Dinosaur Faunas of Egypt—The Terrestrial Late Cretaceous Vertebrate Record

Felix J. Augustin, Josephina Hartung, and Panagiotis Kampouridis

Abstract

Egypt has yielded some of the richest and most spectacular records of Mesozoic terrestrial vertebrates from Africa. Certainly, the best-known and most diverse of these are the vertebrate assemblages of the Upper Cretaceous Bahariya Formation (Cenomanian), which includes numerous different taxa of fishes, abundant remains of turtles and crocodyliforms, as well as several different theropod and sauropod dinosaurs. Originally discovered early in the twentieth century by famous German palaeontologist Ernst Stromer von Reichenbach and fossil collector Richard Markgraf, most of the material has subsequently been destroyed during the Second World War. Aside from the high diversity, the Bahariya Formation also yielded some of the most bizarre and iconic dinosaurs such as the giant theropods *Spinosaurus* and *Carcharodontosaurus* or the enormous sauropod *Paralititan*. Although the Bahariya Oasis has yielded by far the most diverse and extensive remains of Mesozoic terrestrial vertebrates from Egypt, other localities from the Turonian, Campanian and Maastrichtian offer additional important—albeit much less complete—insights into the composition and evolution of African Late Cretaceous terrestrial ecosystems. Some of these assemblages, especially the latest Cretaceous Quseir Formation, have just begun to reveal the richness and diversity of their vertebrate fauna, often with spectacular results, and certainly have the potential to yield further significant insights into the evolution of the Cretaceous life on land. In this chapter, we provide a summary of the terrestrial Mesozoic vertebrate record of Egypt and thus an overview of these remarkable dinosaur faunas.

Keywords

Egypt • Dinosauria • Crocodyliformes • Testudinata • Bahariya Formation • Quseir Formation

1 Introduction

Egypt has yielded one of the richest records of terrestrial vertebrates from the Mesozoic of the African continent. All Egyptian continental Mesozoic vertebrate assemblages are Late Cretaceous in age, spanning from the beginning of that period (Cenomanian) up to the latest Cretaceous (Maastrichtian), representing the final days of the dinosaur era. Although the Mesozoic record of terrestrial ecosystems from Africa is generally extensive, the Cretaceous, and especially the Late Cretaceous, is poorly documented (Rauhut & Werner, 1997; Russell, 1995; Weishampel et al., 2004). Therefore, the Egyptian Late Cretaceous vertebrate assemblages play a key role in our understanding of the evolution of terrestrial ecosystems in Africa during the Cretaceous. Moreover, the Egyptian vertebrate assemblages yielded some of the most astonishing and bizarre land vertebrates, including the large-sized and potentially semi-aquatic carnivorous theropod *Spinosaurus* (Ibrahim et al., 2014, 2020b; Stromer, 1915) or the enormous sauropod *Paralititan*, one of the largest terrestrial animals ever to walk the earth (Smith et al., 2001).

The most famous of these Egyptian terrestrial vertebrate assemblages is the fauna from the Upper Cretaceous (Cenomanian) of the Bahariya Oasis (Fig. 1), which was discovered early in the twentieth century by German palaeontologist Ernst Stromer von Reichenbach and fossil collector Richard Markgraf. Over the course of three years (1912–1914) a diverse array of vertebrates was recovered, including numerous fishes, turtles, crocodyliforms, as well as sauropod and theropod dinosaurs (Stromer, 1936). Although the Bahariya Oasis has yielded by far the most diverse and extensive remains of terrestrial vertebrates, other

F. J. Augustin (✉) · J. Hartung · P. Kampouridis
Department of Geosciences, University of Tübingen,
Hölderlinstraße 12, 72074 Tübingen, Germany
e-mail: felix.augustin@uni-tuebingen.de

Z. Hamimi et al. (eds.), *The Phanerozoic Geology and Natural Resources of Egypt*, Advances in Science, Technology & Innovation, https://doi.org/10.1007/978-3-030-95637-0_9

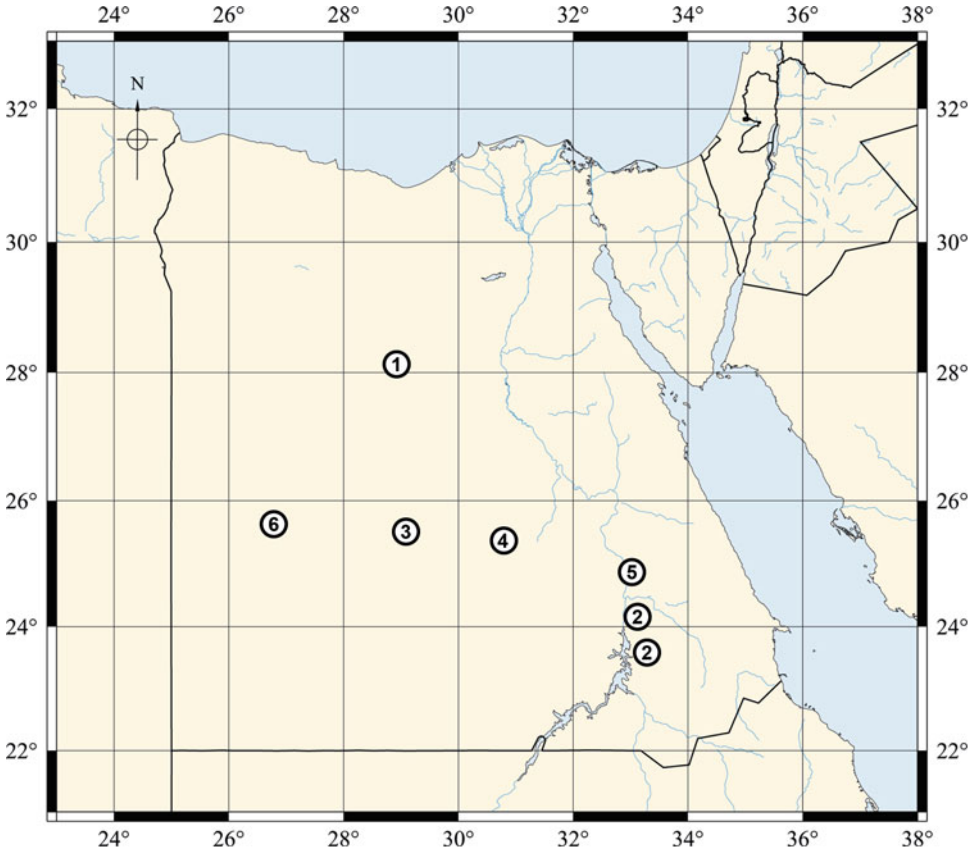

Fig. 1 Map of Egypt with the location of vertebrate-yielding sites from the Cretaceous. *1* Bahariya Oasis (Bahariya Formation); *2* track-sites near Aswan (Abu Agag Formation), 75–80 km south of Aswan and 15 km south of Aswan respectively; *3* Dakhla Oasis (Quseir Formation); *4* Kharga Oasis (Quseir Formation); *5* Nile Valley near Idfu (Quseir Formation); *6* Ammonite Hill Member of the Western Desert (Dakhla Formation). The map was created with GMT6 (Wessel et al. 2013)

localities from the Turonian (Demathieu & Wycisk, 1990), Campanian (Saber et al., 2018; Salem et al., 2021; Sallam et al., 2016, 2018) and Maastrichtian (Rauhut & Werner, 1997; Smith & Lamanna, 2006) offer additional important—albeit sparse—insights into the composition and evolution of African Late Cretaceous terrestrial ecosystems.

In this chapter, a summary of the Cretaceous terrestrial vertebrate assemblages from Egypt is provided. After an overview of the research history of Mesozoic terrestrial vertebrates from Egypt (especially the early phase), each of the different vertebrate assemblages is reviewed, starting with the oldest fauna from the Cenomanian (Bahariya Formation) and ending with the youngest one from the Maastrichtian (Dakhla Formation). As a conclusion, the importance of the Egyptian Mesozoic vertebrate assemblages for our understanding of past terrestrial ecosystems is shortly discussed.

2 Historical Overview

The early research history of the terrestrial Mesozoic vertebrates of Egypt is closely connected to two men, Ernst Stromer von Reichenbach and Richard Markgraf (Fig. 2), who uncovered and studied the rich vertebrate fauna from Bahariya, certainly the most important Mesozoic vertebrate locality from Egypt. Ernst Freiherr Stromer von Reichenbach was a nobleman of an old aristocratic family from the medieval city of Nuremberg and a German palaeontologist. He was a student of the famous German palaeontologist Karl Alfred von Zittel, who conducted some of the first palaeontological fieldwork in Egypt (see below) during expeditions with the famous explorer of Africa Gerhard Rohlf (Zittel, 1883). Stromer travelled three times to Egypt (1902, 1903 and 1910) to discover new fossil sites and collect vertebrate specimens. During his first two expeditions, Stromer primarily collected mammal fossils from the Palaeogene of the Fayum Depression (Kampouridis et al., this volume). During his second and third expedition to Egypt, Stromer was accompanied by fossil collector Richard Markgraf. Richard Markgraf was an Austro-German musician who joined a travelling musical group when he was young, finally ending up sick and impoverished in Cairo. In 1897, he met German palaeontologist Eberhard Fraas, who hired him because of his knowledge in Arabian to assist him in his fieldwork. Fraas trained Markgraf in fossil collection and, after recognising his talent and skills, hired him to

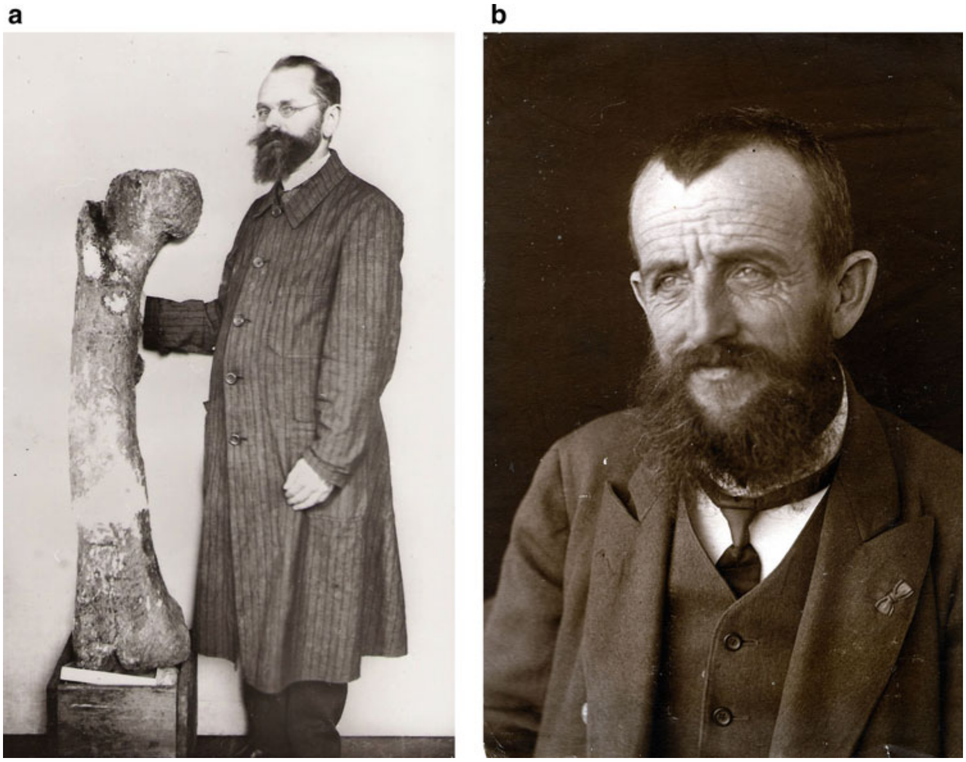

Fig. 2 The German palaeontologist Ernst Stromer von Reichenbach (**a**) and the Austro-German fossil collector Richard Markgraf (**b**), who collected the vast majority of the fossil vertebrates from Bahariya

continue collecting fossils for the Natural History Museum of Stuttgart, Germany. Markgraf was one of the most significant fossil collectors in Egypt, though he did not receive any real fame or fortune for his accomplishments and lived a very simple life.

Originally, the main purpose of Stromer's third expedition to Egypt was the collection of mammal fossils in Wadi el Natrun and in the Nile Valley. Stromer was not able to collect the quantity of fossils he hoped and when his companion Markgraf fell sick in winter 1910, Stromer had to return to Cairo and hire a new guide. In January 1911, he and his new guide travelled to the Bahariya Oasis for the first time, where Stromer was not able to find any mammal fossils but made another awe-inspiring discovery: he found the first dinosaur fossils from Egypt. After Markgraf's recovery, Stromer entrusted him with collecting more fossils from the Bahariya Oasis. In the years 1912–1914 Markgraf continued his work there, gathering an incredibly rich collection of fossils, which he sent to Munich, Germany, to be studied by Stromer and comprising the famous gigantic theropod dinosaur *Spinosaurus* (Stromer, 1915), among others. Markgraf himself collected almost all fossils, that were later published by Stromer and his colleagues, including several new genera and species. Unfortunately, he was unable to continue his fossil collection after 1914, because of the First World War. Due to his sickness, Markgraf died in January 1916 in his home in Sinnuris, in Fayum (Stromer, 1916). The last fossils that Markgraf collected in 1914 were not sent to Stromer in Munich until 1922 (Stromer, 1926). This material comprised several new species, including the dinosaurs *Carcharodontosaurus saharicus* and *Aegyptosaurus baharijensis* (Stromer, 1931, 1934b), as well as the fishes *Markgrafia libyca* and *Stromerichthys aethiopicus*, which were named in honour of collector Markgraf and researcher Stromer, respectively (Weiler, 1935). Unfortunately, during the Second World War almost all of Stromer's material from the Bahariya Oasis that was stored in Munich was destroyed on 24 April 1944 during a bombardment by the Allied Royal Air Force, and only few specimens survived, including the holotypes of *Libycosuchus* and *Aegyptosuchus* among others (Smith et al., 2006).

More recent field activities with the aim to uncover fossil vertebrates from the Mesozoic continental deposits of Egypt have demonstrated the potential of these strata to yield further spectacular and important material. One of the most important among these is probably the field activities of the Technical University of Berlin (1970s and 1980s) that studied the stratigraphy, sedimentology and palaeontology of the Bahariya and Dakhla formations (see below) among others. The Bahariya Dinosaur Project of the University of Pennsylvania continued the search for dinosaurs and other vertebrates in the Upper Cretaceous Bahariya Formation and recovered significant new material, most importantly the holotype of an enormous sauropod dinosaur, *Paralititan stromeri* (for an overview, see Nothdurft & Smith, 2002). More recently, extensive fieldwork was conducted by the Mansoura University in the Bahariya Formation (Salem et al., 2018), and primarily in the latest Cretaceous Quseir Formation (Saber et al., 2018; Sallam et al., 2016, 2018) with spectacular results, including a new sauropod dinosaur (*Mansourasaurus*) and a new crocodilian (*Wahasuchus*) that have important palaeobiogeographic implications.

3 The Vertebrate Fauna of the Bahariya Formation (Cenomanian)

The Bahariya Formation yielded by far the most diverse and richest vertebrate assemblage from the Mesozoic terrestrial deposits of Egypt. The fauna from this formation has been known for more than a century (see above) and is famous for the presence of multiple large-sized carnivorous theropod dinosaurs that lived among gigantic sauropods, several different crocodyliforms, turtles and numerous chondrichthyan and osteichthyan fishes. Unfortunately, most of the fossil vertebrates that were collected in the first half of the twentieth century have been destroyed due to the allied bombing of Munich during the Second World War. Thus, our knowledge of this vertebrate assemblage is largely based on the original descriptions by Stromer. However, more recent fieldwork in the Bahariya Formation has offered important new insights into this unique ecosystem, highlighting the potential of these strata to yield significant new discoveries (Lamanna et al., 2000; Salem et al., 2018; Schweitzer et al., 2003; Smith et al., 2001; Tumarkin-Deratzian et al., 2004).

Vertebrate assemblages that are remarkably similar to that of the Bahariya Formation are relatively widespread in Northern Africa and roughly coeval continental deposits with a comparable vertebrate fauna are known from Algeria (Benyoucef et al., 2015; de Lapparent, 1960), Morocco (Cavin et al., 2010; Ibrahim et al., 2020a; Sereno et al., 1996), Niger (Sereno et al., 2004), Tunisia (Benton et al., 2000; Fanti et al., 2012) and Sudan (Buffetaut et al., 1990; Rauhut, 1999; Werner, 1994). These Upper Cretaceous strata are often referred to the ‘Continental Intercalaire’, an informal unit comprising mostly Lower Cretaceous to Upper Cretaceous continental deposits (de Lapparent, 1960; Kilian, 1931; Lavocat, 1954; Taquet, 1976). Perhaps the most important of these Upper Cretaceous continental deposits in terms of vertebrate diversity is the Kem Kem beds of southern and southeastern Morocco, which yielded remains of chondrichthyan and osteichthyan fishes, amphibians, turtles, squamates, crocodilians, pterosaurs, sauropods and theropods (for a recent overview of the geology and palaeontology of the Kem Kem beds, see Ibrahim et al., 2020a).

3.1 Geological and Palaeoenvironmental Setting

The vertebrate fossils from the Bahariya Formation were collected in the eponymous Bahariya Oasis, a large depression in the Western Desert of Egypt, 320 km southwest of Cairo (Fig. 1). The rocks of this lithostratigraphic unit are well exposed, forming the floor of the Bahariya Oasis and most of the surrounding slopes (Fig. 3). The exposed thickness of the formation varies between 90 m in the central part of the Oasis and about 190 m in the northern parts (Catuneanu et al., 2006; Khalifa & Catuneanu, 2008). The Bahariya Formation has been regarded as Cenomanian in age since the beginning of its research history (Stromer, 1914a), and that age was later corroborated based on ammonite biostratigraphy (Luger & Gröschke, 1989), and comparative studies of vertebrate and plant material (Lejal-Nicol & Dominik, 1990; Schaal, 1984; Werner, 1990). The Bahariya Formation mainly consists of mudstones, siltstones and sandstones that were deposited on a low-gradient, low-energy coastal plain at the southern shore of the Tethys ocean (Khalifa & Catuneanu, 2008; Kirscher, this volume; Lacovara et al., 2003). Most finds of terrestrial vertebrates, including most dinosaurs, were collected from the base of the exposed sequence.

The depositional environments of the Upper Cretaceous sedimentary rocks of the Bahariya Formation range from braided and meandering river systems to coastal floodplains, tidal flats and channels, lagoons, mangrove forests and oyster reefs (Khalifa & Catuneanu, 2008; Lacovara et al., 2003). Several different groups of plants inhabited these extremely productive coastal environments, as evidenced by abundant plant remains of ferns, gymnosperms and angiosperms in the Bahariya beds (Coiffard & El Atfy, this volume; El Atfy et al., 2023; Lejal-Nicol & Dominik, 1990). The coastal areas were colonised by mangrove vegetation dominated by the tree fern *Weichselia*, which probably formed extensive mangrove forests (Lacovara et al., 2003). Recently, evidence for repeated wildfires during the deposition of the Bahariya Formation has been identified (El Atfy et al., 2019). Moreover, invertebrates, such as small decapod crabs, have been found within these mangrove habitats (Schweitzer et al., 2003). The palaeoclimate during the deposition of the Bahariya Formation has been reconstructed as warm and humid (Khalifa & Catuneanu, 2008; Lacovara et al., 2003).

3.2 Fishes

The Bahariya Formation contains an extremely rich and diverse fish fauna with up to twenty species of cartilaginous and more than ten species of bony fish. They are by far the

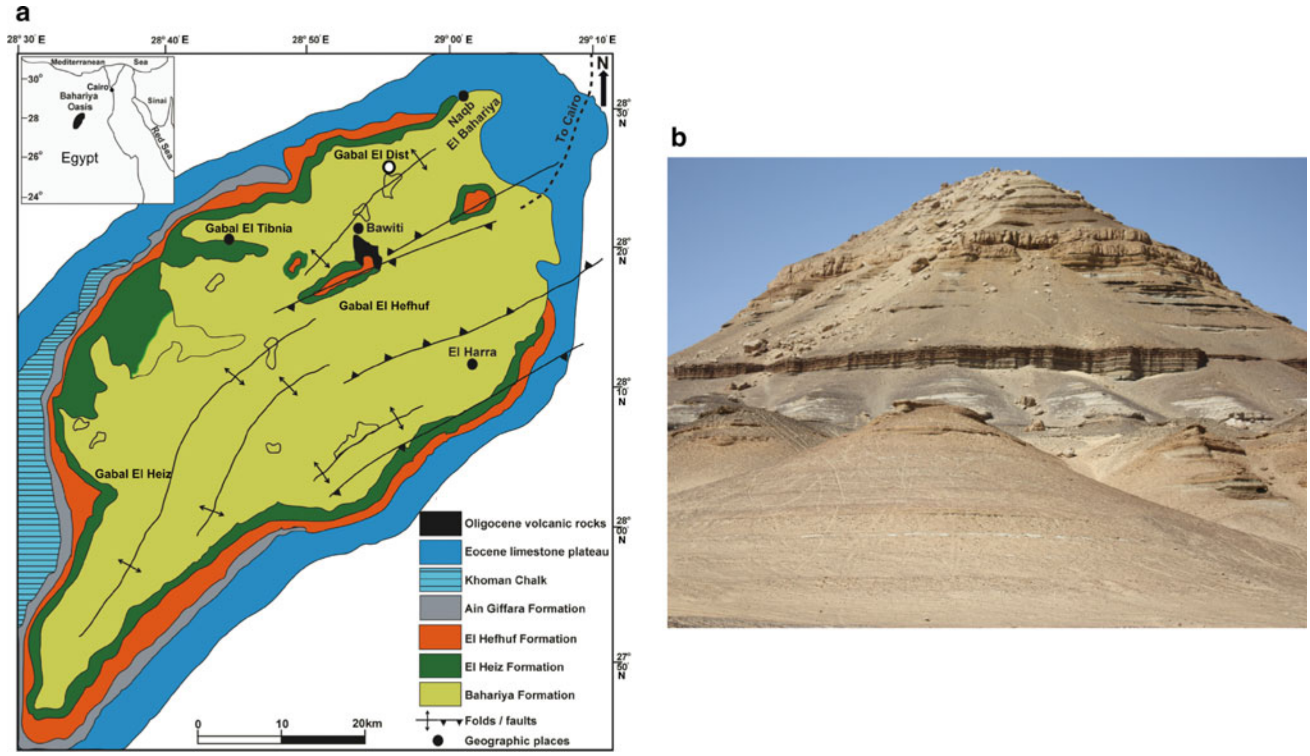

Fig. 3 Geological map of the Bahariya Formation (**a**) and field photo of Gebel El Dist (**b**), from where many important vertebrate specimens have been collected. Geological map modified after El Atfy et al. (2019). Photo of the Gebel El Dist locality kindly provided by Haytham El Atfy

most diverse and abundant vertebrate group in the Bahariya Formation, thus certainly playing a crucial role in this palaeoecosystem, and as such deserve special consideration here.

