Cranial ornamentation in the Late Cretaceous nodosaurid ankylosaur *Hungarosaurus*

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Bony cranial ornamentation is developed by many groups of vertebrates, including ankylosaur dinosaurs. To date, the morphology and ontogenetic origin of cranial ornamentation has primarily focused on a limited number of species from only one of the two major lineages, Ankylosauridae. For members of the sister group Nodosauridae, less is known. Here, we provide new details of the cranial anatomy of the Santonian nodosaurid *Hungarosaurus*. Based on a number of previously described and newly identified fragmentary skulls and skull elements, we identitfy at least three different size classes of *Hungarosaurus* that we interpret as representing different stages of ontogeny. Cranial ornamentation is already well-developed in the earliest ontogenetic stage represented, suggesting that the presence of outgrowths may have played a role in intra- and interspecific recognition. We find no evidence that cranial ornamentation in *Hungarosaurus* involves the contribution of coossified osteoderms. Instead, available evidence indicates that cranial ornamentation forms as a result of the elaboration of individual elements. Dimorphism of cranial ornamentation in *Hungarosaurus*, especially that of the postorbital crest, cannot be excluded, however, a larger sample size is needed to test these predictions.

1 **Cranial ornamentation in the Late Cretaceous nodosaurid ankylosaur**

2 ***Hungarosaurus***

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14 **Key words**: skull; *Hungarosaurus*, ankylosaur; cranial ornamentation; osteoderm fusion; cranial

15 elaboration; sexual dimorphism; Late Cretaceous

19 ABSTRACT

20 Bony cranial ornamentation is developed by many groups of vertebrates, including ankylosaur

21 dinosaurs. To date, the morphology and ontogenetic origin of cranial ornamentation has

22 primarily focused on a limited number of species from only one of the two major lineages,

23 Ankylosauridae. For members of the sister group Nodosauridae, less is known. Here, we provide

24 new details of the cranial anatomy of the Santonian nodosaurid *Hungarosaurus*. Based on a

25 number of previously described and newly identified fragmentary skulls and skull elements, we

26 identitfy at least three different size classes of *Hungarosaurus* that we interpret as representing

27 different stages of ontogeny. Cranial ornamentation is already well-developed in the earliest

28 ontogenetic stage represented, suggesting that the presence of outgrowths may have played a role

29 in intra- and interspecific recognition. We find no evidence that cranial ornamentation in

30 *Hungarosaurus* involves the contribution of coossified osteoderms. Instead, available evidence

31 indicates that cranial ornamentation forms as a result of the elaboration of individual elements.

32 Dimorphism of cranial ornamentation in *Hungarosaurus*, especially that of the postorbital crest,

33 cannot be excluded, however, a larger sample size is needed to test these predictions.

40   INTRODUCTION

41   Development of osseous cranial ornamentation is a relatively common occurence in the

42   evolutionary history of terrestrial vertebrates (Buffrénil, 1982). Among reptiles, cranial

43   ornamentation, including frills, crests, horns, bosses, or casques, is known for representative

44   members of many fossil and extant groups (e.g., Gadow, 1901; Romer, 1956; Clarac et al., 2017;

45   Mayr, 2018). The ultimate morphology of cranial ornamentation, especially among skeletally

46   mature adults, is often highly variable and species-specific (e.g. Otto, 1909; Montanucci, 1987).

47   As currently understood, this vast diversity is the result of two principal modes of

48   morphogenesis: the elaboration of individual cranial elements; and the fusion of additional

49   skeletal elements with the skull (Moss, 1969; Vickaryous, Russell & Currie, 2001). Among

50   reptiles, these additional skeletal elements are most commonly identified as osteoderms.

51   Osteoderms (= dermal sclerifications, osteoscutes) are bone-rich elements that form within the

52   dermis (Moss, 1969; Vickaryous & Sire, 2009). Although they remain often suspended within

53   the skin (e.g., some gekkotan lizards; Paluh; Griffing & Bauer, 2017, Laver et al., 2020), in some

54   taxa they gradually fuse with subadjacent bones of the skull (e.g., helodermatids, xenosaurids;

55   Bhullar, 2011; Maisano et al., 2019). As osteoderms develop within the skin, they are may

56   occupy positions that overlap sutural boundaries (Vickaryous, Russell & Currie, 2001).

57   In addition to the fusion of osteoderms, cranial ornamentation may also develop as a result of the

58   elaboration or exaggerated outgrowth of individual cranial (and mandibular) elements (e.g.

59   Montanucci, 1987; Vickaryous, Russell & Currie, 2001; Hieronymus et al., 2009). In some

60   species, particularly among aged individuals, this form of exaggerated outgrowth may become

61   continuous across multiple adjacent bones (e.g., hummocky rugosities; Hieronymus et al., 2009).

62 Cranial ornamentation is one of the most diagnostic features of the extinct archosaur clade

63 Ankylosauria (Maryanska, 1977; Coombs, 1978; Carpenter et al., 2001; Vickaryous, Maryanska

64 & Weishampel, 2004). For most ankylosaur taxa, the dorsolateral surfaces of the cranium and the

65 posterolateral surface of the mandible are externally (superficially) embossed with cranial

66 ornamentation. Although intraspecific (and possibly ontogenetic) variation exists, details of the

67 size, shape and pattern of cranial ornamentation, often referred to as 'caputegulae' (Blows,

68 2001), have long been recognized as taxonomically informative (e.g. Parks, 1924; Coombs,

69 1971; 1978; Blows, 2001; Penkalski, 2001; Arbour & Currie, 2013; 2016). This includes the

70 classical distinction of the two major clades of ankylosaurs: Ankylosauridae and Nodosauridae

71 (Coombs, 1978).

72 The ontogenetic origin of cranial ornamentation in ankylosaurs has primarily focused on a

73 handful of species, most of which are members of Ankylosauridae (Coombs, 1971; Molnar,

74 1996; Vickaryous, Russell & Currie, 2001; Carpenter et al., 2001; Hill, Witmer & Norell, 2003).

75 Based on the investigation of multiple specimens, including material attributed to subadult (i.e.,

76 not skeletally mature) individuals, the cranial ornamentation of *Euoplocephalus* and

77 *Pinacosaurus* is interpreted involving both the coosification of osteoderms with the skull and the

78 exaggerated outgrowth of individual cranial elements (Vickaryous, Russell & Currie, 2001; Hill,

79 Witmer & Norell, 2003; although see Carpenter et al., 2001). In contrast, osteoderms do not

80 appear to fuse with the skulls of the basal taxa *Cedarpelta* (Carpenter et al., 2001) and *Gastonia*

81 (Kinneer, Carpenter & Shaw, 2016). Hence, cranial ornamentation in these species appears to be

82 exclusively the result of elaborated outgrowth of individual elements. Among nodosaurids, less

83 is known. A partial skull attributed to an unidentified species was reported to demonstrate a

84 rugose external texture, but no evidence of "... overgrowth of dermal bone" (Jacobs et al., 1994).

85   Here we describe several fragmentary skulls and skull elements of the European Late Cretaceous

86   (Santonian) nodosaurid ankylosaur, *Hungarosaurus* (Table 1). These specimens represent at least

87   three different size classes (and likely different stages of ontogeny), and provide new information

88   about the morphological diversity, development and possible function of cranial ornamentation

89   of nodosaurid skulls.

90

91   **Cranial ornamentation in extant forms**

92   Among extant saurospids (turtles, lepidosaurs, crocodiles and birds), representative members of

93   all the main groups develop osseous cranial ornamentation. Ontogenetic development of cranial

94   ornamentation involves two key processes: the fusion of overlying osteoderms and the

95   elaboration of individual dermatocranial elements (Vickaryous, Russell & Currie, 2001, see

96   Table 2). However, the extent to which these processes occur in diffent taxa remains poorly

97   understood.

98

99   *Osteoderm fusion to skull bones*

100   Many extant groups of non-iguanian lizards develop osteoderms across the dorsal and lateral

101   surfaces of the skull (Table 2; see also Gadow, 1901; Moss, 1969; Montanucci, 1987; Etheridge

102   & de Queiroz, 1988; Vickaryous & Sire, 2009). Depending on the species and state of skeletal

103   development, osteoderms may remain embedded within the skin and thus not directly contact the

104   skull, or may partially or even completely fused with the underlying elements (Maisano et al.,

105   2019). With a partial fusion, the degree of coossification is incomplete, resulting in an unossified

106   gap that can be detected using CT scanning (e.g., Fig. 1A, C). Alternatively, in skeletally mature

107   *Heloderma* spp. and xenosaurids, this gap is obliterated and there is no longer any evidence of

108   separation (e.g., Maisano et al., 2019). As a consequence of developing with the skin,

109   osteoderms may overlap cranial sutures and/or form in positions without any subjacent

110   dermatocranial bones (e.g., superficial to cranial fenestrations) (Vickaryous, Russell & Currie,

111   2001).

