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A new deep-sea elasmobranch fauna from the Central Paratethys (Neuhofener Beds, Mitterdorf, near Passau, Germany, Early Miocene, Middle Burdigalian)

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Abstract

In this study, a diverse fauna of fossil elasmobranch teeth from the Early Miocene (Middle Burdigalian) is analysed. The fossil diversity strongly resembles extant deep-water shark and ray assemblages. The fossils were collected from the Upper Marine Molasse of the lower Ottnangian in the Neuhofener Beds location, Mitterdorf, Germany. The collection site is a clay pit in between the Lower Bavarian villages Fürstenzell and Schmidham. The sample revealed 14 shark and four ray species. We present the first record of fossils assigned to taxa *Nanocetorhinus tuberculatus, Deania* and *Apristurus* from Germany. In addition, we describe a hitherto unknown genus and species of shark, *Pseudoapristurus nonstriatus* gen. et sp. nov., based on fossil teeth. The documented diversity is compared to both extant and fossil records of neoselachian deep-water diversities, and it is evident that this Miocene fauna is very similar in composition to indo-pacific deep-water assemblages.

Key words: Bavaria, Early Miocene, deep-water, Chondrichthyes, Ottnangian, Burdigalian, Upper Marine Molasse

Zusammenfassung

Aus der Oberen Meeresmolasse (Neuhofener Schichten, unteres Ottnangium) Niederbayerns (Tongrube zwischen Fürstenzell und Schmidham) wird eine artenreiche Tiefwasser-Elasmobranchierfauna beschrieben. Insgesamt werden 14 Hai- und vier Rochenarten nachgewiesen. Erstnachweise für Deutschland werden von *Nanocetorhinus tuberculatus*, *Apristurus* sp. und *Deania* sp. erbracht. Zusätzlich wird eine bisher unbekannte Neoselachier Gattung und Art (*Pseudoapristurus nonstriatus* nov. gen. et sp.) anhand von Zahnfossilien beschrieben. Ein Vergleich der hier dokumentierten Diversität mit verschiedenen anderen rezenten und fossilen Neoselachier Vergesellschaftungen zeigt, dass die vorliegende Fauna große Übereinstimmungen mit rezenter indo-pazifischer Tiefseediversität aufweist.

Schlüsselwörter: Bayern, Unteres Miozän, Tiefsee, Chondrichthyes, Ottnangium, Burdigalium, Obere Meeresmolasse

1. Introduction

Most fossil remains of Neoselachians are fossilized teeth and dermal denticles, as the cartilaginous skeleton of Chondrichthyes is less prone for fossilization (Maisey 2012). Nevertheless, highly specialized dentitions of many shark and ray species allow for a comparison of fossil teeth with extant taxa based on dental morphological characters.

Despite the presence of a number of deep-water Neogene basins in the Alpine region, records of Miocene deep-sea shark and ray species from the central Paratethys are poorly known (Underwood & Schlögl 2013) and insufficiently documented. Samples analyzed in this study were collected from the Paratethys, a series of elongate basins delimited by the upfolding Alps in the South and the Bohemian Massif in the North. In the East, the Paratethys comprised the extant water bodies of the Black Sea, the Caspian Sea and the Aral Sea. In the West, it encompassed the southwestern German and Swiss parts of the North Alpine Basin and was connected to the Mediterranean basin and the Atlantic Ocean via the Rhone Basin (Pippèrr & Reichenbacher 2010). Moreover, Pippèrr & Reichenbacher (2010) state that the collection site Neuhofener Beds likely had nutrient rich seawater and a significant fresh water inflow from rivers draining surrounding mountains besides high water circulation resulting in increasing oxygen levels in water bodies close to the basin floor. Besides these localized ecological conditions, the biodiversity was likely further influenced by potential migration routes

via connectivity to adjacent oceanic waters: the Atlantic Ocean via the street of Gibraltar and the Rhone trench, connecting eventually to the North Sea, as well as the Indian Ocean via the Red Sea (Rögl 1998; Martini 1990).

In recent years, the Miocene deep-water chondrichthyan fauna was documented in several publications as e.g. Vialle et al. (2011), Underwood & Schlögl (2013), Pollerspöck & Beaury (2014); nevertheless, the information on distribution, composition, and occurrence of taxa is rather scarce compared to shallow water assemblages. A comparison of previously documented Miocene deep-sea neoselachian taxa with extant taxa occurring in the Mediterranean Sea and the North East Atlantic reveals that several taxa in the fossil record are documented based on only few specimens (e.g. genera *Galeus* (Underwood & Schlögl 2013) or *Dalatias* (Brisswalter 2009)), or are completely absent (e.g. genera *Apristurus, Somniosus, Oxynotus*). In contrast to the low shark diversities reported in the fossil record, multiple new extant deep-water species have been described in recent years (White & Iglésias 2011; White et al. 2008; Yearsley et al. 2008; Ebert & Cailliet 2011; Ebert & Wilms 2013; Schaaf-Da Silva & Ebert 2006; Knuckey et al. 2011; Ebert et al. 2011; Straube et al. 2011). Most of these species are assigned to genera, which are also reported in the fossil record based on their tooth morphologies. Here, we report on the diversity of fossils found in the Neuhofener Beds and compare the documented deep-sea neoselachian fauna with other fossil sampling sites as well as geographically documented extant diversity compositions to draw conclusions on geographic and ecological influences which may have shaped the diversity of the Neuhofener Beds.

2. Sampling site

The material described herein was collected at 13.28°E, 48.49°N (WGS84, location Mitterdorf, between Fürstenzell and Schmidham, Bavaria, Germany) and is the site of recently installed clay works (Fig. 1). The exposed horizons of the Neuhofener Beds are part of the Upper Marine Molasse and are assigned to the Lower Ottnangian (= Middle Burdigalian) (Hagn et al. 1981; Unger 1984; Pippèrr & Reichenbacher 2010; Pippèrr 2011). These fully marine sediments of the southern German Molasse Basin are part of the Paratethys.

The Neuhofener Beds sediments are represented by blue to grayish fine marls, including some thin sandstone layers, which became visible in the uppermost part of the outcrop. The diversity of foraminifers found in the Neuhofener Beds is well-documented due to their outstanding preservation quality (Hagn et al. 1981; Pippèrr & Reichenbacher 2010; Pippèrr 2011), whilst the ostracod fauna is also well known (Witt 2009). Pippèrr & Reichenbacher (2010) and Pippèrr (2011) suggest that the Neuhofener Beds represent an euhaline, deep-neritic basin facies of the molasse with an estimated water depth of > 100 m.

3. Material and Methods

Sampling was conducted at three different sites in the clay pit of the Neuhofener Beds from the location Mitterdorf. For details on the samples, refer to Table 1. All samples were dried and thereafter wetted in a hydrogen peroxide solution (concentration 0,1% – 1%). This was repeated two to three times until sediments were fully disaggregated. The residue was washed through 5 mm, 1 mm, 0.5 mm, and 0.25 mm mesh. Fossils were recovered by eye using binoculars (WILD M3Z). In total, 441 partially fragmented fossil elasmobranch teeth and 154 dermal denticles were recovered (Table 3). Only well-preserved teeth were identified to family, genus or species level depending on its preservation quality. Outstanding well-preserved fossils were cleaned in a 2% hydrogen peroxide solution and ultrasonic sound (MEC 300 VAP, MOTOR, Jewelry Cleaner).

These samples 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). GIMP2 (https://www.gimp.org/) was used to excise images and standardize a scale for figure plates. 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 "+".

Table 1: Details on sampling sites.

SAMPLE (FP)	WEIGHT (KG)	LOCATION	DESCRIPTION
1	70	13.28°E, 48.49°N	mixed sediments intended for transportation; July 2013
2A/ 2B	315	13.28°E, 48.49°N	taken at location of 1st depletion site; including ca. 15 kg sediment from a fine sand deposit (FP2B); June 2014
3	300	13.28°E, 48.49°N	taken at bottom of clay pit, August 2014

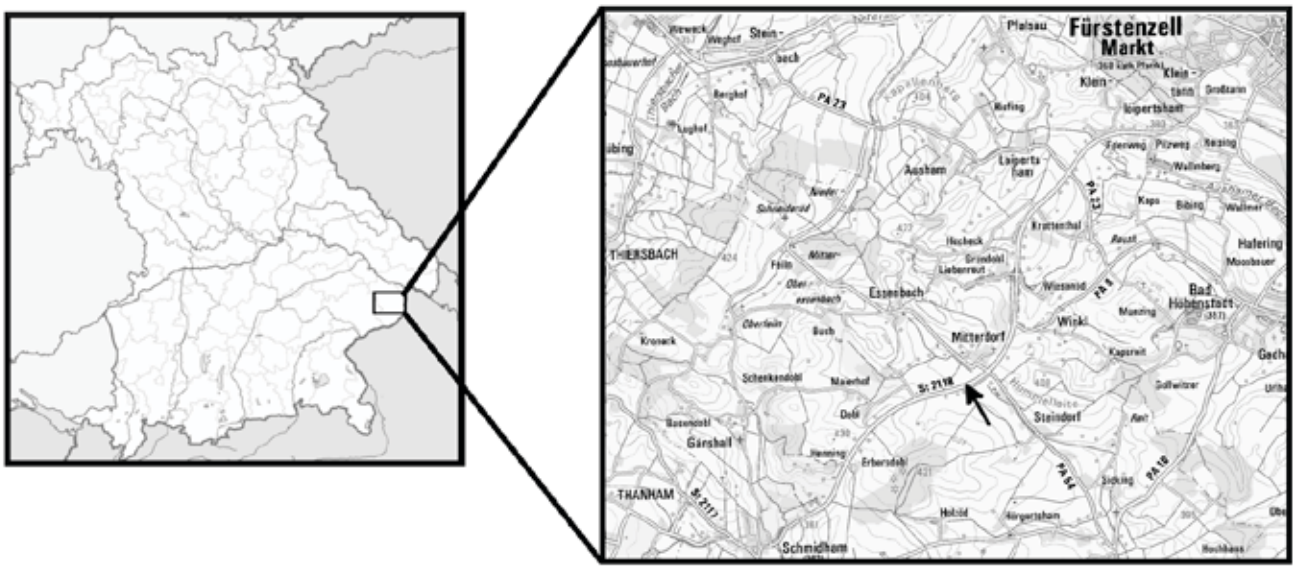


Figure 1: Geographical location of sampling site.

To survey extant and fossil deep-sea elasmobranch diversity, data from peer-reviewed articles dealing with the diversity of deep-sea elasmobranchs on genus level was collected to create a presence/absence matrix of taxa at different geographic localities and fossil sampling sites, respectively. The analyzed articles comprise diversity records from the North Atlantic, the Mediterranean and the adjacent Indian Ocean in depths of up to 4.000 meters. Due to the scarcity of fossils derived from rays, the analysis was conducted on shark taxa only. See Table 2 for the analysed presence and absence matrix resulting from the literature research and the Neuhofener Beds.

For analyzing which fauna most closely resembles the taxa composition of the Neuhofener Beds, we conducted a principal component analysis (PCA) using PAST (Paleontological Statistics Software, Hammer 2015) and computed a most parsimonious network using the software Network (www.fluxus-engineering.com). All fossils analyzed herein are deposited in the Bavarian State Collection for Palaeontology and Geology, Richard-Wagner-Straße 10, D-80333 Munich, collection numbers SNSB-BSPG 2015 III 2-1 – SNSB-BSPG 2015 III 2-128.

4. Results

4.1 Systematic palaeontology

Fossil teeth assignable to the extant order of Squaliformes (Dogfish sharks) represent the largest part of the diversity of the Neuhofener Beds (28.16 %). On species level, the most frequent teeth can be assigned to *Nanocetorhinus tuberculatus* Underwood & Schlögl, 2013 (30.26 %, Neoselachii incertae sedis). See Figure 2 and Table 3 for a detailed evaluation of the faunal survey of the Neuhofener Beds.

This published work and the nomenclatural acts it contains have been registered in ZooBank, the online registration system for the ICZN. The LSID (Life Science Identifier) for this publication is: http://zoobank.org/References/AF040A11-D0E8-4403-B00A-2D42FFD00035

Cohort Euselachii Hay, 1902
Subcohort Neoselachii Compagno, 1977
Order Lamniformes Berg, 1958

Family Cetorhinidae Gill, 1862

Genus *Keasius* Welton, 2013

Keasius parvus (Leriche, 1908)

* 1908: *Cetorhinus parvus* – Leriche: p. 878.
1910: *Cetorhinus parvus* – Leriche: p. 294, figs 91–94.
1991: *Cetorhinus parvus* – Barthelt et al.: p. 202, pl. 2, fig. 12.
1995: *Cetorhinus parvus* – Bolliger et al.: pl. 2, fig. 6.
2007: *Cetorhinus parvus* – Bracher & Unger: p. 94–96, fig. 56, pl. 34.
2009: *Cetorhinus parvus* – Brisswalter et al.: p. 28, 29, pl. 3, figs 1–3.
2011: *Cetorhinus parvus* – Vialle et al.: p. 246.
2013: *Cetorhinus parvus* – Schultz: p. 41, pl. 4, fig. 19, pl. 47, fig. 1.
2013: *Keasius parvus* – Welton: p. 39, 40.

Material: FP 2: 11 fragments of gill rakers (SNSB-BSPG 2015 III 2-79, n=1; SNSB-BSPG 2015 III 2-90, n=10; SNSB-BSPG 2015 III 2-93, Fig. 3); FP 3: 1 oral tooth (SNSB-BSPG 2015 III 2-50); Fig. 3.

Size: SNSB-BSPG 2015 III 2-90, 93: gill rakers (n=11): 1.9+ mm – 4.6+ mm length; SNSB-BSPG 2015 III 2-50: tooth (n=1): height: 0.9+ mm; width: 1.1 mm.

Description: The recovered fragments and especially the fragment shown in Figure 3 of a gill raker

assign the fossils to genus *Keasius*, a small-sized member of the family Cetorhinidae. The fossil gill raker fragment is characterized by a weak curvature of the filament base, the rounded bight shape, and the very small gill rakers (terms follow Welton 2013). The single oral tooth (Fig. 3) is characterized by a triangular crown that widens at the ventral side. The crown displays a slightly convex curvature, weakly developed at the labial but strongly developed at the lingual side. It is completely smooth on both sides unlike teeth of the extant *Cetorhinus*. No pulp cavity can be identified.

Remarks: Two species of *Keasius* have been recorded: the Eocene *K. taylori* (Oregon, Welton 2013) and the Miocene *K. parvus* (Leriche 1908). Both species were described based on gill rakers and single teeth. We assign the Neuhofener Beds fossils to the species *K. parvus* as the fossils discussed here show distinct morphological characters described for *K. parvus* (Welton 2013).

Family Odontaspididae Müller & Henle, 1839

Remarks on the family Odontaspididae Müller & Henle, 1839: So far, the family was described to include the species *Odontaspis ferox, O. noronhai* and *Carcharias taurus*. Naylor et al. (2012a, 2012b) report that the family Odontaspididae is paraphyletic with respect to *C. taurus*, which clusters with *Cetorhinus maximus*.

Genus *Carcharias* Cuvier, 1816
Carcharias acutissimus (Agassiz, 1843)

* 1843: *Lamna (Odontaspis) acutissima* – Agassiz: p. 294, pl. 37a, figs 33, 34.
1879: *Lamna (Odontaspis) reticulata* n.sp. – Probst: p. 145: pl. 2. figs 26–32.
1879: *Lamna (Odontaspis) contortidens* – Probst: p. 144, pl. 2. figs 33–39.
1991: *Synodontaspis acutissima* – Barthelt et al.: p. 200, pl. 2, fig. 3.
1995: *Synodontaspis acutissima* – Holec et al.: p. 40, 41, pl. 10, figs 3–5 & pl. 11, figs 1, 3.
2007: *Carcharias acutissima* – Kocsis: p. 31, figs 4.6–4.11.
2009: *Carcharias acutissima* – Brisswalter et al.: p. 27, pl. 3, figs 6–9, pl. 4, figs 1–3.
2011: *Carcharias* aff. *acutissima* – Vialle et al.: p. 247, figs 3-1, 3-2.
2013: *Carcharias acutissimus* – Schultz: p. 55, pl. 5, figs 7, 8.
2014: *Carcharias acutissimus* – Pollerspöck & Beaury: p. 28, 29, pl. 1, figs 2a, 2b.

Material: FP 3: 1 tooth (only crown).

Size: SNSB-BSPG 2015 III 2-91: height: 7.0+ mm; width: 5.0+ mm.

Description: Only a partial crown fragment of a labial upper jaw tooth was recovered. The characteristic lateral cusplets are absent. The crown is erect, triangular in shape and displays a vertically running, irregular enameloid line on its lingual side, typically characterizing *Carcharias acutissimus.*

Remarks: Fossil remains of this species are frequently found and are recorded from the whole paratethical sea. Its taxonomic history comprises several assignations to different genera (*Lamna, Odontaspis, Synodontaspis, Eugomphodus*), however today it is considered to be a species of the genus *Carcharias* (Agassiz 1843; Leriche 1910; Barthelt et al. 1991; Müller 1996; Compagno & Follet 1986). The fossil record lasts from the Oligocene to the Pliocene without any fossil gaps (Cappetta 2012).

