

Human palaeontology and prehistory

Late Miocene hominoid from Niger

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Received 25 September 2008; accepted after revision 19 November 2008

Available online 4 February 2009

Presented by Philippe Taquet

Abstract

African Late Miocene hominoids are rare, having been reported from six localities in Kenya, Ethiopia and Chad ranging in age from 10.5 to 5.5 Ma. We here report the occurrence of a hominoid in Niger associated with a vertebrate fauna which indicates an age of between 11–5 Ma. The Niger fossil locality is 940 km north of the nearest known extant hominoids, 1000 km west of the nearest recorded fossil hominoid from Chad. **To cite this article:** *M. Pickford et al., C. R. Palevol 8 (2009).*

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Résumé

Un hominoïde du Miocène supérieur au Niger. Les hominoïdes du Miocène supérieur d'Afrique sont encore mal connus aujourd'hui ; ils ne sont présents que dans six localités du Kenya, d'Éthiopie et du Tchad, échelonnées dans le temps entre 10,5 et 5,5 Ma. Dans cet article, nous signalons la présence, au Niger, d'un hominoïde associé à une faune de vertébrés qui indique un âge de 11 à 5 Ma. Le site fossilifère est situé à 940 km au nord de la zone de répartition la plus proche des hominoïdes modernes et à 1000 km à l'ouest du plus proche hominoïde fossile connu au Tchad. **Pour citer cet article :** *M. Pickford et al., C. R. Palevol 8 (2009).*

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Keywords: Niger; Africa; Late Miocene; Hominoid; Mandible; Fauna

Mots clés : Niger ; Afrique ; Miocène supérieur ; Hominoïdé ; Mandibule ; Faune

1. Introduction

Late Miocene hominoids are rare in Africa (Fig. 1). It is therefore of interest to report the recognition of a fauna of this age from Niger containing a hominoid. A small collection of fossils housed at the Muséum national d'histoire naturelle (MNHN) in Paris since 1964 was sent to this institute by the Bataafse Internationale Petroleum

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Fig. 1. Distribution of Late Miocene Hominoidea. The Niger find helps to fill what was a vast gap in the distribution of the group.

Fig. 1. Répartition des Hominoidea au Miocène supérieur. Leur découverte au Niger permet de combler une lacune énorme dans la distribution du groupe.

Maatshappij (now Shell). The material is curated under register no. 1964-27.885. Labels with the fossils are the original typed field labels filled in by the oil company geologist who collected them, Mr Nieuwenhuys (Fig. 2), and there are handwritten labels by Camille Arambourg, at the time honorary professor in the laboratoire de paléontologie. According to correspondence in the MNHN archives the precise point of discovery was marked on a map accompanying the fossils, but the copy of the map sent to the MNHN has since been mislaid. All the fossils collected by Mr Nieuwenhuys

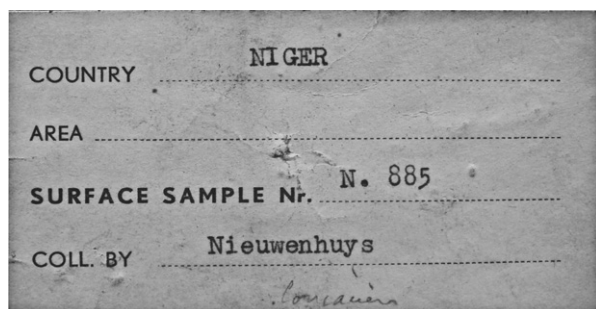


Fig. 2. Label accompanying the fossils described in this paper. Note the handwritten word at the base “Coniacien”, evidence suggesting that they were found on a Cretaceous substrate.

Fig. 2. Étiquette accompagnant les fossiles décrits dans ce papier. Le mot « Coniacien » écrit à la main en bas indique que les fossiles ont été découverts sur des niveaux du Crétacé.

comprising locality numbers 839, 840, 841, 852, 867, 890, 892, 893, 905, 907, 912, 914, 916, 920, 922, 924, 926, 928, 935, 950, 954, 955, 956 belong to Mesozoic taxa. Since locality 885 falls in the middle of this sequence, we consider it likely that the Late Miocene fossils came from the same general area as the others, especially as he was charged with mapping the geology of an oil concession which had precise boundaries. The locality is probably close to longitude 5°43'E: latitude 15°32'N, where Mesozoic Chelonians with the register no. 840 [2] were collected by the same geologist who found the mammals (Fig. 2). Correspondence between the director of the petroleum company and professor Arambourg shows that the geologist considered the entire palaeontological collection to be Cretaceous, which indicates that they were all collected within the general area of Cretaceous outcrops. The label accompanying the fossils indicates the same thing (Fig. 2) especially as it has the word “Coniacien” written on it. Arambourg replied that “certain elements (no. 885), even though collected from a Cretaceous substrate, belong to the Quaternary, and with little doubt consist of (material from) a surface locality” (senior author’s translation from the French). Until a map is found, there will naturally remain some doubt about the exact discovery locus, but the general area of discovery seems assured.

