NOTES ON THE PELVIC ARMOR OF EUROPEAN ANKYLOSAURS (DINOSAURIA: ORNITHISCHIA)

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Key words: Ankylosauria; armor; *Struthiosaurus*; *Hungarosaurus*; Late Cretaceous; Hungary

Abstract

The pelvic armor elements in the ankylosaurian material from the Upper Cretaceous of Iharkút, Hungary are described here. Among these, a new articulated hip region of a small bodied ankylosaur is referred here to cf. *Struthiosaurus* sp. It preserves, uniquely among Late Cretaceous European ankylosaurs, an *in situ* pelvic armor composed of among others four, keeled, oval to circular osteoderms lying centrally and arranged longitudinally above the synsacral neural spines. This is the first indication of this type of pelvic osteoderm arrangement in an ankylosaur, increasing our knowledge on this poorly known part of the ankylosaur skeleton. Some additional pelvic osteoderms are also described that help to reconstruct and distinguish the pelvic armor of the two Late Cretaceous European ankylosaurs *Struthiosaurus* and *Hungarosaurus*. Both taxa have some fused parts in the pelvic armor but most probably neither of them had a single, fused pelvic shield as that of the Early Cretaceous *Polacanthus*. Interwoven texture on the ventral surface of the osteoderms, observed in both European taxa and known in other ankylosaurs (e.g. *Polacanthus*, *Nodosaurus*), is suggested here to be a characteristic feature of the non-keeled, fused pelvic armor elements of Ankylosauria.

1. Introduction

The armor elements (i.e. dermal osteoderms) of ankylosaurs represent a great percent of their skeleton, and these fossils, being represented mainly by isolated but associated elements of different types, are preserved in many specimens. The exact position of the osteoderms and/or their arrangement in the armor are, however, poorly known (Ford, 2000), and in most species armor reconstruction can only be based on comparisons with the rarely preserved, articulated armor of some related taxa. Dorsally, the postcranial armor is composed of cervical (cervical and pectoral in Ford, 2000), thoracic, pelvic and caudal regions (Nopcsa, 1928; Carpenter, 1982, 1984, 2004; Vickaryous et al., 2004; Burns and Currie, 2014). The main difference between the pelvic armor and those of the other regions is the lack of transverse bands separated by unarmored, most probably flexible folds anteroposteriorly (Arbour et al., 2011). *In situ* pelvic armor was preserved only in a few ankylosaurs, including *Polacanthus* (Hulke, 1887; Blows, 2015 and references therein), *Stegopelta* (Moodie, 1910), *Nodosaurus* (Lull, 1921), *Dyoplosaurus* (Parks, 1924; Arbour et al., 2014), *Scolosaurus* (Nopcsa, 1928; Penkalski and Blows, 2013), *Sauropelta* (Carpenter, 1984), *Mymoorapelta* (Kirkland et al., 1998), *Gastonia* (Kirkland, 1998), *Aletopelta* (Ford and Kirkland, 2001) and *Taohelong* (Yang et al., 2013) (see Table 1). In addition, in some species the pelvic armor elements, represented by smaller or larger blocks of fused osteoderms, are associated with the rest of the skeleton, but their exact position on the body is unknown.

Here we describe a partial, articulated pelvic region of a small bodied nodosaurid ankylosaur from the Upper Cretaceous of Iharkút (Hungary) that preserves five articulated osteoderms attaching longitudinally to the dorsal side of the neural arches of the synsacrum. The specimen, referred here to cf. *Struthiosaurus* sp., is the first occurrence of *in situ* pelvic osteoderms in a Late Cretaceous European ankylosaur. In addition, we describe some additional pelvic armor elements from the Iharkút locality that help to clarify the pelvic armor morphology in European ankylosaurs and increase our knowledge on the ankylosaurian pelvic armor construction.

2. Material and methods

The partial skeleton (MTM PAL 2013.59.1), described here, was collected in the Iharkút vertebrate locality in 2012 and is housed in the Vertebrate Paleontological Collection of the Hungarian Natural History Museum. Originally, the specimen was laid on its dorsal surface in the sediment, thus first its ventral surface was cleaned. The specimen was collected using a polyurethane foam jacket to keep the bones in their original position and save them from damage during transportation.

The other armor elements described here were also colllected from the bone-yielding beds of the Iharkút locality. Specimens including the partial skeleton were then prepared mechanically in the lab of the Hungarian Natural History Museum and the bones were fixed by cyanoacrylic glue.

Institutional abbreviations: AMNH, American Museum of Natural History, New York, New York, USA; CEUM, College of Eastern Utah Prehistoric Museum, Price, Utah, USA; DMNH, Denver Museum of Nature and Science, Denver, Colorado, USA; DYM, Dongyang Museum, Dongyang City, Zhejiang, China; FCPTD, Fundación Conjunto Paleontológico de Teruel-Dinópolis, Teruel, Spain; FMNH, Field Museum of Natural History, Chicago, Illinois, USA; GSDM, Gansu Dinosaur Museum, Yangouxia, Yongjing County, Gansu, China; MCNA, Museo de Ciencias Naturales de Alava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz, Spain; MLP, Museo de La Plata, La Plata, Argentina; MTM, Magyar Természettudományi Múzeum, Budapest, Hungary; MWC, Museum of Western Colorado Dinosaur Journey, Fruita, Colorado, USA; NHMUK, The Natural History Museum, London, UK; PIN, Palaeontological

Institute, Russian Academy of Sciences, Moscow, Russia; PIUW, Paläontologische Institut, Universität Wien, Vienna, Austria; QM, Queensland Museum, Brisbane, Australia; ROM, Royal Ontario Museum, Toronto, Ontario, Canada; SDNHM, San Diego Natural History Museum, San Diego, California, USA; UM2, Université des Sciences et Techniques du Languedoc, Montpellier, France; USNM, National Museum of Natural History, Smithsonian, Washington, DC, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA; ZPAL, Zaklad Paleobiologii, Polish Academy of Sciences, Warsaw, Poland.

