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Deep-marine elasmobranchs from the Badenian (Langhian, Middle Miocene) of the Central Paratethys of Austria

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Abstract

This study reports on a rare assemblage of deep-marine elasmobranchs from the middle Badenian (Langhian) of Austria, which has been recovered by extensive bulk sampling of sediment deposited in the Krems embayment. The applied multidisciplinary approach enabled an age assignment, placing the assemblage around the mid Badenian flooding event (14.59 ± 0.2 Ma). Palaeoenvironmental reconstruction, based on a well-preserved foraminifera assemblage and fish otoliths, indicates predominantly oxic to suboxic with partially dysoxic conditions of a rather deep-marine (>100 m) setting, which align with the recovered elasmobranch taxa. Despite analyzing 180 kilograms of sediment, only five elasmobranch teeth were recovered. The low number of teeth and the extraordinarily well-preserved foraminifera argue for an autochthonous deposition and point to high sedimentation rates associated with the flooding event. The teeth represent five different elasmobranch orders (Squaliformes, Squatiniformes, Carcharhiniformes, Torpediniformes, and Myliobatiformes) with a wide range of feeding behaviors, providing new insights into the ecological structure of this deep-marine environment. Despite common genera known from other marine settings of the Paratethyan realm (e.g., *Squatina, Scyliorhinus*, and *Centrophorus*), this study documents the first distinct records of *Torpedo* and *Mobula* from Austria, expanding the known palaeogeographic distribution of these taxa.

1. Introduction

The Central Paratethys Sea played a crucial role in shaping the marine biodiversity of Eurasia before the epicontinental sea transformed into the brackish Lake Pannon (~7 Ma) (Rögl, 1998, 1999; Popov et al., 2004; Harzhauser and Piller, 2007; Harzhauser et al., 2024a). This vast and dynamic system underwent significant palaeoenvironmental and palaeogeographic changes, influenced by global sea-level fluctuations, regional tectonics, and climatic shifts (see Harzhauser et al., 2024a, 2024b). While shallow-water environments of the Central Paratethys are relatively well-documented through extensive fossil records, our understanding of its deep-water ecosystems remains notably incomplete. This concerns particularly marine vertebrates, especially elasmobranchs (sharks, rays, and skates), whose fossil record is mostly limited to isolated teeth. Deep-marine sediments from the Burdigalian, comprising the regional stages of the late Eggenburgian, Ottnangian, and Karpatian, have already provided rare but valuable insights into the diversity of elasmobranchs from that period (e.g., Barthelt et al., 1991; Underwood and Schlögl, 2013; Pollerspöck and Straube, 2017; Marramà et al., 2019; Pollerspöck et al., 2022). However, deep-marine elasmobranch assemblages from the stratigraphically younger sediments of the Langhian (Badenian) have never been described from Austria. To reconstruct the elasmobranch diversity of a deep-marine ecosystem, extensive bulk sampling in meaningful quantities is necessary to adequately assess also teeth of small elasmobranch taxa (e.g., Underwood, 2004). Bulk sampling has become more common over the last decade, enabling the description of several new elasmobranch taxa from different palaeoenvironmental settings from both the Tethys (e.g., Feichtinger et al., 2023, 2024, 2025) and Paratethys (e.g., Underwood and Schlögl, 2013; Pollerspöck and Straube, 2017; Pollerspöck et al., 2018; Feichtinger et al., 2020; Pollerspöck and Straube, 2021). This has been vital for understanding elasmobranch evolution and their spatial and temporal distribution. Here we present a new elasmobranch assemblage of a deep-marine succession of the Langhian from Austria, which significantly contributes to our knowledge on the palaeogeographic distribution of the recovered elasmobranch genera. In order to obtain the best estimate of the environmental conditions, otoliths and foraminifera were used to assess palaeobathymetry and oxygen availability.

2. Geographical and geological settings

The section Heiligenstein (Fig. 1) is situated in the Austrian part of the North Alpine Foreland Basin (NAFB) about 10 km NNE of Krems and about 70 km NW of Vienna. The section is close to the southeastern margin of the Bohemian Massif, which formed the Miocene coastline in the area (Harzhauser et al., 2003). In terms of palaeogeography, the area was part of the Krems embayment, which formed a western embayment of the Central Paratethys Sea during the Badenian (= Langhian) (Gebhardt et al., 2023). For a detailed description of the regional geology see Gebhardt et al. (2023). In the region west of the village of Straß im Straßertal, numerous small outcrops of few meters thickness are accessible along wine-terraces exposing purple-red, continental Permian sandstones of the Zöbing Formation and marine clays, sands and gravels of the Middle Miocene Badenian Gaindorf Formation (Fig. 1). Due to landslides along the terrace boundaries, no continuous profiles can be logged and the contact between the Permian and Miocene is currently not accessible. The herein described Middle Miocene section comprises a basal unit of about 1 m of grey and partly limonitic silts, sandy silts, and gravelly silts. These are overlain by around 1 m of gravelly silts, which contain limonitized plant debris in the top. An approximately 10 cm thick layer of blue-grey clay is overlain by 70 cm of yellowish medium to coarse sand with gravel and pebbles. The sands are abruptly overlain by about 3 m of darkgrey clay, rich in foraminifera and small, often articulated nuculanid bivalves. The samples processed here come from this unit, which extends from 2.30 m - 4.70 m of the section log at Figure 1b.

The abrupt change from coastal sands to deep water clays of this unit (2.30 m - 4.70 m in profile of Fig. 1b) suggests a very rapid flooding of the region. The mechanism causing this rapid change in depositional environments is not solved yet. One might speculate that the Langhian (mid-Badenian) transgression exceeded a swell separating the deeper valley of the eastern North Alpine Foreland Basin from the adjacent Vienna Basin resulting in a rapid flooding of the basin. This hypothesis, however, will need further geological evidence.

3. Material and methods

The elasmobranch teeth and fish otoliths derive from two bulk-samples of 90 kg per horizon, which were collected from lateral equivalents exposed on two different terraces of the vineyards, encompassing a sample from the lower terrace (48°29.1960 N, 15°43.2150 E; 326 m above sea level; Sample 1) and one sample from the upper terrace (48°29.2240 N, 15°43.2030 E; 336 m above sea level; Sample 2). Both samples represent roughly the same horizon, taken from two terraces with a horizontal distance of a few meters. The dark clay was disaggregated with 3% of diluted hydrogen peroxide and washed through a set of sieves down to a mesh size of 320 µm. The teeth and otoliths were manually picked from the residue and photographed with a Keyence VHX-7000 Digital Microscope in the Department of Mineralogy and Petrography (NHM Vienna). In total, the bulk samples yielded five elasmobranch teeth, 213 well-preserved otoliths, and a few bony fish teeth. The same procedure was applied for foraminifera (200 g samples), which were washed through a standard set of sieves (500 µm, 250 µm, 125 µm, 63 µm). The 200 g samples for the micropalaeontological analyses were taken from the 90 kg bulk samples. Approximately 300 individuals were picked from each sample and counted to genus level. Selected specimens identified to species level were photographed with a Keyence VHX-7000 Digital Microscope with automated focus stacking. Foraminiferal species identification was based on Papp and Schmidt (1985), Cicha et al. (1998) and Rögl and Spezzaferri (2003) and cross-checked with the World Foraminifera Database (Hayward et al., 2025) and Mikrotax (Young et al., 2017). For the stratigraphic assignment of planktonic foraminifera, we used Wade et al. (2011) and Lirer et al. (2019). The described fossils are stored in the Geological-Paleontological Department of the Natural History Museum Vienna.

4. Results

4.1. Micropalaeontology

4.1.1. Age assignment and correlation with the mid-Badenian flooding

The co-occurrence of *Orbulina suturalis* and *Praeorbulina circularis* in both samples allows a correlation with the Planktonic Foraminifera Zone M6 after Wade et al. (2011) corresponding to a middle Langhian age (Young et al., 2017) with an age range of 14.67 ± 0.43 Ma. The FO of *Orbulina suturalis* in the Mediterranean is recorded at 14.56 Ma with the base of MMi5a (Lirer et al., 2019). Therefore, the Heiligenstein section corresponds to the middle Bad-

