

A diverse Miocene fish assemblage (Chondrichthyes and Osteichthyes) from the Pécs-Danitzpuszta sand pit (Mecsek Mts, Hungary)

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Egy változatos miocén halfauna a Mecsekből, a pécs-danitzpusztai homokbányából

Összefoglalás

A Középső-Paratethys tengeri üledékeiben igen gyakoriak a porcos- és csontoshal-maradványok, nemcsak szörványleletek, hanem komplex, változatos halfaunák formájában is jelen vannak. Munkánk a pécs-danitzpusztai homokbánya felső miocén (pannóniai) üledékeiből gyűjtött és eddig csak hiányosan tanulmányozott halfaunát mutatja be. Összesen 22 227 halfossziliát vizsgáltunk meg, melyek 17 porcoshal- és 16 csontoshal-taxonot képviselnek. A leletanyag döntő többsége sárga, limonitos, durvaszemcsés, kavicsos homokból került elő izolált leletek formájában. A homokból előkerült halfauna porcoshalai között az Odontaspidae (55,5%) és a Myliobatidae (14,4%) családok dominálnak, míg a csontos halak között a Sparidae (77,1%) család. Recens analógiák alapján a homokból előkerült 17 porcos-, valamint 12 csontoshal-taxon idősebb, középső miocén (badeni) üledékekből halmozódott át. A homok alatti mészmárgából artikulált és asszociált Latidae csontoshal-maradványok kerültek elő. Ezek egykorúak a beágyazó üledékekkel és édesvízi-brakk környezetet jeleznek. Izolált csontoshal-maradványok szintén előkerültek a mészmárgából, úgy mint hallókövek, fogak, pikkelyek, csigolyák és állkapocselemek, melyeket a Gadidae, Gobiidae, Sparidae és Latidae családokhoz soroltunk. Ezek akár áthalmozottak is lehetnek, így paleoökológiai jelentőségük csekély.

Az ismert taxonok recens leszármazottainak ismert ökológiai igényei alapján a homokban talált összes porcoshal és a csontoshalak többsége badeni korú üledékekből halmozódott át. Egyes csontoshal-taxonok maradványai koprolitokból is előkerültek, ami azt bizonyítja, hogy ezek a halak prédaállatként a helyi táplálékhálózat részei voltak. A tengeri- és édesvízi-csontokon felfedezett, nagyragadozó cápáknak tulajdonított harapásnyomok a Középső-Paratethys badeni leletanyagaiból eddig nem voltak ismertek. A homokból előkerült Acipenseridae- és Latidae-maradványok brakk- és/vagy édesvízi üledékekhez köthetőek, emiatt szinte bármely környékbeli miocén formációból áthalmozódhattak.

Tárgyszavak: Paratethys, Pannon-tó, harapásnyomok, anadromous

Abstract

Chondrichthyans and osteichthyans are widely reported from marine sediments of the Central Paratethys, not only by sporadic occurrences, but also by complex, diverse fish assemblages. Here we present a rich fish fauna from the upper Miocene (Pannonian, Tortonian) lacustrine sediments exposed in the Pécs-Danitzpuszta sand pit, in the SW Pannonian Basin. Altogether 22 227 specimens were investigated, and they could be classified into 17 chondrichthyan and 16 osteichthyan taxa. Among the chondrichthyans Odontaspidae (55.5%) and Myliobatidae (14.4%) are the most abundant, while the bony fishes are dominated by the Sparidae (77.1%). The limonitic, yellow, coarse-grained, gravelly sands yielded an extremely large amount of isolated fish fossils. A considerable part of the vertebrate material of the sands is likely reworked from older, middle Miocene (Badenian and Sarmatian, i.e. Langhian and Serravallian) sediments. The late Miocene calcareous marls underlying the sands also yielded a variety of fish remains. From these remains, associated and articulated latid bones are coeval with the sediment and suggest freshwater and brackish conditions in the area, in accord with other biotic data. Other, isolated fossils, namely teeth, otoliths, cycloid scales and jaw elements of Gadidae, Gobiidae, Sparidae and Latidae could have been reworked and thus have a very limited palaeoecological significance.

Based on habitat preferences of extant relatives, all chondrichthyans and most osteichthyan taxa found in the sands must be of Badenian origin. The abundant remains allow for some inferences on the environmental conditions during the Badenian. They suggest tropical-subtropical climate and a shallow, coastal environment with connection to more open water habitats. Remains of some osteichthyan taxa were found in coprolites, showing that these taxa were part of the food

chain as prey items. Sirenian ribs and odontocete limb bones bearing tooth marks refer to trophic relations between marine mammals and large macropredatory sharks. The Pécs-Danitzpuszta record of shark-attributed bite marks on marine mammal bones is only the second one in the Badenian of the Central Paratethys after recent report from the Styrian Basin. Acipenserids and latids of the sands, linked to brackish and/or freshwater environments, could have originated from any Miocene stratigraphic units.

Keywords: Paratethys, Lake Pannon, bite marks, anadromous

Introduction

The Central Paratethys was a widely extended part of the epicontinental Paratethys sea, covering large areas of the Pannonian Basin System (RÖGL 1998, KOVÁČ et al. 2007, TER BORGH et al. 2013). The Paratethys was isolated from the Tethys during the late Eocene – early Oligocene (RÖGL & STEININGER 1983, STEININGER et al. 1988, RÖGL 1998; DERCOURT et al. 2000), and was last connected to the Mediterranean Tethys in the Badenian (KOVÁČOVÁ et al. 2009). Repeated closure and reopening of oceanic gateways resulted in a distinct palaeobiogeographical province in the Central Paratethys (BÁLDI 1983, RÖGL 1998). Badenian fish faunas (often with main focus on chondrichthyans and teleost otoliths) are widely reported from Central Paratethyan marine sediments of the Pannonian Basin (SCHUBERT 1902, 1905, 1906, 1912; FERENCZI 1915; NOSZKY 1925; BRZOBOHATÝ & SCHULTZ 1978; KORDOS & SOLT 1984; SOLT 1987; SEBE et al. 2015; SZABÓ 2019; SZABÓ & KOCSIS 2016a and references therein, 2020). These faunas are dominated by marine taxa with a characteristic presence (or sometimes dominance) of chondrichthyans. Meanwhile, the early and middle Badenian otolith associations indicate typical tropical to subtropical marine environments with normal salinity and connections both to the Atlantic and Mediterranean realms. The increasing number of gadids in the otolith assemblages relates to the gradual cooling (due to the expansion of the Antarctic ice sheet) during the late Badenian (BRZOBOHATÝ et al. 2007, KOVÁČOVÁ et al. 2009). A significant transition in the fish fauna reflects immense environmental changes in the late Badenian and early Sarmatian. The abundance of previously dominant mesopelagic fishes declined or they completely disappeared and were replaced by a prosperous shallow water endemic fauna. This altered fish assemblage was more adapted to brackish marine conditions (SCHWARZHANS et al. 2015). The revised and detailed evaluation of these faunas started in the last few years. Documented Sarmatian fish faunas of the Pannonian Basin exclude chondrichthyans, and are mainly based on otoliths (e.g. REICHENBACHER et al. 2018). These faunas indicate nearshore marine to brackish environments.

Despite the available, overwhelmingly rich fossil material, the Miocene fish assemblages of the Mecsek Mountains (southern Hungary) still remain poorly known, although these localities have been recognized for a long time (SEBE et al. 2015), and attract countless palaeontologists and amateur collectors. Besides middle Miocene

sites, several localities exist in the Mecsek Mts where fish remains occur in upper Miocene (Pannonian in Central Paratethys nomenclature) lacustrine deposits. Due to reworking, these deposits include both middle and late Miocene fossils. Some of these localities have been visited and sampled so many times and for such a long time that they can be considered as classic localities for palaeontologists. The famous Pécs-Danitzpuszta sand pit is one of these localities with its extremely rich fossil vertebrate record including various aquatic, semiaquatic and terrestrial taxa (see KRETZOI 1985; KOCSIS 2002; BENE 2003; KORETSKY 2003; JUHÁSZ 2006, 2009; KAZÁR 2003, 2005, 2006, 2010; KAZÁR et al. 2007; KONRÁD et al. 2010; FÖZY & SZENTE 2012, SEBE et al. 2015; SZENTESI et al. 2019; CSERPÁK 2018).

The aim of the present study is to improve our knowledge about the chondrichthyan and osteichthyan diversity of the Central Paratethys basin during the middle and early late Miocene by detailing the diverse ichthyofauna unearthed from the Pécs-Danitzpuszta sand pit and its palaeoenvironmental and palaeobiogeographical aspects.

Geological setting

The Pécs-Danitzpuszta sand pit is located at the eastern edge of the city of Pécs (centre of the western wall: 46°6'1.86"N, 18°16'56.56"E), in SW Hungary, along the southern margin of the Mecsek Mts (*Figure 1*). The sand pit exposes two main lithological units, light grey, white or yellowish grey calcareous marls and silts (Endrőd Marl Formation), and the overlying yellowish brown, coarse limonitic sands (Kálla Member of the Békés Fm). Both were deposited in the brackish Lake Pannon during the late Miocene (KLEB 1973). Due to compression along the marginal fault of the Mecsek Mts, the whole exposed succession is strongly tilted, with beds reaching an overturned position in the northern part of the outcrop (KONRÁD & SEBE 2010, SEBE 2021).

In the top of the calcareous marl unit, a 4-5 metre thick calcareous silt contained some fish remains. These beds, numbered as layers 219–225 in the sedimentary log of the quarry (SEBE et al. 2021), are exposed in the northern wall of the sand pit in subvertical position. They represent a transition from the carbonate-dominated open lacustrine deposits towards the overlying clastics. They contain a diverse thermophilous macroflora (HABLY & SEBE 2016), and a rich brackish sublittoral mollusc assemblage indicating an age of 10.5–10.2 Ma (BOTKA et al. 2021).

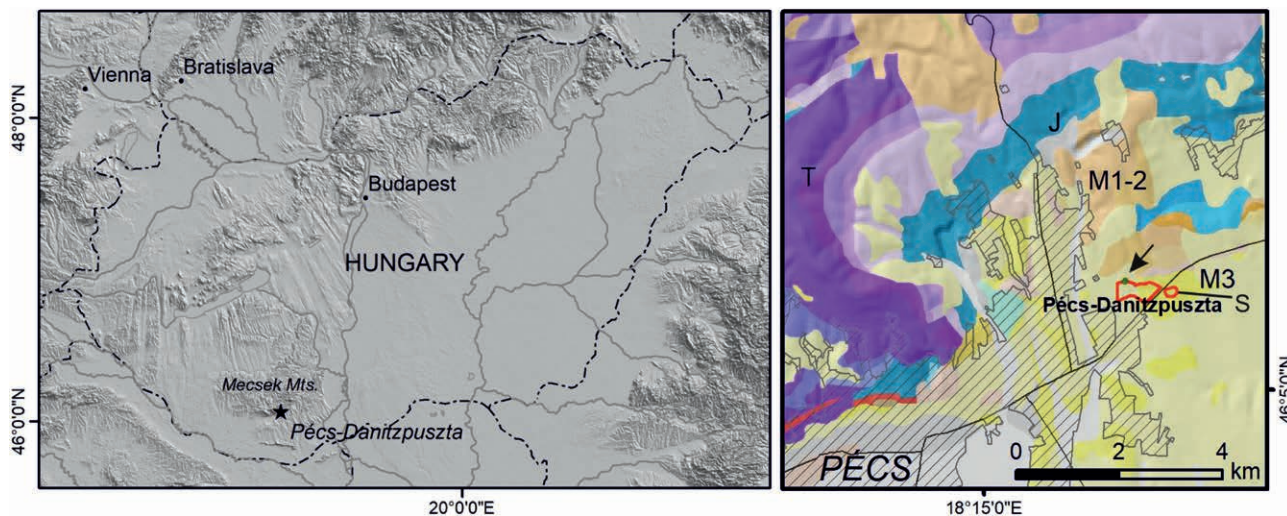


Figure 1. Geological setting of the Pécs-Dánitzpuszta sand pits. Base geological map modified from CHIKÁN & BUDAI (2005). The arrow indicates the location of the exploration trench. Abbreviations: T: Triassic; J: Jurassic; M1–2: lower–middle Miocene; M3: upper Miocene (Pannonian) rocks; “S” indicates the southern sand pit across the main road

1. ábra. A pécs-dánitzpusztai homokbányák elhelyezkedése. Földtani térkép CHIKÁN & BUDAI (2005) után. A nyíl a kutatóárok helyét mutatja. Rövidítések: T: triász; J: jura; M1–2: alsó – középső miocén; M3: felső miocén (pannoniai) kőzetek. Az „S” betű a déli bányagödör helyét jelöli

Beside some scattered bones and teeth, the silt layers provided associated partial skeletons and articulated skeletal parts (*Figure 2B*).

The overwhelming majority of the fish remains were collected from the overlying limonitic sands that are the main product of the sand pit. The sands are exposed in a stratigraphic thickness of at least 140 m, mostly in the western wall of the quarry (SEBE et al. 2021). They are coarse to very coarse grained, often gravelly, with poorly sorted sandy gravel interbeds (*Figure 2A*). The bedding dip gradually decreases southward and upsection, from vertical in the northern part of the sand pit to less than 10°. The sand particles had been sourced from the older

Miocene and basement rocks of the mountains. The age of the sand is 10.2–9.6 Ma based on the recovered mollusk assemblage (BOTKA et al. 2021).

A few fish fossils were unearthed in another sand pit across the main road (*Figure 1B*). This smaller exposure is east of the large sand pit, on the southern side of the road („southern pit”), and exposes sands and sandstones with a smaller average grain size, where fine sands and even thin (<20 cm) clay intercalations occur as well. The bedding dip is less than in the northern sand pit. Although it lies in strike direction of the large sand pit, no individual layers could be correlated between the two sites, thus their stratigraphic relationship is uncertain. The southern quarry probably

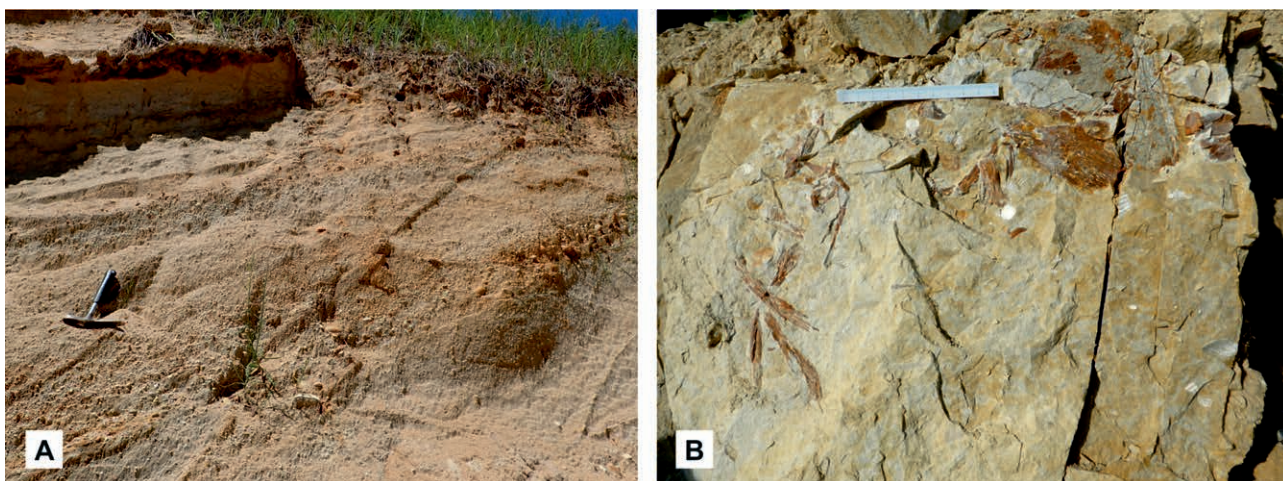


Figure 2. Typical appearance of lithologies providing fish remains. A) Poorly sorted gravelly sand providing inarticulated, mainly reworked vertebrate bones and teeth; B) calcareous silt with mollusk shells (white) and in situ fish remains (brown) (ruler for scale is 10 cm long)

2. ábra. A halmaradványokat tartalmazó két kőzettani egység jellemző megjelenése. A) Rosszul osztályozott kavicsos homok, melyből izolált, főleg áthalmazott csontok és fogak kerültek elő. B) Mészmarga molluszkahéjakkal (fehér) és in situ halmaradványokkal (barna) (a vonalzó hossza 10 cm)

represents sediments somewhat more distal to the shore. Because of the uncertainty, fossils of this southern sand pit are treated separately from the rest of the material.

Material and methods

The vertebrate remains were collected by hand-quarrying, screen-washing, and dry sieving with 2–4 mm sieves. Vertebrate fossils found in the sands are exclusively inarticulated remains, often fragmentary, eroded to a varying degree, and reddish-brown to yellowish in colour due to limonite. Needles and brushes were used for cleaning, and broken specimens were repaired with cyanoacrylate adhesive (superglue).

Both museum and private collection specimens were investigated. Institutional abbreviations: MGSZ – Mining and Geological Survey of Hungary, NHMUS – Hungarian Natural History Museum, PTE – University of Pécs, NHCEU – Natural History Collection of the Eötvös University, JACLMC – József Attila City Library and Museum Collection (Komló).

Systematics and tooth terminology of sharks and rays follow that of CAPPETTA (2012), in accordance with BOR et al. (2012), REINECKE et al. (2011, 2014) and HOVESTADT & HOVESTADT-EULER (2013). Osteichthyan systematics are based on NELSON et al. (2016). Osteological terminology of bony fishes mainly follows CARNEVALE & GODFREY (2018) and PURDY et al. (2001), although latid anatomical terminology follows exclusively that of OTERO (2004). Terminology of otoliths follows that of NOLF (1985).

In case of well-marked heterodonty in some of the described chondrichthyans (e.g., *Odontaspidae* indet., *Notorynchus primigenius*, *Hemipristis serra*) the teeth were figured according to their in-life jaw position. Artificial tooth sets were also illustrated (see *H. serra* and *Galeocерdo aduncus*). For the Systematic Palaeontology (describing *Plate I–XVII*) see Appendix. Digital Annex 1 includes data on the studied museum and private collection materials.

Discussion

Palaeoenvironmental inferences and age of fish remains of the calcareous marls

Fish remains from the older white marls are much less abundant and less diverse than from the younger sands, therefore they allow fewer inferences on the palaeoenvironment. However, only the marls contain fish fossils which are certainly in situ and thus able to provide information on the coeval environmental conditions.

The associable latid cranial and postcranial remains and the articulated actinopterygian hyoid region could not have been redeposited, therefore they must be coeval with the host sediments. Biostratigraphic dating of this interval of the marls gave an age range between 10.5 and 10.2 Ma

(BOTKA et al. 2021), thus these fishes inhabited the brackish Lake Pannon at this time. Latid fishes have already been reported from the middle Miocene sediments of the Central Paratethys (see SCHWARZHANS et al. 2017). Latids generally are of freshwater preference, but some taxa survive in brackish and estuarine waters as well (SORBINI 1975; FROESE & PAULY 2019 and references therein), thus they suggest the presence of freshwater environments (rivers) in the area, connected to the brackish lake. This agrees with the palaeobotanical results, which reconstructed extensive swamps for the lakeshore lowlands and indicated freshwater habitats farther away from the shores as well (HABLY & SEBE 2016). The freshwater interpretation also agrees with the presence of giant salamander remains of possibly Pannonian origin, which require riverine habitats for their reproduction (SZENTESI et al. 2019).

Unfortunately, a precise habitat preference is not possible to infer based on the single gadid otolith found in the marls, as it is not possible to identify the fish more precisely than family rank. Extant sparid fishes are generally marine, but brackish and freshwater taxa are also known among them (NELSON et al. 2016). As the sparid material of the marls is incomplete and not identifiable precisely, it has no palaeoenvironmental significance either. The case is similar to the unidentified actinopterygians: unless they are identified at a lower taxonomic level, their palaeoenvironmental implication is highly limited. Thus, the possible age of the isolated, possibly reworked fossils from the listed taxonomic groups remains unknown as well.

Palaeoenvironmental inferences and age of fish remains of the sands

Preliminary reports on the fish fauna of the sand pit appeared in only few documents. Regarding the chondrichthyan taxa, KOCSIS (2002) reported a fauna list of *Carcharias cuspidata*, *C. acutissima*, *Isurus desori*, *I. hastalis*, *Lamna* sp., *Carcharocles megalodon*, *Hemipristis serra*, *Galeocерdo aduncus*, *Carcharhinus priscus*, *Sphyrna* sp., *Myliobatis* sp., *Aetobatis arcuatus*, *Dasyatis* sp. Most of these taxa were recorded in our study, though with updated views on the taxonomy and taxonomical ranks of the material. Later JUHÁSZ (2006) described a somewhat different fauna composition based on poorly preserved material. However, we consider the JUHÁSZ (2006) report invalid, due to clear misidentifications and/or the lack of informative illustrations in case of the following taxa: *Striatolamia* aff. *macrota*, *Synodontaspis hopei*, *Carcharias* cf. *cuspidata*, *Lamna* sp., *Scyliorhinus distans* and *Negaprion eurybathrodon*. Concerning the bony fish fauna, BENE (2003) reported the genera *Archosargus*, *Chryso-phrys*, *Dentex*, *Diplodus*, *Pagellus*, *Pagrus*, *Sparnodus* and *Sparus* from the same fossiliferous formation of the pit. This material is poorly preserved as well, and except for *Diplodus*, *Pagrus* and *Sparus* (note, that the latter two genera are represented by clearly identifiable bone elements in the sands; see above), we consider these taxa invalid.

Moreover the isolated molariform and conical teeth of these genera are not clearly distinguishable.

The numerous fish taxa of the sands make up a dominantly marine fish fauna, with a wide range of ecological requirements, including forms indicating tropical through subtropical to temperate, and littoral through neritic to pelagic habitats (Digital Annex 2). However, it is known that a considerable percent of the vertebrate remains in the sands is reworked from older, middle Miocene (Badenian and Sarmatian) sediments (KAZÁR et al. 2007, SEBE et al. 2015), and this is obviously the case for the fish fossils as well. Regarding their environmental preferences and the general range of taxa, the fishes found in the sands can be divided into 2 groups.

1. The chondrichthyan faunal elements and most of the osteichthyan forms are typical marine animals and require euhaline conditions. As marine conditions with normal salinity are restricted to the Badenian in the area (PALCU et al. 2015; SEBE et al. 2015, 2019), these fossils must be of Badenian age. Strontium isotope analyses ($^{87}\text{Sr}/^{86}\text{Sr}$) of a shark tooth from Danitzpuszta also corroborate the Badenian origin, however other teeth from here and the nearby Himeshaza reworked site yielded much younger ages, which most possibly reflect diagenetic overprint (KOCIS et al. 2009, KOCIS 2016). The chondrichthyan fauna is very similar to other Badenian assemblages in the Central Parathethys (SZABÓ & KOCIS 2016a) in terms of composition and abundance. The teeth of the Odontaspidae (55.5%) and Myliobatidae (14.4%) families are the most abundant. These forms, accompanied by the also common dasyatids, could indicate widespread shallow, coastal environments in the Badenian, under a subtropical-tropical climate. The presence of relatively large and pelagic forms (e.g., *Isurus*, *Cosmopolitodus*, *Alopias*) together with littoral/neritic habitat taxa (e.g., *Squatina*, *Dasyatis*) could reflect connections toward more open seas. Deeper water can be related to the asymmetric, quickly deepening, rift-related basins, which are known in the area in the Badenian (BÁLDI et al. 2002). The marine osteichthyan fauna is dominated by Sparidae (*Diplodus* sp., *Pagrus cinctus* and *Sparus umbonatus*, not counting the indeterminate sparid remains; altogether 77.1% of the fish material found in the limonitic sands). Sparid fishes are widespread in shallow, temperate-tropical waters. Common inhabitants of pelagic waters (e.g., Sphyraenidae, Scombridae) reflect connection with open water habitats. Labridae and Scaridae are typically reef-associated forms, their presence could refer to a nearby coral reef, which is also testified by re-worked coral fragments found in the sand (DULAI et al. 2021).

