Fossil Record 28 (1) 2025, 45–56 | DOI 10.3897/fr.28.141743

Bioerosional marks in the shells of two sea turtle taxa from the middle Eocene of Belgium

Andrea Guerrero[1], Thierry Smith[2], Adán Pérez-García[1]

1 *Grupo de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional de Educación a Distancia, Avda. Esparta s/n, Las Rozas, 28232 Madrid, Spain*

2 *Directorate Earth & History of Life, Royal Belgian Institute of Natural Sciences, rue Vautier 29, B-1000 Brussels, Belgium*

https://zoobank.org/5721AB39-C9D8-4F26-A12D-80FAF37CD258

Corresponding author: Andrea Guerrero (guerbach@gmail.com)

Academic editor: T. Scheyer ♦ **Received** 13 November 2024 ♦ **Accepted** 23 December 2024 ♦ **Published** 31 January 2025

Abstract

This study analyses the diverse types of bioerosion marks on the shells of two sea turtle specimens from the Lutetian (middle Eocene) of Belgium. The objective is to understand the physical stressors affecting these organisms in ancient marine environments and to identify the potential factors responsible for these changes. The first specimen, the holotype of *Eochelone brabantica*, presents multiple erosive anomalies on its costal plates. The second individual, corresponding to *Puppigerus camperi*, exhibits different types of shell deviations, also of an erosive character. The combination of macroscopic and imaging techniques (i.e., CT scanning and 3D surface scanning) allow us the precise observation and identification of the different alterations. Comparative analyses suggest several external factors as potential causes of the anomalies of the two specimens (i.e., invertebrate feeding traces and trauma). This detailed examination provides specific insights into the types and causes of shell alterations in these Eocene turtles, offering a clearer understanding of their interactions in the marine ecosystem in which they lived.

Key Words

Cheloniidae, Lutetian, paleopathology, shell marks

Introduction

Bioerosion marks serve as frequently encountered indicators of the dynamic interactions between organisms and their environment (Bromley 2004; Augustin et al. 2019). In the vertebrate fossil record, these structures are commonly inferred to signify instances of predation, scavenging, and are inferred to contribute to post-mortem degradation processes (Belaústegui et al. 2012; Higgs et al. 2014; Fernández-Jalvo and Andrews 2016; Ozeki et al. 2020; Szrek et al. 2021; Jamison-Todd et al. 2023). However, in the case of animals with dermal bone, such as turtles, their shells offer a distinctive substrate that is available for the development of bioerosional structure throughout the organism lifespan, unlike other vertebrate bone structures (e.g., Frick et al. 1998; Mader 2006; Pfaller et al. 2008; Zakhama-Sraieb et al. 2010). In fact, shell modifications can encompass a spectrum of alterations, such as encrustations, abrasions, bite marks, and other adaptive changes resulting from a turtle's interactions with its environment (Hutchison and Frye 2001; Reolid et al. 2015; Zonneveld et al. 2015; Gônet et al. 2019; de Valais et al. 2020; El Hedeny et al. 2023; Zonneveld and Bartels 2023). Such bioerosions can be indicative of the type of habitat where the turtles live, their behavioural patterns, and even their state of health (Jacobson 2007; Alfaro et al. 2006; Rothschild et al. 2012; Garner and Jacobson 2020; Zonneveld et al. 2022; El Hedeny et al. 2023; Zonneveld and Bartels 2023). Sea turtles have been extensively studied in the disciplines of biology, evolution, and conservation (Wyneken 2001; Lutz et al. 2002; Orós et al. 2005; Alfaro et al. 2006; Phelan and Eckert 2006; Frick and Pfaller 2013). However, there is relatively scarce information regarding pathology and infectious diseases, especially when extrapolating findings to extinct organisms.

In this context, the objective of the present contribution is to analyse, in detail, diverse typologies of bioerosion marks on the shell of two specimens of sea turtles in order to obtain a better understanding about the interactions between fossil turtles and other organisms in the marine environment. The first specimen analysed herein corresponds favourably with the shell of the holotype of the sea turtle *Eochelone brabantica* Dollo 1903 (i.e., IRSNB R 0001), from the Lutetian (middle Eocene) of the locality of Saint-Remy-Geest (Walloon Brabant, Belgium). The carapace of this *Eochelone brabantica* preserves multiple biomodification traces in several costal plates. The second specimen evaluated in the present contribution corresponds to a carapace of the sea turtle *Puppigerus camperi* (Gray 1831) (i.e., IRSNB R 0004), from the Lutetian (middle Eocene) of Belgium, from the locality of Zaventem, in the Flemish Brabant Province. This specimen displays several types of shell modification traces distributed along the carapace. The analysis of these specimens was performed through detailed macroscopic examination. Additionally, cross-sectional images of traces on *Eochelone brabantica* were provided by CT scanning. Additionally, a 3D model was obtained for *Puppigerus camperi* utilizing photogrammetry. Several external factors are discussed and assessed as potential agents for the anomalies observed on these specimens. As a result, insights into the shell modifications of these two turtle individuals induced by various external agents are provided, enhancing our understanding of both the physical stressors affecting these organisms in ancient marine environments and the identification of the organisms responsible for these changes.

Geological setting

The specimen IRSNB R0001 of *Eochelone brabantica* is registered in the RBINS general inventory under the number IG 2710, which states that it was purchased on February 25th, 1869, from Mr. Lion, quarry master (owner) in Gobertange, a neighbouring village to Saint-Remy-Geest where the specimen was discovered. The specimen was originally embedded in three blocks of sandstone before preparation and mounted for exhibition at RBINS in 1888. Dollo (1903) indicates that the stratigraphic data associated with the specimen were provided by the Belgian geologist Aimé Rutot. The specimen was discovered in a calcareous sandstone of the upper part of the Bruxellian regional stage and the fossil layer associated with bivalves *Crassostrea cymbula* and *Lucina volderiana* corresponds to a littoral facies (Dollo 1903). Today, the Bruxellian is known as the Brussels Sand Formation, an early Lutetian marine stratigraphic unit of Belgium. Micropaleontological analysis of the Brussels Sand Formation in the area of Gobertange has shown that it belongs to the calcareous nannofossil NP 14 biozone (Damblon and Steurbaut 2000; Steurbaut and Nolf 2021).

The specimen IRSNB R 0004 of *Puppigerus camperi* is registered under the number IG 6433, which states that it was purchased on March 5th, 1897, from Mr. Th. Lefèvre, a fossil collector. An old label glued on the back of the specimen indicates that the specimen was found in Saventhem (old name for the city of Zaventem). The specimen is still partially embedded in its original matrix of Bruxellian calcareous sandstone. The Bruxellian of Zaventem has also been correlated with the Lutetian nannofossil NP14 biozone (Herman et al. 2000; Steurbaut and Nolf 2021).

Both specimens belong to the early Lutetian Brussels Sand Formation, which was deposited in the southern part of the North Sea Basin and therefore date from approximatively 46–48 million years ago (Speijer et al. 2020; Steurbaut and Nolf 2021).

Materials and methods

The specimens examined include a partial skeleton with an anomalous carapace, selected for its distinctive markings, along with another specimen consisting of a complete carapace. These specimens represent two distinct taxa of sea turtles (Cheloniidae, Cryptodira) from the Lutetian (middle Eocene) of Belgium. The first individual, IRSNB R 0001 corresponds the shell of the holotype of *Eochelone brabantica* (Fig. 1), from Saint-Remy-Geest (Walloon Brabant). The second specimen, IRSNB R 0004 (Fig. 2), is a carapace of *Puppigerus camperi*, from the locality of Zaventem, in the Flemish Brabant Province. They are currently housed in the Royal Belgian Institute of Natural Sciences (Brussels, Belgium).

