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# A new Middle Miocene selachian assemblage (Chondrichthyes, Elasmobranchii) from the Central Paratethys (Nyirád, Hungary): implications for temporal turnover and biogeography

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**Abstract:** A new Middle Miocene (Langhian–early Serravallian) assemblage with shark and ray teeth from Nyirád (Hungary, Transdanubia, Veszprém County) consists of nine families, with 15 different species. The assemblage shares many common genera with other Middle Miocene assemblages in the Paratethys (*Notorynchus*, *Carcharias*, *Otodus*, *Cosmopolitodus*, *Hemipristis*, *Galeocerdo*, *Carcharhinus*, and *Aetobatus*), and reflects a subtropical climate and a close connection with the Mediterranean Sea. However, a detailed faunal compilation of Miocene selachians reveals that several taxa that were still present in the Mediterranean or lived in the Paratethys during the Lower Miocene disappeared or became very rare by the Middle Miocene in the Central Paratethys (e.g., *Isistius*, *Centrophorus*, *Mitsukurina*, *Carcharoides*, *Parotodus*, *Alopias*). The taxa that went locally extinct in the Paratethys are mainly represented by deep-water or pelagic forms. Their disappearance is most probably related to the gradual separation of the Paratethys from the Mediterranean. The common presence of some large, rather pelagic sharks (e.g., *Otodus*, *Cosmopolitodus*) in the Central Paratethys during the Middle Miocene is explained here by the widespread occurrence of their potential prey represented by marine mammals (e.g., whales and dolphins).

**Key words:** Badenian, Central Paratethys, Hungary, Nyirád, Chondrichthyes, *Carcharoides*.

## Introduction

The Central Paratethys was a part of a large epicontinental sea, the Paratethys, which was isolated from the Tethys Ocean during the late Eocene–early Oligocene (e.g., Báldi 1983, Rögl & Steininger 1983; Rögl 1998). The separation was driven by the Alpine orogeny, but global sea level changes also played important roles in opening and closing seaways towards the open ocean or between the different sub-basins. Complete isolation and reopening of oceanic gateways occurred repeatedly and led to development of a distinct palaeobiological province (e.g., Báldi 1983; Rögl 1998). Fossil remains of cartilaginous fishes (e.g., shark and ray teeth) are often found in the Miocene sediments of the Paratethys and many field-reports and scientific papers have mentioned them since the 19th century (see references in Koch 1903 and Schultz 1971). Generally, in earlier times many fossil species were described (e.g., Agassiz 1843; Probst 1878, 1979), however comparative studies with modern relatives has allowed revising of several previously described fauna and the number of species were reduced in the Paratethys as well (Leriche 1927a,b; Vitális 1942; Schultz 1971; Holec et al. 1995; Kocsis 2007; Schultz et al. 2010).

Here a new Middle Miocene (Badenian) fauna is described from Nyirád (Veszprém County, Hungary). This locality is situated in the Transdanubian Range from where our knowledge on *chondrichthyan* fossils is very sporadic so far (Fig. 1). On the other hand, from other sub-regions of the Central Paratethys the marine Badenian beds often yielded rich shark and ray faunas, among them the Vienna Basin (e.g., Schultz 1971, 2013; Holec 2001), Molasse Basin (Schultz 2003), Styrian Basin (Hiden 1995), the Carpathian Foredeep (Radwański 1965; Schultz 1977; Brzobohatý & Schultz 1978; Wysocka et al. 2012; Reinecke & Radwański 2015) and recently Slovenia (Mikuž 2009; Mikuž & Šoster 2013; Mikuž et al. 2015).

Regarding the Hungarian Badenian beds, so far no detailed investigation was reported on the cartilaginous fish fauna. From northwest Hungary the literature only provides fauna lists (Ferenczi 1915; Noszky 1925; Kordos & Solt 1984), sometimes with photo tables (Solt 1987). Regarding southern Hungary there are some patchy Badenian shark and ray teeth occurrences, but a very rich re-worked fauna is known from the Pannonian (Late Miocene) freshwater deposits, still without comprehensive taxonomical descriptions (Kazár et al. 2001; Sebe et al. 2015). The age of these selachian and ray fossils is assumed to be Karpatian–Badenian (Kocsis 2002; Sebe et al. 2015).

The lack of taxonomical and well-illustrated studies from the Hungarian Badenian beds is evident. The aims of this

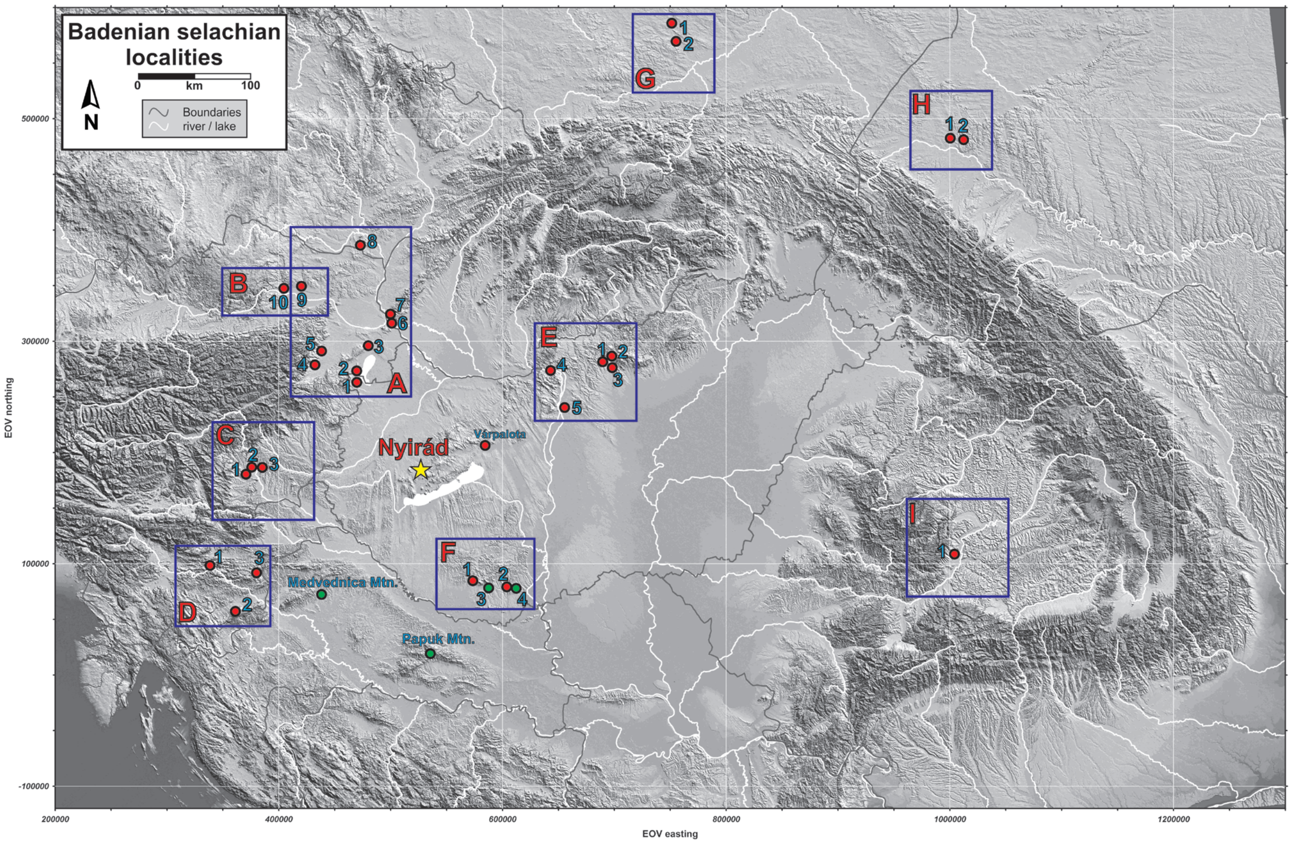


**Fig. 1.** Badenian localities with shark and ray remains in the Central Paratethys. For faunal and stratigraphical details see Table 1 and 2. Note the location of Nyirád, from where the new fauna is described (yellow star symbol). The background map is based on Horváth et al. (2006). The marked regions are the followings: **Vienna Basin** (A); **Lower Austria Molasse** (B); **Styrian Basin** (C); **Sava Basin** (D) with also some occurrences at the Medvednica and Papuk Mountains; **Pannonian Basin** with the investigated locality and some of its sub-regions — North-northeast Hungary (E) and surroundings of the Mecsek Mountain in South Hungary (F); **Carpathian Foredeep** in Poland (G) and Ukraine (H); **Transylvanian basin** (I). The numbers mark the most representative and fossil rich localities within the regions. For the names see Table 1. The colours refer to the online version of the paper

present study were to give a detailed taxonomical description of the shark and ray fauna of Nyirád with clear illustrations of the common taxa, and to fill the aforementioned hiatus about the Badenian cartilaginous fish remains of Hungary. The intensive collection of the last five years at the abandoned gravel pit near Nyirád resulted in hundreds of various fish remains, which allow us to compare the Nyirád fauna with the old literature and museum specimens alongside giving an updated nomenclature. Importantly, the newly described fauna is also put in a wider context of the reported Badenian faunas from the Central Paratethys, together with an updated literature survey on these fossil sites and their ages (see Fig. 1, and references in Tables 1–2). In this sense Schultz's compilation of the Austrian fish fauna (2013) provided a great help regarding some key Middle Miocene localites from the Central Paratethys.

## Locality and background geology

All the vertebrate remains were collected in an abandoned gravel pit located ~3 km southwest from Nyirád (Veszprém County, Transdanubia, Hungary). The site is easy to reach from the public road from Nyirád to Sümeg (Fig. 2A). The fossils have been found in the eastern side of the quarry, where two overlying, fossil-bearing lithostratigraphic units, the Kolontár Member of the Pusztamiske Formation and the Pécsszabolcs Member of the Leitha Limestone Formation can be observed (Fig. 2B, C and Fig. 3) (note that in Hungarian literature the Leitha Fm. often appears as Lajta Fm.). These marine formations cover terrestrial sediments (Somlóvásárhely Formation) in the Transdanubian Range, which was an emerged land during the early Miocene. Transgression reached its southern shores in the earliest Badenian and the investigated fossiliferous sediments were deposited. The layers of this marine sedimentary succession are the best studied in rain-washed gullies and creeps of the Nyirád quarry.

The strata of the Pusztamiske Formation are built up of Lower Badenian coarse- and fine-grained marine sediment. The strata belong to the NN5 nannozone and also yielded Lagenidae-Orbulina foraminifera assemblage (Kercsmár et al. 2015). The formation is known in the western-south-western part of the Bakony Mountains, which means in the Devecser-Nyirád sedimentary basin and in the vicinity of Sümeg, both

**Table 1**: Compilation of Badenian fossil Chondrichthyes localities from the Central Paratethys. Regions (capital letters) with the most important localities (numbers) are plotted on the map in Fig. 1.

