Chronic bone infection in the jaw of *Mosasaurus hoffmanni* (Squamata)

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ABSTRACT – A massive infection appears to have destroyed a considerable portion of the quadrate and the posterior part of the mandible of a specimen of the mosasaurine squamate *Mosasaurus hoffmanni*, housed in the Natuurhistorisch Museum Maastricht collections. The extensive nature of the infection and the formation of reparative bone tissue isolating the infection suggests that the mosasaur survived the infection for a prolonged period of time. The cause of the infection remains speculative.

Key words: *Cretaceous, infection, Maastrichtian, Mosasaurus, pathology, Squamata.*

Infection osseuse chronique de la mâchoire de *Mosasaurus hoffmanni* (Squamata) – Une importante infection a détruit une grande partie du carré et la portion postérieure de la mandibule d'un spécimen du squamate mosasauriné *Mosasaurus hoffmanni* conservé dans les collections du Natuurhistorisch Museum Maastricht. L'importance de l'infection et la présence de tissu osseux de réparation indiquent que le mosasaure a survécu à l'infection sur une période prolongée. La cause de l'infection reste incertaine.

Mots clés: *Crétacé, infection, Maastrichtien, Mosasaurus, pathologie, Squamata.*

INTRODUCTION

Bacterial bone infections (osteomyelitis), given enough time, can have a profound impact on the morphology of bone tissue (e.g., Resnick, 2002; Lingham-Soliar, 2004). In paleopathological studies, where the available material is most often limited to nothing but fossil bone, only those infections serious enough to have attacked bone tissue will leave a recognisable trace (Rothschild & Martin, 1993). Here, a pathological quadrate and posterior mandibular unit of a ~66 million year old mosasaur are described in detail, and diagnosed with osteomyelitis in the jaw joint, possibly triggered by septic arthritis.

Mosasaurs are extinct marine reptiles, closely related to lizards and snakes. They flourished during the last 25 million years of the Cretaceous Period, some 90 to 65 million years ago (Ma). They went extinct at the end of the Cretaceous (Russell, 1967; Bell, 1997, and refs therein). Some mosasaurs reached lengths in excess of 15 metres (e.g. Lingham-Soliar, 1995) well before the end of the Cretaceous. Towards the end of the Cretaceous, they outcompeted sharks and other marine predators, and established themselves at the top predator niche of the Late Cretaceous marine ecosystem (Everhart, 2004a; Rothschild et al., 2005).

Since the first discoveries in the late 18th century, mosasaurs have become a well-known group, with their remains recorded from every continent. Various pathologies have been described in mosasaurs, including infectious spondylitis (Gaudry, 1890), avascular necrosis ('the bends'; Rothschild & L.D. Martin, 1987, 2005), neoplasia (Rothschild & L.D. Martin, 1993), ligamentous ossification of caudal vertebrae due to physical stress (Mulder, 2001), bone fractures (e.g., Schulp et al., 2004 and refs therein), and bite marks and other traumas (e.g. L.D. Martin & Rothschild, 1989; J.E. Martin & Bell, 1995; Rothschild et al., 2005). The common occurrence of traumas suggests that