3. Locality and geological setting

The Iharkút locality is situated close to the villages of Németbánya and Bakonyjákó in the heart of the Bakony Mountains, Veszprém County, western Hungary (47° 13' 52'' N, 17° 39' 01''E; see Fig. 1A). The locality is in an abandoned open-pit bauxite mine (Fig. 1B) belonging now to Dino Park Ltd.

The thick basement of the Iharkút locality is formed by the Upper Triassic Main Dolomite Formation. Deep (50 to 90 m), tectonically controlled sinkholes on the karstified surface of this dolomite were filled up by the Cretaceous (pre-Santonian) bauxite. The bauxite and the karstified paleosurface were covered by the fluvial deposits of the Csehbánya Formation, an alluvial flood plain deposit consisting of alternating coarse basal breccia, sandstone, siltstone and paleosol beds (Jocha-Edelényi, 1988; Ősi and Mindszenty, 2009; for a detailed geology and sedimentology of the locality see Botfalvai et al., 2016, fig. 1C). Bone-yielding beds occur in this formation which, on the basis of palynological results, has a Santonian age (Knauer and Siegl-Farkas, 1992; Bodor and Baranyi, 2012). The most productive beds are exposed in the SZ-6 site of the open-pit (Fig. 1B, C). These beds produced a rich and diverse vertebrate fossil assemblage (Ősi et al., 2012 and references therein), including five published

(Ősi, 2005; Ősi and Makádi, 2009) and seven still undescribed partial skeletons of nodosaurid ankylosaurs (Ősi et al. in prep.).

4. Description and comparisons

In this section, the ankylosaurian pelvic armor elements, referred to cf. *Struthiosaurus* sp. from the Upper Cretaceous of Iharkút, are described. Other skeletal elements are discussed briefly only in MTM PAL 2013.59.1., since here the armor is in an *in situ* position. Likewise, other pelvic armor elements from Iharkút belonging to *Hungarosaurus tormai* are described below.

4.1. Cf. *Struthiosaurus* sp.

4.1.1. Partial skeleton MTM PAL 2013.59.1.

Specimen MTM PAL 2013.59.1. is the eighth and smallest partial ankylosaur skeleton discovered in Iharkút. It is an articulated hip region consisting of the last free dorsal vertebra with one left posterior dorsal rib, the synsacrum with four fused dorsal, one sacrodorsal, three sacral and one sacrocaudal vertebrae, three left sacral ribs, the left ilium including the acetabular region (the pubis and ischium are missing), tendons and five *in situ* osteoderms (Fig. 2).

Dorsal vertebra and rib. A free posterior dorsal vertebra (Fig. 2B, C) is preserved close to the anterior end of the fused sacral rod. It was in a close association with a left dorsal rib, the latter having a T-shaped cross-section in its anterior half (Fig. 2A). The vertebral centrum is hourglass-shaped, but not as concave ventrally and laterally as the last dorsal of *Struthiosaurus languedocensis* (UM2 OLV-D50; Garcia and Pereda-Suberbiola, 2003). The ventral and lateral margins of the anterior, slightly concave articular surface are slightly eroded. Dorsal ribs were fused to the transverse processes. The dorsal end of the neural spine is thickened laterally forming a massive rod-like end as frequently seen in sacral vertebrae. The vertebra and the neural arch otherwise show the same features present in other ankylosaurian dorsals (Vickaryous et al., 2004).

Synsacrum. The synsacrum is composed of nine vertebrae: four dorsal and one dorsosacral vertebrae forming the fused sacral rod, and three wide fused sacrals and one sacrocaudal vertebra (Fig. 2D-H). Dorsal vertebral centra are strongly compressed lateromedially, but ventrally they are not as concave as the last free dorsal. The neural arches are slightly damaged and some parts are still in the matrix, but it is obvious that the distal end of the neural arches of at least the second and third dorsals are fused as seen in other ankylosaurs, including *Hungarosaurus* (MTM PAL 2013.58.1.) and *Struthiosaurus* (UM2 OLV-D50). The last element of the sacral rod (a sacrodorsal) is strongly widened posteriorly, as typically seen in many ankylosaurs (Vickaryous et al., 2004). Within the synsacrum no sutures can be observed between any of the vertebrae. Massive, anteroposteriorly concave sacral ribs fused to the sacral vertebrae are preserved connecting the ilium to the axial column. The ventral half of the sacrocaudal vertebra was broken due to diagenetic events and moved to the ventral side of the last sacral. Its neural arch is, however, in original position with the free postzygapophyses pointing posteriorly.

Pelvic elements. The left partial ilium is preserved (Fig. 2D-F). Its anterior part is misssing and its central part just behind the acetabular region is compressed anteroposteriorly (Fig. 2D-E). The postacetabular region is relatively short with a pointed, triangular posterior end, more similar to that of *Struthiosaurus languedocensis* (UM 2 OLV-D50) than to the elongate posteromedially oriented process seen in an articulated hip region of *Hungarosaurus* (MTM PAL 2013.58.1.). Two posterior dorsal rib fragments are fused to the ventral surface of the anterior end of the ilium. The acetabular region is quite compressed, the pubis is not preserved due to preservational biases, and only the proximal fused part of the ischium is preserved. The lateral margin of the ilium is slightly concave with its anterior end diverging laterally. The dorsal surface of the ilium is relatively smooth; no fusion of any osteoderms or tendons can be observed.

