# THE DIRTY DOZEN: TAXONOMICAL AND TAPHONOMICAL OVERVIEW OF AN UNIQUE ANKYLOSAURIAN (DINOSAURIA: ORNITHISCHIA) ASSEMBLAGE FROM THE SANTONIAN IHARKÚT LOCALITY, HUNGARY

Attila Ősi[1, 2, *], Gábor Botfalvai [2,3], Gáspár Albert[4], Zsófia Hajdu[5]

[1]Eötvös University, Department of Paleontology, Pázmány Péter sétány 1/C, Budapest 1117, Hungary, hungaros@gmail.com

[2]Hungarian Natural History Museum, Ludovika tér 2, Budapest, 1083, Hungary

[3] Eötvös University, Department of Physical and Appiled Geology, Pázmány Péter sétány 1/C, Budapest 111

[4]Eötvös University, Department of Cartography and Geoinformatics, Pázmány Péter sétány 1/A, Budapest 1117, Hungary

[5]MTA–ELTE Lendület Dinosaur Research Group, Budapest, Hungary

[*]Corresponding author: Attila Ősi, +36 30 374 87 63, hungaros@gmail.com

**Key words:** *Hungarosaurus*; *Struthiosaurus*; mass death assemblage, bone mapping, Late Cretaceous; Hungary.

## Acknowledgements

We are grateful to Xabier Pereda-Suberbiola and James Kirkland for their constructive comments that greatly improverd the manuscript. We thank to R. Kalmár (Hungarian Natural History Museum, Budapest) for technical assistance both on the field and in the collection. We thank the 2001–2016 field crews for their assistance in the fieldwork. We are grateful to the Bakony Bauxite Mines and to Geovolán Zrt. for their logistic help. Field and laboratory work was supported by the Hungarian Natural History Museum, the National Geographic Society (Grant Nos. 7228-02, 7508-03), the Hungarian Scientific Research Fund (OTKA T-38045, PD 73021, NF 84193). This project was supported by the National Research, Development and Innovation Office (Grant no. NKFIH, 116665), Lendület Program of the Hungarian Academy of Sciences (Grant no. 95102), the Jurassic Foundation, the Hungarian Dinosaur Foundation, the ÚNKP-17-3 New National Excellence Program of the Ministry of Human Capacities (Grant no. ELTE/12422/16) and the Sepkoski Grants for 2018 of Paleontological Society International Research Program (PalSIRP).

## Abstract

Ankylosaurian fossils are usually standard elements of Cretaceous continental vertebrate localities, however bone-yielding horizons including more than one individual are extremely rare. Here we present a unique assemblage of 12 partial articulated or associated ankylosaurian skeletons and thousands of isolated bones and teeth discovered from the Santonian Iharkút vertebrate locality, western Hungary. Collected from an area of 600 $m^2$ and from a single bone bed, this material is one of the richest ankylosaurian accumulation worldwide. The 12 skeletons are not monospecific but, mostly based on the pelvic armor composition, six of them are from *Hungarosaurus*, two are referred to *Struthiosaurus* and four can be assigned to Nodosauridae indet.

Sedimentological and taphonomical examinations revealed a single mass mortality event as the cause of the death and accumulation of these quadruped animals that are described here. The ankylosaur assemblage from Iharkút suggests at least a temporarily gregarious behavior of these animals and also shows that *Hungarosaurus* and *Struthiosaurus* might lived in the same moist habitat or at least preferred relatively close environments.

## 1. Introduction

Remains of ankylosaurian dinosaurs are relatively rare in Europe. Though their fossils are known from sediments ranging from the Middle Jurassic to the uppermost Cretaceous, specimens are in many cases fragmentary with poorly preserved cranial material (see Ősi 2015 for a review). Multiple articulated or associated specimens of a single genus are only known in a few taxa: the Valanginian *Hylaeosaurus* based on two partial skeletons (Mantell 1833, 1841, Owen 1858; Pereda-Suberbiola 1993a; Carpenter 2001), the Barremian-early Aptian *Polacanthus* based on three partial skeletons (Owen 1865; Hulke 1882; 1888; Blows 1982; 1987; 1996; 2015; Pereda-Suberbiola 1994; Naish and Martill 2001), the Albian *Europelta* based on five skeletons (Kirkland et al. 2013; Luis Alcalá, pers. comm, 2014), and the Santonian *Hungarosaurus* based on six associated skeletons (Ősi 2005; Ősi and Makádi 2009; Ősi 2015; in the paper). The Santonian to Maastrichtian ranged *Struthiosaurus* is known by 10 different associated skeletons (Nopcsa 1929; Pereda-Suberbiola and Galton 2001, Garcia and Pereda-Suberbiola 2003; Ősi and Pereda-Suberbiola 2017), but they came from different tectonical units (Romania, Austria, Hungary, Spain) and the remains are poorly overlapping with each other to prevent comparative work.

The aim of the present study is to give an overview of the Santonain ankylosaur material from the Iharkút locality, western Hungary. Though the first five (Ősi 2005; Ősi and Makádi 2009) and the 8th skeletons (Ősi and Pereda-Suberbiola 2017) have been already published, along with the six unpublished additional specimens they bear important features that helps for a better understanding of European ankylosaur taxonomy and diversity and some aspects of ankylosaur paleoecology as well.

We summarize the remains of 12 partial skeletons discovered by the excavations of the last 17 years, with descriptions of their skeletal components emphasizing the most important and useful characters available on the specimens. We also discuss their taxonomical position and taphonomic history.

**Institutional abbreviations**: MCNA, Museo de Ciencias Naturales de Alava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz, Spain; MTM, Magyar Természettudományi Múzeum, Budapest, Hungary; PIUW, Paläontologische Institut, Universität Wien, Vienna, Austria.

## 2. Material and methods

Besides turtle postcranial elements, ankylosaurian remains are the most frequent fossils in the Iharkút continental vertebrate locality (Botfalvai et al. 2015). Two articulated and ten associated partial skeletons represent the basis of this work. Except for the 1st, 3rd and 10th skeleton, all the associated or articulated remains possess the complete or fragmentary synsacrum indicating that they certainly represent different ankylosaurian individuals. Besides the 12 associated or articulated specimens discussed in this paper, hundreds of isolated specimens including almost all parts of the skeleton have been discovered as well, belonging to both *Hungarosaurus* and *Struthiosaurus* (Botfalvai and Ősi, 2017). The associated material was collected in the Iharkút vertebrate locality between 2001 and 2016 and is housed in the Vertebrate Paleontological Collection of the Hungarian Natural History Museum. Scaled bone maps were drawn from all the skeletons during the excavation (Supplementary Data 1). From 2013 all vertebrate findings were usually surveyed with high-precision geodetic instruments (Total Station in 2013 and RTK GPS later) yielding approximately 700–1100 data records in each exploration season. Measurements are stored in a geodatabase, and 2D/3D GIS tools were used to analyse the possible relations of the bones (Albert et al. 2017; Albert et al. in review). Specimen or parts of them were collected using either a plaster or a polyurethane foam jacket to keep the bones in their original position and save them from damage during transportation. Skeletal elements were then prepared mechanically in the labs of the Department of Paleontology of the Eötvös University and the Hungarian Natural History Museum, and the bones were fixed by cyanoacrylic glue. Ankylosaurian specimens are discussed in taxonomical order.

## 3. Locality and geological setting

The Iharkút vertebrate locality, discovered in Cretaceous beds of a recultivated bauxite open-pit mine between Bakonyjákó and Németbánya villages in Bakony Mountains (western Hungary), has provided a rich and diverse assemblage (>60.000 specimens) of Late Cretaceous (Santonian) continental vertebrates (Fig. 1). The vertebrate material includes remains of fish, amphibians, turtles, lizards, pterosaurs, crocodilians, non-avian and avian dinosaurs, representing at least 32 different taxa (Ősi et al. 2012). All the vertebrate fossils came from bone-yielding horizons of the Csehbánya Formation (Fig. 1a, d). The outcrops of the formation at the locality are interpreted to have been deposited by an anastomosing fluvial system in a topographically low-level, wet, alluvial plain environment controlled by a dominantly humid, but seasonal climate (Botfalvai et al. 2016). Palynological studies of the Iharkút section show that sedimentation took place during the *Oculopollis zaklinskaiae - Brecolpites globosus* palynozones *Oculopollis-Triatriopollenites* subzone, which was correlated to the CC16 Nannoplankton zone (Siegl-Farkas and Wagreich 1996). This indicates a Late Santonian age of the formation in Iharkút (Bodor and Baranyi 2012). Vertebrate remains have been unearthed from multiple horizons in Iharkút, but the site SZ-6 is the only one containing associated and articulated ankylosaur skeletal materials (Fig. 1b). The site SZ-6 is an asymmetrical lenticular channel fill, underlain by a green claystone, and can be divided into three sedimentary units.

**Unit 1** is a 10 to 60 cm thick basal breccia layer composed of grey-green sand, siltstone, clayclasts, pebbles, plant debris and bones and it is the richest fossil-bearing horizon in the locality (Fig. 1a, b). The poorly sorted sandstone breccia layer contains several laminated siltstone/claystone horizons. The presence of smaller or larger ripped-up clayclasts of flood plain origin, the larger-sized tree trunks, and pebbles indicate high-energy conditions associated with rapid flooding events, resulting in efficient reworking of the material of the interfluve areas (Botfalvai et al. 2016). The high energy conditions, however, were by far not constant during the deposition of Unit 1, because the deposition of the basal breccia was interrupted several times by quiet-water sediments (laminated siltstone, claystone) deposited from suspension in standing water following the flow events (Botfalvai et al. 2016). Depositional area of Unit 1 of site SZ-6 acted as a trap where the current velocity suddenly decreased and the poorly sorted sediments and different density (i.e. bones, plant and eggs) and sized (microfossils and partial ankylosaur skeletons) fossils were accumulated altogether at same time (Botfalvai et al. 2015; 2016; Prondvai et al. 2017; Segesdi et al. 2017). The stacked series of Unit 1 (and thus most of the vertebrate fossils in the Iharkút assemblage) was deposited in a relatively short time (e.g. single wet season) by successive flood events (Botfalvai et al. 2016). Due to its rich fossil content, the Unit 1 was the main target of the piecewise geodetic surveying. Between 2013 and 2017, the location of 4765 macroscopic findings were measured in this unit.

**Unit 2** represents a 30-50 centimeter think, grey, cemented sandstone bed showing a poorly developed upward-fining trend (Fig. 1a, b). This Unit indicates a reduction in flow velocity either when the channels were abandoned or possibly at the end of the flood events, when finer sediment (fine- to medium-grained sand) could have been deposited over the basal breccia layer.

**Unit 3** is a 30 to 50 cm thick, laminated, greyish, brownish siltstone layer which contains plant debris, a few bones and two associated, incomplete ankylosaur skeletons (Ősi, 2005, Fig. 1a, c). The closing bed at site SZ-6 (Unit 3) refers to open lacustrine conditions following the flood events (Botfalvai et al. 2016).

The depositional environment of site SZ-6 can be summarized as follows. The underlying green claystone indicates that the area was a low-level floodplain and reflects the depositional environment of a shallow lake or pond before the flow event. When the peak flood discharge reached this depression, the sediment-charged flow heavily eroded the underlying claystone bed. The peak discharge probably lasted for a few hours. Thereafter, in the later stage of the flood, as discharge declined (probably a few hours after the peak discharge) first coarser sediment deposited on the eroded surface of the claystone layer. The shallow depression indicated by the geometry of the green claystone layer behaved as a sediment trap and was filled by a poorly sorted mix of coarser- and finer-grained materials. After the deposition of the basal breccia layers (Unit 1) flow velocity was reduced and sandstone became the dominant sediment while the amount of clayclasts and bones decreased (Unit 2). At site SZ-6 quiet open-lacustrine conditions established soon following the flood events and the deposition of siltstone (Unit 3). Based on the above characters, site SZ-6 is interpreted as one of the abandoned channels formed and filled up by ephemeral high density flash flood events.

Except for the 9th skeletal material, all of the ankylosaurian skeletons were discovered from the channel fill deposit of site SZ-6 indicating that most, if not all of the ankylosaur carcasses was transported and deposited by the same flood event. The material of 9th skeleton came from a greyish/bluish siltstone located between two hydromorf paleosol horizons. The enclosing sediment indicates that the 9th incomplete skeleton was deposited in floodplain environment and not in the channel. This bone-yielding siltstone bed is situated in the same stratigraphic level as the channel fill deposit of site SZ-6 and shows a weak lateral connection to the basal breccia layer of Unit 1 (Fig. 1c). This bone bearing horizon can be interpreted as a floodplain area of the channel of site SZ-6 and probably includes coeval bone accumulations.

## 4. Description and comparisons

### *4.1.* Hungarosaurus tormai

Dinosauria Owen, 1842
Ankylosauria Osborn, 1923
Nodosauridae Marsh, 1890
*Hungarosaurus* Ősi, 2005
*Hungarosaurus tormai* Ősi, 2005

*Revised diagnosis* (based on Ősi 2005; Ősi and Makádi 2009; Ősi et al. 2014a, Ősi and Pereda-Suberbiola 2017). Armored dinosaur, estimated body length ca. 4–4.5 m. Differs from all other known ankylosaurs in having a postorbital bearing a high and anterodorsal–posteroventrally elongated crest; a thin, rod-like, dorsoventrally flat jugal; a large, inverted U-shaped premaxillary notch that is as high dorsoventrally as wide mediolaterally; a forelimb–hindlimb length ratio of 1.0 (humerus/femur = 0.92); and a centrally positioned, massive, boomerang shaped osteoderm with two posteriorly projecting spikes.

*Hungarosaurus* is distinguished from the other European Late Cretaceous ankylosaur, *Struthiosaurus*, by the following features: the dorsoventrally wide quadratojugal ornamented by a large, rounded protuberance laterally; mandibular quadrate condyle being more robust with rhomboidal articular surface; presence of interpterygoid vacuity; postacetabular process comprising approximately 38% of the total ilium length; the elongated ‘neck’ region of the basioccipital; height/width ratio and shape of the occipital condyle; the different flexure of the medulla relative to the forebrain; humerus gracile, elongate with relatively small deltopectoral crest and lack or has reduced muscle scars posteriorly; ulna quite elongate distally; pelvic armor composed of at least partially non-keeled, polygonal osteoderms; medial plate on the cervical half-ring with concave posterior edge; lateral plate on the cervical half-ring anteroposteriorly longer than high and posteriorly projected.

4.1.1. 1st skeleton (Fig. 2)

*Reference No.*: MTM 2007.22.1

*Year of discovery*: 2001.

*Material*: anterior dorsal vertebra (Fig. 2a), cervical half-ring (Fig. 2a), two additional osteoderms (Fig. 2c), three dorsal ribs (fig. 2b, d).

*Description and comparisons*: The most diagnostic element of this specimen is a complete cervical half-ring, composed by a wide and S-shaped base and two plate-like crests (Fig. 2a). The base of this element has a slightly concave and smooth ventral side and a crennelated margin. The larger, medially positioned plate reminds the shape of a shark fin having a convex anterior and concave posterior edge and a posterodorsally pointed apex. The smaller, lateral plate is rather triangular with a lower dorsal apex and straight, anterodorsal and posterodorsal edges. The two plates are not parallel with each other but make an angle of ca. 100°. The dorsal surface of the base between the two plates in only weekly ornamented and is not a clear composition of smaller osteoderms as it can be observed in *Struthiosaurus* (e.g. PIUW 2349/14, MTM VER 2016.507., MTM VER 2016.541., MTM VER 2016.577.). The strongly posteriorly projected medial plate with concave posterior edge (Fig. 2a) markedly differs from those of the triangular *Struthiosaurus* (e.g. PIUW 2349/13, MTM VER 2016.507., MTM VER 2016.577.), but identical with that medial plate of the cervical half-rings of the holotype of *Hungarosaurus tormai*, thus this specimen is referred to *H. tormai*. The anterior dorsal vertebra with anteroposteriorly very short centrum and strongly widened posterior articular surface is identical with those of holotype specimen (Ősi 2005:fig. 8A), but, since this type of vertebra is unknown in *Struthiosaurus*, we cannot use it as a diagnostic element of *Hungarosaurus*. Based on the diameter of ribs (Fig. 2b), and the size of the cervical half-ring, this specimen is the largest of all the ankylosaur specimens from Iharkút.

