Cranial ornamentation in the Late Cretaceous nodosaurid ankylosaur *Hungarosaurus* (#53928)

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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.

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Key words: skull; *Hungarosaurus*, ankylosaur; cranial ornamentation; osteoderm fusion; cranial elaboration; sexual dimorphism; Late Cretaceous

ABSTRACT

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*[illegible]ased 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.

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 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 skul loss, 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 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 clade Ankylosauria (Maryanska, 1977; Coombs, 1978; Carpenter et al., 2001; Vickaryous, Maryanska & 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 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). 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 basal taxa *Cedarpelta* (Carpenter et al., 2001) and *Gastonia* (Kinneer, Carpenter & Shaw, 2016). Hence, cranial ornamentation in these species appears to be exclusively the result of elaborated outgrowth of individual elements. 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 rospids (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 ain embedded within the skin and thus not directly contact the skull, or may partially or ~~even~~ completely fused h the underlying elements (Maisano et al., 2019). With a partial ion, 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 g., Maisano et al., 2019). As a consequence of developing with 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 demonstrates considerable taxonomic ation (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 osteoderm have only been reported for aged marine iguanas (*Amblyrhynchus cristatus*; Etheridge & de Queiroz, 1988). 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 nifests 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* l s 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, 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. *atosuchus* Schmidt, 1938; Bartels, 1984, I chu, 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 nany 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 itecture 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 trabecular bone, but is reportedly solid bone in the greater helmeted hornill (*Buceros vigil*) (Gamble, 2007).

To sum up, the fusion of osteoderms to cranial bones characterizes only a few groups of squamates, and is not present in extant archosaurs (Table 2). In terms of cranial ornamentation, almost all these forms are sexually monomorphic and the architecture of oramentation 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 I kút 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 lls (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 n 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 [illegible] 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. [illegible] images were converted to 3D images using 3DF Zephyr software. [illegible] images of bones also show the original t[illegible]ure 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[illegible]e 3D reconstructions of the three [illegible]died skull [illegible] in the video files (Video S1-S6; https://zenodo.org/record/4117812#.X5FfUO28o2w).

Specimens are [illegible] allowed to 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 m[illegible]e in the laboratory of the Carl Zeiss IMT Austria GmbH (Budaörs, Hungary). Scanning of the bones has been made [illegible] 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 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 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 ger 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 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 MTM PAL 2020.31.1., MTM PAL 2020.32.1. and 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), milarly to the premaxillae, nasals are unfused, a feature that is characteristic of skeletally immature ankylosaurs (e.g. *Pinacosaurus*, ZPAL MgD-II, Maryanska, 1977; a juvenile nodosaurid from the Paw Paw Formation, Jacobs al., 1994) and *Kunbarrasaurus* (Molnar, 1996, ahey 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. kull demonstrates evidence of weathering (Fig. 3F) 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[illegible] mm) pits and grooves (1-5 mm). The isolated frontal (Fig. 4B) is ornamented by various small, deep pits and grooves.[illegible]croCT 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 holes 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 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 is more rounded. Using microCT imaging, there is no evidence that these bosses are separate elements from the quadratojugal. 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, 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.

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., 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 specimen 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 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 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 that 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 n 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 ckaryous, Russell & Currie, 2001; Hill, Witmer & Norell, 2003), in mo elevant clades of dinosaurs (e.g. theropods, hadrosaurs, other ceratopsians, pachycephalosaurs) the cranial ornaments appear to be exclusively the result of elaboration of cranial bones ur study revealed that this was 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 number of specimens or preservation of the cranial remains was far enough from 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 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. 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 *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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References

Alexander, G. D., Houston, D. C., & Campbell, M. (1994). A possible acoustic function for the casque structure in hornbills (Aves: Bucerotidae). Journal of Zoology, 233(1), 57-67.

Anderson, R. A., & Vitt, L. J. (1990). Sexual selection versus alternative causes of sexual dimorphism in teiid lizards. Oecologia, 84(2), 145-157.

Arbour, V. M., & Currie, P. J. (2013). *Euoplocephalus tutus* and the diversity of ankylosaurid dinosaurs in the Late Cretaceous of Alberta, Canada, and Montana, USA. PLoS One, 8(5), e62421.

Arbour, V. M., & Currie, P. J. (2016). Systematics, phylogeny and palaeobiogeography of the ankylosaurid dinosaurs. Journal of Systematic Palaeontology, 14(5), 385-444.

Bartels, W. S. (1984). Osteology and systematic affinities of the horned alligator *Ceratosuchus* (Reptilia, Crocodilia). Journal of Paleontology, 1347-1353.

Bennett, S. C. (1992). Sexual dimorphism of *Pteranodon* and other pterosaurs, with comments on cranial crests. Journal of Vertebrate Paleontology, 12(4), 422-434.

Bennett, S. C. (2001). The osteology and functional morphology of the Late Cretaceous pterosaur Pteranodon Part II. Size and functional morphology. Palaeontographica Abteilung A, 113-153.

Bhullar, B. S. (2011). The power and utility of morphological characters in systematics: a fully resolved phylogeny of *Xenosaurus* and its fossil relatives (Squamata: Anguimorpha). Bulletin of the Museum of Comparative Zoology, 160(3), 65-181.

Bickelmann, C., & Klein, N. (2009). The late Pleistocene horned crocodile *Voay robustus* (Grandidier & Vaillant, 1872) from Madagascar in the Museum für Naturkunde Berlin. Fossil Record, 12(1), 13-21.

Blows W. T. (2001). Dermal armor of the polacanthine dinosaurs. In Carpenter, K. (Ed.). The Armored Dinosaurs. Bloomington: Indiana University Press, pp. 363-385.

