Cranial ornamentation in the Late Cretaceous nodosaurid ankylosaur *Hungarosaurus*

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ABSTRACT

Bony cranial ornamentation is developed by many groups of vertebrates, including ankylosaur dinosaurs. To date, the morphology and ontogenetic origin of ankylosaurian 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 herein, 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. Sexual(?) 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.

INTRODUCTION

Development of osseous cranial ornamentation is a relatively common occurence in the evolutionary history of terrestrial vertebrates (Buffrénil, 1982). Among reptiles, cranial ornamentation, including frills, crests, horns, bosses, or casques, is known for representative members of many fossil and extant groups (e.g. Gadow, 1901; Romer, 1956; Clarac et al., 2017; Mayr, 2018). The ultimate (optimum? ideal?) morphology of cranial ornamentation, especially among skeletally mature adults, is often highly variable and species-specific (e.g. Otto, 1909; Montanucci, 1987). As currently understood, this vast diversity is the result of two principal modes of morphogenesis: the elaboration of individual cranial elements; and the fusion of additional skeletal elements with the skull (Moss, 1969; Vickaryous, Russell & Currie, 2001). Among reptiles, these additional skeletal elements are most commonly identified as osteoderms.

Osteoderms (= dermal sclerifications, osteoscutes) are bone-rich elements that form within the dermis (Moss, 1969; Vickaryous & Sire, 2009). Although they remain often suspended within the skin (e.g. some gekkotan lizards; Paluh; Griffing & Bauer, 2017, Laver et al., 2020), in some taxa they gradually fuse with subadjacent bones of the skull (e.g. helodermatids, xenosaurids; Bhullar, 2011; Maisano et al., 2019). As osteoderms develop within the skin, they ~~are~~ may occupy positions that overlap sutural boundaries (Vickaryous, Russell & Currie, 2001).

In addition to the fusion of osteoderms, cranial ornamentation may also develop as a result of the elaboration or exaggerated outgrowth of individual cranial (and mandibular) elements (e.g. Montanucci, 1987; Vickaryous, Russell & Currie, 2001; Hieronymus et al., 2009). In some species, particularly among aged individuals, this form of exaggerated outgrowth may become continuous across multiple adjacent bones (e.g. "hummocky rugosities"; Hieronymus et al., 2009).

Cranial ornamentation is one of the most diagnostic features of the extinct archosaur dinosaurian? clade Ankylosauria (Maryańska, 1977; Coombs, 1978; Carpenter et al., 2001; Vickaryous, Maryańska & Weishampel, 2004). For most ankylosaur taxa, the dorsolateral surfaces of the cranium and the posterolateral surface of the mandible are externally (superficially) embossed with cranial ornamentation. Although intraspecific (and possibly ontogenetic) variation exists, details of the size, shape and pattern of cranial ornamentation, often referred to as 'caputegulae' (Blows, 2001), ~~have~~ has long been recognized as taxonomically informative (e.g. Parks, 1924; Coombs, 1971; 1978; Blows, 2001; Penkalski, 2001; Arbour & Currie, 2013; 2016). This includes the classical distinction of the two major clades of ankylosaurs: Ankylosauridae and Nodosauridae (Coombs, 1978).

The ontogenetic origin of cranial ornamentation in ankylosaurs has primarily focused on a handful of species, most of which are members of Ankylosauridae (Coombs, 1971; Molnar, 1996; Vickaryous, Russell & Currie, 2001; Carpenter et al., 2001; Hill, Witmer & Norell, 2003). see notes Based on the investigation of multiple specimens, including material attributed to subadult (i.e., not skeletally mature) individuals, the cranial ornamentation of *Euoplocephalus* and *Pinacosaurus* is interpreted involving both the coosification of osteoderms with the skull and the exaggerated outgrowth of individual cranial elements (Vickaryous, Russell & Currie, 2001; Hill, Witmer & Norell, 2003; although see Carpenter et al., 2001). In contrast, osteoderms do not appear to fuse with the skulls of ~~the~~ Some basal taxa e.g. *Cedarpelta* (Carpenter et al., 2001) and *Gastonia* (Kinneer, Carpenter & Shaw, 2016). ~~Hence,~~ The cranial ornamentation in these species appears to be exclusively the result of elaborated outgrowth of individual elements. see notes Among nodosaurids, less is known. A partial skull attributed to an unidentified species was reported to demonstrate a rugose external texture, but no evidence of "... overgrowth of dermal bone" (Jacobs et al., 1994).

Here we describe several fragmentary skulls and skull elements of the European Late Cretaceous (Santonian) nodosaurid ankylosaur, *Hungarosaurus* (Table 1). These specimens represent at least three different size classes (and likely different stages of ontogeny), and provide new information about the morphological diversity, development and possible function of cranial ornamentation of nodosaurid skulls.

Cranial ornamentation in extant forms

Among extant saurospids (turtles, lepidosaurs, crocodiles and birds), representative members of all the main groups develop osseous cranial ornamentation. Ontogenetic development of cranial ornamentation involves two key processes: the fusion of overlying osteoderms and the elaboration of individual dermatocranial elements (Vickaryous, Russell & Currie, 2001, see Table 2). However, the extent to which these processes occur in diffent taxa remains poorly understood.

Osteoderm fusion to skull bones

Many extant groups of non-iguanian lizards develop osteoderms across the dorsal and lateral surfaces of the skull (Table 2; see also Gadow, 1901; Moss, 1969; Montanucci, 1987; Etheridge & de Queiroz, 1988; Vickaryous & Sire, 2009). Depending on the species and state of skeletal development, osteoderms may remain embedded within the skin and thus not directly contact the skull, or may partially or even completely fused with the underlying cranial elements (Maisano et al., 2019). With a partial fusion, the degree of coossification is incomplete, resulting in an unossified gap that can be detected using CT scanning (e.g., Fig. 1A, C). Alternatively, in skeletally mature *Heloderma* spp. and xenosaurids, this gap is obliterated and there is no longer any evidence of separation (e.g., Maisano et al., 2019). As a consequence of developing with the skin, osteoderms may overlap cranial sutures and/or form in positions without any subjacent dermatocranial bones (e.g., superficial to cranial fenestrations) (Vickaryous, Russell & Currie, 2001).

The morphology and arrangement of osteoderms across the skull in non-iguanian lizards(?) demonstrates considerable taxonomic variation (e.g., Fig. 1A-D; see also Mead et al., 2012; Ledesma & Scarpetta, 2018). To date, there is no evidence of any differences associated with sexual dimorphism (Table 2), with both males and females developing comparable arrangements of osteoderm-mediated ornamentation (see references in Table 2). Among iguanid lizards, cranial osteoderms have only been reported for aged marine iguanas (*Amblyrhynchus cristatus*; Etheridge & de Queiroz, 1988). In marine iguanas, these structures are reportedly used by males during the breeding season. Females are characterized by a similar albeit less developed version of this ornamentation (Eibl-Eibesfeldt, 1966).

