



HAL
open science

NEW PLIOCENE HOMINID FOSSILS FROM BARINGO COUNTY, KENYA

Martin Pickford, Brigitte Senut, Dominique Gommery, Joseph Kipkech

► **To cite this version:**

Martin Pickford, Brigitte Senut, Dominique Gommery, Joseph Kipkech. NEW PLIOCENE HOMINID FOSSILS FROM BARINGO COUNTY, KENYA. *Fossil Imprint*, 2022, 78 (2), pp.451-488. 10.37520/fi.2022.020 . hal-03908263

HAL Id: hal-03908263

<https://hal.science/hal-03908263v1>

Submitted on 13 Jan 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

New Pliocene hominid fossils from Baringo County, Kenya

Martin Pickford¹, Brigitte Senut¹, Dominique Gommery², Joseph Kipkech³

¹ Centre de Recherche en Paléontologie – Paris (CR2P), Muséum national d'Histoire naturelle, CNRS, Sorbonne Université, CP 38, 8 rue Buffon, 75005 Paris, FRANCE. martin.pickford@mnhn.fr, brigitte.senut@mnhn.fr

² Centre de Recherche en Paléontologie – Paris (CR2P), CNRS, Muséum national d'Histoire naturelle, Sorbonne Université, Campus Pierre et Marie Curie-SU, T.46-56, E.5, 4 Place Jussieu, 75005 Paris, FRANCE. dominique.gommery@sorbonne-universite.fr

³ Orrorin Community Organisation (OCO), P.O. Box 232-3040, Kabartonjo, KENYA.

Abstract

During field surveys between 2005 and 2011 in the Tugen Hills by the Franco-Kenyan Kenya Palaeontology Expedition, several hominid specimens were discovered in the Pliocene Mabaget Formation. One mandible fragment, three isolated teeth and a pedal phalanx collected from the Pelion Member (base of the formation aged 5.0-4.5 Ma) are compatible in dimensions with *Orrorin tugenensis* and *Ardipithecus ramidus* whilst a mandible from the Sinibo Member, a younger level in the formation (ca 3.4-3.0 Ma) represents an appreciably larger species, as big as, or bigger than, *Praeanthropus afarensis* (ex-*Australopithecus afarensis*) from locality AL 333, Ethiopia.

The small hominid mandible and an isolated p/3 were found in the type section of the Mabaget Formation at localities 2/211 and 2/210 respectively, in deposits aged ca 5.0-4.5 Ma. An isolated upper milk molar, a lower third molar and a pedal phalanx are from Sagatia, near Rondinin, also aged between 5 and 4.5 Ma. The large mandible was collected at Sinibo, near Kipcherere, from sediments above the local occurrence of the Tulu Bor Tuff (= Sidi Hakoma Tuff) which is dated at 3.446 Ma. The aim of this paper is to describe and interpret these hominid fossils and to place them within their geological, stratigraphic and palaeoenvironmental contexts.

Key words

Pliocene, East Africa, Kenya, Hominidae, Dento-gnathic, Phalanx

Introduction

The Tugen Hills stratigraphic succession spans (with gaps) much of the Neogene, the lowermost sediments, the Kamego Beds (ca 17 Ma) overlying Mozambique Belt gneisses (PreCambrian). The youngest strata in the region are Recent (Fig. 1). Hominoid fossils have been found in various units through the succession, the oldest and most diverse assemblage being from the Muruyur Formation at Kipsaraman aged ca 14.5 Ma (Pickford & Kunitatsu, 2005; Sherwood *et al.* 2002b; Ward *et al.* 1999a). Other fossil hominoid specimens are known from the Ngorora Formation (between 13.2 and 10.3 Ma) (Pickford & Senut, 2005a, 2005b), the Lukeino Formation (6.2-5.7 Ma) (Sawada *et al.* 2002; Senut *et al.* 2001, 2018), the Toluk Beds of the Kaparaina Formation (ca 5.7-5.3 Ma) (Pickford *et al.* 2009), the Mabaget Formation (5.1-3.0 Ma) (Pickford *et al.* 1983; Ward & Hill, 1987; Hill & Ward, 1988), the Chemeron Formation (2.4-1.7 Ma) (Deino & Hill, 2002; Sherwood *et al.* 2002a) and the Kapthurin Formation (0.8-0.4 Ma) (Deino & McBrearty, 2002) (Fig. 1).

The only hominid specimens previously reported from the Mabaget Formation (Fig. 2) comprise a proximal humerus (KNM BC 1745) from the Mabaget locality (Pickford *et al.* 1983; Senut, 1983) and a fragmentary mandible containing two molars (KNM TH 13150) from Tabarin (Hill, 1985, 1994; Ward & Hill, 1987; Boaz, 1988; Ferguson, 1989; Deino *et al.* 2002; Kissel & Hawks, 2015). Mention has been made in the literature of a hominid tooth from Sagatia dubbed the Black Cusp (Hill, 2002) but it has not been described. Binetti (2011) wrote that Sagatia had yielded no hominid fossils, which suggests that

the Black Cusp specimen may belong to another mammal. Whatever the case, the specimen remains enigmatic.

Despite the extended duration of the hominoid fossil record in Baringo County, the total quantity of fossils is rather low (fewer than 100 specimens) most of which are fragmentary jaws or isolated teeth, so each new discovery represents a precious addition to the debate about hominoid and hominid origins. We here describe and interpret several hominid specimens found in the Pliocene Mabaget Formation during field surveys by the Franco-Kenyan Kenya Palaeontology Expedition (KPE) between 2005 and 2011.

The Mabaget Formation crops out in the eastern foothills of the Tugen Hills, Baringo County, Kenya (Pickford *et al.* 2009). This formation is of early to middle Pliocene age. The older of the two mandibular specimens described herein (ca 5.0-4.5 Ma) came from locality 2/211 (Mabaget) which is close to the type area of the Mabaget Formation (Loc. 2/210). Locality 2/211 had previously yielded a proximal humerus of a hominid (Pickford *et al.* 1983). An isolated p/3 of a hominid was found at locality 2/210 (Pelion) where the type section of the formation was measured (Fig. 2). A pedal phalanx, a lower third molar and an upper deciduous molar of a chimpanzee-sized form were found in 2005 and 2010 at Sagatia, close to Rondinin. The latter specimens are older than 4 Ma. Finally, two fragments of a large hominid mandible were found at Sinibo, not far from Kipcherere, in the southern outcrops of the same formation but from higher in the stratigraphic succession (Sinibo Member) slightly younger than 3.4 Ma. The latter locality also yielded suids; several specimens of *Nyanzachoerus kanamensis* from the base of the stratigraphic succession, and two teeth of *Kolpochoerus heseloni* (or *olduvaiensis*) from high in the exposures. On the basis of the dimensions of the teeth of *Kolpochoerus olduvaiensis* (m/2 length 36.0 mm x breadth 25.5 mm; m/3 length 70 mm x breadth 25.9 mm) the uppermost sedimentary levels at Sinibo could be of Pleistocene age.

The Sinibo hominid jaw is considerably older than the Chemeron hominid temporal bone (KNM BC 1) aged ca 2.4 Ma, identified as *Homo* sp. by Hill *et al.* 1985. As such, according to MacLachy *et al.* (2010) the latter specimen could be one of the oldest records of the genus *Homo*, being not much younger than specimens from Ledi-Geraru, (2.8 Ma, Ethiopia) (Villmoare *et al.* 2015) that have been interpreted as the earliest known members of the genus *Homo*.

It is worth pointing out that all these fossils were found in what used to be called the Chemeron Formation (Hill *et al.* 1985). Additional surveys by the Kenya Palaeontology Expedition (Pickford *et al.* 2009) provided evidence that has led to the subdivision of this unit which, as previously mapped, was an unnatural grouping of heterochronic sedimentary units that accumulated in two separate rift basins, one west and north of the Kaparaina volcanic massif, the other to its east. What used to be called the Chemeron Formation (Northern Extension) is now known as the Mabaget Formation, which comprises two members, a basal Pelion Member aged between 5.0 and 4.5 Ma, and an upper Sinibo Member aged between 4.1 and 3.0 Ma with the possibility of Pleistocene beds near the top of the exposures at Sinibo. The Chemeron Formation, *sensu stricto* (i.e. in its type area) is aged ca 2.4 to 1.7 Ma (Deino *et al.* 2002). Hominid fossils have been found in all three of these units.

Because the fossils described herein occur several, to tens of, metres above dated tuffs, there is a degree of uncertainty about their precise correlation to the Geological Time Scale. Instead of the terms Early and Late Pliocene (with the adjectives in capital letters) in this paper we employ the informal terms basal, mid- and upper Pliocene (with lower case adjectives).

Material and Methods

Table 1. List of hominid material from the Mabaget Formation, Tugen Hills, Baringo County, Kenya.

Catalogue	Anatomy	Locality	Age	Collector
KNM BC 1745	Proximal humerus	2/211, Mabaget	5.0-4.5 Ma	M. Pickford
KNM TH 13150	Mandible	2/267, Tabarin	5.0-4.5 Ma	Kiptalam Cheboi

OCO BAR 500'05	Left m/3	2/232, Sagatia	5.0-4.5 Ma	Team
OCO BAR 1'08	Right p/3	2/210, Pelion	5.0-4.5 Ma	David Rerimoi
OCO BAR 150'10	Pedal phalanx	2/232, Sagatia	5.0-4.5 Ma	Team
OCO BAR 151'10	Right D4/	2/232, Sagatia	5.0-4.5 Ma	Team
OCO BAR 900'11	Right and left mandible fragments	Sinibo	3.3-3.0 Ma	Rosaline Cheptumo
OCO BAR 1046'11	Right mandible fragment with p/4-m/1	2/211, Mabaget	5.0-4.5 Ma	Zaphania Chetalam

The fossils with prefix OCO are curated at the Orrorin Community Organisation, Kipsaraman Museum. Those with the prefix KNM are housed at the National Museums of Kenya, Nairobi (Table 1).

Measurements were made with sliding calipers to an accuracy of 0.1 mm. It is evident from the literature that measurements of the same specimen by different authors, or even by the same authors in different publications can vary substantially (see for example Leakey *et al.* 1995 and Ward *et al.* 1999b). The published measurements of the p/3 in particular can differ by as much as 35%. For this reason we provide classic mesio-distal and bucco-lingual diameters of the p/3 as well as maximum oblique diameter and minimum diameter at right angles to the former. For teeth that have undergone interstitial wear, we have adjusted the length measurement to account for the missing elements. The sources of measurements from the literature used for comparisons and for compiling the bivariate length/breadth bivariate plots (Figs 17, 21-22) are shown in Table 2. Measurements of the hominid teeth from the Mabaget Formation are provided in Table 6.

During this study enamel thickness was not measured by scanning techniques but visual assessments were made for some teeth classing them as thin-enamelled (ca 1 mm or less) or thick-enamelled (more than 1.5 mm) (see descriptions for details). Enamel thickness varies over the tooth so providing accurate measurements requires sophisticated scanning techniques, and it is evident from the literature that methods of measuring the thickness vary alot, making comparisons of the raw data hazardous. Our assessments were based on natural exposures of the enamel-dentine junction at wear facets or at breaks in the crowns.

Table 2. Sources of measurements of late Miocene to Pliocene hominid teeth compared with the Tugen Hills fossils arranged by locality in alphabetical order.

Locality	Authors
Aramis	White <i>et al.</i> 2015
As Duma (Gona)	Semaw <i>et al.</i> 2005
Burtele	Haile-Selassie <i>et al.</i> 2015
Cheboit	Senut <i>et al.</i> 2001
Drimolen	Moggi-Cecchi <i>et al.</i> 2010; Rak <i>et al.</i> 2021
East Turkana	Ward <i>et al.</i> 2001
Hadar	Kimbel <i>et al.</i> 2004
Kanapoi	Ward <i>et al.</i> 2001
Kapsomin	Senut <i>et al.</i> 2001; 2018
Koro Toro	Brunet <i>et al.</i> 1996
Kuseralee	White <i>et al.</i> 2015
Laetoli	Harrison, 2011, White 1980
Ledi-Geraru	Villmoare <i>et al.</i> 2015; Villmoare, 2018
Lomekwi	Skinner <i>et al.</i> 2020
Malapa	Berger <i>et al.</i> 2010
Middle Awash	Haile-Selassie, 2001; Haile-Selassie <i>et al.</i> 2004
Olduvai	Moggi-Cecchi <i>et al.</i> 2010
Omo	Moggi-Cecchi <i>et al.</i> 2010
Sagantole	White <i>et al.</i> 2015
Sterkfontein	Moggi-Cecchi <i>et al.</i> 2006
Swartkrans	Grine, 2004; Moggi-Cecchi <i>et al.</i> 2010
Tabarin	Hill, 1985
Toros Menalla	Brunet <i>et al.</i> 2005
Uraha	Bromage <i>et al.</i> 1995
West Turkana	Moggi-Cecchi <i>et al.</i> 2010
Woranso-Mille	Haile-Selassie <i>et al.</i> 2022

Figures 21 and 22 compare the dimensions of fossil hominid teeth on a locality by locality basis, which is known and not open to modification. This is done to avoid the uncertainty that surrounds the taxonomic identification of the material that pervades the literature. Some localities, such as Swartkrans, have yielded specimens of both *Homo* and *Australopithecus*, but this does not invalidate the metric comparisons.

Geographic co-ordinates were obtained with GPS set to WGS 84 datum. It is noted that co-ordinates taken before 2011 are no longer accurate in 2021, there being an offset of up to 100 metres.