*Remarks*: This specimen is the only one without an exact location, since it was found on the refuse dump of the Iharkút bauxite open pit mine. The mining company, however, informed us that that part of the refuse dump is the overburden of the bauxite lens Németbánya III, in the wall of which the 2nd and 3rd skeletons were discovered in the same year (2001). This raises the possibility that the 1st skeleton, missing a sacrum, might have been part of any of these. However, the 2nd and 3rd skeletons came from Unit 3 and not from Unit 2 (see below). Concerning the other possibility that the 1st skeleton might have been part of the later discovered, 4th to 12th skeletons is also unlikely, since in 2001 these specimens still were laid a minimum of 50 meters eastwards deep in the hill (see Fig. 1).

*Stratigraphic position*: The exact stratigraphic position is unknown. The embedding matrix is coarse grained sandstone with ripped up clay clasts. This type of litofacies is known from several points of the Iharkút mine associated with the bottom of the channel fill deposits (e.g. site SZ-1 and SZ-6; Botfalvai et al. 2015). The sedimentological (e.g. grain size, colour of the sediment and presence of the clayclasts on the bottom of the sandstone block) and taphonomical features (e.g. colour of the bones, *in-situ* breakage) of the 1st skeleton and the embedding sediment indicate that this incomplete skeleton most probably belong to the material of Unit 2 of site SZ-6.

*Taphonomic features*: Bones are not in original contact. They are not abraded and weathered, the articulation surfaces of ribs are undamaged, but the distal ends were not found on the field. The taphonomical features indicate that this part of the skeleton was not exposed to mechanical stress or impact during the transportation, but suffered significant destruction after accumulation. The bones are pressed to each other and *in situ* breakages were detectable in this assemblage where there were no displacements along the cracks. The *in situ* breakage is likely to have been caused by trampling in this case because not all of the discovered bones were pressed (e.g. the vertebral body was not deformed), which would be expected during the forceful sediment compaction. During mining the rest of the skeleton was removed, thus it is unknown how much and what kind of parts of skeleton were preserved in the original associated skeleton.

### 4.1.2. 2nd skeleton (holotype)

*Reference No.*: MTM 2007.26.1-2007.26.34. (Figs. 3-11).

*Year of discovery*: 2001.

*Material*: left and right premaxilla (Fig. 3a-d, e-g), right postorbital and jugal (Fig. 3n-o), ?left prefrontal, lacrimal (Fig. 3p, q), and frontal (Fig. 3i-m), posterior part of the pterygoid (Fig. 4f, g), left and right quadrate (Fig. 3h-k), condylus occipitalis (Fig. 4d, e), 22 teeth (Fig. 4m-q), one hyoid? bone, ?vomer (Fig. 4c), anterior end of left nasal (Fig. 4h), right fragmentary mandible (Fig. 4i-l), 3 cervical (Fig. 5a-k), 6 dorsal (Fig. 5l-o, Fig. 6a-d), fragments of the synsacrum (Fig. 6e-i), 10 caudal vertebrae (Fig. 6j-t), 9 cervical ribs (Fig. 4r-t), 38 complete or fragmentary dorsal (Fig. 4u) and 6 sacral ribs, 5 chevrons (Fig. 4v, w), 2 tendons, left complete (Fig. 7a-c) and right fragmentary scapulocoracoideum (Fig. 7d-e), left and right fragmentary ilium (Fig. 7h-k), left ischium (Fig. 7f, g), right femur (Fig. 7l, m), right fibula (Fig. 7n, o), phalanges and ungual phalanges (Fig. 7r-x), several dozens of osteoderms (Fig. 8-11): cervical half rings, dorsal scute-like osteoderms, rectangular pelvic armor fragments, caudal osteoderms.

*Description and comparisons*: This is the most complete ankylosaur specimen discovered in Iharkút so far and is the type material of *Hungarosaurus tormai*. Its initial description was done by Ősi (2005), and the reidentification of some bones has been made by Ősi and Makádi (2009).

Based on some later discovered specimens, the anterior end of the left nasal is preserved in the holotype (Fig. 4h). It is a relatively thin bone (max. 4-5 mm thick) and its dorsal surface is only slightly ornamented. Its medial margin is a straight edge with the anterior end receiving the nasal process of the left premaxilla (Fig. 4h). Its anterolateral margin is the dorsal edge of the external nares that is a relatively straight and posteriorly extended edge.

The armor of this skeleton (Fig. 8-11) among others consists of at least three bands of cervical half-rings which elements differ from those of *Struthiosaurus*. As noted in case of the cervical half-ring preserved in the 1st skeleton, the strongly posteriorly projected medial plate with concave posterior edge (Fig. 8a-d, 9a, b, e, f) markedly differs from the triangular, dorsally projected medial plate of *Struthiosaurus* (e.g. PIUW 2349/13, MTM VER 2016.507., MTM VER 2016.577.). In addition, the lateral plate in *Hungarosaurus*, though much lower than the medial one, is anteroposteriorly elongate and pointed posterodorsally (Fig. 8e, 9c), whereas that of *Struthiosaurus* (e.g. PIUW 2349/14, MTM VER 2016.507., MCNA 6532-6533) is higher than anteroposteriorly long, and triangular plate- or spike-like (Ősi and Rudolf 2017).

Ősi and Pereda-Suberbiola (2017) found evidence of a composit of polygonal pelvic armor elements in *Hungarosaurus* that is markedly different from that of *Struthiosaurus*. These elements are flat or only very slightly concave dorsally and has an interwoven texture ventrally, being characteristic for non-keeled pelvic osteoderms in ankylosaurs. In the holotype skeleton there is no evidence for the fusion of these polygonal osteoderms (Fig. 10h-k) as that seen in the 9th skeleton, however, this might have been the result of taphonomical biases (see below).

*Stratigraphic position:* This skeleton was discovered from a greyish-brownish siltstone layer (Unit 3) which is appropriate for the closing bed of SZ-6 site.

*Taphonomic features*: Skeletal elements of the holotype skeleton were in a disarticulated but associated position discovered from an area of 48 m$^2$. The skeleton is fragmentary (more than the half of the skeletal parts was broken) and the intact joints of limbs are often incomplete (see e.g. Fig. 7p, q). Abrasion was limited and the weathering features were not detectable on the bone surfaces. The broken pieces of coherent elements (e.g. skull and mandibular elements, synsacral elements, Fig. 6e-i) were situated close to each other in a delineated area (see Supplementary data 1.). The frequency of bones decreases from SSW to NNE, the maximum concentration of bones is in the SSW part of the SZ-2 site where dozens of bone elements were accumulated on each other. The percentage of total skeletal completeness was about 47% (see Supplementary Data 2). Based on the taphonomical investigations, the 2nd ankylosaur skeleton was disarticulated by biological affect (e.g. trampling, decay, predations/scavenging), and transportation was only slightly responsible for the disarticulation and dispersion (Botfalvai et al. 2015). The resistant elements, such as the synsacrum or skull can only be broken due to significant mechanical effects; however their dispersion was limited (see Supplementary Data 1.). These two factors may prove that trampling was a significant impact in the destruction of the 2nd ankylosaur skeleton, which is often the destruction agent in the soft substrate of abandoned channel environment (Capaldo and Peters 1995). The enclosing sediment indicates reduced current velocities which made the deposition of carcass possible. The carcass has been exposed to biological and mechanical agents (e.g. trampling, scavenging), but this exposure was not long enough for weathering or the carcass may have been covered (intermittently or continuously) with water, which saved the bone surfaces against subaerial destructive processes. Furthermore the vertebrate scavengers may removed bones or parts of the carcasses from the skeleton, which strongly reduced the percentage of skeletal completeness as it was pointed out in other vertebrate specimens (Hill 1979; Cameron and Oxenham 2012). The skeletal material of this incomplete skeleton represents different disarticulation sequences including both the earliest disarticulated (cervical vertebrate, ribs, osteoderms) and most resistant elements (limbs and lumbar vertebrate) together (according to Tooth 1965; Hill 1979; Hill and Behrensmeyer 1984; Cambra-Moo and Buscalioni 2003; Cameron and Oxham 2012), which indicate that the disarticulation of the skeleton began after the final deposition of the carcass and there is no evidence for (long term) transportation of the skeletal elements from a primary accumulation place to the final one.

### 4.1.3. 3rd skeleton

Reference No.: MTM 2007.24.1.-2007.24.10. (Fig. 12).

Year of discovery: 2001.

Material: two caudal vertebrae (Fig. 12a, b), proximal part of left ulna (Fig. 12h, i), right fragmentary femur (Fig. 12j, k), one metapodium (Fig. 12l, m), limb bone fragments including a possible distal end of humerus (Fig. 12e, g, n, o), five osteoderms including one pelvic osteoderm (Fig. 12p, q), one proximal chevron (Fig. 12c, d), rib and unidentifiable bone fragments.

*Description and comparisons*: Of the ulna only the proximal part is preserved (Fig. 12h, i), so its total length and proportions are unknown to prevent taxonomic assignment. The only diagnostic element of this skeleton is a polygonal unfused osteoderm suggested to be a pelvic armor element (Fig. 12p, q). The dorsal surface is slightly convex, with a very weakly developed bump in its central part. The ventral surface shows a slightly interwoven texture similar to those of the pelvic elements of the 2nd and 9th skeletons (Ősi and Pereda-Suberbiola 2017) or that of *Nodosaurus textilis* (Marsh, 1889: text-fig. 1). Its margin is receded to accept the surrounding osteoderms. Since this type of pelvic osteoderms are unknown in specimens of *Struthiosaurus*, and it resembles the flat, polygonal pelvic osteoderms of the holotype, here we support the earlier assignment (Ősi 2005) to refer the 3rd ankylosaur skeleton to *Hungarosaurus tormai*.

*Stratigraphic position:* Skeletal elements of MTM 2007.24 were discovered from the same greyish-brownish siltstone layer (Unit 3) with plant fragments as that of the 2nd, holotype skeleton, but is situated 20 cm higher up in this layer.

*Taphonomic features*: All of the limb bones were broken in the biostratonomic phase while the compact structure bones (e.g. metapodial and caudal vertebrae) were complete. The existing intact joints of the limbs were abraded (Fig. 12e, h, k), which may indicate mechanical damage of short term transportation or scavenging. The plastic deformation was detected on most elements (Fig. 12a, b) that resulted in a significant flattening of bones. This incomplete skeleton contains highly fragmented limb bones, which are one of the most resistant elements of the skeleton against disarticulation based on empirical observation (Tooth 1965; Hill 1979; Hill and Behrensmeyer 1984; Cameron and Oxham 2012). On the other hand the limb bones are one of the most popular food source for the scavengers due to their relatively high marrow wet weights (Capaldo and Peters 1995). The low skeletal completeness and the high fragmentation rate of the limb bone assemblage probably indicate that the scavenger animals (e.g. crocodiles) played a major role in the disarticulation processes of this skeleton.

### 4.1.4. 4th skeleton

*Reference No.*: MTM 2007.23.1.-2007.23.4; 2007.90.1., 2007.90.2. (Fig. 13).

*Year of discovery*: 2003.

*Material*: synsacrum with sacral rod and three sacral ribs (Fig. 13e, f), fragmentary left and right ilia (Fig. 13g, h), left and right ischia (Fig. 13a, d), boomerang shaped, fused, central osteoderm with two conical spikes (Fig. 13i-o), small oval osteoderm.

*Description and comparisons*: Though the synsacrum is known in almost all the ankylosaur skeletons from Iharkút, it does not bear unambiguous diagnostic characters to distinguish *Hungarosaurus* and *Struthiosaurus*. Some difference between the ischia of the two genera has been documented (Ősi and Pereda-Suberbiola 2017). In *Struthiosaurus* (UM2 OLV-D50) the ischium lacks a blunt, anteroposteriorly expanded, knob-like structure at its distal end that is not present in *Hungarosaurus*.

The most peculiar element of this skeleton is a thick, boomerang shaped central osteoderm with two conical spikes projecting slightly posteriorly (Ősi 2005, Fig. 13a-o). Fragments of this osteoderm is also known in the 9th skeleton (see below), which can be certainly referred to *Hungarosaurus* on the basis of the posteriorly projecting plates of the cervical half-rings. This indicates that the 4th skeleton can be also referred to *Hungarosaurus* as it was suggested by Ősi (2005). A conical spike, being almost identical both in size and shape with the spikes from Iharkút and being probably a fragment of a larger symmetrical central osteoderm, is known in the Muthmannsdorf (Austria) ankylosaurian material (PIUW 2349/15, Bunzel 1871; Seeley 1881; see Ősi and Pereda-Suberbiola 2017 for comparison). The position of this boomerang shaped osteoderm is still ambiguous. Since it was associated with pelvic elements, as the only remains of the 4th skeleton, we suppose its position on the posterior pelvic or anterior caudal region (Ősi and Makádi 2009).

*Stratigraphic position:* The skeletal elements were discovered in the Unit 1 layer of SZ-6 site. The bone-yielding beds are composed of grey sand and clay clasts. A seven-meter-long angiosperm tree trunk was found near the skeletal elements suggesting high density (energy) flow depositional environment.

*Taphonomic features*: All of the skeletal elements were broken in the biostratonomic phase (oblique fracture type), suggesting a significant biological or physical impact before the fossil diagenetic phase of bones. Plastic deformation can be observed on the synsacrum and ilia, and mechanical damage was not remarkable on the bones' surfaces. Pelvic girdle elements alike were in an articulated position when they were deposited, because the disarticulation had preceded the scattering.

4.1.5. 5th skeleton

*Reference No.*: MTM 2007.25.1.-2007.25.30. (Figs. 14-17).

*Year of discovery*: 2006.

*Material*: left mandible (Fig. 14b), right dentary (Fig. 14a), three dorsal vertebrae (Fig. 14c-e), synsacrum with sacral ribs (Fig. 14j, k), 15 caudal vertebra (Fig. 14l-t), various complete and fragmentary dorsal ribs (Fig. 14f), three fragmentary cervical ribs (Fig. 14g), four chevrons (Fig. 14h, i), one paravertebral element (Fig. 14u), left scapulocoracoid (Fig. 15a), right humerus (Fig. 15i, j), both ulnae (Fig. 15m-p) , ?right radius (Fig. 15k, l), eight metapodium (Fig. 16i-p), both ilia (Fig. 15c-f), right ischium (Fig. 15g, h), both femora (Fig. 16a-d), ?right tibia (Fig. 16g, h), left fibula (Fig. 16e, f), two phalanges (Fig. 16v, w), two ungual phalanges (Fig. 16r, u), three cervical half-ring osteoderms (Fig. 16x-a', Fig. 17a-f), 60 oval, circular or lance-shaped dorsal osteoderms (Fig. 17g-r), and one crested caudal osteoderm (Fig. 17s-u).

*Description and comparisons*: The most important elements of this skeleton was described by Ősi and Makádi (2009), but a few notes can be added here. Diagnostic elements are the fused, double-plated cervical half-rings (Fig. 16x-a') where both the medial and lateral plates project posteriorly. Based on the mandibular features and those of the cervical half-rings this skeleton can be referred to *Hungarosaurus*.

