



The shark and ray teeth of the Lower Miocene (Upper Marine Molasse) from Ballendorf, Baden-Württemberg, Southern Germany

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Abstract

In an abandoned sand pit near Ballendorf (Alb-Donau District, Baden-Württemberg), sediments of the Upper Marine Molasse (Lower Miocene) are present. In these sediments, 39 shark and ray species belonging to 29 genera were identified (*Aetobatus*, *Alopias*, *Araloselachus*, *Carcharhinus*, *Carcharias*, *Centrophorus*, *Chaenogaleus*, *Dasyatis*, *Galeocerdo*, *Hemipristis*, *Iago*, *Isistius*, *Keasius*, *Notorynchus*, *Pachyscyllium*, *Paragaleus*, *Physogaleus*, *Pristiophorus*, *Raja*, *Rhinobatos*, *Rhinoptera*, *Rhizoprionodon*, *Rhynchobatus*, *Scyliorhinus*, *Sphyrna*, *Squalus*, *Squatina*, *Taeniurops*, *Triakis*). However, in this paper we only illustrate and describe the 23 taxa not already discussed in previous publications on the Upper Marine Molasse deposits of Äpfingen, Rengetsweiler and Ursendorf, apart from two exceptions: teeth from jaw positions not previously illustrated, and specimens that are better preserved than those in previous publications. Specimens only determined as “sp.” were illustrated because it cannot be ruled out that they represent different species to the ones published earlier. Nearly all of the taxa found have Recent relatives; only *Araloselachus*, *Keasius* and *Physogaleus* are extinct. Most of the recovered taxa lived on or near the bottom in the shelf region. *Alopias* and possibly also *Keasius* lived higher in the water column. With *Isistius*, a taxon living in the oceanic realm was present, and the Recent representatives of *Centrophorus* live in deeper waters. Nearly all taxa fed on invertebrates and/or fishes; *Isistius* also fed as an ectoparasite. Additionally, two generalist feeders (*Galeocerdo*, *Notorynchus*) and one filter feeder (*Keasius*) were identified. The species *Carcharias crassidens*, which is not common in the Upper Marine Molasse, was also verified. Other fossils found in this deposit include remnants of odontocete cetaceans, molluscs, balanid barnacles, algae, and teeth of terrestrial mammals. The palaeoenvironment was a warm, shallow-water habitat. Based on greater proximity to the palaeo-coastline, the water depth was probably less than in other Upper Marine Molasse deposits.

Keywords Elasmobranchii · Teeth · Lower Miocene · Upper Marine Molasse · Paratethys

Introduction

The deposit of Ballendorf is located within the Sediments of the Upper Marine Molasse (here abbreviated as OMM, from the German name “Obere Meresmolasse”).

It is only ca. 3 km away from the “Klifflinie” (cliff line representing the shoreline) of the ancient OMM sea. In 2008, a large collection containing fossil shark and ray teeth as well as other fossils from this deposit came into the collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS). This collection was compiled by one of the authors (H. Bracher) during scientific excavations in an abandoned sand pit near Ballendorf. In the mid-1980s, he organised a school project from the Verbandshauptschule Altheim/Alb (near Ballendorf), during which pupils searched for fossils in the aforementioned sand pit. Based on this project and his long-term fossil collecting efforts, a paper concerning the fauna of Ballendorf was privately published by H. Bracher in 2000.

Publications about the shark and ray fauna of the OMM in Baden-Württemberg are rare. In recent years,

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the localities of Ursendorf, Rengetsweiler and Äpfingen were examined by Höltke et al. (2020, 2022a, b). Ulm-Ermingen was discussed in Baier et al. (2004) and Walbertsweiler by Pfeil (1991). Feichtinger and Pollerspöck (2021) illustrated and described the elasmobranch fauna of the whole OMM. The Miocene sharks and rays of Baltringen were the subjects of the famous publications of Probst (1877, 1878, 1879). The large number of elasmobranch teeth, especially those of microscopic size, makes the Ballendorf collection very valuable.

In this paper, we study and present the shark and ray teeth of the Ballendorf deposit. We also provide an overview of the geology, including a description of the sediment profile. The palaeoecology of this deposit is reconstructed and the shark and ray fauna are compared with the other localities in the OMM of Baden-Württemberg. The large Ballendorf collection provides a unique insight into the Lower Miocene shark and ray fauna of the OMM in Baden-Württemberg, especially concerning very small teeth.

Locality

The abandoned sand pit is located in the municipal forest of Ballendorf, which is named “Obere Häu“ (see Fig. 1). It is ca. 1.5 km northwest of the village Ballendorf. The sandpit has the coordinates 48°33′53.29″ N, 10°3′28.72″ E.

Geological overview

The deposit of Ballendorf is located in the Lower Miocene OMM. During that time, large parts of South Germany, Austria and Switzerland were covered by an ancient sea. During the maximum extension of the OMM sea (Lower Miocene, Ottnangian, ca. 17.8 Ma), this sea was connected to the Mediterranean in the Southwest, and the Paratethys in the North (Höltke et al. 2022a). The OMM in Baden-Württemberg ranged from the early to the middle Ottnangian (Heckeberg et al. 2010). See Kuhlemann and Kempf (2002); Pippèrr et al. (2016) and Pippèrr et al. (2018) for details regarding the evolution of the OMM.

Concerning of the age of the Ballendorf deposit, there are some discrepancies. Vennemann and Hegner (1998) determined the age to be 22 ± 2 Ma using Sr-isotopes; this value corresponds to the Paratethyan Eggenburgian stage (see stratigraphic table in Fig. 2). However, according to Heckeberg et al. (2010) and Pippèrr et al. (2016), the OMM sediments of Baden-Württemberg are all of an Ottnangian age. What can be definitively said is that the Ballendorf deposit is of an Early Miocene (Burdigalian) age. There are also some sharks species present which, according to Feichtinger and Pollerspöck (2021), are only known beginning in the Ottnangian: *Isistius triangulus* (Probst, 1879), *Pristiophorus suevicus* Jaekel, 1890, *Iago angustidens* (Cappetta, 1973), *Paragaleus tenuis* (Probst,

Fig. 1 Geographic position of Ballendorf

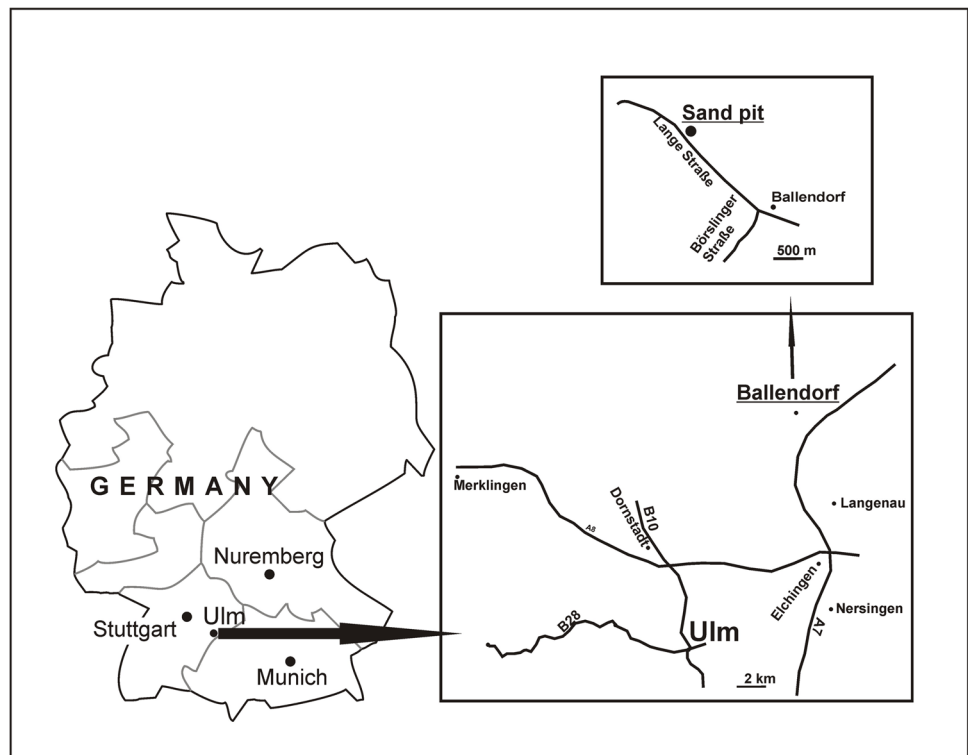
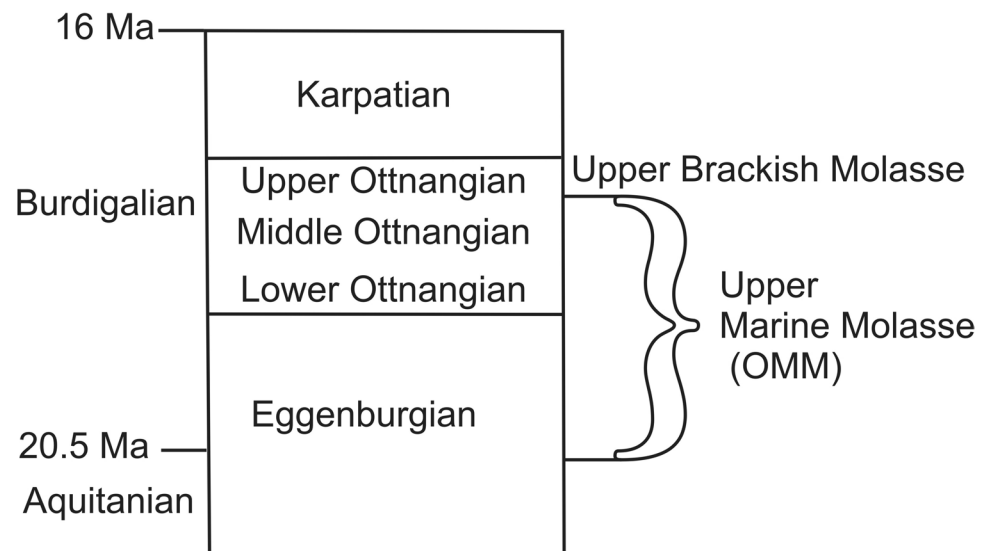


Fig. 2 Early Miocene stratigraphic succession in the Molasse Basin



1878), *Rhizoprionodon fischeuri* (Joleaud, 1912) and *Carcharhinus similis* (Probst, 1878).

Profile description

A lacquer-profile of the sedimentary succession of the Ballendorf sand pit was taken by the SMNS in October 1988. The profile is on display in the exhibition of the SMNS (see Figs. 3 and 4). The floor strata of the profile are built on Upper Jurassic limestone with traces of boring bivalves on its surface representing the marine transgression (see Fig. 5.) This Upper Jurassic base is not part of the lacquer-profile. In the profile, three horizons can be identified (see Figs. 3, 4):

1. ca. 33 cm of very coarse, poorly sorted brown sands with gravels up to 25 mm in size and remnants of oysters and one shark tooth.
2. ca. 66 cm of beige coloured, poorly sorted, very coarse sands. These sands contain larger remnants of oysters.
3. The top of the profile consists of ca. 90 cm of brown, well-sorted medium sands with laminations.

All the fossils came from the two coarse grained horizons. In the top horizon (3), no fossils were found.

Material and methods

For this paper, the Ballendorf collection of one of the authors (H. Bracher) was examined. This collection is housed in the Staatliches Museum für Naturkunde Stuttgart

(SMNS) and contains several hundred teeth with different states of preservation, as well as remnants of other vertebrates. All the fossils came from the Ballendorf sand pit and were collected by fossicking and sieving down to a mesh of 2 mm. Achieving new material and sieving down to a mesh of 1 mm or lower is not possible at the moment because the sand pit is now overgrown by plants. Additionally, invertebrate fossils and some shark teeth from the collection of the SMNS were studied. These teeth also came from the sandpit, but in the case of the invertebrates, the exact locality in Ballendorf is unknown. The teeth were examined under a Wild Heerbrugg-microscope with a magnification up to 50x. Photos were made with a Keyence microscope as well as a Nikon Z 5 camera. Tooth terminology and systematics are according to Cappetta (2012). For the determination, the literature cited in the “References” section was used. For comparisons with Recent relatives and the determination of tooth position, the following references were used: Bigelow and Schroeder (1948), Herman et al. (1988), Herman et al. (1989), Herman et al. (1991), Kent (1994), Reinecke et al. (2011), Voigt and Weber (2011), Froese and Pauly (2022), Pollerspöck and Straube (2022). Dried jaws of *Centrophorus cf. granulosus* (Bloch and Schneider, 1801) in a private collection were examined; the sex and size of this specimen are unknown. For the grain size determination in the profile, a plastic grain size card from TU Bergakademie Freiberg was used.

