C. R. Palevol 1 (2002) 213–219

S1631068302000295/FLA

General Palaeontology / Paléontologie générale
(Palaeoecology / Paléoécologie)

Early Miocene grassland ecosystem at Bukwa, Mount Elgon, Uganda

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Received 22 February 2002; accepted 8 July 2002

Presented by Yves Coppens

Abstract – Fossil plants and terrestrial gastropods collected by the Uganda Palaeontology Expedition at Bukwa site I in 1997 and 1998, throw light on the palaeoenvironmental conditions that characterised the area during the end of the Early Miocene, some 17.5 Ma ago. Some of the evidence indicates the presence of grasslands in situ at the locality, but part of the fossil gastropod assemblage and some of the plants suggest the presence of woodland to forest nearby. ***To cite this article: M. Pickford, C. R. Palevol 1 (2002) 213–219.*** © 2002 Académie des Sciences / Éditions scientifiques et médicales Elsevier SAS

Early Miocene / palaeoenvironment / grassland ecosystem / terrestrial gastropods / palaeosols / volcanic ashes / Uganda

Résumé – Un écosystème de prairie dans le Miocène inférieur à Bukwa, mont Elgon, Ouganda. Des plantes et des gastropodes terrestres fossiles récoltés par l'Uganda Palaeontology Expedition sur le site I de Bukwa, en 1997 et en 1998, précisent la question des conditions de paléoenvironnement qui caractérisaient la région pendant la fin du Miocène inférieur, il y a environ 17,5 Ma. Une partie des témoins indique la présence de prairies in situ dans la localité, mais une partie de l'assortiment de gastropodes fossiles et quelques plantes suggèrent toutefois la proximité de zones boisées ou de forêts. ***Pour citer cet article : M. Pickford, C. R. Palevol 1 (2002) 213–219.*** © 2002 Académie des Sciences / Éditions scientifiques et médicales Elsevier SAS

Miocène inférieur / paléoenvironnement / savane / gastéropodes terrestres / paléosols / cendres volcaniques / Ouganda

Version abrégée

1. Introduction

L'origine des écosystèmes de prairie (*grasslands*) en Afrique de l'Est est d'actualité [8–9,11,15,17,24–27,32], parce qu'il a été postulé que l'ouverture de la végétation de cette région tropicale africaine au Cénozoïque pourrait avoir influencé certains aspects de l'évolution des hominoïdés et des hominidés. L'extension des prairies n'a pas d'effet sur le régime alimentaire des hominoïdés, puisque aucune des lignées connues ne consommait de graminées, mais les conséquences engendrées par cette extension ont plutôt joué un rôle dans les changements environnementaux. Quand la végétation d'une région s'ouvrait, la couverture arborée diminuait, réduisant de ce fait l'habitat des espèces arboricoles en appauvrissant l'approvisionnement alimentaire (typiquement constitué de fruits) dont ils dépendaient.

Bonnefille [8,9] a montré que les prairies étaient répandues en Afrique de l'Est au Pliocène et au Pléistocène, ainsi que dans une localité du Miocène moyen. Des travaux plus récents ont confirmé la présence de prairies au Miocène moyen en Afrique de l'Est [11,25]. Il n'y a pas eu d'attestation de prairies en Afrique de l'Est avant 16 Ma environ [25, fig. 3], même si des graminées fossiles sont connues dans des sites plus anciens du Kenya occidental [21,27].

L'Uganda Palaeontology Expedition a exploré Bukwa en Ouganda (Fig. 1) [10,18,20,30–31] et a trouvé de nombreuses preuves de graminées dans plusieurs horizons. Une date radio-isotopique d'environ 22 Ma a été obtenue dans une lave considérée comme superposée aux sédiments de Bukwa [7,10]. Toutefois, les couches de Bukwa sont considérable-

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ment plus jeunes que 22 Ma, la faune mammalienne suggérant un âge plus récent que celui de Rusinga (17,8 Ma) [16].