In contrast to squamates no extant member of the Archosauria (i.e. crocodylians and birds) has been reported to have cranial osteoderms, with the possible exception of the bony palpebral (eyelid bone) (Vickaryous & Hall, 2008).

Elaboration/outgrowth of cranial elements

Among various iguanians, cranial ornamentation is dominated by the elaboration and outgrowth of individual dermatocranial elements (Etheridge & de Queiroz, 1988). While this form of cranial ornamentation often manifests as rugosities with variably developed crests, pits and bumps (Hieronymous et al., 2009; Fig. 1E-F), some taxa develop large horn-like outgrowths. For example, in species of *Phrynosoma* horns and bosses can develop on each of the parietal and squamosal (Lang, 1989; Vickaryous, Russell & Currie, 2001; Powell et al., 2017). Although the number, morphology and orientation of these protuberances can vary among *Phrynosoma* species, they do not appear to be sexual dimorphic (Powell et al., 2017; see Table 2). Similarly, anoles (Dactyloidae) also have taxon-specific cranial ornamentation that is present in both sexes (Etheridge & de Queiroz, 1988).

The development of bony horns and crests is also characteristic of some archosaurs, including fossil (e.g. *Ceratosuchus* Schmidt, 1938; Bartels, 1984, Brochu, 2006; 2007; Bickelmann & Klein, 2009) and extant (e.g. *Crocodylus rhombifer*; Brochu et al., 2010) crocodylians. Among recent taxa, these protuberances are not sexually dimorphic (Bartels, 1984). It has been speculated that these horns may be used for species recognition in ecosystems where multiple taxa of crocodylians exist (Bartels, 1984). Cranial ornamentation is also characterstic of many taxa of birds (Table 2). In most cases these elaborations and outgrowths are monomorphic (Mayr, 2018). One of the most obvious examples are cassowaries (*Casuarius* spp.), where males and females are similarly ornamented with elaborate casques on the skull roof (Naish & Perron, 2016). The bony architecture of this cranial ornamentation can also vary. For example, the casque on the upper bills of bucorvid and some bucerotid birds is typically dominated by an air-filled cavity and thin trabecular bone, but is reportedly solid bone in the greater helmeted hornill (*Buceros vigil*) (Gamble, 2007).

To ~~sum up~~ summarize, the fusion of osteoderms to cranial bones ~~characterizes~~ only occurs in a few groups of squamates, and is not present in extant archosaurs (Table 2). In terms of cranial ornamentation,

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almost all these forms are sexually monomorphic and the architecture of oramentation is frequently taxon-specific. On the other hand, elaboration or outgrowth of cranial bones appears to be a more frequent phenomenon not only in squamates but also in birds and even in some species of crocodylians.

MATERIAL AND METHODS

Specimens

The Hungarian nodosaurid ankylosaur specimens used in this study (Table 1) are from the Upper Cretaceous (Santonian) Csehbánya Formation of Iharkút vertebrate site, Bakony Mountains, western Hungary (Ősi et al., 2019; for geology and taphonomy~~,~~ see Botfalvai, Ősi & Mindszenty, 2015; Botfalvai et al., 2016). Four partial ankylosaur skulls (Fig. 2) and various isolated skull elements (see Table 1 for all used specimens) from Iharkút are briefly described and compared in detail particularly focusing on the morphology, topographic distribution and origin of the cranial ornamentations. Two of the fragmentary skulls (holotype, MTM PAL 2013.23.1., Fig. 2A, D) and some isolated elements have been already described in more detail (Ősi, 2005; Ősi & Makádi, 2009; Ősi, Pereda-Suberbiola & Földes, 2014; Ősi et al., 2019) but cranial ornamentation was not discussed. The two new ~~additional~~ partial skulls (MTM PAL 2020.31.1., MTM PAL 2020.32.1., Fig. 2B, C, Data S1) have ~~never~~ not been described in detail, the comparative osteological description of these specimens are in Data S1.

The basis of this work is that all four skulls and isolated remains are thought to belong to *Hungarosaurus*. Although the presence of the much smaller *Struthiosaurus* at the site has also been confirmed by postcranial findings (Ősi & Prondvai, 2013; Ősi & Pereda-Suberbiola, 2017), the two new skulls are closer to *Hungarosaurus* based on the osteological features listed in Data S1. The postorbital crest of the specimen MTM PAL 2020.32.1. is, however, somewhat different from that of the holotype of *Hungarosaurus*, that we interpret as presumably due to ontogenetic or intersexual differences (see discussion below).

Methods

Specimens were collected between 2001 and 2019, and all of them are housed in the Vertebrate Paleontological Collection of the Hungarian Natural History Museum, Budapest (MTM). Specimens were prepared mechanically in the labs of the Department of Paleontology of the Eötvös University and the Hungarian Natural History Museum, and the bones were fixed by cyanoacrylic glue.

For 3D reconstruction of the skulls (Fig. 2), we photographed each bone with a Canon EOS 600D DS126311 camera using a photogrammetric technique. 2D images were converted to 3D images using 3DF Zephyr software. 3D images of bones also show the original texture of the bones. 3D files of each bone were assembled within the free Blender software using Polygonal modeling and Sculpting techniques. Finally, we rendered a turntable video of the "finished" skull in Marmoset Toolbag 3. The 3D reconstructions of the three studied skull are in the video files (Video S1-S6; https://zenodo.org/record/4117812#.X5FfUO28o2w).

Specimens ~~are not allowed to~~ were not permitted to be cut for histological purposes, thus microtomographic (microCT) imaging was used to investigate the inner structure of cranial elements and ornamentation. MicroCT scanning of fossil and recent bones ~~have been made in the~~ were conducted at the laboratory of ~~the~~ Carl Zeiss IMT Austria GmbH (Budaörs, Hungary), ~~Scanning of the bones has been made by~~ using a Zeiss Metrotom computer tomograph with a distance ~~between each slices~~ of 130 µm.

Institutional abbreviations: IGM, Institute of Geology, Ulaan Baatar, Mongolia; MTM, Hungarian Natural History Museum, Budapest, Hungary; TMP, Royal Tyrrell Museum, Drumheller, Canada.

