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Fossils from the Upper Miocene (Pannonian) sands of the Pécsvárad sand pit (Eastern Mecsek Mts., SW Hungary)

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Abstract. The Mecsek Mountains in SW Hungary represent an uplifted basement block of the Pannonian Basin. Their Neogene cover includes deposits both from the Middle Miocene Central Paratethys and from its Late Miocene (Pannonian) brackish-water descendant, Lake Pannon. Along the mountain front, the Pannonian sands of the Pécsvárad sand pit contain a mixed vertebrate fossil assemblage, which gives insight into terrestrial and aquatic biota during various time intervals of the Miocene.

The fossil-bearing sands accumulated between 7.6–6.8 Ma, in a high-energy littoral setting of Lake Pannon, as indicated by the mollusc remains. The vertebrate fossil assemblage is relatively diverse compared to the number of finds. The most abundant group, aquatic mammals, encompasses a minimum of four odontocete species and a few mysticete taxa, which originally lived in the Paratethys during the Badenian and the Sarmatian. Rhinocerotid remains are reworked from sediments aged somewhere between the Karpatian and earliest Pannonian. The single shark tooth must be Badenian, and the scombrid fishes probably also date back to that age. Fossils of other fishes (sparids, latids and acipenserids), giant salamanders, turtles, crocodilians and cervids might originate from older Miocene deposits but can be coeval with the host sands as well. Tapirs and giraffids must have lived on the lakeshores of Lake Pannon, probably contemporaneously with sand deposition or not much earlier. The erosion, enrichment and mixing of the fauna is a result of the uplift and denudation of the Mecsek Mountains during Lake Pannon sedimentation, caused by neotectonic basin inversion. This example shows that in spite of the uncertainties in the dating of some fossils, mixed faunas can provide important data on the evolution history of an area.

Key words:
Lake Pannon,
Central Paratethys, Mecsek Mountains, mixed assemblage, basin inversion

Апстракт. Планине Mecsek у ЈЗ Мађарској представљају издигнути подински блок Панонског басена. Њихов неогенски покривач обухвата наслаге како из средњомиоценског Централног Паратетиса, тако и из

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касномиоценског (панонског) бочатног језера Панон. Дуж планинског фронта, панонски песак Pécsvárad пешчаре садржи мешовиту фосилну заједницу кичмењака, која даје увид у копнене и водене животињске врсте током различитих временских интервала миоцена.
Фосилоносни песак акумулиран је пре 7,6–6,8 милиона година, у високоенергетском литоралном окружењу Панонског језера, на шта указују остаци мекушаца. Фосилна заједница кичмењака је релативно разнолика у поређењу са бројем пронађених фосила. Најраспрострањенија група водених сисара, обухвата најмање четири врсте одонтоцета и неколико таксона мистицета, који су првобитно живели у Паратетису током бадена и сармата. Остаци носорога су преталожени из седимената карпатске и најраније панонске старости. Један зуб ајкуле је сигурне баденске старости, а рибе из фамилије скуша такође, вероватно датирају из тог периода. Фосили других риба (спарида, латида и аципенсерида), џиновских даждевњака, корњача, крокодила и јелена могу потицати из старијих миоценских наслага, али могу бити и синхрони са песковитим наслагама. Тапири и жирафе су сигурно живели на обалама Панонског језера, вероватно истовремено кад су и таложене наслаге песка, али не много раније. Ерозија, приношење и мешање фауне резултат је издизања и денудационих процеса на планинама Mecsek током седиментационих процеса у Панонском језеру, изазваних неотектонском инверзијом басена. Овај пример показује да упркос несигурности у одредби старости неких фосила, мешовита фауна може пружити важне податке о еволуцији неког подручја.

Кључне речи:
Панонско језеро, Централни Паратетис, планине Mecsek, мешовита фосилна заједница, инверзија басена

Introduction

The Mecsek Mountains in SW Hungary represent an uplifted basement block of the Pannonian Basin, built up of upper Paleozoic and Mesozoic rocks. Their Neogene cover includes deposits both from the Middle Miocene Central Paratethys and from its Late Miocene brackish-water descendant, Lake Pannon. Upper Miocene (Pannonian in the Central Paratethys regional stratigraphy) limonitic sands are typical marginal deposits of Lake Pannon and occur all along the margin of the mountains. At some localities, like Pécs-Danitzpuszta (Sebe et al., 2021a) or Himesháza (Budai et al., 2019), they contain a mixed vertebrate assemblage, produced by the erosion of fossils from various older Miocene units and their redeposition together with the Late Miocene fauna. A common feature of these exposures is that coastal processes of Lake Pannon winnowed the reworked material of older Miocene sediments and enriched the fossil content (Szabó et al., 2021; Botfalvai et al., 2023); it is thus possible to obtain more fossils from various time intervals of the Miocene at these sites than by investigating the in situ Lower or Middle Miocene sediments. The sand pit of Pécsvárad is one of these localities, with a not especially abundant but relatively diverse vertebrate assemblage, collected mostly recently. Here we give a brief presentation and evaluation of the Pécsvárad fauna.

Study area

The active sand pit, traditionally called „marketplace sand pit" [46°08'23.2"N 18°24'05.4"E], lies SW of the town Pécsvárad, at the SE margin of the Mecsek Mts. (Fig. 1). It covers an area of ~300×400 m with a depth of ~35 m. It exploits feldspar-bearing sands for industrial utilization, e.g. to produce fine ceramics.

The exposed sand is brownish yellow, limonitic, dominantly medium to coarse-grained, with pebbles. It is ~60 m thick as indicated by boreholes (Klespitz, 2009). At the lowest level of the sand pit, the sand is cemented by carbonate into irregular sandstone bodies. Gravel in the sand occurs scattered or as gravel seams. Clast material is quartz, chert, limestone and marl, originating from the Jurassic and Miocene

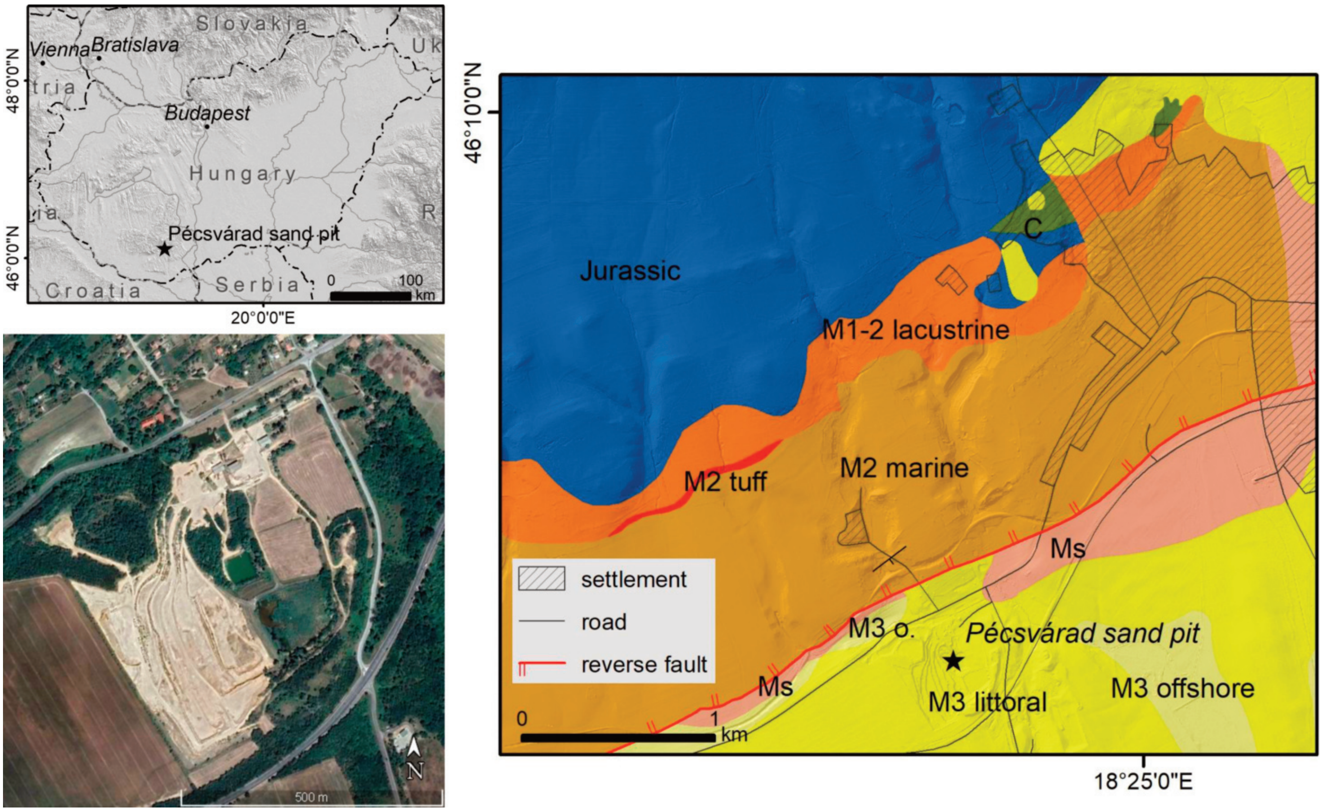


Fig. 1. Location of the Pécsvárad sand pit. Geological map modified from Hetényi *et al. (1982). Satellite image from GoogleEarth, taken on 23.06.2021.*