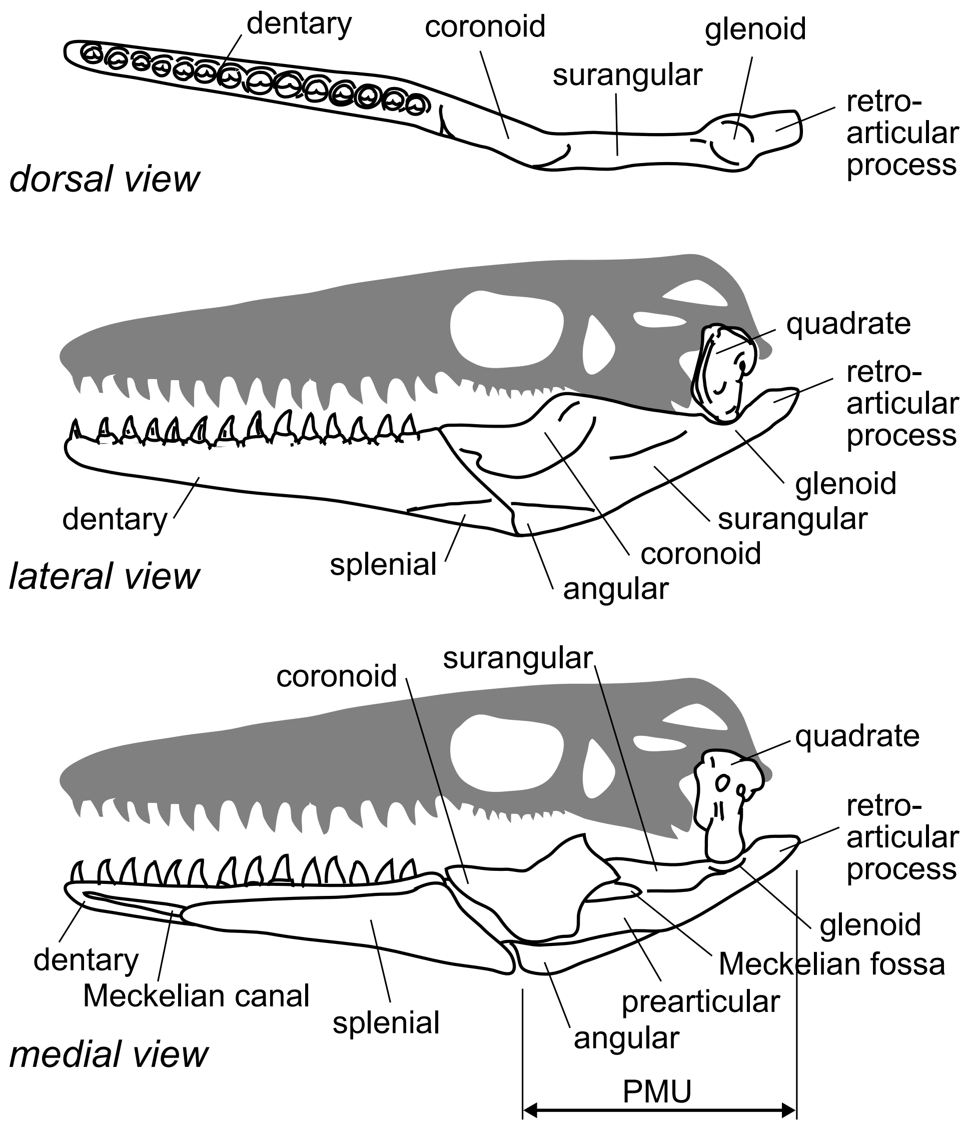


Figure 1 (left) – Schematic osteology and nomenclature of the quadrate and mandibular unit of *Mosasaurus hoffmanni* in dorsal, lateral and medial view. Redrawn and simplified after Russell (1967) and Lingham-Soliar (1995).

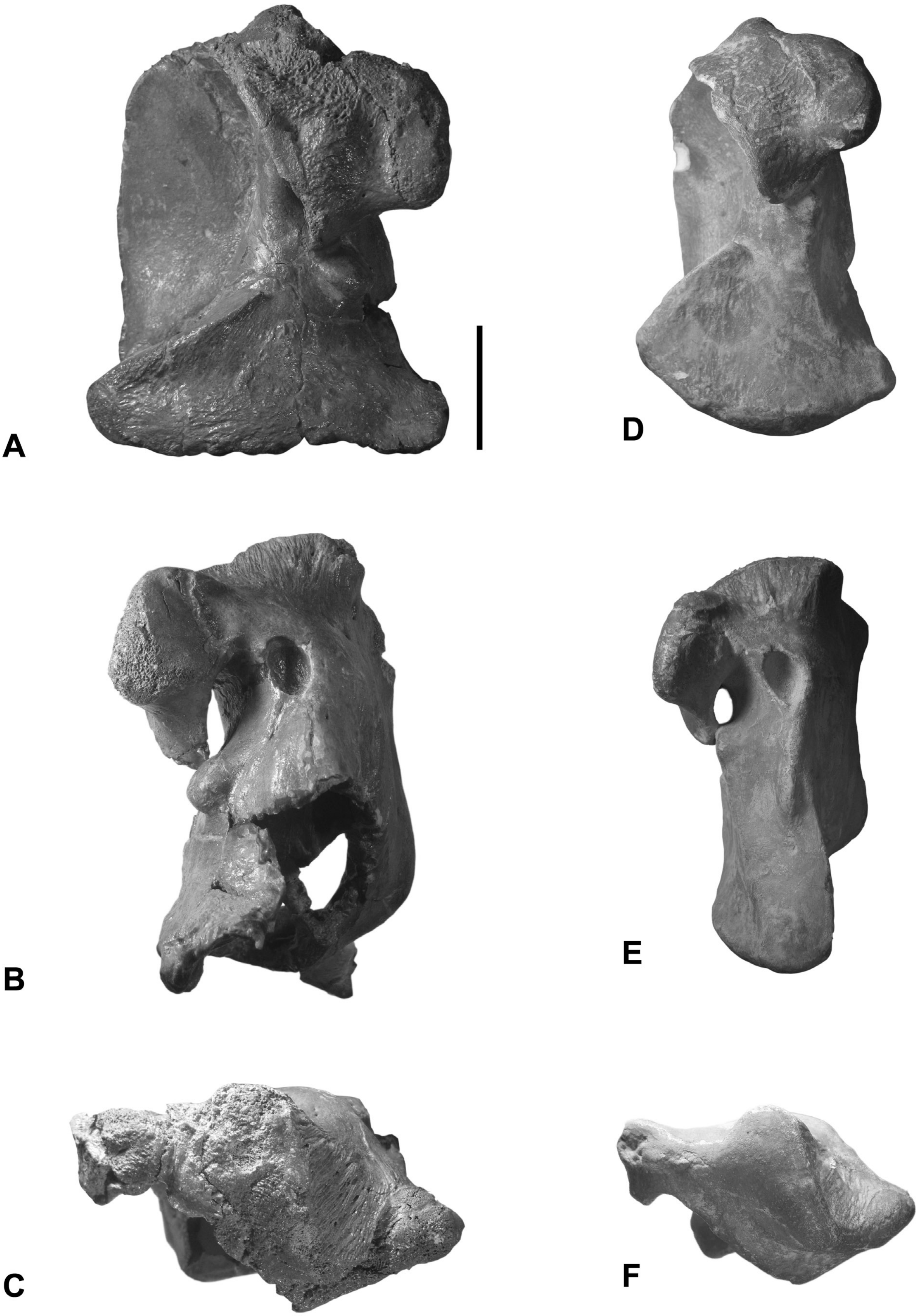
Figure 2 (right) – Pathological left quadrate of *Mosasaurus hoffmanni* NHMM 006696 in posterior (A), medial (B) and dorsal (C) view; Normal left quadrate of *Mosasaurus hoffmanni*, cast of MNHN(P) AC 9648, in posterior (D), medial (E) and dorsal (F) view for comparison. Scale bar equals 5 cm.

mosasaurs lead a violent and aggressive life (e.g., Williston, 1914), and, in an earlier reference, Williston (1898, p. 214) already noted that "...they were pugnacious in the extreme is very evident from the many scars and mutilations which they suffered during life. I have observed exostosial growth in their lower jaws, the vertebrae, expecially those of the tail, and in the paddles, especially the digits." Additional, and more conclusive evidence of intraspecific aggression in mosasaurs was reported by Bell & J.E. Martin (1995) and in the holotype of *Tylosaurus kansasensis* Everhart 2005.

