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Indications for a humid climate in the Western Desert of Egypt 11–10 Myr ago: evidence from Galagidae (Primates, Mammalia)

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Abstract

The timing of desertification of the Sahara Desert is poorly understood, with recent estimates indicating an onset of hyper-aridity during the Latest Miocene. Field work in Egypt in 2005 has led to the discovery of evidence that indicates that 11–10 Ma the Western Desert was covered in woodland. Fossiliferous cave breccia at Sheikh Abdallah, Western Desert, Egypt, has yielded a Late Miocene (11–10 Ma) microvertebrate fauna, which contains Galagidae, Microchiroptera, Macroscelididae, Soricidae, Erinaceidae, and Rodentia. The locality also yielded the remains of frogs, snakes, lizards, and birds. The fauna indicates a mean annual rainfall in excess of 500 mm and perhaps as much as 1,200 mm. This palaeoclimatic information is important because it reveals that the Sahara Desert, which is today the largest in the world, was either considerably smaller during the Late Miocene than it is today, or that it did not yet exist as a continuous hyper-arid belt right across the continent. This data accords with estimates of a Latest Miocene (8–7 Ma) increase in aridity in the Sahara. ***To cite this article: M. Pickford et al., C. R. Palevol 5 (2006)***.

Résumé

Climat humide dans le désert Libyque d'Égypte il y a 11 à 10 millions d'années : mise en évidence des Galagidae (Primates, Mammalia). La chronologie de la désertification du désert du Sahara est mal connue, mais des travaux récents suggèrent un début d'hyperaridité au cours du Miocène supérieur. La découverte récente de restes fossiles en Égypte a permis de montrer que le désert Libyque était couvert d'une prairie boisée il y a 10 à 11 Ma. C'est sur le site de Sheikh Abdallah que furent trouvées des brèches renfermant une microfaune du Miocène supérieur, composée de Galagidae, de Microchiroptera, de Macroscelididae, de Soricidae, d'Erinaceidae et de Rodentia. On peut également signaler la présence de grenouilles, de lacertiliens et d'oiseaux. La faune indique que la moyenne des précipitations annuelles devait être supérieure à 500 mm et peut-être atteindre

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1200 mm. Ceci indique que le désert du Sahara, aujourd'hui le plus grand du monde, était, ou bien plus réduit au Miocène supérieur qu'il ne l'est aujourd'hui, ou bien qu'il ne formait pas une ceinture hyperaride continue à travers le continent. Ces données concordent avec l'hypothèse d'un accroissement en aridité du Sahara au Miocène terminal (8–7 Ma).

Keywords: Egypt; Galagidae; Late Miocene; Palaeoclimate; Sahara; Western Desert

Mots clés : Égypte ; Galagidae ; Miocène supérieur ; Paléoclimat ; Sahara ; Désert occidental

Version française abrégée

Introduction

L'origine de l'établissement des conditions arides dans le Sahara est mal connue, mais il est admis qu'il devint hyperaride vers 8–7 Ma [19,21]. En revanche, le désert de Namib en Afrique australe est bien plus vieux [21,22,26,27,29,30], aux alentours de 17–16 Ma. La découverte de micromammifères du Miocène supérieur dans le désert Libyque en Égypte jette une lumière nouvelle sur son paléoenvironnement.

La faune des dépôts karstiques de Sheikh Abdallah se corrèle avec la zone MN 9 de la zonation mammalienne européenne, âgée de 11–10 Ma environ [9,17]. Parmi les fossiles récoltés sur le site, il faut signaler plusieurs restes de galagidés.

