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THE OCCURRENCE AND GEOLOGICAL SETTING OF CRETACEOUS DINOSAURS, MOSASAURS, PLESIOSAURS, AND TURTLES FROM ANGOLA

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Abstract: Vertebrate-bearing fossiliferous outcrops of Cretaceous age in sub-Saharan Africa are rare because of younger superficial deposits, vegetation cover, and the widespread occurrence of Precambrian metamorphic plateau basement comprising much of the continent. However, one area of extensive marine and nonmarine Cretaceous exposures is found between the plateau and the coast in Angola. The Angolan margin was formed in conjunction with the breakup of Gondwana and subsequent growth of the South Atlantic. Cretaceous deposits are constrained in age by the emplacement of oceanic crust, which began no later than magnetozone M3 (approximately 128 Ma, Barremian). Shallow marine facies are exposed in sea cliffs but equivalent facies become increasingly terrestrial inland. Few vertebrate fossils have been described from Angola aside from sharks. Notable exceptions are the late Turonian mosasaurs *Angolasaurus bocagei* and *Tylosaurus iembeensis* from northern Angola. Those taxa are significant because they are among the earliest derived mosasaurs. Recent field work led to the discovery of a new skull of *Angolasaursus* as well as sharks, fish, plesiosaurs, the skull of a new taxon of turtle, additional mosasaurs, and the articulated forelimb of a sauropod dinosaur, the first reported dinosaur from Angola. In southern Angola, marine sediments spanning the Cretaceous-Paleogene boundary are found.

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

INTRODUCTION

We have embarked on what we hope will be a long-term field-based exploration of the vertebrate paleontology of Angola. There are no better exposures of Cretaceous and Paleogene rocks in all of sub-Saharan Africa than those along the coast of Angola (8°S to 15°S). Sea cliffs and extensive outcrops, especially in the south, are visible between the structural zone separating the metamorphic plateau in the east from the coastal plain leading to the South Atlantic Ocean in the west (Fig. 1).

Outcrops are richly fossiliferous in both invertebrates and vertebrates and comprise a variety of sedimentary lithologies and volcanic rocks. Rocks range in age from late Early Cretaceous through the Cenozoic, with vertebrate fossils reported from most units, especially important for this paper, from the Turonian, Campanian, and Maastrichtian stages. Older and younger vertebrate fossils are known, most notably from the Paleogene. There was even the report of a Miocene rhinoceros, but Cenozoic verte-

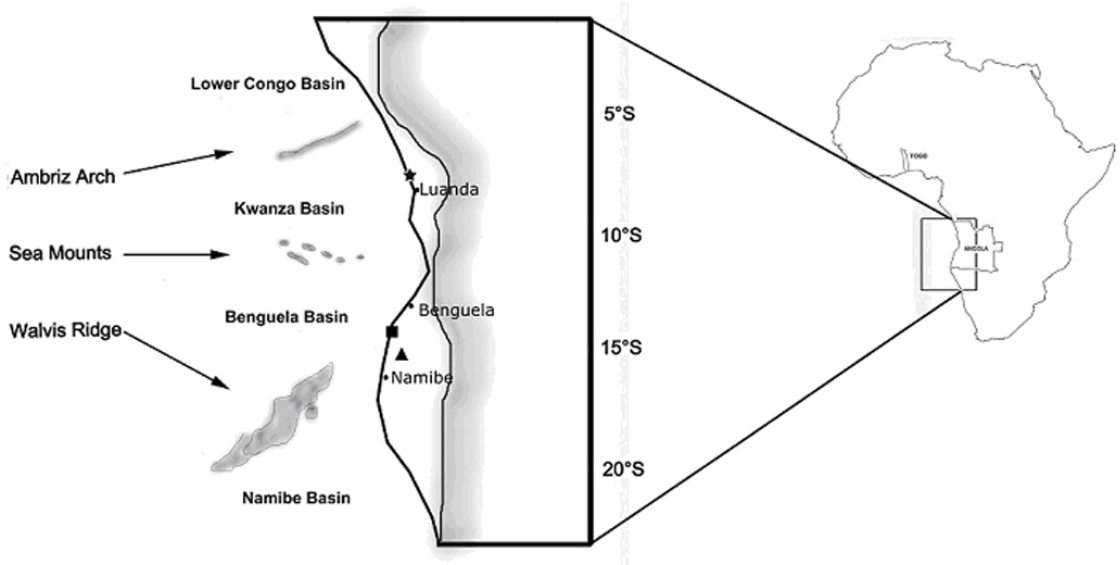

Fig. 1. General geographic representation of coastal Angola and its offshore basins. Cretaceous and Paleogene rocks crop out along the coast and eastward to the hinge zone at the edge of the metamorphic plateau (shaded area). Areas mentioned in text are shown by symbols: Tadi (star north of Luanda), Bentiaba (square south of Benguela), Fazenda dos Cavaleiros (triangle).

brates are beyond the focus of the conference for which this report was prepared.

The most recent comprehensive study of the stratigraphy and paleontology of the Angolan coast was that of Antunes (1964). More recently, Antunes and Cappetta (2002) published a systematic description of sharks collected primarily during the 1960's by Antunes. (The surname Antunes has been inconsistently and incorrectly cited as Telles-Antunes or Telles Antunes; e.g., Bardet *et al*., 2005; Bell, 1997a, but not 1997b; Bell and Polcyn, 2005, but not Polcyn and Bell, 2005; Lingham-Soliar, 1994).

Previous studies of outcrop between the coast and the interior plateau of Angola were completed prior to the general acceptance and full development of plate tectonic concepts, magnetostratigraphy, seismic and sequence stratigraphy, and high precision radiometric dating. Antunes (1964) predated the general use of phylogenetic systematic techniques, the recognition of bolide impact at the Cretaceous-Paleogene transition, the application of stable isotopes to chemostratigraphic, paleoenvironmental, and paleoecological problems, and the advent of such analytical and field tools as high resolution X-ray computed tomography or GIS/GPS positioning. Nor have collections been improved by methodical acquisition of new material of known or additional taxa since the work of Antunes in the early 1960's.

In contrast, offshore basins of Angola are recognized as being extremely important economically and geologically for their petroleum resources and as a geological record of the opening of the South Atlantic Ocean during the breakup of Gondwana. Consequently, there is an important and growing body of seismic and core data from the South Atlantic relevant to a more thorough understanding of the coastal deposits of onshore Angola. This is not only with respect to the initial formation of the South Atlantic, but as an environmental record of changing climatic, atmospheric, and oceanic conditions as the sea floor widened during the Late Cretaceous and Cenozoic. Therefore, we begin this paper with a discussion of offshore geology as a background to understanding the geological history of vertebrate-bearing deposits of Angola, then we discuss the localities visited in our 2005 field season, including preliminary observations and conclusions regarding fossils obtained at that time.

GEOLOGICAL SETTING

PLATE TECTONICS, OFFSHORE BASIN HISTORY, AND STRATIGRAPHY

The geographic significance of Angola from a plate tectonic perspective is that it is the eastern border of the South Atlantic Ocean, formed in the breakup of Gondwana during the Mesozoic Era. Rifting was heralded in the area destined to become the southernmost South Atlantic by regional uplift and volcanism during the Jurassic Period, which continued progressively northward through the Early Cretaceous (Emery and Uchupi, 1984; Nurnberg and Muller, 1991). Flooding of the South Atlantic Ocean after initial volcanism began south of Angola during Jurassic and Early Cretaceous time. Prior to the Barremian, subsidence of intracratonic rift basins farther north, in the area that is now Angola, resulted in deposition of more than a kilometer of clastic detritus over pre-existing metamorphic basement rocks (Brice *et al*., 1982; Karner and Driscoll, 1999). Emplacement of oceanic crust along the Mid-Atlantic Ridge at the coast of Angola began no later than magnetozone M3, or approximately 128 Ma (Barremian; Ogg and Smith, 2004). Rifting appears to have been propagated from the Walvis Ridge hotspot (Fig. 1; Standlee *et al*., 1982).

