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A large new mosasaur from the Upper Cretaceous of The Netherlands

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Abstract

We report the discovery of a new species of marine reptile, a mosasaur, from the Upper Cretaceous (Maastrichtian) of The Netherlands. *Prognathodon saturator* sp. nov. is represented by an almost complete skull and much of the postcranial skeleton, and is one of the largest mosasaurs discovered to date. The stout skull and extremely massive jaws are more powerfully built than in any other known mosasaur. Bite marks, the partial disarticulation and scattering of the skeleton, and the presence of associated teeth of *Squalicorax* and *Plicatoscyllium* suggest extensive scavenging by sharks.

Keywords: Mosasaurs, *Prognathodon*, Maastrichtian, Upper Cretaceous, The Netherlands.

Introduction

Mosasaur remains have been known as rare discoveries from the Maastrichtian type area since 1766 (Bardet & Jagt, 1996). Historically, these fossils played an important part in the development of the concept of extinction by the French anatomist Baron G. Cuvier. Other reptiles known from the Maastrichtian type area include plesiosaurs, crocodiles, turtles and dinosaurs (Mulder et al., 1998). This, combined with an excellent stratigraphic control and the generally superb state of preservation of its vertebrate fossils, has made the Maastrichtian type area a classic site in the history of palaeontology. Despite the ever-increasing collecting efforts of a large group of amateur palaeontologists around Maastricht, discoveries of articulated mosasaur material from the type Maastrichtian remain extremely rare.

Here we describe the partial skeleton of the first reasonably complete mosasaur to be reported from the Maastricht area since 1957 (Kruytzer, 1957). The specimen was discovered by one of the authors (RWD) in the calcarenites of the upper Lanaye Member (Gulpen Formation, Late Maastrichtian, *Belemnitella junior* Cephalopod Zone) at the ENCI-Maastricht B.V. quarry (Fig. 1), south of the city of Maastricht, and adjacent to the type section of the Maastrichtian Stage (Schiøler et al., 1997). Strontium-isotope curve fitting (Vonhof & Smit, 1996) suggests an age of 66,1 million years (Ma). The specimen includes an almost complete skull, the greater portion of the neck and trunk, elements of the pectoral girdle and the forelimb, and 12 disarticulated pygal and caudal vertebrae. A fair number of shed shark teeth were discovered associated with the skeleton, and several elements display *post-mortem* shark bite marks.

Description

Mosasaur genera known from the Maastricht area so far included *Mosasaurus*, *Leiodon*, *Carinodens*, *Plate-*

