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The first North American record of *Carinodens belgicus* (Squamata, Mosasauridae) and correlation with the youngest *in situ* examples from the Maastrichtian type area: palaeoecological implications•

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Abstract

Four recently collected tooth crowns of the rare latest Cretaceous (late Maastrichtian) durophagous mosasaur *Carinodens belgicus* are discussed; the first record from the Atlantic coast of North America (Maryland), and three additional *in situ* examples from the Maastrichtian type area in the southeast Netherlands and northeast Belgium. Also presented are an updated overview of the material recorded to date, and a discussion of the palaeobiogeographical and palaeoenvironmental distribution of the genus. Towards the end of the Cretaceous, *Carinodens* appears to have been successful in exploiting the margins of both the proto-Atlantic Ocean and the Tethyan Realm.

Keywords: Mosasaurs, Late Cretaceous, Maastrichtian, Maryland, the Netherlands, palaeobiogeography

Introduction

On several occasions during the evolutionary history of tetrapods, secondarily aquatic vertebrates adapted a durophagous mode of life, as is demonstrated by such widely divergent groups as placodonts, crocodilians and squamates (e.g., Carroll, 1988; Brinkmann, 1992; Sullivan & Lucas, 2003; Schulp et al., 2004; Martin, 2007; Polcyn et al., 2010). In Late Cretaceous mosasaurid marine squamates, durophagy developed within the Globidensini, the tribe which is thought to comprise the genera *Prognathodon*, *Globidens* and *Carinodens*. Both *Globidens* and *Carinodens* share a markedly heterodont dentition with pointed teeth in the anterior, and blunt bulbous ones in the medial and posterior portions of the jaws, decreasing in size posteriorly (Martin, 2007, figs 5, 6; Schulp et al., 2010, figs 1C, 3C, 4). The tooth crowns have anastomosing enamel ridges in common with some species of *Prognathodon*.

Recent discoveries of the latest Cretaceous mosasaur *Carinodens* have significantly improved our knowledge of the morphology, biomechanics, dietary preferences, distribution and diversity of this small-sized marine squamate (Schulp et al., 2004, 2006, 2010, 2013; Schulp, 2005; Bardet et al., 2008; Kaddumi, 2009). Although examples of this mosasaur remain extraordinarily rare, the combined effort of dozens of amateur and professional collectors alike has resulted in over forty isolated tooth crowns, as well as seven (partial) dentaries (Dollo, 1913; Schulp et al., 2004, 2010), both from the type area of the Maastrichtian Stage and from correlative strata in Morocco, and a partial skeleton from Jordan described by Kaddumi (2009).

In addition to the thirty-odd isolated tooth crowns recognised from the Maastrichtian type area (e.g., Kuypers et al., 1998; Mulder et al., 1998; Schulp et al., 2004), other examples of *Carinodens* include tooth crowns from Brazil (Price, 1957), the Congo Basin (Polcyn et al., 2010), Angola (Schulp et al., 2013),

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Morocco (Arambourg, 1952; Bardet et al., 2008; Schulp et al., 2010), Jordan (Mustafa & Zalmout, 2001), Bulgaria (Tzankov, 1939), Russia and the Ukraine (Schulp et al., 2006), suggesting that the genus ranged through most of the Atlantic and Tethyan realms (Fig. 1). Intriguingly, it had not yet been recorded from the Atlantic coast of North America (compare Bardet, 2012). Here, however, we describe the first example of *Carinodens belgicus* from the Late Maastrichtian Severn Formation of Maryland, USA (Fig. 2A-D), as well as the youngest *in situ* records to date from the Maastrichtian type area (Fig. 2E-Q).

Institutional abbreviations

ANSP – Academy of Natural Sciences, Philadelphia, Pennsylvania, USA; IRScNB – Institut royal des Sciences naturelles de Belgique (Bruxelles); NHMM – Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands.

Systematic palaeontology

Order Squamata Oppel, 1811
Family Mosasauridae Gervais, 1853
Genus Carinodens *Thurmond, 1969*
Carinodens belgicus *(Woodward, 1891)*

1799-1803 '... animaux qu'on ne sauroit déterminer'; Faujas de Saint-Fond, pl. 18, fig. 5.
1891 *Bottosaurus belgicus* Woodward, p. 114, pl. 3, fig. 18a-d.
1913 *Globidens Fraasi* Dollo, p. 610, pl. 24.
2010 *Carinodens belgicus*; Schulp et al., p. 163, figs 1A-D, 2A-D, 3A-D (with additional synonymy).

