

New information about African late middle Miocene to latest Miocene (13-5.5 Ma) African Hominoidea

Helke Mocke¹, Martin Pickford², Brigitte Senut² & Dominique Gommery³

1. Geological Survey of Namibia, National Earth Science Museum, 6 Aviation Road, Private Bag 13297, Windhoek, Namibia (helke.mocke@mme.gov.na)
2. Centre de Recherche en Paléontologie - Paris (CR2P) Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, CP38, 8 rue Buffon, 75005, Paris, France (martin.pickford@mnhn.fr) (brigitte.senut@mnhn.fr)
- 3.- Centre de Recherche en Paléontologie - Paris (CR2P) Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, Campus Pierre et Marie Curie-SU, T.46-56, E.5, 4 Place Jussieu, 75005 Paris, France.(dominique.gommery@sorbonne-universite.fr)

Abstract : In Africa, relatively few hominoid fossils are known from the late middle Miocene and late Miocene periods corresponding to the time span 13-5.5 million years ago, compared to the preceding and subsequent periods from which several thousand specimens have been reported from many different localities. In Eurasia, in contrast, many hominoid fossils are known from the Late Miocene period from diverse localities scattered from Spain in the west to China in the East. The scarcity of hominoid fossils from this period in Africa lent support to the hypothesis that the ancestors of extant African Apes and hominids may have evolved in Eurasia and then dispersed to Africa during the late Miocene where they gave rise to the extant *Gorilla*, *Pan* and *Homo* lineages.

We herein document additional hominoid fossils from Berg Aukas, Namibia, aged ca 12-13 Ma, and rectify the locality data concerning the Niger proto-chimpanzee fossil. The new data indicate that Africa was not devoid of hominoids during the period under discussion, and they support the hypothesis that the extant African Apes and hominids may have evolved autochthonously within the continent.

Key words : Late Miocene, Hominoidea, Diversity, Africa, Provenance, Biogeography

To cite this paper : Mocke, H., Pickford, M., Senut, B. & Gommery, D. 2021. New information about African late middle Miocene to latest Miocene (13-5.5 Ma) African Hominoidea. *Communications of the Geological Survey of Namibia*, **24**, BBBB-BBBB.

Introduction

The African Late Miocene fossil record of Hominoidea is sparse (Campbell & Bernor, 1976; Conroy *et al.* 1992; Ishida & Pickford, 1997; Senut *et al.* 2001; Haile-Selassie, 2001; Brunet *et al.* 2002; Haile-Selassie *et al.* 2004; Pickford & Senut, 2005; Kuniyatsu *et al.* 2007; Suwa *et al.* 2007; Pickford *et al.* 2009a; Pickford & Senut, 2010; Senut, 2010, 2014; Senut & Gommery, 1997; Simpson *et al.* 2015; Kuniyatsu *et al.* 2016). Currently, 12 localities in Africa are known to have yielded hominoid fossils from the period 13-5.5 million years. Despite the rarity of fossils, the diversity of hominoids is relatively great, comprising *Otaviapithecus*, cf *Kenyapithecus*, *Chororapithecus*, *Nakalipithecus*, *Samburupithecus*, *Orrorin*, *Ardipithecus* and *Sahelanthropus*, as well as several poorly preserved un-named

specimens with some gorilla-like and chimpanzee-like attributes (Pickford & Senut, 2005).

In contrast, Eurasian localities spanning the same period of time have yielded several hundred specimens of Hominoidea (Begun, 2001; Begun *et al.* 2012) comprising many taxa. Particularly rich assemblages are known from Spain (*Dryopithecus*, *Anoiapithecus*, *Pierolapithecus*, *Hispanopithecus* - Moyà-Solà & Köhler, 1996; Alba, 2012; Pina *et al.* 2014; Almécija *et al.* 2021), France (*Dryopithecus* - Lartet, 1856), Germany (*Danuvius* - Böhme *et al.* 2019), Italy (*Oreopithecus* - Harrison, 1986; Sarmiento, 1987), Turkey (*Ankarapithecus* - Kappelman *et al.* 2003), Greece (*Graecopithecus*, *Ouranopithecus* - de Bonis *et al.* 1990) Indo-Pakistan (*Sivapithecus*, *Giganto-*

pithecus - Pilbeam, 1980; Kelley, 2002), Myanmar (*Khoratpithecus* - Jaeger *et al.* 2011; Takai *et al.* 2021) and China (*Lufengpithecus* - Harrison *et al.* 2002; Qi *et al.* 2006).

Partly because of the perceived imbalance between the hominoid fossil records of the late Miocene of Africa and Eurasia, some researchers (Begun, 2001) have hypothesised that the ancestors of the extant African apes and humans evolved in Eurasia and then dispersed to Africa towards the end of the late Miocene, eventually to give rise to the gorilla, chimpanzee and human lineages, or that the human lineage split from that of the apes in Europe, and that humans then dispersed back to Africa at the very end of the Miocene (Boehme *et al.* 2020).

Cote (2004) discussed the issues, contrasting the allochthonous and autochthonous alternatives, and pointed out that at least seven African localities in the 13 Ma to 5 Ma time span have yielded hominoid fossils. One of these records (Nkondo, Uganda) is erased, because the isolated tooth upon which it was based (Moggi-Cecchi & Pickford, 1989) is not from a primate.

The presence of a relatively high diversity of hominoids in the late Miocene fossil record of Africa, now known to belong to 8 or more genera (despite the small quantity of fossil material) from at least 12 localities, indicates that it is perhaps more likely that the extant African Ape and Human lineages evolved autochthonously within the continent (Pickford & Senut, 2005; Almécija *et al.* 2021).

A third scenario is that Africa and much of mid-latitude Eurasia formed a single biogeographic province during the middle and early parts of the late Miocene, with many mammalian lineages such as proboscideans, rhinos, equids, ruminants, primates and carnivores, moving relatively freely between the three continents between 15 and 8 million years ago (Campbell & Bernor, 1976; Pickford & Senut, 2005; Senut, 2011, 2020). At ca 8 Ma, global cooling related to uplift of the Himalayas to critical altitudes (Molnar, 2005) and the

growth of the Arctic Ice Cap, led to borealisation of much of mid-latitude Eurasia (Pickford, 1997, 1998) with the consequence that many tropically adapted mammalian lineages, including hominoids, could no longer survive there (Pickford & Morales, 1994; Pickford, 1997, 1998) whereas they continued to flourish in the more humid tropics of Africa and Asia. Over the same time span, dessication of the Paratethys Ocean and its resulting sub-basins across eastern Europe and Asia led to regional aridification (Popov *et al.* 2006; Palcu *et al.* 2019; Sakuma *et al.* 2021) and this process may also have played a role in the disappearance of hominoids from mid-latitude Eurasia ca 8 Ma. Also related to the uplift of the Himalayas and the installation of the monsoon climate, it was towards the end of the Miocene that the Sahara was transformed from a humid subtropical environment to a hyper-arid one (Pickford *et al.* 2006, 2008b, 2010; Wanas *et al.* 2009).

Because the African hominoid fossil record is relatively poor for the period 13-5.5 Ma, each new discovery or precision about previous discoveries is welcome, as it improves our understanding of their diversity and evolution during the remote period during which the split of the human lineage away from that of the apes occurred, currently thought to be sometime between 12 and 8 million years ago (Pickford & Senut, 2005).

For this reason, the present contribution has two aims. The first is to place on record the discovery of additional hominoid fossils aged about 12-13 Ma from the palaeokarst locality of Berg Aukas, Namibia (Pickford & Senut, 2010) and the second is to rectify the locality data concerning a fossil hominoid mandible from the late Miocene of Niger (Pickford *et al.* 2008a).

Both of these localities are far distant from the cluster of sites in Eastern Africa that have yielded most of the evidence about hominoids from this period, and they reveal that members of this superfamily were widespread over the continent during the late Miocene, more so than extant African apes.

Definition

We confine the family Hominidae to mean extant humans (*Homo*) and their obligate bipedal relatives from the late Miocene, Pliocene and Pleistocene, represented by *Orrorin*, *Praeanthropus*, *Kenyanthropus*,

Australopithecus and *Paranthropus* (Senut, 1995, 2011, 2020). Under this usage the hominid status of *Ardipithecus ramidus* and *Sahelanthropus tchadensis* is doubtful, both taxa possessing cranial and post-cranial features

that indicate closer affinities to apes than to humans, in particular their quadrupedal locomotor repertoires (*Sahelanthropus*, *Ardipithecus*) (Sarmiento, 2010; Harrison, 2010; Senut, 2014; Fleagle & Lieberman, 2015; White *et al.* 2015; Macchiarelli *et al.* 2020) and the ape-like angle between planes of the foramen magnum and the orbits in *Sahelanthropus* (Pickford, 2005). Some of the fossils attributed to *Ardipithecus kadabba* (Haile-Selassie, 2001; Simpson *et al.* 2015)

could represent early bipedal hominids, indicating that revision of the material may be required. The latter was already suggested by Senut *et al.* (2018) who considered that the hypodigm of *Ardipithecus kadabba* comprised a chimera of two taxa.

Haile-Selassie *et al.* (2004) suggested that *Sahelanthropus*, *Ardipithecus* and *Orrorin* were synonyms, but the morphological differences between these taxa suggest otherwise.

Part 1. New hominoid fossils from Berg Aukas, Namibia

The first Miocene hominoid fossil reported from south of the Equator, *Otaviapithecus namibiensis*, was discovered at Berg Aukas in 1991 (Conroy *et al.* 1992). During subsequent field surveys additional hominoid fossils were found (Pickford *et al.* 1997; Pickford & Senut, 2010). However, it

transpires that these were not the first ones found at the site, because several specimens are now known to have been collected during the late 1960's by Mr Faan van der Merwe who worked at Berg Aukas mine during its second phase of exploitation (Fig. 1).

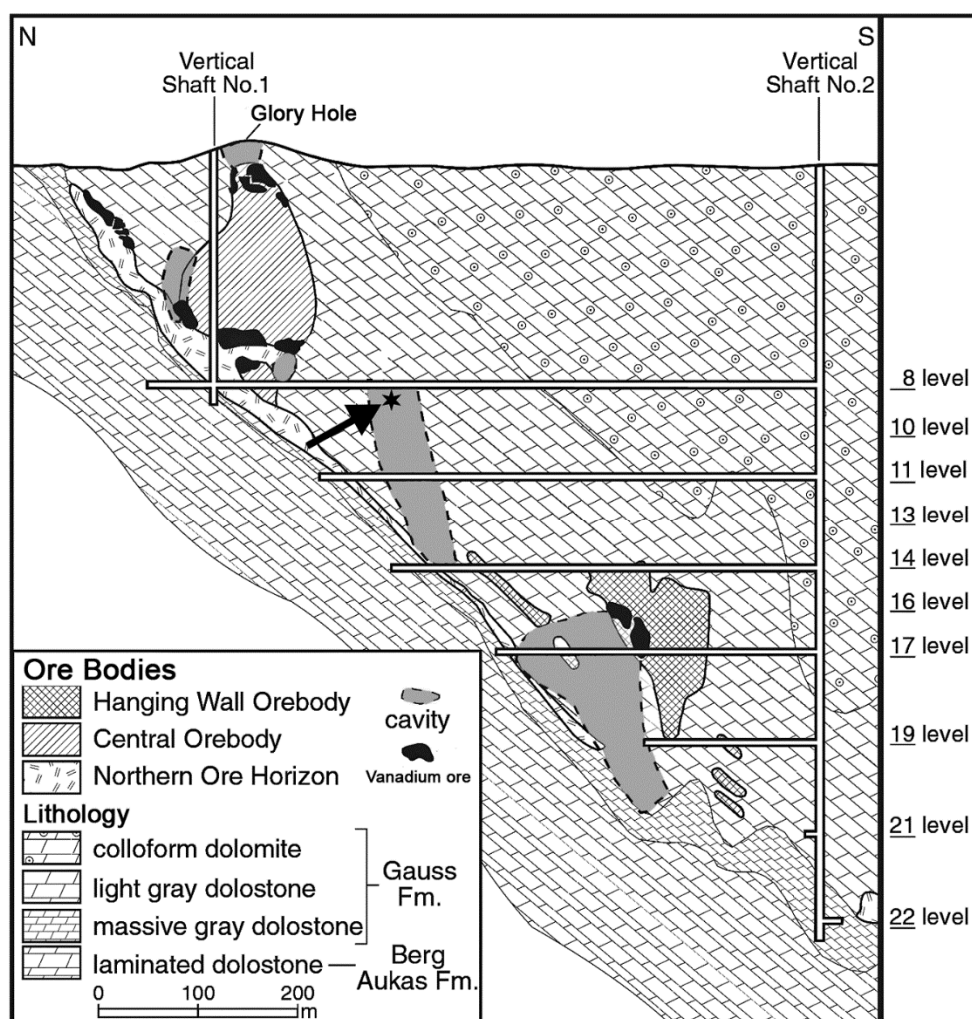


Figure 1. Schematic North-South section through the Berg Aukas Mine highlighting natural cavities in the dolostones (grey zones) and the likely discovery context of the fossils collected by Mr F. van der Merve at level 8.5 (arrowed star symbol). Section modified from Misiewicz, 1988, and Boni *et al.* 2007.

The Berg Aukas lead-zinc-vanadium mine was discovered in 1913 and mined from 1920 to 1928, and again from 1950 to 1978 (Fig. 1). The vanadium ore is associated with spelean and epikarst deposits (Misiewicz, 1988; Boni *et al.* 2007). Beginning in 1991, the systematic sampling and analysis of the breccias from Berg Aukas by the Namibia Palaeontology Expedition (NPE) established a range of ages for the breccias spanning the mid-Miocene to Recent periods (Senut *et al.* 1992; Pickford & Senut, 2010). The fossil faunas discovered at Berg Aukas include Chiroptera, Rodentia, Insectivora, Macroscelidea, Hyracoidea, Artiodactyla, Primates, Carnivora, birds, Squamata and Amphibia.

During the late 1960s Mr. Faan van der Merwe collected fossils from a sandy pocket from level 8.5 in the mine, i.e. 850 ft underground. The mine had carried out a dewatering process three years before he found them. The hominoid specimens were associated with diverse remains of medium-sized to large mammals including a carnivore and a hyracoid (Fig. 2).

On the basis of the preservation characters (colour of bones and teeth, surface characters of the fossils) the new specimens are considered to correspond to samples from breccias of late middle Miocene age (13-12 Ma) (Pickford & Senut, 2010) corresponding the Berg Aukas MM1 or MM2 (MM - micromammal assemblage, Pickford, 2000).



Figure 2. Fossil mammals from the Berg Aukas Mine collected by Mr F. van der Merwe during the late 1960s. 1) hominoid distal tibia, 2) hominoid cranial fragment, 3) primate distal humerus, 4) clavicle, 5) 6-7) long bone fragments, 8) hominoid tibial diaphysis, 9) carnivore distal metapodial, 10) hyracoid talus, 11) hominoid right mandible fragment containing m/1-m/3, 12) hominoid upper molar, 13) hominoid atlas vertebra (in two pieces), 14) primate proximal manual phalanx, 15) indeterminate bone. Specimens 11 and 14 are 44 mm and 37 mm long respectively.

Cranial fragment

An interesting fragment of cranial vault is preserved in the undescribed collection from Berg Aukas (Fig. 3). The specimen shows clearly the ridges and depressions on the inner surface of the bone corresponding to the gyri in

the brain. One edge of the specimen shows a sinus between the inner and outer surfaces of the bone, as in a previously described frontal bone attributed to *Otavipithecus namibiensis* by Pickford *et al.* (1997).

