New records and specimens to the Badenian fish fauna of Nyirád (Hungary), including the first report of *Galeocerdo cuvier* from the Middle Miocene of Europe

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Abstract – The Nyirád I. outcrop is extremely rich in fossils of marine vertebrates, including chondrichthyans, osteichthyans and marine mammals. Rarely, remains of terrestrial vertebrates are also found. The present paper adds important data to the vertebrate faunal list of the two Badenian formations of the outcrop, namely the Pusztamiske and Leitha Limestone Formations. Altogether, remains of 38 chondrichthyan and 13 osteichthyan taxa, cetaceans and two terrestrial tetrapods have been documented from the outcrop so far. The most important new result is the occurrence of teeth most similar to those of the tiger shark *Galeocerdo cuvier*. This data provides the first evidence from the Badenian of the Central Paratethys for the co-existence of two species of the genus *Galeocerdo* in the same habitat. With 141 figures and 1 table.

Key words – Central Paratethys, Chondrichthyes, *Isistius*, *Keasius*, *Mobula*, Osteichthyes

INTRODUCTION

Re-evaluation of Badenian (Middle Miocene) marine vertebrates of the Pannonian Basin has restarted in the 2010s. Materials of numerous localities throughout Hungary are still waiting for a revision; however, the fossil-rich Cenozoic beds of the Devecser–Nyirád Basin attracted scientific attention in particular.
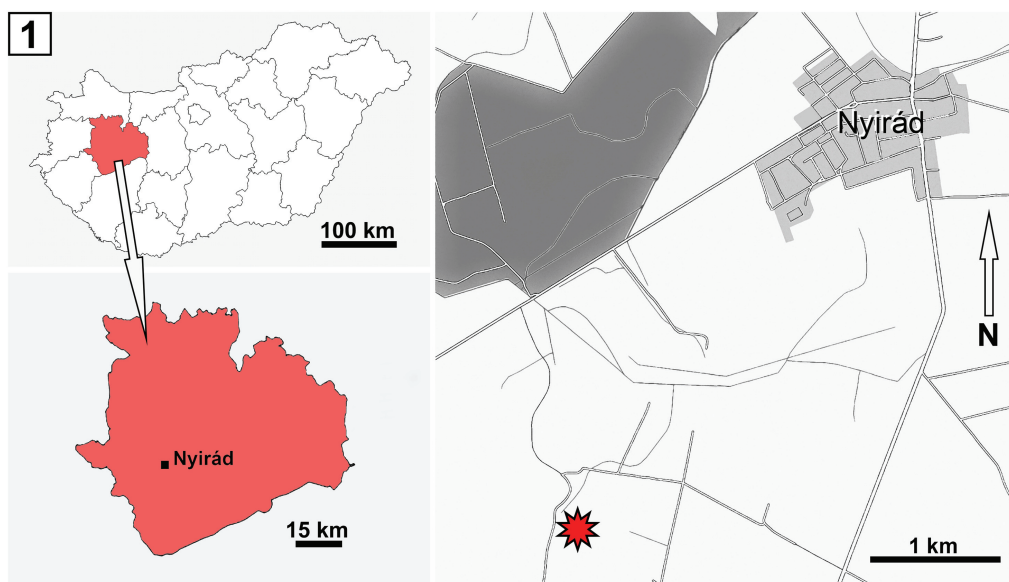
The Devecser–Nyirád Basin was investigated by several authors from geological (Noszky 1938; Kovács 1951, 1952; Selmeczi 1989), tectonical

(Ottlik 1959), and palaeontological points of view (Csepreghy-Meznerics 1958; Bohn-Havas & Selmeczi 1999; Kókay 1967, 1985, 1992, 1996; Müller 1984; Dulai 2005, 2007; Selmeczi 2004; Hyžný & Müller 2010). Systematic collecting trips for Middle Miocene marine vertebrate remains started in an outcrop nearby Nyirád in 2012, however, by that time this locality had long been known by amateur collectors. The first report on fish remains discovered in the Nyirád I. outcrop was published by Szabó & Kocsis (2016). This was followed by Dulai (2017), who reported the occurrence of Discinidae brachiopods from the same outcrop. Later on, more details have been added to the vertebrate faunal list (Szabó & Kocsis 2020), together with remains found in a neighbouring outcrop, exposing the same fossiliferous beds.

The present paper deal with fish remains recently discovered in the Nyirád I. outcrop, and puts them in a wider context regarding Middle Miocene marine vertebrate faunas of the Central Paratethys.

GEOLOGICAL BACKGROUND

The Nyirád I. outcrop is a gravel pit, which is located ~3 km southwest from the village of Nyirád in western Hungary (Fig. 1). Two fossil-rich lithostratigraphic units are documented from the pit: the Kolontár Member of the Pusztamiske Formation, with a gradual transition upwards into the overlying Pécsszabolcs Member of the Leitha Limestone Formation (see Szabó & Kocsis

Fig. 1. The location of the Nyirád I. outcrop within Hungary, Veszprém county and nearby the village of Nyirád

2020, text-fig. 1B). The former one is extremely rich in marine vertebrate fossils and relatively poor in invertebrate remains, while the latter formation yielded a diverse invertebrate assemblage and only a few vertebrate fossils (Szabó & Kocsis 2016, 2020).

The strata of the Pusztamiske Formation consist of Lower Badenian marine sediment, which belongs to the NN5 nannozone (Kercsmár *et al.* 2015). The formation is dominantly made up of coarse- and medium-grained, calc-cemented, grey, greenish grey sandstone. Coarse-grained abrasive gravel and conglomerate have been deposited at the base of the formation, while in its upper section siltstone and marl intercalations are more frequent. The formation is known in the western–south-western part of the Bakony Mountains (= the Devecser–Nyirád sedimentary basin and the vicinity of Sümeg), its average thickness is 50 m (Kercsmár *et al.* 2015). For further details on the geology of the outcrop and the wider area see Selmeczi (1996), Selmeczi *et al.* (2002), Kercsmár *et al.* (2015) and references therein.
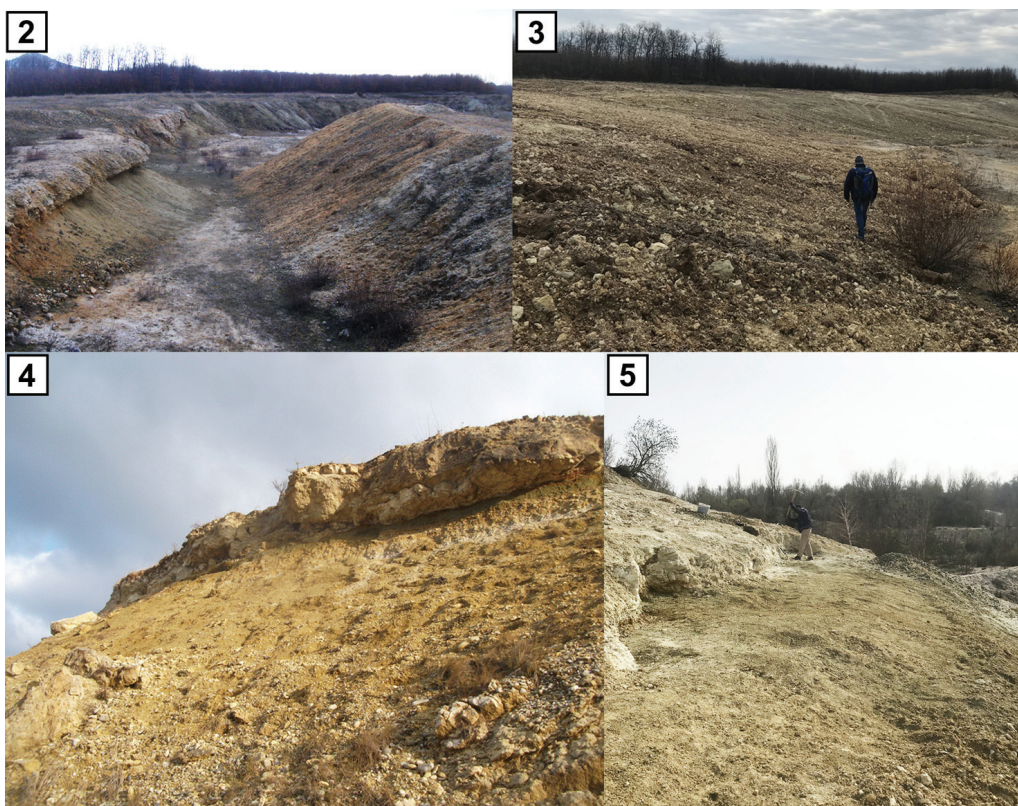
The eastern wall of the Nyirád gravel pit (Nyirád I. outcrop in Szabó & Kocsis 2020) went through a reclamation and restoration process during the winter of 2019 (Figs 2–3). This is gratifying, because overlying rocks of the Leitha Limestone meant a serious risk of accident (Fig. 4). Opening new sections after the restoration required serious efforts, but thanks to the indefatigable work of amateur collectors Péter Gulyás and Zoltán Békési, the two underlying fossiliferous formations are partly exposed again (Fig. 5).

