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On the taphonomy of the late Maastrichtian (Late Cretaceous) marine turtle *Allopleuron hofmanni*[*]

R. Janssen[1,*], R.R. van Baal[1] & A.S. Schulp[2]

1 Faculteit der Aard- en Levenswetenschappen, Vrije Universiteit Amsterdam, De Boelelaan 1085, NL-1081 HV Amsterdam, the Netherlands.
2 Natuurhistorisch Museum Maastricht, de Bosquetplein 6-7, NL-6211 KJ Maastricht, the Netherlands.
* Corresponding author. Email: rjn600@falw.vu.nl.

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Abstract

An exhaustive screening of public collections containing remains of the latest Cretaceous (late Maastrichtian) marine turtle *Allopleuron hofmanni* (Gray, 1831) from the type area of the Maastrichtian Stage (southeast Netherlands, northeast Belgium) shows the available material to represent almost exclusively adult individuals. The various skeletal elements are not preserved in proportionally equal abundance, with portions of carapace, pectoral girdle, cranium and mandible overrepresented. These observations can be explained by population characteristics and taphonomic factors. During the late Maastrichtian, while hatchlings and juveniles in all likelihood lived and fed elsewhere, extensive seagrass meadows might have supported a population of only adult marine turtles.

Keywords: *Allopleuron hofmanni*, Cretaceous, Maastrichtian, marine turtles, population characteristics, taphonomy

Introduction

Pioneer vertebrate palaeontologist Petrus Camper was the first to describe the large-sized marine turtles from the type Maastrichtian, referring to them as a 'large turtle' (Camper, 1786). An apt term, because *Allopleuron hofmanni* attains average carapace lengths of 1.4 m, this being comparable to the modern-day leatherback, *Dermochelys coriacea*. The generic name, derived from the Greek, translates as 'different pleurals', because the costals (formerly referred to as pleurals) are highly reduced in this species. The specific epithet was given by Gray (1831) in honour of the renowned fossil collector Jean-Leonard Hoffmann. The rules of Zoological Nomenclature require Gray's misspelling, '*hofmanni*' with a single 'f', to be maintained.

The fact that marine turtles are usually restricted to the tropical realm did not escape Ubaghs's (1883) attention, which resulted in an early palaeoclimatological interpretation of the type Maastrichtian seas using vertebrate fossils. He observed (p. 25), '... une certaine analogie des mers tropicales avec celle à laquelle nous devons la formation de la craie supérieure de Maestricht, analogie que j'ai trouvée dans la richesse de celle-ci en restes fossiles de tortues marines, si fréquentes dans les mers tropicales.' In spite of having presumably limited material available for study, Ubaghs added a few poignant remarks (p. 25) on the preservation of the material, the scarcity of articulated material being particularly striking, 'Malgré le grand nombre d'ossements isolés qu'on trouve disséminés partout dans notre dépôt, il est extrêmement rare qu'on y rencontre un squelette entier ou tant soit peu complet.' Ubaghs explained (p. 25) this pattern by wave and current action; for articulated material to be preserved, '... il aurait fallu que l'animal, immédiatement après sa mort, eût été entièrement enseveli dans la vase; mais comme le plus souvent il n'en a pas été ainsi, les extrémités les plus exposées, librement articulées en non protégées par la carapace, ont été décomposées en enlevées.'

Well over a century later, skeletal remains of *A. hofmanni* are still exclusively recovered from a relatively small geographic area and from a limited stratigraphic range: the Maastrichtian type area in southern Limburg (the Netherlands) and adjacent provinces of Limburg and Liège in northeast Belgium. During the

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Late Cretaceous this area was covered by a shallow subtropical sea (Jagt, 1999; Herngreen & Wong, 2007), all material of *A. hofmanni* being preserved in rather coarse-grained biocalcarenitic limestones laid down here.

The most comprehensive study of *A. hofmanni* to date is that by Mulder (2003), who investigated some thirty specimens, all of them representing adult individuals. Younger growth stages of *A. hofmanni* are conspicuously absent. This suggests that there is a marked preservation bias against smaller, and thus younger, individuals, an extreme collecting bias skewed to larger individuals, the absence of young individuals as inhabitants of this area, or a combination of these factors. The correct interpretation of any one of these scenarios has significant implications for the reconstruction of this taxon's palaeobiology and palaeoecology. For the present note, we have studied the relative size distribution and the presence or absence of skeletal elements in order to gain a better understanding of the absence of juvenile individuals in collections.

Material and methods

We compiled a detailed and exhaustive overview of material of *Allopleuron hofmanni* housed in the collections of the following public institutions: Natuurhistorisch Museum Maastricht (NHMM; Maastricht, the Netherlands), Teylers Museum (TM; Haarlem, the Netherlands), Nederlands Centrum voor Biodiversiteit (Naturalis; NCB-RGM; Leiden, the Netherlands), Natuurhistorisch Universitair Museum Utrecht (NHUMU; Utrecht, the Netherlands), Geologisch Museum Hofland (Laren, the Netherlands), Natuurmuseum Brabant (NMB; Tilburg, the Netherlands), Institut royal des Sciences naturelles de Belgique (IRScNB; Brussels, Belgium), The Natural History Museum (NHM; London, England), Muséum national d'Histoire naturelle (MNHN; Paris, France), Museum für Naturkunde (MFN; Berlin, Germany) and Yale Peabody Museum (YPM; New Haven, Connecticut, USA).

