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Oldest evidence of the genus *Squalus* in the north alpine realm with remarks on its evolution and distribution through time.

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Abstract

The distinct morphology of teeth of the dogfish sharks *Squalus* spp. allows for tracking its evolutionary history. Fossils of the genus are known since the early Cretaceous; however, fossilized teeth of *Squalus* from that period are scarce. Here, we report on the oldest finding of a Squalus tooth fossil (upper Campanian - lower Maastrichtian) from the north alpine realm. The tooth is assigned to S. vondermarcki based on its morphological characters. Our finding adds information on the distribution of the genus during the Cretaceous period supporting a Tethyan origin in the early Cretaceous and subsequent distribution to other ancient oceans.

keywords: Cretaceous, Maastrichtian, Campanian, Squalidae, tooth morphology, chondrichthyes

Introduction

In earth history the Late Cretaceous holds a crucial role in evolution leading to modern biota. Based on drastic climatic changes from the Cretaceous Thermal Maximum in the early-mid Turonian, the onset of a cooling trend continued during the Campanian and culminated in the Maastrichtian (Cramer et al. 2011; Huber et al. 2018). The significant change of climate and environmental conditions entailed both the demise and evolution of new species of terrestrial (e.g. Condamine et al. 2021) and marine vertebrates including speciation in cartilaginous fishes (e.g. Guinot 2013; Condamine et al. 2019; Guinot & Cavin 2020). Here, we focus on the origination of the selachian genus *Squalus*, which appeared in the fossil record for the first time during the beginning of the Cretaceous Thermal Maximum, endured the severe global cooling in the Late Cretaceous, the mass extinction event at the end of the Cretaceous and persists until today.

The basis of this study is an isolated tooth from a building pit in Bad Adelholzen, Germany. The village Bad Adelholzen is well known for the production of mineral water, which enabled the exposure of the complete succession of the North Helvetic Nappe (Late Cretaceous to Late Eocene) during an expansion of the Adelholzener Alpenquellen company in 1994. This outcrop was frequently visited by amateur collectors of fossils, who made some extraordinary findings. The most famous is the first Bavarian *Hadrosaurus* (Wellnhofer 1992). However, the more common findings are belemnites. Hence, the herein described tooth of the order Squaliformes is the first record of sharks within this section of the Pattenau Formation and represents the oldest evidence of this order from the north alpine realm.

Böhm (1891) and Ganss (1956) published on the fauna of the Helvetic cretaceous formations but did not mention any shark fossils from the Pattenau Formation (“Pattenauer Mergel”). Our study documents the first selachian fossil from this formation.

Geographical and geological settings

Bad Adelholzen is located about 100 km south-east from Munich belonging to the municipality of Siegsdorf (Upper Bavaria) near the northern edge of the Alps (fig. 1A). Cretaceous sediments were only accessible during construction works. It must be mentioned that the sketch of the outcrop and the corresponding stratigraphic horizons of figure 1 rely on informal notes from the one of the authors (BB) during 1994 with only some rough measurements. During the Cretaceous to the Late Eocene, sediments were deposited on the southern continental shelf of Europe in the Tethys Ocean (Helvetic Unit). Hagn (1960) assumed the Tethys Sea to comprise two sea basins divided by the Ultrahelvetic Ridge. This ridge was formed regionally differently as an island chain or as a submarine bar (Heyng 2012). Therefore, these sediments are divided in a southern (South Helvetic Unit) and a northern part (Northern Helvetic Unit), respectively (Hagn 1960). The described outcrop comprises only sediments of the Northern Helvetic Unit. Bad Adelholzen is geographically located in the collision zone of the Helvetic nappe and the North Alpine Foreland Basin.