| Region | Place | Selachian Literature | Lithology and/or Lithostratigraphy | Stage - Zone | Age (Ma) | Literature on Stratigraphy |
|---|---|---|---|---|---|---|
| **Vienna Basin (A)** | Baden-Soos (stratotype locality for the Badenian) (5) | Rögl et al. 2008; Schultz, 2013 | Baden Fm.<br>Clay - "Badener Tegel" | Upper Lagenidae Zone - NN5 | 14.2 | Rögl et al. 2008 |
| | _Austria_: e.g. St. Margarethen (2), Bruck a.d. Leitha (3), Bad Vöslau (4), _Hungary_: Fertőrákos (1) | Noszky 1925; Schultz 1971, 2013; Brzobohatý & Schultz 1978; Schmid et al. 2001 Schultz, 2013 | corallinacean limestones<br>aka Leitha limestone | Upper Lagenidae Zone - NN5 | | Schmid et al. 2001,<br>Harzhauser et al. 2003 |
| | _Slovakia_: Devínska Kobyla (6), Devinska Nova Ves (7) | Noszky 1925; Schultz 1971, 2013; Brzobohatý & Schultz 1978; Holec 2001 | Studienka and Sandberg Formations | Bolivina-Bulimina Zone - NN6 | 13.58 | Hyžný et al. 2012 |
| | _Czech Republic_: Kienberg at Mikulov (8) | Schultz et al. 2010; Schultz 2013 | Lanžhot Formation<br>Hrušky Formation | Upper Lagenidae Zone - NN5 | | Brzobohatý et al. 2007 |
| **Molasse Basin (B)** | Grund near Hollabrunn (9),<br>Mühlbach am Manhartsberg (10), | Schultz 2003, 2013; Daxner-Höck et al. 2004 | Grund Formation<br>Gaindorf Formation | Lower Lagenidae Zone - NN5 | 15–15.1 | Harzhauser et al. 2003,<br>Daxner-Höck et al. 2004,<br>Ćorić et al. 2004 |
| **Styrian Basin (C)** | e.g., St. Florian (1), Tobbisegg (2), Weissenegg (3) | Brzobohatý & Schultz 1978; Hiden 1995; Schultz 2013 | Weissenegg Formation<br>St. Florian Member | Lower Lagenidae Zone - NN5 | | Hiden 1995,<br>Harzhauser et al. 2003 |
| **Sava Basin** | _Slovenia_(D): Plesko quarry, near Trbovlje (1);<br>Orehovica, Dolenjska (2); Virštanj (3) | Mikuž et al. 2013,<br>Mikuž 2009; Mikuž & Šoster 2013; Mikuž et al. 2015 | marlstones and lithothamnium limestones<br>marlstone | upper part of NN5<br>?Upper Badenian | | Mikuž & Bartol 2011 |
| | _Croatia_: Medvednica Mtn.<br>Papuk Mtn. | | Lithothamnium limestone<br>Sandy depoits | Lagenidae Zone - NN5<br>_most are reworked --> ?Badenian_ | | Ćorić et al. 2009 |
| **Pannonian Basin (Hungary)** | | | | | | |
| **Bakony Mountains** | **Nyirád** | **this study** | Pusztamiske Fm. &<br>Leitha Limestone Fm. - Pécsszabolcs Member | Lagenidae Zone - NN5 | | Selmeczi 2003; Kercsmár et al. 2015<br>Gyalog & Buda 2004 |
| | Várpalota (Szabó-bánya) | not studied yet - preliminary fauna list given here | Pusztamiske Fm. &<br>Leitha Limestone Fm. - Pécsszabolcs Member | Lagenidae Zone - NN5 | | Katona et al, 2011; Kókay, 2013; |
| ***(E) Mátra & Cserhát Mountains*** | Mátraszőllős (1); Sámsonháza (2); Mátraverebély (3);<br>?Mátrahasznos; | Noszky 1925; Vitális 1915, 1942; Solt 1987, 1991 | Leitha Limestone Fm. - Pécsszabolcs Member | Lower Badenian ~Lagenidae Zone | | Müller 1984, Moissette et al. 2007,<br>Gyalog & Buda 2004 |
| ***Budapest and its region*** | Zebegény (4), Kemence, Törökmező<br>Őrs vezér tér (5); Rákos - Budapest; | Solt & Kordos 1984 | Leitha Limestone Fm. - Pécsszabolcs Member<br>Leitha Limestone Fm. - Rákos Member | Lower Badenian ~Lagenidae Zone<br>Late Badenian ~ Bolivina-Bulimina Zone | | Müller 1984, Moissette et al. 2007,<br>Gyalog & Buda 2004 |
| ***(F) Mecsek Mountain*** | Hetvehely (1), Fazekasboda (2) | Sebe et al. 2015 | Pécszabolcs Limestone Fm.<br>"Lower Leitha limestone" | | | Sebe et al. 2015 |
| | Danitz-puszta (3) | Kazár et al. 2001; Kocsis 2002; Juhász 2006; Sebe et al. 2015 | Pannonian sand with redeposited fish remains | _reworked fauna--> Badenian_ | | Sebe et al. 2015 |
| | Hímesháza (4) | Kocsis 2002 | Pannonian sand with redeposited fish remains | _reworked fauna--> Badenian_ | | |
| **Carpathian Foredeep** | _Poland_ (G): Korytnica (1) | Schultz 1977, 1979, 2013; Reinecke & Radwański 2015 | Korytnica Clays | Lower Lagenidae Zone | | Rögl & Brandstätter 1993 |
| | Pińczów (2) | Pawlowska 1960; Radwanski 1965 | "Lower Leitha limestone" | Lower Badenian ~ Lagenidae Zone | | |
| | _Ukraine_ (H): e.g. Khorosno (1), Gleboviti (2), Pidiarkiv, Berezhany | Wysocka et al. 2012 | Mykolaiv Sands - coeval with Korytnica Clay | presence of _Orbulina suturalis_<br>~ Lower Lagenidae Zone - NN5 | | Andreyeva-Grigorovich et al. 1997<br>Wysocka et al. 2002 |
| **Transylvanian Basin** | Gârbova de Sus (Felsö-Orbó) | Noszky 1925 | Sand & "Leitha limestone"<br>Gârbova de Sus Fm. | Upper Lagenidae Zone - NN5 | | Filipescu & Gríbacea 1997 |

***The capital letters and numbers are references to Figure 1.***

from boreholes and surface outcrops. It is made up of the following sediments: abrasional gravel and conglomerate, shallow water–nearshore calcareous glauconitic sand, sandstone and silt as well as clay marl and marl consisting of corallinacean limestone lenses. In some places tuff, tuffite or bentonite interbeddings occur in the succession. Several transitions from the looser, sandy-pebblic variation to the strongly cemented, hard-faced, lime-bounded conglomerate can be observed.

The sediments are grey, yellowish-grey, often with reddish-brown tint derived from limonite (Selmeczi 1996, 2003; Selmeczi et al. 2002). The size of the pebbles ranges from 0.5–2 cm up to 10–15 cm; the quantity of the latter is subordinated (in the wider area the average size of the pebbles is 1–2 cm). The pebbly sediment of the Pusztamiske Formation is rich in fossils (e.g., molluscs, mostly *Pectinidae; Balanus* sp.-fragments; chondrichthyan and osteichthyan remains, rarely sea mammals). There is a gradual transition from the Kolontár Member of the Pusztamiske Formation into the Pécsszabolcs Member of the Leitha Limestone Formation, which is very rich in fossil remains. The Leitha Limestone is a common shallow water facies in the Central Paratethys. It was named after the Leitha Mountain in Austria (i.e., Leitha-kalk), but in literature it is often referred to as corallinacean limestones, lithothamnium limestone or algal limestone. In Hungary two members are distinguished: the older Pécsszabolcs Member corresponding to late Lower-Middle Badenian, while the Rákos Member is Upper Badenian (Gyalog & Budai 2004). Chondrichthyan remains are often reported from these limestones (see Table 2), but at Nyirád the majority of the teeth come from the Pusztamiske Formation underneath.

## Regional outlook

The Middle Miocene Badenian stage of the Central Paratethys generally corresponds to the Langhian and early Serravallian age on the global chronostratigraphic chart (e.g., Kováč et al. 2007; Rögl et al. 2008). However, recently Hohenegger et al. (2014) argued that the lower boundary of the Badenian predates the Langhian/Burdigalian boundary by about 300 kys (Fig. 2). Nevertheless, the subdivision of the Badenian is often confusing due to two- (lower and upper) or threefold (lower–middle–upper or early–middle–late) subdivisions, where also the boundaries vary regarding different biostratigraphic approaches and depending on the authors (e.g., Papp & Cicha 1968; Rögl 1998; Harzhauser et al. 2003; Piller et al. 2007). This often makes it difficult to correlate sites from where chondrichthyan fossils are reported.

**Table 2:** Summary of the Badenian faunas from the Central Paratethys. For geographical and stratigraphic details see Fig. 1 and Table 1.

| | Vienna Basin & adjacent area | | | LAM Basin | Styrian Basin | Sava Basin | | | Pannonian Basin | | | | | | | | | Carpathian Foredeep | | | Transylv. Basin |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | Austrian sites (e.g., Sankt Margarethen, Baden-Soos, etc.) | Devínska Kobyla & Devínska Nová Ves (SK) | Kienberg at Mikulov (CZK) | Molasse Basin (AU) - Gaindorf & Grund Formations | Weissenegg Formation & St. Florian Member | Plesko quarry, near Trbovlje (SLO) | Orehovica, Dolenjska & Virštanj (SLO) | Papuk National Park (HR) | **Nyírád locality (HU) - Pusztamiske Fm. and Leitha Fm.** | Várpalota, Szabó-bánya (HU) | *N-NW Hungary - Mátra & Cserhát Mountains* Mátraszőllős; Sámsonháza; Mátraverebély; Hasznos | *N-NW Hungary - Budapest and its region* Kemence, Zebegény, Törökmező, Őrs vezér tér, etc. | *Mecsek Mountain and its surroundings:* | Hetvehely; Leitha Fm. | Fazekasboda; Leitha Fm. | Danitz-puszta | Hímesháza | Korytnica Clays (PL) | Pińczów (PL) - Leitha limestone | Mykolaiv Sand (UKR) | Gârbova de Sus (Felsö-Orbó) (RO) |
| **Hexanchiformes** | | | | | | | | | | | | | | | | | | | | | |
| *Notorynchus primigenius* (Agassiz, 1843) | X | X | | X | X | | | | **X** | | X | X | | | | X | X | X | X | | |
| **Squaliformes** | | | | | | | | | | | | | | | | | | | | | |
| *Squalus* sp. | X | | X | | | | | | | | | | | | | | | | | | |
| **Squatiniformes** | | | | | | | | | | | | | | | | | | | | | |
| *Squatina subserrata* (Münster, 1846) | X | X | X | | | | | | | | X | | | | | | X | X | | | |
| **Orectolobiformes** | | | | | | | | | | | | | | | | | | | | | |
| *Ginglymostoma delfortriei* Daimeries, 1889 | | | | | X | | | | | | | | | | | | | | | | |
| **Lamniformes** | | | | | | | | | | | | | | | | | | | | | |
| *Carcharias* sp. | | X | X | | | | X | | | X | | | | | | X | | | | | X |
| *Carcharias acutissima* (Agassiz, 1844) | X | X | X | X | X | | | | **X** | X | X | X | | | | X | X | X | X | X | X |
| *Araloselachus cuspidatus* (Agassiz, 1844) - earlier *Carcharias* | X | X | X | X | X | | | | **X** | | X | X | | X | | X | X | X | X | X | X |
| *Carcharoides* cf. *catticus* (Philippi, 1846) | | | | | | | | | **X** | | | | | | | | | | | | |
| *Cosmopolitodus hastalis* (Agassiz, 1843) - earlier *Isurus* | X | X | X | X | X | X | X | X | **X** | ?X | X | | | | X | X | | X | X | X | X |
| *Isurus desori* (Agassiz, 1844) | X | X | | | | | | | | | X | | | | | X | X | | X | | X |
| *Isurus* sp. | | | | | | | | | | | | X | | | | | | | | | |
| *Otodus* (*Megaselachus*) *megalodon* (Agassiz, 1843) | X | X | X | | X | | X | | **X** | X | X | | | X | | X | X | X | X | X | X |
| *Alopias exigua* (Probst, 1879) | | | | | | | | | | | | | | | | | | X | | | |
| *Anotodus retroflexus* (Agassiz, 1843) - earlier *Isurus* | X | X | | | | | | | | | X | | | | | | | | | ?X | |
| *Cetorhinus maximus* (Gunnerus, 1765) | X | | X | | | | | | | | | | | | | | | | | | |
| **Carcharhiniformes** | | | | | | | | | | | | | | | | | | | | | |
| *Pachyscyllium dachiardii* (Lawley, 1876) | | | X | X | | | | | | | | | | | | | | X | | | |
| *Pachyscyllium distans* (Probst, 1879) - earlier *Scyliorhinus* | X | | | X | X | | | | | | | | | | | | | X | | | |
| ?*Scyliorhinus* sp. | | X | | | | | | | | | | | | | | X | | | | | |
| *Galeorhinus cf. goncalvesi* Antunes, Balbino & Cappetta, 1999 | | | | | | | | | | | | | | | | | | X | | | |
| *Chaenogaleus affinis* (Probst, 1878) | X | X | X | | X | | | | | | X | | | | | | ?X | X | | | |
| *Hemipristis serra* Agassiz, 1843 | X | X | X | X | X | | | X | **X** | X | X | | | X | | X | X | | X | X | |
| *Paragaleus pulchellus* (Jonet, 1966) | | | X | | | | | | | | | | | | | | | X | | | |
| *Paragaleus* sp. | | | | | | | | | | | X | | | | | | | X | ?X | | |
| *Carcharhinus priscus* (Agassiz, 1843) | X | X | X | X | X | | | | **X** | X | X | | | X | X | X | X | X | X | | |
| *Carcharhinus* sp. | | | | | | | | | | X | X | X | | | | | | | | | |
| *Galeocerdo aduncus* Agassiz, 1843 | X | X | X | X | X | | | | **X** | | X | | | X | X | X | X | X | X | X | |
| *Galeocerdo* sp. | | | | | | | | X | | X | | | | | | | | | | | |
| *Isogomphodon acuarius* (Probst, 1879) | | | | | | | | | | | | | | | | | X | | | | |
| *Negaprion* sp. | | | | | X | | | | **X** | ?X | | | | | | X | X | | | | |
| *Negaprion kraussi* (Probst, 1878) | | | | | X | | | | | | | | | | | | | | | | |
| *Rhizoprionodon* sp. | | | | | | | | | | | X | | | | | X | X | | | | |
| *Rhizoprionodon fischeuri* (Joleaud, 1912) | | | | | X | | | | | | | | | | | | | | | | |
| *Sphyrna* sp. | | | X | X | | | | | | | | | | | | X | X | X | | | |
| *Sphyrna zygaena* (Linnaeus, 1758) | | X | | | | | | | **X** | | | | | X | | X | X | | | | |
| *Sphyrna laevissima* (Cope, 1867) | | | | | | | | | | | | | | | | | | X | | | |
| **Myliobatiformes** | | | | | | | | | | | | | | | | | | | | | |
| *Dasyatis* sp. | X | X | X | X | X | | | | **X** | | X | | | | | X | | | X | | |
| *Dasyatis delfortriei* Cappetta, 1970 | | | | | X | | | | | | | | | | | | | | | | |
| *Dasyatis probsti* Cappetta, 1970 | | | | | X | | | | **X** | | | | | | | | | X | | | |
| *Dasyatis rugosa* (Probst, 1877) | | | | X | X | | | | **X** | | | | | | | | | X | | | |
| *Dasyatis strangulata* (Probst, 1877) | | | | | | | | | | | | | | | | | | X | | | |
| *Taeniurops cavernosus* (Probst, 1877) - earlier *Dasyatis* | | | | | | | | | | | | | | | | | | X | | | |
| *Gymnura* sp. | | | | | X | | | | | | | | | | | | | | | | |
| *Aetobatus arcuatus* (Agassiz, 1843) | X | X | X | X | X | | | | **X** | | X | | | X | | X | X | | X | | |
| *Aetomylaeus* sp. | | | | | X | | | | | | | | | | | | | | | | |
| *Myliobatis* sp. | X | X | X | X | X | | | | **?X** | | X | | | X | | X | X | X | | X | |
| *Myliobatis* cf. *meridionalis* | | | | | | | | | | | | | | | | | | | X | | |
| *Rhinoptera* sp. | | X | | X | | | | | | | | | | | | | | | | | |
| *Rhinoptera schultzi* Hiden, 1994-95 | | | | | X | | | | | | | | | | | | | X | | | |
| *Rhinoptera studeri* (Agassiz, 1843) | | X | | X | X | | | | | | X | | | | | | | | | | |
| *Mobula loupianensis* Cappetta, 1970 | | | | | | | | | | | | | | | | | | X | | | |
| **Rajiformes** | | | | | | | | | | | | | | | | | | | | | |
| *Rhynchobatus pristinus* (Probst, 1877) | | | X | | X | | | | | | | | | | | | | | | | |
| *Rhinobatos antunesi* (Jonet, 1968) | | | | X | | | | | | | | | | | | | | | | | |
| *Dipturus olisiponensis* (Jonet, 1968) | | | X | | | | | | | | | | | | | | | | | | |
| *Raja* sp. | | | X | | | | | | | | | | | | | | | | | | |
| ?*Pristis* sp. | X | | | | X | | | | | | | | | | | | | | | | |