Bancroft [3–6] a décrit des bois fossiles du mont Elgon, tandis que Chaney [12–14] a signalé des feuilles fossiles dans les grès de Bugishu. Le matériel de Chaney consiste en une paléoflore variée de feuilles, que Bonnefille [9] compare à celle des régions boisées actuelles soudano-zambéziennes. Celles-ci subissaient un climat saisonnier, avec alternance de saisons sèches et humides, ce qui, de ce fait, implique la présence de savanes et donc de prairies. Hamilton [18] a décrit des feuilles fossiles et des fleurs provenant de Bukwa ; il en a déduit que la paléoflore de Bukwa consistait en espèces de forêts pluviales de basses terres tropicales, une conclusion approuvée par Bonnefille [9].

2. Le paléoenvironnement de Bukwa

2.1. Les gastéropodes terrestres

La nouvelle récolte de gastéropodes de Bukwa comprend 136 spécimens, appartenant à 15 genres (Tableau 1), qui suggèrent qu'il y avait indubitablement une forêt dans la région [22,28] – mais une partie de la végétation pouvait très bien avoir été plutôt ouverte – ou bien encore une forêt sèche. D'un intérêt particulier sont la découverte de *Trochonanina*, genre de prairie, préservé à la base d'un amas de graminées fossilisées, et la présence d'*Helicarion* et de *Chlamydarion*, qui suggèrent des conditions relativement ouvertes à Bukwa au moment du dépôt.

2.2. Paléobotanique

Il y a à Bukwa plusieurs horizons de cendres volcaniques à grain fin, avec des amas de graminées fossilisées in situ, dans leur position de croissance avec le système radiculaire préservé dans les paléosols sous-jacents. D'après Vesey-Fitzgerald [29], la distribution actuelle d'« amas » ou de « touffes » d'herbes (*clump grass*) dépend plus du type de pluviosité et de son intensité que du feu. En règle générale, ce type de prairies se développe quand les précipitations sont comprises entre 500 et 1500 mm par an et là où existe une saison sèche annuelle marquée. Les fruits et les autres fossiles s'accordent à ces conditions [8,20,30–31]. Il faut noter que les fossiles d'herbes sont préservés à Bukwa là où ces végétaux poussaient, tandis que les feuilles de dicotylédones, les fleurs, les fruits et les branches ont été transportés sur des distances que l'on ne peut préciser avant leur dépôt.

Dans l'état actuel de nos connaissances, le gisement de Bukwa offre la première preuve certaine d'un écosystème de prairie en Afrique de l'Est vers 17,5 Ma, la présence plus ancienne d'un tel écosystème à Bugishu reposant indirectement sur l'interprétation de la flore de dicotylédones. Les preuves ultérieures sont celles de Nyakach (environ 15 Ma) et de Fort Ternan (12,5–13 Ma), au Kenya.

3. Discussions et conclusions

Des graminées fossilisées dans des horizons de cendres volcaniques à grain fin à Bukwa (Miocène inférieur, Ouganda), complètes, avec leur système radiculaire en place dans les paléosols, livrent la première preuve évidente de l'existence d'écosystèmes de prairie (*grassland ecosystems*) en Afrique tropicale. Jusqu'à présent, le plus ancien écosystème connu de ce type était celui de Nyakach (environ 15 Ma), au Kenya occidental.

L'étude des gastéropodes fossiles terrestres de Bukwa appuie la thèse de sédiments accumulés dans un environnement de prairie, mais suggère, cependant, qu'il y avait des espaces boisées ou des forêts au voisinage au moment du dépôt, cette suggestion étant confortée par les macrorestes végétaux trouvés dans la localité [18]. La plupart des sites fossiles du Miocène inférieur d'Afrique de l'Est ont livré d'abondantes preuves de la présence de primates hominoïdes [19,21–22]. Bukwa est exceptionnel par la seule découverte de deux dents hominoïdes isolées. Il serait possible que cette rareté en primates fossiles à Bukwa soit due au fait que la région de dépôt ait été couverte de prairies.

