Cretaceous amniotes from Angola: dinosaurs, pterosaurs, mosasaurs, plesiosaurs, and turtles

Amniotas cretácicos de Angola: dinosaurios, pterosaurios, mosasaurios, plesiosaurios y tortugas

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Abstract

Although rich in Cretaceous vertebrate fossils, prior to 2005 the amniote fossil record of Angola was poorly known. Two horizons and localities have yielded the majority of the vertebrate fossils collected thus far; the Turonian Itombe Formation of Iembe in Bengo Province and the Maastrichtian Mocuio Formation of Bentiaba in Namibe Province. Amniotes of the Mesozoic of Angola are currently restricted to the Cretaceous and include eucryptodire turtles, plesiosaurs, mosasaurs, pterosaurs, and dinosaurs. Recent collecting efforts have greatly expanded our knowledge of the amniote fauna of Angola and most of the taxa reported here were unknown prior to 2005.

Key words: Angola, Africa, mosasaurs, plesiosaurs, turtles, dinosaurs, pterosaurs, Cretaceous

Resumen

Aunque rica en fósiles de vertebrados del Cretácico, el registro fósil amniotas de Angola es poco conocido con anterioridad al 2005. La mayoría de los vertebrados fósiles recogidos hasta el momento provienen de la Formación Itombe, Turoniense de Iembe en la provincia de Bengo y del Maastrichtiense, Formación Mocuio de Bentiaba en la provincia de Namibe. El registro fósil de amniotas del Mesozoico de Angola está actualmente restringido al Cretácico e incluye las tortugas eucryptodiras, plesiosaurios, pterosaurios y dinosaurios. Los recientes esfuerzos del trabajo de campo han ampliado en gran medida nuestro conocimiento de la fauna de los amniotas de Angola y la mayoría de los taxones que se presentan no se conocían antes de 2005.

Palabras clave: Angola, África, mosasaurios, plesiosaurios, tortugas, dinosaurios, pterosaurios, Cretácico.
INTRODUCTION

Angola has the best Southern Hemisphere record of Late Cretaceous marine amniotes, including mosasaurs, plesiosaurs and chelonians (all refs). It has also produced pterosaurs and dinosaurs (refs) preserved in marine sediments. This faunal richness is particularly relevant in the context of the mid-Cretaceous opening of the South Atlantic (Jacobs et al., 2006a, 2006b, 2009a, 2009b) and the general paucity of records for that region of the Earth (Jacobs et al., 2011).

The main sedimentary packages of the Angolan Mesozoic can be broadly grouped into three divisions: (1) Karoo-like continental basin deposits (with Triassic fishes), at Baixa de Cassange; (2) Cretaceous marine sediments related to the opening and expansion of the South Atlantic (and rich in marine vertebrates); and (3) continental Cretaceous, with no vertebrate record so far, filling rift valley remnants along the coast and broadly distributed in the interior of the country. The latter are poorly known, in part because of the inaccessibility and rareness of outcrops.

The goal of this article is to provide an overview of the fossil amniotes from the Cretaceous of Angola. Additionally, we provide a list of non-amniote taxa reported from Angola (Appendix).

History of Mesozoic amniote paleontology in Angola

According to Nunes (1991: 317), the first reports of fossils in Angola are attributed to Lang, who in 1839 (cit. in Nunes, 1991, without bibliographic reference) wrote “… petrifications of Ammon horns, that show the existence of Mesozoic terrains in the country.” The German explorer Eduard Peschuel-Loesche (German, 1849-1913) prospected that part of Africa between 1873 and 1876, including what are now the provinces of Cabinda and Namibe. O. Lenz (1877) wrote notes on fossils from Cabinda, Barra do Dande, Benguela-Cuio, and eight localities in the Namibe basin.

In addition to mosasaurs, Antunes (1964, 1970) also reported vertebral and girdle elements of two plesiosaur specimens from the Turonian of Iembe, isolated plesiosaur teeth and vertebrae from the Maastrichtian of Cambota, Cabinda, Barra do Dande, Ambrizete, and Bentiba, and teeth from Fazenda dos Cavaleiros (Bero River) Neto (1964: 221) reports the occurrence of reptile teeth from the Maastrichtian of Bentiba (former São Nicolau) and later, Cooper (1972) reported Mosasaurus beaugei from that locality.

South of Sumbe (formerly Novo Redondo), Lapão (1972) reported the presence of one tooth and vertebrae from Maastrichtian sediments, attributing them to Mosasaurus and Plesiosaurus respectively. Referral of Maastrichtian material to Plesiosaurus is doubtful since that is restricted to the Lower Jurassic (Großmann 2007). Lapão (1972) also reported the occurrence of a mosasaur skull but it is now lost or was never collected.

Contributions on other aspects of the history of the geology and paleontology are provided by Andrade and Andrade (1957), Antunes (1964, 1970), Antunes et al. (1990), Nunes (1991) and Brandão (2010).

Angola’s war of independence in the early 1970s, and subsequent civil war persisting until 2002, halted field research during that period. After reaching a peace agreement between the warring factions in 2002, fieldwork became feasible once more, and thus the initiation of the current research cycle. All current paleontological work is conducted under the auspices of the PaleoAngola Project, a scientific collaboration between researchers from Universidade Agostinho Neto (Angola), Southern Methodist University (USA), Universidade Nova de Lisboa (Portugal), and the Natuurhistorisch Museum Maastricht (Netherlands). The current research cycle commenced in May of 2005, and has continued with expeditions in May and July 2006, July of 2007, August of 2009, February of 2010, July of 2010 and is planned for July 2011. All coastal provinces have been visited with the exception of Zaire province in the extreme northwest (Fig. 2).

Field work in Angola has been extremely productive. The first visit resulted in the discovery of a new genus and species of sea turtle, Angolachelys mbaxi (Mateus et al., 2009), the dinosaur Angolatitan adamastor (Mateus et al., 2011), the mosasaur Prognathodon kiandra (Schulp et al., 2008), and new specimens of the mosasaurs.
Angolasaurus bocagei, and Tylosaurus iembensis (Antunes 1964). Later expeditions allowed excavation of new specimens including additional forms never reported from Angola. Publication by Jacobs et al. (2006a, 2006b, 2009a, 2009b, 2010a, 2010b), (Polcyn et al., 2007a, 2007b, 2007c, 2009, 2010), Schulp et al. (2006a, 2006b, 2008), Mateus et al. (2006, 2008, 2009, 2011), and Araújo et al. (2010) are beginning to document the richness of the Late Cretaceous amniote fauna of Angola. The Projecto PaleoAngola set of contributions represents an increase up to five high-rank clades of Mesozoic tetrapods. Prior to 2005 only the genera Angolasaurus, Mosasaurus, Tylosaurus, Globidens, and an indeterminate plesiosaur material were known. Here we report 21 different taxa. The fossils are being prepared in the laboratories of the participating institutions: ML, SMU, and NHMM (see in acronyms), where also replicas of the most important specimens will be made prior to the return of the material to University Agostinho Neto, in Luanda.

ACRONYMS

ML - Museu da Lourinhã, Portugal.
SMU - Southern Methodist University, Dallas, USA.
MRAC: Musée Royal d’Afrique Central, Tervuren, Belgium.

FIGURE 1. Plesiosaur rib (MRAC 2084), formerly identified as dinosaur tooth by Dartevelle and Casier (1943-59).
MAIN CRETACEOUS AMNIOTE LOCALITIES

Projecto PaleoAngola has worked mostly in coastal marine Cretaceous rocks, obtaining abundant fishes (both Chondrichthyes and Osteichthyes, see Antunes and Cappetta, 2002), mosasaurs, plesiosaurs, and marine turtles as well as terrestrial animals including isolated bones of pterosaurs and dinosaurs and the articulated forelimb of a sauropod dinosaur (Mateus et al., 2011). No mammals, amphibians, or birds have been discovered thus far. Of the localities explored by the PaleoAngola Project (Fig. 2), two deserve special mention due to their richness: Iembe, in the province of Bengo and Bentiaba, in the province of Namibe. Being situated in the Southern Hemisphere, which has a relatively poor Late Cretaceous marine vertebrate record when compared to Northern Europe, North America, and Morocco (Bardet et al., 2010), add to the importance of these localities.

Iembe (Turonian)
The locality of Iembe (Fig. 2) is late Turonian in age and yielded fishes, mosasaurs, plesiosaurs and remains of a dinosaur (Fig. 3). The most productive formation in the Iembe area is the Itombe Formation (see Mateus et al., 2011: Fig. 1 for the Mesozoic formations in the Cuanza Basin). This is the type locality of the mosasaurs Angolasaurus bocagei Antunes, 1964, Tylosaurus iembeenses Antunes 1964, and the turtle Angolachelys mbaxi Mateus et al., 2009. It also yielded a forelimb of a sauropod dinosaur that represents the first non-avian dinosaur discovered in Angola, Angolatitan adamastor (Mateus et al., 2011).

Bentiaba (Campanian-Maastrichtian)
The main vertebrate bearing layers at the locality of Bentiaba (Fig. 4) are Late Campanian and Maastrichtian in age, although older rocks are present. Most of the specimens have been collected from the mid Maastrichtian. Bentiaba is one of the most important localities for marine vertebrate fossils by virtue of the: (i) high concentration and abundance, (ii) excellent preservation, (iii) completeness and (iv) taxonomic diversity (see faunal list below). Numerous fish species (Dartevelle, 1942), at least twelve taxa of mosasaurs, three taxa of plesiosaurs, marine turtles, dinosaurs and pterosaurs are present. Hundreds of specimens have been located or collected including partial or complete skeletons and skulls, in an exposure covering less than two square kilometers. Thus far, more than 200 marine reptile specimens were and are being unearthed from a two-meter thick bonebed. Bentiaba is the type locality of
the mosasaur *Prognathodon* *kianda* Schulp et al., 2008 and has provided the most complete *Globidens phosphaticus* skeletons to date (Polcyn et al., 2010). Work in progress shows the occurrence of new taxa of plesiosaurs, turtles, and mosasaurs. Also several isolated bones attributed to dinosaurs were found at this locality. The presence of such a large number of top predators in the Late Cretaceous fossil beds of Angola suggest the high primary productivity of the Benguela upwelling system (Shannon 1985) extends back to the Cretaceous (Jacobs et al., 2009a,b).

**SYSTEMATIC PALEONTOLOGY**

**CHELONIANS**

Although the picture is changing quickly, chelonians are poorly known in the Cretaceous of Angola. The first taxon identified to species level was the recently described and named *Angolachelys mbaxi* (Mateus et al., 2009) from the Turonian of Bengo Province. To date, all turtle remains collected in the Mesozoic of Angola are Cretaceous eucryptodirans, including angolachelonians (Mateus et al., 2009), chelonioids, and a possible dermochelyid, which would be the oldest record for that clade.

**Eucryptodira Gaffney, 1975**

**Angolachelonia Mateus et al., 2009**

**Angolachelys mbaxi** Mateus et al., 2009

Material: MGUAN-PA2, nearly complete skull (Fig. 5), dentary, fragments of vertebrae, carapace, one ungual phalanx.

Locality and horizon: North of Iembe (Bengo Province), Turonian.

Comments: Angolachelonians have mandibular articulation aligned with or posterior to the occiput, and basisphenoid not visible or visibility greatly reduced in ventral view.