Many of the common OMM species have already been illustrated for the localities of Ursendorf, Rengetsweiler and Äpfingen (Fig. 6; see also Hölte et al. 2020, 2022a, b). In this new contribution, we only illustrate and describe teeth that were not covered in these earlier publications. Exceptions were made when a tooth from a jaw position not previously published could be verified or when a better-preserved tooth was

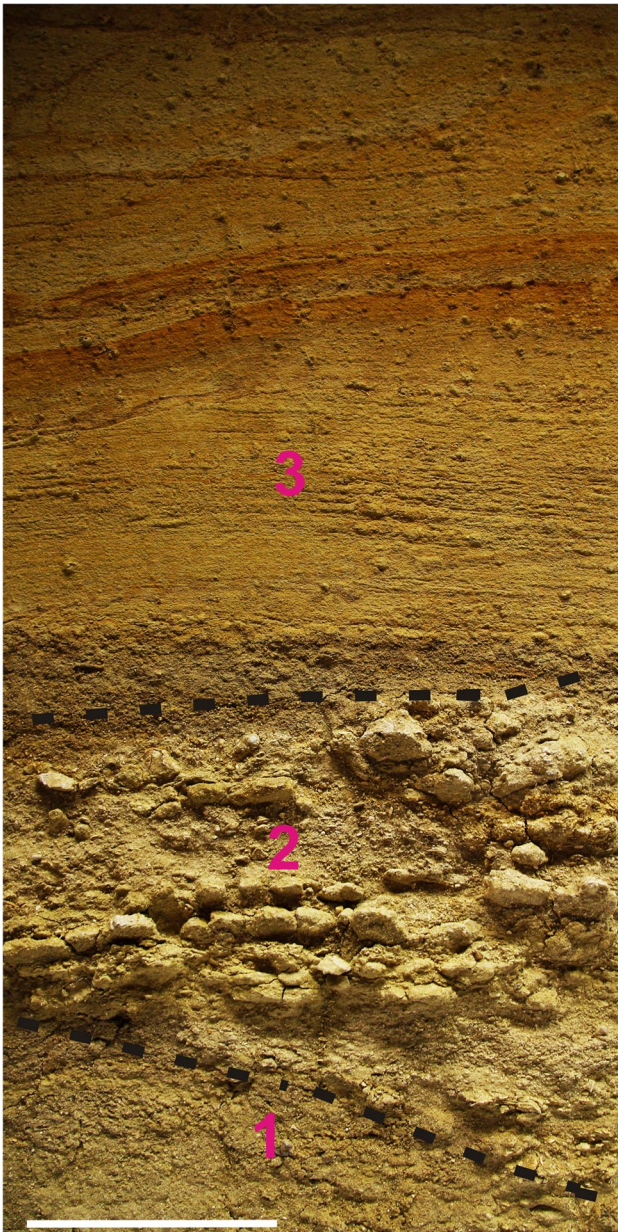


Fig. 3 Lacquer-profile of the OMM at the Obere Häu sandpit, Ballendorf. 1 basal layer of coarse, poorly sorted brown sands with gravels up to 25 mm in size; 2 beige, poorly sorted very coarse sands. 3 brown, well-sorted medium sands with laminations. All fossils discussed in the text originate from the two coarse grained horizons. Scale: 30 cm

available. Specimens only determined as “sp.” were illustrated because it cannot be ruled out that they represent different species to the ones published in the works listed above. For the autecology and other occurrences in the OMM for individual taxa see Hölftke et al. (2020, 2022a, b) and Tab. 1. For taxa not mentioned in these publications, these features are given in the descriptions. To give a full overview of the elasmobranch

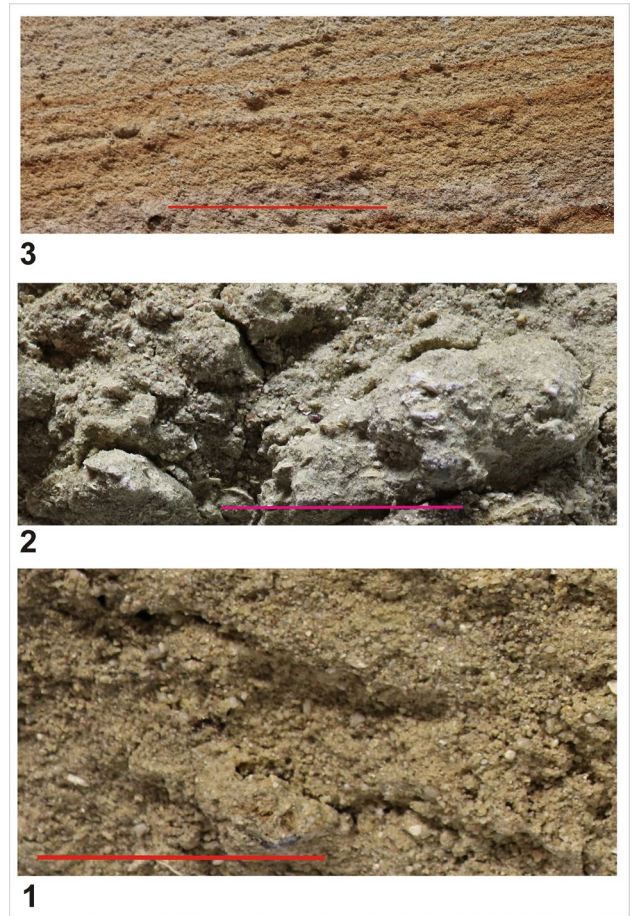
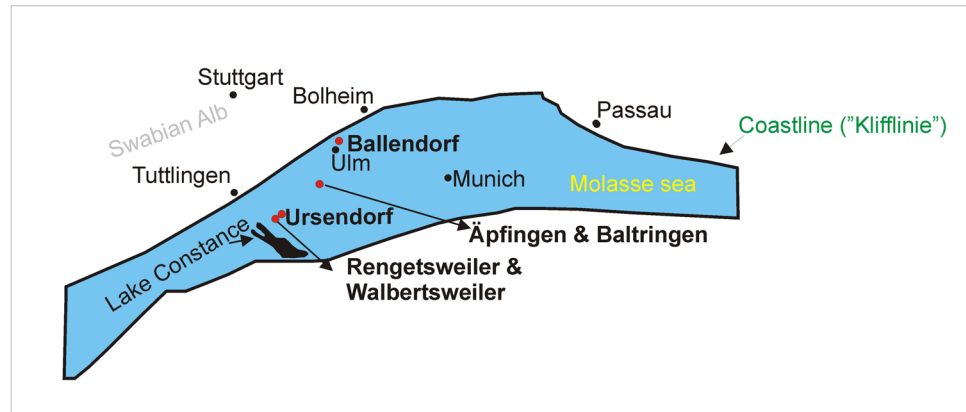


Fig. 4 Details of the lacquer-profile of the OMM at the Obere Häu sandpit, Ballendorf. For an explanation of the numeration of parts, please see Fig. 3. Scale: 10 cm



Fig. 5 Base of the profile consisting of Upper Jurassic limestone with traces of pholadid borings

Fig. 6. Geographic positions of the deposits mentioned in the text in relation to the Northern palaeo-coastline of the Molasse Sea (“Klifflinie”)



fauna of Ballendorf, all the verified shark and ray taxa are summarised in a table, including habitat and diet (see Tab. 1).

Systematics

Class Chondrichthyes Huxley, 1880

Subclass Elasmobranchii Bonaparte, 1838

Superorder Squalomorphii Compagno, 1973

Order Squaliformes Goodrich, 1909.

Family Squalidae Bonaparte, 1834

Squalus sp.

(Figs. 7.1, 7.2)

Material: 27 teeth.

Description: The teeth are all incompletely preserved. Due to changes in the tooth material during the fossilisation process (recrystallization), the crown and the root of the anterolateral tooth SMNS 97056/1 (Fig. 7.1) appear to consist of the same material. The crown of this tooth is distally inclined. In labio-lingual view, the mesial cutting edge is straight; in profile view, the most basal part of the edge is lingually bent. The obliquely oriented distal cutting edge passes with an acute angle into a distal heel, which is separated by a notch. The apical margin of this heel is broken. The lingual crown face is convex. An uvula is visible, but has been ‘melted’ together with the lingual protuberance of the root during fossilisation. On both sides of the uvula, there is a deep depression. At the base of the lingual protuberance, there is a foramen, located slightly distal to the midline of the tooth. The labial crown face is flat. From its base, an apron runs downwards. Both sides of the apron run in an arch-shape towards the base of the tooth; the apron also overhangs the root. If this last detail reflects original morphology or is caused by postmortem erosion of the root is uncertain. On both sides of the apron there are depressions. On the labial root face, there is a foramen next to the apron on the mesial part.

Fig. 7.2 shows another anterolateral tooth (SMNS 97056/2) that has an intact distal heel. The aforementioned foramen near the lingual protuberance is also present. The foramen on the labial root face cannot be seen but this may be due to postmortem erosion. The apron is broader than in SMNS 97056/1.

Discussion: SMNS 97056/1 and 97056/2 show similarities with *Squalus almeidae* Antunes and Jonet, 1970, illustrated in Antunes and Jonet (1970, Pl. 20, Figs. 142, 143, Text Fig. 7). However, in *S. almeidae* the foramen on the lingual root face is on the midline of the tooth (based on Antunes and Jonet 1970, Text Fig. 7), whereas in the teeth described here, this foramen is slightly distal to the midline. *S. almeidae* has three foramina on the mesial part of the labial root face (Antunes and Jonet 1970: text-fig. 7). These foramina are near the apron. As mentioned in the description, only one such foramen can be seen in SMNS 97056/1. This single foramen could be equivalent to the middle one of the three in Antunes and Jonet (1970: text-fig. 7). *S. almeidae* has also six foramina on the distal part of the labial root face. This cannot be observed on the teeth described above. The Oligocene *Squalus alsaticus* (Andreae, 1890) has a narrower apron, a more distally bent crown and only three foramina on the distal part of the labial root face (see Andreae 1890, fig. 2). However, due to incomplete preservation, a species determination of the teeth described above is not possible.

Autecology: Members of *Squalus* can be found in all oceans possibly down to a depth of 1978 m or deeper. Depending on species, their diet consists of bony fishes, invertebrates and occasionally other chondrichthyans. For some species the detailed biology is unknown (Ebert et al. 2021).

Family Centrophoridae Bleeker, 1859

Centrophorus cf. *granulosus* (Bloch and Schneider, 1801) (Figs. 7.3-7.5)

Material: Three teeth.

Tab. 1 Sharks and rays identified from Ballendorf, including autecology and occurrences in other deposits of the OMM in Baden-Württemberg

Taxon	Ballendorf (Number of teeth in brackets)	Äpfingen (Num- ber of teeth in brackets)	Rengetsweiler (Number of teeth in brackets)	Walbertsweiler (according to Pfeil in Barthelt et al. 1991)	Ursendorf (Number of teeth in brack- ets)	Habitat	Diet
Hexanchiformes							
Hexanchidae							
	<i>Notorynchus primigenius</i> Agassiz, 1835.	x (>10)	x (1)	x (>10)	x (>10)	Down to 50 m depth.	Omni vorous.
Squaliformes							
Centrophoridae							
	<i>Centrophorus</i> cf <i>granulosus</i> .	x (>10)		x	? (1, as <i>Centro- phorus</i> sp.)	From 50 to 1500 m depth.	Bony fishes, squid and crustaceans
	<i>Centrophorus</i> sp. 1					From 0 to 3366 m depth	Bony fishes and inver- tebrates.
	<i>Centrophorus</i> sp. 2					From 0 to 3366 m depth	Bony fishes and inver- tebrates.
Dalatiidae							
	<i>Isistius trian- gulus</i> (Probst, 1879)	x (8)	X (2, as cf. <i>Isis- tius triangulus</i>)	X (3, as cf. <i>Isistius</i> <i>triangulus</i>)	x	From epipelagic to bathypelagic regions.	Ectoparasitic on large fishes and cetaceans but feeds also on squids and crusta- ceans.
Squalidae							
	<i>Squalus</i> sp.	x (>10)	x (2)		x	Down to a depth of 1978 m.	Bony fishes, inverte- brates and occasion- ally other chondrich- thyes.
Pristiophoriformes							
Pristiophoridae							
	<i>Pristiophorus</i> <i>suevicus</i> Jaekel, 1890	x (8)	x (2)			Down to a depth of 1240 m.	Bony fishes and crusta- ceans.
Squatiniiformes							
Squatinaidae							
	<i>Squatina</i> sp.	x (>10)	x (1)	x (5)	x (2)	From 1 m to 1300 m depth.	Mollusks, crustaceans and bony fishes.
Lamniformes							
Carchariidae							

Tab. 1 (continued)

Taxon	Ballendorf (Number of teeth in brackets)	Äpfingen (Num- ber of teeth in brackets)	Rengetsweiler (Number of teeth in brackets)	Walbertsweiler (according to Pfeil in Barthelt et al. 1991)	Ursendorf (Number of teeth in brack- ets)	Habitat	Diet
<i>Carcharias contortidens</i> (Agassiz, 1843)	x (2)	x (>10)	x (>10)	x	x (>10)	Shallow waters.	Bony fishes and inver- tebrates.
<i>Carcharias crassidens</i> (Agassiz, 1843)	x (1)		x (as „cf. <i>crassidens</i> “ in Sach 2016)			Shallow waters.	Bony fishes and inver- tebrates.
Odontaspidae							
<i>Araloselachus cf. cuspidatus</i> (Agassiz, 1843)	x (>10)	x (5)	x (>10)	x	x (3)	Shelf region.	Probably bony fishes and invertebrates.
Alopiidae							
<i>Alopias exigua</i> (Probst, 1879)	x	x (2)	x (>10)	x	x (1)	From close inshore to offshore in the open ocean.	Bony fishes and squid.
Lamnidae							
<i>Carcharodon hastalis</i> (Agas- siz, 1838)	? (2 tooth frag- ments)	x (1)	x (>20)	x	x (>10)	Shelf region.	Bony fishes and prob- ably marine mam- mals.
Cetorhinidae							
<i>Keasius</i> sp.	x (2)						
Carcharhiniformes							
Scyliorhinidae							
<i>Pachyscyllium distanis</i> (Probst, 1879)	x (>50)	x (3)	x (1)	x	x (1)	Members of the family Scylio- rhinidae can be found down to a depth of 825 m.	Probably Bony fishes and benthic inver- tebrates.
<i>Scyliorhinus joleaudi</i> Cap- petta, 1970	x (5)	x (2)		x		Near the bottom from 1 to 800 m depth.	Invertebrates and bony fishes.
Triakidae							
<i>Triakis</i> sp.	x (1)		x (1, as ? <i>Triakis</i> sp.)			Neritic realm	Fishes and inverte- brates, depending on species

