

A new species of the enigmatic shark genus *Nanocetorhinus* (Chondrichthyes) from the Oligocene of Austria with palaeoceanographic implications

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KEYWORDS

Paratethys, Egerian, Elasmobranchii, planktivorous, dermal denticle

Abstract

Deep-neritic sediments of the Eferding Formation (Egerian, Upper Oligocene) of Upper Austria from the Kamig kaolinite quarry revealed minute teeth of the putatively planktivorous shark genus *Nanocetorhinus*. This is the oldest unambiguous record of this rarely documented genus, which was known so far only from Miocene deposits of Europe, North America and Japan. Based on previous studies, which showed a positive correlation between sediments of nutrient rich waters and plankton blooms with a majority of ichthyoliths of *Keasius* and *Nanocetorhinus*, we argue for a filter-feeding and migratory lifestyle of the latter. Thus, it is supposed that *Nanocetorhinus* migrated seasonally for foraging, in a similar way to the extant basking shark *Cetorhinus maximus*. This mode of life and the wide paleogeographic distribution of the open marine genus *Nanocetorhinus* requires a deep and fully marine connection between the Paratethys and the Proto-Mediterranean Sea during late Oligocene times, which might have been established via the Slovenian Corridor.

1. Introduction

Ichthyoliths of exclusively marine vertebrates are a heritage of the vanished Paratethys Sea, which evolved during the Eocene and covered most parts of Central Europe until it vanished successively from West to East during the Late Miocene (Rögl, 1998). Its marine connections to the Proto-Mediterranean Sea were strongly controlled by geodynamic events and open connections were a prerequisite for cosmopolitan and migratory elasmobranch species.

During the late Oligocene, the North-Alpine Foreland Basin (NAFB) represented a deep, east-west oriented trough constrained between the advancing Alps in the south and the stable Bohemian Massif in the north (Rögl, 1998; Popov et al., 2004). At that time, the marly clay of the Eferding Fm and the lower Puchkirchen Group were deposited in outer neritic to upper bathyal depositional environments (Rupp and Ćorić, 2015; Grunert et al., 2015). Analyses of the calcareous nannoplankton and foraminiferal assemblages of the Eferding Fm indicate high nutrient flux, occasional phytoplankton blooms and moderately stagnant bottom conditions (Rupp and Ćorić, 2015). The coeval coastal to inner neritic environments are represented by the sandy Linz-Melk Fm (Rupp and Ćorić, 2015) and its mollusc fauna, which documents agitated coasts along the western escarpment of the Bohemian Massif and fringes of mangrove mudflats along the

more protected eastern margin (Harzhauser and Mandić, 2002). The shark assemblages of the Eferding Fm have been studied by Schultz (2013) and Feichtinger et al. (2019a, 2019b) documenting 11 species of the orders Hexanchiformes, Echinorhiniformes, Lamniformes, Carcharhiniformes, and Rajiformes. In addition, deep marine elasmobranchs of the Paratethys Sea have been studied by Underwood and Schlögl (2013), Pollerspöck and Beaury (2014), Reinecke et al. (2014), Pollerspöck and Straube (2017) and Pollerspöck et al. (2018). These studies reveal an unexpected high diversity of bathypelagic sharks in the Paratethys. Herein we document a new occurrence of *Nanocetorhinus*, which was recently erected by Underwood and Schlögl (2013) from the Malé Karpaty Mountains in Slovakia.

The genus had a wide geographic distribution and is documented from the lower Miocene (or possible upper Oligocene) of western Canada (Johns et al., 2005), the middle Miocene of Japan (Nishimatsu and Ujihara, 2019; Nishimatsu, 2019) and several countries in Europe (Switzerland (Bolliger et al., 1995), Slovakia (Underwood and Schlögl, 2013), Germany (Pollerspöck and Straube, 2017; Bracher et al., 2020), and Austria (Pollerspöck et al., 2018)). These tiny, non-functional but morphologically peculiar teeth (Underwood and Schlögl, 2013), which possess striking similarities with dermal denticles (Johns et al., 2005), are typical for *Nanocetorhinus*. Such