Most specimens in museum collections are composed of only one or a handful skeletal elements that are frequently broken. Larger, articulated specimens, comprising more than a few elements, are rare, and most of those consist of co-ossified carapace elements. Because a large proportion of the material comes from older collections, provenance data associated with the specimens generally are very limited. Labels rarely supply more than the name of the quarry or that of the general region where the specimen was found. This precludes the inclusion of a more detailed stratigraphic level and/or sedimentological context into the analysis.

We have personally reviewed, identified and measured all specimens, except for the *A. hofmanni* material in the collections at Paris, New Haven and Berlin. Data on specimens in these collections were compiled from published accounts and correspondence with the curators in charge. Based on these data, the relative abundance of the skeletal elements and the total size of the animals (at the time of death) were calculated. For practical purposes a linear allometric ontogenetic relationship was assumed, with the most complete (albeit not the largest) adult skeleton, NHMM 000001 considered to constitute a '100 per cent' baseline. These data enabled us to evaluate the size distribution of *Allopleuron* fossils from the Maastrichtian type area.

Taphonomy

Due to the often limited provenance data and precise stratigraphic/sedimentological context, realistically available taphonomic data are limited to analysis of bone surface modification, presence or absence of skeletal elements, and bone size distributions. The specimens studied show a general lack of abrasional features other than tooth marks. Most finds consist of single skeletal elements or several articulated ones, whereas more complete skeletons are rare, an observation consistent with that of Ubaghs (1883). The general absence of abrasional features may be the result of limited post-mortem transportation and a relatively quiet setting at final burial. However, Brand et al. (2000, 2003) indicated that, after death, turtles in subaqueous environments can undergo significant transport because of bloating and consequential floating, which does not produce any form of abrasion on bones.

Teeth marks generally consist of small scrapes, shallow and closely spaced, which we attribute to scavengers rather than predators. These marks are found only on the outer surfaces of carapace elements. Scavenging, for instance by sharks of the genus *Squalicorax*, has been reported previously from the Maastrichtian type area (Dortangs et al., 2002). These observations might indicate that *A. hofmanni* was not a regular prey for predators.

The normalised frequency of the various skeletal elements of *A. hofmanni* as represented in museum collections is shown in Fig. 1; it allows the observation that these are not preserved in proportionally equal abundance. The commonest elements are (portions of) the skull, lower jaw, pectoral girdle and carapace. Of the carapace elements, the nuchal is particularly common. Two factors can be considered here. First of all, the commonest elements are sturdy and robust, built to withstand substantial force. This holds true especially for the carapace elements and the skull. The pectoral girdle also is of sturdy build, because most of the propulsive musculature is attached to it (Wyneken, 2001). Secondly, the commonest skeletal elements are all of relatively large size. Large-sized elements can only be processed by large scavengers, thus making it more likely that these are preserved. The opposite is true for small bones and elements belonging to the appendicular skeleton. The smaller elements of tail and limbs are easily accessible meals for predators and scavengers alike. Small bones and bones not connected by ossification or tough ligaments have a lower preservation potential, because they are more prone to