Tab. 1 (continued)

Taxon	Ballendorf (Number of teeth in brackets)	Äpfingen (Num- ber of teeth in brackets)	Rengetsweiler (Number of teeth in brackets)	Walbertsweiler (according to Pfeil in Barthelt et al. 1991)	Ursendorf (Number of teeth in brack- ets)	Habitat	Diet
	<i>Iago angustidens</i> (Cappetta, 1973)	x (1)		x		From 90 to 2195 m depth.	Cephalopods
Hemigaleidae							
	<i>Chaenogaleus affinis</i> (Probst, 1878)	x (>30)	x (1, as „cf. <i>Chaenogaleus affinis</i> “)	x		Down to 59 m depth	Probably small fishes, cephalopods and crus- taceans.
	<i>Hemipristis serra</i> (Agassiz, 1843)	x (10)	x (1)	x (>10)	x (>10)	Between 1 to 132 m depth.	Cephalopods and fishes.
	<i>Paragaleus tenuis</i> (Probst, 1878)	x (>10)		x		Neritic realm	Cephalopods and fishes.
	<i>Paragaleus sp.</i>	x (1)				Neritic realm	Cephalopods and fishes.
Carcharhinidae							
	<i>Rhizoprionon- don fischeuri</i> (Joleaud, 1912)	x (>10)	? (1, as „ <i>Rhizop- rionodon sp.</i> “)	x (1)	x	Shelf region.	Bony fishes and inver- tebrates.
	<i>Carcharhi- nus acuaris</i> (Probst, 1879)	x (>30)			x	Shallow waters	Small schooling fishes
	<i>Carcharhinus priscus</i> (Agas- siz, 1843)	x (>150)	x (3)	x (10)	x	Shelf region.	Probably bony fishes, elasmobranchia and molluscs.
	<i>Carcharhinus similis</i> (Probst, 1878)	x (5)			x	Shelf region.	Probably bony fishes, elasmobranchia and molluscs.
	<i>Physogaleus sin- gularis</i> (Probst, 1878)	x (6)		x (7)	x		
Galeocerdonidae							
	<i>Galeocerdo aduncus</i> (Agas- siz, 1835)	x (>10)	x (3)	x (>10)	x	From the intertidal to at least 1112 m depth.	Omnivorous.
Sphyrnidae							
	<i>Sphyrna integra</i> Probst, 1878	x (3)	x (1)		x	Shelf region.	Fishes and inverte- brates.

Rajiformes

Tab. 1 (continued)

Taxon	Ballendorf (Number of teeth in brackets)	Äpfingen (Num- ber of teeth in brackets)	Rengetsweiler (Number of teeth in brackets)	Walbertsweiler (according to Pfeil in Barthelt et al. 1991)	Ursendorf (Number of teeth in brack- ets)	Habitat	Diet
Rhynchobatidae							
<i>Rhynchobatus pristinus</i> (Probst, 1877)	x	x (1)		x		Shallow waters.	Invertebrates and/or bony fishes.
Rhinobatidae							
<i>Rhinobatos</i> sp.	x			x		Continental shelves and uppermost continental slopes	Molluscs, crustacean and bony fishes
Rajidae							
<i>Raja</i> sp.	x	X (6)		x	x (1, as „cf.“)	Shallow waters to depths of a few hundred meters.	Invertebrates and bony fishes.
Dasyatidae							
<i>Taeniurops cavernosus</i> (Probst, 1877)		x (1)	x (4, as cf. Dasyatidae)				
<i>Dasyatis minuta</i> Cappetta, 1970	x						
<i>Dasyatis probsti</i>	x						
<i>Dasyatis rugosa</i> (Probst, 1877)	x	x (1)		x	x (1, as „?Dasyatis probsti)	Between 1 and 500 m depth.	Bottom fishes, bivalves, crabs and shrimp.
<i>Dasyatis</i> sp.	x						Bony fishes and/or invertebrates.
Myliobatidae							
<i>Aetobatus arcuatus</i> (Agassiz, 1843)	X (2)		x (11)			Mostly in coastal environment.	Bony fishes and/or invertebrates.
Rhinopteridae							
<i>Rhinoptera</i> cf. <i>studeri</i> (Agassiz, 1843)	x	X (> 10, as <i>R. studeri</i>)		x (as <i>R. studeri</i>)	x (> 5)	Shelf region.	Molluscs.

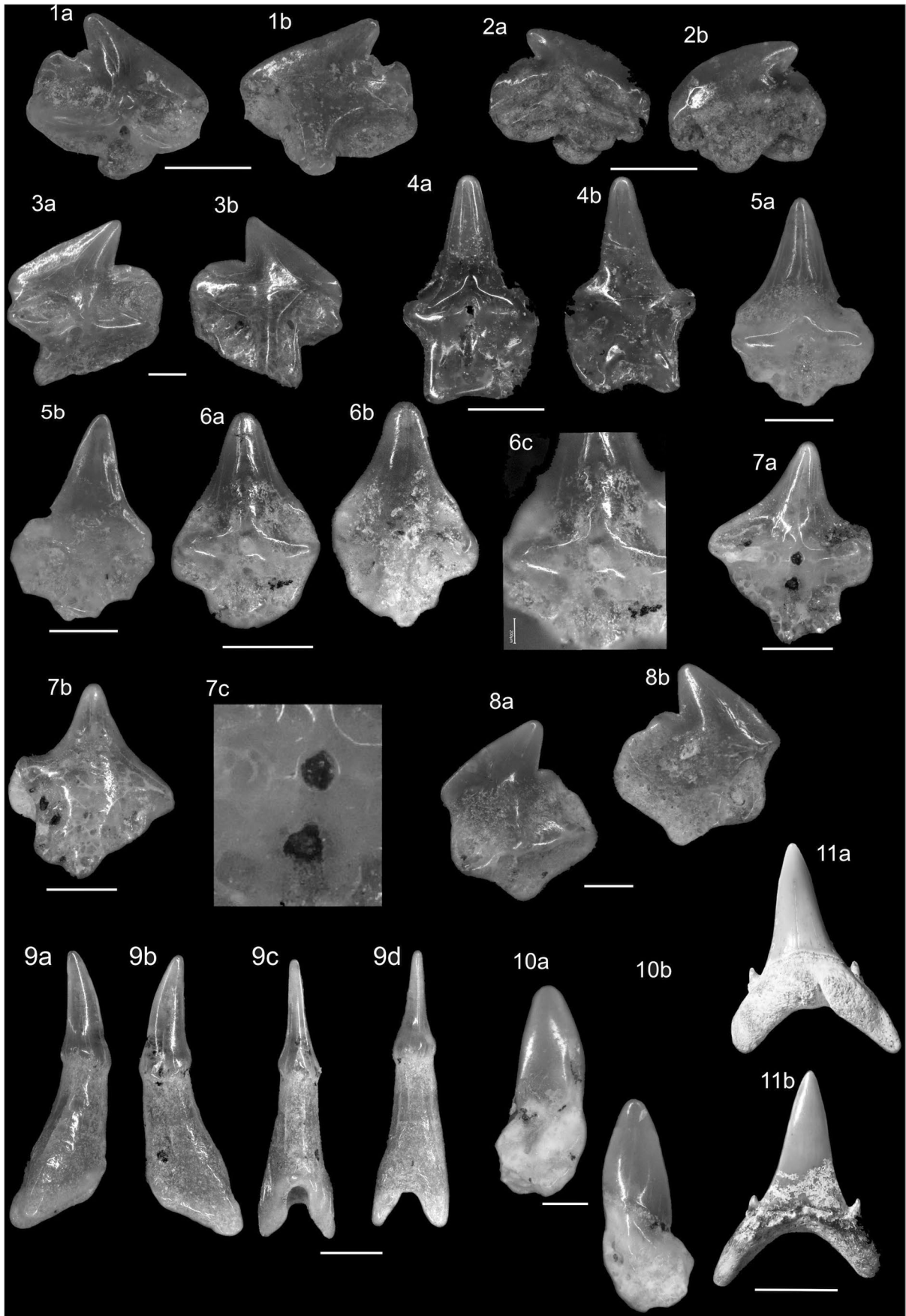


Fig. 7 1 SMNS 97056/1, *Squalus* sp. Antero-lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 2 SMNS 97056/2, *Squalus* sp. Antero-lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 3 SMNS 97056/3, *Centrophorus* cf. *granulosus* (Bloch and Schneider, 1801). Antero-lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 4 SMNS 97056/4, *Centrophorus* cf. *granulosus* (Bloch and Schneider, 1801). Upper parasymphysial tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 5 SMNS 97056/5, *Centrophorus* cf. *granulosus* (Bloch and Schneider, 1801). Parasymphysial tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 6 SMNS 97056/6, *Centrophorus* sp. 1 ?parasymphysial tooth. **a** lingual view; **b** labial view; **c** Detailed view of the second foramen. Scale a, b: 200 μ m; Scale c: 200 μ m. 7 SMNS 97056/7, *Centrophorus* sp. 1 ?parasymphysial tooth. **a** lingual view; **b** labial view. **c** Detailed view of the second foramen. Scale: 1 mm. 8 SMNS 97056/8, *Centrophorus* sp. 2. Antero-lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 9 SMNS 97056/9, *Pristiophorus suevicus* Jaekel, 1890. Rostral denticle. **a** dorsal/ventral view; **b** dorsal/ventral view; **c** mesial view; **d** distal view. Scale: 1 mm. 10 SMNS 97056/10, *Pristiophorus suevicus*? Jaekel, 1890. Rostral denticle. **a** dorsal/ventral view; **b** dorsal/ventral view. Scale: 1 mm. 11 SMNS 97056/11, *Carcharias crassidens* (Agassiz, 1843). Lower lateral tooth. **a** lingual view; **b** labial view. Scale: 10 mm

Description: SMNS 97056/3 (Fig. 7.3) is a lower antero-lateral tooth. It is labio-lingually compressed. Due to changes in the tooth material during fossilisation process (recrystallization), the crown and the root of this tooth appear to consist of the same material. The main cusp is distally bent. Both crown faces are convex. No serration is visible. The distal crown margin continues in a nearly flat distal heel separated by a notch. In profile view, the distal heel is arch-shaped, bent in a lingual direction. The cutting edges are thin and sharp. The uppermost part of the mesial cutting edge is concave, the other parts are nearly straight to very weakly convex. The distal cutting edge is straight. On the lingual crown face, an uvula is visible. On the labial crown face, an apron is present. On the lingual root face, there is a remarkable bulge. The lower end of the uvula lies on this bulge and divides it into two parts. Above the bulge, a pronounced indentation in the root is present on each side of the uvula. Directly below the uvula, marginally offset mesially, there is an infundibulum with traces of a nutrient channel. On the upper margin of the mesial part of the lingual root bulge, there is also a foramen. Distal to the uvula, there are traces of diverse foramina. On the labial root face, foramina and traces of them are present on both sides of the apron. Apart from the lingual bulge, the root is flat and plate-like. The basal parts of the root are not preserved.

Fig. 7.4 shows an upper parasymphysial tooth. Like in the tooth SMNS 97056/3 (Fig. 7.3), here also the crown and the root appear to consist of the same material. The triangular crown is nearly straight, being only weakly bent in a distal direction. No serration is visible. Both cutting edges continue without interruption into a heel. The lingual crown face is bulbous and convex. The labial crown face is flat. On the lingual crown face, a short and convex uvula is present. On the labial crown face, a broad and flat apron is

present. The lingual root face bears a pronounced bulge on which the uvula is resting. To both sides of the uvula there are large and deep indentations. In the middle of the bulge, a deep infundibulum with a nutrient channel can be seen. Also on both sides of the apron, a remarkable indentation is present. Due to the lingual root bulge, the root is slightly wedge-shaped in profile view. Fig. 7.5 shows another upper parasymphysial tooth

Discussion: SMNS 97056/3 (Fig. 7.3) fits to a lower antero-lateral tooth of *C. granulosus* based on the illustrations given by Herman et al. (1989, pl. 11) as well as Pollerspöck and Straube (2022). Based on the shape of the apron and the distribution of the foramina on the lingual root face, this tooth is different from the lower antero-lateral teeth of *Centrophorus squamosus* (Bonnaterre, 1788) and *Centrophorus uyato* (Rafinesque, 1810) (see the illustrations in Pollerspöck and Straube 2022). SMNS 97056/4 (Fig. 7.4) fits to an upper parasymphysial tooth illustrated by Herman et al. (1989, pl. 11). However, based on Ebert et al. (2021), there are nine other Recent species of *Centrophorus* for which no detailed tooth studies have been published. Therefore, the teeth examined here were only determined as “cf. *granulosus*”.

Autecology: The Recent *C. granulosus* lives in the Atlantic, Indian and southwest Pacific Oceans and possibly also in the central and southeast Pacific. It inhabits the continental shelf and slopes, on or near the bottom from 50 to 1500 m depth. This shark feeds on bony fishes, squids and crustaceans (Ebert et al. 2021)

Centrophorus sp. 1
(Figs. 7.6, 7.7)

Material: Two teeth.

