Chapter 4
The Fossil Record of Biodiversity in Angola Through Time: A Paleontological Perspective

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Abstract This chapter provides an overview of the alpha paleobiodiversity of Angola based on the available fossil record that is limited to the sedimentary rocks, ranging in age from Precambrian to the present. The geological period with the highest paleobiodiversity in the Angolan fossil record is the Cretaceous, with more than 80% of the total known fossil taxa, especially marine molluscs, including ammonites as a majority among them. The vertebrates represent about 15% of the known fauna and about one tenth of them are species firstly described based on specimens from Angola.

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Studies of Paleobiodiversity

The study of paleobiodiversity, i.e., the development of biodiversity through geological time, is challenging at multiple levels. In addition to the issues and biases affecting the study of the diversity of modern life, understanding paleobiodiversity faces extra challenges, mostly because of the dependency on the fossil record. Glimpses of entire ecosystems and clades may never reach the paleontologist's eyes if appropriate rocks of that exact time and space were not formed, or if formed, did not preserve fossils, or are eroded away or otherwise inaccessible (see Jackson and Johnson 2001; Crampton et al. 2003).

The study of life's diversity in the past is filtered by the remains that can leave traces and fossilize, remains that actually fossilized, fossils existing today, fossils accessible today, fossils collected (number of fossils accessible to scientists), and species recognised (Fig. 4.1). Moreover, the definition and discrimination of species in the fossil record can be problematic.

Angola has no known fossiliferous rocks from the Paleozoic (541–251 Ma – millions of years ago) nor the Jurassic (199–145 Ma) leaving only windows to life in the territory during the Triassic (251–199 Ma), Cretaceous (145–66 Ma), and Cenozoic (66 Ma -Present) (Fig. 4.2). The chances of finding Paleozoic or Jurassic fossils from Angola are essentially zero. Thus, within the last 550 Ma, the known

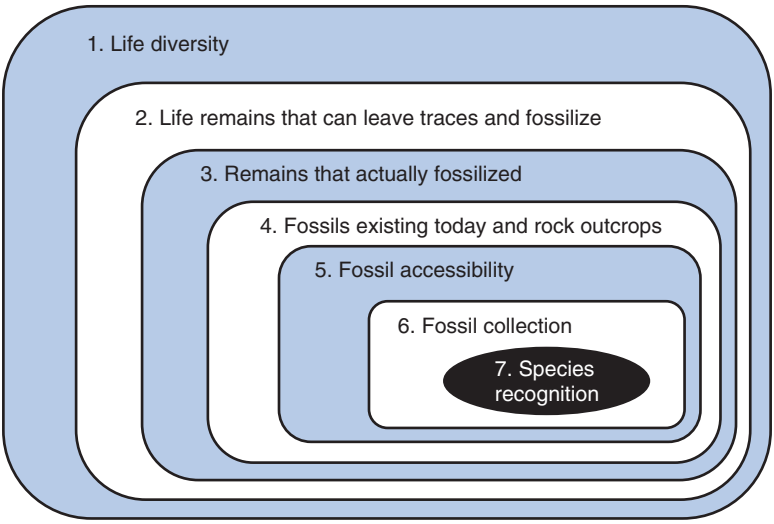

Fig. 4.1 The seven layers of filters of uneven preservation in the fossil record that obscure accurate reconstruction of paleobiodiversity

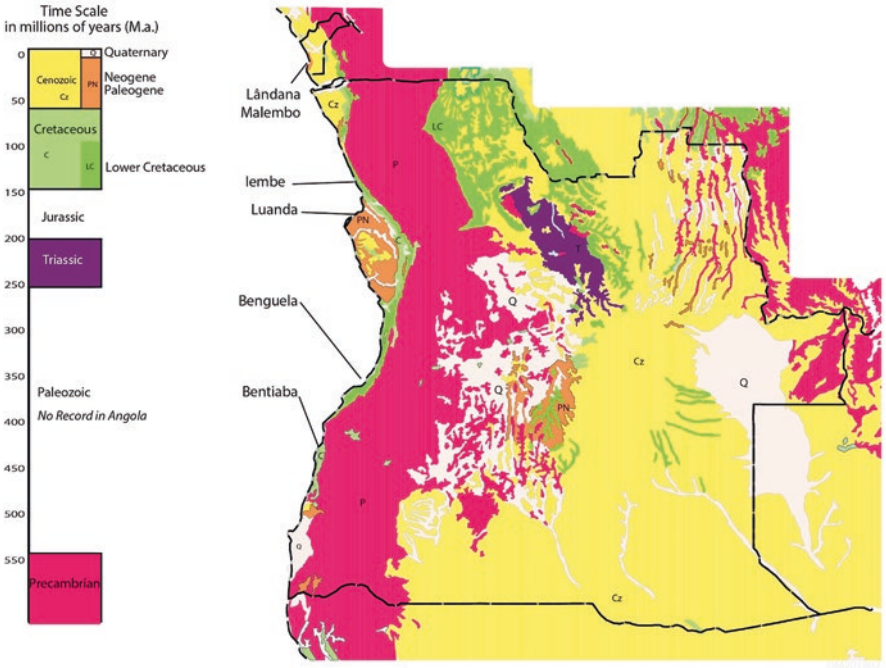

Fig. 4.2 The geological record of Angola, in a stratigraphic log (left) and geological map (right), leaves more than 350 Ma of blank geological record. Map extracted after Africa Geological Map 1:30.000.000 by U.S. Geological Survey, 2002 available at www.uni-koeln.de/sfb389/e/e1

rocks of Angola represent less than 196 million years of geologic time, leaving more than 354 million years (64% of the time) with no known fossil record.

