1 NOTES ON THE PELVIC ARMOR OF EUROPEAN ANKYLOSAURS (DINOSAURIA:

2 ORNITHISCHIA)

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

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26 **Abstract**

27 The pelvic armor elements in the ankylosaurian material from the Upper Cretaceous of

28 Iharkút, Hungary are described here. Among these, a new articulated hip region of a small

29 bodied ankylosaur is referred here to cf. *Struthiosaurus* sp. It preserves, uniquely among Late

30 Cretaceous European ankylosaurs, an *in situ* pelvic armor composed of among others four,

31 keeled, oval to circular osteoderms lying centrally and arranged longitudinally above the

32 synsacral neural spines. This is the first indication of this type of pelvic osteoderm

33 arrangement in an ankylosaur, increasing our knowledge on this poorly known part of the

34 ankylosaur skeleton. Some additional pelvic osteoderms are also described that help to

35 reconstruct and distinguish the pelvic armor of the two Late Cretaceous European ankylosaurs

36 *Struthiosaurus* and *Hungarosaurus*. Both taxa have some fused parts in the pelvic armor but

37 most probably neither of them had a single, fused pelvic shield as that of the Early Cretaceous

38 *Polacanthus*. Interwoven texture on the ventral surface of the osteoderms, observed in both

39 European taxa and known in other ankylosaurs (e.g. *Polacanthus*, *Nodosaurus*), is suggested

40 here to be a characteristic feature of the non-keeled, fused pelvic armor elements of

41 Ankylosauria.

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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

76 morphology in European ankylosaurs and increase our knowledge on the ankylosaurian pelvic

77 armor construction.

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79 **2. Material and methods**

80 The partial skeleton (MTM PAL 2013.59.1), described here, was collected in the Iharkút

81 vertebrate locality in 2012 and is housed in the Vertebrate Paleontological Collection of the

82 Hungarian Natural History Museum. Originally, the specimen was laid on its dorsal surface in

83 the sediment, thus first its ventral surface was cleaned. The specimen was collected using a

84 polyurethane foam jacket to keep the bones in their original position and save them from

85 damage during transportation.

86 The other armor elements described here were also colllected from the bone-yielding beds of

87 the Iharkút locality. Specimens including the partial skeleton were then prepared

88 mechanically in the lab of the Hungarian Natural History Museum and the bones were fixed

89 by cyanoacrylic glue.

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91 Institutional abbreviations: AMNH, American Museum of Natural History, New York, New

92 York, USA; CEUM, College of Eastern Utah Prehistoric Museum, Price, Utah, USA; DMNH,

93 Denver Museum of Nature and Science, Denver, Colorado, USA; DYM, Dongyang Museum,

94 Dongyang City, Zhejiang, China; FCPTD, Fundación Conjunto Paleontológico de Teruel-

95 Dinópolis, Teruel, Spain; FMNH, Field Museum of Natural History, Chicago, Illinois, USA;

96 GSDM, Gansu Dinosaur Museum, Yangouxia, Yongjing County, Gansu, China; MCNA,

97 Museo de Ciencias Naturales de Alava/Arabako Natur Zientzien Museoa, Vitoria-Gasteiz,

98 Spain; MLP, Museo de La Plata, La Plata, Argentina; MTM, Magyar Természettudományi

99 Múzeum, Budapest, Hungary; MWC, Museum of Western Colorado Dinosaur Journey, Fruita,

100 Colorado, USA; NHMUK, The Natural History Museum, London, UK; PIN, Palaeontological

101 Institute, Russian Academy of Sciences, Moscow, Russia; PIUW, Paläontologische Institut,

102 Universität Wien, Vienna, Austria; QM, Queensland Museum, Brisbane, Australia; ROM,

103 Royal Ontario Museum, Toronto, Ontario, Canada; SDNHM, San Diego Natural History

104 Museum, San Diego, California, USA; UM2, Université des Sciences et Techniques du

105 Languedoc, Montpellier, France; USNM, National Museum of Natural History, Smithsonian,

106 Washington, DC, USA; YPM, Yale Peabody Museum, New Haven, Connecticut, USA;

107 ZPAL, Zaklad Paleobiologii, Polish Academy of Sciences, Warsaw, Poland.

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109 **3. Locality and geological setting**

110 The Iharkút locality is situated close to the villages of Németbánya and Bakonyjákó in the

111 heart of the Bakony Mountains, Veszprém County, western Hungary (47° 13' 52'' N, 17° 39'

112 01''E; see Fig. 1A). The locality is in an abandoned open-pit bauxite mine (Fig. 1B)

113 belonging now to Dino Park Ltd.