Order Carcharhiniformes Compagno, 1977

Family Carcharhinidae Jordan & Evermann, 1896

Genus *Rhizoprionodon* Whitley, 1929

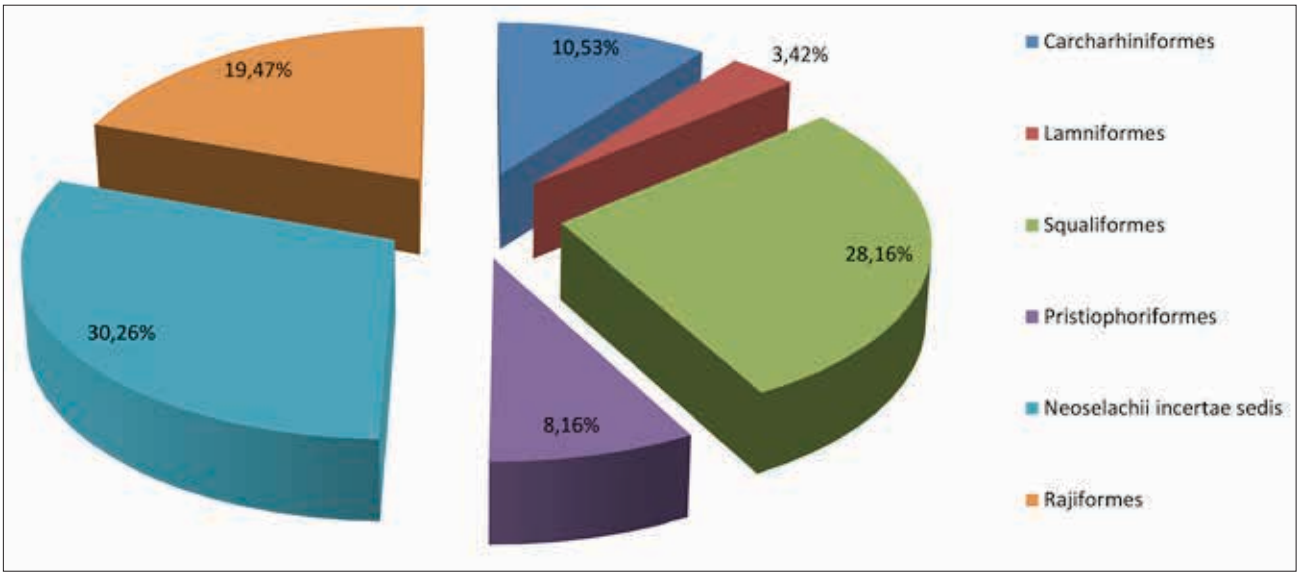


Figure 2: Percentages of excavated fossils on order level.

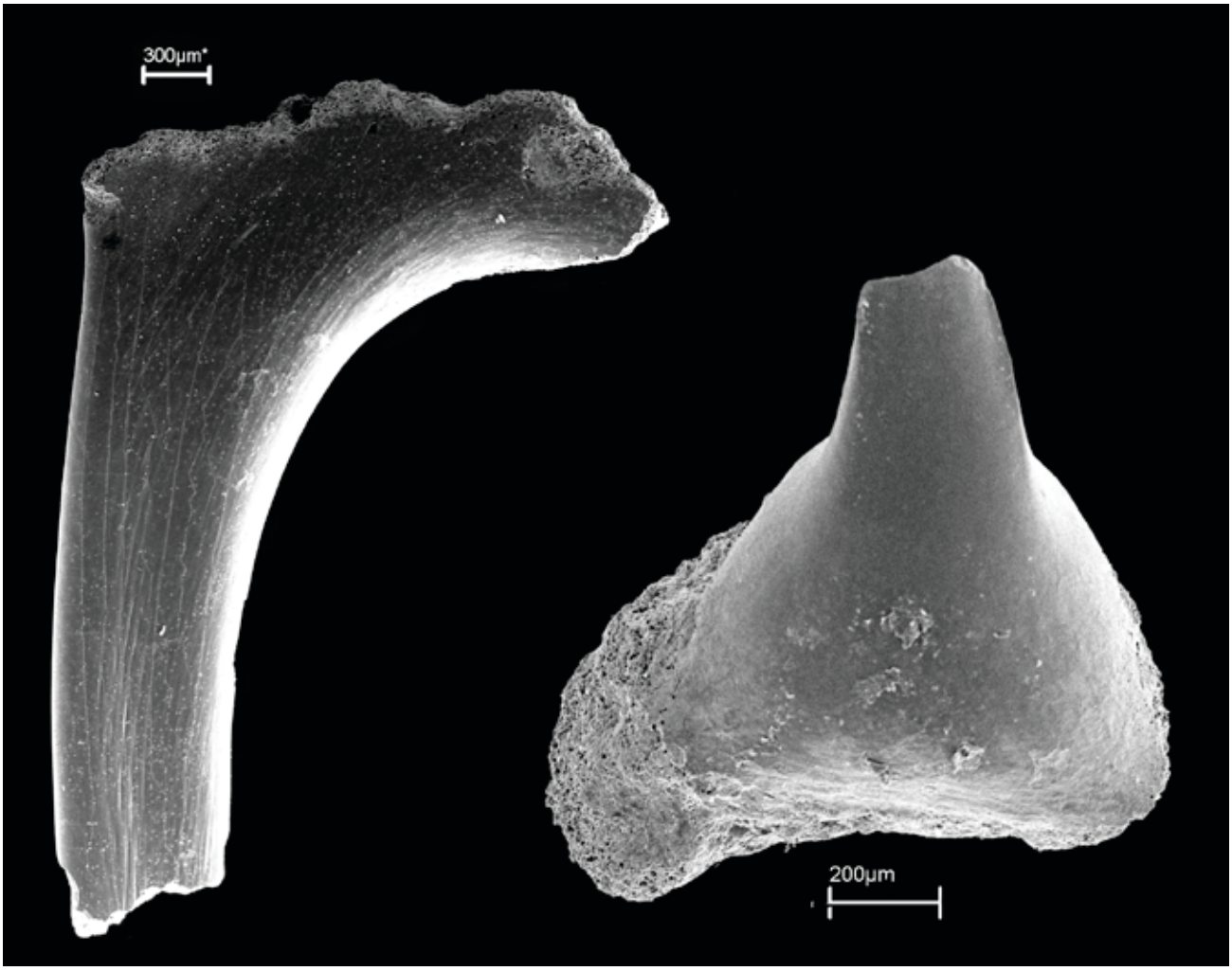


Figure 3: *Keasius parvus* (Leriche, 1908)*:* left: gill raker (SNSB-BSPG 2015 III 2-93), right: oral tooth, labial view (SNSB-BSPG 2015 III 2-50).

cf. *Rhizoprionodon ficheuri* (Joleaud, 1912)

* 1912: *Carcharias (Physodon) ficheuri* – Joleaud: p. 199, pl. 6, figs 4–11 (non figs 1–3).
1970: *Scoliodon taxandriae* – Cappetta: pl. 16, figs 10, 20.
1970: *Physodon fischeuri* – Cappetta: p. 63–65, pl. 15, figs 18–27, pl. 16, figs 1–4.
1991: *Rhizoprionodon ficheuri* – Barthelt et al.: p. 204, pl. 3, fig. 18.
1995: *Rhizoprionodon fischeuri* – Hiden: p. 68, 81, 83, pl. 5, fig. 5.
2007: *Rhizoprionodon fischeuri* – Bracher & Unger: p. 134, 135, pl. 49, 50.
2009: *Rhizoprionodon fischeuri* – Brisswalter: p. 40, 41, pl. 7, fig. 5.
2011: *Rhizoprionodon ficheuri* – Vialle et al.: p. 248, figs 3–7.
2012: *Rhizoprionodon ficheuri* – Cappetta: p. 301, fig. 283.
2013: *Rhizoprionodon ficheuri* – Schultz: p. 89, pl. 10, figs 9a, 9b.

Material: FP 2: SNSB-BSPG 2015 III 2-92: 1 tooth; Fig. 4.

Size: SNSB-BSPG 2015 III 2-92: height: 1.3 mm; width: 2.4 mm.

Description: The single tooth described herein is nearly twice as wide as high. The low tooth crown is mesially concave showing a slightly convex curvature. Its edge is sharp and does not display any serration. A round but damaged cusplet is developed at its distal edge implies a fake serration. The tooth shows distinct drilling channels caused by *Mycelites* sp. post mortem. Similar post mortem damage was reported by Underwood & Schlögl (2013) for deep-water deposits of the central Paratethys.

Remarks: The extant species of the genera *Rhizoprionodon, Loxodon* and *Scoliodon* show highly similar (tooth) morphologies, which were only recently taxonomically reviewed based on both morphological and molecular data (Cappetta 2012; Herman et al. 1991; Springer 1964; Straube et al. 2013; White et al. 2010). Therefore, we assign the fossils found here only preliminary to the genus *Rhizoprionodon*.

Fossils of *Rhizoprionodon ficheuri* have frequently been documented from paratethical deposits, including the Paratethys of France (middle Miocene: Cappetta 1970; Vialle et al. 2011; Canevet 2011; upper Miocene: Brisswalter 2009), Germany (lower Miocene: Barthelt et al. 1991; this study), and Austria (lower and middle Miocene: Schultz 2013).

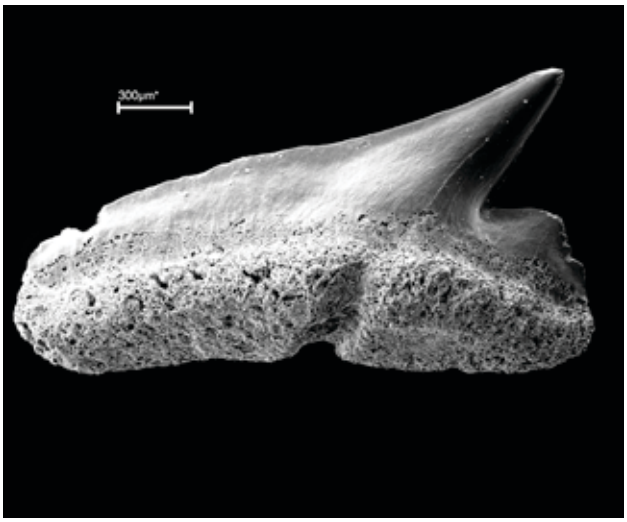


Figure 4: cf. *Rhizoprionodon ficheuri* (Joleaud, 1912) (SNSB-BSPG 2015 III 2-92).

Family Scyliorhinidae Gill, 1862

Remarks on the family Scyliorhinidae Gill, 1862: Recent phylogenetic studies based on DNA sequence data revealed the family to be polyphyletic. Iglésias et al. (2005) resurrected the family name Pentanchidae (Smith & Radclife, in Smith, 1912) comprising genera *Apristurus*, *Asymbolus*, *Cephalurus*, *Galeus*, *Halaelurus*, *Haploblepharus*, *Holohalaelurus*, *Parmaturus*, and *Pentanchus*. Later, Naylor et al. (2012a) described three monophyletic lineages:
- Scyliorhinidae I comprising genera *Apristurus*, *Galeus*, *Asymbolus*, *Figaro*, *Bythaelurus*, *Halaelurus*, *Haploblepharus*, *Holohalaelurus*, and *Parmaturus*;
- Scyliorhinidae II comprising *Atelomycterus*, *Aulohalaelurus*, *Schroederichthys* and *Parmaturus*;
- Scyliorhinidae III including *Cephaloscyllium*, *Poroderma*, and *Scyliorhinus.*

Family Scyliorhinidae sensu Iglésias et al. (2005) or Scyliorhinidae III sensu Naylor et al. (2012a)

Genus *Scyliorhinus* Blainville, 1816

Scyliorhinus cf. *biformis* Reinecke, 2014

Material: 22 teeth: FP1: 1 (SNSB-BSPG 2015 III 2-102); FP2: 18 (SNSB-BSPG 2015 III 2-36, 37, 40, 81); FP3: 3 (SNSB-BSPG 2015 III 2-49, 64, 68); Fig. 5 no. 1–7

Size (only Figs, min/max): 0.47–1.40 mm height: 0.56–1.03 mm width.

Description: The labial view reveals few (from 4 to 12) fine enameloid ridges typical for scyliorhinid teeth. The lingual side reveals less pronounced enameloid folds reaching sporadically to the tip of the crown. In the basal region of the crown folds are arched. The crown is erect or only slightly inclined distally. The labial face of the main cusp, as well as the one to two pairs of lateral cusplets, are strongly convex. If present at all, the outermost lateral cusplets may only be at a very indecisive stage. The root displays two lobes, showing a central foramen in the distinct root protuberance. Between root and crown, a constriction is visible (Fig. 5 no. 3–6).

Remarks: The teeth are preliminary identified as *S.* cf. *biformis*, based on the morphological characters described by Reinecke (2014). The species is reported from the southern North Sea Basin (Reinecke 2014) as well as the Ottnangian, Upper Marine Molasse (this study).

Scyliorhinus sp.

Material: 1 tooth (SNSB-BSPG 2015 III 2-89); Fig. 5 no. 8

Size: BSPG 2015 III 2-89: height: 1.2 mm; width: 1.44 mm.

Description: In contrast to the teeth of *S*. cf. *biformis*, the teeth reported here as *S*. sp. show a distinctly shorter and wider main cusp. The tooth shows wear and in-life damage, we therefore cannot clearly assign the teeth to a species.

Family Pentanchidae sensu Iglésias et al. (2005) or Scyliorhinidae I sensu Naylor et al. (2012a)
Genus *Apristurus* Garman, 1913
Apristurus sp.

Material: 10 teeth: FP1: 3 (SNSB-BSPG 2015 III 2-13, 101); FP2: 3 (SNSB-BSPG 2015 III 2-31, 33, 35); FP3: 4 (SNSB-BSPG 2015 III 2-53, 67, 76, 78); Fig. 6, no. 1–8.

Size (min/max): 0.44–0.71 mm height: 0.45–0.56 mm width.

Description: The fossils assigned to *Apristurus* show the characteristic reticulate (golf ball-like) surface texture near the base of the labial tooth face (Fig. 6, no. 4, 7); this is typical for teeth of genera *Apristurus, Galeus, Haploblepharus, Holohalaelurus, Halaelurus* (Herman et al. 1990). At the base of the enameloid, one to three distinct angular ridges arise, which can reach to the top of some lateral cusplets. The central cusp is strongly angled distally, less distinctly so in the lateral cusplets. The lingual view reveals absent or only weakly developed ornamentation (Fig. 6, no. 1, 2, 3, 5, 6, 8). The distinct ornamentation starts here only in the lower third of the teeth and consists, especially in the main cusp, of several structures of different lengths. The most distal and mesial cusps are less developed, sometimes completely absent. All cusps display a convex curvature. The edge of the enameloid is stretched leading into a blade-like edge around the margins

of the cusps, especially when investigating lateral to lateral-posterior teeth. This enameloid edge extends to the middle of the tooth crown. This creates the illusion that the cusps are broken. The thin edge is often damaged and therefore appears to be serrated. The number of lateral cusplets ranges from two to three reaching in height half of the height of the central cusp. The tooth root is fractioned in two lobes characteristic for scyliorhinid sharks. The two root lobes are "V-shaped", the connection of lobes shows a central foramina.

Remarks: With 38 described extant species, *Apristurus* is the most species rich genus of sharks (Pollerspöck & Straube 2016). Based on both morphological and molecular data, three subgroups within the genus were identified (Flammang et al. 2007; Iglésias et al. 2005; Nakaya & Sato 1999). Detailed morphological analyses dealing with the tooth morphology are only available for *A. laurussonii* (Herman et al. 1990). Without detailed information on inter- and intraspecific morphological characters, the fossils cannot be assigned to any of the described species. Interestingly, the fossil specimen shown herein are distinctly different from species described based on fossil dental remains by their striated surface structures appearing much more differentiated compared to other fossil taxa (*Apristurus sereti* Adnet, 2006, middle Lutetian, Eocene, Angoumé, France, Adnet 2006); *Apristurus* sp. lower Ottnangian, Upper Marine Molasse, Mitterdorf, Bavaria, Germany, this study), *Apristurus* sp. (*Pseudoemiliana lacunose* Zone, lower-middle Pleistocene, Fiumefreddo, Sicily, Italy, Marsili 2007).

Genus *Pseudoapristurus* nov. gen.
http://zoobank.org/NomenclaturalActs/0619A7D5-8DDF-4381-898A-96391ED2EB41

Type species: *Pseudoapristurus nonstriatus* gen. et sp. nov.; see below.

Etymology: Greek: pseudo = pretending, the teeth show a variety of characters as in *Apristurus*, but additionally shows characters which have never been documented in *Apristurus* so far.

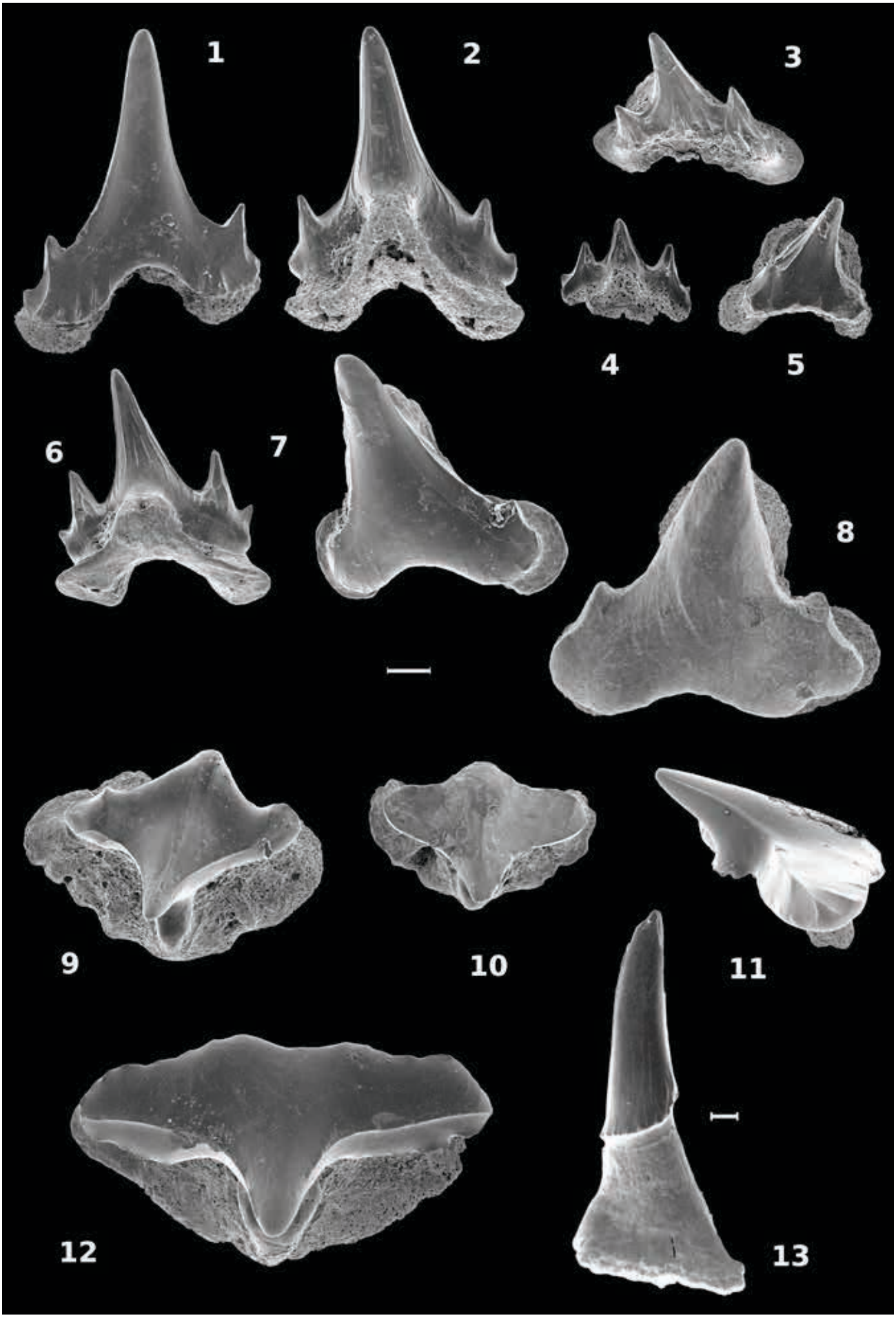
Diagnosis: Teeth 0.5–0.7 mm high, multicuspid with a single to two pairs of lateral cusplets. The first pair of cusplets may reach two thirds of the height of the main cusp. The lingual sides of the main and lateral cusps are convex, less distinct from the labial side. No labial/lingual compression of the crown/root.