Paléontologie des galagidés

Les galagidés du Miocène supérieur sont très mal connus ; les seules localités qui ont livré des restes de la famille sont connues en Namibie (10 Ma) [4,5] et au Kenya (6 Ma) [18]. La famille est mieux représentée dans le Miocène moyen et inférieur d'Afrique orientale, avec de nombreuses espèces du genre *Komba* [6,11,12,16,31,33,34]. Les galagidés sont également présents dans les niveaux plio-pléistocènes d'Afrique orientale, avec une espèce de grande taille appartenant au genre *Galago* [32,34,36]. On les connaît aussi dans l'Oligocène inférieur d'Égypte, où le genre *Saharagalago* est le plus ancien représentant connu de la famille [28].

Considérations phylogénétiques

À la p4, le métaconide de petite taille est proche du protoconide, rappelant la morphologie observée chez *Galago senegalensis* et *Galago alleni* [13]. La canine inférieure et la M3 rappellent également plutôt celles de *Galago senegalensis* que de *Galagoides demidovii*. Des métaconides de grande taille sont présents aux p4 chez les galagidés du Miocène inférieur et moyen [16], mais ils sont réduits ou absents chez les fossiles pliocènes [35] et chez l'espèce actuelle d'*Otolemur* [25]. Les autres genres de galagidés modernes (*Euoticus*, *Galagoides*) présentent généralement un métaconide proéminent, bien isolé du protoconide aux p4, suggérant ainsi que sa perte ou sa réduction chez *Otolemur* représente une condition dérivée. Les restes postcrâniens sont typiques de *Galago* [7,8]. L'ensemble des fossiles donne un cadre pour l'interprétation des analyses moléculaires des galagidés actuels (*Galagoides*, *Galago*, *Euoticus*, *Otolemur*) [14] et impose des contraintes sur les temps de divergence de ces genres [15]. Les galagidés fossiles de Sheikh Abdallah sont attribués à une nouvelle espèce, *Galago farafraensis*.

Paléoclimatologie

Les galagidés sont aujourd'hui restreints à l'Afrique sub-saharienne [37]. Toutes les espèces sont nocturnes et arboricoles, les espèces de petite taille étant principalement insectivores et gommivores [1], alors que les espèces plus grandes consomment aussi des fruits, des insectes et de petits vertébrés [2,3,10]. *Galago senegalensis* est l'espèce la mieux adaptée pour survivre dans des conditions semi-arides, comme l'atteste sa distribution dans toute la zone sub-saharienne. Toutefois, comme les autres espèces de galagidés, il requiert la présence d'arbres, qui offrent des exsudats dont il se nourrit, des cavités où il dort pendant le jour et construit ses nids pendant la saison de reproduction. L'espèce peut habiter les zones ripariennes où les précipitations annuelles sont réduites à 300 mm en moyenne, mais elles nécessitent généralement des précipitations annuelles d'au moins 500 mm (Fig. 6). Dans un cas comme dans l'autre, il apparaît que le désert occidental était bien plus humide il y a environ 11–10 Ma qu'il ne l'est aujourd'hui. Les galagidés sont des primates nocturnes de petite taille qui dépendent des arbres où ils trouvent nourriture et refuge. Leur présence dans le Miocène supérieur du désert Libyque d'Égypte atteste des conditions dans la région beaucoup plus humides aux alentours de 11–10 Ma qu'elles ne le sont aujourd'hui. Les fossiles suggèrent donc que le Sahara devint hyperaride un peu après 9 Ma, confirmant les estimations avancées auparavant (8 à 7 Ma) [20–22,24,29,30].

Conclusions

Les galagidés du Miocène supérieur des dépôts karstiques de Sheikh Abdallah appartiennent à une espèce nouvelle de petite taille, *Galago farafraensis*. La présence de galagidés fossiles dans le désert occidental indique que la région était beaucoup plus humide il y a environ 11–10 Ma qu'il ne l'est aujourd'hui. Ceci apporte une contrainte chronologique sur l'établissement au Sahara de l'hyperaridité, qui semble s'être mise en place vers la fin du Miocène supérieur.