MATERIAL AND METHODS

The specimen described here is a partial skeleton of *Mosasaurus hoffmanni* Mantell 1829, contained in the Natuurhistorisch Museum Maastricht collections under registration number NHMM 006696, and informally referred to as the 'Bemelse mosasaur'. The specimen was discovered in 1953 (Kruytzer, 1957, 1964) in 't Rooth quarry near the village of Bemelen (some 5 km E of Maastricht). It is one of the most complete specimens from the type Maastrichtian area, with portions of the skull, cervical, dorsal, pygal, caudal and terminal vertebrae, right coracoid, right tibia, the right pelvic girdle, some phalanges and rib fragments preserved (see Kuypers et al., 1998, p. 8-9 for a complete listing). With an estimated skull length of 1,44 m, the entire animal in all likelihood would not have been much longer than 15 m (e.g., Kruytzer, 1957). Oddly enough, Kruytzer (1964: 154) presented a length estimate of 18 m. Russell (1967, p. 210) considered the lower jaw length of a *Mosasaurus* specimen at the YPM to represent 10% of the body length.

The specimen comes from the 'Mc' of the type Maastrichtian (Hofker, 1957); corresponding to the Nekum Member in the current local lithostratigraphic framework (see Schiøler et al., 1997, and references therein, for an overview of local stratigraphy). The Nekum Member is of Late Maastrichtian age, and was deposited only a few hundred thousands of years before the K/T event (Vonhof &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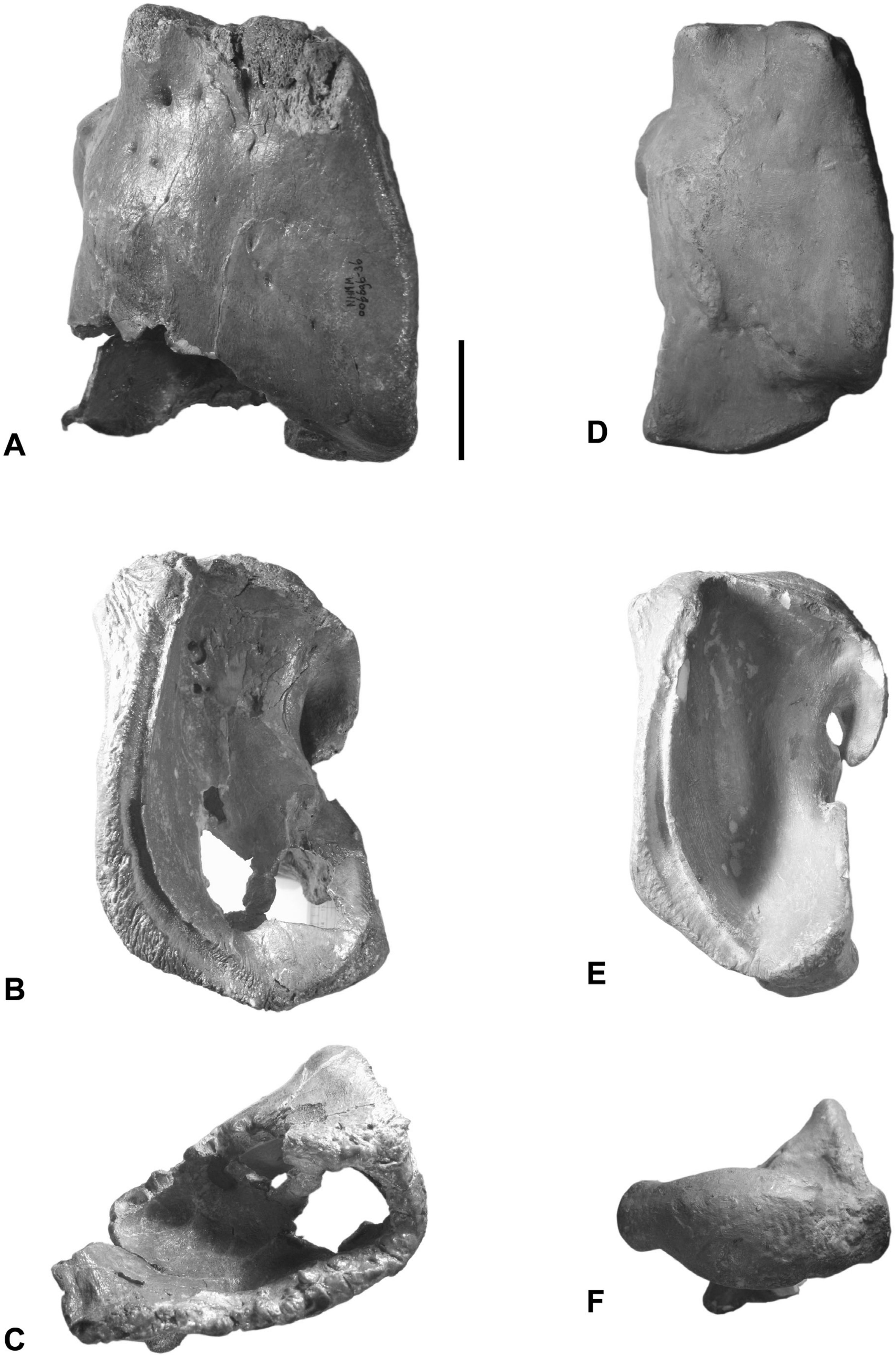
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Smit, 1996).

In most mosasaurs, the quadrate is a dense, powerfully constructed bone (Figure 1). It articulates at its mandibular condyle with the glenoid fossa in the posterior mandibular unit of the lower jaw, together forming the main 'jaw hinge' (Russell, 1967: 46-49). The posterior mandibular unit (PMU) consists of the angular, surangular, coronoid and the prearticular-articular (Russell, 1967: 51-54).

