NEW RECORDS OF TERRESTRIAL MAMMALS FROM THE UPPER EOCENE QASR EL SAGHA FORMATION, FAYUM DEPRESSION, EGYPT

by

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ABSTRACT

New records of terrestrial mammals from the Qasr el Sagha Formation, Fayum Depression, Egypt are reported, and the stratigraphic occurrences of these fossils noted. These include additional specimens of *Moeritherium, Barytherium*, and anthracotheres, as well as the oldest record of a hyracoid in the Fayum. These Eocene mammals occur almost exclusively in the alluvial deposits of the Dir Abu Lifa Member of the Qasr el Sagha Formation and show close affinities to the faunas from the lower sequence of the Jebel Qatrani Formation. There is no evidence of a more marked faunal discontinuity between the Qasr el Sagha and Jebel Qatrani Formations than there is across any of the three major breaks in sedimentation that exist within the Jebel Qatrani Formation. The faunal similarities between fossils of the Iower sequence of the Jebel Qatrani Formation and of the upper part of the Qasr el Sagha Formation is consistent with recent paleomagnetic dating that suggests that these rocks differ in age by only one to two million years.

RESUME

De nouvelles occurrences de mammifères terrestres dans la Formation Qasr el Sagha, au Fayoum, sont données, avec la provenance stratigraphique de ces fossiles. Elles comprennent de nouveaux spécimens de *Moeritherium, Barytherium*, d'anthracothères, ainsi que le plus ancien hyracoïde du Fayoum. Ces mammifères éocènes proviennent presque exclusivement des dépôts alluviaux du membre Dir Abu Lifa de la Formation Qasr el Sagha; ils sont proches de ceux de la séquence inférieure de la Formation Jebel Qatrani. Il n'y a pas d'indication de discontinuité faunique plus marquée entre les formations Qasr el Sagha et Jebel Qatrani qu'il n'y en a au niveau des trois coupures de sédimentation majeures, qui existent au sein de la Formation Jebel Qatrani. La similarité entre les faunes fossiles de la séquence inférieure de la Formation Jebel Qatrani et la partie supérieure de la Formation Qasr el Sagha est cohérente avec les datations paléomagnétiques récentes, qui suggèrent que ces couches different en âge par seulement un ou deux millions d'années.

INTRODUCTION

Late Eocene fossil-bearing rocks in North Africa primarily record nearshore marine conditions. Remains of terrestrial or partly-terrestrial/semi-aquatic mammals are rare in these rocks and occur only at a handful of localities, the most important being in the "Evaporite Unit" at Dur et Talhah in Libya (Savage 1969, 1971, Wight 1980) and in the Qasr el Sagha Formation of the Fayum Depression, Egypt. Records of mammals from the Qasr el Sagha Formation are particularly important because of their biostratigraphic continuity with the well-known faunas of the overlying Jebel Qatrani Formation and because they occur together with potentially datable marine invertebrates and in rock units for which ages have been determined from paleomagnetic reversal stratigraphy. Most African Eocene fossils occur at widely-separated localities that cannot be easily linked to one another either geologically or through faunal comparisons. Consequently, the combined faunas of the Qasr el Sagha and Jebel Qatrani Formations provide the most complete record of successive, stratigraphicallydocumented vertebrate faunas (about 100 localities) in the African Paleogene. The last comprehensive description of mammalian fossils from the Qasr el Sagha Formation was Andrews' (1906) monograph on the Fayum fauna. Subsequently, brief reports or descriptions of additional *Moeritherium* (Simons 1964, Tassy 1981), marine mammal (Gingerich 1992), and creodont (Simons & Gingerich 1976) remains have been made. The most recent report on the Qasr el Sagha Formation fauna was Simons (1968) which provided a faunal list but did not describe new material. Restudy of older collections and continued collecting efforts by joint Duke University/Geological Survey and Mining Authority of Egypt expeditions have documented several new occurrences of relatively rare terrestrial and amphibious mammals of the Qasr el Sagha Formation. Other than the Yale and Duke collections the repositories with relevant fossils are the Cairo Geological Museum and British Museum (Natural History). A number of specimens at the University of California-Berkeley were collected on a "Pan-African" expedition from that institution in 1947.

Abbreviations used:

- AMNH American Museum of Natural History, New York.
- BMNH British Museum of Natural History.
- CGM Cairo Geological Museum, Cairo.
- DPC Duke Primate Center, Durham, North Carolina.
- L- Locality.
- UCMP University of California, Museum of Paleontology, Berkeley, California.
- YPM Yale Peabody Museum, New Haven, Connecticut.

GEOLOGY AND LOCALITY INFORMATION

The Qasr el Sagha Formation comprises about 200 meters of crossbedded sand, sandy mud, limestone and carbonaceous shale and constitutes all of the lower of three principal escarpments that bound the margin of the Fayum Depression, north of Birket Qarun. These rocks were deposited in a subsiding W-SW to E-NE oriented basin bounded by highlands to the north (Bown & Kraus 1988). Bown and Kraus (1988) divided the Qasr el Sagha Formation into two distinct members: the Temple Member for the lower 123 meters (largely shallow marine), and the Dir Abu Lifa Member, covering the upper 77 meters (largely alluvial). The Dir Abu Lifa Member is exposed throughout much of the Fayum Depression and it is from this unit that most of the mammalian remains of the Qasr el Sagha Formation are known (Bown & Kraus 1988), except for a few bones and teeth of the amphibious *Moeritherium* that have been recovered from the underlying Temple Member of the Qasr el Sagha Formation and from the subadjacent Birket Qarun Formation.