Despite the incompleteness of the fossil record and consequent limitations to the study of the paleobiodiversity, cooperative research and modern databases can, however, improve approximation of the estimated number of species in the fossil record. The PaleoBiology Database (paleobiodb.org) is, by far, the most comprehensive database of fossils, which, together with the scientific literature and our own research, contributed to the Supplementary Material and its summary in Table 4.1 that compiles the list of the fossil taxa in Angola, with updated taxonomy, geological age, locality, and references. The fossil record can be used as a lower limit for the alpha paleobiodiversity for specific times and locations in Angola, although it is likely an underestimate of true paleodiversity in the vast majority of cases. The total of all fossil species is a gross underestimation of paleodiversity for the full extent of the time involved, exacerbated by missing intervals of fossiliferous rocks. However, the pattern through time can inform an understanding of general trends.

Fossil collecting in Angola has been conducted since the nineteenth century with Friederich Welwitsch, José de Anchieta (1885), Freire de Andrade, Augusto Eduardo Neuparth and others (Brandão 2008, 2010; Silva and Geirinhas 2010; Callapez et al. 2011; Masse and Laurent 2016). Numerous paleontologists have contributed to the

Table 4.1 Summary of the known fossil record of Angola

		Period							
COUNT (Genus/sp, Family Indet)		Triassic	Cretaceous	Paleogene	Neogene	Quaternary	Triassic	Grand Total	
Bacteria	Cyanobacteria		1					1	0%
Bacterial total			1					1	0 %
Plantae	Chlorophyta		1					1	0%
	Cycadophyta		1					1	0%
	Ginkgophyta		1					1	0%
	Pinophyta	1	1				1	2	0%
	Pteridosperma-tophyta	4					4	4	0%
	Rhodophyceae		2					2	0%
Plantae total		5	6				5	9	1%
Protista and Invertebrates	Foraminifera		207					207	16%
	Anthozoa		1	1	2	2		6	0%
	Brachiopoda		1					1	0%
	Mollusca		677	27	22	72		798	61%
	Echinodermata		61	1	4	1		67	5%
	Arthropoda	13	3	1	1	2	13	20	2%
Protista and invertebrates total		13	950	30	29	77	13	1102	84%
Vertebrata	Chondrichthyes	2	63	1	18		2	84	6%
	Actinopterygii	6	10		5		6	21	2%
	Sarcopterygii	3					3	3	0%
	Reptilia		21	5				26	2%
	Mammalia			12	1	54		67	5%
Vertebrata total		11	94	18	24	54	11	201	15%
Grand Total		**29**	**1052**	**48**	**53**	**131**	**29**	**1313**	**100%**
		2%	80%	4%	4%	10%	2%	100%	

understanding the paleobiodiversity of Angola, since the first explorations and studies: Fernando Mouta, Paul Choffat, Carlos Teixeira, Carlos Freire de Andrade, Edgard Casier, A Jamotte, M Leriche, Heitor de Carvalho, E Dartevelle, Miguel Telles Antunes, Alexandre Borges, Philippe Brebion, Gaspar Soares de Carvalho, Louis Dollo, Henri Douvillé, Otto Haas, Manuel Mascarenhas Neto, Arménio Tavares da Rocha, Gumerzindo Henriques da Silva, LF Spath, António Ferreira Soares, Maurice Collignon, among many others (see bibliography compiled by Nunes 1991). In vertebrate paleontology the work of Miguel Telles Antunes and co-authors is noteworthy. Today, various researchers work on the paleontology of Angola, among them is the team of the Projecto PaleoAngola (paleolabs.org/paleoangola), with regular yearly scientific expeditions since 2005 (Jacobs et al. 2006, 2016).

A Brief Geological History and Context of Angola

The most significant geological event governing the paleogeography of Angola is the opening of the South Atlantic Ocean, in which Africa and South America rifted apart beginning in the Early Cretaceous Epoch about 134 million years ago and the subsequent drifting apart of these continents as the South Atlantic grew (Guiraud and Maurin 1991; Buta-Neto et al. 2006; Quirk et al. 2013; Pérez-Díaz and Eagles 2017). After about 120 million years ago, marine deposition along the coast began to preserve fossils. Africa's place in Gondwana prior to this time resulted in the lack of a marine record for the entire Paleozoic Era and the consequent lack of a fossil record for that time.

As the South Atlantic opened it was colonised by species moving in from the southern ocean and, as a connection between the North Atlantic and South Atlantic oceans developed, from the north. Sea turtles (*Angolachelys mbaxi*) and mosasaurs (*Angolasaurus bocagei* and *Tylosaurus iembeensis*), with relatives to the north, first occur at about 88 million years ago. Along with them were plesiosaurs, probably with southern affinities. Washed into the sea and found with marine creatures, is the sauropod dinosaur *Angolatitan adamastor*, which is probably a remnant of a more broadly distributed Gondwanan dinosaur assemblage. At that time, coastal Angola lay approximately 10–12 degrees further south than today.

Geologic uplift along the coast resulted in the erosion of rock and loss of the fossil record from effected strata. Permian and Jurassic uplift eliminated those intervals from the terrestrial fossil record. Early and Late Cretaceous uplift also occurred, prior to burial of the remaining Cretaceous with up to 1.5–2 km of sediments, since removed by erosion accompanying mid-Cenozoic uplift beginning around 30 Ma and 20 Ma (Green and Machado 2015). Uplift from as young as 45,000 years ago also has been recorded along the Angolan coast (Walker et al. 2016), resulting in a large diversity of fossiliferous raised-beach deposits, frequently associated with pre-historic shell-middens with Paleolithic industries.

