The Eocene–Oligocene Vertebrate Assemblages of the Fayum Depression, Egypt

Panagiotis Kampouridis, Josephina Hartung, and Felix J. Augustin

Abstract

The Fayum has yielded one of the oldest and richest records of fossil mammals from Africa. Today, the Fayum Depression represents an oasis in the Western Desert of Egypt, south of Cairo, and contains several localities that are world renowned for their diverse Eocene to Oligocene vertebrate assemblages. The fossil sites of the Fayum area have provided numerous extraordinarily well-preserved vertebrate remains including complete skulls and partial skeletons of turtles, crocodiles, birds, and mammals. Thus, the Fayum Depression has shed light onto the evolution and biogeography of vertebrates during the Paleogene leading to the establishment of two new orders, several new families and subfamilies, and numerous new species of mammals. In recent years, these fossils have provided clues about ecological aspects of some groups using new methods such as stable isotope analysis and µCT scanning. Despite the fact that the Fayum Depression represents a historical excavation site that has been excavated and studied by numerous famous palaeontologists since the nineteenth century, the area continues to provide new insights into the evolution of mammals during the Eocene to Oligocene, greatly improving our understanding of early Cenozoic vertebrate evolution. This chapter presents a historical review of the excavations in the Fayum Depression and a taxonomic overview of its fossil fauna. Special focus was placed on the taxonomy and, where applicable, ecology of terrestrial mammals from the historical Paleogene Fayum localities.

Keywords

Egypt • Fayum Depression • Cenozoic • Paleogene • Mammalia • Vertebrate assemblages • Fossil fauna

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Abbreviations

AMNH	American Museum of Natural History, New York City, USA
BSPG	Bayerische Staatssammlung für Paläontologie und Geologie in München, Germany
DPC	Duke Lemur Center, Division of Fossil Primates, Durham, North Carolina, USA
GPIT	Palaeontological Collection of the University of Tübingen, Germany
MNHN	Muséum national d'Histoire naturelle, Paris, France
NHMUK	Natural History Museum of the United Kingdom London, UK
NHMW	Naturhistorisches Museum in Wien, Austria
SMNS	Staatliches Museum für Naturkunde Stuttgart, Germany

1 Introduction

The Fayum Depression (Fig. 1) represents today an oasis approximately 80 km southwest of Cairo, in the Western Desert of Egypt (El-Shabrawy & Dumont, 2009). The region is renowned for its plethora of fossiliferous localities, which demonstrate extremely rich and diverse Eocene to Oligocene vertebrate assemblages (Andrews, 1906a; Seiffert et al., 2008; Simons & Rasmussen, 1990). These vertebrate localities of the Fayum Depression have been excavated and studied extensively by numerous famous palaeontologists since the nineteenth century, including Charles W. Andrews, Eberhard Fraas, Ernst Stromer von Reichenbach, and Henry F. Osborn. These palaeontologists, along with many others after them, provided detailed studies about the Fayum fossils and revealed new information about the Eocene to Oligocene mammal communities of Africa, thereby elucidating the origin and early evolution of many mammal groups (e.g. de

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Vries et al., 2021; Simons, 2008; Simons & Rasmussen, 1990). Some of the most extensively studied mammal groups include the Proboscidea, Cetacea, and Primates, which significantly advanced our knowledge on these groups.

The aim of this chapter is mainly twofold: first, we present a historical review of the excavations that were carried out in the Fayum Depression, and second, we provide a taxonomic overview of its fossil vertebrate fauna. For this, we almost exclusively focused on the terrestrial vertebrates, but also refer to aquatic mammals, cetaceans, and sirenians, while other aquatic taxa such as fishes were excluded. As the majority of studies dealing with the palaeontology of the Fayum Depression focused on terrestrial mammals and cetaceans, this is also reflected herein and accordingly, these groups received the most attention, seconded by reptiles and birds. Moreover, a short introduction to the geology of the Fayum Depression and the three different terrestrial vertebrate-bearing formations is given at the beginning. Finally, as a conclusion, we discuss the importance of the Fayum Depression for our understanding of mammalian evolution.

2 Historical Overview

The first fossils from the Fayum Depression were discovered by Orlebar (1845), who studied the geology of the Egyptian deserts. He described many fossils, including several invertebrates, as well as plant remains, comprising up to 20-m-long tree trunks. Orlebar (1845) even reported some mammalian remains, without any description of the specimens though.

The German botanist Georg August Schweinfurth was the first to conduct a detailed geological survey in the area of the Fayum Depression in 1877. In 1879, he collected several shark teeth and cetacean bones from Gezirit El Qarn, a small island within the Birket Qarun Lake. Shortly after, this material was studied by Dames (1883a). Schweinfurth continued his work in the Fayum Depression, uncovering more vertebrate fossils (Schweinfurth, 1886). After receiving further material from Schweinfurth, Dames (1894) described the first fossil whale species from Egypt, *Zeuglodon osiris* (today known as *Saghacetus osiris*).

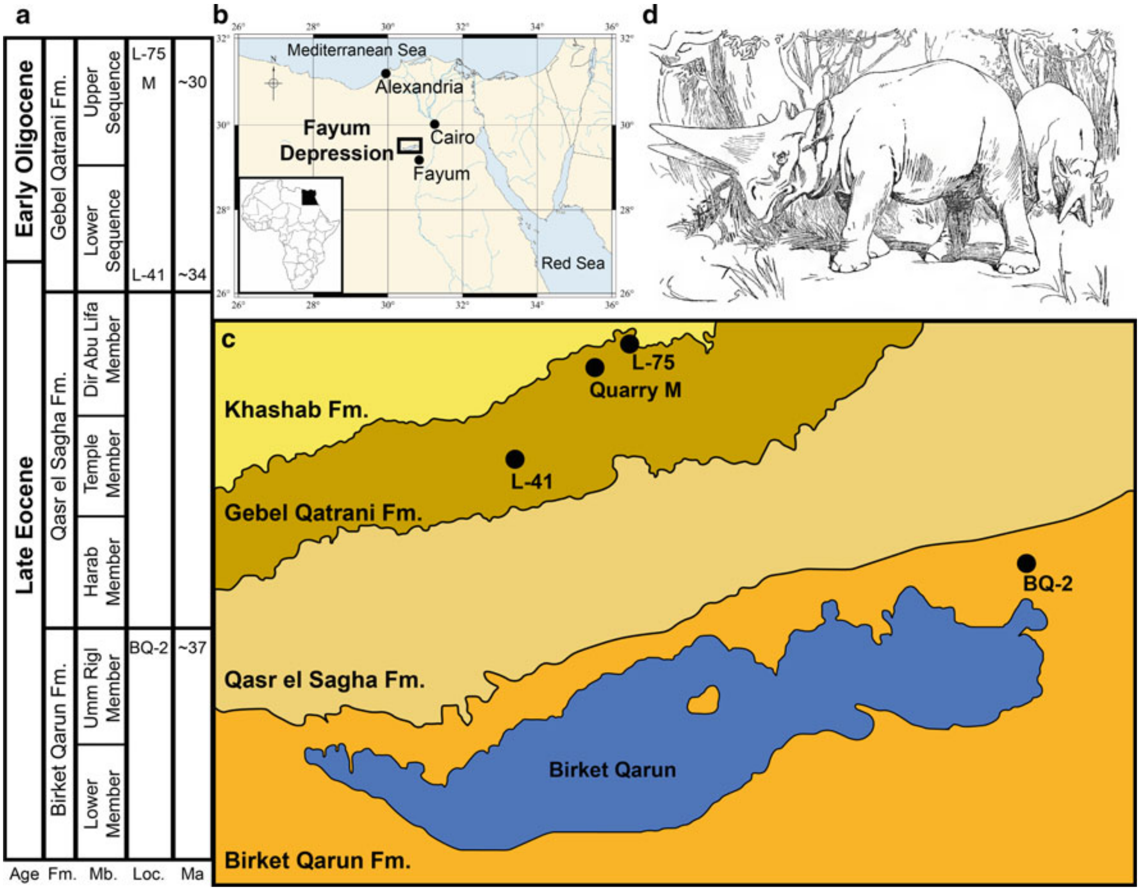

Fig. 1 Geographical and stratigraphical setting of the Fayum Depression (Egypt): **a** stratigraphical context of the Upper Eocene to Lower Oligocene Fayum deposits. **b** Geographical map of Egypt showing the position of the Fayum Depression, created with GMT6 (Wessel et al., 2013). **c** Geological map of the northern part of the Fayum Depression (modified after Sallam et al., 2011). **d** Reconstruction of the iconic *Arsinoitherium* in the Early Oligocene Fayum forest (Andrews, 1906a)

Later, in 1898, the British geologist Hugh John Llewellyn Beadnell was employed by the Egyptian Geological Survey to conduct a geological expedition to the Fayum Depression. Beadnell published his findings initially as a preliminary report on the Fayum Depression and its Paleogene fauna (Beadnell, 1901) and later in a monograph about the geology of the region (Beadnell, 1905). During his fieldwork in the marine sediments north of Birket Qarun, Beadnell and his team found numerous vertebrate fossils, which he sent to the Natural History Museum of the UK in London. There they were studied by British palaeontologist Andrews (1899), who was intrigued by the material and subsequently travelled several times to the Fayum Depression himself to collect fossils. In April 1901, Beadnell was accompanied by Andrews in his fieldwork in the Fayum Depression. Andrews returned to Egypt in the spring of 1902 and 1903, collecting a considerable number of specimens, which he included in his monumental monograph on the vertebrates from the Fayum fauna (Andrews, 1906a). This work represents, to this day, the most important and extensive study on the macrovertebrate fossils from Egypt.

Between 1897 and 1899, the German geologist Max Blanckenhorn was employed by the Geological Survey of Egypt to study the geology and collect fossils from Egypt. He published his findings in 1900, including an examination of the stratigraphy of the Fayum Depression (Blanckenhorn, 1900). In 1902, he returned to Egypt together with the German palaeontologist Ernst Freiherr Stromer von Reichenbach to collect fossils, including a large collection of mammal remains, which were sent to the palaeontological collection in Munich (Stromer, 1902). In November 1903, Stromer returned to Egypt for three months, mainly for the collection of Tertiary mammals, from the Fayum Depression (Stromer, 1904).

There, he met Richard Markgraf, an Austro-German fossil collector who was among the most important people who excavated fossils in the Paleogene as well as in the Cretaceous (see Augustin et al., 2023) of Egypt. In 1897, Markgraf joined the team of German palaeontologist Eberhard Fraas from Stuttgart, in a palaeontological expedition to the Fayum. Fraas taught Markgraf how to excavate fossils, and later, after recognising his skills, he hired him to continue collecting fossils for the Staatliches Museum für Naturkunde Stuttgart in Germany (SMNS) for many years. During his second expedition to the Fayum Depression, in 1903, Stromer was accompanied by Markgraf who was extremely helpful and remained there collecting many more fossils, which he sent to Munich for Stromer to study them (e.g. Stromer, 1903, 1904, 1908). In 1906, Fraas planned another expedition to the Fayum, which was organised and carried out thanks to Markgraf. They uncovered many important specimens that were sent to Stuttgart. Markgraf continued collecting fossils from the Paleogene of the Fayum Depression and the Cretaceous of the Bahariya Oasis (Augustin et al., 2023) until the First World War. He brought to light some of the most important finds from the Fayum area, such as a number of primate fossils. Because of his astonishing achievements in the collection of fossils in Egypt, Markgraf received the silver medal of Bene Merenti from the Bavarian Academy of Sciences in 1902 and the Medal of Merit of the Royal Württemberg Crown Order in 1904. Furthermore, several species were named in his honour, including the primates *Propliopithecus markgrafi* from the Fayum Depression (Schlosser, 1910) and *Libypithecus markgrafi* from the Miocene Wadi el Natrun (Stromer, 1913). Nonetheless, he did not receive any real fame or fortune for his services and lived a very simple life. Unfortunately, nowadays his name has fallen into oblivion, despite his incredible impact on the knowledge of the fossil vertebrate faunas of Africa and their significance for our understanding of vertebrate evolution during the Paleogene.

Another palaeontological expedition to the Fayum Depression was organised by Marcellin Boule and Jean Albert Gaudry from the Muséum national d'Histoire naturelle (MNHN) in Paris and carried out in 1904 by René Fourtau. He was a French civil engineer who worked for the Geological Survey of Egypt and studied invertebrates, mainly echinoderms. During their two-week expedition they were able to collect about 30 mammalian fossils that were transferred to the MNHN (Tabuce, 2016).

Henry Fairfield Osborn, an American palaeontologist who worked intensively on the evolution of Proboscidea at the American Museum of Natural History (AMNH), decided to organise an expedition to the Fayum Depression, in 1907, after reading the findings of Andrews (1906a), that had a significant impact on the understanding of proboscideans. Osborn's team was joined by Walter Granger and George Olsen, who oversaw the expedition that represented America's first palaeontological expedition in the Old World and was supported by President Roosevelt (Morgan & Lucas, 2002). Osborn left the group after a short time and hired Markgraf to assist the expedition. This expedition collected about 550 fossils that were later studied by Osborn (1908), who erected, among others, the new family of Ptolemaiidae, a peculiar group of mammals, which today is placed in its own order, the Ptolemaiida.

The material collected by these first expeditions was later studied by many renowned palaeontologists and gave significant insights into the evolution of several vertebrate groups, such as Primates, Proboscidea, Sirenia, and Cetacea (Andrews, 1899, 1906a; Osborn, 1908; Schlosser, 1911; Stromer, 1916). Nevertheless, the Fayum fossil localities remained forgotten for almost five decades, mainly due to the two world wars, with the only expedition in the area carried out in 1947 by a team led by American archaeologist Wendell Phillips, from the University of California at Berkeley. Then, a renewed period of extensive excavations in the Fayum

Depression began with Elwyn LaVerne Simons. After describing a skull fragment of an anthropoid, Simons (1959) initiated a new series of excavations in the area that lasted from 1961 until 1967. The main purpose of these expeditions was the search for further primate remains and small mammals, which were under-represented in the old Fayum collections (Simons & Rasmussen, 1990). In 1971, the exploration for the Fayum fossils continued under the leadership of Simons. This time the fieldwork and studies carried out in the Fayum area were marked by the interdisciplinary approach of the researchers, with the inclusion of specialists from different fields that also led to the first precise dating of the sedimentary rocks in the Fayum Depression (Bown & Kraus, 1988; Kappelman, 1992; Kappelman et al., 1992; Seiffert, 2006; Seiffert et al., 2008; Van Couvering & Harris, 1991). The efforts of Simons and his team shed new light on the classical vertebrate assemblages of the Fayum Depression, revealing previously unknown details about the locality and many new extraordinary fossils. Palaeontological excavations in the area and the study of the new, but also the re-evaluation of old material continue to this day, producing consistently new research about the Paleogene fauna of Egypt (e.g. Al-Ashqar et al., 2021; El-Sayed et al., 2020; Gohar et al., 2021; Sallam & Seiffert, 2019).

3 Geology of the Fayum Depression

The geology of the Fayum Depression has been studied by numerous researchers over the last two centuries. The most important studies on the geology of the Fayum area include Beadnell (1905), Bown and Kraus (1988), and Gingerich (1992). The Fayum Depression represents a 120-km-wide Graben structure filled with Eocene–Oligocene sediments that have been deposited unconformably on top of Upper Cretaceous sediments (Salem, 1976). The terrestrial vertebrate-yielding sediments in the northern part of the Fayum Depression (Fig. 1) belong to three different formations, which range in age from the Late Eocene to the Early Oligocene and are overlain by the Widan el Faras Basalt. The thickness of this basalt varies from 2 to 25 m, and it has been radio-isotopically (^{40}Ar/^{39}Ar) dated to 23.64 ± 0.035 Ma (Kappelman et al., 1992). Both the Paleogene sediments and the Widan el Faras Basalt are overlain by Neogene sediments of the Khashab Formation.

