Chapter 2

Taphonomy and paleopathology of the Late Cretaceous marine turtle *Allopleuron hofmanni*

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Abstract

We inventory *Allopleuron hofmanni* specimens in public collections, and here provide an overview of our taphonomic and paleopathological findings. A preservation and collection bias has resulted in an overrepresentation of the large, robust skeletal elements of the skull, carapace and pectoral girdle. Tooth marks present on 6-12% of carapace specimens do not occur on other parts of the skeleton, and mostly seem to be inflicted post-mortem by scavengers. Shallow semi-circular lesions occur on 30% of carapace specimens and are likely to be barnacle attachment sites. Most abnormalities in carapace morphology occur in the posterior portion, with 21% of suprapygal elements affected. All reconstructed carapace lengths are >90 cm, suggesting that the collections almost exclusively consist of adult individuals. We hypothesize that this is due to spatial niche partitioning between adults and younger individuals, whereby the home range of the latter group is located outside of the Maastrichtian type area.
2.1 Introduction

In the Late Cretaceous (c. 67-66 Ma) a shallow subtropical sea covered the area which is now the southeast of the Netherlands and the northeast of Belgium (Fig. 2.1; Herngreen and Wong, 2007; Van der Ham et al., 2007; Jagt and Jagt-Yazykova, 2012). Highly fossiliferous carbonate sediments attest of the presence of sharks, rays, turtles, mosasaurs, elasmosaurs and crocodiles in this Maastrichtian sea (Dortangs et al., 2002; Mulder, 2003; Mulder et al., 2005; Schulp, 2006). Delicate remains of stems and foliage reveal the presence of one of the world’s earliest sea grass communities (Voigt and Domke, 1955; Moody, 1997; Van der Ham et al., 2007).

Among the cheloniid turtles living in this sea was *Allopleuron hofmanni* (Camper, 1786; Gray, 1831). This large turtle (with a maximum carapace length of ca. 1.4 m) is found solely in a relatively small geographic area and stratigraphic range (Mulder, 2003), namely the Maastrichtian type area in southern Limburg (the Netherlands) and the adjacent provinces of Limburg and Liege (northeast Belgium). The fact that the occurrence of most marine turtles is restricted to the (sub)tropics resulted in an early paleoclimatological characterization of the Maastrichtian sea (Ubaghs, 1883). In this chapter we explore *A. hofmanni* taphonomy, population dynamics, and how this species’ occurrence can contribute to our understanding of ecological patterns in the Maastrichtian sea.

![Figure 2.1](image)  
*Figure 2.1* Paleogeographic reconstruction of Maastrichtian northwestern Europe (adapted from Ziegler, 1990). White denotes land; gray is sea (with shallow areas in lighter gray). The star marks the study area.
2.2 Collections

As part of this study we compiled an extensive overview of *A. hofmanni* specimens housed in museum collections (Table 1).

<table>
<thead>
<tr>
<th>Museums housing Allopleuron hofmanni specimens.</th>
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<tr>
<td>Natuurhistorisch Museum Maastricht</td>
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<td>Teylers Museum</td>
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<td>Naturalis Biodiversity Center</td>
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<td>Natuurhistorisch Universitair Museum Utrecht</td>
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<td>Geologisch Museum Hofland</td>
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<td>Natuurmuseum Brabant</td>
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<td>Institut Royal des Sciences Naturelles de Belgique</td>
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<td>Natural History Museum</td>
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<td>Museum national d’Histoire naturelle</td>
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<td>Museum für Naturkunde</td>
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<td>Yale Peabody Museum</td>
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Our analyses were based on a total of 281 specimens. Near-complete skeletons are rare; most finds are composed of only one or a few isolated bones. A large part of the material in the collections was acquired over a century ago, and information about the provenance of these specimens is often limited to the name of the quarry or even the general region. The exact stratigraphic and sedimentological context is thus unknown for most specimens.

