

# Re-evaluation of the Lower Miocene (Burdigalian, Ottnangian) elasmobranch fauna (Elasmobranchii, Neoselachii) from Upper Austria (Allerding, near Schärding, Austria) with comments on the palaeogeographic distribution of the recorded squaliform sharks

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(with 9 figures and 2 tables)

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## Abstract

The newly collected shark and ray tooth fossils from the marine sediments of the Upper Marine Molasse close to Allerding (4.8 km SE of Schärding, Austria) allow for a review of the hitherto known diversity comprising a taxonomic update and the documentation of additional taxa. Besides ten taxa already known from the area, the following taxa were collected for the first time from the site: *Galeocерdo aduncus* AGASSIZ, 1835, *Rhizoprionodon* sp., *Hemipristis serra* AGASSIZ, 1835, *Apristurus* sp., *Pseudoapristurus nonstriatus* POLLERSPÖCK & STRAUBE, 2017, *Scyliorhinus* sp., *Keasius* sp., *Mitsukurina lineata* (PROBST, 1879), *Odontaspis molassica* PROBST, 1879, *Otodus (Megaselachus) chubutensis* (AMEGHINO, 1901), *Chlamydoselachus bracheri* PFEIL, 1983, Hexanchidae indet., *Parahepbranchias repens* (PROBST, 1879), *Notorynchus primigenius* (AGASSIZ, 1843), *Deania* sp., *Isistius triangulus* (PROBST, 1879), *Euprotomicrus* sp., *Etmopterus* sp., *Pristiophorus* sp., *Nanocetorhinus tuberculatus* UNDERWOOD & SCHLÖGL, 2013, *Raja gentili* JOLEAUD, 1912, Rajidae sp. indet., *Rhinobatos* sp., *Aetobatus arcuatus* (AGASSIZ, 1843), and *Dasyatis rugosa* (PROBST, 1877). Fossil teeth of *Euprotomicrus* represent the first fossil evidence of this taxon ever. Our results indicate a typical Miocene coastal shallow and continental shelf associated diversity. In addition, we reviewed the palaeogeographic distribution ranges of the squaliform genera listed herein to test, if we can identify the origin of specific squaliform genera.

**Keywords:** Chondrichthyes, Upper Marine Molasse, Central Paratethys, Ottnangian Formation, Neogene.

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## Zusammenfassung

Die neu aufgesammelten Hai- und Rochenzähne aus den marinen Sedimenten der Oberen Meeresmolasse von Allerding (4,8 km südöstlich von Schärding, Österreich) erlauben es, die bisher in der Literatur bekannte Artenliste zu aktualisieren und zu erweitern. Neben den bisher dokumentierten und beschriebenen zehn Haiarten konnten erstmals für diese Fundstelle folgende Taxa neu nachgewiesen werden: *Galeocерdo aduncus* AGASSIZ, 1835, *Rhizoprionodon* sp., *Hemipristis serra* AGASSIZ, 1835, *Apristurus* sp., *Pseudoapristurus nonstriatus* POLLERSPÖCK & STRAUBE, 2017, *Scyliorhinus* sp., *Keasius* sp., *Mitsukurina lineata* (PROBST, 1879), *Odontaspis molassica* PROBST, 1879, *Otodus (Megaselachus) chubutensis* (AMEGHINO, 1901), *Chlamydoselachus bracheri* PFEIL, 1983, Hexanchidae indet., *Paraheptracthias repens* (PROBST, 1879), *Notorynchus primigenius* (AGASSIZ, 1843), *Deania* sp., *Isistius triangulus* (PROBST, 1879), *Euprotomicrus* sp., *Etmopterus* sp., *Pristiophorus* sp., *Nanocetorhinus tuberculatus* UNDERWOOD & SCHLÖGL, 2013, *Raja gentili* JOLEAUD, 1912, Rajidae sp. indet., *Rhinobatos* sp., *Aetobatus arcuatus* (AGASSIZ, 1843), und *Dasyatis rugosa* (PROBST, 1877). *Euprotomicrus* wurde erstmals fossil nachgewiesen. Die Ergebnisse weisen auf eine typische miozäne küstennahe Flachwasser- bzw. Schelffauna mit Nähe zu Tiefseebereichen hin. Darüber hinaus wurde die paläogeographische Verbreitung der nachgewiesenen squaliformen Gattungen aktualisiert und überprüft, ob es anhand der aktuellen Datenlage möglich ist, den bisher angenommenen Ursprung der squaliformen Haie zu bestätigen.

**Schlüsselwörter:** Chondrichthyes, Obere Meeresmolasse, Zentrale Paratethys, Ottnangian-Formation, Neogen.

## Introduction

The fossils presented herein were collected from sediments of the lower marine Miocene of the Upper Marine Molasse located in South Eastern Bavaria (Passau) to Upper Austria (Schärding). These sediments overlie discordant on the crystalline part of the Bohemian Massif (RUPP *et al.* 2011). Already by the end of the 19<sup>th</sup> century, TAUSCH (1896) reported on multiple fossil remains of marine mammals and sharks from granite pits in the area around Schärding. SUESS (1891), STADLER (1916), and MARIAN (1926) reported on similar findings.

The aforementioned publications did not identify the collected fossils to species level and only little is known of the whereabouts of the reported fossils. Some of them are deposited in the Haus der Natur of natural history museum located in Salzburg (Austria), however. In the museum's geological collection, some fossil shark teeth collected in Allerding 1913 are deposited and assigned to the "Freiherr von Schwarz'schen Mineraliensammlung", which is the basis of the contemporary museum's collection (pers. comment. Dr. Anna BIENIOK, curator of geosciences). SCHULTZ (1972) was the first to document the partial mass accumulations of fish tooth fossils of both bony and cartilaginous fish systematically. This work plus amendments mentioned in SCHULTZ (2013) form the basis for the diversity known to date. In addition, several publications deal with the rich invertebrate fauna of the area (CARRIOL & SCHNEIDER 2008, 2016; BITNER & SCHNEIDER 2009; FRIELING *et al.* 2009; JÄGER & SCHNEIDER 2009; SCHNEIDER *et al.* 2009; HARZHAUSER *et al.* 2014; HYŽNÝ *et al.* 2015).

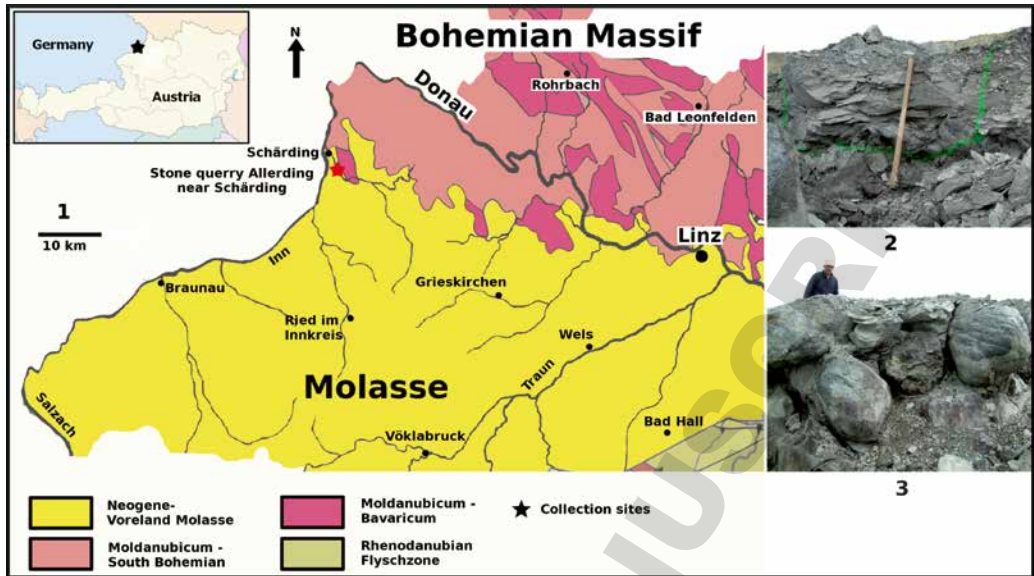


Fig. 1. Geological and geographical settings. 1: overview of the geological situation; 2: sampling area of Sample 3a/3c; 3: sampling area of Sample 2. Images show the globular granite blocks in the lower area and the fine, gray marl of the “Ottnanger Schlier”.

In this study, we review and report on the overall elasmobranch diversity of the Upper Marine Molasse close to Allerding including several first records of species in the area as well as the first fossil record of the enigmatic extant deep-sea shark *Euprotomicrus*.

### Geological settings

The analyzed material was collected from excavation sites in the granite pit of the Schärddinger Granit Industrie AG close to Allerding (Upper Austria, 4.8 km SE of Schärdding), which were only accessible for a short period of time due to the ongoing mining. HARZHAUSER *et al.* (2014) documents granite blocks of the former coastline, which served as a base for marine gastropods. Especially sediments between the almost globular granite blocks contain a diverse macrofauna, whereas the overlying marly clay is almost free of macrofossils (Figs 1.2, 1.3). The Allerding sediments representing the Upper Marine Molasse are bluish-grey mica-rich silts, which are characterized by being hardly sorted and clayey to sandy. They are attributed to the Ottnanger Schlier (Ottnangian-Formation, Lower Ottnangian, Burdigalian) (RUPP *et al.* 2011). The sampled sediments were mostly indistinctly deposited (5–10 cm depositions) or fully admixed.

The fully marine sediments of the Upper Marine Molasse are mica-rich and poorly sorted clayey sandy silts. When wet, the colour is dark gray. RUPP *et al.* (2011) estimate the chalk contents of these marly clays as 25%. Occurring minerals are quartz crystals,

calcite, dolomite, feldspar, and silicate deposits, which are dominating. Heavy minerals comprise garnet, rutile, and tourmaline excluding epidote and zoisite. The composition of the heavy minerals hints to a non-alpine origin of the marly clays, *i. e.*, an origin in the granite areas of the Bohemian Massif. These fully marine sediments of the upper Austrian Molasse basin are part of the Central Paratethys and ca. 17.6–18.5 mio years in age.

## Material and methods

In the years 2014 to 2017, we sampled five times at the northern part of the granite pit (48.419612° N, 13.481296° E) (Fig. 1.1). In this area of the pit, regular blasts were conducted for granite mining. The larger part of sampling was conducted in the overlaying marly clays of the granite blocks (ca. 0–50 cm, Figs 1.2, 1.3) and additionally from filling material between the blocks. In detail, the following samples were taken: sample 1 (S1, collected by Thomas GÜTHNER): mixed sample (ca. 200 kg) of sediments from the range limit of the granite blocks and the marly clays of the overlaying Ottnanger Schlier. Here microfossil-rich layers characterized by echinoderm fossils were preferred. Sample 2 (S2, collected by Jürgen POLLERSPÖCK): mixed sample from sediments collected from filling material in gaps between granite blocks (ca. 35 kg) as well as the overlaying layers of the Ottnanger Schlier (ca. 65 kg, Fig. 1.3).

Sample 3a/3c (S3a/3c, collected by Jürgen POLLERSPÖCK): sample collected from the layers of the Ottnanger Schlier (600 kg, Fig. 1.2) overlaying the granite blocks. Sample 3b (S3b, collected by Jürgen POLLERSPÖCK): sample taken from sediments filling gaps between granite blocks (20 kg).

The collected material (Table 1) was completely dried and thereafter wetted in water and a hydrogen peroxide solution (concentration 0.1 %–1 %). This was on average repeated two times until sediments were fully disaggregated. The residing material was washed through 1 mm and 0.3 mm mesh widths. Fossils were recovered using binoculars (Wild M3Z) and are listed in Table 1. Findings comprise 137 tooth fossils (partially broken) as well as 15 fossil dermal denticles. Fossils were further cleaned using a 2 % hydrogen peroxide solution and ultrasonic sound (MEC 300 VAP, Motor, Jewelry Cleaner). Sample S1 was washed out mechanically to reduce weight at the sampling location and thereafter filtered, dried, sieve fractionated and fossils extracted using binoculars (Zeiss Stemi 305). Recovered fossils were subsequently cleaned using ultrasonic sound, partially pre-cleaned with Rewoquat® surfactant. Tooth fossils ranging in size from 1.5 to 22.5 mm were photographed using a binocular camera (Leica IC80 HD, Software Leica Application Suite). Where appropriate, three to seven images were stacked using CombineZP (HADLEY 2010). GIMP2 (<https://www.gimp.org/>) was used to excise images and standardize a scale for the figures. Twelve smaller sized fossil teeth and denticles (<1 mm) were mounted on Scanning Electron Microscopy (SEM) stubs and prepared for SEM imaging using a Polaron E5100 SEM coating system. Subsequently, SEM images were taken using a LEO 1430 VP (Carl Zeiss, Jena).

Table 1. Fauna list of Allerding, Upper Austria, Otnangian, Upper Marine Molasse. Abbreviation column “private collector”: Haus der Natur Salzburg (HdN), Stefan HIERMANN (SH), Thomas GÜTHNER (TG), Wolfgang DANNINGER (WD). Numbers in brackets are the number of specimens studied in each collection.

Species	total this study (NHMW)	SCHULTZ 1972	private collector/ museums collections	Remarks, References, and Repository Numbers
<i>Galeocerdo aduncus</i> AGASSIZ, 1835			WD (1)	
<i>Rhizoprionodon</i> sp.		11	WD, TG (4) WD, SH (1)	SCHULTZ 2013 (p. 82)
<i>Carcharhinus priscus</i> (AGASSIZ, 1843)				
<i>Hemipristis serra</i> AGASSIZ, 1835				
<i>Apristurus</i> sp.	1			
<i>Pseudoapristurus nonstriatus</i> POLLERSPÖCK & STRAUBE, 2017	1			
<i>Scyliorhinus</i> sp.	3		TG (9)	
<i>Pachyscyllium distans</i> (PROBST, 1879)	1		NHM, WD	SCHULTZ 2013 (p. 94), NHMW 2011/0174/0002
<i>Anotodus retroflexus</i> (AGASSIZ, 1838)		1	WD, SH	SCHULTZ 2013 (p. 39)
<i>Keasius</i> sp.	1			
<i>Carcharodon hastalis</i> (AGASSIZ, 1843)		230	WD, SH	SCHULTZ 2013 (p. 45)
<i>Mitsukurina lineata</i> (PROBST, 1879)	4		WD, SH, TG (27)	
<i>Araloselachus cuspidatus</i> (AGASSIZ, 1843)		180	WD, SH	SCHULTZ 2013 (p. 64)
<i>Carcharias acutissimus</i> (AGASSIZ, 1843)		2690	WD, SH, TG (16)	SCHULTZ 2013 (p. 58)
<i>Odontaspis molassica</i> PROBST, 1879	10		WD	SMNS 96995-1, SMNS 96995-2, and SMNS 96995-3
<i>Otodus</i> ( <i>Megaselachus</i> ) <i>megalodon</i> (AGASSIZ, 1837)				see: <i>Otodus</i> ( <i>Megaselachus</i> ) <i>chubutensis</i> (AMEGHINO, 1901)
<i>Otodus</i> ( <i>Megaselachus</i> ) <i>chubutensis</i> (AMEGHINO, 1901)			SH, HdN, WD	SCHULTZ 2013 (p. 73) as <i>Otodus</i> ( <i>Megaselachus</i> ) <i>megalodon</i> (Agassiz, 1837)
Lamniformes indet.			SH	SCHULTZ 2013 (p. 37); MARIAN 1926 (pp. 15, 17)
<i>Chlamydoselachus bracheri</i> Pfeil, 1983	1			
Hexanchidae indet.			TG (1)	
<i>Parahexanchias repens</i> (PROBST, 1879)	1		TG (2)	

Species	total this study (NHMW)	SCHULTZ 1972	private collector/museums collections	Remarks, References, and Repository Numbers
<i>Notorynchus primigenius</i> (AGASSIZ, 1843)				
<i>Centrophorus</i> sp.	32		WD (1), SH (2) NHM, WD, TG (64)	SCHULTZ 2013 (p. 31), NHMW 2011/0174/0001, 2018/0309/0003 (Fig. 2.3), 2018/0309/0004 (Fig. 2.4), 2018/0309/0005 (Fig. 2.5), 2018/0309/0006
<i>Deania</i> sp.	5			
<i>Isistius triangulus</i> (PROBST, 1879)	12		WD, TG (19)	
<i>Euprotomicrus</i> sp.	8			
<i>Etmopterus</i> sp.	2		TG (1)	
<i>Pristiophorus</i> sp. oral	1		TG (2)	
<i>Pristiophorus</i> sp. rostral	3		WD, SH, TG (16)	
<i>Squatina subserata</i> (MÜNSTER, 1846)		28	WD	SCHULTZ 2013 (p. 33)
<i>Nanocetorhinus tuberculatus</i> UNDERWOOD & SCHLÖGL, 2013	1			
<i>Raja gentilli</i> JOLEAUD, 1912	5		WD, TG (10)	
Rajidae sp. indet.	1			
<i>Rhinobatos</i> sp.	1		TG (1)	
<i>Aetobatus arcuatus</i> (AGASSIZ, 1843)			SH, WD, TG (2)	
<i>Dasyatis rugosa</i> (PROBST 1877)	5		TG (12)	
Denticles	15		TG (1)	
Elasmobranchii indet.	38		TG (51)	
<b>Total:</b>	<b>152</b>	<b>3140</b>		



Further, two private collections (Wolfgang DANNINGER, Austria; Stefan HIERMANN, Austria), as well as the collection of the “Haus der Natur Salzburg” were reviewed regarding hitherto unknown species (Table 1).

For the identification of taxa, morphological characters described in CAPPETTA (2012) were used. Measurements were taken using the width and height of teeth at homologous landmark sites. Damaged teeth are subsequently marked with the symbol “+”.

All fossils analyzed and discussed herein are deposited in the Museum of Natural History Vienna (collection numbers NHMW 2018/0309/0001 to 2018/0309/0044) and in the State Museum of Natural History Stuttgart (only additional material of *Odontaspis molassica*, collection numbers SMNS 96995-1, SMNS 96995-2, and SMNS 96995-3).

### Palaeogeographic distribution

For preparing palaeogeographic distribution maps of the five collected fossil squaliform shark genera *Centrophorus*, *Deania*, *Isistius*, *Squaliolus* (replacing *Euprotopomicros*, which collection in this study represents the first fossil record of the genus), and *Etmopterus* appropriate literature was consulted using the bibliographic database [www.shark-references.com](http://www.shark-references.com) (POLLERSPÖCK & STRAUBE 2019), where synonyms were taken into account. The identified publications were checked for completeness using the database [www.fossilworks.org](http://www.fossilworks.org) as well as CAPPETTA (2012). Subsequently, the resulting literature was checked for further occurrences of the five genera (Table 2, Supplement Table S1). Based on the aforementioned information two distribution maps per genus were established, one for the Cretaceous/Paleogene and one for the Neogene distributions of taxa.

## Results

### Systematic palaeontology

Cohort Euselachii HAY, 1902

Subcohort Neoselachii COMPAGNO, 1977

Order Hexanchiformes DE BUEN, 1926

Family Chlamydoselachidae GARMAN, 1884

Genus *Chlamydoselachus* GARMAN, 1884

Type species: *Chlamydoselachus anguineus* GARMAN, 1884, type by monotypy.

***Chlamydoselachus bracheri* PFEIL, 1983**  
(Figs 2.1a, 2.1b)

- \* 1983 *Chlamydoselachus bracheri* – PFEIL: 84–99; figs 49–54.  
 1991 *Chlamydoselachus bracheri* – BARTHELT *et al.*: 198; pl. 1, fig. 1.  
 2001 *Chlamydoselachus* sp. indet. – TAKAKUWA *et al.*: 22–25; figs 4–7.  
 2004 *Chlamydoselachus bracheri* – GOTO *et al.*: 365–369; figs 13–15.  
 2006 *Chlamydoselachus bracheri* – TAKAKUWA: 28; figs 3-1, 4-1.  
 2007 *Chlamydoselachus bracheri* – BRACHER & UNGER: 15–16; pl. 1–2.  
 2012 *Chlamydoselachus bracheri* – CAPPETTA: 90. [name only]  
 2013 *Chlamydoselachus bracheri* – SCHULTZ: 21–22; pl. 8, figs 6a–d, 7a–d, 8a–d.

Material: single tooth fragment (NHMW 2018/0309/0001, Figs 2.1a, 2.1b).

Size: Height: +3.7 mm; Width: +1.1 mm.

Description: The fossil is a single cusp. Characteristic features of *C. bracheri* are distinct, the cusp is slightly curved sigmoid and display an apical turning. The mesial and distal cutting edge reaches to the basis of the crown with the crown only slightly pointing basal. Longitudinal and irregular enameloid folds on the mesial and distal sides are clearly developed and reaching up to two thirds of the crown's height. The crown is labially and lingually convex, making a cross-section at the basis almost circular. The root is missing.

Remarks: To date *C. bracheri* was documented from Paratethys deposits in several Austrian locations (SCHULTZ 2013) and a single locality in Germany (BARTHELT *et al.* 1991). Outside of Europe, the species was reported from the Miocene of Japan (TAKAKUWA *et al.* 2001; GOTO *et al.* 2004; TAKAKUWA *et al.* 2006).