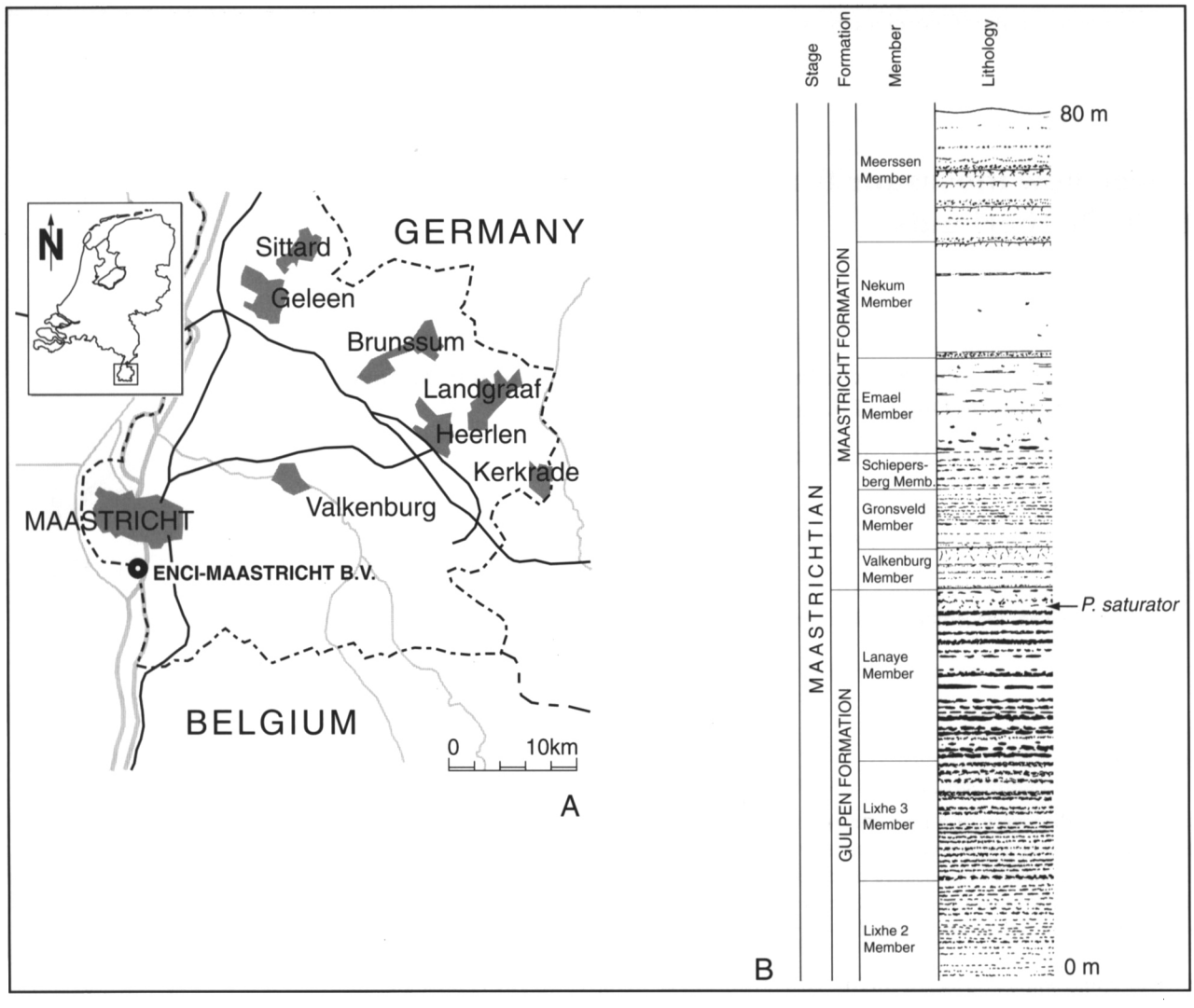

Fig. 1. Location of the ENCI-Maastricht B.V. quarry, 3 km south of the city of Maastricht, The Netherlands (A) and stratigraphic position of the specimen (B).

carpus and *Plioplatecarpus* (Kuypers et al., 1998). We refer the present discovery to the genus *Prognathodon*, making it the first unambiguous record of this genus from the Maastrichtian type area. Several autapomorphies distinguish this specimen from previously described species of *Prognathodon*, leading us to designate a new species:

Prognathodon saturator sp. nov.

Etymology

saturator (Latin): *he who gives satisfaction* (both to Maastrichtian sharks as well as Recent palaeontologists).

Holotype

NHMM 1998141 (collections of Natuurhistorisch Museum Maastricht, The Netherlands).

Locality

ENCI-Maastricht B.V. quarry, 3 km S of Maastricht, The Netherlands (50°49'N latitude, 5°41'E longitude).

Material

Near-complete skull, articulated cervical and anterior dorsal vertebrae with cervical and dorsal ribs, isolated pygal and caudal vertebrae, scapula-coracoid and scattered elements of appendicular skeleton.

Diagnosis

A large and massively built mosasaur. Quadrate massive, lacking the ala ridge dorsolaterally on the anterior face of the ala and the thin, high crest on the dorsal median ridge, found in other members of the genus. Dentaries relatively tall with a prominently concave dorsal dental margin. Ventral margin of maxilla slightly convex. Zygosphenes and zygantra present.