The specimens were evaluated by physical examination. A detailed description of the traces is presented. Photographs (taken with a monochrome background, with a digital camera) and schematic drawings (using with Adobe Illustrator CS6) of the anomalous carapaces are included in this study. Additionally, computerized axial tomography was used to confirm and further characterise the origin of some of the biomodification traces on the holotype of *Eochelone brabantica*, particularly those with evident bone remodelling. Externally visible pathological osseous modifications are commonly associated with changes in skeletal microstructure (Hallock et al. 2016). Therefore, cross-sectional images of the plates obtained by CT scanning provided a means with which to assess the potential causes of the alterations, as well as on the nature of the healing processes. The specimen of *Eochelone brabantica* was scanned by the technical service using a RX Solutions micro-CT scanner at the Royal Belgian Institute of Natural Sciences (Brussels, Belgium). The scanning parameters included a voltage of 118 kV, a current of 364 mA, and a resolution of 60.64 μm. A total of 3,882 images were acquired in TIFF format. The data were imported into the Avizo 7.1 software (VSG, Germany) for visualisation and analysis. A 3D model of *Puppigerus camperi* was created using photogrammetry in order to better visualise alterations to the carapace. Images of both specimens were subjected to differential diagnoses following paleopathology methods outlined in Rothschild and Martin (2006).

The discussion was based on the comparison of both medical and veterinary bone pathology literature, so that a presumptive diagnosis was provided. The description of the shell anomalies was performed following the terminology described by Zonneveld and Bartels (2022). Thus, in this study, the term "hole" is used to describe a perforation that penetrates from the outer to the inner surface of the shell bone, while "pit" is used to identify erosions that do not fully penetrate the bone (for more details see Zonneveld and Bartels 2022, and references therein). In this study, the criterion employed to differentiate premortem marks from post-mortem ones is the presence of bone remodelling (Zulfatunnadiroh et al. 2018). The detection of bone regrowth serves as unequivocal evidence that the organism was alive when the pathologies were inflicted by external agents. Consequently, all anomalies accompanied by bone remodelling have been conclusively ascribed to premortem shell marks, while those lacking such bone alterations cannot definitively be linked to premortem events.

Description of the bioerosion marks

Identification of the bioerosion marks of the *Eochelone brabantica* carapace

The holotype (i.e., IRSNB R 0001) of the sea turtle *Eochelone brabantica* consists of a partial skeleton that includes numerous disarticulated elements of the carapace (Fig. 1). Erosive alterations occur in several costal plates, two of which exhibit associated bone remodelling (Figs 1c–f, 3, 4). Of these two, the most prominent mark, both in size and bone remodelling, is located in the left first costal plate of the individual (Fig. 1c, d). This anomaly extends through the external cortex into the cancellous bone. The erosion is characterised to be an amorphous penetrative lesion of about 4.5 cm in length and 2.5 cm in width. It presents smooth margins and evidence of bone remodelling on the inner surface. An asymmetric ridge-shaped bone growth of variable thickness is identified within the base of the erosion (Fig. 1c). This ridge exhibits a smooth contour, with a polished surface in appearance, and is nearly as long as the erosive lesion. In ventral view, the specimen presents an asymmetric bone growth with well-defined rounded margins (Fig. 1d). The dimensions of this structure are 3 cm long, 2.5 cm wide, and it protrudes 0.5 cm past the inner bone surface. The surface of this osseous growth is polished in appearance. The second mark associated with bone remodelling corresponds to a circular erosion located on the anterior margin of the left second costal plate (Fig. 1e, f). The hole, with well-defined lateral margins, is about 1.7 cm in diameter and shows a depth of about 0.3 cm. The erosion presents a hemispherical profile, and a relatively flattened base (Fig. 1e). It penetrates perpendicular to the shell surface and through the external cortex and inner cancellous layers reaching the internal cortex layer of the plate. The bone growth associated with the hole is 1.8 cm long, 1 cm wide, and it extends 0.4 cm over the plate surface. It presents relatively well-defined rounded margins, and an apparently polished surface (Fig. 1f). Cross-sectional images obtained through CT scanning reveal the internal morphology of both anomalies and the associated bone remodelling (Figs 1c–f, 3, 4). CT scans of the second costal plate anomaly display an irregular morphology, with a rounded base of the erosion. Additionally, a hyperdense bone region is visible in certain slices, located around the area of the lesion. This corresponds to newly formed bone, indicative of the healing process (e.g., Fig. 3, b1). Multiplanar and three-dimensional imaging of the circular erosion in the third costal plate further corroborate the macroscopic observations (Fig. 4a, b). These images reveal a subcircular erosion, with a relatively flattened base. In this case, the variations in bone density are less pronounced than those observed in the first costal plate. Nevertheless, a hypodense bone structure is apparent in certain slices (e.g., Fig. 4, a4). The similarities in bone density across slices may suggest a more advanced stage of the healing process, as newly formed tissue typically restores its physical and mechanical properties over time.

The specimen of *Eochelone brabantica* presents other shell anomalies on its carapace, without evidence of bone remodelling (Fig. 1b, g–j). Such deviations are characterised by being relatively penetrative (i.e., some of them reaching the inner cortex layer of the bone), and subcircular in morphology, with well-defined margins. These shell erosions range from 0.2 cm to 0.5 cm in diameter. All of them are perpendicular to the plate surface, being distributed without a specific pattern over the plates.

Identification of the bioerosion marks of the *Puppigerus camperi* carapace

The carapace of the sea turtle *Puppigerus camperi* (IRSNB R 0004) displays various types of alterations, including abnormal erosion of the shell and superficial marks (Fig. 2). Two regions in the posterior area show abnormal absence of some carapacial areas (Fig 2c). The first erosive lesion corresponds a healed fracture and extends from the left ninth peripheral plate to the centre of the carapace, at least reaching the suprapygal (Fig. 2d). It shows a smooth and irregular contour. This pathology results in the partial loss of the left ninth peripheral and the left last costal plate, with the width of the erosion decreasing towards the centre of the carapace. The second abnormal erosion affects the right eleventh peripheral and the pygal, leading to partial loss of these plates, also displaying a smooth and irregular contour (Fig. 2f). Pits and linear grooves are scattered across the