2.3 Relative frequencies of skeletal elements

A schematic overview of the relative abundance of *A. hofmanni* skeletal parts (Fig. 2.2) shows that most common are (fragments of) the cranium, lower jaw, pectoral girdle and carapace. The nuchal, the large anterior carapace plate located above the neck, is the most abundant skeletal element. Bones of the appendicular skeleton, plastron elements, and vertebrae are significantly underrepresented in the collections.

A number of factors might explain this frequency distribution. Firstly, the skeletal elements most commonly encountered are relatively large in size, making them less likely to be damaged beyond recognition by scavengers. They can withstand substantial force; the carapace is built to protect, and the pectoral girdle is sturdy because most of the propulsive
Figure 2.2 ‘Exploded view’ of an Allopleuron hofmanni skeleton, with relative abundance color-coded on a logarithmic scale. Counts have been normalized to the relative number of bone elements in the skeleton.
musculature is attached to it (Wyneken, 2001). Furthermore, *A. hofmanni* carapace elements are often found in articulation and fractures regularly do not follow the sutures between carapace plates. The robustness of these bones and their attachments to each other makes them more likely to be preserved intact. In contrast, small elements (especially bones belonging to the appendicular skeleton) are more prone to disarticulation, being easily accessible for predators and scavengers and more likely to be scattered by current action (as Ubaghs, 1883 already noted). Additionally, larger elements are more likely to be spotted in an outcrop, and more easily recognized as belonging to *A. hofmanni*. In contrast, small elements are more difficult to prepare and more easily damaged in the process. Material in early collections was often acquired from private collectors, whom might have considered larger fossils to be more spectacular and valuable.

An interesting exception to this pattern is the relative rarity of plastron elements (the ventral parts of the shell) in the collections. Despite the size and robustness of its elements, the plastron is found almost 10 times less often than the carapace. The long, finger-like bone projections may be more prone to fracturing, leaving these bones unrecognizably damaged. In addition, predators and scavengers presumably reached the turtle’s internal organs via the ventral side, making damage to and scattering of plastron elements likely.

### 2.4 Pathologies

To further assess the potential taphonomic impact of predators and scavengers, we turn our attention to the incidence of damage marks. Mosasaurs from the Maastrichtian type area have been the subject of a number of paleopathological studies (Dortangs et al., 2002; Schulp et al., 2004; Rothschild and Martin, 2005; Rothschild et al., 2005), but less is known about pathologies occurring in other type Maastrichtian reptiles. The only instance of predatory marks on *A. hofmanni* fossils previously reported are two large pits on a peripheral, possibly caused by mosasaur predation (specimen TM7431, Mulder, 2003).

In our own investigations we solely found tooth marks on the outer surfaces of the carapace elements. Of all specimens consisting of at least one carapace element, 6-12% carries damage likely to be caused by teeth. Often these are fine, shallow, closely spaced scrapes which show no signs of healing (Fig. 2.3a). This type of damage is likely to be inflicted post-mortem by small scavengers who repeatedly dragged their teeth across the bone surface, gnawing off the overlying dermal plates. Sharks, for instance of the genus *Squalicorax*, are potential candidates for the inflicts of these marks (Schwimmer et al., 1997; Dortangs et al., 2002). Some larger tooth marks have partially or completely healed (Fig. 2.3b), suggesting failed predation attempts. However, bite marks of a severity directly life-threatening to an adult marine turtle are absent, with the exception of the 5 cm wide pit in TM7431. The only
evidence of feeding that is not on the carapace are the radula scrapes on the scapula of TM11305 (Fig. 2.3c). These are probably caused by the feeding apparatus of a molluscan as it grazed algae off the bone surface, as they resemble the feeding marks of the extant marine...
gastropod *Gibbula* in Thompson et al. (1997) and *Radulichnus* traces as described by Voigt (1977) and Jagt (2003).