rocks of the immediate background, but also sand, silt and limonitic concretions produced by the reworking of Pannonian sediments. According to the studies of Kleb (1973), the source of the coarse sand is Carboniferous granite and to some extent Miocene sediments (Lower Miocene Szászvár Fm. and Lower–Middle Miocene Budafa Fm.) based on the high feldspar content and the heavy mineral assemblage. Limonite typically follows the (hardly identifiable) bedding, except for the upper southern part of the sand pit, where limonitic bands crosscut layering and dip to the north. Though lignite seams and blocks were reported from the sand pit (Kleb, 1973), field observations showed that the brownish bands and spots are caused by limonite and not by lignite. While the boundary of the sands with the underlying offshore calcareous marls is roughly horizontal (Klespitz, 2009), bedding dip in the sands ranges from a few degrees up to 20° to the SE (Fig. 2). The coarse grain size and the dip angles of the sand refer to a high-energy, littoral depositional environment. Because of its local origin, the succession is stratigraphically classified into the Kálla Member of the Békés Fm.

Fig. 2. Coarse sands in the SW wall of the Pécsvárad sand pit.

The limonitic sands are overlain by 2 m of fine- to medium-grained, grey-brown sands, with coarse sand and gravel interbeds, containing reworked *Lymnocardium* fossils as well. Its varied sedimentary features – cross-bedding, cross-lamination, channel fills – still refer to littoral conditions. After an unconformity, the succession is draped by Quaternary alluvial gravel, loess and reddish paleosol.

The roughly horizontal boundary of the sands with the underlying calcareous marls indicates that most of the sand body has not experienced significant tectonic tilting, and therefore the bedding dips observed in the sands are primary bedding orientations. Tectonic features, namely reverse faults probably with a horizontal component and related folds, have only been observed in the northernmost part of the sand pit (Konrád & Sebe, 2010) and can be linked to the activity of the boundary fault of the mountains.

The sands contain abundant mollusc fossils, mostly imprints. In his work on molluscs, Sümeghy (1939) mentioned Pécsvárad but did not provide a faunal list for the locality, only a summarised one for the entire southern foreland of the Mecsek Mts. The comprehensive book of Kleb (1973) and the thesis work of Szöllősy (1994) reported the mollusc fauna of the sands, the latter also from the continuation of the sand pit on the opposite, southern side of the main road number 6. They inferred a littoral sedimentary environment and a late Pannonian age from the molluscs.

Although it has long been known that from time to time vertebrate fossils are revealed at the sand pit, so far no systematic collecting activity has been carried out targeting this group. The majority of sporadic vertebrate finds deposited in museums or owned by private collectors have not been classified taxonomically yet. Consequently, the fossil fauna of the locality is poorly known. According to Kazár (2003), reworked fossils of marine vertebrates, predominantly shark and bony fish teeth, had been found in the sand pit.

This paper aims to provide an overview of the fauna found in the sand pit in order to create a basis for possible later detailed studies. For this reason, we do not provide a systematic palaeontological section. The fossils are compared to relevant species or groups already reported from the Mecsek region or – if the latter is absent – from the Central Paratethys basin.

Methods

In the field, fossils were collected during several visits to the sand pit. We paid special attention to the >4 mm sized residue left after industrial sieving of the sands. Besides looking for vertebrate remains, molluscs were targets of the collecting campaigns as well. In the next phase, we surveyed the fossils stored at museums (Janus Pannonius Museum, Pécs (JPM); József Attila City Library and Museum Collection, Komló; Hungarian Natural History Museum (HNHM), Budapest; and Supervisory Authority of Regulatory Affairs (SARA), Geological Directorate, Budapest) and in private collections. Unfortunately, some items in the inventory of the JPM seem to have been lost, probably during the renovation and relocation of the museum in 2023, so these were unavailable for study. Private collectors who provided fossils for investigation were Mihály Pasin, an employee of the KŐKA Kő-és Kavicsbányászati Kft. operating the Pécsvárad sand pit, and László Kanizsai, Károly Kübler and Arnold Kübler from Komló. Máté Gregorits (University of Szeged) offered his collection for study and inclusion in a museum collection. This was deposited together with the fossils collected as part of this project at the Hungarian Natural History Museum in Budapest. The inventory numbers of the specimens discussed in the manuscript are given together with the description of the specimen. The newly inventoried but here not presented material of the locality is the following: INV 2024.1. to INV 2024.7: Late Miocene molluscs; HNHM VER 2024.185: Testudines indet. plastron fragment; HNHM VER 2024.186: Testudines indet. shell fragment; HNHM VER 2024.187: Testudines indet. ?humerus fragment.

The fossil assemblage

Except for the Upper Miocene molluscs, other fossils occur sporadically. Vertebrate remains are disarticulated, often worn and/or broken due to redeposition. Compared to the number of finds, the vertebrate fauna is relatively diverse and includes both aquatic and terrestrial vertebrates. Here we present the important representatives of the fossil assemblage.

Invertebrates

Late Miocene molluscs

The limonitic sands contain abundant mollusc fossils that are coeval with the sands. They often occur as shell beds, but also as in situ specimens (Fig. 3). The aragonitic shell material was completely dissolved, and only moulds and imprints were preserved.

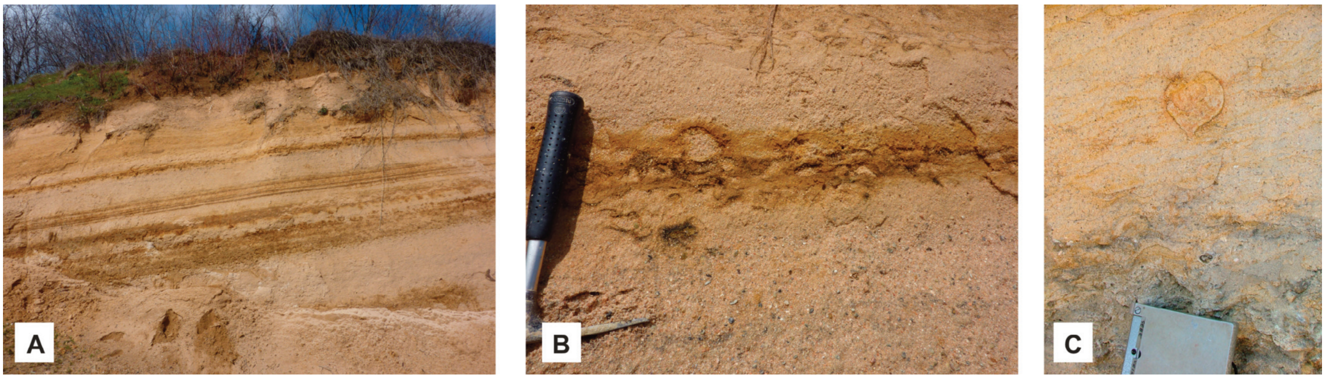


Fig. 3. *Molluscs in the coarse sand, as shell beds **(A–B)** and preserved in situ (**C**; Lymnocardium schmidti).*

János Böckh first collected fossils in the Pécsvárad sandpit in 1874 and identified two dreissenid species, *Congeria partschi* and *C. triangularis* (Böckh, 1876). His specimens, reposited in the paleontological collection of the Royal Hungarian Geological Institute, are still available for study at SARA. His "*C. partschi*" moulds (# Pl.4213) can be determined as *Congeria* sp., whereas his "*C. triangularis*" specimens (#Pl.4212) as *C.* cf. *triangularis* and *C.* cf. *ungulacaprae*.

Kleb (1973, p. 800) listed 7 species from Pécsvárad: *Congeria balatonica*, C. *rhomboidea*, *C. triangularis*, *C. ungulacaprae*, *C. sharpei*, *Lymnocardium schmidti* and *L. haueri*, but only *C. ungulacaprae*, *C. balatonica* and *L. schmidti* were documented with illustrations.