114 The thick basement of the Iharkút locality is formed by the Upper Triassic Main Dolomite

115 Formation. Deep (50 to 90 m), tectonically controlled sinkholes on the karstified surface of

116 this dolomite were filled up by the Cretaceous (pre-Santonian) bauxite. The bauxite and the

117 karstified paleosurface were covered by the fluvial deposits of the Csehbánya Formation, an

118 alluvial flood plain deposit consisting of alternating coarse basal breccia, sandstone, siltstone

119 and paleosol beds (Jocha-Edelényi, 1988; Ősi and Mindszenty, 2009; for a detailed geology

120 and sedimentology of the locality see Botfalvai et al., 2016, fig. 1C). Bone-yielding beds

121 occur in this formation which, on the basis of palynological results, has a Santonian age

122 (Knauer and Siegl-Farkas, 1992; Bodor and Baranyi, 2012). The most productive beds are

123 exposed in the SZ-6 site of the open-pit (Fig. 1B, C). These beds produced a rich and diverse

124 vertebrate fossil assemblage (Ősi et al., 2012 and references therein), including five published

125 (Ősi, 2005; Ősi and Makádi, 2009) and seven still undescribed partial skeletons of nodosaurid

126 ankylosaurs (Ősi et al. in prep.).

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128 **4. Description and comparisons**

129 In this section, the ankylosaurian pelvic armor elements, referred to cf. *Struthiosaurus* sp.

130 from the Upper Cretaceous of Iharkút, are described. Other skeletal elements are discussed

131 briefly only in MTM PAL 2013.59.1., since here the armor is in an *in situ* position. Likewise,

132 other pelvic armor elements from Iharkút belonging to *Hungarosaurus tormai* are described

133 below.

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135 4.1. Cf. *Struthiosaurus* sp.

136 *4.1.1. Partial skeleton MTM PAL 2013.59.1.*

137 Specimen MTM PAL 2013.59.1. is the eighth and smallest partial ankylosaur skeleton

138 discovered in Iharkút. It is an articulated hip region consisting of the last free dorsal vertebra

139 with one left posterior dorsal rib, the synsacrum with four fused dorsal, one sacrodorsal, three

140 sacral and one sacrocaudal vertebrae, three left sacral ribs, the left ilium including the

141 acetabular region (the pubis and ischium are missing), tendons and five *in situ* osteoderms

142 (Fig. 2).

143 ***Dorsal vertebra and rib***. A free posterior dorsal vertebra (Fig. 2B, C) is preserved close to the

144 anterior end of the fused sacral rod. It was in a close association with a left dorsal rib, the

145 latter having a T-shaped cross-section in its anterior half (Fig. 2A). The vertebral centrum is

146 hourglass-shaped, but not as concave ventrally and laterally as the last dorsal of

147 *Struthiosaurus languedocensis* (UM2 OLV-D50; Garcia and Pereda-Suberbiola, 2003). The

148 ventral and lateral margins of the anterior, slightly concave articular surface are slightly

149 eroded. Dorsal ribs were fused to the transverse processes. The dorsal end of the neural spine

150   is thickened laterally forming a massive rod-like end as frequently seen in sacral vertebrae.

151   The vertebra and the neural arch otherwise show the same features present in other

152   ankylosaurian dorsals (Vickaryous et al., 2004).

153   *Synsacrum*. The synsacrum is composed of nine vertebrae: four dorsal and one dorsosacral

154   vertebrae forming the fused sacral rod, and three wide fused sacrals and one sacrocaudal

155   vertebra (Fig. 2D-H). Dorsal vertebral centra are strongly compressed lateromedially, but

156   ventrally they are not as concave as the last free dorsal. The neural arches are slightly

157   damaged and some parts are still in the matrix, but it is obvious that the distal end of the

158   neural arches of at least the second and third dorsals are fused as seen in other ankylosaurs,

159   including *Hungarosaurus* (MTM PAL 2013.58.1.) and *Struthiosaurus* (UM2 OLV-D50). The

160   last element of the sacral rod (a sacrodorsal) is strongly widened posteriorly, as typically seen

161   in many ankylosaurs (Vickaryous et al., 2004). Within the synsacrum no sutures can be

162   observed between any of the vertebrae. Massive, anteroposteriorly concave sacral ribs fused

163   to the sacral vertebrae are preserved connecting the ilium to the axial column. The ventral half

164   of the sacrocaudal vertebra was broken due to diagenetic events and moved to the ventral side

165   of the last sacral. Its neural arch is, however, in original position with the free

166   postzygapophyses pointing posteriorly.

167   *Pelvic elements*. The left partial ilium is preserved (Fig. 2D-F). Its anterior part is misssing

168   and its central part just behind the acetabular region is compressed anteroposteriorly (Fig. 2D-

169   E). The postacetabular region is relatively short with a pointed, triangular posterior end, more

170   similar to that of *Struthiosaurus languedocensis* (UM 2 OLV-D50) than to the elongate

171   posteromedially oriented process seen in an articulated hip region of *Hungarosaurus* (MTM

172   PAL 2013.58.1.). Two posterior dorsal rib fragments are fused to the ventral surface of the

173   anterior end of the ilium. The acetabular region is quite compressed, the pubis is not

174   preserved due to preservational biases, and only the proximal fused part of the ischium is

175   preserved. The lateral margin of the ilium is slightly concave with its anterior end diverging

176   laterally. The dorsal surface of the ilium is relatively smooth; no fusion of any osteoderms or

177   tendons can be observed.

