Revised age estimates for the later Paleogene mammal faunas of Egypt and Oman

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The Jebel Qatrani Formation of northern Egypt has produced Afro-Arabia’s primary record of Paleogene mammalian evolution, including the world’s most complete remains of early anthropoid primates. Recent studies of Fayum mammals have assumed that the Jebel Qatrani Formation contains a significant Eocene component (~150 of 340 m), and that most taxa from that succession are between 35.4 and 33.3 million years old (Ma), i.e., latest Eocene to earliest Oligocene in age. Reanalysis of the chronological evidence shared by later Paleogene strata exposed in Egypt and Oman (Taqah and Thatyniti areas, Dhofar Province) reveals that this hypothesis is no longer tenable. Revised correlation of the Fayum and Dhofar magnetostratigraphies indicates that (i) only the lowest 48 m of the Jebel Qatrani Formation are likely to be Eocene in age; (ii) the youngest Fayum anthropoids, including well known species such as Aegyptopithecus zeuxis and Apidium phiomense, are probably between 30.2 and 29.5 Ma, ~3–4 Ma younger than previously thought; (iii) oligopithecid anthropoids did not go extinct at the Eocene–Oligocene boundary but rather persisted for at least another 2.5 Ma; (iv) propliopithecid anthropoids first appear in the Fayum area at ~31.5 Ma, long after the Eocene–Oligocene boundary; and (v) the youngest Fayum mammals may be only ~1 Ma older than the 28–27-Ma mammals from Chilga, Ethiopia, and not 4–5 Ma older, as previously thought. Whatever gap exists in the Oligocene record of Afro-Arabian mammal evolution is now limited primarily to a poorly sampled 27- to 23-Ma window in the latest Oligocene.

The later Paleogene Jebel Qatrani Formation, which is broadly exposed north of Birket Qarun in the Fayum Depression, Egypt, has produced Afro-Arabia’s primary record of late Eocene and early Oligocene mammalian evolution. The succession is particularly well known for its diverse anthropoid primate fauna (1–5) and is increasingly notable for its record of early strepsirrhine primate evolution (6–10). Members of the endemic afrotherian mammal orders Hyracoidea, Embrithopoda, Proboscidea, Sirenia, Macroscelidea, Afrosoricida, and Ptolemaida are also represented, along with hyaenodontid creodonts and immigrant hystricognathous rodents, chiropithecans, anhydracothervid artiodactyls, and marsupials (11).

The position of the Eocene–Oligocene boundary ([EOB), ~33.9 million years old (Ma) (12)] in the Fayum area has been a matter of consistent debate over the course of the last century, and at various times it has been suggested that the Jebel Qatrani Formation is either entirely Eocene in age (13), entirely Oligocene in age (14, 15), or composed of both late Eocene and early Oligocene sediments (16, 17). Biostratigraphic information bearing on the age of the Formation is limited, because its vertebrate record is many millions of years younger than all previous estimates for the age of the youngest Jebel Qatrani vertebrates. The most useful chronological evidence currently available from the Formation itself is the magnetostratigraphy developed by Kappelman et al. (17) (Fig. 1A), but there remain multiple possible correlations of that magnetostratigraphy to the geomagnetic polarity time scale (GPTS).

The Jebel Qatrani Formation is divided into upper and lower sequences (15), with the boundary between these units being the 4- to 10-m-thick cliff-forming “Barite Sandstone” that unconformably overlies the upper red sandstone of the lower sequence. Rasmussen et al. (16) suggested that the approximate position of the EOB is probably marked by this unconformity, and this interpretation was consistent with Kappelman et al.’s (17) preferred correlation of the Jebel Qatrani magnetostratigraphy to the GPTS, which placed all of the major mammal localities between magnetic polarity Chrons C15r and C13n (i.e., between 35.4 and 33.3 Ma) (Fig. 24). Numerous subsequent publications have accepted the ages of major fossil vertebrate localities required by this correlation (18–21). Placement of the EOB at the division between the upper and lower sequences is not only convenient but also could have implications for primate response to early Oligocene climate change; part of Rasmussen et al.’s (16) justification for their suggested placement of the EOB was a perceived “break” in the anthropoid primate faunas at about the level of the Barite Sandstone, just above which specialized propliopithecid catarrhines and parapithecine parapithecids make their first appearance. The morphological and dietary adaptations differentiating these taxa from their relatives in the lower sequence have been interpreted as possible responses to global cooling in the earliest Oligocene (22).