2. Two noteworthy taxa, acipenserids (sturgeons) and latids (latid perches) might have different palaeoenvironmental significance. Modern acipenserids typically inhabit high-energy environments, including freshwater lacustrine and riverine, estuarine, and less typically nearshore marine habitats (BEMIS & KYNARD 1997). Extant sturgeons are considered to be anadromous (NELSON et al. 2016), meaning that adults migrate upstream to spawn but they spend most

of their lives feeding in river deltas and estuaries. The other interesting taxon is *Lates* sp., represented by the largest variety of skeletal elements. Extant African *Lates* species have a freshwater preference, but *Lates niloticus* (Nile perch), the latid geographically and anatomically closest to the studied fossil material, has been reported to survive in brackish and estuarine waters as well (e.g., Lake Maryut in Egypt) (SORBINI 1975; FROESE & PAULY 2019 and references therein). The lifestyle of these two fishes, especially that of acipenserids, which require fluvial environments for spawning, is related to freshwater, which indicates the presence of a nearby, probably fluvial environment. Given the wide salinity tolerance of latids, and that riverine environments are reconstructed both for the late Miocene and – based on various vertebrate remains – for the middle Miocene (e.g., KAZÁR et al. 2007), the original age of these fish fossils remains unknown.

Trophic interactions of the marine vertebrate fauna found in the sands

Extremely large amounts of vertebrate coprolites were found in the limonitic sands. They are irregular to elongate, usually with rounded edges, most of them are straight, but a few specimens have weakly curved axes. It is unknown if the producers of these coprolites were aquatic, semiaquatic or terrestrial animals. However, some coprolite specimens contain vertebrate inclusions, such as jaws of various osteichthyan taxa like sparids and scarids (Figure 3). These occur in several coprolite morphotypes, suggesting that fish served as prey for various animals.

As several large predators occur among the fish taxa described here, it is also worth examining what could have provided their food source. Based on the feeding habits of their extant relatives and fossil evidence of feeding habits, the presence of five selachians from the sands (*Notorynchus primigenius*, *Cosmopolitodus hastalis*, *Isurus oxyrinchus*, *Otodus (Megaselachus) megalodon* and *Galeocerdo aduncus*) can be related to the presence of marine mammals. The modern hexanchid *Notorynchus cepedianus* consumes a wide variety of prey, including elasmobranchs, teleosts and even marine mammals (EBERT 2002 and references therein). Modern *Isurus* species (ecologically close ancestors of *C. hastalis*) prey on a wide variety of cartilaginous and bony fishes, cephalopods and various further invertebrates, but very large individuals could occasionally catch small pelagic cetaceans (dolphins) (COMPAGNO 2002). The trophic spectrum of *Otodus (Megaselachus) megalodon* could have covered a wide range of prey items, e.g. invertebrates, chondrichthyans, osteichthyans, marine reptiles, seabirds, sirenians, various cetaceans and seals (COLLARETA et al. 2017). The modern tiger shark *Galeocerdo cuvier* also preys on a large variety of invertebrates, chondrichthyans, osteichthyans, sea turtles and marine mammals (COMPAGNO 1984).

Over the years of collecting, a large range of marine mammals has been collected in the Pécs-Danitzpuszta sand

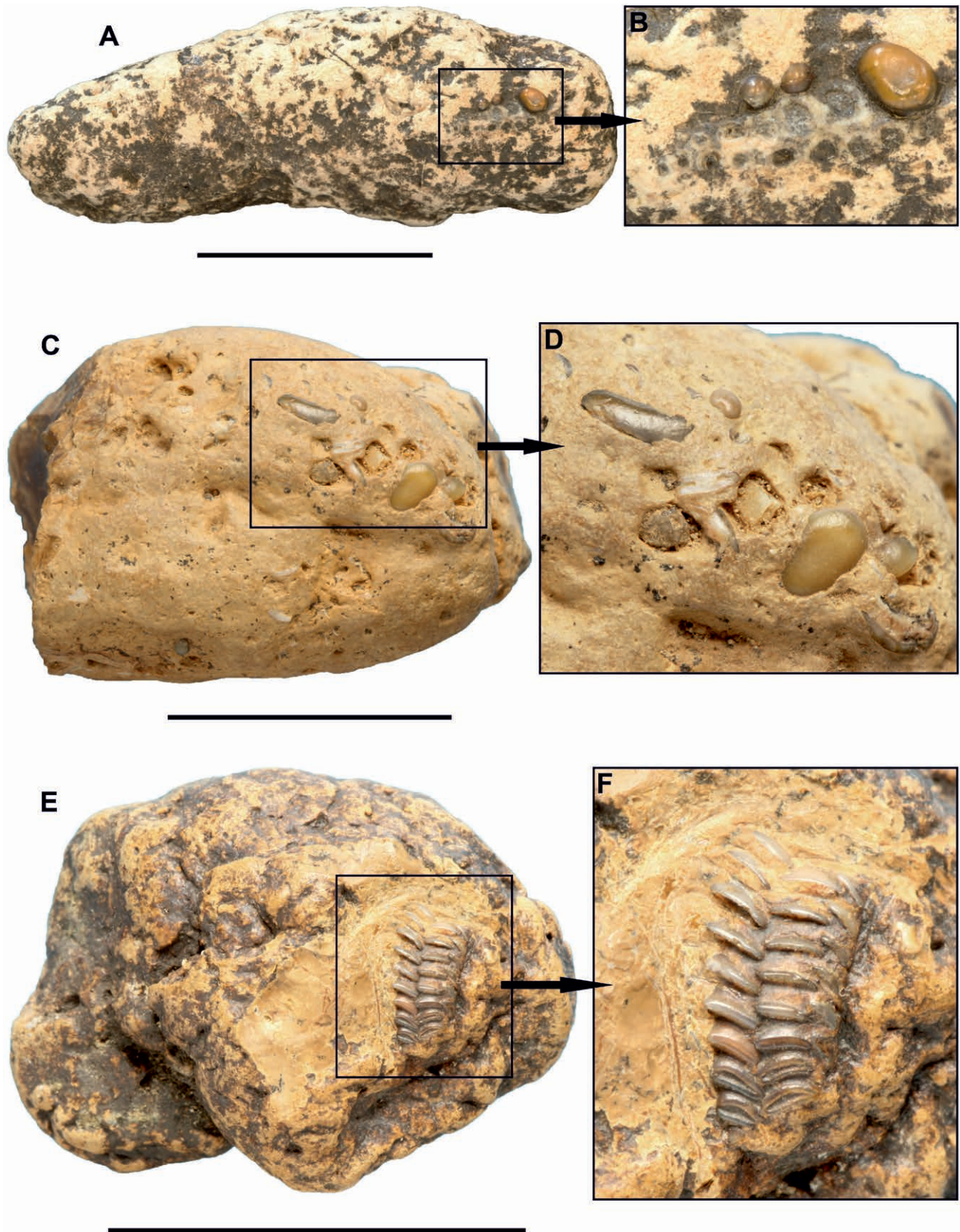


Figure 3. Coprolites from the limonitic sands

A) Sparidae indet. jaw element in coprolite (KANIZSAI L. coll.). B) Close-up of image A. C) Sparidae indet. teeth in coprolite (CSERPAK F. coll., inv. nr: Dp9164). D) Close-up of image C. E) *Calotomus* sp. upper pharyngeal tooth plate in coprolite (CSERPAK F. coll., inv. nr.: Dp3923). F) Close-up of image E. Scale bars: 20 mm

3. ábra. Koproliatok a limonitos homokból

A) Sparidae indet. állkapocselem koproliatban (KANIZSAI L. gyűjteménye), B) Közeli kép az A ábráról. C) Sparidae indet. fogak koproliatban (CSERPAK F. gyűjteménye, leltári szám: Dp9164), D) Közeli kép a C ábráról. E) *Calotomus* sp. garatfoglemez koproliatban (CSERPAK F. gyűjteménye, leltári száma: Dp3923), F) Közeli kép az E ábráról. Méretarányok: 20 mm

pit. These marine mammals could have served as preys for large sharks. KAZÁR (2003, 2005, 2006, 2010) reported the following odontocetes from Pécs-Danitzpuszta: *Acrodelphis letochae*, *Pachyacanthus suessi*, Delphinoidea indet., Kentriodontidae indet., *Kentriodon fuchsii*, ?*Kentriodon* sp., *Sophianacetus commenticius*. CSERPÁK (2018) reported humeri of mysticetes cf. *Cetotherium priscum*, „*Cetotherium*” aff. *maiopicum* and cf. *Cetotheriidae* indet. in detail. One phocid species, *Praepusa magyaricus* has been described from the locality (KORETSKY 2003, GASPARIK M. in SEBE et al. 2015). Sirenians are also known from the pit, they are most commonly represented by rib fragments, occasionally by isolated teeth, but incomplete limb bones and vertebrae are also known in private collections. The hundreds of unidentified sirenian remains most probably belong to the genus *Metaxytherium* (GASPARIK in SEBE et al. 2015). Odontocetes from the limonitic sands are attributed to the Sarmatian, however, family Kentriodontidae occurs in the Badenian of the Central Paratethys as well (KAZÁR 2006), therefore it can not be excluded that some Pécs-Danitzpuszta kentriodontids may originate from the Badenian. It cannot be excluded that two of the cetotheriid baleen whale taxa („*Cetotherium*” aff. *maiopicum* and cf. *Cetotheriidae* indet.) are of Badenian origin (CSERPÁK 2018). The seal remains probably belong to the Sarmatian Stage (KORETSKY 2003), while the sirenians most likely represent the Badenian (KAZÁR 2003, after KORDOS L. pers. comm.). Thus, the middle Miocene marine mammals known from the area (some kentriodontid odontocetes, mysticetes and sirenians) could have served as preys for the large sharks during the Badenian.

Cetotheriidae (a cetacean family known from the sands, CSERPÁK 2018) is an extinct baleen whale family, characterized by generally small body sizes (2.5–7 metres of length) (BOUETEL & DE MUIZON 2006, BOESSENECKER 2013, GOL'DIN 2018), which made these mysticetes suitable for predation by adult *Otodus* (*Megaselachus*) *megalodon*. As an example, COLLARETA et al. (2017) identified *Piscobalaena nana*, member of family Cetotheriidae as prey or scavenging item for *Otodus* (*Megaselachus*) *megalodon* in the upper Miocene deposits of southern Peru. During the early to middle Badenian, sirenians were also abundant in the Central Paratethys (KRETZOI 1951; KORDOS 1985, 1992). These generally slow-moving, herbivorous mammals could have also been common prey items for the Pécs-Danitzpuszta *Otodus* (*Megaselachus*) *megalodon* individuals, since their body provided a large amount of fat required to fulfil the caloric demands of these large-sized sharks (after LAMBERT et al. 2010).

In order to confirm direct trophic connections between predator and prey, we checked the available marine mammal material for tooth marks. Up to now, a radius of a kentriodontid, a radius of an indeterminate odontocete, and a sirenian rib (all are housed in private collections) have been found to bear tooth marks possibly corresponding to sharks (Figure 4). It is worth mentioning that the low number of shark vs. marine mammal predational evidence may be linked to the re-deposition of these remains, which might have damaged the

bones or eroded away fine surface structures (e.g. tooth marks). Based on the suggested age of the local marine mammals (see above), it is highly plausible that kentriodontids, cetotheriids, and sirenians provided a stable food source (either as living preys or carcasses) for macropredatory sharks in the Mecsek area during the Badenian. Up to the present paper, only a single occurrence of similar remains has been published from the middle Miocene of the Central Paratethys by FEICHTINGER et al. (2021), who reported a shark-bitten partial skeleton of an immature sirenian (*Metaxytherium* cf. *medium*) from the Styrian Basin (Austria).

A major marine extinction event occurred in the Central Paratethys at the Badenian–Sarmatian boundary (RÖGL et al. 1978, PALCU et al. 2015). At this time, the conditions changed from open marine to brackish, caused by sea level drop of the Mediterranean and the resulting closure of the Slovenian Strait. During the early Sarmatian the Central Paratethys has regained connection to the Mediterranean through the Eastern Paratethys (RÖGL 1998) and new pinnipedian and cetacean taxa – particularly small odontocetes – arrived, replacing the Badenian taxa (= Sarmatian Marine Mammal Event; GRIGORESCU & KAZÁR 2006). However, no post-Badenian occurrence of these large sized macropredatory sharks have been reported from the Central Paratethys, indicating that these taxa did not return to the region after the Badenian.

Fish fossils and the reworking of older sediments

Fish remains not only provide palaeoecological data, they can also be used to constrain the sedimentary units that got reworked to build up the sand body of Danitzpuszta. Based on the mineralogical composition, KLEB (1973) proposed that the provenance of the sands had been older Miocene rocks. Fish fossils provided data to identify the source units.

Chondrichthyans restricted to normal marine conditions must come from Badenian sediments. Potential lithostratigraphic units supplying these remains are the lower–middle Badenian nearshore Budafa Formation and its offshore counterpart, the Tekeres Schlieren Member of the Baden Fm, the middle and upper Badenian littoral Lajta Limestone Fm, and the upper Badenian Szilágy Claymarl Member of the Baden Fm. Other taxa that tolerated brackish or freshwater may have originated from any Badenian or younger Miocene rock units of the area.

No vertebrate fossils have been reported from the middle Miocene rocks in the direct surroundings of the sand pit. However, the lithostratigraphic units in question are known to contain fish remains elsewhere in the Mecsek region. Among Badenian marine deposits, shark and sparid teeth occur in the Budafa Fm. and in the Lajta Limestone Fm in the western Mecsek Mts. (KORDOS & SOLT 1984, SZABÓ in SEBE et al. 2015), and various otoliths dominated by gobiids and gadids in the Szilágy Claymarl (BOSNAKOFF 2013). In the Badenian brackish-water Hidas Lignite Fm. a gobiid-dominated otolith assemblage was reported from the eastern

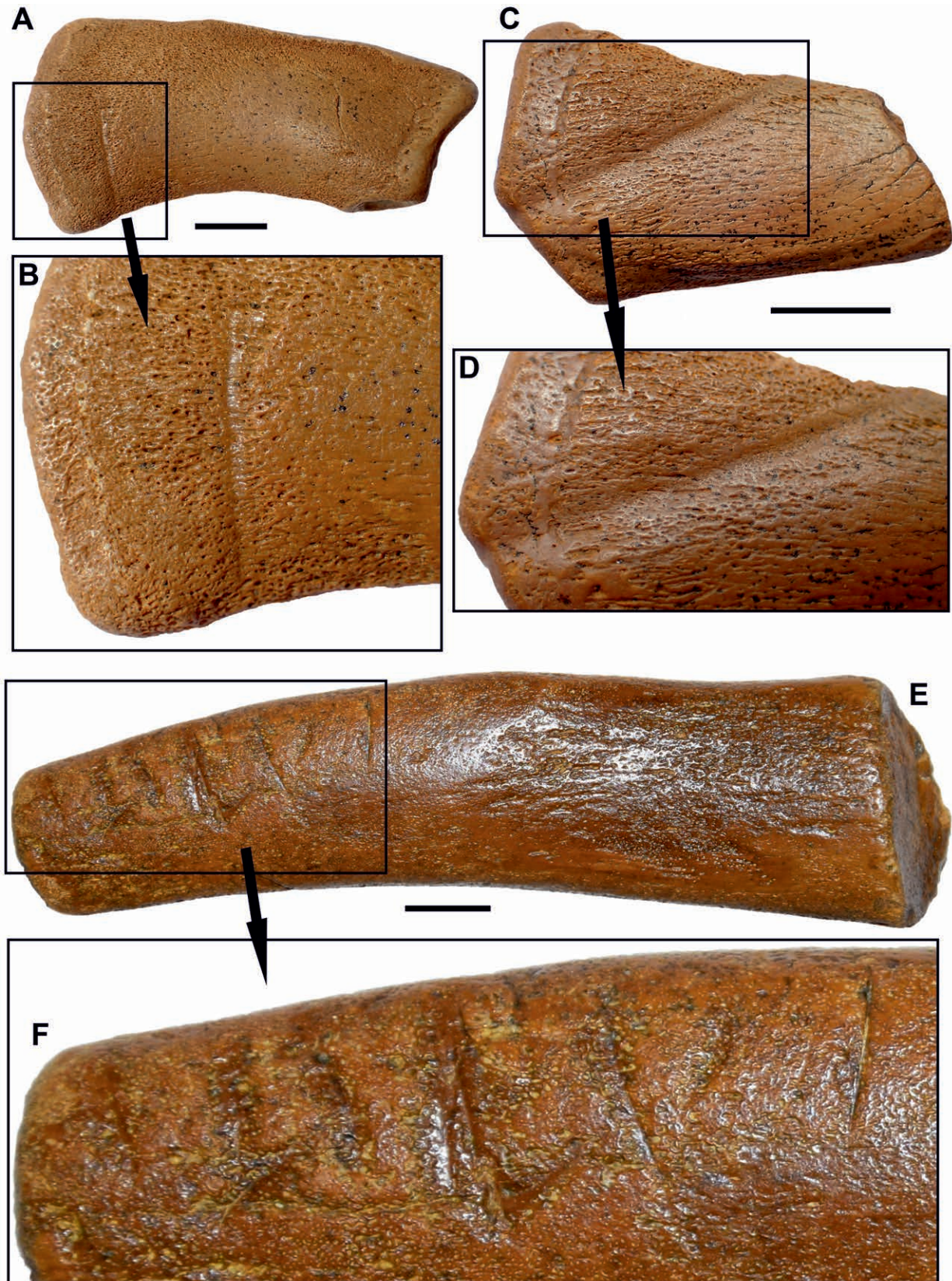


Figure 4. Bite marks on marine mammal bones from the limonitic sands

A) Kentriodontidae indet. radius (KANIZSAI L. coll.), B) Close-up of the tooth mark in figure A. C) Odontoceti indet. distal fragment of ulna (KANIZSAI L. coll.), D) Close-up of the tooth mark in figure C. E) Sirenian rib (KANIZSAI L. coll.), F) Close-up of the tooth marks in figure E. Scale bars: 10 mm

4. ábra. Harapásnyomok a limonitos homokból származó tengeri emlős-csontokon.

A) Kentriodontidae indet. radius (KANIZSAI L. gyűjteménye), B) Közelkép az A ábrán látható harapásnyomról. C) Odontoceti indet. ulna disztális töredéke (KANIZSAI L. gyűjteménye), D) Közelkép a C ábrán látható harapásnyomról. E) Tengeritehén-borda (KANIZSAI L. gyűjteménye), F) Közelkép az E ábrán látható harapásnyomokról. Méretarányok: 10 mm

Mecsek Mts (BARANYAI 2010). Sarmatian laminites in the western part of the mountains contain yet unidentified fish skeletons (KORDOS & SOLT 1984, KONRÁD & DULAI 2013).

Direct evidence for reworking possibilities was provided by an exploration trench excavated in the NW part of the sand pit in order to reveal the underlying rock units (Figure 1; SEBE et al. 221). The trench exposed upper Badenian and Sarmatian deposits below the upper Miocene ones. In the Upper Badenian sandy limestone layer D-71 of the trench, a shark tooth with close relation to the Odontaspidae genus *Araloselachus* was found (Figure 5A, B). Similar teeth occur in the Lake Pannon sands of the pit (see above). The

difference between the teeth in the Pannonian and Badenian sediments is that the fresh, in situ tooth in the middle Miocene limestone is reddish white and all the fine surface characteristics are preserved on its main cusp, while teeth in the Pannonian sands are heavily worn and rusty brown due to limonite impregnation. Sarmatian deposits also revealed unidentifiable fish bone fragments.

Although no vertebrate fossils have been reported from the lower and middle Miocene rocks of the area, in the Danitzpuszta sand pit dozens of vertebrate, dominantly fish remains – mostly teeth and bone fragments – can be collected during a single visit without major effort, by hand-

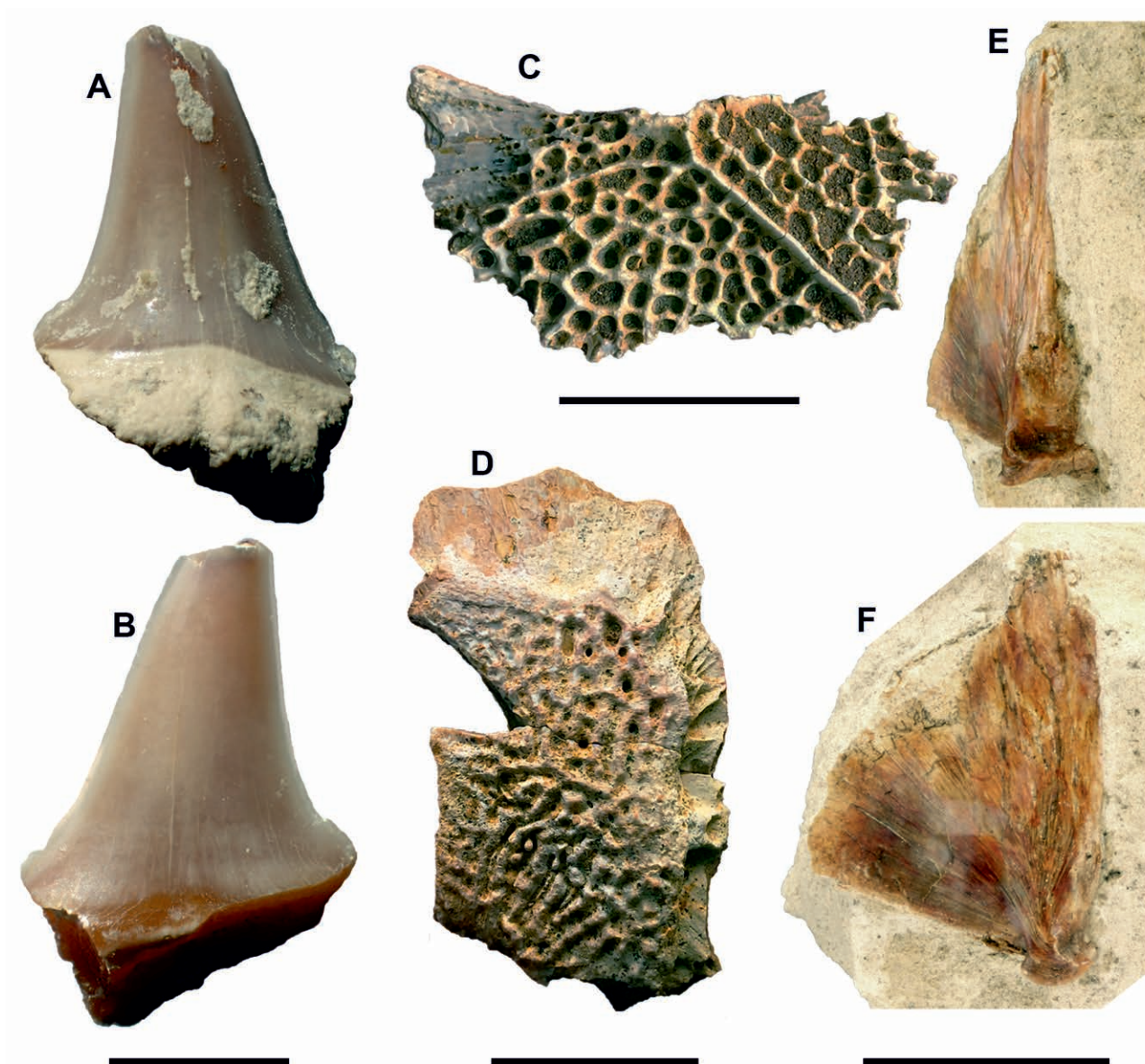


Figure 5. Fish remains from the exploration trench (A, B) and the southern pit (C-F)

A, B) *Odontaspidae* indet. tooth (PTE_5161). C, D) *Acipenseridae* indet. dermal scutes (KRIZSAN S. coll.). E, F) *Lates* sp. quadrate (PTE_5162). A) in lingual view; B) in labial view; C, D) in dorsal view; E) in posterior view; F) in lateral view. Scale bars: A, B) 5 mm; C, D) 20 mm; E, F) 30 mm

5. ábra. Halmaradványok a kutatóárokából (A, B) és a déli bányából (C-F).