Basal eucryptodires and angolachelonians originated in the northern hemisphere (Mateus et al., 2009), thus *Angolachelys* represents one of the first marine amniote
lineages to have invaded the South Atlantic after separation of Africa and South America, as shown by the phylogenetic affinities of angolachelonians (Mateus et al., 2009) with marine eucryptodires from Europe and from Glen Rose in Texas (Mateus et al., 2009; Vineyard, 2009; Vineyard et al., 2009).

Chelonidae Bonaparte 1832
Euclastes Cope 1867
Euclastes sp.

Material: MGUAN-PA14, an incomplete anterior portion of a skull (Fig. 6) and MGUAN-PA157, a new complete skull and mandible, cervical vertebrae, peripheral plates, forelimb (collected in 2010, still mostly unprepared, Fig. 7).

Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian, Mucuio Formation.

Comments: Vineyard et al. (2009) reported the presence of an Euclastes-like turtle from Bentiaba based on specimen MGUAN-PA14. Additional material collected at Bentiaba since the work of Vineyard et al. (2009) improves the quality of the sample of Maastrichtian angolachelonians and will allow evaluation of diversity and relationships among marine eucryptodires.

With respect to MGUAN-PA14, the ventral surface of the palate is flat, smooth and vascularized with a low marginal rim (Fig. 6). In ventral view, the premaxillae are well developed paired bones that form a large contact with the vomer and the maxilla laterally. Sutures are present that form a contact with the palatines, although part of the left palatine is missing. Orbits are anterodorsally positioned on the skull. The vomer is large and roughly rectangular in shape. The dorsal surface floors the fossa nasalis, and foramina praealatina are present. In anterior view, the premaxillae are large, and form the ventral margin of the external narial opening. The maxilla forms the broad and posteriorly inclined margin of the nares. In lateral view the maxilla is large and forms the anteroventral margin of the fossa orbitalis. In posterior view, the vomer pillar is strong, forming the septum between the nasal passages. The posterior extent of the pillar is in line with the posterior margin of the horizontal portion of the vomer. Also in posterior view, a foramen presumed to be the foramen supramaxillare, is present on the maxilla.

Parham (2005) placed Euclastes among the Pancheloniidae (however, see also Jalil et al., 2009 for alternate interpretation). Parham’s (2005) diagnosis of the genus, based on Euclastes wielandi is: (1) V-shaped basisphenoid; (2) secondary palate; (3) closely positioned foramina for the exits of the anterior carotids; and (4) rod-shaped rostrum basisphenoidale, but noted a high variability within the group. Euclastes meridionalis has a more extensive secondary palate, Euclastes planimina has a wider robust head, Euclastes platyops has a shallow tomental ridge, dorsally directed orbits, and non-concave triturating surface; and Euclastes roundsi has a less developed secondary palate. The complete skull and jaw, incomplete postcrania and carapace collected during the 2010 expedition will test and refine the attribution of these specimens to Euclastes.

Chelonioidae Baur, 1893
Protostegidae Cope, 1873
Protostega sp.

Material: MGUAN-PA158, two humeri, three costal plates, one xiphiplastron (Fig. 8), and one peripheral plate (identified as the first or second peripheral) of a single animal.

Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian.

Comments: The PaleoAngola expedition of July 2010 to the Maastrichtian of Namibe Province collected bones of a very large turtle. More bones are still in the field for future excavation. The turtle is identified as a protostegid cryptodire based on its very large size (humerus length is 63 cm), fenestrated carapace, finger-like terminations and curvature of the xiphiplastron, and long and thin costal plates (e.g. Zangerl, 1953, but see Hooks, 1998, for the systematics of Protostegidae).

The long costal plate (98cm long) found in Bentiaba is virtually identical to the holotype of Protostega dixie (CNHM P27314) figured by Zangerl (1953: fig. 39). The xiphiplastron is long, with an acute curve of the
xiphiplastron body, forming a distinct L-shape of the lateral rim, rather than the smooth postero lateral curve for most chelonioids. The anterior end is pointed, while the posterior end is digitiform. These features are also similar to those observed in the xiphiplastron of Protostega dixie (see Zangler, 1953: fig. 45 and 46). The humeri show abundant bite marks, probably caused by sharks. The articular ends of the humerus are broad. The lateral process is moderately projected, not beyond the shaft edge in ventral view.

Protostegidae Cope, 1873

?Calcarichelys

Material: MGUAN-PA 167, neural scute (Fig. 9).
Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian.

Comments: An isolated bone (Fig. 9) found in Bentiaba is here identified as a neural scute, possibly from a Calcarichelys-like protostegid, which would indicate the presence of a second protostegid taxon at Bentiaba. The base has a saddle-like shape, with the conical dorsal face culminating in an acute thorn-like structure. The bone resembles the ankylosaur osteoderms but does not have the typical keel forming a sharp point, and the edges are thin. The surface texture is smooth, contrary to the typically rugose osteoderms of thyreophorans. Calcarichelys gemma Zangler 1953 is known from the Upper Cretaceous of Alabama (Hooks, 1998). Hooks (1998) diagnosed Calcarichelys by the mid-dorsal keel composed of alternating, laterally compressed conical and saddle-shaped elements. The Angolan specimen is known from the above described scute, which is not enough for a detailed attribution. It differs from Calcarichelys because the Angolan scute is totally conical without an elongate
midline keel. The protostegid *Chelosphargis advena* (Hay, 1908) also has sharp scutes (see Hay, 1908: Fig. 257), but they are more keel-like and not as prominent as *Calcarichelys*.

**Toxochelyidae** Baur, 1896

*Toxochelys* sp.

Material: MGUAN-PA168, hyoplastron, peripherals and costals plates (Fig. 10).

Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian.

Comments: Contrary to most cheloinoids, the toxochelyids have rectangular peripheral plates without digitiform terminations, with a socket-like cavity for the rib, and often fenestrated carapace. Nicholls (1988) lists two characters as diagnostic of the genus *Toxochelys* that are visible in the Angolan material: the presence of costoperipheral fontanelles in carapace and the peripheral border smooth, without notches or serrations. The hyoplastron outline is virtually identical to that of *Toxochelys moorevellensis* (see Zangerl, 1980: fig.3c). We tentatively assign this Angolan form to *Toxochelys* sp.

**PLESIOSAURS**

The expeditions of 2007 and 2010 yielded significant plesiosaur material. Several partial skeletons, including cranial material were collected in 2010. Although some plesiosaur vertebrae have been recovered from the Turonian of Iembe, the most productive locality for plesiosaurs is Bentiaba (Fig. 11)

Material: MGUAN-PA85, MGUAN-PA106, MGUAN-PA120, propodials, cervical and pectoral vertebrae and pectoral and pelvic girdle elements.

Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian.

Comments: Referral to this taxon is based on possession of unfaceted distal ends of the propodials, short, straight and robust propodials, presence of low longitudinal ridges
along the distal borders of the propodials, and short and narrow ischia. The Tuarangisaurus-like specimens are important to better understand the phylogenetic status and the ontogeny of this genus, previously reported from Argentina and New Zealand (Gasparini et al., 2003, Wiffen and Moisley, 1986).

Elasmosauridae indet.

Material: MGUAN-PA113, basicranium, MGUAN-PA126, symphyseal region of mandible, various unnumbered specimens, teeth.

Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian.

Comments: The recovered Elasmosauridae mandible portion is ascribed on the basis of straight dentary rami, short symphysis and presence of four symphyseal teeth. Several isolated teeth have been found ascribable to Elasmosauridae on the basis of the recurvature of the tooth crown, thin enamel, fine striae that do not anastomose, and some teeth slightly labiolingually flattened.

Antunes (1964) describes fragmentary plesiosaur material coming from coastal basins except Benguela Basin. The most complete plesiosaur remains, referred to “Cimoliasauridae”, comprise twelve vertebrae and a tooth from Cambota in the Cabinda Enclave. As the “Cimoliasauridae” family is not supported in recent phylogenetic hypotheses (O’Keefe and Street 2009, Ketchum and Benson 2009) the above mentioned material should be referred to Elasmosauridae indet., following Vincent et al., 2010).

MOSASAURS

With the exception of two Turonian taxa described by Antunes (1964), the mosasaur record of Angola was limited to isolated tooth crowns. Since 2005, a collection of relatively complete and well preserved material of several taxa from the late Turonian through the Maastrichtian deposits, now represents the largest collection of Southern Hemisphere mosasaurs. It also provides new information on poorly known taxa and is still producing numerous new species. Mosasaur are the most common amniote found in all Late Cretaceous localities visited in Angola, with dozens of specimens collected to date and many more still in situ. They are also the most taxonomically diverse amniote in the Upper Cretaceous of Angola, with at least ten species identified to date.

Squamata Oppel, 1811
FIGURE 8. Xiphiplastron (MGUAN-PA 158) of the Protostegid turtle *Protostega* sp. from the Maastrichtian of Bentiaba (Namibe Province).

**Mosasauridae** Gervais, 1853

**Mosasaurinae** Gervais, 1853

**Plotosaurini** Russell 1967

*Mosasaurus* sp. aff. *M. hoffmanni* Mantell, 1829

Material: MGUAN-PA35, isolated shed teeth, complete and partial humeri.

Locality and horizon: Baba, Bentiaba, Fazenda Dos Cavaleiros (Namibe Province); middle to upper Maastrichtian.

Comments: The teeth we have referred to *Mosasaurus* are strongly D-shaped in cross section and medially recurved, with minor faceting of the otherwise smooth enamel surface. Previous discoveries of teeth of this genus from Angola have been referred to *Mosasaurus beauei* Arambourg 1952 (Carvalho 1961, Antunes 1964), known from the Maastrichtian of Morocco; however, the isolated teeth reported here are indistinguishable from specimens of *Mosasaurus hoffmanni* from northern Europe and *Mosasaurus maximus* from North America. The European and North American forms likely represent the same species (Russell, 1967; Mulder, 1999). Fernandez et al. (2008) reported a contemporaneous *Mosasaurus* from the upper Maastrichtian of northern Patagonia, referring it to *Mosasaurus* sp. aff. *M. hoffmanni*.

**Globidensini** Russell, 1967

*Prognathodon kianda* Schulp et al., 2008

Material: MGUAN-PA129 (holotype), MGUAN-PA128, MGUAN-PA149, MGUAN-PA150, MGUAN-PA151.
Several specimens of different ontogenetic stages. Shed teeth, isolated bones, partial skulls and skeletons.

Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian.

Comments: *Prognathodon kianda* (Fig. 12 A, B, D) is the most abundant taxon at the Bentiaba locality and previous reports of *Liodon* (Antunes, 1964; Jacobs *et al.*, 2006a) from Bentiaba are referred to that taxon. A new specimen collected in 2010 consists of a largely articulated skeleton and skull, but lacks the portion of the tail posterior to the second caudal vertebra.

*Prognathodon cf. saturator* Dortangs *et al.*, 2002

Material: MGUAN-PA 169. Fragmentary dentary including tooth crown.

Locality and horizon: “Bentiaba 2” locality (Namibe Province); middle Maastrichtian.