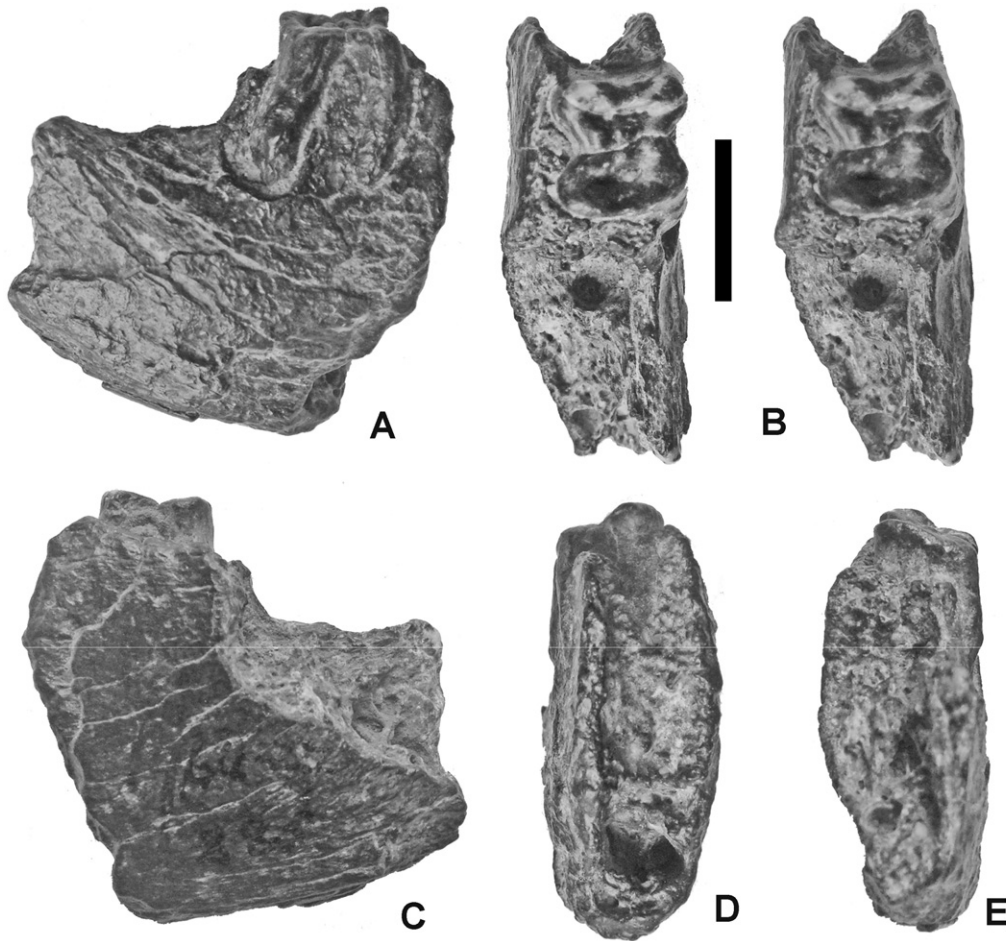


Fig. 3. 1964-27.885, hominoid right mandible fragment from Niger: buccal (A), stereo occlusal (B), lingual (C), anterior (D) and posterior (E) views (scale: 10 mm).

Fig. 3. 1964-27.885, fragment de mandibule droite du Niger, vue buccale (A), vue occlusale stereo (B), vue linguale (C), vue antérieure (D) et vue postérieure (E) (échelle : 10 mm).

The assemblage of fossils comprises lacustrine and terrestrial animals and the specimens are dark brown to black, well mineralised and comprise a preservationally homogeneous sample. The fauna is restricted, but contains remains of Nile Perch (*Lates niloticus*), a crocodile (*Crocodylus* cf. *niloticus*), a chimp-sized hominoid, a medium-sized species of anthracothere (*Libycosaurus* sp.) and a bovid. The combination of a medium-sized species of *Libycosaurus* and a reduncine antelope indicates a probable Late Miocene age for the assemblage.

The fish remains, crocodile, the anthracothere and a reduncine antelope, as well as the presence of a hominoid primate, indicate that the region was appreciably more humid during the Late Miocene than it is today.

2. Palaeontology

Pisces *Lates niloticus* (Nile Perch) is represented at the Niger site by the posterior basal part of the skull. The distal surface of the bone is ovoid with a conical depression much like those developed on vertebrae. Well developed growth ridges are developed inside the conical depression. The ventral part of the specimen is scored by longitudinal grooves and the dorsal surface shows an articular surface for the rest 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. The mandible is the most diagnostic specimen, and preserves the canine

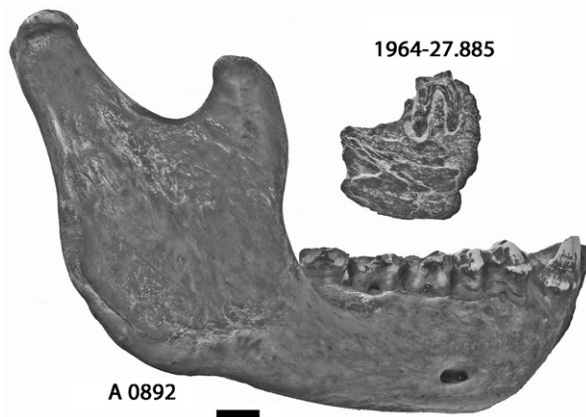


Fig. 4. Comparison of Hominoid right mandible fragment from Niger with *Pan troglodytes*, right lateral views (scale bar: 10 mm).

Fig. 4. Comparaison de la mandibule droite de l'homoïde du Niger avec celle de *Pan troglodytes*, vues latérales droites (barre d'échelle: 10 mm).

alveolus opposite the rear of the symphysis. The anterior part of the symphysis is broken, but two complete and one damaged precanine alveoli are present. The form of the symphysis and the disposition of the precanine and canine alveoli reveal that the mandible belongs to a brevirostrine crocodile. There are six complete and one broken postcanine alveoli preserved. The alveolar process descends behind the canine, levels out at the third and fourth postcanine teeth and ascends towards the seventh alveolus. The buccal margin of the alveolar process is indented between the teeth, such that in lateral view, the bases of the alveoli stand proud of the rest of the jaw, but lingually the alveoli are confluent with the rest of the jaw. These buccal depressions would receive the upper teeth when the jaws are closed. Immediately to the lingual side of the postcanine alveoli there is a line of emissary pits. Mesial to the canine there is a large foramen in the dorsal surface of the jaw. On the lingual side of the specimen, there is a deep groove leading anteriorly from the zone where the splenial terminates, revealing that the splenial was not implicated in the symphysis. This groove leads into a large fossa in the symphysis.

Hominoidea is represented at site N 885 by a right mandible fragment (Figs. 3–5) containing the roots of the first molar. After comparing the Niger specimen with other mammals, including cercopithecids, hominoids, many ungulates, and carnivores, 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. Particular points of resemblance to African apes are the overall morphology of the jaw, the length and orientation of the roots,

and the buccolingual fusion of the roots, a combination that rules out most mammals except for primates.