*Abbreviations:* ***LAM*** *- Lower Austria Molasse; AU - Austria;* ***SK*** *- Slovakia;* ***CZK*** *- Czech Republic;* ***SLO*** *- Slovenia;* ***HR*** *- Croatia;* ***HU*** *- Hungary;* ***PL*** *- Poland;* ***UKR*** *- Ukraine;* ***RO*** *- Romania.*

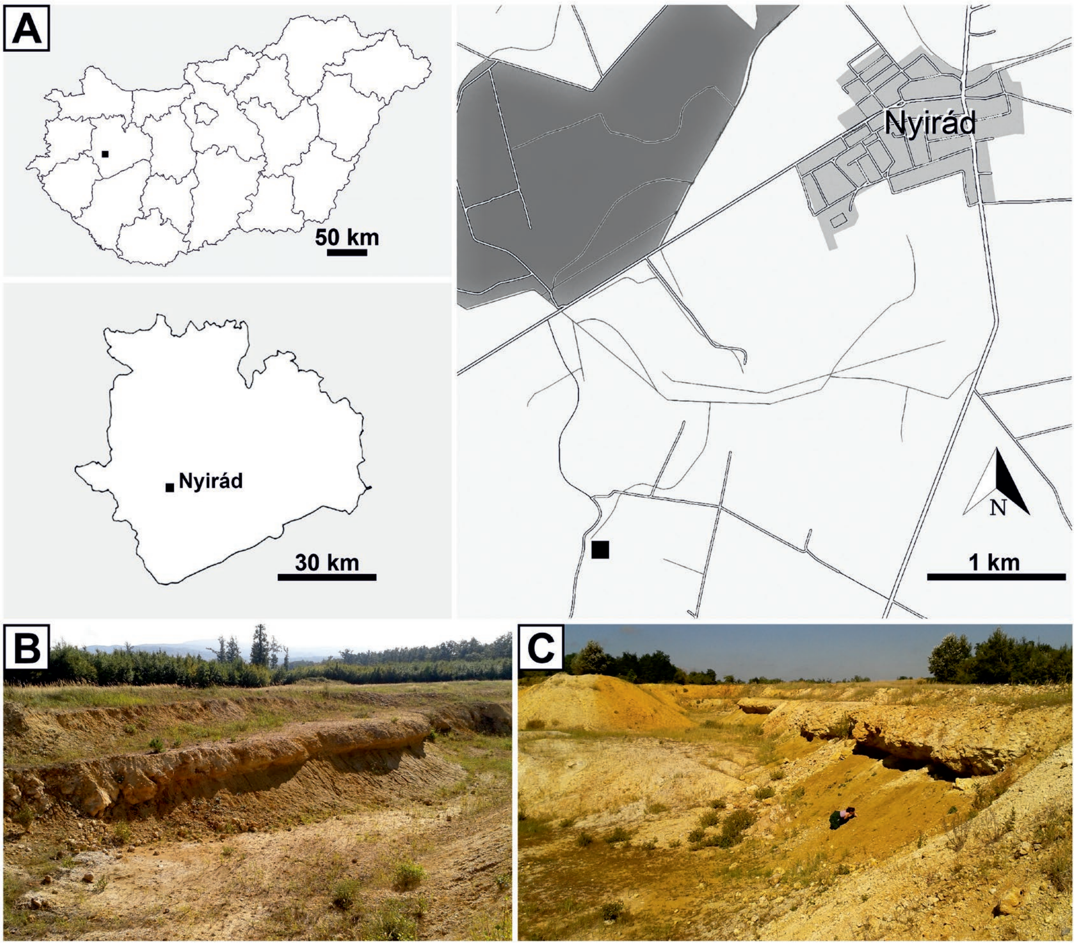


**Fig. 2.** The Nyirád locality. **A** — Location of the shark teeth site of Nyirád (the abandoned gravel pit is indicated by a black square). **B, C** — The eastern side of the open pit mine.

Regarding the palaeogeographic and palaeoceanic conditions, the Central Paratethys was connected with the Mediterranean via the Slovenian Corridor in the south-west during the early–mid Badenian (calcareous nannozones between NN4–NN5/6 boundary), while by the late Badenian this seaway ceased and east-south-east connections existed till the end of the Badenian (Kováč et al. 2007, fig. 2B).

## Materials and methods

All the remains have been collected from the eastern side of the gravel pit during fieldwork conducted in springs and summers of 2012–2016. The specimens were housed in the collection of the Geological and Geophysical Institute of Hungary (MFGI). The chondrichthyan remains have been picked one by one from the sediment surface or collected by screening the sediment. The Pusztamiske Formation was investigated at the eastern side of the open pit mine, along two wall sections of 30 and 20 metres width, respectively (Fig. 3B,C). Above these walls the Leitha Limestone was sampled by hand-quarrying. Due to the steep wall, collecting directly from the pebble succession was difficult and resulted in only a small amount of fossils. The pebble matrix of the Pusztamiske Formation was also screen-washed for micro-remains. About to 75 kilograms of pebble matrix was screened, which gave (quantitatively) the vast majority of the vertebrate fossils (more, than 90 per cent). The collected fossils were cleaned in tap water, and were prepared according to necessity with cyanoacrylate adhesive (superglue).

Most of the shark teeth are poorly preserved, their roots are usually missing or broken, the crowns are often fragmentary, and the cusplets and/or the point of the main cusp are usually missing. The number of the crown and root fragments is high as well. These features indicate that the remains were transported and destructed in high energy environments (i.e., above the wave base). Altogether 854 shark and ray teeth, and two placoid scales were found in the Pusztamiske Formation. Due to the bad preservation, 308 teeth could be described only as Selachimorpha indet. Much less chondrichthyan fossils, only 27 tooth remains came from the Leitha Limestone Formation. It must be mentioned that the teeth are very similar in colour and appearance in both formations, therefore it cannot be ruled out that a few fish remains may have fallen from the Leitha Limestone Formation into the pebble-material of the Pusztamiske Formation.

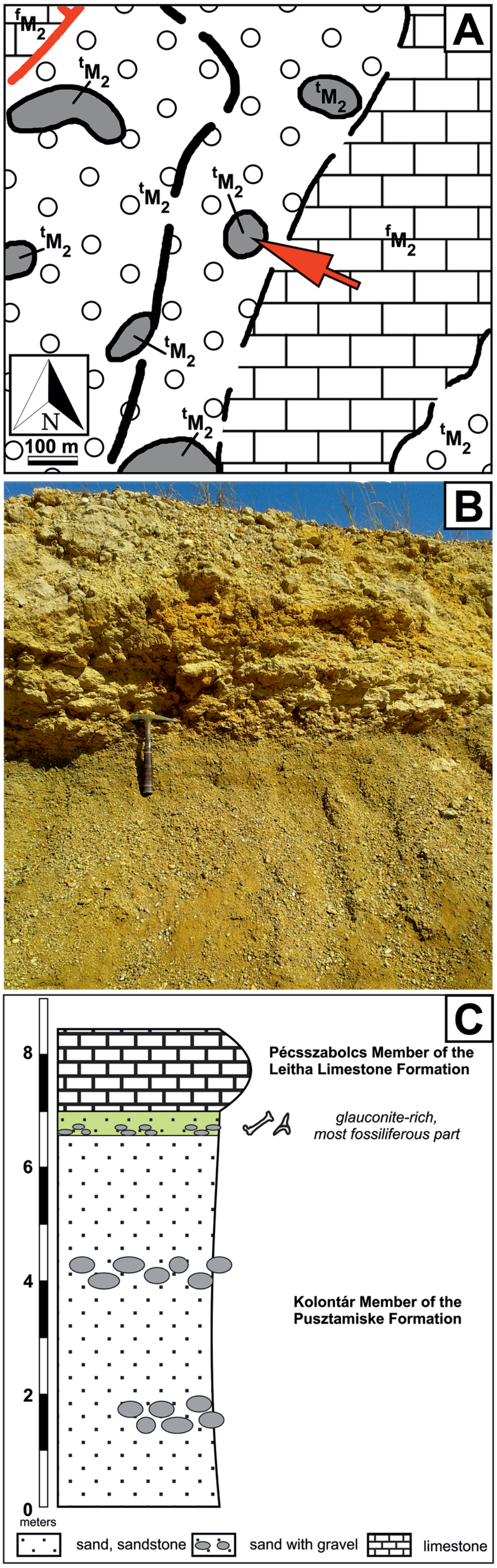


**Fig. 3.** The geological setting of the Nyirád locality. **A** — The areal extent of the site (red arrow symbol) and its region ($^{t}M_2$=Pusztamiske Fm., $^{f}M_2$=Fertőrákos Limestone Fm.) (modified after the geological map of Gyalog & Császár 1982). **B** — The two main formations of the locality; the Leitha Limestone Formation (upper) can be observed clearly on the pebble-matrix of the Pusztamiske Formation (lower). **C** — Simplified sediment profile of the outcropping layers of the fossil bearing formations. The colours refer to the online version of the paper

Over the years we met a few amateur collectors, who have been collecting fossils from the location for years. As a result of their helpfulness, our knowledge about the fish assemblage of the Nyirád locality became more complete.

Below in the systematic chapter the anatomical descriptions of the better preserved teeth are discussed. The classification largely relies on the works of Cappetta (1987, 2012) (Fig. 5), while the fauna and synonym lists are mainly concentrated on Paratethyan and European key localities (see Table 1–2).

## Systematic palaeontology

Class: **Chondrichthyes** Huxley, 1880
Order: **Hexanchiformes** De Buen, 1926
Family: **Hexanchidae** Gray, 1851
Genus: ***Notorynchus*** Ayres, 1855
***Notorynchus primigenius*** (Agassiz, 1843)
Fig. 6 A–B

1843 *Notidanus primigenius* sp. nov.; Agassiz: 218-220, pl. 27: 6-17.
1879 *Notidanus primigenius* Ag.; Probst: 158-162, pl. 3: 12-17.
1965 *Notidanus primigenius* Ag.; Radwański: 268-269, pl. 1: 1, 2.
1970 *Hexanchus primigenius*; Cappetta: pl. 4: 11-19.
1971 *Hexanchus primigenius* (Agassiz); Schultz: 315-316, pl. 1: 1-3.
1978 *Hexanchus primigenius* (Ag.); Brzobohatý and Schultz: 442, pl. 1: 1-3.
1995 *Notorhynchus primigenius* (Agassiz, 1843); Hiden: 55-56, pl. 2: 1.
2001 *Notorynchus primigenius* (Agassiz, 1843); Holec: 119, pl. 1: 1.
2013 *Notorynchus primigenius* (Agassiz, 1835); Schultz: 24-27, pl. 4: 6(a+b) –11(a+b).
2013 *Notorynchus primigenius* (Agassiz, 1835); Šoster and Mikuž: 75-76, pl. 1: 1-3.

Referred tooth material: 1 lateral (?anterolateral) tooth crown (placed in private collection; stratigraphical origin is unknown).