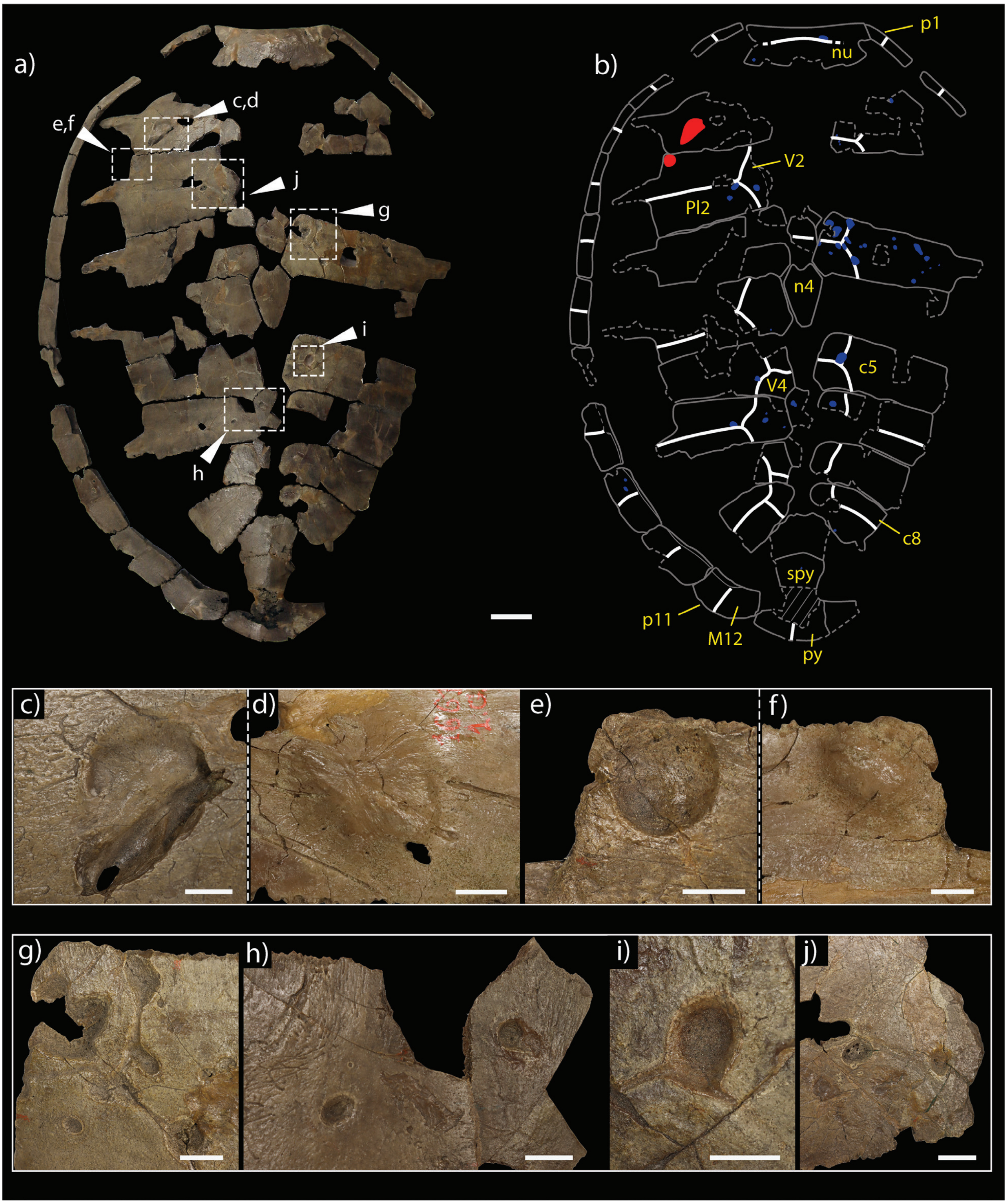

Figure 1. Carapace of the holotype of the sea turtle *Eochelone brabantica* (Cheloniidae, Cryptodira), IRSNB R 0001, from the Lutetian (middle Eocene) of the locality of Saint-Remy-Geest (Walloon Brabant, Belgium). **a, b.** Dorsal view of the carapace; **c–f.** Detail of the shell erosions with a new bone associated, which corresponds to the left second costal plate (**c, d**) and right third costal plate (**e, f**). **g–j.** Detail of the other anomalies identified without evident associated bone remodelling. Scale bars: 5 cm (**a, b**); 1 cm (**c–j**). Anomalies highlighted in blue represent bone modification features not definitively linked to premortem events, while features marked in red are unequivocally attributed as premortem shell damage. Abbreviations for the plates (in lowercase and normal type): c, costal; n, neural; nu, nuchal; p, peripheral; py, pygal; spy, suprapygal. Abbreviations for the scutes (in uppercase and in bold type): M, marginal; Pl, pleural; V, vertebral.

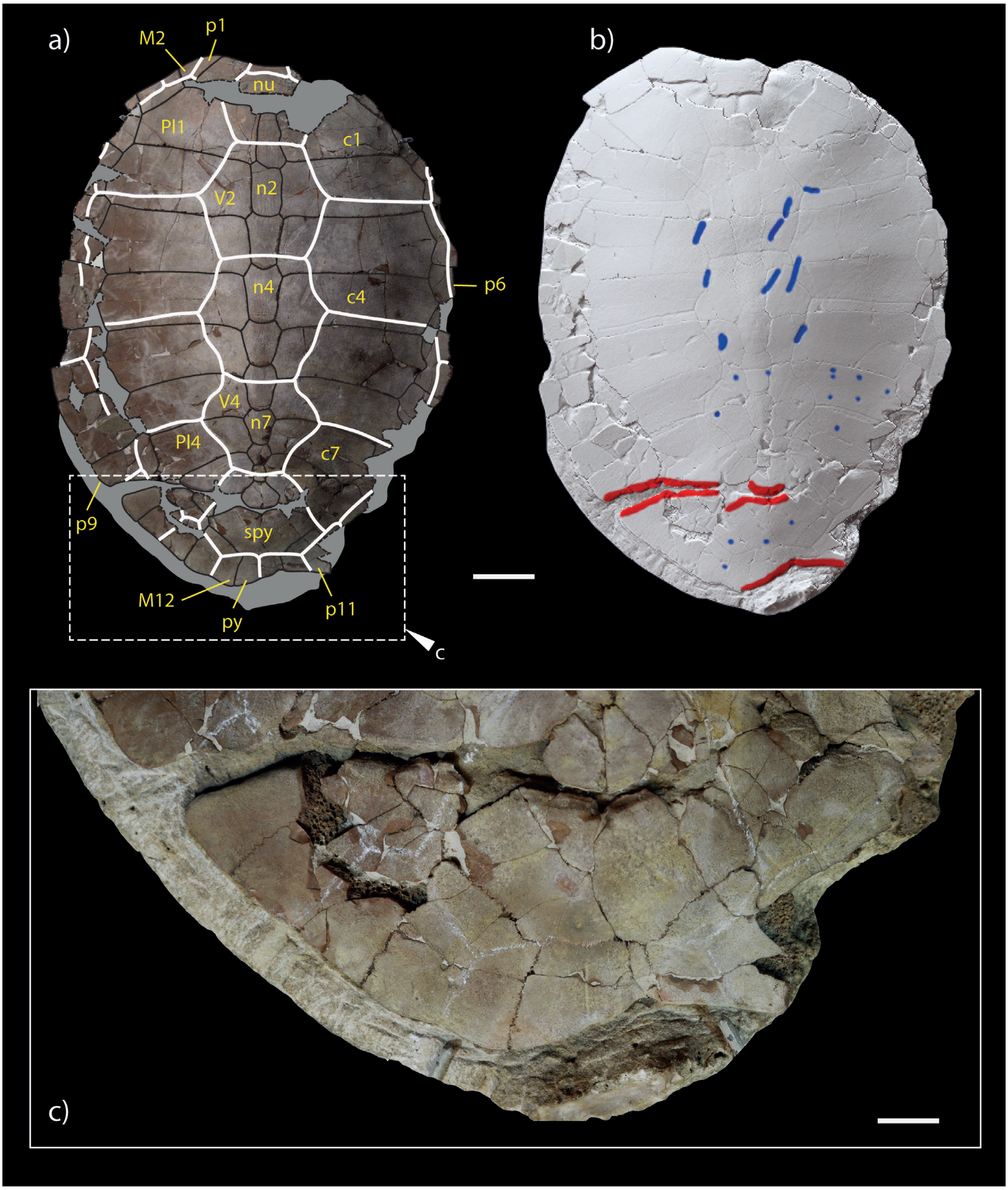

Figure 2. IRSNB R 0004, anomalous carapace of the sea turtle *Puppigerus camperi* (Cheloniidae, Cryptodira), from the Lutetian (middle Eocene) of Belgium, from the locality of Zaventem, in Flemish Brabant Province. **a, b.** Dorsal view of the carapace; **c.** Anomalies with associated bone remodelling in the posterior region of the carapace. Detail of the healed fracture (**d**) and the abnormal erosion of the posterior-most peripheral plates (**e**). Scale bars: 5 cm (**a, b**); 2 cm (**c–e**). Anomalies highlighted in blue represent deviations not definitively linked to premortem events, while deviations marked in red are unequivocally attributed as premortem shell damage. Abbreviations for the plates (in lowercase and normal type): c, costal; n, neural; nu, nuchal; p, peripheral; py, pygal; spy, suprapygal. Abbreviations for the scutes (in uppercase and in bold type): M, marginal; Pl, pleural; V, vertebral.

