

## Post-Gondwana Africa and the vertebrate history of the Angolan Atlantic Coast

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### Abstract

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The separation of Africa from South America and the growth of the South Atlantic are recorded in rocks exposed along the coast of Angola. Tectonic processes that led to the formation of Africa as a continent also controlled sedimentary basins that preserve fossils. The vertebrate fossil record in Angola extends from the Triassic to the Holocene and includes crocodylomorph, dinosaur, and mammalian footprints, but more extensively, bones of fishes, turtles, plesiosaurs, mosasaurs, crocodiles, and cetaceans. Pterosaurs, dinosaurs, and land mammals are rare in Angola. The northward drift of Africa through latitudinal climatic zones provides a method for comparing predicted paleoenvironmental conditions among localities in Angola, and also allows comparison among desert and upwelling areas in Africa, South America, and Australia. South America has shown the least northward drift and its Atacama Desert is the oldest coastal desert among the three continents. Africa's northward drift caused the displacement of the coastal desert to the south as the continent moved north. Australia drifted from far southerly latitudes and entered the climatic arid zone in the Miocene, more recently than South America or Africa, but in addition, a combination of its drift, continental outline, a downwelling eastern boundary current, the Pacific Ocean to Indian Ocean throughflow, and monsoon influence, make Australia unique.

### Keywords

Angola, Africa, South America, Australia, Cretaceous, tectonic drift, upwelling, deserts, paleoenvironments, vertebrate fossils.

### Introduction

The discovery of the dicynodont *Lystrosaurus* in Antarctica was taken at the time as clear evidence of continental drift because the geographic distribution of *Lystrosaurus* demonstrated previously conjoined landmasses during the Triassic (Elliot et al., 1970). However, since the acceptance of plate tectonics, the significance of widespread Jurassic and Early Cretaceous biogeographic distributions, which inform the subsequent breakup of Gondwana, has been less clear because of a dearth of fossils, unresolved phylogenetic relationships, imprecise chronology, and paleoenvironmental uncertainties (Benson et al., 2012; Rich et al., 2014). Thomas H. Rich, to whom this volume is dedicated, through his persevering fieldwork, discoveries, and research on Early Cretaceous vertebrates in Australia, verified that major clades of terrestrial vertebrates were widely distributed across the globe during the

Early Cretaceous, a concept that had not been devised when he began his career, but a necessity as important for understanding the breakup of Gondwana as *Lystrosaurus* was for its existence. Beginning mostly in the Early Cretaceous, Gondwana landmasses drifted apart to become their own largely isolated theaters of evolution while marine amniotes gained access to unbeheld shores through the formation of new seaways.

Africa has a long and important vertebrate fossil record (Durand, 2005). Here we provide a summary of the results obtained by Projecto PaleoAngola from a decade of field expeditions focused on the fossil vertebrates, mainly amniotes, of Angola, southwestern Africa (Jacobs et al., 2006; fig. 1, 2). We provide a general overview of the dispersal of post-Gondwanan land masses to form Africa, the opening of the South Atlantic Ocean, and the distribution of Cretaceous and younger African fossil localities, because accommodation of major tectonic forces conjoins the three. We then present the

chronological sequence of new and historical fossil occurrences in Angola and examine Angola's setting with respect to northward tectonic drift and a growing South Atlantic Ocean, which are fundamental drivers of African paleoenvironmental change through time. We conclude with a brief comparison of the effect of northward drift on paleoenvironmental evolution among Africa, South America, and Australia leading to our modern world.

### **The Mesozoic Formation of Africa and the General Distribution of Sub-Saharan Fossil Localities**

The formation of Africa as a distinct continent is a Mesozoic phenomenon resulting first from the split of Pangea and the opening of the Central Atlantic off northwest Africa beginning in the Triassic (Youbi et al., 2003). The Cretaceous Tethyan edge of African Gondwana was a promontory. This African promontory, with remnants remaining today in the Levant as well as in Europe, was covered with extensive warm, shallow, carbonate platforms, home to snakes with legs and the earliest mosasaurs, which were the unobtrusive precursors of the last major radiation of marine diapsids (Polcyn et al., 1999, 2003, 2005, 2014; Rieppel et al., 2003; Tchernov et al., 2000; Jacobs et al., 2005a, b). Rifted portions from the African promontory drifted northward with Gondwanan fossils, ultimately to construct southern Europe (Dal Sasso and Maganuco, 2011; Müller et al., 2001; Polcyn et al., 1999; Stampfli, 2005; Zarcone et al., 2010). Cenozoic compressional forces, generated through collision of northwestern Africa with Europe in the early Paleogene, formed the Atlas Mountains, followed by mid-Cenozoic collision of northeastern Africa with Eurasia, both events having significant biogeographic consequences for the distribution of terrestrial mammals (Gheerbrant, 1990; Kappelman et al., 2003; Rasmussen and Gutierrez, 2009).

Rifting of Africa's eastern margin was heralded by the Jurassic-aged Karoo Large Igneous Province (LIP; 184–179 Ma; Duncan et al., 1997; Jones et al., 2001; Jacobs et al., 2005c), which was the African portion of the Karoo-Farrar Magmatic Province, extending from southeastern Africa across Antarctica into Australia and Tasmania. Madagascar and India rifted from East Africa, leaving in their wake the Somali Basin and the Cretaceous Anza Graben (fig. 1), an aulacogen extending inland from the coast toward southern Sudan (Tiercelin et al., 2012; Werner, 1994). The final phase in forming the outline of the African continent was the Cretaceous opening of the South Atlantic, producing the iconic puzzle-like fit of the African and South American coastlines (fig. 3). This final phase resulted in a northeastwardly directed aulacogen, the Benue Trough, extending from the Bight of Benin at the mouth of the Niger River on the coast to the Chad Basin (fig. 1).

The crustal movements that culminated in Africa as a unique continent were mainly, but not exclusively, expressions of extensional tectonics. Over the past 100 million years extensional tectonics have opened new oceans that allowed the spread of marine amniotes while reducing dispersal routes for terrestrial animals. Residual effects and accommodation within the continent are especially obvious in sub-Saharan

Africa where they formed aulacogens, rift valleys, and coastal basins on older, preexisting mobile belts. These in turn largely controlled the occurrence and preservation of fossils in Africa during and since the Mesozoic.

The Benue Trough directed from the west coast and the Anza Graben directed from the east, along with East Africa's Great Rift Valley (fig. 1), were developed on older structures. In each, a sequence of basins formed that preserves a progression of vertebrate fossils of decreasing age. Late Cretaceous dinosaurs and other vertebrates are found in Kenya's Anza Graben (O'Connor et al., 2011), an area of crustal thinning and isostatic adjustment (Benoit et al., 2006). Remarkably, the topographic expression of the Anza Graben controlled drainage until the Miocene such that a 17 my old open ocean marine ziphiid whale stranded 740 km up the Anza Graben from the present day Indian Ocean shoreline (Mead, 1975; Wichura et al., 2015), at a present elevation of 620 m, indicating the presence of a large low gradient river in what is now one of the most arid regions of Kenya. The East African Rift Valley in Kenya is structurally developed across the Anza Graben in the Turkana Basin, an area famous for its record of primate evolution extending from Oligocene through Pleistocene (Leakey et al., 2011; Wood and Leakey, 2011). In the Rift Valley of Malawi, fossils of Permian, Early Cretaceous, Pliocene, and Pleistocene age lie in close proximity (Clark et al., 1989; Colin and Jacobs, 1990; Gomani, 1997, 2005; Jacobs et al., 1990, 1992, 1993, 1996, 2005c; Kruger et al., 2015; Schrenk et al., 1993). In the nearby Rukwa Basin of Tanzania, within the Rift Valley, a variety of fossils, including fish, crocodyliforms, dinosaur eggshell and bones, a Cretaceous mammal, and Oligocene primates and other mammals are found (Gorscak et al., 2014; Gottfried et al., 2004, 2009; Krause et al., 2003; O'Connor et al., 2010; Roberts et al., 2004, 2010, 2012; Sertich and O'Connor, 2014; Stevens et al., 2008, 2013).

