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SMALL-BODIED ANTHROPOID (PRIMATES, CATARRHINI) FROM THE EARLY MIOCENE OF MOGHARA, EGYPT

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Abstract: The Early Miocene fluvio-marine and terrestrial deposits at Moghara, Qattara Depression, northern Egypt, have previously yielded several fragmentary mandibles of cercopithecoids and a humerus of a medium-sized anthropoid. In 2010, while studying Moghara fossils at the Cairo Geological Museum, the first author noticed an unpublished edentulous mandible of a primate that was collected in 1994 (specimen M94-90). The jaw is slightly larger than the type specimen and other material of *Prohylobates tandyi* and initially it was thought to belong to this species, but close examination reveals that it differs in a number of morphological features from mandibles of the latter taxon. All the differences point towards the identification of M94-90 as a hominoid or more likely as a pliopithecoid, and they distance it from the Cercopithecoidea. Its dimensions indicate an animal approximately the size of small gibbons such as *Hylobates*. In addition, there is an isolated lower canine in the Cairo University collections that is compatible in size and morphology with the unpublished mandible. This tooth, that was collected in 2005, is similar to specimens of *Micropithecus clarki* Fleagle et Simons, 1978, from the Early Miocene of Napak, Uganda, but also shows some resemblance to canines of pliopithecoids from Europe.

Key words: Hominoidea, Pliopithecoidea, Anthropoidea, Early Miocene, Northern Egypt, Biogeography, mandible, canine

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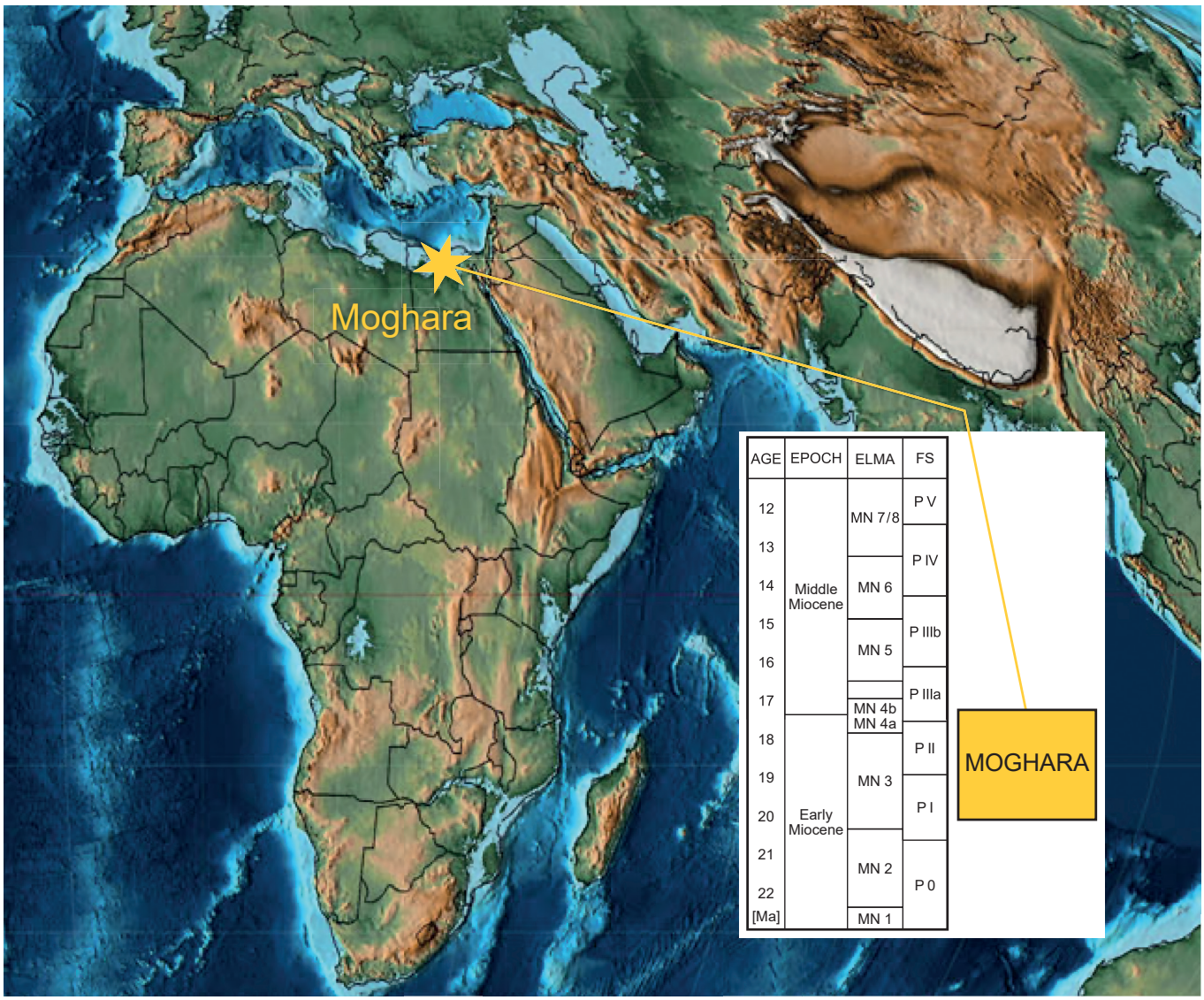
Introduction

Moghara is an extensive fossiliferous area in northern Egypt that, over the past 12 decades, has yielded abundant terrestrial and marine fossils of Early Miocene age (Andrews 1899, Blanckenhorn 1900, Miller et al. 2006).

The escarpment that forms the northeastern margin of the Qattara Depression extends for almost 100 km east-west, with Wadi Faregh to the east, and Siwa Oasis to the west. The south-facing slopes of the escarpment expose a thickness of ca. 200 m of fluvio-marine and terrestrial sediments (Blanckenhorn 1900, Fourtau 1918: fig. 3, Hassan et al. 2012, Hassan 2013) that have yielded abundant fossils of plants, invertebrates and vertebrates (Miller et al. 2006) suggestive of a tropical to sub-tropical, coastal depositional palaeoenvironment (a tide-dominated estuarine setting with abundant palm trees).