The Precambrian – The First Fossils

Precambrian Era (geologic time since the formation of Earth and prior to 541 Ma) rocks worldwide are mostly devoid of fossils as life was unicellular for most time and only macroscopic in the last stages. The shale-limestone series of the Bembe System in Angola includes dolomitic limestones, mostly devoid of fossils, but containing levels with concentrations of coalescent stromatolites (structures due to cyanophilic activity) attributable to the genera *Collenia* and *Conophyton* in Mavoio, Alto Zambeze, and Humpata (Vasconcelos 1951; Antunes 1970; Duarte et al. 2014).

In Angola, no fossils are known from the Paleozoic (Cambrian through Permian periods), which represents a time gap of more than 290 million years (Fig. 4.2).

The Triassic – Inner Basins

The Triassic is a geological period stretching from about 250 to 200 Ma. The beginning and end of this interval are both marked by mass extinction events, the older Permian-Triassic extinction event, concomitant with the Siberian Magmatic event, marking the initiation of the Triassic Period. The vast supercontinent Pangea existed until the Triassic, after which it gradually began to break-up apart, separating the two masses of land, Laurasia to the north and Gondwana to the south. The global climate during the Triassic Period was warm and dry, with deserts covering much of the interior of Pangea. The end of the Triassic was marked by another major mass extinction related with the Central Atlantic Magmatic Province and the early opening of the North Atlantic. Therapsids (a large group containing mammals and their extinct relatives) and archosaurs (dinosaurs, birds, crocodiles and their relatives) were the major terrestrial vertebrates during this time. The dinosaurs first appeared in the Triassic. The first true mammals, which are derived therapsids, evolved during this period, as well as the first flying vertebrates, the pterosaurs.

Triassic outcrops of Angola are restricted to the Baixa de Cassange (Cassange Depression) in Malanje and Lunda-Norte in rocks referred to the Karoo Supergroup geological unit.

Plants and Invertebrates

The Triassic paleoflora of Angola includes the extinct genera *Glossopteris*, *Sphenopteris*, and *Noeggerathiopsis* (Teixeira 1948a, 1961). A few fossils indicate a freshwater environment and a Triassic age. These include the coleopteran Coptoclavidae insect *Coptoclavia africana* and 12 conchostracan crustaceans: *Estheriella moutai* Leriche 1932, *E. cassambensis* Teixeira 1958, *Estheria anchietai* Teixeira 1947, *E. (Echinestheria) marimbensis* Marliére 1950, *E. (Euestheria) mangaliensis* Jones 1862, *Palaeolimnadiopsis reali* Teixeira 1958, *Palaeolimnadia*

(Palaeolimnadia) wianamattensis (Mitchell), *P. (Grandilimnadia) oesterleni* Tasch 1987, *P. (G.) africania* Tasch 1987, *Gabonestheria gabonensis* (Marliére 1950), *Cornia angolata* Tasch 1987, and *Estheriina (Nudusia*) cf. *rewanensis* Tasch 1979.

Vertebrates

The only Triassic vertebrates known from Angola are fishes, including the Elasmobranchii *Lissodus cassangensis,* the paleoniscoids *Perleidus lutoensis* Teixeira 1947, Palaeonisciformes canobiid *Marquesia moutai*, Halecostomi *Angolaichthys lerichei* Teixeira, the ray-finned *Teffichthys lehmani* and *T. lutoensis,* and the Sarcopterygii lungfish *Microceratodus angolensis*.

This faunal assemblage indicates a freshwater environment with insects and a nearly exclusively endemic fauna. Based on the fishes, a Lower Triassic age (252–247 Ma) is indicated for Lunda and Baixa de Cassange rocks (Murray 2000; Antunes et al. 1990). No tetrapods have been collected so far.

The Early Cretaceous – The Opening of South Atlantic

Most of the fossils and outcrops of Cretaceous age in Angola are in Mesozoic-Cenozoic basins of coastal Angola: the Cabinda, Zaire, Cuanza, Benguela, and Namibe sedimentary basins (Antunes 1964; Séranne and Anka 2005; Guiraud et al. 2010), bordered by basement rocks. Almost all formations are mostly marine except for the ichnofauna from the Catoca mine (Marzola et al. 2014; Mateus et al. 2017), in Lunda-Sul. The oldest fossiliferous Cretaceous formations seen in outcrop seem to be Barremian to Aptian lacustrine deposits that contain unidentified gastropods (Ceraldi and Green 2016).

Plants, Protists and Invertebrates

Cretaceous plant remains in Angola seem to be rare (see Supplementary Material), but several examples of unstudied field contexts with transitional facies, namely above the Cuvo units, might come to reveal new fossil sites. The same situation is likely for palynomorphs and dinoflagellates of Early Cretaceous and more recent ages. Plants are known from pollen taxa such as *Classopolis* sp. and *Eucommiidites* sp. *Pachypteris montenegroi* Teixeira 1948 is a Ginkgophyta Umkomasiaceae from Early Albian lagoonal sediments of the Cuanza Basin (Teixeira 1948b; Antunes 1964; Neto 1970; Nunes 1991) and first found in Angola. One species of Chlorophyta, one Cycadophyta, one Rhodophyceae, one Ginkgophyta, and two Pinophyta have been reported from Cabinda, Benguela and Cuanza Basin (Antunes 1964; Neto 1970; Nunes 1991; Araújo and Guimarães 1992; Tavares 2006).

More than 200 foraminifera taxa were identified in the Cretaceous of Angola, and many indicate an Albian age, such as *Globotruncana ventricosa* (Rocha 1984; Antunes and Cappetta 2002; Antunes 1964; Jacobs et al. 2006).