Comments: The specimen is composed of badly weathered fragments of the right dentary (Fig. 12 C). Collectively the fragments preserve three relatively complete alveoli and a single tooth crown. The broad tooth base is elevated above the dorsal margin of the dentary. The tooth crown is extremely robust and ~60 mm in basiapical length. Albeit fragmentary and despite that the only tooth crown lacks the enamel, the specimen preserves some diagnostic characters. The bicarinate tooth is slightly recurved posteriorly, and possesses no medial curvature. It is swollen above the constricted region at its base. This combination of characters allows referral to the genus *Prognathodon* (Bell, 1997; Schulp, 2006). The only Late Maastrichtian species of *Prognathodon* possessing the robustness and proportions seen in the new specimen is *P. saturator* Dortangs *et al.*, 2002, allowing tentative referral to that taxon. This is the first report of this taxon from the South Atlantic region. Antunes (1964, plate 26, fig 4) reported a tooth from the Maastrichtian of Cabinda that he referred to Mosasauridae indet. That tooth may represent an early ontogenetic stage of *P. saturator*.

*Globidens phosphaticus* Bardet and Pereda Suberbiola, 2005b

Material: MGUAN-PA23, MGUAN-PA24, partial skulls, vertebrae and limb material.

Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian, Mocuio Formation.

Comments: *Globidens phosphaticus* was originally described and named on the basis of isolated tooth crowns from Morocco by Bardet *et al.* (2005b). Bardet (2005b) also indicated the presence of that taxon in Angola, based on illustration of an isolated tooth crown in Antunes (1964). Polcyn *et al.* (2010) reported the first skeletal material of this taxon, providing a preliminary description and
confirming the taxonomic validity of the species. Referral of the Angolan material to *G. phosphaticus* was on the basis of the tooth characters given by Bardet *et al.* (2005b). That study also presented character data establishing *Globidens phosphaticus* as the sister-taxon to the late Campanian *G. schurmanni* from North America.

**Plioplatecarpinae Russell, 1967**

*Angolasaurus bocagei* Antunes, 1964

Material: MGUAN-PA 001, Partial skull, MGUAN-PA 063, MGUAN-PA 065, articulated skull, partial postcrania, and nearly complete forelimbs. Locality and horizon: Iembe (Bengo Province); upper Turonian. Comments: The Turonian section at Iembe has yielded new material of *Angolasaurus bocagei* (Fig. 13) allowing an updated phylogenetic analysis and confirming its taxonomic validity. The phylogenetic analysis supports *Angolasaurus* as the sister-taxon of *Selmasaurus*, and along with *Ectenosaurus*, form a clade that apparently diverged from the *Platecarpus*-Plioplatecarpus lineage in the Turonian (Polcyn and Everhart, 2008; Polcyn *et al.*, 2009).

**“Platecarpus” ptychodon** Arambourg, 1952

Material: MGUAN-PA 160 Two partial skulls and skeletons including limb material, isolated tooth crowns. Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian. Comments: This species was erected by Arambourg (1952) on the basis of isolated tooth crowns from the Maastrichtian phosphates of Morocco. Antunes (1964) reported isolated tooth crowns (Antunes, 1964; plate XXVI figures 11 and 11a) that he referred to the same taxon. The new specimens collected in 2010 represent most of the skull elements, the presacral vertebral column, and the pectoral girdle and forelimb. The new material does not support referral to the genus *Platecarpus*, or any named genus of mosasaur.

**Tylosaurinae Williston, 1895**

*Tylosaurus iembeensis* Antunes 1964

Material: MGUAN-PA64, fragmentary skull elements. Locality and horizon: Iembe (Bengo Province); upper Turonian. Comments: *Tylosaurus iembeensis* remains poorly known and the holotype was lost in a fire in Lisbon (Jacobs *et al.*, 2006); however, a fragmentary new specimen has been recovered. The preserved quadrate has a poorly developed infrastapedial process, similar to that seen in *T. kansasensis*, suggesting a relatively basal divergence within Tylosaurinae. However, *T. iembeensis* is significantly larger than *T. kansasensis*, approaching the size of *T. nepaeolicus* and *T. proriger*. 

FIGURE 10. *Toxochelys* sp. from the Maastrichtian of Bentiaba: A-F, peripheral plaque; G, hyoplastron (MGUAN_PA 016).
Halosaurinae Bardet et al., 2005a

*Halisaurus* sp.

Material: MGUAN-PA18, Two partial skeletons including many elements of the skulls, vertebrae, ribs, and limb.

Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian.

Comments: These specimens (Fig. 14 A and B) will be described and named elsewhere; however, preliminary phylogenetic analysis supports its referral as a new species, closely related to *Halisaurus arambourgi* and *H. platyspondylus* (Polcyn et al., 2007a).

*Phosphorosaurus* sp.

Material: MGUAN-PA52, isolated partial frontal.

Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian.

Comments. This isolated partial frontal (Fig. 14 C and D) allows description and comparison with the type material of *Phosphorosaurus ortliebi* from the Maastrichtian of Belgium (IRSNB R34). The frontal is damaged, missing a small portion of the posterior border, the posterolateral edges, and a significant portion anteriorly. The lateral margins, dorsal and ventral surfaces are largely intact. MGUAN-PA52 belongs to a relatively small animal, the frontal measuring 35 mm wide at its widest point anterior to the orbits, and 61 mm long as preserved, thus it belongs to an individual that was approximately 1.5 to 2 meters long.

The dorsal surface bears a strong, tall median ridge along the entire length of the frontal, terminating posteriorly in a prominent triangular boss. There is a significant supraorbital constriction, the preserved lateral margins are strongly convex antorbitally. The dorsal surface is striated, with strong longitudinal ridges near the midline, and more laterally, weaker ridges occur, radiating anterolaterally to meet the lateral margins. Ventrally, the frontal has a broadly open olfactory canal, the descending processes are prominent, forming blunt parallel ridges anteriorly and grading to finer narrow ridges interorbitally, where they trend toward but do not meet the midline, then diverge as low blunt ridges posteriorly. Two sulci are present on this posterior portion, corresponding to the structures labeled by Russell (1967, his text-figure...
FIGURE 12. Select examples of *Prognathodon* specimens. Right maxilla of the holotype of *P. kianda* MGUAN-PA 129 in (A) lateral, and (B) medial views; Fragment of (C) specimen of *P. cf. saturator* MGUAN-PA 159 in right lateral view; photomosaic of an articulated specimen of *P. kianda* excavated during the 2010 field season. All from the Maastrichtian of Bentiaba, Namibe Province. Scale bars = 10 cm.
FIGURE 13. Skull of the mosasaur *Angolasaurus bocagei* from the Turonian of Iembe, Angola.

FIGURE 14. Right quadrate of *Halisaurus novum* sp. from the Maastrichtian of Bentiaba in (A) lateral and (B) medial views; *Phosphorosaurus* sp. from the Maastrichtian of Bentiaba in (C) dorsal and (D) ventral view; *Halosaurinae* n. gen. novum sp. from ?Santonian of Iembe, (E-G) Caudals, (H) dorsal, and (I) cervical vertebrae in right lateral, dorsal, ventral and posterior views. Scale bars = 5 cm.
4) as accommodating the cerebral hemispheres. The articulation for the postorbitofrontal is missing due to breakage. The prefrontal articulation is only weakly developed antorbitally, slightly incising the lateral surface of the descending processes and forming a simple, fibrous lap-joint with ventral surface of the frontal but with no corresponding excavation.

*Phosphorosaurus ortliebi* was described and named by Dollo (1889) and subsequently redescribed and referred to the genus *Halisaaurus* by Lingham-Soliar (1996). Some characters do unite *Phosphorosaurus* with *Halisaaurus*, including the configuration of the quadrate but significant differences also exist, warranting retention of Dollo’s (1889) genus (Polcyn et al., in press). These include the strong median ridge along the entire length of the dorsal surface, terminated posteriorly by a triangular boss and the pineal foramen location on the frontoparietal suture. A weak posteriorly placed triangular boss is visible in *H. platyspondylus* and *H. arambourgi*, but in those taxa, the median ridge is restricted to the anterior part of the frontal and the pineal foramen rests within the parietal table (Holmes and Sues, 2000; Bardet et al., 2005a).

*Halisaurinae* sp.

Material: MGUAN-PA 070 Cervical vertebra, two dorsal vertebrae and four caudal vertebrae (Fig. 14 E - I).

Locality and horizon: Iembe (Bengo Province); Santonian.

Comments: The four caudal vertebrae were found together and two are still articulated. The remaining vertebrae were found as isolated specimens. The single cervical vertebra (Fig. 14 I), is an axis and has an oblique intervertebral articulation, a broadly oval condyle, and relatively large hypapophysis. The dorsal vertebra (Fig. 14 H) bears an oblique intervertebral articulation, has a weak constriction anterior to condyle, its condyle is wider than high, and the synapophyses originate anteriorly. The caudals (Fig. 14 E, F and G) have a roughly symmetrical hexagonal condyle, relatively large haemal arches, a ventral sulcus between haemal arch bases, and large prezygopophyses. Although

FIGURE 15. Left femur (MGUN-PA163) of pterosaur (possible ornithocheiroid) from the Maastrichtian of Angola.
no cranial material has been collected, the combination of characters present in the vertebral elements supports the referral to the Halisaurinae (Polcyn et al., 2009). This specimen is diminutive and judging from the size of individual centra, would have been no more than about 1.5 meters in length. It represents the oldest halisaurine outside North America and presuming the Santonian date as reliable, is approximately as old as the holotype of Eonatator sternbergi (See Bardet et al., 2005a) from the Santonian of Kansas.

PTEROSAURS

So far, pterosaur remains have only been recorded from the Maastrichtian of Bentiaba. Several bones were collected, mainly incomplete and isolated. Here we present the preliminary data on the first report for pterosaurs in Angola.

Pterosauria Kaup 1834
Pterodactyloidea Plieninger 1901
Ornithocheiroidea Seeley 1876

Material: Left femur (MGUN-PA163; Fig. 15).
Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian.
Comments: Attribution of this specimen to the Ornithocheiroidea is due the femoral head with distinct stout neck and steeply directed caput (see Unwin, 2003: character 38). However, this referral is tentative.

DINOSAURS

Dinosaurs were unknown in Angola until the publication of Angolatitan adamastor Mateus et al., 2011. Here we report two additional bones from Bentiaba (Mocuio Formation, middle part of the Maastrichtian) belonging to distinct individuals. Material includes the distal end of a propodial element and a phalanx.

Dinosauria Owen, 1842
Saurischia Seeley, 1888
Sauropoda Marsh, 1878
Eusauropoda Upchurch, 1995
Neosauropoda Wilson and Sereno, 1994
Somphospondyli Wilson and Sereno, 1998
Angolatitan adamastor Mateus et al., 2011

Material: MGUAN-PA3. The only material known is the forelimb and scapular girdle, including the scapula, humerus, ulna, radius, and metacarpals I, III, and IV. Locality and horizon: North of Iembe (Bengo Province); Turonian.
Comments: A forelimb of the sauropod dinosaur Angolatitan adamastor Mateus et al., 2011 (Fig. 16) from the late Turonian of Iembe, represents the first dinosaur

FIGURE 16. Artistic reconstruction of Angolatitan sauropod dinosaur, in the Cretaceous coast of Angola (artwork by Karen Carr).
FIGURE 17. Left pedal phalanx II-2 (MGUAN-PA 176) of Hadrosauroida dinosaur from the Maastrichtian of Angola, in proximal (A), dorsal (B), ventral (C), medial (D), and distal (E) views.

discovery in Angola, and is one of the few occurrences of sauropod dinosaurs in sub-Saharan Africa with a reliable geochronological dating. The marginal marine sediments yielding the specimen are reported to be late Turonian in age (see more on the geology of Iembe in Antunes, 1964, Jacobs et al., 2006), thus it is a non-titanosaurian sauropod in sub-Saharan Africa at a time supposed to be dominated by titanosaurians. Moreover, *Angolatitan adamastor* is the only basal somphospondyl known in the late Cretaceous, which implies the existence of relict forms in Africa. *Angolatitan* is more derived than *Giraffatitan* but less derived than *Euhelopus*, which is notable given its relatively late appearance in the sauropod fossil record. Its habitat is thought to have been an arid setting.