The 200+ metre thick sedimentary succession exposed in the Moghara Escarpment accumulated over a substantial period of time, but overall the sequence is of Early Miocene age (Miller 1999), correlating to East African Faunal Sets PI–PIIIa of Pickford (1981) implying an age of ca. 20–17.5 Ma (Pickford et al. 2021a: fig. 17). In terms of the European Land Mammal Ages, this corresponds to the Burdigalian, i.e., MN 3 to MN 4a (Mein 1989, Steininger 1999) (Text-fig. 1). The bulk of the vertebrate fossils collected from Moghara lack detailed stratigraphic data. On the basis of preservation characters and observations in the field, it is concluded that most of them were collected from lag deposits that are intercalated within the primary sedimentary deposits. Resistant fossils became concentrated in thin layers of sediment that often contain clay balls which were subsequently hardened by ferruginisation, an observation that implies that many of the fossils were locally reworked (remanié) after being fossilised, and were thus collected from secondary (or even tertiary) contexts. However, the differences in age between initial deposition of a specimen and its secondary context are not of major biostratigraphic significance, because most of the Moghara succession accumulated within the time span of MN 3.



Text-fig. 1. Location and biostratigraphic correlation of the Moghara Formation, Egypt. ELMA: European Land Mammal Age, FS: East African Faunal Sets. Base map is modified from Scotese 2014 (Map 7, Early Miocene, Burdigalian and Serravallian, 19.5 Ma, Serravallian Supersequence Boundary, Sea Level +40 m).

Among the fossil mammals described from Moghara (Miller and Simons 1998), there are several specimens of primates, initially attributed to Simiidae by Fourtau (1918) as the species *Prohylobates tandyi* Fourtau, 1918 and (?) *Dryopithecus mogharensis* Fourtau, 1918. Subsequent studies (Simons 1969, 1994) indicated that these two species were synonymous and until recently they were generally considered to represent a single species of Victoriapithecidae von Koenigswald, 1969 in the superfamily Cercopithecoidea Gray, 1821 (Old World Monkeys) (Jablonski and Frost, 2010). However, Miller et al. (2009) concluded that there were indeed two species of fossil monkeys at Moghara, *Prohylobates tandyi* and genus indet. *mogharensis*.

Simons (1994) described a humerus from Moghara that lacks the proximal epiphysis (DPC 6643) that he interpreted to represent a medium-sized "ape-like" species. He noted the overall primitive morphology of the humerus within a hominoid context, such as the presence of an entepicondylar foramen, but he left the specimen in open nomenclature. Thus, Simons (1994) acknowledged the presence of two taxa of anthropoids at Moghara, one that was monkey-like, the other more "ape-like". The humerus of the European pliopithecoid, *Epipliopithecus* Zapfe et Hürzeler, 1957, possesses an entepicondylar foramen (Zapfe 1961), and it thus potentially provides a taxonomic link to the Moghara specimen.

The present paper confirms the occurrence of a species of non-cercopithecoid catarrhine at Moghara, based on an edentulous mandible (CGM M94-90) collected during the 1994 field survey of the area, and an isolated lower canine (CUWM 27) collected in 2005. The jaw shows several morphological features that indicate its appurtenance either to the superfamily Hominoidea Gray, 1825, or (more likely) to Pliopithecoidea Zapfe, 1961, and which distance it from the Cercopithecoidea. Its dimensions suggest that the species had a body size comparable to that of small extant gibbons of the genus *Hylobates* Illiger, 1811, and a suite of extinct small-bodied fossil "apes" from East Africa such as *Micropithecus clarki* Fleagle et Simons, 1978 and *Lomorupithecus evansi* (MacInnes, 1943) (Pickford et al. 2021b) as well as to the smaller fossil pliopithecids from

Europe (Biedermann 1863, Hürzeler 1954, Zapfe 1961, Begun 2002) and Asia (Harrison and Gu 1999, Harrison et al. 2020). Pending the recovery of more informative specimens, the mandible and canine from Moghara are left in open nomenclature.

The aim of this contribution is to augment the record of the presence of a small-bodied anthropoid at Moghara, and to discuss its importance for palaeoprimatology.

Toponomastics

Moghara is the toponym of part of the northern margin of the Qattara Depression in northern Egypt (Fourtau 1918: fig. 1). In much recent literature the place has been referred to as "Moghra" and the alternative usages "Wadi Moghara" and "Wadi Moghra" became widespread after 1969 when Simons (1969) employed the binominal combination for the first time (Black 1978, Pickford 1991, Miller and Simons 1998, Miller 1999, Morlo et al. 2007, Pickford et al. 2010, Miller et al. 2014, Zonneveld et al. 2022).

The origin of the name Moghara is plausibly linked to the presence of a large rock shelter (in Arabic, Moghara = Cavern) at the base of the cliffs 10 km north of the small lake known as Birket Moghara, the lake being so named because of its proximity to the "cavern" (a two-hour walk and the closest permanent water supply to the rock shelter until modern agriculture was developed in the area, with piped water for irrigation). In ancient times, the rock shelter, that formed in the sediments exposed along the foot of the escarpment, would have been a suitable place for sheltering from the heat of the day or for spending the night in the desert (Text-fig. 2).

In his texts, Fourtau (1918, 1920) referred to the area close to the small lake 10 km south of the escarpment as "Hateyet el Moghara" and the fossil-bearing area as "Escarpement de Moghara". In his fig. 1 however, he spelled the name of the area close to the lake as "Hetayet el Moghara". In Arabic, Hateyat or Hetat, means the alluvial materials that are weathered by friction and are transported by rivers and wadis (Mohammed Al-Kindi [Muscat], pers. comm. 2024) – thus in this context Hateyet (hetayet), as employed by Fourtau (1918) most probably signifies "alluvial plain". In most of his appellations, Fourtau (1918) employed the word "Moghara" on its own or he added a prefix such as "escarpement de", "gisement de", "garnison de" and "faune de". This indicates that the name of the area was Moghara.