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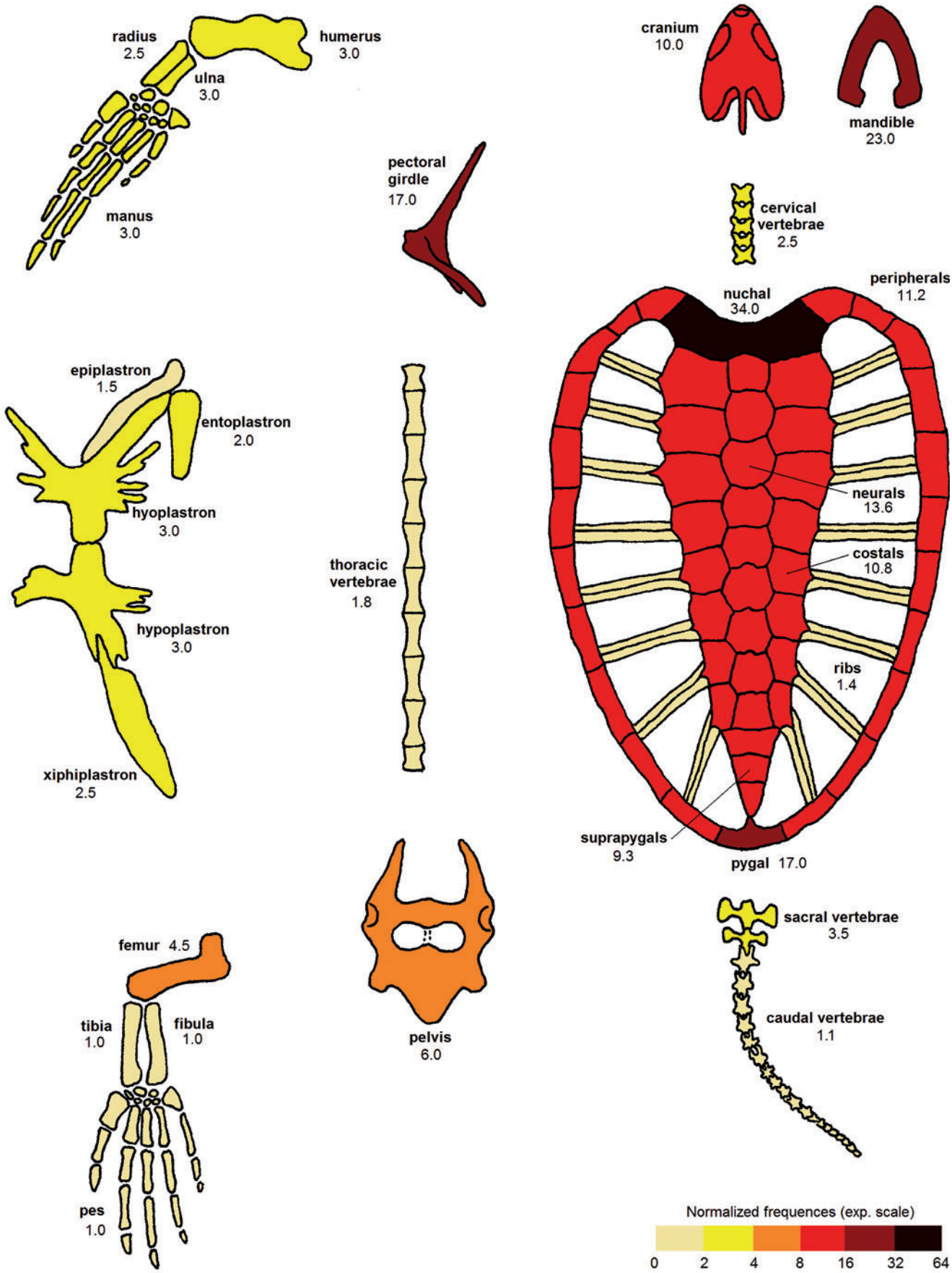

Fig. 1. 'Exploded view' of the skeleton of Allopleuron hofmanni *with colour-coded abundances, corrected for the relative number of bone elements in the animal's skeleton.*

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disarticulation by predator activity or scatter by current action (as noted already by Ubaghs, 1883). Of note is the fact that carapace elements are found relatively often in articulation. Where carapace elements are found disarticulated, fractures do not necessarily follow the sutures. Therefore, we assume that the sutures are not consistently the weakest structural links in the chain. It is interesting to compare these observations to the work by Meyer (1991) on the decomposition of the carapace of the present-day hawksbill turtle, Eretmochelys imbricata; buried in a lagoonal setting the carapace will completely disarticulate within ten days. Differences in size and composition of the carapace as well as the very different burial context (first bloat and float, then deposition) may well explain the different observations.

A collecting bias is certainly involved as well. Larger bones are more easily spotted and collected. Material in early collections was often acquired by private collectors from quarrymen, and larger (i.e., more spectacular) fossils were most sought after. Smaller elements, such as vertebrae, are more difficult to prepare and more easily damaged and perhaps therefore underrepresented in the current collections too.

In Fig. 1, the factors outlined above are reflected by the small numbers of elements of the appendicular skeleton as well as thoracic, caudal and cervical vertebrae. An interesting result is the relative paucity of plastron elements. Like the carapace, plastron bones are relatively large and built for strength; despite this trait, they are remarkably rare. This might be because they are not fused like carapace elements and their long, finger-like processes appear prone to fracturing beyond recognition. We also expect that predators or scavengers gained access to the turtle's internal organs via its ventral side, thereby possibly breaking up and scattering plastron elements.

The type Maastrichtian *Allopleuron hofmanni* population

Although ectothermic vertebrates usually do not display strictly deterministic growth curves (Halliday & Verrell, 1988), correlations between body size and age in extant sea turtles appear reliable enough for rough age estimates (e.g., Chaloupka & Zug, 1997 for *Lepidochelys kempii*; Zug et al., 2002 for *Chelonia mydas*) and certainly for determining if a certain individual was a hatchling, juvenile or adult. We would expect a population of *A. hofmanni* to encompass body sizes ranging from less than 10 centimetres to more than 1.5 metres. To see how this translates into the fossil record as recovered from the type Maastrichtian, we estimated the carapace length of the individuals (wherever possible) by using dimensions of the numerous partial specimens (Fig. 2), and conclude that this range of body sizes is not present at all in specimens of *A. hofmanni*. The majority have a carapace length in excess of one metre (Fig. 2). We are confident in ascribing 99 per cent of all specimens to the late juvenile stage and adult age classes (see Supplementary material).