Moulin *et al*. (2005) utilized deep penetration multi-channel reflection and wide-angle seismic data to document that Early Cretaceous strata are parallel to the base of Aptian evaporites, thereby indicating that pre-Aptian beds were little affected by tectonic deformation during initial rifting. They conclude that environments of deposition were shallow during that phase of rifting and that horizontal motion was less of a factor than vertical motion during basin formation (see also Reston *et al*., 1996). Following Cretaceous rifting, Africa was uplifted in the Cenozoic relative to other continents (Bond, 1978; Sahagian, 1988; Lunde *et al*., 1992; Nyblade and Robinson, 1994). However, neither the rates nor the timing of either Cretaceous or Cenozoic regional or continental vertical motions are precisely known, although it does not seem unlikely that the tectonic style of the formation of the South Atlantic played a role in the initial expression of the continental metamorphic plateau east of the current Angolan coastal plain.

From north to south, the offshore basins of Angola that extend landward are referred to as the Lower Congo, Kwanza, Benguela, and Namibe (Fig. 1). Conjugate basins have been identified on the Brazilian margin of the South Atlantic (Cainelli and Mohriak, 1999), reflecting their common origin. Separating the offshore basins along the Angola passive margin are the Ambriz Arch between the Lower Congo and Kwanza basins (7° to 8°S; Standlee *et al*., 1992), an east-southeast trending chain of volcanic seamounts between the Kwanza and Benguela basins (11°S, Schollnberger, 2001), and the Walvis Ridge, which divides the Benguela from the Namibe Basin (approximately 18°S near the continent; Lehner and de Ruiter, 1977).

("Kwanza" is the English spelling and is used consistently, but not exclusively, in that form in English scientific literature. The spelling in Romance languages is "Cuanza," and it is used in that form in Portuguese scientific literature. We use the term Namibe Basin to conform with the town and the province as they are now called, as opposed to the older synonym, Moçâmedes Basin.)

Cretaceous deposition from Barremian onward is generally comparable among the Angolan offshore basins in terms of lithology and stratigraphic thickness. Above the initial synrift sequence are sandstones up to 200 meters thick, which represent the initiation of marine deposition along the Angola margin (Ala and Selley, 1997; Marton *et al*., 2000). Lower Aptian rocks are dominantly evaporites, which may signify restriction of the Angolan basins from open oceanic circulation by vertical motion along the Walvis Ridge and other topographic features of the South Atlantic seafloor. Above the evaporites are thick carbonate and clastic units (Brognon and Verrier, 1966a, b; Gerrard and Smith, 1982). Post-Aptian salt tectonism is extensive and exacerbated by regional westward tilt (Schollnberger, 2001; Hudec and Jackson,

2004).

Schollnberger (2001) studied two-dimensional seismic profiles of the three northern Angola offshore basins and correlated four unconformity-bounded, second-order (10-100 Ma) sequences, which span the time from the end of the Aptian through the Cenozoic. In addition, Schollnberger (2001) recognized widely varying numbers of third-order (1-10 Ma) and fourth-order (0.2-0.5 Ma) unconformity-bounded sequences among the basins. The mechanisms that can create marine unconformities are sea-level fluctuations, changing circulation patterns, and tectonic activity, including salt tectonism and source-area perturbations that may have affected the distribution of depocenters or sediment provenance. Variation in the number of unconformity-bounded, third- and fourth-order sequences among the Angolan basins suggests basin-specific attributes, the causes of which remain undefined.

Biostratigraphic and lithostratigraphic control for the seismic study of Schollnberger (2001) was provided by a core from DSDP site 364 in the Benguela Basin (Bolli and Ryan, 1978). More recent drilling by the Ocean Drilling Project on ODP leg 208 in the South Atlantic on the northeastern flank of the Walvis Ridge specifically focuses on data relevant to understanding the Cretaceous-Paleogene transition and Paleogene climatic events (Shipboard Scientific Party, 2003). No relevant data are currently available from onshore Africa for rigorous comparison with those data derived from the Walvis Ridge by the ODP, but the most likely prospect for deriving relevant data from the mainland is from outcrops in Angola where Cretaceous and Paleogene deposits are exposed.

ONSHORE STRATIGRAPHY AND PALEONTOLOGY

One needs only examine the maps in Antunes (1964) or Antunes and Cappetta (2002) to see the rich distribution of fossil localities along the coast of Angola, from Cabinda, the northernmost and most vegetated province, to Namibe Province in the south, where vegetation is sparse and exposures are superb. Although the fossils described by Antunes are of a variety of Cretaceous and Cenozoic ages, they are almost exclusively marine. The most abundant fossils pertain to sharks and bony fish, but a suite of marine amniotes, most often fragmentary but occasionally quite complete, were noted.

The most significant fossils studied by Antunes were two of the world's oldest derived mosasaurs, *Angolasaurus bocagei* and *Tylosaurus iembeensis*. He also reported plesiosaurs, turtle, at least two additional mosasaur taxa, and a variety of fish and sharks of Late Cretaceous age (other fossils, including fish, turtle, crocodile, snake, cetaceans, and rhinoceros, were reported from Cenozoic strata). In our field season of 2005 we visited three localities (Fig. 1) near to or identical with those reported by Antunes (1964): Iembe, the type locality of *Angolasaurus bocagei* and *Tylosaurus iembeensis* in the Kwanza Basin, northern Angola; Bentiaba and Fazenda dos Cavaleiros in the Namibe Basin, southern Angola. Antunes obtained time control from ammonites and other invertebrates, and he established a chronology based on sharks and bony fishes. The ichthyofauna identified from the localities we visited are listed in Table 1, compiled from Antunes and Cappetta (2002), which concluded that Iembe is late Turonian in age (but see subsequent discussion) and the other two localities are younger.

Kwanza Basin-The age of Iembe is particularly important because it produces the oldest mosasaurs known from the South Atlantic and it has produced a dinosaur, as well as turtle and plesiosaur. The locality lies near Tadi in the Kwanza Basin, north of Luanda in Bengo Province (817^{o}S, 1321^{o}E; Fig. 1). It is stratigraphically within the Tadi Beds of the Itombe Formation (Fig. 2, 3), which is shown in quotation marks by Antunes and Cappetta (2002, p. 95, but not p. 90) because beds of different ages were lumped together into the same formation. The time discrepancy of the included strata is so great (Turonian versus Campanian; Antunes and Cappetta, 2002) and the facies relationships so ill defined that considering the Tadi Beds as part of the Itombe Formation is unwarranted. The upper portion of the Itombe Formation corresponds to the Middle Campanian *Globotruncata ventricosa* Zone, and the lower portion, the Tadi

Table 1. Ichthyofauna of three Cretaceous localities in Angola (compiled from Antunes and Cappetta, 2002).