The mandible is slender and moderately deep. The jaw beneath m/1 is 13.2 mm thick, and its depth from the alveolar process to the ventral margin is 31.6 mm. The roots of the molar are ca 13 mm long and they curve gently distally. They are fused buccolingually (Fig. 5). The preserved part of the tooth measured at cervix is 9.4 mm × 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 ca 11 mm and the breadth about 9.9 mm. The buccal roots which have been exposed by the removal of alveolar bone by sand blasting (and perhaps by alveolar dehiscence prior to death) show an appreciable amount of flare. The sublingual fossa is shallow and low down.

This mandible fragment is compatible in size and proportions to those of 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) [14] from Hadar, Ethiopia. Comparisons with several hominoids, both extinct and extant, reveal overall similarities to both *Pan troglodytes* (Fig. 4) and *Homo* rather than to any other genera. A low but palpable ridge low down on the lingual side of the jaw beneath m/1 could represent the distal extremity of a simian shelf where it fades into the body of the mandible. In *Homo*, the homologous zone of the jaw is generally hollow and is thus devoid of a ridge. The jaw is slightly less deep than that of *Orrorin* from the Late Miocene of Kenya [30] and the sublingual fossa is not as deeply excavated. The mandible of *Orrorin* is slightly more robust than that of the Niger hominoid.

The scientific value of the 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, except for the Chadian specimens [3].

Anthracotheriidae *Libycosaurus* is represented at the site by a distal metapodial attributed to a medium-sized species, larger than *L. petrocchii* from Beglia and smaller than the large species from Sahabi and Chad [17]. The distal articular facet has a ventral ridge or keel (eroded away by sand-blasting). The dorsal surface of the articulation is smoothly cylindrical without grooves (unlike some hippopotamid specimens which do have shallow grooves that extend onto the dorsal surface from the deep grooves found on the plantar surface), and terminates proximally in a shallow curved depression which separates it from the diaphysis. A shallow ligamentary groove leads proximoaxially from this depression (Fig. 8). The medial and lateral sides of the epiphysis show deep lig-

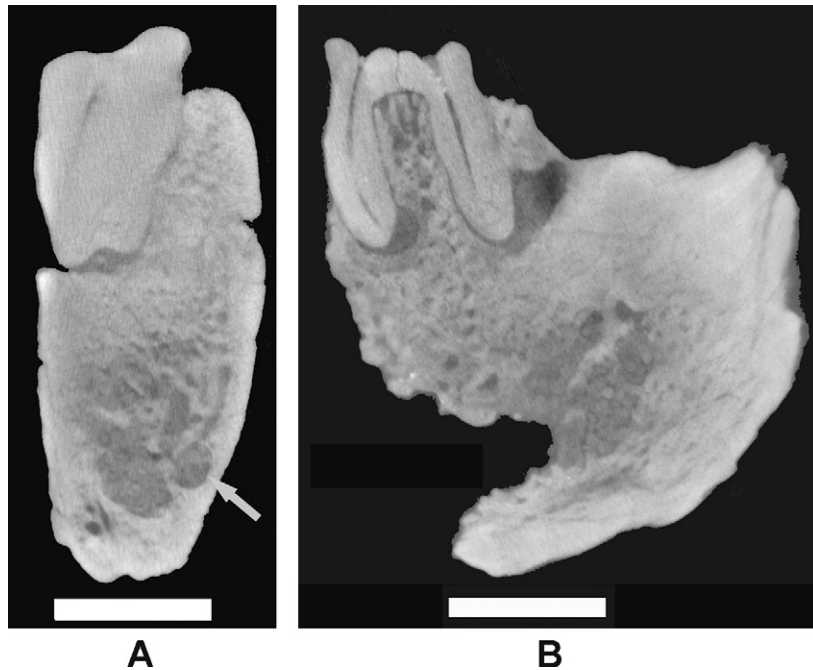


Fig. 5. CT scans of hominoid right mandible from Niger. A. Frontal scan anterior view, (arrow shows the mandibular canal), buccal to the left. B. Sagittal scan, mesial to the left (scale bars: 10 mm) (main specifications of the micro-CT: resolution peripheral CT for measurements of both bone density and bone microarchitecture is $41\text{ }\mu\text{m}$ nominal isotropic, 60 kVp/40 keV [1 mA]).

Fig. 5. Scanners de la mandibule droite de l'humanoïde du Niger. A. Plan frontal, vue antérieure (la flèche indique le canal mandibulaire), partie buccale vers la gauche. B. Plan sagittal, partie mésiale vers la gauche (échelles: 10 mm) (caractères du microscanner: la résolution périphérique CT pour les mesures de la densité osseuse et de la microarchitecture osseuse sont de $41\text{ }\mu\text{m}$ isotropique à 60 kVp/40 keV [1 mA]).

amentary pits. The plantar aspect of the diaphysis is flat, with low marginal ridges. The axial side is relatively flat with two longitudinal grooves near the distal end, without any swelling distally. The dorsal surface is gently curved, sloping more laterally than medially. The section of the bone at the break reveals a compressed dorsoplantar morphology, 22.6 mm dorsoplantar diameter by 42.4 mm mediolateral diameter. The distal end is 44.5 mm broad (Fig. 6). Comparison with a sample of *Brachyodus onoides* metapodials from the Faluns de la Touraine, France, suggests that it is a IVth metatarsal, in which case the Niger fossil would be from the right hind limb.

The Niger metapodial differs from those of hippopotamids in a number of features. Apart from its more dorsoventrally compressed section (Fig. 7) the diaphysis is perpendicular to the distal articular facet, whereas in hippopotamids the abaxial margin of the diaphysis is inclined and not vertical. In hippopotamids the abaxial part of the dorsal surface of the diaphysis usually slopes quite strongly towards the plantar side, making the cross section of the diaphysis sensibly narrower (and with a curved profile) on the abaxial side than the axial one. In anthracotheres, in contrast, the sec-

tion narrows only slightly towards the abaxial side of the bone, as in the Niger specimen (Fig. 6) and the abaxial edge is almost flat. In hippos, the distal end of the metapodial diaphysis sports prominent axial and abaxial swellings close to its zone of fusion with the distal epiphysis (Fig. 8). As a result of this swelling, the diaphysis is wider distally than it is near its centre. In anthracotheres, in contrast, the abaxial swelling is minor and the axial one is nonexistent, and as a consequence, the diaphysis is almost constant in breadth from its centre towards its distal end. This morphology is related to the structure of the foot, which in anthracotheres has the axial metapodials in close contact with each other throughout their length, whereas in hippopotamids, the metapodials splay outwards distally, thereby broadening the feet.