The genus includes only one extant species, *Notorynchus cepedianus* (Péron 1807) (Compagno 1984). The tooth morphology of the cow sharks is easily recognizable. The lower teeth have a main cusp, followed by several cusplets both mesially and distally, reduced in height. The main cusps of these teeth usually sit at the mesial third of the mesiodistal fore-axis. The distal cusplets are bigger than the tiny mesials, there are mostly five-six of them. The lower anterolateral teeth are flattened labiolingually and widened mesiodistally. The root is wide and flattened, it reaches its maximal thickness under the crown-root boundary and it gets thinner towards its base (Holec et al. 1995). Teeth of the upper dentition lack in mesial cusplets, but have a main cusp significantly outgrows the cusplets, which are less in number than those of the lower teeth (usually two–three distal

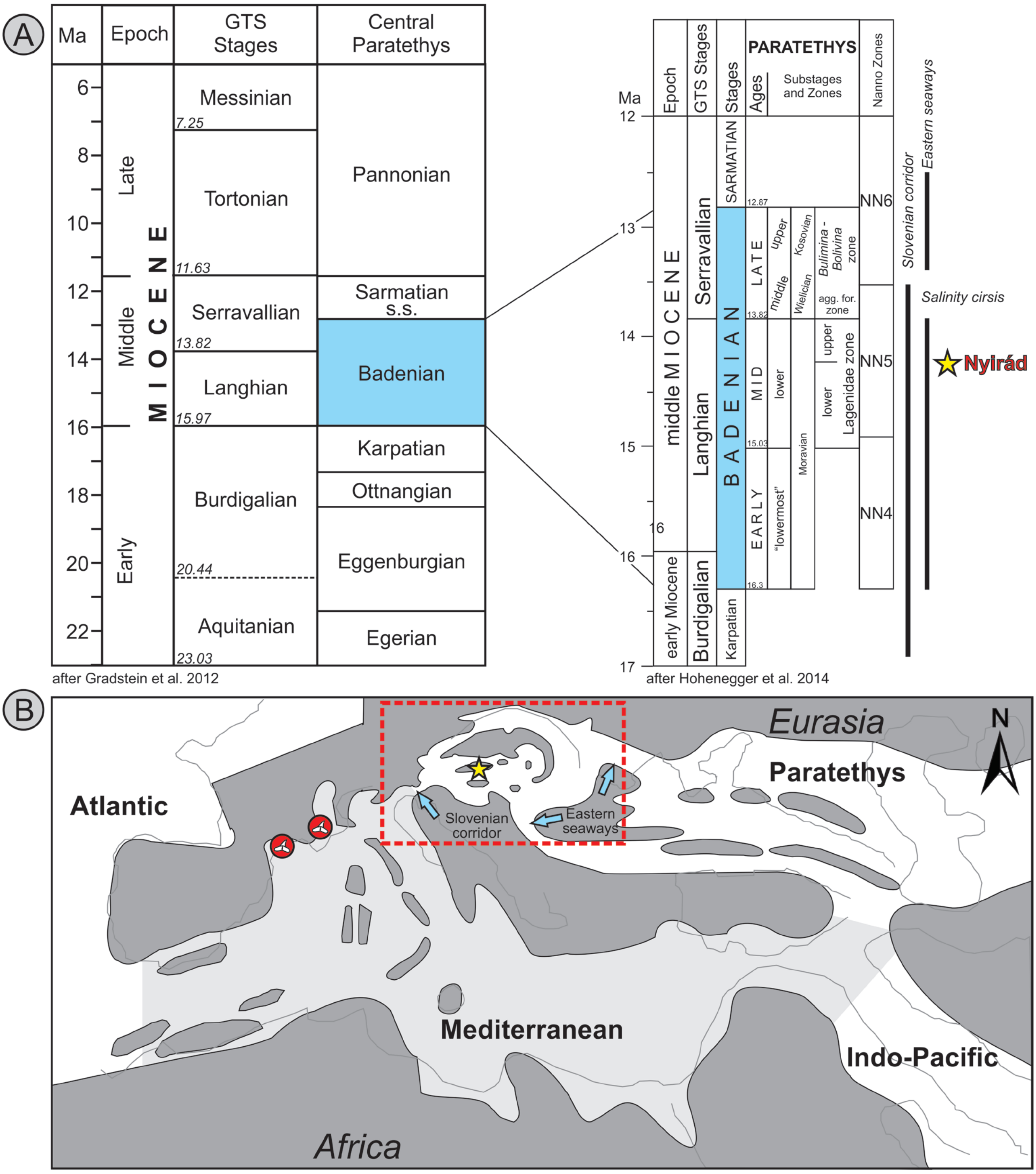


**Fig. 4**. **A** — Comparison between the global Miocene Geological Timescale and the Central Paratethyan regional stages (Gradstein et al. 2012). Note that the subdivision of the Badenian is complicated and its lower limit has been recently proposed to be before the Langhian–Burdigalian boundary (Hohenegger et al. 2014). **B** — Lanhgian palaeogeographic map with the different marine realms (after Rögl 1998; Kováč et al. 2007). The red rectangle marks the Central Paratethys with the Nyirád locality (yellow star symbol). For recent positions and other localities see Fig. 1. Blue arrows show connections with other marine provinces. Red circles are important and rich comparative fauna from the Mediterranean (Cappetta 1970; Vialle et al. 2011). The colours refer to the online version of the paper.

cusplets). The lower symphyseals have a characteristic, nearly symmetrical contour, their detailed morphology is variable. Regarding fossil teeth, Vitális (1942) compared the Badenian *N. primigenius* teeth from Mátraszőlős (northern Hungary, see Fig. 1) with the dentition of living hexanchid species. This work is possibly one of the first well-detailed comparative studies between modern and fossil teeth within this shark group.

The only cow shark tooth found at Nyirád is in a private collection. Unfortunately its stratigraphical origin is unknown

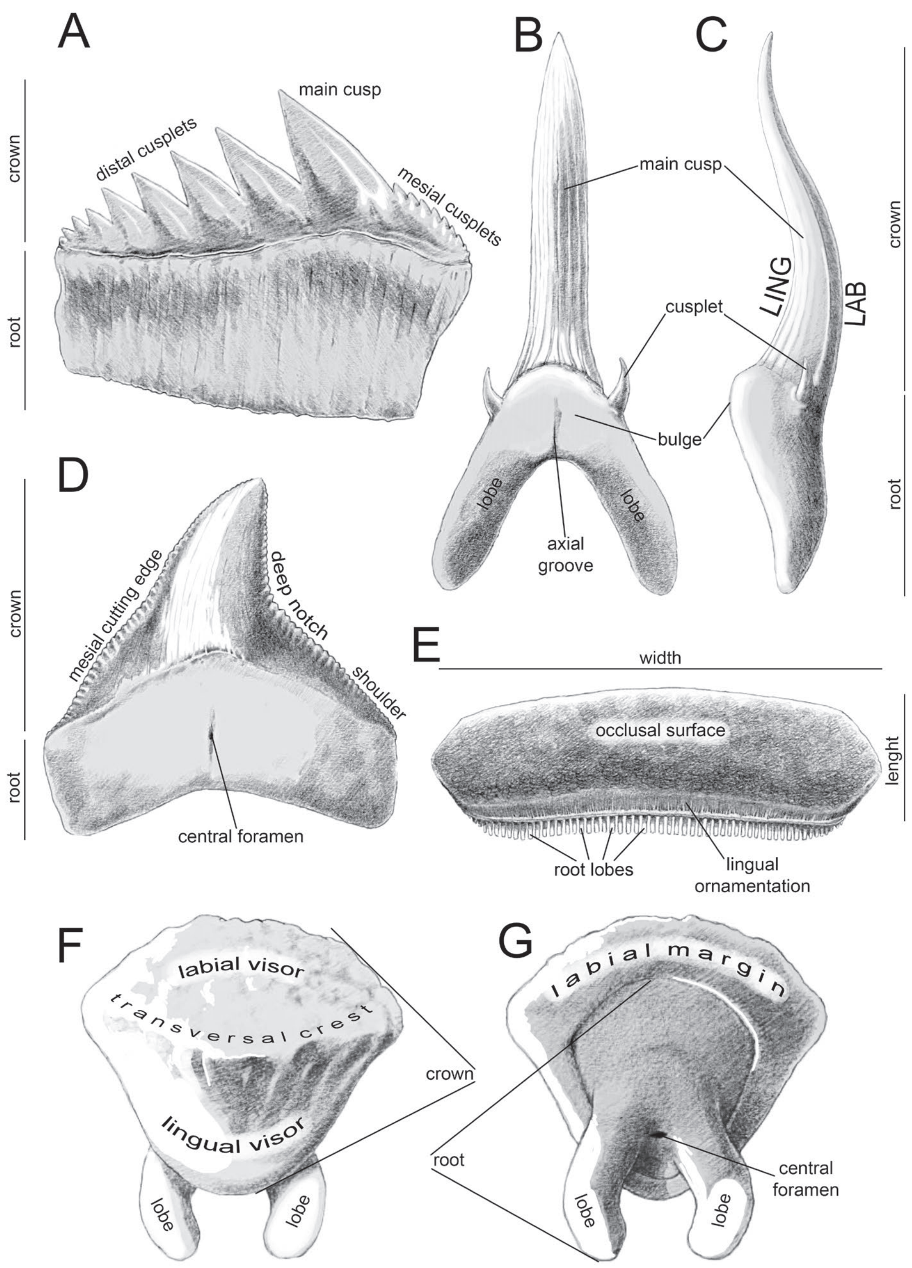


**Fig. 5.** Tooth terminology of the chondrichthyan remains. **A** — Hexanchidae tooth in lingual view. **B** — Odontaspididae tooth in lingual view; C — in mesiodistal view (lab: labial side, lin: lingual side). **D** — Carcharhinidae tooth in lingual view. **E** — Myliobatidae tooth in semi-occlusal/lingual view. **F** — Dasyatidae tooth in occlusal; **G** — in basal view (after Cappetta 2012).

and its root is missing. The number of the mesial cusplets is 6. The main cusp has been preserved as well, just like the following first distal cusplet, which is nearly as big as the main cusp. This feature is referable to the lower lateral and anterolateral teeth.

Order: **Lamniformes** Berg, 1958
Family: **Odontaspididae** Müller and Henle, 1841
Genus: ***Araloselachus*** Glikman, 1964
***Araloselachus cuspidatus*** (Agassiz, 1843)
Fig. 6 C–D

1843 *Lamna cuspidata* sp. nov.; Agassiz: 290, pl. 37a: 43-50.
1970 *Odontaspis cuspidata*; Cappetta: pl. 3: 6-10.
1995 *Carcharias cuspidata* (Agassiz, 1844); Hiden: 58-59, pl. 2: 2.
2001 *Carcharias cuspidatus* (Agassiz, 1843); Holec: 121-123, pl. 1: 5,6a and pl. 2: 1.
2007 *Carcharias cuspidatus* (Agassiz, 1843); Kocsis: 32, fig. 4.12-13.
2010 *Carcharias cuspidatus* (Agassiz, 1983); Schultz et al.; pl. 1: 12,13,15.
2012 *Araloselachus cuspidatus* (Agassiz, 1843); Cappetta: 191, text-fig. 180.
2013 *Carcharias cuspidatus* (Agassiz, 1843); Schultz: 61-66, pl. 5: 5(a+b), 6(a+b)

Collected tooth material: 2 teeth (Pusztamiske Fm.: MFGI V 2014.113.3.1-2.)

This species was long thought to belong to the genus *Carcharias*, but recently Cappetta (2012) placed it into the genus *Araloselachus*. The species is known from the Lower Oligocene to the Middle Miocene in Europe and North America (Reinecke et al. 2001; Cappetta 2012).

The teeth are similar to those of *C. acutissima*, but they are more robust and strong, their main crown is much wider. Another difference is that the striation of the lingual side of the main crown is missing. The lingual face of the main cusp is strongly, while the labial face of it is weakly convex. The cutting edges are smooth all along. The cusplets are low, curved, short on the anteriors, and labiolingually flattened, wide on the laterals.

Two lateral teeth are referred to this species from the locality. The more completely preserved specimen (MFGI V 2014.113.3.2., see Fig. 6C, D) is much more robust than any collected *C. acutissima* tooth (see on Fig. 6). The root is thicker and stronger, just like the main cusp. The places of the denticles are clearly visible on the lobes of the bifurcated, asymmetrical root.

Genus: ***Carcharias*** Rafinesque, 1810
***Carcharias acutissima*** (Agassiz, 1843)
Fig. 6 E–J

1843 *Lamna (Odontaspis) acutissima* sp. nov.; Agassiz: 294, pl. 37a: 33, 34.
1970 *Odontaspis acutissima*; Cappetta: pl. 1: 1-22. and pl. 2: 1-16.
1978 *Odontaspis (Synodontaspis) acutissima acutissima* (Ag.); Brzobohatý and Schultz: 443, pl. 1: 12, 13.
1995*Carcharias acutissima* (Agassiz, 1844); Hiden: 57-58, pl. 1: 1, 2.
1995 *Synodontaspis acutissima* (Agassiz, 1844); Holec et al.: 40-41, pl. 10: 3-5. and pl. 11: 1, 3.
2001 *Carcharias acutissimus* (Agassiz, 1844); Holec: 119-121, pl. 1: 6b, 7.
2007 *Carcharias acutissima* (Agassiz, 1843); Kocsis: 31-32, fig. 4. 6-11.
2013 *Carcharias acutissimus* (Agassiz, 1843); Schultz: 55-60, pl. 5: 7(a+b), 8(a+b)
2014 *Carcharias acutissimus* (Agassiz, 1843); Pollerspöck and Beaury: 30-32, pl. 1: 7a, b
2015 *Carcharias taurus* Rafinesque, 1810; Reinecke and Radwański: 9, pl. 1:D-G

Collected tooth material: 11 teeth (Leitha Limestone Fm.: MFGI V 2014.93.1-3., MFGI V 2014.96.1.; Pusztamiske Fm.: MFGI V 2014.92.3.1-3., MFGI V 2014.91.1., MFGI V 2014.94.1., MFGI V 2014.95.1., MFGI V 2014.113.3.).

The species appeared in the Lutetian (Eocene), and it became widespread in the Miocene epoch (Cappetta 2012). The dentition is strongly heterodont, which is typical for the genus (e.g., Taniuchi 1970; Purdy et al. 2001).

The crown is weakly convex on the labial, while, strongly convex on the lingual face. The root is bifurcated with well developed nutritive groove, and strong internal bulge. The teeth have mostly one pair, but sometimes two pairs of cusplets. The cutting edges are smooth both mesially and distally and they run along the crown.

The anterior teeth (see Fig. 6E–H) are slender, thin, elongated, the shape of the main crown is typically "S"-like in lateral view. The cusplets of the anterior teeth are pointed, thick at their bases and round in section (Cunningham 2000; Antunes & Balbino 2003). The main cusp of the upper lateral teeth (see Fig. 6I, J) are straighter in lateral view, the cusplets of these teeth are mostly flattened labiolingually. The crown is thick at the base, and it slightly bends distally. On some lateral teeth there are two pairs of cusplets (Antunes & Balbino 2003), although it is not typical.

