

## Geological setting and paleoecology of the Upper Cretaceous Bench 19 Marine Vertebrate Bonebed at Bentiaba, Angola

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### Abstract

The Bench 19 Bonebed at Bentiaba, Angola, is a unique concentration of marine vertebrates preserving six species of mosasaurs in sediments best correlated by magnetostratigraphy to chron C32n.1n between 71.4 and 71.64 Ma. The bonebed formed at a paleolatitude near 24°S, with an Atlantic width at that latitude approximating 2700 km, roughly half that of the current width. The locality lies on an uncharacteristically narrow continental shelf near transform faults that controlled the coastal outline of Africa in the formation of the South Atlantic Ocean. Biostratigraphic change through the Bentiaba section indicates that the accumulation occurred in an ecological time dimension within the 240 ky bin delimited by chron 32n.1n. The fauna occurs in a 10 m sand unit in the Mocuio Formation with bones and partial skeletons concentrated in, but not limited to, the basal 1–2 m. The sediment entombing the fossils is an immature feldspathic sand shown by detrital zircon ages to be derived from nearby granitic shield rocks. Specimens do not appear to have a strong preferred orientation and they are not concentrated in a strand line. Stable oxygen isotope analysis of associated bivalve shells indicates a water temperature of 18.5°C. The bonebed is clearly mixed with scattered dinosaur and pterosaur elements in a marine assemblage. Gut contents, scavenging marks and associated shed shark teeth in the Bench 19 Fauna indicate biological association and attrition due to feeding activities. The ecological diversity of mosasaur species is shown by tooth and body-size disparity and by  $\delta^{13}\text{C}$  analysis of tooth enamel, which indicate a variety of foraging areas and dietary niches. The Bench 19 Fauna was formed in arid latitudes along a coastal desert similar to that of modern Namibia on a narrow, tectonically controlled continental shelf, in shallow waters below wave base. The area was used as a foraging ground for diverse species, including molluscivorous *Globidens phosphaticus*, small species expected near the coast, abundant *Prognathodon kianda*, which fed on other mosasaurs at Bench 19, and species that may have been transient and opportunistic feeders in the area.

**Keywords:** mosasaur, paleoecology, continental shelf, detrital zircons, Africa, Cretaceous

### Introduction

Marine sediments at Bentiaba, Angola, have produced one of the most diverse assemblages of marine amniotes known from

the Cretaceous (Mateus et al., 2012; Fig. 1; Table 1), comparable to the type Maastricht fauna of the Netherlands and Belgium (Jagt, 2005) and the Maastrichtian beds of Morocco (Bardet, 2012). The Bentiaba assemblage is of particular



Fig. 1. Location map of Bentiaba. Inset, lower right, shows location of Angola in southwest Africa. Dashed line represents boundary between the Congo Craton and Mesozoic basins, labelled in capital letters. Modified from Strganac et al. (2014).

importance because of the high richness of mosasaurs, a group of extinct marine lizards, and other top predators that have been interpreted as reflecting bottom-up selection pressure within a productive ocean ecosystem during the last 32 million years of Cretaceous time (Polcyn et al., 2014). Bentiaba and other vertebrate fossil localities along the southwest coast of Africa reflect the effects of the growing South Atlantic Ocean on Late Cretaceous marine ecosystems. The Bench 19 Fauna of southern Angola provides a time-constrained glimpse of a marine vertebrate assemblage during the latter phase of this history, placed within the broader context of South Atlantic rifting, sea level, paleoclimate and Late Cretaceous time. In this study we use  $\delta^{13}\text{C}$  values of mosasaur and elasmosaurid plesiosaur tooth enamel to investigate niche differentiation and feeding strategies of the Bench 19 Fauna, and we analyse the geological setting and paleoenvironment of the Bench 19 Bonebed to understand better the biological and physical factors that led to formation of the assemblage (Rogers & Kidwell, 2007).

Differential carbonate cementation in the Mocuio Formation at Bentiaba creates an alternating pattern of more and less resistant beds. The prominent, resistant beds (or benches) were numbered consecutively beginning with the most basal bench in the Mocuio Formation. Overlying Bench 19 in the stratigraphic section are 10 m of fine sandstone, capped at about 138 m in the section by a series of thin lag deposits composed mainly of comminuted fish bone, as well as numerous shark and mosasaur teeth (Strganac et al., 2014; Fig. 2). Although fossil remains of mosasaurs, plesiosaurs and marine turtles are distributed throughout the 10 m of the Mocuio Formation overlying Bench 19, vertebrate specimens are particularly concentrated in a 1–2 m thick zone directly overlying Bench 19, referred to here as the Bench 19 Bonebed and Fauna.

The chronological context for Bentiaba is provided by a  $\delta^{13}\text{C}$  chemostratigraphic curve and magnetic polarity stratigraphy constrained by an  $84.6 \pm 1.5$  Ma  $^{40}\text{Ar}/^{39}\text{Ar}$  whole-rock radiometric date on a basalt of the Ombe Formation and by ammonite biostratigraphy (Strganac et al., 2014). The Bench 19 Bonebed is located near the top of the Bentiaba section, in chron C32n.1n between 71.4 and 71.64 Ma (Husson et al., 2011). Water temperature of  $18.5^\circ\text{C}$  for the Bench 19 Fauna was determined from a  $\delta^{18}\text{O}$  chemostratigraphic curve derived from marine bivalves (Strganac et al., in press).

### Abbreviations

ML – Museu da Lourinhã, Portugal; MGUAN-PA and PA – Museu de Geologia da Universidade Agostinho Neto, Luanda, Angola (PaleoAngola Collection); SMU – Southern Methodist University, Dallas, USA.

### Methods

Locations on the ground of amniote fossils were marked by GPS, recorded in the field and marked on the stratigraphic section. Nearest-neighbour data were compiled from GPS data and the long-axis orientation of the specimens was noted for those that could be identified to taxon and were clearly in place. Remains of bony fish and sharks are found throughout the Mocuio Formation and were collected opportunistically. Precise specimen locality data are on file at SMU. Skeletal completeness and bone modification features were noted during specimen preparation at SMU and ML.

A predicted paleolatitude for Bentiaba from the Ombe Formation dated at  $84.6 \text{ Ma} \pm 1.5 \text{ Ma}$  (Strganac et al., 2014) was determined from oriented paleomagnetic samples collected within the measured section at Bentiaba. Results from three basalt samples yield a mean magnetisation direction of declination ( $D$ ) =  $346.9^\circ$  and inclination ( $I$ ) =  $-42.4^\circ$ , with  $\alpha_{95} = 7.8^\circ$  (Fisher, 1953), which is different from the Earth's present magnetic field direction at the sampling site ( $D = 353.2^\circ$  and  $I = -56.3^\circ$ ). Paleolatitude ( $\lambda$ ) can be calculated by the simple equation:

$$\tan(I) = 2\tan(\lambda)$$

Obtained mean inclination from Ombe Formation basalts yields a paleolatitude of  $24.5^\circ\text{S}$  for the Bentiaba locality. The paleolatitude at 71 Ma was a few degrees lower because of the northward drift of Africa.

The paleolatitudinal trace of Bentiaba from the initial opening of the South Atlantic in the Early Cretaceous to its current latitude is presented in Jacobs et al. (2011), determined using PointTracker (Scotese, 2008). The width of the South Atlantic Ocean at 71 Ma and  $20^\circ\text{S}$  was determined from Earthworks BV (Reeves, 2014). The bathymetric image of the Angolan

Table 1. Annotated vertebrate fauna list for Bench 19 Bonebed.

Taxon	Elements	Notes
Chondrichthyes		
Elasmobranchii		
<i>Squalicorax pristodontus</i>	Numerous shed teeth	Most common shark at Bentiaba; outnumbers Odontaspidae indet. 10:1
Odontaspidae indet.	Shed teeth	
cf. <i>Ganopristis</i> sp.cf. <i>Ganopristis</i> sp.	Two shed teeth	Rare, only two shed teeth found
<i>Brachyrhizodus</i> sp. <i>Brachyrhizodus</i> sp.	Isolated teeth and partial tooth batteries	
Osteichthyes		
cf. <i>Eodiaphyodus</i> sp.cf. <i>Eodiaphyodus</i> sp.	Single fragmentary tooth plate	
<i>Enchodus</i> sp.	Fragmentary skeletons, skull fragments, isolated vertebrae, teeth	Common
Testudines		
Cheloniidae		
<i>Euclastes</i> sp. <i>Euclastes</i> sp.	Two partial skulls	
Protostegidae		
? <i>Calcarichelys</i> sp.? <i>Calcarichelys</i> sp.	Single neural scute	
<i>Protostega</i> sp. <i>Protostega</i> sp.	Large disarticulated skeleton	
Toxochelyidae		
<i>Toxochelys</i> sp.	Fragmentary specimen comprising hyoplastron, peripheral and costal plates	
Squamata		
Mosasauridae		
<i>Globidens phosphaticus</i>	One partial skeleton with skull, two partial skulls with fragmentary postcrania, numerous shed teeth	Second most common mosasaur at Bentiaba
<i>Halisaurus</i> n. sp.	Multiple partial skeletons with skull and limb material, shed teeth	Three partial skeletons found together as gut content, adult and subadult individuals present
<i>Mosasaurus</i> sp.	Rare isolated shed teeth of large morph ( <i>M. cf. hoffmanni</i> ) and two partial skulls, vertebrae, isolated quadrates from a small <i>Mosasaurus</i> sp.	Represented as both gut content (small morph only) and isolated finds; may be ontogenetic stages of a single taxon.
<i>Phosphorosaurus</i> sp.	Partial frontal	
<i>Platecarpus</i> ' <i>ptychodon</i>	Two semi-articulated partial skeletons, shed teeth	Represented as gut content and isolated finds; this taxon was referred to <i>Platecarpus</i> by Arambourg (1952), but considered new unnamed genus
<i>Prognathodon kianda</i>	Multiple partial skeletons, numerous shed teeth	Most common mosasaur at Bentiaba; subadult specimen represented in gut content
Plesiosauria		
Elasmosauridae		
cf. <i>Tuarangisaurus</i>	Four specimens representing pectoral and pelvic girdle elements, propodials, cervical and pectoral vertebrae	Shed teeth are rare
Elasmosauridae indet.	Girdle elements, semi-articulated limb material, vertebrae and fragmentary cranial material	Shed teeth are rare
Pterosauria		
Ornithocheiroidea indet.	Long bones and long bone fragments	
Dinosauria		
Ornithopoda		
Hadrosauoidea indet.	Isolated pedal element	
Ornithopoda indet.	Isolated long bone	