Tendons. One fragmentary tendon, being circular or oval in cross section and ca. 5 cm in anteroposterior length on the left side of the neural spine of the second sacral vertebra is preserved. In addition, a lateromedially flattened tendon fragment starting from the left side of the neural arch of the first sacral vertebra (under the second central osteoderm) is preserved and connects to the dorsal side of the second sacral rib (Fig. 2F). The two tendon fragments might have formed a single parasagittal tendon being narrow and pointed anteriorly and thin and flattened posteriorly, but due to the dorsally positioned central osteoderms the transitional parts are obscured.

Osteoderms. Altogether five *in situ* osteoderms are preserved (Fig. 2E-H). The first morphotype is represented by four oval to circular central osteoderms with an anteroposteriorly oriented sagittal keel. They are preserved in a central position sitting in a line above the neural arches from the last fused dorsal to the middle of the sacrocaudal vertebra. Most of their right part has been eroded, but based on the shape of their margin and thickness, they were symmetrical elements with the sagittal keel positioning exactly centrally. Accepting this hypothesis, the two anterior osteoderms were roughly circular, whereas the last two elements have had a transversely wider than long shape. The sagittal keels are relatively shallow with the posterior, pointed end being slightly higher than the anterior end. This posterior tip is highest (ca. 2 cm measured from the dorsal surface of the osteoderm) on the second and third central osteoderms. Some of these central osteoderms seems to be articulated but not fused with each other. At the posterior end of the first preserved central osteoderm some sediment separating the neural arch from the osteoderm can be observed indicating that they were not ossified with the neural arches. A 2 cm long, 3-4 mm wide, slightly concave articular facet can be observed on the anterior margin of the 3rd and 4th central osteoderms supposedly for connecting the convex posterior margin of the adjoining osteoderm.

These osteoderms of MTM PAL 2013.59.1. are similar to a piece of pelvic armor referred to *Struthiosaurus* sp. (MCNA 7416) from Laño (Spain) in having the same type of keeled elements and the orientation of the keels being in line with each other. On the other hand, the Laño specimen is completely fused and the keels are slightly bent lateromedially.

Besides the central osteoderms, a second morphotype, represented by a small, circular osteoderm on the left side between the 1st and 2nd central osteoderms, is preserved (Fig. 2E, F). It is not fused but almost in connection with the posterolateral margin of the 1st central osteoderm. It is a non-keeled element with a slightly convex, rugose dorsal surface bearing some small grooves and foramina.

4.1.2. MTM VER. 2016.3567.

A complex pelvic armor element with articulated dorsal or sacrodorsal ribs (VER. 2016.3567.; Fig. 3A-F) is an informative specimen from the Iharkút locality. The armor has an average dorsoventral thickness of ca. 5 mm and is a composite of two subcircular keeled osteoderms that are fused together by a composit of smaller osteoderms (Fig. 3C, E). The dorsal surface of the osteoderms is densely pitted and ornamented by some irregular grooves. The osteoderms have a ca. 1.5-2 cm high keel (Fig. 3F) being little higher on one side indicating its posterior end. The keel of the lateral osteoderm is slightly bent medially in a posterior direction. Ventrally, the keeled osteoderms has a concave anteroposterior groove just below the keel. These osteoderms, being wider lateromedially (73 mm and 69 mm) than their anteroposterior length (58 mm), are practically identical with the third central osteoderm lying above the neural spines of MTM PAL 2013.59.1. The similarity is further supported by a 1.5 cm long transverse articular facet on the anterior margin of the lateral keeled osteoderm, as it was pointed out on the anterior 3rd and 4th central osteoderms of MTM PAL 2013.59.1 as well. These type of keeled osteoderms are unknown in the holotype of *Hungarosaurus* and in the 9th skeleton referred to this taxon.

Between the keeled osteoderms most probably two small polygonal osteoderms are fused to each other and to the keeled elements resulting 22 mm distance between the two keeled osteoderms. These small osteoderms show the same dorsal texture as that of the keeled elements but have no apexes or keels. A lateromedially elongate polygonal osteoderm, avoid of any apex or keel dorsally, is also fused to the anterolateral margin of medial keeled osteoderm and to anteromedial margin of the small polygonal osteoderm. These polygonal osteoderms between and anterior to the keeled ones are similar to those of the fused polygonal elements of the 9th skeleton of *Hungarosaurus*. Whereas the ventral surface of the keeled osteoderms is devoid of the interwoven texture, the smaller, non-keeled, flat osteoderms bordering them do show the typical interwoven texture. Since this ventral interwoven texture cannot be observed in any other type (e.g. cervical, dorsal, caudal) of osteoderm in the whole ankylosaurian assemblage from Iharkút, nor on the keeled pelvic osteoderms, this feature is suggested here to be only characteristic for the fused polygonal osteoderms of the pelvic armor.