Ornithopoda Marsh, 1881
Iguanodontia Baur, 1891
Hadrosauroida Sereno, 1986

Material: MGUAN-PA 176, a single phalanx (Fig. 17).
Locality and horizon: Bentiaba (Namibe Province); middle Maastrichtian.
Comments: A single isolated phalanx from Bentiaba is here interpreted as the left pedal phalanx II-2 of an ornithopod, due to the proximodistal short proportion, presence of two assymetrical distal condyles and proximal pits, and trapezoidal outline in distal view. Is not considered a theropod due to the lack of pneumatic cavity, shallow collateral pits and being wider than it is...
long. The ventro-lateral and ventro-medial margins have a expanded lip, which is seen in the pedial phalanx II-2 of hadrosaurs but unusual in other dinosaurs. Prieto-Márquez and Wagner (2009: character 295) consider that length/width proportions of pedial phalanx II2 (http://www.morphbank.net/Show/?id=461032) subsquared, only slightly shorter proximodistally than it is wide mediolaterally is seen in Ouranosaurus nigeriensis and Hadrosauroida, as Probactrosaurus spp., Bactrosaurus johnsoni, Gilmoreosaurus mongoliensis, Lophorhotodon atopus, and Saurolophinae, but not in Lambeosaurinae (except for L. lambei). Therefore, although this is not an unambiguous synapomorphy, it is more distributed in non-lambeosaurine hadrosauroids. The Hadrosauroida clade is not known in the fossil record of Africa, so if this interpretation is correct, this phalanx represents the possible first Hadrosauroida in that continent.

Dinosauria indet.

Material: MGUAN-PA 175, distal part of ?humerus. Locality and horizon: Bentiba (Namibe Province); middle Maastrichtian. Comments: The specimen is the distal end of a large propodial, likely a humerus. Collected in 2010, the specimen is unprepared and identification is preliminary. Assignment to Dinosauria is based on its large size, well formed distal condyles, and long shaft. The very thick medullary region excludes the possibility it belongs to a theropod dinosaur.

Associated fauna (Chondrichthyes, Osteichthyes, and invertebrates)
Although the associated fauna (Chondrichthyes, Osteichthyes and invertebrates) is outside the focus of this article, the Mesozoic of Angola has proven to be very productive of some clades, namely on the Chondrichthyes and marine molluscs. In Appendix 1, we provide the compilation of Mesozoic fossil animal species (excluding amniotes), with the systematic, chronostratigraphic and geographic data, and bibliographic source, compiled using the available scientific publications, including geological maps explanations and recent PhD theses (for example, Tavares, 2006). We recognize that much of the taxonomy might require revision, so we have excluded reports that seem doubtful and pre-1960 citations of genera not existing in the Paleobiology Database (www.paleodb.org). That decision reduces the list of taxa, but guarantees that most taxonomy is updated. This should be seen as a historical list of species reported to Angola. To date, over 700 animal species have been reported from the Cretaceous of Angola. Over 80% of those taxa is represented by molluscs, mainly ammonites, which represent around 70% of the total mollusca species.

Ammonites alone provide more than half of the taxa found and were as such an important component of the Angolan Late Cretaceous marine ecosystem. More than fifty species of Chondrichthyes have been reported in the literature (Antunes and Cappetta, 2002) and represent the most diverse vertebrates in the study area. Other important groups include the Osteichthyes, with 18 species, and the Echinodermata with 60 taxa.

Summary taxa checklist.
Checklist of the Mesozoic amniotes of Angola (see Appendix 1 for invertebrates and non-amniote vertebrates list):

Chelonia
- Eucryptodira
- Angolachelonia
  - Angolachelys mbaxi Mateus et al., 2009 (Turonian)
  - ?Eucallasses sp. (middle part of the Maastrichtian)
- Protostegidae
  - Protostega sp. (middle Maastrichtian)
- Protostegidae indet aff. Calcarichelys (middle part of the Maastrichtian)
- Toxochelyidae
  - Toxochelys sp. (middle Maastrichtian)

Plesiosoria
- Plesiosauroida
cf. Tourangisaurus (middle part of the Maastrichtian)
- Elasmosauridae indet. (middle part of the Maastrichtian)

Squamata
- Mosasauridae
- Mosasaurinae
- Pliosaurini
  - Mosasaurus sp. aff. hoffmanni Mantell 1829 (middle part of the Maastrichtian-late Maastrichtian)
- Globidensini
  - Globidens phosphaticus Bardet and Pereda Suberbiola, 2005b (middle part of the Maastrichtian)
  - Progynothodon kianda Schulp et al., 2008 (Maastrichtian)
  - Progynothodon cf. saturator Dortangs et al. 2002 (Maastrichtian)
- Plioplatecarpinae
  - Angolasaurus bocagei Antunes, 1964 (Turonian)
  - “Platecarpus” psychodon Arambourg, 1952 (Maastrichtian)
- Halisaurinae
  - Halisaurus sp. (Maastrichtian)
Cretaceous amniotes from Angola: dinosaurs, pterosaurs, mosasaurs, plesiosaurs, and turtles

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APPENDIX 1. List of non-amniotes (anthozoans, brachiopods, molluscs, echinoderms, arthropods and fishes) from the Mesozoic of Angola.

This list represents the historical reports of the Mesozoic Angolan fauna (see criteria in the text). There was an attempt for taxonomical updates but revision may be required in most groups, which was out of the scope of this article. Therefore, this list should be regarded critically.

**Anthozoa**
The only Anthozoa species in this list was reported in Galvão (1972).

**Scleractinia: Astrocenioidae**
Astrocoenia konincki (upper Albian; B)

**Brachiopoda**
The only Brachiopoda species is mentioned both in Galvão (1972) and Lapão (1971).

**Rhyynchonellata: Terebratulidae**
Terebratula depressa Lamarck, 1819 (upper Albian; B)

**Mollusca**

_Acera thevestensis_ (Coquand 1862) (upper Albian; B)
_Acera choffiatii_ Rennie 1945 (Senonian; B)

**Mollusca- Bivalvia**


**Arcoida: Arcidae**
_Area (Senilia) senilis_ (Linnaeus, 1758) (upper Albian; B)
_Area sp._ 1758 (lower to upper Albian; B and N)

**Arcoida: Cucullaeidae**
Pseudocucullaea lens Solger, 1903 (Albian to Campanian; N)

**Arcoida: Glycymerididae**
_Trigonarca aff. galdrina_ d’Orbigny 1871 (Cretaceous; N)
_Trigonarca angolensis_ Rennie, 1929 (Coniacian to Maastrichtian; N)
_Trigonarca cameronensis_ Riedel, 1932 (Cretaceous; N)
_Trigonarca cf. diceras_ (Seguenza, 1882) (upper Albian; B and K)
_Trigonarca cf. ligeriensis_ d’Orbigny, 1844 (Albian; B)
_Trigonarca cf. trichinopolitensis_ (Forbes, 1846) (Coniacian to Campanian- Maastrichtian; N)

**Arcoida: Paralleloodontidae**
Nemodon natalsensis (Baily, 1855) (Campanian; N)
_Grammatodon aff. carinatus_ (Sowerby, 1813) (Cretaceous; N)

**Carditoidea: Astartidae**
_Astarte_ sp. Sowerby, 1816 (Albian; K)
_Nicaniella (Nicaniella) aff. trigonoides_ (Stoliczka, 1871) (Cretaceous; N)

**Carditoidea: Carditidae**
_Cardita beaumonti_ d’Archiac & Haime, 1854 (Maastrichtian; N)
_Cardita cf. beaumonti_ d’Archiac & Haime, 1854 (Senonian; B)
_Cardita barroneti_ Munier-Chalmas, 1881 (Senonian; N)
_Glyptoactis_ (Baluchicardia) _ameliae_ Peron 1936 (Maastrichtian; B)
_Venericardia nautilensis_ Cox, 1952 (Senonian; N)

**Carditoidea: Crassatellidae**
_Crassatelles_ sp. Krueger, 1823 (Cretaceous; B)
_Crassatella numidica_ Munier-Chalmas, 1881 (Maastrichtian; N)

**Heterodonta: Poromyidae**
_Lipiopithis_ (Psilomya) _corrugata_ Woods, 1828 (Campanian; N)

**Limoida: Limidae**
_Lima (Mantellum)_ sp. (Campanian-Maastrichtian; N)
_Lima (Plagiostoma) _grenieri_ (Coquand, 1862) (Turonian to Campanian; N)

**Myoida: Corbulidae**
_Corbula elegans_ Sowerby, 1827 (Coniacian; N)
_Corbula truncata_ Sowerby, 1836 (upper Cretaceous; N)

**Mytiloida: Mytilidae**
_Lithodomus_ sp. Cuvier, 1817 (Cretaceous; N)
.Modeiolus _typicus concentrica_ Dartevelle, 1957 (Cenomanian to upper Senonian; N)
_Perna_ sp. Retzius, 1788 (upper Aptian; K and N)
_Volva_ sp. Scopoli, 1777 (Albian; B)

**Nuculoida: Nuculidae**
_Acila (Truncacila) _bivirgata_ (Sowerby, 1836) (upper Albian; B)
_Nucula aff. antiquata_ Sowerby 1825 (upper Albian; B)

