

New material of *Prognathodon* (Squamata, Mosasauridae) from the type Maastrichtian of the Netherlands

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Abstract

A partial quadrate, here assigned to the globidensine mosasaur *Prognathodon* cf. *saturator*, is recorded from the basal Valkenburg Member (Maastricht Formation) in the type area of the Maastrichtian Stage (southeast Netherlands, northeast Belgium). Occurrences of *Prognathodon saturator* in this area are extremely rare, which might well be linked to the offshore habitat preferred by this species.

Key words: Late Cretaceous, Maastrichtian, mosasaurs, new record

Introduction

The globidensine mosasaur genus *Prognathodon* is represented in the Maastrichtian type area by two species, *P. saturator* and *P. sectorius*. In comparison to the three other mosasaur taxa recognised so far in the same strata, both species of *Prognathodon* are very rare, and *P. saturator* even more so than *P. sectorius*. Here we record an additional example of *Prognathodon* cf. *saturator* on the basis of a fragmentary quadrate from the basal Valkenburg Member (Maastricht Formation) at the ENCI-HeidelbergCement Group quarry, Maastricht.

To denote the repositories of material referred to in the text, the following abbreviations are used: NHMM, Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands.

Systematic palaeontology

Order Squamata Opper, 1811

Superfamily Mosasauroidae Gervais, 1853

Family Mosasauridae Gervais, 1853

Subfamily Mosasaurinae Gervais, 1853

Tribe Globidensini Russell, 1967 (see also Bell, 1997)

Prognathodon Dollo, 1889

Prognathodon cf. *saturator* Dortangs, Schulp, Mulder, Jagt, Peeters & De Graaf, 2002

Material

Provenance and geological setting – The specimen presented here, NHMM JJ 15128 (Fig. 1), was collected by the second author in the northeastern corner of the ENCI-HeidelbergCement Group quarry south of Maastricht, in June 2013, from the lowermost portion of the Valkenburg Member, i.e. between 0 and 0.5 m above its base (= Lichtenberg Horizon; see Schiøler et al., 1997 for more details on the stratigraphic setting). Stratigraphically, this approximates the level from which the holotype of *P. saturator* was collected in the uppermost Lanaye Member (Gulpen Formation) (see Schiøler et al., 1997; Dortangs et al., 2002; Jagt and Jagt-Yazykova, 2012). The posterior mandibular unit that has recently been described by Schulp et al. (2013a) originates from the younger (c. 20 kyr) Nekum Member of the Maastricht Formation.

Description and comparisons – As preserved, the present fragment represents the uppermost approximately 25% of a relatively large left quadrate. In lateral view, much of the tympanic cavity is exposed because the greater part of the tympanic crest is missing; only a hint of the dorsal onset of this crest is preserved. The curvature and size of the tympanic cavity closely match the conditions

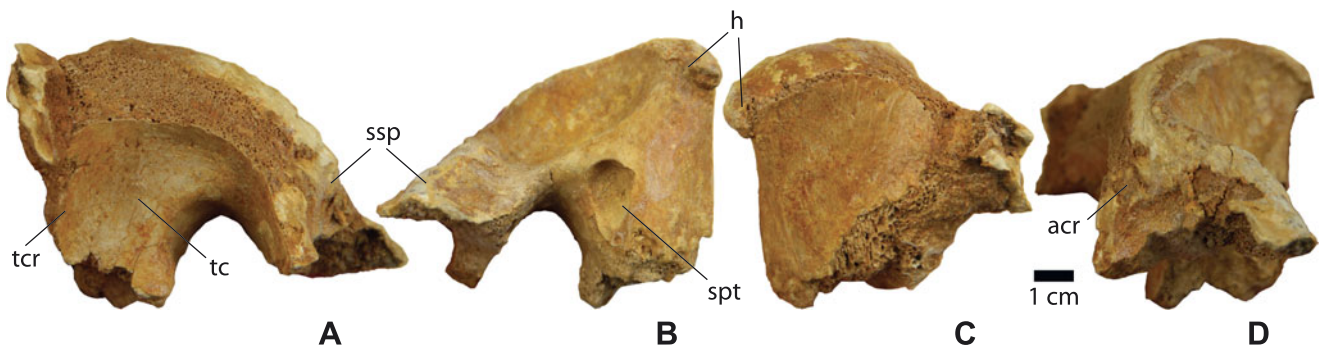


Fig. 1. Left quadrate of *Prognathodon cf. saturator*, NHMM JJ 15128 in lateral (A), medial (B), anterior (C) and posterior (D) views: acr, alar crest; h, head; spt, stapedial pit; ssp, suprastapedial process; tc, tympanic cavity; tcr, tympanic crest.