Two rib fragments extending almost entirely along the armor element are preserved on the ventral side of the armor block. They are not fused to any parts of the armor but separated by 0.5-2 mm thick matrix containing a great amount of pyrite. Whereas the medial end of the ribs shows a dorsoventrally low, but T-shaped cross-section, the lateral end is completely flat. Their shape, the relatively thin body and the weaker dorsoventral bending compared to the more anterior dorsal ribs indicate that these ribs were connected to the last dorsals of the sacral rod and the anterior end of the ilium. Comparison of the ribs to those of the articulated specimen referred to *Hungarosaurus* (Ősi, 2015) and, taking the posterior side of the keeled osteoderms into account, this block represents the right fragment of the pelvic armor positioned between the vertebral column and the preacetabular process of the right ilium anterior to the first sacral rib.

This piece of pelvic armor block is quite similar to a pelvic armor fragment (MCNA 7432) from the Late Cretaceous of Laño, Spain (Pereda-Suberbiola, 1999; Fig. 3I). This element is also composed of two circular, keeled osteoderms fused with smaller rounded or slightly polygonal flat osteoderms. The keeled osteoderms of the Hungarian specimen differs from the Laño specimen being relatively wider lateromedially, and the small osteoderms of the Laño fragment are more markedly separated from each other and from the keeled osteoderms than that of VER. 2016.3567. Furthermore, MCNA 7432 has a much more irregular, even spongy dorsal surface (especially on the keels), being densely ornamented with deep grooves and nutritive foramina, compared to the Iharkút specimen.

4.2. *Hungarosaurus tormai*

4.2.1. Type of Hungarosaurus tormai *MTM 2007.26.32. (formerly Gyn/404)*

Besides the armor of MTM PAL 2013.59.1, many additional pieces of fused or unfused, pelvic armor elements are also known from the Upper Cretaceous Iharkút locality. The holotype of *Hungarosaurus*, exhibiting ca. 70% of the armor (Ősi, 2005) of all the main regions, has some pentagonal to quadrilateral, unfused osteoderms (MTM 2007.26.32) that are suggested to be pelvic armor elements (Fig. 4D, E). Their dorsal surface is flat to slightly convex, with a very weakly developed bump in its central part. The ventral surface shows a slightly interwoven texture similar to that of *Nodosaurus textilis* (Marsh, 1889: text-fig. 1), but this texture is not as heavily developed as that of the armor elements of the 9th skeleton (see below). The margin of these polygonal elements is receded (Fig. 4F) to accept the surrounding osteoderms. In the holotype material of *Hungarosaurus* there is no evidence for fused osteoderms. However, this might be related to some preservational biases and suggested trampling (Botfalvai et al., 2015), since most bones in this associated skeleton are broken elements.

4.2.2. 9th skeleton of Hungarosaurus *MTM PAL 2016.16.1.*

Three relatively large, ossified fragments of pelvic armor (Fig. 4A-C) are preserved in the 9th associated ankylosaur skeleton (MTM PAL 2016.16.1.) from Iharkút. They are composed of pentagonal to quadrilateral, flat osteoderms that are strongly fused to each other, representing Category 3 arrangement of Arbour et al (2011). Their shape and arrangement is very similar to the polygonal armor blocks of *Aletopelta* that covered the acetabular region of the ilia (Coombs and Deméré, 1996; Ford and Kirkland, 2001). Their flat to very slightly concave dorsal surface is ornamented by many small pits and grooves but they do not bear any crests or projections similar to the pelvic osteoderms of the holotype of *Hungarosaurus*. Their ventral surface is markedly ornamented by an interwoven texture (Fig. 4C), as seen in *Nodosaurus* (Marsh, 1889; Lull, 1921).

4.3. Nodosauridae indet.

4.3.1. MTM VER 2016.573.

An isolated armor element (MTM VER 2016.573), composed of two larger (one pentagonal, one quadragular) and one smaller (quadrangular) osteoderm, shows an external morphology not present in any of the former specimens (Fig. 4G). The largest, pentagonal apical osteoderm has a central apex whereas the other osteoderms do not have this feature. The ventral surface of this element has an interwoven texture as well. This type of armor element was most probably part of a fused pelvic armor similar to the blocks of 9th skeleton metioned above, but perhaps represents another segment in the fused block.

5. Discussion

5.1. Taxonomic assignment of the specimens

The pelvic armor of the holotype of *Hungarosaurus* is poorly known (only the few elements described above can be referred to the pelvic armor), but it is clear that some regions were composed of flat, polygonal elements (Fig. 4D, E) with interwoven ventral texture.

The 9th skeleton (MTM PAL 2016.16.1.) is referred to *Hungarosaurus* based on the presence of large polygonal osteoderms with interwoven ventral texture without embedded, keeled, oval shaped osteoderms as seen in MTM PAL 2013.59.1. and VER. 2016.3567. In addition, the shaft of the ischium and the lack of a blunt, knob-like structure at its distal end is more reminiscent to that of *Hungarosaurus* than to *Struthiosaurus* (Ősi et al., in prep.).