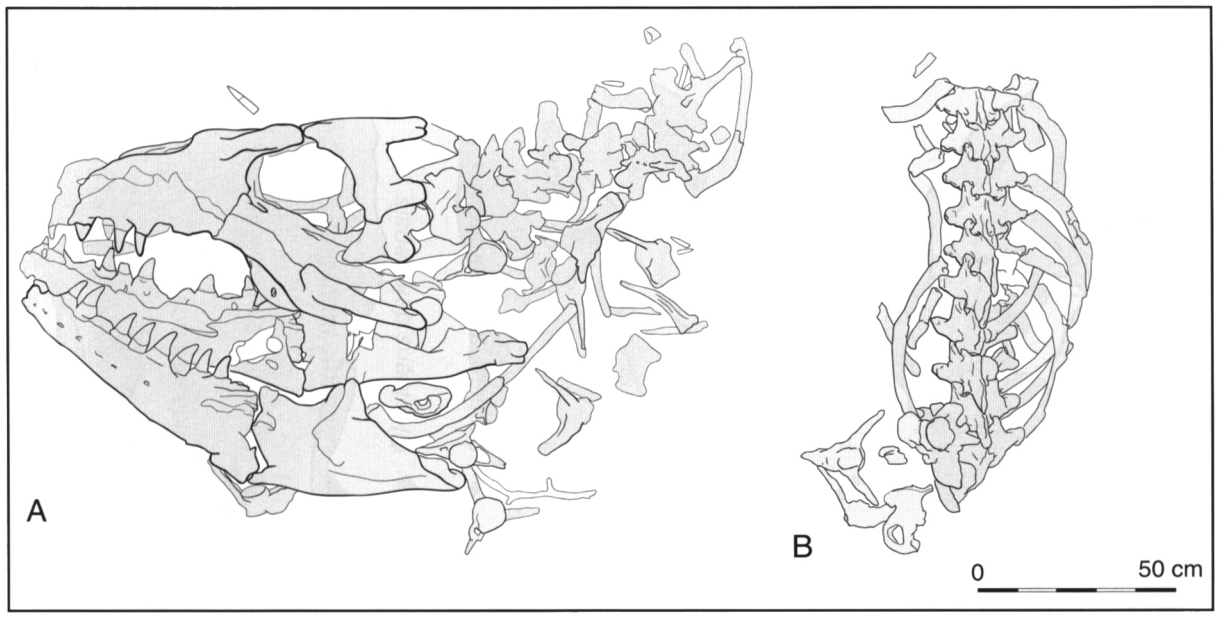

Fig. 2. *Prognathodon saturator* sp. nov. (NHMM 1998141). (A) Skull with cervical vertebrae. (B) Dorsal vertebrae (Rogier Trompert Medical Art).

Description

The skull (Fig. 2A) is near-complete with the exception of the anterior portions of the premaxilla and the dentaries, which have been lost during quarrying prior to the discovery. Although most of the anterior marginal teeth are missing, the inclination of the preserved roots of the first and second dentary teeth suggests that *P. saturator* had procumbent teeth, a condition similar to *P. solvayi* (Lingham-Soliar & Nolf, 1990). The dorsal margin of the dentary is concave; the ventral margin of the maxilla is slightly convex. The marginal teeth are massive, and generally smooth and rounded, as opposed to the facetted and laterally compressed teeth in most other mosasaurs. The mandible is extremely tall and massive, even more so than those of other members of the genus. The equally massive pterygoid contains 6 large, only moderately recurved teeth. The well-preserved left quadrate (Fig. 3) is robust. The greater part of the skull roof is preserved, with only the left side of the wide temporal arcade missing. The temporal region and braincase are all very stout compared to other species of *Prognathodon*. Both the cervical and dorsal vertebrae (Fig. 2A, B) have large and functional zygosphene-zygantrum complexes. The almost completely preserved scapula and coracoid are tightly fused. Characters shared with other members of the genus include the low number of teeth in comparison to other mosasaurs (14 dentary, probably 12 maxillary, 6 pterygoid); pterygoid teeth almost of equal size to marginal teeth and the fusion of the suprastapedial and infrastapedial processes on the quadrate.

Phylogenetic analysis

Phylogenetic analysis confirms the new species' position within *Prognathodon* (Fig. 4 and Table 1). Synapomorphies supporting inclusion in Mosasaurinae (as defined by Bell, 1997) include the presence of fused haemal arches; a prominent supraorbital process of

Table 1. Phylogenetic data, as added to Bell (1997).

Prognathodon saturator (NHMM 1998141)									
???00	??110	?1101	01011	10111	???10	0000?	???20	??111	01010
10000	01100	00101	??3??	2101?	?0100	10100	01201	0?10?	01001
2110?	???01	??0??	?1???	?????	???2?	?????	?????	??	
Prognathodon solvayi (IRScNB R33)									
00?00	00110	00101	01010	10111	11?10	?0005	0?120	?1111	01010
01001	01000	001??	??41?	20011	10100	?000?	01201	??10?	0?00?
2?10?	?????	?????	?11??	?????	?????	?????	?????	??	