MATERIAL AND METHODS

All the remains of the Pusztamiske Formation described here have been collected after the winter of 2019 at the aforementioned, lately opened short sections along the eastern boundary of the Nyirád I. outcrop.

Since the results of Szabó & Kocsis (2020) were published, more than 1,000 kg of sediment from the uppermost, glauconite-rich level of the Pusztamiske Formation have been screen-washed. The microvertebrate remains were sorted under stereomicroscope. Pictures of small specimens were taken with a QImaging MP5.0 digital microscope camera under a Nikon LV 100 polarized light microscope, and processed with Image Pro Insight 8.0 software. For scanning electron microscope imaging we used a Jeol JSR-IT500 HR apparatus (University of Pécs, Szentágothai Research Centre; Pécs).

The majority of the vertebrate remains are housed in the private collections of Péter Gulyás and Zoltán Békési. A few remains were donated to the Hungarian Natural History Museum (HNHM; Budapest, Hungary). Abbreviations "PG"
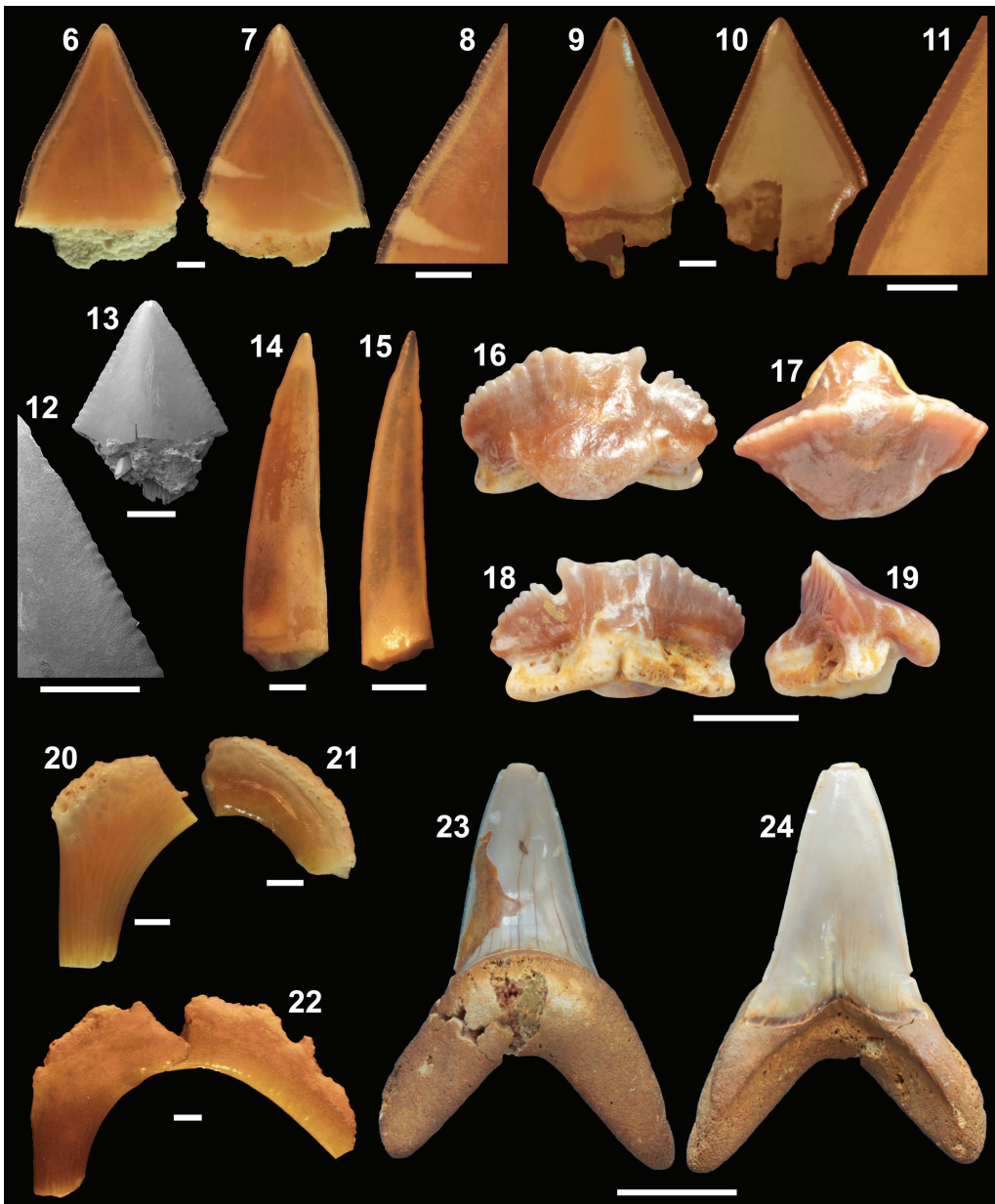
Figs 2–5. The Nyirád I. outcrop. – **Fig. 2.** The eastern wall of the outcrop in the winter of 2017. – **Fig. 3.** The eastern wall of the outcrop in the winter of 2019. – **Fig. 4.** The southern edge of the eastern wall of the outcrop in the winter of 2016. – **Fig. 5.** The southern edge of the eastern wall of the outcrop in the summer of 2021. (Photos by the first author)

and "ZB" refer to the specimens in the private collections of Péter Gulyás and Zoltán Békési, respectively.