Based on pelvic morphology, armor composition and size, specimen MTM PAL 2013.59.1. is referred here to cf. *Struthiosaurus* sp. Although histological evidence is not available at the moment, the completely fused synsacrum, the last free dorsal with completely fused neural arch, the occurrence of ossified tendons, and the presence of pelvic osteoderms, most probably developed in a later ontogenetic stage (see below), suggest that it was not a juvenile but subadult to adult animal. Among the non-osteodermal skeletal elements, the sigmoidal lateral edge of the ilium in dorsal view and the relatively short postacetabular part of the ilium (Fig. 2) is more reminiscent to that of *Struthiosaurus* than of *Hungarosaurus*, further supporting the *Struthiosaurus* affinity of this specimen. The synsacra of *Struthiosaurus languedocensis* from Villeveyrac and *Struthiosaurus* sp. from Laño are composed of ten fused vertebrae (Garcia and Pereda-Suberbiola, 2003); nine vertebrae are known in the cf. *Struthiosaurus* synsacrum from Iharkút and eight or nine elements in the synsacral material of *Hungarosaurus* (Ősi, 2005; Ősi and Makádi, 2009). As it was mentioned above, the morphotype of keeled osteoderms preserved in the pelvic armor of MTM PAL 2013.59.1. and

VER. 2016.3567. are completely unknown in *Hungarosaurus* (including the holotype, the 5th and 9th skeletons), but present in *Struthiosaurus* from Laño (MCNA 7416, 7432; Fig. 4G-I), again, suggesting closer affinity with *Struthiosaurus* and differences between the pelvic armor composition of the two genera. Although the keeled osteoderms represent different positions in the pelvic armor of MTM PAL 2013.59.1 and VER. 2016.3567., their similarly small size and identical external morphology suggest that they both belong to the same taxon. Therefore, we refer provisionally these specimens to as cf. *Struthiosaurus* sp.

Comparison of the size of the skeletal elements of in MTM PAL 2013.59.1. with those of the holotype and the 5th skeleton of *Hungarosaurus* (Ősi and Makádi, 2009), a total body length of ca. 2-2.5 meters can be reconstructed being more closer to the small-sized *Struthiosaurus* (Pereda-Suberbiola, 1992, Ősi and Prondvai, 2013) than to the larger *Hungarosaurus*.

5.2. Pelvic armor in Late Cretaceous European ankylosaurs

The armor of *Struthiosaurus*, the most widespread Late Cretaceous European ankylosaur, is relatively poorly known, though some armor elements are present in all the main assemblages (Transylvanian Basin: Nopcsa, 1929; Ősi et al., 2014; Laño: Pereda-Suberbiola, 1999; Muthmannsdorf: Pereda-Suberbiola and Galton, 2001; Villeveyrac: Garcia and Pereda-Suberbiola, 2003; Iharkút: this paper). In the material referred to *Struthiosaurus* from the Late Cretaceous of Laño, two fused pieces of the pelvic armor (MCNA 7416, 7432) has been described (Pereda-Suberbiola, 1999; see Fig. 3G-I). MCNA 7416 is composed of two subcircular, keeled osteoderms fully ossified with a flat sheet of osteoderm in the latter part of which no individual elements (e.g. smaller ossicles or rosette-like elements) can be recognized (Fig. 3G, H). This fused element was certainly part of the pelvic armor since this type of keeled osteoderms in the preserved position would otherwise represent two transverse bands of dorsal armor separated by a mobile fold (Arbour et al., 2011), which is not the case.

MCNA 7432 is also from the pelvic armor, being very similar to VER. 2016.3567. from Iharkút, a fused block from the anterolateral part of the pelvic armor.

Until now, these two fused elements from Laño were the only evidence for the presence of at least partially fused pelvic armor in a European Late Cretaceous ankylosaur (Pereda-Suberbiola, 1999), since none of the type materials of the three *Struthiosaurus* species (*S. austriacus, S. transylvanicus, S. languedocensis*) or that of *Hungarosaurus* contain fused pelvic armor elements. Only a fragmentary, partially reconstructed, keeled element [PIUW 2349/uncataloged (A1c)], referred to *S. austriacus*, has been described as a possible sacral armor element (Pereda-Suberbiola and Galton, 2001).

Based on MTM PAL 2013.59.1. and VER. 2016.3567. the pelvic armor of *Struthiosaurus* from Iharkút can be partially reconstructed (Fig. 5). The main question is whether the pelvic armor above the synsacrum and ilia was composed of similarly large, keeled osteoderms surrounded by smaller fused elements as seen in VER. 2016.3567., or these regions were covered by fused polygonal armor elements as those preserved in *Hungarosaurus* (see above), *Nodosaurus* and 'stegopeltines' (sensu Ford, 2000; probably not monophyletic, see Arbour and Currie, 2016). Here we suggest that the first type of armor is more plausible in *Struthiosaurus* (Fig. 5), and the presence and absence of fused polygonal osteoderm composition might have been the main difference between the pelvic armor of the two genera. Another question is if these elements were completely fused to form a left and right rigid half-shield (Fig. 5), or they were only fused into smaller armor blocks. VER. 2016.3567. suggests some fusion of these elements, but the extension of fusion is ambiguous. Based on MTM PAL 2013.59.1 some mobility between the sagittally positioned central osteoderms and the lateral elements is suggested (Fig. 5). Although four sagittal osteoderms are preserved *in situ*, a fifth element might have been present anteriorly to cover the anteriormost part of the sacral rod.

The pelvic armor of *Hungarosaurus* is more problematic since no *in situ* osteoderm is preserved. In *Hungarosaurus*, the polygonal elements of the holotype and the three fused armor elements of the 9th skeleton indicate that, in contrast to *Struthiosaurus*, this larger form could have had a completely to at least partially fused pelvic shield composed mainly of flat or very slightly convex, large polygonal elements (Fig. 4A-E), similar to that of *Nodosaurus* (Lull, 1921), *Stegopelta* (Moodie, 1910; Ford, 2000 and references), *Aletopelta* (Ford and Kirkland, 2001) and *Glyptodontopelta* (Ford, 2000; Burns, 2008). The subcircular, keeled elements, present in *Struthiosaurus*, however, appear to have been absent or were a less important osteoderm type in the pelvic armor.