Crustaceans are known from the Decapoda *Parapirimela angolensis* Van Straelen 1937 from the Albian of Iela beach, Benguela Basin (Ferreira 1957; Van Straelen 1937; Antunes 1964) and the ostracods *Chloridella angolia* and *Petrobrasia tenuistriata longinsuela* from Quiçama, Cuanza Basin, (Berry 1939; Antunes 1964) and Cabinda (Araújo and Guimarães 1992), respectively.

The Early Cretaceous of Angola yielded fossils of seven species of Scleractinean corals, one of brachiopod and eight crustaceans.

Of the more than known 600 species of molluscs from the Cretaceous of Angola, the vast majority are ammonites, many are unique to Angola and received related specific epithets such as the *Anisoceras teixeirai, Durnovarites autunesi* Collignon 1978*, Durnovarites netoi, Elobiceras lobitoense* Spath 1922*, Hamitoides angolanus* (Tavares 2006), followed by bivalves such as *Neithea angoliensis* Newton 1917, and gastropods such as "*Cerithium" monteroi* Choffat. By far, the ammonites are the most relevant portion of the Cretaceous biodiversity of Angola (Tavares et al. 2007; Haas 1942, 1943) and also age-indicators for geologists and paleontologists. Haas (1942) described and reported many ammonites from the Albian, some as new species including *Hysteroceras falcicostatum* Haas 1942 and *H. intermedium* Haas 1942. See the Supplementary Material for the complete list.

Echinoderms, mostly echinoids, are remarkably common in the Early Cretaceous of Angola, with about 50 taxa known, but that number depends on the validity and synonymisation of the taxa addressed (see the Supplementary Material for the complete list). A few echinoderms received names after Angolan toponyms and researchers such as the *Douvillaster benguellensis* Loriol 1888 and *D. carvalhoi* Loriol 1888 and *Epiaster catumbelensis* Loriol 1888, and *Holaster domboensis* Loriol 1888 from the Lower Cretaceous of Dombe Grande, Catumbela and Praia da Hanha (Loriol 1888; Ferré and Granier 2001; Tavares 2006; Tavares et al. 2007).

Vertebrates

In the Catoca Diamond Mine, in Lunda-Sul Province, mammaliamorph, crocodylomorph, and sauropod tracks were discovered in Early Cretaceous crater lake sediments. One sauropod track has skin impressions preserved. These are the only fossil vertebrate tracks known in Angola. The most surprising feature is the unexpectedly large size of the mammaliamorph footprints considering the age (Mateus et al. 2017). The Catoca Diamond Mine has an eruption age of around 118 Ma (Aptian; Robles-Cruz et al. 2012). A fragment of a caudal vertebra of a sauropod dinosaur was recovered from Tzimbio, in northern Namibe, from strata that are likely Albian in age.

The Late Cretaceous – Marine Reptiles Flourish

The Late Cretaceous is the time of the Cretaceous Period between 100.5 Ma and 66 million years ago. It is subdivided into the Cenomanian, Turonian, Coniacian, Santonian, Campanian and Maastrichtian ages, from the oldest to the most recent. The climate was warmer than present, although with a cooling trend throughout the period. In the oceans, where the sea-level was much higher than today, mosasaurs (a group of marine lizards) suddenly appeared and underwent a spectacular evolutionary radiation (Polcyn et al. 2014). Modern grade sharks also appeared and plesiosaurs diversified. These predators fed on the numerous teleost fishes, which in turn evolved into new advanced and modern forms (Neoteleostei). Ichthyosaurs and pliosaurs (a group of short-necked plesiosaurs), on the other hand, became extinct during the Cenomanian-Turonian anoxic event (Schlanger et al. 1987) and are not known from Angola. The end of Cretaceous is marked by the mass extinction of some three-quarters of plant and animal species on Earth, known as the Cretaceous-Paleogene (K/Pg) event (Archibald et al. 2010).

Protists and Invertebrates

The Late Cretaceous Foraminifera of Angola were studied by various researchers including Ferreira and Rocha (1957), Lapão and Simões (1972), Rocha (1984) and Blake et al. (1996) who list more than 180 taxa. Foraminifera are known from 15 taxa of Granuloreticulosea, such as the Gavelinellidae *Anomalia berthelini* from the Aptian to Cenomanian of Cabinda, Cuanza and Benguela Basins (Araújo and Guimarães 1992; Rocha 1984).

Molluscs of the Late Cretaceous count more than 240 known taxa, mostly ammonites (see Supplementary Material for the full list). Some were named after Angolan toponyms or after paleontologists that worked in Angola (Borges 1946; Carvalho 1961; Haas 1943; Howarth 1965; Cooper 1972, 1982; Cooper and Kennedy 1979): *Acera choffati* Rennie 1945, *Axonoceras angolanum* Haas 1943, *Didymoceras* cf. *angolaense* Haughton 1924 (Howarth 1965), *Eutrephoceras egitoense* Miller and Carpenter 1956, *Kitchinites angolaensis* Howarth 1965, *Libycoceras dandense* Howarth 1965, *Lucina egitoensis* Rennie 1945, *L. angolensis* Rennie 1929, *Mammites mocamedensis* Howarth 1966, *Nostoceras mariatheresianum* Haas 1943, *Oiophyllites angolaensis* Spath 1953, *Prionocyclus carvalhoi* Howarth 1966, *Protacanthoceras angolaense* Spath 1931, *Prohysteroceras hanhaense* (Haas 1942), *P. angolaense* (Boule et al. 1907), *Protocardia moutai* Rennie 1945, *Pseudocalycoceras angolaense* (Spath 1931), *Pseudomelania salenasensis* Rennie, *Pterotrigonia borgesi* Rennie 1945, *Mortoniceras (Angolaites) stolikzcai* (Spath 1922), *Mortoniceras (?) rochai* Collignon 1978, *M. (Deiradoceras) reali* Collignon 1978, *Collignoniceras (Selwynoceras) reali* Collignon 1978, and *Solenoceras*

bembense Haas 1943. The ammonites are found in almost all Upper Cretaceous sections, including those of the Quissonde Formation from the beaches of Quimbala, Chamure, Cabeça da Baleia, Egito in Benguela Basin, Teba, Bembe in Cuanza Basin, Bentiaba and Salinas in Namibe, and Iembe in Bengo Province (Segundo et al. 2014).

