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Two rare mosasaurs from the Maastrichtian of Angola and the Netherlands

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Abstract

We report here the addition of two rare mosasaur taxa to the Maastrichtian marine amniote fauna of Angola, both of which are also found in northern Europe. The new specimens include a dentary fragment referable to the large carnivore *Prognathodon* cf. *saturator* and an isolated tooth of the small durophage *Carinodens belgicus*. Both were recovered from Maastrichtian outcrops in southern Angola in 2011. Additionally, a complete posterior mandibular unit of a large mosasaur from the type Maastrichtian of the Netherlands, collected some time prior to 1879 and previously identified as '*Mosasaurus giganteus*', is described and reassigned here to *Prognathodon saturator*; historical issues surrounding the taxonomic attribution of this specimen are clarified. The new material extends the known geographic distribution of *Prognathodon saturator* and *Carinodens belgicus*.

Keywords: Mosasauridae, *Prognathodon*, *Carinodens*, Maastrichtian, Angola, the Netherlands

Introduction

In recent years our knowledge of the marine reptile fauna of Angola has been greatly expanded through the efforts of the PaleoAngola Project (Jacobs et al., 2006, 2009; Schulp et al., 2006, 2008; Mateus et al., 2009, 2011; Polcyn et al., 2010; Mateus et al., 2012). A number of new taxa have been reported (Schulp et al., 2008; Mateus et al., 2009, 2011) and skeletal remains of other taxa previously known only from teeth have been described (Polcyn et al., 2010). During the 2011 field season of the PaleoAngola Project, remains of two rare mosasaur taxa were recovered; the extremely large and robust mega-carnivore *Prognathodon* cf. *saturator*, and the diminutive durophagous *Carinodens belgicus*.

Prognathodon saturator Dortangs et al. 2002 was heretofore known only from the holotype material recovered from the type Maastrichtian (~66.1 Ma) of the St Pietersberg (near Maastricht, Limburg Province, the Netherlands); the holotype is now housed in the collections of the Natuurhistorisch Museum Maastricht (NHMM1998-141). This large globidensine mosasaur was a contemporary of the better known *Mosasaurus hoffmanni* Mantell, 1829 and *Plioplatecarpus marshi* Dollo, 1882 (e.g. Kuypers et al., 1998; Mulder, 2003), but evidenced by the extremely massive and robust skull and dentition, was clearly exploiting a separate and unique feeding niche.

In this contribution, we report two new occurrences of *P. saturator*; a short fragment of a dentary recovered by the authors from the Maastrichtian of southern Angola in 2011 and a well-preserved posterior mandibular unit (PMU) collected from the type Maastrichtian of the Netherlands sometime prior to 1879. The latter is currently housed in the collections of the Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium.

Carinodens belgicus Woodward 1891 (see also Dollo, 1913 and Thurmond, 1969) is known primarily from isolated teeth from the Maastrichtian type area of the Netherlands and Belgium (Schulp et al., 2004) and is also known from both shed teeth and relatively complete dentaries from Morocco, and more complete cranial and postcranial material from Jordan (Mustafa & Zalmout, 2001; Bardet et al., 2005, 2008; Kaddumi, 2009; Schulp et al., 2010). The species is known from the Maastrichtian South Atlantic of Brazil (Price, 1957) and from the Congo basin (Polcyn et al., 2010). Here we report the first occurrence from the African Southern Atlantic.

Institutional abbreviations

IRScNB: Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium; NHMM: Natuurhistorisch Museum Maastricht, Maastricht, the Netherlands; MGUAN-PA: Geological Museum, Universidade Agostinho Neto, Luanda, Angola (PaleoAngola collection); MNHN: Muséum National d'Histoire Naturelle, Paris, France; OCP: Office Chérifien des Phosphates, Khouribga, Morocco; TM: Teylers Museum, Haarlem, the Netherlands.

Systematic palaeontology

- Order Squamata Oppel, 1811
- Superfamily Mosasauroidea Gervais, 1853 (nom. transl. Camp, 1923)
- Family Mosasauridae Gervais, 1853
- Subfamily Mosasaurinae Gervais, 1853 (nom. transl. Williston, 1897)
- Tribe Globidensini Russell, 1967 (*sensu* Bell, 1997)
- *Prognathodon* Dollo, 1889
- *Prognathodon saturator* Dortangs et al., 2002

Holotype: NHMM1998-141

Referred specimen

MGUAN-PA 169 (Fig. 1A-C) is a jaw fragment with one preserved tooth.