TAXON	Iembe	Bentiaba	F. d. Cavaleiros
Carcharias heathi		X	X
Ptychodus mortoni	X		
Ptychodus cf. *paucisulcatus*	X		
Ptychodus whipplei	X		
Hexanchus cf. *microdon*	X		
Scapanorhynchus raphiodon	X		
Scapanorhynchus cf. *lewisii*	X		
Cretodus semiplicatus	X		
Cretodus sp.	X		
Cretoxyrhina mantelli	X		
Paranomotodon angustidens	X		
Heterodontus sp.		X	
Cretolamna appendiculata		X	
Squalicorax falcatus	X		
Squalicorax pristodontus		X	X
Cretolamna biauriculata		X	X
Squalicorax sp.	X		
Onchosaurus pharao	X		
Enchodus cf. *elegans*	X		
Enchodus faujasi		X	
Enchodus bursauxi		X	
Enchodus elegans		X	
Eodiaphyodus lerichei		X	
Serratolamna caraibaea		X	X
Serratolamna serrata		X	X
Dalpiazia sp.		X	
Ganopristis sp.		X	
Rhombodus binkhorsti		X	X

Beds, correlates with the Cocaba Beds, southeast of Luanda, which contain the ammonite *Coilpoceras* of Turonian and Coniacian age. The upper limit of the age of the Tadi Beds is constrained by the overlying Pambala Beds, which contain *Texanites* of Coniacian to Campanian age. The Pambala Beds are included in the N'Golome Formation, which also contains the Middle Campanian *Globotruncata ventricosa* Zone (Antunes and Cappetta, 2002), and thus faces the same chronostratigraphic dilemma as the Itombe Formation as these formations are now understood.

Further confusing the issue, Lingham-Soliar (1994, p. 269) states that the Pambala Beds contain the ammonites *Hemitissotia* and *Romaniceras*, which are in fact from the underlying Tadi Beds, not the Pembala Beds, as is clear from Antunes (1964) and Antunes and Cappetta (2002). An additional complexity in the literature is the citation of Howarth (1965, 1985) by Lingham-Soliar (1994) to explain the relevance of the ammonites to the age of the Tadi Beds, but neither of those publications (Howarth 1965,

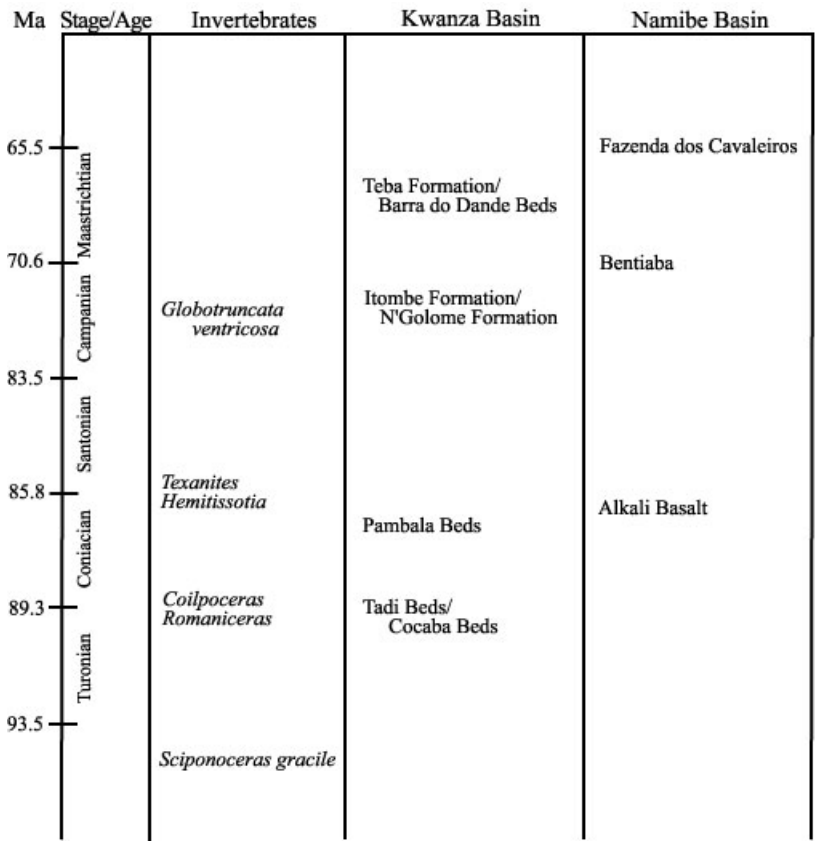

Fig. 2. Correlation of Angolan Cretaceous fossil localities visited in 2005.

Fig. 3. Iembe, near Tadi, at or near the type locality of *Angolasaurus bocagei* and *Tylosaurus iembeensis.* The new skull of *Angolasaurus* was found (by O.M.) approximately at the arrow.

1985) has direct bearing on the age of the Tadi Beds or the Iembe locality. No vertebrates are known from the Pambala Beds (Antunes, 1964), but overlying the Pambala Beds in the Kwanza Basin is the Maastrichtian Teba Formation with the fossiliferous Barra do Dande Beds, which produce shark, bony fish, plesiosaur, and mosasaur teeth.

Brognon *et al*. (1960; cited in Antunes, 1964) reported echinoderms and the ammonites *Hemitissotia*, *Romaniceras*, and *Pachydiscus* from the vicinity of the Iembe site. In Europe, *Hemitissotia* is most characteristic of the Upper Coniacian (Gräfe and Wiedmann, 1998). *Romaniceras deverianum* is a potential primary marker for the Upper Turonian (Ogg *et al*., 2004), but *R. hispanicum* (which we take to be a species of *Romaniceras*) is shown as Coniacian in Gräfe and Wiedmann (1998:fig. 3). *Pachydiscus*, a Campanian and Maastrichtian genus, must be misidentified or the sample is mixed; we will not consider it further as it appears to be of no relevant chronological value in this instance. Based strictly on the ammonites *Hemitissotia* and *Romaniceras* and our understanding of their distributions, it would appear that the age of Iembe might conceivably fall within a maximum range extending from Late Turonian through Coniacian, or about 89±3 Ma.

We accept for the moment the interpretation of Antunes (1964) and Antunes and Capetta (2002) that, based on sharks primarily, the locality of Iembe is Late Turonian in age (which is consistent with the numerical estimate presented here). However, we note that Antunes and Cappetta (2002) provide faunal lists for Cenomanian, Late Turonian, and Santonian-to-Lower-Campanian ichthyofaunas, but they do not provide a locality or a faunal list for Early Turonian or Coniacian ichthyofaunas, which are currently unknown in Angola, rendering it difficult to defend the precision of a Late Turonian age based on strict comparison with other Angolan sites. On the other hand, a Turonian age is supported by the correlation of the ichthyofauna to that of Bula Zambi in the Republic of Congo, which has long been accepted as Turonian in age (e.g., by Haughton, 1963).