The material studied consists of the left (pathological) quadrate (NHMM 006696-36), the left surangular, articular and angular (NHMM 006696-38, -39, and -40, respectively), and, for comparison, the right surangular, articular, angular (all partly reconstructed: NHMM 006696-41, -42, and -43, respectively). Additional material of the same individual is registered under no. NHMM 006699 (partial right dentary; this specimen entered the NHMM collections later; in the initial documentation in some cases erroneously referred to as NHMM 006698). An overview of the material is presented in Kuypers et al. (1998: 8-9). Here the remains of the right quadrate are also mentioned (two fragments; NHMM 006696-72 and -76), but none of these can be assigned with any certainty to a quadrate; the (small) fragments rather appear to represent portions of the humerus.

Part of the material has initially been restored using an undocumented variety of glues, fillers and consolidants, including a brownish substance with appearance and material properties not unlike beeswax. Subsequently, the material has been reinforced with undocumented coating, most likely 'archeoderm', of which the chemical composition has changed over the years (and thus remains undocumented), but has included (according to a variety of sources) most likely a cellulose-based compound, and polyvinyl acetates. Perhaps sodium silicate has been used as well to harden the specimen. The dark discoloration of the bone is most likely at least in part caused by the (mixed) use of these consolidants.

Kruytzer (1957: 126) just hinted at the pathological appearance of the left quadrate and the posterior mandibular unit of NHMM006696: "Het quadratum van Bemelen vertoont [...] een bijzonder iets, dat wel als een pathologische afwijking moet beschouwd worden" [the quadrate from Bemelen shows a peculiarity, that should be considered a pathological abnormality]. The normally convex ventral articular surface of the quadrate is a large concavity instead, and is much wider than normal. Kruytzer considered a malignant tumour to be a possible explanation, without further elaborating on this diagnosis. Mulder (1999) figured the quadrate (fig. 11: 5; fig 12: 1A-1C and fig. 13: 4; the catalogue number is incorrectly stated as NHMM 00696-02), but no mention is made of the pathological appearance, except for "[...] lateral and medial condyle missing" (p. 298). Beyond these studies, no additional work has been done that we are aware of, and nothing more detailed has been published on the pathology of the Bemelen specimen.

DESCRIPTION

In Figures 2 and 3, the quadrate of NHMM 006696 is compared with the cast (in the NHMM collections) of a similar-sized quadrate from the type specimen of *M. hoffmanni*, MNHN(P) AC 9648. NHMM 006696 measures 183 mm in height. The dorsal half of the quadrate appears almost identical to the MNHN(P) specimen, except that the former is slightly wider in posterior and anterior view (Fig 2A/D; Fig 3A/D). In lateral view, the pathology in the NHMM specimen is not very obvious, except for the hole in the tympanic cavity, but in all other views, the lower half of the specimen differs dramatically from the MNHN(P) specimen. The greater part of the medial surface of the quadrate is missing. In ventral view (Figure 3C), the mandibular condyle is almost completely missing, leaving only a swollen, irregularly formed bony rim instead of a massive condyle. In posterior view (Figure 2A), the mandibular condyle has widened considerably. In medial view (Figure 2B), the median ridge is more swollen, along with the infrastapedial process, but apart from that, the morphology remains unchanged in the central part of the element. More ventrally, where the median ridge proceeds towards the mandibular condyle, the bone swells even further, to 'burst open' in the lower third of the element, exposing an open space instead of the massive mandibular condyle.

It is unclear whether all openings in the ventral half of the quadrate (Fig. 2B) represent preservational artefacts, or whether these were (at least partially) present already during life. The rim of the two openings shows large, round excavations, suggesting that the bone must have been severely weakened in vivo, and therefore was easily broken away, either when the mosasaur was still alive, or later during taphonomic processes.

Some of the nutritional foramina, especially on the anterior side, are considerably enlarged, one of them actually cutting through the entire bone, and forming a wide canal giving access to the tympanic cavity. On the inside of the tympanic cavity three radiating grooves and a semi-circular excavation developed around the foramen.

The lower 'rim' of the quadrate, developed more or less parallel to the axis of the original mandibular condyle, features a series of irregular pustules.

The surface of the excavated cavity consists almost entirely of cortical bone. In other words, the usual 'internal'

Figure 3 (left) – Pathological left quadrate of *Mosasaurus hoffmanni* NHMM 006696 in anterior (A), lateral (B) and ventral (C) view; Normal left quadrate of *Mosasaurus hoffmanni*, cast of MNHN(P) AC 9648, in anterior (D), lateral (E) and ventral (F) view for comparison. Scale bar equals 5 cm.