Rennie (1945) describes ten species of gastropods and bivalves from Cabeça da Baleia, Egito-Praia: *Trigonia (Scabrotrigonia) borgesi, Lucina egitoensis, Protocardia moutai, Pseudomelania egitoensis, Confusiscala angolensis, Acirsa (Plesioacirsa?) egitoensis, Dicroloma (Perissoptera) o'donnelli, Paleopsephaea o'donnelli, Acera choffati,* and *Ringicula moutai* (Lapão and Pereira 1971).

More than ten echinoderm taxa are known from the Late Cretaceous of Angola, mostly echinoids, some received Angola-related names, such as the Toxasteridae *Epiaster angolensis* Haughton 1924, collected 150 m below the Itombe Formation at Zenza do Itombe, and *E. carvalhoi* Dartevelle 1953 (Haughton 1924; Kier and Lawson 1978; Néraudeau and Mathey 2000), *Leiostomaster angolanus* Greyling and Cooper 1995, Palaeostomatidae and *Tholaster carvalhoi* Greyling and Cooper 1995, and Holasteridae from the Middle Campanian of Egito Praia, near Quimbala.

Vertebrates

In Angola, a peak of vertebrate paleobiodiversity is observed in the Late Cretaceous, with more than 100 taxa recognised (Antunes 1964; Antunes and Cappetta 2002; Jacobs et al. 2006, 2009, 2016). This peak is in comparison with other time intervals and is likely an artifact of the inadequacies of the fossil record rather than a statement of biological reality. Most known Late Cretaceous sedimentary rocks from Angola are marine, thus the fossil assemblage also reflects this ecosystem. Non-marine organisms are occasionally drifted into a marine setting, including the sauropod dinosaur *Angolatitan adamastor* Mateus et al. (2011) from Iembe, in Bengo Province, originally considered Turonian in age but following the discovery of the ammonite *Protexanites* sp. at Iembe, it is now considered Coniacian. Pterosaurs are known from the Maastrichtian marine sediments of Bentiaba, in Namibe Province. *Angolatitan adamastor* is the first dinosaur found in Angola. Its generic name means 'Titan of Angola' and the specific name refers to Adamastor made famous by Luís de Camões in the *Lusíadas*. It was 13 m long and lived in an arid environment (Mateus et al. 2011). A number of bones of large flying reptiles, pterosaurs, collected in the marine sediments of the Maastrichtian of Bentiaba are the only know pterosaur remains in sub-saharian Africa for this stage.

The fossil record of chondrichthyans shows a peak in Late Cretaceous deposits with 64 species known, including taxa only known in Angola or with Angolan toponyms such as *Angolabatis angolensis, A. benguelaensis, Chlamydoselachus gracilis, Cretascymnus quimbalaensis*, and *Echinorhinus lapaoi* named by Antunes and Cappetta (2002). The diversity of chondrichthyans includes representatives of most of the Cretaceous lineages: Hexanchiformes, Squaliformes, Rajiformes, Orectolobiformes, Odontaspidida, Lamniformes, Carcharhiniformes, and Squaliformes (Antunes and Cappetta 2002).

In contrast to the diversity of chondrichthyans, the Late Cretaceous bony ray-finned fish from Angola are represented by ten taxa only, most likely due to the difficulty of identification of isolated remains, in comparison with the abundance of shark and ray teeth. The teleost genus *Enchodus* is known from various species (*Enchodus bursauxi, E. crenulatus, E. elegans, E. faujasi* and *E. libycus*). Other teleosts include *Eodiaphyodus lerichei, Pseudoegertonia bebianoi*, and *Stephanodus libycus* from the Late Campanian and Maastrichtian in Benguela and Namibe provinces (Antunes and Cappetta 2002) (Fig. 4.3).

Two Upper Cretaceous fossil localities from Angola are remarkably rich in large reptiles: Iembe in Bengo Province (Fig. 4.4) of Coniacian age (~88 Ma), and Bentiaba in Namibe (Maastrichtian). The Coniacian provided the bizarre durophagous cryptodiran turtle *Angolachelys mbaxi* Mateus et al. (2009) that justified the erection of its own clade Angolachelonia, and the sauropod dinosaur *Angolatitan adamastor*. Indeterminate plesiosaur remains have also been recovered from this region. Mosasaurs are represented by *Angolasaurus bocagei* (Fig. 4.3), *Tylosaurus iembeensis* Antunes (1964) and an indeterminate halisaurine.