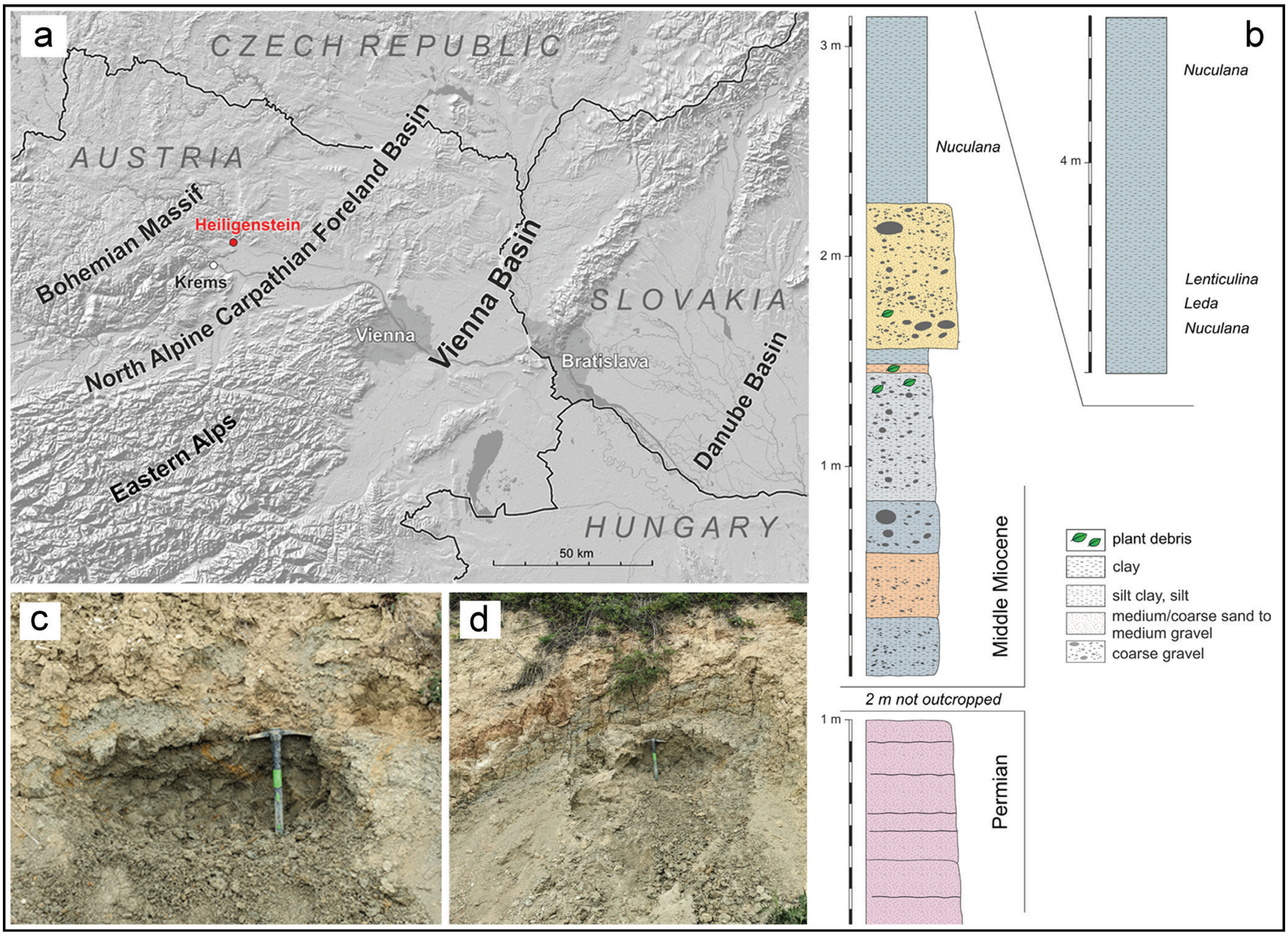

Figure 1: (a) Geographic position of the Heiligenstein section. **(b)** Section log of the succession. The samples derive from the upper part, which comprises dark grey clay of the Gaindorf Formation (Langhian, Middle Miocene). **(c)** Photograph of the sampled horizon (90 kg) from the upper terrace (48°29.2240 N, 15°43.2030 E; Sample 2). **(d)** Photograph of the sampled horizon (90 kg) from the lower terrace (48°29.1960 N, 15°43.2150 E; Sample 1). Basemap (Esri, 2009).

enian of the Vienna Basin as understood by Harzhauser et al. (2020, 2024b) and Siedl et al. (2020). This dating is in accordance with previous data for the Krems embayment as presented by Gebhardt et al. (2023). Therefore, the observed flooding in the Krems embayment corresponds to the mid-Badenian flooding around 14.59 ± 0.2 Ma as described by Šegvić et al. (2022) and Harzhauser et al. (2020, 2024b).

4.1.2. Inference of palaeo-waterdepth and palaeoecology

The inference of the palaeo-waterdepth is based on relatively high abundances (44% and 45%) of deep marine indicator taxa. This indicator taxa includes *Spirorutilus* (Fig. 2a), *Siphonodosaria* (Fig. 2i), *Melonis* (Fig. 2x), *Pullenia* (Fig. 2y), *Heterolepa* (Fig. 2za, zb), *Lenticulina* (Fig. 2c-f), and *Uvigerina* (Fig. 2t, u), which suggest a water depth of at least 100 m or more (e.g., Mandic et al., 2002; Rögl and Spezzaferri, 2003; Spezzaferri, 2004; Tomanová Petrová and Svabenicka, 2007; Kranner et al., 2021). In addition, typical shallow-water taxa of the Badenian, such as *Ammonia* or *Elphidium*, are completely absent.

The micropalaeontological analyses of this section show high abundances (53% and 60%) of cold and cold-temperate indicators such as *Amphicoryna* (Fig. 2g, h), *Sphaeroidina* (Fig. 2v), *Cibicidoides* (Fig. 2w), *Heterolepa* (Fig. 2za, zb), *Lenticulina* (Fig. 2c-f), *Melonis* (Fig. 2x), and *Pullenia* (Fig. 2y), which indicate cold bottom waters (Rögl and Spezzaferri, 2003; Murray, 2006; Tomanová Petrová and Svabenicka, 2007), whereas the planktonic taxa *Praeorbulina* (Fig. 2zc), *Orbulina* (Fig. 2zd), *Trilobatus*, and *Globigerina* are indicative of warm–temperate surface waters (Rögl and Spezzaferri, 2003). The possibility of a local upwelling zone has been discussed in Harzhauser et al. (2003). The benthic assemblages are dominated by *Lenticulina* (Fig. 2c-f) and *Heterolepa* (Fig. 2za, zb) (36% and 43%) pointing to mostly oxic-suboxic conditions in shelf to bathyal settings (Rögl and Spezzaferri, 2003). Dysoxic indicators such as *Amphicoryna* (Fig. 2d, h), *Bolivina* (Fig. 2n, o), *Bulimina* (Fig. 2q), and *Protoglobobulimina* (Fig. 2r) make up 15 and 25% of the assemblage, suggesting at least partially dysoxic conditions (Mandic et al., 2002; Rögl and Spezzaferri, 2003).

