Chapter 2 – New mosasaur material from the Maastrichtian of Angola, with notes on the phylogeny, distribution and palaeoecology of the genus *Prognathodon*

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Introduction

In the present note, we offer a preliminary description of a new, globidensine mosasaur from Namibe Province, Angola. Along with the description of the new material, we present an overview of the mosasaur fauna of the area, and discuss the geographic, temporal and ecological distribution of globidensine mosasaurs.

No fossil vertebrate collecting has been conducted in Angola since the 1960s (Antunes, 1964). In May 2005, two of us (O.M. and L.L.J.) performed a short field reconnaissance in the Angolan provinces of Namibe and Bengo, from where De Carvalho (1961) and Antunes (1964) reported rich Cretaceous faunas, including mosasaurs, fishes, turtles, plesiosaurs and other marine taxa. Material collected during the 2005 field trip includes the two partial mosasaur skulls from the Namibe province here described.

All material collected during this reconnaissance trip will be housed at the Museu Geológico da Universidade Agostinho Neto (MGUAN) in Luanda; however, some specimens, including those described here, have temporarily been transferred to Museu da Lourinhã, Portugal (ML), for preparation, study and description. The material is currently registered under a provisory ML/MGUAN accession number. All specimens will be returned to Angola after study.

Geographic and stratigraphic setting

Upper Cretaceous marine deposits in Africa are largely eustatically controlled and record the Cenomanian-Turonian and Maastrichtian transgressive sequences (Ala & Selley, 1997; Marton et al., 2000). Mosasaurs have been reported from many of these deposits along the northern margin within a northeast-southwest striking epicontinental seaway and along the west coast of Africa reaching as far south as the Republic of South Africa; however, descriptions and identifications have been based largely on fragmentary or poorly preserved material collected during expeditions focused primarily on geological mapping and stratigraphy (e.g., Azzaroli et al., 1972; Lingham-Soliar, 1991, 1994). In recent years, new mosasauroid specimens from Morocco
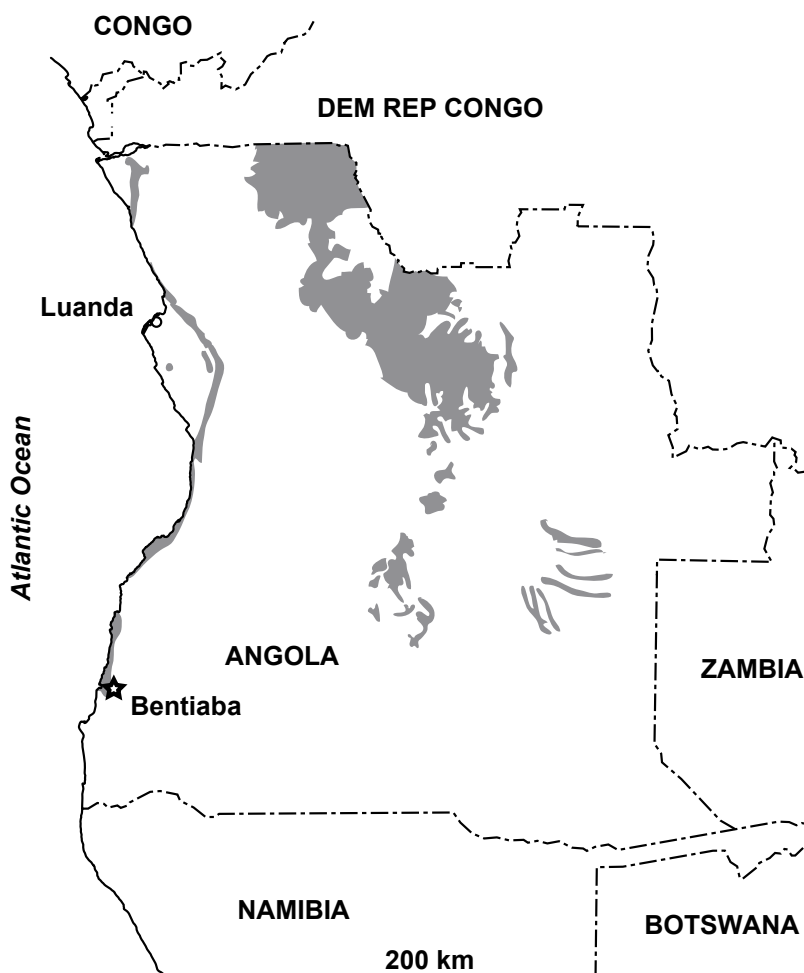

Figure 1. *Provenance of ML/MGUAN05 and ML/MGUAN07, near Bentiaba, Namibe province, southern Angola.*
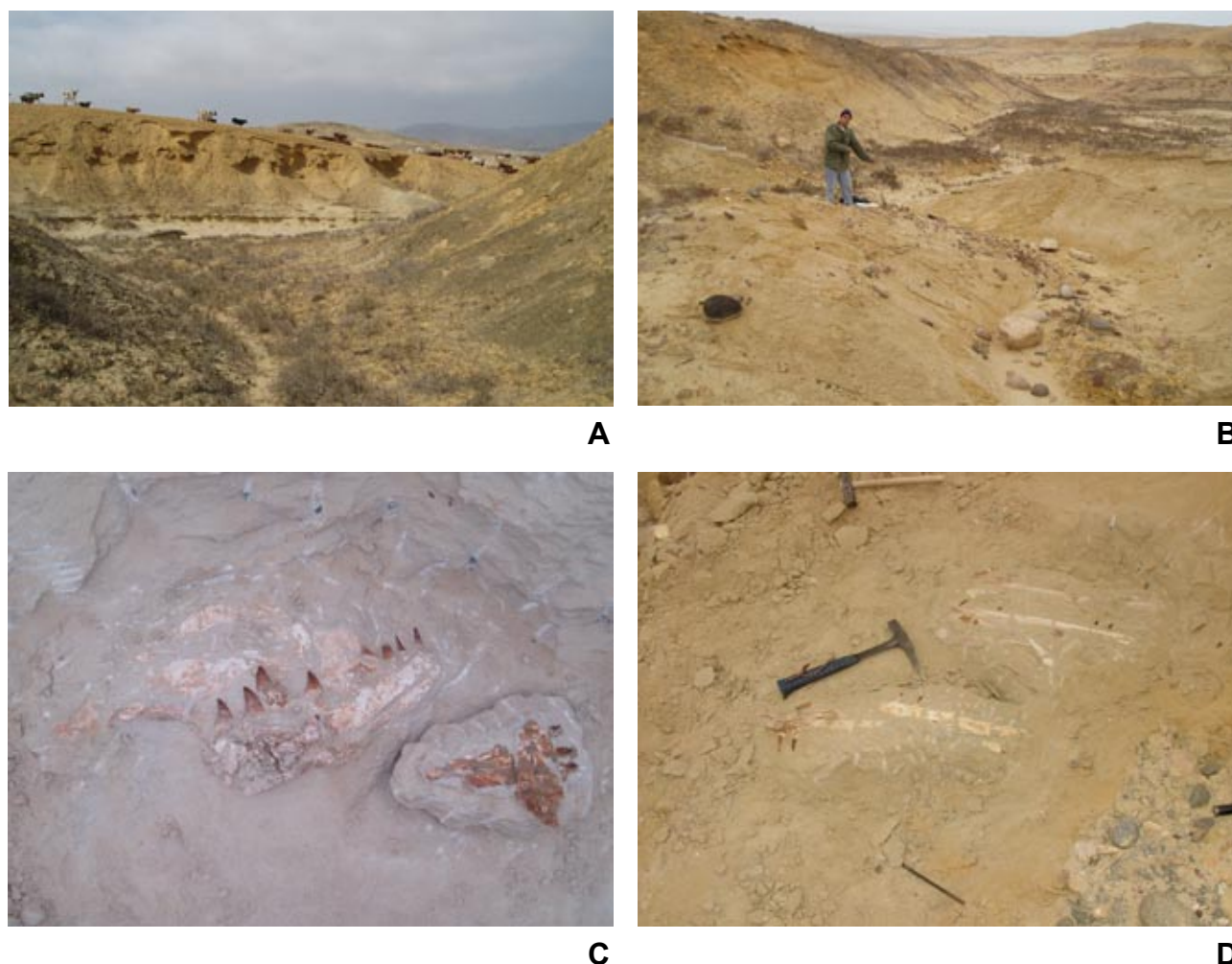
Figure 2. A, B: *Bentiaba sites 05 and 07, respectively;* **C, D:** *ML/MGUAN05 and ML/MGUAN07 specimens in situ.*