3.2.1 Chondrichthyes

Cartilaginous fishes are represented by Elasmobranchii, specifically Euselachii, which comprise sharks and rays. Among euselachians, hybodontiform sharks are well-known from their isolated teeth and vertebrae, as well as their large morphological variety of fin spines (Stromer, 1927, 1936; Weiler, 1935). Besides a comprehensive overview of the taxonomy of the Bahariya elasmobranchian fauna, Stromer (1927), as one of the most detailed studies, investigated the microstructure of these hybodontiform fin spines using thin sections (e.g. Stromer, 1927: pl. III, Figs. 1–14). He furthermore erected two new species of hybodontiform sharks based on material from Bahariya. The fauna also contains a rich and diverse assemblage of neoselachians assigned to Selachimorpha (modern sharks) and Batoidea (rays, skates, and sawfish). Selachimorpha are represented by Lamniformes (mackerel sharks) like *Scapanorhynchus*, *Squalicorax*, *Cretodus*, *Cretalamna* (Murray, 2000; Slaughter & Thurmond, 1974; Smith et al., 2006; Stromer, 1927; Vullo et al., 2007; Werner, 1989, 1990) and *Haimirichia*, which was previously also classified as *Odontaspis*, *Serratolamna* and *Carcharias* (Cavin et al., 2010; Vullo et al., 2016).

Among batoids, Sclerorhynchidae are very similar but not closely related to extant sawfishes. They share an elongated rostrum with lined, lateral protruding, barbed, and hook-like teeth. The family is represented by several different species, like, for example, *Peyeria* and *Markgrafia* (Stromer, 1927; Weiler, 1935). The most extensively studied and best-known taxon is the peculiar sclerorhynchid *Onchopristis numidus* (Fig. 4). Well-preserved, articulated remains of a rostrum, including teeth, were described and figured by Stromer (1917). Isolated teeth are also very abundant in the Kem Kem beds of Morocco (Ibrahim et al., 2020a; Villalobus-Segura et al., 2021). Recent size estimations using the rostrum length revealed a total body length of up to four meters (Villalobus-Segura et al., 2021). Other unusual sclerorhynchid sawfishes are *Schizorhiza* (Stromer and Weiler, 1930) and *Squatina*, the ‘angelshark’ (Slaughter & Thurmond, 1974). The Bahariya batoids also include the enigmatic groups Myliobatidae (eagle rays), represented by *Rhinoptera*, *Hypolophites* and *Trygon* (Stromer, 1927; Weiler, 1935) and Mylobatiformes (butterfly ray) such as *Gymnura* (Weiler, 1935; Werner, 1989).

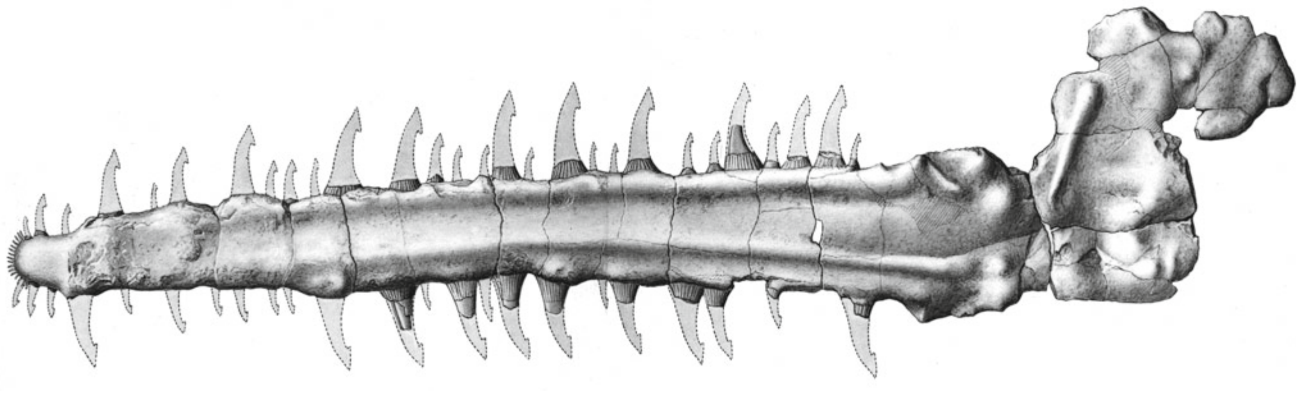

Fig. 4 Rostrum and partial cranium of the large sawfish *Onchopristis numidus* from the Upper Cretaceous Bahariya Formation. Modified after Stromer (1925)

3.2.2 Osteichthyes

Bony fishes are almost as diverse as chondrichthyans in the Bahariya Formation. Actinopterygii (ray-finned fishes) are represented by several taxa such as *Bawitius*, an archaic looking, giant, polypterid bichir (Grandstaff, 2006; Grandstaff et al., 2012; Smith et al., 2006; Stromer, 1936), *Coelodus*, a pycnodontid (Stromer, 1936), and *Enchodus*, an aulopiform (Stromer, 1936; Weiler, 1935). Furthermore, *Lepidotes* (Stromer, 1936; Weiler, 1935) is assumed to occur in the Bahariya Formation based on scales and few isolated teeth (Weiler, 1935: pl. II, Figs. 5–8 and 13). However, the material is probably referable to polypterids such as *Bawitius* (Grandstaff, 2006, 2012; Smith et al., 2006; Stromer, 1936), although *Lepidotes* is a well-known taxon, of which complete skulls are known from the Kem Kem beds of Morocco (Forey et al., 2011). Another actinopterygian is the predatory *Stromerichthys*, known from articulated cranial remains (Stromer, 1936; Weiler, 1935), and named by Weiler (1935) in honour of Ernst Stromer von Reichenbach.

There are three actinopterygian fishes that are under nomenclatural debate such as *Paranogmius* (Cavin & Forey, 2008; Stromer, 1936; Weiler, 1935), which is known from cranial remains and a partial vertebral column (Weiler, 1935; Fig. 4). The specimens, like many other, were destroyed during the Second World War and today it is assumed to be conspecific with *Concavotectum moroccensis* (Cavin & Forey, 2008). The second taxon is *Saurodon*, which was identified by Stromer (1936). Saurodontids were already mentioned by Weiler (1935) based on isolated teeth. Weiler (1935) and Stromer (1936) furthermore mentioned another possible ichthyodectid, *Portheus*, but only few conical teeth were potentially identified. The third taxon is *Plethodus* (Cavin & Forey, 2001; Stromer, 1914a, 1936; Weiler, 1935). Two species were identified based on teeth and palatal remains, but the holotypes were destroyed during the Second World War. Today, some species of *Plethodus* are believed to belong to *Palaeonotopterus* (Cavin & Forey, 2001).

Although Osteichthyes are not as diverse as cartilaginous fishes, they are represented by some peculiar groups such as lungfishes and coelacanths. Both are often referred to as ‘living fossils’ and belong to Sarcopterygii (lobe-finned fishes). Lungfishes (Dipnoi) exhibit a basal sarcopterygian bauplan and retained the ability to breathe air. They are represented by the well-known and abundant *Ceratodus* (Churcher & Iuliis, 2001; Stromer, 1914a, 1914b, 1936), which has an almost worldwide distribution ranging from the early Triassic (Romano et al., 2016) to the earliest Eocene (Cione et al., 2011). *Ceratodus* from Bahariya was studied in detail by Peyer (1925) and Churcher and Iuliis (2001) based on the typically isolated tooth plates. Besides *Ceratodus*, several authors (Churcher & Iuliis, 2001; Slaughter & Thurmond, 1974) reported remains of *Neoceratodus* from the Bahariya Formation and Churcher and Iuliis (2001) suggest that some specimen of *Neoceratodus* belong to another genus, *Retodus* (Churcher et al., 2006). *Ceratodus* probably lived in a freshwater habitat in the Bahariya Formation as Dipnoi are known to live in freshwater environments during the Mesozoic (Cavin et al., 2007). Another freshwater inhabitant is *Mawsonia lybica*, a giant coelacanth, the holotype of which was also lost during the Second World War (Grandstaff, 2006; Stromer, 1936; Weiler, 1935). The number of North African species of *Mawsonia* is currently under debate (Carvalho & Maisey, 2008; Cavin & Forey, 2004). *Mawsonia* is otherwise well-known from the Early Cretaceous of Brazil and could reach up to 6.5 m in body length (e.g. Carvalho & Maisey, 2008). Fossil remains of this genus are very abundant in the Bahariya Formation, especially cranial material, and therefore, it represents one of the most characteristic faunal elements of the Bahariya assemblage (Grandstaff, 2006; Weiler, 1935).

3.3 Testudinata

Turtle remains are numerous in the Upper Cretaceous sedimentary rocks of the Bahariya Formation but usually incomplete and poorly preserved (Stromer, 1934a). Only one genus and species has been named from these deposits to date, *Apertotemporalis baharijensis* (Stromer, 1934a). Additional material was described by Stromer (1934b) and referred to the Pleurodira. This includes several purported pleurodiran carapacial and plastral fragments from Gebel El Dist and Gebel Mandische (Stromer, 1934a). A partial femur, previously described as a testudinid humerus by Daqué (1912), from the upper part of the Gebel El Dist section was tentatively assigned to the Pelomedusidae by Stromer (1934b). Moreover, Stromer (1934b) referred a large cervical vertebrae and fragments of a large carapax, both collected from a basal level near Gebel Majesre, to the Pleurodira, noting some similarities with the Chelidae. Interestingly, the well-known Kem Kem beds of Morocco have also exclusively yielded pleurodiran turtle remains to date (Ibrahim et al., 2020a).

3.3.1 *Apertotemporalis baharijensis*

The genus and species *Apertotemporalis baharijensis* (Fig. 5) was erected for three fragmentary cranial remains discovered at Gebel El Dist (Stromer, 1934a). The specimens were found close to each other in a greyish sandy mudstone layer at the base of the exposed section. Two of them show a perfect fit and together comprise the partial braincase and the ear regions. The third element probably is part of the anterior part of the skull (Stromer, 1934a). Stromer (1934b) noted similarities to several cryptodiran and pleurodiran turtles but did not conclude to which higher taxon the new genus and species belonged. Subsequent studies generally classified *Apertotemporalis* as a bothremydid pleurodiran (de Lapparent de Broin, 2000; Pérez-García, 2017; Zalmout et al., 2005).

3.4 Crocodyliformes

Crocodilian remains are numerous in the Bahariya Formation and belong to at least three, possibly up to five different taxa: *Libycosuchus brevirostris*, *Stomatosuchus inermis* and *Aegyptosuchus peyeri*, as well as two indeterminate genera. These taxa differ markedly from each other in some cases, ranging from small and probably terrestrial forms (*Libycosuchus*) to very large, semi-aquatic and probably piscivorous animals (*Stomatosuchus*).

3.4.1 *Libycosuchus brevirostris*

The first crocodilian described from the Bahariya Formation was *Libycosuchus brevirostris* (Fig. 6), which was founded on a well-preserved skull and lower jaws, as well as three dorsal vertebrae and one caudal vertebra, all assignable to one individual (Stromer, 1914b). The material was collected in 1911 from the lower-most horizon at Gebel El Dist in the northern part of the Bahariya depression. Stromer (1914b) erected the new family Libycosuchidae for the genus, which he presumed to be most closely related to *Notosuchus* and *Theriosuchus* (Stromer, 1914b, 1933, 1936). Stromer reconstructed *Libycosuchus* as a terrestrial carnivorous animal (Stromer, 1914b, 1936), a notion also supported by later studies (Buffetaut, 1976). In contrast to most other vertebrate material described by Stromer, the holotype specimen of *Libycosuchus* survived the Second World War (Sereno & Larsson, 2009; Tumarkin-Deratzian et al., 2004). Additional material of *Libycosuchus* was collected during the early 2000s from the Bahariya Formation, including articulated dentaries and two associated vertebrae from two separate localities (Tumarkin-Deratzian et al., 2004). In general, libycosuchids were a family of small, short-snouted and likely terrestrial predatory crocodilians with a wide distribution across the Cretaceous of northern Africa (Buffetaut, 1976). Recent phylogenetic analyses place *Libycosuchus* (and the family Libycosuchidae) within the Notosuchia, a very successful group of terrestrial crocodyliforms, primarily known from the Cretaceous of Gondwana (Larsson & Sues, 2007; Pol et al., 2014).

3.4.2 *Stomatosuchus inermis*

The holotype of *Stomatosuchus inermis* (Fig. 7) comprises a partial skull, the right lower jaw, as well as a fragmentary cervical and sacral vertebra of one individual (Stromer, 1925). The holotype specimen represents a very large crocodilian, with an estimated skull length of almost 2 m when complete (Stromer, 1925). Aside from the huge size, the cranium of *Stomatosuchus* is also remarkable for its peculiar anatomy, including the long, flat and broad skull, very small teeth and the weak symphysis of the lower jaws (Stromer, 1925). Additional cranial material of the genus was described by Stromer (1933). Due to the peculiar anatomy of the genus, Stromer (1925) erected the new family Stomatosuchidae to encompass this genus, the phylogenetic relationships of which, however, remaining unclear for decades, also because the remains of *Stomatosuchus* were destroyed during the Second World War. Recently, a very similar crocodyliform genus, *Laganosuchus*, has been described based on mandible remains from the Echkar Formation of Niger (*Laganosuchus thaumastos*) and the Kem Kem beds of Morocco (*Laganosuchus maghrebensis*) (Sereno & Larsson, 2009). Like *Stomatosuchus*, *Laganosuchus* is a member of Stomatosuchidae, which was placed within Neosuchia by Sereno and Larsson (2009). Stomatosuchids were reconstructed as semi-aquatic crocodyliforms hunting for fish in shallow water (Sereno &

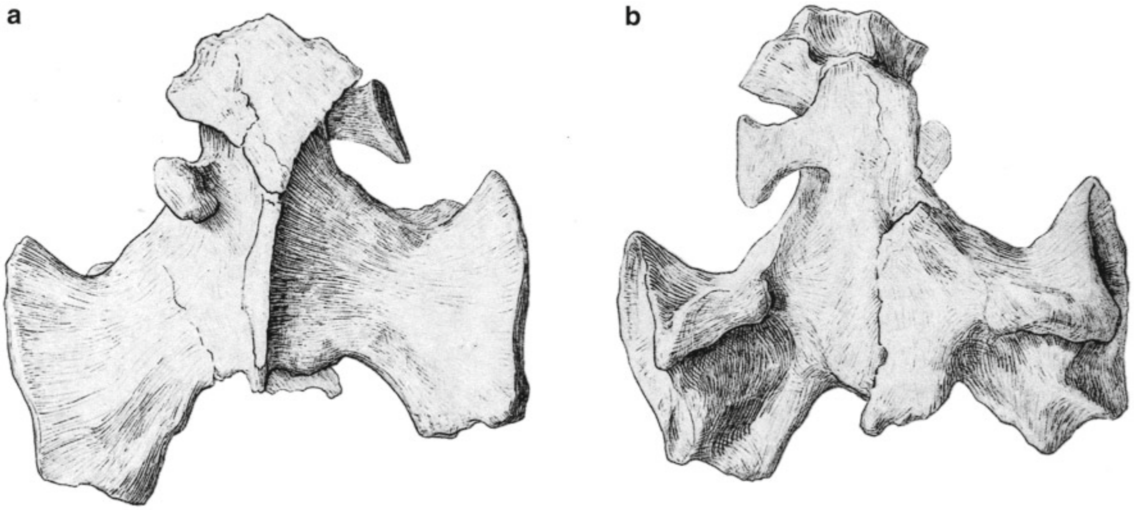

Fig. 5 Holotype partial cranium of the turtle *Apertotemporalis baharijensis* from the Upper Cretaceous Bahariya Formation in dorsal (*1a*) and ventral view (*1b*). Modified after Stromer (1934a)

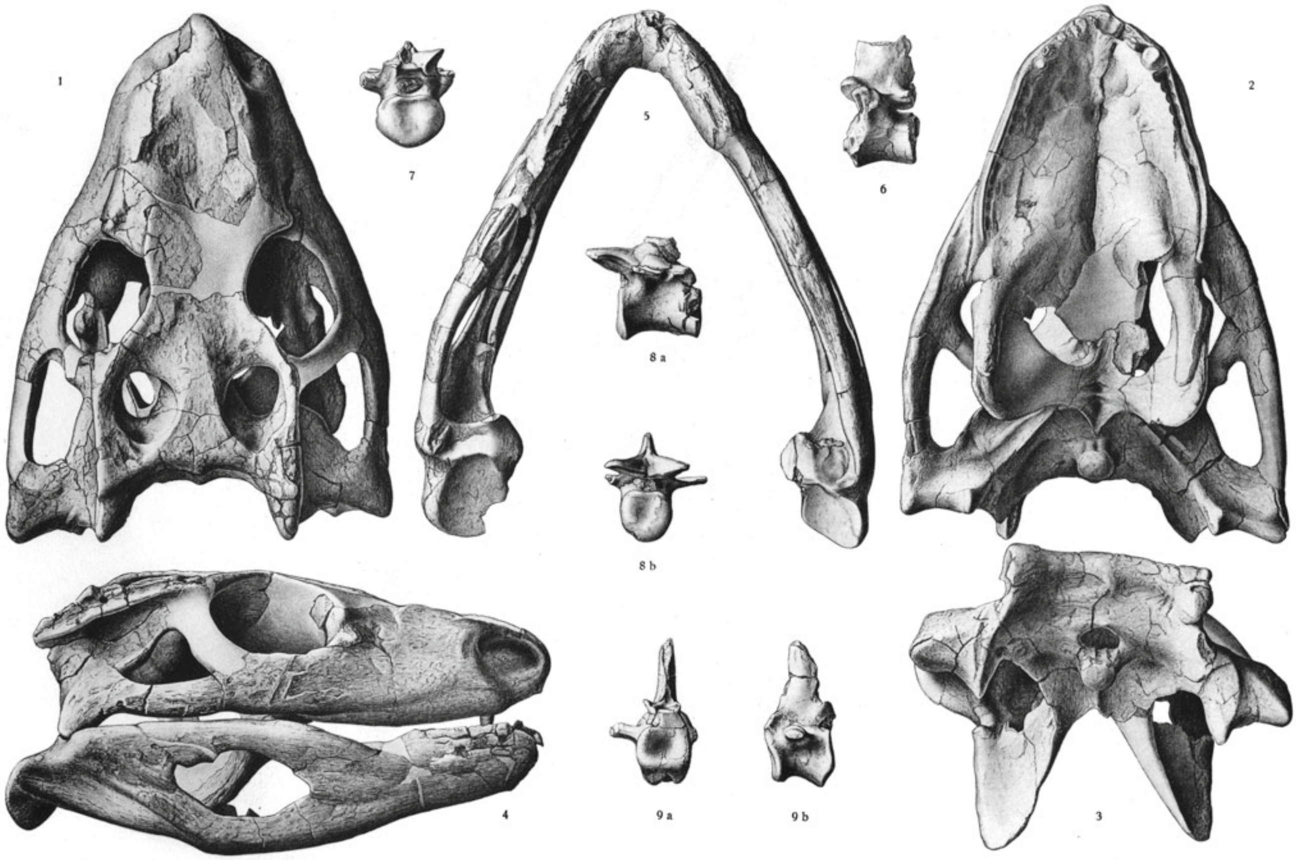

Fig. 6 Holotype material of the crocodyliform *Libycosuchus brevirostris* from the Upper Cretaceous Bahariya Formation. *1–4* Cranium in dorsal (*1*), ventral (*2*), posterior (*3*) and right lateral view (*4*); *5* lower jaw in dorsal view; *6–8* three dorsal vertebrae in right lateral (*6*), posterior (*7*), right lateral (*8a*) and posterior view (*8b*); *9* caudal vertebra in posterior (*9a*) and left lateral view (*9b*). All to the same scale, cranium about 165 mm long. Modified after Stromer (1914b)

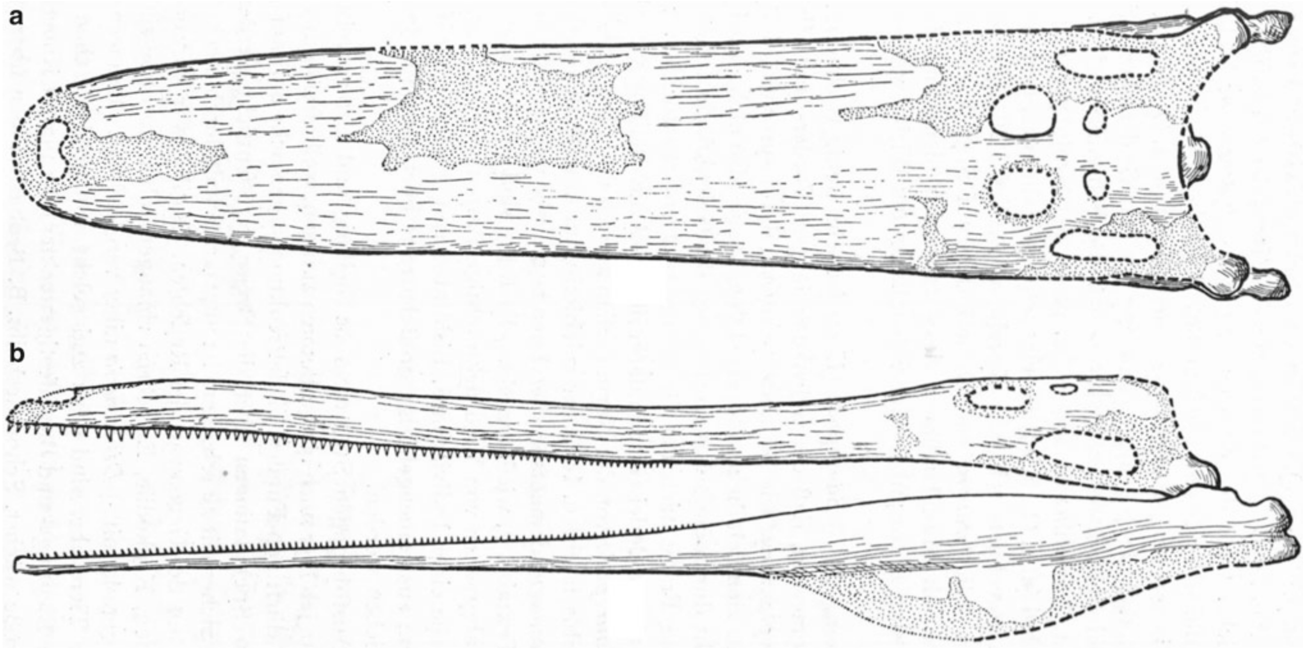

Fig. 7 Reconstruction of the holotype skull of the crocodyliform *Stomatosuchus inermis* from the Upper Cretaceous Bahariya Formation in dorsal (**a**) and left lateral view (**b**). The skull has a length of almost 2 m. Modified after Stromer (1936)

Larsson, 2009; Stromer, 1936); it has even been suggested that *Stomatosuchus* possessed a pelican-like gular pouch below the lower jaw (Nopcsa, 1926; Stromer, 1933), though there is currently no evidence for this (Sereno & Larsson, 2009).

