INFERRED BITE MARKS ON A LATE CRETACEOUS (SANTONIAN) BOTHREMYDID TURTLE AND A HYLAEOCHAMPSID CROCODILIAN FROM HUNGARY

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Abstract

The Iharkút vertebrate locality, an open-pit mine in the Bakony Mountains (western Hungary), has provided a rich and diverse assemblage of Late Cretaceous (Santonian) fossils in the last 13 years. Here we present two fossil specimens of this assemblage, a plate fragment of the bothremydid turtle *Foxemys trabanti*, and a partial skull roof of the hylaeochampsid crocodilian *Iharkutosuchus makadii*, that exhibit pathological traits on their surface. These pathologies can be described as shallow and deep pits, bisected pits, scores, and in the case of the skull roof also a hole piercing through the entire bone thickness. Morphological and bone histological features of these pathological traits imply that they probably represent bite marks. Post-mortem invertebrate feeding traces and microbial activity, as well as different shell diseases and infections are less likely sources of these secondary alterations, because no unequivocal morphological and histological features associated with these alternative causes are detected in the fossil bones. Morphological similarities with experimentally investigated crocodilian tooth marks suggest that both elements bear the bite marks of a crocodilian predator with typical conical teeth. Four different taxa of Mesoeucrocodylia are documented from the Iharkút vertebrate assemblage, among which only the *Allodaposuchus*-like crocodile had conical teeth and therefore might have been responsible for the bite marks in both cases. The inferred tooth marks on the dorsal surface of the *Iharkutosuchus* skull roof indicate a predator-prey interaction rarely documented between two different crocodilian taxa rather than antagonistic behaviour over common resources. Nevertheless, to draw firm conclusions and establish the basis for future investigations of fossil bone pathologies, more comparative studies are needed on the different traumatic as well as non-traumatic bone pathologies that may eventuate in bite-mark-like abnormalities.

1. Introduction

The study of bite marks represents a significant research field in paleontology because such traces on the fossil bone surface indicate a factual interaction between two animals (either antagonistic or predator-prey interaction). As such, it may provide direct evidence on the feeding behaviour of extinct carnivores and information on the trophic structure of the palaeocommunity. Crushing the bones of the prey to access the nutritious marrow is a common behaviour among mammalian carnivores and related traces are frequently found in modern ecosystems as well as in fossil assemblages (e.g. Haynes, 1983; Weigelt, 1989; Fiorill, 1991; Domínguez-Rodrigo, 1999; Hu et al., 2005; Faith and Behrensmeyer, 2006; Faith et al., 2007). However, direct evidence of bones showing such mammal-like bone-crushing activity is quite rare among sauropsid groups due to their usually different dentition and feeding behaviour (Fiorillo, 1991; Farlow and Holtz, 2002; Hone and Rauhut, 2009; D'Amore and Blumenschine, 2009). The number of studies focusing on fossil bones with sauropsid bite marks has increased lately (Fiorill, 1991; Carpenter, 1998; Jacobsen, 1998; Farlow and Holtz, 2002; Avilla et al., 2004; Buffetaut et al., 2004; Hone and Rauhut, 2009; Fiorelli, 2010; Longrich et al., 2010; Milàn et. al., 2010; Schwimmer, 2010; Bell, et al., 2012; Noto et al., 2012; Boyd et al., 2013), and some experiments have been conducted on the feeding traces of extant sauropsids as well (Njau and Blumenschine, 2006; D'Amore and Blumenschine, 2009, 2012; Vasconcellos and Carvalho, 2010). In most investigations of sauropsid feeding behaviour, the study objects were restricted to dinosaurs (e.g. Fiorill, 1991; Erickson and Olson, 1996; Carpenter, 1998; Jacobsen, 1998; Farlow and Holtz, 2002; Rogers et al., 2003; Fowler and Sulivan, 2006; Hone and Rauhut, 2009; Peterson et al., 2009; Hone et al., 2010; Paik et al., 2011) while feeding traces of other sauropsids, such as crocodilians, have only recently received attention (e.g. Karl and Tichy, 2004; Njau and Blumenschine, 2006; 2012 Fiorelli 2010; Schwimmer, 2010; Vasconcellos and Carvalho, 2010; Boyd et al., 2013; Martin, 2013). The predator-prey interaction between crocodyliforms and turtles has long been recognized in modern and ancient ecosystems. However, the number of systematic descriptions of this interaction in the fossil assemblages is limited (Carpenter and Lindsey, 1980; Hutchinson and Frye, 2001; Schwimmer, 2002; 2010; McCoy et al., 2012; Noto et al., 2012) because most studies focus on different taxonomic and/or more general palaeoecological aspects, and less on these specific interactions (Antunes and de Broin, 1988; Mead et al., 2006; Mikulás and Dvorák, 2010).

The aim of the present study is to explore and investigate potential bite marks on fossil bones of the vertebrate assemblage from Iharkút, Hungary, and to interpret the characteristics of these traces in order to assess possible predator-prey interactions in the palaeocommunity. We provide both morphological and histological descriptions and comparisons of the pathological features to assess the probability that they indeed represent bite marks. After arguing for a tooth mark origin, we attempt to infer the identity of the putative predator responsible for the bite marks on the fossil bones, and discuss their significance for possible trophic interactions in this ancient palaeocommunity.

2. Stratigraphy, geological setting and faunal composition

The Iharkút vertebrate locality is situated in a rehabilitated open-pit bauxite mine in the northern part of the Bakony Mountains (Transdanubian Central Range), western Hungary, near the villages of Németbánya and Bakonyjákó (Fig. 1A).