Namibe Basin-At Bentiaba (1416°S, 1221°E, Fig. 1), we discovered rich deposits of relatively complete mosasaurs and plesiosaurs. Exposures are extensive (Fig. 4). Low in the section at Bentiaba an alkali basalt flow is interbedded with near shore marine strata (Fig. 5; Borges, 1946; Carvalho; 1961). Cooper (1972) noted the lack of pillow structures in the basalt. He (Cooper, 1978) also documented the occurrence of Cenomanian and Turonian ammonites below the basalt and Santonian and Campanian ammonites above the basalt. He therefore, based on stratigraphy and invertebrate biochronology, considered that the basalts were extruded during an emergent interval during the Coniacian, probably Late Coniacian (i.e., 86 Ma, *fide* Gradstein *et al*., 2004). He did not find a rich Upper Campanian fauna similar to that of Egito or a Maastrichtian fauna like that found in the Kwanza Basin. Cooper recognized, as we did, the beds rich in sharks and other vertebrates, including what he (and Carvalho, 1961:fig. 128) called *Mosasaurus beaugei* (although we have not identified that taxon from Bentiaba). Cooper (1972) concluded that there was not enough section present above the basalt to have a complete record from Santonian through Maastrichtian, and he concluded that the section ended in the Campanian with the Late Campanian and Maastrichtian not present. Soares (1965) reported Campanian (?) bivalves from the area.

On the other hand, Antunes (1964, 1966) had several localities overlying the basalt in the vicinity of the town of Bentiaba (which he referred to as São Nicolau), in the same area that Cooper worked later. Antunes (1964, 1966) and Antunes and Cappetta (2002) determined the age of the beds as Campanian and Maastrichtian based on the invertebrates and the ichthyofauna (Table 1), including *Squalicorax pristodontus*, which they recognize as a Maastrichtian species in Angola, consistent with its occurrence elsewhere, and other shark taxa that were also mentioned by Cooper (1972).

Near the town of Namibe, Antunes recognized the Cretaceous-Paleogene transition at Fazenda dos Cavaleiros, a site we visited in 2005 (158°S, 1213°E; Antunes, 1964:plate 9:figs. 21, 22; our Fig. 6).

Fig. 4. Late Cretaceous (Campanian-Maastrichtian *fide* Antunes and Cappetta, 2002) beds of Bentiaba (photo by OM).

Fig. 5. Volcanic flow intercalated with late Cretaceous shallow marine sediments, north of Bentiaba (photo by OM).

Within the section, high-energy terrigenous conglomerates are interbedded with nearshore marine sands. The conglomerates can be traced laterally for extended distances, some at least, into more terrestrial channel and overbank facies associated with volcanics and evaporites (Fig. 7). The evaporites presumably were emplaced via post-Aptian salt tectonics as is also seen in offshore seismic sections. Neither the volcanics at Bentiaba or east of Fazenda dos Cavaleiros have been radiometrically dated.

Facies Relations-Coupled with the marine record, from the point of view of exploration, there is entic-

Fig. 6. Fazenda dos Cavaleiros. Cretaceous-Paleogene transition is about midway up the outcrop face (photo by OM).

Fig. 7. Cretaceous terrestrial sediments with evaporites juxtaposed along igneous rocks in western Namibe Province (photo by LLJ).

ing evidence along much of the passive margin of coastal West Africa that marine facies grade into more terrestrial facies and that both are fossiliferous. From the Eocene of Togo, for instance, Gingerich *et al*. (1992) reported sharks, whales, and sirenians, as well as possible land mammals. In Cabinda, marine vertebrates have long been known from the Paleogene of Landana (e.g., most recently Schwarz, 2003) and terrestrial fossils have been recognized from Malembo, near Landana. Antunes (1964:plate 12:fig. 28) indicates a rhinoceros from Miocene strata near the coast of Angola. A similar marine-nonmarine facies

relationship also pertains to the Cretaceous in all three of the areas we visited. The section at Fazenda dos Cavaleirosin the Namibe Basin comprises near shore marine sands with interbedded terrigenous conglomerates that can be traced into terrestrial facies. Marine to terrestrial facies relationships in the southern Kwanza Basin were recognized by Brognon and Verrier (1965a, b). The section at Iembe in the northern Kwanza Basin shows clear indications of terrestrial influx, and including ferruginous alternations, and as mentioned, it has produced a dinosaur. In Angola, and along great expanses of coastal areas of sub-Saharan Africa on both sides of the continent, the possibilities of marine to nonmarine facies transitions are encapsulated in relatively narrow and often poorly exposed rocks of the coastal plain between the shoreline and the crystalline plateau, which comprises much of the continental interior. Deposition along that swath reflects regional basin evolution, continental source areas, and sedimentation during transgressive-regressive cycles, and presents opportunities for investigations of the geological and paleontological history of Africa.

PALEONTOLOGICAL RESULTS

The best known amniote fossil taxa from Angola are those described by Antunes (1964), that is, the mosasaurs *Angolasaurus bocagei* and *Tylosaurus iembeensis.* The holotype of the latter taxon may have been lost in a fire. Although no systematic collections have been made since Antunes, in our short time in Angola during 2005, a variety of vertebrate fossils in various degrees of completeness were found. Among those, one of us (Octávio Mateus) discovered several important specimens that deserve further comment.

Chelonia-An apparently new taxon of turtle is represented by a nearly complete but fractured skull (Fig. 8) from near the Iembe *Angolasaurus* site. The specimen has not been fully prepared, but it appears to have a suite of derived and primitive characters, among others, divided nares, an extensive secondary palate, incisura columellae auris enclosing stapes, elongate squamosal processes, narrow interorbital

Fig. 8. Turtle skull from Iembe coast (4.5 km north of Tadi; photo by OM).

width, and dorsally directed orbits. A closed incisura columella and extensive secondary palate have evolved multiple times, the secondary palate to various degrees. Although found in marine sediments, the Iembe turtle is excluded from membership in the chelonioid sea turtles. It has a more extensive secondary palate than modern sea turtles but similar to some other marine cryptodires, such as the Aptian *Sandownia* (Meylan *et al*., 2000).

Plesiosauria-Antunes (1964) reported a relatively complete plesiosaur specimen from a locality near Iembe, but it has never been studied. Several other localities mentioned in his monograph include fragmentary plesiosaurs in the faunal list. We found plesiosaur remains in each of the three areas we visited (Fig. 9). Bentiaba appears to be particularly rich in plesiosaur remains.

***Angolasaurus*-**Mosasaurs are well represented at least in the Late Turonian and Campanian-Maastrichtian portions of the Angola Cretaceous section. In 1960, M.G. Mascarenhas Neto, then a geologist in Serviços de Geologia e Minas, and Miguel Telles Antunes obtained a skull with some postcrania from Iembe. Antunes (1961) initially identified the material as *Platecarpus* sp. but later (Antunes, 1964) studied it more fully and erected the name *Angolasaurus bocagei* for it. Antunes placed *Angolasaurus* within the Mosasaurinae. Its age is considered to be Late Turonian as explained previously, although the taxon itself appears rather derived for such an early age relative to the history of mosasaurs. The specimen was later studied by Lingham-Soliar (1994), who recognized it as a member of the Subfamily Plioplatecarpinae. As a result of his study, he synonymized the genus *Angolasaurus* with *Platecarpus*; however, he retained the species and placed it (as *P. bocagei*) in his Tribe Platecarpini, which is shown in his figure 8 to be a paraphyletic group.

More recently, Polcyn and Bell (2005; see also Bell and Polcyn, 2005) included *Angolasaurus* in their phylogenetic analysis. The matrix they employed was largely based on Bell (1997b), constructed for Adriatic and North American mosasaurs, but expanded somewhat. There is not total concordance of the taxa or characters utilized in the analyses of Polcyn and Bell as compared to that of Lingham-Soliar, and consequently, the hypotheses presented by those different authors are not strictly comparable. Specifically, according to Lingham-Soliar (1994), *Prognathodon solvayi* and *Halisaurus ortliebi* nest within the

Fig. 9. In situ plesiosaur remains at Bentiaba.