RESULTS

Cranial ornamentation in *Hungarosaurus*

Premaxilla

Premaxillae are preserved in four specimens, including two isolated elements along with the holotype skull and in MTM PAL 2020.31.1. (Fig. 3A-D). The smallest premaxilla (MTM V.2003.12) is almost half the size of the holotype (Fig. 3A), and thus likely represents a juvenile or subadult individual (Ősi & Makádi, 2009). Premaxillae are unfused ~~with~~ to each other in all specimens. Ornamentation can be observed on all the specimens including the smallest element, but does not overlap the sutures between the two premaxillae, or the borders with the nasals and maxillae. On the smallest specimen (MTM V.2003.12), the ornamentation is formed by various deep, relatively large pits and grooves present both anteriorly and laterally reaching the premaxilla-maxilla contact. In addition, various nutritive foramina are present further suggesting the still active growth of this bone. This ornamentation is thickest along the anterior margin. On the larger specimens, the surface of the ornamentation is very slightly irregular, pitting is less extensive and various shallow holes (diameter 2-3 mm) are present (Fig. 3C, D). Ornamentation in larger specimens is restricted to the anterolateral and ventrolateral magins of the premaxilla (Fig. 3D) and composed of irregularly shaped, 1-3 mm thick, flat bumbs with branching morphology. Pits and grooves are less ~~and~~ but wider.

MicroCT scanning of the three smallest premaxillae (Fig. 3A-C) indicates that there is no separation between the superficial ornamentation and the underlying cranial element.

Nasal

Nasals (Fig. 3E-H) are preserved ~~in~~ for the skulls of MTM PAL 2020.31.1., MTM PAL 2020.32.1. and the holotype ~~skulls~~ (Ősi et al., 2019, Fig. 3E, F, H, Data S1, Video S1-S6). There is also an isolated, complete right nasal (MTM PAL 2020.34.1., Fig. 3G). Similarly to the premaxillae, the nasals are unfused, a feature that ~~is characteristic of~~ may indicate skeletally immature ankylosaurs (e.g. *Pinacosaurus*, ZPAL MgD-II, Maryanska, 1977; ~~a juvenile nodosaurid from the Paw Paw Formation, Jacobs et al., 1994)~~ no nasals recovered for this specimen and *Kunbarrasaurus* (Molnar, 1996, Leahey et al., 2015), but otherwise uncommon to ankylosaurs. Ornamentation is present along the dorsal surface of all the nasals, although the MTM PAL 2020.31.1.skull demonstrates evidence of weathering (Fig. 3F) On one of the smallest specimens (MTM PAL 2020.32.1.), the cranial ornamentation consists of four or five transversely oriented, hummocky ridges that are slightly shingled in longitudinal profile (Fig. 3E). A comparable, hummocky-shingled ornamentation is also observed on the nasals of *Pawpawsaurus* (Lee, 1996) in cross-sectional view using microCT imaging (Paulina-Carabajal, Lee & Jacobs, 2016, digimorph.org). Although this hummocky ornamentation is also preserved on the larger specimen (MTM PAL 2020.34.1., Fig. 3G), the shingled arrangement is present but less obvious. The hummocky ornamentation is further characterized by a network of small (diameter: 0.5-3 mm) pits and grooves (length: 5-20 mm). Ornamentation on the nasal does not reach the premaxilla-nasal, internasal and maxilla-nasal sutural borders. Along the maxillary and prefrontal sutural borders, the nasal thins and the ornamentation abruptly ends, resulting in an irregular, step-like raised edge towards the maxilla and prefrontal. The nasal connects to the frontal via a scarf joint and, unlike the other sutural contacts, the pattern of cranial ornamentation appears to overlap the nasal process of the frontal (Data S1).

MicroCT scans from the nasals of three different individuals revealed that this bone is initially composed of compact bone, and that cancellous (spongy) bone is present in the lower two-thirds of the largest specimens (Fig. 3E-G). The upper third layer is more compact and only a few holes and channels are present that open either onto the dorsal surface or connect ventrally to the cancellous lower part.

Prefrontal-supraorbital-frontal complex

The skull roof between the orbits is partly preserved from a number of specimens (Table 1), including MTM PAL 2020.32.1., and an isolated left frontal (MTM 2007.27.1), and fragmentary skull including a portion of the partial and basicranium (MTM PAL 2013.23.1) (Fig. 4A-C). In all specimens, the dermatocranial elements posterior to the nasals (i.e., the temporal region of Vickaryous & Russell, 2003) are completely fused and their sutural boundaries obliterated. Cranial ornamentation on MTM PAL 2020.32.1. (Fig. 4A, Suppl. Fig. 2, Data S1, Video S3-S6) includes a number of large, deep (diameter: 2-4 mm) pits and relatively short, shallow grooves. These grooves appear to radiate from a near-central domed area, corresponding to the position of the parietals. Similar to the nasals, the surface of these elements is further ornamented by very small (0.2-1 mm) pits and grooves (1-5 mm). The isolated frontal (Fig. 4B) is ornamented by various small, deep pits and grooves. MicroCT scans revealed an inner structure similar to the nasal (MTM PAL 2020.34.1.), dominated by compact bone superficially and cancellous bone deeper inside the element. Some pits pass through the compact bone into the deeper cancellous bone whereas some ~~2-3 mm wide~~ wider holes (2-3 mm) and channels of the cancellous part enter into the upper compact bone.

Postorbital-jugal

Portions of the postorbital and jugal are preserved that represent a number of different size classes (and presumably ontogenetic stages), including MTM PAL 2020.32.1. (Fig. 4D), two isolated specimens, MTM 2007.28.1. (Fig. 4E) and MTM 2010.1.1. (Fig. 4F), and the holotype (Fig. 4G, Data S1, Video S1-S6). Characteristically, the long axis of the postorbital of *Hungarosaurus* passes along the posterodorsal margin of the orbit with a variably projecting crest-like caputegulum. In the smallest referred specimens (MTM PAL 2020.32.1., MTM 2007.28.1., Fig. 4D, E), this crest has a dorsoventral height/anterodorsal-posteroventral length ratio of 0.58, whereas in the larger specimens this ratio is reduced to 0.5-0.45 (MTM 2010.1.1., holotype, Fig. 4F, G). As a result, the crests in the larger specimens encircle more of the orbit, both dorsally and caudally (i.e. towards the jugal process). In addition, the crests of the smaller specimens are more rugose than the larger specimens, and are ornamented by a larger number of small, deeply opening pits and/or neurovascular canals. In the largest specimen, these canals are largely absent. MicroCT images of the postorbital elements revealed a cancellous core surrounded by a compact cortex (Fig. 4D-F).