3.1 Birket Qarun Formation

The stratigraphically lowest formation that includes terrestrial fossils is the Birket Qarun Formation (Birket el Qarun Series after Beadnell, 1905). The thickness of the Birket Qarun Formation ranges from 20 to 85 m and includes mainly clays, shales, thick fine-grained sandstones, but also ferruginous bioclasts and calcareous grits (Anan & El Shahat, 2014; Zalmout & Gingerich, 2012). One of its most characteristic layers is the Camp White Layer, which can be up to 2 m thick. It is known for its richness in marine mammals (Gingerich, 1992) and for the existence of vertical, rod-like structures which had been interpreted as “mangrove pneumatophores”, but were most recently re-evaluated and described as burrows of different invertebrates (Gee et al., 2019).

The Birket Qarun Formation comprises an unnamed lower member and the Umm Rigl Member. The assignment of the Umm Rigl Member to the Birket Qarun Formation has been questioned in the past (see King et al., 2014) and its attribution to the overlying Qasr el Sagha Formation has been proposed instead (Gingerich, 1992). Seiffert et al. (2008) discussed the history of the Birket Qarun Formation, including the Umm Rigl Member, and supported the original position of the latter in the Birket Qarun Formation, because it is consistent with previous works and because of the lack of any distinctive features that would allow its association with the Qasr el Sagha Formation. Herein we follow Seiffert et al. (2008) in regarding the Umm Rigl Member as part of the Birket Qarun Formation.

The Birket Qarun Formation contains in total nine fossiliferous localities (Rasmussen et al., 1992; Sileem et al., 2015), whereas the Umm Rigl Member specifically includes one of the richest fossil sites, called Birket Qarun Locality-2 (BQ-2, see Fig. 1a and c). It was discovered in 2000 and has yielded a very rich fauna with an age of ∼ 37 Ma, representing one of the most diverse vertebrate localities in the Paleogene of Afro-Arabia (Seiffert et al., 2008). BQ-2 represents the oldest primate-bearing locality in Egypt, with the coexistence of five primate taxa: *Karanisia clarki* and *Saharagalago misrensis* (Seiffert et al., 2003), *Biretia fayumensis* and *Biretia megalopsis* (Seiffert et al., 2005), and *Masradapis tahai* (Seiffert et al., 2018). The fauna also contains several fish taxa (El-Sayed et al., 2020; Murray et al., 2010), snakes (McCartney & Seiffert, 2016), and a very rich mammalian assemblage, including proboscideans, hyracoids, herodotiines, ptolemaiids, creodonts, anomaluroid and hystricognathous rodents, chiropterans, and insectivores (Seiffert et al., 2005, 2008; Simmons et al., 2016).

The palaeoenvironment of the Birket Qarun Formation, including BQ-2, has traditionally been regarded as marine (Anan & El Shahat, 2014; Beadnell, 1905; Gingerich, 1992; Kappelman et al., 1992; Van Couvering & Harris, 1991; Wanas, 2008). Gingerich (1992) suggested that the Birket Qarun Formation represents an offshore barrier bar complex parallel to the Tethys shoreline. However, Seiffert et al. (2005, 2008) suggested that BQ-2 represents a fluvial environment. The ichthyofauna from BQ-2 has recently been studied in detail and suggests a freshwater environment, with some nearshore marine influences (El-Sayed et al., 2020; Murray et al., 2010).

3.2 Qasr el Sagha Formation

The Qasr el Sagha Formation was initially described as the "Qasr el Sagha Series" by Beadnell (1905) and later also used by Said (1962). It includes Late Eocene sediments that can be up to 200 m thick and can be divided into two to four members, depending on the authors (El-Younsy & Salman, 2021; Gingerich, 1992, 1993). As already mentioned above, herein the Umm Rigl Member will be considered as part of the Birket Qarun Formation (following Seiffert et al., 2008). Therefore, the lowermost part of the Qasr el Sagha Formation is the Harab Member, which consists of 30–40 m of brown shales (Gingerich, 1992). It is overlain by the Temple Member, which can be up to 80 m thick. It consists of thin layers of highly fossiliferous, glauconitic and limonitic arenaceous limestones, fine rippled, cross-laminated and highly bioturbated siliceous sandstones interbedded with thick laminated siltstones and gypsiferous sandy mudstones (El-Younsy & Salman, 2021). The upper part of the Qasr el Sagha Formation is composed of the Dir Abu Lifa Member, which can be up to 80 m thick. It comprises colourful, cross-stratified sandstones, alternating with siltstone, silty claystone and shale, topped by a yellow, fine-to-coarse sandy limestone, with many gradational to erosional surfaces in between (El-Younsy & Salman, 2021). The Dir Abu Lifa Member is overlain by the Gebel Qatrani Formation with an erosional contact.

The Upper Eocene Qasr el Sagha Formation contains eight fossiliferous localities (Rasmussen et al., 1992; Sileem et al., 2015). The Temple Member has yielded only few, and mostly marine, mammals (Bown & Kraus, 1988; Holroyd et al., 1996). Most vertebrate fossils have been recovered from the Dir Abu Lifa Member (Bown & Kraus, 1988), including fishes, crocodilians, turtles, snakes, and some mammalian representatives, including sirenians, cetaceans, and proboscideans. Recent re-evaluation of the sequence stratigraphy of the Qasr el Sagha Formation shows that it was deposited in a range of depositional environments, from shallow marine to fluvial environments (El-Younsy & Salman, 2021).

3.3 Gebel Qatrani Formation

The Gebel Qatrani Formation (also referred to as Jebel Qatrani, Gabal Qatrani, and Djebel Qatrani Formation) was initially named "Fluvio-Marine Series" by Beadnell (1905), but was later re-described by Said (1962). It lies unconformably on the Qasr el Sagha Formation and is topped by the Widan el Faras Basalt. The Gebel Qatrani Formation is of Late Eocene to Early Oligocene age (Beadnell, 1905; Bown et al., 1982; Kappelman et al., 1992; Murray, 2004) and can be up to 300 m thick. The Gebel Qatrani Formation contains variegated sandstones and mudstones with minor carbonates and chert pebble conglomerates and pebbly mudstones (Bown et al., 1982). It has been suggested that it can be subdivided into three members (see El-Younsy & Salman, 2021).

The Gebel Qatrani Formation has been divided into two sequences, the "Lower Fossil Wood Zone" and the "Upper Fossil Wood Zone" (Simons & Wood, 1968). These two zones are separated by a marker bed, consisting of cliff-forming baryte sandstones. The formation consists mainly of alluvial sediments of meandering rivers deposited during the Oligocene (Bown et al., 1982). Remarkably, it represents the first major terrestrial sedimentation in Egypt since the Cretaceous (Bown & Kraus, 1988). Some minor developments of shorelines and shallow marine facies continuing for short periods of time are also present however, as indicated by thin sandstones bearing marine molluscs (Bown & Kraus, 1988; Salem, 1976). Bown et al. (1982) proposed that the environment of the Gebel Qatrani Formation, in which several primate taxa coexisted, represented a sub-tropical to tropical lowland plain, with several large meandering streams and extensive ponds (contra Kortlandt, 1980). Murray (2004) studied the fish assemblage from the Gebel Qatrani Formation, which supports the existence of swampy rivers with overgrown banks, along with abundant vegetation, as also proposed by previous studies (Rasmussen et al., 1987; Wing & Tiffney, 1982). Fossil flora evidence outlined that during the Paleogene, a belt of tropical forests stretched along the coast of the Tethys Ocean, surrounding the Fayum area and its vicinity, whereas some distance further inland a belt of open wood land or even a steppe-like vegetation existed during large parts of the Paleogene (e.g., El Atfy et al., 2021).

The vast majority of the over 100 vertebrate localities of the Fayum Depression are distributed throughout the Gebel Qatrani Formation (Rasmussen et al., 1992). Of these, eight have produced almost 90% of the total mammalian remains (Rasmussen et al., 1992; Sileem et al., 2015); these sites are the quarries A, B, E, G, I, M, V, and Locality 41 (L-41). The site L-41 represents, with an age of about 34 Ma, the oldest and richest fossiliferous locality in the Gebel Qatrani Formation (Sallam et al., 2011; Simons, 2008) and has brought to light a very diverse fauna, comprising fishes (Murray, 2004), birds (Miller et al., 1997; Rasmussen et al., 2001), and a very rich mammalian fauna. It consists mainly of hyracoids, as well as rodents, primates, creodonts, macroscelideans, and anthracotheres, indicating a forested environment (Gagnon, 1997).

4 Fauna Overview

4.1 Reptilia

4.1.1 Serpentes

The fossil record of snakes in the Fayum Depression is rather limited. Andrews (1901a) described the very large

Gigantophis garstini, based on a series of 20 associated vertebrae from the Qasr el Sagha Formation. He originally compared it to the extant genus *Python*, while assigning it to the Boidae (Andrews, 1906a). Recently, however, this taxon was placed in the Madtsoiidae (McCartney & Seiffert, 2016). One year later, a revision of this taxon suggested an estimated length of about 7 m, a sister-taxon relationship to the latest Cretaceous Indian snake *Madtsoia pisdurensis* and discussed potential biogeographical implications for the group (Rio & Mannion, 2017).

Andrews (1901a) described another somewhat smaller, but still relatively large, snake species, *Moeriophis schweinfurthi*, based on vertebrae from the Qasr el Sagha Formation. A few years later, Andrews (1906a) assigned this species to the palaeophiid genus *Pterosphenus*, erected by Lucas (1898). Andrews (1906a) also suggested that *Pterosphenus schweinfurthi* was aquatic, as indicated by the high frequency of its remains in the Qasr el Sagha Formation along with fully aquatic vertebrates like fishes, sirenians, and whales; this notion was also supported by a more recent study (McCartney & Seiffert, 2016).

Recently, the new excavations at BQ-2 in the Birket Qarun Formation brought to light a large collection of snake material (McCartney & Seiffert, 2016). McCartney and Seiffert (2016) recognised the two previously described Fayum snakes together with a variety of other snake taxa, including two distinct booids, a tropidophiid, a probable russellophiid, and a new colubroid, *Renenutet enmerwer*. The authors also suggested a niche partitioning between the smaller snakes, where small mammals, including rodents, small hyracoids, and primates, as well as small fishes and lizards would be potential prey items for these species (McCartney & Seiffert, 2016).

4.1.2 Varanidae

Since the first discovery of vertebrate fossils in the Fayum Depression, in the nineteenth century, no lizards had been found in its Paleogene deposits until recently. Smith et al. (2008) reported a single posterior presacral vertebra of a varanid, from the Early Oligocene Quarry I of the Gebel Qatrani Formation. This vertebra was considered the oldest African record of a stem *Varanus* (Smith et al., 2008). Soon after, Holmes et al. (2010) studied a large collection of vertebrae, from the Late Eocene BQ-2 of the Birket Qarun Formation and from the Oligocene Quarries I and M of the Gebel Qatrani Formation, which they assigned to the genus *Varanus*. Based on this material, the authors argued for a potential African origin for the genus and discussed its dispersal to the Eurasian and Australian continents (Holmes et al., 2010). Holmes et al. (2010) pointed out some morphological differences between their material and the vertebra described by Smith et al. (2008), the latter of which they considered as an indeterminate varanid.

4.1.3 Testudines

Turtles are a well-represented group in the Paleogene sediments of the Fayum Depression. The first chelonian remains were reported by Andrews (1901a) who erected three new species, *Psephophorus eocaenus*, represented by some isolated fragmentary postcranial elements, *Thalassochelys libyca*, represented by several skulls, and the pleurodiran *Stereogenys cromeri*, also represented by several well-preserved skulls, all from the Qasr el Sagha Formation. Two years later, the same author described three new pleurodiran species *Stereogenys libyca*, founded on an almost complete carapace from the Gebel Qatrani Formation, *Podocnemis antiqua* from the Qasr el Sagha Formation, and *Podocnemis fajumensis* from the Gebel Qatrani Formation (Andrews, 1903a).

In the same year, a new large tortoise, *Testudo ammon*, was described from a complete carapace from the Gebel Qatrani Formation (Andrews, 1903b, 1904a, 1906a). In his monograph about the Fayum fauna, Andrews (1906a) studied a large collection of new turtle material from the Fayum Depression, re-examining the previously described species and erected two new species of tortoises, *Testudo beadnelli* and *Testudo isis*. Later, all Fayum tortoises were synonymised and placed under a different generic name, as *Gigantochersina ammon* (Holroyd & Parham, 2003; Lapparent de Broin, 2000).

Half a century after the description of the first pleurodirans from the Fayum Depression, Williams (1954) described the new pleurodiran genus and species *Dacquemys paleomorpha* from its Upper Eocene strata. More recently, Gaffney et al. (2011), in their revision of the pleurodiran family Podocnemididae, described the new pleurodiran genus and species *Albertwoodemys testudinum* based on a shell from the Early Oligocene Fayum deposits, placed "*Podocnemis*" *fajumensis* in the genus *Neochelys*, and erected the new genus *Cordichelys*, for *Cordichelys antiqua* (originally *P. antiqua*; Andrews, 1903a). Cherney et al. (2020) studied new pleurodiran material, which they referred to *C. antiqua*, including a skull and a shell from the Late Eocene Birket Qarun Formation, thus, extending the stratigraphical distribution of this taxon and adding insights about its ecology, as it was probably inhabiting marine waters.

4.1.4 Crocodyliformes

Crocodyliformes are important representatives of the Fayum faunal assemblages. Overall, eight new species of crocodilians have been described based on material from the Fayum Depression (Andrews, 1901a, 1905a; Brochu & Gingerich, 2000; Müller, 1927). Although, many of these were later synonymised; at least five distinct Crocodyliformes seem to have occurred in the Eocene to Oligocene deposits of the Fayum Depression (Brochu & Gingerich, 2000; Stefanic et al., 2019). Andrews (1901a) described the new species

Tomistoma africanum (now referred as *Eogavialis africanum*; Stefanic et al., 2019) from the Qasr el Sagha Formation and mentioned that crocodilian remains are very common in this formation. Later, Andrews (1905a) erected four new species of crocodilians from the Fayum area. He assigned two of them to the genus *Crocodylus*, the "narrow-snouted" *Crocodylus articeps* and the "broad-snouted" *Crocodylus megarhinus*, based on well-preserved skulls from the Gebel Qatrani Formation (Andrews, 1905a). The other two new species were referred to *Tomistoma* by him (Andrews, 1905a). *Tomistoma gavialoides* is very common in the Gebel Qatrani Formation, and *Tomistoma kerunense* is present in the Birket Qarun Formation (Andrews, 1905a), though both of them are now attributed to *Eogavialis* (see Brochu & Gingerich, 2000). Andrews (1906a) offered a detailed description of crocodilian material from the Fayum, referring to all five previously described species, and to one indeterminate crocodilian from the Qasr el Sagha Formation, referred to as *Crocodylus* sp.

Müller (1927) studied the crocodilian material from the Paleogene of Egypt, collected by Markgraf for Fraas and Stromer. This work represents the most detailed study that is dedicated solely to the Paleogene crocodilians of Egypt. He described two new species. The first is *Tomistoma cairense*, based on a skull from the Middle Eocene marine deposits of the Mokattam Formation (Müller, 1927). The second is *Tomistoma tenuirostre*, which he erected based on two mandibular symphyses from the Gebel Qatrani Formation in the Fayum Depression (Müller, 1927). The latter species was afterwards assigned to the genus *Eogavialis* (Brochu & Gingerich, 2000).