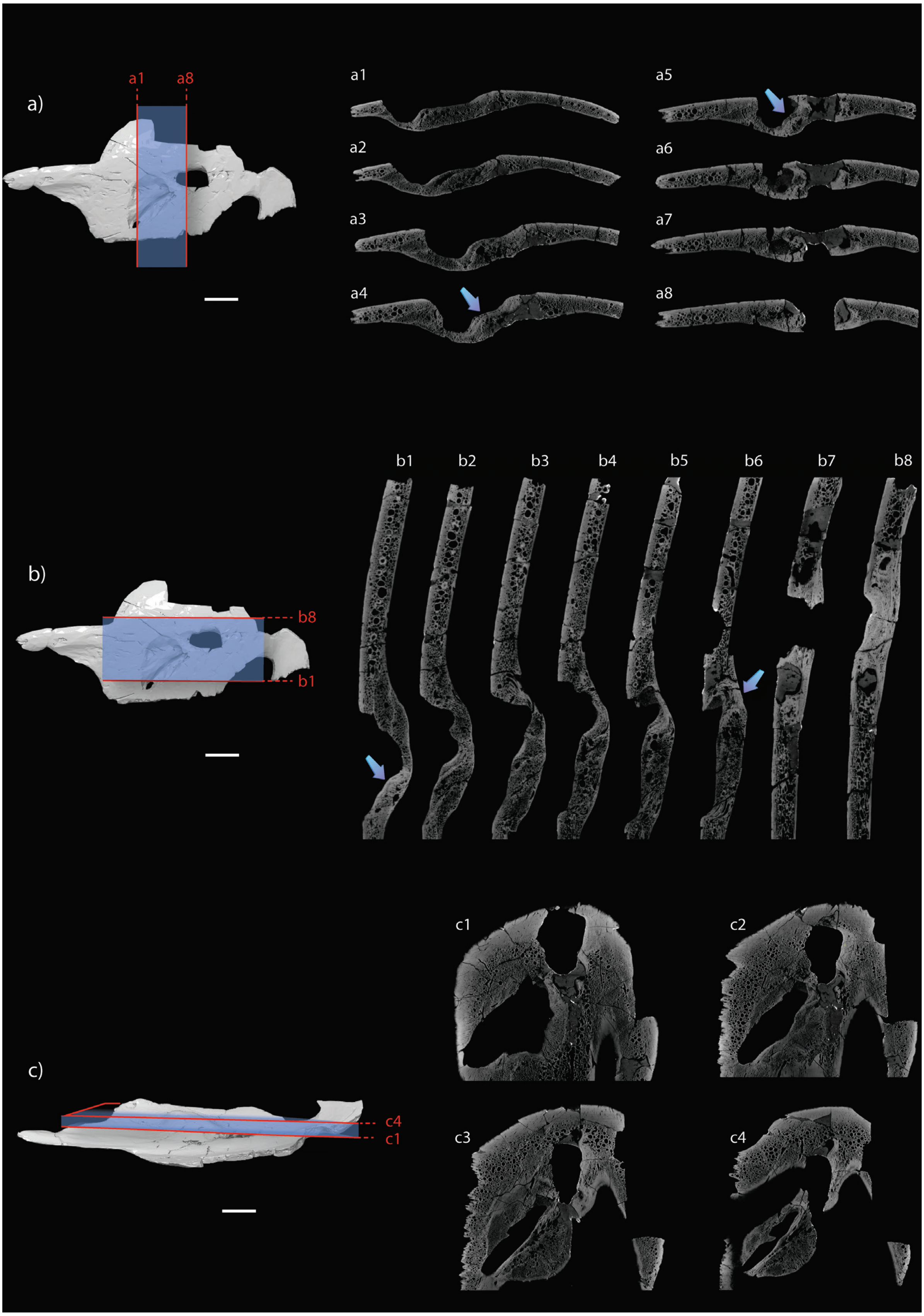

Figure 3. Cross-sectional slices of the left first costal plate obtained through CT scanning of the carapace of the holotype of *Eochelone brabantica* (specimen IRSNB R 0001) from the Lutetian (middle Eocene) of the Saint-Remy-Geest locality (Walloon Brabant, Belgium). **a–c.** 3D models of the ventral (**a, b**) and lateral (**c**) views digitized by photogrammetry. **a1–a8.** Perpendicular view of the hole along the XY plane; **b1–b8.** Perpendicular view of the hole along the YZ plane; **c1–c4.** Parallel view of the hole along the XZ plane. Scale bars: 2 cm. The arrow indicates the hypodense bone structure.

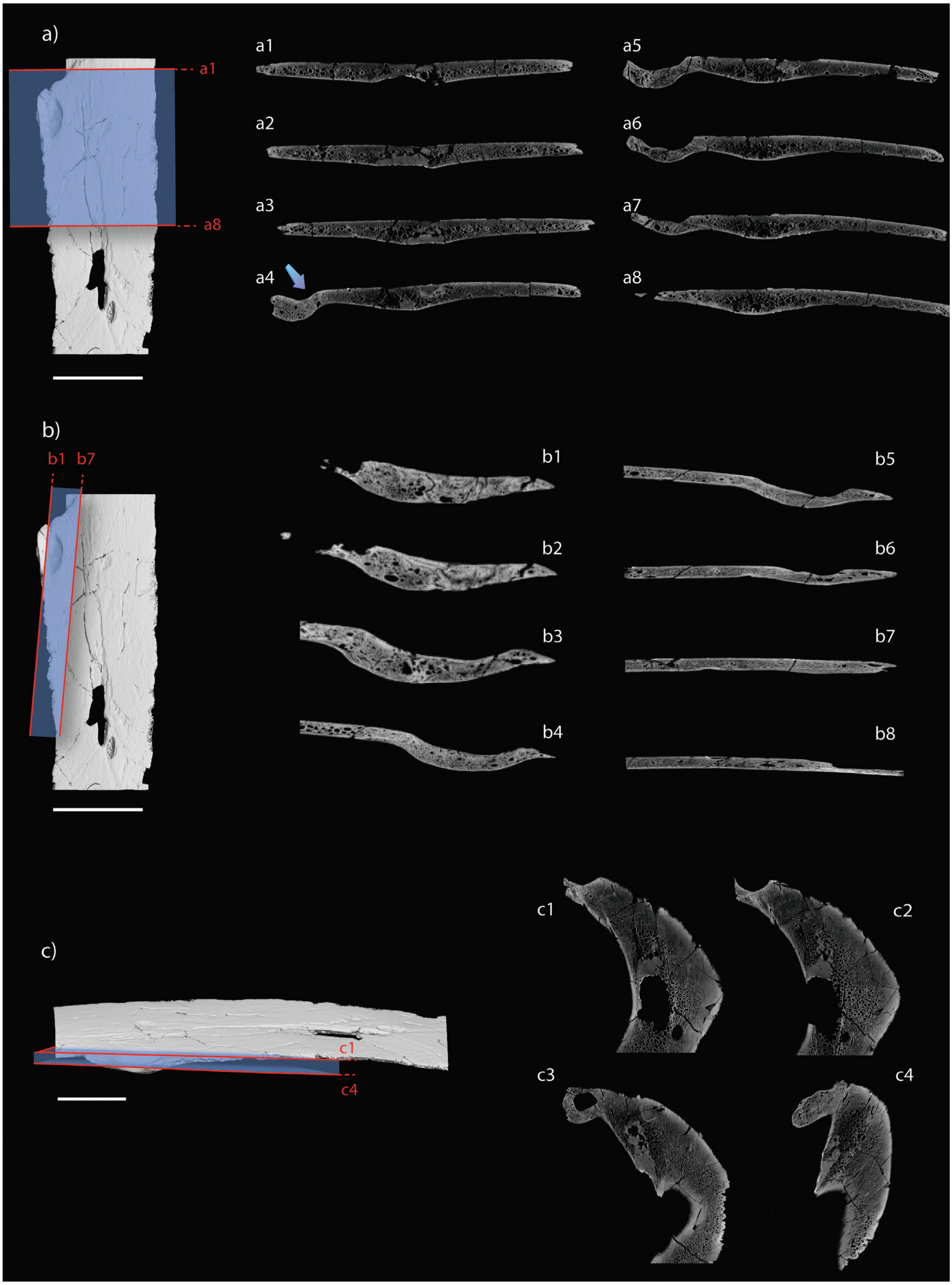

Figure 4. Cross-sectional slices of the left second costal plate obtained through CT scanning of the holotype of *Eochelone brabantica* (specimen IRSNB R 0001) from the Lutetian (middle Eocene) of the Saint-Remy-Geest locality (Walloon Brabant, Belgium). **a–c.** 3D models of the ventral (**a, b**) and lateral (**c**) views digitized by photogrammetry. **a1–a8.** Perpendicular view of the hole along the XY plane. **b1–b7.** Perpendicular view of the hole along the YZ plane. **c1–c4.** Parallel view of the hole along the XZ plane. Scale bars: 4 cm (**a, b**); 2 cm (**c**). The arrow indicates the hypodense bone structure.

carapace, without a discernible pattern (Fig. 2b). None of them fully penetrate the external cortical bone layer. Consequently, no bone remodelling is associated with these superficial anomalies. The pits measure approximately 0.2 cm in diameter, while the linear grooves are about 2.5 cm long and 0.5 cm wide.