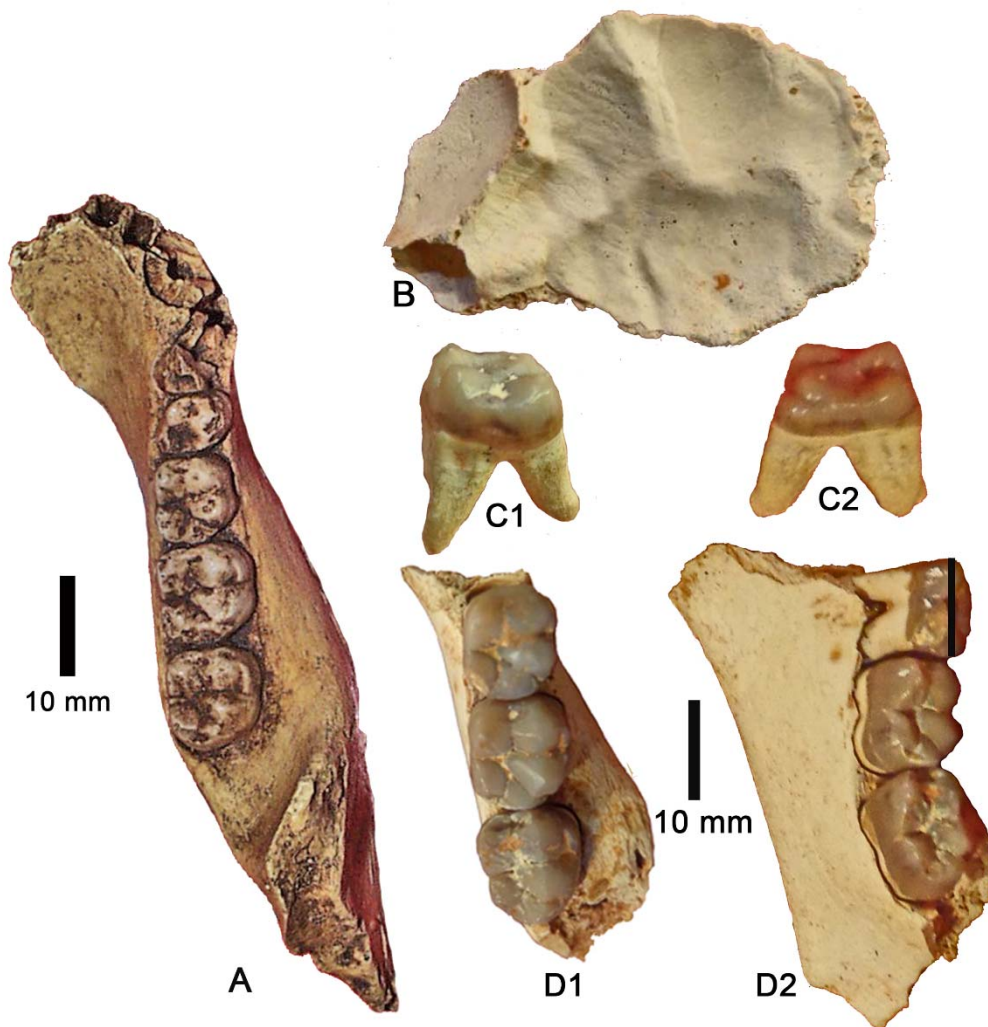


Figure 3. The holotype mandible of *Otavipithecus namibiensis* (A, cast) and the new fossils from Berg Aukas, mine level 8.5 (B-D). A) GSN Ber 1'91, right mandible with p/3-m/3, root of canine and alveoli of incisors in occlusal view. B) GSN BA 2'21, fragment of brain case, internal view, C) GSN BA 12'21, right upper molar, oblique distal and mesial views, D) GSN BA 11'21, right mandible fragment containing m/1-m/3, occlusal and oblique lingual views (scale : 10 mm).

Dentognathic elements

Incisors

Three isolated hominoid incisors were found in breccia blocks from Berg Aukas. They were illustrated by Pickford & Senut (2010) but were not described in detail.

The upper central incisor (Fig. 4A) has a spatulate crown with a convex labial surface and a concave lingual one, in which there is a prominent triangular central pillar. The broad base of the pillar is slightly separated from the

lingual cingulum and it narrows apically giving rise to two narrow enamel wrinkles. The distal margin of the crown overhangs the root by a small margin and the lingual cingulum is deep. There is a well-developed interproximal wear facet. The stout root is twice as tall as the crown and it has shallow longitudinal sulci extending along its mesial and distal sides.

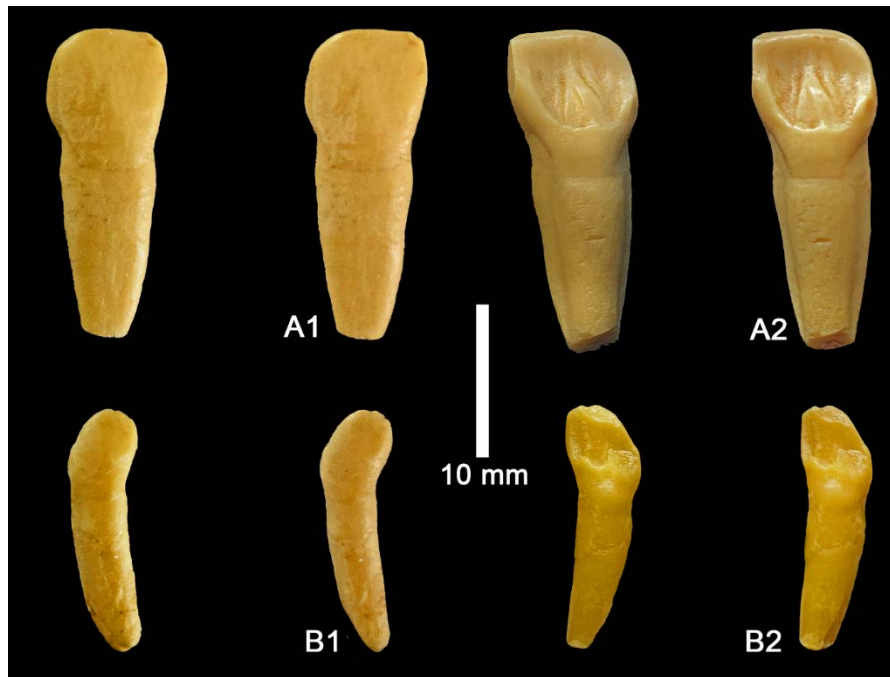


Figure 4. Stereo images of upper incisors (casts) of *Otavipithecus namibiensis* from the late Middle Miocene of Berg Aukas, Namibia. A) left upper central incisor (A1 - labial view, A2 - lingual view), B) left upper lateral incisor (B1 - labial view, B2 - lingual view) (scale : 10 mm).

The upper lateral incisor (Fig. 4b) is rather small, being compatible in its dimensions with what would be expected for *Otavipithecus namibiensis*. Its crown is convex labially and concave lingually with a well-developed lingual cingulum. The crown is canted on the root, the lingual side overhanging the root to a marked extent. The root is twice as tall as the crown and like the upper central incisor, there are shallow longitudinal sulci on its mesial and distal sides that extend the length of the root which tapers to a point.

The left lower second incisor (Fig. 5) from Berg Aukas is rather small, being

compatible in dimensions with the incisor alveoli of the holotype mandible of *Otavipithecus namibiensis*. The root has broken off, but the crown is reasonably well preserved and has undergone only slight wear. It has a straight mesial margin and a slightly convex distal edge. The lingual surface has a low central swelling running from cervix to apex, and there are moderately well developed mesial and distal marginal ridges that fade out apically. The sharp cutting edge of the tooth is angled with respect to the height axis of the tooth suggesting that the tooth may have been somewhat splayed out laterally in the mandible.

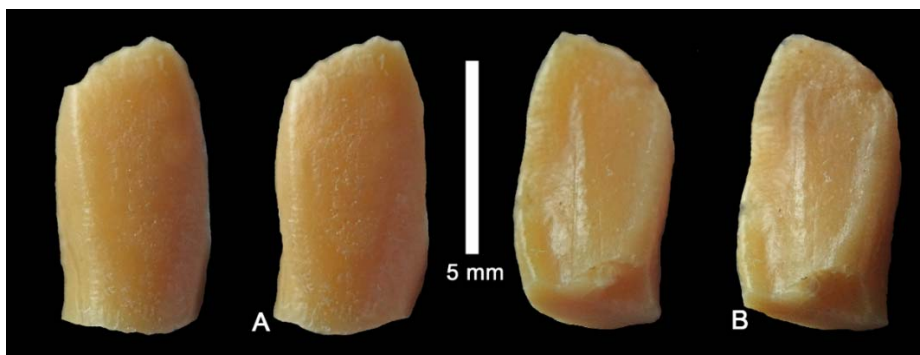


Figure 5. Stereo images of a left lower lateral incisor (cast) of *Otavipithecus namibiensis* from late Middle Miocene breccia from Berg Aukas, Namibia. A) labial view, B) lingual view (scale : 5 mm).

Table 1. Measurements (in mm) of incisors of *Otavipithecus namibiensis* from Berg Aukas, Namibia (e - estimated).

Taxon	Tooth	Mesio-distal length	Labio-lingual breadth	Lingual crown height	Lingual root height
<i>O. namibiensis</i>	I1/ lt	8.1	6.0	10.0	15e
<i>O. namibiensis</i>	I2/ lt	4.2	4.7	5.0	11.0
<i>O. namibiensis</i>	i/1 lt	4.1	--	--	--
<i>O. namibiensis</i>	i/2 lt	4.0	4.0	7e	--

Discussion

The upper incisors of *Kenyapithecus kizili* have a strongly v-shaped lingual crown base where the mesial and distal marginal ridges meet, and the lingual surface of the crown lacks a prominent central tubercle (Kelley *et al.* 2008). In *Kenyapithecus wickeri* from Fort Ternan, the lingual cingulum is not as deep as in the Berg Aukas specimen and the lingual pillar is reduced to a series of low wrinkles.

The Berg Aukas specimen is thus more like specimens of *Griphopithecus alpani*, (Tekkaya, 1974) but it is substantially smaller than any of the specimens of this species (Kelley *et al.* 2008). It shares some resemblances to upper central incisors of *Equatorius africanus* from Maboko, Kenya (Pickford, 1985; Ward *et al.* 1999) but it is appreciably smaller. For these reasons, the Namibian specimen is attributed to *Otavipithecus namibiensis*.

Premolars

There are two isolated hominoid right p/4s from Berg Aukas (Fig. 6) which have been illustrated previously but not described in detail (Pickford & Senut, 2010, pl. 8). An unworn specimen is similar to the corresponding tooth in the holotype mandible of *Otavipithecus namibiensis*, but the other is broader and more

The upper lateral incisor from Berg Aukas differs from that of *Kenyapithecus* by the strong canting of the crown on the root. In *Kenyapithecus kizili* from Paşalar, Turkey, and *Kenyapithecus wickeri* from Fort Ternan, the crown of the I2/ is symmetrically posed on the root (Kelley *et al.* 2008). The dimensions of the Berg Aukas tooth are considerably lower than those of *Kenyapithecus kizili* and *Griphopithecus alpani* from Turkey. The form of its lingual cingulum recalls that of *Equatorius africanus* (Ward *et al.* 1999) but the tooth is smaller, so we attribute the Berg Aukas specimen to *Otavipithecus namibiensis*.

The lower lateral incisor from Berg Aukas differs from that of *Kenyapithecus*, not only by its smaller dimensions, but also by the more U-shaped base of the crown in lingual view. In *Kenyapithecus*, the base of the crown is more sharply V-shaped (Kelley *et al.* 2008).

bunodont, and was attributed to *Kenyapithecus* sp. by these authors in the same paper. The material is re-illustrated in stereo and detailed comparisons are made.

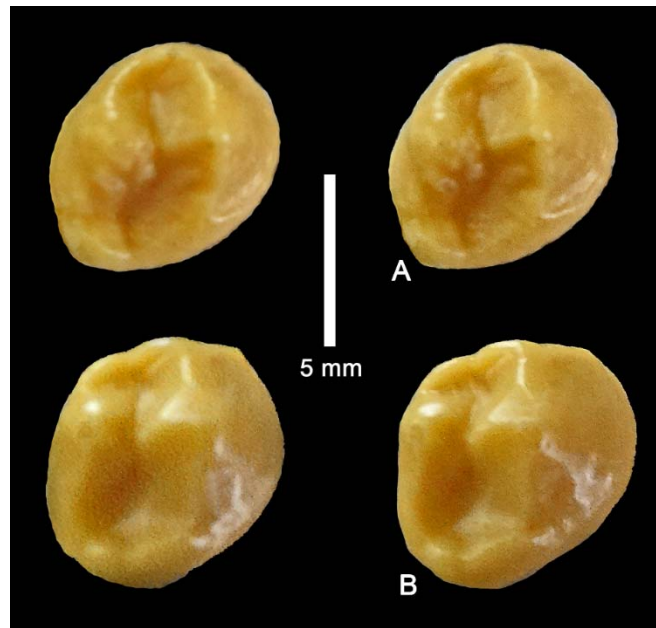


Figure 6. Stereo occlusal views of hominoid right p/4s (casts) from the late Middle Miocene of Berg Aukas, Namibia, A) *Otavipithecus namibiensis*, B) cf *Kenyapithecus* sp.

The p/4 of *Otavipithecus namibiensis* is slightly broader than its length, and the premetacristid and preprotocristid descend anteriorly from the apices of the corresponding cusps, the premetacristid curving buccally as it goes, whereas the preprotocristid is almost straight, both cristids blending into the mesial cingulum, thereby closing off the mesial fovea which is relatively capacious. The metaconid and protoconid possess endocristids that approach each other in the midline of the crown, but which remain separated from each other by the longitudinal valley. The postmetacristid is weak and rounded and descends steeply towards a minute entoconid. The postprotocristid descends directly distally then curves lingually near its base where it joins the distal cingulum, with barely any hint of the presence of a hypoconid. The distal fovea is shallow. On the buccal aspect of the protoconid, there is a low distal fold, which fades out towards the cervix.

Discussion

In *Otavipithecus namibiensis*, the p/4 has poorly developed hypoconid and entoconid, which are more like cingular swellings than distinct cusps. In *Kenyapithecus wickeri* in contrast, these two cusplets are better developed, even though they are considerably smaller and lower than the protoconid and metaconid. The same applies to the p/4 of *Equatorius africanus* (Le Gros Clark & Leakey, 1950) (Ward *et al.* 1999) from Maboko and

The p/4 from Berg Aukas previously attributed to cf *Kenyapithecus* is very slightly broader than its length, and the premetacristid does not extend apically as far as the tip of the cusp. The preprotocristid is short and swollen, and as a result, the mesial fovea is shallow and reduced in area compared to that of *O. namibiensis*. The endocristid of the metaconid is almost obsolete, and that of the protoconid is swollen and is separated from the entoconid by the longitudinal valley. The postmetacristid descends towards a small, but distinct entoconid, and the inflated postprotocristid ends basally at the small hypoconid which is distinguished from the entoconid by subtle, shallow mesial and distal sulci. The distal fovea is shallow and is rimmed distally by the small but inflated entoconid and hypoconid. The buccal fold on the distal aspect of the protoconid is weakly expressed.