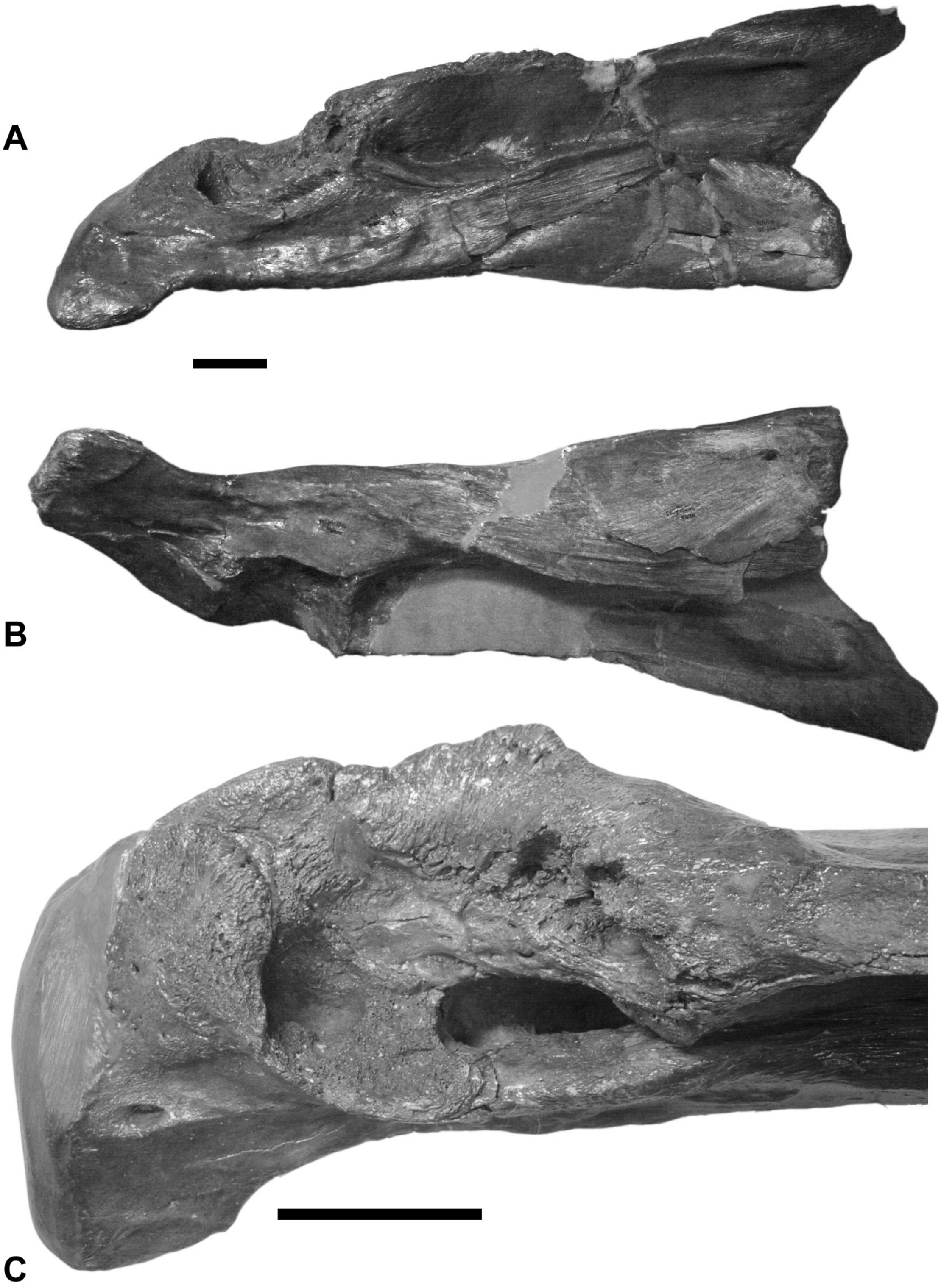

Figure 4 – Left (A) and right (B) posterior mandibular units (PMU) of NHMM 006696 in dorsolingual view; close-up of left posterior PMU in dorsal view (C). Scale bars equal 5 cm.

Figure 5 (opposite page) – Series of CT slices through the left (L) and right (R) PMU of NHMM 006696 from halfway anterior (1) to posterior (6) end. The opaque grey areas are plaster restorations; the white circle is a metal reinforcement rod.

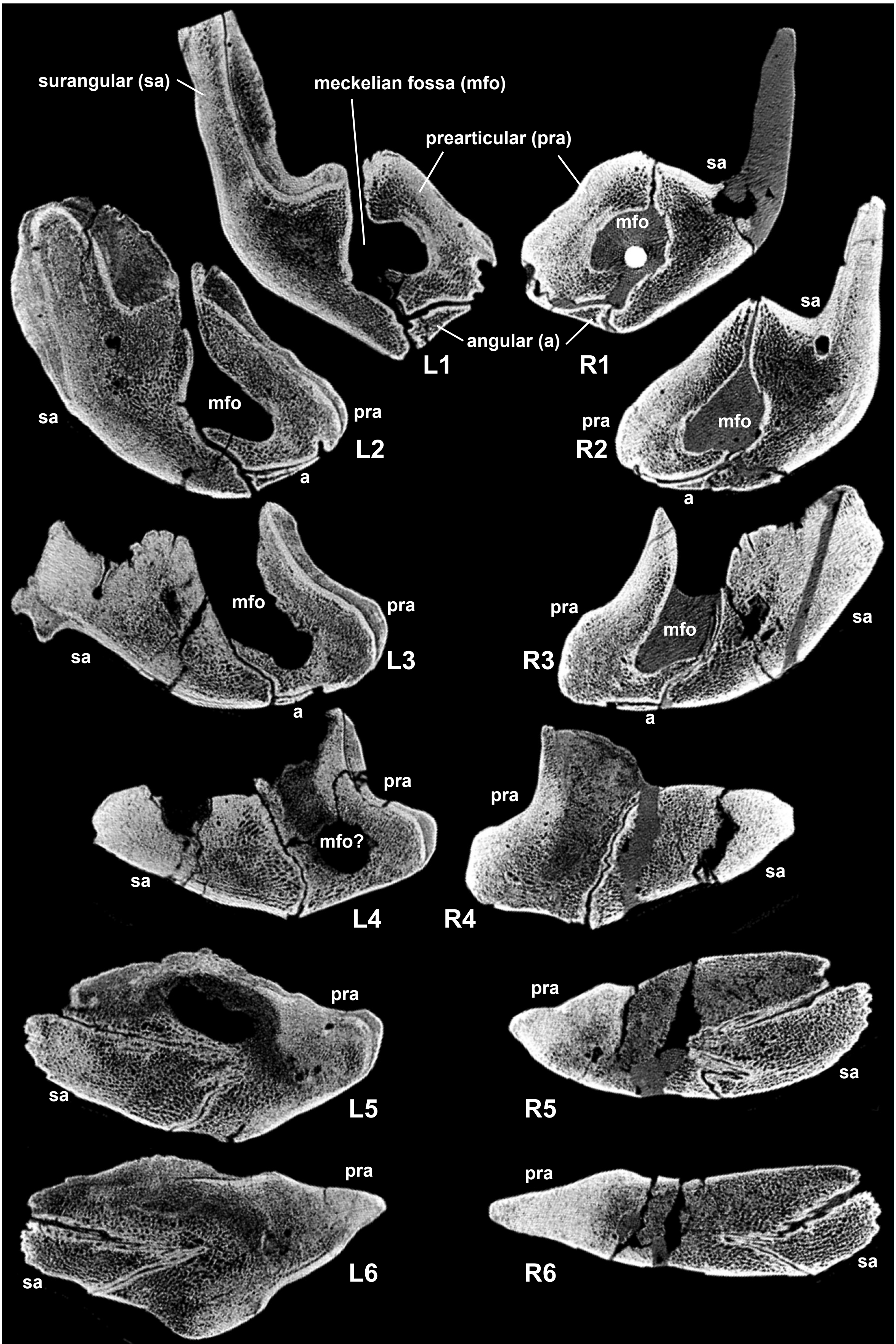
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Figure 6 – Series of CT slices through the quadrate of NHMM 006696 from the relatively unaffected, 'healthy' dorsal articular surface (1) down to the pathological glenoid articular surface (6).