Identification of the chondricthyan remains is based on CAPPETTA (2012), BOR *et al.* (2012), and REINECKE *et al.* (2011, 2014), while that of the osteichthyan remains is based on SCHULTZ (2013).

PALAEONTOLOGY

Pusztamiske Formation – Various, locally new chondrichthyan and osteichthyan taxa have been discovered in the uppermost, glauconite-rich level of the Pusztamiske Formation. *Isistius triangulus* is represented by rootless teeth with triangular crown and smooth to finely serrated cutting edges (Figs 6–13). The Nyirád specimens can be distinguished from the teeth of the Paleocene–Eocene species, *I. trituratus*, and the two extant species, *I. brasiliensis* and *I. plutodus*, as

Figs 6–13. *Isistius triangulus* teeth. – **Figs 6–9.** PG coll. – **Figs 10–11.** ZB coll. – **Figs 12–13.** HNHM VER 2023.1.; labial and lingual aspects are unidentifiable. – **Figs 8**, **11** and **12.** Close-up image of the cutting edges. – **Figs 14–15.** *Pristiophorus* sp. rostral teeth – **Fig. 14.** HNHM VER 2023.2. – **Fig. 15.** PG coll.; aspects are unidentifiable. – **Figs 16–19.** *Ginglymostoma* sp., ZB coll. – **Fig. 16.** Labial view. – **Fig. 17.** Apical view. – **Fig. 18.** Lingual view. – **Fig. 19.** Profile view. – **Figs 20–22.** *Keasius* sp. gill rakers. – **Fig. 20.** HNHM VER 2023.3. – **Fig. 21.** HNHM VER 2023.4. Specimens of Figs 20 and 21 have been found separately and they do not belong together. – **Fig. 22.** ZB coll. – **Fig. 23.** *Anotodus retroflexus* tooth, ZB coll., lingual view. – **Fig. 24.** Labial view. Private collection specimens: Figs 6–11, 15–24.

Scale bars: Figs 6–11, 20–22: 0.6 mm; Figs 12, 13: 0.5 mm; Figs 16–19: 3 mm; Figs 23, 24: 10 mm
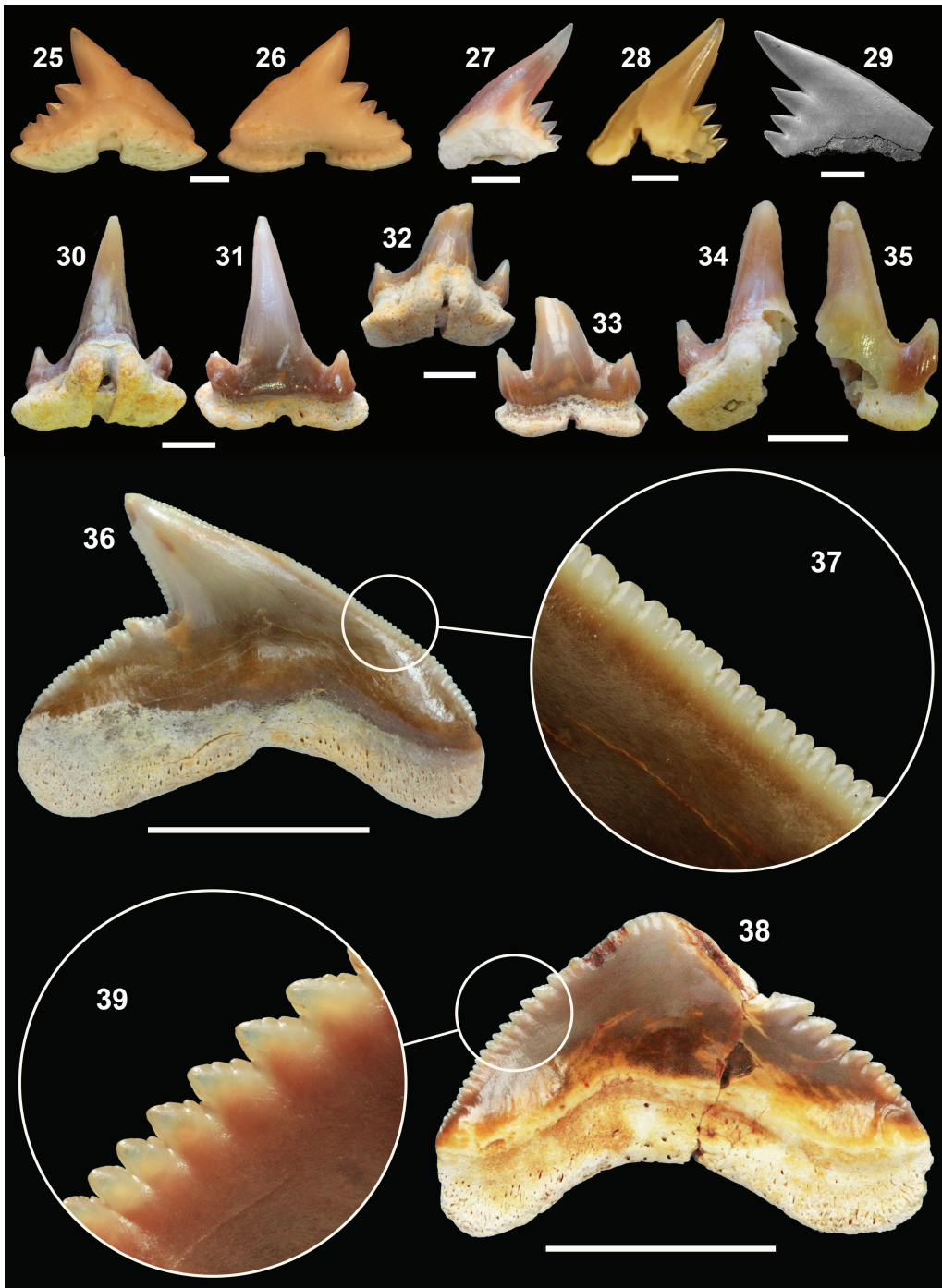
the teeth of these species have smooth cutting edges (Iserbyt & De Schutter 2012; Carlsen & Cuny 2014; de Figueiredo Petean & de Carvalho 2018). *Pristiophorus* sp. is represented by two partial rostral teeth (Figs 14–15). Since specific identification of *Pristiophorus* remains is mainly based on oral teeth, and morphology of *Pristriophorus* rostral teeth can be very variable within the same individual, the Nyirád specimens are identified only as *Pristiophorus* sp. One tooth is referable to Ginglymostomatidae (Figs 16–19). The preserved portions of the crown draw a symmetrical outline in labial and lingual views, the apron is broad and does not reach the level of the base (see Fig. 19). These features are characteristic for genus *Ginglymostoma* (Cappetta 2012). Fragmentary gill rakers, referred to as *Keasius* sp., have been also discovered (Figs 20–22). The Nyirád cetorhinid material seems to show affinities with species *K. septemtrionalis* (based on the delicate gill raker remains, with sickle-shaped raker base; see Reinecke *et al.* 2015), but remains are too poorly preserved for specific determination. A large tooth is referable to *Anotodus retroflexus* (formerly often published as *Isurus retroflexus*) by its smooth and sharp cutting edges, the broad dental band marking at the lingual crown-root boundary, and the strongly bifurcated root (Bor *et al.* 2012; Reinecke *et al.* 2011; see Figs 23–24).