Kipsaraman, Kenya. The p/4 from Berg Aukas previously attributed to cf *Kenyapithecus* (Pickford & Senut, 2010) has a relatively small entoconid, but the hypoconid is somewhat larger. Morphologically and metrically it is closest to *Kenyapithecus wickeri*, but the differences in the dimensions of the entoconid and hypoconid indicate that it may belong to a different species.

Mandible and lower molars

The holotype right mandible of *Otavipithecus namibiensis* is re-illustrated in stereo for convenient comparison with the new fossils from Berg Aukas (Fig. 7, 8). The specimen has been analysed by several

specialists (Conroy *et al.* 1992; Schwartz & Conroy, 1996; Singleton, 1998, 2000) but its phylogenetic and systematic position remains contentious.



Figure 7. Stereo occlusal images of BER 1, 1'91, holotype right mandible of *Otavipithecus namibiensis* (cast) from the late Middle Miocene of Berg Aukas, Namibia.



Figure 8. GSN BER I, 1'91, holotype mandible of *Otavipithecus namibiensis* from Berg Aukas. A) lingual view, B) buccal view (scale : 5 cm).

The undescribed right mandible fragment from Berg Aukas (Fig. 9) contains the three molars in light to medium wear, the m/1 being partly out of its alveolus. The lingual surface of the jaw starts to curve towards the symphysis opposite the mesial end of m/1, and the root of the ascending ramus rises at the middle of m/2, such that in lateral view the rear of the m/3 would be obscured by the anterior margin of the ramus, had it not been broken off.

The m/1 is ca 9.0 mm long by ca 7.0 mm broad. The anterior lobe is almost the same breadth as the second one. The protoconid and hypoconid are broader than the metaconid and entoconid, such that the longitudinal valley between the buccal and lingual cusps is slightly to the lingual side of the midline of the crown. The preprotocristid and postprotocristid are short and inflated, as is the endoprotocristid which is oriented at right angles to the long axis of the crown. The prehypocristid and posthypocristid are also short and inflated. The endohypocristid is more elongated and extends mesio-lingually between the metaconid and entoconid at an angle of ca 45° to the long axis of the tooth. The hypoconulid is larger than the entoconid, and is strongly attached to the hypoconid, forming a substantial cusp at the rear of the tooth. The metaconid possesses inflated pre- and posteristids, and the

endometacristid extends towards the endoprotocristid closing off the rear of the mesial fovea. The entoconid is the smallest cusp with short pre- and posteristids. There is a small remnant of a buccal cingulid at the base of the buccal notch between the protoconid and hypoconid.

The m/2 is ca 9.0 mm long by 9.0 mm broad, and is constructed along similar lines to the m/1 except that proportionally the hypoconulid is appreciably smaller, being slightly smaller than the entoconid. In addition, the buccal cingular fold is better developed than in the m/1.

The m/3 is a 10.0 mm long and ca 9.0 mm broad. It differs from the m/2 in having a narrower distal lophid than the anterior one, with a smaller hypoconulid and entoconid which imparts a triangular outline to the rear of the tooth. The preprotocristid and premetacristid are lightly worn and they curve mesio-centrally to meet in the mid-line of the crown, closing off the front of a bucco-lingually broad, but mesio-distally narrow, mesial fovea. This fovea is closed distally by the endoprotocristid and the endometacristid. The postmetacristid is longer than in the preceding molars and shows a slight detachment near its apex. The buccal cingulid is well developed.

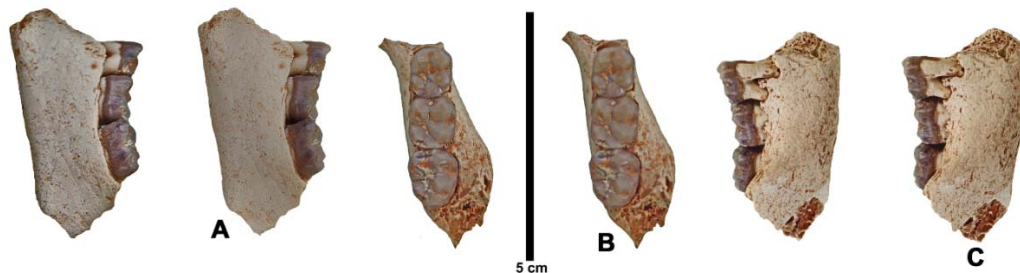


Figure 9. Stereo images of GSN BA 11'21, right mandible from Berg aukas Mine level 8.5, attributed to *Kenyapithecus* sp. A) lingual view, B) occlusal view, C) buccal view (scale : 5 cm).

Discussion

The molars in the new mandible fragment from Berg Aukas differ in several ways from those in the holotype jaw of *Otavipithecus namibiensis* (Conroy *et al.* 1992; Singleton, 1998, 2000). The mesial lophid of the m/1 in the latter species is somewhat narrower than the second lophid, whereas in the new fossil the two lophids are subequal in breadth. In *Otavipithecus*, the hypoconulid of the m/1 is smaller than the entoconid, the opposite of the case in the new fossil. In the m/2 and m/3 of *Otavipithecus*, the buccal cingular fold is more

extensive than it is in the new fossils, extending further mesially along the side of the protoconid.

The m/1 and m/2 in the new hominoid mandible from Berg Aukas are slightly shorter than the corresponding teeth of *Otavipithecus*, and their occlusal outline is more rectangular. However, in the new specimen the m/3 is longer than that of *Otavipithecus namibiensis*, whereas in the latter species the third molar is shorter than the m/2.

Table 2. Measurements (in mm) of cheek teeth of *Otavipithecus namibiensis* and the new specimens from Berg Aukas attributed to cf *Kenyapithecus* sp.

Taxon	Tooth	Mesio-distal length	Bucco-lingual breadth	MD/BL
cf <i>Kenyapithecus</i> sp.	p/4 rt	7.2	7.4	0.97
cf <i>Kenyapithecus</i> sp.	m/1 rt	9.0	7.0	
cf <i>Kenyapithecus</i> sp.	m/2 rt	9.0	9.0	
cf <i>Kenyapithecus</i> sp.	m/3 rt	10.0	9.0	
<i>O. namibiensis</i>	p/4 rt	6.7	7.0	0.96
<i>O. namibiensis</i>	p/4 rt	6.5	6.4	1.01
<i>O. namibiensis</i>	m/1 rt	8.5	7.6	1.18
<i>O. namibiensis</i>	m/2 rt	10.0	9.2	1.08
<i>O. namibiensis</i>	m/3 rt	9.6	7.8	1.23
Cf <i>Kenyapithecus</i> sp.	M*/ rt	9.0	11.0	

In view of the differences in the dimensions, proportions of the lower molars and the cusp morphology that the new Berg Aukas fossils display when compared to their counterparts in *Otavipithecus namibiensis*, we conclude that the new fossil mandible probably represents a distinct species. The presence of a second taxon of hominoid at the site has already been evoked by Pickford & Senut (2010) on the basis of an isolated p/4 that differs from that in

the holotype mandible of *Otavipithecus namibiensis*. It was identified by these authors as *Kenyapithecus* sp. This p/4 (Pickford & Senut, 2010, pl. 8, fig. 4) is compatible in dimensions and morphology with what would be expected for the new mandible, from which it is inferred that it probably belongs to *Kenyapithecus* sp. The new mandible recalls *Kenyapithecus* by its dental morphology (McCrossin & Benefit, 1997).

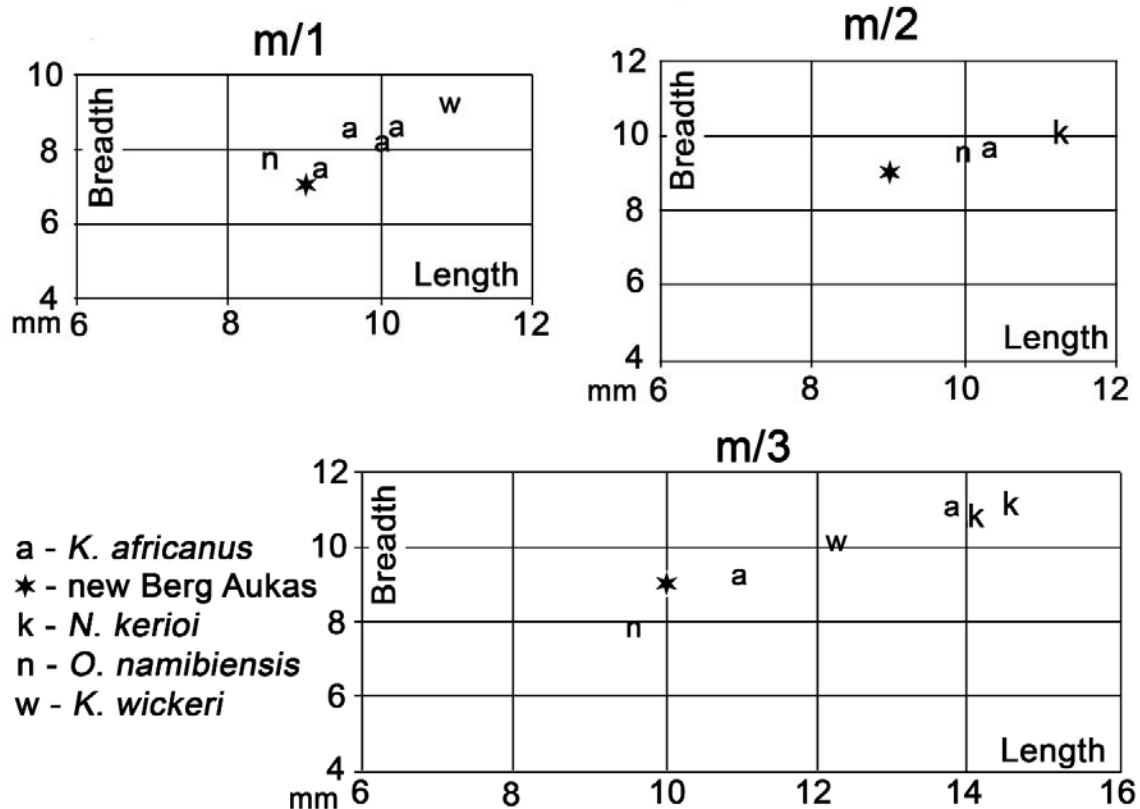


Figure 10. Metric comparison of lower molars of *Otavipithecus namibiensis* and the new specimen from Berg Aukas, against *Kenyapithecus africanus* from Maboko, *Kenyapithecus wickeri* from Fort Ternan and *Nacholapithecus kerioi* from Nachola (data for Kenyan specimens from Pickford, 1985b; Ishida *et al.* 1999 and Kanimatsu *et al.* 2004, data for *Otavipithecus* from Conroy *et al.* 1992).

The Berg Aukas hominoid lower molars are smaller than the corresponding teeth of *Kenyapithecus africanus* from Maboko,

Kenyapithecus wickeri from Fort Ternan and *Nacholapithecus kerioi* from Nachola (Kenya).

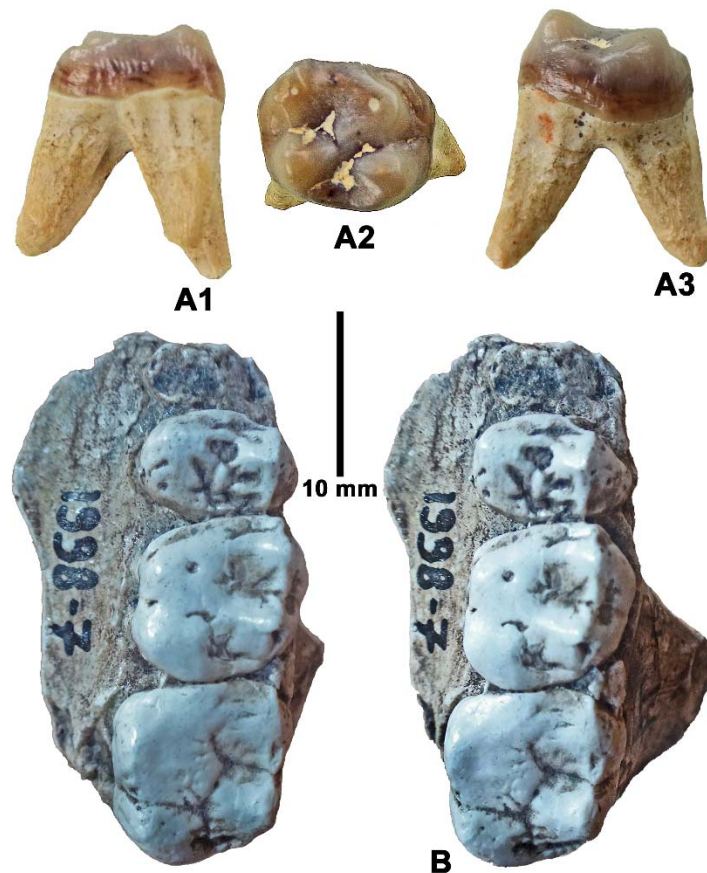


Figure 11. A) GSN BA 12'21, right upper molar of *Otavipithecus namibiensis* from Berg Aukas Mine level 8.5. A1) mesial view, A2) occlusal view, A3) distal view, (B) KNM FT 46, left maxilla of *Kenyapithecus wickeri* with P4/-M2/ from Fort Ternan, Kenya (cast in MNHN 1998-7) (scale : 10 mm).

The isolated right upper molar from Berg Aukas (GSN BA 12'21, Fig. 11) is 9 mm long by 11 mm broad. It is in medium wear and has three stout roots, two buccally and one lingually. The protocone has a low, but swollen cingulum on its mesial and lingual sides. The trigon is clearly expressed, with the crests from the protocone, paracone and metacone forming a triangular ensemble. The mesial and distal cingula are inflated, so that the mesial and distal fovea are reduced in capacity.

There is a prominent cingular structure on the lingual and mesial edges of the protocone but it fades out distally. The hypocone is as

large as the protocone. The mesial fovea is small, contrasting with the large distal fovea. The paracone and metacone have sharp pre- and post-crista. The postparacrista meets the premetacrista at the buccal edge of the trigon basin, forming the buccal notch.

Wear has advanced to the stage that dentine exposures are present on the protocone and paracone but not on the metacone and hypocone.

The enamel in the upper molar and the lower molars appear to be thick, the cusps having an inflated and bunodont aspect.

Discussion

GSN BA 12'21 differs from upper molars of *Kenyapithecus wickeri* in that the cingulum on the protocone in the latter genus is reduced to absent, and the hypocone is sensibly

smaller than the protocone. In addition, the dentine exposures in the Berg Aukas tooth are clearly visible in this relatively lightly worn individual, whereas in the *Kenyapithecus* type

specimen, which is more heavily worn, there is no exposure of dentine on the paracone and only a small one on the protocone. This indicates that the Berg Aukas specimen has thinner occlusal enamel than *Kenyapithecus* does.