112   The morphology and arrangement of osteoderms across the skull demonstrates considerable

113   taxonomic variation (e.g., Fig. 1A-D; see also Mead et al., 2012; Ledesma & Scarpetta, 2018).

114   To date, there is no evidence of any differences associated with sexual dimorphism (Table 2),

115   with both males and females developing comparable arrangements of osteoderm-mediated

116   ornamentation (see references in Table 2). Among iguanid lizards, cranial osteoderm have only

117   been reported for aged marine iguanas (*Amblyrhynchus cristatus*; Etheridge & de Queiroz,

118   1988). In marine iguanas, these structures are reportedly used by males during the breeding

119   season. Females are characterized by a similar albeit less developed version of this

120   ornamentation (Eibl-Eibesfeldt, 1966).

121   In contrast to squamates no extant member of the Archosauria (i.e. crocodylians and birds) has

122   been reported to have cranial osteoderms, with the possible exception of the bony palpebral

123   (eyelid bone) (Vickaryous & Hall, 2008).

124

125   *Elaboration/outgrowth of cranial elements*

126   Among various iguanians, cranial ornamentation is dominated by the elaboration and outgrowth

127   of individual dermatocranial elements (Etheridge & de Queiroz, 1988). While this form of

128 cranial ornamentation often manifests as rugosities with variably developed crests, pits and

129 bumps (Hieronymous et al., 2009, Fig. 1E-F), some taxa develop large horn-like outgrowths. For

130 example, in species of *Phrynosoma* horns and bosses can develop on each of the parietal and

131 squamosal (Lang, 1989; Vickaryous, Russell & Currie, 2001; Powell et al., 2017). Although the

132 number, morphology and orientation of these protuberances can vary among *Phrynosoma*

133 species, they do not appear to be sexual dimorphic (Powell et al., 2017, Table 2). Similarly,

134 anoles (Dactyloidae) also have taxon-specific cranial ornamentation that is present in both sexes

135 (Etheridge & de Queiroz, 1988).

136 The development of bony horns and crests is also characteristic of some archosaurs, including

137 fossil (e.g. *Ceratosuchus* Schmidt, 1938; Bartels, 1984, Brochu, 2006; 2007; Bickelmann &

138 Klein, 2009) and extant (e.g. *Crocodylus rhombifer*; Brochu et al., 2010) crocodylians. Among

139 recent taxa, these protuberances are not sexually dimorphic (Bartels, 1984). It has been

140 speculated that these horns may be used for species recognition in ecosystems where multiple

141 taxa of crocodylians exist (Bartels, 1984). Cranial ornamentation is also characterstic of many

142 taxa of birds (Table 2). In most cases these elaborations and outgrowths are monomorphic

143 (Mayr, 2018). One of the most obvious examples are cassowaries (*Casuarius* spp.), where males

144 and females are similarly ornamented with elaborate casques on the skull roof (Naish & Perron,

145 2016). The bony architecture of this cranial ornamentation can also vary. For example, the

146 casque on the upper bills of bucorvid and some bucerotid birds is typically dominated by an air-

147 filled cavity and thin trabecular bone, but is reportedly solid bone in the greater helmeted hornill

148 (*Buceros vigil*) (Gamble, 2007).

149 To sum up, the fusion of osteoderms to cranial bones characterizes only a few groups of

150 squamates, and is not present in extant archosaurs (Table 2). In terms of cranial ornamentation,

151   almost all these forms are sexually monomorphic and the architecture of oramentation is

152   frequently taxon-specific. On the other hand, elaboration or outgrowth of cranial bones appears

153   to be a more frequent phenomenon not only in squamates but also in birds and even in some

154   species of crocodylians.

155

156   MATERIAL AND METHODS

157   **Specimens**

158   The Hungarian nodosaurid ankylosaur specimens used in this study (Table 1) are from the Upper

159   Cretaceous (Santonian) Csehbánya Formation of Iharkút vertebrate site, Bakony Mountains,

160   western Hungary (Ősi et al., 2019; for geology and taphonomy, see Botfalvai, Ősi &

161   Mindszenty, 2015; Botfalvai et al., 2016). Four partial ankylosaur skulls (Fig. 2) and various

162   isolated skull elements (see Table 1 for all used specimens) from Iharkút are briefly described

163   and compared in detail particularly focusing on the morphology, topographic distribution and

164   origin of the cranial ornamentations. Two of the fragmentary skulls (holotype, MTM PAL

165   2013.23.1., Fig. 2A, D) and some isolated elements have been already described in more detail

166   (Ősi, 2005; Ősi & Makádi, 2009; Ősi, Pereda-Suberbiola & Földes, 2014; Ősi et al., 2019) but

167   cranial ornamentation was not discussed. The two new additional partial skulls (MTM PAL

168   2020.31.1., MTM PAL 2020.32.1., Fig. 2B, C, Data S1) have never been described in detail, the

169   comparative osteological description of these specimens are in Data S1.

170   The basis of this work is that all four skulls and isolated remains are thought to belong to

171   *Hungarosaurus*. Although the presence of the much smaller *Struthiosaurus* at the site has also

172   been confirmed by postcranial findings (Ősi & Prondvai, 2013; Ősi & Pereda-Suberbiola, 2017),

173   the two new skulls are closer to *Hungarosaurus* based on the osteological features listed in Data

174   S1. The postorbital crest of the specimen MTM PAL 2020.32.1. is, however, somewhat different

175   from that of the holotype of *Hungarosaurus*, that we interpret as presumably due to ontogenetic

176   or intersexual differences (see discussion below).

177   **Methods**

178   Specimens were collected between 2001 and 2019 and all of them are housed in the Vertebrate

179   Paleontological Collection of the Hungarian Natural History Museum, Budapest (MTM).

180   Specimens were prepared mechanically in the labs of the Department of Paleontology of the

181   Eötvös University and the Hungarian Natural History Museum, and the bones were fixed by

182   cyanoacrylic glue.

183   For 3D reconstruction of the skulls (Fig. 2), we photographed each bone with a Canon EOS

184   600D DS126311 camera using a photogrammetric technique. 2D images were converted to 3D

185   images using 3DF Zephyr software. 3D images of bones also show the original texture of the

186   bones. 3D files of each bone were assembled within the free Blender software using Polygonal

187   modeling and Sculpting techniques. Finally, we rendered a turntable video of the "finished" skull

188   in Marmoset Toolbag 3. The 3D reconstructions of the three studied skull are in the video files

189   (Video S1-S6; https://zenodo.org/record/4117812#.X5FfUO28o2w).

190   Specimens are not allowed to cut for histological purposes, thus microtomographic (microCT)

191   imaging was used to investigate the inner structure of cranial elements and ornamentation.

192   MicroCT scanning of fossil and recent bones have been made in the laboratory of the Carl Zeiss

193   IMT Austria GmbH (Budaörs, Hungary). Scanning of the bones has been made by a Zeiss

194   Metrotom computer tomograph with a distance between each slices of 130 μm.

195   **Institutional abbreviations**: IGM, Institute of Geology, Ulaan Baatar, Mongolia; MTM,

196   Hungarian Natural History Museum, Budapest, Hungary; TMP, Royal Tyrrell Museum,

197   Drumheller, Canada.

198

199   RESULTS

200   **Cranial ornamentation in *Hungarosaurus***

201   *Premaxilla*

202   Premaxillae are preserved in four specimens, including two isolated elements along with the

203   holotype skull and in MTM PAL 2020.31.1. (Fig. 3A-D). The smallest premaxilla (MTM

204   V.2003.12) is almost half the size of the holotype (Fig. 3A), and thus likely represents a juvenile

205   or subadult individual (Ősi & Makádi, 2009). Premaxillae are unfused with each other in all

206   specimens. Ornamentation can be observed on all the specimens including the smallest element,

207   but does not overlap the sutures between the two premaxillae, or the borders with the nasals and

208   maxillae. On the smallest specimen (MTM V.2003.12), the ornamentation is formed by various

209   deep, relatively large pits and grooves present both anteriorly and laterally reaching the

210   premaxilla-maxilla contact. In addition, various nutritive foramina are present further suggesting

211   the still active growth of this bone. This ornamentation is thickest along the anterior margin. On

212   the larger specimens, the surface of the ornamentation is very slightly irregular, pitting is less

213   extensive and various shallow holes (diameter 2-3 mm) are present (Fig. 3C, D). Ornamentation

214   in larger specimens is restricted to the anterolateral and ventrolateral magins of the premaxilla

215   (Fig. 3D) and composed of irregularly shaped, 1-3 mm thick, flat bumbs with branching

216   morphology. Pits and grooves are less and wider.