3.4.3 *Aegyptosuchus peyeri*

A partial skull, comprising the braincase and skull roof as well as several isolated teeth discovered in 1912 at Gebel El Dist several meters above the basal-most dinosaur layer, were the basis for the erection of a new genus and species, *Aegyptosuchus peyeri* (Stromer, 1933). Additional referred material includes an articular, and several cervical, dorsal and caudal vertebrae, a coracoid, scapula, ilium, ischium, pubis, femur and a metatarsal (Stromer, 1933). However, Stromer (1933) cautioned that the referral of these postcranial specimens to *Aegyptosuchus* is somewhat speculative. The holotype of *Aegyptosuchus* was one of the few remains that survived the Allied bombing of Munich during the Second World War. Like for the other peculiar crocodyliform taxa from the Bahariya Formation, Stromer (1933) erected a distinct family for the genus, Aegyptosuchidae. Recent cladistic phylogenetic analyses recovered *Aegyptosuchus* as a derived eusuchian, most closely related to *Aegisuchus* from the Upper Cretaceous Kem Kem beds of Morocco (Holliday & Gardner, 2012). Notably, Ibrahim et al. (2020a) suggested that *Aegyptosuchus* is almost indistinguishable from *Stomatosuchus* based on the preserved elements and that the former might turn out to be a junior synonym of the latter; the same might then be true for *Aegisuchus* and *Laganosuchus*, respectively (Ibrahim et al., 2020a). In this case, the family Aegyptosuchidae would be synonymous with Stomatosuchidae (Ibrahim et al., 2020a).

3.4.4 Indeterminate Crocodyliforms (‘Krokodilier G and F’)

Due to the fragmentary nature of most crocodilian remains from the Bahariya Formation and an associated lack of overlapping material, Stromer (1933) discussed the difficulties of deciding how many crocodyliforms were really present in the assemblage. He concluded that a minimum of five genera are probably represented by the material: *Libycosuchus brevirostris*, *Stomatosuchus inermis* and *Aegyptosuchus baharijensis*, as well as two indeterminate crocodyliforms (Stromer, 1933, 1936). The two indeterminate forms are Stromer’s ‘Krokodilier (crocodilian) G’ and ‘Krokodilier F’, which differ significantly from all the other known crocodilians of the Bahariya Oasis (Stromer, 1933). ‘Krokodilier G’ is based on a partial lower jaw from an unknown locality of the Bahariya Oasis (Stromer, 1933). ‘Krokodilier F’ is known too from a fragmentary lower jaw that was collected three kilometres east of Ain Gedid (Stromer, 1933). Stromer (1933) noted that ‘Krokodilier F’ is overall similar to *Bottosaurus* from the Upper Cretaceous of North America but, based on some noteworthy anatomical differences and the spatio-temporal separation of the two forms, he concluded that they are probably not congeneric (Stromer, 1933). Later, Kuhn (1936) erected two genera, *Stromerosuchus* and *Baharijodon*, which he based on fragmentary and indeterminate material of Stromer; these are, however, nowadays considered to represent nomina dubia (e.g. Nothdurft & Smith, 2002).

3.5 Dinosauria

At least five different genera of dinosaurs have been identified in the Cenomanian deposits of the Bahariya Formation, including three theropods and two sauropods: *Spinosaurus aegyptiacus*, *Carcharodontosaurus saharicus* and *Bahariasaurus ingens*, as well as *Aegyptosaurus baharijensis* and *Paralititan stromeri*. Furthermore, additional but indeterminate mid- to large-sized theropods and two more sauropods were possibly present in the faunal assemblage of the Bahariya Formation (see below). The vertebrate fauna is thus characterised by the presence of three (possibly up to five) large-bodied carnivorous theropods. This rather unusual faunal composition, also known as 'Stromer's Riddle' (McGowan & Dyke, 2009), has also been observed in some other North African localities, most famously the Kem Kem Beds of Morocco (Ibrahim et al., 2020a). Despite early reports to the contrary (Stromer, 1914a, 1914b), ornithischians are apparently absent from the Bahariya Formation. Evidence of ornithischians is extremely rare in the contemporaneous well-known (and better sampled) Kem Kem beds of Morocco, consisting of one fragmentary tooth crown and a footprint (Ibrahim et al., 2020a).

3.5.1 *Spinosaurus aegyptiacus*

Spinosaurus (Figs. 8, 9 and 10) is probably the most famous Egyptian dinosaur and one of the most iconic dinosaurs in general, mostly owing to its bizarre anatomy and the enormous size of the animal as well as its inferred palaeoecological adaptations. The type material of this genus was found in 1912 by Richard Markgraf approximately 3 km north of Gebel El Dist in the northern part of the Bahariya Oasis and described by Stromer in 1915. The material was recovered from a white muddy sandstone layer situated at the base of the Gebel El Dist profile near the floor of the Bahariya Oasis (Stromer, 1914a, 1915). The bones were found close to each other but were disarticulated, randomly arranged and some of them suffered minor distortion and breakage (Stromer, 1915). The type material comprises the left and right partial mandibles with teeth but missing the posterior parts, a left angular, a fragment of the left maxilla, more than a dozen isolated teeth, two cervical vertebrae, seven dorsal vertebrae, three sacral vertebrae, one anterior caudal vertebra, fragmentary dorsal ribs and several gastralia, all belonging to one individual (Stromer, 1915). Later, Stromer (1933) questioned the assignment of the caudal vertebra to the holotype individual. More recently, the referral of the holotype material to one individual was also questioned by Rauhut (2003), though most authors agree with Stromer's (1915) interpretation of all the holotype material being derived from one individual (Dal Sasso et al., 2005; Evers et al., 2015; Ibrahim et al., 2020a). The specimen was probably exposed to surficial weathering before discovery as indicated by the bleached and cracked appearance of some bones; most bones are, however, well-preserved with delicate processes and laminae being present (Stromer, 1915). Interestingly, the right dentary exhibits a weak thickening, likely representing a pathology caused by injury (Stromer, 1915).

Stromer (1915) noted that *Spinosaurus* likely had a long and narrow snout, conical teeth and exceptionally long spinal processes (up to eight times higher than the centrum). He rejected the idea of these extremely elongated spinal processes having functioned as attachment sites for muscles or as a fatty hump, and compared them to pelycosaurs and extant lacertilians concluding that they instead likely formed a narrow sail (Stromer, 1915); later, he suggested them to be akin to display structures (Stromer, 1936). Based on the holotype description of *Spinosaurus*, Stromer (1915) erected the Spinosauridae, a diverse family now including several different genera from South America, Africa, Asia and Europe (for an overview of spinosaurid diversity, see Evers et al., 2015; Hone & Holtz, 2017). Additional remains probably also referable to the type species *S. aegyptiacus* comprising vertebrae, teeth and ribs are known from a similar horizon near Gebel El Dist and from Gebel Maisara to the south (Stromer, 1915).

Another specimen comprising isolated teeth, five cervical and dorsal vertebrae, and a series of seven caudal vertebrae from Gebel El Harra was referred to '*Spinosaurus* B', differing from the type material and perhaps representing another species (Stromer, 1934b). Russell (1996) referred '*Spinosaurus* B' to the new genus and species *Sigilmassasaurus brevicollis*, which he based on isolated material from the Kem Kem beds of Morocco; in the same paper, he also erected a new species of *Spinosaurus*, *Spinosaurus maroccanus*, for material from Morocco (Russell, 1996). Alternatively, the material pertaining to '*Spinosaurus* B' was also referred to *C. saharicus* (Sereno et al., 1996). For a detailed discussion of '*Spinosaurus* B' and its systematic affinities (including a potential synonymy with *S. aegyptiacus* or *Sigilmassasaurus*), see Evers et al. (2015) and Ibrahim et al. (2020a). In addition, Stromer (1934a) described further postcranial material, including a femur and tibiae that he referred to '*Spinosaurus* B'. Although the *Spinosaurus* remains described by Stromer have been destroyed during the Second World War in Munich, they are still among the best-preserved and most complete specimens of the genus.

Additional material discovered since then in Algeria, Tunisia and most prominently a partial skeleton from the

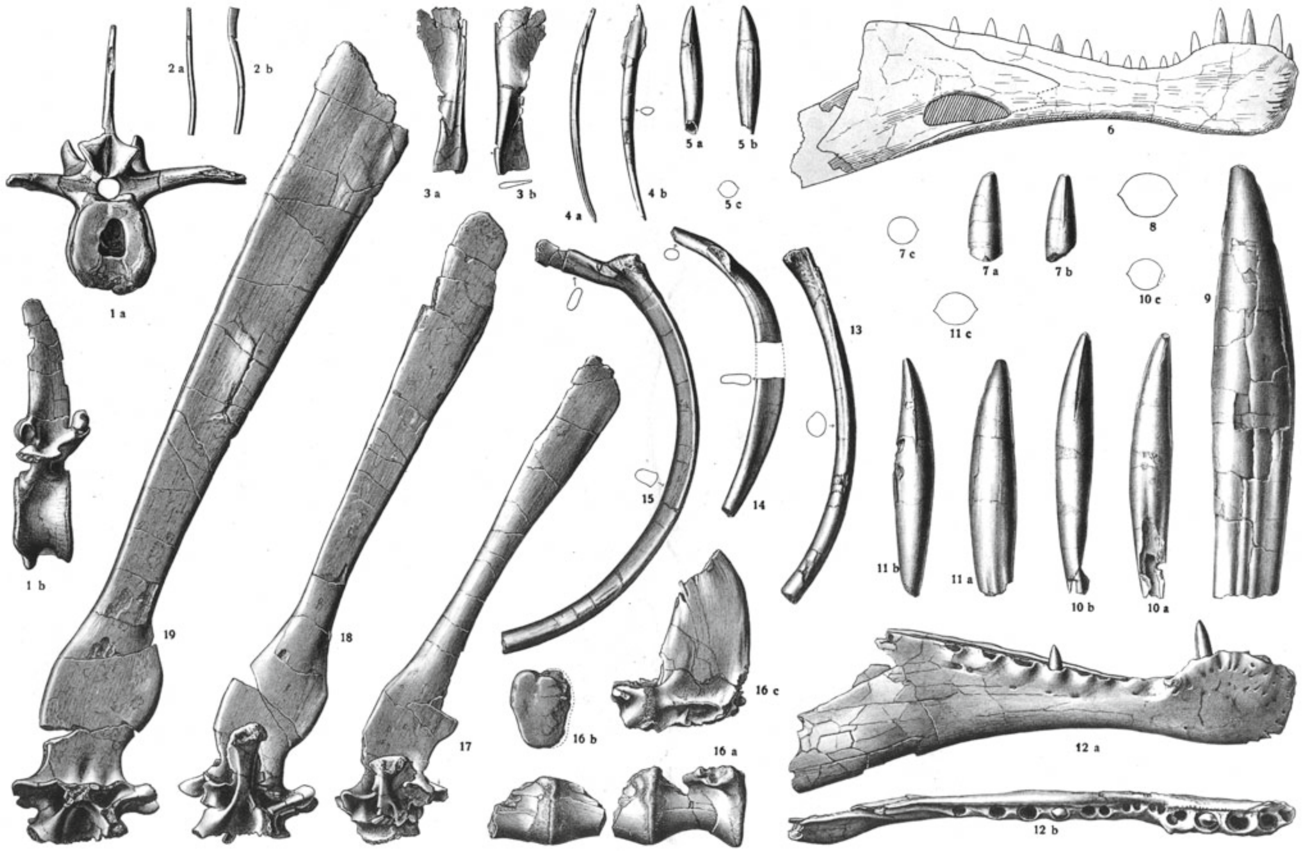

Fig. 8 Holotype material of the theropod dinosaur *Spinosaurus aegyptiacus* from the Upper Cretaceous Bahariya Formation. *1* Anterior caudal vertebra in posterior (*1a*) and right lateral view (*1b*); *2* fragmentary gastral rib; *3* left angular in external (*3a*) and internal view (*3b*); *4* gastral rib; *5* smallest tooth; *6* left lower jaw in internal view; *7* first left tooth of the lower jaw; *8* second largest isolated tooth from the right upper jaw; *9* largest isolated tooth from the right upper jaw; *10–11* two medium-sized teeth from the posterior part of the upper jaw; *12* right lower jaw in external and dorsal view; *13–15* three fragmentary ribs; *16* three sacral vertebrae in right lateral view (*16a*), anterior view of sacral vertebra (*16b*), and neural arch of sacral vertebra in right lateral view (*16c*); *17–19* neural arch and spinal processes of anterior dorsal vertebrae in right lateral view. Figures 1–4, 6 and 12–19 as well as 5 and 7–11 to the same scale, respectively. Modified after Stromer (1915)

Kem Kem beds of Morocco (Ibrahim et al., 2014, 2020b; this specimen was also suggested as a neotype for the genus, but see Evers et al., 2015 for an alternative view on the association of the material), have shed new light on the anatomy and palaeoecology of *Spinosaurus*. Especially the partial skeleton from Morocco has been interpreted as showing several features (e.g. weakly developed hind limbs and a unique tail anatomy indicating a propulsive function in water) that indicate semi-aquatic habits of *Spinosaurus* (Ibrahim et al., 2014, 2020b), a notion independently confirmed by stable isotope data of spinosaurid bones and teeth (Amiot et al., 2010a), as well as taphonomical data (Beevor et al., 2021). This interpretation has been questioned recently, however, based on taphonomical, biomechanical and anatomical considerations (Evers et al., 2015; Henderson, 2018; Hone & Holtz, 2019, 2021). Concordant with a presumed semi-aquatic habit, *Spinosaurus* and related genera have been interpreted as (at least partially) piscivorous animals based on a gut content (Charig & Milner, 1997), biomechanical modelling (Cuff & Rayfield, 2013) and stable isotope analysis (Amiot et al., 2010a; Hassler et al., 2018); this idea of a fish-eating *Spinosaurus* has also been proposed already by Stromer (1936: 71). Moreover, based on these new specimens (primarily a partial snout from Morocco), it has been shown that *Spinosaurus* was among the largest of all theropod dinosaurs (Dal Sasso et al., 2005).

3.5.2 *Carcharodontosaurus saharicus*

The second theropod genus that was described from the Bahariya deposits is *Carcharodontosaurus saharicus* (Figs. 11 and 12), an extremely large-sized carnivorous dinosaur, rivalling the famous *Tyrannosaurus* in size (Sereno et al., 1996). The holotype of this genus was collected in 1914 by Richard Markgraf from a basal marl horizon at Gebel Harra (Stromer, 1931). The holotype comprises two femora, a left fibula, both pubes, a left ischium, three cervical vertebrae, a caudal vertebra, a fragmentary rib and chevron as well as a fragmentary cranium including the

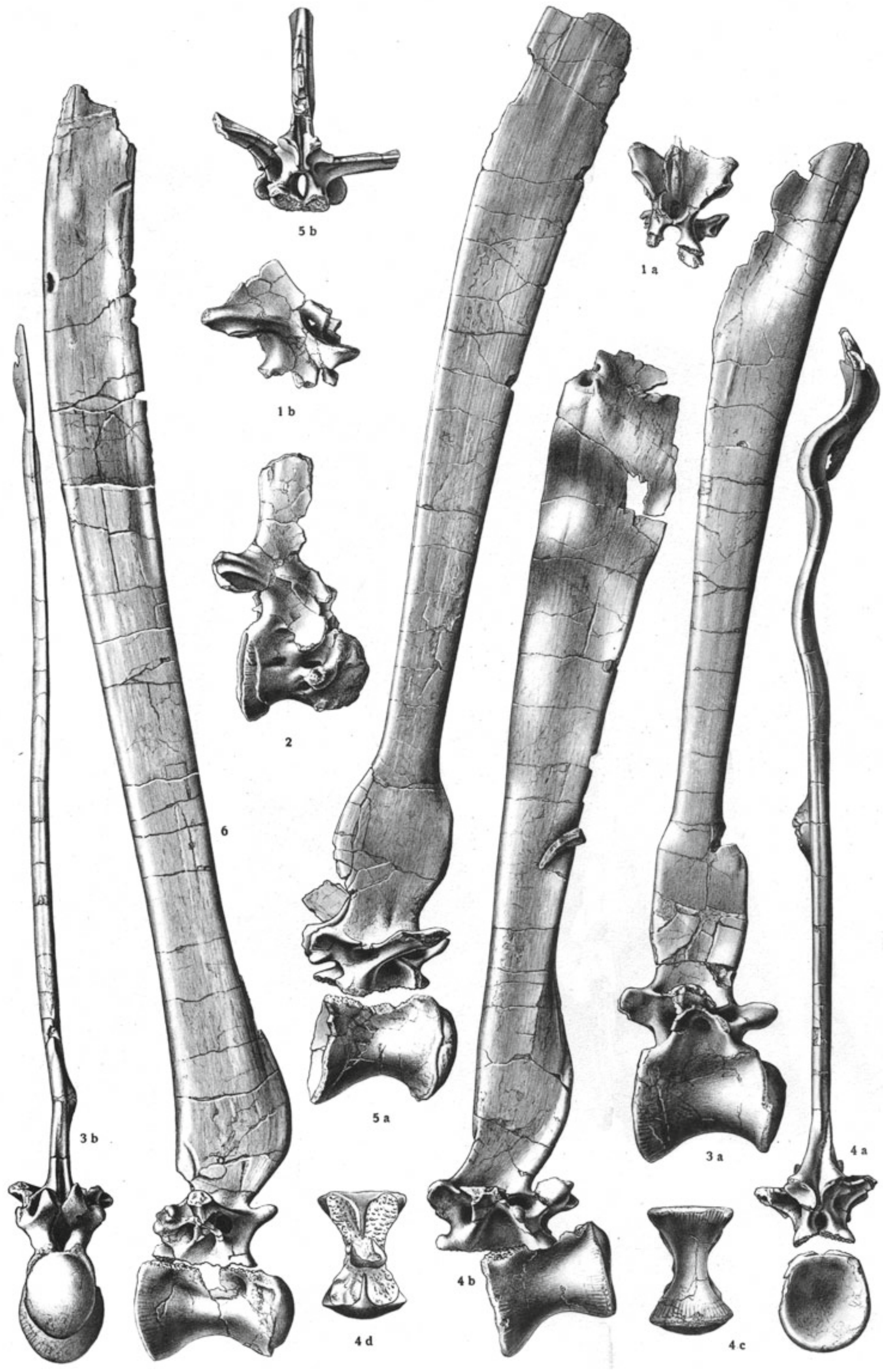

Fig. 9 Holotype material of the theropod dinosaur *Spinosaurus aegyptiacus* from the Upper Cretaceous Bahariya Formation. *1* Neural arch of an anterior cervical vertebra in posterior (*1a*), and right lateral view (*1b*); *2* middle or posterior cervical vertebra in right lateral view; *3* middle dorsal vertebra in right lateral (*3a*), and anterior view (*3b*); *4* middle dorsal vertebra in posterior (*4a*), right lateral (*4b*), ventral (*4c*) and dorsal view (*4d*); *5* posterior dorsal vertebra in right lateral (*5a*) and posterior view (*5b*); *6* posterior dorsal vertebra in right lateral view. All to the same scale. Modified after Stromer (1915)

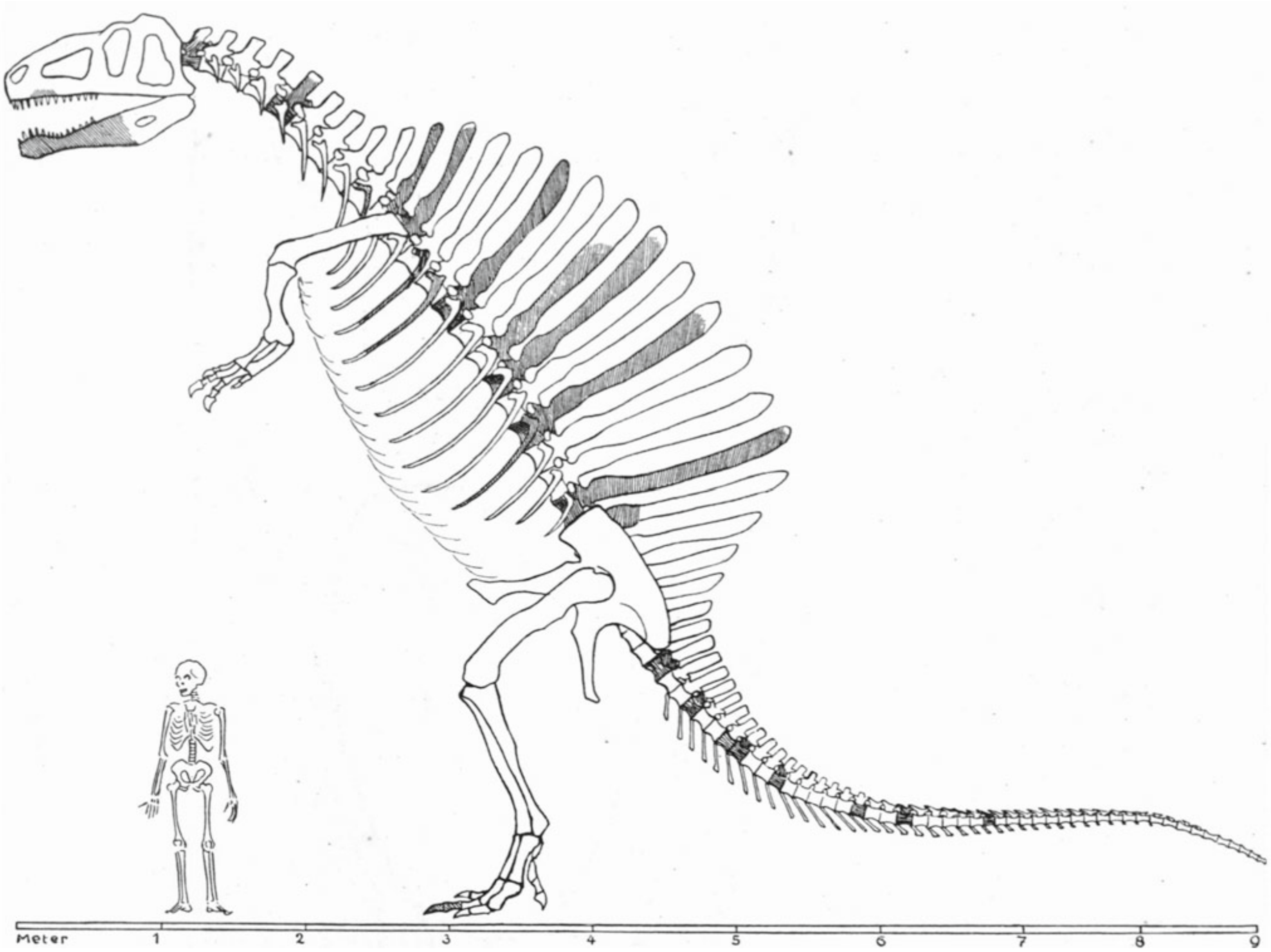

Fig. 10 Reconstruction of the skeleton of *Spinosaurus aegyptiacus*. The parts of the skeleton that were known to Stromer are shaded. Modified after Stromer (1936)

braincase, frontals and parietals, nasals, maxilla and teeth (Stromer, 1931). Based on the resemblance of the teeth to those of the shark genus *Carcharodon*, Stromer (1931) named the new theropod *Carcharodontosaurus*. He also referred teeth from the 'Continental Intercalaire' of Algeria to this genus, originally described as *Megalosaurus saharicus* (Deparet & Savornin, 1925). Based on the description of this material, Stromer (1931) coined the family Carcharodontosauridae, a highly successful family of very large carnivorous dinosaurs, mainly known from the Cretaceous of Gondwana (for an overview of carcharodontosaurid diversity, see Novas et al., 2005, 2013). Additional remains, including a right ilium, from the lower-most level at Gebel el Dist were later assigned to *Carcharodontosaurus* (Stromer, 1934b), though their referral to this genus is questionable (Rauhut, 1995).

