

The North African Mosasaur *Globidens phosphaticus* from the Maastrichtian of Angola

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(Received 2 September 2009; final version received 23 December 2009)

New mosasaur fossils from Maastrichtian beds at Bentiaba, Angola, representing elements of the skull and postcranial axial skeleton from two individuals of the durophagous genus *Globidens*, are reported. Based on dental morphology, specifically the inflated posterior surface and vertical sulci, the Bentiaba specimens are identified as *Globidens phosphaticus*, a species defined by characters of a composite dentition from the Maastrichtian of Morocco. Comparisons indicate that *G. phosphaticus* is most closely related to *G. schurmanni*, from the late Campanian of South Dakota, the youngest north American *Globidens* species at about 72.5 Ma. The morphology of the premaxilla and its relationship with the maxillae is unique among mosasaurs, and supports the taxonomic validity of *G. phosphaticus*. In contrast with earlier species of the genus, *G. phosphaticus* is currently known from north and west Africa, the Middle East and the central eastern margin of South America, suggesting it may have been restricted to the Maastrichtian tropical zone as previously hypothesised.

Keywords: durophagous; *Globidens*; mosasaur; biogeography; Angola

Introduction

Mosasaurid squamates possess a range of tooth morphologies, but most can be generally described as some combination of a piercing or sectorial type; however, some mosasaurs such as the relatively rare genus *Globidens* (Gilmore 1912) possessed a durophagous dentition suitable for processing hard-shelled prey. *Globidens* belongs to the mosasaurid subfamily Mosasaurinae (Bell 1997), that first appears in the middle Turonian (Bell and Polcyn 2005). That group apparently undergoes a radiation in the Campanian, giving rise to a number of clades, including the globidensini (sensu Bell 1997), a speciose, monophyletic group which includes the genera *Prognathodon*, *Plesiotylosaurus*, *Globidens*, *Carinodens* and *Igdamansaurus*, and taxa previously included in the genus *Liodon* (Schulp et al. 2008). The globidensini exhibit extreme variation in tooth form, ranging from laterally compressed, sectorial forms such as *Prognathodon sectorius* to forms with bulbous, nearly spherical teeth such as *Globidens*.

Globidens is known from North America, from localities along the Gulf and east coasts, and the Western Interior Seaway in the lower part of the Campanian, represented by *Globidens alabamaensis* (Gilmore 1912; Thurmond 1969; Gallagher 2005; Polcyn and Bell 2005) and *Globidens dakotensis* (Russell 1975; see also Everhart

2008). The stratigraphic occurrence of the type of *G. alabamaensis* (Gilmore 1912) is poorly constrained; however, Kiernan (2002) stated it may come from the lower unnamed member or the Arcola limestone member of the Mooreville Formation, which would suggest a mid-Campanian age. The New Jersey material from the Marshalltown Formation was reported by Gallagher (2005) as mid-Campanian. The Texas *G. alabamaensis* material (Thurmond 1969; Polcyn and Bell 2005) first appears in an un-named condensed zone within the Ozan Formation that spans the *Baculites aquilaensis* through the *B. mclearnii* Biozones of Echols (1984) and Cobban (1993) of about 79 Ma. The Kansas material is from the *B. asperiformis* zone (Everhart 2008), closer to the *B. obtusus* Zone and is also estimated to be approximately 79 Ma (based on Hicks et al. 1999, interpolated dates for ammonite zones, their figure 9), consistent with the Texas occurrence. The type of *G. dakotensis* was recovered from the upper part of the Sharon Springs member in South Dakota (Russell 1975), an interval Martin (2007) notes as middle Campanian, suggesting the presence of two contemporaneous but geographically segregated species of *Globidens* in the middle Campanian of North America. Outside of North America, *G. alabamaensis* was reported by Dollo (1924), (see also Lingham-Soliar 1999) from the

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Obourg Chalk Formation, that report reassigned to *G. dakotensis* by Russell (1975). *B. aquilaensis* is found at the base of the Obourg Chalk Formation (Jagt 2005) and is consistent with the lower to mid-Campanian age of the North American occurrences. That pattern of dispersal is in accord with the first occurrences of the mosasaurine genus *Clidastes* in Europe and Scandinavia (Lindgren 1998; Lindgren and Siverson 2004; Caldwell and Diedrich 2005), a taxon apparently restricted to the Western Interior Seaway prior to that time (Polcyn et al. 2008). Martin (2007) described a new species of *Globidens*, *Globidens schurmanni*, from the Campanian of South Dakota on the basis of a relatively complete but poorly preserved skull and postcranial skeleton. The specimen was recovered from the *Baculites compressus* Biozone of Cobban (1993) or about 72.5 Ma, and is thus the youngest species of *Globidens* recovered from North America (Martin 2007).

Phosphatic deposits of late Cretaceous age are present along the northern margin of Africa and extend into the Middle East, and have produced a rich and diverse marine reptile fauna largely dominated by mosasaurs (Zdansky 1935; Avnimelech 1949; Arambourg 1952; Arambourg et al. 1959; Raab 1963; Bardet et al. 1999, 2000, 2004, 2005a, 2005b; Mustafa and Zalmout 2001; Bardet and Pereda Suberbiola 2002; Christiansen and Bonde 2002). Bardet et al. (2005b) erected a new species of *Globidens*, *Globidens phosphaticus*, from the Moroccan phosphate deposits on the basis of isolated teeth, referring material to that species from multiple localities across north Africa and the Middle East as well as material reported by Antunes (1964) from Angola and by Price (1953) from Brazil. The age of the Moroccan specimens ranges from earliest to latest Maastrichtian, based on selachians (Bardet et al. 2005b).