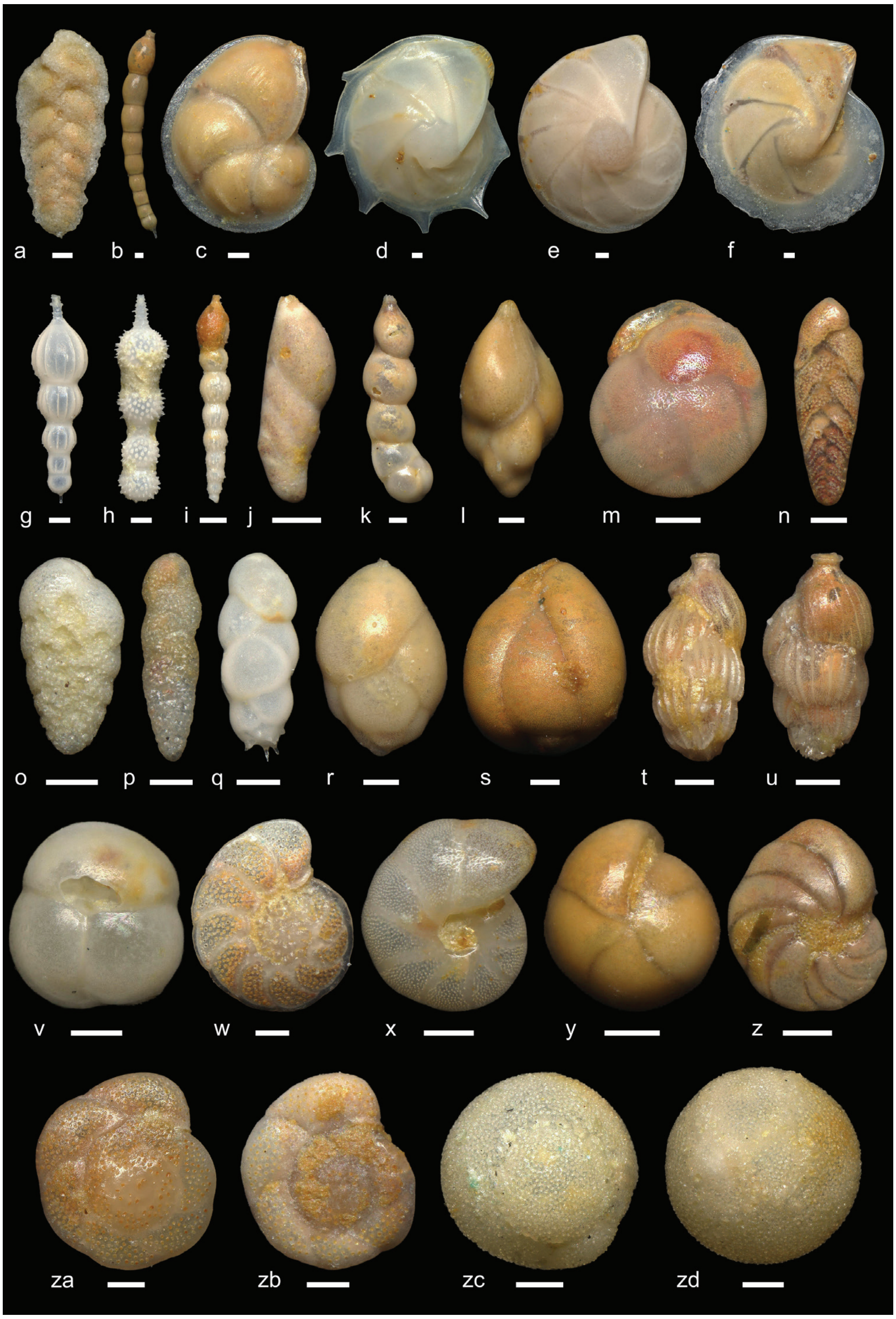

Figure 2: Selected Foraminifera from Heiligenstein. All scale bars are 100 µm. **(a)** *Spirorutilus carinatus* (d'Orbigny, 1846), NHMW-GEO-2025-0077-0001. **(b)** *Laevidentalina elegans* (d'Orbigny, 1846), NHMW-GEO-2025-0077-0003. **(c)** *Lenticulina ariminensis* (d'Orbigny, 1846), NHMW-GEO-2025-0077-0004. **(d)** *Lenticulina calcar* (Linnaeus, 1758), NHMW-GEO-2025-0078-0001. **(e)** *Lenticulina clypeiformis* (d'Orbigny, 1846), NHMW-GEO-2025-0077-0005. **(f)** *Lenticulina cultrata* (Montfort, 1808), NHMW-GEO-2025-0077-0006. **(g)** *Amphicoryna badenensis* (d'Orbigny, 1846), NHMW-GEO-2025-0078-0009. **(h)** *Amphicoryna hirsuta* (d'Orbigny, 1826), NHMW-GEO-2025-0078-0003. **(i)** *Siphonodosaria scripta* (d'Orbigny, 1846), NHMW-GEO-2025-0077-0019. **(j)** *Marginulina eximia* Neugeboren, 1851, NHMW-GEO-2025-0077-0010. **(k)** *Vaginulinopsis pedum* (d'Orbigny, 1846), NHMW-GEO-2025-0078-0004. **(l)** *Guttulina austriaca* d'Orbigny, 1846, NHMW-GEO-2025-0077-0012. **(m)** *Cassidulina laevigata* d'Orbigny, 1826, NHMW-GEO-2025-0077-0014. **(n)** *Bolivina antiqua* d'Orbigny, 1846, NHMW-GEO-2025-0077-0013. **(o)** *Bolivina hebes* Macfadyen, 1930, NHMW-GEO-2025-0078-0006. **(p)** *Lapugyina schmidi* Popescu, 1998, NHMW-GEO-2025-0077-0018. **(q)** *Bulimina subulata* Cushman and Parker, 1937, NHMW-GEO-2025-0078-0007. **(r)** *Protoglobobulimina pupoides* (d'Orbigny, 1846), NHMW-GEO-2025-0078-0008. **(s)** *Globobulimina pyrula* (d'Orbigny, 1846), NHMW-GEO-2025-0077-0015. **(t)** *Uvigerina pygmoides* Papp and Turnovsky, 1953, NHMW-GEO-2025-0077-0016. **(u)** *Uvigerina semiornata* d'Orbigny, 1846, NHMW-GEO-2025-0077-0017. **(v)** *Sphaeroidina bulloides* d'Orbigny in Deshayes, 1832, NHMW-GEO-2025-0078-0009. **(w)** *Cibicidoides ungerianus* (d'Orbigny, 1846), NHMW-GEO-2025-0077-0020. **(x)** *Melonis pompilioides* (Fichtel and Moll, 1798), NHMW-GEO-2025-0078-0010. **(y)** *Pullenia bulloides* (d'Orbigny, 1846), NHMW-GEO-2025-0077-0022. **(z)** *Nonion commune* (d'Orbigny, 1846), NHMW-GEO-2025-0077-0023. **(za)** *Heterolepa praecincta* (Karrer, 1868), NHMW-GEO-2025-0077-0024. **(zb)** *Heterolepa dutemplei* (d'Orbigny, 1846), NHMW-GEO-2025-0078-0011. **(zc)** *Praeorbulina circularis* (Blow, 1956), NHMW-GEO-2025-0077-0026. **(zd)** *Orbulina suturalis* Brönnimann, 1951, NHMW-GEO-2025-0077-0025.

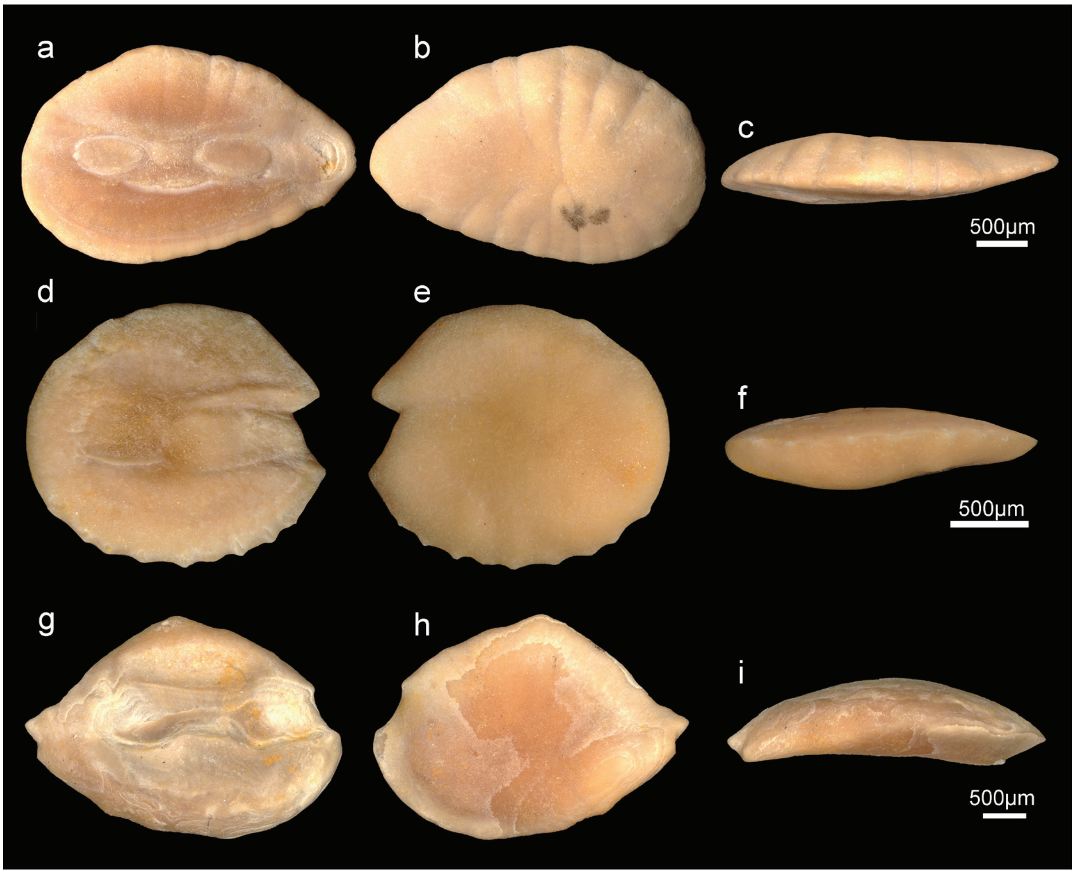

Figure 3: Otoliths from Heiligenstein (Langhian, Miocene). **(a–c)** *Gadiculus argenteus* Guichenot, 1850, (NHMW-GEO-2025-0110-0009) recovered from Sample 1. **(d–f)** *Diaphus austriacus* (Koken, 1891), (NHMW-GEO-2025-0110-0007) recovered from Sample 1 and 2. **(g–i)** *Peristedion* sp. (NHMW-GEO-2025-0110-0005) from Sample 1.

4.2. Otolith assemblage

Material: 12 specimens of *Gadiculus argenteus* Guichenot, 1850 (Fig. 3a-c, Sample 1); 120 specimens of *Diaphus austriacus* (Koken, 1891) (Fig. 3d-f, Sample 1); 1 specimen *Peristedion* sp. (Sample 1); 80 specimens of *Diaphus austriacus* (Koken, 1891) (Fig.3 g-i, Sample 2).

Remarks: Otoliths are relatively common in the studied samples but show a very low diversity. The assemblage is dominated by mesopelagic fishes (*Diaphus austriacus* and *Gadiculus argenteus*), which are both common throughout the middle Badenian of the Central Paratethys (Schwarzhans and Radwańska, 2022 and 2025 in press). Their abundance in combination with the lack of demersal shelf fishes (with the singular exception of one specimen of *Peristedion* sp.) indicates an offshore environment. The absence of bathydemersal fishes may point to suboxic to dysoxic conditions at the sea bottom which would be an adverse ecologic environment for fishes of this guild. Elsewhere in coeval deeper settings of the Central Paratethys, bathydemersal fishes (for instance of the family Macrouridae) are common and diverse (Schwarzhans and Radwańska, 2025 in press).

4.3. Systematic palaeontology of elasmobranchs

The dental terminology and systematic scheme employed here largely follow those of Cappetta (2012).

Order Squaliformes Compagno, 1973
Family Centrophoridae Bleeker, 1859
Genus *Centrophorus* Müller and Henle, 1837
Centrophorus sp.
Figure 4a–b
Material: One tooth (NHMW-GEO-2025-0109-0001); Sample 2

Description: Strongly labio-lingual compressed tooth of the lower jaw, which is slightly higher (2.6 mm) than wide (2.3 mm). The distally bent cusp possesses a faint serration of the sigmoidal curved mesial cutting edge and is flanked by a distal heel. The labial face bears a long and narrow apron, which does not reach the basal root edge (Fig. 4a). Several foramina open mesially and distally of the apron. The lingual crown possesses a small, but acute uvula (Fig. 4b). A well-developed interlocking surface is developed below the distal heel of the lingual root face, which ends at the height of the elongated root bulge. The root bulge extends from the distal interlocking surface to the mesial root edge and is pierced by one central foramen. A faint nutritive groove continues from the central foramen towards the basal root edge. Additional lingual foramina open along the crown-root transition.

Remarks: To date, the genus *Centrophorus* encompasses 13 extant species (Pollerspöck and Straube, 2025), which inhabit mainly deepwater environments with a depth-range of 1000 – 1500 m (Compagno, 2005). So far, three of the modern species have been identified in the fossil record. The species *C. atromarginatus* Garman, 1913 was mentioned to have been found in the Miocene of Japan (Suzuki, 2012). Teeth of the species *C. squamosus* (Bonnaterre, 1788) are mentioned from different Cenozoic strata of New Zealand (Keyes, 1984) and from the Pliocene of Italy (Cigala-Fulgosi, 1986). Unfortunately, none of the mentioned fossil occurrences of both extant species have been figured. Teeth of the third living species, *C. granulosus*, have often been identified among fossil assemblages of different strata (Cappetta, 2012). However, it is important to note that living species can exhibit considerable intraspecific variations of the tooth morphology, though this remains poorly documented (White et al., 2013, 2017, 2022). Nevertheless, several fossil specimens have been attributed to *C. granulosus* or classified as *Centrophorus* sp., the latter being a more reliable assignment given the limited data on dental variation of extant species (e.g., Barthelt et al., 1991; Pollerspöck and Straube 2017; Pollerspöck et al., 2022; Höltke et al., 2022; Pollerspöck and Unger, 2024). Although we prefer to leave this tooth in open nomenclature, this tooth represents the first record of the genus *Centrophorus* from the Langhian of Austria.

