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A new species of the durophagous mosasaur *Carinodens* (Squamata, Mosasauridae) and additional material of *Carinodens belgicus* from the Maastrichtian phosphates of Morocco

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Abstract

Five new dentaries, representing three individuals of the poorly known durophagous mosasaur *Carinodens* are described from the Maastrichtian phosphates of Morocco. Contrary to previous assumptions, the dentary of *Carinodens* holds 17-18 teeth, rather than 13. One pair of dentaries represents a new species, *Carinodens minalmamar*, characterised by laterally flattened teeth with two relatively pronounced sulci, a tooth count of 18, and a more slender general aspect of the dentary itself. The new material requires adjustment of previous reconstructions, assumptions on jaw mechanics, and palaeobiological interpretations of *Carinodens*.

Keywords: Mosasauridae, *Carinodens*, Maastrichtian, Late Cretaceous, Morocco

Introduction

Despite its wide geographic distribution, the Late Cretaceous durophagous mosasaur *Carinodens belgicus* (Woodward, 1891) was until recently exclusively known by two fragmentary dentaries from the Maastrichtian type area (Dollo, 1913; Schulp et al., 2004), and a few dozen isolated tooth crowns from sites elsewhere (see Schulp et al., 2006; Bardet et al., 2008, and references therein). Here we describe five new, complete dentaries, representing three individuals, from the Maastrichtian phosphates of Morocco. One pair of dentaries represents a new species of *Carinodens*, the others significantly improve our knowledge of *C. belgicus*.

Material

Numerous vertebrate fossils from the Late Cretaceous – Early Paleogene phosphates of Morocco find their way into the fossil trade. With large, sharp teeth generally fetching the highest prices on the fossil market, we can safely assume a commercially driven collecting bias to exist against durophagous mosasaurs in general, and small durophagous mosasaurs such as *Carinodens* in particular. Moreover, until recently only a brief note existed on *Carinodens* from Morocco (Arambourg 1952). It took more than five decades for additional isolated teeth from Morocco to be recognised and published (Bardet et al., 2008). Contrary to Bardet et al. (2005), the tooth described by Arambourg is in the collections of the Muséum National d'Histoire Naturelle (Paris), where it has been rediscovered recently.

One pair of *Carinodens* dentaries from Morocco was identified as such by amateur fossil collectors Jan and Annemarie van de Steeg at a fossil fair in the Dutch city of Enschede, where the fossil was labelled as a 'crocodile jaw'. Its provenance was, according to the salesman, nothing more specific than 'Morocco'. The specimen was subsequently acquired and brought to our attention by the couple, and kindly donated by them to the Office Chérifien des Phosphates palaeontological collections at Khouribga, Morocco. The adhering matrix allowed us to identify the specimen as coming from the phosphatic deposits of the area. The specimen is described here as OCP DEK/GE 453. Three

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additional specimens, also dentaries, and attributable to *C. belgicus*, were recovered from the fossil market by a French amateur collector, Gérard Barbe. Mr. Barbe also kindly donated the material to the OCP collections; this material is described here as OCP DEK/GE 454 and OCP DEK/GE 455.

Although the exact geographical and stratigraphical provenance of the specimens within the phosphatic deposits of Morocco is unknown, some data can be deduced (N.B., pers. obs.): the general characters (colour of matrix and fossil, granulometry, selachian tooth content) of the phosphatic matrix in which all fossils were still embedded, as well as the (limited) information provided by the fossil dealers, allow us to narrow down the provenance of all three specimens to the upper Maastrichtian 'Couche III' of the Sidi Chennane area, a zone which has recently seen intensive exploitation, located in the southeastern part of the Oulad Abdoun phosphatic basin of Morocco.

Institutional abbreviations

IRScNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; NHMM: Natuurhistorisch Museum Maastricht, the Netherlands; OCP: Office Chérifien des Phosphates, Khouribga, Morocco; ZIN PH: Palaeoherpetological collection of the Zoological Institute, Russian Academy of Sciences, St Petersburg, Russia.

