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A preliminary report on the Early Oligocene (Rupelian, Kiscellian) selachians from the Kiscell Formation (Buda Mts, Hungary), with the re-discovery of Wilhelm Weiler's shark teeth

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Abstract – An Early Oligocene (Rupelian, Kiscellian), partially published shark tooth material, unearthed from the Kiscell Clay (Budapest, Hungary) is shortly reviewed here. A few shark taxa have been published by Wilhelm Weiler in 1933 and 1938, and some of this material was re-discovered in the Hungarian Natural History Museum. The here described shark taxa are *Notorynchus primigenius*, *Hexanchus agassizi*, *Heptranchias howelli*, *Araloselachus cuspidatus*, *Carcharias* spp., *Carcharoides catticus*, *Isurolamna gracilis*, *Otodus* (*Carcharocles*) *angustidens*, *Alopias* cf. *exigua*, *Carcharhinus* sp., and *Physogaleus latus*. The results indicate a relatively diverse shark fauna with mixed ecological needs. The revised list of the local selachian taxa suggests that a detailed review of all Kiscell shark material (collected in the last century), placed both in public and private collections, is needed. With 73 figures, 1 table and 1 appendix.

Key words – *Heptranchias*, Hungary, Kiscell Clay, Oligocene, Rupelian, selachian, Weiler

INTRODUCTION

The Early Oligocene (Rupelian, Kiscellian) Kiscell Formation is a widely known and studied formation of the Central Paratethys. The sediments of the Kiscell Clay were mined in several brickyards of the Buda Mountains for nearly 100 years. While the brickyards of the Budapest area were open, macrofossils were collected in large numbers. However, the remains are dominated by microfossils.

The extremely diverse Foraminifera fauna (nearly 500 species) was first described by Hantken (1875), followed by Majzon (1966), Sztrákos (1974), and Gellai-Nagy (1989). The macrofauna of the Kiscell Clay consists of numerous invertebrate and vertebrate taxa. The rich mollusc fauna was reported by many authors, such as Hofmann (1873), Bogsch (1929), Noszky (1939, 1940), and Báldi (1983, 1986). Decapod crustaceans were published by Beurlen

(1939) and Hyžný & Dulai (2014), while ostracods by Monostori (1982, 2004). The brachiopods are represented by the species *Terebratulina caputserpentis* (Meznerics 1944), while among the echinoderms a questionable Kiscellian ophiuroid, *Pseudaspidura hungarica* was described by Kolosváry (1941).

The Kiscell Clay is also rich in fish otoliths, especially in the Eger area (eastern occurrence of the formation), where this fauna was studied by Nolf & Brzobohatý (1994). Other fish remains are reported by Weiler (1933, 1938), who mainly presented sharks and bony fishes. Földváry (1988) published a paleoichthyological faunal list about this geological epoch of the Buda Hills.

Regarding other vertebrates, reptile and sea mammal (sirenian and cetacean) remains from the Kiscell Clay are also found in the collection of the Hungarian Natural History Museum (see Appendix). The latter group was investigated by Kretzoi (1941).

Since Weiler, other descriptive and/or well-illustrated work about the selachians of the Kiscell Clay has not been written, however, other Rupelian chondrichthyan faunas around the Carpathian Basin were described in great details. From Hungary it is worth mentioning that Solt (1988) described the odontaspid shark *Odontaspis* (*Synodontaspis*) *divergens* from the Rupelian Tard Clay of the Csillaghegy brickyard (Budapest).

The aims of this study were to give a short description of the Kiscell Clay shark material stored in the collection of the Hungarian Natural History Museum with clear illustrations, representing some specimens attributed to Weiler.

HISTORICAL BACKGROUND

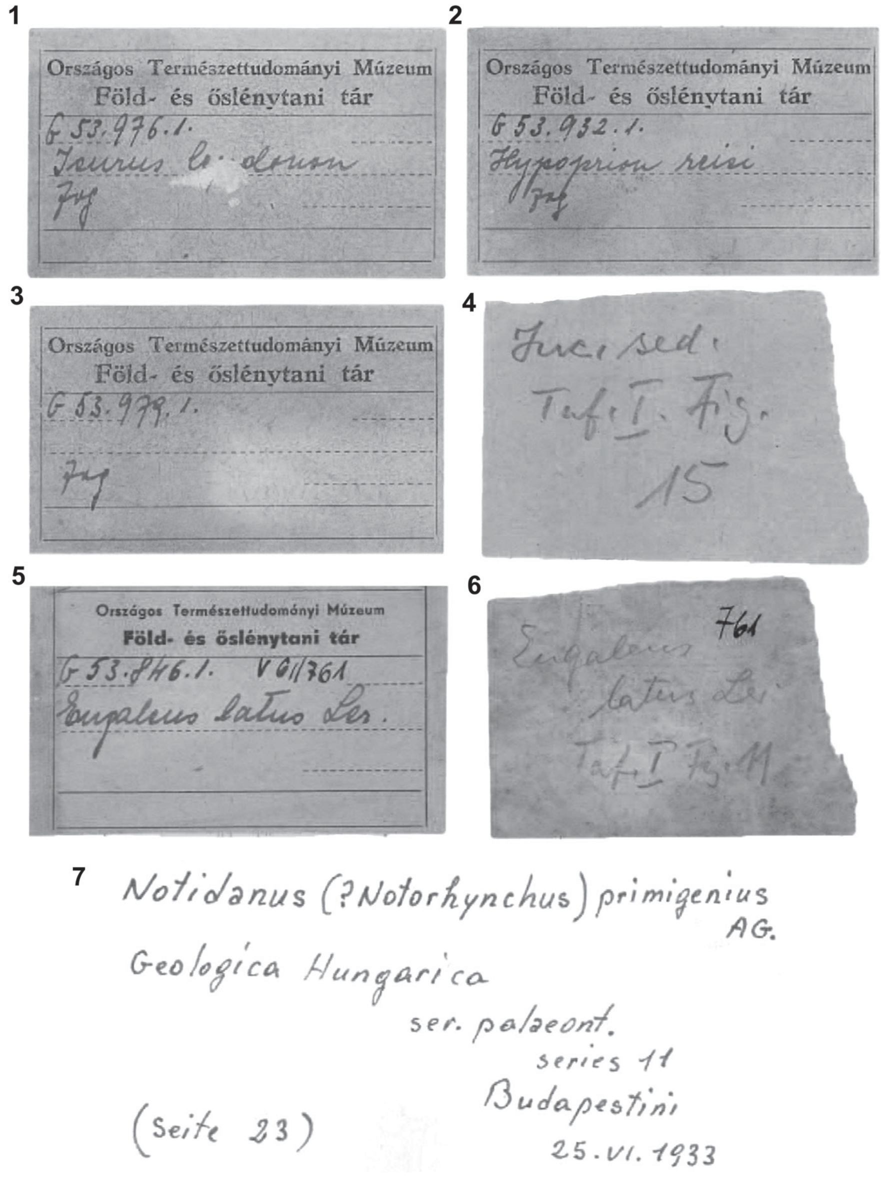
The Hungarian Natural History Museum had tragic events in its past. On the 25th of October in 1956 (and the following days), the museum was bombed. Due to this devastating and destroying event the Mineralogical, Palaeontological, Zoological, and Anthropological departments suffered irreparable damages. At that time, the Palaeontological Department was placed in the main building of the Hungarian National Museum on the Museum Boulevard of Budapest. The exact level of the departmental damages is only a rough estimation. Besides the losses of the fossil collections and the materials of the departmental library, 20 inventory volumes (1952–56), 32,000 index cards, 850 box indexes, 4500 maps, and numerous palaeontological artworks were annihilated by the conflagration. The destroyed fossil material contained many type specimens, 80% of the home and partly foreign scientific and comparative material was lost. However, the losses are barely calculable quantitatively, since a significant part of the inventory books and index cards was burnt, and of course, some losses are scientifically invaluable (Boros 1957). The safely, and/or partially preserved inventory volumes do not include any data about Weiler's shark material.

Decades later, the museum moved to a new building-complex at the Ludovika square in Budapest. In 2012–2013, students of the Eötvös Loránd University (led by Attila Virág) separated the non-inventoried and/or invalidly inventoried specimens in the vertebrate collection of the Palaeontological and Geological Department of the Hungarian Natural History Museum. Published specimens of Weiler (see below in the Systematic Palaeontology section) were found among this separated material in January, 2016. The old inventory numbers starting with letter "G" (after the word "gerinces", Hungarian translation of "vertebrate"), were valid until 1958 (see Figs 1–3 and 5). The specimens got new inventory numbers, and they have been placed back into the collection. The original illustrations of Weiler are very poor, but handwritten labels were found under some specimens (some of them are attributed possibly to Weiler himself), revealing that the specimens were published and figured by Weiler (Figs 4, 6, 7).

LOCALITY AND GEOLOGICAL SETTINGS

The Kiscell Formation was named after the Kiscell plateau located in the Buda Hills (Northwest Budapest, Hungary). It was mined in the area of Budapest (e.g., Bohn brickyard, Nagybátony brickyard, Újlak brickyard) and Eger (in the vicinity of Novaj and Noszvaj; see Nolf & Brzobohatý 1994, Fig. 8). Kiscell (Óbuda, Budapest) is the type area of the Kiscellian Stage, which is a regional stage in the Central Paratethys. The type locality of the Kiscell Clay was in the Újlak brickyard (Óbuda), and most of the material was collected here. Unfortunately, the brickyard localities of Budapest have disappeared or have been recultivated by now, therefore the type locality is no longer available (Hyžný & Dulai 2014). Up to the recent past, the Kiscell Clay has still been mined at Pilisborosjenő and Törökbálint (Horváth 2002), and the mine dumps at Törökbálint are still available for investigation.

The sediment of the Kiscell Formation is unstratified and non-laminated, but hardly bioturbated. It is mostly built up of grey to greenish-grey, sometimes yellowish-brown calcareous clay and clayey marl (Báldi 1983, 1986). The dark colouration of the grey clay is caused by pyrite, while limonite causes the yellowish colour (Vendl 1932; Görög & Török 2007). The formation is rich in foraminifers, ostracods, and calcareous nannofossils, which refer to bathyal depositional conditions. The sedimentation rate has been calculated to 400–500 m/Ma. The thickness of the formation varies between 30 and 800 m (Báldi 1986). It is made up of clay (40–50%), silt (50–60%), and sand (not more than 6–7%) fractions (Báldi 1983).