The Dir Abu Lifa Member of the Qasr el Sagha Formation (and the Qasr el Sagha Formation in general) differs from the overlying Jebel Qatrani Formation in the absence of variegated beds, in the paucity of gravels, and in containing greater proportions of limestone, carbonaceous mudrock, and drab shales (Bown & Kraus 1988). The Dir Abu Lifa Member differs from the underlying Temple Member of the Qasr el Sagha

Formation in having large or giant-scale cross-stratified sandstone and/or mudrock deposits indicative of deposition on immense side-attached bars in stream channels. Although these units are separated by one or more units of shallow marine origin, the Temple Member lacks fluvial rocks entirely. Gingerich (1992) has alternatively interpreted the deposits of the Dir Abu Lifa Member as evidence of a prograding delta front and delta distributionary deposits. Independent of which depositional regime may better describe these rocks, it is clear that the Dir Abu Lifa Member was laid down in a near-shore setting.

Eight sedimentologically-contained units make up the Dir Abu Lifa Member of the Qasr el Sagha Formation (Fig. 1), the lowest of which (the giant crossbedded sandstone sequence) rests with erosional unconformity on the Temple Member of the Qasr el Sagha Formation. The Dir Abu Lifa Member includes three dominantly fluvial units that consist largely of stacked, multistory in-channel and point bar deposits. These units are: (1) the giant crossbedded sandstone sequence (31.5 m — unit 2 in Fig. 1 — all thicknesses vary laterally and are recorded from sections measured above Qasr el Sagha Temple), which is the lowest unit of the member; (2) the lower crossbedded sandstone

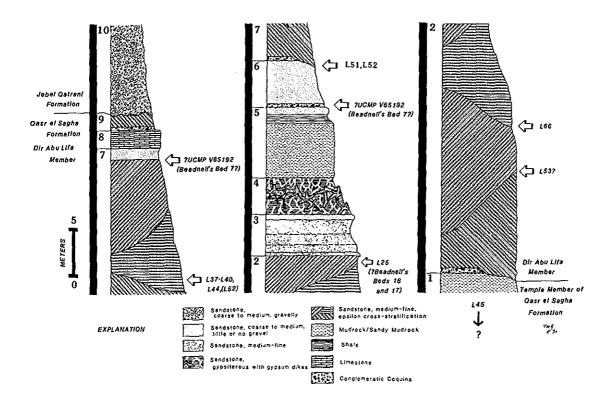


Figure 1.— Stratigraphic column showing lithologies and positions of numbered mammal-bearing localities in the Dir Abu Lifa Member of the Qasr el Sagha Formation in the area between Qasr el Sagha Temple and Dir Abu Lifa. Based on Bown & Kraus 1988, fig. 5. L-52 probably occurs near the top of Unit 6; however, an alternate interpretation may place it within Unit 7, where it is shown listed in brackets. UCMP Locality V65192 may be equivalent to Beadnell's Bed 7; however, its stratigraphic position cannot be ascertained from Beadnell's section other than to say that it probably occurs between the base of Bed 6 and near the top of Bed 7 as shown above.

and mudrock sequence (20.3 m — unit 7 in Fig. 1) near the top of the member; and (3) the upper crossbedded sandstone and mudrock sequence (0-8 m — unit 9 in Fig. 1) that forms the top of the formation (Bown & Kraus 1988).

Internal sedimentary structures indicate that these units were deposited by streams that flowed principally from northeast to southwest. The deposit geometry of the Dir Abu Lifa Member demonstrates that it accumulated in an elongate, mobile, synclinal trough situated between basement and clastic sources in the northern part of the Eastern Desert (Jebel el Galala el Bahariya region) and a southeast-trending embayment of the Tethys seaway located in the vicinity of the Bahariya Oasis (Bown & Kraus 1988). Deposition of the Dir Abu Lifa Member was influenced by a mobile strandline which migrated up and down this trough. The remaining five units of the Dir Abu Lifa Member are principally of nearshore, shallow shelf marine origin (Fig. 1; Bown & Kraus 1988, fig. 5).

The contacts of the alluvial units with underlying units of more marine aspect are invariably erosional, and the erosional troughs contain strandline lag accumulations of both continental and marine fossils (Bown & Kraus 1988). In addition, large-scale erosional surfaces bound troughs in the lower crossbedded sandstone and mudrock sequence and in the giant crossbedded sandstone sequence, and these are also floored with lag accumulations of fossils of both marine and continental origin. Although vertebrate remains are found in other units of the Dir Abu Lifa Member, their occurrences are infrequent and are not generally typified by12 concentrations. Bown and Kraus (1988) determined that the erosional troughs at the bases of and within the fluvial Dir Abu Lifa sequences were formed by a period of erosion concomitant with strandline retreat and that the strandline accumulations of fossils flooring these scours were buried by prograding alluvial sedimentation. Marine transgressive phases are recorded by lags of transported, fragmentary tests of molluscs in the rock sequences of more marine aspect that separate the three fluvial sequences of the Dir Abu Lifa Member.