Material

Four isolated tooth crowns, ANSP 23308 (Fig. 2A-D), NHMM JJ 13527 (Fig. 2E-H), NHMM WR 1846 (Fig. 2I-L) and NHMM 2012 033 (Fig. 2M-Q). ANSP 23308, from near Bowie, Maryland, was purchased from an amateur collector by one of us (PF); it has recently been donated to the Academy of Natural Sciences, Philadelphia. NHMM JJ 13527 stems from subunit IVf-6 of the Meerssen Member (Maastricht Formation; see Fig. 3) at the ENCI-Heidelberg Cement Group quarry, south of Maastricht, the Netherlands, while NHMM WR 1846 is from the highest 0.4 m of the same subunit at the former Ankerpoort-Curfs quarry, Geulhem; it was collected by private collector Erik van Rijsselt. NHMM 2012 033 was recovered by another collector, Jacques Severijns, from a lag deposit at the top of subunit IVf-6 of the Meerssen Member in a temporary exposure along the Albert Canal (western bank), just north of Vroenhoven bridge, northeast Belgium.

Geological and stratigraphical framework

Severn Formation, Maryland, USA

The locality which yielded ANSP 23308 is at the end of Science Drive at Bowie, Prince George's County, Maryland. The coordinates are 38°57'49" N / 76°42'37" W. Here, strata assigned to the Severn Formation were in recent years temporarily exposed on the northern side of a stream. Permanent outcrops of this unit are situated within a kilometre of the locality.

The Severn Formation exposed here comprises a dark greyish green, clayey, micaceous glauconitic fine sand. In Maryland, this unit represents a continuation of the Maastrichtian Monmouth Group beds of southern New Jersey, trending southwestwards

