

First hominoid from the Late Miocene of Niger

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Since the discovery of *Orrorin tugenensis* in the Late Miocene Lukeino Formation, Tugen Hills, Kenya, it is generally admitted that the origin of bipedal hominids occurred earlier than 6 Myr ago and that the adaptation to bipedal stance and locomotion initially occurred in a forested or well-wooded setting. In Africa, eight localities aged between 13 and 5.5 Myr have yielded hominoid fossils belonging to nine species. We here report the occurrence of a Late Miocene hominoid in Niger, associated with a restricted fauna which indicates an age of c. 11–8 Myr. The Niger fossil locality is 940 km north of the nearest known extant hominoids, and 1000 km west of the nearest recorded fossil hominoid from Chad. The scientific value of the Niger specimen resides in its discovery locus far from any other known fossil hominoids, its Late Miocene age and the attention that it will focus on the Neogene fossil record of West Africa, currently almost unknown.

Introduction

It is now widely accepted that the family Hominidae originated in Africa during the Late Miocene. However, the African fossil record for this time period is not well endowed with hominoid fossils, making it difficult to trace the transition from pre-hominid to hominid status. Since 1997, nine hominoid taxa have been reported from eight localities in Africa, ranging in age between 13 and 5 Myr: one species in Namibia [*Otavipithecus* (12–13 Myr)]; five taxa in Kenya^{14,25,28} [a chimp-like hominoid (12.5 Myr), *Nakalipithecus* (9.5–10 Myr), *Samburupithecus* (9.5 Myr), a gorilla-like hominoid (6 Myr), and *Orrorin* (6 Myr)]; two in Ethiopia²⁹ [*Chororapithecus* (10–10.5 Myr) and *Ardipithecus* (5.7 Myr)]; and one in Chad³ [*Sahelanthropus* (6–10 Myr)²³]. Despite the drawbacks of its Late Miocene fossil record, Africa has now yielded a respectable diversity of hominoids comparable with that of Europe and Asia, making it more likely to be the cradle of hominid evolution than Eurasia.¹ All these African Late Miocene taxa are poorly known, and a considerable amount of debate has taken place, even concerning some relatively well-preserved specimens.³ Each addition to the African Late Miocene hominoid fossil sample is therefore precious.

In 1964, a small collection of vertebrate fossils from Niger, which includes a fragment of hominoid mandible, was sent to the Muséum National d'Histoire Naturelle in Paris by the Bataafse Internationale Petroleum Maatshappij (now Shell), where it is curated under register No. 1964-27.885. The precise point of discovery is not known, but it is probably close to 5°43'E, 15°32'N, where some Mesozoic Chelonians² with the register No. 840 were collected by a Mr Nieuwenhuys, who found the mammals.

Palaeontology

The assemblage of fossils from N 885, Niger, comprises well-mineralized skeletal remains of lacustrine and terrestrial animals stained dark brown to black. The fauna is restricted, but contains a Nile perch (*Lates niloticus*), a crocodile (*Crocodylus cf. niloticus*), a chimp-sized hominoid, a medium-sized species of anthracothere (*Libycosaurus* sp.), and a bovid.

Pisces: *Lates niloticus* (Nile perch) is represented at the Niger site by the posterior basal part of the skull.

Crocodylia: *Crocodylus cf. niloticus* (Nile crocodile) is represented at locality N 885 by a brevirostrine mandible with buccal depressions between the teeth, two dermal scutes, two articulated vertebrae, the occipital part of a skull and diverse fragments of skull.

Hominoidea is represented at site N 885 by a right mandible fragment (Fig. 1) containing the roots of the first molar. The mandible is slender and moderately deep. The jaw beneath m1 is 13.2 mm thick, and its depth from the alveolar process to the ventral margin is 31.6 mm. The preserved part of the tooth measured at cervix is 9.4 × 9.7 mm, but judging from the position of the alveoli mesial and distal to the preserved roots, the crown length would originally have been c. 11 mm and the breadth about 9.9 mm. The

sublingual fossa is shallow and low down.

