General Palaeontology (Palaeontology)

Early Pliocene Tragulidae and peafowls in the Rift Valley, Kenya: evidence for rainforest in East Africa

Presented by Yves Coppens

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Abstract

The Early Pliocene Mabaget Formation (5.3–4.5 Ma), Tugen Hills, Kenya, has yielded remains of the African tragulid *Hyemoschus aquaticus*, which is today confined to rainforests of West Africa and the Congo Basin as far east as western Uganda. The same unit has also yielded a peafowl, *Pavo* sp. The Mabaget Formation has yielded early hominid fossils variously attributed to *Australopithecus praegens* or *Ardipithecus ramidus*. This sedimentary deposit joins the list of very early hominid units that preserve evidence of forest in the vicinity of the basin at the time of deposition. This discovery adds weight to the suggestion that the earliest hominids inhabited well wooded to forested regions rather than open country. It now seems more likely that bipedalism evolved in wooded to forested ecosystems and was, for several million years, linked to arborealism and that only after it was perfected did hominids spread into more open environments as fully functional bipeds. If so, then there is no reason to postulate a quadrupedal 'knuckle-walking' stage in the evolution of hominids. *To cite this article: M. Pickford et al., C. R. Palevol (2004).*
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Résumé

Un Tragulidae et des paons dans le Pliocène basal de la vallée du Rift kenyan : preuve d'une forêt tropicale humide en Afrique orientale. La formation de Mabaget (collines Tugen, Kenya), datée du Pliocène basal (5,3 à 4,5 Ma), a livré des restes du tragulidé africain *Hyemoschus aquaticus*, aujourd'hui confiné aux forêts humides de l'Afrique de l'Ouest et du bassin du Congo, et dont la répartititon s'étend jusqu'à l'Ouest de l'Ouganda. Dans cette même formation ont été découverts des restes de paons (*Pavo* sp.) ainsi que des hominidés fossiles attribués à *Australopithecus praegens* ou *Ardipithecus ramidus*. Les sites de la formation de Mabaget complètent la liste des sites à hominidés très anciens, à proximité desquels des forêts existaient au

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moment du dépôt. Cette découverte renforce l'hypothèse selon laquelle les hominidés anciens auraient évolué plutôt dans des habitats forestiers ou bien boisés que dans des environnements de pays ouvert. Elle montre également que la bipédie de type humain se serait développée dans des écosystèmes boisés à forestiers : pendant des millions d'années, la bipédie a été associée à l'arboricolie et ce n'est qu'après son perfectionnement que les hominidés, bipèdes complètement fonctionnels, se seraient déployés dans des milieux plus ouverts. ***Pour citer cet article : M. Pickford et al., C. R. Palevol (2004).***
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Version française abrégée

1. Introduction

Depuis 1998, la *Kenya Palaeontology Expedition* a découvert des restes de Tragulidae à Mosionin (en 1998) et Tabarin (en 2003), et un paon à Sagatia, toutes des localités de la formation pliocène de Mabaget (5,3–4,5 Ma), situées au pied des collines Tugen, dans le Nord du Kenya. Ces découvertes sont très importantes, car elles prouvent la présence d'une forêt tropicale humide au moment du dépôt et confirment que les hominidés, qui sont connus dans cinq localités de la formation, sont associés à des paléoenvironnements forestiers.

2. Géologie et datation

La formation de Mabaget (Fig. 1) (appelée précédemment formation de Chemeron – Northern Extension [30]) recouvre les trachytes et les basaltes de la formation Kaparaina, dont le sommet est âgé de 5,3 Ma environ. Les ignimbrites et les cendres volcaniques de la formation de Mabaget ont livré des âges de 5,3 Ma et 4,3 Ma [6,30]. Ces dépôts volcanogéniques encadrent les principaux niveaux fossilifères, qui contiennent une faune abondante et variée incluant des hominidés anciens, dont l'âge est estimé compris entre 5,3 et 4,5 Ma. Cette date est légèrement plus ancienne que celle de 4,49–4,41 Ma, publiée par Deino et al. [6] pour la mandibule de l'hominidé de Tabarin [12]. Les hominidés fossiles ont maintenant été reconnus dans six localités de la formation de Mabaget; Mabaget [30,41], Pelion, Tabarin [12], Ngetabkwony, Sagatia et Tabarin North. Toutes ces localités sont situées dans la partie basale de la formation. Des restes de tragulidé ont été également trouvés à ce niveau, mais dans des sites de

Mosionin et Tabarin, ainsi qu'un paon dans le gisement de Sagatia.

3. Le tragulidé de Mosionin et de Tabarin

Le tragulidé de Mosionin est connu par une M^1 (BAR 21'98) non usée, à laquelle il manque le métacône (Fig. 2(1)), et celui de Tabarin par une deuxième incisive droite (BAR 2236'03), également non usée (Fig. 2(2)).

Le protocône de M^1 (longueur mésio-distale : 8 mm; largeur bucco-linguale : 9,5 mm) est brachysélénodonte, avec un cingulum buccal proéminent et acéré qui s'étend jusque sur la face antérieure de la cuspide. La crête antérieure du protocône s'étend buccalement et rejoint le style antérieur du paracône. La crête postérieure du protocône se termine au milieu de la couronne et ne rejoint pas la crête antérieure de l'hypocône. Le paracône est conique, avec des styles forts, l'antérieur étant en outre assez bas et le postérieur faible. Il présente une crête antérieure forte, qui s'étend de l'apex de la couronne au style antérieur courant parallèlement à une gouttière antéro-linguale, qui se termine à la base du style antérieur sur son bord buccal. L'hypocône est brachysélénodonte ; son cingulum distal s'étend vers le bord lingual, où il forme un faible renflement vers le collet. La crête antérieure de l'hypocône traverse la couronne et se termine à la base du métacône ; toutefois, elle n'atteint pas la crête postérieure du paracône. La crête postérieure de l'hypocône prend fin à la base du métacône. L'émail est faiblement ridulé. Les deux racines linguales sont fusionnées sur toute leur longueur, la distale étant plus petite que la mésiale (Fig. 2(1c)), comme c'est généralement le cas sur les M^1 du genre, les M^3 possédant souvent de très courtes racines, surtout la distale qui peut même être absente.