Concentrations of many kinds of fossils occur in both the transgressive and regressive deposits of the Dir Abu Lifa Member. Though terrestrial mammal fossils are rare, vertebrate coprolites, fish vertebrae and spines, shark teeth, skate and ray mouth parts, catfish bones, sawfish bones, crocodile and turtle bones, sea snake vertebrae, sirenian bones, whale bones, macerated tests of gastropods and bivalves, corals and bryozoans, polychaete worm tubes, iron silicate petrifactions of fruits, gypsiferous limonitized wood, silicified wood, and discrete examples of filled borings of Teredolites are common. The fossils occur as clasts in 10-15 cm thick beds of friable to well-cemented conglomerate with a ferruginous matrix of hollow, broken, reddishbrown oxyhydrate nodules (some of which almost certainly were originally coprolites and clay intraclasts), gypsum and ironstone steinkerns of coprolites, and granular sand and pebble gravel. Much of the silicified wood is water-worn. The proportion of aquatic mammals (e.g., whales and sirenians) to terrestrial mammals is relatively small in the fluvial sequences and relatively greater in the nearshore marine units. Trace fossils abound throughout the Dir Abu Lifa section; those of the fluvial units are dominated by rhizoliths, Teredolites (in fossil wood), and termitaria of two distinct types.

Bown and Kraus (1988) demonstrated that the Dir Abu Lifa Member represents

nearshore marine and alluvial deposits that record fluctuations of the marine strandline prior to the advent of predominantly continental conditions recorded in the overlying Jebel Qatrani Formation. There is considerable evidence arguing against the premise that Dir Abu Lifa deposits were formed on a rapidly prograding delta front (Bown & Kraus 1988) as has been argued by Vondra (1974) and Gingerich (1992) and repeated by Salem (1976) and Said (1990).

Beadnell (1905: p. 54) described in detail the preservation and chemical composition of fossil bone from the Jebel Qatrani Formation. Although some vertebrate bones from the Qasr el Sagha Formation are as well preserved as those of the Jebel Qatrani Formation, the majority appear to have undergone secondary and possibly additional phases of diagenetic replacement. It appears that many of the bones may have initially been permineralized by removal of organic matter and introduction of anhydrite (CaSO₄) or gypsum (CaSO₄•2H₂0) after which the SO₄⁻⁻ ions were secondarily replaced by CO_3^{-1} ions. This or a similar diagenetic phenomenon resulted in considerable loss of surface detail in bone and tooth structure. Bown and Kraus (1988) suggested that the concentration of gypsum in certain units of the Jebel Oatrani Formation was related to the presence of carbonaceous sediments in directly overlying parts of the section and that the sulfur in the gypsum was from the decay of plant material. Carbonaceous deposits in the Dir Abu Lifa Member are most abundant overlying the centers of broad channeliform scours and are less abundant at the margins of and lateral to such scours. As the incidence of crystalline gypsum in the Dir Abu Lifa Member (perhaps now in a secondary form) is largely limited by scour geometry, a similar origin is suggested for the origin of sulfur and gypsum deposits in the Dir Abu Lifa Member.

Ten numbered DPC localities of known stratigraphic position in the Dir Abu Lifa Member have yielded terrestrial mammal remains. These are (in numerical order): L-25, L-37, L-38, L-39, L-40, L-44, L-52, L-53, L-66. The youngest occurs in unit 7 and the oldest in unit 2. A series of other localities have also produced terrestrial mammals (Yale Quarries H, K, and U; UCMP V4754 and V65192; AMNH Beadnell's Beds 7, 16, and 17), but these could not be accurately placed in the stratigraphic column. Comparison of Beadnell's (1905) sections with those of Bown and Kraus (1988) suggest that Beadnell's Bed 7 (the same as UCMP V65192, according to UCMP locality files) lies in the coquina at the base of unit 6 or near the top of unit 7. Beadnell's Beds 16 and 17 appear to lie at the same stratigraphic level (and perhaps are the same) as DPC L-25. A single numbered locality, L-45, is known from the Temple Member of the Qasr el Sagha Formation, but its stratigraphic position is unclear. A single tooth of *Moeritherium* is also known from the underlying Birket Qarun Formation.