Figs 1–7. Old inventory cards and labels in the HNHM collection. – **1.** Old inventory card of specimen VER 2016.3451., as *Isurus lepdonon* (most probably misspelled version of *Isurus leptodon*). – **2.** Old inventory card of specimen VER 2016.3454., as *Hypoprion reisi*. – **3.** Old inventory card of specimen VER 2016.3453., as "fog" ("tooth" in Hungarian). – **4.** Old, handwritten label belonging to specimen VER 2016.3453. – **5.** Old inventory card of specimen V.61.761., determined as *Eugaleus latus*. – **6.** Old, handwritten label belonging to specimen V.61.761. – **7.** Old, handwritten label belonging to specimen V.61.672C

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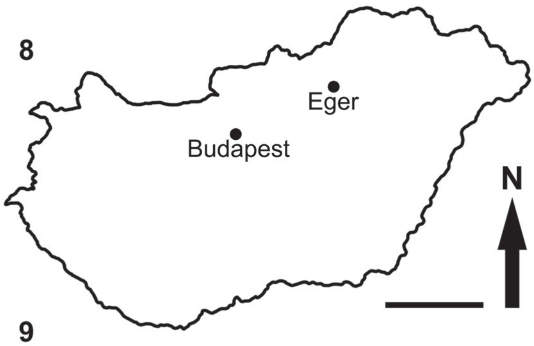

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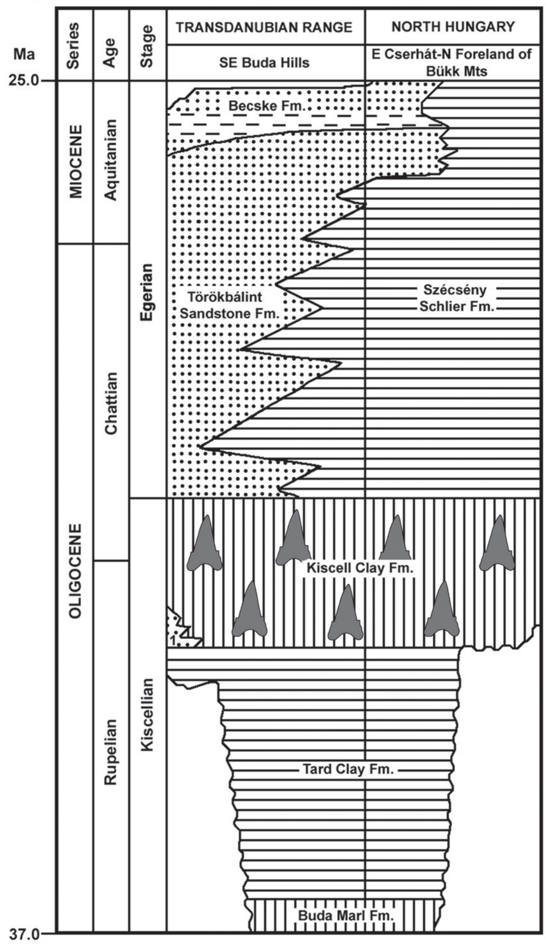


Figs 8–9. Geological background. – **8.** Localities in Hungary, where the Kiscell Formation was mined; Scale bar: 100 km. – **9.** Lithostratigraphic units of the Oligocene at the Buda Hills area (Hungary) (modified after HYŽNÝ & DULAI 2014)

The Kiscell Formation belongs to the lower part of the NP 24 nannoplankton zone, which indicates the Late Kiscellian stage (Nagymarosy & Báldi-Beke 1988). The Kiscellian regional stage is used for part of the Central Paratethyan Lower Oligocene (Rupelian to lowest Chattian; see Báldi *et al.* 1999; Piller *et al.* 2007).

Nolf & Brzobohatý (1994) stated that the regional Kiscellian stage is made up of the Kiscell Formation, and the underlying Tard Clay and Buda Marl (Fig. 9). The Tard Clay grades upwards into the Kiscell Clay without hiatus, but with clear faunal changes (Báldi 1986). The Eger Formation (Egerian stage) overlies the Kiscell Clay with sedimentary and faunal changes (Nolf & Brzobohatý 1994).

MATERIAL AND METHODS

Almost all the specimens described here are placed in the collection of the Hungarian Natural History Museum (HNHM), but a few of them are in private collections. Old, hardly readable labels are placed under some of the non-catalogued, Kiscell Clay shark teeth of the HNHM, which allowed us to identify them undeniably as Weiler's specimens. Most of the teeth are in very poor condition due to oxidization (caused by the high pyrite content of the formation; see Vendl 1932).

The Kiscell Clay shark tooth remains are typically dark, black, brown or greyish in colour. During the last decades, due to the oxidization of pyrite, the non-conserved specimens started to fall apart, most of them (including the shark teeth described below) are already in very poor condition (e.g., most of the teeth have no root preserved). The remains were cleaned in tap water, then prepared with needles and finally for better conservation superglue and polyvinyl butyral (PVB) were used.

The HNHM Kiscell Clay shark material is inventoried with a lot of missing information. Dozens of teeth are catalogued with location data "Budapest" or "Óbuda", and with age data "Oligocene", which do not allow us to refer them to exact locality or age. This is important, since other shark tooth bearing formations (e.g., Tard Formation) have been also mined in Budapest (Óbuda) (see above). We do not report these teeth here, since we focus on the fauna of the Kiscell Clay, as Weiler's work dealt with this formation.

Under some inventory numbers several teeth or different taxa are placed. In these cases we used letter-associated numbering, for separating the specimens. Synonym-lists were mostly set after first authors and remains from the Paratethys.

SYSTEMATIC PALAEONTOLOGY

Class Chondrichthyes Huxley, 1880
Order Hexanchiformes De Buen, 1926
Family Hexanchidae Gray, 1851
Genus *Notorynchus* Ayres, 1855

Notorynchus primigenius (Agassiz, 1843)
(Figs 10–13)

1843 *Notidanus primigenius* n. sp. – Agassiz, pp. 218–220, pl. 27, figs 6–17.
1933 *Notidanus* (?*Notorhynchus*) *primigenius* Ag. – Weiler, p. 23, text-fig. 11.
1938 *Notidanus* (?*Notorhynchus*) *primigenius* Ag. – Weiler, p. 7, pl. 1, fig. 16.
1970 *Hexanchus primigenius* (L. Agassiz, 1843) – Brzobohatý & Kalabis, p. 42, figs 3, 4.
1970 *Hexanchus primigenius* (Agassiz) – Cappetta, pl. 4, figs 11–19.
1993 *Notorynchus primigenius* (Agassiz, 1843) – Baut, p. 3, figs 3–4.
1999 *Notorynchus primigenius* (Agassiz, 1843) – Baut & Génault, pp. 10–11, pl. 1, figs 1–4.
2001 *Notorynchus primigenius* (Agassiz, 1843) – Reinecke *et al.*, pp. 7–8, pls 1–5.
2005 *Notorynchus primigenius* (Agassiz, 1835) – Reinecke *et al.*, pp. 8–9, pls 1–2.
2010 *Notorynchus primigenius* (Agassiz, 1843) – Hovestadt *et al.*, p. 60, fig. 14.
2013 *Notorynchus primigenius* (Agassiz, 1835) – Schultz, pp. 24–27, pl. 4, figs 9a, b.
2014 *Notorynchus primigenius* (Agassiz, 1835) – Reinecke *et al.*, pp. 8–9, pls 1–2.

Referred material: 13 teeth (V.61.672C., V.61.794., V.61.818., V.61.834., V.61.862., VER 2016.3418., VER 2016.3429., VER 2016.3455.).

Remarks: The here referred material consists mostly of lower lateral teeth. Lower laterals have a wide and high, labiolingually flattened root, typical for lower laterals of hexanchid sharks. This root is getting thicker to the root-crown boundary (Holec *et al.* 1995). The crown of lower laterals is made up of small mesial cusplets, a main (or *principal*) cusp, and distal cusplets (usually 3–6 distal cusplets, distally decreasing in size). The lower symphyseals are variable in detailed morphology, however, they mostly have a symmetrical, or nearly symmetrical contour. The upper anteriors have no distal or mesial cusplets, but an elongated main cusp, sigmoid in shape. The root of upper laterals is similar to that of lower ones, but their main cusp is significantly bigger than all other cusplets (these files have mostly 2–3 distal cusplets, often with missing mesial cusplets).

The HNHM specimens are mostly fragmentary or poorly preserved, most of them has no root. Even if some teeth are preserved as fragments only, they can be distinguished from the teeth of *Hexanchus* (see below) by the dimensions, size, number and proportions of the cusplets. Two lower laterals (V.61.794. and V.61.818.) are in relatively good condition, almost their whole crown is preserved. One lower symphyseal tooth is also known (VER 2016.3455., Fig. 10).

The specimen is in very good condition, it has nearly symmetrical shape in labiolingual view. However, it had no inventory label, but it was identifiable as the tooth was figured by Weiler (1938, pl. 1, fig. 16; also Fig. 11 of this work). The characteristic symmetry, the number of cusplets and the shape of the preserved portions of the root allow this matching. This specimen (VER 2016.3455.) was already figured by Főzy & Szente (2012), without exact locality.

Under specimen V.61.672C. a handwritten label was found (Fig. 7), which refers this specimen to one of Weiler's figure (1933, text-fig. 11). It is easily imaginable that specimen V.61.672C. and Weiler's figured one are the same, since the preserved partial outline of the tooth in the clay (Fig. 12) is similar to Weiler's specimen. However, in this case Weiler's figure is horizontally mirrored (Fig. 13). It is also worth mentioning that the old label of V.61.672C. was written in German, but the style of handwriting differs from those of the two other handwritten labels found under the specimens of Weiler (see Figs 4, 6, and 7).

The genus *Notorynchus* is known from the Early Cretaceous, with one recent species, *Notorynchus cepedianus* Péron, 1807 (Compagno 1984). *N. primigenius* ranges from the Oligocene to the Miocene, and it was reported widely from shallow marine sediments (see in Cappetta 2012; Reinecke *et al.* 2014).

