New *Moeritherium* material from the Fayum area, Egypt

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ONE of the best places in Africa to study the evolution of Eocene and Oligocene vertebrates is the Fayum province in north Western Desert Egypt. It is the richest site for *Moeritherium*, which consists of extensive cranial and postcranial remains. *Moeritherium* is an extinct primitive mammal that denotes an early stage in the proboscidean evolution. An early stage in the formation of the well-known elephant tusks was represented by the highly developed anterior incisors in the upper and lower jaws. The nearshore marine and fluvial Upper Eocene Qasr El Sagha Formation, which is overlain by the fluvial Oligocene Jebel Qatrani Formation and Widan El Faras Basalt, makes up the Upper Palaeogene sequence in the Fayum Province. This study focuses on a new specimen of *Moeritherium* from the Fayum depression. During the Eocene, *Moeritherium* has been reported from Egypt, Algeria, Libya, Mali, Senegal, Ethiopia, and Oman. During the Oligocene, they were reported from Egypt, Libya, Tunisia, Ethiopia and Angola. One of the greatest mysteries of all is the appearance and disappearance of *Moeritherium* in Egypt and even in Africa.

Keywords: *Moeritherium*, Eocene, Oligocene, Fayum.

1. Introduction
The Fayum area has a great history in paleontology. Long ago, the Fayum was a lowland area distinguished by tropical, coastal rainforest with a probable monsoonal climate. The Fayum forest was characterized by tall trees, expansive vines, and mangroves closely resembling to the extant forests in Borneo and other Malaysian districts (Bown *et al.*, 1982). In addition, the past environment of this region resembles the tropical swampy rivers of present-day central Africa (Olson and Rasmussen, 1986; Rasmussen *et al.*, 1987), and these were the dominant conditions of the Fayum Province during Late Eocene-Early Oligocene times. The paleoenvironmental conditions made the Fayum depression suitable for many orders of terrestrial and marine mammals. These animals inhabited the Fayum for a period of about 17.4 my (Simons, 2005).

One of the foremost marvelous stories in mammalian evolution is that of the order Proboscidea, *Moeritherium*, elephants, and their relatives (Romer, 1966). Proboscidea was an endemic member among the resident taxa in the Fayum province through the Late Eocene and Early Oligocene times. *Moeritherium* is an extinct genus of paenungulate mammal that belongs to the order Proboscidea, which includes elephants and their extinct relatives, such as mammoths and mastodons. Although, as it were three elephant species are lively nowadays, more than 160 terminated proboscidean species have been distinguished from remains found on all landmasses but Australia and Antarctica. Most of these were called gomphotheres, which had a place to a distinctive family from elephants. Elephants and mammoths both have a place to the only surviving proboscidean family, Elephantidae. *Moeritherium* was semiaquatic and lived in freshwater swamp or riverine...
environments, where it feed on freshwater vegetation. These results support the hypothesis that Oligocene-to-Recent proboscideans were derived from amphibious ancestors. They originated in North Africa and migrated to the South along the coastal regions of the continent. However, they did not cross into Europe and remained inside Africa. The Early Oligocene Gebel Qatrani Formation, North of Birket Qarun and Qasr El Sagha Formations, are Egypt’s main sites yielding these fossils. They are composed of continental and fluvo-marine sediments.

Fossils of Moeritherium reported from (see also Sanders, 2023) the Eocene of Egypt (Andrews, 1901a, b; Andrews, 1902; Andrews and Beadnell, 1902; Seiffert, 2006); from Algeria (Delmer et al., 2006; Pickford and Tassy, 1980); from Libya (Arambourg and Magnier, 1961; Savage, 1969, 1971; Wight, 1980; Shoshani et al., 1996); from Mali (Andrews, 1901b); from Senegal (Andrews, 1901b) and Ethiopia (Sanders et al., 2004; Kappelman et al., 2003); from Oman (Thomas et al., 1989a, b, 1999; Seiffert, 2006) and the Oligocene of Egypt (Andrews, 1904; 1906; Schlosser, 1911; Matsumoto, 1923; Osborn, 1936; Coppens and Beden, 1978; Seiffert, 2006; Andrews and Beadnell, 1902); from Libya (Savage, 1971; Wight, 1980; Andrews and Beadnell, 1902; Arambourg and Magnier, 1961); from Ethiopia (Sanders et al., 2004; Kappelman et al., 2003); from Tunisia (Andrews and Beadnell, 1902; Arambourg and Burrollet, 1962) and Angola (Pickford, 1986, 1987) and Oman (Thomas et al., 1999; Whybrow and Clements, 1999; Seiffert, 2006).