tiny and non-functional teeth are presumably indicative for planktivorous sharks (Shimada, 2002; Underwood and Schlögl, 2013; Welton, 2013). Therefore, the occurrence of such teeth shed by *Nanocetorhinus tuberculatus* Underwood and Schlögl, 2013 in the Paratethys (Bolliger et al., 1995; Underwood and Schlögl, 2013; Pollerspöck and Straube, 2017; Pollerspöck et al., 2018; Bracher et al., 2020), the Mediterranean (Sylvain Adnet pers. comm., 2020), and the Pacific (Nishimatsu and Ujihara, 2019; Nishimatsu, 2019) demonstrates a wide geographic distribution of single species, which suggests a migratory lifestyle as also documented for the extant basking shark *Cetorhinus maximus* (Berrow and Heardman, 1994; Sims et al., 1997; Sims et al., 2005; Soldo et al., 2008). However, a planktivorous lifestyle requires waters with high productivity, which is often correlated with high nutrient influx and/or upwelling conditions (Behrenfeld and Boss, 2014; Sims and Quayle, 1998). The seasonal nature of such plankton blooms (Behrenfeld et al., 2013) stimulates generally the migratory behavior of grazers (Longhurst, 2007) and correlates positively with extant basking shark (Sims and Quayle, 1998) or devil ray (Anderson et al., 2011) occurrences.

In the present study, we report on three teeth of *Nanocetorhinus* that are referred to a new species, *N. zeitlingeri* sp. nov. Furthermore, we discuss regional and palaeoceanographic implications of this seemingly planktivorous shark, which might have lived a migratory lifestyle and entered occasionally the Paratethys Sea during seasonal plankton blooms.

1.2 Geographic position and geological setting

The active Kamig quarry is located at Kriechbaum, northeast of Allerheiligen im Mühlkreis in Upper Austria (48° 18' 21.7" N, 14° 36' 49.3" E) (Fig. 1). Continuous mining of kaolinite, which represents the base of the quarry, warrants access to the overlying sediments of the littoral Linz-Melk Fm and the deep-marine Eferding Fm, which represents an erosional relict of marine sediments trapped by the northwest to southeast trending Kettental Fault (Krenmayr et al., 2006). The Eferding Fm, which is exposed in the Kamig quarry, consists of about 20 m of dark gray, argillaceous to sandy marls with scattered pyrite concretions, fish ichthyoliths, and bivalves. The underlying Linz-Melk Fm is represented by uniform, yellow to white sands without any fossils. Based on this succession, a deepening upward sequence from the basal Linz-Melk Fm to the deep-marine sediments of the overlying Eferding Fm can be reconstructed (own data).

Micropaleontological data from the Eferding Fm allow a correlation with the calcareous nannoplankton zone NP25 of the late Chattian and early Egerian, which represent a regional Paratethyan stage (Lobitzer and Giacomini, 1988; Rupp and Ćorić, 2015; Feichtinger et al., 2019a).

2. Material and methods

Isolated teeth of the herein described new species were extracted from 300 kg of sediment sampled from two

sample points in the uppermost level exposed in the quarry. The sediment was dried, dissolved in diluted hydrogen peroxide and screen washed using a 350 µm mesh size. For preparing Scanning Electron Microscope (SEM) pictures, the teeth were mounted on stubs and coated with a gold alloy for photographing with a JEOL JSM Neoscope at the Geological-Palaeontological Department of the Natural History Museum (NHM) Vienna. The teeth are stored in the NHM Vienna with the following inventory numbers ranging from NHMW/2019/0165/0029 to NHMW/2019/0165/0031. The new species introduced in the present work is registered in ZooBank, together with the electronic publication LSIDurn:lsid:zoobank.org:pub:8DCFFA4E-43D2-4A87-B32F-1A4C4C6724E0.

3. Systematic paleontology

Euselachii Hay, 1902

Neoselachii Compagno, 1977

Neoselachii incertae sedis

Nanocetorhinus Underwood and Schlögl, 2013

Type species: *Nanocetorhinus tuberculatus* Underwood and Schlögl, 2013. Early Miocene, Karpatian (late Burdigalian), Slovakia.