Genus *Hexanchus* Rafinesque, 1810

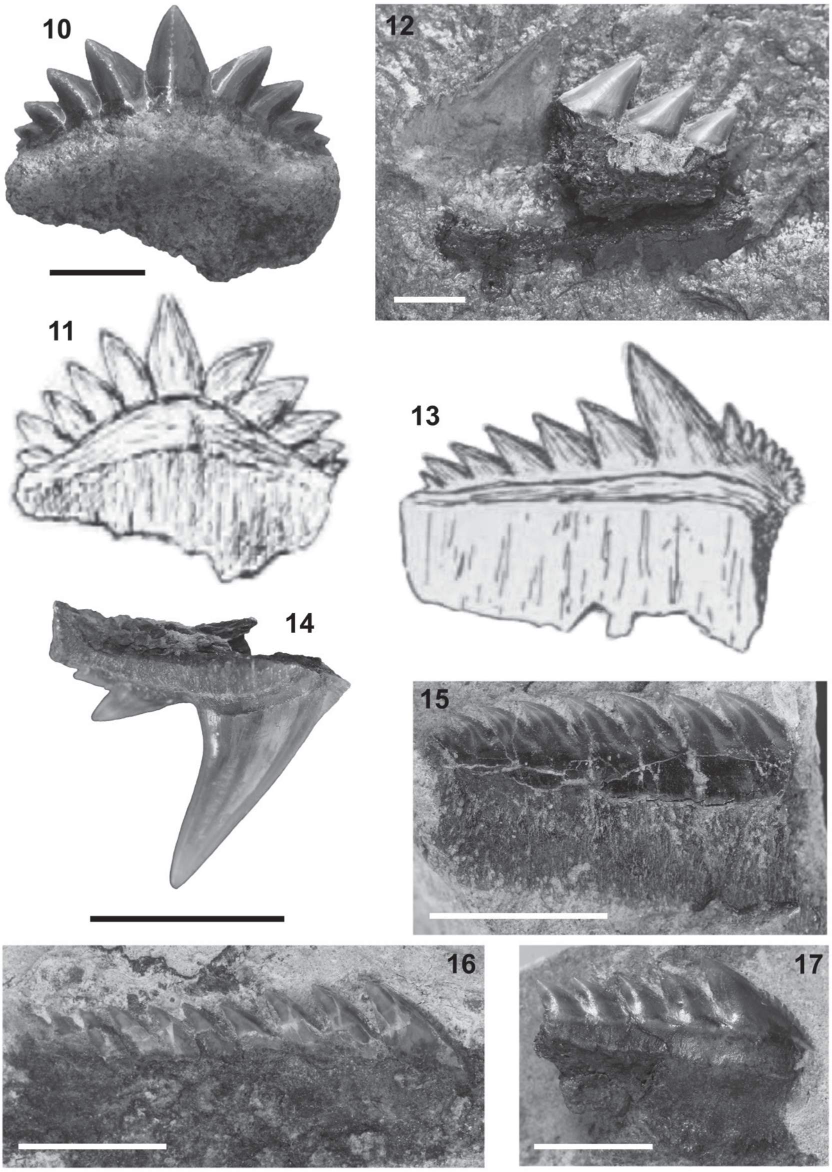
Hexanchus agassizi Cappetta, 1976
(Figs 14–17)

1976 *Hexanchus agassizi* n. sp. – Cappetta, pp. 553–554, pl. 1, figs 5, 7, 8.
1979 *Hexanchus agassizi* Cappetta, 1976 – Ward, pp. 114–115, pl. 2, figs 1–2.
2005 *Hexanchus* sp. – Reinecke *et al.*, p. 9, pl. 3, figs 1a-b.
2012 *Hexanchus agassizi* Cappetta, 1976 – Cappetta, pp. 92–93, fig. 82.
2013 *Hexanchus agassizi* Cappetta, 1976 – Schultz, pp. 23–24, pl. 4, figs 4a, b, 5.
2014 *Hexanchus* cf. *agassizi* Cappetta, 1976 – Reinecke *et al.*, pp. 9–10, pls 3–4.

Referred material: 17 teeth (V.61.282., V.61.285A., V.61.770., VER 2016.3449., VER 2016.3456., VER 2016.3457., VER 2016.3458.).

Remarks: These teeth are similar to those of *N. primigenius* in general morphology, however, they are visually different in their much smaller size, and in having much more distal cusplets on the lower lateral teeth. The upper anteriors are higher than wide, with one slender, sinuous cusp without mesial or distal cusplets. The lower anterolateral-lateral files could be extremely wider than high, with mostly 7–9 distal cusplets reduced in height distally (Figs 15–17).

Most of the HNHM material of *H. agassizi* is in very poor condition, however, some of the specimens have very well-preserved crown. All specimens show



Figs 10–13. *Notorynchus primigenius* (Agassiz, 1843). – **10.** Lower symphyseal tooth (VER 2016.3455.), lingual view. – **11.** Specimen VER 2016.3455. as figured by Weiler (1938). – **12.** Lower lateral tooth (V.61.672C.), lingual view. – **13.** Suggested specimen V.61.672C., as figured by Weiler (1933). – **Figs 14–17.** *Hexanchus agassizi* Cappetta, 1976. – **14.** Upper anterolateral tooth (V.61.285.), lingual view. – **15.** Lower lateral tooth (V.61.770.), lingual view. – **16.** Lower lateral tooth (VER 2016.3456.), labial view. – **17.** Lower lateral tooth (VER 2016.3457.), lingual view. Scale bars: 5 mm

close morphological affinities with the *H. agassizi* teeth figured by CAPPETTA (2012, p. 92, fig. 82).

Hexanchus agassizi was a widespread species from the Early Eocene to the Late Oligocene; its remains have been recovered from deep water sediments (see in CAPPETTA 2012; REINECKE *et al.* 2014).

Genus *Heptranchias* Rafinesque, 1810

Heptranchias howelli (Reed, 1946)
(Figs 18–23)

1938 Fam. et gen. indet. (Inc. sed.) – WEILER, pl. 1, fig. 15.
1946 *Notidanion howelli* n. sp. – REED, pp. 1–3, figs 1–4.
1995 *Heptranchias* sp. – SIVERSON, pp. 4–5, figs 2A-C.
2009 *Heptranchias howelli* (Reed, 1946) – BIEŃKOWSKA-WASILUK & RADWAŃSKI, pp. 238–239, pl. 1, figs 1–5.
2012 *Heptranchias howelli* (Reed, 1946) – CAPPETTA, p. 99, fig. 86.
2014 *Heptranchias howelli* Reed, 1946 – CARLSEN & CUNY, p. 64, figs 16A-B.
2014 *Heptranchias* sp. – REINECKE *et al.*, pp. 10–11, pl. 5, figs 1–5.
2015 *Heptranchias howelli* (Reed, 1946) – ADOLFFSEN & WARD, pp. 7–8, figs 2L-M.

Referred material: 3 teeth (V.61.814., VER 2016.3452., VER 2016.3453.).

Remarks: In general, teeth of *Heptranchias* have typical hexanchid morphology (see above at *N. primigenius* and *H. agassizi*). The lower teeth are wider than the upper teeth, while cusplets of the upper teeth are distally bent, and more elongated. The upper anteriors bear no cusplets, but an elongated main cusp, strongly sigmoid in shape from labiolingual view (Figs 18–19). The upper lateral teeth have a distally bent (or sometimes weakly sigmoid) main cusp, which outgrows the distally also bent distal and mesial cusplets (Figs 20–21). The principal cusp of the lower lateral teeth is longer than the distal cusplets, which are nearly in the same size – except the most distal 1–2 cusplets (Figs 22–23; see CAPPETTA 2012, fig. 86E-F; TRIKOLIDI 2014, fig. 15). The root is mesiodistally wide, and labiolingually flattened on every file. Among all tooth positions, lower laterals are the taxonomically most significant.

One upper anterior tooth (morphologically identical with the figured specimen of CAPPETTA 2012, fig. 86A) is known in the collection of the HNHM (Figs 18–19). The upper lateral figured by WEILER (1938, pl. 1, fig. 15; also Fig. 21 of this work) is closely identical with the one figured by CAPPETTA (2012, fig. 86C, D). This tooth (VER 2016.3453.) was found among the non-catalogued HNHM material, with an old, handwritten label under it ("*Inc. sed. Taf. I. Fig. 15*").

Heptranchias is a neritic (relatively deep water) form known from the Late Cretaceous (Campanian), exists up to nowadays with one recent species, *Heptranchias perlo* (Bonnaterre, 1788), also known as sharpnose sevengill shark. Fossils of the genus are all isolated tooth remains, which are not common in any geological deposits (Cappetta 2012). The genus has also been reported by Reinecke *et al.* (2014) from the Chattian of the Thalberg Beds (Bavaria, Germany), which material seems to show affinity with the species *H. howelli*, however, only upper anteriors and upper laterals have been published there. Lower laterals of *H. howelli* have been reported from the Lower Oligocene Menilite Formation of the Polish Outer Carpathians (Bieńkowska-Wasiluk & Radwański 2009), from the Early Paleocene (Danian) of Denmark (Adolffsen & Ward 2015) and from the Middle Eocene (Late Ypresian to Middle Lutetian) Lillebælt Clay of Denmark (Carlsen & Cuny 2014).

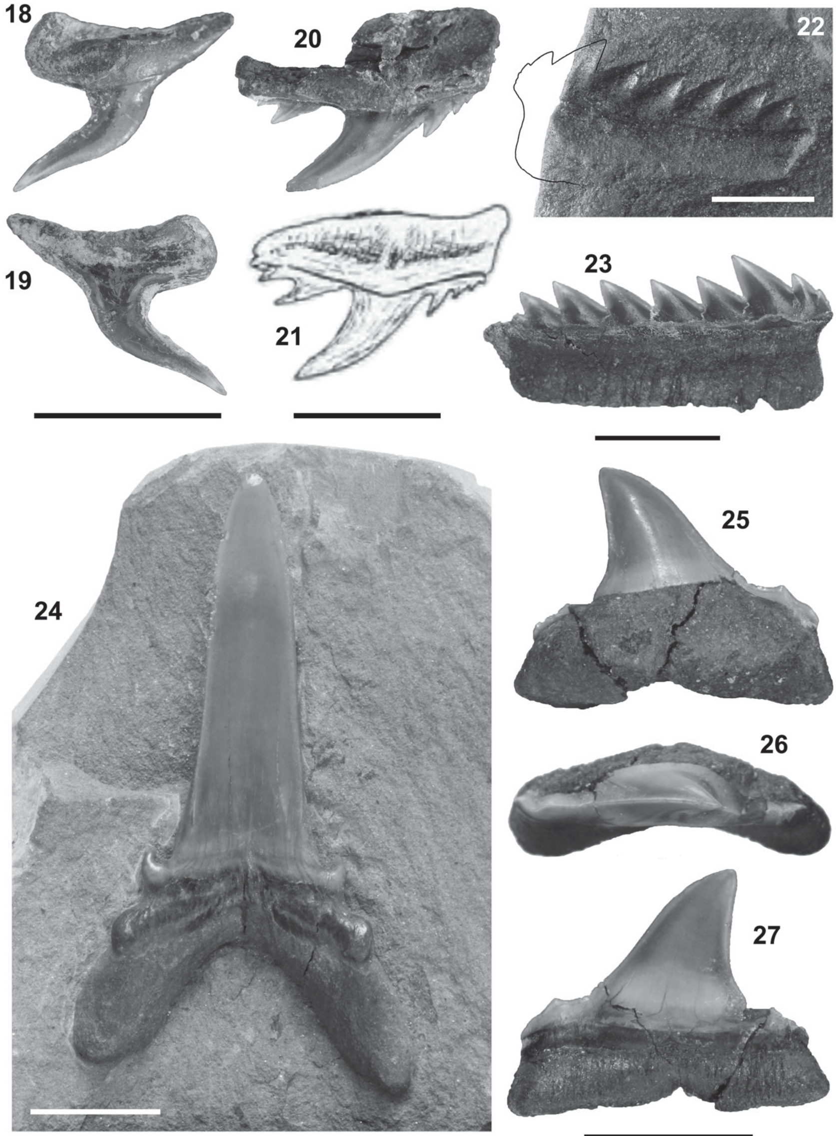
Order Lamniformes Berg, 1958
Family Odontaspididae Müller et Henle, 1839
Genus *Araloselachus* Glikman, 1964