178   *Tendons*. One fragmentary tendon, being circular or oval in cross section and ca. 5 cm in

179   anteroposterior length on the left side of the neural spine of the second sacral vertebra is

180   preserved. In addition, a lateromedially flattened tendon fragment starting from the left side of

181   the neural arch of the first sacral vertebra (under the second central osteoderm) is preserved

182   and connects to the dorsal side of the second sacral rib (Fig. 2F). The two tendon fragments

183   might have formed a single parasagittal tendon being narrow and pointed anteriorly and thin

184   and flattened posteriorly, but due to the dorsally positioned central osteoderms the transitional

185   parts are obscured.

186   *Osteoderms*. Altogether five *in situ* osteoderms are preserved (Fig. 2E-H). The first

187   morphotype is represented by four oval to circular central osteoderms with an

188   anteroposteriorly oriented sagittal keel. They are preserved in a central position sitting in a

189   line above the neural arches from the last fused dorsal to the middle of the sacrocaudal

190   vertebra. Most of their right part has been eroded, but based on the shape of their margin and

191   thickness, they were symmetrical elements with the sagittal keel positioning exactly centrally.

192   Accepting this hypothesis, the two anterior osteoderms were roughly circular, whereas the last

193   two elements have had a transversely wider than long shape. The sagittal keels are relatively

194   shallow with the posterior, pointed end being slightly higher than the anterior end. This

195   posterior tip is highest (ca. 2 cm measured from the dorsal surface of the osteoderm) on the

196   second and third central osteoderms. Some of these central osteoderms seems to be articulated

197   but not fused with each other. At the posterior end of the first preserved central osteoderm

198   some sediment separating the neural arch from the osteoderm can be observed indicating that

199   they were not ossified with the neural arches. A 2 cm long, 3-4 mm wide, slightly concave

200   articular facet can be observed on the anterior margin of the 3rd and 4th central osteoderms

201   supposedly for connecting the convex posterior margin of the adjoining osteoderm.

202   These osteoderms of MTM PAL 2013.59.1. are similar to a piece of pelvic armor referred to

203   *Struthiosaurus* sp. (MCNA 7416) from Laño (Spain) in having the same type of keeled

204   elements and the orientation of the keels being in line with each other. On the other hand, the

205   Laño specimen is completely fused and the keels are slightly bent lateromedially.

206   Besides the central osteoderms, a second morphotype, represented by a small, circular

207   osteoderm on the left side between the 1st and 2nd central osteoderms, is preserved (Fig. 2E,

208   F). It is not fused but almost in connection with the posterolateral margin of the 1st central

209   osteoderm. It is a non-keeled element with a slightly convex, rugose dorsal surface bearing

210   some small grooves and foramina.

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212   *4.1.2. MTM VER. 2016.3567.*

213   A complex pelvic armor element with articulated dorsal or sacrodorsal ribs (VER. 2016.3567.;

214   Fig. 3A-F) is an informative specimen from the Iharkút locality. The armor has an average

215   dorsoventral thickness of ca. 5 mm and is a composite of two subcircular keeled osteoderms

216   that are fused together by a composit of smaller osteoderms (Fig. 3C, E). The dorsal surface

217   of the osteoderms is densely pitted and ornamented by some irregular grooves. The

218   osteoderms have a ca. 1.5-2 cm high keel (Fig. 3F) being little higher on one side indicating

219   its posterior end. The keel of the lateral osteoderm is slightly bent medially in a posterior

220   direction. Ventrally, the keeled osteoderms has a concave anteroposterior groove just below

221   the keel. These osteoderms, being wider lateromedially (73 mm and 69 mm) than their

222   anteroposterior length (58 mm), are practically identical with the third central osteoderm lying

223   above the neural spines of MTM PAL 2013.59.1. The similarity is further supported by a 1.5

224   cm long transverse articular facet on the anterior margin of the lateral keeled osteoderm, as it

225 was pointed out on the anterior 3rd and 4th central osteoderms of MTM PAL 2013.59.1 as

226 well. These type of keeled osteoderms are unknown in the holotype of *Hungarosaurus* and in

227 the 9th skeleton referred to this taxon.

228 Between the keeled osteoderms most probably two small polygonal osteoderms are fused to

229 each other and to the keeled elements resulting 22 mm distance between the two keeled

230 osteoderms. These small osteoderms show the same dorsal texture as that of the keeled

231 elements but have no apexes or keels. A lateromedially elongate polygonal osteoderm, avoid

232 of any apex or keel dorsally, is also fused to the anterolateral margin of medial keeled

233 osteoderm and to anteromedial margin of the small polygonal osteoderm. These polygonal

234 osteoderms between and anterior to the keeled ones are similar to those of the fused polygonal

235 elements of the 9th skeleton of *Hungarosaurus*. Whereas the ventral surface of the keeled

236 osteoderms is devoid of the interwoven texture, the smaller, non-keeled, flat osteoderms

237 bordering them do show the typical interwoven texture. Since this ventral interwoven texture

238 cannot be observed in any other type (e.g. cervical, dorsal, caudal) of osteoderm in the whole

239 ankylosaurian assemblage from Iharkút, nor on the keeled pelvic osteoderms, this feature is

240 suggested here to be only characteristic for the fused polygonal osteoderms of the pelvic

241 armor.