Carcharodontosaurus seems to have been relatively widespread in the Upper Cretaceous of Northern Africa, remains of this genus having been recovered from Algeria (Benyoucef et al., 2015), Morocco (Sereno et al., 1996), Niger (Brusatte & Sereno, 2007) and Tunisia (Fanti et al., 2012). As for *Spinosaurus*, especially spectacular discoveries in the Kem Kem beds of Morocco, including a well-preserved skull missing the lower jaws, have greatly improved our understanding of this taxon (Sereno et al., 1996). This skull, which was also proposed to serve as the neotype for the genus (Brusatte & Sereno, 2007), has an estimated total length of 1.6 m, which is longer than that of the famous *Tyrannosaurus rex* from North America, making *C. saharicus* one of the largest meat-eating land vertebrates of all time (Sereno et al., 1996). More recently, cranial remains from the Upper Cretaceous (Cenomanian) Echkar Formation of Niger were designated as the holotype of a new species of *Carcharodontosaurus*, *C. iguidensis* (Brusatte & Sereno, 2007). In contrast to *Spinosaurus*, *Carcharodontosaurus* is regarded as a terrestrial animal preying mostly upon large-sized land vertebrates (Amiot et al., 2010a, 2010b; Beevor et al., 2021; Hassler et al., 2018; Stromer, 1936).

Fig. 11 Holotype material of the theropod dinosaur *Carcharodontosaurus saharicus* from the Upper Cretaceous Bahariya Formation. *1* Isolated tooth; *2* unerupted anterior tooth from the left maxilla; *3* cross-section of a right unerupted maxillary tooth; *4* cranium in right lateral (*4a*), dorsal (*4b*), and posterior view (*4c*); *5* endocast of the brain cavity in right lateral (*5a*) and dorsal view (*5b*); *6* left maxilla in internal (*6a*) and external view (*6b*); *7* right nasal in dorsal and external (*7a*) and internal (*7b*) view; *8* axis in anterior view; *9* anterior cervical vertebra in left lateral view; *10* anterior caudal vertebra in right lateral (*10a*) and anterior view (*10b*); *11* chevron in right lateral (*11a*), anterior (*11b*) and dorsal view (*11c*); *12* left ischium; *13* left pubis (*13a*) with cross-sectional views of the shaft (*13b–c*); *14* left femur in anterior view (*14a*) and reconstructed ventral view of the right femur (*14b*); *15* left fibula in anterior view (*15a*) and cross-sectional views (*15b–d*). Figures 1–3 and 4–15 to the same scale, respectively

3.5.3 *Bahariasaurus ingens* and *Deltadromeus agilis*

The third large-bodied theropod dinosaur from Bahariya is the enigmatic and rather poorly known *Bahariasaurus ingens* (Figs. 13 and 14). The holotype material of this genus has been recovered from a mudstone horizon at Gebel Ghorabi near the northern margin of the Bahariya depression (Stromer, 1934b). The material comprises two dorsal vertebrae, a neural arch, ribs, three coalesced sacral vertebrae, a right ischium and both pubes, all attributable to one individual (Stromer, 1934b). Moreover, Stromer (1934a) referred several additional specimens to this taxon, including a cervical vertebra and two dorsal vertebrae discovered 4 km south of Gebel Ghorabi, a left and right pubis from Gebel Ghorabi, a right scapula from Ain Murun in the northwestern part of the depression, a right ischium discovered 2.5 km east of Gebel El Dist, two caudal vertebrae and two small conjoined pubes discovered 3.5 km east of Gebel El Dist, a small right ischium discovered 1 km south of Gebel El Dist, as well as three dorsal vertebrae, two caudal vertebrae, a neural arch, a left and right femur, and a left fibula from Gebel El Dist. In addition, he assigned a cranial fragment, nine caudal vertebrae, a left scapula and a left coracoid from Gebel El Dist to this genus (Stromer, 1934b). Like *Spinosaurus* and *Carcharodontosaurus*, *Bahariasaurus* was an extremely large-sized theropod (Stromer, 1934b), the right femur from Gebel El Dist being only slightly shorter than that of *T. rex* (Sereno et al., 1996).

In light of the poor preservation and the size differences of the material mentioned above, Stromer (1934a) cautioned that the material might pertain to more than one species or even genus. In fact, the classification and taxonomic status of *Bahariasaurus* has proven to be especially challenging. Although Stromer (1934a) did not regard *Bahariasaurus* as being closely related to the other theropod genera of the Bahariya Formation, Rauhut (1995) suggested that both *Bahariasaurus* and *Carcharodontosaurus* might in fact belong to the Carcharodontosauridae. Some of the material

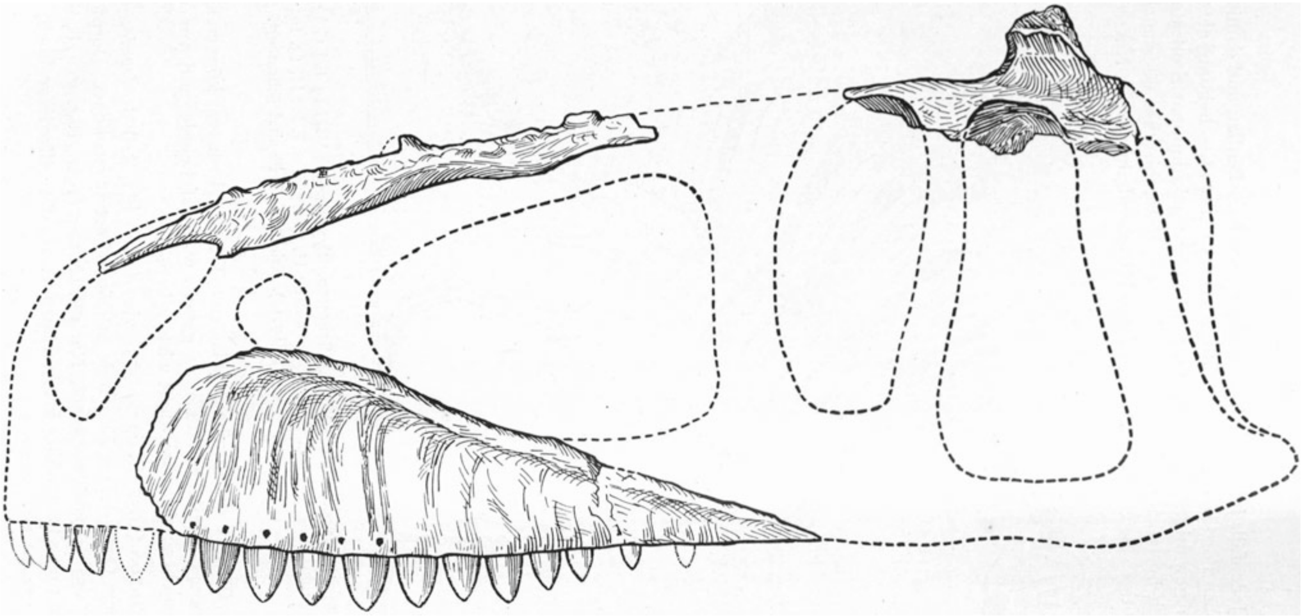

Fig. 12 Reconstruction of the holotype cranium of *Carcharodontosaurus saharicus* in left lateral view. Modified after Stromer (1936)

(including left coracoid, pubes, right tibia, left fibula, right femur), referred to *Bahariasaurus* by Stromer (1934a), was later assigned to *Deltadromeus agilis*, which was founded on a partial skeleton from the Kem Kem beds of Morocco (Sereno et al., 1996). Recently, *Bahariasaurus* was even regarded as a nomen dubium, while several elements assigned to it were referred to *Deltadromeus* (Ibrahim et al., 2020a), thus agreeing with the classification of Sereno et al. (1996). *Deltadromeus* in turn has been classified as a basal coelurosaur (Sereno et al., 1996), as being closely related to ornithomimosaurs (Rauhut, 2003), as a noasaurid (Sereno et al., 2004), a basal ceratosaur (Carrano & Sampson, 2008; Chiarenza & Cau, 2016) or a neovenatorid, and thus closely related to *Carcharodontosaurus* (Apesteguía et al., 2016). In yet another recent study, *Bahariasaurus* was considered as a valid taxon distinct from *Deltadromeus*, but closely related to the latter and both, together with *Aoniraptor* from South America, forming the Bahariasauridae, a family (originally coined by von Huene, 1948) of megaraptoran theropods (Motta et al., 2016). Therefore, at least three, but possibly five (if *Bahariasaurus* and *Deltadromeus* as well as *S. aegyp*tiacus and '*Spinosaurus* B' are indeed distinct), different large-bodied theropods were likely present in the Bahariya faunal assemblage. Remains of *Bahariasaurus*, including six caudal vertebrae, have also been found in the 'Continental Intercalaire' of Niger (de Lapparent, 1960).

3.5.4 Indeterminate Theropods (aff. *Erectopus sauvagei* and cf. *Elaphrosaurus bambergi*)

Stromer (1934a) referred the distal part of a right femur to aff. *Erectopus sauvagei* (Fig. 14), a taxon originally known from the Lower Cretaceous of France (von Huene, 1932). The femur was recovered in 1912 from a basal mudstone horizon at Gebel El Dist (Stromer, 1934b). A proximal tibia found in approximately the same horizon from Ain Murun was referred to the same taxon as the femur (Stromer, 1934a). A third element, a much smaller distal tibia, from Gebel Mandische was also tentatively assigned to aff. *E. sauvagei*, though likely representing a younger individual than the other two elements (Stromer, 1934a). All the material referred to aff. *E. sauvagei* most probably represents an indeterminate theropod (Weishampel et al., 2004). Two tibiae from Gebel El Dist were referred to aff. *Elaphrosaurus bambergi* (Fig. 14) (Stromer, 1934b), a taxon originally known from the famous Upper Jurassic dinosaur beds of Tendaguru, Tanzania (Janensch, 1920). Stromer (1934a) also assigned a right femur from Gebel Mandische to this taxon, that he initially classified as an ornithopod dinosaur (Stromer, 1914a). It should be noted that Stromer (1934a: 43–44) cautioned that the elements are overall similar to *Elaphrosaurus*, but do show significant differences and thus—together with the markedly different age—they certainly represent a different species but might be related to *Elaphrosaurus*. Like the other indeterminate theropod material mentioned above, the specimens referred to cf. *Elaphrosaurus* likely represent an indeterminate theropod dinosaur (Weishampel et al., 2004). Recently, the presence of an indeterminate abelisaurid has been preliminarily reported based on a cervical vertebra (Salem et al., 2018; Salem et al., 2022).

3.5.5 *Aegyptosaurus baharijensis*

The first sauropod remains described from the Bahariya Formation were unearthed in 1911 by Richard Markgraf

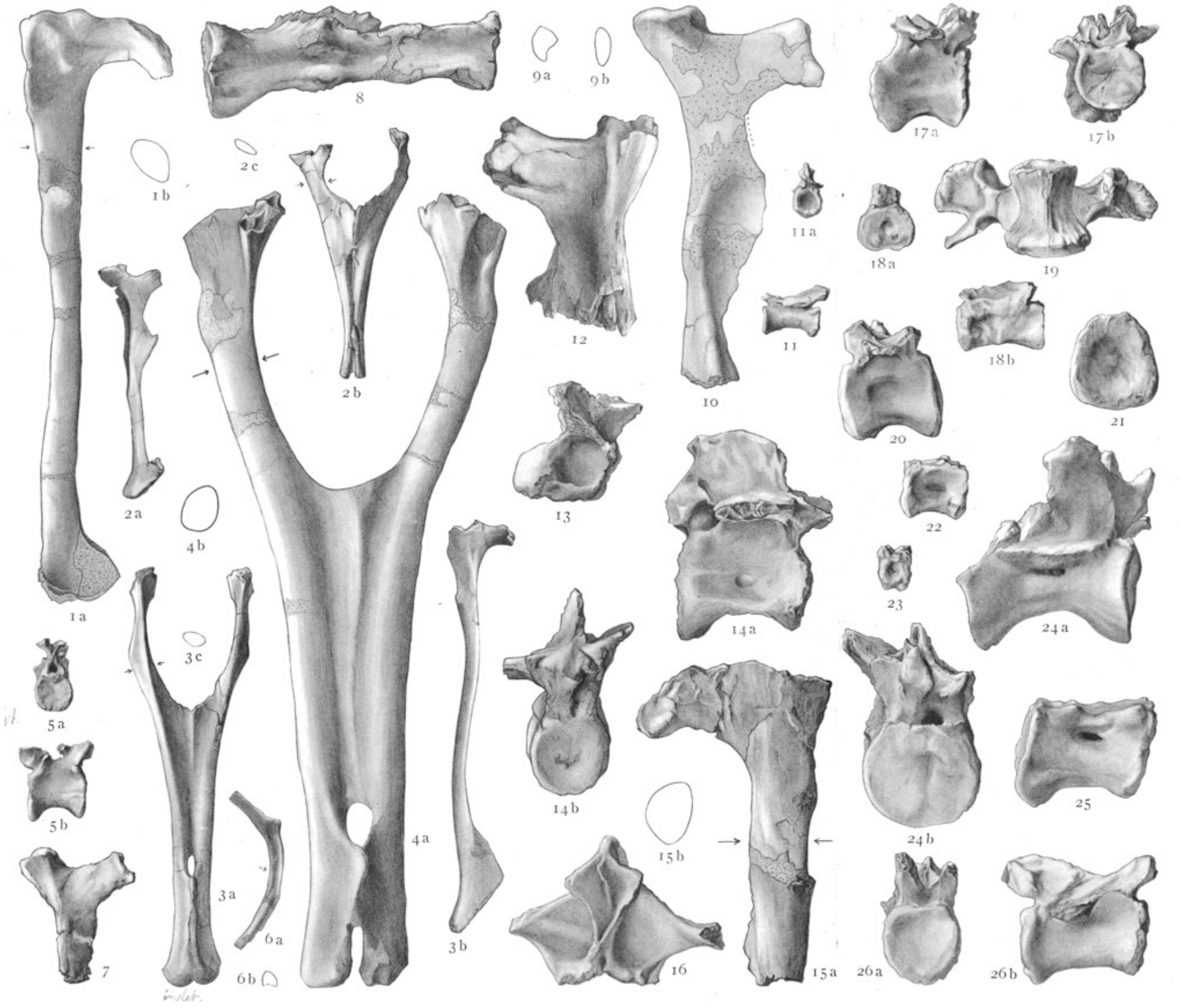

Fig. 13 Material of the theropod dinosaur *Bahariasaurus ingens*, including the holotype (*4*, *9*, *10*), and indeterminate theropods from the Upper Cretaceous Bahariya Formation. *1* Pubes of *Bahariasaurus* in left lateral view (*1a*) and in cross-sectional view (*1b*); *2* pubes of an indet. theropod in left lateral (*2a*), posterior (*2b*), and cross-sectional view (*2c*); *3* pubes of *Bahariasaurus* in posterior (*3a*) and cross-sectional view (*3b*); *4* pubes of *Bahariasaurus* in posterior (*4a*) and cross-sectional view (*4b*); *5* dorsal vertebra of an indeterminate theropod in posterior (*5a*) and right lateral view (*5b*); *6* fragmentary rib of an indeterminate theropod; *7* right ischium of *Bahariasaurus*; *8* three sacral vertebrae of *Bahariasaurus* in ventral view; *9* rib of *Bahariasaurus*; *10* right ischium of *Bahariasaurus*; *11* middle caudal vertebra of *Bahariasaurus* in posterior (*11a*) and left lateral view (*11b*); *12* left ischium of *Bahariasaurus*; *13* posterior cervical vertebra of *Bahariasaurus* in left lateral view; *14* posterior dorsal vertebra of *Bahariasaurus* in right lateral (*14a*) and anterior view (*14b*); *15* right pubis of *Bahariasaurus* in right lateral (*15a*) and cross-sectional view (*15b*); *16* neural arch of an anterior caudal vertebra of *Bahariasaurus* in posterior view; *17* anterior caudal vertebra of *Bahariasaurus* in left lateral (*17a*) and anterior view (*17b*); *18* posterior caudal vertebra of *Bahariasaurus* in anterior (*18a*) and left lateral view (*18b*); *19–23* posterior caudal vertebrae of indeterminate theropods in ventral (*19*), right lateral (*20*), anterior (*21*), right lateral (*22*) and anterior view (*23*); *24* posterior dorsal vertebra of *Bahariasaurus* in right lateral (*24a*) and anterior view (*24b*); *25* anterior caudal vertebra of *Bahariasaurus* in right lateral view; *26* middle caudal vertebra of *Bahariasaurus* in anterior (*25a*) and right lateral view (*25b*). All to the same scale. Modified after Stromer (1934b)

at Gebel El Dist (Stromer, 1932). The material comprises a dorsal vertebra, two caudal vertebrae, a left fragmentary scapula, left humerus, both ulnae, both radii, both femora and the left tibia, all belonging to one individual. Upon this material Stromer (1932) erected the new genus and species *Aegyptosaurus baharijensis* (Fig. 15), which he referred to the Titanosauridae, a relatively widespread family of sauropods from the Cretaceous known primarily from Gondwana. Additional material belonging to a much smaller individual was tentatively assigned to this taxon by Stromer (1932), including an indeterminate vertebra, one caudal vertebra and two cervical vertebrae from

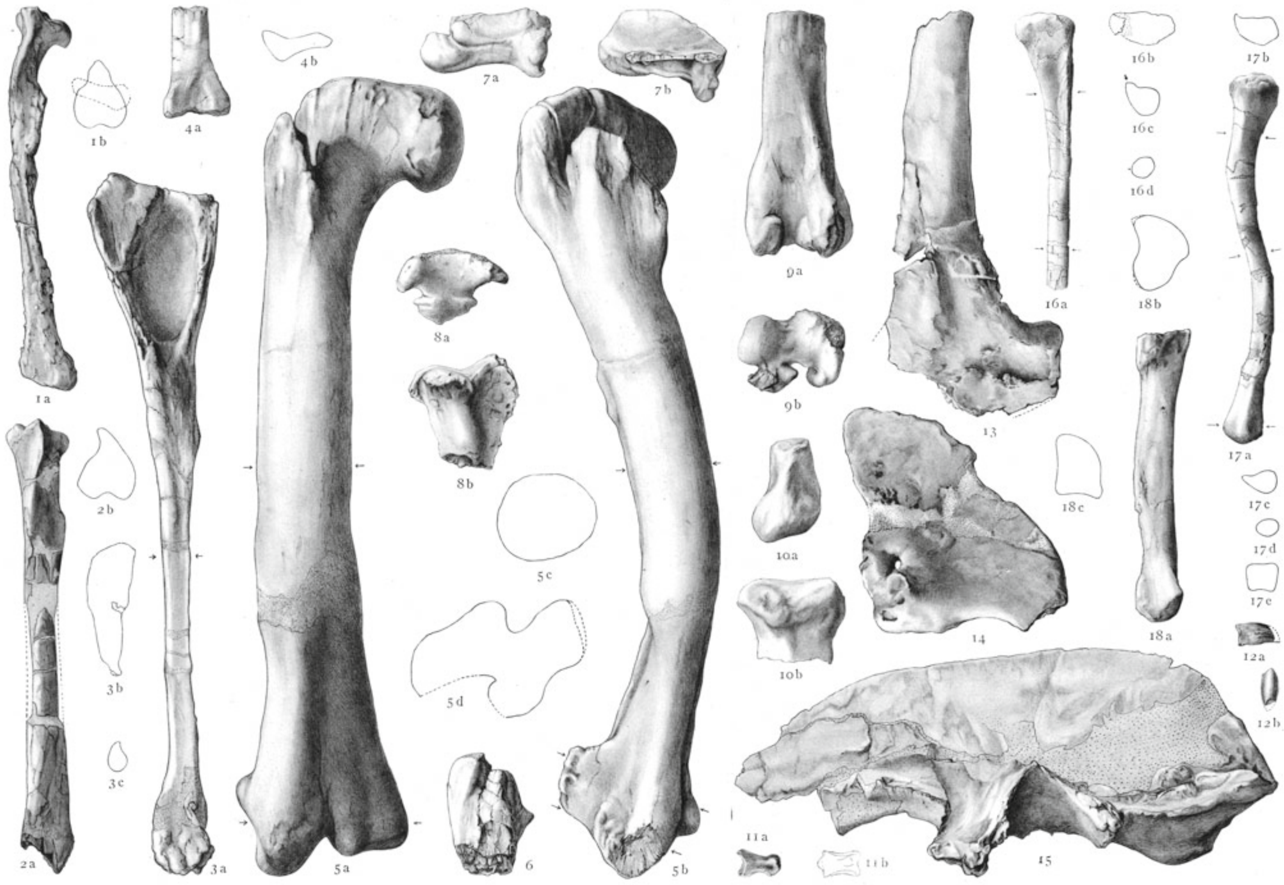

Fig. 14 Material of theropod dinosaurs from the Upper Cretaceous Bahariya Formation. *1* Left tibia of cf. *Elaphrosaurus* in anterior (*1a*) and cross-sectional view (*1b*); *2* left tibia of cf. *Elaphrosaurus* in anterior (*2a*) and cross-sectional view (*2b*); *3* left fibula of *Bahariasaurus* in medial (*3a*) and cross-sectional view (*3b–c*); *4* left tibia of aff. *Erectopus* in anterior (*4a*) and cross-sectional view (*4b*); *5* right femur of *Bahariasaurus* in anterior (*5a*), lateral (*5b*) and cross-sectional view (*5c–d*); *6* right proximal femur of cf. *Elaphrosaurus* in lateral view; *7* partial astragalus of an indeterminate theropod dinosaur in anterior (*7a*) and dorsal view (*7b*); *8* right proximal tibia of aff. *Erectopus* in dorsal (*8a*) and lateral view (*8b*); *9* right distal femur of aff. *Erectopus* in posterior (*9a*) and ventral view (*9b*); *10* right proximal femur of an indeterminate theropod in dorsal (*10a*) and posterior view (*10b*); *11* phalanx of an indeterminate theropod in right lateral (*11a*) and dorsal view (*11b*); *12* ungual phalanx of an indeterminate theropod in right lateral (*12a*) and dorsal view (*12b*); *13* left scapula of *Bahariasaurus* in lateral view; *14* left coracoid of *Bahariasaurus* in medial view; *15* right ilium of *Carcharodontosaurus* in medial view; *16* left proximal humerus of an indeterminate theropod in anterior (*16a*) and cross-sectional view (*16b–d*); *17* left humerus of an indeterminate theropod in posterior (*17a*) and cross-sectional view (*17b–e*); *18* right metatarsal IV of an indeterminate theropod in posterior (*18a*), dorsal (*18b*) and ventral view (*18c*). All to the same scale. Modified after Stromer (1936)

Gebel El Dist. Moreover, an isolated ungual phalanx of a large-sized sauropod (comparable in size to the holotype specimen) found at Gebel El Dist was referred to *Aegyptosaurus* (Stromer, 1932). Subsequently, fragmentary material from the 'Continental Intercalaire' of Niger has been referred to *Aegyptosaurus* by de Lapparent (1960), comprising caudal vertebrae, a partial rib and proximal portions of two metatarsals; this material might, however, represent indeterminate sauropod remains (Weishampel et al., 2004). More recently *Aegyptosaurus* was placed as a basal member of Titanosauria (Upchurch et al., 2004).