trabecular (sponge-like) bone structure one would expect to be exposed on the inside of the excavated quadrate is almost fully covered by a new layer of cortical bone.

In the PMU (Figure 4), the pathology is not unlike the situation in the ventral half of the quadrate. Here, too, a large amount of bone tissue appears to be missing when compared to the right PMU. In a semi-circular area radiating from the centre of the glenoid fossa, bone is removed, in an irregular fashion, clearly exposing the Meckelian fossa. Within the excavated area, smaller, concave 'pockets' can be discerned, each a few centimetres wide and, on average, about a centimetre deep. Two pockets are in the posterior ventral surface of the Meckelian fossa, the other five in the 'crater' at the site of the original glenoid fossa. Part of the bone exposed in the crater appears covered (again) with cortical bone, but more than half of the surface has the appearance of trabecular bone.

Unfortunately, in the right PMU this area has been considerably restored, making the comparison of features such as the width and the amount of exposure of the Meckelian fossa difficult. Apart from those details, the difference between the pathological (left) and healthy (right) PMU is obvious.

A CT scan of the PMU, made at the AzM Maastricht Academic Hospital by P.A.M.H. (Figure 5), reveals that not only bone has been removed, but also that new layers of bone have been deposited on top of the original cortical bone; the initial layer of cortical bone remains clearly visible (particularly in L1-L2-L3). It had not yet been resorbed to make room for cortical bone. Similar bone apposition features are visible in the CT-scan of the quadrate (Figure 6).

Although growth line patterns in teeth could potentially reflect stressful events in the life history of an individual, no clear signs of interrupted growth could be discerned on the available teeth of this specimen.

DISCUSSION

A wide variety of diseases leave traces that can be recognised in fossil bone. Cancer, gout, fractures and infections, rickets (osteomalacia, vitamin-D-deficiency) and inflammatory arthritis all can have a considerable impact on bone morphology (Resnick, 2002). Most of these possibilities can be ruled out in the case of the Bemelen mosasaur.

Mosasaurs have been diagnosed with tumours previously (Rothschild & L.D. Martin, 1993). A tumour, as suggested by Kruytzer (1957), however appears an unlikely

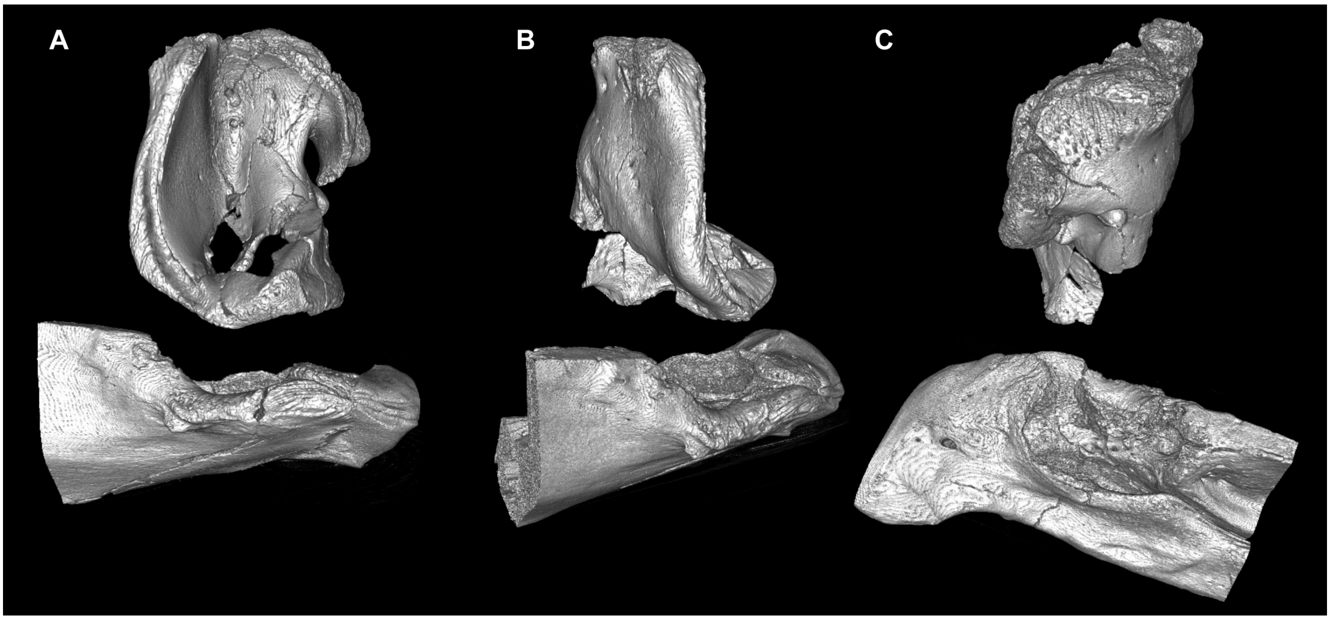

Figure 7 – Left jaw joint in lateral (A), antero-lateral (B) and oblique antero-medial (C) exploded view. Images generated using OsiriX (Rosset et al., 2004).