From 1972 to 1981, fossiliferous localities in the Tugen Hills were numbered with prefix 1/** and 2/** for the localities south and north of latitude 0°40'N respectively. Local place names were also employed along with the numbering system (Pickford, 1975; Pickford *et al.* 2009). In 1982 an alternative system was put in place by which all the localities were renumbered and given the prefix BPRP. This dual numbering system has caused confusion (Binetti, 2011) so in this paper we use the first system which is well documented (Pickford, 1975; Pickford *et al.* 2009) but also provide the alternative number, where known, so that readers can cross-check for themselves. As examples of misinformation, Hill (1985) wrote that Tabarin was a newly discovered site and Binetti (2011) wrote that the sites of Tabarin and Sagatia were first discovered by the BPRP, but they both feature in Pickford's (1975) doctoral thesis as localities 2/267 and 2/232 respectively (Pickford *et al.* 2009).

In accordance with general mammalian palaeontology, we call the posterior deciduous tooth in the maxilla the D4/ rather than the D2/ (or dM2/) as is often done by dentists and palaeoanthropologists. It is replaced by the P4/, not the P2/.

The systematics of African apes and humans have developed into a Gordian Knot such that virtually every author has his or her separate schema for arranging the taxa into genera, subtribes, tribes, subfamilies, and families. For some authors Hominidae comprises the African apes and humans (indeed some go as far as to include the chimpanzee in the genus *Homo* (Watson *et al.* 2001; Goodman *et al.* 2001)) whereas for others, Hominidae is restricted to obligate bipedal taxa that are more closely related to humans than to either chimpanzees or gorillas. Because of the unresolved debate about the validity of *Paranthropus* versus *Australopithecus* and *Praeanthropus*, some authors, such as Prentice & Denton (1998) omitted generic names when discussing *afarensis*, *aethiopicus*, *robustus* and *boisei*. Without entering into details or into the merits and demerits of each scheme, we employ the family name Hominidae to include *Orrorin*, *Praeanthropus*, *Australopithecus*, *Paranthropus*, *Kenyanthropus* and *Homo* (Senut, 1995, 1996). Under this usage the hominid status of *Ardipithecus* and *Sahelanthropus* is doubtful, both taxa possessing cranial and post-cranial features (femur, ulnae) that indicate closer affinities to quadrupedal apes than to humans (Pickford, 2004, 2005a; White *et al.* 2015; Macchiarelli *et al.* 2020; Daver *et al.* 2022).

In this paper, the Hominoidea is defined as a superfamily of catarrhines comprising extant humans, gorillas, chimpanzees and orang-utans as well as gibbons and siamangs (Hylobatidae), and diverse fossil lineages of Oligo-Miocene to Pleistocene age which are more closely related to these extant genera than they are to cercopithecoids (monkeys). The authors exclude gorillas, chimpanzees and orang-utans from the family Hominidae, which is restricted to bipedal hominoids that are more closely related to *Homo* than to *Pan* or *Gorilla*, the latter two genera being classed in Gorillidae. *Pongo* is classed in a separate family, Pongidae. *Sahelanthropus* and *Ardipithecus* are both classed as Gorillidae, their postcranial skeletons indicating that neither was an obligate biped.

A further source of confusion in studies of hominid evolution is the quantity of species epithets that have been proposed for African Plio-Pleistocene hominids (Table 3) (Gyenis, 2002; Bond, 2011). We provide a full list in order that the readers can assess the publications and decide the issues for themselves.

Table 3. List of African latest Miocene to early Pleistocene hominid genera and species arranged in the order of their naming (nn = *nomen nudum*, no holotype or type species designated).

Nomen	Proposed by	Type specimen	Age Ma
<i>Australopithecus africanus</i>	Dart, 1925	Taung 1	2.8-2.6
<i>Plesianthropus transvaalensis</i>	(Broom, 1936)	TM 1511 + STS 60	2.5-2.15
<i>Paranthropus robustus</i>	Broom, 1938	TM 1517	2.0-1.7
<i>Australopithecus prometheus</i>	Dart, 1948	MLD 1	3.2-2.9
<i>Praeanthropus</i>	Hennig, 1948	nn	3.8-3.5
<i>Telanthropus capensis</i>	Broom & Robinson, 1949a (1949b)	SK 15	1.8-1.5
<i>Meganthropus africanus</i>	(Weinert, 1950)	Garussi 1	3.8-3.5
<i>Atlantropus mauritanicus</i>	Arambourg, 1954	1954-7-825, Ternifine 1 (Atl 1)	1.6-1.4
<i>Paranthropus crassidens</i>	Broom, 1952 (Broom & Robinson, 1952)	SK 6	1.8-1.5
<i>Praeanthropus</i>	Şenyürek, 1955	Garussi 1	3.8-3.5
<i>Zinjanthropus boisei</i>	Leakey, 1959	OH 5	1.8-1.2
<i>Homo leakeyi</i>	Heberer, 1963	OH 9	1.8-1.5
<i>Homo habilis</i>	Leakey <i>et al.</i> 1964	OH 7	1.8-1.5
<i>Paraaustralopithecus aethiopicus</i>	Arambourg & Coppens, 1967 (1968)	OMO 18-1967-18	2.6-2.3
<i>Homo ergaster</i>	Groves & Mazak, 1975	KNM ER 992	1.9-1.5
<i>Australopithecus afarensis</i>	Johanson, 1978	LH 4	3.8-3.5
<i>Australopithecus africanus afarensis</i>	Tobias, 1980a	nn	3.4-3.0
<i>Australopithecus africanus aethiopicus</i>	Tobias, 1980a	nn	3.4-3.0
<i>Australopithecus africanus tanzaniensis</i>	Tobias, 1980b	nn	3.8-3.5
<i>Homo antiquus</i>	Ferguson, 1984	AL 288-1	3.4-3.0
<i>Homo (Proanthropus) louisleakeyi</i>	Kretzoi, 1984	OH 9	1.8-1.5
<i>Homo rudolfensis</i>	Alexeev, 1986	KNM ER 1470	1.9
<i>Australopithecus africanus miodentatus</i>	Ferguson, 1987	AL 266-1	3.8-3.5
<i>Australopithecus walkeri</i>	Ferguson, 1989a	KNM WT 17000	2.5
<i>Homo antiquus praegens</i>	Ferguson, 1989b	KNM TH 13150	4.5-4.4
<i>Ardipithecus ramidus</i>	(White <i>et al.</i> 1994)	ARA-VP-6/1	4.5-4.3
<i>Homo microcranus</i>	Ferguson, 1995	KNM ER 1813	1.65
<i>Australopithecus anamensis</i>	Leakey <i>et al.</i> 1995	KNM KP 29281	4.2-3.8
<i>Australopithecus bahrelghazali</i>	Brunet <i>et al.</i> 1996	KT12/H1	?3.5
<i>Australopithecus garhi</i>	Asfaw <i>et al.</i> 1999	BOU-VP-12/130	2.5
<i>Homo okotensis</i>	Zeitoun, 2000	KNM ER 3883	2.0-1.4
<i>Homo kenyaensis</i>	Zeitoun, 2000	KNM ER 3733	1.9
<i>Orrorin tugenensis</i>	Senut <i>et al.</i> 2001	OCO BAR 1000'00	6.2-5.8
<i>Kenyanthropus platyops</i>	Leakey <i>et al.</i> 2001	KNM WT 40000	3.6-3.3
<i>Sahelanthropus tchadensis</i>	Brunet <i>et al.</i> 2002	TM 266-01-060-1	?7
<i>Ardipithecus ramidus kadabba</i>	Haile-Selassie <i>et al.</i> 2004	ALA-VP-2/10	5.8-5.2
<i>Homo hadar</i>	Bonde & Westergarde, 2004	AL 333-45	3.3
<i>Praeanthropus lothagamensis</i>	Bonde & Westergarde, 2004	KNM LT 329	5-4.2
<i>Australopithecus sediba</i>	Berger <i>et al.</i> 2010	MH 1	1.9-1.8
<i>Homo gautengensis</i>	Curnoe, 2010	STW 53	?3.5-3.0
<i>Afaranthropus antiquus</i>	Bonde, 2011	AL 288-1	3.4-3.0
<i>Australopithecus deyiremeda</i>	Haile-Selassie <i>et al.</i> 2015	BRT-VP-3/1	3.5-3.3

Comparative Base

Casts of several of the Hadar specimens attributed to *Australopithecus afarensis* were available for comparison, as were casts of *Orrorin tugenensis*, *Australopithecus bahrelghazali*, *Australopithecus africanus* (holotype), *Paranthropus robustus* and *Paranthropus aethiopicus*. For other taxa, reference has been made to the literature (Tables 2, 3).

Abbreviations

BAR - Baringo

BC - Baringo Chemeron

BPRP - Baringo Paleontological Research Project

KNM - Kenya National Museums, Nairobi

KPE - Kenya Palaeontology Expedition

OCO - Orrorin Community Organisation, Kipsaraman, Kenya

TH - Tugen Hills

Geological Context

The Mabaget Formation is an areally extensive sedimentary unit cropping out in the eastern foothills of the Tugen Hills, Baringo County, Kenya. In the north it unconformably overlies the Lukeino Formation (6.3-5.7 Ma) and in the south it overlies the Kaparaina Basalt Formation (5.7-5.4 Ma). It is overlain by diverse volcanic and sedimentary units of late Pliocene to Recent age (Fig. 1, 2).

The Mabaget Formation is herein subdivided into two members, the basal Pelion Member and the younger Sinibo Member. The type section of the Pelion Member is at Locality 2/210 (Fig. 2) and the succession spans the period 5.1-4.7 Ma, and the type section of the Sinibo Member (Fig. 11) is in the Kipcherere badlands and spans the period 3.5-3.0 Ma with a capping of Pleistocene deposits.

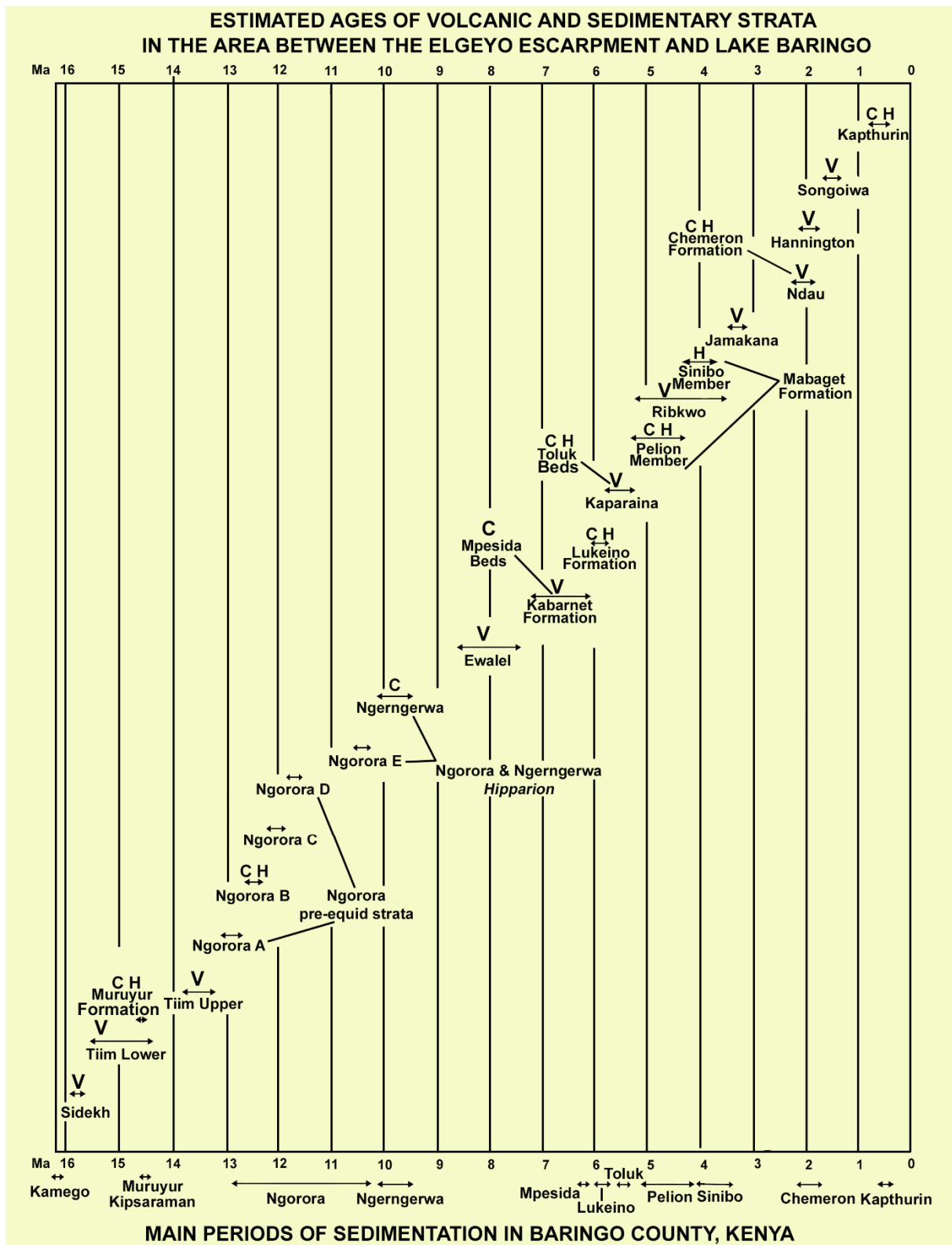


Figure 1. Neogene to Recent stratigraphic succession of the Tugen Hills, Baringo County, Kenya. The time spans of the main sedimentary units are depicted at the foot of the figure. C - cercopithecoids, H - hominoids, V - volcanic rocks.

