary lineages can be recognized in the dentition of the European squalodontid taxa. One of these is represented by the genus *Neosqualodon*. The posterior buccal teeth have retained three large, blade-like anterior and posterior accessory denticles; the main denticle is hardly distinguishable. This primitive tooth crown morphology is connected with an extreme polydonta, a specialization unique to this genus among the Squalodontidae. Their teeth often sit so close together that not only are diastemata completely absent but the tooth crowns may overlap (FABIANI 1949: Figs. a & b).

The second lineage is characterized by the tendency to reduce the anterior accessory denticles. The main denticle is always considerably larger than the accessory denticles. Within this group, some have retained the primitive state of having three posterior denticles (*S. bariensis*, *S. bellunensis*); others have an increased number of posterior accessory denticles (five to six in *S. catulli*). *S. bellunensis* is a primitive representative of this lineage in that it has only 11 upper buccal teeth and the posteriormost upper teeth sometimes retain a third root. On the other hand, it is advanced in having small accessory denticles (small ID values) and 10-11 cristae rugosae per 5 mm. In this respect, *S. catulli* is similarly advanced (small ID values, large number of cristae rugosae). *S. bariensis* has 12 upper buccals that is an advanced state but the relatively low number of cristae rugosae and the larger ID values are regarded as primitive.

The phylogenetic position of the genus *Eosqualodon* is unsettled. ROTHAUSEN (1968) included two species within the genus: *E. latirostris* (CAPELLINI, 1904) and *E. langewieschei* ROTHAUSEN, 1968. Both are characterized by symmetrical tooth crowns with maximum 4 anterior and 4 posterior accessory denticles and 7-9 cristae rugosae per 5 mm. *E. langewieschei* has 12 buccal teeth whereas the number of teeth is unknown in the holotype of *E. latirostris*. ROTHAUSEN (1968) used the genus as a grade: a more primitive phase of his "eusqualodontides Stadium". Based on the available material it is impossible to state whether the two species of *Eosqualodon* are ancestral to some of the more advanced *Squalodon*, or they represent a third lineage where the tendency is to increase the number of the anterior and posterior accessory denticles above the primitive three. The low density of cristae rugosae suggests that *Eosqualodon* is a generalized form; on the other hand, the number of buccal teeth is already larger than in some *Squalodon* spp. (*S. bellunensis*). If future finds verify the theory of Rothausen, then the nomenclature he used (ROTHAUSEN 1968) must be reconsidered.

Squalodon kelloggi ROTHAUSEN, 1968 was described as a new species based on its peculiar mandible morphology (the only element known in this species). The diagnosis of the species includes the shortness of the mandibles (ROTHAUSEN 1968: 93). This is in conflict with Muizon's definition of the Squalodontidae (MUIZON 1990 and above) and *S. kelloggi* must, therefore, be regarded as *Odontoceti incertae sedis*.

Palaeobiogeographic considerations

The Squalodontidae have an extensive palaeontological record in the Mediterranean and Paratethys region. Here we restrict our discussion to the genus *Squalodon*, since the new find presented in this paper is a member of this taxon. Table 2 is a checklist of remains of *Squalodon* spp. in Europe and Figure 4 shows these occurrences in a palaeogeographical context.

In Europe, the oldest remains assigned to *Squalodon* are from the Oligocene of Rumania (PAUCĂ1931). However, the material consists of a single caudal vertebra that has little diagnostic value and thus, its assignment to *Squalodon* is dubious. The presence of the genus is much better documented from the Early Miocene (Aquitanian and Burdigalian Ages in the Mediterranean and the Northeast Atlantic as well as Eggenburgian Stage in the Central Paratethys). In the Aquitanian (23.8-20.5 Ma, according to RÖGL 1998) and in the Early Burdigalian (20.5-18.8 Ma; RÖGL 1998), the Mediterranean had a broad connection with the Indian Ocean and the Atlantic Ocean. The warm-water transgression spreading from the Middle East introduced warm-water invertebrate faunas and ensured tropical-subtropical climatic conditions (RÖGL 1998). The Central Paratethys communicated with the Mediterranean through the Western Paratethys and perhaps via a narrow seaway in the present-day Anatolia (RÖGL 1998). The rich material of the Belluno Sandstones (North Italy) and the *Squalodon* occurrences reported from Mučín (HOLEC at al. 1995) and Felsőesztergály (KOCH 1904) are from this period. The age of the new find from Tsotilion, Greece is Early Miocene but based on its close morphologic match with *Squalodon bellunensis*, a species described from the Aquitanian of North Italy, it is likely that the Greek specimen, too, originates from the Aquitanian.