Small teeth showing the characteristics of the triakid *Galeorhinus goncalvesi* (Figs 25–26) and the hemigaleid *Chaenogaleus affinis* were also documented (Figs 27–29). Teeth assigned to *Galeorhinus goncalvesi* have a triangular main cusp followed by smaller distal cusplets decreasing in size distally, and the crown strongly overhangs the root at the labial crown base. The main cusp of teeth of *Chaenogaleus affinis* is elongate and slightly sinuous, followed by smaller triangular distal cusplets. Tooth remains of two scyliorhinid taxa, namely *Pachyscyllium dachiardii* (Figs 30–33) and *P. distans* (Figs 34–35) have been unearthed. Teeth of *P. dachiardii* have been distinguished from those of *P. distans* by their smooth labial crown base.
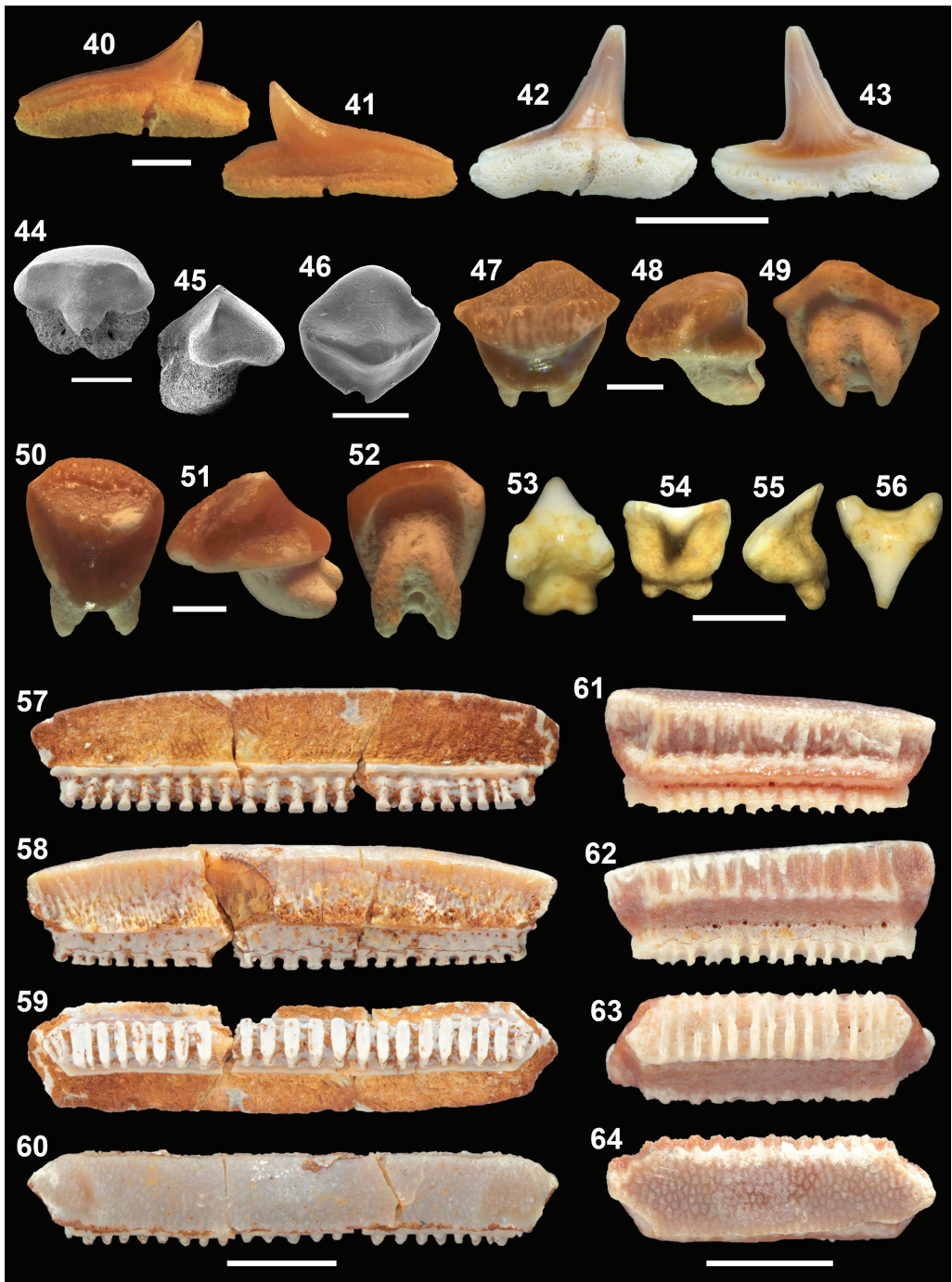
Galeocerdo aduncus, a tiger shark species common in the Neogene sediments of Europe, has been previously reported from Nyirád (Fig. 36). Teeth of this species have cutting edges with irregular, but relatively fine serrations without secondary serrations (Fig. 37). However, a few *Galeocerdo* teeth have been identified in the material (Fig. 38) which possesses cutting edges with coarse serrae bearing secondary serrations (Fig. 39). These teeth are also larger than those identified as *G. aduncus* and they are most similar to the teeth of the extant species, *G. cuvier*, which has a fossil record dating back to the Middle Miocene (Türtscher *et al.* 2021). These teeth are separable from those of *G. mayumbensis*, and other Miocene species of

Figs 25–26. *Galeorhinus goncalvesi* tooth, PG coll. – **Fig. 25.** Lingual view. – **Fig. 26.** Labial view. – **Figs 27–29.** *Chaenogaleus affinis* teeth, lingual view. – **Figs 27, 28.** ZB coll. – **Fig. 29.** HNHM VER 2023.5. – **Figs 30–33.** *Pachyscyllium dachiardii* teeth, ZB coll. – **Figs 30, 32.** Lingual view. – **Figs 31, 33.** Labial view. – **Figs 34–35.** *Pachyscyllium distans* tooth, PG coll. – **Fig. 34.** Lingual view. –

Fig. 35. Labial view. – **Figs 36–37.** *Galeocerdo aduncus* tooth, ZB coll. – **Fig. 36.** Labial view. – **Fig. 37.** Mesial cutting edge of the same specimen. – **Figs 38–39.** *Galeocerdo* cf. *cuvier* tooth, ZB coll. – **Fig. 38.** Labial view. – **Fig. 39.** Mesial cutting edge of the same specimen. Both specimens are housed in private collection. Scale bars: Figs 25–29: 1 mm; Figs 30–35: 2 mm; Figs 36–39: 10 mm

Figs 40–41. *Rhizoprionodon* sp. tooth, PG coll. – **Fig. 40.** Lingual view. – **Fig. 41.** Labial view. – **Figs 42–43.** *Sphyrna integra* tooth, ZB coll. – **Fig. 42.** Lingual view. – **Fig. 43.** Labial view. – **Figs 44–45.** *Rhinobatos* sp. tooth, HNHM VER 2023.6. – **Fig. 44.** Occlusal view. – **Fig. 45.** Profile view. – **Fig. 46.** Rajidae indet. female tooth, HNHM VER 2023.7., occlusal view. – **Figs 47–49.** *Dasyatis*

Galeocerdo, by the convex outline of the distal enamel heel (*G. mayumbensis* has straight to slightly concave distal heel; Andrianavalona *et al.* 2015).