The geographic extent of the Mabaget and Chemeron formations is depicted in Figure 2. The Mabaget Formation extends north and south of latitude 0°45'N over a distance of ca 50 km and its east-west extent is between 2 and 10 km just west of longitude 36°E.

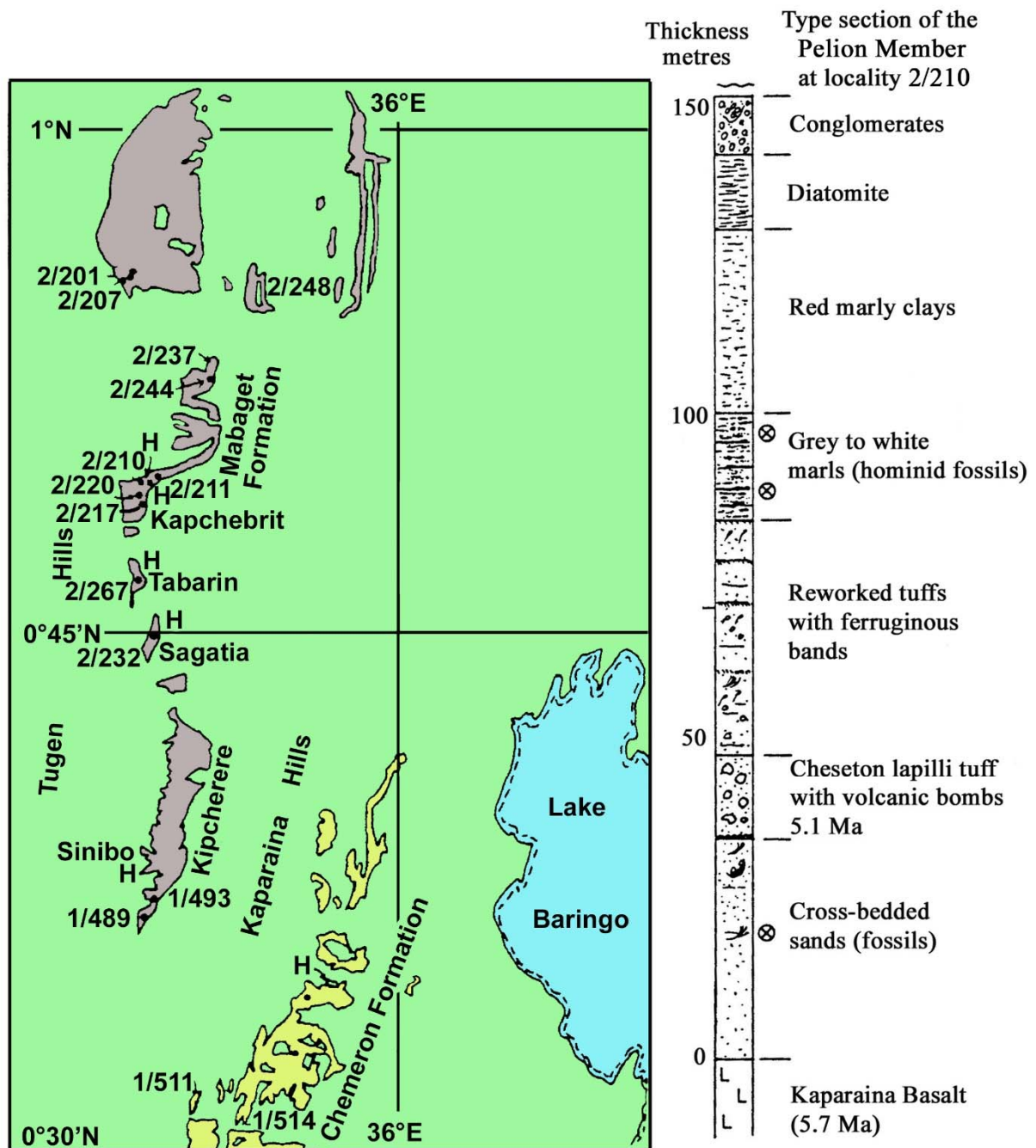
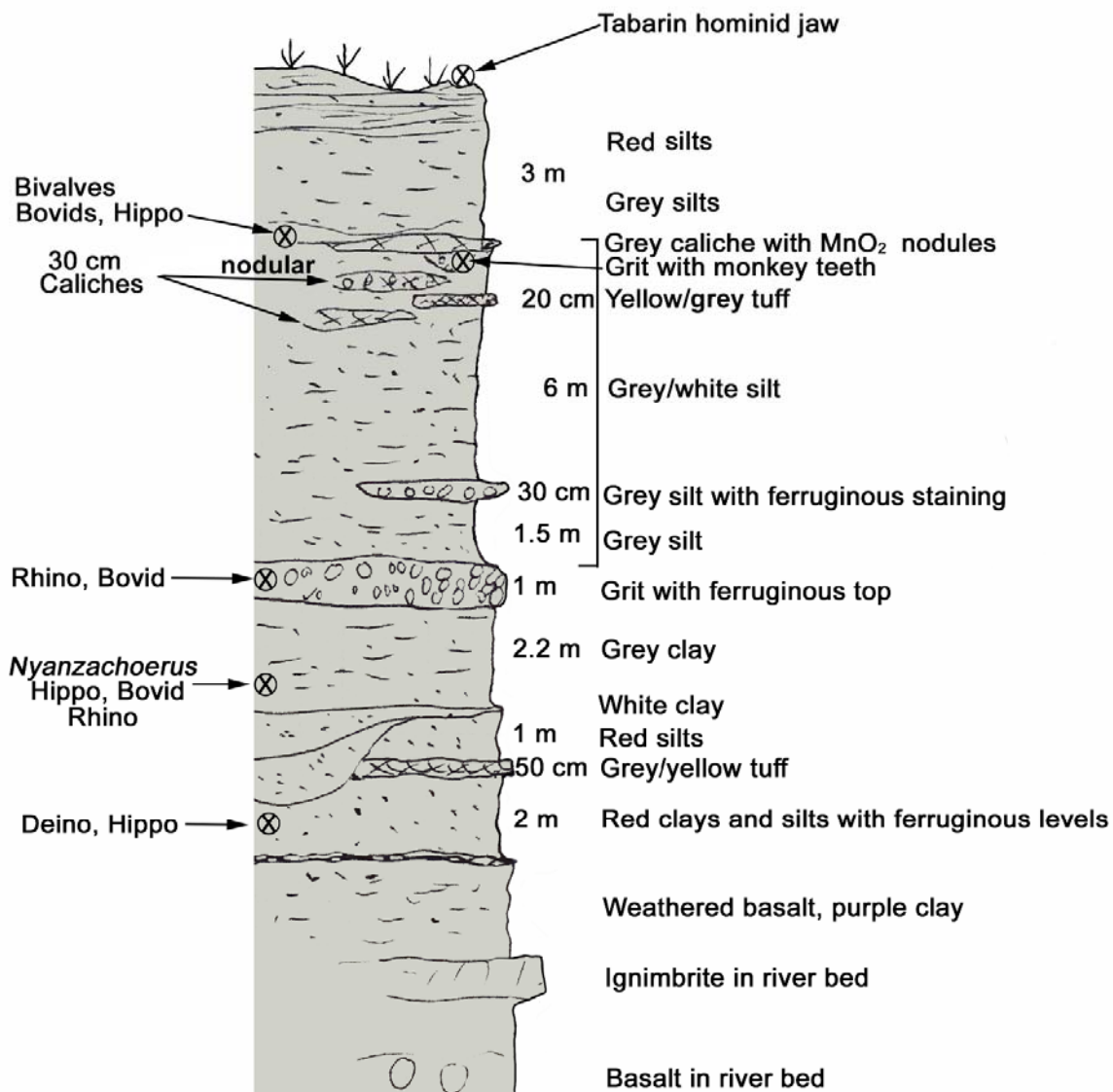


Figure 2. Geographic distribution of the Mabaget (grey) and Chemeron (yellow) formations, and type section of the Pelion Member at locality 2/210, showing the position of the Mabaget hominid fossils. (Green represents the Kaparaina Basalts and other rock units, both older and younger than the Mabaget Formation). H - hominid fossils. Fossiliferous localities north of 0°40'N latitude having the prefix 2/, and those south of it, the prefix 1/ (see Pickford, 1975, and Pickford *et al.* 2009).

Locality 2/211 (Mabaget, BPRP K037) is close to the Yatya-Toluk 4x4 vehicle track at 00°48'58.8''N : 35°52'05.9''E (1210 m altitude). The nearby locality of Pelion at 00°49'10.1''N : 35°52'22.9''E (1210 m altitude) (= locality 2/210, the place name means 'Elephant' in the Tugen dialect of Kalenjin) is beside the same track and yielded a lower third premolar of a hominid.

The co-ordinates of locality 2/267 (= BPRP 77) that yielded the Tabarin hominid mandible (Fig. 3) are 00°45'39.3''N : 35°51'42.8''E. The deposits have been dated to 4.42 Ma using radio-isotopic methods (Deino *et al.* 2002). Delson *et al.* (2000) gave the age of the Tabarin hominid fossil as 4.5 Ma in their

table, page 15, but as 4.2-3.9 Ma in their text, page 26. Note, however, that the Tabarin mandible was a surface find at the top of the succession (Fig. 3).



STRATIGRAPHIC SECTION AT TABARIN

Thickness 17 m, dipping west at 15° +/-

Figure 3. Stratigraphic section at Tabarin, with fossil occurrences at diverse stratigraphic levels. The Tabarin mandible was a surface find at the top of the section (Deino – *Deinotherium*, Hippo – *Hippopotamus*, Rhino - rhinocerotid).

Sagatia (locality 2/232 = BPRP 75) is close to Rondinin (= Tamarind Grove in the Tugen dialect). The upper deciduous molar was collected at 00°44'21.2''N : 35°52'04.8''E and the pedal phalanx at 00°44'20.6''N : 35°52'04.4''E.

The Sinibo locality is at 00°37'36.4''N : 35°52'28.9''E (1245 m altitude) near Kipcherere (Place of Vervet Monkeys in Tugen) and Uswonin (Pickford *et al.* 2009).

The mammalian fauna from the lower sections of the Mabaget Formation (i.e. the Pelion Member) (Table 4) is of middle Pliocene aspect, with species such as *Dasychoerus arvernensis*, *Nyanzachoerus jaegeri*, *Anancus kenyensis*, *Agriotherium aecuatorialis* and *Sivaonyx ekecaman* (Pickford & Obada,

2016; Pickford *et al.* 2009). An age range of ca 5.0-4.5 Ma is estimated for these lower beds (Pickford, 2013).

The higher levels of the Mabaget Formation (i.e. the Sinibo Member) yield a more advanced fauna than the Mabaget Member, comprising, among other taxa, the nyanzachoerine suid, *Nyanzachoerus kanamensis* from the base of the section and a large kolpochoerine suid (several mandible fragments and isolated teeth), *Kolpochoerus heseloni* (or *K. olduvaiensis*) (two teeth) from high in the stratigraphic section, the bovid *Menelikia lyrocera* (or perhaps *Menelikia leakeyi*) (Gentry, 2010) and the elephantid, *Elephas africanavus* (Sanders *et al.* 2010). The estimated age range of the upper beds of the Mabaget Formation spans the period ca 4.1 to 3.0 Ma. The summital strata at Sinibo could be of Pleistocene age (*Kolpochoerus olduvaiensis*).

Table 4. Fauna from the Mabaget Member (5.0-4.5 Ma), Tugen Hills, Baringo County, Kenya.

Ostracoda	
	Indet.
Mollusca	
	Gastropoda
	Viviparidae
	<i>Bellamyia unicolor</i>
	Ampullariidae
	<i>Pila ovata</i>
	Thiariidae
	<i>Melanoides tuberculata</i>
	Bivalvia
	Unionidae
	<i>Coelatura hauttecoeuri</i>
	Iridinidae
	<i>Cameronia mohariensis</i>
	<i>Chambardia trapezia</i>
Pisces	
	Clariidae
	indet.
	Cichlidae
	Indet.
	Cyprinidae
	<i>Barbus</i> sp.
Reptilia	
	Chelonii
	Trionychidae
	cf <i>Trionyx</i> sp.
	Pelomedusidae
	Indet. sp.
	Testudinidae?
	Indet. sp.
	Crocodylia
	Crocodylidae
	<i>Crocodylus</i> sp.
Aves	
	Phasianidae
	<i>Pavo</i> sp.
	Anhingidae
	<i>Anhinga</i> sp. large
Mammalia	
	Chiroptera
	Molossidae indet.
	Insectivora
	Soricidae indet.
	Carnivora

Ursidae
 Agriotherium aecuatorialis
 Hyaenidae
 Ikelohyaena abronia
 Hyaenictitherium namaquensis
 Hyaenictis hendeyi
 Viverridae
 Civettictis howelli
 Herpestidae
 Indet. sp.
 Mustelidae
 Sivaonyx ekecaman
 Primates
 Galagidae
 Galago sadimanensis
 Cercopithecidae
 Hominidae
 Orrorin praegens
 Lagomorpha
 Leporidae
 Serengetilagus sp.
 Rodentia
 Muridae
 Tectonomys africanus
 Saidomys sp.
 Thryonomyidae
 Thryonomys sp.
 Hystricidae
 Hystrix sp.
 Proboscidea
 Gomphotheriidae
 Anancus kenyensis
 Elephantidae
 ?*Primelephas* sp.
 Deinotheriidae
 Deinotherium bozasi
 Perissodactyla
 Rhinocerotidae
 Brachypotherium lewisi
 Diceros cf *pachygnathus*
 Chalicotheriidae
 Ancylotherium cf *cheboitense*
 Equidae
 Hipparion cf *sitifense*
 Artiodactyla
 Hippopotamidae
 Hippopotamus spp.
 Suidae
 Nyanzachoerus jaegeri
 Dasychoerus arvernensis (ex *Kolpochoerus deheinzlini*)
 Tragulidae
 Hyemoschus aquaticus
 Giraffidae
 Sivatherium sp.