Order Squatiniformes De Buen, 1926
Family Squatinidae Bonaparte, 1838
Genus *Squatina* Dumeril, 1805
Squatina sp.
Figure 4c–d
Material: One tooth (NHMW-GEO-2025-0110-0001); Sample 1

Description: The incomplete tooth has a triangular cusp with a narrow apron, which protrudes below the flat root base (Fig. 4d). The combination of a triangular cusp with smooth cutting edges, which continue towards the mesial and distal root in combination with the apron, a flat root base with a lingual root protuberance, is characteristic for the genus *Squatina*.

Remarks: The genus *Squatina* includes 26 living species and 14 extinct species (Pollerspöck and Straube, 2025), with its earliest known records dating back to the Jurassic (Cappetta, 2012). Since *Squatina* species exhibit subtle differences in their tooth morphologies, distinguishing between Cenozoic species based solely on dental characters remains challenging. The recovered tooth of this study is poorly preserved, which precludes precise species identification. Extant representatives occupy environments from the intertidal zone down to 1000 m water depth (Compagno et al., 2005).

Order Carcharhiniformes Compagno, 1977
Family Scyliorhinidae Gill, 1862
Genus *Scyliorhinus* De Blainville, 1816
Scyliorhinus sp.
Figure 4 e-f
Material: One tooth (NHMW-GEO-2025-0109-0003); Sample 2

Description: A small scyliorhinid not exceeding a tooth width of 600 µm. The main cusp is slightly bent in distal direction and is flanked by two pairs of lateral cusps. The first pair of lateral cusps reaches the height of one third of the main cusp. The second pair is significantly smaller, but the distal cusplet is not preserved. The labial crown face bears very well-developed enameloid ridges, which extend from the crown base up to half of the total crown height at the main cusp and almost to the apex at the lateral cusplets (Fig. 4e). The lingual crown face possesses only faint enameloid striations (Fig. 4f). The root is not well-preserved.

Remarks: The fossil record of *Scyliorhinus* dates back to the Cretaceous, however, the origin of the genus based on tooth fossils is poorly known (Underwood and Mitchell, 1999; Cappetta, 2012). Although the genus *Scyliorhinus* comprises almost 40 extinct species, it is not possible to attribute the tooth of this study to a distinct species. These small, bottom-dwelling sharks are well represented in the fossil record and show a wide palaeogeographic distribution (Cappetta, 2012). The majority of extant species dwell in fairly deep waters of the continental shelf or upper slope (Compagno et al., 2005; Soares and Carvalho, 2019).

Order Torpediniformes De Buen, 1926
Family Torpedinidae Bonaparte, 1838
Genus *Torpedo* Dumeril, 1805
Figure 4g–j
Material: One tooth (NHMW-GEO-2025-0110-0002); Sample 1

Description: An antero-lateral, asymmetrical tooth not exceeding a crown height of 1.5 mm. The cusp is strongly bent lingually, which exhibits only faint cutting edges. The cutting edges disappear at the cusp base and thus, do not continue towards the labial or lingual crown margin. The crown base is rectangular in basal view (Fig. 4j), with a deep indentation of the lingual crown face (Fig. 4g). The labial visor is thick and distinctly overhangs the bilobed root (Fig. 4h-j). Both root lobes are small but protrude below the lingual crown (Fig. 4g-h). One large foraminal opening is situated between the root lobes (Fig. 4j).

Remarks: The single tooth described in this study exhibits typical morphological characters of the genus *Torpedo*. The genus comprises twelve modern representatives and four extinct species (Pollerspöck and Straube, 2025). Although the tooth from Heiligenstein is very well preserved, it is difficult to attribute this single tooth to a distinct species. Teeth of the species *T. chattica* Reinecke, 2015, *T. dormaalensis* Smith, 1999, and *T. pessanti* Adnet, 2006 exhibit a very well-developed cutting edge of the cusp, which continues towards the mesial and distal crown margins. Teeth of *T. acarinata* Adnet, 2006 differs by a convex visor, which is straight at the tooth described in this study. In addition, the almost rectangular outline of the crown of the described specimen separates this tooth from all known fossil *Torpedo* species.

Teeth of the genus *Torpedo* are extraordinarily scarce in the fossil record. The stratigraphically oldest record of this genus is known from the Thanetian of Belgium (Smith, 1999). In Europe, the records comprise teeth from the Eocene from Germany and France (Adnet, 2006; Reinecke et al., 2024) and from the Oligocene of Germany (Reinecke et al., 2005; Reinecke, 2015). To date, only two records from the Miocene have been figured, which comprise specimens from Portugal (Fialho et al., 2019) and Switzerland (Bolliger et al., 1995). Additional Miocene reports were mentioned from Belgium (Hoedemakers and Dufraing, 2015), Germany (Von der Hocht, 1986), and France (Cappetta et al., 1967), but none of the mentioned specimens have been figured. The only records from Austria were mentioned by Pfeil (1984) and the same record was listed in Schultz (2013), but the teeth have never been scientifically described or figured and the mentioned teeth are not stored in a public collection. Thus, the tooth described in this study represents the first distinct record of *Torpedo* from Austria.

Order Myliobatiformes
Family Mobulidae Bonaparte, 1838
Genus *Mobula* Rafinesque, 1810
Mobula sp.
Figure 4k–n
Material: One tooth (NHMW-GEO-2025-0109-0002); Sample 2

Description: A small tooth, not exceeding 1.25 mm in width with a monocuspid crown (Fig. 4k-n). The crown is smooth and almost triangular in occlusal view. In profile view, the occlusal face of the crown appears almost flat with the apex of the cusp slightly exceeding the lingual root margin (Fig. 4m). The labial visor is straight (Fig. 4k), but the labial and lingual crown-root transition is strongly narrowed (Fig. 4k-m). The height of the root is lower than the crown, but protrudes below the crown in basal view (Fig. 4n). The broad root represents a reduced polyaulacorhize stage.

Remarks: The phylogeny and taxonomy of extant representatives of the family Mobulidae have long been debated (Adnet et al., 2012; Naylor et al., 2012; Paig-Tran et al., 2013; Aschliman, 2014; Poortvliet et al., 2015). Until recently, the family Mobulidae comprised two modern genera (*Mobula* and *Manta*), whose phylogenetic position has been revised based on DNA data and morphological information (White et al., 2018). Based on this comprehensive analysis, the genus *Manta* was placed in synonymy with *Mobula* (White et al., 2018), making the latter the only remaining extant genus within the family Mobulidae.

The stratigraphically oldest record of *Mobula* dates back to the Danian (Noubhani and Cappetta, 1997). In addition, the family comprises seven extinct genera (*Argoubia* Adnet, Cappetta, Guinot and Notarbartolo Di Sciara, 2012, *Arnomobula* Leder, 2015, *Burnhamia* Cappetta, 1976, *Eomanta* Pfeil, 1981, *Eoplinthicus* Cappetta and Stringer, 2002, *Oromobula* Adnet, Cappetta, Guinot and Notarbartolo Di Sciara, 2012, *Plinthicus* Cope, 1869). Among these, the teeth of *Arnomobula, Argoubia, Eomanta, Plinthicus*, and *Oromobula* possess very strong crown ornamentation (e.g., furrows and irregular granules) and thus, differ distinctly from the tooth described in this study.

The teeth of the remaining extinct genera, *Eoplinthicus* and *Burnhamia*, exhibit a marked transverse groove or depression on the occlusal face of the crown, which differs distinctly from the smooth and flat crown of the tooth from Heiligenstein. Although the teeth of the genus *Mobula* display a wide range of morphological variations (Adnet et al., 2012), the described tooth of this study shows the greatest similarity to the latter. The tooth morphology of this genus comprises three main morphotypes: (1) peg-like teeth with a high, tubular crown with a holaulacorhize root, (2) cobblestone shaped tooth plates with a crown that is higher than the small polyaulacorhize root, which enables an interlocking of the tooth files, and (3) comb-like shapes, which comprises small teeth with smooth or ornamented crown faces of mono- or cuspidate cusps, combined with a low holaulacorhize or polyaulacorhize root. The teeth of the latter do not typically interlock but instead represent the most common type found in both extinct and extant *Mobula* species (Adnet et al., 2012). Within the genus *Mobula*, the tooth from Heiligenstein shares most similarities with teeth of the species *M. loupianensis* (Cappetta, 1970). However, the tooth described in this study differs from *M. loupianensis* by the broad and massive root, which leads us to leave this single tooth in open nomenclature. It is noteworthy, however, that teeth with a similar morphology to the tooth from Heiligenstein have also been reported from the Langhian in France, which was classified as *M. loupianensis* (Pl. 9 in Brisswalter, 2009).

Although distributed circumglobally, the total number of recovered devil ray teeth in the fossil record is low. Fossil teeth from Europe are known from the Oligocene of Germany (Pfeil, 1981, Reinecke et al., 2014; Reinecke, 2015) and from the Miocene of the Netherlands (Bor et al., 2012), Germany (Barthelt et al., 1991), France (Cappetta, 1970; Brisswalter, 2009; Vialle et al., 2011), Portugal (Jonet, 1976; Antunes et al., 1981; Fialho et al., 2019), Hungary (Szabó et al., 2022), and Poland (Schultz, 1977; Reinecke and Radwański, 2015). The only record from Austria was listed in Schultz (2013), but the mentioned tooth has never been figured and is not housed in a public accessible collection. Thus, the tooth from this study represents the first distinct record of the genus *Mobula* from Austria.