As with many other scyliorhinid shark teeth, there is a reticulate ornamentation reminiscent of the surface of a golf ball on the labial side of the teeth. The cutting edges cover the entire occlusal edge in all cusps. The root shows two lobes with two central foramina. The lingual protuberance of the root is only weakly developed; there is no nutritive groove between the two root lobes. The root is holaulacorhizid and the type of dentition is likely of the clutching-type (Cappetta 2012).

Remarks: The teeth described here show morphological characters which have not been reported in neither any extant nor a fossil species so far and will therefore be described as a new genus and species. The teeth display an ornamentation comparable to that of scyliorhinid shark teeth, however their morphology partially also resembles that of some carcharhinid shark genera (Cappetta 2012; Herman et al. 1988, 1990, 1991).

Squalomorph and some higher galeomorph taxa can be excluded due to the absence of the following characters (Cappetta 2012; Herman et al. 1988, 1989, 1990, 1991, 1992): no lingual protuberance of the root, strong labio-lingual compressed teeth and root, interlocking teeth with a particular depression of the root, two root lobes (Hexanchiformes, Squaliformes), a batoid type dentition with staggered, bulky teeth (Pristiophoriformes, Heterodontiformes), no pairs of mesial and distal cusplets (Squatiniformes, Heterodontiformes lateral teeth) and the presence of a labial apron (Squatiniformes, Orectolobiformes, Heterodontiformes anterior teeth) and no tricuspid main cusps (Hexanchiformes: Chlamydoselachidae). We conclude that the taxon is much more likely a galeomorph shark fossil. The following higher-level galeomorph taxa can be excluded, because the teeth of *Pseudoapristurus* display no serration of the main cusp (Lamniformes: e.g. ex Lamnidae/Otodontidae/Cretoxyrhinidae), high and slender mesial and distal cusplets (Lamniformes: Pseudocarchariidae/Alopiidae/Cetorhinidae/Megachasmidae/Mitsukurinidae), and a weakly developed lingual protuberance of the root (Lamniformes: Pseudoscapanorhynchidae). Due to the aforementioned characters, we conclude that the teeth originally stem from a carcharhiniform taxon. Following the differential odontological characterisation of carcharhiniform subgenera in Herman et al. (1991) as well as the fact that a median root groove is absent in *Pseudoapristurus,* three extant families remain as options: Leptochariidae or Scylirohinidae/Pentanchidae. Leptochariidae is a monotypic family and genus and can be exclud-

Figure 5: (1–7) *Scyliorhinus* cf. *biformis* Reinecke, 2014, scale bar: 200 µm. No. 1: FP 3: SNSB-BSPG 2015 III 2-49: labial view. No. 2: FP 3: SNSB-BSPG 2015 III 2-49: lingual view. No. 3: FP 2: SNSB-BSPG 2015 III 2-37: lingual view. No. 4: FP 3: SNSB-BSPG 2015 III 2-68: lingual view. No. 5: FP 3: SNSB-BSPG 2015 III 2-64: labial view. No. 6: FP 2: SNSB-BSPG 2015 III 2-36: lingual view. No. 7: FP 2: SNSB-BSPG 2015 III 2-40: labial view. **(8, 9)** *Scyliorhinus* sp., scale bar: 200 µm. No. 8: FP 2: SNSB-BSPG 2015 III 2-31: labial view. **(10–13)** *Pristiophorus striatus* Underwood & Schlögl, 2013, scale bar: 200 µm (Figs 9–12), 300 µm (Fig. 13). No. 9: FP 2: SNSB-BSPG 2015 III 2-61: oral tooth, occlusal view. No. 10: FP 2: SNSB-BSPG 2015 III 2-9: oral tooth, occlusal view. No. 11: FP 2: SNSB-BSPG 2015 III 2-38: oral tooth, distal view. No. 12: FP 2: SNSB-BSPG 2015 III 2-46: oral tooth, occlusal view. No. 13: FP 2: SNSB-BSPG 2015 III 2-96: rostral tooth, height 4,10 mm.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ed due to the morphology of the main cusp (broad based and strongly inclined distal main cusp). Due to the similarities of the tooth morphology with the genera *Apristurus* and *Galeus*, we assign *Pseudoapristurus* to the extant family Pentanchidae (sensu Iglésias et al. 2005 or Scyliorhinidae I sensu Naylor et al. 2012a).

Pseudoapristurus nonstriatus sp. nov.
http://zoobank.org/NomenclaturalActs/A5C6627E-6C29-4BF2-8D87-482A158BC72D

Etymology: The genus is named for its the morphological similarity of teeth to the deep-water catsharks of the genus *Apristurus*. The species name refers to the absence of the typical enameloid tooth folds found in *Apristurus*.

Holotype: SNSB-BSPG 2015 III 2-24 (Fig. 7 no. 1).

Paratype: SNSB-BSPG 2015 III 2-34 (Fig. 7 no. 3), SNSB-BSPG 2015 III 2-79 (Fig. 7 no. 8).

Type locality: Mitterdorf, Lower Bavaria, Germany.

Type horizon: Neuhofener Beds, Upper Marine Molasse, late Ottnangian (equivalent to middle Burdigalian).

Material: 9 teeth (incl. types): FP2: 4 (SNSB-BSPG 2015 III 2-24, 27, 30, 34); FP3: 5 (SNSB-BSPG 2015 III 2-66, 70, 77, 79, 86); Fig. 7 no. 1–8.

Diagnosis: As for genus.

Description: Holotype SNSB-BSPG 2015 III 2-24 (Fig. 7 no. 1a, 1b): The holotype specimen displays a slender main cusp angled distally that is flanked by two pairs of lateral cusplets. The first pair of cusplets is two thirds in its height compared to the main cusp. The lateral cusplets appear circular in cross-section (Fig. 7 no. 1b), the first mesial cusplet is angled mesially whereas the first distal cusplet points distally. All cusps show a cutting edge reaching to the top of each cusp. The main cusp has a more convex lingual than labial face and has a base that is widely separated from the bases of the lateral cusplets. Cusps are smooth showing no striations typical of many scyliorhinid shark teeth (e.g. Fig. 7 no. 1). The lingual root surface displays two foramina, one close to the edge of the crown, the second on the basal surface. The ornamentation continues labially.

In our sampling, two types of teeth were found: teeth morphologically highly similar to the type specimen and teeth morphologically similar to the defined paratype specimen, which, in contrast to the holotype, lacks elongated, dagger-like lateral cusplets (Fig. 7 no. 1–3), but instead has cusplets that are wide and oval in cross-section (Fig. 7 no. 4–8). We speculate that these two forms may represent upper- and lower jaw teeth, with teeth showing the distinct slender, elongated cusps may represent upper jaw teeth. Another explanation could be a form of sexual dimorphism described from several extant scyliorhinid sharks (Herman et al. 1990).

The ornamentation reminding of a golf ball surface is frequently documented in scyliorhinid shark teeth (Herman et al. 1990). We therefore place the new genus within the family Scyliorhinidae.

Order Pristiophoriformes Compagno, 1973

Family Pristiophoridae Bleeker, 1859

Genus *Pristiophorus* Müller & Henle, 1837
Pristiophorus striatus Underwood & Schlögl, 2013

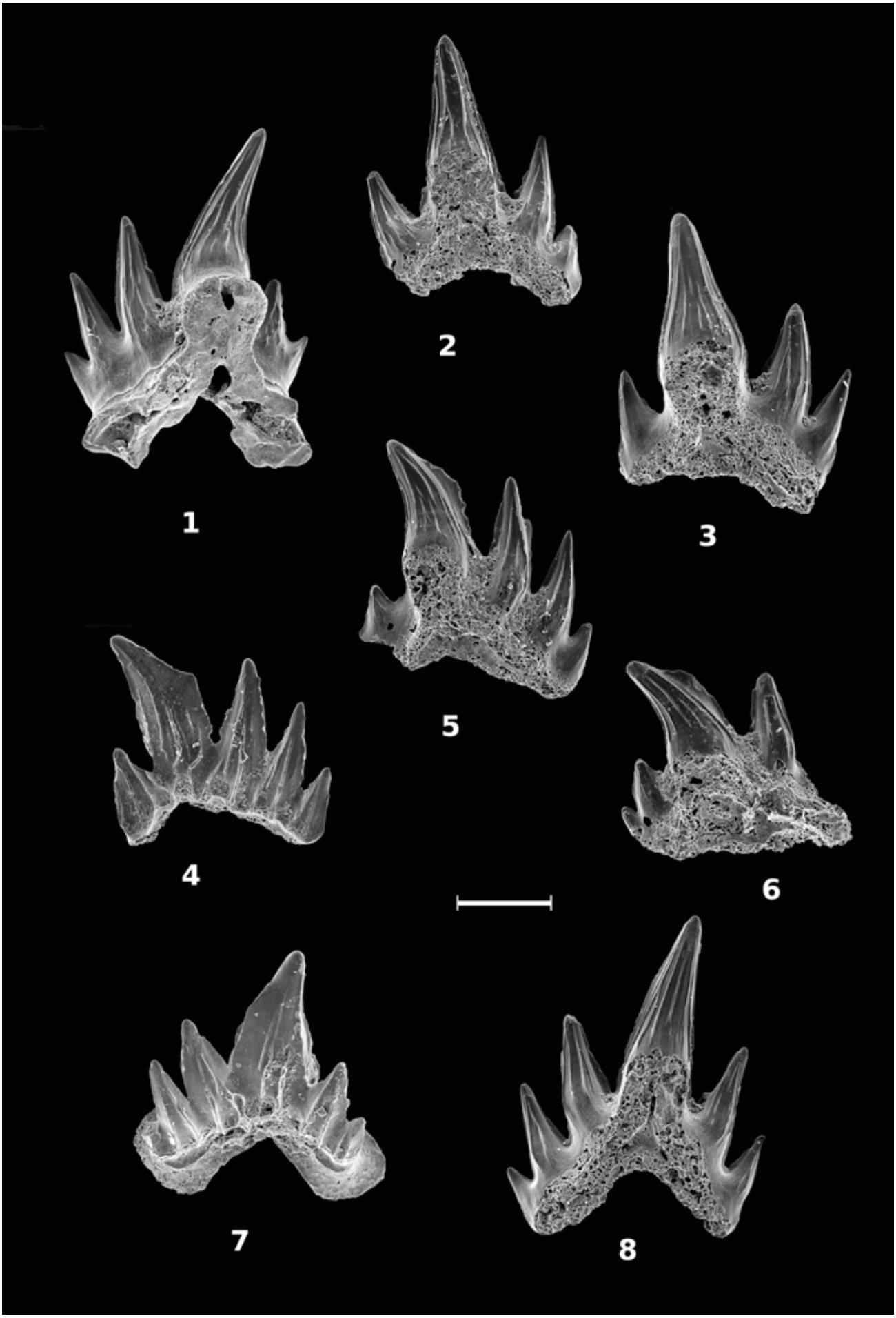
Material: 6 oral teeth, 29 rostral teeth: FP1: 2 rostral teeth (SNSB-BSPG 2015 III 2-9, 103); FP2: 10 rostral oral, 4 oral teeth (SNSB-BSPG 2015 III 2-38, 96, 104); FP3: 17 rostral teeth, 2 oral teeth (SNSB-BSPG 2015 III 2-46, 61, 105); Fig. 5 no. 9–13.

Size (only Figs, min/max): 1.00–1.843 mm width.

Description: On the labial side oral teeth are distinct enameloid ridges in the center of the main cusp, beginning at the crown basis continuing up to the top of the cusp. In most instances, this fold is accompanied by two further folds located mesially and distally at the outer edge of the tooth (Fig. 5 no. 9, 10). In some instances, more of these accompanying folds can occur, e.g. Fig. 5 no. 12. On its lingual side, the main cusp does not show ridges, whereas its labial side may show ridges at the mesial and/or distal extensions of the tooth crown. Some teeth (e.g. Fig. 5 no. 12) do not display central ridges. The labial edge of the crown is highly variable: it can be distinct, showing a triangular shape (Fig. 5 no. 9), but may also display a rounded crown overlap (Fig. 5 no. 10) or even show a slightly wavy crown basis (Fig. 5 no. 12).

Remarks: Herman et al. (1992) show teeth of a male specimen of *Pristiophorus cirratus* (Latham, 1794), which clearly display a number of morphological varieties as described herein. Further, *Pliotrema warreni* Regan, 1906 (Herman et al. 1992) has enam-

Figure 6: (1–8) *Apristurus* sp., scale bar: 200 µm. No. 1: FP 3: SNSB-BSPG 2015 III 2-78: height 0.70 mm; width 0.55 mm; lingual view. No. 2: FP 3: SNSB-BSPG 2015 III 2-67: height 0.58 mm; width 0.45 mm; lingual view. No. 3: FP 2: SNSB-BSPG 2015 III 2-35: height 0.63 mm; width 0.46 mm; lingual view. No. 4: FP 3: SNSB-BSPG 2015 III 2-53: height 0.45 mm; width 0.45 mm; labial view. No. 5: FP 2: SNSB-BSPG 2015 III 2-33: height 0.54 mm; width 0.50 mm; lingual view. No. 6: FP 3: SNSB-BSPG 2015 III 2-76: height 0.44 mm; width 0.49 mm; lingual view. No. 7: FP 1: SNSB-BSPG 2015 III 2-13: height 0.55 mm; width 0.56 mm; labial view. No. 8: FP 2: SNSB-BSPG 2015 III 2-31: height 0.71 mm; width 0.55 mm; lingual view.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eloid folds present in all upper teeth, while lower teeth only irregularly show a distinct fold. Therefore, we suggest that the presence or absence of labial folds in the fossils described herein cannot be used for its species identification. Underwood & Schlögl (2013) describe the species based on two single teeth. Here, we can provide further information regarding the morphological variability of the species.

Order Squaliformes Compagno, 1973

Family Centrophoridae Bleeker, 1859

Genus *Centrophorus* Müller & Henle, 1837
Centrophorus sp.

1879: *Acanthias radicans* n. sp. – Probst: p. 173, 174, pl. 3, figs 31, 32.
1879: *Acanthias serratus* n. sp. – Probst: p. 174, pl. 3, fig. 33.
1930: *Centrophorus* spec. – Fischli: p. 148, pl. 1, fig. 7.
1972: *Centrophorus granulosus* – Ledoux: p. 145–148, fig. 5.
1991: *Centrophorus* cf. *granulosus* – Barthelt et al.: p. 199, pl. 1, fig. 7.
1995: *Squalus* sp. – Holec et al.: p. 39, pl. 9, figs 3, 4.
2009: *Centrophorus* cf. *granulosus* – Brisswalter et al.: p. 22, pl. 2, figs 3–7.
2011: *Centrophorus* aff. *granulosus* – Vialle et al.: p. 243, fig. 2-1.
2014: *Centrophorus* cf. *granulosus* – Pollerspöck & Beaury, p. 26, pl. 2, figs 1a, 1b.

Material: 92 teeth FP1: 4 (SNSB-BSPG 2015 III 2-106); FP2: 29 (SNSB-BSPG 2015 III 2-107); FP2a: 5 (SNSB-BSPG 2015 III 2-108); FP3: 54 (SNSB-BSPG 2015 III 2-48, 109); Fig. 8.

Size (Fig. 8): 3.02 mm height: 1.76 mm width.

Description: The sampling sites contained numerous centrophorid teeth, identified following Herman et al. (1989). Due to the dignathic heterodont dentition, distinctly different lower and upper jaw teeth are identified. Teeth of this morphology are represented with fossil remains in nearly all deposits of the Upper Marine Molasse. The lower jaw teeth are labio-lingually compressed with a distally angled cusp. The cusp`s mesial crown edge is distinctly but irregularly serrated. The convex distal blade is separated from the main cusp by a deep groove. The elongated root lobe shows clear overlapping areas to neighboring teeth to form a cutting edge. On the labial side of the root, a wide, clearly distinct apron points ventrally, its basal edge unregularly marked. Total width of the root displays a swelling on its lingual side, which is ruptured by a central foramen. A shallow groove originating at the central foramen is pointing ventrally.

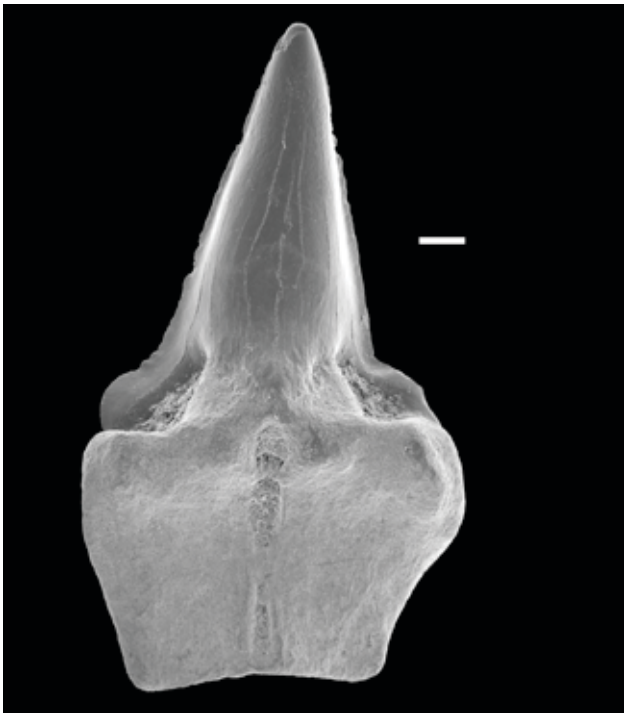


Figure 8: *Centrophorus* sp., (SNSB-BSPG 2015 III 2-48), upper jaw, parasymphysial tooth, lingual view, scale bar: 200 µm.