The posteroventral margin of the orbit receives contributions from the jugal (and possibly the quadratojugal). In *Hungarosaurus*, the jugal is preserved in the holotype and by an isolated element (MTM 2010.1.1., Fig. 4F, G). The isolated specimen includes a relatively small quadratojugal boss with a short, ventrally pointed process, whereas that of the ~~holotypic~~ holotype is more rounded. ~~Using~~ MicroCT imaging, revealed there is no evidence that these bosses are separate elements from the quadratojugal. might be good to add an image of this. In all specimens, the surfaces are ornamented with rugose bone, including short (1-8 mm long) neurovascular grooves and small pits (0.3-1 mm); similar to the postorbital crests, the smaller specimens are more heavily ornamented than the larger specimens. MicroCT images of the jugal ornamentation does not show any layering or distinct inner textural differentiation. The inside is more or less ~~uniform;~~ uniformly? spongious, whereas the outer margin, especially that of the jugal boss is more compact, apparently the thickening of the cortex, as seen on the nasal and frontal.

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Parietal

The area of the skull roof corresponding with the parietal is preserved in the MTM PAL 2020.32.1. (Fig. 4A, Data S1, Video S1-S6) and MTM PAL 2013.23.1. (Fig. 4C). This area forms a domed or vaulted complex, and most of its dorsal surface is relatively smooth or ornamented by shallow, short grooves and small (0.5-1 mm) pits. On MTM PAL 2020.32.1., comparatively deep and wide (> 5mm) grooves and large pits appear to roughly correspond with the positions of contact with the frontal, supraorbital and postorbital bones. Although MTM PAL 2013.23.1. (Fig. 4C) is at least 1.5 times larger than in MTM PAL 2020.32.1., and thus representing different ontogenetic stages, there is no indication (suture, different surface texture) that any osteoderms have fused with this region based on external morphology and microCT imaging (Fig. 4A).

DISCUSSION

Ontogeny of cranial ornamentation in *Hungarosaurus*

Cranial ornamentation is a hallmark feature of ankylosaurs (Coombs, 1978; Vickaryous, Maryanska & Weishampel, 2004), and an emerging source of phylogenetic information (e.g., Arbour & Currie, 2013; 2016). Although the skeletally mature pattern of cranial ornamentation may take the form of a series of variably shaped and sized polygons (referred to as caputegulae; Blows, 2001; see also Arbour & Currie, 2013), in some species these discrete features are not present. Regardless of the pattern formed, cranial ornamentation appears to form as a result of two potentially congruent processes: the coossification of overlying osteoderms with the skull, and the exaggerated outgrowth of individual cranial elements (Vickaryous, Russell & Currie, 2001; Hill, Witmer & Norell, 2003). The cranial material described here provides a rare opportunity to investigate the contribution of each of these processes in a European nodosaurid.

Using size as a proxy for age, we interpret the described specimens as representing a partial ontogenetic series of *Hungarosaurus* (Fig. 2-4). The smallest specimen (MTM V.2003.12; estimated total skull length ~15-17 cm) is approximately half the size of the largest (the holotype and MTM PAL 2013.23.1; estimated total skull length ~34-36 cm). A fourth skull (MTM PAL 2020.32.1.; estimated total skull length ~25 cm), is intermediate in size. Our findings reveal that cranial ornamentation, in the form of rugose texturing across the premaxilla and nasal, ~~and~~ as well as a sharp crest-like ridge along the postorbital, is already present in the smallest (= ontogenetically youngest) individuals examined. Although the pattern of cranial ornamentation changes as the individual gets larger, we found no evidence for the fusion or coossification of osteoderms with the underlying skull.

In *Hungarosaurus*, the smallest (= ontogenetically youngest) specimens have a more well-defined pattern of cranial ornamentation compared to larger (and presumably older) specimens. For example, the premaxilla of the smallest specimen has a more deeply pitted rugosity profile when compared to the larger specimens. Similarly, the pattern of small pits and grooves across the prefrontal-supraorbital-frontal complex and the parietal is more obvious on the smallest specimen. And while the nasal bone also demonstrates a well-developed pattern of transversely oriented pattern of hummocky rugosity, in smaller specimens these features form an anteriorly imbricated or shingle-like arrangement. In larger individuals this angled profile is replaced by a more flattened surface but still retains the hummocky rugosity. These specimens suggest that the size of this rugosity relative to the nasal did not change in later phases of ontogeny, i.e. the same level of ornamentation was present but on a larger element. In addition sexual dimorphism, as an explanation for the difference of relative size and arrangemnet of ornaments, cannot be excluded.

One of the most characteristic features of *Hungarosaurus* is the formation of a well-defined crest-like caputegulum on the postorbital. This structure is present in the smallest specimens (MTM PAL 2020.32.1., MTM 2007.28.1, Fig. 4D-G), suggesting that it develops relative early during ontogeny, similar to the supraorbital horns of ceratopsians (Horner & Goodwin, 2006). MicroCT images reveal no evidence that this crest is formed by the coossification of multiple elements. As for other features of cranial ornamentation, the morphology of the postorbital crest changes during ontogeny. In the smallest specimens, the shape of the postorbital crest is more acute compared with larger (and presumably ontogenetically older) individuals. Near the margin of the orbit, the postorbital demonstrates a pronounced basal sulcus or 'lip' (sensu Hieronymus et al., 2009, Fig. 4D-G). Although this feature was previously characterized as a fused osteoderm (Ősi et al., 2012), it is reinterpreted here as evidence for a cornified sheath. A similar, well demarcated basal sulcus on the postorbital has also been reported for *Euoplocephalus* (Vickaryous, Russell & Currie, 2001).

Osteoderms do not contribute to the cranial ornamentation across the skull of *Hungarosaurus*. Our microCT data ~~do~~ does not reveal any evidence that the cranial elements received a separate superifical contribution of bone, and there are no signs of osteoderms superimposed across sutural boundaries. Consequently, we ~~predict~~ infer that the cranial ornamentation in *Hungarosaurus*, similar to the basal ankylosaurid *Cedarpelta*, is the result of elaborated (exaggerated or exostotic) outgrowth of individual cranial elements. The development of elaborated outgrowth on individual skull bones is also reported for non-ankylosaur ankylosauromorphs such as *Scelidosaurus* and *Emausaurus* (Norman, 2019). In contrast, among some ankylosaurine ankylosaurids (e.g. *Euoplocephalus*, *Pinacosaurus*), and some species of modern squamates (e.g. scincids, cordylids, helodermatids; Maisano et al., 2019, Table 2), the coossification of osteoderms does contribute to the formation of cranial ornamentation (Vickaryous, Russell & Currie, 2001; Hill, Witmer & Norell, 2003).

