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Bone damage in *Allopleuron hofmanni* (Cheloniidae, Late Cretaceous)•

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Abstract

We describe pathologies and post-mortem damage observed in specimens of the late Maastrichtian marine cheloniid turtle *Allopleuron hofmanni*. Shallow circular lesions on carapace bones are common and possibly illustrate barnacle attachment/embedment. Deep, pit-like marks are confined to the neural rim and the inner surface of peripheral elements; these may have been caused either by barnacle attachment or disease. A number of linear marks found on outer carapace surfaces are identified as tooth marks of scavengers, others as possible domichnia of boring bivalves. A fragmentary scapula and prescapular process displays radular traces of molluscs (gastropods and/or polyplacophorans; ichnogenus *Radulichnus*). These diverse types of bone damage suggest both live and dead marine turtles to have been commonly utilised by predators, scavengers and encrusters in the type Maastrichtian marine ecosystem.

Keywords: Testudines, Maastrichtian, pathology, scavenging, molluscs, barnacles

Introduction

To date, the latest Cretaceous (late Maastrichtian) marine turtle *Allopleuron hofmanni* (Gray, 1831) is known exclusively from the Maastrichtian type area in the southeast Netherlands and northeast Belgium (Mulder, 2003; Janssen et al., 2011). During this time interval, a subtropical epeiric sea covered the area in which coarse-grained biocalcarenites were laid down (Felder, 1994; Schiøler et al., 1997; Jagt, 1999; Herngreen & Wong, 2007; Jagt & Jagt-Yazykova, 2012). This shallow sea supported a wide variety of marine fauna and flora, including common sharks and rays, belemnites and ammonites, echinoderms and mosasaurs (Dortangs et al., 2002; Schulp, 2006), while elasmosaurs and crocodiles were much rarer (Mulder, 1998; Mulder et al., 2000). Delicate remains of stems and foliage, occasionally silicified, provide evidence for the presence of one of the earth's earliest sea grass communities (Voigt & Domke, 1955; Van der Ham et al., 2007).

Whereas several palaeopathological studies on Maastrichtian type area mosasaurs have been conducted (Dortangs et al., 2002; Schulp et al., 2004; Rothschild & Martin, 2005; Rothschild et al., 2005), less is known about the pathologies of other type Maastrichtian reptiles such as *A. hofmanni*. Mulder (2003) described and illustrated a carapace element displaying two holes possibly attributable to predation by a mosasaur. Here we record various other types of damage observed on carapace and appendicular skeletal bones of *A. hofmanni*.

Material

The present study targets skeletal material of *A. hofmanni* from all public collections known to contain such: Natuurhistorisch Museum Maastricht (NHMM; Maastricht, the Netherlands), Teylers Museum (TM; Haarlem, the Netherlands), Naturalis Biodiversity Center (NNM; Leiden, the Netherlands), Natuurhistorisch

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Universitair Museum Utrecht (NHUMU; Utrecht, the Netherlands), Geologisch Museum Hofland (Laren, the Netherlands), Natuurmuseum Brabant (Tilburg, the Netherlands), Institut royal des Sciences naturelles de Belgique (Brussels, Belgium), The Natural History Museum (London, United Kingdom), Muséum national d'Histoire naturelle (Paris, France), Museum für Naturkunde (Berlin, Germany) and Yale Peabody Museum (New Haven, Connecticut, United States of America). In a recent study of *A. hofmanni* it was concluded that articulated specimens are rare; most findings comprise a single or merely a couple of skeletal elements (Janssen et al., 2011) and elements of carapace, pectoral girdle and skull are commonest.

Description of pathologies

Shallow lesions constitute the commonest type of pathology found on skeletal elements of *A. hofmanni* (Fig. 1). They are characterised by a well-defined and often circular outline (5-10 mm in diameter) and a surface that is rough and slightly depressed in comparison to the surrounding (healthy) bone. This surface is either level or, in the minority of cases, displays a slightly elevated centre. In three specimens (TM 11357, NNM 76819 and NNM 446895) a much larger, irregular shaped area is affected (Fig. 2A). In specimen TM 11357, the central area of several lesions is not depressed but rather made up of bone tissue similar in thickness and texture to the normal bone surface (Fig. 2B).

Strikingly, these shallow lesions are situated exclusively on the outer face of the carapace; affected most often (normalised for collection bias and surface area) are the anterior and posterior ends of the carapace, i.e., the nuchal, pygal and suprapygals. Nearly a third of all specimens that include at least one carapace element (n = 162) exhibit this particular type of pathology. The lesions have a multifocal character, with specimens often afflicted multiple times and involving a number of different carapace elements and afflictions not clustering in a single location. Near-complete carapaces, such as NHMM 000001 and NHMM 1995 014 illustrate this best, with shallow lesions distributed randomly over every type of carapace element.

