A NEW SPECIES OF *PROGNATHODON* (SQUAMATA, MOSASAURIDAE) FROM THE MAASTRICHTIAN OF ANGOLA, AND THE AFFINITIES OF THE MOSASAUR GENUS *LIODON*

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ABSTRACT: Here we describe a new species of the mosasaurine genus *Prognathodon* from the Maastrichtian of Namibe, Angola, on the basis of five specimens which represent most of the cranial skeleton including the diagnostic quadrate. Phylogenetic analysis shows this new taxon, *P. kianda* nov. sp., to be the sister taxon to all other species of *Prognathodon*. It is unique amongst *Prognathodon* in possessing a high marginal tooth count and relatively small pterygoid teeth. The tooth morphology in the new taxon is reminiscent of some species of the genus *Liodon*, allowing association of *Liodon*-like dentition with otherwise *Prognathodon*-like crania, and thus resolves the long-standing question of the phylogenetic affinities of *Liodon*.

INTRODUCTION

Fieldwork in 2005 through 2007 at outcrops of Maastrichtian strata in southern Angola has yielded a rich fauna of mosasaurs, fishes, turtles, plesiosaurs and other marine vertebrates (Jacobs et al., 2006). The material described herein was collected near the village of Bentiaba, Namibe Province, southwestern Angola (Fig. 1). An overview of the geology of the Namibe (formerly Moçâmedes) area was presented by de Carvalho (1961), including the first record of mosasaur teeth from this area. Antunes (1964) recorded a diverse fauna of Maastrichtian marine vertebrates, based primarily on shed teeth, at outcrops near the village of Bentiaba (formerly São Nicolau). For a discussion of the geology of Maastrichtian deposits at Bentiaba, and a more detailed account of previous work, see Jacobs et al. (2006).

Among the material recovered during the 2005 reconnaissance fieldwork are remains of two individuals of a new species of *Prognathodon*, of which a preliminary description was presented in Schulp et al. (2006). Following preparation of additional material collected in 2006 and 2007, we can now provide a more detailed description and formally name this new taxon. For the sake of completeness, relevant portions of the description given in Schulp et al. (2006) are repeated here.

Institutional abbreviations - BMNH: The Natural History Museum, London, UK; MGUAN: Museo Geológico da Universidade Agostino Neto, Luanda, Angola; MNHN: Muséum National d'Histoire Naturelle, Paris, France; NHMM: Natuurhistorisch Museum Maastricht, Maastricht, The Netherlands.

NEW MATERIAL

One relatively complete skull with disarticulated postcranial elements was referred to by its preliminary registration number 07 in Schulp et al. (2006) and now registered at the Museo Geológico da Universidade Agostino Neto collection as MGUAN PA 129 (PA denoting the PaleoAngola Project). Additional material referred to the same taxon includes cranial material from the same locality (field number 05 in Schulp et al. [2006]; now registered as MGUAN PA 128). A braincase and incomplete frontal-parietal (MGUAN PA149, MGUAN PA150, respectively) of the same taxon were recovered from near PA129, and are tentatively assigned to the same individual. Dentaries, frontal, parietal, postorbital and squamosal of the same taxon exposed in a nearby wash (PA151) allow confident referral of skull roof and temporal arcade to the new taxon.

SYSTEMATIC PALEONTOLOGY

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 KIANDA nov. sp.

Figure 1. Provenance of *Prognathodon kianda* nov. sp., from Bentiaba, Namibe Province, Angola.

Etymology - Named after Kianda (name used in apposition), an Angolan mythological deity who rules the ocean and its fish. In one tale, Kianda appears in the form of a skull.

Holotype - MGUAN PA 129.

Paratypes - MGUAN PA 128, MGUAN PA 149, MGUAN PA 150, MGUAN PA 151.