Revised genus diagnosis: Teeth minute, rarely exceeding 1 mm in height, with single cusp overlying irregular, bi- or trilobed root. Weak heterodonty in form of mesio-distally compressed symphyseal teeth. Cusp slender, more than three times as long as wide, straight or faintly curved. Lingual cusp face strongly convex, labial cusp face slightly to strongly convex, with very well developed cutting edge, bearing weak, very irregular serrations. Labial face of cusp smooth or with well developed granulae or irregularly granulated ridges. Flared collar at base of cusp with finely pitted or granulated ornamentation. Root rather irregular with two or three lobes. Basal root face with irregular or incompletely closed foramina, resulting in a single, very large basal foramen.

Nanocetorhinus zeitlingeri sp. nov.

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Figure 2A-F

Holotype: NHMW/2019/0165/0030 (Fig 2A-C)

Type locality: Kamig quarry, Kriechbaum, Allerheiligen im Mühlkreis, Upper Austria.

Type horizon: Eferding Fm, lower Egerian, Late Chattian, upper Oligocene.

Material: Three complete teeth, NHMW/2019/0165/0029 – NHMW/2019/0165/0031

Etymology: In honor of Franz Zeitlinger, curator of the Kaolinum Mining Museum in Kriechbaum (Austria).

Diagnosis: Minute teeth with single cusp, not exceeding 1 mm in height. Irregular cutting edges not reaching the base of the cusp. Crown constricts from apex to base at two thirds of height of cusp, resulting in a spearhead-shaped crown morphology. Crown ending basally with basal

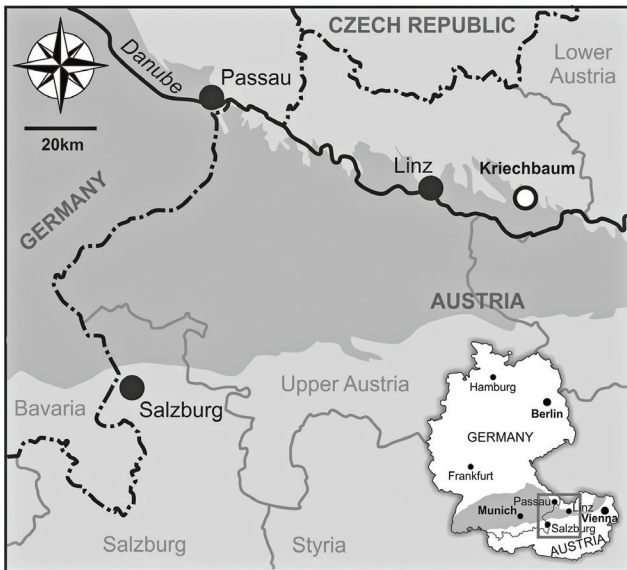


Figure 1: Geographic map of the Kamig quarry at Kriechbaum in Austria. Dark grey color indicates Oligocene and Miocene sediments of the North Alpine Foreland Basin (modified after Grunert et al., 2015).

collar as typical for genus. Labial crown face smooth with occasional enameloid protuberances situated near crown neck, where the cusp narrows. Lingual crown face strongly convex. Bi- or trilobate root with numerous, small foraminal openings piercing the tooth base.

Description: The tiny teeth of this new species are less than 1 mm in height and differ in their width/height ratio from higher than wide in teeth with bilobate root lobes (Fig. 2A, E-F) to equal in teeth when trilobate roots are present (Fig. 2D). The teeth consist of a single, central cusp with a rather acute apex, which narrows distinctly from the apex to the base at two thirds of the height of the crown, resulting in an arrowhead-contour of the crown (Fig. 2A, E, D). In profile view (Fig. 2B), the labial crown face is smooth and flat near the apex but becomes slightly convex towards the prominent crown-neck. The lingual crown face is smooth, and strongly convex. Occasionally, a pronounced protuberance may occur labially, which is situated slightly below the neck (Fig. 2A, C). The lingual face is strongly convex with some longitudinal enameloid striations (Fig. 2F). A seemingly blunt cutting edge occurs, extending from the rounded apex to the crown neck, where it fades out. Below this neck, the crown attains a circular cross-section and ends in a well-pronounced collar, which bears a slight granulate ornamentation (Fig. 2A-D). The root is bi- (Fig. 2A-B, E-F) or trilobate (Fig. 2D), possesses round terminations, and bears scattered foraminal openings (Fig. 2F). Furthermore, the root lobes are rather straight, elongated, and uniform.