The lingual side of the main crown is slightly folded vertically, especially on the anterior teeth. This striation is not as strong as in the family Mitsukurinidae (goblin sharks), moreover the taxonomical relevance of this feature for the *Carcharias* teeth is questionable (Kocsis 2007). The striation is more visible on the juvenile teeth, and it extends beyond the half of the height of the main crown, while this striae pattern on the teeth of adult animals is not very visible, and it becomes weaker at about the middle height of the main crown (Cappetta 1970; Antunes & Balbino 2003).

**Odontaspididae** indet.

Collected tooth material: 302 teeth (Leitha Limestone Fm.: MFGI V 2014.117.10.1-10., MFGI V 2014.101.4.1-4.; Pusztamiske Fm.: MFGI V 2014.97.85.1-85., MFGI V 2014.100.39.1-39., MFGI V 2014.104.20.1-20., MFGI V 2014.105.2.1., MFGI V 2016.20.1.).

Tooth remains of Odontaspididae sharks (sand tiger sharks) are typical chondrichthyan remains of the Miocene marine sediments worldwide. The anterior teeth are easily distinguishable by their sigmoid profile. The lateral teeth are more blade-like, they bend distally, but they are less curved in lateral view than the anterior teeth.

At Nyirád the teeth of this family are the most common (altogether 315 specimens), however, most of them can be identified only as indeterminate Odontaspididae, because of their missing root and cusplets.

Family: **Lamnidae** Müller and Henle, 1838
Genus: ***Carcharoides*** Ameghino, 1901
***Carcharoides cf. catticus*** (Philippi, 1846)
Fig. 7 A–G

1846 *Otodus catticus* sp. nov.; Philippi: 24, pl. 2: 5-7.
1879 *Otodus debilis* sp. nov.; Probst: 155, pl.2: 78-81.
1970 *Lamna cattica*; Cappetta: pl. 4: 1-9.
1995 *Carcharoides catticus* (Philippi, 1846); Holec et al.: 42, pl. 12: 2.
2007 *Carcharoides catticus* (Philippi, 1851); Kocsis: 33, fig. 5. 1-3.
2011 *Carcharoides catticus* (von Philippi, 1846); Vialle et al.: 246, fig. 2. 10.

Collected tooth material: 14 teeth (Pusztamiske Fm.: MFGI V 2016.38.1., MFGI V 2016.39.1., MFGI V 2016.40.1., MFGI V 2016.41.1.).

The *Carcharoides* remains from Nyirád are very fragmentary. The material consists of isolated main crowns (Fig. 7A–C and E–G) and other isolated, asymmetrical cusplets (typical feature for lateral to distal teeth; see Fig. 7D), therefore we refer to them only as *Carcharoides* cf. *catticus*. The pointed anterior teeth are straight, relatively high and symmetrical, while the laterals and the distals are distally bent, with asymmetrical main crown and cusplets. The cutting edge is smooth, a feature that distinguishes the species from *Carcharoides totuserratus* (Ameghino, 1901). The main crown of the anterior files is a little bit more concave on both faces, than those of the lateral to distal files. The cusplets are relatively big, pointed and roundish in cross section on anteriors, while triangular and flattened on lateral-distal teeth. On lateral-distal teeth the main cusp is pointed, flattened labiolingually, and just weakly concave on both faces. Of these teeth the cutting edges of the main cusp run down to the crown-root boundary, where they connects to those of the cusplets.

The teeth of this extinct lamnoid shark are known from several Tertiary sediments of Europe. They have been reported from Hungary too, from the Eggenburgian of Ipolytarnóc (Kocsis 2007), and from the Rupelian to early Chattian Kiscell Clay Formation of the Buda Hills (Weiler 1933, 1938), which is one of the oldest records of the species (see Reinecke et al. 2014). Regarding the Paratethyan shark faunas, this is the very first *Carcharoides* discovery from the Badenian. The habitat of this shark is not well known, but the sudden rarity of this taxon by the Badenian may relate to reduction of its habitat that probably can be linked to the gradual separation of the Paratethys from the Mediterranean. This may suggest a rather open-water, pelagic habitat. Nevertheless, globally the genus died out at the end of the Langhian (Cappetta 2012) and their presence in the palaeo-Mediterranean also decreased gradually. Therefore, the disappearance of the genus from the Paratethys is not unique.

Genus: ***Cosmopolitodus*** Glikman, 1964
***Cosmopolitodus hastalis*** (Agassiz, 1843)
Fig. 7 H–K

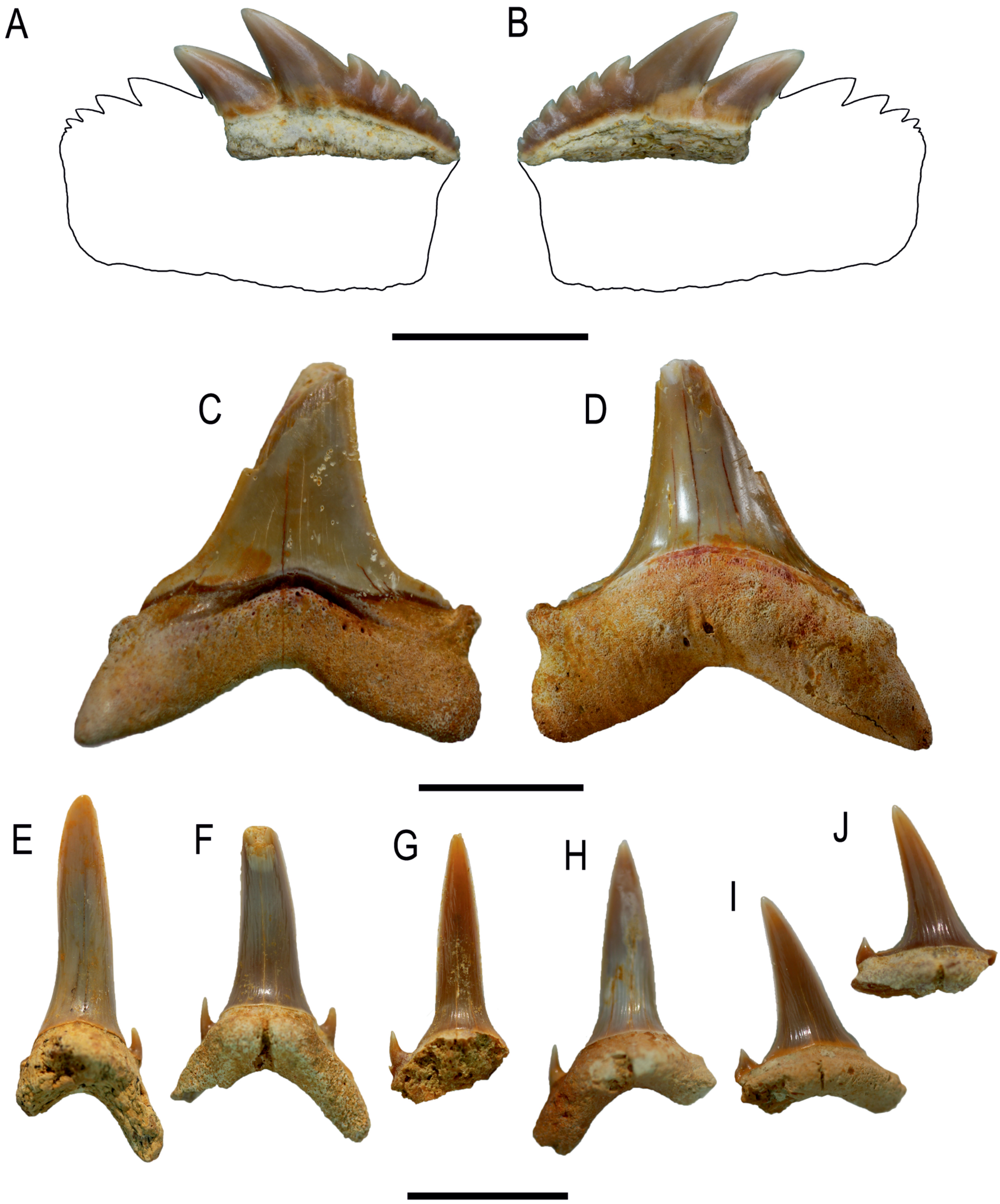


**Fig. 6.** Badenian selachian teeth from the Nyirád locality. **A–B:** *Notorynchus primigenius* lower lateral (?anterolateral) tooth; A — in lingual view; B — in labial view. **C–D:** *Araloselachus cuspidatus* upper lateral tooth (MFGI V 2014.113.3.2.); C — in labial view, D — in lingual view. **E–J:** *Carcharias acutissima*; E–H — anterior teeth in lingual view (E: MFGI V 2014.92.3.1., F: MFGI V 2014.92.3.2., G: V 2014.92.3.3., H: MFGI V 2014.91.1.); I–J — upper lateral teeth in lingual view (I: MFGI V 2014.113.3., J: MFGI V 2014.94.1.). Specimens placed in private collections: A (B). Scale bars: 10 mm

1843 *Oxyrhina hastalis* sp. nov.; Agassiz 1843: 277-278, pl. 34: 3, 6,13-18.
1879 *Oxyrhina hastalis* Ag.; Probst: 129-131, pl. 2: 1-6.
1965 *Oxyrhina hastalis* Agassiz, 1843; Radwański: 269-270, pl. 1: 3.
1970 *Isurus hastalis*; Cappetta: pl. 5: 1-13.
1978 *Isurus hastalis hastalis* (Ag.); Brzobohatý and Schultz: 443, pl. 2: 18, 19.
1995 *Isurus hastalis* (Agassiz, 1843); Holec et al.: 42-43, pl. 12: 4.
2007 *Isurus hastalis* (Agassiz, 1843); Kocsis: 34-35, fig. 5.7-8.
2010 *Cosmopolitodus hastalis* (Agassiz, 1843); Schultz et al.: pl. 1: 9-11.
2013 *Cosmopolitodus hastalis* (Agassiz, 1838); Mikuž et al.: 122-125, pl. 1: 1, 2.
2013 *Cosmopolitodus hastalis* (Agassiz, 1843); Schultz: 43-47, pl. 4: 17, 21, 22(a+b)
2013 *Cosmopolitodus hastalis* (Agassiz, 1838); Šoster and Mikuž: 78, pl. 3: 19, 20.

Collected tooth material: 10 teeth (Leitha Limestone Fm.: MFGI V 2014.11.5.1-2.; Pusztamiske Fm.: MFGI V 2014.114.5.1-5., MFGI V 2016.2.1.).

The genus is known from the Lower Miocene and widespread till the late Pliocene (Cappetta 2012). The crown of the upper teeth is strongly flattened labiolingually. The lower anterior teeth are narrower, and more convex in their lingual face, than the upper anteriors. The tooth crown is not considerably thick on the upper teeth, but the lower dentition has visibly thicker crowns. The thickness of the crown of all teeth reaches its maximum near the root (Holec et al. 1995). Both sides of the crown have smooth surface, the cutting edges run from the apex to the crown-root boundary both on the mesial and the distal side. The carinae are not serrated, cusplets cannot be observed.

The crown of the anteriors is straight and is more elongated apicobasally than that of the laterals (see Fig. 7H). The lateral (see Fig. 7I) and anterolateral (see Fig. 7J) teeth have a typically triangle shaped crown. The distal teeth (see Fig. 7K) are curved distally. The root is strongly bifurcated on the lower teeth, but weakly bifurcated and mesiodistally widened on the teeth of the upper dentition.

Family: **Otodontidae** Glikman, 1964
Genus: ***Otodus*** Agassiz, 1838
Subgenus: ***Otodus (Megaselachus)*** Glikman, 1964
***Otodus (Megaselachus) megalodon*** (Agassiz, 1843)
Fig. 7 L–P

1843 *Carcharodon megalodon* sp. nov.; Agassiz: 247-249, pl. 29: 1-7.
1970 *Procarcharodon megalodon*; Cappetta: pl. 6: 2.
1978 *Procarcharodon megalodon megalodon* (Ag.); Brzobohatý and Schultz: 443, pl. 3: 23.
1979 *Procarcharodon megalodon* (Agassiz, 1843); Schultz: 291, pl. 1: 1.
1995 *Carcharocles megalodon* (Agassiz, 1843); Hiden: 61-62, pl. 2, pl. 3: 1, 2.
1999 *Carcharocles megalodon* (Agassiz, 1843); Mikuž: 144-146, pl. 1: 1a, b
2001 *Carcharocles megalodon* (Agassiz, 1843); Holec: 123, pl. 3: 2.
2007 *Carcharocles* sp.; Kocsis: 34, fig. 5. 10.
2010 *Megaselachus megalodon* (Agassiz, 1835); Schultz et al.; pl. 1: 1, 2.
2012 *Otodus (Megaselachus) megalodon* (Agassiz, 1835); Cappetta: 224-227, text-fig. 210.
2013 *Megaselachus megalodon* (Agassiz, 1835); Schultz: 70-75, pl. 6: 1(a+b)-6(a+b)
2015 *Megaselachus megalodon* (Agassiz, 1835); Mikuž et al.: 79-83, pl. 1-8 with all figures

Collected tooth material: 2 tooth fragments (MFGI V 2014.90.2.1-2.).

This species is the biggest, currently known macropredatory shark that ever lived (Pimiento et al. 2010). Its massive tooth remains are probably the most spectacular shark tooth fossils of the Miocene sediments worldwide. Fossils of the species were reported from the Middle Miocene to Pliocene, the newest results show that this shark species went extinct around 2.6 million years ago, around the Pliocene-Pleistocene boundary (Pimiento and Clements, 2014). The taxonomic assignment of this shark species has been debated for decades, but Cappetta (2012) classified it into the genus *Otodus* Agassiz, 1838, then he separated the genus into three subgenera: *Otodus (Otodus)* Agassiz 1838, *Otodus (Carcharocles)* Jordan and Hannibal 1923 and *Otodus (Megaselachus)* Glikman 1964 (Cappetta 2012).