Diagnosis – Medium-sized *Prognathodon*, characterized by anteriorly deep maxillae, slender dentary, a relatively clearly defined dorsal keel of the internarial bar, fifteen dentary teeth and comparatively small pterygoid dentition.

DESCRIPTIONS AND COMPARISONS

Premaxilla—The overhang of the predental rostrum of the premaxilla (Fig. 2A-C) is minimal (5 mm). In cross-section, the element is almost triangular at the anterior end of the internarial bar (‘inverted’ triangle, apex ventral, sensu Bell, 1997). In dorsal view, the internarial bar reaches its maximum lateral constriction dorsal to the fifth maxillary tooth position. The dorsal surface of the internarial bar tapers slightly, and has 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 yet more triangular. The premaxillo-maxillary suture extends almost to the fourth maxillary tooth position. In lateral view, the premaxillo-maxillary suture faintly curves posteriorly (as is typical of mosasaurines), but it is exceptionally long in *P. kianda*, 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. The dentition is moderately prognate, with the anterior teeth protruding at an angle of almost 45 degrees with respect to the internarial bar, which corresponds to an angle of about 65 degrees with the maxillary dental margin. Teeth are relatively slender; their aspect ratio in lateral view is about 12:24 mm and 12:26 mm for the first and second tooth respectively. The teeth have minimal recurvature, and show a weak, unserrated anterior carina; posteriorly no carina is developed.

Maxilla—The dorsal rims of both maxillae (Fig. 3; only right maxilla figured) are damaged, and portions are missing (particularly in the left maxilla); the ventral margin is straight, and >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, the total length amounts to 440 mm. The maxilla would have held 13 teeth, which posteriorly become more laterally compressed. The teeth are bicarinate, except for the four anteriormost ones which have a pronounced anterior carina only. The carinae are unserrated. The enamel surface is smooth with only very fine anastomosing ridges visible. The roots can be at least as tall as the crown, as observed in the seventh position in the left maxilla. The base of the posteriormost tooth crowns is inflated.

Jugal— The anteriormost 95 mm of the right jugal is preserved in MGUAN PA 128; the holotype, MGUAN PA 129, preserves a near-complete right jugal (Fig. 4A, B). The jugal broadly overlaps the maxilla. There is no sign of the ectopterygoid meeting the maxilla, but articulates more posteriorly on the medial jugal. The jugal has a prominent posteroventral process, most closely resembling that of *P. waiparaensis* and *P. saturator* in gross morphology.

Pterygoid—A heavily crushed partial pterygoid (Fig. 5A, B) is preserved in MGUAN PA 129. Pterygoid tooth count cannot be established; preserved pterygoid teeth are relatively small with tooth size approaching the size of the smaller mandibular teeth only. The teeth, as preserved, are only moderately recurved.

Parietal – The parietal (Figure 6A, B) is described based on MGUAN PA 150 and MGUAN PA 151. MGUAN PA 150 was found in close association with MGUAN PA 129; MGUAN PA 151 was found associated with the frontal, right postorbitofrontal and squamosal and the right dentary, allowing referral to *P. kianda*. The parietal can be divided into a short, broad anterior portion and an elongate subrectangular

Figure 2. *Prognathodon kianda* nov. sp. MGUAN PA 129, holotype. **A-C:** premaxilla in dorsal (A), right lateral (B) and ventral (C) view, respectively. Scale bar equals 1 cm.

posterior portion, slightly constricted at two-third its posterior length. The posterior terminus is concave and the posterior table slightly depressed anterior to about the point of the medial constriction. The anterolateral portion bears deep slots to accept corresponding processes of the postorbitofrontal. A small, slightly oval pineal foramen lies within the parietal table, well separated from the frontoparietal suture. Posteriorly, the parietal bears broad, short diverging parietal rami. Ventrolaterally, there appears to be well-developed lateral descending processes, but these are slightly damaged and obscured.