(e.g., Bardet et al., 2003, 2004, 2005), Syria (Bardet et al., 2000) and Israel (Polcyn et al., 1999, 2003; Christiansen & Bonde, 2002; Haber & Polcyn, 2005), have added to our knowledge of African and eastern Tethyan mosasaurs, but these specimens are from strata that were deposited in a palaeo-equatorial region along the northern and northeastern Gondwanan margins during the Cenomanian-Turonian and Maastrichtian stages (Gealey 1988; Schettino & Scotese, 2002).

The rocks in which the new material was found were deposited in a nearshore setting on the west African continental margin bordering the South Atlantic Ocean at approximately 30° S palaeo-latitude (e.g. Patzkowski et al., 1991). The fossils were found near the village of Bentiaba, Namibe Province, southwestern Angola (Figure 1). The geological framework of Namibe (formerly Moçâmedes) is given by de Carvalho (1961), who recorded and illustrated the presence of mosasaur teeth for the first time. Fieldwork in the early 1960s confirmed the presence of a rich and diverse Maastrichtian fauna at outcrops on the right bank of the Bentiaba River, near the village of Bentiaba (formerly São Nicolau); for example at the Bentiaba-1[A] locality, as referenced by Antunes (1964, fig. 9), and as earlier described by de Carvalho (1961), yielding, amongst other things "peixes, mosasáurios – incluindo *Globidens* – e moluscos"

(Antunes, 1964, p. 91). The recent reconnaissance visit to the area by two of us (O.M., L.L.J.) has yielded many shark teeth, plesiosaur vertebrae, a few plesiosaur teeth, an isolated aff. *Globidens* tooth and other (isolated) mosasaur teeth and bones, in addition to the specimens described here.

Based on isolated teeth, as summarised by Antunes (1964), the Maastrichtian mosasaur fauna of Angola comprises at least four taxa: a *Mosasaurus*-like taxon (Antunes, 1964, pl. XXVI, fig. 1), a large *Prognathodon*-like taxon (ibid., pl. XXVI, fig. 4), a plioplatecarpine (ibid., pl. XXVI, fig. 11), and a *Globidens*-like taxon (ibid., pl. XXVI, figs. 12-14). The shark fauna of the area has recently been described by Antunes & Cappetta (2002).