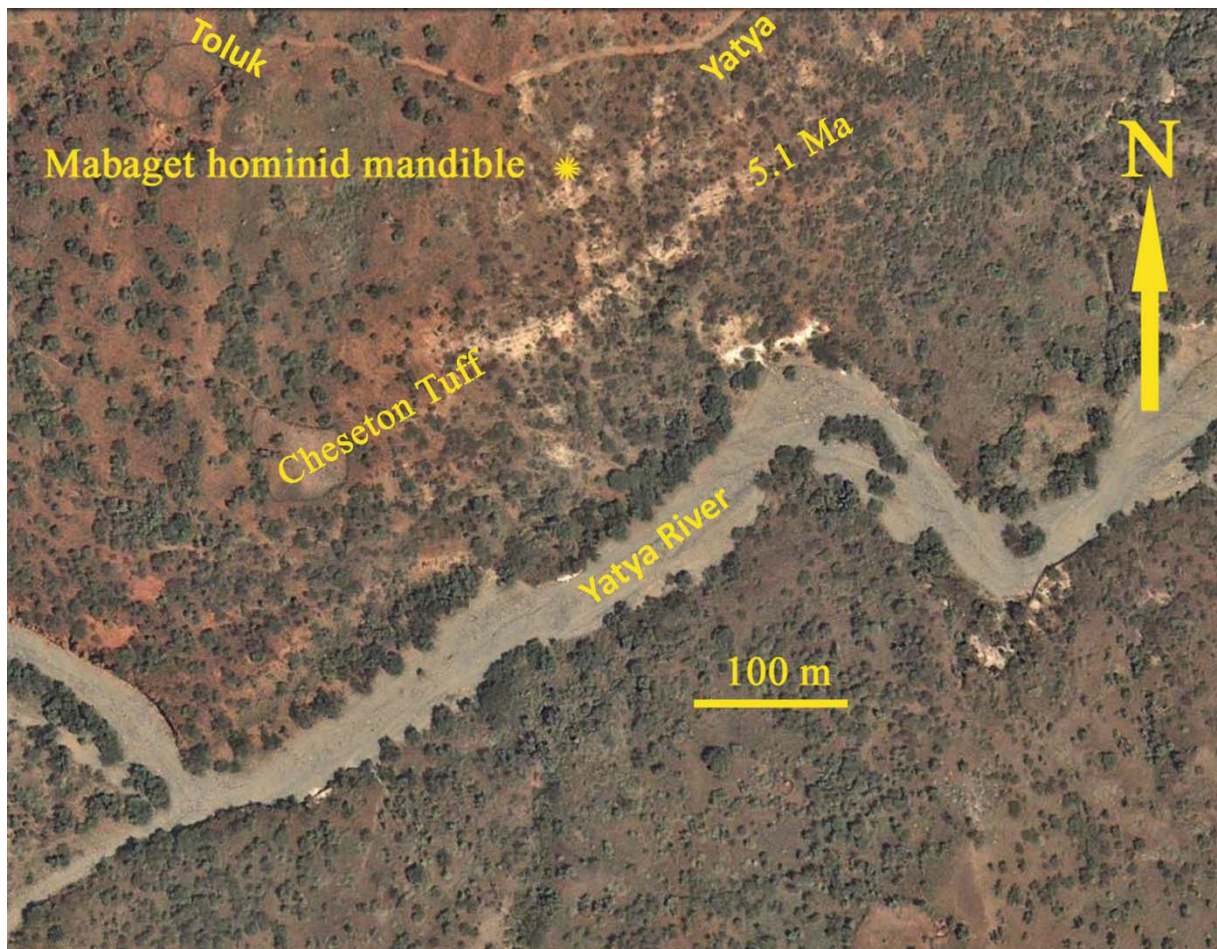


Figure 4. Location of the Mabaget hominid fossil site (2/211) (map modified from Google Earth).

In the type area of the Mabaget Formation (Fig. 2, 4) there is a good exposure of the Cheseton Lapilli Tuff that has been dated, at this precise locality, to 5.1 Ma (Pickford *et al.* 1983). The hominid mandible and proximal humerus were collected from grey to white marly deposits ca 40 metres above the Cheseton Lapilli Tuff at locality 2/211 and an isolated p/3 at the nearby locality 2/210. The Mabaget fossils (OCO BAR 1046'11 and KNM BC 1745) are thus likely to be ca 5.0-4.5 Ma.



Figure 5. Locality 2/211 (=BPRP 37), Pelion Member, Tugen Hills, Baringo County, Kenya. Hominid mandible OCO BAR 1046'11 was found in the gully close to the lady wearing the beige trousers.

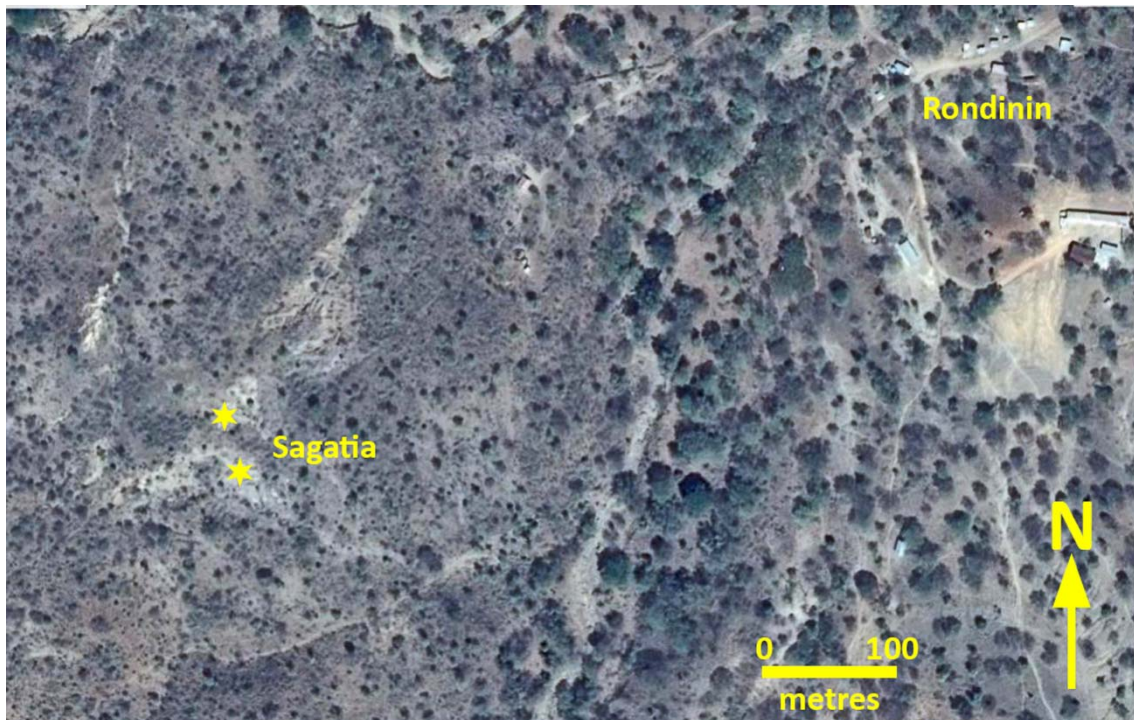


Figure 6. Location of the Sagatia gully system (2/232 = BPRP 75) that yielded hominid remains in 2010 (yellow stars). Map modified from Google Earth.

The Sagatia hominid fossils were collected from the gully system 500 metres southwest of Rondinin Village (Fig. 6, 7).

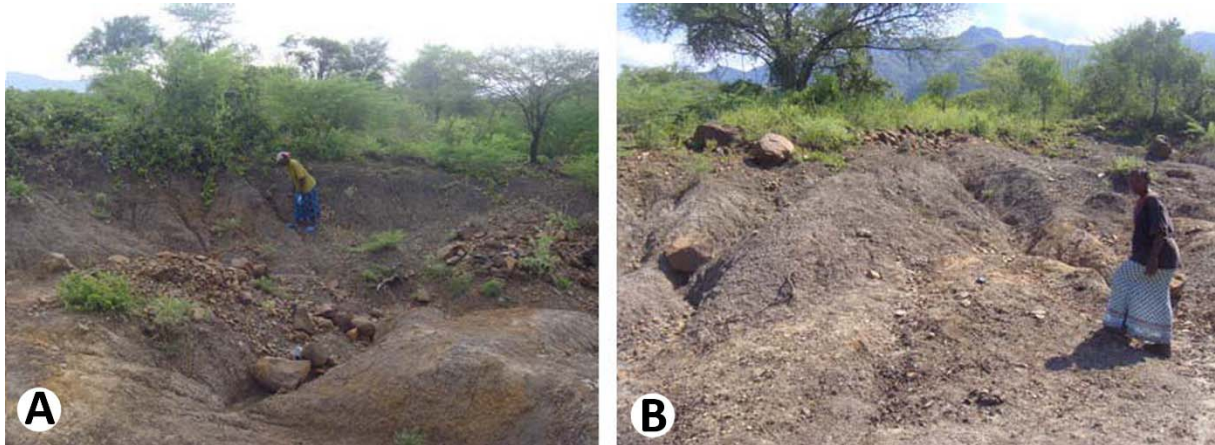


Figure 7. Discovery loci of hominid fossils at Sagatia, Baringo County, Kenya. A) OCO BAR 151'10, upper deciduous molar, B) OCO BAR 150'10, pedal phalanx (Tugen Hills in the background).

The Sinibo hominid specimen was collected from the badlands not far from Kipcherere, in pebbly silty layers that overlie local outcrops of the Tulu Bor Tuff (= Sidi Hakoma Tuff) aged 3.446 Ma (Namwamba, 1993; Brown, 1982, 1994; Feibel 2003; WoldeGabriel *et al.* 2013) (Fig. 8-10).

Table 5. Fauna from the Sinibo Member (4.1-3.0 Ma) Tugen Hills, Baringo County, Kenya. The record of *Kolpochoerus heseloni (olduvaiensis)* indicates the likely presence of Pleistocene sediments at the top of the Sinibo succession.

Mammalia	
Primates	
	Cercopithecidae
	<i>Paracolobus chemeroni</i>
	Hominidae
	<i>Praeanthropus afarensis</i>
Proboscidea	
	Elephantidae
	<i>Elephas africanavus</i>
Perissodactyla	
	Rhinocerotidae
	<i>Ceratotherium praecox</i>
	<i>Diceros bicornis</i>
Artiodactyla	
	Suidae
	<i>Nyanzachoerus kanamensis</i>
	<i>Kolpochoerus heseloni (olduvaiensis)</i>
	Giraffidae
	<i>Giraffa cf jumae</i>
	Bovidae
	<i>Syncerus</i> sp.
	<i>Taurotragus</i> sp.
	<i>Menelikia lyrocera</i> or <i>M. leakeyi</i>
	<i>Gazella</i> sp. 2-3 spp.

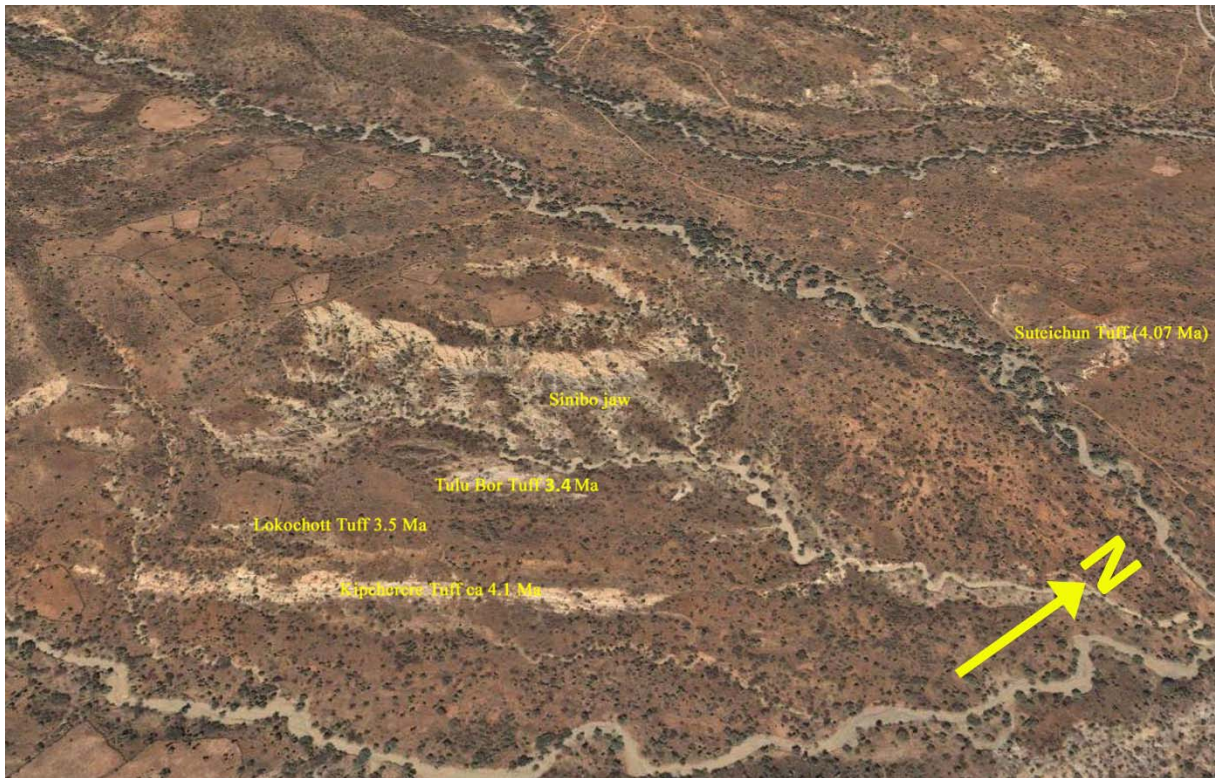


Figure 8. Discovery locus of the Sinibo mandible in the badlands close to Kipcherere, Baringo County, Kenya. Oblique view from Google Earth highlighting the outcrops of tuffs.