The upper jaw tooth shown in Figure 8 is a symphyseal tooth as in Herman et al. (1989). The central foramen is distinct, located at the end of a shallow, broken groove originating at the tooth basis. The root forms a nearly rectangular shape; its crown is upright, lingually convex with a serrated edge.

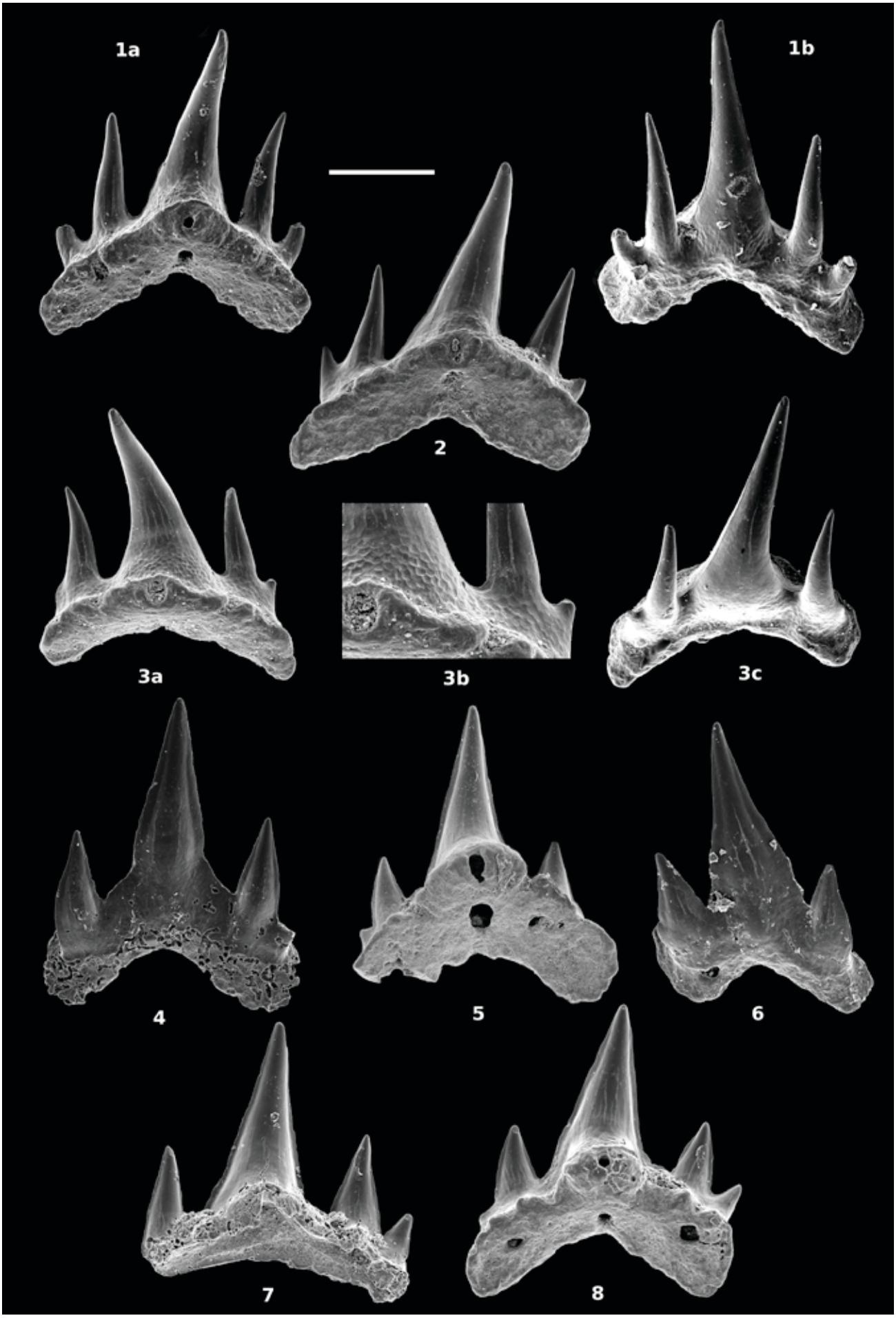
Remarks: Teeth assigned to *Centrophorus* sp. herein show high morphological similarities to the specimen assigned to the extant species *C. granulosus* by Herman et al. (1989), as well as a number of fossil teeth previously described (see above).

Morphologically highly similar teeth are known from the German Molasse basin (Probst 1879; Barthelt et al. 1991; Pollerspöck & Beaury 2014; this study), Austria (Schultz 2013), Switzerland (Fischli 1930), France (Ledoux 1972; Brisswalter 2009; Vialle et al. 2011) and Slovakia (Holec et al. 1995 as *Squalus* sp.).

The taxonomy of extant species of the genus *Centrophorus* is still debated (Verrssimo et al. 2014; White et al. 2013) and studies dealing with the morphological variability of tooth characters are still lacking. Therefore, we refrain from assigning the fossils to an extant species.

Genus *Deania* Jordan & Snyder, 1902
Deania sp.

Figure 7: (1–8) *Pseudoapristurus nonstriatus* sp. nov., scale bar: 200 µm. No. 1: FP 2: SNSB-BSPG 2015 III 2-24: holotype, 1a) lingual view, 1b) labial view. No. 2: FP 3: SNSB-BSPG 2015 III 2-66: lingual view. No. 3: FP 2: SNSB-BSPG 2015 III 2-34: paratype, 3a) lingual view, 3b) detail view of the ornamentation, 3c) labial view. No. 4: FP 2: SNSB-BSPG 2015 III 2-30: labial view. No. 5: FP 3: SNSB-BSPG 2015 III 2-86: lingual view. No. 6: FP 3: SNSB-BSPG 2015 III 2-77: labial view. No. 7: FP 3: SNSB-BSPG 2015 III 2-70: lingual view. No. 8: FP 3: SNSB-BSPG 2015 III 2-79: paratype, lingual view.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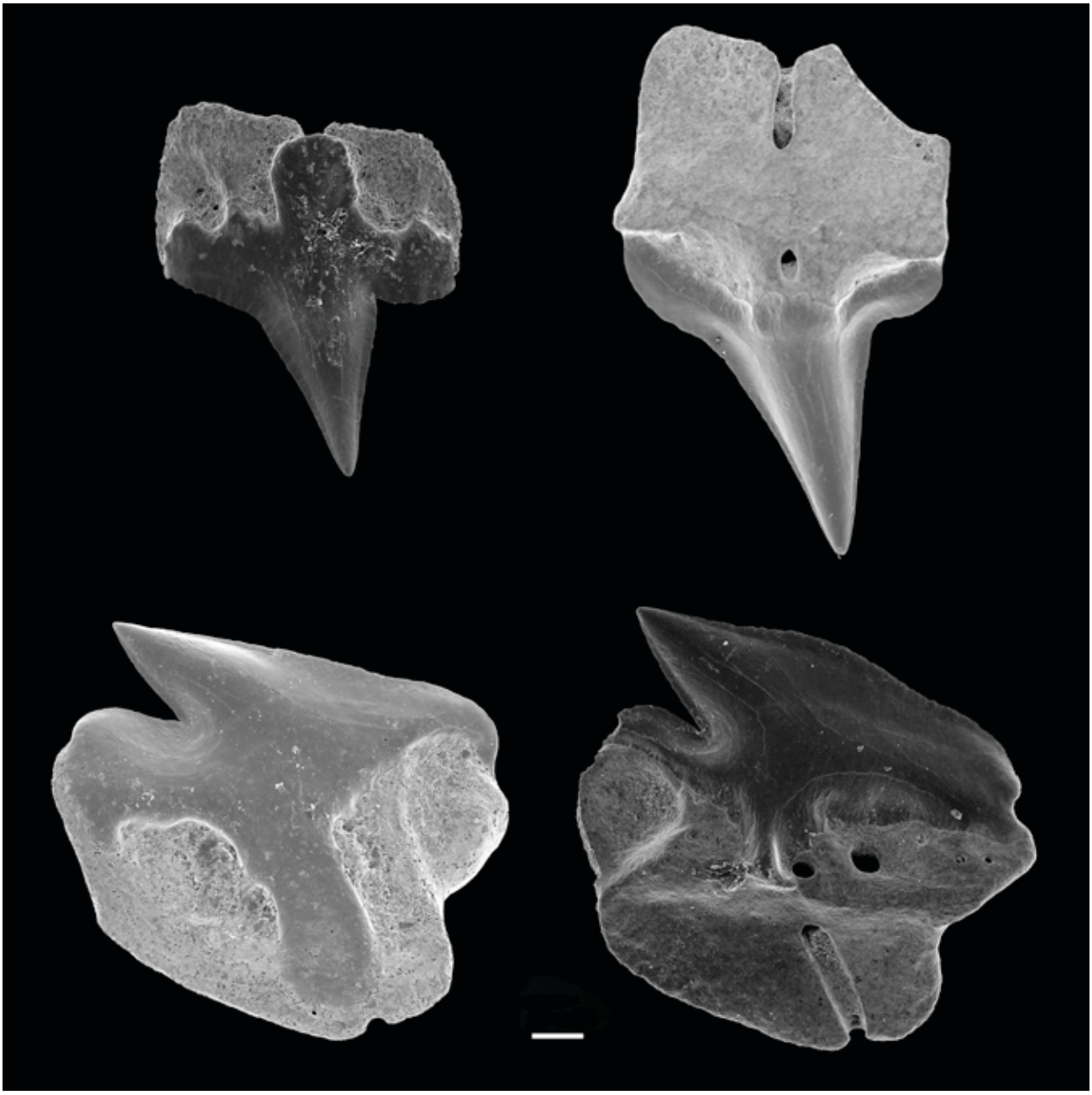


Figure 9: *Deania* sp., upper jaw: left, labial view (SNSB-BSPG 2015 III 2-54), right, lingual view (SNSB-BSPG 2015 III 2-47); lower jaw, left, labial view (SNSB-BSPG 2015 III 2-45), right, lingual view (SNSB-BSPG 2015 III 2-23); scale bar: 200 µm.

Material: 5 teeth: FP2: 2 (SNSB-BSPG 2015 III 2-23); FP3: 3 (SNSB-BSPG 2015 III 2-45, 47, 54); Fig. 9.

Size (only Fig. 9): 1.4–1.76 mm height; 1.16–1.76 mm width.

Description: Three upper and two lower jaw teeth were collected. These teeth show remarkable morphological similarities to teeth to the extant genus *Deania* (Herman et al. 1989).

Remarks: This is the first record of the genus from the German Molasse. So far, the genus has been documented in the Molasse Basin/Mediterranean in France (Ledoux 1972; Vialle et al. 2011) and from the Pliocene of Italy (Marsili & Tabanelli 2007). Schultz (2013) mentions the taxon as present in Austria based on the accompanying diversity of fossil teeth of *Chlamydoselachus* in (Pfeil 1983). Cappetta (2012) cites Probst (1879) and Barthelt et al. (1991) as reference for the genus` occurrence in Germany. However, the species *Acanthias radicans* described in Probst (1879) is a synonym to *Centrophorus* cf. *granulosus* (Barthelt et al. 1991), therefore *Deania* has not yet been reported from Germany.

Order Squaliformes Compagno, 1973

Family Dalatiidae Gray, 1851

Genus *Isistius* Gill, 1865

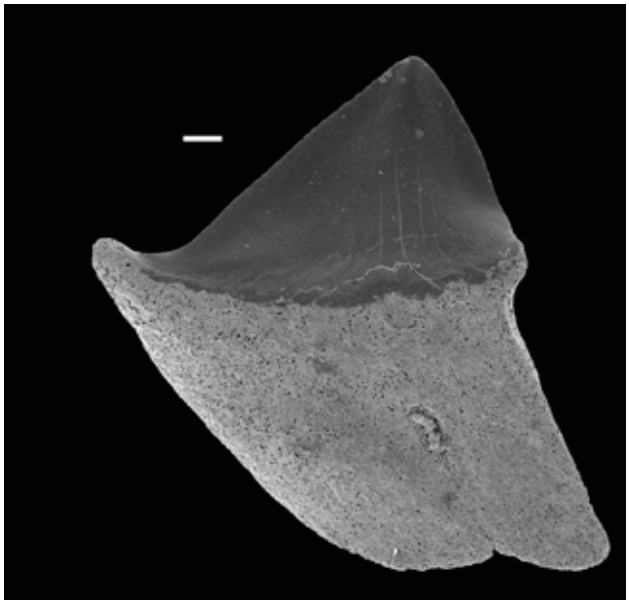


Figure 10: *Isistius triangulus* (Probst, 1879), (SNSB-BSPG 2015 III 2-41), commissural tooth, lingual view, scale bar: 200 µm.

Isistius triangulus (Probst, 1879)

* 1879: *Scymnus triangulus* - Probst: p. 175, 176, pl. 3, figs 35, 36.
1930: *Isistius trituratus* – Fischli: p. 148, pl. 1, fig. 7.
1972: *Isistius triangulus* – Ledoux: p. 161–163, fig. 13.
1991: *Isistius triangulus* – Barthelt et al.: p. 199, pl. 1, fig. 10.
1995: *Isistius triangulus* – Holec et al.: p. 39, pl. 9, figs 1, 2.
2007: *Isistius* cf. *triangulus* – Kocsis: p. 29, fig. 3.6
2009: *Isistius triangulus* – Brisswalter et al.: p. 24, pl. 2, fig. 8.
2011: *Isistius triangulus* – Vialle et al.: p. 243, 244, figs 2–4.
2013: *Isistius triangulus* – Schultz: p. 31, pl. 9, figs 7–9.
2014: *Isistius triangulus* – Pollerspöck & Beaury, p. 26, 27, pl. 2, figs 3 a, b.

Material: 10 lower jaw teeth (FP1: 2, SNSB-BSPG 2015 III 2-97; FP2: 2, SNSB-BSPG 2015 III 2-98; FP2a: 1 SNSB-BSPG 2015 III 2-99; FP3: 5, SNSB-BSPG 2015 III 2-100) including a single commissural tooth from a mouth corner (SNSB-BSPG 2015 III 2-41), Fig. 10.

Size: SNSB-BSPG 2015 III 2-41: height: 2.4 mm; width: 2.4 mm.

Description: The genus is documented based on a series of damaged and complete lower teeth including a commissural tooth (Fig. 10). The teeth are assigned to *Isistius triangulus* (Probst, 1879) due to the strong labio-lingual compression; its triangular crown showing a smooth to finely serrated edge. In contrast to the lingual side, the labial enameloid covers a large part of the root, which shows a central foramen. On its lingual side, approximately in the middle of the tooth, central foramina can be found. Another foramen is visible at the lower half of the rectangular root, terminating a shallow groove originating at the root basis.

Remarks: *Isistius* tooth fossils are also well known and widespread in the Upper Marine Molasse (Vialle et al. 2011; Pollerspöck & Beaury 2014). It is noteworthy that so far, no upper jaw teeth were ever reported (Cappetta 2012). Today, *Isistius* has not been documented to occur in the Mediterranean Sea. The distribution range of the two extant species *I. brasiliensis* and *I. plutodus* seems limited to the Atlantic and Pacific Ocean (Ebert 2013; Ebert et al. 2015; Pollerspöck & Straube 2016), where the Azores form the most northern boundary in the Atlantic (Zidowitz et al. 2004).

Family Etmopteridae Fowler, 1941

Genus *Etmopterus* Rafinesque, 1810
Etmopterus sp.

2013: *Etmopterus* sp. – Underwood & Schlögl: p. 496–498, figs 7 A–G (excl. C1, C2)

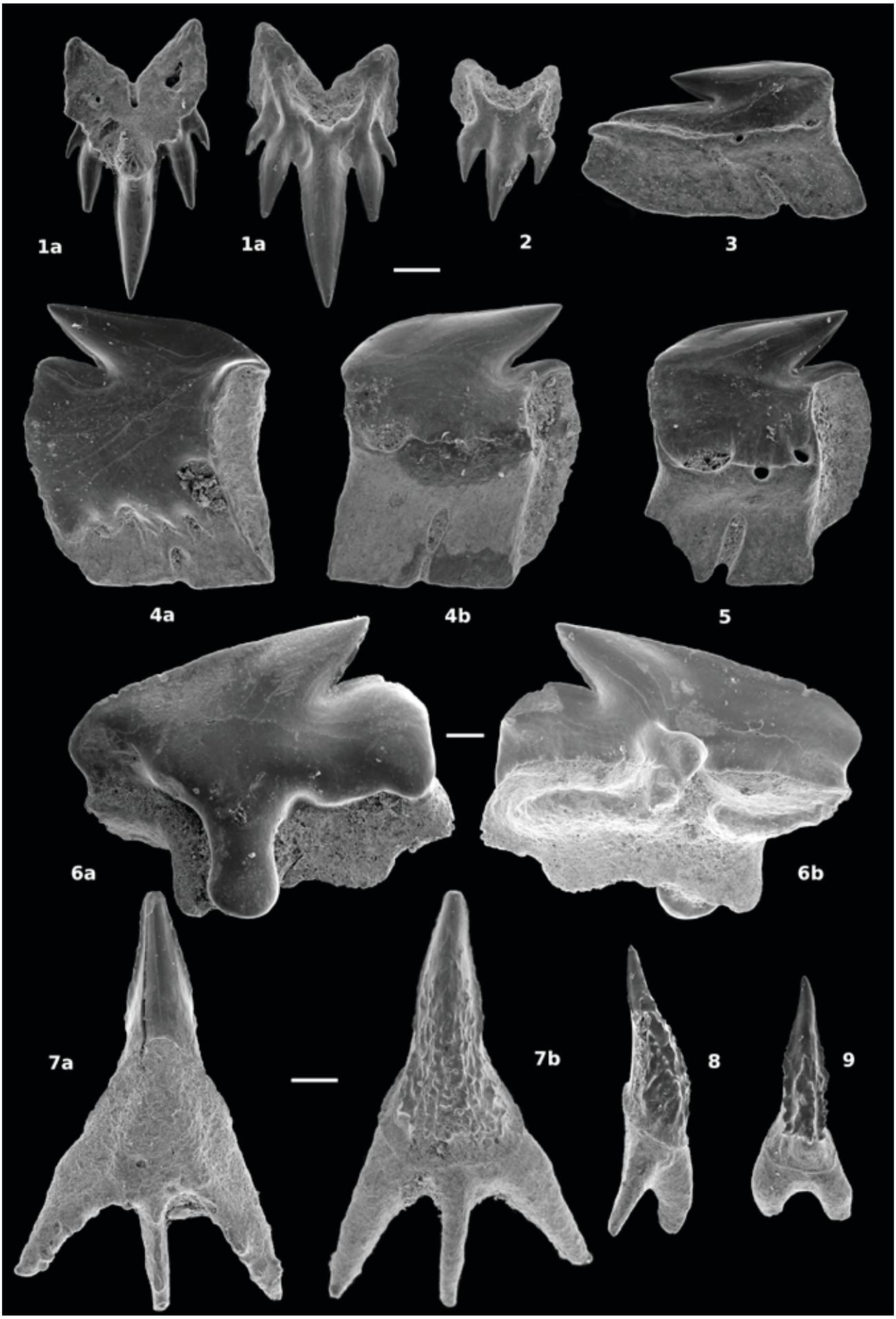
Material: 41 teeth (FP1: 6, SNSB-BSPG 2015 III 2-1-6; FP2: 24, SNSB-BSPG 2015 III 2-17–22, 25, 26, 28, 32, 94, 95; FP3: 11, SNSB-BSPG 2015 III 2-83–85, 87); Fig. 11 no. 1-5.