Discussion

Etiology for the bioerosion marks of *Eochelone brabantica*

Circular to subcircular pits and holes resembling those observed in the carapace of the holotype of *Eochelone brabantica* (Fig. 1) commonly serve as indicators of predation or parasitism in modern sea turtles (Frick et al. 2002; Alfaro et al. 2006; Domènech et al. 2015). Notably, the anomalies observed on the carapace of the holotype specimen (IRSNB R 0001) that can be unequivocally attributed to premortem shell marks are illustrated in Fig. 1c–f. As remarked by Zonneveld et al. (2022), this typology of shell erosions is frequently observed on fossilised turtles, being commonly interpreted as resulting from vertebrate bite marks, parasitism, as well as post-mortem scavenging invertebrates (Erickson 1984; Jiménez-Fuentes 2003; Milàn et al. 2010; Noto et al. 2012: Botfalvai et al. 2014; Myrvold et al. 2018; Gônet et al. 2019; Jagt et al. 2020; De La Garza et al. 2021; Drumheller et al. 2023). In the case of the carapace of IRSNB R 0001, the anomalies identified have been ruled out as resulting from predation by a vertebrate organism. This determination is based on several criteria: the lesions do not follow a specific pattern indicative of predator teeth structure; they lack associated drag-out structures, being well-defined without broken edges (e.g., Fig. 1h, i); and no other typologies of shell lesions, such as punctures, scratches, or mechanical deformations, are associated with those observed in the specimen.

Extant sea turtles can harbour a wide variety of epibionts that can compromise the integrity of their shells, leading to the development of various types of shell lesions (Pfaller et al. 2008). Among the epibionts commonly found on turtle shells and capable of causing lesions are cnidarians (e.g., hydrozoans; Pfaller et al. 2008), mollusks (e.g., boring bivalves; Frazier et al. 1985), arthropods (e.g., barnacles; Caine 1986), platyhelminths (e.g., saltwater leeches; Göpper et al. 2018), and algae (e.g., Rhodophyceae; Abel Sentíes et al. 1999). While some of these epibionts act as commensals and cause minimal damage (i.e., hydrozoans and algae), some may function as parasites (i.e., mollusks, leeches or barnacles), inflicting significant lesions, as those observed in IRSNB R 0001. In this context saltwater leeches and mollusks exhibit inconsistencies that make them unlikely contributors to the anomalies observed in *Eochelone brabantica*. Saltwater leeches have been identified as contributors to certain infections found on the body and carapaces of sea turtles, resulting in erosive lesions on the skin and shell where they attach (Davies and Chapman 1974; Göpper et al. 2018). However, although the morphology of the lesions caused by saltwater leeches may coincide with those observed on the carapace of *Eochelone brabantica* (e.g., subcircular erosions with well-defined margins), their size does not match with those produced by these parasites. Saltwater leeches that affect sea turtles (i.e., those belonging to the genus *Ozobranchus*) range in size from 5 to 30 mm (Apathy 1890; Cordero 1929; Ghosh et al. 1963). While it is theoretically possible that fossil leeches capable of causing such lesions could differ in clade or size from extant *Ozobranchus* species, there is currently no evidence supporting the existence of larger leeches exhibiting similar parasitic behaviour on sea turtles. The lesions on the shell of IRSNB R 0001, with the smallest measuring 80 mm, far exceed the size range associated with any known leeches, whether fossil or extant. Therefore, based on the best available data, saltwater leeches are unlikely to be responsible for the anomalies observed in *Eochelone* brabantica. Similarly, molluscan organisms such as boring bivalves (pholadids) have also been reported in sea turtles as contributors to shell pitting (e.g., Sato and Jenkins 2020). However, although the size may align with the anomalies observed in *Eochelone brabantica*, the morphology of the shell erosions typically associated with boring bivalves does not match with that described in IRSNB R 0001. Specifically, boring bivalves are known to produce clavate or tear-shaped lesions (Bromley 2004; Jenkins et al. 2017; Sato and Jenkins 2020), which differ significantly from the circular to subcircular marks discussed here.

Coronuloidea barnacles (i.e., barnacles that are primarily parasites) are epibiotic organisms that live cemented to inert substrates such as rocks or the external surfaces of various marine vertebrates, such as cetaceans or turtles (Kearn 2005). Currently, these cirripedes are classified into three families (Coronulidae, Chelonibiidae, and Platylepadidae, Ross and Frick 2011; Hayashi et al. 2013), with Chelonibiidae and Platylepadidae being mostly known as turtle barnacles (Ross 1963a, b; Ross and Newman 1967; Caine 1986). The association between barnacles and their chelonian hosts has persisted for more than 30 million years (Collareta et al. 2023). Thus, reports of their activity tracks in the form of attachment scars on several marine turtles in the fossil record are prevalent in the literature (e.g., Hayashi et al. 2013; Janssen et al. 2013; Collareta et al. 2019; Collareta et al. 2022a, b). They are often found partly embedded in the turtle carapace and plastron and can cause minimal stress (e.g., increased surface drag) or more serious damage to the shell, leading to bacterial or fungal infections. These parasites commonly penetrate the bone, thus occupying an intermediate position (i.e., mesoparasites), between ectoparasites and endoparasites (Zonneveld et al. 2022). Depending on the shell shape, the ontogenetic stage, and the anchoring apparatus of the barnacles creating the traces, the resulting scars on the turtle shell may vary in shape from shallow circular and hemispherical pits to deep cylindrical holes (i.e., penetrating through the outer dense bone layer into the more cancellous bone beneath, Seigel 1983) (Zonneveld et al. 2015, 2022; Collareta et al. 2022a, b). In this sense, the shell marks produced by barnacles coincide both in size and morphology with those observed in the carapace of *Eochelone brabantica* (Fig. 1). Specifically, the morphology of these marks includes smooth internal surfaces within the pits, consistent with bone erosion caused by the attachment structures of barnacles, and well-defined but irregular margins that reflect the invasive anchoring apparatus of the cirripedes. The smaller pits (e.g., Fig. 1g) probably represent non-adult barnacles, whereas the deep perforations (e.g., Fig. 1e) suggest that the cirripedes had enough time to develop and acquire significant size. Similarly, shell lesions with amorphous morphology (Fig. 1c) have been interpreted as a probable association of two or more barnacles causing the development of significant scar tissue or some type of infection produced by these parasites. Additionally, distribution of the multifocal shell marks in the individual of *Eochelone brabantica* are also compatible with the presence of barnacles, as these are commonly located on the shell without a specific pattern, sometimes grouped in a region of the shell or distributed across all areas. Thus, based on the size, internal texture, and marginal shape of the lesions, as well as their distribution, arthropods, particularly barnacles (crustaceans of the subclass Cirripedia), are the most likely to induce lesions similar to those observed in the carapace of IRSNB R 0001.

Etiology for the bioerosion marks of *Puppigerus camperi*

The IRSNB R 0004 specimen of *Puppigerus camperi* exhibits various types of erosive anomalies on its carapace (Fig. 2): pits, grooves, and an abnormal absence of a shell region (i.e., including a healed fracture and the erosion of the posterior-most region of the carapace). Notably, the abnormal absence of two shell regions is the only type of injury that can be unequivocally identified as pre-mortem damage and it is the focus of the present discussion (Fig. 2d, e). Determining a specific cause for the fracture is complex, as numerous factors during the turtle lifetime could have led to this type of shell lesion, making it difficult to attribute it to a concrete cause. In this context, some type of traumatism has been considered as the more probable cause for the healed fracture of IRSNB R 0004 (Fig. 2c, d). Likewise, anomalies similar to that observed in the carapace of *Puppigerus camperi* are commonly associated with traumatic injury in extant sea turtles. When the origin of such anomalies is unknown, they are typically attributed, by default, to boat strikes or predator attacks (i.e., shark attack) (e.g., Orós et al. 2005; Phelan et al. 2006). In this case, it is considered improbable that a predator attack caused the injury, since, as mentioned above, it would be expected to see associated marks of predation (e.g., mechanical deformation or tooth marks), which are not present in this specimen. Consequently, given the lack of specific indicators elucidating the etiology of this trauma, it is deemed inappropriate to provide a definitive diagnosis for the fracture. As a healing process, the shell can regenerate and remodel when injured, as observed in the case of the healed fracture of IRSNB R 0004. In the literature on extant turtles, it is often noted that open shell fractures in aquatic turtles carry a high risk of infection (Mader 2006). Consequently, it is uncertain whether the fracture observed in the fossil was solely caused by the initial physical trauma, whether the injury was more extensive and we are observing the result of subsequent healing, or if minor injuries subsequently became infected, leading to more extensive areas of necrosis. Regardless, the fracture did not involve any particularly vulnerable parts of the body, as the spinal column does not extend this far caudally in the carapace. Therefore, it did not result in the immediate death of the specimen.