Szöllősy (1994) identified 5 species: *Dreissena auricularis*, *Congeria balatonica*, *C. croatica*, *Lymnocardium schmidti* and *L. dumicici*. Of these forms, *C. balatonica* and *L. dumicici* were documented with photographs (although the diagnostic features of the species cannot be observed in the pictures).

In 2014 and 2018, we collected the following species: *Dreissena auricularis* (Fig. 4e), *Congeria balatonica* (Fig. 4d), *C.* cf. *ungulacaprae*, *Lymnocardium schmidti* (Fig. 4c), *L. hungaricum* (Fig. 4a, b), „*Pontalmyra*" *budmani* (Fig. 4f, g), *Pseudocatillus simplex* (Fuchs), various unidentifiable Lymnocardiinae species and *Zagrabica* sp.

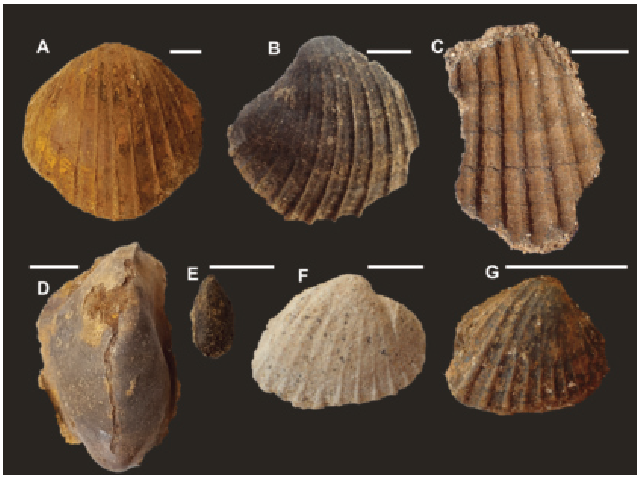


Fig. 4. *Lake Pannon cockles and dreissenids from the Pécsvárad sandpit. **A, B:** L. hungaricum (Hörnes); **C:** Lymnocardium schmidti (Hörnes); **D:** Congeria balatonica Partsch; **E:** Dreissena auricularis (Fuchs); **F, G:** „Pontalmyra" budmani (Brusina). Scale bars: 1 cm*

Other invertebrates

The sands contain invertebrate fossils that are obviously older and reworked. Heavily worn belemnite rostra as well as crionid ossicles and stem fragments originate from the Jurassic sediments.

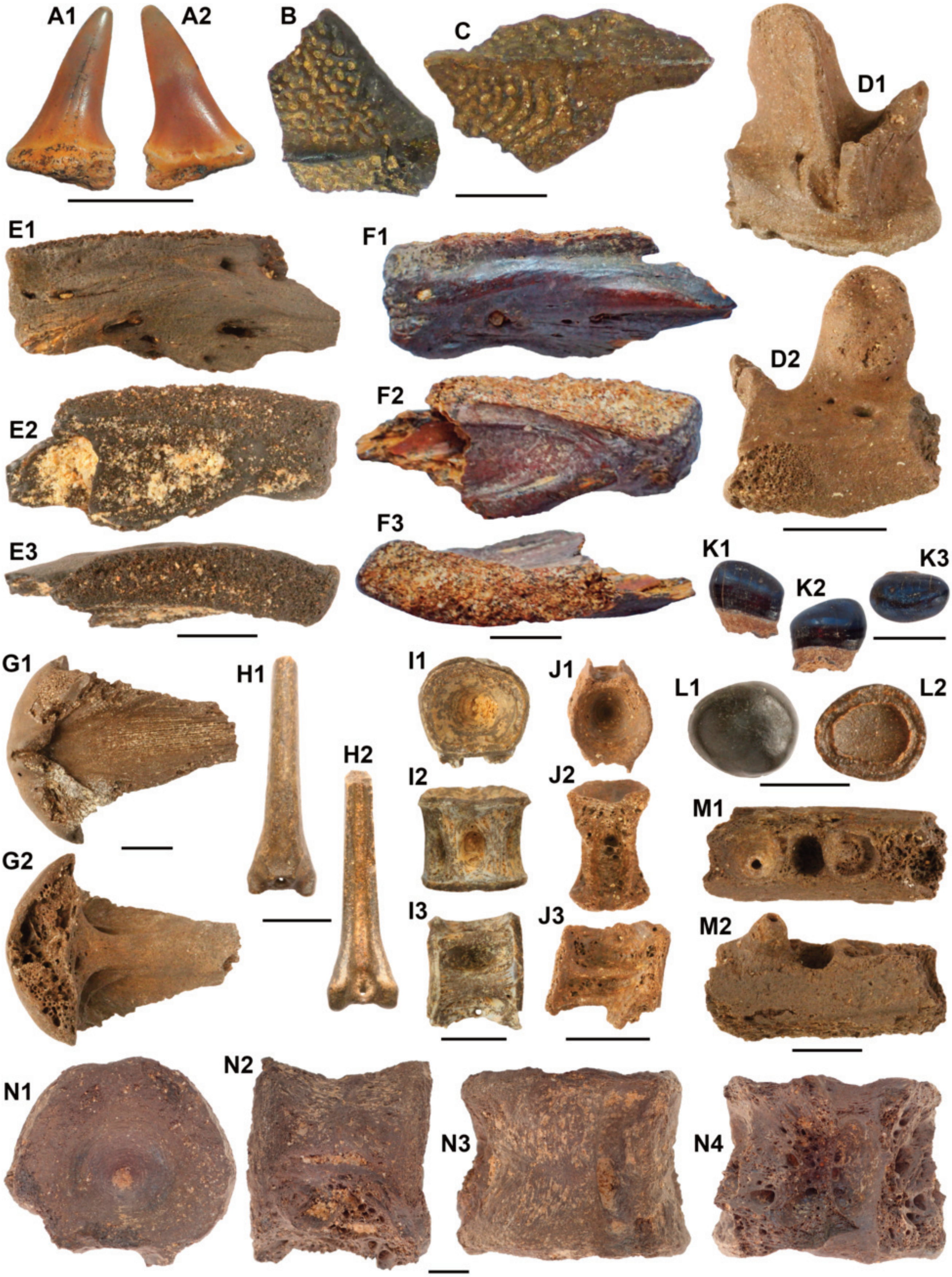
Fishes

The unearthed Pécsvárad fish fauna is composed of both chondrichthyans and osteichthyans. The only Pécsvárad shark tooth is worn and fragmentary (SARA collection, V 2024.8.1; Fig. 5 A). The branches of the root (with possible cusplets) are missing. The crown is slender, pointed, and labiolingually flattened. Both the labial and the lingual face are smooth, striations are absent (however, this could be in connection with the wear of the tooth). The cutting edges show no signs of serrations. The crown is labiolingually straight, while slightly bending distally. These features indicate that the specimen represents an upper lateral tooth of an odontaspid shark.

Characteristic scutes housed in private (Fig. 5 B, C) and museum collections (HNHM VER 2024.167., not figured) are referred to Acipenseridae. Among acipenseriform fishes, members of the family Acipenseridae typically possess longitudinal rows of scutes (arranged in dorsal, lateral and ventral rows), variable in size and shape. On their outer surface, these bony plates exhibit intricate ornamentation characterized by irregular, honeycomb-like patterns, with circular units that vary in shape, size, and positioning relative to each other. A distinct ridge runs anteroposteriorly along the exposed surface. The outer surface is angularly convex, while the inner side is usually concave, therefore scutes are triangular to V-shaped in cross-section. Otherwise, the inner face is smooth. Both lateral scutes (Fig. 5 B) and free dorsal scutes (Fig. 5 C) are identified in the Pécsvárad fish material (see Hilton et al., 2011, figs 98–103).

The genus *Lates* is represented by premaxillae, dentaries, one vomer, fin spines and vertebral centra, housed in museum (HNHM VER 2024.170.-175.) and private collections. Latid premaxillae (Fig. 5 D) have a long ascending process (incomplete or missing in all Pécsvárad specimens). These bone elements bear a large and globular articular process with a large foramen situated at its lateral base. The tooth plate develops along the ventromedial surface of the premaxillary. The dentaries (Fig. 5 E, F) are similar to that of the extant species *Lates niloticus* (see Otero, 2004, figs. 23 and 24). They have several sensory canal pores preserved on the lateral surface, arranged similarly to those of the aforementioned species. A well-defined groove runs anteroposteriorly along the lateral surface. The upper (superior) foramen of the dentaries is situated in this groove. A ventral notch is visible in the lateral (and medial) view. The medio-ventral side of the dentaries is made up of a ventral plate, characteristic of latid fishes. The main dentary sensory canal runs in a bony tube in this plate (Otero, 2004). The only Pécsvárad latid vomer is large and well-preserved (Fig. 5 G). It has a rounded anterior margin, and it bears a fused, arched tooth patch. Following parsimony, large median fin spines with a generalized perciform morphology are hereby referred to *Lates* (Fig. 5 H). The anterior abdominal vertebral centra of *Lates* (Fig. 5 I) have large and deep primary lateral fossa. Postabdominal vertebral centra (Fig. 5 J) of *Lates* have a large lower and an upper lateral fossa, separated by a massive bone ridge.