Atlas

Although split into two, the new atlas from Berg Aukas (Fig. 12) shows the classic anatomical features of this type of vertebra. The cranial surface is well preserved, while the caudal surface is slightly damaged with chips of bone missing from the ventral and dorsal arches, while the lower parts of the inferior articular facets have slight erosional damage. The tips of both transverse processes are broken. The vertebra is 42 mm broad and its total dorso-ventral height is 23 mm. The dorso-ventral diameter of the vertebral canal is 16 mm. The superior articular facets are about 15.8 mm long and 3.7 mm broad, the inferior articular facets are 8 mm long (longer axis) and 7 mm wide. The facets are slightly inclined to the horizontal as in hominoids. The retroglenoid tubercles protrude weakly at the posterior end of the superior articular facets and look more towards the vertebral canal. The aspect of the lateral side of the right lateral mass of this atlas is similar to that of GSN BA 104'91 (Conroy *et al.*, 1996). The lateral side of the left lateral mass differs by the presence of a vertical bony bridge between the retroglenoid bridge (posterior to the superior articular facet) and the transverse foramen. This vertical bridge closes the groove of the vertebral artery and the different ramus of the

For these reasons we attribute the new upper molar from Berg Aukas to *Otavipithecus namibiensis*. In accordance with this, it is noted that *Otavipithecus* has better developed cingular structures in the lower molars than does *Kenyapithecus*.

suboccipital nerve. This groove is generally open in hominoids and closed in the Old World monkey, but some variation exists. The opening of the groove seems to correlate to a more important vertebral artery in hominoids. The transverse processes are elongated and present a gracile aspect. The base of these processes with the lateral mass is greatly occupied by the transverse foramen as in hominoids and GSN BA 104'91. Although the ventral arch is broken, the anterior tubercle is blunt as in GSN BA 104'91 and in hominoids, and differs from the situation in cercopithecoids with a spine-like anterior tubercle.

Although this new atlas is slightly smaller than the previously described hominoid atlas vertebra from Berg Aukas (GSN BA 104'91, Fig. 13) (Conroy *et al.*, 1996; Senut & Gommery, 1997; Gommery, 2000), it exhibits several hominoid-like features such as a more horizontal orientation of the cranial and inferior articular facets, the morphology and orientation of retroglenoid tubercle, the morphology of the anterior tubercle, an overall reduction in the relative size and proportions of the transverse processes and the morphology of the anterior tubercle.

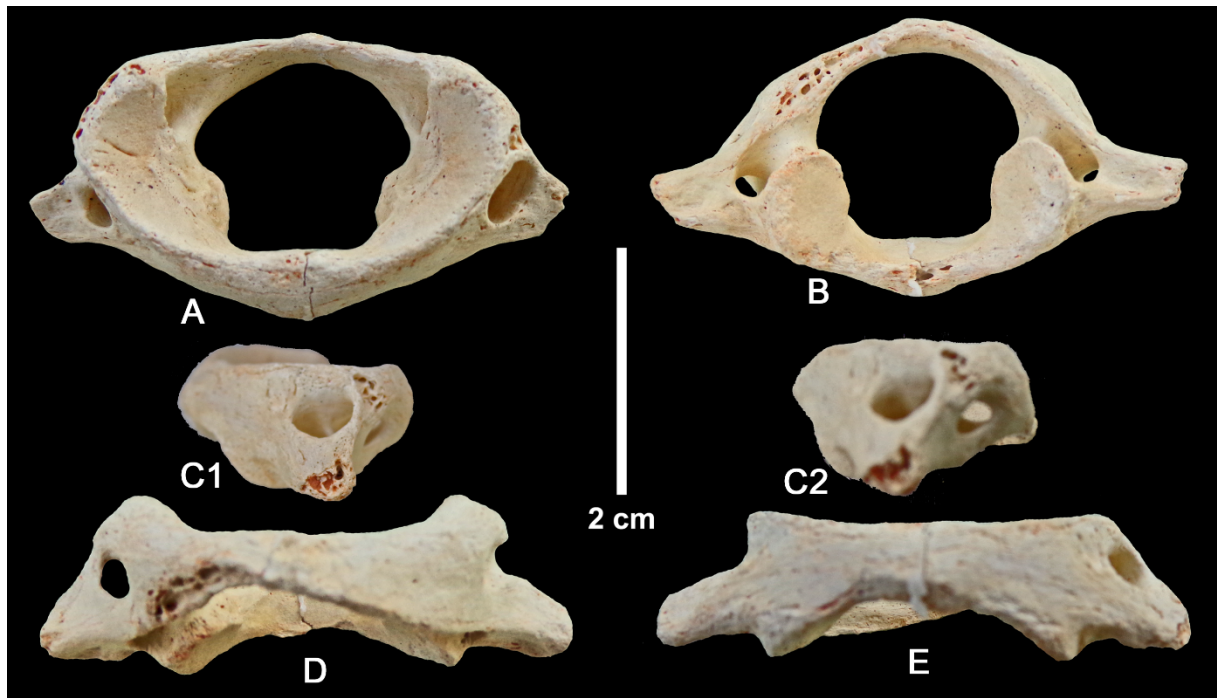


Figure 12. GSN BA 13'21, hominoid atlas vertebra from Berg Aukas Mine level 8.5. A) cranial view, B) caudal view, C1 and C2) lateral views, D) dorsal view, e) ventral view (scale : 2 cm).

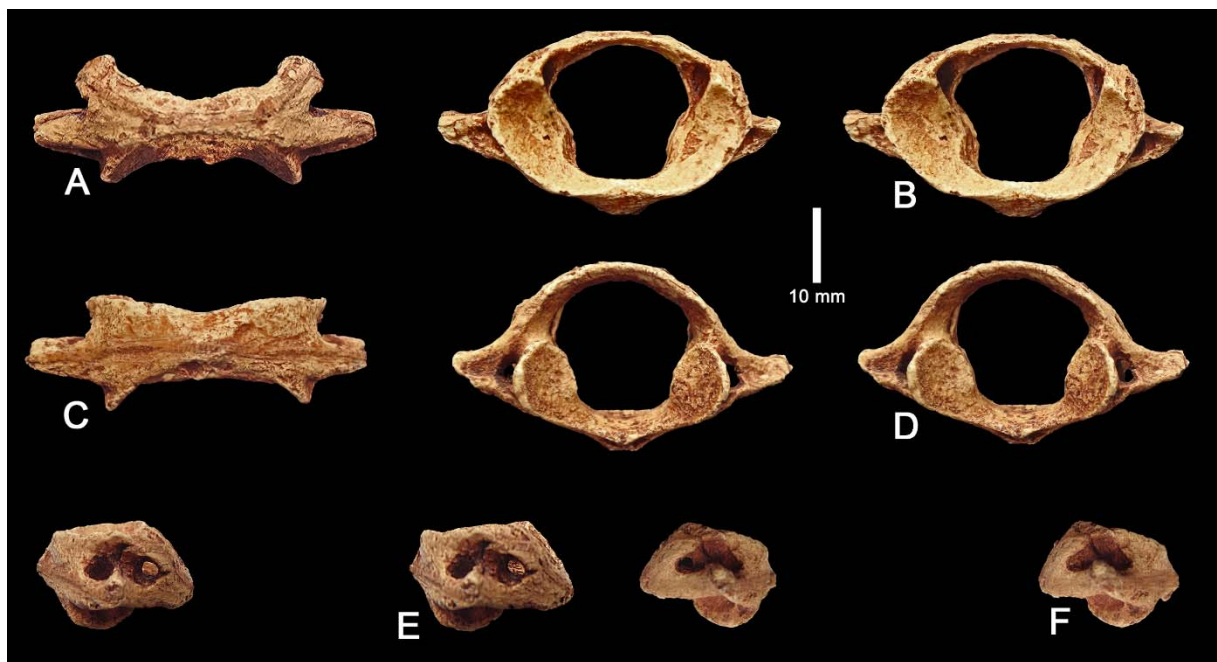


Figure 13. GSN BA 91'104, atlas vertebra (cast) attributed to *Otavipithecus namibiensis*. A) dorsal view, B) stereo cranial view, C) ventral view, D) caudal view, E) stereo left lateral view, F) stereo right lateral view (scale : 10 mm).

Forelimb

Humerus

The distal left humerus from Berg Aukas (Fig. 14) is broken off beneath the middle of the diaphysis, the distal articulation being in good condition. As preserved the

specimen is 76 mm long and the greatest breadth of the distal end is ca 40 mm.

In anterior view (Fig. 14 A2), the humeral trochlea has the classic pulley-like form of hominoids. Its medial lip is abraded, the

zona conoidea is symmetrical and has two weakly inclined margins. The *capitulum humeri* is spherical and projects anteriorly. The diaphysis extends slightly laterally and upwards and the anterior margin extends slightly medially. It terminates above the extension of the *zona conoidea*.

The lateral epicondyle projects above the capitulum and slightly laterally, but mainly posteriorly.

The lateral border of the humerus is rectilinear and the marked extent of the brachioradialis muscle is evident.

Above the articulation, the two fossettes (radial and coronoid) are well marked and separated by the distal extension of the anterior crest.

In posterior view (Fig. 14 A1), the triangular *fossa olecrani*, with its apex oriented

upwards, is deep. It is bordered by two pillars, the lateral one being broader than the medial one. There is a strong acerate crest lateral to the olecranon fossa. The postepitrochlear fossette is clearly marked and opens proximally into the olecranon fossa. The epitrochlea (*epicondylus medialis*) is weakly developed and twisted posteriorly.

Compared with other Miocene hominoid distal humeri, the fossil from Berg Aukas is closest to a specimen from Fort Ternan, Kenya (Andrews & Walker, 1976; Senut, 1989; McCrossin & Benefit, 2004). However, it is slightly smaller suggesting either the presence of sexual dimorphism or that it possibly represents a different species of the genus.

Table 3. Measurements (in mm) of the distal humerus (KNM FT 2751) of *Kenyapithecus wickeri* from Fort Ternan, Kenya.

Maximal width distal end	45.3
Articular width distal end	33.5
Trochlear width (taken posteriorly)	16.6
Capitular width (anterior view)	11.5
Lateral pillar to fossa olecrani	17.2
Medial pillar to fossa olecrani	5.7
Medial epicondyle height (in distal view)	10.3

Without taking measurements directly on the fossil, it is difficult to be precise about the dimensions of the Berg Aukas fossil. However, on the basis of the scaled images, it is slightly smaller than that of *Kenyapithecus wickeri* (total breadth of the distal end is 45.3 mm in *K. wickeri* and ca 40 mm in GSN BA 3'21).

The medial pillar is somewhat more developed than on the Kenyan specimen. From a functional perspective, it shows stabilisation of the elbow joint with a projecting *zona*

conoidea, even though less projecting than in other fossil hominoids, but suggesting a partly arboreal life with reinforcement of the flexor muscles (straightness of the lateral part of the bone). The posterior crest lateral to the olecranon fossa indicates strong stabilisation of the elbow during quadrupedal walking and recalls what is observed in terrestrial quadrupeds. Thus, the Berg Aukas humerus indicates a duality of locomotor repertoires : terrestrial and arboreal.

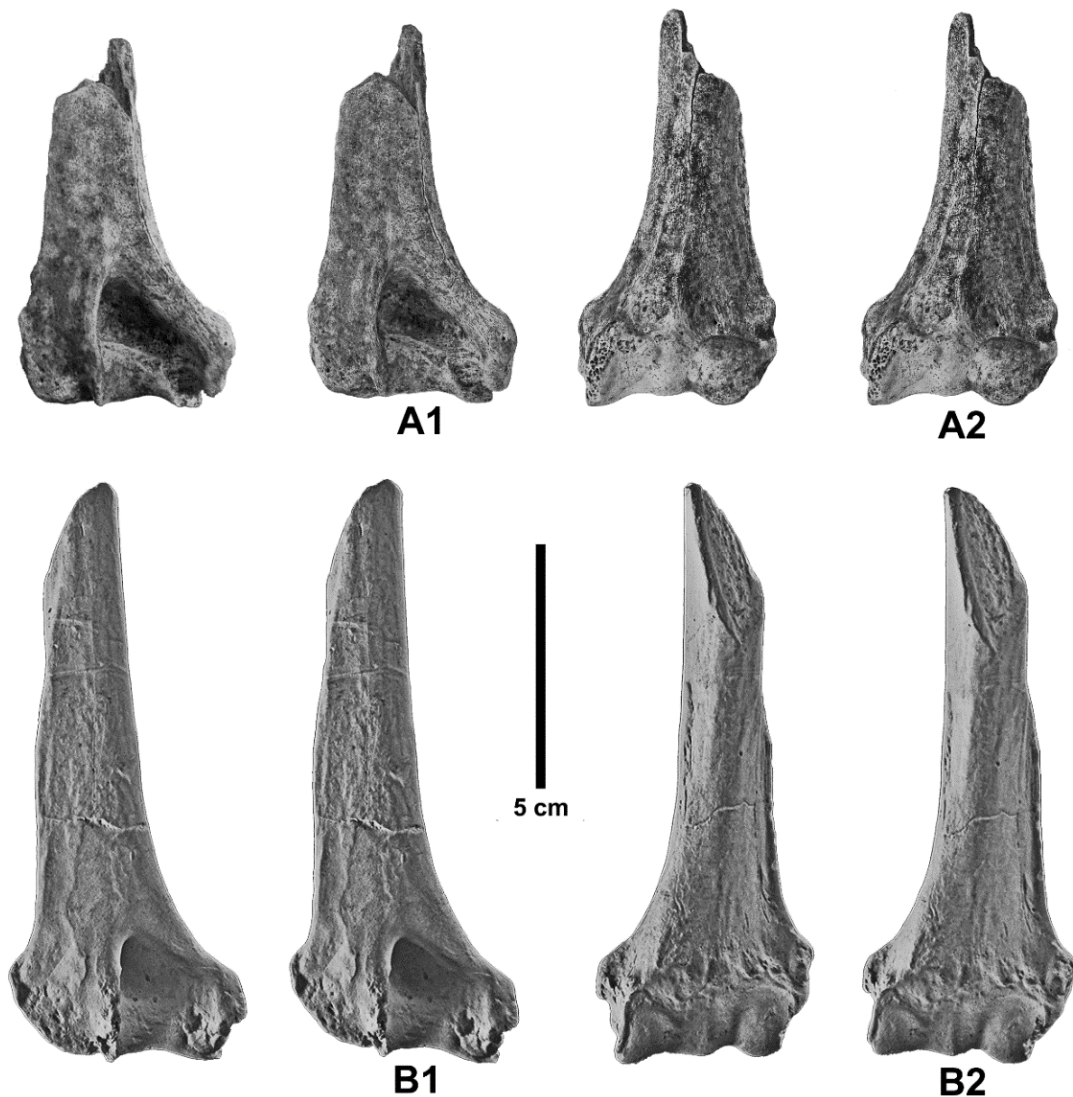


Figure 14. Stereo images of primate distal humeri (A) GSN BA 3'21, distal right humerus from Berg Aukas Mine level 8.5, A1) posterior view, A2) anterior view (B) KNM FT 2751, distal left humerus (cast - reversed) attributed to *Kenyapithecus wickeri*, B1) posterior view, B2) anterior view (scale : 5 cm).

Ulna

The proximal right ulna (GSN BA 91.4a, Fig. 15) from Berg Aukas was briefly mentioned by Conroy *et al.* (1993) Senut & Gommery (1997) and Singleton (1998) who concluded that its morphological features indicated that *Otavipithecus* was “a slow-moving arboreal quadruped”.

The olecranon process is damaged but it appears to have been short, and part of the coronoid process of the humeral articular facet has broken off. The sigmoid notch is broad and the anterior lip projects a short distance out from the shaft. The medial side of the proximal part

of the diaphysis has a deep groove (radial fossa) that curves from proximo-medial to disto-anterior as it descends the shaft which is broken off some 4 cm beneath the anterior lip of the sigmoid notch. This fossa accepts the proximal part of the radial shaft during pronation. The preserved parts of the shaft are robust, but the ulnar tuberosity is weakly developed.