The most productive later Paleogene Afro-Arabian mammal localities outside of the Fayum area are found in the Dhofar Province of Oman, where restricted exposures of the Ashawq Formation in the Taqah and Thatyniti areas have produced mammalian assemblages that are very similar to those from the Jebel Qatrani Formation (23–30). Importantly, the mammals from the Ashawq Formation occur in stratigraphic sections that preserve marine invertebrates (nummulitid and lepidocycline foraminifers) that allow for age estimates independent of the mammals themselves. Magnetostratigraphic sampling in the Taqah and Thatyniti sections helps to further constrain the ages of these mammal-bearing strata (Fig. 1 B and C) (24, 25, 29). The Omani mammals thus hold great promise for helping to reveal the most probable correlation of the Jebel Qatrani magnetostratigraphy to the current GPTS, but as yet there has been no attempt to draw the available magnetostratigraphic and biostratigraphic data from the Fayum and Dhofar areas into an internally consistent biochroonostratigraphic hypothesis. The present study provides such a synthesis, and reveals that the Jebel Qatrani Formation is likely to be almost entirely Oligocene in age.

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Abbreviations: EOB, Eocene–Oligocene boundary; GPTS, geomagnetic polarity time scale; Ma, million years old; kyr, thousand years.

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Results

Magnetostratigraphic and Nonmammalian Biostratigraphic Evidence from the Ashawq Formation. A maximum age for the Taqah mammal locality is constrained by stratigraphically lower occurrences of the benthic foraminifera *Nummulites fichteli* (an early Oligocene index fossil) and *Eulepidina dilatata* (Fig. 1B), with first occurrences of key foraminifera. The Taqah fossil mammal locality is marked by a horizontal gray bar. (A) Magnetostratigraphy of the Taqah section, modified from Roger et al. (29), with the first occurrence of key foraminifera. The Taqah fossil mammal locality is marked by a horizontal gray bar. (B) Magnetostratigraphy of the Thaytiniti section, modified from Thomas et al. (24), with labeling as in B. VGP, virtual geomagnetic pole.

Fig. 1. Magnetostratigraphic and nonmammalian biostratigraphic data from the Jebel Qatrani Formation, Egypt, and the Ashawq Formation, Oman. (A) Magnetostratigraphy of the Qasr el-Sagha, Qasr el-Mtitn, and upper Birket Qarun Formations, modified from Kappelman et al. (17) and Seiffert et al. (19). The stratigraphic positions of major fossil mammal localities (A, B, E, G, I, M, V, and L-41) are marked by horizontal gray bars. (B) Magnetostratigraphy of the Taqah section, modified from Roger et al. (29), with first occurrences of key foraminifera. The Taqah fossil mammal locality is marked by a horizontal gray bar. (C) Magnetostratigraphy of the Thaytiniti section, modified from Thomas et al. (24), with labeling as in B. VGP, virtual geomagnetic pole.

Thus it remains possible that *E. dilatata’s* first appearance along the southern margins of the Arabian Peninsula occurs in the very latest stages of the long reversed polarity Chron C12r (Fig. 2). The Taqah mammals occur at the top of a long zone of reversed magnetic polarity, stratigraphically above the first appearance of both *N. fichteli* and *E. dilatata* in the Shizar Member (Fig. 1B), and taken together, these stratigraphic relationships suggest a placement in the very latest part of Chron 12r (~31.5 Ma) (Fig. 2C). The normal polarity zone at the base of the Taqah magnetostratigraphy would then be Chron C13n. The only other option, favored by Roger et al. (29), would be to place the Taqah mammal locality in Chron C11r (30.63–30.22 Ma), but because the Taqah section of the Shizar Formation is likely to contain a considerable amount of time in only a ~2.15-Ma-long Chron C12r intervene between the Taqah and Thaytiniti mammals but nevertheless be completely unsampled in the
magnetostratigraphies from both areas, even though much shorter normal (C13n, \( \approx 470 \) kyr; C12n, \( \approx 490 \) kyr) and reversed (C11r, \( \approx 410 \) kyr) zones are densely sampled in one area or the other. Regardless, the age difference between Roger et al.’s (29) placement of the Taqah mammal locality and that proposed here is potentially \( < 500 \) kyr, and the most important point is that the Taqah mammals, based on combined magnetostratigraphic and invertebrate biostratigraphic constraints, are unlikely to be older than 31.5 Ma and are potentially as young as 30.22 Ma.