Similar to the healed fracture, the abnormal erosion affecting the right eleventh peripheral and pygal plate (Fig. 2e, f) may be attributed to various external factors. For instance, this erosion could be compatible with a healed fracture caused by some type of trauma or could correspond to a set of healed plates eroded by an epibiont (e.g., a mollusk, Hayward and Ryland 1990) rasping on the shell margins when the turtle was not fully developed, as occurs in some extant sea turtles. In any case, this pathology appears not to have impacted the primary functions of the body. It cannot be confirmed whether this abnormal erosion is associated with the healed fracture discussed above or represents separate anomalies. The available evidence does not allow for a definitive conclusion on whether the anomalies in the posterior region of the carapace have a common origin. However, the most parsimonious explanation suggests that both erosive lesions are likely caused by the same factor, given their similar characteristics and location.

Several superficial pits have been observed scattered across the carapace (Fig. 2b). These marks are consistent with two potential etiologies: small invasive barnacles (see section 4.2 for more details), this area being the most likely region in extant turtles to accumulate such organisms; or by some vertebrate or invertebrate activity during the postmortem process. Regarding the linear grooves (Fig. 2b), they are consistent with marks typically associated with organic processes during the postmortem interval, such as invertebrate activity, solution marks made by plants or microorganisms (Fernández-Jalvo and Andrews 2016). Specifically, these grooves are characterized by their U-shaped profile, smooth contours, lack of ornamentation, and gently convex or slightly flattened cross-sections, which align with the morphology expected from such processes (Fernández-Jalvo and Andrews 2016 and references therein). However, it cannot be definitively confirmed that these grooves did not originate while the organism was alive, thus their precise etiology remains uncertain.

Conclusions

Diverse types of bioerosion marks on the shells of two sea turtle specimens from the Lutetian (middle Eocene) of Belgium have been analysed here. The first specimen corresponds to the shell of the holotype of the sea turtle *Eochelone brabantica* (i.e., IRSNB R 0001), from Saint-Remy-Geest (Walloon Brabant). The second individual evaluated in the present contribution corresponds to a carapace of the sea turtle *Puppigerus camperi* IRSNB R 0004, from Zaventem, in the Flemish Brabant Province. Both specimens present various types of erosive shell deviations distributed along their carapace. Specifically, several erosive alterations (i.e., with different morphologies and depths) have been identified on various costal plates of the holotype of *Eochelone brabantica*, two of which exhibit associated bone remodelling. Regarding *Puppigerus camperi*, various types of alterations have been described, including abnormal erosion of the carapace (i.e., a healed fracture and the abrasion of the posterior-most region of the carapace) and superficial marks (pits and grooves). Of these anomalies, only those with bone remodelling have been conclusively ascribed to premortem shell marks, while those lacking such bone alterations cannot definitively be linked to premortem events (e.g., the superficial pits and grooves).

The combination of macroscopic examination, imaging techniques (i.e., CT scanning and 3D surface scanning), and comparative analyses with similar anomalies observed in extant turtles facilitated the identification of potential agents responsible for the anomalies of the two Belgian sea turtle fossils. Specifically, the erosions of *Eochelone brabantica* have been attributed to an association of epibiotic organisms, particularly barnacles. The shell marks produced by barnacles coincide both in size and morphology with those observed in the carapace of this individual. The healed fracture displayed by the *Puppigerus camperi* individual is suggested to result from some type of trauma, whereas the abnormal erosion of the posterior-most region of the carapace is likely due to abrasion by invertebrate organisms (e.g., mollusks) or to a trauma. The superficial marks of *Puppigerus camperi* (pits and grooves) have been attributed to barnacle activity (i.e., in the case of the pits), and other organic processes (i.e., in the case of grooves). In neither fossil did the skeletal anomalies appear to involve particularly vulnerable parts of the body, and thus, the cause of death of these sea turtles is not likely linked to these lesions.

Acknowledgments

This research was funded by an FPI UNED fellowship and by the Ministerio de Ciencia e Innovación (PID2019-111488RB-I00). The authors express their gratitude to the Royal Belgian Institute of Natural Sciences (Brussels, Belgium) for the CT scanning of the specimen IRSNB R 0001, for providing photographs of the two specimens analysed here, and curator Dr. Annelise Folie for access to the specimens and for sharing valuable information about them. Additionally, the authors sincerely thank Dr. Jeanette Wyneken (Florida Atlantic University) and Dr. Amy Bonka (Sea Turtle Inc.) for invaluable suggestions regarding the anomalies observed in the specimens. The authors also thank the editors Florian Witzmann and Torsten Scheyer, and the reviewers John-Paul Zonneveld (University of Alberta, Canada) and Stephanie K. Drumheller (University of Tennessee, United States of America) for their useful comments and their constructive reviews.

References

Abel Sentíes G, Espinoza-Avalos J, Zurita JC (1999) Epizoic algae of nesting sea turtles *Caretta caretta* (L.) and *Chelonia mydas* (L.) from the Mexican Caribbean. Bulletin of marine science 64: 185–188.

Alfaro A, Køie M, Buchmann K (2008) Synopsis of infections in sea turtles caused by virus, bacteria and parasites: an ecological review. In: 27th annual symposium on sea turtle biology and conservation. NOAA Tech Memo Myrtle Beach.

Apathy ST (1890) *Pseudobranchellion margoi* (Nova familia Hirudinearum). OrvosTermeszettudomanyi Eresito 15: 122–127.

Augustin FJ, Matzke AT, Csiki-Sava Z, Pfretzschner HU (2019) Bioerosion on vertebrate remains from the Upper Cretaceous of the Haţeg Basin, Romania and its taphonomic implications. Palaeogeography, Palaeoclimatology, Palaeoecology 534: 109318. https://doi.org/10.1016/j.palaeo.2019.109318

Belaústegui Z, de Gibert JM, Domènech R, Muñiz F, Martinell J (2012) Clavate borings in a Miocene cetacean skeleton from Tarragona (NE Spain) and the fossil record of marine bone bioerosion. Palaeogeography, Palaeoclimatology, Palaeoecology 323: 68–74. https://doi.org/10.1016/j.palaeo.2012.01.031

Botfalvai G, Prondvai E, Ősi A (2014) Inferred bite marks on a Late Cretaceous (Santonian) bothremydid turtle and a hylaeochampsid crocodilian from Hungary. Cretaceous Research 50: 304–317. https://doi.org/10.1016/j.cretres.2014.05.006

Bromley RG (2004) A stratigraphy of marine bioerosion. Geological Society, London, Special Publications 228: 455–479. https://doi.org/10.1144/GSL.SP.2004.228.01.20

Caine EA (1986) Carapace epibionts of nesting loggerhead sea turtles: Atlantic coast of USA. Journal of Experimental Marine Biology and Ecology 95: 15–26. https://doi.org/10.1016/0022-0981(86)90084-5

Collareta A, Reitano A, Rosso A, Sanflippo R, Bosselaers M, Bianucci G, Insacco G (2019) The oldest platylepadid turtle barnacle (Cirripedia, Coronuloidea): A new species of Platylepas from the Lower Pleistocene of Italy. European Journal of Taxonomy 516: 1–17. https://doi.org/10.5852/ejt.2019.516