Sub-Saharan African reports of mosasaurs are scarce and have been based largely on poorly preserved and isolated material (Broom 1912; Azzaroli et al. 1972; Lingham-Soliar 1991, 1992b, 1994, 1998). A notable exception is found in Angola where Antunes (1964) reported two new taxa from Turonian sediments, representing the oldest southern hemisphere mosasaurs. Antunes (1964) also reported mosasaur teeth from multiple localities including the durophagous mosasaur genus *Globidens* from a locality in Cabinda (northern Angola) later referred to as *G. phosphaticus* by Bardet et al. (2005b). Due to internal conflicts, including a protracted civil war, there was a hiatus of paleontological research in Angola that spanned over 40 years. In 2005, paleontological field work in Angola was resumed by us and continued with extended field seasons in 2006, 2007 and 2009. These expeditions have yielded significant new collections of mosasaurs, plesiosaurs, turtles, pterosaurs, dinosaurs and fish (Jacobs et al. 2006; Schulp et al. 2008; Jacobs et al. 2009; Mateus et al. 2009). Field seasons of 2005 and 2006 yielded isolated teeth of *Globidens* at Bentiaba (Figure 1) and the 2007 field season yielded two

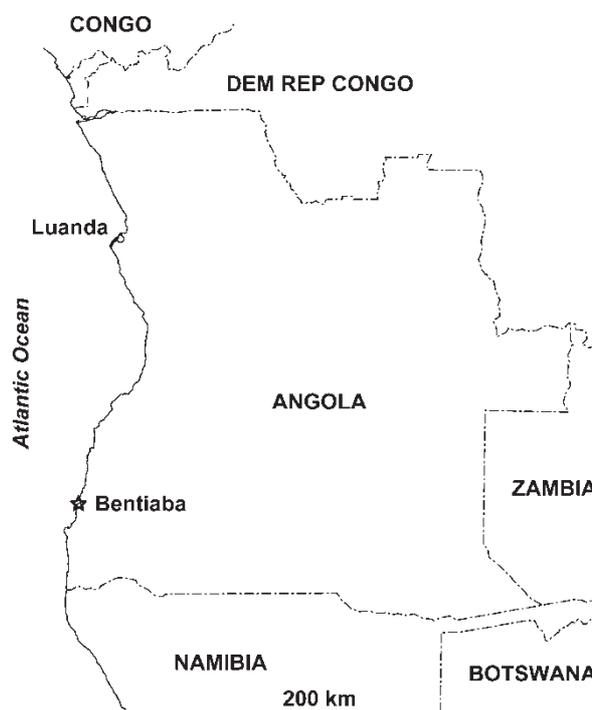


Figure 1. Locality of material described herein. PA23 and PA24 were collected at Bentiaba (indicated by star), Namibe Province, Angola. After Schulp et al. (2008).

skeletal specimens of *G. phosphaticus* at that locality. The new material has been partially prepared and now allows a preliminary description and an assessment of relationships and taxonomic validity of *G. phosphaticus* (Bardet et al. 2005b). We conclude with a brief discussion of the distribution and biogeography of *G. phosphaticus*.

Institutional abbreviations

OCP, Office Chérifien des Phosphates, Khouribga, Morocco; PA, Paleo Angola Project; RMCA, Royal Museum for Central Africa, Tervuren, Belgium; SDSMT, Museum of Geology, South Dakota School of Mines and Technology, Rapid City, SD, USA; SMU, Shuler Museum of Paleontology at Southern Methodist University, Dallas, TX, USA; USNM, United States National Museum, Washington, DC, USA.

Systematic paleontology

Squamata Oppel, 1811

Mososauridae Gervais, 1853

Mososaurinae Gervais, 1853

Globidensini Russell, 1967

Globidens Gilmore, 1912

G. phosphaticus Bardet and Pereda Suberbiola 2005

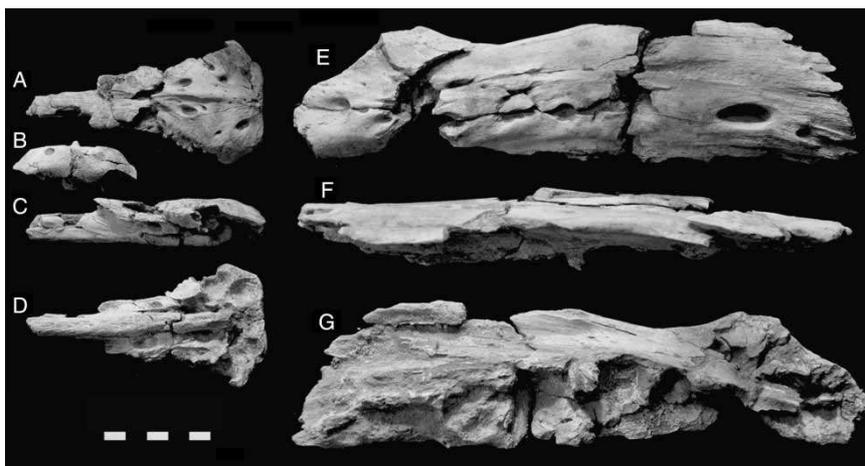


Figure 2. Premaxilla of *G. phosphaticus*, specimen PA24; in dorsal (A), anterior (B), right lateral (C) and ventral (D), views; left maxilla of *G. phosphaticus* in lateral (E), dorsal (F) and medial (G) views. Scale = 5 cm.

