Cretaceous paleogeography, paleoclimatology, and amniote biogeography of the low and mid-latitude South Atlantic Ocean

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Key-words. – Paleobiogeography, Angola, South Atlantic, Cretaceous, Mosasaur, *Angolasaurus*, Turtles, Chelonians, Squamates

Abstract. – The Cretaceous tropical Atlantic Ocean was the setting for an initial tectonically controlled late Aptian shallow water (≤ 300 m) connection between the northern and southern portions of the Atlantic, followed by a deep-water connection by the Turonian. Ocean currents changed with deepening of the South Atlantic and progressive widening of the Equatorial Atlantic Gateway. Aptian evaporite deposition came to a halt. The Albian-Turonian interval includes a trend toward increasing sea level and was characterized by globally warm sea surface temperatures. Productive areas of coastal upwelling led to the deposition of organic-rich sediments varying in position along the African coast with time, culminating in the Benguela Upwelling that commenced in the Miocene. The drift of Africa in the Late Cretaceous indicates that throughout most of this period, the coastal area around the fossil locality of Iembe, north of Luanda, Angola, lay in arid latitudes (15° S to 30° S), which are generally characterized by sparse vegetation. This presumption is consistent with the utter lack of macroscopic terrestrial plant debris washed into near shore sedimentary environments and indicates that organic rich marine shales have a minimal terrestrial carbon component. The connection of the North and South Atlantic oceans severed a direct terrestrial dispersal route between South America and Africa, but opened a north-south dispersal route for marine amniotes. This seaway was used by late Turonian mosasaurs and sea turtles as evidenced by *Angolasaurus* and a new turtle taxon close to *Sandownia*, both found at Iembe and derived from northern clades. The presence of a sauropod in late Turonian sediments, also from Iembe, suggests that this animal was tolerant of warm, arid conditions as the desert elephants of Namibia are today. Further, it suggests that the waning terrestrial dispersal route between South America and Africa was situated in a region where high temperature, low rainfall, and sparse vegetation would be expected to restrict the movement of more mesic and ecologically sensitive species.

La paléogéographie, la paléoclimatologie et la biogéographie des amniotes pendant le Crétacé aux basses et moyennes latitudes de l'océan Sud-Atlantique

Mots-clés. – Paléobiogéographie, Angola, Atlantique Sud, Crétacé, Mosasaurides, *Angolasaurus*, Tortues, Chéloniens, Squamates.

Résumé. – L'océan Atlantique tropical crétacé a été le siège de la connection, contrôlée par la tectonique, en eaux peu profondes (≤ 300 m) à l'Albien supérieur, entre les parties nord et sud de l'océan. Elle sera suivie par une connection en eaux profondes au Turonien. Les courants océaniques changent avec l'approfondissement de l'Atlantique sud et l'élargissement progressif de l'Atlantique équatorial (golfe de Guinée) qui se traduit par l'arrêt des dépôts évaporitiques marquants l'Aptien. L'intervalle Albien-Turonien est caractérisé par une tendance à l'augmentation du niveau marin et des températures des eaux de surface. Des régions productives d'upwellings côtiers conduisent au dépôt de sédiments riches en matière organique migrant le long de la côte africaine avec le temps, aboutissant à l'upwelling de Benguela qui a débuté au Miocène. La dérive de l'Afrique durant le Crétacé supérieur indique que durant la majeure partie de cette période, le secteur côtier autour de la localité fossile d'Iembe, nord de Luanda, Angola, était situé sous des latitudes arides (15° S à 30° S), qui sont généralement caractérisées par une végétation clairsemée. Cette présomption est appuyée par le manque total de débris terrestres macroscopiques de plantes dans les environnements sédimentaires et indique que les shales marins riches en matière organique avaient un taux de carbone terrestre faible.

Le raccordement de l'océan Atlantique Nord et Sud a clos la route terrestre directe de dispersion entre l'Amérique du Sud et l'Afrique, mais a ouvert un itinéraire de dispersion Nord-Sud pour les amniotes marins. Cette voie marine a été utilisée dès le Turonien supérieur par les mosasaures et les tortues, du genre *Angolasaurus* et un nouveau taxon proche de *Sandownia*, les deux dérivés de clades d'origine septentrionale et trouvés à Iembe. La présence à Iembe d'un sauropode dans le Turonien supérieur suggère que cet animal tolérait des conditions chaudes et arides comme les

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éléphants actuels du désert de Namibie. De plus, elle suggère que l'itinéraire de dispersion (de plus en plus limité) entre l'Amérique du Sud et l'Afrique était situé dans une région où les hautes températures, les basses précipitations, et la végétation clairsemée ont probablement dû limiter les mouvements des espèces écologiquement plus sensibles.

INTRODUCTION

The origin of the South Atlantic Ocean has long been the premier example of plate tectonics, obvious from the puzzle-like fit of conjugate South American and African continental margins coupled with mirror-image magnetic stripes on the ocean floor [Cande *et al.*, 1989]. It is also a premier example of paleobiogeography, of ocean currents that transfer heat between the northern and southern hemispheres, and of depositional basins that accumulate organic sediments and produce oil [Berger and Wefer, 1996; Brownfield and Charpentier, 2006]. Our purpose in this paper is to examine the biogeography of the low and mid-latitude southern Atlantic Ocean from the perspective of our work on Cretaceous vertebrate fossils from coastal Angola.