242 Two rib fragments extending almost entirely along the armor element are preserved on the

243 ventral side of the armor block. They are not fused to any parts of the armor but separated by

244 0.5-2 mm thick matrix containing a great amount of pyrite. Whereas the medial end of the ribs

245 shows a dorsoventrally low, but T-shaped cross-section, the lateral end is completely flat.

246 Their shape, the relatively thin body and the weaker dorsoventral bending compared to the

247 more anterior dorsal ribs indicate that these ribs were connected to the last dorsals of the

248 sacral rod and the anterior end of the ilium. Comparison of the ribs to those of the articulated

249 specimen referred to *Hungarosaurus* (Ősi, 2015) and, taking the posterior side of the keeled

250 osteoderms into account, this block represents the right fragment of the pelvic armor

251 positioned between the vertebral column and the preacetabular process of the right ilium

252 anterior to the first sacral rib.

253 This piece of pelvic armor block is quite similar to a pelvic armor fragment (MCNA 7432)

254 from the Late Cretaceous of Laño, Spain (Pereda-Suberbiola, 1999; Fig. 3I). This element is

255 also composed of two circular, keeled osteoderms fused with smaller rounded or slightly

256 polygonal flat osteoderms. The keeled osteoderms of the Hungarian specimen differs from the

257 Laño specimen being relatively wider lateromedially, and the small osteoderms of the Laño

258 fragment are more markedly separated from each other and from the keeled osteoderms than

259 that of VER. 2016.3567. Furthermore, MCNA 7432 has a much more irregular, even spongy

260 dorsal surface (especially on the keels), being densely ornamented with deep grooves and

261 nutritive foramina, compared to the Iharkút specimen.

262

263 4.2. *Hungarosaurus tormai*

264 *4.2.1. Type of* Hungarosaurus tormai *MTM 2007.26.32. (formerly Gyn/404)*

265 Besides the armor of MTM PAL 2013.59.1, many additional pieces of fused or unfused,

266 pelvic armor elements are also known from the Upper Cretaceous Iharkút locality. The

267 holotype of *Hungarosaurus*, exhibiting ca. 70% of the armor (Ősi, 2005) of all the main

268 regions, has some pentagonal to quadrilateral, unfused osteoderms (MTM 2007.26.32) that

269 are suggested to be pelvic armor elements (Fig. 4D, E). Their dorsal surface is flat to slightly

270 convex, with a very weakly developed bump in its central part. The ventral surface shows a

271 slightly interwoven texture similar to that of *Nodosaurus textilis* (Marsh, 1889: text-fig. 1),

272 but this texture is not as heavily developed as that of the armor elements of the 9th skeleton

273 (see below). The margin of these polygonal elements is receded (Fig. 4F) to accept the

274 surrounding osteoderms. In the holotype material of *Hungarosaurus* there is no evidence for

275 fused osteoderms. However, this might be related to some preservational biases and suggested

276 trampling (Botfalvai et al., 2015), since most bones in this associated skeleton are broken

277 elements.

278

279 *4.2.2. 9th skeleton of* Hungarosaurus *MTM PAL 2016.16.1.*

280 Three relatively large, ossified fragments of pelvic armor (Fig. 4A-C) are preserved in the 9th

281 associated ankylosaur skeleton (MTM PAL 2016.16.1.) from Iharkút. They are composed of

282 pentagonal to quadrilateral, flat osteoderms that are strongly fused to each other, representing

283 Category 3 arrangement of Arbour et al (2011). Their shape and arrangement is very similar

284 to the polygonal armor blocks of *Aletopelta* that covered the acetabular region of the ilia

285 (Coombs and Deméré, 1996; Ford and Kirkland, 2001). Their flat to very slightly concave

286 dorsal surface is ornamented by many small pits and grooves but they do not bear any crests

287 or projections similar to the pelvic osteoderms of the holotype of *Hungarosaurus*. Their

288 ventral surface is markedly ornamented by an interwoven texture (Fig. 4C), as seen in

289 *Nodosaurus* (Marsh, 1889; Lull, 1921).

290

291 4.3. Nodosauridae indet.

292 *4.3.1. MTM VER 2016.573.*

293 An isolated armor element (MTM VER 2016.573), composed of two larger (one pentagonal,

294 one quadragular) and one smaller (quadrangular) osteoderm, shows an external morphology

295 not present in any of the former specimens (Fig. 4G). The largest, pentagonal apical

296 osteoderm has a central apex whereas the other osteoderms do not have this feature. The

297 ventral surface of this element has an interwoven texture as well. This type of armor element

298 was most probably part of a fused pelvic armor similar to the blocks of 9th skeleton metioned

299 above, but perhaps represents another segment in the fused block.