Having, in 1969, started the trend for naming the fossiliferous area "Wadi Moghara", two decades later Simons (1994) wrote that Fourtau (1918) referred to the "Wadi Moghara Fauna", and then commented that „there is no Wadi Moghara, only a freshwater lake". However, examination of the literature reveals that Fourtau (1918, 1920) never used the combination "Wadi Moghara". In his geomorphological cross-section of the region Fourtau (1918: fig. 2) employed the term Birket Moghara (= Moghara Freshwater Reservoir), for the small lake in the northeastern sector of the Qattara Depression, but he distinguished this place from the fossiliferous deposits exposed along the slopes of the escarpment 8–10 km north of the Birket. Despite the subsequent declaration by Simons (1994) pointing out the invalid usage of the term "Wadi Moghara", he, his colleagues and several other authors continued to employ

Text-fig. 2. Cavities eroded into soft layers near the base of the sedimentary succession at Moghara. These cavities plausibly explain why the region is called Moghara (Cavern in Arabic). Note the large cylindrical petrified tree trunks in the foreground, mostly palm stems. Note also that the end of the ridge above the cavities collapsed recently, thereby reducing the amount of undercut in the hillside.

the incorrect toponym for the fossil-bearing area (Miller and Simons 1998). It wasn't until Pickford et al. (2021a) that the correct toponym was re-established.

Abbreviations

CGM	abbreviation of "Cairo Geological Museum" which is attached to fossils catalogued in its collections; however, the institution is now known as the Egyptian Geological Museum, Cairo
CUWM	Cairo University (Wadi) Moghara collection, Geology Department, Faculty of Science, Cairo University, Giza
DPC	Duke Primate Centre, Durham, North Carolina
KNM	Kenya National Museum, Nairobi
UM	Uganda Museums, Kampala

Systematic palaeontology

Order Primates Linnaeus, 1758
Suborder Anthropoidea Mivart, 1864
Infraorder Catarrhini Geoffroy Saint-Hilaire, 1812
Superfamily Hominoidea Gray, 1825
or Pliopithecoidea Zapfe, 1961

Genus and species indet.

Material. CGM M94-90, edentulous left mandible preserved from the distal part of the canine alveolus to the distal alveolus of the m/3 (Text-fig. 3). CUWM 27, left lower canine (Text-fig. 4).

Locality. Moghara, Egypt (Text-fig. 1).

Age. Early Miocene (Faunal Set PI–PIIIa (Pickford 1981), ca. 19.5–16.5 Ma (Pickford et al. 2021a)) (Text-fig. 1).

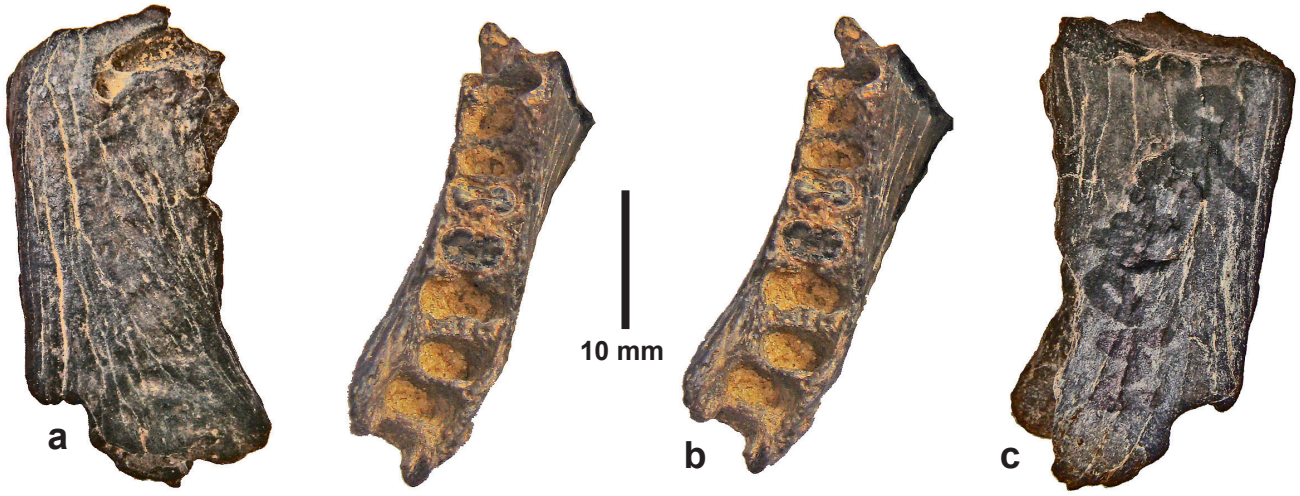
Description. **The mandible**. M94-90 is an edentulous left mandibular ramus extending from the posterior part of the left canine alveolus to the incomplete distal alveolus of the m/3 (Text-fig. 3). The base of the jaw in M94-90 is well preserved from beneath the p/3 as far distally as the m/2. The depth of the jaw is 15.5 mm at the level of the m/1, where it is 7.8 mm thick. The mental foramen is positioned slightly beneath mid-height of the ramus between the buccal apices of the roots of p/3 and p/4. The length from the mesial side of m/1 to the distal end of the m/3 is estimated to have been ca. 23 mm.

The mandible fragment is slightly over 3.2 cm long, measured from the anterior alveolus of the p/3 to the distal alveolus of the m/3. It retains the roots of the m/1, but the other alveoli are empty. In lateral and medial views, the ramus is slightly deeper mesially than distally, and in superior view, it is clear that the cheek tooth row was almost straight from p/3 to m/2 after which it curves laterally such that the alveoli of the m/3 are no longer in line with, nor parallel to those of the anterior teeth, as a result of which the alveoli of the m/3 were shifted laterally and twisted at an angle of ca. 25–30° with respect to the long axis of the tooth row (Text-fig. 9).

