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Central Paratethyan shark fauna (Ipolytarnóc, Hungary)

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Abstract: Previously described selachian remains from the Lower Miocene sandstone at Ipolytarnóc (north-eastern Hungary) have been revised, together with recently collected material from the same locality. The fauna is diverse and includes 19 genera with 16 certain species, from which 5 newly reported from this locality (*Squalus, Centrophorus, Isistius, Mitsukurina,* Scyliorhinidae). The earlier described four species that originated from the area — *Notidanus paucidens* Koch, 1903, *Notidanus diffusidens* Koch, 1904, *Lamna tarnoczensis* Koch, 1903, *Oxyrhina neogradensis* Koch, 1903 — have been redetermined as *Notorynchus primigenius*, *Carcharias acutissima* and *Parotodus benedeni*. The Chondrichthyes fauna represents a warm-temperate, subtropical climate with wide habitation range that was typical in the Alpine Foreland Basin and the Central Paratethys during the Lower Miocene.

Key words: Lower Miocene, Paratethys, Ipolytarnóc, molasse, shark teeth.

Introduction

The natural geological Museum of Ipolytarnóc is located in NE Hungary (48°14′12″ N; 19°39′25″ E) near to the Slovak border (Fig. 1). The area has been known for its fossils for more than 150 years. Detailed descriptions of footprints of different Miocene mammals and birds, and the fossil flora were published by Kordos (1985) and Hably (1985).

The shark teeth rich marine beds of Ipolytarnóc were first reported by Koch (1903, 1904). He described 25 species from 8 genera, with 4 new species among them: *Notidanus paucidens*, *Lamna tarnoczensis*, *Oxyrhina neogradensis* and *Notidanus diffusidens*.

The aim of this work is to give a detailed revision of this shark fauna according to the modern nomenclature and systematic paleontology. Morphology of the shark teeth often shows striking differences with respect to the two jaws of the shark (dignathic heterodonty) but differences occur even within one jaw (monognathic heterodonty). Morphological variations could be more complex if ontogenetic changes (e.g. Taniuchi 1970; Compagno 1984) and sexual dimorphism (e.g. Bass et al. 1973) are also taken into account. Hence, detailed investigation of the recent material is rather important from the paleontological point of view (e.g. Sadowsky 1970; Bourdon 2003). Lack of such knowledge resulted in a high number of fossil species in the early times (e.g. Agassiz 1833–43). The selachian remains from Ipolytarnóc were examined and revised in view of modern studies.

Since Koch's works, Leriche (1910), Vitális (1942), Hano & Seneš (1952) and Schultz (1969) took this fauna into account and included some of the species in their fauna lists. In 1984, Kordos & Solt reported a revised and reduced fauna list without any details, mentioning 12 species from 9 genera.

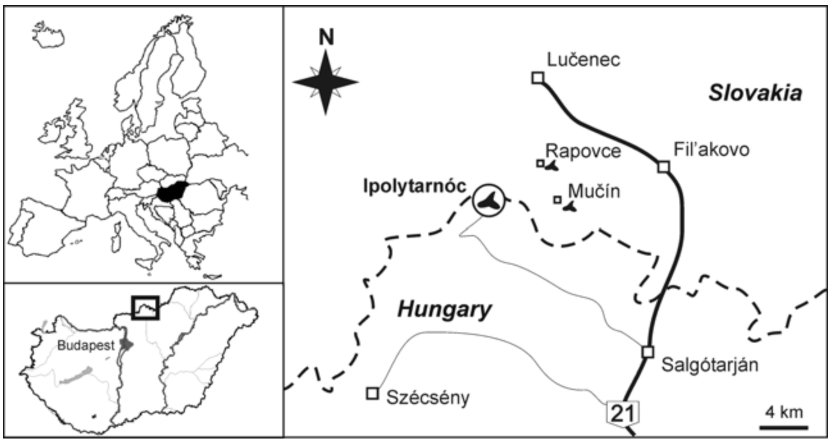

Fig. 1. Location of the site.

Most of the teeth described by Koch (1903, 1904) were placed in the collection of the Hungarian Geological Institution (MÁFI) and the Hungarian Museum of Natural History (MTM). In the last 100 years many other shark teeth have arrived in these museums from the area. In 1944 the fossil sites of Ipolytarnóc became protected and since then many remains have been deposited in the National Park Collection as well (IT).

The revision was performed on the fossils in these three collections. The latter one was completed by fossils collected recently in the framework of systematic field investigations in summer 2002 and 2003. During detailed excavation procedures and screen-washing, several new taxa for the locality have been discovered. However, most of the teeth have been shown to be broken, fragmented and worn. The amount of determinable teeth is comparatively small and does not allow reconstruction of complete artificial dentition sets. Altogether more than 1500 items have been studied, for the revision only the well-preserved remains were classified (see Appendix in data repository or web version at www.geologicacarpathica.sk).

The remains were compared with the fauna of Mučín (pers. com. Hornáček 2003) in Slovakia, which is very close to the state boundary (Fig. 1). It is characterized by teeth collected from beds of comparable facies and age.

The systematic chapter and the anatomical description of the teeth largely rely on the works of Cappetta (1987) and Purdy et al. (2001). The fauna lists are restricted mostly for the type species; the remains figured by Koch (1903, 1904) and those references closely related to the Central Paratethys. The teeth are figured according to their position in the jaw (e.g. upper teeth pointed downwards) and usually in lingual view. Hereafter, the following abbreviations are used: H — height and W — width of the teeth in mm. The different view of the teeth as: lin — lingual, lab — labial, mes — mesial, oc — occlusal, bas — basal.

Abbreviations of the different collections are MÁFI — Hungarian Geological Institution; MTM — Hungarian Museum of Natural History and IT — National Park at Ipolytarnóc, which is followed by the collection number (see Figures and Appendix in web version).

Geological setting

The marine Miocene sediments of Ipolytarnóc are part of the Upper Eocene to Lower Miocene fill of the North Hungarian Paleogene Basin, which overlies the Paleozoic crystalline basement (e.g. Báldi 1983). In the Oligocene and the Early Miocene the area was a part of the Central Paratethys and two formations of marine beds are exposed at Ipolytarnóc (Fig. 2). The Szécsény Formation is a fine-grained, pelagic unit, representing a deep sublittoral to shallow bathyal environment. Upsection the regressional sequence grades into the Pétervására Formation, which was formed under shallow-marine, near-shore conditions and contains the shark-teeth bearing beds. Biostratigraphical data clearly demonstrate an Eggenburgian age for the Pétervására Formation (e.g. Bartkó 1985).

The marine basin was filled up at the end of the Eggenburgian or at least in the Early Ottnangian and was covered by terrestrial beds of the Zagyvapálfalva Formation. These layers contain the famous petrified pine tree, the footprint sandstones ("Ipolytarnóc beds") and the abundant Miocene plant remains. Subsequently, the succession was buried by the "lower rhyolite tuff" (Gyulakeszi Formation), which displays a K/Ar age of 19.6 ± 1.4 Ma (Bartkó 1985), however recently these tuff layers were re-dated by subsequent methods (Pálfy et al. 2006) showing a younger age of 17.5 Ma.

Systematic Paleontology

Classis: **Chondrichthyes** Huxley, 1880
Ordo: **Hexanchiformes** Buen, 1926
Familia: **Hexanchidae** Gray, 1851
Genus: ***Notorynchus*** Ayres, 1855

The family of the six and seven gills sharks includes three recent genera: *Heptranchias*, *Hexanchus* and *Notorynchus*. They show a strong dignathic and monognathic heterodonty. The upper jaw contains one or two symphysials (one of them could be medial), six to nine anterolaterals and 11–13 posteriors; the lower jaw have one medial, six anterolaterals and 8 to 9 posteriors (Compagno 1984; Purdy et al. 2001).

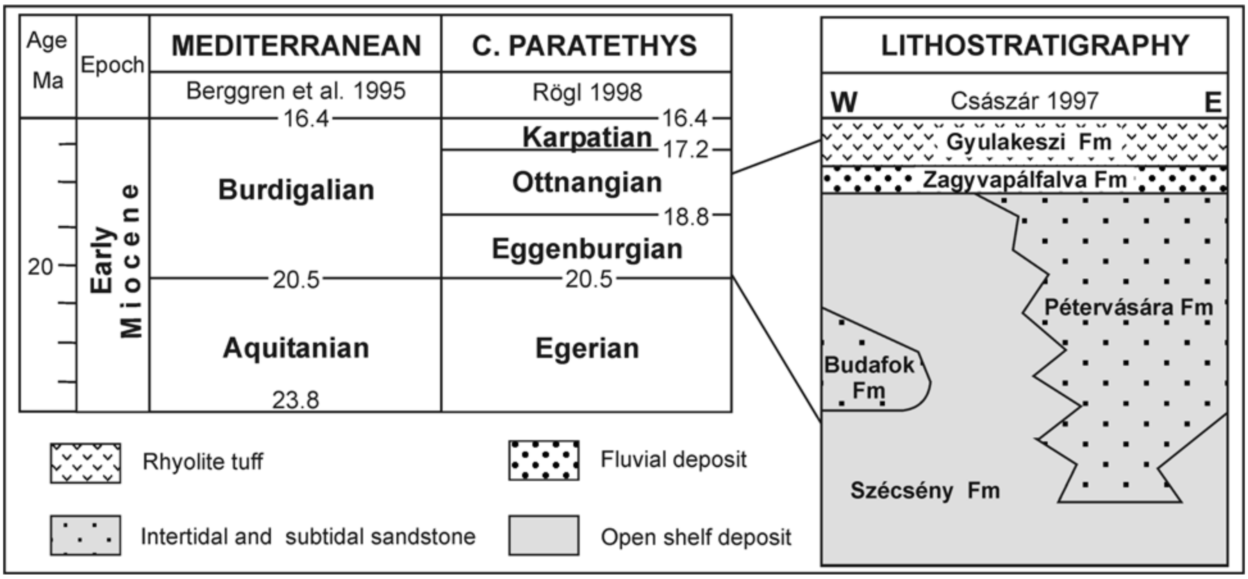

Fig. 2. Stratigraphic position of the Lower Miocene beds at Ipolytarnóc.