In the Benue Trough (Obaje, 2009), the aulacogen on the opposite side of the continent from the Anza Graben, Early Cretaceous (Barremian) non-marine vertebrates are found in the Koum (Congleton et al., 1992; Jacobs et al., 1989; Flynn et al., 1987), Mayo Oulo Léré (Brunet et al., 1988a), and Barbouri-Figil (Michard et al., 1990; Colin et al., 1992) basins, prior to formation of the deep water connection between the North and South Atlantics. Late Cretaceous marine fish (*Vullo* and Courville, 2014), turtles, crocodiles, and the mosasaurs *Goronyosaurus* and *Pluridens* were discovered to the north and west in the Benue Trough and associated rift system (Azzaroli et al., 1975; Halstead, 1979; Soliar, 1988; Lingham-Soliar, 1994, 1998). Stevens et al. (2011) described a Paleocene marine ichthyofauna from Nigeria. The Benue Trough extends northeastward to the Chad Basin, which contains terrestrial Neogene rocks with a diverse Late Miocene mammalian fauna including the oldest known hominid, *Sahelanthropus* (Brunet et al., 2002). Toward the west of the Chad Basin, Cretaceous rocks of Niger have yielded a remarkable fauna of Cretaceous dinosaurs and other vertebrates (Taquet, 1976; Sereno et al., 2008). Toward the east, Cretaceous deposits are found in Sudan (Werner, 1994) and on to the Anza Graben.

Of course, the Mesozoic and younger fossils of Africa, like those of other Gondwana island continents, represent

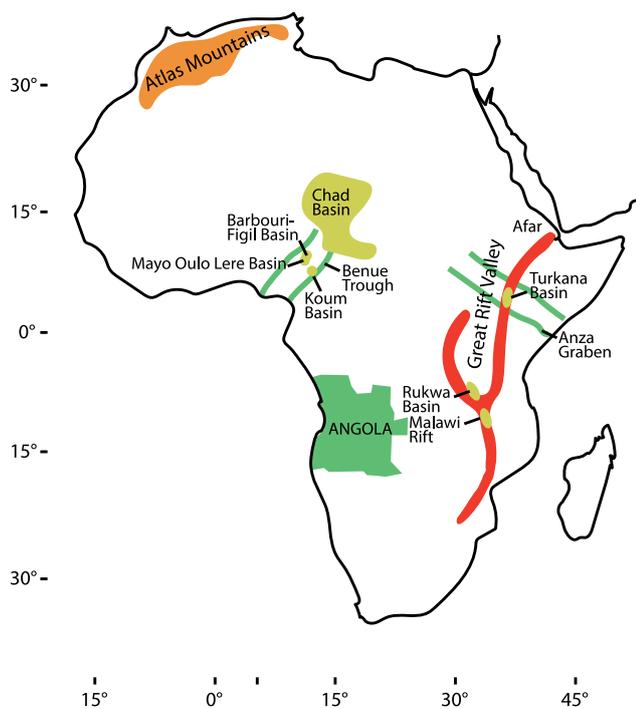


Figure 1. Map of Africa showing location of Angola and simplified major structural features controlling placement of some important fossiliferous regions. Coastal basins are not included.

populations evolving, dying, and being preserved since rifting began and the continent drifted. In the breakup of Gondwana, the relative motion of individual landmasses was largely away from each other and to the north (Jacobs et al., 2011). Their northward journeys, to the extent that each traveled, moved the continents across latitudinal climate zones denoted by atmospheric circulation, most notably the descending limbs of Hadley Cells, causing high-pressure arid zones. The northward progression of post-Gondwana continents through essentially fixed climate zones provides a method for large-scale, first-order comparison of their environmental histories and a context for their preserved fossil records.

### Coastal Angola and the Africa - South America Split

A chronology of the growth of the South Atlantic Ocean and concomitant northward drift of Africa is shown in Figure 3. Africa's drift can be followed especially well because conjugate basins shared between Africa and South America provide fixed starting points (Brownfield and Charpentier, 2006), and because of seafloor magnetic stripes (Cande et al., 1989; Müller et al., 1997; He et al., 2008), hot spot traces (O'Connor and le Roex, 1992; O'Connor et al., 1999), predicted paleolatitudes determined from igneous rocks (Strganac et al., 2014a), and fault zones that can be followed from the Mid-Atlantic Ridge to the coast of Africa (fig. 4) (Eagles, 2007; Guiraud et al., 2010).

Numerous geophysical models address the opening and growth of the South Atlantic (Eagles, 2007; Gaina et al., 2013;

Pérez-Díaz and Eagles, 2014; Torsvik et al., 2009). Uncertainties are introduced through an imprecise understanding of the extension of continental crust and the placement of the continent-ocean boundary, imprecise estimates of the amount and geographic effect of intracontinental structural accommodation to large scale plate motions; and in identifying the oldest magnetic chronos at specific positions along the African margin (Cande et al., 1989; Müller et al., 1997; Gradstein et al., 2004, 2012; He et al., 2008). These uncertainties affect estimates of the initial timing of the opening and of the width of the seaway at specific times and latitudes early in its history.

Eagles (2007) estimated the diachronous south to north opening of the South Atlantic took place over 40 my. Gaina et al. (2013) recognized older magnetic isochrons south of the Walvis Ridge, but only younger isochrons north of the Walvis ridge. According to Gaina et al. (2013), the generation of oceanic crust north of the Walvis Ridge probably was initiated at about the beginning the Cretaceous Normal Superchron (120.6 Ma).

Torsvik et al. (2009) noted two Cretaceous magmatic episodes around the South Atlantic, the earlier being the Etendeka-Paraná LIP (133–130 Ma), heralding the opening of the South Atlantic, the younger peaking at about 84 Ma. The Etendeka Basalt is dated in Namibia at  $132 \pm 1$  Ma (Renne et al., 1996) and tholeiitic rocks in the Kwanza Basin, Angola, are  $\sim 132$  Ma (Marzoli et al., 1999). These represent the older magmatic event. Soon after Etendeka magmatism, oceanic crust began to form south of the Walvis Ridge, but not to the north of it, as determined because none of the M magnetic chronos are clearly recognized north of the Walvis Ridge (Gaina et al., 2013). Chron M0 marks the base of the Aptian Stage, so regardless of numerical calibration of M isochrons, crustal extension occurred along the Angolan coast during the Barremian (125–130 Ma) and into the Aptian, culminating in Aptian seafloor spreading at around 121 Ma.

Kimberlite was emplaced along the Lucapa Fault Zone, which helps control continental shelf width along the southern Angola coast, at 117 Ma (mid-Aptian) (fig. 4). Marine fossils with northern affinities are first noted in the South Atlantic in the Sergipe and other northern basins in Brazil at 115 Ma (Bengston and Koutsoukos, 1992; Arai, 2014), while a deepwater passage between the North and South Atlantics developed between 100 and 90 Ma (Eagles, 2007; Handoh et al., 1999). The younger South Atlantic magmatic event of Torsvik et al. (2009) is recorded in Angola by the Ombe Basalt at Bentiaba in Namibe Province, dated at  $84.6 \pm 1.5$  Ma (Strganac et al., 2014b). Predicted paleolatitude of the Ombe Basalt at its emplacement determined from oriented paleomagnetic samples was  $24.5^\circ$  S. The width of the South Atlantic was some 2700 km at that time and latitude, roughly half that of its current width (Strganac et al., 2014a; Reeves, 2014).

Angola is unique in having excellent exposures that illuminate this profound geological history. These exposures were well mapped by Carvalho (1961) in Namibe Province in southern Angola, although his work predated the acceptance of plate tectonics (see also Masse and Laurent, 2015). Field



Figure 2. Location map of major fossil localities and cities in Angola.

relationships of rocks between Bentiaba and Piambo, a distance of ~50 km to the south of Bentiaba, are shown in Figure 5. The South Atlantic boundary fault separates Precambrian granitic rocks to the east from younger volcanic and sedimentary units to the west. Both magmatic events of Torsvik et al. (2009; *i.e.*, Etendeka and Ombe) are represented in outcrop, with gypsum and conglomerates in between. The boundary fault is overstepped at Piambo by biostratigraphically-dated Late Cretaceous (Maastrichtian) marine sediments equivalent to the upper fossiliferous beds at Bentiaba and Cacoto (Bentiaba II) 50 km to the north. This section is an exemplary geological representation of the opening and growth of the South Atlantic Ocean.

In addition, as exemplified in Namibe Province, the fault zones propagating from the Mid-Atlantic Ridge controlled the width of the continental shelf and hence played a direct role in the depositional setting that preserved fossils on the shelf some 40 million years after the South Atlantic started to open (Strganac et al., 2014b; fig. 4, 5). The Luçapa and Benguela fault zones established margins for the narrowest continental shelf in West Africa. The Luçapa Fault Zone can be traced inland to the Catoca diamond mine where it is characterized by kimberlites with U-Pb zircon ages of ~117 Ma (Pervov et al., 2011). The Luxinga Field, 80 km to the southwest of Catoca, has dates derived from kimberlites of 145–113 Ma (Pervov et al., 2011). Activity on the Luçapa fault zone, taken with the chronology of the opening of the South Atlantic and the biochronology of fossils (Tavares et al., 2006), constrains the formation of the continental shelf, as opposed to the South Atlantic opening, to late Early Cretaceous (Aptian), around 117 Ma.