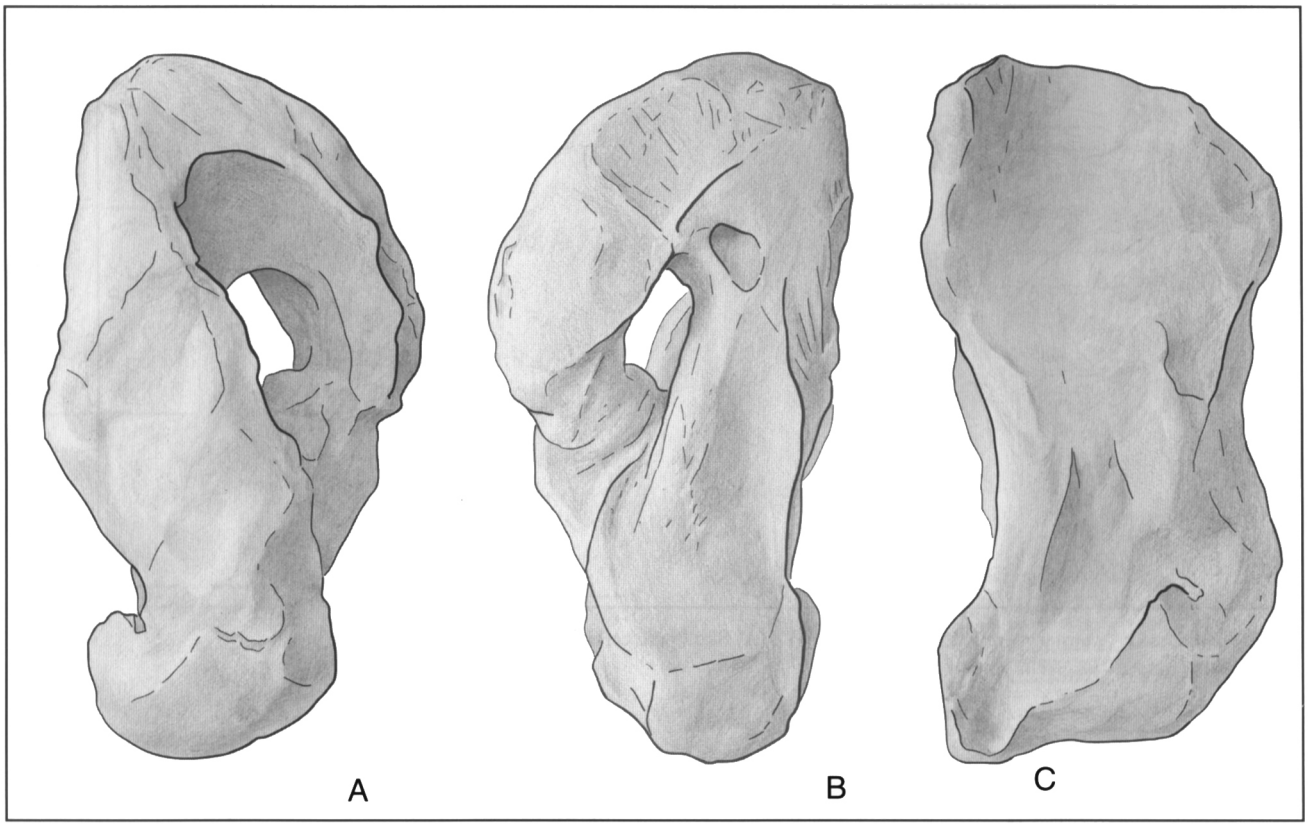

Fig. 3. Quadrate of *Prognathodon saturator* sp. nov. (NHMM 1998141) in frontal (A), lateral (B) and medial (C) view (Rogier Trompert Medical Art).

the prefrontal; the greatly expanded posterior wing of the coronoid; a high, thin surangular coronoid buttress and equidimensional condyles of anteriormost trunk vertebrae. Although haemal arches that are 1,5 times longer than neural arches of the same vertebra are considered a synapomorphy in Mosasaurinae (Bell, 1997), this condition is reversed in the present specimen with haemal arches barely longer than the neural arches. Synapomorphies linking the present specimen with *Prognathodon* and *Plesiotylosaurus* include anterior pterygoid teeth that approach the size of marginal teeth.