**Pectinoida: Pectinidae**
_Camptonectes virgatus_ Nilsson, 1827 (Coniacian; N)
Pecten curvatus Geinitz, 1843 (Cretaceous; N)
Neithea quadricostata Sowerby, 1814 (Albian; B)
Neithea quinquecostata Sowerby, 1814 (Albian; B)
Pecten sp. Müller (1776) (upper Albian; B)
Neithea aequicostata (Lamarck, 1819) (upper Albian to Turonian?; B)
Neithea tricostata Coquand (Albian to Cenomanian; B and K)
Neithea angoliensi Newton, 1916 (Albian; B)
Neithea shawi Pervinquiére (middle part of the Albian to upper Albian; B)
Neithea salinasensis Rennie, 1930 (Senonian; N)
Eopecten studeri (Pictet and Roux) (upper Albian; B)
Pectinoida: Plicatulidae
Plicatula cf. jerryi Coquand (Turonian to Maastrichtian; N)
Plicatula ferryi Coquand, 1862 (Cretaceous; N)
Plicatula instabilis Stoliczka, 1871 (Cretaceous; N)
Plicatula sp. Lamarck (1801) (upper Albian to Turonian?; B and K)
Pectinoida: Spondylidae
Spondylus angolensis sp. (Cretaceous; N)
Pholadomyoida: Laterulidae
Ceromya gurgitis Pictet & Campiche, 1865 (upper Albian; B)
Pholadomyoida: Pholadomyidae
Pholadomya aff. tigris Noetling (Senonian; K)
Pholadomya pleuromyaformis Choffat (lower Aptian to Albian; B and N)
Pholadomya vinnesi Latet, 1877 (upper Albian; B)
Pterioida: Gryphaeidae
Exogyra (Costagryra) olisiponensis Sharpe, 1850 (Cenomanian- Turonian; B, K and N)
Exogyra aff. olisiponensis Sharpe, 1850 (upper Albian?; B)
Exogyra cf. conica Sowerby, 1813 (Albian; K)
Exogyra cf. flabellata (Goldfuss, 1833) (Albian; B)
Exogyra ostracina Lamarck, 1801 (Aptian- Albian; B and N)
Exogyra overweigide Buch (upper Albian; B)
Pycnodonta cf. vesicularis Lamarck, 1806 (upper Albian; B)
Pycnodonta f'icky Pervinquiére (Senonian; B)
Pycnodonta vesicularis Lamarck, 1806 (Cenomanian-Turonian; B)
Rhyynchostreon cf. suborbiculatum (Lamarck, 1801) (Cenomanian; N)
Rhyynchostreon cf. suborbiculatum Cooper, 1972 (upper Cenomanian; N)
Rhyynchostreon suborbiculatum Cooper, 1972 (upper Cenomanian- lower Turonian; N)
Pterioida: Inoceramidae
Inoceramus expansus Baily, 1855 (Maastrichtian, Senonian; B)
Inoceramus regularis d’Orbigny, 1842 (Campanian/ Maastrichtian; K)
Inoceramus sp. (Cenomanian to Senonian; B, N and K)
Tethyoceramus madagascariensis Heinz, 1933 (Maastrichtian; B)
Pterioida: Isognomonidae
Isognomon neivai Soares, 1965 (Senonian (Campanian?); N)
Pterioida: Ostreidae
Lopha cf. diluviana Linnaeus, 1767 (upper Albian; B)
Lopha cf. lombardi Freneix (Santonian to Campanian; N)
Lopha syphax Coquand, 1854 (upper Albian; B)
Ostrea baylei, Guer (Cenomanian- Turonian?; B)
Ostrea szajnochai Choffat (Cenomanian- Turonian?; B and N)
Pycnodonte (Pycnodonte) biauriculatum (Lamarck, 1819) (Albian; K)
Pterioida: Pinnaidae
Pinna cf. robinaldina d’Orbigny, 1844 (Cenomanian ?; B)
Pinna petrina White, 1874 (Cretaceous; N)
Pterioida: Pteriidae
Avicula sp. Bruguieres (1791) (Cretaceous; N)
Trigonioida: Trigonidae
Pterotrignia (Acanthotrignia) shepstonei (Griesbach, 1871) (Senonian (Campanian?); N)
Pterotrignia (Scabrotrignia) cf. scabra (Lamarck, 1819) (Cretaceous; N)
Pterotrignia (Scabrotrignia) scabra (Lamarck, 1819) (Cretaceous; N)
Trigonia (Scabrotrignia) borgesi Rennie (Senonian; B)
Trigonia (Scabrotrignia) shepstonei Griesbach, 1871 (Campanian-Maastrichtian; N)
Trigonia af. spinosa Parkinson, 1811 (Cretaceous; N)
Trigonia aliformis (Parkinson) Roemer, 1849 (Cretaceous; N)
Trigonia scabra Lamarck, 1819 (Coniacian; N)
Trigonia sp. Bruguieres, 1789 (Aptian to Albian; B)
Veneroida
Agelasina plenodonta Riedel, 1932 (Coniacian to Maastrichtian; N)
Veneroida: Arcticae
Cyprina (Venilicardia) cf. barrosi Coquand (Coniacian; N)
Cyprina sp. Schumacher (1817) (Cretaceous; N)
Venilia duri Munier-Chalmas, 1881 (Turonian to Maastrichtian; B and N)
Venilia forbesiana Stoliczka, 1871 (Cenomanian to Maastrichtian; B and N)
Venilicardia odonelli Rennie 1945 (Maastrichtian; B)
Veneroida: Cardiidae
Cardium sp. Linnaeus, 1758 (Cretaceous; B)
Cardium (Trachycardium) reynoldsi Rennie, 1929 (Senonian; B and N)
Cardium cf. gentianum Sowerby, 1796 (upper Albian; B)
Cardium hillanum Sowerby, 1813 (Cretaceous; N)
Granocardium (Granocardium) productum Sowerby, 1832 (Albian to Campanian; N)
Granocardium (Granocardium) reynoldsi (Rennie) (Cenomanian to Maastrichtian; B and N)
Integricardium aphaeroideum Forbes (upper Albian; B)
Globocardinum cf. sphaeroideum Forbes, 1845 (upper Aptian; B)
Globocardinum Integrigradum sphaeroxideum Forbes, 1845 (upper Albian; B)
Protocardinia cf. hillina Sowerby, 1813 (upper Albian; B)
Protocardinia hillina Sowerby, 1813 (Cenomanian; K and N)
Protocardinia moutai Rennie, 1940 (Senonian; B)
Veneroida: Lucinidae
Lucina angolensis Rennie, 1929 (Cretaceous; B)
Lucina egitoensis Rennie, 1940 (Senonian; B)
Lucina reinckeii Rennie, 1929 (Cretaceous; K)
Veneroida: Tellinidae
Tellina (Palaeomeore) sp. Linnaeus, 1758 (Campanian; N)
Veneroida: Thyasiridae
Thyasira cretaee Whiteaves, 1903 (Maastrichtian, Senonian; B)
Veneroida: Veneridae
Aphrodina (Mesocallistida) cf. andersoni Newton (lower Albian; N)
Trigonocallista umzambiensis (Woods) (Campanian? to Campanian-Maastrichtian; N)
Venus plana Sowerby, 1812 (Coniacian; N)

Mollusca - Cephalopoda

Ammonoidea: Acanthoceratidae
Acanthoceras cf. tunetana Pervinquière, 1907 (Cenomanian; B)
Calycoceras annulatum Collington, 1964 (Cenomanian; B)
Calycoceras coloroense perostata Collington, 1964 (Cenomanian; B)
Calycoceras naviculare (Mantell, 1822) (lower Turonian; B)
Eucalycoceras sp. Spath (1923) (upper Cenomanian; N and B)
Euomphaloceras (Kanabericeras) septem-seriatum (Cragin, 1893) (L. Cenom.- E. Turon.; B and N)
Euomphaloceras cunningtoni meridionium Stoliczka, 1864 (Cenomanian; B)
Euomphaloceras cunningtoni, Sharpe (lower Cenomanian to middle Cenomanian; B)
Euomphaloceras euphemalum (Sharpe, 1855) (Cenomanian-Turonian?; B)
Mammites mocamedensis Howarth, 1966 (middle Turonian to lower Coniacian; N)
Mantelliceras cf. saxbii Sharpe, 1857 (lower Conomanian; K)
Mantelliceras sp. Hyatt, 1903 (Turonian to Santonian; B)
Metoicoceras cf. whitei Hyatt, 1903 (upper Cenomanian; N)

Metoicoceras gibbosum Hyatt, 1903 (upper Cenomanian-Lower Turonian; N)
Protacanthoceras sp. Spath, 1923 (upper Cenomanian; N)
Protacanthoceras angolaense Spath, 1931 (Cenomanian; N)
Pseudaspisoceras foetidum Stolickzka, 1864 (lower Turonian; B)
Pseudaspisoceras sp. Spath, 1903 (lower Turonian; B)
Pseudocalycoceras aff. haugi (Pervinquière, 1907) (upper Cenomanian- lower Turonian; N)
Pseudocalycoceras angolaense (Spith, 1931) (upper Cenomanian- lower Turonian; N)
Romaniaceras sp. Spath, 1923 (Turonian; K)
Sharpeiceras florenciae Spath, 1925 (lower Cenomanian; B)
Sharpeiceras goliath Haas, 1942 (Turonian to Santonian; K)
Sharpeiceras indicum Kossmat (upper Albian? to lower Cenomanian; B)
Sharpeiceras lataviculum Sharpe, 1855 (lower Cenomanian; K)
Sharpeiceras mexicanum Böse, 1928 (lower Cenomanian; B)
Sharpeiceras schlueteri Hyatt, 1903 (upper Albian? to lower Cenomanian; B)
Watinoceras coloradoense (Henderson, 1908) (upper Cenomanian- lower Turonian; N)

Ammonoidea: Anisocrateridae
Anisoceras aff. armatum (Sowerby, 1817) (upper Albian; B)
Anisoceras armatum (Sowerby, 1817) (lower to Upper Albian; B)
Anisoceras arrogans (Giebel, 1852) (upper Albian; B)
Anisoceras jacobi (Breistroffer) (upper Albian; B)
Anisoceras perarmatum Pictet & Campiche, 1861 (upper Albian; B)
Anisoceras picteti Spath, 1926 (upper Albian; B)
Anisoceras plicatile (Sowerby, 1819) (Cenomanian; B)
Anisoceras pseudoelgans Pictet & Campiche, 1861 (upper Albian; B)
Anisoceras reni Kotetishvili, 1984 (upper Albian; B)
Anisoceras saussureanum spinosa Haas, 1942 (upper Albian; B)
Anisoceras subarcuratum Spath, 1938 (upper Albian; B)
Anisoceras teixeirai Collington, 1978 (upper Albian; B)
Hysterceras cf. varicosum (Sowerby, 1824) (upper Albian; B)
Idiohamites spiniger (Sowerby, 1818) (upper Albian; B)
Idiohamites subspiniger Spath, 1939 (upper Albian; B)
Protanisoceras sp. (upper Albian; B)

Ammonoidea: Baculitidae
Baculites aff. asper Morton, 1830 (upper Senonian; N)
Baculites anceps Lamarck, 1822 (Turonian to Santonian; K)
Baculites capensis Woods, 1906 (lower Campanian; K)
Baculites cf. anceps Lamarck, 1822 (Turonian to Santonian; K)
Baculites subanceps Haughton, 1925 (upper Campanian; K)
Sciponoceras gracile (Shumard, 1861) (upper Cenomanian-lower Turonian; K and N)
Ammonoidea: Brancoceratidae