The dimensions of this metapodial are greater than those of *Libycosaurus petrocchii* from Beglia, Tunisia, and belong to the smaller of the two unnamed anthracotheres that occur in Chad and Libya [17,24,25] (Fig. 9). Of these the smaller species ranges in age from about 10 to 8 Ma and the larger from ca 8 Ma to perhaps as young as 6–5 Ma [24]. On this basis the Niger collection is expected to be between 10 and 8 Ma but we

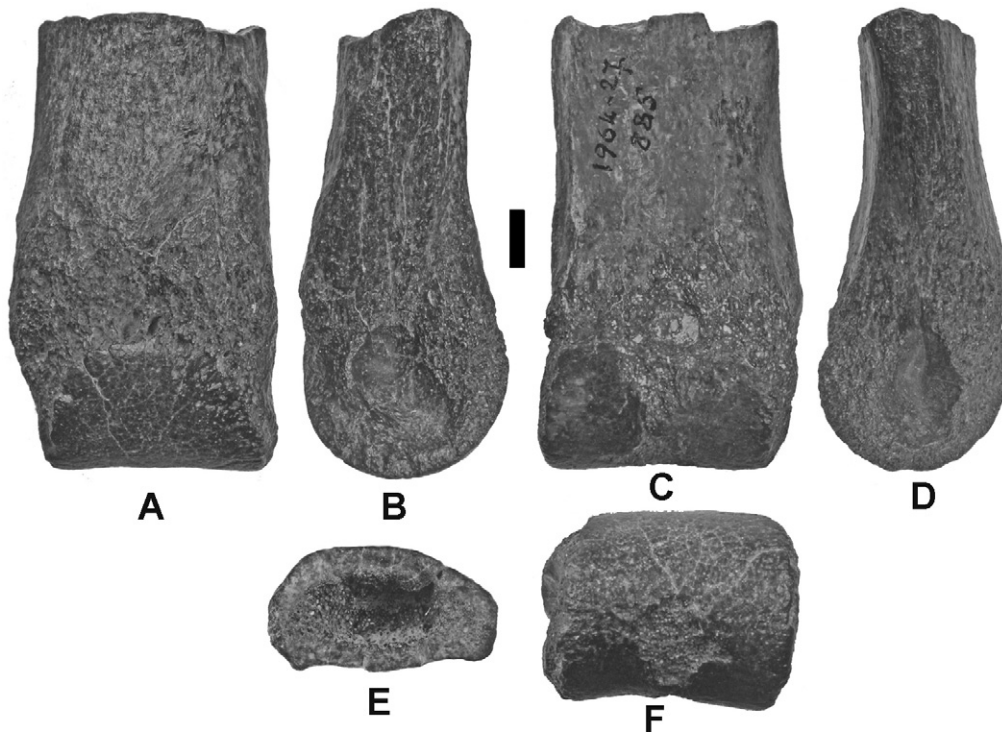


Fig. 6. *Libycosaurus* medium-sized sp. distal metapodial, probably right Mt IV, from Niger dorsal (A), medial (B), plantar (C), lateral (D), proximal (E) view of broken surface to show compressed section of diaphysis, and distal (F) views (scale: 10 mm).

Fig. 6. Extrémité distale de métapode (probablement un Mt IV droit) d'une espèce de taille moyenne de *Libycosaurus* provenant du Niger. Vue dorsale (A), vue médiale (B), vue plantaire (C), vue latérale (D), vue proximale (E) de la surface cassée qui montre la section comprimée de la diaphyse et vue distale (F) (échelle: 10 mm).

take a cautious view and correlate it to the Late Miocene (11–5 Ma).

The value of this anthracothere specimen, even in its fragmentary state, is that it yields evidence of the age of the deposits from which it came. Secondly, it indicates the former presence of shallow swamps or lake margins in what is now an extremely arid part of the world.

Bovidae. The family Bovidae is represented at point N 885 by a left frontal with horn core (Fig. 10) a distal left radius and a left calcaneum lacking the talar process and part of the sustentaculum tali. The base of the horn core is 34 mm mediolateral diameter by 29 mm antero-posterior. It is inserted above the orbit, and its base on the lateral side is lower than the dorsal edge of the frontal. The frontal bears a precornual fossa. The horn core itself has no obvious sign of transverse ridges. The frontal is thick, the pedicle short, and there is no penetration of a sinus into the base of horn core, only a foramen in the roof of the orbit. It preserves the interfrontal suture and a part of the parietal suture. The postcornual fossa is deep and relatively large (8 mm × 5 mm) and is located in a posterolateral position. The medial keel is well marked,

although displaced posteriorly and the lateral one is weakly marked. The vertical grooves are exceptionally deep where associated with the medial keel. The horn core slopes backwards at a marked angle and diverges at about 30° from the sagittal plane. The apex of the horn core is broken off, but as preserved it is 77 mm long measured anteriorly from the top of the pedicle.