As the South Atlantic basin developed through the separation of the African and South American landmasses, the east-west terrestrial dispersal route for Gondwana, exclusive of Antarctica, was severed while enabling a new route for north-south marine dispersal to and from the Tethyan realm. In considering the biogeography of dispersal, we must also consider the geography and position of the African continent from the initial opening of the South Atlantic to the achievement of its current latitude, because latitude has a first order effect on climate and therefore environment, both of which affect vertebrate distribution. Moreover, as the connection between the northern and southern portions of the Atlantic grew deeper and wider, and as continental reorganization continued to change through the Cretaceous and Cenozoic, deep, intermediate, and shallow ocean currents were modified, influencing climate, productivity, and depositional patterns. Below we review these topics briefly and speculate on a model of marine amniote dispersal and climatic control of terrestrial amniote dispersal.

Figure 1 shows a series of maps for the late Turonian South Atlantic, a time chosen because it contains the first good record of marine amniotes in Angola. These maps represent models of paleogeography, rainfall and land runoff, and upwelling zones. For a discussion of assumptions associated with maps such as these, see Sewall *et al.* [2007]. The salient points to recognize are a narrow South Atlantic with a connection to the North Atlantic, the position of Angola within a low rainfall and runoff area, and the placement of West African upwelling to the north.

The isolation of Africa progressed from the eastern portion of the continent near the beginning of the Jurassic ($\approx$ 200 Ma), continuing south with the formation of the nascent Indian Ocean, then around the Cape of Good Hope, and northward until the final separation from South America [Hay *et al.*, 1999]. Our concern in this paper is with the formation of the west coast of Africa, which began in the Jurassic and culminated in the middle portion of the Cretaceous [Emery and Uchupi, 1984; Nurnberg and Muller, 1991; Jacobs *et al.*, 2006]. We are specifically interested in Aptian through Turonian (125 – 89 Ma), when the southern

Atlantic began as a narrow, highly saline sea, which has continued widening along the Mid-Atlantic Ridge until today.

The coast of Angola, including the province of Cabinda, lies today between approximately 5°S to 17°S. The Walvis Ridge, which is an important structure with respect to ocean currents, extends from the African coast at about 20°S southwestward toward the Mid-Atlantic Ridge. The Walvis Ridge (or Tristan) and Saint Helena hotspots served to propagate rifting during the opening of the Atlantic [Standlee *et al.*, 1992; O'Connor and le Roex, 1992]. The oldest known oceanic crust along the coast of Angola [magnetozone M3, Cande *et al.*, 1989] is approximately 128 Ma (Early Cretaceous, Barremian) [Ogg and Smith, 2004].

The opening of the South Atlantic through tectonic processes, with concomitant development and modification of ocean currents, has resulted in characteristic patterns of marine sedimentation through time. Lower Cretaceous (Aptian, 125 – 112 Ma) rocks are dominantly evaporites, which signify restriction from open oceanic circulation [Hay *et al.*, 1999]. Above the evaporites are thick carbonate and clastic units [Brognon and Verrier, 1966; Gerrard and Smith, 1982]. Carbon isotope analyses show a greater influx of terrigenous carbon into the marine Angola Basin in the Aptian and early Albian with little terrestrial component after that time [Foresman, 1978]. The fossiliferous, amniote-bearing, marine rocks of the Angola coast are fine-grained near-shore silts and sands [Jacobs *et al.,* 2006]. Those that we have studied range in age from Turonian through Maastrichtian (93 – 66 Ma). While the west coast of Africa is a passive margin, it is not without structure and igneous activity. The Angola coastline shows numerous faults and Late Cretaceous volcanics [Lunde *et al.*, 1992; Jacobs *et al.*, 2006]. We have observed Late Cenozoic shorelines in Angola now standing 30 meters or more above current sea level.