300

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

325   VER. 2016.3567. are completely unknown in *Hungarosaurus* (including the holotype, the 5th

326   and 9th skeletons), but present in *Struthiosaurus* from Laño (MCNA 7416, 7432; Fig. 4G-I),

327   again, suggesting closer affinity with *Struthiosaurus* and differences between the pelvic armor

328   composition of the two genera. Although the keeled osteoderms represent different positions

329   in the pelvic armor of MTM PAL 2013.59.1 and VER. 2016.3567., their similarly small size

330   and identical external morphology suggest that they both belong to the same taxon. Therefore,

331   we refer provisionally these specimens to as cf. *Struthiosaurus* sp.

332   Comparison of the size of the skeletal elements of in MTM PAL 2013.59.1. with those of the

333   holotype and the 5th skeleton of *Hungarosaurus* (Ősi and Makádi, 2009), a total body length

334   of ca. 2-2.5 meters can be reconstructed being more closer to the small-sized *Struthiosaurus*

335   (Pereda-Suberbiola, 1992, Ősi and Prondvai, 2013) than to the larger *Hungarosaurus*.

336

337   *5.2. Pelvic armor in Late Cretaceous European ankylosaurs*

338   The armor of *Struthiosaurus*, the most widespread Late Cretaceous European ankylosaur, is

339   relatively poorly known, though some armor elements are present in all the main assemblages

340   (Transylvanian Basin: Nopcsa, 1929; Ősi et al., 2014; Laño: Pereda-Suberbiola, 1999;

341   Muthmannsdorf: Pereda-Suberbiola and Galton, 2001; Villeveyrac: Garcia and Pereda-

342   Suberbiola, 2003; Iharkút: this paper). In the material referred to *Struthiosaurus* from the Late

343   Cretaceous of Laño, two fused pieces of the pelvic armor (MCNA 7416, 7432) has been

344   described (Pereda-Suberbiola, 1999; see Fig. 3G-I). MCNA 7416 is composed of two

345   subcircular, keeled osteoderms fully ossified with a flat sheet of osteoderm in the latter part of

346   which no individual elements (e.g. smaller ossicles or rosette-like elements) can be

347   recognized (Fig. 3G, H). This fused element was certainly part of the pelvic armor since this

348   type of keeled osteoderms in the preserved position would otherwise represent two transverse

349   bands of dorsal armor separated by a mobile fold (Arbour et al., 2011), which is not the case.

350   MCNA 7432 is also from the pelvic armor, being very similar to VER. 2016.3567. from

351   Iharkút, a fused block from the anterolateral part of the pelvic armor.

352   Until now, these two fused elements from Laño were the only evidence for the presence of at

353   least partially fused pelvic armor in a European Late Cretaceous ankylosaur (Pereda-

354   Suberbiola, 1999), since none of the type materials of the three *Struthiosaurus* species (*S.*

355   *austriacus, S. transylvanicus, S. languedocensis*) or that of *Hungarosaurus* contain fused

356   pelvic armor elements. Only a fragmentary, partially reconstructed, keeled element [PIUW

357   2349/uncataloged (A1c)], referred to *S. austriacus*, has been described as a possible sacral

358   armor element (Pereda-Suberbiola and Galton, 2001).

359   Based on MTM PAL 2013.59.1. and VER. 2016.3567. the pelvic armor of *Struthiosaurus*

360   from Iharkút can be partially reconstructed (Fig. 5). The main question is whether the pelvic

361   armor above the synsacrum and ilia was composed of similarly large, keeled osteoderms

362   surrounded by smaller fused elements as seen in VER. 2016.3567., or these regions were

363   covered by fused polygonal armor elements as those preserved in *Hungarosaurus* (see above),

364   *Nodosaurus* and 'stegopeltines' (sensu Ford, 2000; probably not monophyletic, see Arbour

365   and Currie, 2016). Here we suggest that the first type of armor is more plausible in

366   *Struthiosaurus* (Fig. 5), and the presence and absence of fused polygonal osteoderm

367   composition might have been the main difference between the pelvic armor of the two genera.

368   Another question is if these elements were completely fused to form a left and right rigid half-

369   shield (Fig. 5), or they were only fused into smaller armor blocks. VER. 2016.3567. suggests

370   some fusion of these elements, but the extension of fusion is ambiguous. Based on MTM PAL

371   2013.59.1 some mobility between the sagittally positioned central osteoderms and the lateral

372   elements is suggested (Fig. 5). Although four sagittal osteoderms are preserved *in situ*, a fifth

373   element might have been present anteriorly to cover the anteriormost part of the sacral rod.