Type series

The type series includes the holotype, OCP.DEK/GE 361, a mid-posterior tooth and paratypes, OCP.DEK/GE 338, an anterior tooth and OCP.DEK/GE 339–343, all median teeth. Holotype and paratype material are illustrated in Bardet et al. (2008) their Figure 2. See also Bardet et al. (2006) for correction of holotype number.

Referred specimens

Those specimens referred by Bardet et al. (2008), PA24, a partial skeleton including many elements of the skull and some postcrania, and PA23, a fragmentary skull and posterior dorsal vertebra (Figures 2–5).

Amended diagnosis

Premaxillae dorsoventrally compressed, nearly straight anterior border, dorsal surface bears a median ridge and numerous large foramina, and terminates posteriorly at anterior extent of external nares in a v-shaped notch, emarginating the recessed dorsal surface of internarial bar; internarial bar almost circular in cross section posteriorly, extends anteriorly as a strong ventral ridge and terminates just posterior to the anterior alveoli; anterior maxillae depressed, articulating with premaxilla in a long narrow laterally oriented suture, anterior terminus of external nares defined by dorsomedial processes of maxillae nearly meet at the midline and overlay the markedly recessed internarial process of the premaxilla; anterior teeth broadly conical, taller than long, posteriorly recurved then straight, with discrete apical carinae; mid-posterior teeth bulbous, anteriorly taller than long becoming longer than tall posteriorly, irregularly oval in cross section, with an inflated posterior surface, a large eccentric and recurved apical

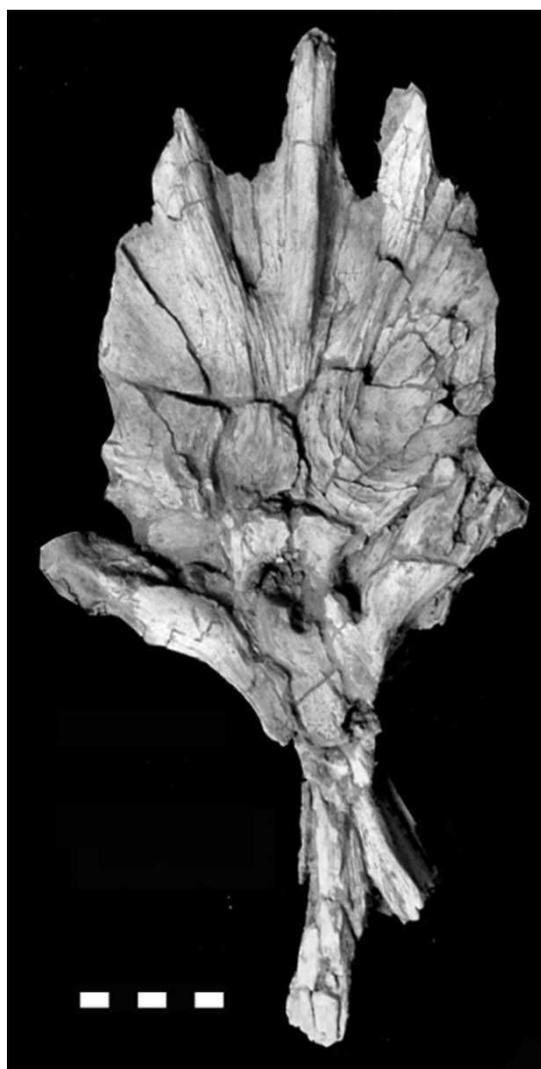


Figure 3. Frontal and parietal of *G. phosphaticus* in dorsal view. Scale = 5 cm.

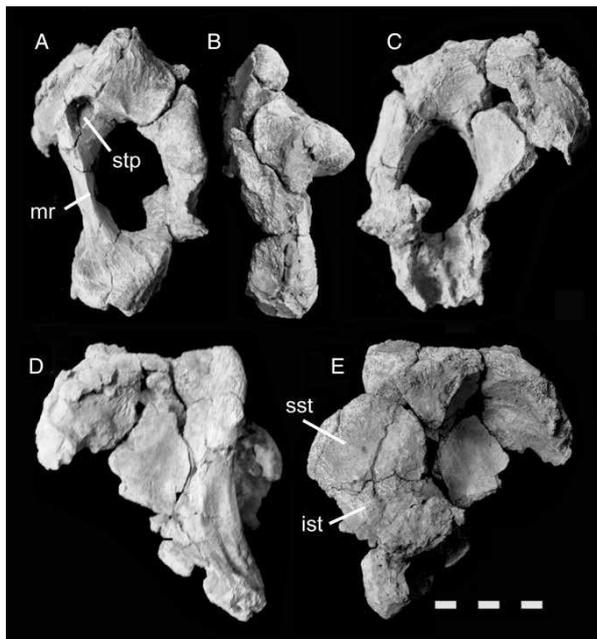


Figure 4. (A)–(E), right quadrate of *G. phosphaticus* in medial (A), dorsal (B), lateral (C), anterior (D) and posterior (E) views. Abbreviations: mr, medial ridge; ist, infrastapedial; sst, suprastapedial; stp, stapedial pit. Scale = 5 cm.

nubbin, vertical sulci on medial and lateral faces, no carinae and enamel surface covered by crude anastomosing ridges.