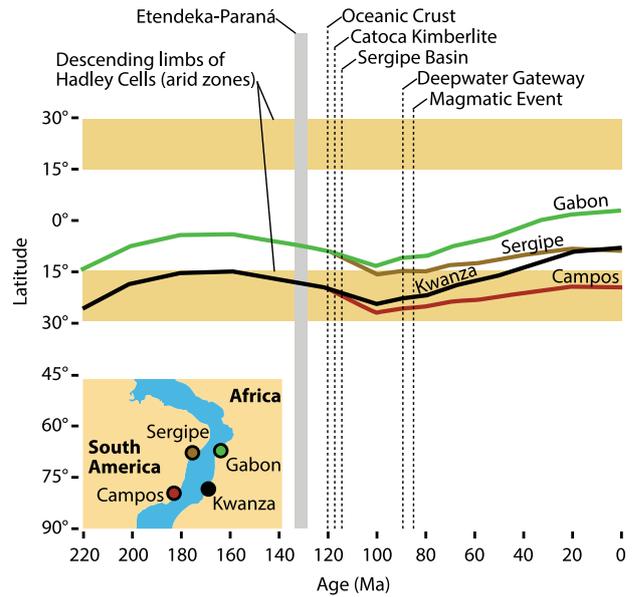


Figure 3. Northward drift of African and South American conjugate basins relative to Hadley Cells and the chronology of the South Atlantic Ocean. Inset shows conjugate Serpige-Gabon and Campos-Kwanza basins in South America and Africa. From the initial opening of the South Atlantic Ocean heralded by the Etendeka-Paraná Large Igneous Province (LIP), the basins drifted from their starting position in interior Gondwana. As the width of the South Atlantic has grown, Africa has also drifted north relative to South America and through the latitudes of the descending limb of the southern Hadley Cell.

### The Fossil Record of Amniotes in Angola

The first comprehensive review of Angolan vertebrate fossils was that of Antunes (1964). More recently, Cretaceous amniote faunas of Angola were reviewed by Mateus et al. (2012). Sharks were reviewed by Antunes and Cappetta (2002; Balbino and Antunes, 2007). Since 2005 Projecto PaleoAngola has discovered new sites and visited most of the sites discussed by Antunes (1964) that are still accessible, although some have been lost to growth or the ravages of former prolonged conflict. Antunes (1964, his plate 3, fig. 5) illustrated a whale “bone graveyard” (*cemitério dos ossos*) that has since been engulfed by the capital city of Luanda.

The main localities worked by Projecto PaleoAngola (fig. 2) are discussed below in geographical and roughly chronological order (fig. 6). Most of these sites are in coastal basins along the continental margin with sedimentation controlled by eustatic sea level (Müller et al., 2008) in conjunction with structural motions ascribed to salt tectonics and movements along preexisting faults (Brognon and Verrier, 1966; Cauxeiro et al., 2014; Ciampo et al., 2001; Guiraud et al., 2010; Hudec and Jackson, 2002; Jackson and Hudec, 2005).

Only two known Mesozoic Angolan fossiliferous areas are fully continental and found inland from the coast. One of these, the Cassange Depression (Triassic), predates the initial opening of the South Atlantic, and the second, the Catoca Diamond Mine, dates from the late Early Cretaceous, some 15

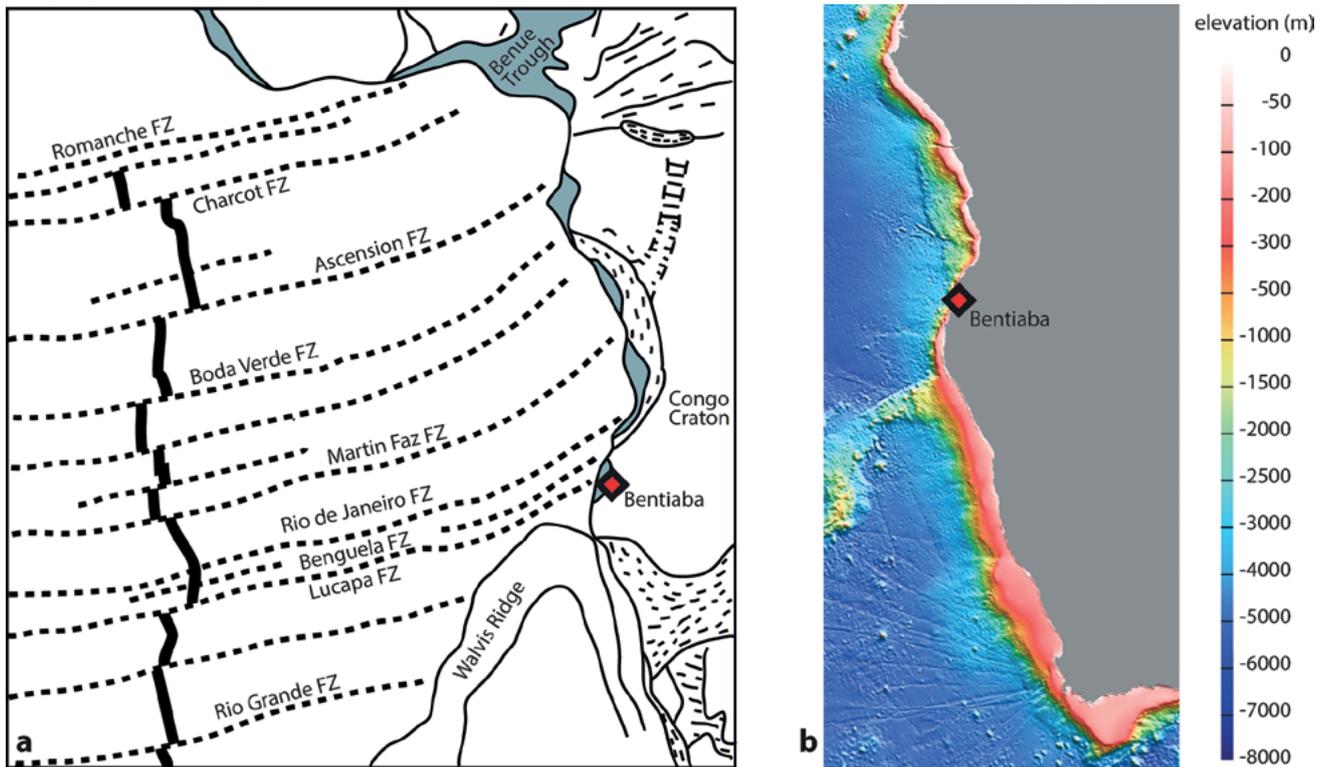


Figure 4. Trace of fault zones (FZ) from Mid-Atlantic Ridge to the African coast (a) and bathymetric map of coastal Africa showing width of continental shelf (b). The rich marine amniote fossil locality of Bentiaba was formed on the fault-controlled, narrow portion of the continental shelf (modified from Strganac et al., 2015a).

million years after Africa and South America began to separate, but during kimberlite emplacement on the Lucapa fault zone (Pervov et al., 2011).

**Cassange Depression.** The Cassange Depression lies west of the city of Malanje in Malanje and Lunda Norte Provinces, northeastern Angola (fig. 2). Catuneanu et al. (2005) considered the Cassanje Depression to be a sag basin, at times holding a saline inland lake (Oesterlen, 1976, 1979), extending in age from the Late Permian to the Middle or Late Triassic. Five genera and six species of freshwater fish represented by nicely preserved specimens in laminated shale have been reported from there, but it appears no vertebrate paleontologist has ever yet visited the sites and no systematic collecting effort in the Cassange Depression has been undertaken (Antunes et al., 1990; Mouta, 1954; Mouta and Dartevelle, 1954). Projecto PaleoAngola attempted to prospect the area in 2012, but was thwarted by the presence of landmines and unexploded ordnance remaining from Angola's war years prior to 2003. The fauna listed by Murray (2000) from the Cassange Depression includes the shark *Lissodus cassangensis*, *Angolaichthys lerichei* (*Halecostomi incertae sedis*), the paleoniscoids *Perleidus lutoensis*, *Marquesia moutai* (*Canobiidae incertae sedis*), and *Microceratodus* sp., a lungfish. Plants, crustaceans, and an insect, in addition to fish, have been reported (Nunes, 1991; Schlüter, 2003). Antunes et al. (1990) assigned an Early Triassic age to the assemblage.