The overall aspect of the specimen is comparable to the ulnae of *Ekembo*, a medium-sized catarrhine from Rusinga Island, Kenya (Walker & Pickford, 1983).

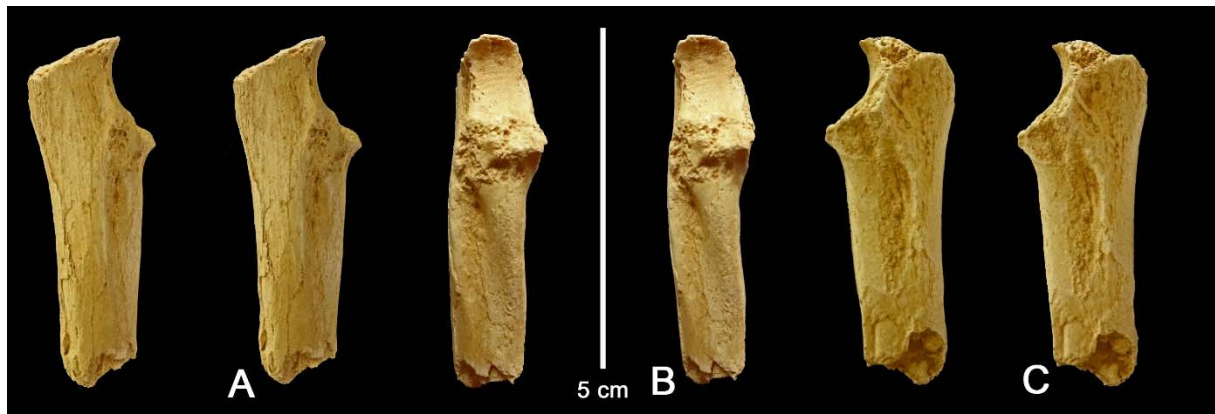


Figure 15. Stereo images of proximal right ulna (cast) from Berg Aukas attributed to *Otavipithecus namibiensis*. A) lateral view, B) anterior view, C) medial view (scale : 5 cm).

Senut & Gommery (1997) remarked that the obliquity of the inferior part of the sigmoid cavity of the Berg Aukas ulna resembled the morphology observed in certain platyrrhines that had a less stabilised

articulation than terrestrial quadrupeds, which indicates that the Berg Aukas ulna probably represents an arboreal quadruped somewhat similar to *Ekembo heseloni* from Rusinga, Kenya (Senut, 1989).

Manual phalanx



Figure 16. GSN BA 14'21, hominoid manual phalanx from Berg Aukas Mine level 8.5, A) medial view, B) dorsal view, C) palmar view, D) lateral view (scale : 2 cm).

GSN BA 14'21 is a well-preserved proximal manual phalanx (Fig. 16) from one of the digits II to IV. The morphology of the trochlea at the distal extremity and the palmar tubercles (especially the more developed aspect of the median or radial palmar tubercle relatively to the other (on the right in palmar view suggest that this phalanx is from the right hand. The length is 37 mm and the breadth of the proximal part is 10 mm and 7 mm for the distal articular extremity. The breadth of the shaft at the proximal termination of the flexor sheath ridges, is 7 mm.

The phalanx presents a long, dorso-palmarly compressed shaft and seems to be moderately curved as in *Ekembo* from Kenya and material from Paşalar (Turkey), as well as in *Pierolapithecus* from Spain, but is not as curved as in *Dryopithecus*, *Hispanopithecus* and *Danuvius* from Europe, or *Pongo* from Asia (Almécija *et al.* 2009; Begun *et al.* 1994; Böhme *et al.* 2019; Ersoy *et al.* 2008; Moyà-Solà *et al.* 2004; Susman, 1979).

In palmar view, there are flexor sheath ridges developed in the medium third to distal third of the shaft. The distal articular surface is broader than the proximal articular surface. At

the distal extremity, the trochlear groove is narrow as in several Miocene hominoids except *Sivapithecus* from the Indian subcontinent (Almécija *et al.* 2009). At the distal extremity, well-developed and separated volar tubercles surround a deep central depression but less so than in IPS 21350.14 of *Pierolapithecus*

catalaunicus (Moyà-Solà *et al.* 2004). The proximal articular facet is tilted proximodorsally. These anatomical features are considered to be primitive hominoid characters and could indicate the use of the hands in palmigrady.

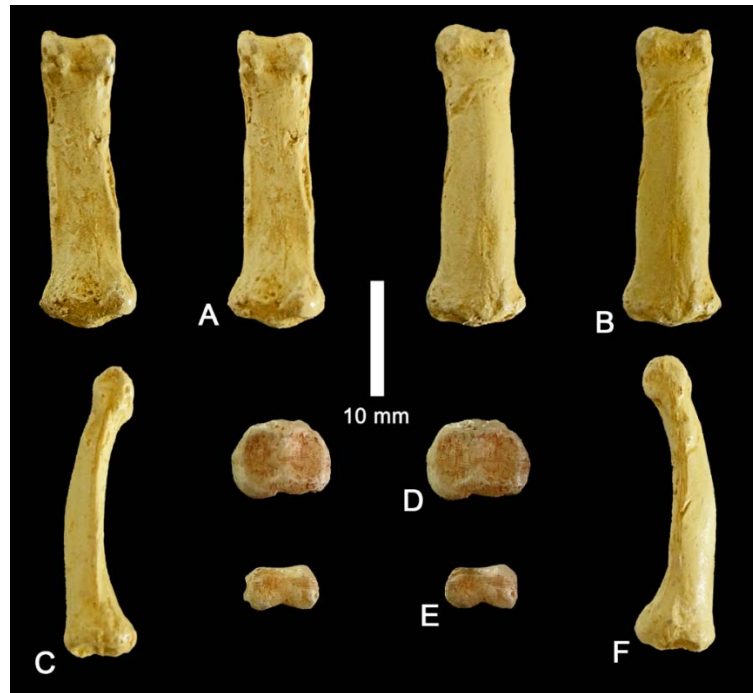


Figure 17. GSN BA 23'91 + 20'92, hominoid manual phalanx (cast) from Berg Aukas, Namibia, A) stereo palmar view, B) stereo dorsal view, C) side view, D) stereo proximal view, E) stereo distal view, F) side view (scale : 10 mm).

The second manual phalanx, GSN BA 23'91+20'92 (Fig. 17), was described by Senut & Gommery (1997) who interpreted it as displaying arboreal quadrupedal features.

Other Miocene hominoid manual phalanges from African fossil sites have been described (Allen & McCrossin, 2007; Arney *et al.* 2019) which attest to a diversity of

locomotor repertoires, ranging from more arboreally adapted species to more terrestrial taxa. Berg Aukas, thus join the list of localities at which hominoids with different locomotor adaptations are preserved, one more arboreal, the other more terrestrial but with some arboreal capabilities.

Hind Limb *Tibia*

The right distal tibia with much of the diaphysis from Berg Aukas (Fig. 18) is attributed to Hominoidea. Its dimensions are compatible with the hominoid dentognathic remains, the atlas vertebra and the manual phalanx from the same site (Fig. 2). The specimen is 124 mm long. It comprises the distal and middle part of the shaft and the distal articulation. The shaft is gracile and is 12 mm wide in the middle part. The shaft is fairly well

preserved except for the proximal part of the anterior surface which is slightly abraded.

In anterior and posterior views, the shaft widens proximally. In Hominoidea it is widest at the level of the tibial tuberosity, but this is not preserved in the specimen from Berg Aukas. Proximally, the diaphysis is flatter latero-medially as in chimpanzees and some extinct Hominoidea such as *Ugandapithecus major* (cf. NAP IX' AUG 62; Gommery *et al.* 1998), *Hispanopithecus laietanus* (IPS34575h ;

Alba *et al.* 2012) and *Ekembo nyanzae* (KNM-MW 13142A; Ward *et al.* 1993). On the lateral side, there is a crest distally which is rounded in its proximal third. This crest corresponds to the interosseus border (*margo interosseus*).

The distal end measures approximately 19 mm anteroposteriorly and about 29 mm mediolaterally as in some hominoids and large platyrrhines (Rose, 1993). The distal part is missing some cortical bone, and has a spongy aspect which is probably related to the biological age of the individual, a young adult(?), but this does not affect its overall morphology. The medial malleolus (*malleolus medialis*) is robust and long. It is similar to those of *Pan troglodytes* (Swindler & Wood, 1973) and *Pan paniscus* (pers. obs.), and is much shorter than those of baboons in which it is very elongated (Swindler & Wood, 1973). The articular facet is missing a chip of bone antero-laterally. Despite this, the malleolus does not appear to curve laterally near its apex and does not produce a deep sulcus as in baboons (Swindler & Wood, 1975) but seems straight and we can observe a narrow depression posterior to the tip as in the chimpanzee sample and the fossil tibiae NAP I 1958 (*Ugandapithecus major*) and YGSP 1656 (*Sivapithecus indicus*; DeSilva *et al.* 2010).

The tibio-talar articulation has a low central ridge with shallow depressions medially and laterally, indicating that the talus would have possessed a low relief trochlea (with saddle morphology: Olivier & Fenart, 1956), as in primates in general and unlike most carnivores. The tibio-talar articulation is trapezoidal with an expanded antero-lateral

corner (19 mm long and ca 20.9 mm wide). The lateral part of the articulation makes an angle with the long axis of the shaft while the medial part is perpendicular. Similar morphology is present in YGSP 1656 and NAP I 1958 as well as in chimpanzees but also in some other primates such as baboons and *Semnopithecus* (Olivier & Fenart, 1956). This is also reported by Aiello & Dean (1990) to be the case for the global inclination of the articulation in chimpanzees, but not in humans. The morphology of the distal part of the Berg Aukas fossil tibia is similar to those of YGSP 1656 (*Sivapithecus indicus*) and NAP I 1958 (*Ugandapithecus major*) and it also shows some similarities to tibiae of chimpanzees.

In anterior view, the edge of the tibio-talar articulation is not straight but convex (or with a disto-laterally salient apex). The lateral surface presents a shallow elongated triangular depression which corresponds to the fibular notch, the postero-lateral corner of which is damaged and it is impossible to observe the articulation for the fibula. In posterior view, the distal tibial tuberosity is salient and robust, and the retromalleolar groove which accepts the *flexor longus digitorum* is clearly developed.

Concerning the fossil tibia from Chinji in Pakistan, YGSP 1656 (*Sivapithecus indicus*), DeSilva *et al.* (2010) suggested that this hominoid had a mobile ankle indicating adaptations for general pronograde arboreal quadrupedalism and vertical climbing. *Ugandapithecus major* presents adaptation to powerful vertical climbing (Gommery *et al.* 1998, Senut *et al.* 2000).



Figure 18. GSN BA 1'21, hominoid distal right tibia from Berg Aukas Mine level 8.5, A) slightly oblique posterior view to highlight the retromalleolar groove, B) posterior view, C) lateral view, D) distal view, E) anterior view, F) medial view (scale 10 cm).

Discussion

On the basis of the mandibular and dental evidence, it is clear that there are two taxa of Hominoidea in the late Middle Miocene cave breccias of Berg Aukas, Namibia, a conclusion already reached by Pickford & Senut (2010). Some of the new material differs in dimensions and morphology from remains of *Otavipithecus namibiensis*, and agrees better with fossils attributed to *Kenyapithecus wickeri* from Fort Ternan, Kenya, but it is not an exact match to that species. Given the rather poor representation of the latter species at its type locality, and also the limited nature of the specimens from Berg Aukas, it is possible that the Namibian fossils represent a different but closely related species. Although the m/2 in the new Berg Aukas jaw is similar in dimensions to that of *Nacholapithecus kerioi* from Nachola, Kenya (Ishida *et al.* 1999; Kunitatsu *et al.* 2004) the m/3 of the latter species is substantially larger than the corresponding tooth in the Berg Aukas mandible. For these reasons we adopt a cautious taxonomic approach and attribute the new mandible from Berg Aukas to cf *Kenyapithecus* sp.

In contrast, the upper molar from Berg Aukas differs from the corresponding tooth in the holotype of *Kenyapithecus wickeri*, notably by the difference in proportions of the protocone and hypocone. For this reason, we attribute the new upper molar to *Otavipithecus namibiensis*.

Because the two hominoid taxa from Berg Aukas are almost the same size, it is difficult to attribute the post-cranial elements to one or other of the species. The morphometric differences between the articular surfaces of the distal humeri from Berg Aukas and Fort Ternan suggest that they belong to different species, in which case it is possible that the Namibian specimen represents a second species of *Kenyapithecus*.

The ulna from Berg Aukas is incompatible with the humerus, so we consider it likely that it represents *Otavipithecus*. *Kenyapithecus* shows more terrestrial adaptations (with a climbing component) than *Otavipithecus* which was likely more arboreally adapted.

Part 2. Precision concerning the locality of a Late Miocene hominoid from Niger

The precise position of the discovery locus of a Late Miocene fauna from Niger containing a hominoid fossil was in doubt although, on the basis of the available archives, the general area of the find was reasonably considered to be in central Niger at 15°32'N : 5°40'E (Pickford *et al.*, 2008a, 2009b). However, examination of the Shell Company archives in The Hague by Dr Shirley E. van Heck, Senior Stratigrapher at Shell International Exploration and Production B.V., The Netherlands, has led to the discovery of an unpublished report that considerably clarifies the matter (Nieuwenhuis *et al.* 1963). This report contains geological maps and stratigraphic sections that include the position of locality N 885 that yielded the late Miocene fossils. Locality N 885 is positioned in Section D1 in sediments that are topographically close to the base of the Zakak Formation of Upper Senonian age in west central Niger, ca 20 km east of the frontier with Mali. Nieuwenhuis *et al.* (1963) mapped ferruginised deposits containing fossils at about this level, but considered that they were likely to be Quaternary (Fig. 19).

By overlaying the map in the field report onto Google Earth, locality N 885 is estimated to be at approximately 17°52'N : 4°26'E but it could be as much as 15 km further

southwards (see possibilities in Fig. 19). This locality is 1,375 km west of the type locality of *Sahelanthropus tchadensis* (TM 266 Chad) and is about 1,100 km north of the nearest population of extant chimpanzees (Fig. 20-22). It is ca 300 km northwest of the location previously thought to have yielded the fossils.

The geological map in the field report focuses on the Mesozoic and Palaeogene strata, but handwritten notes on the map indicate that the area surveyed has an incomplete cover of various sediments of «Quaternary» and Recent age including sand and ferruginous deposits, consolidated dunes, active dunes and alluvium. Some of the sediments mapped as «Quaternary» could be of late Miocene age. The only mammalian fossils collected are from locality N 885, erroneously thought to be Cretaceous by Nieuwenhuis (Fig. 19 - label accompanying the fossils). The nature of the samples from N 881 - N 883 has not been communicated to the authors. The geographic co-ordinates of the locality were estimated by superposing the map onto Google Earth, but clearly there is a margin of error of several hundred metres. Ground survey is required to settle the issue.

Figures 19-22 show the position of the locality N 885 as now understood. Further precision concerning the locality and its geological context will require field survey.