217   MicroCT scanning of the three smallest premaxillae (Fig. 3A-C) indicates that there is no

218   separation between the superficial ornamentation and the underlying cranial element.

219

220   *Nasal*

221   Nasals (Fig. 3E-H) are preserved in MTM PAL 2020.31.1., MTM PAL 2020.32.1. and holotype

222   skulls (Ősi et al., 2019, Fig. 3E, F, H, Data S1, Video S1-S6). There is also an isolated, complete

223   right nasal (MTM PAL 2020.34.1., Fig. 3G). Similarly to the premaxillae, nasals are unfused, a

224   feature that is characteristic of skeletally immature ankylosaurs (e.g. *Pinacosaurus*, ZPAL MgD-

225   II, Maryanska, 1977; a juvenile nodosaurid from the Paw Paw Formation, Jacobs et al., 1994)

226   and *Kunbarrasaurus* (Molnar, 1996, Leahey et al., 2015), but otherwise uncommon to

227   ankylosaurs. Ornamentation is present along the dorsal surface of all the nasals, although the

228   MTM PAL 2020.31.1.skull demonstrates evidence of weathering (Fig. 3F) On one of the

229   smallest specimens (MTM PAL 2020.32.1.), the cranial ornamentation consists of four or five

230   transversely oriented, hummocky ridges that are slightly shingled in longitudinal profile (Fig.

231   3E). A comparable, hummocky-shingled ornamentation is also observed on the nasals of

232   *Pawpawsaurus* (Lee, 1996) in cross-sectional view using microCT imaging (Paulina-Carabajal,

233   Lee & Jacobs, 2016, digimorph.org). Although this hummocky ornamentation is also preserved

234   on the larger specimen (MTM PAL 2020.34.1., Fig. 3G), the shingled arrangement is present but

235   less obvious. The hummocky ornamentation is further characterized by a network of small

236   (diameter: 0.5-3 mm) pits and grooves (length: 5-20 mm). Ornamentation on the nasal does not

237   reach the premaxilla-nasal, internasal and maxilla-nasal sutural borders. Along the maxillary and

238   prefrontal sutural borders, the nasal thins and the ornamentation abruptly ends, resulting in an

239 irregular, step-like raised edge towards the maxilla and prefrontal. The nasal connects to the

240 frontal via a scarf joint and, unlike the other sutural contacts, the pattern of cranial ornamentation

241 appears to overlap the nasal process of the frontal (Data S1).

242 MicroCT scans from the nasals of three different individuals revealed that this bone is initially

243 composed of compact bone, and that cancellous (spongy) bone is present in the lower two-thirds

244 of the largest specimens (Fig. 3E-G). The upper third layer is more compact and only a few holes

245 and channels are present that open either onto the dorsal surface or connect ventrally to the

246 cancellous lower part.

247

248 *Prefrontal-supraorbital-frontal complex*

249 The skull roof between the orbits is partly preserved from a number of specimens (Table 1),

250 including MTM PAL 2020.32.1., and an isolated left frontal (MTM 2007.27.1), and fragmentary

251 skull including a portion of the partial and basicranium (MTM PAL 2013.23.1) (Fig. 4A-C). In

252 all specimens, the dermatocranial elements posterior to the nasals (i.e., the temporal region of

253 Vickaryous & Russell, 2003) are completely fused and their sutural boundaries obliterated.

254 Cranial ornamentation on MTM PAL 2020.32.1. (Fig. 4A, Suppl. Fig. 2, Data S1, Video S3-S6)

255 includes a number of large, deep (diameter: 2-4 mm) pits and relatively short, shallow grooves.

256 These grooves appear to radiate from a near-central domed area, corresponding to the position of

257 the parietals. Similar to the nasals, the surface of these elements is further ornamented by very

258 small (0.2-1 mm) pits and grooves (1-5 mm). The isolated frontal (Fig. 4B) is ornamented by

259 various small, deep pits and grooves. MicroCT scans revealed an inner structure similar to the

260 nasal (MTM PAL 2020.34.1.), dominated by compact bone superficially and cancellous bone

261 deeper inside the element. Some pits pass through the compact bone into the deeper cancellous

262 bone whereas some 2-3 mm wide holes and channels of the cancellous part enter into the upper

263 compact bone.

264

265 *Postorbital-jugal*

266 Portions of the postorbital and jugal are preserved that represent a number of different size

267 classes (and presumably ontogenetic stages), including MTM PAL 2020.32.1. (Fig. 4D), two

268 isolated specimens, MTM 2007.28.1. (Fig. 4E) and MTM 2010.1.1. (Fig. 4F), and the holotype

269 (Fig. 4G, Data S1, Video S1-S6). Characteristically, the long axis of the postorbital of

270 *Hungarosaurus* passes along the posterodorsal margin of the orbit with a variably projecting

271 crest-like caputegulum. In the smallest referred specimens (MTM PAL 2020.32.1., MTM

272 2007.28.1., Fig. 4D, E), this crest has a dorsoventral height/anterodorsal-posteroventral length

273 ratio of 0.58, whereas in the larger specimens this ratio is reduced to 0.5-0.45 (MTM 2010.1.1.,

274 holotype, Fig. 4F, G). As a result, the crests in the larger specimens encircle more of the orbit,

275 both dorsally and caudally (i.e., towards the jugal process). In addition, the crests of the smaller

276 specimens are more rugose than the larger specimens, and are ornamented by a larger number of

277 small, deeply opening pits and/or neurovascular canals. In the largest specimen, these canals are

278 largely absent. MicroCT images of the postorbital elements revealed a cancellous core

279 surrounded by a compact cortex (Fig. 4D-F).

280 The posteroventral margin of the orbit receives contributions from the jugal (and possibly the

281 quadratojugal). In *Hungarosaurus*, the jugal is preserved in the holotype and by an isolated

282 element (MTM 2010.1.1., Fig. 4F, G). The isolated specimen includes a relatively small

283   quadratojugal boss with a short, ventrally pointed process, whereas that of the holotypic is more

284   rounded. Using microCT imaging, there is no evidence that these bosses are separate elements

285   from the quadratojugal. In all specimens, the surfaces are ornamented with rugose bone,

286   including short (1-8 mm long) neurovascular grooves and small pits (0.3-1 mm); similar to the

287   postorbital crests, the smaller specimens are more heavily ornamented than the larger specimens.

288   MicroCT images of the jugal ornamentation does not show any layering or distinct inner textural

289   differentiation. The inside is more or less uniform, spongious whereas the outer margin,

290   especially that of the jugal boss is more compact, apparently the thickening of the cortex, as seen

291   on the nasal and frontal.

292

293   *Parietal*

294   The area of the skull roof corresponding with the parietal is preserved in the MTM PAL

295   2020.32.1. (Fig. 4A, Data S1, Video S1-S6) and MTM PAL 2013.23.1. (Fig. 4C). This area

296   forms a domed or vaulted complex, and most of its dorsal surface is relatively smooth or

297   ornamented by shallow, short grooves and small (0.5-1 mm) pits. On MTM PAL 2020.32.1.,

298   comparatively deep and wide (> 5mm) grooves and large pits appear to roughly correspond with

299   the positions of contact with the frontal, supraorbital and postorbital bones. Although MTM PAL

300   2013.23.1. (Fig. 4C) is at least 1.5 times larger than in MTM PAL 2020.32.1., representing

301   different ontogenetic stages, there is no indication (suture, different surface texture) that any

302   osteoderms have fused with this region based on external morphology and microCT imaging

303   (Fig. 4A).