A, B) *Odontaspidae* indet. fog (PTE_5161). C, D) *Acipenseridae* indet. bőrcsontok (KRIZSAN S. gyűjteménye). E, F) *Lates* sp. *quadratum* (PTE_5162). A) linguális nézet; B) labiális nézet; C, D) dorzális nézet; E) poszterior nézet; F) laterális nézet. Méretarányok: A, B) 5 mm; C, D) 20 mm; E, F) 30 mm

picking. The strong enrichment of vertebrate fossils in the Lake Pannon sands indicates intense denudation of the terrestrial hinterland at the time of sedimentation. When older Miocene rocks were exposed at, or transported to the lake, wave action could continue their comminution, while winnowing effect could have removed the fine siliclastic fractions, leaving the coarse material (i.e., coarse sand, gravel, and gravel-sized fossils) to accumulate. The high carbonate content of some limestone- or marl-dominated units could become dissolved. The syn-sedimentary uplift of the mountains (SEBE 2021) could further increase the denudation rate.

The smaller southern sand pit contains much fewer fossils than the northern one, and fish remains found here exclusively belong to fresh- or brackish-water, euhaline forms, namely acipenserids and latids (Figure 5C–F). This may be linked to the fact that it represents partly an upward and partly a lakeward continuation of the succession exposed in the northern sand pit. Vertebrate remains redeposited from older sediments are enriched in the basal layers of the sand unit – in the northern pit – and did not seem to travel far from the shore either. These, together with the taxonomic composition of the fossils suggest that acipenserid remains found here may not be redeposited, but these fishes may have lived in Lake Pannon.

Conclusions

The upper Miocene brackish lacustrine sediments of the Pécs-Danitzpuszta sand pit yielded a wealth of fish remains. 22 227 specimens were investigated, and they were classified into a total of 33 taxa. Following analogies of modern relatives, all the 17 chondrichthyans (namely *Notorynchus primigenius*, *Squatina* sp., *Odontaspidae* indet., *Cosmopolitodus hastalis*, *Isurus oxyrinchus*, *Otodus* (*Megaselachus*) *megalodon*, *Alopias exigua*, *Antodus retroflexus*, *Hemipristis serra*, *Carcharhinus priscus*, *Galeocercus aduncus*, *Sphyrna laevis*, *Dasyatidae* indet., *Aetobatus arcuatus*, *Aetomylaeus* sp., *Myliobatis* sp., *Rhinoptera* cf. *schantzi*) and 12 identified osteichthyan taxa (namely *Carangidae* indet., *Sphyrna* sp., cf. *Thunnus* sp., *Scombridae* indet., *Labrodon* sp., *Trigonodon jugleri*, *Calotomus* sp., *Sciaenidae* indet., *Diplodus* sp., *Pagrus cinctus*, *Sparus umbonatus*, *Tetraodontiformes* indet.) found in the sands are regarded to belong to the Badenian Stage and must therefore have been redeposited into the upper Miocene sediments from Badenian rocks. Vast majority of the fossils came from the limonitic sands, among these specimens chondrichthyans are dominated by *Odontaspidae* (55.5%) and *Myliobatidae* (14.4%), while among the bony fishes the *Sparidae* (77.1%) are the most abundant. Acipenserids and latids do not fit into the typical marine conditions of the Badenian. Extant adult sturgeons inhabit freshwater and brackish habitats (river deltas and estuaries), and modern latids prefer brackish and freshwater environments. Brackish or freshwater could be present in the area throughout the Miocene, thus remains of

these taxa may have been re-deposited from any Miocene stratigraphic units. Bone elements bearing tooth marks and coprolites prove that sparids, scarids and some marine mammals – sirenians and some of the local kentriodontids – were part of the food chain as preys, hunted among others by macropredatory sharks. As the Pécs-Danitzpuszta sirenians are attributed to the Badenian, the proof of their trophic interaction further supports their suggested age. The Pécs-Danitzpuszta record of shark-attributed bite marks on bones of marine mammals is the second one in the Badenian of the Central Paratethys.

The calcareous marls underlying the sands yielded associated latid cranial and postcranial fossils and an articulated hyoid region of an indeterminate actinopterygian, which must be coeval with the host sediment, i.e., upper Miocene (Pannonian). The detailed evaluation of the latter remain could be part of a future study, as articulated Miocene fishes are very rare in the Mecsek Mts. Latids suggest freshwater and brackish conditions in the area, in accordance with other biotic data. The age of isolated fish remains (representing *Gadidae*, *Gobiidae*, *Sparidae* and further, yet indeterminate actinopterygian taxa) coming from the same layers is unsure, as they do not provide environmental implications.

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Plate I – I. tábla**Fish remains from the calcareous marls – Halmaradványok a mészmárgából**

A, B, Gadidae indet. otolith (PTE_5151), A, internal view, B, external view. C–E, Gobiidae indet. teeth (PTE_5152, PTE_5153), C and D, profile view, E, labial view. F, Gobiidae indet. otolith (PTE_5154) in internal view. G–P, *Lates* sp.; G, associated parasphenoid and ethmoid bones (PTE_5155); H–L, associable postabdominal vertebrae (PTE_5148); H, set of vertebrae in a piece of the embedding calcareous marl; I, J, prepared vertebra; K, L, prepared vertebra; M, N, second abdominal vertebra (PTE_5149); O, P, *Lates* sp. caudal vertebra (PTE_5150). A, F in internal view; B in external view; C, E in profile view; D in labial view; I, K, M, O in lateral view; J, L, N in articular view; P in anterior view. Scale bars: A, B, 5 mm; C, F, 0.5 mm; D, E, 0.25 mm; G–P, 10 mm

A, B, Gadidae indet. otolith (PTE_5151), A, belső nézet, B, külső nézet. C–E, Gobiidae indet. fogak (PTE_5152, PTE_5153), C és D, profilnézet, E, labiális nézet. F, Gobiidae indet. otolith (PTE_5154) belső nézetben. G–P, *Lates* sp.; G, asszociált parasphenoid és ethmoideumok (PTE_5155); H–L, asszociált posztabdominális csigolyák (PTE_5148); H, mészmárgában ülő csigolyák; I, J, kipreparált csigolya; K, L, kipreparált csigolya; M, N, második abdominális csigolya (PTE_5149); O, P, *Lates* sp. farki csigolya (PTE_5150). A, F, belső nézet; B, külső nézet; C, E, profilnézet; D, labiális nézet; I, K, M, O, laterális nézet; J, L, N, ízesülési felület felőli nézet; P, anterior nézet. Méretarányok: A, B, 5 mm; C, F, 0.5 mm; D, E, 0.25 mm; G–P, 10 mm

Plate II – II. tábla**Fish remains from the calcareous marls – Halmaradványok a mészmárgából**

A, Sparidae indet. premaxilla (PTE_5156) in medial view. B, Actinopterygii indet. tooth (PTE_5157). C, Actinopterygii indet. tooth (PTE_5158). D, Actinopterygii indet. cycloid scale (PTE_5159). E, Actinopterygii indet. articulated hyoid elements (PTE_5160). Scale bars: A, 10 mm; B, C, 1 mm; D, 5 mm; E, 50 mm

Halmaradványok a mészmárgából. A, Sparidae indet. premaxilla (PTE_5156) mediális nézetben. B, Actinopterygii indet. fog (PTE_5157). C, Actinopterygii indet. fog (PTE_5158). D, Actinopterygii indet. cycloid pikkely (PTE_5159). E, Actinopterygii indet. artikulált hyoid csontelemek (PTE_5160). Méretarányok: A, 10 mm; B, C, 1 mm; D, 5 mm; E, 50 mm

Plate III – III. tábla**Chondrichthyan remains from the limonitic sands – Porcoshal-maradványok a limonitos homokból**

A–R, *Notorynchus primigenius*; A–C, upper anterior tooth (PTE_5005); D–F, upper anterior tooth (SÖVÉR L. coll.); G, H, upper anterolateral tooth (KANIZSAI L. coll.); I, J, upper anterolateral tooth (PTE_5002); K, L, upper anterolateral/ lateral tooth (PTE_5000); M, N, lower anterolateral/ lateral tooth (PTE_5003); O, P, lower anterolateral/ lateral tooth (BÉCSI L. coll.); Q, R, lower lateral tooth (PTE_5004). S–X, *Squatina* sp.; S–U, anterior tooth (NHMUS VER 2020.178.); V–X, lateral tooth (KANIZSAI L. coll.). A, D, G, I, K, M, O, Q, S, V in lingual view; B, E, T, W in profile view; C, F, H, J, L, N, P, R, U, X in labial view. Scale bars: A–R, 10 mm; S–X, 5 mm

A–R, *Notorynchus primigenius*; A–C, felső anterior fog (PTE_5005); D–F, felső anterior fog (SÖVÉR L. gyűjteménye); G, H, felső anterolaterális fog (KANIZSAI L. gyűjteménye); I, J, felső anterolaterális fog (PTE_5002); K, L, felső anterolaterális/ laterális fog (PTE_5000); M, N, alsó anterolaterális/ laterális fog (PTE_5003); O, P, alsó anterolaterális/ laterális fog (BÉCSI L. gyűjteménye); Q, R, alsó laterális fog (PTE_5004). S–X, *Squatina* sp.; S–U, anterior fog (NHMUS VER 2020.178.); V–X, laterális fog (KANIZSAI L. gyűjteménye). A, D, G, I, K, M, O, Q, S, V, linguális nézet; B, E, T, W, profilnézet; C, F, H, J, L, N, P, R, U, X, labiális nézet. Méretarányok: A–R, 10 mm; S–X, 5 mm

Plate IV – IV. tábla**Chondrichthyan remains from the limonitic sands – Porcoshal-maradványok a limonitos homokból**

A–H, Odontaspidae indet.; A, B, anterior tooth (PTE_5020); D–F, anterior tooth (PTE_5021); G, H, upper lateral tooth (PTE_5038). I–R, *Cosmopolitodus hastalis*; I, upper tooth (PTE_5056); J, lower tooth (PTE_5054); K, upper tooth (SÖVÉR L. coll.); L, upper tooth (SÖVÉR L. coll.); M, upper tooth (SÖVÉR L. coll.); N, upper tooth (KANIZSAI L. coll.); O, upper tooth (KANIZSAI L. coll.); P, upper tooth (KANIZSAI L. coll.); Q, upper tooth (KANIZSAI L. coll.); R, upper tooth (KANIZSAI L. coll.). S–V, *Isurus oxyrinchus*; S, T, upper tooth (KANIZSAI L. coll.); U, V, upper tooth (KANIZSAI L. coll.). A, D, G, I–R, S, U in lingual view; B, E in profile view; C, F, H, T, V in labial view. Scale bars: 10 mm

A–H, *Odontaspidae* indet.; A, B, anterior fog (PTE_5020); D–F, anterior fog (PTE_5021); G, H, felső laterális fog (PTE_5038). I–R, *Cosmopolitodus hastalis*; I, felső fog (PTE_5056); J, alsó fog (PTE_5054); K, felső fog (SÖVÉR L. gyűjteménye); L, felső fog (SÖVÉR L. gyűjteménye); M, felső fog (SÖVÉR L. gyűjteménye); N, felső fog (KANIZSAI L. gyűjteménye); O, felső fog (KANIZSAI L. gyűjteménye); P, felső fog (KANIZSAI L. gyűjteménye); Q, felső fog (KANIZSAI L. gyűjteménye); R, felső fog (KANIZSAI L. gyűjteménye). S–V, *Isurus oxyrinchus*; S,

T, felső fog (KANIZSAI L. gyűjteménye); U, V, felső fog (KANIZSAI L. gyűjteménye). A, D, G, I–R, S, U, linguális nézet; B, E, profilnézet; C, F, H, T, V, labiális nézet. Méretarányok: 10 mm

Plate V – V. tábla

Chondrichthyan remains from the limonitic sands. *Otodus (Megaselachus) megalodon* teeth – Porcoshal-maradványok a limonitos homokból: *Otodus (Megaselachus) megalodon* fogak

A, B, upper anterior tooth (KANIZSAI L. coll.); C, D, upper anterior tooth (PTE_5014); E–H, ?anterolateral tooth with pathological deformity (BÉCSI L. coll.); G, H, close-ups of the pathological section of the distal cutting edge); I, J, lower anterior tooth (KOCSESI L. coll.); K, L, distal tooth (BÉCSI L. coll.); M, N, posterior tooth (CSERPÁK F. coll., inv. nr.: Dp2095); O, P, juvenile anterior tooth (BÉCSI L. coll.). A, C, E, I, K, M, O in lingual view; B, D, F, J, L, N, P in labial view. Scale bars: A–F, I, J, 50 mm; K, L, 20 mm; M–P, 10 mm

A, B, felső anterior fog (KANIZSAI L. gyűjteménye); C, D, felső anterior fog (PTE_5014); E–H, patológiás ?anterolaterális fog (BÉCSI L. gyűjteménye); G, H, Közeli képek a disztális vágóél patológiás részéről); I, J, alsó anterior fog (KOCSESI L. gyűjteménye); K, L, disztális fog (BÉCSI L. gyűjteménye); M, N, poszterior fog (CSERPÁK F. gyűjteménye, leltári szám: Dp2095); O, P, fiatal egyed anterior foga (BÉCSI L. gyűjteménye). A, C, E, I, K, M, O, linguális nézet; B, D, F, J, L, N, P, labiális nézet. Méretarányok: A–F, I, J, 50 mm; K, L, 20 mm; M–P, 10 mm

Plate VI – VI. tábla

Chondrichthyan remains from the limonitic sands – Porcoshal-maradványok a limonitos homokból

A–D, *Alopias exigua*; A, B, lateral-anterolateral tooth (BÉCSI L. coll.); C, D, lateral-anterolateral tooth (A. ANDERSON coll.). E–P, *Anotodus retroflexus*; E, F, lateral tooth (KANIZSAI L. coll.); G, H, ?anterolateral tooth (CSERPÁK F. coll.); I, J, lateral tooth (KANIZSAI L. coll.); K, L, lateral tooth (KANIZSAI L. coll.); M, N, anterolateral tooth (KANIZSAI L. coll.); O, P, ?anterolateral tooth (KANIZSAI L. coll.). A, C, E, G, I, K, M, O in lingual view; B, D, F, H, J, L, N, P in labial view. Scale bars: A–D, 5 mm; E–P, 10 mm

A–D, *Alopias exigua*; A, B, laterális-anterolaterális (BÉCSI L. gyűjteménye); C, D, laterális-anterolaterális fog (A. ANDERSON gyűjteménye). E–P, *Anotodus retroflexus*; E, F, laterális fog (KANIZSAI L. gyűjteménye); G, H, ?anterolaterális fog (CSERPÁK F. gyűjteménye); I, J, laterális fog (KANIZSAI L. gyűjteménye); K, L, laterális fog (KANIZSAI L. gyűjteménye); M, N, anterolaterális fog (KANIZSAI L. gyűjteménye); O, P, ?anterolaterális fog (KANIZSAI L. gyűjteménye). A, C, E, G, I, K, M, O, linguális nézet; B, D, F, H, J, L, N, P, labiális nézet. Méretarányok: A–D, 5 mm; E–P, 10 mm

Plate VII – VII. tábla

Chondrichthyan remains from the limonitic sands – Porcoshal-maradványok a limonitos homokból

A–K, *Hemipristis serra* artificial tooth set; A, B, upper lateral tooth (SÖVÉR L. coll.); C, D, upper anterior tooth (PTE_5047); E, upper anterior tooth (PTE_5043); F–H, lower lateral tooth (PTE_5042); I–K, lower anterior tooth (PTE_5041). L–U, *Galeocerdo aduncus* artificial tooth set; L, M, distal tooth (PTE_5012); N, O, lateral tooth (PTE_5011); P, Q, lateral tooth (PTE_5009); R, S, anterolateral tooth (PTE_5008); T, U, anterior tooth (PTE_5006). V–A', *Carcharhinus priscus*; V, W, anterior tooth (PTE_5030); X, Y, lateral tooth (PTE_5032); Z, A', lateral tooth (PTE_5029). B'–E', *Sphyrna laevissima*; B', C', lateral tooth (PTE_5017); D', E', lateral tooth (BÉCSI L. coll.). A, C, E, F, I, L, N, P, R, T, V, X, Z, B', D' in lingual view; G, J in profile view; B, D, H, K, U, S, Q, O, M, W, Y, A', C', E' in labial view. Scale bars: A–M, 10 mm; V–E', 5 mm

A–K, *Hemipristis serra sematicus kompozit fogazati*; A, B, felső laterális fog (SÖVÉR L. gyűjteménye); C, D, felső anterior fog (PTE_5047); E, felső anterior fog (PTE_5043); F–H, alsó laterális fog (PTE_5042); I–K, alsó anterior fog (PTE_5041). L–U, *Galeocerdo aduncus sematicus kompozit fogazati*; L, M, disztális fog (PTE_5012); N, O, laterális fog (PTE_5011); P, Q, laterális fog (PTE_5009); R, S, anterolaterális fog (PTE_5008); T, U, anterior fog (PTE_5006). V–A', *Carcharhinus priscus*; V, W, anterior fog (PTE_5030); X, Y, laterális fog (PTE_5032); Z, A', laterális fog (PTE_5029). B'–E', *Sphyrna laevissima*; B', C', laterális fog (PTE_5017); D', E', laterális fog (BÉCSI L. coll.). A, C, E, F, I, L, N, P, R, T, V, X, Z, B', D', linguális nézet; G, J, profilnézet; B, D, H, K, U, S, Q, O, M, W, Y, A', C', E', labiális nézet. Méretarányok: A–M, 10 mm; V–E', 5 mm

Plate VIII – VIII. tábla

Chondrichthyan remains from the limonitic sands – Porcoshal-maradványok a limonitos homokból

A–C, Dasyatidae indet. female-type tooth (NHMUS VER 2020.209.). D–F, ?Dasyatidae indet. female-type tooth (NHMUS VER 2020.210.). G–Q, *Aetobatus arcuatus*; G, lower tooth plate (NHMUS VER 2020.146.) specimen embedded in a piece of limonitized sand in occlusal view, H, Close-up of image G; I, J, lower tooth plate (PTE_5065); K, L, lower tooth plate (PTE_5064); M–Q, upper tooth plate (NHCEU coll.). R–A', *Aetomylaeus* sp.; R–V, tooth plate (NHCEU coll.); W–A', tooth plate (PTE_5070). A, D, G, H, I, K, M, R, W, in

occlusal view; C, F, J, L, P, U, Z in basal view; B, E, Q, V, A' in profile view; N, S, X in lingual view; O, T, Y in labial view. A–C, 2 mm; D–F, 1 mm; G, I–Q, W–A', 10 mm; R–V, 20 mm

A–C, *Dasyatidae* indet. nőstény fog (NHMUS VER 2020.209.). D–F, ?*Dasyatidae* indet. nőstény fog (NHMUS VER 2020.210.). G–Q, *Aetobatus arcuatus*; G, alsó fog (NHMUS VER 2020.146.) egy darab limonitos homokba ágyazva, H, Közeli kép a G ábráról; I, J, alsó fog (PTE_5065); K, L, alsó fog (PTE_5064); M–Q, felső fog (NHCEU gyűjtemény). R–A', *Aetomylaeus* sp.; R–V, fog (NHCEU gyűjtemény); W–A', töredékes fog (PTE_5070). A, D, G, H, I, K, M, R, W, okkluzális nézet; C, F, J, L, P, U, Z, bazális nézet; B, E, Q, V, A', profilnézet; N, S, X, linguális nézet; O, T, Y, labiális nézet. Méretarányok: A–C, 2 mm; D–F, 1 mm; G, I–Q, W–A', 10 mm; R–V, 20 mm

Plate IX – IX. tábla

Chondrichthyan remains from the limonitic sands – Porcoshal-maradványok a limonitos homokból

A–T, *Myliobatis* sp.; A–D, partial lower tooth plate (PTE_5068); E–H, partial upper tooth plate (CSERPÁK F. coll.); I–L, partial lower tooth plate (NHCEU coll.); M–Q, incomplete medial tooth (KANIZSAI L. coll.); R–T, lateral tooth (PTE_5069). U–I', *Rhinoptera* cf. *schultzi*; U–Y, lateral tooth (NHCEU coll.); Z–D', lateral tooth (PTE_5071); E'–I', lateral tooth (NHCEU coll.). J'–M', K', *Myliobatiformes* indet.; J', K', partial caudal spine (PTE_5079); L', M', partial caudal spine (PTE_5078). A, E, I, M, R, U, Z, E' in occlusal view; B, F, J, N, S, X, C', H' in basal view; C, G, K, Q, T, Y, D', F', I' in lateral view; O, V, B', G' in labial view; D, H, L, P, W, A' in lingual view; J', L' in dorsal view; K', M' in ventral view. Scale bars: A–L, U–M', 10 mm; M–T, 5 mm

A–T, *Myliobatis* sp.; A–D, részleges alsó rágólemezt (PTE_5068); E–H, részleges felső rágólemezt (CSERPÁK F. gyűjteménye); I–L, részleges alsó rágólemezt (NHCEU gyűjtemény); M–Q, töredékes mediális fog (KANIZSAI L. gyűjtemény); R–T, laterális fog (PTE_5069). U–I', *Rhinoptera* cf. *schultzi*; U–Y, laterális fog (NHCEU gyűjtemény); Z–D', laterális fog (PTE_5071); E'–I', laterális fog (NHCEU coll.). J'–M', K', *Myliobatiformes* indet.; J', K', részleges faroktövis (PTE_5079); L', M', részleges faroktövis (PTE_5078). A, E, I, M, R, U, Z, E', okkluzális nézet; B, F, J, N, S, X, C', H', bazális nézet; C, G, K, Q, T, Y, D', F', I', laterális nézet; O, V, B', G', labiális nézet; D, H, L, P, W, A', linguális nézet; J', L', dorzális nézet; K', M', ventrális nézet. Méretarányok: A–L, U–M', 10 mm; M–T, 5 mm

Plate X – X. tábla

Chondrichthyan remains from the limonitic sands – Porcoshal-maradványok a limonitos homokból

A–H, *Chondrichthyes* indet. vertebrae; A, B, vertebra morphotype 1 (KANIZSAI L. coll.); C–E, vertebra morphotype 1 (CSERPÁK F. coll., inv. nr.: Dp6291); F–H, vertebra morphotype 2 (CSERPÁK F. coll., inv. nr.: Dp1826). I, J, *Chondrichthyes* indet. cartilage (CSERPÁK F. coll., inv. nr.: Dp7690). A, C in articular view; B, D in profile view; E, H in medial view; F, in dorsal or ventral view; G, in oblique view; I, in outer view; J, in inner view. Scale bars: 10 mm