Intragenetic comparisons: The teeth of *N. zeitlinger* sp. nov. differ from those of *N. tuberculatus* Underwood and Schlögl, 2013 in the absence of irregular tubercles on the labial crown face. Additionally, teeth of *N. tuberculatus* are generally more massive compared to the rather gracile teeth of *N. zeitlinger* sp. nov., which possess a slender, spearhead-shaped tooth crown, with noticeable elongated root lobes.

Remarks: Teeth of the genus *Nanocetorhinus* are rare in the fossil record (Fig. 3). The stratigraphically oldest known European record is reported from deep-marine sediments of the upper Egerian (Aquitanian) of Upper Austria (Pollerspöck et al., 2018) with subsequent younger records from the Ottnangian (Burdigalian) of Mitterdorf (Pollerspöck & Straube, 2017) and Walbertsweiler (Bracher et al., 2020) of Germany, of Allerding (Pollerspöck et al., 2020) and Wallern of Upper Austria, and from sediments of the Upper Marine Molasse (Burdigalian) of Switzerland (Bolliger et al., 1995). Teeth from the Karpatian (upper Burdigalian) are known of the Slovakian part of the Vienna Basin (Underwood and Schlögl, 2013), which represents the type locality of *Nanocetorhinus*. The youngest European record of this genus comes from the Langhian of the Mediterranean of southern France (pers. comm. Sylvain Adnet, 2020).

A record from the upper Oligocene or lower Miocene of western Canada (Johns et al., 2005) and two records from the lower and middle Miocene of Japan (Nishimatsu and Ujihara, 2019; Nishimatsu, 2019) testify a Pacific distribution of the genus.

Although most colleagues follow the diagnosis of Underwood and Schlögl (2013) that these ichthyoliths represent oral teeth rather than dermal denticles, we would seize this issue for further discussions. As stated by the latter authors, the root morphology is very indicative for teeth and not for dermal denticles. A direct comparison with dermal denticles of Rajidae demonstrates, however, some similarities. In particular, teeth with the trilobate root-type resembles dermal denticles of the extant ray *Raja clavata* (Gravendeel et al., 2002). However, the trilobate root-type of *Nanocetorhinus* seems to be a variation within the morphological range of this peculiar teeth. As figured in the type-series in Underwood and Schlögl (Fig. 9, C1-C2, 2013) a beginning development of a third root lobe can be observed. Further examples of the high degree of variations within this tooth type can be seen in teeth of *N. tuberculatus* from Mitterdorf (Germany, Early Miocene) in Pollerspöck and Straube (Fig. 11, 7a-7b, 2017), which shows also three separated root lobes. Within the assemblage of Mitterdorf, merely six out of 120 teeth possess a trilobate root and 15 teeth show a distinct projection of a third lobe. Thus, there are bi- and trilobate ichthyoliths within one assemblage. This argues against dermal denticles because denticles always possess more than two lobes (e.g. Rajidae) or a flat root base and this would exclude the bilobate ichthyoliths to be denticles.