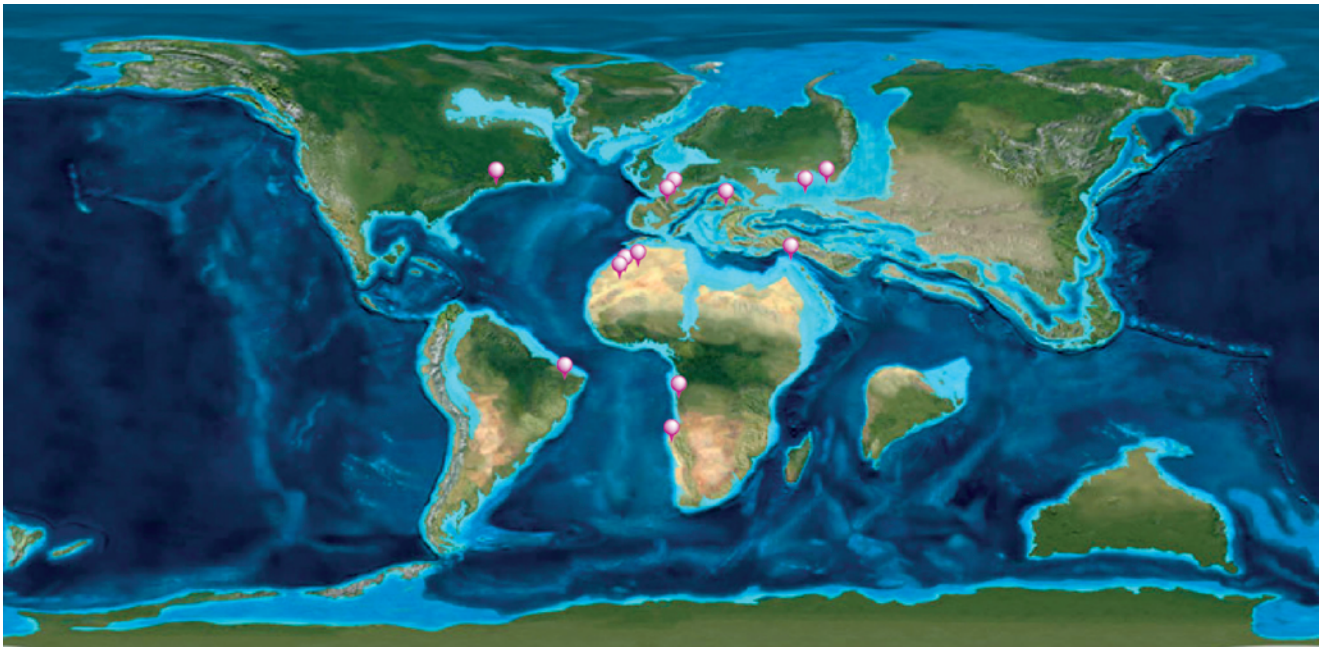

Fig. 1. Distribution of the Maastrichtian durophagous mosasaur genus Carinodens (palaeogeographical map courtesy of Ron Blakey).

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Fig. 2. Carinodens belgicus *(Woodward, 1891), isolated tooth crowns. A-D: ANSP 23308, in various aspects; Science Drive, Bowie, Prince George's County, Maryland, Severn Formation. E-H: NHMM JJ 13527, in various aspects; ENCI-HeidelbergCement Group quarry, Maastricht, the Netherlands, Maastricht Formation, Meerssen Member, subunit IVf-6. I-L: NHMM WR 1846, in various aspects; former Ankerpoort-Curfs quarry, Geulhem, Maastricht Formation, Meerssen Member, subunit IVf-6, 0-40 cm below Berg en Terblijt Horizont. M-Q: NHMM 2012 033, in various aspects; temporary outcrops just northwest of Vroenhoven bridge, Albert Canal, Belgium, Maastricht Formation, Meerssen Member, highest part of subunit IVf-6. Scale bars equal 10 mm.*

across the western Chesapeake region towards the border with Virginia. The Severn Formation is part of the general Maastrichtian transgressive phase that is roughly correlatable with the New Egypt, Red Bank and Tinton formations of the Atlantic Coastal Plain of northern New Jersey (Gallagher, 1993).

Age constraints

On ammonite evidence, a late Maastrichtian age can be assigned to the Severn Formation (Kennedy et al., 1997). The unit rests unconformably on the Campanian Mount Laurel and Matawan formations, and is overlain unconformably by the Paleocene Brightseat Formation. Although ANSP 23308 represents a reworked tooth crown, for the time being we assume that the specimen did not originate from older (i.e., Campanian) levels, because at present there are no pre-(Late) Maastrichtian records of *Carinodens*.

Palaeoenvironment and palaeodepth

A nearshore to mid-shelf setting is hinted at by the fossil biota, which include a diverse array of marine invertebrates, sharks, rays and bony fish (Hartstein & Decina, 1986; Hartstein et al., 1999). Amongst marine reptiles from the Severn Formation

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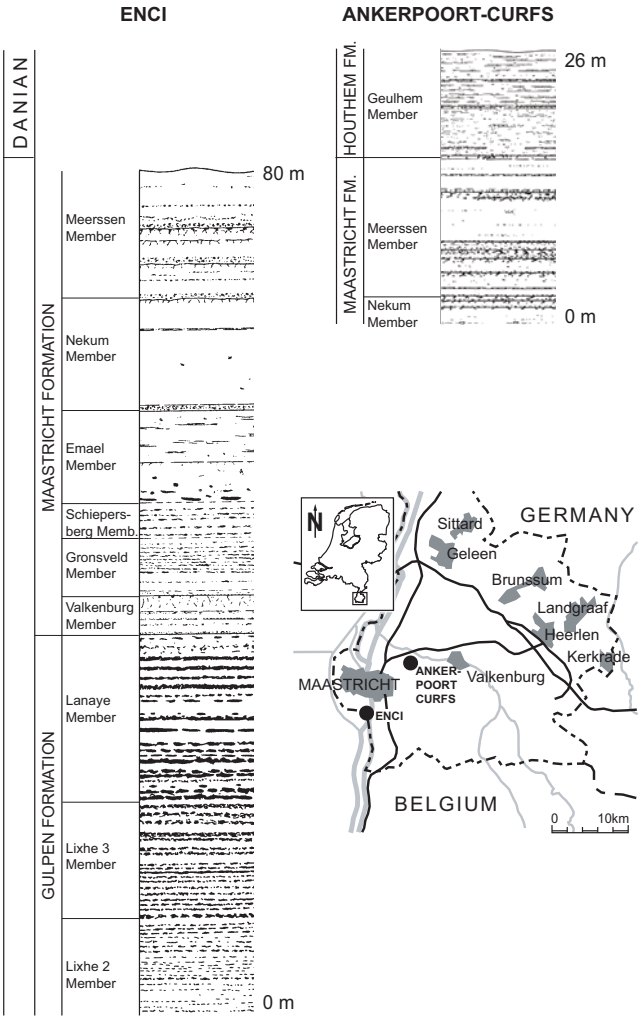