New material

Two incomplete mosasaur skulls have been collected at the Bentiaba River site (Figure 2). The first specimen to be discovered, a rather incomplete mosasaur skull (ML/MGUAN05) was collected by O.M. and L.L.J. on May 20, 2005 (Figure 2C); a preliminary excavation suggested that the remainder of the skeleton had probably eroded away already. Co-ordinates of the site are on file at the participating institutions. During a second visit to the area, on May 22, 2005, a second, more complete skull (ML/MGUAN07) was collected by O.M. (Figures 2D). Due to time constraints,
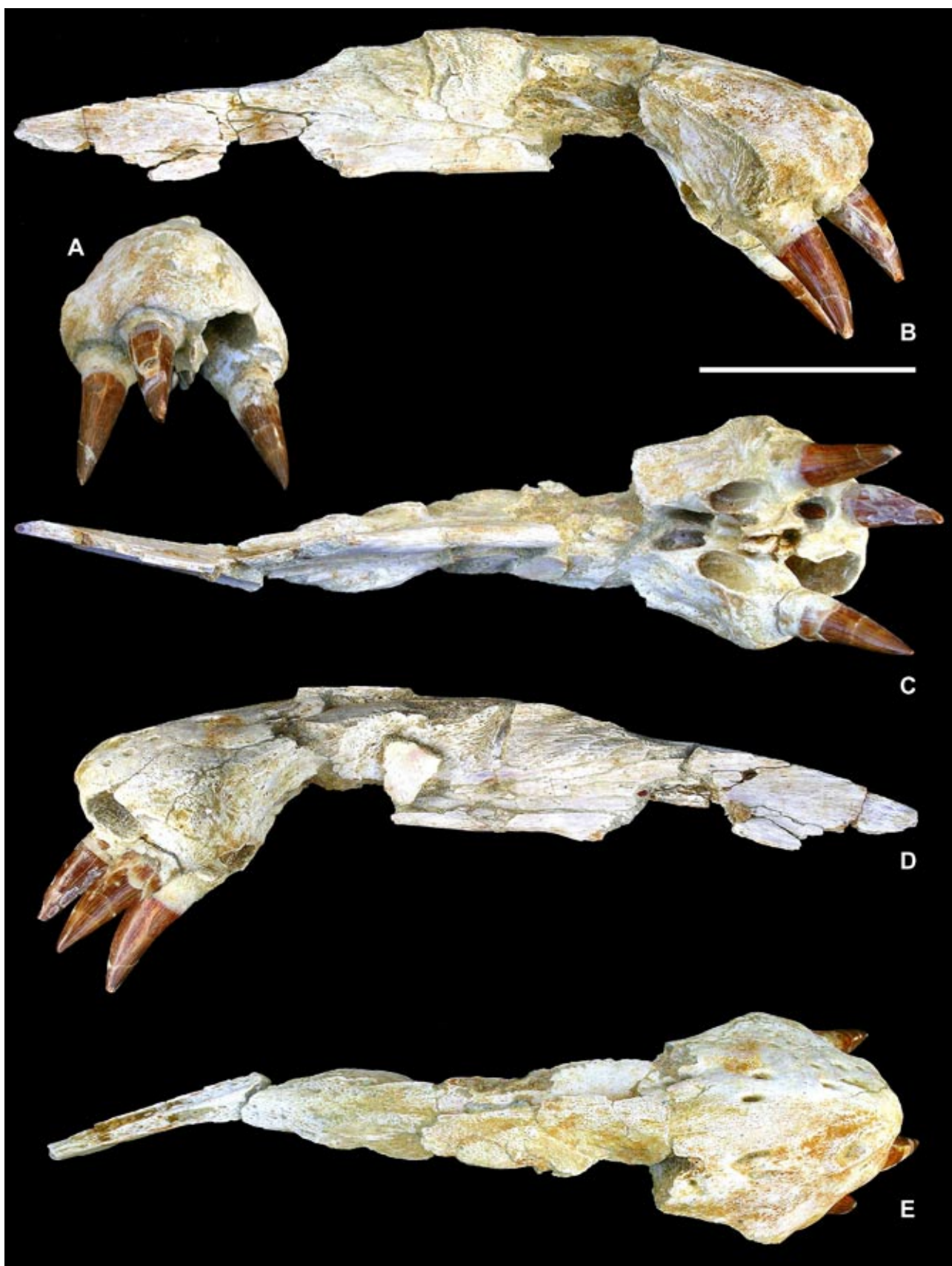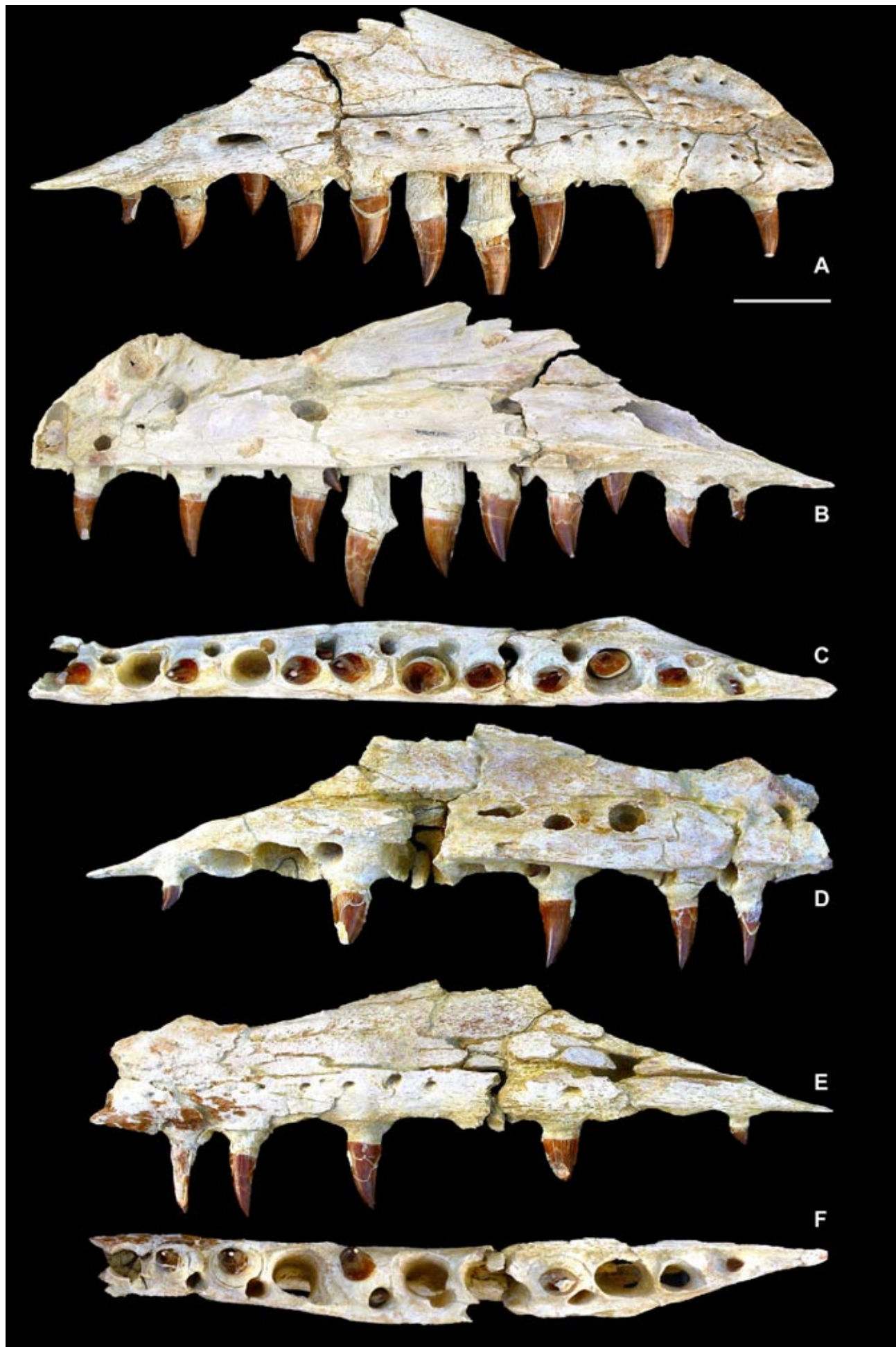
Figure 3. Prognathodon sp., *ML/MGUAN07. Premaxilla in* **A:** *anterior,* **B:** *right lateral,* **C:** *ventral,* **D:** *left lateral and* **E:** *dorsal view. Scale bar equals 5 cm.*

only part of the skull was recovered. Both specimens have been prepared by staff members (O.M., Alexandra Tomás) and expert volunteers at the Lourinhã dinosaur museum in Portugal, during the summer of 2005.

Description: ML/MGUAN07

Premaxilla

The premaxilla (Figure 3) is almost complete, its maximum anterior width being 53 mm; the overhang of the predental rostrum is minimal (5 mm). In cross-section, the premaxilla is almost triangular ('inverted' triangle as in Bell, 1997: apex ventral) at the anterior end of the internarial bar. The internarial bar (in dorsal view) reaches its maximum lateral constriction dorsal to the fifth maxillary tooth position. The dorsal surface of the internarial bar tapers slightly, featuring a central ridge around the fourth and fifth maxillary tooth position; its dorsal surface becomes slightly wider posteriorly, making the cross-section of the internarial bar at that point a little more triangular again. The maxillary-premaxillary suture extends almost to the fourth maxillary tooth position. In lateral view, the maxillary-premaxillary suture gently curves posteriorly (as is typical of mosasaurines), but here it is exceptionally long, reflecting a tall maxilla in lateral aspect. In dorsal view, the anteriormost portion of the premaxilla is a near-equidimensional triangle with a slightly flattened apex.

Premaxillary dentition

The dentition is clearly prognate – the anterior teeth protrude at an angle of almost 45 degrees with respect to the horizontal. This is a value similar to that seen in *Prognathodon solvayi* Dollo, 1889 (compare Lingham-Soliar & Nolf, 1990). Teeth are relatively slender; their aspect ratio in lateral view is about 12:24 mm (first) and 12:26 mm (second tooth). The teeth have minimal recurvature, and show a weak, unserrated anterior carina; posteriorly no carinae are present.