Locality and Horizon

The specimen comes from the Tzimbio locality (initially reported as the 'Bentiaba 2'-locality in Mateus et al., 2012), some 15 km NE of the richly fossiliferous locality of Bentiaba, Namibe Province, Angola (Jacobs et al., 2006). This site exposes strata from the Maastrichtian Mocuio Formation. Inoceramid shell fragments characteristically present in the lower part of the section at nearby Bentiaba are absent in the higher part of the section at both Bentiaba and Tzimbio. Inoceramids became extinct in the mid Maastrichtian (MacLeod, 1996), suggesting this part of the section (and the fossils therein) fall within the upper part of the Maastrichtian and thus MGUAN-PA 169 is part of a slightly younger fauna than the material described so far from the Bentiaba site (e.g. Schulp et al., 2008; Polcyn et al., 2010; Mateus et al., 2012).

Description

The specimen is severely weathered, and is composed of portions of the right dentary. It preserves two complete alveoli, multiple isolated bone fragments, a single tooth crown and a few tooth fragments. The teeth are ankylosed to the dentary by a broad tooth base elevated above the dorsal margin of the dentary. The single preserved tooth crown is robust, and measures 68 mm tall. It is missing the enamel, but allows description of diagnostic features. The tooth is bicarinate and only very slightly recurved posteriorly. There is no medial curvature. The tooth is constricted at the base and shows the swelling just above the base that is characteristic of *Prognathodon* (Bell, 1997; Bardet et al., 2000; Schulp, 2006).

This combination of characters allows referral to the genus Prognathodon and other closely related forms. Although the outer layer of enamel is exfoliated from the dentine, the remaining surface is smooth and shows no signs of fluting or other ornamentation, ruling out *P. overtoni* and *P. solvayi* in which the teeth possess these features. Smooth surfaces are known in *Prognathodon* (*Dollosaurus*) *lutugini*, *P. stadtmani*, *P. waiparaensis*, *P. kianda* and the species previously referred to the genus *Liodon* (see Schulp, 2006 and Schulp et al., 2008). The robust nature of the specimen and the nearly circular cross-section of the teeth rules out *Prognathodon kianda* and other *Prognathodon* species that have previously been referred to the genus *Liodon* (Schulp et al, 2008), in which the teeth are more laterally compressed. *P. currii* and *Igdamanosaurus* are ruled out on the basis of their domed appearance. Additionally, *P. currii* teeth are not elevated on a bony base of attachment. The specimen described herein has tooth crowns elevated above the bony margin of the jaw by the bony base of attachment as in *P. giganteus*, *P.* (*Dollosaurus*) *lutugini* (Lindgren, 2005), *P. saturator*, and *P. overtoni* (Lindgren 2005). *P. overtoni* was ruled out on the basis of possession of fluted surfaces. Morphologically, the specimen described here is similar to *P.* (*Dollosaurus*) *lutugini* (Lindgren, 2005) which comes from the Lower Campanian of Sweden and the upper Campanian of the Ukraine (Lindgren, 2005), *Prognathodon saturator* from the Maastrichtian of the Netherlands (Dortangs et al., 2002), and *Prognathodon giganteus* from the Upper Campanian of France (Bardet et al., 1997; Jagt, 2005). *Dollosaurus,* however, is a much smaller species. *P. giganteus* and *P. saturator* are similar in size, and although Dortangs et al. (2002) provided character justification for separation of *P. saturator* from *P. giganteus*, those characters are not preserved in the specimen described here. Additionally, a range extension of either of those species cannot be conclusively ruled out. Nonetheless, the specimen described herein is most similar in size, morphology, and age to *P. saturator* (which is also Maastrichtian in age) and we therefore tentatively refer the new material to that species.