Notorynchus primigenius (Agassiz, 1843)
Fig. 3.1–3

1833–43 *Notidanus primigenius* n. sp. — Agassiz, p. 218–220, pl. 27, figs. 6–17
1903 *Notidanus primigenius,* Ag. — Koch, p. 27, pl. I, fig. 1
1903 *Notidanus* cfr. *serratissimus,* Ag. — Koch, p. 27, pl. I, fig. 2
1903 *Notidanus paucidens* n. sp. — Koch, p. 27–28, pl. I, fig. 3
1904 *Notidanus diffusidens* n. fr. — Koch, p. 202, text-fig. 1
1952 *Notidanus gigas* Sismd. — Hano & Seneš, p. 331–332, pl. L, figs. 3a–d
1969 *Hexanchus primigenius* (Agassiz, 1843) — Schultz, p. 68–73, pl. I, figs. 1–7
1970 *Hexanchus primigenius* (Agassiz, 1843) — Cappetta, p. 15–17, pl. 4, figs. 11–19
1971 *Hexanchus primigenius* (Ag.) — Brzobohatý & Schultz, p. 720–721, pl. 1, figs. 1–9

Referred material: 10 lower anterolateral, 2 lower medial, 1 upper anterolateral teeth.

The lower anterolaterals are labiolingually compressed and mesiodistally elongated with one main cusp followed by gradually decreasing lateral cusplets. Most of them are broken, but the typical *Notorynchus* character — the small unequal denticles, increasing in size apically on the mesial side of the main cusp (Applegate 1965) — can be observed on them (Fig. 3.1).

The two lower medials (Fig. 3.2: Koch's *Notidanus diffusidens* and IT-III-140, H: 12, W: 12) have a main cusp with 3–4 lateral cusplets on both sides. These teeth look like two lower anterolaterals merged in one.

The only upper anterolateral is large in size (H: 21, W: 20) having a main cusp with one mesial and two distal, separated lateral cusplets. Koch (1903) based his *Notidanus paucidens* on this tooth (Fig. 3.3).

Notorynchus primigenius was defined by Agassiz (1833–43) based on lower anterolaterals. Koch assigned most of the lower anterolaterals to this species. For those teeth originating from different jaw positions, he introduced the above-mentioned two species. Vitális (1942) studied the recent Hexanchidae species, reconstructed the jaw of this fossil form and placed the Ipolytarnóc teeth in the right position. Earlier Leriche (1910) and later Schultz (1969) made the same notion for the *N. paucidens*.

The genus is known from the Early Cretaceous. The *N. primigenius* first occurred in the Oligocene and was widespread in the Miocene (Cappetta 1987).

The recent *N. cepedianus* (Peron 1807) favours shallow water habitat in the shelf region and sometimes may show up near the shore. These forms are bottom-dwellers; their maximum size is 3–4 meters (Compagno 1984).

Ordo: **Squaliformes** Goodrich, 1909
Familia: **Squalidae** Bonaparte, 1834
Genus: ***Squalus*** Linnaeus, 1758

Squalus sp.
Fig. 3.4

Referred material: 2 anterolateral teeth.

The teeth are labiolingually flattened; their crowns curve distally and have a broad cusp. After a notch the cusp is followed by a convex, distal enamel shoulder. The apron passes through the basal edge of the root.

The figured specimen is larger (H: 2; W: 2.5) and better preserved, but its condition does not allow identification at the species level. The upper and lower teeth of the *Squalus* are very similar; the only difference is that the lower ones are somewhat wider. The Ipolytarnóc teeth are either left upper or right lower anterolaterals.

The genus is known from the Late Cretaceous. The only European Miocene species, *S. almeidae*, has been described from France and Portugal (Cappetta 1987).

From the 14 extant species, the *S. acanthias* Smith et Radscliffe, 1912 is the most common in the European seas. It inhabits boreal to warm temperate waters from the intertidal zone down to 900 m. Its maximum size is 1.6 meter (Compagno et al. 2005).

Familia: **Centrophoridae** Bleeker, 1859
Genus: ***Centrophorus*** Müller et Henle, 1837

Centrophorus sp.
Fig. 3.5

Referred material: 1 anterolateral tooth.

The tooth is labiolingually flattened (H: 3.5; W: 2.8) and shows a distally curved, broad crown with a convex distal enamel shoulder and smooth cutting edge. The apron does not reach the basal edge of the root. The root itself has a well-developed distolingual hollow. In the centre of the lingual side, under the uvula, a big foramen (infundibulum) opens, where a deep groove divides the root into two parts. The tooth shows a strong resemblance to *Deania* as well, however the infundibulum is out of the axis of the uvula, opens in a more mesial position in this genus (pers. comm. Cappetta 2005).

The *Centrophorus* is known from the Late Cretaceous. Its teeth are frequent in Miocene bathyal deposits in France (Cappetta 1987). Holec et al. (1995) has presented two *Squalus* sp. teeth from Mučín, which belong to this genus as well.

From the ten recent species the *C. granulosus* (Bloch et Schneider, 1801) is the best known. It is a common deepwater shark of the outer continental shelves and the upper part of the continental slopes (100–1200 m). Its maximum size is 1.5 meter (Compagno et al. 2005).

Familia: **Dalatiidae** Gill, 1893
Genus: ***Isistius*** Gill, 1864

Isistius cf. *triangulus* (Probst, 1879)
Fig. 3.6

1879 *Scymnus triangulus* n. sp. — Probst, p. 175–176, pl. III, figs. 35–36
1995 *Isistius triangulus* (Probst, 1879) — Holec et al., p. 39, pl. IX, figs. 1–2

Referred material: 21 lower teeth.

Most of the remains are merely the typical labiolingually flattened, thin, triangular crowns of the lower teeth, which characterize this genus. Their cutting edges are smooth. The largest tooth has a height of 3.5 mm and a width of 4.2 mm.

Some teeth are more complete (Fig. 3.6). Their crown has a wide, thin apron, which goes down to an elliptical hole, called a button hole. Their root is also very thin and has a mediolingual foramen. A kind of overlapping margin, a hollow runs both sides of the teeth, where they connect to each other in the jaw.

The upper teeth are very different from the lower ones (dignathic heterodonty). These are narrow, pointed teeth, without lateral cusplet (Compagno 1984). This kind of tooth has not been found yet.

The genus is known from the Late Paleocene. From the Miocene the *Isistius triangulus* (Probst, 1879) was described. Probst's figure shows a well-marked margin under the crown and the mediolingual foramen opens in the middle of this margin involving the crown area as well. This feature is restricted only for the root area on the examined teeth, and therefore they were described as *I.* cf. *triangulus*. The *Isistius* was widespread in Europe (Leriche, 1910; Holec et al. 1995), but teeth have turned up in South-America (Cappetta 1987) and North-America (Purdy et al. 2001) as well.

Three recent species exist, out of which the *I. brasiliensis* (Quay et Gaimard, 1824) shows closer relations to the fossil species. This is a tropical, epipelagic to bathypelagic (85 to even 3000 m) shark; younger individuals could be found in shallower water. Its maximum size is 0.5 meter (Compagno et al. 2005).

Ordo: **Squatiniformes** Buen, 1926
Familia: **Squatinidae** Bonaparte, 1838
Genus: ***Squatina*** Duméril, 1906

Squatina sp.
Fig. 3.7

Referred material: 22 lateral teeth.

The crown of these teeth has only one lingually curved cusp. At its base a low enamel edge runs distally and mesially. On the labial side the enamel overhangs the root and forms a small apron. The root is usually flat at its base and has a triangular shape in basal view with a large foramen in its center (Fig. 3.7/b). On some more anterior teeth the root lobes bend downwards.

Usually two species has been reported from the Miocene: *S. subserrata* and *S. biforis*. The previous one was widespread in the entire Paratethys; the latter was reported only from Rapovce (Fig. 1) (Brzobohatý & Schultz 1971). Koch (1903) described this kind of teeth as *Sphyrna subserrata*.

The angel sharks are known from the Upper-Jurassic on. Since then their dentition has barely changed (Cappetta 1987). The teeth of the 18 extant species are very similar to each other and one can hardly distinguish among them. Therefore until a precise study is made, it is expedient to describe them only at the genus level.

The angel sharks are dorsoventrally flattened. Their appearance makes them similar to rays, but unlike rays their mouth is in terminal position and their pectoral fins are separated from their trunk. They are widespread, inhabiting boreal to tropical waters, from the intertidal zone to the upper continental slope (Compagno et al. 2005).

Ordo: **Lamniformes** Berg, 1958
Familia: **Odontaspididae** Müller et Henle, 1839

Teeth of this family are commonly found in Neogene marine sediments. Among them, S-shaped anterior teeth are the most frequent. Early authors have thus already described many different Odontaspididae usually under the genus name of *Lamna* (e.g. Agassiz 1833–43; Probst, 1879). Only from Ipolytarnóc seven different species were reported (Koch 1903). When the knowledge of extant species widened many fossil species were merged together (e.g. Leriche 1910).

In many publications a number of further genus names are found, like *Odontaspis* (e.g. Leriche 1910), *Eugomphodus* (e.g. Compagno 1984), *Synodontaspis* (e.g. Cappetta 1987) and *Carcharias*

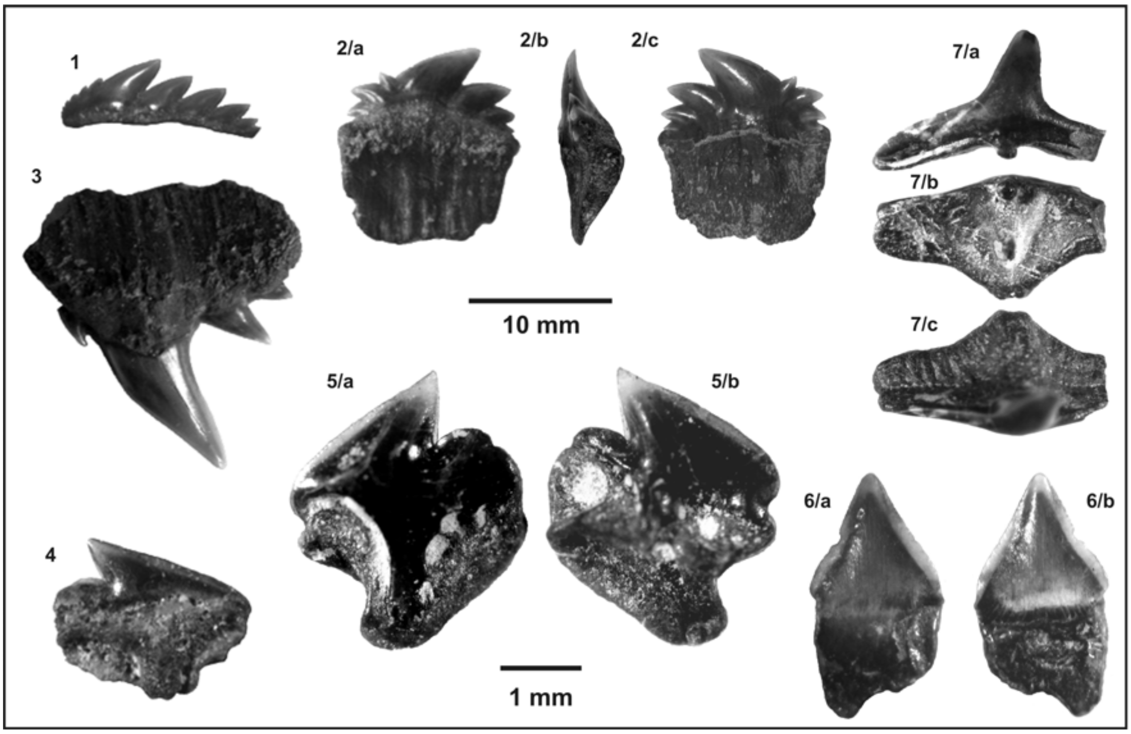

Fig. 3. 1–3 — *Notorynchus primigenius*: 1 — anterolateral (MÁFI-V14907); 2 — anterolateral (MÁFI-V14947), lin (a), mes (b), lab (c); 3 — medial (MÁFI-V14945). **4** — Squalus sp.: anterolateral (IT-M4-3), lab. **5** — *Centrophorus* sp.: anterolateral (IT-III-115), lab (a), lin (b). **6** — *Isistius* cf. *triangulus*: lower tooth (IT-M4-2), lab (a), lin (b) (scale bar: 1 mm). **7** — *Squatina* sp.: lateral (IT-M6-1/a), lab (a), bas (b) and oc (c). (1 mm scale for Figs. 3–6.)