Borkovic, B. (2013). Investigating sexual dimorphism in Ceratopsid Horncores. Unpublished Master's thesis, University of Calgary, Calgary, Canada, 203 pp.

Botfalvai, G., Ősi, A., & Mindszenty, A. (2015). Taphonomic and paleoecologic investigations of the Late Cretaceous (Santonian) Iharkút vertebrate assemblage (Bakony Mts, northwestern Hungary). Palaeogeography, Palaeoclimatology, Palaeoecology, 417, 379-405.

Botfalvai, G., Prondvai, E., & Ősi, A. (2020). Living alone or moving in herds? A holistic approach highlights complexity in the social lifestyle of Cretaceous ankylosaurs. Cretaceous Research, 118, 104633.

Botfalvai, G., Haas, J., Bodor, E. R., Mindszenty, A., & Ősi, A. (2016). Facies architecture and palaeoenvironmental implications of the Upper Cretaceous (Santonian) Csehbánya formation at the Iharkút vertebrate locality (Bakony Mountains, Northwestern Hungary). Palaeogeography, Palaeoclimatology, Palaeoecology, 441, 659-678.

Brochu, C. A. (2006). A new miniature horned crocodile from the Quaternary of Aldabra Atoll, western Indian Ocean. Copeia, 2006(2), 149-158.

Brochu, C. A. (2007). Morphology, relationships, and biogeographical significance of an extinct horned crocodile (Crocodylia, Crocodylidae) from the Quaternary of Madagascar. Zoological Journal of the Linnean Society, 150(4), 835-863.

Brochu, C. A., Njau, J., Blumenschine, R. J., & Densmore, L. D. (2010). A new horned crocodile from the Plio-Pleistocene hominid sites at Olduvai Gorge, Tanzania. PLoS One, 5(2).

Broeckhoven, C., de Kock, C., & Hui, C. (2018). Sexual dimorphism in the dermal armour of cordyline lizards (Squamata: Cordylinae). Biological Journal of the Linnean Society, 125(1), 30-36.

Broeckhoven, C., de Kock, C., & Mouton, P. L. F. N. (2017). Sexual dimorphism in osteoderm expression and the role of male intrasexual aggression. Biological Journal of the Linnean Society, 122(2), 329-339.

Broeckhoven, C., du Plessis, A., & Hui, C. (2017). Functional trade-off between strength and thermal capacity of dermal armor: insights from girdled lizards. Journal of the mechanical behavior of biomedical materials, 74, 189-194.

Buchholz, R. (1991) Older males have bigger knobs: correlates of ornamentation in two species of curassow. Auk 198:153–160

de Buffrénil, V. (1982). Morphogenesis of bone ornamentation in extant and extinct crocodilians. *Zoomorphology*, 99(2), 155-166.

Carpenter, K., Kirkland, J. I., Burge, D., & Bird, J. (2001). Disarticulated Skull of a New Primitive Ankylosaurid from the Lower Cretaceous of Eastern Utah. In Carpenter, K. (Ed.). The Armored Dinosaurs. Indiana University Press, Bloomingron. pp. 318-340.

Čerňanský, A., & Hutchinson, M. N. (2013). A new large fossil species of Tiliqua (Squamata; Scincidae) from the Pliocene of the Wellington Caves (New South Wales, Australia). Alcheringa: An Australasian Journal of Palaeontology, 37(1), 131-136.

Čerňanský, A., & Syromyatnikova, E. V. (2019). The first Miocene fossils of *Lacerta* cf. *trilineata* (Squamata, Lacertidae) with a comparative study of the main cranial osteological differences in green lizards and their relatives. PloS one, 14(8).

Clarac, F., De Buffrenil, V., Brochu, C., & Cubo, J. (2017). The evolution of bone ornamentation in Pseudosuchia: morphological contraints versus ecological adaptation. Biological Journal of the Linnean Society, 121: 395-408

Coombs Jr., W. P. (1971). The Ankylosauria. PhD dissertation, Columbia University, New York, 487 p.

Coombs Jr., W. P. (1978). The families of the ornithischian dinosaur Order Ankylosauria. Palaeontology, 21,143-170.

Doughty, P., & Shine, R. (1995). Life in two dimensions: natural history of the southern leaf-tailed gecko, *Phyllurus platurus*. Herpetologica, 51, 193-201.

Eastick, D. L., Tattersall, G. J., Watson, S. J., Lesku, J. A., & Robert, K. A. (2019). Cassowary casques act as thermal windows. Scientific Reports, 9(1), 1-7.

Eckhardt, F. S., Gehring, P. S., Bartel, L., Bellmann, J., Beuker, J., Hahne, J., Korte, V., Knittel, M., Mensch, D., Nagel, M., Vences, C., Rostosky, V., Vierath, V., Wilms, J. Zenk & Pohl, M. (2012). Assessing sexual dimorphism in a species of Malagasy chameleon (*Calumma* *boettgeri*) with a newly defined set of morphometric and meristic measurements. Herpetology Notes, 5, 335-344.

Eibl-Eibesfeldt, I. (1966). The fighting behaviour of marine iguanas. Philosophical Transactions of the Royal Society B: Biological Sciences, 251, 475-476.

Etheridge, R., & de Queiroz, K. (1988). A phylogeny of Iguanidae. In Estes R., & Pergil, G. (Eds.) Phylogenetic relationships of the lizard families, Essays Commemorating Charles L. Camp, pp. 283-367.

Evans, R. M., & Knopf, F. L. (1993). American white pelican (*Pelecanus erythrorhynchos*). In Poole, A. & Gill, F. (Eds.), The birds of North America No. 57. American Ornithologists Union, Washington, DC.