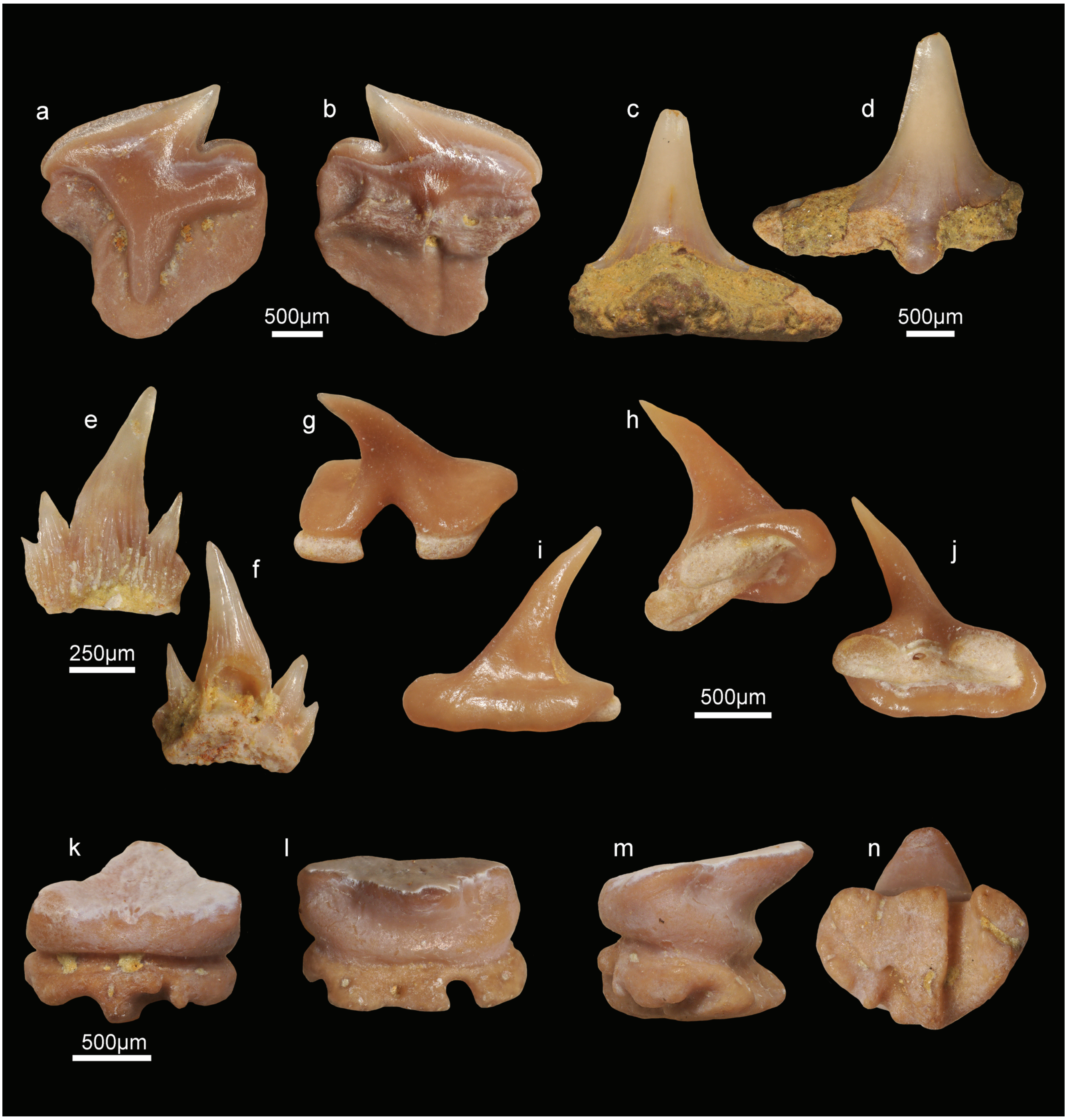

Figure 4: Elasmobranch teeth from Heiligenstein (Langhian, Miocene). **(a–b)** *Centrophorus* sp. (NHMW-GEO-2025-0109-0001; Sample 2), **(a)** labial view, **(b)** lingual view. **(c–d)** *Squatina* sp. (NHMW-GEO-2025-0110-0001; Sample 1), **(c)** lingual view, **(d)** labial view. **(e–f)** *Scyliorhinus* sp. (NHMW-GEO-2025-0109-0003; Sample 2), **(e)** labial view, **(f)** lingual view. **(g–j)** *Torpedo* sp. (NHMW-GEO-2025-0110-0002; Sample 1), **(g)** lingual view, **(h)** profile view, **(i)** labial view, **(j)** basal view. **(k–n)** *Mobula* sp. (NHMW-GEO-2025-0109-0002; Sample 2), **(k)** labial view, **(l)** lingual view, **(m)** profile view, **(n)** basal view.

5. Discussion

The studied section at Heiligenstein is dated to the middle Badenian, based on the co-occurrence of the planktonic foraminifera *Orbulina suturalis* and *Praeorbulina circularis* (Wade et al., 2011; Lirer et al., 2019). The section documents a major flooding, which corresponds to the mid-Badenian flooding around 14.59 ± 0.2 Ma as described by Šegvić et al. (2022) and Harzhauser et al. (2020, 2024b).

The analysis of microfossils such as benthic foraminifera and otoliths suggests a medium to deep-marine environment with water depths of at least 100 m or more (e.g., Mandic et al., 2002; Rögl and Spezzaferri, 2003; Kranner et al., 2021) with cool bottom waters and warm-temperate surface waters (Rögl and Spezzaferri, 2003; Murray, 2006). Foraminiferal indicators points to mostly oxic to suboxic conditions with periodically dysoxic intervals (Mandic et al., 2002; Rögl and Spezzaferri, 2003). A comparable setting was described by Harzhauser et al. (2003) from the close-by Mühlbach section, where deep water settings existed in close vicinity to the coast due to the deep cliffs of the Bohemian Massif. The possibility of a local upwelling zone, corresponding to the variable temperature regimes, was discussed therein (Harzhauser et al., 2003).

The processed sediment (180 kg) of this section yielded five teeth of five different elasmobranch orders, pointing to a moderate diverse assemblage of cartilaginous fishes recovered from a deep-marine environment, which are accompanied by a low diversity bony fish fauna. The identified elasmobranch orders are Squaliformes (dogfish sharks), Squatiniformes (angel sharks), Carcharhiniformes (ground sharks), Torpediniformes (electric rays), and Myliobatiformes (stingrays and their relatives).

The associated bony fish fauna comprises otoliths of the species *Gadiculus argenteus*, *Diaphus austriacus*, and one single otolith of *Peristedion* sp., the latter of which may be of allochthonous shallow water origin. Otherwise, the otolith assemblage indicates a pelagic environment of at least 100 m water depth. Myctophids (*Diaphus austriacus*), which are the most common, are known for undertaking diel migrations living at depths of 300 to 1000 m during the day and migrating to the sea surface at night (Robison et al., 2020). *Gadiculus argenteus* is one of the few fish species from the Middle Miocene that still exists today. This species is found in the oceanic pelagic zone at depths ranging from 100 to 1000 meters (Froese and Pauly, 2025). The absence of demersal fishes, particularly of the bathydemersal guild, speaks for suboxic to dysoxic conditions at the sea bottom.

Sample 1 has yielded one tooth attributed to the genus *Torpedo*, which represents the first documented occurrence of an electric ray in Austria. This discovery significantly contributes to our knowledge of the spatial distribution and expands the palaeogeographic range of this genus to the Central Paratethys. The second recovered tooth from Sample 1 has been identified as *Squatina*, which is a common faunal element in different palaeoenvironments of the Central Paratethys. Both electric rays (*Torpedo*) and angel sharks (*Squatina*) are highly specialized benthic predators characterized by a predominantly demersal lifestyle (Capapé et al., 2007; Baremore et al., 2010; El Kamel-Moutalibi, 2013; Velázquez-Chiquito et al., 2021), which indicates habitable conditions for bottom-dwelling taxa of the depositional environment. Although *Torpedo* and *Squatina* are both bottom dwellers, their hunting behavior differs distinctly. *Torpedo* rays possess electrogenic organs, which they use to generate electric discharges to paralyze prey. In contrast, angel sharks are ambush predators that bury themselves in sand or mud, patiently waiting for their prey. Extant relatives of electric rays occupy different environments ranging from coral reefs of coastal regions down to the upper continental slope (De Carvalho et al., 2016 [in Last et al., 2016]), which is in accordance with the preferred habitat of angel sharks (Compagno et al., 2005).

The recovered teeth from the second sample (Sample 2) comprise the genera *Centrophorus*, *Scyliorhinus*, and *Mobula*. Teeth of gulper sharks (*Centrophorus*) and cat sharks (*Scyliorhinus*) are common in different palaeoenvironments of the Central Paratethys including the North Alpine Foreland Basin (e.g., Schultz, 2013). However, teeth of large pelagic devil rays (*Mobula*) are scarce in sediments of the North Alpine Foreland Basin (e.g., Cappetta, 2012; Schultz, 2013). Giant devil and manta rays exhibit a planktivorous feeding behavior, with a diet mainly composed of small crustaceans (Burgess et al., 2016; Bennett et al., 2017). Thus, all three identified elasmobranch genera, recovered from the second sample (Sample 2), exhibit different hunting strategies and feeding preferences. As mentioned, devil rays feed on planktonic organisms, which are sieved from the water using their branchial filter plates (White and Last, 2016). In contrast, gulper and catsharks hunt more actively using their perfectly adapted dentitions. Whereas gulper sharks (*Centrophorus*) possess dignathic heterodonty, with needle-like upper jaw teeth and overlapping, blade-like lower jaw teeth referred to as clutching-cutting dentition, catsharks (*Scyliorhinus*) exhibit only weak monognathic heterodonty, characterized by small, multicuspid teeth of a clutching-type dentition. Although both genera primarily feed on small invertebrates and bony fish, their hunting behavior differs significantly due to variations in their lifestyle. Whereas catsharks are opportunistic, benthic ambush predators, gulper sharks are active mesopelagic hunters that preferentially prey on larger fish and cephalopods. Considering the habitat range of modern gulper and catsharks, which occupy fairly deep environments (Compagno et al., 2005), teeth of both genera are typical deep-water indicators of a fossil assemblage.