Maxillae

The right maxilla (Figure 4A-C) is almost complete; the left maxilla (Figure 4D-F) lacks the anterior portion. The dorsal rim in both maxillae is damaged, and in parts even missing; the ventral margin is straight, and more than 90 mm in height at its tallest point measured from the ventral margin. The total length of the right maxilla is 414 mm; with the premaxilla attached to this, the total length would amount to 440 mm.

Maxillary dentition

The maxilla would have held 13 teeth. The teeth are bicarinate, except for the four anteriormost ones which only have a pronounced anterior carina. The carinae are unserrated. The enamel surface is smooth. The roots can be at least as tall as the crown, as observed in the seventh position. The base of the posteriormost tooth crowns is inflated.

Dentary

The right dentary (Figure 5) is almost complete; of the left dentary only a fragment remains with the anteriormost seven alveoli, and a separate, more posterior fragment preserving teeth #8, 9 and 11. The dorsal surface of the dentary is only very slightly concave, less so when compared to most other species of *Prognathodon*. Underneath the anteriormost two tooth positions, at least 10 mental foramina can be counted (in each dentary). At the tallest point, at tooth position #14, the dentary is at least 94 mm in height. The splenial probably extended anteriorly to between the fourth and fifth alveolus. The splenial itself is not preserved, apart from a possible splinter of bone preserved in the Meckelian canal. The Meckelian canal has a marked constriction near the seventh tooth position.

Dentary dentition

The dentary would have held 15 teeth. The anteriormost tooth is ever so slightly prognate, but much less so than in the premaxilla. Replacement teeth erupt from subdental crypts, medioposteriorly to 'active' teeth. The teeth are unserrated, as in the maxilla. The enamel surface is smooth. Posteriorly from the sixth dentary tooth the teeth are bicarinate; the anteriormost five teeth show anterior carinae only. The teeth are relatively slender; the aspect ratio of the crowns in lateral view is 13:28 mm and 14:32 mm (5th and 4th dentary tooth, respectively). The basal inflation of the teeth becomes more pronounced from the eighth or ninth tooth and further posteriorly, reaching an aspect ratio in lateral view of about 1:1 at the posteriormost tooth. The posterior recurvature of teeth increases posteriorly along the dentary.

Jugal

The anteriormost 95 mm of the right jugal is preserved; it articulates well with maxilla. There is no sign of the ectopterygoid meeting the maxilla, nor of articulation of the ectopterygoid with the preserved portion, so the ectopterygoid was more posteriorly placed.

Description: ML/MGUAN05

Although ML/MGUAN05 is much less complete, we confidently attribute it to the same species, based on the striking similarities (even in size) between the dentaries. As this specimen also has an associated, partially preserved, semi-articulated posterior mandibular unit, a description is added here.

Mandibular material

The anterior mandibular material consists of a left dentary with the anteriormost six alveoli preserved (Figure 6F), with the anterior three alveoli preserving teeth. Again, the orientation of the anteriormost two teeth is prognate, slightly more so than in the right dentary of ML/MGUAN07, most likely because this tooth is slightly better developed. A separate block of matrix holds the considerably weathered remains of the left dentary teeth 7 through 10 (Figure 6E). The right dentary is preserved with the anteriormost four alveoli preserved, and the anteriormost three alveoli still hold teeth.

Figure 4 (opposite page). Prognathodon *sp., ML/MGUAN07. Right maxilla in* **A:** *lateral,* **B:** *medial and* **C:** *occlusal view. Left maxilla in* **D:** *medial,* **E:** *lateral and* **F:** *occlusal view. Scale bar equals 5 cm.*

Figure 5. Prognathodon sp., *ML/MGUAN07. Right dentary in* **A:** *medial,* **B:** *lateral and* **C:** *occlusal view. Scale bar equals 5 cm.*

Posterior mandibular unit

The right coronoid is preserved (Figure 6A, B); it is 175 mm long, 33 mm wide, and approximately 112 mm in height. The posteromedial wing contacted the angular medially high on the surangular coronoid ascending buttress. The anteromedial process is not deep and likely exposed the surangular in medial view. The surangular is preserved for the largest part and displays a steeply ascending coronoid buttress (Figure 6C, D); it measures 173 mm in length. The articular suture descends from about the mid-glenoid laterally and gently curves anteriorly.

Cladistic analysis

Characters have been scored following the phylogenetic analysis in Chapter 1, largely based on Bell & Polcyn (2005), with the data on the Angolan specimen added (Table 1).

The Angolan specimen possesses a number of mosasaurine characters, and therefore only members of Mosasaurinae covered in Bell & Polcyn (2005) were used for this analysis; *Clidastes* was used as an outgroup. Of other published data on *Prognathodon*, those for *P. currii* (Christiansen & Bonde 2002), are not included here, but rather the data set as scored by the first author (A.S.) on the holotype at Ber Sheva, Israel; details on differences in interpretation on this particular specimen are discussed in Chapter 1. *Prognathodon rapax* material was not available for study, and has been omitted from the analysis presented here. Character 34 in the matrix of Bell (1997) is swapped back to the intended order (as mentioned in Christiansen & Bonde,

2002 and Bell & Polcyn, 2005).

The analysis was performed using PAUP* 4.0 (Swofford, 2000), and tree topologies and character distribution were subsequently studied using MacClade (Maddison & Maddison, 2000). All characters were equally weighted and unordered. The analysis was performed using heuristic search mode, as in Bell (1997), with the DELTRAN character optimisation option selected. Only 26 of the 144 characters could be scored in the present specimen. The analysis, limited to 90 cranial characters only, yielded four equally parsimonious trees with a tree length of 109 steps. Consistency and Retention Index values were 0,606 and 0,779, respectively. Figure 7 illustrates a hypothesis of the relationships of the Angola taxon. The differences between the four equally parsimonious trees are limited to minor instabilities in *Clidastes* (as in Bell & Polcyn, p. 189). In Figure 7, the different species of the genera *Clidastes*, *Mosasaurus* and *Plotosaurus* have been collapsed into one branch each for clarity.