Another type of damage found solely on the outer surface of *A. hofmanni* carapace elements are shallow depressions with discrete margins, mostly semi-circular and 5-10 mm in diameter (Fig. 2.3d). About 30% of specimens that consist of at least one carapace element exhibit this feature. In affected individuals this type of lesion occurs repeatedly over different carapace elements, although the nuchal, pygal and suprapygal are most often affected. In several specimens, what is supposedly the same type of pathology has created much larger, irregularly shaped lesions (Fig. 2.3e). Bone regrowth seems to have occurred in part of these lesions, implying a non-lethal attack. The more common circular lesions do not show any sign of bone renewal, possibly because the limited extent of the damage did not trigger such processes. These features do not match the typical appearance of common forms of osteomyelitis and shell disease in turtles (Rothschild et al., 2013), but it resembles lesions inflicted by some types of barnacles (as described by Weems, 1974 and noted by Michael G. Frick, pers. comm.)

Eight *A. hofmanni* specimens (5%) exhibit deeper lesions of ca. 10 mm in diameter, which are sometimes surrounded by a thickened rim indicating a bone repair reaction (Fig. 2.3f). These pits only occur inside the nook of the peripheral and centrally on the neural rim. Specimen NHMM003903 has five pits in a single peripheral, and IRScNB REG-1737 has two pits on two adjoining peripherals. Deeper lesions on the carapace could perhaps be caused by the teeth of predators, but this explanation is unlikely given the observed distribution. Boring epibionts can prefer specific locations on the turtle carapace, and some species may be able to penetrate as far as the inside of the peripheral (Michael G. Frick., pers. comm.). Alternatively, pitting may be caused by bone-damaging ulcers triggered by infections (Cooper and Jackson, 1981) or cancers such as histiocytosis and myeloma (Bruce Rothschild, pers. comm.; S. Vincent Rajkumar, pers. com., 2011).

### 2.5 Morphological abnormalities

In the Testudine order, the configuration of carapace elements and overlying epidermal scutes is subject to a high degree of variation between individuals of the same species (Zangerl and Johnson, 1957). While the general arrangement of the carapace plates has remained fixed since the Late Triassic, subnumerary or supernumerary plates are common (Velo-Antón et al., 2011). Such anomalies could be caused by disturbances during ontogenetic development (Hildebrand, 1930; Lynn and Ullrich, 1950; Hill, 1971) or low genetic diversity in the population (Soulé, 1979; Velo-Antón et al., 2011).
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The carapace of some *Allopleuron hofmanni* individuals likewise exhibits abnormalities. Mulder (2003) describes the 9th neural of specimen IRScNB3668 protruding between the 8th right pleural and the suprapygal, and asymmetrical arrangement of the suprapygals in specimen IRScNB3668. We further observed carapaces in which several plates are completely fused or the location of sutures is abnormal (Fig. 2.4). Interestingly, most abnormalities occur in the posterior part of the carapace. Suprapygals are most often affected (21%), followed by the neurals and costals (5%). Despite the abundance of peripherals in the
collections, we identified no abnormalities affecting them. However, due to the shape and often non-articulated occurrence of these skeletal elements, abnormal peripherals may more easily go unrecognized than other carapace elements deviating from the morphological norm.

**Figure 2.5** Lengths of 4th left and right *Allopleuron hofmanni* peripherals. Reconstructed carapace lengths based on these measurements range from 100 to 150 cm.

### 2.6 Size distribution

Studying the collections, it becomes apparent that *A. hofmanni* skeletal elements occur in a relatively narrow size range. Skeletal elements belonging to 15 *A. hofmanni* individuals measured by Mulder (2003) all seem to belong to adults. Smaller skeletal elements belonging to juvenile turtles are conspicuously absent from the collections. To take a frequently found carapace element as an example, the length of the 4th peripheral was found to be on average 14.7 cm, with a relatively small standard deviation of 2.3 cm (Fig. 2.5).