Frontal/prefrontal – Of the frontal assigned to the holotype, MGUAN PA 150, only a posterior fragment is preserved. The description is augmented by an essentially complete, relatively well-preserved referred specimen, MGUAN PA 151 (further reconstructed in Fig. 6C). The referred specimen is approximately the same size as MGUAN PA 150, approximately 200 mm in length, and 170 mm wide at the parietal suture. The interorbital width is 115 mm. The frontal is subtriangular, has a broadly convex anterolateral margin and gently concave supraorbital margin. There is no anterolateral narial emargination. The posterolateral margin is gently rounded. The frontal is broadly embraced by the parietal posteriorly, with posterior paramedian tabs overlying the parietal. The frontal bears a well-defined anteriorly placed median ridge. Anteroventrally, the frontal bears a broad olfactory canal medially and broad overlapping suture with the prefrontals anterolaterally. The prefrontal meets the postorbitofrontal, forming the supraorbital margin, but does not protrude laterally beyond the lateral margin of the frontal.

Figure 3. *Prognathodon kianda* nov. sp. MGUAN PA 129, holotype. Right maxilla in lateral view. Scale bar equals 1 cm.

Postorbitofrontal – The postorbitofrontal is a hatchet shaped element (Fig. 6D, E). It deeply underlies the frontoparietal suture medially and forms a large overhanging lateral process, articulating with the jugal ventromedially. The posterior ramus nearly meets the posterior terminus of the supratemporal fenestra.

Squamosal – The squamosal forms a long medial trough for nearly its entire length for articulation with the postorbitofrontal (Fig. 6F, G). In lateral view it forms a pedestal-like posteroventral terminus. Posterodorsally, a relatively short ascending process overlaps the supratemporal, but likely did not meet the relatively short parietal rami.

Braincase – The braincase (MGUAN PA149; Figure 6H, I) is complete, but crushed and deformed, and found in close association with MGUAN PA 150 and MGUAN PA 129. The size, close association with both MGUAN PA 129 and MGUAN PA 150, and extremely long supratemporals to accommodate the correspondingly short parietal rami noted in MGUAN PA 150 and MGUAN PA 151, warrant referral to *P. kianda*. The basicranium is displaced anteriorly relative to the dorsal elements. The paroccipital processes are crushed and pushed forward. The caudal face of the robust basioccipital is reniform. The basal tubera are broad and subrounded. The basisphenoid is longer than the basioccipital with which it shares a simple transverse ventral suture. The basipterygoid processes are broad, and somewhat anterolaterally oriented, and continue anteriorly following the lateral margins on the strongly upturned long parasphenoid rostrum to its anterior terminus. The dorsal elements are more or less in articulation. As far as now can be determined, the morphology conforms closely to Russell's (1967) description of these elements in *Clidastes*, but differs in possessing a poorly developed otosphenoidal crest and a large prominent foramen for the facial nerve (VII) on the posterolateral face of the inferior process of the prootic. The supraoccipital is blocky in shape and has a broad subrectangular dorsal surface, indicating a broad contact with the parietal. In dorsal view, the posterior margin is V-shaped and forms the roof of the foramen magnum. The parietal processes of the supratemporals are extremely long, consistent with the short parietal rami.

Quadrate—The right quadrate (Fig. 7A-F) is almost complete. The element is not distorted, considering that it is perfectly mirrored by its left counterpart, which is only slightly less complete (not figured). The element is 113 mm tall. The suprastapedial process is fused to the infrastapedial process only slightly below midheight of the element. In lateral view, the element compares favorably in general appearance with both *P. saturator* as well as *P. waiparaensis* Welles & Gregg (1971). The outline of the anterior surface however is more convex in lateral view compared to *P. saturator* Dortangs et al. (2002), and the ventral condyle is slightly more slender in lateral view. In medial view, the infrastapedial process is less developed and less visible than in *P. saturator*; it lacks the distinct muscle scar seen protruding in profile in medial view on the lower third of the anterior surface in *P. waiparaensis*. The stapedial pit is broadly oval, 10 mm tall and 8 mm wide. The inflection of the lower quarter of the median ridge in *P. waiparensis* is nearly absent in *P. kianda* nov. sp. The quadrate is transversely relatively wide; its aspect ratio is closer to that of *P. waiparaensis* than to the relatively taller (hence more slender) *P. saturator* or *P. overtoni* Williston (1897). In anterior view, the