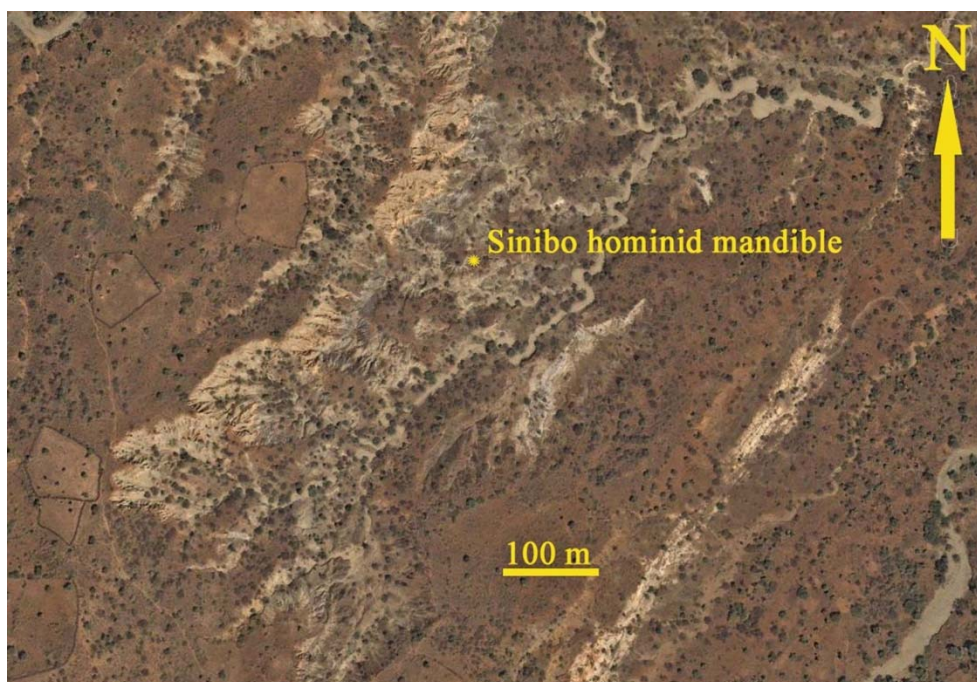


Figure 9. Discovery locus of the Sinibo hominid mandible in the badlands not far from Kipcherere, Tugen Hills, Baringo County, Kenya. Map modified from Google Earth.



Figure 10. Discovery locus of the Sinibo hominid mandible (yellow arrow points to searchers on site). View northwestwards towards the Tugen Hills in the background. A - Tulu Bor Tuff, B - Brown-green Tuff (see Fig. 11).

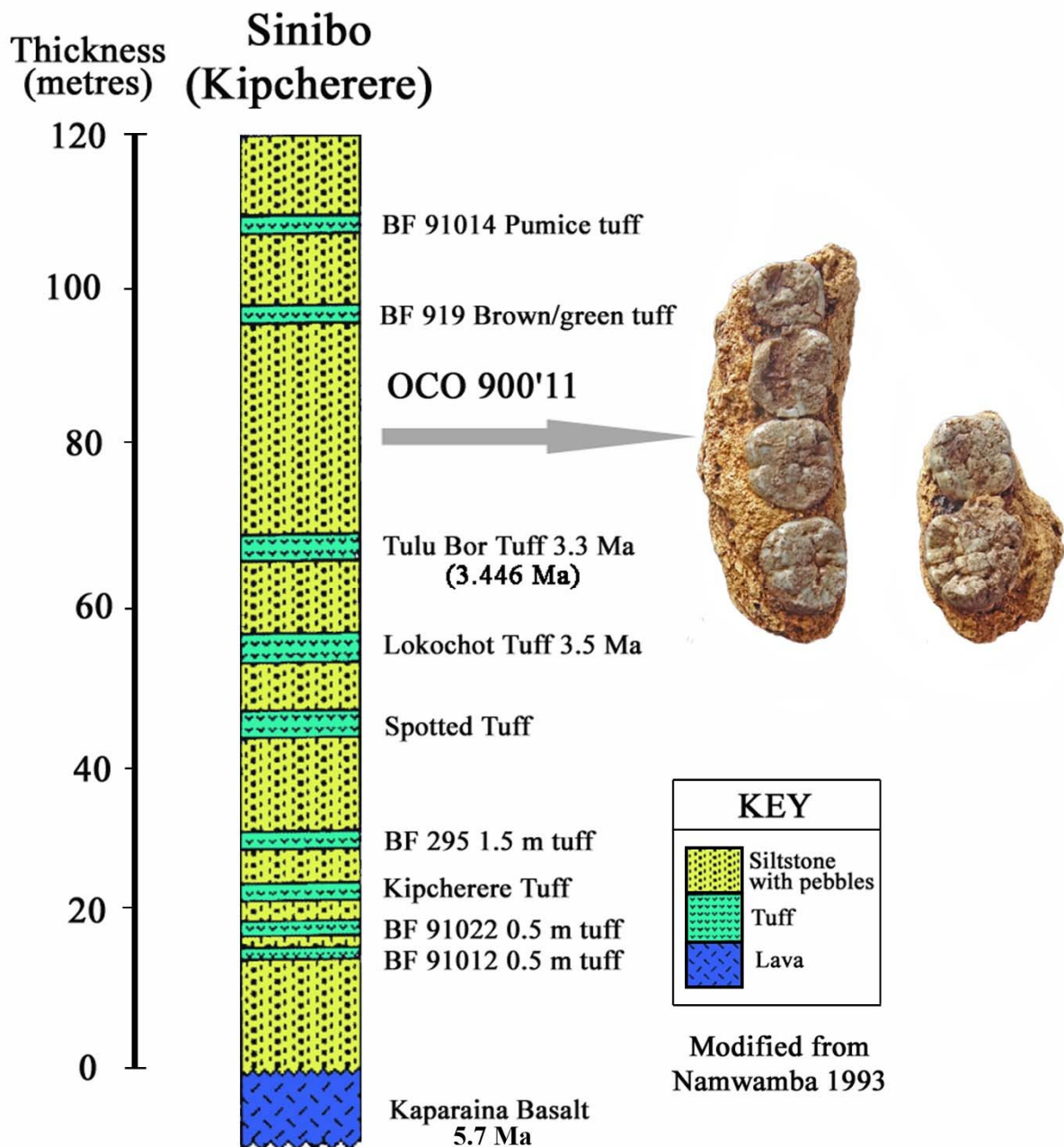


Figure 11. Stratigraphic succession of the Sinibo Member of the Mabaget Formation in the badlands not far from Kipcherere, highlighting the volcanic tuffs intercalated between clastic sediments. The Sinibo hominid mandible was collected from pebbly siltstone deposits ca 15 metres above the local occurrence of the Tulu Bor Tuff (=Sidi Hakoma Tuff). The section is adapted from Namwamba (1993) who listed the age of the Tulu Bor Tuff as 3.3 Ma, but later work has redated the tuff to 3.446 Ma calculated with updated ^{40}K decay constants (WoldeGabriel *et al.* 2013). The Kipcherere Tuff is dated 4.1 Ma.

Palaeoenvironment

The lowermost strata of the Mabaget Formation (older than 4 Ma) have yielded fossils suggestive of tropical forest conditions (*Hyemoschus aquaticus*, *Pavo* sp, fruit bats) (Pickford *et al.* 2004). Binetti (2011) supported an interpretation in which afro-montane vegetation was the probable biotope of *Ardipithecus ramidus*, in which she included the Tabarin mandible.

The Sinibo Member of the Mabaget Formation is younger than 4.1 Ma and it yields a different faunal assemblage from that in the Pelion Member, including taxa more often associated with open woodland to savannah settings, such as *Kolpochoerus heseloni* or *K. olduvaiensis*, *Elephas africanus* and gazelles.

Systematic Palaeontology

Order Primates Linnaeus, 1758

Superfamily Hominoidea Gray, 1825

Family Hominidae Gray, 1825

Genus *Orrorin* Senut *et al.* 2001

Species *Orrorin praegens* (Ferguson, 1989b)

Material: OCO BAR 151'10, right D4/; OCO BAR 1'08, right p/3; OCO BAR 1046'11, right mandible fragment containing p/4-m/1; OCO BAR 500'05, left m/3; KNM TH 13150, mandible with m/1-m/2; KNM BC 1745, proximal humerus.

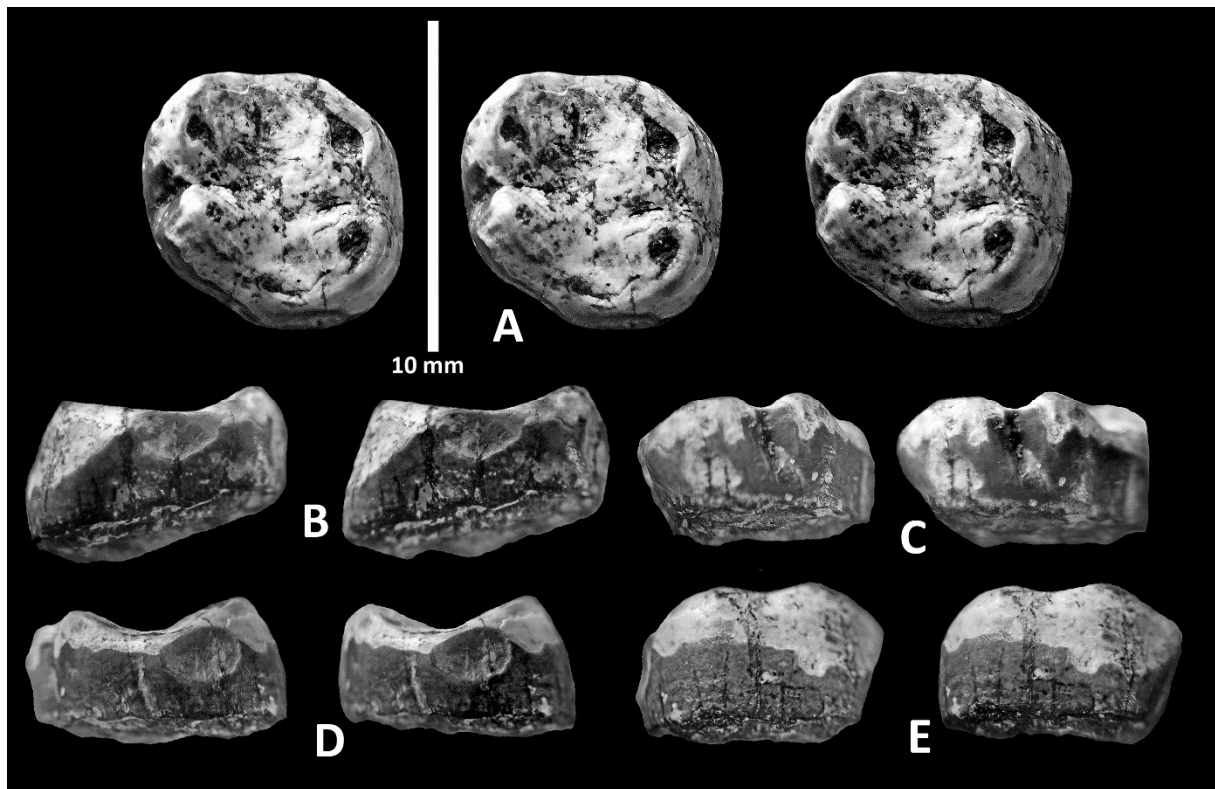


Figure 12. Stereo images of OCO BAR 151'10, hominid right D4/ from Sagatia, Tugen Hills, Baringo County, Kenya. A) occlusal views, B) mesial view, C) buccal view, D) distal view, E) lingual view (scale : 10 mm).

Descriptions

The D4/

OCO BAR 151'10 is an isolated right D4/ crown in medium wear (Fig. 12). The roots are missing, and may have been partly resorbed prior to the tooth being shed, or the individual dying. There are prominent interstitial wear facets mesially and distally, the one on the distal surface being located mostly to the lingual side of the mesio-distal midline of the crown, and is thus to the rear of the hypocone. The mesial

facet is centrally positioned. Thin layers of enamel have spalled off parts of the lingual and buccal sides of the tooth, and some enamel is missing from the occlusal aspect of the mesial cingulum. Apart from this post-mortem damage, the tooth is in good condition.