G. phosphaticus differs from *G. alabamaensis* and *G. dakotensis* in the morphology of the adult teeth which are nearly spherical, the frontal which bears only a low anterior medial ridge, and the pineal foramen that lies completely within the parietal table in those taxa. It differs from all other *Globidens* species in the morphology of the premaxilla and anterior maxillae. *G. phosphaticus* can further be differentiated from *Globidens schurmanni* by the latter taxon's possession of more slender and elongate anterior teeth, lack of inflated surface of marginal teeth, an unusually broad suprastapedial process of the quadrate, and an accessory flange on posterodorsolateral squamosal.

Comments

G. phosphaticus shares with *G. schurmanni* a broad short frontal bearing a strong anterior median ridge and two anterolaterally oriented ridges, pineal foramen sits on the frontal–parietal suture, reduced marginal tooth count and a high thin central median ridge of quadrate, unlike *G. dakotensis* in which the median ridge is low and broadly rounded in cross section. These characters indicate a close relationship between *G. phosphaticus* and *G. schurmanni*.

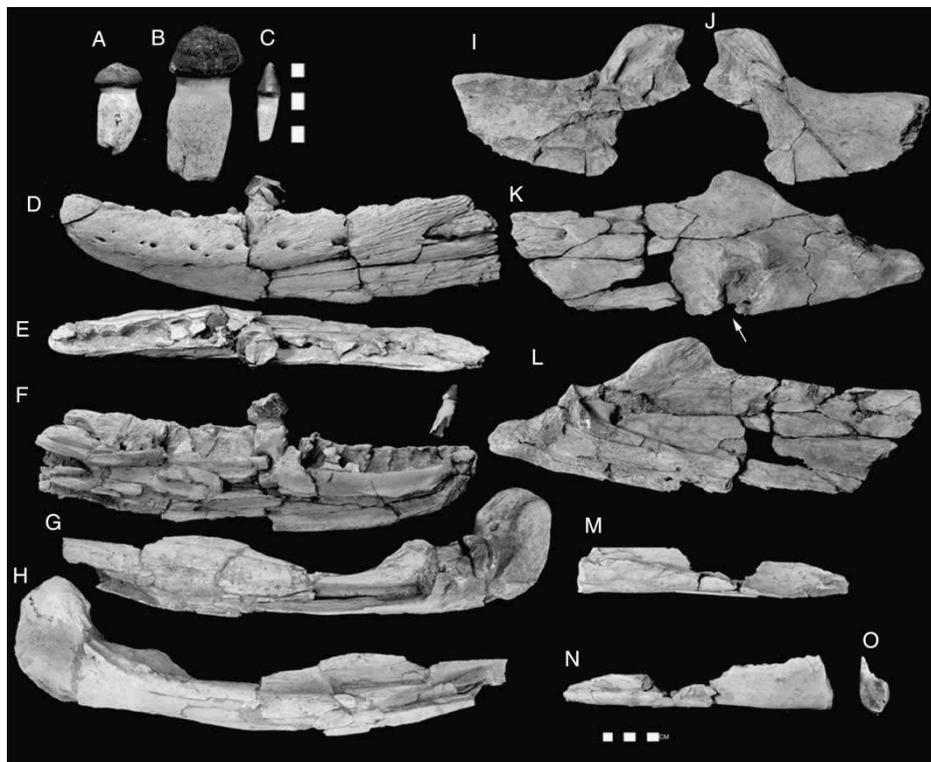


Figure 5. Representative marginal teeth of *G. phosphaticus* from posterior (A), mid-posterior (B) and anterior (C), position; left dentary in lateral (D), dorsal (E) and medial (F) views; left articular in lateral (G) and medial (H) views; left coronoid in lateral (I) and medial (J) views; left surangular in lateral (K) and medial (L) views; left splenial in medial (M), lateral (N) and anterior (O) views; Arrow indicates area of healed abscess. Scale = 5 cm; scale near top of figure for (A)–(C) only.

Restudy of *G. schurmanni* in the context of the new Angolan material allowed recognition of certain morphology that will require rediagnosis of that species and the genus *Globidens*; however, such an exercise is beyond the scope of this contribution and should only be undertaken upon completion of a systematic revision of *Globidensini*.

Description

Two individuals are used for the following description. One specimen, PA24, is the more complete of the two and preserves many elements of the skull and some postcrania. It was found near the surface and although the bone is well mineralised and retains great surface detail, preservation is compromised by root damage and weathering of many elements. The second specimen, PA23, includes a few cranial elements and a single dorsal vertebra is used to augment the description. The specimens are only partially prepared and only selected elements that facilitate diagnosis are described here.

Premaxilla

The premaxilla is broad and dorsoventrally short, the anterior margin is nearly straight and terminates abruptly just anterior to the tooth root (Figure 2(A)–(D)). The dorsal surface bears a high, thin median ridge and numerous large foramina. In dorsal view, the straight anterior margin, curves posterolaterally a short distance and then turns sharply and trends posteromedially. This posteromedial edge bears rugosities and sculpting. At the posterior terminus of the articulation with the maxillae, the dorsal surface of the premaxilla terminates posteriorly in an anteriorly converging, v-shaped notch, the internarial bar recessed below the dorsal surface of the anterior premaxilla, a condition unique among mosasaurs. The internarial bar is broken posteriorly but is robust and nearly round in cross section. In ventral view, the internarial bar continues forward as a robust ventral ridge, terminating somewhat posterior to the alveoli of the medial tooth positions. The premaxillary branch of the facial nerve enters at a point dorsal to a point between the second and third maxillary tooth position. The articulation with the maxillae is narrow and more laterally oriented, and suggests a relatively flexible and broad snout.

