

## **Trophic relationships in the Early Miocene Upper Marine Molasse of Baden-Württemberg, Southwest Germany, with special emphasis on the elasmobranch fauna**

**Olaf Höltke, Rodrigo B. Salvador, and Michael W. Rasser**

### **ABSTRACT**

The Early Miocene Upper Marine Molasse (OMM) in south-western Germany contains a diverse fossil ecosystem in which elasmobranch teeth are especially abundant. However, the scarcity of outcrops and sometimes poor preservation of fossils resulted in scant recent literature about the OMM. Here, we focus on the elasmobranch fauna to determine the trophic relationships within the OMM, using fossil teeth as proxies for diet and trophic levels based on functional morphology and an actualistic species- or genus-level approach. Herein we present a fresh and comprehensive palaeoecological reconstruction of the OMM ecosystem in Baden-Württemberg. All five outcrop areas available for the present analysis (Baltringen, Meßkirch-Rengetsweiler, Meßkirch-Walbertsweiler, Ulm-Ermingen, and Ursendorf) exhibit a similar faunal composition, with the apex predator being *Otodus (Megaselachus)* sp. Among the other elasmobranchs, there are mostly piscivorous and malacophagous species; taxa that feed on a variety of other invertebrates or amniotes (including marine mammals) are also present. The OMM sediments deposited in shallow-water settings, but there are fossils of more oceanic species that might, at times, have approached the shore. With a soft bottom, partly covered by sea grass, the OMM environment would have been like the present-day warm-waters settings of the Mediterranean.

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## INTRODUCTION

Trophic relationships or food chains are a common theme in the literature about modern marine ecosystems (e.g., Lindeman, 1942; Arias-Gonzalez et al., 1997; Heithaus and Vaudo, 2012; Heithaus et al., 2012; Wetherbee et al., 2012; Bănaru et al., 2013; Bornatowski et al., 2014, 2018), as well as about palaeoecosystems (e.g., Scott, 1978; Maisey, 1994; Bianucci et al., 2000; Westgate, 2001; Stanton Jr., 2006; Aguilera and de Aguilera, 2014; Perez et al., 2017, 2021; Alberti and Reich, 2018 and references therein; Collareta, 2021).

Recently, isotopes from shark teeth have been used to determine the trophic position of extant and extinct species (see Martin et al., 2015; Kast et al., 2022; and McCormack et al., 2022). In palaeoecosystems, several of the parameters observable in their extant counterparts are generally not available, including stomach content, primary productivity data, and information on dietary energy levels between trophic levels (TL). Another important difference between recent and fossil ecosystems is the time factor. In modern ecosystems, the “everyday” (or seasonal, annual, etc.) conditions are directly accessible to study. Even ‘long-term’ studies conducted in modern ecosystems represent an insignificant time interval when compared to the fossil record. Indeed, a typical fossil assemblage usually represents a broad interval of geological time (time-averaging), whose duration is often difficult to estimate. Additionally, the time intervals for analysis need to be defined in accordance with litho- and sedimentological evidence, to properly acknowledge possible environmental changes throughout the section (e.g., from shallow to deep waters). Understanding the trophic relationships is a valuable tool for getting a better and more detailed picture of the paleoenvironment.

The sediments of the Upper Marine Molasse (“Obere Meeresmolasse” in German, abbreviated as OMM) in Baden-Württemberg, southwestern Germany, contains a diverse fossil ecosystem in which sharks and rays are especially abundant, being mostly represented by isolated teeth. The OMM fossil assemblage represents a relatively short timespan in the Miocene (early to middle Ottnangian, ca. 18 to 17.6 myr). Therefore, it can be assumed that the faunal elements present in the OMM in Baden-Württemberg inhabited the same

suite of palaeohabitats and were largely contemporaneous. However, many of the elasmobranch fossil teeth are poorly preserved. The amount of determinable shark and ray teeth are much lower than that of other similar deposits, such as those of northern Germany. Other macrofossils are also often poorly preserved. This may be the reason for the scant recent literature about OMM macrofossils in Baden-Württemberg (Barthelt et al., 1991; Pfeil, 1991; Baier et al., 2004; Höltke, 2009; Nebelsick et al., 2019; Höltke et al., 2020; Feichtinger and Pöllerspöck, 2021; Höltke et al., 2022; see also the informative outreach website by Feichtinger et al., 2022).

In the present study, we focused on the elasmobranch fauna to determine the trophic relationships within the OMM by using fossil teeth as proxies for diet and trophic levels based on functional morphology and an actualistic genus or species-level approach (Rasser et al., 2019). We present a novel and comprehensive palaeoecological reconstruction of the OMM ecosystem in Baden-Württemberg.

## GEOLOGICAL OVERVIEW

In southern Germany, the sediments within the North Alpine Foreland Basin are divided in the following units: Lower Marine Molasse, Lower Freshwater Molasse, Upper Marine Molasse, Brackish Molasse, and Upper Freshwater Molasse. The Upper Marine Molasse (OMM) in Baden-Württemberg belongs to the early Miocene and ranges from the early to the middle Ottnangian (middle Burdigalian, ca. 18 to 17.6 myr; for details, see Geyer and Gwinner, 1991; Heckeberg et al., 2010). During the deposition of the Brackish Molasse (upper Ottnangian), the so-called “Graupensandrinne” level was formed, which eroded most of the underlying OMM sediments (Geyer and Gwinner, 1991). Only parts of the OMM sediments were preserved within this Graupensandrinne; they are called “Grobsandzug”.

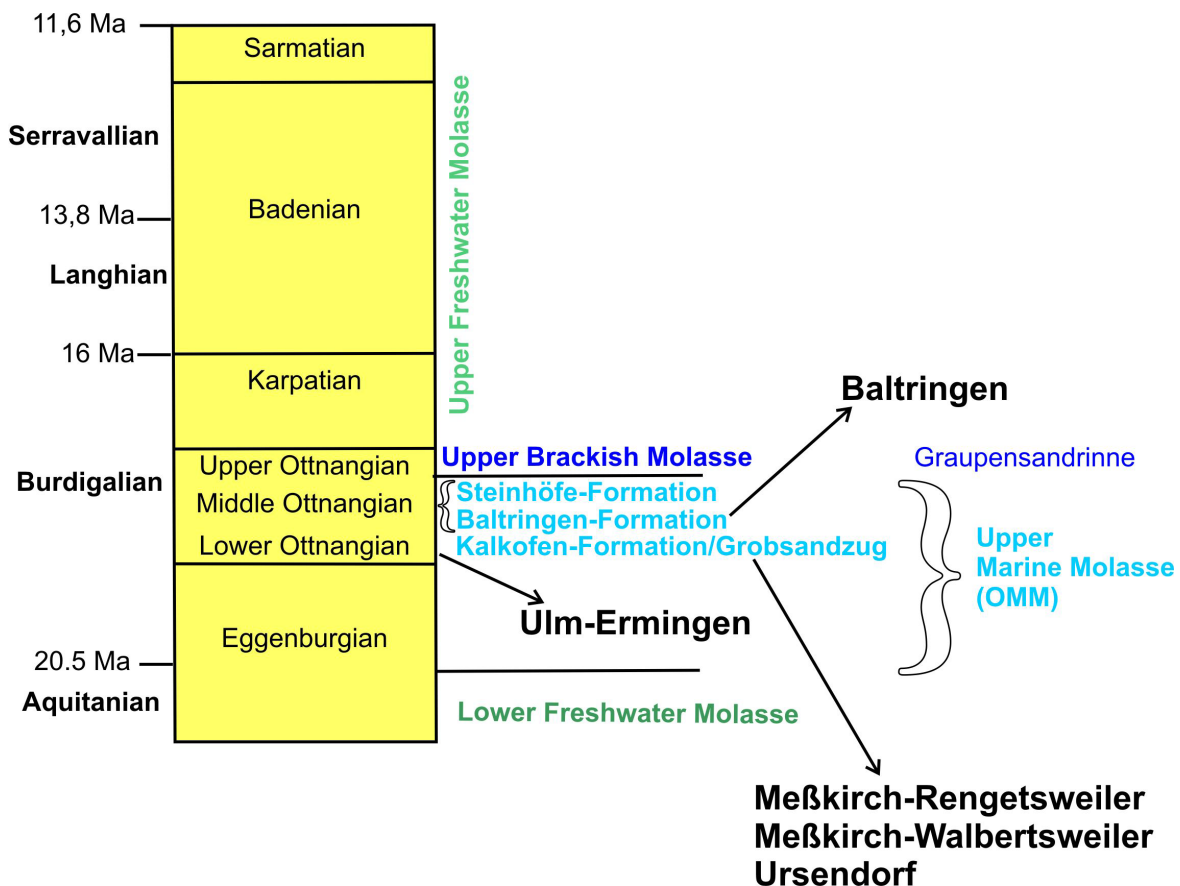
The Grobsandzug is time-equivalent to the early Ottnangian Kalkofen Formation, an OMM formation of the Molasse Basin of Southern Germany (Heckeberg et al., 2010) (Figure 1). The authors defined a new lithostratigraphic terminology for the Ottnangian deposits of the OMM in Southwest Germany. The hanging of the Kalkofen Formation is formed by the Baltringen Formation and the Stein-

höfe Formation (Figure 1). For more specific details about OMM geology, we refer the reader to previous works (Schreiner, 1966; Geyer and Gwinner, 1991; Kuhlemann and Kempf, 2002; Höltke, 2009; Heckeberg et al., 2010). We focus our analysis on the following OMM fossiliferous deposits: Baltringen (middle Ottnangian), Meßkirch-Rengetsweiler (early Ottnangian), Meßkirch-Walbertsweiler (early Ottnangian), Ulm-Ermingen (early Ottnangian), and Ursendorf (early Ottnangian) (Figure 2). Meßkirch-Rengetsweiler, Meßkirch-Walbertsweiler, and Ursendorf are part of the Grobsandzug mentioned above. In addition to shark and ray teeth, fossil remains of other taxa were also recovered from these deposits, including bonyfish teeth and molluscs.

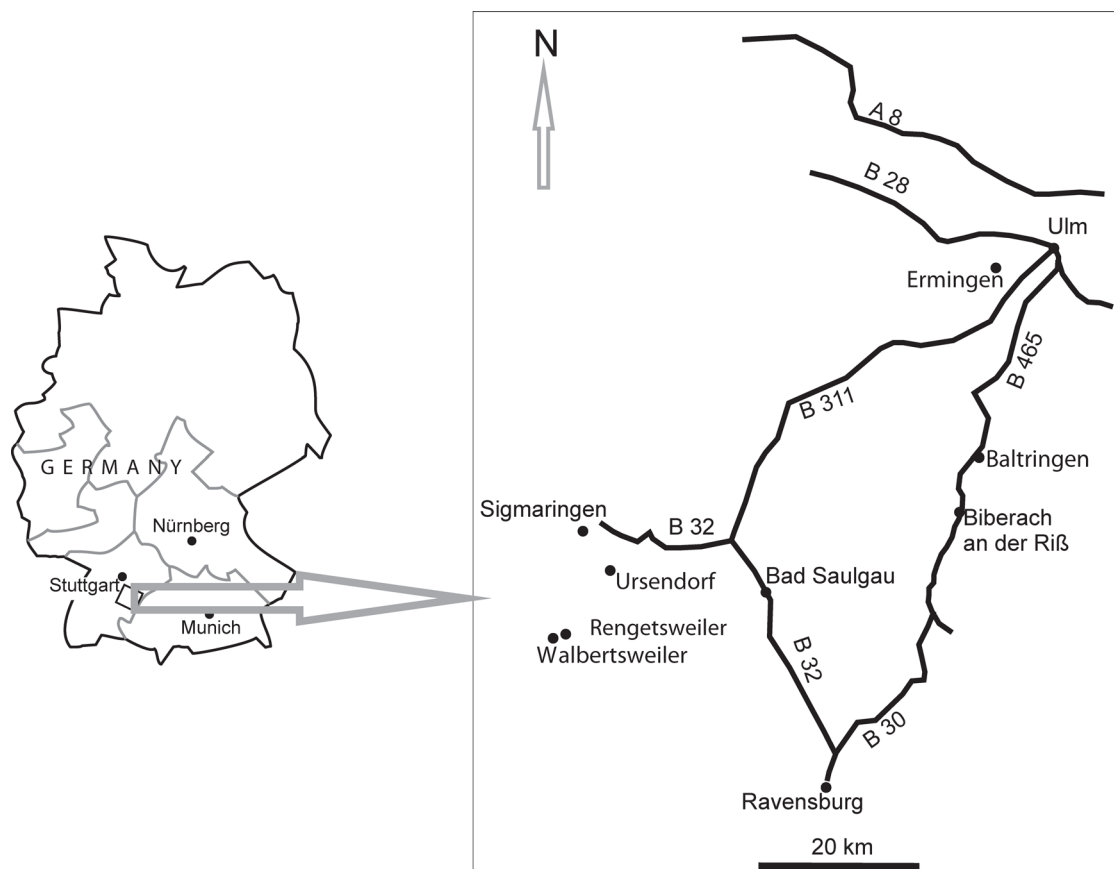
### Ulm-Ermingen (early Ottnangian)

Ermingen is famous for the so-called “Ermingen Turritellenplatte”, a mass accumulation of gastropod shells belonging to the genus *Turritella* Lamarck, 1799 (Baier, 2008; Höltke, 2009; Nebelsick et al., 2019). A succession of 3.5 m of

the Turritellenplatte was excavated in 2005 by a team from the Staatliches Museum für Naturkunde Stuttgart (SMNS; Stuttgart, Germany). The *Turritella* shells are firmly cemented within bioclastic, coarse grained-sandstone with a calcareous matrix that can pass into a quartz-rich limestones (Nebelsick et al., 2019). According to Nebelsick et al. (2019), silty marls with sands are also present, containing isolated specimens of *Turritella* and bivalves (Veneridae). Towards the top of the excavated succession, unconsolidated sands appear that are rich in *Turritella* specimens, followed by large blocks in situ (Nebelsick et al., 2019). The changes in the fabric of the *Turritella*-dominated beds were used by Nebelsick et al. (2019) to reconstruct a generally deepening environment that corresponds to an Early Miocene transgression. Despite this deepening, a shallow-water, soft-bottom community persisted, with endo- and epibenthic and pelagic organisms, like recent faunas of warm-temperate to (sub)tropical continental shelves. The mass occurrence of the semi-infaunal gastropod genus *Turritella* indicates a nutrient-rich



**FIGURE 1.** New lithostratigraphic terminology for the Ottnangian deposits of the OMM in Southwest Germany. Modified after Heckeberg et al. (2010).