Remarks: Figs. 7.6, 7.7 (SMNS 97056/6 and SMNS 97056/7) show teeth of similar shape to the parasymphysial tooth in Fig. 7.4, but differing in having less pronounced indentations on the sides of the uvula. However, this could be the result of postmortem erosion. The important difference is the present of a second foramen above the infundibulum (see Fig. 7.6c). Both foramina lie on top of each other with a space between them (see Fig. 7.7c). Based on the illustrations given by Herman et al. (1989, pl. 11) as well as Pollerspöck and Straube (2022), *C. granulosus* also has upper teeth with two foramina on the lingual bulge, but these teeth are lateral ones and have more distally bent crowns. SMNS 97056/6 and SMNS 97056/7 also do not fit to the two other *Centrophorus* species discussed above. Therefore, a species determination is not possible at the moment.

Autecology: Recent representatives of *Centrophorus* are deep water, bottom-dwelling sharks with an almost worldwide distribution (Ebert et al. 2021). They are known from depths down to 3366 m (Ebert et al. 2021). Recent species

with known diet feed on fishes, cephalopods and crustaceans (Megalofonou and Chatzisyrou 2007; Ebert et al. 2021)

Centrophorus sp. 2
(Fig. 7.8)

Material: One tooth.

Remarks: The incomplete tooth in Fig. 7.8 is similar in shape to SMNS 97056/3 (Fig. 7.3) and is also a lower antero-lateral tooth. It differs in having a convex distal heel as well as a single large foramen directly mesial to the apron. Above this foramen, there is a trace of another small foramen. Because this is the only tooth with these features and because of its incompleteness, open nomenclature was chosen.

Autecology: See *Centrophorus* sp. 1.

Order Pristiophoriformes Berg, 1958

Family Pristiophoridae Bleeker, 1859

Pristiophorus suevicus Jaekel, 1890

(Figs. 7.9, ?7.10)

?1877 *Pristis* sp. - Probst, p. 81, 103, pl. 1, figs. 21-22 (rostral denticles)

*1890 *Pristiophorus suevicus* n. sp. – Jaekel, pp. 116-117, pl. 3, figs. 1-2, pl. 4, fig. 1, pl. 5 (rostral denticles)

?1930 *Pristiophorus suevicus* Jaekel, 1890 – Fischli, p. 148, pl. 2, fig. 7 (rostral denticles)

1991 *Pristiophorus suevicus* Jaekel, 1890 – Pfeil, p. 199, pl. 1, figs. 12 (rostral denticle), 13 (oral tooth)

2013 *Pristiophorus suevicus* Jaekel, 1890 – Schultz, p. 32, pl. 4, figs. 12-13 (rostral denticles)

2014 *Pristiophorus suevicus* Jaekel, 1890 – Pollerspöck and Beaury, pp. 27-28, pl. 1, fig. 6 (rostral denticle)

?2016 *Pristiophorus* sp. – Jost et al, p. 15, fig. 8k (rostral denticle)

?2022b *Pristiophorus* sp. – Höltke et al. p. 328, figs. 3.5 (oral tooth), 3.6 (rostral denticle)

Material: Eight rostral denticles.

Description: The denticle in Fig. 7.9 consists of a crown and a root. The crown is bent in a posterior direction and is also slightly inclined in a ventral direction. It has a compressed, blade-like shape but with a thickened basis. The posterior cutting edge reaches the base of the crown. The anterior one is only present in the apical ¼ of the crown. On the posterior side, the crown base shows an apically oriented indentation. The crown overhangs the root. The root is somewhat higher than the crown and has an oval cross section, diverging in its lower part into two dorsoventrally compressed root lobes. The denticle in Fig. 7.10 could also be from *P. suevicus*, but due to incomplete preservation a reliable determination of the species is not possible.

Remarks: Details on this species can be found in Reinecke et al. (2020).

Other occurrences in the OMM: Germany, Baden-Württemberg: ?Äpfingen (Höltke et al. 2022b, as “*Pristiophorus* sp.”), ?Baltringen (Probst, 1877, as “*Pristis* sp.”), Walbertsweiler (Pfeil, 1991). Bavaria: Heigelsberger Graben near Teisendorf (Pollerspöck and Beaury 2014). Austria, Upper Austria: Höbmansbach (Schultz 2013). Switzerland, Kanton Zürich: ?Benken (Fischli, 1930). Kanton Luzern: ? Roggliswil-Hornwald (Jost et al. 2016 as “*Pristiophorus* sp.”).

Autecology: Members of this genus can be found in the warm waters of the Pacific, the Indian Ocean as well as the Northwest Atlantic. They are known from a depth down to 1240 m (Ebert et al. 2021). The latter authors mentioned seven extant species of this genus. Some feed on bony fishes and crustaceans, the biology of others is unknown.

Superorder Galeomorphii Compagno, 1973

Order Lamniformes Berg, 1837

Family Carchariidae Müller and Henle, 1838

Carcharias crassidens (Agassiz, 1843)

(Fig. 7.11)

* 1843 *Lamna crassidens* – Agassiz, Vol. 3, pl. 35, figs. 8-21
1879 *Lamna crassidens* Ag. – Probst, pp. 153-154, pl. 2, figs. 64-68

1910 *Lamna crassidens* (Ag.) – Fraas, p. 224, pl. 68, fig. 7
1927 *Odontaspis crassidens*, L. Agassiz – Leriche, pp. 63-65, pl. 9, figs. 1-14

1930 *Lamna (Odontaspis) crassidens* Ag. – Fischli, p. 150, pl. 3, fig. 3

2016 *Carcharias crassidens* - Sach, fig. 61

Material: One nearly complete tooth.

Description: SMNS 97056/11 (Fig. 7.11) is a lower lateral tooth. It is massive with a triangular crown. The crown tapers regularly in an apical direction; the upper third is weakly bent in a distal direction. In profile view, the crown is distally bent. The lingual crown face is remarkable convex. The labial crown face is flat. Both crown faces and the cutting edges are smooth. At the base of the labial crown face, there is a slight indentation. Both cutting edges reach the base of the crown. On each side of the crown, there is one lateral cusplet. The cusplets are connected to the main cusp. The enamel of the crown continues on the apical margin and labial face of the root lobes. The cusplets have a rounded base and taper in an apical direction. Both faces of the cusplets are convex. The apices are hook-like, bent toward the main cusp. Both cusplets are also bent in a lingual direction. On the distal side of the mesial cusplet is a small and low hump that could be the remnant of a secondary cusplet. The labial crown face overhangs the root. The root lobes are well separated. On the lingual root face, there is a

lingual protuberance. The labial root face is flat. The distal root lobe is longer than the mesial one. On the lingual root face, there is a groove distal to the midline. Based on its position, it is not a nutrient channel and may result from postmortem erosion. The end of the mesial root lobe is flattened and rounded. The end of the distal root lobe is also flattened, but is much narrower in a mesio-distal direction and is slightly tapered.

Discussion: SMNS 97056/11 fits to the illustrations of *Lamna crassidens* (Agassiz, 1843; pl. 35, figs. 8–21). In its basic morphology, the tooth is similar to a lower lateral tooth of the Recent *Carcharias taurus* Rafinesque, 1810 illustrated by Pollerspöck and Straube (2022). SMNS 97056/11 differs from *C. taurus* teeth in having a more massive crown, especially in the lower half of the main cusp. The same feature distinguishes it from *C. contortidens* (Agassiz, 1843). SMNS 97056/11 differs from *Araloselachus cuspidatus* (Agassiz, 1843) in having a more lingually bent crown. Following Probst (1879), the material on which the description of Agassiz (1843) was based came from the “bean ore” (“Bohnerze”); in the original description of Agassiz: “couche de fer pisolitique”) of Messkirch-Heudorf in Baden-Württemberg. According to Probst (1879), the cited material is stored in the “Stuttgarter Sammlung” (= the SMNS); however, this material could not be located in the collection of the SMNS. Based on the private collections in which Agassiz studied the material (collections: Herr Klausung (Karlsruhe), Prof. Walchner (Freiburg, later Karlsruhe), Herr Hermann von Meyer, Frankfurt), these teeth are unlikely to ever have been housed at the SMNS; Probst may have confused *L. crassidens* teeth from the Alberti collection (SMNS) with the Agassiz specimens. The teeth from this historical collection came from the same locality (Messkirch-Heudorf) as the ones examined by Agassiz.

Other occurrences in the OMM: Germany: Baden-Württemberg: Baltringen, Rengetsweiler (Sach 2016, as “cf. *crassidens*”), Riedern am Sand (Leriche 1927). Switzerland: Kanton Aargau: ? Kilchberg near Brittnau (Leriche 1927). Kanton Freiburg: Châbles, Le Mont-Vully near Môtiers (Leriche 1927). Kanton Waadt: La Chau-de-Sainte-Croix (Leriche 1927). Kanton Zürich: Wildensbuch near Trüllikon (Leriche 1927), Kohlfürst near Benken (Leriche 1927; Fischli 1930).

Occurrences in the Brackish water Molasse: Germany: Baden-Württemberg: Messkirch-Heudorf (Probst 1879), Altheim-Breitenlauh near Ehingen/Donau (Sach 2016); Eggingen-Mittelhart near Ulm (Sach 2016). Bavaria: Lake at the Iller River near Senden-Freudenegg (Sach 2016).

Autecology: This species probably occupied a similar niche as the Recent *Carcharias taurus* Rafinesque, 1810, which inhabits coastal waters in warm-temperate and tropical seas and feeds on wide range of fishes as well as invertebrates (Ebert et al. 2021).

Family Cetorhinidae Gill, 1861

Keasius sp.

(Fig. 8.1)

Material: Two broken gill rakers.

Remarks: Due to incomplete preservation, a species determination is not possible. For details on the species of *Keasius* see Reinecke et al. (2015).

Autecology: The closest Recent relative is *Cetorhinus maximus* (Gunnerus, 1765). This species has a worldwide distribution in cold- to warm temperate waters as well as in deep water below the thermocline in tropical and equatorial regions. It lives from the coastal region to the continental edge and slope down to a depth of 1264 m. *C. maximus* is a plankton-feeder (Ebert et al. 2021).

Order Carcharhiniformes Compagno, 1973

Family Triakidae Gray, 1851

Triakis sp.

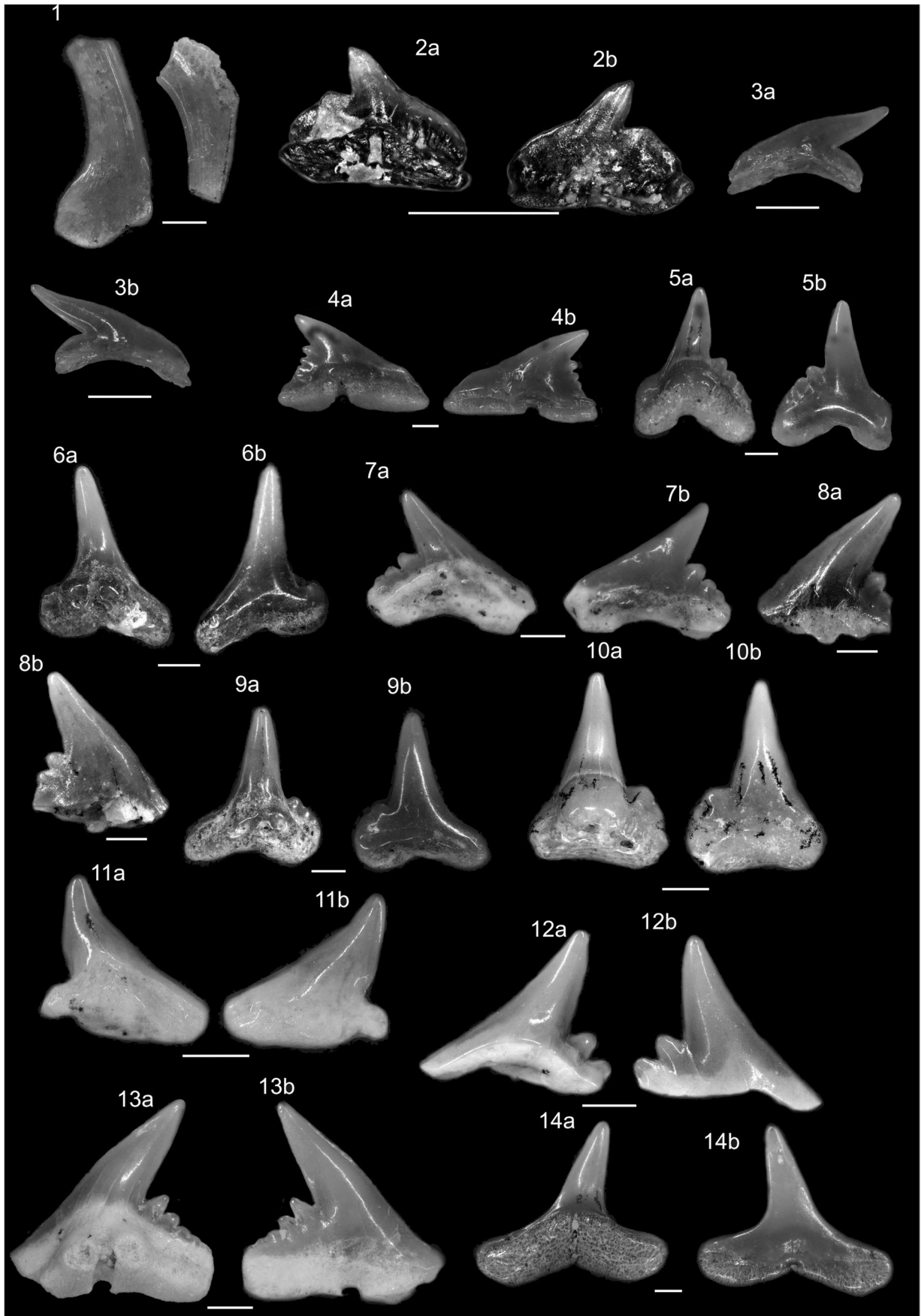
(Fig. 8.2)

Material: One tooth.