Dental wear analysis fulfilled on the *in situ* teeth of this specimen shows that a palinal jaw movement completed the powerstroke of *Hungarosaurus* (Ősi et al. 2014b). Although the teeth of *S. languedocensis* from France (Garcia and Pereda-Suberbiola 2003; Ősi et al. 2016) and those referred to *S. austriacus* (Nopcsa 1929) also bear dental wear due to tooth-tooth contact (precise shearing bite), scratch orientation is still unknown thus the direction of jaw movement in *Struthiosaurus* is ambiguous.

*Stratigraphic position*: MTM 2007.25 was discovered from the strongly cemented grey sandstone bed (Unit 2), which is the covering bed of the most important fossiliferous layer (Unit 1).

*Taphonomic features*: The fifth skeleton is associated and the elements are not abraded or weathered. The osteoderms and ribs were broken (in most cases, damage category cannot be detected), but the limbs, vertebrae, mandibular and pelvic girdle elements are mostly complete. The epiphyses of limb bones were complete and the dentaries with well preserved teeth were found. The percentage of total skeletal completeness of this skeleton is about 21% (see Supplementary Data 2). The enclosing sediment (coarse sandstone), composition (several parts of the body are represented in the material) and taphonomical features of the 5th ankylosaur skeletal material indicate that when the carcass was floated by currents into the site, some soft tissue (ligaments, muscles) should have kept together the parts of the body (this is also suggested by two articulated dorsal vertebrae, the only elements preserved in articulated position). The fore- and hindlimbs, lumbar vertebrae and mandibles preserved within the skeleton indicate that the disarticulation process had not really started until the carcass stopped and became covered by sediment, because the limbs in terrestrial tetrapods become easily detached from the girdle region in early stage of decomposition (see e.g. Tooth 1965; Dodson 1971; Cameron and Oxham 2012). When the transportation of the carcass stopped, currents were still sufficiently enough to slightly move the parts of the body and progressively dislocated some skeletal elements. The skull or its elements were not found in the skeletal material due to the decay processes. Experimental data on vertebrate carcasses shows that the skull is usually the first element being separated from the body by transportation or decay and therefore it often deposited in a different place (Dodson 1971; Capaldo and Peters 1995). Nevertheless, the mandibles were preserved with deposited elements questioning an early disarticulation of skull. However, empirical data on disarticulation sequences show that while the lower jaws are usually preserved close to the other parts of the skeleton, after being disconnected, the skull is more easily moved away from them by currents (Tooth 1965; Dodson 1971; Holz and Barberena 1994; Capaldo and Peters 1995).

### 4.1.6. 9th skeleton

*Reference No.*: MTM PAL 2016.16.1. (Fig. 18-20).

*Year of discovery*: 2014.

*Material*: posterior half of right mandible (Fig. 18a, b), atlas (Fig. 18f, g), six fragmentary dorsal vertebrae (Fig. 18h-l), one fragmentary neural arch, one fragmentary cervical rib (Fig. 18c), several fragmentary dorsal ribs (Fig. 18d, e), very fragmentary synsacrum, one fragmentary caudal vertebra (Fig. 18m-p), left scapula with the glenoidal fragment of coracoid (Fig. 19a, b), proximal and distal ends of left humerus (Fig. 19c, d), proximal end of right humerus, proximal part of an ulna (Fig. 19e), one ischium (Fig. 19f, g), fragmentary ilium, distal end of femur (Fig. 19h), proximal fragment of tibia, distal end of a metapodium (Fig. 19i, j), two ungual phalanges, three fragmentary cervical halfrings (Fig. 20a), five blocks of fused, polygonal pelvic osteoderms (Fig. 20h-k), fragments of the boomerang shaped central osteoderm with conical spikes (Fig. 20l-n), circular, oval dorsal and/or pelvic osteoderms (Fig. 20d-g), and one crested caudal osteoderm (Fig. 20o, p).

*Description and comparisons*: Among the cranial remains, only a posterior half of the right mandible is preserved (Fig. 18a, b). The coronoid process is complete, showing the insertion surfaces of the external adductor muscles. The prearticular and posterior parts of the splenial are preserved but they were slightly compressed lateromedially. The posterior edge of the splenial is slightly concave bordering anteromedially the mandibular adductor chamber. The suture between the splenial and angular can be observed in medial view, that is perforated by a one centimeter large, anteroposteriorly elongate foramen. The articular region is similar to that of the holotype mandible of *Hungarosaurus*, but the glenoid is compressed lateromedially. The retroarticular process is only a one centimeter long knob-like structure. Laterally, the posterior end of the mandible is ornamented by an oval-shaped, well pitted osteoderm that is completely fused to the angular-surangular block suggesting a subadult or adult ontogenetic status of this specimen (Hill et al. 2003).

Of the axial column the vertebrae are fragmentary and show the same features as those seen in the holotype specimen of *Hungarosaurus*. This skeleton, however, contains a nearly complete, dorsoventrally slightly complete atlas (Fig. 18f, g) that was still unknown in any ankylosaur from Iharkút. The centrum of the atlas is as long as wide and the neural arch and the ribs are completely fused to the centrum. Whereas the end of the right rib is broken, the left one is complete having a length of 7.3 cm. The hypapophysis cannot be observed due to the compaction of the specimen. The anterior articulation surface is deeply concave. This atlas is very similar to that of *Struthiosaurus transylvanicus* (Nopcsa 1929) both in size and in general morphology.

From the synsacrum only the possibly three sacral vertebrae and ribs are preserved in very poor condition (broken into hundreds of small pieces). The fragmentary left scapulocoracoid (Fig. 19a, b) is preserved showing similar size and morphology to that of the holotype specimen. The acromion process extends from the dorsal edge of the scapular blade and projects anteroventrally toward the insertion surface for M. supracoracoideus anterior. In this specimen, the very end of the acromion process is preserved showing a rugose articulation surface. The scapula and coracoid are massively fused.

The left humerus is more complete than the right one, having the proximal and distal parts preserved (Fig. 19c, d). The bicipital crest is more or less preserved. It has a straight medial margin, and proximally it is not separated from the humeral head by a demarcation as in *Struthiosaurus* (Ősi and Prondvai 2013). The proximal surface of the bicipital crest is ornamented by a rugose insertion surface that seems to be more developed than in *Struthiosaurus*. The posterior surface of the shaft and deltopectoral crest is not preserved. Thus, it is unknown whether the muscle insertion areas documented here in *Struthiosaurus* were present here or not. The distal end of the humerus is relatively wide lateromedially, but this might be also the result of strong anteroposterior compression. Distally the lateral and medial condyles are similar in size. The lateral condyle is bordered laterally by a massive, rugose ectepicondyle whereas the medial condyle has also medially a shallow, anteriorly grooved medial entepicondyle. Though the shaft of the humerus is unkwown, based on its proximal part, it much more resembles to the humerus of *Hungarosaurus* than that of *Struthiosaurus*. A proximal fragment of one of the ulnae is preserved. Its humeral articulation is missing, but most of the olecranon process is preserved. It is quite elongate proximodistally being almost identical to that of the fifth skeleton (Ősi and Makádi 2009) suggesting a similarly long ulna of the 9th skeleton.

From the pelvic elements, one straight ischium (Fig. 19f-g) and some poorly preserved fragments of the ilium are preserved. The ischium is quite similar to that of the holotype, the 4th, 5th, and 6th skeletons in general morphology. Some slight difference in the anteroposterior curvature of the ischial shaft can be observed that is partly due to diagenetic processes.

Among the femora, a distal end (Fig. 19h) is present that is strongly compressed lateromedially. As usually seen in ankylosaurs (Vickaryous et al. 2004), including *Struthiosaurus austriacus* as well (Seeley 1881), the distal condyles are massive and well developed anteroposteriorly.

A significant part of the dermal armor is preserved in the 9th skeleton. Of the cervical-pectoral region, fragmentary half-rings with posteriorly projected plates (Fig. 20a) are present, clearly indicating the *Hungarosaurus* affinity. After the 4th skeleton, this 9th skeleton provides evidence for the boomerang shaped central osteoderm with two posteriorly projecting spikes. In this specimen one of the broken conical spikes (length ca. 17 cm, Fig. 20l, m) and an eight-centimeter-long anaterolateral fragment of the boomerang shaped base (Fig. 20n) are preserved. The conical spike is anteroposterioly compressed and has a strongly rugose anterior surface of the bone. The basal fragment bears the anteromedial basal margin of one of the conical spikes that should have been originally completely ossified with the basal element, and has an anteromedially oriented crest along the anterolateral margin of the osteoderm (Fig. 20n).

Besides these dermal elements, the 9th skeleton consists of at least eight oval shaped, fragmentary keeled osteoderms from the dorsal and/or the pelvic region and six larger and many small fused blocks from the pelvic armor (Fig. 20h-k). These fused blocks are composed of non-keeled, flat or slightly convex, polygonal elements that were partly or completely fused above the pelvic and synsacrum (Ősi and Pereda-Suberbiola 2017).

Based on the morphology of the humerus and that of the cervical half-rings and pelvic osteoderms, we follow Ősi and Pereda-Suberbiola (2017) in assigning this specimen to *Hungarosaurus*.

*Stratigraphic position*: Remains of the 9th skeleton were discovered from a greyish/bluish siltstone located between two hydromorf paleosol horizons. This siltstone crops out in the same stratigraphic level as the channel fill deposit of site SZ-6 and shows a weak lateral connection to the basal breccia layer of Unit 1. Based on the field observations, we suggest that this bone-bearing horizon can be interpreted as a floodplain deposit situated close to the channel fill deposit of site SZ-6.

*Taphonomic features*: Skeletal elements of the 9th skeleton were in a disarticulated but associated position, discovered from an area of 14 $m^2$ and the percentage of total skeletal completeness was about 17% (see Table 1). The bones were not abraded or weathered but most of them were broken before the bone fossilization (oblique and longitudinal breakages). Most of the skeletal elements are cracked due to the sediment compaction (similar to that described by Evans et al. 2015) and the broken end of limb bones frequently show the type of the rotting bone modification (e.g. naturally excavated trabecular bone of Eberth, 2015). The 9th skeleton contains different skeletal elements from the earliest and the latest disarticulation sequences (vertebrae, limb bones and mandibular fragments were present together, as in other vertebrate examples: Cambra-Moo and Buscalioni 2003), indicating that the disarticulation began after the final deposition of the carcass. The taphonomical history of this incomplete skeleton is similar to that presented at 2nd and 5th skeletons where the percentage of skeletal completeness were higher, and the enclosing sediment indicates reduction in flow velocity compared to the other skeletal materials from the Unit 1 of site SZ-6.

### 4.1.7. Isolated material

*Year of discovery*: 2001-2017.

*Material and reference number*: basicranium with partial skull roof (MTM PAL 2013.23.1), postorbital region (MTM V 2010.1.1), premaxilla–maxilla fragment (MTM V.2003.12); left fragmentary postorbital (MTM 2007.28.1), boomerang shaped central osteoderm fragments with conical spikes (MTM VER 2017.66, VER 2016.578, VER 2016.578).

*Description and comparisons*: Of the isolated cranial remains, a partial skull with the basicranium and central part of the skull roof has been described by Ősi et al. (2014a) and the premaxilla–maxilla fragment and left fragmentary postorbital were described by Ősi and Makádi (2009). In addition, an orbital rim preserving the typical anteroposteriorly oriented postorbital crest and the ventrally pointed jugal horn has been also referred to *Hungarosaurus tormai* (Ősi et al. 2012).

Multiple fragments of the boomerang shaped central osteoderm with conical spikes have been described by Ősi and Makádi (2009) and Ősi and Pereda-Suberbiola (2017).

*4.2.* Struthiosaurus sp.

Nodosauridae Marsh, 1890

*Struthiosaurus* Bunzel, 1871

*Revised diagnosis*. Pereda-Suberbiola and Galton (2001) gave the last diagnosis of the genus that is used and extended here. Armored dinosaur, estimated body length ca. 2.5–3 m. Differs from all other known ankylosaurs in having relatively narrow, high occipital region, ventrally projected basisphenoid; small, oval, almost symmetrical distal quadrate condyle; longer than wide cervical vertebrae; ridge-like lesser trochanter of the femur; three cervical bands (saggitally unfused half-rings) with two, fused, complex elements in each band. Cervical armor elements built up by the fusion of: a high, triangular, posteriorly not bending lateral plate with straight or slightly convex anteroposterior edge; a central base formed by two to sixteen, circular to polygonal, sometimes pointed or crested osteoderms; and a medial, dorsally or slightly posterodorsally oriented, short triangular plate or spike. Pelvic armour is composed of oval-shaped, crested osteoderms that are surrounded by a fused matrix of small polygonal osteoderms, and these oval, crested osteoderms are present centrally just above the fused neural arch of the synsacral vertebral series as well (Ősi and Pereda-Suberbiola 2017).

Cf. *Struthiosaurus* sp.

### 4.2.1. 8th skeleton

Reference No.: MTM PAL 2013.59.1. (Fig. 21).

Year of discovery: 2013.

*Material*: two posterior dorsal vertebrae (Fig. 21a-d), a dorsal rib, left ilium with articulated elements of a fragmentary synsacrum and sacral ribs (Fig. 21e-h), five articulated osteoderms (Fig. 21e, g).

*Description and comparisons*: This partial hip region was described in detail by Ősi and Pereda-Suberbiola (2017) and referred to as cf. *Struthiosaurus* sp. The most important and diagnostic part of this specimen is the pelvic armor region that certainly differs from that of *Hungarosaurus* in having at least four (but probably five) centrally positioned oval to subcircular crested osteoderms positioned just above the neural arch of the sacral vertebrae. The crest of the osteoderms is slightly higher posteriorly than anteriorly. In the 12th skeleton, almost identical osteoderms were present at least lateral to the anterior central osteoderms and they were fused together with small polygonal shaped osteoderms just above the last dorsal ribs. In addition, these types of crested osteoderms are present in the Laño (Spain) ankylosaur material (see Pereda-Suberbiola 1999) strengthening the view that both the 8th and the 12th skeletons belong to *Struthiosaurus*.

*Stratigraphic position*: This partial skeleton was discovered from the basal breccia layer (Unit 1) of site SZ-6 from an area of 0.2 m$^2$. From this year (2013) the geodetic survey of the site made it possible to create and maintain a 3D model of the bone-bearing layer (Unit 1) and to analyse the spatial distribution of the bones. At the location of the 8th skeleton the Unit 1 thins to 30–35 cm and the parts are positioned 17–31 cm from the base layer of the bone-bed.

*Taphonomic features*: The remains of the 8th nodosaurid skeleton include different bones of the pelvic region and two additional bones (dorsal vertebra and rib) from the more distal parts of the dorsal axial skeleton. The bones of hip region show articulate preservation where most of the elements were retained in their original anatomical position, while the two dorsal vertebrae and a rib were preserved disarticulated but in associated position. The taphonomic history of this partial skeleton could have been similar to that of the 6th skeleton (both of them were discovered from the same horizon and represent bones from the hip region in articulated position) with the exception that in this case three additional bones were also preserved next to the articulated skeletal parts. The last two free dorsal vertebrae and the left posterior dorsal rib were preserved close to the anterior end of the sacral rod (almost in original anatomical position, see Supplementary data 1) indicating that the disarticulation of the vertebrae and the rib occurred after the deposition. *In situ* preservation of the central osteoderms on the sacral rod also indicates that the partial skeleton was buried relatively shortly after the time of deposition. The elements are distributed along a WNW-ESE axis (Fig. 22).

### 4.2.2. 12th skeleton

*Reference No.*: MTM VER. 2016.3567., MTM PAL 2018.5.1. (Fig. 23).

*Year of discovery*: 2016.