(e.g. Kemp 1991). Since the decision of the International Commission on Zoological Nomenclature in 1987 (Opinion 1459), the *Carcharias* should be regarded as the valid name whereas *Eugomphodus* and *Synodontaspis* are junior synonyms (e.g. Kent 1994). At present two extant genera exist: *Odontaspis* and *Carcharias*. Table 1 summarizes the main characteristic differences between them (Purdy et al. 2001).

Many important studies were inspired by observations of recent species (e.g. *Carcharias taurus* Rafinesque, 1810: in: Cunningham 2000; Sadowsky 1970; Taniuchi 1970). These authors have shown that the dentition can be very variable and, for example, the numbers of the lateral cusplet or difference between laterals are insufficient features to distinguish among species. Other marks, such as lingual striation on the crown turned out to have not much taxonomical relevance. Taking into account these works, two *Odontaspis* groups and 2 or 3 *Carcharias* species can be distinguished in the Ipolytarnóc fauna.

Genus: ***Odontaspis*** Agassiz, 1838

Odontaspis sp. 1.
Fig. 4.1–4

1903 *Lamna* (*Odontaspis*) cfr. *subulata,* Ag. — Koch, p. 34, pl. II, fig. 19
1903 *Lamna* (*Odontaspis*) cfr. *duplex,* Ag. — Koch, p. 34–35, pl. II, fig. 20

Referred material: 1 anterior, 7 lateral teeth.

These teeth are small and usually have two pairs of spike-like cusplets. The proximal ones are straight and diverge from the main cusp. Each upper lateral has a distally curved cusp (Fig. 4.1); those of the lower laterals are straight and they recurve a bit lingually (Fig. 4.3–4). Some teeth have striation on the lingual side of the crown. There are teeth that have only one pair of cusplets, however the shape of these teeth is the same as the others' (Fig. 4.3).

Koch (1903) named those teeth, which have two pairs of cusplets as *Lamna* (*Odontaspis*) cfr. *duplex* and those ones, which have only one as *Lamna* (*Odontaspis*) cfr. *subulata*.

Odontaspis sp. 2.
Fig. 4.5

1903 *Lamna* (*Odontaspis*) *dubia,* Ag. — Koch, p. 33, pl. I, fig. 15

Referred material: 6 anterior teeth.

Four teeth are well-preserved anteriors, each with a straight and slightly lingually curved crown. Each has one pair of long, straight, narrow cusplets, which curve a bit. This curvature, however, differs from that of the *Carcharias,* which is rather hook-like. One tooth has weak striation, the rests are smooth (Fig. 4.5). The cutting edges of the cusps do not reach the base of their crowns. The remaining teeth are broken, not well-preserved, but a straight narrow cusplet beside the main cusp is still observable.

The genus *Odontaspis* first appeared in the Late Cretaceous. Of the two extant species, knowledge on *O. ferox* is more extensive. This shark favours warm-temperate and tropical waters and inhabits the bottom of the shelf and the upper continental slope between 15–420 meters. Its maximum size is 3.6 meters (Compagno 1984).

Genus: ***Carcharias*** Rafinesque, 1810

Carcharias acutissima (Agassiz, 1843)
Fig. 4.6–11

1833–43 *Lamna contortidens* n. sp. — Agassiz, p. 294–295, pl. 37a, figs. 21–23
1903 *Lamna* (*Odontaspis*) *contortidens,* Ag. — Koch, p. 32–33, pl. I, fig. 14
1903 *Lamna tarnoczensis*, n. sp. — Koch, p. 33, pl. I, fig. 16
1910 *Odontaspis acutissima* Agassiz 1844 — Leriche, p. 261–268, pl. XIV, figs. 1–27
1995 *Synodontaspis acutissima* (Agassiz, 1844) — Holec et al., p. 40–41, pl. X, figs. 3–5 & pl. XI, figs. 1, 3

Referred material: 28 anterior, 1 intermediate, 48 lateral teeth.

This is one of the most abundant species in Ipolytarnóc. The anteriors are slender, having usually one pair of hook-like cusplets. The lingual side of the crown is usually striated. Their heights range between 14–25 mm and their width between 7–14 mm. One small intermediate tooth was found (see Fig. 4.9). The laterals are highly variable. The lower laterals have a straight main cusp, whereas crowns of the upper ones curve distally and their cusplets are flattened labiolingually.

The holotype (Koch 1903: fig. a–c) of *Lamna tarnoczensis* Koch, 1903 is missing from the collections, only 8 paratypes can be found (MÁFI V14948). All of them are broken, only 5 are valuable and can be identified as laterals of this species.

The detailed description of *C. acutissima* was first given by Leriche (1910). He merged Agassiz's (1833–43) three species *Lamna acutissima*, *L. contortidens* and *L. dubia* under the name of *Odontaspis acutissima*. Since Leriche's revision many authors cited this species (e.g. Schultz 1969; Cappetta 1970) or even reported reconstructed dentation sets (Reinecke et al. 2001). Recently Purdy et al. (2001) questioned the validity of this species, based on Agassiz's (1843–44) pioneer work. However according to paragraph 23.9.1.2 of the International Code of Zoological Nomenclature (ICZN 1999) the *Carcharias acutissima* could be regarded as a valid name.

The *C. acutissima* is known from the Oligocene. In the Miocene it became widespread as shown by its abundant preservation in

Table 1: Differences between the dentition of the genera *Odontaspis* and *Carcharias*.

	Carcharias	*Odontaspis*
Heterodonty	Strong	Weakly
Anteriors	3–3 row both sides of the symphysial Stout and wide tipped main cusp Short and strongly hooked cusplets	2–2 row both sides of the symphysial Slender and narrow-tipped main cusp Long, straight, weakly curved not hook-like cusplets
Laterals	Compressed labiolingually Bladelike with flattened cusplets	Less compressed labiolingually Not bladelike with little flattened cusplets
Posteriors	Carinate molariform crushers	Not differentiated as molariform crushers

most of the shark-teeth-bearing beds. There are some Pliocene occurrences too, but these can hardly be separated from the extant *C. taurus* (see e.g. Cappetta 1987).

Carcharias cuspidatus (Agassiz, 1843)
Fig. 4.12–13

1833–43 *Lamna cuspidata* n. sp. — Agassiz, p. 290, pl. 37a, figs. 43–50
1903 *Lamna* (*Odontaspis*) *cuspidata,* Ag. — Koch, p. 32, pl. I, fig. 13
1903 *Lamna denticulata,* Ag. — Koch, p. 34, pl. I, fig. 18
1995 *Synodontaspis cuspidata* (Agassiz, 1844) — Holec et al., p. 40–41, pl. XI, figs. 2, 4–6 & pl. XII, fig. 1

Referred material: 1 symphysial, 8 anterior, 6 lateral teeth.

As compared to the previous species, these teeth are more robust, their crowns are wider, their cusplets are smaller and the lingual side of the crown is usually smooth. One symphysial (Fig. 4.13) was distinguished. The anteriors have heights of 18–32 mm and widths of 13–18 mm. The laterals (H: 20–22; W: 20–21) often have two pairs of cusplets (Fig. 4.12).

The species is known from the European and North American Oligocene to Miocene strata (Cappetta 1987).

Carcharias sp.
Fig. 4.14

Referred material: 1 lateral tooth.

One tiny upper lateral tooth which could not be assigned to any *Carcharias* species. Its crown is wrinkled at its base and it has two pair of slightly hook-like cusplets. This tooth may come from a juvenile *C. cuspidatus*.

The genus *Carcharias* first appeared in the Early Cretaceous. The above-mentioned two species were widespread in the Mi-