Dipoloceras aff. quadratum Spath, 1921 (upper Albian; B)
Dipoloceras bouchardianum (d’Orbigny, 1841) (upper Albian; B)
Dipoloceras cf. subdelkaruei Spath, 1931 (upper Albian; B)
Dipoloceras pseudaoon moliniformis Spath (middle to upper Albian; B)
Dipoloceras rectangulare Spath (upper Albian; B)
Dipoloceras remotum Spath, 1931 (middle to upper Albian; B)
Dipoloceras symmetricum Sowerby (upper Albian; B)
Hysteroceras aff. antipodeum Etheridge, 1902 (upper Albian; B)
Hysteroceras binum (Sowerby, 1815) (upper Albian; B)
Hysteroceras binum lobitoensis Haas, 1942 (upper Albian; B)
Hysteroceras carinatum Spith, 1922 (upper Albian; B)
Hysteroceras carinatum haasi Collignon, 1978 (upper Albian; B)
Hysteroceras cf. subbinum Spath, 1934 (upper Albian; B)
Hysteroceras choifati Spath, 1925 (upper Albian; B)
Hysteroceras falcisatum Haas, 1942 (upper Albian; B)
Hysteroceras orbignyi minor Haas, 1942 (upper Albian; B)
Hysteroceras orbignyi (Spith, 1922) (upper Albian; B)
Hysteroceras propinquum Haas, 1942 (upper Albian; B)
Hysteroceras semileve Haas, 1942 (upper Albian; B)
Hysteroceras cf. simplicostatum (Spith, 1934) (upper Albian; B)
Hysteroceras varicosum angolatum Haas, 1942 (upper Albian; B)
Hysteroceras varicosum Sowerby, 1824 (upper Albian; B)
Mortoniceras (Angolaites) gregoryi Spath, 1922 (upper Albian; B)
Mortoniceras (Angolaites) simplex Choffat, 1905 (upper Albian; B)
Mortoniceras (Angolaites) vicina Haas, 1942 (upper Albian; B)
Mortoniceras (Angolaites) wintoni Adkins, 1920; upper Albian; B)
Mortoniceras (Boesites) aff. barbouri Haas, 1942 (upper Albian; B)
Mortoniceras (Boesites) barbouri Haas, 1942 (upper Albian; B)
Mortoniceras (Boesites) haasi Collignon, 1978 (upper Albian; B)
Mortoniceras (Boesites) howelli Haas, 1942 (upper Albian; B)
Mortoniceras (Boesites) proteus (Haas, 1942) (upper Albian; B)
Mortoniceras (Boesites) romeri Haas, 1942 (upper Albian; B)
Mortoniceras (Boesites) stoliczki Spath, 1922 (upper Albian; B)
Mortoniceras (?Boesites) vokesi (Haas, 1942) (upper Albian; B)
Mortoniceras (Pervinquieria) ferecostata (Haas, 1942) (upper Albian; B)
Mortoniceras (Pervinquieria) howelli (Haas, 1942) (upper Albian; B)
Mortoniceras (Pervinquieria) inflatum Sowerby, 1818 (upper Albian; B)
Mortoniceras (Pervinquieria) margarita (Haas, 1942) (upper Albian; B)
Mortoniceras (Pervinquieria) margaritatum Haas (upper Albian; B)
Mortoniceras (Pervinquieria) montraynaudensis (Haas, 1942) (upper Albian; B)
Mortoniceras (Pervinquieria) perarmata (Haas, 1942) (upper Albian; B)
Mortoniceras (Pervinquieria) pricei intermedia Spath, 1932 (upper Albian; B)
Mortoniceras (Pervinquieria) proteus (Haas, 1942) (upper Albian; B)
Mortoniceras (Pervinquieria) rochall Collignon, 1978 (upper Albian; B)
Mortoniceras (Pervinquieria) romeri (Haas, 1942) (upper Albian; B)
Mortoniceras (Pervinquieria) stoliczkae (Spath, 1922) (upper Albian; B)
Mortoniceras (Pervinquieria) velliferum van Hoepen (upper Albian; B)
Mortoniceras (Pervinquieria) vicinia (Haas, 1942) (upper Albian; B)
Mortoniceras (subgenus ?) rochall (Collignon, 1978) (upper Albian; B)
Mortoniceras (Subschloenbachia) aequatorialis Kosmat (upper Albian; B)
Mortoniceras (Subschloenbachia) angolanus Collignon, 1978 (upper Albian; B)
Mortoniceras (Subschloenbachia) antunesi Collignon, 1978 (upper Albian; B)
Mortoniceras (Subschloenbachia) cf. subquadratum Spath, 1933 (upper Albian; B)
Mortoniceras (Subschloenbachia) crassicostatum Spath, 1922 (upper Albian; B)
Mortoniceras (Subschloenbachia) depressum Spath, 1922 (upper Albian; B)
Mortoniceras (Subschloenbachia) depressum Spath, 1922 (upper Albian; B)
Mortoniceras (Subschloenbachia) gracillima Kosmat, 1895 (upper Albian; B)
Mortoniceras (Subschloenbachia) inflata Sowerby, 1847 (upper Albian to Cenomanian; B and N)
Mortoniceras (Subschloenbachia) irregularis Collignon, 1978 (upper Albian; B)
Mortoniceras (Subschloenbachia) netoi Collignon, 1978 (upper Albian; B)
Mortoniceras (Subschloenbachia) af. perinflatus Spath 1932 (upper Albian; B)
Mortoniceras (Subschloenbachia) perinflatus Spath, 1932 (upper Albian; B)
Mortoniceras (Subschloenbachia) cf. quadratum Spath, 1933 (upper Albian; B)
Mortoniceras (Subschloenbachia) rectangulatus Collignon, 1978 (upper Albian; B)
Mortoniceras (Subschloenbachia) rostratum Sowerby, 1817 (upper Albian; B)
Mortoniceras (Subschloenbachia) cf. subquadratum crassicostatum Spath, 1933 (upper Albian; B)
Mortoniceras (Subschloenbachia) subquadratatus Spath, 1933 (upper Albian; B)
Mortoniceras (Subschloenbachia) dacestai (Collignon 1978) (upper Albian; B)
Mortoniceras (Subschloenbachia) vicinia (Haas, 1942) (upper Albian; B)
Mortoniceras (Subschloenbachia) perinflatus Spath, 1932 (upper Albian; B)
Mortoniceras (Subschloenbachia) angolanus Collignon, 1978 (upper Albian; B)
Mortoniceras (Subschloenbachia) curvicornu (Spath, 1922) (upper Albian; B)
Mortoniceras (Subschloenbachia) crassicostatum Spath, 1922 (upper Albian; B)
Mortoniceras (Subschloenbachia) costatum Haas, 1942 (upper Albian; B)
Mortoniceras (Subschloenbachia) crassicostatum Howarth, 1965 (upper Albian; B)
Mortoniceras (Subschloenbachia) curvicornu Spath, 1922 (upper Albian; B)
Mortoniceras (Subschloenbachia) gr. corvicornu (Spath, 1921) (upper Albian; B)
Mortoniceras (Subschloenbachia) magnum Haas, 1942 (upper Albian; B)
Mortoniceras (Subschloenbachia) pseudovaricosum Spath, 1922 (upper Albian; B)
Mortoniceras (Subschloenbachia) singulare Haas, 1942 (upper Albian; B)
Mortoniceras (Subschloenbachia) subruberculatum Spath, 1922; Upper Albian; B)
Mortoniceras (Subschloenbachia) trituberculatum Howarth, 1965 (upper Albian; B)
Mortoniceras (Subschloenbachia) subruberculatum Spath, 1922; Upper Albian; B)
Mortoniceras (Subschloenbachia) trituberculatum Howarth, 1965 (upper Albian; B)
Oxytropidoceras (Manuamniceras) sp. (Spath, 1925) (middle Albian; B)
Oxytropidoceras (Mirapelia) aff. mirapelium (d’Orbigny, 1850) (middle Albian; B)
Oxytropidoceras (Mirapelia) sergipense (White, 1887) (middle Albian; B)
Oxytropidoceras (Oxytropidoceras) bisei (Knechtel, 1947) (middle Albian; B)
Oxytropidoceras (Mirapelia) bauerianum (White, 1887) (middle Albian; B)
Ammonoidea: Coilopoceratidae
Coilopoceras sp. (Lower Turonian to Coniacian; CB and K)
**Ammonoidea: Collignoniceratidae**

*Benuites* sp. (Lower Turonian; B)

*Prionocyclus carvalhoi* Howarth, 1966 (middle Turonian to Lower Coniacian; N)

*Prontexanites* sp. (lower Santonian; N)

*Submartinoceras mariscalense* Young, 1963 (lower Campanian; K)

*Subprionocyclus* sp. Shimizu 1932 (upper Turonian to Lower Coniacian; N and K)

**Texanites angolanus** Haas, 1942 (Turonian to Santonian; K)

*Texanites quiuenodosus* Redtenbacher (Santonian; K)

*Texanites roeneri* (Yabe & Shimizu, 1923) (lower Campanian; K)

**Ammonoidea: Desmoceratidae**

*Beudanticeras* aff. *newtoni* Casey, 1961 (lower to Middle Albian; B)

*Beudanticeras beudanti* Brongniart, 1822 (upper Albian; B)

*Beudanticeras dupianum* (d’Orbigny, 1841) (lower to Middle Albian; B)

*Desmesites aimaunus* Matsumoto, 1957 (middle Turonian to Lower Coniacian; N)

*Desmesites* sp. Matsumoto, 1942 (lower Santonian; N and K)

*Desmoceras* (Desmoceras) *latidorsatum* lemon (Collignon (lower Cenomanian; B)

*Desmoceras* (Desmoceras) *latidorsatum* periflatum Cooper & Kennedy, 1979 (upper Albian; B)

*Desmoceras* (Desmoceras) *latidorsatum* Michelin, 1838 (upper Albian to Lower Cenomanian, B)

*Desmoceras* (Pseudouhligella) aff. *ezoanum* Matsumoto, 1942 (L. Cenomanian- E. Turonian; N)

*Desmoceras* aff. *latidorsatum* Michelin, 1838 (upper Albian; B)

*Desmoceras constrictum* Collignon, 1978 (middle to Upper Albian; B)

*Desmoceras latidorsatum* (Michelin, 1838) (upper Albian; B)

*Desmoceras latidorsatum* periflatum Cooper & Kennedy, 1979 (upper Albian; B)

*Desmophyllites diphylloides* Forbes, 1846 (Senonian; B)

*Haueritites gardini* (?) Baily (Campanian?; B)

*Kitchinites angolaensis* Howarth, 1965 (upper Campanian; B)

*Kitchinites* sp. Spath, 1922 (upper Campanian? to Maastrichtian; B)

*Mesopuzosia yubarensis* Jimbo, 1894 (middle Turonian; N)

*Parapuzosia* (Austiniceras) *dibleyi* Spath, 1922 (upper Cenomanian; N)

*Polyptychoceras pseudogautinum* Yokoyama, 1890 (upper Campanian; B)

*Polyptychoceras* sp. Yabe, 1927 (upper Campanian? to Maastrichtian; B)

*Puzosia* (Anapuzosia) *dibleyi* (Spath, 1922) (L. Cenomanian- E. Turonian; N)

*Puzosia* (Austiniceras) *intermedia orientalis* Matsumoto, 1959 (L. Cenomanian- E. Turonian; N)

*Puzosia* aff. *deficilis* d’Orbigny (upper Albian; B)

*Puzosia* aff. *spathianum* Venzo, 1936 (upper Albian; B)

*Puzosia* bisirctica (White, 1887) (middle Albian; B)

*Puzosia* cf. *mayoriana* (d’Orbigny, 1841) (upper Albian; B)

*Puzosia* cf. *tenuis* Haas, 1942 (upper Albian; B)

*Puzosia* *matheroni* (d’Orbigny, 1840) (lower Cenomanian; B)

*Puzosia* *quenstedti* Parona and Bonarelli, 1897 (upper Albian; B)

*Puzosia* *spathi* Venzo, 1936 (upper Albian; B)

**Ammonoidea: Diplomoceratidae**

*Puzosia* *tenuis* Haas, 1942 (upper Albian; B)

*Scalarites* sp. Wright & Matsumoto, 1954 (lower Coniacian; N)

*Solenoceras bembense* Haas, 1943 (Turonian to Santonian; K)

**Ammonoidea: Diplomoceratidae**

*Aidoceras hoepeni* Collignon, 1978 (upper Albian; B)