La découverte d'un écosystème de prairie dans les couches du Miocène inférieur de Bukwa, Ouganda, est importante pour comprendre l'évolution des types de végétation sous les tropiques en Afrique. Premièrement, elle conduit à réfuter l'idée de forêts tropicales étendues en une ceinture continue depuis les rivages africains de l'Atlantique jusqu'à ceux de l'Océan indien pendant le Miocène inférieur [1]. Elle révèle que la présence de mosaïques de végétation a été un trait caractéristique de l'Afrique tropicale depuis au moins 17,5 Ma [2]. Deuxièmement, la rareté en hominoïdes sur le site devient compréhensible quand l'existence de prairies dans le paléoenvironnement est prise en compte. Troisièmement, la présence d'un écosystème de prairie à Bukwa est antérieure d'environ 10 Ma aux origines de la famille des Hominidés.

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1. Introduction

The origin of grassland ecosystems in East Africa is of current interest [8–9,11,17,24–27,32] because it has been postulated that opening up of the tropical African countryside during the Cainozoic may have driven some aspects of hominoid and hominid evolution [15]. It has long been suggested that there is a direct link between the development of hypsodonty and cementodonty in various mammalian lineages that exploited grasses in their diet, including Elephantidae, Suidae, equids, grazing rhinocerotids, hippopotamids, antelopes of various kinds, and so on. The effects of grassland expansion on hominoids was not so much to do with diet, since none of the known lineages eat grass, but it is more to do with the environmental

Fig. 1. Location of fossiliferous areas in Uganda, showing Bukwa on the northeast flanks of Mount Elgon.

Fig. 1. Localisation des gisements fossilifères en Ouganda. Bukwa se trouve sur le flanc nord-est du mont Elgon.

changes that grassland expansion engendered. Thus as the countryside opened up, tree cover diminished, thereby reducing the habitat of arboreal species and impoverishing the food supplies (typically fruit) that they were dependent on.

As studies of tropical African palaeovegetation have progressed, there has been a trend to discover older and older evidence of grasslands. Bonnefille [8–9] showed that grasses were widespread in East Africa during the Pliocene and Pleistocene, and at one locality in the Middle Miocene (Bugishu Sandstone, Uganda, probably of Early Miocene age). More recent work has confirmed the presence of grasslands in the Middle Miocene of East Africa at sites such as Fort Ternan and Nyakach [11,25] in Kenya. Prior to about 16 Ma, grasslands have not been reported in East Africa [25, fig. 3] even if fossil grass (usually broad leafed species) has been recorded from some sites in Western Kenya [21,27] that are older than this. Such broad-leafed species are thought to have grown in the understory of forests, and thus should not be taken to denote the existence of grasslands which are usually considered to imply some degree of treelessness in the environment.

In 1997 and 1998, the Uganda Palaeontology Expedition made surveys of the fossil sites at Bukwa (Fig. 1) (01°17’00.0”N, 34°47’07.8”E) on the northeastern slopes of Mount Elgon, Uganda [10,18,20,30,31] and found abundant evidence of grass *in situ* at several horizons (Fig. 1). The fossil terrestrial gastropods from Bukwa provide additional palaeoenvironmental information about the site, suggesting that it was surrounded by a mosaic of vegetation types, of which grassland was locally the most important. The combination of fossil terrestrial gastropods and in situ grass fossils in fine-grained volcanic ash with their root systems in the underlying palaeosols provides good evidence about past environmental conditions at Bukwa during the Early Miocene.

2. Bukwa age

Bukwa has long been considered one of the oldest known fossil sites in East Africa, a radioisotopic date of ca 22 Ma having been obtained from a lava thought to overlie the sediments [7,10]. However, the strata at Bukwa are probably considerably younger than 22 Ma,

the mammalian fauna suggesting an age younger than Rusinga, which is 17.8 Ma [16]. The few mammal fossils found by the Uganda Palaeontology Expedition (*Bathyergoides neotertiarius*, a large *Palaeomeryx*, *Nguruwe kijivium*, *Kenyasus namaquensis*, and *Diamantohyus africanus*) suggest an age of ca 17.5 Ma for the deposits. As such the fossil grassland at Bukwa is currently the oldest known in tropical Africa, and predates the previous record by about 1.5 Myr.