The richest vertebrate locality in Angola is near Bentiaba in Namibe province (Strganac et al. 2014, 2015a, b). The reptile list includes the cheloniid turtles *Euclastes* sp., *Protostega* sp. and *Toxochelys* sp. Terrestrial reptiles include isolated remains that allow undetermined large pterosaurs, an undetermined sauropod based on a metapodial, and a possible hadrosaur based on an isolated phalanx (Mateus et al. 2012). The squamate mosasaurs are, by far, the most abundant and speciose group of tetrapods, and include *Globidens phosphaticus*, *Prognathodon kianda*, *Halisaurus* sp., *Mosasaurus* sp., *Phosphorosaurus* sp., and '*Platecarpus*' *ptychodon* (Polcyn et al. 2007, 2010, 2014; Schulp et al. 2006, 2008, 2013). The plesiosaur

Fig. 4.3 The mosasaur *Angolasaurus bocagei* skull and anterior postcrania (Museum of Geology, Universidade Agostinho Neto). (Photo: Hillsman Jackson, Southern Methodist University)

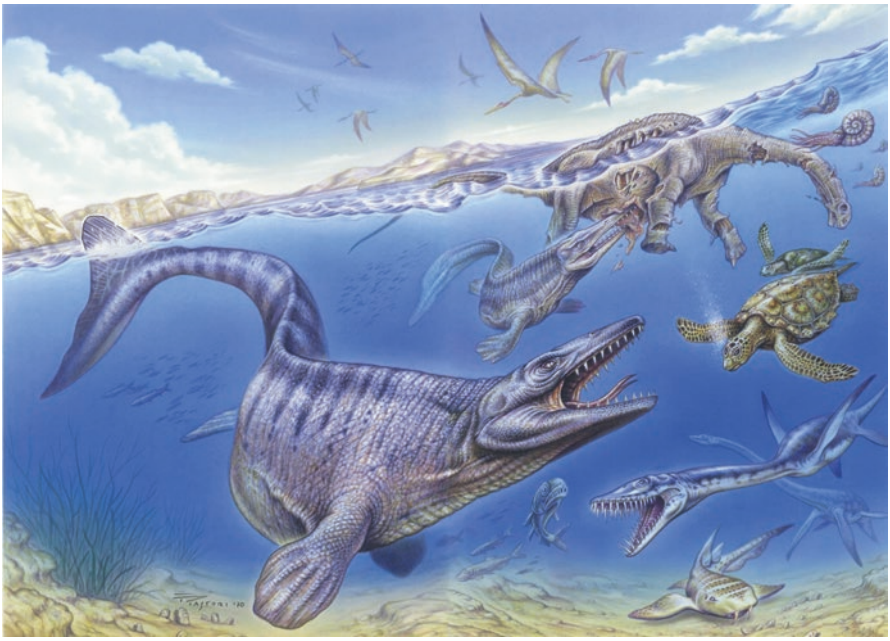

Fig. 4.4 Reconstruction of the fauna during the Late Cretaceous, based on the Coniacian fauna of Iembe. Illustration using acrylic painting with brush by Fabio Pastori

Elasmosauridae are also abundant at Bentiaba where two taxa are known: Aristonectinae indet. and *Cardiocorax mukulu* (Araújo et al. 2015a, b).

The Paleogene – Mammals Take Over

The Paleogene Period begins at the end of the Cretaceous (66 Ma) and lasted until the Neogene Period 23.03 Ma. The Paleogene is the interval of Earth's history in which mammals diversified and flourished after the K/Pg mass extinction, when most large reptiles, and belemnites and ammonites went extinct. There is a dearth of terrestrial vertebrates, especially mammals, from the Paleogene of Angola. During the global Paleocene-Eocene Thermal Maximum (PETM), 55.8 million years ago, there occurred a sudden change of the climate that marked the end of the Paleocene and the beginning of the Eocene, one of the most significant periods of climate change in the Cenozoic era (Zachos et al. 2005). The best known Paleogene geologic section in Angola is that of Lândana in Cabinda Province. A recent study of the Paleocene and Eocene biota and strata of Lândana indicated that the PETM is missing from that section, either because the event was too short to be recorded at the sampling interval used or that it falls within one of the several stratigraphic gaps documented in the Lândana section (Solé et al. 2018).

Protista and Invertebrates

Among the protists, foraminifera stand out as the most important and well-known taxonomic group in the Angolan marine series of Paleogene age, due to their importance for biostratigraphic correlations in offshore oil drilling and their equivalence with landward outcrops. Important works include those of Rocha (1973) and Kender et al. (2008), which include many Eocene and Oligocene characteristic taxa such as: *Cyclammina* cf. *compressa*, *Nonion centrosulcatum*, *Cassidulina subglobosa*, *Globigerina ampliapertura*, *Bolivina* cf. *pygmaea*, *Bulimina alsatica*, *B. kacksonensis* and *B. nkomi*.

In the Paleogene of Angola, molluscs remain the most speciose clade of invertebrates, comprising at least three nautiloids, 14 bivalves, and 21 gastropods (see Supplementary Material). The bivalves are mainly known from the Eocene (Lutetian) Quimbriz Formation along the Luculo River (Tavares et al. 2007) and include *Leda africae, Noetia veatchi, 'Cardium' luculensis, 'C.' sandigii, Crassatella schoonoverae, Lucina* cf. *landanensis, Macrocallista palmerae, Metis olssoni, Pitar quimbrizensis, P. quipayensis, Protonoetia nigeriensis, Raetomya schweinfurthi, Venericardia angolae,* and *V. heroyi* (Tavares et al. 2007). The three nautiloids are *Cimomia landanensis, Deltoidonautilus caheni, Hercoglossa diderrichi* from the Danian of Cabinda Basin, Landana (Soares 1965), and the gastropods are also mainly known from the Eocene, Lutetian of Luculo River (Tavares et al. 2007): *Ficula roscheni, Fulguroficus harrisi, Pleurotoma angolae, P. rebeccae, Polinices (Neverita) angolae, Ringicula hughesae, Sinum dusenberryi, Surcula* cf. *ingens,* and *Turricula (Knefastia) angolensis.*

Other groups such as Anthozoa, Arthropoda and Echinodermata, exist but are low in numbers (Dartevelle 1953).