2. Geological Setting
The Fayum is around 65 km South-West of Cairo, lies between latitudes 29° 05’ and 29° 45’ N and longitudes 30° 00’ and 31° 00’ E and it is one of the richest vertebrate sites of the Eocene-Oligocene in the world. The Fayum Depression area is about 440 km². The Paleogene deposits are exposed in benches North of Birket Qarun. Paleogene deposits in Fayum had been accumulated in a basin aligned West-southwest- East-northeast isolated from the Tethys Sea at the North by structural highs (Bown and Kraus, 1988).

The Upper Eocene - Lower Oligocene formations are the Birket Qarun, Qasr - El Sagha, and the Jebel Qatrani. They are underlain by the Middle Eocene Gehannam Formation and overlain by the Lower to Middle Oligocene Widan-El Faras Basalt and Lower Miocene fluvial deposits of the Khashab Formation (Fig.1).

Qasr el-Sagha Formation. This formation was named by Beadnell (1905). He founded the type section of this unit at the Qasr el-Sagha Temple in the northern Fayum Depression. Said (1962) coined the formal term Qasr el-Sagha Formation. It is 180 m. of shale, limestone, and sandstone. It has an unconformity relationship with the underlying Gebel Qatrani Formation and is deposited conformably above the Birket Qarun Formation. Gingerich (1992) established the lower two members, whereas Bown and Kraus (1988) established the upper two. Gingerich (1992) measured the entire section, which consists of the four individuals, along a transect running from Wadi Hitran to Minqar Abyad in the northwest Fayum Depression. From bottom to top, they are as follows:

- Umm Rigl Member, comprises 35 m of carbonate facies, claystone, and siltstone facies.
- Harab Member comprises 30-40 m brown shale, considered a barren interval.
- Temple Member consists mainly of sandy limestones, and fine sandstones interbedded with thicker sandy and carbonaceous mudstone.
- Dir Abu Lifa Member consists of Sandstone, claystone, and siltstone cross-bedded with one another dominate the lithology.

According to Issawi et al., (1999), the Qasr el-Sagha Formation extends significantly from Fayum to Bahariya to the southern approaches of the Qattara Depression and Cairo-Helwan. It was assigned Late-Late Eocene (Priaebonian) (Gingerich, 1992). At that time (Late- Late Eocene) Qasr el-Sagha Formation was marshy region and was at least partly aquatic, full of vegetation and plants, and these conditions make from Qasr el-Sagha a suitable environment for many creatures including Moeritherium.

3. Material and methods
The specimen is housed and preserved in the Egyptian Geological Museum, Egypt. Its catalogue number is CGM29784.

Abbreviations: I, Incisors; C, Canine; P, Premolar; M, molar.
Location of the specimen: Dir Abulifa member, Qasr El Sagha Fm.

4. Systematic paleontology
Class Mammalia Linnaeus, 1758
Order Proboscidea Illiger, 1811
Family Moeritheriidae Andrews, 1906
Genus Moeritherium Andrews, 1901a, b
(Fig. 2)

Moeritherium fossils have been discovered in strata in northern Africa that belong to the early Oligocene Epoch (33.9–23 million years ago) and the Eocene...
Epoch (55.8–33.9 million years ago) (Andrews, 1901a, b). It was roughly the size of a tapir. Its body was somewhat long, its tail was short and had powerful, short legs. Moeritherium had broad feet that ended in toes with flat hooves. The eyes were positioned far forward, and the skull and cheekbones were long. Moeritherium most likely possessed a short, flexible proboscis, like a tapir, although it is doubtful that an elephantine trunk was present given the location of the nasal apertures on the upper side of the skull. An early stage in the formation of the well-known elephant tusks was represented by the highly developed anterior incisors in the upper and lower jaws. The broad back of the skull was connected to powerful neck muscles (Andrews, 1901a, b). Moeritherium was at least partially aquatic, living in marshy areas and consuming aquatic plants (Andrews, 1901a, b).