Fig. 5. *Fish fossils from the Pécsvárad sand pit.* ***A)*** *Odontaspididae indet. shark tooth (SARA, V 2024.8.1);* ***A1:*** *labial view;* ***A2:*** *lingual view.* ***B, C)*** *Acipenseridae indet. scutes, in dorsal view (Kübler coll.).* ***D)*** *Lates* sp. *premaxilla (HNHM VER 2024.172.);* ***D1:*** *lateral view;* ***D2:*** *medial view.* ***E, F)*** *Lates* sp. *dentaries (**E:** HNHM VER 2024.171.; **F:** JPM 57.109.142.;* ***E1, F1:*** *lateral view;* ***E2, F2:*** *medial view;* ***E3, F3:*** *dorsal view.* ***G)*** *Lates* sp. *vomer (HNHM VER 2024.173.);* ***G1:*** *dorsal view;* ***G2:*** *ventral view.* ***H)*** *Lates* sp.*, median fin spine (HNHM VER 2024.174.);* ***H1:*** *anterior view;* ***H2:*** *posterior view.* ***I, J)*** *Lates* sp.*, vertebral centra (HNHM VER 2024.175.);* ***I1, J1:*** *articular view;* ***I2, J2:*** *ventral view;* ***I3, J:*** *lateral view.* ***K)*** *?Sparidae indet. incisiform tooth (HNHM VER 2024.168.);* ***K1:*** *lingual view;* ***K2:*** *labial view;* ***K3:*** *occlusal view.* ***L)*** *Sparidae indet. molariform tooth (HNHM VER 2024.169.);* ***L1:*** *occlusal view;* ***L2:*** *basal view.* ***M)*** *Scombridae indet. dentary (HNHM VER 2024.176.);* ***M1:*** *dorsal view;* ***M2:*** *medial view.* ***N)*** *Scombridae indet. vertebral centrum (HNHM VER 2024.179.);* ***N1:*** *articular view;* ***N2:*** *lateral view;* ***N3:*** *ventral view;* ***N3****: dorsal view. Scale bars: 1 cm*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Numerous incisiform (Fig. 5 K) and molariform teeth (Fig. 5 L) are attributed to sparid fishes (HNHM VER 2024.168.-169. and private collections). The incisiform teeth are thick, massive, and labiolingually weakly compressed. They have a trapezoid outline in labial and lingual views. The molariform teeth possess a thick layer of shiny enamel. Only their crown is preserved, while their root is missing. The teeth are rounded to slightly oval in apical and basal views. All specimens show a strongly concave basal surface, the thickness of the enamel is also visible in this view. As the overall condition of these remains is poor, and tooth morphologies of different sparid taxa are often very similar, here we identify these remains only at the family level.

Scombridae fishes are represented by dentaries and vertebral centra (HNHM VER 2024.176.-179.). The dentaries (Fig. 5 M) are massive, labiolingually thick with a triangular cross-section outline. They possess circular empty tooth positions in dorsal view, if teeth are preserved, they are simple and conical. The vertebral centra (Fig. 5 N) are nearly as wide as high, and a little wider than long. The articular view is circular to weakly trapezoid. Schultz (2013, pl. 71, fig. 5) figured vertebra of *Pelamcycybium partschi*, and they are very similar to the Pécsvárad Scombridae vertebral centra in all visible features.

Apart from the aforementioned remains, numerous fragmentary fish fossils are known from the site (HNHM VER 2024.180.-181., not figured). These are in poor condition, therefore their closer identification is currently not possible.

Amphibians

The only amphibian material found is a single fragmentary caudal vertebra of the giant salamander *Andrias* cf. *scheuchzeri* (Fig. 6 H).

Reptiles

Reptiles are represented by turtles and crocodiles. Turtle remains are not uncommon, they include mostly carapax fragments, plus a cervical vertebra and some limb bones (femora, humeri) (Fig. 6). Most of them are fragmentary and do not allow a more precise identification than Testudines indet. More closely identifiable finds indicate the presence of at least three genera. *Testudo* sp. carapax fragments are massive, thick pieces (Fig. 6 A). A cf. *Ptychogaster* sp. nuchal fragment was identified based on its thickness and a wavy edge divided by a plate boundary (Fig. 6 B). Softshell turtles are represented by a decorated *Trionyx* costale and a Pan-Trionychidae indet. femur (Fig. 6 C, D). Crocodilian remains are comprised of a tooth and a few osteoderm fragments and can be attributed to the genus *Diplocynodon* (Fig. 6 E, F, G).

Mammals

The bulk of the mammal material originates from aquatic groups: toothed whales, baleen whales and sirenians. In addition, several terrestrial taxa occur in the fauna.

The most numerous fossils belong to odontocetes. Within the group, at least four different taxa can be identified. Remains attributable to *Kentriodon fuchsii* are the most abundant and include a left periotic, an axis, possibly atlas fragments, other vertebrae, humeri, ulna, and rib (Fig. 7). These are non-pachyostotic bones of relatively small sizes; identifications are based on Brandt (1873) and Kazár (2003, 2005a, 2006b). For another kentriodontid, the larger *Sophianaecetus commenticius*, Kazár (2003) reported and imaged a right humerus (V.60/707 in the HNHM collection) from the Pécsvárad sand pit (in the table caption the locality is erroneously given as Pécs-Danitzpuszta). In our material, an atlas fragment and a radius are tentatively attributed to this species based on the relatively large size of bones and their morphology similar to that presented by Brandt (1873) and Kazár (2005b): the base of the narrow ventral process on the atlas fragment and the arched shape of the radius. A right humerus of *Acrodelphis letochae* (V.18381 in the SARA geological collection) was identified and presented by Kazár (2003 and 2005a). One of the newly found humeri strongly resembles that one but is smaller and somewhat more slender. A massive, thick, and unfortunately fragmentary limb bone is tentatively classified as the distal part of the ulna of *Pachyacanthus suessi*, a relatively large toothed whale featuring pachyostotic bones (Kazár 2010).