Collareta A, Harzhauser M, Rasser MW (2022a) New and overlooked occurrences of the rarely reported protochelonibiine "turtle" barnacles from the Oligocene and Miocene of Europe. PalZ 96: 197–206. https://doi.org/10.1007/s12542-021-00576-5

Collareta A, Merella M, Bosselaers M, Casati S, Di Cencio A, Bianucci G (2022b) A *Karethraichnus* boring on a turtle shell bone from the Miocene of Italy is assessed as the attachment scar of a platylepadid symbiont. Neues Jahrbuch Für Geologie Und Paläontologie Abhandlungen 303: 327–337. https://doi.org/10.1127/njgpa/2022/1052

Collareta A, Rasser MW, Frey E, Harzhauser M (2023) Turtle barnacles have been turtle riders for more than 30 million years. PalZ 97: 353–363. https://doi.org/10.1007/s12542-022-00641-7

Cordero EH (1929) Notes sur les hirudinées, I. Quelques observations sur la morphologie externe d'*Ozobranchus margoi* (Apathy). Annales de Parasitologie Humaine et Comparée 7: 209–217. https://doi.org/10.1051/parasite/1929073209

Davies RW, Chapman CG (1974) First record from North America of the piscicolid leech, *Ozobranchus margoi*, a parasite of marine turtles. Journal of the Fisheries Board of Canada 31: 104–106. https://doi.org/10.1139/f74-016

De La Garza RG, Madsen H, Eriksson ME, Lindgren J (2021) A fossil sea turtle (Reptilia, Pan-Cheloniidae) with preserved soft tissues from the Eocene Fur Formation of Denmark. Journal of Vertebrate Paleontology 41: e1938590. https://doi.org/10.1080/02724634.2021.1938590

de Valais S, Díaz-Martínez I, Citton P, Maniel I, de la Fuente M (2020) A predation attempt in a Late Cretaceous pleurodire turtle from Patagonia. Cretaceous Research 107: 104290. https://doi.org/10.1016/j.cretres.2019.104290

Dollo L (1903) *Eochelone brabantica*, tortue marine nouvelle du Bruxellien (Eocène moyen) de la Belgique et l'évolution des chéloniens marins, Bulletins de l'Académie royale des sciences, des lettres et des beaux-arts de Belgique 8: 792–801.

Domènech F, Badillo FJ, Tomás J, Raga JA, Aznar FJ (2015) Epibiont communities of loggerhead marine turtles (*Caretta caretta*) in the western Mediterranean: influence of geographic and ecological factors. Journal of the marine biological Association of the United Kingdom 95: 851–861. https://doi.org/10.1017/S0025315414001520

Drumheller SK, Maddox H, Stocker MR, Tech V, Noto CR (2023) Differentiating convergent pathologies in turtle shells using computed tomographic scanning of modern and fossil bone. Palaeontologia Electronica 26: a15. https://doi.org/10.26879/1230

El Hedeny M, Mohesn S, Tantawy AA, El-Sabbagh A, AbdelGawad M, El-Kheir GA (2023) Bioerosion traces on the Campanian turtle remains: New data from the lagoonal deposits of the Quseir Formation, Kharga Oasis, Egypt. Palaeontologia Electronica 26: a40. https://doi.org/10.26879/1315

Erickson BR (1984) Chelonivorous habits of the Paleocene crocodile *Leidyosuchus formidabilis*. Scientific Publications of The Science Museum of Minnesota 5: 3–9.

Fernández-Jalvo Y, Andrews P (2016) Atlas of taphonomic identifications: 1001+ images of fossil and recent mammal bone modification. Springer, 359 pp. https://doi.org/10.1007/978-94-017-7432-1

Frazier JG, Margaritoulis D, Muldoon K, Potter CW, Rosewater J, Ruckdeschel C, Salas S (1985) Epizoan communities on marine turtles. I. Bivalve and gastropod mollusks. Marine Ecology 6: 127–140. https://doi.org/10.1111/j.1439-0485.1985.tb00134.x

Frick MG, Williams KL, Robinson M (1998) Epibionts associated with nesting loggerhead sea turtles (*Caretta caretta*) in Georgia, USA. Herpetological Review 29: 211.

Frick MG, Pfaller JB (2013) 15 sea turtle epibiosis. In: Wyneken J, Lohmann K, Musick J (Eds) The Biology of Sea Turtles, Volume III, 399–426. https://doi.org/10.1201/b13895-16

Frick MG, Williams KL, Veljacic DC (2002) New records of epibionts from loggerhead sea turtles *Caretta caretta* (L.). Bulletin of Marine Science 70: 953–956.

Garner MM, Jacobson ER (2020) Noninfectious Diseases and Pathology of Reptiles: Color Atlas and Text, Diseases and Pathology of Reptiles, Volume 2. CRC Press, 534 pp. https://doi.org/10.1201/9780429154317

Ghosh JM (1963) On the Occurrence of the Leech *Ozobranchus Branchiatus* (Menzies 1791) (Hirudinea) in India (Gulf of Kutch). The Journal of the Bombay Natural History Society 60: 469–471.

Gônet J, Rozada L, Bourgeais R, Allain R (2019) Taphonomic study of a pleurosternid turtle shell from the Early Cretaceous of Angeac-Charente, southwest France. Lethaia 52: 232–243. https://doi.org/10.1111/let.12309

Göpper BM, Voogt NM, Ganswindt A (2018) First record of the marine turtle leech (*Ozobranchus margoi*) on hawksbill turtles (*Eretmochelys imbricata*) in the inner granitic Seychelles. Onderstepoort Journal of Veterinary Research 85: 1–3. https://doi.org/10.4102/ojvr.v85i1.1604

Gray JE (1831) Synopsis Reptilium; or short descriptions of the species of Reptiles (Vol 1). Treuttel, Wurts, and Company, London, 122 pp. https://doi.org/10.5962/bhl.title.4697

Hayashi R, Chan BKK, Simon-Blecher N, Watanabe H, Guy-Haim T, Yonezawa T, Levy Y, Shuto T, Achituv Y (2013) Phylogenetic position and evolutionary history of the turtle and whale barnacles (Cirripedia: Balanomorpha: Coronuloidea). Molecular Phylogenetics and Evolution 67: 9–14. https://doi.org/10.1016/j.ympev.2012.12.018

Hayward PJ, Ryland JS (1990) Bivalve molluscs as epibionts. In: Bivalves: Their Ecology and Physiology. Springer, Dordrecht, 417–439.

Herman J, Steurbaut E, Vandenberghe N (2001) The boundary between the Middle Eocene Brussel Sand and the Lede Sand formations in the Zaventem-Nederokkerzeel area (Northeast of Brussels, Belgium). Geologica Belgica 3(3–4): 231–255. https://doi.org/10.20341/gb.2014.031

Higgs ND, Glover AG, Dahlgren TG, Smith CR, Fujiwara Y, Pradillon F, Johnson SB, Vrijenhoek RC, Little CTS (2014) The morphological diversity of *Osedax* worm borings (Annelida: Siboglinidae). Journal of the Marine Biological Association of the United Kingdom 94: 1429–1439. https://doi.org/10.1017/S0025315414000770

Hutchison JH, Frye FL (2001) Evidence of pathology in early Cenozoic turtles. PaleoBios 21: 12–19.

Jacobson ER (2007) Infectious diseases and pathology of reptiles: Color atlas and text. CRC Press, 736 pp. https://doi.org/10.1201/9781420004038

Jagt JW, Deckers MJ, De Leebeeck M, Donovan SK, Nieuwenhuis E (2020) Episkeletozoans and bioerosional ichnotaxa on isolated bones of Late Cretaceous mosasaurs and cheloniid turtles from the Maastricht area, the Netherlands. Geologos 26: 39–49. https://doi.org/10.2478/logos-2020-0003

Jamison-Todd S, Upchurch P, Mannion PD (2023) The prevalence of invertebrate bioerosion on Mesozoic marine reptile bone from the Jurassic and Cretaceous of the United Kingdom: new data and implications for taphonomy and environment. Geological Magazine 160: 1701–1710. https://doi.org/10.1017/S0016756823000651

Janssen R, van Baal RR, Schulp AS (2013) Bone damage in *Allopleuron hofmanni* (Cheloniidae, Late Cretaceous). Netherlands Journal of Geosciences 92: 153–157. https://doi.org/10.1017/S0016774600000081

Jenkins RG, Kaim A, Sato K, Moriya K, Hikida Y, Hirayama R (2017) Discovery of chemosynthesis-based association on the Cretaceous basal leatherback sea turtle from Japan. Acta Palaeontologica Polonica 62: 683–690. https://doi.org/10.4202/app.00405.2017

Jiménez-Fuentes E (2003) Predación crocodiliana a quelonios. Un *Neochelys* (Pelomedusidae), del Eoceno de Zamora, lisiado por un *Asiatosuchus*. Studia Geologica Salmanticensia 39: 11–23.