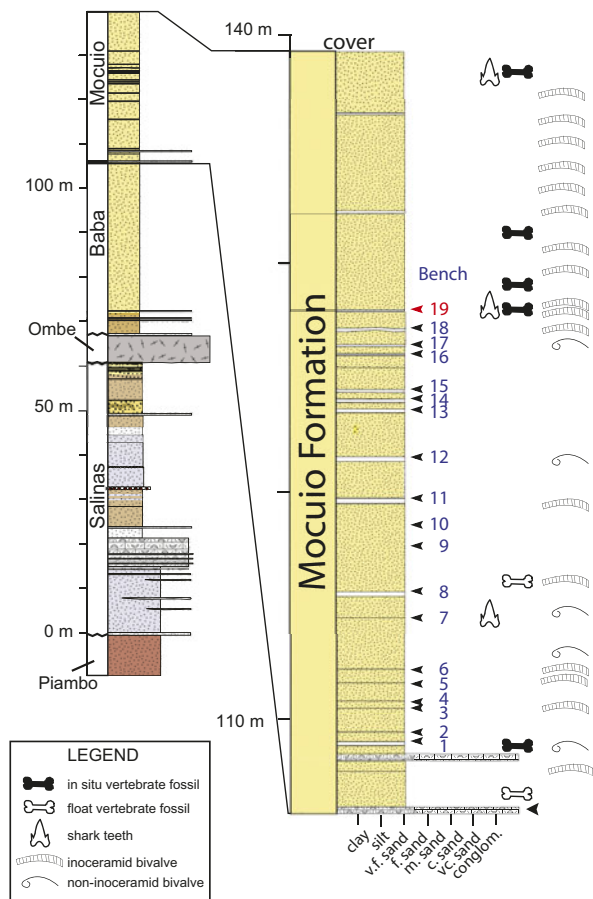


Fig. 2. Stratigraphic section at Bentiaba, with Mocuio Formation enlarged. The Ombe Formation is a basalt dated at  $84.6 \pm 1.5$  Ma (Strganac et al., 2014), within the Santonian. The overlying Baba and Mocuio formations are Campanian–Maastrichtian.

continental shelf discussed below was constructed from [http://cmtt.tori.org.tw/data/App\\_map/maplist.htm](http://cmtt.tori.org.tw/data/App_map/maplist.htm).

Sediment samples from the Bench 19 Bonebed were taken from the field jacket containing a specimen of *Prognathodon kianda* (PA 183) at the base of the Bench 19 Bonebed and analysed for mineral composition, grain size and detrital zircon ages. A second sample was taken from the jacket of a *Prognathodon* sp. (PA 186) near the top of the unit. To determine the mineralogy of the Bench 19 Bonebed matrix, a small amount of material was powdered with a mortar and pestle and analysed at SMU using a Rigaku III Ultima X-ray diffractometer with a step size of  $0.05^\circ$  over a range of  $2\text{--}60^\circ 2\theta$ . Grain size was determined by sonicating a matrix sample in deionised water to disaggregate it and sieving the dried matrix to separate the size fractions.

A single sample of sandstone (MJP 2006A) was analysed for detrital zircon geochronology to investigate sediment provenance. This sample comprises sand from the Mocuio Formation that was excavated from one of the plaster jackets containing a *Prognathodon kianda* (PA 183). Detrital zircons were analysed using laser ablation inductively coupled plasma mass spectrometry

(LA-ICPMS) at the Arizona LaserChron Center ([www.laserchron.org](http://www.laserchron.org)) using methods described by Gehrels et al. (2006, 2008).

Isolated teeth of mosasaurs and plesiosaurs collected from the Bench 19 Fauna were identified by comparison with specimens at the Shuler Museum of Paleontology at SMU and published literature (Bardet & Pereda Suberbiola, 2002; Schulp et al., 2006, 2008; Polcyn et al., 2010; Araújo et al., submitted A; submitted B). Tooth specimens were soaked in 10% acetic acid for at least 72 hours to remove diagenetic carbonate encrustation and rinsed with deionised water. The samples were then sonicated, treated with methanol, rinsed again in a deionised water bath and dried. Enamel was sampled using a carbide-tipped hand drill and the resulting enamel powders were placed in vacuum-sealed reaction vessels with 100% orthophosphoric acid at  $25^\circ\text{C}$  for a minimum of 4 hours. The evolved gas was cryogenically purified to isolated  $\text{CO}_2$ , which was analysed with a Finnegan MAT 252 isotope ratio mass spectrometer to determine its  $\delta^{13}\text{C}$  and  $\delta^{18}\text{O}$  values, reported here in permil units relative to the Vienna Pee-Dee Belemnite standard (VPDB). Data obtained for individuals or groups of taxa were compared statistically using the nonparametric Mann–Whitney U test for two groups of data and Kruskal–Wallis ANOVA for three or more groups.

## Results

### Sedimentology and detrital zircons

The Mocuio Formation at Bentiaba is composed primarily of massive fine-grained sandstone with, near the top, occasional low-angle cross-bedding and some thin fossiliferous lag deposits. Scour marks are minor and rare, and there is no evidence of high-energy deposition or wave action, such as hummocky cross-stratification, indicating that depth was below storm wave base. The macroinvertebrate assemblage is relatively sparse and comprises fragments of the pteriomorphian bivalve *Inoceramus*, dissolution moulds of non-inoceramid bivalves and irregular vertical burrows.

Although vertebrate fossils occur sporadically throughout the upper Mocuio Formation, they are concentrated in a 1–2 m thick bonebed overlying Bench 19, although the Bench 19 Fauna (Table 1) occurs throughout the overlying 10 m. The base of Bench 19 is planar and the overlying fossil-bearing sediments grade upward rapidly into friable sand that forms steep walls, overlain by more frequent, albeit uncommon, cross-beds and fossiliferous lags. Terrestrial influence in Bench 19 and the overlying 10 m includes rare oxidised, unidentifiable plant remains and occasional isolated dinosaur and pterosaur bones (Mateus et al., 2012), indicating proximity to shore. No pollen or microfossils were recovered.

The basal Bench 19 Bonebed sediment (sample from PA183; Fig. 3A) comprises a pale yellow (2.5Y 8/2) to white (2.5Y 8/1) poorly sorted, subangular to subrounded, silty, fine-grained feldspathic arenite, weakly cemented by calcite. Clast size

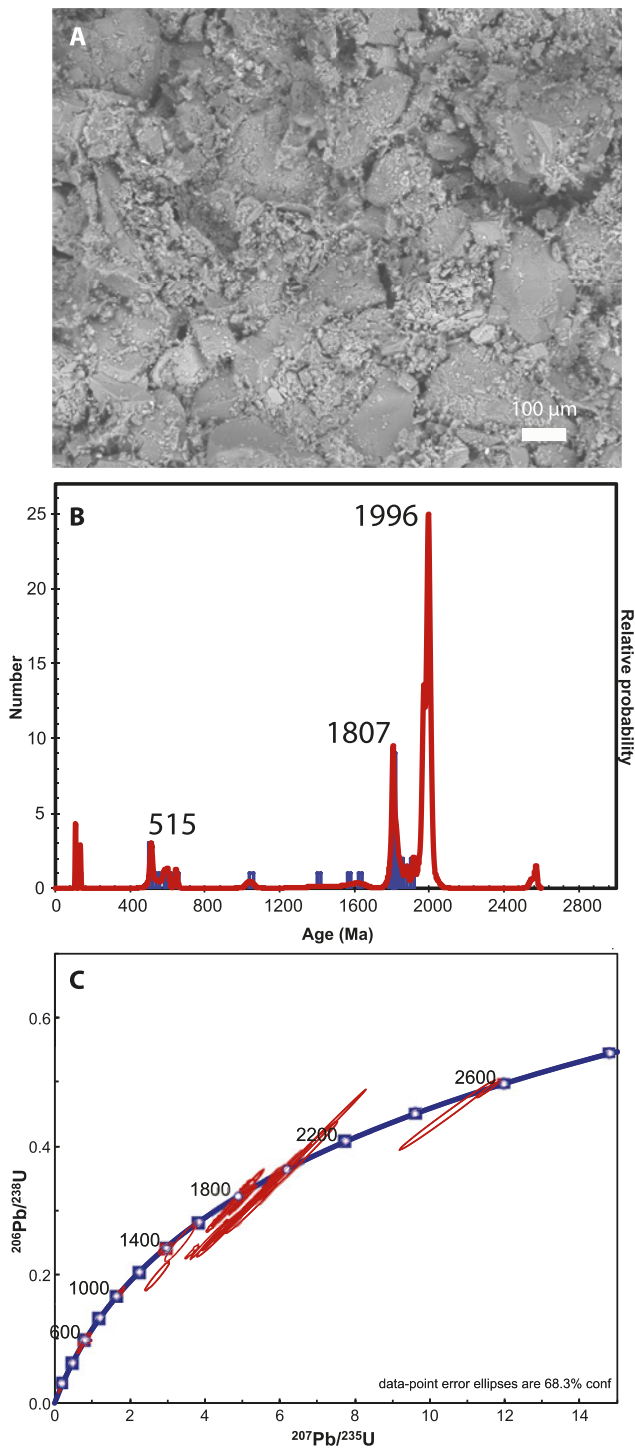


Fig. 3. Bench 19 sediments and zircon age analysis. A. SEM image of sediment samples from main bonebed layer above Bench 19 taken from PA183. Large grains are quartz and small grains are feldspathic. B. Detrital zircon age probability distribution (red) and histogram (blue) for sample MJP2006A from the Bonebed sandstone in the Mocúio Formation. Age of key probability peaks is shown on the figure. C. Concordia plot for detrital zircons from MJP2006A showing error ellipses from resulting  $^{206}\text{Pb}/^{238}\text{U}$  and  $^{207}\text{Pb}/^{235}\text{U}$  values.

ranges from coarse sand to silt-size, with a positively skewed distribution. Larger clasts are lithics and quartz, and smaller

clasts are predominantly microcline and anorthite. There is an indistinct and gradual facies change in the upper part of the Bench 19 unit (sample from PA 186). This part of the unit comprises a well-sorted, subrounded to rounded, very fine-grained yellow (2.5Y 7/6) to olive yellow (2.5Y 6/6) silty sand. XRD analysis indicates it is also a feldspathic arenite with a relatively high abundance of quartz (75–90%). This level has a greater textural and compositional maturity relative to the lower part of the Bench 19 Bonebed.