374 The pelvic armor of *Hungarosaurus* is more problematic since no *in situ* osteoderm is

375 preserved. In *Hungarosaurus*, the polygonal elements of the holotype and the three fused

376 armor elements of the 9th skeleton indicate that, in contrast to *Struthiosaurus*, this larger form

377 could have had a completely to at least partially fused pelvic shield composed mainly of flat

378 or very slightly convex, large polygonal elements (Fig. 4A-E), similar to that of *Nodosaurus*

379 (Lull, 1921), *Stegopelta* (Moodie, 1910; Ford, 2000 and references), *Aletopelta* (Ford and

380 Kirkland, 2001) and *Glyptodontopelta* (Ford, 2000; Burns, 2008). The subcircular, keeled

381 elements, present in *Struthiosaurus*, however, appear to have been absent or were a less

382 important osteoderm type in the pelvic armor.

383 One problematic type of fused osteoderm is a large, symmetrical, ca. 30 cm wide,

384 dorsoventrally thick, boomerang shaped centrally positioned element (MTM 2007.23.1) with

385 two high (ca. 15 cm), slightly posteriorly projecting conical spikes laterally on its dorsal side

386 (Fig. 6A-E). This element was discovered in Iharkút in 2003 with an associated hip region

387 (ilia, ischia, synsacrum) of the fourth nodosaurid skeleton that has been referred to

388 *Hungarosaurus* (Ősi, 2005). Later on, some additional, but isolated conical spikes have been

389 discovered as well (MTM 2007.30.1; Ősi and Makádi, 2009, Fig. 6F, G). One identical

390 conical spike (PIUW 2349/15) is also known from the Campanian of Muthmannsdorf (Austria)

391 and referred to *Struthiosaurus* (Seeley, 1881; Pereda-Suberbiola and Galton, 2001; Fig. 6H).

392 Ősi and Makádi (2009) reconstructed this element from Iharkút as being in the posterior

393 segment of the pelvic or the anterior margin of the caudal armor in *Hungarosaurus*. This

394 hypothesis was only based on the association of this fused osteoderm with the pelvic-sacral

395 elements, but they were not in articulation, so it cannot be ruled out that it might represent

396 some part of the cervical-dorsal armor. Furthermore, it is also ambiguous, whether this dermal

397 element was present in both taxa or was charateristic only for *Hungarosaurus*.

398

399 *5.3. Osteoderm fusion and arrangement*

400 Using 13 taxa with preserved elements of the pelvic region, ankylosaur pelvic armor

401 morphology has been classified into three categories on the basis of the shape and fusional

402 degree of the osteoderms (Arbour et al., 2011): 1) not coossified but tightly interlocking

403 osteoderms; 2) coossified osteoderms forming rosettes; 3) coossified polygonal osteoderms of

404 similar size. Updated information on the pelvic armor of ankylosaurs is presented in Table 1,

405 including data from 25 taxa, 16 of them with *in situ* osteoderms. As noted by Arbour et al.

406 (2011), this classification of pelvic armor arrangement should not be used to support any

407 monophyletic grouping within the Ankylosauria until there is a global phylogenetic analysis

408 that includes pelvic armor characters, but it is useful to understand the morphological

409 variations among taxa.

410 According to this interpretation, the pelvic armor of sagittally positioned and tightly

411 interlocking but unfused osteoderms, preserved dorsal to the synsacral neural spines of MTM

412 PAL 2013.59.1, here referred to cf. *Struthiosaurus* p., belongs to Category 1 of Arbour et al.

413 (2011). Similarly unfused but interlocking osteoderms has been reported in the Early

414 Cretaceous nodosaurid *Sauropelta* from North America (and in several Late Cretaceous

415 ankylosaurids from North America and Asia, Arbour et al., 2011, 2013, 2014; see Table 1).

416 These forms, however, show a different arrangement of osteoderms, having widely spaced,

417 large circular elements surrounded by smaller ones (Arbour et al., 2014), whereas in the

418 Iharkút specimen the large central osteoderms are in a continuous sagittal line not interrupted

419 by smaller elements. The large circular elements of *Sauropelta* are non-keeled (Carpenter,

420 1984; Coombs and Maryańska, 1990), while the large pelvic osteoderms of *Scolosaurus* bear

421 an anteroposteriorly oriented keel (Arbour et al., 2011; Penkalski and Blows, 2013). These

422 differences further support the hypothesis that the ankylosaur armor or some parts of it

423 (Carpenter, 1990; Blows, 2001, Ford, 2000), or even the external and internal morphology of

424 a single osteoderm (Burns 2008, 2010), are distinctive to at least the generic level allowing

425 the identification of an ankylosaur genus based solely on osteoderms.

426 Since there is not a single ankylosaurian species represented by more individuals of different

427 ontogenetic stages with preserved pelvic armor (Burns, 2008; Arbour et al., 2011), it is

428 unknown, how the fusional degree of the pelvic armor changed in ankylosaurs during

429 ontogeny. Burns (2010) reported that the juvenile specimen of *Pinacosaurus* do not exhibit

430 postcranial osteoderms beyond the cervical half rings, suggesting that their osteoderms

431 exhibited a delayed onset of osteoderm skeletogenesis relative to the remainder of the body

432 skeleton, as demonstrated in *Stegosaurus* (Hayashi et al., 2009), extant archosaurs

433 (Vickaryous and Hall, 2008) and armadillos (Vickaryous and Hall, 2006). This means that the

434 pelvic armor developed most likely in a relatively later phase of ontogeny than the more

435 anteriorly positioned pectoral and possibly also the dorsal armor elements.