OCEAN CURRENTS

The Atlantic Ocean is an excellent example to demonstrate the effect of changing continental configurations on the development of ocean currents through geologic time. Surface currents of the southern Atlantic today are predictably controlled by Earth's rotation and prevailing winds, and notably give rise to the cold upwelling, highly productive, Benguela Current from the coast of Namibia north to the southern portion of Angola where it turns northwest [Shannon and Nelson, 1996]. It forms the eastern boundary of the Subtropical Gyre. Upwelling of the Benguela Current has a Miocene origin, approximately 10.5 Ma [Siesser, 1980; Diester-Haass *et al.,* 2002], although other areas of productive upwelling occurred along the West African coast in the past [Handoh *et al.*, 1999]. The South Equatorial Current skirts the northern edge of the Subtropical Gyre from southeast to northwest where it merges with the Gulf Stream to deliver warm water to the north.
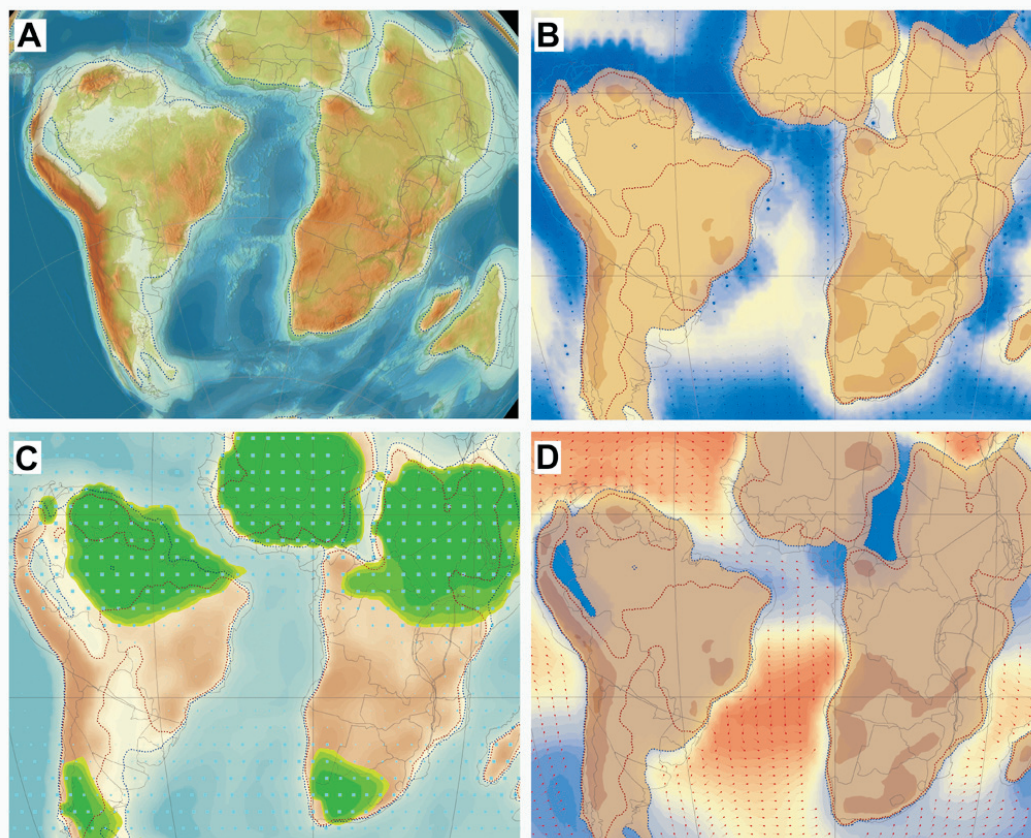
FIG. 1. – A, Late Turonian (90 Ma) lowstand paleogeography of the South Atlantic region; B, Late Turonian upwelling in the South Atlantic region (blue areas = upwelling; size of blue dots represents volume of upwelling X persistence); C, Late Turonian rainfall and runoff pattern the South Atlantic region (green = land runoff; size of cyan squares represents average annual rainfall); D, Late Turonian salinity (red = more salty; blue = less salty; arrows = summer surface ocean currents). Blue dashed lines = lowstand; brown dashed lines = highstand [Scotese, 2008].

FIG. 1. – A, *Paléogéographie au niveau le plus bas de l'océan dans la région Sud-Atlantique au Turonien supérieur (90 Ma). B, Remontée d'eau ('Upwelling') dans la région Sud-Atlantique au Turonien supérieur. Aires bleues = upwelling ; la taille des points représente le volume de persistence de l'upwelling au Turonien supérieur (90 Ma). C, Pluviosité et ruissellement de la région Sud-Atlantique au Turonien supérieur. Vert = ruissellement ; la taille du carré cyan indique la moyenne annuelle de pluie. D, Salinité au Turonien supérieur. Rouge = plus salin ; bleu = salin; flèche = courants océaniques de surface en été. Tirets bleus = niveau bas de l'océan ; tirets brun = niveau haut de l'océan [Scotese, 2008].*

Deep currents in the Atlantic are induced as cold, saline North Atlantic Deep Water sinks and flows southward. The warm southern hemisphere South Equatorial Current described above flows to the north at shallower depths, above the south flowing North Atlantic Deep Water, creating an Atlantic heat conveyor [Berger and Wefer, 1996]. Frigid Antarctic Bottom Water flows northward at greater depth, below the North Atlantic Deep Water Current with which it eventually mixes, extending farther to the north on the western side of the Atlantic and hindered in its progress on the east by bottom structures, notably the Walvis Ridge. While cold-water drainage from the Antarctic has likely always been a factor to some extent, the Paleogene isolation of Antarctica and the consequent development of the Circumpolar Current almost certainly exacerbated its effect. Thus, modern Atlantic Ocean currents require an open Atlantic and an isolated Antarctica. Therefore, they are much derived from what is to be expected in the nascent Atlantic Ocean.