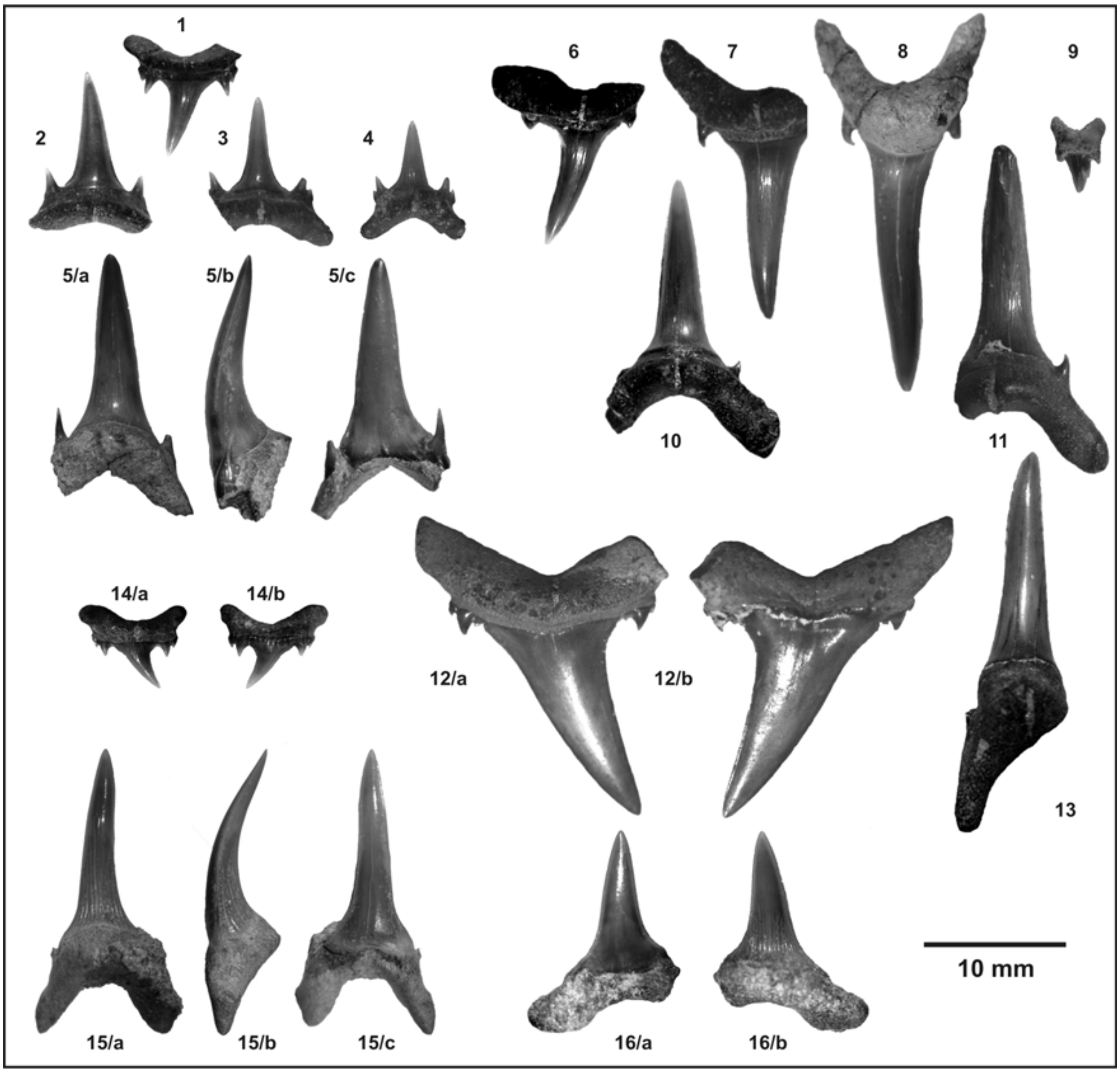

Fig. 4. 1–4 — *Odontaspis* sp. 1.: 1 — lateral (MÁFI-V14908); 2 — anterior (?) (MÁFI-V14922); 3–4 — laterals (MÁFI-V14908). **5** — *Odontaspis* sp. 2.: anterior (IT-III-65), lin (a), mes (b), lab (c). **6–11** — *Carcharias acutissima*: 6 — lateral (MÁFI-V5095); 7 — third anterior (MÁFI-V1621); 8 — first anterior (IT-III-137); 9 — intermediate (IT-108); 10 — lateral (II-133); 11 — first anterior (MTM-V61-322). **12–13** — *Carcharias cuspidatus*: 12 — lateral (MÁFI-V14937), lin (a), lab (b); 13 — symphysial (MÁFI-V2273&V2275). **14** — *Carcharias* sp.: lateral (IT-M18-2), lin (a), lab (b). **15–16** — *Mitsukurina lineata*: 15 — lateral (IT-103), lab (a), lin (b); 16 — anterior (IT-82), lin (a), mes (b), lab (c).

ocene (Cappetta 1987). The extant species *C. taurus* is very common in the littoral region of temperate and tropical waters, to depths of up to 190 m. Its maximum size is 3–3.1 meters (Compagno et al. 2005).

Familia: **Mitsukurinidae** Jordan, 1898
Genus: ***Mitsukurina*** Jordan, 1898

Mitsukurina lineata (Probst, 1879)
Fig. 4.15–16

1879 *Lamna (Odontaspis) lineata* n. sp. — Probst, p. 147–149, pl. II, figs. 41–43
1987 *Mitsukurina lineata* (Probst, 1879) — Cappetta, p. 92, text-figs. 81/A–C
1995 *Mitsukurina lineata* (Probst, 1879) — Holec et al., p. 42, pl. X, fig. 6

Referred material: 5 anterior, 3 lateral teeth.

These teeth resemble the Odontaspididae, but they are more slender and more elongated, and do not have lateral cusplets, only occasionally very small ones may occur. The lingual side of the crown is strongly striated. These ridges are closely spaced, quite regular and nearly extend to the apex.

Four of the teeth are lower anteriors (H: 20–25, W: 8.5–10). Their crowns curve lingually in a sigmoidal shape. The specimen in Fig. 4.15 has a slightly distally curved crown thus this can be placed in the 2nd or 3rd position of the lower anterior series. One first upper anterior was distinguished (IT-120, H: 20; W: 10.5), with its tip recurving labially in lateral view. The rest of the teeth are laterals (H: 10–12; W: ~8–10; see e.g. Fig. 4.16).

The *M. lineata* is the only reported species from the Miocene. Its remains mainly occur in Europe (Cappetta 1987). The extant *Mitsukurina owstoni* Jordan, 1898, the goblin shark, is a bottom-dweller at the outer shelves and on the upper continental slopes (to over 550 meters). It is of rather unusual appearance: peculiarities include a pinkish-white colour, soft and flabby body, long caudal fin, elongated paddlefish-like snout and highly protrusible jaws. Its maximum size is 3.3 meters (Compagno 1984; Bourdon 2003).

Familia: **Lamnidae** Müller et Henle, 1838
Genus: ***Carcharoides*** Ameghino, 1901

Carcharoides catticus (Philippi, 1851)
Fig. 5.1–3

1851 *Otodus catticus* n. sp. — Philippi, p. 24, pl. 2, figs. 5–7
1903 *Lamna* cfr. *compressa,* Ag. — Koch, p. 33–34, pl. I, fig. 17
1952 *Lamna compressa* Ag. — Hano & Seneš, p. 337, pl. LVII, figs. 4–6
1969 *Lamna cattica* (Philippi 1846) — Schultz, p. 82–83, pl. 4, fig. 58
1970 *Lamna cattica* (Philippi 1846) — Cappetta, p. 23–25, pl. 4, figs. 5–9
1995 *Carcharoides catticus* (Philippi 1846) — Holec et al., p. 42, pl. XII, fig. 2

Referred material: 3 anterior, 26 lateral teeth.

These teeth have a very thin, labiolingually flattened crown with a pair of triangular denticles, which are at least as high as one quarter of the main cusp. Two small, slightly broken (IT-M10-1, H: ~6; W: ~4) teeth and one bigger (Fig. 5.2) straight crowned anterior tooth were distinguished. The other teeth are laterals with wide crowns at their base (Fig. 5.1). The upper ones curve more distally (Fig. 5.3) than the lowers. The mesial cutting edge is straight and convex, while the distal is straight or concave. The root is small, thin and extends laterally.

The fossil species was first described as *Otodus catticus* by Philippi (1851). Cappetta (1987) classified these teeth into the Lamnidae and named as *Carcharoides catticus*. Opposite to this, Purdy et al. (2001) found that these sorts of teeth belong to the recent Carcharhinidae species *Triaenodon obesus* (Rüppell, 1835). Comparing the Ipolytarnóc teeth to the *T. obesus* (e.g. Bourdon 2003), the recent species appears to be smaller and their roots has more developed groove on the lingual side. On the other hand, the main difference between the Lamniformes and Carcharhiniformes is that the premier one has a crown without pulp cavity (pers. comm. Cappetta 2005), as is the case of the teeth of Ipolytarnóc.

The remains of this genus are known from the Middle Oligocene till the Middle Miocene (Cappetta 1987).

Genus: ***Isurus*** Rafinesque, 1810

The dentitions of the mako sharks are characterized by teeth that are never serrated; they are smooth on both labial and lingual sides and usually lack lateral cusplets. On the root the nutritive groove is weakly developed, sometimes not visible. The dentition of extant species includes 2 anteriors, 1 intermediate, 5–7 laterals and 3–4 posteriors in the upper jaw and 3 anteriors, 5–7 laterals and 3–4 posteriors in the lower jaw (Compagno 1984). The extant species, *I. oxyrinchus* Rafinesque, 1809, displays signs of ontogenetical changes. It could be observed that as the teeth became more robust, the cutting edge became less sinuous and the cusps of the laterals curved more distally (cf. Kemp 1991).

Isurus desori (Agassiz, 1843)
Fig. 5.4–6

1833–43 *Oxyrhina desori* n. sp. — Agassiz, p. 282–283, pl. 37, fig. 9
1903 *Oxyrhina xiphodon,* Nötling non Ag. — Koch, p. 35–36, pl. II, figs. 21a–c
1903 *Oxyrhina leptodon,* Ag. — Koch, p. 36, pl. II, figs. 22
1969 *Oxyrhina desori* Agassiz, 1843 — Schultz, p. 79–80, pl. 3, figs. 41–49
1971 *Isurus desori* L. Agassiz 1843 — Brzobohatý & Schultz, p. 732–733, pl. 3, fig. 2
1995 *Isurus desori* (Agassiz, 1843) — Holec et al., p. 43, pl. XIII, figs. 3–4

Referred material: 7 anteriors, 1 lateral, 2 posterior teeth.

This species is characterized by narrow, erect and symmetrical first lower anteriors and distally a bit curved first upper anteriors (Fig. 5.4–5). These teeth are lingually curved; but the tips of the uppers recurve a bit labially. The tooth shown in Fig. 5.4 is smaller, has a flexuous crown with cutting edges that do not reach the base of the crown. It can be attributed to a juvenile individual, while that in Fig. 5.5 derives from an adult specimen.

Second upper anteriors have longer mesial cutting edge and their root projects over the base of the crown. From Koch's (1903) description, the *Oxyrhina leptodon* and *Oxyrhina xiphodon* (*O. desori*) were in such a position. The previous is from a juvenile, the latter is a tooth of an adult specimen.

The crown of the laterals and posteriors (Fig. 5.6) are narrow; the lowers are erect, the uppers curve distally. Their root projects over the base of the crown mesially and distally.

The *I. desori* is thought to be the ancestor of the recent *I. oxyrinchus* (see Kent, 1994), whereas Purdy et al. (2001) claims that the two species are the same.

Isurus hastalis (Agassiz, 1843)
Fig. 5.7-8

1833-43 *Oxyrhina hastalis* n. sp. — Agassiz, p. 277-278, pl. 34, figs. 3, 6 & 13-18
1903 *Oxyrhina xiphodon*, Nötling non Ag. — Koch, p. 35-36, pl. II, figs. 21d-f
1952 *Oxyrhina hastalis* Ag. — Hano & Seneš, p. 336, pl. LVI, figs. 4-5
1969 *Oxyrhina hastalis* Agassiz, 1843 — Schultz, p. 77-79, pl. 2, figs. 27-28
1995 *Isurus hastalis* (Agassiz, 1843) — Holec et al., p. 42-43, pl. XII, fig. 4

Referred material: 1 anterior, 2 lateral, 2 posteriors teeth.