This mandible fragment is compatible in size and proportions to medium-sized hominoids with slender mandibular rami. It is too gracile to belong to an australopithecine, even a small individual such as AL 288-1 (Lucy)¹³ from Hadar, Ethiopia. Comparisons with several hominoids, both extinct and extant, reveal overall similarities to both *Pan troglodytes* (Fig. 1) and *Homo* rather than to any other genera. The jaw is slightly less deep and more gracile than that of *Orrorin*²⁸ and the sublingual fossa is not as deeply excavated.

We consider that the best match for the Niger hominoid fossil is with *Pan*, but because the fossil is fragmentary, we hesitate to attribute it to this or to any other hominoid genus.

Anthracotheriidae: *Libycosaurus* is represented at the Niger site by a distal metapodial attributed to a medium-sized species, larger than *L. petrochii* and smaller than the large species from Sahabi and Chad.^{16,23} The section of the bone at the break reveals a marked degree of dorso-plantar compression which distinguishes this fossil from hippopotamid metapodials²⁴ with which it might otherwise be confused.

Bovidae: The family Bovidae is represented at point N 885 by a left frontal with horn core, a distal left radius and a damaged left calcaneum. The horn core belongs to a reduncine antelope, morphologically close to but smaller than *Redunca darti*.^{8,10}

Age of the Niger fossils

Two specimens from the Niger locality are useful for biochronology. The most telling evidence is the presence of an anthracothere, *Libycosaurus* sp., equivalent to the medium-sized species from Toros-Ménalla, Chad and Sahabi, Libya.^{16,23} Secondly, the bovid horn core has some resemblances to, but is smaller than, material from Sahabi¹⁵ (Libya), Lukeino,³⁰ Mpésida³⁰ and Lothagam¹¹ (Kenya) and Langebaanweg⁹ (South Africa). An age of between 11 and 8 Myr is possible for the deposits that yielded these fossils.

Palaeoenvironment and palaeoclimatology

The presence of Nile perch, *Lates niloticus*, in the Niger deposits indicates the former presence of a freshwater lake or large river in the country. The anthracothere *Libycosaurus* was likely a denizen of shallow swampy parts of a palaeolake, and the reduncine probably lived close to water. This evidence, combined with the

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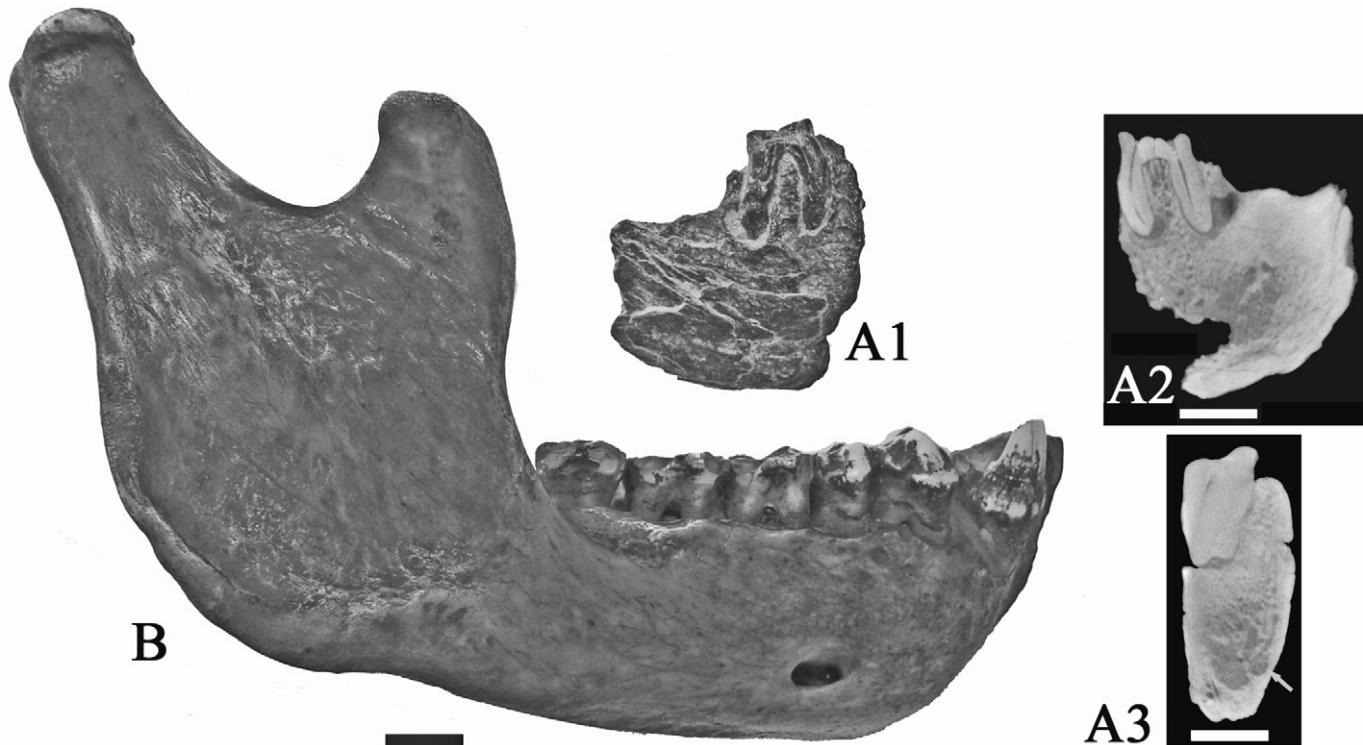