The age of the Thaytiniti mammal locality is less well constrained by biostratigraphic data. The locality must be early Oligocene in age, based on the occurrence of \( N. fichteli \) (24) and is at least slightly older than Taqah, given its occurrence near the base of the Shizar Member in a zone of normal magnetic polarity (24) (Fig. 1C). If, as suggested here, the Taqah mammals are most likely to fall within the \(<31.5\) Ma part of Chron 12r, then the only possible placement of Thaytiniti is in Chron 13n, the only older zone of normal polarity in the early Oligocene. If this is the case, then the Thaytiniti mammals are no older than \( \approx 33.7 \) Ma. This correlation is consistent with the interpretation of Roger et al. (29) and Thomas et al. (25), based on the biostratigraphic and magnetostratigraphic data available to them. A less plausible alternative correlation would place the Thaytiniti mammals in Chron 13n (\( \approx 30.6-31.1 \) Ma) and would require the Taqah mammal layer to be correlated with Chron C11r. For additional discussion of the Dhofar magnetostratigraphies, see Supporting Text, which is published as supporting information on the PNAS web site.

**Comparison of Chronological Data Shared by the Fayum and Dhofar Localities.** The magnetostratigraphic and nonmammalian biostratigraphic evidence summarized above suggests that the ages of the Taqah and Thaytiniti mammal localities are probably \( \approx 31.0-31.5 \) and 33.7–33.3 Ma, respectively. Kappelman et al.’s (17) preferred correlation of the Jebel Qatrani magnetostratigraphy to the GPTS places all of the major mammal localities in that Formation between Chron 13n and Chron 15r and requires that the youngest primate-bearing quarries (I and M) would be no less than 33.3 Ma, whereas the oldest (L-41) is no older than 35.4 Ma (Fig. 1A). This correlation would imply that the Taqah mammals are \( \approx 2 \) Ma younger than the youngest primate-bearing Jebel Qatrani quarries (I and M), whereas Thaytiniti would be of approximately the same age as quarries I and M.

The mammalian biostratigraphic evidence from the Fayum and Dhofar localities is completely inconsistent with this scenario. Although many of the mammals from Taqah and Thaytiniti remain undescribed, available evidence strongly suggests that both Omani localities are older than quarries I and M and probably intermediate in age between the oldest localities of the Jebel Qatrani upper sequence (quarries G and V, a few meters above the Barite Sandstone) and the oldest productive locality from the lower sequence (quarry L-41) (Fig. 2B). Thus far, the only taxa from the Fayum and Dhofar areas that can be directly compared are anthropoid primates and hyracoids; the Taqah and Thaytiniti rodent assemblages should be of great use in this regard but are, as yet, largely undescribed.

According to the faunal list of Thomas et al. (25), two mammalian species, the hyracoid Thyrohyrax meyeri and the propliopithecid anthropoid Moeripithecus markgrafi, are shared by the Jebel Qatrani and Taqah faunas. In Oman, \( T. \) meyeri is found at Taqah, and “\( cf. \) \( T. \) meyeri” is found at Thaytiniti; in Egypt, \( T. \) meyeri is found only at quarry L-41 (33). Another hyracoid from Thaytiniti has been described as \( cf. \) Saghatherium bowni; like \( T. \) meyeri, \( S. \) bowni occurs only at quarry L-41 (33), and the genus Saghatherium does not occur at all in the Jebel Qatrani’s upper sequence. The propliopithecid from Taqah,
so the occurrence of these stem strepsirrhines at Taqah again or crown) above the 48-m level in the Jebel Qatrani Formation, L-41 (6). There are no undoubted records of Strepsirrhini (stem which are closely related to ""[Image 9x9 to 28x824]

EOB is marked by a gray line and the letters ""EOB."" 