Discussion

Phylogenetic analysis

The preliminary cladistic analysis of the new Angolan taxon confirms that assignment to the genus *Prognathodon* would be appropriate. In the analysis, the taxon occupies a basal position between *Globidens* and *Prognathodon* (Figure 7). Characters supporting inclusion in *Prognathodon* are, amongst other features, (1) the basal inflation of teeth and
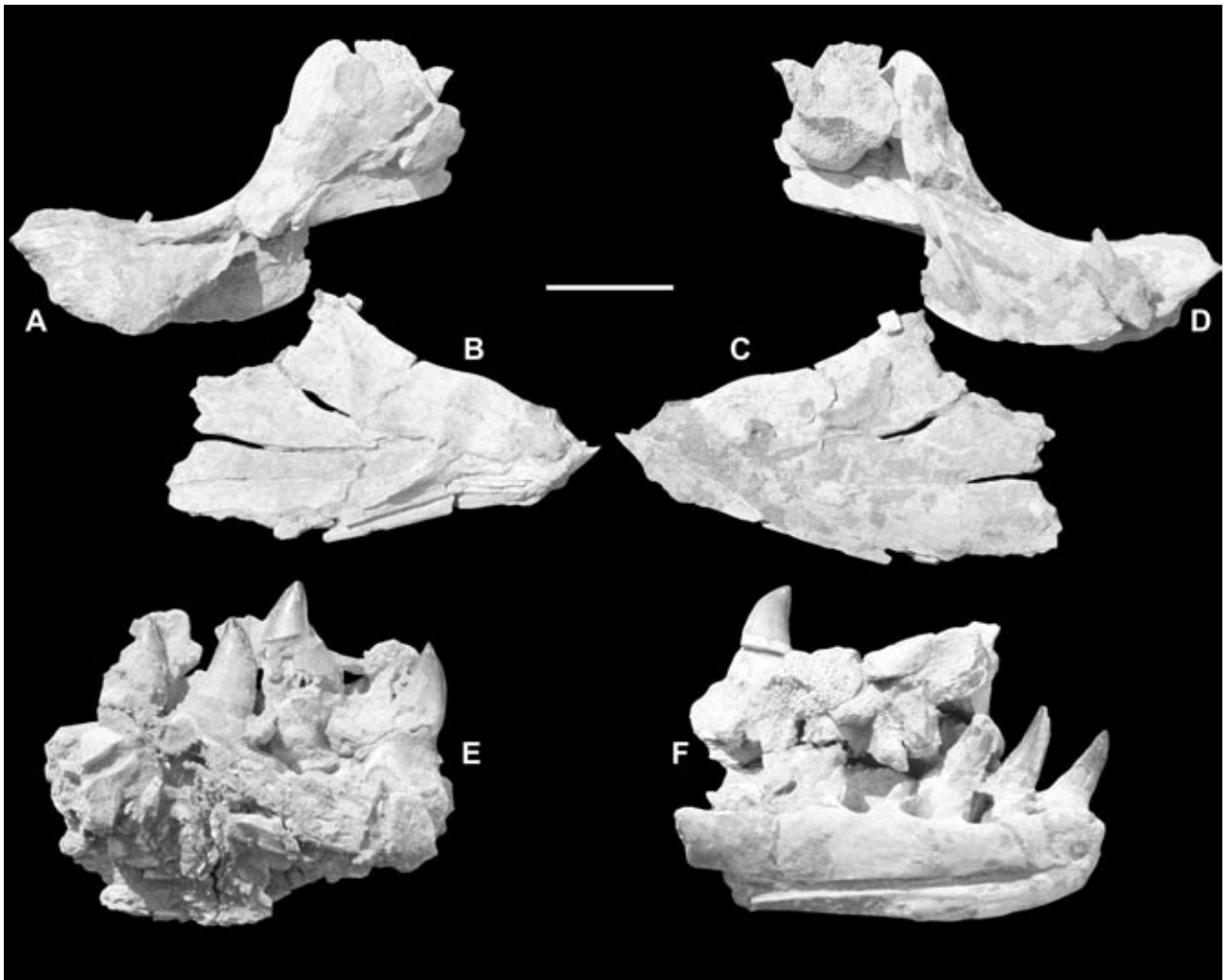
Figure 6. Prognathodon *sp., ML/MGUAN05.* **A, D:** *Right coronoid in lateral and medial view;* **B, C:** *Angular in lateral and medial view;* **E, F:** *left dentary fragments, medial view. Scale bar equals 5 cm.*

(2) the low maxillary and dentary tooth count, but also – although not as such included in the character matrix by Bell (1997), Bell & Polcyn (2005) nor in Chapter 1 – (3) the prognate condition of the anteriormost dentition, and (4) the (slight) concave recurvature of the dorsal margin of the dentary. Although (5) the smooth-surfaced dentition shows some very faint 'anastomosing' ridges, this character is not as well developed as in most other species of *Prognathodon*. Autapomophies of this new taxon include (1) gracile tooth form and (2) a more clearly defined dorsal keel of the internarial bar. Comparison with other *Prognathodon* material suggests that the material from Bentiaba represents a new species of this genus; however, at this stage, we prefer not to name it formally pending further excavations planned.

It should be noted, that the concave curvature in the dorsal margin of the dentary is much less pronounced in the Angolan specimen than in any other species of *Prognathodon*. Only *P. waiparaensis* has a straighter dorsal dentary margin, but upon inspection of the holotype (C.M. zfr 108) at the Canterbury Museum in Christchurch, New Zealand, it seems this is more likely an artifact of preparation and subsequent restoration rather than a primary anatomical feature,

contrary to the reconstruction of Welles & Gregg (1971).
The teeth, particularly the anteriormost ones, are relatively slender compared to most other species of *Prognathodon* (with the exception of *P. solvayi*) – and also relatively slender compared to most other mosasaurs for that matter. The teeth figured by Antunes (1964, pl. XXVI, figs 1-3) do not exhibit a basal swelling or constriction of the root, yet do display facetting, and are therefore likely not assignable to the taxon described here.

Habitat partitioning and dentition

The Maastrichtian mosasaur fauna of Angola includes to date at least five taxa: *Globidens*, a large *Prognathodon*, *Plioplatecarpus*, an indeterminate large mosasaurine taxon (Antunes 1964), and the new *Prognathodon*-like taxon described here.

Habitat partitioning has been discussed previously in terms of prey preference based on tooth form (Massare 1987), or partitioning of the water column based on histological analysis of bone samples (Sheldon 1997). We cannot currently test the water column partitioning hypothesis because prior collecting has yielded mainly isolated teeth. However, we do have sufficient tooth samples to place them