**Catoca Diamond Mine.** Mammalian, crocodylimorph, and sauropod tracks were discovered in lacustrine diatreme sediments at the Catoca Diamond Mine, the fourth largest diamond mine in the world, Lunda Sul Province, northeastern Angola (fig. 2). One sauropod track has skin impressions preserved (Marzola et al., 2014). The most surprising feature is the unexpectedly large size of the mammalian footprints, measured in centimeters, considering their age is Early Cretaceous. The Catoca Mine is located in the southern Congo Basin, which has recently been the subject of renewed investigation (de Wit et al., 2015). Other Cretaceous vertebrates reported from the correlative Kwango Group (Roberts et al., 2015) in the general region include sauropod bones and a pterosaur (Cahen, 1954; Swinton, 1948).

Mining activities at Catoca are focused on a kimberlite pipe emplaced along the continental extension of the Lucapa fault zone, which can be traced seaward to the Mid-Atlantic Ridge. U-Pb SHRIMP eruption age dates on zircons from the kimberlite pipe are  $117 \pm 0.7$  Ma (Aptian), providing a maximum age for the track-bearing sediments of the diatreme associated with the diamond-producing kimberlite. Early Cretaceous vertebrate localities in Africa have little to constrain their ages (Le Loeuff et al., 2012). The Catoca Mine provides one of the few limiting quantitative age estimates for Early Cretaceous vertebrate fossils in Africa. More broadly, Linol et al. (2015) correlate the Kwango Group, in which by

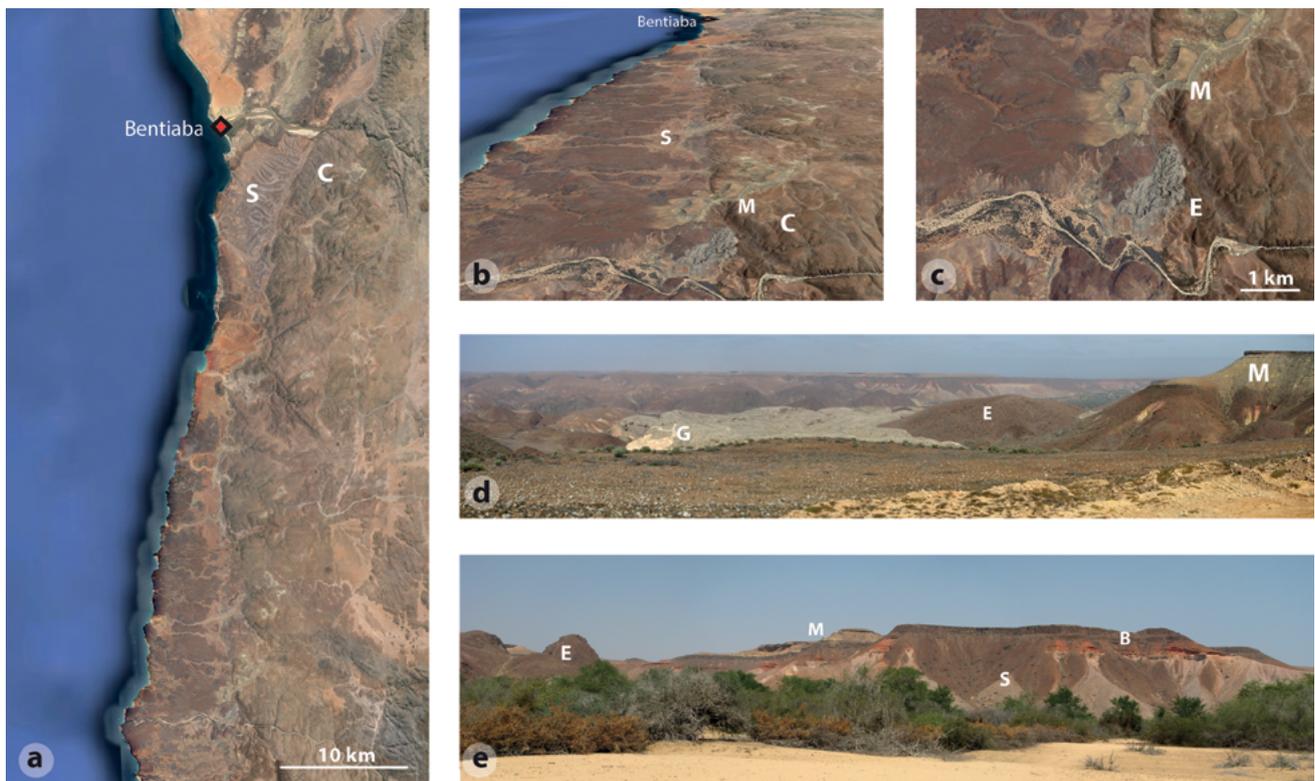


Figure 5. Angolan coastal geology between Bentiaba in the north and Piambo in the south, a distance of ~50 km, in Google Earth™ (a, b, and c) and outcrop views (d and e): a, boundary fault trace lies between synrift terrestrial deposits (S) and crystalline basement (C); b, oblique view showing gray gypsum deposited on Entendeka Basalt at Piambo with Bentiaba in the distance; c, plan view of Piambo showing gray gypsum, Entendeka Basalt (E), and marine Maastrichtian (M) overstepping boundary fault; d, looking from crystalline basement (near M in c) to southwest, base is Etendeka (E) followed by gypsum (G) and synrift conglomerates capped by dark Ombe Basalt topped by marine Maastrichtian (M); e, looking across valley showing pointed hill of Etendeka (E) on left, overlain by synrift conglomerates (S), and flat-lying Ombe Basalt (B), capped by Maastrichtian marine sands (M).

extension we would include sediments in the Catoca crater, with the Bauru Group in the Paraná Basin of Brazil, which has produced a number of sauropods and other vertebrate taxa, but only one jaw fragment with a premolar of a small mammal (Candeiro et al., 2006). A larger mammal, *Vincelestes*, is known from the Early Cretaceous of Argentina.

In sub-Saharan West Africa, the only known Early Cretaceous mammals are the minute tooth taxon *Abelodon abeli*, identified as a peramurid, and a few other teeth, plus a jaw fragment from the Early Cretaceous of the Koum Basin, Cameroon (Brunet et al., 1988b, Brunet et al., 1990; Jacobs et al., 1988). A gondwanatherian was described from a single tooth-bearing dentary from mid-Cretaceous deposits of Tanzania (Krause et al., 2003), but the mammalian tracks from Catoca are too large to have been made by any known African Cretaceous mammal. The newly described gondwanatherian *Vintana sertichi* from Madagascar is quite large, perhaps large enough to produce the tracks, although its feet are unknown and it is some 50 my younger (Krause, 2014; Krause et al., 2014). Nevertheless, Africa and Madagascar split in the Early Cretaceous (Jacobs et al., 2011) and gondwanatherians and other mammals were widely

distributed across Gondwana at that time; however, their diversity and disparity remain elusive but expanded by the tracks at Catoca.

*Iembe*. The Tadi beds of the Itombe Formation (Mateus et al., 2011), near the village of Iembe in Bengo Province north of Luanda (fig. 2), is the type locality for the turtle *Angolachelys mbaxi* (Mateus et al., 2009), the mosasaurs *Angolasaurus bocagei* and *Tylosaurus iembeensis* named by Antunes (1964), and the first dinosaur discovered in Angola (Mateus et al., 2011), the titanosauriform sauropod *Angolatitan adamastor*. The age of the Tadi beds was determined as late Turonian by Antunes (1961, 1964; Lingham-Soliar, 1994) and Antunes and Cappetta (2002) based on the ichthyofauna. Projecto PaleoAngola has measured approximately 150 m of section at the site. Vertebrates, especially fishes, occur throughout the section (Mateus et al., 2009). *Angolasaurus* falls within the lower third to half of the section and is biochronologically consistent with a late Turonian age, about 90 Ma. However, small and distinctive mosasaur vertebrae and the sharks found at the top of the section suggest it may extend into the Coniacian or possibly lower Santonian.

*Bentiaba*. The section at Bentiaba, Namibe Province (fig. 2), extends from Cenomanian to late Maastrichtian and is dated by carbon isotope chemostratigraphy and magnetostratigraphy, anchored by <sup>40</sup>Ar/<sup>39</sup>Ar dates on the intercalated Ombe Basalt (84.6±1.5 Ma; Santonian; Strganac et al., 2014b). Invertebrate fossils of the Bentiaba area were studied by Cooper (1972, 1976, 1978, 2003a, 2003b), who also collected shark teeth and a tetrapod jaw now in the Iziko South African Museum. Vertebrate occurrences are scattered throughout the section above the Ombe Basalt in the Baba and Mocuio formations. The Campanian assemblage from the Baba Formation includes russellosaurine and mosasaurine mosasaurs distinct from those found at Maastrichtian levels in the Mocuio Formation, most notably, the overlying Bench 19 Fauna.