Was cranial ornamentation of *Hungarosaurus* sexually dimorphic?

Although fused osteoderms to cranial bones have been reported in a few ceratopsids, e.g. *Triceratops* (the epinasal horn, Horner & Goodwin, 2006) and some ankylosaurids (Vickaryous, Russell & Currie, 2001; Hill, Witmer & Norell, 2003), in most relevant clades of dinosaurs (e.g. theropods, hadrosaurs, other ceratopsians, pachycephalosaurs) the cranial ornaments appear to be exclusively the result of elaboration of cranial bones. References needed. Our study revealed that this was also the case in the nodosaurid ankylosaur *Hungarosaurus* ~~as well~~. In addition, the specimens we examined also showed that cranial ornamentation changes during ontogeny. Whether cranial ornamentation is a sexually selected or dimorphic trait remains unclear, owing to the limited number of specimens. Among the ornamented elements described herein, we did find differences in size and shape, although this variation cannot be separated from changes in body size. However, the potential use of these features as dimorphic signals cannot be ruled out. For example, the postorbital crest of the holotype and MTM V 2010.1.1. encircle more of the orbit, both dorsally and caudally, than those of MTM PAL 2020.32.1. and MTM 2007.28.1. (Fig. 4D-G). Though the latter specimens are from much smaller individuals, it remains possible that the different morphologies represent dimorphism.

Dimorphism of cranial ornamentations in fossil archosaurs has already been suggested, for example, in pterosaurs (Bennett, 1992; 2001; Naish & Martill, 2003), ceratopsian dinosaurs (Lehman, 1990; Sampson, Ryan & Tanke, 1997; Knell & Sampson, 2011, Borkovic, 2013; Hone & Naish, 2013) and the ankylosaurid *Pinacosaurus* (Godefroit et al., 1999). In most cases, however, the limited number of specimens or preservation of the cranial remains was ~~far enough from~~ insufficient in establishing firm conclusions (? but see Bennett, 1992).

Although the phenomenon of dimorphic cranial ornamentation among extant sauropsid reptiles has been documented, the overall function of the various horns, crests, and polygonal-ornaments remains poorly understood. Among lizards and birds, monomorphic and dimorphic forms of cranial ornamentation exist, with dimorphic ~~species~~ forms being rarer (e.g. agamids, corytophanids, chameleons, some anatids, cracids or bucerotids, see Table 2.). While skull ornamentation in birds is solely the result of cranial elaboration (Mayr, 2018), osteoderm fusion is common to many groups of lizards (e.g. xenosaurids, helodermatids, Moss, 1969; Montanucci, 1987; Etheridge & de Queiroz, 1988). However, with the possible exception of the marine iguana, dimorphic cranial ornamentation appears to be restricted to the species exaggerating the outgrowth of individual elements. Fossil and extant examples have made it clear that cranial ornamentation is highly varaible, and that using these features as taxonomic characteristics should be viewed with caution (Godefroit et al., 1999; Martill & Naish 2006). Future work on the cranial ornamentation of recent forms may bring us closer to the understanding of the cranial ornamentation of fossil taxa as well.

Conclusions

The Santonian nodosaurid *Hungarosaurus* is represented by multiple individuals, including a partial ontogenetic series. As for other ankylosaurs, the skull of *Hungarosaurus* is characterized by cranial ornamentation ?only. This osseous ornamentation is restricted to individual elements, and does not appear to include the incorporation of osteoderms similar to the basal ankylosaurids *Cedarpelta* and *Gastonia*, and the ankylomorphan ?see previous comment *Scelidosaurus*. Cranial ornamentation was already well-formed in the smallest (= youngest) individuals. Although the role of ankylosaur cranial ornamentation in species recognition and/or sexual dimorphism cannot be ruled out, a larger sample size is needed to test these predictions.

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Supplementary data to the manuscript entitled:

Cranial ornamentation in the Late Cretaceous nodosaurid ankylosaur *Hungarosaurus*

Attila Ősi*[1], János Magyar[1], Károly Rosta[2], Matthew Vickaryous[3]

Two of the specimens (MTM PAL 2020.31.1., MTM PAL 2020.32.1.) used in this study have not been osteologically described and taxonomically assigned yet. Here we give a detailed comparative osteological description to support the taxonomic assignment of these specimens.

Description, comparison and taxonomic assignment of the two new skulls

1) MTM PAL 2020.31.1.

This skull (estimated length between 26-32 cm) consists of most of the rostrum including the premaxillae, nasals, the right fragmentary maxilla and the right frontal-supraorbital-?prefrontal-?lacrimal complex (Suppl. Fig. 1). Premaxillae and nasals ~~did~~ do not fuse to each ① other resulting in clearly observable sutural surfaces. Dorsomedial compression and pre-depositional weathering strongly eroded the outer suface of the bones preventing the clear identification of cranial ornamentation. Only the premaxillae ~~show~~ shows some of ② the original texture of ornamentation. The dorsoventrally as high as mediolaterally wide, ③ large, ④ inverted U-shaped premaxillary notch, being a diagnostic feature of *Hungarosaurus* (Ősi et al. 2019), is present on MTM PAL 2020.31.1. ⑤ Other features, such as the ventrally concave, anterolaterally and laterally rounded cutting margin, the elongate nasal processes (Suppl. Fig. 1C, D), the anteroventrally oblique shelf of the external nares, and the presence of premaxillary alveoli are ~~all~~ also featues shared with *Hungarosaurus*. The posterior end of the nasal process is