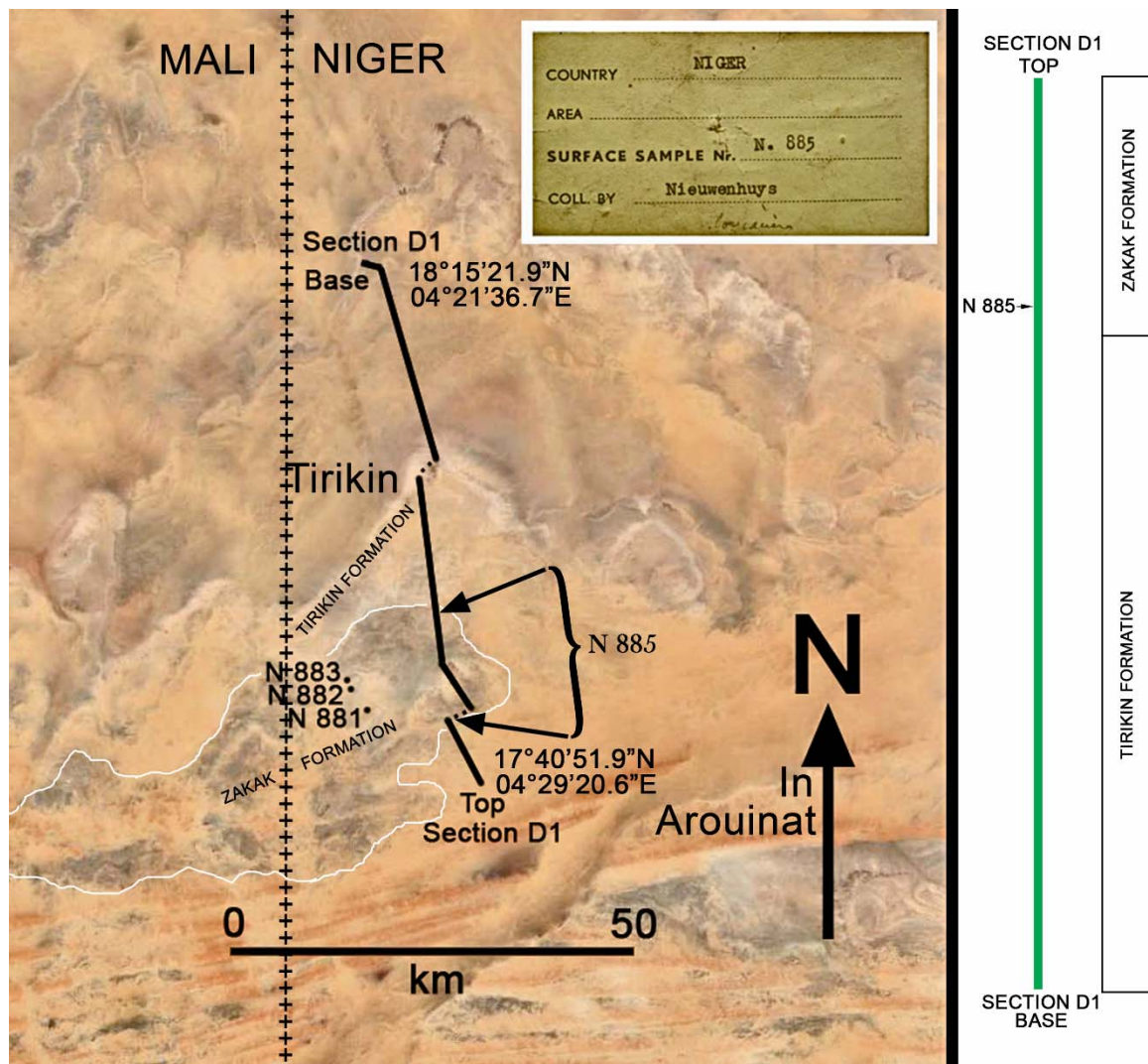


Figure 19. Superposition of locality data and Section D1 from the unpublished field report by Nieuwenhuis *et al.* (1963) onto a satellite map modified from Google Earth. Locality N 885 is located towards the top of section D1, topographically near the base of the Zakak Formation. The approximate co-ordinates of the northern and southern ends of Section D1 have been estimated from Google Earth. To the right is an extract from the sections in the field report showing the position of locality N 885. In the main map, the outcrop of the Zakak Formation is outlined in white. The two arrows show possible positions of N 885 near the basal outcrops of the Zakak Formation, the northern one being the preferred position based on the section data. The insert is a copy of the label accompanying the late Miocene fossils – note the hand-written correlation ‘Coniacian’ at the bottom of the label (the spelling of Nieuwenhuys in the label is erroneous).



Figure 20. Location of point N 885, Niger. Also indicated is the type locality of the Cretaceous chelonian *Nigermys gigantea* Bergounioux & Crouzel, 1968, initially thought to have been found close to the late Miocene fossils. Scale for the hominoid mandible is 10 mm.

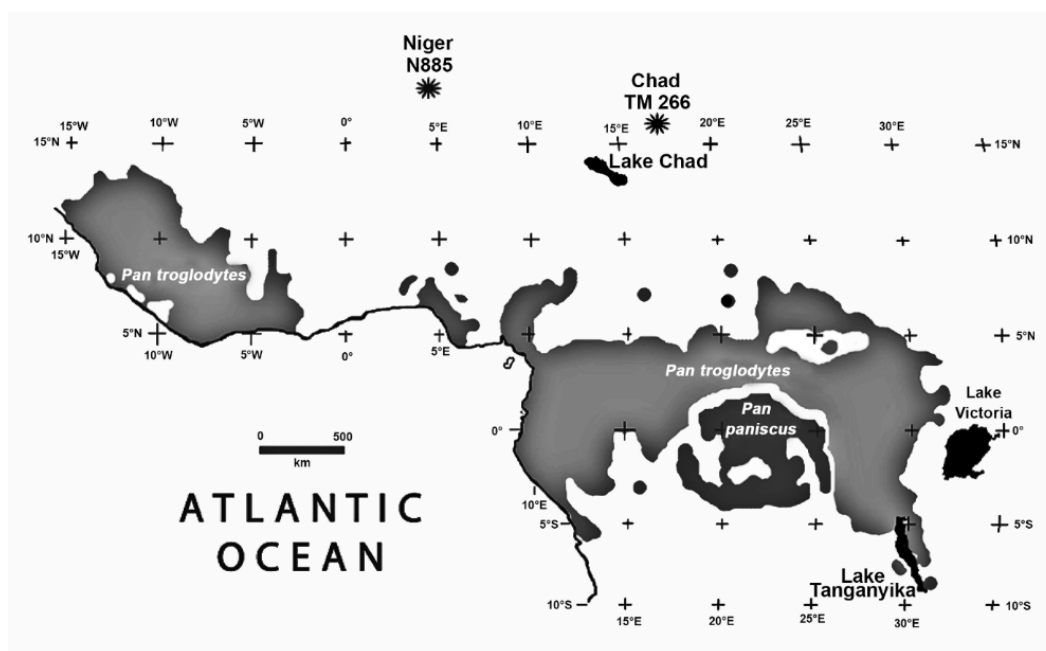


Figure 21. Distribution of extant species of chimpanzee relative to the Late Miocene hominoids from locality N 885, Niger and TM 266, Chad.

Discussion

Even though it is restricted in diversity, the late Miocene mammalian fauna from western Niger, originally considered to date somewhere between 11 and 5 Ma (Pickford *et al.* 2009b) is important for palaeoanthropology because it contains remains of a hominoid. The late Miocene hominoid fossil record of Africa (Fig. 22) is quite sparse, meaning that every new record is precious for throwing light on the diversity and possible evolutionary pathways within this superfamily during the time that early hominids were splitting away from the African Great Apes (chimpanzee, gorilla) estimated to have occurred between 12 and 8 million years ago (Pickford, 2012).

In addition to a hominoid, the fauna from Niger locality N 885 comprises an anthracothere and a reduncine bovid, as well as Nile Perch and a crocodile, all of which indicate that the local palaeoclimate was appreciably more humid during the late Miocene than the hyper-arid climate that prevails in the region today (Pickford *et al.* 2008a; Senut *et al.* 2010).

Other African hominoids of late Miocene age (Fig. 22) are known from Ethiopia (Ch'orora, *Chororapithecus* Suwa *et al.* 2007. Awash, *Ardipithecus kadabba* Haile-Selasie, 2001; Haile-Selassie *et al.* 2004), Gona, *Ardipithecus kadabba* - Simpson *et al.* 2015); Kenya (Samburu Hills, *Samburupithecus*, Ishida & Pickford, 1997, Pickford & Ishida, 1998; Nakali, *Nakalipithecus* Kunimatsu *et al.* 2007; indeterminate genus (Kunimatsu *et al.* 2016), Lothagam (indeterminate genus, Leakey & Walker, 2003), Lukeino (*Orrorin*, Senut *et al.* 2001, gorilla-like species, chimpanzee-like

species Pickford & Senut, 2005); Tolut (indeterminate hominoid, Pickford *et al.* 2009a); Chad (*Sahelanthropus*, Brunet *et al.* 2002, published as ca 7 Ma (Lebatard *et al.* 2008, but the precise age within the late Miocene contested - Pickford (2009) estimated that on the basis of the associated fauna it could be somewhere between 10 and 6 Ma). Terminal middle Miocene hominoids are known from Ngorora, Kenya (indeterminate genus, Pickford & Senut, 2005) and Berg Aukas, Namibia (*Otavipithecus* Conroy *et al.* 1992; cf *Kenyapithecus* Pickford & Senut, 2010, this paper).

The report of the presence of a possibly late Miocene chimpanzee fossil at Kikorongo Crater, Uganda (DeSilva *et al.* 2006) is not retained, because the femur upon which this record was based belongs to a late Pleistocene human. Even if the fossil were from a chimpanzee, the chronological record is untenable, because it was collected from the surficial lake margin deposits in the floor of the crater (J. Wilson, manuscript label) the oldest beds of which are late Pleistocene as shown by the presence in them of Middle Stone Age tools.

Likewise the human mandible from Kanam, Kenya, is not retained because it did not come from the late Miocene to basal Pliocene Kanam Formation as thought by Leakey (1936) but from the late Pleistocene Apoko Formation which unconformably overlies the Kanam Formation, as demonstrated by Pickford (1986a, 1986b, 1987). Leakey (1936) correlated the Kanam Formation beds to the Pliocene, but they are older than 5 Ma (Pickford, 1986b).

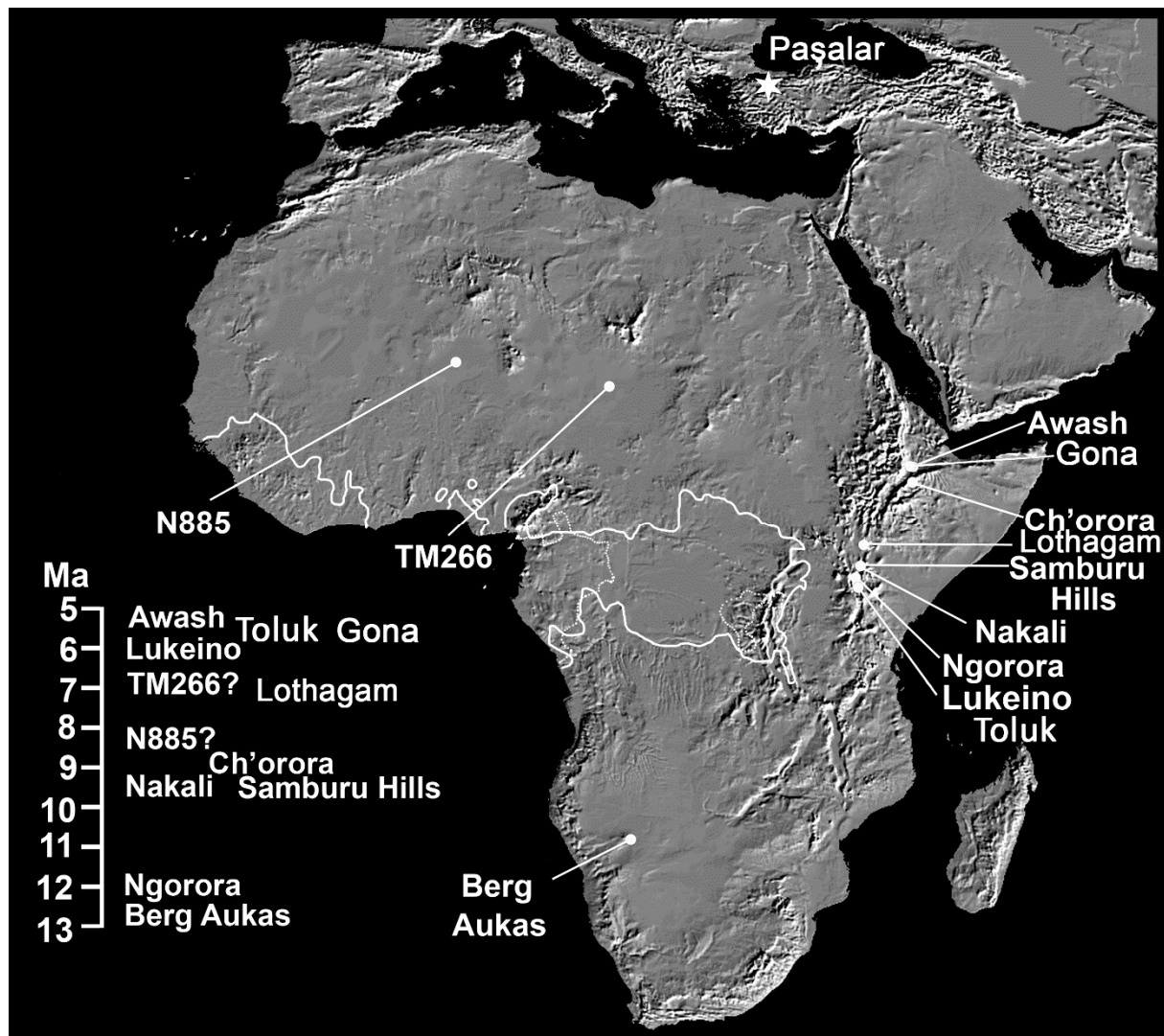


Figure 22. Distribution of late middle Miocene to late Miocene (13 to 5.5 Ma) African hominoid fossils. The continuous white contours show the distribution of extant chimpanzees, the dotted contours, that of gorillas. Also shown is the middle Miocene locality of Paşalar, Turkey, which yielded abundant dentognathic remains that have been attributed to *Kenyapithecus*.

An important aspect of the presence of a high diversity of late Miocene hominoids in Africa, even though the records are few and far between (Fig. 22) and are rather fragmentary, is that it proves that the continent was not devoid of large hominoids during this period. Indeed, the geographic distribution of the known late Miocene hominoids of Africa covers a greater latitudinal extent than the combined ranges of extant gorillas and chimpanzees. In Eurasia, late

Miocene hominoids are abundant and quite diverse, and on this basis it has been proposed by some researchers that the extant African Apes and humans descended from a Eurasian lineage (or lineages) that dispersed back to Africa (Begun, 2001, 2012). It is perhaps more likely that the extant African Apes and hominids descended from lineages that had persisted in the continent during the late Miocene.

Conclusion

Examination of the Nieuwenhuis archives held in the Shell Company Headquarters, The Hague, pertaining to field surveys carried out in Niger during the early

1960's, has revealed that the location of the late Miocene fauna from point N 885 is close to the frontier between Niger and Mali, about 300 km northwest of where it was originally thought to

be on the basis of labels and correspondence kept with the fossils in Paris. This locality is over 1,000 km north of the closest extant chimpanzee population, and it attests to a considerably more humid palaeoclimate in

western Niger than its present-day arid to hyper-arid climate (Senut *et al.* 2010). Further advances in knowledge about the site and the fauna will require additional field surveys.