Angola specimens ML/MGUAN05 & -07
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10100 1???? ????? ????? ????? ????? ????4 0???? 1???? ?????
????? ????? ????? ??200 2??1? 1?110 ??100 01201
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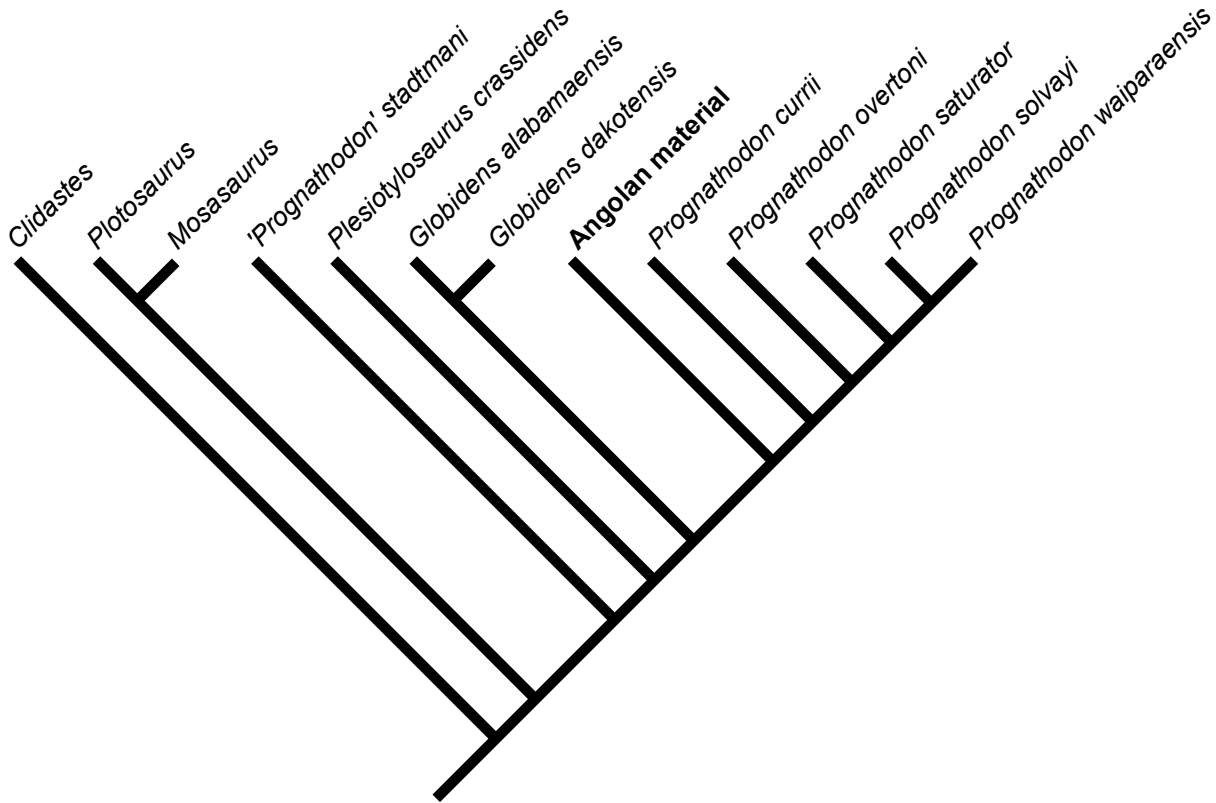**Table 1.** *Phylogenetic data, as added to the analysis in Chapter 1.*

Figure 7. *Phylogenetic relationships of the new Angolan* Prognathodon, *following the phylogenetic analysis in Chapter 1 and Bell & Polcyn (2005). Species in the genera* Clidastes, Mosasaurus *and* Plotosaurus *have been collapsed into one branch each for clarity.*

within Massare's scheme, and to compare assemblages from the Maastrichtian of The Netherlands with the Angolan ones.

One of the most striking characteristics of globidensine mosasaurs compared to other mosasaurs is the pronounced degree of heterodonty, both in terms of shape as well as size (Lingham-Soliar & Nolf, 1990; Schulp et al., 2004; Schulp, 2005). Both tooth morphology and wear patterns can help evaluate assumptions on possible feeding preferences and feeding behaviour of mosasaurs. Massare (1987) recognised seven different feeding guilds, based on tooth morphology. All seven guilds occupy a limited area in a triangular diagram, where each corner represents an end member in tooth shape and function: (1) slender, pointed, piercing teeth; (2) blunter, robust and more suited for crushing; and (3) sharp, robust, cutting teeth. An attempt to plot a selection of mosasaurs (the Angolan specimens, all species from the Maastrichtian type area, and a selection of globidensine mosasaurs known from elsewhere) into the diagram illustrated by Massare (1987, figs. 14-16) is presented in Figure 8.

The position of the teeth in the diagram is approximate, as no exact, quantitative criteria were provided by Massare; hence their position was determined mainly by comparing teeth with those of other mosasaurs already plotted by Massare. Particularly in globidensine mosasaurs revealing a pronounced heterodont dentition, this is a somewhat subjective issue; however, the essence (and value) of the diagram lies in the *relative* position of different taxa.

Carinodens is placed slightly to the right of *Globidens*, as the teeth are somewhat more pointed, laterally flattened, and show vestiges of a cutting edge when compared to *Globidens*, but still falls within the 'Crush' guild (compare Chapter 8). The massive, thick, pointed teeth with a blunt apex of *Prognathodon saturator* fall between the 'Cut' and 'Crush' guild, which brings them somewhat closer to the 'General' guild. The much sharper teeth of *Plioplatecarpus marshi*, *Liodon sectorius*, *Mosasaurus lemonnieri* and *Mosasaurus hoffmanni* all fall within the 'Cut' guild, with *Liodon* and *Plioplatecarpus* approaching the 'Pierce II' guild. *Prognathodon currii* has a blunter, 'crunching/crushing' dentition compared to *Prognathodon saturator*, but the teeth are still more pointed than those of *Globidens*. The
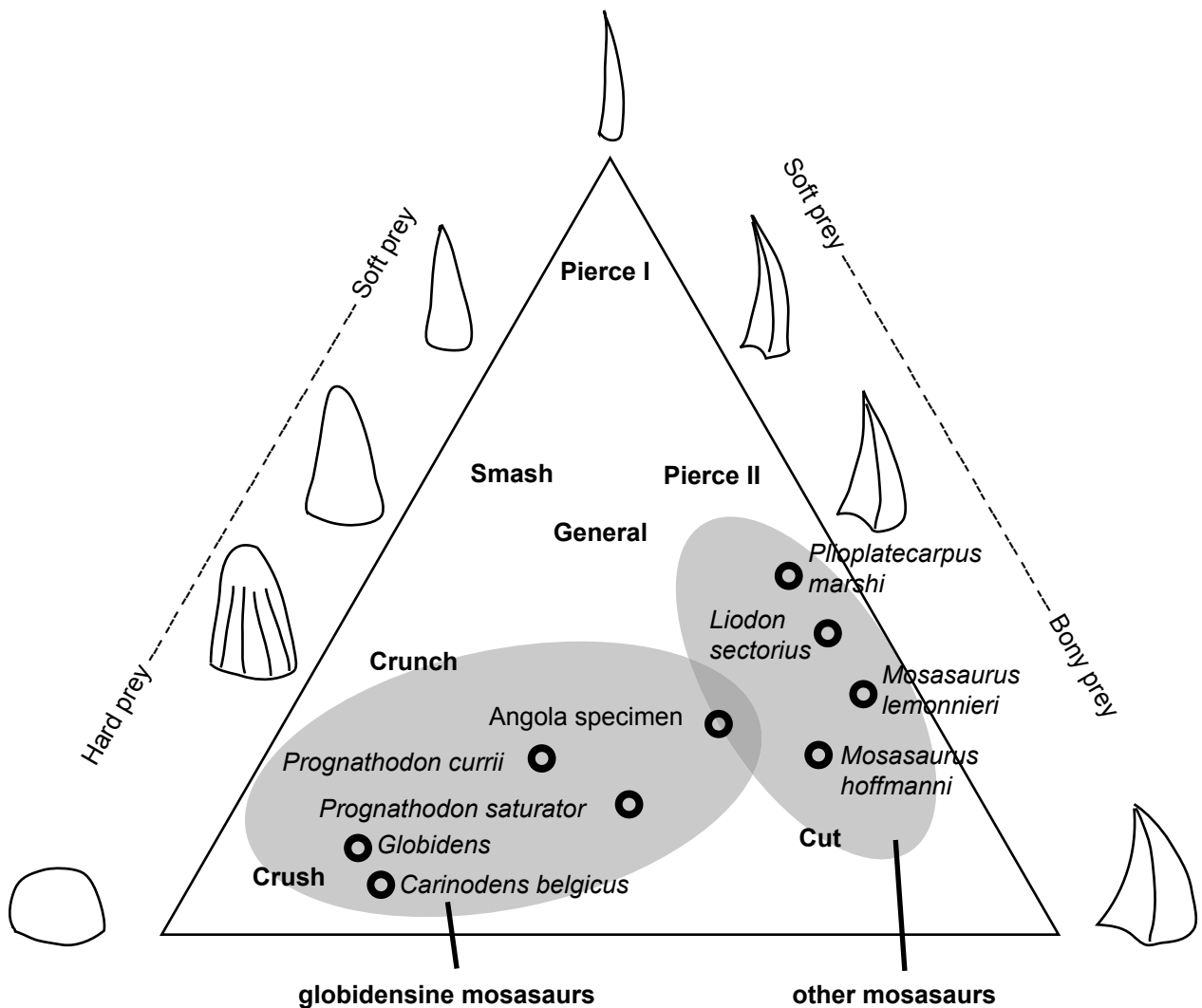
Figure 8. *Feeding guilds presumably occupied by globidensine mosasaurs, based on dental morphology (modified after Massare, 1987).*