Fig. 3. Generalised lithostratigraphical logs of the upper Gulpen Formation and Maastricht Formation and their respective members at the ENCI (Maastricht) and former Curfs quarries (Geulhem); inset – map of the study area. The Cretaceous-Paleogene (K/Pg) boundary corresponds to the top of Meerssen Member, subunit IVf-6.

Baird (1986) listed cheloniid turtles (*Peritresius ornatus* (Leidy, 1856) and *Osteopygis emarginatus* Cope, 1869), crocodiles (*Thoracosaurus neocesariensis* (DeKay, 1842)) as well as several mosasaurid taxa including *Halisaurus platyspondylus* Marsh, 1869, *Prognathodon rapax* (Hay, 1902), *Mosasaurus hoffmanni* Mantell, 1829 and *M. conodon* (Cope, 1881). Terrestrial faunal elements in this unit comprise fragmentary dinosaur remains; the presence of lignite in the sequence also points to a nearshore setting, while glauconite is indicative of deposition below wave base.

Palaeotemperature

Based on data presented by Olsson et al. (2002), K.G. Miller and J.D. Wright (pers. comm. to WBG, 2012) estimate minimum mean annual temperatures of the North Atlantic near New Jersey to have ranged between 20 and 24° C.

Palaeolatitude and ocean currents

The latitude of the Late Cretaceous 'New Jersey coastline' was only slightly south of today's coast. Circulation in the North Atlantic basin was different from today's; with a smaller basin and a poorly mixed water column, temperature differences within the water mass did not drive strong circulating surface and bottom currents.

Gulpen and Maastricht formations, southeast Netherlands and northeast Belgium

Coordinates of the ENCI-HeidelbergCement Group quarry, the former Ankerpoort-Curfs quarry and the temporary exposures at Vroenhoven are 50°49'18" N / 5°41'04" E, 50°52'06" N / 5°45'60" E and 50°49'58" N / 5°39'25" E, respectively.

On current evidence, the stratigraphic range of *Carinodens belgicus* in the type area of the Maastrichtian Stage includes the upper Gulpen Formation (Lanaye Member) and the entire overlying Maastricht Formation (Fig. 3). The Lanaye Member is a pure, coccolithic bioclastic, silty and homogeneously bioturbated packstone, with well-developed planar-parallel flint nodule levels occurring at 0.5-1.5 m interspaces. The overlying Valkenburg, Gronsveld, Schiepersberg and Emael members (Maastricht Formation) represent fining-upward cycles with a phosphatic, glauconitic-pyritic, bioclastic sands (gravelly intrabiomicrosparites) at the base, with bioturbated, fine-grained, purer carbonate sediment at the top (Jagt, 1999).

The Nekum Member (Maastricht Formation) is a poorly indurated, white-yellowish, coarse-grained homogeneous biocalcarenite, while the overlying Meerssen Member comprises medium- to coarse-grained biocalcarenites (mainly packstones and grainstones; gravelly intrabiomicrosparites), with very coarse bioclastic sands resting on erosional surfaces. Of note is an increase of average bed thickness and hardground development within this member, in particular in the lower/middle portion (see Jagt, 1999; Jagt & Jagt-Yazykova, 2012).

Age constraints

Keutgen & Jagt (2009, table 1) dated the base and top of the Lanaye Member at 67.8 and 67.4 Ma, and the base of the Maastricht Formation at 66.2 Ma, respectively. For the Cretaceous/Paleogene (K/Pg), they used 65.5 Ma. On ammonite evidence, the entire Maastricht Formation is of latest Maastrichtian age. Assemblages from Maryland (Kennedy et al., 1997) and the type area have quite a number of elements in common amongst sphenodiscids (*Sphenodiscus lobatus*, of which *S. binckhorsti* probably is a synonym), baculitids (*Baculites vertebralis*, *Eubaculites* spp.), diplomoceratids (*Glyptoxoceras rugatum*) and scaphitids (*Hoploscaphites* spp.). Correlation with the New Jersey Coastal Plain, as favoured by Keutgen & Jagt (2009), would equate the top of Navesink I (dated at 67.0 Ma) to a level close

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to the top of the Lanaye Member (67.4 Ma), and the base of Navesink II (dated at 66.0 Ma) to a level close to the base of the Maastricht Formation (66.2 Ma).