The oldest rocks in the Iharkút open-pit mine are Late Triassic shallow marine dolomites (Main Dolomite Formation) the irregular karstic surface of which was filled by bauxite (Nagytárkány Bauxite Formation) during the Late Cretaceous (pre-Santonian) subaerial exposure phase (Bárdossy and Mindszenty, 2013). The dolomite and the bauxite deposits are overlain by the Upper Cretaceous Csehbánya Formation, rich in both plant and vertebrate fossils. The Csehbánya Formation represents a typical alluvial, flood-plain deposit consisting mainly of fine-grained silty-clayey overbank sediments with several palaeosol horizons and are crosscut by shallow channel-filling sandstones (Ősi and Mindszenty, 2009; Tuba et al., 2006; Botfalvai et al., 2012). Absence of desiccation cracks and subordinate pedogenic carbonate accumulation in the paleosol horizons indicate humid climate in agreement with the reconstructed subtropical floodplain forest vegetation (Bodor et al., 2012). At some places in the quarry, higher up in the stratigraphic sequence, Middle Eocene (Lutetian) conglomerates and limestones unconformably cover the Csehbánya Formation (Bárdossy and Mindszenty, 2013). The youngest deposit exposed in the mine is Pleistocene loess forming a discontinuous blanket over most of the area (Fig. 1B).

Most of the vertebrate fossils were discovered in the basal breccia of the site SZ-6. This layer is 10 to 50 cm thick, composed of grey sand, siltstone, clay clasts, pebbles and plant debris, and occasionally contains complete, but more frequently fragmentary bones (Fig. 1C). Normal gradation of this unit suggests that energy conditions changed during the deposition of the bone bed complex. The basal breccia layer of site SZ-6 is covered by a less fossiliferous sandstone bed. The uppermost bed of this sequence is a 30 to 50 cm thick, laminated, greyish siltstone which contains fewer bones and sometimes incomplete skeletons of *Hungarosaurus*. Vertebrate fossils are common in the coarse-grained poorly sorted sediments of the lower segment of sequence SZ-6, while they are only rarely encountered in the upper laminated deposit. The age of the bone beds at site SZ-6 was examined by palynological methods which resulted in an age corresponding to the Santonian *Oculopollis zaklinskaiae*-*Tetracolporopollenites* (*Brecolpites*) *globosus* Zone (Bodor and Baranyi, 2012). The fossils presented in this study were recovered from the basal breccia of site SZ-6 and represent part of the attritional isolated bone assemblage of the Iharkút vertebrate material (Botfalvai et al., submitted.).

The Late Cretaceous vertebrate locality of Iharkút yielded a very rich and diverse fauna of terrestrial and freshwater animals, the composition of which is similar to other Late Cretaceous continental vertebrate faunas of Europe (see e.g. Buffetaut and Le Loeuff, 1991; Allain and Pereda Suberbiola, 2003; Weishampel et al., 2010). The fish fauna recovered from Iharkút includes one pycnodontiform and one lepisosteiform taxa (Ősi et al., 2012a). Amphibians were a diverse group in this palaeoenvironment and are represented by both allocaudatans (albanerpetontid) and anurans (e.g. Szentesi and Vencel, 2010; Szentesi et al., 2013). Turtle fossils are the most frequent remains in the Iharkút bone assemblage and represent at least four different taxa. Among these, isolated postcranial elements and skulls of the bothremydid *Foxemys trabanti* Rabi, Tong and Botfalvai, 2012 are the most abundant, whereas remains of dortokid turtles and *Kallokibotion* sp. are less common (Rabi et al., 2012 Ősi et al., 2012a). Squamates show a high diversity, including at least seven, small to medium-sized taxa of lizards and the freshwater mosasaur *Pannoniasaurus inexpectatus* Makádi, Caldwell and Ősi, 2012 (Makádi et al., 2012; Makádi, 2013a,b). The crocodyliform assemblage is relatively diverse being represented by two terrestrial (*Doratodon* sp. and a *Theriosuchus*-like neosuchian) and two semi-aquatic taxa (*Iharkutosuchus makadii* Ősi, Clark and Weishampel, 2007 and an *Allodaposuchus*-related form; Ősi, 2008; Ősi et al., 2012a). One of the characteristics of the Iharkút palaeocommunity is the surprisingly high individual number of pterosaurs including members of the family Azhdarchidae and indeterminate pterodactyloids (Ősi et al., 2011, Prondvai et al., in press.). At least ten different taxa of dinosaurs can be distinguished: the theropods are represented by five different taxa (Tetanurae indet, Abelisauridae indet, *Pneumatoraptor fodori* Ősi, Apesteguía and Kowalewski, 2010 Paraves indet., *Bauxitornis mindszentyae* Dyke and Ősi 2010 , Enantiornithes indet.), whereas the known herbivorous dinosaur fauna includes two nodosaurid ankylosaurs (*Hungarosaurus tormai* Ősi 2005, cf. *Struthiosaurus sp.*), a small-bodied rhabdodontid (*Mochlodon vorosi* Ősi et al., 2012) and a ceratopsian dinosaur (*Ajkaceratops kozmai* Ősi, Butler and Weishampel 2010), the latter of which is the first undisputable evidence for the European occurrence of the clade Ceratopsia (e.g. Ősi and Buffetaut, 2011; Ősi et al., 2010; Ősi et al., 2012a,b; Ősi and Prondvai 2013).