304

305 DISCUSSION

306 **Ontogeny of cranial ornamentation in *Hungarosaurus***

307 Cranial ornamentation is a hallmark feature of ankylosaurs (Coombs, 1978; Vickaryous,

308 Maryanska & Weishampel, 2004), and an emerging source of phylogenetic information (e.g.,

309 Arbour & Currie, 2013; 2016). Although the skeletally mature pattern of cranial ornamentation

310 may take the form of a series of variably shaped and sized polygons (referred to as caputegulae;

311 Blows, 2001; see also Arbour & Currie, 2013), in some species these discrete features are not

312 present. Regardless of the pattern formed, cranial ornamentation appears to form as a result of

313 two potentially congruent processes: the coossification of overlying osteoderms with the skull,

314 and the exaggerated outgrowth of individual cranial elements (Vickaryous, Russell & Currie,

315 2001; Hill, Witmer & Norell, 2003). The cranial material described here provides a rare

316 opportunity to investigate the contribution of each of these processes in a European nodosaurid.

317 Using size as a proxy for age, we interpret the described specimen as representing a partial

318 ontogenetic series of *Hungarosaurus* (Fig. 2-4). The smallest specimen (MTM V.2003.12;

319 estimated total skull length ~15-17 cm) is approximately half the size of the largest (the holotype

320 and MTM PAL 2013.23.1; estimated total skull length ~34-36 cm). A fourth skull (MTM PAL

321 2020.32.1.; estimated total skull length ~25 cm), is intermediate in size. Our findings reveal that

322 cranial ornamentation, in the form of rugose texturing across the premaxilla and nasal, and a

323 sharp crest-like ridge along the postorbital, is already present in the smallest (= ontogenetically

324 youngest) individuals examined. Although the pattern of cranial ornamentation changes as the

325 individual gets larger, we found no evidence for the fusion or coossification of osteoderms with

326 the underlying skull.

327   In *Hungarosaurus*, the smallest (= ontogenetically youngest) specimens have a more well-

328   defined pattern of cranial ornamentation compared to larger (and presumably older) specimens.

329   For example, the premaxilla of the smallest specimen has a more deeply pitted rugosity profile

330   when compared to the larger specimens. Similarly, the pattern of small pits and grooves across

331   the prefrontal-supraorbital-frontal complex and the parietal is more obvious on the smallest

332   specimen. And while the nasal bone also demonstrates a well-developed pattern of transversely

333   oriented pattern of hummocky rugosity, in smaller specimens these features form an anteriorly

334   imbricated or shingle-like arrangement. In larger individuals this angled profile is replaced by a

335   more flattened surface but still retains the hummocky rugosity. These specimens suggest that the

336   size of this rugosity relative to the nasal did not change in later phases of ontogeny, i.e. the same

337   level of ornamentation was present but on a larger element. In addition sexual dimorphism, as an

338   explanation for the difference of relative size and arrangemnet of ornaments, cannot be excluded.

339   One of the most characteristic features of *Hungarosaurus* is the formation of a well-defined

340   crest-like caputegulum on the postorbital. This structure is present in the smallest specimens

341   (MTM PAL 2020.32.1., MTM 2007.28.1, Fig. 4D-G), suggesting that it develops relative early

342   during ontogeny, similar to the supraorbital horns of ceratopsians (Horner & Goodwin, 2006).

343   MicroCT images reveal no evidence that this crest is formed by the coossification of multiple

344   elements. As for other features of cranial ornamentation, the morphology of the postorbital crest

345   changes during ontogeny. In the smallest specimens, the shape of the postorbital crest is more

346   acute compared with larger (and presumably ontogenetically older) individuals. Near the margin

347   of the orbit, the postorbital demonstrates a pronounced basal sulcus or 'lip' (sensu Hieronymus et

348   al., 2009, Fig. 4D-G). Although this feature was previously characterized as a fused osteoderm

349   (Ősi et al., 2012), it is reinterpreted here as evidence for a cornified sheath. A similar, well

350   demarcated basal sulcus on the postorbital has also been reported for *Euoplocephalus*

351   (Vickaryous, Russell & Currie, 2001).

352   Osteoderms do not contribute to the cranial ornamentation across the skull of *Hungarosaurus*.

353   Our microCT data do not reveal any evidence that the cranial elements received a separate

354   superifical contribution of bone, and there are no signs of osteoderms superimposed across

355   sutural boundaries. Consequently, we predict that cranial ornamentation in *Hungarosaurus*,

356   similar to the basal ankylosaurid *Cedarpelta*, is the result of elaborated (exaggerated or

357   exostotic) outgrowth of individual cranial elements. The development of elaborated outgrowth

358   on individual skull bones is also reported for non-ankylosaur ankylosauromorphs such as

359   *Scelidosaurus* and *Emausaurus* (Norman, 2019). In contrast, among some ankylosaurine

360   ankylosaurids (e.g., *Euoplocephalus*, *Pinacosaurus*), and some species of modern squamates

361   (e.g., scincids, cordylids, helodermatids; Maisano et al., 2019, Table 2), the coossification of

362   osteoderms does contribute to the formation of cranial ornamentation (Vickaryous, Russell &

363   Currie, 2001; Hill, Witmer & Norell, 2003).

364

365   **Was cranial ornamentation of *Hungarosaurus* sexually dimorphic?**

366   Although fused osteoderms to cranial bones have been reported in a few ceratopsids, e.g.

367   *Triceratops* (the epinasal horn, Horner & Goodwin, 2006) and some ankylosaurids (Vickaryous,

368   Russell & Currie, 2001; Hill, Witmer & Norell, 2003), in most relevant clades of dinosaurs (e.g.

369   theropods, hadrosaurs, other ceratopsians, pachycephalosaurs) the cranial ornaments appear to be

370   exclusively the result of elaboration of cranial bones. Our study revealed that this was the case in

371   the nodosaurid ankylosaur *Hungarosaurus* as well. In addition, the specimens we examined also

372   showed that cranial ornamentation changes during ontogeny. Whether cranial ornamentation is a

373   sexually selected or dimorphic trait remains unclear, owing to the limited number of specimens.

374   Among the ornamented elements described herein, we did find differences in size and shape,

375   although this variation cannot be separated from changes in body size. However, the potential

376   use of these features as dimorphic signals cannot be ruled out. For example, the postorbital crest

377   of the holotype and MTM V 2010.1.1. encircle more of the orbit, both dorsally and caudally,

378   than those of MTM PAL 2020.32.1. and MTM 2007.28.1. (Fig. 4D-G). Though the latter

379   specimens are from much smaller individuals, it remains possible that the different morphologies

380   represent dimorphism.

381   Dimorphism of cranial ornamentations in fossil archosaurs has already been suggested, for

382   example, in pterosaurs (Bennett, 1992; 2001; Naish & Martill, 2003), ceratopsian dinosaurs

383   (Lehman, 1990; Sampson, Ryan & Tanke, 1997; Knell & Sampson, 2011, Borkovic, 2013; Hone

384   & Naish, 2013) and the ankylosaurid *Pinacosaurus* (Godefroit et al., 1999). In most cases,

385   however, the number of specimens or preservation of the cranial remains was far enough from

386   establishing firm conclusions (but see Bennett, 1992).

387   Although the phenomenon of dimorphic cranial ornamentation among extant sauropsid reptiles

388   has been documented, the overall function of the various horns, crests, and polygonal-ornaments

389   remains poorly understood. Among lizards and birds, monomorphic and dimorphic forms of

390   cranial ornamentation exist, with dimorphic species being rarer (e.g. agamids, corytophanids,

391   chameleons, some anatids, cracids or bucerotids, see Table 2.). While skull ornamentation in

392   birds is solely the result of cranial elaboration (Mayr, 2018), osteoderm fusion is common to

393   many groups of lizards (e.g. xenosaurids, helodermatids, Moss, 1969; Montanucci, 1987;

394   Etheridge & de Queiroz, 1988). However, with the possible exception of the marine iguana,

395 dimorphic cranial ornamentation appears to be restricted to the species exaggerating the

396 outgrowth of individual elements. Fossil and extant examples have made it clear that cranial

397 ornamentation is highly varaible, and that using these features as taxonomic characteristics

398 should be viewed with caution (Godefroit et al., 1999; Martill & Naish 2006). Future work on

399 the cranial ornamentation of recent forms may bring us closer to the understanding of the cranial

400 ornamentation of fossil taxa as well.

401

402 **Conclusions**

403 The Santonian nodosaurid *Hungarosaurus* is represented by multiple individuals, including a

404 partial ontogenetic series. As for other ankylosaurs, the skull of *Hungarosaurus* is characterized

405 by cranial ornamentation. This osseous ornamentation is restricted to individual elements, and

406 does not appear to include the incorporation of osteoderms similar to the basal ankylosaurids

407 *Cedarpelta* and *Gastonia*, and the ankylomorphan *Scelidosaurus*. Cranial ornamentation was

408 already well-formed in the smallest (= youngest) individuals. Although the role of ankylosaur

409 cranial ornamentation in species recognition and/or sexual dimorphism cannot be ruled out, a

410 larger sample size is needed to test these predictions.