Flemming, A., Bates, M., & Broeckhoven, C. (2018). The relationship between generation gland morphology and armour in Dragon Lizards (*Smaug*): a reassessment of ancestral states for the Cordylidae. Amphibia-Reptilia, 39(4), 457-470.

Fraga, R. M., & Kreft, S. (2007). Natural history and breeding behavior of the olive (*Psarocolius yuracares*) and yellow-billed (*P. angustifrons alfredi*) oropendolas in Chapare Province, Bolivia. Ornitología Neotropical, 18:251–261.

Gadow, H. (1901). Amphibia and reptiles. The Cambridge natural history. Vol. 8. London, Macmillan, 13(668), 181.

Gaffney, E. S. (1979). Comparative cranial morphology of Recent and fossil turtles. Bulletin of the American Museum of Natural History; v. 164, article 2.

Gamble, K. C. (2007). Internal anatomy of the hornbill casque described by radiography, contrast radiography, and computed tomography. Journal of Avian Medicine and Surgery, 21(1), 38-49.

Garbin, R. C., & Caramaschi, U. (2015). Is the matamata only one species? Morphological variation and color polymorphism in the South American turtle *Chelus fimbriatus* (Schneider, 1783) (Pleurodira: Chelidae). PeerJ PrePrints. 3 (2015), Article e1072.

Godefroit, P., Pereda-Suberbiola, X., Li, H., & Dong, Z. M. (1999). A new species of the ankylosaurid dinosaur Pinacosaurus from the Late Cretaceous of Inner Mongolia (PR China). Bulletin de l'Institut Royal des Sciences Naturelles de Belgique, Sciences de la Terre, 69(Suppl B), 17-36.

González-García, F. (1995). Reproductive biology and vocalizations of the Horned Guan *Oreophasis derbianus* in Mexico. The Condor, 97(2), 415-426.

Green, T., & Gignac, P. (2019). Ontogeny of Southern Cassowary, Maleo, and Helmeted Guinea Fowl Casques: Implications for the Study of Bony Patterning in Non-avian Dinosaur Cranial Ornaments. The FASEB Journal, 33(1_supplement), 452-13.

Hieronymus, T. L., Witmer, L. M., Tanke, D. H., & Currie, P. J. (2009). The facial integument of centrosaurine ceratopsids: morphological and histological correlates of novel skin structures. Anatomical Record, 292(9), 1370-1396.

Hill, R. V., Witmer, L. W. & Norell, M. A. (2003). A new specimen of *Pinacosaurus grangeri* (Dinosauria: Ornithischia) from the Late Cretaceous of Mongolia: ontogeny and phylogeny of ankylosaurs. American Museum Novitates, 3395, 1-29.

Hone, D. W. E., & Naish, D. (2013). The 'species recognition hypothesis' does not explain the presence and evolution of exaggerated structures in non-avialan dinosaurs. Journal of Zoology, 290(3), 172-180.

Horner, J. R., & Goodwin, M. B. (2006). Major cranial changes during *Triceratops* ontogeny. Proceedings of the Royal Society B: Biological Sciences, 273(1602), 2757-2761.

Horrocks, N., Perrins, C., & Charmantier, A. (2009). Seasonal changes in male and female bill knob size in the mute swan *Cygnus olor*. Journal of avian biology, 40(5), 511-519.

Jacobs, L. L., Winkler, D. A., Murry, P. A., & Maurice, J. M. (1994). A nodosaurid scuteling from the Texas shore of the Western Interior Seaway. In Carpenter, K., Hirsch K. F. & Horner J. R. (Eds.). Dinosaur eggs and babies, pp. 337-346.

Jones, I. L. (1993). Sexual differences in bill shape and external measurements of Crested Auklets. The Wilson Bulletin, 105(3), 525-529.

Jouventin, P. & Viot, C. R. (1985). Morphological and genetic variability of Snow Petrels *Pagodroma nivea*. Ibis, 127(4), 430-441.

Kemp, A. C. (2001) Family Bucerotidae (Hornbills). In del Hoyo J, Elliott A, & Sargatal J (Eds.) Handbook of the birds of the world, vol 6. Mousebirds to Hornbills. Lynx Edicions, Barcelona, pp 436–523

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

Kirby, A., Vickaryous, M., Boyde, A., Olivo, A., Moazen, M., Bertazzo, S., & Evans, S. (2020). A comparative histological study of the osteoderms in the lizards *Heloderma suspectum* (Squamata: Helodermatidae) and *Varanus komodoensis* (Squamata: Varanidae). Journal of anatomy, 236(6), 1035-1043.

Klembara, J., Dobiašová, K., Hain, M., & Yaryhin, O. (2017). Skull anatomy and ontogeny of legless lizard *Pseudopus apodus* (Pallas, 1775): heterochronic influences on form. The Anatomical Record, 300(3), 460-502.

Knell, R. J., & Sampson, S. D. (2011). Bizarre structures in dinosaurs. Journal of Zoology, 283, 18-22.

Kopij, G. (1998). Behavioural patterns in the Southern Bald Ibis (Geronticus calvus) at breeding sites. Vogelwarte, 39, 248-263.

Lang, M. (1989). Phylogenetic and Biogeographic Patterns of Basiliscine Iguanians. Bonner Zoologische Monographien, Nr. 28, Herausgeber: Zoologisches Forschungsinstitut und Museum Alexander Koening, Bonn, p. 172.

Laver, R. J., Morales, C. H., Heinicke, M. P., Gamble, T., Longoria, K., Bauer, A. M., & Daza, J. D. (2020). The development of cephalic armor in the tokay gecko (Squamata: Gekkonidae: *Gekko gecko*). Journal of morphology, 281(2), 213-228.