General discussion and conclusions

It is now generally accepted that the dichotomy between the African Apes on the one hand, and Humans on the other, took place sometime between 12 and 8 Ma, but there is still debate about whether the Human and/or the African Ape lineages originated in Asia or in Africa (Campbell & Bernor, 1976; Begun, 2001; Cote, 2004; Senut, 2011, 2020). When Cote (2004) discussed the alternative hypotheses, seven localities in Africa (of which one is invalid) were reported to have yielded fossil hominoids, but there are now 12 African localities from which a minimum of eight genera are known.

The quantity of African hominoid fossils from the period 13-5 Ma is restricted, and the quality of the material is limited, but efforts over the past 15 years to increase the data base have improved the situation, making it more likely that the dichotomy between the African Apes and Humans took place within Africa rather than in Europe or Asia (Kunimatsu *et al.* 2004). Overall, the African late Miocene sites that have yielded hominoid fossils (Niger, Chad, Ethiopia, Kenya, Namibia) span a greater latitudinal extent of the continent (17°45'N to

19°30'S) than the extant distribution of gorillas and chimpanzees (14°N to 10°S latitude).

Hominoid fossils from Berg Aukas, Namibia, estimated to be about 13-12 Ma, reveal that there were two taxa in the deposits, *Otaviapithecus namibiensis* and a form close to *Kenyapithecus wickeri* (Pickford & Senut, 2010). Interestingly, a species of *Kenyapithecus* (*K. kizili* Kelley *et al.* 2008) has been recorded from the late Middle Miocene of Paşalar, Turkey, which means that, with the exception of the genus *Homo*, this extinct genus had by far the greatest latitudinal distribution range known for any hominoid (39°58'N to 19°30'S). If the attribution of the Paşalar and Berg Aukas fossils to *Kenyapithecus* is valid, then it implies that the genus was possibly more eurytopic (more adaptable) than other hominoid genera which were more restricted in their latitudinal ranges and were thus probably more stenotopic, as are extant chimpanzees and gorillas (Senut *et al.* 2017).

Finally, rectification of the geographic position of a locality in Niger that yielded a fragmentary mandible of a late Miocene hominoid (Pickford *et al.* 2008a) is important for future research efforts in the country.

Acknowledgements

We thank Mr Faan Van der Merwe for rescuing the fossils from Berg Aukas Mine and keeping them in good condition, and for providing access to them for detailed study. The Namibia National Heritage Council authorised the Namibia Palaeontology Expedition to carry out research in the country. The NPE is a collaborative project undertaken by the National Museum of Natural History and the University of Paris, and the Geological Survey of Namibia.

The authors are anxious to thank Dr John Van Couvering and Dr Shirley van Heck

for helping to track down the Nieuwenhuis archives which contain the information concerning locality N 885. Comments from two anonymous referees led to improvement of the paper.

Funding for the studies of the Namibian karst deposits was provided by the CNRS, the French Embassy in Namibia (Service de coopération de l'ambassade de France) and the Collège de France (Chaire de Paléo-anthropologie et de Préhistoire, Yves Coppens).

References

- Aiello, L. & Dean, C. 1990. The hominoid knee joint and lower leg. *Introduction to Human Evolutionary Anatomy*. Academic Press, Harcourt Brace & Company, Publishers, London, pp. 483-506.
- Alba, D.M. 2012. Fossil apes from the Vallès-Penedès basin. *Evolutionary Anthropology: Issues, News, and Reviews*, **21**, 254-269.
- Alba, D.M., Almécija, S., Casanovas-Vilar, I., Méndez, J.M. & Moyà-Solà, S. 2012. A partial skeleton of the fossil great ape *Hispanopithecus laietanus* from Can Feu and the mosaic evolution of Crown-Hominoid positional behaviors. *PloS One*, **7**, 6, e39617. Doi:10.1371/Journal.pone.0039617.t002
- Allen, K.L. & McCrossin, M. 2007. Functional morphology of the *Kenyapithecus* hand from Maboko Island (Kenya). *American Journal of Physical Anthropology*, **132** (Supplement 4) p. 62.
- Almécija, S., Alba, D.M. & Moyà-Solà, S. 2009. *Pierolapithecus* and the functional morphology of Miocene ape hand phalanges: paleobiological and evolutionary implications. *Journal of Human Evolution*, **57**, 284-297.
- Almécija, S., Hammond, A.S., Thompson, N.E., Pugh, K.D., Moyà-Solà, S. & Alba, D. 2021. Fossil apes and Human Evolution. *Science*, **372**, eabb4363 (2021). DOI: 10.1126/science.abb4363
- Andrews, P. & Walker, A. 1976. The primate and other fauna from Fort Ternan, Kenya. In: Isaac, G.L. & McCown, E.R. (Eds) *Human Origins : Louis Leakey and the East African Evidence*, pp. 279-304. Menlo, W.A. Benjamin.
- Arney, I.D., McCrossin, M., Benefit, B. & Nengo, I. 2019. Moving through time : intermediate phalanges from East African early and middle Miocene catarrhines reveal locomotor changes. *The 88th Annual Meeting of the American Association of Physical Anthropologists (2019), Poster Session Abstract*.
- Begun, D.R. 2001. African and Eurasian Miocene hominoids and the origins of Hominidae. In: de Bonis, L., Koufos, G. & Andrews, P. (Eds) *Hominoid Evolution and Climate Change in Europe*, volume 2, *Phylogeny of the Neogene Hominoid Primates of Eurasia*. Cambridge University Press, Cambridge, pp. 231-253.
- Begun, D., Nargolwalla, M.C. & Kordos, L. 2012. European Miocene hominids and the origin of the African Ape and Human clade. *Evolutionary Anthropology*, **21**, 10-23
- Begun, D.R., Teaford, M.F. & Walker, A. 1994. Comparative and functional anatomy of *Proconsul* phalanges from Kaswanga Primate Site, Rusinga Island, Kenya. *Journal of Human Evolution*, **26**, 89-165.
- Bergounioux, F. & Crouzel, F. 1968. Deux tortues fossiles d'Afrique. *Bulletin de la Société d'Histoire Naturelle, Toulouse*, **104**, 179-186.
- Böhme, M., Braun, R. & Breier, F. 2020. *Ancient Bones : Unearthing the Astonishing New Story of How We Became Human*. (translated by Billinghamurst, J.). Vancouver, Greystone Books, 376 pp.
- Böhme, M., Spassov, N., Fuss, J., Tröscher, A., Dean, A.S., Prieto, J., Kirscher, U., Lechner, T. & Begun, D.R. 2019. A new Miocene ape and locomotion in the ancestor of great apes and humans. *Nature*, doi.org/10.1038/s41586-019-1731-0
- Boni, M., Terracciano, R., Evans, N.J., Laukamp, C., Schneider, J. & Bechstädt, T. 2007. Genesis of Vanadium ores in the Otavi Mountainland, Namibia. *Economic Geology*, **102**, 441-469.
- Bonis, L. de, Bouvrain, G., Geraads, D. & Koufos, G. 1990. New hominoid skull material from the late Miocene of Macedonia in northern Greece. *Nature*, **345**, 712-714
- Brunet, M., Guy, F., Pilbeam, D., Taisso Mackaye, H., Likius, A., Ahounta, D., Beauvilain, A., Blondel, C., Bocherens, H., Boissérie, J.-R., de Bonis, L., Coppens, Y., Dejax, J., Denys, C., Düringer, P., Eisenmann, V., Fanone, G., Fronty, P., Geraads, D., Lehmann, T., Lihoreau, F., Louchart, A., Mahamat, A., Merceron, G., Mouchelin, G., Otero, O., Pelaez Campomanes, P., Ponce De Leon, M., Rage, J.-C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A. & Zollikofer, C.P.E. 2002. A new hominid from the Upper Miocene of Chad, Central Africa. *Nature*, **418** (6894) 145-151.
- Campbell, B.G. & Bernor, R. 1976. The origin of the Hominidae: Africa or Asia? *Journal of Human Evolution*, **5**, 441-454.
- Conroy, G., Pickford, M., Senut, B., Van Couvering, J. & Mein, P. 1992. *Otaviapithecus namibiensis*, first Miocene hominoid from Southern Africa (Berg Aukas, Namibia). *Nature*, **356**, 144-148.
- Conroy, G.C., Pickford, M., Senut, B. & Mein, P. 1993. Diamonds in the desert: the discovery of *Otaviapithecus namibiensis*. *Evolutionary Anthropology*, pp. 46-52, Wiley-Liss, Inc.

- Conroy, G.C., Senut, B., Gommery, D., Pickford, M. & Mein, P. 1996. Brief Communication: New Primate remains from the Miocene of Namibia, Southern Africa. *American Journal of Physical Anthropology*, **99**, 487-492.
- Cote, S.M. 2004. Origins of the African hominoids: an assessment of the palaeobiogeographical evidence. *Comptes Rendus Palevol*, **3**, 323-340.
- DeSilva, J.M., Morgan, M.E., Barry, J.C. & Pilbeam, D. 2010. A hominoid distal tibia from the Miocene of Pakistan. *Journal of Human Evolution*, **58**, 147-154.
- DeSilva, J., Shoreman, E. & MacLatchy, L. 2006. A fossil hominoid proximal femur from Kikorongo Crater, southwestern Uganda. *Journal of Human Evolution*, **50** (6), 687-695.
- Ersoy, A., Kelley, J., Andrews, P. & Alpagut, B. 2008. Hominoid phalanges from the middle Miocene site of Paşalar, Turkey. *Journal of Human Evolution*, **54**, 518-529.
- Fleagle, J. & Lieberman, D. 2015. Major transformations in the Evolution of Primate locomotion. In: Dial, K.P., Shubin, N. & Brainerd, E.L. (Eds). *Great Transformations in Vertebrate Evolution*, University of Chicago Press, pp. 257-278.
- Gommery, D. 2000. Superior cervical vertebrae of a Miocene hominoid and a Plio-Pleistocene hominid from Southern Africa. *Palaeontologia africana*, **36**, 139-145.
- Gommery, D., Senut, B. & Pickford, M. 1998. Nouveaux restes postcrâniens d'Hominoidea du Miocène inférieur de Napak, Ouganda. Hommage à W.W. Bishop. *Annales de Paléontologie*, **84** (3-4), 287-306.
- Haile-Selassie, Y. 2001. Late Miocene hominids from the Middle Awash, Ethiopia. *Nature*, **412**, 177-181.
- Haile-Selassie, Y., Suwa, G. & White, T.D. 2004. Late Miocene teeth from Middle Awash, Ethiopia, and early hominid dental evolution. *Science*, **303**, 1503-1505.
- Harrison, T. 1986. A reassessment of the phylogenetic relationships of *Oreopithecus bambolii* Gervais. *Journal of Human Evolution*, **15**, 541-583.
- Harrison, T. 2010. Dendropithecoidea, Proconsuloidea, and Hominoidea. In: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*. Berkeley, Los Angeles, London, University of California Press, pp. 429-469.
- Harrison, T., Ji, X. & Su, D. 2002. On the systematic status of the Late Neogene hominoids from Yunnan Province, China. *Journal of Human Evolution*, **43**, 207-227.
- Ishida, H., Kunimatsu, Y., Nakatsukasa, M. & Nakano Y. 1999. New hominoid genus from the middle Miocene of Nachola, Kenya. *Anthropological Science*, **107**, 189-191.
- Ishida, H. & Pickford, M. 1997. A new late Miocene hominoid from Kenya: *Samburupithecus kiptalami* gen. et sp. nov. *Comptes Rendus de l'Académie des Sciences, Paris*, **325**, 823-829.
- Jaeger, J.-J., Soe, A.N., Chavasseau, O., Coster, P., Emonet, E.-G., Guy, F., Lebrun, R., Maung, A., Khyaw, A.A., Shwe, H., Tun, S.T., Oo, K.L., Rugbunrung, M., Bocherens, H., Benammi, M., Chaivanich, K., Tafforeau, P. & Chaimanee, Y. 2011. First hominoid from the Late Miocene of the Irrawaddy Formation (Myanmar). *PLoS One, Public Library of Science*, **6** (4), pp.e17065. [ff10.1371/journal.pone.0017065ff](https://doi.org/10.1371/journal.pone.0017065)
- Kappelman, J., Richmond, B.G., Seiffert, E.R., Maga, A.M. & Ryan, T.M. 2003. Hominoidea (Primates). In: Fortelius M., Kappelman J., Sen S. & Bernor R.L. (Eds) *Geology and Paleontology of the Miocene Sinap Formation, Turkey*. Columbia University Press, New York, pp. 90-124.
- Kelley, J. 2002. The hominoid radiation in Asia. In: Hartwig, W.C. (Ed.) *The Primate Fossil Record*. Cambridge, Cambridge University Press, pp 385-397.
- Kelley, J., Andrews, P. & Alpagut, B. 2008. A new hominoid species from the middle Miocene site of Paşalar, Turkey. *Journal of Human Evolution*, **54** (4) 455-479.
- Kunimatsu, Y., Ishida, H., Nakatsukasa, M., Nakano, Y., Sawada, Y. & Nakayama, K. 2004. Maxillae and associated gnathodental specimens of *Nacholapithecus kerioi*, a large-bodied hominoid from Nachola, northern Kenya. *Journal of Human Evolution*, **46**, 365-400.
- Kunimatsu, Y., Nakatsukasa, M., Sawada, Y., Sakai, T., Hyodo, M., Hyodo, H., Itaya, T., Nakaya, H., Saegusa, H., Mazurier, A., Saneyoshi, M., Tsujikawa, H., Yamamoto, A. & Mbua, E. 2007. A new late Miocene great ape from Kenya and its implications for the origins of African great apes and humans. *Proceedings of the National Academy of Sciences of the United States of America*, **104**, 19220-19225.
- Kunimatsu, Y., Nakatsukasa, M., Sawada, Y., Sakai, T., Saneyoshi, M., Nakaya, H., Yamamoto, A. & Mbua, E. 2016. A second