Uranium-lead ages were obtained from 76 zircons extracted from a single sample from the Bench 19 Bonebed sandstone with a total age distribution of  $107 \pm 2$  Ma to  $2571 \pm 7$  Ma. A standard age probability distribution (Fig. 3B) shows major grain populations at  $\sim 1996$  Ma and  $\sim 1807$  Ma, and a late Precambrian to Cambrian population with an age peak at  $\sim 515$  Ma. Uranium concentrations for all grains is  $< 600$  ppm. As illustrated in Fig. 3C, some of the Paleoproterozoic grains depart from the concordia, suggesting potential lead loss during the Pan-African orogenic event.

#### Fossil spatial distribution and orientation

The Bench 19 Fauna was collected from a contiguous band of badland outcrops within an area approximately 500 m north-south by 200 m east-west, with additional specimens obtained from sporadic outcrops extending some 300 m east (Fig. 4A). The Bench 19 unit intersects the eroded surface along a trace approximately 1.5–2 km in length, estimated by connecting the fossil occurrences on a map. The dip of the strata approximates the surface of Bench 19 in some places and in others the intersection is along steep faces. Fragments of pterosaur bones were found throughout the interval, but more complete bones were discovered by their cross-sections in steep outcrop faces, which afforded them protection from deeper weathering and erosion. Bony fish and sharks, although not systematically collected, appear broadly distributed, but shark teeth, especially *Squalicorax* (Antunes & Cappetta, 2002) are closely intermingled with amniote skeletal remains. A histogram of amniote nearest-neighbour distances shows a peak between 2.5 and 5 m ( $n = 192$ , range = 0–35 m,  $\bar{x} = 8.5$ ,  $\sigma = 6.5$ ; Fig. 4B). The closest associations of amniotes (0 m) are interpreted as gut contents because of the position of one individual within the gut area of a presumed consumer and the etched condition of bones and teeth in consumed individuals (see discussion below).

There is no preferred orientation of elements and all specimens rest parallel to the bedding plane (Fig. 4C). The spatial distribution of amniote specimens and their separation by metres indicates a scattered distribution over the sea floor, lacking linear orientation as in a strand, or concentration by currents or other agents into a tight mass. The fossils are not concentrated in ravinements or on scoured surfaces. There is no evidence of turbulence in the sediments or of transport in the condition of the bone.

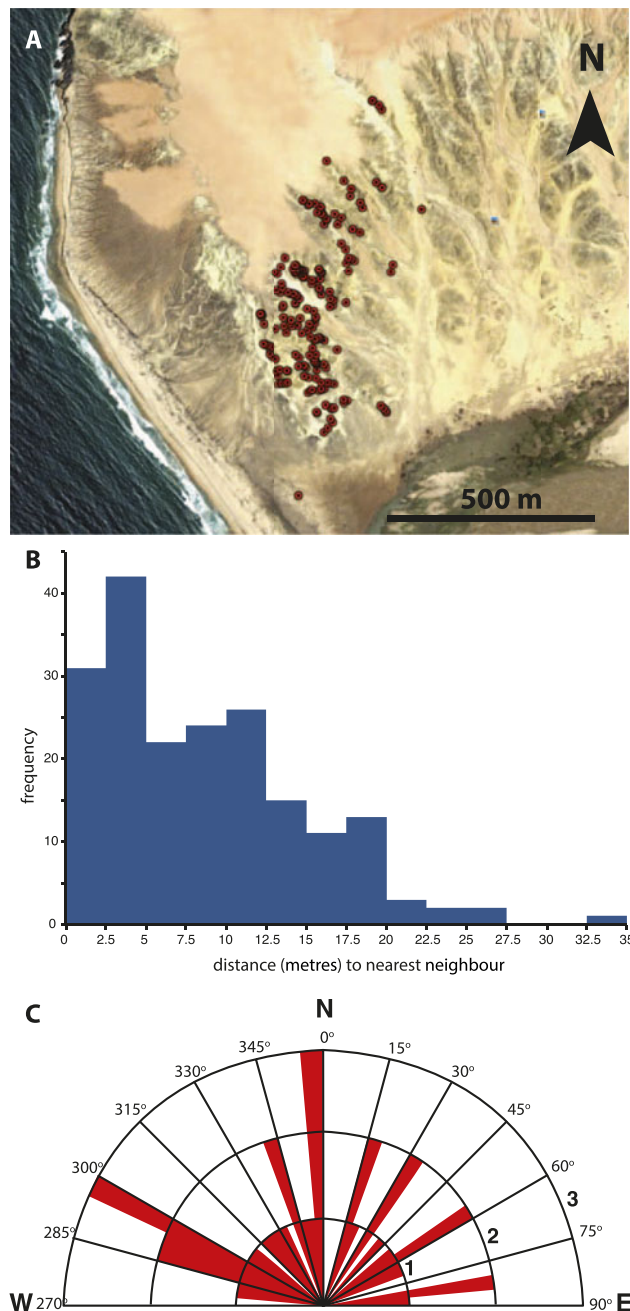


Fig. 4. A. Satellite image of Bentiaba (map data: Google, DigitalGlobe). Red dots represent locations of specimens recovered from Bench 19 Bonebed. B. Histogram of nearest-neighbour distances among fossils at Bench 19. C. Rose diagram for orientations of elongate fossil elements at Bench 19.

### Bone modification

Amniote fossils occur as partially articulated skeletons, disarticulated but associated partial skeletons and isolated elements. All specimens within the bonebed, except those interpreted as gut contents, exhibit a similar preservation style. Postburial crushing, indicated by longitudinal cracks, is common, but fossils appear more completely permineralised with less apparent postburial crushing in the upper part of the Bench 19 Bonebed.

Irrespective of position within the Bench 19 Bonebed, pitting and erosion of cortical bone is present only in juvenile plesiosaur limbs. No bioencrustation or microboring was observed. Evidence of transport (abrasion, rounding or polishing) is absent and bone surfaces are generally pristine (Fig. 5A).

Most specimens show evidence of scavenging by sharks. Bite marks and scratches most closely match the size and serration pattern of *Squalicorax pristodontus* teeth, displaying secondary lineations perpendicular to the main grooves (Schwimmer et al., 1997; Shimada et al., 2010). Marks from shark scavenging are common on limb elements and ribs but rare on vertebrae, irrespective of taxon (Fig. 5B).

Mosasaur-on-mosasaur predation or scavenging is present in one specimen of *Prognathodon kianda* (PA 183), which comprises the skull, some proximal rib portions and the vertebral column complete to the anterior caudals, but is missing the limbs, girdles and most of the ribs. The skeleton shows bite marks attributed to sharks and numerous *Squalicorax pristodontus* teeth were found with the specimen. Partial skulls of *Platecarpus ptychodon*, *Mosasaurus* sp. and an indeterminate mosasaurine were found in the gut region of PA 183 (Fig. 5C). In these gut-content specimens, the skull roof, snout and other areas thinly fleshed in life are etched, and tooth crowns are dissolved above the gum line.

A second mass of bones exhibiting similar modification to those seen in the gut area of PA 183 comprises the partial skeletons of three *Halisaurus* specimens (PA 179) and a juvenile *P. kianda* (PA 25). Individual bones show no modification by sharks. At the time of discovery and excavation, the mass was thought to be isolated and a consumer remains undiscovered, possibly still in the quarry. The size of the bone mass, if in fact it is gut contents, suggests the consumer was a large mosasaur.

### Results of $\delta^{13}\text{C}$

The 49 enamel carbonate  $\delta^{13}\text{C}$  values derived from 37 tooth specimens of five mosasaur taxa and four plesiosaur teeth from Bench 19 Bonebed are presented in Table 2 and Fig. 6. PA 314 (*Halisaurus*) yielded a  $\delta^{13}\text{C}$  value of  $-7.2\text{‰}$ . Specimens PA 177 and PA 312 (*P. ptychodon*) produced an average  $\delta^{13}\text{C}$  value of  $-7.3\text{‰}$ . Twenty-one teeth assigned to *Prognathodon kianda* produced an average  $\delta^{13}\text{C}$  value of  $-10.1\text{‰}$  and ranged from  $-14.1$  to  $-5.2\text{‰}$ . Three teeth of *Mosasaurus* sp. yielded an average  $\delta^{13}\text{C}$  value of  $11.6\text{‰}$  and ranged from  $-12.9$  to  $-10.2\text{‰}$ . Eleven *Globidens phosphaticus* teeth yielded an average  $\delta^{13}\text{C}$  value of  $13.0\text{‰}$  and ranged from  $-16.1$  to  $-10.8\text{‰}$ . Four plesiosaur teeth produced an average  $\delta^{13}\text{C}$  of  $-13.1\text{‰}$  and ranged from  $-14.0$  to  $-12.2\text{‰}$ .

*Halisaurus* and *P. ptychodon* are grouped together for analyses due to their small body size (<5 m in length; Polcyn et al., 2014) and their similar  $\delta^{13}\text{C}$  values. The standard deviation of *Halisaurus* + *P. ptychodon* ( $-7.3 \pm 0.4$ ) does not overlap with those of *Prognathodon* ( $-10.3 \pm 2.4$ ), *Globidens* ( $-13.1 \pm 1.6$ ) or plesiosaurs ( $-13.1 \pm 0.7$ ) and is therefore statistically different.