Araloselachus cuspidatus (Agassiz, 1843)
(Figs 24–27)

1843 *Lamna cuspidata* n. sp. – Agassiz, p. 290, pl. 37a, figs 43–50.
1993 *Carcharias cuspidata* (Agassiz, 1843) – Baut, p. 4, figs 22, 24.
1999 *Carcharias cuspidata* (Agassiz, 1844) – Baut & Génault, pp. 15–16, pl. 3, figs 3–6.
2005 *Carcharias cuspidatus* (Agassiz, 1843) – Reinecke *et al.*, pp. 24–25, pl. 9, figs 1–7.
2007 *Carcharias cuspidatus* (Agassiz, 1843) – Kocsis, p. 32, pl. 4, figs 12–13.
2010 *Carcharias cuspidata* (Agassiz, 1843) – Hovestadt *et al.*, p. 60, figs 5–7.
2012 *Araloselachus cuspidatus* (Agassiz, 1843) – Cappetta, p. 191, fig. 180.
2013 *Carcharias cuspidatus* (Agassiz, 1843) – Schultz, pp. 61–66, pl. 5, figs 5a, b.
2014 *Araloselachus cuspidatus* (Agassiz, 1843) – Reinecke *et al.*, pp. 17–20, pls 16–18.

Referred material: 5 teeth (V.61.671., V.61.677F-I., VER 2016.3447.)

Remarks: The teeth are robust and massive among odontaspids. The cutting edges are smooth, they usually do not reach the tooth-crown boundary, except for some upper lateral-distal files (see below). The labial face is nearly flat, while the lingual is convex. The root is typically bifurcated with a large nutritive groove on a central bulge. The root-lobes are less angled on upper laterals. Anterior to lateral teeth could bear one or two pairs of relatively small and pointed cusplets. The lateral cusplets of the anteriors are typically circular in cross-section, while those of laterals and distals are labiolingually flattened. The anterior files have straight, narrow, high main cusp (Fig. 24). The crown of the lower laterals is also symmetrical, straight, and narrow, but these files are much lower than the anteriors. The upper laterals-distals are distally bent with low,



Figs 18–23. *Heptranchias howelli* (Reed, 1946). – **18–19.** Upper anterior tooth (VER 2016.3452.). – **18.** Lingual view. – **19.** Labial view. – **20.** Upper lateral tooth (VER 2016.3453.), lingual view. – **21.** Specimen VER 2016.3453. as figured by Weiler (1938). – **22.** Imprint of a lower lateral tooth (V.61.814.); tooth contour of the specimen has been reconstructed based on the specimen on Fig. 23. – **23.** Lower lateral tooth, lingual view (specimen in private collection of Peter Picard). – **Figs 24–27.** *Araloselachus cuspidatus* (Agassiz, 1843). – **24.** Anterior tooth (V.61.671.), labial view. – **25–27.** Distal tooth (VER 2016.3447.). – **25.** Lingual view. – **26.** Apical view. – **27.** Labial view. Scale bars: 18–20, 22–23: 5 mm; 24–27: 10 mm

triangular main crown. The cutting edge of these files sometimes continues in the cutting edges of the cusplets (Figs 25–27).

Odontaspids are common and widespread in many Paleogene and Neogene marine deposits. This species is widely known from Europe and North America, from the Lower Oligocene to the boundary of the Middle and Upper Miocene (Cappetta 1987; Holec *et al.* 1995; Reinecke *et al.* 2014). Weiler (1933, p. 23 and 1938, p. 8) also reported the species from the Kiscell Clay as *Odontaspis cuspidata*.

Genus *Carcharias* Rafinesque, 1810

The dentition is strongly heterodont, the teeth have typical odontaspid tooth morphology. All teeth have long, pointed main crown, bifurcated root with one or two pairs of cusplets. The cutting edges are smooth all along, they do not reach the base of the main crown. The anteriors are thin and slender, their main crown is elongated, symmetrical in labiolingual view, while strongly sigmoid in profile view. The lower laterals are similar to the anterior, but they are shorter, and less sigmoid. The distals and the upper laterals have a distally bent main crown.

The root has two, slender branches, with a massive central bulge on the lingual side. This bulge bears a visual nutritive groove. The cusplets of the anteriors are pointed and also slender, they are usually circular in cross-section. The laterals and distals have labiolingually straight, triangular cusplets. Weiler (1933, 1938) reported *Carcharias acutissima* (as *Odontaspis acutissima*) from the Kiscell Clay, however, he did not figure these teeth, and he did not mention any detail about a possible ornamentation of the lingual face of the main crown, therefore this report could belong to any of the here detailed *Carcharias* morphogroups (see below).

Carcharias sp. 1
(Figs 28–30)

Referred material: 7 teeth (VER 2016.3411., VER 2016.3425., VER 2016.3441., VER 2016.3442.).

Remarks: The lingual face of the main crown bears fine apicobasal striation, which disappears towards the tip (this striation is not as visible and well-developed as that of members of the family Mitsukurinidae). The labial face is smooth, without any ornamentation.

In having striated lingual face, these teeth show affinities to the species *Carcharias acutissima* (Agassiz, 1843). This species is known from the Eocene and became abundant in the Miocene (Cappetta 2012). All the Kiscell Clay specimens referred here bear the lingual striation of the main crown, however, only one (VER 2016.3441.; Figs 28–30) has lateral cusplets preserved. This cusplet is not so bent to the main crown, as it is typical for the species. It is weakly bent labiolingually, it has weak, flattened edges to the tip. This difference could have been caused by intraspecific variability, due to the strong heterodonty, but for a certain taxonomic determination more specimens are needed.

It is worth mentioning that Weiler (1933, p. 23 and 1938, p. 8) reported the species *Carcharias acutissima* as *Odontaspis acutissima*, therefore its presence seems to be supported.

Carcharias sp. 2
(Figs 31–33)

Referred material: 8 teeth (V.61.866., VER 2016.3424., VER 2016.3439.).

Remarks: Most teeth of this morphogroup are very poorly preserved. The most completely preserved tooth (V.61.866.) is similar to the first morphogroup in size, but in contrast to the teeth of *Carcharias* sp. 1, the main crown is more robust, labiolingually wider at the base, and both faces are more convex to the tip. One cusplet is preserved which is similar to those of *Carcharias* sp. 1 in being pointed and having flattened edges, but while the cusplets are simply bent both mesiodistally and labiolingually on *Carcharias* sp. 1, the only preserved cusplet of *Carcharias* sp. 2 is weakly sigmoid.

The lingual face of the main crown is smooth all along, no striation is present. According to Hovestadt & Hovestadt-Euler (2010), this feature assigns this tooth with uncertain affinities to the species *Carcharias gustrowensis* (Winkler, 1875). This species was widely distributed in the North Sea Basin during the Late Oligocene and the Early to Middle Miocene (Reinecke *et al.* 2014).

Odontaspididae indet.

Referred material: 106 teeth (V.61.667A-E., V.61.672D., V.61.736., V.61.737., V.61.811., V.63.691., V.63.695., V.61.820., V.61.829., V.61.838., V.61.842., V.61.848., V.61.881., VER 2016.3407., VER 2016.3412., VER 2016.3415., VER 2016.3417., VER 2016.3420., VER 2016.3430., VER 2016.3432., VER 2016.3433., VER 2016.3440.).

Remarks: These teeth are too fragmentary for closer identification, however, there are many of them. Various tooth positions are represented. Most of them consist only of the main crown, or elongated, sigmoid enamel-fragments. The qualitative damages of these teeth could have been caused by the oxidization of the pyrite and/or during the transportation of the material.

Figs 28–30. *Carcharias* sp. 1 anterior tooth (VER 2016.3441.). – **28.** Lingual view. – **29.** Profile view. – **30.** Labial view. – **Figs 31–33.** *Carcharias* sp. 2 anterior tooth (V.61.866.). – **31.** Lingual view. – **32.** Profile view. – **33.** Labial view. Scale bars: 10 mm

Family Lamnidae Müller et Henle, 1838
Genus *Carcharoides* Ameghino, 1901

Carcharoides catticus (Philippi, 1846)
(Figs 34–36)

1846 *Otodus catticus* n. sp. – Philippi, p. 24, pl. 2, figs 5–7.
1933 *Lamna cattica* Philippi – Weiler, p. 24, text-fig. 13.
1999 *Carcharoides catticus* (Philippi, 1846) – Müller, pl. 3, figs 9–12.
2005 *Carcharoides catticus* (Philippi, 1846) – Reinecke *et al.*, pp. 28–30, pl. 19, figs 3–6.
2007 *Carcharoides catticus* (Philippi, 1851) – Kocsis, p. 33, figs 5.1–5.3.
2014 *Carcharoides catticus* (Philippi, 1846) – Reinecke *et al.*, p. 20, pl. 20, figs 1–6.

Referred material: 15 teeth (VER 2016.3414., VER 2016.3419., VER 2016.3428., VER 2016.3431., VER 2016.3445., VER 2016.3446., VER 2016.3450.).

Remarks: The teeth are very characteristic, and easy to identify. The main crown is pointed on all files, it bears no striation or any other kind of ornamentation. Anteriors and lower laterals have narrow, straight main crown, but those of upper laterals are triangular, and distally bent (Figs 34–36). The main crown of upper laterals is strongly flattened, only the lingual surface shows weak convexity. The lateral cusplets are relatively big, they are narrow and pointed on anteriors and lower laterals, while labiolingually flattened, triangular on upper laterals (the lateral cusplets of the anterior and lower lateral files are usually circular in cross- section). The carinae of the main crown are smooth all along, they often run down to the root-crown boundary (sometimes the carinae of the main crown are continuous with the flattened edges of the lateral cusplets; see Verwey 2013; fig. 4). The root is bifurcated, flattened, its lingual side bears a central bulge with a transversal groove. The anteriors and lower laterals have symmetrical root, while the distals and upper laterals have asymmetrical root.