Figure 4. *Prognathodon kianda* nov. sp. MGUAN PA 129, holotype. **A, B:** right jugal in medial (A) and lateral view (B), respectively. Scale bar equals 1 cm.

cephalic condyle is clearly less developed than in *P. waiparaensis* but rather more comparable in proportions to *P. saturator*. Conversely, in dorsal view the median part of the anterior surface is much more, and very characteristically developed in *P. kianda* nov. sp. In posterior view, the muscle scar in the supra-stapedial process in *P. kianda* nov. sp. is relatively small, compared to *P. saturator* and *P. waiparaensis*. The suprastapedial process has a broad dorsal exposure, similar to the condition seen in *P. saturator*.

Dentary—The dentaries (Fig. 8A-D) are almost complete; the dentary tooth count is fifteen. Additional preparation has revealed that the dorsal dental margin of the dentary (*contra* Schulp et al., 2006) actually *is* concave, similar to most other species of *Prognathodon*. A predental projection is negligible. Below the anterior 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 deep. The splenial probably extended anteriorly to between the fourth and fifth alveolus. The Meckelian canal has a marked constriction near the seventh tooth position. Based on dental characters, the dentary of MGUAN PA 128 can be assigned to the same taxon. The anteriormost tooth is slightly prognate, but less so than that in the premaxilla. Replacement teeth erupt from subdental crypts, positioned posteromedially to active teeth. The teeth are unserrated, as in the maxilla. The enamel surface is generally smooth, although some very fine anastomosing ridges can be discerned. Posteriorly from the sixth dentary tooth onwards the teeth are bicarinate; the anterior five teeth show anterior carinae only. The teeth are relatively slender; the aspect ratio of the crowns in lateral view is 14:32 and 13:28 mm (4th and 5th 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 in the posteriormost tooth. The posterior recurvature of teeth increases posteriorly along the dentary.

Splenial—The posterior parts of the splenials (Fig. 9A-B) are preserved in the holotype as isolated elements, with the anterodorsal portions crushed and incomplete. The elements are relatively elongate. The articular surface with the angular is laterally compressed. The perpendicular keel on the articular surface is relatively well developed.