Maxilla

Both maxillae are present in PA24, although the ventral margin of the right is badly damaged, it retains the anterior articulation with the premaxilla. The anterior end of the left maxilla in PA24 is damaged and somewhat displaced (Figure 2(E)–(G)). The left maxilla of PA23 is preserved and provides additional details. The maxillae have 10 tooth positions. Most of the teeth, retaining their roots, have

fallen from their respective sockets; however, the depth of the alveoli, documented positions of loose teeth, and teeth retained in life position give a guide to reconstruct the dental series. The largest teeth are in positions seven and eight. The posterior teeth become progressively lower and broad. The anterior teeth become smaller, but proportionally similar to the mid-tooth-row, and the anteriormost two positions are subconical and robust with wide bases and are prognathid. The deepest alveoli are positions six and seven and are progressively less deep both anteriorly and posteriorly. The facial nerve exits are large posteriorly and form a single row until about the fifth tooth position anterior to which is an irregular array of foramina, with a large anteriormost foramen. The anterior maxillae appear to twist medially, such that their anterior portion is more horizontally than vertically oriented. This is consistent with the nature of the unusual articulation with the premaxillae. Visible on the anterior portion of the right maxilla, the articulation is long and narrow and lacks the broad anteromedial articulation typical of other *Globidens* species. This suggests a relatively flexible articulation with the premaxilla, consistent with the prominent muscle scars visible on both the dorsal surface of the anterior maxillae and the premaxilla. Posterior to the articulation with the premaxillae, a well-developed dorsomedial process overlies the internarial bar of the premaxilla a short distance; however, it is unclear whether these processes of the maxillae were in contact with one another.

Frontal

The frontal is completely preserved in PA24 (Figure 3). In dorsal view, it is subrectangular, and wide. It bears a strong median ridge that originates in the centre of the frontal table and extends forward, separating the posterior external nares a significant distance. The frontal also bears two other ridges that originate in the centre of the frontal and trend anterolaterally and form the posterolateral margin of the external nares. The lateral margins of the frontal are nearly parallel most of its length, curving anteromedially a short distance, then turning anterior, forming the lateral margin of the anterolateral ridges. The contact with the parietal is complex, the posterior margin trending posteromedially then turning sharply posterior to form tabs that straddle similar structures of the parietal and forms the anterior border of the pineal foramen that lies on the frontoparietal suture. In ventral view, the posterior part of the frontal is obscured; however, the olfactory canal is broadly open, widening anteriorly and bears deep longitudinal striae. The articulation with the prefrontal is extensive and it appears that the anterolateral dorsal ridges of the frontal overlies the medial margin of the prefrontal articulation and anteriorly likely contacted the anterior portion of the prefrontal forming the posterolateral nares.

Parietal

The parietal is anteriorly broad, but narrows quickly, forming an anterior subtriangular table, then diverging posteriorly at about mid-length, to form the parietal rami (Figure 3). The confluence of the rami forms an anteriorly narrowing posterior shelf. The parietal has an extensive and complex articulation composed of a lateral portion that embraces the frontal from behind and below posterolaterally, a recess to accept posterior projecting tabs of the frontal, and more medial anteriorly placed tabs that embrace both the frontal tabs laterally and the posterior and lateral margins of the pineal foramen medially. The relatively short rami sandwich the supratemporals from above and below as in *G. dakotensis*.

Prefrontal

The right prefrontal (not figured) is present, but is poorly preserved; however, a few comments are possible. The preserved portion indicates that the prefrontal projected laterally a significant distance, but the articulation with the maxilla and the posterior articulation with the postorbitofrontal are badly damaged. The posterior margin of the maxilla rises sharply, suggesting it overlaid much of the anterior portion of the prefrontal. The prefrontal deeply underlies the frontal, and also clasped the anterolateral margin of the frontal within a narrow groove on its dorsal surface.

Quadrate

Both quadrates are damaged, but the right is more complete, missing the ventrolateral portion due to weathering (Figure 4). The left is also severely weathered but preserves the ventral condyle. The suprastapedial process is medially constricted in dorsal view. The large infrastapedial process is fused to the suprastapedial process. The medial surface bears a sharp, thin ridge that runs from the anterior margin of the broadly oval stapedial pit to the anteroventral margin of the stapedial meatus. The cephalic head of the quadrate is tall and heavily sculpted, slanting slightly posterior relative to the long axis of the quadrate. The ventral condyle is broadly convex.

Dentary

Both dentaries are present in PA24. The left dentary is better preserved (Figure 5(D)–(F)). The right dentary (not figured) retains multiple teeth in their respective alveoli, and together with the documented position of displaced teeth allows reconstruction of the tooth row. There are 11 tooth positions. The right dentary retains four erupted teeth in place in positions 5, 6, 8 and 10, and pre-erupted teeth in positions 1, 7 and 11. Positions 1 and 2 are slender and conical (e.g. Figure 5(D)), positions 3–6 increase in size

and robustness. Positions 7–10 are large and are extremely inflated posteriorly (e.g. Figure 5(B)) and the last two positions are relatively low and broad (e.g. Figure 5(A)). The dentary is massively built and curved, forming a slightly concave dorsal margin. There are deep striae in the posterior third of the dentary suggesting significant soft tissue attachment to the posterior portion of the mandible. There is a single row of facial nerve exits posteriorly, and additional smaller irregularly placed exits anteriorly, starting at about the eighth tooth position. The posterior-most exit is the largest as in the maxilla. The Meckel groove is broadly open anteriorly. The medial parapet is tall and interdental bone separate alveoli. The eighth tooth position's alveolus is the deepest. The alveoli shallow both posteriorly and anteriorly, the anterior tooth positions inclined anteriorly.