- hominoid species in the early Late Miocene fauna of Nakali (Kenya). *Anthropological Science*, **124**, 75-83.
- Lartet, E. 1856. Note sur un grand singe fossile qui s'attache au groupe des singes supérieurs. *Comptes Rendus de l'Académie des Sciences*, **43**, 219-223.
- Leakey, L.S.B. 1936. Fossil human remains from Kanam and Kanjera, Kenya Colony. *Nature*, **138**, 643-644.
- Leakey, M.G. & Walker, A.C. 2003. The Lothagam hominids. In: Leakey, M.G. & Harris, J.M. (Eds) *Lothagam: The Dawn of Humanity in Eastern Africa*. New York, Columbia University Press, pp. 249-258.
- Lebatard, A.-E., Bourlès, D., Düringer, P., Jolivet, M., Braucher, R., Carcaillet, J., Schuster, M., Arnaud, N., Monié, P., Lihoreau, F., Likius, A., Mackaye, H.T., Vignaud, P. & Brunet, M. 2008. Cosmogenic nuclide dating of *Sahelanthropus tchadensis* and *Australopithecus bahrelghazali* : Mio-Pliocene hominids from Chad. *Proceedings of the National Academy of Sciences of the United States of America*, **105** (9), 3226-3231.
- Le Gros Clark, W.E. & Leakey, L.S.B. 1950. Diagnoses of East African Miocene Hominoidea. *Proceedings of the Zoological Society of London*, **105**, 260-262.
- Macchiarelli, R., Bergeret-Medina, A., Marchi, D. & Wood, B. 2020. Nature and relationships of *Sahelanthropus tchadensis*. *Journal of Human Evolution*, **149**, 102898.
- McCrossin, M. & Benefit, B. 1997. On the relationships and adaptations of *Kenyapithecus*, a large-bodied hominoid from the Middle Miocene of Eastern Africa. In: Begun, D., Ward, C.V. & Rose, M.D. (Eds) *Function, Phylogeny and Fossils - Miocene Hominoid Evolution and Adaptations*, Plenum Press, New York, pp. 241-267.
- McCrossin, M. & Benefit, B. 2004
- Misiewicz, J.E. 1988. *The geology and metallogeny of the Otavi Mountain Land, Damara Orogen, SWA/Namibia, with particular reference to the Berg Aukas Zn-Pb-V deposit: A model of ore genesis*. Unpublished M.Sc. Thesis, Grahamstown, South Africa, Rhodes University, 143 pp.
- Moggi Cecchi, J. & Pickford, M. 1989. Une nouvelle technique non destructive de détermination de la structure prismatique de l'émail des dents chez les mammifères fossiles. *Comptes Rendus de l'Académie des Sciences, Paris*, **308**, 1651-1654.
- Molnar, P. 2005. Mio-Pliocene growth of the Tibetan Plateau and evolution of East Asian climate. *Palaeontologia Electronica*, **8** (1: 2A) 23 pp.
- Moyà-Solà, S. & Köhler, M. 1996. A *Dryopithecus* skeleton and the origins of great-ape locomotion. *Nature*, **379**, 156.
- Moyà-Solà, S., Köhler, M., Alba, D.M., Casanovas-Vilar, I. & Galindo, J. 2004. *Pierolapithecus catalaunicus*, a new Middle Miocene great ape from Spain. *Science*, **306**, 1339-1344.
- Nieuwenhuis, W.H., van der Vlugt, W.R., Brennand, T.P. & Cuche, D.J. 1963. *Roving Geological Survey of the Niger Basin*. Unpublished Report # 34532, Bataafse Internationale Petroleum Maatschappij B.V., The Hague.
- Olivier, G. & Fenart, R. 1956. Les os de la jambe du semnopithèque. *Mammalia*, **20**, 248-275.
- Palcu, D.V., Vasiliev, I., Stoica, M. & Krigsman, W. 2019. The end of the great Khersonian drying of Eurasia: Magnetostratigraphic dating of the Maeotian transgression in Eastern Paratethys. *Basin Research*, **31**, 33-58.
- Pickford, M. 1985. A new look at *Kenyapithecus* based on recent collections from Western Kenya. *Journal of Human Evolution*, **14**, 113-143.
- Pickford, M. 1986a. Cainozoic palaeontological sites of Western Kenya. *Münchner Geowissenschaftliche Abhandlungen*, **A 8**, 1-151.
- Pickford, M., 1986b. The geochronology of Miocene higher primate faunas of East Africa. In: Else, J. & Lee, P. (Eds) *Primate Evolution*. Cambridge, Cambridge University Press, pp. 19-45.
- Pickford, M. 1987. The geology and palaeontology of the Kanam erosion gullies (Kenya). *Mainzer Geowissenschaftliche Mitteilungen*, **16**, 209-226.
- Pickford, M. 1997. Interplay between global tectonics and the palaeobiosphere during the Cainozoic. In: Aguirre, E., Morales, J. & Soria, D. (Eds) *Registros fósiles e historia de la Tierra*, Madrid, Edit. Complutense, pp. 27-55.
- Pickford, M. 1998. Dating of the Neogene Old World anthropoid fossil record: essential base for phylogenetic analysis, biogeography and palaeoecology. *Primatologie*, **1**, 27-92.
- Pickford, M. 2000. Neogene and Quaternary vertebrate biochronology of the Sperrgebiet and Otavi Mountainland, Namibia. *Communications of the Geological Survey of Namibia*, **12**, 359-365.

- Pickford, M. 2005. Orientation of the foramen magnum in Late Miocene to extant African apes and hominids. Jan Jelinek Commemorative volume. *Anthropologie*, **43**, 103-110.
- Pickford, M. 2009. Metric variation in *Afromeryx* and *Libycosaurus* (Anthracotheriidae: Mammalia) and its utility for biochronology. *Revista Española de Paleontología*, **24**, 107-120.
- Pickford, M. 2012. *Orrorin* and the African Ape / Hominid dichotomy. In: Reynolds, S.C. & Gallagher, A. (Eds) *African Genesis : Perspectives on Hominin Evolution*. Cambridge, Cambridge University Press, pp. 99-119.
- Pickford, M., Coppens, Y., Senut, B., Morales, J. & Braga J. 2009b. Late Miocene hominoid from Niger. *Comptes Rendus Palevol*, **8**, 413-425.
- Pickford, M. & Ishida, H. 1998. Interpretation of *Samburupithecus*, an upper Miocene hominoid from Kenya. *Comptes Rendus de l'Académie des Sciences, Paris*, **326**, 299-306.
- Pickford, M. & Morales, J. 1994. Biostratigraphy and palaeobiogeography of East Africa and the Iberian Peninsula. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **112**, 297-322.
- Pickford, M., Moyà Solà, S. & Köhler, M. 1997. Phylogenetic implications of the first African Middle Miocene hominoid frontal bone from Otavi, Namibia. *Comptes Rendus de l'Académie des Sciences, Paris*, **325**, 459-466.
- Pickford, M. & Senut, B. 2005 Hominoid teeth with chimpanzee- and gorilla-like features from the Miocene of Kenya : implications for the chronology of the ape-human divergence and biogeography of Miocene hominoids. *Anthropological Science*, **113**, 95-102.
- Pickford, M. & Senut, B. 2010. Karst Geology and Palaeobiology of Northern Namibia. *Memoir of the Geological Survey of Namibia*, **21**, 1-74.
- Pickford, M., Senut, B. & Cheboi, K. 2009a. The Geology and Palaeobiology of the Tugen Hills, Kenya: Rift tectonics, Basin Formation, Volcanics and Sedimentation. *Geo-Pal Kenya*, **1**, 4-134.
- Pickford, M., Senut, B., Morales, J. & Braga, J. 2008a. First hominoid from the Late Miocene of Niger. *South African Journal of Science*, **104**, 337-339.
- Pickford, M., Wanas, H., Mein, P., Ségalen, L. & Soliman, H. 2010. The extent of palaeokarst and fluvio-lacustrine features in the Western Desert, Egypt: Late Miocene subaerial and subterranean palaeohydrology of the Bahariya-Farafrā area. *Bulletin of the Tethys Geological Society, Cairo*, **5**, 35-42.
- Pickford, M., Wanas, H., Mein, P. & Soliman, H. 2008b. Humid conditions in the Western Desert of Egypt during the Vallesian (Late Miocene). *Bulletin of the Tethys Geological Society*, **3**, 63-79.
- Pickford, M., Wanas, H. & Soliman, H. 2006. Indications for a humid climate in the Western Desert of Egypt 11-10 million years ago: evidence from Galagidae (Primates, Mammalia). *Comptes Rendus Palevol*, **5**, 935-943.
- Pilbeam, D.R. 1980. Miocene hominoids from Pakistan. *Postilla*, **181**, 1-94.
- Pina, M., Almécija, S., Alba, D.M., O'Neill, M.C. & Moyà-Solà, S. 2014. The middle Miocene ape *Pierolapithecus catalaunicus* exhibits extant great ape-like morphometric affinities on its patella: inferences on knee function and evolution. *PloS One*, **9**, e91944.
- Popov, S.V., Scherba, I.G., Ilyina, L.B., Nevesskaya, L.A., Paramanova, N.P., Khondkarian, S.O. & Magyar, I. 2006. Late Miocene to Pliocene palaeogeography of the Paratethys and its relation to the Mediterranean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **238** (1-4), 91-106.
- Qi, G-Q., Dong, W., Zheng, L., Zhao, L., Gao, F., Yue, L. & Zhang, Y. 2006. Taxonomy, age and environment status of the Yuanmou hominoids. *Chinese Science Bulletin*, **51**, 704-712.
- Rose, M.D. 1993. Locomotor anatomy of Miocene Hominoids. In: Gebo, D (Ed.) *Postcranial Adaptation in Nonhuman Primates*, Northern Illinois University Press, DeKalb, pp. 252-272.
- Sakuma, A., Tada, R., Yoshida, T., Hasegawa, H., Sugiura, N., Karasuda, A., Wang, K. & Zheng, H. 2021. Relationship between tectonism and desertification inferred from provenance and lithofacies changes in the Cenozoic terrestrial sequence of the southwestern Tarim Basin. *Progress in Earth and Planetary Science*, **8** (44) 21 pp.
- Sarmiento, E. 1987. The phylogenetic position of *Oreopithecus* and its significance in the origin of the Hominoidea. *American Museum Novitates*, **2881**, 1-44.
- Sarmiento, E. 2010. Comment on the Paleobiology and Classification of *Ardipithecus ramidus*. *Science*, **328**, 1105, 10.1126/science.1184148.
- Schwartz, G.T. & Conroy, G.C. 1996. Cross-Sectional geometric properties of the *Otaviapithecus* mandible. *American Journal of Physical Anthropology*, **99**, 613-623.
- Senut, B. 1989. Le coude des primates hominoïdes : anatomie, fonction, taxonomie, évolution.

- Cahiers de Paléanthropologie*, Paris, CNRS. 231 pp.
- Senut, B. 1995. D'*Australopithecus* à *Prae-anthropus* ou du respect du Code de Nomenclature. *Annales de Paléontologie, (Vertebrata-Invertebrata)*, **81** (4), 279-281
- Senut B. 2010. Upper Miocene Hominoid distribution and the origin of hominids revisited. *Historical Biology*, **22** (1-3), 260-267. <https://doi.org/10.1080/08912961003603175>
- Senut B. 2011. Origin of hominids: European or African origin, neither or both? *Estudios Geológicos*, **67** (2), 395-409. <http://dx.doi.org/10.3989/egol.40613.196>.
- Senut B. 2014. The Miocene hominoids and the earliest putative hominids. In: Henke, W. & Tattersall, I. (Eds), *Handbook of Palaeoanthropology*, Volume III: *Phylogeny of Hominines*. Springer, pp. 1-20. DOI: 10.1007/SpringerReference_135084; URL: <http://www.springerreference.com/index/chapterdbid/135084>; 2013 doi.org/10.1007/978-3-642-27800-6_49-2
- Senut, B. 2020. *Orrorin tugenensis* et les origines de l'homme : une synthèse. *Bulletin de l'Académie National de Médecine*, **204**, 258-267.
- Senut, B. & Gommery, D. 1997. Squelette post-crânien d'*Otavipithecus*, Hominoidea du Miocène moyen de Namibie *Annales de Paléontologie, (Vertébrés-Invertébrés)*, **83**, (3), 267-284.
- Senut, B., Pickford; M. & Gommery, D. 2018 Dental anatomy of the early hominid, *Orrorin tugenensis*, from the Lukeino Formation, Tugen Hills, Kenya. *Revue de Paléobiologie*, **37** (2), 577-591. DOI: 10.5281/zenodo.2545075
- Senut, B., Pickford, M., Gommery, D., Mein, P., Cheboi, K. & Coppens, Y. 2001. First hominid from the Miocene (Lukeino Formation, Kenya). *Comptes Rendus de l'Académie des Sciences, Paris*, **332**, 137-144.
- Senut, B., Pickford, M., Gommery, G. & Ségalen, L. 2017. Palaeoenvironments and the origin of hominid bipedalism. *Historical Biology*, **30** (1-2), 284-296. Special Issue: *Tribute to Percy Milton Butler*, <http://dx.doi.org/10.1080/08912963.2017.1286337>
- Senut, B., Pickford, M., Mein, P., Conroy, G. & Van Couvering, J. 1992. Discovery of 12 new late Cainozoic fossiliferous sites in palaeokarsts of the Otavi Mountains, Namibia. *Comptes Rendus de l'Académie des Sciences, Paris*, **314**, 727-733.
- Senut, B., Pickford, M., Ségalen, L., Roche, D. & Gommery, D. 2010. Paléoenvironnements néogènes et évolution des hominoïdes. In: Barbault, R. & Foucault, A. (Eds) *Changements climatiques et biodiversité*. Paris, Vuibert-AFAS, pp. 125-144.
- Simpson, S.W., Kleinsasser, L., Quade, J., Levin, N.E., McIntosh, W.C., Dunbar, N., Semaw, S. & Rogers, M.J. 2015. Late Miocene hominin teeth from the Gona Paleoanthropological Research Project area, Afar, Ethiopia. *Journal of Human Evolution*, **81**, 68-82.
- Singleton, A.-M. 1998. *The Phylogenetic Position of Otavipithecus namibiensis: Quantitative Character Coding in Hominoid Phylogeny Reconstruction*. PhD Thesis, Washington University, Saint Louis, Missouri, 344 pp.
- Singleton, M. 2000. The phylogenetic affinities of *Otavipithecus namibiensis*. *Journal of Human Evolution*, **38**, 537-573.
- Susman, R.L. 1979. Comparative and functional morphology of hominoid fingers. *American Journal of Physical Anthropology*, **50**, 215-236.
- Suwa, G., Kono, R.T., Katoh, S., Asfaw, B. & Beyene, Y. 2007. A new species of great ape from the late Miocene epoch in Ethiopia. *Nature*. **448** (7156), 921-924.
- Swindler, R.R. & Wood, C.D. 1973. *An Atlas of Primate Gross Anatomy. Baboon, Chimpanzee, and Man*. University of Washington Press, Seattle and London, 370 pp.
- Takai, M., Nyo, K., Kono, R.T., Htike, T., Kusuhashi, N. & Thein, S.M.M. 2021. New hominoid mandible from the early Late Miocene Irrawaddy Formation in Tebingan area, central Myanmar. *Anthropological Science*, DOI: 10.1537/ase.2012131.
- Tekkaya, I. 1974. A new species of Tortonian anthropoid (Primates, Mammalia) from Anatolia. *Bulletin of the Mineral Research and Exploration Institute of Turkey, Ankara*, **83**, 148-165.
- Walker, M. & Pickford, M. 1983. New postcranial fossils of *Proconsul africanus* and *Proconsul nyanzae*. In: Ciochon, R. & Corruccini, R. (Eds) *New Interpretations of Ape and Human Ancestry*. New York, Plenum, pp. 325-351.
- Wanas, H., Pickford, M., Mein, P., Soliman, H. & Segalen, L. 2009. Late Miocene karst system at Sheikh Abdallah, between Bahariya and Farafra, Western Desert, Egypt: Implications for palaeoclimate and geomorphology. *Geologica Acta*, **7** (4), 475-487.
- Ward, S., Brown, B., Hill, A., Kelley, J. & Downs, W. 1999. *Equatorius* : A new hominoid genus

from the Middle Miocene of Kenya. *Science*, **285**, 1382-1386.

White, T.D., Lovejoy, C.O., Asfaw, B., Carlson, J.P. & Suwa, G. 2015. Neither chimpanzee nor human, *Ardipithecus* reveals the surprising ancestry of both. *Proceedings of the National Academy of Sciences of the United States of America*, **112**, 4877-4884.