**FIGURE 2.** Map showing the fossiliferous localities studied herein.

palaeoenvironment, which in turn, implies a high degree of water movement within the Molasse Sea, with nutrients being readily available from local upwelling and tidal current transport (Nebelsick et al., 2019). *Turritella*-dominated assemblages are also known from other rich palaeoecosystems such as the Gatun Formation from the Upper Miocene of Panama (Anderson et al. 2017) as well as from the Pisco Formation (Late Miocene) of Cerro Los Quesos, Ica Desert, Peru (Di Celma et al., 2015).

#### **Meßkirch-Rengetsweiler (early Ottnangian, Grobsandzug)**

Not far away from the open sand pit in Walbertsweiler (see below), the active sand pit owned by the Steidle Company takes its place in Rengetsweiler. The geology of the Grobsand deposit occurring herein was documented by Bieg et al. (2007) based on an excavation by an SMNS team in September 2006. These sediments belong to the European Neogene Mammal Zones MN 2b to MN 3 (Sach, 2016). They consist of sand with muddy intercalations. The palaeoenvironment was proba-

bly shallow water like the one in Walbertsweiler, and evidence for tides is present, including flaser bedding and ripple bedding (following Bieg et al., 2007). The presence of *Metaxytherium* sp. (Sirenia) is an indication of the presence of sea grass meadows.

#### **Meßkirch-Walbertsweiler (early Ottnangian, Grobsandzug)**

The fossils originate from an open sand pit near Meßkirch-Walbertsweiler (Barthelt et al., 1991). Sediments consist of alternated sands and marls and were deposited in a sublittoral environment at a water depth of less than 50 m (Barthelt et al., 1991). Most fossils (especially invertebrates) are abraded and eroded, so data is scarce. Sirenian fossils have also been found at this locality, which indicates the presence of sea grass weed.

#### **Ursendorf (early Ottnangian, Grobsandzug)**

The geology of Ursendorf was described by Bieg et al. (2007) based on an excavation conducted by an SMNS team in the sand pit of the Teufel Company. The sediments consist of sands

with different grain size (Bieg et al., 2007, Hölftke, 2009), with fossils coming from coarse-grained and poorly sorted sands. In the late eighteenth and early nineteenth centuries, there were more (and similarly coarse-grained) sand pits in the surroundings of the present-day pit, hence some fossils in the SMNS collection probably come from these older pits. The sedimentary succession examined during the excavation in 2006 showed a cross-bedding that indicates a high-energy regime (Bieg et al., 2007) and a palaeoenvironment comprised of a soft bottom, with a rich bryozoan and sea-grass community (Hölftke, 2009). However, based on the fossil content, there were also habitats below the storm wave base. The fossils of Ursendorf were the main theme of part of some publications: Molluscs (Hölftke, 2009), elasmobranchs (Hölftke et al., 2020), bryozoans (Miller, 1875), echinoderms, and sponges (Schütze, 1904).

### Baltringen (middle Otnangian)

The fossil fauna of Baltringen was examined by Probst (1877, 1878, 1879a), who extensively described the elasmobranchs and bony fishes. That author erected several new taxa, many of which were later put into synonymy. A more recent list of fossil fish from this locality was published by Sach (2016). Pollerspöck and Unger (2022) published a re-evaluation of the new ray taxa erected by Probst (1877). Baltringen is the type locality of the Baltringen Formation, which consist of sands with silt lenses (Heimann et al., 2009; Heckeberg et al., 2010). This formation was deposited in a tide-influenced subtidal environment (Heckeberg et al., 2010) and has been assigned to the Mammal Zone MN 4a (Sach, 2016). The presence of Sirenia (*Metaxytherium* sp.) is indicative of sea grass.

## MATERIAL AND METHODS

The localities studied here were chosen based on the number of fossils of elasmobranchs (sharks and rays) available in the palaeontological collection of the Staatliches Museum für Naturkunde Stuttgart (SMNS, Stuttgart, Germany) as well as on the number of studies available in the literature detailing the fossil content of these deposits (Tables 1 and 2). For reconstructing the food chain, other fossils (vertebrates and invertebrates; Table 3) were also considered, as they were the potential prey of the ancient elasmobranchs.

We also included two instances of personal communications with collectors: the finding of a dactylus of a crab in Meßkirch-Rengetsweiler (pers. comm. Member of the “Mineralien- und Fossilienfreunde Ulm / Neu-Ulm e.V.” with the first author, 2007) and the presence of remnants of Cetacea and Sirenia in Meßkirch-Walbertsweiler (pers. comm. Elmar Unger with the first author, 2019). Animals comprising mainly soft tissues, such as worms, cephalopods, and even “soft-shelled” creatures like shrimps and prawns, rarely preserve in the fossil record, though their presence in the OMM can be inferred given their ubiquity in shallow marine environments globally. In Ursendorf, there had been different sand pits in the past and only remnants of them are readily visible today, apart from one active sand pit. So, it cannot be determined from which sand pit each fossil came, but all the outcrops show the same lithofacies. The same is the case for Baltringen. Probst (1871, 1877, 1878, 1879a, 1879b) collected at different sites in Baltringen, all with the same lithofacies. No reworked material from the underlying

**TABLE 1.** Fossiliferous localities studied herein, references for published elasmobranch data, and indication of whether fossils from paleontological collections were used to complement the study (see Material and Methods for more information).

Localities	References consulted	Collection material
Baltringen	Probst (1871, 1877, 1878, 1879a, 1879b), Barthelt et al. (1991), Pfeil (1991), Reinecke et al. (2011), Bor et al. (2012), Sach (2016)	x
Meßkirch-Rengetsweiler	Bieg et al. (2007), Heckeberg et al. (2010), Sach (2016), Hölftke et al. (2022)	x
Meßkirch-Walbertsweiler	Pfeil in Barthelt et al. (1991), Heckeberg et al. (2010), Sach (2016), Feichtinger et al. (2022)	
Ulm-Ermingen	Probst (1879b), Lutzeier (1922), Baier et al. (2004), Baier (2008), Hölftke (2009), Nebelsick et al. (2019)	x
Ursendorf	Miller (1875), Miller (1877), Probst (1879b), Schütze (1904), Hölftke (2009), Heckeberg et al. (2010), Hölftke et al. (2020)	x

**TABLE 2.** Elasmobranch taxa, their potential diet, and localities where they have been found. Taxa are listed alphabetically for ease of use. Symbols: ? = uncertain dietary item or unconfirmed occurrence of species in locality; cf. = uncertain identification; \* = identified as *Centrophorus cf. granulatus* in the literature (Müller and Henle, 1837); \*\* = identified as *Myliobatis canaliculatus* in the literature (Lutzeier, 1922); \*\*\* = identified as *Raja ornata* in the literature (Lutzeier, 1922).

Taxon	Tooth type	Potential prey items											Localities						
		Plankton invertebrates (undetermined)	Jellyfish.	Molluscs (undetermined)	Bivalves	Gastropods	Cephalopods	Crustaceans	Crabs	Other (non-crab) crustaceans	Elaasmobranchii	Osteichthyes	Marine reptiles and birds	Marine mammals	Baltringen	Meßkirch- Rengetsweiler	Meßkirch- Walbertsweiler	Ulm-Ermingen	Ursendorf
<i>Aetobatus arcuatus</i>	Grinding				x										x	x	x	x	x
<i>Aetobatus</i> sp.	Grinding																	x	
<i>Alopias exigua</i>	Tearing						x					x			x	x	x	x	x
<i>Araloselachus cuspidatus</i>	Tearing											x			x	cf.	x	x	x
<i>Centrophorus</i> sp.	Cutting-clutching											x			x	x	x	x*	x
<i>Centroscymnus</i> sp.	Cutting-clutching											x					x		
<i>Chaenogaleus affinis</i>	Cutting-clutching						x	x				x			x		x		
<i>Dasyatis probsti</i>	Crushing (female), Clutching (male)								x							?			
<i>Dasyatis rugosa</i>	Crushing (female), Clutching (male)									x					x		x		x
<i>Dasyatis strangulata</i>	Crushing (female), Clutching (male)								x						x				
<i>Dasyatis</i> sp.	Crushing (female), Clutching (male)								x								x	x	
Dasyatidae(?) gen. et sp. indet.	Crushing (female), Clutching (male)								x							x			x
<i>Echinorhinus pfauntschi</i>	Cutting-clutching										x	x					x		x
<i>Etmopterus</i> sp.	Cutting-clutching							x					x				x		
<i>Galeocerdo aduncus</i>	Cutting		x			x	x		x	x	x	x	x	x	x	x	x	x	x
<i>Ginglymostoma grandis</i>	Clutching						x	x							x				
<i>Gymnura</i> sp.	Clutching												x				x		
<i>Hemipristis serra</i>	Cutting-clutching						x							x	x	x	x	x	x
<i>Heptranchias</i> sp.	Cutting-clutching						x										x		
<i>Iago angustidens</i>	Clutching						x										x	x	
<i>Iago</i> sp.	Clutching						x										x		
<i>Isistius triangulus</i>	Cutting-clutching						x								x	cf.	x		
<i>Isurus oxyrinchus</i>	Tearing											x	x		x	x			x
<i>Isurus retroflexus</i>	Tearing (tending towards cutting)						x								x	x			x
<i>Keasius parvus</i>	Clutching	x															x		
<i>Megalolamna paradoxodon</i>	Tearing and grasping on anterior teeth; cutting on lateral ones													x			x		
<i>Megascyliorhinus miocaenicus</i>	Clutching						x	x									x		

TABLE 2 (continued).

Taxon	Tooth type	Potential prey items											Localities						
		Plankton	invertebrates (undetermined)	Jellyfish.	Molluscs (undetermined)	Bivalves	Gastropods	Cephalopods	Crustaceans	Crabs	Other (non-crab) crustaceans	Elasmobranchii	Osteichthyes	Marine reptiles and birds	Marine mammals	Baltringen	Meßkirch- Rengetsweiler	Meßkirch- Walbertsweiler	Ulm-Ermingen
<i>Mitsukurina lineata</i>	Tearing												x		x	x	x	x	x
<i>Mobula</i> sp.	Clutching	x															x		
<i>Myliobatis</i> sp.	Grinding					x	x		x						x	cf.	x	x**	
<i>Notorynchus primigenius</i>	Cutting-clutching						x	x	x		x	x		x	x	x	x	x	x
<i>Odontaspis molassica</i>	Tearing									x		x			x	x	x	x	x
<i>Otodus (Megaselachus)</i> sp.	Cutting										?	?		x	x	x	x	x	x
<i>Pachyscyllium dachiardii</i>	Clutching		x					x	x			x					x		x
<i>Pachyscyllium distans</i>	Clutching		x						x			x			x	x	x		x
? <i>Pachyscyllium</i> sp.	Clutching							x								x			
<i>Paragaleus tenuis</i>	Cutting-clutching									x					x		x		
<i>Parahepbranchias repens</i>	Cutting-clutching							x				x			x		x		
<i>Physogaleus contortus</i>	Clutching											x			x	x			
<i>Physogaleus singularis</i>	Cutting-clutching									x					x	x	x		x
<i>Physogaleus</i> sp.	?Cutting-clutching																		x
<i>Pristiophorus suevicus</i>	Clutching								x				x		x		x		
<i>Pseudocarcharias kamoharai(?)</i>	Tearing									x			x		x	x	x		x
<i>Raja</i> sp.	Crushing (female), Clutching (male)									x			x				x	x***	x
<i>Rhinobatos</i> sp.	Crushing				x								x				x		
<i>Rhinoptera stuederi</i>	Grinding				x										x		x	x	x
<i>Rhinoptera</i> sp.	Grinding																		x
<i>Rhizoprionodon fischeuri</i>	Cutting-clutching												x			x	x		x
<i>Rhizoprionodon</i> sp.	Cutting-clutching												x						x
<i>Rhynchobatus pristinus</i>	Crushing		x											x			x		
<i>Rolfodon bracheri</i>	Clutching										x	x						x	
<i>Scyliorhinus fossilis</i>	Clutching									x	x							x	
<i>Scyliorhinus</i> sp.	Clutching									x	x						x	x	
<i>Sphyrna integra</i>	Cutting-clutching												x				x		
<i>Sphyrna laevisima</i>	Cutting-clutching									x					x				
<i>Sphyrna</i> sp.	Cutting-clutching																		x

TABLE 2 (continued).