It is important to note that the relation between age, growth, and osteological development is less than straightforward in most ectothermic vertebrates due to individual differences in growth (Halliday and Verrell, 1988). In extant turtles, some individuals will grow rapidly and reach their maximum body size early in life, whereas others grow much slower and attain maximum body size relatively late in life. As a result, the exact age of turtles is not easily deduced from their size. Nonetheless, the correlation between age and body size is strong enough to allow rough estimates of the developmental stage – whether the individual was a hatchling, juvenile or adult (e.g. Chaloupka and Zug, 1997 for *Lepidochelys kempii*; Zug et al., 2002 for *Chelonia mydas*).
To test the premise that the majority of *A. hofmanni* specimens is derived from adult individuals, we estimated the total carapace length for all elements in the collections whose degree of preservation allowed the necessary measurements, by comparing their dimensions to the largely complete skeleton of specimen NHMM000001. The average reconstructed carapace length is 142 cm, and it is striking that none of the 92 specimens seems to have originated from an individual with a carapace length of less than 90 cm (Fig. 2.6). These computations confirm that juveniles of *A. hofmanni* are rare in the collections; virtually all of the examined individuals died in the late juvenile to adult stage of life.

Two possible explanations may account for the observed bias towards adult *A. hofmanni* remains. Firstly, the distribution could be due to preservation and collecting biases. Young turtles would be especially vulnerable to attack by predators such as marine crocodiles and mosasours, and predation decreases the odds of fossilization (Shipman, 1981). In contrast, large marine turtles experience relatively low rates of predator-induced mortality (e.g. Bjorndal et al., 2003; Heithaus et al., 2008) and predators and scavengers are less likely to transfigure and scatter large skeletal remains. Large articulated fossils are also more easily recognized in the field and especially sought after by collectors. Yet the same taphonomic processes fail to produce as strong a bias in other fossil vertebrates; a much wider size range is observed for other marine reptile taxa in the type Maastrichtian (e.g. Kuypers et al., 1998).

We therefore suggest that in addition to the taphonomic factors outlined above, the age distribution of the regional population was skewed toward adult *A. hofmanni* individuals. What could have caused an area to have a large population of adult sea turtles and not many younger individuals? Many modern-day marine turtles show dramatic changes in diet and habitat type from one life cycle phase to the next. For instance, green turtles (*Chelonia mydas*) are carnivores during their juvenile stage and only become benthic seagrass feeders in the adult stage of life (Lutz et al., 2003; Reich et al., 2007). The stratigraphic and spatial distribution of *A. hofmanni* coincides with that of the seagrass species *Thalassotaenia debeyi* (Brasier, 1975; Van der Ham et al., 2007). The extensive seagrass meadows of the Maastrichtian type area may thus have provided a food source and habitat for adult *A. hofmanni* turtles (Hirayama, 1997; Moody, 1997; Mulder, 2003), a possibility affirmed by their broad, U-shaped beak (compare with *C. mydas*; Wyneken, 2001). This would provide a parsimonious explanation for both the restricted regional occurrence of *A. hofmanni* and the seeming spatial niche partitioning between adults and juveniles.
Figure 2.6 Frequency distribution of reconstructed carapace lengths of specimens of *Allopleuron hofmanni* based on 92 specimens. Carapace length was estimated using the near-complete specimen NHMM 000001 as a reference.

### 2.7 Conclusions

Taphonomic and paleopathological analysis of a large sample of *Allopleuron hofmanni* specimens attests of the activity of predators, scavengers and encrusters, but there is scant evidence of potentially lethal predation. Large and sturdy bones are most likely to have been preserved and to have made their way into the collections. However, this taphonomic bias is not sufficient to explain why *A. hofmanni* fossils almost exclusively derive from adult individuals. We hypothesize that the ultimate factor in producing the observed size distribution is spatial niche partitioning between adult *A. hofmanni* individuals in the seagrass meadows of the Maastrichtian type area and younger individuals elsewhere. The application of carbon isotope analysis could elucidate whether the diet of *A. hofmanni* indeed consisted of seagrass.