The age of the Taqah mammals is constrained by marine invertebrates that can be correlated across numerous areas exposed throughout the Tethyan region and is highly unlikely to be any older than the latest part of Chron C12r (&lt;~31.5 Ma). The Jebel Qatrani Formation has no such biostratigraphic constraints, and the only 40Ar/39Ar radioisotopic age constraint (from the Widan el-Faras basalt) is much younger (31.5 Ma). There is clearly a profound mismatch between the mammalian biostratigraphic data and the currently accepted correlation of the Fayum magnetostratigraphy with the GPTS. Given Kappelman et al.’s (17) preferred magnetostratigraphic correlation, the Fayum occurrence of P. ankelí would predate that from Taqah by &gt;2 million years, the youngest documented Fayum oligopithecid (Oligopithecus savagei from quarry E) would be ~3 million years older than the Taqah species, and Fayum records of stem strepsirrhines and the hyracoid T. meyeri would be between 3.5 and 4 Ma older than those from Taqah. The fact that Taqah appears to contain taxa from localities distributed throughout the lower 165 m of the Jebel Qatrani Formation is problematic, but the mammalian correlation becomes irreconcilable if Taqah is, in fact, at least 2 million years younger than the youngest Jebel Qatrani quarries.

A New Correlation of the Fayum Magnetostratigraphy to the GPTS. The age of the Taqah mammals is constrained by marine invertebrates that can be correlated across numerous areas exposed throughout the Tethyan region and is highly unlikely to be any older than the latest part of Chron C12r (&lt;~31.5 Ma). The Jebel Qatrani Formation has no such biostratigraphic constraints, and the only 40Ar/39Ar radioisotopic age constraint (from the Widan el-Faras basalt) is much younger (~23.6 Ma) than the suggested age of the Taqah mammals, so the correlation of the Fayum magnetostratigraphy to the GPTS can and should be shifted to resolve the mismatch between the magnetostratigraphic and mammalian biostratigraphic data from the Fayum

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**Fig. 3.** Revised correlation of the mammal localities from Egypt and Oman. (A) Correlation of the Fayum, Taqah, and Thaytiniti magnetostratigraphies to the GPTS. Major, moderate, and minor unconformities in the Fayum section are marked by black lines on the right side of the Fayum magnetostratigraphic column. (B and C) Phylogenetic relationships of later Paleogene anthropoid primates, based on the Adams consensus tree published by Seiffert et al. (19), plotted against the revised age correlation (B) and the age correlation preferred by Kappelman et al. (17) (C). Broken lines indicate uncertainty in the temporal placement of species; minimum species’ durations are arbitrarily figured as being ~1 Ma. The provenance of M. markgrafi, Parapithecus fraasi, and Propliopithecus haeckei is unknown. The temporal position of the Taqah anthropoids in C is that previously proposed by Rasmussen et al. (16) and Rasmussen (18). The position of the EOB is marked by a gray line and the letters “EOB.”
and Dhofar areas. The correlation of the Fayum magnetostratigraphy to the GPTS proposed here (Fig. 3) hinges on the strong probability that the Taqah locality, based on its mammalian fauna, is of approximately the same age or older than the Jebel Qatrani quarries G and V (16, 18, 25, 26, 36). Forging a sequence of ages proposed here. Rasmussen et al.’s (16) recommended placement of the EOB around the position of the Barite Sandstone is less likely on these magnetostratigraphic grounds, because samples from the 20 m of sediment overlying that unconformity are all of reversed and not normal polarity, as would be expected if erosion and the subsequent resumption of deposition occurred within Chron C13n. The placement of the EOB proposed here gains additional support from the observation that the net loss of sediment from the unconformity just above L-41 is likely to have been considerably greater than the amount eroded before the onset of Barite Sandstone deposition (T. M. Bown, personal communication).