Taxon	Tooth type	Potential prey items											Localities							
		Plankton	invertebrates (undetermined)	Jellyfish.	Molluscs (undetermined)	Bivalves	Gastropods	Cephalopods	Crustaceans	Crabs	Other (non-crab) crustaceans	Elasmobranchii	Osteichthyes	Marine reptiles and birds	Marine mammals	Baltringen	Meßkirch-Rengetsweiler	Meßkirch-Walbertweiler	Ulm-Ermingen	Ursendorf
<i>Squaliolus</i> sp.	Cutting-clutching							x				x						x		
<i>Squalus</i> sp.	Cutting											x							x	
<i>Squatina</i> sp.	Clutching											x			x	x	x	x	x	x
<i>Taeniurops cavernosus</i>	Crushing (female), Clutching (male)					x				x	x	x			x		x			x
? <i>Triakis</i> sp.	Clutching	x										x					x			

Jurassic or Lower Freshwater Molasse sediments—as evidenced by the very different faunas and preservation—were found in the present study; furthermore, there are no mentions of reworked fossils in the literature.

### Tooth Morphology and Diet

We focused on the fossil teeth of elasmobranchs as a proxy for establishing the diet of these species. As a first step, we used the actualistic approach described by Rasser et al. (2019), which is based on comparisons with ecological data of living congeners. When possible, this was done on the species level, otherwise it was done on the genus-level. The data on recent species was extracted from specialized literature, mostly Ebert (2003), Compagno et al. (2005), Ebert et al. (2021), and Froese and Pauly (2019). More specific works were also used and are highlighted in the species' entries below when pertinent. Special attention was paid to the work of Cortés (1999), which provides precise proportions of the different prey items that make up the diets of the sharks, thus enabling us to determine whether a given species has a favored food item (referred to as “staple food” herein). In extant sharks, a dietary shift during ontogeny can often be observed (e.g., of Tricas and McCosker 1984; Tricas, 1985; Powter et al., 2010; Goodman et al., 2022). Based on comparisons with modern shark teeth as well as the size and morphology of the OMM teeth used herein, they were probably all from adult specimens, so the reconstructed trophic relationships presented here pertains to adult specimens.

Tooth morphology provides clues to the diet of extinct taxa, as tooth shape strongly correlates with diet in extant shark species (Moss, 1977; Cappetta, 1986, 2012; Powter et al., 2010; Pollerspöck and

Straube, 2019; Straube and Pollerspöck, 2020; Bazzi et al., 2021; Goodman et al., 2022). In the works of Cappetta (1986, 2012), elasmobranch teeth were classified into eight dental types according to their morphology, each corresponding to a type of trophic adaptation: 1) clutching; 2) tearing; 3) cutting (with the subtypes “*sensu stricto* cutting” and “cutting-clutching”); 4) crushing; 5) grinding; 6) clutching-grinding; 7) cutting-grinding; 8) crushing-grinding. Out of these eight dental types, five are known from the OMM deposits named above (1, 2, 3, 4, 5; type 3 includes both subtypes) (Figure 3). However, contrary opinions concerning the role of tooth shape can be found in the literature; e.g., the study of Whitenack and Motta (2010) concluded that shark tooth morphology is a poor predictor of trophic level. There is definitively a dietary overlap between, for example, sharks with “tearing-type” dentition (e.g., *Carcharias*, *Mitsukurina* and *Pseudocarcharias*) and ones with “cutting-type” dentition (e.g., *Galeocerdo*); both feed on bony fishes, but *Galeocerdo* also takes marine mammals, reptiles, and birds. Animals belonging to the ray families Myliobatidae and Rhinopteridae have teeth adapted for “grinding” hard-shelled invertebrates. According to the works of Tricas and McCosker (1984) as well as Tricas (1985), Great White sharks (*Carcharodon carcharias*) with a total length of < 3 m feed mostly on fishes and therefore, they have narrow tooth shape for grasping; when the sharks become larger, the teeth broaden at the base and achieve the typical triangular serrated shape, which is suitable for preying on marine mammals. Therefore, tooth morphology is not an unequivocal method for a detailed prey determination of living or fossil taxa, but it can be used to provide valuable data regarding a species' dietary spectrum. The teeth were classified accord-



TABLE 3. Marine non-elasmobranch taxa.

Ulm-Ermingen	Meßkirch- Rengetsweiler	Meßkirch- Walbertsweiler	Ursendorf	Baltringen
<b>Sponges</b>	<b>Foraminifera:</b>	<b>Foraminifera</b>	<b>Foraminifera</b>	<b>Foraminifera</b>
<b>Worms:</b>	<i>Elphidium</i> sp.	<b>Bivalves:</b>	<b>Sponges:</b>	<b>Bivalves:</b>
<i>Serpula</i>	<b>Sponges:</b>	Ostreidae	<i>Cliona</i>	Arcidae
<b>Bivalves:</b>	<i>Cliona</i>	Pectinidae	<b>Corals:</b>	Cardiidae
Arcidae	<b>Bivalves:</b>	<b>Crustacea:</b>	Ballanophyllia	Mytilidae
Chamidae	Anomiidae	Ostracods	<b>Bivalves:</b>	Ostreidae
Cardiidae	Ostreidae	<i>“Callianassa”</i>	Anomiidae	Pectinidae
Carditidae	Pectinidae	<b>Bryozoans</b>	Carditidae	Pholadidae
Glycymerididae	Pholadidae	<b>Marine mammals:</b>	Corbulidae	Veneridae
Mytilidae	<b>Gastropods:</b>	Sirenia	Glycymerididae	<b>Gastropods:</b>
Ostreidae	Cerithiidae	Cetacea	Limidae	<i>Turritella</i>
Pectinidae	Conidae		Ostreidae	<b>Scaphopods:</b>
Pholadidae	<i>Ficus</i>		Pectinidae	? <i>Dentalium</i>
Veneridae	Trochidae		Pholadidae	<b>Crustacea:</b>
<b>Gastropods:</b>	<b>Scaphopods</b>		<b>Gastropods:</b>	Balanids
<i>Calyptrea</i>	<b>Crustacea:</b>		<i>Calyptrea</i>	<b>Bony fishes:</b>
Cerithiidae	Balanids		Conidae	Labridae
Fasciolaridae	Brachyura		Cypraeidae	Sparidae
Ficidae	<i>“Callianassa”</i>		Epitoniidae	<b>Reptiles:</b>
Fissurellidae	<b>Brachiopods:</b>		Fasciolaridae	<i>Trionyx</i>
Naticidae	<i>Terebratula</i>		Ficidae	<b>Marine mammals:</b>
Olividae	<b>Echinoidea:</b>		Mitridae	Sirenia
Turridae	Cidaroida		Naticidae	Cetacea (see Sach, 2016)
<i>Turritella</i>	Irregularia		Trochidae	
Xenophoridae	Bryozoan		<b>Scaphopods</b>	
<b>Scaphopods</b>	<b>Bony fishes:</b>		<b>Crustacea:</b>	
<b>Crustacea:</b>	Sparidae		Balanids	
Balanids	<b>Reptiles:</b>		Brachyura	
Bryozoan	Chelonioidea		<i>“Callianassa”</i>	
<b>Bony fishes:</b>	<b>Marine mammals:</b>		<b>Brachiopods:</b>	
Labridae	Sirenia		<i>Terebratula</i>	
Sparidae	cf. <i>Squalodelphis</i> sp.		<b>Crinoidea:</b>	
<b>Reptiles:</b>	Squalodontidae indet.		<i>Antedon</i>	
<i>Trionyx</i>	Odontoceti indet.		<b>Echinoidea:</b>	
<b>Marine mammals:</b>			<i>Psammechinus</i>	
<i>Schizodelphis</i>			<i>Stirechinus</i>	
			Cidaridae	
			<i>Amphiope</i>	
			<i>Fibularia</i>	
			<i>Scutella</i>	
			<i>Spatangus</i>	

TABLE 3 (continued).

Ulm-Ermingen	Meßkirch- Rengetsweiler	Meßkirch- Walbertsweiler	Ursendorf	Baltringen
			Bryozoans	
			Bony fishes:	
			Sparidae	
			Marine mammals:	
			Sirenia	

ing to the definitions and descriptions provided by Cappetta (2012, p. 16-23).

When available, isotope data were also considered (Kast et al., 2022; McCormack et al., 2022). McCormack et al. (2022), analysed Zn isotopes in fossil teeth of selected species (i.e., *Otodus (Megaselachus) chubutensis*, *Carcharodon hastalis*, *Araloselachus cuspidatus*, *Carcharias contortidens*, *Galeocerdo aduncus*, *Hemipristis serra*, *Mitsukurina lineata*, *Pseudocarcharias rigida*) from Walbertsweiler, one of the localities studied herein. They observed that relative  $\delta^{66}\text{Zn}$  values for tested taxa (e.g., *Carcharias* spp., *Galeocerdo* spp.) showed no statistical variation with geologic age and locality, indicating relatively stable trophic levels and ecological niches across time and space. For extinct OMM genera, where the closest living taxa are uncertain, tooth morphology alone was used as a guide to the preferred prey type. As explained by Cappetta (2012), similar dentition in recent and fossil forms—even without direct systematic relationship—is indicative of comparable feeding habits, diets and, to a lesser extent, similar modes of life. When more than one recent congener is known and dental morphology is invariant across various species (e.g., *Squatina*), a consensus on prey items had to be acquired. In some cases (e.g., Scyliorhinidae), the staple food of most extant species is unknown, so our interpretations are necessarily based on the few species for which the diet is known and as such, they need to be taken cautiously. For extinct genera (e.g., *Physogaleus*), we relied entirely on dental morphology, compared with that of allied recent species. Recent literature dealing with diet and stomach contents of sharks and rays which have fishes on their diet (e.g., Rasmussen, 2018 and references therein) suggest that these predators have no preferences for specific prey taxa, feeding on members of different families according to availability and size.

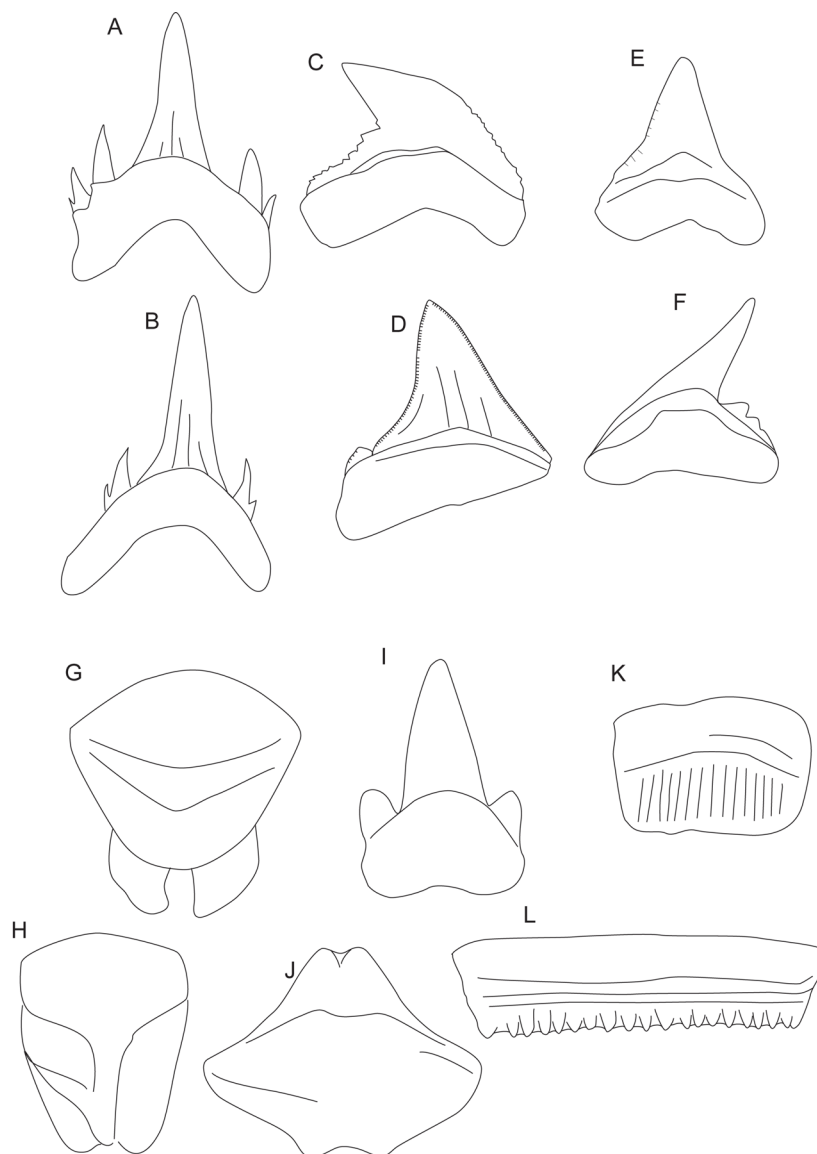
## RESULTS AND DISCUSSION

A full list of species found in the studied OMM deposits and their tooth types (sensu Cappetta, 2012) are given in Table 2. Some taxa do not match exactly one type: the two taxa with tearing-type dentition, *Carcharodon hastalis* (Agassiz, 1843) and *Isurus retroflexus* (Agassiz, 1843), display a tendency toward the cutting type due to widening of the lateral of the teeth (see also Cappetta, 2012, p. 18).