Leahey, L. G., Molnar, R. E., Carpenter, K., Witmer, L. M., & Salisbury, S. W. (2015). Cranial osteology of the ankylosaurian dinosaur formerly known as *Minmi* sp. (Ornithischia: Thyreophora) from the Lower Cretaceous Allaru Mudstone of Richmond, Queensland, Australia. PeerJ, 3, e1475.

Ledesma, D. T., & Scarpetta, S. G. (2018). The skull of the gerrhonotine lizard *Elgaria panamintina* (Squamata: Anguidae). PloS one, 13(6), e0199584.

Lee, Y. N. (1996). A new nodosaurid ankylosaur (Dinosauria: Ornithischia) from the Paw Paw Formation (late Albian) of Texas. Journal of Vertebrate Paleontology, 16(2), 232-245.

Lehman, T. M. (1990). The ceratopsian subfamily Chasmosaurinae: sexual dimorphism and systematics. In Currie P. J. & Carpenter k. (Eds.). Dinosaur systematics symposium, pp. 211-229.

Levrat-Calviac, V., & Zylberberg, L. (1986). The structure of the osteoderms in the gekko: *Tarentola mauritanica*. American Journal of Anatomy, 176(4), 437-446.

Lindén, H., & Väisänen, R. A. (1986). Growth and sexual dimorphism in the skull of the Capercaillie *Tetrao urogallus*: a multivariate study of geographical variation. Ornis Scandinavica, 85-98.

Lowe, P. R. (1916) Studies on the Charadriiformes. IV. An Additional note on the Sheath-bills: Some points in the osteology of the skull of an embryo of *Chionarchus* "*minor*" from Kerguelen.—V. Some notes on the Crab-Plover (Dromas ardeola Paykull). Ibis 58:313–337.

Lüps, P. (1990) Wozu besitzen Höckerschwäne Cygnus olor. Höcker? Der Ornithologische Beobachter, 87:1–11

Maisano, J. A., Bell, C. J., Gauthier, J. A., & Rowe, T. (2002). The osteoderms and palpebral in *Lanthanotus borneensis* (Squamata: Anguimorpha). Journal of Herpetology, 36(4), 678-682.

Maisano, J. A., Laduc, T. J., Bell, C. J., & Barber, D. (2019). The cephalic osteoderms of Varanus komodoensis as revealed by high-resolution X-ray computed tomography. The Anatomical Record, 302(10), 1675-1680.

Martill, D. M., & Naish, D. (2006). Cranial crest development in the azhdarchoid pterosaur *Tupuxuara*, with a review of the genus and tapejarid monophyly. Palaeontology, 49(4), 925-941.

Maryanska, T. (1977). Ankylosauridae (Dinosauria) from Mongolia. Palaeontologia Polonica, 37,85-151.

Mayr, G. (2018). A survey of casques, frontal humps, and other extravagant bony cranial protuberances in birds. Zoomorphology, 137(3), 457-472.

Mead, J. I., Schubert, B. W., Wallace, S. C., & Swift, S. L. (2012). Helodermatid lizard from the Mio-Pliocene oak-hickory forest of Tennessee, eastern USA, and a review of monstersaurian osteoderms. Acta Palaeontologica Polonica, 57(1), 111-121.

Molnar, R. E. (1996). Preliminary report on a new ankylosaur from the Early Cretaceous of Queensland, Australia. Memoirs of the Queensland Museum, 39, 653-668.

Montanucci, R. R. (1987). A phylogenetic study of the horned lizards, genus *Phrynosoma*, based on skeletal and external morphology. Contrib. in science/Natural history museum of Los Angeles county, 113, 1–26.

Moss, M. L. (1969). Comparative osteology of dermal sclerifications in reptiles. Acta anatomica, 73, 510-533.

Naish, D., & Martill, D. M. (2003). Pterosaurs- a successful invasion of prehistoric skies. Biologist, 50(5), 213–216.

Naish, D., & Perron, R. (2016). Structure and function of the cassowary's casque and its implications for cassowary history, biology and evolution. Historical Biology, 28(4), 507-518.

Nance, H. A. (2007). Cranial osteology of the African gerrhosaurid *Angolosaurus skoogi* (Squamata; Gerrhosauridae). African Journal of Herpetology, 56(1), 39-75.

Norman, D. B. (2020). *Scelidosaurus harrisonii* from the Early Jurassic of Dorset, England: cranial anatomy. Zoological Journal of the Linnean Society, 188(1), 1-81.

Otto, H. (1909). Die Beschuppung der Brevilinguier und Ascalaboten. Jena Z Naturwiss, 44, 193–252.

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

Ősi, A., & Makádi, L. (2009). New remains of *Hungarosaurus tormai* (Ankylosauria, Dinosauria) from the Upper Cretaceous of Hungary: skeletal reconstruction and body mass estimation. Paläontologische Zeitschrift, 83(2), 227-245.

Ősi, A., & Pereda-Suberbiola, X. (2017). Notes on the pelvic armor of European ankylosaurs (Dinosauria: Ornithischia). Cretaceous Research, 75, 11-22.

Ősi, A., Pereda-Suberbiola, X., & Földes, T. (2014). Partial skull and endocranial cast of the ankylosaurian dinosaur Hungarosaurus from the Late Cretaceous of Hungary: implications for locomotion. Palaeontologia Electronica, Article-nr.

Ősi, A., & Prondvai, E. (2013). Sympatry of two ankylosaurs (*Hungarosaurus* and cf. *Struthiosaurus*) in the Santonian of Hungary. Cretaceous Research, 44, 58-63.