AGE AND CORRELATIONS OF THE QASR EL SAGHA FORMATION

The Qasr el Sagha Formation has conventionally been considered late Eocene in age and the overlying Jebel Qatrani Formation has usually been judged early Oligocene

(see e.g., Gingerich 1992). The contact between the two formations was long regarded as the Eocene-Oligocene boundary in Egypt (Said 1962, 1990, Simons 1968, Vondra 1974, Bown *et al.* 1982, Fleagle *et al.* 1986, Bown & Kraus 1988, Gingerich 1992). However, as pointed out most recently by Said (1990), the exact age of many Eocene formations in Egypt is uncertain because the planktonic foraminifera most useful for correlation are not available in most cases, being restricted in occurrence to pelagic facies having very limited distribution. Consequently, the age of the Qasr el Sagha Formation can only be inferred from data on its paleomagnetic reversal stratigraphy taken from the top of the formation, and by the correlation of the even less adequate macroinvertebrate faunas with faunas from rocks elsewhere in Egypt. Unfortunately, the invertebrate faunas of the Dir Abu Lifa Member (in contrast to those of the Temple Member) have received little attention.

Recent magnetostratigraphic studies of the Fayum sediments support a late Eocene age for the rocks of the Dir Abu Lifa Member as well as for the overlying sediments of the lower sequence of the Jebel Qatrani Formation (Kappelman 1992, Kappelman *et al.* 1992). Kappelman and colleagues sampled the upper 60 meters of the Dir Abu Lifa Member and found that most of this sequence (including levels where the majority of mammalian fossils were found) can be placed in Chron C16.2N. Therefore, the mammal bearing sediments of the Dir Abu Lifa Member appear to have been deposited during an approximately 300,000-year interval between approximately 35.7 to 36.4 Ma (based on the time scale of Cande & Kent 1992).

Strougo and Boukhary (1987) most recently reviewed the invertebrate evidence for dating and revised the position of the middle Eocene-late Eocene boundary in Egypt to coincide with the first occurrence of the macroinvertebrate *Carolia placunoides*. *C. placunoides* first appears in the Fayum area in the Temple Member of the Qasr el Sagha (Beadnell 1905, Strougo 1979), and this fossil is common throughout the Temple and Dir Abu Lifa Members (Beadnell 1905, Bown & Kraus 1988). Thus, the Dir Abu Lifa Member and its fauna appear to be entirely late Eocene in age; however, parts of the Temple Member may be middle Eocene in age. Therefore, *Moeritherium* and hyaenodontine remains discussed below from L-45 (of unclear stratigraphic provenance in the Temple Member) and from the subadjacent Birket Qarun Formation may be late middle Eocene (Bartonian) occurrences of these animals.

SYSTEMATIC PALEONTOLOGY

Order ARTIODACTYLA Family ANTHRACOTHERIIDAE cf. *Bothriogenys* sp.

The presence of anthracotheres (?Brachyodus sp.) in the late Eocene of Africa was first documented in Simons' (1968) faunal list, based upon the recovery of an astragalus from a surface deposit subsequently designated L-25. Bothriogenys, rather

than *Brachyodus*, is now regarded as the correct generic nomen for Fayum anthracotheres (Black 1978, Pickford 1991).

DPC 2545 (Pl. 1A-B), a weathered right distal humerus and shaft from Locality 25, provides additional evidence of anthracotheres in the Qasr el Sagha Formation. Morphologically, DPC 2545 is similar to humeri referred by Schmidt (1913) to *Bothriogenys* from the lower sequence of the Jebel Qatrani Formation.

Like all artiodactyls, the shaft of DPC 2545 is compressed mediolaterally in its proximal portion. A distinct but not strongly developed line courses approximately halfway down the anterior face of the shaft for the attachment of the mm. deltoideus. This line is attenuated in the form of a ridge that turns laterally to end at the lateral edge of the distal articular surface.

Distally, the shaft is triangular in cross-section. The epicondyles are not projecting. The medial epicondyle is anteroposteriorly longer than the lateral and extends further posteriorly to form a right angle to the shaft. The lateral epicondyle does not extend far posteriorly but curves sharply upward. A deep olecranon fossa is present that does not appear to perforate the shaft to form a supratrochlear foramen. However, the specimen is covered with a thin layer of mineral deposits that cannot be easily removed and that could obscure the presence of a small supratrochlear foramen.

The distal articular surface is eroded, but the medial portion of the trochlear surface and the most proximal portion of the capitular surface are present. The medial trochlear ridge is sharp and pronounced. The trochlear surface is strongly concave and approximately 30 per cent larger than the capitular surface. The capitulum is modified into a cylindrical shape and is cranially placed relative to the trochlea. The proximal surface of the capitulum slopes upward from its medial to lateral side.

This specimen is similar to humeri referable to *Bothriogenys* in size and overall morphology (Schmidt 1913). DPC 2545 differs from Fayum anthracotheriid humeri from stratigraphically higher levels in the more craniad orientation and upwardly sloping surface of the capitulum. Dimensions of DPC 2545 are: biepicondylar width, 50.7 mm; anteroposterior depth at medial epicondyle, 48.3 mm; at lateral epicondyle, 39.7 mm; maximum anteroposterior shaft width, 42.5 mm; maximum mediolateral dimension of shaft, 30.9 mm.