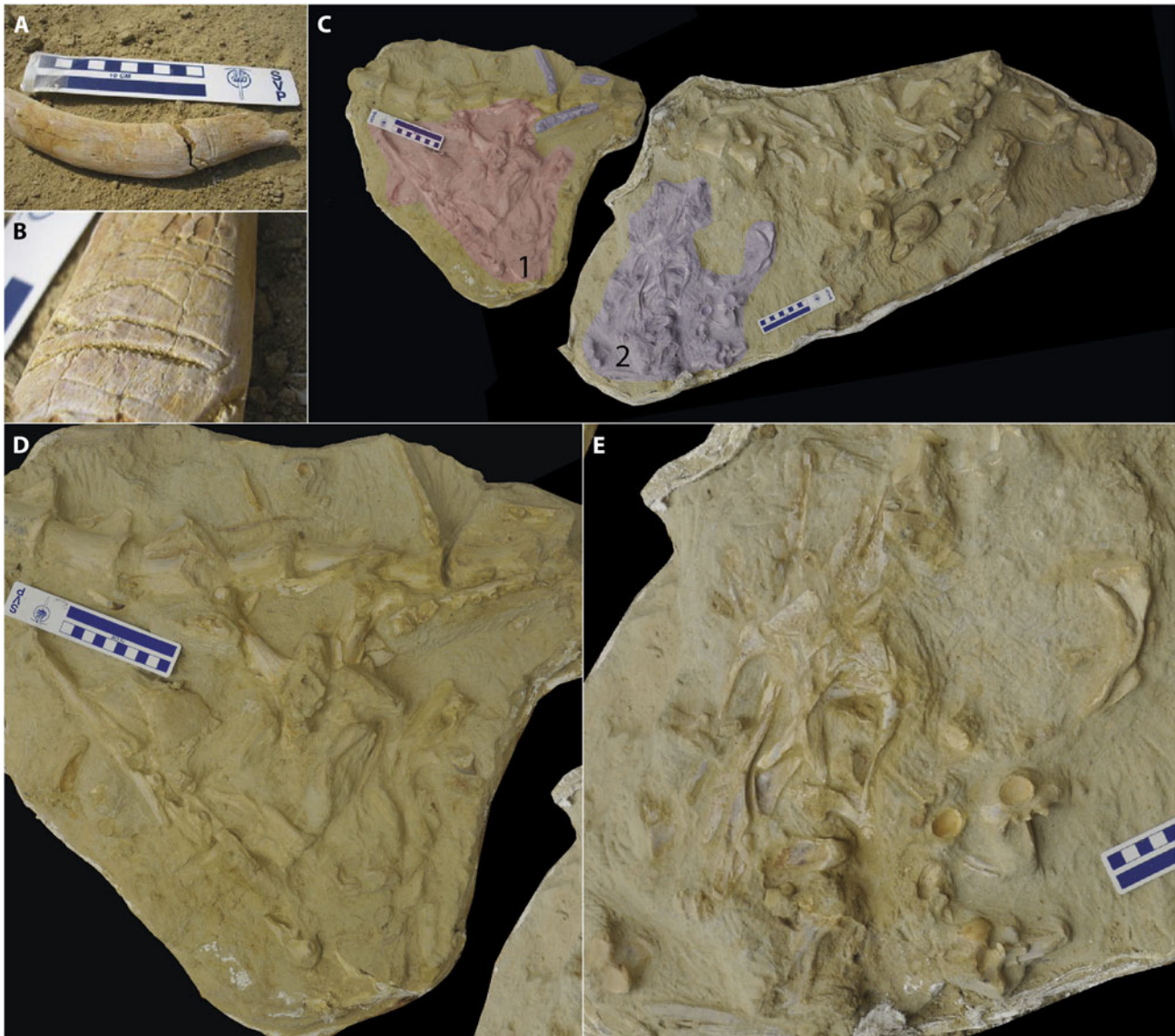


Fig. 5. A. Bite marks attributed to the shark *Squalicorax pristodontus* on a mosasaur rib from the Bench 19 Bonebed, enlarged in B. Note short transverse marks along major groove from serrations on teeth. C. Specimen PA183, *Prognathodon kianda*, with preserved gut contents. Two specimens in the gut are shown as highlighted regions 1 and 2, and are enlarged in D and E, respectively. A third specimen was recovered between the blocks and is not shown.

Mann–Whitney U tests (Table 3) were used to compare  $\delta^{13}\text{C}$  values between two taxa or groups at significance levels of 0.05. *Globidens* values are significantly different from *Prognathodon* ( $p = 0.001$ ), but not from plesiosaurs ( $p = 0.862$ ) or *Mosasaurus* ( $p = 0.223$ ). *Mosasaurus* is not significantly different from *Prognathodon* ( $p = 0.316$ ) or plesiosaurs ( $p = 0.114$ ). The  $\delta^{13}\text{C}$  values of *Prognathodon* are not significantly different from ‘P.’ *ptychodon* + *Halisaurus* ( $p = 0.046$ ).

In comparing the  $\delta^{13}\text{C}$  values between more than two taxa, Kruskal–Wallis ANOVA tests indicate *Globidens*, *Mosasaurus* and plesiosaurs were not significantly different ( $p = 0.293$ ). The group is significantly different when *Prognathodon* is included ( $p = 0.003$ ). There is a significant difference in  $\delta^{13}\text{C}$  values derived from *Mosasaurus*, *Prognathodon* and plesiosaurs

( $p = 0.046$ ), and *Globidens*, *Prognathodon* and plesiosaurs ( $p = 0.001$ ).

## Discussion

The modern marine ecosystem off the shore of southern Angola and Namibia is highly productive due to the Benguela Current and coastal upwelling system (Shannon & Nelson, 1996). The Benguela upwelling zone provides nutrient-rich waters that support a diverse marine ecosystem containing ~70% of the marine mammal species in the South Atlantic Ocean (Cury et al., 2000). Although the modern Benguela upwelling system is purported to have originated in the late Miocene (Diester-Haas et al., 2002), the presence of organic-rich Cenomanian–Turonian

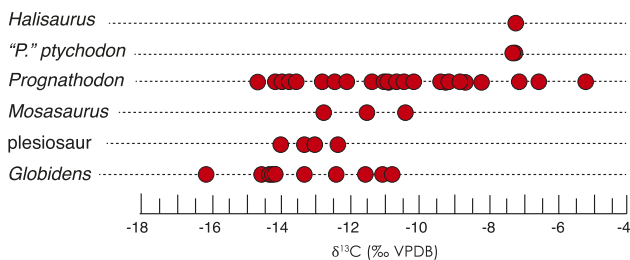
Table 2.  $\delta^{13}\text{C}$  values of tooth enamel carbonate in Bench 19 mosasaurs and plesiosaurs. Length estimates from Polcyn et al. (2014).

Taxon	Length (m)	Specimen #	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$		
<i>Globidens</i>	4-6	PA 04	-14.6	-2.1		
		PA 05	-13.2	-1.7		
		PA 29	-14.3	-1.2		
		PA 30	-10.8	-1.3		
		PA 301	-12.6	-1.1		
		PA 307	-11.6	-1.7		
		PA 31	-12.4	-1.1		
		PA 313	-12.5	-1.5		
		PA 33	-11	-2.4		
		PA 500	-16.1	-2.1		
		PA 61	-14.3	-1.6		
		<i>Halisaurus</i>	3	PA 314	-7.2	-2.2
		<i>Mosasaurus</i>	17	PA 309r1	-10.2	-1.4
PA 309r2	-8.9			-1.4		
PA 44	-11.6			-2.6		
PA 46	-12.9			-1.9		
"P." <i>ptychodon</i>	1.5	PA 177	-7.2	-2.1		
		PA 312r1	-7.2	-2.1		
		PA 312r2	-7.6	-2.4		
<i>Prognathodon</i>	7-9	PA 177r1	-9.2	-2.6		
		PA 177r2	-9.2	-3.2		
		PA 321	-8.2	-2.3		
		PA 38	-10.9	-1.5		
		PA 55	-8.7	-3.6		
		PA 173	-9.1	-1.7		
		PA 173	-9.2	-2.3		
		PA 28r1	-11.1	-1.6		
		PA 28r2	-11.4	-2.3		
		PA 304r1	-6.9	-1.8		
		PA 304r2	-7.3	-1.5		
		PA 306	-12.1	-2.4		
		PA 315	-10.1	-1.8		
		PA 318	-12.4	-2.4		
		PA 35	-10.7	-1.5		
		PA 40	-11	-1.7		
		PA 41	-5.2	-1.9		
		PA 45	-10.4	-3.3		
		PA 47	-13.7	-2.4		
		PA 48	-10.9	-1.6		
PA 50r1	-14.1	-3.7				
PA 50r2	-13.4	-1.9				
PA 53	-12.8	-3.5				
PA 56	-6.6	-2				
Plesiosauria		PA 173	-12.2	-2.5		



Table 2. Continued.

Taxon	Length (m)	Specimen #	$\delta^{13}\text{C}$	$\delta^{18}\text{O}$
		PA 305	-12.5	-1.5
		PA 305	-13.5	-2
		PA 320	-14	-1
		PA 36	-12.7	-2.7
		PA 36	-13.7	-2.5

Fig. 6.  $\delta^{13}\text{C}$  values of mosasaurs and plesiosaurs at Bench 19.

deposits offshore in western Africa and the rich marine vertebrate fauna preserved in Turonian, Campanian and Maastrichtian coastal outcrops of Angola indicate that latitudinally controlled, high-productivity environments consistent with upwelling existed in the Late Cretaceous (Handoh et al., 1999; Jacobs et al., 2006, 2009; Polcyn et al., 2014).

The paleolatitude of Bentiaba, at the time of the accumulation of the Bench 19 Fauna (C32n.1n; 71.40–71.64, using the calibration of Husson et al., 2011; see Strganac et al., 2014) was not more than the  $-24^\circ$  as calculated for the Ombe Formation basalt ( $84.6 \pm 1.5$  Ma  $^{40}\text{Ar}/^{39}\text{Ar}$  whole-rock radiometric date; Strganac et al., 2014) and as reported by Jacobs et al. (2011). The width of the South Atlantic at paleolatitude  $20^\circ\text{S}$  and 71 Ma was approximately 2700 km calculated from Reeves (2014), roughly half the current width. Thus, the Bench 19 Fauna was emplaced at a paleolatitude analogous to the position of Walvis Bay in the present-day latitudinal position of Africa, although in a wide but narrower than present-day ocean. This latitude is well within the area of the high-pressure, descending limb of the southern Hadley cell, driving rich upwelling along the coastal desert. Oceanic upwelling cells provide nutrients that enhance primary productivity, which has been suggested as a driver of mosasaur evolution generally (Jacobs et al., 2009; Polcyn et al., 2014). The presence of abundant marine amniote fossils in coastal Angola, specifically at Bentiaba, is consistent with that hypothesis.

The continental shelf at Bentiaba is much narrower than in northern Namibia (100–160 km in Walvis Bay, as opposed to <10 km at Bentiaba; Fig. 7). The extremely narrow width of the continental shelf and the orientation of the continental margin in the Bentiaba region are controlled by the tectonics of the Benguela and Lucapa transform faults, relating to the opening of the South Atlantic (as discussed by Guiraud et al.,

2010; see also Moulin et al., 2012). The depth of the shelf near Bentiaba was shallow throughout the Late Cretaceous (Strganac et al., 2014). The 84.6 Ma Ombe Formation basalt flowed across the coastline, but based on paleomagnetic and  $\delta^{13}\text{C}$  chemostratigraphic correlations (Strganac et al., 2014), the Bentiaba coast was emergent as indicated by the missing section shown by 5 my of time not represented by strata subjacent to the Ombe Formation and 6 my of missing strata superjacent to a thin veneer of sediment atop the Ombe Formation. Examination of sea-level curves presented by Müller et al. (2008) and Miller et al. (2011) does not suggest an apparent link to eustatic sea-level fall as the cause for these hiatuses, but tectonically induced stratigraphic hiatuses have been documented in the Benguela basin to the north (Giraud et al., 2010). At Bentiaba, the two Late Cretaceous episodes of relative sea-level fall were caused by local to regional uplift. The intervening Ombe Formation defines sea level at the time by crossing the Santonian shoreline. The fossiliferous upper Campanian to lower Maastrichtian Baba Formation, which overlies the unconformity, and the Mocuio Formation, which contains the Bench 19 Fauna, represent shelf flooding resulting from relaxation and subsidence. The narrow shallow shelf may have served to concentrate prey items and attract predators in a relatively small area compared to the shelf to the north and south. Cenozoic faulting and eustatic sea level change culminated in a Pliocene or younger terrace that truncates Cretaceous deposits at Bentiaba, perhaps comparable to terraces seen farther south in the Namibe basin (Sessa et al., 2013).