Other circular lesions are much deeper, approximately 10 millimetres in diameter, and occasionally encircled by a slightly thickened rim (Figs 3, 4). Such traces have been noted in eight specimens, i.e., 5 % of all specimens comprising one or more carapace elements. These pit-like features have only been observed at two particular locations of the carapace: centrally

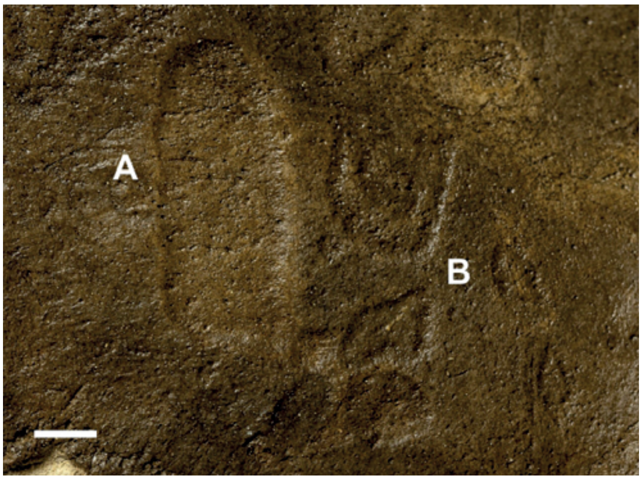

Fig. 2. Multiple shallow lesions on a nuchal (TM 11357); large irregular surface (A); elevated central area (B). The scale bar equals 10 mm.

Fig. 3. Pit-like lesions in the anterior peripheral rim (NHMM 003903). The scale bar equals 50 mm.

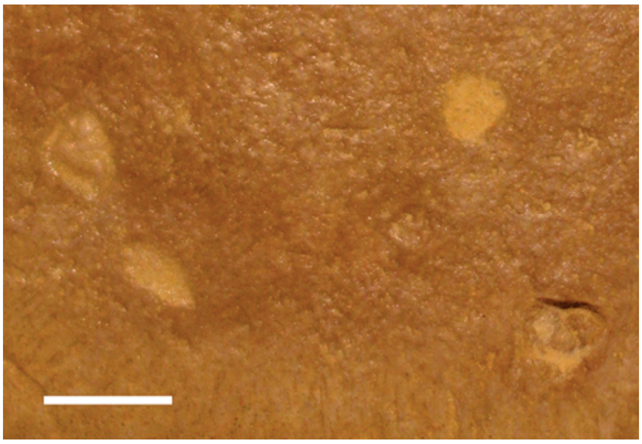

Fig. 1. Shallow circular lesions on a carapace (NHMM 1995 014). The scale bar equals 10 mm.

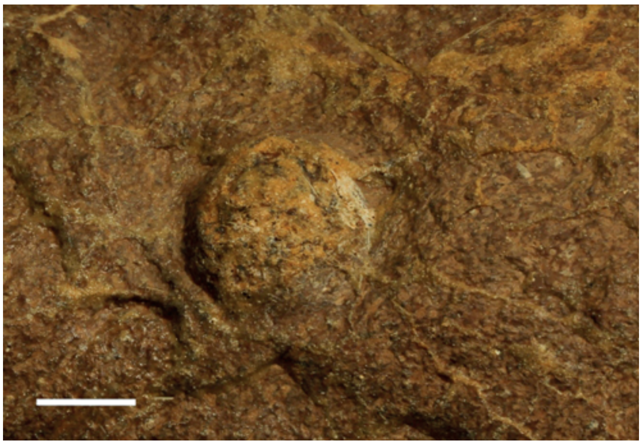

Fig. 4. Close-up of one of the pit-like lesions in Fig. 3 (NHMM 003903). The scale bar equals 10 mm.

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placed on the rim of the dorsal side of the neural (n = 4; see Fig. 5) and on the inside nook of the peripheral (n = 4). Five specimens exhibit a single pit-like lesion, while two others have several lesions on a single peripheral element (NHMM 003903 and NNM 446907). Specimen IRScNB REG-1737 displays two pit-like lesions on two adjoining peripherals.

Fig. 5. Deep circular lesion on a neural (NHUMU G768.1881).The scale bar equals 10 mm.

Multiple linear scratch marks were found on seven specimens, all located on the outer surfaces of carapace elements. Some are short and occur in a chaotic arrangement; others are longer and unidirectional. For instance, NHMM 003890 consists of a posterior peripheral showing an array of fine, closely spaced, mostly parallel scrapings only a fraction of a millimetre in width (Fig. 6). Such traces differ from tooth impressions on dinosaur and whale bones described and named by Jacobsen & Bromley (2009). Specimens TM 7452 and TM 11360 feature elongated elevations on the peripheral and costal plates, respectively (Fig. 7).

Specimen TM 11305, consisting of a joint fragmentary scapula and prescapular process, displays two groups of closely spaced scrape marks in a slightly depressed surface (Fig. 8).

Fig. 6. Fine scrapings on a posterior peripheral (NHMM 003890). The scale bar equals 10 mm.