436 Nevertheless, the fusional degree of the different pelvic armor regions might have been

437 variable even in a single specimen similar to that seen in the Late Cretaeous North American

438 *Aletopelta* (Coombs and Deméré, 1996, Ford and Kirkland, 2001). In this form, the lateral

439 side of the pelvic armor is more solid with fused hexagonal to quadrilateral osteoderms,

440 whereas centrally some of these angular elements are unfused (Coombs and Deméré, 1996:

441 fig. 1). Since the central pelvic armor elements are mostly missing in this taxon, it is

442 ambiguous whether these lateral coossified blocks were fused with the central elements or not.

443 Although we have pelvic armor elements fused with several smaller and larger osteoderms in

444 various ankylosaur taxa, a single, massive block of pelvic shield covering the hip region is

445 unambiguously present only in *Polacanthus* (Hulke, 1887). The presence of a solid pelvic

446 shield has also been assumed for other North American 'polacanthines', such as *Gastonia*,

447 *Mymoorapelta*, *Hoplitosaurus* and *Gargoyleosaurus* (Kirkland, 1998; Kirkland et al., 1998;

448 Blows, 2001; Carpenter, 2001) and potentially in *Taohelong*, *Sauroplites* and *Shamosaurus*

449   (Arbour and Currie, 2016), although in these taxa the fossil evidence is still incomplete.

450   Recently, Kinneer et al. (2015) have raised the possibility that the pelvic shield of

451   *Gargoyleosaurus* may have been made of multiple smaller coossified sections rather than a

452   single unit. So, it cannot be ruled out that the pelvic armor of some taxa of Category 2 of

453   Arbour et al. (2011) was not a single, rigid construction as that of *Polacanthus*, but rather

454   composed of several fused and unfused blocks covering the synsacral and pelvic regions, as it

455   is suggested in the Hungarian cf. *Struthiosaurus* (Fig. 5). Here, the sagittal row of osteoderms

456   representing Category 1 of Arbour et al. (2011) could have bordered by at least one to one

457   fused block of osteoderms in a system of Category 2 of Arbour et al. (2011). Thus, cf.

458   *Struthiosaurus* may be unique among ankylosaurs in falling under categories 1 and 2 of pelvic

459   armor fusion and arrangement.

460   Although the ankylosaurian pelvic armor should have been a more or less rigid construction

461   due to the ossified synsacral-iliac block, it apparently was set up by some sort of transverse

462   bands that were either fused with each other by smaller (e.g. polygonal) osteoderms or were

463   separated by an unmobile fold (in contrast to the mobile folds of the cervical-dorsal region;

464   Arbour et al., 2011). *Struthiosaurus* had four *in situ* sagittal osteoderms but a fifth element

465   (actually the very first) might have been covered the anterior end of the sacral rod, thus it is

466   reconstructed here with five transverse bands incorporated into the pelvic armor (Fig. 5). It

467   differs therefore from other ankylosaurs, such as the ankylosaurid *Scolosaurus* (NHMUK

468   R5161), which has three transverse bands (Arbour et al., 2011; Penkalski and Blows, 2013)

469   and the nodosaurid *Sauropelta* (AMNH 3036), with probably six transverse bands (Carpenter,

470   1984, 2012). The rigid pelvic shield of *Polacanthus* (NHMUK R175) consists of at least 8

471   (and may be 9 or 10) transverse bands of osteoderms (Hulke, 1887; Blows, 2001).

472   With regard to *Hungarosaurus*, its pelvic armor is composed of polygonal, flat osteoderms

473   that are fused to each other, and so represents Category 3 of Arbour et al (2011). This

474 category is mainly represented in nodosaurids from the mid-Cretaceous of North America,

475 Asia and Europe, and the Upper Cretaceous of North America and Antarctica, as well as in

476 the ankylosaurid *Aletopelta* from North America (see Arbour and Currie, 2016). Previously

477 reported in *Europelta* from the Albian of Teruel in Spain (Kirkland et al., 2013),

478 *Hungarosaurus* would be the only Late Cretaceous European ankylosaur included in this

479 category of pelvic morphology (Table 1).

480 According to Arbour and Currie (2016), the presence of a pelvic shield in numerous basal

481 ankylosaurs, as well as in more derived members of both the Nodosauridae and

482 Ankylosauridae, suggests that fused pelvic osteoderms are plesiomorphic for ankylosaurs, and

483 not a synapomorphy of a polacanthid or polacanthine clade. An unossified pelvic armor

484 (Category 1 of Arbour et al., 2011) seems to be present in *Kunbarrasaurus* (Molnar, 2001),

485 the most basal ankylosaur (following the phylogenetic analysis of Arbour and Currie 2016),

486 and also in basal thyreophorans, such as *Scelidosaurus* and *Scutellosaurus* (Owen, 1861;

487 Colbert, 1981). Thus, a pelvic armor having unfused but tighly interlocking osteoderms may

488 be the plesiomorphic condition for Ankylosauria.