Description: The small, lateral tooth has a broad crown base and a narrow main cusp. The main cusp is distally bent. The lingual face of the main cusp is convex. On the labial crown face, the main cusp is weakly convex. The mesial cutting edge of the main cusp is weakly arched into a mesial heel. This results in a long concave mesial cutting edge; the distal cutting edge also continues into a heel separated by a notch, forming an acute angle with the main cusp. The mesial part of the distal heel is straight, extending upwards with a weakly oblique orientation, then downwards in an arch-shaped manner. The cutting edges are sharp and thin. At the base of the mesial lingual crown face, there are seven pronounced short vertical ridges. On the labial crown face, similar ridges are present across the whole base. The ridges are only partially regularly arranged. The root is flat with widely separated root lobes. The basal part of the root lobes widen remarkably. The underside of the flat root lobes both have an irregular ovate shape. The lingual root face is convex, with a nutrient channel that separates the root into two halves. The lingual root face remarkably overhangs the crown. On the labial side, the labial crown face slightly overhangs the root. The nutrient channel forms a recess in the middle of the labial root face.

Remarks: Following López et al. (2006), the genus *Triakis* is polyphyletic.

Autecology: Recent species of *Triakis* live in cool to warm-temperate and tropical waters of the Atlantic and Pacific (Ebert et al. 2021). They inhabit the neritic realm (Ebert et al. 2021). According to the latter authors, these sharks feed on fishes and invertebrates, depending on species. For some species, however, the diet is unknown.



◀**Fig. 8** 1 SMNS 97056/12, *Keasius* sp. Two broken gill rakers. Scale: 1 mm. 2 SMNS 97056/13, *Triakis* sp. Lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 3 SMNS 97056/14, *Iago angustidens* (Cappetta, 1973). Lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 4 SMNS 97056/15, *Chaenogaleus affinis* (Probst, 1878). Upper lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 5 SMNS 97056/16, *Chaenogaleus affinis* (Probst, 1878). Upper anterior tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 6 SMNS 97056/17, *Chaenogaleus affinis* (Probst, 1878). Lower antero-lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 7 SMNS 97056/18, *Paragaleus tenuis* (Probst, 1878). Upper antero-lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 8 SMNS 97056/19, *Paragaleus tenuis* (Probst, 1878). Upper antero-lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 9 SMNS 97056/20, *Paragaleus tenuis* (Probst, 1878). ?Upper anterior tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 10 SMNS 97056/21, *Paragaleus tenuis* (Probst, 1878). ?Upper anterior tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 11 SMNS 97056/22, *Paragaleus tenuis* (Probst, 1878). Lower lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 12 SMNS 97056/23, *Paragaleus tenuis* (Probst, 1878). Lower lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 13 SMNS 97056/24, *Paragaleus* sp. Upper lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. 14 SMNS 97056/25, *Carcharhinus acuarius* (Probst, 1879). Lateral tooth. **a** lingual view; **b**:labial view. Scale: 1 mm

Iago angustidens (Cappetta, 1973)
(Fig. 8.3)

*1973 *Triakis angustidens* – Cappetta, pp. 216–218, pl. 12, figs. 23–32
1991 *Triakis angustidens* Cappetta, 1973 – Pfeil, p. 202, pl. 3, fig. 5
2021 *Iago angustidens* (Cappetta, 1973) – Feichtinger and Pollerspöck, pp. 204–205

Material: One tooth.

Description: The small, lateral tooth has a wide crown base but a slender crown, such that the crown tapers strongly shortly about the base. The main cusp is strongly distally bent. Both crown faces as well as the cutting edges are smooth. Both crown faces are convex, but the lingual one is slightly more convex than the labial face. The mesial cutting edge continues into a mesial heel, forming a long cutting edge. The lowest third of the mesial cutting edge is nearly straight, the middle third is very weakly convex and the upper third is remarkably concave. In profile view, the lower half of the mesial cutting edge is concave. The distal cutting edge is very weakly convex. The distal cutting edge continues in an acute angle into a distal heel. The most mesial part of this heel runs straight, then downwards in a weak arch. In profile view, this downward-directed part is also arched, bent in a lingual direction. The root seems to be only rudimentarily preserved. The parts that might belong to the root appear to consist of the same enamel-like material as the crown. The root lobes are well separated, and the lingual root face seems to be convex. The labial root face is remarkably concave.

Remarks: The tooth fits to the illustrations of *Triakis angustidens* Cappetta, 1973 given by Cappetta (1973, pl. 12, figs. 23–32).

Autecology: Recent members of *Iago* can be found between 0 and 2195 m depth in the Western Indian Ocean (Red Sea, Gulf of Aqaba, Gulf of Aden and Gulf of Oman to Pakistan and southwestern India) and in the Western Central Pacific (Australia, including Western Australia, Vanuatu and the Philippines) (Froese and Pauly 2022). They feed on cephalopods and bony fishes (Ebert et al. 2021).

Family Hemigaleidae Hasse, 1878
Chaenogaleus affinis (Probst, 1878)
(Figs. 8.4–8.6)

*1878 *Galeus affinis* n. sp. – Probst, pp. 139–140, pl. 1, figs. 64–70

For other synonyms see Höltke et al. (2022b).

Material: 60 teeth.

Remarks: This species has been often described in the literature; see Reinecke et al. (2011); Bor et al. (2012); Höltke et al. (2022b). Fig. 8.4 shows an upper antero-lateral tooth, Fig. 8.5 probably an upper anterior one and Fig. 8.6 shows a lower antero-lateral tooth.

Discussion: As can be seen in the upper teeth of the Recent relative *Chaenogaleus macrostoma* (Bleeker, 1852) illustrated in Herman et al. (1991, pl. 14, 15), the number of lateral denticles differs according to position. The teeth in Figs. 8.4–8.6 fit to the illustrations given by Probst (1878), illustrated in Reinecke et al. (2011 text-figs. 18, 19) as well as to the teeth determined as *G. affinis* pictured in Reinecke et al. (2011, pl. 57–60). The jaw positions of the aforementioned teeth were determined based on the teeth of the Recent *C. macrostoma* illustrated in Compagno, (1988, pl. 19, figs. 15–18, pl. 20, figs. M, N).

Autecology: The Recent *Chaenogaleus macrostoma* can be found on the shelves in the Indo-West Pacific down to a depth of 59 m. It probably feeds on small fishes, cephalopods, and crustaceans (Froese and Pauly 2022).

Paragaleus tenuis (Probst, 1878)
(Figs. 8.7–8.12)

*1878 *Galeus tenuis* n. sp. – Probst, p. 140, pl. 11, figs. 68–70
1991 *Paragalues tenuis* (Probst, 1878) – Pfeil, p. 204, pl. 2, fig. 8
2021 *Paragaleus tenuis* (Probst, 1878) – Feichtinger and Pollerspöck, pp. 184–185

Material: 27 teeth, all incomplete.

Description: Upper antero-lateral teeth (Figs. 8.7, 8.8): In SMNS 97056/18 (Fig. 8.7), the main triangular cusp is strongly distally inclined. The lingual crown face is convex whereas the labial one is only weakly convex. In profile view, the crown is weakly sigmoidal. The cutting edges and both crown faces are smooth. The long mesial cutting edge is concave; the distal one is straight. There are no traces of lateral denticles on the mesial cutting edge. The distal cutting edge continues into a heel that contains three lateral denticles, which decrease in size distally. The denticles have blunt, arc-shaped apices, and in occlusal and lateral views have a slight duckbill shape. The last denticle remarkably ends before the distal end of the tooth. The root has been stabilised with glue and in labio-lingual view has an arch shape. The root is not completely preserved, but the labial crown face seems to overhang the root, at least at the main cusp. On the mesial part of the labial root face there is a significant bulge. However, it cannot be said if this is natural or if it is due to the stabilising glue. Fig. 8.8 shows another tooth but here the root is not preserved.

?Upper anterior teeth (Figs. 8.9, 8.10): SMNS 97056/20 (Fig. 8.9) has an upright triangular crown, which is weakly distally bent. The lingual crown face is convex and the labial one is only weakly convex. In profile view, the crown is lingually bent. The tooth and both cutting edges are smooth. The mesial cutting edge is weakly convex, and continues directly into a mesial heel; both together form a coherent concave mesial cutting edge. On the distal side, the cutting edge also continues into a heel that contains two blunt and bulbous lateral denticles. Both are eroded but they seemed to have the same duckbill shape as on SMNS 97056/18. The root has well separated root lobes and a salient lingual protuberance, which, however, seems to have been lowered by erosion. Traces of a nutrient channel and a foramen can be seen. The mesial root lobe has a rounded end. The distal one is not preserved. Because of the incomplete root, it is not clear if the labial crown base overhangs the root. Fig. 8.10 shows another probable upper anterior tooth.

Figs. 8.11 and 8.12 show two incomplete lower lateral teeth from a more distal position with the salient concave mesial cutting edge.

Discussion: The teeth in Figs. 8.7–8.9 fit to two teeth named and described as *Galeus tenuis* by Probst (1878, pl. 1, figs. 69, 70). According to Reinecke et al. (2011), the type material of *G. tenuis* could not be relocated. From the outline, SMNS 97056/20 and 97056/21 (Figs. 8.9, 8.10) are similar in shape to upper anterior teeth based on the illustration of the jaws of the Recent *Paragaleus pectoralis* (Garman, 1906) given by Bigelow and Schroeder (1948, fig. 45). The upper anterior teeth of *Paragaleus leucolomatus* Compagno and Smale, 1985 also have a similar shape to SMNS 97056/20 and 97056/21 (see Compagno and Smale, 1985, fig. 4). The teeth in Figs. 8.11, 8.12 have the same concave mesial cutting edge as some lower lateral teeth in the

illustration in Bigelow and Schroeder (1948, fig. 45). The upper teeth in Figs. 8.7, 8.8 have a weaker concave mesial cutting edge than the lower ones, which is also the case for the upper teeth in the illustration given by Bigelow and Schroeder (1948, fig. 45). The upper teeth of *Paragaleus tengi* (Chen, 1963) (see Compagno 1988, pl. 20, fig. A) also show some similarities to the outline of the upper teeth of *P. tenuis* (Figs. 8.7, 8.8).

There are two other *Paragaleus* species named in the literature for the Miocene, *Paragaleus pulchellus* Jonet, 1966 and *P. antunesi* Balbino and Cappetta 2000. The corresponding teeth of *Paragaleus tenuis* differ from *P. pulchellus* in having lateral denticles only on the distal side of the tooth (see Antunes and Jonet, 1970, pl. 12, figs. 68–74). *P. antunesi* has a greater number of lateral denticles on the distal heel, as well as a basal bulge on the labial crown face that is not present in *Paragaleus tenuis* (see Balbino and Cappetta 2000, pl. 1, 2).

Distribution in the OMM: Baden-Württemberg, South Germany: Baltringen (Probst 1878; Sach 2016), Walbertsweiler (Pfeil, 1991).

Autecology: *Paragaleus* contains four Recent species. Members of the genus are known from the Pacific, Indian and East Atlantic Oceans. All species live in warm to tropical waters from the surfline down to a depth of 100 m (Ebert et al. 2021). Only the diet of *P. pectoralis* is known; this shark feeds on cephalopods and small fishes.

Paragaleus sp.
(Fig. 8.13)

Material: One tooth.

Description: SMNS 97056/24 is a lateral tooth from the upper jaw. The triangular crown is distally bent. Both crown faces are convex. The cutting edges and the crown faces are smooth. In profile view, the crown is slightly bent in a lingual direction, and the apical region is weakly labially bent. The mesial side of the tooth is incomplete. The mesial cutting edge continues into a mesial heel without interruption and thus forms a long cutting edge. In profile view, the mesial cutting edge shows a concave course, and the distal cutting edge shows a convex course. In labio-lingual view, the mesial cutting edge shows a convex course, and the distal cutting edge is nearly straight. Only in its upper part does the distal cutting edge trend weakly in a mesial direction. The distal cutting edge also continues without interruption into a distal heel, which bears a serration. The five denticles decrease in size in a distal direction. The first has an upright, triangular shape with a blunt apex. The second, shorter one is also upright but with a blunt, arc-shaped apex. The following three are very low with a pectinate apex. All five denticles have convex labial and lingual faces. The root has widely separated root lobes. The lingual root face has a

salient lingual protuberance. A nutrient channel divides the lingual protuberance and the basal root face into two halves. The labial root face is concave. Whether the base of the labial crown face overhangs the root cannot be confirmed due to preservation. In the middle of the labial root face, the nutrient channel forms an arc-shaped notch. The distal root lobe has a squared end. The end of the mesial root lobe is not preserved.

Discussion: The tooth of *Paragaleus* sp. differs from *P. tenuis* in the following details: 1. Larger size; 2. Both crown faces are convex; 3. Five lateral denticles are present. Because only one specimen of this type of tooth could be verified, for now it is named only as *Paragaleus* sp.

Autecology: See *P. tenuis*.