Size (only Figs): height: 0.7–1.14 mm; width: 0.48–1.17 mm.

Description: Our sampling revealed 41 mostly intact teeth representing various jaw positions. The upper teeth of *Etmopterus* comprise a two-lobed root and two to four lateral cusplets flanking a “dagger-like” main cusp. Lower jaw teeth show a single strongly inclined cusp with small distal blade. Distally, lower jaw teeth display a distinct groove, which shows a large foramen. At the basis of the crown, three to four further foramina are visible as well as a central foramina located at the middle of the root. A groove extends to the base of the root from the aforementioned foramen in several specimens. On their labial sides, the basal edge of the enameloid (half of the lingual side) undulates. There are several foramina along this edge as well as a central foramen in the lower part of the root.

Remarks: Research dealing with tooth morphologies allowing for a species-specific diagnosis were

Figure 11: (1–5) *Etmopterus* sp., scale bar: 200 µm. No. 1: FP 2: SNSB-BSPG 2015 III 2-21: upper jaw, 1a) lingual view, 1b) labial view. No. 2: FP 3: SNSB-BSPG 2015 III 2-84: upper jaw, labial view. No. 3: FP 2: SNSB-BSPG 2015 III 2-32: lower jaw, commissural tooth, lingual view. No. 4: FP 2: SNSB-BSPG 2015 III 2-25: lower jaw, 4a) labial view, 4b) lingual view. No. 5: FP 2: SNSB-BSPG 2015 III 2-22: lower jaw, lingual view. **(6)** *Squalus* sp., scale bar: 200 µm. No. 6: FP 3: SNSB-BSPG 2015 III 2-52: Height 1.6 mm; Width 2.0 mm; 6a labial view, 6b lingual view. **(7–9)** *Nanocetorhinus tuberculatus* Underwood & Schlögl, 2013, scale bar: 200 µm. No. 7: FP 2: SNSB-BSPG 2015 III 2-55: 7a) lingual view, 1b) labial view. No. 8: FP 2: SNSB-BSPG 2015 III 2-60: labial view. No. 9: FP 2: SNSB-BSPG 2015 III 2-65: labial view.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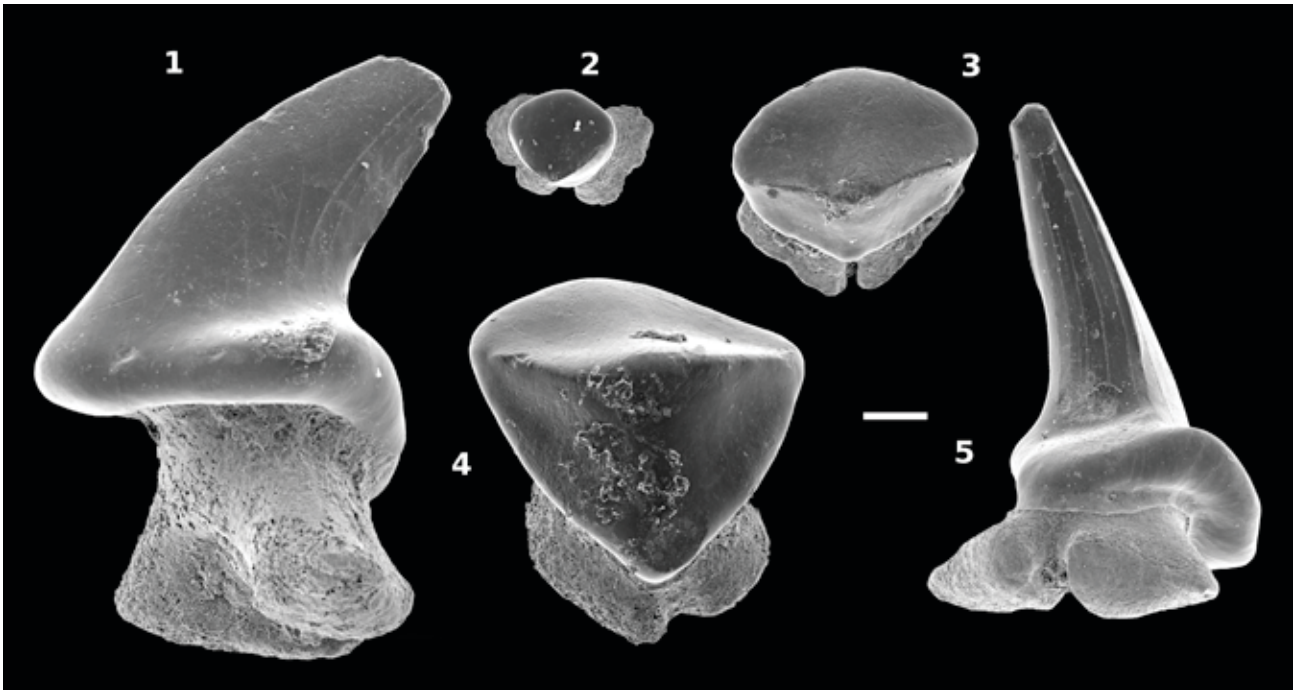

Figure 12: (1–5) *Raja gentili* Joleaud, 1912, scale bar: 200 µm. No. 1: FP 1: SNSB-BSPG 2015 III 2-51: male, lateral view. No. 2–3: FP 1: SNSB-BSPG 2015 III 2-10, 16: female, occlusal view. No. 4: FP 3: SNSB-BSPG 2015 III 2-73: female, occlusal view. No. 5: FP 2: SNSB-BSPG 2015 III 2-42: male, lateral view.

so far only conducted for two *(E. spinax* and *E. granulosus*) of the 39 extant species (Herman et al. 1989; Straube et al. 2008; Pollerspöck & Straube 2016). Nevertheless, a genetic study revealed four subclades within the genus, which are in congruence with morphological characters. In the future, the four extant subclades will be analyzed for potential clade-specific dental characters, which may allow assignment of the fossil teeth described here to one of the *Etmopterus* subclades.

We were not able to detect any dental morphological or morphometrical differences between fossil teeth anaylsed herein and the specimen shown in Underwood & Schlögl (2013).

Family Squalidae Bonaparte, 1834

Genus *Squalus* Linné, 1758
Squalus sp.

Material: 6 teeth (FP2: 2, SNSB-BSPG 2015 III 2-114; FP3: 4, SNSB-BSPG 2015 III 2-52, 82, 115); Fig. 11 no. 6.

Size: height: 1.3–1.7 mm; width: 1.0–2.4 mm.

Description: Teeth described here are very small compared to *Squalus almeidae* and *S. alsaticus* (Antunes & Jonet 1970; Reinecke et al. 2005, 2014). Nevertheless, they show typical characters allowing an assignation to the genus *Squalus*. The crown is low and strongly bent distally. Its edge is smooth and without ornamentation. The apron is nearly erect in relation to the crown basis and extends beyond the root base on its labial side (Fig. 11 no. 6a). The crown's edge gently undulates; the characteristic foramina seen on the basal edge of the crown in many *Squalus* teeth display are completely missing in this specimen.

Remarks: Today, 25 *Squalus* species are described (Pollerspöck & Straube 2016). Detailed analyses dealing with tooth morphologies of extant species were only conducted for *Squalus acanthias* (Herman et al. 1989; Ledoux 1970; Bass et al. 1976), *Squalus megalops* (Bass et al. 1976), *Cirrhigaleus asper* (Bass et al. 1976) and *Cirrhigaleus barbifer* (Herman et al. 1989). *S. acanthias* differs significantly from the fossils described herein, for example *S. acanthias* displays a shorter, more slender apron not overhanging the root. The fossil *Squalus alsaticus* (Bor et al. 2012; Reinecke et al. 2014) differs from the fossils described here by the reduction of the labial foramina as well as its size (Reinecke et al. 2014).

Neoselachii incertae sedis

Genus *Nanocetorhinus* Underwood & Schlögl, 2013
Nanocetorhinus tuberculatus
Underwood & Schlögl, 2013

1995: *Cetorhinus* sp. – Bolliger et al.: pl. 2, fig. 7.
2005: Elasmobranch dermal denticle or possible tooth, Form I – Johns et al.: p. 39 fig. 37.
* 2013: *Nanocetorhinus tuberculatus* – Underwood & Schlögl: p. 502–504, figs 9 A–H.

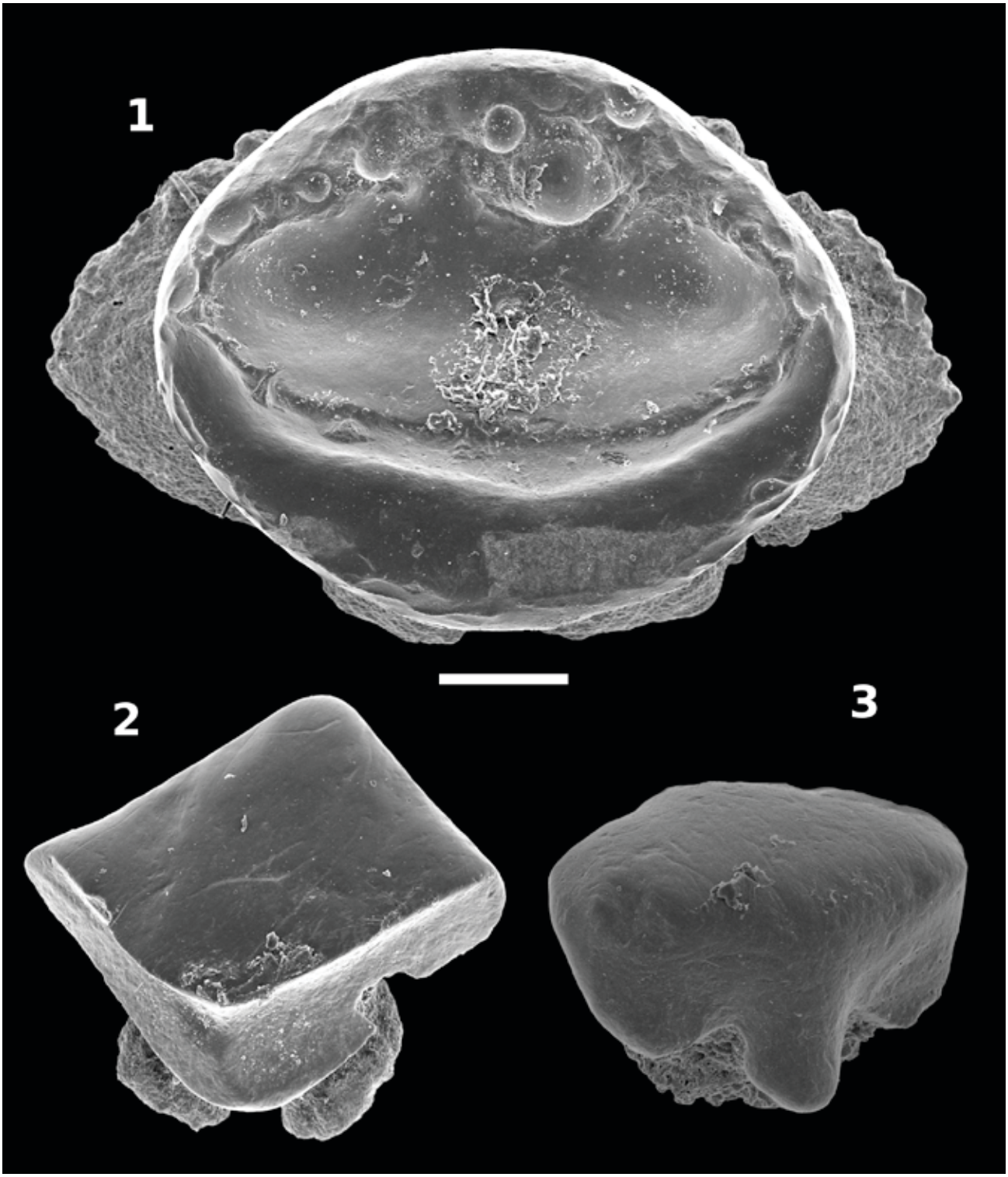

Figure 13: (1) Rajidae sp. indet., FP 1: SNSB-BSPG 2015 III 2-15: occlusal view. **(2)** Urolophidae indet., FP 1: SNSB-BSPG 2015 III 2-12: occlusal view. **(3)** *Rhinobatos* sp., FP 3: SNSB-BSPG 2015 III 2-125: labial view. Scale bar: 200 µm.

Material: 126 teeth (FP1: 11, SNSB-BSPG 2015 III 2-116; FP2: 57, SNSB-BSPG 2015 III 2-117; FP3: 58, SNSB-BSPG 2015 III 2-55–60, 65, 118); Fig. 11 no. 7–9.

Size (only Figs): height: 1.01–1.77 mm; width: 0.40–1.13 mm.

Description: The frequent fossils found here are assigned to *Nanocetorhinus tuberculatus* because they morphologically resemble the fossils described in Underwood & Schlögl (2013). Both two- and three-lobed tooth roots are found. Six out of 120 teeth actually show three distinct root lobes, another 15 teeth show at least a projection of a third lobe.

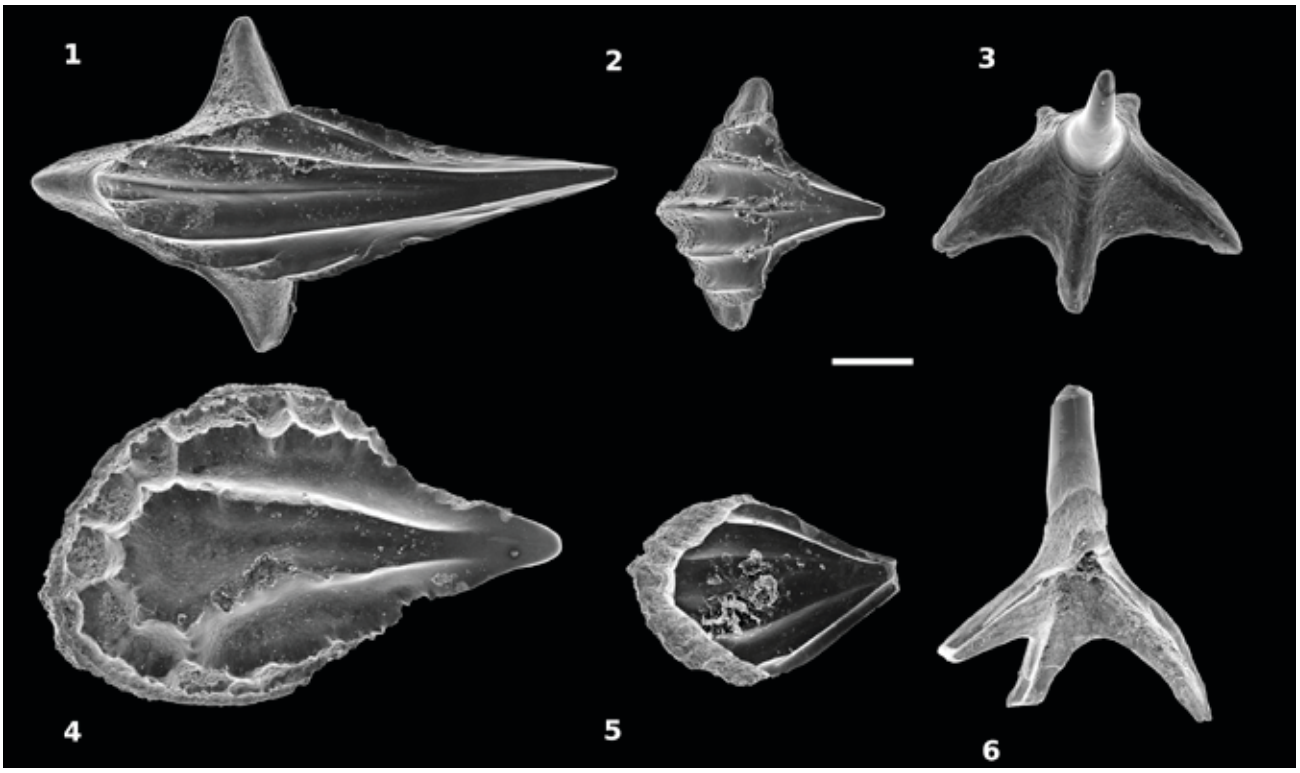

Figure 14: (1–5) Dermal denticles. No. 1, 2: "scyliorhinid/pentanchid" denticles: FP 3: SNSB-BSPG 2015 III 2-72, 80. No. 3: "rajid" denticle: FP 2: SNSB-BSPG 2015 III 2-29. No. 4: "squatinid" denticle: SNSB-BSPG 2015 III 2-63. No. 5: "squalid" denticle: FP 3: SNSB-BSPG 2015 III 2-69. No. 6: "rajid" denticle: FP 1: SNSB-BSPG 2015 III 2-7. Scale bar: 200 µm.

Remarks: This fossil taxon is known from the Latest Burdigalian (Karpatian) Slovak Republic, eastern margin of the Vienna Basin (Underwood & Schlögl 2013), the Upper Egerian, Finklham, Austria, Älterer Schlier (own collection); Ottnangian, Mitterdorf, Germany (this study) and Bollwies, Hummelberg and Curtiberg, Switzerland, Upper Marine Molasse (Eggenburgian, Ottnangian, Bolliger et al. 1975). Note that we consider the fossil described as *Cetorhinus* sp. in Bolliger et al. (1975) as *Nanocetorhinus tuberculatus.* Therefore, the species seems to be widely distributed and common across the complete Molasse Basin.