Ősi, A., Rabi, M., Makádi, L., Szentesi, Z., Botfalvai, G., Gulyás, P., & Godefroit, P. (2012). The Late Cretaceous continental vertebrate fauna from Iharkút (Western Hungary): a review. Bernissart Dinosaurs and Early Cretaceous Terrestrial Ecosystems. Indiana University Press, Bloomington, 532-569.

Ősi, A., Botfalvai, G., Albert, G., & Hajdu, Z. (2019). The dirty dozen: taxonomical and taphonomical overview of a unique ankylosaurian (Dinosauria: Ornithischia) assemblage from the Santonian Iharkút locality, Hungary. Palaeobiodiversity and Palaeoenvironments, 99(2), 195-240.

Paluh, D. J., Griffing, A. H., & Bauer, A. M. (2017). Sheddable armour: identification of osteoderms in the integument of *Geckolepis maculata* (Gekkota). African Journal of Herpetology, 66(1), 12-24.

Parks, W. A. (1924). *Dyoplosaurus acutosquameus*: a new genus and species of armoured dinosaur; and notes on a skeleton of *Prosaurolophus maximus*. Univ. Toronto Studies, Geological series, 18, 1-35.

Paulina-Carabajal, A., Lee, Y. N., & Jacobs, L. L. (2016). Neuroanatomy of the primitive nodosaurid dinosaur *Pawpawsaurus campbelli* and paleobiological implications of some endocranial features. PLoS One, 11, e0150845.

Penkalski, P. (2001). Variation in specimens referred to *Euoplocephalus tutus*. In Carpenter, K. (Ed.). The Armored Dinosaurs. Bloomington: Indiana University Press, pp. 363–385.

Peterson, J. A., & Bezy, R. L. (1985). The microstructure and evolution of scale surfaces in xantusiid lizards. Herpetologica, 41, 298-324.

Posso, S. R, & Donatelli, R. J. (2001) Cranial osteology and systematic implications in Crotophaginae (Aves, Cuculidae). Journal of Zoological Systematics and Evolutionary Research, 39, 247–256.

Powell, G. L., Russell, A. P., Jamniczky, H. A., & Hallgrímsson, B. (2017). Shape variation in the Dermatocranium of the greater short-horned Lizard *Phrynosoma hernandesi* (Reptilia: Squamata: Phrynosomatidae). Evolutionary Biology, 44(2), 240-260.

Ramírez-Bautista, A., Vitt, L., Ramírez-Hernández, A., Quijano, F. M., & Smith, G. (2008). Reproduction and sexual dimorphism of *Lepidophyma sylvaticum* (Squamata: Xantusiidae), a tropical night lizard from Tlanchinol, Hidalgo, Mexico. Amphibia-Reptilia, 29(2), 207-216.

Rand, A. S. (1961). A suggested function of the ornamentation of East African forest chameleons. Copeia, 1961(4), 411-414.

Romer, A. S. (1956). Osteology of the Reptiles. University of Chicago Press, Chicago, Illinois, 772 p.

Sampson, S. D., Ryan, M. J., & Tanke, D. H. (1997). Craniofacial ontogeny in centrosaurine dinosaurs (Ornithischia: Ceratopsidae): taxonomic and behavioral implications. Zoological Journal of the Linnean Society, 121(3), 293-337.

Schmidt, K. P. (1938). New crocodilians from the upper Paleocene of western Colorado. Geological Series of the field museum of natural history, 6(21), 315-321.

Smith, K. T. (2011). The evolution of mid-latitude faunas during the Eocene: late Eocene lizards of the Medicine Pole Hills reconsidered. Bulletin of the Peabody Museum of Natural History, 52(1), 3-105.

Smith, G. R., Lemos-Espinal, J. A., & Ballinger, R. E. (1997). Sexual dimorphism in two species of knob-scaled lizards (genus *Xenosaurus*) from Mexico. Herpetologica, 53, 200-205.

Taylor, G. W., Santos, J. C., Perrault, B. J., Morando, M., Vásquez Almazán, C. R., & Sites Jr., J. W. (2017). Sexual dimorphism, phenotypic integration, and the evolution of head structure in casque-headed lizards. Ecology and evolution, 7(21), 8989-8998.

Tinius, A. (2019). Cranial Ornamentation in *Anolis baleatus*. Available at https://www.anoleannals.org/2019/08/28/cranial-ornamentation-in-anolis-baleatus/ (accessed 08 August 2019.)

Vaurie, C. (1968) Taxonomy of the Cracidae (Aves). Bulleton of the American Museum of Natural History, 138,1–259.

Vickaryous, M. K., & Hall, B. K. (2008). Development of the dermal skeleton in *Alligator mississippiensis* (Archosauria, Crocodylia) with comments on the homology of osteoderms. Journal of morphology, 269(4), 398-422.

Vickaryous, M. K., Maryanska, T., & Weishampel, D. B. (2004). Ankylosauria. In Weishampel D. B, Dodson P, & Osmolska H. (Eds.). The Dinosauria (Second Edition). University of California Press, Berkeley, pp. 363-392.

Vickaryous, M. K., & Russell, A. P. (2003). A redescription of the skull of Euoplocephalus tutus (Archosauria: Ornithischia): a foundation for comparative and systematic studies of ankylosaurian dinosaurs. Zoological Journal of the Linnean Society, 137(1), 157-186.

Vickaryous, M. K., Russell, A. P., & Currie, P. J. (2001). Cranial Ornamentation of Ankylosaurs (Ornithischia: Thyerophora): Reappraisal of Developmental Hypotheses. In Carpenter, K. (Ed.). The Armored Dinosaurs. Indiana University Press, Bloomington and Indianapolis, pp. 318-340.