explanation for the pathological appearance of the quadrate of the Bemelen mosasaur. Benign bone tumours are often characterised by a radiolucent growth centre and sclerotic perimeter, while there is no periostial reaction (Rothschild & L.D. Martin, 1993). This is not the case here. The amount of removed bone is far too large to be explained by gout; additionally, the absence of new bone overgrowing the lesion (producing an overhang) allows us to eliminate gout from the differential diagnosis (Rothschild et al., 1997; Resnick, 2002). A poorly repaired fracture does not appear a feasible explanation either, in the absence of fracture-like lines and callus formation (compare Schulp et al., 2004); nor can a fracture explain the amount of removed bone tissue. The same can be said for osteomalacia (Resnick, 2002; Schulp et al., 2004). So far, no fractured quadrates have been reported in the fossil record of mosasaurs (Everhart, pers. comm.)

A massive bone infection (osteomyelitis) of the jaw joint appears the most likely explanation for the pathologies observed in the Bemelen specimen. The elements forming the jaw joint show considerable amount of bone removal, at a site where wear ('arthritis') or trauma would not likely have removed it. The spongy nature and remodelling of bone (periosteal bone apposition, where a layer of new, dense smooth cortical bone is formed on top of the originally present bone; Figure 5), and areas that appear not unlike pus drains are all features that are best explained as a massive, chronic bone infection (Walenkamp, 1997; Resnick, 2002). Considering that this infection affected the jaw joint, the pathology may perhaps also be classified as secondary osteomyelitis, initiated by septic arthritis; the infection may have either spread from one element to the opposite element in the joint, or the infection may have actually initiated in the joint space itself.

From the appearance of the bone, it seems likely that the infection developed until most of the articular surface between the posterior mandibular unit and the quadrate consisted of virtually nothing but a void filled with pus: one large abscess. An attempt to determine the size of the abscess by inserting water-filled plastic bags in the opening suggests that about half a litre of bone tissue was removed, and this measurement excludes a possible extension of the infection into the Meckelian canal. Three exploded views of the jaw joint are given in Fig. 7.

In palaeopathological cases, bone infection, or osteomyelitis, may have been caused by (a) an endogenic infection (hematogenic, spreading from the blood into the bone, or, in case of septic arthritis, from the joint) or (b) an exogenic infection (e.g. a complicated open fracture) (Walenkamp, 1997).

Bone regeneration is a dynamic process involving osteoclasts and osteoblasts, with the former being cells that 'eat' away bone, the latter instead forming new bone. Normally these two types of cells act in balance, but certain diseases or circumstances may affect the equilibrium, leading to loss of bone tissue (lysis) or overgrowth of bone (hyperostosis). In osteomyelitis, disequilibrium between lysis and hyperostosis leads to disorganisation of the trabecular framework of the spongy bone (e.g., Rothschild & Berman, 1991).

In humans, "Healing of chronic osteomyelitis demands a well performed, often aggressive, combination of operative and antibiotic treatment. Avascular tissue that cannot sufficiently be penetrated by antibiotics should be removed", and even in current medical practise, "healing in