As discussed above, taphonomic processes exert a bias towards large fossil remains, some very obvious: young turtles can be swallowed whole by predators, adult turtles cannot. Old turtles can die of old age, juveniles not. And large fossils are more sought after by collectors. These factors all provide a partial explanation for the observed population characteristics. Yet, the same processes have an impact on all vertebrates, failing to produce a bias as strong as the one we have observed. It is statistically very unlikely for these biases to explain away the 99 per cent representation of subadult and older. Many other marine reptile taxa such as mosasaurs are represented by a much wider size range in the type Maastrichtian (e.g. Kuypers

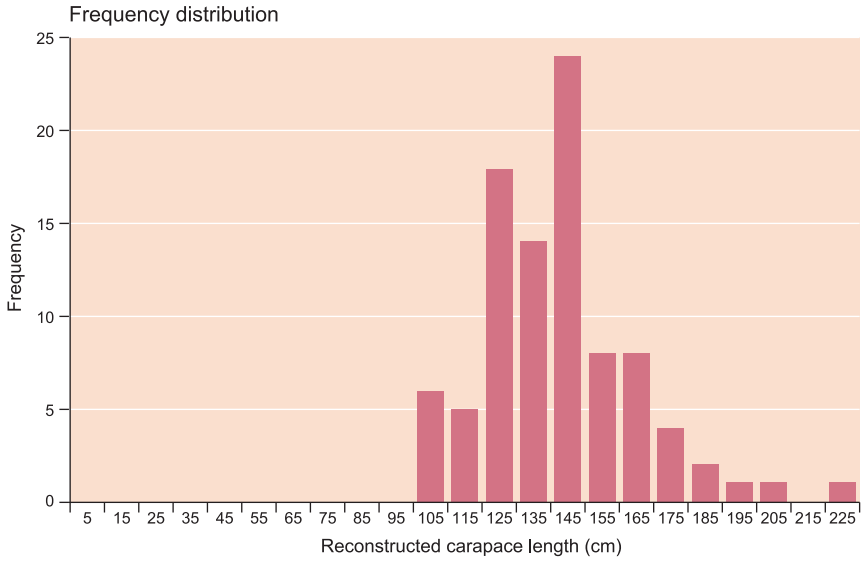

Fig. 2. Frequency distribution of carapace lengths of specimens of Allopleuron hofmanni. *In most cases, no complete carapace was present, and carapace lengths were estimated using specimen NHMM 000001 as a reference. A total of 92 specimens were used to construct this graph; other specimens were excluded because of uncertain identification of the skeletal element involved or incomplete preservation. Due to intraspecific variation between the relative size of particular skeletal elements and total body size, this figure primarily provides an indication of the general range of carapace lengths (all >90 cm), and should not be interpreted as a precise record of the original carapace lengths.*

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et al., 1998). Therefore we propose that, in addition to the taphonomic factors outlined above, the regional population composition is also a major factor. The stratigraphic and spatial distribution of *A. hofmanni* coincides remarkably well with that of the seagrass species *Thalassotaenia debeyi* (Van der Ham et al., 2007). It is not unthinkable that the seagrass meadows were the primary food source and provided a habitat during the adult life stage. If the population was composed solely of adult individuals, this would suggest that *A. hofmanni* moved through different, specific habitats during the various ontogenetic stages. This development can be compared with the life cycle of the extant green turtle, *Chelonia mydas*, which displays dramatic changes in lifestyle and habitat when reaching the adult stage. Like other contemporary marine turtles, green turtle hatchlings and juveniles hide in floating seaweed patches in the open ocean, feeding on shrimp, fish and jellyfish, in what are termed 'the lost years' (sensu Perrine, 2003). After this phase, the turtles move inshore and change their diet (Reich et al., 2007). At this stage in life, the green turtle develops into a herbivorous bottom-dwelling adult (Lutz et al., 2003). Hypothetically, a similar life cycle development may have been responsible for geographic separation of individuals of *A. hofmanni* of different ages.

Conclusions

The fossil record of *Allopleuron hofmanni* is composed almost entirely of remains of adult specimens. This may be explained by the assumption that the population consisted almost exclusively of adult individuals in this particular habitat, and by taphonomic processes which introduced a bias towards large, strong and robust skeletal elements. We can hypothesise that adult individuals inhabited the coastal, shallow environment of the Maastrichtian type area, while hatchlings and juveniles lived elsewhere, in yet unknown habitats. Taphonomic processes alone would produce a more gradual bias, leaving more specimens of small- and medium-sized *A. hofmanni* to be found in the Maastrichtian type area.

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Supplementary material

List of all specimens, including reconstructed carapace length and bone affection types; these data were used to compile Fig. 1.