Splénial

The left splénial is preserved, but damaged (Figure 5(M)–(O)). The articulation with the angular is broad and dorsally subdivided by a sharp vertical ridge. Adjacent to the ridge, the articulation is slightly indented both medially and laterally, but as a whole is somewhat flattened and appears to have shared a largely immobile contact with the angular. There is a strongly developed ossification visible on the posterolateral surface or the splénial adjacent to the articulation, but along with the flattened appearance of the articulation, this may possibly be pathological. The anterior mylohyoid foramen is low on the medial surface about 3 cm from the posterior terminus. There is a marked trough anterolaterally to receive the dentary, but the splénial was probably obscured in later view by the dentary, anterior to about the seventh tooth position.

Surangular

Left surangular of PA24 is preserved (Figure 5(K) and (L)). It bears remnants of a healed abscess on its lateral face near its ventral margin just ventral to the posterior terminus of the coronoid. The suture with the articular runs posteriorly from the posterior terminus of the glenoid a short distance, before turning anterior in a relatively tight arc, and then proceeds anterior, and largely parallels the dorsal margin of the surangular. On the dorsal margin, the surangular forms a high and robust buttress that meets the posterior coronoid.

Articular

Only the posterior portion of the articular of PA24 is preserved, the right articular of PA23 is better preserved and augments this description (Figure 5(G) and (H)). The articulation with the surangular is described above. The anterior margin of the glenoid is strongly buttressed.

The retroarticular turns sharply medially and bears large muscle scars. The anterior portion of the articular is composed of a robust posteroventral and ventral portion and a dorsally oriented blade-like process that meets the medial wall of the surangular and continues anteriorly across the intramandibular joint to insert between the dorsal laminae of the splenial. The tallest portion of this blade-like process lies ventral to the coronoid.

Coronoid

The left coronoid is present, but most of the lateral portion is damaged (Figure 5(I) and (J)). The coronoid is saddle shaped with a tall posterior portion and an anterior portion that largely parallels the dorsal margin of the surangular. A large anteromedial process is present, but does not meet the angular nor does it contact or overlay the articular.

Axial skeleton

There are a number of vertebrae preserved with the specimen, but most are still in matrix, pending preparation, and are not figured here; however, a few descriptive comments can be made. The atlas neural arch is similar to *Clidastes* but the posterior process is not as elaborated and is generally more heavily built. They also appear to have a much broader neural spine in lateral view, in part due to the strong development of the posterodorsal process. The prezygapophyses are broadly spaced and articulate at a high angle with the more medially placed postzygapophyses. These articulations are augmented by strongly developed zygosphenes and zygantra, and appear to be present into the posterior dorsal vertebra. Fragments of caudal vertebrae bear remnants of fused chevron bones as in other mosasaurine mosasaurs.

Discussion

Relationships

A cladistic analysis is beyond the scope of this paper and will be addressed elsewhere pending preparation of additional material; however, the prepared material reported here allows comparisons and assessment of the relationships of *G. phosphaticus*. The new material can be assigned to Mosasaurinae by possession of a tall, dorsal buttress of the surangular, meeting the coronoid posteriorly, fused haemal arches of caudal vertebrae, and medial constriction of suprastapedial process of quadrate, and can be assigned to Globidensini (*sensu* Bell, 1997) by possession of prognathous anterior teeth, infrastapedial and suprastapedial processes of quadrate in contact or fused, and the anterior wall of the sella turcica lying at nearly a right angle to the floor of the medullary cavity. The latter character is present in *Prognathodon kianda* (Schulp et al. 2008), has not been verified in other *Prognathodon* taxa, but is clearly present

in *G. alabamaensis*. The new material can be confidently referred to *Globidens* (Gilmore 1912) based on broadly inflated, durophagous tooth morphology with anastomosing ridges and further can be referred to *G. phosphaticus* based on the inflated posterior surface and vertical sulci of the marginal dentition.

The new material can be excluded from referral to *G. alabamaensis* and *G. dakotensis* on the basis of maxillary tooth count, frontal and parietal morphology and details of the quadrate. The maxillary tooth count in *G. dakotensis* is 13 (Russell 1975) as in *G. alabamaensis* (SMU76279). *G. phosphaticus* possesses 10 maxillary tooth positions. The maxilla of *G. schurmanni* was described as having 12 or 13 tooth positions (Martin 2007); however, the first author was only able to count 11 tooth positions. The frontal is stoutly built in both *G. dakotensis* and *G. alabamaensis*, but differs in its relationship with the postorbitofrontal and prefrontal. In *G. alabamaensis*, the lateral margin of the anterior ramus of the postorbitofrontal curves medially to intersect with the frontal margin as in *Prognathodon overtoni* and *P. kianda*. In *G. dakotensis*, the postorbitofrontal anterior ramus is extremely broad, runs parallel to the lateral margin of the frontal and meets the broad posterior process of the prefrontal, both elements together separating the frontal from the supraorbital margin a significant distance. The frontals of both *G. dakotensis* and *G. alabamaensis* both possess a low anterior median ridge. The anterior median ridge in *G. phosphaticus* is extremely well developed and also possesses two additional ridges that originate near the centre of the frontal and radiate anterolaterally. *G. schurmanni* possesses a similar condition (contra Martin 2007). Additionally, the condition of the prefrontal and postorbitofrontal in *G. schurmanni* is similar to *G. dakotensis* but is more stoutly built and appears to have more extensive overlap of those elements. The pineal foramen is located within the parietal table in *G. dakotensis* and *G. alabamaensis* but lies on the frontoparietal suture in *G. phosphaticus* and *G. schurmanni*. In addition to both taxa sharing the triradiate ridges on the frontal, the frontal dimensions and the posterior margin of the frontal and its relationship to the parietal and pineal foramen are nearly identical in *G. phosphaticus* and *G. schurmanni*. The pineal foramen lies on the frontoparietal suture and is straddled by two anterior tabs of the parietal which in turn is straddled by two posterior tabs of the frontal. The quadrates of *G. phosphaticus* and *G. schurmanni*, are also quite similar and share a high, thin central median ridge of quadrate, derived relative to the low rounded median surface in *G. dakotensis* which is more similar to *Clidastes* in that regard.