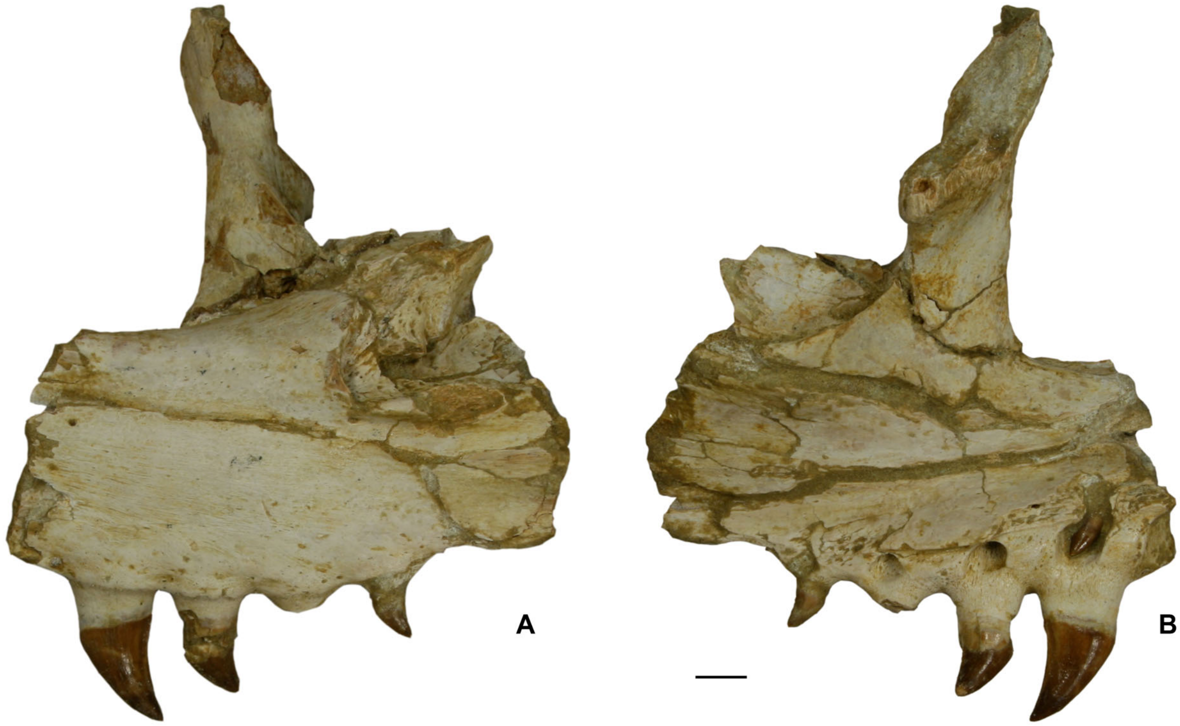

Figure 5. *Prognathodon kianda* nov. sp. MGUAN PA 129, holotype. **A, B:** right pterygoid in lateral (A) and medial view (B), respectively. Scale bar equals 1 cm.

Posterior mandibular unit—Measuring 355 mm, the posterior mandibular unit (PMU) (Fig. 9A-B) occupies 42% of the mandibular length, similar to the value seen in other species of the genus. The PMU is relatively slender, particularly when compared to *P. saturator*, or to *P. currii* Christiansen & Bonde, 2002. The articular surface of the angular is laterally compressed. The posteromedial wing contacts the angular medially high on the surangular coronoid ascending buttress. The anteromedial process is shallow and exposes the surangular in medial view. The surangular displays a steeply ascending coronoid buttress. In lateral view, the articular-prearticular is exposed over a relatively tall portion of the unit.

DISCUSSION AND CONCLUSIONS

Schulp (2006) and Schulp et al. (2006) performed a cladistic analysis of the genus *Prognathodon* and found *Prognathodon kianda* (referred to as 'Angolan material' in Schulp et al., 2006) to be the most basal species of that clade. That preliminary analysis supported inclusion of the Angolan material in the genus *Prognathodon* by possession of five synapomophies including (1) the basal inflation of teeth, (2) the relatively low maxillary and dentary tooth count compared to *Mosasaurus*, (3) the prognate condition of the anteriormost dentition, (4) the slight concave recurvature of the dorsal margin of the dentary, and (5) the smooth-surfaced dentition showing some very faint anastomosing ridges. Preparation of new material confirms that initial finding of relationships on the basis of the distinct morphology of the quadrate and the skull roof. Although bootstrap analysis collapses the recovered tree of Schulp et al (2006) to a polytomy of all *Prognathodon* species, the finding of *P. kianda* as the most basal species of *Prognathodon* can be supported by retention of plesiomorphic characters such as the higher marginal tooth count and relatively small pterygoid dentition.