The Bench 19 Bonebed at Bentiaba has produced one of the richest Cretaceous marine amniote faunas known (table 1), including turtles (Mateus et al., 2012), mosasaurs (Polcyn et al., 2010; Schulp et al., 2006, 2008), and plesiosaurs (Araújo et al., 2015a, b), with rare pterosaur and dinosaur bones (Mateus et al., 2012). It is a unique concentration of marine vertebrates because it was preserved on an uncharacteristically narrow continental shelf near the Lucapa fault zone that appears to have controlled the coastal outline of Africa in the formation of the South Atlantic Ocean (fig. 4). The Lucapa Fault Zone links the shelf to the Mid-Atlantic Ridge on the one hand and to the Catoca kimberlite on the other. The sediments of the Bench 19 interval are immature feldspathic sands, determined by detrital zircon provenance to be derived from nearby granitic rocks, transported to the narrow shelf by short, intermittent rivers, similar to the setting seen today at analogous latitudes in Namibia. The age of Bench 19 was determined by magnetostratigraphic correlation to chron C32n.1n, between 71.4 and 71.64 Ma (Strganac et al., 2014b). The Bonebed formed at a paleolatitude near 24°S, when the Atlantic width at that latitude approximated 2700 km, roughly half that of the current width. Biostratigraphic uniformity of the Bench 19 fauna, evidence of interspecies interactions, including gut contents and scavenging marks, and the presence of pterosaur and dinosaur bones in a marine setting, indicate that the accumulation was attritional but occurred in an ecological time dimension within the 240 ky bin delimited by chron 32n.1n (71.40–71.64 Ma). The spatial distribution and taphonomy of fossils suggest a rich feeding area for diverse top consumers in waters 50–100 m in depth and at a water temperature based on δ<sup>18</sup>O from bivalve shells of 18.5° C (Strganac et al., 2014a, 2015).

The upper beds at Bentiaba, above the Bench 19 interval, and at nearby Cacoto (Bentiaba II) are biostratigraphically distinct from those containing the Bench 19 fauna. Most notably, they contain the mosasaur genus *Carinodens* and a large *Prognathodon* similar in grade to *P. saturator* from Europe (Schulp et al., 2013). *Globidens*, known by several individuals from the Bench 19 Fauna, is not known from Bentiaba upper levels, nor is the thick-shelled bivalve *Inoceramus*, which *Globidens* is known to have eaten (Polcyn et al., 2010). Nurse sharks (Ginglymostomatidae) are first seen in the upper levels and *Squalicorax* teeth obtain more extreme size classes (larger and smaller) than those from the Bench 19 interval.

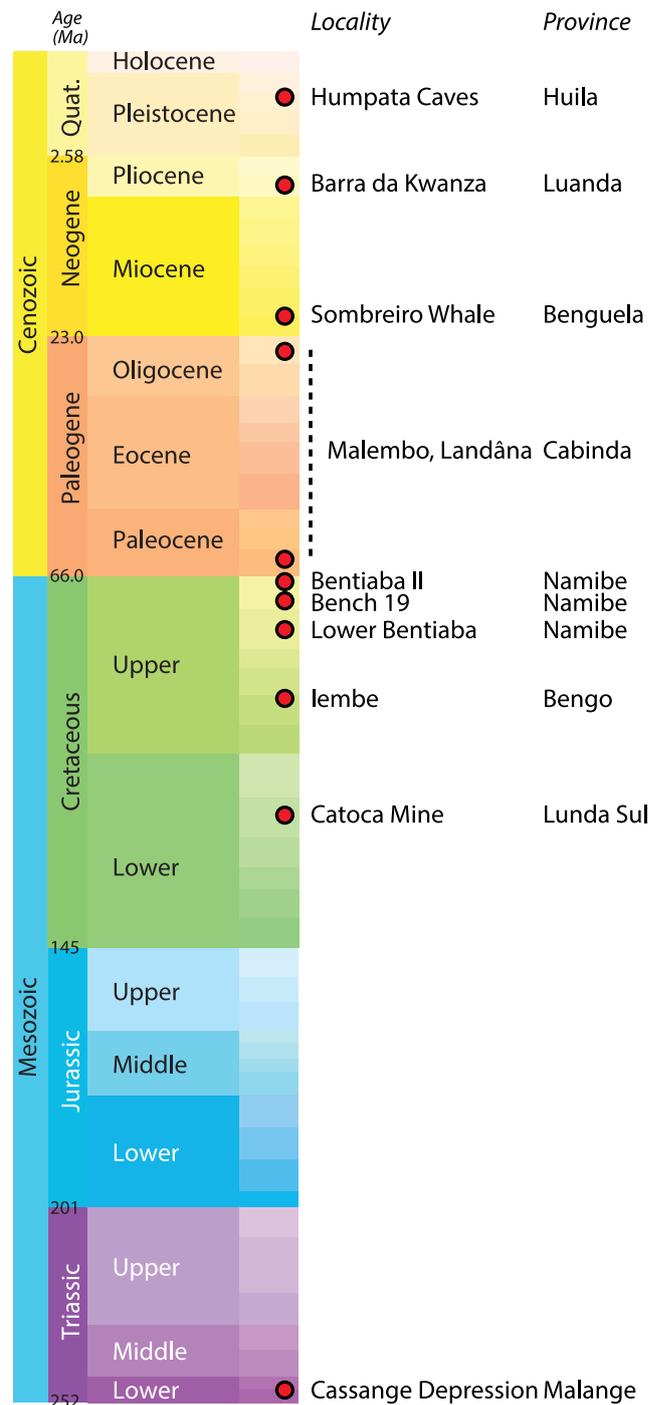


Figure 6. Chronological sequence of major vertebrate-bearing localities investigated by Projecto PaleoAngola; chronostratigraphy following IUGS/ICS v. 2014/2 (www.stratigraphy.org).

In the Tzimbio Valley, between Bentiaba and Cacoto, a few fragments of fossil wood, bivalve shells, and dinosaur bone were found in layers mapped as Albian. Near Bentiaba, late Neogene or younger sea-level change resulted in a terrace (Sessa et al., 2013) topped with beach deposits of tossed Cretaceous red sandstone beach boulders with barnacles distributed over their entire surfaces. The Cretaceous section at Bentiaba is capped by a Pleistocene caliche with rare fragmentary carbonate encrusted mammal bones and teeth and ostrich eggshell.

*Benguela*. Fragmentary whales, sirenians, and large *Carcharocles* sharks (following Ehret et al., 2009) were discovered in the lower Sombreiro sandstones of Burdigalian age (late early Miocene, 20.4–15.97 Ma, Gradstein et al., 2012; Brownfield and Charpentier, 2006; Brognon and Verrier, 1966;

Guiraud et al., 2010), 13 km southwest of the provincial capital of Benguela (fig. 2). A partial whale skull shares derived characters with the Pygmy Right Whale (*Caperea*) and with rorqual whales. Late Neogene whale bones are found in concretions and as isolated elements along the shore at Baía Farta and neighboring bays (Antunes, 1964). In 1931, the German geographer Professor O. Jessen visited what he referred to as Bahia Farla [sic], indicated by his map to be Bahia Farta (Jessen, 1936), where he picked up a few vertebrae and a jaw fragment, now at the Eberhard-Karls University in Tübingen. A Pleistocene, nearly complete, rorqual skeleton identified as Blue Whale (*Balaenoptera* sp.) was discovered in Benguela, and is now at the Benguela Archaeology Museum (Gutierrez et al., 2001, 2011). An exceptionally large fossil dentary of Blue Whale (*Balaenoptera musculus*) without data is present in the Natural History Museum in Luanda. Plant leaf impressions in carbonate are known from north of Benguela, presumably from karst fissures, but no collections have been made to date.

Table 1. Bench 19 faunal list (after Strganac et al., 2014a).

Chondrichthyes

Elasmobranchii

*Squalicorax pristodontus*  
Odontaspidae indet.  
cf. *Ganopristis* sp.  
*Brachyrhizodus* sp.

Osteichthyes

cf. *Eodiaphyodus* sp.  
*Enchodus* sp.  
?Sphyræniidae sp.

Testudines

Cheloniidae  
*Euclastes* sp.  
Protostegidae  
? *Calcarichelys* sp.  
*Protostega* sp.  
Toxochelyiidae  
*Toxochelys* sp.

Squamata

Mosasauridae  
*Globidens phosphaticus*  
*Halisaurus* sp.  
*Mosasaurus* sp.  
*Phosphorosaurus* sp.  
“*Platecarpus*” *ptychodon*  
*Prognathodon kianda*

Sauropterygia

Plesiosauria  
Elasmosauridae  
Aristonectinae indet.  
*Cardiocorax mukulu*

Pterosauria

Ornithocheiroidea indet.