Plioplatecarpinae as more dervived than *Angolasaurus bocagei*. According to Polcyn and Bell (2005) both fall outside the Plioplatecarpinae, with *Prognathodon* (at least *P. rapax*) grouped as a globidensine and *Halisaurus* represented in the sister group to Russellosaurina plus Plioplatecarpinae plus Tylosaurinae.

In contrast to Lingham-Soliar (1994), in the cladogram of Bell and Polcyn (2005) and Polcyn and Bell (2005), *Angolasaurus bocagei* falls on its own branch, suggesting that it is in fact a valid taxon. Nevertheless, their (Bell and Polcyn, 2005; Polcyn and Bell, 2005) results show *Angolasaurus* nested with *Ectenosaurus*, *Platecarpus*, and *Plioplatecarpus*, forming a monophyletic group (Plioplatecarpinae) that would include both the Platecarpini and Plioplatecarpini of Lingham-Soliar (1994). However, their cladogram places *Angolasaurus* between *Platecarpus planifrons* and *Platecarpus tympanicus*, highlighting an inconsistency: Either the genus *Platecarpus* is paraphyletic, or the resolution surrounding *Angolasaurus* is incorrect.

Our field work in May, 2005, resulted in the collection of a second skull of *Angolasaurus* (Fig. 10). For now, our tentative conclusions are that the cladogram of Polcyn and Bell (2005) presents a viable hypothesis, that *Angolasaurus bocagei* is a valid taxon, and that because *Platecarpus tympanicus* is the type species of the genus, *P. planifrons* should be placed in its own genus, separate from either *Platecarpus* or *Angolasaurus*.

Globidensine mosasaurs-Globidensine mosasaurs are characterized (in part) by the robust nature, peculiar morphology, and reduced number of their teeth, most obviously developed in *Globidens*, teeth of which were reported from Bentiaba and from Chibuete near the border with the Republic of Congo by Antunes (1964). However, excellent skull material tentatively referred to the globidensine *Prognathodon* (Fig. 11) was recovered from Bentiaba in 2005, further documenting ecological differentiation among mosasaurs during the Campanian and Maastrichtian over a broad geographic area in both the northern and southern hemispheres.

Sauropoda-Arguably, the most important fossil found in the 2005 expedition is the articulated forelimb of a sauropod dinosaur (Fig. 12), because it is the first Cretaceous terrestrial vertebrate discovered in Angola and therefore opens the door to a new fossil field for African Cretaceous terrestrial biota.

Fig. 10. New skull of *Angolasaurus* at Tadi (photo by OM).

Fig. 11. *Prognathodon* sp. skull at Bentiaba (Photos by OM and Carlos Natário).

Fig. 12. Sauropod ulna and manus elements at Iembe near type locality of *Angolasaurus* (photo by OM).

Although the specimen was found in near shore marine sediments, the association of the bones and the terrigenous input into the strata indicates proximity to the paleoshoreline. Moreover, this specimen, found in sediments at or near the end of the Turonian, is probably the most precisely dated Cretaceous dinosaur in sub-Saharan Africa. The morphology of the ulna suggests that the forelimb does not belong to a titanosaurian (Mateus *et al*., submitted).

DISCUSSION

In Angola, Cretaceous deposits are of mostly shallow marine facies along the coast but may become

increasingly terrestrial inland until the metamorphic plateau is reached. Terrigenous detritus and torrential beds in marine facies can be traced landward into terrestrial facies with the possibility of approaching a stratigraphically controlled sequence of both terrestrial and marine vertebrates spanning the Cretaceous-Paleogene transition. Further, Angola offers the best opportunity for correlation of the onshore African rock record to the much better-known and calibrated record of the South Atlantic Ocean. Recent drilling on ODP leg 208 in the South Atlantic on the northeastern flank of the Walvis Ridge specifically focuses on data relevant to understanding the Cretaceous-Paleogene transition, the Early Eocene Climatic Optimum, the Paleocene-Eocene Thermal Maximum, and the Early Oligocene Glacial Maximum (Shipboard Scientific Party, 2003). No relevant data are currently available from onshore Africa for rigorous comparison with those derived from the Walvis Ridge by the ODP, but the most likely prospect for deriving relevant data from the mainland is from outcrops in Angola where Cretaceous and Paleogene deposits are exposed.

From a biogeographic and tectonic perspective, the location of Angola along the eastern margin of the South Atlantic has particular significance. Hay *et al*. (1999) suggest that the early South Atlantic was similar in its parallel-sided geometry to the Red Sea, only three times as long. It lay in latitudes in which evaporation exceeded precipitation, and at the time, did not receive influx from major rivers, such as it does today with respect to the Congo and the Amazon. The result was elevated salinity as is evident from extensive evaporite deposits. The connection of the North and South Atlantic oceans, at least with respect to surface circulation, occurred during the Albian (Reyment and Dingle, 1987; Maisey, 2000; Albian comprises the interval 112-99.6 Ma following Gradstein *et al*., 2004). Cooper (1978) noted that the latest Albian was a time of lowered global sea level but the Angolan ammonite fauna of that time includes a number of European forms, confirming connection of the North and South Atlantic during Albian low sea stand. However, while it appears true that short-term sea-level change may have caused fluctuations, the overall trend from Early Albian through the Cenomanian was a rising sea level (Haq *et al*., 1988). Ocean modeling of reduced-gravity to determine upwelling has simulated the Cenomanian Atlantic Ocean connection to have been $\leq$300 m deep (Handoh *et al*., 1999). The connection between the North and South Atlantics grew stronger, in general, as sea level rose throughout the middle part of the Cretaceous. This interval was one of high sea-surface temperatures, and Late Cenomanian to Early Turonian ammonite zones are widely distributed, including in the Western Interior Seaway of North America, in inundated areas of northwest Africa, and in Angola (Cooper, 1978; Jacobs *et al*., 2005a,b). Numerical simulations, as well as the marine record, suggest that the initiation of completion of the Atlantic Ocean drove climatic and oceanographic changes surrounding the Cenomanian-Turonian boundary (Poulsen *et al*., 2001).

Biogeographic precision concerning when, where, and how many times the three major marine amniote groups in Angola during the Cretaceous (turtles, plesiosaurs, and mosasaurs) dispersed into the South Atlantic must await phylogenetic analysis of Angolan representatives in conjunction with tectonic history, precise chronology, and global distribution of relevant taxa. Turtles and plesiosaurs have a longer aquatic history than mosasaurs and could have entered the opening ocean from the south, if they were not hampered by factors of prior distribution or elevated salinity. (Leatherback, loggerhead, and green sea turtles all inhabit the Red Sea today, but all possess a salt gland as well.) Early Cretaceous plesiosaurs and sea turtles are known from Australia (Kear, 2003).

The Australian elasmosaurid *Eramangosaurus* from the Toolebuc Formation is Albian in age. In a consensus tree presented by Kear (2005), it falls as the sister to *Libonectes* from north central Texas (probably Turonian; "uppermost Eagle Ford shale" *fide* Welles, 1949). Known Albian sea turtles from Australia are protostegids, also from the Toolebuc Formation (Kear and Lee, 2005). However, the most similar turtles to that from Iembe appear to be such Northern Hemisphere forms as *Sandownia* from the

Aptian of the Isle of Wight and an undescribed Albian taxon from north central Texas (D. Vineyard, pers. com.), based on structure of the palate and ear. Thus, we interpret the Iembe specimen to represent a marine turtle because it was found in marine sediments, as are the skulls with which it appears to share some derived characters, if judgments made at this stage of the study have validity. Outside of Angola, only one questionable Cretaceous record of marine turtle is known from Africa and that is a specimen reported in 1855 from Umtata River Mouth, South Africa. Its age is given as Albian-Cenomanian (de Broin, 2000), but its location at the southeastern part of the southern extent of Africa may be relevant with respect to both the sea turtles of Australia and to the fauna of the South Atlantic.