Tab. 2: European occurrences of the genus *Squalodon* GRATELOUP, 1840 and sources of data.

Species	Locality (country)	Age / Stage	References
<i>Squalodon</i> sp.	Visiano, Parma (Italy)	early Serravallian, Middle Miocene	CIGALA-FULGOSI & PILLERI (1985)
<i>S. imperator</i> CIGALA-FULGOSI & PILLERI, 1985	Visiano, Parma (Italy)	early Serravallian, Middle Miocene	CIGALA-FULGOSI & PILLERI (1985)
<i>S. zitteli</i> PAQUIER, 1893	Bleichenbach (Germany)	Middle Miocene	KELLOGG (1923)
<i>S. servatus</i> (VON MEYER, 1841)	Baltringen, Württemberg (Germany)	"Vindobonian", Middle Miocene	KELLOGG (1923)
<i>S. molassicus</i> (BRONN, 1837)	Baltringen, Württemberg (Germany)	"Vindobonian", Middle Miocene	KELLOGG (1923)
<i>Squalodon</i> sp.	Apulia (Italy)	"Pietra leccese", late Early to Late Miocene	BIANUCCI et al. (1994)
<i>S. dalpiazii</i> FABIANI, 1949	Ragusa, Sicily (Italy)	upper Burdigalian, late Early Miocene	KELLOGG (1923)
<i>Squalodon</i> "a" ROTHAUSEN, 1968	Antwerp (Belgium)	Anversian (=Burdigalian), Early Miocene	ROTHAUSEN (1968)
<i>S. antwerpiensis</i> VAN BENEDEEN, 1861	Antwerp (Belgium)	Anversian (=Burdigalian), Early Miocene	KELLOGG (1923)
<i>S. bariensis</i> (JOURDAN, 1861)	Barie (France)	Burdigalian, Early Miocene	KELLOGG (1923)
<i>S. melitensis</i> (BLAINVILLE, 1840)	Malta	Burdigalian, Early Miocene	ROTHAUSEN (1968)
<i>S. grateloupii</i> VON MEYER, 1843	Léognan, Bordeaux (France)	Burdigalian, Early Miocene	KELLOGG (1923)
<i>Squalodon</i> sp.	Felsősztergály (Slovakia)	Eggenburgian, Early Miocene	KOCH (1904)
<i>Squalodon</i> sp.	Mučín (Slovakia)	Eggenburgian, Early Miocene	HOLEC et al. (1995)
<i>Squalodon</i> cf. <i>bellunensis</i>	Anargyroi, Tsotilion (Greece)	Aquitanian, Early Burdigalian	present paper
<i>S. peregrinus</i> DAL PIAZ, 1971	Belluno (Italy)	Aquitanian, Early Miocene	PILLERI (1985)
<i>S. bellunensis</i> DAL PIAZ, 1900	Belluno (Italy)	Aquitanian, Early Miocene	PILLERI (1985)
<i>S. catulli</i> MOLIN, 1859	Belluno (Italy)	Aquitanian, Early Miocene	ZIGNO (1876) and ROTHAUSEN (1968)
<i>Squalodon</i> sp.	Suslânești (Rumania)	Oligocene	PAUCĂ (1931)

During the Middle and Late Burdigalian (18.8-16.4 Ma; RÖGL 1998), the seaway between the Mediterranean and the Indian Ocean closed but the broad seaway to the Atlantic Ocean remained open (RÖGL 1998). The Eastern Paratethys lost its connections to the Central Paratethys and the Mediterranean, and became isolated (RÖGL 1998). The Central Paratethys Sea regressed extensively, and thus, marine vertebrate remains are scarce in the region (KORDOS & SOLT 1984). The Mediterranean and the Atlantic Ocean, however, remained hospitable to shark-toothed odontocetes and thus, records of *Squalodon* spp. continue during this period in the Mediterranean and the Northeast Atlantic (Table 2, Fig. 4).