The morphological features of this fossil frontal and horn core are only encountered in representatives of the bovid subfamily Hippotraginae, and more particularly in members of the tribe Reduncini. In overall aspect it differs from species of *Kobus* (which is well represented in the African fossil record) by the transverse section of the horn core, which is more circular in *Kobus*, with the mediolateral diameter slightly greater than the antero-posterior one. Lehmann and Thomas [16] used the more circular outline of the section of the horn core as the basis for attributing two frontals and a horn core from the Late Miocene of Sahabi, Libya, to *Redunca* aff. *darti*, differentiating them from *Kobus subdolos* from the Latest Miocene of Langebaanweg, South Africa [9], and the reduncines from the Late Miocene of Mpesida and Lukeino, Kenya [32]. For the same reasons, the Niger

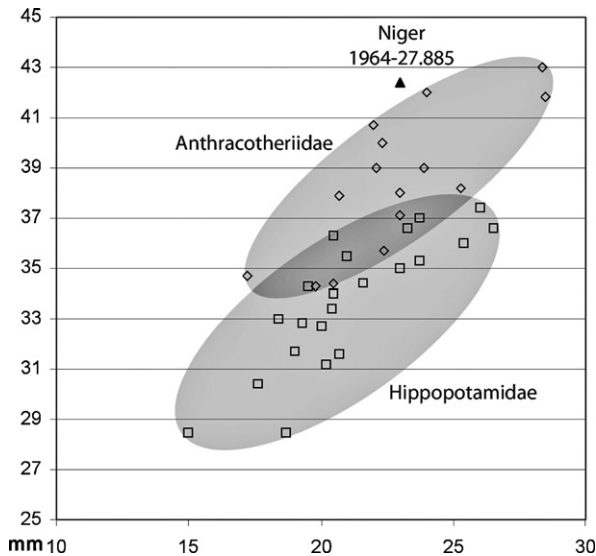


Fig. 7. Bivariate scatter plot of metapodial diaphyses dorsoplantar thickness (horizontal axis) and mediolateral diameter (vertical axis) of *Brachyodus onoides* and *Hippopotamus* spp. from Omo, Ethiopia. 1964–27.885 falls close to the range of variation of anthracotheres and far from that of hippos. The Niger fossil is therefore attributed to *Libycosaurus* sp. [24].

Fig. 7. Variation des dimensions d'épaisseur dorsoplantaire (axe horizontal) et médiolatérale (axe vertical) des diaphyses de métapodes de *Brachyodus onoides* et *Hippopotamus* spp. de l'Omo, Éthiopie. 1964–27.885 tombe dans la variation des anthracothères et loin de celle des hippopotames. Le fossile du Niger est donc attribué à *Libycosaurus* sp. [24].

specimen differs from the reduncines from the Late Miocene of Lothagam, Kenya [12].

The Niger bovid species is smaller than *Redunca darti* from Middle Pliocene of Makapansgat, South Africa (type locality of the species), and from *Redunca* aff. *darti* from Sahabi, Libya [16], although it shares morphological affinities with the latter specimens.

Lehman and Thomas [16] described a bovid frontal from the Late Miocene of Sahabi, Libya, which they attributed to *R. darti*, which differs from the Niger specimen by the greater divergence of its horn cores, but in other respects the two specimens are concordant, save in their dimensions, the Niger specimen being appreciably smaller than the Sahabi ones. Gentry [11] in contrast, considered that the Sahabi specimens previously attributed to *R. darti*, belong instead to *Kobus* aff. *subdolus*. The Niger fossil shows some similarities to a horn core from Lukeino, Kenya, attributed to *Kobus porrecticornis* by Thomas [32] although the latter specimen does not show the posteromedial flattening at the base, although it does show flattening near the apex. *K. porrecticornis* was first described from the Middle Siwaliks of Pakistan (Dhok Pathan Zone, ca 7 Ma)

and similar fossils occur at Sahabi, Lothagam, Langebaanweg, Lukeino [8] and other Late Miocene sites in Africa.

Zephyreduncinus oundagaisus from the Late Miocene of Ethiopia [33] is markedly divergent from the Niger species. The Ethiopian species has strong horn core compression, the opposite of the Niger specimen and, in addition, the disposition of the keels is different. In *Zephyreduncinus* (Vrba and Haile-Selassie [33], figure 2) the keel is anterior with slight torsion outwards, whereas in the Niger specimen the keels of the horn are medial and lateral.

Both *Redunca* and *Kobus* are aquaphile bovids [10,32] living close to water, or in tall grass plains, although they can inhabit quite open country but usually not far from riparian woodland to forests.

3. Age of the Niger fossils

Despite the restricted quantity of fossils from the Niger locality, two specimens are useful for biochronology. The most evocative evidence is that of an anthracothere, *Libycosaurus* sp. equivalent to the medium-sized species from Toros-Ménalla, Chad and Sahabi, Libya [17,24]. Secondly, the bovid horn core has some resemblances to material from Sahabi (Libya), Lukeino, Mpesida and Lothagam (Kenya) and Langebaanweg (South Africa). Combined, the two fossils suggest that an age between 11 and 5 Ma is possible for the deposits that yielded these fossils.

4. Palaeoenvironment and palaeoclimatology

The presence of Nile Perch, *Lates niloticus*, in the Niger Late Miocene deposits indicates the former presence of a freshwater lake or large river in the country. It is not known whether this would have been part of Late Miocene Palaeolake Chad (not to be confused with Holocene and Late Pleistocene Megachad) [21], or whether it was a separate lake. If the latitude and longitude of the locality are close to those indicated by Bergounioux and Crouzel [2] for the type skull of *Nigermys gigantea* as suggested by the field label (Fig. 2), then it would in all probability have been a separate lake. The anthracothere *Libycosaurus* was likely a denizen of shallow swampy parts of the palaeolake or river, and the reduncine probably lived close to water. The palaeoenvironment was possibly rather like that of the extant Lechwe (*Kobus leche*) which is common in the Okavango Swamp, Botswana. Unlike the Okavango, however, the Niger palaeolake had vast and deep fully