Family Hexanchidae GRAY, 1851

Genus *Parahepbranchias* PFEIL, 1981

Type species: *Notidanus repens* PROBST, 1879, type by monotypy.

***Parahepbranchias repens* (PROBST, 1879)**  
(Figs 2.2a, 2.2b.)

- \* 1879 *Notidanus repens* n. sp. – PROBST: 163–166; pl. 3, figs 19–21, 22a.  
 1912 *Notidanus avenionensis* – JOLEAUD: 255–256; pl. 4, fig. 4.  
 1981 *Parahepbranchias repens* – PFEIL: 361.  
 1991 *Parahepbranchias repens* – BARTHELT *et al.*: 198; pl. 1, figs 4–5.  
 2007 *Parahepbranchias repens* – BRACHER & UNGER: 23–24; pl. 5, 5a.  
 2011 *Parahepbranchias repens* – VIALLE *et al.*: 243.  
 2012 *Parahepbranchias repens* – CAPPETTA: 99; fig. 87.  
 2013 *Parahepbranchias repens* – SCHULTZ: 23; pl. 9, figs 1a–c, 2a–c, 3a+b, 4a+b.

Material: single tooth fragment (NHMW 2018/0309/0002, ex collection GÜTHNER, Figs 2.2a–b).



Size: Height: +6.0 mm; Width: +2.5 mm.

Description: The fragment is a secondary or following main cusp of a lower jaw tooth, as distinctive rudimentary secondary cusps at the mesial side are present (BARTHELT *et al.* 1991: fig. 4). The slender cusp is sigmoid and upright. The mesial edge of the crown reaches to the tooth basis and merges with the typical small secondary cusps.

Remarks: *P. repens* is exclusively known from Miocene sediments of the Paratethys from Austria (SCHULTZ 2013), Germany (PROBST 1879; BARTHELT *et al.* 1991), Switzerland (JORDAN *et al.* 2011; GRAF *et al.* 2012; JOST *et al.* 2016) and France (VIALLE *et al.* 2011). The presence of secondary cusps in lower teeth is characteristic for the genus *Parahepbranchias* and separates it from its assumed sister taxon *Hepbranchias*.

Order Squaliformes COMPAGNO, 1973

Family Centrophoridae BLEEKER, 1859

Genus *Centrophorus* MÜLLER & HENLE, 1837

Type species: *Squalus granulosus* BLOCH & SCHNEIDER, 1801, type by monotypy.

***Centrophorus* sp.**

(Figs 2.3a, 2.3b, 2.4a, 2.4b, 2.5a, 2.5b)

- 1879 *Acanthias radicans* n. sp. – PROBST: 173–174; pl. 3, figs 31–32.
- 1879 *Acanthias serratus* n. sp. – PROBST: 174; pl. 3, fig. 33.
- 1930 *Centrophorus* spec. – FISCHLI: 148; pl. 1, fig. 7.
- 1972 *Centrophorus granulosus* – LEDOUX: 145–148; fig. 5.
- 1991 *Centrophorus* cf. *granulosus* – BARTHELT *et al.*: 199; pl. 1, fig. 7.
- 1995 *Squalus* sp. – HOLEC *et al.*: 39; pl. 9, figs 3, 4.
- 2009 *Centrophorus* cf. *granulosus* – BRISSWALTER: 22; pl. 2, figs 3–7.
- 2011 *Centrophorus* aff. *granulosus* – VIALLE *et al.*: 243; fig. 2-1.
- 2013 *Centrophorus* sp. (2) – SCHULTZ: 30–31; pl. 9, figs 10a+b–16a+b.
- 2014 *Centrophorus* cf. *granulosus* – POLLERSPÖCK & BEAURY: 26; pl. 2, figs 1 a, b.
- 2017 *Centrophorus* sp. – POLLERSPÖCK & STRAUBE: 90; fig. 8.

Material: 32 teeth/tooth fragments (NHMW 2018/0309/0003–0005, Figs 2.3–2.5; NHMW 2018/0309/0006).

Size (only Figs): NHMW 2018/0309/0003–0005: Height: 2.2 mm (Fig. 2.3), 5.3 mm (Fig. 2.4), 2.3 mm (Fig. 2.5); Width: 3.2 mm (Fig. 2.3), 4.8 mm (Fig. 2.4), 1.4 mm (Fig. 2.5).

Description: The lower jaw tooth shown in Figs 2.4a, 2.4b is marked by the distinct serration of the mesial cutting edge. The first two thirds of the edge show a remarkably rough serration, which directly transfers in a more smooth serration within the upper third of the edge. Further distinct characters are lingual bulge of the root ruptured by the infundibulum (central lingual foramina), only weakly developed lingual root grooves

and a crown, which is distinctly more upright compared to *Deania*. The upper jaw tooth shown in Figs 2.5a, 2.5b is a parasymphysial tooth, recognizable by the upright, slender, and almost symmetrical smooth crown, the absence of a distal talon, the square root and the absence of overlapping areas.

Remarks: DE SCHUTTER & WIJNKER (2012) documented a lower lateral tooth with a similar rough serration of the mesial cutting edge. Fossil teeth from the Miocene of the Paratethys and the Pliocene of the Mediterranean, respectively, are usually assigned to *Centrophorus granulosus* (e.g., BARTHELT *et al.* 1991; CAPPETTA & CAVALLO 2006; CIGALA-FULGOSI *et al.* 2009; VIALLE *et al.* 2011; POLLERSPÖCK & BEAURY 2014). Today, 13 extant species of *Centrophorus* are described (POLLERSPÖCK & STRAUBE 2019), the genus is under taxonomic revision (WHITE *et al.* 2013, 2017) and until now no detailed tooth morphological studies have been published, which show that species can be distinguished based on dental characters. Therefore, the fossil teeth herein cannot be assigned to an extant species.

#### Genus *Deania* JORDAN & SNYDER, 1902

Type species: *Deania eglantina* JORDAN & SNYDER, 1902, type by monotypy.

#### ***Deania* sp.**

(Figs 2.6a, 2.6b, 2.7a, 2.7b)

2013 *Deania* sp. – SCHULTZ: 31.

Material: 5 teeth/teeth fragments (NHMW 2018/0309/0007–0008, Figs 2.6, 2.7; NHMW 2018/0309/0009).

Size (only Figs): NHMW 2018/0309/0007–0008: Height: 2.2 mm (Fig. 2.6), 2.5 mm (Fig. 2.7); Width: 2.5 mm (Fig. 2.6), 1.7 mm (Fig. 2.7).

Description: Figs 2.6a, 2.6b show a well-preserved lower jaw tooth, which is labio-lingually compressed. The mesial cutting edge is weakly serrated. The crown's cusp is oblique pointing distally. The lingual side of the root shows two central foramina, one of each above and below the lingual bulge of the root running along the complete width of the root. The distinct basal groove reaches from the central foramen to the root's basis. The upper jaw tooth shown in Figs 2.7a, 2.7b is an anterior tooth, due to its almost symmetrical shape.

Remarks: Lower teeth of the genus *Deania* can be distinguished from *Centrophorus* in having two lingual central foramina, one of each above and below the lingual bulge of the root running along the complete width of the root (vs. *Centrophorus* showing only one lingual central foramen at the level of the lingual bulge). Upper jaw teeth of the genus can be distinguished by broadly developed aprons, which flows around single foramina (Fig. 2.7b) and the absence of overlapping areas (Fig. 2.7a). Extant *Deania*

comprises four described species (POLLERSPÖCK & STRAUBE 2019). Studies based on DNA sequence data show that a taxonomic revision of the genus is required (STRAUBE *et al.* 2013). No studies exist, which show how the four species could be distinguished based on dental characters alone. *Deania calcea* (LOWE, 1839) is the only species for which a detailed description of its dentition is available (HERMAN *et al.* 1989).

Family Dalatiidae GRAY, 1851

Genus *Isistius* GILL, 1865a

Type species: *Scymnus brasiliensis* QUOY & GAIMARD, 1824, type by monotypy.

***Isistius triangulus* (PROBST, 1879)**

(Figs 2.8a, 2.8b)

- \* 1879 *Scymnus triangulus* n. sp. – PROBST: 175–176; pl. 3, figs 35, 36.  
 1930 *Isistius trituratorus* – FISCHLI: 148; pl. 1, fig. 7.  
 1972 *Isistius triangulus* – LEDOUX: 161–163; fig. 13.  
 1991 *Isistius triangulus* – BARTHELT *et al.*: 199; pl. 1, fig. 10.  
 1995 *Isistius triangulus* – HOLEC *et al.*: 39; pl. 9, figs 1, 2.  
 2007 *Isistius* cf. *triangulus* – KOC SIS: 29; fig. 3.6.  
 2009 *Isistius triangulus* – BRISSWALTER: 24; pl. 2, fig. 8.  
 2011 *Isistius triangulus* – VIALLE *et al.*: 243–244; fig. 2-4.  
 2012 *Isistius triangulus* – CAPPETTA: 136; figs 125E–L.  
 2013 *Isistius triangulus* – SCHULTZ: 31; pl. 9, figs 7–9.  
 2014 *Isistius triangulus* – POLLERSPÖCK & BEAURY: 26–27; pl. 2, figs 3 a, b.  
 2017 *Isistius triangulus* – POLLERSPÖCK & STRAUBE: 39–40; fig. 10.

Material: 12 teeth/teeth fragments (NHMW 2018/0309/0010, Figs 2.8a–b, NHMW 2018/0309/0011).

Size (only Fig. 2.8): NHMW 2018/0309/0010: Height: 2.2 mm; Width: 2.5 mm.

Description: Our findings comprise multiple mostly fragmented lower jaw teeth (Figs 2.8a, 2.8b). Teeth including a well-preserved root were not found, however, *Isistius* can be recognized by its upright labio-lingually compressed triangular symmetrical crown. Further, the mesial and distal cutting edge is distinctly serrated.

Remarks: Genus-rich Dalatiidae comprise seven extant genera (POLLERSPÖCK & STRAUBE 2019). Molecular phylogenetic analyses showed the presence of two intra-familial clades, one comprising the *Dalatiidae/Isistius* lineages and the sister clade including mainly *Squaliolus* and *Euprotomicrus* (NAYLOR *et al.* 2012b; STRAUBE *et al.* 2015; FLAMMENSBECK *et al.* 2018). The genus *Isistius* is, in comparison with other taxa from the family, not only the most frequent dalatiid fossil, but also the most widely distributed in the Miocene (Table S1). A reason for these patterns may be its predatory behaviour, which assumes a gathering of *Isistius* along with larger fish species as well as marine mammals (*e.g.*, REDDA CLIFF 1988; SOUTO *et al.* 2009). Especially marine mammals



are well documented from the excavation site (GÜTHNER pers. comm., TAUSCH 1896; MARIAN 1926). Further reasons could be the vertical movement of *Isistius* (*e.g.*, PARIN 1966; NAKANO & TABUCHI 1990) and schooling activities (WIDDER 1986; PARIN 1966). The aforementioned factors may be causing the high frequency of fossils in coastal sediments (*e.g.*, BRISSWALTER 2009; CARRILLO-BRICEÑO *et al.* 2015). Besides teeth of *Centrophorus*, *Isistius* teeth are the most frequent squaliform teeth.

### Genus *Euprotomicrus* GILL, 1865a

Type species: *Scymnus (Laemargus) labordii* MÜLLER & HENLE, 1839, type by monotypy.

#### ***Euprotomicrus* sp.**

(Figs 3.1–3.4)

Material: single complete lower tooth, ex. collection GÜTHNER (NHMW 2018/0309/0012, Fig. 3.4), single lower tooth (NHMW 2018/0309/0013, Fig. 3.3), 2 upper teeth (NHMW 2018/0309/0014–0015, Figs 3.1–3.2), 4 fragment of lower teeth (NHMW 2018/0309/0016).

Size (only Figs): NHMW 2018/0309/0012–0015: Height: 0.7 mm (Fig. 3.3), 1.6 mm (Fig. 3.4), 1.3 mm (Fig. 3.1); 1.3 mm (Fig. 3.2); Width: 0.5 mm (Fig. 3.3), 1.0 mm (Fig. 3.4), 0.5 mm (Fig. 3.1), 0.8 mm (Fig. 3.2).

Description: Lower jaw teeth are labio-lingually compressed; the cusp is very strongly distally inclined, a well developed distal talon is present. A single central foramen is available on the lingual side. The labial overlapping area is reaching to the basis of the square root (Fig. 3.3). On the labial side, a large, central foramen is present, which is flanked by a bilobed apron. A dalatiid character is the splitting of the apron based on the aforementioned situation. The labial side of the root may show additional small foramina, which are flanking the central foramen or are present at in the overlapping area (Figs 3.3, 3.4).

- ◀ Fig. 2. **1:** *Chlamydoselachus bracheri* PFEIL, 1983 (NHMW 2018/0309/0001; a: profile view, b: labial view); **2:** *Paraheptracthias repens* (PROBST, 1879) (NHMW 2018/0309/0002; lower tooth; a: labial view, b: lingual view); **3:** *Centrophorus* sp. (NHMW 2018/0309/0003; lower tooth; a: lingual view, b: labial view); **4:** *Centrophorus* sp. (NHMW 2018/0309/0004; lower tooth; a: lingual view, b: labial view); **5:** *Centrophorus* sp. (NHMW 2018/0309/0005; upper tooth; a: lingual view, b: labial view); **6:** *Deania* sp. (NHMW 2018/0309/0007; lower tooth, a: labial view, b: lingual view); **7:** *Deania* sp. (NHMW 2018/0309/0008; upper tooth; a: lingual view, b: labial view); **8:** *Isistius triangulus* (PROBST, 1879) (NHMW 2018/0309/0010; lower tooth; a: lingual view, b: labial view).



Both upper jaw teeth shown in Figs 3.1–3.2 show a split labial apron, which is characteristic for the genus along with the large central foramen. The anterior teeth display an upright crown (Figs 3.1a, 3.1b, HERMAN *et al.* 1989), while lateral crowns are pointing distally (Figs 3.2a, 3.2b). In lateral upper teeth both the apron as well as the root lobes are differentially developed in length.

Remarks: Fossil teeth presented in this study mark the first fossil record for this genus. Morphologically similar fossil teeth of the genus *Squaliolus* were only rarely observed (Table S1). The French Eocene and the Slovakian Miocene are the only two locations so far, where multiple teeth were recovered allowing for the description of the morphological variation within the genus (*Squaliolus gasconensis*, ADNET, 2006; *Squaliolus cf. schaubi*, UNDERWOOD & SCHLÖGL, 2013) (Table S1). HERMAN *et al.* (1989) state that extant teeth of *Euprotomicrus*, *Squaliolus*, and *Heteroscymnoides* are highly similar. In *Euprotomicrus bispinatus* and *Squaliolus laticaudus* HERMAN *et al.* (1989) report on a sexual dimorphism of tooth morphologies: the mesial cutting edge of the cusp of male teeth is sigmoid and the cusp is more slender compared to females. In contrast, females show a straight mesial cutting edge and more strongly cusps (HERMAN *et al.* 1989).

Even though this is supported in SMITH (1912) and SEIGEL (1978), more detailed studies and enlarged sampling are necessary for confirmation. HERMAN *et al.* (1989) analysed only a single male and four female specimens. Further, SEIGEL (1978) display a single tooth without the sigmoid curvature. Besides that, HERMAN *et al.* (1989) show a lower jaw tooth of a female, which carries the potential male character of a sigmoid cutting edge (HERMAN *et al.* 1989: pl. 21, tooth of the latero-posterior position, marked with “lp”).

HERMAN *et al.* (1989) display teeth of *E. bispinatus* from a 200 mm total length male and from a 115 mm female, which are suggested to document the lower jaw teeth sexual dimorphism. In contrast to the images shown in HERMAN *et al.* (1989), HUBBS & MCHUGH (1951) show the jaws from a 223 mm female, which shows a distinct sigmoid crown edge as well. This may indicate that this type of differences between specimens may in fact be an ontogenetic heterodonty, as all *E. bispinatus* is assumed to reach maturity at a total length of 170–190 mm for males and 220–230 mm for females (EBERT 2016). Ontogenetic heterodonty is known from several extant and extinct taxa (*e. g.*, ADNET *et al.* 2006; CIGALA-FULGOSI *et al.* 2009; DELPIANI *et al.* 2012; MOYER & BEMIS 2016; VORIS & HECKERT 2017).

Based on the figured teeth in HERMAN *et al.* (1989) teeth of *Euprotomicrus* can be distinguished from *Squaliolus* and *Heteroscymnoides* using the following characteristics:

- lower jaw teeth of *Euprotomicrus* differ by an enlarged distance between both labial apron lobes, which covers a third of the root;
- the mesial lower part of the apron is distinct, conical and is clearly separated from the root;
- presence of a symmetrical symphyseal tooth with an upright crown in the lower jaw (see also HUBBS *et al.* 1967);



- crown of anterior upper jaw teeth are upright and almost symmetrical;
- lateral upper jaw teeth do not show a decrease in size and the crown is only slightly bent distally;
- the distance of labial apron lobes of upper jaw teeth is remarkably larger compared to *Squaliolus* and *Heteroscymnoides*.

Due to the aforementioned characteristics documented for the fossils described herein, we assign these fossil teeth to *Euprotomicrus*.

Family Etmopteridae FOWLER, 1941

Genus *Etmopterus* RAFINESQUE, 1810

Type species: *Etmopterus aculeatus* RAFINESQUE, 1810, type by monotypy.

***Etmopterus* sp.**

(Figs 3.5, 3.6)

Material: single lower tooth (NHMW 2018/0309/0017, Fig. 3.6), single upper tooth (NHMW 2018/0309/0018, Fig. 3.5), single fragment of lower tooth (NHMW 2018/0309/0019).

Size (only Figs): NHMW 2018/0309/0017–0018: Height: 1.5 mm (Fig. 3.6), 1.3 mm (Fig. 3.5); Width: 1.1 mm (Fig. 3.6), 0.7 mm (Fig. 3.5).

Description: Three fossil teeth were collected, two lower and a single upper jaw tooth. The teeth indicate the typical dignathic heterodonty of etmopterids. The upper jaw tooth is multicuspid and asymmetrical; the main cusp is upright and flanked by two cusplets on one and only a single cusplet on the other side. The cusplets next to the main cusp are larger and reach up to the middle of the main cusp. The labial basis of the crown shows strongly vertical enameloid folds, the basal edge of the crown is sickle-shaped and reaches as a conus to the middle of the root lobes. The labio-lingually compressed lower jaw tooth shows distally an overlapping depression to former neighboring teeth, which reaches down to the basis of the root and is s-shaped. Further, the cusp is bent distally, a distal talon is present as well as four foramen at the crown basis, a large central one and three smaller, flanking ones.

Remarks: This large extant genus comprises 44 described species (POLLERSPÖCK & STRAUBE 2019) and is separated into four subclades (STRAUBE *et al.* 2010). Due to missing information on potential specific dental features characterizing the species and/or subclades, the fossil teeth presented herein can only be assigned to the genus. In comparison to the teeth collected in the deep-sea in Mitterdorf (POLLERSPÖCK & STRAUBE 2017), we did not find distinct differences and therefore regard the teeth found here as conspecific.

## Order Carcharhiniformes COMPAGNO, 1977

## Family Scyliorhinidae GILL, 1862

Remarks to the family Scyliorhinidae GILL, 1862: Phylogenetic studies by IGLÉSIAS *et al.* (2005) and NAYLOR *et al.* (2012a) have shown that the family is polyphyletic.

Family Pentanchidae *sensu* IGLÉSIAS *et al.*, 2005or Scyliorhinidae I *sensu* NAYLOR *et al.*, 2012aGenus *Apristurus* GARMAN, 1913

Type species: *Scylliorhinus indicus* BRAUER, 1906, type by original designation.

***Apristurus* sp.**

(Fig. 3.7)

Material: single tooth (NHMW 2018/0309/0023, Fig. 3.7)

Size: Height: 0.8 mm; Width: 1.0 mm.

Description: The fossil tooth shown in Fig. 3.7 almost completely lacks the characteristic lingual reticulate (golf ball-like) ornamentation present in *Apristurus*. Only the mesial edge of the mesial cusplet displays the ornamentation. The distinct angular ridges of the crown starts already at the lower third of the cusp and consists of several parallel striations of different lengths – especially notable for the main cusp. Only inner cusplets show striations. Both main cusp and cusplets are strongly convex. The typically present thin and wide enameloid edged is damaged likely due to extensive usage displaying undamaged parts only at the mesial lower part of the main cusp. Two distinct cusplets are present mesially, distally only a single cusplet is present. The root has two lobes – a typical character for scyliorhinid teeth – and reaches lingually far up, shows a V-shape and the lobes are arranged in a pointed angle. The lingual root protuberance displays a central foramen.