The tooth of *I. hastalis* has a broad, labiolingually flattened crown that reaches the mesial and distal edge of the root. Notably, the crown of the upper posterior tooth (Fig. 5.8) is broader than the tooth of *I. desori* in the same position (Fig. 5.6).

This species is regarded by some authors (e.g. Siverson 1999) as the ancestor of the great white shark (*Carcharodon carcharias* Linnaeus, 1758) and might be sorted in a different genus and named as *Cosmopolitodus hastalis*.

Isurus retroflexus (Agassiz, 1843)
Fig. 5.9

1833-43 *Oxyrhina retroflexa* n. sp. — Agassiz, p. 281, pl. 33, fig. 10
1952 *Oxyrhina hastalis* Ag. — Hano & Seneš, p. 336, pl. LVII, fig. 1
1969 *Oxyrhina retroflexa* Agassiz, 1843 — Schultz, p. 80-81, pl. 2, figs. 37-38
1995 *Isurus retroflexus* (Agassiz, 1843) — Holec et al., p. 43-44, pl. XII, figs. 3, 5 & pl. XIII, figs. 1-2

Referred material: 1 anterior, 2 lateral teeth.

These teeth are more robust compared to the other *Isurus* species. The main character is the labial platform-like margin on the root (Fig. 5.9/a). The laterals have more globular crown tips. The root projects mesially and distally over the base of the crown. The distal cutting edge meets the base of the crown with right angles on the upper lateral teeth. According to Kent (1994) this species might be the ancestor of the other extant form the *I. paucus* Guitart, 1966.

The first appearance of the genus was in the Late Paleocene (Cappetta 1987). The taxon includes the above-mentioned two extant species *I. oxyrinchus* and *I. paucus*. Although both sharks are pelagic, *I. oxyrinchus* occupies more near-shore habitats. They favour tropical and warm waters (over 150 meters), but may occur in boreal areas as well. Their maximum size is 3.8-4 meters (Compagno 1984).

Familia: **Otodontidae** Glückman, 1964
Genus: ***Carcharocles*** Jordan et Hanibal, 1923

Carcharocles sp.
Fig. 5.10

Referred material: 3 teeth.

Although the teeth are worn and broken, remarkable features, such as the strong, serrated cutting edge can be confidently identified on all of them. Two specimens exhibit symmetrical crowns. The third one has a distally curved crown (Fig. 5.10) with convex mesial and concave distal cutting edge.

In the Miocene the *Carcharocles megalodon* — huge teeth, lacking lateral cusplets — and the *C. chubutensis* — broad crown with a pair of lateral cusplets — were widespread forms (Cappetta 1987). The latter was redefined by Purdy et al. (2001) as *C. subauriculatus*. These authors reconstructed its dentition from large number of teeth from the Lee Creek Formation (North America).

The *C. megalodon* is a well-known and well-studied species. Several jaw reconstructions were performed by various authors. Taking all these into account, dimensions of this shark could reach 14-15 meters (Purdy et al. 2001).

Genus: ***Parotodus*** Cappetta, 1980

Parotodus benedeni (Le Hon, 1871)
Fig. 5.11-12

1871 *Oxyrhina Benedenii* — Le Hon, p. 6 with figures
1903 *Oxyrhina neogradensis,* n. sp. — Koch, p. 36-37, pl. II, fig. 23
1903 *Oxyrhina xiphodon,* Nötling non Ag. — Koch, p. 35-36, pl. II, figs. 21j-l
1969 *Oxyrhina* cf. *benedeni* Le Hon, 1871 — Schultz, p. 81-82, pl. 2, figs. 37-38
1995 *Isurus benedeni* (Le Hon, 1871) — Holec et al., p. 44, pl. XIV, fig. 1-2
2001 *Parotodus benedenii* (Le Hon, 1871) — Purdy et al., p. 110-113, text-figs. 23-24

Referred material: 1 anterior, 1 lateral and 1 posterior teeth.

All the three teeth have the same features: the labial side of the crown is flat; the lingual one is strongly convex. The crown is intensely curved distally. The mesial cutting edge is convex; the distal one is concave. They have a broad crown-neck between the root and the crown. The root is very thick; the ends of the lobes are globular and robust; the torus is salient and lacks the nutrient groove.

This species was described from Pliocene sediments by Le Hon (1871). Its earliest appearance was in the Oligocene (Leriche 1910). Purdy et al. (2001) reconstructed the dentition of this species based on eighty-five teeth from Lee Creek Mine (North-America). Le Hon's holotype is a 2nd anterior tooth in their artificial dentition set.

The holotype of *Oxyrhina neogradensis* Koch, 1903 (Fig. 5.11) is a 2nd anterior tooth of this species. The second tooth (IT-72) is broken and might be an upper lateral tooth. The third one is a small tooth (Fig. 5.12) that could be in posterior position. This latter resembles the lateral teeth of Leriche's (1910) *Alopias latidens*, but our tooth is more robust and its crown-neck is broader.

The *Parotodus benedeni* was a pelagic shark; based on the reconstructed dentition its estimated maximum size is 6-7.5 meters. The genus died out at the end of the Pliocene (Cappetta 1987).

Familia: **Alopiidae** Bonaparte, 1838
Genus: ***Alopias*** Rafinesque, 1810

Alopias exigua (Probst, 1879)
Fig. 5.13-14

1879 *Oxyrhina exigua* n. sp. — Probst, p. 135-137, pl. II, figs. 21, 23-24
1903 *Oxyrhina exigua* — Koch, p. 37, pl. II, fig. 24
1969 *Alopecias exigua* (Probst, 1879) — Schultz, p. 85-86, pl. IV, figs. 52-56

Referred material: 3 anteriors, 13 lateral teeth.

One main cusp without any cusplet marks these teeth. The crown is smooth on both sides and hangs over the root on the labial side. The cutting edges do not reach the base of the crown.

The laterals curve distally, their mesial cutting edge is convex and the distal one is concave. The mesial one has a remarkable sinuous curvature, which is well developed on the upper laterals (Fig. 5.14).

The species was described by Probst (1879). The holotype is slightly broken, but Leriche (1910) gave a detailed description of this form and his figures are compatible with the Ipolytarnóc teeth.

The genus is known from the Early Eocene; the *A. exigua* was present from the Early Oligocene to the Middle Miocene (Cappetta 1987). Three species live nowadays from which *A. superciliosus* (Lowe, 1839) resembles the fossil teeth. It has a wide occurrence, inhabits coastal waters in the shallow region but can often be found in the open ocean. This shark has a very long caudal fin thus its maximum size is 4–4.5 meters (Compagno 1984).

Ordo: Carcharhiniformes Compagno, 1973
Familia: **Scyliorhinidae** Gill, 1862
Genus: ***Scyliorhinus*** Blainville, 1816

?*Scyliorhinus* sp.
Fig. 6.1

Referred material: 1 tooth.

One broken and worn tooth is assigned to this genus (H: 6; W: 4.5). The crown is erect and its cutting edges are complete; it curves lingually and its tip recurves labially. Beside the main cusp

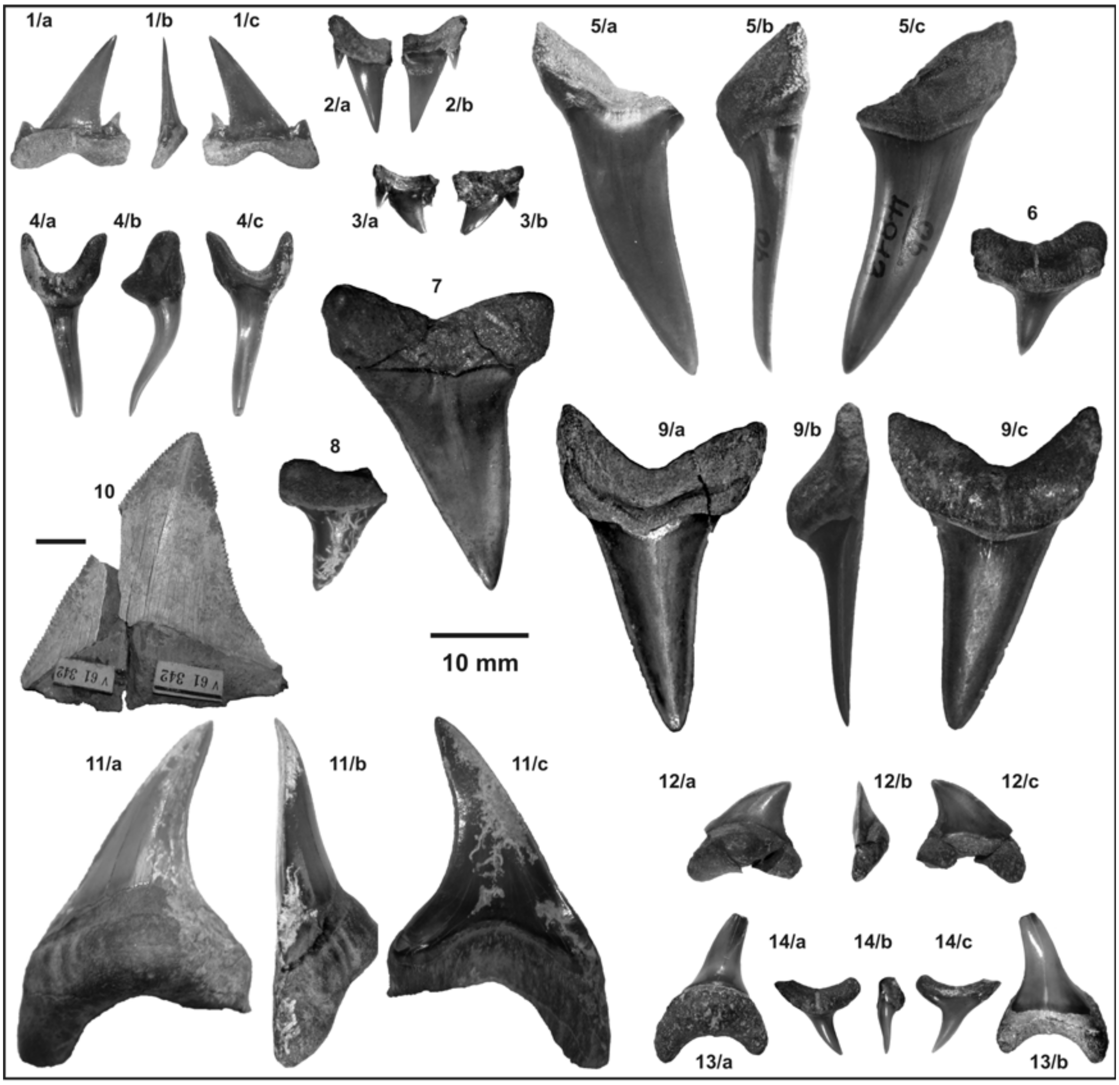

Fig. 5. 1–3 — *Carcharoides catticus*: 1 — lateral (IT-98), lin (a), mes (b), lab (c); 2 — anterior (IT-98) lin (a), lab (b); 3 — lateral (IT-M16-3) lab (a), lin (b). **4–6** — *Isurus desori*: 4 — second anterior (IT-III-134) from juvenile specimens, lin (a), mes (b) and lab (c); 5 — second anterior from adult specimen (MÁFI-V4813), lab (a), mes (b) and lin (c); 6 — posterior (IT-8). **7–8** — *Isurus hastalis*: 7 — first lateral (MÁFI-V14928), lab; 8 — posterior (MÁFI-V1616). **9** — *Isurus retroflexus*: anterior (MÁFI-V14928), lab (a), mes (b), lin (c). **10** — *Carcharocles* sp: lateral (?) (MTM-V61-342). **11–12** — *Parotodus benedeni*: 11 — second anterior (MÁFI-V14946) and 12 — posterior (MÁFI-V14940), lin (a), mes (b) lab (c). **13–14** — *Alopias exigua*: 13 — first lateral (IT-118), lin (a) lab (b); 14 — lateral (IT-87), lin (a), mes (b) lab (c). (The small scale bar (10 mm) for Fig. 7.)

it used to have one pair of cusplets, from which one is missing. The root shows a strongly developed torus.