P. kianda can be differentiated from other species of *Prognathodon* by possession of three autapomophies: (1) a gracile tooth form, (2) more clearly defined dorsal keel of the internarial bar, and (3) higher tooth count than other species of *Prognathodon*. The teeth, particularly the anterior ones, are relatively slender compared to most other species of *Prognathodon* (with the exception of *P. solvayi*), and most other mosasaurs, for that matter, but are similar to fragmentary material reported from Morocco and Syria as cf. *Liodon anceps* (Depéret & Russo, 1925; Arambourg, 1935; Bardet et al., 2000). Therefore, we

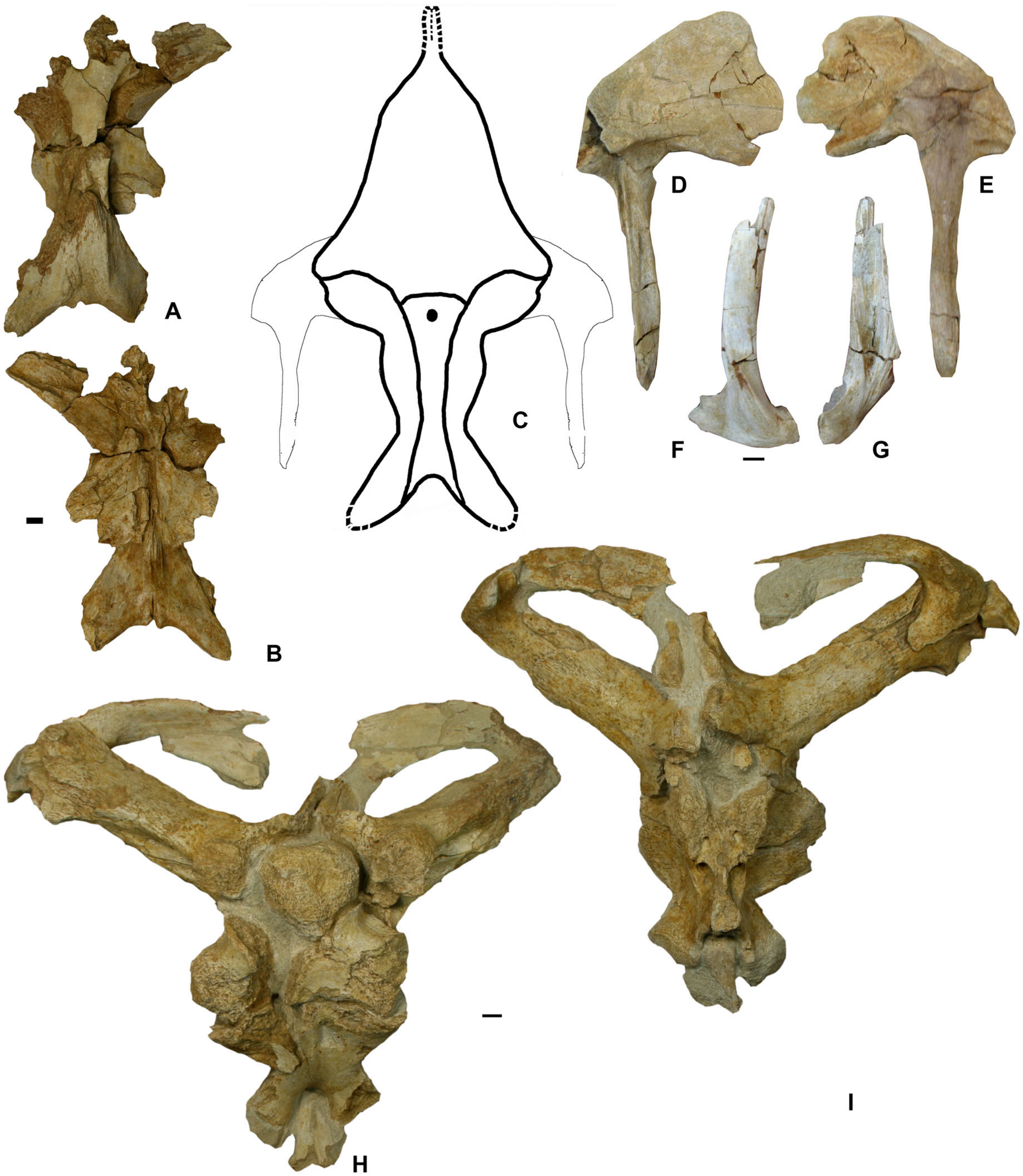

Figure 6. *Prognathodon kianda* nov. sp. MGUAN PA 150 (A, B), MGUAN PA 151 (C; D-G) and MGUAN PA 149 (H, I); **A, B:** frontal-parietal in dorsal (A) and ventral (B) view, respectively; **C:** outline drawing based on composite of all preserved skull roof elements; **D, E:** right postorbitofrontal in upper left ventral (D) and upper right dorsal (E) view; **F, G:** squamosal in lower right (F) and medial view; **H, I:** braincase in posteroventral (H) and anterodorsal (I) view, respectively. Scale bar equals 1 cm.

Figure 7. *Prognathodon kianda* nov. sp. MGUAN PA 129, holotype. **A-F:** right quadrate in medial (A), anterior (B), dorsal (C), lateral (D), posterior (E), and ventral (F) view, respectively. Scale bar equals 1 cm.

compared *P. kianda* with material assigned to the enigmatic genus *Liodon*.

Lingham-Soliar (1993) and Lindgren & Siverson (2002) discussed the taxonomic history of the genus in detail, of which but a brief summary is reproduced here. *Leiodon* was introduced by Owen (1841-1845) based on two tooth fragments and a small portion of the corresponding jaw bone. Agassiz (1846) noted that the genus name was preoccupied by *Leiodon* Swainson, 1839 and replaced it with *Liodon*. In the second half of the nineteenth century, three additional species of *Liodon* were introduced: *Liodon sectorius* Cope, 1871; *Liodon mosasauroides* Gaudry, 1892, and *Liodon compressidens* Gaudry, 1892. Lingham-Soliar (1993) suggested that the genus *Liodon* could be diagnosed. However, the type species of *Liodon*, *L. anceps* (BMNH 41639), is now missing the teeth, the diagnostic feature of the specimen as described, and thus we consider the genus *Liodon nomen dubium*.