Vertebrates

Paleogene marine sediments have been studied mostly in the Benguela Basin and in Cabinda. Adnet et al. (2009) recognized a new species of Eocene lamniform shark, *Xiphodolamia serrata*, from Benguela. Sharks and bony fishes from Cabinda have been listed by Solé et al. (2018), and Taverne (2016) has provided new information about osteoglossid fishes from Lândana. The tetrapods from the Paleogene of Angola are mostly from the fossil sites of Lândana (Solé et al. 2018) and Malembo in Cabinda. The section begins with Lower Paleocene strata at Lândana. Reptiles comprise the dyrosaurid crocodylomorph *Congosaurus bequaerti,* and indeterminate crocodilians (Jouve and Schwarz 2004; Schwarz 2003; Schwarz et al. 2006), the turtles *Taphrosphys congolensis*, a toxochelyid, and *Cabindachelys landanensis* (Myers et al. 2017). Along the Chiloango River, Cabinda, a vertebra of the snake *Palaeophis* was reported by Antunes (1964).

The youngest portion of the Cabinda section is at Malembo Point, south of Lândana, which was originally considered Miocene. The Malembo mammal fauna is comparable to the Early Oligocene fauna of the Fayum, Egypt because of the

presence of the embrithopod *Arsinoitherium*, hyracoids such as *Geniohyus* aff. *Mirus* and *Bunohyrax* aff. *Fajumensis*, the proboscidean cf. *Phiomia* or *Hemimastodon,* the sirenian *Halitherium,* and a reported anthropoid canine (Hooijer 1963; Pickford 1986; Jacobs et al. 2016). Recent findings by *Projecto PaleoAngola* in Malembo include a ptolemaiidan molar more similar to *Kelba* from the Miocene of Songhor, Kenya (19.5 Ma) than to Fayum *Ptolemaia*, and an isolated premolar tooth of a large primate comparable in size to that of a female gorilla, likely an undescribed taxon (Jacobs et al. 2016), and not representing any of the numerous Fayum primate taxa. In addition, *Arsinoitherium* is now known from the latest Oligocene of Kenya. The presence of a Kelba-like ptolemaiadan, a unique primate, and Arsinoitherium may indicate a latest Oligocene or even earliest Miocene age for Malembo Point. The assemblage certainly has differences from the Fatum fauna and may indicate the presence of a lowland West Africa faunal province near the Paleogene-Neogene boundary in age and distinct from other regions such as the East African Rift Valley or the Fayum.

The Neogene – The Founding of Modern Biodiversity

The Neogene began about 23 Ma and extends until the Pleistocene (1.8 Ma). It is divided into Miocene (23 Ma to 5.3 Ma) and Pliocene (5.3 Ma to 2.6 Ma), from the oldest to the more recent. This period saw the expansion of the large mammals, and the appearance of hominids. In the Miocene the climate warms again and grasslands and savannas spread. In the Pliocene, the Earth had become similar to the one we know today.

Protists and Invertebrates

The Neogene foraminifera of the Angolan coastal basins, including those from the Miocene Quifandongo series of the Cuanza Basin, are known from a diversity of planktonic and benthic taxa widely used in oil industry offshore correlations or as palaeoenvironmental indicators. Rocha (1957), Graham et al. (1965), Mcmillan and Fourie (1999) and Kender et al. (2009), among others describe the essentials of these West African foraminiferal assemblages, which include planktonic taxa such as *Globigerina praebulloides*, *Globigerinella obesa*, *Globigerinoides bisphericus*, *G. immaturus*, *G. trilobus*, *Globorotalia peripheroronda* and *Orbulina bilobata*.

Invertebrates are surprisingly poorly known and comprise, at least, the nautiloid mollusc *Aturia luculoensis,* the decapod crustacean *Callianassa floridana* from the Miocene Burdigalian of Cabinda Basin (Newton 1917), several taxa of Miocene echinoid echinoderms such as *Clypeaster borgesi, Echinolampas antunesi, Rotula deciesdigitata, Rotuloidea vieirai, Amphiope neuparthi*, and *Plagiobrissus* sp. (Loriol 1905; Dartevelle 1953; Gonçalves 1971; Kroh 2010; Silva and Pereira 2014; Pereira and Stara 2018), and two species of anthozoan corals *Flabellum extensum*

and *Stylophora raristella* (Chevalier 1970). Nevertheless, bivalve and gastropod molluscs are undoubtedly the most diverse and abundant invertebrate taxa of the marine Neogene of Luanda, Benguela and Namibe, with several rich fossil sites, some of them presently in course of study. The molluscan faunas of these coastal basin areas, including new species such as *Pereiraea africana*, *Clavatula loandensis* or *Chlamys silvai* Antunes (1964), were the focus of Douvillé (1933), Keller (1934), Dartevelle (1952, 1953), Dartevelle and Roger (1954), Soares (1961, 1962), Silva (1962), Silva and Soares (1962), Antunes (1964), and more recently Antunes (1984), Lozouet and Gourgues (1995), among others.

Vertebrates

Mammals are known from Benguela and the Cuanza provinces where Projecto PaleoAngola collected skulls of fossil baleen whales. An odontocete has also been found from Barra da Cuanza.

In Angola the most abundant group of Neogene vertebrates are the Elasmobranchii chondrichthyans (18 taxa; see Supplementary Material). The following taxa are from the Pliocene of Farol das Lagostas (Cuanza Basin): *Aetobatus, Carcharhinus egertoni, Carcharhinus priscus, Carcharias taurus, Carcharocles megalodon*, *Carcharodon carcharias, Galeocerdo cuvier, Hemipristis serra, Isurus benedeni, Isurus oxyrinchus, Mitsukurina, Myliobatis, Negaprion brevirostris, Paragaleus, Pristis, Pteromylaeus bovina, Rhinoptera brasiliensis,* and *Sphyrna zygaena* (Antunes 1964). Five bony fishes are known, the actinopterygians *Cybium, Sparus, Sphyraena barracuda, Tachysurus,* and *Tetrodon*.