Part of the root of the ascending ramus is preserved in M94-90 (Text-fig. 3), which shows that its anterior end becomes distinct as a feature at the level of the junction between m/1 and m/2, and that it rises above the alveolar plane opposite the midline of the m/2 (Text-fig. 9) but, being of low relief, it does not greatly affect the thickness of the mandible.

In M94-90, the distal portion of the canine alveolus is extensive and deep, suggesting that the individual was possibly a male.

In buccal view, one observes that the lateral part of the alveolus of the p/3 in M94-90 has broken away, exposing the extent of the root which penetrated to just over half the depth of the jaw, which accords with male status of the individual. The mesial alveolus of the p/3 is positioned slightly anteriorly and well laterally with respect to its distal alveolus, which indicates that the tooth was oriented obliquely mesiolingually-distobuccally with respect to the long axis of the cheek tooth row.



Text-fig. 3. CGM M94-90, edentulous left mandible of a small-bodied anthropoid from Moghara, Egypt. a: buccal view, b: stereo dorsal view, c: lingual view.

Text-fig. 4. Stereo images of CUWM 27, left lower canine of a small-bodied anthropoid from Moghara, Egypt. a: distal views, b: lingual views, c: labial views, d: mesial views.

The two alveoli of the p/4 are sub-equal in dimensions and are ovoid in outline, with the long axis of the ovals oriented bucco-lingually. The mesial alveolus is not offset laterally, being in line with the distal alveolus of the tooth and to those of the m/1 behind. Likewise, the mesial and distal roots of the m/1 are ovoid and of almost the same bucco-lingual diameter. In contrast, the distal alveolus of the m/2 appears to be distinctly narrower bucco-lingually than the mesial alveolus of the same tooth, but this impression could be due to damage that the jaw has suffered at this point.

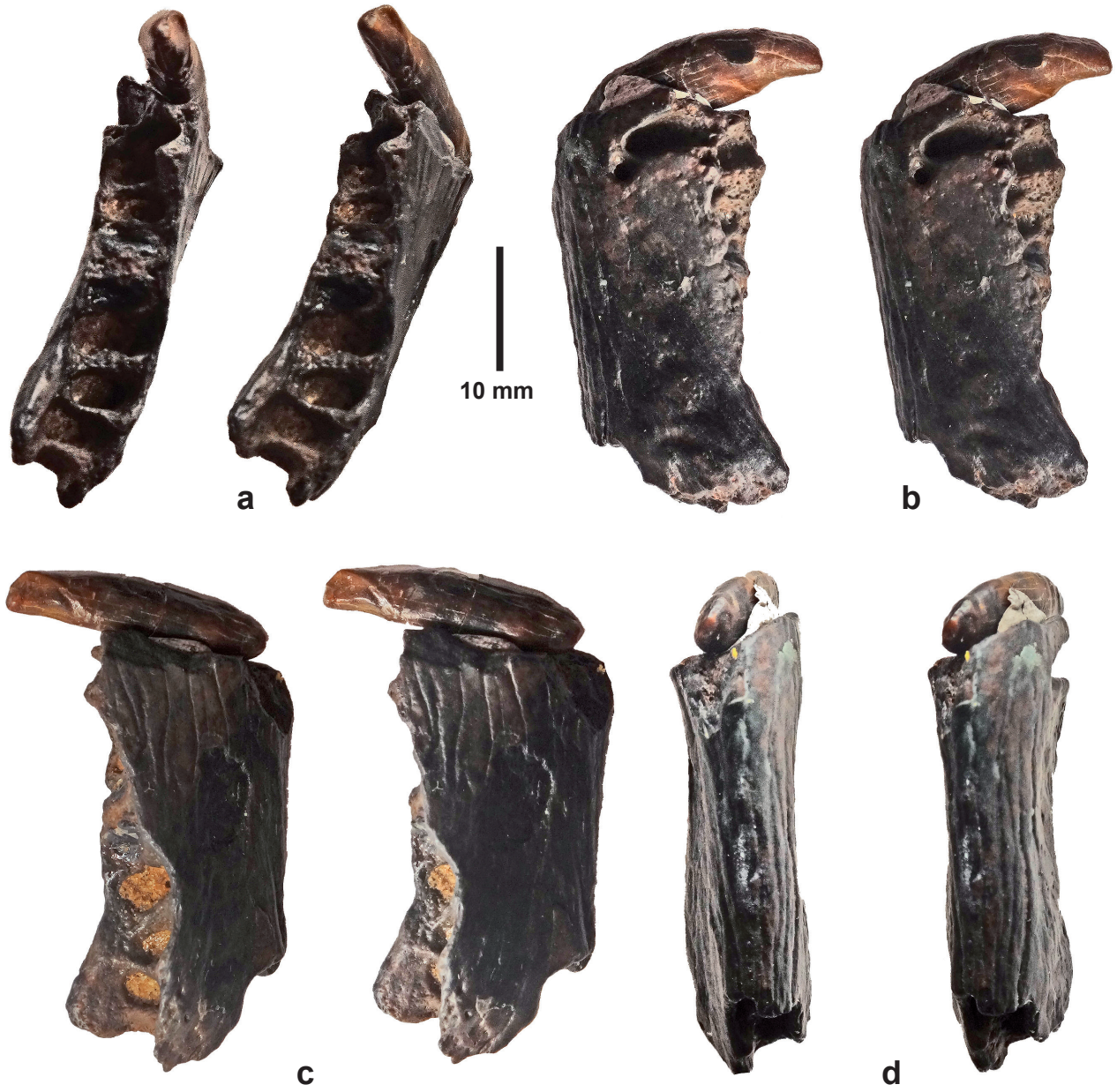
The alveoli of m/2 are substantially broader than those of the m/1 suggesting that the crown of the tooth would have been appreciably longer and wider than that of the m/1.