L'incisive inférieure de Tabarin, à couronne longue et étroite, présente une courbure distincte, située à environ un tiers du collet vers l'apex (Fig. 2(2a–e)). La couronne est légèrement comprimée labio-lingualement. Sur sa face linguale, on observe une crête verticale forte, issue d'un tubercule basal qui se termine près de l'apex de la dent ; par ailleurs, les bords mésial et distal sont renforcés par de fortes crêtes. La surface labiale est mousse et relativement plate. La racine, à section circulaire, est longue (5,6 mm). La couronne mesure 1,4 mm mésio-distalement, 1,6 mm labio-lingualement et 4,9 mm de hauteur.

Les comparaisons effectuées avec les incisives d'autres ruminants actuels ont montré que la dent est très proche morphologiquement et métriquement des i/2 du chevrotain d'eau, *Hyemoschus aquaticus* (Fig. 2(3)). Elle diffère des i/3 et de la canine des Tragulidae, qui présentent des couronnes à courbure continue et non pas à inclinaison brutale (Fig. 2(3)). La i/1 des Tragulidae est spatulée, avec une dépression distale dans laquelle vient se loger la couronne inclinée de la i/2 (Fig. 3). Les Bovidae, tels que *Ourebia* et *Cephalophus*, possèdent des i/2 dont les couronnes ne sont pas très spatulées, rappelant superficiellement celles des Tragulidae, mais l'inclinaison de la couronne se situe au niveau du collet et non pas au milieu de celle-ci. Par ailleurs, les crêtes linguales tendent à être moins développées qu'elles ne le sont chez *Hyemoschus*. La plupart des autres Bovidae ont des i/2 qui sont nettement plus spatulées que la dent de Tabarin. On peut ainsi éliminer l'hypothèse de l'attribution de cette dent aux Bovidae.

Par leurs mesures et leurs caractères morphologiques, les dents du tragulidé de Mosionin et de Tabarin tombent dans la variation du tragulidé africain *Hyemoschus aquaticus*. Cette espèce est aujourd'hui confinée aux forêts humides de l'Afrique occidentale, du bassin du Congo jusqu'à l'Ouest de l'Ouganda.

4. Le paon de Mabaget

Les paons actuels comportent deux espèces de grande taille, *Pavo cristatus* et *Pavo muticus*, qui vivent en Asie du Sud et du Sud-Est, et une espèce de petite taille, *Afropavo congensis*, qui vit dans les forêts équatoriales d'Afrique centrale. Deux espèces éteintes ont été décrites en Europe, *Pavo aesculapi* (Gaudry), du Miocène supérieur et du Pliocène inférieur, connu

uniquement en Europe sud-orientale et centrale, et *Pavo bravardi* (Gervais), du Pliocène, connu à la fois à l'Est et à l'Ouest. *Pavo bravardi* est une forme de grande taille, parfois supérieure à celles des espèces actuelles du genre *Pavo*. Il a disparu à la fin du Pliocène, sans doute en raison des premiers grands refroidissements du Pléistocène [2,21,22].

Des restes d'une grande forme de paon ont récemment été signalés en Afrique, dans les gisements d'Aramis 1 et d'Aramis 6, en Éthiopie, datés du Pliocène inférieur [19]. Cette forme est très proche à la fois de l'espèce actuelle *P. muticus* et de l'espèce éteinte *P. bravardi*, et elle a été désignée provisoirement comme *Pavo* sp.

Les restes provenant de la formation de Mabaget sont deux extrémités distales de tibiotarse, une droite et une gauche, provenant sans doute d'un même individu. Ils présentent les caractères morphologiques du genre *Pavo* et leur taille est légèrement inférieure à celle des tibiotarses connus pour l'espèce *P. bravardi*, mais il y a un fort dimorphisme sexuel chez les paons, et leur taille est comprise dans l'intervalle de variation des deux espèces actuelles (on ne peut pas comparer leurs dimensions à celles d'Aramis 1 et 6, car ces restes ne comportent pas de tibiotarses). Leurs dimensions sont très nettement supérieures à celles d'*Afropavo congensis*. On peut également désigner ce matériel comme *Pavo* sp.

La présence d'un paon dans le matériel de la formation de Mabaget a une importante signification paléoécologique. Le paon bleu, *Pavo cristatus*, vit dans les forêts ouvertes, généralement de feuillus, avec une végétation de sous-bois, le long des cours d'eaux. Le paon spicifère, *Pavo muticus*, vit en Thaïlande dans des forêts-galeries et, à Java ; on le trouve dans des forêts ouvertes, ou en bordure de forêt, mais pas au cœur des forêts pluviales équatoriales [7]. On peut en conclure que le milieu correspondant au dépôt des sédiments était un milieu forestier, avec des cours d'eau.