Fig. 1. Location map of the Fayum Depression in Egypt; and geological map showing the distribution of the Late Eocene – Oligocene deposits (modified after Sileem and Abu El-Kheir, 2022).
Fig. 2. The Moeritherium specimen CGM29784. A, photograph of the ventral view; B, Line drawing of the ventral view; and dorsal view.
Description and discussion: The well-preserved maxilla have a short diastema between the alveoli of the canine and the P2, which is in contact with the P3/, P4/, M1/, M2/, and M3/ on both sides. The canines are missing from the maxilla but are represented by their alveoli. The dorsal surface of the maxilla is straight or very slightly concave from before backward. The point of junction of the lambdoidal and sagittal ridges posteriorly and the nasals anteriorly is the highest portions of the skullroof. The anterior prominence is probably due to the deepening of the maxilla. The nasals are absent. The anterior region’s upper surface has a deep groove in the mid-line, which is made deeper by the prominent ridges on each side of it. The large alveoli of I2/ form the prominences that are situated outside of these ridges and are separated from them by tiny depressions. Because the nasals are absent, the floor of the nasal cavity is exposed for a considerable amount of distance and is formed by the upper surface of the bones. The front of the snout’s ridges and grooves could be a sign of a small proboscis or a movable top lip that needs an extensive muscle attachment. The following description of the teeth is based on a nearly complete specimen belonging to a young individual. Molars are quadriruberucular and bilophodont. The last premolar is not bilophodont; molars are bilophodont. Premolars are trisphenic. The canine is followed by a short diastema (about 2.5 cm).

The P2/ has an almost triangular shape, with one angle directed anteriorly. The crown is made up of a shelf-like projection on the postero-internal side and an outer row of cusps. The blade is made up of two primary cusps (a.e., p.e.) that are positioned relatively obliquely and tightly together. Out of all of these, the anterior (a.e.) merges with the cingulum at the inner border of the crown after continuing within as a transverse ridge. A little but noticeable cusp, most likely the parastyle (p.s.), forms the anterior angle of the tooth in front of these major cusps. There is a tiny auxiliary cusp located behind the main cusps. The cingulum, which is well-developed and crimped over the entire inner side of the tooth, provides a raised border that forms a broad, slightly concave shelf along the postero-internal portion of the tooth. Comparatively speaking, the anterior premolar (P2/) is tiny and narrow from side to side.

The next premolar (P3/) is distinct from the P2/ in that it has a large antero-internal cusp (deuterocone), which (a.i.) forms a transverse ridge with the anteroexternal cusp (a.e.). There is a posterior auxiliary cusp and a parastyle (p-s.). Also, it is larger and wider; it consists of a high anterior portion and a posterior talon. Three cusps make up the anterior portion of the tooth; one of them forms the antero-internal angle, while behind these the other two imperfectly separated cusps form the transverse ridge. In wear, the talon’s surface—which has a ridge toward its outer side and rises into a tubercle posteriorly—unites with the abraded surface of the antero-internal cusp, which is continuous with that of the outer cusp of the transverse pair. The last premolar, P4/, resembles P3/ but is a little smaller in size. The transverse pair’s inner cusp, on the other hand, is significantly larger and more noticeable. Additionally, the talon has a more pronounced postero-external cusp. The cingulum is slightly developed on the posterior and outer sides of the third and fourth premolars; on the latter, it produces an elevated edge of the talon.

The premolars exhibit a protostyle and anteriorly prominent paracune; P4/ has stronger development of the metacone and hypocone than P3/.

No chevronting, no choerodonty, and no advancement of the pretrite mesaconule anterior to the posttrite half loph are present in the upper molars. The molars are bilophodont, with a lower,
blunter, and more worn inner cusp and a higher, slightly pointed outer cusp on each transverse crest. The pattern depicted in M1/occurs when the postero-internal cusp wears down and tends to be stretched backwards into a little blunt lobe. There is no cementum, and traces of cingulae are weakly expressed on both sides of the crown in the lateral margins of the transverse valleys. The modest thickness of the enamel is distinguished by a sculpture made up of many irregular wrinkles; these are particularly noticeable on the cingulum, to which, in some cases, they give a beaded appearance. The cingulum is well developed on the anterior and lingual surfaces of the teeth. The molars have small, single mesoconelets, and its lophs are transversely aligned straight across the crown. Anterior and posterior pretrite accessory conules are present in association with each loph. The molars have vertical wrinkling of the enamel and lack a continuous centrocrista and well-defined ectoflexus. On molar crowns, posttrite accessory conules are tiny and may be dispersed erratically. The pretrite side of the tritoloph is composed of a stout conelet that may be subdivided into two apical digitations and is accompanied on the posttrite side by a single diminutive conelet. With each loph, there are anterior and posterior pretrite accessory conules.