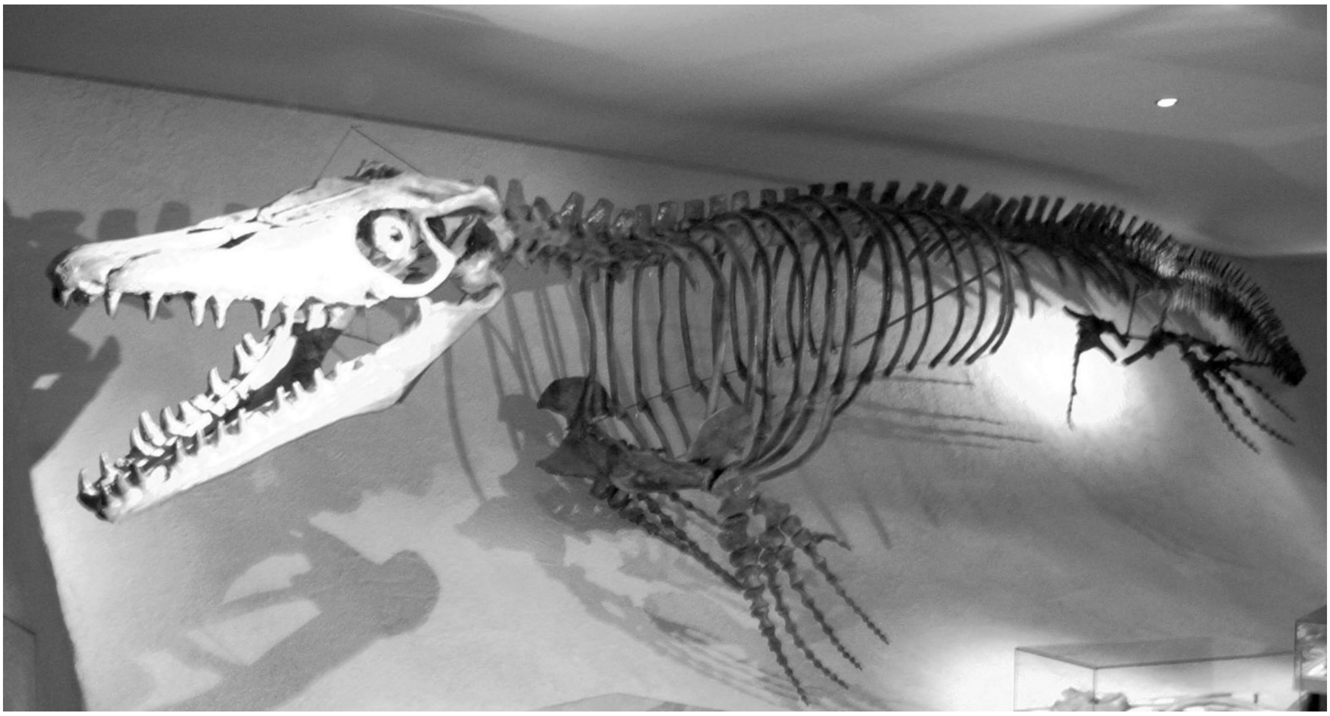

Figure 8 – Skeletal reconstruction of *Mosasaurus hoffmanni* NHMM 006696 by Hans Brinkerink of Vista Natura, Baarn, The Netherlands; on display at the Natuurhistorisch Museum Maastricht.

chronic osteomyelitis should be defined in terms of relapse-free years, and survival analysis makes more sense than healing percentages" (Walenkamp, 1997: 497-498). In other words, bone infections are difficult to treat. Then how long can we expect an infection to have taken to remove such a massive amount of bone tissue from the quadrate of the Bemelen mosasaur? How long did it possibly last until new bone tissue was deposited? And how long did the Bemelen mosasaur survive the infection? In humans, osteomyelitis can remove considerable amounts of bone in a matter of weeks. The presence of cortical bone on the inside of the removed bone in the Bemelen specimen suggests that after these 'weeks', the infected area became encapsulated by newly formed bone tissue, isolating the abscess. How long the animal survived after that, is not exactly clear from the bones, but assuming that the periosteal bone apposition on the left PMU was indeed initiated by the infection, this would suggest that the animal would have survived well over a few months.

To what degree did the infection impair the mosasaur's ability to acquire food? Considering that all elements in the jaw hinge were thoroughly ruined by the infection (Fig. 7), any movement of this joint must have been tremendously painful. In humans, the characteristics of osteomyelitis include "[...] cyclic pain, increasing to severe deep intense pain with fever [...], especially if pain, fever and redness disappear when pus breaks out in a fistula" (Walenkamp, 1997). Of course the amount of cushioning provided by the remaining cartilage remains unknown, but we may safely assume that the infection had a severely debilitating effect on this particular mosasaur.

Perhaps surprisingly, the quadrate did not collapse under the stresses it would have normally been subjected to. If, during the development of the infection, the mosasaur kept on feeding in the usual way, and thus using its mandible, considerable forces must have acted on the quadrate. This may suggest that the Bemelen mosasaur had to shift to a "lighter" diet, which allowed to forage without having to use its jaws too much, if at all.

The mosasaur either survived on eating soft food (such as squid, or small prey which could be swallowed whole; see e.g. Massare (1987) for a review of mosasaur feeding), depended on its right jaw for a prolonged period of time, or survived on eating nothing at all. Because of their relatively high intra-cranial mobility, this mosasaur may have used its other jaw somewhat independently of the affected one. Lingham-Soliar (2004) extensively discussed the difficulties mosasaurs experienced during the healing process of a unilateral jaw fracture. The present specimen confirms his conclusion that a broken or otherwise immobilised jaw is not necessarily immediately fatal.

Another problem with an enormous abscess in the jaw joint is a possible effect on respiration. The airway could become narrowed or even obstructed by a bulging abscess in the jawbone. Obviously, the latter was not the case here, as the mosasaur did survive the infection for a longer period of time.

The cause of the infection remains unexplained, but might include a bite attack injury, probably by another mosasaur (Bell and Martin 1995 noted that a tooth from the atacking mosasaur had penetrated the left quadrate of another mosasaur). In this case, the attacking mosasaur must have managed to pierce the lower part of the quadrate (tympanic cavity), creating a porte d'entrée for the infection. Such a scenario would also explain the hole(s) in the tympanic cavity; the size of the two holes approximates the tooth size of a large mosasaur, but of course all this remains entirely speculative. We know of no other animals in the Maastricht seas that would have been able to inflict such a large wound in one bite, but an encounter with an attacking shark could also have started the infection (see Everhart 2004b and Rothschild et al., 2005 for a discussion of mosasaur/shark interactions). Interspecific acts of violence amongst mosasaurs are not unusual, and even intraspecific violent encounters, perhaps even of a cannibalistic nature have been reported; even from the Maastrichtian type area, we know of examples of this (e.g. Schulp et al., 2004 and refs therein).

An alternative porte d'entrée for the infection could have been the dentary, where a tooth infection may have spread through the Meckelian canal towards the quadrate/glenoid joint. We could think of a sharp, hard food item that accidentally pierced the gums, providing a starting point for an infection, but also the tooth replacement process or simply tooth fractures may have provided an opportunity for an infection to settle. The possibility of a 'spontaneous', haematogenic infection cannot be ruled out either.

CONCLUSION

The 'Bemelen specimen' of *Mosasaurus hoffmanni* suffered from a chronic osteomyelitis. Both the position of the infection as well as the amount of removed bone tissue must have been severely debilitating to the animal; however, the amount of new bone tissue deposited on the PMU and the quadrate indicate that the animal survived the infection for a prolonged period of time. The exact cause of the infection remains unknown.

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INSTITUTIONAL ABBREVIATIONS:

NHMM: Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands
MNHN(P): Muséum National d'Histoire Naturelle, Paléontologie, Paris, France
YPM: Yale Peabody Museum, New Haven, CT, USA

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