5. Discussion

La formation de Mabaget a livré les restes d'Hominidae attribués à *Australopithecus praegens* ou *Ardipithecus ramidus*. Elle appartient à toute une série de formations renfermant des sites à hominidés très anciens, comme ceux de la formation de Lukeino au

Kenya (6 Ma), ceux de la bordure occidentale de la vallée moyenne de l'Aouache (5,7–5,2 Ma) et d'Aramis (4,2 Ma) en Éthiopie. Dans ces derniers, une forêt était présente à proximité du bassin au moment du dépôt. Les données suggèrent que la région des collines Tugen était très largement recouverte de forêts au Miocène supérieur et à la base du Pliocène, mais ceci n'exclut pas la possibilité de présence de zones localisées de végétation herbacée dans le bassin, comme on l'observe aujourd'hui en Ouganda occidental et au Congo oriental. Ces données supportent l'idée que les hominidés anciens ont habité des régions bien boisées à forestières, plutôt que des zones de savane ouverte. La bipédie semble avoir émergé avant l'expansion des hominidés dans des environnements de savane, ce qui réfute l'hypothèse classiquement admise d'une origine dans la savane où les proto-hominidés auraient pratiqué le *knuckle-walking* avant d'évoluer vers une locomotion bipède. Il semble aujourd'hui plus probable que la bipédie, associée à une composante arboricole, a évolué dans des écosystèmes boisés à forestiers pendant des millions d'années. Il apparaît donc que la bipédie s'est développée dans des environnements de végétation fermée, et ce n'est qu'après avoir perfectionné cette bipédie que les hominidés, complètement bipèdes, auraient conquis des milieux plus ouverts. L'hypothèse d'un précurseur *knuckle-walker* des hominidés semble donc de moins en moins crédible.

1. Introduction

In 1998 and 2003, the Kenya Palaeontology Expedition discovered tragulid remains at Mosionin and Tabarin, Early Pliocene (5.3–4.5 Ma) and a peafowl at Sagatia, all localities in the Mabaget Formation, foothills of the Tugen Hills, northern Kenya. These finds are of great significance as they indicate the presence of tropical forest in the region at the time of deposition. Early hominids, which have been found at six localities in the same formation, are thus associated with forest palaeoenvironments.

2. Geology, stratigraphy and age

The Mabaget Formation (Fig. 1), previously called the Chemeron Formation – Northern Extension) [30],
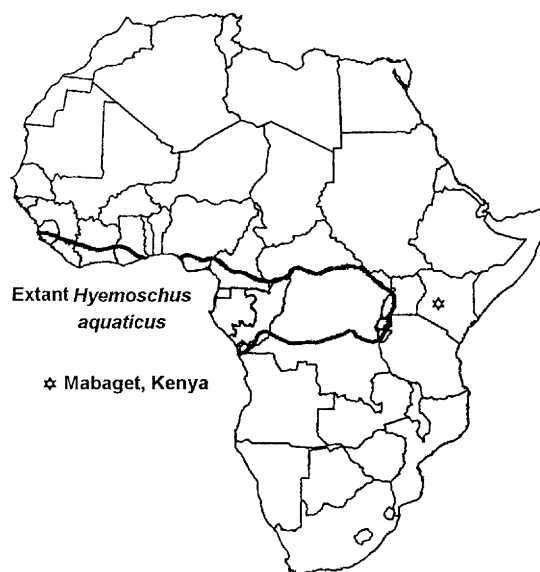

Fig. 1. Pliocene and present-day distribution of *Hyemoschus aquaticus* in Africa.
Fig. 1. Répartition actuelle et pliocène de *Hyemoschus aquaticus* en Afrique.

is underlain by trachytes and basalts of the Kaparaina Formation, the top of which is aged ca 5.3 Ma. Ignimbrites and volcanic tuffs within the Mabaget Formation have yielded ages of 5.3 Ma and 4.3 Ma [6,30]. These volcanogenic deposits respectively underlie and overlie the main fossiliferous levels, which contain a diverse and abundant fauna, including early hominids and an age of between 5.3 Ma and 4.5 Ma is inferred for them. This estimate is slightly older than the age of 4.49–4.41 Ma published by Deino et al., [6] for the Tabarin hominid mandible [12]. Hominid fossils have now been recovered from six separate localities in the Mabaget Formation, i.e. Mabaget [30,41], Pelion, Ngetabkwony, Tabarin [12], Sagatia, and Tabarin North, all in the basal part of the formation. The tragulid specimens were also found at this level, at Mosionin and Tabarin and the peafowl at Sagatia.

3. The Mosionin and Tabarin tragulid specimens

Bar 21'98, from Mosionin, is an unworn left upper M1/ lacking its metacone (Fig. 2(1)) while BAR 2236'03, from Tabarin, is an unworn right second incisor (Fig. 2(2)).

The M1/ is slightly more than 8 mm in mesiodistal length and 9.5 mm in buccolingual breadth (Fig. 1(1)). The protocone is brachyselenodont with a prominent, sharp, lingual cingulum, which extends onto the anterior aspect of the cusp. The anterior crest of the protocone extends buccally and reaches the anterior paracone style. The posterior crest of the protocone ends in the midline of the crown but does not join the anterior crest of the hypocone. The paracone is conical, with strong but low anterior and weak posterior styles, and a prominent anterior crest running from the apex of the cusp to the anterior style paralleling an antero-buccal groove that ends at the base of the anterior style on its buccal side. The hypocone is brachyselenodont with a distal cingulum that extends lingually where it forms a low swelling near cervix. The anterior hypocone crest extends across the crown and ends at the base of the metacone, but it does not reach the posterior crest of the paracone. The posterior crest of the hypocone ends at the base of the metacone. The enamel is lightly wrinkled. The two lingual roots are fused throughout their length, the distal root being smaller than the mesial one (Fig. 2(1c)), as is typical of M1/s of the genus, the M3/ often having very short roots, especially the distal one, which may even be absent.