Family Carcharhinidae Jordan and Evermann, 1896

Carcharhinus acuarius (Probst, 1879)

(Figs. 8.14; 9.1–9.3)

*1879 *Alopecias acuarius* n.sp. – Probst, p. 140, Pl. 2, figs. 76, 77

1991 *Isogomphodon acuarius* (Probst, 1879) – Pfeil, p. 204, Pl. 3, fig. 11

1995 *Isogomphodon acuarius* (Probst, 1879) – Bolliger et al., Pl. 2, fig. 5

2020 *Isogomphodon acuarius* (Probst, 1879) – Villafaña et al., pp. 738–739, fig. 60, p.

2021 *Isogomphodon acuarius* (Probst, 1879) – Feichtinger and and Pollerspöck, pp. 168–169

Material: 50 teeth.

Description: Lateral teeth (Figs. 8.14, 9.1). SMNS 97056/25 (Fig. 8.14) has a slender crown that is distally inclined. The lingual crown face is convex and the labial one is flat. Both crown faces are smooth. In profile view, the crown shows a slightly sigmoidal shape. On the lingual crown face, a neck zone is visible. Both cutting edges continue into a heel on each side of the crown. The mesial heels runs obliquely downwards to the tip of the root lobe. The distal heel runs in a flatter, less inclined manner downwards to the tip of the root lobe. Through this continuation on the heels, both cutting edges are remarkable long. In labio-lingual view, both cutting edges form a concavity where they pass into the heel. In profile view, both cutting edges show a convexity. The root has widely separated root lobes. On the lingual root face, there is a lingual protuberance with a nutrient channel dividing the root. The lingual root face is convex. Most of the labial root face is flat; only the middle part is concave. The nutrient channel forms a rounded recess on the base of the labial root face. The ends of the root lobes are flat. Fig. 9.1 shows another lateral tooth, in which it can be seen that on the labial tooth side, only the base of the main cusp overhangs the root. The base of the heels are at the same height as the root.

SMNS 97056/27 (Fig. 9.2) is possibly from an anterior position. The crown is upright apart from the upper third, which is slightly bent in a distal direction. The root lobes are closer together and the lingual root face bears a more pronounced lingual protuberance. Fig. 9.3 shows another probable anterior tooth; here the whole crown is upright. Both possible anterior teeth are more strongly lingually bent than the lateral teeth described above.

Remarks: The next Recent relative is *Carcharhinus oxyrhynchus* (Müller and Henle, 1839). Following Feichtinger and Pollerspöck (2021), this species shows no dignathic heterodonty but weak monognathic heterodonty. Unfortunately, no dried jaws of the Recent relative were available, nor a detailed illustration of the complete dentition of *C. oxyrhynchus*. Only Bigelow and Schroeder (1948, fig. 73c) have provided a drawing of a complete dentition of *C. oxyrhynchus*, which was the base for our assessment of tooth positions. The Recent species was formerly placed in the genus *Isogomphodon* Gill, 1862. According to the genetic studies by da Silva Rodrigues-Filho et al. (2023), the species *oxyrhynchus* is a member of the genus *Carcharhinus*.

Other occurrences in the OMM: Baden-Württemberg: Baltringen (Probst 1879; Sach 2016), Walbertsweiler (Pfeil 1991), Ulm-Ermingen (Baier et al. 2004). Bavaria: Simssee area (Villafaña et al. 2020).

Autecology: The extant species lives near the bottom in the tropical Western Atlantic down to a depth of 15 m. It lives in marine and brackish waters and feeds on small schooling fishes (Froese and Pauly 2022).

Carcharhinus priscus (Agassiz, 1843)

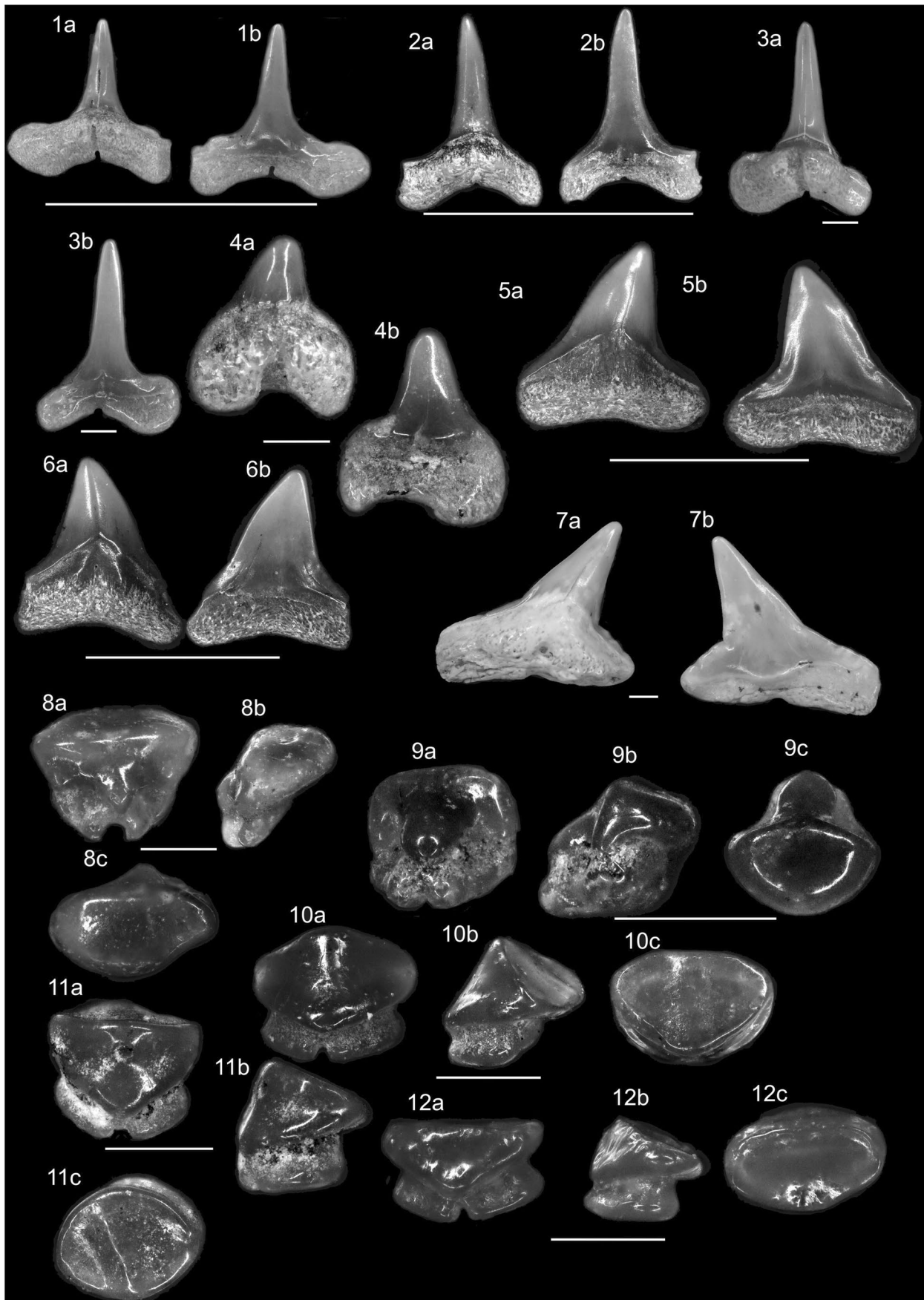
(Fig. 9.4)

*1843 *Sphyrna prisca* - Agassiz, pl. 26a, figs. 35–50

For other synonyms see Reinecke et al. (2011) and Höltke et al. (2020).

Material: ca. 250 teeth.

Description: SMNS 97056/29 Fig. 9.4 is a symphyial tooth. This eroded tooth has an upright, triangular crown, which is slightly bent in a distal direction. The crown tapers regularly in an apical direction. It is low in height compared to the root. The lingual crown face is convex and the labial one is flat. Both crown faces and the cutting edges are smooth. The root is high and massive, seemingly fully calcified. The lingual root face is convex. The nutrient channel on the lingual root face is similar to that in the upper lateral teeth apart from one aspect: despite a broken piece at the distal root lobe, it can be seen that the channel widens further on the basal root face than in it does in the upper laterals. The root seems to be originally symmetrical; the observed asymmetry is due to the broken part at the nutrient channel mentioned above. Both root lobes seem to have rounded ends. The labial root



◀**Fig. 9 1** SMNS 97056/26, *Carcharhinus acuarius* (Probst, 1879). Lateral tooth. **a** lingual view; **b** labial view. Scale: 10 mm. **2** SMNS 97056/27, *Carcharhinus acuarius* (Probst, 1879). ?Anterior tooth. **a** lingual view; **b** labial view. Scale: 10 mm. **3** SMNS 97056/28, *Carcharhinus acuarius* (Probst, 1879). ?Anterior tooth. **a** lingual view; **b** labial view. Scale: 1 mm. **4** SMNS 97056/29, *Carcharhinus priscus* (Agassiz, 1843). Symphyseal tooth. **a** lingual view; **b** labial view. Scale: 1 mm. **5** SMNS 97056/30, *Carcharhinus similis* (Probst, 1878). Upper lateral tooth. **a** lingual view; **b** labial view. Scale: 10 mm. **6** SMNS 97056/31, *Carcharhinus similis* (Probst, 1878). Upper lateral tooth. **a** lingual view; **b** labial view. Scale: 10 mm. **7** SMNS 97056/32, *Sphyrna integra* Probst, 1878. Lateral tooth. **a** lingual view; **b** labial view. Scale: 1 mm. **8** SMNS 97056/33, *Rhinobatos* sp. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **9** SMNS 97056/34, *Rhinobatos* sp. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **10** SMNS 97056/35, *Raja* sp. Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **11** SMNS 97056/36, *Raja* sp. Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **12** SMNS 97056/37, *Raja* sp. Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm

face is flat and the labial crown face remarkably overhangs the root. However, the last point could also be due to post-mortem erosion.

Remarks: Upper and lower anterior and lateral teeth of this species have often been described in the literature, including from the OMM (see Reinecke et al. 2011; Höltnke et al. 2020, 2022a). In the deposit of Ballendorf, a symphyseal tooth of this species could be verified which has not been illustrated for the OMM before.

The syntypes of *C. priscus* illustrated by Agassiz (1843; pl. 26a, figs. 35–50) came partly from Malta (figs. 35–38); the origin of the other teeth was uncertain. Probst (1878) didn't mentioned this species in his work on the shark and ray fauna of Baltringen although he was familiar with the work of Agassiz. Instead, Probst (1878) used the name *Sphyrna serrata* Münster, 1846 for one *priscus*-shaped tooth (Probst 1878, fig. 45), and designated two new species for four *priscus*-shaped teeth (Probst 1878: *C. Aprion brevis*, fig. 4; *C. Aprion stellatus*, figs. 1–3). All the three aforementioned taxa were later synonymized with *C. priscus* (see Reinecke et al. 2011). The first authors to use the species name *priscus* for teeth from the OMM were Leriche (1927, as *Sphyrna prisca*, pp. 85–86, pl. 14, fig. 8) and von Ihering (1927, *Sphyrna prisca*, p. 485). Both authors listed *Sphyrna serrata* Münster, 1846 as a synonym of *C. priscus*. Since then, similar teeth in the Lower Miocene have been referred to as *Carcharhinus priscus* in the literature.

Autecology: Recent members of this genus can be found worldwide in warm-temperate and tropical oceans (see Voigt and Weber 2011; Ebert et al. 2021). Most of the species live in the neritic realm but some species can be also found at several hundred meters depth (see Ebert et al. 2021 for details). Depending on species, the diet consists of fishes and/or invertebrates (see Ebert et al. 2021 for details).

Carcharhinus similis (Probst, 1878)
(Figs. 9.5, 9.6)

*1878 *Prionodon similis* n. sp. – Probst, pp. 125–127, pl. 1, figs. 12–19
1991 *Carcharhinus similis* (Probst 1878) – Pfeil, p. 204, pl. 3, figs. 14, 15
2021 *Carcharhinus similis* (Probst 1878) – Feichtinger and Pollerspöck, pp. 166–167

Material: Five incomplete teeth.

Description: The teeth are upper lateral ones. All the teeth have been eroded; the teeth in Figs. 9.5, 9.6 are the best preserved examples. The teeth are remarkably thin. The lingual crown face is weakly convex and the labial one is flat. They have a triangular crown with a broad base. Shortly above the base, the crown tapers strongly, then more regularly in an apical direction. The crown is distally bent. On the distal and mesial sides, the cutting edges continue without a notch onto the root lobes. On the distal side, this can be named as a talon. Only a slight indentation is present, where the distal cutting edge goes over into the distal talon. Both faces of the crown are smooth. The cutting edges are also smooth, but weak traces of a former serration can be seen. The labial crown face slightly overhangs the root. The lingual root face is weakly convex and higher than the labial one; the labial root face is weakly concave. The root has widely separated root lobes, and consists of a shiny, brown material.

Distribution in the OMM: Baden-Württemberg, South Germany: Baltringen (Probst 1878; Sach 2016), Ulm-Ermingen (Baier et al. 2004), Walbertsweiler (Pfeil 1991). Switzerland: Kanton Aargau: Würenlos (Leriche 1927).

Autecology: Following Reinecke et al. (2011), the teeth of *Carcharhinus similis* show some morphological similarities with the extant *C. amboinensis* (Müller and Henle, 1839) and *C. leucas* (Valenciennes, 1839, in Müller and Henle, 1839).

Family Sphyrnidae Bonaparte, 1840
Sphyrna integra Probst, 1878
(Fig. 9.7)

*1878 *Sphyrna integra* n. sp. – Probst, pp. 152, pl. 1, figs. 46, 47

For further synonyms see Reinecke et al. (2011).