In occlusal view the largest cusp is the protocone followed by subequal paracone and hypocone and a smaller metacone. As a consequence of the different cusp sizes, the occlusal outline of the tooth is trapezoidal rather than square, the lateral surface of the metacone slanting disto-lingually at an angle of 45°, the other cusp surfaces at right angles to each other but with rounded corners. The metacone and paracone are closer to each other than are the protocone and hypocone.

Cusp relief is minimal and crests are low and blunt. The preprotocrista extends mesio-buccally to terminate at the mesial midline of the crown. A slight interruption in its thickness suggests that it fuses with the mesial cingulum which is reduced in stature. The mesial fovea and trigon basin are coalescent with no obvious ridge of enamel between the two. The crista obliqua is a low relief, rounded ridge which reaches the middle of the crown, barely separating the trigon basin from the distal fovea. The postprotocrista and the prehypocrista extend towards each other but are separated lingually by a narrow slit that broadens buccally between the hypocone and the crista obliqua. The posthypocrista curves distally and buccally where it fuses with the distal cingulum.

The preparacrista is low (partly due to wear) and curves mesially and lingually where it joins the mesial cingulum. The postparacrista is short and rather lingually positioned and it touches the premetacrista, thereby forming a buccal notch or sulcus. The postmetacrista is low and is angled at 45° towards the distal cingulum.

Wear in this tooth has reached the stage in which dentine is exposed on all four main cusps, the exposures on the protocone and hypocone being substantially greater than those on the paracone and metacone. There is also dentine exposed along the preprotocrista, part of the posthypocrista and the distal cingulum.

In mesial view, the crown is deeper beneath the protocone than the paracone, despite the fact that the paracone is higher than the protocone. As a consequence, the cervix of the tooth slants at an angle of ca 5-10° with respect to the occlusal plane. In distal view the hypocone is slightly taller than the metacone. In lateral view the mesial surface of the crown is angled such that the mesial edge of the occlusal surface is substantially anterior to the root. The distal surface of the crown is more vertically oriented.

The enamel in this tooth appears to be thin (ca 1 mm where the dentine-enamel junction is exposed), an aspect that has been enhanced by the loss of enamel from parts of the lingual surface.

The p/3

OCO BAR 1'08 is a lightly worn right p/3 lacking parts of the mesial and distal roots (Fig. 13). There is a small dentine exposure on the protoconid and the enamel appears to be thick (ca 3 mm where the dentine-enamel junction is exposed occlusally). The crown is ovoid in occlusal outline, shorter mesio-distally than the bucco-lingual breadth. The protoconid dominates the crown and is centrally positioned, with broad, prominent pre- and postcrisids as well as a broad cristid leading lingually towards the very reduced metaconid. This lingual cristid (protocrisid in Ferguson, 1984; transverse crest in Delezené & Kimbel, 2011) separates the small mesial fovea from the larger and deeper distal fovea. There is a stylid at the mesio-buccal side of the preprotocrisid (mesial protoconid crest in Delezené & Kimbel, 2011), and a smaller stylid at the disto-buccal end of the postprotocrisid (distal protoconid crest in Delezené & Kimbel 2011). The buccal surface of the crown between these stylids is convex and has slightly rugose enamel (polished to a small extent by abrasion).

Viewed under the microscope, the wear facet on the postprotocrisid is observed to have several parallel scratches of variable depth and diameter, oriented bucco-lingually and descending from buccal to lingual. There is almost no tooth-to-tooth wear on the buccal surface of this tooth, indicating that there

was no honing function between it and the upper canine. The wear facet at the apex of the protoconid slopes gently lingually.

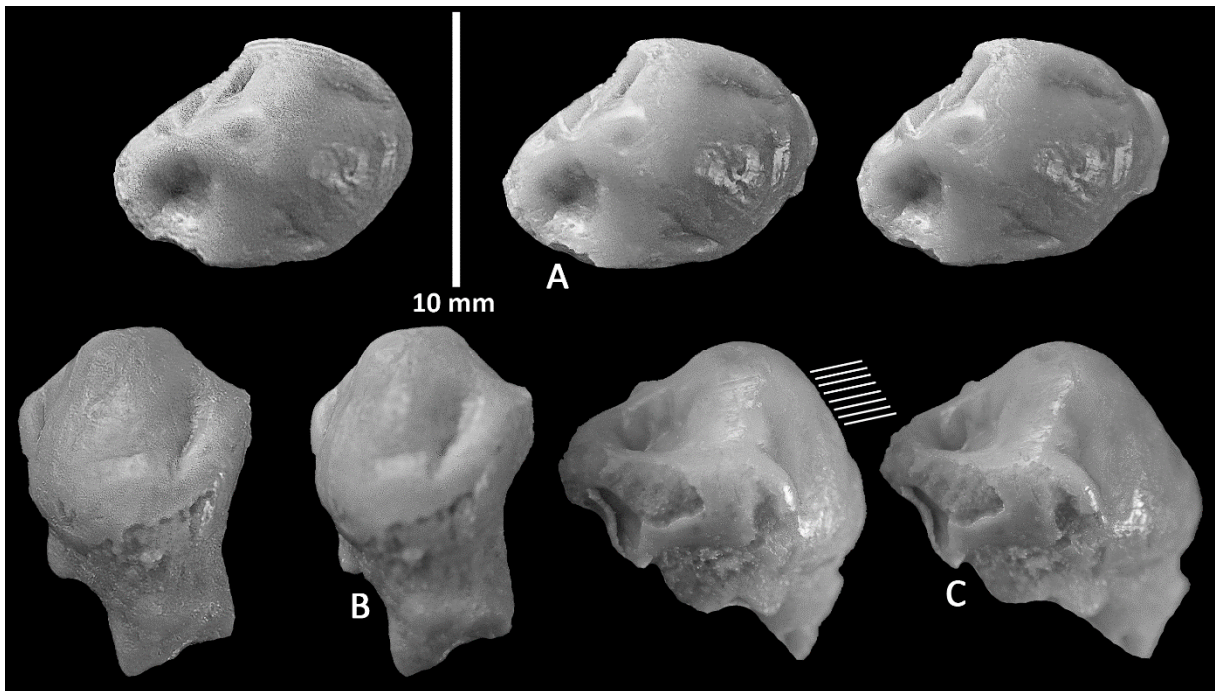


Figure 13. Stereo images of OCO BAR 1'08, cast of right p/3, from locality 2/210 in the Pelion Member, A) occlusal views, B) buccal view, C) distal view to show orientation of wear scratches on the postprotocristid (white parallel lines) (scale : 10 mm).

The mandible

OCO BAR 1046'11 is a right mandible fragment containing moderately worn p/4 and m/1, part of the distal root of the p/3 and portions of the alveoli of the mesial root of the m/2 (Fig. 14-15). The subgingival parts of the mandible are relatively gracile but its base is broken away. There is no sign of the mental foramen in the preserved parts of the jaw. In superior view, one observes the lingual side of the body curving mesio-sagittally, starting gently at the rear of the p/4 but curving more sharply opposite the p/3.

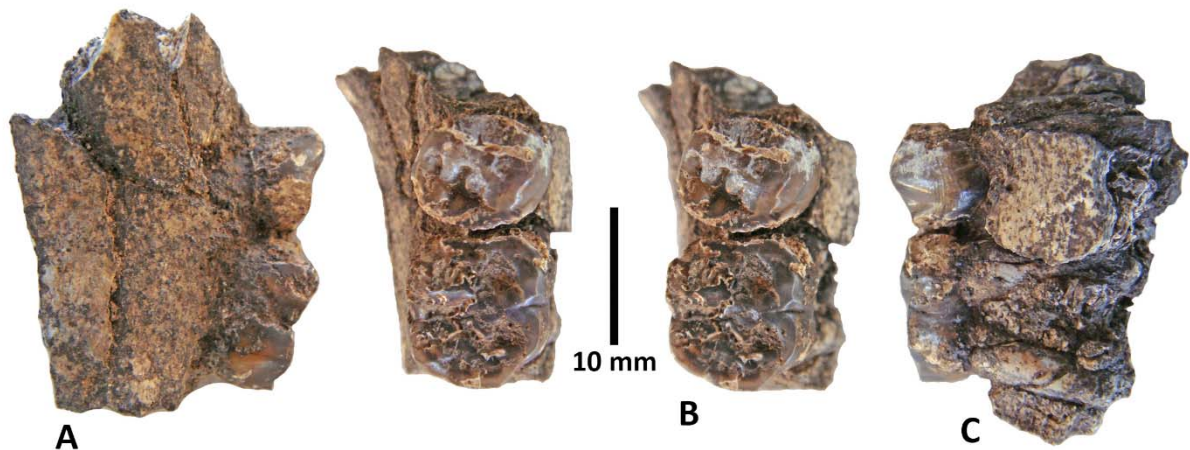


Figure 14. OCO BAR 1046'11, right mandible fragment containing p/4-m/1 from locality 2/211, Pelion Member, Tugen Hills, Kenya. A - lingual, B - stereo occlusal, C - buccal views (scale : 10 mm).

The p/4

In the p/4, there is a small amount of damage to the mesial cingulum such that the mesial stylid on the buccal side has broken off. Dentine is exposed at the apices of the protoconid and metaconid. The enamel is remarkably thick in the protoconid (ca 2 mm on the buccal side of the cuspid).

The protoconid is the largest cusp, the metaconid being about half its dimensions and the entoconid or distal cingulum low and small. The protoconid has three main cristids; a preprotocristid extending mesio-lingually to terminate in the mesial midline of the crown, a broad postprotocristid leading distally and a lingually directed cristid that bifurcates, the mesial branch leading towards the metaconid, and a distal branch leading disto-lingually into the talonid basin. The metaconid has rather narrow premetacristid and postmetacristid, but its lingually directed cristid is broad and, like the corresponding cristid in the protoconid, it bifurcates, one branch leading towards the protoconid, the other directed distally into the talonid basin. There is a prominent distal cingulum, possibly representing a nascent hypoconid.

In buccal view two stylids are present, one mesially which is damaged, and one distally which slants occluso-distally to cervico-mesially, but fading out at about half the height of the crown.

Wear in the p/4 is almost planar, horizontal, leaving low crown relief.

The apex of the mesial root of the p/4 is exposed where bone has broken off. The root is almost twice as tall (13 mm) as the crown is high (7.5 mm) and appears to be straight and vertically oriented.

The m/1

The lower first molar in mandible OCO BAR 1046'11 is almost rectangular in occlusal contour. The tooth has five main cusps, large protoconid and hypoconid, with bucco-lingually narrower metaconid and entoconid, and a small hypoconulid positioned distally in the midline of the tooth. There is a shallow notch between the protoconid and hypoconid which fades out well above the cervix, and another between the metaconid and entoconid which possibly extends to cervix (some enamel has spalled away making the extent of the notch uncertain, but the curvature of the damaged area suggests that it extended as far as the cervix). In buccal view there is a small stylid closely applied to the protoconid but it fades out at about a quarter of the height of the crown. There does not appear to be a tuberculum sextum in this tooth.

The crown of the m/1 is more deeply worn than that of the p/4, and the dentine exposures are larger. Those on the protoconid and hypoconid are larger and deeper than the exposures on the metaconid, entoconid and hypoconulid. Even though much of the occlusal surface is almost planar, the dentine exposures on the protoconid and hypoconid are still separated from each other. The apices of the metaconid and entoconid are slightly taller than the protoconid and hypoconid, with a sharp angle between the occlusal and lingual surfaces, unlike the more rounded shape of the lingual edges of the protoconid and hypoconid. The occlusal surface of the hypoconulid is planar and almost horizontal.

The thickness of the enamel on the buccal side of the protoconid is ca 2 mm.

The roots of the m/1 are partly visible on the buccal side of the specimen. The mesial one is 12.5 mm tall for a remaining crown height (at protoconid) of 4.8 mm. The apex of the mesial root is bent distally. The distal root is 11.5 mm tall for a remaining crown height (at hypoconid) of 4.2 mm. The latter root is inclined distally in the mandible such that its apex underlies the anterior part of the protoconid of the m/2.