*Material*: a fragmentary sacral rod (Fig. 23b), one larger block of two posterior dorsal or sacrodorsal ribs with a composite of articulated osteoderms (Ősi and Pereda-Suberbiola 2017; Fig. 23f), one larger (ca. 8 cm) piece of the right ilium (Fig. 23d) and a smaller piece of the anterior part of the ilium with two rib fragments (Fig. 23i, j), 16 rib fragments (Fig. 23a, c), 2 large (9 cm ×10.5 cm) triangular, plate-like osteoderms, four pieces of fused block of osteoderms (Fig. 23e), 40 small to medium sized (up to 12 cm) oval to circular, low keeled osteoderms, and over 10 small (<3 cm) ossicles (Fig. 23g-h, k-v).

*Description and comparisons*: Based on rib size, preserved underneath the fused osteoderms (Ősi and Pereda-Suberbiola 2017), this partial skeleton belonged to a relatively small individual (up to 2.5–3 m). Parts of the pelvic/sacral region are preserved and probably most of the osteoderms also represent this region (Fig. 23d-f). However, they were only associated elements, and thus, this hypothesis cannot be proved at the moment.

The sacral rod contains three very poorly preserved, fused posterior dorsal vertebrae and they lack the whole neural arch (Fig. 23b). Of the ilium fragments the dorsal surface of the larger piece (Fig. 23d) shows similar interwowen structure as those of many non-keeled pelvic armor elements (Ősi and Pereda-Suberbiola 2017).

The two large, plate-like osteoderms are close to identical in morphology. They have a deeply excavated, spongious ventral attachment surface and straight to slightly convex anterior and posterior edges of the plates. The material contains a block of fused osteoderms (MTM VER. 2016.3567), which were preserved with two rib fragments ventral to them (Fig. 23f). It is composed of two subcricular, crested osteoderms surrounded by fused, small polygonal elements. This specimen was described by Ősi and Pereda-Suberbiola (2017) in detail, and, based on osteoderm morphology and composition, it is referred to *Struthiosaurus*. Four additional armor elements are preserved in this assemblage. One of them contains a larger, keeled osteoderm that is fused on one side with two small flat osteoderms (Fig. 23e). The keeled osteoderm is almost identical with those preserved in the 8th skeleton above the neural spines. The three other fused blocks contains small, non-keeled, flat elements which most probably were situated between the keeled elements.

Besides thes fused elements, a great number of smaller osteoderms were found in a small, but quite dense accumulation. These osteoderms represent two different morphotypes: the first is the classical, oval-shaped osteoderm with a shallow, longitudinal keel positioned more or less centrally (Fig. 23g, h, u, v); the second type is usually 2–4 cm large, circular or slightly rhomboidal scute with only a very shallow, diagonal ridge (Fig. 23s, t).

*Stratigraphic position*: The skeletal elements were discovered from the basal breccia layer (Unit 1) of the channel fill deposit at the site SZ-6. Though this specimen came from the basal breccia layer, it was excavated from a tectonically separated block ca. 100 m southwards from the main locality within the open-pit, preventing the geodetic measuring of the bones and connection them to the main assemblage measured between 2013 and 2017.

*Taphonomic features*: The 12th skeleton shows relatively high percentage of skeletal completeness (about 9%) because several part of the pelvic region including *in situ* pelvic osteoderms are preserved in this material (see Table 1). The sacral region was broken in the biostratonomic phase (oblique and longitudinal fracture type), suggesting a significant biological or physical impact before the fossil-diagenetic phase of bones. All of the elements of 12th skeleton represent a low food value due to their limited marrow content, which probably suggest that the scavenger effect might have been significant during the disarticulation. The scavengers preferably consume the bones with high marrow content (e.g. limb bones) because these elements are the most nutritious parts of the prey, while most of the marrow-poor elements remain intact (Capaldo and Peters, 1995). The predominance of marrow-poor bones in the assemblage of the 12th skeleton suggests that the carcass suffered scavenging by selective carnivores that removed the most nutritious part of the prey, leaving behind mainly osteoderms and ribs as it was documented in other vertebrate accumulations (e.g. Haynes 1980; Behrensmeyer 1991; Müller et al. 2015). Theropod teeth, or bitemarks as direct evidence of scavenging were not found associated with the skeletal material.

### 4.2.3. Isolated material

*Year of discovery*: 2001-2017.

*Material and reference number*: right humerus (MTM PAL 2012.30.1), six cervical armor elements (MTM VER 2016.507., VER 2016.541., VER 2016.577., VER 2016.579., VER 2016.580., VER 2016.580.), fused block of pelvic armor (MTM VER 2018.836.)

*Description and comparisons*: A right complete humerus has been described in detail by Ősi and Prondvai (2013). Based on histology, this small sized (21.5 cm) specimen represents a fully grown adult animal. It is markedly differs from the humerus of *Hungarosaurus* in having a very short shaft, massive, laterally well expanded deltopectoral crest and a quite divergent distal epiphysis.

Three complex cervical armor elements can be referred to *Struthiosaurus* (Ősi and Rudolf 2017). Though their detailed description is in progress (Rudolf, in prep.), their most important character is that the lateral plate is triangular with straight or slightly convex distal edge and the plate project laterally and not posterolaterally as those of *Hungarosaurus*.

A fused block of the pelvic armor is almost identical to that of the 12th skeleton. Two subcircular crested osteoderms are fused together with small polygonal shaped osteoderms surrounding them. The crest of the large osteoderms is slightly higher posteriorly than anteriorly.

## 4.3. Nodosauridae indet.

### 4.3.1. 6th skeleton

*Reference No.*: MTM PAL 2013.58.1. (Fig. 24).

*Year of discovery*: 2012.

Material: complete hip region with sysnsacrum, articulated ilia, ischia, and right pubis, sacral and dorsal ribs.

*Description and comparisons*: Based on ilium length, MTM PAL 2013.58.1. represents one of the largest ankylosaur specimens from Iharkút being nearly equal in length to the fifth skeleton of *Hungarosaurus*. The specimen is slightly compressed dorsoventrally and lateromedially, thus the sacral rod is weakly rotated along its long axis, and slightly compressed lateromedially (Fig. 24). The ischia were pushed laterally and medially close to the ventral surface of the acetabular region (Fig. 24a). The distal end of the left ilium is slightly rotated and deformed as well. The synsacrum is composed of six posterior dorsal, one sacrodorsal, three sacral and one sacrocaudal vertebrae (so altogehter 11 vertebrae) that are massively fused to each other (Fig. 24a). The neural arch of the whole synsacrum is fused into a massive block. The dorsal end of the neural spines are fused into a single elongate block as well, and are slightly wider lateromedially than the rest of the spines (Fig. 24b).

Dorsal ribs are ankylosed with the posterior dorsal vertebrae (Fig. 24a) and laterally they fused to the ventral side of the ilia. Hourglass shaped sacral ribs strongly connect the sacral vertebrae to the acetabular region of the ilia. Ischia bend slightly anteriorly as seen in specimens of *Hungarosaurus*. The acetabulum is deep and rounded bordered medially-posteromedially by the ischium and anteromedially by the pubis. In this specimen only the right pubis is preserved that is ca. 10 cm long, elongate and curved posteriorly. Due to compression it is lying on the ventral surface of the right ilium just in the line of the first sacral rib. Anteriorly, the lateral margin of the ilium sligthly diverges laterally, whereas just behind the level of the acetabulum it abruptly bends posteromedially with an angle of ca. 70°. The posterior end of the ilium is proportionally slightly longer and more pointed posteromedially than that of *Struthiosaurus languedocensis*.

To sum up, based on the shape of the ilium and its size, this specimen is slightly more similar to *Hungarosaurus* than to *Struthiosaurus*. However, there is not enough diagnostic features at present to certainly refer it to any genus.

*Stratigraphic position*: The MTM PAL 2013.58.1. is an articulated skeleton from the Iharkút mine and was discovered from the basal breccia of SZ-6. This fossiliferous layer is composed of grey sand and clay clasts with plant fragments and isolated bones. It was situated on the boundary of the coarse sand and clay clasts horizons, 10 cm above the greenish clay layer.

*Taphonomic features*: Though slightly compressed dorsoventrally, the bones were undamaged and most of the elements were retained in their original anatomical position. The greatest width was 63 cm and the length was 71 cm of the articulated segment, and the orientation was SSW to NNE, i.e. similar to that of the 2nd skeletal material. The original skeleton presumably began to decompose by biological or physical effects after transportation and the parts of the skeleton were separated to each other. The pelvic girdle may remain articulated far longer than the other parts of the body because their elements were ossified and hardly connected by ligaments and other connective tissues. It is plausible that these parts of the ankylosaur skeleton might have been dispersed by water with different flow rates compared to the others (Nasti 2005), because the hydraulic transport potential of articulated remains is often greater than that of the disarticulated bones (Coard and Dennell 1995). After deposition it was not exposed to be trampled and for scavenger effect so bones could remain together in their original position.

4.3.2. 7th skeleton.

*Reference No.*: MTM PAL 2013.57.1. (Fig. 25).

*Year of discovery*: 2012

*Material*: dorsal rib fragments (Fig. 25c, d), fragmentary synsacrum with sacral ribs and sacral rod (Fig. 25e, f), fragmentary anterior caudal vertebra (Fig. 25a), partial left and right ilia (Fig. 25g-j), one ischium fragment, few complete (Fig. 25k, l) and fragmentary osteoderms including some fused pelvic osteoderms.

*Description and comparisons*: Of this very poorly preserved skeleton most elements are non-diagnostic. The caudal vertebra is compressed and only the centrum is preserved (Fig. 25a).

From the synsacrum, the sacral rod composed of four fused vertebrae and the two anterior sacral vertebrae are preserved, but their dorsal surface with the neural arch is strongly eroded. Among the sacral ribs, the medial chunk of the two first sacral ribs and one broken sacral rib are preserved.

One large bone fragment might be a piece of a scapulocoracoid bearing a small surface with rugose articular surface. Of the right ilium, most of the pre-acetabular part including the anterior and anteromedial side of the acetabulum is preserved (Fig. 25g, h), but the medial side with the sacral and posterior dorsal rib connections are missing. From the left ilium, only one larger piece of the pre-acetabular segment is preserved (Fig. 25i, j).

Among the few armor elements, three oval shaped, longitudinally crested osteoderms are present. In the largest one the crest is quite eroded. The second largest osteoderm is a marginal element with posteriorly projecting, slightly laterally bending shallow crest (Fig. 25k, l).

The fourth preserved osteoderm is a triangular plated element that should have been from the lateral side of the body. Two additional pieces of thin and flat elements do not bear any crest or protuberance dorsally, and they might be from the medial part of the ilium. Their ventral and dorsal surfaces are quite eroded and no interwoven texture, characteristic of non crested, pelvic osteoderms (Ősi and Pereda-Suberbiola 2017), can be seen.

*Stratigraphic position*: MTM PAL 2013.57.1. is a partial skeleton discovered from the basal breccia layer of SZ-6 site.

*Taphonomic features*: The remains of this associated skeleton show significant fragmentation with fractures formed in the biostratonomic phase of bones. The bones were not abraded or weathered. All of the bones were related with the pelvic region, thus this assemblage is considered as a partial skeleton. The taphonomic history of this partial skeleton could have been similar to that of the 4th skeleton, because both of them contains the similar pelvic-sacral elements and they were discovered from the same horizon of the Iharkút mine (Unit 1 of site SZ-6).

### 4.3.3. 10th skeleton

*Reference No.*: MTM PAL 2018.3.1. (Fig. 26).

*Year of discovery*: 2014.

*Material*: one distal caudal vertebra, four dorsal rib fragments (Fig. 26a, b), one fragmentary tendon, one metapodium (Fig. 26c), and three dozens of osteoderms (Fig. 26d-r).

*Description and comparisons*: The caudal vertebra, the dorsal ribs and the metapodium have the typical ankylosaurian morphology, but they do not bring any low-level taxonomical information. Of the osteoderms, the classical oval to circular-shaped forms with a shallow or more developed crest are the most frequent elements (Fig. 26d-r). Three of these are longitudinally quite elongate reaching the length of 9–12 cm (Fig. 26j-l). One flat, pentagonal osteoderm has an interwoven texture ventrally (Fig. 26m) as seen on the polygonal elements of the 9th skeleton referred to *Hungarosaurus*. There is a block of two fused osteoderms, composed of a larger and a smaller one, each of them having slightly convex dorsal surface and polygonal to rounded shape. These osteoderms might suggest the *Hungarosaurus* affinity but more material, i.e. larger, more complex blocks of the pelvic armor would be essential to justify this hypothesis.

*Stratigraphic position*: The bones of the 10th skeletons were discovered from the lowermost part of Unit 2 of site SZ-6 from an area of 5 m$^2$. The embedding sediment is medium grained sandstones which is a transition horizon from the Unit 1 to the Unit 2. This bone-yielding level is only a few centimenters thick horizon where several nodosaurid osteoderms and ribs were discovered close to each other. The remains were subject of a piecewise geodesic survey producing high resolution 3D data. The material is distributed in an elongated-shaped area which longer axis strikes WNW-ESE (Fig. 22).

*Taphonomic features*: The material of the 10th skeleton contains nearly the same sized isolated bones from different parts of the body raising the possibility that this material resulted from the processes of hydraulic concentration and not necessarily represent bones from the same individual. However, the dispersal potential of the disc- (e.g. osteoderms) and the rod-like (e.g. ribs) bones is significantly different (Frostic and Reid 1983), which probably contradicts the theory of hydraulic concentration in this specimen. Furthermore, the remains of the 10th skeleton were situated close to each other in a very thin horizon and represent different shape, density bones from the same taxon. The mentioned taphonomic features indicate that this material represent bones from a single individual. However, based on the available anatomical and taxonomical data (especially the lack of sacrum that is present in most of the other skeletons), it cannot be excluded that this material is not part of another skeleton mentioned in the text. Among the other unearthed skeletons, the 11th was found closest to the 10th skeleton (Fig. 22). The 11th skeleton was discovered from almost the same horizon of the Unit 2 of site SZ-6 and the bone mapping data and its analyses raise the possibility that the 10th and 11th partial skeletons represent different body parts of the same carcass (see the analysis of the 11th skeleton below).

To estimate the probability of the relation between the 10th skeleton and further isolated Nodosauridae indet. remains, a geometric analysis was done (see Albert et al. 2017). For the analysis the 3D stratigraphic model of the Unit 1 and the geodatabase of the findings were used. The method searches for those findings that belong to the same category (in this case they were all Nodosauridae) and located within a certain buffer distance from each other. Using the maximum spatial distance that was calculated from the associated bone material of the 10th skeleton, a query was done in the database to select those findings that belongs to the

Nodosauridae category and are positioned less than 40 cm from each other. Since the skeleton is situated only a few centimeter above the border of Unit 1 and 2, the result of the query was filtered for this horizon excluding those results that are positioned at the bottom level of Unit 1 (Fig. 22). The spatial connections forming a 3D network may give hints about those findings that are discovered, but yet unidentified parts of the skeleton (isolated materials). Most of these records are categorized as osteoderm fragments, but a few ribs, vertebrae and tendons were also amongst them. Unfortunately these elements are not definitive enough to use them for more precize taxonomic assignment. However, the density of the created network of associated findings can also indicate taphonomic features. It was discovered that the WNW-ESE striking elongated area of the 10th skeleton has a high network density in the western and lower network density in the Eastern end of the area (see Fig. 22). It may refer to the flow direction of the river from west to eastwards, which scattered the material downstream.

### 4.3.4. 11th skeleton

*Reference No.:* MTM PAL 2018.4.1. (Fig. 27).

*Year of discovery:* 2016.