3.5.6 *Paralititan stromeri*

The second named sauropod dinosaur from the Bahariya faunal assemblage and the largest animal from this fauna is *Paralititan stromeri* (Smith et al., 2001). In fact, the genus represents the only tetrapod taxon from Bahariya named since Stromer's descriptions of this vertebrate assemblage. It was founded on a partial skeleton, including two fused sacral vertebrae, two caudal vertebrae, dorsal and sacral ribs, both fragmentary scapulae, both humeri, and the distal part of a metacarpal (Smith et al., 2001). The specimen represents one of the largest known sauropods, with a humeral length of 1.69 m (Smith et al., 2001). A dorsal vertebra from Gebel El

Dist (Fig. 15) originally described by Stromer (1932) was tentatively referred to *Paralititan* (Smith et al., 2001). The initial phylogenetic analysis of Smith et al. (2001) recovered *Paralititan* as a titanosaurid, while later, it was classified as a lithostrotian titanosaur (Upchurch et al., 2004). Recent studies recovered *Paralititan* as a saltasaurid titanosaur together with several other Late Cretaceous titanosaurs (Gorscak & O'Connor, 2019; Sallam et al., 2018). The holotype material of *P. stromeri* was discovered at Gebel Fagga in strata representing tidal channel and tidal flat facies, thus indicating that sauropods habitually entered mangrove environments (Smith et al., 2001). A shed tooth crown of *Carcharodontosaurus* was discovered between the bones of the holotype, indicating that the theropod scavenged on the carcass of *Paralititan* (Smith et al., 2001). Due to a presumed low water energy at the site, the carcass and the theropod tooth were most likely not transported to this locality, suggesting an autochthonous assemblage (Smith et al., 2001).

3.5.7 Indeterminate Sauropods (cf. *Dicraeosaurus* sp. and an Indeterminate Rebbachisaurid)

A poorly preserved caudal vertebra recovered from an unknown locality was referred to cf. *Dicraeosaurus* sp. by Stromer (1932). *Dicraeosaurus* is originally known from the Upper Jurassic dinosaur beds of Tendaguru, Tanzania (Janensch, 1914). Due to the fragmentary nature of the specimen and the temporal separation from other *Dicraeosaurus* occurrences, however, Stromer (1932) emphasised the tentative nature of this referral. In addition, Smith et al.

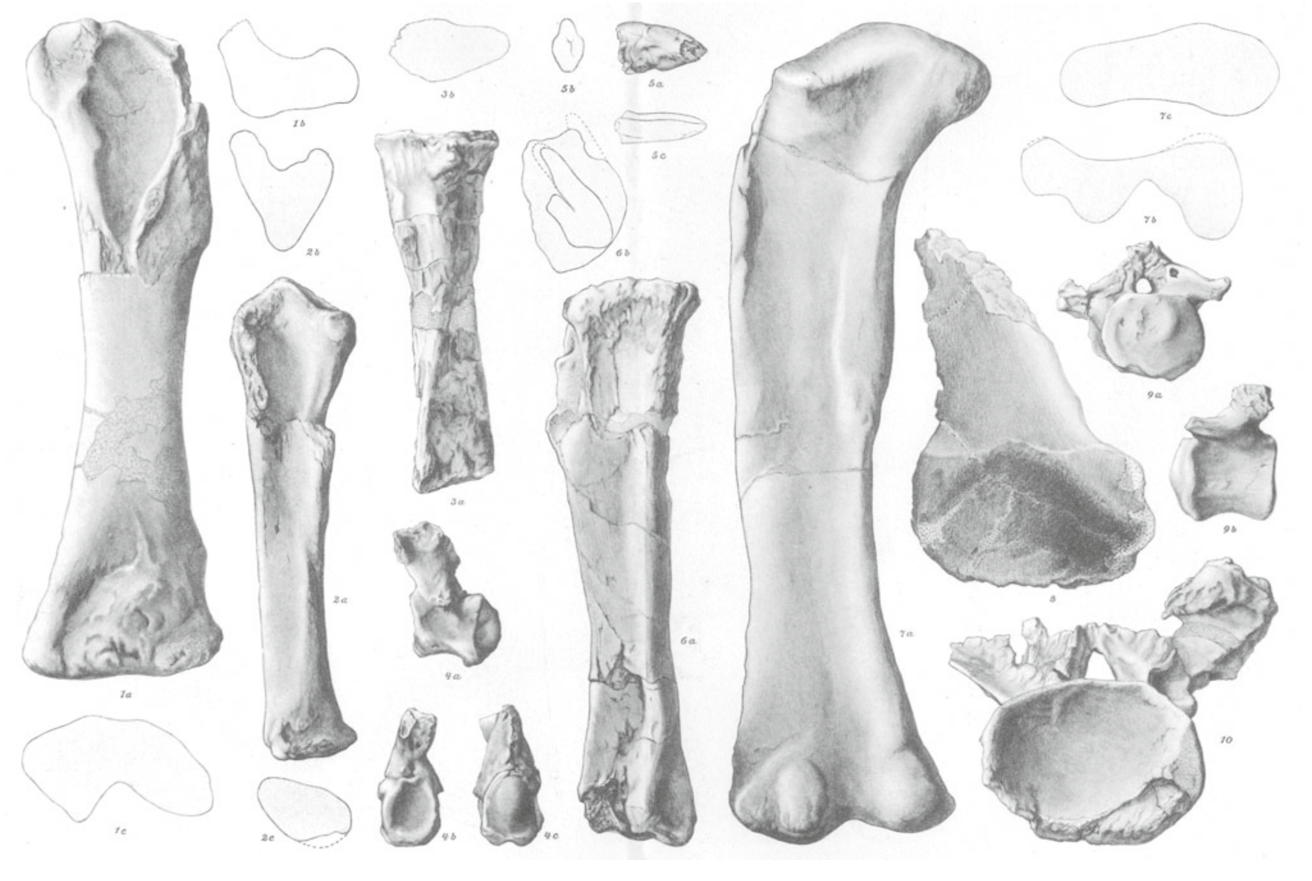

Fig. 15 Holotype material of the sauropod dinosaur *Aegyptosaurus baharijensis* (*1–9*) and an indeterminate sauropod dinosaur (*10*), both from the Upper Cretaceous Bahariya Formation. *1* Left humerus in anterior (*1a*) and cross-sectional view (*1b–c*); *2* right ulna in anterior (*2a*) and cross-sectional view (*2b–c*); *3* left radius in posterior (*3a*) and cross-sectional view (*3b*); *4* middle caudal vertebra in left lateral (*4a*), anterior (*4b*) and posterior view (*4c*); *5* ungual pedal phalanx in medial (*5a*) and cross-sectional view (*5b–c*); *6* left tibia in lateral (*6a*) and cross-sectional view (*6b*); *7* left femur in posterior (*7a*) and cross-sectional view (*7b–c*); *8* left scapula in lateral view; *9* anterior caudal vertebra in posterior (*9a*) and right lateral view (*9b*); *10* dorsal vertebra of an indeterminate sauropod dinosaur (might pertain to *Paralititan stromeri*, see text for explanations and Smith et al., 2001). All to the same scale. Modified after Stromer (1932)

(2001) noted the presence of a possible rebbachisaurid in the Bahariya faunal assemblage based on an isolated scapula. Rebbachisaurid remains are also known from several coeval deposits of northern Africa, including the Kem Kem beds of Morocco (Ibrahim et al., 2020a; Lavocat, 1954), and the 'Continental Intercalaire' of Tunisia (Fanti et al., 2012).

3.6 Plesiosauria

Remains of plesiosaurs are relatively common in the deposits of the Bahariya Formation but they mostly occur as isolated and fragmentary specimens (Stromer, 1935). Intriguingly, the fossils of plesiosaurs seem not to occur in the basal-most layers of the Bahariya depression, from which the majority of the vertebrate material was recovered (especially terrestrial ones), but instead they derive from a higher position in the sequence that probably reflects a marine depositional environment (Stromer, 1935). Moreover, the remains of plesiosaurs differ from those of the terrestrial vertebrates (e.g. dinosaurs) in terms of preservation and mostly comprise brownish bones as opposed to the often greyish to whitish bones of the dinosaurs (Stromer, 1935). This is in accordance of the presumed habitat of these predatory marine reptiles (Stromer, 1935, 1936). Similar to the other vertebrate groups, however, the most abundant and best-preserved specimens of plesiosaurs are known from Gebel El Dist (Stromer, 1935).

Although Stromer (1935) expected at least part of the plesiosaur material to belong to previously known species (because of the marine habitat and thus an assumed wider geographic distribution), he was unable to assign any of the material to a pre-existing plesiosaur taxon. Moreover, due to the fragmentary nature of the plesiosaur remains, Stromer (1935) also refrained from erecting a new genus or species based on the available material. Nonetheless, he distinguished at least four, and possibly up to seven, different plesiosaurs ('Plesiosaurier A–D') represented by isolated and associated cranial and postcranial material. Stromer (1936) noted that 'Plesiosaurier D' closely resembles *Trinacromerum* from the Upper Cretaceous of North America, thus suggesting a possible close relationship to that genus. Stromer (1936) favoured a near-shore and/or brackish habitat for the plesiosaurs of the Bahariya Formation, a hypothesis agreeing well with the presumed distinctiveness of the plesiosaur fauna. Interestingly, plesiosaur remains have not yet been reported from the Kem Kem beds of Morocco (Ibrahim et al., 2020a), despite a high degree of faunal similarity between both the Kem Kem and the Bahariya faunas and plesiosaurs representing a common faunal element in the latter.

3.7 Squamata (*Simoliophis* sp.)

Stromer (1914a, 1914b) reported the remains of a small snake from the Bahariya Formation, which were later described in detail by Nopcsa (1925). The material comprises numerous cervical, dorsal and caudal vertebrae, as well as rib fragments belonging to several individuals (Nopcsa, 1925). The remains were mostly recovered by Richard Markgraf, except for one individual that was collected by Ernst Stromer von Reichenbach (Nopcsa, 1925). Nearly all of the specimens originate from marine strata above the basal-most dinosaur bearing horizon, only one weathered vertebra was collected from this lower-most horizon (Nopcsa, 1925). Both Stromer (1914b) and Nopcsa (1925) referred the material to *Simoliophis* (spelled '*Symoliophis*'), otherwise known from the Cenomanian of France and Portugal, and at the time representing the oldest snake in the fossil record. Nopcsa (1925) also erected the family Simoliophidae for this genus. Originally referred to the type species, *Simoliophis rochebrunei*, the material from Egypt probably represents a new unnamed species of *Simoliophis* (Rage & Escuillié, 2003). Moreover, according to Rage and Escuillié (2003), Nopcsa (1925) actually mixed the vertebrae of two distinct snakes, one of them representing an unnamed genus; however, this view was subsequently challenged by Rage et al. (2016), who argued in favour of only one species (*Simoliophis* sp.) being represented by the material from Bahariya.

The dorsal vertebrae and dorsal ribs are remarkably thick and show a dense bone microstructure (pachyostosis), which, together with the predominantly marine depositional setting for most *Simoliophis* remains, led Nopcsa (1925) to conclude that *Simoliophis* inhabited marine environments. This interpretation was recently confirmed by Rage et al. (2016), who regarded *Simoliophis* as a slow swimmer, capable of long but shallow dives and inhabiting shallow marine and brackish environments. The pachyostotic vertebrae and ribs, already noted by Nopcsa (1925), might have been an adaptation to counteract buoyancy caused by the air-filled lungs (Nopcsa, 1925; Rage et al., 2016). The roughly coeval Kem Kem beds of Morocco yielded a diverse snake fauna with five different taxa of snakes, including *Simoliophis* (Ibrahim et al., 2020a). Thus, snakes probably were a common and diverse faunal element in the early Late Cretaceous of North Africa.

3.8 Palaeoecology

The palaeontology of the Bahariya Formation indicates an extremely productive ecosystem, comprising a wide range of fluviatile, brackish, tidal and near-shore marine environments, which supported a diverse vegetation dominated by extensive mangrove forests. The palaeoecosystem of the Bahariya Formation is characterised by a very high faunal diversity of vertebrates and an overabundance of predatory taxa, the latter of which has also been referred to as 'Stromer's Riddle' (McGowan & Dyke, 2009). Like in other roughly contemporaneous North African deposits (see above), aquatic and semi-aquatic taxa dominate the vertebrate assemblage from the Bahariya Formation. Especially numerous and diverse are the fishes with more than 20 taxa of cartilaginous fishes and more than 10 taxa of bony fishes. The fishes are not only taxonomically diverse but also with regard to their palaeoecology—some groups like lungfishes and polypterids likely inhabited freshwater ecosystems, while others such as hybodontid sharks were inhabitants of the marine realm (Stromer, 1936); still others likely lived in brackish environments, like the large coelacanth *Mawsonia* and the huge sawfish *Onchopristis* (Ibrahim et al., 2020a). Many tetrapods of the Bahariya Formation likely were at least partially dependent on this rich fish assemblage. This includes the abundant plesiosaurs, which likely hunted in brackish to near-shore marine environments as originally suggested by Stromer (1936). Moreover, at least three and up to five different crocodyliforms are present in the Bahariya ecosystem, most of which probably had a piscivorous diet. The small and likely terrestrial *Libycosuchus* is a notable exception and likely hunted small prey on land.

The overabundance of large-sized theropods in the local faunal assemblage is one of the most outstanding features of the Bahariya Formation and was originally also noted by Stromer (1936). At least five, and potentially up to eight, different theropods have been reported from the Bahariya Formation, three of which (*Spinosaurus*, *Carcharodontosaurus* and *Bahariasaurus*/*Deltadromeus*) are among the largest terrestrial carnivores of all time. This peculiarity has also been observed in coeval deposits of Northern Africa, most prominently in the Kem Kem beds of Morocco (Cavin et al., 2010; Ibrahim et al., 2020a; Russell, 1996). Based on the high diversity and abundance of fishes in the early Late Cretaceous of North Africa, it has been suggested that the great majority of carnivorous tetrapods, including the theropods, fed on aquatic prey items (Russell, 1996; Stromer, 1936). This might be particularly true for the spinosaurids from the Bahariya assemblage (*Spinosaurus aegyptiacus* and '*Spinosaurus* B'/*Sigilmassasaurus*) which likely subsisted on a fish diet (see above). An alternative theory that has been brought forward to account for the dominance of large carnivorous dinosaurs, is a sampling bias towards large theropods (McGowan & Dyke, 2009); however, this hypothesis has been rejected recently, and thus the overabundance of predators might indeed be real (Ibrahim et al., 2020a).

The abundance of large terrestrial (or semi-aquatic) carnivores contrasts sharply with the rarity of terrestrial herbivores, which so far only comprise sauropod dinosaurs. This includes the large-sized *Aegyptosaurus*, the gigantic *Paralititan* and two indeterminate sauropods (a dicraeosaurid and a rebbachisaurid). Again, this situation is similar to that of other North African vertebrate assemblages of a similar age (Benyoucef et al., 2015; Ibrahim et al., 2020a). One potential reason for this might be the patchy distribution of vegetation in these coastal environments (Ibrahim et al., 2020a). Evidence for theropod dinosaurs feeding on the sauropods exists in the form of a shed tooth crown of the large-sized *Carcharodontosaurus* between the holotype skeleton of *Paralititan* (Smith et al., 2001). Ornithischians, albeit being a common faunal component in most Early and Late Cretaceous Mesozoic terrestrial ecosystems, are completely absent from the Bahariya Formation. Mammals and birds are also completely absent from the Bahariya Formation thus far. Furthermore, neither of them has been described from the well-sampled Kem Kem beds of Morocco, or other contemporaneous deposits of Northern Africa that yielded a similar vertebrate fauna (Ibrahim et al., 2020a). It has been hypothesised that small multicuspid crocodyliforms with a presumed insectivorous and herbivorous diet replaced mammals in the Kem Kem ecosystem (Ibrahim et al., 2020a) and the same might have been true for the Bahariya ecosystem. Other small-sized terrestrial vertebrates are unknown from the Bahariya assemblage as well, the small marine squamate *Simoliophis* being the only exception. Pterosaurs have only recently been reported from the Bahariya Formation based on an isolated first-wing phalanx (Salem et al., 2018), although they are a common faunal element in the very similar Kem Kem beds (e.g. Martill et al., 2020).

4 Tetrapod Trackways from the Abu Agag Formation (Turonian)

The Abu Agag Formation has yielded tetrapod footprints from the Upper Cretaceous (Demathieu & Wycisk, 1990). The tracks were originally discovered in the 1980s during stratigraphical and sedimentological fieldwork by the Technical University of Berlin in southeastern Egypt (Fig. 1) and northern Sudan (Demathieu & Wycisk, 1990). As vertebrate tracks are generally rarely reported in the Cretaceous of Northern Africa and the time interval covered by the Abu Agag Formation is poorly known in the region, these footprints offer important insights into the composition and palaeoecology of these terrestrial ecosystems.

4.1 Geological and Palaeoenvironmental Setting

The fluviatile sedimentary rocks of the Abu Agag Formation comprise basal conglomerates that grade up into coarse-grained cross-bedded sandstones and mudstones, directly overlying Precambrian basement (Demathieu & Wycisk, 1990; El Sharkawi & Mesaed, 1996; Klitzsch & Wycisk, 1987). The Abu Agag Formation represents a regressional phase in the area and is in turn overlain by the shallow marine Upper Cretaceous (Coniacian–Santonian) Timsah Formation (El Sharkawi & Mesaed, 1996). The depositional environments of the Abu Agag Formation range from channel lag deposits (basal conglomerates) to distal channels of low sinuosity rivers and braided streams (cross-bedded sandstones), as well as to floodplain deposits with occasional paleosol development (mudstone-dominated facies to the top) (Demathieu & Wycisk, 1990; El Sharkawi & Mesaed, 1996). The age of the formation is considered to be Turonian (El Sharkawi & Mesaed, 1996; Hendriks et al., 1987; Klitzsch & Wycisk, 1987), though it might turn out to be somewhat older due to the lack of conclusive dating for the succession (Demathieu & Wycisk, 1990).

4.2 Tetrapod Trackways

The tracks of the Abu Agag Formation occur in several different stratigraphic horizons at three different locations in Egypt, 75–80 km south and 15–30 km north of Aswan (Demathieu & Wycisk, 1990). The first location, situated 80 km south of Aswan, preserves four different trackways, for which tracemakers could be identified (Demathieu & Wycisk, 1990). The first of these trackways is a small pentadactyl trackway resembling the ichnogenus *Capitosauroides* and probably representing a small amphibian, similar to a salamander with an estimated total length of 40 cm. The second trackway comprises two footprints that are comparable to the ichnotaxon *Rhynchosauroides* and likely were produced by a small lepidosaur, about 20 cm in length. The third trackway shows similarities to *Rotodactylus* and consists of two left footprints of a small quadrupedal animal, probably an archosaur with long limbs. The fourth trackway comprises a manus imprint and two small tridactyl footprints that are comparable to the ichnogenus *Amblydactylus* and were likely made by a very small ornithischian dinosaur. In addition, the site yielded indeterminate tracks that were probably made on wet mud and thus are badly preserved; in contrast, the identifiable tracks were likely produced on dry sediment.

The second locality from the Abu Agag Formation that preserves tetrapod tracks is situated 75 km south of Aswan (Demathieu & Wycisk, 1990). Although the footprints from this site are generally poorly preserved, two different trackways were identified. Among them is a small trackway that resembles the ichnotaxon *Rhynchosauroides*, and was likely produced by a small lepidosaur with a length of about 40 cm. The second trackway consists of two footprints from a small quadrupedal animal of uncertain affinities, comparable to the ichnogenus *Gallegosichnus*, but it might have been produced by a mammal-like animal. The third location, 15 km north of Aswan, yielded indeterminate tracks that were made in wet mud and thus are badly preserved, as well as one large and well-preserved four-toed footprint resembling *Chirotherium* (Demathieu & Wycisk, 1990). The latter probably represents a large archosaur with an estimated total length of 4–5 m.

The tracks are all preserved in fluviatile to lacustrine sedimentary rocks that were laid down in low-energy environments of channel and overbank deposits (Demathieu & Wycisk, 1990). Remarkably, the tracks are mostly assignable to small animals—tracks of large vertebrates are missing with the exception of one footprint of a large-sized archosaur. The local vertebrate assemblage as reconstructed from the ichnites includes amphibians, lepidosaurs, mammal-like animals, small (ornithischian?) dinosaurs, as well as small and large archosaurs of uncertain affinities (Demathieu & Wycisk, 1990). If some of the small tracks from the Abu Agag Formation indeed represent ornithischians, as suggested by Demathieu and Wycisk (1990), this would constitute one of the only (if not the only) record of ornithischians from post-Cenomanian deposits in Africa (see also Lamanna et al., 2004). Similarly, the small tracks potentially produced by mammals (Demathieu & Wycisk, 1990) would represent one of the very few mammalian occurrences in Upper Cretaceous deposits from continental Africa. Unfortunately, the poor preservation of these tracks makes their assignment uncertain (Demathieu & Wycisk, 1990; Lamanna et al., 2004).

5 The Vertebrate Fauna of the Quseir Formation (Campanian)

The Upper Cretaceous Quseir Formation has yielded a diverse fauna of terrestrial vertebrates, representing the second richest Cretaceous continental assemblage from Egypt after the Bahariya Formation (see above). Numerous different groups are known from these deposits, including fishes, turtles, crocodyliforms and dinosaurs. Due to the young age of the formation, this vertebrate fauna offers most important insights into latest Cretaceous (Campanian–Maastrichtian) terrestrial ecosystems of continental Africa, a time period that is extremely underrepresented on this continent.

5.1 Geological and Palaeoenvironmental Setting

The Quseir Formation has a widespread distribution in Egypt but the majority of fossil vertebrate material has been reported from the Dakhla and Kharga Oases in the Western Desert of Egypt as well as from the Nile Valley (Fig. 1). The Quseir Formation is also known as the 'variegated shale' of the Nubia Formation (Awad & Ghobrial, 1966; Lamanna et al., 2004; Said, 1962), Baris Formation (Hendriks et al., 1987; Lamanna et al., 2004), Mut Formation (Barthel & Herrmann-Degen, 1981; Mahmoud, 2003), or the upper part of the Nubia Sandstone (Klitzsch et al., 1979; Mahmoud, 2003); the 'Nubian Sandstones' (German 'Nubischer Sandstein') of Stromer and Weiler (1930) from the Nile Valley are probably also referable to the Quseir Formation. The formation consists of variegated shales, mudstones and siltstone, with occasional phosphatic horizons (Sallam et al., 2016).