One of the most similar species to this tooth is the *S. distans*, which was reported from the Miocene Bavarian Molasse Basin (Probst 1879; Barthelt et al. 1991). The tooth also resembles other genera such as *Premontreia (Oxyscyllium)* that is known from the Paleocene–Eocene (Cappetta 1992; Noubhani & Cappetta 1997) till the Pliocene (Cappetta & Cavallo, in print) and also shows strong similarities to the Oligocene-Miocene genus *Pachyscyllium* (Reinecke et al. 2005).

Finally the tooth was named *Scyliorhinus* because this is the closest scyliorhinid shark from the Miocene Paratethys, but due to the incompleteness and the similarity to other genera, the name was signed with a question mark. If more and better preserved teeth turn up it would be worth discussing this group further.

The catsharks are known from the Late Jurassic. Many fossils have been described so far (Cappetta 1987). The extant ones count 160 species in 16 genera. The genus *Scyliorhinus* itself contains 15 species from which the *S. canicula* (Linnaeus, 1758) is the most common in the European seas. This shark is a bottom-dweller, it equally inhabits on pebbly, sandy and muddy bottom surfaces. It commonly occurs from the nearshore to 110 meters depth. Its maximum size is 1 meter (Compagno et al. 2005).

Familia: **Hemigaleidae** Hasse, 1879
Genus: ***Paragaleus*** Budker, 1935

?*Paragaleus* sp.
Fig. 6.2–4

Referred material: 8 anterolateral teeth.

All the teeth are broken and most of them quite worn thus closer classification is not possible.

In the future they might be resorted to another group. The main feature of these teeth is the distally curved main cusp that is flat on the labial and convex on the lingual side. The mesial cutting edge runs along the mesial root lobe and forms a smooth enamel shoulder. On the distal root lobe small lateral cusplets can be observed (Fig. 6.2) gradually decreasing in size (note: this is eroded from tooth Fig. 6.2). The base line of the root runs horizontally and bears a strong torus with deep nutritive groove.

There is one tooth (Fig. 6.4), already reported by Koch (1903) as *Galeocerdo* cf. *gibberulus* and it resembles these teeth, however, it is bigger (H: 9 mm; W: ~9 mm) and its torus is more prominent. Till similar finds do not appear this tooth is assigned to this group as well.

The genus turned up in the Lower Miocene of Europe (Cappetta 1984) and in North-America (Purdy et al. 2001). At present four species are known, of which the *P. pectoralis* (Garman, 1906) is the better studied. This shark inhabits the shallower region (max. 100 m) of the tropical, warm-temperate waters. Its maximum size is 1.2–1.3 meters (Compagno et al. 2005).

Genus: ***Hemipristis*** Agassiz, 1843

Hemipristis serra Agassiz, 1843
Fig. 6.5–6

1843 *Hemipristis serra* n. sp. — Agassiz, p. 237, pl. 27, figs. 18–30
1903 *Hemipristis serra,* Ag. — Koch, p. 30–31, pl. I, fig. 8
1952 *Hemipristis serra* Ag. — Hano & Seneš, p. 368–369, pl. LVIII, figs. 7–8 & LIX, figs. 1–3
1969 *Hemipristis serra* Agassiz, 1843 — Schultz, p. 90, pl. 4, figs. 66–74
1971 *Hemipristis serra* L. Agassiz 1843 — Brzobohatý & Schultz, p. 725–726, pl. 4, fig. 7
1995 *Hemipristis serra* Agassiz, 1843 — Holec et al., p. 45–46, pl. XVI, figs. 1–4 & pl. XVII, figs. 1–3

Referred material: 2 anterior, 14 lateral teeth.

This species has a strong dignathic heterodonty. Two characteristic tooth types can be distinguished. The first is awl-like with lingual curvatures and with cutting edge that runs only to one third of the crown. Teeth of these types are the upper and lower symphysials and the lower anteriors and the first two lower laterals. On these latter ones small lateral denticles can be observed (Fig. 6.5).

The second type has a rather broad, flattened crown with strong serration on its cutting edge, which gradually increases towards the tip but does not reach it. This form corresponds to the upper anteriors and upper laterals (Fig. 6.6). In the lower jaw the dentition changes gradually into this type from the previous one. The laterals curve distally; their mesial cutting edge is convex, the distal one is concave or straight.

Both types have a strong torus, marked with a long groove. The base of the roots become nearly horizontal on the upper laterals, unlike in the lower ones.

The genus is known from the Middle Eocene. The remains of *H. serra* occur all over the world in Miocene marine sediments (Cappetta 1987). The extant species *H. elongata* (Klunzzinger 1871) lives in tropical, shallow, near-shore waters (1–30 m). Its maximum size is 2.3–2.4 meters (Compagno 1984).

Familia: **Carcharhinidae** Jordan & Evermann, 1896
Genus: ***Carcharhinus*** Blainville, 1816

The most common feature of this genus is the dignathic heterodonty. The dentition is composed of lower and upper medials (maybe alternals), usually lower symphysial, upper anteriors, upper lateroposteriors and lower anteroposteriors (Purdy et al. 2001). The different species have very similar lower dentitions, thus they can be distinguished mostly by their upper teeth.

The remains of this genus are the most abundant at Ipolytarnóc and a total of 163 teeth were examined.

Carcharhinus priscus (Agassiz, 1843)
Fig. 6.7–12

1843 *Sphyrna prisca* n. sp. — Agassiz, p. 234–235, pl. 26a, figs. 44, 47
1903 *Galeocerdo minor* Ag. — Koch, p. 29–30, pl. I, fig. 6a–c
1903 *Carcharias* (*Aprionodon*) *stellatus* Probst — Koch, p. 31, pl. I, fig. 10
1952 *Sphyrna prisca* Ag. — Hano & Seneš, p. 339, pl. LX, figs. 1–14
1969 *Carcharhinus* (*Hypoprion*) *acanthodon* (Le Hon 1871) — Schultz, p. 88, pl. 4, figs. 77–81
1971 *Sphyrna prisca* Ag. — Brzobohatý & Schultz, p. 724, pl. 5, fig. 7
1995 *Carcharhinus priscus* (Agassiz, 1843) — Holec et al., p. 46, pl. XVIII, figs. 1–2
1995 *Carcharhinus similis* (Probst, 1878) — Holec et al., p. 46–47, pl. XVIII, figs. 3–4

Referred material: 1 medial, 5 anterior, 128 lateroposterior and 29 lower anteroposterior teeth.

The crown of each upper tooth has a triangular shape. The anteriors are erect and narrow, while the lateroposteriors curve distally and their roots are elongated horizontally. The cutting edge could be smooth or slightly serrated, which gradually disappears towards the tip. The enamel runs to the margin of the root in the both directions (mesial-distal) and it is strongly serrated. The transition towards the crown is more continuous on the mesial side, while distally it has a strong notch.

Most of the teeth are lateroposteriors; their height varies between 6–10 mm and their width between 6.5–13 mm. One small upper medial tooth (Fig. 6.7) and at least five anteriors (Fig. 6.8–9) were distinguished.

The lower teeth are simpler. They have one single narrow cusp that could curve slightly distally. The enamel is elongated on the labial side and on some teeth extends upwards and forms a smooth enamel shoulder. The root is projected mesiodistally and runs horizontally. Their size is similar to the upper ones.

Koch (1903) distinguished between the upper and lower teeth and described the upper teeth as *Galeocerdo minor*, the lower ones as *Carcharias* (*Aprionodon*) *stellatus*.

There are two very similar species in the Miocene. Names of both species are in common use. One, originating from Agassiz (1833–43), is *Sphyrna prisca*, which has upper teeth similar to our upper teeth. The other named *Galeocerdo acanthodon* derives from Le Hon (1871). It has a lower tooth with straight crown and serrated enamel shoulder.

Lack of this latter feature on the examined Ipolytarnóc lower teeth suggests that these correspond to Agassiz's species, and thus they are described here as *Carcharhinus priscus*.