In most respects of their cranial morphology, *G. phosphaticus* and *G. schurmanni* appear to be closely related; however, they can be differentiated by characters of the quadrate, premaxilla, maxilla and marginal dentition.

The quadrate of *G. schurmanni* is more robust and possesses a relatively wider suprastapedial process compared to *G. phosphaticus*. Additionally, the squamosal of *G. schurmanni* possesses an accessory flange on posterodorsolateral squamosal. The squamosal in *G. phosphaticus* is unknown. In addition to being diagnostic of the species, the most distinctive aspect of *G. phosphaticus* is the anteriorly depressed and laterally expanded snout. The morphology of the premaxilla and its articulation with the maxillae is unique among mosasaurs and is likely an adaptation for prey acquisition and handling. The maxillae nearly meet at the midline anteriorly, obscuring the internarial process of the premaxilla in dorsal view. In the *G. phosphaticus* specimens described here, nearly all of the marginal dentition was found slightly displaced or separated from their respective sockets, suggesting that the teeth were loosely socketed and periodontal ligaments did not mineralise in life (Luan et al. 2009). This is different from the condition in other derived mosasaurines (Luan et al. 2009) and may be an adaptation to accommodate the increased loading associated with durophagous feeding. This characteristic may also be shared with *G. schurmanni* as some of the teeth in the type specimen appear to protrude an unusual distance from the dentary.

Detailed description of the tooth morphology of *G. phosphaticus* was given by Bardet et al. (2008) and is consistent with the new material described here. Additionally, the hypothetical reconstruction they proposed is largely supported by the new material with the minor exceptions in tooth size and position noted in the description of the new material. The presence of an inflated posterior surface and vertical sulci on the teeth of *G. phosphaticus* does appear to be a unique feature of that taxon. Martin (2007) justified erection of *G. schurmanni* in part based on distinctions in the morphology of the marginal dentition. However, the degree of ontogenetic variation in *G. schurmanni* and *G. phosphaticus* is currently unknown. Polcyn and Bell (2005) noted dramatic ontogenetic variation in the tooth morphology of *G. alabamaensis* ranging from a sectorial dentition in young animals to low-crowned bulbous teeth in mature individuals. Therefore, the dental characters diagnosing *G. phosphaticus* and *G. schurmanni* should be used cautiously until the full range of ontogenetic variation can be assessed. Nonetheless, the specimens described here are inferred to be mature individuals based on some aspects of morphology described above (e.g. the strong medial and anterolateral ridges of the frontal, deep striae in the posterior third of the dentary and large muscle scars on the retroarticular processes). Isolated teeth, approximately 15% larger than the largest described here, are also found at the same locality, and share a similar morphology. Thus, the diagnostic dental characters given for

G. phosphaticus appear to be reliable at least in mature individuals.

Distribution

Globidens, by virtue of its tooth morphology (Massare 1987; Schulp 2005) and stomach contents (Martin and Fox 2007), had a durophagous diet, although variation in tooth morphology (Polcyn and Bell 2005) and stable carbon isotope analysis (Robbins et al. 2008) indicate an ontogenetic change in food selection, at least in *G. alabamaensis*. Six genera of mosasaurs (*Mosasaurus*, *Plioplatecarpus*, *Halisaurus*, *Phosphorosaurus*, *Prognathodon* and *Platecarpus*), a polycotyloid and two elasmosaurid plesiosaur taxa are found at Bentiaba, and are interpreted as active predators. The number of well-preserved mosasaur and plesiosaur specimens at Bentiaba indicates rich and productive seas. While the fossils are found essentially at the paleoshoreline (Jacobs et al. 2006), in life mosasaur species probably partitioned resources through foraging at varying depths and distances from shore (Robbins et al. 2008).

Productive areas of upwelling in modern oceans often result from prevailing winds that move surface water away from continents, allowing deeper, nutrient rich water to rise to the surface, enabling the bloom of plankton. The richness of plankton leads to availability of food higher up the food chain, affecting the distribution of marine mammals in modern ecosystems (e.g. Sydeman and Allen 1999). These areas of upwelling occur at predictable latitudes, notably at the descending limb of Hadley Cells, or about 15–30° latitude (Hartley et al. 2005). In these latitudes along the western margins of continents, upwelling zones lie alongside deserts, such as the Namib Desert in Africa or the Atacama Desert in South America. There are many factors that affect marine productivity and the distribution of deserts, but continental position relative to Hadley Cells is clearly a first-order determinant.