Teeth referable to the carcharhinid genus *Rhizoprionodon* (Figs 40–41), and to the sphyrnid *Sphyrna integra* have been found (Figs 42–43). Teeth of the taxa *Rhizoprionodon* sp. and *Sphyrna integra* are generally similar, but they can be separated by their relative size and the height of the cusp compared to the mesiodistal width of the root. In addition, in *Sphyrna*, it seems that there is a break between the mesial enamel heel and the mesial cutting edge of the cusp, while in *Rhizoprionodon*, this transition is much smoother.

Sorting the screen washed residue of the glauconite-rich matrix resulted in teeth of *Rhinobatos* sp. (Figs 44–45), Rajidae indet. (Fig. 46, female morphotype), *Dasyatis strangulata* (Figs 47–49, female morphotype), *Taeniurops cavernosus* (Figs 50–52, female morphotype), and *Gymnura* sp. (Figs 53–56). Teeth of *Aetomylaeus* sp. (Figs 57–60) and *Rhinoptera* sp. (Figs 61–64) were also identified in private collections. The teeth of *Rhynchobatus* (a genus previously reported from Nyirád) and *Rhinobatos* are generally similar in morphology; however, *Rhinobatos* has much smaller teeth lacking fine occlusal sculpting. The discovered Rajidae teeth are small and rootless, the crown is rhomboid in occlusal view and low in profile view, bearing a small uvula lingually. Since the root of the Nyirád rajid teeth is missing, we leave them with open nomenclature. *Dasyatis strangulata* teeth are massive with well-developed, wide transversal crest and very thick crown (other Nyirád *Dasyatis* spp. teeth are comparably less thick and also more gracile). *Taeniurops cavernosus* teeth are very similar to those of *Dasyatis* spp., however, their lingual visor is larger, and the labial and lingual crown edge is round-arched in occlusal/basal view. The two *Gymnura* sp. teeth are tiny, with characteristic crown, showing a Y-shaped outline in occlusal view. *Aetomylaeus* has teeth with crown medially higher than laterally. The Nyirád *Rhinoptera* tooth remains are very similar to those of *Myliobatis* (previously reported from the Nyirád I. outcrop by a high number of teeth), but they differ from those in having a labial and lingual crown ornamentation composed of apicobasally running ridges. The Nyirád *Rhinoptera* teeth are the most similar to *R. studeri*, however, due to the low number of the here referred specimens, and the limited availability

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strangulata female tooth, PG coll. – **Fig. 47.** Occlusal view. – **Fig. 48.** Profile view. – **Fig. 49.** Basal view. – **Figs 50–52.** *Taeniurops cavernosus* female tooth, PG coll. – **Fig. 50.** Occlusal view. – **Fig. 51.** Profile view. – **Fig. 52.** Basal view. – **Figs 53–56.** *Gymnura* sp. tooth, HNHM VER 2023.8. – **Fig. 53.** Labial view. – **Fig. 54.** Lingual view. – **Fig. 55.** Profile view. – **Fig. 56.** Occlusal view. – **Figs 57–60.** *Aetomylaeus* sp. tooth, ZB coll. – **Fig. 57.** Lingual view. – **Fig. 58.** Labial view. – **Fig. 59.** Basal view. – **Fig. 60.** Occlusal view. – **Figs 61–64.** *Rhinoptera* sp. tooth, ZB coll. – **Fig. 61.** Lingual view. – **Fig. 62.** Labial view. – **Fig. 63.** Basal view. – **Fig. 64.** Occlusal view. Scale bars: Figs 40, 41, 47–56: 1 mm; Figs 42, 43, 57–64: 5 mm; Figs 44–46: 0.5 mm

Figs 65–68. *Mobula fragilis* tooth, HNHM VER 2023.9. – **Fig. 65.** Labial view. – **Fig. 66.** Apical view. – **Fig. 67.** Basal view. – **Fig. 68.** Profile view. – **Figs 69–97.** *Mobula loupianensis* teeth. – **Figs 69, 74, 79, 84, 89, 94:** Labial view. – **Figs 70, 75, 80, 85, 90, 95:** Lingual view. – **Figs 71, 76, 81,**

of the holotype specimens of the two Badenian *Rhinoptera* species reported from the Central Parathethys sediments, here they are left in open nomenclature.
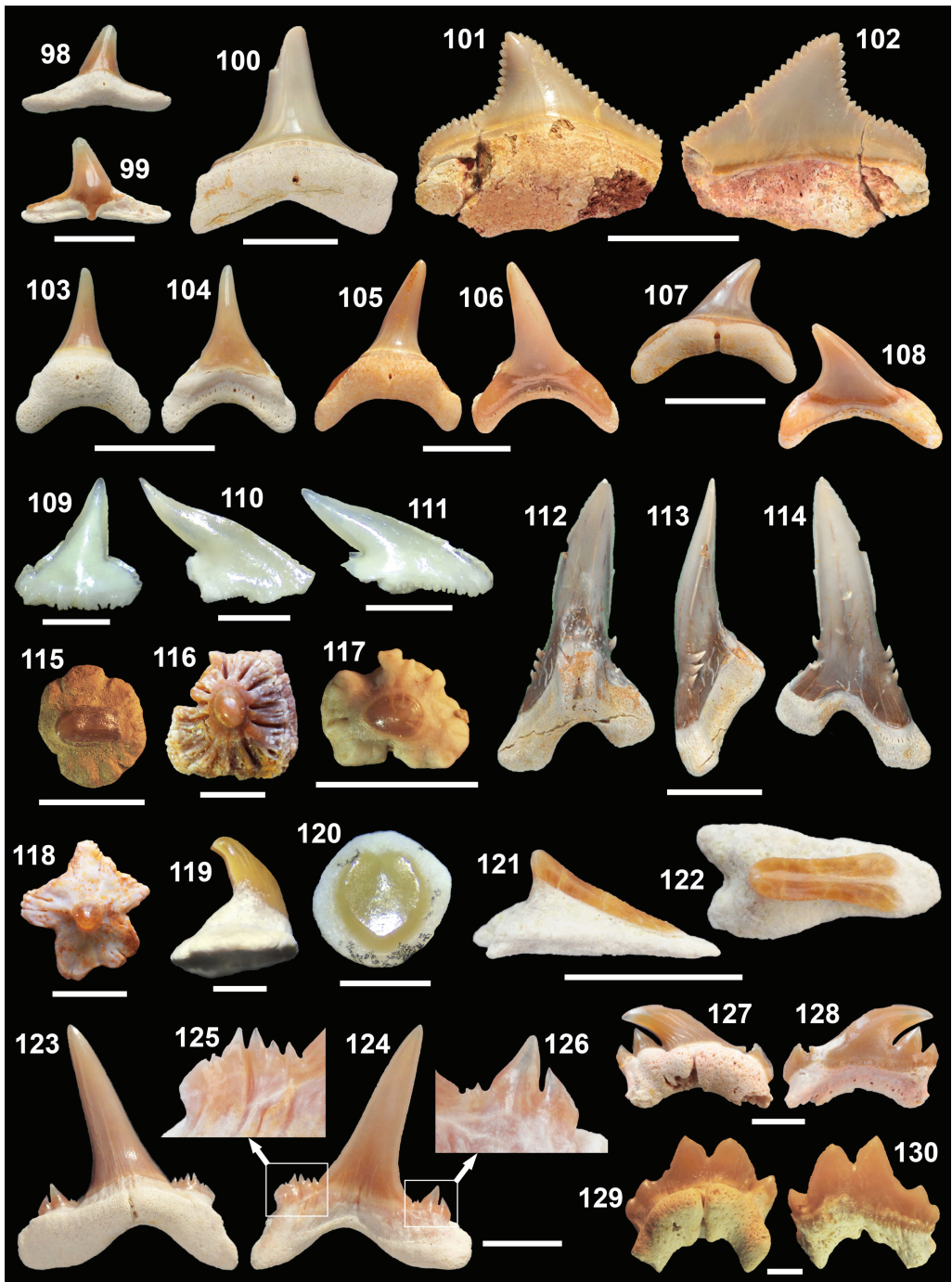
The teeth of at least two mobulid taxa, namely *Mobula fragilis* (Figs 65–68) and *Mobula loupianensis* (Figs 69–97, both male and female morphotypes) were discovered in the water screened residue. The teeth of *Mobula fragilis* from Nyirád have a labiolingually flattened, and mesiodistally expanded crown, ornamented by folds labially, and by fine ridges lingually. The cutting edge of these teeth is lingually directed and irregular. The root is low and is built up by numerous lobes. The species *Mobula loupianensis* possesses a strong dental sexual dimorphism: female teeth have drop-shaped, lingually bent crown without cusplets, while male teeth have crown with a prominent central cusp, flanked by a pair of cusplets. The basal labial crown face of both sexes bears folds and ridges. A few teeth possess bicuspid or asymmetrical crown (Figs 89–93). Similar mobulid teeth with bicuspid crown have been described from the Middle Miocene of southern France as *Mobula pectinata* (Cappetta 1970). Here we follow Cicimurri & Knight (2009), who placed *M. loupianensis* and *M. pectinata* in synonymy, leaving *M. loupianensis* as valid taxon. An amateur collection specimen (Figs 94–97) is nearly three times wider than high, and is identical with a tooth included in the figured type material of *M. loupianensis* (see Cappetta 1970, pl. 26, fig. 5, as a lateral tooth). The same two species of the genus *Mobula* have recently been reported from the Mecsek Mts., southern Hungary (Szabó *et al.* 2022).