3. Previous palaeobotanic studies of Mount Elgon

Bancroft [3–6] described fossil wood from various sites on the Ugandan side of Mount Elgon, while Chaney [12–14] reported on fossil leaves from the Bugishu Sandstones, a prevolcanic deposit that crops out near Mbale, Uganda. Most of Bancroft's material seems to have come from coarse agglomerates that erupted onto vegetation that was growing on the flanks of the volcano. The picture that emerged from these early studies was that Elgon was clothed in forest and woodland during the Early Miocene. However, agglomerates tend to over-represent macrobotanical remains and under-represent small plants, such as grasses, and the ages of the agglomerates are not well constrained, even if they are indeed most likely to be of Early Miocene age. They are younger than the Bukwa sites, since the latter immediately overlie basement complex gneisses.

Chaney's material came from pre-volcanic sandstones and consists of a diverse leaf palaeoflora, comprising Caesalpiniaceae (*Bauhinia*, *Berlinia*, *Cassia*), Papilionaceae (*Dalbergia*), Rosaceae (*Parinari*), Combretaceae (*Terminalia*), Pittosporaceae (*Pittosporum*), and Dipterocarpaceae (*Monotes* and *Marquesia*). According to Bonnefille [9], such a flora occurs typically in Sudano-Zambezian woodlands that experience a seasonal climate with alternating dry and wet seasons, and thus it implies the presence of savannah, and thus grassland. The age of the Bugishu sandstone is unknown, but, being pre-volcanic, it is probably earlier than Bukwa, which consists of volcanic ashes overlying basement complex rocks.

Because of the sedimentological bias, it is interesting to examine plants preserved in finer grained sediments, such as those that occur at Bukwa. Hamilton [18] described fossil leaves and flowers that he assigned to Melianthiaceae (*Bersema*) and Sterculiaceae (*Cola* and *Pterygota*), on which basis he deduced that the Bukwa palaeoflora consisted of tropical lowland rainforest species, a conclusion supported by Bonnefille [9]. Thus Bukwa has yielded an interesting 'mélange' of fossils, implying the existence of open and closed vegetation types at the time of deposition.

4. The paucity of fossil primates at Bukwa

Most Early Miocene fossil sites in East Africa have yielded abundant evidence of hominoid primates [19,21,22]. Bukwa is exceptional in that very few primates have been recovered from it, the order being represented by only two isolated teeth. Previous literature [31] is somewhat misleading to the extent that some fragmentary suiform fossils (teeth of *Diamantohyus africanus* and *Kenyasus namaquensis*) were misidentified as *Proconsul*, which gave the false impression of the presence of these hominoids at the site. There are only two primate teeth from Bukwa: both are poorly preserved but have been identified as *Limnopithecus legetet* [19].

UMP 68–22	Bukwa II	left lower m/1	*Limnopithecus legetet*
UMP 68–26/27	Bukwa II	upper left I1/	*Limnopithecus legetet*

It is possible that the rarity of primate fossils at Bukwa could be due to the fact that the depositional area was covered in grassland, with woodland and forest some distance away.

5. Bukwa palaeoenvironment

Terrestrial gastropods

Two field seasons of the Uganda Palaeontology Expedition at Bukwa in 1997 and 1998 resulted in the collection of numerous fossils, the most important of which were terrestrial gastropods. The 1967 collections from the site contained only 22 specimens, belonging to six taxa (*Oreohomorus*, *Thapsia*, *Maizania*, *Tayloria*, *Achatina leakeyi* and *Burtoa nilotica*), but previous identifications of these specimens contained several errors [31]. A supposed *Archachatina* from Bukwa is more likely to represent *Achatina leakeyi*. The new collections comprise 136 additional specimens belonging to 15 genera (Table 1). From the enlarged assemblage, it is now possible to reconstruct the palaeoenvironment of Bukwa more satisfactorily than was hitherto possible.