Remarks: Today, there are 39 extant species described (POLLERSPÖCK & STRAUBE 2019), which are distinguished in three morphological groups (NAKAYA & SATO 1999; IGLÉSIAS *et al.* 2005; FLAMMANG *et al.* 2007). Dental morphological descriptions are only available for a single species, *A. laurussonii* (HERMAN *et al.* 1990). The extant genus is not reported from the Mediterranean Sea. Six species are known from the North Atlantic, two of which are assigned to the *brunneus*-group (*A. laurussonii*, *A. melanoasper*) and four species are designated as members of the *spongiceps*-group (*A. microps*, *A. manis*, *A. apyodes*, and *A. profundorum*) (EBERT & STEHMANN 2013).

The extant genus *Apristurus* is distributed worldwide at sea mounts and continental shelves excluding the polar regions and species occur in depths of 400–2000 m (NAKAYA

*et al.* 2008). The fossil teeth shown in this study are not differing in morphology from fossils collected in the Neuhofener Beds (Lower Ottnangian, Bavaria) (POLLERSPÖCK & STRAUBE 2017) and are therefore the second record for this genus within the Northern Alpine Molasse and the first record for Austria.

Genus *Pseudoapristurus* POLLERSPÖCK & STRAUBE, 2017

Type species: *Pseudoapristurus nonstriatus* POLLERSPÖCK & STRAUBE, 2017, type by monotypy.

***Pseudoapristurus nonstriatus* POLLERSPÖCK & STRAUBE, 2017**

(Fig. 3.8)

\* 2017 *Pseudoapristurus nonstriatus* – POLLERSPÖCK & STRAUBE: 34; fig. 7.

Material: single tooth, (NHMW 2018/0309/0024, Fig. 3.8)

Size: Height: 0.63 mm; Width: 0.65 mm.

Description: The fossil described herein is characterized by distinctly high cusplets typical for the genus. The tooth is approximately 0.6 mm in height and width. Here, the first mesial cusplet is almost reaching the distally bent main cusp in height. The first distal cusplet is significantly lower in height and triangular. The thin and wide enameloid edge is distinct and present at both the main cusp as well as the cusplets. This type of fold is typical for scyliorhinid teeth of genera *Pseudoapristurus*, *Apristurus*, or *Galeus* (HERMAN *et al.* 1990; POLLERSPÖCK & STRAUBE 2017). No folds are present on the lingual and labial sides. We suggest that the tooth is of posterior lower jaw origin, as the main cusp is strongly bent distally and widely resembles the type 2 morphology shown in POLLERSPÖCK & STRAUBE (2017).

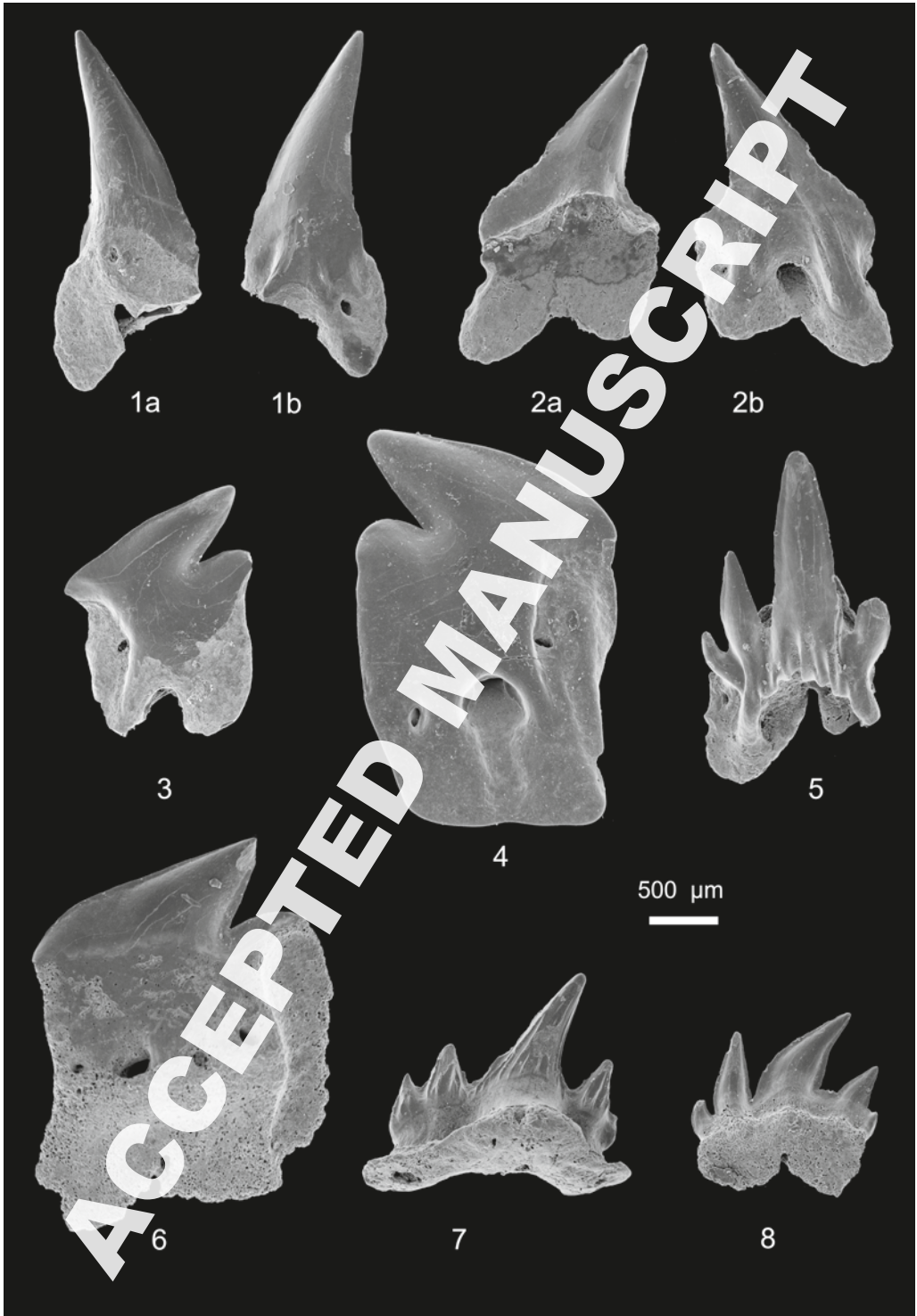
Remarks: This second record of *P. nonstriatus* from another locality further aligns with the suggestion by POLLERSPÖCK & STRAUBE (2017) that there are morphological differences between upper and lower jaw teeth and generally, how posterior teeth in this species are shaped.

Family Scyliorhinidae *sensu* IGLÉSIAS *et al.*, 2005

or Scyliorhinidae III *sensu* NAYLOR *et al.*, 2012a

Genus *Pachyscyllium* REINECKE, MOTHS, GRANT & BREITKREUZ, 2005

Type species: *Pachyscyllium albigensis* REINECKE, MOTHS, GRANT & BREITKREUZ, 2005, by original designation.



***Pachyscyllium distans* (PROBST, 1879)**

(Fig. 4.1)

- \* 1879 *Scyllium distans* n. sp. – PROBST: 170; pl. 3, figs 24, ?23 and ?25, non 26.  
 1971 *Scyliorhinus distans* – SCHULTZ: 325. [name only]  
 1978 *Scyliorhinus distans* – BRZOBOHATÝ & SCHULTZ: 442. [name only]  
 1991 *Scyliorhinus distans* – BARTHELT *et al.*: 202; pl. 3, figs 2, 4.  
 1995 *Scyliorhinus distans* – HIDEN: 62; pl. 5, fig. 3.  
 1995 *Scyliorhinus distans* – BOLLIGER *et al.*: 892–893; pl. 1, fig. 12.  
 1998 *Scyliorhinus distans* – SCHULTZ: 297; pl. 1, figs 4–9.  
 2003 *Scyliorhinus distans* – SCHULTZ: 187. [name only]  
 2004 *Scyliorhinus distans* – DAXNER-HÖCK *et al.*: 192. [name only]  
 2004 *Scyliorhinus distans* – SCHULTZ: 258; pl. 1, figs 7, 8.  
 2007 *Premontreia (Oxyscyllium) distans* – BRACHER & UNGER: 100; fig. 60, pl. 36.  
 2011 *Pachyscyllium* aff. *dachiardii* – VIALLE *et al.*: 250; figs 3-8, 3-9.  
 2012 *Pachyscyllium dachiardii* – CAPPETTA: 267; fig. 247.  
 2013 *Pachyscyllium dachiardii* – SCHULTZ: 94; pl. 10, figs 14a, b, 15a, b.  
 2014 *Pachyscyllium* aff. *distans* – REINECKE *et al.*: 28; pl. 11, figs 4–5.  
 2016 *Premontreia distans* – JOST *et al.*: fig. 8 c.  
 2016 *Scyliorhinus distans* – SACH: 105. [name only]  
 2016 *Scyliorhinus (Pachyscyllium)* cf. *distans* – SCHLUNEGGER *et al.*: 22. [name only]

Material: single tooth, (NHMW 2018/0309/0025, Figs 4.1a, 4.1b)

Size: Height: 2.4 mm; Width: 2.0 mm.

Description: The tooth shows a massive main cusp, which is only slightly bent distally. The labial and lingual crown area is strongly convex and show labial and lingual distinct enameloid folds reaching a third of the main cusp's total height and almost the full height in the cusplets. The crown's cutting edge covers the whole main cusp as well as the mesial and distal sides of cusplets. The root is only fragmentarily preserved. The former lingual bulge and the nutritive groove are still recognizable.

Remarks: REINECKE *et al.* (2005) described the genus *Pachyscyllium* based on the type species *Pachyscyllium albigensis*, and placed the teeth of *P. distans* in the “*distans*” group of the genus *Scyliorhinus*, as the excavated material was not sufficient for a revision of the “*Scyliorhinus*” *distans* group. Later, CAPPETTA (2006) assigned the species to the genus *Premontreia (Oxyscyllium)* and suggested that *P. (Oxyscyllium) distans* is a synonym to the Pliocene species *P. (Oxyscyllium) dachiardii* (LAWLEY, 1876) collected in

- ◀ Fig. 3. 1: *Euprotomicrus* sp. (NHMW 2018/0309/0014; upper tooth; a: lingual view, b: labial view); 2: *Euprotomicrus* sp. (NHMW 2018/0309/0015; upper tooth; a: lingual view, b: labial view); 3: *Euprotomicrus* sp. (NHMW 2018/0309/0013; lower tooth; labial view); 4: *Euprotomicrus* sp. (NHMW 2018/0309/0012; lower tooth; lingual view); 5: *Etmopterus* sp. (NHMW 2018/0309/0018; upper tooth; labial view); 6: *Etmopterus* sp. (NHMW 2018/0309/0017; lower tooth; lingual view); 7: *Apristurus* sp. (NHMW 2018/0309/0023; lingual view); 8: *Pseudoapristurus nonstriatus* POLLERSPÖCK & STRAUBE, 2017 (NHMW 2018/0309/0024; upper tooth; lingual view).

Italy. REINECKE *et al.* (2011) concluded, after comparing the original syntypes collected by PROBST (1879), that the species “*distans*” is valid, but doubted their assignment to the genus *Premontreia*. CAPPETTA (2012) finally suggested that the “*dachiardii-distans*” group belongs to the genus *Pachyscyllium*, neglecting REINECKE *et al.* (2011) and placed the “*distans*” species as a synonym to *Pachyscyllium dachiardii*. Here, we follow REINECKE *et al.* (2011) and consider the species as valid based on the aforementioned dental morphological differences (*i. e.*, morphology of cusplets, distally bent lateral and commissural teeth).

Genus *Scyliorhinus* BLAINVILLE, 1816

Type species: *Squalus canicula* LINNÉ, 1758, type by subsequent designation.

***Scyliorhinus* sp.**  
(Figs 4.2a, 4.2b)

Material: 3 tooth (mostly fragments), (NHMW 2018/0309/0026, Figs 4.2a, 4.2b; NHMW 2018/0309/0027)

Size (only Fig.): NHMW 2018/0309/0026: Height: 1.6 mm; Width: 1.2 mm (Fig. 4.2).

Description: The larger part of teeth is only preserved fragmentary or strongly polished, which does not allow for identification to species level. Exclusively the tooth shown in Fig. 4.2. allows a description. The crown is almost smooth labially and does not show enameloid folds. On its lingual side, the folds are prominently developed and cover the cusplets completely. The crown is upright. Both crown and cusplets are convex lingually, while only weakly convex on its labial side. The root displays two lobes, is rather wide and reaches far up lingually. REINECKE (2014) discusses a sexual dimorphism and places teeth of the aforementioned morphology to males of *Scyliorhinus biformis*. According to REINECKE (2014), teeth of male origin do not show labial enameloid folds, while females display such folds.

Remarks: Morphologically highly similar teeth were also reported in POLLERSPÖCK & STRAUBE (2017) from the geographically nearby site Neuhofener Beds (Ottangian, Upper Marine Molasse). The figured tooth shows typical morphological character of the genus *Scyliorhinus*, like the shape of the poorly developed cusplets, the cusp which is weakly convex in labial and strongly convex in lingual view, and the lingual striae.

Order Pristiophoriformes COMPAGNO, 1973

Family Pristiophoridae BLEEKER, 1859

Genus *Pristiophorus* MÜLLER & HENLE, 1837

Type species: *Pristis cirratus* LATHAM, 1794, type by monotypy.



***Pristiophorus* sp.**

(Figs 4.3, 4.4)

**Material:** 1 oral tooth (NHMW 2018/0309/0020, Fig. 4.3), 2 rostral teeth (NHMW 2018/0309/0021, Fig. 4.4, NHMW 2018/0309/0022).

**Size (only Figs):** NHMW 2018/0309/0020–0021): Height: 1.4 mm (Fig. 4.3), 10.8 mm (Fig. 4.4); Width: 1.6 mm (Fig. 4.3), 2.7 mm (Fig. 4.4).

**Description:** Three collected oral teeth are roundish, do not show any kind of enameloid structures and miss roots. The figured tooth shows a triangular cusp flanked by laterally heels. The labial surface is smooth, shows a axial ridge in the apical part of the crown, and a pointed, triangular apron. No rostral teeth including a root were collected.

**Remarks:** Fossil records of *Pristiophorus*, which are in many cases rostral teeth found in remains of the Miocene Paratethys, are mostly assigned to *P. suevicus* JAEKEL, 1890 (FISCHLI 1930; BARTHELT *et al.* 1991; BRISSWALTER 2009; VIALLE *et al.* 2011; SCHULTZ 2013; POLLERSPÖCK & BEAURY 2014). The species was exclusively described based on the rostral teeth. If the rostral teeth carry characters allowing for a species-level identification is questionable. UNDERWOOD & SCHLÖGL (2013) described *P. striatus* from the early Miocene of Slovakia (Burdigalian, Central Paratethys) based on three oral teeth and suggested conspecificity with *P. suevicus*. Further, the authors suggested to mention *Pristiophorus* species described exclusively on rostral teeth as nomina dubia.

Order Lamniformes BERG, 1937

Family Cetorhinidae GILL, 1862

Genus *Keasius* WELTON, 2013

**Type species:** *Keasius taylori* WELTON, 2013, type by subsequent designation.

***Keasius* sp.**

(Fig. 4.5)

**Material:** single gill raker fragment (NHMW 2018/0309/0028, Fig. 4.5)

**Size:** 8.3 mm Length.

**Description:** The single specimen is part of a gill raker consisting of a partial base and its connected filament. Distinctive characters for identification such as the distal protuberance, the mesial and basal edge, and the medial process are missing. The rounded bight and the low base height are well recognizable.

**Remarks:** An identification of *Keasius* species is only possible, if oral teeth are available. Today, the following species are described: *K. taylori* (Eocene of Oregon, USA) (WELTON 2013), *K. septemtrionalis* (Late Oligocene, Chattian, Germany) and *K.*

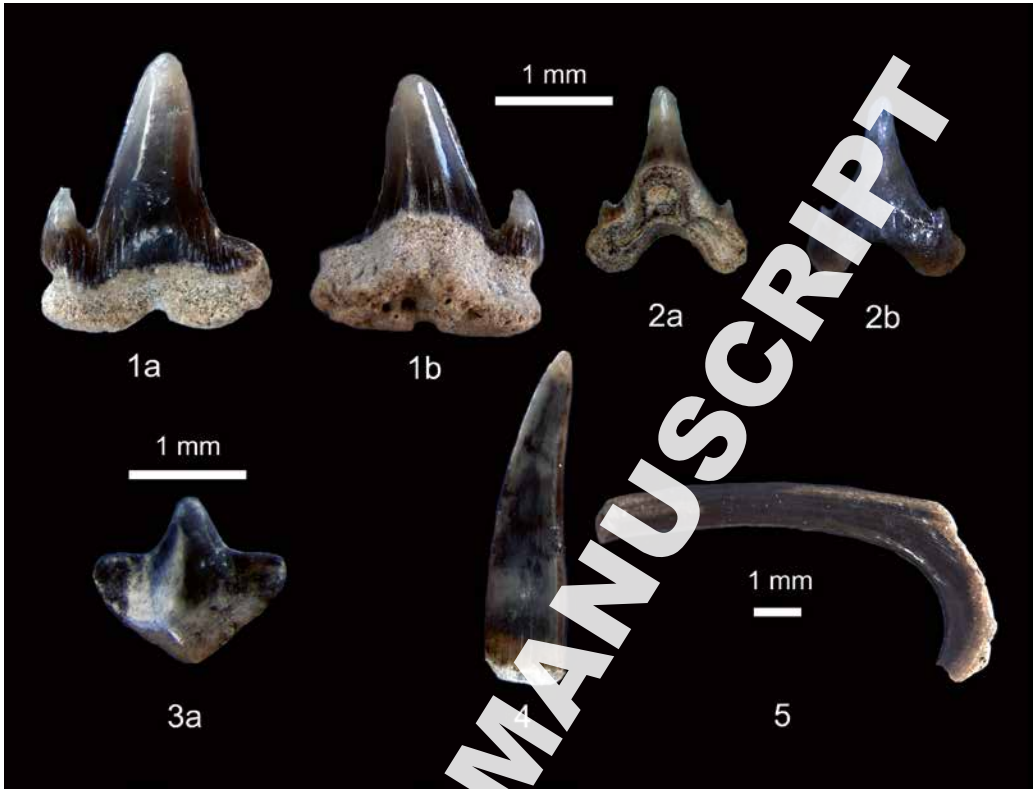


Fig. 4. **1:** *Pachyscyllium distans* (PROBST, 1879) (NHMW 2018/0309/0025; a: labial view, b: lingual view); **2:** *Scyliorhinus* sp. (NHMW 2018/0309/0026; a: labial view, b: lingual view); **3:** *Pristiophorus* sp. (NHMW 2018/0309/0020; oral tooth; labial view); **4:** *Pristiophorus* sp. (NHMW 2018/0309/0021; rostral tooth); **5:** *Keasius* sp. (NHMW 2018/0309/0028; fragment of gill raker).

*rhenanus* (Early Miocene, Burdigalian, Germany) (REINECKE *et al.* 2015), as well as *K. parvus* (Early Oligocene, Rupelian; Belgium and Germany) (LERICHE 1908; REINECKE *et al.* 2015).

Family Mitsukurinidae JORDAN, 1898

Genus *Mitsukurina* JORDAN, 1898

Type species: *Mitsukurina owstoni* JORDAN, 1898, type by monotypy.

***Mitsukurina lineata* (PROBST, 1879)**

(Figs 5.1a, 5.1b, 5.1c)

- \* 1879 *Lamna (Odontaspis) lineata* n. sp. – PROBST: 147–149; pl. 2, figs 40–46.  
 1930 *Odontaspis acutissima* – FISCHLI: 150; pl. 3, fig. 1.  
 1991 *Mitsukurina lineata* – BARTHELT *et al.*: 200; pl. 2, fig. 6.

- 1992 *Mitsukurina lineata* – SCHOLZ & BIENERTH: 12; pl. 2, figs 5, 6.  
 1995 *Mitsukurina lineata* – BOLLIGER *et al.*: 893; pl. 2, fig. 9.  
 2004 *Mitsukurina lineata* – BAIER *et al.*: 365; pl. 1, fig. 1.  
 2007 *Mitsukurina lineata* – BRACHER & UNGER: 82–83; pl. 30.  
 2011 *Mitsukurina lineata* – VIALLE *et al.*: 247; fig. 2-12.  
 2012 *Mitsukurina lineata* – CAPPETTA: 186; figs 175A–C.  
 2013 *Mitsukurina lineata* – SCHULTZ: 51; pl. 5, figs 1–3.  
 2014 *Mitsukurina lineata* – POLLERSPÖCK & BEAURY: 28; pl. 1, figs 3a, b.  
 2016 *Mitsukurina lineata* – JOST *et al.*: fig. 8e.

Material: 4 teeth, (NHMW 2018/0309/0029, Figs 5.1a–c, NHMW 2018/0309/0030)

Size (only Figs): NHMW 2018/0309/0029: Height: 10.0 mm; Width: 10.6 mm (Figs 5.1a–c).

Description: *M. lineata* is characterized by distinct parallel enameloid folds, which are only present at the lingual side of the crown. Lateral teeth display pointed triangular cusps, which are upright in lower jaw teeth, while they are distally bent in upper jaw teeth. Figs 5.1a–5.1c shows a completely preserved lateral upper jaw tooth. Projections of mesial and distal cusplets are further visible, typically small and bent inwards in this species. The basis of the mesial cusplet is visible, while the distal cusplet is broken. Root lobes are widespread and flattened at the outer edges. Labially, the root lobes show multiple small foramina, the lingual sides carry a single large central foramen.