411

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737 **Table and figure captions**

738

739 **Table 1.** List of specimens used in this study.

740 **Table 2**. Osseous cranial ornamentation in extant sauropsid vertebrates.

741

742 **Figure 1**. Surface view and microCT cross sectional images (in level of the green line) of cranial

743 ornamentation developed as either osteodermal fusion (A-D) or elaboration of skull bones (E-H)

744 in squamates. A, *Tiliqua scincoides* skull in dorsal view and inner structure of the skull bones

745 and covering osteoderms. B, partially fused polygonal osteoderms on the skull of *T. scincoides*.

746 C, *Tiliqua nigrolutea* skull in dorsal view and inner structure of the skull bones and covering

747 osteoderms. D, partially fused polygonal osteoderms on the skull of *T. nigrolutea.* E, *Iguana*

748 *iguana* skull in dorsal view and inner structure of the elaborated skull bones. F, elaboration of

749 skull bones in *I. iguana*. G, *Chamaeleo calyptratus* skull in lateral view and inner structure of the

750 elaborated skull bones. H, elaboration of skull bones in *C. calyptratus*. Abbreviations: cb,

751 cancellous bone; cel, cranial elaboration; cob, compact bone; fr, frontal; glo, globular

752 ornamentation; mx, maxilla; or, orbit, os, osteoderm; pa, parietal; pcr, parietal crest; pfos,

753 partially fused osteoderms; plos, polygonal osteoderms; po, postorbital; uno, unossified part

754 between osteoderm and skull bone; sp, small pits.

755

756 **Figure 2.** Cranial specimens of the Late Cretaceous (Santonian) nodosaurid ankylosaur,

757 *Hungarosaurus tormai* in 3D reconstruction (for 3D reconstruction see Video S1-S6). A,

758   holotype skull, B, MTM PAL 2020.31.1., C, MTM PAL 2020.32.1. D, basicranium and partial

759   skull roof MTM PAL 2013.23.1. Not to scale.

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761   **Figure 3.** Ontogenetic change of the cranial ornamentation on the premaxillae (A-D) and nasals

762   (E-H) of *Hungarosaurus*. Each element is visualized in surface view, three-dimensional surface

763   rendering of microCT images, and microCT cross-sectional view. A, right premaxilla of MTM V

764   2003.12. (mirrored) in left lateral view. B, left premaxilla of MTM PAL 2020.33.1. in left lateral

765   view. C, premaxilla of MTM PAL 2020.31.1. in left lateral view. D, holotype premaxilla in left

766   lateral view. E, nasals of MTM PAL 2020.32.1. in dorsal view. F, right nasal from MTM PAL

767   2020.31.1., G, right nasal (MTM PAL 2020.34.1.) in doral view. H, holotype nasal fragment

768   (mirrored) Abbreviations: cb, cancellous bone; cob, compact bone; den, dorsal margin of

769   external nares; en, external nares; es, eroded surface; gr, groove; ins, internasal suture; lp, large

770   pits; or, ornamentation; re, raised edge; sho, ornamentation in shingled arrangement; sp, small

771   pits.

772

773   **Figure 4.** Ontogenetic change of the cranial ornamentation on the skull roof and orbital region of

774   *Hungarosaurus*. Each element is visualized in surface view, three-dimensional surface rendering

775   of microCT images, and microCT cross-sectional view. A, skull roof of MTM PAL 2020.32.1. in

776   dorsal view. B, MTM 2007.27.1. left fragmentary frontal in dorsal view. C, MTM PAL

777   2013.23.1. basicranium and partial sull roof in dorsal view. D, postorbital of MTM PAL

778   2020.32.1.. E, MTM 2007.28.1. left postorbital. F, MTM 2010.1.1. left postorbital and jugal. G,

779   holotype postorbital and jugal (mirrored). Abbreviations: cb, cancellous bone; cob, compact

780   bone; efe, edge of frontal elaboration; gr, groove; lip, depressed „lip" at transition to softer skin;

781   lp, large pits; npf, nasal process of frontal; orb, orbit; pa, parietal; po, postorbital; poc, postorbital

782   crest; sp, small pits.

783

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List of specimens used in this study.

Reference No.	Preserved skull elements (elements with bold used in this study)	Ontogenetic stage	First described in:
Holotype, MTM 2007.26.1.-2007.26.34.	Partial skull including the **premaxillae**, **right postorbital and jugal**, ?left prefrontal, lacrimal, and **frontal**, posterior part of the pterygoid, both quadrates, condylus occipitalis, 22 teeth, one hyoid? bone, ?vomer, **anterior end of left nasal**	adult	Ősi, 2005; Ősi and Makádi 2009; Ősi et al., 2019; Botfalvai, Prondvai & Ősi, 2020
MTM PAL 2013.23.1	Skull fragment with **parietal** and basicranium	adult?	Ősi, Pereda-Suberbiola & Földes, 2014
MTM PAL 2020.31.1.	Partial skull with most of the rostrum including the **premaxillae**, **nasals**, the right fragmentary maxilla and the right **frontal-supraorbital-?prefrontal-?lacrimal** complex.	subadult-to adult?	This study
MTM PAL 2020.32.1.	Partial skull including the partial basicranium, most of the **skull roof** (frontal, postfrontal, parietal) between and behind the orbits, the **two nasals**, the **left postorbital**, left squamosal, most of the left quadrate and the distal end of the right quadrate.	subadult?	This study
MTM V.2003.12	Isolated **left premaxilla** and partial maxilla	juvenile	Ősi and Makádi, 2009
MTM PAL 2020.33.1.	Isolated **Left premaxilla**	subadult?	This study
MTM V 2010.1.1.	Isolated **left postorbital and jugal**	subadult?	Ősi et al., 2012
MTM 2007.28.1.	Isolated **left postorbital**	subadult?	Ősi and Makádi, 2009
MTM 2007.27.1.	Isolated **left frontal** (originally described as nasal)	subadult? to adult	Ősi and Makádi, 2009
MTM PAL 2020.34.1.	Isolated **right nasal**	adult?	This study

Osseous cranial ornamentation in extant sauropsid vertebrates.