Systematic palaeontology

Squamata Oppel, 1811
Mosasauridae Gervais, 1853
Mosasaurinae Gervais, 1853
Globidensini Russell, 1967
Carinodens Thurmond, 1969
Carinodens belgicus (Woodward, 1891)

Referred material

OCP DEK/GE 454, a left and right dentary (of the same individual) from the Oulad Abdoun basin of Morocco, and OCP DEK/GE 455, a right dentary of the same provenance; both specimens in all likelihood originate from the upper Maastrichtian 'Couche III' of the Sidi Chennane area.

Revised diagnosis

Relatively small mosasaur with seventeen tooth positions in dentary. Dentary most massive from 8th through 13th tooth position, and laterally diverging posteriorly to the 13th tooth position. Strongly heterodont both in tooth size and morphology. All teeth somewhat labiolingually flattened. Anterior teeth small, with swollen base; median part of the dentary ramus with much larger, blunt and rounded teeth. Posteriormost teeth small and slightly pointed and recurved.

General preservation

OCP DEK/GE 454 (Figs 1B-3B, 1C-3C) comprise two complete dentaries from the same individual. The left one is better preserved than the right, which is partially distorted in dorsal view. The left dentary preserves teeth #8, 10 (base only), 11, 13, 14, 16 and 17, versus teeth #2, 4, 6, 8, 11, 13, and 15-17 in the right one. OCP DEK/GE 455 (Figs 1D-3D) is a right incomplete dentary of a smaller individual than OCP DEK/GE 454, preserved up to the 15th tooth position. It is slightly distorted in dorsal view and its postero-ventral part is lacking. Teeth #5 and 8-11 are preserved but are heavily damaged. Replacement tooth 11th is preserved and well exposed.

Description and comparison

OCP DEK/GE 454 very closely matches the preserved part of IRScNB R 43, the holotype dentary of *Carinodens belgicus* from the type Maastrichtian (Dollo, 1913). The length from the anterior tip to the posterior margin of tooth #12 is 16.2 cm in OCP DEK/GE 454, which makes it comparable in size to the holotype. Total length of both dentaries is about 21.5 cm. The dentary bears a small rostrum anterior to the first tooth position. Labial and lingual parapets are at about the same level. The dentary ends posterior to the last tooth without an edentulous process. The posterior margin of the dentary is expanded and bears a dorsally located groove like the one present in e.g. *Prognathodon overtoni* Williston 1897 (see Russell, 1967, fig. 90) or *P. kianda* Schulp et al., 2008 (see Schulp et al., 2008, fig. 8). Lingually, the Meckelian canal can be followed all the way to the anteriormost tooth position; the opening widens considerably posterior to the 10th tooth position. Tooth replacement positions are large and located medio-posteriorly to the functional tooth. Labially, the primary row of foramina follows quite closely the midline at half-height of the dentary; the foramina are only slightly marked. In dorsal view, starting between the 12th and 13th tooth position, both dentaries have a distinct lateral curvature of the posterior end, making this portion of the ramus clearly divergent from the main axis of the bone. Both dentaries bear seventeen tooth positions. About half of the alveoli preserve teeth in each dentary, for the first time allowing assembly of a full composite reconstruction of the dentition of *Carinodens belgicus* (Fig. 4). The anterior teeth are relatively small, only slightly laterally flattened, with an almost round crown in lateral view. From position #6 onwards, the teeth become larger, with positions #10 through #13 holding the largest teeth. The largest teeth are bulbous in lateral view, with a swollen base just above the onset of the enamel cover, and part of the prominently thinner roots raised above the dorsal dental margin, giving the teeth a 'waisted', almost mushroom-like aspect. At this portion of the dental ramus, teeth are laterally flattened to an aspect ratio of about 1.6 : 1 when seen in occlusal view. Teeth become more asymmetrical in lateral view here, with the apical nubbin positioned slightly posterior to the midline of the tooth. Tooth size reduces quite

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Fig. 1A-D. Carinodens belgicus *dentaries in lateral view: A – holotype IRScNB R 43; B – OCP DEK/GE 454 left dentary; C – OCP DEK/GE 454 right dentary; D – OCP DEK/GE 455 right dentary; E, F –* Carinodens minalmamar *nov. sp. dentaries in lateral view: holotype pair OCP DEK/GE 453 left dentary (E) and right dentary (F). Scale bar equals 1 cm.*

abruptly posterior to the 14th tooth position, with the posterior-most teeth (position #15-17) at about one quarter the size of the largest teeth. The posterior teeth are more or less triangular in lateral view, slightly posteriorly recurved and with a slightly rounded apex. Roots here are wider than the area at the base of the enamel-covered portion of the teeth, leaving them with less of a 'swollen' aspect, much rather continuing the triangular shape.