Order Rajiformes Berg, 1940

Family Rajidae Bonaparte, 1831

Genus *Raja* Linné, 1758
Raja gentili Joleaud, 1912

Material: 84 teeth (FP1: 6, SNSB-BSPG 2015 III 2-10, 11, 16, 119; FP2: 36, SNSB-BSPG 2015 III 2-42, 43, 120; FP2a: 3, SNSB-BSPG 2015 III 2-124; FP3: 39, SNSB-BSPG 2015 III 2-51, 73, 121); Fig. 12 no. 1–5.

Size (Fig. 12 no. 1–5): height: 0.5–2.0 mm; width: 0.5–1.2 mm.

* 1912: *Raja gentili* – Joleaud: pl. 8, figs 37–44, non figs 45, 46.
1930: *Raja gentili* – Fischli: p. 157, fig. 4.
1970: *Raja gentili* – Cappetta: p. 84, 85, pl. 20, figs 28–32.
2001: *Raja gentili* – Ward & Bonavia: p. 143, pl. 2, figs f, g.
2007: *Raja* cf. *gentili* – Bracher & Unger: p. 147–149, pl. 53.
2009: *Raja gentili* – Brisswalter: p. 44, pl. 9, fig. 3.
2011: *Raja gentili* – Vialle et al.: p. 252, figs 4-3, 4-4.

Description: The fossils assigned to this taxon represent the most frequent rajid fossil, and agree well with previous descriptions of the species. Castillo-Géniz et al. (2007) as well as Feduccia & Slaughter (1974) speculate that a sexual dimorphism comparable for example to extant species *Raja texana, R. ocellata* or *R. clavata* can be observed in their specimen. If this is accurate, then the specimen in this study shows the same dimorphism, i.e. potential male teeth are erect and pointed forming a cutting edge on their labial sides. Female type teeth display a smooth unornamented crown surface, and a low crown profile. The root shows two widely separated lobes that are broadly expanded in meso-distally direction and is strongly overhung by the crown (Fig. 12 no. 2–4). Fossils of this type are known from Miocene deposits of France (Joleaud 1912; Cappetta 1970; Brisswalter 2009; Vialle et al. 2011), Switzerland (Fischli 1930), Malta (Ward & Bonavia 2001), and Germany (this study).

Rajidae sp. indet.

Material: 3 teeth (FP1: 2, SNSB-BSPG 2015 III 2-15, 122; FP3:1, SNSB-BSPG 2015 III 2-123); Fig. 13 no. 1.

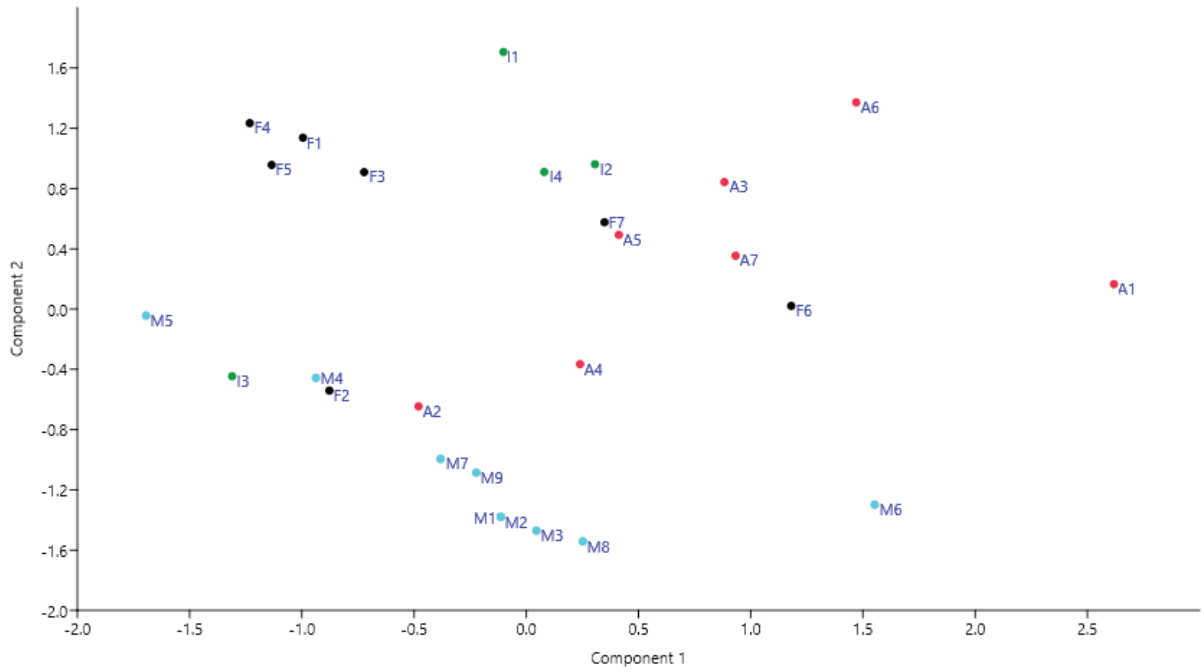

Figure 15: Principal component analysis (PCA) of selected faunas listed in Table 2.

Size (Fig. 13 no. 1): width: 1.42 mm.

Description: The single tooth assignable to this species is marked by an oval crown, and a root characterized by two lobes, which widely overarch by the crown on both sides. This overall morphology is characteristic for teeth occurring in the family Rajidae (Herman et al. 1995). In occlusal view, teeth show an oval shape with the root wider than the crown. The occlusal face is separated into an occluso-lingual and labial subarea by a sharp, convex ridge. The occlusal subarea is impressed and shows ornamentation comprising an incomplete oval ridge.

Remark: Here we do not assign the fossils to a ray genus or species as too few specimens are available for allowing a detailed analysis.

Family Rhinobatidae Bonaparte, 1835
Rhinobatos Linck, 1790
Rhinobatos sp.

Material: 1 tooth (FP3: SNSB-BSPG 2015 III 2-125); Fig. 13 no. 3.
Size: width: 0.6 mm.

Description: The single specimen described here lacks a root due to damage. The crown is separated into two areas by a distinct but blunt occlusal ridge. The occlusal surface is smooth and shows no structure. The labial side of the crown shows a distinct uvula at its lower end. The mesial and distal edges show further weakly developed uvulae resembling as an oscillating crown edge. The uvulae are less strongly developed than in many “rhinobatid” taxa.

Remark: *Rhinobatos* fossils are documented since the Barremian (Cappetta 2012). In the Upper Marine Molasse Fischli (1930) already reported the genus.

Order Myliobatiformes Compagno, 1973

Family Urolophidae Müller & Henle, 1841
Urolophidae indet.

Material: 1 tooth (FP1: SNSB-BSPG 2015 III 2-12); Fig. 13 no. 2.

Size: width: 0.74 mm.

Description: The single specimen collected shows a symmetrical and rhombic occlusal surface. The root shows two lobes, which are angled lingually, separated by a basal groove.
There is no ornamentation and no concavity on the occlusal surface as e.g. as seen in *Dasyatis* (Cappetta 2012). Nevertheless it can be clearly assigned to the family Dasyatidae due to the overall tooth form (Herman et al. 1998, 1999).

Remarks: Even though teeth of the genus *Hexatrygon* appear very similar to the specimen shown in Fig. 13b, we refrain from assigning the specimen to *Hexatrygon*, as the lower lingual edge of the crown of *Hexatrygon* shows a horizontal edge (Herman et al. 1998), unlike the tapered edge of the specimen shown here.

Dermal denticles.

Material: 154 denticles (FP1: SNSB-BSPG 2015 III

2-7, 8, 14, 126; FP2: SNSB-BSPG 2015 III 2-29, 39, 44, 127; FP3: SNSB-BSPG 2015 III 2-62, 63, 69, 71, 72, 74, 75, 80, 128); Figs 14 no. 1–6.

Description: More than a hundred dermal denticles were collected from the Neuhofener Beds. Here, we figure examples of some of the more diagnostic morphotypes, which allow a preliminary taxonomic assignation (Figs 14 no. 1–6). Two of the denticles show the typical characters known to occur in scyliorhinid and pentanchid sharks (e.g. genus *Scyliorhinus*: Meyer & Seegers 2012; Manzanares et al. 2014; genus *Apristurus*: Kawauchi et al. 2014; genus *Galeus*: Konstantinou et al. 2000) (Figs14 no. 1, 2). Figure 14 no. 1 represents the most frequently found scyliorhinid/pentanchid-type denticle (FP1: n=8, FP2A: n=15; FP3: n=42) Dermal denticles showing a thorn-like morphology can be assigned to the Rajidae (Figs 14 no. 3, 6) (e.g. McEachran & Konstantinou 1996). Rajid tooth fossils found in the Neuhofener Beds were assigned to *Raja gentili* as mentioned above. We speculate that the rajid dermal denticles may be fossil remains of the same species. The largest dermal denticle (Fig. 14 no. 4) displays a morphology that is comparable to that of *Squatina* denticles (Vaz & de Carvalho 2013). Figure 14 no. 5 shows a dermal denticle which morphology strongly resembles denticles of *Centrophorus* as shown in White et al. 2013.

5. Discussion

5.1. Palaeoecology

The diversity of the Neuhofener Beds is dominated by elasmobranch tooth fossils, which can be assigned to extant genera. Most of these extant taxa are found in deep-water habitats today comprising depths of 200 to 2000 meters, e.g. *Etmopterus, Pristiophorus, Centrophorus, Deania,* and *Raja* (Patokina & Litvinov 2004). We therefore conclude that the Neuhofener Beds sediments stem from the marine Miocene Paratethys, which were characterized by ecological circumstances likely comparable to the habitats inhabited by extant deep-water taxa. Information from the foraminifer in the Neuhofener Beds suggests that the Miocene depth of the sampling site was estimated to be approximately 100 meters (Pippèrr & Reichenbacher 2010; Pippèrr 2011), apparently in disagreement with the deep-water chondrichthyan assemblage. Today, taxa assumed to predominantly occur in the deep-sea may occur in rather shallow depths in some cool water fjords (Försterra & Häussermann 2003; Försterra et al. 2013; Claes et al. 2010). Factors that contributed to the presence of deep-water taxa in fjords likely include a fresh-water layer overlying the saline marine water that absorbs most UV light by the presence of fresh water algae. This may create an environment comparable to the twilight zone in depths of only four to five meters, which is usually found at much larger depths ranging from 200 to 2000 meters. We speculate that the Neuhofener Beds once must have displayed similar ecological conditions as in extant fjord regions, i.e. a light absorbing fresh water layer. However, a re-deposition of fossils may be an alternative explanation of the species composition described herein.

5.2 Palaeodiversity

The diversity of fishes in the Paratethys was shaped by migration of taxa from other marine ecosystems as well as regional ecological factors such as salinity and oxygen content. An example would be the presence of fossil teeth of the sawshark *Pristiophorus*. Today, the genus is not distributed in the Mediterranean Sea, the North East Atlantic or the Red Sea. Its main distribution range rather comprises the North West Atlantic (Caribbean Sea) as well as the Indian and Pacific Ocean (Ebert 2013). Contrasting, Miocene/Pliocene fossil remains show a much wider distribution range that also includes the North East Atlantic and Mediterranean (this study; Underwood & Schlögl 2013; Vialle et al. 2011; Marsili & Tabanelli 2007; Cigala-Fulgosi 1986).

For testing which extant as well as fossil deep-water fauna is most closely related to the Neuhofener Beds the data presented in Table 2 was analyzed using a principal component analysis (PCA) as well as a most parsimonious network reconstruction. Both analyses show that the diversity of the Neuhofener Beds (F1) are mostly resembling fossil faunas F3 (Southern France, Middle Miocene), F4 (Switzerland, Miocene) and F5 (Italy, Plio- to Pleistocene) from the present-day Mediterranean region (M1-M9). Interestingly, F5 represents a post Messinian salinity crisis diversity, which is both linked with older fossil diversities (F1, F3), but also with the extant diversity reported from M5. Closest extant faunas to F1 are I4 (Indian Ocean) as well as M5 (Mediterranean). It is noteworthy that the Atlantic Ocean faunas included in our analysis seem not to be involved in shaping the Neuhofener Bed diversity. Therefore, the diversity of the Neuhofener Beds may have been mainly shaped by migration events from the Indian Ocean to the Paratethys, but not from the Atlantic Ocean. A close connectivity between Indian Ocean and Parathetical faunas is reported for the early Miocene (Roegl 1998).

When comparing the Neuhofener Beds with the geographically closest, slightly younger fossil fauna described from the Vienna Basin (Central Paratethys, Slovakia, lower Karpatium, Underwood & Schlögl 2013; F2), a distinct difference in the faunal composition is revealed (Fig. 15, Fig. 16). Even though both sampling sites show a number of alike taxa (e.g. *Nanocetorhinus tuberculatus*, *Pristiophorus striatus*, *Etmopterus* sp.), other taxa present in F2 are completely absent in the Neuhofener Beds

Table 2: Presence and absence matrix. (abbr. references: F1: This Study, F2: Underwood & Schlögl 2013; F3: Vialle et al. 2011; F4: Bolliger et al. 1995; F5: Marsili & Tabanelli 2007; F6: Cigala-Fulgosi 1986; F7: Marsili 2007; M1: D'Onghia et al. 2004; M2: Sion et al. 2004; M3: Ferretti et al. 2005; M4: D'Onghia et al. 2012; M5: Psomadakis et al. 2012; M6: Ragonese et al. 2013; M7: García-Ruiz et al. 2015; M8: Goren & Galil 2015; M9: Ramírez-Amaro et al. 2015; A1: Lloris et al. 1991; A2: Dolgov 2000; A3: Shestopal et al. 2002; A4: Patokina & Litvinov 2004; A5: Clarke et al. 2005; A6: Gulyugin et al. 2006; A8: Clarke 2009; I1: Parin et al. 2008; I2: Akhilesh et al. 2011; I3: Petersen et al. 2009; I4: Manilo & Bogorodsky 2003)

Indian Ocean				Atlantic Ocean							Mediterranean Sea									Fossil records (from extant Mediterrenean region)							Genus
I4	I3	I2	I1	A7	A6	A5	A4	A3	A2	A1	M9	M8	M7	M6	M5	M4	M3	M2	M1	F7	F6	F5	F4	F3	F2	F1	
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	1	1	*Pristiophorus/Pliotrema*
1	0	1	1	1	1	1	1	1	0	1	1	1	1	1	0	1	1	1	1	1	1	1	1	1	0	1	*Centrophorus*
0	0	1	1	1	1	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	1	1	1	1	0	1	*Deania*
0	0	0	0	1	1	0	1	1	0	1	1	1	1	1	0	0	1	1	1	0	1	0	0	1	1	0	*Dalatias/†Squaliodalatias/†Oligodalatias*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Euprotomicroides*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Euprotomicrus*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Heteroscymnoides*
0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	1	0	1	*Isistius*
0	0	0	0	0	1	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	1	1	1	0	*Squaliolus/†Eosqualiolus*
1	0	1	0	0	0	0	0	0	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	*Echinorhinus*
1	0	0	0	1	1	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Centroscyllium*
1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	1	0	1	1	*Etmopterus/†Paraetmopterus*
0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	0	0	1	1	1	0	1	0	0	0	0	0	*Oxynotus*
1	0	0	1	1	1	1	0	1	0	1	0	0	0	1	0	0	0	0	0	1	1	0	0	0	0	0	*Centroscymnus*
0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Centroselachus*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Proscymnodon*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Scymnodalatias*
0	0	0	0	0	1	1	1	0	0	1	0	0	0	0	0	0	0	0	0	1	1	1	0	0	0	0	*Scymnodon*
0	0	0	0	0	0	0	0	0	1	1	0	1	0	1	0	0	0	0	0	0	1	0	0	0	0	0	*Somniosus*
0	0	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Zameus*
0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	*Cirrhigaleus*
1	0	1	0	1	0	0	1	0	1	1	1	1	0	1	0	0	1	0	0	0	0	0	1	0	0	1	*Squalus*
1	0	1	0	0	1	0	0	1	0	1	0	0	0	1	0	0	0	0	0	0	0	0	0	1	0	0	*Heptranchias/†Paraheptranchias*
0	1	1	0	0	0	1	0	0	0	1	0	1	0	1	0	0	1	1	1	0	1	0	0	1	0	0	*Hexanchus*
1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	*Notorhynchus*
0	0	0	1	0	1	0	0	0	1	1	0	0	0	0	0	0	0	0	0	1	1	0	0	0	0	0	*Chlamydoselachus*
0	0	1	1	1	1	0	0	1	0	1	0	0	0	0	0	0	0	0	0	1	0	0	0	0	0	1	*Apristurus*
0	0	0	0	1	1	1	1	1	1	1	1	1	1	1	0	1	1	1	1	1	1	0	0	0	1	0	*Galeus*
1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	*Iago*
1	1	1	0	1	0	0	1	0	0	1	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	*Mustelus*
0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1	0	0	*Mitsukurina*

Table 3: Faunal survey of the Neuhofener Beds from the clay pit (only FP2A/FP3).