In the late Aptian and the earlier portion of the Albian, the southern Atlantic was narrow and the northern end was open through a shallow to intermediate connection, but not deep circulation. The evidence for an initial Equatorial Atlantic Gateway derives from northeastern Brazil. A variety of marine invertebrates of northern affinity in the Sergipe Basin [Bengston and Koutsoukos, 1992; Koutsoukos, 1992] and the distribution of fish [Maisey, 2000] indicate a marine incursion into Brazil by late Aptian time (Aptian = 125 – 112 Ma) [Ogg *et al.*, 2004]. Valença *et al.* [2003] recognize two short marine transgressions (late Aptian and Albian) over much of the region. However, the Sergipe Basin was apparently continuously marine from the late Aptian to the Holocene [Koutsoukos *et al.*, 1991]. The widespread abundance of evaporites during the Aptian indicates restricted circulation, and intervals of early to mid-Cretaceous anoxia in the offshore Angola Basin are explained by a Red Sea circulation model [Shipboard Scientific Party, 1978; Hay *et al.,* 1999] driven by reduced influx and high evaporation.

Poulsen *et al.* [2001] point out that major oceanic anoxic events in the Aptian-early Albian (112 Ma) and at the Cenomanian-Turonian (93.5 Ma) boundary, as well as mid-Cretaceous increased biological turnover and a thermal maximum were coincident with high seafloor spreading rates and volcanic outgassing. Their model experiments support the hypothesis that climatic and oceanographic changes surrounding the Cenomanian-Turonian boundary, as compared

to the Albian, were driven by the initiation of deep flow between the northern and southern Atlantic Oceans.

Handoh *et al.* [1999], utilizing a reduced-gravity ocean model, conclude that the distribution of organic-rich sediments inferred to result from upwelling zones suggests an initial shallow gateway (≤ 300 m) persisting through the Cenomanian (99.6 – 93.5 Ma), followed by a late Turonian (90 Ma) deep-water connection across the Equatorial Atlantic Gateway. According to this model, some regions of upwelling changed as geography changed, resulting in organic-rich shales more localized than those formed due to a general anoxia of ocean bottom waters. This view is consistent with the geographically facultative development or intensification of upwelling zones such as the Benguela Current in the late Miocene or later [Diester-Haass *et al.,* 2002, 2004].

At a finer scale, river discharge driven by orbital precession during the Coniacian to Campanian interval is reported to have influenced anoxia by delivery of nutrients into the marine environment near Ivory Coast in the Gulf of Guinea, north of Angola, culminating in the deposition of black shales [Beckmann *et al.*, 2005]. Nevertheless, the position of the black shales near Ivory Coast is consistent with the model of Handoh *et al.* [1999].

The Handoh *et al.* [1999] model allows a geographic arrangement of oceans and continents that facilitates marine dispersal beginning in the late Aptian but halts terrestrial dispersal even as tectonic processes continue. Although this scenario seems reasonable to us, it is difficult to portray ocean depths of the magnitude of ≤ 300 m on maps of the scale shown in figure 1, regardless of their apparent paleobiogeographic impact. It is clear that continental configuration played a major role in the development of currents and that other factors imposed modifications to regional productivity.

GLOBAL TEMPERATURES

General circulation models of mid-Cretaceous climate indicate that temperatures were at their maximum during the Cenomanian and Turonian, with warmer temperatures extending to higher latitudes [Bice and Norris, 2002; Bice *et al.,* 2003]. One potential problem is the mechanism for raising high latitude temperatures without unrealistically raising tropical temperatures. Small-bodied marine squamates such as snakes, coniasaurs, and plesiopedal mosasaurs, which are known to occur in relatively low latitudes are not likely to have existed habitually in surface waters appreciably above 30°C without behavioral or other mechanisms for survival [Jacobs, Polcyn *et al.,* 2005]. Bice *et al.* [2006] interpreted $\delta^{18}O$ values of Turonian foraminifera as indicating sea surface temperatures over the Demara Rise (9°-14°N) between 33°C and 42°C, which is indeed a high sea surface temperature.

The Cenomanian and Turonian position of Iembe, Angola, north of Luanda, was 20° to 25°S latitude. Pucéat *et al.* [2007] presented two paleotemperature estimates (26.6° ± 1.4°C and 28.9° ± 1.4°C) for upper ocean temperature of coastal Angola during the Cenomanian, utilizing a $\delta^{18}O$ value determined by Kolodny and Luz [1991] from phosphate of a shark tooth (*Cretalamna appendiculata*).

These are comparable sea surface temperatures to the modern Caribbean Sea. The paleolatitude for the sample is given by Pucéat *et al.* [2007] as 23°S, but there are no further locality data, and no further justification for the age. Indeed, *Cretalamna appendiculata* has a long temporal range in the Cretaceous of Angola [Antunes and Cappetta, 2002].

Amiot *et al.* [2004] analyzed phosphate from the teeth of Campanian and Maastrichtian continental vertebrates, well after the Cenomanian – Turonian thermal maximum. While they concluded that the latitudinal temperature gradient was less than today because of higher temperatures at higher latitudes, as modeled for the Cenomanian and Turonian, the average annual air temperatures at lower latitudes were roughly 30°C at the equator, dropping to approximately 20°C at 20° latitude.