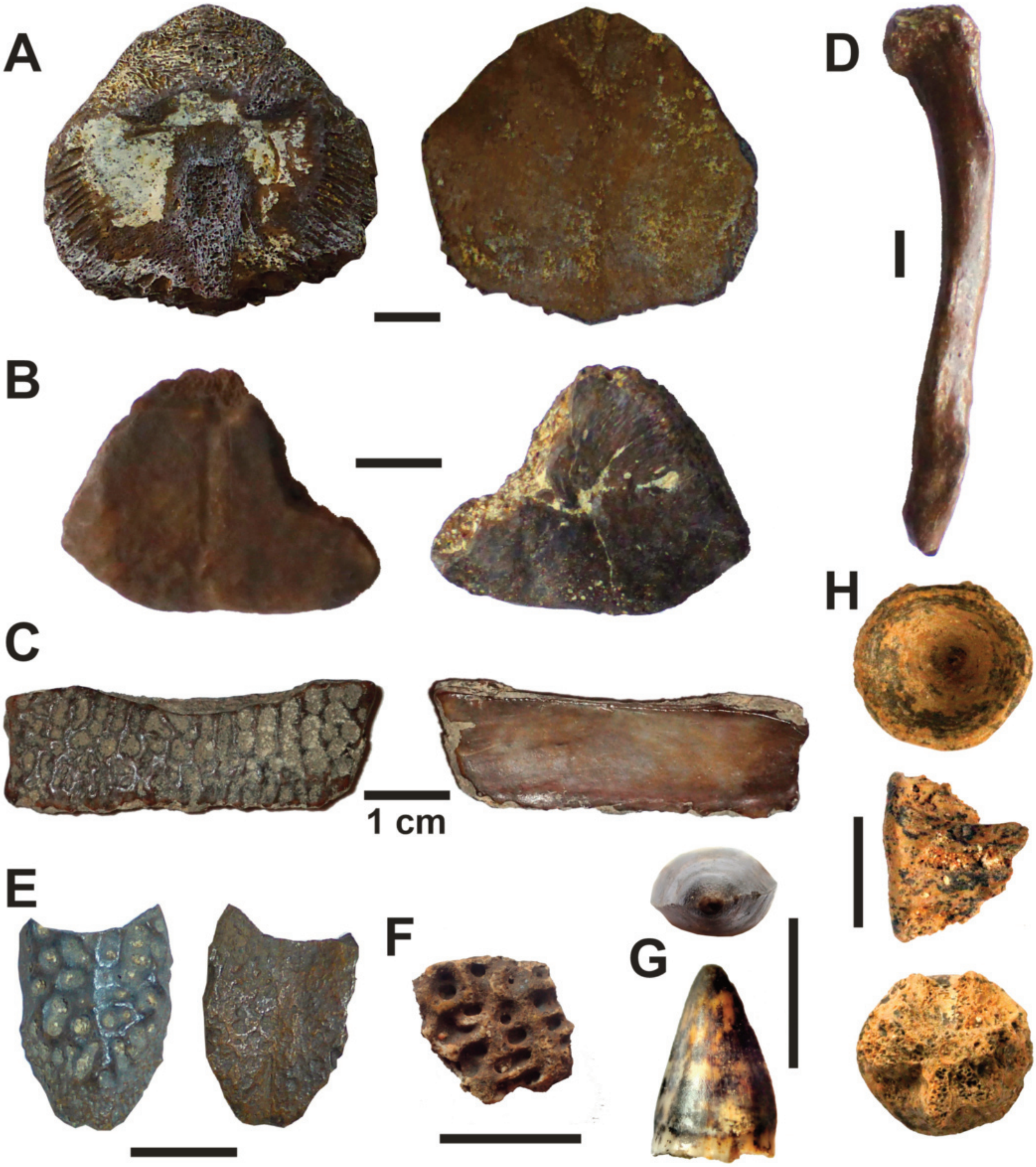

Fig. 6. *Amphibian and reptile remains from the Pécsvárad sand pit.* ***A)*** cf. *Testudo carapace fragment (?nuchal), internal and external view (Kübler coll.);* ***B)*** cf. *Ptychogaster* sp. *nuchal, external and internal view (JPM);* ***C)*** *Trionyx carapace fragment (costale), external and internal view (JPM 57.94.1);* ***D)*** *Pan-Trionychidae indet. femur, ?posterior view;* ***E, F)*** *Diplocynodon osteoderms (Kübler coll. & SARA),* ***E-*** *external and internal view,* ***F-*** *external view;* ***G)*** *Diplocynodon tooth (HNHM VER 2024.188), occlusal and labial view;* ***H)*** *Andrias* cf. *scheuchzeri caudal vertebra (HNHM VER 2024.166), anterior, dorsal and posterior view*

Fig. 7. *Odontocete fossils from the Pécsvárad sand pit.* ***A)*** *Kentriodon fuchsii left periotic (JPM 57.109.142);* ***B)*** cf. *Sophianaecetus commenticius atlas fragment (JPM 57.109.142);* ***C)*** *Odontoceti indet. atlas fragment (JPM 57.98.2);* ***D)*** *Kentriodon fuchsii axis (JPM 57.97.1);* ***E)*** *Odontoceti indet scapula fragment (JPM 57.100.1);* ***F)*** *Sophianaecetus commenticius right humerus (HNHM V.60/707; det. Kazár 2003);* ***G)*** aff. *Acrodelphis* sp. *(JPM 57.102.4);* ***H, I)*** *Kentriodon fuchsii humeri (JPM 57.109.142);* ***J)*** *Kentriodon fuchsii ulna (JPM 57.88.5);* ***K)*** *Sophianaecetus commenticius radius (JPM 57.88.5); arrows indicate possible shark bite mark;* ***L)*** *Pachyacanthus suessi ulna fragment (JPM 57.109.142);* ***M)*** *Odontoceti indet. metacarpal (JPM 57.88.5);* ***N)*** *Odontoceti indet. (JPM 57.109.142);* ***O)*** *Kentriodon fuchsii rib fragment (JPM 57.108.3)*

Some stout, thick vertebral spinous processes found at the locality, similar to those referred to this species from Pécs-Danitzpuszta by Kazár (2010), are attributed to *Pachyacanthus suessi* as well, where the highly pachyostotic thickening of the vertebral spines is typical (Kazár 2010). Odontocetes are further represented by an unidentified scapula fragment, possibly belonging to a kentriodontid; a metacarpal and phalanges; several vertebrae; and spinous processes of various vertebrae belonging to multiple taxa, among them the thin, slender ones probably attributable to *Kentriodon fuchsii* or some similar small-sized kentriodontid.

Mysticetes are represented by two mandible fragments, a humerus, possibly a rib, and a few vertebrae (Fig. 8). Mandible fragments (Fig. 8 A, B) do not allow any closer identification. The numerous baleen whale humeri found in similarly Upper Miocene sands in the nearby sand pit of Pécs-Danitzpuszta were investigated by Cserpák (2018). Based on the morphological characters provided by him – primarily the dimensions and the more slender build than that of the two other taxa, i.e. the lower ratio of the caput humeri relative to the complete length of the humerus – the Pécsvárad humerus (Fig. 8 C) can be identified as *Cetotherium priscum*. With its length of 17–18 cm, the specimen is above the upper limit of the size range presented by Cserpák (2018), it might have belonged to a whale longer than 3.5 m. The vertebrae are all worn, with their processes broken off (Fig. 8 E–G). The non-pachyostotic vertebrae can only be identified as Mysticeti indet. The largest one (V60.698 JPM, Fig. 8 E) is comparable in its general shape (high ratio of antero-posterior vs. dorsoventral measures, round shape of epiphyseal plate) and size to the *Mesocetus* remains described from the Central Paratethys: *M. hungaricus* (Kadić, 1907) or *M. agrami* (van Beneden, 1884; Paunović, 1993). One vertebra (Fig. 8 F) must have belonged to a young animal, as the epiphyseal plate is not fused on the body of the vertebra. Pachyostotic vertebrae belong to cetotheriids (Fig. 8 G). Two pachyostotic rib fragments are inventoried in the Pécs museum (JPM) as belonging to sirenians. One is too fragmentary to allow identification. The other one still bears the base of the epiphysis and is relatively flattened next to it (Fig. 8); this shape suggests attribution to a small cetotheriid baleen whale rather than to a sirenian. Middle Miocene cetotheriids may also show pachyostosis, which appeared convergently in

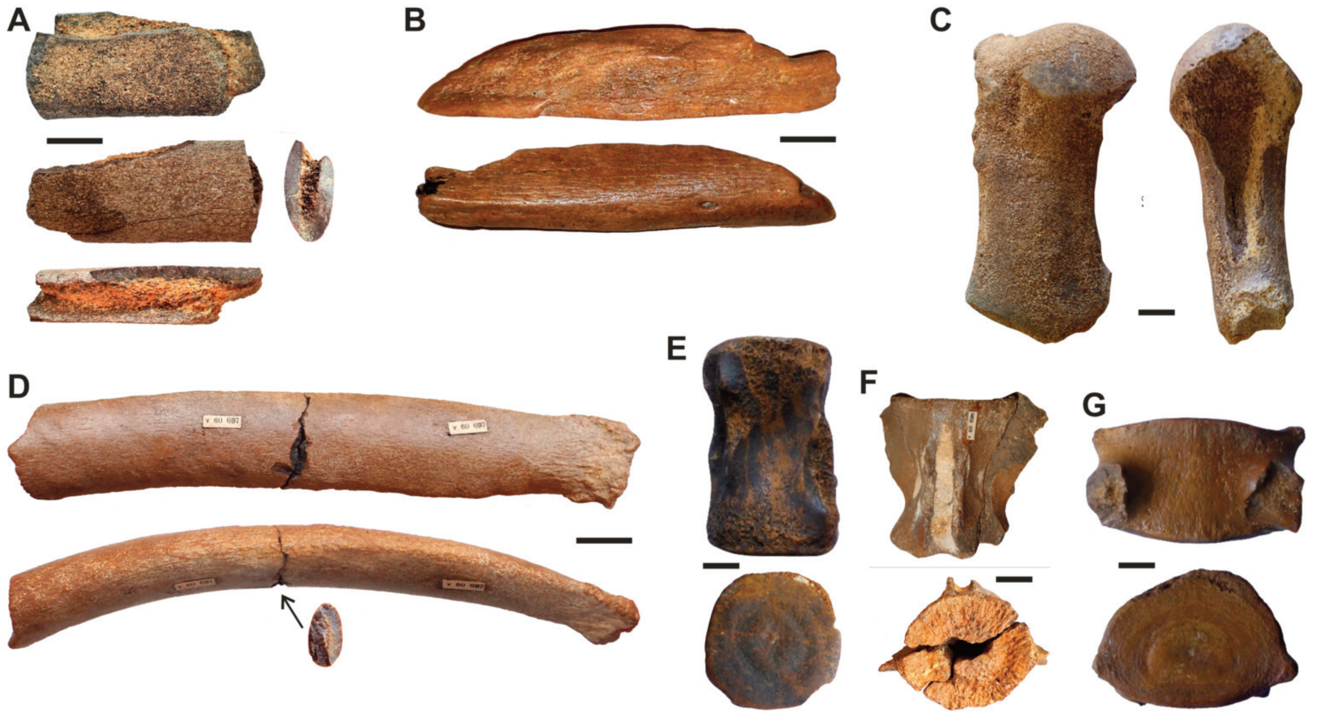

Fig. 8. *Mysticete remains from the Pécsvárad sand pit.* ***A, B)*** *Mysticeti indet. mandible fragments (****A:*** *HNHM VER 2024.189.;* ***B:*** *JPM 57.109.142);* ***C)*** cf. *Cetotherium priscum left humerus;* ***D)*** *Cetotheriidae indet. rib fragment (HNHM V60.697);* ***E, F)*** *Mysticeti indet. vertebrae (JPM 57.84.3, HNHM V60.698);* ***G)*** *Cetotheriidae indet. vertebra (JPM 57.87.1)*

various marine mammal groups in the Central Paratethys, presumably as a response to elevated salinities (Dewaele et al., 2022).