Order	Family	Species	FP2A	FP3	Total	%-Species	%-Family	%-Anteil Order
Carcharhiniformes	Carcharhinidae	*Rhizoprionodon ficheuri* (Joleaud, 1912)	1		1	0,26	0,26	
Carcharhiniformes	Scyliorhinidae	*Apristurus* sp.	3	4	7	1,84		
Carcharhiniformes	Scyliorhinidae	*Pseudoapristurus nonstriatus* nov. gen. et sp.	4	4	8	2,11		
Carcharhiniformes	Scyliorhinidae	*Scyliorhinus* cf. *biformis* Reinecke, 2014	18	4	22	5,79		
Carcharhiniformes	Scyliorhinidae	*Scyliorhinus* sp.		2	2	0,53	10,27	10,53
Lamniformes	Cetorhinidae	*Keasius parvus* (Leriche, 1908)	11	1	12	3,16	3,16	
Lamniformes	Odontaspididae	*Carcharias acutissimus* (Agassiz, 1843)		1	1	0,26	0,26	3,42
Squaliformes	Centrophoridae	*Centrophorus granulosus* (Bloch & Schneider, 1801)	29	46	75	19,74		
Squaliformes	Centrophoridae	*Deania* aff. *calcea* (Lowe, 1839)	2	3	5	1,32	21,06	
Squaliformes	Dalatiidae	*Isistius triangulus* (Probst, 1879)	2	5	7	1,84	1,84	
Squaliformes	Etmopteridae	*Etmopterus* sp.	12	4	16	4,21	4,21	
Squaliformes	Squalidae	*Squalus* sp.	2	2	4	1,05	1,05	28,16
Pristiophoriformes	Pristiophoridae	*Pristiophorus striatus* Underwood & Schlögl, 2013	13	18	31	8,16	8,16	8,16
Neoselachii incertae sedis		*Nanocetorhinus tuberculatus* Underwood & Schlögl, 2013	57	58	115	30,26	30,26	30,26
Rajiformes	Rajidae	*Raja gentili* Joleaud, 1912	33	39	72	18,95		
Rajiformes	Rajidae	Rajidae sp. indet.		1	1	0,26	19,21	
Rajiformes	Rhinobatidae	*Rhinobatos* sp.		1	1	0,26	0,26	19,47
		Total:	**187**	**193**	**380**	**100**	**100**	**100**

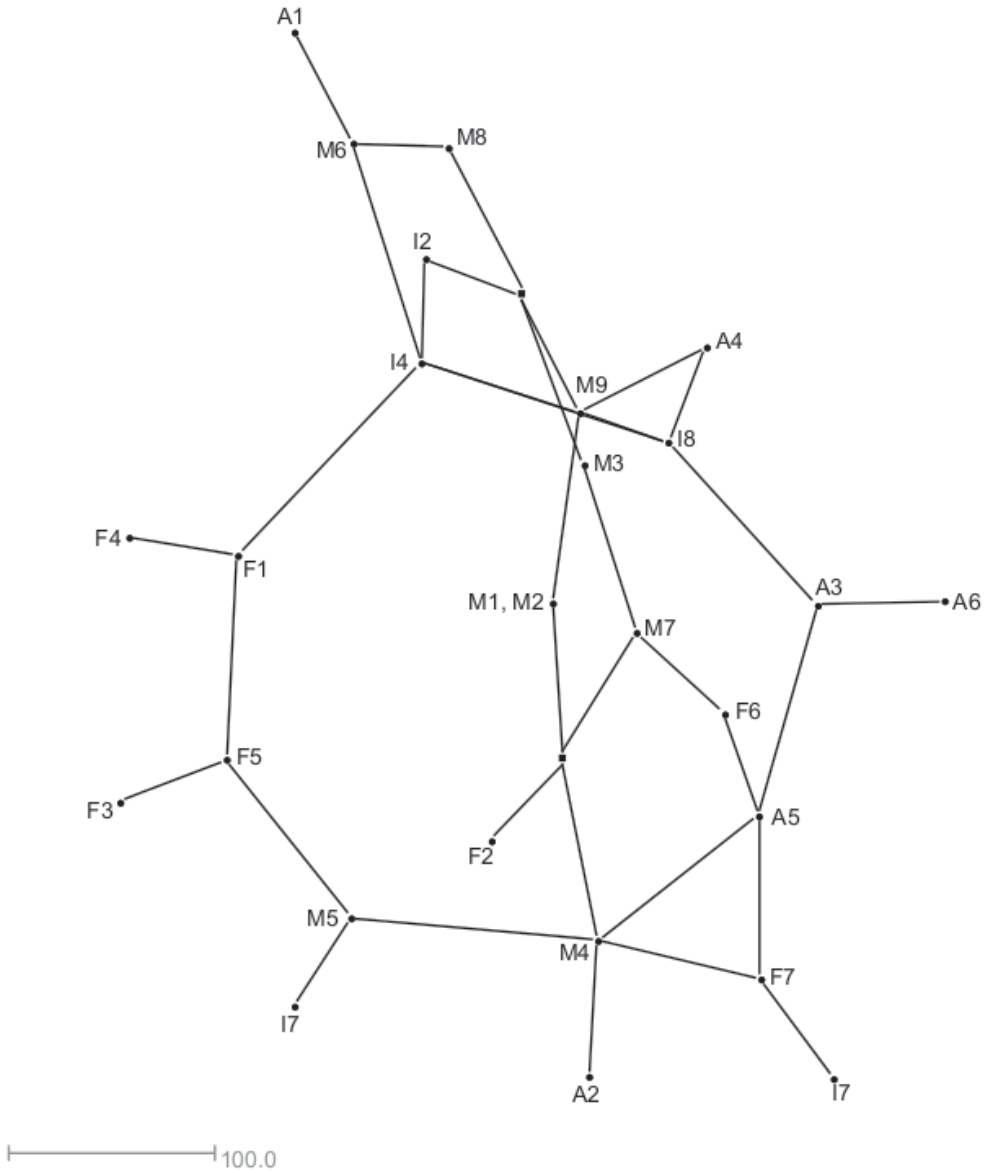

Figure 16: Parsimonious network reconstruction of selected faunas listed in Table 2.

(e.g. *Squaliolus* cf. *schaubi*, *Eosqualiolus skrovinai*, *Paraetmopterus horvathi*). These differences are further supported by the quantity of individual fossils. Both studies were based on a similar number of individual teeth, i.e. 380 in this study and 343 in Underwood & Schlögl (2013). However, the Vienna Basin fauna is dominated by two species adding up to 80% of all individual fossils: *Squaliolus* cf. *schaubi* with 222 specimen equaling 64,7% of the individual fossils and *Paraetmopterus horvathi* with 52 specimen equaling 15,2 % of all individual fossils. These two species are not reported from the Neuhofener Beds. Contrasting, the Neuhofener Beds show a high proportion of fossils, which can be assigned to benthic species, *Pristiophorus striatus* (31 specimen, 8,2 % of all excavated fossils) und *Raja gentili* (72 specimen, 18,9 %). These results support Pippèrr & Reichenbacher (2010) documenting the presence of benthic foraminifera that serve as indicators for advantageous environmental surroundings for the benefit of other marine organisms in the Ottnangium, such as benthic rays and saw sharks.

The Vienna Basin sediments were deposited during low water levels in the Upper Karpatian, which is further supported by the benthic foraminiferan diversity (Schlögl et al. 2011; Piller et al. 2007). This shows that the analysis of fossils assignable to the deep-sea elasmobranchs can be used to collect evidence for regionally and timely limited environmental conditions. In this specific case, the presence of likely benthic rays and saw sharks is indicative for well-oxygenated sea-water at the sea floor, while the absence of benthic elasmobranchs in Underwood & Schlögl (2013) may indicate hostile oxygen conditions at the sea floor.

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6. References

Adnet S. 2006. Nouvelles faunes de sélaciens (Elasmobranchii, Neoselachii) de l'Éocène des Landes (Sud-Ouest, France). Implication dans les connaissances des communautés d'eaux profondes. Palaeo Ichthyologica 10, 1–128.

Agassiz L. 1843. Recherches sur les poissons fossiles. Volume 3. Neuchâtel, Imprimerie de Petitpierre et Prince.

Akhilesh KV, Ganga U, Pillai NGK, Vivekanandan E, Bineesh KK, Shanis CPR, Hashim M. 2011. Deep-sea fishing for chondrichthyan resources and sustainability concerns - a case study from southwest coast of India. Indian Journal of Geo-Marine Sciences 40, 347–355.

Antunes MT, Jonet S. 1970. Requins de l'Helvétien supérieur et du Tortonien de Lisbonne. Revista da Faculdade de Ciências de Lisboa 16, 119–280.

Barthelt D, Fejfar O, Pfeil FH, Unger E. 1991. Notizen zu einem Profil der Selachier-Fundstelle Walbertsweiler im Bereich der miozänen Oberen Meeresmolasse Süddeutschlands. Münchner Geowissenschaftliche Abhandlungen (A) 19, 195–208.

Bass AJ, d'Aubrey JD, Kistnasamy N. 1976. Sharks of the east coast of Southern Africa. VI. The families Oxynotidae, Squalidae, Dalatiidae and Echinorhinidae. Investigational Report Oceanographic Research Institute 45, 1–103.

Berg LS. 1958. System der Rezenten und Fossilen Fischartigen und Fische. Hochschulbücher für Biologie, Berlin, 310 pp.

Blainville HMD de. 1816. Prodrome d'une nouvelle distribution sytématique du règne animal. Bulletin des Sciences, par la Société Philomatique de Paris 8, 105–124.

Bleeker P. 1859. Enumeratio specierum piscium hucusque in Archipelago indico observatarum. Acta Societatis scientiarum Indo-Neerlandae 6, 276 pp.

Bolliger T, Kindlimann R, Wegmüller U. 1995. Die marinen Sedimente (jüngere OMM, St. Galler-Formation) am Südwestrand der Hörnlischüttung (Ostschweiz) und die palökologische Interpretation ihres Fossilinhaltes. Eclogae Geologicae Helvetiae 88, 885–909.

Bonaparte CL. 1831. Saggio di una distribuzione metodica degli animali vertebrati. Roma, 78 pp.

Bonaparte CL. 1832–41. Iconografia della fauna italica per le quattro classi degli animali vertebrati. Tomo III. Pesci, 556 pp.

Bor TJ, Reinecke T, Verschueren S. 2012. Miocene Chondrichthyes from Winterswijk – Miste, the Netherlands. Palaeontos 21, 1–136.

Bracher H, Unger E. 2007. Untermiozäne Haie und Rochen. Altheim, 183 pp.

Brisswalter G. 2009. Inventaire des Elasmobranches (requins, raies, chimères) des dépôts molassiques du Sud-Luberon (Miocène supérieur), à Cabrières d'Aigues (Vaucluse) France. Courriers scientifiques du Parc Régional du Lubéron, Hors Série, 1–100.

Canevet JM. 2011. Les Chondrichthyens du Miocène moyen (Serravallien) de Salles (Gironde, France). Cossmanniana 13, 59–76.

Cappetta H. 1970. Les Sélaciens du Miocène de la région de Montpellier. Palaeovertebrata, Mém. ext. 1970, 139 pp.

Cappetta H. 2012. Handbook of Paleoichthyology, Vol. 3E: Chondrichthyes Mesozoic and Cenozoic Elasmobranchii: Teeth. Verlag Dr. Friedrich Pfeil, 512 pp.

Castillo-Géniz JL, Sosa-Nishizaki O, Perez JC. 2007. Morphological variation and sexual dimorphism in the California skate, *Raja inornata* Jordan and Gilbert, 1881 from the Gulf of California, Mexico. Zootaxa 1545, 1–16.

Cigala-Fulgosi F. 1986. A deep water elasmobranch fauna from a lower Pliocene outcropping (Northern Italy). In: Uyeno T, Arai R, Taniuchi T, Matsuura K. (eds) Proceedings of the second international conference on Indo-Pacific fishes. Ichthyological Society of Japan, Tokyo, 133–139.

Claes JM, Aksnes DL, Mallefet J. 2010. Phantom hunter of the fjords: Camouflage by counterillumination in a shark (*Etmopterus spinax*). Journal of Experimental Marine Biology and Ecology 388, 28–32.

Clarke MW, Borges L, Officer RA. 2005. Comparisons of Trawl and Longline Catches of Deepwater Elasmobranchs West and North of Ireland. Journal of Northwest Atlantic Fishery Science 35, 429–442.

Clarke MW. 2009. Sharks, skates and rays in the northeast Atlantic: population status, advice and management. Journal of Applied Ichthyology 25, 3–8.

Compagno LJV. 1973. Interrelationships of living elasmobranchs. Zoological Journal of the Linnean Society 53 (Supplement 1), 15–61.

Compagno LJV. 1977. Phyletic relationships of living sharks and rays. American Zoologist 17, 303–322.

Compagno LJV, Follett WI. 1986. *Carcharias* Rafinesque, 1810 (Chondrichthyes, Lamniformes): Proposed Conservation by the Use of the Relative Precedence Procedure; Z.N.(S) 2414. Bulletin of Zoological Nomenclature 43, 89–92.

Cuvier GLCFD. 1816. Le Règne Animal distribué d'après son organisation pour servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparée. Les reptiles, les poissons, les mollusques et les annélides. Deterville, Paris, 532 pp.

Dolgov AV. 2000. New data on composition and distribution of the Barents Sea ichthyofauna. ICES CM Documents 2000, Mini12, 13pp.

D'Onghia G, Maiorano P, Carlucci R, Capezzuto F, Carluccio A, Tursi A, Sion L. 2012. Comparing Deep-Sea Fish Fauna between Coral and Non-Coral "Megahabitats" in the Santa Maria di Leuca Cold-Water Coral Province (Mediterranean Sea). PLoS ONE 7, e44509.

D'Onghia G, Politou C-Y, Bozzano A, Lloris D, Rotllant G, Sion L, Mastrototaro F. 2004. Deep-water fish assemblages in the Mediterranean Sea. Scientia Marina 68, 87–99.

Ebert DA. 2013. Deep-sea Cartilaginous Fishes of the Indian Ocean. Volume 1. Sharks. FAO Species Catalogue for Fishery Purposes. No. 8, Vol. 1. Rome, FAO. 256 pp.

Ebert DA, Cailliet GM. 2011. *Pristiophorus nancyae*, a new species of Sawshark (Chondrichthyes: Pristiophoridae) from Southern Africa. Bulletin of Marine Science 87, 501–512.

Ebert DA, Compagno LJV, De Vries MJ. 2011. A New Lanternshark (Squaliformes: Etmopteridae: *Etmopterus*) from Southern Africa. Copeia 2011, 379–384.

Ebert DA, Pien C, Kamikawa DJ. 2015. Confirmation of the cookiecutter shark, *Isistius brasiliensis*, from the eastern North Pacific Ocean (Squaliformes: Dalatiidae). Marine Biodiversity Records 8, e118.

Ebert DA, Wilms, HA. 2013. *Pristiophorus lanae* sp. nov., a new sawshark species from the Western North Pacific, with comments on the genus *Pristiophorus* Müller & Henle, 1837 (Chondrichthyes: Pristiophoridae). Zootaxa 3752, 86–100.

Feduccia A, Slaughter BH. 1974. Sexual dimorphism in skates (Rajidae) and its posible role in diffferential niche utilization. Evolution 28, 164–168.

Ferretti F, Myers, RA, Serena F, Sartor P. 2005. Long term dynamics of chondrichthyan fish community in the upper Tyrrhenian Sea.

ICES CM Documents 2005 25, 1–34.
Fischli H. 1930. Die Fossilien der Quarzsande von Benken (Kt. Zürich). Mitteilungen der naturwissenschaftlichen Gesellschaft Winterthur 17/18, 131–167.
Flammang BE, Ebert DA, Cailliet GM. 2007. Egg cases of the genus *Apristurus* (Chondrichthyes: Scyliorhinidae): Phylogenetic and ecological implications. Zoology 110, 308–317.
Försterra G, Häussermann V. 2003. First report on large scleractinian (Cnidaria: Anthozoa) accumulations in cold-temperate shallow water of south Chilean fjordsm. Zoologische Verhandelingen 345, 117–128.
Försterra G, Häussermann V, Melzer RR, Weis A. 2013. A deep water pycnogonid close to the beach: *Colossendeis macerrima* Hoek, 1881 spotted at 18 m in the Chilean fjords (Chelicerata, Pycnogonida, Colossendeidae). Spixiana 36, 20.
Fowler HW. 1941. Contributions to the biology of the Philippine archipelago and adjacent regions. The fishes of the groups Elasmocephalii, Holocephali, Isospondyli, and Ostariophysi obtained by the United States Fisheries Steamer "Albatross" in 1907 to 1910, chiefly in the Philippine islands and adjacent seas. Bulletin of the United States National Museum 100, 879 pp.
García-Ruiz C, Lloris D, Rueda JL, García-Martínez, C, Gil De Sola L. 2015. Spatial distribution of ichthyofauna in the northern Alboran Sea (western Mediterranean). Journal of Natural History 49, 1191–1224.
Garman S. 1913. The Plagiostomia (Sharks, Skates and Rays). Memoirs of the Museum of Comparative Zoology at Harvard College 36, 528 pp.
Gill T. 1862. Analytical synopsis of the Order of Squali and revision of the nomenclature of the genera. Annals of the Lyceum of Natural History of New York 7, 367–408.
Gill T. 1865. Synopsis of the eastern American sharks. Proceedings of the Academy of Natural Sciences of Philadelphia 16, 258–265.
Goren M, Galil BS. 2015. A checklist of the deep sea fishes of the Levant Sea, Mediterranean Sea. Zootaxa 3994, 507–530.
Gray JE. 1851. List of the specimens of fish in the collection of the British Museum. Part I. Chondropterygii. British Museum (Natural History), London, 160 pp.
Gulyugin SY, Litvinov FF, Sirota AM. 2006. The distribution and relative abundance of elasmobranch species along North-Western African shelf and slope (from Gibraltar to 16°N) as compared to retrospective data (70s–80s) and environment. ICES CM 2006/ Session D, 03, 35 pp.
Hagn H, Malz H, Martini E. 1981. Miozäne Vorland Molasse Niederbayerns und Kreide von Regensburg. Exkursion G2: Mitterdorf. In: Hagn H (Ed.), Die Bayerischen Alpen und ihr Vorland in mikropaläontologischer Sicht: Geologica Bavarica 82, 267–269.
Hammer Ø. 2015. The past and future of PAST – Paleontological Statistics Software, version 3. http://folk.uio.no/ohammer/past/
Hay OP. 1902. Bibliography and catalogue of the fossil Vertebrata of North America. Bulletin of the United States Geological and Geographical Survey of the Territories 179, 868 pp.
Herman J, Hovestadt-Euler M, Hovestadt DC. 1988. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living superaspecific taxa of Chondrichthyan fishes. Part A: Selachii. No. 2a: Carcharhiniformes - Family: Triakidae. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 58, 99–126.
Herman J, Hovestadt-Euler M, Hovestadt DC. 1989. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living superspecific taxa of Chondrichthyan fishes. Part A: Selachii. No. 3: Order: Squaliformes – Families: Echinorhinidae, Oxynotidae and Squalidae. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 59, 101–158.
Herman J, Hovestadt-Euler M, Hovestadt DC. 1990. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living superspecific taxa of Chondrichthyan fishes. Part A: Selachii. No. 2b: Order: Carcharhiniformes – Familiy: Scyliorhinidae. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 60, 181–230.
Herman J, Hovestadt-Euler M, Hovestadt DC. 1991. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living superspecific taxa of Chondrichthyan fishes. Part A: Selachii. No. 2c: Order: Carcharhiniformes Families: Proscylliidae, Hemigaleidae, Pseudotriakidae, Leptochariidae and Carcharhinidae. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 61, 73–120.
Herman J, Hovestadt-Euler M, Hovestadt DC. 1992. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living superspecific taxa of Chondrichthyan fishes. Part A: Selachii. No. 4: Order: Orectolobiformes Families: Brachaeluridae, Giglymostomatidae, Hemiscylliidae, Orectolobidae, Parascylliidae, Rhiniodontidae, Stegostomatidae. Order: Pristiophoriformes – Family: Pristiophoridae Order: Squatiniformes – Family: Squatinidae. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 62, 193–254.
Herman J, Hovestadt-Euler M, Hovestadt DC, Stehmann M. 1995. Contributions to the study of the comparative morphology of teeth and other relevant ichthyodorulites in living supraspecific taxa of chondrichthyan fishes. Part B: Batomorphii No. 1b: Order: Rajoidei - Family: Rajidae Genera and Subgenera: *Bathyraja* (with a deep-water, shallow-water and transitional morphotype) *Psammobatis*, *Raja (Amblyraja), Raja (Dipturus), Raja (Leucoraja), Raja (Raja), Raja (Rajella)* (with two morphotypes), *Raja (Rioraja), Raja (Rostroraja), Raja lintea* and *Sympterygia*. Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Biologie 65, 237–307.
Hiden HR. 1995. Elasmobranchier (Pisces, Chondrichthyes) aus dem Badenium (Mittleres Miozän) des Steirischen Beckens (Österreich). Mitteilungen der Abteilung für Geologie und Paläontologie am Landesmuseum Joanneum 52/53, 41–110.
Holec P, Hornácek M, Sykora M. 1995. Lower Miocene Shark (Chondrichthys, Elasmobranchii) and Whale Faunas near Mučín, Southern Slovakia. Geologické práce, Správy 100, 37–52.
Iglésias SP, Lecointre G, Sellos DY. 2005. Extensive paraphylies within sharks of the order Carcharhiniformes inferred from nuclear and mitochondrial genes. Molecular Phylogenetics and Evolution 34, 569–583.
Johns MJ, Barnes CR, Narayan YR. 2005. Cenozoic and Cretaceous Ichthyoliths from the Tofino Basin and Western Vancouver Island, British Columbia, Canada. Palaeontologia Electronica 8 (2) 29A, 1–202.
Joleaud L. 1912. Géologie et paléontologie de la Plaine du Comtat et de ses abords. Description des terrains néogènes. Montpellier: impr. Montane, Sicardi et Valentin 2, 255–285.
Jordan DS, Evermann, BW. 1896. The fishes of North and Middle America: a descriptive catalogue of the species of fish-like vertebrates found in the waters of North America, north of the Isthmus of Panama. Part I. Bulletin of the United States National Museum 47, 1–1240.
Jordan DS, Snyder JO. 1902. Descriptions of two new species of squaloid sharks from Japan. Proceedings of the United States National Museum 25 (1279), 79–81.
Knuckey JDS, Ebert DA, Burgess GH. 2011. *Etmopterus joungi* n. sp., a new species of lanternshark (Squaliformes: Etmopteridae) from Taiwan. Aqua, International Journal of Ichthyology 17, 61–72.
Kawauchi J, Weigmann S, Nakaya K. 2014. *Apristurus breviventralis*, a new species of deep-water catshark (Chondrichthyes: Carcharhiniformes: Scyliorhinidae) from the Gulf of Aden. Zootaxa 3881, 1–16.
Kocsis L. 2007. Central Paratethyan shark fauna (Ipolytarnóc, Hungary). Geologica Carpathica 58, 27–40.
Konstantinou H, McEachran JD, Woolley JB. 2000. The systematics and reproductive biology of the *Galeus arae* subspecific complex (Chondrichthyes: Scyliorhinidae). Environmental Biology of Fishes 57, 117–129.
Latham J. 1794. An essay on the various species of Sawfish. Transactions of the Linnean Society of London 2, 273–282.
Ledoux J-C. 1970. Les dents des Squalidés de la Méditerranée occidentale et de l'Atlantique Nord-ouest africain. Vie et Milieu,