Legend

- Adult, based on well-defined measurement
- Adult, based on measurements of unidentified or very fragmental bone elements
- Unknown, measurements available but not enough qualitative information
- Juvenile
- RCL Reconstructed carapace length

Specimen number	Skeletal elements present	No.	Life phase	RCL (cm)
Natuurhistorisch Museum Maastricht (the Netherlands)				
NHMM000001	Peripherals	19	Adult	143
	Neurals	9		
	Costals	16		
	Nuchal	1		
	Pygal	1		
	Suprapygals	3		
	Xiphiplastrons	2		
	Hypoplastrons	2		
	Cranium	1		
	Ceratobranchials	2		
	Paired Atlas Neural Arch Pieces	2		
	Mandible	1		
	Cervical Vertebrae	4		
	Ribs	5		
	Pectoral Girdle	2		
	Humeri	2		
	Ulna	1		
	Radii	2		
	Manus	2		
	Femur	1		
	Tibia/Fibula	1		
	Caudal Vertebrae	2		
NHMM383	Costal	1	Adult	
NHMM881	Thoracic rib pairs 1 to 6	12	Adult	129
NHMM001406	Peripheral	1	Adult	143
NHMM001413	Peripherals	2	Adult	
NHMM002056	Cranium	1	Adult	128
	Mandible	1		
NHMM003836	Costal	1	Adult	
NHMM003889	Costal	1	Adult	103
NHMM003890	Peripheral	1	Adult	164
NHMM003891	Peripheral	1	Adult	
NHMM003894	Peripherals	2	Adult	
NHMM003901	Pectoral girdle	1	Adult	
NHMM003903	Peripherals	3	Adult	124
NHMM003906	Sacral vertebrae	2	Adult	
	Caudal vertebra	1		
	Unidentified bone fragment	1		
NHMM003910	Unidentified vertebra	1	Adult	
NHMM007978	Nuchal	1	Adult	145
	Costals	2		
	Neurals	2		
	Peripheral	1		
NHMM009005	Cranium	1	Adult	125
NHMM009012	Tibia	1	Adult	
	Fibula	1		
	Pes	1		
NHMM009016	Nuchal	1	Adult	134
	Neurals	8		
	Costals	8		
	Thoracic vertebrae	7		
	Ribs	7		
	Suprapygal	1		
	Pectoral girdle	1		
	Femur	2		
	Cranium	1		
	Mandible	1		
	Ceratobranchial	1		
	Humerus	1		
	Paired Atlas Neural Arch Piece	1		
	Ulna	1		
	Radius	1		
	Manus	1		
	Pygal	1		
NHMM009017	Manus	2	Adult	149
	Peripherals	8		
	Humerus	1		
	Radius	1		
	Ulna	1		
	Hypoplastron	2		
	Pygal	1		
	Pelvis	1		
	Femurs	2		
	Tibia	1		
	Fibula	1		
	Xiphiplastron	1		

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	Hyoplastron	1		
	Epiplastron	1		
	Entoplastron	1		
	Cervical vertebra	1		
	Caudal vertebrae	3		
	Unidentified vertebra	1		
	Pes	1		
	Cranium	1		
	Mandible	1		
NHMM198350	Plastron fragment	1	Adult	
NHMM198351	Peripheral	1	Adult	
NHMM1991051	Peripheral	1	Adult	147
NHMM1992087	Peripherals	2	Adult	
NHMM1992183	Costal	1	Adult	
NHMM1995014	Nuchal	1	Adult	
	Peripherals	2		
	Neurals	9		
	Costals	16		
	Suprapygal	3		
NHMM2010144	Pygal	1	Adult	176
	Peripherals	2		
NHMM2010145	Peripheral	1	Adult	142
NHMM2010146	Peripheral	1	Adult	132
NHMM2010147	Peripheral	1	Adult	129
NHMM2010148	Peripheral	1	Adult	147
NHMM2010149	Pygal	1	Adult	107
NHMM2010150	Peripheral	1	Adult	121
NHMM2010151	Unidentified bone fragment	1	Adult	
NHMM2010152	Unidentified bone fragments	2	Adult	
NHMM2010153	Unidentified bone fragments	4	Adult	
NHMM2010154	Unidentified bone fragment	1	Unknown	
NHMM2010155	Unidentified bone fragments	*	Unknown	
NHMM2010156	Neurals	3	Adult	147
	Costals	4		
	Nuchal	1		
NHMM2010157	Neurals	4	Adult	131
	Costals	8		
	Suprapygal	1		
NHMM2010158	Pygal	1	Adult	
NHMM2010159	Peripheral	1	Adult	
NHMM2010160	Mandible	1	Adult	
NHMM2010161	Femur	1	Adult	150
NHMM2010162	Peripherals	2?	Adult	
NHMM2010163	Nuchal	1	Adult	155
	Neurals	2		
	Costals	4		
	Peripherals	4		
	Pygal	1		

Teylers Museum (Haarlem, the Netherlands)