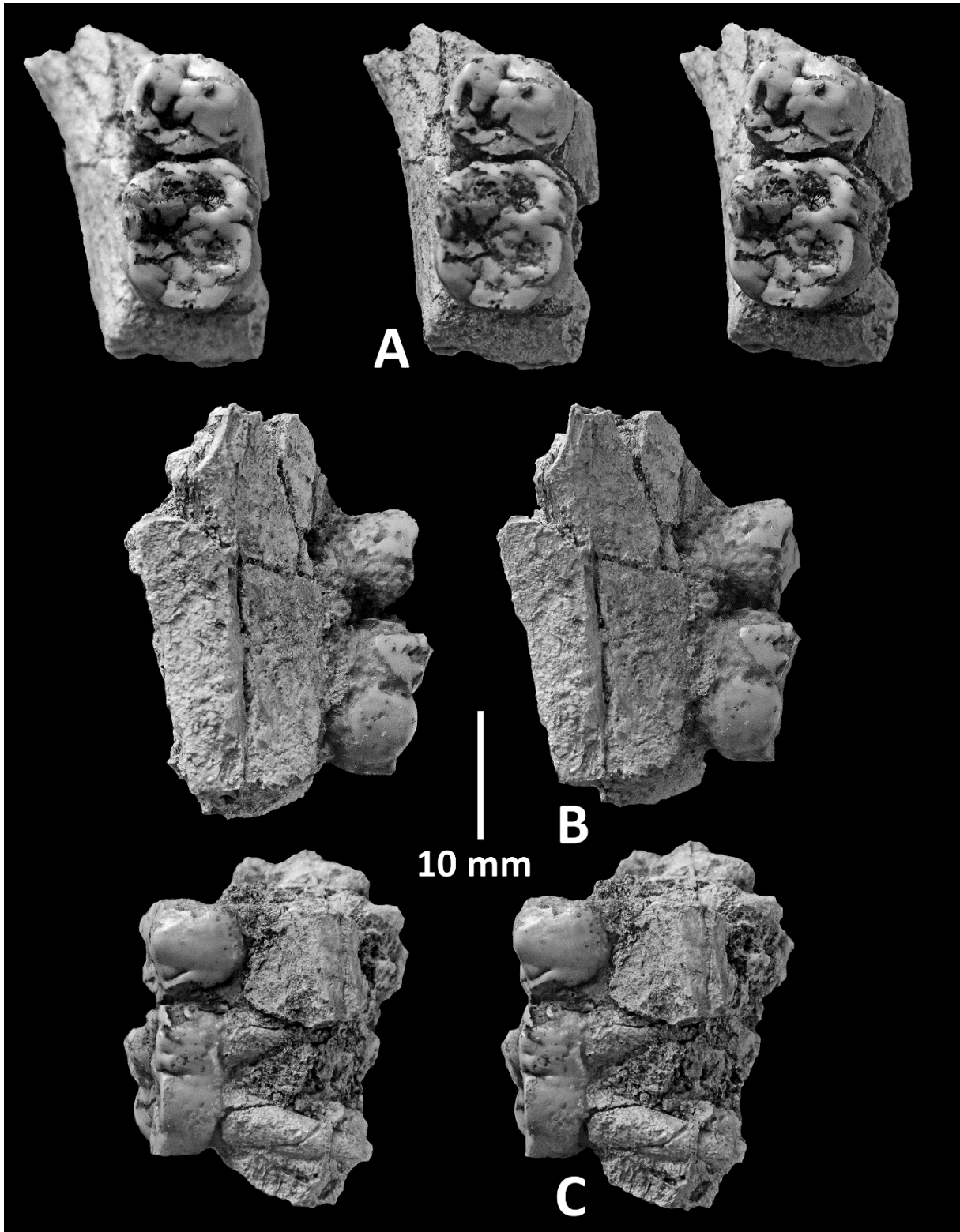


Figure 15. Stereo images of OCO BAR 1046'11, cast of right mandible fragment containing p/4-m/1 from locality 2/211, Pelion Member, Tugen Hills, Baringo County, Kenya. A - occlusal views, B - lingual view, C - buccal view (scale : 10 mm).

Table 6. Measurements (in mm) of hominid teeth from the Pelion Member (5.0-4.5 Ma) of the Mabaget Formation, Tugen Hills, Baringo County. In brackets are the maximum and minimum diameters of the p/3. Measurements of KNM TH 13150 are from Hill, 1985 (e = estimated measurement).

Catalogue	Tooth	Mesio-distal length	Bucco-lingual breadth
OCO BAR 151'10	D4/ right	7.5	8.2
OCO BAR 500'05	m/3 left	11.7 e	11.0 e
OCO BAR 1'08	p/3 right	8.4 (11.0)	10.4 (7.8)
OCO BAR 1046'11	p/4 right	7.6	9.5
OCO BAR 1046'11	m/1 right	11.0	10.7
KNM TH 13150	m/1 right	11.1	10.4
KNM TH 13150	m/2 right	13.1	11.4

The m/3

The lower third molar collected at Sagatia in 2005 (OCO BAR 500'05) has lost enamel from the lingual, mesial and part of the buccal sides, but retains much of the occlusal enamel cap (Fig. 16). The tooth is lightly worn, the main cusps being clearly delineated by the intercuspatal groove system. The mesial end of the tooth has a caries-like lesion which has left a deep, smooth-walled cavity beneath the protoconid and part of the metaconid. There is no interstitial contact facet on the distal surface of the tooth.

The distal root is substantially shorter (ca 10.5 mm for a crown height of 5.4 mm at the tuberculum sextum) than the mesial one which is ca 14 mm tall for a crown height estimated to be ca 5 mm at the metaconid. The mesial root curves distally from cervix to apex, and the distal root is inclined slightly distally. In distal view the bucco-lingual breadth of the distal root decreases sensibly from cervix to apex, whereas the mesial root tapers less rapidly than it. For these reasons, OCO BAR 500'00 is interpreted to be a lower third molar rather than an m/2 or m/1. Both roots possess a broad central sulcus extending from cervix to apex.

What remains of the protoconid suggests that it was somewhat greater in dimensions than the metaconid. The hypoconid is complete save for a chip of enamel missing from its buccal surface. It is smaller than the protoconid and its endocristid extends well across the crown towards the entoconid. The hypoconulid is small and is clearly distinct from the tuberculum sextum, being separated from it by a groove in the midline of the crown. The only enamel preserved on the metaconid and entoconid is on their buccal aspect. The vertical enamel thickness at the entoconid, as exposed by damage, is ca 1.5 mm.

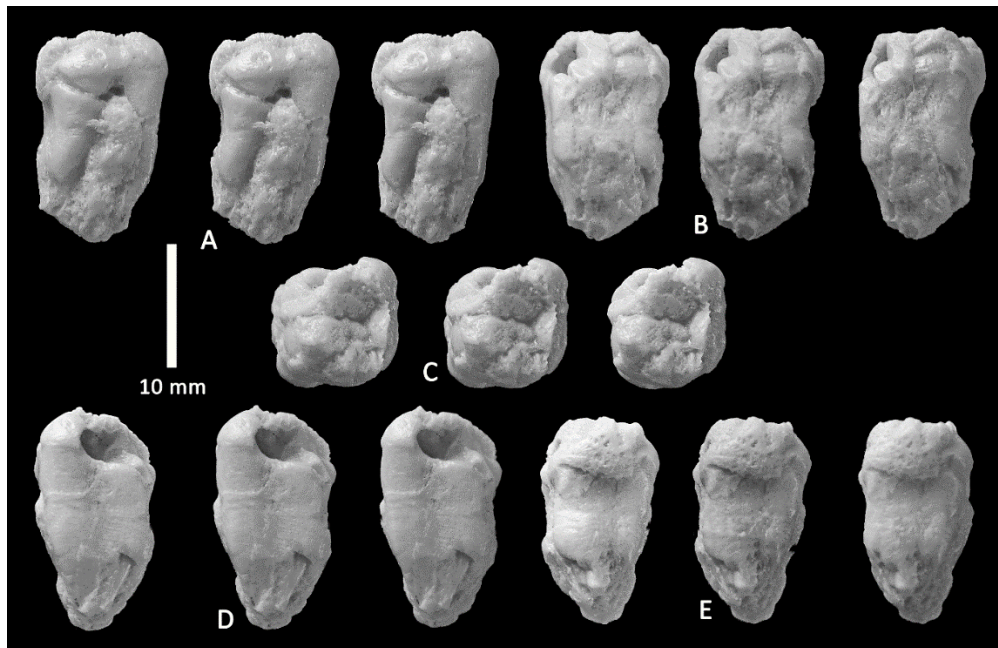


Figure 16. Stereo images of a cast of OCO BAR 500'05, left m/3 from Sagatia, Pelion Member, Tugen Hills, Baringo County, Kenya. A - lingual view, B - buccal view, C - occlusal view, D - mesial view, E - distal view (scale : 10 mm).

Comparisons and Interpretation

The trapezoidal outline of the crown of the D4/ (OCO BAR 151'10) the mesial overhang of the crown and the thin enamel indicate that this is a deciduous tooth. The lingual position of the distal interstitial wear facet caused by rubbing against the M1/, also suggests that the tooth is a deciduous one.

OCO BAR 151'10 corresponds to an individual aged ca 7.5 to 8 years if the chimpanzee ontogenic clock is used (Zihlman *et al.* 2004).

The p/3 from Pelion (OCO BAR 1'08) has thick enamel and there is no evidence of a honing facet on the buccal aspect of the crown. In the latter feature it differs from *Ardipithecus kadabba* (Haile-Selassie *et al.* 2004, 2009). The transverse crest is much shorter than it is in *Pan* and *Gorilla*, and does not produce a lingual cusplet as in australopithecines and *Homo* (Deleuzene & Kimbel, 2011). Thus, this p/3 is unlike those of African apes, but it also differs from those of *Australopithecus* and *Homo*. However, its enamel is thicker than those of *Pan* and *Gorilla*, and the absence of a honing facet indicates affinities with hominids (*sensu stricto*) such as *Orrorin* (Senut *et al.* 2018). The reduced mesial fovea and somewhat larger distal fovea in the Pelion p/3 are similar to the proportions observed in OCO BAR 1900'01, the p/3 of *Orrorin tugenensis* from Kapsomin.

Mandible OCO BAR 1046'11 is of an animal similar in size to *Orrorin tugenensis* and its teeth are approximately the dimensions of those of *Ardipithecus ramidus*. It is closely similar in overall dimensions to the Tabarin mandible (KNM TH 13150) from the same formation. The latter specimen was classified as *Australopithecus cf. afarensis* by Hill (1983) and Ward & Hill (1987) but most specimens of *Australopithecus afarensis* from Hadar and all of the specimens from the type locality of the species, Laetoli, are appreciably larger than the Tabarin specimen. Ferguson (1989) erected the subspecies *Homo antiquus praegens* on the basis of the Tabarin mandible, the species *Homo antiquus* Ferguson, 1984, being erected for the smaller of the Hadar specimens attributed to *Australopithecus afarensis*, the « Lucy » specimen being nominated as the holotype. However in this instance the species name proposed by Ferguson (1984) is a junior homonym of *Homo antiquus* Adloff, 1908, and is thus invalid when applied to the Hadar or any other fossils from Africa (Delson *et al.* 2000; Harrison, 2011). Furthermore, the femur of the AL 288-1 skeleton is typical of australopithecines (lesser trochanter pointing posteriorly rather than medially, for example) and unlike that of *Orrorin* or *Homo*, in which the lesser trochanter is directed medially (Pickford *et al.* 2002). However, the name *praegens* is valid and has priority if the Tabarin mandible proves to belong to a species erected after 1989.

The occlusal surfaces of the cheek teeth in KNM TH 13150 are so deeply worn that little remains of the cusp and crest morphology which renders interpretation difficult. Ward & Hill (1987) described the enamel as thick, whereas MacLatchy *et al.* (2010) wrote that it was thin, but this impression could be due to the deeply worn state of the molars (enamel thickness diminishes towards the cervix in all primates). *Ardipithecus ramidus* possesses thin occlusal enamel in the cheek teeth (Suwa *et al.* 2009) which has prompted some authors to classify the Tabarin mandible within this species (MacLatchy *et al.* 2010; Binetti, 2011). However, the enamel in cheek teeth from Mabaget and Sagatia that are less worn than those in the Tabarin specimen reveal that the hominid specimens from the Pelion Member possess thick occlusal enamel, and are thus unlike *Ardipithecus ramidus*. It has also been claimed that the Tabarin mandible possesses narrower molars than *Ardipithecus ramidus* (MacLatchy *et al.* 2010) but the m/1 is as broad as those of the Aramis species, and the m/1 in the new mandible (OCO BAR 1046'11) is broader than any of the Ethiopian specimens. The m/2 in KNM TH 13150 is indeed rather narrow, but this could be a case of individual variation. The isolated m/3 from Sagatia is slightly narrower than the m/2 in KNM TH 13150, but it plots within the range of metric variation of *Ardipithecus ramidus*. Indeed, relative to its length, its breadth falls at the upper end of the range of variation of the Aramis material.

Thus the combination of metric and morphological data indicates that the Mabaget hominid fossils do not belong to *Ardipithecus ramidus*. If, however, the two samples are considered to be conspecific as has been proposed by MacLatchy *et al.* (2010) and Binetti (2011), then the name with priority would be *Ardipithecus praegens* (Ferguson, 1989) and not *Ardipithecus ramidus* (White *et al.* 1994).

The thick enamel and planar occlusal wear surfaces on the p/4 and m/1 of OCO BAR 1046'11 indicate that this fossil does not belong to a chimpanzee or gorilla. In these and other features the teeth in the specimen are more like those of *Orrorin*, australopithecines and *Homo*. Although it is difficult to obtain an idea of mandibular robusticity because the base of the jaw is broken, it seems to be more robust than mandibles of *Homo*, so it is inferred that this mandible most likely belongs to *Orrorin*.

The p/4 in OCO BAR 1046'11 is slightly smaller than the smallest specimen from Hadar attributed to *Australopithecus afarensis* by Kimbel *et al.* (2004) but it falls within the range of variation of specimens from As Duma and Aramis attributed to *Ardipithecus ramidus* by Semaw *et al.* (2005) and White *et al.* (2015) and is close in size to the p/4 of *Ardipithecus ramidus kadabba* from the Middle Awash (Haile-Selassie, 2001; Haile-Selassie *et al.* 2004) (Fig. 17). The p/4 in the Mabaget specimen is close in dimensions to two p/4s attributed to *Orrorin tugenensis* by Senut *et al.* (2001, 2015) and it is also compatible in mesio-distal length to the p/4 in *Sahelanthropus tchadensis* (TM 266-02-154-1) (Brunet *et al.* 2005). It is also similar in dimensions to the smallest of the three specimens from East Turkana (KNM ER 35228) included in *Australopithecus anamensis* but it is much smaller than the other two specimens (KNM ER 20432 and KNM ER 22683) suggesting that the ER material may be a mixture of two taxa. The Mabaget p/4 is smaller than the smallest of the specimens from Kanapoi attributed to *Australopithecus anamensis*. At the latter locality too, there is a bimodal distribution of p/4s suggesting the possibility of the presence, either of a high degree of sexual bimodality, or of two taxa in the sample.