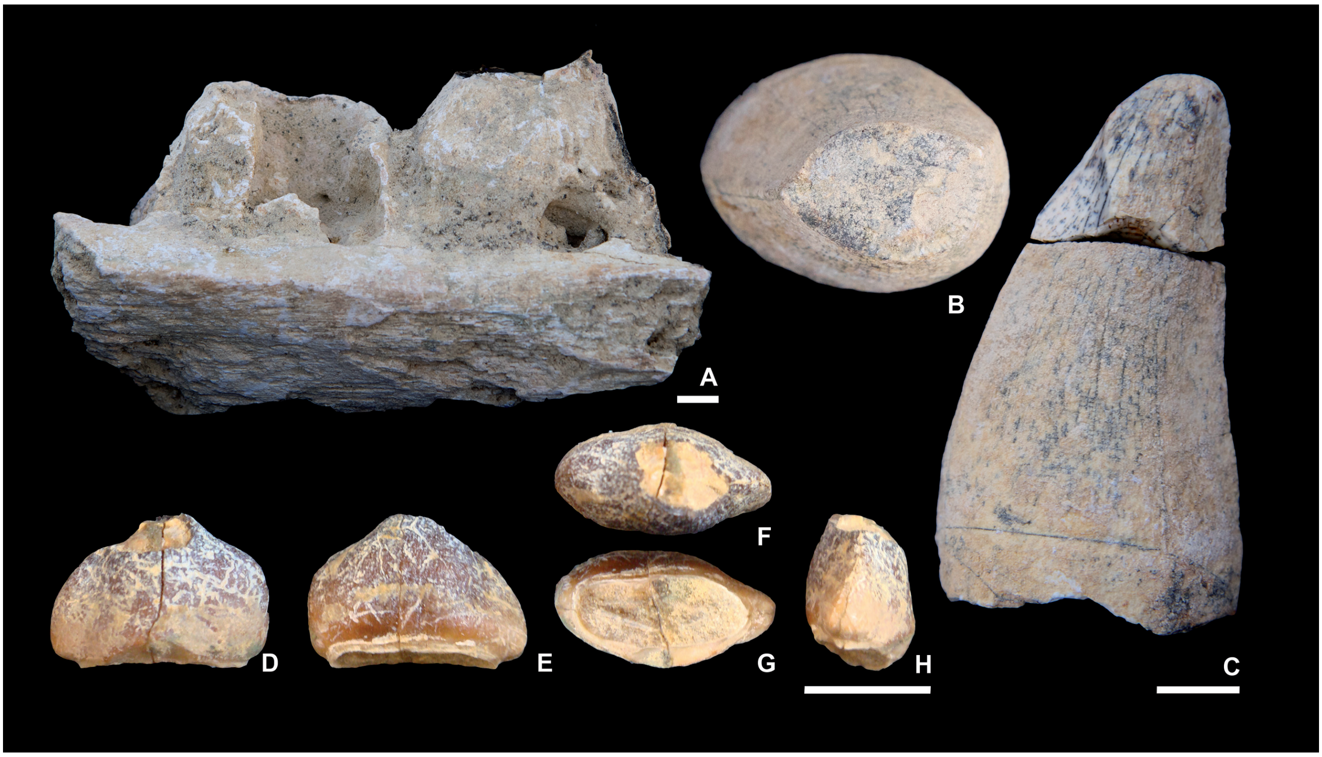

Fig. 1. Prognathodon *cf.* saturator *Dortangs et al., 2002, right dentary fragment MGUAN-PA-169, in medial view (A), tooth crown in occlusal (B) and lateral (C) views; Carinodens belgicus (Woodward, 1891), isolated tooth crown MGUAN-PA-171, in buccal (D), lingual (E), occlusal (F), basal (G) and posterior (H) views. Scale bars equal 1 cm.*

Referred specimen

IRScNB R24 (Fig. 2A-D) is a complete and well preserved left posterior mandibular unit (PMU) of a large mosasaur.

Locality and Horizon

The labels filed with the specimen make reference to the previous collection number IG4286 and 'registre 1506'. The locality as stated in the collection registration (linked to those previous specimen numbers) is 'Montagne St-Pierre Tuffeau de Maestricht' and identified as 'Maxillaire inférieur (extrémité postérieur)'. Thus, IRScNB R24 comes from the type Maastrichtian limestones of the St Pietersberg, SW of Maastricht. At the time of discovery of IRScNB R24 (the second half of the 19th century; Ubaghs, 1879a, b), the limestone was quarried almost exclusively in underground galleries, in the Nekum Member only, as the near-absence of flint made this member the best choice for building stone. Therefore, we can safely assume that IRScNB R24 is from the Late Maastrichtian Nekum Member (see Schiøler et al., 1997 for an overview of the lithostratigraphy).

Description

The posterior mandibular units (PMU) of the holotype of *P. saturator* are crushed and only partially exposed (see Schulp, 2006: p. 23), and the medial morphology is largely obscured. The Brussels specimen IRScNB R24 is well preserved, uncrushed, and completely free of matrix, and thus allows description of these elements and augments previous descriptions of *P. saturator* (Dortangs et al., 2002; Schulp, 2006). IRScNB R24 is larger than the holotype, measuring 68 cm from the anterior tip of the coronoid to the posterior end of the retroarticular process compared to the (slightly crushed) holotype of *P. saturator* measuring about 57 cm (i.e. almost 20% longer). All elements are tightly sutured as in the holotype of *P. saturator*.