The bonebed sandstone is compositionally immature and texturally submature. Its poor sorting, incomplete rounding and feldspathic composition indicate close proximity to a granitic source. The suite of ages exhibited by detrital zircons (Fig. 3B) show significant populations at 1996 Ma and 1807 Ma with lesser populations at 515 and  $\sim 2500$  Ma. The observed age probability distribution is consistent with a nearby source terrain for the Mocuio Formation sandstones. Within close proximity to the present-day outcrops, Angolan basement yields radiometric ages of 1795–2243 Ma (Hanson, 2003). Angolan basement is dominated by Paleoproterozoic granitic and gneissic lithologies with inliers of Archean crust consistent with the dominance of Paleoproterozoic detrital zircon ages (62 of the 76 grains studied) and occasional Archean grains. Granitoid rocks of the Pan-African Kaoko Belt, south of Bentiaba, yield

Table 3. Results for statistical analysis of variance for marine amniote  $\delta^{13}\text{C}$  values.

Test	Independent variables		P value	Significance level
Mann-Whitney U	<i>Globidens</i>	Plesiosauria	0.862	0.05
Mann-Whitney U	<i>Globidens</i>	<i>Mosasaurus</i>	0.223	0.05
Mann-Whitney U	<i>Globidens</i>	<i>Prognathodon</i>	0.001	0.05
Mann-Whitney U	Plesiosauria	<i>Mosasaurus</i>	0.114	0.05
Mann-Whitney U	Plesiosauria	<i>Prognathodon</i>	0.021	0.05
Mann-Whitney U	<i>Prognathodon</i>	small	0.046	0.05
Mann-Whitney U	<i>Prognathodon</i>	<i>Mosasaurus</i>	0.316	0.05
Kruskal-Wallis ANOVA	<i>Globidens</i>	<i>Mosasaurus</i>	0.293	0.05
	Plesiosauria			
Kruskal-Wallis ANOVA	<i>Globidens</i>	Plesiosauria	0.003	0.05
	<i>Mosasaurus</i>	<i>Prognathodon</i>		
Kruskal-Wallis ANOVA	Plesiosauria	<i>Prognathodon</i>	0.046	0.05
	<i>Mosasaurus</i>			
Kruskal-Wallis ANOVA	Plesiosauria	<i>Prognathodon</i>	0.001	0.05
	<i>Globidens</i>			

radiometric ages of 505–656 Ma (Hanson, 2003; Goscombe et al., 2005). The youngest detrital zircon grains at 107 Ma and 132 Ma are significantly older than the depositional age of the Mocuio Formation. They may represent minor sediment derivation from Early Cretaceous kimberlites and carbonatites emplaced along the Lucapa fault zone (Giuraud et al., 2010). While not providing a unique fingerprint of sediment provenance, detrital zircon ages from the bonebed sandstone are consistent with derivation from nearby basement outcrops and do not require long distance sediment transport. The detrital zircon data show that the Precambrian basement was exhumed by the Cretaceous and that Bench 19 sedimentary rocks could have been derived from a nearby source area. Thus, mineralogy, physical characteristics of grains, detrital zircon ages and proximity of the granitic shield to the coast at Bentiaba all indicate sediment transport by short intermittent or seasonal rivers draining the shield and flowing directly to the sea. This is consistent with the sedimentation in the arid environment seen today in northern Namibia (Calvert & Price, 1983). However, in northern Namibia, a 70-km band of organic-rich diatom ooze is deposited at depths shallower than 140 m (Calvert & Price, 1983) and along the shelf where terrigenous input from the coastal arid region is insufficient to dilute planktonic and skeletal organic matter. At Bentiaba, there is no evidence of diatom ooze.

The Bench 19 unit was deposited relatively near the shore based on the paleogeography of the Bentiaba coast, as shown by the shoreline observed in the Ombe Formation, the narrow shelf, and the composition and texture of the sediment. On the other hand, it is interpreted to have been deposited below storm wave base (Peters & Loss, 2012) because sedimentary

structures such as hummocky cross-stratification and significant scour surfaces are absent. Furthermore, there is no evidence of postmortem, pre-burial, subaerial weathering on the bones of the marine species (Behrensmeyer, 1978), indicating that the life, death and burial of these animals was completely below the surface of the ocean. While the Bench 19 Bonebed preserves a range of completeness of specimens, none appears to have bloated and floated from gases released during decomposition. The presence of relatively complete carcasses in the bonebed suggests that the volume of gas generated and captured in the carcasses was insufficient to overcome hydrostatic pressure, leaving the carcasses on the bottom. Reisdorf et al. (2012), in their study of ichthyosaur taphonomy and bathymetry, concluded that intact articulated carcasses remaining on the sea bed due to hydrostatic pressure at certain localities were indicative of water depths >50 m because putrifying carcasses sometimes rise from depths of 50 m but do not rise from depths of 100 m or more. Variability in the tendency to rise, especially at shallower depths, is temperature dependent due to the solubility of gases. The water temperature at Bentiaba immediately below Bench 19 as determined from  $\delta^{18}\text{O}$  of *Inoceramus* shells was 18.5°C (Strganac et al., in press). Assuming a maximum shelf depth of 150 m, a reasonable range of depths for the formation the Bench 19 Bonebed is below wave base, between 50 and 150 m.

The amniote fauna of the Bench 19 Bonebed was reviewed by Mateus et al. (2012) and an updated, annotated faunal list is provided in Table 1. Schulp et al. (2013) documented the presence of a large *Prognathodon* sp. and *Carinodens* sp., neither of which is known from the Bench 19 Fauna, but rather from higher stratigraphic levels. Lower in the section, in the Baba

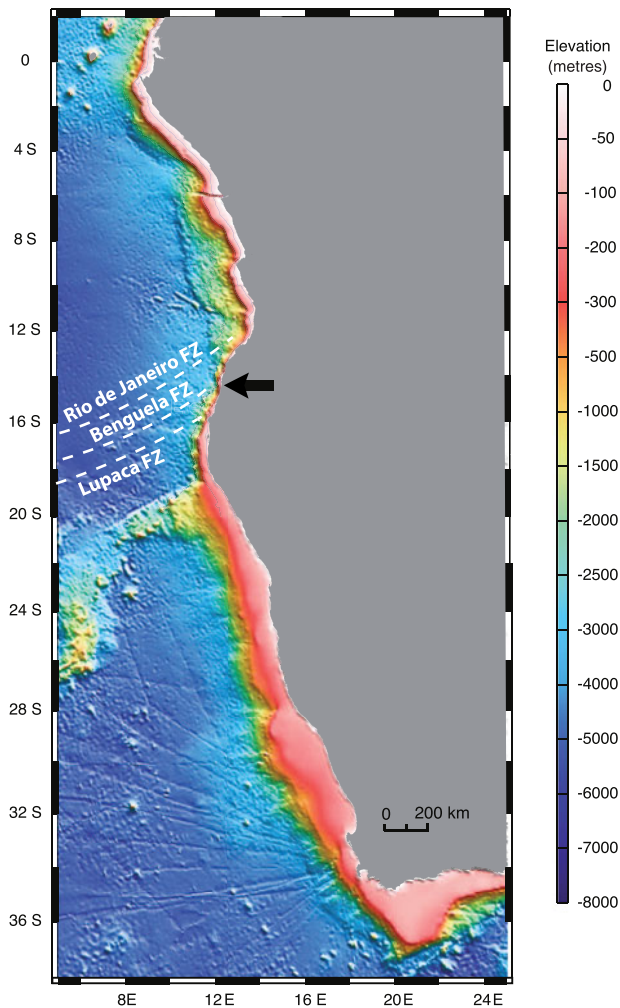


Fig. 7. Bathymetric map of southwest Africa. Arrow points to Bentiaba. Dashed lines indicate fracture zones (FZ), which can be traced to transform faults at the Mid-Atlantic Ridge. South of the Walvis Ridge is Walvis Bay. Note the width of the continental shelf at Bentiaba compared to Walvis Bay. In the early Maastrichtian (Late Cretaceous), Bentiaba lay approximately  $10^\circ$  further south at a latitude analogous to that of modern Walvis Bay.

Formation, below the Bench 19 unit, a small russellosaurine mosasaur (*sensu* Polcyn & Bell, 2005) is found. Russellosaurina is the clade that includes the subfamilies Plioplatecarpinae and Tylosaurinae, representatives of which are found in the Bench 19 Fauna, but the Baba specimen is distinct from those found higher in the section. Thus, the amniote fauna from the Bench 19 Bonebed is taxonomically consistent but distinct taxonomically from levels above and below Bench 19. In addition, above the Bench 19, the bivalve *Inoceramus*, common in the bonebed, has its last appearance in the section, nurse sharks (Ginglymostomatidae) have their first appearance and *Squalicorax* teeth obtain a larger maximum size co-occurring with smaller forms. The taxonomic internal consistency of the Bench 19 Fauna and the short time bin into which it fits, compared to the fauna above and below, suggests accumulation of the Bench 19 Bonebed on an ecological rather than a geological timescale.

The fossiliferous fine-grained sandstone Bench 19 Bonebed in the upper Mocuio Formation preserves an attritional fossil assemblage, as indicated by the stratigraphic distribution of specimens and a faunal list that includes pterosaurs and dinosaurs as rare and isolated elements among an overwhelmingly marine fauna. Attritional accumulations forming bonebeds have an excess of bones relative to sediment input, and hence exhibit some amount of time averaging. There is no evidence of past exhumation and reburial of individual fossils within the Bench 19 Bonebed, consequently the stratigraphic position of fossils within the bonebed is a time-ordered sequence and the fauna must be considered time-averaged in the strictest sense, of a relatively short duration. Temporal limits on the duration of the Bench 19 Bonebed are set by the length of chron C32n.1n, which is the 240 ky bin between 71.4 and 71.64 Ma (Strganac et al., 2014).