Brochu and Gingerich (2000) offered a short review of the Fayum crocodylians and described the new genus and species *Paratomistoma courti*, based on a partial skull and mandible from the Middle Eocene Gehennam Formation in Wadi al Hitan. They also discussed the taxonomic and phylogenetic status of the Fayum gavialoids and proposed that *Eogavialis gavialoides*, *Eogavialis kerunense*, and *Eogavialis tenuirostre* represent junior synonyms of *E. africanum*. The four previously suggested distinct species are morphologically indistinguishable and only differ in their stratigraphical position, ranging from the Late Eocene Qasr el Sagha Formation to the Early Oligocene Gebel Qatrani Formation (Brochu & Gingerich, 2000). Furthermore, Brochu and Gingerich (2000) suggested that *C. articeps* represents a juvenile *C. megarhinus*.

Fig. 2 Skull (GPIT-PV-41686) of *Eogavialis africanum* (sensu Brochu & Gingerich, 2000) from the Late Eocene to Early Oligocene Gebel Qatrani Formation of the Fayum Depression (Egypt) collected by Richard Markgraf in 1905 (originally described as *Eogavialis gavialoides* by Müller, 1927). Scale bar is 10 cm

Stefanic et al. (2019) studied the new crocodyliform material from BQ-2, of the Birket Qarun Formation. They described some material assignable to Crocodylia, as well as a non-crocodylian mesoeucrocodylian partial right dentary, which they referred to the extinct crocodyliform clade of Sebecosuchia. This is the first report of Sebecosuchia from the Fayum Depression and one of its youngest records in Africa (Stefanic et al., 2019).

4.2 Aves

The Fayum Depression has yielded the oldest diverse avifauna from Africa, including at least seven orders of birds (Rasmussen et al., 1987). However, its avifauna remained rather poorly known until the study of Rasmussen et al. (1987), in which they offered a detailed overview of the Fayum birds. Until then, only four species of birds had been known from the Fayum fauna (Andrews, 1904b; Lambrecht, 1929, 1930).

One of the most interesting features of the Fayum avifauna is certainly the existence of a large flightless bird. Andrews (1904b) described the new ratite *Eremopezus eocaenus*, based on a distal end of a large left tibiotarsus from the Gebel Qatrani Formation. Later, Lambrecht (1929) described the new species *Stromeria fajumensis*, based on a distal end of a right tarsometatarsus from the Gebel Qatrani Formation, which he assigned to the Aepyornithidae. Later, it was noted that these two species might in fact be synonymous (Moustafa, 1974; Rasmussen et al., 1987, 2001). Rasmussen et al. (2001) studied several newly found specimens of a large bird from the Late Eocene site L-41 of the Gebel Qatrani Formation and, based on this material, they revised the flightless, cursorial bird from the Fayum fauna, concluding that *S. fajumensis* does in fact represent a junior synonym of *E. eocaenus*. In addition, they suggested that *Eremopezus* belongs to its own family, Eremopezidae, which is not closer related to any ratite lineage or any other large bird (Rasmussen et al., 2001).

In their review of the Fayum avifauna, Rasmussen et al. (1987) also described four new species, *Nupharanassa* *bulotorum*, *Nupharanassa tolutaria*, *Janipes nymphaeobates*, and *Xenerodiops mycter* and erected the new family Xenerodiopidae for the latter one. In total, they reported the presence of at least 17 different species, belonging to 13 families. Remains of another relatively large, potentially flightless, bird were uncovered in the Early Oligocene Quarry E of the Gebel Qatrani Formation, which they tentatively attributed to Ameghinornithidae (Stidham & Smith, 2015). More recently, Smith et al. (2020) described the oldest fossil owl from Africa, based on a distal end of a left tibiotarsus from the Early Oligocene Quarry I of the Gebel Qatrani Formation, whereas one year later El Adli et al. (2021) described the oldest remains of a pelican from the Birket Qarun Formation in Wadi el Hitan, based on which they founded the new genus and species *Eopelecanus aegyptiacus*.

4.3 Mammalia

4.3.1 Marsupialia

The most basal mammalian group in the Fayum Depression is represented by the marsupials. Only few fragmentary specimens have been discovered, but have led to the description of two distinct new marsupial taxa, which represent the first record of marsupials in Africa (Bown & Simons, 1984; Gunnell, 2010). The first specimens comprise three fragmentary mandibles, which come from the Early Oligocene of Quarry M (Gebel Qatrani Formation) and were initially published by Bown and Simons (1984). Later that same year, they were described as the new species *Peratherium africanum* (Simons & Bown, 1984). Crochet et al. (1992) erected the new genus *Qatranitherium* for this species. Subsequently, Hooker et al. (2008) described some new material of *Peratherium africanum*, including the first maxilla, from the same fossil site where the holotype came from. They concluded that *Qatranitherium* represents a junior synonym of *Peratherium* and provided information about the phylogenetic position of this species, indicating a European origin for this "didelphimorph" species.

Sánchez-Villagra et al. (2007) described the new potential "didelphimorphian" marsupial *Ghamidtherium dimaiensis*, based on a fragmentary right mandible from the Late Eocene of BQ-2 (Birket Qarun Formation), which weighed about 300–500 g. The same authors also reported an isolated lower tooth that might belong to the same species or could represent a close relative, and two isolated upper molars, which can be referred to another potential marsupialian taxon, from the same locality. However, the exact systematic position of the BQ-2 specimens could not be assessed and an association to a marsupial-like chiropteran cannot be excluded (Sánchez-Villagra et al., 2007).

4.3.2 Ptolemaiida

The Ptolemaiida is an enigmatic group of medium- to small-sized mammals, potentially assignable to Afrotheria, comprising three genera and five species, almost exclusively known from the Early Oligocene deposits of the Gebel Qatrani Formation in the Fayum Depression. Over a century ago, Osborn (1908) described the first taxon of this group, *Ptolemaia lyonsi*, based on a dog-sized left mandible, only missing the p4 and the front teeth (Fig. 3A). He erected the new family Ptolemaiidae for this peculiar animal. He also noted that it might represent a new order and that it is evidently very different from any primate or ungulate (Osborn, 1908). Due to the fragmentary state of the specimen, Osborn (1908) was not able to make any suggestions about the animal's ecology. Schlosser (1911) described new material, including two mandibles, several isolated teeth and possibly a radius, which he attributed to the same species. Based on these new specimens he concluded that *P. lyonsi* must belong to the carnivorous "creodont" family of Hyaenodontidae (Schlosser, 1911). Matthew (1918) noted that this

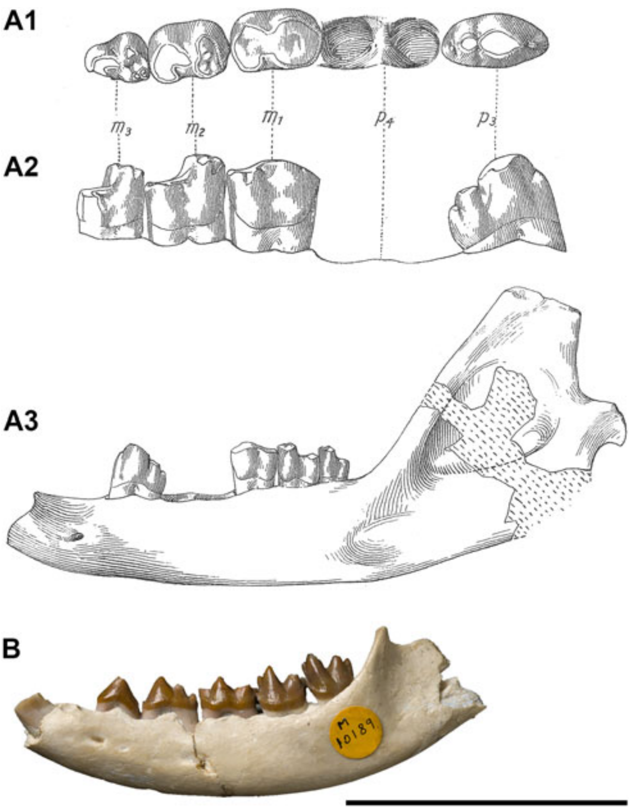

Fig. 3 Ptolemaiida material from the Late Eocene to Early Oligocene Gebel Qatrani Formation of the Fayum Depression (Egypt): **A** left mandible (holotype) of *Ptolemaia lyonsi* (Amer. Mus. No. 13269; Osborn, 1908, figs. 1 and 2). 1, occlusal view of the dentition; 2, lingual view of the dentition; and 3, buccal view of the mandible. **B** left mandible (holotype) of *Qarunavus meyeri* (NHMUK PV M 10189; Simons & Gingerich, 1974), originally referred to *Ptolemaia lyonsi* (Schlosser, 1911). Scale bar is 10 cm for **A1–2** and 5 cm for **A3** and **B**

new material, described by Schlosser (1911), did not belong to the genus *Ptolemaia*. Subsequently, Simons and Gingerich (1974) included this material in their new genus and species *Qarunavus meyeri*, which they referred to the Ptolemaiidae, order incertae sedis, along with *Ptolemaia lyonsi*. Bown and Simons (1987) erected the new species *Ptolemaia grangeri*, based on a left m3 from Quarry V (Gebel Qatrani Formation), and the new genus *Cleopatrodon*, comprising two new species *Cleopatrodon ayeshae*, from Quarry V (Gebel Qatrani Formation) and *Cleopatrodon robusta*, from Quarry I (Gebel Qatrani Formation), which were described based on relatively well-preserved mandibles. The same authors argued about a close phylogenetic relationship between the genera *Qarunavus* and *Cleopatrodon*, to the exclusion of *Ptolemaia*.

The origin and systematic position of the ptolemaiids has been a matter of considerable debate, and the family has been assigned to various groups, including creodonts, pantolestids, tubulidentates, and chiropterans (Gunnell et al., 2010; Van Valen, 1966). Simons and Bown (1995) described new material of ptolemaiids from the Quarry V (Gebel Qatrani Formation), including an almost complete, but distorted, skull of *Ptolemaia grangeri*. Based on this new material, they revised the previously described ptolemaiid material and erected the new order Ptolemaiida for the genera *Ptolemaia*, *Qarunavus*, and *Cleopatrodon*. Later, the group Ptolemaiida was included in Afrotheria (Cote et al., 2007; Nishihara et al., 2005). Seiffert (2007) also placed the ptolemaiids within the Afrotheria and supported the previous suggestions that they might be allied with aardvarks (Cote et al., 2007; Simons & Gingerich, 1974). A revision of the two mandibles of *Qarunavus meyeri* supports the notion of Bown and Simons (1987) that it shares a closer phylogenetic relationship with *Cleopatrodon* than with *Ptolemaia* and further supports an inclusion into the Afrotheria (Kampouridis et al. In prep).

The ecology of the ptolemaiids has remained elusive ever since their first discovery, because the fragmentary nature of the material does not allow for any decisive conclusions about their preferred environment, feeding habits or any other aspect of their ecology (Osborn, 1908; Schlosser, 1911; Simons & Bown, 1995). Simons and Rasmussen (1990) suggested that *Q. meyeri* may have been a racoon-like, omnivorous animal, which preferred small riverside prey.

Overall, the Fayum ptolemaiids are known from only few and mostly fragmentary specimens that record three genera and five species (Simons & Bown, 1995). Until recently, ptolemaiids were known exclusively from the Oligocene deposits of the Gebel Qatrani Formation, in the Fayum Depression. However, material assigned to *Ptolemaia* has recently been reported from the Late Oligocene of Western Turkana, in Kenya (Miller et al., 2015). Lastly, the genus *Kelba*, which is known from several Miocene localities in East Africa (Cote et al., 2007), has also been suggested to belong to the Ptolemaiida, thus, potentially expanding the temporal distribution of the group significantly.

4.3.3 Macroscelidea

This group was long regarded as closely related to the Eulipotyphla, due to their overall similar appearance. Their fossil record is extremely scanty, which has made the investigation of their origin and phylogenetic position very difficult (e.g. Senut & Pickford, 2021; Stevens et al., 2021). Schlosser (1910) described the first macroscelidean from the Fayum Depression, which he named *Metoldobotes stromeri* in honour of Ernst Stromer von Reichenbach, based on a mandible, though he initially regarded it as an insectivoran (Schlosser, 1911). More recently, Simons et al. (1991) studied new macroscelidean material from the Gebel Qatrani Formation. They assigned part of this material to *Metoldobotes stromeri*, while the rest of the material was used to describe the new genus and species *Herodotius pattersoni*. The genus was named after the ancient Greek historian Herodotus who had travelled to and written about the Fayum, while the species was named in honour of Harvard Professor Bryan Patterson, who extensively studied the clade Macroscelidea. Subsequently, Simons et al. (1991) erected two new subfamilies for these species, Metoldobotinae and Herodotinae. The Fayum macroscelideans seem to be relatively primitive representatives of this group and their morphological affinities support their inclusion in the afrotheres (Simons et al., 1991). Later, Holroyd (2010) included in the Herodotinae also the genera *Nementchatherium*, from the Eocene of Algeria and *Chambius*, from the Eocene of Tunisia and Algeria.

4.3.4 Afrosoricida

Today, this enigmatic group includes the tenrecs (Tenrecoidea) and golden moles (Chrysochloridea). In the past, these animals were associated with the Eulipotyphla. They have a very poor fossil record and thus much about their systematic position and origin had remained ambiguous. Relatively recently, the first remains of these animals were uncovered from the Paleogene sediments of the Fayum Depression (Seiffert, 2010; Seiffert & Simons, 2000; Seiffert et al., 2007). Seiffert and Simons (2000) described the new genus *Widanelfarasia*, which included the two new species *Widanelfarasia bowni* and *Widanelfarasia rasmusseni*, based on partial mandibles from the Late Eocene site L-41 of the Gebel Qatrani Formation. In the initial description, their systematic position was not completely clear; they were regarded as potential relatives of either the Afrosoricida or the Eulipotyphla, though the former hypothesis was regarded as more likely by Seiffert and Simons (2000). Seiffert et al. (2007) described additional material of *W. bowni*, which they regarded as a tenrecomorph and also erected the new tenrecomorph afrosoricid *Jawharia tenrecoides*, as well as the new purported chrysochlorid afrosoricid *Eochrysochloris* *tribosphenus*. Both new taxa were found in the Early Oligocene site Quarry E of the Gebel Qatrani Formation (Seiffert et al., 2007). Seiffert (2010) studied further afrosoricid material from the Fayum Depression and described two additional new species. The first was named *Dilambdogale gheerbranti*, based on dental material from the Late Eocene locality BQ-2 of the Birket Qarun Formation, representing the oldest record of an afrosoricid from the Fayum succession. The second species was named *Qatranilestes oligocaenus*, based on a right mandibular fragment from the Early Oligocene site Quarry I of the Gebel Qatrani Formation and represents the youngest find of an afrosoricid from the Fayum. In his phylogenetic analysis, *Dilambdogale* and *Widanelfarasia* are placed as sister taxa of crown afrosoricids, though it could not be excluded that they actually represent stem tenrecoids (Seiffert, 2010). Furthermore, it has been argued that *Eochrysochloris* might be a member of the tenrecs rather than a golden mole (Pickford, 2015a).