*Material*: synsacrum (Fig. 27a-b, h-i), sacral ribs, almost complete left (Fig. 27c) and fragmentary right ilia (Fig. 27f-g), and osteoderm (Fig. 27d-e).

*Description and comparisons*: The synsacrum is composed of four or five fused posterior dorsal, three sacral, and one sacrocaudal vertebra (Fig. 27a) and shows the same morphological features as those described in the other skeletons. The left ilium preserves most of the pre- and postacetabular parts with a lateral outline (Fig. 27c) similar to that of the 5th and 6th skeleton. The acetabular region is poorly preserved. A single, high keeled osteoderm was preserved associated with the pelvic-sacral elements which, based on its hollow base, was part of the anterolateral caudal armor (Fig. 27d, e).

*Stratigraphic position*: The position of the 11th skeleton is nearly the same horizon as that of the 10th mentioned above (lowermost part of Unit 2). It was discovered in an area covering 0.25 $m^2$. Due to the preliminary preservation processes, the parts of this skeleton were not subjected to piecewise geodetic survey. The location was reconstructed on the map based on photodocumentation (Fig. 22).

*Taphonomic features*: The specimen was accidentally unearthed by the excavator when cleaning the overburden of the SZ-6 site, thus only a few information is available from the original position of the bones (see Supplementary Data 1). All bones of the 11th skeleton were related with the pelvic region, thus this material is considered as a partial skeleton. The bones are well preserved and most of them are complete. The sacral ribs are almost complete and fused to the sacral vertebrae while the ilium is disarticulated but show an associated position with the sacral region. The ischium is absent from the material, which is an unexpected phenomenon because all of the pelvic-sacral blocks discovered from Iharkút site contains at least one fragmentary ischium. Based on the available taphonomical characters, the taphonomical history of the 11th skeleton could have been similar to that of the 4th and 7th skeletons mentioned in the text above.

The Nodosauridae indet. material was also subjected for spatial analysis in the vicinity of the 11th skeleton using the same parameters as in the case of the 10th one. Within sixty centimeters, osteoderm and rib fragments were detected showing high network density that refers to close association level. Furthermore, the direction, bearing the strike axis of the 10th skeleton, points towards the location of the 11th skeleton and the perimeter of the 10th skeleton's distribution area is only one meter from the location of the 11th skeleton. This also emphasizes the possibility that the 10th and 11th skeletons are just slightly separated associations of the same ankylosaur specimen (Fig. 22).

### 4.3.4. Isolated material

*Year of discovery*: 2001-2017

*Material and reference number*: The isolated material referred to Nodosauridae indet. is quite abundant including hundreds of worn, unworn or broken teeth, some of them with root, mandibular fragments, several fragmentary cervical, dorsal vertebrae, a few sacrum fragments, dozens of caudal vertebrae from all part of the tail, hundreds of fragmentary to almost complete cervical and dorsal ribs, one humerus, several fragmentary limb elements, chevrons, many hundreds of complete or almost complete osteoderms and osteoderm fragments representing all part of the armor.

## 5. Discussion

### *5.1. Late Cretaceous ankylosaur diversity in Europe*

The 12 partial skeletons and the thousands of isolated ankylosaur elements discovered in the Santonian beds of Iharkút, unambiguously make this locality one of the richest ankylosaur sites worldwide and add significant information on the ankylosaur diversity of Europe. Skeletal remains indicate the occurrence of at least two, clearly different taxa: the larger *Hungarosaurus* that is, based on the number of skeletons, more frequent than the smaller sized *Struthiosaurus*. In addition, thousands of mostly fragmentary ankylosaurian elements are known as well, but most of them are too poorly preserved for a more precise taxonomic assignment.

Besides the Iharkút material, an ankylosaurian tooth and an osteoderm are known from the Ajka Coal Formation as well (Ősi et al. 2016). Although they cannot be identified at more precise taxonomical level, according to palynological and nannoplankton studies (Siegl-Farkas and Wagreich 1996; Bodrogi et al. 1998; Bodor and Baranyi 2012) the osteoderm is from the *Oculopollis - Complexiopollis* palynozone. With this age this osteoderm represents the oldest ankylosaur fossil in the area dating back the temporal range of the Bakony ankylosaurs within two palynological zones (most probably early Santonian) relative to the age of the Iharkút ankylosaurs (*Oculopollis-Triatriopollenites* subzone of the *Oculopollis zaklinskaiae - Brecolpites globosus* palynozone).

Whereas *Hungarosaurus* has only been reported from the Santonian of Iharkút (Ősi 2005; Ősi and Makádi 2009), *Struthiosaurus* appears to be more widespread in Europe. True ankylosaurian diversity in Europe is, however, greatly masked by the lack of overlapping diagnostic elements in many assemblages (Ősi 2015). Thus, except for a few elements (Pereda-Suberbiola 1993a), all the Campanian-Maastrichtian ankylosaur material have been referred to as *Struthiosaurus* (Bunzel 1871; Seeley 1881; Nopcsa 1915; 1929; Pereda-Suberbiola 1992; 1993b; 1999; Pereda-Suberbiola and Galton 1994; 2001; Garcia and Pereda-Suberbiola 2003; Company 2004; Ősi et al. 2014c; Ősi and Pereda-Suberbiola 2017). Study and reconstruction of armor composition and cervical and pelvic armor morphology might help to challenge this view in the future (Burns 2008; Arbour et al. 2014; Burns and Currie 2014; Ősi and Pereda-Suberbiola 2017; Ősi and Rudolf 2017).

Cervical armour elements of *Hungarosaurus* markedly differ from those referred to *Struthiosaurus* in having strongly posteriorly projecting lateral and medial plates (see e.g. Fig. 8-9). Cervical armour elements referred to *Struthiosaurus* are known from at least five European sites. These bones are generally similar to each other, but some differences between the base (flat or formed by the fusion of well developed polygonal or rounded osteoderms) or the shape of the lateral plate can be recognized (Ősi and Rudolf 2017). This might be the result of interspecific differences but for a firm conclusion the reconstruction of a more complete cervical series is necessary. Nevertheless, the available record (two-two bands are known in the Iharkút and Muthmannsdorf *Struthiosaurus* and only one-one in the western European [Cruzy, France; Laño and Chera, Spain] assemblages) may suggest that the western European *Struthiosaurus* had more than one species (besides *S. languedocensis* where cervical armour is unknown). This would not be surprising since the stratigraphic range of *Struthiosaurus* on the Ibero-Armorican landmass is ca. 15 My (Garcia and Pereda-Suberbiola 2003).

The Early Campanian Muthmannsdorf ankylosaurian material contains a large conical spike (PIUW 2349/15, Bunzel 1871, Seeley 1881), an element that is also known in the 4th and 9th skeletons referred to *Hungarosaurus* and from isolated specimens in Iharkút (see Ősi and Pereda-Suberbiola 2017 for comparison). Though the Austrian specimen has been referred to *Struthiosaurus austriacus* (Nopcsa 1929; Pereda-Suberbiola and Galton 2001), it cannot be ruled out that it might belong to another ankylosaur (as it was proposed by Seeley 1881). In the Hungarian material, this conical spike is part of a large, boomerang-shaped central osteoderm. The Austrian spike was also part of a larger, obviously fused osteoderm, since it has a massive, thick base with broken edges. In Iharkút this element was only identified certainly in *Hungarosaurus*. The identical conical spikes in Iharkút, Hungary and Muthmannsdorf, Austria suggest that this element in the Austrian assemblage might have not belonged to *S. austriacus* but rather to an other, more robust taxon, as it was originally proposed by Seeley (1881). A more complete *Struthiosaurus* material either from Austria or Hungary certaily would solve this problem. Whatever is the case, the ankylosaurian occurrences with different cervical armor elements morphology suggest that ankylosaur diversity during the last 20 My of the Late Cretaceous European archipelago was more diverse than previously thought.

The ankylosaur matrial from Iharkút adds some further information about the body length of these quadruped herbivores. Based on the first five skeletons referred to *Hungarosaurus* this taxon had a body length of 4-4.5 meters (Ősi and Makádi 2009). The new, 9th skeleton also referred to *Hungarosaurus*, fits well with this estimation since the bones of this assemblage are similar in size to that of largest specimens of the other five skeletons.

In case of *Struthiosaurus* a body length of 2.5-3 meters has been estimated by earlier workers (Pereda-Suberbiola and Galton 2001, Garcia and Pereda-Suberbiola 2003). The two specimens in the Iharkút assemblage (along with the fragmentary new material from Transylvania; Ősi et al. 2014c) well correlates with these estimates. Though histological studies still need to be done for establishing the ontogenetic status of the Hungarian *Struthiosaurus* specimens, the well-ossified sacral region, and the fused centrum and the neural arch of the associated dorsal vertebrae suggest a non-juvenile but at least subadult ontogenetic stage. This shows that *Struthiosaurus* in Iharkút could have an estimated total body length of ca. 3 meters, similar to its other European cousins, and that it was smaller than *Hungarosaurus*.

## *5.2. Genesis of the ankylosaur skeleton concentration*

Based on the accurate taphonomical investigations of the Iharkút vertebrate remains (Botfalvai et al. 2015), we have previously demonstrated that the associated and articulated remains of nodosaurid ankylosaurs most probably represent a mass death assemblage, because 1) the skeletal remains have almost uniform taphonomic features; 2) skeletons were found close to each other in a channel fill sequence and most of them were discovered from the same horizon (e.g. 2nd-4th, 6th-7th ankylosaur skeletons); 3) the material represents a monotaxic assemblage; 4) the closing layer shows rapid deposition (Botfalvai et al. 2016), which is a sedimentological criterion of a mass-killed assemblage (see the more detailed description in Botfalvai et al. 2015).

These interpretations were based only on the first seven skeletons (1st-7th skeletons from Iharkút) available in 2012 for study by Botfalvai et al. (2015). After 2012, however, five additional, partial and incomplete articulated or associated skeletons (8th-12th) have been found in Iharkút, further strengthening the above mentioned mass death hypothesis giving new opportunities for additional taphonomical investigations.

Except for the 9th skeleton, all of the newly discovered skeletons came from the same channel fill deposit (Unit 1-3) of site SZ-6 (see Table 1) as the previous ones, further supporting that a high density flash flood event played a major role in their concentration. The number of the skeletal parts in the channel fill deposit of site SZ-6 shows a negative correlation with the suspected flow energy, because the sediment association of Unit 1 reflects upper flow regime conditions containing more skeletal remains than Unit 2 and 3 characterized by decreasing energy conditions (see Botfalvai et al. 2016).

The Unit 1 of site SZ-6 includes the 4th, 6th, 7th, 8th and 12th incomplete or partial skeletons, which were transported by a high energy flash flood event. The accumulation of these skeletons began after the culmination of a high flood process, when current strength suddenly decreased and different density (i.e. bones, plant and eggs) and sized (microfossils and partial ankylosaur skeletons) fossils accumulated together at the same time (Botfalvai et al. 2015; Prondvai et al. 2017).

Four additional incomplete skeletons (1st, 5th, 10th and 11th; see Table 1) were transported in somewhat lower energetic environment, compared to that of the skeletal material of Unit 1. The 10th and the 11th skeletons came from a transitional horizon from Unit 1 to the Unit 2 (the lowermost part of Unit 2) suggesting a depositional mode similar to the skeletons discovered in Unit 1. The remains of the 5th skeleton were discovered from a typical sandstone bed of Unit 2 of site SZ-6 indicating reduction in flow velocity either when the channel was abandoned or possibly at the end of the flooding event (Botfalvai et al. 2016). Fossils of this skeleton have a higher percentage of skeletal completeness (about 21%) compared to the skeletal remains of Unit 1, containing a diverse skeletal representation from all parts of the body (see Supplementary Data 2).

The closing bed at site SZ-6 (Unit 3) is a greyish-brownish siltstone layer representing open lacustrine conditions following the flood events (Botfalvai et al. 2016). This layer also contained two associated skeletons (2nd and 3rd skeletons), where the 2nd one is the most complete, holotype skeleton of *Hungarosaurus* (percentage of skeletal completeness is about 47%) (Ősi 2005).

The 9th skeleton was discovered from the floodplain sediments and not in the channel fill deposit as the other skeletons. However, based on the stratigraphical and sedimentological observations, we suggest that the depositional place of the 9th skeleton was situated along the same horizon as the channel fill of site Sz-6 (Fig. 1c), within a small area and thus the 9th skeleton probably represents the same deposition event that buried the other skeletons as well. The embedding siltstone-mudstone of the 9th skeleton indicates that the bones were not transported through a tractive flow, because the bones were not theoretically equivalent with the dominant sizes of quartz grains of enclosing sediment (e.g. Behrensmeyer 1975; Fiorillo et al. 2000; Müller et al. 2015; Botfalvai et al. 2017). The absence of hydraulic equivalence indicates that the material probably were transported as a whole carcass and the disarticulation processes were begun in the floodplain environment after the deposition. In addition, it cannot be excluded that the individual of the 9th skeleton died in unknown death event and was buried *in situ* in the floodplain environment prior to the deposition of other skeletons at Iharkút site. However, the same stratigraphical position, the similar preservation mode and disarticulation history perhaps reinforces the assumption that this carcass was also transported by the same event as the other skeletons and it was just drifted from the channel to the floodplain during the transportation.

There is no unequivocal evidence that the deposition of Unit 2 and 3 skeletons were part of the same mass death event resulted in a unique skeletal concentration in Unit 1 (see above). However, the sedimentological features suggest a relatively short time passed between the accumulation of Unit 1 and 3 supported by the followings: 1) this kind of flood events are restricted in time, usually not exceeding a few hours indicating that a significant part of the channel fill was deposited under extremely short time (Botfalvai et al. 2016); 2) the lack of bioturbation (indicated by lamination of the siltstone) and soil formation, 3) the lenticular geometry, the absence of point bar accretion and the infrequent cross-bedding suggest a rapid vertical aggradation while the lateral accretion was moderate during the channel fill processes. Based on these sedimentological features, it is conceivable that all of the ankylosaur skeletons discovered from the site SZ-6 (Unit 1-3) represent a single mass death assemblage, the individuals of which might have died over a very brief time span due to the same event.

The cause of death of the Iharkút ankylosaurs was probably drowning when their herds time to time attempted to cross the flooded river, because 1) the bonebed layer was deposited during a heavy flood event (Botfalvai et al. 2016); 2) their body structure might have been unfavourable for swimming across the flooded river; 3) the ankylosaur skeletal material from Iharkút site indicates that the animals were congragated in a group before their death and drowning is a frequent cause of death in terrestrial herding lifestyle animals (Weigelt 1989; Capaldo and Peters 1995; Ryan et al. 2001; Rogers and Kidwell 2007; Kinneer et al. 2016; Subalusky et al. 2017); 4) there are no evidences for possible other causes of death e.g. drought, disease, forest fire or miring (Botfalvai et al. 2015).

After the death, the ankylosaur carcasses were transported by fluvial currents as floating bodies into the place of site Sz-6 where they were finally deposited. The mass deposited carcasses provide important resource pulses for scavengers and microbial activity, which can facilitate carcass decomposition and disarticulation (e.g. Kahlke and Gaudzinski 2005; Subalusky et al. 2017). The relatively low percentages of skeletal completeness (see Table 1, Supplementary Data 2) in Iharkút indicate that the deposited carcasses were exposed to destruction processes (e.g. decay and scavenger) in the water, resulting in the disarticulation of the body and destroy of certain parts of the skeleton, as it was documented in other cases as well (e.g. Capaldo and Peters 1995; Davis and Briggs 1998; Brand et al. 2003; Cameron and Oxenham 2012; Subalusky et al. 2017). Besides the decaying (microbial processes), the notable reduction of the skeletons might have been caused by vertebrate scavengers in the aquatic habitats of Iharkút. This hypothesis is suggested on the basis of 2600 coprolites with high phosphorous content discovered from the same excavated area (ca. 600 m$^2$) of Unit 1 which are indicators of *quasi in situ* high scavenger activity around the accumulated carcasses (Segesdi et al. 2017). Fishes play a significant role in carcass decomposition in freshwater habits (Subalusky et al. 2017) and the presence of coiled and spiral coprolites in the Iharkút material (Segesdi et al. 2017) probably also indicate that the fishes (such as *Atractosteus*) could have played a significant role during the decomposition of these ankylosaur carcasses. The decomposition and disarticulation of the ankylosaur skeletons was *in situ* in the channel fill in a water logged environment. The partial skeletons from Unit 1 and 2 were buried during the following flooding event that brought enough sediment to cover their disarticulated carcasses, while the 2nd and 3rd skeletons of Unit 3 were buried by quiet-water sediments indicative of deposition from suspension in close to standing water following the flood events.