4. Discussion

Due to its complex geodynamic setting, the Central Paratethys Sea underwent continuous paleogeographic changes, which affected marine circulation patterns and led to phases of partial or full isolation (Rögl, 1998; Popov et al., 2004; Grunert et al., 2010a). Phases with open marine gateways to the adjacent Proto-Mediterranean Sea provided migration routes for cosmopolitan species into the Atlantic Ocean and – at least until the

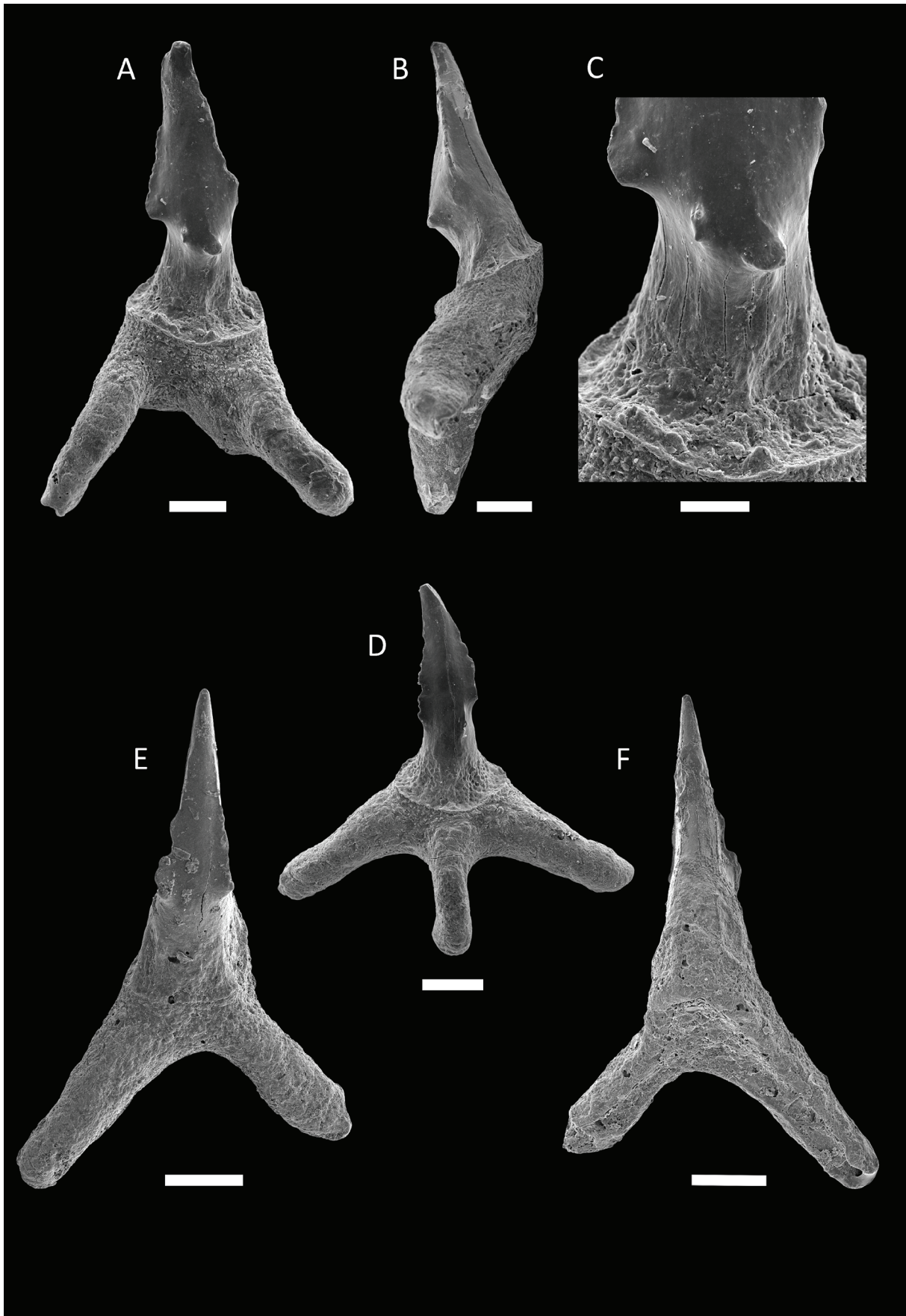


Figure 2: A-C: Holotype of *Nanocetorhinus zeitlingeri* sp. nov. (NHMW/2019/0165/0030). A: labial view, B: profile view. C: close up of the characteristic collar with granulate ornamentation pattern. D: Paratype of *Nanocetorhinus zeitlingeri* sp. nov. (NHMW/2019/0165/0029): labial view. E-F: Paratype of *Nanocetorhinus zeitlingeri* sp. nov. (NHMW/2019/0165/0031). E: labial view, F: lingual view. Scale bars A-B, D-E: 200 μ m; C 50 μ m.