4.3.5 Embrithopoda

The Embrithopoda is a group of impressive large-sized, but poorly known, afrotherians that lived during the Paleogene. The most emblematic representative of the clade is *Arsinoitherium*. This taxon is characterised by the presence of two huge anterior horns formed by the nasal bones and two smaller, posterior horns formed by the frontal bones, as well as peculiar hypsodont teeth (Court, 1992a; Sanders et al., 2010a). Two species of *Arsinoitherium* have been erected based on material from the Gebel Qatrani Formation of the Fayum Depression. The first is *Arsinoitherium zitteli* (Fig. 4), which was erected by Beadnell (1902) and represents the type species of the order. Lankester (1903) erected a second species, *Arsinoitherium andrewsi*, based on a mandible from the Fayum (Fig. 5c), that is about one-third larger than the previously described arsinoithere material, and also reported an almost complete skull of *Arsinoitherium zitteli*. Andrews (1906a) studied a large amount of *Arsinoitherium* material from the Fayum area, recognising both previously described species, with *Arsinoitherium zitteli* representing the more abundant one. Later, Osborn (1907, 1908) reported the presence of *Arsinoitherium* sp. in their material from the Gebel Qatrani Formation, without any detailed description. Sanders et al. (2004) suggested that *Arsinoitherium andrewsi* in fact represents a junior synonym of *Arsinoitherium zitteli* and that the metric variation between those two suggested species is within the expected range of a sexually dimorphic species, with the “*Arsinoitherium andrewsi*” holotype representing the largest known individual of *Arsinoitherium* from the Fayum. However, Pickford (2015b) suggested that there is significant variability within the *Arsinoitherium* material from the Fayum Depression and considered *Arsinoitherium andrewsi* as a valid species, based on some variable dental features and their postcranial size difference. The genus *Arsinoitherium* is present throughout the Gebel Qatrani Formation in the Fayum Depression (Sanders et al., 2010a), from L-41 at the base to Quarry M at the top of the formation (Fig. 1a), spanning a range of approximately 34 to 30 Ma (Kappelman, 1992; Seiffert, 2006).

The Embrithopoda was known only from the Fayum deposits for many decades, until some discoveries of fragmentary remains in other Oligocene localities in Africa (Pickford, 1986, 2017; Thomas et al., 1989; Vialle et al., 2013; Wight, 1980). Further, material associated with *Arsinoitherium* has also been found on the Arabian Peninsula, in the Early Oligocene of Oman (Al-Sayigh et al., 2008; Pickford, 2015b; Thomas et al., 1989, 1999) and Saudi Arabia (Zalmout et al., 2010). Sanders et al. (2004) described numerous fragmentary embrithopod remains from the Late Oligocene of Chilga (Ethiopia) (Kappelman et al.,

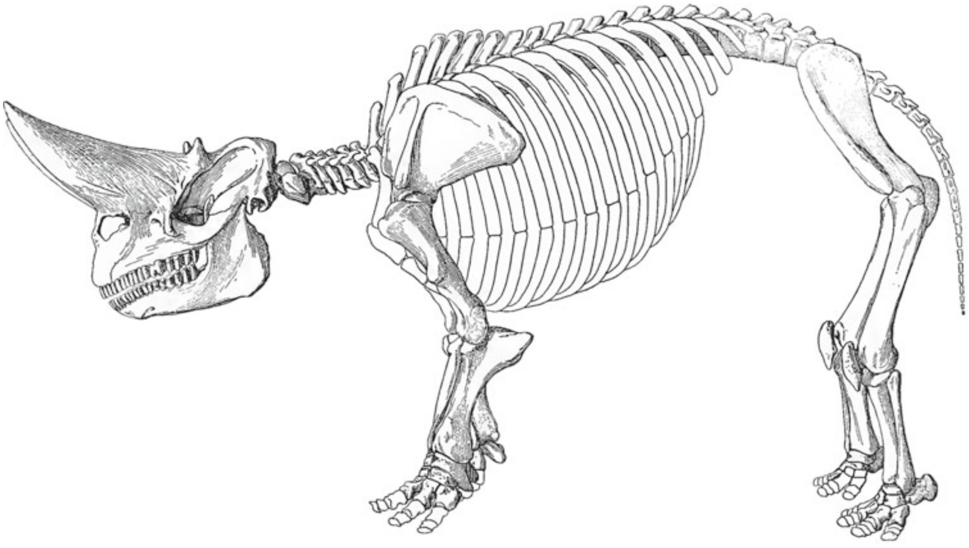

Fig. 4 *Arsinoitherium zitteli* skeleton reconstruction (Andrews, 1906a, text—fig. 36)

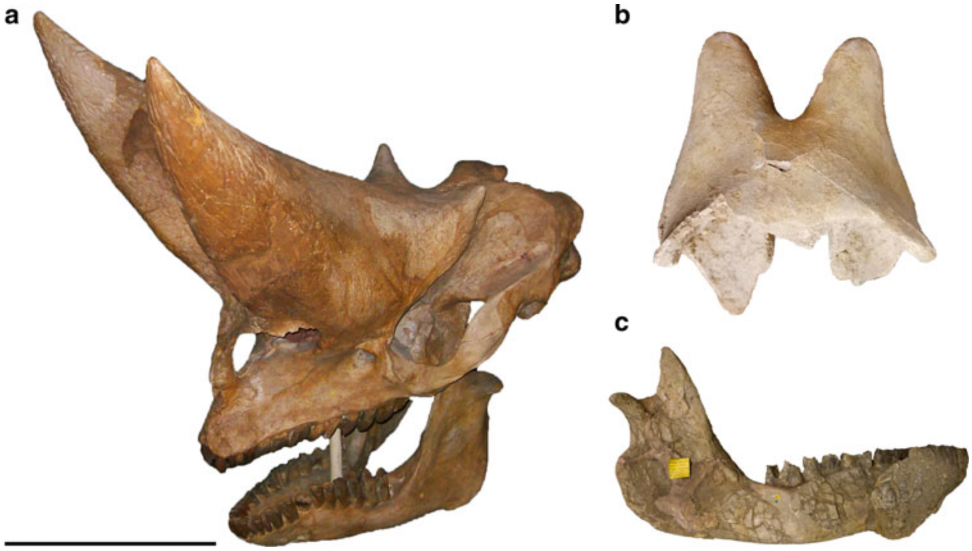

Fig. 5 Embrithopoda material from the Late Eocene to Early Oligocene Gebel Qatrani Formation of the Fayum Depression (Egypt): **a** complete skull and mandible of *Arsinoitherium zitteli* (NHMUK PV M 8463; Andrews, 1906a); **b** nasal horns of a juvenile *Arsinoitherium zitteli* (SMNS-P-12611); and **c** mandible of *Arsinoitherium zitteli* (NHMUK PV M 8461b) (holotype of *Arsinoitherium andrewsi* Lankester, 1903). Scale bar 40 cm for **a** and **c** and 10 cm for **b**

2003), which he referred to their new species *Arsinoitherium giganteum*. This species differs from *Arsinoitherium zitteli* in having larger dental dimensions, with the M2 of the holotype of *Arsinoitherium giganteum* exceeding even the large "*Arsinoitherium andrewsi*" from the Fayum in size (Sanders et al., 2004). Pickford et al. (2008) described the embrithopod *Namatherium blackcrowense* from the Middle Eocene of Namibia, which is characterised by its very wide zygomatic arches. Recently, Gheerbrant et al. (2021) described the oldest and basal-most embrithopod from the Eocene of Morocco, erecting the new family Stylolophidae, which includes the two species *Stylolophus major* and *Stylolophus minor* (Gheerbrant et al., 2018, 2021). Thus, a total of three genera and five species of Embrithopoda have been suggested to be present in the Eocene to Oligocene of Africa (Andrews, 1906a; Beadnell, 1902; Gheerbrant et al., 2018, 2021; Pickford et al., 2008; Sanders et al., 2004).

For many years, the Embrithopoda was considered endemic to Africa (Sen, 2013). Matthew and Granger (1925) studied the Paleogene fauna of the Gashato Formation (Mongolia) and described the new genus and species *Phenacolophus fallax*, which they did compare, but not attribute, to arsinoitheres. More than 50 years later, McKenna and Manning (1977) described further material of this taxon and suggested that it represents a primitive arsinoithere. Some new studies support the position of *Phenacolophus* as a potential stem-group member of Embrithopoda (Erdal et al., 2016; Sen, 2013), although other recent studies have argued against its inclusion in this order (Gheerbrant et al., 2021; von Koenigswald, 2013).

Almost half a century ago, Radulescu et al. (1976) studied the geology of the Haţeg Basin (Romania) and founded the new taxon *Crivadiatherium mackennai*, based on three lower teeth from Lower Oligocene freshwater limestones in Crivadia (Romania). Radulescu and Sudre (1985) described some teeth from the same locality, which they referred to the new species *Crivadiatherium iliescui*, characterised by its larger size, compared to *Crivadiatherium mackennai*. In general, *Crivadiatherium* from the Oligocene of Romania seems to be smaller, and exhibit more primitive features than *Arsinoitherium* (Radulescu & Sudre, 1985; Radulescu et al., 1976).

Rich embrithopod material has been also described from Paleogene coal deposits of Anatolia, which was mainly attributed to *Palaeoamasia kansui*, initially regarded as a chalicotheriid perissodactyl (Ozansoy, 1966). Later, Sen and Heintz (1979) revised this taxon, included it in the Embrithopoda, and erected the new subfamily Palaeoamasiinae for this species, including also *Crivadiatherium* from Romania. Some of the oldest embrithopods, from the Late Palaeocene to Early Eocene of Turkey (Uzunçarşıdere Formation), were used to establish the new embrithopod *Hypsamasia seni* (Maas et al., 1998). Moreover, the youngest specimens from Turkey (Cemalettin Formation) were suggested to belong to a new species of *Palaeoamasia* (referred to as "*Palaeoamasia* sp. nov."), without any formal description of the species (Sanders et al., 2014).

In his initial description of *Arsinoitherium*, Beadnell (1902) suggested that the genus may be an ancestor of today's rhinoceroses, based on the dentition, though noting some similarities to the strange, horned Dinocerata. Soon after its first description, *Arsinoitherium* was included by Andrews (1904c) in the order Amblypoda, which also included the Dinocerata. In another contribution in the same volume, Andrews (1904d) argued against this assignment and in fact erected the new order Barypoda for the genus *Arsinoitherium*. However, the name Barypoda had already been used earlier by Haeckel (1866) for a group of marsupials. Therefore, two years after its creation, Andrews (1906b) published a note discussing this issue and proposing the new name Embrithopoda for the order that includes *Arsinoitherium*. In his monograph on the vertebrate assemblages of the Fayum Depression, Andrews (1906a) still uses the term Barypoda, but added a footnote mentioning the aforementioned issues with this name and that the alternative Embrithopoda has been proposed (Andrews, 1906a, p. xiv).

The exact phylogenetic position of embrithopods has long been debated (e.g. Andrews, 1904d, 1906a; Court, 1992a; Gheerbrant et al., 2014; Pickford et al., 2008; Tabuce et al., 2007). In the afrotherian phylogenetic analysis performed by Seiffert (2007), *Arsinoitherium zitteli* was recovered as the sister taxon to the Sirenia. More recently, comprehensive phylogenetic analyses performed to recover the systematic affinities of the Embrithopoda (Erdal et al., 2016; Gheerbrant et al., 2018, 2021) confirmed their placement in the Paenungulata, within the Afrotheria, and suggest a close relationship to Proboscidea, Sirenia, and Hyracoidea.

The phylogenetic relationships within the Embrithopoda have been the focus of many studies (e.g. Erdal et al., 2016; Gheerbrant et al., 2021; Sen & Heintz, 1979) but still remain somewhat controversial. The phylogenetic analysis of Erdal et al. (2016) supports the separation of Embrithopoda into Arsinoitheriinae (*Arsinoitherium*) and Palaeoamasiinae (*Palaeoamasia*, *Hypsamasia* and *Crivadiatherium*), as previously proposed by Sen and Heintz (1979), and implies *Namatherium* as the sister group to all other embrithopods. The phylogenetic analysis performed by Gheerbrant et al. (2021) offers different results, with *Palaeoamasia* being distinct from all other embrithopods and *Stylolophus* being placed as the most basal embrithopod. It has to be noted that in both analyses most embrithopods were recovered to form a polytomy (Erdal et al., 2016; Gheerbrant et al., 2021).

The iconic massive horns of *Arsinoitherium* are formed mainly by the nasals which are fused even in juvenile individuals (Fig. 5b; Andrews, 1906a, pl. III, fig. 2). The base of the horns is composed by the frontals, which also form a smaller, posterior pair of horns (Andrews, 1906a). There, numerous grooves, probably representing impressions of blood vessels, run across the surface of the horns, on the nasals and frontals. Based on this feature, Andrews (1906a, p. 7) suggested that the horns were covered by keratin, similar to modern-day bovids (Sanders et al., 2010a; Simons & Rasmussen, 1990; Tanner, 1978). Other authors suggested that the horns were covered only by skin (Pickford et al., 2008; Prothero & Schoch, 2002; Rose, 2006). Despite their massive appearance, at the centrum of the horns, the bone is at some places as thin as 1 cm (Andrews, 1906a, p. 7), bearing a large sinus. Pickford et al. (2008) discussed the possible functions of the horns, supporting the hypothesis of the sinus within the horns acting as a resonance chamber, implying that vocalisation played an important role in the animal's ecology. Subsequently, Benoit et al. (2013) studied the inner ear of *Arsinoitherium*, leading them to conclude that the animals might have been able to hear very low frequencies, and proposed that *Arsinoitherium* was most probably able to communicate through seismic vibrations similar to extant elephants. Pickford et al. (2008) suggested that the horns were covered by skin and were used secondarily for visual signals and not for intraspecific combat purposes. Furthermore, a visible sexual dimorphism in the horns has been suggested by many authors, with males bearing larger, pointed horn and females smaller, rounded ones (e.g. Andrews, 1906a; Prothero & Schoch, 2002).

The dentition is another peculiar feature, characteristic for *Arsinoitherium*. This and its mandibular morphology are probably associated with a specialised masticatory apparatus, and it has been proposed that it represents a highly selective browser (Court, 1992b). This would also be consistent with the high $\delta^{13}C$ values measured in the enamel of *Arsinoitherium* by Clementz et al. (2008). Regarding the ecology of *Arsinoitherium*, also a semi-aquatic lifestyle has been proposed based on the reconstructed palaeoenvironmental context and the postcranial morphology (Carroll, 1988; Court, 1993; Moustapha, 1955; Sen & Heintz, 1979). However, Clementz et al. (2008) argued that the $\delta^{18}O$ values obtained for *Arsinoitherium* point to a terrestrial lifestyle, as also supported by Sanders et al. (2010a), who based their interpretation on the graviportal features exhibited by *Arsinoitherium*.

In total, only eight rather complete *Arsinoitherium* skulls have been uncovered, including three adult, four sub-adult, and one juvenile skull (Court, 1992a; Osborn, 1907). An additional complete skull, allegedly representing the largest of the species was unfortunately destroyed during its transport (Osborn, 1907). The detailed study of this limited cranial material, along with the rich postcranial elements found in the Fayum area, also with new and innovative methods has significantly added to our understanding about this peculiar animal (e.g. Benoit et al., 2013; Clementz et al., 2008; Court, 1992a, 1992b, 1993).

4.3.6 Proboscidea

Proboscidea is one of the most fascinating mammal groups from the Fayum Depression and indeed, it was this group that primarily sparked the interest of American palaeontologist Henry F. Osborn to start excavations in the Fayum

Depression (Osborn, 1907). The first proboscideans were described by Andrews (1901b). He erected three new genera and species of proboscideans, *Palaeomastodon beadnelli*, *Moeritherium lyonsi*, and *Barytherium grave* (Andrews, 1901b). A more detailed description of these species was provided later in the same year (Andrews, 1901c).