The existence of monospecific skeletal material in a layer deposited under high energy conditions raises the possibility that all or some of the ankylosaurs were killed by instantaneous events when they attempted to cross the flooded river. The carcasses of the drowned animals drifted downstream by flotation until the current velocity decreased (or water column become too shallow). The deposited carcasses were exposed to destruction processes (decay, trampling or scavenger) during which the parts of the body disarticulated and certain parts of the skeleton were destroyed or transported to the different places. The mass deposited carcasses represent an important source of food for the scavengers (macro- and microbial decomposition) which can cause a notable reduction of the skeleton. After the decomposition and disarticulation, the ankylosaur skeletons were buried *in-situ* in the channel fill deposit of site SZ-6 due to the following flooding event or covered by quiet-water sediments from suspension following the flood.

Despite that the ankylosaur remains are relatively common fossils in Cretaceous costal and floodplain sediments (Vickaryous et al. 2004; Arbour et al. 2016), bonebeds containing more than one individual are extremely rare (but see e.g. Kirkland 1998; Carpenter et al. 2001; Burns et al. 2011; Kinneer et al. 2016). Therefore, the discovery of twelve ankylosaurian individuals from a single, few hundred square meters large vertebrate site is unique in ankylosaurian dinosaurs. The association of these specimens at Iharkút locality may correspond to a natural aggregation during life (Botfalvai et al in prep.). Moreover, beside of the twelve associated and articulated skeletons, more than 2700 ankylosaur isolated elements were also collected from the site SZ-6, making this group one of the most abundant taxa (after turtles) in the Iharkút assemblage (Botfalvai et al. 2016). The extraordinary abundant ankylosaur material discovered from Iharkút vertebrate locality is unrivalled in the Cretaceous vertebrate record and might contradict the hypothesis that the adult ankylosaurs were solitary living animals (e.g. Vickaryous et al. 2004; Burns et al. 2011; Arbour and Mallon 2017).

## 6. Conclusions

1) The ankylosaurian remains discovered from the Santonian of Iharkút represent one of the richest ankylosaurian assemblages worldwide. Excavated from an area of ca. 600 $m^2$ in a sedimentary sequence deposited during a relatively fast and single event, the 12 partial associated or articulated skeletons and thousands of isolated elements play a critical role in the understanting of European ankylosaur taxonomy and diversity but they also shed light on the paleoecological aspects of the group.

2) Sedimentological and taphonomical investigations indicate the following succession of events led to the concentration of this unique nodosaurid assemblage: 1) aggregation of ankylosaur population as might be the result of their gregarious lifestyle; 2) mass mortality by a flash flood event perhaps when their herds time to time attempted to cross the flooded river; 3) soft tissue decomposition by scavenger action and microbial activity after water transportation generated disarticulated but associated bone assemblages; 4) the disarticulated bones were dispersed more or less by low velocity water currents that modified the bone spectrum remaining at the site.

3) The assemblage is not monospecific, but six of the 12 ankylosaur skeletons are assigned to *Hungarosaurus*, whereas two others belong to *Struthiosaurus* and four additional ones can only be referred to Nodosauridae indet. This suggests that *Hungarosaurus* and *Struthiosaurus* might lived in a same community closer to the site of deposition and preferred wetland habits such as fluvial system.

4) The material presented here strengthens the previous hypothesis that cervical and pelvic armor elements can be a good tool for distinguishing different ankylosaur taxa in a single vertebrate assemblage. Assuming the available information on these armor elements

from different sites of Europe we think that ankylosaur diversity during the last 20 My of the Late Cretaceous European archipelago was more diverse than previously thought.

## Conflict of Interest statement

The authors declare that they have no conflict of interest.

## References

Albert, G., Botfalvai, G., Ősi, A. (2017). Making high resolution 3D model of a bonebed from GPS data to assist taphonomical analyses – case study of the Santonian vertebrate site of Iharkút (Hungary). Vienna, Austria: 8th International Meeting on Taphonomy and Fossilization, Abstract Book, 36 pp.

Albert, G., Botfalvai, G., Ősi, A.  (in review). Mapping the past: GIS and intra site spatial analyses of fossil deposits in paleontological sites and their applications in taxonomy, taphonomy and paleoecology.

Arbour, V. M., & Mallon, J. C. (2017). Unusual cranial and postcranial anatomy int he archetypal ankylosaur *Ankylosaurus magniventris*, *FACETS*, 2, 764-794. https://doi.org/10.1139/facets-2017-0063

Arbour, V. M., Burns, M. E., Bell, P. R., Currie, P. J. (2014). Epidermal and dermal integumentary structures of ankylosaurian dinosaurs. *Journal of Morphology*, 275, 39-50. https://doi.org/10.1002/jmor.20194

Arbour, V. M., Zanno, L. E., Gates, T. (2016). Ankylosaurian dinosaur palaeoenvironmental associations were influenced by extirpation, sea-level fluctuation, and geodispersal. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 449, 289-299. https://doi.org/10.1016/j.palaeo.2016.02.033

Badgley, C. (1986). Counting Individuals in Mammalian Fossil Assemblages from Fluvial Environments. *Palaios*, 1(3), 328-338. https://.doi.org/10.2307/3514695

Behrensmeyer, A. K. (1975). The taphonomy and paleoecology of Plio-Pleistocene vertebrate assemblages east of Lake Rudolf, Kenya. *Bulletin of the Museum of Comparative Zoology*, 146(10), 1-106.

Behrensmeyer, A. K. (1991). Terrestrial vertebrate accumulations. In P. A. Allison, & D. E. G. Briggs (Eds.), *Taphonomy: releasing the data locked in the fossil record* (pp. 291-335). New York: Plenum Press.

Blows, W. T. (1982). A preliminary account of a new specimen *Polacanthus foxi* (Ankylosauria, Reptilia) from the Wealden of the Isle of Wight. *Proceedings of the Isle of Wight Natural History and Archaeological Society*, 7(5), 303-306.

Blows, W. T. (1987). The armoured dinosaur *Polacanthus foxi* from the Lower Cretaceous of the Isle of Wight. *Palaeontology*, 30(3), 557-580.

Blows, W. T. (1996). A new species of *Polacanthus* (Ornithischia: Ankylosauria) from the Lower Cretaceous of Sussex, England. *Geological Magazine*, 133(6), 671-682. https://.doi.org/10.1017/S0016756800024535

Blows, W. T. (2015). British Polacanthid Dinosaurs – Observations on the History and Palaeontology of the UK Polacanthid Armoured Dinosaurs and their Relatives, Siri Scientific Press, 220 pp.

Bodor, E., & Baranyi, V. (2012). Palynomorphs of the Normapolles group and related plant mesofossils from the Iharkút vertebrate site, Bakony Mountains (Hungary). *Central European Geology*, 55, 259-292. https://.doi.org/10.1556/CEuGeol.55.2012.3.3

Bodrogi, I., Fogarasi, A., Yazikova, E. A., Sztanó, O., Báldi-Beke, M. (1998). Upper Cretaceous of the Bakony Mts.(Hungary): sedimentology, biostratigraphy, correlation. *Zentralblatt für Geologie und Paläontologie*, 1(11/12), 1179-1194.

Botfalvai, G., Csiki-Sava, Z., Grigorescu, D., Vasile, S. (2017). Taphonomical and palaeoecological investigation of the Late Cretaceous (Maastrichtian) Tuştea vertebrate assemblage (Romania; Haţeg Basin) - insights into a unique dinosaur nesting locality. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 468, 228-262. https://.doi.org/10.1016/j.palaeo.2016.12.003

Botfalvai, G., Haas, J., Mindszenty, A., Ősi, A. (2016). Facies Architecture and Paleoenvironmental implications of the Upper Cretaceous (Santonian) Csehbánya Formation at the Iharkút vertebrate locality (Bakony Mountains, northwestern Hungary). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 441, 659-678. https://.doi.org/10.1016/j.palaeo.2015.10.018

Botfalvai, G., Ősi., A. (2017). Ankylosaur mass death assemblage from the Late Cretaceous of Iharkut (Hungary) and its effect on an ancient river ecosystem. In: Zuschin, M., Harzhauser, M. and Mayrhofer, S. (Eds.), 8th Internacional Meeting on Taphonomy and Fossilization (Taphos 2017), Vienna, Austria, 14-17 September 2017, pp. 36-37.

Botfalvai, G., Ősi, A., Mindszenty, A. (2015). Taphonomic and paleoecologic investigations of the Late Cretaceous (Santonian) Iharkút vertebrate assemblage (Bakony Mts, northwestern Hungary). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 417, 379-405. https://.doi.org/10.1016/j.palaeo.2014.09.032

Botfalvai, G., Prondvai, E., Ősi, A., in prep. Group living or solitary lifestyle? Determination of the social behaviour of ankylosaurs.

Brand, L., Hussey, M., Taylor, J. (2003). Taphonomy of freshwater turtles: Decay and disarticulation in controlled experiments. *Journal of Taphonomy*, 1, 233–245.

Bunzel, E. (1871). Die Reptilfauna der Gosauformation in der Neuen Welt bei Weiner-Neustadt. *Abhandlungen der Kaiserlich-Königlichen Geologischen Reichsanstalt*, 5, 1-18.

Burns, M. E. (2008). Taxonomic utility of ankylosaur (Dinosauria, Ornithischia) osteoderms: *Glyptodontopelta mimus* FORD, 2000: a test case. *Journal of Vertebrate Paleontology*, 1102-1109. https://.doi.org/10.1671/0272-4634-28.4.1102

Burns, M. E., Currie, P. J., Sissons, R. L., Arbour, V. M. (2011). Juvenile specimens of *Pinacosaurus grangeri* Gilmore, 1933 (Ornithischia: Ankylosauria) from the Late Cretaceous of China, with comments on the specific taxonomy of *Pinacosaurus*. *Cretaceous Research*, 32, 174–186. https://.doi.org/10.1016/j.cretres.2010.11.007

Burns, M. E., & Currie, P. J. (2014). External and internal structure of ankylosaur (Dinosauria, Ornithischia) osteoderms and their systematic relevance. *Journal of Vertebrate Paleontology*, 34, 835-851. https://.doi.org/10.1080/02724634.2014.840309

Cambra-Moo, O., & Buscalioni, A. D. (2003). Biostratinomic Patterns in Archosaur Fossils: Influence of Morphological Organization on Dispersal. *Journal of Taphonomy*, 1(4), 247-275.

Cameron, A. C., & Oxenham, M. (2012). Disarticulation sequences and scattering patterns in temperate southeastern Australia. *Australian Journal of Forensic Science*s, 44(2), 197-211. https://.doi.org/10.1080/00450618.2011.650206

Capaldo, S. D., & Peters, C. R. (1995). Skeletal Inventories from Wildebeest Drownings at Lakes Masek and Ndutu in the Serengeti Ecosystem of Tanzania. *Journal of Archaeological Science*, 22(3), 385-408. https://.doi.org/10.1006/jasc.1995.0039

Carpenter, K. (2001). Skull of the polacanthid ankylosaur *Hylaeosaurus armatus* Mantell, 1833, from the Lower Cretaceous of England. In K. Carpenter (Ed.), *The Armored Dinosaurs* (pp. 169-172). Bloomington: Indiana University Press.

Carpenter, K., Kirkland, J. I., Burge, D., Bird, J. (2001). Disarticulated skull of a new primitive ankylosaurid from the Lower Cretaceous of eastern Utah. In K. Carpenter (Ed.), *The Armored Dinosaurs* (pp. 211-238). Bloomington: IndianaUniversity Press.

Coard, R., & Dennell, R. W. (1995). Taphonomy of Some Articulated Skeletal Remains: Transport Potential in an Artificial Environment. *Journal of Archaeological Science*, 22(3), 441-448. https://doi.org/10.1006/jasc.1995.0043

Company, J. (2004). Vertebrados continentales del Cretácico Superior (Campaniense–Maastrichtiense) de Valencia. Tesis doctoral, Universidad de Valencia Spain, 410 pp. (Unpublished).

Davis, P. G., & Briggs, D. E. G. (1998). The impact of decay and disarticulation on the preservation of fossil birds. *Palaios*, 13(1), 3-13. https://doi.org/10.1043/0883-1351(1998)013<0003:TIODAD>2.0.CO;2

Dodson, P. (1971). Sedimentology and taphonomy of the Oldman Formation (Campanian), Dinosaur Provincial Park, Alberta (Canada). *Palaeogeography, Palaeoclimatology, Palaeoecology*, 10(1), 21-74. https://doi.org/10.1016/0031-0182(71)90044-7

Eberth, D. A. (2015). Origins of dinosaur bonebeds in the Cretaceous of Alberta, Canada. *Canadian Journal of Earth Sciences*, 52(8), 655-681. https://doi.org/10.1139/cjes-2014-0200

Evans, D. C., Eberth, D. A., Ryan, M. J. (2015). Hadrosaurid (*Edmontosaurus*) bonebeds from the Horseshoe Canyon Formation (Horsethief Member) at Drumheller, Alberta, Canada: geology, preliminary taphonomy, and significance. *Canadian Journal of Earth Science*, 52(8), 642- 654. https://doi.org/10.1139/cjes-2014-0184

Fiorillo, A. R., Padian, K., Musikasinthorn, C. (2000). Taphonomy and Depositional Setting of the Placerias Quarry (Chinle Formation: Late Triassic, Arizona). *Palaios*, 15(5), 373-386. https://doi.org/10.1669/0883-1351(2000)015<0373:TADSOT>2.0.CO;2

Frostic, L., & Reid, I. (1983). Taphonomic significance of sub-aerial transport of vertebrate fossils on steep semi-arid slopes. *Lethaia*, 16(2), 157-164. https://doi.org/10.1111/j.1502-3931.1983.tb01711.x

Garcia, G., & Pereda-Suberbiola, X. (2003). A new species of *Struthiosaurus* (Dinosauria: Ankylosauria) from the Upper Cretaceous of Villeveyrac (Southern France). *Journal of Vertebrate Paleontology*, 23, 156–165. https://doi.org/10.1671/0272-4634(2003)23[156:ANSOSD]2.0.CO;2

Haynes, G. (1980). Prey bones and predators: potential ecologic information from analysis of bone sites. *Ossa*, 7, 75-97.