Remarks: *M. lineata* is a common and frequently reported species from the Molasse Basin (PROBST 1879). The genus comprises only a single extant species, *M. owstoni* JORDAN, 1898, which is rarely recorded from tropical and subtropical deep waters (100–960 m depth) of the Atlantic, Indian and Pacific Oceans (ORLOV *et al.* 2017).

Family Odontaspidae MÜLLER & HENLE, 1839

Genus *Odontaspis* CUVIER, 1816

Type species: *Squalus ferox* RISSO, 1810, type by monotypy.

***Odontaspis molassica* (PROBST, 1879)**

(Figs 5.2a, 5.2b)

- \* 1879 *Lamna (Odontaspis) molassica* n. sp. – PROBST: 150; pl. 2, figs 47–52.  
 1907 *Odontaspis molassica* – JOLEAUD: 139.  
 1912 *Odontaspis molassica* – JOLEAUD: 266; pl. 4, figs 29–31.  
 1991 *Odontaspis molassica* – BARTHELT *et al.*: 200; pl. 2, fig. 2.  
 2006 *Carcharias sternbergensis* – CAPPETTA: 208. [name only]  
 2007 *Odontaspis molassica* – BRACHER & UNGER: 65–66; pl. 23.  
 2011 *Carcharias sternbergensis* – VIALLE *et al.*: 247  
 2013 *Carcharias acutissimus* – SCHULTZ: 67.  
 2016 *Odontaspis molassica* – SACH: 107. [name only]

**Material:** single tooth (incomplete tooth, NHMW 2018/0309/0031, Figs 5.2a–b), ex. collection DANNINGER.

**Additional material:** 3 teeth of Walbertsweiler, Germany (Ottngian, ex. coll. Unger, now SMNS 96995-1, SMNS 96995-2, and SMNS 96995-3, Figs 5.3–5.5).

**Size:** NHMW 2018/0309/0031: Height: +7.4 mm; Width: +6.5 mm (Fig. 5.2); additional material: SMNS 96995-1: Height: 25.2 mm; Width: 16.0 mm (Fig. 5.3), SMNS 96995-2: Height: 14.5 mm; Width: 11.6 mm (Fig. 5.4), SMNS 96995-3: Height: +14.4 mm; Width: 14.5 mm (Fig. 5.5).

**Description:** This fossil is a lateral lower jaw tooth displaying an erect central cusp and three mesially flanking cusplets. The cusplet directly neighbouring the central main cusp is broken. The tooth shows the typical features characterizing *O. molassica*, i. e., a labially linear running basal crown edge with small vertical enameloid folds at its basis (Fig. 5.2). The mesial and distal cutting edge reaches almost to the crown's basis, the cusplets do not show a cutting edge and are therefore almost circular in cross section. The two root lobes are not well-preserved, foramina etc. are not recognizable. Three well-preserved teeth are documented from Walbertsweiler (Ottngian, Upper Marine Molasse) (Figs 5.3–5.5), which display all characteristics of this species.

**Differential diagnosis:** Following COMPAGNO & FOLLETT (1986) and CAPPETTA (2012) the genus *Odontaspis* can be distinguished from the genus *Carcharias* in having no or only a weakly sigmoidal profile of anterior teeth (CAPPETTA 2012: fig. 192), up to three pairs of lateral cusplets (vs. up to two pairs in *Carcharias*), a distinctly concave basal edge of the root, a distinctly reduced upper parasymphysial tooth, an upper symphyseal tooth (usually absent in *Carcharias*), two rows of upper anterior teeth on either side of symphysis (vs. three rows in *Carcharias*), lateral teeth slightly compressed and not blade-like, with cusps slightly flattened (vs. lateral teeth compressed and blade-like, with flattened cusps in *Carcharias*), and cusplets on anterior teeth with a long and straight or weakly curved morphology, not hooked, and cusps slender and narrow-tipped (vs. short and strongly hooked, and cusps stout and broad-tipped in *Carcharias*).

**Remarks:** CAPPETTA (2006) synonymized the species described in PROBST (1879) with *Carcharias acutissimus*. Additional specimens attributed to *C. molassica* by JOLEAUD (1907, 1912) were attributed to *Carcharias sternbergensis* described in REINECKE *et al.* (2005) from the Oligocene (Chattian) without discussing the reason. VIALLE *et al.* (2011) followed this suggestion. Comparing the original description of *O. molassica* (PROBST, 1879) and *C. sternbergensis* (REINECKE *et al.* 2005) a massive size difference gets obvious. While teeth of *C. sternbergensis* are of 3–13 mm in height (REINECKE *et al.* 2005), teeth of *O. molassica* can reach heights of more than 30 mm (BRACHER & UNGER 2007; PROBST 1879). Further, cusplets of *O. molassica* are larger, without a cutting edge and circular in cross-section. In addition, teeth may show both mesially and distally several cusplets. The transition from the enameloid of the crown to root on the labial side is straight and shifted downwards. We suggest that *O. molassica* can be distinguished from *C. sternbergensis*, as well as further sympatric odontaspids as e. g., *C. acutissima* and must be therefore considered as valid species.

## Family Otodontidae GLIKMAN, 1964

Genus *Otodus* AGASSIZ, 1838

Type species: *Squalus auriculatus* BLAINVILLE, 1818 non AGASSIZ, 1835 [1843], type by subsequent designation.

***Otodus (Megaselachus) chubutensis* (AMEGHINO, 1901)**

(Figs 5.6a, 5.6b)

- \* 1901 *Cacharodon chubutensis* n. sp. – AMEGHINO: 83.  
 1927 *Carcharodon megalodon* var. *chubutensis* – LERICHE: 80–81; pl. 12–13, figs 1–3.  
 1968 *Carcharodon megalodon megalodon* – SCHULTZ: 83–84; pl. 3, figs 50, 51.  
 1968 *Carcharodon megalodon chubutensis* – SCHULTZ: 84–85; pl. 2, figs 39, 40.  
 1971 *Carcharodon megalodon chubutensis* – BRZOBHATÝ & SCHULTZ: 730; pl. 4, fig. 5.  
 1973 *Carcharodon megalodon chubutensis* – BRZOBHATÝ & SCHULTZ: 664; pl. 2, fig. 14.  
 1975 *Procarcharodon megalodon chubutensis* – BRZOBHATÝ *et al.*: 462.  
 1991 *Procarcharodon megalodon* – BARTHELT *et al.*: 202; pl. 2, figs 9–10.  
 1995 *Procarcharodon chubutensis* – HOLEC *et al.*: 44–45; pl. 14, fig. 3, pl. 15, figs 1, 2.  
 2012 *Otodus (Megaselachus) chubutensis* – CAPPETTA: 227.

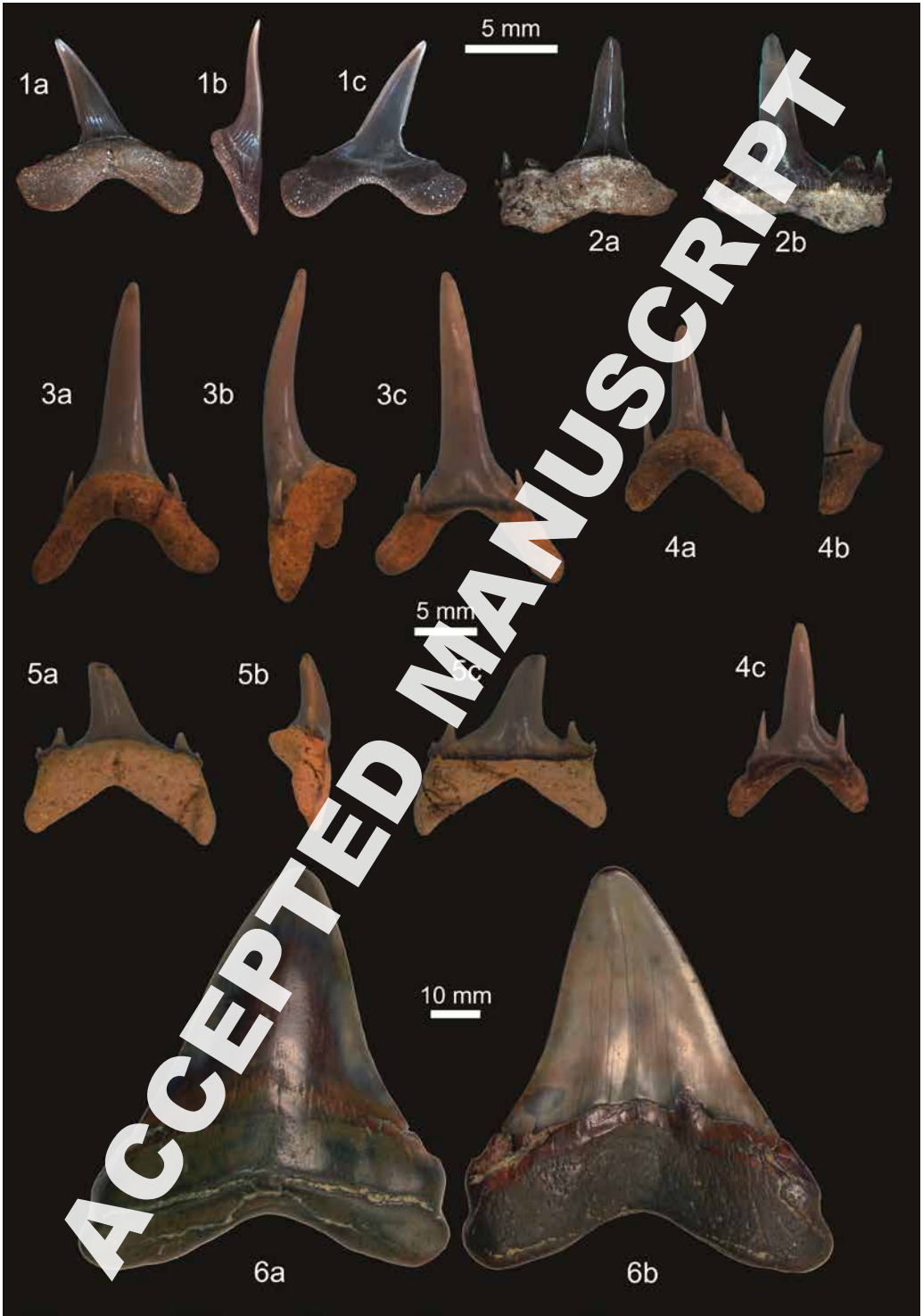
Material: single tooth (P 00367 Haus der Natur, Salzburg, Figs 5.6a–b).

Additional material: 4 teeth collection GÜTHNER, 24 teeth collection DANNINGER and HIERMANN (Supplement Table 2).

Description: Several teeth of *Otodus* are documented from Allerding – especially from private collectors (Table S2, Fig. 5.6). The teeth can reach 100 mm in height and display typical characters such as a triangular serrated crown. A detailed analysis of the collections by DANNINGER, HIERMANN, and GÜTHNER regarding the presence or absence of cusplets (24 teeth in total) resulted in 13 teeth (54.2%) with cusplets, seven teeth without cusplets (29.2%), and four teeth (16.6%) which conditions prevented collecting data. (Table S2). The size of teeth with cusplets ranges from 55 mm to 100 mm, teeth without cusplets are 60 mm to 95 mm. Therefore an ontogenetic heterodonty as described for *O. megalodon* (PIMIENTO *et al.* 2010), can be excluded. A dignathic heterodonty can be excluded as well, as upper (Supplement Table 2: Figs 2, 5, 9, 12, 15) and lower jaw teeth (Supplement Table 2: Figs 1, 14) show or do not show cusplets. A disjunct heterodonty can further not be taken into account, as anterior (Supplement Table 2: Fig. 1) as well as posterior teeth (Supplement Table 2: Fig. 5) show cusplets.

Remarks: SCHULTZ (1968) described both putative *Otodus* species, *O. (Megaselachus) chubutensis* and *O. (Megaselachus) megalodon* from Plesching (Upper Austria, Ottnangian, Molasse Basin), as well as teeth with lateral cusplets from the putative (sub-) species *O. chubutensis*. Teeth without cusplets were assigned to *O. megalodon*. This view was later shared by several authors such as BRZOBHATÝ & SCHULTZ (1971, 1973), BRZOBHATÝ *et al.* (1975), whereas HOLEC *et al.* (1995) already discussed the possibility that the lower Miocene *O. (Megaselachus) chubutensis* may be the direct ancestor of *O. (Megaselachus) megalodon*. CAPPETTA (2012) notes that *O. (Megaselachus)*







*chubutensis* specimens with or without cusplets exist. This suggestion is shared by BRACHER *et al.* (2019), which report that 60% of teeth collected at the deposits in the lower Miocene deposits Rengetsweiler and Ursendorf show well-developed lateral cusplets. Remaining 30% do not have cusplets and 10% were in poor condition. The stratigraphic distribution of *O. (Megaselachus) chubutensis* ranges from the early to middle Miocene, while *O. (Megaselachus) megalodon* ranges from the middle Miocene to the Pliocene (PIMIENTO *et al.* 2010, 2013). Sexual dimorphism as explanation for the occurrence of teeth with and without cusplets seems unlikely when reviewing the morphological changes in *Otodus* teeth over time showing a shift from teeth exclusively showing cusplets to absence of those (Oligocene to Pliocene).

CAPPETTA (2012) suggests the existence of different populations with different phenotypes, *i. e.*, populations differing in the presence or absence of cusplets. Regarding the fact that cusplets seem to disappear in younger fossils (CAPPETTA 2012), this hypothesis seems more likely compared to sexual dimorphism. Migration of individuals carrying a dominant character, *i. e.*, no cusplets, may have gradually replaced the recessive phenotype with cusplets. A migration between different geographically distant populations would have been possible, as connections to the Mediterranean as well as Atlantic Ocean existed (RÖGL 1998) and large-scale migration is widely documented in the extant top predator *Carcharodon carcharias* (BONFIL *et al.* 2005; WENG *et al.* 2007; DOMEIER & NASBY-LUCAS 2008; JORGENSEN *et al.* 2010; DEL RAYE *et al.* 2013), which may have formed a similar ecological niche as *O. (Megaselachus) chubutensis* (PIMIENTO *et al.* 2010; FERRÓN 2017).

#### Neoselachii incertae sedis

#### Genus *Nanocetorhinus* UNDERWOOD & SCHLÖGL, 2013

Type species: *Nanocetorhinus tuberculatus* UNDERWOOD & SCHLÖGL, 2013, type by monotypy.

- ◀ Fig. 5: **1:** *Mitsukurina lineata* (PROBST, 1879) (NHMW 2018/0309/0029; upper tooth; a: lingual view, b: profile view, c: labial view); **2:** *Odontaspis molassica* PROBST, 1879 (NHMW 2018/0309/0031; lower tooth; a: lingual view, b: labial view); **3:** *Odontaspis molassica* PROBST, 1879 (SMNS 96995-1; lower tooth; a: lingual view, b: profile view, c: labial view; Walbertsweiler, Ottnangian, ex. coll. Elmar UNGER); **4:** *Odontaspis molassica* PROBST, 1879 (SMNS 96995-2; lower tooth; a: lingual view, b: profile view, c: labial view; Walbertsweiler, Ottnangian, ex. coll. Elmar UNGER); **5:** *Odontaspis molassica* PROBST, 1879 (SMNS 96995-3; upper tooth; a: lingual view, b: profile view, c: labial view; Walbertsweiler, Ottnangian, ex. coll. Elmar UNGER). **6:** *Otodus (Megaselachus) chubutensis* (AMEGHINO, 1901) (P 00367; Haus der Natur Salzburg; a: lingual view, b: labial view).

***Nanocetorhinus tuberculatus* UNDERWOOD & SCHLÖGL, 2013**  
(Fig. 6.1)

1995 *Cetorhinus* sp. – BOLLIGER *et al.*: pl. 2, fig. 7.

2005 Elasmobranch dermal denticle or possible tooth, Form I – JOHNS *et al.*: 39; fig. 37.

- \* 2013 *Nanocetorhinus tuberculatus* – UNDERWOOD & SCHLÖGL: 502–504; figs 9 A–H.  
2017 *Nanocetorhinus tuberculatus* – POLLERSPÖCK & STRAUBE: 42–43; fig. 11 no. 7–9.  
2018 *Nanocetorhinus tuberculatus* – POLLERSPÖCK *et al.*: name only (suppl. tab. 1).

Material: single tooth, (NHMW 2018/0309/0032, Fig. 6.1)

Size: Height: 1.45 mm; Width: 0.6 mm.

Description: Fig. 6.1 shows a characteristic tooth of that species in labial view with its distinct ornamentation. The dental enamel is strongly structured without any recognizable patterns. Enameloid folds are absent. Contrasting, the lingual side is smooth. The basis of the crown is circular in cross-section, the crown is upright and slender. The root consists of two lobes and does not show a foramen labially.

Remarks: After the species was first described from the central Paratethys (Slovakia, Latest Burdigalian (Karpatian) in UNDERWOOD & SCHLÖGL (2013), we report this species from another locality in Austria. This suggests that the species was both geographically (Switzerland, Austria, Germany and Slovakia) as well as stratigraphically at least from the Egerian (POLLERSPÖCK *et al.* 2018), during the Ottnangian (POLLERSPÖCK & STRAUBE 2017; BRACHER *et al.* 2019, this study) to the Karpatian (UNDERWOOD & SCHLÖGL 2013) widespread.

Order Rajiformes BERG, 1940

Family Rajidae BLAINVILLE, 1816

Genus *Raja* LINNÉ, 1758

Type species: *Raja miraletus* LINNÉ, 1758, type by subsequent designation.

***Raja gentili* JOLEAUD, 1912**  
(Figs 6.2a, 6.2b)

- \* 1912 *Raja gentili* – JOLEAUD: pl. 8, figs 37–44, non figs 45–46.  
1930 *Raja gentili* – FISCHLI: 157; fig. 4.  
1970 *Raja gentili* – CAPPETTA: 84–85; pl. 20, figs 28–32.  
2001 *Raja gentili* – WARD & BONAVIA: 143; pl. 2, figs f, g.  
2007 *Raja* cf. *gentili* – BRACHER & UNGER: 147–149; pl. 53.  
2009 *Raja gentili* – BRISSWALTER: 44; pl. 9, fig. 3.  
2011 *Raja gentili* – VIALLE *et al.*: 252; figs 4-3, 4-4.  
2012 *Raja gentili* – CAPPETTA: 360.  
2017 *Raja gentili* – POLLERSPÖCK & STRAUBE: 44; fig. 12 no. 1–5.

Material: 5 teeth (female/male morphotyps, NHMW 2018/0309/0033, Figs 6.2a–b; NHMW 2018/0309/0034),

Size (only Fig.): NHMW 2018/0309/0033: Height: 1.25 mm; Width: 1.8 mm (Fig. 6.2).

Description: Figs 6.2a and 6.2b shows a female morphotype (FEDUCCIA & SLAUGHTER 1974; HERMAN *et al.* 1995; CASTILLO-GÉNIZ *et al.* 2007) characterized by smooth dental enameloid, a low crown, which chewing area is separated into a labial and a lingual side by a distinct transverse crest. The wide root, which often projects beyond the crown, is separated into two root lobes by a deep nutritive groove showing a central foramen.

Remarks: This species, along with other rajids is an example for a sexual dental dimorphism (POLLERSPÖCK & STRAUBE 2017). Male dental morphotypes show in contrast to the female morphotype described above pointed erect crowns (FEDUCCIA & SLAUGHTER 1974; HERMAN *et al.* 1995; CASTILLO-GÉNIZ *et al.* 2007).

### **Rajidae sp. indet.**

(Fig. 6.3)

Material: single tooth (NHMW 2018/0309/0035, Fig. 6.3).

Size: Width: 0.5 mm.

Description: This single tooth fossil displays an almost oval chewing area without any structuring. Its edge appears bent downward. The crown is low, a cusp is not developed. A transverse keel and an apron is lacking. The root shows two distinct foramina, it is not projecting beyond the crown.

Remarks: This single tooth does not allow a further more detailed identification. Comparing with HERMAN *et al.* (1994, 1995, 1996), we can only preliminary assign the tooth to Rajidae. This is based on lacking a median lingual ridge in the lingual face of the crown, the smooth crown with absence of any ornamentation, the absence of a transverse crest and the form of the bilobed root.

Order Myliobatiformes COMPAGNO, 1973

Family Aetobatidae AGASSIZ, 1858

Genus *Aetobatus* BLAINVILLE, 1816

Type species: *Raja aquila* LINNÉ, 1758, type by subsequent designation

***Aetobatus arcuatus* AGASSIZ, 1843**

(Fig. 6.4)

- \* 1843 *Aetobatis arcuatus* – AGASSIZ: 327–328.
- 1877 *Aetobates arcuatus* – PROBST: 84; pl. 1, fig. 28.
- 1930 *Aetobates arcuatus* – FISCHLI: 160; pl. 5, fig. 9.
- 1968 *Aetobatis arcuatus* – SCHULTZ: 91; pl. 4, fig. 82.
- 1971 *Aetobatis arcuatus* – SCHULTZ: 332–333; pl. 4, fig. 24.
- 1991 *Aetobatus arcuatus* – BARTHELT *et al.*: 206. [name only]
- 1995 *Aetobatus arcuatus* – HIDEN: 73–74; pl. 7, figs 3, 9.