TM1353	Costal	1	Adult	143
TM3949	Thoracic vertebrae	3	Adult	
TM5226	Carapace fragment	1	Unknown	
TM5239	Carapace fragment	1	Adult	
TM5253	Carapace fragment	1	Adult	
TM7430	Costal	1	Adult	
TM7431	Peripheral	1	Adult	155
TM7432	Scapula-prescapular process	1	Adult	
TM7434	Plastron	1	Adult	
TM7451	Nuchal	1	Adult	140
	Neurals	4		
	Costals	8		
	Peripherals	2		
	Suprapygals	3		
TM7452	Nuchal	1	Adult	127
	Peripherals	4		
	Costals	2		
TM7453	Mandible	1	Adult	176
TM7454	Rib fragments?	2	Adult	
TM7455	Peripherals	2	Adult	149
TM7456	Peripheral	1	Adult	132
TM11208	Unidentified bone fragment	1	Adult	
TM11221	Unidentified bone fragment	1	Adult	
TM11240	Unidentified bone fragment	1	Adult	
TM11259	Pygal	1	Adult	
TM11263	Peripheral	1	Adult	
TM11264	Neural	1	Adult	
TM11265	Costal	1	Adult	131
TM11266	Peripheral	1	Adult	
TM11267	Neural	1	Adult	115
TM11268	Peripheral	1	Adult	
TM11269	Cranium	1	Adult	102
	Cervical vertebrae	3 or 4		
TM11270	Scapula-prescapular process	1	Adult	
TM11275	Unidentified bone fragment	1	Unknown	
TM11277	Nuchal	1	Adult	110
	Peripherals	2		
	Neurals	3		
	Costals	6		
TM11279	Unidentified bone fragment	1	Unknown	
TM11280	Procoracoid	1	Adult	
TM11281	Peripheral	1	Adult	
TM11282	Procoracoid	1	Adult	
TM11283	Unidentified bone fragment	1	Adult	
TM11284	Scapula-prescapular process	1	Adult	
TM11285	Neural	1	Adult	
TM11286	Peripheral	1	Adult	180
TM11288	Peripherals	2	Adult	144
TM11289	Nuchal	1	Adult	137
	Neurals	7		
	Costals	13		
	Suprapygal	2		
TM11290	Mandible	1	Adult	176
TM11291	Pelvis	1	Adult	
TM11292	Costal	1	Adult	144
	Suprapygal	1		
	Neural	1		

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TM11294	Ulna	1	Adult	201
TM11295	Scapula-prescapular process	1	Adult	
TM11296	Unidentified bone fragment	1	Adult	
TM11297	Unidentified bone fragment	1	Unknown	
TM11298	Unidentified bone fragment	1	Unknown	
TM11299	Pygal	1	Adult	166
	Peripheral	1		
TM11300	Scapula-prescapular process	1	Adult	
TM11301	Scapula-prescapular process	1	Unknown	
TM11302	Unidentified bone fragment	1	Unknown	
TM11303	Peripheral	1	Adult	
TM11305	Scapula-prescapular process	1	Unknown	
TM11306	Unidentified carapace element	1	Adult	
TM11308	Unidentified bone fragment	1	Unknown	
TM11309	Unidentified bone fragment	1	Unknown	
TM11323	Unidentified bone fragment	1	Unknown	
TM11332	Peripheral	1	Adult	
TM11335	Peripheral	1	Adult	
TM11336	Unidentified carapace element	1	Adult	
TM11337	Peripheral	1	Adult	
TM11338	Nuchal	1	Adult	
TM11339	Peripheral	1	Adult	146
TM11352	Peripheral	1	Adult	166
	Pygal	1		
TM11353	Peripherals	2	Unknown	
TM11354	Peripheral	1	Unknown	
	Unidentified bone fragment	1		
TM11355	Peripherals	1	Unknown	
TM11357	Nuchal	1	Adult	136
	Peripheral	1		
TM11359	Peripherals	8	Adult	149
	Pygal	1		
TM11360	Neurals	3	Adult	144
	Costals	2		
TM11361	Mandible	1	Adult	
TM11366	Peripheral	1	Unknown	
TM11390	Unidentified bone fragment	1	Unknown	
TM11394	Unidentified bone fragment	1	Unknown	
TM11397	Unidentified bone fragment	1	Unknown	
TM11399	Cranium fragment	1	Adult	
TM11404	Peripheral	1	Adult	151
TM12744	Unidentified bone fragment	1	Unknown	
TM13264	Neurals	3	Adult	132
	Costals	6		
	Nuchal	1		
	Peripheral	1		
	Scapula-prescapular process	1		
TM13265	Peripherals	5	Adult	142
TM13266	Pectoral girdle	1	Adult	
TM13268	Pectoral girdle	1	Adult	
TM13269	Thoracic vertebrae	2	Adult	
TM13270	Thoracic vertebrae	2	Adult	
TM13271	Procoracoid	1	Adult	
TM13272	Peripherals	2	Adult	195
TM13273	Peripheral	1	Adult	127
TM13274	Peripheral	1	Adult	
TM13275	Costals	2	Adult	148
	Rib	1		
TM13277	Unidentified bone fragment	1	Adult	
TM13278	Nuchal	1	Adult	
TM16793	Unidentified bone fragments	5	Unknown	
TM16794	Unidentified bone fragments	a lot	Unknown	
TM17129	Cervical vertebra	1	Adult	
TM17130	Cervical vertebrae	2	Adult	
TM17235	Unidentified bone fragment	1	Unknown	
TM17237	Carapace element	1	Adult	
TM17252	Unidentified appendage fragment	1	Adult	
TM21849	Peripheral	1	Unknown	
TM21850	Peripheral	1	Unknown	
TM218451	Carapace fragments	5	Unknown	
TM218452	Unidentified fragments	2	Unknown	
TM218454	Appendage fragment	1	Adult	
TM218459	Unidentified fragments	2	Unknown	