Order HYRACOIDEA Family PLIOHYRACIDAE

pliohyracid, genus and species indeterminate

The first record of Hyracoidea in the Qasr el Sagha Formation is represented by AMNH 13445 (Pl. 1E-F), a weathered and broken edentulous right mandibular corpus, found 1/2 mile east of Qasr el Sagha Temple during the 1907 expedition by the American Museum of Natural History. This locality probably occurs within the Temple Member of the formation. Matsumoto (1923) considered this mandible to be a juvenile specimen of *Moeritherium gracile*. Further cleaning by one of us (PAH) revealed its hyracoid affinity.

In this specimen the ascending ramus arises beside the last molar alveolus. A small oval alveolus is preserved at the front of the fragment, probably for the third incisor. There is a short diastema posterior to it and a series of broken alveoli for the canine, premolars, and molars. The post-incisor tooth row is 83 mm in length. There is a strong lingual alveolar torus. A large condyloid canal courses distally and ventrally. The mandibular ramus contains a greatly expanded chamber that is 13 mm at its greatest width. The chamber extends the length of the post-incisor tooth row, ending anteriorly beneath the diastema. The lateral mandibular wall is extremely robust, measuring 8.0 mm at its greatest thickness.

This mandible cannot be assigned to any known hyracoid genus. It bears similarities to *Geniohyus* in the curvature of the lingual wall of the mandible and in having a strong alveolar torus. In pliohyracids the lingual mandibular wall is typically perpendicular to the tooth row. However, *Geniohyus* is distinct from other pliohyracids in having only a mandibular fossa rather than the internal mandibular chamber that AMNH 13445 possesses. Among pliohyracids, an expanded internal mandibular chamber occurs in only one sex, probably females (Meyer 1978). In its degree of mandibular expansion, this specimen is most similar to the genus *Thyrohyrax*. As noted by Meyer (1978), *Thyrohyrax* differs from all other hyracoids in possessing a greatly inflated mandibular chamber that extends beneath (but is not connected to) the tooth row and posteriorly into the base of the ascending ramus. AMNH 13445 shares with *Thyrohyrax* a greatly inflated ramus and swollen chamber unconnected to the dental series, but there is no evidence that the chamber in this specimen extends into the ascending ramus.

Order CREODONTA Family HYAENODONTIDAE Apterodon ANDREWS, 1904

Simons and Gingerich (1976) described as Apterodon saghensis a left mandibular fragment containing P_2 - P_4 and a broken M_1 from an unspecified locality in the Qasr el Sagha Formation. Subsequently, this locality has been designated Locality 25.

Apterodon is also represented in the Qasr el Sagha Formation by DPC 5441 (Pl. 2A), a right mandibular ramus containing P_3 and M_1-M_2 found by one of us (ELS) at Locality 66, and UCMP 41597, a humerus from UCMP Locality V65192. The teeth of DPC 5441 are very poorly preserved, but it is clear that the molars had a large protoconid, smaller lingually-placed paraconid, very small metaconid, and a short talonid as in other species of Apterodon. In size and morphology, this specimen is closest to A. macrognathus that occurs commonly at Quarries A and B in the lower sequence of the Jebel Qatrani Formation. It does not differ in size from A. macrognathus, but is much larger than Apterodon sp. from the stratigraphically intermediate Locality 41 (Holroyd, pers. obs.) and is slightly larger than the type of A. saghensis. It is unlikely that more than one species of the genus is present, but the poor quality of DPC 5441, its similarity in size to A. macrognathus, and its lack of comparable teeth (except P_3) with A. saghensis make it difficult to assign it to either species.

UCMP 41597 is a humerus that is mineralized with poor surface detail, but which is otherwise complete. Its greatest length (from the top of the greater trochanter to the most distal point of the humeral condyle) is 23 cm. The greatest width of the proximal end is 5.7 cm. The middle of the shaft (measured from side to side) is 1.6 cm at its narrowest point and from front to back is 4.2 cm. The distal end at its widest point is 7.3 cm. This humerus is virtually identical, in both size and morphology, to that figured and described by Andrews (1906) from the Jebel Qatrani Formation, and it further corroborates the presence of *Apterodon* in the Dir Abu Lifa Member.

An additional specimen may be provisionally referred to Apterodon, DPC 4061 (Pl. 2B), an eroded left mandibular corpus having alveoli and roots for P_3-M_3 from L-45 in the Temple Member. There are two roots per tooth, and M_1 is smaller than P_4 , M_2 and M_3 , all three of which are subequal in size. The corpus is shallow, and there is a mandibular foramen beneath P_4 . In overall size and in the proportions of the premolars, this specimen is closest to Apterodon saghensis. The length of the three molar alveoli is 35 mm and that of the two premolars is 22 mm in DPC 4061. In Apterodon saghensis the combined length of the last two premolar alveoli is almost exactly the same, 22.1 mm.