The depositional environment, in which these sediments were laid down, ranges from fluviatile, to brackish and shallow marine (Sallam et al., 2016). The palaeoflora as reconstructed by studies of the palynomorph assemblage from central Egypt is dominated by angiosperms, but pteridophytes, aquatic plants and freshwater algae seem to have been abundant as well, indicating warm and humid palaeoclimatic conditions (Mahmoud, 2003). Recently, evidence for wildfires in the ecosystems of the Quseir Formation has been mentioned based on the presence of charcoal attributable to gymnosperms (El Atfy et al., 2016). The Quseir Formation has been interpreted to be early to middle Campanian in age (Mahmoud, 2003; Sallam et al., 2016). In addition to the terrestrial (or semi-terrestrial) vertebrates outlined below, the Quseir Formation also yielded diverse but mostly fragmentary remains of elasmobranchians, teleosts and lungfishes (Churcher, 1995; Churcher & Iuliis, 2001; Churcher et al., 2006; Claeson et al., 2014; Stromer & Weiler, 1930), as well as scarce remains of marine reptiles including elasmosaurid sauropterygians and mosasaurs (Churcher, 1995; Stromer & Weiler, 1930).

5.2 Testudinata Indet.

Turtle remains are abundant in the Quseir Formation of the Kharga and Dakhla Oases and mostly consist of isolated shell elements—so far no cranial remains of turtles are known from the Quseir Formation (Sallam et al., 2016). Noteworthy among these turtle remains is a well-preserved and nearly complete shell that comprises both the carapace and plastron, missing most of the peripherals and the epiplastron (Sallam et al., 2016). The specimen belongs to a medium-sized turtle with an estimated carapace length of 50 cm and was discovered by a team from the Mansoura University south of Kharga Oasis in the basal part of the formation (Sallam et al., 2016). The turtle has been referred to the Pleurodira and shows similarities to Pelomedusoides (Sallam et al., 2016). In addition, four well-preserved and mostly complete turtle shells have been preliminarily reported, three of them comprising a complete plastron with a partial carapace and one comprising a plastron and carapace (Gawad & Abuelkheir, 2018). The specimens were discovered south of Kharga Oasis in the upper part of the Quseir Formation (Sallam et al., 2016). All of them probably belong to bothremydid pleurodires.

5.3 Crocodyliforms

Numerous crocodyliform remains have been collected from the Quseir Formation, comprising both cranial and postcranial remains of at least three different neosuchians (Saber et al., 2018; Sallam et al., 2016). These include an indeterminate dyrosaurid (Lamanna et al., 2004), a gavialoid neosuchian (Saber et al., 2020; Sallam et al., 2016) and the recently described *Wahasuchus egyptensis* (Saber et al., 2018).

5.3.1 *Wahasuchus egyptensis*

The type material of *Wahasuchus* was collected in the early 2000s from the Dakhla Oasis by a team of the Mansoura University (Saber et al., 2018). The holotype consists of a partial skull and a fragmentary left mandible assignable to one individual (Saber et al., 2018). Referred material comprises a partial braincase and skull roof, a partial left maxilla, a partial right premaxilla, a left dentary, a partial right mandible, two dorsal vertebrae, a right femur, a distal right tibia and a proximal left humerus (Saber et al., 2018). *Wahasuchus* probably represents a basal neosuchian that is remarkably different from both Gondwanan and European Late Cretaceous crocodyliforms, pointing to some degree of endemism in the Late Cretaceous terrestrial vertebrate faunas of Northern Africa (Saber et al., 2018). Therefore, Saber et al. (2018) suggested that some representatives of this Late Cretaceous North African fauna may have been regionally adapted to the southern Tethys area. This contrasts with the supposed affinities of other Late Cretaceous vertebrate groups such as titanosaurian sauropods, which show close relationships to members of neighbouring landmasses (South America, Eurasia) and thus suggests some degree of faunal interchange (Sallam et al., 2018). *Wahasuchus* likely was a semi-aquatic generalist preying upon fishes, turtles and terrestrial vertebrates (Saber et al., 2018).

5.3.2 Crocodyliformes Indet.

A left humerus, originally described as pertaining to an ornithischian (Awad & Ghobrial, 1966), was later referred to an indeterminate dyrosaurid crocodilian (Lamanna et al., 2004). The presence of dyrosaurids in the Quseir Formation has previously been also suggested by Churcher and Iuliis (2001). Dyrosaurids are generally regarded as predators of marine to brackish environments with a wide distribution and ranging from the Upper Cretaceous to the Eocene (de Andrade & Sayão, 2014; Khosla et al., 2009). Furthermore, well-preserved cranial remains of a long-snouted neosuchian crocodilian are known from the Kharga Oasis near Baris (Sallam et al., 2016). The largely complete skull probably pertains to a ‘thoracosaur’ gavialoid and thus might represent the oldest member of the Gavialoidea (Saber et al., 2020; Sallam et al., 2016). Stromer and Weiler (1930) reported on isolated crocodilian teeth and a partial femur from the ‘Nubian Sandstone’ of the Nile Valley that they referred to the Goniopholidae. Interestingly, these goniopholid teeth seem to be different from those described by Gemmellaro (1921) from the overlying Duwi Formation of the Nile Valley (see below).

5.4 Dinosauria

Dinosaur remains are relatively common in the deposits of the Quseir Formation, belonging to both theropod and sauropod dinosaurs (Salem et al., 2021; Sallam et al., 2016). Recently, a reasonably complete and well-preserved sauropod, *Mansourasaurus shahinae*, has been described from this formation representing the first named dinosaur taxon from the post-Cenomanian of Egypt (Sallam et al., 2018). Ornithischian remains mentioned by Awad and Ghobrial (1966) were later shown to represent a dyrosaurid crocodilian, thus limiting the occurrence of ornithischians to pre-Turonian times in continental Africa (Lamanna et al., 2004).

5.4.1 Theropoda Indet.

Theropods are represented mostly by isolated, fragmentary and indeterminate remains. Two isolated teeth that were found in 1993 near El Atrun in the Kharga Oasis by Dale Russell and Charles Churcher were tentatively referred to *Spinosaurus* and *Carcharodontosaurus* but were never described in detail (Churcher, 1995). An indeterminate partial caudal vertebra and a proximal fibula were recovered during expeditions of the Mansoura University from the Dakhla and Kharga Oasis respectively (Salem et al., 2021). The fibula described by Salem et al. (2021) resembles those of abelisaurids and might indicate the presence of this theropod family in the Quseir Formation. Abelisaurids are in general poorly documented from the Upper Cretaceous of Africa (for an overview, see Salem et al., 2021); a tooth from the overlying Duwi Formation of the Nile Valley near Idfu (see below) has also been referred to the Abelisauridae by Smith and Lamanna (2006). A small proximal theropod tibia from the ‘Nubian Sandstones’ of the Nile Valley was described by Stromer and Weiler (1930), and might potentially also belong to an abelisaurid (Smith & Lamanna, 2006).

5.4.2 *Mansourasaurus shahinae*

Mansourasaurus has a special role in the vertebrate assemblages of Egypt as it represents the best-known terrestrial vertebrate from the post-Cenomanian of the entire African continent (excluding Madagascar) and as such offers unique insights into the relationships of Egyptian Late Cretaceous ecosystems (Sallam et al., 2018). The holotype of *Mansourasaurus* comprises cranial fragments, both dentaries, cervical and dorsal vertebrae, ribs, scapulocoracoid, sternal plate, both humeri, a radius, metacarpal III, three metatarsals, osteoderms and indeterminate fragments, all pertaining to one individual (Sallam et al., 2018). This partial skeleton was discovered during an expedition of the Mansoura University in the upper part of the Quseir Formation in the Dakhla Oasis (Sallam et al., 2018). A phylogenetic analysis performed by Sallam et al. (2018) recovered *Mansourasaurus* as a saltasaurid titanosaurian and, more specifically, as the sister taxon of the Late Cretaceous European titanosaur *Lohuecotitan*. This clade (*Mansourasaurus* and *Lohuecotitan*), in turn, is closely related to Late Cretaceous titanosaurs from central Asia (*Nemegtosaurus* and *Opisthocoelicaudia*) and Europe (*Ampelosaurus* and *Paludititan*) (Sallam et al., 2018).

Therefore, *Mansourasaurus* offers new insights into the palaeobiogeography of African terrestrial vertebrates during the Late Cretaceous, providing evidence for a latest Cretaceous dispersal between Europe and northern Africa (Sallam et al., 2018). This theory has been previously proposed by several authors, although the exact timing and nature of these dispersals have remained controversial (for an overview of Late Cretaceous biogeographical relationships between Europe and Africa, see Buffetaut & Le Loeuff, 1991; Csiki-Sava et al., 2015; Gheerbrant & Rage, 2006; Pereda-Suberbiola, 2009; Rabi & Sebők, 2015). *Mansourasaurus* provides additional and important evidence for a close biogeographic connection between Africa and Europe (Sallam et al., 2018).

5.4.3 Sauropoda Indet.

Aside from the well-preserved holotype specimen of *Mansourasaurus shahinae*, the Quseir Formation has yielded two more partial skeletons of titanosaur sauropods. Both of them have been recovered from the Kharga Oasis, but neither of them has been properly described in detail yet (Lamanna et al., 2017; Salem et al., 2020). The first was discovered in the 1970s by a team of the Technical University of Berlin and comprises five dorsal vertebrae, and several appendicular elements (Díez Díaz et al., 2017; Lamanna et al., 2017). This specimen was only described in an unpublished thesis thus far, but a detailed study of the material is currently ongoing (Lamanna et al., 2017). The second skeleton was discovered in 2017 by a team from the Mansoura University and includes a cervical vertebra, five dorsal vertebrae, a caudal vertebra, and the articulated right tibia and astragalus (Salem et al., 2020). Work is currently in progress to describe this specimen as well (Salem et al., 2020). The preliminary results point to the presence of at least two different titanosaur sauropods in the Quseir Formation of Egypt (Salem et al., 2020).

In addition, several indeterminate sauropod remains have been described from the Quseir Formation recently. This includes a partial left femur from the Kharga Oasis, and the associated proximal parts of both the right tibia and fibula from the Dakhla Oasis, all referable to titanosauriform sauropods (Salem et al., 2021). Moreover, Salem et al. (2021) described a partial titanosauriform cervical vertebra from the Kharga Oasis, and two isolated titanosaurian caudal vertebrae from the Dakhla Oasis. Interestingly, one of the isolated caudal vertebrae exhibits a camellate internal morphology that is also found in saltasaurine titanosaurians and thus might suggest affinities of at least one sauropod from the Dakhla Oasis to this clade of Late Cretaceous South American titanosaurs (Salem et al., 2021). The sauropod dinosaurs from the Quseir Formation thus possibly show affinities to both South American and Laurasian titanosaurs (see above), indicating more complex biogeographical relationships of the Late Cretaceous dinosaurs from this region than previously thought.

5.4.4 Mammalia? Indet.

Stromer and Weiler (1930) reported a very small tooth from the 'Nubia Sandstone' of the Nile Valley that was discovered near Mahamid. The tooth has a preserved length of 5 mm, but the lower part (at least 3 mm) was lost during excavation (Stromer & Weiler, 1930). The tooth is elongated and flat with an oval cross-section at the base and a chisel-like morphology near the apical part (Stromer & Weiler, 1930: pl. I, Fig. 4a–e). Due to its peculiar morphology that is uncommon in reptiles, Stromer and Weiler (1930) referred it tentatively to an indeterminate mammal. At the same time, however, they stress that this referral should be viewed with caution due to the fragmentary preservation of the tooth and its peculiar morphology. Although the assignment of the tooth to a mammal is far from certain, it deserves a notion here, being the only report of a Mesozoic mammalian from Egypt.

6 The Vertebrate Fauna of the Duwi Formation (Campanian–Maastrichtian)

Fragmentary remains of abelisaurid theropods and crocodyliforms are known from the uppermost Cretaceous Duwi Formation of the Nile Valley (Fig. 1) (Gemmellaro, 1921; Smith & Lamanna, 2006). This represents one of only two occurrences of terrestrial vertebrates from the Maastrichtian of Egypt, the other being sauropod and turtle remains from the overlying Dakhla Formation (see below).

6.1 Geological and Palaeoenvironmental Setting

The Duwi Formation has a widespread distribution in central and southern Egypt, including the Dakhla and Kharga Oases as well as the Nile Valley. It is underlain by the Quseir Formation and overlain by the Dakhla Formation (El-Younsy et al., 2017), both of which also yielded terrestrial vertebrates, including dinosaurs (see above and below). The formation mainly consists of shales, limestones and phosphates and several massive oyster layers (Abdelhady et al., 2020; El-Ayyat & Kassab, 2004). The sediments were deposited in a shallow marine setting and marked the onset of fully marine conditions in Egypt following the late Cretaceous marine transgression of the region (El Ayyat, 2015; El-Ayyat & Kassab, 2004). The Duwi Formation is considered to be late Campanian to early Maastrichtian in age (El Ayyat, 2015; El Beialy, 1995; Hamama & Kassab, 1990; Kassab & Mohamed, 1996). The 'Phosphates' (German 'Phosphate') of Stromer and Weiler (1930) from the Nile Valley between Mahamid and Edfu (= Idfu) are probably referable to the Duwi Formation based on: (i) their distinctive richness in phosphatic layers; (ii) the abundance of oyster shell layers; and (iii) the 'Phosphates' are overlying the 'Nubian Sandstone' (the latter likely representing the Quseir Formation, which underlies the Duwi Formation, see below).

The marine deposits of the Duwi Formation have yielded a fauna of relatively low diversity, including invertebrates (El-Ayyat & Kassab, 2004; Hamama & Kassab, 1990; Kassab & Mohamed, 1996), osteichthyan and chondrichthyan fishes (Holloway et al., 2017; Salama et al., 2021; Sallam et al., 2016; Stromer & Weiler, 1930), and marine tetrapods such as sauropterygians (plesiosaurs) and mosasaurs (Churcher & Iuliis, 2001; Gemmellaro, 1921; Sallam et al., 2016). Terrestrial vertebrates are represented only by the presence of isolated and fragmentary crocodyliform and theropod remains (Gemmellaro, 1921; Smith & Lamanna, 2006). Isolated teeth of crocodyliforms were referred to the marine dyrosaurid *Dyrosaurus phosphaticus* and to an indeterminate member of the Goniopholidae (Gemmellaro, 1921). The terrestrial vertebrates (theropod dinosaurs and the semi-aquatic goniopholid crocodyliforms) were likely washed into the sea and thus offer insights into the faunal composition of the nearby coast. The low faunal diversity of the Duwi Formation and the occurrence of autochthonous oyster beds probably are the result of stressed environmental conditions (Abdelhady et al., 2020); additionally, the oyster shell layers are indicative of repetitive storm events (Abdelhady et al., 2020). The palaeoclimate was probably humid and tropical as evidenced by the palynomorph assemblage (El Beialy, 1995).

6.2 Abelisauridae Indet.

Gemmellaro (1921) reported the occurrence of several isolated theropod tooth crowns and an ungual phalanx that were recovered from Upper Cretaceous strata of the Nile Valley near Idfu (for details, see also Smith & Lamanna, 2006). Originally, the teeth were assigned to '*Megalosaurus*' *crenatissimus* (Gemmellaro, 1921), a theropod known from the Upper Cretaceous of Madagascar (Depéret, 1896), which was later referred to the new genus *Majungasaurus crenatissimus* (Lavocat, 1955). Subsequent discoveries of more complete skeletal material from Madagascar showed *Majungasaurus crenatissimus* (= '*Majungatholus*' *crenatissimus*) to be a derived abelisaurid theropod (Krause et al., 2007; Sampson et al., 1998). More recently, Smith and Lamanna (2006) re-evaluated the affinities of the theropod teeth from the Duwi Formation, showing that one tooth almost certainly belongs to an abelisaurid theropod (Smith & Lamanna, 2006). Although it is unlikely that the tooth indeed belongs to *Majungasaurus crenatissimus* due to the isolation of Madagascar prior to the Late Cretaceous, the study demonstrates that it represents a derived (instead of a more basal) abelisaurid (Smith & Lamanna, 2006). The presence of a derived abelisaurid in uppermost Cretaceous (post-Cenomanian) deposits from continental Africa has important biogeographic implications, suggesting connections between Africa and South America (where these derived abelisaurids likely originated) until the Late Cretaceous and thus weakens the hypothesis that Cretaceous African land vertebrates developed in isolation (Smith & Lamanna, 2006).

7 The Vertebrate Fauna of the Dakhla Formation (Maastrichtian–Palaeocene)

The Maastrichtian strata of the Dakhla Formation have yielded an isolated but well-preserved sauropod femur (Rauhut & Werner, 1997) that is one of only two Maastrichtian occurrences of terrestrial vertebrates from of Egypt (Fig. 1)—the other being isolated theropod and crocodyliform remains from the slightly older Duwi Formation of the Nile Valley near Idfu (see above). In addition, abundant and diverse remains of marine turtles are known from the same strata of the Dakhla Formation (Ammonite Hill Member) as the sauropod femur (de Lapparent de Broin & Werner, 1998). Although earlier fieldwork in the region conducted by the famous German palaeontologist Karl Alfred von Zittel from the University of Munich already lead to the discovery of marine reptiles and turtles, the material was unfortunately destroyed during the Second World War, similar to the famous Bahariya collection of Ernst Stromer von Reichenbach (see above). Subsequent expeditions of the Technical University of Berlin recovered a rich vertebrate assemblage, including the sauropod femur and most of the turtle remains.

7.1 Geological and Palaeoenvironmental Setting

The Dakhla Formation consists of dark grey shales that are often intercalated with fossiliferous siltstones and sandstones (Tantawy et al., 2001). The age of the Dakhla Formation ranges from the Campanian–Maastrichtian boundary to the early Palaeocene based on macrofossil (bivalves, ammonites) and microfossil (foraminifera, calcareous nannofossils) biostratigraphy (Tantawy et al., 2001). The sauropod femur described by Rauhut and Werner (1997) was found in the Ammonite Hill Member of the Dakhla Formation, which crops out only in the westernmost margin of the Dakhla Basin and comprises a lower Maastrichtian and an upper Palaeocene part (Rauhut & Werner, 1997). The Ammonite Hill Member consists of highly fossiliferous mudstones, siltstones, sandstones and limestones that represent an interfingering of distal alluvial to deltaic shallow marine depositional settings (Barthel & Herrmann-Degen, 1981; Rauhut & Werner, 1997). The palaeoclimate as inferred from clay minerals during the time of the deposition has been reconstructed as tropical to subtropical with seasonal humid conditions (Tantawy et al., 2001).

The fauna of the Ammonite Hill Member includes numerous invertebrate groups (bioturbation trace fossils of crustaceans, ammonites, bivalves, gastropods, echinoids, corals), plant remains (fruits of the mangrove plant *Nypa*), fishes (osteichthyans, elasmobranchians), as well as marine and terrestrial tetrapods (Barthel & Herrmann-Degen, 1981; Hedeny et al., 2021; Rauhut & Werner, 1997). Among the marine tetrapods are fragmentary remains of mosasaurs (*Prognathodon*), and elasmosaurid plesiosaurs (Rauhut & Werner, 1997; Werner & Bardet, 1996). Additionally, abundant and diverse remains of marine to brackish turtles were collected from the Ammonite Hill Member, probably representing at least six different species (de Lapparent de Broin & Werner, 1998). A sauropod femur is the only definitive representative of the terrestrial vertebrate fauna and indicates near-shore conditions (Rauhut & Werner, 1997).

7.2 Testudinata

Turtles are the most abundant vertebrates from the Ammonite Hill Member of the Dakhla Formation (de Lapparent de Broin & Werner, 1998). The material ranges from isolated remains to nearly complete skulls and shells, belonging to at least six different species (de Lapparent de Broin & Werner, 1998). The vast majority of the turtle specimens was collected in 1979 and 1980 by a team from the Technical University of Berlin under the leadership of Werner Barthel. Five different species of bothremydid pleurodirans and one indeterminate cryptodiran (known only from a humerus) are present in the assemblage (de Lapparent de Broin & Werner, 1998). Based on the humerus morphology of the indeterminate cryptodiran that closely resembles extant marine turtles, it was regarded as a marine turtle (de Lapparent de Broin & Werner, 1998). The bothremydids comprise indeterminate forms, *Taphrosphys* sp. and *T.* cf. *sulcatus*, as well as *Arenila krebsi* and *Zolhafah bella*, the last two of which were newly erected for material recovered from the Ammonite Hill Member (de Lapparent de Broin & Werner, 1998). Due to the marine depositional environment in which their remains have been found and the peculiar shell ornamentation, the bothremydids are likewise interpreted as inhabitants of marine and perhaps brackish environments (de Lapparent de Broin & Werner, 1998).

7.3 Sauropoda Indet.

The sauropod femur from the Dakhla Formation was also recovered in 1980 by the team from the Technical University of Berlin, from the Great Sand Sea of the Western Desert of Egypt, west of the Dakhla Oasis (Rauhut & Werner, 1997). The femur is well-preserved and nearly complete, only the proximal and distal portions are slightly abraded. Based on the presence of a well-developed lateral bulge of the femur, Rauhut and Werner (1997) argue that the femur might belong to either a brachiosaurid or a titanosaur sauropod. Due to the overall greater resemblance to brachiosaurids (and *Brachiosaurus* in particular) than to titanosaurs, the authors favour close affinities to this family and thus refer the femur to a brachiosaurid. The relatively small size of the specimen (proximo-distal length of 724 mm), together with the probable adult ontogenetic stage of the individual as indicated by the robustness of the shaft, suggests that the sauropod represented by the femur was a comparatively small animal (Rauhut & Werner, 1997). If indeed belonging to a brachiosaurid, the femur would represent the youngest record of the family in the fossil record, providing evidence for the survival of the lineage up to the latest Cretaceous. Moreover, the femur underscores how little is actually known of Late Cretaceous terrestrial ecosystems from continental Africa.

8 The Importance of Egyptian Mesozoic Terrestrial Ecosystems

The Mesozoic terrestrial vertebrate assemblages of Egypt as a whole offer significant insights into the diversity of terrestrial vertebrates in Africa and the evolution of continental Mesozoic ecosystems. Among these assemblages, the Bahariya Formation yielded by far the richest and most diverse vertebrate fauna, including numerous different chondrichthyan and osteichthyan fishes, abundant remains of turtles, several different crocodyliforms, as well as theropod and sauropod dinosaurs. In addition, it was the first well-known Cretaceous vertebrate fauna from Africa and many families that are now known from numerous different localities around the world (especially from Gondwana), have first been established on material from Bahariya. Most prominently, this includes the holotypes of the very large theropods *Spinosaurus* and *Carcharodontosaurus*, serving as the basis for the Spinosauridae and Carcharodontosauridae, respectively. Although similar faunas are now known to have been widespread across Northern Africa, the fauna from the Bahariya Formation represents the first well-studied of these early Late Cretaceous vertebrate assemblages and also yielded some of the best specimens (e.g. the holotypes of *Spinosaurus*, *Carcharodontosaurus*, *Bahariasaurus*, *Aegyptosaurus*) if not the only material of the respective vertebrate taxa known so far (e.g. *Paralititan*, *Libycosuchus*, *Stomatosuchus*).