In the OMM, two large-toothed *Otodus* species are known: *O. (Megaselachus) chubutensis* (Ameghino, 1901), which had teeth with lateral cusplets, and *O. (Megaselachus) megalodon* (Agassiz, 1843), which had teeth without lateral cusplets. Because there are transitional forms between both taxa, which have only weakly pronounced lateral cusplets, an exact determination is often problematic (Kent, 1994; Perez et al., 2019; Feichtinger and Pollerspöck, 2021; Pollerspöck et al., 2022). Concerning the diet reconstruction, the presence or absence of lateral cusplets on this tooth type is negligible. Because there is not enough well-preserved *Otodus*-material to separate them according to the presence/absence of lateral cusplets, the *Otodus*-teeth here are only determined on subgenus level. The name *O. chubutensis* is often used for Early Miocene “megalodon-like teeth” with lateral cusplets, whereas typical *megalodon* adult teeth have no lateral cusplets (Kent 1994; Applegate and Espinosa-Arrubarrena, 1996; Pollerspöck et al., 2022).

A full list of the elasmobranch species known from the OMM can be found in the Appendix, with detailed description of the palaeoecology of each species and comments on their probable diet and trophic level. The results below are a summary of that information focusing on the more important points and constructing a bigger picture for each studied site.

Table 2 summarizes the prey items that have thus been reconstructed for each elasmobranch



**FIGURE 3.** **A.** Tearing type [*Odontaspis molassica* (Probst, 1878)]. Tooth height: c. 9.8 mm. Locality: Messkirch-Walbertsweiler. Redrawn after Pfeil (1991, pl. 2, fig. 2). **B.** Tearing type [*Carcharias contortidens* (Agassiz, 1843)]. Tooth height: c. 17.9 mm. Locality: Messkirch-Walbertsweiler. Redrawn after Pfeil (1991, pl. 2, fig. 3, named here as “*Synodontaspis acutissima*”). **C.** Cutting type - sensu stricto cutting subtype [*Galeocerdo aduncus* (Agassiz, 1843)]. Tooth width: c. 14.2 mm. Locality: Messkirch-Walbertsweiler. Redrawn after Pfeil (1991, pl. 3, fig. 16). **D.** Cutting type - sensu stricto cutting subtype [*Otodus (Megaselachus) chubutensis* (Ameghino, 1901)]. Tooth height: c. 65 mm. Locality: Messkirch-Walbertsweiler. Redrawn after Pfeil (1991, pl. 2, fig. 10, named here as “*Procarcharodon megalodon*”). **E.** Cutting type – cutting-clutching subtype [*Carcharhinus similis* (Probst, 1878)]. Tooth height: c. 12.9 mm. Locality: Baltringen. Redrawn after Probst (1878, pl. 1, fig. 19). Size according to Reinecke et al. (2011, Text-Fig. 21). **F.** Cutting type – cutting-clutching subtype [*Paragaleus tenuis* (Probst, 1878)]. Tooth height: c. 4 mm. Locality: Messkirch-Walbertsweiler. Redrawn after Pfeil (1991, pl. 3, fig. 8). **G.** Crushing type [*Dasyatis rugosa* (Probst, 1877)]. Tooth height: c. 3 mm. Locality: Messkirch-Walbertsweiler. Redrawn after Pfeil (1991, pl. 4, fig. 9). **H.** Crushing type [*Rynchobatus pristinus* (Probst, 1877)]. Tooth height: c. 4 mm. Locality: Baltringen. Redrawn after Probst (1877, pl. 1, fig. 19). **I.** Clutching type [*Pachyscyllium dachiardii* (Lawley, 1876)]. Tooth height c. 6 mm. Locality: Ursendorf. Redrawn after Höltke et al. (2020, pl. 7, fig. 1). **J.** Clutching type [*Ginglymostoma delfortriei* Daimeries, 1889)]. Tooth width. c. 7.6 mm. Locality: Baltringen. Redrawn after Pfeil [1991, pl. 2, fig. 1 named here as “*Ginglymostoma grandis*”). **K.** Grinding type [*Aeobatus arcuatus* (Agassiz, 1843)]. Tooth width. C. 14 mm. Locality: Ursendorf. Redrawn after Höltke et al. (2020, pl. 9, fig. 8). **L.** Grinding type [*Rhinoptera cf. studeri* (Agassiz, 1843)]. Tooth width: c. 23 mm. Locality: Ursendorf. Redrawn after Höltke et al. (2020, pl. 9, fig. 11).

species including the tooth type. In Table 3, the other occurring taxa were listed. Figure 4 shows a generalized food chain with all the taxa that are known from the five OMM localities, with special emphasis on the sharks and rays. According to the analysis of Höltke et al. (2022b), all the localities studied here have a similar shark and ray fauna, although there are still a few differences in the faunal composition of the single deposits. Figure 5, reproduced from Höltke et al. (2020; 2022b), shows the cluster analysis of the similarity in elasmobranch faunas across OMM deposits in Baden-Württemberg in comparison to the ones outside of Baden-Württemberg. The reasons for the clusters were the palaeogeographic and palaeoenvironmental settings (Höltke et al. 2020), but biases due to differing collection effort might have influenced the analysis to some extent (see discussion in Höltke et al. 2020; 2022b). Each of the five deposits is discussed below on its own, and a summary is presented afterwards.

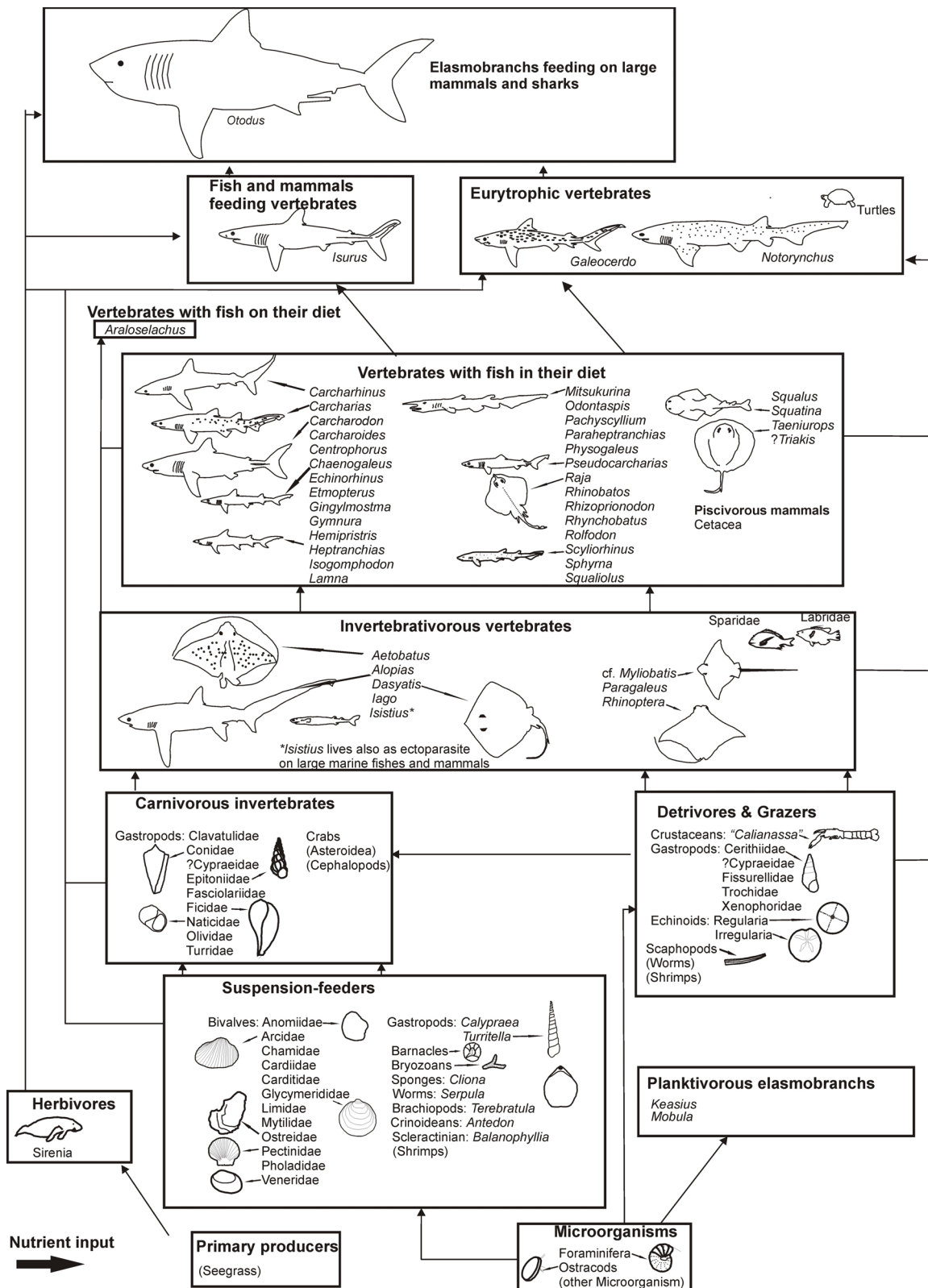
### Fossil Assemblages and Food Chains

**Ulm-Ermingen (early Ottnangian).** The mass-occurring *Turritella* is a suspension feeder (Höltke 2009), alongside bivalves (Arcidae, Chamidae, Cardiidae, Carditidae, Glycymerididae, Mytilidae, Ostreidae, Pectinidae, Pholadidae, Veneridae), other gastropods (*Calyptrea* Lamarck, 1799), bryozoans, barnacles, worms (*Serpula* Linnaeus, 1758) and sponges. Grazers and detritivores were represented by gastropods (Fissurellidae, Cerithiidae, Xenophoridae) and scaphopods. Carnivorous gastropods were represented by Fasciolaridae, Ficidae, Naticidae, Olividae, and Turridae; the Naticidae, in particular, fed on *Turritella*, as shown by the occurrence of typical drill holes on the shells. A remarkable aspect of this deposit is the high number of preserved molluscan shells in comparison to the other four deposits. As it can be seen in Table 3, the locality Ursendorf (discussed below) has a similar number of molluscan taxa, but these are mostly only found as steinkerns. Two families of bony fishes (Labridae, Sparidae) are observed in Ermingen, typically feeding on shelled invertebrates. Omnivorous turtles (*Trionyx* sp.) were also present. Among the elasmobranchs, there are a few molluscivores, such as *Aetobatus arcuatus*, *Aetobatus* sp., *Rhinoptera studeri* and *R.* sp. (feeding on bivalves), *Myliobatis* sp. (gastropods and bivalves), *Iago angustidens* and *Alopias exigua* (cephalopods). *Myliobatis* sp. would also have fed on crustaceans, a diet shared with *Dasyatis* sp. and *Raja* sp. The latter probably also have fed on

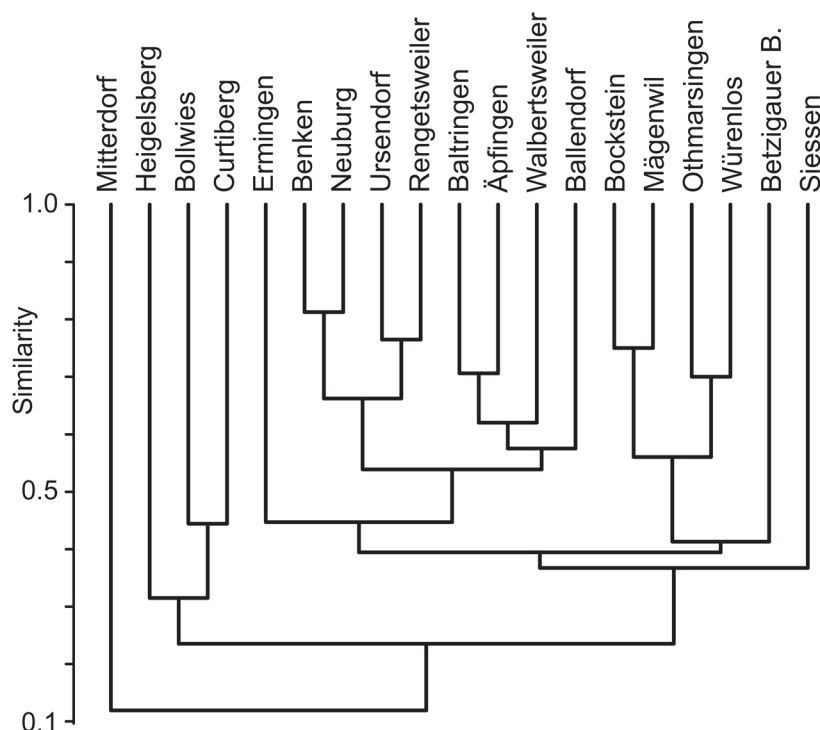
bony fishes. Most elasmobranchs were naturally piscivores, but several also preyed up on cephalopods (see Table 2). The top predators in the ancient sea of Ermingen were the two eurytrophic sharks *Galeocerdo aduncus* and *Notorynchus primigenius*, as well as *Carcharodon hastalis*. Lutzeier (1922) also mentioned *Otodus (Megaselachus) megalodon* from Ermingen, which would have been the topmost predator, as it probably fed on larger sharks and cetaceans. That author also mentioned the long-snouted dolphin *Schizodelphis* sp. from this locality, which would have fed on bony fishes.