A–H, *Chondrichthyes* indet. csigolyák; A, B, csigolya morfotípus 1 (KANIZSAI L. gyűjteménye); C–E, csigolya morfotípus 1 (CSERPÁK F. gyűjteménye, leltári szám: Dp6291); F–H, csigolya morfotípus 2 (CSERPÁK F. gyűjteménye, leltári szám: Dp1826). I, J, *Chondrichthyes* indet. porcmaradvány (CSERPÁK F. gyűjteménye, leltári szám: Dp7690). A, C, artikulációs felület felőli nézet; B, D, profilnézet; E, H, mediális nézet; F, dorzális vagy ventrális nézet; G, döntött nézet; I, külső nézet; J, belső nézet. Méretarány: 10 mm

Plate XI – XI. tábla

Osteichthyan remains from the limonitic sands – Csontosshal-maradványok a limonitos homokból

A–J, *Acipenseridae* indet.; A, B, skull element (KANIZSAI L. coll.); C, D: dermal scute (PTE_5163); E, F, dermal scute (NHMUS VER 2020.212.); G, H, pectoral spine (PTE_5135). I–N, *Carangidae* indet.; I–K, dentary (KANIZSAI L. coll.); L–N, dentary (NHMUS VER 2020.158.). O, P, *Sphyræna* sp. tooth (PTE_5083) in two different views. A, C, E, J, M in dorsal view; B in ventral view; D, F in anterior or posterior view; G, I, L in lateral view; H in posterior view; K, N in medial view. Scale bars: 10 mm

A–J, *Acipenseridae* indet.; A, B, koponyaelem (KANIZSAI L. gyűjteménye); C, D: bőrcsont (PTE_5163); E, F, bőrcsont (NHMUS VER 2020.212.); G, H, mellúsó-tövis (PTE_5135). I–N, *Carangidae* indet.; I–K, dentale (KANIZSAI L. gyűjteménye); L–N, dentale (NHMUS VER 2020.158.). O, P, *Sphyræna* sp. fog (PTE_5083) két nézetben. A, C, E, J, M, dorzális nézet; B, ventrális nézet; D, F, anterior vagy poszterior nézet; G, I, L, laterális nézet; H, poszterior nézet; K, N, mediális nézet. Méretarányok: 10 mm

Plate XII – XII. tábla

Osteichthyan remains from the limonitic sands – Csontosshal-maradványok a limonitos homokból

A–O, cf. *Thunnus* sp.; A–C, premaxilla (KANIZSAI L. coll.); D–F, dentary (NHMUS VER 2020.161.); G–I, dentary (MGSH coll.); J–L, abdominal vertebra (MGSH coll.); M–O, caudal vertebra (NHMUS VER 2020.174). P–A', *Scombridae* indet.; P, Q, premaxilla (PTE_5094); S–U, dentary (PTE_5097); V–X, dentary (PTE_5095); Y–A', dentary (PTE_5096). A, D, G, K, N, P, S, V, Y in lateral view;

B, Q in ventral view; M in ?ventral view; C, F, I, R, U, X, A' in medial view; E, H, J, T, W, Z in dorsal view; L, O in ?anterior view. Scale bars: 10 mm

A–O, cf. *Thunnus* sp.; A–C, premaxilla (KANIZSAI L. gyűjtemény); D–F, dentale (NHMUS VER 2020.161.); G–I, dentale (MGSH gyűjtemény); J–L, abdominális csigolya (MGSH gyűjtemény); M–O, farki csigolya (NHMUS VER 2020.174.). P–A', Scombridae indet.; P, Q, premaxilla (PTE_5094); S–U, dentale (PTE_5097); V–X, dentale (PTE_5095); Y–A', dentale (PTE_5096). A, D, G, K, N, P, S, V, Y, laterális nézet; B, Q, ventrális nézet; M, ?ventrális nézet; C, F, I, R, U, X, A', mediális nézet; E, H, J, T, W, Z, dorzális nézet; L, O, ?anterior nézet. Méretarányok: 10 mm

Plate XIII – XIII. tábla

Osteichthyan remains from the limonitic sands – Csontosshal-maradványok a limonitos homokból

A–D, *Labrodon* sp.; A, B, pharyngeal tooth plate (PTE_5082); C, D, pharyngeal tooth plate (KANIZSAI L. coll.). E–H, *Trigonodon jugleri* tooth (CSERPÁK F. coll., inv. nr.: Dp2792). I, J, *Calotomus* sp. pharyngeal tooth plate (CSERPÁK F. coll., inv. nr.: Dp 3923) in two different views. A, C, G in occlusal view; B, D in basal view; E in labial view; F in lingual view; H in profile view. Scale bars: 5 mm

A–D, *Labrodon* sp.; A, B, garatfoglemez (PTE_5082); C, D, garatfoglemez (KANIZSAI L. gyűjteménye). E–H, *Trigonodon jugleri* fog (CSERPÁK F. gyűjteménye, leltári szám: Dp2792). I, J, *Calotomus* sp. garatfoglemez (CSERPÁK F. gyűjteménye, leltári szám: Dp 3923) két nézet. A, C, G, okkluzális nézet; B, D, bazális nézet; E, labiális nézet; F, linguális nézet; H, profilnézet. Méretarányok: 5 mm

Plate XIV – XIV. tábla

Osteichthyan remains from the limonitic sands – Csontosshal-maradványok a limonitos homokból

A–N, *Lates* sp.; A, B, vomer (JACLMEC 2006.156.74); C–E, parasphenoid (NHMUS VER 2020.248.); F, basioccipital (NHMUS VER 2020.154.); G, H, quadrate (JACLMEC 2006.145.113); I, J, quadrate (PTE_5109); K, L, premaxilla (KANIZSAI L. coll.); M, N, premaxilla (NHMUS VER 2020.165.). A, C, F in ventral view; B, E in dorsal view; D, H, I, K, M in lateral view; G, J in posterior view; L, N in medial view. Scale bars: 10 mm

A–N, *Lates* sp.; A, B, vomer (JACLMEC 2006.156.74); C–E, parasphenoideum (NHMUS VER 2020.248.); F, basioccipitale (NHMUS VER 2020.154.); G, H, quadratum (JACLMEC 2006.145.113); I, J, quadratum (PTE_5109); K, L, premaxilla (KANIZSAI L. gyűjteménye); M, N, premaxilla (NHMUS VER 2020.165.). A, C, F, ventrális nézet; B, E, dorzális nézet; D, H, I, K, M, laterális nézet; G, J, poszterior nézet; L, N, mediális nézet. Méretarányok: 10 mm

Plate XV – XV. tábla

Osteichthyan remains from the limonitic sands – Csontosshal-maradványok a limonitos homokból

A–L, *Lates* sp.; A, B, maxilla (JACLMEC 2006.145.114); C, D, dentary (KANIZSAI L. coll.); E, dentary (KANIZSAI L. coll.); F, angulo-articular (JACLMEC 2015.9.84); G, angulo-articular (JACLMEC 2015.9.120); H, anterior abdominal vertebra (PTE_5130); I, anterior abdominal vertebra (NHMUS VER 2020.148.); J, postabdominal vertebra (MGSH coll.); K, L, median fin spine (PTE_5113). M–R, Sciaenidae indet.; M–O, premaxilla (PTE_5106); P–R, premaxilla (PTE_5105). A, C, E, F, G, H, I, J, M, P in lateral view; B, K in anterior view; D, O, R in medial view; L in posterior view, N, Q in ventral view. Scale bars: 10 mm

A–L, *Lates* sp.; A, B, maxilla (JACLMEC 2006.145.114); C, D, dentale (KANIZSAI L. gyűjteménye); E, dentale (KANIZSAI L. gyűjteménye); F, angulo-articulare (JACLMEC 2015.9.84); G, angulo-articulare (JACLMEC 2015.9.120); H, anterior abdominális csigolya (PTE_5130); I, anterior abdominális csigolya (NHMUS VER 2020.148.); J, postabdominális csigolya (MGSH coll.); K, L, medián úszótüske (PTE_5113). M–R, Sciaenidae indet.; M–O, premaxilla (PTE_5106); P–R, premaxilla (PTE_5105). A, C, E, F, G, H, I, J, M, P, laterális nézet; B, K, anterior nézet; D, O, R, mediális nézet; L, poszterior nézet, N, Q, ventrális nézet. Méretarányok: 10 mm

Plate XVI – XVI. tábla

Osteichthyan remains from the limonitic sands – Csontosshal-maradványok a limonitos homokból

A, B, *Diplodus* sp.; tooth (NHMUS VER 2020.211.). C–K, *Pagrus cinctus*; C, D, premaxilla (SÖVÉR L. coll.); E, F, premaxilla (KANIZSAI L. coll.); G, H, premaxilla (KANIZSAI L. coll.); I–K, dentary (PTE_5090). L–U, *Sparus umbonatus*; L, M, premaxilla (PTE_5088); N, O, premaxilla (PTE_5089); P–R, dentary (NHMUS VER 2020.172.); S–U, enlarged crushing tooth (PTE_5085). V–Z, Tetraodontiformes indet.; V–X, tooth plate (A. ANDERSON coll.); W, close-up of the occlusal surface; Y, Z, tooth plate (SÖVÉR L. coll.). A in labial view; B in lingual view; C, E, G, M, O in lateral view; I, P in ?lateral view; D, F, H, L, N in medial view; K, R in ?medial view; J, Q in dorsal view; S, V, Y in occlusal view; T in profile view; U, X, Z in basal view. Scale bars: A, B, 1 mm; C–V, X–Z, 10 mm

A, B, *Diplodus* sp. fog (NHMUS VER 2020.211.). C–K; *Pagrus cinctus*; C, D, premaxilla (SÖVÉR L. gyűjteménye); E, F, premaxilla (KANIZSAI L. gyűjteménye); G, H, premaxilla (KANIZSAI L. gyűjteménye); I–K, dentale (PTE_5090). L–U, *Sparus umbonatus*; L, M, premaxilla (PTE_5088); N, O, premaxilla (PTE_5089); P–R, dentale (NHMUS VER 2020.172.); S–U, megnagyobbodott, őrlésre módosult fog (PTE_5085). V–Z, *Tetraodontiformes* indet.; V–X, foglemezek (A. ANDERSON gyűjteménye; W, Közeli kép az okklúzális felszínről); Y, Z, foglemezek (SÖVÉR L. gyűjteménye). A, labiális nézet; B, linguális nézet; C, E, G, M, O, laterális nézet; I, P ?laterális nézet; D, F, H, L, N, mediális nézet; K, R, ?mediális nézet; J, Q, dorzális nézet; S, V, Y, okklúzális nézet; T, profilnézet; U, X, Z, bazális nézet. Méretarányok: A, B, 1 mm; C–V, X–Z, 10 mm

Plate XVII – XVII. tábla

Osteichthyan remains from the limonitic sands – Csontoshal-maradványok a limonitos homokból

A–L, Actinopterygii indet. hyperostotic bone elements; A, B, ?rib (MGSH coll.); C, D, ?rib (KANIZSAI L. coll.); E, F, ?rib (MGSH coll.); G, H, ?rib (NHMUS VER 2020.170.); I, J, vertebra (MGSH coll.); K, L, vertebra (MGSH coll.). A, C, E, G, J, L in lateral view; B, D, F, H, I, K in medial view. Scale bars: 10 mm

A–L, Actinopterygii indet. hiperosztotikus csontelemek; A, B, ?borda (MGSH gyűjtemény); C, D, ?borda (KANIZSAI L. gyűjteménye); E, F, ?borda (MGSH gyűjtemény); G, H, ?borda (NHMUS VER 2020.170.); I, J, csigolya (MGSH gyűjtemény); K, L, csigolya (MGSH gyűjtemény). A, C, E, G, J, L, laterális nézet; B, D, F, H, I, K, mediális nézet. Méretarányok: 10 mm

Plate I – I. tábla

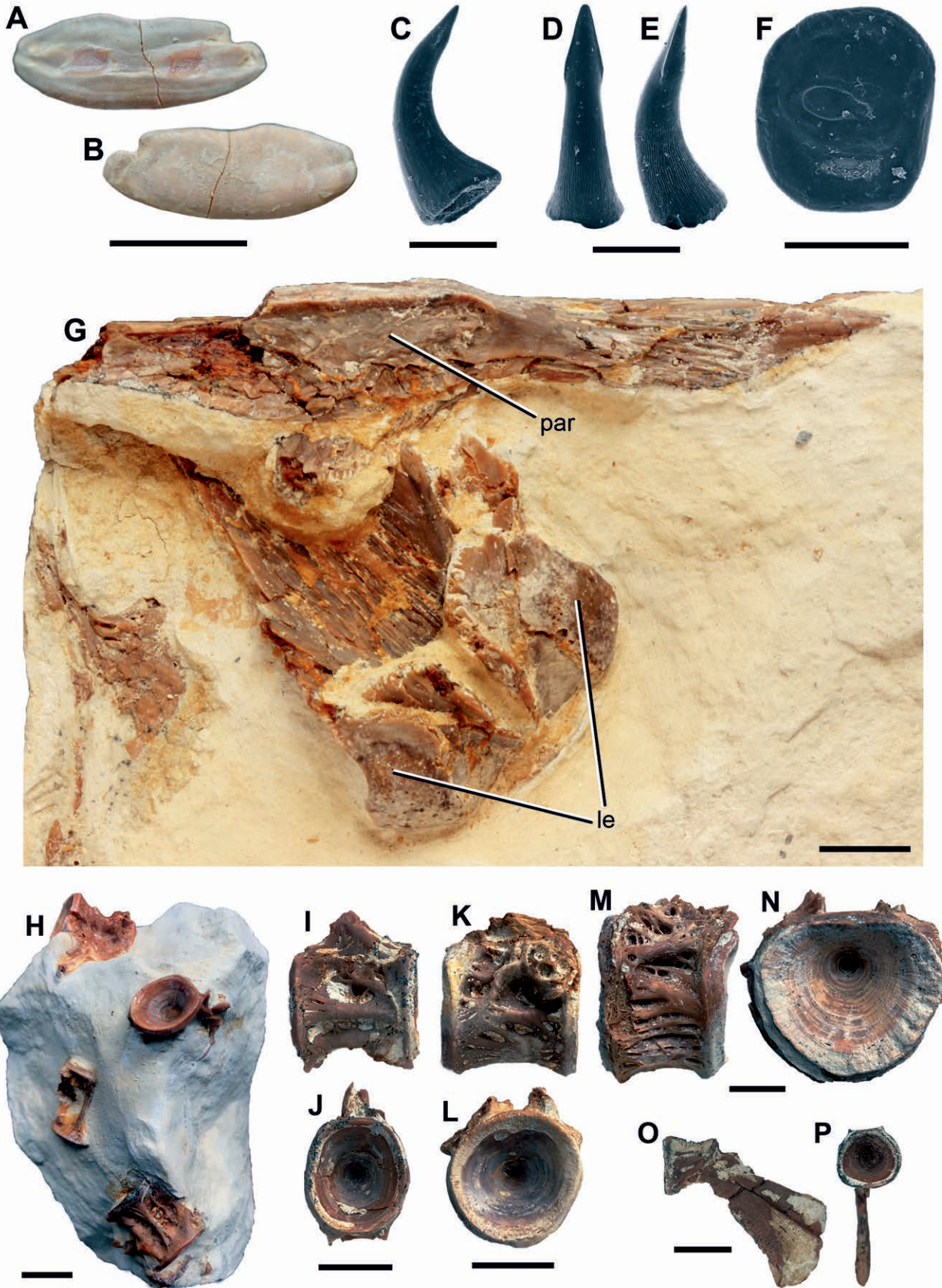


Plate II – II. tábla

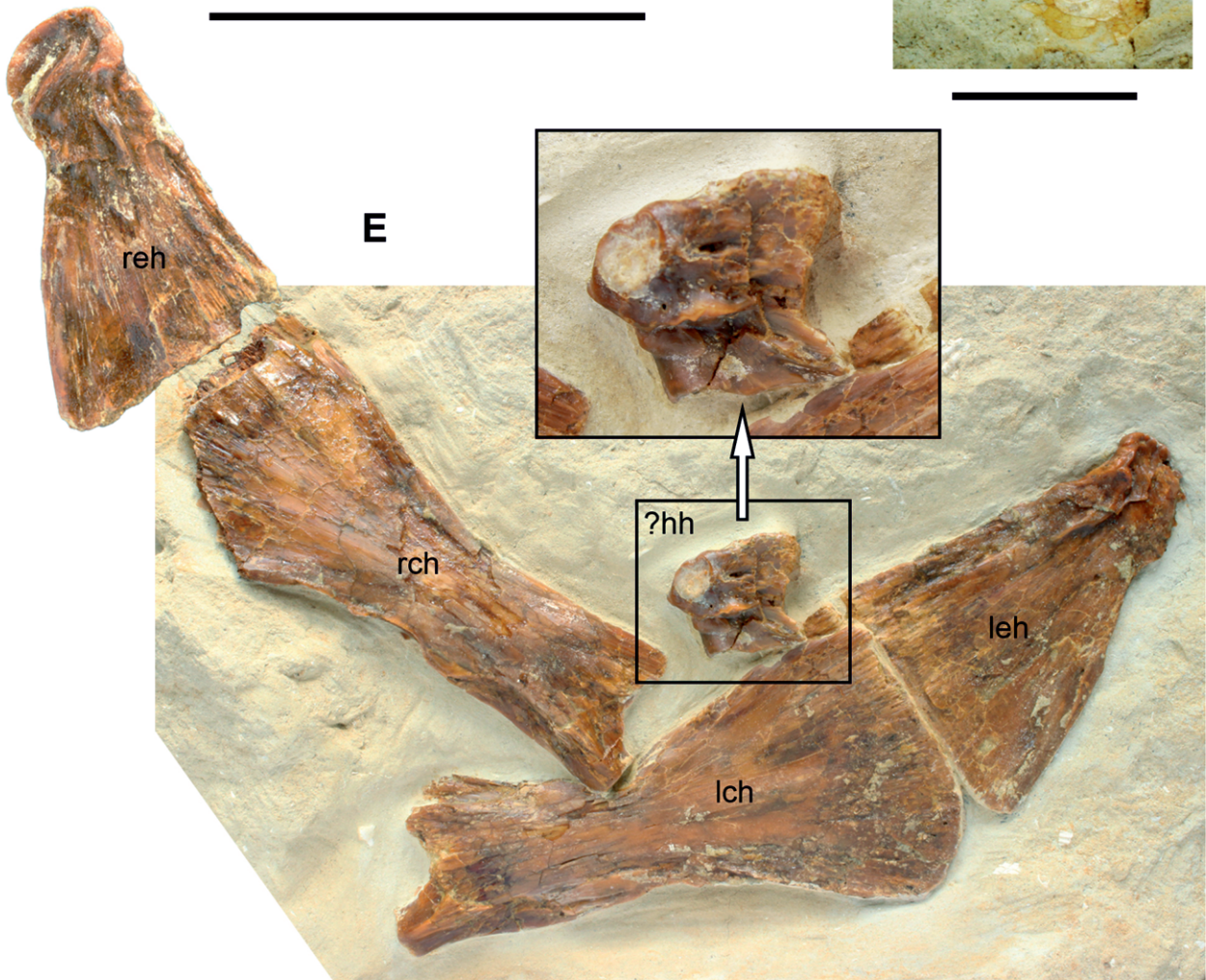
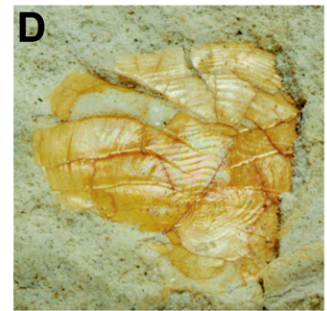
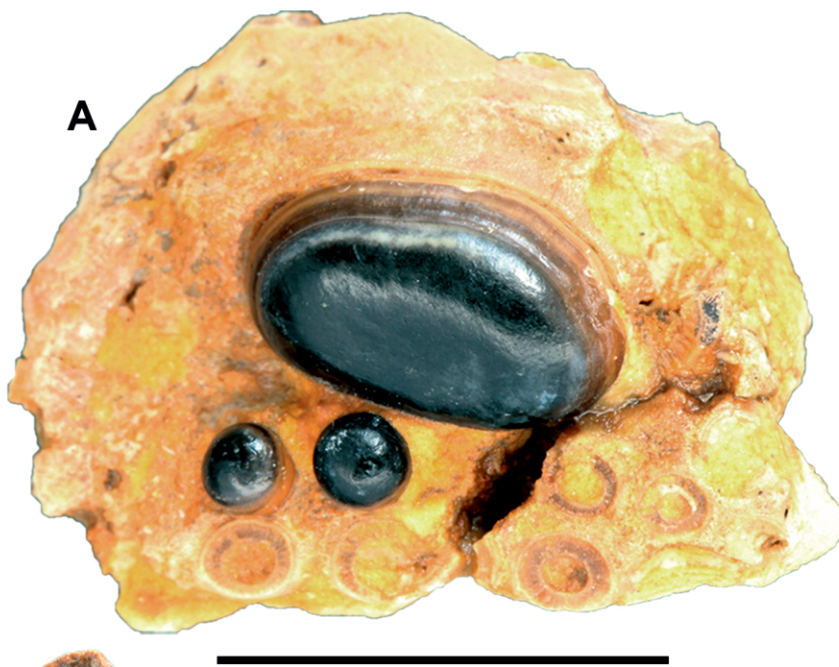