The Mosionin molar differs from those of *Dorcatherium* species in its more selenodont cusps, but most importantly by the orientation of the posterior crest of the protocone. In European and African *Dorcatherium* species similar in size to or slightly larger than *Hyemoschus aquaticus*, this crest is oriented directly distally [28,50], whereas in *Hyemoschus* and the Mosionin tooth it is directed disto-buccally. Furthermore, at its termination there is a tiny swelling that, with wear, gives a curved appearance to the crest, more evident in worn teeth than in unworn ones. Thus, the Mosionin tooth is much closer morphologically to *Hyemoschus* than to *Dorcatherium* or other Miocene tragulids such as *Dorcabune* [33] and *Siamotragulus* [44] or extant ones such as *Tragulus*.

Comparison of measurements of the upper molars of *Hyemoschus aquaticus* with the fossil from Mosionin shows that it falls within the range of metric variation of the upper first molars of the extant species (Fig. 3). Because the Mosionin tooth is close in size and morphology to the upper first molars of *Hyemoschus aquaticus*, we assign it to this species. This is the first record of fossil *Hyemoschus* in Africa. Tragulidae are common in Early and Middle Miocene deposits of Africa [27,28], but they have all been attributed to the genus *Dorcatherium*, which is close to *Hyemoschus* in many features, although the dentition of the former genus seems to be slightly more bunoselenodont.

The second lower incisor from Tabarin has a long, narrow crown with a distinctive bend one third of the distance from cervix to apex (Fig. 2(2a–e)). The crown is slightly compressed labio-lingually with a prominent lingual ridge that emanates from a low basal tubercle and ends near the apex of the tooth (Fig. 2(2e)). On the lingual side of the crown, the mesial and distal edges are marked by sharp crests. The labial surface is smooth and relatively flat. The root is long and circular in section. The crown is 1.4 mm mesio-distally, 1.6 mm labio-lingually, the crown is 4.9 mm high and the root is 5.6 mm long.

Comparisons with extant ruminant incisors reveal that the Tabarin tooth is similar morphologically and metrically to lower second incisors of the water chevrotain *Hyemoschus aquaticus* (Fig. 2(3)). It differs from the third incisor and canine of tragulids, the crowns of which are more uniformly curved, but not bent. The first incisor of tragulids is spatulate with a re-entrant angle distally into which fits the bent crown of the second incisor (Fig. 3b). Bovids such as *Ourebia* and *Cephalophus* possess second incisor crowns, which are not very spatulate, superficially recalling those of tragulids, but the bend in the incisor occurs at the crown/root margin rather than within the crown. In addition, the lingual crests tend to be less well developed than they are in *Hyemoschus*. Most other bovids have second incisors that are appreciably more spatulate than the Tabarin tooth, and any close relationship between this tooth and those of bovids can be dismissed.

A specimen (1952–1980) of *Hyemoschus aquaticus* in the Department of Comparative Anatomy of the 'Muséum national d'histoire naturelle', Paris, has an i/2 crown that is 5.1 mm high, ca 1.8 mm mesio-distal and 2.1 mm labio-lingual, which is quite similar in dimensions to the Tabarin tooth. Because of the metric and morphological similarities of BAR 2236'03 to lower second incisors of *Hyemoschus aquaticus*, we conclude that it should be identified as such rather than as any other ruminant.
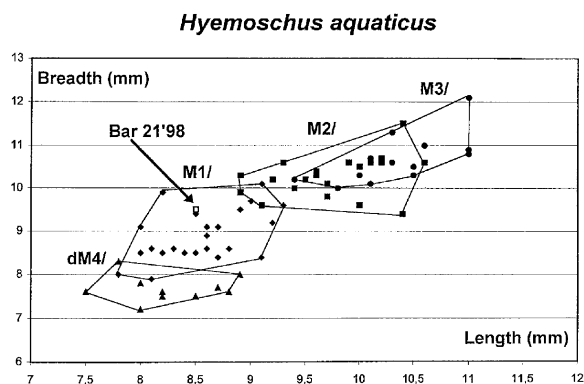
1a 1b 1c 2a 2b 2c 2d 2e 3a 3b 4a 4b 5a 5b

Hyemoschus aquaticus

Fig. 3. Length/breadth plots of upper molars and dM4/ of extant and fossil *Hyemoschus aquaticus*.

Fig. 3. Représentation bivariée du rapport longueur sur largeur des molaires supérieures et des dM4/ des *Hyemoschus aquaticus* fossiles et actuels.

4. Significance of the presence of fossil *Hyemoschus* in Kenya

The 'water chevrotain' *Hyemoschus aquaticus* is a small nocturnal African ruminant that dwells exclusively in rain forest and is never found far from water [13]. It is predominantly a frugivore, eating fruits that have fallen to the forest floor [8], but it is known to devour crabs, molluscs and carrion. It also eats vegetation that it ruminates. It has a highly developed sense of olfaction, searching for food on the forest floor at night. When alarmed, it seeks water that it dives into, hiding under waterweeds or under overhanging banks and roots of trees.

Its present-day distribution is limited to tropical forest in which fruit is available for more than nine months per year [10,23,36]. This kind of forest is of very low seasonality. As such, the discovery of fossils of *Hyemoschus aquaticus* in Kenya signifies the former presence of rain forest in the vicinity of the

basin at the time of sedimentation, between 5.3 Ma and 4.5 Ma. This suggests a significant expansion of tropical forest eastwards of its present day limits (Fig. 1). Extant African tragulids are confined to regions in which the mean annual rainfall is equal to, or greater than, 1500 mm per annum. They do not occur in areas that have less than 40 kg m^{-2} yr^{-1} of precipitable water in the atmosphere [25] and which are even moderately seasonally arid.