1. Introduction

The timing of the onset of desert conditions in the Sahara is poorly constrained, with a consensus emerging that it became hyper-arid by about 8–7 Ma [19–21]. In contrast, the Namib Desert of southwestern Africa is considerably older [21,22,26,27,29,30], hyper-arid conditions setting in between 17 and 16 Ma. Given the paucity of geochronological data upon which to base the palaeoclimatic evolution of the Sahara, the discovery of Late Miocene micromammals in the Western Desert, Egypt, is important not only for the biochronological data that they yield, but also for the palaeoenvironmental evidence.

The karst deposits at Sheikh Abdallah, between Farafra and Baharia Oases (Fig. 1) [9], have yielded well over 1000 dental specimens of micromammals, rodents for the most part, which provide good evidence as to the age of the infillings. The fauna correlates with MN 9 of the European and North African mammal zonation, which is considered to be between 11 and 10 Ma [17]. Among the fossils retrieved from Sheikh Abdallah are several teeth and post-cranial bones of at least two individuals of galagid. Galagids are small nocturnal primates that are dependent upon trees for food and shelter. Their presence in the Late Miocene deposits of the Western Desert, Egypt, provides sound evidence that the region was considerably more humid 11–10 Ma than it is today. As such the fossils suggest that the Sahara became hyper-arid somewhat later than 9 Ma, in support of previous estimates of an origin between 8 and 7 Ma [20,24].

Fig. 1. Red sandy karst deposits infilling a Late Miocene cave system eroded into Cretaceous or Palaeogene chalk [23] at Sheikh Abdallah, Western Desert, Egypt.
Fig. 1. Remplissage de sables rouges dans un réseau de grotte du Miocène supérieur, creusé dans la craie crétacée ou paléogène [23] à Sheikh Abdallah, dans le désert Libyque d'Égypte.

2. Taphonomy

The Sheikh Abdallah fossils are concentrated in calcified quartz sands that accumulated in a cave eroded into Cretaceous or Palaeogene Chalk [9,23]. The assemblage consists exclusively of small vertebrates, predominantly rodents, but with a range of mammals, birds, reptiles and anurans (Fig. 2). The fact that many of the bones are complete indicates that the concentrations were not made by a carnivore but more likely represent disaggregated regurgitation pellets of owls.

Fig. 2. Cave breccia from Sheikh Abdallah in the process of acid preparation, rich in the remains of micromammals.
Fig. 2. Préparation à l'acide des brèches riches en restes de micromammifères provenant de Sheikh Abdallah.

Galagids are small nocturnal primates, and the main predators of the smaller species comprise owls, genets, palm civets and snakes [10]. During the daylight hours, galagids are extracted from their sleeping holes in trees by goshawks, which have elongated lower leg elements, with a hyper-extensible proximal tarso-metatarsal joint. However, goshawks are diurnal and at night they perch in trees and do not generally enter caves. For these reasons, it is considered likely that the Sheikh Abdallah galagids represent the prey of owls.

3. Galagid palaeontology

Late Miocene galagids are extremely poorly known, the only localities that have yielded the family being in Namibia (10 Ma) [4,5] and Kenya (6 Ma) [18], where isolated teeth have been found, but which throw little light on galagid evolution. The family is better known from Early and Middle Miocene deposits in East Africa (various *Komba* species) [6,11,12,16,31–34]. They are also represented in Plio-Pleistocene levels in East Africa (large *Galago* species) [32,35,36]. Early Oligocene fossils (*Saharagalago*) from Egypt [28] are the earliest known representatives of the family.

There are lengthy gaps in the galagid fossil record, which makes the Late Miocene Sheikh Abdallah occurrence particularly valuable, since it helps to fill what was a 10-million-year gap in galagid evolutionary history, between Middle Miocene *Komba* on the one hand, and Plio-Pleistocene *Galago* on the other. Its dimensions are close to those of extant *Galagoides demidovii*, but it has dental morphology (lower p/4 metaconid reduced in size and close to protoconid, reduced size of metaconule and paraconule in the upper molars) more like that of *Galago senegalensis*, suggesting that the latter genus was already in existence ca 10 Myr. This possibility, if valid, provides constraints for the interpretation of molecular analyses of extant galagid genera (*Galagoides*, *Galago*, *Euoticus*, *Otolemur*) [14] and may provide constraints on the timing of the splits between the various genera [15].