cf. Hyaenodon brachycephalus

AMNH 128553 (Pl. 2C-D), an eroded left mandibular corpus labelled as having been found "near Qasr el Sagha," is that of a hyaenodontine creodont. The fragment preserves only the roots and bases of P_3-M_3 . The dimensions (in mm) of the alveoli in AMNH 128553 are: P_3 length, 15.1; P_4 length, 14.3; M_1 length, 9.2; M_2 length, 14.1; M_3 length, 15.1. Alveolar width could not be accurately measured due to the poor preservation of the lateral surface of the specimen. The corpus is deep, measuring 35.6 mm beneath M_2 . The posterior part of the symphyseal region is preserved along the lower half of the corpus beneath P_3 . The base of the ascending ramus is preserved posterior to the M_3 alveolus and bears a strong masseteric crest. The ascending ramus is more vertically oriented than in *Pterodon*. In size and in aspects of the mandibular morphology (the location and posterior extent of the symphysis and the more vertical orientation of the ascending ramus), this specimen is most similar to *Hyaenodon brachycephalus* (AMNH 13264 labelled from "west of Quarry A" in the lower sequence of the Jebel Qatrani Formation) and to AMNH 13262 from Quarry B, described by Osborn (1909) as ?*Hyaenodon*.

Order PROBOSCIDEA Family BARYTHERIIDAE

Barytherium cf. B. grave ANDREWS, 1901

Two teeth referable to *Barytherium* have been recovered: DPC 2917 (Pl. 1C), an unworn left M^2 from Locality 25; and DPC 4071 (Pl. 1D), a right lower premolar from an unspecified location in the Qasr el Sagha Formation. These specimens are not as heavily worn as the holotype and paratype of *B. grave* described by Andrews (1901,

1904, 1906) and, consequently, contribute new information on the dental morphology of this unusual mammal.

DPC 4071 is probably a worn P_3 , on the basis of comparisons with the dimensions of the holotype of *B. grave*. The tooth is square in outline, measuring 43.2 mm in length and 41.9 mm in width. The trigonid is worn flat to the same level as the talonid, forming a large rectangular facet. The labial side is worn more deeply than the lingual. The talonid is short, approximately one-half the length of the trigonid, but is slightly broader. There are no distinct cusps present on the talonid. Instead, a broad, low and anteriorly-inclined loph spans the width of the tooth. A very short cristid obliqua meets the posterior wall of the trigonid. A small, low posterior cingulum runs from the base of the lingual side of the tooth labially and cranially to end just short of the labial edge of the tooth. There are pronounced anterior and posterior interstitial wear facets.

DPC 2917 is a roughly square tooth composed of two tall, well-separated lophs. The protoloph is curved posteriorly and is lower than the metaloph. A poorly-developed postprotocrista runs down the distolabial face of the protocone, ending in the center of the tooth. A slight postparacrista is present on the distal face of the paracone and meets a weak premetacrista in the transverse valley between the lophs. The metaloph is similarly curved, and a narrow crescentic facet is present on the anterior face of this loph. A distinct posthypocrista runs posteriorly in a broad arc to meet the posterior cingulum at the midline of the tooth. The posterior cingulum is the only cingulum on the tooth.

The dimensions of DPC 2917 are: length, 55.2 mm; width at protoloph, 52.2 mm; width at metaloph, 56.8 mm. This tooth is somewhat smaller than the molars of the holotype, but also differs from the type in being proportionately longer, possibly due to the lack of extensive interstitial wear on this specimen. The dental morphology described here supports the suggestion made by Harris (1978) and Mahboubi *et al.* (1984) that there is a close relationship between *Barytherium* and deinotheres.

Family MOERITHERIIDAE

Moeritherium lyonsi ANDREWS, 1901

Newly referred material and occurrences:

- L-25: DPC 2679, lower incisor; DPC 2544, left femur; DPC 2551, thoracic vertebra; DPC 2718, edentulous mandible; DPC 3178, upper molar
- L-37: DPC 4102, left humeral fragment; DPC 4133, left? ulnar fragment; DPC 4149, maxillary fragment with P⁴-M¹.
- L-38: DPC 4453, left M₂-M₃.
- L-45: DPC 4048, M₃ in bony coquina.
- L-52: DPC 4951, left P₄; DPC 5229, left M₁; DPC 5047, M² or M³.
- L-66 (= "slopes near Dir Abu Lifa Monastery"): DPC 5435, right M₁; DPC 8873, rib; DPC 8874, right lower canine; DPC 8875, left zygomatic arch.

Beadnell's Bed 17: YPM 18238, left maxillary fragment with partial P⁴; YPM 18181, mandible with right P₃-M₃ and left P₄-M₃.

Quarry H: YPM 24839, partial skeleton.

Near Quarry H: YPM 18237, right juvenile dentary with partial M₃.

Quarry K: YPM 24811, left upper tusk; YPM 24812, left M₃ and two upper molars; YPM 24826, right and left squamosals.

Quarry U: YPM 34764, left juvenile mandible with DP₂-DP₄, M₁.