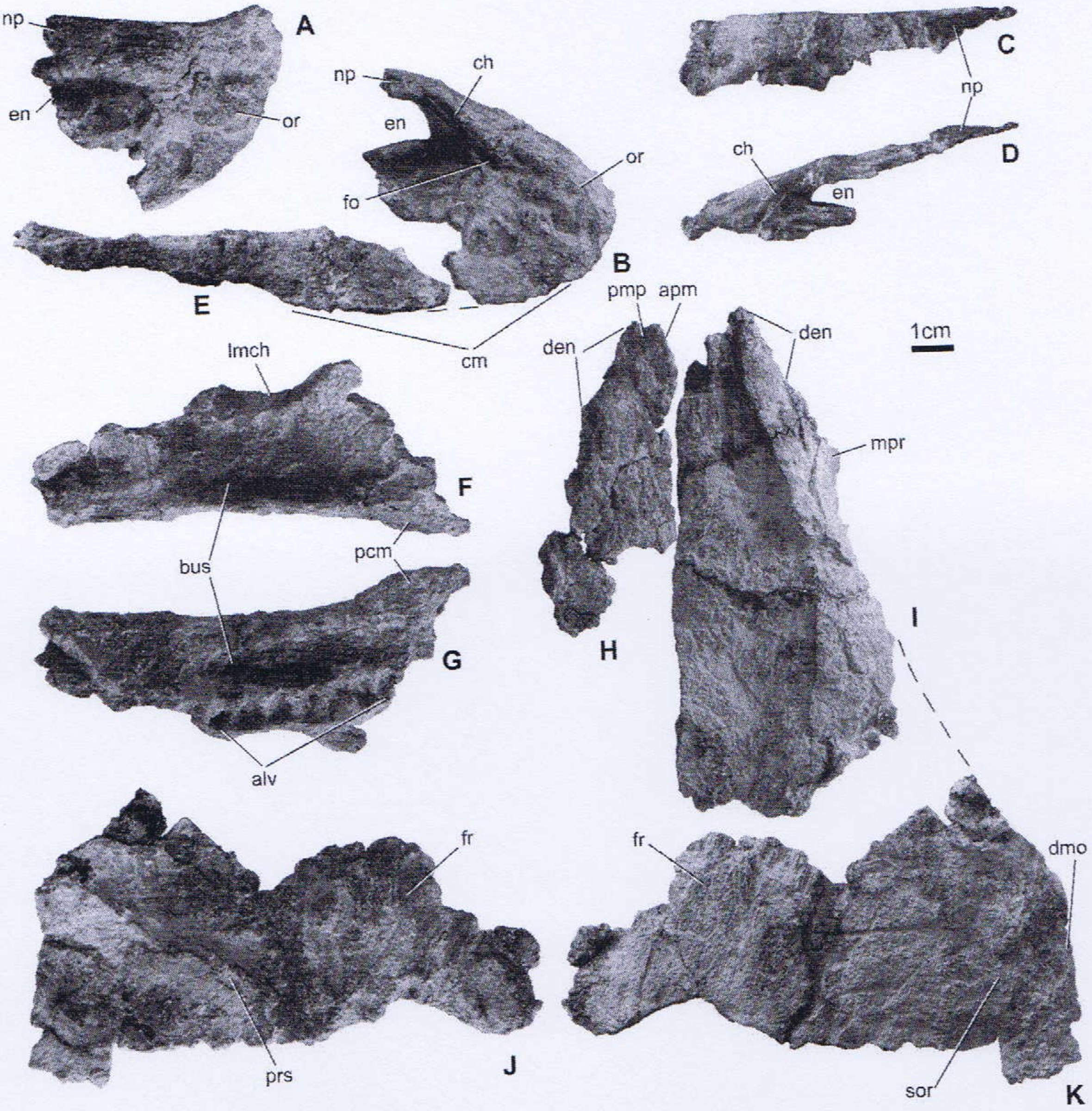

Figure 1. Partial skull MTM PAL 2020.31.1. referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. A, right premaxilla in dorsal, B, lateral view. C, left premaxilla in dorsal, D, lateral view. E, right maxilla in lateral, F, dorsal, G, ventral view. H, left nasal in dorsal view. I, right nasal in dorsal view. J, interorbital part of the skull roof in ventral, K, dorsal view. Abreviations: alv, alveoli; apm, articular surface for premaxilla; bus, buccal shelf; ch, channel; cm, cutting margin; den, dorsal margin of external nares; dmo, dorsal margin of the orbit; en, external nares; fo, foramen; fr, frontal; lmch, lateral margin of choana; mpr, maxillary process of nasal; np, nasal process; or, orbit; pcm, posterior end of cutting margin; pmp, premaxillary process of nasal; prs, preocular shelf; sor, supraorbital.

completely preserved on the left premaxilla having a triangular, very pointed tip (Suppl. Fig. 1C, D) that slightly overlaps the anterodorsomedial margin of the left nasal. Close to the basal part of the nasal process both premaxillae have a ventrally, anteroventrally oriented, laterally opened channel that breaks thorough the premaxilla (Suppl. Fig. 1B) and on the ventral side, ⑥ it opens into a relatively large (3-4 mm in diameter) foramen. This feature cannot be seen on the holotype of *Hungarosaurus*, ~~that~~ and as such might be an ontogenetic or sexual difference. However, it seems to be present on an even smaller, isolated premaxilla (MTM V 2003.12., Ősi and Makádi 2009) suggesting that it might have had the function to supply the ontogenetically growing ornamentation in this region. ⑦

Of the two nasals, the right one is more complete being more than twice as long as wide. Anteriorly it becomes narrow to connect to the premaxilla, laterally it curves ventrally to connect with the maxilla and posteriorly it is ~~the~~ widest, with some slightly eroded scarf joints on its medioventral surface (Suppl. Fig. 1H, I). The internasal suture is a straight, slightly waving, ca. 3 mm thick surface ⑧. Its outer surface is strongly weathered. The anterior part of the left nasal is better preserved having a rounded anterolateral margin bordering dorsally the external nares. ~~This~~ The smaller specimen (Suppl. Fig. 1H) is almost identical with the left nasal of the holotype of *Hungarosaurus*.

The fragmentary right maxilla has an anteriorly slightly widening morphology (Suppl. Fig. 1F, G). Anterolaterally the ventral side of the maxilla forms the posteriorly widened cutting margin of the premaxilla. Eight alveoli ~~is~~ are preserved in the maxilla, but the posterior half of the alveolar row is missing suggesting at least the double this number of alveoli. This bone is also compressed dorsomedially, but has a significant buccal shelf (1.5-2 cm wide lateromedially), lateral to the alveolar row as is present ~~as~~ in most ankylosaurs (Vickaryous et al. 2004). Mediodorsal to the anterior alveoli, is a 1 cm long process which curves anterodorsally. ~~that could have been~~ This may represent the anteriormost margin of the choana.