- 2003 *Aetobatus arcuatus* – SCHULTZ: 187.  
 2007 *Aetobatus arcuatus* – BRACHER & UNGER: 167–168; pl. 62.  
 2010 *Aetobatus arcuatus* – SCHULTZ *et al.*: 495; pl. 3, fig. 4.  
 2012 *Aetobatus arcuatus* – CAPPETTA: 445.  
 2013 *Aetobatus arcuatus* – SCHULTZ: 106–109; pl. 11, figs 9–13.  
 2016 *Aetobatus arcuatus* – SACH: 105. [name only]

Material: single teeth (part of the dental plate), ex. collection DANNINGER (NHMW 2018/0309/0036, Fig. 6.4).

Size: Width: +16.8 mm.

Description: The studied fossil (Fig. 6.4) is a piece of the lower dental plate of *Aetobatus arcuatus*. The crown is low, the occlusal face of the crown is smooth and shows several furrows. The polyaulacorhize and lingually bent root is long and shows numerous parallel grooves.

Remarks: AGASSIZ (1858) described the family Aëtobatinae for the genus *Aetobatis*. This family was changed to Aetobatinae in GILL (1865b). POEY (1868) assigned the genus to the Myliobatidae and Aetobatinae were discarded. Recent molecular and morphological analyses of Eagle Rays resulted in the resurrection of the family Aetobatidae (WHITE & NAYLOR 2016). Today, this family comprises a single genus and five species (POLLERSPÖCK & STRAUBE 2019).

Characteristic for these dental plates are the chewing areas, which are touching each other in a right angle at the middle of the chewing areas and a lingually weakly developed root area, which is marked by several parallel ridges and grooves. *A. arcuatus* is only documented by few fossils and is hitherto the only evidence of large-toothed rays at Allerding.

#### Family Dasyatidae JORDAN & GILBERT, 1879

##### Genus *Dasyatis* RAFINESQUE, 1810

Type species: *Dasyatis ujo* RAFINESQUE, 1810, type by monotypy.

#### ***Dasyatis rugosa* (PROBST, 1877)**

(Fig. 6.5)

- \* 1877 *Raja rugosa* n. sp. – PROBST: 76; pl. 1, figs 5–7, ?8, ?9.  
 1970 *Dasyatis rugosa* – CAPPETTA: 95–97; pl. 21, figs 1–14.  
 1991 *Dasyatis rugosa* – BARTHELT *et al.*: 205; pl. 4, figs 5–8.  
 1995 *Dasyatis rugosa* – HIDEN: 71; pl. 6, figs 2–4.  
 2003 *Dasyatis* cf. *rugosa* – SCHULTZ: 187. [name only]  
 2007 *Dasyatis rugosa* – BRACHER & UNGER: 155; pl. 57.  
 2012 *Dasyatis rugosa* – CAPPETTA: 417; fig. 408.  
 2013 *Dasyatis* cf. *rugosa* – SCHULTZ: 102.  
 2014 *Dasyatis rugosa* – POLLERSPÖCK & BEAURY: 32; pl. 2, fig. 8.  
 2015 *Dasyatis* cf. *rugosa* – REINECKE: 20–21; fig. 12.

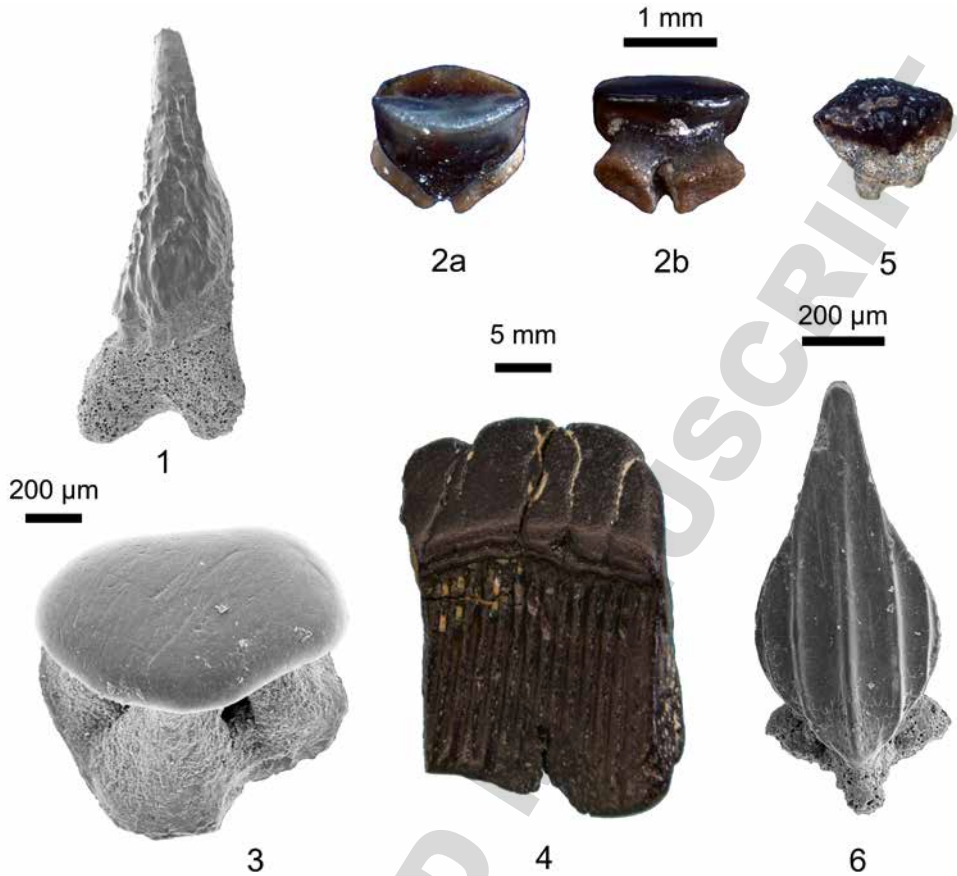


Fig. 6. **1:** *Nanocetorhinus tuberculatus* UNDERWOOD & SCHLÖGL, 2013 (NHMW 2018/0309/0032; labial view); **2:** *Raja gentili* JOLEAUD, 1912 (NHMW 2018/0309/0033; female morphotyp; a: lingual view, b: labial view); **3:** Rajidae indet. (NHMW 2018/0309/0035; lingual view); **4:** *Aetobatus arcuatus* AGASSIZ, 1843 (NHMW 2018/0309/0036; lower tooth plate; lingual view); **5:** *Dasyatis rugosa* (PROBST, 1877) (NHMW 2018/0309/0037; female morphotyp; lingual view); **6:** “scyliorhinid/pentanchid” denticle (NHMW 2018/0309/0039).

Material: 5 teeth, (NHMW 2018/0309/0037, Fig. 6.5, NHMW 2018/0309/0038).

Size (only Fig.): Width: 1.7 mm (Fig. 6.5).

Description: All collected teeth are in bad condition and only fragmentarily preserved. The tooth shown in Fig. 6.5, however, displays all characters necessary to identify the species and further allows to identify the female type morphology. The flat labial crown area is heavily ornamented and marked by deep grooves and sharp ridges. Contrasting, the lingual area is lacking any ornamentation. The root is not completely preserved.

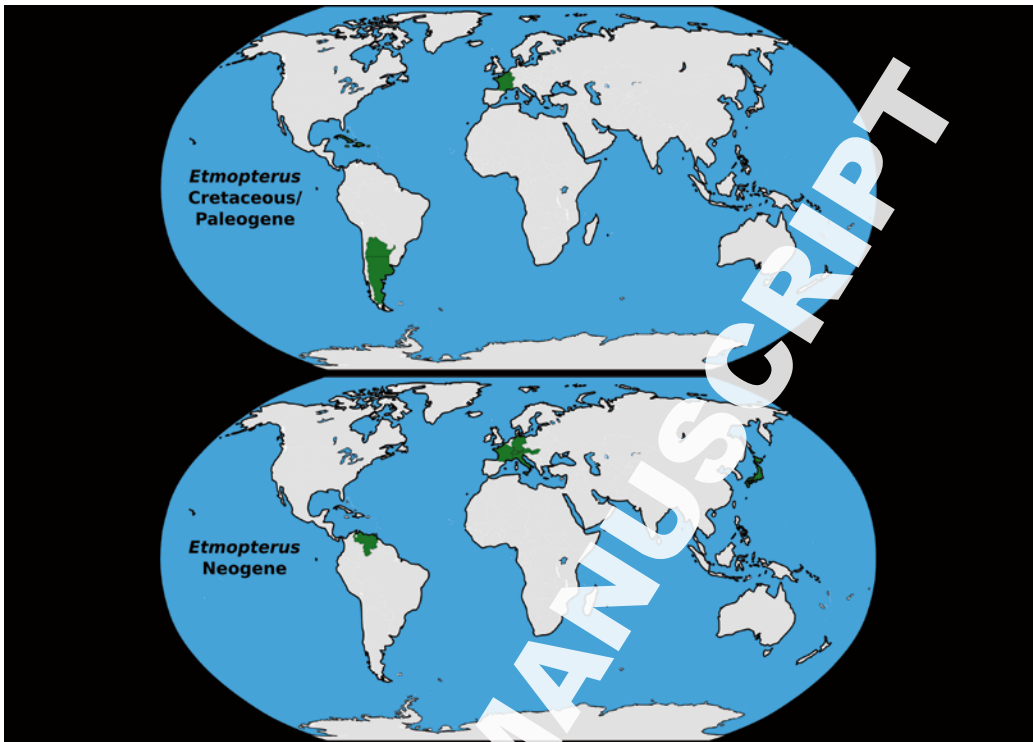


Fig. 7. Palaeogeographic distribution of the squaliform genus *Etmopterus*.

Remarks: *D. rugosa* is a common and frequently collected species of stingray from the Ottnangian sediments of the Paratethys (PROBST 1877; BRACHER & UNGER 2007). The species is reported from the Chattian for the first time and is then documented until the Serravallian (REINECKE 2015).

### Dermal Denticles

Material: 15 denticles (NHMW 2018/0309/0039, Fig. 6.6, NHMW 2018/0309/0040)

Description: Only few fossilized dermal denticles were collected. The majority can be assigned to the scyliorhinid type described in POLLERSPÖCK & STRAUBE (2017), *i. e.*, smooth elongated denticles with three to five parallel ridges and a typical bowl-like shape at the basis as in extant scyliorhinid sharks (POLLERSPÖCK & STRAUBE 2017).

### Distribution of the recorded squaliform sharks

Resulting from an extensive literature research, 108 studies were found (Supplement Table 1) comprising 210 records containing records of the genera *Centrophorus* (73 records), *Deania* (24 records), *Etmopterus* (25 records), *Isistius* (72 records), and *Squaliolus* (16 records) (Table 2). The majority of records stems from the Miocene



Table 2. Number of records and distribution of the following squaliform sharks genera: *Centrophorus*, *Deania*, *Isistius*, *Squaliolus*, and *Etmopterus*.

Genus	Continent	Country	Epoch/number of records											
			Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene					
	Antarctica	Antarctica			2									
	Asia	Japan						3						
	Australia	New Zealand	1	2	1	2	2	2	1					
	Europa	Belgium						1						
		Denmark			1									
		Austria			1			2						
		Switzerland						4						
		Czech Republic			1	1								
		Hungary						1						
		Germany		1		1		6						
		France			2			5			1			
		Italy								9		3		
		Spain									1			
	Central America	Antilles				3								
		Panama						2						
	North America	British Columbia	1											
		California		1				1						
		Mexico						1						
	South America	Chile											1	
		Colombia						1						
		Ecuador						1					1	
		Venezuela						3					1	

*Centrophorus*



Genus	Continent	Country	Epoch/number of records									
			Cretaceous	Paleocene	Eocene	Oligocene	Miocene	Pliocene	Pleistocene			
<i>Isistius</i>	Africa	Algeria, Tunisia		1	1							
	Asia	Marocco	2	1								
		Japan					1					
Europe	Uzbekistan			1								
	Netherland			2								
	Belgium			7						1		
	Denmark			1								
	Austria							2				
	Switzerland							4				
	Hungary							1				
	Slovakia							1				
	Germany				1	3			4			
	France					4			6			
	Portugal								4			
	Spain									1		
	United Kingdom					4						
Central America	Antilles						2					
	Costa Rica								2		1	
	Panama								1			
North America	California		1									
	Florida											1
	Maryland					1						
	Mexico								1			
	North Carolina										2	
	Virginia					2						
South America	Ecuador									2		1
	Venezuela									1		1

Genus	Continent	Country	Cretaceous	Paleocene	Eocene	Epoch/number of records					
						Oligocene	Miocene	Pliocene	Pleistocene		
<i>Squaliolus</i>	Asia	Japan					1				
	Europa	Austria			1			2			
		Switzerland				1					
		Slovakia				1					
		Germany				1					
		France			1			3			
		Spain						1			
		Central America	Antilles				2		2		
		<b>Total:</b>		3	11	40	13	105	30		6

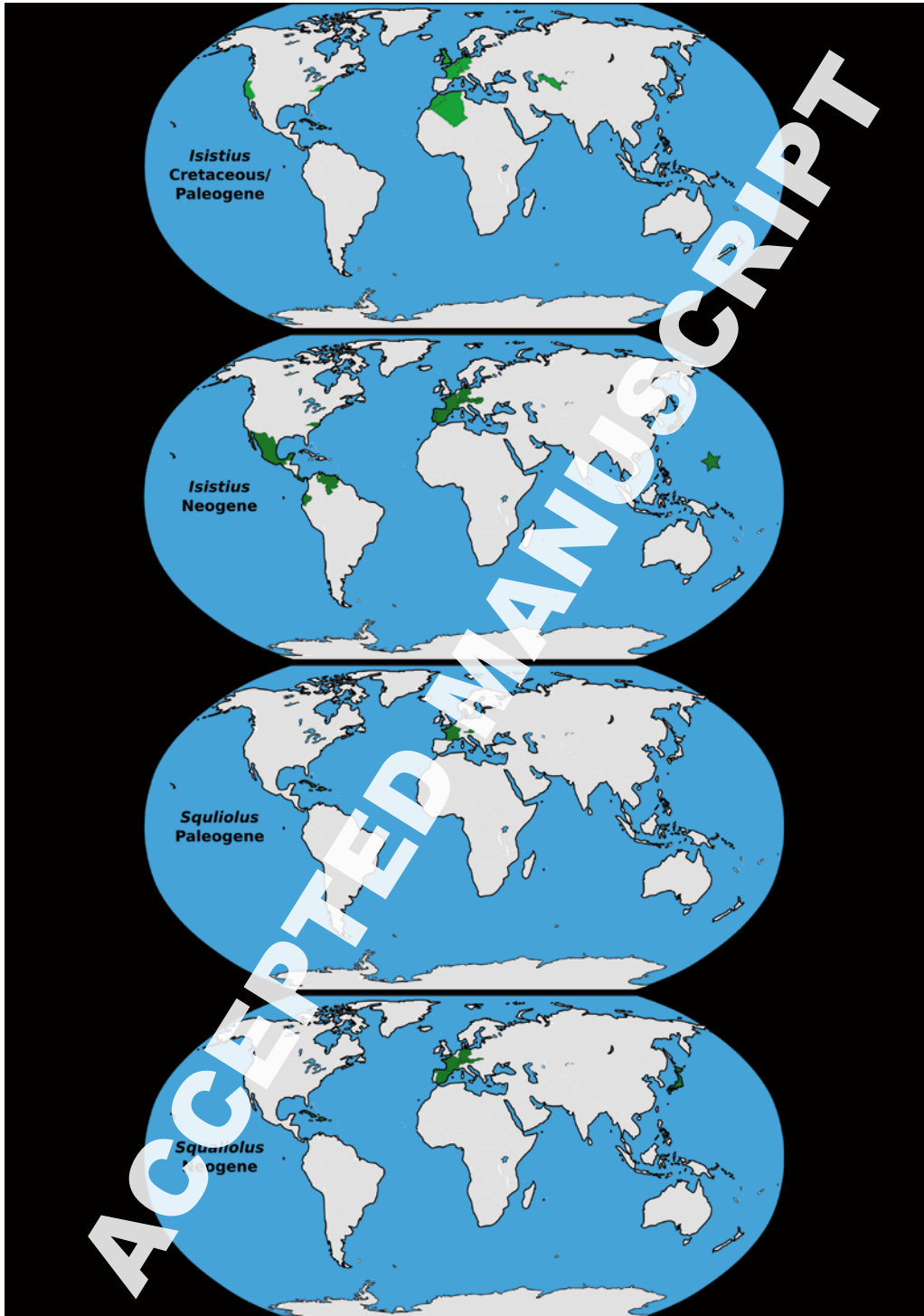


Fig. 8. Palaeogeographic distribution of the squaliform genera *Isistius* and *Squaliolus*.

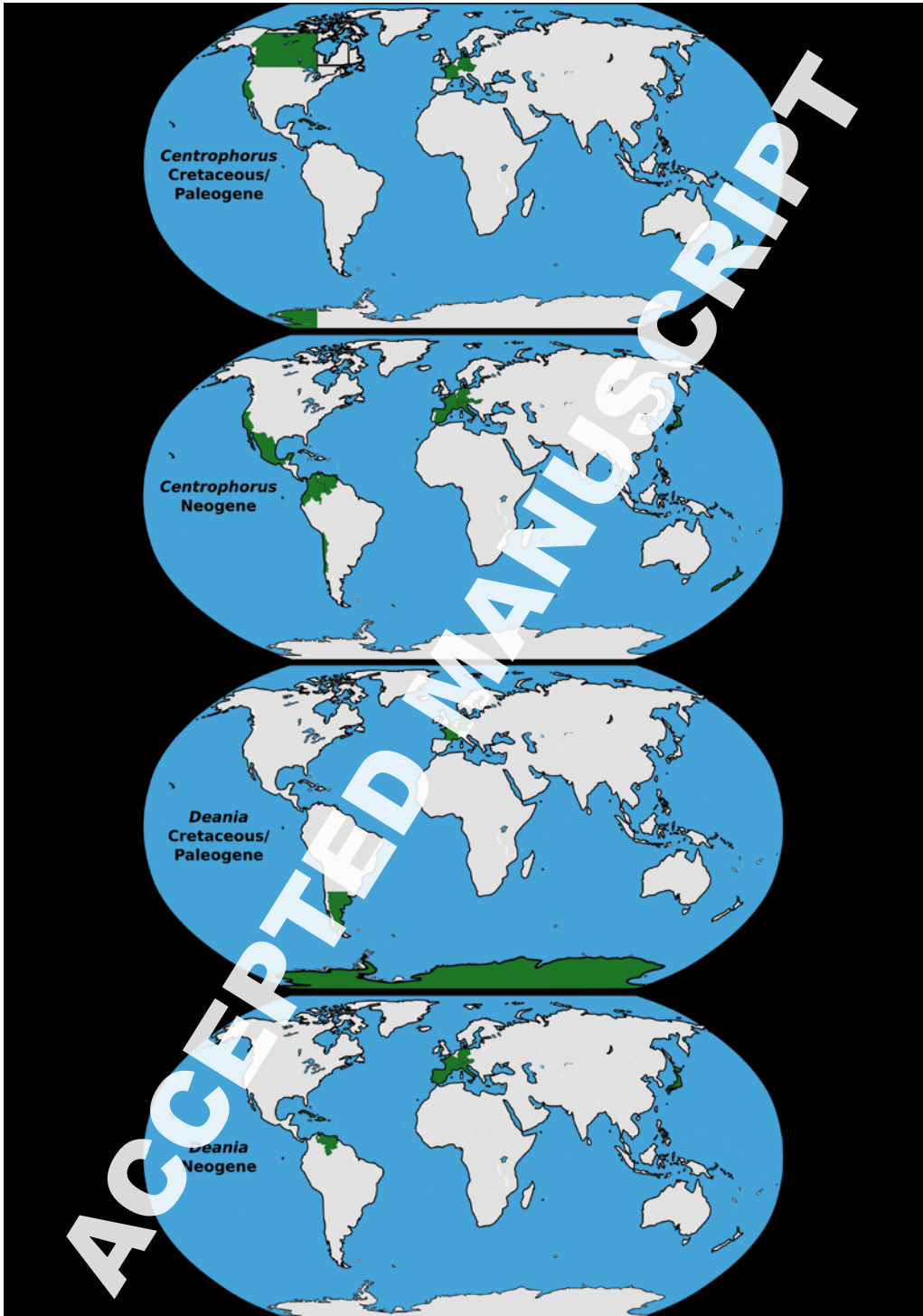


Fig. 9. Palaeogeographic distribution of the squaliform genera *Centrophorus* and *Deania*.