Nederlands Centrum voor Biodiversiteit Naturals (Leiden, the Netherlands)

NNM12459	Nuchal	1	Adult	122
	Neurals	9		
	Costals	16		
	Suprapygals	2		
	Peripherals	2		
NNM14000	Peripheral	1		
NNM14016	Mandible	1		
NNM14061	Mandible	1	Adult	148
NNM14062	Cranium	1	Adult	138
	Mandible	1		
NNM14063	Sacral vertebrae	2	Adult	
	Caudal vertebra	1		
NNM27639	Peripheral	1	Adult	162
NNM440902	Unidentified bone element	1	Unknown	
NNM446890	Peripheral	1	Adult	
NNM446891	Peripheral	1	Adult	122
NNM446892	Carapace fragment	1	Unknown	
NNM446894	Peripheral	1	Unknown	
NNM446895	Peripheral	1	Adult	126
NNM446896	Costal	1	Adult	146
NNM446897	Unidentified bone element	1	Unknown	
NNM446898	Unidentified carapace element	1	Unknown	
NNM446899	Nuchal	1	Adult	
NNM446900	Peripheral	1	Adult	119
NNM446901	Nuchal	1	Unknown	
NNM446903	Peripheral	1	Adult	118
NNM446904	Peripherals	2	Adult	
NNM446905	Peripheral	1	Adult	
NNM446906	Neural	1	Adult	
NNM446907	Peripheral	1	Adult	133
NNM446908	Unidentified bone element	1	Unknown	

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NNM446909	Peripheral	1	Adult	
NNM446910	Unidentified bone element	1	Unknown	
NNM446911	Unidentified bone element	1	Unknown	
NNM446912	Unidentified bone element	1	Unknown	
NNM446913	Nuchal	1	Unknown	
NNM76729	Nuchal	1	Unknown	
NNM76735	Pectoral girdle	1	Adult	
NNM76819	Peripheral	1	Adult	110
NNM76820	Peripheral	1	Adult	
NNM78240	Unidentified carapace element	1	Unknown	
NNM94273	Peripheral	1	Unknown	
NNM-RR008	Peripheral	1	Adult	132
	Pygal	1		
Universiteitsmuseum Utrecht (the Netherlands)				
G768.1881	Neural	1	Adult	
G788.1883	Peripheral	1	Adult	
G797.1883	Peripheral	1	Adult	
G811.1883	Peripheral	1	Adult	
G812.1883	Peripheral	1	Unknown	
G819.1883	Peripherals	2	Adult	124
G824.1883	Unidentified bone fragment	1	Unknown	
G092.1903	Peripheral	1	Adult	
Natuurmuseum Brabant (Tilburg, the Netherlands)				
041.334	Neural	1	Adult	
	Carapace or plastron element	1		
	Carapace element	1		
041.242	Unidentified bone element	1	Unknown	
042.222	Mandible	1	Adult	
Geologisch Museum Hofland (Laren, the Netherlands)				
1184	Mandible	1	Adult	
1685	Peripheral	1	Adult	
Peabody Museum of Natural History (Yale, Unites States)				
YPM9773	Peripheral	1	Adult	174
YPM9774	Peripheral	1	Adult	163
YPM17826	Nuchal	1	Adult	111
	Neurals	9		
	Costals	10		
	Peripherals	5		
	Suprapygals	2		
	Pygal	1		
YPM uncat A	Unidentified bone fragments	24	Unknown	
YPM uncat B	Suprapygals	2	Adult	
YPM uncat C	Costal	1	Unknown	
YPM uncat D	Unidentified bone fragments	4	Adult	
YPM uncat E	Unidentified bone fragments	6	Unknown	
YPM uncat F	Peripherals	2	Adult	180
Museum fur Naturkunde Berlin (Germany)				
MBR2534	Mandible	1	Adult	
MBR2535	Peripheral	1	Adult	
Muséum National d'Histoire Naturelle Paris (France)				
AC8324	Nuchal	1	Adult	124
	Neural	1		
	Costals	2		
	Peripherals	3		
AC8556	Nuchal	1	Adult	
	Neurals	3		
	Costals	3		
	Peripherals	3		
AC8627	Pectoral girdle	1	Adult	
AC uncat 1	Neural	1	Adult	
AC uncat 2	Neural	1	Adult	104
	Costals	2		
	Suprapygals	2		
AC uncat 3	Femur	1	Adult	265
AC uncat 4	Unidentified plastron element	3	Unknown	
AC uncat 5	Unidentified bone fragment	1	Unknown	
AC uncat 6	Peripherals	?	Unknown	
AC uncat 7	Unidentified bone fragments	a lot	Unknown	
Institut Royal des Sciences Naturelles de Belgique (Brussels, Belgium)				
1619	Hyoplastron	2	Adult	130
	Hypoplastron	1		
	Pectoral girdle	2		
	Nuchal	4		
	Peripherals	12		
1620	Sacral vertebrae	2	Adult	
	Caudal vertebrae	5		
1623	Mandible	1	Adult	144
	Mandible	1		
3106	Peripherals	6?	Adult	
	Neurals	4		
	Costals	3?		
	Unidentified carapace fragments	7		
C44-8 (3175)	Nuchal	1	Adult	123
	Peripherals	4		
	Costals	2		
	Neurals	3		
	Unidentified bone fragment	1		
IG8444	Peripherals	2	Adult	
IG8612	Peripherals	2	Adult	148
	Ulna	1		
	Unidentified carapace fragment	1		
	Suprapygal	1		
	Pectoral girdle	1		
IG8912	Peripheral	1	Adult	
	Neural	1		
	Costal	1		
IG9694	Peripherals	5	Adult	127
	Unidentified bone fragments	3		
	Unidentified vertebra	1		
	Pectoral girdle	1		
IG9708	Pygal	1	Adult	145
IRScNB EFR 9 (1623)	Mandible	1	Adult	142
REG1737	Peripherals	7	Adult	123
	Unidentified plastron elements	12		