Hill, A. (1979). Disarticulation and scattering of mammal skeletons. *Paleobiology*, 5(3), 261-274. https://doi.org/10.1017/S0094837300006552

Hill, A., & Behrensmeyer A. K. (1984). Disarticulation patterns of some modern East African mammals. *Paleobiology*, 10(3), 366-376. https://doi.org/10.1017/S0094837300008332

Hill, R.V.,Witmer, L. M., Norell, M. A. (2003). A newspecimen of *Pinacosaurus grangeri* (Dinosauria: Ornithischia) from the Late Cretaceous of Mongolia: ontogeny and phylogeny of ankylosaurs. *American Museum Novitates*, 3395, 1–29. https://doi.org/10.1206/0003-0082(2003)395<0001:ANSOPG>2.0.CO;2

Holz, M., & Barberena, M. C. (1994). Taphonomy of the south Brazilian Triassic paleoherpetofauna: pattern of death, transport and burial. *Palaeogeography, Palaeoclimatology, Palaeoecology*, 107(1-2), 179-197. https://doi.org/10.1016/0031-0182(94)90170-8

Hulke, J. W. (1882). *Polacanthus foxii*, a large undescribed dinosaur from the Wealden Formation in the Isle of Wight. *Philosophical Transactions of the Royal Society of London*, 172, 653-662. https://doi.org/10.1098/rstl.1881.0015

Hulke, J. W. (1888). Supplemental note on *Polacanthus foxii*, describing the dorsal shield and some parts of the endoskeleton, imperfectly known in 1881. *Philosophical Transactions of the Royal Society of London*, 178, 169-172.

Kahlke, R. D., & Gaudzinski S. (2005). The blessing of a great flood: differentiation of mortality patterns in the large mammal record of the Lower Pleistocene fluvial site of Untermassfeld (Germany) and its relevance for the interpretation of faunal assemblages from archaeological sites. *Journal of Archaeological Science*, 32(8), 1202-1222. https://doi.org/10.1016/j.jas.2005.03.004

Kinneer, B., Carpenter, K., Shaw, A. (2016). Redescription of *Gastonia burgei* (Dinosauria: Ankylosauria, Polacanthidae), and description of a new species. *Neues Jahrbuch für Geologie und Paläontologie - Abhandlungen*, 282(1), 37-80. https://doi.org/10.1127/njgpa/2016/0605

Kirkland, J. I. (1998). A polacanthine ankylosaur (Ornithischia: Dinosauria) from the Early Cretaceous (Barremian) of eastern Utah. *New Mexico Museum of Natural History and Science Bulletin*, 14, 271-281.

Kirkland, J. I., Alcalá, L., Loewen, M. A., Espílez, E., Mampei, L., Wiersma, J. P. (2013). The basal nodosaurid *Europelta carbonensis* n. gen., n. sp. from the Lower Cretaceous (Lower Albian) Escucha Formation of northeastern Spain. *PLoS One*, 8(12), 1-40. https://doi.org/10.1371/journal.pone.0080405

Mantell, G. A. (1833). *The Geology of the South-East of England*. London: Longman Ltd. 415 pp. https://doi.org/10.5962/bhl.title.106921

Mantell, G. A. (1841). Memoir on a portion of the lower jaw of the *Iguanodon,* and on the remains of the *Hylaeosaurus* and other saurians, discovered in the strata of the Tilgate Forest, in Sussex. *Philosophical Transactions of the Royal Society of London*, 131**,** 131-151.

Marsh, O. C. (1889). Notice of gigantic horned Dinosauria from the Cretaceous. *American Journal of Science*, 39, 418–426. https://doi.org/10.2475/ajs.s3-38.224.173

Marsh, C. O. (1890). Additional characters of the Ceratopsidae with notice of new Cretaceous dinosaurus. *American Journal of Science*, 39, 418–426.

Müller, R. T., de Araújo-Júnior, H. I., Aires, A. S. S., Roberto-da-Silva, L., Dias-da-Silva, S. (2015). Biogenic control on the origin of a vertebrate monotypic accumulation from the Late Triassic of southern Brazil. *Geobios*, 48, 331-340. https://doi.org/10.1016/j.geobios.2015.05.001

Naish, D., & Martill, D. M. (2001). Armoured dinosaurs: thyreophorans. In D. M. Martill, & D. Naish (Eds.), *Dinosaurs of the Isle of Wight* (pp. 147-184). London: Palaeontological Association.

Nasti, A. (2005). Dragging and Scattering of Camelid Bones by Fluvial Action in the Real Grande Gorge, Province of Catamarca, Southern Argentinean Puna. *Journal of Taphonomy*, 3(4), 173-183.

Nopcsa, F. (1915). Die Dinosaurier der Siebenbürgischen Landesteile Ungarns. *Mitteilungen aus dem Jahrbuch der königlichen Ungarischen Geologischen Reichsanstalt Budapest*, 23(1), 1-24.

Nopcsa, F. (1929). Dinosaurier reste aus Siebenbürgen. *V. Geologica Hungarica. Series Palaeontologica*, 4, 1-76.

Osborn, H. F. (1923). Two Lower Cretaceous dinosaurs from Mongolia. *American Museum Novitates*, 95,110.

Owen, R. (1842). Report on British fossil reptiles, part II. *Report of the British Association for the Advancement of Science*, 11, 60–204.

Owen, R. (1858). Monograph on the fossil Reptilia of the Wealden and Purbeck Formations. − Part IV. Dinosauria (*Hylaeosaurus*). Wealden: The Palaeontological Society London, 8-26 pp.

Owen, R. (1865). The Reptilia of the Liassic formations, part III. *Monograph of the Palaeontographical Society*, 1-40 pp.

Ősi, A. (2005). *Hungarosaurus tormai*, a new ankylosaur (Dinosauria) from the Upper Cretaceous of Hungary. *Journal of Vertebrate Paleontology*, 25(2), 370-383.

Ősi, A. (2015). The European ankylosaur record: a review. *Hantkeniana*, 10, 89-106.

Ősi, A., & Makádi, L. (2009). New remains of *Hungarosaurus tormai* (Ankylosauria, Dinosauria) from the Upper Cretaceous of Hungary: skeletal reconstruction and body mass estimation. *Paläontologische Zeitschrift*, 83, 227–245.

Ősi, A., & Pereda-Suberbiola, X. (2017). Notes on the pelvic armor of European ankylosaurs (Dinosauria: Ornithischia). *Cretaceous Research*, 75, 11-22. doi.org/10.1016/j.cretres.2017.03.007

Ősi, A., & Prondvai E. (2013). Sympatry of two ankylosaurs (*Hungarosaurus* and cf. *Struthiosaurus*) in the Santonian of Hungary. *Cretaceous Research*, 75, 11-22. https://doi.org/10.1016/j.cretres.2013.03.006

Ősi, A., & Rudolf, J. (2017). Systematics of Late Cretaceous European ankylosaurs: the importance of the dermal armour. Birmingham, UK: Abstract volume of the 65th Symposium on Vertebrate Palaeontology and Comparative Anatomy, 72 pp.

Ősi, A., Barrett, P., Földes, T., Tokai, R. (2014b). Wear Pattern, Dental Function, and Jaw Mechanism in the Late Cretaceous Ankylosaur *Hungarosaurus*. *The Anatomical Record*, 297, 1165-1180. https://doi.org/10.1002/ar.22910

Ősi, A., Bodor, E. R., Makádi, L., Rabi, M. (2016). Vertebrate remains from the Upper Cretaceous (Santonian) Ajka Coal Formation, western Hungary. *Cretaceous Research*, 57, 228–238. https://doi.org/10.1016/j.cretres.2015.04.014

Ősi, A., Rabi, M., Makádi, L., Szentesi Z., Botfalvai, G., Gulyás, P. (2012). The Late Cretaceous continental vertebrate fauna from Iharkút (Western Hungary): a review. In P.

Godefroit (Ed.), *Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems* (532–569 pp). Bloomington: Indiana University Press.

Ősi, A., Pereda-Suberbiola, X., Földes, T. (2014a). Partial skull and endocranial cast of the ankylosaurian dinosaur *Hungarosaurus* from the Late Cretaceous of Hungary: implications for locomotion. *Palaeontologia Electronica*. http://palaeo-electronica.org/content/pdfs/405.pdf.

Ősi, A., Prondvai, E., Csiki-Sava, Z. (2014c). New ankylosaurian material from the Upper Cretaceous of Transylvania. *Annales de Paléontologie*, 100: 257-271. https://doi.org/10.1016/j.annpal.2014.02.001

Ősi, A., Prondvai, E., Mallon, J., Bodor, E. R. (2016). Diversity and convergences in the evolution of feeding adaptations in ankylosaurs (Dinosauria: Ornithischia). *Historical Biology*, 29 (4), 539-570. https://doi.org/10.1080/08912963.2016.1208194

Pereda-Suberbiola, X. (1992). A revised census of European Late Cretaceous nodosaurids (Ornithischia: Ankylosauria): last occurrence and possible extinction scenarios. *Terra Nova*, 4(6), 641-648. https://doi.org/10.1111/j.1365-3121.1992.tb00613.x

Pereda-Suberbiola, X. (1993a). *Hylaeosaurus*, *Polacanthus*, and the systematics and stratigraphy of Wealden armoured dinosaurs. *Geological Magazine*, 130(6), 767-781. https://doi.org/10.1017/S0016756800023141

Pereda-Suberbiola, X. (1993b). Un dinosaure cuirassé (Ornithischia, Ankylosauria) dans le Crétacé supérieur de Laño (Bassin Basco-Cantabrique). *Paleontologia i Evolució*, 26–27, 231–235.

Pereda-Suberbiola, X. (1994). *Polacanthus* (Ornithischia, Ankylosauria), a transatlantic armoured dinosaur from the Early Cretaceous of Europe and North America. *Palaeontographica Abteilung A*, 232, 133-159.

Pereda-Suberbiola, X. (1999). Ankylosaurian dinosaur remains from the Upper Cretaceous of Laño (Iberian Peninsula). *Estudios del Museo de Ciencias Naturales de Alava*, 14(1), 273–288.

Pereda-Suberbiola, X., & Galton, P. M. (1994). A revision of the cranial features of the dinosaur *Struthiosaurus austriacus* BUNZEL (Ornithischia: Ankylosauria) from the Late Cretaceous of Europe. *Neues Jahrbuch fur Geologie und Palaontologie-Abhandlungen*, 191(3), 173-200.

Pereda-Suberbiola, X., & Galton, P. M. (2001). Reappraisal of the nodosaurid ankylosaur *Struthiosaurus austriacus* Bunzel from the Upper Cretaceous Gosau Beds of Austria. In K. Carpenter (Ed.), *The Armored Dinosaurs* (pp. 173-210). Bloomington, Indiana: Indiana University Press.

Prondvai, E., Botfalvai, G., Stein, K., Szentesi, Z., Ősi, A. (2017). Collection of the thinnest: A unique eggshell assemblage from the Late Cretaceous vertebrate locality of Iharkút (Hungary). *Central European Geology*, 60(1), 73-133. https://doi.org/10.1556/24.60.2017.004

Rogers, R. R., & Kidwell, S. M. (2007). A conceptual framework for the genesis and analysis of vertebrate skeletal concentrations. In R. R. Rogers, D. A. Eberth, A. R. Fiorillo (Eds.), *Bonebeds: genesis, analysis, and paleobiological significance* (pp. 1-61). Chichago and London: The University of Chichago Press.

Ryan, M. J., Russel, A. P., Eberth, D. A., Currie, P. J. (2001). The Taphonomy of a Centrosaurus (Ornithischia: Certopsidae) Bone Bed from the Dinosaur Park Formation (Upper Campanian), Alberta, Canada, with Comments on Cranial Ontogeny. *Palaios,* 16(5), 482-506. https://doi.org/10.1669/0883-1351(2001)016<0482:TTOACO>2.0.CO;2

Seeley, H. G. (1881). The reptile fauna of the Gosau Formation preserved in the Geological Museum of the University of Vienna. *Quarterly Journal of the Geological Society of London*, 37(148), 620-707. https://doi.org/10.1144/GSL.JGS.1881.037.01-04.49

Segesdi, M., Botfalvai, G., Bodor, E. R., Ősi, A., Buczkó, K., Dallos, Zs., Tokai, R., Földes, T. (2017). First report on vertebrate coprolites from the Upper Cretaceous (Santonian) Csehbánya Formation of Iharkút, Hungary. *Cretaceous Research*, 74, 87-99. https://doi.org/10.1016/j.cretres.2017.02.010

Siegel-Farkas, A., & Wagreich, M. (1996). Age and palaeoenvironment of the spherulite-bearing. Polány Marl Formation (Late Cretaceous, Hungary) on the basis of palynological and nannonplankton investigations. *Acta Biolgica Szegediensis*, 35, 23-36.

Subalusky, A. L., Dutton, C. L., Rosi, E. J., Post, D. M. (2017). Annual mass drownings of the Serengeti wildebeest migration influence nutrient cycling and storage in the Mara River. *Proceedings of the National Academy of Sciences of the United States of America*, 114(29), 7647–7652. https://doi.org/10.1073/pnas.1614778114

Tooth, H. (1965). Sequence of disarticulation in mammalian skeletons. *Rocky Mountain Geology*, 4(1), 37-39.

Vickaryous, M. K., Maryanska, T., Weishampel, D. B. (2004). Ankylosauria. In D. B. Weishampel, P. Dodson, H. Osmólska (Eds.), *The Dinosauria*, Second Edi-tion (pp. 363-392). Berkeley: University of California Press.

Weigelt, J. (1989). *Recent Vertebrate carcass and their archaeological implications*. Chicago: University of  Chicago Press, 1-198 pp.

## Figure captions

**Fig. 1.** Geological and geographical background of the skeletons. **a** schematic stratigraphic section of the site SZ-6 showing the main palaeoenvironments and lithofacies associations. **b** close up of the Unit 1 layers of site SZ-6. **c** the positions of the ankylosaur skeletons in the channel fill deposit. **d** position of the 12 ankylosaur skeletons discovered in the Iharkút vertebrate locality. Note that the position of the 1st skeleton is uncertain, but sedimentological date indicate that it cam from Unit 2 of site SZ-6.

**Fig. 2.** The 1st ankylosaur skeleton (MTM 2007.22.1) referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. **a** main block with an anterior dorsal vertebra (the centrum is covered by the plate-like osteoderm), a right? fused cervical half-ring, three fragmentary dorsal ribs and a rectangular osteoderm below one of the ribs. **b** two proximal dorsal rib fragments. **c** reactangular flat osteoderm. **d** distal dorsal rib fragment.

**Fig. 3.** The holotype of *Hungarosaurus tormai* (2nd ankylosaur skeleton, MTM 2007.26.1-2007.26.34.) from the Santonian of Iharkút, Hungary. **a** right premaxilla in lateral, **b** medial view. **c** left premaxilla in lateral, **d** medial view. **e** posteroventral, alveolar fragment of left premaxilla in ventral, **f** medial, **g** lateral view. **h** right quadrate in anterior, **i** posterior view. **j** left distal quadrate in posterior, **k** anterior view. **l** left? frontal in ventral, **m** dorsal view; **n** right postorbial and jugal in medial, **o** lateral view. **p** left ?prefrontal and ?lacrimal in lateral, **q** medial view. **r** cranial fragment in medial, **s** lateral view.

**Fig. 4.** The holotype of *Hungarosaurus tormai* (2nd ankylosaur skeleton, MTM 2007.26.1-2007.26.34.) from the Santonian of Iharkút, Hungary. **a** cranial fragment in medial, **b** lateral view. **c** anterior part of the vomer. **d** occipital condyle in posterior, **e** dorsal view. **f** pterygoid

in anteroventral, **g** posterodorsal view. **h** anterior part of left nasal in dorsal view. **i** right dentary in medial view. **j** post-dentary part of the right mandible in medial view. **k** post-dentary part of the right mandible in lateral view. **l** right dentary in lateral view. **m** dentary tooth in labial, **n** ?mesial, **o** lingual view. **p** complete tooth crown in ?lingual and ?labial view. **r** anterior cervical rib. **s-t** posterior cervical ribs. **u** dorsal rib in posterior view. **v** distally positioned chevron. **w** anteriorly positioned chevron.