- "Moeritherium locality": YPM 18102 associated partial Moeritherium skull, mandible, ribs, vertebrae, sacrum and partial pelvis. This specimen gives the Moeritherium locality its name. The location of the find is "about 5 miles NE of Qasr el Sagha Temple". [This specimen is also the basis of the Peabody Museum mounted skeleton, but the appendicular skeleton in that exhibit is restored from casts from other sites and partly modeled hypothetically]; YPM 24809, upper right tusk.
- "100 m from '61 *Moeritherium* Locality": DPC 9683, left femur; DPC 9489, thoracic vertebra.
- "1.5 miles west of *Moeritherium* skeleton (YPM 18102)": YPM 18107 "many *Moeritherium* vertebrae".
- UCMP Locality V4754: UCMP 41327, vertebral column with axis, four cervicals, and four thoracic vertebrae; UCMP 100025, upper tusk; UCMP 100024, poorly-preserved tusk fragment.
- Locality unknown: BMNH M10229, skull and mandible (Pl. 3); BMNH nos. 10230-10232, various ribs, vertebrae and other postcranial elements; BMNH M10233, poorly preserved mandibular fragment; BMNH 12068, imperfect skull.

Moeritherium lyonsi has previously been reported from the Qasr el Sagha Formation by Andrews (1906), Matsumoto (1923), and Simons (1964, 1968). Remains of a smaller form, named *M. gracile*, have been described from these levels (Andrews 1902, 1906, Matsumoto 1922). However, as Tobien (1978) has shown and Wight (1980) has also stated that, these specimens probably represent the female morph of a sexually dimorphic species and should be synonymized with *M. lyonsi*. Deraniyagala (1955, 1968) described two additional species —*M. ancestralis* and *M. pharoahensis* — on the basis of specimens from the University of California-Berkeley Fayum expedition

MAXILLAE Specimen		P ⁴		M ¹		M ²		М ³		
Number			L	W	L	W	L	w	L	W
DPC 4149			19.5	23.0	21.0	21.5		<u> </u>		
YPM 24812									33.3	27.3
YPM 24839									30.2	27.8
MANDIBULAE					A			··· <u>··</u> ·· <u>··</u> ··		
Specimen Number	P. L	3 W	P L	4 W	M L	W	L	2 W	L	w W
DPC 5229					27.0	21.5				
DPC 5435					24.5	19.0				
YPM 18181	21.4	16.1	21.9	17.6	24.3	19.5	27.2	23.4	-	

Table 1.- Moeritherium dental measurements (all measurements in mm).

and now housed in Ceylon. It is unlikely that these specimens represent a species different from *M. lyonsi*. *M. lyonsi* is the only species of *Moeritherium* definitely known from the Qasr el Sagha Formation.

The vast majority of the newly-referred specimens duplicate the better-preserved material previously described for this species by Andrews (1906) and Tassy (1981). The primary contribution of these specimens lies in their having provided more accurate data on stratigraphic distribution. Dental measurements for specimens having adequate preservation to permit reliable measurement are given in Table 1.

UCMP 41327 (Locality V4754) provides some new information on the vertebral column of this species. The specimen is a partially-complete vertebral column consisting of the axis, first through fourth cervicals, and four thoracic vertebrae. The cervical series is articulated, as are two of the thoracic vertebrae. The remaining two thoracic vertebrae are isolated. All of the bones were encrusted with a hard red matrix, which was only partially removed in preparation. The axis and thoracic vertebrae are like those described by Andrews (1906). Andrews also described what he believed to be a third or fourth cervical vertebra. It has bifid transverse processes with a small, upwardly-directed flange and a longer, downwardly-directed flange. Comparison with UCMP 41327 reveals Andrew's specimen to be a fourth cervical. The first three cervicals have progressively developed transverse processes, with the first ending fairly bluntly, the second showing some development of the small, upwardly-directed flange, and the third with a fairly well-developed upward flange, although the downward flange is much shorter and blunter than on the fourth cervical. In other respects, the first three cervicals are similar to the fourth. The axis is 131 mm from the top of the dens to the posterior point of the neural spine and 90 mm across the widest points of the condyles. The first cervical is 96 mm wide at the widest point of the transverse processes. Cervical two is 102 mm wide, cervical three is 117 mm wide, and cervical four is 118 mm wide,

Order Artiodactyla Family Anthracotheriidae cf <i>. Bothriogenys</i> sp. (Schmidt 1913)
Order Creodonta
Family Hyaenodontidae
Apterodon saghensis SIMONS & GINGERICH, 1976 cf. Hyaenodon brachycephalus OSBORN, 1908
Order Hyracoidea
Family Pliohyracidae
genus and species indeterminate
Order Proboscidea
Family Barytheriidae
Barytherium cf. B. grave ANDREWS, 1904
Family Moeritheriidae
Moeritherium lyonsi Andrews, 1901

Table 2.— A revised list of non-marine mammals from the Qasr el Sagha Formation, Fayum Depression, Egypt.

Two additional specimens, UCMP 100024 and 100025, are questionably assigned to *M. lyonsi*. UCMP 100025 is a relatively complete tusk that is crushed and broken at its proximal end. In cross-section, it is convex anteriorly and flattened posteriorly. It is 216 mm long from tip to tip in a straight line, 39 mm transverse diameter at its widest point, and 36 mm in antero-posterior diameter. UCMP 100024 is a very badly corroded distal end of a tusk and little can be observed other than it is also convex anteriorly and flattened posteriorly. This specimen is 117 mm long from tip to broken end.