Although a precise analysis of the environmental conditions is still pending, the extraordinarily well-preserved foraminifera from this section likely indicate an elevated sedimentation rate, potentially triggered by the mid-Langhian (Badenian) transgression.

6. Conclusion

The Heiligenstein section represents a rare snapshot of the trophic structure of a deep-marine realm of the North Alpine Foreland Basin during the middle Badenian (Langhian). In total, the sampled sediment enabled the documentation of five different elasmobranch taxa, including the first distinct record of *Torpedo* and *Mobula* from Austria. Specialized hunting strategies among these taxa further highlight their ecological diversity: *Mobula* filters plankton, *Torpedo* paralyzes prey with electric discharges, *Scyliorhinus* and *Squatina* ambush benthic prey, and *Centrophorus* actively hunts in the mesopelagic zone. The elasmobranch fauna is accompanied by typical deep-marine bony fish such as *Gadiculus argenteus* and *Diaphus austriacus*. The absence of bathydemersal fishes in the sediment points to low-oxygen (suboxic to dysoxic) bottom-water conditions that were likely unsuitable for many deep-sea fish. However, the presence of bottom-dwelling elasmobranchs like *Torpedo* and *Squatina* - which usually require more oxygen - suggests that conditions may have been more favorable at times. This is supported by foraminiferal data indicating oxic to suboxic environments. The mixed signals make this interpretation somewhat uncertain, and more detailed, fine-scale sampling is needed to better understand short-term changes in bottom-water conditions. Nevertheless, the combination of vertebrate and micropalaeontological data offers a rare insight into the palaeoecology of this deep-marine realm in the Central Paratethys Sea. However, due to the small number of recovered teeth further and more extensive bulk-sampling is necessary to reconstruct a more precise trophic structure of this deep-marine ecosystem.

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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.

Adnet S., Cappetta H., Guinot G., Notarbartolo di Sciara G., 2012. Evolutionary history of the devilrays (Chondrichthyes: Myliobatiformes) from fossil and morphological inference. Zoological Journal of the Linnean Society, 166, 132–159. https://doi.org/10.1111/j.1096-3642.2012.00844.x

Antunes M.T., Jonet S., Nascimento A., 1981. Vertébrés (crocodiliens, poissons) du Miocène marin de l'Argarve occidentale. Ciências da Terra (UNL), 6, 9–38.

Aschliman N.C., 2014. Interrelationships of the durophagous stingrays (Batoidea: Myliobatidae). Environmental Biology of Fishes, 97, 967–979. https://doi.org/10.1007/s10641-014-0261-8

Baremore I.E., Murie D.J., Carlson J.K., 2010 Seasonal and size-related differences in diet of the Atlantic angel shark *Squatina dumeril* in the northeastern Gulf of Mexico. Aquatic Biology, 8, 125–136. https://doi.org/10.3354/ab00214

Barthelt D., Fejfar O., Pfeil F.H., Unger E., 1991. Notizen zu einem Profil der Selachier-Fundstelle Walbertsweiler im Bereich der miozänen Oberen Meeresmolasse Süddeutschlands. Münchner Geowissenschaftliche Abhandlungen, Reihe A, Geologie und Paläontologie, 19, 195–208.

Bennett M.B., Coman F.F., Townsend K.A., Couturier L.I.E., Jaine F.R.A., Richardson A.J., 2017. A historical and contemporary consideration of the diet of the reef manta ray (*Manta alfredi*) from the Great Barrier Reef, Australia. Marine and Freshwater Research, 68/5, 993–997. https://doi.org/10.1071/MF16046

Bleeker P., 1859. Over eenige vischsoorten van de Kaap de Goede Hoop. Natuurkundig Tijdschrift voor Nederlandsch Indie, 21, 49–80.

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, 88/3, 885–909.

Bonaparte C.L., 1838. Selachorum tabula analytica. Nuovi Annali della Science Naturali Bologna, 1/2, 195–214.

Bonnaterre J.P., 1788. Ichthyologie. Tableau encyclopédique et méthodique des trois règnes de la nature. Paris, 215 p., pl. A-B + 1–100.

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

Brisswalter G., 2009. Inventaire des Élasmobranches (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.

Burgess K.B., Couturier L.I.E., Marshall A.D., Richardson A.J., Weeks S.J., Bennett M.B., 2016. *Manta birostris*, predator of the deep? Insight into the diet of the giant manta ray through stable isotope analysis. Royal Society Open Science, 3/11, 160717. https://doi.org/10.1098/rsos.160717

Capapé C., Crouzet S., Clément C., Vergne Y., Guélorget O., 2007. Diet of the marbled electric ray *Torpedo marmorata* (Chondrichthyes: Torpedinidae) off the Languedocian Coast (Southern France, Northern Mediterranean). Annales, Series Historia Naturalis, 17/1, 17–22.

Cappetta H., 1970. Les Sélaciens du Miocène de la région de Montpellier. Palaeovertebrata, Mémoire extraordinaire, 1970, 1–139.

Cappetta H., 1976. Sélaciens nouveaux du London Clay de l'Essex (Yprésien du Bassin de Londres). Geobios, 9/5, 551–575. https://doi.org/10.1016/S0016-6995(76)80024-1

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

Cappetta H., Granier J., Ledoux J.C., 1967. Deux faunes de sélaciens du Miocène méditerranéen de France et leur signification bathymétrique. Compte Rendu sommaire des Séances de la Société Géologique de France, 7, 292–293.

Cappetta H., Stringer G.L., 2002. A new batoid genus (Neoselachii: Myliobatiformes) from the Yazoo Clay (Upper Eocène) of Louisiana, U.S.A. Tertiary Research, 21/1–4, 51–56.

Cicha I., Rögl F., Rupp C., Čtyroká J. with the collaboration of the members of the "Working group on the foraminifera of the Central Paratethys", 1998. Oligocene-Miocene foraminifera of the Central Paratethys. Abhandlungen der Senckenbergischen Naturforschenden Gesellschaft, 549, 1–325. Frankfurt am Main, Waldemar Kramer.

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.

Compagno L.J.V., 1973. Interrelationships of living elasmobranchs. Zoological Journal of the Linnean Society, 53, 15–61.

Compagno L.J.V., 1977. Phyletic relationships of living sharks and rays. American Zoologist, 17/2, 303–322.

Compagno L.J.V., Dando M., Fowler S., 2005. Sharks of the World. Princeton University Press, p. 496.

Cope E.D., 1869. Descriptions of some extinct fishes previously unknown. Proceedings of the Boston Society of Natural History, 12, 310–317.

De Blainville H.M.D., 1816. Prodrome d'une nouvelle distribution systématique du règne animal. Bulletin des Sciences, par la Société Philomatique de Paris, 8, 105–124.

De Buen F., 1926. Catalogo ictiologico del Mediterraneo Español y de Marruecos, recopilando lo publicado sobrepeces de las costas mediterraneas y proximas del Atlantico (Mar de España). Resultados de las ampafias Realizadas por Acuerdos Internacionales. Instituto Español de Oceanografia, 2, 1–221.

De Carvalho M.R., Last P.R., Séret B., 2016. Torpedo rays, Family Torpedinidae. In Last P.R., White W.T., Carvalho M.R. de, Séret B., Stehmann M.F.W, and Naylor G.J.P(Eds.) Rays of the World. CSIRO Publishing, Melbourne: 184–203.

Dumeril A.H.A., 1805. Zoologie analytique, ou méthode naturelle de classification des animaux. Paris, 1–344.

El Kamel-Moutalibi O., Mnasri N., Boumaiza M., Reynaud C., Capapé C., 2013. Diet of common torpedo *Torpedo torpedo* (Chondrichthyes:

Torpedinidae) from the Lagoon of Bizerte (northeastern Tunisia, central Mediterranean). Cahiers de Biologie Marine, 54/2, 209–220.

Esri, 2009. Basemap. World Shaded Relief. https://services.arcgisonline.com/ArcGIS/rest/services/World_Shaded_Relief/MapServer

Feichtinger I., Pollerspöck J., Harzhauser M., 2020. A new species of the enigmatic shark genus *Nanocetorhinus* (Chondrichthyes) from the Oligocene of Austria with palaeoceanographic implications. Austrian Journal of Earth Sciences, 113/2, 229–236. https://doi.org/10.17738/ajes.2020.0014

Feichtinger I., Pollerspöck J., Harzhauser M., Auer G., Ćorić S., Kranner M., Guinot G., 2023. Shifts in composition of northern Tethyan elasmobranch assemblages during the last millennia of the Cretaceous. Cretaceous Research, 142, 105414. https://doi.org/10.1016/j.cretres.2022.105414

Feichtinger I., Pollerspöck J., Harzhauser M., Auer G., Ćorić S., Kranner M., Beaury B., Guinot G., 2024. Earliest Danian outer neritic elasmobranch assemblages reveal an environmentally controlled faunal turnover at the Cretaceous - Palaeogene boundary in the northern Tethyan Realm (Austria). Papers in Palaeontology, 10/1, Article e1547. https://doi.org/10.1002/spp2.1547

Feichtinger I., Beaury B., S. Ćorić, Straube N., Harzhauser M., Kranner M., Auer G., Guinot G., Pollerspöck J. 2025. A new deep-marine elasmobranch fauna from the Late Cretaceous of Bergen (Bavaria, Germany) dominated by squaliform sharks. Paläontologische Zeitschrift, 99, 71–93. https://doi.org/ 10.1007/s12542-024-00713-w

Fialho P., Balbino A., Antues M.T., 2019. Langhian rays (Chondrichthyes, Batomorphii) from Brielas, Lower Tagus Basin, Portugal. Geologica Acta, 17/7, 1–16. https://doi.org/10.1344/GeologicaActa2019.17.7

Froese R., Pauly D., 2025. FishBase. World Wide Web electronic publication. www.fishbase.org. Version (02/2024). Electronic version accessed March 2025.