**Fig. 5.** The holotype of *Hungarosaurus tormai* (2nd ankylosaur skeleton, MTM 2007.26.1-2007.26.34.) from the Santonian of Iharkút, Hungary. **a** ?8th cervical vertebra in anterior, **b** left lateral, **c** ventral view. **d** ?6th cervical vertebra in posterior, **e** left lateral, **f** ventral, **g** dorsal view. **h** 4th cervical vertebra in left lateral, **i** posterior, **j** ventral, **k** dorsal view. **l** anterior dorsal vertebra in posterior, **m** left lateral, **n** dorsal, **o** ventral view.

**Fig. 6.** The holotype of *Hungarosaurus tormai* (2nd ankylosaur skeleton, MTM 2007.26.1-2007.26.34.) from the Santonian of Iharkút, Hungary. **a** dorsal vertebra in left lateral, **b** anterior, **c** ventral, **d** dorsal view. **e** fragment from the sacrum and sacral ribs. **f** sacral rod (fused lumbar vertebrae) in left lateral view (contra Ősi 2005: Fig. 11C, D). **g-i**, sacral ribs in dorsal view. **j** anterior caudal vertebra in ventral, **k** posterior, **l** dorsal view. **m** middle caudal vertebra in left lateral, **n** anterior, **o** ventral, **p** dorsal view. **q** distal caudal vertebra in left lateral, **r** posterior, **s** ventral, **t** dorsal view.

**Fig. 7.** The holotype of *Hungarosaurus tormai* (2nd ankylosaur skeleton, MTM 2007.26.1-2007.26.34.) from the Santonian of Iharkút, Hungary. **a** right scapula in lateral view. **b** fragmentary right coracoid in ventral, **c** anterolateral view. **d** left scapulocoracoid in lateral, **e** medial view. **f** fragmentary ischium in lateral, **g** medial view. **h** Fragmentary left ilium in

dorsal, **i** ventral view. **j-k** ilium fragments. **l** right femur in anterior, **m** posterior view. **n** rigth fibula in lateral, **o** medial view. **p-q** limb bone fragment. **r** ungual phalanx in dorsal, **s** ventral view. **t** ungual phalanx in dorsal, **u** ventral view. **v** second or third phalanx in dorsal, **w** proximal, **x** distal view.

**Fig. 8.** The holotype of *Hungarosaurus tormai* (2nd ankylosaur skeleton, MTM 2007.26.1-2007.26.34.) from the Santonian of Iharkút, Hungary. **a** plate of an anterior cervical half-ring in ?lateral, **b** ?medial view. **c** plate of an anterior cervical half-ring in ?lateral, **d** ?medial view. **e** lateral plate and the base of a cervical half-ring in ventral, **f** dorsal view. **g** small lateral plate and the base of a posterior cervical half-ring in ventral, **h** dorsal view. **i** fragmentary plate of an anterior cervical half-ring in ?lateral, **j** ?medial view.

**Fig. 9.** The holotype of *Hungarosaurus tormai* (2nd ankylosaur skeleton, MTM 2007.26.1-2007.26.34.) from the Santonian of Iharkút, Hungary. **a** complete ?left distal cervical half-ring in ?medial, **b** ?lateral view. **c** lateral plate and fragmentary base of a cervical half-ring in ventral, **d** dorsal view. **e** ?right distal cervical half-ring in ?lateral, **f** ?medial view. **g-h** oval shaped dorsal osteoderms in dorsal view. **i** oval shaped, massive, fused osteoderm from the ?pelvic region in dorsal view. **j** subcircular shallow keeled osteoderm in dorsal view.

**Fig. 10.** The holotype of *Hungarosaurus tormai* (2nd ankylosaur skeleton, MTM 2007.26.1-2007.26.34.) from the Santonian of Iharkút, Hungary. **a-g** oval shaped, keeled, dorsal osteoderms in dorsal view. **h** polygonal pelvic osteoderm in dorsal, **i** ventral view. **j** polygonal pelvic osteoderm in dorsal, **k** ventral view. **l** oval shaped, keeled osteoderm in ventral, **m** dorsal view. **n** oval shaped, slightly keeled osteoderm in ventral, **o** dorsal view. **r** osteoderm from the ?dorsal region in ventral, **s** dorsal view. **t** osteoderm from the ?dorsal region in

dorsal, **u** ventral view. **v** osteoderm from the ?dorsal region in dorsal, **w** ventral view. **x** osteoderm from the ?dorsal region in ?ventral, **y** ?dorsal view.

**Fig. 11.** The holotype of *Hungarosaurus tormai* (2nd ankylosaur skeleton, MTM 2007.26.1-2007.26.34.) from the Santonian of Iharkút, Hungary. **a** keeled, lateral osteoderm in ventral, **b** dorsal view. **c** keeled, rhomboidal, dorsal osteoderm in dorsal, **d** ventral view. **e** keeled osteoderm in dorsal, **f** ventral view. **g** keeled, oval, dorsal osteoderm in dorsal, **h** ventral view. **i** keeled, oval, dorsal osteoderm in dorsal, **j** ventral view. **k** keeled, oval, dorsal osteoderm in dorsal, **l** ventral view. **m** keeled, oval, dorsal osteoderm in dorsal, **n** ventral view. **o** Keeled, oval, small ?dorsal osteoderm in dorsal, **p** ventral view. **q** crested, oval, lateral osteoderm in ?medial, **r** lateral view. **s** crested, oval, caudal osteoderm in ?ventral, **t** medial view.

**Fig. 12**. The 3rd ankylosaur skeleton (MTM 2007.24.1.-2007.24.10.) referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. **a** proximal caudal vertebra in left lateral, **b** posteror view. **c** anterior chevron in posterior, **d** lateral view. **e** distal half of a ?humerus in ?lateral, **f** posterior, **g** anterior view. **h** proximal end of ulna in lateral, I, medial view. **j** fragmentary right femur in posterior, **k** anterior view. **l** metapodium in ?medial, **m** lateral view. **n** unidentified limb element (?radius) in ?lateral, **o** medial view. **p** fused pelvic osteoderm in ventral, **q** dorsal view.

**Fig. 13**. The 4th ankylosaur skeleton (MTM 2007.23.1.-2007.23.4; 2007.90.1., 2007.90.2.) referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. **a** left ischium in lateral, **b** anterior view. **c** right ischium in medial, **d** lateral view. **e** synsacrum in dorsal, **f** ventral view. **g** left fragmentary ilium in dorsal, **h** ventral view. **i** boomerang shaped symmetrical, centrally positioned dermal element with two posterodorsally projecting conical

spikes (broken, see n, o) laterally on its dorsal side in anterior, **j** dorsal, **k** ventral, **l** left lateral, **m** right lateral view. **n** broken conical spike from the boomerang shaped symmetrical, centrally positioned element in ?lateral, **o** ?medial view.

**Fig. 14**. The 5th ankylosaur skeleton (MTM 2007.26.1-2007.26.34.) referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. **a** right dentary in lateral view. **b** left mandible in lateral view. **c** dorsal vertebra in lateral view. **d** dorsal vertebra in lateral, **e** ventral view. **f** dorsal rib in posterior view. **g** fragmentary cervical rib. **h** chevron in anterior, **i** lateral view. **j** synsacrum in ventral, **k** dorsal view. **l** proximal caudal verebra in ?anterior, **m** ventral view. **n** middle caudal vertebra in posterior, **o** lateral, **o** ventral, **q** dorsal view. **r** distal caudal vertebra in anterior, **s** lateral, **t** ventral view. **u** paravertebral element with broken spines in dorsal view.

**Fig. 15**. The 5th ankylosaur skeleton (MTM 2007.26.1-2007.26.34.) referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. **a** left scapulocoracoid in lateral, **b** medial view. **c** left fragmentary ilium in dorsal, **d** ventral view. **e** right ilium with the associated left ischium in ventral, **f** dorsal view. **g** right ischium in lateral, **h** medial view. **i** right humerus in anterior, **j** posterior view. **k** ?right radius in lateral, **l** medial view. **m** right ulna in medial, **n** lateral view. **o** left fragmentary ulna in lateral, **p** medial view.

**Fig. 16**. The 5th ankylosaur skeleton (MTM 2007.26.1-2007.26.34.) referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. **a** right femur in posterior, **b** anterior view. **c** left femur in posterior, **d** anterior view. **e** left fibula in lateral, **f** medial view. **g** ?right tibia in posterior, **h** anterior view. **i-o** metepodium dorsal view. **p** metapodium in proximal, **q** lateral view. **r** ungual phalanx in dorsal, **s** ventral view. **t** ungual phalanx in

dorsal, **u** ventral view. **v** phalanx in proximal, **w** dorsal view. **x** anterior cervical half-ring with two posteriorly projecting plates in dorsal, **y** posterior, **z** ventral view. **a'**, anterior cervical half-ring with two posteriorly projecting plates in ventral view.

**Fig. 17**. The 5th ankylosaur skeleton (MTM 2007.26.1-2007.26.34.) referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. **a** posteriorly projecting plate of an anterior cervical half-ring in ?lateral, **b** dorsal, **c** ventral view. **d-e** fragmentary posteriorly projecting plate of an anterior cervical half-ring in lateral/medial, **f** anterior view. **g** subcircular osteoderm in dorsal, **h** ventral view. **i** subcircular osteoderm in dorsal, **j** ventral view. **k** oval dorsal osteoderm in dorsal, **l** ventral view. **m** oval dorsal osteoderm in dorsal, **n** ventral view. **o** oval dorsal osteoderm in dorsal, **p** ventral view. **q** oval, elongate, dorsal osteoderm in dorsal, **r** ventral view. **s** caudal osteoderm with high crest in dorsal, **t** ventral, **u** lateral view.

**Fig. 18**. The 9th ankylosaur skeleton (MTM PAL 2016.16.1.) referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. **a** postdentary part of the right mandible in lateral, **b** medial view. **c** cervical rib fragment. **d-e** dorsal rib fragment. **f** atlas in ventral, **g** dorsal view. **h** dorsal vertebra in lateral, **i** ventral view. **j** dorsal vertebral centrum in ?anterior, **k** ventral, **l** lateral view. **m** middle caudal vertebral centrum in proximal, **n** dorsal, **o** lateral, **p** ventral view.

**Fig. 19**. The 9th ankylosaur skeleton (MTM PAL 2016.16.1.) referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. **a** left scapula with the glenoidal part of the coracoid in medial, **b** lateral view. **c** proximal and distal parts of left humerus in posterior, **d**

anterior view. **e** proximal part of the an ulna. **f** fragmentary ischium in lateral, **g** medial view. **h** distal end of femur. **i-j** distal end of a metapodium.

**Fig. 20**. The 9th ankylosaur skeleton (MTM PAL 2016.16.1.) referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. **a** fragmentary cervical half-ring in ventral view. **b** oval, shallow crested, dorsal or pelvic osteoderm in dorsal, **c** ventral view. **d** small, ?dorsal osteoderm in dorsal, **e** ventral view. **f** small, ?dorsal osteoderm in dorsal, **g** ventral view. **h** fused blocks of polygonal osteoderms with a dorsal rib fragment in dorsal, **i** ventral view. **j** fused blocks of polygonal osteoderms in ventral, **k** dorsal view. **l** broken conical spike from the boomerang shaped symmetrical, centrally positioned element in anterior, **m** posterior view. **n** anterior fragment from the base of the boomerang shaped symmetrical, centrally positioned element in dorsal view. **o-p** crested caudal osteoderm in lateral view.

**Fig. 21**. The 8th ankylosaur skeleton (MTM PAL 2013.59.1.) referred to cf. *Struthiosaurus* from the Santonian of Iharkút, Hungary. **a** dorsal vertebra in left lateral, **b** posterior view. **c** dorsal vertebral centrum right lateral, **d** posterior view. **e** synsacrum with articulated, crested, central osteoderms in left lateral view. **f** left ilium in dorsal view. **g** synsacrum with articulated, crested, central osteoderms in dorsal, **h** ventral view. **i** left ilium in ventral view.

**Fig. 22**. Bone map with the position of the 8th (cf. *Struthiosaurus* sp.), 10th and 11th (Nodosauridae indet.) skeletons and other findings surveyed between 2013 and 2017 at the site SZ-6.

**Fig. 23**. The 12th ankylosaur skeleton (MTM VER. 2016.3567., MTM  PAL 2018.5.1.) referred to cf. *Struthiosaurus* from the Santonian of Iharkút, Hungary. **a** proximal dorsal rib

fragment. **b** anterior end of sacral rod. **c** dorsal rib fragment. **d** ilium fragment. **e** small block of fused pelvic osteoderms with one crested element. **e** block of fused pelvic osteoderms with one crested element (see Ősi and Pereda-Suberbiola 2017). **g** oval, crested dorsal osteoderm. **h** crested osteoderm. **i** small fused block of pelvic osteoderms with two small attached rib fragments in dorsal, **j** ventral view. **k-l** associated one crested high caudal and one crested pelvic osteoderm in lateral, **m** ventral view. **n** crested ?lateral osteoderm in ?ventral, **o** dorsal, **p** lateral view. **q** rectangular crested osteoderm in dorsal, **r** ventral view. **s** subcircular crested osteoderm in dorsal, **t** ventral view. **u** oval, crested osteoderm in dorsal, **v** ventral view.

**Fig. 24**. The 6th ankylosaur skeleton (MTM PAL 2013.58.1.) referred to Nodosauridae indet. from the Santonian of Iharkút, Hungary. **a** pelvic region with synsacrum, sacral and dorsal ribs, both ilia, ischia and right pubis in ventral, **b** dorsal view.

**Fig. 25**. The 7th ankylosaur skeleton (MTM PAL 2013.57.1.) referred to Nodosauridae indet. from the Santonian of Iharkút, Hungary. **a** caudal vertebra ?anterodorsal, **b** posterodorsal view. **c-d** rib fragments. **e** fragmentary synsacrum in ventral, **f** dorsal view. **g** right fragmentary ilium in dorsal, **h** ventral view. **i** left ilium fragment in dorsal, **j** ventral view. **k** crested lateral osteoderm in ventral, **l** dorsal view.

**Fig. 26**. The 10th ankylosaur skeleton (MTM PAL 2018.3.1.) referred to Nodosauridae indet. from the Santonian of Iharkút, Hungary. **a** dorsal rib in lateral, **b** medial view. **c** metapodium in lateral view. **d** crested oval dorsal osteoderm in dorsal, **e** ventral view. **f** crested oval dorsal osteoderm in dorsal, **g** ventral view. **h** crested subcircular dorsal osteoderm in dorsal, **i** ventral view. **j** crested oval dorsal osteoderm in dorsal, **k** ventral view. **l** two crested oval dorsal

osteoderms and a small osteoderm in dorsal, **m** ventral view. **n-o,** crested caudal osteoderm in lateroventral, **p**, lateral view. **q**, small oval dorsal osteoderm in ventral, **r**, dorsal view.

**Fig. 27**. The 11th ankylosaur skeleton (MTM PAL 2018.4.1.) referred to Nodosauridae indet. from the Santonian of Iharkút, Hungary. **a** partial synsacrum with a sacrocaudal vertebra and a fragment of the right ilium in ventral, **b** dorsal view. **c** left ilium in dorsal view. **d** crested ?caudal osteoderm in lateral, **e** ventral view. **f-g** ilium fragment. **h-i** fragment of the sacral rod.

**Table 1**. Summary of the taphonomical, sedimentological and taxonomical data of the ankylosaur skeletons discovered from the Iharkút locality. The calculations of skeletal completeness are persent in the Supplementary Data 2.

**Supplementary Data 1**. Bone maps of the ankylosaur skeletons discovered in Iharkút, Hungary. From the 12th skeleton no bone map could have drawn due to technical and logistical problems.

**Supplementary Data 2**. Skeletal completeness data of the ankylosaur skeletons discovered from the Iharkút locality.