C. catticus specimens from the Kiscell Clay are mostly fragmentary, only a few of them have some portions of the root, or the lateral cusplets preserved. According to Reinecke *et al.* (2014), the reports on the Rupelian presence of the species in the Buda Hills (Weiler 1933, 1938; Földváry 1988) is one of the oldest records of the species. *C. catticus* is thought to be a neritic, medium sized form. The species has been reported from Western Africa and Europe, from the middle Oligocene to the middle Miocene (Cappetta 1987), however, exceptional Eocene reports are also known (Otero *et al.* 2012, 2013).

Genus *Isurolamna* Cappetta, 1976

Isurolamna gracilis (Le Hon, 1871)
(Figs 37–44)

1871 *Oxyrhina gracilis* n. sp. – Le Hon, p. 11, text-fig. 2.
1933 *Lamna rupeliensis* Le Hon – Weiler, p. 24, text-fig. 12.
1993 *Lamna rupeliensis* (Le Hon, 1871) – Baut, p. 4, figs 8–9.
2001 *Isurolamna gracilis* (Le Hon, 1871) – Reinecke *et al.*, pp. 21–23, pls 31, 32 (with fig. b), 33, 34.
2005 *Isurolamna gracilis* (Le Hon, 1871) – Reinecke *et al.*, p. 30, pl. 20, figs 4–6.
2012 *Isurolamna gracilis* (Le Hon, 1871) – Cappetta, p. 217, fig. 202.

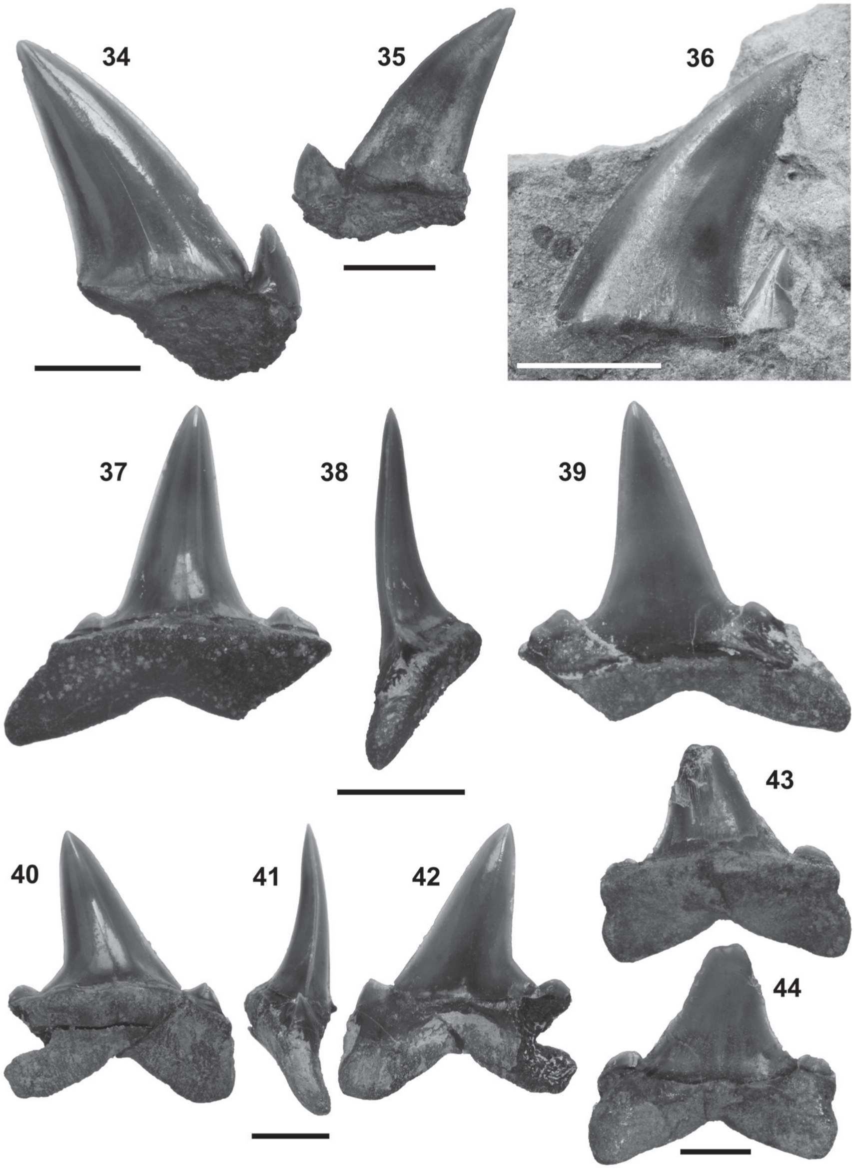
Referred material: 5 teeth (VER 2016.3416., VER 2016.3427., VER 2016.3436., VER 2016.3437., VER 2016.3438.).

Remarks: The crown is pointed and triangular, slender and narrow on lower files (Figs 37–39), while labiolingually and mesiodistally wide at the base on uppers. Both faces are smooth, the cutting edges are smooth all along, in continuing in the edges of the flattened lateral cusplets both mesially and distally. The lateral cusplets are low, typically rounded, or triangular, and pointed. On the lingual side the root bears a wide, convex crest, runs mesiodistally between the lateral cusplets, under the root-crown boundary. The root has two large, flattened lobes, with a visual nutritive groove in the middle. The lobes are angled on their mesial and distal edges. The anterior teeth are typically straight (or nearly straight), while the laterals and distals have distally directed main crown (Figs 40–44). Teeth of upper and lower jaw are easily distinguishable due to the dignathic heterodonty.

We assign a possible relation to *I. gracilis*, since the presence of lateral cusplets is not typical for *Isurus oxyrinchus* (reported from the Chattian of Germany; Reinecke *et al.* 2005, 2014). Hopefully later on more better preserved Kiscell Clay specimens of this species are going to be re-discovered in museum collections.

Weiler (1933, p. 24, text-fig. 12) reported and figured *I. gracilis* as *Lamna rupeliensis* from the Kiscellian of Budapest, but his figured specimen seems to be lost. However, other specimens have been found in the HNHM collection, labelled as *Lamna rupeliensis*, but these remains are fragmentary, and do not give any additional information to our description.

During the Rupelian *Isurolamna gracilis* was the predominant lamnid shark (Reinecke *et al.* 2014).



Figs 34–36. *Carcharoides catticus* (Philippi, 1846). – **34.** Upper lateral tooth (VER 2016.3446.), lingual view. – **35.** Upper lateral tooth (VER 2016.3445.), labial view. – **36.** Upper lateral tooth (VER 2016.3450.), labial view. – **Figs 37–44.** *Isurolamna gracilis* (Le Hon, 1871). – **37–39.** Lower anterolateral tooth (VER 2016.3436.). – **37.** Lingual view. – **38.** Profile view. – **39.** Labial view. – **40–42.** ?Upper lateral tooth (VER 2016.3437.). – **40.** Lingual view. – **41.** Profile view. – **42.** Labial view. – **43–44.** Lower lateral tooth (VER 2016.3438.). – **43.** Lingual view. – **44.** Labial view. Scale bars: 5 mm

Lamnidae indet.

Referred material: 70 teeth (V.61.672A., V.61.779., V.61.813., V.61.826., V.61.845., V.61.852., V.61.875., VER 2016.3397., VER 2016.3398., VER 2016.3408., VER 2016.3409., VER 2016.3413., VER 2016.3421., VER 2016.3422., VER 2016.3423., VER 2016.3434.).

Remarks: These teeth are rootless, mostly broken crowns. They represent various sizes and tooth positions, however, they are too fragmentary for closer identification.

Family Otodontidae Glikman, 1964
Genus *Otodus* Agassiz, 1843
Subgenus *Otodus* (*Carcharocles*) Jordan et Hannibal, 1923

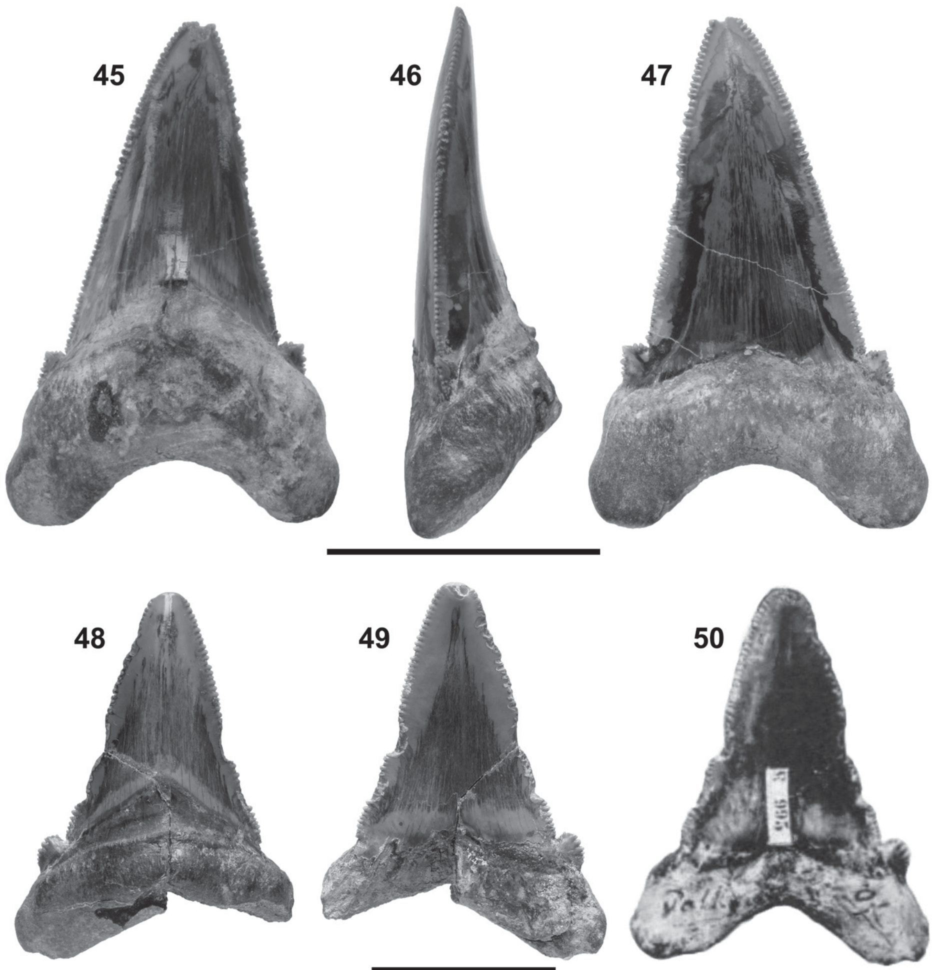
Otodus (*Carcharocles*) *angustidens* (Agassiz, 1843)
(Figs 45–50)