Garman S., 1913. The Plagiostomia (Sharks, Skates and Rays). Memoirs of the Museum of Comparative Zoology at Harvard College, 36, 1–528.

Gebhardt H., Schenk B., Enge A., Ćorić S., Ranftl E.-M., Heinz P., 2023. The Lower - Middle Miocene transition in the Krems Embayment (Central Paratethys, Lower Austria): a multistratigraphic approach and the role of the Diendorf-Boskovice Fault System. Austrian Journal of Earth Sciences, 116, 117–134. https://doi.org/10.17738/ajes.2023.0006

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, 7/32, 367–408.

Guichenot, A., 1850. Histoire naturelle des reptiles et des poissons. In: Exploration scientifique de l'Algérie pendant les années 1840, 1841, 1842. Zoologie, Paris.

Harzhauser M., Piller W.E., 2007. Benchmark data of a changing sea - palaeogeography, palaeobiogeography and events in the Central Paratethys during the Miocene. Palaeogeography, Palaeoclimatology, Palaeoecology, 253, 8–31. https://doi.org/10.1016/j.palaeo.2007.03.031

Harzhauser M., Daxner-Höck G., Boon-Kristkoiz E., Ćorić S., Mandic O., Miklas-Tempfer P., Roetzel R., Rögl F., Schultz O., Spezzaferri S., Ziegler R., Zorn I., 2003. Palaeoecology and biostratigraphy of the section Mühlbach (Gaindorf Formation, lower Middle Miocene, Lower Badenian, Austria). Annalen des Naturhistorischen Museums in Wien, Serie A, 104A, 323–334.

Harzhauser M., Kranner M., Mandic O., Strauss P., Siedl W., Piller W.E., 2020. Miocene lithostratigraphy of the northern and central Vienna Basin (Austria). Austrian Journal of Earth Sciences, 113, 169–200. https://doi.org/10.17738/ajes.2020.0011

Harzhauser M., Landau B., Mandic O., Neubauer T., 2024a. The Central Paratethys Sea – rise and demise of a Miocene European marine biodiversity hotspot. Scientific Reports, 14, 16288. https://doi.org/10.1038/s41598-024-67370-6

Harzhauser M., Kranner M., Siedl W., Conradi F., Piller W.E., 2024b. The Neogene of the Vienna Basin – a synthesis. In: Tari G.C., Kitchka A., Krézsek C., Lučić D., Markič M., Radivojević D., Sachsenhofer R.F., Šujan M. (Eds) The Miocene Extensional Pannonian Superbasin, Volume 1: Regional Geology. Geological Society, London, Special Publications, 554. https://doi.org/10.1144/SP554-2023-168

Hayward B.W., Le Coze F., Vachard D., Gross O., 2025. World Foraminifera Database. (Last Accessed at https://www.marinespecies.org/foraminifera on 2025-03-14).

Hoedemakers K., Dufraing L., 2015. Elasmobranchii in de ontsluiting aan de luchthaven te Borsbeek (prov. Antwerpen, België) Afzettingen WTKG, 36/1, 12–19.

Höltke O., Maxwell E.E., Pollerspöck J., Rasser M.W., 2022. The shark and ray fauna of the Upper Marine Molasse (Lower Miocene) of Rengetsweiler (Baden-Württemberg, SW Germany). Neues Jahrbuch für Geologie und Paläontologie, Abhandlungen, 303/1, 89–122. https://doi.org/10.1127/njgpa/2022/1038

Jonet S., 1976. Notes d'ichthyologie miocène. VII. La famille des Mobulidae au Portugal. Boletim da Sociedade Geológica de Portugal, 20/1–2, 53–64.

Keyes I.W., 1984. New records of fossil elasmobranch genera *Megascyliorhinus*, *Centrophorus,* and *Dalatias* (Order Selachii) in New Zealand. New Zealand Journal of Geology and Geophysics, 27/2, 203–216.

Koken E. 1891. Neue Untersuchungen an tertiären Fisch-Otolithen II. Zeitschrift der deutschen geologischen Gesellschaft, 43, 77–170.

Kranner M., Harzhauser M., Mandic O., Strauss P., Siedl W., Piller W.E., 2021. Early and middle Miocene paleobathymetry of the Vienna Basin (Austria). Marine and Petroleum Geology, 132, 105187. https://doi.org/10.1016/j.marpetgeo.2021.105187

Leder R.M., 2015. Fossile Reste von Selachiern und Chimaeren aus dem Muschelschluff und Phosphoritknollenhorizont von Zwenkau bei Leipzig. [Fossil remains of selachiens and chimaera from the Muschelschluff and Phosphoritknollenhorizont of Zwenkau near Leipzig]. Geologica Saxonica, 61/1, 73–90.

Lirer F., Foresi L.M., Iaccarino S.M., Salvatorini G., Turco E., Cosentino C., Sierro F.J., Caruso A., 2019. Mediterranean Neogene planktonic foraminifer biozonation and biochronology. Earth Science Reviews, 196, 102869. https://doi.org/10.1016/j.earscirev.2019.05.013

Mandic O., Harzhauser M., Spezzaferri S., Zuschin M., 2002. The paleoenvironment of an early Middle Miocene Paratethys sequence in NE Austria with special emphasis on paleoecology of mollusks and foraminifera. Geobios, 35 (Supplement 1), 193–206. https://doi.org/10.1016/S0016-6995(02)00059-1

Marramà G., Schultz O., Kriwet J., 2019. A new Miocene skate from the Central Paratethys (Upper Austria): the first unambiguous skeletal record for the Rajiformes (Chondrichthyes: Batomorphii). Journal of Systematic Palaeontology, 17/11, 937–960. https://doi.org/10.1080/14772019.2018.1486336

Müller J., Henle F.G.J., 1837. Gattungen der Haifische und Rochen nach einer von ihm mit Hrn. Henle unternommenen gemeinschaftlichen Arbeit über die Naturgeschichte der Knorpelfische. Berichte der Königlichen Preussischen Akademie der Wissenschaften zu Berlin, 1837, 111–118.

Murray J., 2006. Ecology and Applications of Benthic Foraminifera. Cambridge University Press, Cambridge, UK, 426 pp.

Naylor G., Caira J., Jensen K., Rosana K., White W., Last P., 2012. 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, 1–262.

Noubhani A., Cappetta H., 1997. Les Orectolobiformes, Carcharhiniformes et Myliobatiformes (Elasmobranchii, Neoselachii) des Bassins à phosphate du Maroc (Maastrichtien-Lutétien basal). Systématique, biostratigraphie, évolution et dynamique des faunes. Palaeo Ichthyologica, 8, 1–327.

Paig-Tran E.W., Kleinteich T., Summers A.P., 2013. The filter pads and filtration mechanisms of the devil rays: Variation at macro and microscopic scales. Journal of Morphology, 274, 1026–1043. https://doi.org/10.1002/jmor.20160

Papp A., Schmid M.E., 1985. The Fossil Foraminifera of the Tertiary Basin of Vienna. Revision of the monograph by Alcide d'Orbigny (1846). Abhandlungen der Geologischen Bundesanstalt 37, 1–311.

Pfeil F.H., 1981. Eine nektonische Fischfauna aus dem unteroligozänen Schönecker Fischschiefer des Galon-Grabens in Oberbayern. Geologica Bavarica, 82, 357–388.

Pfeil F.H., 1984. Wallern - ein bedeutender Mosaikstein für die Evolution der Fische. Festschrift zur Markterhebung der Gemeinde Wallern, 1984, 6–8.

Pollerspöck J., Straube N., 2017. A new deep-sea elasmobranch fauna from the Central Paratethys (Neuhofener Beds, Mitterdorf, near Passau, Germany, Early Miocene, Middle Burdigalian). Zitteliana, 90, 27–53. https://doi.org/10.5282/ubm/epub.40476

Pollerspöck J., Straube N., 2021. Phylogenetic placement and description of an extinct genus and species of kitefin shark based on tooth fossils (Squaliformes: Dalatiidae). Journal of Systematic Palaeontology, 19/15, 1083–1096. https://doi.org/10.1080/14772019.2021.2012537

Pollerspöck J., Straube N., 2025. www.shark-references.com, World Wide Web electronic publication, Version 2025.

Pollerspöck J., Unger E., 2024. „Beiträge zur Kenntniss der fossilen Fische aus der Molasse von Baltringen" – Revision zum 200. Geburtstag von Pfarrer Josef Probst. Teil Hayfische (Selachoidei A. Günther) (Schluss) (Probst 1879). Jahreshefte der Gesellschaft für Naturkunde Württemberg, 180, 401–500.

Pollerspöck J., Flammensbeck C.K., Straube N., 2018. *Palaeocentroscymnus* (Chondrichthyes: Somniosidae), a new sleeper shark genus from Miocene deposits of Austria (Europe). Paläontologische Zeitschrift, 92/3, 443–456. https://doi.org/10.1007/s12542-017-0398-9

Pollerspöck J., Güthner T., Straube N., 2022. Re-evaluation of the Lower Miocene (Burdigalian, Ottnangian) elasmobranch fauna (Elasmobranchii, Neoselachii) from Upper Austria (Allerding, near Schärding, Austria) with comments on the paleogeographic distribution of the recorded squaliform sharks. Annalen des Naturhistorischen Museums in Wien, Series A, 122, 87–163.