Because of their relatively late origin, geologically short duration, morphological diversity, and global distribution, mosasaurs may prove to be profoundly useful for studies of Cretaceous biogeography of the South Atlantic. Mosasaurs are generally considered to have taken to the ocean during the Cenomanian. Their earliest undisputed record is 98 Ma (Cenomanian) from the Middle East, but they have other Cenomanian records and a complex biogeographic Cenomanian and Turonian biogeographic history influenced by tectonics, sea level, and sea surface temperature in the Middle East, Europe, North Africa, North America, and South America (Jacobs *et al*., 2005a,b; Polcyn *et al*., 1999; Rage and Néraudeau, 2004). We dismiss the report of a vertebra from the Molecap Greensand, Australia, as being as old as Cenomanian. The authors of the report (Kear *et al*., 2005) note that the age of the Molecap Greensand is contentious, with palynomorphs used to indicate a Cenomanian to early Turonian range. In the same paper the authors indicate the presence of the sharks *Cretolamna gunsoni*, *Cretolamna appendiculata*, and *Squalicorax kaupi* from the Molecap. *Cretolamna gunsoni* is endemic to Australia, including the Albian-Cenomanian Alinga Formation. *Cretolamna appendiculata* and *Squalicorax kaupi* are known from Angola, the former from the late Turonian through Maastrichtian, the latter from the Santonian through Maastrichtian (Antunes and Cappetta, 2002). We are not in a position to evaluate the age of the Alinga Formation, but it appears to us that the Molecap cannot be defended on present evidence as producing a Cenomanian mosasaur. Moreover, the fragmentary vertebra illustrated by Kear *et al*. (2005:fig. 2) is larger than known, clearly Cenomanian mosasaurs.

All substantiated Cenomanian records are of plesiopedal forms that retain feet and do not possess limbs strongly modified to paddles. The oldest record of mosasaurs in Angola is *Angolasaurus*, and nothing of the group is known definitively in the Southern Hemisphere prior to that occurrence. With regard to their presence in the South Atlantic, it seems most probable that mosasaurs entered there no earlier than the Cenomanian (<99.6). Plesiosaurs and turtles may have had a more complex history, entering once or more than once, from the south in the Early Cretaceous and possibly from the north in the Late Cretaceous. However, possible affinities of Angolan specimens with Northern Hemisphere taxa, and the clear dispersal of ammonites during the middle portion of the Cretaceous as the Atlantic was completed, certainly suggest equatorial dispersal into the South Atlantic of all three groups at least by Turonian time. Those loose hypotheses remain to be tested by the fossil record of Angola.

The sauropod specimen from Iembe is interesting as far as it goes, but we predict that the sample of dinosaurs and other terrestrial vertebrates will improve as field work continues. For now, it is reasonable to conclude that the Iembe sauropod represents a taxon descended from sauropods in Africa at the completion of the South Atlantic Ocean and the isolation of Africa. Thus, from a biogeographic perspective, the development of the South Atlantic has significance for dinosaurs equal to that which it has for mosasaurs, in the first case leading to restriction of faunal dispersal, in the second to a new dispersal route for marine organisms. Sereno *et al*. (2004) suggested that trans-Atlantic interchange, and hence a dry land passage between South America and Africa, may have existed as late as 95 Ma, based on their reckoning of the age of the abelisaurid dinosaur *Rugops* from the Echkar Formation, Niger. Although they state the age as Cenomanian and give an absolute age estimate of "ca. 95 Myr ago" for the specimen (Sereno *et*

al., 2004:2), no evidence for the age is provided. Taquet (1976), on which the dating of fossil localities in Niger appears to rely, places the Echkar Formation in the Albian. By the Late Cenomanian, marine transgression had put an end to the deposition of the Continentale Intercalaire, of which the Echar Formation is a part. Until chronological data are brought forth to justify a Cenomanian age for *Rugops*, its significance for indicating trans-Atlantic interchange at 95 Ma should be questioned because that age estimate stands contrary to indications that the Atlantic was complete by Albian time (which ended at 99.6 Ma), and Niger was inundated by marine waters by Late Cenomanian time, or about at the target age of 95 Ma.

CONCLUSIONS

We began this paper by stating that we have embarked on what we hope will be a long-term field-based exploration of the vertebrate paleontology of Angola. During the course of writing this paper several specific issues became obvious as to what can be done and what should be done with respect to our project. From what we know now, it is clear that the fossil record of mosasaurs, plesiosaurs, and turtles can be significantly augmented through field work in Angola, and that those studies will have an impact on phylogenetic studies of those groups. Advances will take place on fossils from at least two time horizons, the first approximately the Late Turonian and the second Campanian-Maastrichtian. We accept that statement as likely because we have collected fossils in those intervals, but that does not preclude the discovery of fossils at other stratigraphic levels. It is also a reasonable assumption that we will obtain a better sample of dinosaurs and other terrestrial fossils.

All of the fossils that we collect are likely to influence models of biogeography of marine vertebrates on the one hand, and of terrestrial vertebrates on the other, because of the strategic position of Angola with respect to the completion of the Atlantic Ocean permitting the exchange of Northern with Southern Hemisphere marine species in a strictly circumscribed area both temporally and geographically, and because the completion of the Atlantic Ocean resulted in the final isolation of Africa and its terrestrial fauna. To approach its full potential with respect to formulating and testing biogeographic models, however, it has become abundantly clear that fossils need to be collected with extreme concern for stratigraphic context, and that multiple approaches to chronological control, including radiometric dating, should be applied.

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앙골라에서 산출된 백악기 공룡, 모사사우루스, 수장룡, 거북과 그 지질환경

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요 약: 아프리카 사하라 지역에 척추동물화석을 배태한 백악기 지층의 노출은 매우 적다. 왜냐하면 대륙의 상당 부분을 선캄브리아기 변성암 육괴가 넓게 분포하고 있을 뿐 아니라 젊은 시대의 지층들과 식물들이 이들 백악기 지층을 덮고 있기 때문이다. 그러나 백악기 해성층과 육성층이 넓게 발달한 지역이 앙골라 해안과 내륙 사이에서 발견되었다. 앙골라의 주변부는 곤드와나 대륙이 갈라지면서 남대서양이 확장되는 것과 관련되어 형성되었다. 백악기 퇴적층은 해양지각의 덮고 있어 시대는 매우 제한적이며 가장 오래된 지층은 지자기대 (magnetozone) M3 (대략 128Ma, Barremian) 보다 오래되지 않았다. 얕은 해양퇴적 환경은 해안가에 드러나 있지만 내륙으로 점점 육성퇴적 환경이 증가한다. 상어 화석이외에는 앙골라에서 척추화석이 거의 발견되지 않았었다. 예외적인 화석은 앙골라 북부에서 산출된 후기 Turonian 모사사우루스 *Angolasaurus bocagei* 와 *Tylosaurus iembeensis* 이다. 이들 화석은 가장 초창기에 진화된 모사사우루스들이기 때문에 중요하다. 최근 야외조사를 통해 새로운 *Angolasaurus* 의 머리뼈뿐만 아니라 상어, 물고기, 수장룡, 새로운 거북의 머리뼈, 앙골라에서는 처음 발견되는 용각류의 앞다리가 발견되었다. 앙골라 남부에는 백악기에서 팔레오세 경계까지 퇴적된 해양퇴적층이 발견된다.