A large part of the anterior skull roof between the orbits is preserved. Its strongly weathered (and relatively thin with max. thickness of 4-6 mm) outer surface is not too informative but laterally and anterolaterally it preserves the dorsal and anterodorsal margin of the orbit. No crest or other distinctive cranial ornamentation is present on this part of the orbital margin. The posterior section of the orbit, present in the holotype of *Hungarosaurus*, is not preserved for MTM 2020.31.1 ~~here~~ (Suppl. Fig. 1K) thus the presence or absence of a postorbital crest is unkown. Ventrally the preocular shelf extends into the anteroventrally bending, anterodorsal corner of the orbital rim (Suppl. Fig. 1J). Sutures between the individual cranial elements on this piece of bone cannot be observed, but according to the position of this element most of the right prefrontal-supraorbital-frontal complex is preserved. ⑩

Since there are no ~~overlapping~~ corresponding elements with any of the ~~fragmentary skulls~~ cranial material of *Struthiosaurus* spp. (Seeley 1881, Nopcsa 1929, Pereda-Suberbiola and Galton 1994, 2001), the preserved elements of MTM PAL 2020.31.1. only allow ~~to compare it only~~ comparisons with those of *Hungarosaurus*. Most of the rostrum of this form MTM 2020.31.1 ? is poorly known as well, and only the premaxilla and anterior end of the nasal can be compared. As mentioned earlier, these bones are extremely similar to the bones found in the holotype of *Hungarosaurus* and no different features can be recognized except for the channel dorsoventrally crossing the premaxilla. ~~According to~~ Based on these features, the most parsimonious scenario is to herein refer MTM PAL 2020.31.1. to *Hungarosaurus tormai*, ~~until more complete material helps for a better identification~~. "I don't think this last bit is really necessary"

2) MTM PAL 2020.32.1.

This specimen represents the smallest among the four skulls. It consists of the partial basicranium, most of the skull roof between and ~~behind~~ posterior to the orbits, the two nasals, the left postorbital, left squamosal, most of the left quadrate and the distal end of the right quadrate (Suppl. Fig. 2).

In contrast to MTM PAL 2020.31.1., this specimen is ~~well~~ better preserved showing many details of the cranial ornamentation on the dorsal elements. The specimen is slightly compressed dorsoventrally thus the basicranium was pushed into braincase. Posterior to the frontal all bones of the skull roof, braincase and orbital region are completely fused and no sutures can be recognized (Suppl. Fig. 2A, B). Although the two nasals are preserved together, the bones are not fused to each other. Neither are they fused to the maxillae and the postnasal ? bones as it can be seen by the overlapping articulation surfaces preserved on the nasals.

⑪ Nasals are anteroposteriorly two times longer than wide (though anteriorly not completely preserved), dorsally highly ornamented (for details see main text), trapezoid elements. In the nasal-frontal contacts the nasals overlap the anterior process of the frontals (Suppl. Fig. 2A, B). Similar sutural contact can be ~~supposed~~ assumed between the nasal and prefrontal, ~~though~~ despite the prefrontals ~~are not~~ not being preserved, ~~only~~ as the posterolaterally facing, wedge-like articulation surfaces of the nasals suggest this condition (Suppl. Fig. 2B). An ~~I~~interfrontal suture ⑫ may be present between the anterior part of the bones (also seen weekly on the ventral side), but cranial ornamentation mostly masks it. The anterior part of the nasals are not preserved preventing comparison with that of the holotype of *Hungarosaurus*.

The dorsal surface of the skull roof is highly ornamented. The parietal region is highly vaulted, as seen ~~both~~ in *Struthiosaurus* spp. (reference), a referred specimen of *Hungarosaurus* (MTM PAL 2013.23.1.) ~~or in~~ and *Pawpawsaurus* (Lee 1996). The supraoccipital is strongly fused with the parietal and exoccipitals, it bears a short saggital crest. remove extra space Laterodorsal to the foramen magnum, the exoccipital bears an oval, dorsally-posterodorsally facing protuberance, similar to that of MTM PAL 2013.23.1. The condylus occipitalis is wider than high but rather