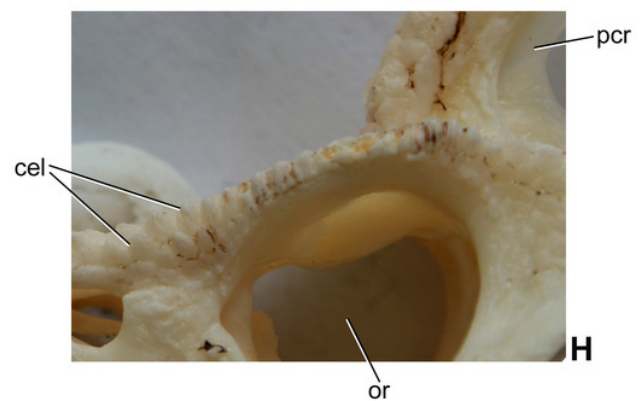
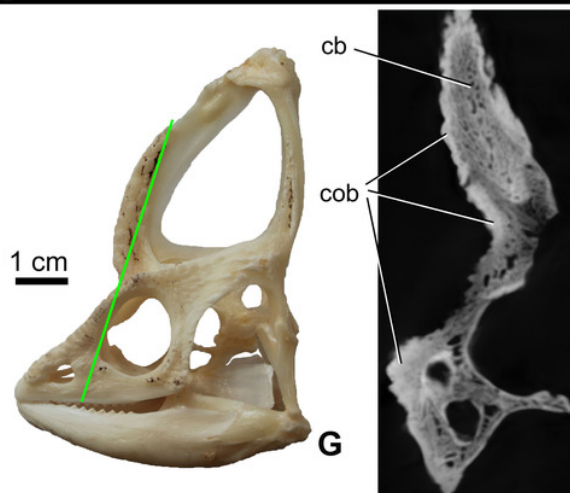
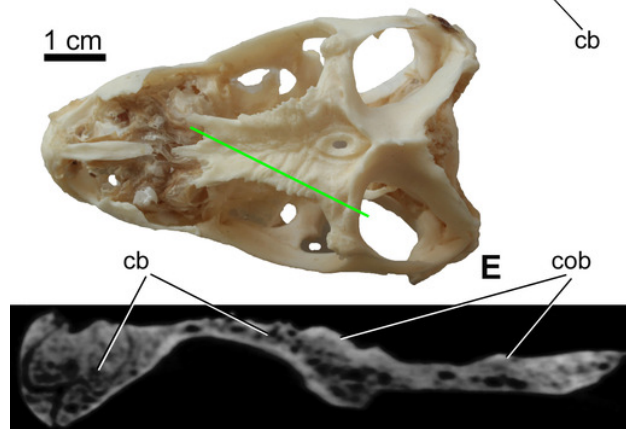
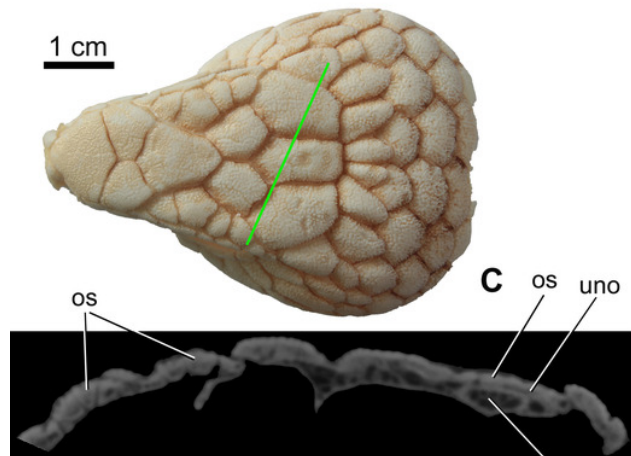
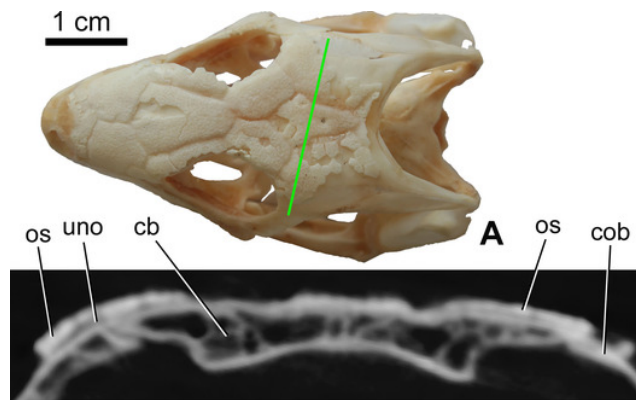
Development of cranial ornamentation	Sexual variation	Higher-level taxon	Family	*Genus/species* example	Morphology	Function	Reference
Osteoderms	**monomorphic**	squmates	Helodermatidae	*Heloderma*	flat, scale-like	?	Mead et al., 2012
Osteoderms	**monomorphic**	squmates	Gerrhonotide	*Abronia, Barisia, Mesaspis*	flat, scale-like	?	Ledesma & Scarpetta, 2018
Osteoderms	**monomorphic**	squmates	Gerrhosauridae	*Angolosaurus, Tracheloptychus*	flat, scale-like or harply keeled scales	?	Nance, 2007
Osteoderms	**monomorphic**	squmates	Scincidae	*Eugongylus, Eumeces, Tiliqua*	flat, polygonal	?	Čerňanský & Hutchinson, 2013
Osteoderms	**monomorphic**	squmates	Xenosauridae	*Xenosaurus*	flat, scale-like	?	Smith et al., 1997
Osteoderms	**monomorphic**	squmates	Xantusiidae	*Lepidophyma gaigeae*	flat, scale-like	Physical protection?	Peterson & Bezy, 1985; Ramírez-Bautista et al., 2008
Osteoderms	**monomorphic**	squmates	Cordylidae	*Ouroborus, Cordylus cataphractus*	flat or slightly domed, pointed	intrasexual fight	Broeckhoven et al., 2017a, b, 2018; Flemming et al., 2018
Osteoderms	**monomorphic**	squmates	Lanthanotidae	*Lanthanotus borneensis*	small, flat to convex	?	Maisano et al., 2002
Osteoderms	**monomorphic**	squmates	Lacertidae	*Lacerta strigata, Xantusia riversiana*	flat, scale-like	?	Čerňanský & SyromyatnikovaI, 2019
Osteoderms	**monomorphic**	squmates	Gekkonidae	*Gekko gecko*	flat, scale-like	?	Laver et al., 2020
Osteoderms	**monomorphic**	squmates	Phyllodactylidae	*Tarentola mauritanica*	flat, scale-like	?	Paluh et al., 2017; Levrat-Calviac & Zylberg, 1986
Osteoderms	**monomorphic**	squmates	Varanidae	*Varanus komodoensis*	small, vermiform osteoderms	?	Maisano et al., 2019; Kirby et al., 2020
Osteoderms	**dimorphic**	squmates	Iguanidae	*Amblyrhynchus*	knob-like	interlock the horns during breeding	Eibl-Eibesfeldt, 1966; Wikelski & Trillmich, 1997
Skull elaboration	**monomorphic**	squmates	Phrynosomatidae	*Phrynosoma*	high spikes	interspecific	Montanucci, 1987; Powell et al., 2017
Skull elaboration	**monomorphic**	squmates	Dactyloidae	*Anolis* spp.	hummocky rugosity, small crests	interspecific	Etheridge & de Queiroz, 1988; Tinius, 2019
Skull elaboration	**monomorphic**	squmates	Carphodactylidae	*Phyllurus cornutus*	hummocky rugosity	?	Doughty & Shine, 1995
Skull elaboration	**monomorphic**	squmates	Teiidae	*Cnemidophorus lemniscatus*	hummocky rugosity, small crests	?	Anderson & Vitt, 1990

Skull elaboration	monomorphic	squmates	Corytophanidae	*Corytophanes*	casque, crest	?	Lang, 1989; Taylor et al., 2017; Smith, 2011
Skull elaboration	monomorphic	turtles	Chelidae	*Chelus fimbriata*	shallow hummocky rugosity	?	Garbin, 2015
Skull elaboration	monomorphic	turtles	Chelydridae	*Macrochelys temminckii*	hummocky rugosity, small grooves	?	-
Skull elaboration	monomorphic	turtles	Testudinidae	*Geochelone denticulata*	hummocky rugosity, small grooves	?	Gaffney, 1979
Skull elaboration	monomorphic	crocodiles	Crocodylidae	*Crocodylus rhombifer*	squamosal horn	interspecific	Bartels, 1984; Brochu et al., 2010
Skull elaboration	monomorphic	birds	Casuariidae	*Casuarius* spp.	casque	thermal radiator	Naish & Perron, 2016; Eastick et al., 2019
Skull elaboration	monomorphic	birds	Bucorvidae	*Bucorvus* spp.	frontal hump	species recognition, amplify communication	Alexander et al., 1994
Skull elaboration	monomorphic	birds	Numididae	*Numida meleagris*	casque	thermoregulation, vocalisation and intraspecific combat?	Mayr, 2018
Skull elaboration	monomorphic	birds	Megapodiidae	*Macrocephalon maleo*	vauled skull	?	Green & Gignac, 2019
Skull elaboration	monomorphic	birds	Gruidae	*Balearica regulorum*	frontal hump, horn-like tubercles on parietal	?	Mayr, 2018
Skull elaboration	monomorphic	birds	Anatidae	*Anas gibberifrons*	frontal hump	physiological, sensory, or acoustic function?	Mayr, 2018
Skull elaboration	monomorphic	birds	Cracidae	*Oreophasis derbianus, Pauxi*	casque	demonstrative of ability to survive	Vaurie, 1968; González-García, 1995; Mayr, 2018
Skull elaboration	monomorphic	birds	Alcidae	*Fratercula arctica, Cerorhinca monocerata*	crest or horn on the upper beak	beak stregthening?	Jones, 1993
Skull elaboration	monomorphic	birds	Pelecanidae	*Pelecanus erythrorhynchos*	Crest on the upper beak	display during breading	Evans & Knopf, 1993
Skull elaboration	monomorphic	birds	Procellariidae	*Pagodroma nivea, Fulmarus*	Crest on the upper beak	?	Jouventin & Viot, 1984