Angolan material adds a medium-sized, relatively slender species to this list, with a dentition slightly more specialised in cutting and piercing softer food, expanding the range of tooth morphologies encountered within globidensine mosasaurs even further.

Following the functional constraints placed by each and every type of tooth morphology, this model allows for assumptions to be made about the feeding guild and ecological niche occupied by each taxon. The diagram illustrates that towards the end of the Cretaceous, globidensine mosasaurs as a group were equipped with a wide repertoire of feeding habits.

The applicability of Massare's prey preference model is only one component of a multivariate approach to resolve questions on habitat partitioning. Other factors that need to be considered are size, position in the water column, and temporal factors such as day/night feeding cycles and seasonal habitat segregation. Because some of these factors can be difficult to observe in the fossil record, only the size ranges will be discussed here.

Size range of globidensine mosasaurs

If we apply the measurements of the present specimens to the discussion in Christiansen & Bonde (2002, p. 639), assuming that maxillary length (414 mm) equals slightly less than half the skull length, and that the total length of the animal is in the order of eight times the skull length, a reasonable estimate would be that the present specimens would have reached a total length of just over seven metres, implying a medium-sized *Prognathodon*. The smallest species of *Prognathodon* is *P. solvayi*, at less than five metres (Dollo, 1889); *P. currii* would arguably have been the largest, at approximately 11 metres (Christiansen & Bonde, 2002). Considering that the smallest globidensine mosasaur, the c. 2,5 m long *Carinodens belgicus*, has a body mass almost 100 times less than the largest globidensine *Prognathodon currii* (compare Chapter 3 and Christiansen & Bonde, 2002), it is safe to say, based on differences in body mass alone, that this group diversified widely enough to occupy a wide variety of niches successfully.
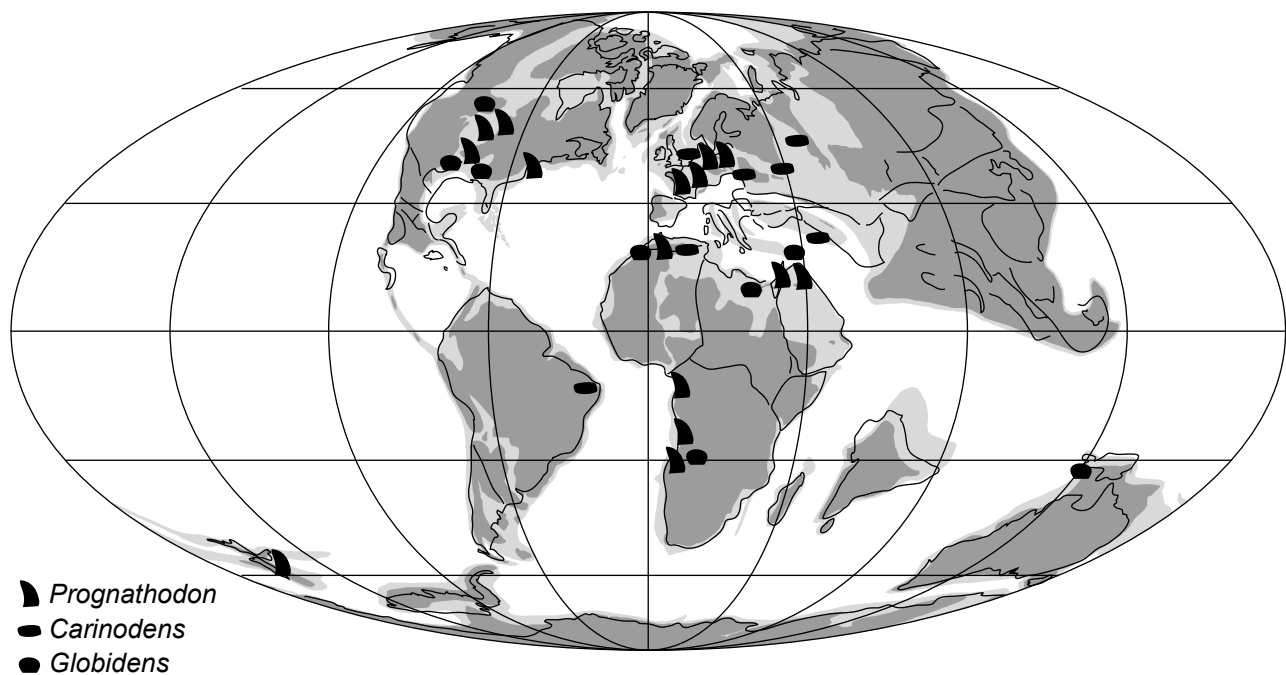
Figure 9. *Distribution of globidensine mosasaurs. Palaeogeography after Patzkowski et al. (1991).*

Distribution of globidensine mosasaurs

The clade comprising *Prognathodon*, *Globidens* and *Carinodens* (see Chapter 3) shows a worldwide distribution. Here an attempt is made to compile a list of all globidensine mosasaurs, and graphically present their distribution on a palaeogeographical map of the Maastrichtian (Table 2, Figure 9). Most occurrences are Maastrichtian or late Campanian (ignoring material labelled with less precision). All occurrences seem to be distributed over a wide band from 50° north to 60° south palaeolatitude. The worldwide distribution of globidensine mosasaurs shows that not only did they successfully diversify, but also spread and flourished towards the end of the Cretaceous.