주요어: 백악기, 공룡, 모사사우루스, 수장룡, 거북, 앙골라

REFERENCES

Ala, M. A. and Selley, R. C. 1997. The western African coastal basins; pp. 173-186 in Selley, R. C. (ed.) and Hsu, K.J. (series ed.), African Basins (Sedimentary Basins of the World, 3). Elsevier Science, Saint Louis, Missouri.

Antunes, M. T. 1964. O neocretácico e o cenozóico do litoral de Angola. Junta de Investigações do Ultramar, Lisboa, 254 pp.

Antunes, M. T. 1966. Contribuiçã para o conhecimento dos nautilóides fóssies de Angola. Conclusões estratigráficas sobre o Cretácico terminal da Bacia de Moçâmede, a propósito dos dos cefalópodes de S. Nicolau. Garcia de Orta (Lisboa) 14:109-138.

Antunes, M. T. and Cappetta, H. 2002. Sélaciens du Crétacé (Albien-Maastrichtien) d'Angola. Palaeontographica 264:85-146.

Bardet, N., Pereda Superbiola, X., Iarochène, M., Amalik, M. and Bouya, B. 2005. Durophagous Mosasauridae (Squamata) from the Upper Cretaceous phosphates of Morocco. Netherlands Journal of Geosciences 84:167-175.

Bell, G. L., Jr. 1997. Part IV Mosasauridae. Introduction; pp. 281-292 in Callaway, J. M. and Nicholls, E. L. (eds.), Ancient Marine Reptiles. Academic Press, San Diego.

Bell, G. L., Jr. 1997. A phylogenetic revision of North American and Adriatic Mosasauroidea; pp. 293-332 in Callaway, J. M. and Nicholls, E. L. (eds.), Ancient Marine Reptiles. Academic Press, San Diego.

Bell, G. L., Jr. and Polcyn, M. J. 2005. *Dallasaurus turneri*, a new primitive mosasauroid from the middle Turonian

of Texas and comments on the polyphyly of Mosasauridae (Squamata). Netherlands Journal of Geosciences 84:174-194.

Bolli, H. M., Ryan, W. B. F. *et al*. 1978. Initial reports of the Deep-Sea Drilling Project, Volume 40. U.S. Government Printing Office, Washington, D.C.

Bond, G. 1978. Evidence for late Tertiary uplift of Africa relative to North America, South America, Australia, and Europe. Journal of Geology 86:47-65.

Borge, A. 1946. A costa de Angola da Baía da Lucira à Foz do Bentiaba. Boletim Soc. Geologia Portugal 5:141-150.

Brice, S. E., Cochran, M. D., Pardo, G. and Edwards, A. D. 1982. Tectonics and sedimentation of the South Atlantic Rift sequence: Cabinda, Angola; pp. 5-18 in Watkins, J. S. and Drake, C. L. (eds.), Studies in Continental Margin Geology. American Association of Petroleum Geologists Memoir 34.

Brognon, G. P. and Verrier, G. V. 1966a. Tectonique et sedimentation dans le basin du Cuanza (Angola). Serviços de Geologia e Minas de Angola Boletim 11:5-90.

Brognon, G. P. and Verrier, G. V. 1966b. Oil and geology in Cuanza Basin of Angola. American Association of Petroleum Geologists Bulletin 50:108-158.

Broin, F. de L. de. 2000. African chelonians from the Jurassic to the Present: Phases of development and preliminary catalogue of the fossils record. Palaeontologia Africana 36:43-82.

Cainelli, C. and Mohriak, W. U. 1999. Some remarks on the evolution of sedimentary basins along the eastern Brazilian continental margin. Episodes, Journal of International Geoscience 22:206-216.

Carvalho, G. S. de. 1961. Geologia do deserto de Moçâmedes (Angola). Junta de Investigações do Ultramar, Lisboa, 227 pp.

Cooper, M. R. 1972. The Cretaceous stratigraphy of San Nicolau and Salinas, Angola. Annals of the South African Museum 72:245-251.

Cooper, M. R. 1978. Uppermost Cenomanian-basal Turonian ammonites from Salinas, Angola. Annals of the South African Museum 75:51-152.

Emery, K. O. and Uchupi, E. 1984. The Geology of the Atlantic Ocean. Springer, New York, 1050 pp.

Gerrard, I. and Smith, G. C. 1982. Post-Paleozoic succession and structure of the southwestern African continental margin; pp. 49-74 in Watkins, J. S. and Drake, C. L. (eds.), Studies in Continental Margin Geology. American Association of Petroleum Geologists Memoir 34.

Gingerich, P. D., Cappetta, H. and Traverse, M. 1992. Marine mammals (Cetacea and Sirenia) from the middle Eocene of Kpogamé-Hahotoéin Togo. Journal of Vertebrate Paleontology 12(Supplement to 3):29A-30A (abstract).

Gradstein, F., Ogg, J. and Smith, A. (eds.). 2004. A Geological Timescale 2004. Cambridge University Press, 589 pp.

Gräfe, K.-U. and Wiedmann, J. 1998. Sequence stratigraphy on a carbonate ramp: The Late Cretaceous Basco-Cantabrian Basin (Northern Spain); pp. 333-341 in de Graciansky, P.-C., Hardenbol, J., Jacquin, T. and Vail, P. R. (eds.), Mesozoic and Cenozoic Sequence Stratigraphy of European basins. SEPM Special Publication 60.

Handoh, I. C., Bigg, G. R., Jones, E. J. W. and Inoue, M. 1999. An ocean modeling study of the Cenomanian Atlantic: Equatorial paleo-upwelling, organic-rich sediments and the consequences for a connection between the proto-North and South Atlantic. Geophysical Research Letters 26:223-226.

Haq, B. U., Hardenbol, J. and Vail, P. R. 1988. Mesozoic and Cenozoic chronostratigraphy and cycles of sea-level change. Sea-level Changes: An Integrated Approach. SEPM Special Publication 42:71-108.

Haughton, S. H. 1963. The Stratigraphic History of Africa South of the Sahara. Oliver & Boyd, Edinburgh, 365 pp.

Hay, W. W., DeConto, R. M., Wold, C. N., Wilson, K. M., Volgt, S., Schulz, M., Wold, A. R., Dullo, W.-C., Ronov, A. B., Balukhovsky, A. N. and Söding, E. 1999. Alternative global Cretaceous paleogeography; pp. 1-47 in Barrera, E. and Johnson, C. C. (eds.), Evolution of the Cretaceous Ocean-Climate System. Geological Society of America Special Paper 332.

Howarth, M. K. 1965. Cretaceous ammonites and nautiloids from Angola. Bulletin of the British Museum (Natural History), Geology 10:339-412.

Howarth, M. K. 1985. Cenomanian and Turonian ammonites from the Novo Redondo area, Angola. Bulletin of the British Museum (Natural History), Geology 39:73-105.

Hudec, M. R. and Jackson, M. P. A. 2004. Regional restoration across the Kwanza Basin, Angola: salt tectonics triggered by repeated uplift of a metastable passive margin. American Association of Petroleum Geologists Bulletin 88:971-990.