Palaeoenvironment and palaeodepth

The Lanaye Member represents deposition in a subtropical, platform (middle sublittoral) setting with minor open ocean influence, at water depths of between 40 and 80 m. During this interval there was an increased Tethyan/proto-Mediterranean influence, as demonstrated by ostracods, mosasaurids and cheloniid turtles. The lower and middle portion of the Maastricht Formation (Valkenburg, Gronsveld, Schiepersberg and Emael members) were laid down at shallower depths (20-40 m), in a subtropical setting free from oceanic influence. Sediment reworking resulted in homogenisation of sediments over a depth of some decimetres, leaving a relatively solid sea floor and clear waters. This interval is characterised by the occurrence of sea grass communities (Jagt, 1999). The Nekum and Meerssen members continue this trend, comprising high-energy deposits laid down in shallow to very shallow (2-15 m) setting, with an elevated production of carbonate detritus leading to the establishment of a broad, shallow, well-lit, warm carbonate platform with rich phytal associations. Water temperatures are held to have risen to 20-25° C, allowing the growth of scleractinian corals and rudistid bivalves, especially in the lower and middle portions of the Meerssen Member (Jagt, 1999). The upper portion of the latter member was deposited in deeper, colder water, as demonstrated by the general lack of scleractinians and rudistid bivalves and the presence of coleoid cephalopods typical of Boreal settings of the Russian Platform and northeast Europe (Jagt & Jagt-Yazykova, 2012).

Palaeotemperature

To date, there are no isotope data available to allow reliable temperature estimates to be made. Only in general terms may it be stated that deposition of the upper Gulpen Formation and the entire Maastricht Formation reflects subtropical conditions, with increasing shallowing and a concomitant rise of water temperature to values around 20-25° C near the top of the sequence. The climatic 'deterioration' in the uppermost Maastricht Formation probably is related to a change in ocean currents.

Description

ANSP 23308 (Fig. 2A-D) appears to be reworked, thus conforming to most elements of the 'Bowie vertebrate assemblage' (*sensu* Hartstein et al., 1999). This tooth crown is incomplete, the posterior portion having broken off. As preserved, its anteroposterior length is 15.2 mm, its labiolingual width and height being 10.2 mm and 12.1 mm, respectively. Enamel and dentine have the same black colour and are mineralised to such an extent that they hardly can be distinguished from each other. The enamel layer is worn and shows some cracks. The carina, normally present in teeth of *Carinodens*, has been lost due to erosion. The enamel surface is irregularly rugose. At the apex the dentine can be seen, due to the state of erosion of the enamel. The preserved anterior part of the crown is convex, as such forming a distinct 'shoulder'. ANSP 23308 is referred to *Carinodens belgicus* because it matches very well the teeth preserved in the type dentary of this species. The present tooth crown might have occupied the 9th to 14th position in the jaw.

NHMM JJ 13527 (Fig. 2E-H) is bicuspid and fairly well preserved, although a substantial part of the enamel layer anterior to the dorsal apex is missing, as can be seen in occlusal view (Fig. 2F). Its anteroposterior length is 20.1 mm, the labiolingual width and height being 10.6 and 9.2 mm, respectively. Enamel rugosity, as preserved, is obvious. The anterior carina is prominent, extending over the entire crown, as seen in occlusal view. The anterior 'shoulder' is sufficiently prominent as to feature a short convex stretch in outline. The posterior 'shoulder' remains concave throughout. It bears a small wear facet, exposing the dentine. This tooth crown corresponds to the 11th to 13th position in the jaw (compare Schulp et al., 2010, fig. 4).