The mesial alveolus of the m/3 is oriented at an angle with respect to alveoli of the m/1 and m/2 indicating that the roots of the tooth were not in line with the anterior cheek teeth but were somewhat twisted in the jaw and were positioned slightly lateral to the long axis of the other teeth. The distal alveolus of the m/3, even though it is damaged distally, is distinctly narrower than its mesial alveolus and it is positioned laterally.

The lingual margin of the alveolar process is straight from the p/3 to the mesial root of m/2, but then it bends disto-laterally at the level of the distal root of the m/2 continuing as far as the distal root of the m/3.

In summary, it is deduced that in the mandible M94-90, the tooth rows were straight from the p/3 to the m/2, after which there was a distinct outward bend of the part of the jaw that carried the m/3.

The canine. CUWM 27 is a well-preserved left lower canine from Moghara (Text-figs 4, 5, Tab. 1). The crown is 7 mm tall on the lingual side and the root is twice as tall as the crown. The lingual side of the crown shows a low central ridge that descends from the distal part of the apical margin of the tooth crown to the cervix terminating close to the centre of the lingual side of the tooth. The cutting edge of the crown is relatively straight, but is slightly oblique with respect to the axis of the crown-root ensemble. The mesial side of the crown is low, whereas the distal margin is twice as tall as it. The labial side of the tooth is slightly convex with parallel margins. The root is robust with no sign of a sulcus on its mesial surface, unlike the lower canines of Victoriapithecidae which have a prominent sulcus extending from the cervix to the apex of the root (Pickford et al. 2021b: fig. 8).

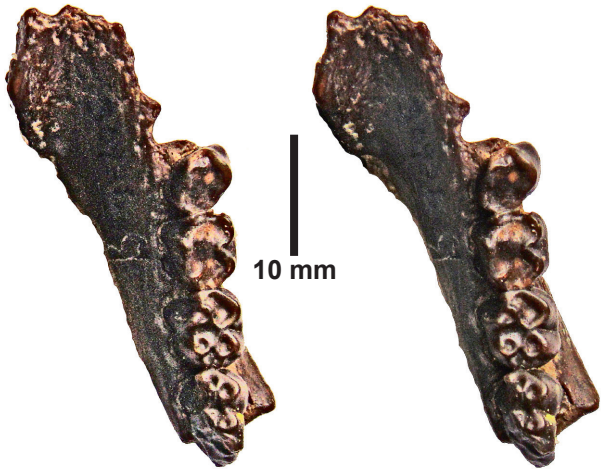


Text-fig. 5. Stereo images of CUWM 27 (canine) and CGM 94M-90 (mandible) reconstructed to demonstrate the compatibility of the dimensions of the two specimens. a: superior view, b: lateral view, c: medial view, d: ventral view.

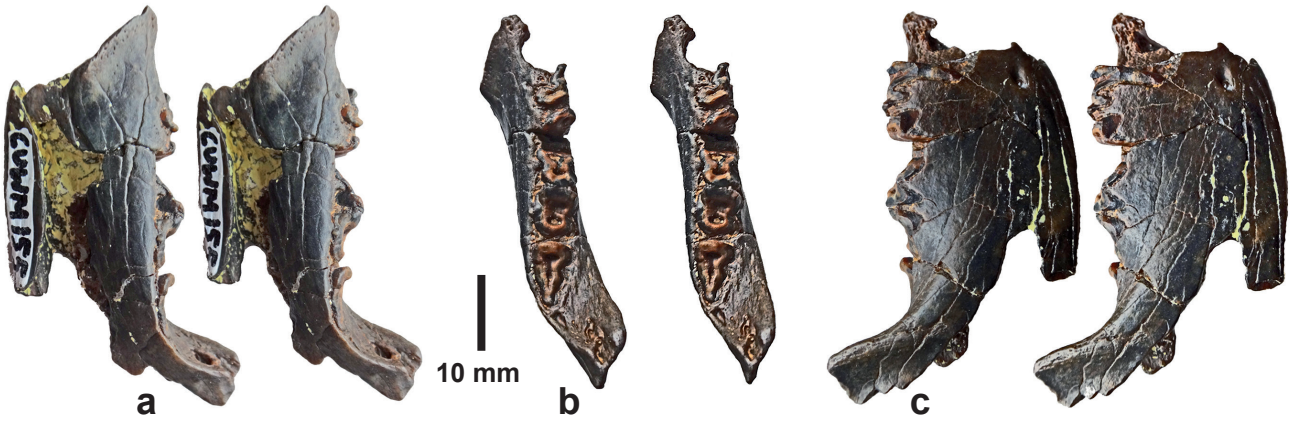
Discussion

Even though mandible M94-90 is comparable in overall dimensions to the type specimens of *Prohylobates tandyi* (Text-figs 6, 9) and genus indet *mogharensis* (Text-fig. 8) it differs from them in a number of morphological features, including mandibular depth, the thickness of the ramus and the length of m/1–m/3, as well as the positions of the distal pole of the symphysis and the mental foramen. Furthermore, in M94-90, the jaw becomes shallower from mesial to distal, whereas in genus indet. *mogharensis*, the mandible deepens posteriorly (Text-figs 7, 8). The sublingual fossa is shallow in M94-90, whereas in both species of Moghara cercopithecoids, it is deep and extensive.

In *Prohylobates* Fourtau, 1918 the distal root of the p/3 is in a lingual position when compared to the roots of the p/4 (Text-figs 6, 8). In M94-90, the corresponding root of the p/3



Text-fig. 6. Stereo occlusal view of CGM 30936, holotype right mandible of *Prohylobates tandyi*, Early Miocene, Moghara, Egypt.