Terrestrial mammals give further diversity to the assemblage. The largest fossil found is a portion of mandibular horizontal ramus preserving the roots of some teeth (Fig. 9 A). The anterior roots of each tooth display a straight anterior at the contact with the alveolus, and the internal borders of both anterior and posterior roots are slightly concave, similarly to the *Tapirus* specimen HNHM V.71.30 from Ajnácskő and contrary to Rhinocerotidae, where the anterior and posterior borders of the roots are characterized by a strong constriction in the middle. Accordingly, shape and size of the specimen suggest an attribution to the family Tapiridae. During the Miocene, Tapiridae are documented in Europe through the presence of two genera, *Tapirus* and *Tapiriscus* (Pandolfi et al., 2023). Considering the preservation of the specimen it is not possible to assign it under either of the two genera. Rhinocerotids are represented by postcranial bones. A left metatarsal is long (maximal length 192 mm) and slender (diameter of the diaphysis 39.4 mm) featuring a sinuous anterior border of the proximal articular surface (Fig. 9 B). The specimen closely resembles *Lartetotherium sansaniense* in both morphology and dimensions (cf. Cerdeño 1986; Pandolfi & Martino, 2023). Another bone can be identified as a proximal phalanx of digit III (Fig. 9 C) but it does not allow a classification closer than Rhinocerotidae. A small, heavily worn antler documents the presence of cervids in the assemblage (Fig. 9 E). It is not possible to decide whether the angle at its upper third marks a point of dichotomy or just a curve. The small length and diameter of the antler suggest that it belonged to a young individual. A proximal phalanx belongs to a giraffid (Fig. 9 D). From Hungary, two Miocene giraffid genera have been reported: *Csakvarotherium,* named after the finding locality Csákvár cave (Kretzoi, 1954), and *Helladotherium* (Gaál, 1943; Kormos, 1911). The upward strongly widening Pécsvárad specimen can rather be attributed to *Csakvarotherium*.

Fig. 9. *Terrestrial mammal fossils and coprolites from the Pécsvárad sand pit.* ***A)*** *Tapiridae indet. mandible (HNHM VER 2024.190.);* ***B)*** *cf. Lartetotherium sansaniense left metatarsal (JPM 57.85.1.);* ***C)*** *Rhinocerotidae indet. proximal phalanx of digit III (JPM 57.99.1.);* ***D)*** cf. *Csakvarotherium proximal phalanx (Kübler collection);* ***E)*** *Cervidae indet. antler (HNHM VER 2024.191.);* ***F)*** *various coprolites (JPM 57.101.8);* ***G)*** *detail of the first coprolite with fish bones*

Several vertebrate coprolites of various sizes and shapes are also part of the Pécsvárad assemblage (Fig. 9). Some of them contain large amounts of fish bones, among them vertebrae (Fig. 9 G), indicating a piscivorous diet of the producer. Lacking any desiccation features, the coprolites must have been produced by aquatic animals, similarly to those of the nearby Pécs-Danitzpuszta sand pit (Román et al., 2024).

In the Hungarian Natural History Museum, an amphicyonide tooth (*Hubacyon* (*Kanicyon*) *pannonicus*) is inventoried with the location Pécsvárad.

Kretzoi (1985) wrote that the tooth had been found „in Lower Pannonian sands", „in the sand pit east of the city Pécs, along the road to Pécsvárad". This description fits the sand pit of Pécs-Danitzpuszta and not that of Pécsvárad. We therefore consider this specimen erroneously localised in the museum inventory and do not discuss it together with the Pécsvárad assemblage.

Discussion

Depositional environment and age of the sediment

The Pannonian mollusc fauna of the Pécsvárad sandpit represents a littoral assemblage that lived in the shallow, agitated waters of Lake Pannon. *Dreissena auricularis*, *Congeria balatonica*, *Lymnocardium dumicici*, *„Pontalmyra" budmani* and *Pseudocatillus simplex* were all exclusively shallow-water dwellers (e.g., Müller & Szónoky, 1990; Mező et al., 1999), whereas *Congeria ungulacaprae*, *Lymnocardium schmidti* and L. *hungaricum* lived both in the littoral and sublittoral zones of the lake (cf. Magyar, 1992 and Cziczer et al., 2009; Lennert et al., 1999 and Szónoky et al., 1999). The original diversity of the Pécsvárad assemblage was likely higher, but poor preservation hinders the species-level identification of additional forms.

The biostratigraphic position of the Pécsvárad layers is constrained by the presence of *Lymnocardium schmidti*, which first appears in the littoral *Prosodacnomya carbonifera* Zone (Müller & Magyar, 1992; Geary et al., 2010), and by *L. hungaricum*, having its earliest known record in the *Prosodacnomya dainellii* Zone (Lennert et al., 1999). The rest of the species appeared considerably earlier than these two forms. The base of the *Prosodacnomya carbonifera* Zone is dated at 8.1 Ma, whereas that of the *P. dainellii* Zone at 7.6 Ma (Magyar & Geary, 2012; Sztanó et al., 2013; Magyar et al., 2019; Magyar, 2021). The top of the Miocene was regionally eroded as a consequence of tectonic inversion (Sacchi et al., 1999; Magyar & Sztanó, 2008; Sebe et al., 2020), and the age of the youngest Miocene deposits in the basin margins is about 6.8 Ma (Kelder et al., 2018). Therefore, the age of the Pécsvard sand can be estimated at 7.6–6.8 Ma.

Origin of vertebrate fossils

The vertebrate fossils obviously represent a mixed assemblage. Here we investigate each group to determine from which age or sedimentary unit they may have originated through reworking.

Odontaspididae (sand tiger sharks) are among the dominant selachians of the Paratethys. Extant odontaspidids mostly prefer warm, shallow waters, where they feed on a wide variety of bony fishes, other sharks, rays, cephalopods and crustaceans (Cappetta, 2012; Compagno, 2002).

Adult individuals of modern acipenserids (sturgeons) inhabit high-energy environments, including freshwater lacustrine, riverine, estuarine, and sometimes nearshore marine habitats (Bemis & Kynard, 1997) and brackish environments (river deltas and estuaries). Extant sturgeons are anadromous (Nelson et al., 2016), which means that adult individuals migrate upstream to spawn, however, they spend most of their lives feeding in river deltas and estuaries (Nelson et al., 2016). Following the ecological needs of modern taxa, the occurrence of this family in the Pécsvárad assemblage indicates the nearby presence of freshwater habitats during the Miocene. Acipenseridae fossils have also been reported from the nearby Pécs-Danitzpuszta sand pit (Szabó et al., 2021).

It is believed that the family Latidae (lates perches) originated in the marine environments of the Tethys Sea (Kovalchuk et al., 2024). Extant latids generally prefer freshwater environments, however, some taxa survive in brackish and estuarine waters as well (Sorbini, 1975; Froese & Pauly, 2024 and references therein). Fossils of Latidae have already been reported from the Miocene of the Paratethys (Szabó et al., 2021; Kovalchuk et al., 2024).

Extant sparid fishes (porgies) are primarily found in marine environments, with only occasional occurrences in freshwater and brackish waters (Nelson et al., 2016). Nowadays, they are widespread in shallow, temperate-tropical waters, where they occupy a wide variety of habitats. The Pécsvárad

Sparidae material is not identified closer than family rank, so they are not useful for paleoecological implications. Isolated tooth fossils of Sparidae are widespread and are widely reported from the Miocene marine and Upper Miocene lacustrine sediments of the Paratethys and Lake Pannon, representing various saltwater habitats (e.g., Solt, 1991; Schultz et al., 2010; Mikuž & Šoster, 2013; Schultz, 2013; Bosnakoff, 2014; Szabó, 2019; Szabó & Kocsis, 2020; Szabó et al., 2021).