4. Systematic description

Order Primates Linnaeus, 1758
Infraorder Lorisiformes Gregory, 1915
Family Galagidae Mivart, 1864
Genus *Galago* Geoffroy, 1796
Species *Galago farafraensis* nov.

Diagnosis: Minute species of *Galago* similar in size to *Galagoides demidovii*, but with metaconid on p/4 reduced in size and closely applied to the protoconid, metaconules and paraconules in upper molars reduced or indiscernible, hypocone of M3/ reduced, with triangular occlusal outline.

Derivatio nominis: The species name is for Farafra Oasis, 90 km south of Sheikh Abdallah.

Holotype: SA 1′05, right P4/ (Figs. 3, 4).

Referred material: SA 2′05, right M1/; SA 3′05, right M2/; SA 4′05, right M3/; SA 5′05, left P4/; SA 6′05, left M1/; SA 7′05, right lower canine; SA 8′05, right p/4; SA 9′05, right m/1; SA 10′05, right m/3; SA 11′05, right m/3 talonid; SA 12′05, left talus (Fig. 3); SA 13′05, distal femur (Fig. 5); SA 14′05, terminal phalanx (Fig. 5); SA 15′05, terminal phalanx (Fig. 5).

Type locality: Sheikh Abdallah, Western Desert, Egypt, mid-way between Baharia and Farafra Oases.

Age: Late Miocene, MN 9, ca 11–10 Ma.

Description: Dental terminology is based on Schwartz & Tattersall [25] and Maier [13].

4.1. Lower dentition

The lower canine possesses a central lingual ridge and clear anterior and posterior cingula and a curved burin-like apex, which is similar in morphology to that of *Galago senegalensis* and *G. alleni*. It is unlike the blade-like lower canine lacking cingula of *Euoticus elegantulus*. The canine crown height is 2.5 mm. In the p/4 the metaconid is close to the protoconid and slightly lower than it (Fig. 4, G1), unlike the widely separated metaconid that occurs in *Galagoides* and the much reduced metaconid that occurs in *Otolemur*. In the m/1 the trigonid is reduced in mesiodistal length due to the tiny dimensions of the paraconid, but it is high, and the talonid is low. In the m/3, the trigonid is high with a reduced basin, the talonid is low but long, the hypoconulid being well separated from the entoconid and hypoconid, the floor of the talonid basin is smooth, and not deeply indented (pit-like) as in *Galagoides demidovii*. In these respects the m/3 is similar to those of *Galago senegalensis* and *G. alleni*, but the talonid is more elongated in *G. farafraensis*.

4.2. Upper dentition (Table 1)

The paraconule and metaconule in the upper P4/ and the anterior two molars are reduced in stature, as in *G. senegalensis* unlike the prominent conules that occur in *Galagoides demidovii*. In the P4/, M1/ and M2/, the postmetacrista descends bucco-distally as in