3. Material and Methods

Among the vertebrate remains, only two specimens, a carapace fragment (MTM PAL 2013.93.1) of the turtle *Foxemys trabanti* and a partial skull roof (MTM PAL 2013.94.1) of the crocodilian *Iharkutosuchus makadii* showed clear pathological traits resembling tooth marks, and hence were suitable for this study (Figs. 2 and 3). The fossils are housed in the vertebrate paleontological collection of the Hungarian Natural History Museum (MTM) in Budapest. Morphologies of the inferred tooth marks were described following Njau and Blumenschine (2006).

Both elements showing bite-mark-like deformities were cut through the pathologic regions for histological investigation. Two samples were taken from the anterior margin of the carapace fragment (MTM PAL 2013.93.1, Fig. 2A): one right through the largest presumed tooth mark on the left peripheral 1, whereas the other from an intact area on the right peripheral 1 to compare the histological characteristics of a healthy and a pathological region. The transverse (i.e., vertical) section plane was directed parallel to the natural free margin of the peripheral (Fig. 2B). By contrast, the entire skull roof fragment was cut in half through the parietal and the frontal (Fig. 3B) slicing through areas that looked intact as well as through the most distinct, tooth mark looking depressions, including a hole piercing the entire bone thickness. Transverse thin sections of these samples were prepared following standard methods (Wells, 1989) and examined under Nicon LV 100 polarized light microscope. Pictures of the histological slides were acquired with QImaging MP5.0 digital microscope camera and processed with Image Pro Insight software. Interpretative figures were obtained using CorelDRAW X5 software. Histological descriptions follow the nomenclature of Marotti (2010) and Stein and Prondvai (2014) and partially that of Scheyer and Sander (2007).

4. Results

4.1. Examination and description of pathologies detected on the turtle plate fragment (MTM PAL 2013.93.1)

Material and description: The turtle shell fragment exhibiting the pathological marks (MTM PAL 2013.93.1) is 13.9 cm in length and 6.8 cm in width and represents the anterior edge of the carapace, including the nuchal and both peripherals 1 (Fig. 2). Of the scutes, the anterior fourth of the first vertebral and four marginals can be observed. The left and right first two marginals are complete, whereas the second marginals on both sides preserve only their medial portion. The specimen is assigned to *Foxemys trabanti* on the basis of its size, the emarginated nuchal, the absence of characteristic surface decoration, and the absence of a cervical scale (Rabi et al., 2012, 2013, Ősi et al., 2012).

Taphonomical features: The dorsal surface of the turtle carapace fragment is moderately well preserved, with no significant abrasion or weathering, whereas the ventral surface is more worn due to physical or chemical effects. The margin of the carapace fragment is interrupted by two pathological depressions, but there are a number of other pits distributed on the dorsal and ventral surface of the element (Fig. 2). The edges of some of these marks are rounded, which indicates that the bone surface experienced some abrasion after the depressions were formed. The rounded margins and the abraded ventral side of the plate fragment indicate that it was exposed to the physical impacts of transportation before the burial. As in the case of this specimen, the dorsal sides of fossil turtle plates often show better preservation than the ventral side due to the protective horny scales covering the dorsal but missing from the ventral surface making the dorsal side more resistant to physical impacts (e.g. Brand et al., 2003). The carapace was deformed and bent along the scale sulci probably due to mechanical impact.

Morphology of the pathological traits: Several pathological depressions can be detected on the ventral, dorsal and lateral surfaces of the plate showing different morphologies (Fig. 2). The pit marks appear as irregular or bowl-shaped depressions on the plate surface, vary in diameter from 1 to 13.5 mm, show U-shaped cross-section, and a circular to oval outline in dorsal view. Most of the pit marks are arranged in rows of different orientations. Some of them look bisected via a slight linear depression, but this feature was observed only in a few pits. There are two large circular marks situated in the marginal region of the specimen, which completely pass through the carapace. Score marks also appear on the more proximal part of the shell, ranging 13-38 mm in length and 1-4 mm in width. They are shallow and U-shaped in cross section, and in many cases they originate from the pit marks. The scores are mostly perpendicular to the rows of pits and diagonal to the long axis of the carapace. On the ventral surface of the carapace there is a pathological region with deformations of complex morphology including one shallow and three deeper pits which coalesce into a deep groove (Fig. 2D,E).

Bone histology: Although the staining effect of the pyrite obscures details of fibre orientation and osteocyte lacuna features in most areas, the microstructural preservation of the turtle shell fragment is sufficient for comparing the healthy and pathologic bone tissue (Figs. 4 and 5). Histology of the intact area of the shell reveals a diploe structure common in terrestrial and semi-aquatic turtles (Scheyer 2007a; Scheyer and Sander, 2007) with cancellous bone sandwiched between the well-developed external and internal compact cortices (Fig. 4A). Apart from being slightly thinner, the external cortex (Fig. 4B) appears to have the same microstructural features as the internal cortex (Fig. 4F) in this section. In this context, however, it is noteworthy that the peripheral was sampled at its free, rounded margin, and therefore the external and internal cortices in this area correspond to the dorsal and ventral compact bone of the plate fragment, respectively. Hence, the ventral compact bone must be considered external cortex, as well (Scheyer, 2007a) which may explain the unexpected symmetrical diploe structure in the peripheral of this turtle in contrast to the reduced internal cortex in the shell of other bothremydid turtles that is considered a synapomorphic trait (Scheyer, 2007a). Growth marks mostly eventuating in lines of arrested growth (LAGs) are visible, locally even in the highly porous cancellous bone, although not in the innermost middle layer. The spacing of these growth marks is variable; some are densely packed, others are more distantly spaced. Primary vascular canals run radially, longitudinally or irregularly in both the dorsal and ventral cortices, and towards the cancellous layer the canals have progressively wider lumen and scalloped outlines due to secondary resorption (Fig. 4B,D,F). In the cancellous areas (Fig. 4D), most of the large cavities are also the result of extensive secondary resorption, although deposition of secondary bone tissue on these irregular resorption surfaces is also evident mainly at the transitional region between the cancellous and dorsal compact bone. Well-compacted secondary osteons, however, are not present in any area of this section, and most of the bony material in the cancellous layer is also primary. The entire primary cortex is invaded by extrinsic structural fibres mostly running parallel to the surface of the plate fragment (Fig. 4C,D). There are extensive, apparently acellular cortical areas, although the lack of osteocyte lacunae in these regions may be a preservational artefact (Fig. 4C).