489

490 **6. Conclusions**

491 Burns (2008) and Burns and Currie (2014) suggested that ankylosaurian armor can be a great

492 tool for low-level taxonomic identification since external and/or internal features of even a

493 single osteoderm can reveal taxonomic affinity. This can be especially true for complex

494 elements or fused blocks (cervical or pelvic elements) of the armor. The ankylosaur material

495 described here further supports this hypothesis, and the armor elements from the Iharkút

496 locality of Hungary provide significant information about the pelvic armor morphology and

497 arrangement in Late Cretaceous European ankylosaurs. Cf. *Struthiosaurus* is characterized by

498 having interlocked but unfused keeled, oval to circular osteoderms arranged sagittally in a

499   row over the synsacral neural spines (Category 1 of Arbour et al., 2011), combined with at

500   least two fused blocks of keeled, subcircular osteoderms above the ilia that are coossified

501   together by a composite of smaller polygonal scutes. So far, this is the only known ankylosaur

502   whose pelvic armor combines unfused osteoderms with coossified blocks (i.e. Category 1 and

503   2 of Arbour et al., 2011). As reconstructed here, cf. *Struthiosaurus* has a pelvic armor formed

504   of at least four but probably five transverse bands, and can be also differentiated from many

505   other ankylosaurs on the basis of this quantitative character. On the other hand, the pelvic

506   armor of *Hungarosaurus* was rather more of a composit of pentagonal to quadrilateral, flat

507   osteoderms that were fused at least in some parts (Category 3 of Arbour et al., 2011).

508   Interwoven texture is observed only on the ventral side of polygonal elements but is not

509   present on the oval to circular, keeled osteoderms, suggesting some difference in their

510   skeletogenesis.

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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

780   armor fragment and one of the sacrodorsal ribs (VER. 2016.3567.) in anterior view. G-I,

781   fragmentary pelvic armor elements from Laño, Spain. G, MCNA 7416 in dorsal view, and H,

782   in ventral view. I, MCNA 7432 in dorsal view. Anatomical abbreviations: **gr**, groove; **iw**,

783   interwoven texture; **ko**, keeled osteoderm; **pos**, polygonal osteoderm; **r**, rib; **se**, sediment.

784   [Planned with double column width, color in online only]

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786   **Figure 4.** Pelvic armor elements of *Hungarosaurus* from the Upper Cretaceous of Iharkút,

787   Hungary. A-B, fused blocks of polygonal osteoderms from the 9th skeleton (MTM PAL

788   2016.16.1.) in dorsal view. C, fused block of polygonal osteoderms from the 9th skeleton

789   (MTM PAL 2016.16.1.) in ventral view. D-E, polygonal osteoderms (MTM 2007.26.32) from

790   the holotype of *Hungarosaurus tormai* in dorsal view. F, the receding margin of the polygonal

791   osteoderm seen in Fig. 3D in dorsal view. G, fused pelvic osteoderm MTM VER 2016.573 in

792   dorsal view. Anatomical abbreviations: **iw**, interwoven texture; **oaf**, osteoderm articulation

793   facet; **pos**, polygonal osteoderm. [Planned with double column width, color in online only]

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795   **Figure 5.** Partially reconstructed pelvic armor of cf. *Struthiosaurus* from Iharkút. Dark grey

796   elements are preserved, light grey elements are reconstructed. Anatomical abbreviations: **co**,

797   central osteoderms; **il**, ilium; **r**, rib; **sr**, sacral rib; **sro**, synsacral rod. [Planned with double

798   column width]

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800   **Figure 6.** Problematic osteoderms with conical spikes in European Late Cretaceous

801   nodosaurids. A, boomerang shaped symmetrical, centrally positioned element (MTM

802   2007.23.1) with two high, slightly posteriorly projecting conical spikes laterally on its dorsal

803   side in dorsal; B, ventral; C, anterior; D, posterior; E left dorsolateral view. This element was

804   associated with the fourth skeleton referred to *Hungarosaurus* from Iharkút (Ősi 2005). F,

805   isolated fragmentary boomerang shaped element with a conical spike (MTM VER 2017.66.)

806   from Iharkút. G, isolated fragmentary boomerang shaped element with a conical spike (MTM

807   VER 2016.578.) from Iharkút. H, isolated fragmentary fused element with a conical spike of

808   *Struthiosaurus austriacus* (PIUW 2349/15) from the lower Campanian of Muthmannsdorf,

809   Austria. Anatomical abbreviations: **bsp**, broken conical spike; **fb**, fused basement of the

810   osteoderm; **ri**, ridge [Planned with double column width]

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