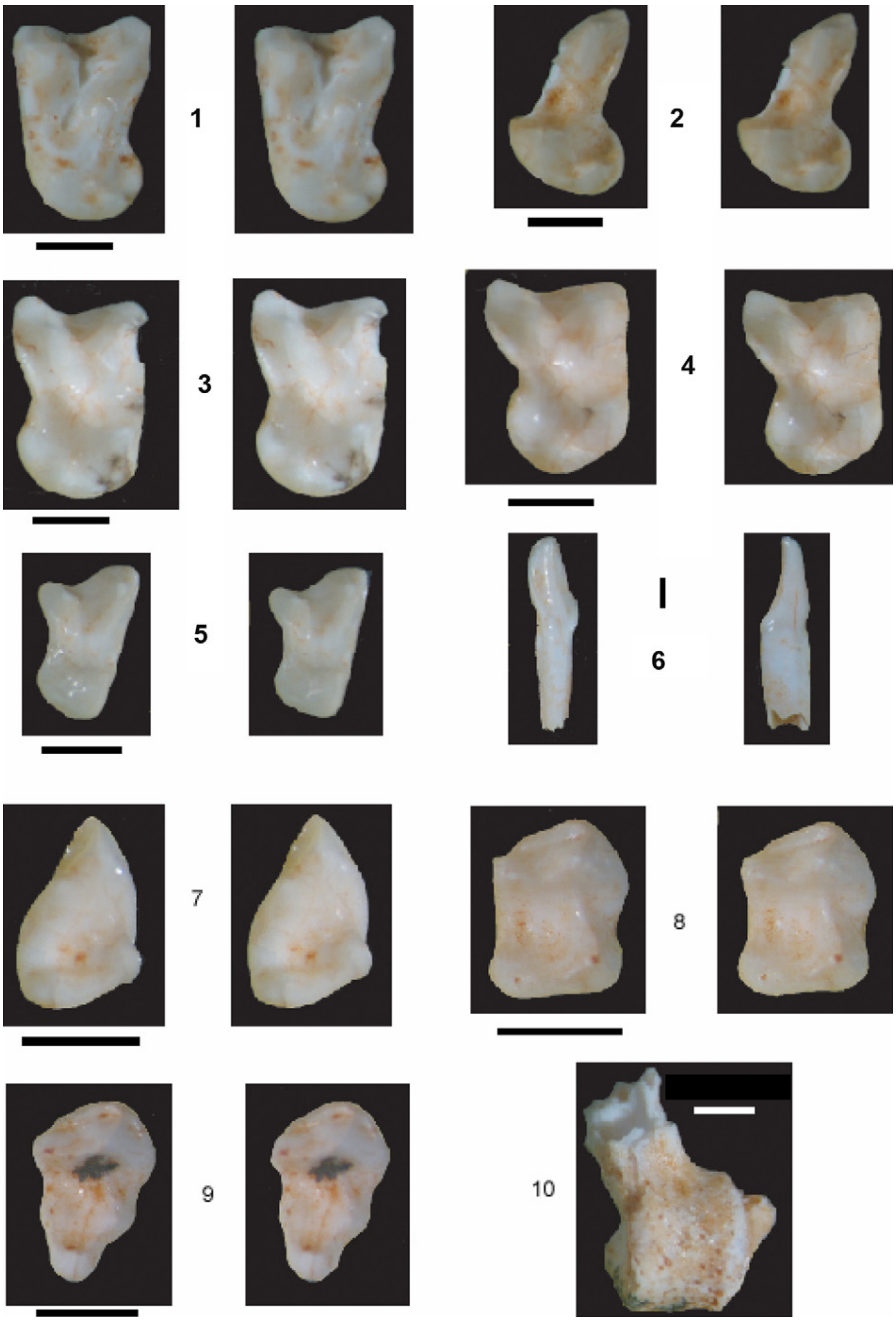

Fig. 3. *Galago farafraensis* sp. nov. dental and postcranial remains from Sheikh Abdallah, Late Miocene (MN 9) Western Desert, Egypt (stereo pairs, scales: 1 mm). (**1**) SA 2′05, right M1/, (**2**) SA 5′05, left P4/, (**3**) SA 3′05, right M2/, (**4**) SA 1′05, right P4/ (holotype), (**5**) SA 4′05, right M3/, (**6**) SA 7′05, right c/1, (**7**) SA 8′05, right p/4, (**8**) SA 9′05, right m/1, (**9**) SA 10′05, right m/3, (**10**) SA 12′05, left talus.