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Unnumbered 1	Pectoral girdle	1	Adult	
Unnumbered 3	Peripheral	1	Adult	
Unnumbered 4	Peripherals	2	Adult	121
Unnumbered 5	Peripherals	2	Adult	
Unnumbered 6	Peripheral	1	Unknown	
Unnumbered 7	Pectoral girdle	1	Unknown	
Unnumbered 8	Peripherals	2	Adult	127
Unnumbered 9	Unidentified plastron element	1	Unknown	
Unnumbered 10	Unidentified bone fragment	1	Unknown	
Unnumbered 11	Unidentified vertebra	1	Unknown	
Natural History Museum London (United Kingdom)				
NHM-R921	Nuchal	1	Adult	
NHM11603	Peripheral	1	Unknown	
NHM40173	Costal	1	Adult	
NHM42889	Mandible	1		163
NHM42890	Mandible	1		160
NHM42891	Mandible	1		152
NHM42892	Mandible	1		153
NHM42893	Manus	1		150
	Humerus	1		
	Radius	1		
	Ulna	1		
	Presum. Hyoid bone	1		
NHM42894	Pelvis	1	Adult	
	Thoracic vertebrae	2		
	Plastron element	1		
	Femur	1		
	Sacral vertebra	1		
NHM42895	Pelvis	1	Adult	
NHM42896	Neural	1	Adult	
NHM42897	Peripheral	1	Adult	
NHM42898	Peripheral	1	Adult	
NHM42899	Suprapygals	2	Adult	
	Pygal	1		
	Peripherals	2		
	Caudal vertebrae	5		
NHM42901	Plastron element	1	Unknown	
NHM42902	Scapula/prescapular process	1	Adult	
NHM42903	Scapula/prescapular process	1	Adult	
NHM42904	Pectoral girdle	1	Adult	
NHM42907	Unidentified bone fragments	3	Adult	
NHM42910+	Nuchal	1	Adult	
NHM42911	Costals	4		
	Peripherals	3		
NHM42912	Cervical vertebrae	6		143
	Scapula	1		
	Pectoral girdle	1		
	Neurals	9		
	Suprapygals	3		
	Nuchal	1		
	Costals	11		
	Peripherals	8		
	Pygal	1		
	Pectoral girdle elements	2		
NHM42913	Pelvis	1		168
	Hyoplastron	1		
	Plastron element	1		
	Peripherals	5		
	Unidentified bone fragments	4		
	Neurals	2		
	Mandible	1		
	Cranium	1		
NHM42914	Pectoral girdle	1	Adult	
	Peripherals	3		
	Cervical vertebrae	3		
NHM42915	Nuchal	1		119
	Peripherals	3		
	Neurals	7		
	Costals	10		
NHM42916	Peripherals	3	Adult	
	Pygal	1		
	Neurals	3		
	Costal	1		
NHM429165a	Nuchal	1		152
	Peripherals	4		
	Neural	1		
NHM42964	Caudal vertebrae	6	Adult	
NHM42965	Nuchal	1		132
	Peripherals	2		
NHM42967	Neurals	2	Adult	
	Dorsal vertebrae	2		
NHM42968	Presum. Left hyoplastron	1	Adult	
NHM42970	Plastron element	1	Unknown	
NHM42971	Humerus	1	Adult	
NHM42972	Scapula	1		
NHM42973	Femur	1		
NHM42997	Cranium	1		
NHM42999	Peripherals	9		144
	Nuchal	1		
	Pelvis	1		
	Carapace element	1		
	Unknown element	1		
	Rib	1		
	Neurals	2		
	Vertebra	1		
	Mandible	1		
	Plastron element	1		
	Unknown elements	6?		
	Scapula/prescapular process	1	Juvenile	
NHM43467	Neural	1	Adult	

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