Poortvliet M., Olsen J.L., Croll D.A., Bernardi G., Newton K., Kollias S., O'Sullivan J., Fernando D., Stevens G., Galván Magaña F., Séret B., Wintner S., Hoarau G., 2015. A dated molecular phylogeny of manta and devil rays (Mobulidae) based on mitogenome and nuclear sequences. Molecular Phylogenetics and Evolution, 83, 72–85. https://doi.org/10.1016/j.ympev.2014.10.012

Popov S.V., Rögl F., Rozanov A.Y., Steininger F.F., Shcherba I.G., Kovac M., 2004. Lithological-Paleogeographic maps of the Paratethys. 10 maps Late Eocene to Pliocene. Courier Forschungsinstitut Senckenberg, 250, 1–46.

Rafinesque C.S., 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 involves fishes, pp. [i–iv] 3–69 [70 blank], Part 2 with slightly different title, pp. ia–iva + 71–105 [106 blank]).

Reinecke T., 2015. Batoids (Rajiformes, Torpediniformes, Myliobatiformes) from the Sülstorf Beds (Chattian, Late Oligocene) of Mecklenburg, northeastern Germany: a revision and description of three new species. Palaeovertebrata, 39, Article e2.

Reinecke T., Radwański A., 2015. Fossil sharks and batoids from the Korytnica-clays, early Badenian (Langhian, Middle Miocene), Fore-Carpathian basin, central Poland – a revision and updated record. Palaeontos, 28, 1–32.

Reinecke T., Moths H., Grant A., Breitkreuz H., 2005. Die Elasmobranchier des norddeutschen Chattiums, insbesondere des Sternberger Gesteins (Eochattium, Oligozän). Palaeontos, 8, 1–135.

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, 1–127.

Reinecke T., Mollen F.H., Gijsen B., D'haeze B., Hoedemakers K., 2024. Batomorphs (Elasmobranchii: Rhinopristiformes, Rajiformes, Torpediniformes, Myliobatiformes) of the middle to late Ypresian, early Eocene, in the Anglo-Belgian Basin (south-western North Sea Basin) – a review and description of new taxa. Palaeontos, 35, 1–172.

Robison B.H., Sherlock R.E., Reisenbichler K.R., McGill P.R., 2020. Running the gauntlet: assessing the threats to vertical migrators. Frontiers in Marine Science, 7, 64. https://doi.org/10.3389/fmars.2020.00064

Rögl F., 1998. Palaeogeographic considerations for Mediterranean and Paratethys Seaways (Oligocene to Miocene). Annalen des Naturhistorischen Museums Wien, Serie A, 99, 279–310.

Rögl F., 1999. Mediterranean and Paratethys. Facts and hypotheses of an Oligocene to Miocene paleogeography (short overview). Geologica Carpathica, 50, 339–349.

Rögl F., Spezzaferri S., 2003. Foraminifera paleoecology and biostratigraphy of the Mühlbach section (Gaindorf Formation, Lower Badenian), Lower Austria. Annalen des Naturhistorischen Museums in Wien, Serie A, 104, 23–75.

Schultz O., 1977. Elasmobranch and teleost fish remains from the Koryntica Clays (Middle Miocene; Holy Cross Mountains, Central Poland). Acta Geologica Polonica, 27/2, 201–209.

Schultz O., 2013. Pisces. In Piller W.E. (ed.) Catalogus Fossilium Austriae, Band 3 - Verlag der Österreichischen Akademie der Wissenschaften, Wien, ISBN13: 978-3-7001-7238-3, 576 pp.

Schwarzhans W., Radwańska U., 2022. A review of lanternfish otoliths (Myctophidae, Teleostei) of the early Badenian (Langhian, middle Miocene) from Bęczyn, southern Poland. Cainozoic Research, 22, 9–24.

Schwarzhans W., Radwańska U., 2025 (in press). The hidden fish diversity from the Langhian (Middle Miocene, Badenian) of the Central Paratethys – Tales from an extinct biodiversity hotspot. Contributions from the Museum of Paleontology, University of Michigan.

Šegvić B., Lukács R., Mandic O., Strauss P., Badurina L., Guillong M., Harzhauser M., 2022. U-Pb zircon age and mineralogy of St. Georgen halloysite tuff shed light on the timing of the middle Badenian transgression, ash dispersal and paleoenvironmental conditions in the central Vienna Basin, Austria, Journal of the Geological Society, 180/2, jgs2022-106. https://doi.org/10.1144/jgs2022-106

Siedl W., Strauss P., Sachsenhofer R.F., Harzhauser M., Kuffner T., Kranner M., 2020. Revised Badenian (middle Miocene) depositional systems of the Austrian Vienna Basin based on a new sequence stratigraphic framework. Austrian Journal of Earth Sciences, 113/1, 87–110. https://doi.org/10.17738/ajes.2020.0006

Smith R., 1999. Elasmobranches nouveaux de la transition Paléocène-Eocène de Dormaal (Belgique). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, 69, 173–185.

Soares K.D.A., de Carvalho M.R., 2019. The catshark genus *Scyliorhinus* (Chondrichthyes: Carcharhiniformes: Scyliorhinidae): taxonomy, morphology and distribution. Zootaxa, 4601/1, 001–147. https://doi.org/10.11646/zootaxa.4601.1.1

Spezzaferri S., 2004. Foraminiferal paleoecology and biostratigraphy of the Grund Formation (Molasse Basin, Lower Austria). Geologica Carpathica, 55/2, 155–164.

Suzuki H., 2012. A fossil deep-sea shark assemblage from the Middle Miocene, Ueda City, Nagano Prefecture, central Japan. [in japanese] Earth Science (Chikyu Kagaku), 66(2), 47–61.

Szabó M., Kocsis L., Tóth E., Szabó P., Németh T., Sebe K., 2022. Chondrichthyan (Holocephali, Squalomorphii and Batomorphii) remains from the Badenian of southern Hungary (Tekeres, Mecsek Mountains): the first deepwater cartilaginous fishes from the Middle Miocene of the Central Paratethys. Papers in Palaeontology, 8/6, Article e1471. https://doi.org/10.1002/spp2.1471

Tomanová Petrová P., Švábenická L., 2007. Lower Badenian biostratigraphy and paleoecology: a case study from the Carpathian Foredeep (Czech Republic). Geologica Carpathica, 58/4, 333–352.

Underwood C.J., 2004. Environmental controls on the distribution of neoselachian sharks and rays within the British Bathonian (Middle Jurassic). Palaeogeography, Palaeoclimatology, Palaeoecology 203/1–2, 107e126. https://doi.org/10.1016/S0031-0182(03)00663-1

Underwood C.J., Mitchell S.F., 1999. Albian and Cenomanian (Cretaceous) selachian faunas from north east England. Special Papers in Palaeontology, 60, 9–56.

Underwood C.J., Schlögl J., 2013. Deep-water chondrichthyans from the Early Miocene of the Vienna Basin (Central Paratethys, Slovakia). Acta Palaeontologica Polonica, 58/3, 487–509. https://doi.org/10.4202/app.2011.0101

Velázquez-Chiquito V.M., Méndez-Macías J.S., Estupiñán-Montaño C., Galván-Magaña F., 2021. Dietary ecology and trophic level of adults of the Chilean angel shark *Squatina armata* Philippi 1887 in the Central-Eastern Pacific Ocean. Regional Studies in Marine Science, 43, 101675. https://doi.org/10.1016/j.rsma.2021.101675

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, 130/2, 241–258. https://doi.org/10.1007/s13358-011-0025-4

Von der Hocht F., 1986. Stand der Untersuchungen an der Chondrichthyes-Fauna des nordwestdeutschen Tertiärs. Beiträge zur regionalen Geologie der Erde, 18, 503–509.

Wade B.S., Pearson P.N., Berggren W.A., Pälike H., 2011. Review and revision of Cenozoic tropical planktonic foraminiferal biostratigraphy and calibration to the geomagnetic polarity and astronomical time scale. Earth-Science Reviews, 104, 111–142. https://doi.org/10.1016/j.earscirev.2010.09.003

White W.T., Last P.R., 2016. Eagle rays, Family Myliobatidae. In Last P.R., White W.T., Carvalho M.R. de, Séret B., Stehmann M.F.W and Naylor G.J.P. (Eds) Rays of the World. CSIRO Publishing, Melbourne, 706–725.

White W.T., Ebert D.A., Naylor G.J.P., Ho H.-C., Clerkin P.J., Veríssimo A., Cotton C.F., 2013. Revision of the genus *Centrophorus* (Squaliformes: Centrophoridae): Part 1 – Redescription of *Centrophorus granulosus* (Bloch and Schneider), a senior synonym of *C. acus* Garman and *C. niaukang* Teng. Zootaxa, 3752, 35–72. https://doi.org/10.11646/zootaxa.3752.1.5

White W.T., Ebert D.A., Naylor G.J.P., 2017. Revision of the genus *Centrophorus* (Squaliformes: Centrophoridae): Part 2 – Description of two new species of *Centrophorus* and clarification of the status of *Centrophorus lusitanicus* Barbosa du Bocage and de Brito Capello, 1864. Zootaxa, 4344/1, 86–114. https://doi.org/10.11646/zootaxa.4344.1.3

White W.T., Corrigan S., Yang L., Henderson A.C., Bazinet A.L., Swofford D.L., Naylor G.J.P., 2018. Phylogeny of the manta and devilrays (Chondrichthyes: Mobulidae), with an updated taxonomic arrangement for the family. Zoological Journal of the Linnean Society, 182/1, 50–75. https://doi.org/10.1093/zoolinnean/zlx018

White W.T., Guallart J., Ebert D.A., Naylor G.J.P., Mo A.V., Cotton C.F., Harris M., Serena F., Iglésias S.P., 2022. Revision of the genus *Centrophorus* (Squaliformes: Centrophoridae): Part 3 – Redescription of *Centrophorus uyato* (Rafinesque) with a discussion of its complicated nomenclatural history. Zootaxa, 5155/1, 1–51. https://doi.org/10.11646/zootaxa.5155.1.1

Young J.R., Wade B.S., Huber B.T. (Eds), 2017. pforams@mikrotax. (Last Accessed at https://www.mikrotax.org/pforams/ on 2025-03-14).

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