The appearance of the bone tissue in the pathologic region (Fig. 5) suggests mechanical abrasion of the dorsal compact bone in the U-shaped pit that exposed the inner cancellous layer (Fig. 5A-D,G). This exposed cancellous layer contains cavities of diverse sizes and shapes most of which have smooth rims formed by a thin layer of secondary bone (Fig. 5C). It is observable by naked eye as well that the loss of the dorsal cortex is restricted to the area of the U-shaped depression. Unequivocal microstructural characteristics of osteomyelitis such as irregular lesion or necrosis of the bony tissue caused by different shell diseases (Lovich et al., 1996; Garner et al., 1997; Homer et al., 1998; Hernandez-Divers et al., 2009; Aleksić-Kovačević et al., 2013; Rothschild et al., 2013 and references therein) cannot be detected. No callus-like tissue or other pathological secondary bone tissues disfiguring shell disease or referring to wound healing can be observed. Apart from the erosion of the dorsal cortex in the U-shaped pit, the microstructure of this region of the plate corresponds with that of the intact region (compare Figs. 4 and 5), and there is no other evidently pathological condition observed in this thin section.

4.2. Examination and description of pathologies detected on the Iharkutosuchus *skull roof (MTM PAL 2013.94.1)*

Material and description: The skull roof fragment of *Iharkutosuchus makadii* (MTM PAL 2013.94.1) exhibits at least eleven pathological marks on its dorsal surface (Fig. 3). The anteroposterior length of this specimen is 4 cm and its mediolateral width is 3.1 cm. It represents the anterior part of the skull table preserving the posterior part of the frontal, the anterior and central portions of the parietal, the medial sides of both postorbitals, and the anteromedial corner of the right squamosal. As it is characteristic for *Iharkutosuchus*, this specimen has also closed supratemporal fenestrae. The dorsal ornamentation of the skull elements is similar to that seen in the holotype of *I. makadii* (MTM PAL 2006.52.1). On the ventral side of the frontal, the posterior ends of the cristae cranii frontales can be observed. On the ventral side of the parietal, only the crests for the connection with the lateral side of the braincase are preserved. The specimen represents a skull approximately 75% of the 11.1 cm long holotype specimen, so the estimated total body length of MTM PAL 2013.94.1 is about 55-60 cm.

Taphonomical features: The *Iharkutosuchus* skull roof is well preserved showing neither abrasion nor weathering. Most of the broken edges outlining the skull fragment (irregular and step fractures) were created during the pre-fossil diagenetic phase. The margins of the pit marks are not abraded. Good preservation indicates that the bone was not exposed to fluvial transportation before the burial and raises the possibility that the skull fragment was broken off the rest of the skull due to biological impact such as feeding or trampling.

Morphology of the pathological traits: There are approximately 11 pathological features on the dorsal surface of the skull roof and they all show similar morphology. All of the marks were U-shaped in cross-section and had an oval outline in dorsal view, and some of them could be identified as bisected pit marks (e.g. Njau and Blumenschine, 2006, 2012). The largest detected pathological trait on this skull fragment is a hole that penetrates the element at the border of the parietal and frontal, and is 0.9 mm in diameter. The other, bowl-shaped depressions on the dorsal surface of the skull roof are relatively deep (1-3 mm) and have rounded margins.

Bone histology: The complete transverse section of the partial skull roof reveals a smaller piece of the frontal and a larger piece of the parietal separated by the pathologic hole (Figs. 6A and 7A). The ventral and dorsal surfaces, including the surface of sculptural and pathological pits on the dorsal side, uniformly appear very smooth under the microscope. This may be due to pre-burial external factors that very finely polished the surface of the element. Extensive areas along the margin of the section show infiltration of a staining mineral into the bone tissue obscuring details of fibre arrangement and osteocyte lacuna morphologies. The general microstructure of the skull fragment corresponds to that of a typical dermal bone with partially distinct, partially transitional border between the middle, highly cancellous bone layer and the compact cortex surrounding it. In a larger area, the external (dorsal) cortex consists of longitudinally oriented (i.e. parallel to the bone surface) fine parallel-fibred bone with low birefringence (Fig. 6D) and abundant Sharpey's fibres that run roughly perpendicular or oblique to the dorsal surface of the bone. In other areas, the orientation of the parallel-fibred bone is variable partially following the orientation of the vascular canals. Osteocyte lacunae are sparse in the majority of the dorsal cortex with areas that seem to be void of lacunae; however, the latter may be a pure preservational artefact. No evident plywood-like arrangement can be observed. Some indistinct incremental lines can be detected but usually cannot be followed all along the length of the section. Vascular canals are sparse but of relatively wide lumen, and they run mostly radially and parallel to the dorsal surface of the bone. Secondary remodelling can also be observed around some vascular. A distinct structural change characterizes the border between the external cortex and the middle cancellous bone layer. Here, the fine parallel-fibred bone of the dorsal cortex with low lacunar densities and low birefringence abruptly changes into the strongly birefringent parallel-fibred bone of the middle cancellous layer which shows much higher lacunar densities (Fig. 6D). The majority of the parallel-fibred bone in the middle layer is primary and oriented parallel or subparallel to the external and internal cortical surfaces (Fig. 7A), but in small areas interwoven structural fibres characteristic of dermal bones (e.g., Scheyer 2007a,b; Scheyer and Sander, 2007; Witzmann 2009) also occur. External structural fibres are also present in this middle layer. Secondary remodelling by lamellar parallel-fibred bone is restricted to the margin of some medium-sized secondary osteons and the large erosion cavities. There is no distinct border between the middle cancellous layer and the internal (ventral) cortex; the parallel-fibred bone of the middle layer continues in the ventral compacta without any structural interruption (Figs. 6C and 7C). In the ventral cortex, parallel-fibred bone is oriented mainly parallel to the internal bone surface, and locally it shows lamellation (Figs. 6C and 7A,C). As in the dorsal cortex, Sharpey's fibres abundantly cross the internal compacta perpendicular or oblique to its surface. Vascularity is much lower than in the external cortex with a few radially oriented canals and large, entirely avascular areas. Numerous growth marks are present which, in contrast to e.g., the frontal bone of the eocene *Crocodylus* cf. *affinis* and the recent *C. niloticus* (Buffrenil and Buffetaut, 1981), are much more distinct than in the dorsal cortex.