seen in the holotype of *P. saturator*. The cavity does not show the marked anterodorsal expansion of the tympanic cavity that is seen in *Mosasaurus hoffmanni* (e.g. Mulder, 2003: 139), nor the much smaller and more flattened condition in *Plioplatecarpus* (e.g. Lingham-Soliar, 1994: 185). The suprastapedial process, as far as preserved, reveals a marked downward curvature, suggesting that it would have reached the condition of fusion with the infrastapedial process that is characteristic of *Prognathodon*. The suprastapedial process would have been much smaller and have a greater taper in *Mosasaurus* (e.g. Mulder, 2003: 139). In medial view, comparison with the quadrate of the holotype of *P. saturator* is hampered by the fact that the dorsomedial area above the stapedial pit in the latter has suffered from deformation by a flint nodule next to it. NHMM JJ 15128 has a small yet pronounced medial protuberance at the head. The stapedial pit is identical in size and shape to that in the holotype of *P. saturator*. The anteromedial surface (as far as preserved) is less rugose than in the latter, but comparable in gross morphology otherwise. In anterior view, the slightly more pronounced head in NHMM JJ 15128 is clear when compared with the (deformed) condition in *P. saturator*; in all other respects its morphology closely matches that of that species. In posterior and dorsal views, it is difficult to assess other morphological traits because almost all cortical bone has disappeared. Nevertheless, the orientation of the alar crest and the remaining stretch of well-preserved bone surface does correspond to the morphology in the holotype of *P. saturator*. Even though NHMM JJ 15128 constitutes only a small portion of a left quadrate, we consider the similarities to the holotype of *P. saturator* to be such that attribution to that species, albeit with query, appears warranted. Two other large mosasaurs from the type Maastrichtian, *Plioplatecarpus marshi* and *Mosasaurus hoffmanni*, can be ruled out beyond doubt (as discussed above), and the sheer size of the fragment immediately excludes the diminutive globidensine *Carinodens belgicus* from consideration. Of the second species of *Prognathodon* from the type Maastrichtian, *P. sectorius*, no quadrates have been identified to date. However, in view of the more gracile dental and cranial morphology, we would expect, from a biomechanical point of view, this slightly smaller form to have had a much more lightly built quadrate. In view of this, we here assign the newly collected

specimen to *Prognathodon saturator*, at least for the time being. If correctly interpreted, NHMM JJ 15128 adds to our knowledge of quadrate morphology in *P. saturator*, in which in the holotype, the dorsal part of the medial surface has suffered post-mortem distortion.

Discussion

To date, the remains of only two individuals of *P. saturator* have been identified from the Maastrichtian type section. The holotype of *P. saturator* was recovered in 1998 (Dortangs et al., 2002), while the only other skeletal material that we are aware of, a posterior mandibular unit, lay hidden in collections made in the latter part of the 19th century, having been labelled *Mosasaurus hoffmanni*, until its 'rediscovery' well over a decade later (Schulp et al., 2013a). *Prognathodon sectorius*, earlier referred to as *L(e)iodon sectorius* (see Schulp et al., 2008), is almost equally rare (e.g. Kuypers et al., 1998). So far, of this taxon only partial jaws and isolated teeth crowns are available. Thus, this new material not only provides a welcome addition to a scant record, it has also prompted us to reflect on the paucity of *Prognathodon*, and more specifically *Prognathodon saturator*, in comparison to relatively common mosasaur taxa in area such as *Mosasaurus* and *Plioplatecarpus*, and even *Carinodens*, although the latter is mainly represented by isolated (shed) tooth crowns. Much progress has been made recently in identifying niche exploitation and resource partitioning in the type Maastrichtian mosasaur fauna (Schulp, 2006; Schulp et al., 2013b) and, more generally, in aspects of the geographic and stratigraphic distribution of tetrapods (Mulder, 2003) and vertebrate taphonomy in the Maastrichtian type area (e.g. Janssen et al., 2011). The relatively depleted carbon stable isotopic values recorded for tooth enamel (Schulp et al., 2013b) suggest that both species of *Prognathodon* would have foraged in more offshore and/or deeper-water settings, thus differentiating them from the less depleted taxa *Carinodens* and *Plioplatecarpus*. This alone, however, does not provide an adequate explanation of the rarity of *Prognathodon* as compared with *Mosasaurus*, which exhibits an isotope signature ranging from roughly similar to even more depleted values.

Even though tooth morphology suggests that a difference in preferred prey existed between *M. hoffmanni* and *P. saturator*, the question remains whether the shallow marine type Maastrichtian ecosystem would have supported two similarly large apex predators at the same time. A degree of habitat partitioning, with *P. saturator* further offshore in an open marine setting, appears likely. Tooth morphology of and bite force estimates for *Prognathodon saturator* both suggest that large marine turtles could have formed part of its diet (Schulp, 2006). Although the holotype of *P. saturator* does not preserve any stomach contents, turtle fragments from the gut of a smaller-sized specimen of *Prognathodon* from the late Campanian of Alberta, Canada, lends support to such a scenario (Konishi et al., 2011). The large marine turtle *Allopleuron hofmanni* has previously been suggested to have exploited the sea grass meadows of the type Maastrichtian (Mulder, 2003). Seen in this light, the relatively common occurrence of *Allopleuron* vs the rarity of *Prognathodon saturator* would be puzzling even if a population size difference in this assumed predator–prey ratio of more than an order of magnitude is being considered. An interesting hypothesis could be that smaller juvenile or subadult specimens were a more convenient prey for *P. saturator*. In view of the fact that some extant marine turtles are known to undergo a shift in diet and foraging area during ontogeny (e.g. Reich et al., 2007), the observed absence of juvenile *Allopleuron* in the type Maastrichtian (Janssen et al., 2011) would offer a possible explanation for the paucity of *P. saturator* in the area. If, indeed, both *P. saturator* and juvenile *Allopleuron* spent most of their time in more offshore waters, this would indeed account for their near-absence in the shallow, near-shore setting of the type Maastrichtian. However, testing this hypothesis requires the unlikely discovery of (multiple) *P. saturator* skeletons with preserved gut contents featuring the recognisable remains of juvenile *Allopleuron*.

Along a different line of reasoning, we are not aware of any record of (isolated, i.e. shed) tooth crowns of *P. saturator* from the Maastrichtian type area. This observation does lend support to the idea that *P. saturator* would have preferred a habitat further offshore, avoiding the near-shore shallows of the Maastricht area. In this case only floating carcasses and the occasional disoriented individual would have ended up in the type Maastrichtian strata.

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