The analysis was based on the phylogenetic revision of the North American and Adriatic Mosasauroidea by Bell (1997), to which we added data on the specimen described here and on the holotype (IRScNB 33) of the Early Maastrichtian *P. solvayi* (see Lingham-Soliar & Nolf, 1990). Three other species of *Prognathodon*, viz. *P. waiparaensis*, *P. giganteus* and *P. stadtmani* were not included in this analysis, because data available were too limited to warrant a meaningful comparison, but attribution of the present specimen to *P. stadtmani*, *P. waiparaensis* or *P. giganteus* can be excluded with confidence, on the following grounds. *Prognathodon saturator* may be differentiated from these congeners in being much larger than any previously recorded *Prognathodon* and generally being considerably more massive. The Early Campanian *P. stadtmani* (see Kass, 1999; Kass & Smith, 2001) differs from *P. saturator* in having a much more slender dentary and coronoid and recumbent anteriormost dentary teeth. *Prognathodon waiparaensis* (see Welles & Gregg, 1971) also differs from *P. saturator* in having a much more slender dentary, with a nearly straight dorsal dental margin and an elongate posterior mandibular unit inclined at almost 45°. *Prognathodon giganteus* (see Lingham-Soliar & Nolf, 1990) can be distinguished from *P. saturator* by its straight dorsal dental margin, small coronoid, rectangular posterior mandibular unit with short and blunt retroarticular process and a considerably less massive quadrate.

Phylogenetic trees, rooted in *Clidastes liodontus*, were generated using PAUP* (Swofford, 2000) and analysed using MacClade (Maddison & Maddison, 2000). A branch-and-bound search yielded six equally most parsimonious trees of 128 steps (consistency index 0,62; retention index 0,76). Of the total of 142 characters (all unordered and unweighted), 61 were phylogenetically informative within Mosasaurinae.

Discussion

The robust quadrate, the large temporal arcade and the stout mandible of *P. saturator* suggest this animal