The Bukwa gastropod fauna suggests that there was undoubtedly forest in the region, as shown by the

Table 1. Terrestrial gastropods from Bukwa, Uganda.
Tableau 1. Gastéropodes terrestres de Bukwa, Uganda.

Taxon/Year/Total	1967	1997	1998	Total
Maizania	3	5	6	14
Edouardia	—	2	—	2
Subulinidae indet.	—	—	21	21
Opeas	—	6	—	6
Oreohomorus	2	35	—	37
Subuliniscus	—	3	—	3
Pseudoglessula	—	—	1	1
Achatina leakeyi	6	19	9	34
Burtoa nilotica	9	9	3	21
Trochonanina	—	2	1	3
Thapsia	1	2	2	5
Ptychotrema	—	1	1	2
Tayloria	1	4	1	6
Helicarion	—	1	—	1
Trochozonites	—	—	1	1
Chlamydarion	—	—	1	1

presence of *Ptychotrema*, *Tayloria*, *Trochozonites*, and large Subulinidae (*Oreohomorus* and *Subuliniscus*) [23,28], but some of the forest may well have been rather open, or dry forest, because of the presence of *Burtoa nilotica*, *Pseudoglessula* and *Maizania*. Of particular interest is the discovery of a grassland type of *Trochonanina* preserved in the base of a clump of fossilised grass, similar to extant species that hide in the base of such clumps where they are protected from desiccation during dry seasons or from being burnt during grass fires. The presence of *Helicarion* and *Chlamydarion* also suggests relatively open conditions at Bukwa at the time of deposition.

Even if, at first glance, the snails that indicate open country at Bukwa appear to occur in relatively low numbers and are thus numerically subordinate to forest adapted lineages, two things need to be remembered. Firstly, large, robust shells of achatinids and subulinids tend to preserve better than small thin shells of urocyclids and helicarionids. This taphonomic bias can lead to under-representation of grassland species at the expense of woodland to forest types. Secondly, the population density and taxonomic diversity of snails in grasslands tends to be considerably lower than it is in forests and woodlands, and this can give a false impression about the relative importance of forest versus grassland species at a site. The combination of taphonomic and biological biases could thus yield the erroneous view that the sediments at Bukwa accumulated in a forested setting. The fossil grasses and the palaeosols indicate otherwise, and the few grassland types of snails support this conclusion.

6. Palaeobotany

Fossil grass occurs abundantly at Bukwa I. There are several fine-grained volcanic ash horizons with clumps of grass fossilised as imprints of leaves and three-dimensional stems in situ in their positions of growth with the root systems preserved in the underlying palaeosols. This indicates that there were grasslands at the site at the time of deposition. The closest analogy in terms of diameter and straightness of stems and size of clumps that we have found for the Bukwa grass fossils is the long grass plains of Karamoja, where grass grows in clumps rather than as a continuous cover. According to Vesey-Fitzgerald [29] present-day distribution of ‘clump’ or ‘bunch’ grasses (*Panicum*, *Hyparrhenia*, or *Andropogon*) is dependent more upon rainfall pattern and intensity than on fire. This type of grassland as a rule occurs where precipitation is between 500–1500 mm (20–60 inches) per year and where there is a marked annual dry season. Grass stems from Bukwa are straight and range in diameter from 1.6–3.2 mm. Further study of microscopic details of the leaves and stems is required for a definitive identification, but the gross morphology of the stems and leaves, as well as the clumped growth habitus, is sufficient to indicate that it could belong to one or other of the genera listed above, or to a species with similar growth habitus.

Near watercourses in grassy plains dominated by clump grasses, there is usually riparian forest, and this may well have been what Bukwa looked like at the time of deposition. The fossil fruits and other macrobotanical remains found by the UPE and by previous researchers accord with this scenario [18,20,30,31]. It should be noted that the grass fossils at Bukwa are preserved where they grew, whereas the dicotyledon leaves, flowers, fruits and branches were transported unknown distances before deposition. Thus, when reconstructing the palaeoenvironment at Bukwa, greater significance should be given to the grass fossils than to the other plant remains. Fossil wood, fruit and seeds that occur in the Bukwa succession [18] indicate that there was lowland tropical forest in the vicinity. This environmental reconstruction accords with the evidence yielded by the gastropod fauna.