Dinosauria

Hadrosaurioidea indet.

Dinosauria indet.

*Barra da Cuanza* (also spelled *Kwanza*, *Kuanza* and *Quanza*). A large number of cetacean bones and a crocodylian skull, most encrusted on all surfaces with limestone containing abundant mollusks and megatoothed shark teeth, were found approximately 5 km north of the Kwanza River mouth in Luanda Province (fig. 2). The sediments there correlate with the spectacular cliffs of Miradouro da Lua studied by Cauxeiro et al. (2014), who consider the age of unit 2 to be Messinian (Late Miocene), or about 6 Ma, to the north of the Barra da Cuanza section. Fossils at Barra da Cuanza occur in unit 2 of Cauxeiro et al. (2014). The crocodile skull is not fully prepared but appears to be a very large *Crocodylus* and probably an early record for the genus (Brochu and Storrs, 2012). Of the whale fossils, the most spectacular is a mysticete skull lacking the anterior portion of the rostrum, with two fish preserved in its blowhole.

Although the fossil record of neobalaenid whales is sparse (Buono et al., 2014; Fitzgerald, 2012), both the Benguela and the Kwanza skulls share three synapomorphies with the Pygmy Right Whale, *Caperea marginata*, traditionally considered the only living species of the family Neobalaenidae. Recently, however, Fordyce and Marx (2012) posited that *Caperea* was the last of the cetotheres, formerly known only as fossils, thereby invalidating Neobalaenidae as a family and reducing it to a subfamily within Cetotheriidae. The Angolan specimens appear to have a significant bearing on the relationships of neobalaenids, balaenopterids, and cetotheres.

*Cabinda*. Fossils from Cabinda (fig. 2), Angola’s northernmost province, were discovered and reported by Belgians in the first half of the 20<sup>th</sup> Century (Vincent et al., 1913). Cabinda is a tropical enclave north of the Congo River. Localities are nearshore marine and purportedly range in age from Cretaceous through Oligocene or possibly Early Miocene. Reported Cretaceous localities are currently grown over. Projecto PaleoAngola was unable to locate the fossiliferous Paleogene limestone of Sassa Zau along the Chiloango River, reported by Antunes (1964) to contain fish, turtle carapace and plastron fragments, vertebrae of the snake *Palaeophis*, and crocodile teeth and bones. The main exposures in Cabinda are

along sea cliffs between Lândana and Sapho, as the stretch along the southern shore of Malembo Point is called. The oldest locality Projecto PaleoAngola visited in Cabinda is Lândana (Paleocene), best known for marine fish (Vincent et al., 1913; Cahen, 1954; Casier, 1960; Darteville and Casier, 1943, 1949, 1959; Hussakof, 1917), turtles (Dollo, 1925; Wood, 1973, 1975), and dyrosaurid crocodylians (Jouve and Schwarz, 2004; Schwarz, 2003; Swinton, 1950). Between Lândana and Malembo the intervening strata contain mainly shark teeth. The dark sediments at Malembo contain carbonized plant fragments, standing in contrast to Paleogene and Neogene sediments in southern Angola, which are consistently light colored and lack carbonized plant material.

Malembo Point (called Malembe in older literature but Malembo on maps and signs, Antunes, 1964) is a promontory headland on the south side of a small bay. Beta m'Bembe is on the north side of Malembo Bay, and Sapho lies along the south side of the promontory. Rare, isolated, sometimes abraded and phosphatized mammal teeth and sirenian rib fragments, first reported by Darteville (1935a, b), along with shark and ray teeth and crocodile fragments, are found along this stretch of sea cliffs. Hooijer (1963) described the mammals and considered them to be Early Miocene in age. Pickford (1986) revised their identifications and assigned an Early Oligocene age. An incisor originally identified as the chalicothere *Macrotherium* (?) was reidentified as *Arsinoitherium*. Hooijer's new anthracothere genus *Anthracotheriidarum* was reidentified as the hyrax *Geniohyus* aff. *mirus*, and Hooijer's suiform species *Palaeochoerus dartevelli* was reidentified as *Bunohyrax* aff. *fajumensis*. The proboscidean *Trilophodon angustidens* was reidentified as cf. *Phiomia* or *Hemimastodon*. An incisor identified by R.J.G. Savage as cf. *Amphicyon* (reported in Hooijer, 1963) was reidentified by Pickford (1986) as an anthropoid canine, but its whereabouts are no longer known. The effect of these re-identifications was to characterize the Malembo fauna as essentially like that of the Fayum, Egypt, implying a widespread geographic uniformity of the African Paleogene mammalian fauna.

Tooth-producing sediments of the Malembo promontory range from pebbly clay to coarse conglomerate and crop out at sea level on active beaches. All known mammal fossils from there, except sirenian rib fragments, which are pachyosteosclerotic (Domning and de Buffrénil, 1991), were preserved as single teeth or pieces, occasionally in jaw fragments. Given the high-energy geological context of the fossils and the active shore processes eroding them out, Projecto PaleoAngola prospects these outcrops yearly. Two new specimens, while poorly preserved, are sufficient to indicate that the Malembo fauna is distinct in composition from any level of the Fayum. The first is a ptolemaiidan molar more similar to *Kelba* from Songhor, Kenya (19.5 Ma) than to Fayum *Ptolemaia* because it has mesial and distal cingula and the paracone and metacone are widely separated. The second specimen from Malembo is the P<sup>4</sup> of a large primate unlike any described taxon, and being comparable in size to that of a female gorilla, it is certainly larger than Fayum primates. In addition, an arsiniothere anterior tooth from Malembo is apparently smaller than in other arsiniotheres (Sanders et al., 2004).

No radiometric dates have been determined for Malembo or other sites in Cabinda (contra the *lapsus* in Seiffert, 2010, his table 2.1, where the indication was likely meant for Rukwa, one step up in the table). Seiffert (2010) accepted an Oligocene age for Malembo based on Pickford's (1986) analysis of mammals, but states that more informative fossils or radiometric dates are necessary to determine whether the age of Malembo is Early Oligocene or Late Oligocene. The closer similarity of the Malembo ptolemaiidan tooth to East African Miocene *Kelba* than to Fayum *Ptolemaia*, and its association with arsiniotheres, suggests a late, if not latest Oligocene age for Malembo, perhaps comparable in age to Chilga, Ethiopia (Kappelman et al., 2003), Nakwai, Kenya (Rasmussen and Gutierrez, 2009), or Rukwa, Tanzania (Roberts et al., 2012), or between about 25 and 23 Ma. While following Pickford (1986) there were no taxa identified to lend West Africa a distinction in faunal composition from other areas of Africa. However, the presence of a new ptolemaiidan, the unnamed but new primate, and perhaps the small arsiniothere provides the first indications of faunal differentiation between East, West, and North Africa during this time interval.

*Humpata Caves*. The coastal region of Angola is delimited from the interior by the main boundary fault (shown at Bentiaba in fig. 5) and a spectacular escarpment called the Serra da Chela, especially along the border of Namibe and Huila provinces. The Serra da Chela is the edge of a plateau formed primarily of Precambrian granitic rocks but overlain in places by the Chela Dolomite. In the area around Humpata southwest of Lubango (fig. 2), the Chela Dolomite hosts caves and fissures exposed in quarrying operations for cement. Many of these are fossiliferous (Amaral, 1973; Antunes, 1965; Arambourg and Mouta, 1952; Beetz, 1933; Dart, 1950; Franca, 1964; Mason, 1976; Mouta, 1950). Pickford et al. (1990, 1992, 1994) listed 44 taxa of vertebrates, most of which are mammals, mainly rodents, from these Humpata Caves. The most thoroughly studied of the Humpata fossils are those of the extinct baboon referred to as *Theropithecus (Omopithecus) baringensis* or *Papio (Dinopithecus) quadratiostris* (Delson and Dean, 1992; Jablonski, 1994; Jablonski and Frost, 2010; Minkoff, 1972). Pickford et al. (1992) attribute a Pliocene-Pleistocene age to the fossils, but recognize that ages may vary among localities. Gilbert et al. (2009) compared taphonomic features of the Humpata fossils with those of Taung and other southern African fissure localities and concluded that the Humpata bones were concentrated by raptor predation. Off the plateau, near the coast along Rio Curoca, Projecto PaleoAngola discovered a Holocene midden, which has not yet been adequately collected.

### Northward Drift of Africa

As alluded to above, the position of a continent below a high pressure descending limb of an atmospheric Hadley Cell is a first order predictor of continental aridity and coastal upwelling between 15° and 30° latitude, notwithstanding significant but regional, transient, or smaller scale perturbations and trends (Etourneau et al., 2009; Heyman et al., 2004; Jung et al., 2014; Rommerskirchen et al., 2011; Shuster, 2006;

Zhang, 2014). Africa currently straddles the descending limbs of both the northern and southern hemisphere Hadley cells, it has done so since it became defined as a continent, and it is the only continent with that distinction.