5. The peafowl from the Mabaget Formation, Kenya

Extant peafowls comprise two large species, *Pavo cristatus* and *Pavo muticus*, which live in southern and southeastern Asia, and a small species, *Afropavo congensis*, which lives in tropical forest of central Africa. Two extinct species have been described in Europe, *Pavo aesculapi* (Gaudry), from the Late Miocene and Early Pliocene, known only from southwestern and central Europe, and *Pavo bravardi* (Gervais), from the Pliocene, known from both eastern and western Europe. *Pavo bravardi* is a large form, somewhat larger than the extant species of the genus. It disappeared at the end of the Pliocene, most probably due to the onset of major cooling at the start of the Pleistocene [2,21,22].

Remains of a large peafowl were recently reported in Africa, at Aramis 1 and Aramis 6, in Ethiopia, dating from the Early Pliocene [19]. This form is close to both the extant species, *P. muticus*, and the extinct one, *P. bravardi*, and it has been identified provisionally as *Pavo* sp.

The specimens from the Mabaget Formation comprise two distal extremities of tibiotarsus, a left and a right, probably from a single individual. They present

Fig. 2. Tragulid and phasianid specimens from the Mabaget Formation, Early Pliocene, Tugen Hills, Kenya. (**1**) BAR 21'98, *Hyemoschus aquaticus*, left M1/ (8+ × 9.5 mm) from Mosionin: **a–c**, stereo occlusal, anterior and lingual views. (**2**) BAR 2236'03, *Hyemoschus aquaticus*, right i/2 (total height of tooth including root 10.7 mm) from Tabarin: **a–d**, anterior, lingual posterior and labial views; **e**, enlargement of lingual view. (**3**) **a–b**, Labial and lingual views of the incisors and canine of *Hyemoschus aquaticus*. (**4**) **a–b**, Cranial and caudal views of Bar 849'03, *Pavo* sp. right tibiotarsus, distal part. (**5**) **a–b**, Cranial and caudal views of Bar 976'03, *Pavo* sp. left tibiotarsus, distal part. (Scale bars: 10 mm).
Fig. 2. Tragulidés et Phasianidae de la formation de Mabaget, Pliocène inférieur, Collines Tugen, Kenya. (**1**) BAR 21'98, *Hyemoschus aquaticus*, M1 supérieure gauche (8 + × 9,5 mm) de Mosionin : **a-c**, vues occlusale stéréo, antérieure et linguale. (**2**) BAR 2236'03, *Hyemoschus aquaticus*, i/2 droite de Tabarin (hauteur totale de la dent, racine comprise = 10,7 mm), **a–d**, vues antérieure, linguale, postérieure et labiale ; **e**, agrandissement de la vue linguale. (**3**) **a–b**, Vues labiale et linguale des incisives et de la canine de *Hyemoschus aquaticus*. (**4**) **a–b**, vues crâniale et caudale de Bar 849'03, *Pavo* sp. tibiotarse droit, partie distale. (**5**) **a–b**, vues crâniale et caudale de Bar 796'03, *Pavo* sp. tibiotarse gauche, partie distale. (barres d'échelle : 10 mm).

typical morphology of the genus *Pavo* and their dimensions are slightly lower than known tibiotarsi of *P. bravardi*, but there is strong sexual dimorphism in peafowls, and the size of the specimens falls between the ranges of variation of the two extant species (we are not able to make direct comparisons with material from Aramis, as no tibiotarsi have been reported from there). Their dimensions are clearly greater than those of *Afropavo congensis* the Congo Peafowl. The Mabaget material is thus identified as *Pavo* sp.

The presence of a peafowl in the Mabaget fauna is important from the point of view of palaeoecology. The Blue Peafowl, *Pavo cristatus*, lives in open, generally deciduous, forest, with a vegetation understory, along watercourses. The Green Peafowl, *Pavo muticus*, occurs in Thailand in riverine forests and in Java where it lives in open forest, or forest edges, but not in dense tropical rainforest [7]. From this we can conclude that the depositional environment of the Mabaget Formation was close to or in forest, with watercourses. The environment indicated by the presence of peafowls accords with that suggested by the water chevrotain.

6. Palaeosols and palaeoclimate

The Mabaget Formation comprises fluvial, lacustrine and volcanic sediments intercalated with several palaeosols. These palaeosols are laterally widespread in the formation and consist of dark brown to black, iron-rich, almost lateritic horizons with abundant ferruginous pisoliths. At present, this kind of deposit forms in humid climates, and is notable for the lack of carbonate nodules. Palaeosols in the underlying Kaparaina Basalt Formation are also lateritic in affinities. In the latter formation there are at least four thick red palaeosols devoid of carbonate nodules intercalated between lava flows. The evidence suggests that the climate was extremely humid at the time of deposition of both the Kaparaina and Mabaget Formations and that dry seasons, if they occurred, did not result in the formation of carbonate nodules. Evidence from the underlying Lukeino Formation suggests the same thing [29] and the even older Mpesida Beds (6.3 Ma) are known for the fossil forests [15] with abundant, 20–30-m-tall trees, some of which possess buttress roots and others of which were draped in large lianas. All this

evidence suggests that the Tugen Hills region was considerably more humid and far less seasonal from 6.3 to 4.5 Ma than it is today, and that it was probably covered in tropical rain forest. Compatible results have been obtained for the same stratigraphic sequence using stable isotopes of herbivore enamel, soil carbonate nodules and palaeoflora [14] as well as ecomorphological and stable isotope studies of suid fossils [1]. The available data suggests that the Tugen Hills region was heavily forested through the Late Miocene and basal Pliocene, but this does not exclude the possibility of localised patches of grassland existing within the basin, as occurs for example, in present day Western Uganda and Eastern Congo (Albert-Edward Rift) [31].