The complete section reveals the pathologic as well as the presumably intact areas of the skull fragment, including a supposedly intact sculptural pit of the external surface. The most important microstructural difference between the ornamental and the pathological pits lies in the apparently pathological loss of a larger amount of bone in the bite-mark-like pits and around the hole piercing through the entire element. Although the surface of the element is uniformly smoothened, in contrast to the sculptural pit, where the external cortex is still thick and the fibres seem to follow the undulation of the dorsal surface, in all pathological pits the external cortex is lost or reduced to a thin layer and there is an abrupt termination of the longitudinally oriented parallel-fibred bone at the margin of the pits and the hole (Figs. 6C and 7A,C). The preserved bone layers do not exhibit any other histological difference compared to the intact region of the bone which shows no apparent deviations from the characteristic microstructure of dermal bones, either (e.g., Buffrenil and Buffetaut, 1981; Scheyer, 2007a,b; Scheyer and Sander, 2007; Witzmann, 2009). Hence, as in the turtle plate fragment MTM PAL 2013.94.1, no histological features indicate that pre-mortem pathogens were responsible for the formation of the bite-mark-like pits. The microstructure of this skull roof fragment rather suggests an external, strong mechanical impact that removed the dorsal cortex in the pits and broke through the entire bone thickness in the thinner part of the element.

5. Discussion

Some morphological features (spatial distribution and shapes) of the diverse pits, bisected marks and scores detected on the surface of the carapace fragment and the skull roof imply that they probably represent feeding traces. In addition, histological comparison of the intact and pathologic regions of both elements is consistent with the hypothesis that the investigated pits have resulted from the massive intrusion of conical objects, most probably teeth, into the bones. The abundant fractures and deformations present in both elements may also be the result of powerful mechanical impacts to which the specimens were exposed prior to fossilization (e.g. Noto et al., 2012). Post-mortem invertebrate feeding traces (Hutchinson and Frye, 2001; Farinati and Zavala, 2002; Bader et al., 2009; Saneyoshi et al., 2011; Holden et al., 2013) and microbial activity (Pereda Suberbiola et al., 2000; Hutchinson and Frye, 2001; Slater et al., 2011), as well as different shell diseases and infections (Lovich et al., 1996; Garner et al., 1997; Homer et al., 1998; Knotkova et al., 2005; Hernandez-Divers et al., 2009; Rothschild et al., 2013) are less likely sources of these secondary alterations, because no unequivocal morphological and histological features associated with these alternative causes are detected in the fossil bones. Traces of neither post-mortem microbial activities (fungal and bacterial) nor shell diseases are likely to be spatially restricted to evenly distributed, coherent rows of pits, as is the case in our fossils. However, it must be noted that, at present, inadequate morphological and histological descriptions and illustrations of pathologies occurring in dermal bones (such as skull bones or turtle shells) with known causes (including trauma, infection and metabolic diseases) prevent precise comparison (Rothschild et al., 2013) and hence inferences on the unknown agent of pathologies in fossils. As a consequence, most reports on inferred bite marks (Antunes and de Broin, 1988; Schwimmer, 2002, 2010; Steadman et al., 2007; Milàn et al., 2011; Noto et al., 2012; Valais et al., 2012; Karl, 2012,; McCoy et al., 2012; Morgan and Albury, 2013) do not take non-traumatic origin of the detected pathologies into account which are otherwise very common in both extant and fossil turtle shells (Hutchison and Frye, 2001; Rothschild, 2010; Rothschild et al., 2013 and references therein). Non-traumatic skeletal pathologies resulting in holes and grooves near the articular surfaces have also been documented in crocodilians (Rothschild, 2010); however not in their skull bones. Bone pathological evaluation of fossil specimens is even more problematic because post-mortem alterations of the bone surface due to diagenetic processes, weathering, and different microbial and invertebrate feeding activities sometimes eventuating in bite-mark-like pathologies (Hutchison and Frye, 2001; Fejfar and Kaiser, 2005; Fernández-Jalvo et al., 2010; Holden et al., 2013) cannot be assessed with high confidence. Nevertheless, based on the comparison of morphological and histological features of the pathologies detected in our specimens with those reported in other studies, the bite mark origin is still consistent in both elements studied here.