Fig. 3. Restes dentaires et postcrâniens de *Galago farafraensis* sp. nov. provenant de Sheikh Abdallah, Miocène supérieur (MN 9) du désert Libyque d'Égypte (stéréophotos, échelles : 1 mm). (**1**) SA 2′05, M1/ droite, (**2**) SA 5′05, P4/ gauche, (**3**) SA 3′05, M2/ droite, (**4**) SA 1′05, P4/ (holotype) droite, (**5**) SA 4′05, M3/ droite, (**6**) SA 7′05, c/1 droite, (**7**) SA 8′05, p/4 droite, (**8**) SA 9′05, m/1 droite, (**9**) SA 10′05, m/3 droite, (**10**) SA 12′05, astragale gauche.

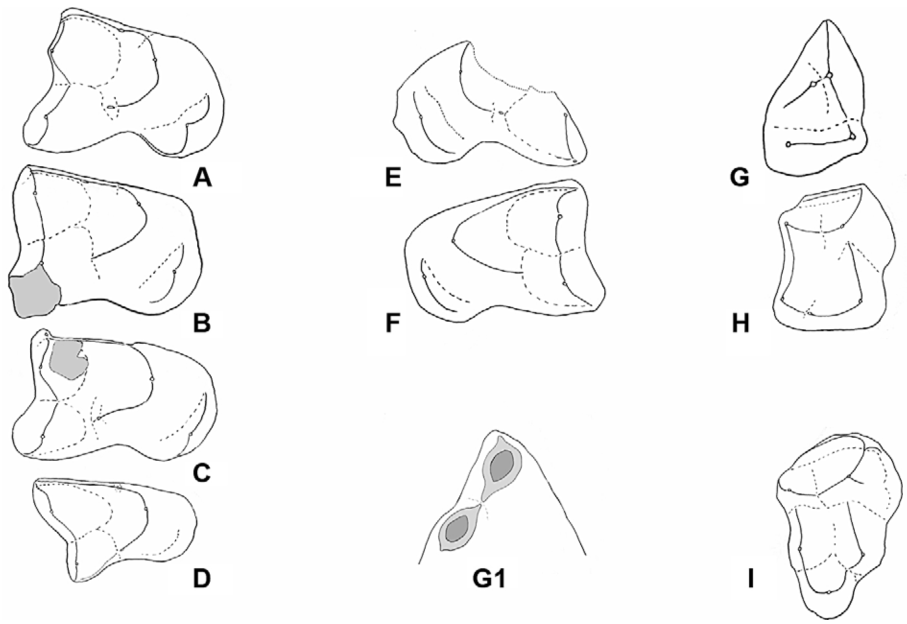

Fig. 4. *Galago farafraensis* sp. nov. interpretive drawings of dental remains from Sheikh Abdallah, MN 9, Western Desert, Egypt. (**A**) right P4/, (**B**) right M1/, (**C**) right M2/, (**D**) right M3/, (**E**) left P4/, (**F**) left M1/, (**G**) right p/4, (**G1**) detail of protoconid and metaconid of right p/4, (**H**) right m/1, (**I**) right m/3.

Fig. 4. Dessins interprétatifs des restes dentaires de *Galago farafraensis* sp. nov. provenant de Sheikh Abdallah, MN 9, désert Libyque d'Égypte. (**A**) P4/ droite, (**B**) M1/ droite, (**C**) M2/ droite, (**D**) M3/ droite, (**E**) P4/ gauche, (**F**) M1/ gauche, (**G**) p/4 droite, (**G1**) détail des protoconide et métaconide de la p/4 droite, (**H**) m/1 droite, (**I**) m/3 droite.