The paleo-position of Africa since the Cretaceous is well constrained by hot-spot traces, particularly the Walvis Ridge (Jacobs et al. 2009), which extends northeast from the Mid-Atlantic Ridge and intersects the African Coast at about the Angola–Namibia border. The trend of the Walvis Ridge documents the northward drift of Africa since the Cretaceous. The fossil locality of Bentiaba lay at about 25°S when its sediments and fossils were deposited (calculated using Scotese [2008] and well within the predicted area of upwelling). Therefore, it is reasonable to conclude that the rich mosasaur and plesiosaur fauna, both taxonomically and numerically, found at Bentiaba, reflects this geographically induced offshore primary productivity transferred up the trophic structure.

Globidens-producing phosphatic localities in Morocco, such as Oulad Abdoun, now at nearly 33°N, were formed at a Maastrichtian position of approximately

24°N, under the descending limb of the northern Hadley Cell. Phosphate deposits are generally considered to be derived from bacterially mediated precipitates produced in upwelling centres, with subsequent winnowing (e.g. Hiatt and Budd 2001). The sedimentary context, and geophysical models of upwelling centres for the early part of the late Cretaceous (Handoh et al. 1999), indicates that the abundance of marine amniotes in Morocco is associated with upwelling productivity during the Maastrichtian, probably driven by Hadley Cell circulation.

The latitudinal position and intensity of upwelling cells, and therefore productivity, varies seasonally and on other ecologically significant timescales (Wefer et al. 1996; Pillar et al. 1998). The north–south shifting of northern and southern upwelling zones in relation to the productive areas induced at the Intertropical Convergence Zone may have well facilitated the migration and dispersal of Cretaceous marine amniotes along the west coast of Africa as they sought out and followed food stocks. This model provides a biogeographic context for evaluating patterns such as antitropicality (Hubbs 1952), as is seen in some species of modern whales (Davies 1963; Fordyce and Muizon 2001), in Cretaceous and younger marine amniotes, for example, in comparing the mosasaur genus *Globidens* in Morocco and Angola.

As noted by Bardet et al. (2005b), *G. phosphaticus* is known from localities across north Africa and the Middle East as well as Brazil and Angola. The material reported by Price (1953) as *Globidens fraasi* is from the Gramame Formation, State of Pernambuco, Brazil, which was at about 10°S paleolatitude during the Maastrichtian. His figured specimens of *G. fraasi* (Plate 1, figures 1–9, Price 1953) actually included two taxa, correctly identified as *G. phosphaticus* and *Carinodens belgicus* by Bardet et al. (2005b). Antunes (1964) reported teeth attributed to *Globidens aegypticus* from the Congo basin in northern Angola, also correctly identified as *G. phosphaticus* by Bardet et al. (2005b). The material described here from Bentiaba is the southernmost occurrence of *G. phosphaticus* at approximately 25°S paleolatitude. Additionally, a collection of reptile teeth housed in the Royal Museum for Central Africa in Tervuren, Belgium, from localities along the Congo River, includes both *G. phosphaticus* and *Carinodens cf. belgicus*. Although this collection has no precise locality or stratigraphic data available, it does document the occurrence of these taxa at approximately 13°S paleolatitude during the Maastrichtian. Thus, it appears that *G. phosphaticus* inhabited not only areas of increased productivity, due to upwelling, but also exploited other marginal areas between approximately 25°N to 25°S. Given the small number of specimens, it is impossible to know whether these occurrences on both sides of the Atlantic represent a single homogeneous population; however, the occurrence of *G. phosphaticus* in Brazil indicates that they did traverse a deep ocean basin

in the Maastrichtian. One would assume their durophagous diet would obligate them to exploit shelf habitats. However, ontogenetic variation in tooth form in *Globidens* as evidenced by *G. alabamaensis* (Polcyn and Bell 2005), likely allowed exploitation of a variety of food sources during early ontogeny, and thus aided their ability to actively range across the Campanian and Maastrichtian Atlantic. Alternatively, their distribution may be an accident of dispersal aided by ocean currents (e.g. Renner 2004). In any event, although *G. phosphaticus* did range across the Maastrichtian Atlantic it appears to have had a more restrictive latitudinal distribution, roughly within the tropics as hypothesised by Bardet et al. (2008). This is in sharp contrast to other mosasaurs genera (e.g. *Mosasaurus*, *Prognathodon*, *Halisaurus* and *Phosphorosaurus*) that exhibit a wide geographic and latitudinal range in the Maastrichtian.

Acknowledgements

We thank our Angolan friends and colleagues for all of their help with planning and assistance with our expeditions, including Margarida Ventura, Andre Neto Buto, Tatiana Tavares, Maria Luísa and Eduardo Morais. We thank graduate students Chris Strganac, Rui Castanhinha and Bruno Pereira who were the backbone of our 2007 field crew. Initial preparation of the fossils was performed by Rui Castanhinha and Ricardo Araújo at the Museu da Lourinhã, in Portugal and by Vicky Quick at SMU. The bulk of the preparation to date was performed by Bill Johnson at SMU. Field work was supported by National Geographic, the Petroleum Research Fund of the American Chemical Society, the Institute for the Study of Earth and Man at SMU, the Royal Netherlands Embassy in Luanda, Angola and TAP Airlines. For collections access and assistance, we thank Jim Martin, Sally Shelton, Bill Simpson, Michael Brett-Surman, Pascal Godefroit, Mary Bade and Nathalie Bardet. We thank our reviewers for providing useful comments and criticisms.

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