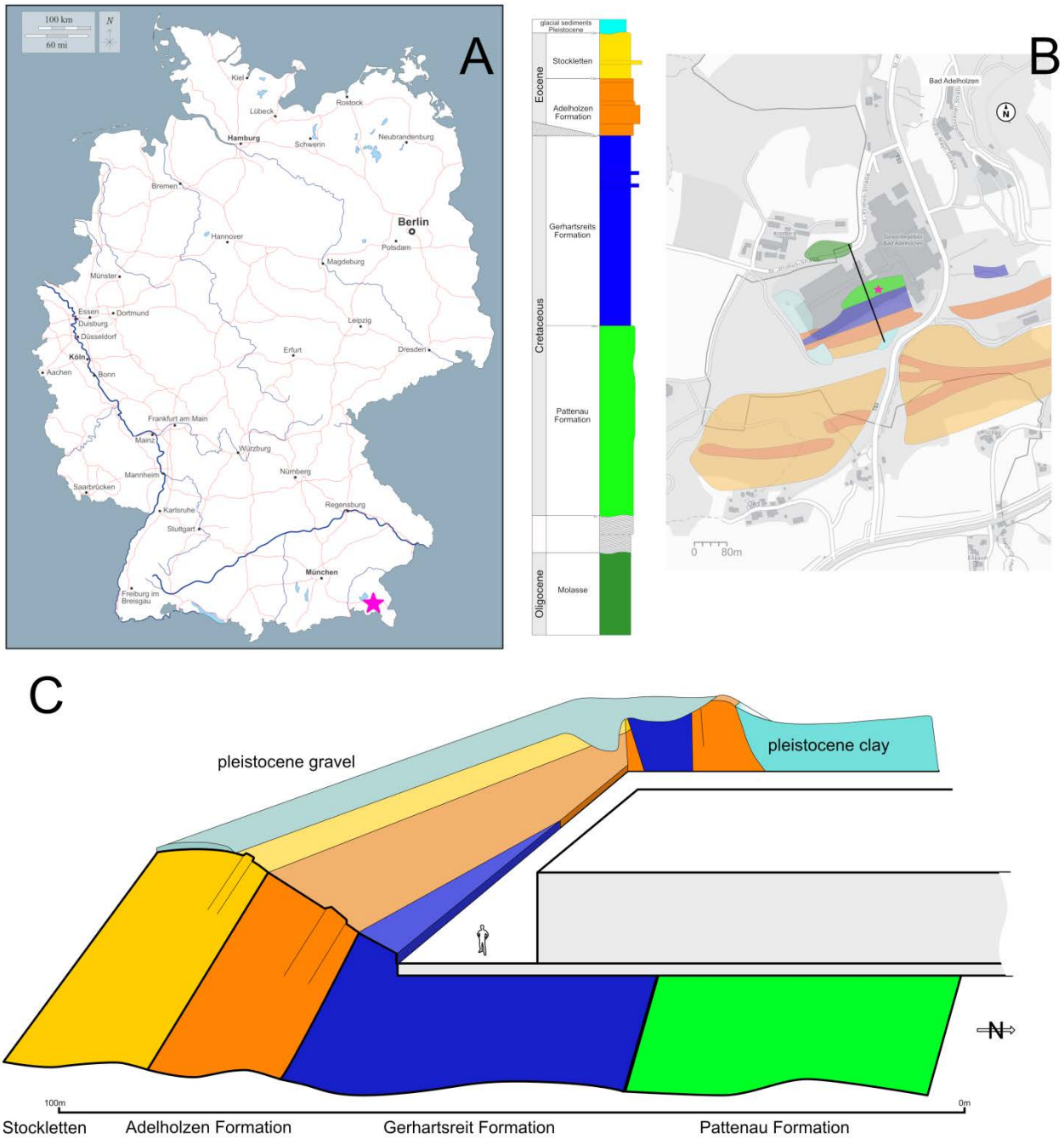

fig. 1. Geographical and geological settings. A: The locality Adelholzen (star) in the very south-east of Germany. B: Simplified geological setting. Locality marked by star. C: Sketch of the geological cross section after completion of construction.