Galago senegalensis rather than buccally as in *Galagoides*. Cristae on buccal cusps are sharp and the valley between the protocone and hypocone is wide and smooth. There are no signs of buccal cingula. The M2/ has a large re-entrant distally and the M3/ is triangular in occlusal outline, bucco-lingually broader than the mesio-distal length and it has a reduced hypocone, unlike the enlarged hypocone in *Galagoides*. The M3/ is appreciably smaller than the M2/ but is not as reduced as it is in *G. senegalensis* and *G. alleni*.

4.3. Postcranial bones

The postcranial bones are typically galagid in morphology [7,8], but are extremely small. They compare in dimensions with those of *Galagoides demidovii.* The breadth of the distal epiphysis of the femur is 5 mm (Fig. 5), which compares with a range of 4.3–4.7 mm in *Galagoides demidovii*, 7.5–9.6 in *Galago senegalensis,* 8.2 mm in *Galago moholi,* 12 mm in *Otolemur crassicaudatus* and 12.5 mm in *Otolemur garnetti.* The trochlea of the talus (Fig. 3) has a dorsal breadth of 2 mm. The terminal phalanges are morphologically similar to those of galagids in general but are very small (Fig. 5). They possess well developed apical tufts and robust proximal epiphyses with slender diaphyses.

5. Phylogenetic considerations

The dentition of the Sheikh Abdallah galagid is closest metrically to that of the extant dwarf galago, *Galagoides*, but there are several morphological features that indicate closer affinities with the genus *Galago*. The fossils have a small metaconid on the p/4, which is close to the protoconid similar to the situation in *Galago senegalensis* and *Galago alleni*, a structure that is much larger and more offset from the protoconid in *Galagoides demidovii*. Similarly the morphology of the lower canine and the upper M3/ of the Sheikh Abdallah species is closer to the species *Galago senegalensis* than to *Galagoides demidovii*. Large metaconids are present in the p/4s of Early and Middle Miocene galagids [16] but are reduced or absent in Pliocene [35] and extant species of *Otolemur* [25]. Other genera of extant galagids (*Euoticus*, *Galagoides*) generally possess a prominent p/4 metaconid well set off from the protoconid, suggesting that its loss or reduction in *Otolemur* species represents a derived condition.

Fig. 5. *Galago farafraensis* sp. nov. postcranial remains from Sheikh Abdallah, MN 9, Western Desert, Egypt. (**A**–**C**) SA 13′05 right femur, (**A**) anterior view, (**B**) distal view, (**C**) posterior view, (**D**–**E**) SA 14′05 terminal phalanx (**D**) volar view, (**E**) dorsal view, (**F**–**G**) SA 15′05 terminal phalanx, (**F**) volar view, (**G**) dorsal view (scale for femur: 5 mm, for phalanges: 1 mm).

Fig. 5. Restes postcrâniens de *Galago farafraensis* sp. nov. provenant de Sheikh Abdallah, MN 9, désert Libyque d'Égypte. (**A**–**C**) SA 13′05 fémur droit, (**A**) vue antérieure, (**B**) vue distale, (**C**) vue postérieure, (**D**–**E**) SA 14′05 phalange distale, (**D**) vue palmaire, (**E**) vue dorsale, (**F**–**G**) SA 15′05 phalange distale, (**F**) vue palmaire, (**G**) vue dorsale (échelle pour le fémur : 5 mm, échelle pour les phalanges : 1 mm).

Because of the morphological similarities of the fossils to extant *Galago senegalensis* and *G. alleni* we prefer to place it in the genus *Galago*, but on account of its diminutive size, it represents a new species, about 60% of the linear dimensions of *Galago senegalensis*.