Despite the sparse and often fragmentary terrestrial vertebrate remains recovered from the other Upper Cretaceous formations of Egypt (i.e. Abu Agag, Quseir, Duwi and Dakhla formations), they nonetheless offer significant insights into the evolution of life on land in the later parts of the Late Cretaceous, including the latest Cretaceous (Campanian, Maastrichtian)—a period, which is extremely poorly represented in continental Africa. Even isolated finds (single teeth and bones) can thus hold valuable information on palaeobiogeography (e.g. the abelisaurid tooth from the Duwi Formation) and the faunal composition of these latest Cretaceous vertebrate faunas (e.g. the sauropod femur from the Dakhla Formation). Some of these formations (especially the Quseir Formation) have just begun to reveal the richness and diversity of their vertebrate fauna, often with spectacular results—the holotype specimen of *Mansourasaurus* and its implications for the palaeobiogeography of the latest Cretaceous Tethys realm being a prime example. In the future, these rather poorly known vertebrate assemblages from the later part of the Late Cretaceous have a great potential to yield further significant insights into the evolution of the Cretaceous life on land in what is still one of the most enigmatic continents with respect to its vertebrate palaeontology—Africa.

Acknowledgements We would like to thank Haytham El Atfy (Mansoura University, Egypt and University of Tübingen, Germany) for the invitation to write this chapter and thus to contribute to this volume. In addition, it was a great chance to dive deeply into the Mesozoic terrestrial ecosystems of Egypt, which fascinated us for a long time. We would also like to express our gratitude to Zakaria Hamimi (Benha University, Egypt) for the kind assistance during the publication of this book chapter. We are thankful to two reviewers for their helpful comments and critical evaluation of this manuscript.

References

Abdelhady, A. A., Seuss, B., Fürsich, F. T., Ali, A., Abdel-Raheem, K. H. M., & Mohamed, R. S. A. (2020). Paleoenvironmental significance of the monospecific biostromes in the Campanian-Maastrichtian Duwi Formation (Eastern Desert, Egypt). *Sedimentary Geology, 408*, 105772.

Amiot, R., Buffetaut, E., Lécuyer, C., Wang, X., Boudad, L., Ding, Z., Fourel, F., Hutt, S., Martineau, F., Medeiros, M. A., Mo, J., Simon, L., Suteethorn, V., Sweetman, S., Tong, H., Zhang, F., & Zhou, Z. (2010a). Oxygen isotope evidence for semi-aquatic habits among spinosaurid theropods. *Geology, 38*, 139–142.

Amiot, R., Wang, X., Lécuyer, C., Buffetaut, E., Boudad, L., Cavin, L., Ding, Z., Fluteau, F., Kellner, A. W. A., Tong, H., & Zhang, F. (2010b). Oxygen and carbon isotope compositions of middle Cretaceous vertebrates from North Africa and Brazil: Ecological and environmental significance. *Palaeogeography, Palaeoclimatology, Palaeoecology, 297*, 439–451.

Apesteguía, S., Smith, N. D., Valieri, R. J., & Makovicky, P. J. (2016). An unusual new theropod with a didactyl manus from the Upper Cretaceous of Patagonia, Argentina. *PLoS ONE, 11*, e0157793.

Awad, G. H., & Ghobrial, M. G. (1966). Zonal stratigraphy of the Kharga Oasis. *General Egyptian Organization for Geological Research and Mining, 34*, 1–77.

Barthel, K. W., & Herrmann-Degen, W. (1981). Late Cretaceous and early Tertiary stratigraphy in the Great Sand Sea and its SE margins (Farafra and Dakhla oases), SW desert, Egypt. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie, 21*, 141–182.

Beevor, T., Quigley, A., Smith, R. E., Smyth, R. S. H., Ibrahim, N., Zouhri, S., & Martill, D. M. (2021). Taphonomic evidence supports an aquatic lifestyle for *Spinosaurus*. *Cretaceous Research, 117*, 104627.

Benton, M. J., Bouaziz, S., Buffetaut, E., Martill, D., Ouaja, M., Soussi, M., & Trueman, C. (2000). Dinosaurs and other fossil vertebrates from fluvial deposits in the Lower Cretaceous of southern Tunisia. *Palaeogeography, Palaeoclimatology, Palaeoecology, 157*, 227–246.

Benyoucef, M., Läng, E., Cavin, L., Mebarki, K., Adaci, M., & Bensalah, M. (2015). Overabundance of piscivorous dinosaurs (Theropoda: Spinosauridae) in the mid-Cretaceous of North Africa: The Algerian dilemma. *Cretaceous Research, 55*, 44–55.

Brusatte, S. L., & Sereno, P. C. (2007). A new species of *Carcharodontosaurus* (Dinosauria: Theropoda) from the Cenomanian of Niger and a revision of the genus. *Journal of Vertebrate Paleontology, 27*, 902–916.

Buffetaut, E. (1976). Der Land-Krokodilier *Libycosuchus* Stromer und die Familie Libycosuchidae (Crocodylia, Mesosuchia) aus der Kreide Afrikas. *Mitteilungen der Bayerischen Staatssammlung für Paläontologie und Historische Geologie, 51*, 1–20.

Buffetaut, E., Bussert, R., & Brinkmann, W. (1990). A new nonmarine vertebrate fauna in the Upper Cretaceous of northern Sudan. *Berliner Geowissenschaftliche Abhandlungen A, 120*, 183–202.

Buffetaut, E., & Le Loeuff, J. (1991). Late Cretaceous dinosaur faunas of Europe: Some correlation problems. *Cretaceous Research, 12*, 159–176.

Carrano, M. T., & Sampson, S. D. (2008). The phylogeny of Ceratosauria (Dinosauria: Theropoda). *Journal of Systematic Palaeontology, 6*, 183–236.

Carvalho, M. S. S., & Maisey, J. G. (2008). New occurrence of *Mawsonia* (Sarcopterygii: Actinistia) from the Early Cretaceous of the Sanfranciscana Basin, Minas Gerais, southeastern Brazil. *Geological Society, London, Special Publications, 295*, 109–144.

Catuneanu, O., Khalifa, M. A., & Wanas, H. A. (2006). Sequence stratigraphy of the Lower Cenomanian Bahariya Formation, Bahariya Oasis, Western Desert, Egypt. *Sedimentary Geology, 190*, 121–137.

Cavin, L., & Forey, P. L. (2001). Osteology and systematic affinities of *Palaeonotopterus greenwoodi* Forey 1997 (Teleostei: Osteoglossomorpha). *Zoological Journal of the Linnean Society, 133*, 25–52.

Cavin, L., & Forey, P. L. (2004). New mawsoniid coelacanth (Sarcopterygii: Actinistia) remains from the Cretaceous of the Kem Kem beds, Southern Morocco. In G. Arratia & A. Tintori (Eds.), *Mesozoic fishes 3—Systematics, paleoenvironments and biodiversity* (pp. 493–506). Verlag Dr. Friedrich Pfeil.

Cavin, L., & Forey, P. L. (2008). A new tselfatiiform teleost from the Upper Cretaceous (Cenomanian) of the Kem Kem beds, Southern Morocco. In G. Arratia, H.-P. Schultze, & M. V. H. Wilson (Eds.), *Mesozoic fishes 4—Homology and phylogeny* (pp. 199–216). Verlag Dr. Friedrich Pfeil.

Cavin, L., Suteethorn, V., Buffetaut, E., & Tong, H. (2007). A new Thai Mesozoic lungfish (Sarcopterygii, Dipnoi) with an insight into post-Palaeozoic dipnoan evolution. *Zoological Journal of the Linnean Society, 149*, 141–177.

Cavin, L., Tong, H., Boudad, L., Meister, C., Piuz, A., Tabouelle, J., Aarab, M., Amiot, R., Buffetaut, E., Dyke, G., Hua, S., & Le Loeuff, J. (2010). Vertebrate assemblages from the early Late Cretaceous of southeastern Morocco: An overview. *Journal of African Earth Sciences, 57*, 391–412.

Charig, A. J., & Milner, A. C. (1997). *Baryonyx walkeri*, a fish-eating dinosaur from the Wealden of Surrey. *Bulletin of the Natural History Museum Geology, 53*, 11–70.

Chiarenza, A. A., & Cau, A. (2016). A large abelisaurid (Dinosauria, Theropoda) from Morocco and comments on the Cenomanian theropods from North Africa. *PeerJ, 4*, e1754.

Churcher, C. S. (1995). Giant Cretaceous lungfish *Neoceratodus tuberculatus* from a deltaic environment in the Quseir (=Baris) Formation of Kharga oasis, western desert of Egypt. *Journal of Vertebrate Paleontology, 15*, 845–849.

Churcher, C. S., & Iuliis, G. D. (2001). A new species of *Protopterus* and a revision of *Ceratodus humei* (Dipnoi: Ceratodontiformes) from the Late Cretaceous Mut Formation of eastern Dakhleh Oasis, Western Desert of Egypt. *Palaeontology, 44*, 305–323.

Churcher, C. S., Iuliis, G. D., & Kleindienst, M. R. (2006). A new genus for the dipnoan species *Ceratodus tuberculatus* Tabaste, 1963. *Geodiversitas, 28*, 635–647.

Cione, A. L., Gouiric-Cavalli, S., Gelfo, J. N., & Goin, F. J. (2011). The youngest non-lepidosirenid lungfish of South America (Dipnoi, latest Paleocene–earliest Eocene, Argentina). *Alcheringa: An Australasian Journal of Palaeontology, 35*, 193–198.

Claeson, K. M., Sallam, H. M., O'Connor, P. M., & Sertich, J. J. W. (2014). A revision of the Upper Cretaceous lepidosirenid lungfishes from the Quseir Formation, Western Desert, central Egypt. *Journal of Vertebrate Paleontology, 34*, 760–766.

Coiffard, C., El Atfy, H. (this volume). The evolution of vegetation through the Cretaceous of Egypt. In: Z. Hamimi, H. Khozyem, T. Adatte, F. H. Nader, F. Oboh-Ikuenobe, M. K. Zobaa, H. El Atfy (Eds.), The Phanerozoic geology and natural resources of Egypt. Springer.

Csiki-Sava, Z., Buffetaut, E., Ősi, A., Pereda-Suberbiola, X., & Brusatte, S. L. (2015). Island life in the Cretaceous—Faunal composition, biogeography, evolution, and extinction of land-living vertebrates on the Late Cretaceous European archipelago. *ZooKeys, 469*, 1–161.

Cuff, A. R., & Rayfield, E. J. (2013). Feeding mechanics in spinosaurid theropods and extant crocodilians. *PLoS ONE, 8*, e65295.

Dal Sasso, C., Maganuco, S., Buffetaut, E., & Mendez, M. A. (2005). New information on the skull of the enigmatic theropod *Spinosaurus*, with remarks on its size and affinities. *Journal of Vertebrate Paleontology, 25*, 888–896.

Daqué, E. (1912). Die fossilen Schildkröten Ägyptens. *Geologische und Paläontologische Abhandlungen, Neue Folge, 10*, 275.

de Andrade, R. C. L. P., & Sayão, J. M. (2014). Paleohistology and lifestyle inferences of a dyrosaurid (Archosauria: Crocodylomorpha) from Paraíba Basin (Northeastern Brazil). *PLoS ONE, 9*, e102189.

de Lapparent, A. F. (1960). Les dinosauriens du "continental intercalaire" du Sahara central. *Mémoires de la Société Géologique de France, 88A*, 1–57.

de Lapparent de Broin, F. (2000). African chelonians from the Jurassic to the present: Phases of development and preliminary catalogue of the fossil record. *Palaeontologia Africana, 36*, 43–82.

de Lapparent de Broin, F., & Werner, C. (1998). New late Cretaceous turtles from the Western Desert of Egypt. *Annales de Paléontologie, 84*, 131–214.

Demathieu, G. R., & Wycisk, P. (1990). Tetrapod trackways from Southern Egypt and Northern Sudan. *Journal of African Earth Sciences (and the Middle East), 10*, 435–443.

Deparet, C., & Savornin, J. (1925). Sur la decouverte d'une faune de vertebres albiens a Timimoun (Sahara occidental). *Comptes Rendus de l'Académie des Sciences de Paris, 181*, 1108–1111.

Depéret, C. (1896). Note sur les dinosauriens sauropodes et théropodes du Crétacé supérieur de Madagascar. *Bulletin de la Société Géologique de France, 3*(24), 176–196.

Díez Díaz, V., Gorscak, E., Lamanna, M. C., Schwarz, D., & El-Dawoudi, I. (2017). The metatarsus of a Late Cretaceous titanosaur (Dinosauria: Sauropoda) from the Kharga Oasis of Egypt. In *15th Annual Meeting of the European Association of Vertebrate Palaeontologists. Information and Abstracts*.

El Atfy, H., Anan, T., Jasper, A., & Uhl, D. (2019). Repeated occurrence of palaeo-wildfires during deposition of the Bahariya Formation (early Cenomanian) of Egypt. *Journal of Palaeogeography, 8*, 28.

El Atfy, H., Sallam, H., Jasper, A., & Uhl, D. (2016). The first evidence of paleo-wildfire from the Campanian (Late Cretaceous) of North Africa. *Cretaceous Research, 57*, 306–310.

El Atfy, H., Coiffard, C., El Beialy, S. Y., & Uhl, D. (2023). Vegetation and climate change at the southern margin of the Neo-Tethys during the Cenomanian (Late Cretaceous): Evidence from Egypt. Plos One. https://doi.org/10.1371/journal.pone.0281008

El Ayyat, A. M. (2015). Lithostratigraphy, sedimentology, and cyclicity of the Duwi Formation (late Cretaceous) at Abu Tartur plateau, Western Desert of Egypt: Evidences for reworking and redeposition. *Arabian Journal of Geosciences, 8*, 99–124.

El-Ayyat, A. M., & Kassab, A. S. (2004). Biostratinomy and facies analysis of the Upper Cretaceous oyster storm shell beds of the Duwi Formation, Qusseir District, Red Sea Region, Egypt. *Journal of African Earth Sciences, 39*, 421–428.

El Beialy, S. Y. (1995). Campanian-Maastrichtian palynomorphs from the Duwi (Phosphate) Formation of the Hamrawein and Umm El Hueitat mines, Red Sea Coast, Egypt. *Review of Palaeobotany and Palynology, 85*, 303–317.

El Sharkawi, M. A., & Mesaed, A. A. (1996). Stratigraphic setting and paleoenvironment of the Coniacian-Santonian ironstones of Aswan, South Egypt. *Geological Society of Egypt, Special Publications, 2*, 243–278.

El-Younsy, A. R. M., Obaidalla, N. A., Philobbos, E. R., & Salman, A. M. (2017). High-resolution sequence stratigraphy of the Upper Cretaceous-Lower Paleogene succession, Gabal Qreiya area, Upper Egypt. *Arabian Journal of Geosciences, 10*, 531.

Evers, S. W., Rauhut, O. W. M., Milner, A. C., McFeeters, B., & Allain, R. (2015). A reappraisal of the morphology and systematic position of the theropod dinosaur *Sigilmassasaurus* from the "middle" Cretaceous of Morocco. *PeerJ, 3*, e1323.

Fanti, F., Contessi, M., & Franchi, F. (2012). The "Continental Intercalaire" of southern Tunisia: Stratigraphy, paleontology, and paleoecology. *Journal of African Earth Sciences, 73–74*, 1–23.

Forey, P. L., López-Arbarello, A., & MacLeod, N. (2011). A new species of *Lepidotes* (Actinopterygii: Semiontiformes) from the Cenomanian (Upper Cretaceous) of Morocco. *Palaeontologia Electronica, 14*, 1–12.

Gawad, A. M. K., & Abuelkheir, G. (2018). Quseir Testudines remains from the Late Cretaceous Kharga area, south western desert, Egypt. In *78th Annual Meeting 2018 of the Society of Vertebrate Paleontology. Abstract Volume*.

Gemmellaro, M. (1921). Rettili maëstrichtiani d'Egitto. *Giornale di Scienze Naturali ed Economiche, 32*, 339–351.

Gheerbrant, E., & Rage, J.-C. (2006). Paleobiogeography of Africa: How distinct from Gondwana and Laurasia? *Palaeogeography, Palaeoclimatology, Palaeoecology, 241*, 224–246.

Gorscak, E., & O'Connor, P. M. (2019). A new African titanosaurian sauropod dinosaur from the middle Cretaceous Galula Formation (Mtuka Member), Rukwa Rift Basin, Southwestern Tanzania. *PLoS ONE, 14*, e0211412.

Grandstaff, B. S. (2006). *Giant fishes from the Bahariya Formation, Bahariya Oasis, Western Desert, Egypt* [Ph.D. thesis] (pp. 1–185). University of Pennsylvania, Philadelphia.

Grandstaff, B. S., Smith, J. B., Lamanna, M. C., Lacovara, K. J., & Abdel-Ghani, M. S. (2012). *Bawitius*, gen. nov., a giant polypterid (Osteichthyes, Actinopterygii) from the Upper Cretaceous Bahariya Formation of Egypt. *Journal of Vertebrate Paleontology, 32*, 17–26.

Hamama, H. H., & Kassab, A. S. (1990). Upper Cretaceous ammonites of Duwi Formation in Gabal Abu Had and Wadi Hamama, Eastern Desert, Egypt. *Journal of African Earth Sciences (and the Middle East), 10*, 453–464.

Hassler, A., Martin, J. E., Amiot, R., Tacail, T., Godet, F. A., Allain, R., & Balter, V. (2018). Calcium isotopes offer clues on resource partitioning among Cretaceous predatory dinosaurs. *Proceedings of the Royal Society B: Biological Sciences, 285*, 20180197.

Hedeny, M. E., Kassab, W., Rashwan, M., El-Kheir, G. A., & Gawad, A. M. K. (2021). Bivalve borings in Maastrichtian fossil *Nypa* fruits: Dakhla Formation, Bir Abu Minqar, South Western Desert, Egypt. *Ichnos, 28*, 24–33.

Henderson, D. M. (2018). A buoyancy, balance and stability challenge to the hypothesis of a semi-aquatic *Spinosaurus* Stromer, 1915 (Dinosauria: Theropoda). *PeerJ, 6*, e5409.

Hendriks, F. L., Bowitz, J. P., & Kallenbach, H. (1987). Evolution of the depositional environments of SE-Egypt during the Cretaceous and early Tertiary. *Berliner Geowissenschaftliche Abhandlungen A, 75*, 49–52.

Holliday, C. M., & Gardner, N. M. (2012). A new eusuchian crocodyliform with novel cranial integument and its significance for the origin and evolution of Crocodylia. *PLoS ONE, 7*, e30471.

Holloway, W., Claeson, K., Sallam, H., El-Sayed, S., Kora, M., Sertich, J., & O'Connor, P. (2017). A new species of the neopterygian fish *Enchodus* from the Duwi Formation, Campanian, Late Cretaceous, Western Desert, central Egypt. *Acta Palaeontologica Polonica, 62*, 603–611.

Hone, D., & Holtz, T. (2021). Evaluating the ecology of *Spinosaurus*: Shoreline generalist or aquatic pursuit specialist? *Palaeontologia Electronica,* 1–28.

Hone, D. W. E., & Holtz, T. R. (2017). A century of *Spinosaurs*—A review and revision of the Spinosauridae with comments on their ecology. *Acta Geologica Sinica—English Edition, 91*, 1120–1132.

Hone, D. W. E., & Holtz, T. R. (2019). Comment on: Aquatic adaptation in the skull of carnivorous dinosaurs (Theropoda: Spinosauridae) and the evolution of aquatic habits in spinosaurids. *Cretaceous Research, 93*, 275–284.

brahim, N., Sereno, P. C., Varricchio, D. J., Martill, D. M., Dutheil, D. B., Unwin, D. M., Baidder, L., Larsson, H. C. E., Zouhri, S., & Kaoukaya, A. (2020a). Geology and paleontology of the Upper Cretaceous Kem Kem Group of eastern Morocco. *ZooKeys, 928*, 1–216.

Ibrahim, N., Maganuco, S., Dal Sasso, C., Fabbri, M., Auditore, M., Bindellini, G., Martill, D. M., Zouhri, S., Mattarelli, D. A., Unwin, D. M., Wiemann, J., Bonadonna, D., Amane, A., Jakubczak, J., Joger, U., Lauder, G. V., & Pierce, S. E. (2020b). Tail-propelled aquatic locomotion in a theropod dinosaur. *Nature, 581*, 67–70.

Ibrahim, N., Sereno, P. C., Sasso, C. D., Maganuco, S., Fabbri, M., Martill, D. M., Zouhri, S., Myhrvold, N., & Iurino, D. A. (2014). Semiaquatic adaptations in a giant predatory dinosaur. *Science, 345*, 1613–1616.

Janensch, W. (1914). Übersicht über die Wirbeltierfauna der Tendaguru-Schichten, nebst einer kurzen Charakterisierung der neu aufgeführten Arten Sauropoden. *Archiv für Biontologie, 3*, 81–110.

Janensch, W. (1920). Über *Elaphrosaurus bambergi* und die Megalosaurier aus den Tendaguru–Schichten Deutsch–Ostafrikas. In *Sitzungsberichte Der Gesellschaft Naturforschender Freunde Zu Berlin* (pp. 225–235).

Kampouridis, P., Hartung, J., & Augustin, F. J. (this volume). The Eocene – Oligocene vertebrate assemblages of the Fayum Depression, Egypt. In: Z. Hamimi, H. Khozyem, T. Adatte, F. H. Nader, F. Oboh-Ikuenobe, M. K. Zobaa, H. El Atfy (Eds.), The Phanerozoic geology and natural resources of Egypt. Springer.

Kassab, A. S., & Mohamed, A. S. (1996). Upper Cretaceous macrofossils from the Duwi Formation of the Nile Valley, southern Egypt. *Neues Jahrbuch für Geologie und Paläontologie—Abhandlungen,* 259–284.

Khalifa, M. A., & Catuneanu, O. (2008). Sedimentology of the fluvial and fluvio-marine facies of the Bahariya Formation (Early Cenomanian), Bahariya Oasis, Western Desert, Egypt. *Journal of African Earth Sciences, 51*, 89–103.

Khosla, A., Sertich, J. J. W., Prasad, G. V. R., & Verma, O. (2009). Dyrosaurid remains from the Intertrappean Beds of India and the Late Cretaceous distribution of Dyrosauridae. *Journal of Vertebrate Paleontology, 29*, 1321–1326.

Kilian, C. (1931). Des principaux complexes continentaux du Sahara. *Comptes Rendus de la Société Géologique de France, 9*, 109–111.

Klitzsch, E., Harms, J. C., Lejal-Nicol, A., & List, F. K. (1979). Major subdivisions and depositional environments of Nubia Strata, Southwestern Egypt. *AAPG Bulletin, 63*, 967–974.

Klitzsch, E., & Wycisk, P. (1987). Geology of the sedimentary basins of northern Sudan and bordering areas. *Berliner Geowissenschaftliche Abhandlungen A, 75*, 97–136.

Krause, D. W., Sampson, S. D., Carrano, M. T., & O'Connor, P. M. (2007). Overview of the history of discovery, taxonomy, phylogeny, and biogeography of *Majungasaurus crenatissimus* (Theropoda: Abelisauridae) from the Late Cretaceous of Madagascar. *Journal of Vertebrate Paleontology, 27*, 1–20.