THE NORTHWARD DRIFT OF AFRICA

Regardless of superimposed effects of climate drivers such as atmospheric CO_2 concentration, a first order approximation of climate of the Angola coast can be derived from its latitudinal position through time, assuming that changes in atmospheric circulation cells due to temperature gradient or other factors are relatively trivial. Figure 2 is a plot for the latitude (as the measure of the northward component of drift) versus time for the fossil locality of Iembe, our northernmost Angolan Cretaceous locality, now at 8°S. There is a general northward drift throughout the Cretaceous and Cenozoic, as is obvious from hotspot traces [O'Connor and le Roex, 1992]. The rate of northward drift lessens at about 20 Ma, consistent with O'Connor *et al.* [1999]. There is a strong deflection at about 100 Ma. This deflection indicates a shift in direction from that followed by the continent during the eruption of Jurassic Karroo flood basalts and Early Cretaceous Entendeka lavas [O'Connor and Duncan, 1990]. This change in course may represent larger scale plate reorganization, rather than a tracing of single plate movement along hotspots [Wang and Liu, 2006]. Throughout the Cenomanian and Turonian, Iembe lay between 20° and 25°S latitude. These latitudes today would indicate an arid environment.
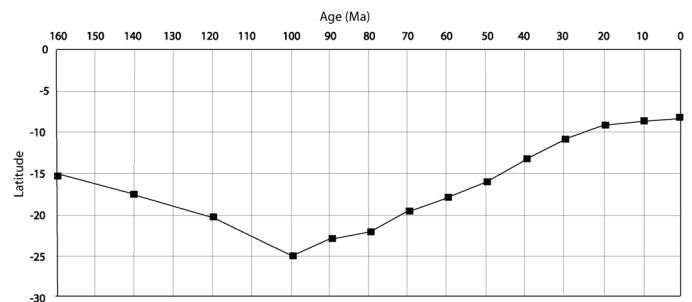

FIG. 2. – Latitude as a function of time for the late Turonian (90 Ma) fossil locality of Iembe, Angola. Current latitude = 8°S [Latitudes from Scotese, 2008].

FIG. 2. – *Déplacement de la latitude au cours du temps de la localité des fossiles de Iembe, Angola au Turonien supériur (90 Ma). Latitude actuelle : 8°S [latitudes de Scotese, 2008].*

THE COMPLETION OF THE ATLANTIC OCEAN AS A MARINE AMNIOTE DISPERSAL CORRIDOR

The completion of the Atlantic Ocean by the opening of the Equatorial Atlantic Gateway occurred in the Early Cretaceous (late Aptian, approximately 115 Ma) based on the presence of ammonites and other invertebrates from the north extending their range to the south through an open corridor. It also appears as if a new taxon of marine turtle and two mosasaurs, *Angolasaurus* and *Tylosaurus*, from Iembe were derived from northern source areas.

The turtle is derived in having an extensive palate and elongate squamosal bones. Phylogenetic analysis indicates a close relationship with an unnamed taxon of Albian turtle from Texas, and with *Sandownia* from the Aptian of the Isle of Wight (fig. 3) [Vineyard, 2007]. A phylogenetic analysis was conducted using a matrix of 25 chelonian taxa and 49 cranial characters presented by Joyce [2007], modified to include characters of the secondary palate. Maximum parsimony analyses using heuristic search in PAUP* [Swofford, 2002] yielded 2241 trees. A majority rule consensus (CI = 0.5217) agrees with Joyce's preferred phylogenetic hypotheses [Joyce, 2007, his Figure 18) of Eucryptodira. The Angola and Texas taxa form a monophyletic group with *Sandownia* within Eucryptodira based on possession of a well-developed secondary palate involving vomer, elongate squamosal bones, incisura columellae auris enclosing the stapes, broad vomer-premaxillae contact, and foramen posterius canalis carotici interni formed by the pterygoid near the posterior end of the basisphenoid. The Angola and Texas taxa are derived relative to *Sandownia* in having reduced prefrontal bones that are anteriorly positioned, and a well-developed crista supraoccipitalis that extends significantly posteriorly beyond the occipital region. Conversely, the Angola and Texas taxa appear primitive relative to *Sandownia* in the presence of paired nasals, absence of a contribution by palatines to the anterior extension of the lateral braincase wall, and the presence of an epipterygoid that forms the anteroventral portion of the foramen nervi trigimini. The extensive palate and associated features of the lower jaw, such as broad symphysis, suggest a durophagous diet, as has also been suggested for osteopygine turtles [Lynch and Parham, 2003].

Mosasaurs from Iembe were originally studied by Antunes [1964]. Our recent fieldwork produced three skulls and postcrania of *Angolasaurus bocagei* and a new specimen of *Tylosaurus iembeensis* [Jacobs *et al*., 2006]. Figure 4 is a

cladogram of the phylogenetic relationships of *Angolasaurus* and *Tylosaurus iembeensis* among mosasaurs based on Polcyn and Bell [2005]. *Angolasaurus* is relatively basal among plioplatecarpine mosasaurs, distinct from *Platecarpus* by retention of the plesiomorphic states of a narrow frontal, position of pineal foramen in the center of the triangular parietal table, basilar artery entering basioccipital floor as two foramen, and the autapomorphic condition of an enlarged posteroventral process of the parietal meeting the supraoccipital.