In lateral view the surangular broadly overlaps both the angular and the articular. The suture with the articular originates at the posterior terminus of the glenoid and trends posteroventrally, closely paralleling the posterodorsal margin of the articular, extending to the posterior terminus of the PMU and ventrally to a point at which the articular bends sharply medially to form the retroarticular. At that point, the ventral margin turns anteriorly, again closely paralleling the ventral margin of the PMU and exposing only a small portion of the angular in lateral view along the ventral margin. Anteriorly, the surangular ventral margin trends anterodorsally exposing the anterolateral portion of the angular broadly. Dorsal to the angular, the anterior margin of the surangular trends dorsal at a sharper angle, its most dorsal portion underlying the coronoid. Posteriorly, the dorsal margin slopes anterodorsally, buttressing the posterior portion of the coronoid. In lateral view the anterodorsal portion of the coronoid protrudes anteriorly beyond the anterior terminus of the surangular. Its anterior margin trends posteroventrally and is sharply emarginated at the surangular foramen that carries the intramandibular artery, and more posteriorly forms a gently curved ventral

Fig. 2. Prognathodon saturator *Dortangs et al., 2002, posterior mandibular unit IRScNB R24, in dorsal (A), medial (B), anterior (C) and lateral (D) views. Scale bar equals 10 cm.*

margin. The posterior portion of the coronoid is dorsoventrally wide and broadly overlaps the surangular. In medial view the surangular is largely covered on three sides by the other constituent elements of the PMU, but a large central portion is exposed and provided a portion of the insertion of the adductor muscles. The articular is deeply emarginated dorsally by this insertion area just anterior to the glenoid, the anterior portion has parallel sides and is obscured anteriorly by the coronoid. Posteriorly, the articular is sharply deflected medially, forming the retroarticular process. In medial view the coronoid is broad and dorsoventrally deep, the ventral portion overlapping the articular and contacting the angular broadly, forming a posteriorly directed process that is accommodated by a recess in the underlying articular. The posterodorsal portion forms an extensive contact with the medial ascending process of the surangular. The anterior margin is nearly vertical.

Comments and specific attribution

IRScNB R24 was first described and figured by Ubaghs in two publications which saw only limited distribution (1879a: pl. I; 1879b: pl. I). In his comparison of IRScNB R24 with the holotype of *M. hoffmanni*, Ubaghs noted differences in proportion ("On n'a pas oublié que notre échantillon dépasse en longueur celui de Paris (MNHN AC 9648) d'un quart, mais d'à peu près le double en largeur"), but apparently did not consider these differences taxonomically significant. Instead, he attributed the specimen to *M. camperi* (i.e. the name under which the 'Paris' and 'Haarlem' specimens of *M. hoffmanni* were known at that time). His referral was noted by him to be prompted by the fact that the corresponding elements in the Paris specimen (MNHN AC 9648) were only partially exposed, and (mostly) missing in the Haarlem specimen (TM 7424).

The specimen is clearly a mosasaurine by possession of a surangular buttress of the coronoid. It shares with derived (see Bell, 1997; Schulp, 2006) *Prognathodon* species (e.g. *P. overtoni* Williston, 1897; *P. waiparaensis* Welles & Gregg 1971) contact of the anteroventromedial coronoid with the angular. It shares with *P. saturator* the nearly complete concealment of the angular in lateral view by the surangular, only exposed anteriorly, and the relatively tall aspect ratio in lateral view (compare fig. 19 in Schulp, 2006). Because we now know *M. hoffmanni* from many well-preserved specimens, we can exclude IRScNB R24 from referral to *M. hoffmanni* (compare Lingham-Soliar 1995: fig 14; note the ventral extension of the coronoid in medial view). Instead, IRScNB R24 is almost indistinguishable in all respects which can be compared to the holotype of *Prognathodon saturator* Dortangs et al., 2002, and can now be confidently referred to that taxon (we consider the differences in proportions of the coronoid compared to the holotype to be the result of crushing and deformation of the bone by flint – now removed – in the holotype).