Fig. 1. Hominoid right mandible fragment from Niger (A) compared with a chimpanzee mandible (B): A1) buccal view; A2) sagittal scan, mesial to the left; A3) frontal scan, buccal to the left (arrow points to the mandibular canal). (Scale bars: 10 mm)

presence of a hominoid primate, indicates that the region was appreciably more humid (at least 750 mm mean annual rainfall) during the Late Miocene than it is today (ranging from sahel to total desert over large areas of the country).

Discussion

Apart from humans, hominoids are today confined to forest and woodland, but the common chimpanzee can survive in sub-humid environments as long as there are enough trees to supply adequate food and security.¹⁷ This means that the longest dry period should not exceed two months, and that the area should be well endowed with riparian forest so that there is always a supply of fresh vegetation in the form of fruit, leaves, pith and bark, even during the driest months of the year. In general, however, chimpanzees and gorillas flourish best in tropical rainforest of Guineo-Congolian affinities.³¹ At present, the most arid environment inhabited by chimpanzees is wooded savanna in Liberia and Miombo woodland in Tanzania.^{17,32} The presence of a chimp-sized hominoid in the Late Miocene of Niger therefore provides evidence that the country was considerably more humid then than it is today, and was at least covered in wooded savanna if not denser vegetation categories.

The discovery of a Late Miocene aquatic and terrestrial fauna in Niger confirms

the view that the Sahara is a relatively young desert, post-dating the Late Miocene. Recent work in Egypt has revealed that central Egypt was covered in woodland to forest some 11–10 Myr ago^{26,27} and Chad is long known to have been more humid in the past than it is today^{5,6,20} as were Libya⁷ and Tunisia.^{21,22}

At present, the chimpanzees living closest to the Niger fossil site occur 940 km to the south in Ghana and Nigeria and 1700 km to the west in Mali (Fig. 2).^{4,32} Niger thus joins an increasing list of African countries that have yielded remains of Late Miocene (c. 11–5.5 Myr ago) hominoids including: Kenya (Lukeino, 6 Myr, two taxa);^{19,25,28} (Samburu Hills, 9.5 Myr);¹² (Nakali, c. 10 Myr);¹⁴ Ethiopia (Ch'orora, c. 10.5 Myr, Middle Awash, c. 5.7 Myr)²⁹ and Chad (Toros-Menalla, c. 10–6 Myr)^{3,23} and it indicates that further research in West Africa will undoubtedly add fuel to the debate about hominid origins. It is clear that during the Late Miocene, hominoids were widespread in Africa and, although the quantity of fossils is limited, the diversity is large, with at least seven lineages already recognized in the time range 11–5.5 Myr ago (in the order in which they were reported: *Samburupithecus*, *Orrorin*, *Ardipithecus*, *Sahelanthropus*, an unnamed protogorilla-like form, *Chororapithecus*, and *Nakalipithecus*) and two between 13 and 11 Myr ago (*Otavipithecus* and an unnamed