Andrews (1901c) described the type mandible of *Palaeomastodon beadnelli* from the Gebel Qatrani Formation and noted the similarities to some Miocene proboscideans. Later, Andrews (1904e) reported a right mandibular ramus from the same formation, differing from *Palaeomastodon beadnelli* and established for it the new species *Palaeomastodon minor*, due to its smaller size. In the next year, Andrews (1905b) described two additional species of *Palaeomastodon*. The first was named *Palaeomastodon parvus*, because of its smaller size in comparison to the type species. The second species, named *Palaeomastodon wintoni*, is morphologically more similar to *Palaeomastodon minor*, but much larger, though smaller than the type species. Andrews (1905b) also noted that this last species is the most common one in the Gebel Qatrani Formation, from which almost all *Palaeomastodon* material was derived. Andrews (1906a) erected the new family Palaeomastodontidae to include originally the genera *Palaeomastodon*, *Tetrabelodon*, and potentially *Phiomia*. Nowadays, the family includes only the genera *Palaeomastodon* and *Phiomia*, which can be regarded as the most primitive elephantiforms (e.g. Hautier et al., 2021; Sanders et al., 2010b; Seiffert, 2006; Tobien, 1978). Though, the validity of the species within *Palaeomastodon* remains a complex issue that has been discussed repeatedly (e.g. Sanders et al., 2004, 2010b). Recently, Sanders et al. (2004) discussed the presence of two new *Palaeomastodon* species from the Late Oligocene of Chilga in Ethiopia, without naming them.

Andrews (1901b) suggested *Moeritherium lyonsi* as an ancestor of proboscideans. He also mentioned that *Moeritherium* is quite common in the Qasr el Sagha Formation and that it has the size of a large tapir and is known from cranial and postcranial elements, though only describing the cranial and dental features (Andrews, 1901c). In the following year, Andrews (1902) described the new species *Moeritherium gracile* from the Qasr el Sagha Formation, which he regarded as smaller than the type species *Moeritherium lyonsi*. Two years later, Andrews (1904e) described a third species for this genus, *Moeritherium trigodon* (later referred to as *Moeritherium trigonodon* by Andrews (1906a) and *Moeritherium trigonodum* by Schlosser, 1911), based on a right mandibular ramus from the Gebel Qatrani Formation. He noted that the dental morphology of this latter species seems to differ considerably from other material of *Moeritherium* and that it might in fact represent a distinct genus (Andrews, 1904e). Andrews (1906a) proposed that the genus *Moeritherium* constitutes a distinct family, called Moeritheriidae, in the Proboscidea. Half a decade later, Schlosser (1911) studied a large collection of *Moeritherium* material and decided to erect the new species *Moeritherium andrewsi* for material from the Gebel Qatrani Formation. Later, Matsumoto (1922, 1923) suggested that all four species were valid and that *M. lyonsi* and *M. gracile* might represent potential ancestors of *M. andrewsi* and *M. trigodon*, respectively. Petronievics (1923) described the new species, *Moeritherium ancestrale*, based on a well-preserved skull from the Qasr el Sagha Formation found by Baron Franz Nopcsa, during a short trip to the Fayum Depression in 1905. Over half a century after the initial description of the genus *Moeritherium*, Deraniyagala (1955) described the two new species *Moeritherium latidens* and *Moeritherium pharaonensis*, based on two partial mandibles collected by the African Expedition of the University of California. Later, Holroyd et al. (1996) reported the presence of *M. lyonsi* at the base of the Qasr el Sagha Formation. More recently, Delmer et al. (2006) described the new species *Moeritherium chehbeurameuri* from the Eocene of Algeria. Since the first description of the various species of *Moeritherium,* many authors have discussed their validity and potential synonymy. Most *Moeritherium* species have been synonymised and probably only *M. lyonsi* and *M. trigodon* can be regarded as valid (for an overview see Delmer et al., 2006; Sanders et al., 2010b).

In addition to his extensive work on *Palaeomastodon* and *Moeritherium*, Andrews (1901c) described a peculiar mandible that he referred to as "*Bradytherium*" *grave*. However, in the same year Andrews (1901d) noted that the genus name *Bradytherium* was already preoccupied for the Madagascan purported edentate *Bradytherium madagascariense*, which is now synonymised with the primate *Palaeopropithecus ingens* (MacPhee & Raholimavo, 1988). Andrews (1901d) accordingly proposed the name *Barytherium* to replace it. Andrews (1904d) discussed the controversial systematic position of this genus and proposed the name Barytheria for the clade that at the time only included *Barytherium grave*. He also suggested that Barytheria can be included in the Amblypoda and are of the same rank as Dinocerata (Andrews, 1904d). In his extensive description of the Fayum fauna, Andrews (1906a) erected also the new family Barytheriidae for *Barytherium grave*, but did not assign it to any definite order or suborder. Later, it was suggested that Barytheriidae, including only *Barytherium*, was closely related to the proboscidean Numidotheriidae, including several species of *Numidotherium*, and together constituted the Barytherioidea (for an overview, see Sanders et al., 2010b). Recently, Seiffert et al. (2012) described the new proboscidean genus and species *Omanitherium dhofarensis*, based on a partial mandible from the Oligocene of Oman and regarded it as the sister taxon of *Barytherium*.

The last proboscidean genus to date that was named from the Fayum area is *Phiomia*. Andrews and Beadnell (1902) described the new genus and species *Phiomia serridens* based on a partial left mandible from the Gebel Qatrani Formation. The authors initially thought that this animal might have been a specialised creodont (Andrews & Beadnell, 1902). Andrews (1906a) later re-examined the type mandible of *Phiomia serridens* and compared it to *Palaeomastodon*, suggesting a close relationship, following Schlosser (1905). Matsumoto (1922) described the new species *Phiomia osborni* based on a complete mandible from the Gebel Qatrani Formation (Fig. 6a) and referred some *Palaeomastodon* species to the genus *Phiomia*, "*Phiomia* (*minus*) *minor*" and "*Phiomia wintoni*". Subsequently, Sanders et al. (2004) described the new species *Phiomia major* based on several dental remains from the Late Oligocene of Chilga in Ethiopia, which are considerably larger than *Phiomia serridens*. Today, only the last described species, *Phiomia major*, and the type species, *Phiomia serridens* are regarded as valid (Sanders et al., 2004, 2010b).

Concerning the ecology of these early proboscideans, some interesting points as to their preferred habitat have been discussed. The primitive proboscidean *Moeritherium*, whose remains were very abundant in the Qasr el Sagha Formation and also present in the marine Birket Qarun Formation, was relatively small and had a relatively stout body plan, remarkably similar to extant hippos. Based on this, Andrews (1906a) regarded it as a swamp inhabitant. Matsumoto (1923) discussed the features of *Moeritherium* that point to either aquatic or non-aquatic lifestyle, concluding that although it might not have been as adapted to an aquatic lifestyle as extant hippos; it probably preferred environments close to water bodies. *Palaeomastodon* and *Phiomia*, on the other hand, seem more similar to the more derived elephantiforms and are usually regarded as terrestrial. In more recent studies, the isotopic signature of these species was compared, leading to the conclusion that *Moeritherium* and *Barytherium* were at least semi-aquatic, whereas the other Fayum proboscideans were fully terrestrial (Clementz et al., 2008; Liu et al., 2008).

4.3.7 Hyracoidea

The hyracoids represent one of the most diverse groups in the Fayum (Matsumoto, 1926; Rasmussen & Gutiérrez, 2010; Rasmussen & Simons, 1988a; Tabuce et al., 2021), including both small taxa such as *Saghatherium* and *Thyrohyrax* (Barrow et al., 2010; Rasmussen & Simons, 1991), comparable in size to modern-day hyraxes, and very large ones such as *Titanohyrax* that may have weighed up to a ton (Schwartz et al., 1995; Tabuce, 2016).

The first remains of hyracoids were reported by Andrews and Beadnell (1902), for which they erected the new small-sized hyracoid genus *Saghatherium*, including the two new species *Saghatherium antiquum* and *Saghatherium minus* from the Gebel Qatrani Formation. Subsequently, however, these two taxa have been synonymised (Tabuce, 2016). Thus, *Saghatherium* represented the oldest hyracoid finds at the time and the second hyracoid fossil taxon ever described, after *Pliohyrax graecus* from the famous Greek Late Miocene locality Pikermi (Gaudry, 1862; Roussiakis et al., 2019). One year after the initial description of *Saghatherium*, Andrews (1903c) described a new genus and species of a large-sized hyracoid, *Megalohyrax eocaenus*. In the following year, Andrews (1904c) described the new genus *Geniohyus*, with two new species, *Geniohyus mirus* and *Geniohyus fajumensis*, which he originally considered as "pig-like" and later even referred to the Suidae (Andrews, 1906a). Andrews (1904f) founded three further new species for previously described genera, *Geniohyus major*, *Megalohyrax minor*, and *Saghatherium magnum*, based on dental

Fig. 6 Proboscidea material from the Late Eocene to Early Oligocene of the Fayum Depression (Egypt): **a** complete mandible of *Phiomia serridens* (NHMUK PV M 9449, holotype of *Phiomia osborni*); **b** skull of *Moeritherium lyonsi* (SMNS-P-12617); and **c** skull and mandible of *Palaeomastodon beadnelli* (NHMUK PV M 8464; Andrews, 1906a, pl. XII, fig. 1). Not to scale

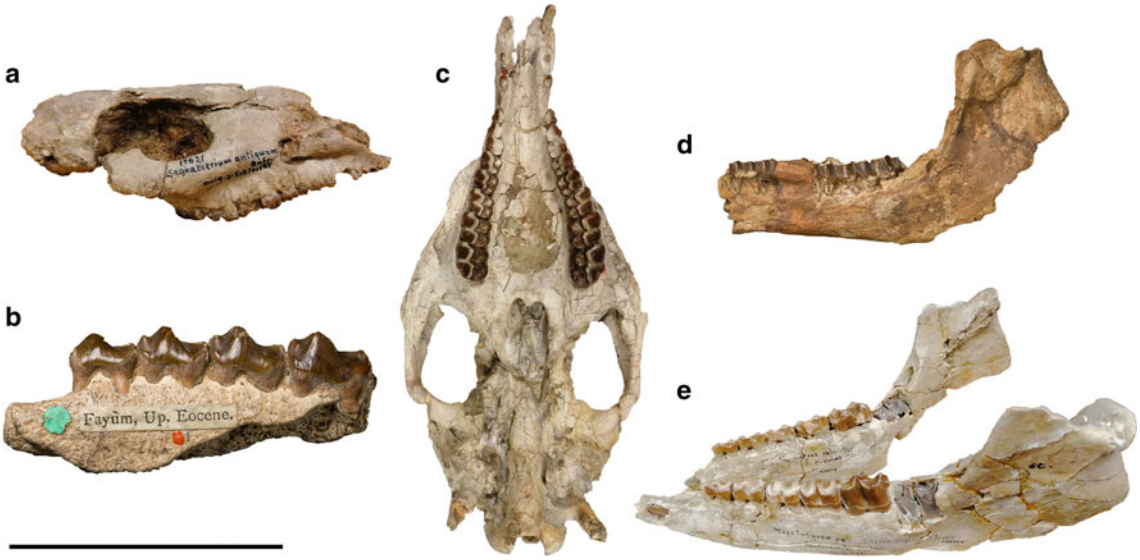

Fig. 7 Hyracoidea material from the Late Eocene to Early Oligocene Gebel Qatrani Formation of the Fayum Depression (Egypt): **a** skull of *Saghatherium antiquum* (SMNS-P-12621; Schlosser, 1911, taf. II, fig. 12), in right lateral view; **b** fragment of a mandibular ramus of *Bunohyrax fajumensis* (NHMUK PV M 8435), originally described as *Geniohyus fajumensis* (Andrews, 1904c), in lateral view; **c**, type skull of *Megalohyrax niloticus* (SMNS-P-12624), originally referred to as *Mixohyrax niloticus* (Schlosser, 1910, 1911, taf. VII, figs. 1 and 8), in ventral view; **d** mandible of *Titanohyrax andrewsi* (NHMUK PV M 9220), in lateral view; and **e** mandible of *Titanohyrax palaeotherioides* (SMNS-P-43922) originally referred as *Megalohyrax palaeotherioides* (Schlosser, 1911, taf. IV, fig. 1), in right lateral view. Scale bar is 10 cm for **a**, 5 cm for **b**, 20 cm for **C**, and 15 cm for **d** and **e**

remains from the Gebel Qatrani Formation. Two years later, Andrews (1906a) erected the medium-sized species *Saghatherium majus* and introduced the family Saghatheriidae for the Fayum hyracoids. Schlosser (1910) proposed the name Palaeohyracidae to include these primitive hyracoids and the subfamily Saghatheriinae for the selenodont representatives of this group. He also included *Geniohyus* in the Hyracoidea and described several new species of this group, including *Geniohyus minutus* and *Megalohyrax palaeotherioides*, as well as the new genera *Pachyhyrax*, with the relatively rare *Pachyhyrax crassidentatus*, *Mixohyrax*, with the three species *Mixohyrax andrewsi*, *Mixohyrax niloticus* (Fig. 7c), *Mixohyrax suillus*, and *Bunohyrax*, in which he included the previously described species *Bunohyrax* (= *Geniohyus*) *fajumensis*. One year later, Schlosser (1911) offered detailed descriptions of the rich hyracoid material from the Fayum Depression, including all species he previously erected and also described the new species *Geniohyus macrognathus*, which he referred tentatively to the genus *Geniohyus*. Matsumoto (1921) revised the hyracoid genus *Megalohyrax* in which he included the species *Megalohyrax eocaenus*, *Megalohyrax minor*, *Megalohyrax niloticus* (originally *Mixohyrax niloticus*), *Megalohyrax suillus* (originally *Mixohyrax suillus*), and the new species *Megalohyrax pygmaeus*. He also erected the new genus *Titanohyrax* for very large-sized hyracoids, in which he included the new species *Titanohyrax ultimus*, *Titanohyrax schlosseri*, *Titanohyrax andrewsi*, and *Titanohyrax palaeotherioides* as the type species (originally *Megalohyrax palaeotherioides*). Five years later, Matsumoto (1926) revised all Fayum hyracoids, erecting three new families. He named the first Geniohyidae, and included in this the three bunodont genera *Geniohyus*, with the new species *Geniohyus gigas*, *Geniohyus subgigas* and *Geniohyus diphycus*, *Bunohyrax*, for which he described the new species *Bunohyrax affinis*, and *Megalohyrax*. The second family is Titanohyracidae, which includes only the genus *Titanohyrax*. The third family is Pliohyracidae, a family that actually had already been established by Osborn (1899) for the Miocene genus *Pliohyrax* (Pickford et al., 2021). In this family, Matsumoto (1926) included the monospecific genus *Pachyhyrax* and the genus *Saghatherium*, for which he described four new species, *Saghatherium macrodon*, *Saghatherium euryodon*, *Saghatherium annectens*, and *Saghatherium sobrina*. Almost half a century later, Meyer (1973) described a new genus and species of saghatheriine hyracoid, *Thyrohyrax domorictus*, known from several Early Oligocene fossil sites (Quarries M, G, I) of the Gebel Qatrani Formation. Rasmussen and Simons (1988a) studied new hyracoid material from the Fayum Depression and erected the new large hyracoid species *Titanohyrax angustidens*, the small *Saghatherium humarum*, and the new genus and species *Selenohyrax chatrathi*, all from the Oligocene of the Gebel Qatrani Formation. Shortly after, Rasmussen and Simons (1991) studied the hyracoid material from the Late Eocene site L-41 of the Gebel Qatrani Formation and described three new species. The first one is *Saghatherium bowni*, which is fairly common in L-41 and exhibits a considerable size-related sexual dimorphism (Rasmussen & Simons, 1991). The other two species are *Thyrohyrax meyeri* and *Thyrohyrax litholagus*, representing more primitive relatives to the somewhat bigger and more derived *Thyrohyrax domorictus* and *Thyrohyrax pygmaeus*, respectively (Rasmussen & Simons, 1991). Almost a decade later, the same authors (Rasmussen & Simons, 2000) described a new titanohyracine species, *Antilohyrax pectidens*, from the Late Eocene site L-41 of the Gebel Qatrani Formation, based on its comb-like first incisor. This new species is of medium size and seems to be related to the huge *Titanohyrax* based on their similarly selenodont cheek teeth and broad incisors, among other features (Rasmussen & Simons, 2000). Barrow et al. (2010) described the new small species *Dimaitherium patnaiki*, based on a partial left mandible as the holotype and numerous isolated dental elements from the Late Eocene locality BQ-2, all from the Birket Qarun Formation. A partial cranium from the Late Eocene locality BQ-7 can also be referred to this species. Thus, *Dimaitherium patnaiki* represents the oldest and most primitive hyracoid taxon from the Fayum Depression and seems to be most closely related to the genus *Thyrohyrax* (Barrow et al., 2010).