As the South Atlantic widened since its opening, Africa drifted  $\sim 12^\circ$  north and rotated  $\sim 45^\circ$  degrees counterclockwise (calculated using Scotese, 2008). Figure 7 shows the northward drift of selected coastal Angola sites to illustrate their passage through the Southern Hemisphere subtropical arid zone resulting from Hadley circulation. Also included is the trace for the Dekese drill core, Democratic Republic of the Congo (Cahen et al., 1960), and for the Orange River mouth in South Africa. The Dekese core includes Jurassic and Early Cretaceous strata similar to those in the Samba Core (Cahen et al., 1959) deposited prior to the split of Africa and South America. Isotopic analysis of paleosols sampled by the Samba core indicate a hot, arid climate in interior Gondwana (Myers et al., 2011, 2012), consistent with climate models (Sellwood and Valdes, 2006, 2008; Valdes and Sellwood, 1992). The location of the Samba core drill site now lies in the tropics but its location was in the arid subtropics in the Jurassic and Cretaceous. Fossil plants of Coniacian age from the Orange River indicate a temperate climate (Stevenson et al., 2003), but it now lies at the southern margin of the hyper-arid Namib Desert, also called the Skeleton Coast.

All the localities discovered at Iembe and Bentiaba were formed under climatic conditions imposed by the descending Hadley limb. Iembe has since drifted into the tropics and Bentiaba lies at the northern limit of the Skeleton Coast desert (fig. 7). Strganac et al. (2014a) argue that Bentiaba was formed in a setting similar to that of the Skeleton Coast, between  $20^\circ$  and  $24^\circ$ S paleolatitude. An inference of coastal upwelling is based on the prevalence and abundance of marine top-consumers and coeval petroleum source rocks with type II kerogen derived from marine plankton (Zimmerman et al., 1987). Coastal desert is suggested by short intermittent rivers draining into the sea inferred from provenance of detrital zircons in sediments from mosasaur excavations (Strganac et al., 2014a). If these interpretations are correct, they can be extended to Iembe because of its paleolatitude at the time of formation. Thus, the position of upwelling cells and coastal deserts are inferred from paleogeography to have migrated south along the coast as Africa drifted north (Jacobs et al., 2009). The Benguela Large Marine Ecosystem and Skeleton Coast are the modern manifestations of this environmental setting.

The hypothesis that the Cretaceous coastal sites of Angola formed in an environment similar to the modern Skeleton Coast raises the question of the age of the desert (Torquato, 1970). The Skeleton Coast, extending from southern Angola through Namibia into South Africa (Seeley, 1990), is a classic coastal desert (Glennie, 1987) resulting from the orientation of the coastline below the high-pressure, descending limb of the Southern Hemisphere Hadley cell between  $15^\circ$  and  $30^\circ$ S, exacerbated by upwelling that brings cold, nutrient-rich water to the surface. The stratigraphic evidence for aridity in that region is the lithified aeolianites of the Etjo Sandstone underlying the Etendeka Basalts in the Huab Basin, Namibia

(Catuneanu et al., 2005; Jerram et al., 2000a, b; Mountney et al., 1998, 1999a, b). This relationship of fossilized sand dunes underneath basalts of the Etendeka-Paraná LIP establishes arid conditions in this portion of Gondwana prior to 133 Ma. While this has been used as evidence for an Early Cretaceous age of the Skeleton Coast Desert (Goudie and Eckardt, 1999; Jerram et al., 2000a, b; Vogel, 1989; Ward and Corbett, 1990), it essentially predates the formation of the South Atlantic, reflecting instead the aridity of Gondwana, consistent with data from the Samba core (Myers et al., 2011, 2012).

However, the Benguela Current and associated upwelling (Shannon and Nelson, 1996), currently the foundation of the highly productive Benguela Large Marine Ecosystem (Cury and Shannon, 2004), is generally considered to be about 10 million years old (Miocene; Siesser, 1978, 1980), and therefore apparently too young to explain Cretaceous productivity (Dupont et al., 2005; Diester-Haass et al., 2002, 2004). We would suggest that while the intensification and other trends in the Benguela Current documented since the Miocene are valid, aridity on the continent and upwelling along the coast at the appropriate latitudes are likely and supported by the lines of evidence discussed above, although on a geologic timescale their position relative to the continent has changed. Thus, the age of the Skeleton Coast and associated upwelling varies along the African South Atlantic margin.

The Paleogene localities of Lândana and Malembo in the northern province of Cabinda fall along the latitudinal trace of the Dekese core. Lândana was formed at  $15^\circ$ S paleolatitude, the predicted northern margin of the southern arid zone at the time. Malembo formed slightly south of its current  $5^\circ$ S in an interval of slow northward drift. That paleogeographic setting lends the few terrestrial mammals from Malembo, which are both low latitude and low elevation, a greater measure of significance as they are currently the only West African window into that environment.

This study has focused on the Angolan record; however, as stated previously, Africa straddles the descending limbs of both the northern and southern Hadley cells. Interestingly, the Cenozoic stratigraphy of the Sahara as presented by Swezey (2009) can plausibly be interpreted as having elements of drift-controlled paleoenvironmental change, suggesting that the gross antitropical patterns and historical distributions of environments have a common, specifically African, first-order cause related to northward drift.

### **Comparison of the drift paths of Africa, South America, and Australia**

In addition to examining the effects of latitudinal drift on the eastern South Atlantic Coast, we compared the latitudinal drift of Africa, South America, and Australia at  $25^\circ$ S present day latitude from 160 Ma to the present (fig. 8). This latitude was chosen because it is that of the main Namib Desert Sand Sea and the strongest upwelling cell of the Benguela Current, well within the  $15^\circ$ – $30^\circ$  subtropical arid zone. The latitude of  $25^\circ$ S in Africa today falls between Walvis Bay and Lüderitz, Namibia, in South America near Taltal, Chile, and at Shark Bay, Australia.

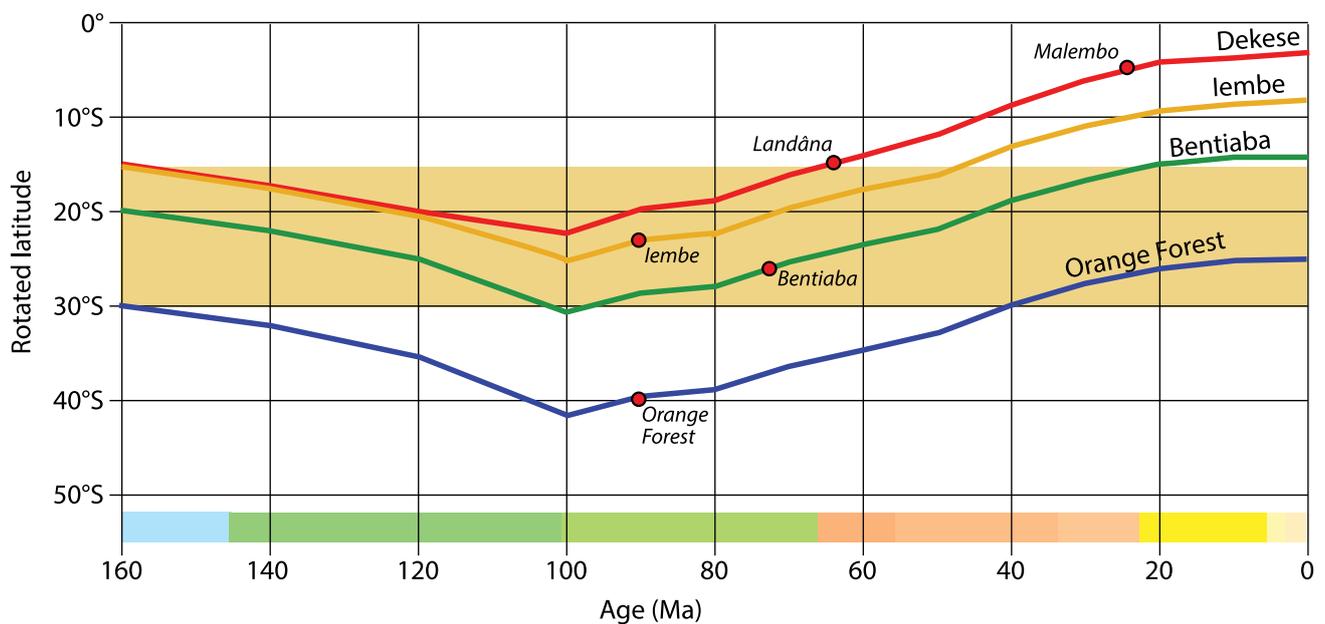


Figure 7. Northward drift of Angolan fossil localities, the Dekese core from the Democratic Republic of Congo, and the Orange Forest, a submerged forest at the mouth of the Orange River, South Africa. The Cretaceous localities of Iembe and Bentiaba formed in latitudes expected to have upwelling and coastal deserts. The Dekese and Samba cores (Cahen et al., 1959, 1960) sampled sediments deposited in the Congo Basin at arid subtropical latitudes although they are now in the tropics. The Orange Forest grew in the temperate zone but now lies in the Skeleton Coast.