7. Micromammals

The rodent fauna from the Mabaget Formation (Mein, pers. comm.) based on several hundred specimens, has no representation of gerbillids, which are common in the older Lukeino Formation, and are abundant today in woodland, savannah and steppe settings. The apparent absence of gerbillids in the Mabaget Formation accords with the forested palaeoenvironment deduced from other evidence.

8. Significance for early hominid habitats

For the past 40 years and more, the prevailing hypothesis about hominid origins has been that the family evolved in open country from a quadrupedal precursor, often described as a knuckle-walker [32,34,47,54]. The East Side Story of Coppens [5] is a variant of the 'savannah hypothesis', with chronological, palaeoecological, geographic and geological details added, but without a specified ancestral taxon. The central theme of Coppens' hypothesis is that opening up of the countryside due to rifting and domal uplift, which caused the aridification of East Africa, led to the emergence of Hominidae at the end of the Miocene, some 8–7 Ma ago. In this and other versions of the 'savannah hypothesis', the emergence of the family is visualised as occurring in open country.

However, it was long ago suggested that 3 Ma 'Lucy' (*Australopithecus antiquus seu afarensis*) from Ethiopia, inhabited montane forest rather than savan-

nah [3] and recent discoveries of Late Miocene and Early Pliocene hominids reveal that all the sites older than 4 Ma at which they have been found, represent well-wooded to forested palaeohabitats. *Orrorin tugenensis*, a 6–5.7 Ma bipedal hominid, is associated with abundant colobine monkey fossils, suggesting an abundance of trees in the basin [29,43]. The same applies to the Western Margin sites in the Middle Awash (5.7–5.2 Ma) [11] and the 4.2 Ma site of Aramis, Ethiopia [48,49,53] as well as the 4.5–5.3 Ma sites in the Mabaget Formation, which have yielded *Ardipithecus ramidus* (or *A. praegens* [9]). The Lothagam hominid mandible (Apak Member), which was for many years thought to be Late Miocene in age [24] has recently been redated [20] and is more likely to be Early Pliocene in age (older than 4.2 Ma and younger than 5 Ma). It appears to be associated with well-vegetated conditions with some open country habitats nearby, while two slightly older specimens (Upper Nawata Member: 6.5–5 Ma) are also associated with well-vegetated palaeoenvironments [17,18].

It now seems increasingly unlikely that protohominids ventured into the savannah as quadrupeds, then went through a knuckle-walking stage before becoming bipedal, a conclusion already suggested nearly four decades ago by Tuttle [45], subsequently by Senut [37–40] and re-iterated more recently by Senut [42,43], Tuttle [46] and Clarke [4].

9. Discussion on East African Pliocene palaeoenvironments

Williamson [51,52] proposed, on the basis of the freshwater snail genus *Potadoma* found in Late Pliocene to Early Pleistocene deposits of West Turkana, that there was an extension of the tropical rainforest to the Turkana Basin, Kenya. Today, this snail is confined to rivers in heavily forested areas. On the basis of faunal studies, Pickford [26] concluded that during the Late Miocene and Early Pliocene the Tugen Hills region was considerably more humid and better vegetated than it is today. The recent discovery of tragulids in the Early Pliocene deposits of the region confirms that rainforest was present in Kenya from about 5.3 Ma to 4.5 Ma, while forest and dense woodland has been inferred even earlier in the basin, in the Lukeino Formation (ca 6 Ma) [29] and the Mpesida

Beds (6.3 Ma) [14]. This evidence is in general agreement with the stable isotope studies carried out by Kingston [14,16] who analysed carbonate nodules from palaeosols in the Tugen Hills succession. Forest palaeosols usually do not develop carbonate nodules, and thus these palaeosols could not be included in the previous studies. By omitting the humid palaeosols, the sampling programme biased the results, highlighting the C4 grassland contribution at the expense of the more prevalent humid ones, but even so, it is evident that there was forest in the region [14]. Basically similar conclusions were reached by Bishop et al. [1], on the basis of the study of stable isotopes of suid enamel and suid ecomorphology, but the authors pointed out that some of their results suggested 'either seasonality, some aridity, low moisture or a combination of these conditions'. For the base of the Mabaget Formation, it is more likely that seasonality was minimal, even if other horizons in the succession contain evidence of more marked seasonality.

The faunal studies and examination of palaeosols in the Lukeino, Kaparaina and Mabaget Formations indicate that throughout the period represented by these formations (6–4.5 Ma), the Tugen Hills area was close to or within tropical forest, and that signs of semi-arid to arid conditions are rare to non-existent.

10. Conclusions

The discovery of fossil tragulid remains attributed to the extant species *Hyemoschus aquaticus* and of a peafowl, *Pavo* sp., in the 4.5–5.3 Ma Mabaget Formation, Tugen Hills, Kenya, indicates that the region was endowed with tropical rainforest at the time of deposition and that seasonality was minimal. This is important for understanding the early stages of hominid evolution, because it now appears that Late Miocene and Early Pliocene hominids inhabited forested areas, and that the family had perhaps not yet ventured into open country. This inference has important implications for the origins of bipedalism, suggesting not only that the traditional 'savannah hypothesis' of human origins is invalid, but also that the idea that protohominids went through a knuckle-walking stage [35] prior to evolving bipedalism is obsolete. It is more likely that early bipeds evolved in wooded to forested environments and that for several million years they combined

bipedalism with arboreal climbing [29,43]. This combination of locomotor repertoires persisted in Middle and Late Pliocene australopithecines [38–40], but climbing adaptations were eventually reduced and bipedal adaptations accentuated in the *Praeanthropus* and *Homo* lineages.