				glacialis			
Skull elaboration	**monomorphic**	birds	Chionididae	*Chionis minor*	Shield-like callosity	physiological role?	Lowe, 1916; Mayr, 2018
Skull elaboration	**monomorphic**	birds	Musophagidae	*Musophaga violacea*	casque	?	Mayr, 2018
Skull elaboration	**monomorphic**	birds	Icteridae	*Psarocolius decumanus*	crest on the upper beak	?	Webster, 1992; Fraga & Kreft, 2007
Skull elaboration	**monomorphic**	birds	Threskiornithidae	*Geronticus calvus*		?	Kopij 1998
Skull elaboration	**monomorphic**	birds	Meliphagidae	*Philemon corniculatus*	Crest on the beak	?	Mayr, 2018
Skull elaboration	**monomorphic**	birds	Cuculidae	*Crotophaga sulcirostris*	deep upper beak	?	Posso & Donatelli, 2001; Mayr, 2018
Skull elaboration	**dimorphic**	squamates	Corytophanidae	*Basiliscus*	casque, crest	intersexual	Lang, 1989; Taylor et al., 2017; Smith, 2011
Skull elaboration	**dimorphic**	squamates	Chamaeleonidae	*Chameleo jacksoni, Triceros*	crest, horns	social significance, species recognition	Rand, 1961; Eckhardt et al., 2012
Skull elaboration	**dimorphic**	birds	Phasianidae	*Tetrao urogallus*	preorbital ridge	?	Lindén & Vaisanen, 1986
Skull elaboration	**dimorphic**	birds	Anatidae	*Cygnus, Melanitta, Oxyura*	frontal hump	fat reservoir indicating individual fitness	Horrocks et al., 2009; Lüps, 1990; Mayr, 2018
Skull elaboration	**dimorphic**	birds	Anseranatidae	*Anseranas*	frontal hump	?	Mayr, 2018
Skull elaboration	**dimorphic**	birds	Cracidae	*Crax*	casque	demonstrative of ability to survive	Buchholz, 1991; Mayr, 2018
Skull elaboration	**dimorphic**	birds	Bucerotidae	*Rhyticeros*	casque on upper beak	?	Kemp, 2001; Mayr, 2018
Osteoderms and skull elaboration	**monomorphic**	squamates	Anguidae	*Pseudopus (Ophisaurus) apodus*	flat, scale-like, pitted osteoderms; grooved nasal, frontal, parietal	?	Klembara et al., 2017

Figure 1

Surface view and microCT cross sectional images (in level of the green line) of cranial ornamentation developed as either osteodermal fusion (A-D) or elaboration of skull bones (E-H) in squamates.

A, *Tiliqua scincoides* skull in dorsal view and inner structure of the skull bones and covering osteoderms. B, partially fused polygonal osteoderms on the skull of *T. scincoides*. C, *Tiliqua nigrolutea* skull in dorsal view and inner structure of the skull bones and covering osteoderms. D, partially fused polygonal osteoderms on the skull of *T. nigrolutea.* E, *Iguana iguana* skull in dorsal view and inner structure of the elaborated skull bones. F, elaboration of skull bones in *I. iguana*. G, *Chamaeleo calyptratus* skull in lateral view and inner structure of the elaborated skull bones. H, elaboration of skull bones in *C. calyptratus*. Abbreviations: cb, cancellous bone; cel, cranial elaboration; cob, compact bone; fr, frontal; glo, globular ornamentation; mx, maxilla; or, orbit, os, osteoderm; pa, parietal; pcr, parietal crest; pfos, partially fused osteoderms; plos, polygonal osteoderms; po, postorbital; uno, unossified part between osteoderm and skull bone; sp, small pits.

A os uno cb os cob

B po plos sp

C os os uno cb

D pfos or mx glo

E cb cob

F cel fr pa

G cb cob

H pcr cel or

Figure 2

Cranial specimens of the Late Cretaceous (Santonian) nodosaurid ankylosaur, *Hungarosaurus tormai* in 3D reconstruction (for 3D reconstruction see Video S1-S6).

A, holotype skull, B, MTM PAL 2020.31.1., C, MTM PAL 2020.32.1. D, basicranium and partial skull roof MTM PAL 2013.23.1. Not to scale.

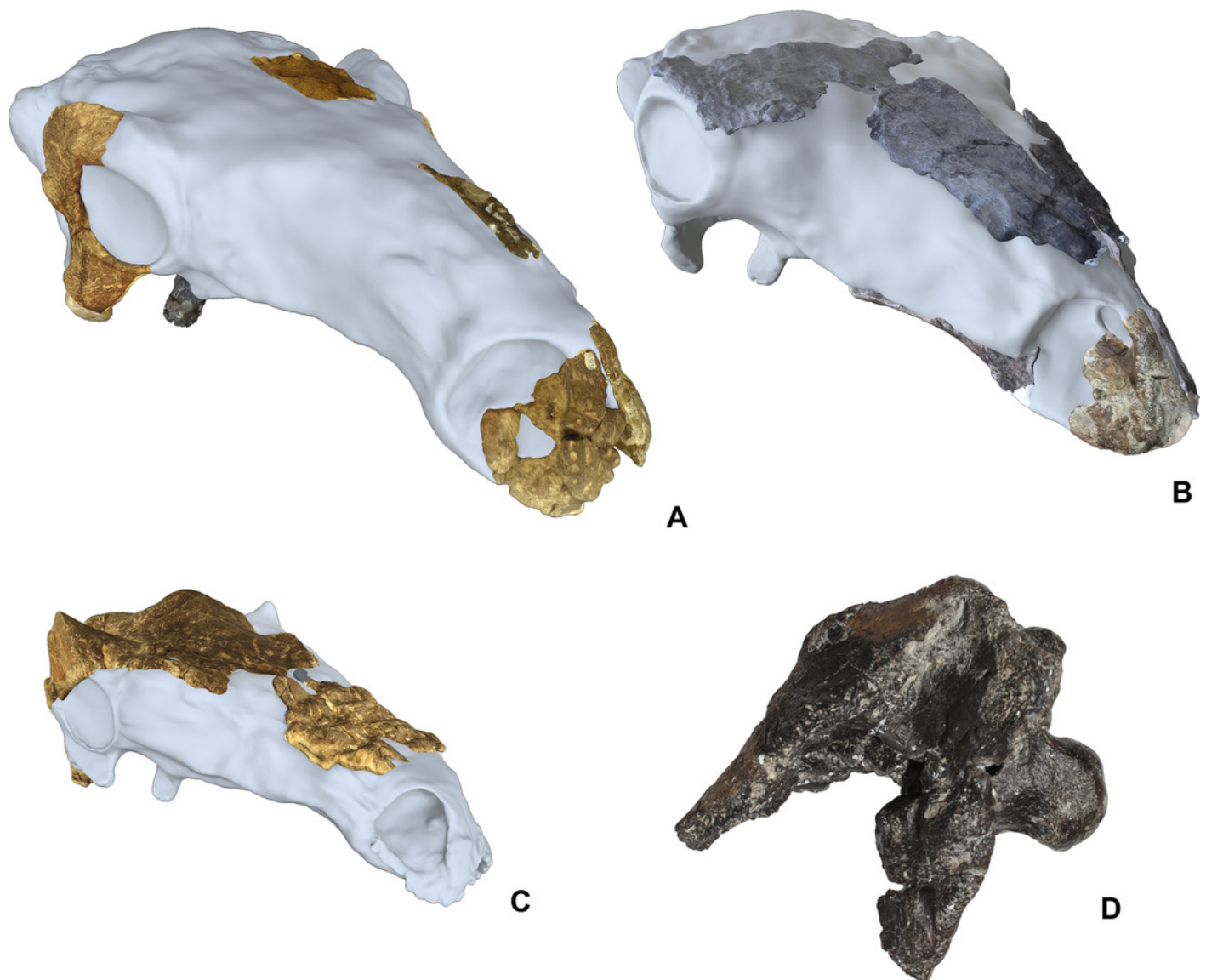



Figure 3

Ontogenetic change of the cranial ornamentation on the premaxillae (A-D) and nasals (E-H) of *Hungarosaurus*.

Each element is visualized in surface view, three-dimensional surface rendering of microCT images, and microCT cross-sectional view. A, right premaxilla of MTM V 2003.12. (mirrored) in left lateral view. B, left premaxilla of MTM PAL 2020.33.1. in left lateral view. C, premaxilla of MTM PAL 2020.31.1. in left lateral view. D, holotype premaxilla in left lateral view. E, nasals of MTM PAL 2020.32.1. in dorsal view. F, right nasal from MTM PAL 2020.31.1., G, right nasal (MTM PAL 2020.34.1.) in doral view. H, holotype nasal fragment (mirrored) Abbreviations: cb, cancellous bone; cob, compact bone; den, dorsal margin of external nares; en, external nares; es, eroded surface; gr, groove; ins, internasal suture; lp, large pits; or, ornamentation; re, raised edge; sho, ornamentation in shingled arrangement; sp, small pits.