Tylosaurus iembeensis is known from the Turonian of Angola [Antunes, 1964]. It retains a plesiomorphic quadrate morphology exemplified by the absence of a developed infrastapedial process, comparable to the condition in *T. kansasensis* from the Coniacian of Kansas [Everhart, 2005]. Earlier occurrences of *Tylosaurus* are documented from the Turonian of Texas and New Mexico [Polcyn *et al.*, 2008]. The distribution of these early tylosaurines is comparable to that of *Angolasaurus* and confirms communication between the Western Interior Seaway of North America and the South Atlantic during the late Turonian.

The presence of *Angolasaurus* and an early *Tylosaurus* at Iembe is biogeographically informative because they represent the earliest record of mosasaurs in the southern ocean. Currently the oldest mosasaur record (early Cenomanian, 98 Ma) is *Haasiasaurus*, a plesiopedal form [*sensu* Bell and Polcyn, 2005] from 'Ein Yabrud in the Middle East [Polcyn *et al.*, 1999, 2003; Jacobs, Ferguson *et al.*, 2005], the sister taxon to (*Halisaurus* + (Tylosaurinae + Plioplatecarpinae)). Its age and phylogenetic position demonstrates that mosasaurines diverged from plioplatecarpines plus tylosaurines by 98 Ma. The oldest known mosasaurine is *Dallasaurus* from Texas at 92.5 Ma (early Turonian). The oldest known and most basal plioplatecarpine is *Russellosaurus*, also from Texas and also 92.5 Ma [Polcyn and Bell, 2005]. Its age demonstrates that the cladogenetic event between plioplatecarpines and tylosaurines occurred at least by that time.

By 90 Ma (late Turonian), derived mosasaurids are known from the northern and southern hemispheres, notably Angola. Significantly, *Angolasaurus* is reported from Texas based on two partial skulls, and from the Sergipe Basin, Brazil, based on size, proportions, and pattern of striations of two teeth [Polcyn *et al.*, 2007; Bengtson and Lindgren, 2005]. Both *Angolasaurus* and *Tylosaurus* from Iembe are relatively basal within their respective subfamilies. The phylogenetic relationships of *Angolasaurus* and *Tylosaurus iembeensis*, and the geographic distribution of Cenomanian and Turonian mosasaurs, suggest a dispersal route from North to South through the Gulf of Guinea soon after the subfamilial diversification of mosasaurids.

Accepting the record at face value, and comparing with modern marine mammals and sea turtles, a hypothesis of dispersal biology can be constructed based on $\delta^{13}C$ values of the carbonate component of mosasaur tooth enamel. In the modern oceans, the $\delta^{13}C$ values of primary producers vary in parallel with the values of particulate organic matter; both have decreasing $\delta^{13}C$ values with increasing distance from shore and increasing latitude [Clementz and Koch, 2001; Rau *et al.*, 1982]. These geographic variations in carbon isotope value are transmitted up the marine food chain, and are evident in the $\delta^{13}C$ values of structural
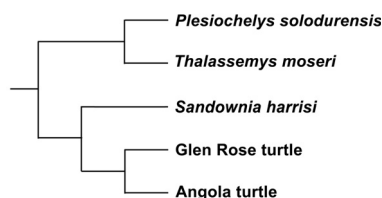

FIG. 3. – Phylogenetic relationships of a new basal eucryptodiran turtle from Iembe, Angola, based on Vineyard [2007]. The Angolan taxon nests with a new species from the Albian of Texas and with *Sandownia* from the late Aptian of England.

FIG. 3. – *Relation phylogénétique d'une nouvelle tortue eucryptodiran basale de Iembe, Angola, d'après Vineyard [2007]. Le taxon d'Angola se groupe avec une nouvelle espèce de l'Albien du Texas, et avec* Sandownia *de l'Aptien d'Angleterre.*

carbonate in marine mammals [Walker and Macko, 1999]. Their enamel $\delta^{13}C$ values vary systematically with the distance from shore of the foraging area the animal occupies. Animals that forage near shore have more positive $\delta^{13}C$ enamel values than those that forage in the open ocean [Clementz and Koch, 2001; Clementz et al., 2007].

In addition to the effects of geographic variation in foraging behavior, physiological differences between shallow– and deep-diving marine amniotes may contribute to carbon isotope differences among species. Biasatti [2004] found that the carbonate component of bone apatite in shallow-diving sea turtles had $\delta^{13}C$ values much more positive (~ 0‰) than those in the bone apatite of deep-diving sea turtles (–6 to –12‰), a difference which is likely caused in part by the Bohr effect.