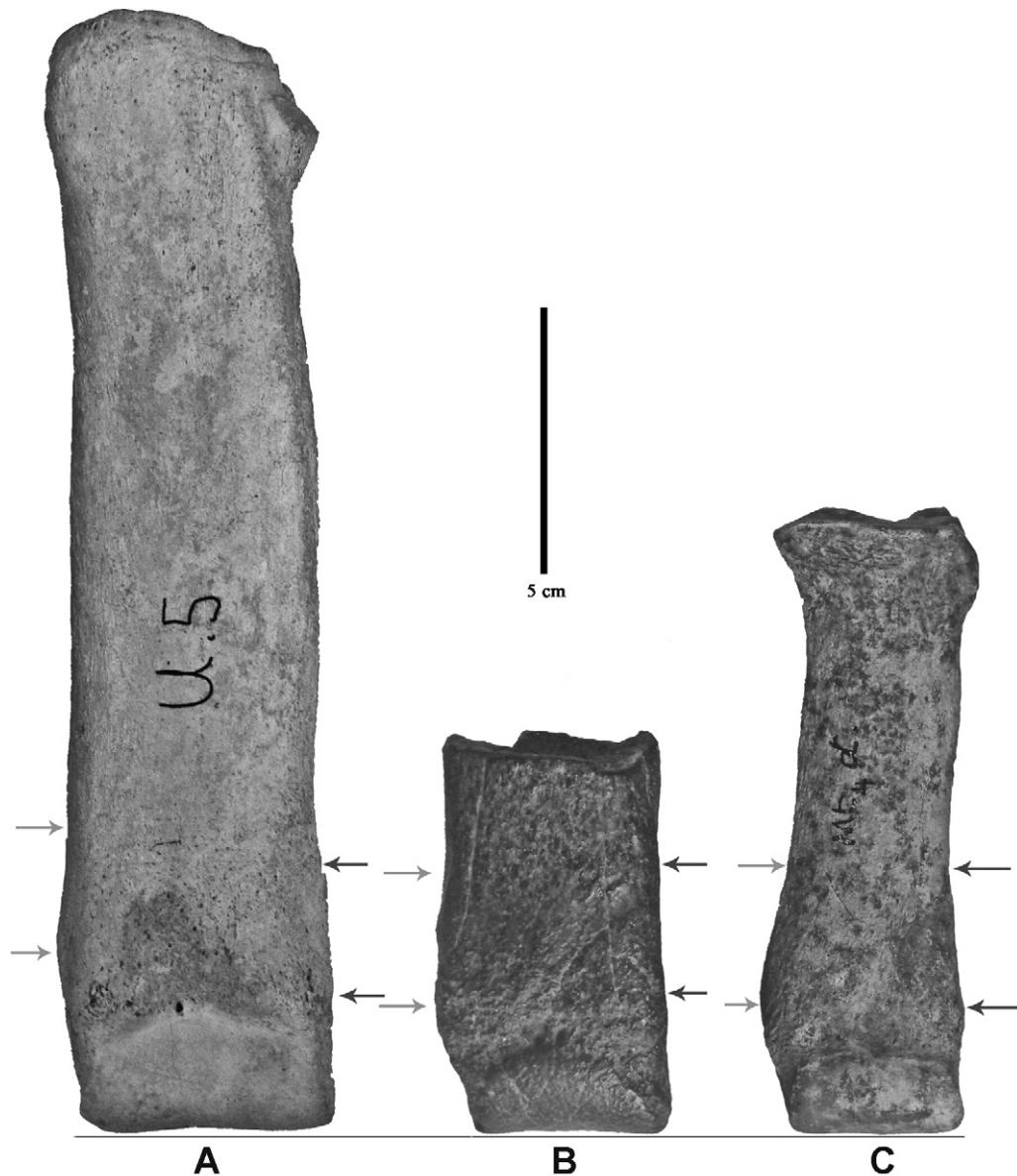


Fig. 8. Comparison of metapodials of the Niger anthracothere, *Brachyodus* and a hippopotamid, distal ends oriented horizontally, dorsal views. A. NHM U5, right MT IV, *Brachyodus aequatorialis* from Gebel Zelten, Libya. B. Niger 1964-27.885 distal metapodial, probably right MT IV, *Libycosaurus* sp. C. 1933-9.490 hippopotamid right MT IV from Omo, Ethiopia. Note the distal swelling of the diaphysis close to the epiphyseal suture in the hippo, a structure that is absent or much less evident in anthracotheres (grey arrows: abaxial side, black arrows: axial side). The margins of the anthracothere metapodial are vertical with respect to the distal articulation, whereas in the hippo metapodial the abaxial margin slants proximoaxially. In hippos, there is a swelling on the axial side of the distal end of the epiphysis (lower black arrow), a structure that is reduced or absent in anthracothere metapodials.

Fig. 8. Comparaison de métapode de l'anthracothère du Niger avec ceux de *Brachyodus* et d'un hippopotame, vues dorsales. A. NHM U5, MT IV droit, *Brachyodus aequatorialis* du Gebel Zelten, Libye. B. Niger 1964-27.885 métapode distal, probablement MT IV droit de *Libycosaurus*. C. 1933-9.490 MT IV droit d'un hippopotame de l'Omo, Éthiopie. Noter le gonflement distal de la diaphyse près de la suture de l'épiphyse chez l'hippopotame qui est absent ou moins marqué chez l'anthracothère (flèches grises: côté abaxial, flèches noires: côté axial). Les bords du métapode de l'anthracothère sont verticaux par rapport avec l'articulation distale; en revanche, chez l'hippopotame, le bord abaxial est incliné proximoaxialement. Chez les hippopotames, il y a un gonflement sur le bord axial de la partie distale de la diaphyse du métapode (flèche noire la plus basse), qui n'existe pas chez l'anthracothère.

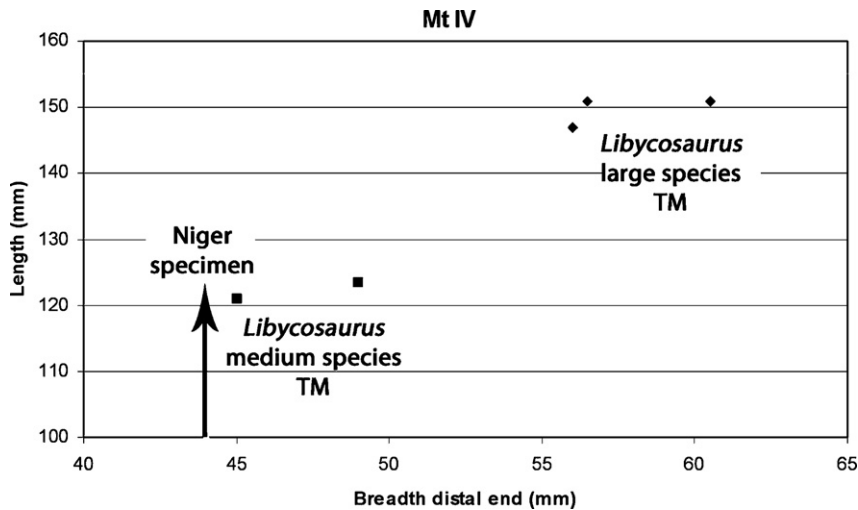


Fig. 9. Dimensions of the distal end of Mt IV in *Libycosaurus* species from Toros-Ménalla, Chad, and Niger. The medium-sized species is considered to range in age from ca 10–8 Ma, and the large species from ca 8–7 Ma [24,25] (TM data from ref [17]).