The history of taxonomic issues surrounding the specimen IRScNB R24 and the broader applications of the species name *gigantea* (or *giganteus*) are significant, and will be addressed here. Ubaghs identified the specimen, at that time in his personal collection, as '*Mosasaurus Camperi* H. V. Meyer'. The Ubaghs Collection was later transferred to the museum in Brussels, where the specimen is currently registered as IRScNB R24. Accepting Ubaghs identification, Dollo (1882: p. 62) listed the specimen as '*Mosasaurus Camperi*, v. Meyer'; however, in 1882 he then refers to the specimen as '*Mosasaurus giganteus* Sömmering 1820' (Dollo, 1882: p. 68) without providing justification for this new referral – nonetheless, identification has not been challenged until now.

The confusion arises in large part from the original construction of the species name given by Von Sömmering (1820) for Late Jurassic crocodilian material from Bavaria, Germany. At that time, he considered his new material conspecific with the holotype of *M. hoffmanni*, which at that time carried only informal names, referring both the crocodile and mosasaur material to *Lacerta gigantea*, creating a composite holotype (see Bardet & Jagt, 1996 for historical background).

Cuvier (1824) separated the crocodile and the holotype *M. hoffmanni* by transferring the crocodile material to the newly erected genus *Geosaurus*, and specifically stated that reference of the species name *giganteus* to the genus *Geosaurus* would be inappropriate, but was silent on continued use of it (Cuvier, 1824, p. 343: "Je ne peux lui laisser l'épithète de gigantesque, car, dans le grand genre *lacerta*, nous avons d'abord l'animal de Maestricht ou mosasaurus qui le surpasse de beaucoup, et nous allons en voir un autre (le mégalosaurus) qui lui est aussi très-supérieur.").

Dollo mistakenly resurrected the species name, identifying IRScNB R24 as *Mosasaurus giganteus* Sömmering, 1820 (adapting the gender to match masculine *Mosasaurus*). His considerations to maintain the species name *giganteus* (Dollo, 1890, pp. 160-161) essentially repeated Cuvier's argumentation. To make matters more complicated, in 1904, Dollo introduced a potential source of confusion by using the species name *giganteus* in his description of a new species of *Prognathodon* (holotype IRScNB R106 / formerly 3103; incomplete skull and postcranial skeleton from the upper Campanian of the Ciply area, southern Belgium; Jagt, 2005); see also Schulp (2006): p. 22.

Although Cuvier's statement on the assignment of the species name *giganteus* is understandable in light of the less than gigantic size of *Geosaurus*, ICZN rules do not allow for exceptions in priority issues because of 'inappropriateness' (Article 18: "... are not to be rejected because of a claim that they denote a character or distribution not possessed by the taxon."; article 23.3.7). Although formal rules governing taxonomy were not published till some decades after the time of Cuvier's act, in the interest of maintaining a reasonable taxonomy these ICZN rules should also apply retrospectively. In absence of ICZN governance of Cuvier's act, and in light of his silence on the continued use of the species name, Camp (1942, p. 45) suggested that: "By inference, the specific name *gigantea* would, from Cuvier's date, rest with *Geosaurus*. It should not be applied to the mosasaur as has frequently been done (Kuhn, 1929 (sic!)). Lydekker (1888) restudied von Sömmering's Bavarian type of *Lacerta gigantea* and confirmed Cuvier's reference of that form to the genus *Geosaurus*. This fixed the name *gigantea*, and it has subsequently been consistently used".

Of note is the fact that, although *Mosasaurus hoffmanni* Mantell 1829 takes priority over *Mosasaurus camperi* von Meyer, 1832, Ubaghs (1879a) referred to the Paris (MNHN AC 9648) and Teylers (TM 7424) specimens, as well as the Brussels material (IRScNB R24) discussed here, as *Mosasaurus Camperi* H. V. Meyer, even though this synonymy had been noted in the literature as early as 1845 (Russell, 1967).

- *Carinodens* Thurmond, 1969
- *Carinodens belgicus* (Woodward, 1891)

Holotype: IRScNB R43

Referred specimen

MGUAN-PA 171 (Fig 1D-H), an isolated tooth crown of a small durophagous mosasaur.

Locality and horizon

The specimen was collected from the upper reaches of the Bentiaba locality in 2011. The highest levels of this locality are characterized in part by the absence of *Inoceramus* and is thus likely Upper Maastrichtian (*fide* MacLeod, 1996).