One problematic type of fused osteoderm is a large, symmetrical, ca. 30 cm wide, dorsoventrally thick, boomerang shaped centrally positioned element (MTM 2007.23.1) with two high (ca. 15 cm), slightly posteriorly projecting conical spikes laterally on its dorsal side (Fig. 6A-E). This element was discovered in Iharkút in 2003 with an associated hip region (ilia, ischia, synsacrum) of the fourth nodosaurid skeleton that has been referred to *Hungarosaurus* (Ősi, 2005). Later on, some additional, but isolated conical spikes have been discovered as well (MTM 2007.30.1; Ősi and Makádi, 2009, Fig. 6F, G). One identical conical spike (PIUW 2349/15) is also known from the Campanian of Muthmannsdorf (Austria) and referred to *Struthiosaurus* (Seeley, 1881; Pereda-Suberbiola and Galton, 2001; Fig. 6H). Ősi and Makádi (2009) reconstructed this element from Iharkút as being in the posterior segment of the pelvic or the anterior margin of the caudal armor in *Hungarosaurus*. This hypothesis was only based on the association of this fused osteoderm with the pelvic-sacral elements, but they were not in articulation, so it cannot be ruled out that it might represent some part of the cervical-dorsal armor. Furthermore, it is also ambiguous, whether this dermal element was present in both taxa or was charateristic only for *Hungarosaurus*.

5.3. Osteoderm fusion and arrangement

Using 13 taxa with preserved elements of the pelvic region, ankylosaur pelvic armor morphology has been classified into three categories on the basis of the shape and fusional degree of the osteoderms (Arbour et al., 2011): 1) not coossified but tightly interlocking osteoderms; 2) coossified osteoderms forming rosettes; 3) coossified polygonal osteoderms of similar size. Updated information on the pelvic armor of ankylosaurs is presented in Table 1, including data from 25 taxa, 16 of them with *in situ* osteoderms. As noted by Arbour et al. (2011), this classification of pelvic armor arrangement should not be used to support any monophyletic grouping within the Ankylosauria until there is a global phylogenetic analysis that includes pelvic armor characters, but it is useful to understand the morphological variations among taxa.

According to this interpretation, the pelvic armor of sagittally positioned and tightly interlocking but unfused osteoderms, preserved dorsal to the synsacral neural spines of MTM PAL 2013.59.1, here referred to cf. *Struthiosaurus* p., belongs to Category 1 of Arbour et al. (2011). Similarly unfused but interlocking osteoderms has been reported in the Early Cretaceous nodosaurid *Sauropelta* from North America (and in several Late Cretaceous ankylosaurids from North America and Asia, Arbour et al., 2011, 2013, 2014; see Table 1). These forms, however, show a different arrangement of osteoderms, having widely spaced, large circular elements surrounded by smaller ones (Arbour et al., 2014), whereas in the Iharkút specimen the large central osteoderms are in a continuous sagittal line not interrupted by smaller elements. The large circular elements of *Sauropelta* are non-keeled (Carpenter, 1984; Coombs and Maryańska, 1990), while the large pelvic osteoderms of *Scolosaurus* bear an anteroposteriorly oriented keel (Arbour et al., 2011; Penkalski and Blows, 2013). These differences further support the hypothesis that the ankylosaur armor or some parts of it (Carpenter, 1990; Blows, 2001, Ford, 2000), or even the external and internal morphology of a single osteoderm (Burns 2008, 2010), are distinctive to at least the generic level allowing the identification of an ankylosaur genus based solely on osteoderms.

Since there is not a single ankylosaurian species represented by more individuals of different ontogenetic stages with preserved pelvic armor (Burns, 2008; Arbour et al., 2011), it is unknown, how the fusional degree of the pelvic armor changed in ankylosaurs during ontogeny. Burns (2010) reported that the juvenile specimen of *Pinacosaurus* do not exhibit postcranial osteoderms beyond the cervical half rings, suggesting that their osteoderms exhibited a delayed onset of osteoderm skeletogenesis relative to the remainder of the body skeleton, as demonstrated in *Stegosaurus* (Hayashi et al., 2009), extant archosaurs (Vickaryous and Hall, 2008) and armadillos (Vickaryous and Hall, 2006). This means that the pelvic armor developed most likely in a relatively later phase of ontogeny than the more anteriorly positioned pectoral and possibly also the dorsal armor elements.

Nevertheless, the fusional degree of the different pelvic armor regions might have been variable even in a single specimen similar to that seen in the Late Cretaeous North American *Aletopelta* (Coombs and Deméré, 1996, Ford and Kirkland, 2001). In this form, the lateral side of the pelvic armor is more solid with fused hexagonal to quadrilateral osteoderms, whereas centrally some of these angular elements are unfused (Coombs and Deméré, 1996: fig. 1). Since the central pelvic armor elements are mostly missing in this taxon, it is ambiguous whether these lateral coossified blocks were fused with the central elements or not.