Regardless of whether the EOB is tied directly to the 48-Ma level unconformity, the new magnetostratigraphic correlation requires that almost two-thirds of the lower sequence of the Jebel Qatrani Formation is early Oligocene, and not late Eocene, in age as previously thought. The sediments at quarries A and B are of uncertain position relative to the EOB, but the younger Quarry E, which has produced remains of the anthropoids O. savagei and Qatrania wingi, is now best placed near the bottom of Chron C12r, a position thus unambiguously early Oligocene (perhaps ~33 Ma) in age. Proplopiocnids do not appear in the Jebel Qatrani Formation until the upper part of Chron C12r, probably later than ~31.5 Ma. Because the propliopithecids from quarries G and V could be almost 1.5 Ma younger than the next-oldest anthropoids in the Formation (from quarry E), their first appearance was not necessarily a sudden event, and can no longer be directly tied to earliest Oligocene cooling, given the ~2.5-Ma gap between the EOB and their first appearance. The absence of more primitive catarrhines that are intermediate in morphology between oligopithecids and propliopithecids may simply be due to sampling and/or sedimentary gaps between the ~90- and ~165-Ma levels of the Formation. The new correlation also indicates that the extinction of oligopithecids cannot be tied to the EOB, although local extinction of strepsirrhines in the Fayum area could be, because there are no undoubted records of that group above the 48-Ma-level unconformity. As has already been noted by Rasmussen et al. (16), there are no major shifts or extinctions in the nonprimate mammalian fauna of the Jebel Qatrani Formation that could be linked to climate change at the EOB. Other long-term trends, such as increasing selenodonty and lophodonty in some hyracoid lineages and increased body size and bunodonty among anthropoids, could nevertheless represent delayed adaptive reactions to environmental changes associated with early Oligocene cooling.

The revised ages for Fayum quarries also have implications for the timing of crown anthropoid origins. All specialists agree that the oldest definitive crown anthropoids occur in the Jebel Qatrani Formation, but there is ongoing debate surrounding whether oligopithecids or propliopithecids are the oldest known stem catarrhines (19, 42). Regardless, it should be noted that both groups’ first appearance is later than previously thought. The oldest oligopithecids, Catopithecus browni, should now be considered latest Eocene (or, less likely, for the reasons enumerated above, earliest Oligocene) in age or ~34.8–33.9 Ma. This is not a major shift from the previous estimate of 35.4–35.0 Ma. The implications are much more dramatic if Kay et al. (42) are correct in arguing that propliopithecids are the oldest known stem catarrhines and crown anthropoids, for their first appearance is now likely to be ~31.0–31.5, at least 2 Ma later than previously thought. Recent multigene molecular estimates for the origin of crown Anthropoidea extend back to the middle Eocene, around 44 Ma (43).

A much younger age for many of the Jebel Qatrani mammal localities helps to make sense of other faunal patterns documented in the later Paleogene of Afro-Arabia. For instance, the
recently described late Oligocene paenungulates (hyracoids, embrithopods, and proboscideans) from Chilga, Ethiopia, bear great overall similarity to the paenungulates from the Jebel Qatrani Formation despite having been radioisotopically and magnetostatigraphically dated to Chron C9n (∼28–27 Ma) (44). Indeed, as noted by Salders et al. (ref. 45), the similarity between the Chilga and Fayum mammals “is remarkable in light of their tremendous differences in geological time, distance, and elevation.” However, the great temporal gap that was thought to separate these faunas largely disappears under the magnetostatigraphic correlation proposed here. Quarries such as I and M are probably only ∼2 Ma older than the Chilga localities (and not ∼5.5 Ma older, as previously thought), and the very youngest localities in the Jebel Qatrani Formation might be <1 Ma older than the oldest mammals from the Chilga region. Therefore, the unique proboscidean groups documented at Chilga, such as deinotheriods and gomphotheriods, probably did not appear suddenly in the short amount of time separating the Fayum and Chilga beds but rather are missing from the Fayum area for environmental reasons. This hypothesis is consistent with phylogenetic analyses that imply a long ghost lineage for deinotheriids in Af tro-Arabia (46, 47).

Meaningful inferences about evolutionary patterns in the mammalian fossil record and the possible links of such phenom-
ena to changes in global climate cannot be made until the fossil mammals of interest can be confidently situated on the global time scale. Unfortunately, the ages of many important Paleogene Afro-Arabian mammal faunas, such as those from Chambi (48) in Tunisia and the Hammadou du Dra region of Algeria (49), remain very poorly constrained, and this problem continues to hinder our understanding of early mammalian evolution in Africa. However, the precise dating of the Chilga mammal localities (44) and the recent discovery of a middle Eocene mammal fauna in Morocco (Aznaq) that can be dated to 45.8–43.6 Ma based on associated foraminifera (50) represent major improvements to this situation. Placement of the Fayum and Dhofar mammals into an internally consistent biochronostatigraphic framework represents another major advance of the utmost importance, for this revised chronology will inform all future analyses of the taxa from these, the richest of all Paleogene Afro-Arabian mammal localities.

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