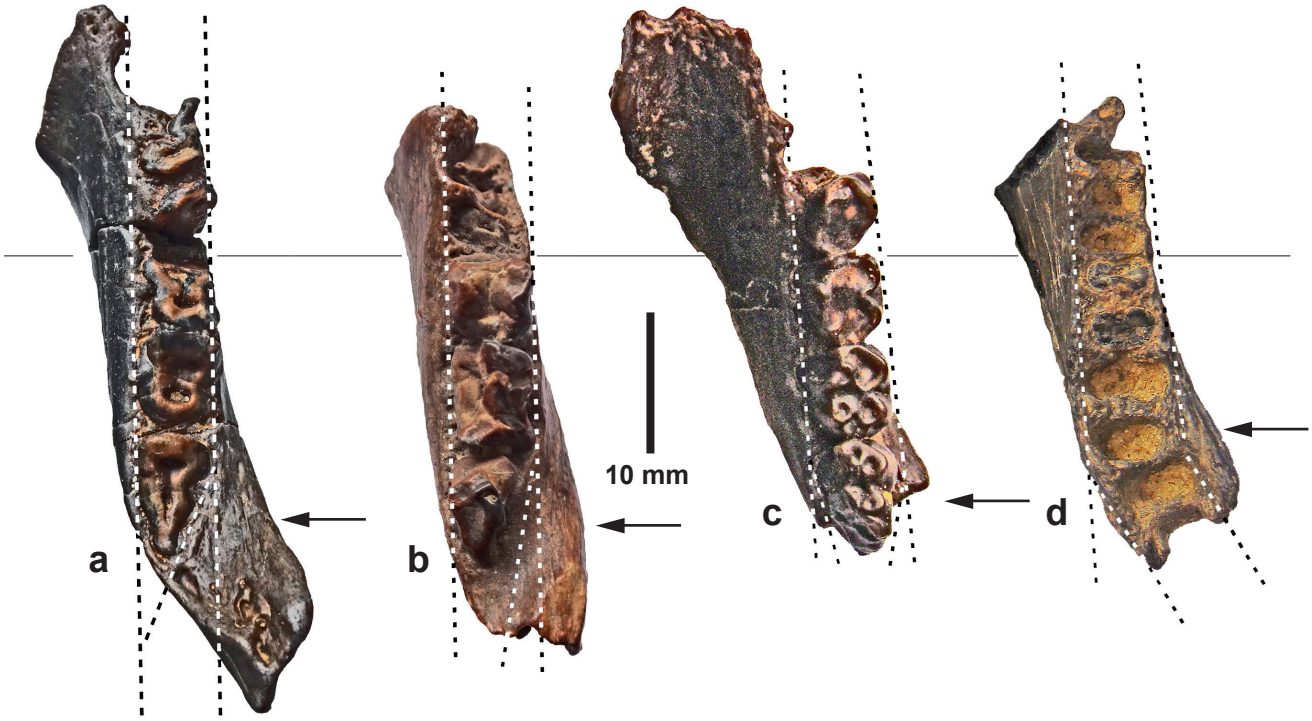
Text-fig. 7. Stereo images of CUWM 155, edentulous right mandible of genus indet. *mogharensis* from Moghara. a: lingual view, b: occlusal view, c: buccal view.

Text-fig. 8. Comparison between CGM 30937, right mandible of genus indet. *mogharensis* (a) and CGM M94-90 plus CUWM 27 (b), left mandible and canine of a small anthropoid (images reversed). Note the great difference in depths of the mandibles, the position of the distal pole of the symphysis, the thickness of the root of the ascending ramus and the fact that the jaw of the cercopithecoid deepens posteriorly, whereas that of M94-90 becomes shallower distally. 1: lateral view, 2: occlusal view, 3: medial view.

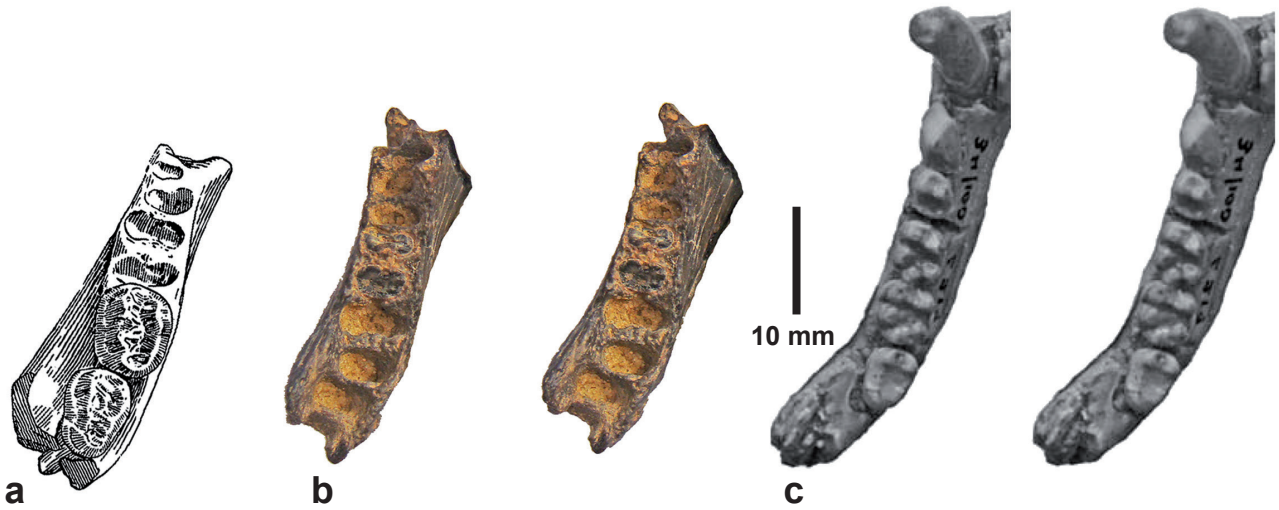
Table 1. Measurements of CUWM 27, left lower canine of a small hominoid or pliopithecoid from Moghara, Egypt.