Although we have pelvic armor elements fused with several smaller and larger osteoderms in various ankylosaur taxa, a single, massive block of pelvic shield covering the hip region is unambiguously present only in *Polacanthus* (Hulke, 1887). The presence of a solid pelvic shield has also been assumed for other North American ’polacanthines’, such as *Gastonia*, *Mymoorapelta*, *Hoplitosaurus* and *Gargoyleosaurus* (Kirkland, 1998; Kirkland et al., 1998; Blows, 2001; Carpenter, 2001) and potentially in *Taohelong*, *Sauroplites* and *Shamosaurus*

(Arbour and Currie, 2016), although in these taxa the fossil evidence is still incomplete. Recently, Kinneer et al. (2015) have raised the possibility that the pelvic shield of *Gargoyleosaurus* may have been made of multiple smaller coossified sections rather than a single unit. So, it cannot be ruled out that the pelvic armor of some taxa of Category 2 of Arbour et al. (2011) was not a single, rigid construction as that of *Polacanthus*, but rather composed of several fused and unfused blocks covering the synsacral and pelvic regions, as it is suggested in the Hungarian cf. *Struthiosaurus* (Fig. 5). Here, the sagittal row of osteoderms representing Category 1 of Arbour et al. (2011) could have bordered by at least one to one fused block of osteoderms in a system of Category 2 of Arbour et al. (2011). Thus, cf. *Struthiosaurus* may be unique among ankylosaurs in falling under categories 1 and 2 of pelvic armor fusion and arrangement.

Although the ankylosaurian pelvic armor should have been a more or less rigid construction due to the ossified synsacral-iliac block, it apparently was set up by some sort of transverse bands that were either fused with each other by smaller (e.g. polygonal) osteoderms or were separated by an unmobile fold (in contrast to the mobile folds of the cervical-dorsal region; Arbour et al., 2011). *Struthiosaurus* had four *in situ* sagittal osteoderms but a fifth element (actually the very first) might have been covered the anterior end of the sacral rod, thus it is reconstructed here with five transverse bands incorporated into the pelvic armor (Fig. 5). It differs therefore from other ankylosaurs, such as the ankylosaurid *Scolosaurus* (NHMUK R5161), which has three transverse bands (Arbour et al., 2011; Penkalski and Blows, 2013) and the nodosaurid *Sauropelta* (AMNH 3036), with probably six transverse bands (Carpenter, 1984, 2012). The rigid pelvic shield of *Polacanthus* (NHMUK R175) consists of at least 8 (and may be 9 or 10) transverse bands of osteoderms (Hulke, 1887; Blows, 2001).

With regard to *Hungarosaurus*, its pelvic armor is composed of polygonal, flat osteoderms that are fused to each other, and so represents Category 3 of Arbour et al (2011). This category is mainly represented in nodosaurids from the mid-Cretaceous of North America, Asia and Europe, and the Upper Cretaceous of North America and Antarctica, as well as in the ankylosaurid *Aletopelta* from North America (see Arbour and Currie, 2016). Previously reported in *Europelta* from the Albian of Teruel in Spain (Kirkland et al., 2013), *Hungarosaurus* would be the only Late Cretaceous European ankylosaur included in this category of pelvic morphology (Table 1).

According to Arbour and Currie (2016), the presence of a pelvic shield in numerous basal ankylosaurs, as well as in more derived members of both the Nodosauridae and Ankylosauridae, suggests that fused pelvic osteoderms are plesiomorphic for ankylosaurs, and not a synapomorphy of a polacanthid or polacanthine clade. An unossified pelvic armor (Category 1 of Arbour et al., 2011) seems to be present in *Kunbarrasaurus* (Molnar, 2001), the most basal ankylosaur (following the phylogenetic analysis of Arbour and Currie 2016), and also in basal thyreophorans, such as *Scelidosaurus* and *Scutellosaurus* (Owen, 1861; Colbert, 1981). Thus, a pelvic armor having unfused but tighly interlocking osteoderms may be the plesiomorphic condition for Ankylosauria.

6. Conclusions

Burns (2008) and Burns and Currie (2014) suggested that ankylosaurian armor can be a great tool for low-level taxonomic identification since external and/or internal features of even a single osteoderm can reveal taxonomic affinity. This can be especially true for complex elements or fused blocks (cervical or pelvic elements) of the armor. The ankylosaur material described here further supports this hypothesis, and the armor elements from the Iharkút locality of Hungary provide significant information about the pelvic armor morphology and arrangement in Late Cretaceous European ankylosaurs. Cf. *Struthiosaurus* is characterized by having interlocked but unfused keeled, oval to circular osteoderms arranged sagittally in a row over the synsacral neural spines (Category 1 of Arbour et al., 2011), combined with at least two fused blocks of keeled, subcircular osteoderms above the ilia that are coossified together by a composite of smaller polygonal scutes. So far, this is the only known ankylosaur whose pelvic armor combines unfused osteoderms with coossified blocks (i.e. Category 1 and 2 of Arbour et al., 2011). As reconstructed here, cf. *Struthiosaurus* has a pelvic armor formed of at least four but probably five transverse bands, and can be also differentiated from many other ankylosaurs on the basis of this quantitative character. On the other hand, the pelvic armor of *Hungarosaurus* was rather more of a composit of pentagonal to quadrilateral, flat osteoderms that were fused at least in some parts (Category 3 of Arbour et al., 2011). Interwoven texture is observed only on the ventral side of polygonal elements but is not present on the oval to circular, keeled osteoderms, suggesting some difference in their skeletogenesis.