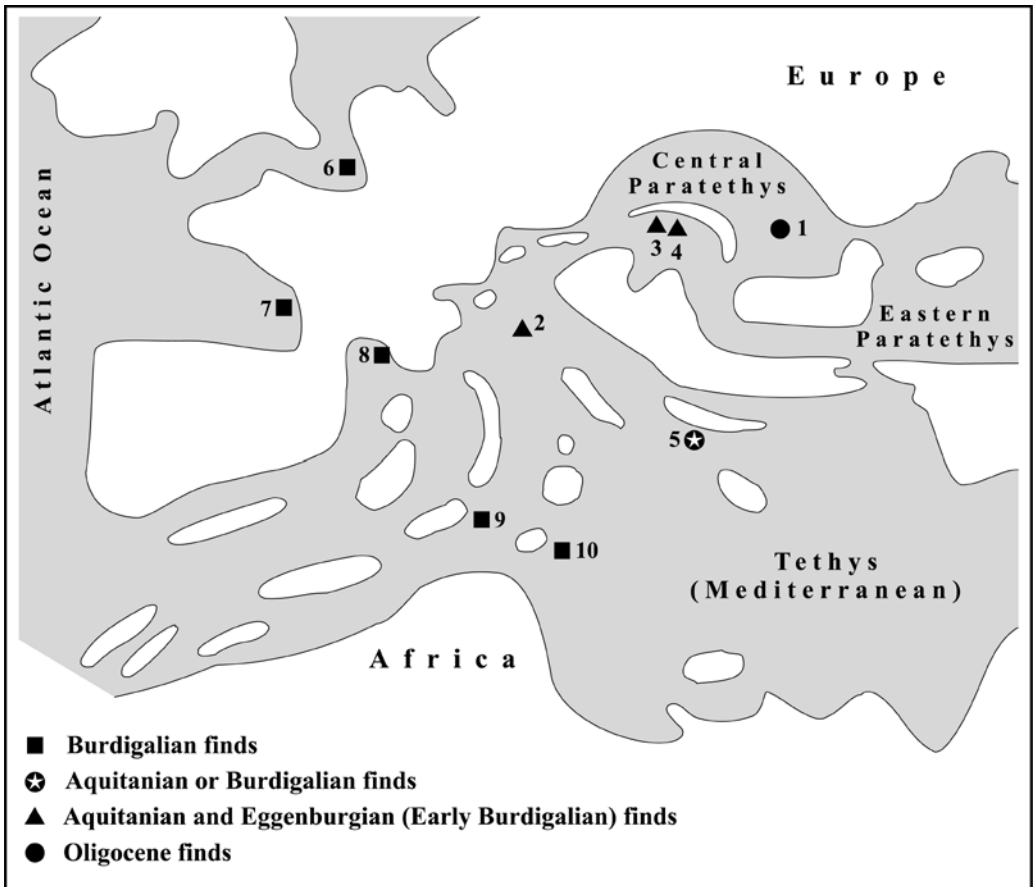


Fig. 4: European occurrences of the genus *Squalodon* from Late Oligocene and Early Miocene deposits. The paleogeographic situation corresponds to the Aquitanian Age (Early Miocene). 1 – Suslânești; 2 – Belluno; 3 – Felsősztergály (Horné Strháre); 4 – Mučín; 5 – Tsotilion; 6 – Antwerp; 7 – Léognan, Bordeaux; 8 – Barie, Saint-Paul-Trois-Châteaux; 9 – Ragusa, Sicily; 10 – Malta. (For more detail see Table 2; paleogeographic map redrawn after RÖGL 1998.)

From deposits younger than the Burdigalian there are only few records of *Squalodon*. They are from North Italy and from South Germany (if the latter localities are autochthonous) (Table 2). The beginning of the Middle Miocene was characterized by a far-reaching transgression in the entire circum-Mediterranean area (RÖGL 1998). Again, the broad communication between the Mediterranean and the Indian Ocean was established, and tropical faunal elements of Indo-Pacific origin appeared in the region (RÖGL 1998). The decline of the populations of *Squalodon* spp. in the Mediterranean – Paratethyan area is probably due to the appearance of more modern odontocetes rather than to environmental changes.

Conclusions

The fossil remains described in this paper from the Early Miocene marine marls of Tsotilion (West Macedonia, Greece) are recognized as representatives of the genus *Squalodon* (Squalodontidae). The specimen has 11 upper buccal teeth with three posterior denticles, whereas the anterior denticles of the buccal teeth tend to reduce. All buccal teeth have a large density of cristae rugosae, small ID values and large main denticles. These features indicate that the specimen is closely related to *S. bellunensis* DAL PIAZ, 1900. The new specimen is the first record of the genus *Squalodon* from the Eastern Mediterranean area.