Vickaryous, M. K., & Sire, J. Y. (2009). The integumentary skeleton of tetrapods: origin, evolution, and development. Journal of Anatomy, 214(4), 441-464.

Webster, M. S. (1992). Sexual dimorphism, mating system and body size in New World blackbirds (Icterinae). Evolution, 46(6), 1621-1641.

Wikelski, M., & Trillmich, F. (1997). Body size and sexual size dimorphism in marine iguanas fluctuate as a result of opposing natural and sexual selection: an island comparison. Evolution, 51(3), 922-936.

Table and figure captions

Table 1. List of specimens used in this study.

Table 2. Osseous cranial ornamentation in extant sauropsid vertebrates.

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.

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.

Table 1(on next page)

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

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Table 2(on next page)

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**	squmates	Corytophanidae	*Basiliscus*	casque, crest	intersexual	Lang, 1989; Taylor et al., 2017; Smith, 2011
Skull elaboration	**dimorphic**	squmates	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**	squmates	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.

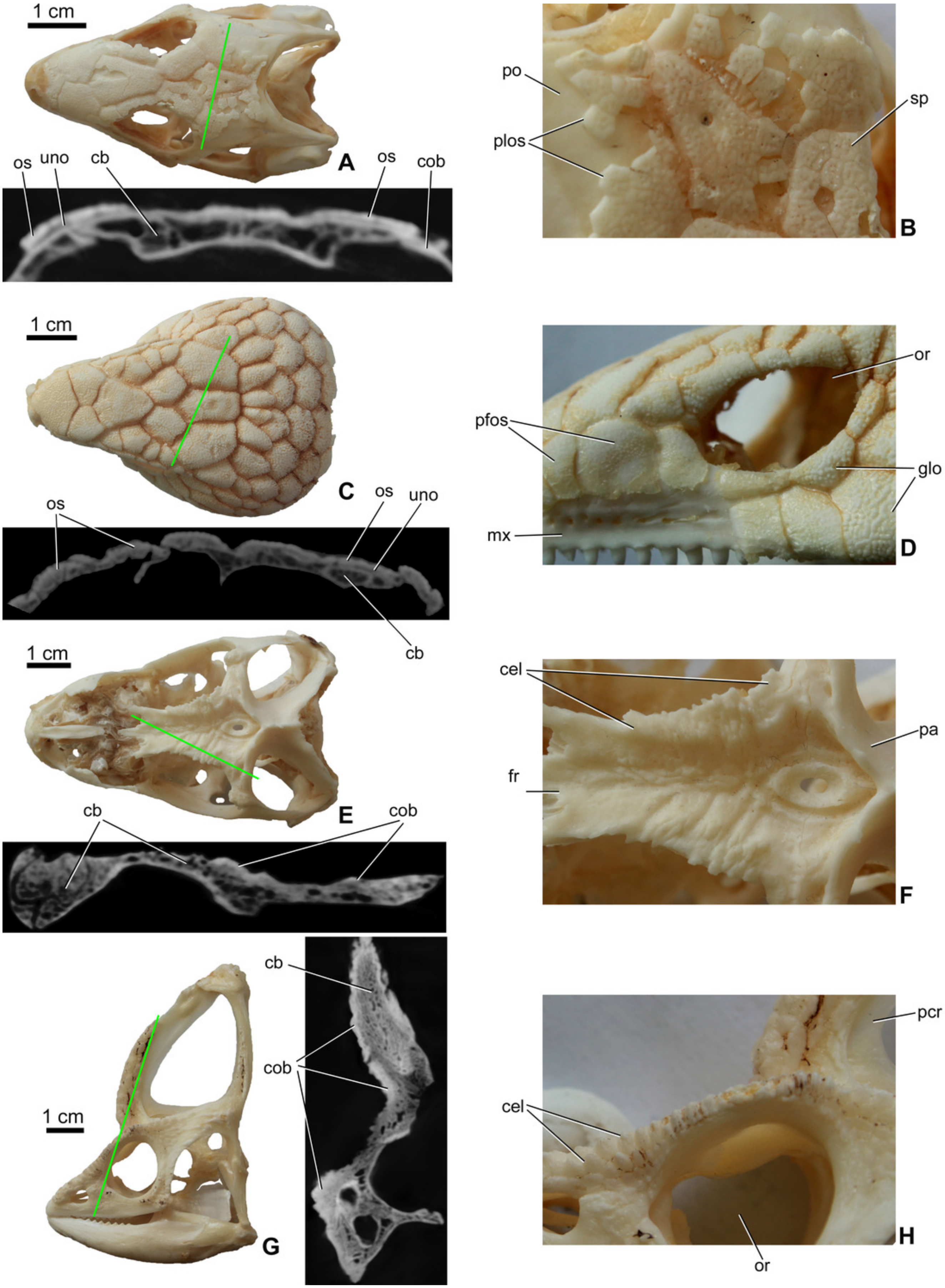
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Figure 2

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.