If these biogeographic and physiological differences in $\delta^{13}C$ values shown by modern marine mammals and sea turtles hold for mosasaur tooth enamel, then the $\delta^{13}C$ values of mosasaur teeth can be used to examine mosasaur foraging strategies and to determine dispersal patterns of near-shore, shallow water *versus* offshore, deeper water species. As a preliminary test we determined the $\delta^{13}C$ value of the carbonate component of enamel of one specimen of *Coniasaurus* from Texas, among others [Robbins et al., 2008], and from one tooth of *Angolasaurus* from Iembe. *Coniasaurus* has a value of –1.2‰, which suggests a preferential near shore habitat, an environment not surprising for a small marine squamate. *Angolasaurus* has a value of –7.4‰, which may indicate a more open ocean foraging strategy compared to *Coniasaurus*, a greater reliance on deep diving during

foraging, or some combination of the two. Other factors, such as latitude, may have an effect and should be tested. However, carbon isotope values presented by Robbins et al. [2008] indicate that foraging habitat is important in mosasaur carbon isotope variation, as it is in marine mammals, even if *Angolasaurus* is excluded from the Robbins et al. [2008] data set.

Given the Cretaceous history of the opening of the South Atlantic, *Coniasaurus* and other small marine squamates including primitive plesiopedal mosasaurs might be expected to have dispersed along routes close to shore, during the initial, shallow water connection with the North Atlantic. Dispersal of the deeper water, open-ocean foraging mosasaurs such as *Angolasaurus* would not have been hindered by a deep-water connection established in the Turonian.

THE ENVIRONMENT OF THE TERRESTRIAL DISPERSAL ROUTE AS THE ATLANTIC OCEAN OPENED

A marine barrier is a strong (but not complete) inhibitor of terrestrial dispersal. However, the environmental conditions along a corridor as it narrows over geologic time can limit carrying capacity and filter ecologically sensitive species. The latitude of Iembe through the Cretaceous, between 20 and 25°S, would suggest arid conditions because those latitudes lie below the high-pressure limb of the atmospheric Hadley Cell, the southeasterly trade winds of those latitudes are drained of moisture as they traverse the continent, and
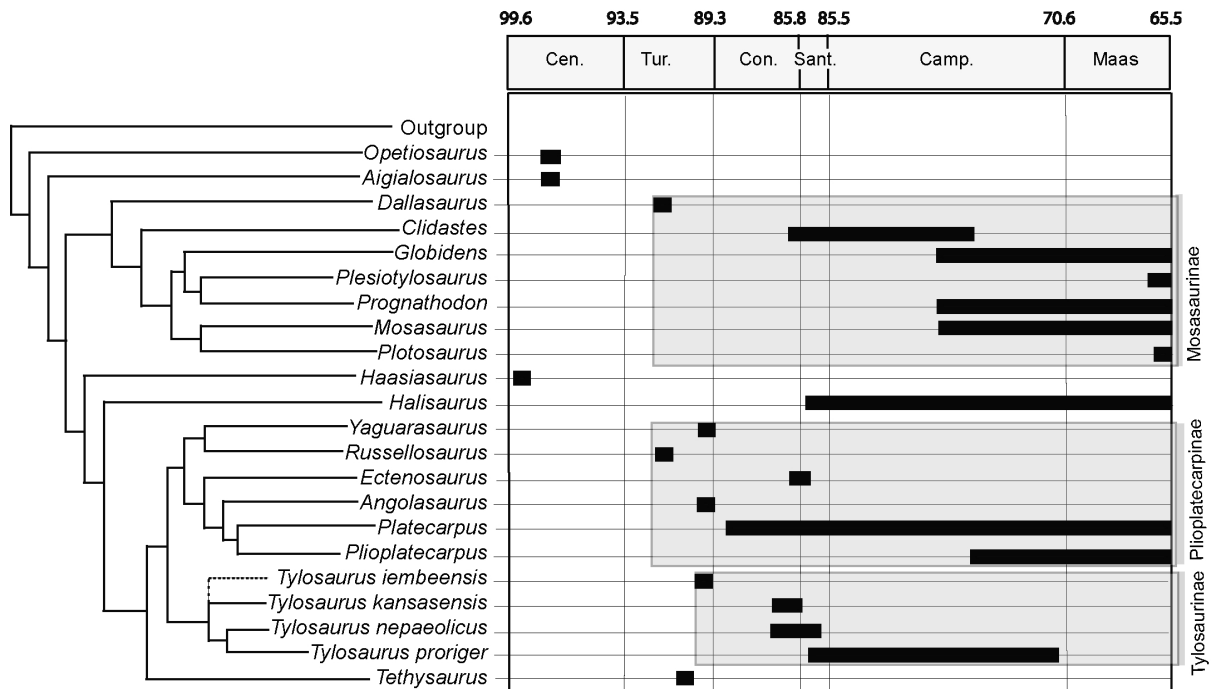

FIG. 4. – Phylogenetic relationships of *Angolasaurus* and *Tylosaurus iembeensis* from Iembe, Angola, modified from Polcyn and Bell [2005]. Phylogenetic position of *T. iembeensis* inferred from quadrate morphology. The phylogenetic positions and the age of the two Angolan taxa relative to other mosasaurs indicates a northern source area. Time scale from Ogg et al. [2004]; range data from Bardet et al. [2005, 2006], Cuthbertson et al. [2007], Everhart [2001, 2005], Polcyn et al. [2009], and Russell [1967].