Fig. 9. Mensurations de l'extrémité distale du Mt IV des espèces de *Libycosaurus* de Toros-Ménalla (Tchad) et du Niger. L'espèce de taille moyenne aurait un âge de 10 à 8 Ma environ et la grande espèce de 7 à 8 Ma [24,25] (les données sur Toros-Ménalla sont tirées de Lihoreau [17]).

lacustrine zones in which Nile Perch could grow to large dimensions.

5. Discussion

Nonhuman hominoids are today confined to forests and woodlands, but the common chimpanzee can survive in subhumid environments as long as there are enough trees to supply adequate food and security [18]. This means that the longest dry period should not exceed two months, and that the area should be 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 rainforests of Guineo-Congolian affinities [34]. At present, the most arid environment inhabited by chimpanzees is wooded savannah in Liberia and Miombo woodland in Tanzania [18,34,35]. If the sort of “prechimp” represented by the Niger fossil can be considered as having the same habits as the extant species, then it may indicate that the country was considerably more humid then than it is today, and was at least covered in wooded savannah if not denser vegetation categories.

The inferred former presence of a Late Miocene palaeolake or large river in Niger inhabited by Nile Perch, surrounded by countryside covered in wooded savannah if not denser vegetation, suggests that the mean annual rainfall was probably greater than 750 mm, and possibly as much as 1200 mm. At present, Niger is one of

the driest countries in Africa, much of it, such as Tenéré, being total desert.

The discovery of a Late Miocene aquatic and terrestrial vertebrate fauna in Niger confirms the view that the Sahara is a relatively young desert, postdating the Late Miocene. Recent work in Egypt has revealed that central Egypt was covered in woodland to forests some 11–10 Ma [28,29] and Chad is long known to have been more humid in the past than it is today [5,6] as was Libya [7] and Tunisia [22,23].

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. 11) [4,34,35]. Niger thus joins an increasing list of African countries that have yielded remains of Late Miocene (ca 11–5.5 Ma) hominoids including, Kenya (Lukeino, 6 Ma, two taxa [20,29]; Samburu Hills, 9.5 Ma [13]; Nakali, ca 10 Ma) [15], Ethiopia (Ch'orora, ca 10.5 Ma) [31] and Chad (Toros-Menalla, ca 10–6 Ma) [24] 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 (Fig. 1) and although the quantity of fossils is restricted, the diversity is large, with at least eight lineages already recognised (in the order in which they were reported: *Otaviapithecus*, *Samburupithecus*, *Orrorin*, *Ardipithecus*, *Sahelanthropus*, an unnamed protogorilla-like form, *Chororapithecus*, and *Nakalipithecus*) [26]. Under the circumstances, it is necessary to reconsider the “Back to Africa” hypoth-