Consequently, the North Alpine Foreland Basin has been successively overthrusted by the Helvetic nappe during alpine orogenesis (Hagn 1960).
Simplified, all strata are running more or less in east-west direction. From north to south, sediments from the Oligocene are found first in the north of the company site, followed by the Northern Helvetic nappe in the south. The contact zone was never accessible due to a Pleistocene glacier outflow of the Chiemsee glacier, removing the autochthonous sediments and replacing them with allochthonous gravel or clay.
The accessible succession started with the Pattenau Formation (Campanian-Maastrichtian) in the north of the ancient outcrop (fig. 1B, C) and is followed by the Gerhartsreit Formation (Maastrichtian). Sediments from the Palaeocene and lower Eocene sediments are missing due to a rather large hiatus. Consequently, the Adelholzen Formation (type locality) follows the Gerhartsreit Formation at this site, which represents sediments from the middle to upper Eocene. The top of autochthonous sedimentation is represented by the deposition of the Stockletten. The sketch (fig. 3B, C) is showing the former geological exposure overlayed on today's situation. Hagn et al. (1981) described the formation of interest, Pattenau Formation, as "light grey, calcareous, chunky marls with a tinge of blue or green". Throughout the section, several layers with fossil accumulations could be observed, dominated by belemnites, molluscs (*Inoceramus*), and echinoids among others.

Material & methods

The tooth-bearing sediments from the Pattenau Formation (5 kg) were collected by one of the authors (BB) in 1994. The tooth was extracted from the sediment in 2013 by using diluted hydrogen peroxide in combination with screen-washing down to a mesh size of 300µm. The accompanying fauna consists particularly of belemnites as well as a rich micro fauna. The tooth analyzed herein is deposited in the Natural History Museum (NHM) Vienna with the inventory number NHMW/2021/0136/0001.