Extant members of the family Scombridae (mackerels and tunas) are dominantly marine fishes, which commonly inhabit pelagic waters of tropical and subtropical seas (Nelson et al., 2016), therefore their presence in the Pécsvárad fish fauna reflects a connection to open marine habitats. Scombridae fossils are also known from the Miocene sands of the Pécs-Danitzpuszta sand pit (Szabó et al., 2021).

To sum up, the Pécsvárad fish fauna represents an ecological mixture, composed of taxa with a wide variety of habitat preferences, which reduces its paleoecological significance. Considering the ecological needs of their extant relatives, Odontaspididae sharks, scombrids and possibly sparids are most likely re-deposited from the Badenian marine sediments. In contrast, Acipenseridae and Latidae fishes could have been inhabitants of freshwater environments, therefore their remains could be coeval with the embedding sands or might come from earlier intervals of the Miocene as well.

In the Mecsek area, giant salamander fossils have so far been reported only from the Pécs-Danitzpuszta sand pit (Szentesi et al., 2020; Szentesi, 2021). Both extant and extinct giant salamanders are known to live in freshwater, usually in fast-flowing streams, on high-relief terrain and under frost-free climates. Considering the environmental requirements the fossils from the Mecsek Mts. can even be coeval with Lake Pannon, although they might also originate from older time intervals of the Miocene as well (Szentesi et al., 2020).

Testudo and *Tryonix* fossils in the Mecsek Mts. are known from the Karpatian–Badenian (i.e., late Burdigalian to early Serravallian) lacustrine deposits, though „turtle remains" without further specification have also been reported from the Eggenburgian–Badenian fluvial succession (Vadász, 1935; Kordos, 1985). They are abundant in the mixed, to a great part reworked assemblage of the Upper Miocene sands in Pécs-Danitzpuszta (Sebe et al., 2021a, b). Testudinids occupy various terrestrial environments from forests to deserts (Ernst & Barbour, 1989). *Ptychogaster* species prefer arid and warm habitats (Młynarski & Roček, 1985). The warm subtropical climate in the Mecsek area lasted until at least the early Late Miocene based on macrofloral remains (Hably & Sebe, 2016). Relatively dry habitats could be found here during this interval based on the abundant lauraceous plants (Hably & Sebe, 2016), but could also have occurred earlier, in the Early Miocene, considering the explicitly arid climate reconstructed for the nearby North Croatian Basin and Serbia (Pavelić et al., 2016, 2022; Andrić-Tomašević et al., 2021). Trionychids prefer freshwater or slightly brackish environments: slow-moving rivers, swamps, and ponds (Holec, 2006). In Central and Eastern Europe, Trionychidae are known up to MN13 (Ernst & Barbour, 1989; Danilov et al., 2012). Thus, turtles can originate from any part of the Miocene before the deposition of the Pécsvárad sands or can even be coeval with them.

Crocodilian (*Diplocynodon*) remains have been found in the southern foreland of the Mecsek Mts. in Karpatian–Badenian lacustrine deposits (Kordos, 1985). In 1873, a partial *Diplocynodon* skeleton (coll. János Böckh) was found SE of the settlement Orfű-Bános, in the same stratigraphic unit (unpublished; stored in the Hungarian Natural History Museum collection). The genus has also been reported from the Upper Badenian paralic lignite series (Kordos, 1985). *Diplocynodon* finds indicate a warm, subtropical climate and permanent water bodies (Markwick, 1998; Böhme, 2003). In the Central Paratethys basin, the known temporal range of *Diplocynodon* extends up to the zone MN7, as documented at localities in Romania (Venczel, 2007; Hír et al., 2002). Conditions could have been appropriate for *Diplocynodon* during the deposition of the Pécsvárad sands as well: the mean annual temperature (16°C) and the temperature of the coldest month (5 °C) reconstructed from macroflora for the not much older Pécs-Danitzpuszta locality (Hably & Sebe, 2016) just fit in the range tolerated by these crocodilians (Markwick, 1998).

Among toothed whales, *Kentriodon fuchsii* was a widespread early Sarmatian (late Serravallian) small species occurring at several localities in the Central Paratethys basin (Kazár, 2003, 2006b; Grigorescu & Kazár, 2006 and references within). Its remains are the most frequent odontocete fossils in the nearby Pécs-Danitzpuszta sand pit but up until now, they have not been reported from other localities in the Mecsek area (Kazár, 2005a). *Sophianaecetus commenticius* was described from the Sarmatian of the Mecsek Mts. (Kazár, 2005b, 2006a). *Pachyacanthus suessi*, a toothed whale resembling the modern river dolphins, has occurrences in the Sarmatian deposits of the Central Paratethys (Kazár, 2010). According to Kazár, (2003), the Sarmatian *Acrodelphis letochae* (Brandt, 1873) is a descendant of the smaller-sized Badenian cf. *Acrodelphis* sp., which is described from the Vienna Basin, and points to an evolutionary trend of strong size increase. Based on this, the new indeterminate humerus from Pécsvárad might have belonged to the older, Badenian form. So, apart from this latter find, the majority of the Pécsvárad odontocete remains have their origins in Sarmatian sediments.

The *Sophianaecetus commenticius* radius bears a straight groove (Fig. 7 K), which resembles bone injuries that have been interpreted as shark bite marks in similar fossil assemblages containing both marine mammal and shark remains (Collareta et al., 2017; Merella et al., 2021; Szabó et al., 2021; Feichtinger et al., 2021). If this interpretation is correct, it would mean that the temporal range of *Sophianaecetus* was not restricted to the Sarmatian but extended down into the Badenian as well, since sharks disappeared from the area (and from the Central Paratethys as a whole) at the end of the Badenian. Badenian occurrence in addition to the Sarmatian has already been suggested for some toothed whales of the Mecsek region based on similar bite marks (Szabó et al., 2021).

The dimensions of all mysticete remains show that they must have belonged to small-sized whales typical of the Central Paratethys during the Sarmatian and partly also during the Badenian (Brandt, 1873; van Beneden, 1884; Gorjanović-Kramberger, 1884; Kadić, 1907; Pia, 1937; Paunović, 1993; Gol'din & Radović, 2018; Cserpák, 2018). According to Cserpák (2018), *Cetotherium priscum* remains of the Central Paratethys found in situ come from Sarmatian deposits (Brandt, 1873; Gorjanović-Kramberger, 1884; Pia, 1937) and represent the most abundant baleen whale species of the time. However, *C. priscum* has recently been considered as nomen dubium and the taxonomically undiagnostic type specimens should belong to some yet unidentified Cethotheriinae (Gol'din & Startsev, 2016). Considering that – even if restricted – marine conditions were last present in the study area during the Sarmatian, the Pécsvárad humerus could be attributed to one of the two oldest genera of Cethotheriinae, *Zygiocetus* and *Kurdalagonus*, appearing in the late Sarmatian in the Eastern Paratethys (Tarasenko & Lopatin, 2012; Gol'din & Startsev, 2016). *Mesocetus* fossils were found both in Badenian and Sarmatian sediments of the Central Paratethys (van Beneden, 1884; Kadić, 1907; Paunović, 1993; Holec & Sabol, 1996). Thus, at least some of the Pécsvárad remains must have had their provenance in Sarmatian deposits, while a part of them might have also come from the Badenian.

Tapiridae were present in Europe in the earliest Miocene and then from the Badenian onward (Pandolfi et al., 2023). In the Miocene of the Pannonian Basin, the small *Tapiriscus pannonicus* has been reported from the MN11 locality Csákvár in Hungary (Kretzoi, 1951; Guérin & Eisenmann, 1994), and from the Turolian site Șărmășag in Romania (Codrea, 1994), which are approximately coeval with the deposition of the Pécsvárad sands. Although the preservation of the Pécsvárad mandible does not allow for a taxonomic identification even at the generic level, its small size does not exclude that it belonged to *Tapiriscus pannonicus*. Tapirs prefer warm swampy forests, which were present along the shores of Lake Pannon (Hably & Sebe, 2016).

The rhinocerotid *Lartetotherium sansaniense* occurred in Europe from MN4 to MN9 (Heissig, 2012), so the specimen identified in the Pécsvárad assemblage must have been reworked.