Acknowlegements

We thank Victoria Arbour and an anonymous reviewer for their constructive comments that highly improved the manuscript. We thank the 2000–2016 field crew for their assistance in the fieldwork. We are especially grateful to the Bakony Bauxite Mining Company and the Geovolán Zrt. for their logistic help. We thank Réka Kalmár and Márton Szabó (Hungarian Natural History Museum, Budapest) and J. Carmelo Corral (MCNA, Vitoria-Gasteiz) for their technical assistance. Field and laboratory work was supported by the MTA–ELTE Lendület Dinosaur Research Group (Grant no. 95102), Hungarian Scientific Research Fund and National Research, Development and Innovation Office (OTKA T–38045, PD 73021, NF 84193, K 116665), National Geographic Society (Grant No. 7228–02, 7508–03), Bolyai Fellowship, Hungarian Natural History Museum, Eötvös Loránd University, the

Jurassic Foundation and the Hungarian Dinosaur Foundation. Research work of XPS was supported by the Spanish project CGL2013-47521-P of the Ministerio de Economía y Competitividad (MINECO), the European Regional Development Fund (FEDER), and the research groups IT834-13 and IT1044-16 of the Eusko Jaurlaritza/Gobierno Vasco. Photograph of Fig. 3I was kindly provided by J. Carmelo Corral (MCNA, Vitoria-Gasteiz).

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Figure captions:

Figure 1. Locality and geological background of the Iharkút SZ-6 site (Hungary). A, Location map of the Iharkút vertebrate locality. B, Aerial photo of the Iharkút open-pit, showing the position of the SZ-6 site. C, Stratigraphic section of the Csehbánya Formation exposed in the open-pit with SZ-6 site (modified after Botfalvai et al., 2016). [Planned with double column width, color in online only]

Figure 2. Articulated partial hip region of an ankylosaur (MTM PAL 2013.59.1.) referred to cf. *Struthiosaurus* sp. from the Upper Cretaceous of Iharkút, Hungary. A, position of the specimen on the field exposed in ventral view. B, last free dorsal vertebra in posterior, C, and left lateral view. D, synsacrum and left ilium in ventral view. E-F, synsacrum and left ilium with *in situ* centrally positioned osteoderms in dorsal view. G-H, synsacrum with *in situ* centrally positioned osteoderms in left lateral view. Anatomical abbreviations: **co**, central osteoderms; **gr**, groove; **il**, ilium; **os**, osteoderm; **pzy**, postzygapophysis; **rfi**, ribs fused to the ilium; **sr**, sacral rib; **sro**, synsacral rod; **te**, tendon. [Planned with double column width, color in online only]

Figure 3. Ankylosaurian pelvic armor fragments from the Late Cretaceous of Europe. A-F, VER. 2016.3567. pelvic armor fragment referred to cf. *Struthiosaurus* sp. from Iharkút, Hungary. A, details of the anterior margin in one of the keeled osteoderms with sacrodorsal rib ventrally, the osteoderm dorsally with an articulation surface, and sediment between the two bones. B, interwoven texture of the ventral surface of the non-keeled osteoderms anterior to the keeled ones in VER. 2016.3567. C, Fused pelvic armor fragment (VER. 2016.3567.) in dorsal view. D, fused pelvic armor fragment (VER. 2016.3567.) in ventral view. E, technical drawing of the fused pelvic armor fragment (VER. 2016.3567.) in dorsal view. F, fused pelvic

armor fragment and one of the sacrodorsal ribs (VER. 2016.3567.) in anterior view. G-I, fragmentary pelvic armor elements from Laño, Spain. G, MCNA 7416 in dorsal view, and H, in ventral view. I, MCNA 7432 in dorsal view. Anatomical abbreviations: **gr**, groove; **iw**, interwoven texture; **ko**, keeled osteoderm; **pos**, polygonal osteoderm; **r**, rib; **se**, sediment. [Planned with double column width, color in online only]

Figure 4. Pelvic armor elements of *Hungarosaurus* from the Upper Cretaceous of Iharkút, Hungary. A-B, fused blocks of polygonal osteoderms from the 9th skeleton (MTM PAL 2016.16.1.) in dorsal view. C, fused block of polygonal osteoderms from the 9th skeleton (MTM PAL 2016.16.1.) in ventral view. D-E, polygonal osteoderms (MTM 2007.26.32) from the holotype of *Hungarosaurus tormai* in dorsal view. F, the receding margin of the polygonal osteoderm seen in Fig. 3D in dorsal view. G, fused pelvic osteoderm MTM VER 2016.573 in dorsal view. Anatomical abbreviations: **iw**, interwoven texture; **oaf**, osteoderm articulation facet; **pos**, polygonal osteoderm. [Planned with double column width, color in online only]

Figure 5. Partially reconstructed pelvic armor of cf. *Struthiosaurus* from Iharkút. Dark grey elements are preserved, light grey elements are reconstructed. Anatomical abbreviations: **co**, central osteoderms; **il**, ilium; **r**, rib; **sr**, sacral rib; **sro**, synsacral rod. [Planned with double column width]

Figure 6. Problematic osteoderms with conical spikes in European Late Cretaceous nodosaurids. A, boomerang shaped symmetrical, centrally positioned element (MTM 2007.23.1) with two high, slightly posteriorly projecting conical spikes laterally on its dorsal side in dorsal; B, ventral; C, anterior; D, posterior; E left dorsolateral view. This element was associated with the fourth skeleton referred to *Hungarosaurus* from Iharkút (Ősi 2005). F,

isolated fragmentary boomerang shaped element with a conical spike (MTM VER 2017.66.) from Iharkút. G, isolated fragmentary boomerang shaped element with a conical spike (MTM VER 2016.578.) from Iharkút. H, isolated fragmentary fused element with a conical spike of *Struthiosaurus austriacus* (PIUW 2349/15) from the lower Campanian of Muthmannsdorf, Austria. Anatomical abbreviations: **bsp**, broken conical spike; **fb**, fused basement of the osteoderm; **ri**, ridge [Planned with double column width]