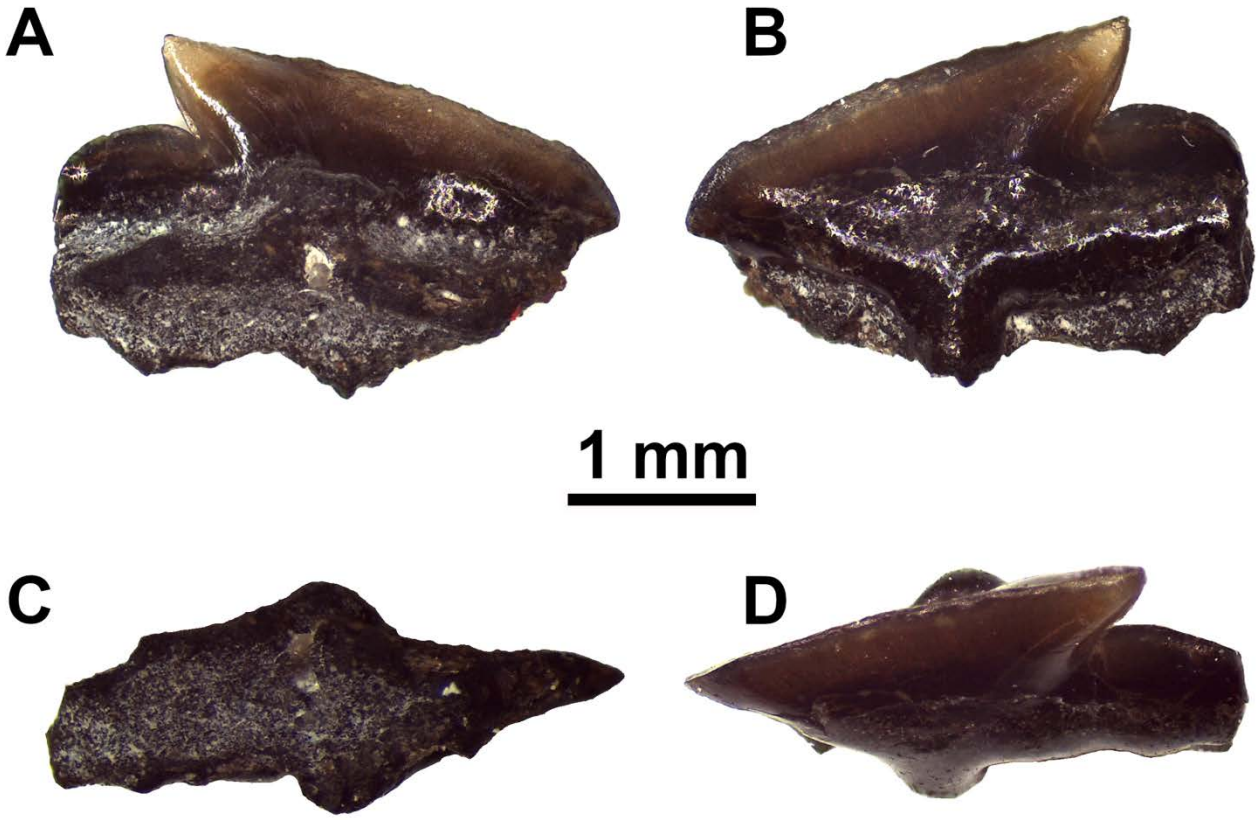

fig. 2. *Squalus vondermarcki* Müller & Schöllmann, 1989, Pattenau Formation, Collection No. NHMW/2021/0136/0001
A: lingual view, B: labial view, C: basal view, D: occlusal view.

Results

1. Systematic palaeontology

cohort	EUSELACHII	Hay, 1902
subcohort	NEOSELACHII	Compagno, 1977
order	Squaliformes	Compagno, 1977
family	Squalidae	Blainville, 1816
genus	*Squalus*	Linné, 1758
type species	*S. acanthias*	Linné, 1758 | by subsequent designation

Squalus vondermarcki Müller & Schöllmann, 1989

1977 *Squalus* cfr. *latidens* - Herman: 139, pl. 5 fig. 9
1982a *Centrosqualus appendiculatus* - Herman: 133-134 (partim), pl. 1 fig. 4a

figure 2 A-D
material: 1 tooth (NHMW/2021/0136/0001).
size: height: 1.90 mm; width: 3.03 mm.
distribution: Germany, Maastrichtian-Campanian (Müller 1989, 1991; Müller & Schöllmann 1989; Thies & Müller 1993; Zacke 2003), Angola (Antunes & Cappetta 2002), ?Canada (Cappetta et al. 2019).

2. Description

The tooth is strongly labio-lingually compressed. Its width is 3.02 mm, the height is 1.93 mm and the angle of inclination of the main cusp measures 28.4°. The broad, triangular main cusp is strongly bent distally. The crown is smooth and biconvex. Folds or ornamentations are absent. The mesial cutting edge shows no serration, is convex in the lower two-thirds and straight near the tip of the cusp. The short distal cutting edge is weakly convex. The semi-circular distal heel takes up about a quarter of the total width. The labial short and approximately rectangular apron overhangs insignificant the base of the root. Several small foramina are located on both sides of the apron directly below the crown base. The lingual side of the tooth shows a prominent, high medially uvula with a central infundibulum. Similar to the labial side of the tooth there are several small foramina on both sides of the uvula. The compressed and narrow root shows a flat basal face and a well marked lingual bulge.

3. Remarks

The tooth described here shows great similarity with the tooth illustrated by Müller & Schöllmann (1989, fig. 4) and described as *Squalus vondermarcki*. The morphological differences from the valid species mentioned below are described in detail in Antunes & Cappetta (2002). Cappetta et al. (2019) reported *S. vondermarcki* from the Campanian of Hornby Island, British Columbia, Canada. It is remarkable that, in contrast to the teeth from the Campanian of Northern Germany and the tooth shown herein, the teeth from Hornby Island possess aprons that distinctly overhang the bases of roots. Müller & Schöllmann (1989) write in their species diagnosis that the apron generally slightly overhangs the base of the root, however, not as distinct as shown in Cappetta et al. (2019). We therefore suggest a taxonomic re-analysis of fossil teeth from Hornby Island.
In addition to the genera *Squalus* and *Cirrhigaleus*, the extinct genera †*Centrosqualus* Signeux, 1950, †*Protosqualus* Cappetta, 1977, †*Megasqualus* Herman, 1982b, and †*Centrophoides* Davis, 1887, are included in the family Squalidae. Apart from *S. vondermarcki*, the following valid *Squalus* species are currently known from the Cretaceous: *S. worlandensis* Case, 1987, *S. huntensis* Case & Cappetta, 1997, *S. ballingsloevensis* Siverson, 1993, *S. balsvikensis* Siverson, 1993, *S. gabrielsoni* Siverson, 1993, *S. nicholsae* Cappetta, Morrison & Adnet, 2019, *S. argentinensis* (Bogan, Agnolín & Novas, 2016), and *S. chiconis* (Jordan, 1907).
Squalus chiconis (Jordan, 1907) was originally described as *Hemipristis chiconis* Jordan, 1907 and later placed in *Notidanion chicone* (Jordan & Hannibal, 1923). The holotype was examined by Welton & Alderson (1981) and clearly identified as *Squalus*. Due to the only fragmentary preservation and the lack of the complete root, the morphological characteristics decisive for species identification are missing and the species has to be evaluated as a nomen dubium.