Plate III – III. tábla

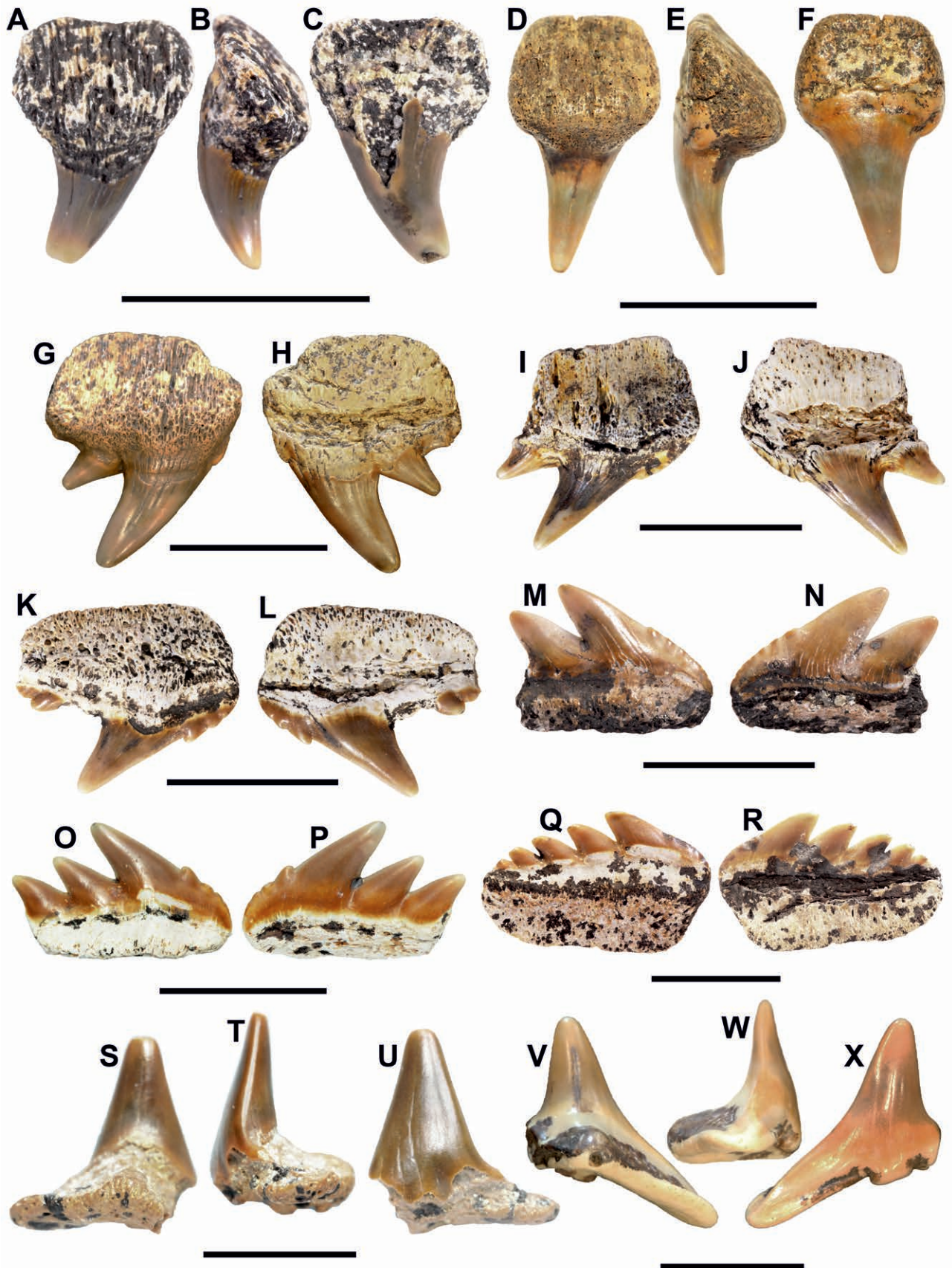


Plate IV – IV. tábla

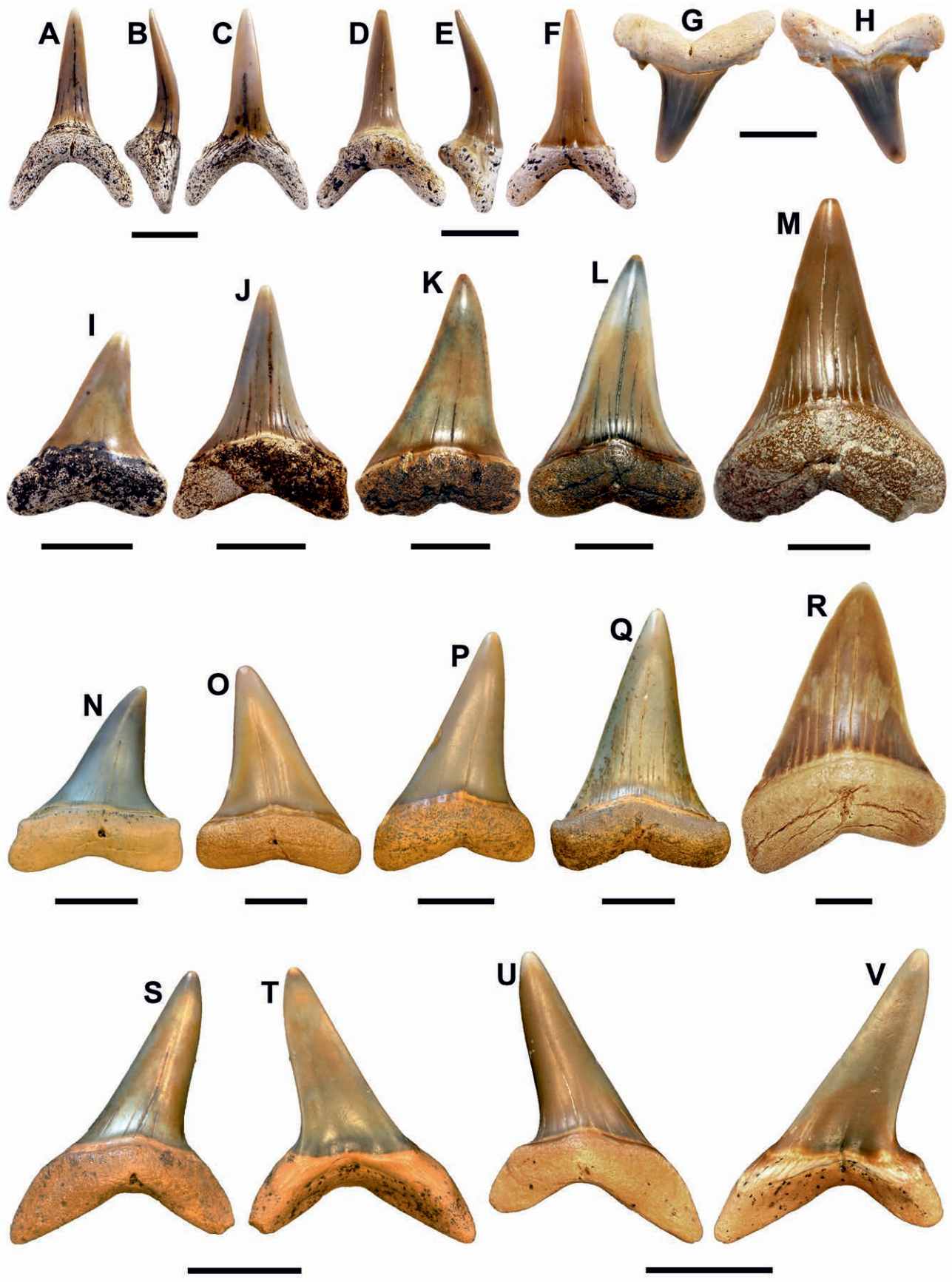


Plate V – V. tábla

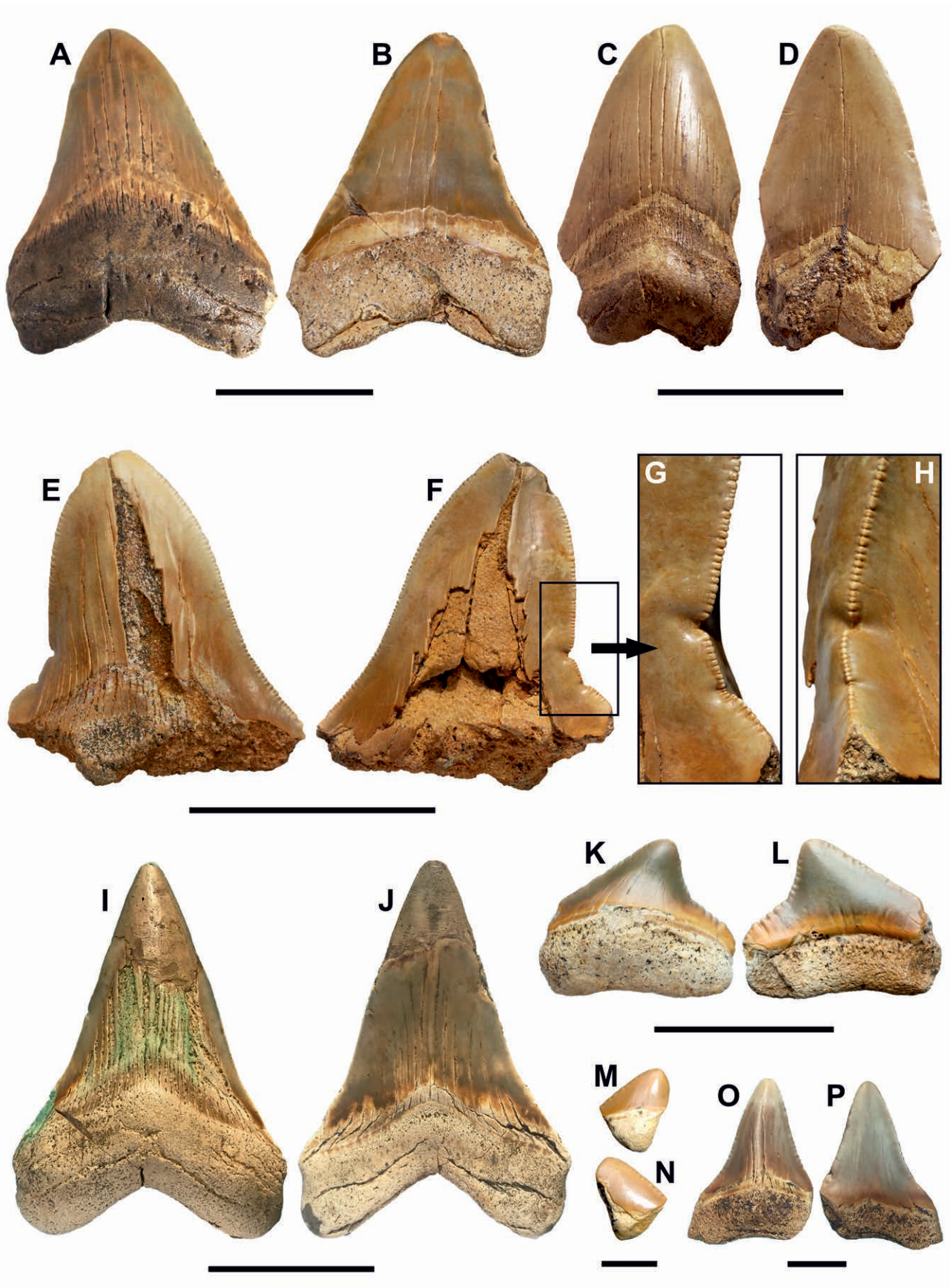


Plate VI – VI. tábla

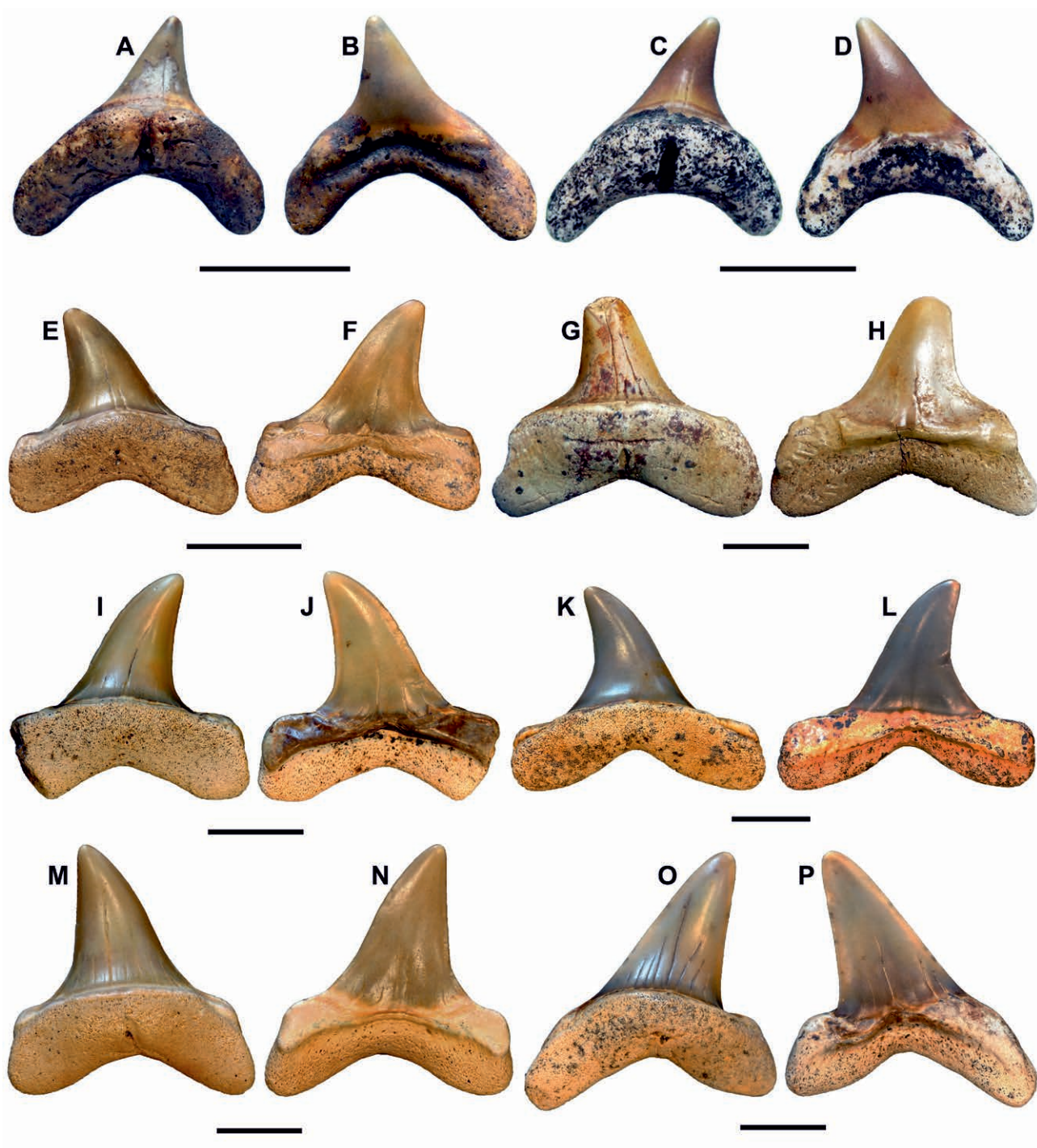


Plate VII – VII. tábla

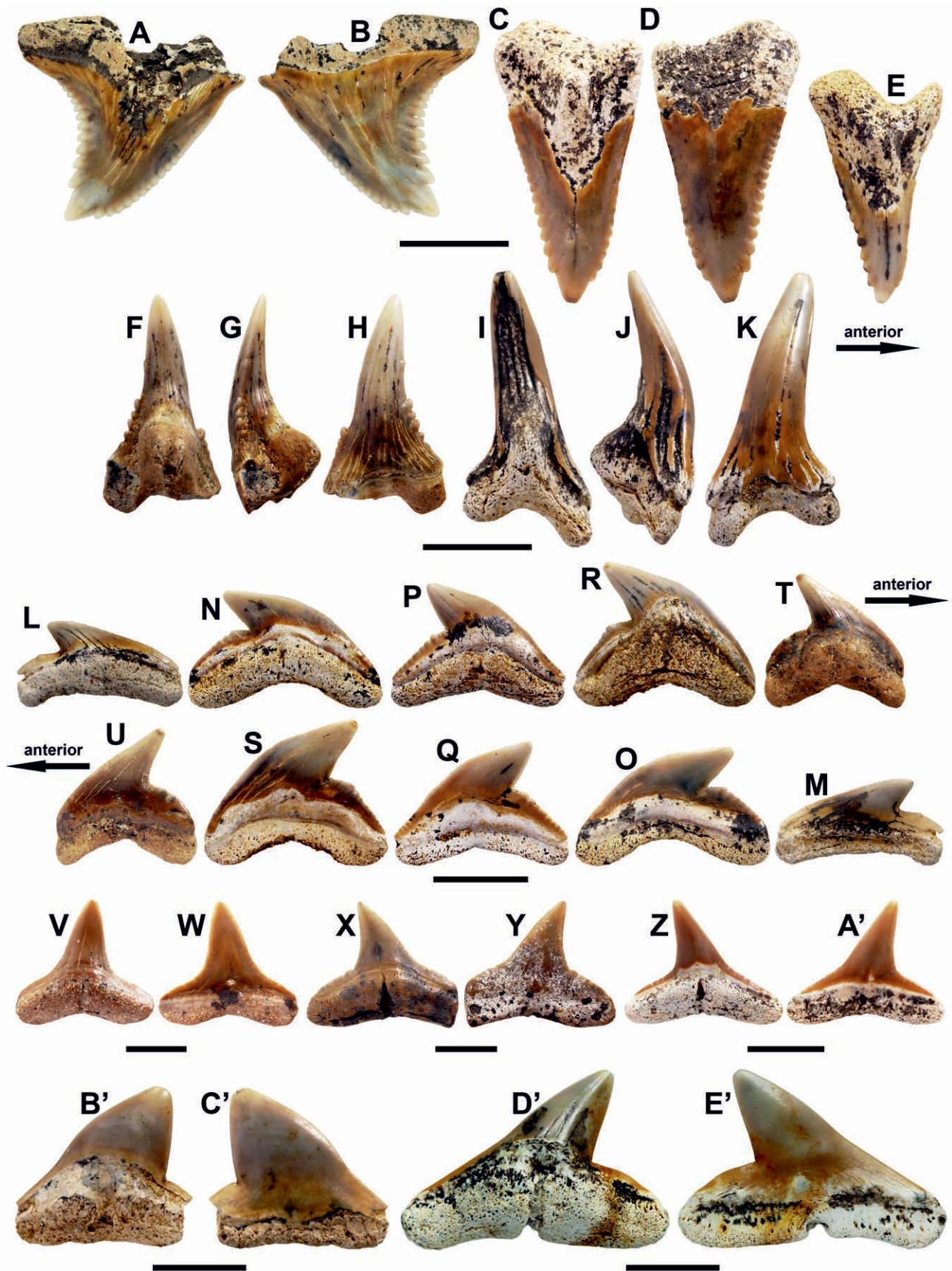


Plate VIII – VIII. tábla



Plate IX – IX. tábla



Plate X – X. tábla

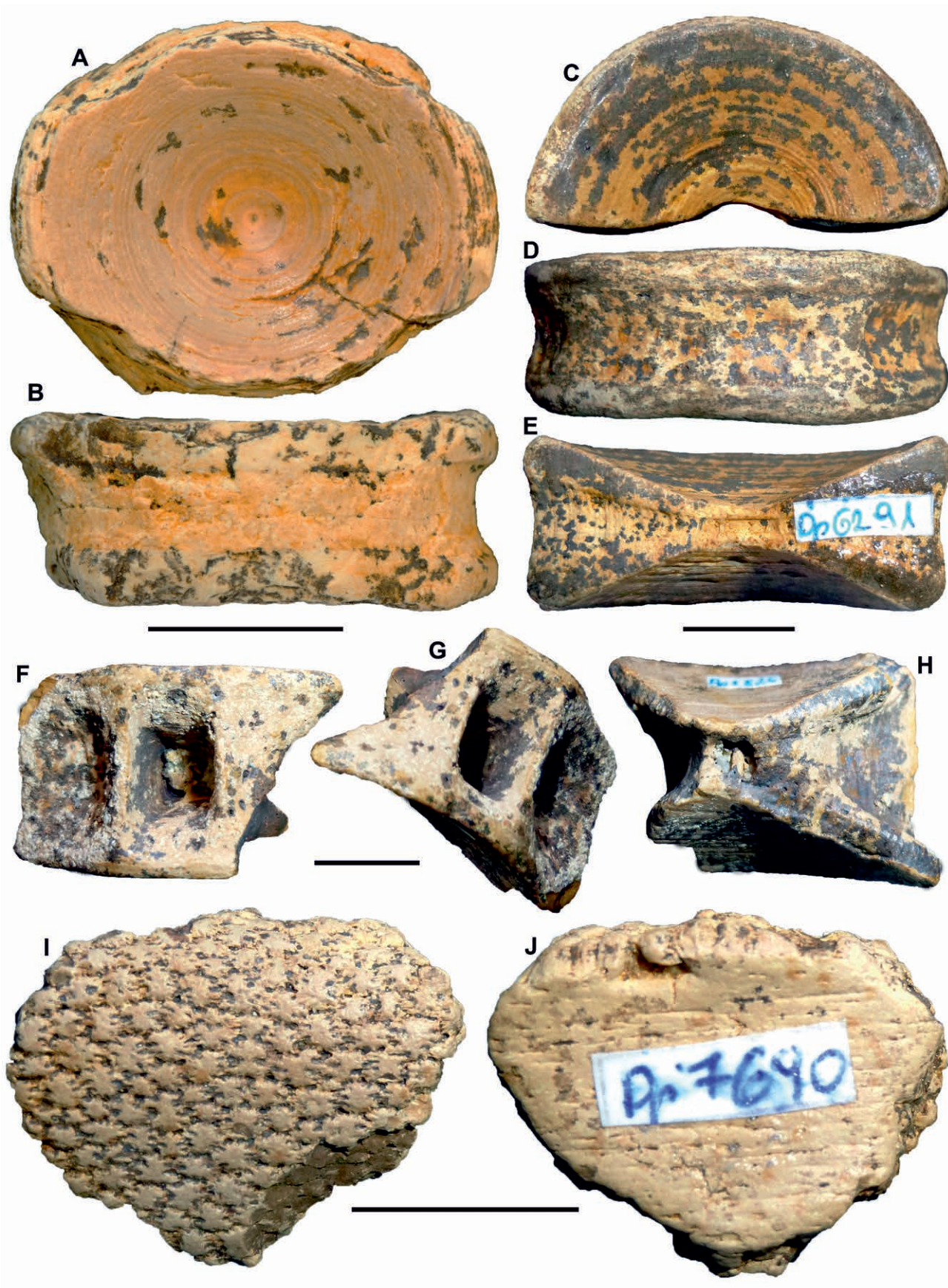


Plate XI – XI. tábla

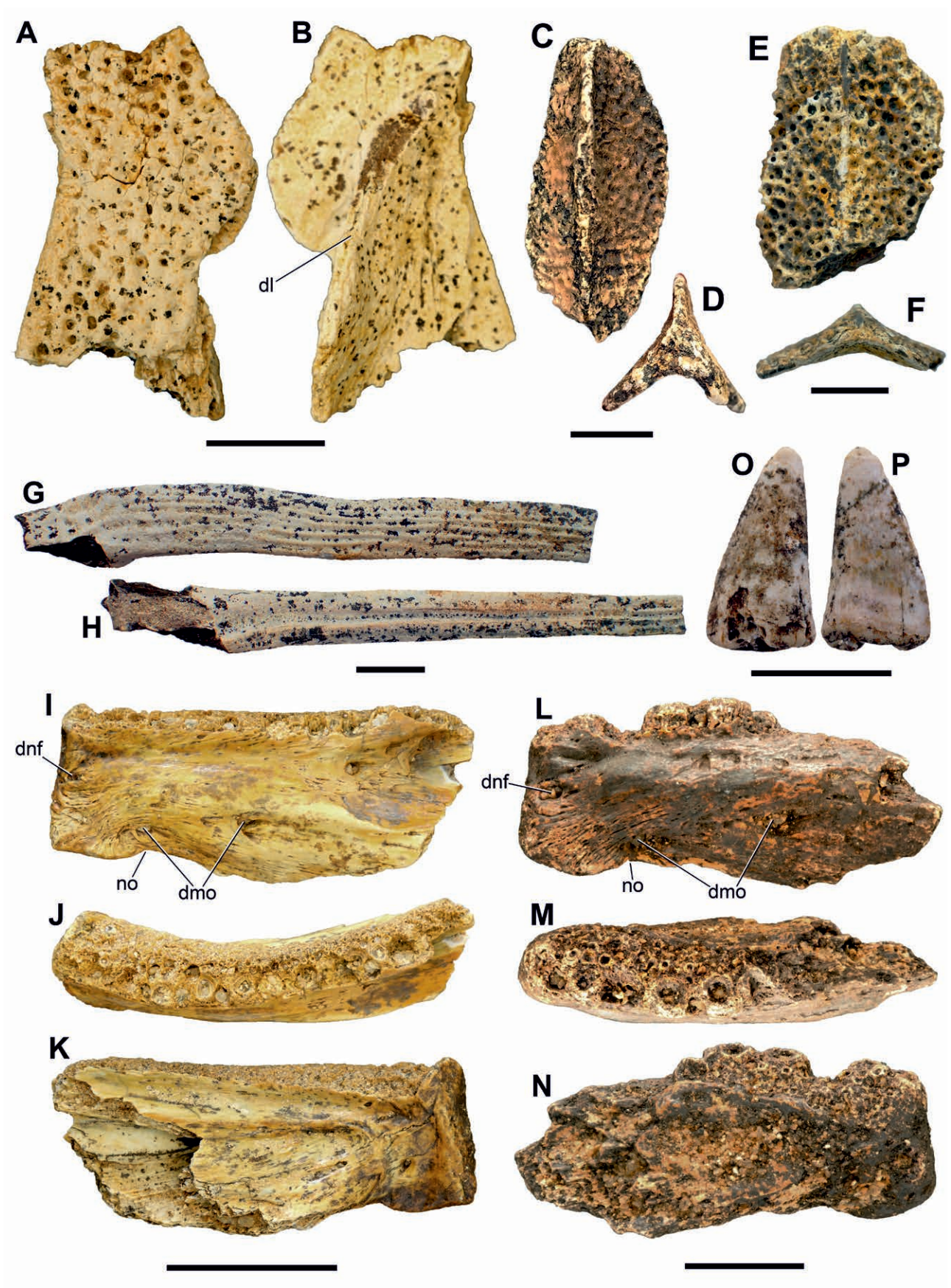


Plate XII – XII. tábla

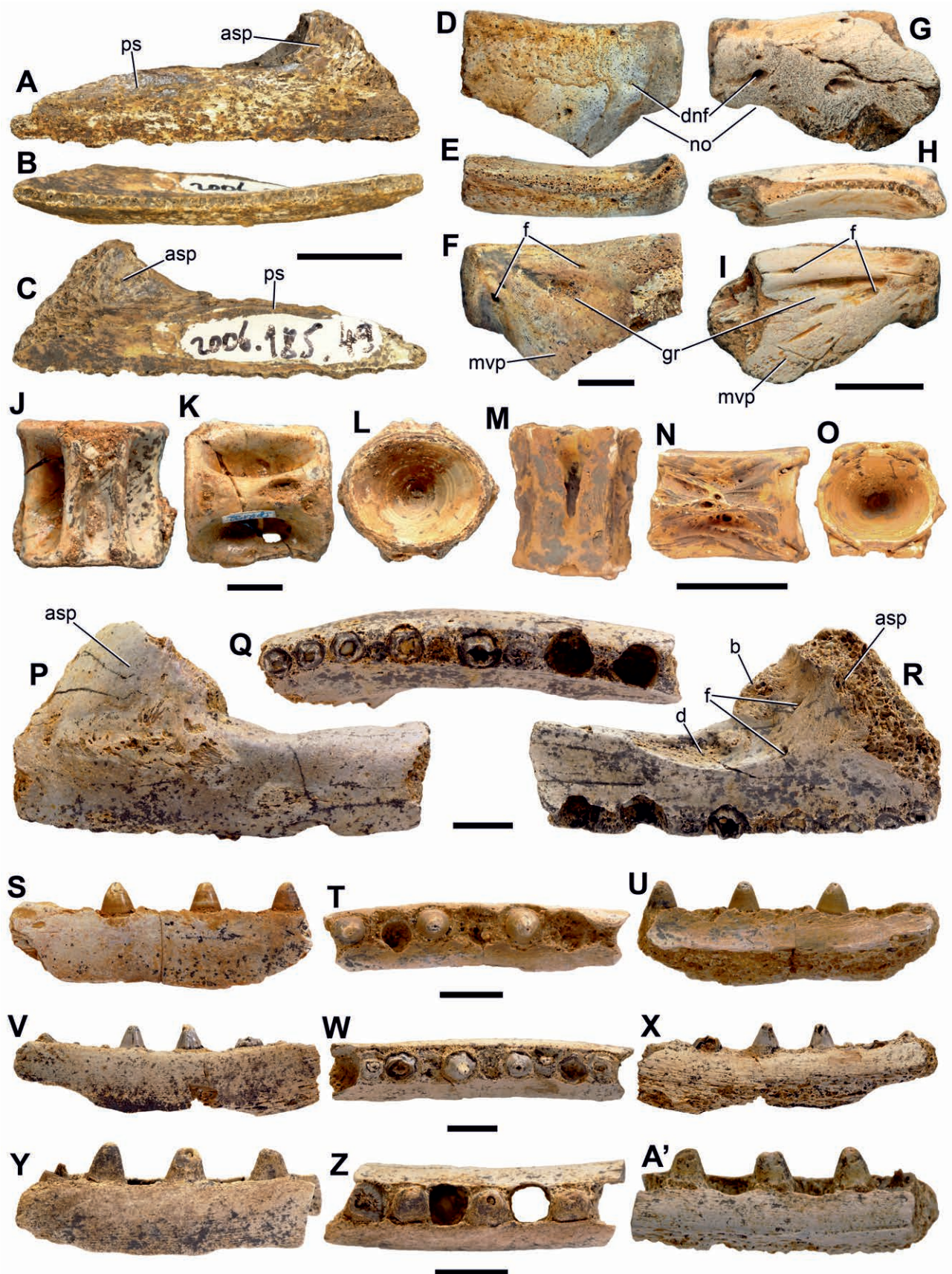


Plate XIII – XIII. tábla

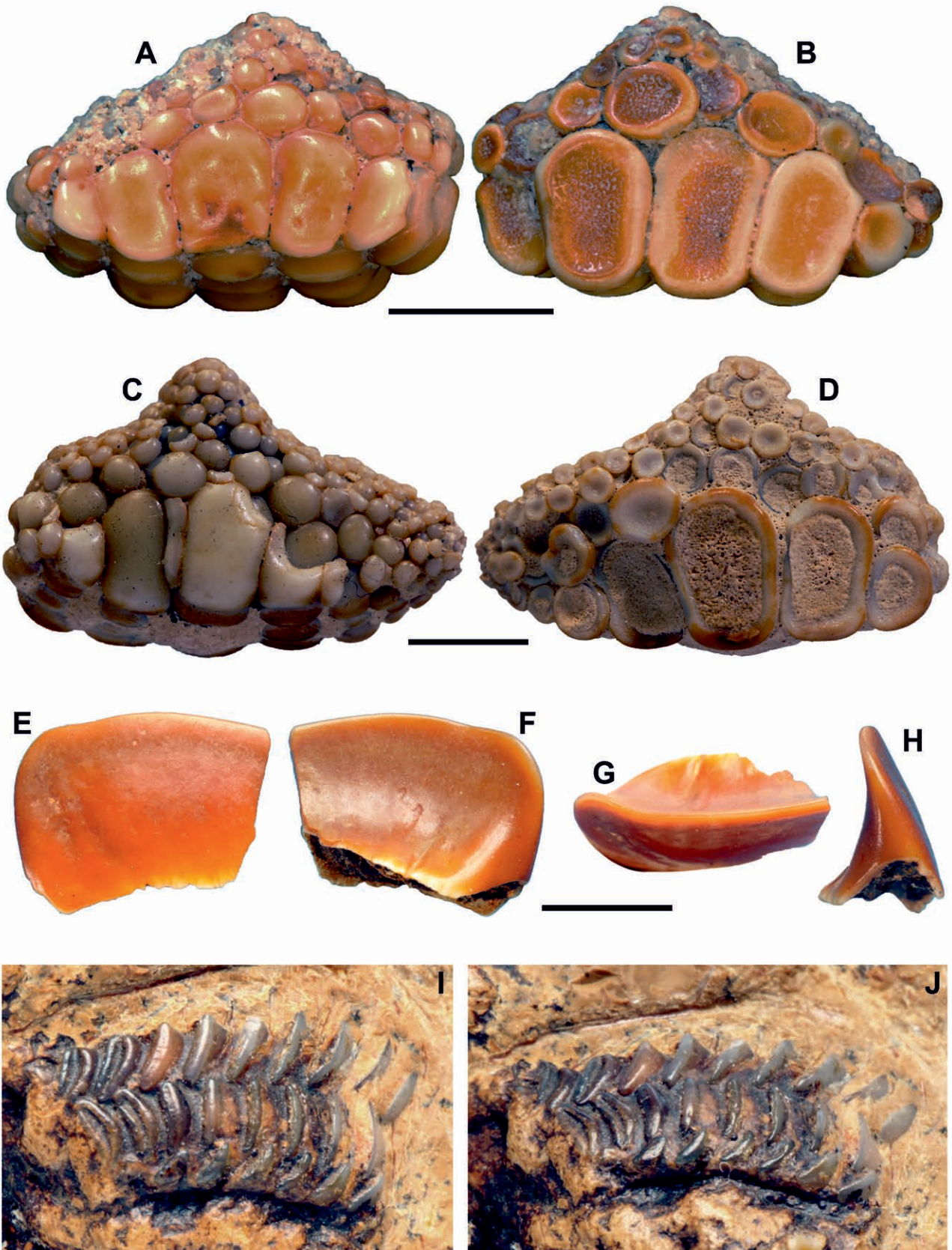


Plate XIV – XIV. tábla

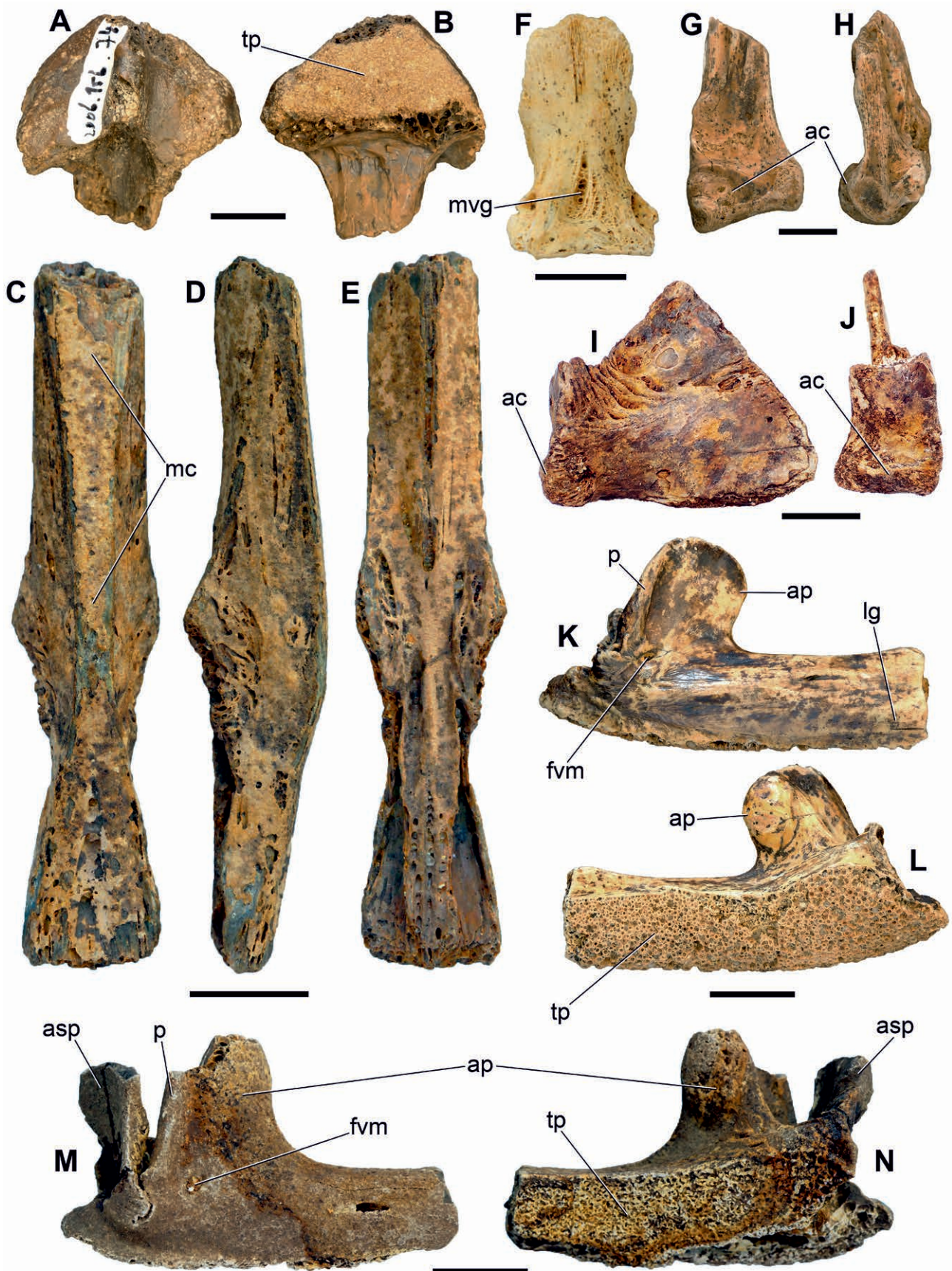


Plate XV – XV. tábla

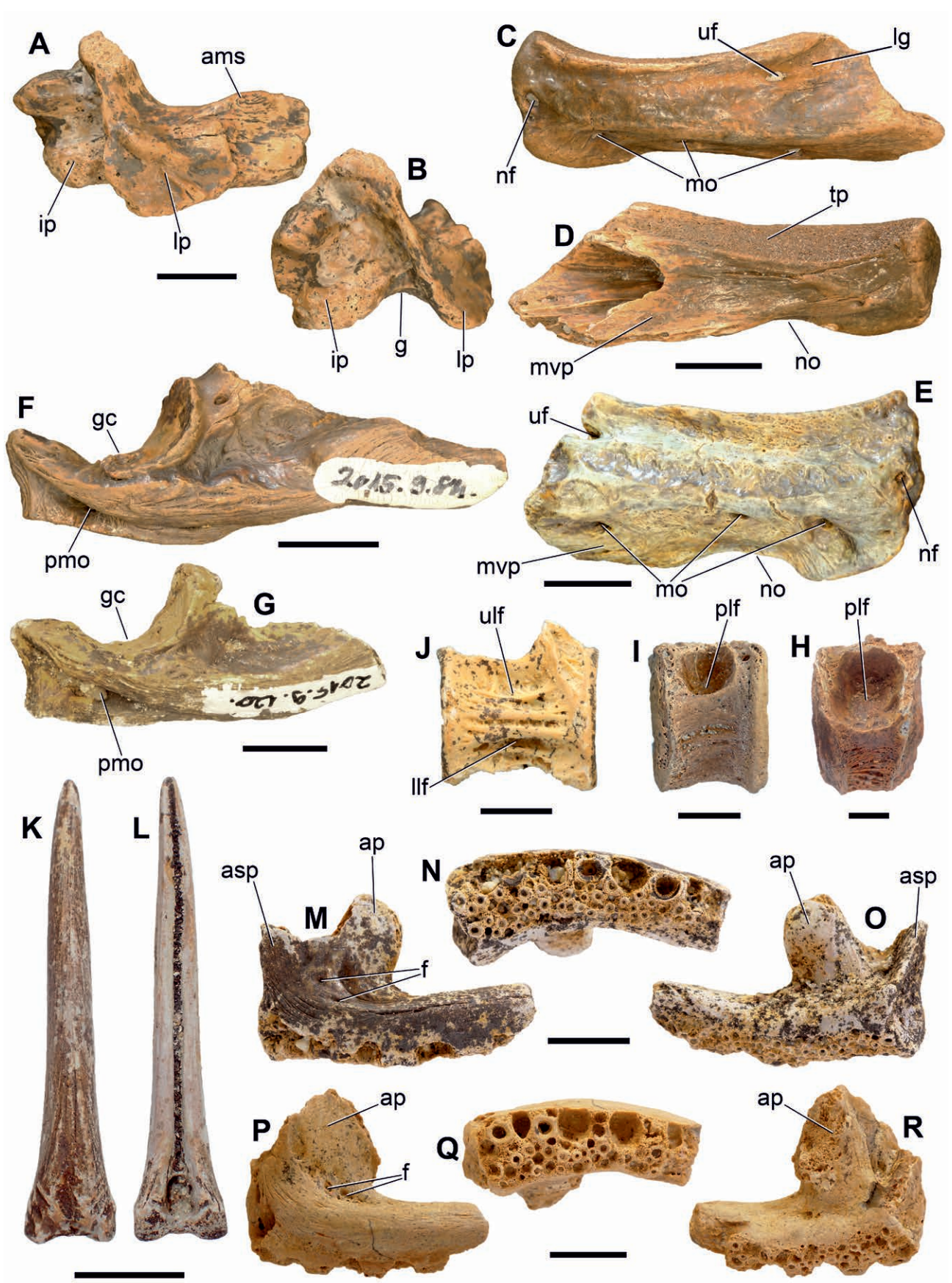
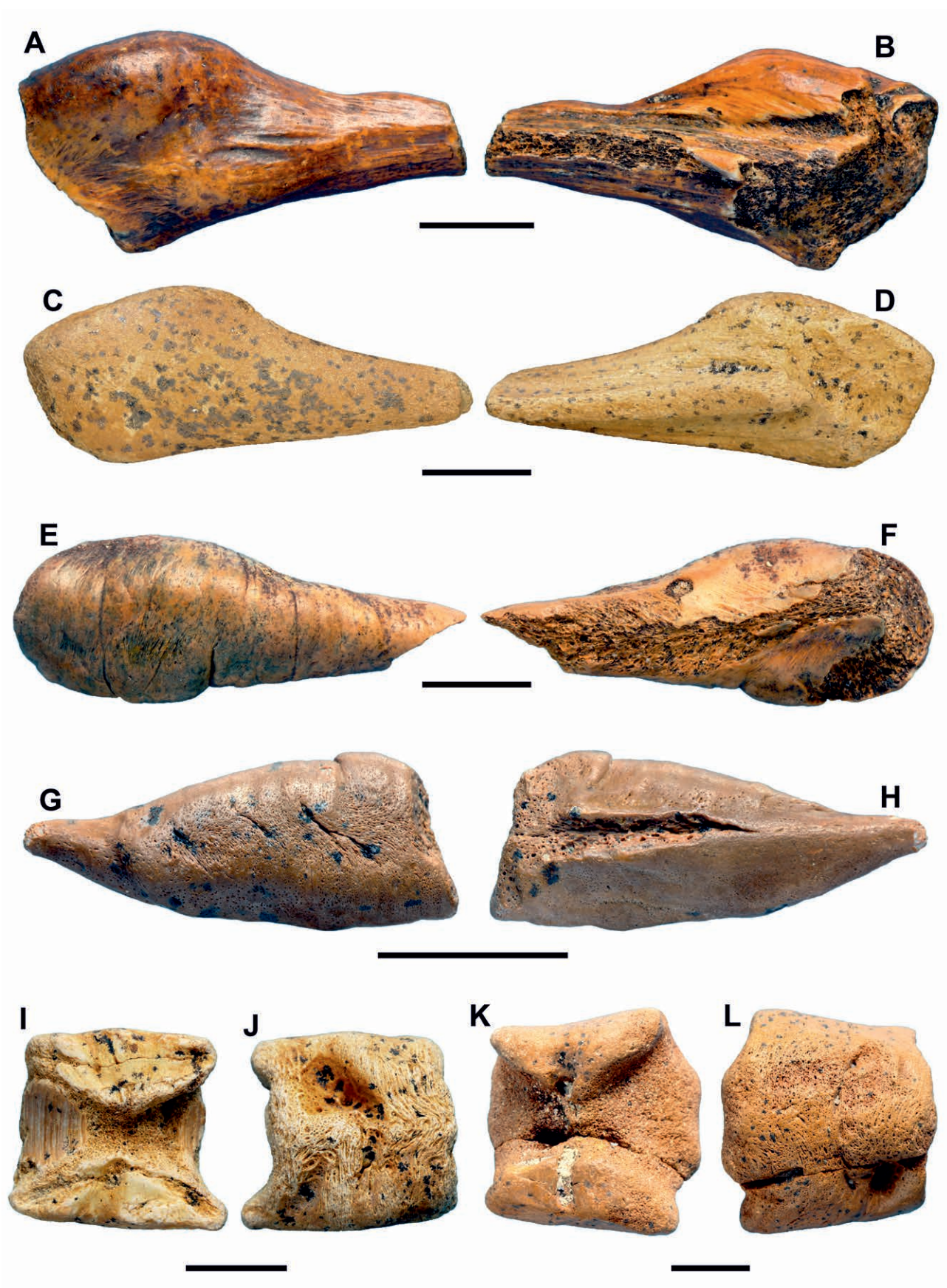


Plate XVII – XVII. tábla



Appendix

Systematic Palaeontology

Calcareous marls (Endrőd Marl Fm)

Class Osteichthyes HUXLEY, 1880
Subclass Actinopterygii KLEIN, 1885
Order Gadiformes GOODRICH, 1909
Family Gadidae RAFINESQUE, 1810

Gadidae indet. Plate I, A–E

Referred material: 1 otolith, 2 teeth.

Description: A relatively large otolith was referred to an indeterminate gadid taxon (*Plate I, A, B*). The otolith is elongated with smooth rims. The outer surface is smooth without ornamentation except a well-defined furrow at the rostral end. The inner face is moderately convex lengthwise. The ventral rim is gently curved towards both the anterior and the posterior tips, slightly rounded anteriorly. The dorsal rim has a weakly developed pre-dorsal angle, the medio-dorsal part is slightly depressed, the postdorsal angle is marked. The dorsal rim bears a deep pinch between the postdorsal angle and the posterior tip. The anterior tip is bluntly pointed above the tiny rostrum. The rather shallow sulcus is straight with median position, ending in a narrow channel towards the anterior rim. The ostium is slightly shorter than the cauda, the collum is rather wide. The colliculi are shallow and do not extend to the margins. The ostial colliculum is smaller and has a trapezoidal shape. The caudal colliculum is fading away towards the posterior rim. The pseudocolliculum is well-developed. The ventral furrow is distinct and close to the ventral rim.