The genus is known from the Middle Eocene. The species appeared first in the Oligocene then it was widespread in the Miocene (Cappetta 1987). *Carcharhinus* is flourishing at present and it includes 31 different recent species (Compagno et al. 2005). Three of them — *C. brachyurus* (Günther, 1870), *C. perezi* (Poey, 1876) and *C. melanopterus* (Quoy et Gaimard, 1824) — bear close resemblance to the Ipolytarnóc species. The first one is related to the fossil species by many authors (e.g. Kemp 1991). It inhabits warm-

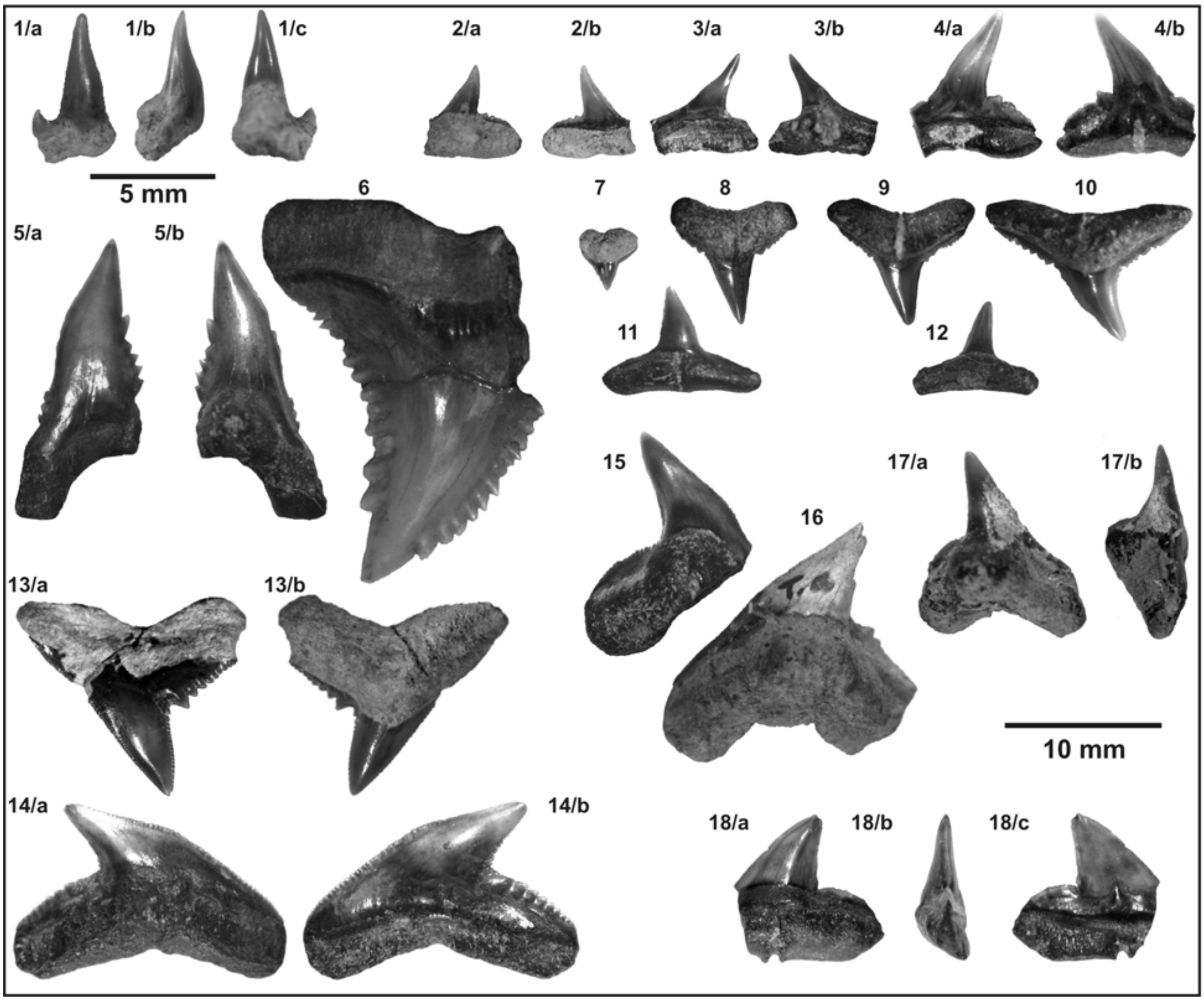

Fig. 6. **1** — ?*Scyliorhinus* sp.: anteroposterior (IT-M19-8), lab (a), mes (b), lin (c), (scale bar: 5 mm). **2–4** — ?*Paragaleus* sp.: anterolaterals 2 — lin (a), lab (b) (IT-V-6); 3 — lab (a), lin (b) (IT-II-36); 4 — lab (a), lin (b) (MÁFI-V14906). **5–6** — *Hemipristis serra*: 5 — first lateral (MÁFI-V14939), lab (a) lin (b); 6 — lateral (MÁFI-V14911), lab. **7–12** — *Carcharhinus priscus*: 7 — medial (IT-M16-4); 8–9 — anterior (IT-100 and IT-II-70); 10 — lateroposterior (IT-119); 11–12 — anteroposteriors (MÁFI-V1623 and IT-III-62). **13–14** — *Galeocerdo aduncus*: 13 — medial (IT-III-23), lab (a), lin (b); 14 — anteroposterior (MÁFI-V14905), lin (a), lab (b). **15–17** — *Galeocerdo contortus*: 15 — anteroposterior (IT-35); 16 — anterolateral (MÁFI-V14905); 17 — symphysial (MÁFI-V14907), lin (a), mes (b). **18** — *Sphyrna* cf. *zygaena*: lateral (MÁFI-V14934), lin (a), mes (b), lab (c). (5 mm scale for Fig. 1.)

temperate waters, close to the coastline. Its maximum size is 2.8–2.9 meters (Compagno 1984).

Genus: ***Galeocerdo*** Müller et Henle, 1837

The upper and lower dentitions of the tiger sharks are very similar. The medials and the lower symphysial tooth differ from the anteroposterior teeth (monognathic heterodonty). The size of the teeth decrease gradually in both anteroposterior series and they become wider and lower towards the corner of the jaw (Compagno 1984).

Galeocerdo aduncus Agassiz, 1843
Fig. 6.13–14

1843 *Galeocerdo aduncus* n. sp. — Agassiz, p. 231, pl. 26, figs. 25–28
1903 *Galeocerdo* cfr. *aduncus,* Ag. — Koch, p. 28–29, pl. I, fig. 4
1903 *Galeocerdo latidens,* Ag. — Koch, p. 29, pl. I, fig. 5
1952 *Galeocerdo aduncus* Ag. — Hano & Seneš, p. 338, pl. LVII, figs. 7–8 & LVIII figs. 1, 2–5
1969 *Galeocerdo aduncus* Agassiz 1843 — Schultz, p. 89, pl. 4, figs. 59–65
1971 *Galeocerdo aduncus* L. Agassiz, 1843 — Brzobohatý & Schultz, p. 724, pl. 5, figs. 1–6
1995 *Galeocerdo aduncus* Agassiz, 1843 — Holec et al., p. 47–48, pl. XIX, figs. 1–5

Referred material: 1 medial, 7 anteroposterior teeth.

Most of the teeth are anteroposteriors (Fig. 6.14), characterized by distally curved, serrated main cusp with an elongated convex mesial cutting edge. The main cusp is separated from a distal enamel shoulder by a deep notch and its serration decreases distally. In basal view the root lobes recurve slightly lingually. One medial tooth was found (Fig. 6.13), which shows a less curved cusp and has straight mesial cutting edge.

This species is known from the Early Oligocene and was widespread in the Miocene. Some remains occur in the Pliocene beds of Japan as well (Cappetta 1987).

Purdy et al. (2001) supposed that it resembled to the extant *G. cuvier* (Peron et LeSueur, 1822). The main difference is that the recent one has pointed, compound serration on the mesial cutting edge instead of simple pointed serration. This feature cannot be observed on the Ipolytarnóc teeth and the medial tooth obviously differs from the extant species, thus these teeth were described as *G. aduncus*.

Galeocerdo cf. *contortus* Gibbes, 1848–1849
Fig. 6.15–17

1903 *Galeocerdo minor* Ag. — Koch, p. 29–30, pl. I, fig. 6d–f
2001 *Galeocerdo contortus* Gibbes, 1948–1949 — Purdy et al., p. 146–147, text-fig. 50

Referred material: 1 symphysial, 2 anteroposterior teeth.

The crown of this species is more elongated; the mesial cutting edge is sinuous and the serration of the distal enamel shoulder is faint (Fig. 6.15). Another important feature is the thick root with very strong torus (e.g. Fig. 6.16–17). One lower symphysial (Fig. 6.17) was distinguished, which has a straight mesial cutting edge.

The remains of *G. contortus* mainly occur in the Miocene of North-America (Cappetta 1987). Its dentition was reconstructed by Purdy et al. (2001). After studying the Slovak (Mučín) Miocene material some teeth were found there as well that clearly belong to this species.

The genus *Galeocerdo* is known from the Early Eocene (Cappetta 1987). One cosmopolitan species lives nowadays, the *G. cuvier*, which occurs from tropical to temperate waters and from the surface to a depth of 140 meters. Its maximum size is 4–4.5 meters (Compagno 1984).

Familia: **Sphyrnidae** Gill, 1872
Genus: ***Sphyrna*** Rafinesque, 1810

Sphyrna cf. *zygaena* (Linnaeus, 1758)
Fig. 6.18

1903 *Carcharias* (*Scoliodon*) *Krausi*, Probst? — Koch, p. 32, pl. I, fig. 11

Referred material: 1 lateral tooth.

One tooth belongs to this species. The base of its crown is wide; the tip curves distally; its cutting edges are smooth; the mesial one is convex, while the distal one is almost perpendicular to the root line. After a deep notch, the convex, smooth enamel shoulder follows the main cusp. The root is massive; the lobes run horizontally and between them a deep basal nutritive groove can be observed.

The hammerhead sharks are known from the Early Miocene of Europe and Asia (Cappetta 1987), moreover Purdy et al. (2001) reported three species from the North-American Early Miocene that are identified as certain extant species.

There are seven extant species, from which the Ipolytarnóc tooth best resembles the *S. zygaena* (Linnaeus, 1758). The incomplete preservation of the tooth allows its description as *S.* cf. *zygaena*. This species inhabits tropical and temperate waters and it is frequent both in the near-shore and pelagic environments. It preferably lives close to the water surface in an average depth of 20 meters. Its maximum size is 3.7–4 meters (Compagno et al. 2005).

Paleoenvironment

Numerous Lower Miocene selachian remains were found at Ipolytarnóc, in Hungary. In addition to the shark teeth, also shark vertebra and, owing to the screen-washing technique, other Chondrichthyes groups such as rays (*Dasyatis* and *Aetobatus*) turned up at the site. The well preserved shark teeth were identified properly and classified at specific taxonomical level and the results of the classification suggest that the fauna is highly diverse.

Most of the teeth, about 63 %, belong to the Carcharhinidae and Odontaspididae. Both families are widespread in warm-temperate and tropical waters, which mostly applies to the rest of the fauna as well. However, there are also taxa with rather warm-temperate and boreal distribution (e.g. *Squalus*).