Species	Age	Number of specimens	County	Ocean	Reference
Squalus sp.	Maastrichtian	1	Chile	East Pacific	Muñoz-Ramírez et al. 2007
Squalus gabrielsoni Siverson, 1993	Maastrichtian	36	Denmark	North Atlantic	Adolfssen & Ward 2014
Squalus ballingsloevensis Siverson, 1993	Maastrichtian	>100	Sweden	North Atlantic	Siverson 1993
Squalus balsvikensis Siverson, 1993	Maastrichtian	several hundred teeth	Sweden	North Atlantic	Siverson 1993
Squalus gabrielsoni Siverson, 1993	Maastrichtian	about 50 teeth	Sweden	North Atlantic	Siverson 1993
Squalus huntensis Case & Cappetta, 1997	Maastrichtian	1	US, North Carolina	North East Atlantic	Case et al. 2017
Squalus chiconis (=sp.) (Jordan, 1907)	Maastrichtian	1	US, California	Ost Pacific	Jordan 1907
Squalus argentinensis (Bogan, Agnolin & Novas, 2016)	Maastrichtian	18	Argentina	South East Atlantic	Bogan et al. 2016
Squalus sp.	Maastrichtian	1	Germany	Tethys	Pollerspöck & Beaury 2014
Squalus vondermarcki Müller & Schöllmann, 1989	Maastrichtian	5	Germany	Tethys	Zacke 2003
Squalus sp.	Maastrichtian	?	Maroc	Tethys	Noubhani & Cappetta 1997
Squalus ballingsloevensis Siverson, 1993	Maastrichtian	153	US, North Dakota	Western Interior Seaway	Hoganson et al. 2019
Squalus sp.	Maastrichtian	4	US, North Dakota	Western Interior Seaway	Hoganson et al. 2019
Squalus huntensis Case & Cappetta, 1997	Maastrichtian	2	US, Texas	Western Interior Seaway/East Atlantic	Case & Cappetta 1997
Squalus nicholsae Cappetta, Morrison & Adnet, 2019	Campanian	154	CA, British Columbia	East Pacific	Cappetta et al. 2019
Squalus sp.	Campanian	1	CA, British Columbia	East Pacific	Cappetta et al. 2019
Squalus vondermarcki Müller & Schöllmann, 1989	Campanian	343	CA, British Columbia	East Pacific	Cappetta et al. 2019
Squalus sp.	Campanian	2	US, California	East Pacific	Welton & Alderson 1981
Squalus vondermarcki Müller & Schöllmann, 1989	Early Camp./Late Maastr.	10	Angola	South West Atlantic	Antunes & Cappetta 2002
Squalus vondermarcki Müller & Schöllmann, 1989	Campanian	>50	Germany	Tethys	Müller 1989
Squalus vondermarcki Müller & Schöllmann, 1989	Campanian	6 (plus fragments)	Germany	Tethys	Müller & Schöllmann 1989
Squalus vondermarcki Müller & Schöllmann, 1989	Campanian	2	Germany	Tethys	Thies & Müller 1993
Squalus vondermarcki Müller & Schöllmann, 1989	Campanian	20	Germany	Tethys	Müller 1991
Squalus vondermarcki Müller & Schöllmann, 1989	Campanian	1	Germany	Tethys	this study
Squalus sp.	Campanian	?	Israel	Tethys	Lewy & Cappetta 1989
Squalus worlandensis (Case, 1987)	Campanian	4	CA, Alberta	Western Interior Seaway	Cook et al. 2017
Squalus sp.	Campanian	>200	US, South Dakota	Western Interior Seaway	Martin & Fox 2007
Squalus worlandensis (Case, 1987)	Campanian	numerous teeth (100?)	US, Wyoming	Western Interior Seaway	Case 1987
Squalus worlandensis (Case, 1987)	Campanian	?	US, Wyoming	Western Interior Seaway	Demar & Breithaupt 2006
Squalus sp.	Turonian	(?, one fin spine)	Germany	Tethys	Fischer et al. 2017
Squalus sp.	Cenomanian	1	Lithuanian	North Atlantic	Adnet et al. 2008
Squalus sp.	Cenomanian	>10	Kazakhstan	Tethys	Kennedy et al. 2008
Squalus sp.	Cenomanian	?	Russia	Tethys	Popov & Lapkin 2000
Squalus sp.	Cenomanian	2	United Kingdom	Tethys	Underwood & Mitchell 1999