Additionally, new, better preserved tooth remains of already reported rare chondrichthyan taxa from the Nyirád I. outcrop (Szabó & Kocsis 2016, 2020) have been found and displayed here (Figs 98–114). Some of these remains are in exceptionally good preservation such as *Squatina* sp. (Figs 98–99), *Carcharodon hastalis* (Fig. 100; this species was originally assigned to genus *Oxyrhina*, later to *Isurus*, then *Cosmopolitodus* – see Ehret *et al.* 2012), *Otodus* (*Megaselachus*) *megalodon* (Figs 101–102), *Alopias exigua* (Figs 103–108), *Iago angustidens* (Figs 109–111), and *Hemipristis serra* (Figs 112–114). Well-preserved myliobatiform dermal denticles have been discovered as well (Figs 115–122). Note, that specimen HNHM VER 2023.14. (Fig. 120) has a low, heart-shaped crown, which refers it to close relation with Dasyatidae (see Marramà *et al.* 2018, figs 7A–C). Pathological teeth, referable to the sand tiger shark species *Carcharias acutissima* have been discovered as well (Figs 123–130).

Trichiurid teeth different from those previously reported from the locality (see Szabó & Kocsis 2020) have been also found. They have a circular cross-section and markedly hooked apex. Altogether these remains are the most similar to
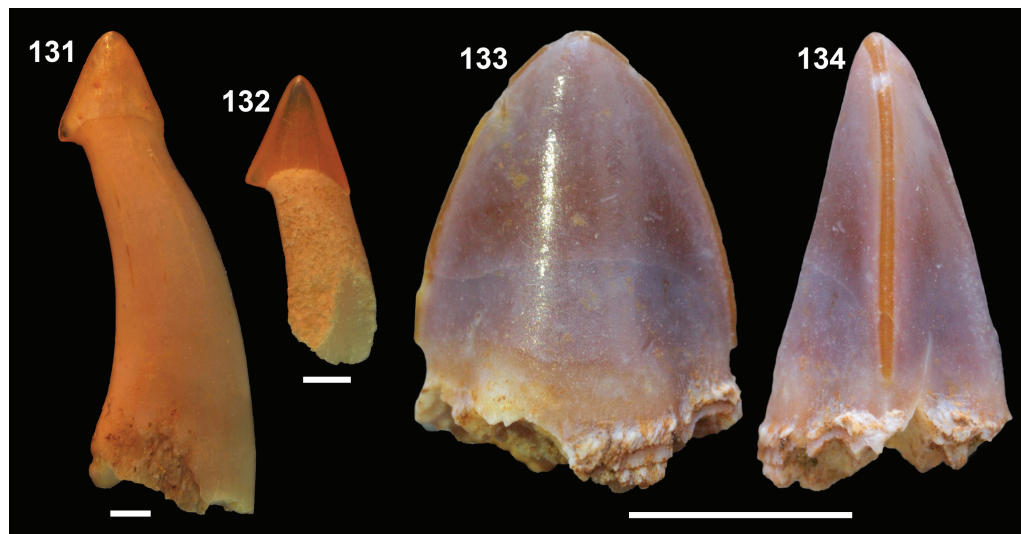

86, 91, 96: Occlusal view. – **Figs 72, 77, 82, 87, 92, 97:** Basal view. – **Figs 73, 78, 83, 88, 93:** Profile view. Except Figs 65–68, all specimens are housed in private collection. Scale bars: 1 mm

Figs 98–99. *Squatina* sp. tooth, ZB coll. – **Fig. 98.** Lingual view. – **Fig. 99.** Labial view. – **Fig. 100.** *Carcharodon hastalis* lower tooth, ZB coll., lingual view. – **Figs 101–102.** *Otodus* (*Megaselachus*) *megalodon* distal tooth, ZB coll. – **Fig. 101.** Lingual view. – **Fig. 102.** Labial view. – **Figs 103–108.** *Alopias exigua* teeth. – **Figs 103, 105, 107:** Lingual view. – **Figs 104, 106, 108.** Labial view. –
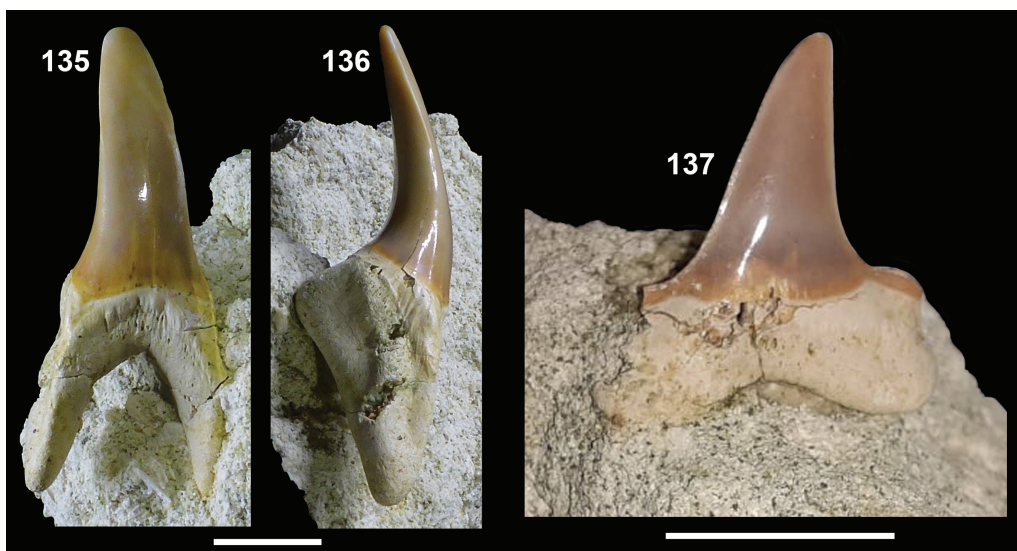
teeth reported as *Trichiurus miocaenicus* (Figs 131–132; see SCHULTZ 2003). A single, triangular bony fish tooth thickening to its base and with smooth cutting edges is tentatively referred to an indeterminate Scombridae fish (Figs 133–134).