The lingual side of the crown is strongly convex, while the labial side is typically flat. The cutting edges are strongly serrated in their full length both on the mesial and distal sides. The root is bifurcated and usually symmetric. The crown of the anteriors is high, triangle shaped, wide with clearly visible crown-root boundary. Going backwards distally the height of the teeth reduces, and the crowns get more curved distally as well.

Most of the *Otodus (Megaselachus) megalodon* teeth fossils from Nyirád were collected by private collectors.

Order: **Carcharhiniformes** Compagno, 1973
Family: **Hemigaleidae** Hasse, 1879
Genus: ***Hemipristis*** Agassiz, 1843
***Hemipristis serra*** Agassiz, 1843
Fig. 8 A–E

1843 *Hemipristis serra* sp. nov.; Agassiz: 237, pl. 27: 18-30.
1970 *Hemipristis serra*; Cappetta: pl. 11: 1-18.
1878 *Hemipristis klunzingeri* sp. nov.; Probst: 146-149, pl. 1: 58-63.
1878 *Hemipristis serra* Ag.; Probst: 143-146, pl. 1: 49-57.
1978 *Hemipristis serra* Ag.; Brzobohatý and Schultz: 443, pl. 1: 6.
1995 *Hemipristis serra* Agassiz, 1843; Hiden: 64-65, pl. 4: 1-2.
1995 *Hemipristis serra* Agassiz, 1843; Holec et al.: 45-46, pl. 16: 1-4. and pl. 17: 1-3.
2001 *Hemipristis serra* Agassiz, 1843; Holec: 127, 129, pl. 2: 10. and pl. 3: 1.
2007 *Hemipristis serra* Agassiz, 1843; Kocsis: 36, fig. 6. 5-6.
2010 *Hemipristis serra* Agassiz, 1835; Schultz et al.; pl. 1: 3-5.
2013 *Hemipristis serra* Agassiz, 1835; Schultz: 90-93, pl. 7: 5(a+b), 8(a+b)-10(a+b)

Collected tooth material: 4 teeth (Pusztamiske Fm.: MFGI V 2014.110.4.1-4.).

Snaggletooth sharks typically have dignathic heterodont dentition. The upper teeth are labiolingually flattened, distally

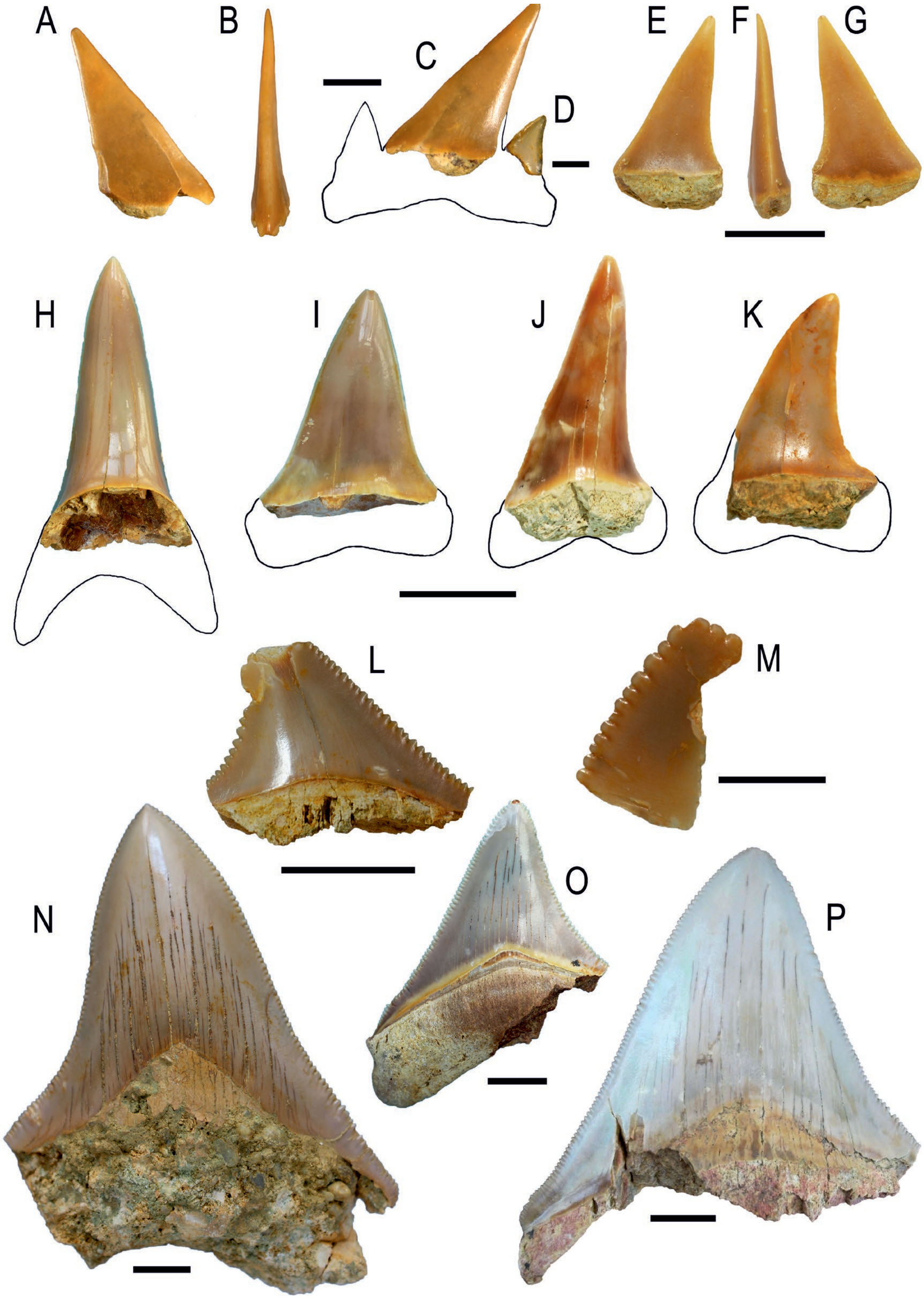


**Fig. 7.** Badenian selachian teeth from the Nyirád locality. **A–G:** *Carcharoides* cf. *catticus;* A — main cusp of an upper lateral tooth (MFGI V 2016.38.1.) in labial view; B — in mesial view; C — in lingual view; D — cusplet of an upper lateral tooth (MFGI V 2016.39.1.) in ?lingual view; E — main cusp of an upper lateral tooth (MFGI V 2016.40.1.) in lingual view; F — in mesial view; G — in labial view. **H–K:** *Cosmopolitodus hastalis*; H–I — anterior teeth in lingual view; J–K — lateral teeth in lingual view (J: MFGI V 2014.114.5.1., K: MFGIV 2014.114.5.2.). **L–P:** *Otodus (Megaselachus) megalodon*; L — distal tooth in lingual view; M — tooth crown tip in ?labial view (MFGI V 2014.90.2.1.); N–P — anterolateral teeth in lingual view. Tooth root contours of *Cosmopolitodus hastalis* teeth have been reconstructed based on specimens seen in private collection. Specimens placed in private collections: H, I, L, N, O, P. Scale bars: A–C: 2 mm, D: 1mm, E–G and M: 5 mm, L and N–P: 10 mm.

bent, triangle shaped with wide crown and visibly serrated cutting edges, except the symphyseals. The distal cutting edge of these teeth is concave, while the mesial is strongly convex. These features make them similar to the teeth in the distal third of the lower jaw. The lower and upper symphyseals, the lower anteriors and the first few lateral teeth have an awl-like contour in lingual view. The cutting edge is not serrated on these lingually curved teeth, and it runs only to the apical half of the tooth crown. Several cusplets can be also observed on these teeth.

The tooth remains of *Hemipristis serra* are common and abundant worldwide in Miocene marine sediments. The modern species of the genus is the *Hemipristis elongata* (Klunzinger, 1871). Although the dentition of *H. elongata* and *H. serra* is closely similar, the main difference between them are the more numerous serrations on the upper laterals of the modern species. Additionally, an increase in tooth size with age was also reported for the genus from the Lee Creek Mine (Chandler et al. 2006).

Family: **Carcharhinidae** Jordan and Evermann, 1896
Genus: ***Carcharhinus*** Blainville, 1816
***Carcharhinus priscus*** (Agassiz, 1843)
Fig. 8 F–L

1843 *Sphyrna prisca* sp. nov.; Agassiz: 234-235, pl. 26a: 44, 47.
1970 *Carcharhinus priscus*; Cappetta: pl. 13:1-20 and pl. 14: 1-20.
1978 *Carcharhinus priscus* (Ag.); Brzobohatý and Schultz: 442, pl. 1: 9.
1995 *Carcharhinus priscus* (Agassiz, 1843); Hiden: 65-66, pl. 5: 2.
1995 *Carcharhinus priscus* (Agassiz, 1843); Holec et al.: 46, pl. 18: 1, 2.
1995 *Carcharhinus similis* (Probst, 1878); Holec et al.: 46-47, pl. 18: 3-4.
2001 *Carcharhinus priscus* (Agassiz, 1843); Holec: 123-125, pl. 2: 4, 6.
2001 *Carcharhinus similis* (Probst, 1878); Holec: 125, pl. 2: 5.
2007 *Carcharhinus priscus* (Agassiz, 1843); Kocsis: 36-38, fig. 6.7-12.
2010 *Carcharhinus priscus* (Agassiz, 1843); Schultz et al.; pl. 2: 11.
2013 *Carcharhinus priscus* (Agassiz, 1843); Schultz: 80-84, pl. 7: 6(a+b), 7(a+b)
2015 *Carcharhinus priscus* (Agassiz, 1843); Reinecke and Radwański: 13, pl. 4: A-R

Collected tooth material: 28 teeth (Leitha Limestone Fm.: MFGI V 2014.106.2.1-2.; Pusztamiske Fm.: MFGI V 2014.108.10.1-10., MFGI V 2016.22.1.).

The genus has a typical dignathic heterodonty in its dentition. The lower dentition of the different species can be very similar, and therefore the species are mainly best distinguished by their upper dentition (see e.g., Bourdon 1997–2013, Cappetta 2012). The lower teeth are simpler than the upper ones, but their corresponding counterpart is similar in size.

The tooth crown of this genus is typically not higher than the width of the tooth (anteriors are the highest), it is narrow triangle shaped (sometimes weakly bent distally) on the anterior teeth, while strongly bent distally on the laterals. The cutting edges run downward, and continue on the lobes of the root on both sides, while creating the enamel-shoulders. The serration of the cutting edges is strongest on the enamel-shoulders. The root is widened mesiodistally, usually there is an axial groove on the middle of the lingual side.

The genus is known from the Lutetian (Cappetta 2012) and become widespread and radiated during the Miocene and Pliocene. The *C. priscus* was a very common form in the Palaeo-Mediterranean Sea and the Paratethys. In the Lower and Middle Miocene sometimes another species, *C. similis* is mentioned (Probst 1878, Barthelt et al. 1991; Holec et al. 1995, 2001), and its teeth are often confused with the *C. priscus* (see the synonym list).

Genus: ***Galeocerdo*** Müller and Henle, 1837
***Galeocerdo aduncus*** Agassiz, 1843
Fig. 8 M–R

1843 *Galeocerdo aduncus* sp. nov.; Agassiz: 231, pl. 26: 25-28.
1970 *Galeocerdo aduncus*; Cappetta: pl. 12:1-21.
1978 *Galeocerdo aduncus* Ag.; Brzobohaty and Schultz: 442-443, pl. 1: 10.
1995 *Galeocerdo aduncus* Agassiz, 1843; Hiden: 66-67, pl. 4: 4.
1995 *Galeocerdo aduncus* Agassiz, 1843; Holec et al.: 47-48, pl. 19: 1, 2, 4-6.
2001 *Galeocerdo aduncus* Agassiz, 1843; Holec: 125-127, pl. 2: 9.
2007 *Galeocerdo aduncus* Agassiz, 1843; Kocsis: 38, fig. 6.13-14.
2010 *Galeocerdo aduncus* (Agassiz, 1835); Schultz et al.: pl. 1: 6-8.
2013 *Galeocerdo aduncus* (Agassiz, 1835); Schultz: 84-87, pl. 7: 11(a+b), 12(a+b)
2015 *Galeocerdo aduncus* Agassiz, 1835; Reinecke and Radwański: 12-13, pl. 1: H-I

Collected tooth material: 9 teeth (Leitha Limestone Fm.: MFGI V 2014.111.2.1-2.; Pusztamiske Fm.: MFGI V 2014.112.6.1-6., MFGI V 2014.105.2.2.).

The genus is known from the early Eocene. The species *G. aduncus* appeared in the early Oligocene, and became widespread in the Miocene Epoch (Cappetta 2012).

The dentition of the upper and the lower jaw is very similar (Compagno 1984), but the teeth sitting in the same jaw can be distinguished by their position (monognathic heterodonty). The teeth reduce in height and increase in width distally from the symphysis (Kocsis 2007). The mesial cutting edge is convex and visibly serrated, while the distal cutting edge wears a deep notch, which separates the main cusp from the distal shoulder of the tooth. The tooth-shoulder wears a massive, distally reducing serration. The root lobes are slightly curved lingually.

Genus: ***Negaprion*** Whitley, 1940
***Negaprion*** sp.
Fig. 8 S–T

Collected tooth material: 1 tooth (Pusztamiske Fm.: MFGI V. 2014.107.1.).