Measurement	mm
Mesio-distal length of crown	3.5
Bucco-lingual breadth of crown	4.9
Crown height lingual side	7
Root height lingual side	14

is only slightly lingual to the p/4 root (Text-fig. 3). The p/4 in *Prohylobates tandyi* is oriented slightly obliquely in the jaw (Simons 1969) whereas in M94-90, the mesial and distal roots of the tooth are in line with the roots of the m/1 and m/2, indicating that the tooth was probably not as obliquely oriented as it is in *Prohylobates*. The m/3 in *Prohylobates* is positioned slightly to the lingual side of the midline of the cheek tooth row (Fourtau 1918, Simons 1969, Miller et al. 2009) whereas in M94-90, the alveoli of the m/3 are positioned well lateral to the midline of the cheek tooth row



Text-fig. 9. Comparison between mandibles; a: CUWM 155, genus indet. *mogharensis*, b: CGM 30937, genus indet. *mogharensis*, c: CGM 30936, *Prohylobates tandyi*, d: CGM M94-90, hominoid or pliopithecoid indet. (image reversed), to highlight the orientation of the m/3 in relation to that of the other cheek teeth, and to show the level at which the ascending ramus rises above the alveolar plane (arrows). The position of the ascending ramus is not preserved in CGM 30936, but it is present in CGM 30937 (given as CGM 28971 in Simons 1969: fig. 1c) and CUWM 155. The mandibles are aligned at the mesial edge of m/1 (horizontal line).



Text-fig. 10. Superior views of mandible CGM M94-90 (b) compared with the type specimens of *Pliopithecus piveteaui* (a) (image from Hürzeler 1954: drawing reversed), and *Micropithecus chamtwaraensis* (c) (cast of right mandible of specimen KNM CA 380, image reversed) to show the similar outward bending of the ramus at the level of the m/2–m/3. For ease of comparison, the sketch of the mandible of *Pliopithecus piveteaui* has been brought to the same dimensions as CGM M94-90.

(Text-fig. 9), and furthermore, the distal root is even more laterally positioned than the mesial root, indicating a twist in the orientation of the tooth. Similar outward bend in the mandible is evident in the small-bodied ape *Micropithecus chamtwaraensis* Pickford, Senut, Gommery, Musalizi et Ssebuyungo, 2021 (Pickford et al. 2021b: fig. 71) from the Early Miocene of Kenya, and the same can be said of the mandibles of European *Epipliopithecus vindobonensis* Zapfe et Hürzeler, 1957 (Zapfe 1961, Begun 2002) and *Pliopithecus piveteaui* Hürzeler, 1954 (Text-fig. 10).

In the fossil monkeys, *Prohylobates tandyi* and genus indet. *mogharensis* (Text-figs 7, 8), the anterior margin of the ascending ramus of the lower jaw rises above the alveolar plane at about the middle of the m/3 (Simons 1969: fig. 1c) whereas in M94-90, it is positioned further anteriorly, rising above the alveolar plane at the level of the middle of the second lower molar (Text-fig. 9).

Another difference between these mandibles, concerns the position of the mental foramen, which is located at about half the depth of the mandible in M94-90, but is lower in *Prohylobates*, ca. 1/3 of the way up from the ventral margin (Text-fig. 8).

The mandible CGM M94-90 is slender and shallow when compared to those of *Prohylobates* and genus indet. *mogharensis* (Tab. 2). Thus, even though the length of m/1–m/3 in *Prohylobates* is less than that in CGM M94-90, the jaws of the cercopithecoids are appreciable thicker and deeper at m/1 than the corresponding parts of CGM M94-90. The lateral swelling of the mandible where the ascending ramus takes root, is prominent in *Prohylobates*, increasing visibly from m/1 to m/3, but in M94-90, the jaw remains slender right up to the middle of the m/3, and possibly beyond, although the specimen is broken at this point, so it cannot be observed directly.

Furthermore, in *Prohylobates tandyi* and genus indet. *mogharensis* the distal pole of the mandibular symphysis is observed to be beneath the level of the junction between p/3-p/4, but in M94-90, it is not present, even beneath the alveolus of the canine, suggesting that the symphysis terminated in a more anterior position in the latter fossil. However, damage to the specimen may be biasing the observation.

All the features by which M94-90 differs from *Prohylobates* are universal or common in hominoids and pliopithecoids, whereas they are rare or inexistant in Cercopithecoidea. For this reason, it is concluded that M94-90 represents a small-bodied anthropoid ("ape"), which had more or less the same dimensions as small extant gibbons such as *Hylobates* Illiger, 1811, as well as a suite of extinct small-bodied "apes" from the Early Miocene of East Africa such as *Micropithecus clarki*, or *Lomorupithecus evansi* (Pickford et al. 2021b) in Napak Uganda (UM collections), but was slightly smaller than the extinct European genera *Pliopithecus* Gervais, 1849 and *Epipliopithecus* (Begun 2002). Being edentulous, however, it is not possible to arrive at a secure identification of the mandible at the genus or family rank, so the specimen is attributed to Hominoidea or (more likely) Pliopithecoidea, genus and species indet.

The recognition of the mandible M94-90 as that of a small-bodied anthropoid confirms that a hominoid or pliopithecoid, as opposed to a cercopithecoid, was present at Moghara during the Early Miocene (Simons 1994). The m/1–m/3 length of the Moghara mandible is close to that of *Pliopithecus platyodon* Biedermann, 1863, from Elgg (MN 5), Switzerland.

The primate lower canine from Moghara differs from the corresponding teeth of victoriapithecid monkeys in that it does not have a sulcus on the mesial side of the root (Pickford et al. 2021b), the crown is less tall and it has a central lingual crest that is absent or subtle in the lower canines of Victoriapithecidae. Comparisons with small ape teeth reveals that the specimen is close in size and morphology to teeth of *Micropithecus clarki* and *Lomorupithecus evansi* from East Africa (Pickford et al. 2021b) and apart from the lower crown, it recalls to some extent the lower canines of *Epipliopithecus* (Zapfe 1961).