Two teeth were referred to indeterminate gadid fishes (*Plate I, C–E*). Their base is curved, and circular in cross-section. The tooth base bears fine or moderately coarse apicobasal striations. The slightly reclining cap is lanceolate.

Remarks: The morphology of the teeth does not provide specific characteristics; therefore identification on a level closer than Gadidae indet. is not possible. Morphologically similar or identical teeth were published in BRZOBOHATÝ & PANĀ (1985, pl. 58, fig. 28) and BOTKA et al. (2019, fig. 9A–D) as gadid teeth. The otolith specimen is similar to otoliths of *Gadiculus* (NOLF 2013) or *Palimphemus* (BRATISHKO et al. 2015), but its closer identification requires further specimens.

Family Gobiidae CUVIER, 1816

Gobiidae indet. Plate I, F

Referred material: 1 otolith.

Description: Well-preserved, very small otolith. It is rounded, and the sulcus is hardly visible. The sulcus is wide with high ostial lobe and small cauda. The ventral furrow is broad, running far from the ventral rim of the otolith. The outer surface is convex and smooth without ornamentation.

Remarks: This specimen represents a juvenile individual, therefore is mentioned only at family level.

Order Perciformes BLEEKER, 1859

Family Latidae JORDAN, 1888

Genus *Lates* CUVIER & VALENCIENNES, 1828

Lates sp. Plate I, G–P

Referred material: 1 partial skeleton, 1 block of associate vertebrae, 2 isolated vertebrae.

Description: An incomplete parasphenoid with associate ethmoid bones embedded in a piece of marl (*Plate I, G*). The parasphenoid (*Plate I, G, par*) is elongated and in lateral view, it has a slightly curved ventral border. The lateral ethmoids (*Plate I, G, le*) are slightly deformed, but they possess the palatine facets.

A block of marl includes associate vertebrae (of which two were prepared for closer examination) representing the postabdominal section of the spine (*Plate I, H–L*).

A large, isolated vertebra possibly belongs to the second abdominal position (*Plate I, M, N*). Based on its long haemal spine another isolated vertebra represents the caudal skeleton (*Plate I, O, P*).