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Plate 1

Cranial fragment of *Squalodon cf. bellunensis* from Tsotilion, Greece. – NHMW 2003z0024/0001.

Fig. 1: Dorsal view.

Fig. 2: Ventral view.

Scale bar equals 5 cm.

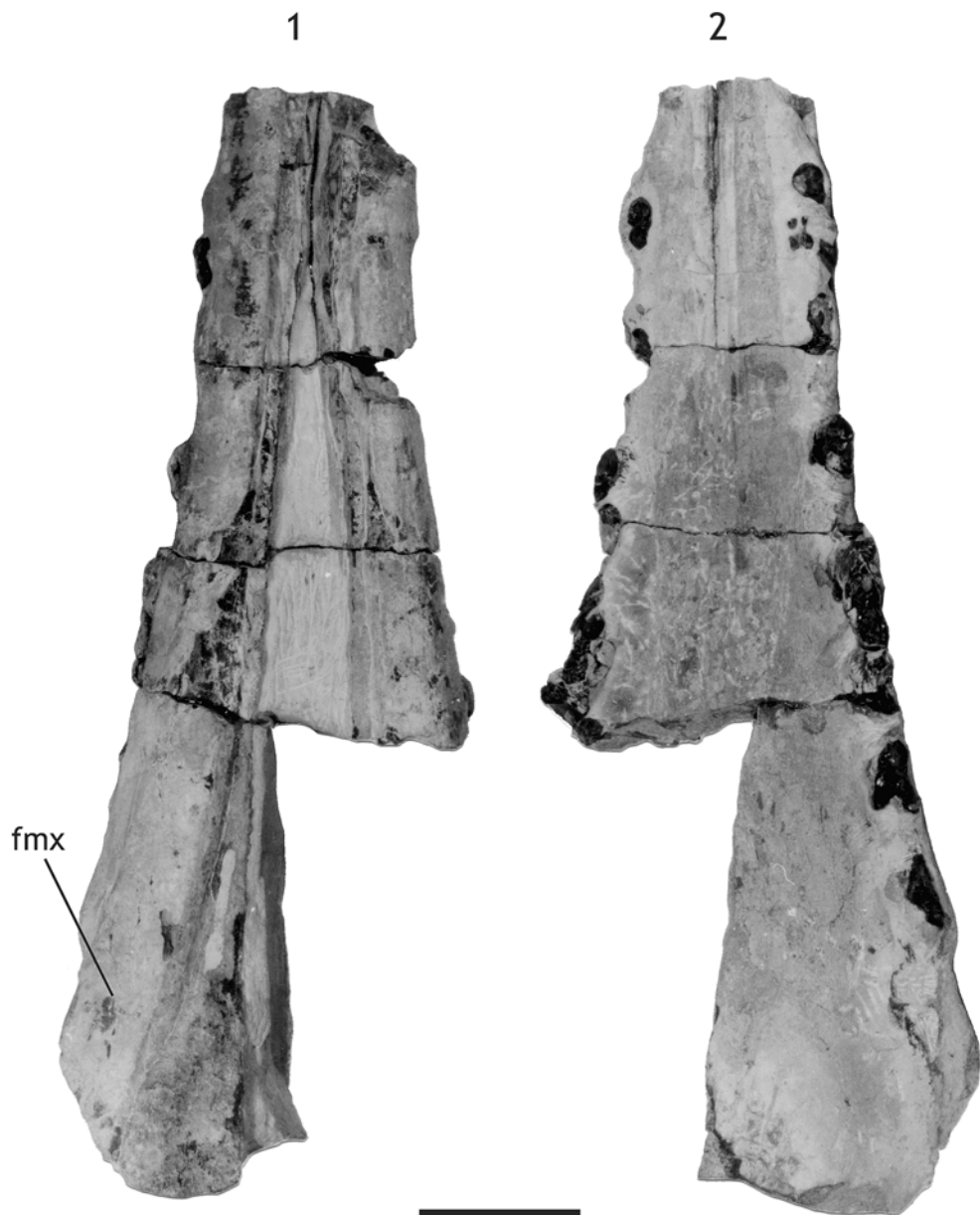


Plate 2

Mandibular fragment of *Squalodon* cf. *bellunensis* from Tsotilion, Greece. – NHMW 2003z0024/0002.