The Bench 19 Fauna does not appear to be a catastrophic death assemblage such as reported in marine mammal strandings caused by harmful algal blooms (Brongersma-Sanders, 1948, 1957; Brongersma-Sanders et al., 1980; Pyenson et al., 2014) because at Bentiaba individuals do not align with strand, the bones are not limited to a single plane and there is definitive evidence of active predation or scavenging. Pyenson et al. (2009) studied the formation of the Miocene Shark Tooth Hill Bonebed of California and concluded that this rich accumulation, which is both larger and denser than the Bench 19 Bonebed, was a winnowed, attritional accumulation formed under sediment-starved conditions and terminated when sediment input increased. The time averaged in the Shark Tooth Hill Bonebed is as much as 700 ky. At Bentiaba there is no evidence of significant winnowing and mixing by bottom currents, large specimens are partially articulated and scavenged, and biological interactions related to feeding are clear.

Bench 19 does not fit the model of preservation in a subaqueous gravity flow as presented by Adams (2009) because the shelf setting of Bentiaba is inconsistent with the geological setting and depositional environment reflected in sedimentary textures and structures expected of active margins. However, the Pisco Formation along the coast of western South America in latitudes comparable to the paleolatitude of Bentiaba is also on an active margin, yet preserves a diverse cetacean fauna, including articulated skeletons with baleen. Sediments are both diatomaceous and tuffaceous, and most fossil occurrences appear to be rapidly buried falls (Esperante et al., 2002, 2008; Brand et al., 2004, 2011) or strandings (Pyenson et al., 2014) in embayments. Along passive margins, Calvert Cliffs, Maryland, preserves a rich cetacean fauna, but the accumulation is attritional over millions of years (Vogt & Eshelman, 1987; Gottfried et al., 1994). In Africa, the Cretaceous upwelling area along Morocco is the antitropical equivalent of that which occurred at the same time along the Bentiaba coast and it has produced a rich and varied marine fauna (Bardet et al., 2010; Bardet, 2012). However, upwelling in Morocco

produced phosphatic sediments and specimens are not concentrated as in the Bench 19 Fauna.

In the case of the Bench 19 Bonebed, it is clear that a large number of carcasses accumulated individually soon after death, presenting a food source that attracted large numbers of mobile scavengers, as evidenced by numerous associated shark teeth. Decomposition was truncated by burial at varying stages, but none of the carcasses remained on the seafloor long enough to transition beyond the mobile scavenger phase (*sensu* Smith & Baco, 2003).

**Stable carbon isotopes**

Whole-body  $\delta^{13}\text{C}$  values of consumer species largely reflect the carbon isotope values of primary producers on which they ultimately feed, albeit with an  $\sim 0\text{--}1\%$  enrichment in  $^{13}\text{C}$  per trophic step (Koch, 2007). The  $\delta^{13}\text{C}$  of tooth enamel carbonate, as opposed to whole-body values, is typically  $\sim 9\%$  more positive relative to diet, but differences in the  $\delta^{13}\text{C}$  of tooth enamel carbonate among marine species still largely reflects the  $\delta^{13}\text{C}$  values of primary producers (Koch, 2007). In marine settings the  $\delta^{13}\text{C}$  values of primary producers and particulate organic matter become depleted with increasing distance from shore and

depth, possibly due to a more diverse group of primary producers found in highly productive nearshore environments, including  $^{13}\text{C}$ -enriched kelp beds and benthic macrophytes, relative to offshore where  $^{13}\text{C}$  depleted marine phytoplankton are the dominant primary producers (Clementz & Koch, 2001; Michener & Kaufman, 2007). Clementz & Koch (2001) used these relationships to examine the  $\delta^{13}\text{C}$  values derived from tooth enamel belonging to modern and recent marine mammals. They demonstrated that a variety of niches were used in the California upwelling zone and reflected the trend of depleted  $\delta^{13}\text{C}$  values in primary producers located farther from shore (Fig. 8A).

Robbins et al. (2008) examined stable carbon isotopes from a diverse sample of mosasaur teeth from numerous Upper Cretaceous localities and interpreted the  $\delta^{13}\text{C}$  values as reflecting feeding distance from shore and diving duration, showing that the  $\delta^{13}\text{C}$  values generally correlated with body size. Schulp et al. (2013) examined five mosasaur taxa from the type Maastrichtian section and found a strong correlation between larger body size and lower  $\delta^{13}\text{C}$  values.

The  $\delta^{13}\text{C}$  values derived from tooth enamel (Fig. 6, Table 2) from the Bench 19 Fauna show a general trend of decreasing average  $\delta^{13}\text{C}$  values with increasing body size, the pattern previously documented in mosasaurs (Robbins et al., 2008;

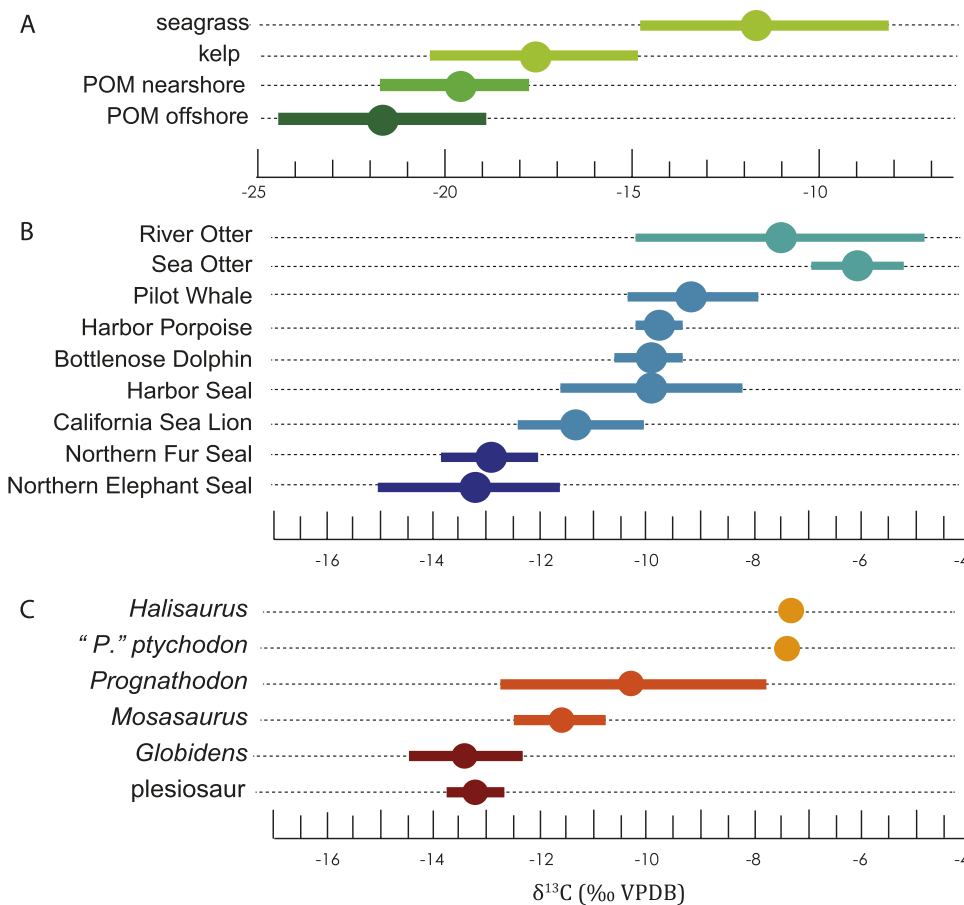


Fig. 8. Comparison of  $\delta^{13}\text{C}$  values of (A) modern primary producers and particulate organic matter (POM), (B) modern marine mammals (modified from Clementz & Koch, 2001), and (C) tooth enamel carbonate of Bench 19 mosasaurs and plesiosaurs.

Schulp et al., 2013). *Halisaurus* and '*P.*' *ptychodon* exhibit enriched  $\delta^{13}\text{C}$  values similar to modern sea otters and reflect a shallow marine feeding habitat at the coastline.  $\delta^{13}\text{C}$  values of *Mosasaurus* and *Prognathodon* are similar in value ( $\sim -12$  to  $-8\text{‰}$ ) to cetaceans and pinnipeds that feed in near-shore California waters (Clementz & Koch, 2001). *Prognathodon* teeth from Bentiaba have a much broader range of  $\delta^{13}\text{C}$  values ( $-14.8$  to  $-5.2\text{‰}$ ) than those reported from the Netherlands ( $-13.6$  to  $-12.3\text{‰}$ ; Schulp et al., 2013). This greater range may be a product of the larger sample size in this study, or it may indicate that Bentiaba mosasaurs used a greater variety of habitats or had broader diets. Average *Globidens*  $\delta^{13}\text{C}$  values are more depleted than expected for their body size, and are statistically indistinguishable from those of plesiosaurs. The  $\delta^{13}\text{C}$  values of plesiosaurs are consistent with foraging far from shore (Cicimurri & Everhart, 2001), but this does not explain the values seen in *Globidens*. The relatively depleted  $\delta^{13}\text{C}$  values in *Globidens* are similar to northern fur seals and elephant seals, whereas the values of the latter species are probably affected by routine dives  $>300$  m in depth (Clementz & Koch, 2001). Thus, *Globidens*  $\delta^{13}\text{C}$  values can be explained by foraging behaviour that involved increased dive time (Biasatti, 2004) required by a diet of mollusks consistent with reported stomach contents (Martin, 2007; Martin & Fox, 2007) and with durophagus tooth morphology.

The  $\delta^{13}\text{C}$  values of Bench 19 mosasaurs indicate that they occupied a variety of niches as do modern marine mammals in the upwelling waters off California. At least six mosasaur taxa are represented in the Bench 19 Fauna, five of which were analysed for  $\delta^{13}\text{C}$  (Table 2).  $\delta^{13}\text{C}$  values of tooth enamel, body size and tooth-form disparity suggest niche differentiation in preferred foraging zones ranging from nearshore to open ocean. Although differentiation of foraging strategies would be expected in a rich upwelling zone, the five Bench 19 mosasaur taxa are associated in a short time horizon and a small area, and are not spatially segregated as the  $\delta^{13}\text{C}$  values predict.