OCP DEK/GE 455 (Figs 1D-3D) is, at 14.8 cm, a much smaller dentary. It has suffered much more damage, but preserves the same traits as described above and provides some additional morphological information. This dentary holds some poorly preserved teeth at positions #9 through #12. The clearly 'imbricated', somewhat unusual arrangement in occlusal view of adjoining teeth is clearly visible in this specimen.

Of note is the fact that the reconstruction of the holotype IRScNB R 43 of *Carinodens belgicus* by Dollo (1913) features thirteen teeth only; Dollo assumed that the dentary did not extend much further. ('La façon dont le dentaire se termine postérieurement (posterior of the 13th alveolus) me fait penser qu'il n'en contenait pas davantage'). A re-examination of the holotype (illustrated here in Figs 1A-3A) and comparison with OCP DEK/GE 454 clearly proves this assumption to be incorrect. It also reveals the onset of the same distinctive lateral divergence of the dental ramus posterior to the 12th tooth position.

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Fig. 2A-D. Carinodens belgicus *dentaries in occlusal view: A – holotype IRScNB R 43; B – OCP DEK/GE 454 left dentary; C – OCP DEK/GE 454 right dentary; D – OCP DEK/GE 455 right dentary; E, F –* Carinodens minalmamar *nov. sp. dentaries in occlusal view: holotype pair OCP DEK/GE 453 left dentary (E) and right dentary (F). Scale bar equals 1 cm.*

Carinodens minalmamar nov. sp.

Etymology

In recognition of the Dutch amateur fossil collectors Jan and Annemarie van de Steeg; 'min al-mamar' meaning 'from the alley' or '-corridor' in Arabic, both referring to the Dutch family name *Van de Steeg* as well as to the relatively compressed dentary (a dental 'corridor') of the species.

Holotype

OCP DEK/GE 453, near-complete left and right dentary of the same individual, with two teeth preserved in left dentary.

Type locality and horizon

'Couche III' phosphatic level, upper Maastrichtian (Cappetta, 1987), Oulad Abdoun Basin (probably Sidi Chennane area), Morocco.

Diagnosis

Small mosasaur with eighteen tooth positions in dentary. Relatively slender and straight dentary. Teeth labiolingually flattened with an aspect ratio of ⩾2.2 : 1 in occlusal view. Labial surface of largest teeth characterised by two prominent sulci.

General preservation

In the two dentaries (Figs 1E-3E, 1F-3F), only the left preserves two fully developed teeth. The specimen was acquired from the market in what appears to have been the original matrix, although presumably for aesthetic/commercial reasons part of the block was found to have been 'enhanced' with a mixture of glue and ground matrix.

Description and comparison

The left dentary of OCP DEK/GE 453 is fully preserved, and measures 16,9 cm along the length of the ramus. There was either a minor left/right asymmetry in life, some minor post-mortem deformation, or a combination of both, as the right dentary, also completely preserved, measures 17.5 cm. The posteriormost part of the dentary, approximately the part with the four posteriormost alveoli, curves laterally and slightly dorsally; similar to but much less pronounced so than observed in OCP DEK/GE 454 (*Carinodens belgicus*). In general appearance the dentary is more slender and straighter compared to *C. belgicus*; it is both in lateral view less tall, as well as narrower in dorsal/occlusal view. The anterior ventro-medial margin of the dentary is much less massively developed than in *C. belgicus*. The keel above the Meckelian canal along the posterior half of the dental ramus is more pronounced in *C. minalmamar* nov. sp. The dorsal dental margin is straighter compared to the rather laterally flanging in *C. belgicus*. The two preserved teeth (at