tab. 1.
Fossil records of the genus *Squalus*.

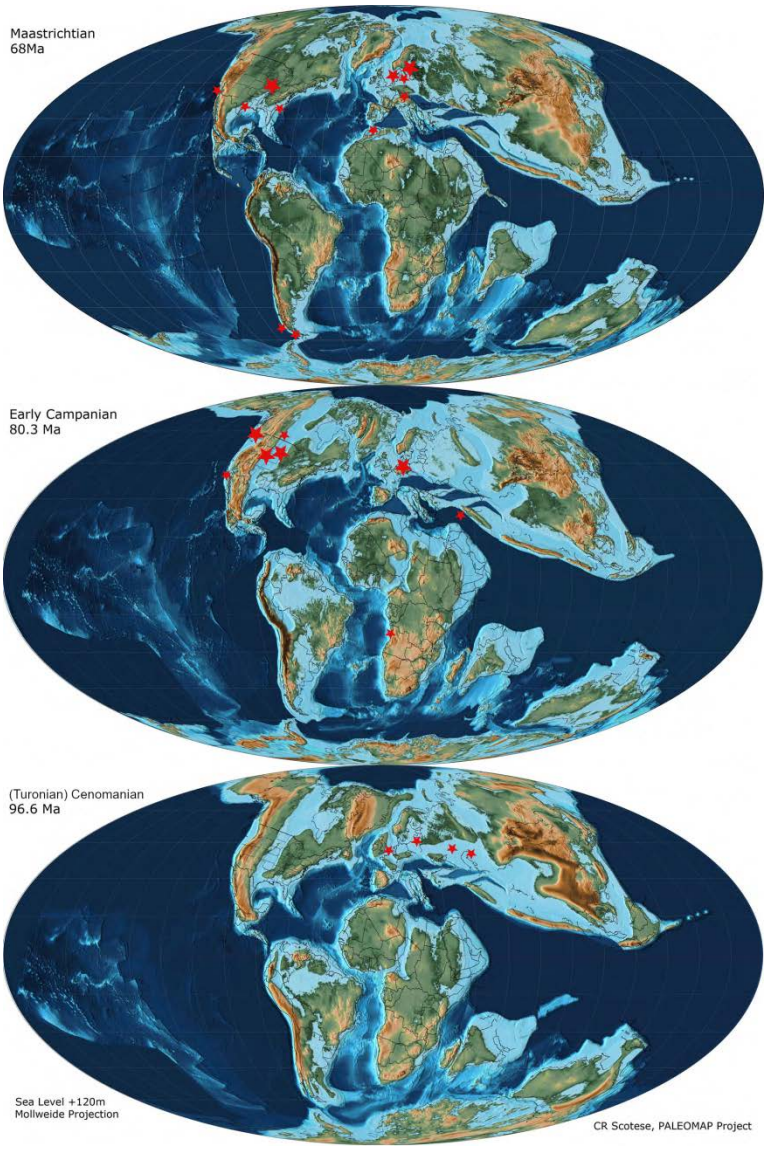

fig. 3.
Paleogeographic records of the genus *Squalus* during the Cretaceous indicated by red stars, big star (n>100), medium star (n>20<100), small star (n<20) (Palaeomaps after Scotese 2014).