Morphological similarities with experimentally investigated crocodilian tooth marks (e.g. Njau and Blumenschine, 2006, 2012) suggest that both the carapace and skull roof fragments studied here bear the bite marks of a crocodilian with typical conical teeth. This hypothesis is also supported by (1) the presence of bisected pits typical for crocodilian tooth marks; (2) the U-shaped cross section and the circular outline of tooth marks in dorsal view lacking extensive punctures or furrows which have been associated with mammalian style of chewing (Noto et al., 2012); (3) the high concentration of feeding traces in a small area (Boyd et al., 2013); and (4) the lack of diagnostic marks from serrated ziphodont teeth, such as parallel clusters of elongate and narrow marks or striations, which are characteristic of most theropod dinosaurs and some crocodilians (Fiorillo, 1991; Farlow and Holtz, 2002; Rogers et al., 2003; D’Amore and Blumenschine, 2009; Hone and Rauhut, 2009; Paik et al., 2011).

Pannoniasaurus, a potential top predator known from the locality, has slender, pointed and slightly distally curved teeth (Makádi et al. 2012); a tooth morphology that, in contrast to conical teeth, is considered to be inadequate for crushing hard food items, such as bony elements (e.g. Massare, 1987). Therefore it is also highly unlikely that *Pannoniasaurus* was responsible for the feeding traces detected on the investigated carapace and the skull roof fragments.

The differently oriented rows of tooth marks on the turtle plate are likely the result of rotating the shell in the mouth during which the crocodile, by quick motions of the head and jaws, tried to place the food item in the most adequate position for swallowing; a process also demonstrated by Noto et al. (2012) and Milán et al. (2010).

5.1. Paleoecology

If the feeding trace hypothesis is true, the bite marks detected on the *Iharkutosuchus* skull roof fragment most probably represent traces of a predator-prey interaction between two crocodilian species rather than scavenging, because the skull is an undesirable food item for a scavenger (Dodson, 1971; Weigelt, 1989). Antagonistic behaviour due to competition over common resources is also very unlikely, since *Iharkutosuchus* was a small-bodied crocodile (estimated body length 50–100 cm) with spatulate anterior and flat, molariform posterior teeth referring to oral food processing and a specialized omnivorous/herbivorous diet (Ősi and Weishampel, 2009), whereas its attacker was apparently a larger species with tooth morphologies typical for generalist crocodilian predators (e.g.; Buffetaut, 1983). Hence, it is more likely that these tooth marks were created when the *Iharkutosuchus* specimen was caught by another, larger-bodied crocodile species that tried to kill its prey by perforating the skull roof, which injury may have caused the death of this *Iharkutosuchus* individual.

Having restricted the circle of possible predators to a crocodilian, the most probable identity of the attacker can be assessed. Four different taxa of Mesoeucrocodylia are documented from the Iharkút vertebrate assemblage (Ősi et al., 2007; Ősi et al., 2012a). *Doratodon* sp. is represented by several serrated, labiolingually compressed (i.e., ziphodont) teeth, an incomplete dentary and a maxilla (Ősi et al., 2012a). The occurrence of a second mesoeucrocodylian taxon is inferred from the presence of labiolingually compressed teeth lacking serration (i.e., pseudoziphodont teeth). This tooth morphology is similar to that found in the genus *Theriosuchus* (Ősi et al., 2012a). The remains of the other two, semiaquatic mesoeucrocodylians, an indeterminate neosuchian and the hylaeochampsid eusuchian *Iharkutosuchus*, yield the richest diagnostic crocodilian material of the Iharkút vertebrate assemblage. *Iharkutosuchus* is known on the basis of nearly complete skulls and skull fragments, dentaries, and teeth (Ősi et al., 2007; Ősi et al., 2012a). The indeterminate neosuchian taxon is represented by conical teeth with sharp mesial and distal carinae, dentaries, and different skull elements which are reminiscent of those of *Allodaposuchus* (Rabi, 2006; Ősi et al., 2012a; Rabi and Delfino, 2012); a taxon reported from numerous European Late Cretaceous vertebrate localities (e.g. Buscalioni et al., 2001; Delfino et al., 2008; Martin, 2010; Puértolas-Pascual, 2013). Among the abundant remains of *Iharkutosuchus*, the most unmistakable elements are its unique molariform, multicuspid teeth (Ősi et al., 2007; Ősi, 2008) which suggest specialized feeding involving elaborate chewing mechanism (Ősi and Weishampel, 2009). Differences in tooth morphology and presumed lifestyle of these four crocodilian taxa suggest distinct feeding strategies.

The tooth morphology and enamel microstructure of *Iharkutosuchus makadii* suggest that its diet could have included fibrous plants, fruits, arthropods, and possibly small-bodied vertebrates (Ősi and Weishampel, 2009). These features, combined with its relatively small body size shows that *Iharkutosuchus* certainly did not belong to the top predators of the

Iharkút paleocommunity. Instead, it may have represented an important food source for the top predators of the area. The other crocodilians were probably more generalist carnivores. The largest of them, the *Allodaposuchus*-like neosuchian, may have been among the top predators at least in the aquatic environment along with the mosasaur *Pannoniasaurus*.