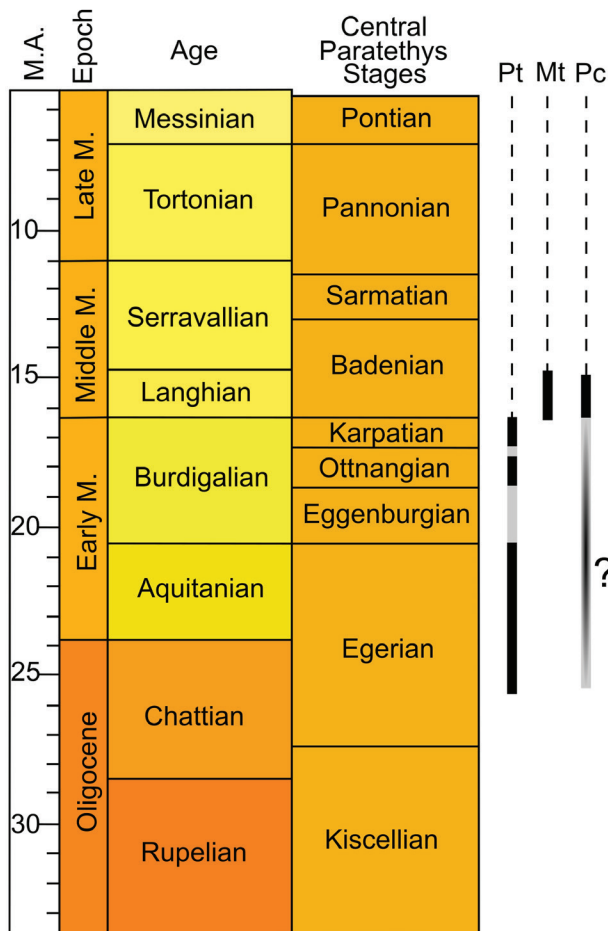


Figure 3: Stratigraphic overview of known occurrences of the genus *Nanocetorhinus*. Black line marks secured records, grey line indicate ghost lineages. Occurrences after Pollerspöck et al. (2018, 2020), Pollerspöck and Straube (2017), Bracher et al. (2020), Bolliger et al. (1995), Underwood and Schlögl (2013), Sylvain Adnet pers. comm. (2020), Johns et al. (2005), Nishimatsu and Ujihara (2019), Nishimatsu (2019), and the present work. Abbreviations: **Pt** = Paratethys; **Mt** = Mediterranean; **Pc** = Pacific.

closure of the Tethys Gateway during the early Miocene (Harzhauser et al., 2007) – also into the Indo-West Pacific.

Present-day representatives of cosmopolitan, large planktivorous sharks are the giant whale shark *Rhincodon typus* Smith, 1828, the megamouth shark *Megachasma pelagios* Taylor, Compagno and Struhsaker, 1983 and the basking shark *Cetorhinus maximus* (Gunnerus, 1765). In particular the latter is highly migratory and follows seasonal plankton blooms (Berrow and Heardman, 1994; Sims et al., 1997; Sims et al., 2005; Soldo et al., 2008). However, this behavior is not limited to sharks but is also known from the devil rays (Mobulidae), which are sieving plankton through their highly modified branchial filter plates (Anderson et al., 2011; Rohner et al., 2017). Therefore, the presence of *Nanocetorhinus* in the Paratethys during the late Oligocene seemingly evokes two pre-requisites, namely, the presence of nutrient-rich surface waters and open marine gateways. The western gateway that opened into the western part of the Proto-Mediterranean Sea across the Rhône Valley was closed during

the late Oligocene and the North Alpine Foreland Basin formed a deep marine embayment (Popov et al., 2004). The eastern route across the Thracian Basin, as shown by Rögl (1998), was a very shallow sill (İslamoğlu et al., 2008), which most probably provided an effective barrier for open pelagic organisms. Therefore, only the central route via the Hungarian Basin and the Slovenian Basin provided a potential gateway for *Nanocetorhinus* between the Paratethys and the Proto-Mediterranean Sea. This in turn suggests that this Slovenian Corridor (Rögl, 1998; Bartol, 2009) was a deep connection between the Paratethys and the Proto-Mediterranean Sea.