Fig. 1: Dorsal view.

Fig. 2: Ventral view.

Scale bar equals 5 cm.

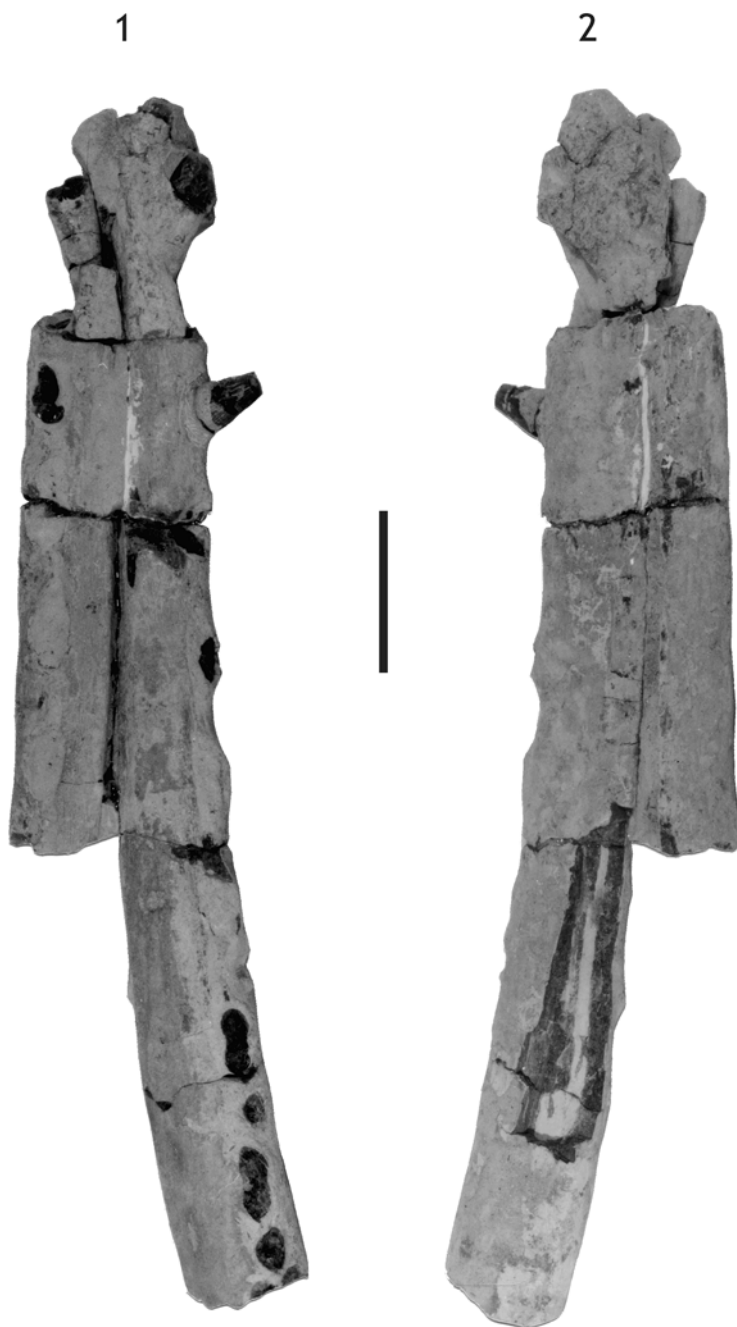


Plate 3

Squalodon cf. bellunensis from Tsotilion, Greece.

Fig. 1: Fragments of in situ left B7 (left) and B8 (right) with attached b8 between them. Lateral view. – NHMW 2003z0024/0001.

Fig. 2: Anterior ?buccal tooth in lateral view. – NHMW 2003z0024/0004.

Fig. 3: Left caninus or anterior buccal tooth in medial view. – NHMW 2003z0024/0005.

Fig. 4: Right caninus or anterior buccal tooth in lateral view. – NHMW 2003z0024/0006.

Fig. 5: ?right i3 in medial view. – NHMW 2003z0024/0007.

Fig. 6: Left B9 or B10 in medial view. – NHMW 2003z0024/0008.

Fig. 7: Left i1. – NHMW 2003z0024/0009.

Scale bars equal 1 cm.