The ziphodont and pseudoziphodont teeth of *Doratodon* and the *Theriosuchus*-like crocodilian suggest different feeding strategies from the *Allodaposuchus*-like neosuchian with conical tooth morphology. Whereas ziphodont and pseudoziphodont teeth are more suitable for cutting and slicing, conical teeth have more potential for crushing hard elements, such as bones (e.g. Massare, 1987; Fiorillo, 1991; Farlow and Holtz, 2002; D'Amore and Blumenschine, 2009, 2012). Hence, it is most likely that the bite marks detected on the *Iharkutosuchus* skull roof fragment (MTM PAL 2013.94.1) originated from this *Allodaposuchus*-like predator. This hypothesis is further supported by the presence of bowl-shaped deep depressions and bisected-like tooth marks, which is exactly the expected pattern if conical teeth with sharp mesial and distal carinae intrude the bone. Such tooth marks were observed on the bone surface bitten by extant *Crocodylus niloticus* with similar tooth morphologies (Njau and Blumenschine, 2006). By contrast, the ziphodont teeth of *Doratodon* and the pseudoziphodont teeth of the *Theriosuchus*-like crocodilian tend to create deeper marks with a more oval outline in dorsal view and V-shaped cross section (Noto et al., 2012). Thus, based on these parameters it is conceivable that the bite marks observed on the *Iharkutosuchus* skull roof fragment originate from the *Allodaposuchus*-like neosuchian crocodilian.

Studies focusing on predator-prey interaction or cannibalism among extant crocodilians based on stomach content investigations in modern ecosystems are rare (e.g. Delany and Abercrombie, 1986; Gabrey, 2010). Reports on crocodilian-crocodilian interaction in the fossil record are also scarce, and most of them are interpreted as intraspecific antagonistic behaviour rather than predation or scavenging (Buffetaut, 1983; Williamson 1996; Avilla et al., 2004; Vasconcellos and Carvalho, 2010; Martin, 2013). Interspecific predator-prey interactions among different crocodilian taxa are also poorly documented (Fiorelli, 2010). Therefore, the inferred tooth marks on the dorsal surface of the *Iharkutosuchus* skull roof (MTM PAL 2013.94.1) indicating a predator-prey interaction between two different crocodilian taxa are of great importance. Considering its abundance in the locality, it is possible that, besides turtles, the small-bodied, semiaquatic *Iharkutosuchus* was also a potential prey for larger-bodied carnivores in the palaeoenvironment of Iharkút, including the *Allodaposuchus*-like crocodilians.

Turtles are the most common and most important sauropsid food source for the wild populations of larger-bodied (>3 m) extant alligators (*Alligator mississippiensis*) in Florida and Louisiana where, based on stomach content investigations, turtles give ~15% of the total volume of consumed prey (Delany and Abercrombie, 1986; Gabrey, 2010). Predator-prey interaction between eusuchian crocodilians and turtles has been inferred from the fossil record, including many Cretaceous ecosystems, as well (Carpenter and Lindsey, 1980; Antunes and de Broin, 1988; Joyce, 2000, Hutchison and Frye, 2001; Schwimmer, 2002, 2010; Karl and Tichy, 2004; Mead et al., 2006; Steadman et al. 2007; Joyce et al., 2009; Milàn et al., 2010; McCoy et al., 2012; Noto et al., 2012). Bothremydid turtles were common members of Late Cretaceous aquatic communities along the northern coasts of Africa, the European archipelago and North America (Schwimmer, 2002; Gaffney et al., 2006; Rabi et al., 2012), and their fossils are often found together with conical-tooth-bearing eusuchians, such as *Allodaposuchus, Musturzabalsuchus, Massaliasuchus, Brachychampsa* or *Deinosuchus* (Buscalioni et al., 1999; Martin and Buffetaut, 2008, Ortega et al., 2008, Martin 2010, Schwimmer, 2002; Ősi et al., 2012a).

However, assessing predator-prey interaction between the *Allodaposuchus*-like neosuchian crocodiles and the adult *Foxemys* turtles in the Iharkút paleocommunity is problematic because the largest known remains of *Foxemys trabanti* (Rabi et al., 2012), which also include the plate fragment bearing the inferred bite marks, indicate that shell length and carapace/plastron thickness could have reached 70-80 cm and 0.5-1 cm, respectively. These dimensions probably did not define an adequate prey size for an *Allodaposuchus*-like crocodilian with an estimated adult body length of 170 cm and a skull length of 25 cm based on its scanty fossil remains known from the Iharkút locality. Furthermore, the 13.5 mm wide pit mark on the turtle plate fragment MTM PAL 2013.93.1 is too large compared with the greatest mesiodistal diameter (6-7 mm) of the largest known teeth of the *Allodaposuchus*-like neosuchian. On the other hand, size differences between these teeth and the bite marks might be explained by repeated biting and/or further, post-mortem physical and chemical erosion of the original bite mark. The diameter of the other tooth marks (3-8 mm) on the turtle plate fragment corresponds with the size of the *Allodaposuchus*-like neosuchian teeth recovered so far from the Iharkút assemblage. However, adult *Foxemys* turtles apparently represented an over-sized prey to be attacked and regularly consumed by the *Allodaposuchus*-like neosuchian in this paleocommunity. It is more conceivable that the large plate fragment bears the traces of scavenging activity rather than those of a predatory attack.

In summary, based on the currently available data, the bite mark origin of the pathologies detected on both elements studied here seems probable. Nevertheless, the general shortage of comparative morphological and histological descriptions of similarly looking traumatic and non-traumatic bone pathologies prevents us to draw firm conclusions on the most likely causes of the deformities described in the studied specimens. If the bite mark hypothesis is right, uncertainties further accumulate when questing for the identity of a putative predator responsible for the tooth marks. Even so, all information obtainable at present suggests that the inferred predator was a generalist crocodilian with conical tooth morphology, such as the *Allodaposuchus*-like neosuchian known from the Iharkút locality. This possibility raises further questions on the potential interspecific predator-prey interaction among different crocodilians. Moreover, this study also draws attention to the need for more comparative work on the morphological and histological appearence of bone pathologies induced by different external and internal factors in extant vertebrates before inferring on the origin of fossil bone deformations.