Figs 131, 132. *Trichiurus miocaenicus* teeth, PG coll., labial or lingual view. – **Figs 133–134.** ?Scombridae indet. tooth, PG coll. – **Fig. 133.** Labial or lingual view. – **Fig. 134.** Profile view. All specimens are housed in private collection. Scale bars: Figs 131, 132: 0.6 mm; Figs 133, 134: 5 mm

Leitha Limestone Formation – A large amount of Leitha Limestone has been outcropped due to the restoration process of the Nyirád I. quarry. Numerous vertebrate remains have been found in these rocks, among them a tooth with preserved root has been identified as a lower tooth with close relation to *Isurus desori* (Figs 135–136). Both crown faces are smooth, the lingual is strongly, while the labial is weakly convex. The cutting edges are smooth; they vanish towards the crown base. The root lobes are elongate, they are about as high as the crown itself. An upper lateral tooth, showing close affinities to the teeth of *Anotodus retroflexus* has been found as well (Fig. 137).

Figs 109–111. *Iago angustidens* teeth, labial view. – **Fig. 109.** HNHM VER 2023.10. – **Fig. 110.** HNHM VER 2023.11. – **Fig. 111.** HNHM VER 2023.12. – **Figs 112–114.** *Hemipristis serra* lower tooth, ZB coll. – **Fig. 112.** Lingual view. – **Fig. 113.** Mesial view. – **Fig. 114.** Labial view. – **Figs 115–122.** Batoid dermal elements. – **Figs 115–118, 121, 122.** ZB coll. – **Fig. 119.** HNHM VER 2023.13. – **Fig. 120.** HNHM VER 2023.14. – **Figs 115–118, 120, 122.** Apical view. – **Figs 119, 121.** Profile view. – **Figs 123–130.** *Carcharias acutissima* pathological teeth, ZB coll. – **Figs 123, 127, 129.** Lingual view. – **Figs 124, 128, 130.** Labial view. – **Fig. 125.** Close-up of the mesial cusplet. – **Fig. 126.** Cluse-up of the distal cusplet. Private collection specimens: Figs 98–108, 112–118, 121–130. Scale bars: Figs 109–111, 119, 120, 129, 130: 1 mm; Figs 127, 128: 2 mm; Figs 115–118: 3 mm; Figs 98, 99, 103–108, 121–124: 5 mm; Figs 100–102, 112–114: 10 mm

Figs 135–136. *Isurus* cf. *desori* lower anterior tooth, PG coll. – **Fig. 135.** Labial view. – **Fig. 136.** Profile view. – **Fig. 137.** *Anotodus retroflexus* upper lateral tooth, PG coll., labial view. All specimens are housed in private collection. Scale bars: 10 mm

DISCUSSION

The potential of the Nyirád area for Badenian marine vertebrate remains has been discovered around 2012. Since then, the present study is the third paper which details the extreme diversity of this fauna. The Nyirád I. outcrop is currently the richest of all known Badenian localities in Hungary. An experimental sampling and screen-washing of ~30 kg pebbly glauconitic matrix from the Pusztamiske Formation resulted in 792 vertebrate remains (including both chondrichthyans and osteichthyans). This number is much higher than that of any Badenian marine vertebrate localities of the Pannonian Basin.

Up to now, the genus *Isistius* (represented by *I. triangulus*) has not been reported from the Badenian sediments of the Central Paratethys. However, it occurred in pre-Badenian sediments of the Central Paratethys, i.e. in the Lower Miocene (Middle Burdigalian) of Mitterdorf (Germany) (POLLERSPÖCK & STRAUBE 2017) and in the Lower Miocene (Eggenburgian) of Mučín (Slovakia) and Ipolytarnóc (Hungary) (HOLEC *et al.* 1995; KOCSIS 2007). Extant species of *Isistius* are typical inhabitants of the pelagic-bathypelagic zone between the surface and depths of 3700 m (COMPAGNO *et al.* 2005; FROESE & PAULY 2022). Important vertical migrations have been recorded in extant *Isistius*, meaning that these sharks often perform nocturnal vertical migrations from deep to shallow

waters (Jahn & Haedrich 1987; Nakano & Tabuchi 1990; Kiraly *et al.* 2003; Compagno *et al.* 2005). The migrating behaviour is typically associated with feeding habits in nearshore environments. Extant *Isistius* spp. are facultative ectoparasites on larger marine vertebrates, i.e. marine mammals (cetaceans, pinnipeds, and dugongs), chondrichthyans (sharks and rays), and osteichthyans (Compagno 1984; Hoyos-Padilla *et al.* 2013 and references therein). The Nyirád area has been inhabited by a variety of such marine vertebrates during the Badenian (Szabó & Kocsis 2020; see also below), meaning a stable food source for *Isistius triangulus* (note, that extinct and modern species of *Isistius* share similar dental characteristics, suggesting a similar hunting strategy and feeding behaviour). Therefore, the presence of *I. triangulus* may indicate an upper bathyal palaeoenvironment within a short distance from the coast, allowing a vertical, food-related wandering for this species (after Carrillo-Briceño *et al.* 2014, 2015; Martínez-Pérez *et al.* 2017).

Cetorhinus maximus (the only living representative of Cetorhinidae) is a cosmopolitan, highly migratory species, feeding on zooplankton by filtering (Sims & Quayle 1998; Compagno 2002; Gore *et al.* 2008; Doherty *et al.* 2017; Froese & Pauly 2022). As extant and extinct cetorhinids share the same gill raker characteristics, a similar feeding behaviour is presumed for the fossil taxa. The available fossil data suggests that species of *Keasius* preferred oceans of the Northern Hemisphere at higher latitudes (e.g. the Paratethys) during the Oligocene and Miocene (Reinecke *et al.* 2015). Yet, fossil remains of cetorhinids are unearthed only at very few Badenian localities of the Central Paratethys (Szabó & Kocsis 2016). This is presumably the result of the lack of studies based on marine vertebrate micro-remains yielded from screen-washing. Further excavations including exhaustive screen-washing procedures could reveal if these planktivorous sharks were regular (= seasonal) or occasional visitors of the Central Paratethys during the Badenian.