Material: Three teeth.

Description: The incomplete lateral tooth in Fig. 9.7 has a broad crown base. The main cusp is narrow in comparison to the broad base, tapering regularly in an apical direction. The crown is distally inclined. The cutting edges are smooth, as

are both crown faces. The lingual crown face is convex; the labial face is flat. The mesial cutting edge continues with a kink into a mesial heel. The distal cutting edge also continues into a distal heel, which is separated by a notch. In labio-lingual view, the mesial cutting edge is very weakly convex on the basal half of the crown, then it runs straight. The basal 2/3 of the distal cutting edge is weakly concave; in the apical 1/3, it is straight. The heels on both sides are flat. The distal heel has a slightly undulated apical margin. The labial crown face overhangs the root. The root has widely separated root lobes. Only half of the distal root lobe is preserved. The end of the mesial root lobe is labio-lingually thin.

Autecology: Recent members of *Sphyrna* (hammerheads) are known from the shelf region of all warm oceans, but some species have been found at more than 1000 m depth (Ebert et al. 2021). Their diet consists of invertebrates and fishes (Compagno 1984).

Superorder Batomorphii Cappetta, 1980

Order Rhinopristiformes Naylor, Caira, Jensen, Rosana, Straube, Lakner, 2012

Family Rhinobatidae Müller and Henle, 1838

Rhinobatos sp.

(Figs. 9.8, 9.9)

Material: Three teeth.

Description: The antero-lateral tooth in Fig. 9.8 has a flat crown. On the lingual crown face is a median lingual uvula, which is triangular and pointed in a downward direction. This uvula overhangs the root. A transverse crest separates the lingual crown face from the flat and smooth labial one. On both sides of the median lingual uvula is a foramen. The root lobes are bent in a lingual direction. The lingual notch of the root is arch-shaped and symmetrical. Fig. 9.9 shows another tooth of this taxon.

Autecology: Following Ebert (2003), members of this family live on the continental shelves and uppermost continental slopes in warm-temperate to tropical seas.

Order Rajiformes Berg, 1937

Family Rajidae Blainville, 1816

Raja sp.

(Figs. 9.10, 9.11, 9.12, 10.1)

Material: 17 teeth.

Description: In SMNS 97056/35, the antero-lateral tooth in Fig. 9.10, the lingual crown face together with the transverse crest and the lingual visor have a triangular shape. The transverse crest is convex but inconspicuous. The convex lingual visor is strongly bent in a basal direction. The labial crown face is concave in a mesio-distal direction apart from a shallow but broad ridge, which runs labio-lingually. This ridge divides the labial crown face into two halves. The

labial visor is moderately convex. Where the ridge meets the labial visor is an indentation. Both root lobes are extended in a lingual direction. The distal root lobe is broader than the mesial one. Both root lobes have a flat base and an irregular, oval shape. A foramen is not observed between the root lobes. The lingual ends of the root lobe and the lingual visor are at the same height. The lingual notch of the root has a low and arch-shaped course. Fig. 9.11 shows another antero-lateral tooth with the same features (SMNS 97056/36). Both root lobes of SMNS 97056/37, the antero-lateral tooth in Fig. 9.12, are the same size and the ridge on the labial crown face is absent, differing from SMNS 97056/35 and SMNS 97056/36. The crown of the former tooth is also mesio-distally more elongated and labio-lingually narrower in comparison to SMNS 97056/35 and SMNS 97056/36. In labial view, the labial visor is arch-shaped, bent in a basal direction where the labial crown face is also slightly sunken. The upper margin of the transverse crest has an undulating course.

The tooth in Fig. 10.1 (SMNS 97056/38) is an antero-lateral one with a lingually bent crown. The lingual crown face is convex, as is the tongue-shaped lingual visor. The latter is strongly extended in a lingual direction as well as bent in a basal direction. In profile view, the lingual visor is slightly arch-shaped. The transverse crest is strongly convex but inconspicuous. The labial crown face is moderately convex in a mesio-distal direction and concave in a labio-lingual direction. The labial visor is thick and convex. Both root lobes are lingually extended and have a flat base and an irregular oval shape. The mesial root lobe is broader than the distal one. Between the root lobes, a foramen is present. The lingual notch of the root has a low and arch-shaped course.

Discussion: According to the overall morphology, the teeth in Figs. 9.10–9.12 are from a female whereas the one in Fig. 10.1 represents a tooth from a male (Cappetta 2012, p. 360, fig. 349). If the morphological differences between the female teeth described above (Figs. 9.10–9.12) are due to a heterodont dentition or if they represent different species is unclear. SMNS 97056/35 and SMNS 97056/36 (Figs. 9.10, 9.11) differ from the Neogene species *Raja gentili* Joleaud, 1912 in the arrangement of the root lobes as well as the triangular shape of the lingual crown face (together with the transverse crest and the lingual visor), as does SMNS 97056/37. The lingual crown face of *R. gentili* is also flatter than in SMNS 97056/35 and SMNS 97056/36 (see Joleaud 1912, pl. 8, figs. 37–46). SMNS 97056/35 and SMNS 97056/36 show some similarities in the shape of the labial crown face to *Raja holsatica* Reinecke, Von Der Hocht and Gürs, 2008 from the Vierlandian, Lower Miocene of North-west Germany (see Reinecke et al. 2008, pl. 8, fig. 5). However, based on the illustrations given by Reinecke et al. (2008, pl. 8), the aforementioned teeth have a higher lingual crown face and a wider lingual notch of the root than *R.*

holsatica. In comparison to SMNS 97056/37, the species *R. holsatica* has a more convex lingual crown face. *Dipturus casieri* (Sturbaut and Herman, 1978) differs remarkably in the shape of the root (see Reinecke 2015, pl. 5, figs. A-F.) *Atlantoraja ceciliae* (Sturbaut and Herman, 1978) has a lower lingual crown face than SMNS 97056/35 and SMNS 97056/36 and a higher root than SMNS 97056/37 (see Sturbaut and Herman 1979, pl. 2, fig. 2 as *Raja heinzellini*, which is a synonym of *A. ceciliae* following Reinecke 2015).

The male tooth Fig. 10.1 (SMNS 97056/38) is the only male one that could be verified. The tooth doesn't fit to the male teeth of the taxa listed above. The Rajiformes were revised in 2016 (Last et al. 2016b, c); species formerly placed in *Raja* have also been transferred to other genera (see Froese and Pauly 2022). Unfortunately, no material (jaws or isolated teeth) of the various Recent taxa were available for comparison. Therefore the initial determination is only as "*Raja* sp."

Autecology: The family Rajidae has a cosmopolitan distribution. Their members have benthic lifestyle on soft substrates and most of them feed on benthic crustaceans and bony fishes (Fricke and Al-Hassan 1995; Last et al. 2016b). Their depth range is from shallow waters to depths of a few hundred meters (see Fricke and Al-Hassan 1995; Barreiros and Gadig 2011). However, the biology of some species is poorly known (Last et al. 2016b).

Myliobatiformes Compagno, 1973

Family Dasyatidae Jordan and Gilbert, 1879

Dasyatis minuta Cappetta, 1970

(Figs. 10.2- 10.4)

* 1970 *Dasyatis minuta* nov. sp. – Cappetta, pp. 97-98, Pl. 21, figs. 24-31

Material: 15 teeth.

Description: The antero-lateral tooth in Fig. 10.2 probably came from a female. It has a very convex transverse crest. The lingual visor is also very convex, and runs obliquely downwards in a lingual direction. The median lingual ridge is weakly concave. The lingual zone of the crown has a massive appearance. This zone is divided by a narrow and deep indentation. This indentation is enclosed on three sides by parts of the lingual zone of the crown. On the labial side, it is open and the indentation continues into the convex labial visor. The root consist of two flat root lobes with an obliquely ovate shape. Between the root lobes, a foramen is visible.

The antero-lateral tooth in Fig. 10.3 probably comes from a male. The crown is lingually bent. The median lingual ridge is concave. Both lingual marginal faces of the crown are also concave. The lingual visor is nearly straight in occlusal view. The transverse crest is very convex and nearly

forms a triangle with an acute angle but without a base. The lingual visor slightly overhangs the transverse crest. An indentation is present on the lingual zone of the crown, enclosed on three sides by massive parts of this zone. The indentation runs obliquely downwards in a labial direction. The indentation then continues in a labial zone of the crown oriented obliquely downward. This labial crown zone ends in the convex labial visor. The root lobes are strongly bent forward and overhang the lingual visor. Only one root lobe is complete but it seems that both lobes are the same size. The root lobes have a bulbous, rounded shape. The presence of a foramen between the root lobes cannot be confirmed. Fig. 10.4 shows another antero-lateral tooth which probably came from a male.

Discussion: The examined teeth fit to the illustrations of *Dasyatis minuta* given by Cappetta (1970, pl. 21, figs. 24-31). The pronounced transverse crest and the curvature of this crest fit to the teeth described above. The differentiation between male and female morphs is based on comparisons with other *Dasyatis* species. Cappetta (1970) described *D. minuta* from the Langhian ("Helvétien inférieur") from Loupian, Dept. Hérault, France. This is the only reference to this species in the literature.

Autecology: Extant species of *Dasyatis* can be found in the Atlantic and southwest Indian Oceans and in the Mediterranean (Last et al. 2016a). According to the latter authors, most of the species live in a coastal environment and feed on bony fishes and/or invertebrates (Last et al. 2016a).

Dasyatis probsti Cappetta, 1970

(Figs. 10.5, 10.6)

*1970 *Dasyatis probsti* nov. sp. – Cappetta, pp. 91-92, fig. 12, pl. 21, figs. 15-23

2014 *Dasyatis probsti* Cappetta, 1970 – Pollerspöck and Beury, p. 32, pl. 2, figs. 7a, b, 9a, b

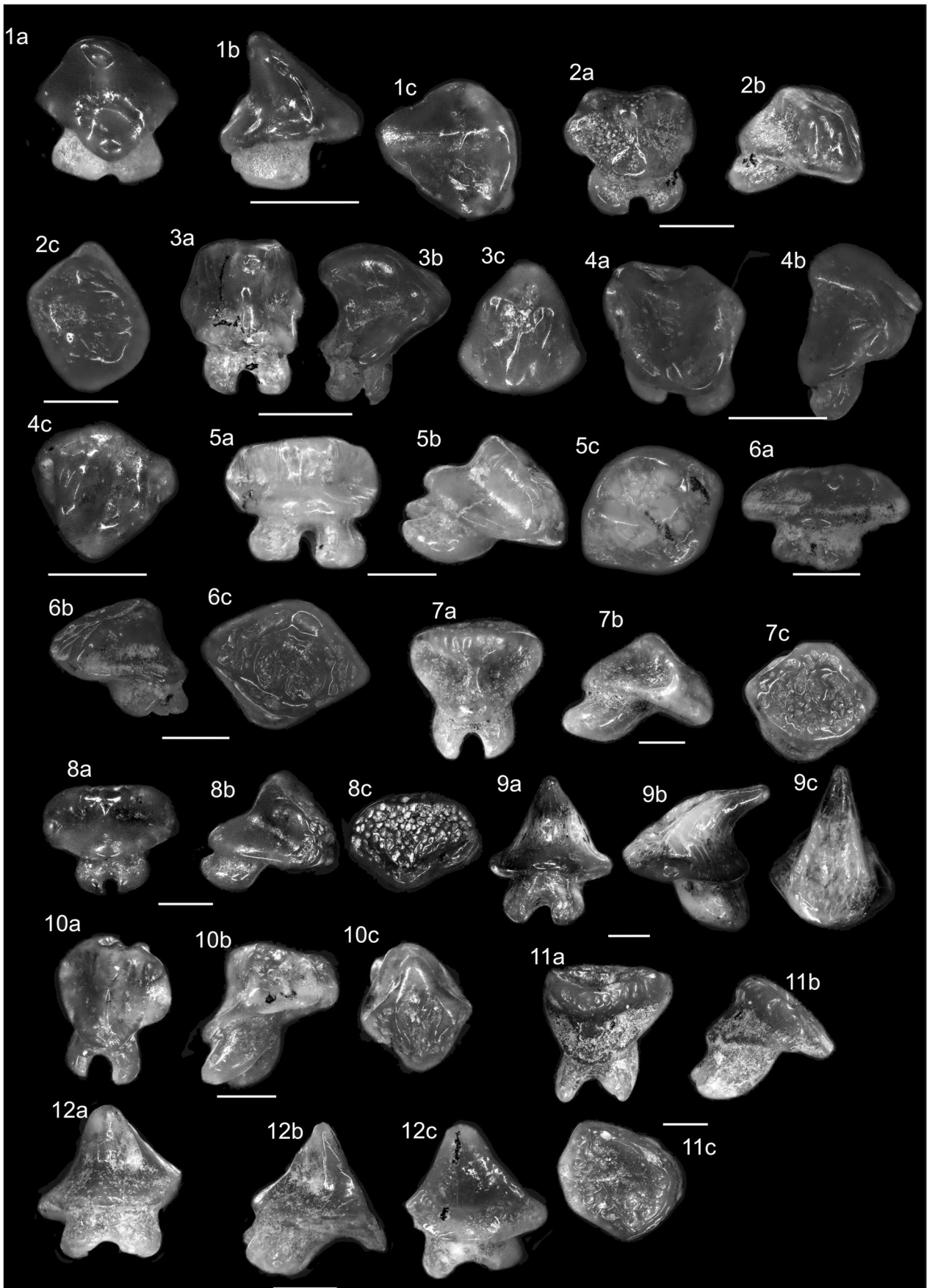
2020 *Dasyatis probsti* Cappetta, 1970 – Villafañá et al., p. 745, figs. 8k, l

2021 *Dasyatis probsti* Cappetta, 1970 – Feichtinger and Pollerspöck, pp. 228-229

2022a ?*Dasyatis probsti* (Cappetta, 1970) – Höltke et al., p.113, fig. 7.7

Material: 22 teeth, mostly eroded.