Jacobs, L. L., Ferguson, K., Polcyn, M. J. and Rennison, C. 2005a. Cretaceous ^{13}C stratigraphy and the age of dolichosaurs and early mosasaurs. Netherlands Journal of Geosciences 84:257-268.

Jacobs, L. L., Polcyn, M. J., Taylor, L. H. and Ferguson, K. 2005b. Sea-surface temperatures and palaeoenvironments

of dolichosaurs and early mosasaurs. Netherlands Journal of Geosciences 84:269-281.
Karner, G. D. and Driscoll, N. W. 1999. Tectonic and stratigraphic development of the West African and eastern Brazilian margins: Insights from quantitative basin modeling, pp. 11-40 in Camron, N. R., Bate, R. H. and Clure (eds.), The Oil and Gas Habitats of the South Atlantic. Geological Society Special Publication 153.
Kear, B. P. 2003. Cretaceous marine reptiles of Australia: A review of taxonomy and distribution. Cretaceous Research 24:277-303.
Kear, B. P. 2005. A new elasmosaurid plesiosaur from the Lower Cretaceous of Queensland, Australia. Journal of Vertebrate Paleontology 25:792-805.
Kear, B. P. and Lee, M. S. Y. 2005. A primitive protostegid from Australia and early sea turtle evolution. Biology Letters of the Royal Society of London doi:10.1098/rsbl.2005.0406.
Kear, B. P., Long, J. A. and Martin, J. E. 2005. A review of Australian mosasaur occurrences. Netherlands Journal of Geosciences 84:307-313.
Lehner, P. and de Ruiter, P. A. C. 1977. Structural history of the Atlantic margin of Africa. American Association of Petroleum Geologists Bulletin 61:961-981.
Lingham-Soliar, T. 1994. The mosasaur "*Angolasaurus*" *bocagei* (Reptilia: Mosasauridae) from the Turonian of Angola re-interpreted as the earliest member of the genus *Platecarpus.* Paläontologische Zeitschrift 68:267-282.
Lunde, G., Aubert, K., Lauritzen, O. and Lorange, E. 1992. Tertiary uplift of the Kwanza Basin in Angola; pp. 99-117 in Curnelle, R. (ed.), Géologie Africaine: Colloque de Stratigraphie et de Paléogéographie des Bassins Sédimentaires Ouest-Africains. Recuell des Communications, 6-8 May 1991, Libreville, Gabon.
Maisey, J. G. 2000. Continental break up and the distribution of fishes of western Gondwana during the Early Cretaceous. Cretaceous Research 21:281-314.
Marton, L. G., Tari, G. C. and Lehman, C. T. 2000. Evolution of the Angolan passive margin, West Africa, with emphasis on post-salt structural styles; pp. 129-149 in Mohriak, W. U. and Talwani, M. (eds.), Geology and Geophysics of Continental Margins. American Geophysical Union Geophysical Monographs 115.
Meylan, P. A., Moody, R. T. J., Walker, C. A. and Chapman, S. D. 2000. *Sandownia harrisi*, a highly derived trionychoid turtle (Testudines: Cryptodira) from the Early Cretaceous of the Isle of Wight, England. Journal of Vertebrate Paleontology 20:522-532.
Moulin, M., Aslanian, D., Olivet, J.-L., Contrucci, I., Matias, L., Géli, L., Klingelhoefer, F., Nouzé, H., Réhault, J.-P.and Unternehr, P. 2005. Geological constraints on the evolution of the Angolan margin based on reflection and refraction seismic data (ZaïAngo Project). Geophysical Journal International 162:1-24.
Nurnberg, D. and Muller, D. 1991. The tectonic evolution of the South Atlantic from the late Jurassic to present. Tectonics 191:27-53.
Nyblade, A. A. and Robinson, S. W. 1994. The African superswell. Geophysical Research Letters 21:765-768.
Ogg, J. G., Agterberg, F. P. and Gradstein, F. M. 2004. The Cretaceous Period; pp. 344-371 in Gradstein, F., Ogg, J. and Smith, A. (eds.), A Geologic Time Scale 2004. Cambridge University Press.
Ogg, J. G. and Smith, A. G. 2004. The geomagnetic polarity time scale; pp. 63-86 in Gradstein, F., Ogg, J. and Smith, A. (eds.), A Geologic Time Scale 2004. Cambridge University Press.
Polcyn, M. J. and Bell, G. L. Jr. 2005. *Russellosaurus coheni* n. gen., n. sp., a 92 million-year-old mosasaur from Texas (USA), and the definition of the parafamily Russellosaurina. Netherlands Journal of Geosciences 84:321-333.
Poulsen, C. J., Barron, E. J., Arthur, M. A. and Peterson, W. H. 2001. Response of the mid-Cretaceous global oceanic circulation to tectonic and CO_2 forcings. Paleoceanography 16:576-592.
Rage, J.-C. and Néraudeau, D. 2004. A new pachyostotic squamate reptile from the Cenomanian of France. Palaeontology 47:1195-1210.
Reston, T. J., Ruoff, O., McBride, J. H., Ranero, C. R. and White, R. S. 1996. Detachment and steep normal faulting in Atlantic Ocean crust west of Africa. Geology 24:811-814.
Reyment, R. A. and Dingle, R. V. 1987. Palaeogeography of Africa during the Cretaceous Period. Palaeogeography, Palaeoclimatology, Palaeoecology 59:93-116.
Sahagian, D. 1988. Epeirogenic motions of Africa as inferred from Cretaceous shoreline deposits. Tectonics 7:125-138.
Schollnberger, E. M. 2001. Seismic sequence stratigraphy of the Lower Congo, Kwanza, and Benguela basins, offshore Angola, Africa. Ph.D. dissertation, Rice University, Houston, Texas, 358 pp.
Schwarz, D. 2003. A procoelous crocodilian vertebra from the lower Tertiary of Central Africa (Cabinda enclave, Angola). Neues Jahrbuch für Geologie und Paläontologie Monatshefte 2003(6):376-384.
Sereno, P. C., Wilson, J. A. and Conrad, J. L. 2004. New dinosaurs link southern landmasses in the mid-Cretaceous.

Proceedings of the Royal Society of London B:DOI 10.1098/rspb.2004.2692.
Shipboard Scientific Party. 2003. Leg 208 preliminary report. ODP Preliminary Report 108:http://www-odp.tamu.edu/publications/prelim/208_prel/208toc.html.
Soares, A. F. 1965. Contribuição para o estudo dos lamelibrânquios Cretácicos da região de Moçâmedes. Serviços de Geologia e Minas de Angola Boletim 11:137-168.
Standlee, L. A., Brumbaugh, W. D. and Cameron, N. R. 1992. Controlling factors in the initiation of the South Atlantic Rift system; pp. 141-152 in Curnelle, R. (ed.), Géologie Africaine: Colloque de Stratigraphie et de Paléogéographie des Bassins Sédimentaires Ouest-Africains. Recuell des Communications, 6-8 May 1991, Libreville, Gabon.
Taquet, P. 1976. Géologie et paléontologie du gisement de Gadoufaoua (Aptien du Niger). Cahiers de Paléontologie, éditions du Centre National de la Recherche Scientifique, Paris, 191 pp.
Welles, S. P. 1949. A new elasmosaur from the Eagle Ford Shale of Texas: Systematic description. Fondren Science Series 1:1-28.