Description

The enamel on the tooth crown is preserved, with the exception of the worn apical nubbin, a condition commonly seen in durophagous mosasaurs. The tooth is wider than tall in lateral aspect, the apical nubbin located slightly off-centre. The base of the crown is constricted, and minute anastomosing ridges on the thick enamel are present. The outline in labial view of MGUAN-PA 171 is quite similar to tooth position #10 to #13 in *Carinodens belgicus* (Schulp et al., 2010: fig 4). The aspect ratio in occlusal view (anteroposterior length / labiolingual length) in MGUAN-PA 171 is 1.87, which corresponds closely with the value of tooth position #11 in *Carinodens belgicus* OCP DEK/GE 454 (1.91). This alone is sufficient to distinguish MGUAN-PA 171 from *Carinodens minalmamar* Schulp et al., 2010, as the teeth in *C. minalmamar* are much more laterally flattened. Prominent sulci are present on the lateral aspect of the teeth of *C. minalmamar* but much less pronounced in MGUAN-PA 171 and other specimens referred to *C. belgicus* (compare Schulp et al., 2010).

Discussion and conclusions

Stratigraphic range and geographic distribution of P. saturator

Previously, the temporal and geographic occurrence of *P. saturator* was restricted to a single specimen from the Maastrichtian type area (Dortangs et al., 2002) from the upper Lanaye Member (Gulpen Formation; late Maastrichtian, *Belemnitella junior* Cephalopod Zone). IRScNB R24 comes from the same area as the holotype of *P. saturator*. With the holotype from the upper Lanaye Member (Gulpen Formation) and IRScNB R24 from the Nekum Member (Maastricht Formation), the minimum range of *P. saturator* can now be defined from the top of the Gulpen Formation throughout most of the Maastricht Formation. The Bentiaba site in Angola (e.g. Jacobs et al., 2006) is extraordinarily rich in fossil marine reptiles, and in the past six years, the lower reaches of the site have been extensively sampled in five field seasons by the PaleoAngola team. The lower reaches, particularly the middle Maastrichtian Mocuio Formation (see Mateus et al., 2012), did not yield any large *Prognathodon* teeth, whereas the smaller globidensine mosasaur *Prognathodon kianda* is present (Schulp et al., 2008), along with *Globidens phosphaticus* (Polcyn et al., 2010), which in turn disappears in the higher part of the section along with inoceramids. Pending more detailed stratigraphic logging, we infer the part of the Tzimbio section that yielded MGUAN-PA-169 to represent slightly younger strata, because of the disappearance of inoceramid shells (MacLeod, 1996), indicating the Angolan *Prognathodon saturator* is mid-Maastrichtian or younger. A tooth mentioned and illustrated by Antunes (1964: plate 26, fig. 4) from Cabinda may represent a large *Prognathodon*. Bardet et al., 2000 ‘tentatively’ identified the specimen as *P. giganteus*, but given the size, proportions and age, referral to *P.* cf. *saturator* would be more conservative on both morphological and temporal grounds. The teeth of the much older Campanian species *P. giganteus* Dollo 1904, preserved in the holotype IRScNB R 106 (see also Lingham-Soliar, 1994 and Bardet et al., 2000) are smaller, and differ in having a more pronounced posterior curvature and a more circular cross-section (Lingham-Soliar, 1994: fig. 1e-f). However, it should also be noted that the diagnostic value of the posterior curvature in *Prognathodon* teeth is relatively limited, and in the holotype of *P. saturator* (NHMM 1998-141), curvature of the posterior carina differs from almost straight to considerably curved from one tooth position to the next in a single individual.

Stratigraphic range and geographic distribution of Carinodens

Our knowledge of the distribution and morphology of *Carinodens* has expanded considerably in recent years (e.g. Kaddumi, 2009; Schulp et al., 2010 and refs therein). In addition to the records from Europe, the North African margin, and Middle East, *Carinodens* has also been reported from the South Atlantic Maastrichtian of Brazil (Price, 1957) and the Congo (Polcyn et al., 2010), both at a paleolatitude of approximately 13° S. This report extends the range of *Carinodens belgicus* to approximately 25° S paleolatitude, mirroring similar occurrences from North Africa and the Middle East.

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Note added in proof

This manuscript was submitted prior to publication of Konishi et al. (2011) in which multiple specimens of *Prognathodon overtoni* were described. For our comparisons, we used a specimen of *P. overtoni* from Tennessee (PPM 1990.2.4) which possesses a somewhat fluted tooth morphology, thus leading us to exclude that species. The tooth enamel is smooth in the specimens described by Konishi et al. (2011), consistent with Russell's comments (Russell, 1967 p.165). In any event, the teeth of *P. overtoni* as described by Konishi et al (2011) are relatively shorter and more robust than the tooth preserved with the specimen described here, and thus do not affect our conclusions.