The fauna from the Bukwa I site confirms its subaerial affinities, with not a single aquatic element known in the assemblage. In contrast, Bukwa II, which is a paludal clay deposit of restricted areal extent, has yielded abundant remains of crabs and ostracods, but few mammals (both the hominoid specimens came from Bukwa II) and none of terrestrial gastropods. The limited areal extent of Bukwa II suggests that it was a

small pond within the Bukwa depositional environment, most of which was sub-aerial.

As far as we know, Bukwa provides the earliest (ca 17.5 Ma) clear evidence of a grassland ecosystem in Eastern Africa, the older Bugishu 'occurrence' being implied from the dicotyledon flora, with no direct evidence of grasses at the site. The next oldest evidence is from Nyakach (ca 15 Ma) and Fort Ternan (12.5–13 Ma), Kenya.

7. Discussion and conclusions

Fossilised grass in fine-grained volcanic ash horizons at Bukwa (Early Miocene, Uganda), complete with the root systems in palaeosols that underlie each ash, provide the earliest good evidence for the existence of grassland ecosystems in tropical Africa. Previously, the earliest such ecosystem was recorded at Nyakach, (ca 15 Ma) in western Kenya [32].

Study of the fossil terrestrial gastropods from Bukwa supports the conclusion that the sediments accumulated in a grassland environment, but suggests that, in addition, there was woodland or forest in the vicinity at the time of deposition, a suggestion comforted by the macrobotanical remains found there [18].

For several reasons, the discovery of a grassland ecosystem in Early Miocene strata at Bukwa, Uganda, is important for understanding the evolution of vegetation types in the African tropics. Firstly, it effectively refutes the idea that tropical forest extended in an unbroken belt from the Atlantic to the Indian Ocean shores of Africa during the Early Miocene [1]. It reveals that vegetation mosaics have been a feature of tropical Africa for at least 17.5 Ma [2]. Secondly, the mammal fauna from Bukwa, with its grassland ecosystem, differs in several respects from Early Miocene faunas found in more wooded to forested locales, including Songhor, Koru, Rusinga and Napak, in which hominoid primates are a relatively common element [19,21,22]. Bukwa is unusual in having yielded very few primate fossils, but such a paucity of hominoids is more understandable when the grassland aspect of the palaeoenvironment is taken into account.

The presence of a grassland ecosystem at Bukwa pre-dates by about 10 Myr the origins of the family Hominidae, as well as the onset of the trend among African large mammals, such as Elephantidae and Suidae, to develop hypsodont cheek teeth endowed with cementum. Small mammals, such as lagomorphs (*Austrolagomys*), macroscelidids (*Myohyrax*), and some rodents (*Diamantomys*, *Bathyergoides*, *Megapedetes*) developed hypsodonty and cementodonty at a much earlier geological epoch, the earliest records of these taxa pre-dating the Bukwa deposits by up to 2 million years. It is thus not beyond the realms of possibility that evidence for the existence of grassland ecosystems even earlier than Bukwa will be found in East Africa when appropriate searches are made.

Acknowledgements. I thank the Uganda National Council for Science and Technology (Drs Nyiira, Kakule, Mugoya), the Uganda Museum (Dr Kamuhangire, Mr Musiime), Makerere University Geology Department (Mrs I. Ssemmanda), the Ministry of Culture, Antiquities and Tourism for authorisation to carry out research and for co-operation within Uganda. The French Embassy in Kampala was of considerable aid to the Uganda Palaeontology Expedition. I am anxious to thank Professors Y. Coppens ('Collège de France') and P. Taquet ('Laboratoire de paléontologie', MNHN, Paris, France) for funds and other assistance. Funding was also supplied by the French Ministry of Foreign Affairs ('Commission des fouilles') and the CNRS (UMR 8569).

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