Tooth types present (number of species in parenthesis; see also Table 2): Clutching (3); Crushing (female), Clutching (male) (2); Cutting (2); Cutting-Clutching (8, but see Table 2 and Appendix); Grinding (5); Tearing (7); Tearing tending towards cutting (1).

**Meßkirch-Rengetsweiler (early Ottnangian, Grobsandzug).** The lowest verified trophic level consists of foraminifera (including *Elphidium* de Montfort, 1808). The next level consists of different suspension-feeders: sponges (*Cliona* Grant, 1826), bryozoans, brachiopods (*Terebratula* Müller, 1776), bivalves (Anomiidae, Ostreidae, Pectinidae, Pholadidae), and balanids. The only identified herbivore was *Metaxytherium* sp. (Sirenia). Grazers were represented by gastropods (Trochoidea) and sea urchins (Cidaroida). Detritivores include gastropods (Cerithiidae), scaphopods, crustaceans (*Callianassa* sp.), and sea urchins (Irregularia). Other invertebrates include carnivorous gastropods (Conidae, *Ficus* sp.) and omnivorous crabs (Brachyura). Bony fishes (Sparidae) and elasmobranchs (*Aetobatus arcuatus* and cf. *Myliobatis* sp.) that fed on shelled molluscs were also present (the latter form may also have fed on crabs). *Alopias exigua* was more specialized for preying on cephalopods, and the same can also be said for *Isistius triangulus*, which probably also lived as an ectoparasite on larger fishes and marine mammals. Crustacean-feeding members of Dasyatidae were also present. As it can be seen in Table 2, other elasmobranchs were mostly piscivorous, with many also feeding on cephalopods and crustaceans. Piscivorous marine mammals (Odontoceti) were also present in this deposit. Sach (2016) named the following representatives of Odontoceti: Squalodontidae indet., cf. *Squalodelphis* sp., Odontoceti indet. Also, remnants of sea turtles (Chelonioidea) were found, which had different ways of life depending on species and genus. The top-predator in the ancient Rengetsweiler sea was



**FIGURE 4.** Generalized trophic interaction scheme of the five OMM deposits discussed in this paper. Some of the fish feeding taxa also feed on invertebrates. A definitive separation in exclusive fish and invertebrate feeders is often not possible. The same problem exists for members of the shark genus *Isistius*, which are ectoparasites of large marine animals but also feed on cephalopods.



**FIGURE 5.** Similarity analyses (cluster analyses) of the shark and ray fauna of the OMM deposits in Baden-Württemberg, Bavaria and Switzerland. Redrawn after Höltke et al. (2020; 2022b).

*Otodus (Megaselachus)* sp. In addition, other top predators included *Carcharodon hastalis*, *Galeocerdo aduncus*, and *Notorynchus primigenius*. Many land mammal remains were found in Rengetsweiler; their carrion was probably also eaten by *G. aduncus* and *N. primigenius*.

Tooth types present (number of species in parenthesis; see also Table 2): Clutching (5); Crushing (female), Clutching (male) (2); Cutting (2); Cutting-Clutching (7); Grinding (2); Tearing (6); Tearing tending towards cutting (2).

**Meßkirch-Walbertsweiler (early Ottnangian, Grobsandzug).** The lowest recorded trophic level consisted of foraminifera and ostracods. Herbivores consisted of Sirenia, and suspension-feeders were represented by bryozoans and bivalves (Pectinidae and Ostreidae). Detritus-feeder included crustaceans ("*Callianassa*" sp. and ostracods). Remnants of echinoids were also reported, nothing more is known about their affinities, and the same applies to the fossil teeth of bony fishes. As seen in Table 3, the fossil record concerning non-elasmobranchs, especially invertebrates, is comparably low in comparison to other localities, which may be simply due to collection bias or taphonomic reasons. Planktivorous elasmobranchs were represented by *Mobula* sp. and *Kea-*

*sius parvus*. Molluscivorous, durophagous elasmobranchs were represented by *Aetobatus arcuatus* and *Rhinoptera studeri*, as well as by *Myliobatis* sp. (which also preyed on crabs) and *Rhinobatos* sp. (which also preyed on crustaceans and small bony fishes). Other elasmobranchs were more specialized on cephalopods: *Alopias exigua*, *Rolfodon bracheri*, *Iago angustidens*, *Iago* sp., *Paragaleus tenuis*, and *Isistius triangulus* (the latter probably being also an ectoparasite of large fishes and marine mammals). Crustaceans were also hunted by *Dasyatis cavernosa*, *D. probsti*, *D. rugosa*, *D.* sp. and *Raja* sp. Several others fed on cephalopods, bony fishes, and crustaceans (Table 2). Since now, this deposit is the only one in the OMM of Germany and from which the shark species *Megalolamna paradoxodon* could be verified, a taxon already designated in 2016. Piscivorous marine mammals (Cetacea) were also present. Like in the previous locality, the top predator was *Otodus (Megaselachus)* sp., followed by *Carcharodon hastalis*, *Notorynchus primigenius*, and *Galeocerdo aduncus*, the latter being potentially a carrion-feeder as well, possibly including remnants of terrestrial mammals in its diet.

Tooth types present (number of species in parenthesis; see also Table 2): Clutching (13);

Crushing (2); Crushing (female), Clutching (male) (4); Cutting (3); Cutting-Clutching (17); Grinding (3); Tearing (8); Tearing and grasping on anterior teeth, cutting on lateral ones (1); Tearing tending towards cutting (2).

#### **Ursendorf (early Ottnangian, Grobsandzug).**

The lowest trophic level recorded for Ursendorf is occupied by foraminifera. As it can be seen in Table 3, a remarkable amount on non-elasmobranch-taxa, especially invertebrates, could be verified for this deposit. The following suspension feeders are known from Ursendorf: sponges (*Cliona*), solitary corals (*Ballanophyllia* Wood, 1844), brachiopods (*Terebratula*), bryozoans, balanids, crinoideans (*Antedon* de Fréminville, 1811), gastropods (*Calyptrea*) and bivalves (Anomiidae, Carditidae, Corbulidae, Glycymerididae, Limidae, Ostreidae, Pectinidae, and Pholadidae). The only strict herbivores were marine mammals (Sirenia). Detritivorous forms include crustaceans (“*Callianassa*” sp.), scaphopods, irregular sea urchins (*Amphiope* Agassiz, 1840, *Fibularia* Lamarck, 1816, *Scutella* Lamarck, 1816 and *Spatangus* Gray, 1825) and gastropods (Cypraeidae). Most species of Cypraeidae are herbivorous grazers, but some are carnivorous, specifically sponge eaters (Passamonti, 2015). In Figure 4 the Cypraeidae are thus mentioned both in the “Carnivore invertebrates” section and in the “Detritivores and Grazers” section, in both cases being marked by a question mark.

Grazers were represented by gastropods (Trochidae) and regular sea urchins (Cidaridae, *Psammechinus* L. Agassiz and Desor, 1846 and *Stirechinus* Desor, 1856). Carnivorous gastropods (Conidae, Epitoniidae, Fasciolaridae, Ficidae, Mitridae, and Naticidae) and crustaceans (crabs) were also present. The occurrence of members of the gastropod family Epitoniidae could also be an indication of the presence of sea anemones (Actinaria), because these animals are their preferred prey (Kilius, 1997). Species of bony fishes (Sparidae) and elasmobranchs (*Aetobatus arcuatus* and *Rhinoptera studei*) fed on the shelled invertebrate fauna. *Alopias exigua* fed on cephalopods and *Raja* sp. and *Dasyatis rugosa* on crustaceans. *Taeniurops cavernosus* fed on crustaceans and bony fishes. The following taxa fed next to bony fishes possibly also on small sharks, squid, and other invertebrates: *Pachyscyllium dachiardii* and *Pachyscyllium distans*. Most of the elasmobranchs were mainly piscivores, but some also featured cephalopods in their diet (Table 2). As other localities above, the top predator was *Otodus (Megasela-*

*chus*) sp., followed by *Carcharodon hastalis*, *Notorynchus primigenius* and *Galeocerdo aduncus*.

Tooth types present (number of species in parenthesis; see also Table 2): Clutching (3); Crushing (female), Clutching (male) (4); Cutting (2); Cutting-Clutching (7); Grinding (2); Tearing (8); Tearing tending towards cutting (2).

**Baltringen (middle Ottnangian).** The lowest trophic level recorded is represented by a distinctive Foraminifera fauna. Several suspension feeders are known from Baltringen: Balanids (*Balanus* Costa, 1778), bivalves (Arcidae, Cardiidae, Ostreidae, Mytilidae, Pectinidae, Pholadidae, and Veneridae) and gastropods (*Turritella*). The only detritus feeder that could be observed was the scaphopod *Dentalium?* sp. Other invertebrates are not known from these sediments. There are no signs of ecological reasons for the missing of other invertebrates so they may be simply not preserved in the fossil record. Herbivores were represented by Sirenia (*Metaxytherium* sp.). Molluscivorous animals were bony fishes (Labridae, Sparidae) and elasmobranchs (*Aetobatus arcuatus*, *Rhinoptera studei*, *Myliobatis* sp., the latter also likely fed on crabs). Cephalopod-eating specialists included: *Alopias exigua*, *Paragaleus tenuis* and, to some extent, *Isistius triangulus* (also reconstructed as a likely ectoparasite on large fishes or marine mammals). Other elasmobranchs featured bony fishes and sometimes cephalopods and/or crustaceans in their diets (Table 2). Piscivorous cetaceans as well as omnivorous turtles (*Trionyx* sp.) are also known from the ancient sea of Baltringen. Sach (2016) mentioned 14 different taxa of Cetacea for this locality. As for most of the investigated localities, the top predator was *Otodus (Megaselachus)* sp., followed by *Carcharodon hastalis*, *Notorynchus primigenius* and *Galeocerdo aduncus*. The latter two were also a likely carrion-feeder that used to feed on drifting carcasses of terrestrial mammals.

Tooth types present (number of species in parenthesis; see also Table 2): Clutching (5); Crushing (1); Crushing (female), Clutching (male) (3); Cutting (2); Cutting-Clutching (12); Grinding (3), Tearing (9); Tearing tending towards cutting (2).

## **CONCLUSION**

The composition of the elasmobranch fauna, and hence the trophic relationships they entail, is very similar across all six investigated localities. Taxa with fish on their diet dominated the elasmobranch fauna, which could be a sign of a more diverse bony fish fauna in the ancient OMM sea

that has not been preserved in the fossil record. Teeth of bony fishes are also not commonly found. That said, there are no recent research efforts focusing on the OMM Osteichthyes (the latest being Probst, 1882) despite the abundant fossil teeth.

In all localities, the apex predator was *Otodus* (*Megaselachus*) sp. The presence of this large shark was accompanied by the presence of marine mammals (Sirenia and/or Cetacea). These mammals probably were the preferred prey for those large sharks (Morgan, 1994; Purdy, 1996; Godfrey and Altman, 2005; Collareta et al., 2017a). Another aspect of note is the presence of the deep-water shark genera *Echinorhinus*, *Isistius*, *Mitsukurina*, and/or *Squaliolus* in the deposits studied herein, especially in Meßkirch-Walberstweiler. The OMM deposits mentioned in this paper were shallow water, featuring no sedimentological evidence of

deep-water habitats (furthermore, all the remaining components of the palaeofauna were inhabitants of the neritic realm). The sharks may have occasionally frequented shallower waters, recalling what is known for the recent *Echinorhinus cookei* and *Mitsukurina owstoni*.

All in all, the trophic data depict a fully marine, shallow-water ecosystem with a soft-bottom and partly covered with sea grass, like recent warm oceans such as the Mediterranean Sea. Further revision of the taxonomic affinities of other faunal elements that comprise the OMM assemblages will certainly improve the present reconstruction of this palaeoenvironment.

### ACKNOWLEDGEMENTS

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## APPENDIX

Below, we provide a list of all elasmobranch species found in the studied fossil sites, with information regarding their tooth morphology alongside palaeoecological data gleaned from the literature of both fossil and recent related forms. Taxonomic information is also provided when necessary.