The lateral bend of the distal part of the mandible M94-90 at the level of the m/2-m/3 (Text-figs 8–10) indicates that the ascending rami and the mandibular condyles may have been further apart than they were in *Prohylobates*. A similar outward bend of the mandible is observed in the small-bodied anthropoid from the Early Miocene of Chamtwara, Kenya, *Micropithecus chamtwaraensis* (Pickford et al. 2021b: fig. 71) and in *Pliopithecus piveteaui* from Europe (Hürzeler 1954) (Text-fig. 10).

Palaeobiogeography

It has long been appreciated that, during the Early Miocene, there was a high diversity of anthropoids in the low latitudes of Africa (Pickford et al. 2021b) and that at higher latitudes of the continent the diversity was lower (Senut et al. 1997, Mocke et al. 2023) and that until the middle of the Early Miocene (ca. 20 Ma) the superfamily was probably absent from Eurasia. Anthropoids dispersed to Eurasia prior to the end of Early Miocene (Harrison et al. 2020) eventually reaching as far north as 50° latitude (Pickford 2013). The Moghara Formation in Egypt, at 30° N latitude, is thus strategically positioned in geological time and geographic coverage to yield evidence concerning the dispersal of anthropoids (and other vertebrates) from Africa to Eurasia, and vice versa, during the Early Miocene.

Table 2. Measurements (in mm) of the mandible CGM M94-90 (hominoid or pliopithecoid) and of cercopithecoids CUWM 155 and CGM 30937 (genus indet. *mogharensis*) and CGM 30936 (*Prohylobates tandyi*) (e – estimated measurement).

Measurement	CGM M94-90	CUWM 155	CGM 30937	CGM 30936
Length m/1–m/3	23e	21.5e	21.5	19.6
Mandible thickness at m/1	7.8	7.8e	9.9	8.9
Mandible depth at m/1	15.5	22.0e	21.9	–

Paradoxically, the most common anthropoid at Moghara (7 specimens described; Fourtau 1918, Simons 1994, Miller et al. 2009) are cercopithecoids, *Prohylobates tandyi* and genus indet. *mogharensis*, both of which are members of a superfamily that is unknown in Eurasia until the Late Miocene some 4 to 5 million years after the deposition of the Moghara sediments. Initially interpreted to be an "Anthropoidae" (sic) (Simiidae) by Fourtau (1918), *Prohylobates* was subsequently transferred to Victoriapithecidae (Simons 1969).

In contrast, the earliest records of anthropoids in Eurasia comprise pliopithecoids (*Pliopithecus* Gervais, 1849, *Platodontopithecus* Gu et Lin, 1983, and close relatives: see Harrison and Gu (1999); *Fanchangia* Harrison et al., 2020) a superfamily that, until M94-90 and CUWM 27 were recognised, was potentially represented at Moghara by a single specimen (a humerus, DPC 6643; Simons 1994). However, the discovery of M94-90 and CUWM 27 opens up new possibilities regarding our understanding of the dispersal of small anthropoids from Africa to Eurasia during MN 3, possibly as early as 19–20 Ma (Harrison and Gu 1999, Harrison et al. 2020). The sequence of fossiliferous deposits at Moghara spans the geological time period concerned (Text-fig. 1), and its geographic position is strategically intermediate between the equatorial deposits of Eastern Africa on the one hand, and the mid-latitude localities in Eurasia, on the other.

It remains to be determined why cercopithecoids, which are more commonly encountered as fossils at Moghara than are anthropoids, did not disperse to Eurasia until many millions of years after the pliopithecoids and hominoids had done so, whereas pliopithecoids, which are rare at Moghara, did manage to disperse to Eurasia, after which they spread rapidly as far as Spain in the west and China in the east (Harrison and Gu 1999).

Conclusion and general discussion

Moghara, an Early Miocene fossiliferous locality in northern Egypt, is known to have yielded several remains of two species of Early Miocene Cercopithecoidea and a single specimen of a medium-sized anthropoid (Fourtau 1918, Simons 1969, 1994, Miller et al. 2009). Simons (1994) attributed all the Moghara cercopithecoid remains to the species *Prohylobates tandyi*, but he left the "ape-like" humerus in open nomenclature, although the presence of an entepicondylar foramen in the humerus suggests affinities with pliopithecoids, such as *Epipliopithecus*, the humerus of which also has an entepicondylar foramen (Zapfe 1961).

Miller et al. (2009) in contrast, considered that there were two species of cercopithecoid monkeys at Moghara based on several mandibles, as well as an "ape-like" species based on the humerus. The present paper documents the presence of two additional "ape-like" specimens (hominoid or, more likely, pliopithecoid) at Moghara, but both of the fossils are left in open nomenclature, pending the recovery of more diagnostic remains. It is noted however, that some aspects of the Moghara non-cercopithecoid fossils recall the genera *Micropithecus* Fleagle et Simons, 1978 from equatorial Africa and *Epipliopithecus* and *Pliopithecus* from mid-latitude Europe. The combined evidence of the mandibular shape and of the presence of an entepicondylar foramen in the humerus suggests closer affinities of the Moghara specimens to Pliopithecoidea than to Hominoidea.

Even though the mandible M94-90 is compatible in dimensions with those of *Prohylobates tandyi* and genus indet. *mogharensis*, its ramus is more slender and appreciably shallower than those of the two cercopithecoid species. The sublingual fossa is shallow in the "ape-like" specimen, whereas it is deep and prominent in the cercopithecoids.

The humerus and mandible of *Epipliopithecus* published by Zapfe (1961), are slightly smaller than those of the humerus from Moghara described by Simons (1994) and the mandible, M94-90, described herein, but the proportions between the dimensions of the humeri and mandibles are similar in the two samples, suggesting that the Moghara fossil mandible (and lower canine) likely represent the same species as the "ape-like" humerus described by Simons (1994). It is thus concluded that Moghara has yielded three kinds of Anthropoidea, comprising two species of Cercopithecoidea (Victoriapithecidae, *Prohylobates tandyi* and genus indet. *mogharensis*), and a single species of Hominoidea or (more likely) Pliopithecoidea, which is yet to be named.

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