Remarks: The morphology of the described remains clearly refers them to the latid genus *Lates* (see MURRAY et al. 2018, OTERO 2004). This taxon is extremely abundant in the sands (see the section of the limonitic sands), from where comparable skeletal elements were unearthed.

Order Spariformes BLEEKER, 1860

Family Sparidae BONAPARTE, 1832

Sparidae indet. Plate II, A

Referred material: 1 premaxilla.

Description: A fragmentary premaxillary bone was referred to a sparid fish. This premaxillary bears an enlarged molariform tooth, oval in occlusal view, and further, smaller, hemispherical molariform teeth and empty tooth positions. The broken tooth bases show radial ridges arranged around a large circular pulp cavity.

Remarks: The specimen is similar to the remains of *Sparus umbonatus* (see in the fauna of the limonitic sands), but it is much smaller, and somewhat less robust, which indicate closer resemblance to other sparids, e.g., *Sparus auratus*.

Actinopterygii indet.

Plate II, B–E

Referred material: 2 teeth, 2 cycloid scales, 1 articulated hyoid region.

Description: A few isolated teeth (Plate II, B, C) and cycloid scales (Plate II, D) were referred to indeterminate actinopterygians. The articulated hyoid region is of large size (Plate II, E), it comprises a left and a right ceratohyal (Plate II, E, *lch* and *rch*) with matching epihyals (Plate II, E, *leh* and *reh*) and a possible hypohyal (Plate II, E, *?hh*).

Remarks: The teeth and cycloid scales referred here are of too general morphology and low number for a closer identification. The investigation of the hyoid elements is yet to be carried out, but it clearly differs from hyoid region of gadiforms (HUSSAIN 1986, ENDO 2002), latids (OTERO 2004) and sparids (DAY 2002). Until more fish remains are found in the Endrőd Formation, here we refer these specimens as unidentified actinopterygian remains.

Limonitic sands (Kálla Member of the Békés Formation)

Class Chondrichthyes HUXLEY, 1880
Superorder Selachimorpha NELSON, 1984
Order Hexanchiformes DE BUEN, 1926
Family Hexanchidae GRAY, 1851
Genus *Notorynchus* AYRES, 1855

Notorynchus primigenius (AGASSIZ, 1835)

Plate III, A–R

Referred material: 17 teeth.

Description: Both upper and lower teeth are known. Upper anterior teeth (Plate III, A–F) have a single cusp, weakly curved lingually. Upper anterolateral and lateral teeth (Plate III, G–L) have a distally inclined main cusp, flanked by cusplets both mesially and distally. The root of upper teeth is flattened and rectangular, it gradually becomes wider than it is high in distal direction along the upper jaw. Lower files (Plate III, M–R), the most characteristic elements of the species have a distally inclined main cusp, followed by up to 5 distal cusplets. Further cusplets, smaller than the distal ones, are situated mesially to the main cusp. This part of the crown is usually eroded in the studied upper anterolateral-lateral and lower hexanchid teeth. The root is wider than it is high, and – similarly to that of upper teeth – it has a rectangular outline in labial and lingual view.

Remarks: The hexanchid species *N. primigenius* is widely reported from the Miocene marine sediments of the Central Paratethys (e.g., HOLEC et al. 1995; KOCSIS 2007; SZABÓ & KOCSIS 2016a, table 2). Its global fossil record consists of isolated teeth only, found in Oligocene–Miocene marine sediments of North America, Europe and Australia (CAPPETTA 2012).

Order Squatiniformes DE BUEN, 1926
Family Squatinidae BONAPARTE, 1838
Genus *Squatina* DUMÉRIL, 1806

Squatina sp.

Plate III, S–X

Referred material: 2 teeth.

Description: Both teeth are incomplete and miss nearly the half of the root. The anterior tooth has an upright main cusp perpendicular to the root (Plate III, S–U), while the cusp of the lateral tooth is distally inclined (Plate III, V–X). The crown of both specimens has convex labial and lingual faces. In profile view, the crown is weakly curved lingually. Both cutting edges are straight, no serrations are present or preserved. The crown basally continues on the root lobes both mesially and distally. Faint remains of the rounded, labial apron (characteristic for the genus) are visible. The preserved root portions refer to a triangular outline in basal view (not illustrated).

Remarks: The dentition of *Squatina* is very stable over geological times, therefore distinguishing species solely based on isolated teeth is not well-established (CAPPETTA 2012). Numerous Oligocene–Miocene reports show the presence of the genus in the Central Paratethys (e.g., HOLEC et al. 1995; KOCSIS 2007; SZABÓ & KOCSIS 2016a, table 2; SZABÓ et al. 2017).

Order Lamniformes BERG, 1958
Family Odontaspidae MÜLLER & HENLE, 1839

Odontaspidae indet.

Plate IV, A–H

Referred material: 1500 teeth.

Description: Anterior teeth are Y-shaped, and symmetrical in labial and lingual views (Plate IV, A–F). The crown is slender and upright, with sigmoid profile. The cutting edges are smooth all along, they run basally from the tip, not reaching the crown base. The lingual face is strongly, while the labial is only weakly convex to flat. Due to reworking it is uncertain if the lingual crown face had any surface ornamentation. The root is bilobate, with well-separated lobes with rounded extremities. The lobes meet in a large lingual protuberance, usually bearing a well-developed nutritive groove. Faint remains of lateral cusplets are present on both lobes of the best preserved specimens. Upper lateral files are distinguishable by their distally inclined main cusp, and non-sigmoid profile outline (Plate IV, G, H).

Remarks: Miocene odontaspids of the Central Paratethys

are represented by the genera *Araloselachus*, *Carcharias* and *Carcharoides* (see SZABÓ 2019; SZABÓ & KOCSIS 2016a, table 2; SZABÓ & KOCSIS 2020). These taxa are easily distinguishable by the fine characteristics of the main cusp (robustness, surface ornamentation, etc.) and the root (number and morphology of cusplets, outline of the root lobes, etc.) (CAPPETTA 2012). All specimens are markedly worn due to reworking, resulting in the disappearance of delicate surface features (e.g., lingual crown ornamentation, such as apicobasal folds), which could help closer identification. We leave the teeth referred here with open nomenclature. Nevertheless, the investigated odontaspid material is most similar to two species, *Carchaias acutissima* and *Araloselachus cuspidatus*, that are commonly reported from the Central Paratethys (SZABÓ & KOCSIS 2016a and references therein).

Family Lamnidae BONAPARTE, 1835
Genus *Cosmopolitodus* GLIKMAN, 1964

Cosmopolitodus hastalis (AGASSIZ, 1838)
Plate IV, I–R

Referred material: 170 teeth.

Description: Due to dignathic heterodonty upper and lower teeth are easy to distinguish. Lower teeth, especially lower anterior files, have a narrower crown, which is more convex on its lingual face than the upper teeth. Upper teeth have a high, triangular crown, with a weakly convex lingual and a practically flat labial face. The cutting edges are running from the tip to the crown base and are entirely smooth. No lateral cusplets are present. The root of uppers is moderately, while that of lowers is strongly bifurcate with a weak lingual protuberance, usually having a foramen (unclear in the Pécs-Danitzpuszta teeth).

Remarks: The species is of worldwide distribution from Miocene to Pliocene marine sediments (CAPPETTA 2012). It is also widespread in the Miocene of the Central Paratethys (e.g. HOLEC et al. 1995; KOCSIS 2007; SZABÓ & KOCSIS 2016a, table 2). Several aspects of the classification and taxonomy of *C. hastalis* have been published in the last few decades, therefore different names have been used for the species. *C. hastalis* was originally grouped in genus *Oxyrhina*, and later in *Isurus*. According to the hypothesis of GLIKMAN (1964), *C. hastalis* and *Carcharodon carcharias* (Great white shark) represent chronospecies as *C. hastalis* is replaced by a morphologically intermediate form, named *Carcharodon hubbelli* and finally *C. carcharias* (EHRET et al. 2012). To clarify this question is beyond the aims of the present paper, and the classification here follows that of CAPPETTA (2012).

Genus *Isurus* RAFINESQUE, 1810

Isurus oxyrinchus RAFINESQUE, 1810
Plate IV, S–V

Referred material: 13 teeth.

Description: The crown is narrow, triangular, distally inclined with a very weak curvature in profile view. The lingual crown face is convex, while the labial face is flat. Both faces

and the cutting edges are entirely smooth. The cutting edges do not reach the base of the crown. No lateral cusplets are present. The root is bilobate and asymmetrical, caused by the distal lobe being shorter than the mesial one. Characteristically, both root lobes have angled extremities. The lingual protuberance is moderately developed, with a nutritive foramen.

Remarks: Fossil teeth of this species are known from Oligocene to Pliocene deposits, and they have been reported from Miocene sediments of the Central Paratethys as well (see REINECKE et al. 2011 and references therein).

Lamnidae indet.

Referred material: 7 teeth.

Description: These teeth are rather poorly preserved crowns, which could belong to both of the Pécs-Danitzpuszta lamnids. The crowns show a triangular outline in labial and lingual view, the crown faces are smooth, and the cutting edges are not serrated.

Remarks: Because of their poor quality, these teeth are not described closer than family rank.

Family Otodontidae GLIKMAN, 1964
Genus *Otodus* AGASSIZ, 1838
Subgenus *Otodus* (*Megaselachus*) GLIKMAN, 1964

Otodus (*Megaselachus*) *megalodon*
(AGASSIZ, 1843)
Plate V

Referred material: 72 teeth.

Description: These massive “megalodon” teeth are the most spectacular among all fish remains of the sands. The crown is broad, triangular, erect, massive, it reaches its maximum thickness at its base. The lingual crown face is strongly convex, while the labial face is usually flat or only slightly convex. The cutting edges are originally strongly serrated, however from some of the Pécs-Danitzpuszta specimens this feature was completely abraded off. The root-crown boundary bears a chevron-shaped band of thinner enameloid on the lingual crown face (= “lingual neck” in BOESSENECKER et al. 2019; also called as “bourlette”). Going backwards distally along the dentition, the height of the teeth decreases, they gradually become wider, with an increasing distal inclination. The root is thick and bifurcate with a massive lingual protuberance. The lobes are usually similar in size, and both have rounded extremities.

Remarks: A strongly pathological tooth is known in a private collection (Plate V, E–H). Based on their size, some teeth are referable to juvenile individuals (Plate V, M–P) (GOTTFRIED et al. 1996, PIMIENTO et al. 2010, SHIMADA 2019).

Family Alopiidae BONAPARTE, 1838
Genus *Alopias* RAFINESQUE, 1810

Alopias exigua (PROBST, 1879)
Plate VI, A–D

Referred material: 2 teeth.

Description: Two lateral teeth were referred here; both are higher than they are wide. The cusp is distally inclined,

the cutting edges are smooth, no lateral cusplets are present. The lingual crown face is strongly convex, while the labial is nearly flat, except for its base, where it continues in calloused enamel shoulders both mesially and distally, overhanging the root. A well-developed lingual protuberance with nutritive grooves is present on both specimens. The root lobes form an arched contour and possess rounded extremities.

Remarks: Fossil teeth of *Alopias* are never common in the Miocene sediments of the Central Paratethys. *A. exigua* ranges from the Early Oligocene to the Middle Miocene (REINECKE & RADWAŃSKI 2015; SZABÓ & KOCSIS 2016b, 2020). This species has previously been reported from only one Badenian locality in Hungary (SZABÓ & KOCSIS 2020).

Genus *Anotodus* LE HON, 1871

Anotodus retroflexus (AGASSIZ, 1843)

Plate VI, E–P

Referred material: 27 teeth.

Description: Medium to large alopiid teeth are typical, relatively common in the studied material. The crown of anteriors (unknown from the Pécs-Danitzpuszta material) is symmetrical and erect, while that of laterals is distally inclined, therefore weakly asymmetrical. In profile view, the crown of all files slightly bends lingually. The cutting edges are smooth, and the crown faces bear no ornamentation. The root is bilobate, and the root lobes are thick and well-separated. The labial crown enamel basally continues on both root lobes as enamel heels. These heels slightly overhang the lobes. The lobes have angled extremities, they meet in a lingual protuberance, bearing a faint nutritive groove, less typical with a large foramen.

Remarks: Genus *Anotodus* was erected by LE HON (1871) and re-classified in Alopiidae by HERMAN (1979). Until recently, the described teeth were widely regarded as *Isurus retroflexus*, as a member of the family Lamnidae, but the species were synonymized and replaced within the Alopiidae (CAPPETTA 2012). KENT (2018) found smaller teeth and anterior teeth of *A. retroflexus* more similar to those of lamnids, and he included the species within Lamnidae as *Isurus retroflexus*.

Order Carcharhiniformes COMPAGNO, 1973

Family Hemigaleidae HASSE, 1879

Genus *Hemipristis* AGASSIZ, 1835

Hemipristis serra AGASSIZ, 1835

Plate VII, A–K

Referred material: 101 teeth.

Description: The species is characterized by clear dognathic heterodonty. Upper teeth – except for the first upper anteriors – have large, labiolingually flattened, triangular, distally inclined crown with strongly serrated cutting edges (Plate VII, A–E). The root of upper files is asymmetrical, high and bilobate, bearing a lingual protuberance. Lower anterior teeth have slender, upright

crown with slightly sigmoid profile view. The cross-section is circular. Lower anterior teeth (Plate VII, I–K) less typically bear a pair of lateral cusplets, which are missing from all Pécs-Danitzpuszta lower anteriors as a result of re-deposition. The cutting edge is smooth, it runs from the apex only to the upper third of the apicobasal height. In lower lateral files the teeth become asymmetrical (the mesial cutting edge becomes longer), the number of lateral cusplets increases (see figs Plate VII, F–H). The roots of all lower files are bilobate, with a well-marked lingual protuberance.

Remarks: Teeth of *H. serra* are characteristic and easy to identify. The species has been widely reported from the Miocene of the Central Paratethys (see SZABÓ & KOCSIS 2016a, table 2).

Family Carcharhinidae JORDAN & EVERMANN, 1896

Genus *Galeocerdo* MÜLLER & HENLE, 1838

Galeocerdo aduncus AGASSIZ, 1835

Plate VII, L–U

Referred material: 163 teeth.

Description: The teeth have a triangular crown bent toward the rear, except for the very anterior teeth, which have a somewhat more erect cusp. The lingual tooth face is convex, while the labial is flat. Both crown faces are smooth. The convex mesial cutting edge bears fine, irregular serrations; however, this feature is worn away in most Pécs-Danitzpuszta teeth. The distal cutting edge is short, straight to slightly convex, finely serrated (all teeth studied here lack this character due to re-working). It continues in a distal enamel shoulder, which has a serration built up by rather large serrations, large enough to be preserved in almost all Pécs-Danitzpuszta teeth. The root is mesiodistally wide, the lingual protuberance is low with a nutritive groove.

Remarks: This species is also widely reported from the Miocene of the Central Paratethys (see SZABÓ & KOCSIS 2016a, table 2). The Pécs-Danitzpuszta material covers all important tooth positions. Teeth of the modern species *G. cuvier* was also reported from late Miocene deposits (e.g. PURDY et al. 2001) but their teeth are rather robust with cutting edges bearing secondary serrations, which is missing from the mesial cutting edge of *G. aduncus* (CIGALA-FULGOSI & MORI 1979). The serration of the Pécs-Danitzpuszta teeth is typically worn, however their size, shape and proportions somewhat differ from teeth of *G. cuvier*.

Genus *Carcharhinus* BLAINVILLE, 1816

Carcharhinus priscus (AGASSIZ, 1843)

Plate VII, V–A'

Referred material: 130 teeth.

Description: Both upper and lower teeth are present in the studied material. Upper jaw dentition includes teeth with triangular crowns. The crown is straight in profile view, upright in anterior files, while distally inclined in lateral and distal teeth. Lower teeth (not illustrated due to their poor pre-

servation) also have an upright crown, more convex faces, and are slightly bent lingually. The root is mesiodistally wide, bilobate, and they meet in a low lingual protuberance with a nutritive groove.

Remarks: This species has widely been reported from the Miocene deposits of Europe, including those of the Central Paratethys (SZABÓ & KOCSIS 2016a, table 2). ANDRIANAVALONA et al. (2015) considered that *C. priscus* may represent a species group rather than a discrete species.

Family Sphyrnidae GILL, 1872
Genus *Sphyrna* RAFINEQUE, 1810

Sphyrna laevis (COPE, 1867)
Plate VII, B'–E'

Referred material: 6 teeth.

Description: Only lateral teeth are known from Pécs-Danitzpuszta. The distally inclined crown has a convex lingual and a flat labial face. Both faces are smooth. The mesial cutting edge is smooth all along; it is straight on its basal half, while slightly convex on the apical half. The distal cutting edge is smooth and short; it continues in a convex and smooth, distal enamel shoulder. The root is mesiodistally wide and bilobate. The lobes have rounded extremities, and they meet in a very low lingual protuberance bearing a large nutritive groove.

Remarks: Hammerhead sharks are relatively uncommon in the middle Miocene sediments of the Central Paratethys (SZABÓ & KOCSIS 2016a, table 2).

Superorder Batomorphii CAPPETTA, 1980
Order Myliobatiformes COMPAGNO, 1973
Family Dasyatidae JORDAN, 1988

Dasyatidae indet.
Plate VIII, A–C

Referred material: 1 tooth.

Description: The only tooth referred here is small and nearly complete; however, it is strongly worn due to re-deposition. The crown is rectangular in occlusal view, and it bears a well-developed but low transversal crest. The crest separates the labial and the lingual visors. This morphology refers the tooth to a female individual. Neither occlusal ornamentation, nor facets on the basal crown surface are visible. The root is bilobate, and a large foramen is situated between the lobes.

Remarks: Various dasyatid species have been reported under the genus *Dasyatis* from the middle Miocene of the Central Paratethys (SZABÓ & KOCSIS 2016a, table 2), but the Pécs-Danitzpuszta material is too worn for a closer identification, therefore we leave it with open nomenclature until further material is unearthed. It must be pointed out that the classification of Dasyatidae has been revised (LAST et al. 2016), and previously described fossil “*Dasyatis*” species might belong to other genera such as *Himantura* or *Maculabatis*.

?Dasyatidae indet.
Plate VIII, D–F

Referred material: 1 tooth.

Description: The crown is low, bearing a lingually arched transversal crest, which separates the labial and lingual faces (or visors). In occlusal view, the crown shows a rounded anterior margin, while the posterior outline is angular. No apron is present. The crown is wider than the root, and the root shows two widely separated lobes. The root lobes are slightly shifted posteriorly. Based on the preserved characteristics, the tooth belongs to a female individual.

Remarks: The only tooth referred here was collected and illustrated by JUHÁSZ (2006, pl. 2, figs 3, 4), who identified it as *Raja* sp. Poorly preserved rajid and dasyatid teeth show similar morphology, therefore the taxonomical assignment of this tooth remains confusing. Nevertheless, it shows more affinity to dasyatids. The specimen was re-housed in the NHMUS collection.

Family Aetobatidae AGASSIZ, 1858
Genus *Aetobatus* BLAINVILLE, 1816

Aetobatus arcuatus (AGASSIZ, 1843)
Plate VIII, G–Q

Referred material: 50 teeth.

Description: Both lower (*Plate VIII, G–L*) and upper teeth (*Plate VIII, M–Q*) were recognized in the Pécs-Danitzpuszta material. Lower teeth are distally arched, they reach their maximal length at their mediolateral midline. The crown is low, it is separated from the root lobes by a lingual bulge. The lingually shifted root is built up by numerous parallel lobes. Upper teeth are fairly rectilinear, except for the lingually bent lateral edges. The root of the upper teeth is less shifted lingually and has about the same height as the crown.

Remarks: *A. arcuatus* is a common eagle ray species in the Miocene marine sediments of Europe (RADWAŃSKI 1965; SZABÓ & KOCSIS 2016a, table 2). Its tooth remains are easily distinguishable from those of other Miocene myliobatiform taxa of Europe.

Family Myliobatidae BONAPARTE, 1838
Genus *Aetomylaeus* GARMAN, 1908

Aetomylaeus sp.
Plate VIII, R–A'

Referred material: 17 teeth.

Description: The dentition of *Aetomylaeus* is similar to that of *Myliobatis* (also present in the limonitic sands), but significant morphological differences can be recognized in the lower dentition. *Aetomylaeus* typically has seven anteroposteriorly running tooth rows: one medial (or central) and three-three lateral ones on both sides (CAPPETTA 2012). Unlike in *Myliobatis*, the medial files of *Aetomylaeus* are arched. The root and the crown of the medial files are thicker medially than laterally, the tooth is oblique in lateral view. The labial side bears a rich ornamentation built up by a dense network of ridges. The slightly lingually directed root is high, at some medial sections it can be higher than the crown.

Remarks: *Aetomylaeus* and *Pteromylaeus* have been traditionally regarded as separate genera (e.g. CAPPETTA 2012). However, systematic analysis by WHITE (2014) suggests that *Pteromylaeus* is a junior synonym of *Aetomylaeus*, and this hypothesis is accepted here. The genus *Aetomylaeus* is known from the middle Miocene, but its appearance in the fossil record could have been much earlier, since their teeth have often been confused with those of *Myliobatis* spp. (CAPPETTA 2012). The genus is very scarce in the middle Miocene of the Central Paratethys (SZABÓ & KOCSIS 2016a, table 2).

Genus *Myliobatis* CUVIER, 1826

Myliobatis sp.
Plate IX, A–T

Referred material: 292 teeth and 3 partial tooth plates.

Description: In the Pécs-Danitzpuszta material *Myliobatis* is represented by tooth plates as well. Currently three, partially preserved tooth plates are known, all have been illustrated (Plate IX, A–L).

The isolated medial (Plate IX, M–Q) and lateral teeth have straight and mediolaterally widened crown, with angled lateral edges. Medial files are mediolaterally wider than laterals (Plate IX, R–T), which are therefore more hexagonal in occlusal view. The root of all files consists of numerous, mediolaterally flattened, parallel lobes.

Remarks: These remains were distinguished from those of *Rhinoptera* (also present in the limonitic sands) by having a relatively lower crown, different root lobe proportions and tooth connection structure. As dental characteristics of *Myliobatis* are conservative over geological time, distinguishing the species only by their isolated teeth is uncertain. For this reason, here we identify these remains only at the genus rank. *Myliobatis* is abundant all over the Miocene marine deposits of Europe, including those of the Central Paratethys (SZABÓ & KOCSIS 2016a, table 2).

Myliobatidae indet.

Referred material: 77 teeth.

Description: Poorly preserved, worn or fragmentary teeth of myliobatid morphology are referred here.

Remarks: Based on the connecting structures of the teeth, they certainly do not represent the family Rhinopteridae. Due to their poor preservation, we do not refer them closer than family rank as multiple myliobatid genera inhabited the area.

Family Rhinopteridae JORDAN & EVERMANN, 1896
Genus *Rhinoptera* CUVIER, 1829

Rhinoptera cf. *schultzi* HIDEN, 1995
Plate IX, U–I'

Referred material: 6 teeth.

Description: The *Rhinoptera* teeth are hexagonal in occlusal view, the occlusal surface is weakly concave. The crown is massive and thick. The root consists of numerous

parallel lobes and is lower apicobasally than the crown. It is also less displaced lingually than those of *Aetomylaeus* and *Myliobatis* (see above).

Remarks: Compared to teeth of *Aetomylaeus* and *Myliobatis*, the root of *Rhinoptera* teeth is not or only slightly shifted lingually (SZABÓ & KOCSIS 2016a). Also, the connection between the teeth is more complex in *Rhinoptera* than in *Aetomylaeus* and *Myliobatis* (so-called „tenon and mortise” connections; BOURDON 2002). Based on these characteristics, the Pécs-Danitzpuszta teeth clearly represent the genus *Rhinoptera*.