1843 *Carcharodon angustidens* n. sp. – Agassiz, p. 255, pl. 28, figs 20–25, pl. 30, fig. 3.
1933 *Carcharodon angustidens* var. *turgidus* Ag. – Weiler, p. 25, pl. 1, fig. 3, pl. 3, fig. 2.
1933 *Carcharodon angustidens* Ag. – Weiler, p. 26, pl. 3, fig. 3.
1993 *Carcharocles angustidens* (Agassiz, 1843) – Baut, p. 5, figs 12–15.
1999 *Carcharocles angustidens* (Agassiz, 1843) – Baut & Génault, pp. 25–26, figs 12–13, pl. 4, fig. 11.
1999 *Carcharocles angustidens* (Agassiz, 1843) – Müller, p. 39, pl. 4, figs 7, 9, 11–13.
2001 *Carcharocles angustidens* (Agassiz, 1843) – Reinecke *et al.*, pp. 19–20, pls 28–30.
2005 *Carcharocles angustidens* (Agassiz, 1843) – Reinecke *et al.*, pp. 35–36, pl. 20, figs 7–9.
2013 *Otodus angustidens* (Agassiz, 1835) – Schultz, pp. 75–76, pl. 5, figs 14a, b.
2014 *Otodus* (*Carcharocles*) sp. – Reinecke *et al.*, p. 23, pl. 22, fig. 2.

Referred material: 50 teeth (V.61.668., V.61.733., V.61.751., V.61.778., V.61.798., V.61.823., V.61.827., V.61.833., V.61.837., V.61.846., V.61.850., V.61.851., V.61.859., V.61.888., V.61.900., V.61.906., V.81.138., VER 2016.3399., VER 2016.3400., VER 2016.3401., VER 2016.3402., VER 2016.3403., VER 2016.3404., VER 2016.3405., VER 2016.3406., VER 2016.3426.).

Remarks: The teeth have triangular, labiolingually straight crown with serrated mesial and distal carinae. The root is wide, massive, and bifurcated. The teeth bear 1–1 lateral cusplets both mesially and distally. The cusplets are variable in shape, and they have also visually serrated carinae. The anterior teeth are symmetrical, while the anterior-lateral-distal teeth show asymmetrical contour in labiolingual view. The species has been reported from other Early Oligocene localities around Europe (see Baut & Génault 1999; Reinecke *et al.* 2001). The species of this genus are among the currently known biggest macropredator sharks ever lived. This species must have been the top predator of the local fauna.

In 1933, Weiler figured a tooth from the Kiscell Clay under the name *Carcharodon angustidens* (Weiler 1933, pl. 3, fig. 3; also Fig. 50 of this work). The identification done by Weiler was absolutely correct, however, since 1933 the species has been re-classified several times. Following Cappetta (2012) the actual name of the species is *Otodus* (*Carcharocles*) *angustidens*. The specimen was found in the collection of the HNHM (re-inventoried as VER 2016.3403.), with some damages on the root (see Figs 48–49). The specimen figured by Weiler



Figs 45–50. *Otodus* (*Carcharocles*) *angustidens* (Agassiz, 1843). – **45–47.** Lower anterior tooth (V.61.822.). – **45.** Labial view. – **46.** Profile view. – **47.** Lingual view. – **48–49.** Lower anterior tooth (VER 2016.3403.). – **48.** Labial view. – **49.** Lingual view. – **50.** Specimen VER 2016.3403. as figured by Weiler (1933). Scale bars: 30 mm

(1933) bears all important features of lower anterior teeth. The cutting edges and the root are damaged, however, the condition of the tooth did not change much since the first publication of Weiler. The tooth is easy to identify by the serrations on the only preserved lateral cusplet and the missing sections of the cutting edges.

Dozens of other specimens are placed in the collection of the HNHM, some of them are more or less complete, or at least complete enough for taxonomic identification.

Family Alopiidae Bonaparte, 1838
Genus *Alopias* Rafinesque, 1810

Alopias cf. *exigua* (Probst, 1879)
(Figs 51–60)

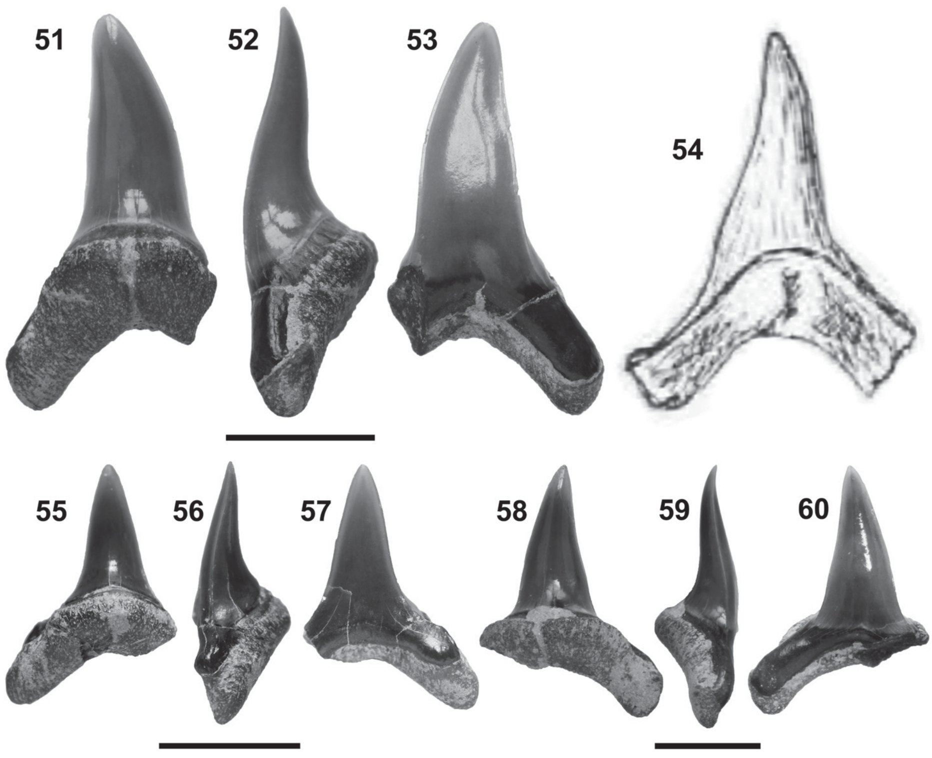
1879 *Oxyrhina exigua* n. sp. – Probst, p. 135, pl. 2, figs 20–25.
1938 *Isurus leptodon* Ag. (= *Isurus gracilis* Le Hon.) – Weiler, pp. 7–8, pl. 1, fig. 17.
1999 *Alopias exigua* (Probst, 1879) – Baut & Génault, p. 27, pl. 7, figs 8–10.
2001 *Alopias exigua* (Probst, 1879) – Reinecke *et al.*, pp. 23–24, pl. 35.
2007 *Alopias exigua* (Probst, 1879) – Kocsis, pp. 34–35, figs 5.13–5.14.
2013 *Alopias exigua* (Probst, 1879) – Schultz, p. 38, pl. 4, figs 15a, b.
2014 *Alopias* aff. *exigua* (Probst, 1879) – Reinecke *et al.*, pp. 23–27, pls 23, 24, pl. 25, figs 1–6.

Referred material: 4 teeth (V.61.840., V.61.853., VER 2016.3410., VER 2016.3451.).

Remarks: The teeth have narrow crown with bifurcated root. The crown is weakly curved labiolingually, it is smooth, and bears no striations. The lingual face is strongly, while the labial is weakly convex. The cutting edges are smooth all along, they usually do not reach the root-crown boundary (Kocsis 2007). The enamel continues towards the root lobes in forming a well-developed enamel shoulder (Figs 53, 57, 60). This shoulder is wide and it weakly overhangs the root on the labial side (Figs 52, 56, 59). The two root lobes typically form a squared to C-like shape in labiolingual view. A well-developed nutritive groove can be seen on the lingual face of the root. No lateral cusplets are present. While the anteriors are typically straight, the laterals curve distally. The visual sinuous-like curvature of the mesial cutting edge of the distals (especially of the upper distals) is typical feature.

Weiler (1938, pl. 1, fig. 17; also Fig. 54 of this work) figured a tooth as *Isurus leptodon*. One Kiscell Clay shark tooth of the HNHM collection is labelled as *Isurus lepdonon* (VER 2016.3451., Figs 51–53; most probably misspelled while cataloguing), and three others (V.61.840., V.61.853., VER 2016.3410.) have been found with similar morphology. The visual enamel-shoulder, the overhanging crown-enamel on the lingual side, and the shape of the root are all can be seen on the specimens, therefore, they are identified as possible remains of *Alopias exigua*. Weiler's illustration is not detailed enough and drawn in a strange angle (Fig. 54), still it shows some resemblance to VER 2016.3451. Because this specimen was found among other Kiscell Clay specimens of Weiler, and also catalogued as *I. leptodon* (misspelled, as *Isurus lepdonon*), therefore it might be the illustrated tooth of Weiler (see Figs 51–54).

The genus is known from the Eocene, the species itself has been reported from the Early Oligocene to the Middle Miocene (Cappetta 1987). Nowadays, three nominal species of thresher sharks live, these are *A. pelagicus*, *A. superciliosus,* and *A. vulpinus* (Pollerspöck & Straube 2016). These sharks live in pelagic waters, and *A. superciliosus* prefers deep waters (Cappetta 2012).



Figs 51–60. *Alopias* cf. *exigua* (Probst, 1879). – **51–53.** Anterior tooth (VER 2016.3451.). – **51.** Lingual view. – **52.** Profile view. – **53.** Labial view. – **54.** Anterior tooth figured by Weiler (1938), which shows some similarities to the specimen of VER 2016.3451. – **55–57.** Anterior tooth (V.61.840.). – **55.** Lingual view. – **56.** Profile view. – **57.** Labial view. – **58–60.** Anterior tooth (V.61.853.). – **58.** Lingual view. – **59.** Profile view. – **60.** Labial view. Scale bars: 5 mm

Order Carcharhiniformes Compagno, 1973
Family Carcharhinidae Jordan et Evermann, 1896
Genus *Carcharhinus* Blainville, 1816

Carcharhinus sp.
(Figs 61–68)

Referred material: 5 teeth (V.61.836., VER 2016.3443., VER 2016.3444., VER 2016.3454., VER 2016.3459.).