The oldest records of teeth assigned to the genus *Squalus* come from the Cenomanian (North East England, Underwood & Mitchell 1999; Russia, Popov & Lapkin 2000; Lithuanian, Adnet et al. 2008; Kazakhstan, Kennedy et al. 2008). Both Underwood & Mitchell (1999) and Adnet et al. (2008) documented a striking dominance of the genus *Protosqualus* relative to the genus *Squalus* at these sites (470/2 in Underwood & Mitchell 1999, and more than 150/1 in Adnet et al. 2008).
Protosqualus differs essentially from *Squalus* in having two separate lingual foramina, whereas the genus *Squalus* usually has one infundibulum. However, Cappetta (1977) already notes in the genus diagnosis of *Protosqualus* that three out of 18 tooth specimens have an infundibulum. The second difference is the shape of the apron. While the apron of *Protosqualus* is usually very broad at the base and continuously tapers towards the bottom, the apron of *Squalus* is usually formed with parallel edges (Underwood & Mitchell 1999). *Protosqualus* has been recorded mainly from the central Tethys (Europe, Russia, Cappetta 2012). It has been reported from Australia (Kemp 1991; Berrell et al. 2020) and India (Underwood et al. 2011). To date, there are no records from North America.

Discussion

Teeth of the genus *Squalus* are relatively rare in Late Cretaceous sediments. A database search at www.shark-references.com (Pollerspöck & Straube 2021a) revealed 832 publications dealing with Late Cretaceous elasmobranch faunas. Of these, 9,85 % report on squaliform tooth fossils. Only 4,69 % of the articles documenting squaliform diversity report on *Squalus* fossils (tab. 1).
Figure 3 summarises the findings of the genus *Squalus* published to date. Contrary to the description in Adnet et al. (2008, fig. 5), which suggests a continuous record of the genus *Squalus* from the Cenomanian to the present day, records are still missing from the Turonian to the Santonian. (tab. 1, fig. 3).
According to current knowledge, the genus *Squalus* appears in the Cenomanian in the area of the Central Tethys, is common in the Campanian in North America both on the Pacific coast and at Western Interior Seaway, but has also already been recorded in the southern Atlantic (Angola) (fig. 3). The geographical distribution continues in the Maastrichtian with first records from the South-East Pacific (Chile). Today, with 37 species (Pollerspöck & Straube 2021b), the genus is distributed almost worldwide in boreal, temperate and tropical seas and is one of the most diverse genera of the order Squaliformes.
Assuming the genus *Squalus* originated in the Central Tethys, it appears to have expanded from there to the Campanian both eastward (Israel, Lewy & Cappetta 1989) and southward along the African continent (Angola, Antunes & Cappetta 2002) and westward (North America). The numerous abundance in the area of the Western Interior Seaway is remarkable (Case 1987; Martin & Fox 2007), since only few specimens were documented from other sites (tab. 1). In the Western Interior Seaway, water depth increased steadily westward, reaching several hundred meters in the Utah area (Kauffman 1984). The two sites mentioned above were located in the central and eastern areas of this sea, respectively, and thus in much shallower waters. The sediments in which the teeth of the fossil *S. worlandensis* (Case, 1987) were found are even attributed to the estuarine phase of the Mesaverde Formation. Comparably shallow habitats as estimated for the Mesaverde Formation are occupied today only by *Cirrhigaleus asper*, *S. acanthias*, and *S. suckleyi*. In contrast, several recent representatives of the family Squalidae usually inhabit depths of 600m and below (Ebert et al. 2013). *Squalus acanthias* and *S. suckleyi* are known to reproduce in shallow nearshore areas (Ebert et al. 2013). The numerically frequent occurrence of *Squalus* fossils in shallow water deposits of the Maastrichtian may indicate at least temporary shallow habitat occupancy.
However, the numerically largest occurrence of fossil *Squalus* teeth is reported from large deep-water submarine fan complexes at the North American Pacific Coast region (Cappetta et al. 2019). Since there was no connection between the Pacific and the Western Interior Seaway in the Maastrichtian, the genus likely spread along the North American Pacific coast via the Central American Seaway. Records from Chile provide further datapoints allowing speculation on a worldwide distribution already in the Maastrichtian.

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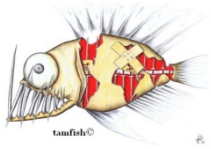

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