Kearn GC (2005) Leeches, lice and lampreys: a natural history of skin and gill parasites of fishes. Springer Science & Business Media, 432 pp. https://doi.org/10.1007/978-1-4020-2926-4

Lutz PL, Musick JA, Wyneken J (2002) The biology of sea turtles, Volume II. CRC press. https://doi.org/10.1201/9781420040807

Mader DR (2006) Reptile medicine and surgery. Saunders Elsevier, Westline Industrial Drive, St. Louis, Missouri, 1242 pp.

Milàn J, Kofoed J, Bromley RG (2010) Crocodylian-chelonian carnivory: bite traces of Dwarf Caiman, Paleosuchus palpebrosus in red-eared slider, *Trachemys scripta* carapaces. New Mexico Museum of Natural History and Science 51: 195–200.

Myrvold KS, Milàn J, Rasmussen JA (2018) Two new finds of turtle remains from the Danian and Selandian (Paleocene) deposits of Denmark with evidence of predation by crocodilians and sharks. Bulletin of the Geological Society of Denmark 66: 211–218. https://doi.org/10.37570/bgsd-2018-66-11

Noto CR, Main DJ, Drumheller SK (2012) Feeding traces and paleobiology of a Cretaceous (Cenomanian) crocodyliform: Example from the Woodbine Formation of Texas. PALAIOS 27: 105–115. https://doi.org/10.2110/palo.2011.p11-052r

Orós J, Torrent A, Calabuig P, Déniz S (2005) Diseases and causes of mortality among sea turtles stranded in the Canary Islands, Spain (1998–2001). Diseases of aquatic organisms 63: 13–24. https://doi.org/10.3354/dao063013

Ozeki CS, Martill DM, Smith RE, Ibrahim N (2020) Biological modification of bones in the Cretaceous of North Africa. Cretaceous Research 114: 104529. https://doi.org/10.1016/j.cretres.2020.104529

Pfaller JB, Bjorndal KA, Reich KJ, Williams KL, Frick MG (2008) Distribution patterns of epibionts on the carapace of loggerhead turtles, *Caretta caretta*. Marine Biodiversity Records 1: e36. https://doi.org/10.1017/S1755267206003812

Phelan SM, Eckert KL (2006) Marine Turtle Trauma Response Procedures: A Field Guide. Wider Caribbean Sea Turtle Conservation Network (WIDECAST) Technical Report 4. Beaufort, North Carolina USA, 71 pp.

Reolid M, Santos A, Mayoral E (2015) Grazing activity as taphonomic record of necrobiotic interaction: A case study of a sea turtle carapace from the Upper Jurassic of the Prebetic (south Spain). Revista mexicana de ciencias geológicas 32: 21–28.

Ross, A (1963a) A new Pleistocene Platylepas from Florida. Quarterly Journal of the Florida Academy of Science 26: 150–158.

Ross A (1963b) Chelonibia in the Neogene of Florida. Quarterly Journal of the Florida Academy of Science 26: 221–233.

Ross A, Frick MF (2011) Nomenclatural emendations of the family-group names Cylindrolepadinae, Stomatolepadinae, Chelolepadinae, Cryptolepadinae, and Tubicinellinae of Ross & Frick, 2007—including current definitions of family-groups within the Coronuloidea (Cirripedia: Balanomorpha). Zootaxa 3106: 60–66. https://doi.org/10.11646/zootaxa.3106.1.4

Ross A, Newman WA (1967) Eocene Balanidae of Florida, including a new genus and species with a unique plan of “ turtle-barnacle” organization. American Museum novitates 2288: 203–205.

Rothschild BM, Schultze HP, Pellegrini R, Rothschild BM, Schultze HP, Pellegrini R (2012) Summary of osseous pathology in amphibians and reptiles. Herpetological Osteopathology: Annotated bibliography of amphibians and reptiles. Springer, New York, 11–53. https://doi.org/10.1007/978-1-4614-0824-6_4

Sato K, Jenkins RG (2020) Mobile home for pholadoid boring bivalves: first example from a Late Cretaceous sea turtle in Hokkaido Japan. Palaios 35: 228–236. https://doi.org/10.2110/palo.2019.077

Seigel RA (1983) Occurrence and efects of barnacle infestations on diamondback terrapins (*Malaclemys terrapin*). American Midland Naturalist 109: 34–39. https://doi.org/10.2307/2425512

Speijer RP, Pälike H, Hollis CJ, Hooker JJ, Ogg JG (2020) The Paleogene Period. In: Gradstein FM, Ogg JG, Schmitz MD, Ogg GM (Eds) Geologic time scale 2020: Volume 2, 1087–1140. Oxford, England: Elsevier. https://doi.org/10.1016/B978-0-12-824360-2.00028-0

Steurbaut E, Nolf D (2021) The Mont-des-Récollets section (N France): a key site for the Ypresian-Lutetian transition at mid-latitudes — reassessment of the boundary criterion for the base-Lutetian GSSP. Geodiversitas 43: 311–363. https://doi.org/10.5252/geodiversitas2021v43a11

Szrek P, Dworczak PG, Wilk O (2021) Bioerosion traces and borings in the Upper Devonian vertebrate remains from the Holy Cross Mountains, Poland Bioerosion in fish remains. bioRxiv. https://doi.org/10.1101/2021.07.23.453559

Wyneken J (2001) The Anatomy of Sea Turtles. U.S. Department of Commerce NOAA Technical Memorandum NMFS-SEFSC-470, 172 pp.

Zakhama-Sraieb R, Karaa S, Bradai MN, Jribi I, Charfi-Cheikhrouha F (2010) Amphipod epibionts of the sea turtles *Caretta caretta* and *Chelonia mydas* from the Gulf of Gabès (central Mediterranean). Marine Biodiversity Records 3: e38. https://doi.org/10.1017/S1755267210000333

Zonneveld JP, Bartels WS, Gunnell GF, McHugh LP (2015) Borings in early Eocene turtle shell from the Wasatch Formation, South Pass, Wyoming. Journal of Paleontology 89: 802–820. https://doi.org/10.1017/jpa.2015.61

Zonneveld JP, Bartels WS (2022) The occurrence of bone modification features in the carapace and plastron of the extant red-eared Slider *Trachemys scripta elegans* (Wied-Neuwied, 1839): implications for paleoecological analyses of fossil turtle assemblages. Palaios 37: 499–519. https://doi.org/10.2110/palo.2022.018

Zonneveld JP, Zonneveld ZEE, Bartels WS, Gingras MK, Head JJ (2022) Bone modification features resulting from barnacle attachment on the bones of loggerhead sea turtles (*Caretta caretta*), Cumberland Island, Georgia, USA: Implications for the paleoecological, and taphonomic analyses of fossil sea turtles. Palaios 37: 650–670. https://doi.org/10.2110/palo.2022.021

Zonneveld JP, Bartels WS (2023) The occurrence and significance of ulcerative Shell disease (USD) on geoemydid turtles, middle Eocene, southwestern Wyoming, United States. Palaios 38: 453–473.

Zulfatunnadiroh LA, Prastyo E, Dimpudus ROY, Dyah M (2018) Bone Damage in the Antemortem, Perimortem, and Postmortem Periods: Looking for Traumatic Indications on Bones for Assessing the Quality of Life of Skeletal Remains. In: Innovation of Technology and Bureaucracy Towards Good Governance to improve the Nation’s Competitiveness, 431–435. https://doi.org/10.5220/0007544404310435