(5.33–23.03 myr, 105 records), followed by Eocene (33.9–56.0 myr, 40 records) and Pliocene records (2.58–5.33 myr, 30 records). Only five Cretaceous records (66.0–145.0 myr) were found. In total 2218 articles dealing with Cretaceous to Holocene Elasmobranch diversities were analysed. The major part of records is reported from Europe (Figs 7–9) (131 records = 62.4%), followed by South-America (19 records = 9.1%), Central-America (18 records = 8.6%), and North-America (12 records = 5.7%). The oldest records are from genera *Centrophorus* (2 records, Cretaceous), *Deania* (2 records, Cretaceous), and *Etmopterus* (1 record, Cretaceous). The genera *Etmopterus* and *Isistius* are reported from the Palaeocene (56.0–66.0 myr) for the first time.

## Discussion

### Palaeodiversity

Our findings increase the diversity reported from Allerding by 25 species. The coastal fauna discussed in SCHULTZ (1971) comprised only seven species and was expanded herein with multiple taxa, which extant representatives are associated with the deep-sea, as *e. g.*, *Chlamydoselachus*, *Etmopterus*, *Centrophorus*, *Deania*, *Isistius*, *Apristurus*, *Odontaspis*, *Mitsukurina*, or *Pristiophorus*. Further typical Oligocene taxa of the Northern Alpine Molasse are documented (*e. g.*, *G. aduncus*, *Rhizoprionodon* sp., *H. serra*). Large-toothed coastal shark and ray species were exclusively found in the horizontal transgression, which is marked in Allerding by microfossil sediments in between the globular granite. Deep-water representatives were collected from clayey marls, overlying the horizontal transgression, which indicates that the seabed has dropped significantly and rapidly (RUPP *et al.* 2011), the water depth has increased, and large amounts of fine sediments were deposited.

The documented diversity largely overlaps in species composition with the geographically nearby Neuhofener Beds (POLLERSPÖCK & STRAUBE 2017).

### Origin of the recorded squaliform sharks

All Cretaceous fossils of squaliform sharks are documented from the Upper Cretaceous, *i. e.*, the Campanian and Maastrichtian. None of the five genera were reported from the Lower Cretaceous. The occurrence of the genus *Deania* in the Lower Cretaceous is still under debate (THIES & MÜLLER 1993; ADNET & CAPPETTA 2001; CAPPETTA 2012).

*Centrophorus* is documented from the Maastrichtian of New Zealand (KEYES 1984), which is considered valid in CAPPETTA (2012) and ADNET & CAPPETTA (2001). HESSIN *et al.* 2007 report on another fossil from the late Campanian to early Maastrichtian (Northumberland Formation, Upper Cretaceous) on Hornby Island, British Columbia, Canada. Older fossil evidence for Centrophoridae are unknown as of today indicating a splitting of genera *Deania* and *Centrophorus* before the late Campanian.

This is in accordance with results from ADNET & CAPPETTA (2001), STRAUBE *et al.* (2015) and FLAMMENSBECK *et al.* (2018), who estimated that the divergence happened in the Upper Cretaceous.

*Isistius* is documented for the first time from the Paleocene of Northern Africa, Germany and California (Table 2, Supplement Table 1). Which of the records represents the oldest record cannot be identified. Records from Northern Africa and Germany are assigned to the Thanetian (Upper Paleocene), the Californian record is assigned to the Ynezian, which comprises the Upper-Middle Paleocene (Thanetian/Selandian). The oldest fossils of the phylogenetically close genus *Dalatias* (STRAUBE *et al.* 2015) are documented from the Danian of New Zealand (MANNERING & HILLER 2008), as well as the Danian of Turkmenistan (GLIKMAN 1964). The species *Somniosus crenulatus* (ARAMBOURG 1952) from the Thanetian was later assigned to a genus morphologically close to *Dalatias* by CAPPETTA (2012), which was also documented from Jordania (CAPPETTA 2012). Both the record from New Zealand and Turkmenistan constitute crown tips, which do not allow for a definite allocation to the genus *Dalatias*. Therefore, the oldest fossil evidence for the *Isistius/Dalatias*-clade comes from the Thanetian. Latest studies estimating divergence times from molecular data (STRAUBE *et al.* 2015) and a combination of fossil morphological and molecular data (FLAMMENSBECK *et al.* 2018) suggest an Upper Cretaceous origin of the clade. The discrepancy of the fossil record and the divergence time estimations may indicate a large fossil gap.

VAN DER BRUGGHEN *et al.* (1993) describe a shark and ray fauna from the Maastrichtian, where the authors depict a tooth fossil identified as *Etmopterus* sp. carrying numerous characters of *Etmopterus* lower jaw teeth. This supports the hypothesis that *Etmopterus* split from the *Trigonognathus/Centroscyllum/Aculeola*-clade in the Upper Cretaceous. Both STRAUBE *et al.* (2015) and FLAMMENSBECK *et al.* (2018) estimate the divergence time to the Campanian.

The two oldest fossil records of *Squaliolus* were collected from Eocene deposits (Table 2, Supplement Table 1). ADNET & CAPPETTA (2001) suggest a split from *Euprotomicrus* already in the Eocene, while FLAMMENSBECK *et al.* (2018) estimate this divergence to the Maastrichtian.

Based on our literature research, we cannot detect a clear geographic origin of squaliform genera. Especially the fossil record of the Centrophoridae disagrees with recent assumptions to its geographic origin. While ADNET *et al.* (2008), KRIWET & KLUG (2009) and MAISEY (2012) suggest a central or northern Tethys origin of all squaliform families, including Centrophoridae, respectively, the oldest records of the family (genus *Centrophorus*) are documented from the North American Pacific coast as well as New Zealand (Fig. 7; HESSIN *et al.* 2007; KEYES 1984). We therefore suggest a more detailed analysis of the geography of fossil findings of squaliformes from their estimated time of origin, *i. e.*, fossils from the Cretaceous and Paleocene, to track geographic origins of taxa (work in progress).

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ACCEPTED MANUSCRIPT

Supplement Table S1. List of references about the paleogeographic distribution of the following squaliform sharks genera: *Centrophorus*, *Deania*, *Isistius*, *Squaliolus*, and *Etmopterus*.

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described Material as	Collectiomr.	Remarks
ADNET 2006	Eocene	Lutetian		Paleogene	Europe	France	Central Tethys	<i>Centrophorus aff. granulosis</i>	+450 teeth	ANG22-28	
ADNET 2006	Eocene	Lutetian		Paleogene	Europe	France	Central Tethys	<i>Deania angoumeensis</i>	+350 teeth	ANG29-35	
ADNET 2006	Eocene	Bartonian	Lutetian	Paleogene	Europe	France	Central Tethys	<i>Etmopterus cahuzad</i>	55 teeth	ANG53-60	
ADNET 2006	Eocene	Lutetian		Paleogene	Europe	France	Central Tethys	<i>Isistius aff. tritiratus</i>	14 teeth	ANG98-100	
ADNET 2006	Eocene	Bartonian	Lutetian	Paleogene	Europe	France	Central Tethys	<i>Squaliolus gasconensis</i>	180 teeth	ANG75-82	
ADNET et al. 2008	Eocene	Bartonian		Paleogene	Europe	France	Central Tethys	<i>Isistius cf. tritiratus</i>			only species list
ADNET et al. 2008	Eocene	Bartonian		Paleogene	Europe	France	Central Tethys	<i>Centrophorus cf. granulosis</i>			only species list
AGUILERA & DE AGUILERA 2001	Miocene	Messinian		Neogene	South America	Venezuela	Caribbean	<i>Deania sp.</i>			only species list
AGUILERA & DE AGUILERA 2001	Pliocene	Zanclean		Neogene	South America	Venezuela	Caribbean	<i>Deania sp.</i>			only species list
AGUILERA & DE AGUILERA 2001	Miocene	Messinian		Neogene	South America	Venezuela	Caribbean	<i>Etmopterus sp.</i>			only species list
AGUILERA & DE AGUILERA 2001	Pliocene	Zanclean		Neogene	South America	Venezuela	Caribbean	<i>Etmopterus sp.</i>			only species list
AGUILERA & DE AGUILERA 2001	Miocene	Messinian		Neogene	South America	Venezuela	Caribbean	<i>Isistius aff. triangulus</i>			only species list
AGUILERA & DE AGUILERA 2001	Pliocene	Zanclean		Neogene	South America	Venezuela	Caribbean	<i>Isistius aff. triangulus</i>			only species list
AGUILERA & DE AGUILERA 2001	Miocene	Messinian		Neogene	South America	Venezuela	Caribbean	<i>Centrophorus sp.</i>			only species list
AGUILERA & DE AGUILERA 2001	Pliocene	Zanclean		Neogene	South America	Venezuela	Caribbean	<i>Centrophorus sp.</i>			only species list
ANTUNES & JONET 1970	Miocene	Langhian	Serravalian	Neogene	Europe	Portugal	Eastern North Atlantic	<i>Deania sp.</i>			only species list
ANTUNES & JONET 1970	Miocene	Langhian	Serravalian	Neogene	Europe	Portugal	Eastern North Atlantic	<i>Isistius triangulus</i>			
ANTUNES et al. 1981	Miocene	Burdigalian		Neogene	Europe	Portugal	Western Mediterranean	<i>Isistius sp.</i>	1		no figure
ARAMBOURG 1952	Paleocene			Paleogene	Africa	Algeria, Tunisia, Morocco	Western Mediterranean	<i>Isistius tritiratus</i>			
ARAMBOURG 1952	Eocene			Paleogene	Africa	Algeria, Tunisia, Morocco	Western Mediterranean	<i>Isistius tritiratus</i>			
BAIER et al. 2004	Miocene	Burdigalian		Neogene	Europe	Germany	Central Paratethys	<i>Centrophorus cf. granulosis</i>			only species list

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described as	Material	Collectionnr.	Remarks
BARTHEL <i>et al.</i> 1991	Miocene	Burdigalian		Neogene	Europe	Germany	Central Paratethys	<i>Centrophorus cf. granulosis</i>				no information about number of specimens
BARTHEL <i>et al.</i> 1991	Miocene	Burdigalian		Neogene	Europe	Germany	Central Paratethys	<i>Etmopterus sp.</i>	1 tooth			no image
BARTHEL <i>et al.</i> 1991	Miocene	Burdigalian		Neogene	Europe	Germany	Central Paratethys	<i>Isistius triangulus</i>				
BARTHEL <i>et al.</i> 1991	Miocene	Burdigalian		Neogene	Europe	Germany	Central Paratethys	<i>Squaliolus sp.</i>				
BARTHEL 1997	Paleocene Danian			Paleogene	South America	Argentina	Western South Atlantic	<i>Deania sp.</i>				only species list
BERNÁRDEZ 1997	Paleocene Danian			Paleogene	South America	Argentina	Western South Atlantic	<i>Etmopterus sp.</i>				only species list
BOLLIGER <i>et al.</i> 1995	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Deania sp.</i>			PIMUZA/I-3053	
BOLLIGER <i>et al.</i> 1995	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Etmopterus sp.</i>			PIMUZA/I-3048, PIMUZA/I-3066	
BOLLIGER <i>et al.</i> 1995	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Isistius sp.</i>				
BOLLIGER <i>et al.</i> 1995	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Squaliolus sp.</i>			PIMUZA/I-3052	
BOLLIGER <i>et al.</i> 1995	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Centrophorus sp.</i>			PIMUZA/I-3055	
BOR 1985	Eocene	Ypresian		Lutetian	Europe	Netherlands	Central Tethys	<i>Isistius triratus</i>	46 LT			
BRISWALTER 2009	Miocene	Langhian		Serravallian	Europe	France	Western Paratethys	<i>Isistius triangulus</i>	500 teeth			
BRISWALTER 2009	Miocene	Langhian		Serravallian	Europe	France	Western Paratethys	<i>Centrophorus cf. granulosis</i>	342 teeth			
BRZOBHATÝ & KALABIS 1970	Oligocene	Rupelian		Paleogene	Europe	Czech Republic	Central Tethys	<i>Centrophorus sp.</i>	Squalus sp. 20 teeth			Geol.-pal. Institut des Mährischen Museums in Brno, Coll. Nr. 16401
CAPPETTA 1970	Miocene	Aquitainian		Neogene	Europe	France	Western Mediterranean	<i>Isistius triangulus</i>	12			
CAPPETTA & CAVALLO 2006	Pliocene	Zanclean		Piacenzian	Europe	Italy	Western Mediterranean	<i>Centrophorus aff. granulosis</i>	1 tooth			
CAPPETTA <i>et al.</i> 1967	Miocene	Langhian		Neogene	Europe	France	Western Mediterranean	<i>Centrophorus cf. granulosis</i>	Acanthias radicans			only species list

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described as	Material	Collectionnr.	Remarks
CAPPETTA <i>et al.</i> 1967	Miocene	Langhian		Neogene	Europe	France	Western Mediterranean	<i>Etmopterus</i> sp.				only species list
CAPPETTA <i>et al.</i> 1967	Miocene	Langhian		Neogene	Europe	France	Western Mediterranean	<i>Isistius triangulus</i>				only species list
CAPPETTA & NOLF 1991	Pliocene	Zanclean		Neogene	Europe	France	Western Mediterranean	<i>Centrophorus</i> aff.		3 LT, 3 UT		
CAPPETTA & NOLF 1991	Pliocene	Zanclean		Neogene	Europe	France	Western Mediterranean	<i>Deania</i> sp.		2 LT, 1 UT		
CARLSEN & CUNY 2014	Eocene	Ypresian	Lutetian	Paleogene	Europe	Denmark	North Sea Basin	<i>Isistius tritiratus</i>		9 LT	DK730 (1 well preserved tooth), Lot MM0002 (5 well preserved teeth) and Lot AWC11.0 (3 fragmentary teeth).	The Trede Ness teeth have smooth cutting edges on the crown and thereby separate from teeth of <i>Isistius triangulus</i> which have serrated cutting edges (LONGBOTTOM, 1979; ADNET, 2006). Teeth of living <i>Isistius brasiliensis</i> (QUOY & GAIMARD, 1824 have higher roots than those of <i>Isistius tritiratus</i> (ARAMBURG, 1952). The Trede Ness teeth are very similar to teeth of <i>Isistius tritiratus</i> , which lack serration (ARAMBURG 1952). <i>I. tritiratus</i> is known from the Lower Eocene of England (CASIER 1966; COOPER 1977; RAYNER <i>et al.</i> 2009), the Eocene of Belgium (NOLF 1988; VAN DEN ECKHAUT & DE SCHUTTER 2009; ISERBYT & DE SCHUTTER 2012) and Morocco (ARAMBURG 1952; WARD & WEST 1990; NOUBHANI & CAPPETTA 1997) and the Lutetian of France (ADNET 2006).
CARLSEN & CUNY 2014	Eocene	Ypresian		Paleogene	Europe	Denmark	North Sea Basin	<i>Centrophorus</i> aff. <i>granulosus</i>		22 teeth	DK731, Lot AWC10.0, Lot SL0001 and Lot MM3118.0	
CARRILLO-BRICENO <i>et al.</i> 2014	Miocene	Messinian		Neogene	South America	Ecuador	Central Eastern Pacific	<i>Isistius cf. triangulus</i>		12 LT	PPP-3484-T-3 (4 teeth), PPP-3492-T-1, PPP-3493-T-2 (7 teeth)	from Camarones River, Onzole Formation (Late Miocene-Early Pliocene)

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described Material as	Collectionnr.	Remarks
CARRILLO-BRICEÑO <i>et al.</i> 2014	Pliocene	Zanclean		Neogene	South America	Ecuador	Central Eastern Pacific	<i>Isistius cf. triangulus</i>	12 LT	PPP-3484-T-3 (4 teeth), PPP-3492-T-1, Pliocene) PPP-3493-T-2 (7 teeth)	from Camarones River, Onzole Formation (Late Miocene-Early Pliocene)
CARRILLO-BRICEÑO <i>et al.</i> 2014	Miocene	Messinian		Neogene	South America	Ecuador	Central Eastern Pacific	<i>Centroprorhus</i> sp.	4 LT	2 teeth from Playa de Oro (PPP-3455-T-2) and Punta Verde Early Pliocene (PPP-3476-T-1), 2 teeth from Camarones River (PPP-3493-T-3)	2 teeth: Angostura Formation (Middle-Late Miocene); 2 teeth: Onzole Formation (Late Miocene-Early Pliocene)
CARRILLO-BRICEÑO <i>et al.</i> 2014	Pliocene	Zanclean		Neogene	South America	Ecuador	Central Eastern Pacific	<i>Centroprorhus</i> sp.	4 LT	2 teeth from Playa de Oro (PPP-3455-T-2) and Punta Verde Early Pliocene (PPP-3476-T-1), 2 teeth from Camarones River (PPP-3493-T-3)	2 teeth: Angostura Formation (Middle-Late Miocene); 2 teeth: Onzole Formation (Late Miocene-Early Pliocene)
CARRILLO-BRICEÑO <i>et al.</i> 2016	Miocene	Aquitanian		Neogene	South America	Colombia	Caribbean	<i>Centroprorhus</i> sp.	5 LT	MUNSTR-39927	The specimen illustrated as <i>Acanthias stehlini</i> by LERICHE (1938: pl. 1, fig. 5) from the locality of Mene de Acosta in Venezuela (San Lorenzo Formation: early-middle Miocene) is, instead, a lower tooth of <i>Centroprorhus</i> (Fig. 3.14–3.15), as previously suggested by Cappetta (2012: p. 116). The poorly preserved single isolated and fragmented tooth used by Leriche (1938) to erect <i>Acanthias stehlini</i> ( <i>Centroprorhus stehlini</i> ) does not exhibit any diagnostic features that may distinguish it from the specimens from the Ujiba Formation or any other known fossil or recent species. We consider Leriche's species a nomen dubium of questionable taxonomical validity.

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described Material as	Collectionnr.	Remarks
CARRILLO-BRICEÑO <i>et al.</i> 2015	Miocene	Tortonian	Messinian	Neogene	Central America	Panama	Caribbean	<i>Isisitus</i> sp.	272	PIMUZ-AI-4202	Pina locality, Chagres Sandstone is the youngest member (~7.9-5.3 Ma), Colon Province
CARRILLO-BRICEÑO <i>et al.</i> 2015	Miocene	Tortonian	Messinian	Neogene	Central America	Panama	Caribbean	<i>Centrophorus</i> aff. <i>granulosus</i>	11	PIMUZ-AI-4267, F; PIMUZ-AI-4268 Ma)	Pina locality, Chagres Sandstone is the youngest member (~7.9-5.3 Ma), Colon Province
CASE <i>et al.</i> 1996	Eocene	Lutetian		Paleogene	Asia	Uzbekistan	Eastern Tethys	<i>Isisitus triturratus</i>	15 LT	(CMGE 57/1217/3), (CMGE 58/1217/3), (CMGE 59/1217/3) and (CMGE 60/1217/3	no image
CASIER 1967	Eocene	Ypresian		Paleogene	Europe	Germany	North Sea Basin	<i>Isisitus triturratus</i>	1 tooth		
CASIER 1966	Oligocene			Paleogene	Central America	Antilles	Caribbean	<i>Centrophorus</i> sp.	2 teeth		
CASIER 1966	Oligocene			Paleogene	Central America	Antilles	Caribbean	<i>Centrophorus squamosus</i>			<i>Cheirostephanus hurzeleri</i>
CASIER 1966	Oligocene			Paleogene	Central America	Antilles	Caribbean	<i>Etmopterus acutidens</i>	2 teeth		<i>Centrosymnus schaubi</i> CASIER, 1958; p. 31, pl. 1, fig. 12 (non fig. 10, non fig. 11); see Casier (1966)
CASIER 1966	Oligocene			Paleogene	Central America	Antilles	Caribbean	<i>Isisitus</i> sp.			
CASIER 1966	Oligocene			Paleogene	Central America	Antilles	Caribbean	<i>Squaliolus schaubi</i>			
CASIER 1958	Oligocene	Chattian		Paleogene	Central America	Antilles	Caribbean	<i>Centrophorus squamosus</i>	1		
CASIER 1958	Oligocene	Chattian		Paleogene	Central America	Antilles	Caribbean	<i>Etmopterus acutidens</i>			<i>Centrosymnus schaubi</i> CASIER, 1958; p. 31, pl. 1, fig. 12 (non fig. 10, non fig. 11); see CASIER (1966)
CASIER 1958	Oligocene	Chattian		Paleogene	Central America	Antilles	Caribbean	<i>Isisitus</i> sp.	1		In 1966 he redescribed them as <i>Sphyaena kugleri</i> Casier and figured more examples. However, his pl. 3, fig. 27 appears to be a specimen of <i>Isisitus triangulus</i> and is thus included in Table 1.



Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described as	Material	Collectionnr.	Remarks
CASIER 1958	Oligocene	Chattian		Paleogene	Central America	Antilles	Caribbean	<i>Squaliolus schaubi</i>	<i>Centroscymnus schaubi</i>	3		
CASIER 1946	Eocene	Ypresian		Paleogene	Europe	Belgium	Central Tethys	<i>Isistius tritiratus</i>		127 teeth		pl. 1, fig. 7, a-k
CASIER & STINTON 1966	Eocene	Ypresian		Paleogene	Europe	United Kingdom	Central Tethys	<i>Isistius tritiratus</i>				
CIGALA-FULGOSI 1986	Pliocene	Zanclean		Neogene	Europe	Italy	Western Mediterranean	<i>Centrophorus cf. granulosus</i>				only species list
CIGALA-FULGOSI 1986	Pliocene	Zanclean		Neogene	Europe	Italy	Western Mediterranean	<i>Centrophorus squamosus</i>				only species list
CIGALA-FULGOSI 1986	Pliocene	Zanclean		Neogene	Europe	Italy	Western Mediterranean	<i>Deania cf. calcea</i>				only species list
CIGALA-FULGOSI 1986	Pliocene	Zanclean		Neogene	Europe	Italy	Western Mediterranean	<i>Etmopterus sp.</i>				only species list
CIGALA-FULGOSI <i>et al.</i> 2009	Pliocene	Piacenzian		Neogene	Europe	Italy	Western Mediterranean	<i>Centrophorus granulosus</i>		180 teeth	CZ-TES 2, 130-310	only species list
COOPER 1977	Eocene	Ypresian		Paleogene	Europe	United Kingdom	Central Tethys	<i>Isistius tritiratus</i>				only species list
DAIMERIES 1889	Eocene	Ypresian		Paleogene	Europe	Belgium	Central Tethys	<i>Isistius tritiratus</i>	<i>Scymnus tritiratus</i>			no image
DAMES 1883	Eocene			Paleogene	Europe	Belgium	Central Tethys	<i>Isistius tritiratus</i>	<i>Centrina tritiratus</i>			no image
DE SCHUTTER & WUNKER 2012	Miocene			Neogene	Europe	Belgium	North Sea Basin	<i>Centrophorus sp.</i>		7 teeth	private collection, DS01-DS04, TL01, LK01-02	
DE SCHUTTER & WUNKER 2012	Pliocene	Zanclean		Neogene	Europe	Belgium	North Sea Basin	<i>Centrophorus sp.</i>				see LANDINI (1977)
DE STEFANO 1909	Pliocene			Neogene	Europe	Italy	Central Paratethys	<i>Centrophorus granulosus</i>	<i>Acanthias vulgaris</i>			only species list
DUTHEIL 1991	Eocene	Ypresian		Paleogene	Europe	France	Central Tethys	<i>Isistius tritiratus</i>				
ENGBRECHT <i>et al.</i> 2017	Eocene	Ypresian	Lutetian	Paleogene	Antarctica	Antarctica	Western South Atlantic	<i>Centrophorus sp.</i>		2 LT	NRM-PZ P15804, NRM-PZ P15807	
FISCHLI 1930	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Isistius triangulus</i>	<i>Isistius tritiratus</i>	>20		

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Country	Ocean	Valid species	Described Material as	Collectionnr.	Remarks
FISCHL 1930	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Centrophorus</i> sp.			
GONZÁLEZ-BARRERA & THIES 2000	Miocene	Tortonian	Messinian	Neogene	North America	Mexico	Central South Pacific	<i>Isistius</i> cf. <i>triangulus</i>			only species list
GONZÁLEZ-BARRERA & THIES 2000	Miocene	Tortonian	Messinian	Neogene	North America	Mexico	Central South Pacific	<i>Centrophorus</i> sp.			only species list
HERMAN <i>et al.</i> 1974	Pliocene	Zanclean		Neogene	Europe	Belgium	North Sea Basin	<i>Isistius</i> sp.	2	Collection C.G.H.	only species list
HESSIN <i>et al.</i> 2007	Cretaceous	Campanian	Maastrichtian	Cretaceous	North America	British Columbia	Western North Pacific	<i>Centrophorus</i> sp.			only species list
HOLEC <i>et al.</i> 1995	Miocene	Burdigalian		Neogene	Europe	Slovakia	Central Paratethys	<i>Isistius triangulus</i>			
ISERBYT & DE SCHUTTER 2012	Eocene	Ypresian		Paleogene	Europe	Belgium	Central Tethys	<i>Isistius triturtatus</i>	58 teeth		see CAPPETTA (1970: p. 74)
JOLEAUD 1912	Miocene			Neogene	Europe	France	Western Mediterranean	<i>Isistius triangulus</i>	<i>Scym-norhinus triangulus</i> <i>Centrophorus radicans</i>		fig. 5–13
JOLEAUD 1912	Miocene			Neogene	Europe	France	Western Mediterranean	<i>Isistius triangulus</i>			
JOST <i>et al.</i> 2016	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Isistius triangulus</i>			Roggiswil-Hornwald, St. Gallen Fm., no systematic part
JOST <i>et al.</i> 2016	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Centrophorus cf. granulatus</i>			Roggiswil-Hornwald, St. Gallen Fm., no systematic part
KEMP <i>et al.</i> 1990	Eocene	Ypresian	Lutelian	Paleogene	Europe	United Kingdom	Central Tethys	<i>Isistius triturtatus</i>			
KENT 1999	Eocene	Ypresian		Paleogene	North America	Virginia	Western North Atlantic	<i>Isistius triturtatus</i>			
KEYES 1984	Cretaceous	Maastrichtian		Cretaceous	Australia	New Zealand	Central South Pacific	<i>Centrophorus squamosus</i>			only species list
KEYES 1984	Paleocene	Danian		Paleogene	Australia	New Zealand	Central South Pacific	<i>Centrophorus squamosus</i>			only species list
KEYES 1984	Eocene	Bartonian		Paleogene	Australia	New Zealand	Central South Pacific	<i>Centrophorus squamosus</i>			only species list
KEYES 1984	Oligocene	Rupelian, Chattian		Paleogene	Australia	New Zealand	Central South Pacific	<i>Centrophorus squamosus</i>			only species list
KEYES 1984	Miocene	Aquitanian, Burdigalian		Neogene	Australia	New Zealand	Central South Pacific	<i>Centrophorus squamosus</i>			only species list

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described as	Material	Collectionnr.	Remarks
KEYES 1984	Pliocene	Zanclean		Neogene	Australia	New Zealand	Central Pacific	<i>Centrophorus squamosus</i>				only species list
Kocsis 2007	Miocene	Burdigalian		Neogene	Europe	Hungary	Central Paratethys	<i>Isistius cf. triangulus</i>		21 lower teeth		
Kocsis 2007	Miocene	Burdigalian		Neogene	Europe	Hungary	Central Paratethys	<i>Centrophorus</i> sp.		1 anterolateral tooth		only dermal denticles
KOIKE <i>et al.</i> 2008	Miocene	Langhian		Neogene	Asia	Japan	Eastern North Pacific	<i>Etmopterus</i> sp.				
LANDINI 1977	Pliocene	Zanclean		Neogene	Europe	Italy	Western Mediterranean	<i>Centrophorus granulosus</i>				
LAURITO MORA 1999	Miocene	Messinian		Neogene	Central America	Costa Rica	Caribbean	<i>Isistius triangulus</i>		29 teeth		
LAURITO MORA 1999	Pliocene	Zanclean		Neogene	Central America	Costa Rica	Caribbean	<i>Isistius triangulus</i>		29 teeth		
LAURITO MORA 1996	Miocene	Messinian		Neogene	Central America	Costa Rica	Caribbean	<i>Isistius triangulus</i>		13 teeth	CLM-016-CLM-028	
LEDoux 1972	Miocene	Burdigalian	Langhian	Neogene	Europe	France	Western Mediterranean	<i>Centrophorus granulosus</i>				= <i>Acanthias serratus</i> PROBST, 1879: p. 174, pl. 3 fig. 33
LEDoux 1972	Miocene	Burdigalian	Langhian	Neogene	Europe	France	Western Mediterranean	<i>Deania calceus</i>				= <i>Acanthia radicans</i> PROBST, 1879: pp. 773–174, pl. 3, fig. 31, 32 (no correct synonym, <i>Acanthia radicans</i> is a synonym of <i>C. granulosus</i> )
LEDoux 1972	Miocene	Burdigalian	Langhian	Neogene	Europe	France	Western Mediterranean	<i>Etmopterus</i> sp.				
LEDoux 1972	Miocene	Burdigalian	Langhian	Neogene	Europe	France	Western Mediterranean	<i>Isistius triangulus</i>				
LEDoux 1972	Miocene	Burdigalian	Langhian	Neogene	Europe	France	Western Mediterranean	<i>Squaliolus schaubi</i>				
LEDoux 1972	Miocene	Burdigalian	Langhian	Neogene	Europe	France	Western Mediterranean	<i>Squaliolus</i> sp.				= <i>Squalifome</i> indet. CAPPETTA (1970: p. 76, fig. 9, pl. 7, fig. 8–9, pl. 8, fig. 1–2)

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described Material as	Collectionnr.	Remarks
LERICHE 1938	Miocene			Neogene	South America	Venezuela	Caribbean	<i>Centrophorus</i> sp.	<i>Acanthias stehlini</i>		see CARRILLO-BRICEÑO <i>et al.</i> (2016): The specimen illustrated as <i>Acanthias stehlini</i> by LERICHE (1938, pl. 1, fig. 5) from the locality of Mene de Acosta in Venezuela (San Lorenzo Formation: early–middle Miocene) is, instead, a lower tooth of <i>Centrophorus</i> (Fig. 3.14–3.15), as previously suggested by CAPPETTA (2012: p. 116). The poorly preserved single isolated and fragmented tooth used by LERICHE (1938) to erect <i>Acanthias stehlini</i> ( <i>Centrophorus stehlini</i> ) does not exhibit any diagnostic features that may distinguish it from the specimens from the Utpa Formation or any other known fossil or recent species. We consider Leriche's species a nomen dubium of questionable taxonomical validity.
LERICHE 1938	Miocene			Neogene	South America	Venezuela	Caribbean	<i>Centrophorus</i> sp.	<i>Nolidanus tenuidens</i>		see CARRILLO-BRICEÑO <i>et al.</i> (2016): It should also be noted that one of the specimens referred to as <i>H. tenuidens</i> by LERICHE (1938: pl. 1, fig. 4) most likely corresponds to an upper anterior tooth of cf. <i>Centrophorus</i> (Fig. 3.16–3.17). doubtful see CAPPETTA (1970: p. 74)
LERICHE 1927	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Isistius triangulus</i>	<i>Scymnus triangulus</i>		
LERICHE 1927	Miocene	Burdigalian		Neogene	Europe	Switzerland	Western Paratethys	<i>Centrophorus</i> cf. <i>granulosus</i>	<i>Acanthias radicans</i>		
LERICHE 1905	Eocene			Paleogene	Europe	Belgium	Central Tethys	<i>Isistius tritiratus</i>			
LONG 1992	Eocene	Ypresian	Lutetian	Paleogene	Antarctica	Antarctica	Western South Atlantic	<i>Centrophorus</i> sp.		20 teeth	nr. of specimen, <i>Centrophorus + Deania!</i>
LONG 1992	Eocene	Ypresian	Lutetian	Paleogene	Antarctica	Antarctica	Western South Atlantic	<i>Deania</i> sp.		20 teeth	nr. of specimen, <i>Centrophorus + Deania!</i>

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described Material as	Collectionnr.	Remarks
Longbottom 1979	Miocene	Tortonian		Neogene	South America	Ecuador	Central Eastern Pacific	<i>Isistius triangulus</i>	3	P.59282-4	CASIER (1958) described specimens of <i>Isistius</i> sp. from Barbados. In 1966 he redescribed them as <i>Sphyræna kugleri</i> Casier and figured more examples. However, his pl. 3, fig. 27 appears to be a specimen of <i>Isistius triangulus</i> and is thus included in Table 1.
MANÉ <i>et al.</i> 1996	Pliocene	Zanclean (?)		Neogene	Europe	Spain	Western Mediterranean	<i>Centrophorus granulosus</i>	5 teeth		unusually large size for the genus, upper jaw teeth up to 10 mm high by 8 mm wide, lower jaw teeth up to 11 mm high by 9.5 mm wide
MANNERING & HILLER 2008	Paleocene	Danian	Seelandian	Paleogene	Australia	New Zealand	Central South Pacific	<i>Centrophorus</i> sp.	7 teeth		only species list
MARSILI 2008	Pliocene	Zanclean	Piacenzian	Neogene	Europe	Italy	Western Mediterranean	<i>Deania cf. calcea</i>			only species list
MARSILI 2008	Pleistocene			Neogene	Europe	Italy	Western Mediterranean	<i>Deania cf. calcea</i>			only species list
MARSILI 2008	Pliocene	Zanclean	Piacenzian	Neogene	Europe	Italy	Western Mediterranean	<i>Centrophorus cf. granulosus</i>			only species list
MARSILI 2008	Pleistocene			Neogene	Europe	Italy	Western Mediterranean	<i>Centrophorus cf. granulosus</i>			only species list
MARSILI 2008	Pliocene	Zanclean	Piacenzian	Neogene	Europe	Italy	Western Mediterranean	<i>Etmopterus</i> sp.			only species list
MARSILI 2008	Pliocene	Zanclean	Piacenzian	Neogene	Europe	Italy	Western Mediterranean	<i>Centrophorus cf. squamosus</i>			only species list
MARSILI 2007	Pleistocene			Quaternary	Europe	Italy	Western Mediterranean	<i>Etmopterus</i> sp.	1 tooth		only species list
MARSILI 2007	Pleistocene			Quaternary	Europe	Italy	Western Mediterranean	<i>Centrophorus cf. granulosus</i>	4 teeth		only species list
MARSILI 2007	Pleistocene			Quaternary	Europe	Italy	Western Mediterranean	<i>Centrophorus cf. squamosus</i>	only scales		only species list
MARSILI & TABANELLI 2007	Pliocene	Zanclean	Piacenzian	Neogene	Europe	Italy	Western Mediterranean	<i>Deania aff. calcea</i>	1 UT	MSNTC 11 2752	
MARSILI & TABANELLI 2007	Pliocene	Zanclean	Piacenzian	Neogene	Europe	Italy	Western Mediterranean	<i>Centrophorus cf. granulosus</i>	5 teeth	MS TC 112750 (2 teeth) MSNTC 112751 (3 teeth)	

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Country	Ocean	Valid species	Described Material as	Collectionnr.	Remarks
MARTINEZ-PÉREZ <i>et al.</i> 2018	Miocene	Serravallian		Neogene	Europe	Spain	Western Mediterranean	<i>Deania calcea</i>	8 LT, 9 UT	MGUV-35862-66; MGUV-35867	
MARTINEZ-PÉREZ <i>et al.</i> 2018	Miocene	Serravallian		Neogene	Europe	Spain	Western Mediterranean	<i>Isistius triangulus</i>	4 LT	MGUV-35868, MGUV-35869	
MARTINEZ-PÉREZ <i>et al.</i> 2018	Miocene	Serravallian		Neogene	Europe	Spain	Western Mediterranean	<i>Squaliolus cf. schaubi</i>	2 UT, 3 LT, 8 fragments	MGUV-35873, MGUV-35874, MGUV-35870-72, MGUV-35875	
MOREAU <i>et al.</i> 2013	Eocene	Ypresian		Paleogene	Europe	France	Central Tethys	<i>Isistius tritiratus</i>	1 LT		questionable, see ADNET & CAPPETTA (2001)
MÜLLER 1989	Cretaceous	Campanian		Cretaceous	Europe	Germany	Central Tethys	<i>Deania</i> sp.			no image
NOETLING 1886	Eocene			Paleogene	Europe	Belgium	Central Tethys	<i>Isistius tritiratus</i>			only species list
NOUBHANI & CAPPETTA 1997	Paleocene	Thanetian	Ypresian	Paleogene	Africa	Marocco	Western Mediterranean	<i>Isistius tritiratus</i>			only species list
OHE & KOIKE 1998	Miocene	Langhian		Neogene	Asia	Japan	Eastern North Pacific	<i>Eriopterus cf. polli</i>			only species list
PEREZ & MARKS 2017	Pleistocene			Quaternary	North America	Florida	Western North Atlantic	<i>Isistius triangulus</i>	201 LT	UF 405059-405073, 413742-413927	
PEREZ <i>et al.</i> 2017	Miocene	Tortonian		Neogene	Central America	Panama	Central Eastern Pacific	<i>Centrophorus</i> sp.	1 LT	STRI 290109	
PREIL 1984	Oligocene	Chattian		Paleogene	Australia	New Zealand	Central South Pacific	<i>Centrophorus</i> sp.	44		both species
PREIL 1984	Miocene	Aquitanian		Neogene	Australia	New Zealand	Central South Pacific	<i>Centrophorus</i> sp.	44		both species
PHILLIPS <i>et al.</i> 1976	Miocene	Aquitanian		Neogene	North America	California	Western North Pacific	<i>Centrophorus</i> sp.	2	UCMP 114596, 114847	
POLLERSPÖCK <i>et al.</i> 2018	Miocene	Burdigalian		Neogene	Europe	Austria	Central Paratethys	<i>Centrophorus</i> sp.	96		
POLLERSPÖCK <i>et al.</i> 2018	Miocene	Burdigalian		Neogene	Europe	Austria	Central Paratethys	<i>Deania</i> sp.	5		
POLLERSPÖCK <i>et al.</i> 2018	Miocene	Burdigalian		Neogene	Europe	Austria	Central Paratethys	<i>Isistius triangulus</i>	31		
POLLERSPÖCK <i>et al.</i> 2018	Miocene	Burdigalian		Neogene	Europe	Austria	Central Paratethys	<i>Euprotomiscus</i> sp.	8		



Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described Material as	Collectionnr.	Remarks
POLLERSPÖCK <i>et al.</i> 2018	Miocene	Burdigalian	Burdigalian	Neogene	Europe	Austria	Central Paratethys	<i>Etmopterus</i> sp.	3		
POLLERSPÖCK & BEAURY 2014	Miocene	Burdigalian	Burdigalian	Neogene	Europe	Germany	Central Paratethys	<i>Isistius triangulus</i>	21 LT	SNSB-BSPG 2013 X 2	
POLLERSPÖCK & BEAURY 2014	Miocene	Burdigalian	Burdigalian	Neogene	Europe	Germany	Central Paratethys	<i>Centrophorus cf. granulatus</i>	31 teeth	SNSB-BSPG 2013 X 1	
POLLERSPÖCK <i>et al.</i> 2018	Miocene	Aquitainian	Aquitainian	Neogene	Europe	Austria	Central Paratethys	<i>Etmopterus</i> sp.	28		
POLLERSPÖCK <i>et al.</i> 2018	Miocene	Aquitainian	Aquitainian	Neogene	Europe	Austria	Central Paratethys	<i>Deania</i> sp.	1		
POLLERSPÖCK & STRAUBE 2017	Miocene	Burdigalian	Burdigalian	Neogene	Europe	Germany	Central Paratethys	<i>Deania aff. calcea</i>	5		
POLLERSPÖCK & STRAUBE 2017	Miocene	Burdigalian	Burdigalian	Neogene	Europe	Germany	Central Paratethys	<i>Etmopterus</i> sp.	16		
POLLERSPÖCK & STRAUBE 2017	Miocene	Burdigalian	Burdigalian	Neogene	Europe	Germany	Central Paratethys	<i>Isistius triangulus</i>	7		
POLLERSPÖCK & STRAUBE 2017	Miocene	Burdigalian	Burdigalian	Neogene	Europe	Germany	Central Paratethys	<i>Centrophorus</i> sp.	75		
PRKRYL & SKUPIEN 2013	Eocene	Priabonian	Priabonian	Paleogene	Europe	Czech Republic	Central Tethys	<i>Centrophorus</i> sp.	2 teeth	99580, 99581	Frydlant Formation, Subsilisian Unit, from unpublished data, they rarely occur in the lower Badenian clays of the Carpathian Foredeep and the Vienna Basin (Bzobohaj, personal communication)
PROBST 1879	Miocene	Burdigalian	Burdigalian	Neogene	Europe	Germany	Central Paratethys	<i>Acanthias radicans</i>			
PROBST 1879	Miocene	Burdigalian	Burdigalian	Neogene	Europe	Germany	Central Paratethys	<i>Acanthias serratus</i>			
PROBST 1879	Miocene	Burdigalian	Burdigalian	Neogene	Europe	Germany	Central Paratethys	<i>Scymnus triangulus</i>			see CAPPETTA (1970: p. 74)
PURDY <i>et al.</i> 2001	Pliocene	Zanclean	Zanclean	Neogene	North America	North Carolina	Western North Atlantic	<i>Isistius</i> sp.	5 teeth	NCSM 11287, 11288, 11291, 11292, USNM 475362	
REYNER <i>et al.</i> 2009	Eocene	Ypresian	Ypresian	Paleogene	Europe	United Kingdom	Central Tethys	<i>Isistius triturratus</i>			