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Fig. 3A-D. Carinodens belgicus *dentaries in medial view: A – holotype IRScNB R 43; B – OCP DEK/GE 454 left dentary; C – OCP DEK/GE 454 right dentary; D – OCP DEK/GE 455 right dentary; E, F –* Carinodens minalmamar *nov. sp. dentaries in medial view: holotype pair OCP DEK/GE 453 left dentary (E) and right dentary (F). Scale bar equals 1 cm.*

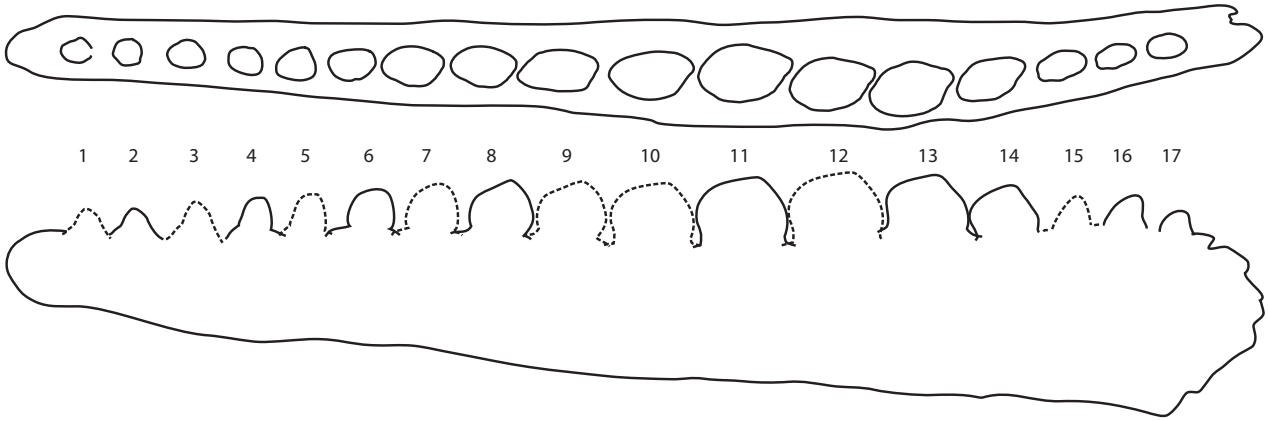

Fig. 4. Composite dentition of Carinodens belgicus based *on IRScNB R43 and OCP DEK/GE 454 and -455. Note that tooth replacement is not considered in this composite. Also compare with Lingham-Soliar (1999).*

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position #8 and #10) are considerably worn, but still preserve enough enamel to allow for an accurate comparison with (and distinction from) *C. belgicus*. The teeth are laterally considerably more flattened compared to *C. belgicus*: for tooth positions #8 and #10, the aspect ratio is ~2.3 in occlusal view, compared to ~1.6 in *C. belgicus* OCP DEK/GE 454 and -455. Both teeth feature two pronounced sulci in lateral (labial) view. The arrangement of the alveoli shows a more pronounced imbricated pattern compared to *C. belgicus* (OCP DEK/GE 454), which corresponds well with the much more laterally flattened aspect of the preserved teeth. When comparing OCP DEK/GE 453 with the holotype of *C. belgicus* and OCP DEK/GE 454 and -455, we can confidently exclude ontogeny as a factor in the differences in morphology observed here. Both the smaller, and hence – if it were the same taxon – presumably younger OCP DEK/GE 455 (14.8 cm dentary length) as well as the large, presumably older OCP DEK/GE 454 (21.5 cm) feature the more swollen tooth morphology; the new taxon with much more laterally compressed teeth is at an intermediate ~ 17.2 cm. Also of note is the difference in tooth count, 18 in *C. minalmamar* nov. sp. rather than 17 in *C. belgicus*, although we do realise that given the natural variation in tooth count within a species of mosasaur, this alone would not be sufficient to separate OCP DEK/GE 453 as a new taxon.

Discussion

The new material shows that within the genus *Carinodens* we can now discern a more heavily built and a more gracile taxon. Several teeth presented earlier, including the isolated tooth described by Arambourg (1952: pl. 40, fig. 3) and the isolated tooth from Russia (ZIN PH 1/61, described in Schulp et al., 2006) can now be attributed to *Carinodens minalmamar* nov. sp.