Hyracoids are extremely diverse and well represented in the Fayum fauna, but almost all finds come from the Late Eocene to Early Oligocene Gebel Qatrani Formation (e.g. Andrews, 1906a; Rasmussen & Simons, 1988a). The Late Eocene fossil site L-41 of this formation preserves the highest diversity of hyracoids in the Fayum succession, including eight genera and nine species (Barrow et al., 2010; Rasmussen & Simons, 1988a, 1991). Only a single fragmentary hyracoid specimen has been described from the underlying Qasr el Sagha Formation (Holroyd et al., 1996), and one primitive taxon, *Dimaitherium patnaiki*, is exclusively found in the Birket Qarun Formation (Umm Rigl Member) (Barrow et al., 2010).

Over the last century, more than 30 hyracoid species have been described from Fayum material. Many of these species have been synonymised and/or referred to different genera afterwards. Beside the taxonomic diversity in the Fayum hyracoids, the representatives of this group seem to cover a wide array of ecological niches. This is indicated by the different dental morphologies including the more generalised *Saghatherium* and *Thyrohyrax* and the bunodont, probably omnivorous *Geniohyus* (Barrow et al., 2010). One of the most peculiar hyracoids of the Fayum fauna is certainly the gazelle-sized *Antilohyrax pectidens* (Rasmussen & Simons, 2000). It exhibits hyper-pectinate lower incisors, but no upper incisors (de Blieux & Simons, 2002). The dentition is sharp-edged selenodont, pointing to a folivorous diet and its postcranial morphology suggests that it was cursorial browser, representing an Eocene analogue to modern bovids (Rasmussen & Simons, 2000).

4.3.8 Sirenia

The sirenians or sea-cows are among the first vertebrate fossils that have been described from Egypt. Owen (1875) described the new species *Eotherium aegyptiacum* from the Eocene of the "Mokattam cliffs" near Cairo, representing the first sirenian species to be described from Egypt. From Middle to Upper Eocene strata of the same area, close to Cairo, four further species have been described, *Manatus coulombi* Filhol, 1878, *Protosiren fraasi* Abel, 1907, *Eosiren abeli* Sickenberg, 1934, and *Eotherium majus* Zdanksy, 1938, of which the holotype is now considered lost (Zalmout & Gingerich, 2012). It is important to note that the genus name *Eotherium* was actually preoccupied, and thus, Palmer (1899) proposed the new name *Eotheroides* for this genus, which is still in use today.

Andrews (1902) described the first sirenian remains from the Fayum Depression. This material comes from the Qasr el Sagha Formation and includes an almost complete skull and associated mandible, for which Andrews (1902) erected the genus and species *Eosiren libyca*. Three decades later, Sickenberg (1934) described the new species *Eosiren stromeri*, in honour of Ernst Stromer von Reichenbach, from the Qasr el Sagha Formation of the Fayum. More than half a century later, Domning et al. (1994) described the new species *Eosiren imenti* based on a cranium from the Early Oligocene of the Gebel Qatrani Formation in the Fayum. Based on the fluviatile environment of the Gebel Qatrani Formation, it is possible that *Eosiren imenti* had a wide salinity tolerance (Domning et al., 1994). In the same year, Domning and Gingerich (1994) described the new species *Protosiren smithae*, based on a partial skeleton that comprises a fairly well-preserved skull, its mandible, and several postcranial elements, from the Gehannam Formation in Wadi al Hitan. More recently, Zalmout and Gingerich (2012) described two additional species of sea-cows, from the Birket Qarun Formation of Wadi al Hitan. The first species is *Eotheroides clavigerum* and was based on a partial skeleton of an adult individual. The second species, *Eotheroides sandersi*, was based on more fragmentary cranial and postcranial elements that were found in association (Zalmout & Gingerich, 2012, fig. 8).

4.3.9 Primates

The Fayum Depression has offered significant insight into the early evolution of primates during the Eocene and Oligocene. When the locality was first discovered in the late nineteenth and early twentieth century, it provided the oldest fossil primates known at that time. More specifically, Osborn (1908) described the small *Apidium phiomense* (originally mentioned as *Apidium phiomensis*) based on a partial left mandibular ramus from the Gebel Qatrani Formation, which he initially compared to bunodont artiodactyls and primates, but was unable to assign it to any of them. It was soon after

Fig. 8 Skull of *Eosiren libyca* (GPIT-PV-41670) from the Fayum Depression (Egypt), collected by Richard Markgraf, in **a** dorsal and **b** left lateral view. Scale bar is 10 cm

referred to a primate (Schlosser, 1911), though the discussion about its systematic position was far from over (Simons, 1960). Fleagle and Simons (1995) studied the limb skeleton of *Apidium phiomense* and compared it to other primates, concluding that it was a very primitive arboreal quadrupedal primate, weighing about 1.6 kg. Today, *Apidium* is well recognised as a primate that belongs to the family of Parapithecidae (Beard et al., 2016; Fleagle & Simons, 1995; Simons, 1995a) and is very common in the Gebel Qatrani Formation (Simons & Rasmussen, 1990). The genus includes three species along with *Apidium phiomense*, *Apidium moustafai* from Quarry G of the Gebel Qatrani Formation (Simons, 1962), *Apidium bowni* from Quarry V of the Gebel Qatrani Formation (Simons, 1995a), and *Apidium zuetina* from the Early Oligocene of the Sirt Basin in central Libya (Beard et al., 2016).

Soon after the description of the first primate material from the Fayum deposits (Osborn, 1908), Schlosser (1910) published a preliminary report on the Fayum fossils collected by Markgraf from the Gebel Qatrani Formation and described three new primate taxa: *Moeripithecus markgrafi*, *Parapithecus fraasi*, and *Propliopithecus haeckeli*. Schlosser (1910) even suggested that *Propliopithecus haeckeli* represents an ancestor of hominids. *Moeripithecus markgrafi* was based on a mandibular ramus fragment with two preserved molars (Schlosser, 1910, 1911). It was later suggested to be a juvenile *Propliopithecus* (Simons, 1967; Szalay & Delson, 1979). Nowadays, the synonymy of *Moeripithecus* and *Propliopithecus* is well established, and the name *Propliopithecus* is used (e.g. Simons & Rasmussen, 1990; Simons et al., 1987). Simons (1965) described the new taxa *Aegyptopithecus zeuxis*, based on two mandibular fragments, and *Aeolopithecus chirobates*, based on a nearly complete mandibular corpus, from Quarry I of the Gebel Qatrani Formation. Since its first description, much more material of *Aegyptopithecus zeuxis* has been found, including several more or less complete skulls (Fig. 9a and b), of both male and female individuals (e.g. Fleagle et al., 1980; Kay et al., 1981; Simons, 1987; Simons et al., 2007). Subsequently, however, the validity of *Aeolopithecus chirobates* has been questioned after its initial description by Gingerich and Arbor (1978), who argued for a potential synonymy with *Propliopithecus haeckeli*. Szalay and Delson (1979) later supported the notion that *Aeolopithecus chiborates* might in fact be assignable to the genus *Propliopithecus*. This was also followed by Kay et al. (1981), who also discussed some ecological aspects of these animals, such as the existence of sexual dimorphism. Furthermore, Simons et al. (1987) erected the new species *Propliopithecus ankeli* based on dental material from Quarry V of the Gebel Qatrani Formation. The genera *Propliopithecus* (including *Aeolopithecus* and *Moeripithecus*) and *Aegyptopithecus* are regarded as members of the Propliopithecidae (Ducrocq, 2001).

Parapithecus fraasi is based on a complete mandible (Fig. 9d), only lacking the right p2 (Schlosser, 1910, 1911). Schlosser (1911) established the new family Parapithecidae for this taxon. Later, Simons (1974) described the new species *Parapithecus grangeri*, based on a mandibular fragment with five teeth preserved, from Quarry I of the Gebel Qatrani Formation that is somewhat larger and presumably stratigraphically younger than the type mandible of *Parapithecus fraasi*. Few years later, Gingerich and Arbor (1978) proposed the synonymy of *Parapithecus fraasi* and *Apidium phiomense* and erected the new genus *Simonsius* for *Parapithecus grangeri*. Although this view was not supported by most authors in the following years (e.g. Kay et al., 1981; Seiffert et al., 2020; Simons & Rasmussen, 1991; Simons, 1986, 1992, 1995b, 2001), it was nevertheless adopted by some and is used even in more recent studies (e.g. Fleagle & Kay, 1985; Harrison, 1987; Mattingly et al., 2021). Mattingly et al. (2021) considered *Simonsius* as a valid genus and described the new species *Simonsius harujensis*, a small (1–1.5 kg) parapithecine from the Early Oligocene of Libya.

Simons and Kay (1983) erected the genus *Qatrania*, with the sole species *Qatrania wingi*, based on some fragmentary dental elements from Quarry E of the Gebel Qatrani Formation. *Qatrania* represents a parapithecid of very small size, ~ 300 g (Mattingly et al., 2021; Simons & Kay, 1983). Five years later, the same authors described the new species *Qatrania fleaglei* based on a fragmentary right hemimandible from Quarry M of the Gebel Qatrani Formation (Simons & Kay, 1988), which constitutes the youngest representative of the genus (Beard & Coster,

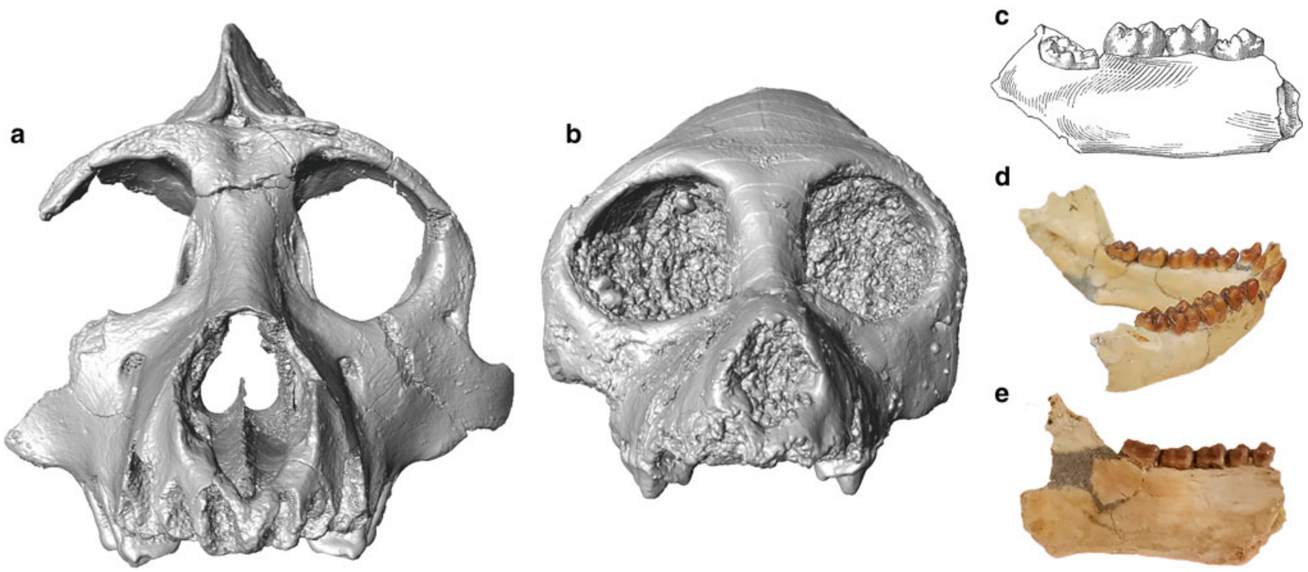

Fig. 9 Primate material from the Late Eocene to Early Oligocene Gebel Qatrani Formation of the Fayum Depression (Egypt): **a** µCT-scan of a male skull of *Aegyptopithecus zeuxis* (DPC 2803), provided by the DPC; **b** µCT-scan of a female skull of *Aegyptopithecus zeuxis* (CGM 85785), provided by the DPC; **c** type mandible of *Apidium phiomense* in medial view (taken from Osborn, 1908, fig. 6A2); **d** type mandible of *Parapithecus fraasi* (SMNS-P-43461) in right lateral view (Schlosser, 1911, taf. I, fig. 3); and **e** type mandible of *Propliopithecus haeckeli* (SMNS-P-12638) in medial view (Schlosser, 1911, taf. I, fig. 1). Not to scale

2016). Simons et al. (2001) erected a new genus and species of Parapithecidae, *Abuqatrania basiodontos*, based on a small mandible from the Late Eocene site L-41 of the Gebel Qatrani Formation. This species was later attributed to the genus *Qatrania* (Beard, 2013; Beard & Coster, 2016; Mattingly et al., 2021).

Simons and Bown (1985) erected the small, peculiar primate *Afrotarsius chatrathi* based on a mandible from the Oligocene site Quarry M, of the Gebel Qatrani Formation. It was initially regarded as a relative of the tarsier (Simons & Bown, 1985). More recently, Jaeger et al. (2010) described a second species for the genus, *Afrotarsius libycus*, from the late Middle Eocene of Libya, whereas Chaimanee et al. (2012) erected a new primate species, *Afrasia djijidae*, from the late Middle Eocene of Myanmar and proposed that it belongs, along with *Afrotarsius libycus*, to the Afrotarsiidae, within the Eosimiiformes.

De Bonis et al. (1988) erected the genus *Biretia* for a potential primitive Catarrhini from the Eocene of Algeria. This genus was later included in the Parapithecoidea (e.g. Mattingly et al., 2021; Seiffert et al., 2005, 2020). Later, two species of *Biretia* were described based on the material from the Fayum Depression: *Biretia fayumensis* and *Biretia megalopsis*, both based on mandibular fragments preserving the m2 and m3 from the Late Oligocene locality BQ-2 of the Birket Qarun Formation (Seiffert et al., 2005).

Simons (1962) described, alongside *Apidium moustafai*, also the new genus and species *Oligopithecus savagei* from Quarry F of the Gebel Qatrani Formation. Later, Rasmussen and Simons (1988b) described further material of *Oligopithecus savagei*, supporting a close relationship to the Propliopithecidae. Simons (1989) described two new small primate taxa, *Catopithecus browni* and *Proteopithecus sylviae*, from the Late Eocene site L-41 of the Gebel Qatrani Formation. The same author erected the Oligopithecinae to include *Oligopithecus*, *Catopithecus* and possibly *Proteopithecus*, though the lower dentition of the latter was still unknown (Simons, 1989). Some years later, a large collection of additional material of *Proteopithecus sylviae* was published, including even a partial skull (Miller & Simons, 1997), which led Simons (1997a) to erect the family Proteopithecidae, with the sole representative being *Proteopithecus sylviae*.