Figure 8. *Prognathodon kianda* nov. sp. MGUAN PA 129, holotype. **A-C:** left dentary in lateral (A), dorsal (B) and medial (C) view, respectively; **D:** right dentary in medial view. Scale bar equals 1 cm

Other species referred to *Liodon* (largely on the basis of laterally compressed dentition) share similarities of dentition with *P. kianda* and are discussed here. The holotype of *L. compressidens* (MNHN-Z-C-1878-5) has a pronounced heterodont dentition, and a concave dorsal dental margin; the anterior teeth are relatively slender and recurved; in the centre of the dental margin the teeth become more inflated at the base with a straighter posterior carina; the posterior teeth are relatively small, with a convex anterior carina and a near-straight posterior carina. The anterior four teeth have no posterior carina, at the fifth and sixth positions a faint carina can be seen along the upper half of the crown, and from the seventh position and onwards the teeth are fully bicarinate. Each of these features correspond to the condition seen in *P. kianda*. However, *L. compressidens* can be differentiated from *P. kianda* by possesion of relatively shorter and less compressed teeth and can be further distinguished from *P. kianda* in possessing a relative slender and low maxilla. *Liodon mosasauroides* also has a heterodont dentition but the labiolingual flattening is much more pronounced than in *P. kianda*. The dentition of the referred material of *L. sectorius* in the NHMM collections (e.g., Meijer, 1980) is similarly heterodont as in the taxa discussed above, but *L. sectorius* is characterized by considerably less slender dentary teeth compared to *P. kianda*, with an aspect ratio in lateral view of about 60-70% of the values observed in *P. kianda* all long the dental ramus (Fig. 10). The

Figure 9. *Prognathodon kianda* nov. sp. MGUAN PA 129, holotype. **A, B:** right posterior mandibular unit and splenial in lateral (A) and medial (B) view, respectively. Scale bar equals 1 cm.

labiolingual flattening in the *L. sectorius* material in the NHMM collections is comparable to *P. kianda*.