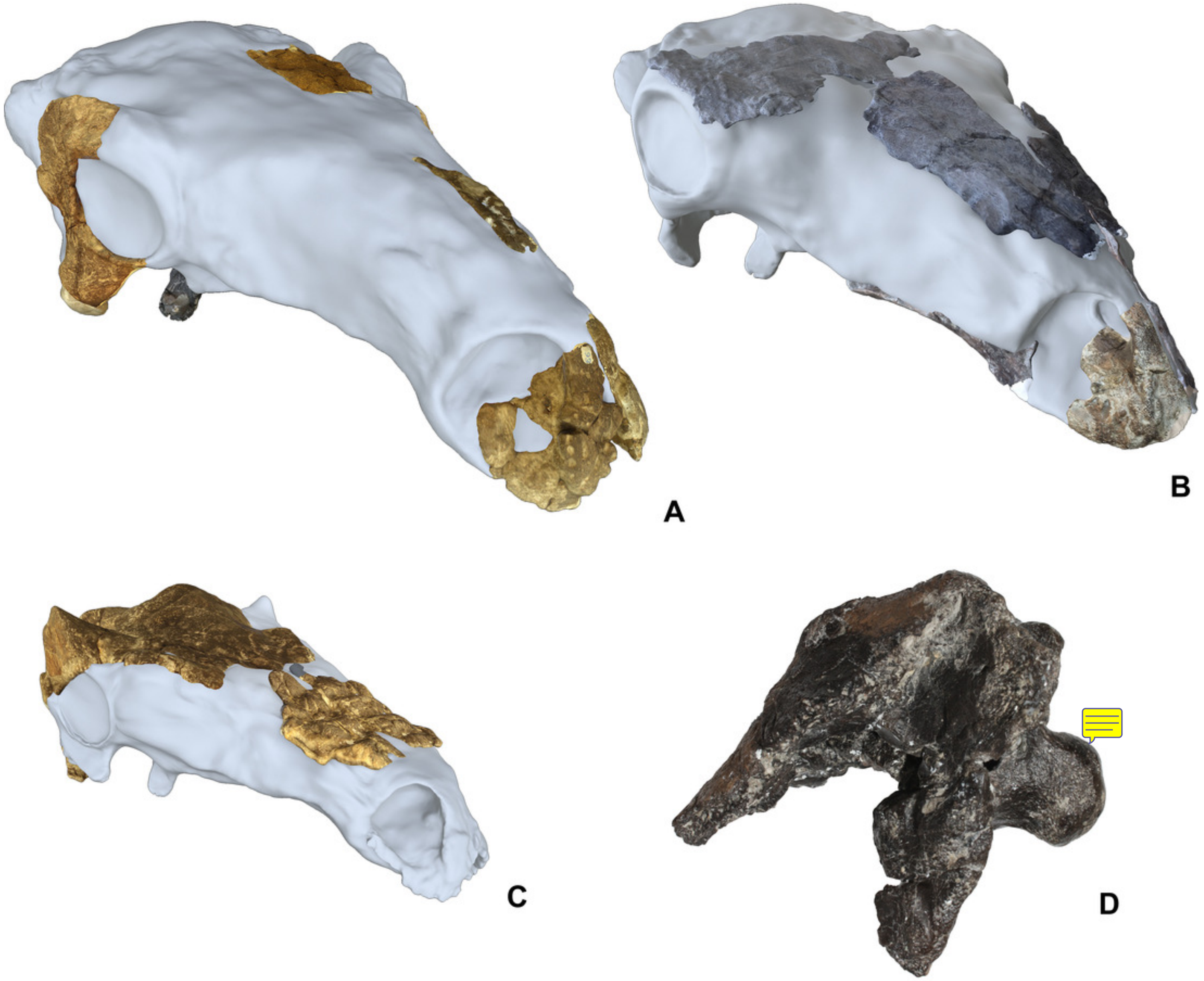

Figure 3

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 eft 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.