FIG. 4. – *Relation phylogénétique de mosasaures* Angolasaurus *et* Tylosaurus iembeensis *de Iembe, Angola, modifié de Polcyn et Bell [2005]. Position phylogénétique de* T. iembeensis *déduite de la morphologie quadrate. Les positions phylogénétiques et l'âge des deux taxa d'Angola, relatifs à d'autres mosasaurids, indiquent une origine d'une région du nord. Chronologie de Ogg* et al. *[2004] ; distribution de Bardet* et al. *[2005, 2006], Cuthbertson* et al. *[2007], Everhart [2001, 2005], Polcyn* et al. *[2009], et Russell [1967].*

the coastal upwelling generated by the trade winds further exacerbates aridity [Hartley *et al.,* 2005]. The fossil localities we have worked in Angola are near shore marine. We have observed no plant material washed into the sediments. It is not unlikely that the surrounding shores were sparsely vegetated due to desert conditions. Deserts are not without fauna, but they have a limited carrying capacity because of limited resources. Nevertheless, today, even large mammals such as elephants can exist in desert conditions, as in Namibia where they obtain water from springs and by excavating streambeds. At Iembe we recovered the forelimb of a small non-titanosaurian sauropod, the first Turonian dinosaur discovered in Africa [Jacobs *et al.*, 2006]. Its presence postdates the formation of the Equatorial Atlantic Gateway by 10 million years or more, so it is not a direct reflection of South America-Africa dispersal. However, if our climatic assumptions are correct, it does show that sauropods could inhabit arid regions. Given the latitude of western Gondwana before the completion of the Atlantic, dispersal may well have been across an inhospitable desert terrain, which may have acted as a filter by reducing carrying capacity and inhibiting the spread of ecologically sensitive species. Conversely, species evolving in Cretaceous arid latitudes were subject to vicariance as the seaway was completed and to ecological constraints as they dispersed into new environments.

DISCUSSION AND CONCLUSIONS

The maps in figure 1 summarize important points relevant to South Atlantic paleobiogeography. The opening of the Equatorial Atlantic Gateway allowed marine migration to occur. Marine productivity patterns were shifted to more northerly parts of the African continent as shown by areas of upwelling (fig. 1B). However, the area of Angola was in an arid region even though the patterns of rainfall and runoff are unique to the time (fig. 1C). The paleolatitude of Iembe, as shown in figure 2, indicates a position in latitudes that are arid currently and indicate a similar pattern of atmospheric cells. Our observations at Iembe indicate that a productive coastal environment lay next to an arid terrestrial environment. Thus, the point locality of Iembe does not contradict the models presented in the maps of figure 1.

The biogeography of Africa was reviewed by Maisey [2000], Krause *et al.* [2006], and Gheerbrant and Rage [2006]. Africa's continental vertebrate biota in the Early Cretaceous is most like that of South America, suggesting subsequent biogeographic vicariance. Africa was essentially isolated through plate tectonics from other landmasses, including the Gondwana continents of India, Australia, and Antarctica, for much of the Early Cretaceous and all of the Late Cretaceous. Moreover, Cretaceous biogeographic relationships with Laurasia, more specifically Europe, are complex and very likely involve what McKenna [1973] termed "beached Viking funeral ships" because fossils preserved in one area (northern African Gondwana) subsequently became incorporated into a new area (Europe), as slices of

continental crust peeled northward and assembled Apulia and other portions of southern Europe [Polcyn *et al*., 1999]. The biota of the Cretaceous sea around West Africa supply the data for the timing of Africa's separation from South America and the conjoining of the northern and southern Atlantic through the Equatorial Atlantic Gateway.

Beginning as early as the late Aptian a shallow gateway existed between north and south, but deep-water connection did not occur until the Turonian [Handoh *et al.,* 1999]. As mosasaurs obtained a size and life style that allowed significant open marine dispersal, they were able to colonize the South Atlantic from the north. At least one marine basal eucryptodire turtle, in addition to mosasaurs, was able to exploit opportunistically the north-south connection in the same time interval.

From a terrestrial perspective, latitudinal position is a first order determinate of climate because of insolation on the globe. Climate zonation is well known, and although it may be modified from time to time for physiographic or other reasons, latitudinal zonation must be considered a primary climate driver in the context of specific locations on drifting continents. This is probably the primary explanation of Namibia's persistent arid climate beginning in the Cretaceous [Goudie and Eckardt, 1999; Ward *et al.,* 1983], and it suggests that Angola lay in arid latitudes for the entire Cretaceous.

The Cenomanian-Turonian was a time of thermal maximum with a reduced latitudinal thermal gradient. This long term, middle Cretaceous warming trend has been implicated in numerous paleobiological scenarios, for example in the establishment of flowering plants [Heimhofer *et al.,* 2005]. Regardless of that possibility, a luxuriance of angiosperms or other plants in the area now Angola does not appear likely because it lay in arid paleolatitudes, and a climatic filter impeding biotic exchange between most of South America and Africa was probably in effect before final separation.

The relevance of geological processes to biological evolution is more than simply providing a physical context to life on Earth. Tectonics and sea-level change appear to have been important macroevolutionary drivers throughout the Phanerozoic [Peters, 2005], and certainly the completion of the Atlantic Ocean, with all its diverse effects on geography, oceanography, and climate has changed life on Earth since the Cretaceous.

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