A single locality in the subadjacent Birket Qarun Formation (commonly considered middle Eocene in age) has also produced a tooth assignable to *Moeritherium lyonsi*. DPC 5906, a right P_4 was found at L-67, a surface locality near the base of the Birket Qarun Formation. Morphologically, this specimen does not differ from those referred to *M. lyonsi* from the Qasr el Sagha Formation.

CONCLUSIONS

The fossils described here from the Dir Abu Lifa and Temple Members of the Qasr el Sagha Formation (Table 2) expand the late Eocene faunal record of the Fayum region by providing the earliest record of both artiodactyls and hyaenodontine creodonts in Africa, as well as the earliest record of a hyracoid in the Fayum. Further, the occurrence of *Apterodon* earlier in Africa than in Europe (see Lange 1967) is now confirmed based on these new specimens of this taxon.

Van Couvering and Harris (1991) recently argued that there is a remarkable shift in diversity between the Qasr el Sagha and Jebel Qatrani Formations. Comparison of the Dir Abu Lifa fauna with that of the lower sequence of the Jebel Qatrani Formation (Fayum Faunal Zones 1 and 2; Rasmussen et al. 1992) demonstrates that as far as we know the mammals from the Qasr el Sagha Formation there is significant faunal continuity between the two formations. Both formations share the presence of closely related species of Apterodon, Moeritherium and Hyaenodon, and both Apterodon and Hyaenodon continue into the lower Oligocene upper sequence of the Jebel Qatrani Formation. There is little evidence supporting a more pronounced faunal discontinuity between the Dir Abu Lifa Member and the lower sequence of the Jebel Qatrani Formation than several that occur within the Jebel Qatrani Formation (see Rasmussen et al. 1992). The terrestrial mammal taxa are largely African endemics and are congeneric with and closely comparable to Jebel Qatrani Formation taxa. The creodonts, in particular, have affinities with species described from Quarries A and B in the lower sequence of the Jebel Qatrani Formation. Only the solitary hyracoid specimen as well as Barytherium grave lack congeners in the Jebel Qatrani Formation. However, Barytherium is known from younger deposits in Oman (Thomas et al. 1989) and was quite abundant in Libya in both the "Evaporite Unit" and "Idam Unit" at Dur at Talhah, Libya (Wight 1980). The latter units correlate broadly with the Qasr el Sagha and Jebel Qatrani Formations, respectively (Wight 1980). The absence of Barytherium in the Jebel Oatrani Formation contrasted with its apparent contemporaneity elsewhere suggests environmental controls on the distribution of Barytherium.

The Dir Abu Lifa Member, Qasr el Sagha Formation, does lack a significant proportion of the fauna found in the lower sequence of the Jebel Qatrani Formation, with no representation of smaller mammals. The absence of small mammals may be at least partly due to the diagenetic alteration of bones from these sites, which could render smaller specimens unrecognizable or even destroy them. However, their absence could mainly be due to taphonomic and facies differences when fossils were deposited. Jebel Qatrani Formation mammals were deposited in meandering streams (Bown *et al.* 1982, Bown & Kraus 1988, Olson & Rasmussen 1986, Rasmussen & Simons 1988) in contrast to the strandline lag accumulations and channel deposits that characterize the Qasr el Sagha Formation.

Excluding dissimilarities due to depositional environment, the compositional differences observed between the Dir Abu Lifa fauna and that of Quarry A and B is no less than and no more than those seen within the Jebel Qatrani Formation, for example, distinctions between faunas at Locality 41 at the 42 meter level and Quarries A and B at the 60 meter level (Rasmussen & Simons 1988, Rasmussen 1989, Rasmussen *et al.* 1992). These data are suggestive of a late Eocene age for both the Dir Abu Lifa Member of the Qasr el Sagha Formation and part or all of the lower sequence of the Jebel Qatrani Formation. This finding also provides additional evidence that late Eocene-early Oligocene faunal changes in the Fayum were not wholesale alterations in the representation of families or higher level taxa. Rather they arose primarily through the appearances and disappearances of species and genera as demonstrated also by Rasmussen *et al.* (1992) based on the study of only the faunas of the Jebel Qatrani Formation.

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LEGENDS OF PLATES

PLATE 1

A-B. cf. *Bothriogenys* sp. DPC 2545, right distal humerus, anterior (A) and posterior (B) views.

- C-D. *Barytherium* sp., cf. *B. grave*. A: DPC 4071, right lower premolar, occlusal view. B: DPC 2917, left M², occlusal view.
- E-F. Indeterminate hyracoid.

AMNH 13445, right mandibular corpus.

PLATE 2

A. Apterodon sp. DPC 5441, right mandibular corpus, lateral view.

- B. ? Apterodon saghensis. DPC 4061, left mandibular corpus, lateral view.
- C-D. cf. Hyaenodon brachycephalus. AMNH 128553, left mandibular corpus, medial (C) and lateral (D) views.

PLATE 3

- A-D. Moeritherium lyonsi skull and associated mandible. BMNH M10229.
 - A: ventral view of skull.
 - B: occlusal view of mandible.
 - C: left lateral view of skull.
 - D: dorsal view of skull.