Lingham-Soliar (1991) introduced the genus *Igdamanosaurus* on the basis of a poorly preserved right dentary (BMNH R11898), and referred *Globidens aegyptiacus* Zdansky 1935 to that genus as well. The preserved tooth crowns in BMNH R11898 are dome shaped, do not appear to have a constricted base and are covered with fine parallel ribbing or striae (see Lingham-Soliar, 1991, fig. 5). The presence of vertical striae led him to refer the new genus to the subfamily Plioplaecarpinae. However, in addition to a wrinkled enamel surface, raised ridges and striae are variably seen on *Globidens* teeth, and thus this character alone does not warrant placement of *Igdamanosaurus* in Plioplatecarpinae. Lingham-Soliar (1991, fig. 5A) shows that the anterior alveoli are smaller than the more posterior, with a marked increase in size at position eight/nine, which suggests that some level of heterodonty is present (see Chapter 8 on heterodonty in globidensine mosasaurs). Additionally, new material assignable to the genera *Prognathodon* and *Globidens* (Christiansen and Bonde, 2002; Bardet et al., 2005) demonstrates the range of variation in globidensine mosasaur dentition. Given the robust nature of the dentary, the apparent heterodonty, and dome-shaped teeth in

Igdamanosaurus it more likely represents a member of the tribe Globidensini (sensu Russell, 1967) than of the subfamily Plioplatecaprinae. In Table 2, *Igdamanosaurus* is listed with *Globidens*.

Bite marks / infection pits
ML/MGUAN07
The ventral surface of the right maxilla shows a few dimples which seem to have been the result of an infection. The articulation surface with the premaxilla is also damaged. The lateral surface of the right dentary (Figure 5) has two infectious lesions at the fifth and ninth tooth position. The right antero-lateral side of the premaxilla also shows the traces of an infected, and subsequently healed, bone lesion.

Conclusions
By Maastrichtian times, globidensine mosasaurs had diversified into an amazing variety of tooth morphologies. On one end of the spectrum, Christiansen & Bonde (2002) even went as far as to consider *P. currii* the 'T. rex of the seas', a comparison certainly validated by the sheer size of the skull and numerous aspects of its dental morphology. The "rather blunt apices [of *P. currii*] would also imply greater resistance to mechanical damage than the more pointed tooth apices common in [other] mosasaurs", they stated (Christiansen & Bonde, 2002, p. 639).

It is worth noting that in the subdivision as proposed by Massare (1987), globidensine mosasaurs occupy a wide range of niches not occupied by any other mosasaur (Figure 8). Interestingly enough, the new mosasaur from Angola expands the area of globidensine mosasaurs in the diagram even further into the playground of other mosasaurs. Whether the new Angolan specimens represent a basal taxon that retained feeding habits of its presumed ancestors, or

Carinodens belgicus	Dollo, 1913; Schulp et al., 2004	Maastrichtian	Netherlands+Belgium
Carinodens belgicus	Tzankov, 1939	Maastrichtian	Bulgaria
Carinodens belgicus	Arambourg, 1952; Schulp et al., 2004	Maastrichtian	Morocco
Carinodens belgicus	Price, 1957	Maastrichtian	Brazil
Carinodens belgicus	Schulp et al., *in press*	Maastrichtian	Russia, Ukraine
Globidens sp. (*Carinodens*?)	Mustafa & Zalmout, 2001	Maastrichtian	Jordan
Globidens alabamaensis	Gilmore, 1912	Campanian	USA
Globidens dakotensis	Dollo, 1924; Jagt, 2005	Campanian	Belgium
Globidens dakotensis	Russell, 1975	Late Cretaceous	USA
Globidens phosphaticus	Bardet et al., 2005	Maastrichtian	Morocco
Globidens timorensis	von Huene, 1935	Late Cretaceous	Indonesia ('Timor')
Globidens sp.	Zdansky, 1935, Leonardi & Malaroda, 1946	Late Cretaceous	Egypt
Globidens sp.	Avnimelech, 1949; Bardet et al., 2002	Campanian	Jordan
Globidens sp.	Raab, 1963	Late Campanian	Israel
Globidens sp.	Antunes, 1964	Maastrichtian	Angola
G. sp. ('*Igdamanosaurus*')	Lingham-Soliar, 1991	Late Cretaceous	Niger
Globidens sp.	Martin & Fox, 2004	Campanian	USA
Globidens sp.	Bardet et al., 2000	Late Cretaceous	Syria
Globidens sp.	Polcyn & Bell, 2005	Campanian	USA
Prognathodon saturator	Dortangs et al., 2002	Maastrichtian	Netherlands
Prognathodon crassartus	Cope, 1872	Campanian	USA
Prognathodon currii	Christiansen & Bonde, 2002	Late Campanian	Israel
Prognathodon currii	Bardet et al., 2005	Maastrichtian	Morocco
Prognathodon waiparaensis	Welles & Gregg, 1971	Late Cretaceous	New Zealand
Prognathodon solvayi	Dollo, 1889	Early Maastrichtian	Belgium
Prognathodon giganteus	Dollo, 1904	Camp. / Maastr.	Belgium
Prognathodon giganteus	Bardet et al., 1997	late Early Campanian	France
Prognathodon giganteus	Bardet et al., 2000	Late Cretaceous	Syria
Prognathodon giganteus	Bardet et al., 2002	Maastrichtian	Jordan
Prognathodon overtoni	Williston, 1897	Maastrichtian	SD, USA
Prognathodon rapax	Hay, 1902	Maastrichtian	NJ, USA
Prognathodon sp.	Machalski et al., 2003	Late Campanian	Poland
Prognathodon sp.	Lingham-Soliar, 1994	Maastrichtian	D.R. Congo ('Zaïre')
Prognathodon sp.	Antunes, 1964	Maastrichtian	Angola
Prognathodon sp.	(This contribution)	Maastrichtian	Angola
Prognathodon stadtmani *)	Kass, 1999	Early Campanian	USA

*) most likely *not* a *Prognathodon;* see Chapter 1.

Table 2. *Overview of globidensine mosasaur occurrences.*

if it represents a further specialisation of globidensine mosasaurs homing in on the dominance of other mosasaurs on the right of the diagram remains to be seen.

The Maastrichtian strata around Bentiaba have proved to yield a rich and diverse mosasaur fauna. A larger-scale, more intensive, long-term excavation project is much needed, and promises to yield a large amount of additional material – amongst others possibly the remainder of the skeleton of ML/MGUAN07.

The diversity of globidensine mosasaurs is greater than previously thought, with five new species having been described in just a few years' time (Kass, 1999, Dortangs et al., 2002, Christiansen & Bonde, 2002; Bardet et al., 2005 and Polcyn & Bell, 2005, although the 'prognathodont' affinities of *P. stadtmani* Kass, 1999 are questionable; see Chapter 1). The specimens described in the present contribution, a possibly new *Prognathodon*-like species from Angola, add yet another taxon to this list. The size and tooth morphology of the new taxon suggests it occupied another spot in the wide range of feeding guilds claimed by globidensine mosasaurs during the latest part of the Cretaceous. The pronounced heterodonty and wide range of variation in tooth morphology in general have doubtlessly played an important role in their success.

Although inconclusive, the assemblage from the Maastrichtian of Angola is comparable to that found in northern Europe, in terms of diversity and habitat partitioning, but not necessarily at the level of precise taxonomic composition. Additionally, the niche of a small durophagous mosasaur is not yet represented in the Angolan fossil record.