Extant members of the *Mobulidae* family are large sized, zooplanktivorous rays inhabiting tropical, subtropical, and temperate coastal waters circumglobally (Couturier *et al.* 2012; Last & Stevens 2009). Modern species of the family are highly mobile and are suited for rapidly traveling large distances. Based on tooth size and morphology, the same can be assumed for the Middle Miocene forms. Together with cetorhinids, these planktivorous migrators are unique elements of the elasmobranch fauna of the Middle Miocene Central Paratethys, and they can be used as tool-taxa for future palaeoenvironmental and palaeobiological implications (e.g. in Szabó *et al.* 2022). The genus *Mobula* is still considered as rare in the Badenian of the Central Paratethys (Szabó & Kocsis 2016; Szabó *et al.* 2022; present study).

The extant species of *Galeocerdo cuvier* has been reported from Miocene beds only from Florida (Middle Miocene – Türtscher *et al.* 2021) and Borneo (Late Miocene 7.2 Myr, Kocsis *et al.* 2019). Its presence in the Middle Miocene Nyirád ecosystem is therefore unique, but not only because the Nyirád report is the first *G. cuvier* from the Middle Miocene of Europe, but also, because it is the first evidence of two *Galeocerdo* species co-existing in the Central Paratethys. However, differences in the tooth morphology of the two species reveal further questions. Cutting edges of *G. aduncus* bear simple, fine, irregular serrations (some secondary serrations may occur on the distal heel), while those of *G. cuvier* possess coarse, large serrae with marked secondary serrations both on the mesial and distal cutting edges and also on the distal enamel heel (Cigala-Fulgosi & Mori 1979, fig. 3; Türtscher *et al.* 2021 and references therein). The diet of the modern tiger shark is well-studied, it is widely considered as one of the least specialized sharks as far as feeding is concerned. This species consumes nearly any kind of prey items, including invertebrates (e.g., cephalopods and crabs), chondrichthyans and osteichthyans, marine reptiles, marine birds, marine mammals, carcasses, and even garbage of human activity (Compagno 1984). Based on generally similar tooth morphology, a similar diet has long been proposed for *G. aduncus*, however, the simpler serrated cutting edges and the less robust teeth might have been suited for a less generalist diet. Therefore, the sympatric co-existence of the two species of *Galeocerdo* in the Middle Miocene Nyirád ecosystem may refer to niche partitioning between the two species through different feeding habits, and different prey-preferences. This theory requires further investigations, which could be ideal for future studies.

Cetaceans were previously reported from the Nyirád I. outcrop by teeth, ribs, and unidentified bone elements (Szabó & Kocsis 2020). Since then, new cetacean fossils have been found both in the Pusztamiske and Leitha Limestone Formations by amateur collectors, their detailed description is yet to be done. Cetaceans inhabited the Nyirád area in both the Pusztamiske and the Leitha Limestone palaeoenvironment, just like their potential predator, *Otodus* (*Megaselachus*) *megalodon*. Unfortunately, no direct evidences of predator-prey interactions between the two groups have been discovered in the Nyirád area so far.

The disarticulated shell of a non-marine turtle was also discovered in an amateur collection (Figs 138–140). The shell fragments have been found in the Pusztamiske Fm., in close vicinity to each other, suggesting that they belonged to the same animal. Due to its poor preservation, the taxonomy of the animal is doubtful. This fossil (together with a previously discovered and reported mammal tooth fragment from the same formation, attributed to a rhinocerotid; Fig. 141) further indicates the vicinity of coastal terrestrial and/or freshwater environments.

Figs 138–140. Turtle shell fragment, in three different views. – **Fig. 141.** ?Rhinocerotidae indet. tooth fragment, in suggested occlusal view. All specimens are housed in private collection. Scale bars: 10 mm

CONCLUSIONS

After the reclamation and restoration of the Nyirád I. outcrop in 2019, further, locally new taxa have been found in the uppermost, glauconite-rich layer of the Pusztamiske Formation, and in stone-blocks originating from the Leitha Limestone Formation. Altogether 38 chondrichthyan and 13 osteichthyan taxa, various cetaceans and two terrestrial tetrapods (a turtle and a suggested rhinocerotid) have been documented from the locality so far (Table 1). The likely occurrence of *Galeocerdo cuvier* teeth (extant tiger shark) at Nyirád provides the first data of this species from the fossil record of Europe, and also suggests that it co-existed with the fossil species of *G. aduncus* in the Central Paratethys during the Badenian. Hopefully, scientific interest aiming at the fossils of the Nyirád I. outcrop will continue to rise. The present study also emphasizes the importance of amateur fossil collections.

*

Table 1. Summary of the vertebrate fauna discovered at the Nyirád I. site

PUSZTAMISKE FORMATION

CHONDRICHTHYES
  Selachimorpha
    Hexanchiformes
      Notorynchus primigenius
    Squaliformes
      Isistius triangulus
    Pristiophoriformes
      Pristiophorus sp.
    Orectolobiformes
      Ginglymostoma sp.
    Squatiniformes
      Squatina sp.
    Lamniformes
      Carcharias acutissima
      Carcharoides catticus
      Cosmopolitodus hastalis
      Isurus sp.
      Otodus (*Megaselachus*)
        megalodon
      Parotodus benedeni
      Keasius sp.
      Alopias exigua
      Anotodus retroflexus
    Carcharhiniformes
      Pachyscyllium dachiardi
      Pachyscyllium distans

Galeorhinus goncalvesi
Iago angustidens
Chaenogaleus affinis
Hemipristis serra
Rhizoprionodon sp.
Carcharhinus priscus
Galeocerdo aduncus
Galeocerdo cf. *cuvier*
Sphyrna integra
Sphyrna laevissima
  Batomorpha
    Rhinopristiformes
      Rhynchobatus sp.
      Rhinobatos sp.
    Rajiformes
      Rajidae indet.
    Myliobatiformes
      Dasyatis probsti
      Dasyatis rugosa
      Dasyatis strangulata
      Taeniurops cavernosus
      Gymnura sp.
      Aetobatus arcuatus
      Aetomylaeus sp.
      Myliobatis sp.
      Rhinoptera sp.

OSTEICHTHYES
  Perciformes
    Crenidens sp.
    Dentex sp.
    Diplodus sp.
    Pagrus sp.
    Sparus sp.
    Labrodon sp.
    Trigonodon jugleri
    Acanthurus sp.
    Sphyraena sp.
    Trichiurus miocaenicus
    Trichiuridae indet.
    ?Scombridae indet.
  Tetraodontiformes
    Tetraodontiformes indet.

REPTILIA
  Testudines
      Testudines indet.

MAMMALIA
  Cetacea
    Odontoceti
    Mysticeti
  Perissodactyla
    ?Rhinocerotidae indet.

LEITHA LIMESTONE FORMATION

CHONDRICHTHYES
  Selachimorpha
    Hexanchiformes
      Notorynchus primigenius
    Lamniformes
      Carcharias acutissima
      Cosmopolitodus hastalis
      Isurus cf. *desori*

Otodus (*Megaselachus*)
  megalodon
Anotodus retroflexus
Carcharhinus priscus
Galeocerdo aduncus
  Batomorpha
    Myliobatiformes
      Myliobatis sp.

OSTEICHTHYES
  Perciformes
    Pagrus sp.
    Sparus sp.

MAMMALIA
  Cetacea
    Odontoceti indet.

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