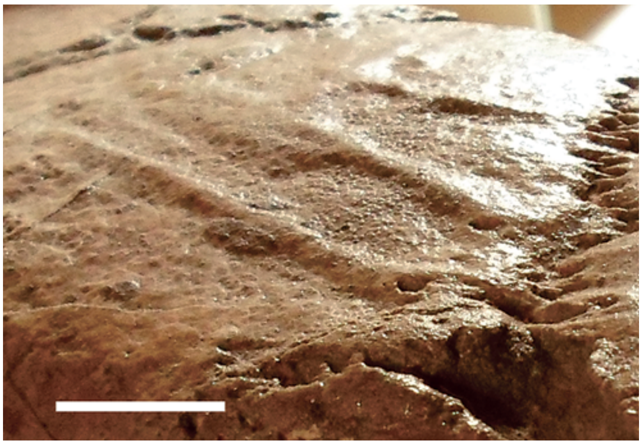

Fig. 7. Elongated, elevated features on a peripheral (TM 7452). The scale bar equals 20 mm.

Fig. 8. Radular traces (ichnogenus Radulichnus *Voigt, 1977) on scapula-prescapular process (TM 11305). The scale bar equals 10 mm.*

Discussion

The bone tissue in the centre of some shallow lesions (Fig. 2B) may be the result of secondary growth in response to the damage inflicted, which implies a non-lethal attack during life. In other shallow lesions the damage did not lead to bone renewal, possibly because of the limited extent both laterally and in depth. CT scans and thin sections do not provide conclusive evidence of secondary bone growth; additional thin sections, prepared specifically for histological analysis, may possibly provide more insight in future. Predator teeth are unable to inflict such shallow and wide damage. A recent extensive review of osseous and other hard-tissue pathologies in turtles has concluded that, 'shell pitting is perhaps the least understood pathological phenomenon' (Rothschild et al., 2013, p. 526). It listed bites, parasites, mixed bacterial and fungal infections as possible causative agents. We here speculate that epibiont attachment and/or embedment to/in the carapace surface is the most likely cause of the type of shallow damage reported here. Many turtle epibionts settle predominantly on the carapace and can cause damage to the bone. Frick et al. (1998) and Pfaller et al. (2006) observed the highest densities of epibionts on the posterior and vertebral zones of the carapace in loggerhead sea turtles. In comparison, the distribution of shallow lesions on the carapace of *Allopleuron hofmanni* shows a slight bias towards anterior and posterior zones. Michael G. Frick (pers. comm., 2012) has noted that the circular lesions we have observed on *A. hofmanni* closely resemble those made by some extant platylepadid barnacles, with the observed differences in depth and the flatness of the surface suggesting infliction by different subspecies. However, the oldest known platylepadids are of Eocene age (Hayashi, 2013), while the superfamily to which they are assigned, the Coronuloidea, originated during the latest Cretaceous (Hayashi et al., 2013). The larger lesions in Figure 2 may have been caused by joint action of such barnacles, boring bivalves and sponges, similar to what has been observed in some modern marine turtles.

The thickened rim around some of the deep pit-like marks again suggests non-lethal wounds. Deep lesions such as these could potentially be teeth marks, but their exclusive appearance on the inner surface of peripherals and central neural rim makes this explanation unlikely. Several types of disease may trigger multifocal bone-damaging ulcers, including infections commonly found in modern-day turtles (e.g., Cooper & Jackson, 1981) and some types of cancer such as histiocytosis and myeloma (Bruce Rothschild, pers. comm., 2011; S. Vincent Rajkumar, pers. comm., 2011). Alternatively, these lesions may have been inflicted by platylepadid barnacles, similar to the shallow lesions. These can leave pit-like scars and prefer specific sites on the turtle carapace, while some species may be able to penetrate enough skin to reach the inside of the peripheral (Michael G. Frick, pers. comm., 2012).

We suggest that the fine, closely spaced marks seen in NHMM 003890 (Fig. 6) are the result of repeated scraping of small teeth. We also identify the marks on specimen TM 7452 as bite marks (compare Schwimmer et al., 1997), whereas the origin of scratch marks on other specimens is less certain. Taking into account both the repetition of the scraping action and the protection of dermal scutes overlying the carapace (Mulder, 2003), we hypothesise that this type of damage was inflicted post mortem by small-sized scavengers.

The elongate elevations in specimens TM 7452 and TM 11360 (Fig. 7) resemble modern-day domichnia of boring bivalves (Michael G. Frick, pers. comm., 2012), whereas the marks on specimen TM 11305 (Fig. 8) certainly constitute radular traces, resulting from the feeding on algae of a molluscan from the bone as it lay exposed on the sea floor. Traces left by the radula of the extant marine gastropod *Gibbula* (see Thompson et al., 1997) and by fossil gastropods and polyplacophorans (see Voigt, 1977; Jagt, 2003; Mulder et al., 2005) are closely similar and can be referred to the ichnogenus *Radulichnus* Voigt, 1977.

The wide range of bone damage types suggests that both live and dead turtles were commonly utilised by an array of predators, scavengers and encrusters in the Late Cretaceous ecosystem represented by the type Maastrichtian.

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