The bilophodont first molar is made up mostly of two transverse ridges, each of which has a small talon and two tubercles. The outer tubercles are the most worn, whereas the inside tubercles are a little higher and sharper. There is a tendency to form small tubercles in the valley between the two main ridges, connecting the inner ends of the outer tubercles. The talon is made up of a tiny, frequently invisible cusp on the inner side and a blunt tubercle nearly in the mid-line. The M1/ shows great wear, such that the pretrite and posttrite sides nearly at the same level. The protoloph of this molar is deeply worn. It is also having a simple crown and exhibits no ptychodonty or cementodonty.

The second molar (M2/) is larger than M1/ and is less worn than it. It is also bilophodont, each half-loph is composed of two conelets, the outer abaxial conelets being larger than the inner mesoconelets. The first pretrite half-loph in each M2/ exhibits a trefoil wear pattern, due to incorporation of small anterior and posterior central accessory conules. The protoloph of this molar is less worn than that of the M1/, thus the dentine of the ectocone is attached to that of the entocone making a linked lobe which in its turn may be connected to the accessory central conule "protoconule" in the interloph. In M1/ and M2/ a crest descends medially from the protocone into the floor of the anterior transverse valley; the postcingulum is an elongate crest attached to the hypocone, enclosing a diminutive talon basin. Shorter crests are present on the buccal side of the lophs as well. The M3/ is like the first two upper molars but is narrower posteriorly and has less well developed or absent crests.

There is a large cusp (hypoconule) located in the center of the postcingulum in M1/-M2/ but in M3/ it is positioned to the pretrite side of the postcingulum. The talon in the third molar (M3/) is significantly larger than in other teeth. The inner cusp is particularly conspicuous, and the larger main cusp tends to split into two. As a result, the talon produces a third transverse ridge in this tooth. From M1/to M3/, the molar size increases. The protoloph of M3/ is clear, the dentine of the ectocone is attached to that of the entocone which in its turn may be connected to the accessory central conule1 "protoconule" in the first interloph. Also, the second interloph has an accessory central conule2 "the posthypoconule". The entocone and ectocone of this tooth are marked by their antero-posterior compression. There is no talon, but a distinct
cingulum beyond the tritoloph. The accessory central conules are restricted to the anterior half of the crown and the accessory central conule "protoconule" is considerably developed and fills the first valley behind the pretrite ectocone of the protoloph.

Table 1. Measurements (in mm) of the teeth of Moeritherium specimen CGM 29784.

<table>
<thead>
<tr>
<th>Tooth</th>
<th>Mesio-distal length</th>
<th>Bucco-lingual breadth</th>
</tr>
</thead>
<tbody>
<tr>
<td>P2/</td>
<td>2.03</td>
<td>2.14</td>
</tr>
<tr>
<td>P3/</td>
<td>2.23</td>
<td>2.7</td>
</tr>
<tr>
<td>P4/</td>
<td>1.96</td>
<td>2.7</td>
</tr>
<tr>
<td>M1/</td>
<td>2.29</td>
<td>2.6</td>
</tr>
<tr>
<td>M2/</td>
<td>2.53</td>
<td>2.57</td>
</tr>
<tr>
<td>M3/</td>
<td>3.19</td>
<td>2.85</td>
</tr>
</tbody>
</table>

The main differences between the M. Iyonsi (CGM29784) and the other Fayum Moeritherium species:

The Fayum contains several species of *Moeritherium*. *Moeritherium lyonsi* Andrews (1901a) from the Late Eocene, Qasr el Sagha Formation, Fayum area, Egypt (including "M. gracile" "M. ancestrale" "M. pharaonensis" and "M. latidens"). *Moeritherium gracile* Andrews (1902) from the Eocene, Fayum area, Egypt. *Moeritherium trigodon* Andrews (1904) from the Early Oligocene, Gebel el Qatrani Formation, Fayum area, Egypt (including "M. andrewsi" and "M. trigonodon"). *Moeritherium* tends to have more complex cheek tooth crowns and its teeth reach a larger size range limit (Sanders, 2023). *Moeritherium gracile* which distinguished from *M. lyonsi* by its:
1- The comparative lightness of structure,
2- The narrowness of the palate,
3- The smaller size of the upper molars and premolars,
4- The particularly of m 3,
5- The strong development of the cingulum in these teeth

6- And by the considerable inflation of the cranial region of the squamosal, which apparently contains extensive air-sinuses (Andrews, 1906).

Petronievics (1923) recommended erection of "Moeritherium ancestrale," for a few specimens from the Qasr el Sagha Formation, based on differences from *M. lyonsi* (Andrews, 1901a) in the angulation of the occipital planum and size of the palatine vacuity between the maxillary inner borders.

Deraniyagala (1955) proposed two additional *Moeritherium* species for the Qasr el Sagha Formation, "M. latidens" and "M. pharaohensis," based on shape and proportions of molars in two dentary fragments. Subsequent researchers have tended to ignore *M. latidens* and *M. pharaohensis* as too poorly diagnostic to merit specific distinction and treated the features of *M. ancestrale* as exhibiting intraspecific variation that could be accommodated within *M. lyonsi* (Tobien, 1971; Delmer et al., 2006; Sanders et al., 2010).

Comparison between *M. chehbeurameuri* (Algeria) and *M. lyonsi* (CGM29784) (Egypt)

In Algeria, there is a record of *Moeritherium*. *M. chehbeurameuri* which is described from the early late Eocene locality (55.8–33.9 million years ago) of Bir ElAter, Algeria. It shares some features with *M. lyonsi* (CGM29784), such as the important increase in size between M1 and M2, the possession of a relatively wide P3 without a buccal cingulum, together with the reduction/absence of a buccal cingulum on the M1. It differs from it by the reduction of its incisor (Delmer et al, 2006).

5. Conclusions

The snout CGM 29784 is attributed to *Moeritherium* because of the short diastema (about 2.5 cm) behind the canine which is a feature that is diagnostic of *Moeritherium*, and because of the dental morphology. Furthermore, the shape of the
maxilla is like that of *Moeritherium*. This specimen is well preserved and retains an almost complete dentition; molars and premolars are present whereas the canines and incisors. It is robust and characterized by the presence of a nasal opening in front of the maxilla and an open sagittal suture between the two maxillae.

*Moeritherium* is restricted to the Africa and Middle East regions in Eocene and Oligocene time.

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6. References


عينة جديدة لحيوان الموريثريوم من منطقة الفيوم، مصر

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تعتبر أحد أفضل الأماكن في أفريقيا لدراسة تطور الفقاريات الأيوسينية والأوليجوسينية هي منطقة الفيوم في شمال الصحراء الغربية، مصر. إنها أغلى موقع للموريثريوم، والذي يتكون من بقايا جمجمة واسعة النطاق. الموريثريوم هي ثدييات بدائية منقرضة تشير إلى مرحلة مبكرة في تطور الفقاريات. تمثلت المرحلة المبكرة في تكوين أنياب الفيل الشهيرة في القواطع الأمامية المنقرضة للغاية في الفكين العلوي والسفلي. يشكل تكوين قصر الصاغ الأيوسيني البحري والهيري القريب من الشاطئ، والذي يعج بتكوين جبل القطاري النهري وودان الفرس البازلت، تسلسل البيولوجي العلوي في محافظة الفيوم. تركز هذه الدراسة على عينة جديدة من الموريثريوم من منخفض الفيوم. خلال العصر الأيوسيني، تم الاكتشاف عن وجود الموريثريوم في مصر والجزائر، وليبيا، والسنغال، والسودان، وأثيوبيا، عمان، خلال العصر الأوليجوسيني، تم الاكتشاف عنهم من مصر، وليبيا، وتونس، وإثيوبيا، وأنغولا. أحد أعظم الألغاز على الإطلاق هو ظهور واختفاء الموريثريوم في مصر وحتى في أفريقيا.