Primitive giraffids are known in Europe from the MN5 zone, while the group diversified in the Late Miocene (Rössner & Hessig, 1999). Giraffid finds from Hungary are all dated to the Late Miocene: Csákvár has most recently been classified into MN11 (Mészáros, 2000), while among the localities which yielded *Helladotherium*, Hatvan belongs to the MN12 (Gaál, 1943; Bernor et al., 2003) and Polgárdi to the MN13 zone (Kormos, 1911; Rabeder, 1990). The Pécsvárad giraffid phalanx can thus be even coeval with the host sands or not much older.

The cervid antler could be identified only at the family level. Based on the presence of a burr and the pronounced longitudinal grooves on the antler, the animal must have lived after MN4, i.e. in the Badenian or later (Rössner & Hessig, 1999).

The detailed investigation of the extremely rich coprolite assemblage of the nearby Pécs-Danitzpuszta sand pit showed that the coprolites in the Upper Miocene sands might have been reworked from any time interval of the Miocene (Román et al., 2024). The earliest in situ coprolites in the Miocene of the area have been found in the Lower–Middle Miocene lacustrine deposits (Sebe et al., 2023).

Evolution of the study area

In the background of the sand pit, in the Mecsek Mts. lying to the north, the Miocene succession overlying the Jurassic and subordinately Cretaceous basement rocks begins with Lower–Middle Miocene lacustrine sediments (Kiskunhalas Fm.) (Hámor et al., 1964) (Fig. 1). It continues with Middle Miocene, Badenian and Sarmatian, dominantly marine (Budafa, Baden, Lajta and Tinnye Fms.), subordinately also brackish and freshwater (Hidas Fm.) deposits, intercalated with pyroclastics (Tar Dacite Tuff). These are overlain by offshore white marls and littoral limonitic sands that accumulated in the brackish Lake Pannon during the Late Miocene.

Based on the fossil assemblage, the provenance area of the Pécsvárad Upper Miocene sands contained Jurassic and Middle Miocene (Badenian and Sarmatian) rocks as well. Compared to the large modern extent of Badenian marine deposits (Fig. 1), the number of definitively Badenian fossils is low. The nearby site of Pécs-Danitzpuszta, similarly in Upper Miocene sands with a mixed reworked vertebrate fauna, provided an especially diverse chondrichtyan assemblage (Szabó et al., 2021), and at another locality to the east, Himesháza, shark and ray teeth are also abundant (Kocsis et al., 2009; Budai et al., 2019), while only a single shark tooth has been found at Pécsvárad. In contrast, today Sarmatian rocks crop out only in a narrow band near the Pécsvárad sand pit, but the amount of Sarmatian fossils is remarkable in the sands. This refers to a composition of the provenance area during the Late Miocene different from that of today: Sarmatian deposits must have built up a considerable part of the source area, while outcrops of Badenian sediments must have been subordinate.

A possible scenario to explain this can be outlined based on our understanding of the structural evolution of the region. The Pécsvárad sand pit lies just in front of the main boundary fault of the Mecsek Mts., along which the range has been thrust upon its southeastern foreland (Fig. 1). Sediments next to the fault are heavily deformed, with steep bedding dips on both sides of the fault, while dips are more gentle away from it. Sarmatian rocks are missing in the hanging wall (NW of the fault) in the vicinity of the sand pit. After the Early to early Late Miocene rifting of the Pannonian Basin, the uplift of the Mecsek Mts. started in the Late Miocene, ~10 Ma ago, and intensified from ~8 Ma due to the neotectonic basin inversion (Konrád & Sebe, 2010; Sebe et al., 2016; Sebe, 2021). Uplift and consequent denudation of the mountains happened partly simultaneously with Lake Pannon deposition. It seems that at Pécsvárad, uplift-related denudation must have been intense during the deposition of the sands, 7.6–6.8 Ma ago, and it destroyed mostly the Sarmatian marine beds, and a minor part of the underlying Badenian marine and Karpatian–Badenian lacustrine deposits. Earlier Miocene sediments were transported into Lake Pannon, where nearshore processes removed much of the sediments and enriched the fossil content. A mixed fossil assemblage was thus produced, providing insights into various parts of the Miocene.

Conclusions

The fossil-bearing sands of the Pécsvárad sand pit accumulated in the Late Miocene, between 7.6–6.8 Ma, in a high-energy littoral setting of the brackish Lake Pannon, as indicated by the mollusc remains. The mixed vertebrate fossil assemblage presents a noteworthy diversity relative to the number of specimens, offering insights into both terrestrial and aquatic biota throughout various time intervals of the Miocene. Aquatic mammals represent the most abundant group, and include at least four odontocete species and a few mysticete genera, which inhabited the Paratethys during the Badenian and the Sarmatian. Rhinocerotid remains are reworked from sediments aged somewhere between Karpatian and earliest Pannonian. The single shark tooth must be Badenian, and probably the scombrid fishes date to that time interval as well. Fossils of other fishes (sparids, latids and acipenserids), giant salamanders, turtles, crocodilians and cervids might have originated from older Miocene deposits but can be coeval with the host sands as well. Tapirs and giraffids must have lived on the shores of Lake Pannon, probably contemporaneously with sand deposition or not much earlier. The erosion, enrichment and mixing of the fauna result from the uplift and denudation of the Mecsek Mountains during Lake Pannon sedimentation, caused by neotectonic basin inversion. This example shows that in spite of their inherently restricted interpretation potential caused by the uncertainties in the dating of some fossils, mixed faunas can provide important data on the evolution history of an area.

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Резиме

Фосили из горњомиоценских (панонских) пескова на локалитету Pécsvárad (источни обод Mecsek планина, ЈЗ Мађарска)

Планине Mecsek на југозападу Мађарске представљају издигнути подински блок Панонског басена, изграђен од стена горњег палеозоика и мезозоика. Њихов неогенски покривач обухвата наслаге средњег миоцена Централног Паратетиса и касномиоценске бракичне седименте Панонског језера. Лимонитски пескови горњег миоцена (панонске старости у регионалној стратиграфији Централног Паратетиса) су типичне наслаге Панонског језера и јављају се дуж целог обода Mecsek планина. На неким локалитетима, као што су Pécs-Danitzpuszta или Himesháza, песковити седименти садрже мешовиту фосилну заједницу кичмењака која је преталожена из различитих старијих миоценских јединица и потом је депонована заједно са фауном касног миоцена. Површински коп песка на локалитету Pécsvárad обилује не посебно богатом, али релативно разноликом заједницом фосилних кичмењака, сакупљених углавном недавно. У раду је приказан кратак опис и процена фосилне фауне локалитета Pécsvárad.

Активни површински коп песка налази се ЈЗ од града Pécsvárad, на ЈИ ободима планине Mecsek. Заузима површину од око 300 x 400 m са дебљином наслага од 35 m. Пескови који садрже фелдспате се експлоатишу за потребе индустрије, нпр, за производњу фине керамике.

Касномиоценске молуске

Лимонитски песак садржи обиље фосилних мекушаца са честим лумакелама. Арагонитске љуштуре су у потпуности растворене, а сачувани су само калупи и отисци. Током 2014 и 2018. године, из пескова су сакупљене и одређене следеће врсте: *Dreissena auricularis* (сл. 4е), *Congeria balatonica* (сл. 4d), *C.* cf. *ungulacaprae*, *Lymnocardium schmidti* (сл. 4c), *L. hungaricum* (сл. 4a, b), „*Pontalmyra*” *budmani* (сл. 4f, g), *Pseudocatillus simplex* (Fuchs), Lymnocardiinae и *Zagrabica* sp.

Други бескичмењаци

Пескови садрже и преталожене јурске белемните и криноидске чашице.

Рибе

Фауна риба се састоји од риба са хрскавиавим скелетом (chondrichthyans) и риба са коштаним скелетом (osteichthyans). Једини пронађен зуб ајкуле је у фрагментираном стању и без корена, али указује на горњи латерални зуб одонтоспаридске ајкуле. Пронађени су и представници фамилија Acipenseridae и Scombridae.

Водоземци

Једини пронађени фосилни материјал водоземаца је представљен фрагментираним каудалним пршљеном џиновског даждевњака *Andrias* cf. *scheuchzeri.*

Гмизавци

Гмизавци су представљени фосилним остацима корњача и крокодила. Остаци корњача су чести и представљени су фрагментима карапакса, вратним пршљеновима и костима удова који дозвољавају идентификацију до Testudines indet. Остаци крокодила састоје се од зуба и неколико фрагмената остеодерма и могу се приписати роду *Diplocynodon* (сл. 6 E, F, G).

Сисари

Највећи део фосилних остатака сисара потиче од китова и делфина. Најбројнији остаци припадају врсти *Kentriodon fuchsii.* Копнени сисари припадају фамилијама Tapiridae и Rhinocerotidae, док су остаци жирафа представљени родом *Csakvarotherium*.

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