*Elobiceras* aff. *intermedium* Spath, 1942 (upper Albian; B)

*Elobiceras* af. *irregulare* Spath, 1922 (upper Albian; B)

*Elobiceras angustum* Spath, 1922 (upper Albian; B)

*Elobiceras browni* Haas, 1942 (upper Albian; B)

*Elobiceras cargumentum* Spath (upper Albian; B)

*Elobiceras cf. *angustum* Spath, 1922 (upper Albian; B)

*Elobiceras cf. *elobiense* Szajnocha (upper Albian; B)

*Elobiceras cf. *flexicostatum* Spath, 1922 (upper Albian; B)

*Elobiceras cf. *spathianum* Haas, 1942 (upper Albian; B)

*Elobiceras conditum* Haas, 1942 (upper Albian; B)

*Elobiceras densicostatum* Spath, 1922 (upper Albian; B)

*Elobiceras elobiense* Szajnocha (upper Albian; B)

*Elobiceras flexicostatum* Spath, 1922 (upper Albian; B)

*Elobiceras haughtoni* Collignon, 1978 (upper Albian; B)

*Elobiceras hexagonum* Haas, 1942 (upper Albian; B)

*Elobiceras intermedium* Spath, 1922 (upper Albian; B)

*Elobiceras irrugulare* rigidecostatum Haas (upper Albian; B)

*Elobiceras irregular* Spath, 1922 (upper Albian; B)

*Elobiceras lobico* Spath, 1922 (upper Albian; B)

*Elobiceras neuparthi* Choffat, 1905 (upper Albian; B)

*Elobiceras orientiformis* Spath (upper Albian; B)

*Elobiceras* *oxypodoceratoides* Haas, 1942 (upper Albian; B)

*Elobiceras primordiale* Haas, 1942 (upper Albian; B)

*Elobiceras raymondii* Haas, 1942 (upper Albian; B)

*Elobiceras rectangulum* arrietiformis Spath, 1922 (upper Albian; B)

*Elobiceras* *spathianum* Haas, 1942 (upper Albian; B)

*Elobiceras subelobiense* Spath (upper Albian; B)

*Goodallitites tremebundum* van Hooen, 1946 (upper Albian; B)

*Hysteroceras* aff. *simplicicostatum* Spath, 1934 (upper Albian; B)

*Hysteroceras* cf. *simplicicostatum* Spath (Albian; B)

*Inflaticeras orientalis* Kossmat (upper Albian; B)

*Inflaticeras stolizkaia* Spath (upper Albian; B)

*Prohysteroceras* aff. *aitchsoni* Young (upper Albian; B)
Prohysteroceras africanum Sornay, 1953 (upper Albian; B)
Prohysteroceras atelchoni Young, 1957 (upper Albian; B)
Prohysteroceras cf. dubium Spath, 1922 (upper Albian; B)
Prohysteroceras decipiens Spath (upper Albian; B)
Prohysteroceras dubium Spath, 1922 (upper Albian; B)
Prohysteroceras gracile Haas, 1942 (upper Albian; B)
Prohysteroceras hanhaense Haas, 1942 (upper Albian; B)
Prohysteroceras nortic Spath (upper Albian; B)
Prohysteroceras wordiei compressa Spath (upper Albian; B)
Prohysteroceras wortelii Spath, 1922 (upper Albian; B)

Ammonoidea: Douvilleiceratidae
Douvilleiceras anequinodum Quenstedt, 1849 (middle Albian; B)
Douvilleiceras inaequidum Quenstedt, 1849 (middle Albian; B)
Douvilleiceras mamillatum anequinodum Quenstedt, 1849 (lower to Middle Albian; B)
Douvilleiceras mamillatum Schlotheim, 1813 (lower to Upper Albian; B)
Douvilleiceras orbignyi Hyatt, 1903 (lower to Middle Albian; B)
Douvilleiceras variabile Tavani, 1949 (middle Albian; B)

Ammonoidea: Forbesiceratidae
Forbesiceras contilni Stephenson (Cenomanian- Turonian; B)
Forbesiceras obtusum Sharpe, 1853 (middle Cenomanian; B)

Ammonoidea: Gaudryceratidae
Anagaudryceras cf. casistianum d’Orbigny, 1850 (upper Cenomanian-Lower Turonian; N)
Anagaudryceras involvulatum (Stoliczka, 1865) (middle Turonian; N)
Anagaudryceras mikobokense Collignon, 1956 (upper Campanian; B)
Gaudryceras (Gaudryceras) isovolynse Collignon, 1964 (upper Cenomanian-Lower Turonian; N)
Gaudryceras aenigma Haas, 1942 (upper Albian; B)
Gaudryceras varigurense Kossmat, 1895 (middle Turonian to Senonian; N and B)

Ammonoidea: Hamitidae
Hamites sp. (upper Albian; B)
Hamites angolensis Choffat (upper Albian; B)
Hamites attenuatus Sowerby, 1814 (lower Albian; B)
Hamites compressus Sowerby, 1814 (middle to Upper Albian; B)
Hamites duplicatus Pictet & Campiche, 1861 (upper Albian; B)
Hamites incurvatus Brown, 1837 (lower Albian; B)
Hamites aff. simplex d’Orbigny, 1842 (Cenomanian; B)
Hamites tenuscostatus Spath, 1941 (lower Albian; B)
Hamites tenuis Sowerby, 1814 (upper Albian; B)
Hamites aff. tenuis Sowerby, 1814 (upper Albian; B)
Hamites venetzianus Pictet, 1847 (upper Albian; B)
Hamites virgulatus Brongniart, 1822 (upper Albian; B)
Hamites aff. virgulatus Brongniart, 1822 (upper Albian; B)
Hamitoides angolanus Haas, 1942 (upper Albian; B)

Ammonoidea: Kossmaticeratidae
Kossmaticeras sp. (lower Coniacian; N)

Ammonoidea: Labeceratidae
Labeceras sp. (upper Albian; B)

Ammonoidea: Libycceratidae
Libycoceras sp. (upper Campanian to Maastrichtian; K)

Ammonoidea: Lyelliceratidae
Stoliczkaia clavigera Neumayr, 1875 (upper Albian; B)
Stoliczkaia dispar d’Orbigny, 1841 (upper Albian; B)
Stoliczkaia dorsetensis Spath, 1832 (upper Albian; B)
Stoliczkaia dorsetensis Spath, 1832 var. compressa Spath (upper Albian; B)
Stoliczkaia notha Seeley, 1865 var. ultima (upper Albian; B)
Stoliczkaia renzi Collignon, 1978 (upper Albian; B)
Stoliczkaia reyrei Collignon, 1978 (upper Albian; B)
Stoliczkaia rhamnomota Spath, 1932 (upper Albian; B)
Stoliczkaia sp. (lower Albian to Cenomanian; N and B)
Stoliczkaia tenuis Renz, 1968 (upper Albian; B)
Tegoceras aff. maderoense Young, 1993 (middle Albian; B)

Ammonoidea: Nostoceratidae
Asonoceras angolanaum Haas, 1943 (Turonian to Campanian; K)
Bosnychoceras sp. (upper Campanian to Maastrichtian; K)
Cirroceras sp. Conrad, 1866 (upper Campanian to Maastrichtian; K and B)
Didymoceras californiae Anderson, 1958 (upper Campanian; K)
Didymoceras cf. angolaense Haughton, 1924 (Campanian-Maastrichtian; K)
Didymoceras hornbyense Whiteaves, 1876 (Campanian; K)
Didymoceras subluberculatum Howarth, 1965 (upper Campanian; B)
Nostoceras helicinus Shumard, 1861 (Turonian to Campanian; B)
Nostoceras hyatti Stephenson, 1941 (upper Campanian; B)
Nostoceras kemense Anderson, 1958 (upper Campanian; B)
Nostoceras mariatheresianum Haas, 1943 (Turonian to Santonian; B)
Nostoceras rotundum Howarth, 1965 (Turonian to Campanian; B)
Nostoceras sp. (upper Campanian; K)

Ammonoidea: Oppelliidae
Aconeeras sp. (upper Albian; B)

Ammonoidea: Pachydiscidae
Eupachydiscus pseudogrossouvrei Collignon, 1955 (Senonian; B)
Eupachydiscus sp. (Campanian? to Maastrichtian; B)
Menuites sp. (upper Campanian; K)

Ammonoidea: Phylloceratidae
Neophylloceras sp. (Maastrichtian; K)
Neophylloceras ultinatum Spath, 1953 (upper Campanian; B)
Phylloceras (Hyphophylloceras) sp. (Cenomanian to Lower Coniacian; N and B)

Cretaceous amniotes from Angola: dinosaurs, pterosaurs, mosasaurs, plesiosaurs, and turtles

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Phylloceras (Hypophylloceras) seresitense Pervinquiére, 1907 (lower Cenomanian; B)
Phylloceras velledae (Michelin, 1834) (upper Albian; B)
Ammonoidea: Placenticeratidae
Hoplitoplacenticeras (Hoplitoplacenticeras) marroti (Coquand, 1859) (upper Campanian; B)
Hoplitoplacenticeras cf. costulosum Schlüter, 1867 (Senonian; B)
Hoplitoplacenticeras cf. marroti Coquand, 1859 (Senonian; B)
Hoplitoplacenticeras costulosum Schlüter, 1867 (Senonian; B)
Placenticeras sp. (lower Senonian; CB)
Proplacenticeras ambiloense Collignon (Conomanian-Turonian; B)
Proplacenticeras fritschi Grossouvre, 1894 (Conianian; K)
Proplacenticeras reinecki Haughton (Conianian; K)
Proplacenticeras sp. (lower Turonian to Lower Conianian; N and B)
Proplacenticeras stantonii Hyatt, 1903 (upper Conomanian; B)
Ammonoidea: Pseudotissotiidae
Hourcquia africana Kroemmelbein, 1965 (Neocomian to Aptian; CB)
Ammonoidea: Ptychoceratidae
Ptychoceras faunier Haas, 1942 (upper Albian; B)
Ammonoidea: Pulchelliidae
Pulchella sp. (lower Conomanian; N)
Ammonoidea: Sphenodiscidae
Eulophoceras globosum Reymont, 1954 (Conomanian-Turonian; B)
Eulophoceras (Paravascoceras) harttii Hyatt, 1870 (upper Conomanian; B)
Eulophoceras (Paravascoceras) cf. caulini Chudeau, 1909 (upper Conomanian-Lower Turonian; N)
Nautilida: Eutrephoceratidae
Eutrephoceras egitoense Miller & Carpenter, 1955 (upper Cretaceous; B)
Eutrephoceras indicum Spengler (upper Senonian; N)
Eutrephoceras similis Spath, 1953 (Senonian; B)
Eutrephoceras sp. (upper Albian to Maastrichtian; B)

Mollusca - Gastropoda

Anaspidae
Akera gregoryi Newton 1917 (upper Albian-Cenomanian; B)
Cephalaspidea: Acteonellidae
Acteonella aff. fusiformis Coquand, 1865 (upper Aptian; K)
Acteonella anchietai Choffat (Aptian to Turonian; N and B)
Acteonella (Trochacteon) cylindracea Stolickza (Conomanian- Turonian; N)
Cephalaspidea: Ringiculidae
Avellana incrassata Sowerby (Cretaceous; K)
Heterobranchia: Architectonicidae
Solarium baily Spath, 1937 (upper Albian; B)
Heterobranchia: Nerineidae
Nerinea kaploi Choffat (Aptian to Turonian; B and N)
Heterostrophia
Mhilaia cf. nerineaformis Coquand (upper Albian; B)
Littorinimorpha: Aporrhaidae
Aporrhais neubaueri Riedel (Campanian to Maastrichtian; N)
Chenopus sp. (Cretaceous; B)
Littorinimorpha: Naticidae
Gyrodes cf. genti Sowerby (Albian; B)
Natica bulbiformis Sowerby, 1870 (Senonian; B)
Natica feiot Choffat (upper Aptian; B)
Echinodermata - Echinoidea