The presence of *Halisaurus* and '*P.*' *ptychodon*, both characterised by relatively small body size and positive  $\delta^{13}\text{C}$  values, is consistent with the near-shore depositional environment of the Bench 19 Bonebed. Likewise, the presence of the durophagous mosasaur *Globidens* can be explained by the abundance of the bivalve *Inoceramus* in the strata in which it is found; the predator-prey relationship between these taxa is established by *Globidens* stomach contents (Martin & Fox, 2007). The stomach contents of *Prognathodon kianda* demonstrate the association of three of the five mosasaur species in the Bench 19 Fauna as a function of predation or scavenging.

*Prognathodon kianda* shows a wide range of  $\delta^{13}\text{C}$  values and it had remains of three mosasaur individuals in its gut area. The biological association of scavenging sharks with a diversity of mosasaurs and plesiosaurs, coupled with the association of three species of mosasaurs within the gut of a fourth, implies that all Bench 19 mosasaurs were contemporary inhabitants of this highly productive shallow, narrow shelf environment.

The association of mosasaur taxa with each other and with the sharks that scavenged their flesh is indicative of the use of this area as a foraging zone by individual taxa either as a relatively permanent home range or as an opportunistic feeding ground.

## Conclusions

The Bench 19 Bonebed at Bentiaba, Angola, formed in a shallow, narrow, highly productive shelf environment characterised by relatively low sedimentation rates compared to bone input. The Bench 19 Bonebed represents a residual accumulation of instantaneous biological interactions that introduced carcasses into the sedimentary system where the animals lived, at the time they died, and in that sense, it is attritional. Although we cannot constrain the amount of time represented to less than 240,000 years, we interpret the Bench 19 Fauna as an accurate representation of the Late Cretaceous marine amniote ecosystem in offshore Angola. The Bench 19 Bonebed contains the richest, temporally constrained and intimately associated assemblage of mosasaurs yet known from the fossil record, and as such it provides an unparalleled window into the ecological relationships of Late Cretaceous marine ecosystems on the southwest African coast of the widening South Atlantic Ocean.

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## References

- Adams, T.L., 2009. Deposition and taphonomy of the Hound Island Late Triassic vertebrate fauna: Fossil preservation within subaqueous gravity flows. *Palaios* 24: 603-615.
- Antunes, M.T. & Cappetta, H., 2002. Sélaciens du Crétacé (Albien-Maastrichtien) d'Angola. *Palaeontographica* 264: 85-146.
- Arambourg, C., 1952. Les vertébrés fossiles des gisements de phosphates (Maroc – Algérie – Tunisie). *Notes et Mémoires du Service Géologique du Maroc* 92: 1-372.
- Araújo, R., Polcyn, M.J., Schulp, A.S., Mateus, O. & Jacobs, L.L., submitted. A new elasmosaurid from the early Maastrichtian of Angola and the implications of girdle morphology on swimming style in plesiosaurs. *Netherlands Journal of Geosciences*.

- Araújo, R., Lindgren, J., Polcyn, M.J., Jacobs, L.L., Schulp, A.S. & Mateus, O.**, submitted. New aristonectine elasmosaurid plesiosaur specimens from the Lower Maastrichtian of Angola and comments on paedomorphism in plesiosaurs. *Netherlands Journal of Geosciences*.
- Bardet, N.**, 2012. Maastrichtian marine reptiles of the Mediterranean Tethys: a palaeobiogeographical approach. *Bulletin de la Société Géologique de France* 183(6): 573-596.
- Bardet, N. & Pereda Superbiola, X.P.**, 2002. Marine reptiles from the Late Cretaceous Phosphates of Jordan: palaeobiogeographical implications. *Geodiversitas* 24(4): 831-839.
- Bardet, N., Pereda Suberbiola, X., Jouve, S., Bourdon, E., Vincent, P., Houssaye, A., Rage, J.-C., Jalil, N.-E., Bouyou, B. & Amaghzaz, M.**, 2010. Reptilian assemblages from the latest Cretaceous–Palaeogene phosphates of Morocco: from Arambourg to present time. *Historical Biology* 22(1–3): 186-199.
- Behrensmeier, A.K.**, 1978. Taphonomic and ecologic information from bone weathering. *Paleobiology* 4: 150-162.
- Biasatti, D.M.**, 2004. Stable carbon isotopic profiles of sea turtle humeri: implications for ecology and physiology. *Palaeogeography, Palaeoclimatology, Palaeoecology* 206(3): 203-216.
- Brand, L.R., Esperante, R., Chadwick, A.V., Porras, O.P. & Alomía, M.** 2004. Fossil whale preservation implies high diatom accumulation rate in the Miocene–Pliocene Pisco Formation of Peru. *Geology* 32: 165-168.
- Brand, L., Urbina, M., Chadwick, A., DeVries, T.J. & Esperante, R.**, 2011. A high resolution stratigraphic framework for the remarkable fossil cetacean assemblage of the Miocene/Pliocene Pisco Formation, Peru. *Journal of South American Earth Sciences* 31: 414-425.
- Brongersma-Sanders, M.**, 1948. The importance of upwelling water to vertebrate paleontology and oil geology: *Verhandelingen der Koninklijke Nederlandsche Akademie van Wetenschappen te Amsterdam. Afdeling Natuurkunde (Amsterdam) Noord-Hollandsche Uitgevers Maatschappij*: 112 pp.
- Brongersma-Sanders, M.**, 1957. Mass mortality in the sea. *In: Hedgepeth, J.W.* (ed.): *Treatise on Marine Ecology and Paleocology*. Geological Society of America Memoire 167: 941-1010.
- Brongersma-Sanders, M., Stephan, K.M., Kwee, T.G. & DeBruin, M.**, 1980. Distribution of minor elements in cores from the southwest Africa shelf with notes on plankton and fish mortality. *Marine Geology* 37: 91-132.
- Calvert, S.E. & Price, N.B.**, 1983. Geochemistry of Namibian shelf sediments. *In: Suess, E. & Thiede, J.* (eds): *Coastal Upwelling, Its Sediment Record, Part A: Responses of the Sedimentary Regime to Present Coastal Upwelling*. Plenum Press (New York): 337-375.
- Cicimurri, D.J. & Everhart, M.J.**, 2001. An elasmosaur with stomach contents and gastroliths from the Pierre Shale (Late Cretaceous) of Kansas. *Transactions of the Kansas Academy of Science* 104(3–4): 129-143.
- Clementz, M.T. & Koch, P.L.**, 2001. Differentiating aquatic mammal habitat and foraging ecology with stable isotopes in tooth enamel. *Oecologia* 129: 461-472.
- Cury, P., Bakun, A., Crawford, R.J.M., Jarre, A., Quinones, R.A., Shannon, L.J. & Verheye, H.M.**, 2000. Small pelagics in upwelling systems: patterns of interaction and structural changes in 'wasp-waist' ecosystems. *ICES Journal of Marine Science* 57: 603-618.
- Diester-Haas, L., Meyers, P.A. & Vidal, L.**, 2002. The late Miocene onset of high productivity in the Benguela Current upwelling system as part of a global pattern. *Marine Geology* 180: 87-103.
- Esperante, R., Brand, L., Chadwick, A. & Poma, O.**, 2002. Taphonomy of fossil whales in the diatomaceous sediments of the Miocene/Pliocene Pisco Formation, Peru. *In: De Renzi, M., Alonzo, M., Belinchon, M., Penalver, E., Montoya, P. & Marquez-Aliaga, A.* (eds): *Current Topics on Taphonomy and Fossilization*. International Conference Taphos 2002, 3rd Meeting on Taphonomy and Fossilization, Valencia, Spain: 337-343.
- Esperante, R., Brand, L., Nick, K.E., Poma, O. & Urbina, M.**, 2008. Exceptional occurrence of fossil baleen in shallow marine sediments of the Neogene Pisco Formation, southern Peru. *Palaeogeography, Palaeoclimatology, Palaeoecology* 257: 344-360.
- Fisher, R.**, 1953. Dispersion of a sphere. *Proceedings of the Royal Society of London* 217: 295-305.
- Gehrels, G.E., Valencia, V. & Pullen, A.**, 2006. Detrital zircon geochronology by Laser-Ablation Multicollector ICPMS at the Arizona LaserChron Center. *In: Loszewski, T. & Huff, W.* (eds): *Geochronology: Emerging Opportunities*. Paleontology Society Short Course: Paleontology Society Papers 11: 10 pp.
- Gehrels, G.E., Valencia, V. & Ruiz, J.**, 2008. Enhanced precision, accuracy, efficiency, and spatial resolution of U-Pb ages by laser ablation–multicollector–inductively coupled plasma–mass spectrometry. *Geochemistry, Geophysics, Geosystems* 9: Q03017.
- Goscombe, B., Gray, D., Armstrong, R., Foster, D.A. & Vogl, J.**, 2005. Event geochronology of the Pan-African Kaoko Belt, Namibia. *Precambrian Research* 140: 103.e1-103.e41.
- Gottfried, M.D., Bohaska, D.J. & Whitmore, F.C. Jr.**, 1994. Miocene cetaceans of the Chesapeake Group. *In: Berta, A. & Deméré, T.* (eds): *Contributions in Marine Mammal Paleontology Honoring Frank C. Whitmore, Jr.* Proceedings of the San Diego Society of Natural History 29: 229-238.
- Guiraud, M., Buta-Neto, A. & Quesne, D.**, 2010. Segmentation and differential post-rift uplift at the Angola margin as recorded by the transform-rifted Benguela and oblique-to-orthogonal-rifted Kwanza basins. *Marine and Petroleum Geology* 27(5): 1040-1068.
- Handoh, I.C., Bigg, G.R., Jones, E.J.W. & Inoue, M.**, 1999. An ocean modelling study of the Cenomanian Atlantic: Equatorial paleo-upwelling, organic-rich sediments and the consequences for a connection between the proto-North and South Atlantic. *Geophysical Research Letters* 26: 223-226.
- Hanson, R.E.**, 2003. Proterozoic geochronology and tectonic evolution of southern Africa. *In: Yoshida, M., Windley, B.E. & Dasgupta, S.* (eds): *Proterozoic East Gondwana: Supercontinent Assembly and Breakup*. Geological Society, London, Special Publications 206: 427-463.
- Husson, D., Galbrun, B., Laskar, J., Hinnov, L.A., Thibault, N., Gardin, S. & Locklair, R.E.**, 2011. Astronomical calibration of the Maastrichtian (late Cretaceous). *Earth and Planetary Science Letters* 305(3): 328-340.
- Jacobs, L.L., Mateus, O., Polcyn, M.J., Schulp, A.S., Antunes, M.T., Morais, M.L. & Da Silva Tavares, T.**, 2006. The occurrence and geological setting of Cretaceous dinosaurs, mosasaurs, plesiosaurs, and turtles from Angola. *Journal of the Paleontological Society of Korea* 22: 91-110.
- Jacobs, L.L., Mateus, O., Polcyn, M.J., Schulp, A.S., Scotese, C.R., Goswami, A., Ferguson, K.M., Robbins, J.A., Vineyard, D.P. & Buta Neto, A.**, 2009. Cretaceous paleogeography, paleoclimatology, and amniote biogeography of the low and mid-latitude South Atlantic Ocean. *Bulletin de la Société Géologique de France* 180(4): 333-341.
- Jacobs, L.L., Strganac, C. & Scotese, C.R.**, 2011. Plate motions, Gondwana dinosaurs, Noah's Arks, Ghost Ships, and Beached Viking Funeral Ships. *Anais da Academia Brasileira de Ciências* 83(1): 3-22.