Remarks: The main crown is low, triangular, and pointed with smooth cutting edges both mesially and distally. Both faces of the main crown are smooth, and weakly convex. The cutting edges continue in a serrated enamel-shoulder both mesially and distally. The root runs mesiodistally, with a well-developed nutritive groove positioned in the middle, and without bearing any lateral cusplets.

Weiler (1932) described a new carcharhinid species of *Hypoprion reisi* (now *Carcharhinus reisi*) from the lower Marine Molasse in Southern Germany. Later Weiler (1933) reported this species from the Buda Hills as well. The Hungarian museum specimen (VER 2016.3454.) is very similar to Weiler's figure (1933, text-fig. 17; also Fig. 66 of this work) but it seems that the drawn tooth is mirrored horizontally (similarly to the *N. primigenius* specimen V.61.672C.; see above). Nevertheless this is the only *H. reisi* tooth in the HNHM collection, and this tooth was found among other figured specimens of Weiler, therefore, we suggest that the only Kiscell Clay shark tooth of the HNHM collection, labelled as *Hypoprion reisi* is Weiler's figured one. It must be mentioned that Reinecke *et al*. (2014) placed *Hypoprion reisi* in the synonym list of *C. gibbesi* when studying the Chattian shark fauna of the Subalpine Molasse Basin in Bavaria, Germany. Based on this study Weiler's species is considered as invalid.

Weiler (1933) reported another carcharhinid species from the Kiscell Clay, *Cestracion elongatus,* today known as *Carcharhinus elongatus*. The only HNHM shark tooth labelled as *Cestracion elongatus* (VER 2016.3459.; Figs 61–62) is very similar to Weiler's (1933, text-fig. 16; also Fig. 63 of this work) figure, and it was found among other Kiscell Clay shark teeth, figured by Weiler. For these reasons we re-catalogued it as Weiler's figured *Cestracion elongatus* tooth.

The Kiscell Clay *Carcharhinus* teeth could belong to two species, *C. elongatus*, or *C. gibbesi*. At this stage classifying the Kiscell Clay requiem shark teeth to any of these species would be problematic due to the low number of the remains, and since different requiem shark species have similar, but still heterodont dentition. In accordance with White (1956), Cicimurri & Knight (2009) described the dignath heterodonty of the species *C. gibbesi* in having strongly serrated enamel shoulder on upper files, while smooth shoulders on lowers.

Cicimurri & Knight (2009) concluded that using this feature, the species could be distinguished from *C. elongatus*, which has weakly serrated or smooth shoulders on upper teeth and weakly serrated on lowers.

However, without enough well-preserved specimens suitable to make tooth sets, we suggest that these reported Kiscell Clay requiem shark teeth could belong to the same species, due to the strong heterodonty of requiem sharks. Since the studied material does not include undeniably informative specimens of various tooth positions, we identify these teeth tentatively as *Carcharhinus* sp., until better preserved specimens are discovered.

Genus *Physogaleus* Cappetta, 1980

Physogaleus latus (Storms, 1894)
(Figs 69–73)

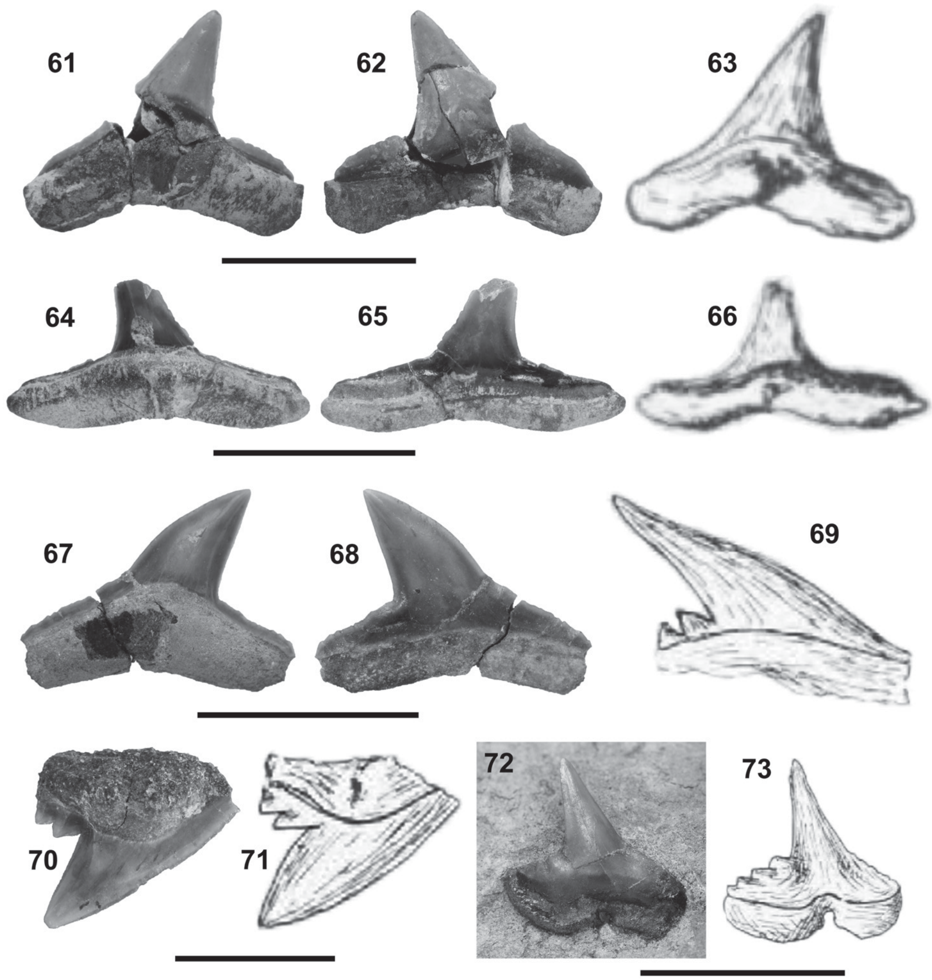
1894 *Protogaleus latus* n. sp. – Storms, p. 78, pl. 6, figs 17a-c.
1938 *Eugaleus latus* Ler. – Weiler, p. 8, pl. 1, figs 10, 11.
1938 ?*Physodon contortus* G. var. *hassiae* Jkl. – Weiler, p. 8, pl. 1, figs 19, 20.
1996 *Physogaleus latus* (Storms, 1894) – Müller, pp. 39–40, pl. 1, figs 3a-c, 7a-b.
1999 *Physogaleus latus* (Storms, 1894) – Müller, pp. 52–53, pl. 6, figs 1–4.
2001 *Physogaleus latus* (Storms, 1894) – Reinecke *et al.*, pp. 30–32, pls 46–49.
2010 *Physogaleus latus* (Storms, 1874) – Hovestadt *et al.*, p. 60, figs 15–28.
2014 *Physogaleus latus* (Storms, 1894) – Reinecke *et al.*, pp. 34–35, pls 31–34.

Referred material: 3 teeth (V.61.761., VER 2016.3435., VER 2016.3448.)

Remarks: The dentition of *Physogaleus* has dignathic and gradient monognathic heterodonty (Reinecke *et al.* 2014). The anteriors are nearly as high as wide, while the lateral-distal teeth are wider than high. The mesial cutting edge is often serrated basally, and the serration vanishes from the half of the mesial cutting edge to the tip. The distal enamel shoulder has stronger serrations. The upper anterolaterals have a convex mesial cutting edge, while that of the lower anterolateral teeth is straight or weakly concave. The root is wide and low, it runs mesiodistally and bears a visual transversal groove. The species has been also reported by Baut & Génault (1999), Hovestadt & Hovestadt-Euler (2010), Hovestadt *et al.* (2010), and Reinecke *et al.* (2001, 2014).

Weiler also mentioned and figured another species, *Physodon contortus* G. var. *hassiae* Jkl. (1938, pl. 1, figs 19–20; also Fig. 69 of this work), which unfortunately was not found in the HNHM collection. Comparing this illustration with other faunas (e.g., Reinecke *et al.* 2014) it is highly possible that this specimen belongs to *P. latus* and represents an upper anterolateral tooth.

Another upper anterolateral tooth figured by Weiler (1938, pl. 1, fig. 10; also Fig. 71 of this work) has features typical for upper anterolaterals of the



Figs 61–68. *Carcharhinus* sp. – **61–62.** Anterolateral-lateral tooth (VER 2016.3459.). – **61.** Lingual view. – **62.** Labial view. – **63.** Presumed same specimen, as figured by Weiler (1933). – **64–65.** Lateral tooth (VER 2016.3454.). – **64.** Lingual view. – **65.** Labial view. – **66.** Presumed same specimen, as figured by Weiler (1933). – **67–68.** Lateral tooth (V.61.836.). – **67.** Lingual view. – **68.** Labial view. – **Figs 69–73.** *Physogaleus latus* (Storms, 1894). – **69.** ?Upper anterolateral tooth figured by Weiler (1938), as *Physodon contortus* var. *hassiae*. – **70.** Upper anterolateral tooth (VER 2016.3448.), lingual view. – **71.** Upper anterolateral tooth figured by Weiler (1938), presumed to be specimen VER 2016.3448. – **72.** Lower anterolateral tooth (V.61.761.), labial view. – **73.** Specimen V.61.761. as figured by Weiler (1938). Scale bars: 61–62, 64–65, 67–68, 72–73: 10 mm; 70–71: 5 mm

species. We suggest that specimen VER 2016.3448. (Fig. 70) is Weiler's figured one, since it was found among other specimens of Weiler, and the preserved portions and size are the same. The major portion of the root and the serrated basal part of the mesial cutting edge are missing, but the first two serrations of the distal shoulder are preserved. The crown is wide, and shows a convex mesial cutting edge.

The lower anterolateral (V.61.761.; Figs 72–73) is sitting on a small piece of clay-matrix in labial aspect. A handwritten label ("*Eugaleus latus Ler. Taf. I Fig. 11*") was found under the specimen, which shows that this is one of Weiler's figured ones (see Weiler 1933, pl. 1, fig. 11; also Fig. 73 of this work). Except some cracks, this tooth is in nearly perfect condition.