The genus is known from the Lower Miocene (Burgidalian) and it exists today as well with two modern species: *Negaprion brevirostris* (Poey, 1868) and *Negaprion acutidens* (Rüppell, 1837) (Compagno 1984; Cappetta 2012; Pimiento et al. 2013b).

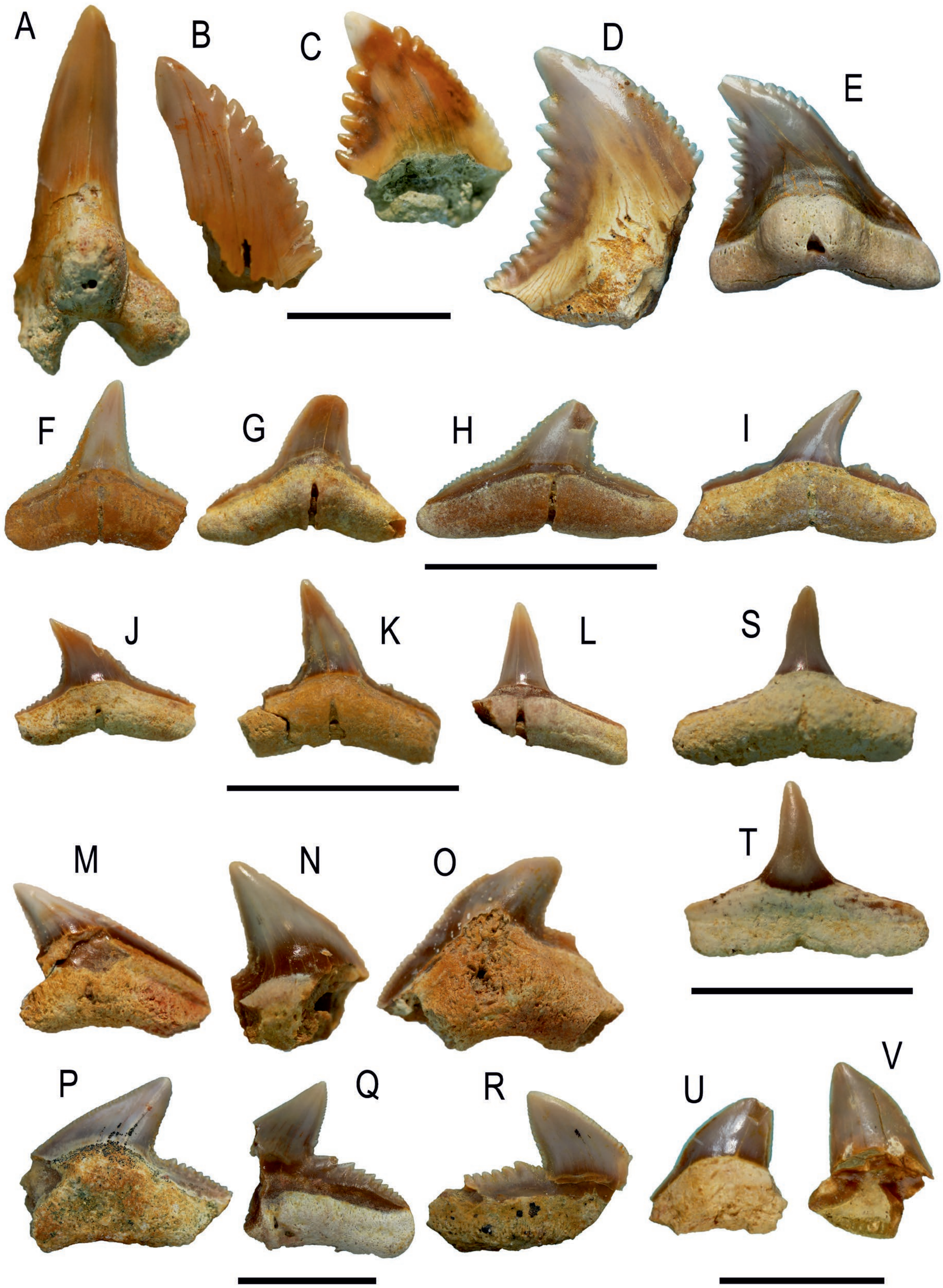


**Fig. 8.** Badenian selachian teeth from the Nyirád locality. **A–E:** *Hemipristis serra*; A — lower anterior tooth (MFGI V 2014.110.4.1.) in lingual view; B–E upper lateral teeth in lingual view (B: MFGI V 2014.110.4.2., C: MFGI V 2014.110.4.3.). **F–L:** *Carcharhinus priscus*; F, L — anterior teeth (L: MFGI V 2014.108.10.4.) in lingual view; G–K — lateral teeth in lingual view (G: MFGI V 2014.108.10.1., J: MFGI V 2014.108.10.2., K: MFGI V 2014.108.10.3.). **M–R:** *Galeocerdo aduncus*; M — posterior tooth (MFGI V 2014.112.6.1.) in lingual view; N–R — anterior (?anterolateral) teeth in lingual view (N: MFGI V 2014.112.6.2., O: MFGI V 2014.112.6.3.). **S–T:** *Negaprion* sp. lower posterior (?anterolateral) tooth (MFGI V.2014.107.1.); S — in lingual view; T — in labial view. **U–V:** *Sphyrna* cf. *zygaena* lateral teeth in lingual view (U: MFGI V 2016.42.1.). Specimens placed in private collections: D, E, F, H, I, P, Q, R, V. Scale bars: 10 mm.

The teeth of the genus have unserrated, sometimes lingually curved, pointed crowns perpendicular or nearly perpendicular to the root. The labial side of the crown is flat, while the lingual side is convex. The root runs mesiodistally, the axial groove usually clearly visible with a central foramen.

*Negaprion* tooth remains are very similar to the lower teeth of the *Carcharhinus* genus, but according to Pimiento et al. (2013a,b), they are easy to distinguish from them by their smooth, unserrated cutting edge, and their thicker root. However, many modern *Carcharhinus* species have lower teeth with smooth cutting edge (Bourdon 1997-2013). Nevertheless, based on the somewhat bulkier root, this tooth from Nyirád is placed under this genus.

**Carcharhinidae** indet.

Collected tooth remains: 118 teeth (Leitha Limestone Fm.: MFGI V 2014.99.1.; Pusztamiske Fm.: MFGI 2014.103.23.1-23., MFGI V 2016.43.1.).

Requiem shark remains are abundant fossils in Miocene marine sediments worldwide. The fragmentary tooth remains of this family at Nyirád are small, none of them is bigger than 5 mm. On some teeth slight serration can be observed on the cutting edges. The anterior crowns are straight, the laterals are weakly curved, and all remains are pointed. The roots and enamel-shoulders of all of these teeth are missing.

Family: **Sphyrnidae** Gill, 1872
Genus: ***Sphyrna*** Rafinesque, 1810
***Sphyrna*** cf. ***zygaena*** (Linnaeus, 1758)
Fig. 8 U–V

2001 *Sphyrna zygaena* (Linnaeus, 1758); Holec: 127, pl. 2: 7.
2001 *Sphyrna zygaena* (Linnaeus, 1758); Purdy et al.: 158-160, text-figs. 59-60
2007 *Sphyrna* cf. *zygaena* (Linnaeus, 1758); Kocsis: 38, fig. 6.18a-c

Collected tooth material: 1 tooth (Pusztamiske Fm.: MFGI V 2016.42.1.).

Hammerhead sharks are known from the early Oligocene (Cappetta 2012), and the taxon still exists with seven extant species (Compagno 2005).

The teeth are flattened labiolingually, the crown is wide at its base, and it slightly bends distally. The cutting edges are smooth both on the mesial and distal sides. The mesial cutting edge is slightly convex, while the distal one is straight, nearly perpendicular to the root, and it creates a deep notch near to the base of the crown. The distal cutting edge continues behind this deep notch on a smooth, convex enamel-shoulder. This feature can-not be observed on the Nyirád tooth as it is quite fragmentary. Part of the root of MFGI V 2016.42.1. is also missing, but it typically runs mesiodistally, and it bears a clearly visible transversal groove.

The hammerhead shark tooth from Nyirád is similar to those of *Sphyrna zygaena*, however, its poor preservation allows us to describe specimen MFGI V 2016.42.1. only as *Sphyrna* cf. *zygaena*.

Order: **Myliobatiformes** Compagno, 1973
Family: **Myliobatidae** Bonaparte, 1838
Genus: ***Aetobatus*** Blainville, 1816
***Aetobatus arcuatus*** (Agassiz, 1843)
Fig. 9 A–C

1843 *Aetobatis arcuatus* sp. nov.; Agassiz; p. 327
1965 *Aetobatis arcuatus* Agassiz, 1843; Radwański: 272, pl. 1: 7.
1970 *Aetobatis arcuatus*; Cappetta: pl. 24: 6-9.
1995 *Aetobatus arcuatus* (Agassiz, 1843);Hiden: 73-74, pl. 7: 3.
1995 *Aetobatis arcuatus* L. Agassiz, 1843; Holec et al.: 48, pl. 20: 1.
2001 *Aetobatus arcuatus* (L. Agassiz, 1843); Holec: 129-130, pl. 3: 5.
2011 *Aetobatus arcuatus* (Agassiz, 1843); Vialle et al.: 253, fig. 4.11.
2013 *Aetobatus arcuatus* (Agassiz, 1843); Schultz: 106-109, pl. 11: 9-13

Collected tooth material: 4 teeth (Pusztamiske Fm.: MFGI V 2014.89.2.1-2., MFGI V 2016.24.1., MFGI V 2016.25.1.).

This species is a relatively common eagle ray species in the Miocene marine sediments of Europe (Radwański 1965), and its tooth remains are easily distinguishable from those of other eagle ray taxa. Most of the typical features of the lower teeth can be well observed on all Nyirád specimens, however, they are all fragmentary.

The lower teeth of *A. arcuatus* are curved distally, they reach their maximal length at their mediolateral midline. The occlusal surface is smooth and shiny. The crown is separated from the root by a lingual bulge, which runs along the posterior side of the plate. The lingually bent root is made up by numerous laminae and grooves. The root reaches its maximal height in the midline of the tooth.

Genus: ***Myliobatis*** Cuvier, 1816
**?*Myliobatis*** sp.
Fig. 9 D–K

Collected tooth material: 44teeth (Leitha Limestone Fm.: MFGI V 2014.98.2.1-2.; Pusztamiske Fm.: MFGI V 2014.116.22.1-22., MFGI V 2016.26.1., MFGI V 2016.27.1., MFGI V 2016.28.1., MFGI V 2016.29.1., MFGI V 2016.30.1.).

This eagle ray genus is widely abundant in Miocene sediments. Numerous isolated, fragmentary ?*Myliobatis* teeth have been collected at the Nyirád site. They are widened mediolaterally, and slightly curved distally. The occlusal surface is shiny and smooth, the root lobes are high and mediolaterally flattened. The lateral edges of the tooth contour are angled in occlusal (and basal) view.

The ?*Myliobatis* sp. tooth remains are distinguished from those of *Rhinoptera* here by their relatively lower crown, the lingual extension of the root and the structure of the connections between the teeth. For the *Rhinoptera* genus the root not or only slightly extended lingually, and the connection between the tooth plates is more complex (so-called "tenon and mortise" connections; see Bourdon 2002). Still, due to the preservation of the teeth (e.g., broken and worn-off features), it is not impossible that some of the teeth may come from the *Rhinoptera* genus.

Family: **Dasyatidae** Jordan, 1888
Genus: ***Dasyatis*** Rafinesque, 1810
***Dasyatis*** cf. ***probsti*** Cappetta, 1970
Fig. 9 L–N

1970 *Dasyatis probsti* sp. nov.; Cappetta: 91-92, pl. 21:15-23.
1977 *Dasyatis* aff. *probsti* Cappetta, 1970; Schultz: 202, pl. 1: 2-3.
1995 *Dasyatis probsti* Cappetta, 1970; Hiden: 70, pl. 6: 5. and text-fig. 8C
2011 *Dasyatis probsti* Cappetta, 1970; Vialle et al: 252, figs. 4.5-6.
2014 *Dasyatis probsti* Cappetta, 1970; Pollerspöck and Beaury: 32, pl. 2: 7 a, b
2015 *Dasyatis probsti* Cappetta, 1970; Reinecke and Radwański: 14, pl. 6: A-D

Collected tooth material: 1 tooth (placed in private collection; stratigraphical origin is unknown).

The only known *Dasyatis* cf. *probsti* tooth from Nyirád is well preserved. The tooth has a two lobed root, both lobes are curved lingually, and have C-shaped contour in basal view. The crown bears a well developed transversal crest, which separates the crown into two visors: an anterior (labial) and a posterior (lingual) one. This feature refers the tooth as tooth of a female specimen. The lingual visor overhangs the root-lobes. The labial visor and the transversal crest have weakly reticulated ornamentation. The lingual margin has two lateral facets and a medial facet in basal view (Fig. 9N), a feature that is referred to this species by Hiden (1995, text-fig. 8C).

***Dasyatis rugosa*** (Probst, 1877)
Fig. 9 O–T

1877 *Raja rugosa* sp. nov.; Probst: 76, pl. 1: 5, 8, 9.
1970 *Dasyatis rugosa*; Cappetta: pl. 21: 1-14.
2011 *Dasyatis rugosa* (Probst, 1877); Vialle et al.: 253, fig. 4.7.
2014 *Dasyatis rugosa* (Probst, 1877); Pollerspöck and Beaury: 32, pl. 2: 8.
2015 *Dasyatis* cf. *rugosa* (Probst, 1877); Reinecke: 20-22, fig. 12.
2015 *Dasyatis rugosa* (Probst, 1877); Reinecke and Radwański: 14, pl. 7: D-F and pl.8: A-B

Collected tooth material: 9 teeth (Pusztamiske Fm.: MFGI V 2016.34.1., MFGI V 2016.35.1., MFGI V 2016.36.1., MFGI V 2016.37.1.).