Two species, *R. schultzi* and *R. studeri* have been reported from the middle Miocene of the Central Paratethys (SZABÓ & KOCSIS 2016a, table 2). *R. schultzi* differs from *R. studeri* in having smaller teeth, with much thinner crown with smaller width/length ratio, and also in the absence of ornamentation of the labial and lingual faces (HIDEN 1995). The differences between the proportions of the teeth of the two species can be easily observed in lateral view (see HIDEN 1995, text-fig. 11 and SZABÓ et al. 2017, figs 9p, u). Based on the observable characters, the Pécs-Danitzpuszta teeth are more similar to *R. schultzi*. However, because of the quality and low number of the specimens referred here, further teeth are required for a more certain identification.

Myliobatiformes indet.
Plate IX, J'–M'

Referred material: 22 caudal spines.

Description: Myliobatiform caudal spines are also known from the Pécs-Danitzpuszta site. All are incomplete, and they have serrated lateral edges.

Remarks: Since all myliobatiform caudal spines have very similar characters (HOVESTADT & HOVESTADT-EULER 2013), and the Pécs-Danitzpuszta specimens are very fragmentary, a closer identification is impossible.

Chondrichthyes indet.
Plate X

Referred material: 22 vertebral centra, 1 piece of fossilized cartilage.

Description: Although the chondrichthyan centra referred here are incomplete, the preserved portions refer to a circular outline in articular view. Centra of morphotype 1 (Plate X, A–E) are aseptate and short in profile view, giving an overall discoid shape to the centra. No large ventral or dorsal foramina are present. Morphotype 2 (Plate X, F–H) bears large dorsal and/or ventral foramina, however, all specimens referred here are fragmentary.

The only cartilage specimen referred here (Plate X, I, J) is built up by stellate units of cartilage tissue. Chondrichthyans are characterized by the presence of tessellate mineralization of the cartilaginous endoskeleton (MAISEY 2012).

Remarks: Vertebral centra morphologically similar to centrum morphotype 1 were published in LOPES et al. (2016, figs 9.1–2) as ray vertebrae. Centra morphotype 2 are generally similar to those of Carcharhiniformes (see PURDY et al. 2001, fig 52; SZABÓ et al. 2017, figs 8k–n; SZABÓ &

KOCSIS 2020, fig. pl. 10, figs 1–12), but they are too incomplete for a close identification; therefore, they are left with open nomenclature.

Fossilized cartilage is exceptionally rare, and it has only been reported in case of a few specimens from the Oligocene–Miocene of the Central Paratethys (SZABÓ 2019). Cartilage that makes up the chondrichthyan skeleton is easily crushed and dissociated during fossilization (MAISEY 2012).

Class Osteichthyes HUXLEY, 1880
Subclass Actinopterygii KLEIN, 1885
Order Acipenseriformes BERG, 1940
Family Acipenseridae BONAPARTE, 1831

Acipenseridae indet.
Plate XI, A–H

Referred material: 1 indeterminate skull element, 4 dermal scutes, 2 pectoral spines.

Description: The skull element (*Plate XI, A, B*) has an ornamented outer surface, while a distinct descending lamina (*Plate XI, B, dl*) is present on its ventral side. The scutes (*Plate XI, C–F*) exhibits a strong, honeycomb like ornamentation on its outer surface and a nearly smooth inner surface. The lateral surfaces of the fin spine (*Plate XI, G, H*) bear marked longitudinal ridges, and the posterior surface have a deep concavity.

Remarks: Following parsimony, here we assign all Pécs-Danitzpuszta acipenserid remains to a single taxon, until further specimens lead us to a different conclusion. Although the dermal scutes are exceptionally similar to that of *Acipenser sturio* (DESSE-BERSET 2011, fig. 7.4C), the studied material is too incomplete for an identification closer than Acipenseridae indet.

Order Carangiformes JORDAN, 1923
Family Carangidae RAFINESQUE, 1815

Carangidae indet.
Plate XI, I–N

Referred material: 2 dentaries.

Description: The dentaries are incomplete; and the preserved portions refer to a subtriangular outline in lateral view. A large neural foramen opens at the middle of the symphyseal edge on the outer surface of the dentary (*Plate XI, I, L, dnf*). The symphyseal edge is high and angular both dorsally and ventrally. A wide longitudinal groove runs along the lateral side of the bone, starting just behind the symphyseal edge. The mandibular sensory canal opens anteriorly on the lateral surface of the bone, posteriorly to the large neural foramen, and on the lateroventral side of the dentary (*Plate XI, I, L, dmo*). The ventral margin of the dentary bears a notch (*Plate XI, I, L, no*). Labially a row of enlarged teeth runs along the dentary. Lingually, much smaller teeth are arranged in multiple rows.

Remarks: Based on the tooth row morphology, the high and angular symphyseal, and the arrangement of the lateral foramina, the dentaries resemble the most those of extant

carangid genera (see TERCEIRE et al. 2019). However, due to the low number and poor quality of the remains here we identify them only as Carangidae indet.

Order Istiophoriformes BETANCUR-R et al., 2013
Family Sphyraenidae RAFINESQUE, 1815
Genus *Sphyraena* KLEIN, 1778

Sphyraena sp.
Plate XI, O, P

Referred material: 1 tooth.

Description: A single tooth is labiolingually flattened, and has a triangular outline in profile view. The tooth bears faint remains of fine striations, and the tip is missing.

Remarks: As the only tooth referred here is heavily worn and incomplete, a species level identification is impossible. Family Sphyraenidae (barracudas) includes genus *Sphyraena* only (GOTTFRIED et al. 2017). Genus *Sphyraena* has previously been reported from the Miocene of the Central Paratethys (SCHULTZ 2013, SCHULTZ et al. 2010, SZABÓ & KOCSIS 2020). There are 28 extant barracuda species around the world, and all are common predators of tropical and subtropical seas (FROESE & PAULY 2019).

Order Scombriformes RAFINESQUE, 1810
Family Scombridae RAFINESQUE, 1815
Genus *Thunnus* SOUTH, 1845

cf. *Thunnus* sp.
Plate XII, A–O

Referred material: 1 premaxilla, 18 dentaries, 3 vertebrae.

Description: The premaxilla (*Plate XII, A–C*) is slender, slightly curved with a single row of small, closely positioned, circular alveoli. Only the very base of the ascending process (*Plate XII, A, C, asp*) is preserved. The posterior shank of the premaxilla (*Plate XII, A, C, ps*) is long. The bone surface is quite eroded; therefore, no characteristic foramina are observable. The dentaries (*Plate XII, D–I*) bear a thick medioventral plate (*Plate XII, F, I, mvp*). A large neural foramen opens behind the symphyseal edge, above a shallow ventral notch (*Plate XII, D, G, dnf* and *no*). The medial bone surface bears a posteriorly widening groove with numerous foramina (*Plate XII, F, I, gr* and *f*). The abdominal centrum (*Plate XII, J–L*) is characterized by deep fossae separated by a strong median ridge along the lateral sides. The caudal vertebral centrum (*Plate XII, M–O*) has rectangular dorsal, ventral, and lateral outline, caused by its dorsoventral compression. In anterior and posterior views, the caudal vertebra shows a hexagonal outline.

Remarks: At the moment it is unclear whether this morphotype represents a single taxon, but based on the general appearance of the bones we tentatively refer the remains to the same morphogroup until more specimens disprove this. The specimens resemble the most those of *Thunnus* (CARNEVALE & GODFREY 2018, Plate I.16A–E, G, H; PURDY et al. 2001, fig. 76; TERCEIRE et al. 2019); however,

further specimens are required for a more precise identification.

Scombridae indet.
Plate XII, P–A'

Referred material: 1 premaxillary, 158 dentaries.

Description: This scombrid morphogroup represents a rather large taxon. The premaxilla (*Plate XII, P–R*) is massive, and it has a wide ascending process (*Plate XII, P, R, asp*), which is only partially preserved. A major part of the posterior shank is missing. The medial side of the premaxilla bears a large, rounded depression with large foramina in it (*Plate XII, R, d* and *f*). Posteriorly to the base of the articular process a large bulge is visible (*Plate XII, R, b*). The dentaries are of poor quality, only their tooth-bearing portions are preserved. Both the premaxillae and the dentaries bear a series of large, closely spaced alveoli. A few specimens still have some fragmentary, subtriangular teeth preserved in situ.

Remarks: Similarly, to the specimen PTE_5094, premaxillae of extant *Euthynnus*, *Scomber* and *Thunnus* bear a bulge-like structure posteriorly to the base of the ascending process (TERCEIRE et al. 2019). However, the fossils here also resemble those of large sized fossil scombrid taxa *Acanthocybium solandri* (CARNEVALE & GODFREY 2018, Plate I.15A–D; PURDY et al. 2001, fig. 77) and *Pelamycybium partschi* (see SCHULTZ 2013, pl. 71, figs 1, 2). These Pécs-Danitzpuszta scombrid elements are too fragmentary for a more precise identification.

Order Labriformes KAUFMAN & LIEM, 1982
Family Labridae CUVIER, 1817
Genus *Labrodon* GERVAIS, 1857

Labrodon sp.
Plate XIII, A–D

Referred material: 2 pharyngeal tooth plates, 1 isolated tooth.

Description: The two pharyngeal tooth plates have triangular outline in occlusal view. Both specimens comprise multiple layers of phyllodont teeth. The posterior rows include larger, oval teeth, while the more anterior rows include teeth with circular outline. An isolated tooth (not illustrated) has been found with screening. Its basal surface is characteristically ornamented by crenulations.

Remarks: Labrid fishes are widely reported from the middle Miocene of the Central Paratethys (see BELLWOOD et al. 2019, SCHULTZ et al. 2010, SZABÓ 2019, SZABÓ & KOCSIS 2020). Based on the shape and proportions of the teeth and the shape of the tooth plates, the Pécs-Danitzpuszta remains resembles most the *L. pavementation* (see ÁVILA et al. 2020, BETANCORT et al 2016).

Genus *Trigonodon* SISMONDA, 1847

Trigonodon jugleri (MÜNSTER, 1846)
Plate XIII, E–H

Referred material: 1 tooth.

Description: A single incomplete tooth is referred here. The specimen is of incisiform morphology; therefore, it belongs to the anterior section of the jaw apparatus.

Remarks: *Diplodus jomnitanus*, a fossil sparid widespread in the Miocene of Europe also has large incisiform teeth, but these are rectangular and more symmetrical in labial view, unlike those of *T. jugleri*, which are mesio-distally much wider, asymmetrical and have a trapezoid to almost triangular outline. *T. jugleri* is widely reported from the middle Miocene of the Central Paratethys, and its oldest fossils are from the early Miocene of Italy and Austria (SCHULTZ & BELLWOOD 2004, SZABÓ & KOCSIS 2020).

Family Scaridae RAFINESQUE, 1810
Genus *Calotomus* GILBERT, 1890

Calotomus sp.
Plate XIII, I, J

Referred material: 1 pharyngeal tooth plate.

Description: The tooth plate is composed of three parallel, anteroposteriorly running rows of small, ovoid to sub-rectangular teeth. The specimen is sitting in a piece of coprolite.

Remarks: Upper pharyngeal bones with 1-3 rows of teeth are a unique character found only in the family Scaridae (BELLWOOD & SCHULTZ 1991). *Calotomus priesli*, a species described from the middle Miocene of Austria (BELLWOOD & SCHULTZ 1991) is the only representative of the genus from the middle Miocene of Europe. As this species has been described from an articulated head region of an individual, it is uncertain if the Pécs-Danitzpuszta fossil represents the same species. Therefore, we describe it as *Calotomus* sp. until further specimens provide more taxonomical details.

Order Perciformes BLEEKER, 1859
Family Latidae JORDAN, 1888
Genus *Lates* CUVIER & VALENCIENNES, 1828

Lates sp.
Plate XIV, A–N and Plate XV A–L

Referred material: 11 vomers, 57 parasphenoids, 51 quadrates, 247 premaxillae, 7 maxillae, 446 dentaries, 80 fragmentary upper or lower jaw elements, 34 angulo-articulars, 776 vertebrae, 114 fin spines.

Description: Vomers (*Plate XIV, A, B*) are stocky, and they have a rounded anterior margin in ventral view. The vomer bears a perfectly fused tooth patch (*Plate XIV, B, tp*) in all latid species. The vomer distally connects to the mesethmoid and the parasphenoid. The parasphenoid (*Plate XIII, C–E*) is an elongated bone element, ranging along the ventral side of the neurocranium. Parasphenoids referred here have a ventral border slightly curved in lateral view. In transverse section, their ventral face is slightly concave. A well-developed median crest (*Plate XIV, C, mc*) is present along the ventral surface, between the orbits. The basioccipital (*Plate XIV, F*) bears a median ventral groove

(Plate XIV, F, *mvg*), which does not reach the parasphenoid (characteristic for all known extant and extinct species of *Lates*). The most complete quadrates (Plate XIV, G–J) are nearly as long as they are high. The articular condyle (Plate XIV, G–J, *ac*) and the base of the posterior border are wide compared to the rest of the bone. Latid premaxillae (Plate XIV, K–N) are characterized by a long ascending process (Plate XIV, M, N, *asp*), which are incomplete or missing in all Pécs-Danitzpuszta specimens. The articular process is large and globular (Plate XIV, K–N, *ap*). The anterior margin of the articular process bears a massive, dorsoventrally running pad (Plate XIV, K, M, *p*). A large foramen for venous vessels and the maxillary nerve branch opens at the base of the articular process (Plate XIV, K, M, *fvm*). Unfortunately, all Pécs-Danitzpuszta latid premaxillae lack the posterior process. A very low longitudinal groove develops along the alveolar process (Plate XIV, K, *lg*); it starts anteriorly just below the articular process. The tooth plate develops along the ventromedial surface of the alveolar process (Plate XIV, L, N, *tp*). The maxilla of latids has a large posterior dorsal plate, but this part of the bone is missing in all Pécs-Danitzpuszta specimens (Plate XV, A, B). The shape of the articular head is intraspecifically variable in extant forms. The premaxillary internal process is medioventrally directed (Plate XV, A, B, *ip*). The adductor mandibulae I surface (Plate XV, A, *ams*) is situated posteriorly of the extended lateral plate (Plate XV, A, B, *lp*). The internal process and the lateral plate are separated by a deep groove (Plate XV, B, *g*). The dentary (Plate XV, C–E) bears a medioventral plate and a large lateral groove (Plate XV, C–E, *mvp* and *lg*). The upper foramen of the dentary is situated anteriorly to the lateral groove (Plate XV, C, E, *uf*). A large neural foramen opens near the middle of the symphyseal edge on the outer surface of the dentary (Plate XV, C, E, *nf*). The mandibular sensory canal runs in a bony tube ventrally bordered by the medioventral plate, it opens anteriorly on the lateral surface of the bone, posteriorly to the large neural foramen, and on the lateroventral side of the dentary (Plate XV, C, E, *mo*). The ventral margin of the dentary bears a notch posterior to the symphysis (Plate XV, D, E, *no*). Angulo-articulars (Plate XV, F, G) have a wide and deep glenoid cavity (Plate XV, F, G, *gc*). The mandibular sensory canal runs in a bony tube with a posterior opening (Plate XV, F, G, *pmo*) in a groove below the glenoid cavity on the lateral side of the bone. Vertebrae (Plate XV, J–H) have striated bone surface with enlarged lateral fossae. The anteriormost vertebral centra are higher than they are long. These proportion turns to the opposite caudally. The anterior abdominal vertebrae have a large and deep primary lateral fossa (Plate XV, I, H, *plf*). Postabdominal vertebrae have a lower and an upper (or dorsal) lateral fossa (Plate XV, J, *llf* and *ulf*), which are separated by a bundle of striated bone. All Pécs-Danitzpuszta specimen lack the neural spine, and only their bases are preserved in some caudal vertebrae. Median fin spines (Plate XV, K, L), similar to those of generalized perciforms are here assigned to the genus *Lates*.

Remarks: Remains of *Lates* sp. are frequent osteichthyan

elements of the Pécs-Danitzpuszta sand pit. Altogether, this is the anatomically best known Pécs-Danitzpuszta osteichthyan.

Fossils of *Lates* are relatively common in the Cenozoic of the old world. They are known from Italy, Portugal, Austria, Moldavia, Croatia, Israel, Oman, Saudi-Arabia and various localities in Africa (CARNEVALE & LANDINI 2001). The oldest representative is from the Oligocene. The genus started its diversification during the Miocene. Most finds are isolated, and their identification is often problematic at specific level (GAGNAISON & COSSARD 2013, MURRAY et al. 2018, OTERO & GAYET 2001). Here we leave the Pécs-Danitzpuszta material undetermined.

Order Acanthuriformes JORDAN, 1923
Family Sciaenidae CUVIER, 1829

Sciaenidae indet.
Plate XV, M–R

Referred material: 61 premaxillae.

Description: The premaxillae are labiolingually curved, they bear a flattened, elongated ascending process (Plate XV, M, O, *asp*) and an oblong, well-developed articular process (Plate XV, M, O, P, R, *ap*). The two processes are incomplete in all investigated Pécs-Danitzpuszta premaxillae. Large foramina open at the base of the articular process (Plate XV, M, P, *f*). The labialmost tooth row consists of enlarged teeth. Lingually to this row, smaller teeth are arranged in multiple rows.

Remarks: The closely spaced labial teeth are similar to those of *Sciaenops* (PURDY et al. 2001). Among all extant genera, based on the labiolingual curvature of the premaxillae and the arrangement and proportions of tooth rows, the Pécs-Danitzpuszta sciaenid material resembles most the *Sciaena* (TERCEIRE et al. 2019). Due to the low number of the specimens referred here we identify them only as Sciaenidae indet., until more specimens provide further information.

Order Spariformes BLEEKER, 1860
Family Sparidae BONAPARTE, 1832
Genus *Diplodus* RAFINESQUE, 1810

Diplodus sp.
Plate XVI, A, B

Referred material: 27 teeth.

Description: The teeth referred here are labiolingually flattened and show a rectangular labial (and lingual) outline. The labial face is convex, while the lingual is concave. Both faces are entirely smooth, and they lack any surface ornamentation.

Remarks: Teeth of the genus are very common in the fossil record of the Central Paratethys (SCHULTZ 2013, SZABÓ & KOCSIS 2020). BENE (2003) assigned 43 molariform crushing teeth to this genus. However, if multiple sparid taxa are present at the same fossil site, it is uncertain if this tooth morphotype of sparids can be referred to a genera. The original report of BENE (2003) does not

include scale bars and the location of the material is currently unknown. Until further material is discovered, here we refer only 24 of the reported incisiform teeth to *Diplodus*.

Genus *Pagrus* CUVIER, 1816

Pagrus cinctus (AGASSIZ, 1839)
Plate XVI, C–K

Referred material: 6 premaxillae, 1 dentary.

Description: The ascending process is missing in all examined Pécs-Danitzpuszta premaxillae (Plate XVI, C–H). In a private collection specimen, only the base of the articular process is preserved (Plate XVI, D, ap). On the medial side of the bone, a large foramen opens at the base of the articular process (Plate XVI, D, F, f). The posterior process (Plate XVI, C, E, G, pp) is low and wide, and it bears well-developed longitudinal striation. Multiple rows of circular tooth positions are running anteroposteriorly. All premaxillae have non-functional teeth preserved inside the bony base. The dentary (Plate XVI, I–K) is incomplete, and it bears massive hemisphaerical teeth of molariform morphology.

Remarks: This species is among the most widely reported osteichthyans of the Miocene sediments of Europe (SCHULTZ 2013, SZABÓ & KOCSIS 2020). Well-preserved premaxillae and dentaries of *P. cinctus* have been illustrated by SCHULTZ (2013, pl. 67, figs 9, 10).

Genus *Sparus* LINNAEUS, 1758

Sparus umbonatus (MÜNSTER, 1846)
Plate XVI, L–U

Referred material: 30 premaxillae, 1 dentary, 15 incomplete upper or lower jaw elements, 16455 isolated teeth.

Description: The premaxillae (Plate XVI, L–O) are shorter and stockier than those of *P. cinctus* (see above). The posterior process (Plate XVI, M, P, pp) is much higher, and bears striation. Only the base of the articular process (Plate XVI, L, N, ap) is preserved in some specimens. Most of the premaxillae have only empty tooth positions, but some have *in situ* the enlarged, posterior molariform tooth preserved (Plate XVI, N, pmt). The dentary (Plate XVI, P–R) is incomplete, massive and stocky. The coronoid process (Plate XVI, P, cp) is high. An enlarged, massive molariform posterior tooth (Plate XVI, Q, R, mtd) is visible, matching that observable in the premaxillae.

Remarks: This fish species was collected in the highest number in the Pécs-Danitzpuszta sand pit. Its isolated, enlarged molariform teeth were found in extremely high numbers. A large percent of them bears signs of functional wear (see BENE 2003), which together with the high number of these teeth, indicates that these teeth regularly dropped out and re-grew. SCHULTZ (2013, pl. 68, fig. 1) illustrated a well-preserved premaxilla of *S. umbonatus*.

Sparidae indet.

Referred material: 569 teeth, 1 upper or lower jaw element in coprolite.

Description: Isolated teeth of sparid morphology – conical anterior and hemisphaerical posterior teeth – are referred here.

Remarks: As isolated teeth of fossil sparids are very similar, in the presence of more than one sparid genera their generic identification is uncertain (except for the enlarged oval crushing teeth of *S. umbonatus*, see above).

Order Tetraodontiformes BERG, 1955

Tetraodontiformes indet.
Plate XVI, V–Z

Referred material: 4 tooth plates.

Description: The tooth plates referred here have subtriangular outline in occlusal view. They are built up of overlapping sheets of teeth that are fused together. The enamel surface is richly crenulated (Plate XVI, W). The size of the tooth-sheets decreases upwards.

Remarks: The order Tetraodontiformes includes numerous extant and fossil families. Several tetraodontiform taxa have been reported from the Miocene of Europe (SCHULTZ 2006, 2013), however, their synonymy remains problematic (see synonym lists in SCHULTZ 2013). More complete dental remains are needed for a definite identification.

Actinopterygii indet.
Plate XVII, A–L

Referred material: 31 hyperostotic ribs, 34 hyperostotic vertebrae, 30 indeterminate fragmentary bone elements, 1 dentary, 1 ?angulo-articular, 11 vertebrae, 1 skull element, 1 gill-arch element, 227 fin spines.

Description: Elongated droplet-shaped bones (Plate XVII, A–H) and massive, stocky vertebrae (Plate XVII, I–L), showing the signs of hyperostosis, are referred here. A very high number of poorly preserved fragmentary fish bones are also included here.

Remarks: Hyperostotic bones (or swollen bones) are the result of hyperostosis, indicating an abnormally high amount of primary bone deposition (FRANCILLON-VIEILLOT et al. 1990, CHANET 2018). Such structures have been observed in 38 different teleost genera, but they are more frequent in trichiurid, carangid and sciaenid taxa (SMITH-VANIZ et al. 1995). As bone characteristics of the specimens referred here are unclear, and both Carangidae and Sciaenidae are recognized in the Pécs-Danitzpuszta fish material, here we refer these remains only as hyperostotic bones of indeterminate actinopterygians. Fossil hyperostotic bones of *Caranx caranopsis*, which are morphologically very similar to the Pécs-Danitzpuszta specimens have been illustrated by SCHULTZ (2013, pl. 67, figs 13–15).

The large numbers of fragmentary actinopterygian bones with no taxonomical characteristics are not identifiable at lower taxonomical ranks.