chimp-like form). In the circumstances, it seems superfluous to invoke a Late Miocene reintroduction of hominoids into Africa from Eurasia in order to give rise to hominids,¹ a view that was attractive only while the Late Miocene hominoid fossil record of Africa was poorly known.

Conclusions

A restricted vertebrate fauna of Late Miocene age from Niger is of interest on account of its age and the presence within it of a hominoid primate and an anthropocene. The discovery helps to fill what was a vast gap in the geographic coverage of fossil hominoids; the nearest known fossil specimen of comparable age being from Chad, over 1000 km to the east and 3500 km from sites in Ethiopia and Kenya that have yielded Late Miocene hominoids. The site is closer to the Spanish Late Miocene hominoid sites (3000 km)¹⁸ than it is to the East African ones. The find site, the position of which is not precisely known at present, is about 940 km north of the closest extant hominoids (*Pan troglodytes*) in Ghana and Nigeria. The fauna as a whole indicates the former presence of a freshwater lake or large river in Niger, and a Late Miocene palaeoclimate considerably more humid than that of today. The scientific value of the Niger hominoid specimen resides in the attention that it will focus on a palaeontologically poorly known part of the continent, which

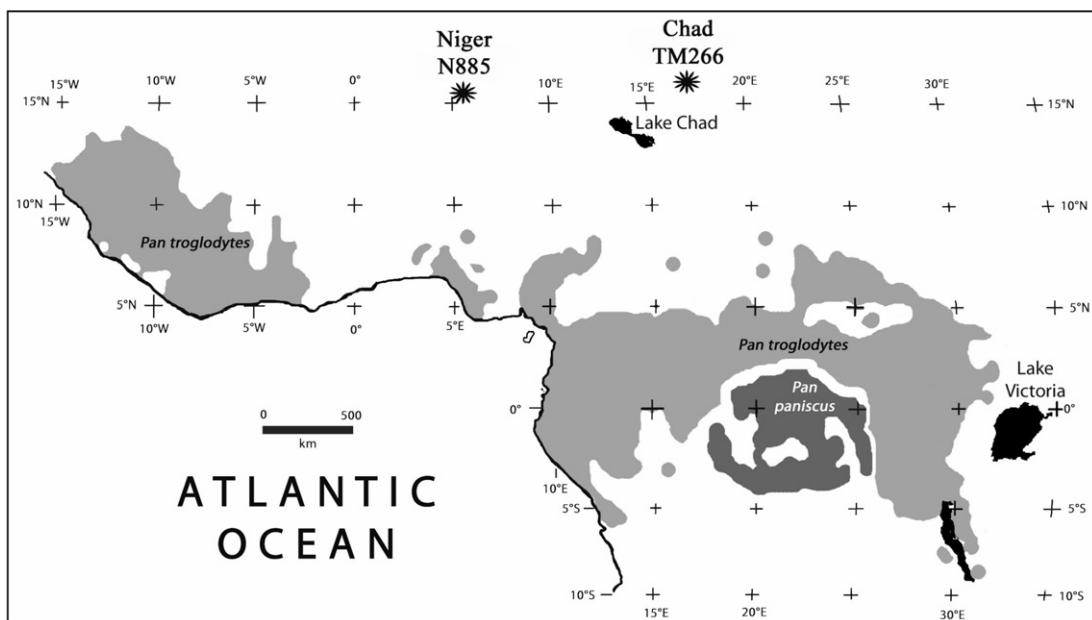


Fig. 2. Extant distribution of species of *Pan*, and the position of two Late Miocene hominoid localities (stars) (*Pan* distribution based on data in Butynski⁴).

nevertheless probably has a great deal to contribute to our knowledge about the origin of hominids.

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