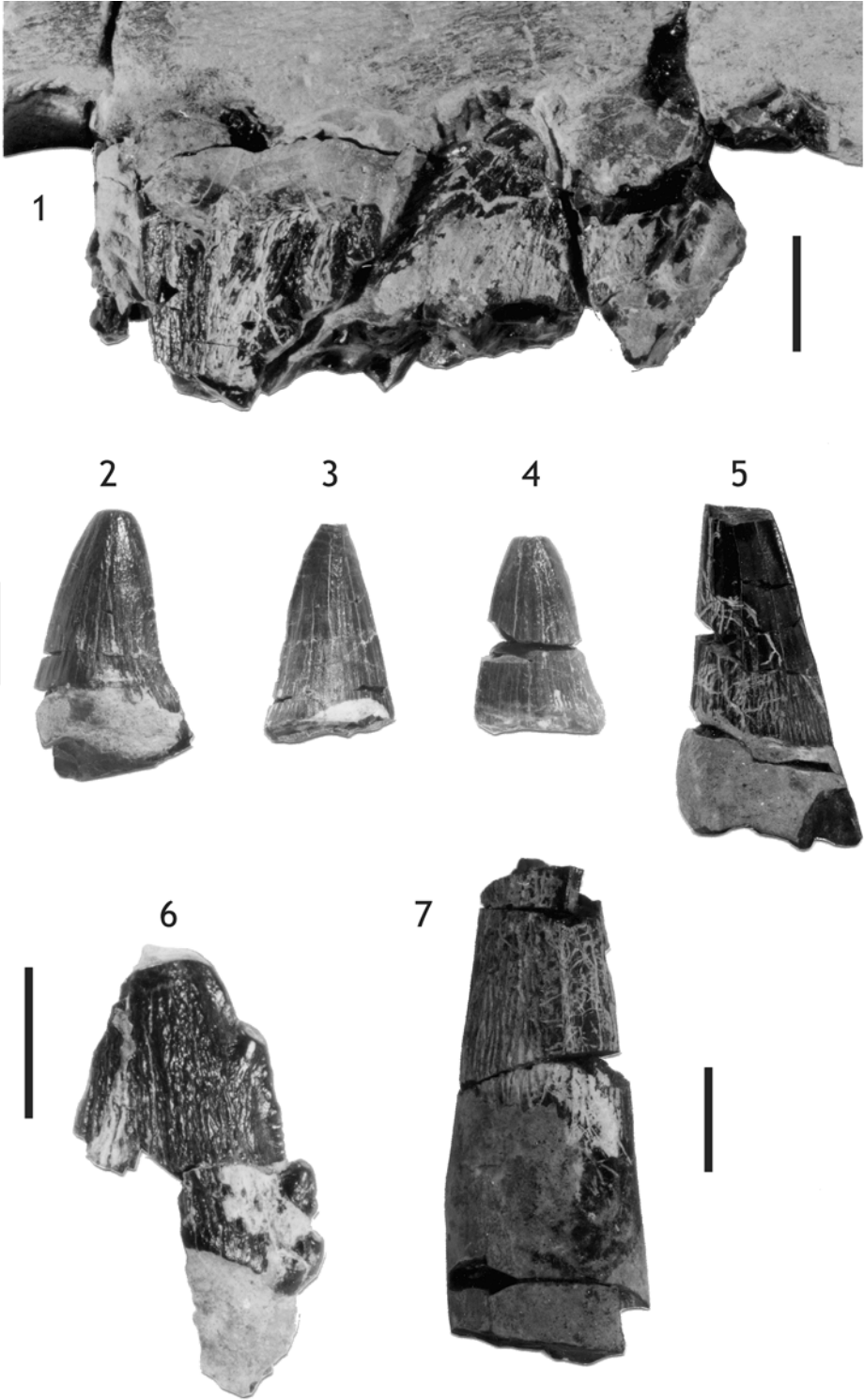


Plate 4

Squalodon cf. bellunensis from Tsotilion, Greece.

Fig. 1: Thoracic vertebra. Scale bar equals 1 cm. – NHMW 2003z0024/0010.

Fig. 2: ?First rib. Scale bar equals 5 cm in Figures 2-5. – NHMW 2003z0024/0011.

Fig. 3: ?Second rib. – NHMW 2003z0024/0012.

Fig. 4: ?Fourth rib. – NHMW 2003z0024/0013.

Fig. 5: ?Fifth rib. – NHMW 2003z0024/0014.



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