Acknowledgements

References

[1] L.C. Bishop, A. Hill, J. Kingston, Palaeoecology of Suidae from the Tugen Hills, Baringo, Kenya, in: P. Andrews, P. Banham (Eds.), Late Cenozoic Environments and Hominid Evolution: a tribute to Bill Bishop, Geological Society, London, 1999, pp. 99–112.

[2] Z. Boev, G. Koufos, Présence de *Pavo bravardi* (Gervais, 1849) (Aves, Phasianidae) in the Ruscinian locality of Megalo Emvolon, Macedonia, Greece, Geol. Balc. 30 (1–2) (2000) 69–74.

[3] R. Bonnefille, A. Vincens, G. Buchet, Palynology, stratigraphy and palaeoenvironment of a Pliocene hominid site (2.9–3.3 Myr) at Hadar, Ethiopia, Palaeogeogr. Palaeoclimatol. Palaeoecol 60 (1987) 249–281.

[4] R.J. Clarke, Newly revealed information on the Sterkfontein Member 2 *Australopithecus* skeleton, S. Afr. J. Sci. 98 (2003) 523–526.

[5] Y. Coppens, East Side Story: the origin of humankind, Scientific American (May 1994) 62–69.

[6] A. Deino, L. Tauxe, M. Monaghan, A. Hill, [40]Ar/[39]Ar geochronology and paleomagnetic stratigraphy of the Lukeino and lower Chemeron Formations at Tabarin and Kapcheberek, Tugen Hills, Kenya, J. Hum. Evol 42 (2002) 117–140.

[7] J. del Hoyo, A. Elliott, J. Sargatal (Eds.), New World Vultures to Guineafowl, 2, Lynx Edicions, Barcelona, Spain, 1994, pp. 638 Handbook of the Birds of the World.

[8] G. Dubost, Comparison of the diets of frugivorous forest ruminants of Gabon, J. Mammal 65 (2) (1984) 298–316.

[9] W.W. Ferguson, Taxonomic status of the hominid mandible KNM TH 13150 from the Middle Pliocene of Tabarin, in Kenya, Primates 30 (1989) 383–387.

[10] P. Grubb, Order Artiodactyla, 2nd ed, in: D.E. Wilson, D.M. Reader (Eds.), Mammal Species of the World, Smithsonian Institution Press, Washington, 1993, pp. 382.

[11] Y. Haile-Selassie, Late Miocene hominids from the Middle Awash, Ethiopia, Nature 412 (2001) 178–181.

[12] A. Hill, Early hominid from Baringo District, Kenya, Nature 315 (1985) 222–224.

[13] J. Kingdon, East African Mammals, III, Academic Press, New York, 1979 Part B.

[14] J. Kingston, Environmental determinants in early hominid evolution: issues and evidence from the Tugen Hills, Kenya, in: P. Andrews, P. Banham (Eds.), Late Cenozoic Environments and Hominid Evolution: a tribute to Bill Bishop, Geological Society, London, 1999, pp. 69–84.

[15] J. Kingston, B.F. Jacobs, A. Hill, A. Deino, Stratigraphy, age and environments of the Late Miocene Mpesida Beds, Tugen Hills, Kenya, J. Hum. Evol. 42 (2002) 95–116.

[16] J. Kingston, B. Marino, A. Hill, Isotopic evidence for Neogene hominid paleoenvironments in the Kenya Rift Valley, Science 264 (1994) 955–959.

[17] M.G. Leakey, C. Feibel, R. Bernor, J.M. Harris, T. Cerling, K. Stewart, J. Storrs, A. Walker, L. Werdelin, A. Winkler, Lothagam: a record of faunal change in the Late Miocene of East Africa, J. Vert. Paleontol. 16 (1996) 556–570.

[18] M. Leakey, M. Teaford, C. Ward, A. Walker, Primates, in: M. Leakey, J.M. Harris (Eds.), Lothagam: the dawn of humanity in Eastern Africa. Columbia, Columbia University Press, 2003.

[19] A. Louchart, A true peafowl in Africa, S. Afr. J. Sci. 99 (2003) 7–8.

[20] I. McDougall, C. Feibel, Numerical age control for the Miocene-Pliocene succession at Lothagam, a hominoid-bearing sequence in the northern Kenya Rift, J. Geol. Soc. Lond. 156 (1999) 731–745.

[21] C. Mourer-Chauviré, A peafowl from the Pliocene of Perpignan, France, Palaeontology 32 (2) (1989) 439–446.

[22] C. Mourer-Chauviré, Les paons du Pliocène et du Pléistocène inférieur d'Europe. Biostratigraphie et Paléoécologie, in: Journée Louis David (Ed.), Documents des Laboratoires de Géologie de Lyon, 1990, pp. 77–91 Hors série n° 9.

[23] R. Nowak, Walker's Mammals of the World, 6th ed, The John's Hopkins University Press, Maryland, 1999.

[24] B. Patterson, K. Behrensmeyer, W.D. Sill, Geology and fauna of a new Pliocene locality in northwestern Kenya, Nature 226 (1970) 918–921.

[25] J.-P. Peixoto, A.H. Oort, Le cycle de l'eau et le climat, La Recherche 221 (1990) 570–579.