The species are presented in systematic order (classification scheme follows Compagno et al., 2005, Cappetta, 2012), with genera and species within the same family ordered alphabetically for ease of use.

The trophic level (TL) data for the modern taxa were delineated by Cortés (1999) and also as available from Froese and Pauly (2019). For skates (*Raja* spp.), the work of Ebert and Bizzarro (2007) was consulted.

ORDER HEXANCHIFORMES De Buen, 1926  
Family Chlamydoselachidae Garman, 1884  
Genus *Rolfodon* Cappetta, Morrison and Adnet,  
2021  
*Rolfodon bracheri* (Pfeil, 1983)

Tooth type: Clutching.

This species was originally placed within the recent genus *Chlamydoselachus* Garman, 1884. However, Cappetta et al. (2021) transferred the species to the extinct genus *Rolfodon*. Regardless of that, both genera have similar trident-shaped teeth and *Chlamydoselachus* seems to be the obvious nearest recent relative of *Rolfodon*. There are two recent species of *Chlamydoselachus*: *C. anguineus* Garman, 1884, living at depths between 17 and 1520 m. (Ebert et al., 2021) and *C. africana* Ebert and Compagno, 2009, living from 300 to 1400 m depth (Ebert et al., 2021). Both these species have very similar teeth (see illustrations in Ebert et al., 2021: p. 97). For *C. anguineus*, Cortés (1999) defined a TL of 4.2 and listed cephalopods as its staple food. Ebert and Compagno (2009) and Ebert et al. (2021) listed members of the Scyliorhinidae and bony fishes as diet for both species. According to the latter authors, *C. anguineus* also feeds on midwater crustaceans.

Family Hexanchidae Gray, 1851  
Genus *Hepranchias* Rafinesque, 1810  
*Hepranchias* sp.

Tooth type: Cutting-clutching.

Only one living species is known in this genus, namely *H. perlo* (Bonnaterre, 1788), which lives from 0 to 1000 m depth (Ebert et al., 2021). Cortés (1999) assigned it a TL of 4.2, mentioning bony fishes and cephalopods as staple foods.

Genus *Parahepranchias* Pfeil, 1981  
*Parahepranchias repens* (Probst, 1879a)

Tooth type: Cutting-clutching.

The genus is extinct. Based on tooth morphology, the species is most similar to the recent *Hepranchias perlo* (see *Hepranchias* sp. above).

Genus *Notorynchus* Ayres, 1855  
*Notorynchus primigenius* Agassiz, 1835

Tooth type: Cutting-clutching.

The only extant relative is *N. cepedianus* (Péron, 1807), which very often feeds on other elasmobranchs such as *Myliobatis* spp., *Dasyatis* spp. and *Squalus* spp. (Ebert, 1991). Other prey items are bony fishes, squids (*Loligo* spp.), octopuses, crustaceans, gastropods, marine mammals (cetaceans and pinnipeds), agnathans and carrion (Ebert, 1991, 2003; Ebert et al., 2021). According to Cortés (1999), marine mammals and elasmobranchs are the staple food for this species, which has a TL of 4.7. This shark is the dominant elasmobranch in the nearshore marine environment, living from the surf line (less than 1 m depth) to at least 570 m depth, but mostly in less than 100 m depth (Ebert, 2003, Ebert et al., 2021).

ORDER SQUALIFORMES Goodrich, 1909  
Family Echinorhinidae Gill, 1862  
Genus *Echinorhinus* Blainville, 1816  
*Echinorhinus pfauntschi* Pfeil, 1983

Tooth type: Cutting-clutching.

There are two recent species of *Echinorhinus*: *E. cookei* Pietschmann, 1928 and *E. brucus* (Bonnaterre, 1788), living from 4 to 1100 m and from 10 to 1214 m depth (Ebert et al., 2021), respectively. The TL of *E. cookei* is circa  $4.4 \pm 0.76$  (Froese and Pauly, 2019) and that of *E. brucus* is 4.4 (Cortés, 1999). Both bony and cartilaginous fishes have been indicated as staple foods of the recent species (Cortés, 1999; Ebert et al., 2021).

Family Squalidae Blainville, 1816  
Genus *Squalus* Linnaeus, 1758  
*Squalus* sp.

Tooth type: Cutting.

Ebert et al. (2021) listed 34 recent *Squalus* species, the biology of some of which are poorly known. Most extant species include bony fishes and several kinds of invertebrates in their diet (Last et al., 2007; Ebert et al., 2021). Cortés (1999) assigned TL values between 3.9 and 4.2 to five *Squalus* species, all with bony fishes as staple food. The members of this genus can be found from 0 to more than 1500 m depth (Ebert et al., 2021).

Family Centrophoridae Bleeker, 1859  
Genus *Centrophorus* Müller and Henle, 1837  
*Centrophorus* sp.

Tooth type: Cutting-clutching.

The *Centrophorus* teeth from the OMM were sometimes identified as belonging to *Centrophorus* cf. *granulosus* (Bloch and Schneider, 1801) (Pfeil, 1991; Vialle et al., 2011; Pollerspöck and Beaury, 2014; Pollerspöck et al., 2022). *Centrophorus granulosus* is a recent species, which feeds mainly on bony fishes and cephalopods (Cortés, 1999), has a TL of 4.1 (Cortés, 1999), and lives in depths from 50 to 1500 m, mostly deeper than 600 m (Ebert et al., 2021).

Family Etmopteridae Fowler, 1934  
Genus *Etmopterus* Rafinesque, 1810a  
*Etmopterus* sp.

Tooth type: Cutting-clutching.

Ebert et al. (2021) listed 42 recent species of *Etmopterus*, the biology of most of which is poorly known. Cortés (1999) listed nine recent species, with TL values ranging from 3.8 to 4.2, which have bony fishes and cephalopods as their staple food. Representatives of this genus can be found from 0 to more than 2490 m depth (Ebert et al., 2021).

Family Somniosidae Jordan, 1888  
Genus *Centroscymnus* Barbosa Du Bocage and De Brito Capello, 1864  
*Centroscymnus* sp.

Tooth type: Cutting-clutching.

Two extant species are known: *C. coelolepis* Barbosa Du Bocage and De Brito Capello, 1864 (128 and 3675 m deep) and *C. owstoni* Garman, 1906 (150 to 1459 m deep) (Ebert et al., 2021). Both species live on or near the bottom (Ebert et al., 2021) and have diets composed of bony fishes and cephalopods, resulting in a TL of 4.2 (Cortés, 1999).

Family Dalatiidae Gray, 1851  
Genus *Isistius* Gill, 1865  
*Isistius triangulus* (Probst, 1879)

Tooth type: Cutting-clutching.

There are only two extant species within this genus: *I. brasiliensis* (Quoy and Gaimard, 1824) and *I. plutodus* Garrick and Springer, 1964. According to de Figueiredo Petean and de Carvalho (2018), members of this genus may not be good swimmers, given that they are ectoparasites of large fishes and cetaceans. Wounds made by *Isistius* spp. have been found on marlins, mackerels, tunas, sharks, rays, seals, whales, and dolphins (de Figueiredo Petean and de Carvalho, 2018). Strasburg (1963) also described squid retrieved from stomach contents and Cortés (1999) listed cephalopods as staple prey of *I. brasiliensis*. Extant *I. brasiliensis* has a TL of 4.3 (Cortés, 1999), whereas *I. plutodus* has a TL of  $4.2 \pm 0.4$  (Froese and Pauly, 2019). *Isistius* spp. live in the oceanic realm, from epipelagic to bathypelagic regions (Ebert et al., 2021). For details on the feeding apparatus of the recent *I. brasiliensis* see Shirai and Nakaya (1992).

*Squaliolus* sp.

Both recent species, *S. aliae* Teng, 1959 and *S. laticaudus* Smith and Radcliffe, 1912, feed on squids and bony fishes (Ebert et al., 2021); the former has a TL of  $4.4 \pm 0.57$  and the latter,  $4.2 \pm 0.73$  (Froese and Pauly, 2019). *S. aliae* lives from 0 to 2000 m deep and *S. laticaudus* from 10 to 750 m (Ebert et al., 2021).

ORDER PRISTIOPHORIFORMES Berg, 1958  
Family Pristiophoridae Bleeker, 1859  
Genus *Pristiophorus* Müller and Henle, 1837  
*Pristiophorus suevicus* Jaekel, 1890

Tooth type: Clutching.

There are seven recent species within this genus, some of which with unknown biology (Ebert et al., 2021). Those whose biology is known feed on small fishes and crustaceans (Ebert et al., 2021). The members of this genus can be subdivided into two groups by habitat (Ebert and Wilms, 2013): one of temperate waters and mostly coastal and continental shelf species, and another of tropical, deep-waters, continental and insular slope species, living near the bottom (maximum known depth of 630 m; Compagno et al., 2005). TL values for the seven recent species range from 3.8 to 4.2 (Froese and Pauly, 2019).

ORDER SQUATINIFORMES De Buen, 1926  
Family Squatinidae Bonaparte, 1838  
Genus *Squatina* Dumeril, 1806  
*Squatina* sp.

Tooth type: Clutching.

Ebert et al. (2021) listed 22 recent species of *Squatina*, the biology of some of which are poorly known. All the species with better known biology have bony fishes as their staple food, with TL values ranging from 4.0 to 4.2 (for six of the living species; Cortés, 1999). *Squatina* spp. live on or near the bottom, from shallow waters to a depth of 1290 m (Ebert et al., 2021).

ORDER ORECTOLOBIFORMES Applegate, 1974  
Family Ginglymostomatidae Gill, 1862  
Genus *Ginglymostoma* Müller and Henle, 1837  
*Ginglymostoma delfortriei* Daimeries, 1889

Tooth type: Clutching.

*Ginglymostoma cirratum* (Bonnaterre, 1788) is the only recent species known, living between 0 and 130 m depth, but mostly at depths shallower than 40 m (Ebert et al., 2021). Its staple foods are crustaceans, bony fishes and cephalopods, and its TL value is 3.8 (Cortés, 1999). For details on the feeding apparatus of the recent *Ginglymostoma cirratum* see Motta et al. (2008).

ORDER LAMNIFORMES Berg, 1937  
Family Odontaspidae Müller and Henle, 1839  
Genus *Araloselachus* Glikman 1964  
*Araloselachus cuspidatus* (Agassiz, 1843)

Tooth type: Tearing.

The genus is extinct. The teeth present a general odontaspidae morphology and can be found nearly worldwide in neritic Oligocene and Miocene sediments. The genus affiliation of this species is under discussion (see Hovestadt, 2020). Based on  $\delta^{66}\text{Zn}$  isotopes from teeth of the OMM of Rengetzweiler and Walbertzweiler, McCormack et al. (2022) found out that this species was placed much higher in the food pyramid than the other piscivore taxa, together with *Carcharias*, *Pseudocarcharias*, *Hemipristris*, *Mitsukurina* and also *Carcharodon* (see also their fig. 2). That conclusion is also supported by the more robust teeth of *A. cuspidatus*. Furthermore, according to McCormack et al. (2022), *A. cuspidatus* had a higher trophic level than *Hemipristris* and *Carcharodon* from the studied OMM deposits, which would mean that *A. cuspidatus* hunted fishes that had a higher position in the trophic chain.

Genus *Carcharoides* Ameghino, 1901  
*Carcharoides catticus* (Philippi, 1846)

Tooth type: Tearing.

The genus is extinct. Teeth of *C. catticus* are found in neritic sediments and have an odontaspidae morphology, being also similar to those of extant *Triaenodon obsesus* (Rüppel, 1837) (family

Carcharhinidae). Because of this similarity, Purdy et al. (2001) placed *Carcharoides* in synonymy with *T. obsesus*, but Ward and Bonavia (2001) later showed that they are different taxa. In spite of the similar tooth shape suggests that *C. catticus* had a similar diet to *T. obsesus*, which consists of bony fish and squids (Cortés, 1999; Ebert et al., 2021).

Genus *Odontaspis* Agassiz, 1838  
*Odontaspis molassica* (Probst, 1879a)

Tooth type: Tearing.

As already mentioned, there are two recent species of *Odontaspis*, *O. noronhai* and *O. ferox*; the teeth of the latter are most similar to *O. molassica* (Bass et al., 1975; Pfeil, 1991). According to Pfeil (1991), *O. molassica* is the ancestor of *O. ferox* (Risso, 1810). The latter species feeds on small bony fishes, including rockfish, as well as squid and shrimp, living between 10 and 1015 m depth (Ebert et al., 2021) and having a TL value of  $4.2 \pm 0.56$  (Froese and Pauly, 2019). *Odontaspis ferox* has a cosmopolitan distribution across warm-temperate and tropical waters, and although it is essentially demersal, it has also been captured pelagically in the mid-ocean (Fergusson et al., 2008).

Family Carchariidae Müller and Henle, 1838  
Genus *Carcharias* Rafinesque, 1810  
*Carcharias contortidens* (Agassiz, 1843)

Tooth type: Tearing.