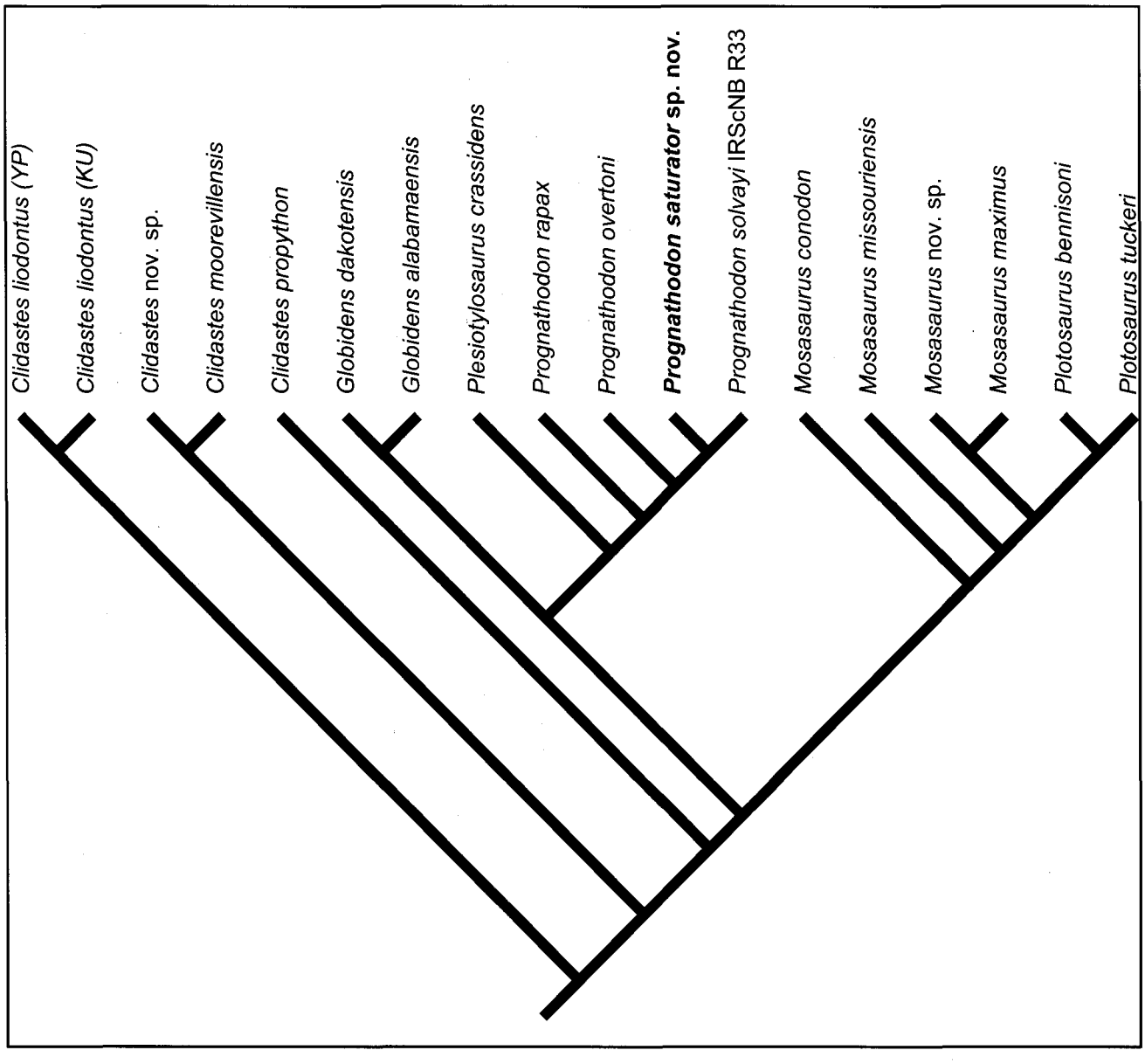

Fig. 4. Cladogram showing position of *Prognathodon saturator* sp. nov. within the Mosasaurinae depicting the preferred hypothesis of 6 equally parsimonious trees (length 128 steps, consistency index 0,62, retention index 0,76).

could achieve bite forces unparallelled by any other mosasaur. The quadrates of the globidensine mosasaurs *Globidens* and *Prognathodon* both have fused suprastapedial and infrastapedial processes, a condition interpreted by Lingham-Soliar & Nolf (1990) as an adaptation to counteract the strong vertical forces exerted on this bone during biting. Compared to the previously described quadrates of Globidensini, that of *P. saturator* is even more strongly built. Russell (1975) calculated the relative power of the jaw musculature in several mosasaurs using the temporal arcade length / overall skull length ratio. The durophagous *Globidens dakotensis* had the highest ratio of 0,27, followed by *P. overtoni* at 0,22. The much larger *P. saturator* has a ratio similar to *P. overtoni* (based on measurements on the reconstructed skull). The leverage provided by the strong jaw musculature in combination with the relatively short and tall dentary would have resulted in an extremely powerful bite.

Having the most powerful jaws present in the Maastrichtian seas, and with examples of large marine turtle (*Allopleuron*) from the Maastricht area with pathologies suggesting healed bite marks (NHMM collections; a detailed description of these specimens is in preparation) available, it is not unlikely that the size range of possible prey items of *P. saturator* ranged up to these 2,90 m long turtles.

Various estimates of *Prognathodon* allometry (Russell, 1967; Lingham-Soliar & Nolf, 1990; Kass, 1999) suggest that the length of the mandible represents 10 – 14 % of the body length. With a reconstructed mandible length of 140 cm, and assuming a similar