[26] M. Pickford, Growth of the Ruwenzoris and their impact on palaeoanthropology, in: Akiyoshi Ehara, et al. (Eds.), Primatology Today, Elsevier, Amsterdam, 1991, pp. 513–516.

[27] M. Pickford, Africa's smallest ruminant: a new tragulid from the Miocene of Kenya and the biostratigraphy of East African Tragulidae, Geobios 34 (2001) 437–447.

[28] M. Pickford, Ruminants from the Early Miocene of Napak, Uganda, Ann. Paléontol. 88 (2002) 85–113.

[29] M. Pickford, B. Senut, The geological and faunal context of Late Miocene hominid remains from Lukeino, Kenya, C. R. Acad. Sci. Paris, Ser. IIa 332 (2001) 145–152.

[30] M. Pickford, D. Johanson, C.O. Lovejoy, T. White, J. Aronson, A hominoid humeral fragment from the Pliocene of Kenya, Am. J. Phys. Anthropol. 60 (1983) 337–346.

[31] M. Pickford, B. Senut, D. Hadoto, Geology and Palaeobiology of the Albertine Rift Valley, Uganda-Zaire, Orléans, CIFEG. Publ. Occas. 24 (1993) 1–190.

[32] D. Pilbeam, Genetic and morphological records of the Hominoidea and hominid origins: a synthesis, Mol. Phylogenet. Evol. 5 (1996) 155–168.

[33] G. Pilgrim, The dentition of the tragulid genus *Dorcabune*, Rec. Geol. Surv. India 45 (1915) 226–238.

[34] B.G. Richmond, D.S. Strait, Evidence that humans evolved from a knuckle-walking ancestor, Nature 404 (2000) 382–385.

[35] B.G. Richmond, D.S. Strait, Les hommes ont-ils eu un ancêtre *knuckle-walker* ? Primatologie 3 (2000) 555–570.

[36] K. Robin, Chevrotains, in: B. Grzimek (Ed.), Grzimek's Encyclopaedia of Mammals, 5, McGraw-Hill Publishing Co., New Jersey, 1999, pp. 118–123.

[37] B. Senut, New data on the humerus and its joints in Plio-Pleistocene hominids, Coll. Anthropol. 4 (1980) 87–93.

[38] B. Senut, Outlines of the distal humerus in hominoid primates: application to some Plio-Pleistocene hominids, in: A.B. Chiarelli, R.S. Corruccini (Eds.), Primate Evolutionary Biology, Springer Verlag, Heidelberg, 1981, pp. 81–92.

[39] B. Senut, L'humérus et ses articulations chez les hominidés plio-pleistocènes, Cah. Paléontol. (Paléoanthropol.) (1981) 1–141.

[40] B. Senut, Humeral outlines in some hominoid primates and in Plio-Pleistocene hominids, Am. J. Phys. Anthropol. 56 (1981) 275–284.

[41] B. Senut, Quelques remarques à propos d'un humérus d'hominoïde pliocène provenant de Chemeron (bassin du lac Baringo, Kenya), Folia Primatol. 41 (1983) 267–276.

[42] B. Senut, Quand les caractères deviennent magiques, Primatologie 3 (2000) 575–576.

[43] B. Senut, M. Pickford, D. Gommery, P. Mein, K. Cheboi, Y. Coppens, First hominid from the Miocene (Lukeino Formation, Kenya), C. R. Acad. Sci. Paris, Ser. IIa 332 (2001) 137–144.

[44] H. Thomas, L. Ginsburg, C. Hintong, V. Suteethorn, A new tragulid, *Siamotragulus sanyathanai* n. g., n. sp. (Artiodactyla, Mammalia) from the Miocene of Thailand (Amphoe Pong, Phayao Province), C. R. Acad. Sci. Paris, Ser. II 310 (1990) 989–995.

[45] R. Tuttle, Knuckle-walking and the evolution of hominoid hands, Am. J. Phys. Anthropol. 26 (2) (1967) 171–206.

[46] R. Tuttle, Le *knuckle-walking* revisité, Primatologie 3 (2000) 571–573.

[47] S. Washburn, Behaviour and the origin of man, The Huxley Memorial Lecture, 1967, Proc. R. Anthropol. Inst. Great Britain and Ireland 3 (1967) 21–27.

[48] T. White, Earliest hominids, in: W.C. Hartwig (Ed.), The Primate Fossil Record, Cambridge University Press, Cambridge, 2002, pp. 407–417.

[49] T. White, G. Suwa, B. Asfaw, *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia, Nature 371 (1994) 306–312 375 (1994) 88.

[50] T. Whitworth, Miocene ruminants of East Africa. Fossil Mammals of Africa, Br. Mus. (Nat. Hist.) 15 (1958) 1–50.

[51] P. Williamson, Evidence for an early Plio-Pleistocene rainforest expansion in East Africa, Nature 315 (1985) 487–489.

[52] P. Williamson, A first record of *Potadoma* (Swainson) (Prosobranchia: Gastropoda) from Eastern Africa, J. Conchol. 32 (1985) 135–139.

[53] G. WoldeGabriel, T. White, G. Suwa, P. Renne, J. de Heinzelin, W. Hart, G. Heiken, Ecological and temporal placement of Early Pliocene hominids at Aramis, Ethiopia, Nature 371 (1994) 330–333.

[54] R. Wrangham, D. Pilbeam, African apes as time machines, in: B. Galdikas, N. Briggs, L. Sheeran, G. Shapiro, J. Goodall (Eds.), All apes great and small, 1, Kluwer Academic/Plenum Publishers, New York, 2001, pp. 5–17 African Apes.