NHMM WR 1846 (Fig. 2I-L) is somewhat eroded, the irregularly rugose surface of the enamel remaining visible. Its anteroposterior length is 15.9 mm, the labiolingual width and height being 8.5 and 11.2 mm, respectively. A faint anterior carina is present. The anterior 'shoulder' is barely convex, while the posterior 'shoulder' is slightly concave; this results in a distinct cusp and gives the apical part of the crown a more or less triangular outline in lingual and labial views. This tooth crown also matches the 11th to 13th position in the jaw (compare Schulp et al., 2010, fig. 4).

NHMM 2012 033 (Fig. 2M-Q) has recently been described by Schulp (2012) as the first record of an anterior tooth of *Carinodens* from the Maastrichtian type area. Its height is 10 mm. The apical rugosity of the enamel transforms downwards into a pattern of anastomosing ridges. In striking contrast to more posterior teeth, the shape of NHMM 2012 033 is more or less conical, although a faint anterior 'shoulder' is present. The crown shows no sign of a carina and most probably reflects the 5th or 6th position in the jaw (Schulp et al., 2010, figs 1C, 3C, 4; compare Martin, 2007, fig. 5C, E).

Discussion and conclusions

Distribution

Despite the general paucity of isolated tooth crowns and a handful of fragmentary dentaries, it is possible to conclude that representatives of the genus *Carinodens* were widely distributed towards the end of the Cretaceous. Schulp et al. (2006, 2010),

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Bardet et al. (2008) and Bardet (2012) noted a late Maastrichtian southern trans-Atlantic epicontinental distribution, and a presence in the shallow waters of the Tethyan Realm. Previously, Mulder (2003) had discussed trans-Atlantic similarities between the mosasaur faunas from the type Maastrichtian and the Late Cretaceous marine deposits of New Jersey, noting in particular the presence of *Mosasaurus hoffmanni* Mantell, 1829 and *Plioplatecarpus marshi* Dollo, 1882 on both sides of the Atlantic. In view of these similarities, the absence of *Carinodens* in eastern North America was intriguing, the more so since the trans-Atlantic distribution of marine squamates may have been stimulated by an ocean current direction pattern, such as suggested by Windley (1977).

The new material now enables a full north and south trans-Atlantic epicontinental distribution to be recognised for *Carinodens*. Until recently, isolated bulbous tooth crowns from outcrops in Maryland were identified as those of durophagous crocodiles of the genera *Brachychampsa* and '*Bottosaurus*' (for comments see Gallagher, 1993; Norell et al., 1994; Sullivan & Lucas, 2003), which is why additional records of *Carinodens* might be expected in the near future.

Palaeoenvironment

The ecosystem of the Late Cretaceous marginal seas of the Maastrichtian type area can be characterised as a sea grass community, with the possible exception of the highest part of the sequence (Moody, 1997; Jagt, 2005), while the Late Cretaceous glauconitic sediments of New Jersey and Maryland reflect muddy water (estuarine) conditions during the Maastrichtian (Gallagher, 1993). In both types of palaeoenvironment, bivalves were abundant (Gallagher, 1993; Jagt, 1999), which is accordance with previous suggestions about preferred diet (Schulp, 2005).

With *Carinodens* now recorded from ten different localities across the Atlantic-Tethyan realm, we may review the sedimentological context of the various occurrences in more general terms. Lithologies range from almost exclusively biocalcarenitic (type Maastrichtian occurrences) to more clastic (sandy) facies, such as in the Ukraine. Records from Russia, Morocco, Brazil and Jordan are all, to varying degrees, related to phosphatic strata; glauconite is reported for the Ukrainian, North American and Bulgarian occurrences. Thus, it can safely be assumed that *Carinodens* preferred a shallow-marine, nearshore setting.

Stratigraphic range

Based on records from the well-dated type section of the Maastrichtian Stage, *Carinodens belgicus* is of an exclusively late Maastrichtian age. An isolated tooth crown (IRScNB R41), originally referred to as '*Bottosaurus*', from an unspecified level within the Obourg Chalk Formation (Late Campanian) near Mons (Ciply area, southern Belgium) can be assigned to *Globidens* (Jagt, 2005). The lowest occurrence of *Carinodens* in the Maastrichtian type area is from the upper Lanaye Member (Gulpen Formation), dated at ca 67.5 Ma (compare Keutgen & Jagt, 2009), the highest being just below the K/Pg boundary, at 65.5 Ma (see also Jagt et al., 2008).

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