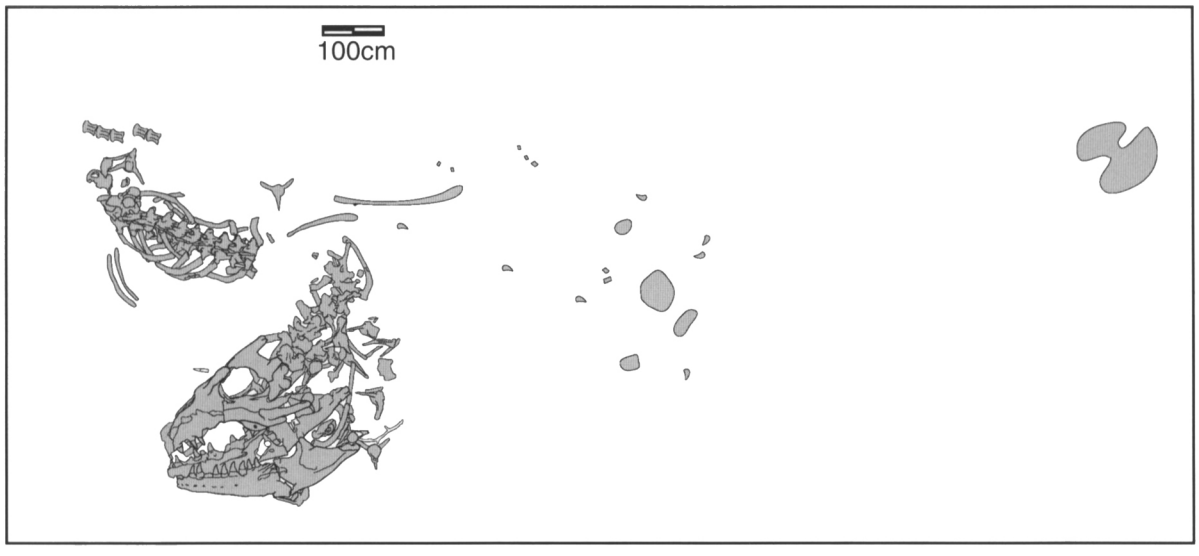

Fig. 5. Original position of skeletal remains at the quarry. Scale bar equals 100 cm.

allometry as previously published estimates, the present specimen could have measured from 10 up to just over 14 m. *P. saturator* probably did not reach the lengths attained by the largest individuals of *Mosasaurus hoffmanni* [for which lengths up to 17,6 m (Lingham-Soliar, 1995) have been calculated], but is still one of the largest marine reptiles known from the Maastrichtian type area, and certainly the most massively built species.

Taphonomy

The present specimen provides an interesting taphonomic case history. We consider age or disease to have been the most likely cause of death of this specimen, as marine predators capable of bringing down an animal of this size are unknown from the type Maastrichtian. The degree of articulation (Fig. 5) suggests that the animal reached the sea floor soon after its death, where it was scavenged by sharks prior to final burial. Indirect evidence of shark scavenging includes the presence of shed teeth of *Squalicorax* and *Plicatoscyllium* amongst the skeletal remains of the mosasaur. The teeth show no evidence of having been attacked by stomach acids, excluding the possibility that the teeth were in the mosasaur's stomach. The number of shark teeth recovered is too high to be explained by background abundance. Moreover, the fact that groups of teeth are all of the same size class and colour would also rule out such an interpretation. The various bite marks on the skeleton (Fig. 6) form direct evidence of shark scavenging. The few remaining portions of the appendicular skeleton were found disarticulated, which corresponds to previously reported patterns of scavenging on large marine reptiles (Kass, 1999; Schwimmer et al., 1997; Everhart, 1999). When the remaining parts of the skeleton were still connected with ligaments, the skeleton was partially covered with relatively coarse material, evidenced by current-aligned belemnites and caudal elements washed against the skull. The premaxilla and anteriormost portions of the dentaries, along with part of the tail, were lost to quarrying prior to the discovery of the specimen.

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Fig. 6. Bite marks on ribs.

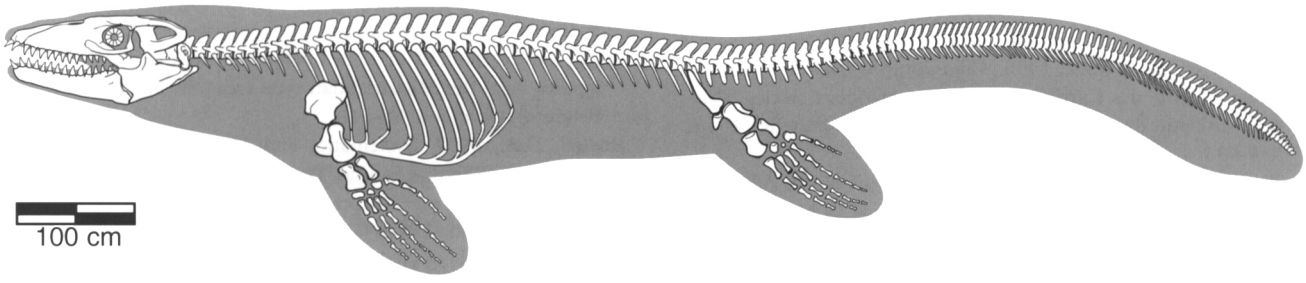

Fig. 7. Reconstruction of *Prognathodon saturator* sp. nov. The premaxilla is reconstructed after *Prognathodon solvayi* (Rogier Trompert Medical Art, outline silhouette courtesy of Dan Varner).

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Fig. 8. Artist's impression of the carcass of *Prognathodon saturator* sp. nov. being scavenged by *Squalicorax* and *Plicatoscyllium sharks* (Dan Varner).

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Institutional abbreviations:

IRScNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
NHMM: Natuurhistorisch Museum Maastricht, The Netherlands