The Quaternary – The Dominance of Humans

The Quaternary (2.6 Ma to present, including the Pleistocene and Holocene) is the third geological period of the Cenozoic era and the most recent in the geological time scale. This period is characterised by the return of glaciations at higher elevations and latitudes, the dominant role of the genus *Homo* in all terrestrial habitats and the extinction of much of the megafauna.

Invertebrates

In Angola, the Quaternary biodiversity is again marked by the high number of mollusc taxa (73 or more), of which 29 are bivalves such as *Arcopsis afra, Barbatia complanata, Cardium indicum, Chama crenulata, Glycymeris concentrica, Lutraria senegalensis, Noetiella congoensis, Ungulina cuneata* from the Middle Pleistocene of Pipas (Namibe Basin) and 44 gastropods mainly known from Namibe Basin, such as *Cantharus viverratus*, *Columbella adansoni*, *Conus babaensis*, *Siphonaria*

capensis, and *Terebra senegalensis* (Miller and Carpenter 1956; Sessa et al. 2013). Other invertebrates such as corals, arthropods and echinoderms are known but reduced to a handful of known taxa, such as *Cladangia carvalhoi* from the Pleistocene of Salinas de Bero, Saco, Namibe (Wood 1973). In most situations they occur in a variety of raised-beach and lagoonal deposits related to coastal uplift and major sea-level changes (Carvalho 1961). The post-glacial Holocene is marked by the accretion of sand-spits and deltaic facies with rich coquinas, including the bivalve *Senilia senilis* as a typical species (Dinis et al. 2016). See Supplementary Material for the updated list.

Vertebrates

A remarkable fossilized jaw (dentary bone) of Blue Whale *Balaenoptera musculus* present in the *Museu Nacional de História Natural* in Luanda measuring nearly seven meters in length is not only the largest known fossilized bone but also one of the largest whales, thus animals, ever recorded. Large land mammals, including *Bubalus*, *Syncerus* cf. *nanus* Boddaert; *Phacochoerus* sp., *Equus*, *Hippotigris* cf. *zebra* have been reported from the site called *Cemitério dos Ossos*, north of Luanda (Antunes 1961).

The caves of Humpata, in Huíla Province, in southern Angola, are formed in Chela Dolomite that hosts fossiliferous caves and fissures (Amaral 1973; Antunes 1965; Arambourg and Mouta 1952; França 1964; Mouta 1950). Pickford et al. (1990, 1992, 1994) listed taxa of mammals from the Humpata Caves. These include the insectivore *Crocidura*, a Macroscelididae, the chiropteran *Rhinolophus, Miniopterus, Nycteris*, 19 genera of rodents (*Uranomys, Acomys, Dasymys, Aethomys, Thallomys, Zelotomys, Mus, Pelomys, Malacomys, Praomys, Grammomys, Dendromus, Steatomys, Petromyscus, Tatera, Otomys, Cryptomys, Graphiurus*, and *Hystrix*), the lagomorph *Serengetilagus*, Mustelidae, Viverridae, Canidae, and the Hyaenidae cf. *Chasmoporthetes*, the Hyracoidea *Gigantohyrax* and *Procavia,* Rhinocerotidae, Equidae, Suidae *Metridiochoerus andrewsi* and the Bovidae Hippotragini and *Connochaetes.*

The most thoroughly studied of the Humpata fossils are those of the extinct baboon. Cercopithecid primates from Humpata caves include *Soromandrillus quadratirostris*, cf. *Theropithecus* sp., and *Cercopithecoides* sp. (dated as ca. 2.0–3.0 Ma) (Minkoff 1972; Jablonski 1994; Jablonski and Frost 2010; Gilbert 2013).

Pleistocene deposits in Namibe provided remains of fossilized ostrich *Struthio* eggshells, artiodactyl bones and numerous human artifacts - including Acheulean hand axes (amygdaloid bifaces) suggesting the presence of early humans, such as *Homo ergaster* or *H. erectus*, whereas bones of early humans are not known in Angola.

Final Remarks on the Fossil Record and Paleobiodiversity

Measuring paleobiodiversity is challenging due to the sparse and limited availability of data, compared with modern extant faunas. The paleobiodiversity of Angola is mostly known from Cretaceous and Cenozoic fossils that comprise 90% or more of all known fossil records of Angolan taxa (see Table 4.1 and Supplementary Material). The vast preponderance of the fossil taxa is marine which is consistent with the geological settings and paleogeography, related to the opening of the South Atlantic and repeated inundation of the Angolan continental margin.

For this study, we compiled a list of taxa using species, genus or the lowest known taxonomical clade reported in the scientific literature for Angola (see Supplementary Material). Of the resulting list of more than 1300 fossil taxa, many may require systematic revision and the final number will depend on the validity of the taxonomy.

By far the most speciose group are the molluscs (about 61% of taxa, more than half being Cretaceous ammonites) and Cretaceous foraminiferans (16%), followed by vertebrates with about 15% of taxa. Chondrichthyes and mammals represent 6% and 5% of taxa, respectively.

About 10% of vertebrate taxa listed are unique or were first recognised in Angola, most of them receiving species names after localities in Angola or of geologists that worked in the country. According to current knowledge, at least 67 taxa (6.1%) of invertebrates are endemic or were first mentioned from Angola.

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