An analogue example for the impact of a small and shallow sill on diversity of e.g. deep-water elasmobranchs can be seen in the modern Mediterranean. Although the modern Mediterranean is rather deep, the diversity of deep-water inhabitants (sharks and rays) is rather low (Bradai et al., 2012). Consequently, broad and deep marine gateways are essential for a balanced elasmobranch diversity today and have been in the past.

Phyto- and/or zooplankton blooms are frequently described from the Oligocene and Miocene of the North-Alpine Foreland Basin (Grunert et al., 2010a, b). A positive correlation between nutrient-rich seawater and the occurrence of filter feeding sharks is likely for the lower Ottnangian Neuhofer beds at Mitterdorf (Bavaria, Germany). From these beds, Pippèr and Reichenbacher (2010) documented abundant *Coccolithus pelagicus*, *Globigerina ottnangiensis*, and *G. praebulloides*, which are indicators for nutrient rich waters, upwelling conditions, and/or are characteristic for environments with high primary productivity (Rögl and Spezzaferri, 2003; Pippèr and Reichenbacher, 2010). From the same deposits, Pollerspöck and Straube (2017) described an outstanding richness of planktivorous teeth. In 685 kg of screen-washed sediment, planktivorous sharks account for 33.5% of the fauna at the species level, including 126 teeth of *Nanocetorhinus tuberculatus* and 12 gill rakers and one oral tooth of *Keasius parvus*. An even higher contribution of 64% filter-feeding species was shown for the late Egerian shark assemblage from Graben (Upper Austria). 440 kg of sediment contained 63 teeth of *N. tuberculatus* as well as 482 fragments of gill rakers and one oral tooth of *K. parvus* (Pollerspöck et al., 2018). The same sample is extraordinarily rich in diatoms and planktonic taxa such as *Globigerina praebulloides*, *G. officinalis*, *G. anguliofficialis*, *Tenuitellinata angustiumbilitata*, and *Tenuitella munda*, account for up to 67% of the foraminiferal assemblages (Krenmayr and Rupp, 1996).

Upwelling conditions, periodic phases of increased nutrient influx and plankton blooms have been documented also for the Polsenz and Unterrudling sections in the Eferding Fm by Rupp and Ćorić (2015).

5. Conclusion

Extensive sampling of deep-marine sediments of the Eferding Fm in the Kamig quarry at Kriechbaum (Upper Austria) provided teeth of a new species of the

presumably planktivorous shark *Nanocetorhinus*. The teeth of the herein described species *N. zeitlingeri* sp. nov. represent the oldest ascertained record of this genus, which extends the fossil record of *Nanocetorhinus* back into the lower Egerian (upper Oligocene).

We notice a correlation between nutrient rich waters, plankton blooms, and accumulations of *Nanocetorhinus* and Keasius as indicated by the mass occurrences of these elasmobranchs at several localities in the NAFB (Pollerspöck and Straube, 2017; Pollerspöck et al., 2018). Coupled with the tiny and non-functional tooth morphology of *Nanocetorhinus*, such a correlation points towards a filter-feeding lifestyle as already supposed by Underwood and Schlögl (2013).

Thus in turn is indicative for the oral origin of these enigmatic ichthyoliths, which were supposed to represent dermal denticles (Johns et al., 2005) rather than oral teeth. Moreover, the wide paleogeographic distribution of the open marine *Nanocetorhinus* suggests a deep and fully marine connection between the Paratethys and the Proto-Mediterranean Sea during late Oligocene times, which might have been established via the Slovenian Corridor.

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