Simons (1992) described three new genera and species of primates, *Serapia eocaena*, *Plesiopithecus teras*, and *Arsinoea kallimos*, based on three partial mandibles from L-41 in the Upper Eocene strata of the Gebel Qatrani Formation. Simons (1992) suggested that *Serapia* belonged to the Parapithecidae, while not being able to attribute the other two new taxa to any family. A new phylogenetic analysis placed *Serapia* as the sister taxon of *Proteopithecus*, forming together the Proteopithecidae, whereas *Arsinoea* seems to represent a basal stem-group member of the Parapithecidae (Seiffert et al., 2020). Seiffert et al. (2020) suggested that the Proteopithecidae and the Parapithecidae belong to the Parapithecoidea, an autochtonous group of Afro-Arabia, with a single representative from the Oligocene of South America, *Ucayalipithecus perdita* (Seiffert et al., 2020).

A new superfamily, the Plesiopithecoidea, and family, the Plesiopithecidae, were erected by Simons and Rasmussen (1991) for the small primate *Plesiopithecus teras*. Simons (1997b) described two new extremely small prosimians (Kirk & Simons, 2001), the new genus and species *Wadilemur elegans* and the new species *Anchomomys milleri*, from the Late Eocene site L-41, of the Gebel Qatrani Formation. In their phylogenetic analysis, Seiffert et al. (2003) placed *Plesiopithecus* as a stem Strepsirrhini. Gunnell et al. (2018) recovered *Plesiopithecus* as a basal Chiromyiiformes and a relative to both the extant Madagascan aye-aye (*Daubentonia*) and the Early Miocene *Propotto* from Kenya. Although, *Propotto* has been suggested to belong to the Megachiroptera (Pickford, 2018).

Seiffert et al. (2003) also erected the lorisiform primates *Karanisia clarki* and *Saharagalago misrensis*, based on a partial mandible and a single lower tooth from BQ-2, respectively, both from the Late Eocene Birket Qarun Formation (Seiffert et al., 2003). A second species was added to *Karanisia*, when Jaeger et al. (2010) described the new *Karanisia arenula* based on an m2 from the late Middle Eocene of Libya. Gunnell et al. (2018) included *Wadilemur*, *Saharagalago*, and *Karanisia* in their phylogenetic analysis, which placed them as relative basal lorisiforms (Gunnell et al., 2018).

Simons et al. (1995) described the new adapid primate *Aframonius dieides*, based on three partial mandibles from the Late Eocene L-41 of the Gebel Qatrani Formation. Seiffert et al. (2009) described a new large adapiform, *Afradapis longicristatus*. Soon after, the description of an astragalus assigned to this species further supported its phylogenetic position (Boyer et al., 2010). More recently, Seiffert et al. (2018) assigned a plethora of isolated dental remains and some partial mandibles to the new adapiform *Masradapis tahai*, which seems to represent a sister taxon to *Aframonius dieides* (Seiffert et al., 2018).

Seiffert et al. (2010) described a puzzling new primate, *Nosmips aenigmaticus*, named after George Gaylord Simpson, based on some isolated teeth from the Late Eocene site BQ-2 of the Birket Qarun Formation. The phylogenetic position of this taxon and its affinities remain uncertain (e.g. Gunnell et al., 2018; Seiffert, 2012; Seiffert et al., 2010). Seiffert et al. (2010) suggested that it might represent a highly specialised representative of an unknown primate lineage, endemic to Africa.

4.3.10 Rodentia

The rodents are well known from the Fayum Depression, especially from the Oligocene of the Gebel Qatrani Formation (Wood, 1968). The most frequent representatives of this group are the hystricomorphs and the anomaluroids (Al Ashgar et al., 2019). Most of the material of this group from the Fayum area was collected during the second half of the twentieth century; before, most collecting efforts aimed principally at large mammals (Simons, 1968).

Nonetheless, the first micromammals were described by Osborn (1908) who erected *Phiomys andrewsi*, named after Charles W. Andrews, for two partial right mandibles, and *Metaphiomys beadnelli*, named after Hugh J. L. Beadnell, for a partial left mandible, both species occurring in the Gebel Qatrani Formation. Wood (1968) presented the first comprehensive study of rodents from the Fayum deposits. He described two new species of *Phiomys*, *Phiomys paraphiomyoides* and *Phiomys lavocati*, the new species *Metaphiomys schaubi* and *Paraphiomys simonsi* and introduced two new genera, *Gaudeamus* and *Phiocricetomys*, from the Oligocene of the Gebel Qatrani Formation (Wood, 1968). Sallam et al. (2009) studied the rodent material from BQ-2, erecting the new species *Protophiomys aegyptensis* and the new genus and species *Waslamys attiai*. They performed a phylogenetic analysis, which recovered both taxa as stem-group members of Hystricognathi, to draw conclusions on the biogeographic history of the hystricognathous evolution and their dispersal from Africa to South America (Sallam et al., 2009). Sallam et al. (2010a, 2010b) studied the anomaluroid rodent material from BQ-2 of the Birket Qarun Formation and described two new species *Shazurus minutus* and *Kabirmys qarunensis*. Both were suggested to be members of the Anomaluridae (Sallam et al., 2010a, 2010b). Sallam et al. (2011) described two new species, *Gaudeamus aslius* and *Gaudeamus hylaeus* from the Late Eocene site L-41 of the Gebel Qatrani Formation. This genus also includes *Gaudeamus aegyptius* as the type species, also known from the Gebel Qatrani Formation, *Gaudeamus lavocati*, and potentially a third species from the Fayum succession, which they referred to as *Gaudeamus* aff. *aslius*. For these taxa, they erected the new hystricognathous family Gaudeamuridae, which they regarded as autochthonous for Afro-Arabia and as potentially being closely related to the hystricids (Sallam et al., 2011, figs. 20 and 21).

A new species of phiomyid, *Acritophiomys bowni*, was described by Sallam et al. (2012) from the Late Eocene site L-41 of the Gebel Qatrani Formation in the Fayum succession. In their phylogenetic analysis, this species was recovered as a basal member of the Phiomorpha (Sallam et al., 2012). Sallam and Seiffert (2016) described two new phiomorphs, *Birkamys korai* and *Mubhammys vadumensis*, from the Late Eocene site L-41 of the Gebel Qatrani Formation, which seem to form a monophyletic group. Later, the same authors (Sallam & Seiffert, 2019) erected the new genus *Monamys* for the previously described species *Monamys simonsi* (originally named *Paraphiomys simonsi* by Wood, 1968), which they regarded as a stem thryonomyoid. Most recently, Al-Ashqar et al. (2021) studied new material of the Phiocricetomyinae and erected a new genus and species, *Qatranimys safroutus*, from the Late Eocene site L-41, from the base of the Gebel Qatrani Formation.

4.3.11 Pholidota

The potential existence of pangolins in the Paleogene of the Fayum Depression was unknown for almost a century. Until Gebo and Rasmussen (1985) reported two distal phalanges, which resemble those of an extant pangolin (i.e. *Manis pentadactyla*). The specimens come from the Early Oligocene deposits of Quarry M and Locality 12 (L-12), of the Gebel Qatrani Formation. Furthermore, numerous termite- and ant-nests have been reported from the Gebel Qatrani Formation, some of which exhibit potential vertebrate excavation marks (Bown, 1982). Thus, despite the ambiguous taxonomy of the two phalanges, it has been suggested that the Fayum pangolin dug and fed on termites, similar to some modern-day pangolins (Gebo & Rasmussen, 1985). Due to the fragmentary nature of the fossils and the absence of any teeth or cranial material from the Fayum Depression, the attribution of these specimens to pangolins has been questioned (Gaudin et al., 2009).

4.3.12 Cetacea

Cetaceans are one of the most extensively studied and best-known fossil vertebrate groups from the Paleogene of Egypt. Complete skeletons have been recovered from the Gehannam Formation and Birket Qarun Formation (from the Wadi al Hitan or Valley of Whales); however, they occur only sparsely in the Qasr el Sagha Formation (Gameil et al., 2016; Gingerich, 1992, 2010). The first fossil whales from Africa were found by Georg Schweinfurth in 1879, representing the first archaeocete cetaceans known from the eastern hemisphere. The remains were found in the Birket Qarun Formation on the island of Geziret el Qarn in the centre of lake Birket Qarun (Dames, 1883a; Gingerich, 2010). These fossils include vertebrae (Dames, 1883a, 1894) and skull fragments (Dames, 1883b) of "*Zeuglodon*" sp. as well as the holotype of "*Zeuglodon*" *osiris* (now *Saghacetus osiris*), an almost complete dentary (Dames, 1894, pl. I; fig. 10).

At the beginning of the twentieth century, Beadnell collected a considerable amount of archaeocete remains from the Birket Qarun Formation, which were briefly described by Andrews (1901c, 1904f). Andrews (1904f) established the species "*Zeuglodon*" *isis* (now *Basilosaurus isis*). The name of this species was originally proposed by Beadnell in a memoire about the geology of the Fayum Province (Beadnell, 1905) that was, however, published after Andrews (1904f). The holotype is a complete mandible containing the entire dentition. Beadnell also collected fossil archaeocetes from an area west of Garet Gehannam. The fossils were so abundant there that he called this area "*Zeuglodon* Valley" (Beadnell, 1905), which was later named Wadi al Hitan or Valley of Whales. During this phase, he collected a complete skull of an archaeocete that was later described as the holotype of "*Prozeuglodon*" *atrox* (now *Dorudon atrox*), by Andrews (1906a). All fossil archaeocetes collected by Beadnell and Andrews at the beginning of the twentieth century were described in detail by Andrews (1906a) in his monograph about the vertebrate fauna of the Fayum.

Andrews (1906a) described the holotype skull of "*Prozeuglodon*" as intermediate between *Protocetus* and "*Zeuglodon*", but in 1908 he revised the specimen, concluding that it instead represented a juvenile with deciduous teeth. Therefore, "*Prozeuglodon*" *atrox* was long thought to be the juvenile form of "*Zeuglodon*" *isis* (e.g. Barnes & Mitchell, 1978; Kellogg, 1936). However, Gingerich et al. (1990) studied complete skeletons of both species and showed that "*Prozeuglodon*" *atrox* is not a juvenile of "*Zeuglodon*" *isis* and thus belongs to a separate genus and species. The archaeocete fossil collected by Andrews and Beadnell were furthermore studied by Dart (1923), who established three new species of "*Zeuglodon*" (*Zeuglodon sensitives*, *Zeuglodon elliotsmithii*, and *Zeuglodon intermedius*) based on natural endocasts of the brain cavity (Fig. 11).

Besides Beadnell and Andrews, Stromer and Fraas also collected archaeocete remains from the Fayum region, north of Birket Qarun. They discovered a new skull and lower jaw of "*Zeuglodon*" *osiris* from the Qasr el Sagha Formation (Stromer, 1902) and, furthermore, established the species "*Zeuglodon*" *zitteli* based on a natural endocast of the nasal region, skull remains, as well as vertebrae (Stromer, 1903, pl. 10–11). More recently, Gingerich (2007) established a new species of archaeocete whale from that region based on the vertebrae collected by Stromer and additional vertebrae from Garet el Esh, which he named in honour to Stromer, *Stromerius nidensis*.

During the same period, Fraas and Markgraf collected a cranium and associated postcranial remains of a small

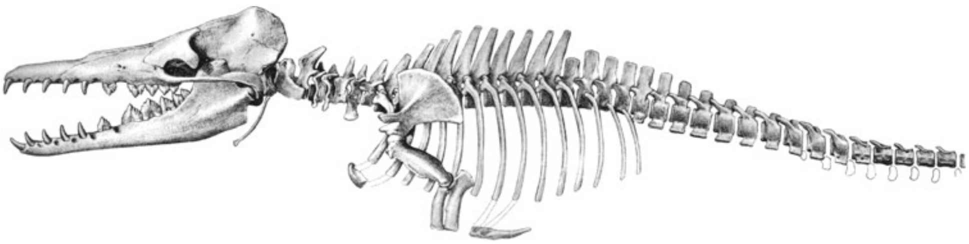

Fig. 10 *Saghacetus osiris* skeleton reconstruction (Stromer, 1908, taf. I, fig. 1)

Fig. 11 Cetacea material from the Eocene of the Fayum Depression (Egypt): **a** skull of *Saghacetus osiris* (NHMUK M 10228) in right lateral view; and **b** "*Zeuglodon intermedius*' (NHMUK M 10173, now *Dorudon atrox*) in left lateral view. Scale bar is 20 cm

archaeocete from Gebel Mokattam. The specimen was described by Fraas (1904) as *Protocetus atavus* a new genus and species, which became the type genus of the new family Protocetidae (Stromer, 1908). Another skull from the same formation was named by Fraas (1904, 1906) as "*Mesocetus*" *schweinfurthi* (now known as *Eocetus schwinfurthi*). In 1906, Fraas and Markgraf excavated a large skeleton of "*Zeuglodon*" *isis* west of Birket Qarun comprising a skull with a length of 1.3 m and a sequence of vertebrae and ribs about 10 m in length (Fraas, 1906; Gingerich, 2010). This skull was described by Stromer (1908) and Slijper (1936) and was later depicted by Heizmann (1991). After the excavations of Fraas and Markgraf, Stromer together with Markgraf went to the Fayum Depression in order to collect fossil whales (Gingerich, 2010). They recovered two large archaeocete vertebrae from Gebel Mokattam, an archaeocete skull with jaws, and some vertebrae from the Birket Qarun Formation (Stromer, 1904).

After the expeditions of Fraas and Stromer, several scientists and fossil collectors from the USA, such as Henry F. Osborn and Walter Granger (in 1907), as well as Robert H. Denison and Paules E. P. Deraniyagala (in 1947) visited the areas around Qasr el Sagha, Birket Qarun, and Wadi al Hitan (Gingerich, 2010). They collected many large zeuglodonts from Wadi al Hitan (Deraniyagala, 1948; Kellogg, 1936; Osborn, 1907) and partial skulls of "*Zeuglodon*" *isis*, as well as endocranial casts of "*Prozeuglodon*" *atrox* (Pilleri, 1991). Kellogg (1936) was the first to mention the use of *Basilosaurus* over *Zeuglodon*, as he regarded them as synonyms. Later, Gingerich et al. (1990) and Uhen (2004) supported this taxonomic assignment. Furthermore, Kellogg (1936) placed "*Zeuglodon*" *osiris* in *Dorudon,* and later Uhen (2004) included "*Prozeuglodon*" *atrox* in *Dorudon* as well. The species "*Zeuglodon*" *osiris* was later placed into *Saghacetus* by Gingerich (1992).

Moustafa (1954) described a partial skull of a subadult "*Zeuglodon*" *isis* in the Birket Qarun Formation that was collected by him in 1950. In the following two decades, the palaeontologists Simons and Meyer visited the area around Birket Qarun, Qasr el Sagha, and Wadi al Hitan (Gingerich, 2010). They found skulls of "*Zeuglodon*" *isis* in the Birket Qarun Formation and some archaeocete remains in the Qasr el Sagha Formation (Simons & Wood, 1968). Barnes and Mitchell (1978) provided a review of African cetaceans, in which they included *Prozeuglodon atavus*, *Eocetus schweinfurthi*, and *Pappocetus lugardi* in Protocetidae. They also placed among others "*Zeuglodon*" *osiris* and "*Zeuglodon*" *isis* into Basilosauridae.