Of note are the pronounced lateral sulci present in *C. minalmamar* nov. sp., a feature also prominent in some teeth of the genus *Globidens* (compare e.g., Bardet et al., 2005, fig. 2). The exact functional importance of these sulci remains somewhat speculative. First of all, the alignment of the sulci appears to be more or less parallel to the presumed direction of the forces concentrated at the apex of the tooth, which could presumably allow for a better distribution of the mechanical stress during biting over a larger amount of enamel. Second, the presence of these sulci increases the contact area between the enamel (which is already unusually thick in globidensine mosasaurs) and the underlying dentine. Considering the slightly different mechanical properties of enamel and dentine (in terms of hardness and hence compressibility), the increased surface area of the contact zone between the enamel and the dentine could presumably also increase the support of the thick enamel at the apex of the tooth.

A *Carinodens belgicus* dentary from the Maastrichtian type area, described in Schulp et al. (2004) was initially interpreted to represent a left dentary from tooth positions #6 through #9, following the assumption by Dollo (1913) and the reconstruction (with splenial) in Lingham-Soliar (1999) that *C. belgicus* had thirteen teeth only. The new material from Morocco, as well as our re-examination of the holotype (now accessible again) now proves this interpretation to be incorrect; rather, this specimen (NHMM 2003-141) represents a fragment of the right dentary, with – probably – tooth positions #13, #15 and #16 preserved. By turning the fossil 180°, this also clarifies the observation that the replacement teeth in NHMM 2003-141 were positioned slightly anteriorly of the centre of the tooth to be replaced rather than slightly posteriorly, as seen in the holotype.

The study presented in Schulp (2005) heavily relied upon the erroneous interpretation of a 13-teeth dentition of *Carinodens*. Biting experiments with a reconstructed *Carinodens* jaw provided a range of possible prey items based on jaw reconstructions following Dollo (1913) and Schulp et al. (2004). The new material now shows that the dentary would have been some 15-20% longer than initially assumed. Consequently, the reconstructed skull presented in Schulp (2005) and the conclusions drawn on feeding opportunities available to *C. belgicus* now also require adjustment. We can assume that the longer dentary would lead to a reduced leverage, hence a lower biting force, and as a result we should consider a slightly smaller feeding envelope than previous interpretation of the simulated biting experiments suggested. With the new material, the functional significance of the different tooth morphologies along the dental ramus becomes more evident, as we can now distinguish between the anterior teeth involved in acquiring and manipulating food, the middle part of the dentition in the rough processing (crushing) of the presumably hard-shelled food, and the posterior dentition playing a role in further processing the just-unshelled food down to smaller chunks prior to swallowing, thus facilitating digestion.

It is interesting to note that the only material of the genus *Carinodens* recognised so far exclusively consists of dentaries and isolated teeth. There is probably a taphonomic bias favouring the preservation of the – presumably – strongest parts of the crania of these taxa; with a disproportionally heavy dentary, the dentaries would also stand a disproportionally good chance of becoming preserved in the fossil record.

It becomes clear now that durophagous mosasaurs successfully exploited a much wider range of niches of the Late Maastrichtian southern Tethys than initially assumed (compare Bardet et al., 2008). We now recognise various specialisations towards a durophagous lifestyle within the globidensine mosasaurs, ranging from the small, slender-snouted *Carinodens minalmamar* and the slightly larger, more heavily equipped *Carinodens belgicus*, via the much larger *Globidens phosphaticus* Bardet et al., 2005 and its relatives, up to the most massive *Prognathodon currii* Christiansen & Bonde, 2002.

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Conclusions

Carinodens is a more diverse genus than initially thought. New material from the upper Maastrichtian phosphates of Morocco proves that *Carinodens belgicus* had more teeth in its jaw than assumed previously: 17 rather than 13. Reconstructions of the genus therefore require adjustment, with a much longer snout and, more generally, probably a larger body size as well. Moreover, we present a new species of *Carinodens* from the upper Maastrichtian phosphates of Morocco, *C. minalmamar*, a small, relatively slender-snouted durophagous mosasaur as compared to *C. belgicus*. Durophagous mosasaurs were more diverse, and managed to exploit successfully an even wider range of niches than initially assumed.

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