Thus, all species previously referred to the genus *Liodon* can be differentiated from *P. kianda* on the basis of dental and skeletal characters. We have considered and rejected the possibility that *P. kianda* represents an early ontogentic stage of one of the named species of *Liodon* because all specimens of *P. kianda* collected appear to be adults based on well finished bone surfaces and solid suturing of braincase elements in MGUAN PA 149. The other aforementioned specimens also appear to be adult forms. Given that the type species of *Liodon* is *nomen dubium*, we include the remaining three species of *Liodon* in the genus *Prognathodon*.

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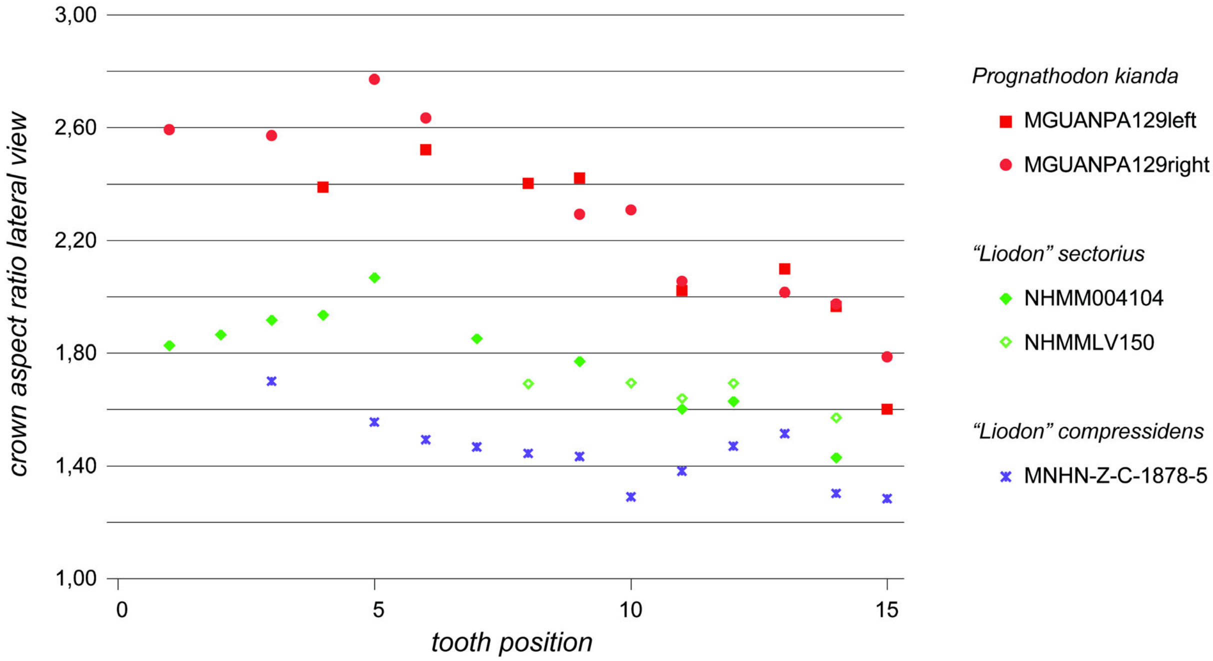

Figure 10. Aspect ratio of dentary tooth crowns in lateral view (crown height / crown basal width) of *Prognathodon kianda*, *Liodon sectorius* (referred material NHMM collections) and *Liodon compressidens* (holotype; measurements made from cast in NHMM collection). Horizontal axis represents position along dental ramus; anterior to the left. Note the higher aspect ratio indicating more slender teeth in *P. kianda*.

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