The only recent species is *C. taurus* Rafinesque, 1810, which has very similar teeth to the above fossil taxon (Reinecke et al., 2011). It feeds mainly on bony fishes and elasmobranchs, including members of the families Carcharhinidae, Dasyatidae, Hexanchidae, Rajidae, and Rhinobatidae (Cortés, 1999; Smale, 2005; Lucifora et al., 2009). It lives near the bottom from 1 to 232 m depth, but mostly between 15 to 25 m (Ebert et al., 2021). TL for recent *C. taurus* is 4.4 (Cortés, 1999).

Family Pseudocarchariidae Taylor, Compagno and Struhsaker, 1983

Genus *Pseudocarcharias* Cadenat, 1963  
*Pseudocarcharias kamoharai* (Matsubara, 1936)

Tooth type: Tearing.

The OMM fossils have been assigned to *P. kamoharai*, which is an extant species. It lives offshore (occasionally closer to the shore), from the surface down to at least 590 m depth (Compagno, 1984; Nelson, 2006; Ebert et al., 2021). It feeds on small pelagic bony fishes, squids as well as shrimps (Compagno 1984; Estupiñán-Montaño



and Galván-Magaña 2021) and has a TL value of  $4.2 \pm 0.60$  (Froese and Pauly, 2019).

Family Mitsukurinidae Jordan, 1898  
Genus *Mitsukurina* Jordan, 1898  
*Mitsukurina lineata* (Probst, 1879)

Tooth type: Tearing.

The only living species is *M. owstoni* Jordan, 1898, which feeds primarily on bony fishes (Yano et al., 2007), having a TL of  $4.1 \pm 0.62$  (Froese and Pauly, 2019). This species lives mostly offshore, from 100 to 1300 m depth, rarely approaching the surface (Compagno, 1984; Yano et al., 2007; Ebert et al., 2021). According to Ebert (2003), *M. owstoni* appears to forage away from the bottom and may in fact occupy more of a midwater habitat than generally assumed.

Family Alopiidae Bonaparte, 1838  
Genus *Alopias* Rafinesque 1810  
*Alopias exigua* (Probst, 1879)

Tooth type: Tearing.

Out of the three recent species of *Alopias* listed in Ebert et al. (2021), the teeth of *A. superciliosus* (Lowe, 1840) display the strongest similarity with those of *A. exigua* (Bigelow and Schroeder, 1948; Bass et al., 1975; Herman et al., 2004; Ebert et al., 2021). Cortés (1999) indicated cephalopods as the main food item of that species, followed by bony fishes, and established a TL of 4.2. *Alopias superciliosus* lives from close inshore to the open ocean, from the surface to 955 m depth, but mostly over 100 m depth (Compagno et al., 2005; Ebert et al., 2021).

Family Cetorhinidae Gill, 1862  
Genus *Keasius* Welton, 2013  
*Keasius parvus* (Leriche, 1908)

Tooth type: Clutching.

This is an extinct genus of basking sharks. Based on the morphology of teeth and gill rakers, the only recent relative taxon is *Cetorhinus maximus* (Gunnerus, 1765), a plankton feeder that lives on the continental shelf and slope (Compagno et al., 2005; Ebert et al., 2021). *Cetorhinus maximus* can dive down to 1264 m depth (Ebert et al., 2021). During summer time, basking sharks can be found near the surface, whereas in winter they move to deeper waters (Compagno et al., 2005). *Cetorhinus maximus* has a TL of 3.2 (Cortés, 1999).

Family Lamnidae Müller and Henle, 1838  
Genus *Carcharodon* Smith, 1838  
*Carcharodon hastalis* (Agassiz, 1843)

Tooth type: Tearing with tendency towards the cutting type.

According to Collareta et al. (2017b), adults of the extinct species *C. hastalis* were in large part piscivorous; they lived in tropical to temperate seas worldwide, probably on the inner shelf (Cappetta, 1987; Bor et al., 2012). The recent white shark *C. carcharias* feeds on bony and cartilaginous fishes as well as on marine mammals (Cortés, 1999; Ebert, 2003), having a TL of 4.5 (Cortés, 1999). If *C. hastalis* also fed on marine mammals can not be said with certainty.

Genus *Isurus* Rafinesque, 1810  
*Isurus oxyrinchus* Rafinesque, 1810

Tooth type: Tearing.

This is a living species that feeds on bony and cartilaginous fishes, having a TL of 4.3 (Cortés, 1999). Large specimens also feed on small cetaceans (Ebert et al., 2021). This species inhabits the open ocean and coastal waters, from the surface to 888 m depth (Ebert et al., 2021).

*Isurus retroflexus* (Agassiz, 1843)

Tooth type: Tearing with tendency towards the cutting type.

The genus level of this species is highly debated. A recent species with similar dental morphology is *I. paucus* Guitart-Manday, 1966, which feeds primarily on schooling fishes and pelagic cephalopods (Ebert, 2003), having a TL of 4.5 (Froese and Pauly, 2019). The blade-like teeth of *I. retroflexus*, it might also feed on marine mammals. *I. paucus* is an epipelagic species that can be found from the surface to 1752 m deep (Compagno 1984; Ebert 2003; Ebert et al., 2021).

Family Otodontidae Glikman, 1964  
Genus *Megalolamna* Shimada, Chandler, Lam, Tanaka and Ward, 2016  
*Megalolamna paradoxodon* Shimada, Chandler, Lam, Tanaka and Ward, 2016

Tooth type: Anterior teeth tearing or grasping type, lateral teeth cutting type (Shimada et al. 2016).

In 2016, Shimada et al. designated this new species and genus for teeth from the early Miocene (Aquitania–Burdigalian) of Japan, Peru and the USA (see Shimada et al. 2016: fig. 2). Pfeil (1991: 200, pl. 2, fig. 8) mentioned and illustrated a tooth from Messkirch-Walbertsweiler as *Lamna* sp. When comparing the illustration of “*Lamna* sp.” with the ones of *Megalolamna paradoxodon*, it became obvious that it belongs to the latter as per the tooth shape and inclination and position of the lateral cusplets. Shimada et al. (2016) assumed bony fishes as prey for this species.

Genus *Otodus* Agassiz, 1843  
 Subgenus *Megaselachus* Glikman, 1964  
*Otodus (Megaselachus)* sp.

Tooth type: Cutting.

Both the genus and the subgenus are extinct, but its species are thought to have inhabited the neritic realm of warm-temperate to tropical oceans worldwide, feeding on marine mammals (Purdy, 1996). Collareta et al. (2017a) proposed that *C. megalodon* was an apex predator whose trophic spectrum was still focused on small-sized baleen whales. They may also have fed on other sharks and rays, similar to recent *Carcharodon carcharias*. According to Kast et al. (2022) teeth of *Otodus (Megaselachus) megalodon* are characterized by a broad range of  $\delta^{15}\text{N}$  values, which could be explained by the individuals feeding across many prey types and different trophic levels. Also, according to those authors, teeth of *O. (Megaselachus) chubutensis* and *O. (Megaselachus) megalodon* display similar isotope signatures. In the OMM, *Otodus (Megaselachus)* sp. did likely feed at the highest trophic levels.

ORDER CARCHARHINIFORMES Compagno, 1977

Family Scyliorhinidae Gill, 1862

Genus *Pachyscyllium* Reinecke, Moths, Grant and Breitzkreuz, 2005

*Pachyscyllium dachiardii* (Lawley, 1876)

Tooth type: Clutching.

The genus is extinct. Based on odontological analogies, the diet of this species was similar to that of the extant members of Scyliorhinidae. Ebert (2003) listed small bony fish, small sharks, crabs, squid and other invertebrates as prey items for members of Scyliorhinidae. Jacobsen and Bennett (2013) proposed an average TL of 3.9 for scyliorhinids. Members of this family can be found from shallow waters to 825 m depth (Ebert and Fowler, 2014).

*Pachyscyllium distans* (Probst, 1879a)

The genus is extinct. See *P. dachiardii* above for details.

Genus *Scyliorhinus* Blainville, 1816  
*Scyliorhinus fossilis* (Leriche, 1927)

Tooth type: Clutching.

This genus contains different recent species, some with poorly-known biology (Compagno et al., 2005; Froese and Pauly, 2019). Cortés (1999) mentioned bony fishes, cephalopods and crustaceans as staple food for five of the extant species and gave a TL of 4.0 to four of them [3.6 to 5.

*canicula* (Linnaeus, 1758)]. Members of this demersal genus live between 1 and 825 m depth (Ebert et al., 2021).

*Scyliorhinus* sp.

See *S. fossilis* above.

Family Triakidae Gray, 1851

Genus *Iago* Compagno and Springer, 1971

*Iago angustidens* (Cappetta, 1973)

Tooth type: Clutching.

There are two recent species, namely, *Iago garricki* Fourmanoir, 1979 and *I. omanensis* (Norman, 1939) (Ebert et al., 2021), both of which forage on cephalopods (Ebert et al., 2021). Cortés (1999) assigned a TL of 4.1 to *I. omanensis*. *I. garricki* can be found from 250 to 477 m depth and *I. omanensis* from circa 90 m to possibly 2195 m depth (Ebert et al., 2021).

*Iago* sp.

See *I. angustidens* above.

Genus *Triakis* Müller and Henle, 1838

?*Triakis* sp.

Tooth type: Clutching.

There are two teeth from Meßkirch-Rengetsweller that possibly belong to *Triakis* (see Höltke et al., 2022). They show similarities to recent *T. scyllium* Müller and Henle, 1839 and *T. semifasciata* Girard, 1855 (Herman et al., 1988). Both these extant species feature bony fishes and invertebrates in their diet and live near the bottom in the neritic realm (Ebert et al., 2021).

Family Hemigaleidae Hasse, 1879

Genus *Chaenogaleus* Gill, 1862

*Chaenogaleus affinis* (Probst, 1879)

Tooth type: Cutting-clutching.

The only recent congener is *C. macrostoma* (Bleeker, 1852), which lives on continental and insular shelves down to 160 m depth (Compagno et al., 2005). Its biology is poorly known (Ebert et al., 2021), but *C. macrostoma* probably feeds on small fishes, cephalopods and crustaceans (Compagno, 1984). Froese and Pauly (2019) indicated a TL of  $4.2 \pm 0.57$  for *C. macrostoma*.

Genus *Hemipristis* Agassiz, 1843

*Hemipristis serra* Agassiz, 1843

Tooth type: Cutting-clutching.

The only recent congener is *H. elongata* (Klunzinger, 1871), which feeds on bony fishes and cephalopods and has a TL of 4.3 (Cortés, 1999). It lives on continental and insular shelves down to 132 m depth (Ebert et al., 2021). However, the Miocene *Hemipristis serra* had larger teeth than extant

*H. elongata*, which may suggest different prey items and, maybe, a slightly higher TL for the extinct species.

*Hemipristis* sp.

See *H. serra* above.

Genus *Paragaleus* Budker, 1935  
*Paragaleus tenuis* (Probst, 1878)

Tooth type: Cutting-clutching.

There are four extant species of *Paragaleus*, living in the neritic realm. They can be found down to a depth of 100 m (Compagno et al., 2005; Ebert et al., 2021). Only one species, *P. pectoralis* (Garman, 1906), has a known diet: it is a specialist feeder on cephalopods but may also take small fishes (Ebert et al., 2021). It has a TL of  $4.3 \pm 0.64$  (Froese and Pauly, 2019). The three other species as well as the extinct *P. tenuis* have similarly structured teeth (Probst, 1878, pl. 1, figs. 68-70; Herman et al., 1991, pl. 17 and 18; Pfeil, 1991, pl. 3, fig. 8; Ebert et al., pp. 499-500), hence equivalent feeding habits can be assumed.

Family Carcharhinidae Jordan and Evermann,  
1896

Genus *Carcharhinus* Blainville, 1816  
*Carcharhinus acuarius* (Probst, 1879)

Tooth type: Tearing.

The next recent congener is *Carcharhinus oxyrhynchus* (Müller and Henle, 1839), which feeds on small schooling fishes and has a TL of 4.5 (Ebert et al., 2021; Froese and Pauly, 2019). This recent species was previously the type species of the monotypic genus *Isogomphodon* Gill, 1862. Based on molecular genetics, da Silva Rodrigues-Filho et al. (2023) mentioned *Isogomphodon* as a synonym of *Carcharhinus*.

This species lives in turbid waters in estuaries, mangroves and river mouths, as well as over shallow banks, in depths between 4 and 40 m (Ebert et al., 2021).

*Carcharhinus priscus* (Agassiz, 1843)

Tooth type: Cutting-clutching.

A comparison of *C. priscus* teeth with the dentition of extant *Carcharhinus* spp. indicates a close morphological relationship with *C. limbatus* (Müller and Henle, 1841), *C. perezii* (Poey, 1876) and *C. brachyurus* (Günther, 1870) (Reinecke et al., 2011; Bor et al., 2012; Andrianavalona et al., 2015; Collareta et al., 2021). That said, the teeth from those three extant species differ in one or more features from *C. priscus* (Bor et al. 2012). According to this morphological affinity, it can be assumed that *C. priscus* had a similar diet and habits as the afore-

mentioned extant species. *Carcharhinus perezii* lives inshore, from the surface to 65 m depth, while *C. limbatus* and *C. brachyurus* live in- and offshore, from the surface to a depth of 100 m (Voigt and Weber, 2011). All these species feature bony fishes in their diet (Voigt and Weber, 2011). Cortés (1999) also mentioned cephalopods as a second component of the diet of *C. brachyurus* and *C. limbatus*, establishing a TL of 4.2 for them. For *C. perezii*, in turn, a TL of  $4.5 \pm 0.8$  has been proposed (Froese and Pauly, 2019).