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Figure captions

Figure 1. Map and stratigraphic-sedimentological sections of the Iharkút locality (see colour version online). A, Location map of the Iharkút vertebrate locality. B, Schematic section of the Iharkút open-pit mine after Ősi and Mindszenty (2009). C, Schematic stratigraphic section of the site SZ-6 showing the main palaeoenvironment and lithofacies associations.

Figure 2. Carapace fragment of the *Foxemys* turtle (MTM PAL 2013.93.1) with pathological traits. A, Actual specimen in dorsal view with the indication of pathologies (white arrows) and the locations of histological sampling (black squares). B, Line drawing of the specimen in dorsal view outlining the pathological traits (solid grey lines), the bony sutures (blue solid lines) between the first peripherals (per1) and the nuchal (nu), the sulci (green dotted lines) between the four marginals (m1, m2) and the vertebral (ver1) scales, and the direction of the histological sectioning (dashed lines). C, Arrangement of scutes in a reconstructed intact carapace with the red outline marking the position of MTM PAL 2013.93.1 in dorsal view (see colour version online). D, Actual specimen and E, its line drawing in ventral view with the indication of the same structures as in A and B. Abbreviations: hs1, location of histological sampling of the intact region; hs2, location of histological sampling through the largest pit mark; m1-2, marginals 1 and 2; nu, nuchal; per1, peripheral 1; ver1, vertebral 1.

Figure 3. Skull roof fragment of the *Iharkutosuchus* (MTM PAL 2013.94.1) with pathological traits. A, Pathological pits (white arrow) in dorsal view. B, Sketch of the same skull fragment with pathological marks indicated by grey line in dorsal view. Dotted lines mark sutures; hatched area indicates the hole piercing the skull roof. Dashed line denotes the

direction of cut of the histological sample. C, Reconstruction of the skull of *Iharkutosuchus* with indication of the position of MTM PAL 2013.94.1 (red line) in dorsal view (see colour version online). Abbreviations: fr, frontal; pa, parietal; po, postorbital; sq, squamosum.

Figure 4. Transverse thin section of the intact region of the turtle plate fragment MTM PAL 2013.93.1. A, Complete section revealing the diploe microanatomy of the shell with dorsal and ventral compact bone (dcb, vcb) and the cancellous bone (cb) sandwiched in between. Labelled squares indicate corresponding magnified areas showing finer details of the tripartite structure in B, D, and F. C, Close-up of the dorsal compact bone with short irregular and circular primary vascular canals (pvc) and abundant bundles of extrinsic structural fibres (esf) appearing as dark stripes. Areas of apparently acellular bone (acb?) are also visible. E, Higher magnification of some preserved osteocyte lacunae probably derived from dynamic osteogenesis (DO-l?), and the extrinsic structural fibres running between them. Further abbreviations: ds, dorsal surface; ec, erosion cavity; so, secondary osteon; vs, ventral surface.

Figure 5. Transverse thin section through the largest pit mark found on the turtle plate fragment MTM PAL 2013.93.1. A, Complete section with indication of the outline-shape of the depression (dashed line) and the direction of the presumed mechanical impact (black arrow) causing it. Labelled squares indicate corresponding magnified areas in B-G showing details of the pathologically eroded surface (pes) and the deeper shell layers. Note, that the only evident pathology compared to the intact section is the lack of the dorsal compact bone which reveals the inner cancellous bone on the dorsal external surface. Further abbreviations: LAG, lines of arrested growth; and as in Figure 4.

Figure 6. Transverse thin section of the *Iharkutosuchus* (MTM PAL 2013.94.1) skull fragment. A, Complete section under plane polarized light showing the general tripartite microstructure of the skull roof (delineated by dotted lines) including intact as well as pathologic regions. Black arrows indicate pathologic depressions, whereas dashed lines the outline of the eroded surfaces of the depressions. Large black arrow marks the pathological hole where the element was pierced through. Letter labels refer to the magnified areas shown in B-D. B, Histological details of the margin of a pathological pit at the broken edge of the fragment under single plane polarizers and C, under cross polarized light. Note the abrupt termination of the bone fibres running parallel to the ventral bone surface and the complete loss of the dorsal compact bone (dcb) in the deeper part of the pit revealing the cancellous layer on the eroded surface. D, Close-up of the intact sculptural pit (scp) and the distinct structural change of the primary parallel-fibred bone (pfb) at the border between the dorsal compact bone (dcb) and the middle cancellous bone (cb). Further abbreviations as in Figures 4-5.

Figure 7. Counterpart of the transverse thin section of the *Iharkutosuchus* (MTM PAL 2013.94.1) skull fragment. A, Complete section showing the general tripartite microstructure under cross polarized light. Black arrows and dashed lines indicate pathologic pits and the outline of their eroded surfaces, respectively. Large black arrow marks the pathological hole where the element was pierced through. Letter labels refer to the magnified areas shown in B-D. B and C, magnified areas of the margins of pathologic pits under crossed plane polarizers revealing the cut-off nature of the bone fibres and vascular canals at the edge of the pits and the loss of the dorsal cortex. D, Close-up of the shallow margin of a pathologic pit at the edge of the broken fragment. Note the apparent erosion cutting off the fibres of secondary osteons close to the surface. Abbreviations as in Figures 4-6.

Figure 8. Scaled silhouette-reconstructions of the studied *Foxemys* specimen, MTM PAL 2013.93.1 (A), and the *Iharkutosuchus* specimen, MTM PAL 2013.94.1 (B), and the estimated maximum body size of the *Allodaposuchus*-like crocodilian (C) based on the known material from the Iharkút assemblage.