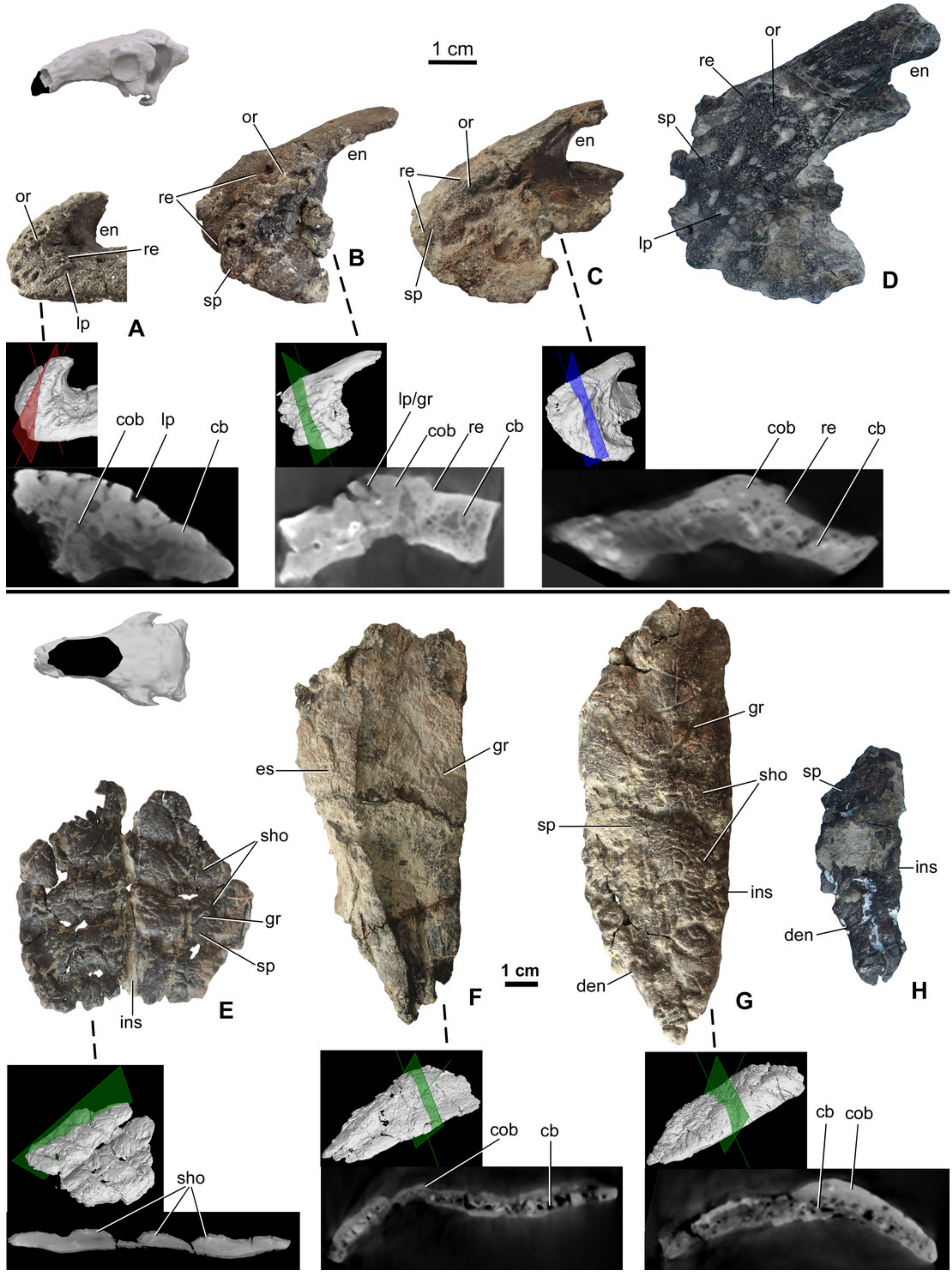
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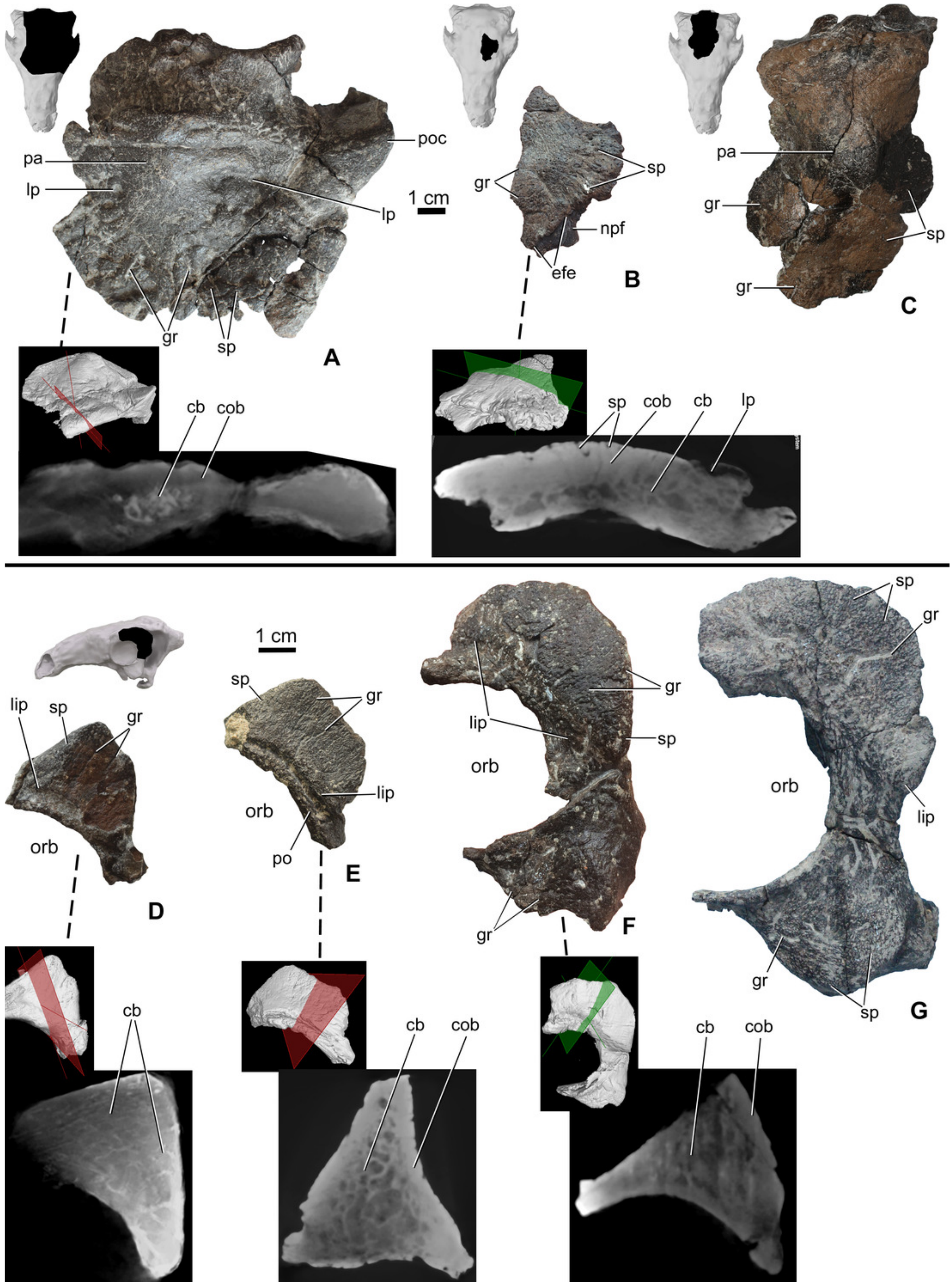
Figure 4

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 [illegible]irrored). 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.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