South America has the longest drift history within arid paleolatitudes, predicting the Atacama as the oldest coastal desert among Africa, South America, or Australia. Hartley et al. (2005) provided sedimentary evidence for Atacama aridity since the Jurassic. In addition, Hartley et al. (2005) noted that the continentality effect, whereby moisture is drained from the atmosphere as it travels west over the continent, is an important factor in the case of the Atacama Desert, enhancing aridity of the west coast even in the Mesozoic absence of the rain-shadowing Andes. Hyperaridity is exacerbated today by the Humboldt Current, which presumably has existed as long as the desert. Marine vertebrate fossils occur in outcrops of Cretaceous through Cenozoic age along the Atacama Coast (Otero et al., 2012; Pyenson et al., 2014).

Australia has had a long northward drift. Dinosaur localities of Early Cretaceous Victoria were formed at the most southerly paleolatitudes of any known dinosaur sites (>70°S; Rich et al., 1988), including those in Antarctica now (Jacobs et al., 2011). During the Cretaceous, Australia and Antarctica were conjoined. The timing of the final separation and deepwater passage between the two continents is problematic, but the opening may have been completed as late as the Eocene-Oligocene boundary (33.9 Ma) (Lawver et al., 2011). Few Paleogene localities are known from Australia. The Early Eocene site of Tingamarra (54.6 Ma) in Queensland, northeastern Australia, is the only terrestrial mammal-bearing locality in Australia between the Early Cretaceous and the Late Oligocene (Woodhead et al., 2014). Eocene mekosuchine crocodylians are also known from localities in Queensland. These faunas reflect, albeit in a depauperate way, the fauna of

Austro-Antarctic Gondwana, from which the endemic fauna of Australia was derived (Beck, 2012; Beck et al., 2008; Buchanan, 2009).

Australia as a whole is an arid continent, but the point currently at 25°S along Australia's western coast lay south of the arid paleolatitudes until about 10 million years ago, predicting mid-Miocene aridification and upwelling. Aridification in the Miocene is consistent with sedimentological data (Bowler, 1976), particularly with the formation and geomorphology of Channel Iron Deposits in western Australia (MacPhail and Stone, 2004; Morris and Ramanidou, 2007), with the paleobotanical and floral record (Martin, 2006), and with faunal observations (Jacobs et al., 1999; Tedford, 1985; Price, 2012). Climate modeling (Herold et al., 2011) shows widespread aridity during the Miocene and later. Conflicts between modeling and paleontological proxies occur in the north at Riversleigh (Travouillon et al., 2009, 2012; Woodhead et al., 2014), where monsoon effects are more difficult to model, presumably complicated by geography and the Pacific to Indian Ocean throughflow.

Australia has no large-scale upwelling system along its west coast, as would have been predicted by its latitudinal position. Currently at 25°S the eastern boundary current along the west coast is the warm, downwelling Leeuwin Current (Cresswell, 1990). In this case, the longshore pressure gradient along the continental shelf edge suppresses wind-driven upwelling (Godfrey and Ridgway, 1985). The presence of the Leeuwin Current may be due to the Northwest Monsoon and Pacific to Indian Ocean throughflow (Gentili, 1972; Godfrey and Ridgway, 1985). Seasonal variation permits

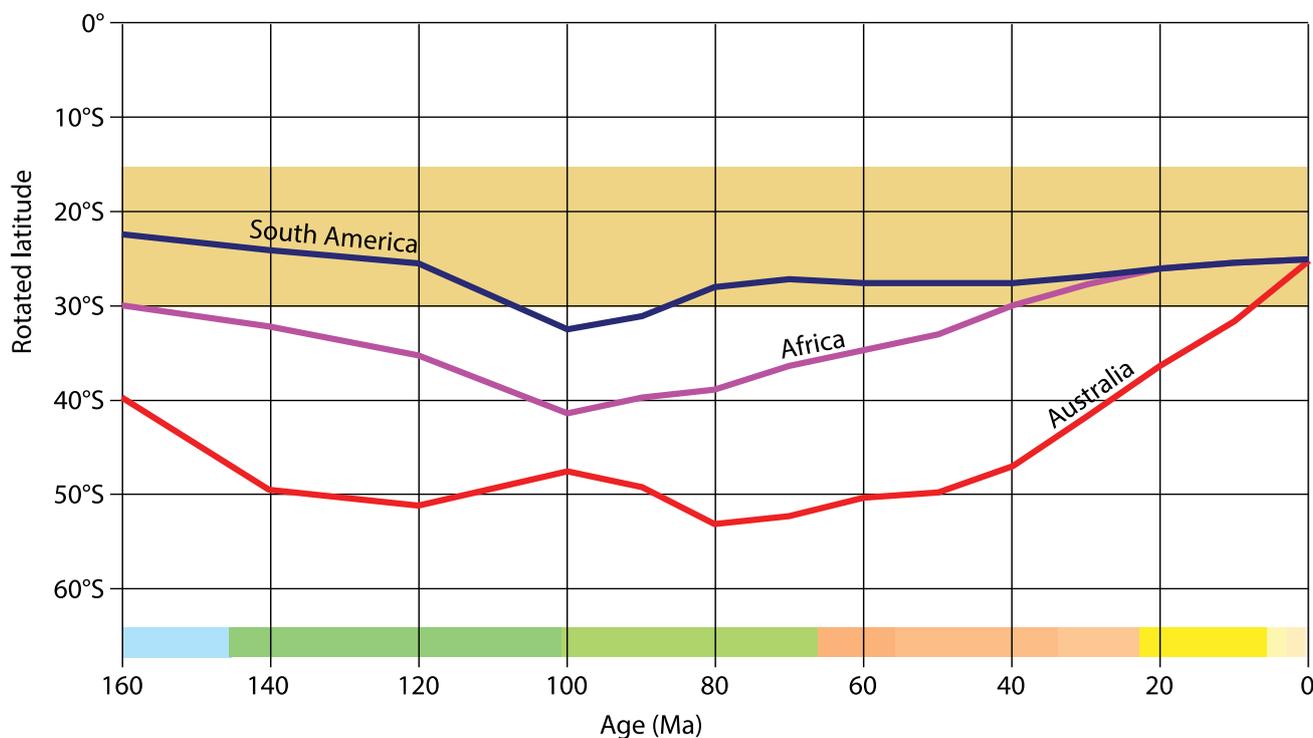


Figure 8. Comparison of northward drift of Africa, South America, and Australia at modern 25°S latitude. South America's Atacama Desert appears to be the oldest among the three continents because of its stable latitudinal position. Africa traversed through the arid zone resulting in southward migration of upwelling and desert relative to the coast. Australia entered the arid latitudes relatively late.

sporadic upwelling in this area (Hanson et al., 2005; Woo et al., 2006). Other local upwelling systems are distributed along Australia controlled by the orientation of the coast relative to seasonal winds.

### Conclusions

The geological setting of coastal Angola and its superb exposures have allowed Projecto PaleoAngola to examine the long record of coastal vertebrates with respect to the opening of the South Atlantic and the northward drift of Africa through climate zones. From this perspective we were able to compare two other post-Gondwanan landmasses that have very different paleolatitudinal and therefore paleoclimatic and paleoenvironmental histories.

At the time of the breakup of Gondwana, major clades of terrestrial vertebrates were already widespread. Dispersing continents disrupted contiguous distributions and reduced probabilities of faunal interchange until halted by Cenozoic continental collisions. The opposite was true for marine vertebrates who found new seas to cross.

Evolution is physically driven by changing environments caused by any number of factors. However, latitudinal position is a first-order determinant of paleoenvironment and therefore a driver of evolution on dispersing land masses and of marine vertebrates in the context of oceanic conditions responding to continental geographies and climatic effects. The

demonstration of the first-order significance of continental position relative to atmospheric cells does not deny the importance of other climate drivers and their effects on biota, but it should provide a more robust platform for their evaluation. The paleontological challenges of studying Gondwana continents and their surrounding seas lie in improving the stratigraphic density of fossils, understanding their associated contexts, and in improving chronology.

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