- Jagt, J.W.M.**, 2005. Stratigraphic ranges of mosasaurs in Belgium and the Netherlands (Late Cretaceous) and cephalopod-based correlations with North America. *Netherlands Journal of Geosciences* 84(3): 283-301.
- Koch, P.L.**, 2007. Chapter 5: Isotopic study of the biology of modern and fossil vertebrates. In: Michener, M. & Lajtha, K. (eds): *Stable isotopes in ecology and environmental science*, 2nd edn. Blackwell Publishing (Malden): 99-154.
- Martin, J.E.**, 2007. A new species of the durophagus mosasaur *Globidens* (Squamata: Mosasauridae) from the Late Cretaceous Pierre Shale Group of central South Dakota, USA. In: Martin, J.E. & Parris, D.C. (eds): *The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas*. Geological Society of America, Special Paper 427: 177-198.
- Martin, J.E. & Fox, J.E.**, 2007. Stomach contents of *Globidens*, a shell-crushing mosasaur (Squamata), from the Late Cretaceous Pierre Shale, Big Bend area of the Missouri River, central South Dakota. In: Martin, J.E. & Parris, D.C. (eds): *The Geology and Paleontology of the Late Cretaceous Marine Deposits of the Dakotas*. Geological Society of America, Special Paper 427: 167-176.
- Mateus, O., Polcyn, M.J., Jacobs, L.L., Araújo, R., Schulp, A.S., Marinheiro, J., Pereira, B. & Vineyard, D.**, 2012. Cretaceous amniotes from Angola: Dinosaurs, pterosaurs, mosasaurs, plesiosaurs, and turtles. *Jornadas Internacionais sobre Paleontología de Dinosaurios y su Entorno*: 75-105.
- Michener, R.H. & Kaufman, L.**, 2007. Chapter 9: Stable isotope ratios as tracers in marine food webs: an update. In: Michener, R. & Lajtha, K. (eds): *Stable isotopes in ecology and environmental science*, 2nd edn. Blackwell Publishing (Malden): 238-282.
- Miller, K.G., Mountain, G.S., Wright, J.D. & Browning, J.V.**, 2011. A 180-million-year record of sea level and ice volume variations from continental margin and deep-sea isotopic records. *Oceanography* 24(2): 40-53. doi: 10.5670/oceanog.2011.26.
- Moulin, M., Aslanian, D., Rabineau, M., Patriat, M. & Matias, L.** 2012. Kinematic keys of the Santos-Namibe basins. In: Mohriak, W.U., Danforth, A., Post, P.J., Brown, D.E., Tari, G.C., Nemcok, M. & Sinha, S.T. (eds): *Conjugate Divergent Margins*. Geological Society (London) Special Publications 369: <http://dx.doi.org/10.1144/SP369.3>.
- Müller, R.D., Sárdias, M., Gaina, C., Steinberger, B. & Heine, C.**, 2008. Long-term sea-level fluctuations driven by ocean basin dynamics. *Science* 319: 1357-1362.
- Peters, S.E. & Loss, D.P.**, 2012. Storm and fair-weather wave base: A relevant distinction? *Geology* 40: 511-514
- Polcyn, M.J. & Bell, G.L.**, 2005. *Russellosaurus coheni* n. gen., n. sp., a 92 million-year-old mosasaur from Texas (USA), and the definition of the parafamily Russellosaurina. *Netherlands Journal of Geosciences* 84(3): 321-333.
- Polcyn, M.J., Jacobs, L.L., Schulp, A.S. & Mateus, O.**, 2010. The North African mosasaur *Globidens phosphaticus* from the Maastrichtian of Angola. *Historical Biology* 22: 175-185.
- Polcyn, M.J., Jacobs, L.L., Araújo, R., Schulp, A.S. & Mateus, O.**, 2014. Physical drivers of mosasaur evolution. *Palaeogeography, Palaeoclimatology, Palaeoecology* 400: 17-27. <http://dx.doi.org/10.1016/j.palaeo.2013.05.018>
- Pyenson, N.D., Irmis, R.B., Lipps, J.H., Barnes, L.G., Mitchell, E.D. Jr. & McLeod, S.A.**, 2009. Origin of a widespread marine bonebed deposited during the middle Miocene Climatic Optimum. *Geology* 37(6): 519-522.
- Pyenson, N.D., Gutstein, C.S., Parham, J.F., Le Roux, J.P., Carreño Chavarría, C., Little, H., Metallo, A., Rossi, V., Valenzuela-Toro, A.M., Velez-Juarbe, J., Santelli, C.M., Rogers, D.R., Cozzuol, M.A. & Suárez, M.E.**, 2014. Repeated mass strandings of Miocene marine mammals from Atacama Region of Chile point to sudden death at sea. *Proceedings of the Royal Society of London B* 281: 20133316.
- Reeves, C.**, 2014. Atlantic Ocean, 2010 December. Earthworks BV. <http://www.reeves.nl/upload/2011SouthAtlantic1.gif>.
- Reisdorf, A.G., Bux, R., Wyler, D., Benecke, M., Klug, C., Maisch, M.W., Fornaro, P. & Wetzel, A.**, 2012. Float, explode or sink: postmortem fate of lung-breathing marine vertebrates. *Palaeobiodiversity and Palaeoenvironments* 92(1): 67-81.
- Robbins, J.A., Ferguson, K.M., Polcyn, M.J. & Jacobs, L.L.**, 2008. Application of stable carbon isotope analysis to mosasaur ecology. Everhart M. (ed.): *Proceedings of the Second Mosasaur Meeting*, Hays, KS, Fort Hays State University: 123-130.
- Rogers, R.R. & Kidwell, S.M.**, 2007. A conceptual framework for the genesis and analysis of vertebrate skeletal concentrations. In: Rogers, R.R., Eberth, D.A., Fiorillo, A.R. (eds): *Bonebeds: Genesis, Analysis, and Paleobiological Significance*. The University of Chicago Press (Chicago): 1-63.
- Schulp, A.S., Polcyn, M.J., Mateus, O., Jacobs, L.L., Morais, M.L. & Da Silva Tavares, T.**, 2006. New mosasaur material from the Maastrichtian of Angola, with notes on the phylogeny, distribution and paleoecology of the genus *Prognathodon*. In: Schulp, A.S. (ed.): *On Maastricht Mosasaurs*. Publicaties van het Natuurhistorisch Genootschap in Limburg 45: 57-67.
- Schulp, A.S., Polcyn, M.J., Mateus, O., Jacobs, L.L. & Morais, M.L.**, 2008. A new species of *Prognathodon* (Squamata, Mosasauridae) from the Maastrichtian of Angola, and the affinities of the mosasaur genus *Liodon*. In: Everhart, M.J. (ed.): *Proceedings of the Second Mosasaur Meeting*, Fort Hays Studies Special Issue 3, Fort Hays State University, Hays, Kansas: 1-12.
- Schulp, A.S., Vonhof, H.B., van der Lubbe, J.H.J.L., Janssen, R. & van Baal, R.R.**, 2013. On diving and diet: resource partitioning in type-Maastrichtian mosasaurs. *Netherlands Journal of Geosciences, Geologie en Mijnbouw* 92(2-3): 165-170.
- Schwimmer, D.R., Stewart, J.D. & Williams, G.D.**, 1997. Scavenging by sharks of the genus *Squalicorax* in the Late Cretaceous of North America. *Palaios* 12: 71-83.
- Scotese, C.R.**, 2008. PALEOMAP project. [www.scotese.com](http://www.scotese.com).
- Sessa, J., Callapez, P.M., Dinis, P.A. & Hendy, A.J.W.**, 2013. Paleoenvironmental and paleobiogeographical implications of a Middle Pleistocene mollusk assemblage from the marine terraces of Baía das Pipas, southwest Angola. *Journal of Paleontology* 87(6): 1016-1040.
- Shannon, L.V. & Nelson, G.** 1996. The Benguela: large scale features and processes and system variability. In: Wefer, G., Berger, W.H., Siedler, G. & Webb, D.J. (eds): *The South Atlantic: Past and Present Circulation*. Springer-Verlag (Heidelberg): 163-210.
- Shimada, K., Tsuihiji, T., Sato, T. & Hasegawa, Y.**, 2010. A remarkable case of a shark-bitten elasmosaurid plesiosaur. *Journal of Vertebrate Paleontology* 30(2): 592-597.
- Smith, C.R. & Baco, A.R.**, 2003. Ecology of whale falls at the deep-sea floor. *Oceanography and Marine Biology* 41: 311-354.
- Strganac, C., Salminen, J., Jacobs, L.L., Polcyn, M.J., Ferguson, K.M., Mateus, O., Schulp, A.S., Morais, M.L., Tavares, T. da S. & Gonçalves, A.O.**, 2014. Carbon isotope stratigraphy, magnetostratigraphy, and  $^{40}\text{Ar}/^{39}\text{Ar}$  age of the Cretaceous South Atlantic coast, Namibe Basin, Angola. *Journal of African Earth Sciences*. <http://dx.doi.org/10.1016/j.jafrearsci.2014.03.003>.
- Strganac, C., Jacobs, L.L., Polcyn, M.J., Ferguson, K.M., Mateus, O., Gonçalves, A.O., Morais, M.L. & Tavares, T. da S.**, in press. Stable oxygen isotope

chemostratigraphy and paleotemperature regime of mosasaurs at Bentiaba, Angola. Netherlands Journal of Geosciences.

**Vogt, P.R. & Eshelman, R., 1987.** Maryland's Cliffs of Calvert: A fossiliferous record mid-Miocene inner shelf and coastal environments. Geological Society of America Field Guide – Northeastern Section 1987: 9-14.