Acroechinoidea: Orthopoida
Orthopsis cf. ruppeli Desor (upper Albian; B)
Orthopsis gr. miliaris (d’Archiac, 1835) (lower to Upper Albian; B)
Orthopsis sp. (Albian- Turonian?; B)

Arbacioida: Arbaciidae
Cottalida aff. benettiae Koenig 1820 (upper Albian; B)
Cassiduloida: Archiaciidae
Acriaster aff. sergipensis Smith, 1991 (upper Albian; B)

Cassiduloida: Clypeidae
Pygopistes sp. (Albian; B)

Cidariidae: Cidariidae
Cidaris vafellus Loriol, 1888 (Cretaceous; B)
Leiocidaris thiebaudi Jeannet, 1955 (Albian; B)
Rhabdocidaris sp. (upper Cretaceous?; B)

Hemicidaroida: family uncertain
Micropedina sphaeroides Stoliczka (Cenomanian- Turonian?; B)

Holasteroida: Holasteridae
Holaster cf. africanus Woods (upper Albian; B)

Cardiaster kelleri Haughton, 1924 (upper Albian; B)
Holaster aff. lerichei Dartvelle, 1953 (Aptian- Albian; B)
Holaster aff. treccensis Leymerie, 1842 (upper Albian; B)

Holoelphidium: Holoelphidium
Passalidae: Passalidae

Orthopodea - Echinoidea
Orthopodea are reported in Blake & Breton (1988), Blake et al., 1996 (upper Coniacian; B)

Littorinimorpha: Tylostomatidiae
Tylostoma aff. rochatianum d’Orbigny, 1850 (upper Albian; B)
Tylostoma globosum Sharpe, 1849 (Cenomanian- Turonian?; B)
Tylostoma perchueli Choixiat (upper Albian; B)

Neotaenioglossa
Pterodonta aff. elongata d’ Orbigny (Cretaceous; K)
Pterodonta cf. inflata d’ Orbigny, 1842 (Albian; B).

Neritopsina: Neritidae
Nerita angolensis Rennie, 1929 (Senonian; K)

Prosobranchia: Prosobranchidae
Afraster scalariformis Blake et al., 1996 (upper Coniacian; K)

Ptenoglossa: Ptenoglossidae
Micropedina sphaeroides Loriol, 1888 (upper Albian; B)

Phosphatolina: Phosphatolinidae
Phymosona binexilis White, 1887 Lower to Upper Albian; B)
Phymosoma cf. binealis White, 1888 (upper Albian; B)
Salenioida: Hyposaleniidae  
*Hyposalenia aff. clathrata* (Woodward, 1856) (lower Albian; B)  
*Hyposalenia* sp. (upper Albian; B)  

Salenioida: Saleniidae  
*Salenia dombeensis* Loriot, 1888 (middle to Upper Albian; B)  
*Salenia* sp. (upper Albian; B)  

Spatangoida: Hemisteriidae  
*Hemiaster cf. forbesi* Baily 1855 (upper Albian; B)  
*Hemiaster* proculivus Cotteau, Peron & Gauthier, 1878 (Aptian to Upper Albian; B)  
*Hemiaster reineckeri* Haughton, 1924 (upper Albian; B)  
*Hemiaster* sp. (middle Upper Albian; B)  
*Leystomaster* sp. Tavares, 2006 (Albian; B)  
*Mecaster* aff. africanus Péron & Gauthier (upper Albian; B)  
*Measter* aff. amaia Péron & Gauthier (upper Albian; B)  
*Measter* cf. africana Coquand, 1862 (upper Albian; B)  
*Measter* cf. amelaea Péron & Gauthier (upper Albian; B)  
*Mecaster* sp. (upper Albian; B)  

Spatangoida: Palaeostomatidae  
*Leystomaster angolanus* Greyling & Cooper, 1995 (middle Campanian; B)  

Spatangoida: Toxasteridae  
*Douvilleaster benguellensis* Loriot, 1888 (upper Albian; B)  
*Douvilleaster* aff. carvalhoi Dartevelle (upper Albian; B)  
*Macraster angolensis* Haughton, 1924 (upper Albian; B)  
*Epistylus carvalhoi* Dartevelle, 1953 (Senonian; B)  
*Heteraster* sp. (Aptian-Albian; B)  

Echinodermata - Crinoidea  
The only reference for the Crinoidea was Ferré & Granier (2001).  

Roveacrinida: Roveacrinidae  
*Roveacrinus communis* Douglas, 1908 (upper Albian; C)  
*Roveacrinus* cf. communis Douglas, 1908 (upper Albian; C)  
*Roveacrinus* aff. geinitzi Schneider, 1989 (upper Albian; C)  
*Roveacrinus* pyramidalis Peck, 1943 (upper Albian; C)  
*Roveacrinus* sp. (upper Albian; C)  

Gnathostomata - Chondrichthyes  

Carcharhiniformes: Scylliorhinidae  
*Pteroscyllium* cf. signeuxi Cappetta, 1980 (upper Campanian-Maastrichtian; B)  

Echinorhiniformes: Echinorhinidae  
*Echinorhinus lapaoi* Antunes & Cappetta, 2002 (upper Campanian-Maastrichtian; B)  

Elasmobranchii: Ptychodontidae  
*Ptychodus* sp. (upper Turonian; B)  
*Ptychodus decurrens* Agassiz, 1838 (upper Turonian; B)  
*Ptychodus latissimus* Agassiz, 1838 (upper Turonian; K)  
*Ptychodus mammillaris* Agassiz, 1838 (upper Turonian; K)  
*Ptychodus mortoni* Mantell, 1836 (upper Turonian; K)  

Psychodus paucisulcatus Agassiz, 1838 (upper Turonian; K)  
Psychodus cf. paucisulcatus Agassiz, 1838 (upper Turonian; K)  
Psychodus whipplei Marcou, 1858 (upper Turonian; K)  

Heterodontiformes: Heterodontidae  
*Heterodontus* sp. (Maastrichtian; N)  

Hexanchiformes: Chlamydoselachidae  
*Chlamydoselachus goliath* Antunes & Cappetta, 1991 (upper Campanian-Maastrichtian; B)  

Hexanchiformes: Hexanchidae  
*Hexanchus cf. microdon* Agassiz, 1843 (upper Turonian to Campanian-Maastrichtian; K and B)  

Lamniformes: Alopidae  
*Paranomotodon angustidens* Reuss, 1845 (upper Turonian; K and B)  

Lamniformes: Acnacoracidae  
*Squalicornis* sp. (upper Albian to Upper Turonian; B and K)  

Lamniformes: Myliorhynchidae  
*Pseudocorax affinis* Agassiz, 1843 (upper Campanian-Maastrichtian; B)  
*Squalicornis* cf. falcatus (Agassiz, 1843) (Cenomanian; B)  
*Squalicornis* falcatus (Agassiz, 1843) (Turonian to Senonian; B and K)  
*Squalicornis* cf. kaupi (Agassiz, 1843) (upper Campanian-Maastrichtian; B)  
*Squalicornis* kaupi (Agassiz, 1843) (Santonian to Maastrichtian; B, CB and N)  
*Squalicornis* pristodontus (Agassiz, 1843) (Santonian to Maastrichtian; N, CB, K and B)  
*Squalicornis* aff. yangaensis Dartevelle & Casier, 1943 (Santonian to Lower Campanian; K)  
*Squalicornis* yangaensis Dartevelle & Casier, 1943 (Santonian to Lower Campanian; B and CB)  

Lamniformes: Eoptolamnidae  
*Leptostyrax macrorhiza* Cope, 1875 (upper Albian; B)  

Myliobatiformes: Myliobatidae  
*Brachyrhinus* cf. wichtenstein Romer, 1942 (upper Campanian-Maastrichtian; B)  

Myliobatiformes: Rhombodontoidea  
*Rhombodus* binkhorsti Dames, 1881 (upper Campanian-Maastrichtian; CB and N)  

Odontaspidida: Cretoxyrhinidae  
*Cretodus cassinidus* Dixon, 1850 (upper Turonian; K)  
*Cretodus semiplicatus* Agassiz, 1843 (Cenomanian to Upper Turonian; B and K)  
*Cretolamna* cf. appendiculata Agassiz, 1843 (Cenomanian; B)
Cretolamna biauriculata Wanner, 1902 (Santonian to Maastrichtian; CB, K, B and N)
Cretothyrrhina mantelli Agassiz, 1843 (Cenomanian to Upper Turonian; B and K)
Carcharias heathi Case & Capetta, 1997 (upper Campanian to Maastrichtian; B, CB and N)
Serratolamna caraibaea Leriche, 1938 (upper Campanian to Maastrichtian; CB and N)
Serratolamna serrata Agassiz, 1843 (upper Campanian-Maastrichtian; N)

Odontaspidida: Odontaspidae
Carcharias amonensis Cappetta & Case, 1975 (Cenomanian to Upper Turonian; B)

Odontaspidida: Scapanorhynchidae
Scapanorhynchus sp. (Senonian (Santonian to Maastrichtian); CB, B and N)
Scapanorhynchus cf. lewesi Davis, 1887 (upper Turonian to Maastrichtian; B)
Scapanorhynchus rapax Quaas, 1902 (upper Cretaceous; B and N)
Scapanorhynchus raphiodon Agassiz, 1843 (Turonian to Senonian; K, B and CB)
Scapanorhynchus cf. texanus Roemer, 1949 (upper Turonian; K)

Orectolobiformes: Ginglymostomatidae
Plicatoscyllium antiquum Case & Cappetta, 1997 (upper Campanian and Maastrichtian; B)

Angolabatis angolensis Antunes & Capetta, 2002 (upper Campanian-Maastrichtian; B)

Rajiformes
Angolaichthys lerichei Teixeira, 1947 (upper Campanian-Maastrichtian; CB)
Enchodus bursauxi Arambourg, 1952 (upper Campanian-Maastrichtian; CB and N)
Enchodus cf. elegans Dartevelle & Casier, 1949 (upper Turonian to Upper Campanian-Maastrichtian; K and N)
Enchodus crenulatus Dartevelle & Casier, 1949 (Santonian-Lower Campanian; CB)
Enchodus elegans Dartevelle & Casier, 1949 (Santonian-Maastrichtian; B, N and CB)
Enchodus faujasi Agassiz, 1835 (upper Campanian-Maastrichtian; N)
Enchodus lemonnier Dollo, 1893 (Maastrichtian; N)
Enchodus libycus Quaas, 1902 (upper Campanian-Maastrichtian; CB)
Enchodus sp. (upper Turonian-Maastrichtian; N and B)

Teleostei: Trigonodontidae
Stephanodus libycus Dames, 1883 (upper Campanian-Maastrichtian; )

SPECIES LIST FULL REFERENCES
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