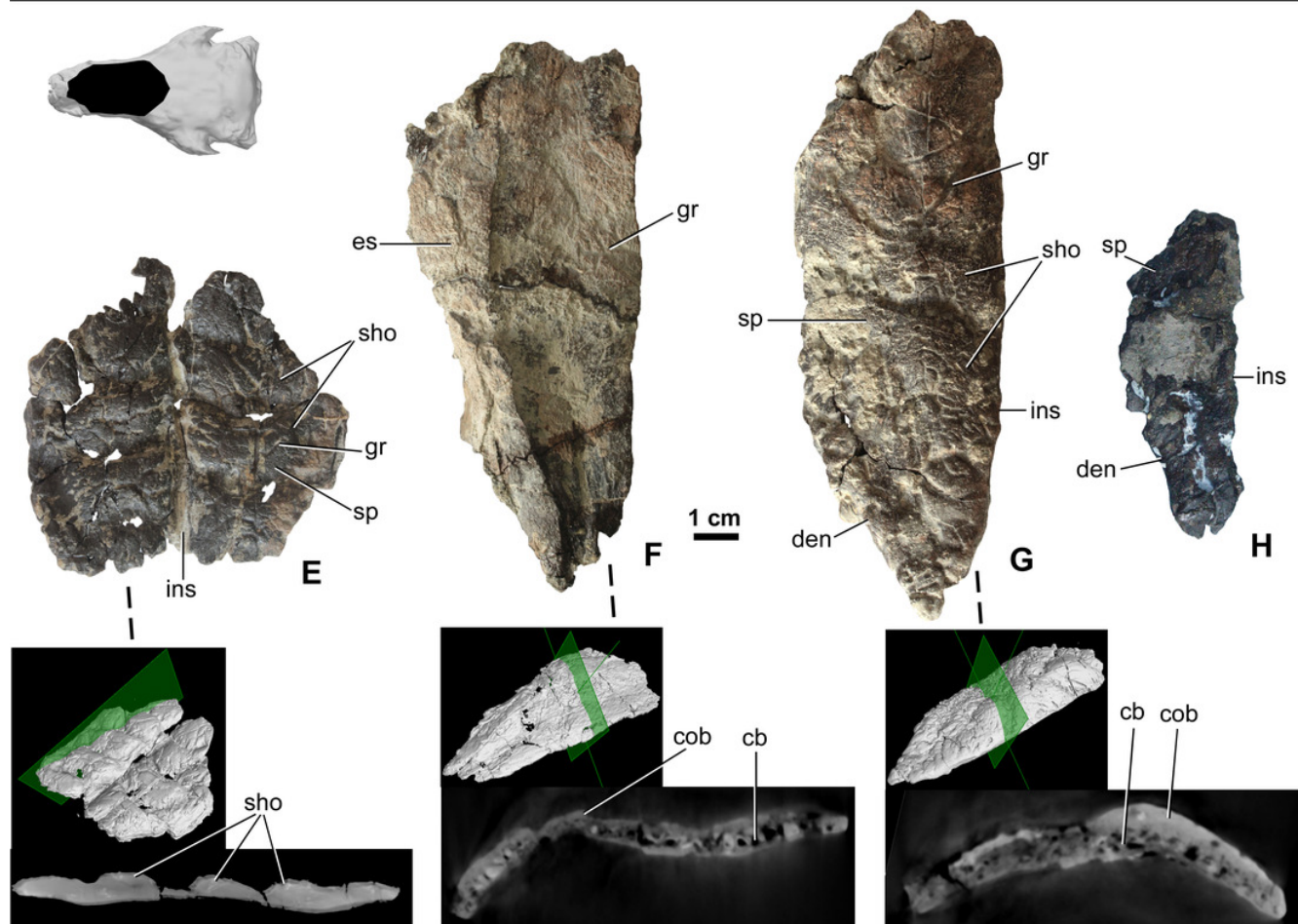
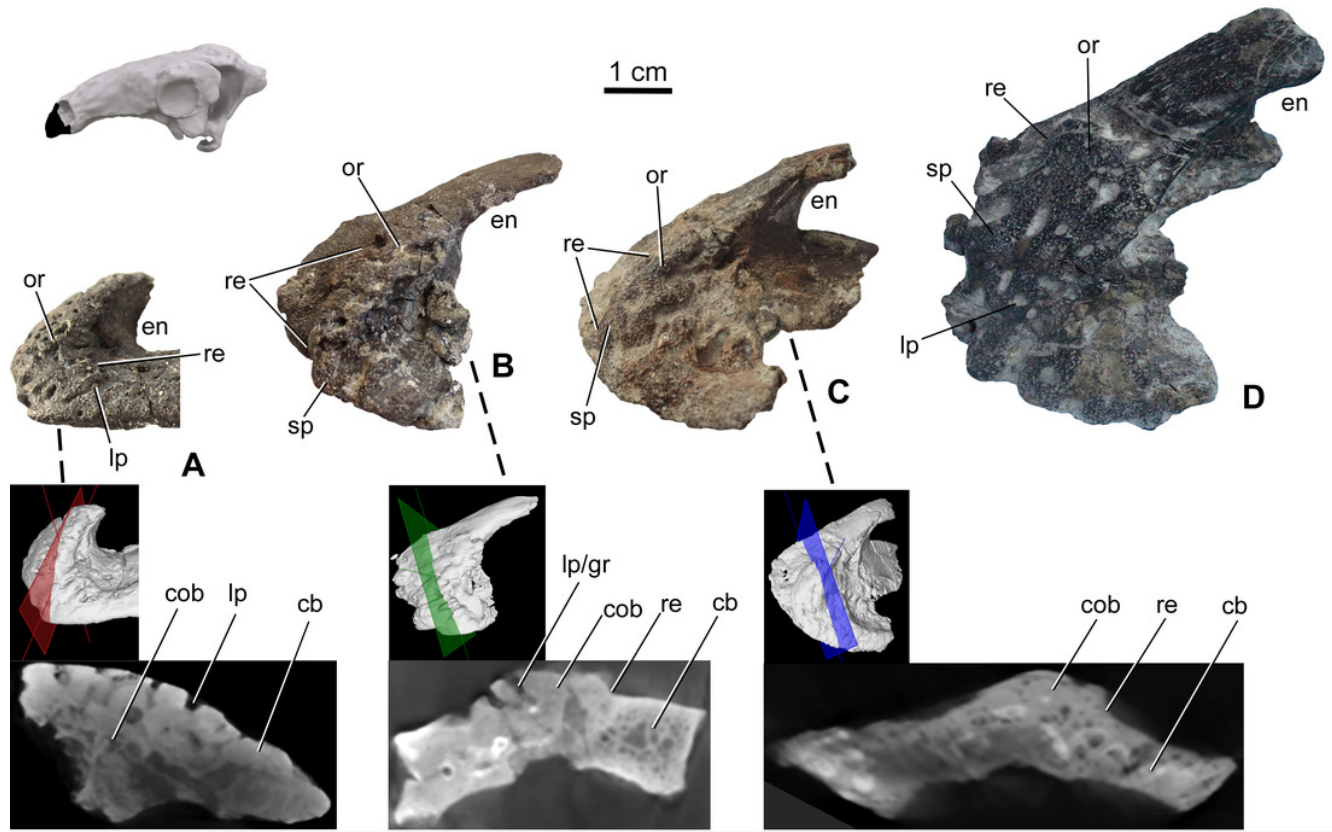



Figure 4

Ontogenetic change of the cranial ornamentation on the skull roof and orbital region of *Hungarosaurus*.

Each element is visualized in surface view, three-dimensional surface rendering of microCT images, and microCT cross-sectional view. A, skull roof of MTM PAL 2020.32.1. in dorsal view. B, MTM 2007.27.1. left fragmentary frontal in dorsal view. C, MTM PAL 2013.23.1. basicranium and partial sull roof in dorsal view. D, postorbital of MTM PAL 2020.32.1.. E, MTM 2007.28.1. left postorbital. F, MTM 2010.1.1. left postorbital and jugal. G, holotype postorbital and jugal (mirrored). Abbreviations: cb, cancellous bone; cob, compact bone; efe, edge of frontal elaboration; gr, groove; lip, depressed „lip" at transition to softer skin; lp, large pits; npf, nasal process of frontal; orb, orbit; pa, parietal; po, postorbital; poc, postorbital crest; sp, small pits.