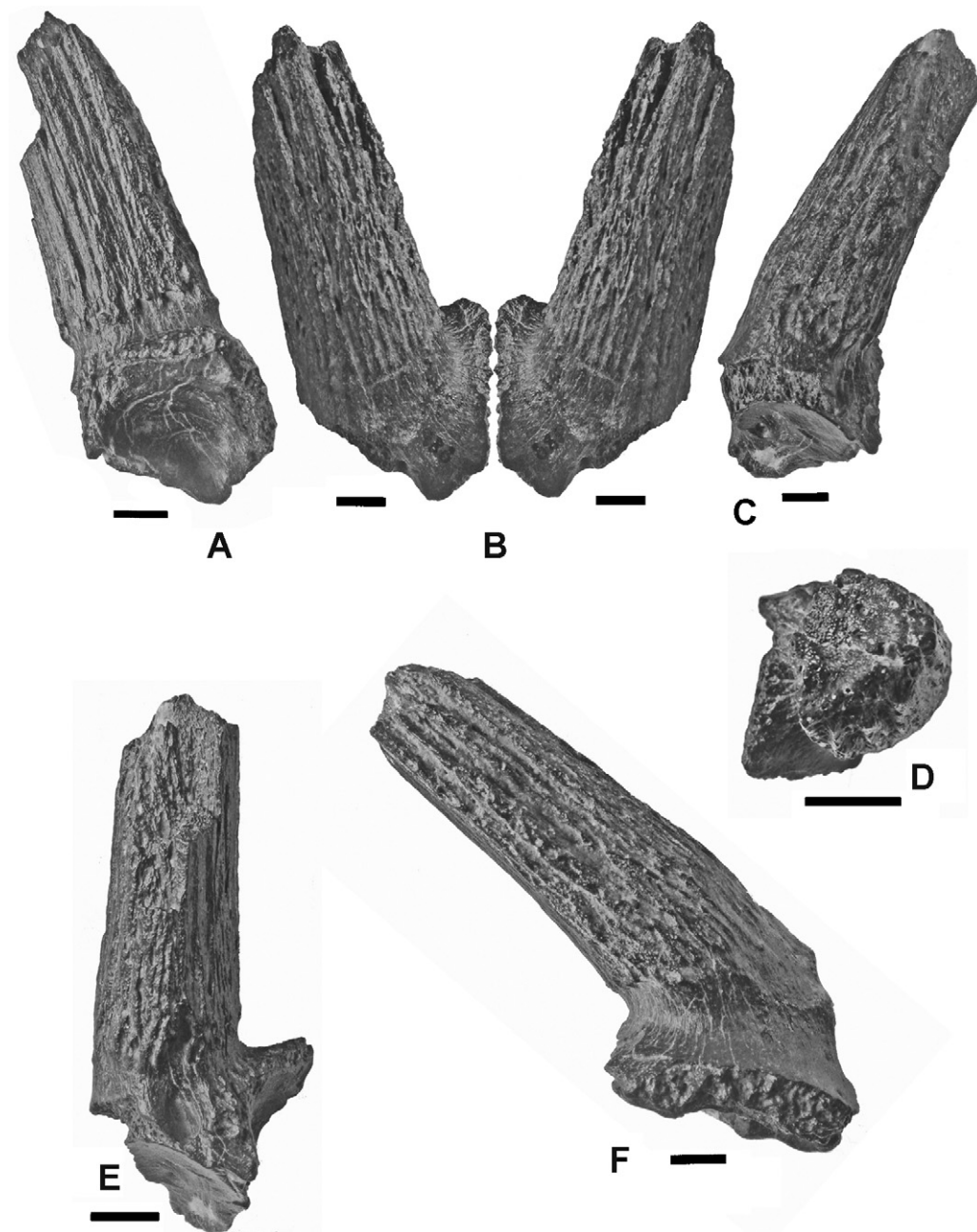


Fig. 10. 1964-27.885, bovid left horn core, medial (A), dorsal view with mirror image (B), oblique posterior view (C), apical view of broken surface to show section (D), posterior view to show postcornual fossa (E), and medial view to show thickened frontal suture indicating adult status for this individual (scales: 10 mm) (F).

Fig. 10. 1964-27.885, cheville osseuse gauche de bovidé, vues médiale (A), dorsale (avec image miroir) (B), postérieure oblique (C), apicale pour montrer la section (D), postérieure (E) pour montrer la fosse postcornuale et médiale (F) pour apprécier l'épaisseur de la suture frontale, qui prouve que l'individu était adulte (échelles : 10 mm).

esis which invokes a Late Miocene reintroduction of hominoids into Africa from Eurasia in order to give rise to extant African apes and hominids [1]. The European genera *Dryopithecus* (*sensu lato*), *Pierolapithecus* [19]

“*Austriacopithecus*” and eventually *Ouranopithecus*, upon which the « Back to Africa » hypothesis is based, could all represent lineages that migrated from Africa towards Europe, rather than the other way round.

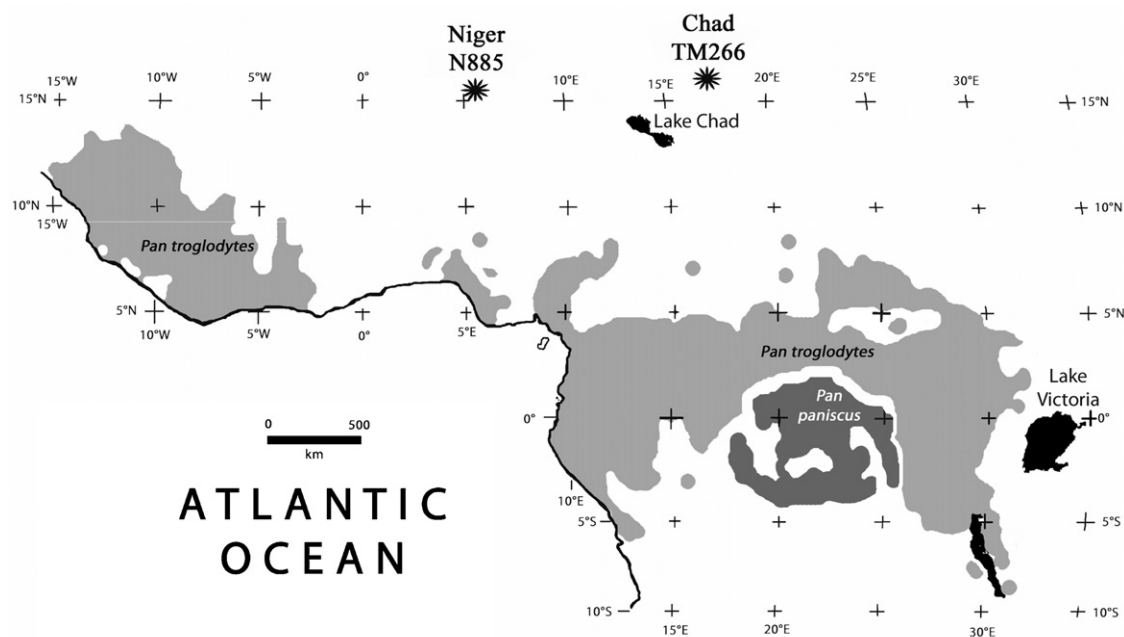


Fig. 11. Extant distribution of species of *Pan*, and the position of two Late Miocene hominoid localities (stars) (*Pan* distribution based on data in ref [4]).

Fig. 11. Répartition actuelle des espèces de chimpanzé et localisation des localités à hominoïdes du Miocène supérieur (étoiles) (les données pour *Pan* sont tirées de Butynski [4]).

Otaviipithecus from 13–12 Ma deposits in Namibia, for example, possessed an atlas vertebra morphometrically close to that of *Pan paniscus*, and its frontal bone [27] shows similar frontal sinus morphology to that of *Pan* and *Gorilla*, which indicates that a late Middle Miocene fossil ape from Africa possessed postcranial and cranial anatomy foreshadowing that of extant African apes, and differing from that of Eurasian apes, both fossil and extant. *Nakalipithecus* [15] from the Late Miocene of Kenya is similar in many ways to *Ouranopithecus*, but it is older than it, suggesting an African origin for this particular lineage. When additional postcranial remains of African Late Miocene hominoids are found, it will be possible to test the «Back to Africa» hypothesis in a more rigorous way, as the hypothesis relies largely on postcranial resemblances between extant African apes and European Late Miocene hominoids.

6. Conclusions

A 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 anthracothere. 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) [19] than it is to the East African ones (3500 km)! The find site, the position of which is not precisely known at present, but lies within the area of outcrop of Mesozoic strata in central Niger, 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.

Acknowledgements

We thank Christine Argot and Claire Sagne for their cheerful and efficient assistance with the collections and registers of fossils at the MNHN. Philippe Taquet, Martine Leroux, Philippe Lapointe, Cristina Perreira and Pascale Heurtel helped in efforts to determine the precise locality of point N 885. Thanks to Philippe Richir for making casts and Jacques Treil (MEDES, Toulouse) for CT scans.

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