6. Palaeoclimatology

At present, galagids are restricted to Africa south of the Sahara [37], their most northerly record being 16°N in Sierra Leone, and 15°N in the Nile valley, Sudan, and 2° to 5° of latitude closer to the equator in between [3]. All species are nocturnal and arboreal, with smaller species being predominantly insectivorous and gumivorous [1], but seasonally also eating fruit, while the larger species include greater quantities of fruit in their diet, but also consume insects and small vertebrates [2,3,10]. *Galago senegalensis* is the species that is currently the best adapted to surviving in semi-arid conditions, and it ranges right across semi-arid Africa immediately south of the Sahara. However, like all other galagids, it requires the presence of trees, not only for the exudates that comprise an essential part of its diet, but also for the holes in which it sleeps during the day, and builds its nests during the breeding season. In areas with sufficient groundwater, such as riparian settings, which favour the growth of trees even in deserts, the species can occur in areas with as

Table 1
Dimensions (in mm) of the teeth of *Galago farafraensis* sp. nov. from Sheikh Abdallah, Egypt
Tableau 1
Dimensions (en mm) des dents de *Galago farafraensis* sp. nov. provenant de Sheikh Abdallah, en Égypte

Catalogue N°	Tooth	Mesio-distal length	Bucco-lingual breadth
SA 1′05	Right P4/	1.6	2.2
SA 2′05	Right M1/	1.8	2.4
SA 3′05	Right M2/	1.8	2.3
SA 4′05	Right M3/	1.3	2.1
SA 5′05	Left P4/	—	2.3
SA 6′05	Left M1/	1.8	2.5
SA 7′05	Right c/1	1.1	0.6
SA 8′05	Right p/4	1.6	1.0
SA 9′05	Right m/1	1.5	1.2

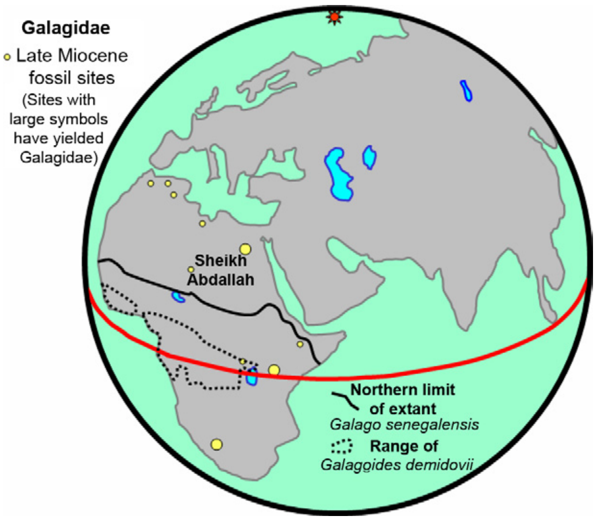

Fig. 6. Distribution of extant and Late Miocene Galagidae.
Fig. 6. Répartition des Galagidae actuels et du Miocène supérieur.

little as 300 mm mean annual rainfall, but removed from these riparian environments, the species requires a mean annual rainfall of at least 500 mm (Fig. 6).

Because the Sheikh Abdallah galagid is closest in size to extant *Galagoides demidovii*, rather than to species of *Galago* such as *G. senegalensis*, it is possible that the palaeoenvironment at the time of deposition could have been more humid than the minimum mean annual rainfall deduced above. This is suggested by the fact that at present, *Galagoides demidovii* ranges through tropical African habitats with more than 1,200 mm mean annual rainfall [10]. However, because the Egyptian fossils show morphological affinities with the genus *Galago*, such as reduction of the size of the p/4 metaconid and diminution of the metaconule and paraconule in the upper molars, it is possible that it survived in somewhat drier environments. Whatever the case, it is clear that the Western Desert of Egypt was considerably more humid 11–10 Myr ago than it is today.

7. Conclusions

The galagids from the basal Late Miocene karst deposits at Sheikh Abdallah belong to a diminutive new species, *Galago farafraensis*. The presence of galagid fossils in the Western Desert indicate that the region was considerably more humid 11–10 Ma than it is today. This discovery provides constraints on the timing of the onset of hyper-aridity in the Sahara which most likely occurred towards the end of the Late Miocene.

Acknowledgements

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