Shortly after, Gingerich and Simons excavated in the Fayum region, uncovering new archaeocete remains from the Birket Qarun Formation (Wadi al Hitan) and Qasr el Sagha Formation in 1983 (Gingerich, 2010). They found many well-preserved skeletons of archaeocete whales. The most common taxa in Wadi al Hitan were *Basilosaurus isis* and *Dorudon atrox*, both represented by equal numbers of individuals (Gingerich, 2010). Both species are described to be morphologically quite similar with slight osteological differences (Gingerich & Smith, 1990; Gingerich et al., 1990; Luo & Gingerich, 1999). Furthermore, recent studies using stable isotopes confirmed that both, *Basilosaurus* and *Dorudon*, were fully aquatic (Clementz et al., 2006). Moreover, Gingerich et al. (1990) focused on the development of the hindlimbs in archaeocetes based on fossils from Wadi al Hitan ultimately providing insights into archaeocete evolution. In addition to *Basilosaurus isis* and *Dorudon atrox*, further archaeocete whales are known from Wadi al Hitan such as *Ancalecetus simonsi* (Gingerich & Uhen, 1996) and *Masracetus markgrafi* (Gingerich, 2007). From the Qasr el Sagha Formation, *Saghacetus osiris* and *Stromerius nidensis* are known (Gingerich, 2007).

Most recently, Gohar et al. (2021) described a new medium-sized protocetid, *Phiomicetus anubis*, from the Middle Eocene Midawara Formation in the south-western part of the Fayum Depression. A partial skeleton, including a fragmentary skull, was reported. The material enabled the authors to establish *Phiomicetus* as the most basal African protocetid and as a highly efficient hunter of elusive prey (Gohar et al., 2021).

4.3.13 Anthracotheriidae

Anthracotheres are among the most abundant fossils recovered from the Fayum Depression (Sileem et al., 2016). They were the first artiodactyls that reached the African continent (Sileem et al., 2016; Simons, 2008; Simons & Rasmussen, 1990); however, the origin of African anthracotheres is still largely unknown. According to Lihoreau and Ducrocq (2007), anthracotheres likely originated in North America or Eurasia with the oldest known fossils from North America (42 Ma) and Myanmar (~ 40 Ma; Zaw et al., 2014). Anthracotheres then spread and diversified throughout Laurasia and Africa. However, Simons and Rasmussen (1990) mentioned that Anthracotheriidae are not related to African Paenungulata, but instead originated from the Eurasian forms (Black, 1978; Schmidt, 1913).

Andrews and Beadnell (1902) reported the first anthracothere material from the Fayum area and described the new species *Ancodus gorringei* from the Gebel Qatrani Formation based on a nearly complete mandible. This species was described in detail by Andrews (1906a) as *Ancodon gorringei*. Andrews (1906a) furthermore established the new species *Ancodon parvus*, in addition to unassigned material of *Ancodon* sp. Specimens of *Ancodon gorringei* and *Ancodon parvus* comprise mainly mandible remains including teeth and provisionally referred postcranial material. Together with the remains of *Ancodon*, Andrews (1906a) also established the species *Rhagatherium aegyptiacum* based on an upper left molar. All fossils described by him in 1906 were recovered from the Gebel Qatrani Formation. Depéret (1908) assigned *Ancodon gorringei* and *Ancodon parvus* to the bunodont anthracothere genus *Brachyodus*, and later Schmidt (1913) mentioned that the unassigned material of *Ancodon* sp. (Andrews, 1906a, p. 191) belonged to *Brachyodus parvus*. Schmidt (1913) reported the presence of the two already known species of *Brachyodus* and erected three new species, *Brachyodus andrewsi*, *Brachyodus fraasi*, and *Brachyodus rugulosus*. He also erected the new subgenus *Bothriogenys* (Schmidt, 1913), which was later raised by Black (1978) to genus rank and since then retained this status (e.g. Black, 1978; Dineur, 1982; Sileem et al., 2015, 2016). In 1997, Ducrocq (1997) erected the genus *Qatraniodon* to which he referred the previously described species *Bothriogenys parvus*.

Fig. 12 Anthracotheriidae material from the Late Eocene to Early Oligocene Gebel Qatrani Formation of the Fayum Depression (Egypt): **a** complete skull of *Bothriogenys fraasi* (NHMUK PV M 10186; Schmidt, 1913, taf. II, fig. 1) in ventral view; and **b** right mandibular ramus of *Bothriogenys gorringei* (SMNS-P-44080; Schmidt, 1913, taf. IV, fig. 9) in lateral view. Scale bar is 10 cm

At present, the existence of three genera of Anthracotheriidae in the Fayum succession is accepted: *Bothriogenys*—including the four species *Bothriogenys gorringei*, *Bothriogenys rugulosus*, *Bothriogenys fraasi*, and *Bothriogenys andrewsi*; *Qatraniodon*—comprising one species, *Qatraniodon parvus*; and *Nabotherium*—replacing *Rhagatherium*, thus including *Nabotherium aegyptiacum*

(Sileem et al., 2015, 2016). These species differ from one another primarily in size, specializations of the anterior dentition, and degree of brachydonty versus selenodonty (Holroyd et al., 2010, fig. 12).

Anthracotheres are absent in the Birket Qarun Formation. They first appear in the Dir Abu Lifa Member of the Qasr el Sagha Formation as Anthracotheriidae indet. Above the Eocene–Oligocene boundary; *Nabotherium*, *Qatraniodon*, and *Bothriogenys* are present in the Gebel Qatrani Formation (Sileem et al., 2015, 2016).

Anthracotheres were large, stout-bodied animals that might have been semi-aquatic (Pickford et al., 2008; Sileem et al., 2016; Simons, 2008). Boisserie et al. (2005) even reaffirmed a distant relationship to hippopotamuses. Simons and Rasmussen (1990) assumed that anthracotheres partially replaced hyracoids, when they arrived in Africa, because hyracoids were the dominant terrestrial plant eating group at that time that had radiated into several species and their number decreased after the arrival of anthracotheres (Simons, 2008).

Schmidt (1913) already implied that the Fayum anthracotheres consisted of two different lineages and later, Sileem et al. (2016) classified *Nabotherium* as bunodont and *Bothriogenys*, as well as *Qatraniodon* as bunoselenodont representatives. He also concluded that the abundant *Bothriogenys* probably had a browsing/grazing adaptation and was eating foliage based on the morphology of its dentition. Due to their hydrophilic nature, it is possible that they also fed on water plants (Pickford et al., 2008; Simons, 2008). In contrast, the bunodont *Nabotherium* was according to Sileem et al. (2016) probably a selective frugivore/herbivore.

4.3.14 Chiroptera

Bats are a quite rare and under-represented group in the Fayum deposits. The first remains were described well over a century ago, when Schlosser (1910) erected the new genus and species *Vampyravus orientalis* for a relatively big humerus from the Gebel Qatrani Formation. This species represents the first fossil bat described from Africa. In his extensive work about the Fayum fauna, Schlosser (1911) actually coined a new genus name for this specimen, *Provampyrus orientalis*, without explaining the reasons behind this change. Of course, the genus name *Vampyravus* has priority over *Provampyrus*, a fact that has been mentioned repeatedly in the literature (e.g. Gunnell et al., 2008; Rosina & Pickford, 2019; Sigé, 1985). The humerus housed in the SMNS that was described by Schlosser (1910, 1911) remains the only known specimen assignable to this species (Gunnell et al., 2008, 2009). Gunnell et al. (2009) studied the holotype of the species and compared it to the other bats that were described later from the Fayum Depression. He concluded that *Vampyravus orientalis* was the largest bat in the Fayum fauna, weighing about 120 g, distinct from any other taxon from the Fayum and probably belonged to a derived bat family, such as the emballonurids or rhinopomatids (Gunnell et al., 2009).

Gunnell et al. (2008) studied new chiropteran material from different localities from the Birket Qarun Formation and the Gebel Qatrani Formation of the Fayum region. They recognised two previously described species and also founded four new genera, *Witwatia*, *Qarunycteris*, *Saharaderma*, and *Khonsunycteris*, and six new species of bats, *Witwatia schlosseri*, *Witwatia eremicus*, *Dhofarella sigei*, *Qarunycteris moerisae*, *Saharaderma pseudovampyrus*, and *Khonsunycteris aegypticus* (Gunnell et al., 2008). Gunnell et al. (2014) erected a new genus of myzopodid bat, *Phasmatonycteris*, to which he referred two new species *Phasmatonycteris phiomensis*, from the Early Oligocene site Quarry I of the Gebel Qatrani Formation, and *Phasmatonycteris butleri*, from the Late Eocene site BQ-2 of the Birket Qarun Formation. Simmons et al. (2016) described the new genus and species *Aegyptonycteris knighteae*, based on a partial right maxilla from the Late Eocene site BQ-2. This large bat differed considerably from any existing bat family, leading the authors to erect the new family Aegyptonycteridae (Simmons et al., 2016).

4.3.15 Hyaenodonta

Large terrestrial carnivores of the Fayum fauna are represented by the hyaenodonts. The first remains of this extinct group in the Fayum deposits were described by Andrews (1903c), who erected the new “creodont” species *Pterodon africanus* for a partial right mandible. One year later, Andrews (1904f) described another new “creodont” species, *Pterodon macrognathus*, based on a partial left mandible from the Gebel Qatrani Formation. In his monograph about the Fayum fauna, Andrews (1906a) offered detailed descriptions of both previously described carnivorous species, re-examining the generic assignment of the second species and referring to it as *Apterodon macrognathus*. He reported the presence of the genus *Hyaenodon*, based on a partial mandible, and described a new small “creodont” species, *Sinopa ethiopica*, based on a partial left fragment of a mandible (Andrews, 1906a). Shortly after, Osborn (1909) described two complete skulls of *Apterodon macrognathus*, one possibly belonging to a female and the other to a male, two mandibles of *Pterodon africanus*, a slender mandible, which he assigned to a new species, *Pterodon leptognathus*, and a somewhat smaller mandible, on the basis of which he founded the new species *Pterodon phiomensis*. Osborn (1909) also erected the new genus and species *Metasinopa fraasi* and the new species *Hyaenodon brachycephalus*, both based on almost complete mandibles from the Gebel Qatrani Formation. Schlosser (1910) described two new species, *Apterodon altidens* and *Apterodon minutus*, and suggested that a giant “creodont”, like *Palaeonictis* or *Pachyaena*, existed in the Fayum fauna, based on a very large carpal bone. Schlosser (1911) offered extensive descriptions and comparisons of his new carnivore material from the Fayum Depression. More than half a century later, Simons and Gingerich (1974) founded the new genus and species *Masrasector aegypticum* on the basis of dental remains from the Gebel Qatrani Formation. Two years later, the same authors (Simons & Gingerich, 1976) described the new carnivore *Apterodon saghensis*, based on a left mandible from the Late Eocene of the Qasr el Sagha Formation. Holroyd (1999) studied the "creodont" assemblage of the Fayum succession and described the new species and included the two species *Metapterodon schlosseri*, and *Metapterodon markgrafi*, both from the Gebel Qatrani Formation, in the genus *Metapterodon*. More recently, Borths et al. (2016) offered a revision of the Fayum hyaenodonts and erected the new genus and species *Brychotherium ephalmos* and the new species *Akhnatenavus nefertiticyon*. One year later, Borths and Seiffert (2017) described the new species *Masrasector nananubis*, of which complete skulls are known from the Late Eocene site L-41 of the Gebel Qatrani Formation.

Other taxa which had been previously associated with the "creodonts" are the ptolemaiids, which have already been discussed above (e.g. Schlosser, 1911; Simons & Gingerich, 1974). The generic status of the carnivore species has been debated by many authors over the past century and many have been reassigned to new genera, adding to the confusion about the Fayum carnivores (e.g. Holroyd, 1999; Lewis & Morlo, 2010; Morales & Pickford, 2017).

5 Importance of the Fayum Depression for Mammalian Evolution

The Fayum Depression represents the first Paleogene locality that was discovered in Africa. In the early years, the remarkable richness and diversity of the Fayum faunal assemblages sparked the interest of many important vertebrate palaeontologists, who were then involved in the collection and description of the Fayum fossils. These palaeontologists include the British Charles W. Andrews, the Germans Eberhard Fraas, Ernst Stromer von Reichenbach, and Max Schlosser, as well as the American Henry F. Osborn.

These Paleogene deposits in the Fayum Depression yielded the oldest well-documented record of fossil vertebrates from Africa at the time and provided important information on many mammalian groups. The Fayum fossils even led to the establishment of two new orders of mammals: the huge horned Embrithopoda, the ecological affinities of which are not entirely clear, and the small enigmatic Ptolemaiida, whose systematic position is still debated. In addition, numerous new families (e.g. Eremopezidae, Moeritheriidae, Saghatheriidae, Parapithecidae, Propliopithecidae, and Aegyptonycteridae) and subfamilies (e.g. Oligopithecinae, Geniohyinae, Titanohyracinae, and Metoldobotinae) were erected for different Fayum taxa. Extremely rich fossil material of clades, such as the proboscideans and cetaceans, helped unravel the origins and early evolutionary histories of these groups. Eocene–Oligocene members of Proboscidea demonstrate the diversity of this group and point to a semi-aquatic lifestyle for some basal representatives such as *Moeritherium*, whereas the cetaceans from the Eocene of the Fayum Depression show how morphologically advanced and diverse their early representatives from this time were. Wadi al Hitan has provided evidence for at least four distinct whale species, *Basilosaurus isis*, *Dorudon atrox*, *Ancalecetus simonsi*, and *Masracetus markgrafi*. Moreover, the Fayum deposits yielded a remarkable diversity of hyracoids and primates, for which over 30 different species have been named, respectively. Regarding the hyracoids, 10 distinct genera have been erected, to include 37 species (some of which have been synonymised over the years). This high number of taxa likely covered a wide array of ecological niches, from the small-sized *Saghatherium*, weighing below 10 kg, to the large-sized *Titanohyrax*, potentially weighing up to a ton, and from the probably climbing *Dimaitherium* to the cursorial, gazelle-sized *Antilohyrax*. The primates from the Fayum Depression have revealed a similar diversity, with about 20 genera, including about 30 species, most of which are still considered valid, representing several different clades. The most common primate group in the Fayum fauna is the Parapithecoidea, which is regarded as a basal group of Anthropoidea and can be divided into the Parapithecidae and Proteopithecidae. This superfamily also includes the first ever described primate from the Fayum Depression, *Apidium phiomense*. Another common family of primates is the Propliopithecidae, known from many species from the Gebel Qatrani Formation. Other primate groups include the Afrotarsiidae, which in the past was regarded as closely related to the extant *Tarsius*, the Lorisiformes, and the Adapidae.

Fossils from the Fayum Depression that were collected at the end of the nineteenth and the beginning of the twentieth century have been distributed throughout many different collections, including some of the largest natural history museums, such as the AMNH, BSPG, MNHN, NHMUK, NHMW, and SMNS. Important collections of Fayum fossils are also housed at the DPC, the Egyptian Geological Museum in Cairo (Egypt) and the Mansoura University Vertebrate Paleontology Center (Egypt). Even in recent years, over one century after the first discovery of fossils in the Fayum Depression, the region continues to yield rich fossil material that keeps providing new insight into vertebrate evolution during the Paleogene. Especially the discovery of rich fossil localities such as L-41 in the Gebel Qatrani Formation and BQ-2 in the Birket Qarun Formation have provided a wealth of information on the faunal diversity of the Fayum succession and the Paleogene of Africa in general. New cranial material of primates such as *Aegyptopithecus zeuxis* has helped to resolve its phylogenetic relationship to other primates and revealed a pronounced sexual dimorphism. Recently, also the use of new methods such as CT scanning and stable isotope analysis of vertebrate remains has significantly enhanced our understanding of many mammals from the Fayum Depression, including the potential ecology of animals such as *Arsinoitherium*, the anthracotheres, and the hyracoids. As the excavations in the area and the study of old and new fossils from the Fayum with new methods continue, many new and exciting studies are to be expected. The Fayum Depression may continue to shed light on the origin and evolution of many mammalian groups during the Eocene–Oligocene.

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