Serie A 21 (2a), 309–362.
Ledoux J-C. 1972. Les Squalidae (Euselachii) miocènes des environs d'Avignon (Vaucluse). Documents des Laboratoires de Geologie de la Facult des Sciences de Lyon, Notes et Mémoirs 52, 133–175.
Leriche M. 1908. Sur un appareil fanonculaire de Cetorhinus trouvé à l'état fossile dans le Pliocène d'Anvers. Comptes Rendus hebdomadaires des séances de l'Academie des Sciences 146, 875–878.
Leriche M. 1910. Les poissons tertiaires de la Belgique. III. Les poissons oligocènes. Mémoires du Musée Royal d'Histoire Naturelle de Belgique 5, 229–363.
Linck HF. 1790. Versuch einer Eintheilung der Fische nach den Zähnen. Magazin für das Neueste aus der Physik und Naturgeschichte 6, 28–38.
Linné C. 1758. Systema Naturae per regna tria naturae, regnum animale, secundum classes, ordines, genera, species, cum characteribus differentiis synonymis, locis. Ed. X., 1, Stockholm (L. Salvius), 824 pp.
Lloris D, Rucabado JA, Figueroa H. 1991. Biogeography of the Macaronesian ichthyofauna (The Azores, Madeira, the Canary Islands, Cape Verde and the African enclave). Boletim do Museu Municipal do Funchal 43, 191–241.
Lowe RT. 1839. A supplement to a synopsis of the fishes of Madeira. Proceedings of the Zoological Society of London 1839 (pt 7), 76–92.
Manilo LG, Bogorodsky SV. 2003. Taxonomic composition, diversity and distribution of coastal fishes of the Arabian Sea. Journal of Ichthyology 43, 75–149.
Manzanares E, Plá C, Martínez-Pérez C, Rasskin D, Botella H. 2014. The enameloid microstructure of euselachian (Chondrichthyes) scales. Paleontological Journal 48, 1060–1066.
Marsili S. 2007. A new bathyal shark fauna from the Pleistocene sediments of Fiumefreddo (Sicily, Italy). Geodiversitas 29, 229–247.
Marsili S, Tabanelli C. 2007. Bathyal sharks from the middle Pliocene of the Romagna Apennines (Italy). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen 244, 247–255.
Martini E. 1990. The Rhinegraben system, a connection between northern and southern seas in the European Tertiary. Veröffentlichungen Übersee-Museum A 10, 83–98.
Maisey JG. 2012. What is an 'elasmobranch'? The impact of palaeontology in understanding elasmobranch phylogeny and evolution. Journal of Fish Biology 80, 918–951.
McEachran JD, Konstantinou H. 1996. Survey of the variation of alar and malar thorns in skates: phylogenetic implications (Chondrichthyes: Rajoidei). Journal of Morphology 228, 165–178.
Meyer W, Seegers U. 2012. Basics of skin structure and function in elasmobranchs: a review. Journal of Fish Biology 80, 1940–1967.
Müller A. 1996. Die Ichthyofauna des Oberoligozäns der Hessischen Senke (Raum Kassel, Deutschland). Leipziger Geowissenschaften 2, 31–115.
Müller J, Henle FGJ. 1837. Ueber die Gattungen der Plagiostomen. Archiv für Naturgeschichte 3, 394–401.
Müller J, Henle FGJ. 1839–1841. Systematische Beschreibung der Plagiostomen. Berlin, Veit, 200 pp.
Nakaya K, Sato K, Iglesias SP, White WT. 2008. Methodology for the taxonomic description of members of the genus *Apristurus* (Chondrichthyes: Carcharhiniformes: Scyliorhinidae). CSIRO Marine and Atmospheric Research Paper 22, 49–60.
Nakaya K, Sato K. 1999. Species grouping within the genus *Apristurus* (Elasmobranchii: Scyliorhinidae). Proceedings of the 5th Indo-Pacific Fish Conference, Nouméa, 1997, 307–320.
Naylor GJP, Caira JN, Jensen K, Rosana KAM, Straube N, Lakner C. 2012a. Elasmobranch Phylogeny: A Mitochondrial Estimate Based on 595 Species. In: Carrier JC, Musick JA, Heithaus MR. (eds) Biology of Sharks and their Relatives, Edition 2. CRC Press, Boca Raton, Florida, 31–56.
Naylor GJP, Caira JN, Jensen K, Rosana KAM, White WT, Last PR. 2012b. A DNA sequence based approach to the identification of shark and ray species and its implications for global elasmobranch diversity and parasitology. Bulletin of the American Museum of Natural History 367, 262 pp.
Parin NV, Timokhin IG, Novikov NP, Shcherbachev YN. 2008. On the composition of talassobathyal ichthyofauna and commercial productivity of Mozambique Seamount (the Indian Ocean). Journal of Ichthyology 48, 361–366.
Patokina FA, Litvinov FF. 2004. Food composition and distribution of demersal elasmobranches on shelf and upper slope of North-West Africa. ICES CM 2004/Session K, 19, 30 pp.
Petersen SL, Honig MB, Ryan PG, Underhill LG, Compagno LJV. 2009. Pelagic shark bycatch in the tuna- and swordfish-directed longline fishery off southern Africa. African Journal of Marine Science 31, 215–225.
Pfeil FH. 1983. Zahnmorphologische Untersuchungen an rezenten und fossilen Haien der Ordnungen Chlamydoselachiformes und Echinorhiniformes. Palaeo Ichthyologica 1, 1–315.
Piller WE, Harzhauser M, Mandic O. 2007. Miocene Central Paratethys stratigraphy - current status and future directions. Stratigraphy 4, 151–168.
Pippèrr M. 2011. Characterisation of Ottnangian (middle Burdigalian) palaeoenvironments in the North Alpine Foreland Basin using benthic foraminifera - A review of the Upper Marine Molasse of southern Germany. Marine Micropaleontology 79, 80–99.
Pippèrr M, Reichenbacher B. 2010. Foraminifera from the borehole Altdorf (SE Germany): proxies for Ottnangian (early Miocene) palaeoenvironments of the Central Paratethys. Palaeogeography, Palaeoclimatology, Palaeoecology 289, 62–80.
Pollerspöck J, Beaury B. 2014. Eine Elasmobranchierfauna (Elasmobranchii, Neoselachii) aus der Oberen Meeresmolasse (Ottnangium, Unteres Miozän) des Heigelsberger Grabens bei Teisendorf, Oberbayern. Zitteliana A54, 23–37.
Pollerspöck J, Straube N. 2016. Bibliography database of living/fossil sharks, rays and chimaeras (Chondrichtyes: Elasmobranchii, Holocephali). www.shark-references.com, World Wide Web electronic publication, Version 2015 [accessed 02-Apr-2016].
Probst J. 1877. Beiträge zur Kenntniss der fossilen Fische aus der Molasse von Baltringen. II: Batoidei A. Günther. Jahreshefte des Vereins für vaterländische Naturkunde in Württemberg 33, 69–103.
Psomadakis PN, Giustino S, Vacchi M. 2012. Mediterranean fish biodiversity: an updated inventory with focus on the Ligurian and Tyrrhenian seas. Zootaxa 3263, 1–46.
Rafinesque CS. 1810. Caratteri di alcuni nuovi generi e nuove specie di animali e pinate della Sicilia, con varie osservazioni sopra i medisimi, lère partie. Part 1, 3–69.
Ragonese S, Vitale S, Dimech M, Mazzola S. 2013. Abundances of Demersal Sharks and Chimaera from 1994–2009 Scientific Surveys in the Central Mediterranean Sea. PLoS ONE 8, e74865.
Ramírez-Amaro S, Ordines F, Terrasa B, Esteban A, García C, Guijarro B, Massutí E. 2015. Demersal chondrichthyans in the western Mediterranean: assemblages and biological parameters of their main species. Marine and Freshwater Research 67, 636–652.
Regan CT. 1906. Descriptions of new or little known fishes from the coast of Natal. Annals of the Natal Government Museum 1, 1–6.
Reinecke T. 2014. Two new scyliorhinid shark species (Elasmobranchii, Carcharhiniformes, Scyliorhinidae), from the Sülstorf Beds (Chattian, Late Oligocene) of the southeastern North Sea Basin, northern Germany. Palaeovertebrata 38, 1–8.
Reinecke T, Balsberger M, Beaury B, Pollerspöck J. 2014. The elasmobranch fauna of the Thalberg Beds, early Egerian (Chattian, Oligocene), in the Subalpine Molasse Basin near Siegsdorf, Bavaria, Germany. Palaeontos 26, 127 pp.
Reinecke T, Moths H, Grant A, Breitkreuz H. 2005. Die Elasmobranchier des norddeutschen Chattiums, insbesondere des Sternberger Gesteins (Eochattium, Oligozän). Palaeontos 8, 135 pp.
Rögl F. 1998. Palaeogeographic Considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). Annalen des Naturhistorischen Museums in Wien 99 A, 279–310.
Schaaf-Da Silva JA, Ebert DA. 2006. *Etmopterus burgessi* sp. nov., a new species of lanternshark (Squaliformes: Etmopteridae) from Taiwan. Zootaxa 1373, 53–64.
Schlögl J, Chirat R, Balter V, Joachimski M, Hudáčková N, Quillévéré

F. 2011. *Aturia* of the Miocene Paratethys: An exceptional window in nautilid habitat and lifestyle. Palaeogeography, Palaeoclimatology, Palaeoecology 308, 330–338.

Schultz O. 2013. Catalogus Fossilium Austriae Band 3 - Pisces. Verlag der Österreichischen Akademie der Wissenschaften, Wien, ISBN13: 978-3-7001-7238-3, 576 pp.

Shestopal IP, Smirnov OV, Grekov AA. 2002. Bottom longline fishing for deepwater sharks on sea-mounts in the International waters of the North Atlantic. NAFO SCR Document 02/100, Ser. No. N4721, 5 pp.

Sion L, Bozzano A, D'Onghia G, Capezzuto F, Panza M. 2004. Chondrichthyes species in deep waters of the Mediterranean Sea. Scientia Marina 68, 153–162.

Springer VG. 1964. A revision of the carcharhinid shark genera *Scoliodon*, *Loxodon*, and *Rhizoprionodon*. Proceedings of the United States National Museum 115 (3493), 559–632.

Straube N, Duhamel G, Gasco N, Kriwet J, Schliewen U. 2011. Description of a new deep-sea lantern shark, *Etmopterus viator* n. sp. (Squaliformes: Etmopteridae) from the southern hemisphere. In: Duhamel G, Welsford D. (eds). The Kerguelen Plateau, Marine Ecosystem and Fisheries. Société Française d´Ichtyologie, 137–150.

Straube N, Schliewen U, Kriwet J. 2008. Dental structure of the Giant lantern shark *Etmopterus baxteri* (Chondrichthyes: Squaliformes) and its taxonomic implications. Environmental Biology of Fishes 82, 133–141.

Straube N, White WT, Ho H-C, Rochel E, Corrigan S, Li C, Naylor, GJP. 2013. A DNA sequence-based identification checklist for Taiwanese chondrichthyans. Zootaxa 3752, 256–278.

Underwood CJ, Schlögl J. 2013 Deep-water chondrichthyans from the Early Miocene of the Vienna Basin (Central Paratethys, Slovakia). Acta Palaeontologica Polonica 58, 487–509.

Unger HJ. 1984. Erläuterungen zur Geologischen Karte von Bayern 1:50000, Blatt L 7544 Griesbach im Rottal. Bayerisches Geologisches Landesamt München, 245pp.

Vaz DFB, de Carvalho MR. 2013. Morphological and taxonomic revision of species of *Squatina* from the Southwestern Atlantic Ocean (Chondrichthyes: Squatiniformes: Squatinidae). Zootaxa 3695, 1–81.

Veríssimo A, Cotton CF, Buch RH, Guallart J, Burgess GH. 2014. Species diversity of the deep-water gulper sharks (Squaliformes: Centrophoridae: *Centrophorus*) in North Atlantic waters – current status and taxonomic issues. Zoological Journal of the Linnean Society 172, 803–830.

Vialle N, Adnet S, Cappetta H. 2011. A new shark and ray fauna from the Middle Miocene of Mazan, Vaucluse (southern France) and its importance in interpreting the paleoenvironment of marine deposits in the southern Rhodanian Basin. Swiss Journal of Palaeontology 130, 241–258.

Ward DJ, Bonavia CG. 2001. Additions to, and a review of, the Miocene shark and ray fauna of Malta. Central Mediterranean Naturalist 3, 131–146.

Welton BJ. 2013. A New Archaic Basking Shark (Lamniformes: Cetorhinidae) from the Late Eocene of Western Oregon, U.S.A., and Description of the Dentition, Gill Rakers and Vertebrae of the Recent Basking Shark *Cetorhinus maximus* (Gunnerus). New Mexico Museum of Natural History and Science, Bulletin 58, 48 pp.

White WT, Ebert DA, Compagno LJV. 2008. Description of two new species of gulper sharks, genus *Centrophorus* (Chondrichthyes: Squaliformes: Centrophoridae) from Australia. CSIRO Marine and Atmospheric Research Paper 22, 1–22.

White WT, Ebert DA, Naylor GJP, Ho H-C, Clerkin PJ, Veríssimo A, Cotton CF. 2013. Revision of the genus *Centrophorus* (Squaliformes: Centrophoridae): Part 1 – Redescription of *Centrophorus granulosus* (Bloch & Schneider), a senior synonym of *C. acus* Garman and *C. niaukang* Teng. Zootaxa 3752, 35–72.

White WT, Iglésias SP. 2011. *Squalus formosus*, a new species of spurdog shark (Squaliformes: Squalidae), from the western North Pacific Ocean. Journal of Fish Biology 79, 954–968.

White WT, Last PR, Naylor GJP. 2010. *Scoliodon macrorhynchos* (Bleeker, 1852), a second species of spadenose shark from the Western Pacific (Carcharhiniformes: Carcharhinidae). CSIRO Marine and Atmospheric Research Paper 32, 61–76.

Whitley GP. 1929. Additions to the check-list of the fishes of New South Wales. No. 2. Australian Zoologist 5, 353–357.

Witt W. 2009. Zur Ostracodenfauna des Ottnangs (Unteres Miozän) der Oberen Meeresmolasse Bayerns. Zitteliana 48A, 49–67.

Yearsley GK, Last PR, White WT. 2008. A new species of sawshark, *Pristiophorus delicatus* sp. nov. (Pristiophoriformes: Pristiophoridae), from northeastern Australia. CSIRO Marine and Atmospheric Research Paper 22, 23–34.

Zidowitz H, Fock HO, Pusch C, Von Westernhagen H. 2004. A first record of *Isistius plutodus* in the north-eastern Atlantic. Journal of Fish Biology 64, 1430–1434.