Kuhn, O. (1936). Fossilium Catalogus I. Animalia Part 75: Crocodilia. W. Junk, Berlin, 144 pp.

Lacovara, K. J., Smith, J. R., Smith, J. B., & Lamanna, M. C. (2003). The Ten Thousand Islands Coast of Florida: A modern analog to low-energy mangrove coasts of Cretaceous epeiric seas. In *Proceedings of the 5th International Conference on Coastal Sediments* (pp. 1773–1784).

Lamanna, M. C., Gorscak, E., Díaz, V. D., Schwarz, D., & El-Dawoudi, I. (2017). Reassessment of a partial titanosaurian sauropod dinosaur skeleton from the Upper Cretaceous (Campanian) Quseir Formation of the Kharga Oasis, Egypt. In *15th Annual Meeting of the European Association of Vertebrate Palaeontologists. Information and Abstracts*.

Lamanna, M. C., Smith, J. B., Attia, Y. S., & Dodson, P. (2004). From dinosaurs to dyrosaurids (Crocodyliformes): Removal of the post-Cenomanian (Late Cretaceous) record of Ornithischia from Africa. *Journal of Vertebrate Paleontology, 24*, 764–768.

Lamanna, M. C., Smith, J. B., Lacovara, K. J., Dodson, P., & Attia, Y. (2000). New vertebrate discoveries from the Cretaceous of Egypt. *Journal of Vertebrate Paleontology, 20*, 53A.

Larsson, H. C. E., & Sues, H.-D. (2007). Cranial osteology and phylogenetic relationships of *Hamadasuchus rebouli* (Crocodyliformes: Mesoeucrocodylia) from the Cretaceous of Morocco. *Zoological Journal of the Linnean Society, 149*, 533–567.

Lavocat, R. (1954). Reconnaissance géologique dans les hammadas des confins algéro-marocains du sud. *Notes et Mémoires Du Service Géologiques, 116*, 1–147.

Lavocat, R. (1955). Les recherches de reptiles fossiles à Madagascar. *National Malgache, 7*, 203–207.

Lejal-Nicol, A., & Dominik, W. (1990). Sur la paleoflore a Weichseliaceae et a angiospermes du Cenomanien de la region de Bahariya (Egypte du Sud-Ouest). *Berliner Geowissenschaftliche Abhandlungen A, 120*, 957–991.

Luger, P., & Gröschke, M. (1989). Late Cretaceous ammonites from the Wadi Qena area in the Egyptian Eastern Desert. *Palaeontology, 32*, 355–407.

Mahmoud, M. S. (2003). Palynology and palaeoenvironment of the Quseir Formation (Campanian) from central Egypt. *Journal of African Earth Sciences, 36*, 135–148.

Martill, D. M., Smith, R., Unwin, D. M., Kao, A., McPhee, J., & Ibrahim, N. (2020). A new tapejarid (Pterosauria, Azhdarchoidea) from the mid-Cretaceous Kem Kem beds of Takmout, southern Morocco. *Cretaceous Research, 112*, 104424.

McGowan, A. J., & Dyke, G. J. (2009). A surfeit of theropods in the Moroccan Late Cretaceous? Comparing diversity estimates from field data and fossil shops. *Geology, 37*, 843–846.

Motta, M. J., Aranciaga Rolando, A. M., Rozadilla, S., Agnolín, F. E., Chimento, N. R., Brissón Egli, F., & Novas, F. E. (2016). New theropod fauna from the Upper Cretaceous (Huincul Formation) of northwestern Patagonia, Argentina. *New Mexico Museum of Natural History and Science Bulletin, 71*, 231–253.

Murray, A. M. (2000). The Palaeozoic, Mesozoic and early Cenozoic fishes of Africa. *Fish and Fisheries, 1*, 111–145.

Nopcsa, F. (1925). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 5. Die *Symoliophis*-Reste. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 30*, 1–27.

Nopcsa, F. (1926). Neue Beobachtungen an *Stomatosuchus*. *Centralblatt fur Mineralogie, Geologie und Paläontologie, 1926*, 212–215.

Nothdurft, W. E., & Smith, J. (2002). *The lost dinosaurs of Egypt* (1st ed., p. 242). Random House.

Novas, F. E., Agnolín, F. L., Ezcurra, M. D., Porfiri, J., & Canale, J. I. (2013). Evolution of the carnivorous dinosaurs during the Cretaceous: The evidence from Patagonia. *Cretaceous Research, 45*, 174–215.

Novas, F. E., de Valais, S., Vickers-Rich, P., & Rich, T. (2005). A large Cretaceous theropod from Patagonia, Argentina, and the evolution of carcharodontosaurids. *Naturwissenschaften, 92*, 226–230.

Pereda-Suberbiola, X. (2009). Biogeographical affinities of Late Cretaceous continental tetrapods of Europe: A review. *Bulletin de la Société Géologique de France, 180*, 57–71.

Pérez-García, A. (2017). A new turtle taxon (Podocnemidoidea, Bothremydidae) reveals the oldest known dispersal event of the crown Pleurodira from Gondwana to Laurasia. *Journal of Systematic Palaeontology, 15*, 709–731.

Peyer, B. (1925). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 6. *Ceratodus*-Funde. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 30*, 1–23.

Pol, D., Nascimento, P. M., Carvalho, A. B., Riccomini, C., Pires-Domingues, R. A., & Zaher, H. (2014). A new notosuchian from the Late Cretaceous of Brazil and the phylogeny of advanced notosuchians. *PLoS ONE, 9*, e93105.

Rabi, M., & Sebők, N. (2015). A revised Eurogondwana model: Late Cretaceous notosuchian crocodyliforms and other vertebrate taxa suggest the retention of episodic faunal links between Europe and Gondwana during most of the Cretaceous. *Gondwana Research, 28*, 1197–1211.

Rage, J.-C., & Escuillié, F. (2003). The Cenomanian: Stage of hindlimbed snakes. *Carnets de Géologie,* 1–11.

Rage, J.-C., Vullo, R., & Néraudeau, D. (2016). The mid-Cretaceous snake *Simoliophis rochebrunei* Sauvage, 1880 (Squamata: Ophidia) from its type area (Charentes, southwestern France): Redescription, distribution, and palaeoecology. *Cretaceous Research, 58*, 234–253.

Rauhut, O. W. M. (1995). Zur systematischen Stellung der afrikanischen Theropoden *Carcharodontosaurus* Stromer 1931 und *Bahariasaurus* Stromer 1934. *Berliner Geowissenschaftliche Abhandlungen A, 16*, 357–375.

Rauhut, O. W. M. (1999). A dinosaur fauna from the Upper Cretaceous (Cenomanian) of northern Sudan. *Palaeontologia Africana, 35*, 61–84.

Rauhut, O. W. M. (2003). The interrelationships and evolution of basal theropod dinosaurs. *Special Papers in Palaeontology, 69*, 1–213.

Rauhut, O. W. M., & Werner, C. (1997). First record of a Maastrichtian sauropod dinosaur from Egypt. *Palaeontologia Africana, 34*, 63–67.

Romano, C., Koot, M. B., Kogan, I., Brayard, A., Minikh, A. V., Brinkmann, W., Bucher, H., & Kriwet, J. (2016). Permian-Triassic Osteichthyes (bony fishes): Diversity dynamics and body size evolution. *Biological Reviews, 91*, 106–147.

Russell, D. A. (1995). China and the lost worlds of the dinosaurian era. *Historical Biology, 10*, 3–12.

Russell, D. A. (1996). Isolated dinosaur bones from the Middle Cretaceous of the Tafilalt, Morocco. *Bulletin du Muséum National d'Histoire Naturelle. Section C, Sciences de La Terre, Paléontologie, Géologie, Minéralogie, 18*, 349–402.

Saber, S., Sertich, J. J. W., El-Kheir, G. A., Ouda, K. A., El-Sayed, S., O'Connor, P. M., Seiffert, E. R., & Sallam, H. M. (2020). The oldest gavialoid crocodyliform ('thoracosaur') from the Campanian Quseir Formation of Baris Oasis, Western Desert, Egypt. In *80th Annual Meeting of the Society of Vertebrate Paleontology. Virtual 2020. Abstract Volume*.

Saber, S., Sertich, J. J. W., Sallam, H. M., Ouda, K. A., O'Connor, P. M., & Seiffert, E. R. (2018). An enigmatic crocodyliform from the Upper Cretaceous Quseir Formation, central Egypt. *Cretaceous Research, 90*, 174–184.

Said, R. (1962). *The geology of Egypt* (p. 377). Elsevier.

Salama, Y., Altoom, N. G., Allam, A. A., Ajarem, J. S., & Abd-Elhameed, S. (2021). Late Cretaceous anacoracid sharks (Squalicorax) from Duwi Formation, Gebel Duwi, central Eastern Desert, Egypt: Qualitative and quantitative analyses. *Historical Biology, 33*, 1–9.

Salem, B. S., El-Kheir, G. A., Lamanna, M. C., Gorscak, E., El-Sayed, S., & Sallam, H. M. (2020). A new titanosaurian sauropod dinosaur partial skeleton from the Late Cretaceous (Campanian) of the Kharga Oasis, Western Desert of Egypt. In *80th Annual Meeting of the Society of Vertebrate Paleontology. Virtual 2020. Abstract Volume*.

Salem, B. S., O'Connor, P. M., Gorscak, E., El-Sayed, S., Sertich, J. J. W., Seiffert, E. R., & Sallam, H. M. (2021). Dinosaur remains from the Upper Cretaceous (Campanian) of the Western Desert, Egypt. *Cretaceous Research, 123*, 104783.

Salem, B. S., Sallam, H. M., El-Sayed, S., Thabet, W., Antar, M. S., & Lamanna, M. C. (2018). New fossil diapsid remains from the Upper Cretaceous (Cenomanian) Bahariya Formation, Bahariya Oasis, Western Desert of Egypt. In *The 56th Annual Scientific Meeting. Scientific Program and Abstracts*. The Geological Society of Egypt.

Sallam, H. M., Gorscak, E., O'Connor, P. M., El-Dawoudi, I. A., El-Sayed, S., Saber, S., Kora, M. A., Sertich, J. J. W., Seiffert, E. R., & Lamanna, M. C. (2018). New Egyptian sauropod reveals Late Cretaceous dinosaur dispersal between Europe and Africa. *Nature Ecology & Evolution, 2*, 445–451.

Sallam, H. M., O'Connor, P. M., Kora, M., Sertich, J. J. W., Seiffert, E. R., Faris, M., Ouda, K., El-Dawoudi, I., Saber, S., & El-Sayed, S. (2016). Vertebrate paleontological exploration of the Upper Cretaceous succession in the Dakhla and Kharga Oases, Western Desert, Egypt. *Journal of African Earth Sciences, 117*, 223–234.

Salem, B. S., Lamanna, M. C., O'Connor, P. M., El-Qot, G. M., Shaker, F., Thabet, W. A., El-Sayed, S., & Sallam,H. M. (2022). First definitive record of Abelisauridae (Theropoda: Ceratosauria) from the Cretaceous Bahariya Formation, Bahariya Oasis, Western Desert of Egypt. *Royal Society Open Science, 9*, 220106.

Sampson, S. D., Witmer, L. M., Forster, C. A., Krause, D. W., O'Connor, P. M., Dodson, P., & Ravoavy, F. (1998). Predatory dinosaur remains from Madagascar: Implications for the Cretaceous biogeography of Gondwana. *Science, 280*, 1048–1051.

Schaal, S. (1984). Oberkretazische Osteichthyes (Knochenfische) aus dem Bereich von Bahariya und Kharga, Ägypten, und ihre Aussagen zur Paläökologie und Stratigraphie. *Berliner Geowissenschaftliche Abhandlungen A, 53*, 79.

Schweitzer, C. E., Lacovara, K. J., Smith, J. B., Lamanna, M. C., Lyon, M. A., & Attia, Y. (2003). Mangrove-dwelling crabs (Decapoda:

Brachyura: Necrocarcinidae) associated with dinosaurs from the Upper Cretaceous (Cenomanian) of Egypt. *Journal of Paleontology, 77*, 888–894.

Sereno, P. C., Dutheil, D. B., Iarochene, M., Larsson, H. C. E., Lyon, G. H., Magwene, P. M., Sidor, C. A., Varricchio, D. J., & Wilson, J. A. (1996). Predatory dinosaurs from the Sahara and Late Cretaceous faunal differentiation. *Science, 272*, 986–991.

Sereno, P. C., & Larsson, H. C. E. (2009). Cretaceous Crocodyliforms from the Sahara. *ZooKeys, 28*, 1–143.

Sereno, P. C., Wilson, J. A., & Conrad, J. L. (2004). New dinosaurs link southern landmasses in the Mid–Cretaceous. *Proceedings of the Royal Society of London. Series B: Biological Sciences, 271*, 1325–1330.

Slaughter, B. H., & Thurmond, J. T. (1974). A lower Cenomanian (Cretaceous) ichthyofauna from the Bahariya Formation of Egypt. *Annals of the Geological Society, Egypt, 4*, 25–40.

Smith, J. B., & Lamanna, M. C. (2006). An abelisaurid from the Late Cretaceous of Egypt: Implications for theropod biogeography. *Naturwissenschaften, 93*, 242–245.

Smith, J. B., Lamanna, M. C., Lacovara, K. J., Dodson, P., Smith, J. R., Poole, J. C., Giegengack, R., & Attia, Y. (2001). A giant sauropod dinosaur from an Upper Cretaceous mangrove deposit in Egypt. *Science, 292*, 1704–1706.

Smith, J. B., Lamanna, M. C., Mayr, H., & Lacovara, K. J. (2006). New information regarding the holotype of *Spinosaurus aegyptiacus* Stromer, 1915. *Journal of Paleontology, 80*, 400–406.

Stromer, E. (1914a). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. I. Die Topographie und Geologie der Strecke Gharaq-Baharije nebst Ausführungen über die geologische Geschichte Ägyptens. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Physikalische Klasse, 26*, 1–78.

Stromer, E. (1914b). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 1. Einleitung und 2. *Libycosuchus*. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Physikalische Klasse, 27*, 1–16.

Stromer, E. (1915). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 3. Das Original des Theropoden *Spinosaurus aegyptiacus* nov. gen., nov. spec. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Physikalische Klasse, 28*, 1–32.

Stromer, E. (1916). Richard Markgraf und seine Bedeutung für die Erforschung der Wirbeltierpaläontologie Ägyptens. *Centralblatt fur Mineralogie, Geologie und Paläontologie, 11*, 287–288.

Stromer, E. (1917). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 4. Die Säge des Pristiden Onchopristis numidus Haug sp. und über die Sägen der Sägehaie. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Physikalische Klasse, 28*, 1–28.

Stromer, E. (1925). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 7. *Stomatosuchus inermis* Stromer, ein schwach bezahnter Krokodilier und 8. Ein Skelettrest des Pristiden *Onchopristis numidus* Haug sp. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, 30*, 1–22.

Stromer, E. (1926). Ergebnisse meiner Forschungsreisen in den Wüsten Ägyptens. *Die Naturwissenschaften, 14*, 353–356.

Stromer, E. (1927). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 9. Die Plagiostomen, mit einem Anhang über käno- und mesozoische Rückenflossenstacheln von Elasmobranchiern. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, 31*, 1–64.

Stromer, E. (1931). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharijestufe (unterstes Cenoman). 10. Ein Skelett-Rest von *Carcharodontosaurus* nov. gen. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 9*, 1–22.

Stromer, E. (1932). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 11. Sauropoda. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 10*, 1–21.

Stromer, E. (1933). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 12. Die procölen Crocodilia. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 15*, 1–55.

Stromer, E. (1934a). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 14. Testudinata. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 25*, 1–26.

Stromer, E. (1934b). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 13. Dinosauria. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 22*, 1–79.

Stromer, E. (1935). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 15. Plesiosauria. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 26*, 1–55.

Stromer, E. (1936). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. VII. Baharije-Kessel und -Stufe mit deren Fauna und Flora. Eine ergänzende Zusammenfassung. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 33*, 1–102.

Stromer, E., & Weiler, W. (1930). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. VI. Beschreibung von Wirbeltier-Resten aus dem nubischen Sandsteine Oberägyptens und aus ägyptischen Phosphaten nebst Bemerkungen über die Geologie der Umgebung von Mahamid in Oberägypten. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 7*, 1–42.

Tantawy, A. A., Keller, G., Adatte, T., Stinnesbeck, W., Kassab, A., & Schulte, P. (2001). Maastrichtian to Paleocene depositional environment of the Dakhla Formation, Western Desert, Egypt: Sedimentology, mineralogy, and integrated micro- and macrofossil biostratigraphies. *Cretaceous Research, 22*, 795–827.

Taquet, P. (1976). Géologie et paleontologie du gisement de Gadoufaoua (Aptien du Niger). *Cahiers de Paléontologie. C.N.R.S.*, 1–191.

Tumarkin-Deratzian, A. R., Grandstaff, B. S., Lamanna, M. C., & Smith, J. B. (2004). New material of *Libycosuchus brevirostris* from the Cenomanian Bahariya Formation of Egypt. *Journal of Vertebrate Paleontology, 24*, 123A.

Upchurch, P., Barrett, P. M., & Dodson, P. (2004). Sauropoda. In D. B. Weishampel, P. Dodson, & H. Osmolska (Eds.), *The Dinosauria* (2nd ed., pp. 259–322). University of California Press.

Villalobus-Segura, E., Kriwet, J., Vullo, R., Stumpf, S., Ward, D. J., & Underwood, C. J. (2021). The skeletal remains of the euryhaline sclerorhynchoid *Onchopristis* (Elasmobranchii) from the 'Mid'-Cretaceous and their palaeontological implications. *Zoological Journal of the Linnean Society, 20*, 1–26.

von Huene, F. (1932). Die fossile Reptilordnung Saurischia: Ihre Entwicklung und Geschichte. 1 (1932). Borntraeger. *Monographien zur Geologie und Paläontologie, I*, 1–361.

von Huene, F. (1948). Short review of the lower tetrapods. *The Royal Society of South Africa Special Publications, Robert Broom Commemorative Volume, 1*, 65–106.

Vullo, R., Cappetta, H., & Néraudeau, D. (2007). New sharks and rays from the Cenomanian and Turonian of Charentes, France. *Acta Palaeontologica Polonica, 52*, 99–116.

Vullo, R., Guinot, G., & Barbe, G. (2016). The first articulated specimen of the Cretaceous mackerel shark *Haimirichia amonensis* gen. nov. (Haimirichiidae fam. nov.) reveals a novel ecomorphological adaptation within the Lamniformes (Elasmobranchii). *Journal of Systematic Palaeontology, 14*, 1003–1024.

Weiler, W. (1935). Ergebnisse der Forschungsreisen Prof. E. Stromers in den Wüsten Ägyptens. II. Wirbeltierreste der Baharije-Stufe (unterstes Cenoman). 16. Neue Untersuchungen an den Fischresten. *Abhandlungen der Bayerischen Akademie der Wissenschaften, Mathematisch-Naturwissenschaftliche Abteilung, Neue Folge, 32*, 1–57.

Weishampel, D. B., Barrett, P. M., Coria, R. A., Loeuff, J. L., Xing, X., Xijin, Z., Sahni, A., Gomani, E. M. P., & Noto, C. R. (2004). Dinosaur distribution. In D. B. Weishampel, P. Dodson, & H. Osmólska (Eds.), *The Dinosauria* (2nd ed., pp. 517–606). University of California Press.

Werner, C. (1989). Die Elasmobranchier-Fauna des Gebel Dist Member der Bahariya Formation (Obercenoman) der Oase Bahariya, Ägypten. *Palaeo Ichthyologica, 5*, 1–112.

Werner, C. (1990). Biostratigraphical results of investigations on the Cenomanian elasmobranchian fauna of Bahariya Oasis, Egypt. *Berliner Geowissenschaftliche Abhandlungen A, 120*, 43–956.

Werner, C. (1994). Die kontinentale Wirbeltierfauna aus der unteren Oberkreide des Sudan (Wadi Milk Formation). *Berliner Geowissenschaftliche Abhandlungen E, 13*, 221–249.

Werner, C., & Bardet, N. (1996). First record of elasmosaurs (Reptilia, Plesiosauria) in the Maastrichtian of the Western Desert of Egypt. *Berliner Geowissenschaftliche Abhandlungen E, 18*, 335–343.

Wessel, P., Smith, W. H. F., Scharroo, R., Luis, J., & Wobbe F. (2013). Generic Mapping Tools: Improved version released. *Eos, 94*, 409–410.

Zalmout, I. S., Mustafa, H. A., & Wilson, J. A. (2005). *Karkaemys arabicus*, a new side-necked turtle (Pleurodira, Bothremydidae) from the Upper Cretaceous Wadi Umm Ghudran Formation of Karak, Jordan. *Contributions from the Museum of Paleontology, University of Michigan, 31*, 155–177.

Zittel, K. A. (1883). Beiträge zut Geologie und Paläontologie der Libyschen Wüste und der angrenzenden Gebiete Ägyptens. *Palaeontographica, 30*, 1–147.

Felix J. Augustin is a paleontologist from Germany who focuses on terrestrial Mesozoic ecosystems. He graduated from the Technical University Freiberg (Germany) in 2016 with a B.Sc. degree and earned an M.Sc. degree from the University of Tübingen (Germany), where he is currently writing his Ph.D. His research interests focus on terrestrial Mesozoic vertebrates, ranging from taxonomy to paleoecology and taphonomy. His research interests span all aspects of vertebrate taxonomy, paleoecology and taphonomy of the Late Jurassic of Germany, the Late Jurassic and Early Cretaceous of northwestern China and the Late Cretaceous of Romania. He has participated in field trips to and excavations in Germany, Romania, Bulgaria and the United States. The Late Cretaceous vertebrates from Egypt have fascinated him for long, especially the peculiar dinosaur faunas.

Josephina Hartung is a vertebrate paleontologist focusing on Cenozoic mammals and Mesozoic sarcopterygians. Her study on mammals focuses on artiodactyls from the Miocene of Europe. She completed her B.Sc. studies at the Freie Universität Berlin and her M.Sc. at the Rheinische Friedrich Wilhelms Universität Bonn, both in Germany. During her M.Sc. degree, she studied the bovids from the late Miocene hominid locality of Hammerschmiede (Germany) and continued her research on ruminants from this locality as her Ph.D. project at the University of Tübingen. Together with the University of Bonn, she works on the evolution of Late Triassic coelacanths from Europe and South America.

Panagiotis Kampouridis is a vertebrate paleontologist with his main focus on the study of Old-World mammals. He completed a B.Sc. degree at the National and Kapodistrian University of Athens (Greece) where he focused on the Neogene and Quaternary terrestrial faunas of Greece and the adjacent region, including the world-renowned late Miocene localities of Pikermi and Samos (Greece). During his M.Sc. studies at the University of Tübingen (Germany) he expanded on the study of non-mammalian vertebrates, while working on the late Miocene hominid locality of Hammerschmiede (Germany). His Ph.D. dissertation focuses on the evolution of the Eurasian rhinocerotid genus *Chilotherium*. During this time, he has also expanded his studies on the Paleogene mammals of the Old-World, including the Eocene–Oligocene fauna of the Fayum (Egypt).