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described Material as	Collectionnr.	Remarks
REINECKE et al. 2014	Oligocene Chattian			Paleogene Europe	Europe	Germany	Central Paratethys	<i>Centrophorus</i> sp.	5 teeth		Based on an incomplete, small tooth, LERICHE (1938) described <i>Acanthias</i> (= <i>Squalus</i> ) <i>stehlini</i> from the El Mene Formation, Chattian, of Venezuela. CAPPETTA (2006) assigned the taxon <i>stehlini</i> to the genus <i>Centrophorus</i> . The details of dental morphology, given by Leriche, are too scarce and indistinct to safely distinguish <i>C. stehlini</i> from other fossil and extant species of <i>Centrophorus</i> . Another two related species, described by Probst (1879) from the Balingen Beds, Upper Marine Molasse, Othmangian (middle Burdigalian), are <i>Acanthias serratus</i> and <i>Acanthias radicans</i> . Both were referred by BARTHELT et al. (1991) to <i>Centrophorus</i> , whereas CAPPETTA (2006) assigned the latter to <i>Deania</i> . BARTHELT et al. (1991: p. 199) stated that Probst's type material "is strongly worn and important characteristics are hardly recognizable". However, based on more complete specimens, recovered from slightly older lower Othmangian deposits at Walberisweiler, Baden-Württemberg, south-western Germany (see BRACHER & UNGER 2007), BARTHELT et al. (1991) referred Probst's species to <i>Centrophorus</i> cf. <i>granulosus</i> (BLOCH & SCHNEIDER, 1801). The probably earliest record of <i>Centrophorus</i> in Oligocene strata of western-central Europe is from the Pouzifany Beds of the Czech Republic (BRZOBORHATY & KALABIS 1970: pl. 1, fig. 2; as <i>Squalus</i> sp., see CAPPETTA 2012: p. 116).
REINECKE & ENGELHARD 1997	Paleocene Thanetian			Paleogene Europe	Europe	Germany	Central Tethys	<i>Centrophorus</i> sp.	1 tooth	TRBo-004	

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described Material as	Collectionnr.	Remarks	
ROMÃO SERRALHEIRO 1954	Miocene	Burdigalian		Neogene	Europe	Portugal	Western Mediterranean	<i>Isistius triangulus</i>	<i>Scymnus 8 lichia</i>		only species List, after BARTHÉLÉMY <i>et al.</i> , (1991)	
SACH 2016	Miocene	Burdigalian		Neogene	Europe	Germany	Central Paratethys	<i>Isistius triangulus</i>			only species List, after BARTHÉLÉMY <i>et al.</i> , (1991)	
SACH 2016	Miocene	Burdigalian		Neogene	Europe	Germany	Central Paratethys	<i>Centrophorus cf. granulatus</i>			only species List, after BARTHÉLÉMY <i>et al.</i> , (1991)	
SCHOLZ & BIENERTH 1992	Miocene	Burdigalian		Neogene	Europe	Germany	Central Paratethys	<i>Centrophorus cf. granulatus</i>	<i>Centrophorus radicans</i>			
SCHULTZ 2013	Eocene	Lutetian		Paleogene	Europe	Austria	Central Tethys	<i>Centrophorus sp.</i>			only literature record after PFEIL (1983), St. Pankraz, Schloßbrunn, 15 km N Salzburg, ESE Oberndorf; Salzburg; PFEIL (1983: p. 238; "Fossilsschicht"; Mittel-Eozän, oberstes Lutet, NP 16)	
SCHULTZ 2013	Eocene	Lutetian		Paleogene	Europe	Austria	Central Tethys	<i>Squaliolus sp.</i>			only literature record after PFEIL (1983), St. Pankraz, Schloßbrunn, 15 km N Salzburg, ESE Oberndorf; Salzburg; PFEIL (1983: p. 238; "Fossilsschicht"; Mittel-Eozän, oberstes Lutet, NP 16)	
SCHULTZ 2013	Miocene	Burdigalian		Neogene	Europe	Austria	Central Paratethys	<i>Centrophorus sp.</i>		NHMWien 2007z0117 10011–10013; Schärding, OÖ: NHMWien 2011/0174/0001 (la., leg. + don. W. Danninger, Andorf). Antiesen-Stiefler, SE Antiesen-höfen, S Schärding; OÖ: NHMWien 2008z0265/0001 (leg. O. Schultz 5.4.1969). Riedau, OÖ; NHMWien 2008z0265/0002; NHMWien 2007z0117/0011–0018 (la.–ex 1978/1966/0012); siehe Taf. 9, Fig. 10a+b–12a+b + Fig. 15a+b + 16a+b.		Überösterreich: PFEIL (1983: pp. 89, 151) Allerding, Steinbruch, SE Schärding, OÖ: NHMWien 2011/0174/0001 (la., leg. + don. W. Danninger, Andorf). Antiesen-Stiefler, SE Antiesen-höfen, S Schärding; OÖ: NHMWien 2008z0265/0001 (la., leg. O. Schultz 5.4.1969). Riedau, OÖ; NHMWien 2008z0265/0002; NHMWien 2007z0117/0011–0018 (la.–ex 1978/1966/0012); siehe Taf. 9, Fig. 10a+b–12a+b + Fig. 15a+b + 16a+b.

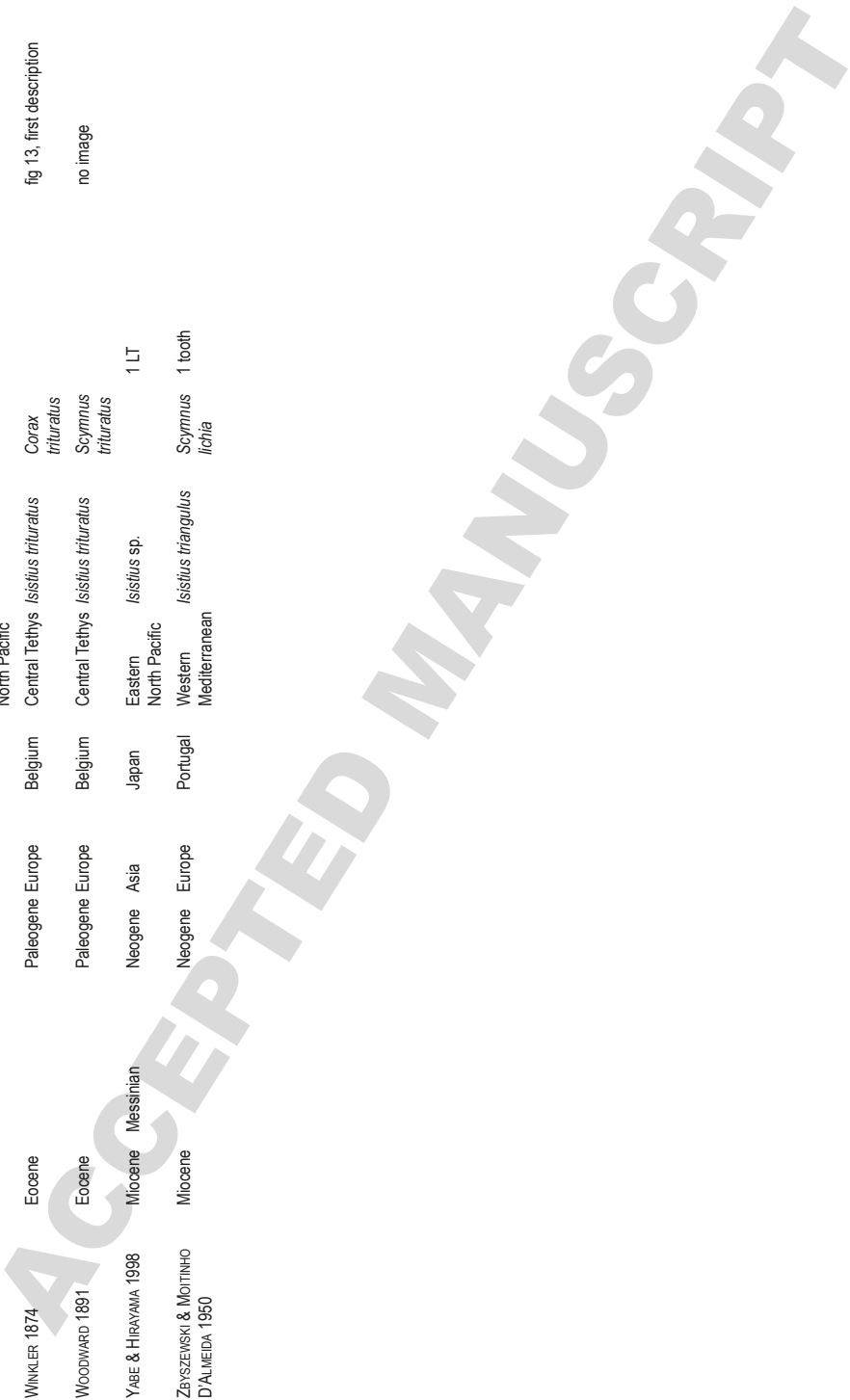
Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described as	Material	Collectionnr.	Remarks
SCHULTZ 2013	Miocene	Burdigalian		Neogene	Europe	Austria	Central Paratethys	<i>Dearia</i> sp.				only literature record after PFEIL (1983), Unter-Miozän: Ober-österreich: PFEIL (1983: pp. 89, 151); Höbmannsbach, ESESchärding; OÖ: PFEIL (1983: p. 151); Wallern an der Trattnach, Ortsteil Holz; OÖ: PFEIL (1983: p. 151)
SCHULTZ 2013	Miocene	Burdigalian		Neogene	Europe	Austria	Central Paratethys	<i>Etmopterus</i> sp.				only literature record after PFEIL (1983), Unter-Miozän, unteres Otnangium: Oberösterreich: PFEIL (1983: pp. 89, 151); Höbmannsbach, ESESchärding; OÖ: PFEIL (1983: p. 151); Wallern an der Trattnach, Ortsteil Holz; OÖ: PFEIL (1983: p. 151)
SCHULTZ 2013	Miocene	Aquitanian		Neogene	Europe	Austria	Central Paratethys	<i>Etmopterus</i> sp.			NHMWien o. Nr.	Egerium: ? Lindach; OÖ: NHM-Wien o. Nr. (Za: Ob. Puchkirchner Serie: Lindach-2, Teufe 1000–1002 m., leg. F. Rögl) no image
SCHULTZ 2013	Miocene	Burdigalian		Neogene	Europe	Austria	Central Paratethys	<i>Isistius triangulus</i>			NHMWien 1978/1966/12 resp. 2007z0117der	unteres Otnangium: Höbmannsbach, Großwiesenhart, Wallern an der Trattnach, Kemating, Upper Austria
SCHULTZ 2013	Miocene	Burdigalian		Neogene	Europe	Austria	Central Paratethys	<i>Squaliolus</i> sp.				only literature record after PFEIL (1983), Unter-Miozän, unteres Otnangium: Oberösterreich: PFEIL (1983: p. 89)
SUÁREZ <i>et al.</i> 2003	Pliocene	Zanclean (?)		Neogene	South America	Chile	Central South Pacific	<i>Centrophorus</i> sp.				only species list
SUZUKI 2012	Miocene	Langhian		Neogene	Asia	Japan	Eastern North Pacific	<i>Dearia cf. calcea</i>				
SUZUKI 2012	Miocene	Langhian		Neogene	Asia	Japan	Eastern North Pacific	<i>Etmopterus cf. spirax</i>				
SUZUKI 2012	Miocene	Langhian		Neogene	Asia	Japan	Eastern North Pacific	<i>Centrophorus atromarginatus</i>				
SUZUKI 2007	Miocene	Langhian		Neogene	Asia	Japan	Eastern North Pacific	<i>Centrophorus</i> sp.				
TAKAKUMA 2006	Miocene	Langhian		Neogene	Asia	Japan	Eastern North Pacific	<i>Dearia</i> sp.		2 teeth	GMNHPV 1701, 1702	

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described Material as	Collectiomr.	Remarks
TAKAKUMA 2006	Miocene	Langhian		Neogene	Asia	Japan	Eastern North Pacific	<i>Etmopterus</i> sp.		GMNHPV 1703, 1822 – 2167	
TAKAKUMA 2006	Miocene	Langhian		Neogene	Asia	Japan	Eastern North Pacific	<i>Squaliolus</i> sp.		GMNII-PV-1428, 1703, 1719, 2195 – 2261	
TAKAKUMA 2006	Miocene	Langhian		Neogene	Asia	Japan	Eastern North Pacific	<i>Centrophorus</i> sp.	1 tooth	GMNHPV-159	
TAKAKUMA <i>et al.</i> 2009	Miocene	Serravallian		Neogene	Asia	Japan	Eastern North Pacific	<i>Etmopterus</i> sp.			
TAVERNE & NOLF 1978	Eocene	Lutetian		Paleogene	Europe	Belgium	Central Tethys	<i>Isistius tritritatus</i>	55		partly only species list
THIES & MÜLLER 1993	Cretaceous	Campanian		Cretaceous	Europe	Germany	Central Tethys	<i>Deania</i> sp. (?)	1 UT	(IGPH 1992-1-5)	questionable, see ADNET & CAPPETTA (2001)
TIMMERMAN & CHANDLER 2011	Pliocene	Zanclean		Neogene	North America	North Carolina	Western North Atlantic	<i>Isistius triangulus</i>			
UNDERWOOD & MITCHELL 2004	Miocene	Aquitanian (?)		Neogene	Central America	Antilles	Caribbean	<i>Deania</i> sp.	1 LT	UF206535	
UNDERWOOD & MITCHELL 2004	Miocene	Aquitanian (?)		Neogene	Central America	Antilles	Caribbean	<i>Squaliolus schaubi</i>	4 teeth	UF 206537, 206538, 206539, 206464	
UNDERWOOD & MITCHELL 2004	Miocene	Aquitanian (?)		Neogene	Central America	Antilles	Caribbean	<i>Squaliolus</i> sp.	1 LT	UF206536	This tooth is larger than any known lower tooth of <i>S. schaubi</i> , and differs in having a far larger and more erect cusp.
UNDERWOOD & MITCHELL 2013	Miocene	Burdigalian		Neogene	Europe	Slovakia	Central Paratethys	<i>Etmopterus</i> sp.	7 LT, 1 UT	SNM Z 27463 to SNM Z 27468	
UNDERWOOD & MITCHELL 2013	Miocene	Burdigalian		Neogene	Europe	Slovakia	Central Paratethys	<i>Squaliolus cf. schaubi</i>	137 LT, 89 UT	SNM Z 27443 to SNM Z 27454	only species list
VAN DEN BOSCH 1980	Eocene			Paleogene	Europe	Netherlands	Central Tethys	<i>Isistius tritritatus</i>			
VAN DEN ECKHAUT & DE SCHUTTER 2009	Eocene	Lutetian		Paleogene	Europe	Belgium	Central Tethys	<i>Isistius tritritatus</i>			
VAN DER BRUGGHEN <i>et al.</i> 1993	Cretaceous	Maastrichtian		Cretaceous	Europe	Netherlands	Central Tethys	<i>Etmopterus</i> sp. (?)			questionable
VIALLE <i>et al.</i> 2011	Miocene	Langhian		Neogene	Europe	France	Western Paratethys	<i>Deania aff. calceus</i>	10 teeth		The number and position of the foramina on the lingual face of these teeth are distinctive of genus <i>Centrophorus</i> and indicative of the recent species <i>Deania calceus</i> . The remains of this genus are very rare in the fossil record but they have been already observed in the bathyal deposits of the Lower and Middle Miocene of Vaucluse (CAPPETTA <i>et al.</i> 1967; LECOUX 1972).

Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described Material as	Collectionnr.	Remarks
VALLE <i>et al.</i> 2011	Miocene	Langhian		Neogene	Europe	France	Western Paratethys	<i>Isistius triangulus</i>	295 lower teeth		The Neogene species <i>I. triangulus</i> differs from the Palaeogene species <i>I. tritiratus</i> (WINKLER, 1874) by the lower position of the 'button-hole' on the labial face of the root and the serrated cutting edges (LEDOUX 1972). The species <i>I. triangulus</i> is very common in the Miocene deposits of north Hemisphere, including the south of France from Hérault (CAPPETTA 1970) to Vacluse (LEDOUX 1972).
VALLE <i>et al.</i> 2011	Miocene	Langhian		Neogene	Europe	France	Western Paratethys	<i>Squaliolus schaubi</i>	3 lower teeth		The absence of lingual marginal foramina on the lingual face of root allows to assign these teeth to <i>S. schaubi</i> . This genus is very rare in the fossil record (CASIER 1958, 1966; BARTHELT <i>et al.</i> 1991) and was only found in Palaeogene and Neogene deep-water deposits. This species was reported in the deposits of the Early and Middle Miocene of southern France (CAPPETTA 1970; LEDOUX 1972).
VALLE <i>et al.</i> 2011	Miocene	Langhian		Neogene	Europe	France	Western Paratethys	<i>Centrophorus aff. granulolus</i>	42 teeth		The presence of a slightly serrated mesial cutting edge and absence of fold on the uvula are indicative of the living species <i>Centrophorus granulolus</i> . This species is widespread in the Miocene sediments of Vacluse, from the Early to Late Miocene (CAPPETTA <i>et al.</i> 1967; LEDOUX 1972; BRISSWALTER 2009).
VON DER HOCHT 1986	Paleocene	Thanetian		Paleogene	Europe	Germany	Central Tethys	<i>Isistius tritiratus</i>			only species list
VON DER HOCHT 1986	Eocene	Ypresian		Paleogene	Europe	Germany	Central Tethys	<i>Isistius tritiratus</i>			only species list
VON DER HOCHT 1979	Eocene	Ypresian		Paleogene	Europe	Germany	Central Tethys	<i>Isistius tritiratus</i>			only species list
WARD & WIEST 1990	Eocene	Ypresian		Paleogene	North America	Maryland, Virginia	Western South Atlantic	<i>Isistius tritiratus</i>			only species list
WELTON 1974	Paleocene			Paleogene	North America	California	Western North Pacific	<i>Centrophorus sp.</i>			only species list



Author	Keyword Time 1	Keyword Time 2	Keyword Time 3	Epoch	Continent	Keyword Country	Ocean	Valid species	Described as	Material	Collectionnr.	Remarks
WELTON 1974	Paleocene			Paleogene	North America	California	Western North Pacific	<i>Isisitus cf. triturratus</i>				only species list
WINKLER 1874	Eocene			Paleogene	Europe	Belgium	Central Tethys	<i>Isisitus triturratus</i>	<i>Corax triturratus</i>			fig 13, first description
WOODWARD 1891	Eocene			Paleogene	Europe	Belgium	Central Tethys	<i>Isisitus triturratus</i>	<i>Scymnus triturratus</i>			no image
YABE & HIRAYAMA 1998	Miocene	Messinian		Neogene	Asia	Japan	Eastern North Pacific	<i>Isisitus</i> sp.		1 LT		
ZBYSZEWSKI & MOTTINHO D'ALMEIDA 1950	Miocene			Neogene	Europe	Portugal	Western Mediterranean	<i>Isisitus triangulus</i>	<i>Scymnus lichia</i>	1 tooth		



Supplement Table S2. *Otodus (Megaselachus) chubutensis* (AMEGINO, 1901), collection DANNINGER and HIERMANN, Austria, from Allerding, Ottnangian. Scale bars equal 1 cm. Teeth without cusplets are highlighted in grey.

			
<p>Coll. Danninger, ca. 10 cm height, with cusplets</p>	<p>Coll. Danninger, ca. 8,5 cm height, with cusplets</p>	<p>Coll. Danninger, ca. +9 cm height, without (?) cusplets</p>	<p>Coll. Danninger, ca. 9,5 cm height, with cusplets</p>
<p>5</p> 	<p>6</p> 	<p>7</p> 	
<p>Coll. Danninger, ca. 5,5 cm height, with cusplets</p>	<p>Coll. Danninger, ca. 7,5 cm height, without cusplets</p>	<p>Coll. Danninger, ca. +5,5 cm height, without (?) cusplets</p>	
<p>8</p>	<p>9</p>	<p>10</p>	<p>11</p>
			
<p>Coll. Hiermann, ca. +5,5 cm height, without cusplets</p>	<p>Coll. Hiermann, ca. +6,5 cm height, with cusplets</p>	<p>Coll. Hiermann, ca. 6,5 cm height, without cusplets</p>	<p>Coll. Hiermann, ca. 9,5 cm height, without cusplets</p>
<p>12</p>	<p>13</p>	<p>14</p>	<p>15</p>
			
<p>Coll. Hiermann, ca. 9,5 cm height, with cusplets</p>	<p>Coll. Hiermann, ca. 8,0 cm height, without cusplets</p>	<p>Coll. Hiermann, ca. 7,5 cm height, with cusplets</p>	<p>Coll. Hiermann, ca. 9,5 cm height, with cusplets</p>
<p>16</p>	<p>17</p>	<p>18</p>	<p>19</p>

			
Coll. Hiermann, ca. 8,0 cm height, with cusplets	Coll. Hiermann, ca. 9,5 cm height, with cusplets	Coll. Hiermann, ca. 7,5 cm height, with cusplets	Coll. Hiermann, ca. +6,0 cm height, without cusplets
<b>20</b>	<b>21</b>	<b>22</b>	<b>23</b>
			
Coll. Hiermann, ca. +9,0 cm height, without (?) cusplets	Coll. Hiermann, ca. 8,5 cm height, with cusplets	Coll. Hiermann, ca. 7,0 cm height, with cusplets	Coll. Hiermann, ca. 6,0 cm height, without cusplets
<b>24</b>			
			
Coll. Hiermann, ca. +9,5 cm height, without (?) cusplets			