This stingray species is abundant in the Miocene sediments of Europe. A few female teeth are known from Nyirád, with a relatively well preserved crown and missing root. Although the root lobes are not preserved, the specimens have typically robust lobes in basal view (see Hiden 1995, text-fig. 8B). The labial visor of these teeth is ornamented with small crenulations. The labial margin of the crown is smooth in basal view (see Fig. 9Q, T and also Hiden 1995, text-fig. 8B).

***Dasyatis*** sp.
Fig. 9 U–V

Collected tooth material: 14 teeth (Pusztamiske Fm.: MFGI V 2016.31.1., MFGI V 2016.32.1., MFGI V 2016.33.1.).

These tooth remains clearly belong to the genus *Dasyatis*, however, they are too fragmentary or worn to be identified on the species level (they could belong to any Nyirád *Dasyatis* form). Most of the remains have crown morphology typical for female individuals. The transversal crest of one specimen is elongated, and distally bent, which refers the tooth as a male tooth (MFGI V 2016.31.1., see Fig. 9U–V).

## Discussion

The shark and ray fauna of Nyirád includes 14 genera of 9 families, with 13 identified species: *Notorynchus primigenius*, *Araloselachus cuspidatus*, *Carcharias acutissima*, *Carcharoides* cf. *catticus*, *Cosmopolitodus hastalis*, *Otodus (Megaselachus) megalodon*, *Hemipristis serra*, *Carcharhinus priscus*, *Galeocerdo aduncus*, *Negaprion* sp., *Sphyrna* cf. *zygaena*, *Aetobatus arcuatus*, ?*Myliobatis* sp., *Dasyatis* cf. *probsti* and *Dasyatis rugosa*. The result indicates a moderately diverse chondrichthyan fauna.

The dominant shark family of the ecosystem was the Odontaspididae (sand tiger sharks), represented by 315 teeth (due to preservation bias 302 teeth could be identified only at family level). In frequency the family Odontaspididae is followed by the Carcharhinidae (requiem sharks) with 156 tooth remains. The dominance of these families would indicate that the ecosystem was filled with smaller fishes, as available potential prey-animals. The remains of these possible prey-animals have also been collected at the locality. The recovered ray taxa, like the *Aetobatus arcuatus*, ?*Myliobatis* sp. and *Dasyatis* spp. can be considered as part of the diet of the sharks. However, there are abundant bony fish tooth remains at the locality as well, such as *Acanthurus* sp., *Dentex* sp., ?*Diplodus* sp., *Pagrus cinctus*, indeterminate Sparidae, indeterminate Tetraodontidae and ?*Trichiurus* sp. teeth. Sea mammal remains have been collected at the locality as well, such as an Odontoceti indet. tooth, a vertebra fragment of a ?Sirenia, and several bone fragments (other sea mammal fossils from the locality are also known in private collections). However, there is still no direct evidence for predational relations between any local shark and other vertebrate taxon. Nevertheless, the top predator of this ecosystem could have undeniably been the *Otodus (Megaselachus) megalodon*, which is the biggest known macropredatory shark of the Neogene.

Among the lifestyles of the species the nectonic (=freely swimming) lifestyle and the tropical-subtropical distribution dominates (Compagno 1984, 2005). The tropical-subtropical shark fauna-elements, together with the other vertebrate and invertebrate taxa found at the locality, represent a subtropical climate with warm-temperate water and also indicate a connection to Mediterranean marine realm. However, the rarity of

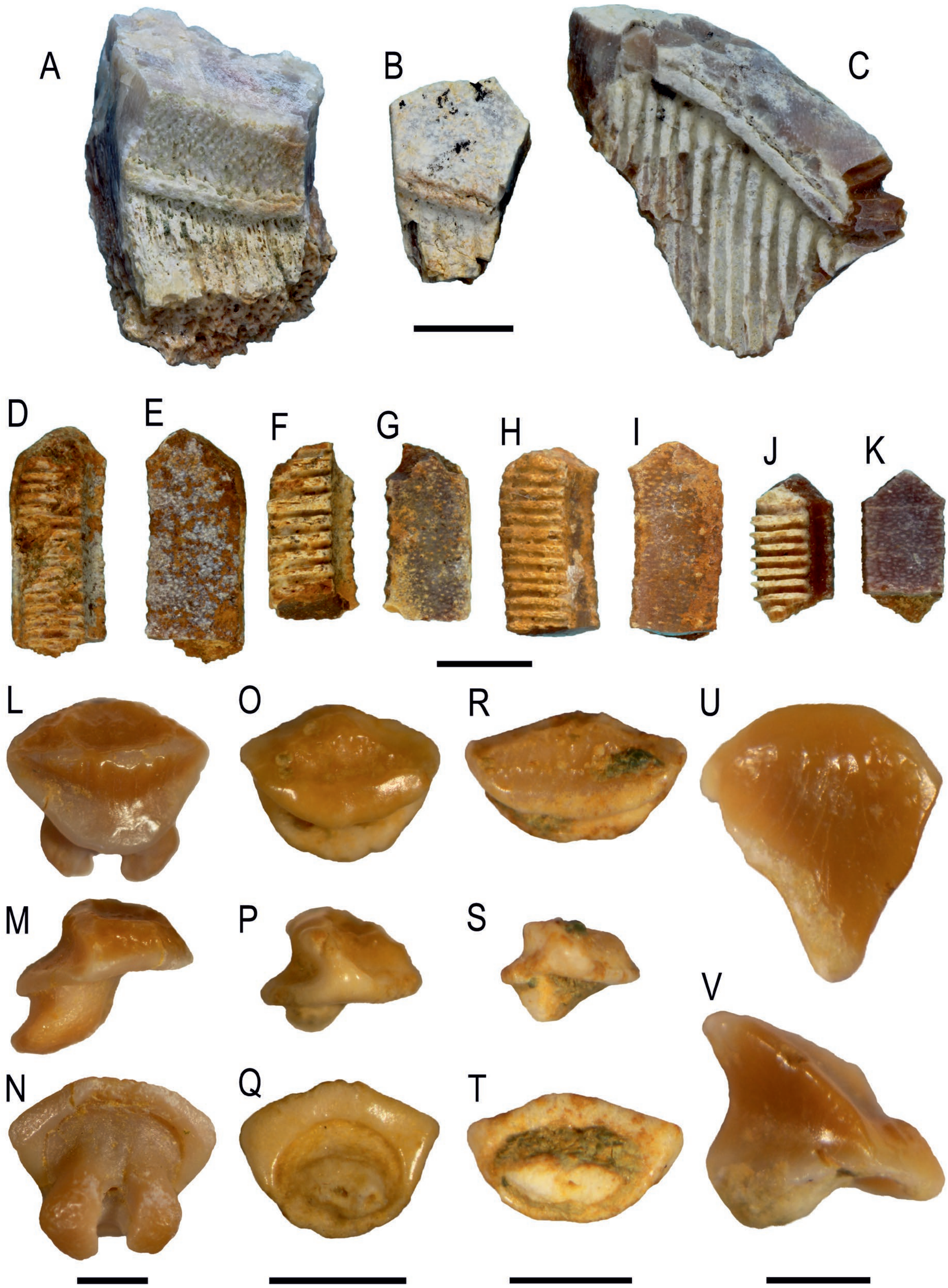


**Fig. 9.** Badenian ray remains from the Nyirád locality. **A–C:** *Aetobatus arcuatus* (in occlusal view) (B: MFGI V 2016.25.1.). **D–K:** ?*Myliobatis* sp. (D, F, H, J — in basal view; E, G, J, K — in occlusal view) (D–E: MFGI V 2016.30.1., F–G: MFGI V 2016.27.1., H–I: MFGI V 2016.28.1., J–K: MFGI V 2016.29.1.). **L–N:** *Dasyatis* cf. *probsti* female tooth; L — in occlusal view; M — in lateral view; N — in basal view. **O–Q:** *Dasyatis rugosa* female tooth (MFGI V 2016.36.1.); O — in occlusal view; P — in lateral view; Q — in basal view. **R–T:** *Dasyatis rugosa* female tooth (MFGI V 2016.37.1.); R — in occlusal view; S — in lateral view; T — in basal view. **U–V:** *Dasyatis* sp. male tooth (MFGI V 2016.31.1.); U — in occlusal view; V — in lateral view. Scale bars: A–K: 5 mm; L–Q: 1 mm; R–V: 2 mm

the tropical genus *Ginglymostoma* is worth mentioning. This taxon yielded only one tooth so far from the Central Paratethys from this period (Hiden 1995).

The Nyirád fauna is very similar to the typical Middle Miocene shark and ray assemblages of the Central Paratethys (Fig. 1, Table 2) and most of the common genera are represented in our record (*Notorynchus*, *Carcharias*, *Otodus*, *Cosmopolitodus*, *Hemipristis*, *Galeocerdo*, *Carcharhinus*, *Sphyrna*). There are a few exceptions like *Squalus* or *Squatina*, and a few rarely mentioned taxa (see Table 2 and e.g., Hiden 1995; Schultz 2003, 2013; Reinecke & Radwański 2015) that have not been discovered at Nyirád. The reason for the lack of these taxa could be (1) preservation bias for the micro-remains, (2) the relatively low volume of sediment searched through and/or (3) the palaeoenvironmental conditions were not suitable for these forms at Nyirád.

The compilation of the Badenian chondrichthyan remains (Tables 1–2), however, also revealed that many groups disappeared or became very rare in the Central Paratethys by the middle Miocene, for example, *Isistius*, *Centrophorus*, *Mitsukurina*, *Carcharoides*, *Parotodus*, *Alopias*. All these genera were common in the Mediterranean during the Miocene (Cappetta 1970; Vialle et al. 2011), and were also present in the Paratethys during the Lower Miocene (Holec et al. 1995; Kocsis 2007; Pollerspöck & Beaury 2014). Moreover, most of them still have modern representatives. The exceptions are the *Carcharoides* that went extinct in the Langhian and the *Parotodus* that died out in the Pliocene (Cappetta 2012). It must be mentioned that *Alopias* is reported from a few Karpatian and Badenian localities in Hungary (Kordos & Solt 1984), however, after re-examining these remains in the MFGI collection these turned out to be Odontaspididae teeth. On the other hand, very recently the presence of *Alopias* in the Badenian was comfirmed by Reinecke and Radwański (2015) who reported one tooth from this genus from Korytnica (Poland).

The disappearance or the rarity of these taxa in the Paratethys is quite intriguing. Most of these groups are deep-water epi- to bathypelagic sharks (e.g., *Isistius*) or pelagic (e.g., *Alopias*) forms, and their vanishing most probably relates to the gradual separation of the Paratethys from the Mediterranean. Still, large predators and pelagic fishes like *Otodus* or *Cosmopolitodus* were quite common in the Badenian. One explanation of their presence may be linked to large prey animals namely to marine vertebrates like whales and dolphins. Numerous fossil remains indicate the widespread present of these animals in the Paratethys at this period (Kazár et al. 2001; Kazár & Venczel 2003; Vrsaljko et al. 2010; Banak et al. 2015). Moreover, some dolphins became endemic and also lived in the Sarmatian period, when more or less brackish conditions set in the Paratethys (Kazár et al. 2004).

## Conclusion

The described shark and ray fauna from Nyirád includes 14 genera from 9 families, with 13 identified species. The fauna is similar to other chondrichthyan assemblages reported from the Badenian in the Central Paratethys. Comparison with Mediterranean and older Paratethyan faunas revealed that some deep-water and pelagic genera vanished or became very rare by the Middle Miocene in the Central Paratethys, which is best explained by the palaeogeographical evolution of the region. Among these taxa, the *Carcharoides* is reported here for the first time from Badenian beds of the Paratethys. Marine mammals are proposed here as prey-animals for the still common Badenian presence of other large sharks like *Otodus (Megaselachus)* or *Cosmopolitodus*.

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## Appendix

Placoid scales from the Pusztamiske Formation: MFGI V 2016.10.1.

Selachimorpha indet. teeth from the Pusztamiske Formation: MFGI V 2016.1.1., MFGI V 2016.15.1., MFGI V 2016.21.1.

*Acanthurus* sp. teeth from the Pusztamiske Formation: MFGI V 2016.11.1.

*Dentex* sp. teeth from the Pusztamiske Formation: MFGI V 2016.16.1.

?*Diplodus* sp. teeth from the Pusztamiske Formation: MFGI V 2016.4.1.

*Pagrus cinctus* teeth from the Pusztamiske Fm.: MFGI V 2014.88.25.1-25., MFGI V 2016.13.1., MFGI V 2016.17.1., MFGI V 2016.18.1., MFGI V 2016.19.1.

Indeterminate fish vertebra from the Leitha Limestone Fm.: MFGI V 2014.87.1.

Indeterminate Sparidae teeth from the Pusztamiske Formation: MFGI V 2016.7.1.

Indeterminate Tetraodontidae teeth from the Pusztamiske Formation: MFGI V 2016.3.1.

?*Trichiurus* sp. teeth from the Pusztamiske Formation: MFGI V 2014.102.1., MFGI V 2016.9.1.

Odontoceti indet. tooth from the Leitha Limestone Formation: MFGI V 2014.109.1.

?Sirenia vertebra from the Leitha Limestone Formation: MFGI V 2016.45.1.

Indeterminate bone fragments from the Pusztamiske Formation: MFGI V 2016.44.1.