The habitat of the species is widely varying. The two most frequent families are characterized by shallow-marine, near-shore habitat (except *Odontaspis*). Another typical neritic, shallow water shark is the *Hemipristis.* The third most common group, the Lamnidae (11 %) are rather pelagic sharks also like other forms: *Carcharocles*, *Alopias* and *Sphyrna.* There are sharks that live near the continental slope at the outer shelf in deeper water such as *Mitsukurina* and *Odontaspis* and some of the sharks have typical bathyal

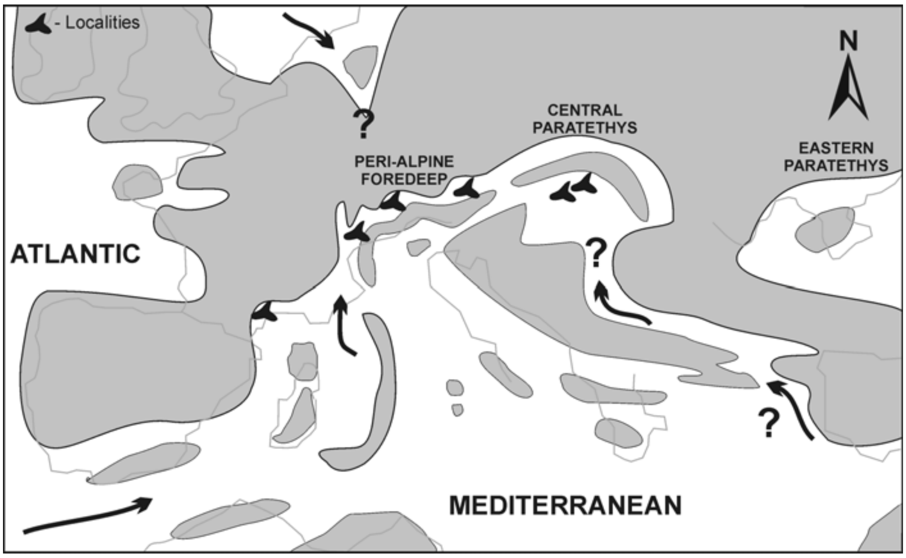

Fig. 7. Lower Miocene paleogeography (after Rögl 1998 modified at Rhine Graben after Kuhlemann & Kempf 2002). The shark teeth localities from west to east: Montpelier region, Swiss Molasse; Bavarian Molasse; Austria; Ipolytarnóc and Southern Slovakia.

habitat like *Isistius* and *Centrophorus*. In addition, some genera are specially bottom-dwellers (e.g. *Squatina*).

Most of the species already appeared in the Oligocene and became major elements of the Miocene faunas. Except the *Parotodus* and the *Carcharoides*, all genera have recent representatives and the majority closely resemble the recent species.

Very similar Lower Miocene faunas were described from the Paratethys: the Swiss Molasse Basin (Leriche 1927a,b), the Bavarian Molasse Basin (Probst 1878, 1879; Barthelt et al. 1991), Linz (Schultz 1969) and many Eggenburgian localities in Austria (Brzobohatý & Schultz 1971), Rapovce (Hano & Seneš 1952) and Mučín (Holec et al. 1995) in Slovakia.

The composition of the Ipolytarnóc shark fauna and comparison with the other faunas suggests that the Paratethys (Fig. 7) was a warm-temperate to subtropical sea, with direct tropical connections in the Lower Miocene (Brzobohatý & Schultz 1971). The Paratethys could have been oriented towards the Mediterranean, upheld by the similar Lower Miocene fauna of Montpelier region (Cappetta 1970) and towards to the Indo-Pacific supported by the presence of *Hemipristis*, which lives nowadays in the Indian Ocean. The connection of these areas is generally accepted (Rögl 1998).

During this time there could be still large, connected open water surfaces, with deeper sea basin, which is indicated by the appearance of the *Isistius* and *Mitsukurina*. The remains of these genera are not known from younger Miocene deposits of the Central Paratethys. In contrast, the two most abundant genera, *Carcharias* and *Carcharhinus*, remained major elements of the late Early-Middle Miocene shark faunas.

Conclusions

The fauna described more than 100 years ago was revised and completed with new finds. The result shows a very diverse Lower Miocene shark community that includes 19 genera with 16 certain species: *Notorynchus primigenius*, *Squalus* sp., *Centrophorus* sp., *Isistius* cf. *triangulus*, *Squatina* sp., *Odontaspis* sp. 1 & 2, *Carcharias acutissima*, *Carcharias cuspidatus*, *Mitsukurina lineata*, *Carcharoides catticus*, *Isurus desori*, *Isurus hastalis*, *Isurus retroflexus*, *Carcharocles* sp., *Parotodus benedeni*, *Alopias exigua*, ?*Scyliorhinus* sp., ?*Paragaleus* sp., *Hemipristis serra*, *Carcharhinus priscus*, *Galeocerdo aduncus*, *Galeocerdo contortus*, *Sphyrna* cf. *zygaena*.

This fauna represents warm-temperate water, a subtropical climate with wide habitation range of the Chondrichthyes. The North Alpine Foreland Basin and the Central Paratethys was directly connected in the Early Miocene (see Rögl 1998) as shown by their identical selachian assemblages.

It should be noted that during fieldwork, a number of other remains like vertebra fragments of fish, bony fish teeth, scales and otoliths were also found, which all await a detailed study. Their examination is expected to complete the knowledge of the Lower Miocene fish fauna of the Paratethys.

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Appendix

Notorynchus primigenius (Agassiz, 1843)	MÁFI: MTM: IT:	V2281; V14907; V14933 (2); V14945; V14947 . V61–333 (2); V63–2030. 76; M4–1; III-18; III-140.
Squalus sp.	IT:	MII-1–2; M4–3.
Centrophorus sp.	IT:	III-115.
Isistius cf. *triangulus* (Probst, 1879)	IT:	106 (2); II-105; III-16; III-45; III-84; MI-2–1; MII-2–1 (2); M4–2 (2); M6–2; M9–1 (2); M11–1; M12–1; M14–1; M17–2; M18–1; M19–2 (2).
Squatina sp.	MÁFI: MTM: IT:	V1625; V2279 (3/1); 14913 (6/4); V14915 (17/1). V61–336; V63–2031. 19; 20; 46; M6–1 (2); M8–1; M15–2, M17–1; M19–1 (3); III-50; III-106.
Odontaspis sp. 1.	MÁFI: MTM: IT:	V14908 (3/3); 14922 (2/1); V14923. V63–2024 (2/1). 70; III-142 (4/1).
Odontaspis sp. 2.	MAFI: IT:	V1620 (2/1). 33; 67; 102; II-45; III-65.
Carcharias acutissima (Agassiz, 1843)	MÁFI: MTM: IT:	V1621 (13/2); V2273 & 2275 (17/4); V5095; V14920 (4/2); V14948 (8/5). V61–315 (16/1); V61–322 (4/1); V63–2024 (2/1); V63–2026 (3/1); V63–2027 (11/2); V63–2029 (2/1). 21–29; 32; 45; 57–66; 80; 81; 83; 84; 90; 97; 101; 105; 108; 121 (2); II-12; II-57; II-84; II-97; II-107; II-115; II-133; III-6; III-35; III-113; III-132; III-137; III-139; III-142 (21/2); MI-2–2; MII-2–2; M1–1 (2); M4–4 (2/1); M-12–3; M14–2; M-16–1; M-17–3.
Carcharias cuspidatus (Agassiz, 1843)	MÁFI: MTM: IT:	V1622; V2272 (4/2); V2273 & 2275 (17/2); V14917; V14931 (2); V14937. V63–2023 (3/1). 30; 31; 44; II-31; II-122.
Carcharias sp.	IT:	M-18–2.
Mitsukurina lineata (Probst, 1879)	MÁFI: MTM: IT:	V2273 & V2275 (17/1). V61–315 (16/1). 82; 103; II-1; II-67; III-122; III-125.
Carcharoides catticus (Philippi, 1851)	MÁFI: MTM: IT:	V14921 (3); V14929 (5). V61–341 (3/1); V63–2016 (7/2). 54–56; 91(2); 98 (2),120; II-93; II-114; II-123 (3/1); II-134 (3/1); V-8; M10–1; M16–2; M16–3; M19–6 (2).
Isurus desori (Agassiz, 1843)	MÁFI: IT:	V2272 (4/1); V4813. 1; 6; 8; 9; 10; 75; III-119; III-134.
Isurus hastalis (Agassiz, 1843)	MÁFI: MTM: IT:	V1616; V14928 (3/1). A11–530. 4; 11.
Isurus retroflexus (Agassiz, 1843)	MÁFI: IT:	V14928 (3/1). 2; 12.
Carcharocles sp.	MÁFI: MTM:	V14916. V61–342; V61–343.
Parotodus benedeni (Le Hon, 1871)	MÁFI: IT:	V14940; V14946. 72.
Alopias exigua (Probst, 1879)	MÁFI: MTM: IT:	V14935 (3); V14936 (3). V63–2018 (5/1). 13; 48–52; 87; 118; III-89.
? *Scyliorhinus* sp.	IT:	M19–8.
? *Paragaleus* sp.	MÁFI: IT:	V14906. II-120; III-36; III-67; III-142 (2/1); V-6; M19–7; M19–9.
Hemipristis serra Agassiz, 1843	MÁFI: MTM: IT:	V1626; V2280; V14911 (2); V14912; V14939 (3). V63–2032. 14–18; 117; M-12–4.
Carcharhinus priscus (Agassiz, 1843)	MÁFI: MTM: IT:	V1509 (2/1); V1623 (5); V2276 (2); V2279 (3/1); V14907 (6/4); V14913 (6/1); V14915 (17/13); V14932 (9); V14934 (2/1). V61–331 (5); V61–337 (2); V61–338 (4/4); V63–2012 (2); V63–2015 (3); V63–2020. 79, 92 (3), 94 (3), 100, 104, 107 (2), 109 (10), 119 (2), (124–132); I-4; II-3, 13, 32, 38, 48, 56, 70, 75, 90, 108, 127 (4/2); 128, 125, 132 (4/2); 134 (3/2); III-8, 13, 32, 40, 46, 49, 62, 66, 68, 70, 72, 80 (3/1), 81, 83, 86, 92, 96, 98, 104, 114, 110, 120; 142 (4), 143; VII-3, 6; MI-2–3; MII-1–1; MII-2–3; MIII-2–1; M3–2; M5–1 (6); M11–2 (4/3); M12–2 (3); M15–3; M16–4; M17–4; M18–3 (2); M19–4 (7).
Galeocerdo aduncus (Agassiz, 1843)	MÁFI: IT:	V14905 (2/1); V14909 (5/3). 71; III-23; III-93; III-100.
Galeocerdo contortus Gibbes, 1848–1849	MÁFI: IT:	V14905 (2/1); V14907 (6/1). 35.
Sphyrna cf. *zygaena* (Linnaeus, 1758)	MÁFI:	V14934 (2/1).

MÁFI: Hungarian Geological Institution (Magyar Állami Földtani Intézet) H-1143, Budapest, Stefánia út 106.
MTM: Hungarian Museum of Natural History, Paleontological Collection (Magyar Természettudományi Múzeum, Őslénytár) H-1083, Budapest, Ludovika tér 2-6.
IT: Collection of Ipolytarnóc, (Ipolytarnóci Ősmaradványok Természetvédelmi Terület) H-3138, Ipolytarnóc, Pf.:1.