DISCUSSION

The re-discovered and revised Kiscell Clay selachian material of the HNHM includes typical Rupelian faunal elements, however, the fauna shows an ecologically mixed composition. Odontaspids were undeniably the dominant sharks, their dominance (in accordance with the high number of fish-eating lamnids) is supported by the rich teleost fauna (see in Weiler 1933, 1938), as possible prey-animals. The presence of the large macropredatory species, *Otodus* (*Carcharocles*) *angustidens* can be linked to the presence of marine mammals, however, no direct evidences of predational relations (e.g., tooth marks on sea cow rib-fragments) have been found yet. The large number and variety of hexanchids refer to an active connection to the deep water ecosystems, since hexanchids are generally frequent in deep waters (Cappetta 1987, 2012). Thresher sharks (Alopiidae) are typically pelagic (Cappetta 1987, 2012), however, their presence seems to be evident due to the large number of smaller, potential prey-fish. Carcharhinids inhabit the most variable ecosystems from coastal, nearshore to clearly oceanic waters, even freshwater environments (Compagno 1984), therefore their presence is not informative of palaeoecological conditions.

It is worth mentioning that the *Heptranchias howelli* specimen figured by Weiler (1938, pl. 1, fig. 15 as "*Inc. sed.*"; also Fig. 21 of this work) and described here is the oldest figured report of the species, even older than the formal description by Reed (1946). Moreover, our work is the first report of this species (and also of this genus) from Hungary. According to all indications, the Kiscell report of *Isurus leptodon* is invalid (even with suggested relations to *Isurus gracilis*; see Weiler 1938). On the other hand, based on the database of Pollerspöck & Straube (2016) the species *I. leptodon* has been referred as a synonym of

Cosmopolitodus hastalis, but the only HNHM specimen of *I. leptodon* (together with other related items) clearly belong to thresher sharks, and not to *C. hastalis*.

Altogether three specimens of Weiler, associated with old, handwritten labels are re-discovered (*Notorynchus primigenius* with V.61.672C., *Heptranchias howelli* with VER 2016.3453., and *Physogaleus latus* with VER 2016.3448.), one has been undeniably re-identified after a photograph figure (*Otodus* (*Carcharocles*) *angustidens* with VER 2016.3403.), and based on the original, but unfortunately poor illustrations of Weiler, five additional teeth are re-discovered (*Notorynchus primigenius* with VER 2016.3455., *Carcharhinus* sp. with VER 2016.3459. and VER 2016.3454., *Physogaleus latus* with VER 2016.3448., and maybe *Alopias* cf. *exigua* with VER 2016.3451.) (Table 1). Some taxa published by Weiler are not represented in the HNHM vertebrate collection (e.g., *Isurus* cf. *benedeni* (valid name: *Parotodus benedenii*), and *Isurus desori*). This could be caused by the moving of the original material (the original specimens may have been lost or fallen apart), or by changes of the nomenclature. However, all these taxa have been reported from other Oligocene localities of Europe (see e.g., Baut 1993; Baut & Génault 1999; Reinecke *et al*. 2001, 2005).

Solt (1988) described an associated sand tiger shark remain as a new species, *Odontaspis* (*Synodontaspis*) *divergens* from the Tard Formation (also Kiscellian in age, adjacent to the Kiscell Formation) of the Csillaghegy locality in Budapest. This material can be found in the collection of the Geological and Geophysical Institute of Hungary (GGIH). In having relatively long lateral cusplets (nearly straight in labiolingual view), and a main cusp without striae on the lingual face, both the GGIH material published by Solt, and some of the aforementioned indeterminate Kiscell odontaspid specimens of the HNHM show affinity with the fossil sand tiger shark species *Carcharias gustrowensis*, however, closer examinations are needed.

In this work we revised Weiler's earlier works (1933, 1938) on the Kiscell Clay cartilaginous fish remains based on the HNHM collection. The results clarified the validity and the presence of some species in the early Oligocene, and draw attention to the necessity of the re-investigation of some fossil materials available both in the HNHM and the GGIH. Among the Rupelian shark material of the GGIH, other specimens of Weiler may be expected. Hopefully more, and better preserved shark tooth specimens of other, here not reported shark species are also placed in the GGIH vertebrate collection. The published bony fish material of Weiler (1933, 1938) may be also worth revising. This material could be the subject of future, more detailed projects on the Rupelian fishes of the Central Paratethyan Oligocene.

Table 1. Review of the nomenclatural changes of Weiler's Kiscell Clay shark taxa, with the summary of the re-discovered specimens. The figured specimens and collection numbers in bold-italic were re-discovered in the HNHM collection.

	Weiler, 1933	Weiler, 1938	This study and valid names	Figures
Notidanus (?*Notorhynchus*) *primigenius* Ag.	***Fig. 11 – drawing (V.61.672C.)***	***Fig. 16 – drawing (VER 2016.3455.)***	*Notorynchus primigenius*	Figs 10–13
			Hexanchus agassizi	Figs 14–17
Inc. sed. Zahn	–	***Fig. 15 – drawing (VER 2016.3453.)***	*Heptranchias howelli*	Figs 18–23
Odontaspis cuspidata (Ag.)	+	+	*Araloselachus cuspidatus*	Figs 24–27
Odontaspis acutissima (Ag.)	+	+	*Carcharias* sp. 1 & 2	Figs 28–33
Lamna cattica Philippi	Fig. 13 – drawing	+	*Carcharoides catticus*	Figs 34–36
Lamna rupeliensis Le Hon	Fig. 12 – drawing	+	*Isurolamna gracilis*	Figs 37–44
Isurus desori (Ag.)	Fig. 14 – drawing	–	not found at HNHM	
Isurus cf. *benedeni* Le Hon	Fig. 15 – drawing	–	not found at HNHM	
Isurus leptodon Ag. (= *Isurus gracilis* Le Hon)	–	Fig. 17 – drawing (maybe VER 2016.3451.)	*Alopias* cf. *exigua*	Figs 51–60
Carcharodon angustidens Ag.	***Tabl. III. Fig 3 – photo (VER 2016.3403.)***	+	*Otodus* (*Carcharocles*) *angustidens*	Figs 45–50
Carcharodon angustidens var. *turgidus* Ag.	Tabl. III. Fig 2 – photo	–	*Otodus* (*Carcharocles*) *angustidens*	Figs 45–50
Cestracion elongatus (Ler.)	Fig. 16 – drawing	+	*Carcharhinus* sp.	Figs 61–68
Hypoprion reisi Weiler	***Fig. 17 – drawing (VER 2016.3459., VER 2016.3454.)***	–	*Carcharhinus* sp.	Figs 61–68
Eugaleus latus Ler.	–	***Figs 10–11 – drawing (VER 2016.3448.)***	*Physogaleus latus*	Figs 69–73
?*Physodon contortus G*. var. *hassiae* Jkl.	–	Figs 19–20 – drawing	*Physogaleus latus* – not found at HNHM	

CONCLUSIONS

Original Rupelian (Kiscellian) shark tooth specimens of Wilhelm Weiler have been re-discovered in the vertebrate palaeontological collection of the HNHM. The material has probably been lost in the second half of the last century as a consequence of the 1956 conflagration of the museum. The teeth represent a typical Rupelian shark fauna with at least 11 different taxa, with clear qualitative odontaspid dominance. Deep water forms (hexanchids) and pelagic-neritic taxa (*Alopias*, *Otodus*) are also represented, just like eurytopic taxa (carcharhinids). Weiler's specimens have been identified by means of handwritten labels placed under some specimens, and by following the preserved features visible to the naked eye. These tooth remains represent a scientifically important part of the paleoichthyology of the Carpathian Basin.

*

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Appendix: Reptile and mammal remains from the Oligocene brickyard localities of the Budapest area (presumed from the Kiscell Formation), now placed in the collection of the Hungarian Natural History Museum.

Inventory number	Taxon/ determination of specimen	Number of specimens	Locality	Age
Reptilia				
V.61.1151.	Reptile imprint	1	Budapest, Újlak brickyard	Rupelian
V.61.1152.	Reptile imprint	1	Budapest, Újlak brickyard	Rupelian
V.61.1129.	Turtle imprint	1	Budapest	Rupelian
V.61.1148.	*Trionyx* sp.	1	Budapest	Rupelian
V.61.1146.	*Trionyx* sp.	2	Budapest	?
V.61.1156.	*Trionyx* sp.	1	Budapest, Óbuda	?
Mammalia				
V.60.649.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.654.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.655.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.644.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.653.	cf. *Manatherium delheidi*	3	Budapest, Újlak brickyard	Middle Oligocene
V.60.660.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.642.	cf. *Manatherium delheidi*	numerous	Budapest, Újlak brickyard	Middle Oligocene
V.60.643.	cf. *Manatherium delheidi*	numerous	Budapest, Újlak brickyard	Middle Oligocene
V.60.645.	cf. *Manatherium delheidi*	3	Budapest, Újlak brickyard	Middle Oligocene
V.60.646.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.647.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.648.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.651.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.656.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene

Appendix (continued)

Inventory number	Taxon/ determination of specimen	Number of specimens	Locality	Age
V.60.664.	cf. *Manatherium delheidi*	3	Budapest, Újlak brickyard	Middle Oligocene
V.60.666.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.668.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.673.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.674.	cf. *Manatherium delheidi*	numerous	Budapest, Újlak brickyard	Middle Oligocene
V.60.675.	cf. *Manatherium delheidi*	numerous	Budapest, Újlak brickyard	Middle Oligocene
V.60.676.	cf. *Manatherium delheidi*	2	Budapest, Újlak brickyard	Middle Oligocene
V.60.659.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.652.	cf. *Manatherium delheidi*	numerous	Budapest, Újlak brickyard	Middle Oligocene
V.60.658.	cf. *Manatherium delheidi*	6	Budapest, Újlak brickyard	Middle Oligocene
V.60.661.	cf. *Manatherium delheidi*	numerous	Budapest, Újlak brickyard	Middle Oligocene
V.60.662.	cf. *Manatherium delheidi*	numerous	Budapest, Újlak brickyard	Middle Oligocene
V.60.663.	cf. *Manatherium delheidi*	numerous	Budapest, Újlak brickyard	Middle Oligocene
V.60.667.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.669.	cf. *Manatherium delheidi*	1	Budapest, Újlak brickyard	Middle Oligocene
V.60.670.	cf. *Manatherium delheidi*	4	Budapest, Újlak brickyard	Middle Oligocene
V.60.695.	Sirenida indet.	26	Budapest, Farkasrét cemetery	Rupelian
V.60.1722.	*Ronsotherium velanum*	1	Budapest, Kiscell Clay	Oligocene
V.60.308.	*Eggysodon* sp.	2	Budapest, Nagybátony-Újlak brickyard	?