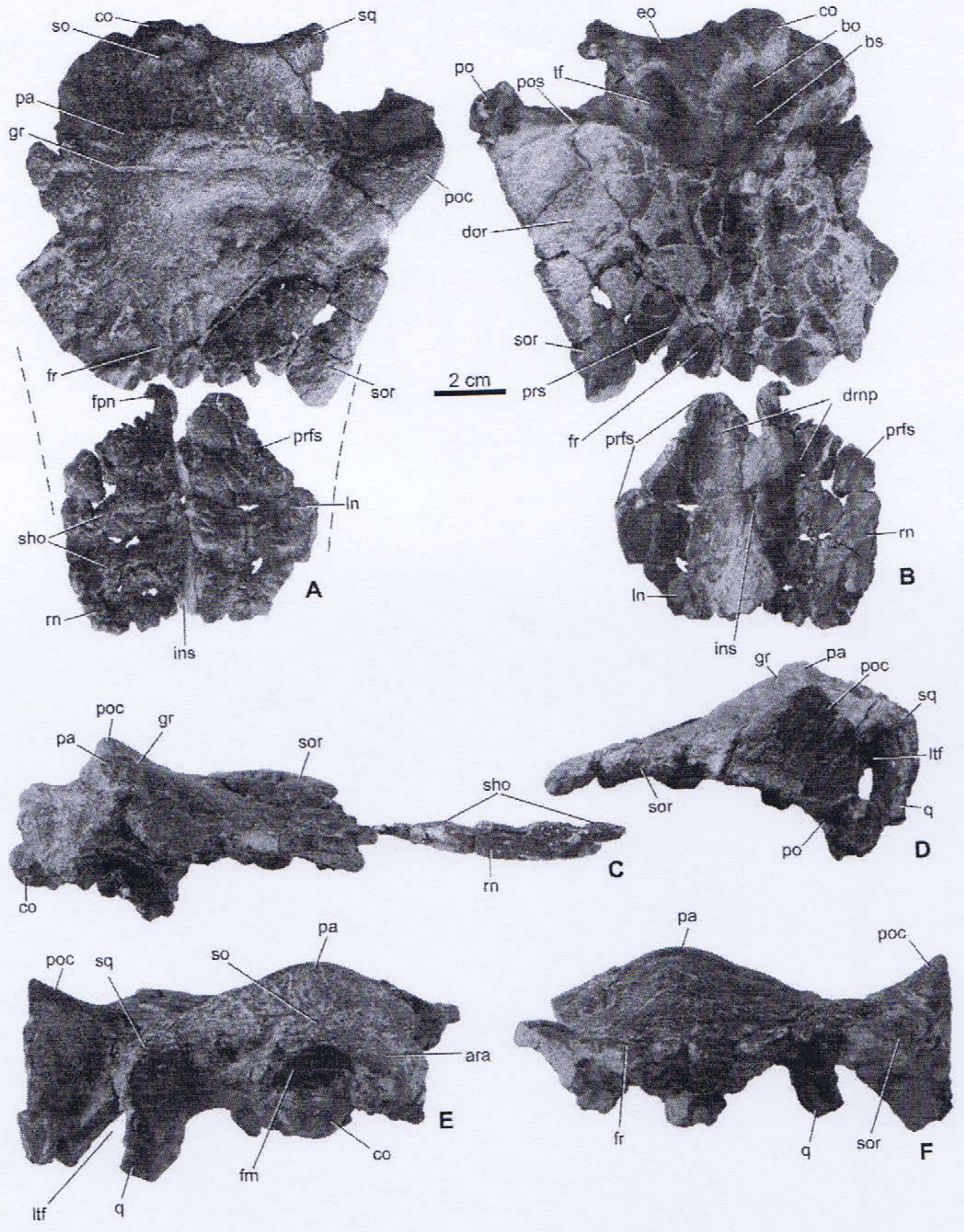

Figure 2. Partial skull MTM PAL 2020.32.1. referred to *Hungarosaurus tormai* from the Santonian of Iharkút, Hungary. A, skull roof and nasals in dorsal, B, ventral, C, right lateral view. D, posterior part of the skull in left lateral, E, posterior, F, anterior view. Abbreviations: ara, articular surface of atlas; bo, basioccipital; bs, basisphenoid; co, condylus occipitalis; dor, dorsal orbital rim; drnp, dorsal rim of narial passage; eo, exoccipital; fm, foramen magnum; fpn, frontal process of nasal; fr, frontal, gr, groove; ins, internasal suture; ln, left nasal; ltf, lateral temporal fenestra; m, maxilla; pa, parietal; po, postorbital; poc, postorbital crest; pos, postocular shelf; prfs, prefrontal suture; prs, preocular shelf; q, quadrate; rn, right nasal; sho, shingled ornamentation; so, supraoccipital; sor, supraorbital; sq, squamosal; tf, temporal fossa.

triangular and heart-shaped in posterior-posteroventral view. This is ~~being~~ slightly different from the ventrally rounded condyle of the holotype of *Hungarosaurus* and ~~or that of~~ MTM PAL 2013.23.1., It ~~but~~ also differs from that of *Struthiosaurus*. The exoccipital-squamosal-quadrate region is a massively fused, L-shaped block. In dorsal view, the squamosal is laterally-posterolaterally oriented and bears no significant ornamentation; only some rugose texture can be seen mediodorsally (Suppl. Fig. 2E), extending towards the exoccipital that might have been served for the attachment of the dorsal neck muscles. ⑬

The dorsal and posterodorsal part of the left orbital region is preserved in MTM PAL 2020.32.1.x Ventrally the orbital fossa is bordered by the posterolaterally extending postocular shelf and anterolaterally by the preocular shelf (Suppl. Fig. 2B). The postorbital bears an anteroposteriorly elongate crest that is relatively shorter and higher than the crest of the holotype of *Hungarosaurus* and ~~or that of~~ MTM 2010.1.1.x However, an isolated postorbital crest (MTM 2007.28.1.) from Iharkút shows similar size and morphology. Anterior to the postorbital crest is a slightly ventrally bending, dorsally ornamented rim ~~is present~~. In lateral view, this margin extends far anteriorly resulting in an abruptly long dorsal margin, consequently ~~and would~~ resulting an enormous orbit. Though the skull was certainly compressed dorsoventrally the pre- and postocular shelfs are at a near vertical ~~really high~~ angle (ca. 85-90°), further suggesting ~~the~~ large sized orbits ~~size of the orbits.~~

One of the quadrates shows the typical L-shape in posterior view, separating proximally the lateral temporal fenestra from the label on image posttemporal fenestra (Suppl. Fig. 3B). Mandibular condyle is complete on the right and fragmentary on the left quadrate. The mandibular articulation surface, though much smaller than the type of *Hungarosaurus* or that of *Struthiosaurus* spp. (PIUW 2349, BMNH R 4966), it is more similar to that of *Hungarosaurus* in having a rather rhomboidal than oval shape in distal view (Suppl. Fig. 3C, E). Furthermore, the lateral

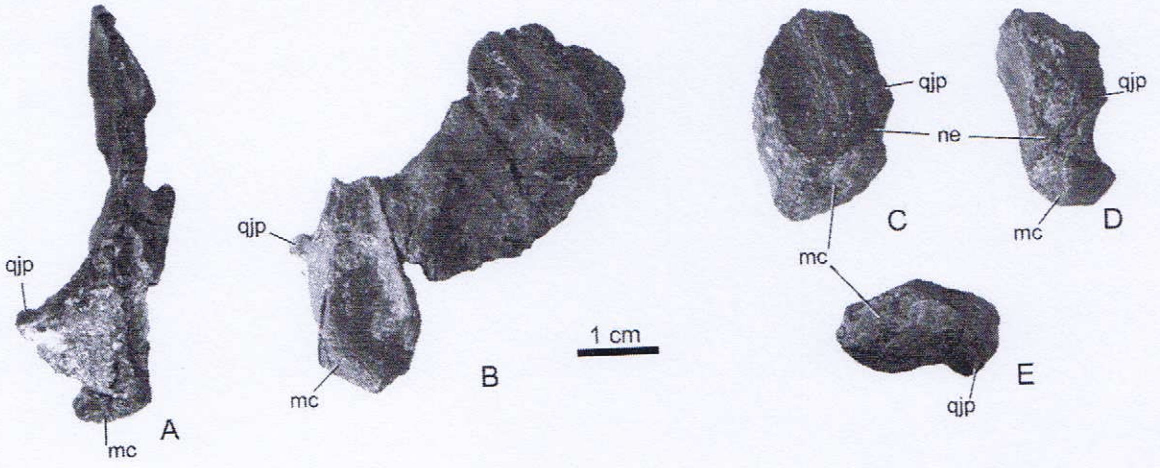

Figure 3. Quadrates of MTM PAL 2020.32.1. referred to *Hungarosaurus* from the Santonian of Iharkút, Hungary. A, left qadrate inlateral, B, posterior view. C, distal part of the right quadrate in posterior, D, lateral, E, distal view.

condyle of the quadrate is separated by a distinct neck from the quadratojugal process (Suppl. Fig. 3C, D), in contrast with the continuous, rounded edge seen in *Struthiosaurus* (BMNH R 4966).

Based on ~~From~~ the diagnostic characters of *Hungarosaurus tormai*, the postorbital bearing a high and anterodorsal–posteroventrally elongated crest and the mandibular quadrate condyle having rhomboidal articular surface (Ősi et al. 2019), though slightly differently, are present on MTM PAL 2020.32.1. These differences, furthermore the relatively large-sized orbits and the unfused preorbital bones are in accordance with the relatively small size of the skull (estimated length between 20-23 cm), suggesting a subadult ontogenetic stage. Based on these characters we refer this specimen to *Hungarosaurus tormai* most probably representing an ontogenetically immature animal. ⑭