*Carcharhinus similis* (Probst, 1978)

Tooth type: Cutting-clutching.

The teeth of *C. similis* display closer morphological affinities with those of the extant species *C. leucas* (Valenciennes, 1839) and *C. amboinensis* (Müller and Henle, 1839), both of which inhabit the neritic realm, from the surface to a depth of 150 m (Reinecke et al., 2011; Voigt and Weber, 2011). The diet of both these species is composed of bony and cartilaginous fishes, and both have a TL of 4.3 (Cortés 1999). Some authors (Cliff and Dudley, 1991a, 1991b; Tillett et al., 2014; Estupiñán-Montaño et al., 2017) provided further detail on the food items of these two species, which appear to include: *Aetobatus* spp., *Dasyatis* spp., *Carcharhinus* spp., *Carcharias* spp., *Isurus oxyrinchus*, *Mobula* spp., *Rhynchobatus* spp., *Rhizoprionodon* spp., *Sphyrna* spp., *Squatina* spp. and Squalidae for *C. leucas*; and Carcharhinidae, Dasyatidae, Gymnuridae, Myliobatidae, Rhinobatidae, Scyliorhinidae, Sphyrnidae and Squatinidae for *C. amboinensis*.

Genus *Physogaleus* Cappetta, 1980  
*Physogaleus contortus* (Gibbes, 1849)

Tooth type: Clutching.

The genus *Physogaleus* is extinct; that said, *P. contortus* might belong to the extant genus *Galeocerdo* J.P. Müller and Henle, 1837 (Kent, 1994; Purdy et al., 2001). We follow Reinecke et al. (2011) in assigning this extinct species to *Physogaleus*. In contrast to *Galeocerdo* teeth, the teeth of *P. contortus* have a weaker serration and a slenderer upper part of the crown (see also Bor et al., 2012). Another difference to *Galeocerdo* is the mesial cutting edge of the *P. contortus* teeth, which is slightly twisted in a lingual direction. The mentioned slenderer upper part of the crown in particular is most suitable for a diet more specialized on fish, and possibly cephalopods, in contrast to the omnivorous diet of *Galeocerdo*. The dental morphology of *P. contortus* matches the clutching type sensu Cappetta (2012) whereas the dentition of

*Galeocerdo* matches the cutting type. The Teeth of *P. contortus* can be found in neritic sediments (Reinecke et al., 2011).

*Physogaleus singularis* (Probst, 1878)

Tooth type: Cutting-clutching.

The generic allocation of this species is debated. Based on illustrations from Voigt and Weber (2011) and Ebert et al. (2021), teeth of the extant species of the *Carcharhinus sealei-dussumieri* group (White 2012) are structured in a similar way to those of *P. singularis*. That group also contains the recent species *C. coatesi* (Whitley, 1939) and *C. tjtjot* (Bleeker, 1852). They live in the shelf region, and their staple food is represented by bony fishes, followed by cephalopods (Cortés 1999; Ebert et al., 2021). According to its tooth shape, the lifestyle and diet of *P. singularis* was likely similar to those of the aforementioned recent species.

*Physogaleus* sp.

Tooth type: Cutting-clutching (?).

Baier et al. (2004) listed *Physogaleus* sp. for Ermingen, but without any illustration, so it is problematic to determine its diet. Considering what already observed for *Physogaleus* spp., at least bony fishes can be surmised.

Genus *Rhizoprionodon* Whitley, 1929

*Rhizoprionodon fischeuri* (Joleaud, 1912)

Tooth type: Cutting-clutching.

The teeth of recent *Rhizoprionodon* spp. are very similar to the fossil representatives (Springer, 1964; Reinecke et al., 2011). Cortés (1999) mentioned bony fishes as staple food for the five extant species, assigning them TL values ranging from 3.8 to 4.2. Members of this genus live in the shelf region as well as offshore, down to depths of 500 m (Ebert et al., 2021).

*Rhizoprionodon* sp.

See *R. fischeuri* above.

Family Galeocerdonidae Poey, 1875

Genus *Galeocerdo* Müller and Henle, 1837

*Galeocerdo aduncus* (Agassiz, 1843)

Tooth type: Cutting

The only extant congener is *G. cuvier* (Péron and Lesueur, 1822), an omnivorous opportunistic feeder that eats crabs, lobsters, horseshoe crabs, gastropods, cephalopods, jellyfish, bony fishes, other elasmobranchs, sea turtles, sea snakes, marine mammals, marine birds, and even carrion of terrestrial mammals (Schwartz, 2000; Ebert, 2003; Dicken et al., 2017; Estupiñán-Montaño et

al., 2017). Like in other elasmobranch taxa, diet of *G. cuvier* changes as the animal grows, shifting from bony fishes and cephalopods in juveniles to larger prey items as size increases (Ebert 2003). Large specimens mostly consume elasmobranchs, sea turtles, marine mammals, sea birds and crustaceans (Ebert 2003). The living tiger shark has a TL of 4.1 (Cortés, 1999), living from the intertidal zone to 1136 m depth, moving closer inshore at night but retreating into deeper waters offshore during daytime (Ebert, 2003; Ebert et al., 2021).

Family Sphyrnidae Gill, 1872

Genus *Sphyrna* Rafinesque, 1810

*Sphyrna integra* Probst, 1878

Tooth type: Cutting-clutching.

The teeth of *S. integra* are closest in morphology to those of the recent *S. lewini* (Griffith and Smith, 1834) and *S. media* Springer, 1940 (Bor et al., 2012). The diet of the latter is unknown, but it has been assigned a TL of  $4.0 \pm 0.4$  (Froese and Pauly, 2019; Ebert et al., 2021); the former mainly feeds on bony fishes, followed by squids, crustaceans and elasmobranchs (Estupiñán-Montaño et al. 2009, 2021; Bornatowski et al., 2014), and has a TL of  $4.1 \pm 0.5$  (Cortés, 1999; Froese and Pauly, 2019). Both species live on the continental shelf, but *S. lewini* can also be found on insular shelves and adjacent waters down to a depth of 1043 m or more (Ebert et al., 2021). Estupiñán-Montaño et al. (2021) mentioned a strong relation of *S. lewini* to coastal regions.

*Sphyrna laevissima* (Cope, 1867)

Tooth type: Cutting-clutching.

In light of tooth morphology, the recent species that is closest to *S. laevissima* is *S. zygaena* (Linnaeus, 1758). Because of such similarity, Purdy et al. (2001) placed *S. laevissima* in synonymy with *S. zygaena*, but Reinecke et al. (2011) demonstrated that these two taxa are indeed different. *Sphyrna zygaena* feeds mainly on cephalopods, followed by bony fishes, and has a TL of 4.2 (Cortés, 1999). It lives on coastal to offshore waters, from the surface to 200 m deep, possibly also down to 500 m deep (Ebert et al., 2021).

ORDER INCERTAE SEDIS

Family Megascyliorhinidae Pfeil, 1984

Genus *Megascyliorhinus* Cappetta and Ward 1977

*Megascyliorhinus miocaenicus* (Antunes and Jonet, 1970)

Tooth type: Clutching.

The genus as well as the family are extinct. A discussion about this species can be found in Man-

ganelli and Spadini (2019). The teeth show odontological analogies to the Scyliorhinidae. See *Pachyscyllium dachiardii* above for details.

ORDER RAJIFORMES Berg, 1940

Family Rhinidae Müller and Henle, 1841

Genus *Rhynchobatus* Müller and Henle, 1837

*Rhynchobatus pristinus* (Probst, 1877)

Tooth type: Crushing.

All eight extant species of *Rhynchobatus* live in shallow water down to 70 m depth and they all feature bony fishes and invertebrates in their diet (Froese and Pauly, 2019). Apart from one species with a TL of 4.5, all the others range from 3.4 to 3.6 in TL (Froese and Pauly, 2019).

Family Rhinobatidae Müller and Henle, 1837

Genus *Rhinobatos* Linck, 1790

*Rhinobatos* sp.

Tooth type: Crushing.

The recent representatives of *Rhinobatos* feed on molluscs and crustaceans but will also take small fish (Froese and Pauly, 2019). They live from coastal habitats to offshore regions, down to 350 m depth (Séret et al., 2016). The TL values of the 21 recent species of *Rhinobatos* range from 3.5 to 4.1 (Froese and Pauly, 2019).

Family Rajidae Blainville, 1816

Genus *Raja* Linnaeus, 1758

*Raja* sp.

Tooth type: Crushing (female), Clutching (male).

All recent *Raja* spp. feed on bony fishes and invertebrates (mostly benthic crustaceans), living on the bottom, from shallow waters down to 800 m depth (Last et al., 2016a). The 24 extant species have TL values between 3.3 and 4.0 (Froese and Pauly, 2019). Ebert and Bizzarro (2007) gave a mean TL value of 3.76 for members of the genus *Raja*.

ORDER MYLIOBATIFORMES Compagno, 1973

Family Aetobatidae Agassiz, 1858

Genus *Aetobatus* Blainville, 1816

*Aetobatus arcuatus* (Agassiz, 1843)

Tooth type: Grinding.

There are five extant species of *Aetobatus* with different diet habits, albeit all of them include bivalves (White and Last, 2016a). *Aetobatus* spp. can be between from 1 to 60 m depth (White and Last, 2016a). Four species have a TL of 3.6, but *A. narinari* (Euphrasen, 1790) has a TL of 4.2 (Froese and Pauly, 2019).

*Aetobatus* sp.

See *A. arcuatus* above.

Family Dasyatidae Jordan, 1888

Genus *Dasyatis* Rafinesque, 1810

*Dasyatis probsti* Cappetta, 1970

Toothy type: Crushing (female), clutching (male).

There is scarce information on the diet of the recent species of *Dasyatis*, though all of the, seem to feed on crustaceans (Ebert and Bizzarro, 2007). The 9 recent *Dasyatis* spp. have been associated to TL values comprised between 3.5 and 4.1 (Froese and Pauly, 2019).

*Dasyatis rugosa* Probst, 1877

See *D. probsti* above.

*Dasyatis strangulata* (Probst, 1877)

See *D. probsti* above.

*Dasyatis* sp.

See *D. probsti* above.

Genus *Taeniurops* Garman, 1913

*Taeniurops cavernosus* (Probst, 1877)

Tooth type: Crushing (female), Clutching (male).

The only recent congener, *T. meyeri* Müller and Henle, 1841, is a benthic organism living between 20 and 60 m depth (Froese and Pauly, 2019). It feeds on bottom fishes, bivalves, crabs and shrimp (Compagno et al., 1989; Froese and Pauly, 2019) and has a TL of 4.2 ±0.69 (Froese and Pauly, 2019).

Family Gymnuridae Fowler, 1934

Genus *Gymnura* van Hasselt, 1823

*Gymnura* sp.

Tooth type: Clutching.

Recent *Gymnura* spp. have different trophic habits, all of which include bony fishes (Yokota et al., 2016). Extant members of this genus live inshore, on the bottom down, to 15 m depth (Yokota et al., 2016), and have TL values ranging from 3.6 and 4.5 (Froese and Pauly, 2019).

Family Myliobatidae Bonaparte, 1835

Genus *Myliobatis* Cuvier, 1816

*Myliobatis* sp.

All the extant congeners feed on bivalves and gastropods, as well as on crabs (White and Last 2016c); the TL of the 12 recent species range from 3.2 to 3.6 (Froese and Pauly, 2019). Members of this genus can be found in coastal and offshore waters down to 420 m depth (White and Last, 2016c).

Family Rhinopterae Jordan and Evermann, 1896

Genus *Rhinoptera* Jordan and Evermann, 1896

*Rhinoptera studeri* Agassiz, 1843

Tooth type: Grinding.

Dietary data is only available for two extant species of *Rhinoptera*, *R. bonasus* (Mitchill, 1815) and *R. brasiliensis* Müller, 1836, both of which feed on molluscs (Myers et al., 2007; Last et al., 2016b). That said, Froese and Pauly (2019) assigned TL values to all seven extant species, ranging from 3.2 to 3.8. Members of *Rhinoptera* live in the benthopelagic zone in the open ocean as well as inshore on the continental shelf, down to a depth of 100 m (Last et al., 2016b).

*Rhinoptera* sp.

See *R. stuederi* above.

Family Mobulidae Gill, 1893

Genus *Mobula* Rafinesque, 1810b

*Mobula* sp.

Tooth type: Clutching.

All recent *Mobula* spp. feed on zooplankton and have a pelagic lifestyle in coastal and offshore areas (White and Last, 2016b). The 11 species of *Mobula* have been associated to TL values ranging between 3.1 and 3.9 (Froese and Pauly, 2019).

#### **OTHER TAXA**

Other marine taxa apart from sharks and rays are listed in Table 3. Remnants of non-marine taxa (birds, reptiles, and mammals) were also found in the deposits and probably came into the palaeoenvironment as carrion (they are not listed in Table 3, but see Table 2 for references).