Description: The antero-lateral tooth in Fig. 10.5 is from a female. The arch-shaped transversal ridge divides the lingual crown margin from the larger labial one. The lingual visor is convex. Both lingual marginal faces of the crown are concave. The median lingual ridge is only weakly developed. On the labial crown face is a pronounced depression, at the bottom of which are folds. The lateral margins of this depression show some folds, but also smooth areas. The other parts of the labial crown face bear some ridges. The upper margin of the transverse crest is smooth. However, the prominence



◀**Fig. 10 1** SMNS 97056/38, *Raja* sp. Male. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **2** SMNS 97056/39, *Dasyatis minuta* Cappetta, 1970. Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale 1 mm. **3** SMNS 97056/40, *Dasyatis minuta* Cappetta, 1970. Male. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **4** SMNS 97056/41, *Dasyatis minuta* Cappetta, 1970. Male. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **5** SMNS 97056/42, *Dasyatis probsti* Cappetta, 1970. Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **6** SMNS 97056/43, *Dasyatis probsti* Cappetta, 1970. Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **7** SMNS 97056/44, *Dasyatis rugosa* (Probst, 1877). Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **8** SMNS 97056/45, *Dasyatis rugosa* (Probst, 1877). Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **9** SMNS 97056/46, *Dasyatis rugosa* (Probst, 1877). Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **10** SMNS 97056/47, *Dasyatis* sp. ?Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **11** SMNS 97056/48, *Taeniurops cavernosus* (Probst, 1877). Female. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm. **12** SMNS 97056/49, *Taeniurops cavernosus* (Probst, 1877). Male. Antero-lateral tooth. **a** lingual view; **b** profile view; **c** occlusal view. Scale: 1 mm

of the folds and ridges could be affected by postmortem erosion. The labial visor has a curved but somewhat irregular course. The last feature may also be caused by postmortem erosion. In basal view, the labial visor together with the lingual one form an oval outline. The root lobes are well separated by a lingual notch. The ends of the root lobes are bent in a lingual direction. Between the root lobes is a foramen. Fig. 10.6 shows another antero-lateral tooth from a female.

Discussion: The teeth fit the illustrations of *D. probsti* in Cappetta (the bottom is characteristic for this species. *Taeniurops cavernosus* (Probst, 1877) also has a pronounced labial depression, but this depression is larger than in *D. probsti* (see the cited material of *T. cavernosus* illustrated in Reinecke et al. 2011, text-fig. 34). Additionally, Following Probst (1877), the labial depression in *T. cavernosus* has a smooth bottom.

Autecology: See *D. minuta* and Tab. 1.

Dasyatis rugosa (Probst, 1877)
(Figs. 10.7–10.9)

*1877 *Raja rugosa* n. sp. – Probst, pp. 66–67, pl. 1, figs. 5–9
For further synonyms see Reinecke et al. (2011) and Höltker et al. (2022b).

Material: More than 50 teeth.

Description: SMNS 97056/44 is an antero-lateral tooth from a female (Fig. 10.7). The tongue-shaped lingual visor runs obliquely downwards in a lingual direction. The median lingual ridge is broad and straight but not very massive. The lingual marginal faces of the crown are convex. The

transverse crest arches between the marginal angles. On the lingual margin of the transverse crest, weakly pronounced ridges are visible. The transverse crest and the lingual visor are at the same height. The labial crown face is slightly sunken. It is covered with ridges and pits. The labial visor is strongly convex. The well separated root lobes are bent in a lingual direction, slightly overhanging the crown. Between the root lobes are two large foramina, positioned side by side. Fig. 10.8 shows another antero-lateral tooth from a female. The median lingual ridge is concave and the ridges on the transverse crest are more pronounced. In contrast to SMNS 97056/44, SMNS 97056/45 (Fig. 10.8) has only one foramen between the root lobes.

Fig. 10.9 shows a tooth from a male. Here, the crown is lingually bent. The tongue-shaped lingual visor runs obliquely downwards in a lingual direction. The lingual faces of the crown are concave. A lingual median ridge is absent, but this area is strongly concave. Both marginal angles are very pronounced. The labial crown face together with the transverse crest tapers strongly in a lingual direction, such that they have a triangular shape in occlusal view. The surface of the labial crown face is covered with ridges and pits. The root lobes are lingually bent and have a flat base. The lingual ends of the root lobes are at the same height as the transverse crest. The root has a deep and arch-shaped lingual notch. Between the root lobes there are traces of two foramina.

Autecology: See *D. minuta* and Tab. 1.

Dasyatis sp. (Fig. 10.10)

Material: One tooth.

Description: SMNS 97056/47 is a comparatively large dasytid-like antero-lateral tooth. It might come from a female. The lingual visor is strongly bent and tapers strongly in a lingual direction. The narrow median lingual ridge is concave. The transverse crest is also strongly bent and tapered in a lingual direction and has therefore a triangular shape. The lingual marginal faces of the crown are concave. The lingual visor overhangs the transverse crest. On the labial crown face is a depression which is remarkably longer than wide. The depression strongly tapers in a labial direction. From its lingual margin, a ridge from the transverse crest protrudes into the depression, such that in occlusal view, the depression looks a bit like a two-pointed fork. The bottom of the depression appears smooth. Outside of the depression, a few pits can be seen but most of the area is smooth. The two well separated root lobes are strongly bent in a lingual direction. The root lobes overhang the crown. Between the root lobes are two foramina side by side. The lingual notch of the root is broad and arch-shaped.

Remarks: The labially elongated depression as well as the ridge protruding into it from the transverse crest differentiate SMNS 97056/47 from the other Miocene *Dasyatis* teeth illustrated in the literature. Because of this and the fact that

only one tooth of this type could be verified, open nomenclature was chosen.

Autecology: See *D. minuta* and Tab. 1.

Taeniurops cavernosus (Probst, 1877)
(Figs. 10.11, 10.12)

*1877 *Raja cavernosa* n. sp. – Probst, pp. 75–76, pl. 1, figs. 1–4
2021 *Taeniurops cavernosa* (Probst, 1877) – Feichtinger and Pollerspöck, pp. 230–231

For further synonyms see Reinecke et al. (2011, p. 95)

Material: 43 teeth.

Remarks: A well preserved female antero-lateral tooth (Fig. 10.11) and a well preserved male antero-lateral tooth (Fig. 10.12) are illustrated. Despite being already described from the OMM, these teeth are figured because of their better preservation than those from Ursendorf and Äpfingen (see Höltke et al. 2020, 2022b). *T. cavernosus* is also remarkably common in Ballendorf, in contrast to the aforementioned localities. Whether the reason for this is simply a collection bias or if other factors played a role is unclear at the moment. A description of this species as well as the autecology of the genus can be found elsewhere in the literature (for example Reinecke et al. 2011; Bor et al. 2012; Höltke et al. 2020; 2022b; Feichtinger and Pollerspöck 2021).

Autecology: There are two Recent species of *Taeniurops* (Froese and Pauly, 2022). One can be found in the Atlantic (including the Mediterranean Sea), the other one in the Indo–West Pacific (Last et al. 2016a). The European species *T. grabatus* (Geoffroy St-Hilaire, 1817) lives on sand and rock-sand bottoms from 10 to 300 m water depth (Froese and Pauly 2022). The Indo-West Pacific species *T. meyeri* (Müller and Henle, 1841) lives mainly inshore but was reported from more than 400 m depth (Last et al. 2016a). According to Froese and Pauly (2022) both species feed on bottom-living fishes and invertebrates.

Palaeoecology

Nearly all the taxa of the Ballendorf shark and ray fauna have Recent relatives; only the genera *Keasius* and *Physogaleus* are extinct. The fauna contains two generalist feeders (*Galeocerdo*, *Notorynchus*), and one filter-feeder (*Keasius*), whereas the majority of taxa likely fed on invertebrates and/or fishes. All Recent relatives are inhabitants of warm-temperate and/or tropical waters, consistent with the isotopically derived palaeo-water temperature of 20° C (± 4° C) at Ballendorf during the Burdigalian (Vennemann and Hegner 1998). Apart from *Isistius*, Recent relatives of all the taxa live in the shelf region or

this is part of their habitat, and based on their fossil occurrences, the two extinct genera probably also lived in warm-water neritic regions. Species of *Isistius* live in the oceanic realm and species of *Centrophorus* live on the outer shelf and upper continental slope in deep water; the mesopelagic taxa *Mitsukurina* and *Pseudocarcharias* were not verified as being present. Most of the taxa recovered lived on the bottom or near the bottom; however, *Keasius*, *Isistius* and *Alopias* lived higher in the water column. *Alopias* was probably the only active pelagic swimming taxon. Apart from two tooth fragments which could belong to *Carcharodon hastalis* (Agassiz, 1843), teeth of large sharks like *Otodus*, *Isurus* and clearly determinable teeth of *C. hastalis* are missing. The same is also true for the extinct genus *Carcharoides*, known from other deposits in the OMM of Baden-Württemberg. Due to the intensity of collecting activity in Ballendorf, a collection bias can likely be ruled out.

Other fossils from this sandpit (Bracher collection) include teeth from bony fishes (Sparidae), remnants of marine mammals (Odontoceti) as well as teeth from small terrestrial mammals. Invertebrates are represented by bivalves: *Mimachlamys varia* (Linnaeus, 1758) Ostreidae, Pholadidae, and gastropod steinkerns: Turritellidae, Gastropoda indet.. The following additional taxa from Ballendorf but not from the Bracher collection include calcareous algae, bivalves (Pectinidae), balanomorph barnacles, and bryozoans. The exact locality in Ballendorf is unknown for the taxa not part of the Bracher collection, but it can be assumed that these fossils are of the same age as the ones from the sand pit.

The elasmobranch assemblage as well as the associated fauna imply a shallow water environment. The sedimentology and proximity to the palaeo-coastline (the so-called “Klifflinie”) agree with this type of habitat. The occurrences of the *Isistius* and *Centrophorus* may be explained through these taxa occasionally frequenting shallow water areas to hunt. The absence of large-toothed predators like *Carcharodon*, *Isurus* and *Otodus* and of the mesopelagic sharks *Mitsukurina* and *Pseudocarcharias* might be due to a shallower water depth in comparison to the other OMM deposits like Äpfingen, Rengetsweiler, Ursendorf and Walbertsweiler. Fig. 6 shows the geographic positions of these deposits in relation to the palaeo-coastline. If *Carcharoides* is absent for the same reason cannot be said because this genus has no Recent relatives. A remarkable aspect of the ancient shark and ray fauna from Ballendorf is the presence of *Carcharias crassidens*, a seldom found species in the OMM of Baden-Württemberg. This species is most abundant in the Upper Brackish Water Molasse in the region around Ulm (see Sach and Heizmann 2001; Sach 2016). If its presence in Ballendorf has implications for palaeoecology cannot be said. The remarkably large number of small to micro-sized teeth from Ballendorf, in contrast to the deposits of Äpfingen, Ursendorf and Rengetsweiler, is clearly due to collection bias at the latter localities.

Conclusion

In total, 39 different species and 29 genera could be verified as present at the Lower Miocene locality of Ballendorf. If the sediments are of Eggenburgian or Ottangian age is not clearly evident. However, six shark species from Ballendorf are only known in Ottangian and younger sediments [*Isistius triangulus* (Probst, 1879), *Pristiophorus suevicus* Jaekel, 1890, *Iago angustidens* (Cappetta, 1973), *Paragaleus tenuis* (Probst, 1878), *Rhizoprionodon fischeuri* (Joleaud, 1912) and *Carcharhinus similis* (Probst, 1878)]. Additionally, there are some undeterminable tooth fragments, including two pieces that could belong to *Carcharodon hastalis*. Apart from these fragments, no teeth from the large taxa *Carcharodon*, *Isurus* and *Otodus* could be verified. The majority of the elasmobranchs present lived in the shelf region on or near the bottom. Only *Alopias* and possibly also *Keasius* lived in the upper part of the water column. The only exceptions to the coastal nature of the fauna are *Isistius* and *Centrophorus*. The first of these lived in the oceanic realm and the second lived in deeper water. Both probably occasionally visited the shelf region to feed. The mesopelagic genera *Mitsukurina* and *Pseudocarcharias*, known from many other OMM localities, are absent. The same is true for the extinct genus *Carcharoides*. Apart from two generalist feeders (*Galeocerdo*, *Notorynchus*) and one filter-feeder (*Keasius*), all the other taxa fed on fishes and/or invertebrates, whereas *Isistius* also lived as an ectoparasite. An uncommon find in the OMM is a tooth of *Carcharias crassidens* from the Ballendorf deposit. Whether the large *Paragaleus* tooth mentioned here as *Paragaleus* sp. represents a new species cannot be said at the moment, because only one specimen could be verified. The whole fauna is consistent with a warm, shallow water community. Due to its close proximity to the palaeo-coastline, the water depth was shallower than in other known deposits of the OMM in Baden-Württemberg. This may explain the absence of the taxa named above.

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Declarations

Availability of data and material The material is stored at the Staatliches Museum für Naturkunde Stuttgart.

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