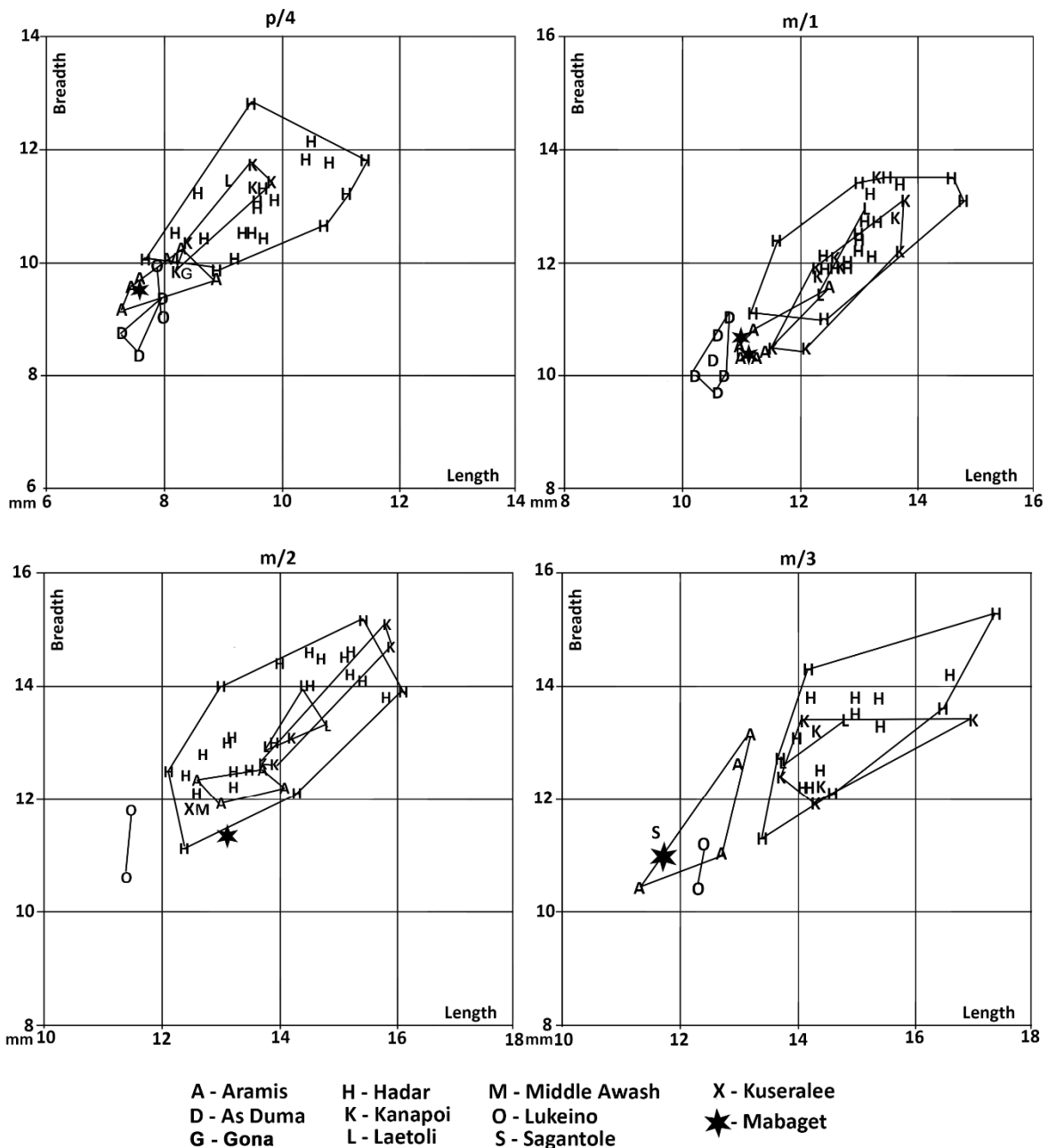


Figure 17. Bivariate plots of lower cheek teeth of hominids from the Mabaget Formation and other late Miocene to mid-Pliocene localities in Eastern Africa.

The two m/1s from the Mabaget Formation (KNM TH 13150 and OCO BAR 1046'11) are close in dimensions to corresponding teeth from Aramis (Fig. 17) attributed to *Ardipithecus ramidus* (White *et al.* 2015) but are marginally larger than specimens from As Duma attributed to the same taxon (Semaw *et al.* 2005). They are slightly smaller than two of the specimens from East Turkana included in « Early *Homo* » by Moggi-Cecchi *et al.* (2010), the remainder of the East Turkana specimens being appreciably larger. One specimen of m/1 from Hadar (AL 128-23) is close in dimensions to the Mabaget teeth but the remainder of the Hadar specimens are substantially larger. The two Mabaget specimens are quite a bit smaller than an m/1 from Burtele (BRT-VP-3/14) attributed to *Australopithecus deyiremeda* by Haile-Selassie *et al.* (2015). The mesio-distal length of the m/1 of *Sahelanthropus tchadensis* is published as 11.0 mm and its breadth as 11.9 mm (Brunet *et al.* 2001). However, interstitial wear has

removed a substantial amount of the mesial part of the crown and some of the distal part, meaning that the tooth would probably have been closer to 12 mm long when unaffected by such wear. As such, the tooth is substantially longer and broader than the m/1 in the Mabaget Formation specimens.

The lower second molar in the Tabarin mandible (KNM TH 13150) falls into the range of metric variation of the corresponding tooth of four taxa (Fig. 17), *Orrorin tugenensis* (Senut *et al.* 2001), *Ardipithecus ramidus* (White *et al.* 2015) and *Ardipithecus ramidus kadabba* from the Middle Awash (Haile-Selassie, 2001; Haile-Selassie *et al.* 2004) as well as to a group of small specimens attributed to *Australopithecus afarensis* from Hadar (Kimbel *et al.* 2014), but not with any of the specimens of the latter taxon from the type locality, Laetoli (Harrison, 2011; White, 1980) which are substantially larger. The m/2 in the Tabarin specimen is somewhat larger than two m/2s of *Orrorin tugenensis* from the Lukeino Formation (Senut *et al.* 2001, 2015). Ferguson (1989) was so impressed by the morphometric data concerning the Tabarin mandible that he erected a new subspecies, *Homo antiquus praegens*, for it, the species *Homo antiquus* being based on small specimens (Lucy) from Hadar previously attributed to *Australopithecus afarensis*.

The m/3 from Sagatia (OCO BAR 500'05) is similar in dimensions and morphology to the corresponding tooth in the holotype of *Orrorin tugenensis*. Like the type specimen from Kapsomin in the 6 million year old Lukeino Formation, the Sagatia tooth has lost enamel from its lingual and buccal sides in rather a similar way. The tooth is also comparable in dimensions to a specimen of *Ardipithecus ramidus* from Sagantole (White *et al.* 2015) but it is slightly smaller than the smallest tooth of this species from Aramis. With a length of 13.3 mm (breadth measurement not available, Haile-Selassie *et al.* 2004) the m/3 in the holotype of *Ardipithecus kadabba* is appreciably greater than that of the m/3 from Sagatia (11.6 x 11.0 mm). The latter tooth is smaller than the smallest hominid m/3 from Hadar (Kimbel *et al.* 2004).

Pedal phalanx OCO BAR 150'10

Description

OCO BAR 150'10 was collected at Sagatia, the same set of gullies that yielded the D4/ (OCO BAR 151'10). It is a complete, undistorted and well-preserved left pedal proximal phalanx. The morphology does not correspond to a hallucial phalanx, so it is most probably from ray II, III, IV or V (we consider it to be from ray II) (Fig. 18). The dimensions of this fossil accord with measurements of proximal pedal phalanges of other Mio-Pliocene hominids (Table 7). The Sagatia phalanx is curved proximo-distally (in lateral and medial view) but is also twisted (torsion) with the medio-distal corner slightly raised dorsally (observed when the phalanx is posed with the proximal extremity in the plantar plane).

The proximal extremity is robust. It is broad in dorsal and plantar views, high in lateral and medial views. The proximal surface (Fig. 18 C) consists of an ovoid proximal articular surface with an apex medially. The long axis of this surface tilts medio-dorsally to latero-plantarly. It is more concave transversally than vertically. The lateral edge is curved and moderately salient proximally. It is close to the lateral proximal plantar tubercle in its lower part. The medial edge forms a rounded V with a dorso-medial apex that is salient proximally. It is close to the medial proximal tubercle in the plantar-median corner that corresponds to the attachment of first dorsal interosseous ligament. There is a slight dorsal cant of the proximal articular surface as observed in many Plio-Pleistocene hominid specimens (Stern & Susman, 1983) but which is absent in chimpanzees. In OCO BAR 150'10, the canting of the facet is approximately 100°. In dorsal view, but also in plantar view, the proximal edges are concave with a more robust and projecting median extremity, which is characteristic of human left proximal phalanges and seems less pronounced than in chimpanzees. This morphology of the proximal extremity corresponds to part of the metatarso-phalangeal joint. The transition between the proximal extremity and the shaft of the phalanx is more concave on the median side than the lateral side (Fig. 18 A & E).

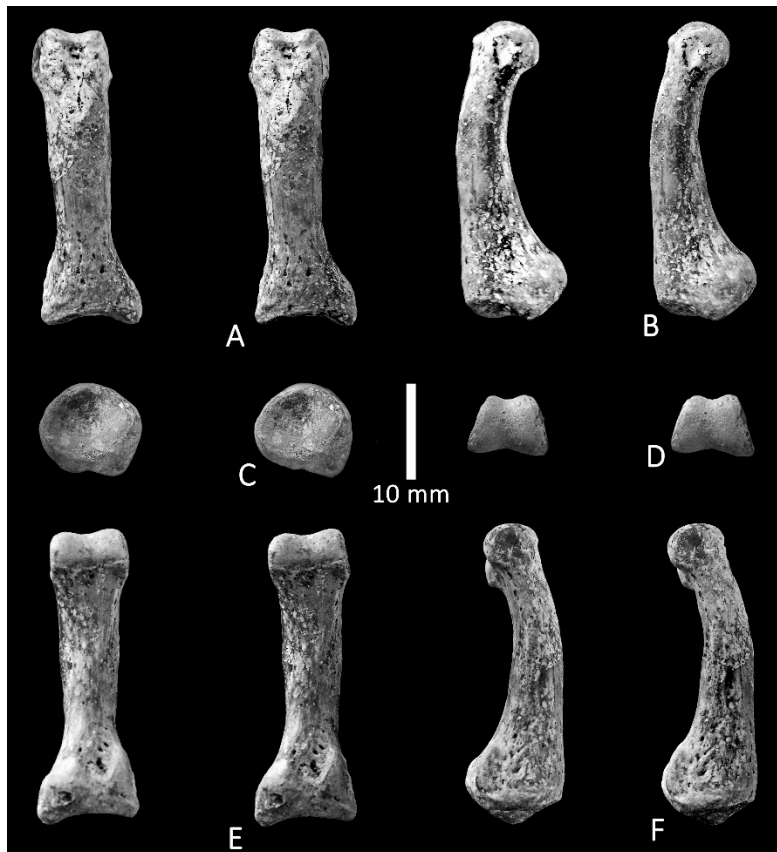


Figure 18. Stereo images of OCO BAR 150'10, hominid pedal phalanx from Sagatia, Baringo County, Kenya. A - dorsal, B - medial, C - proximal, D - distal, E - plantar, F - lateral views (scale : 10 mm).

In plantar view (Fig. 18 E) the median proximal plantar tubercle is more robust and is located more proximally than the lateral proximal plantar tubercle (which corresponds to the plantar part of the attachment of the second dorsal interosseous ligament). The tubercles are extended by a short bulge distally but do not form a ridge as in humans but they are more pronounced than in chimpanzees. A moderate depression is present between the two tubercles but is not deep as in humans, whereas it is a smooth depression in chimpanzees. In lateral view (Fig. 18 F), the lateral proximal plantar tubercle forms a smooth transition with the moderately convex lateral edge of the proximal articular facet. In medial view (Fig. 18 B) the medial proximal plantar tubercle is robust to the apex of the rounded V formed by the medial edge of the proximal articular facet. The apex of the V is strongly salient proximally in medial view. This morphology is developed strongly in the proximal foot phalanx of the second digit in chimpanzees (*Pan paniscus*). The morphology is different in humans where the facet is more rounded and the analogous part of the apex of the V in the median edge is located medio-plantarly.

The shaft of the phalanx is moderately long. The distal third of the shaft is dorso-plantarly compressed and the proximal third is medio-laterally compressed. In plantar view (Fig. 18 E) there are medial and lateral expansions located approximately in the mid-part of the shaft of the phalanx in the region of the flexor sheath insertions, but they seem not to be as well-developed as in A.L.333 Hadar hominids (Stern & Susman, 1983) and are different from the well-developed ridges present in chimpanzees. In OCO BAR 150'10, they look like smooth bulges. These expansions are underlined by shallow and short depressions which correspond to the insertion of collateral ligaments of the pedal interphalangeal joint. The medio-lateral width at mid-shaft is 6.3 mm and the dorso-plantar diameter is 5.3 mm.

In dorsal and plantar views of OCO BAR 150'10, the distal extremity presents a relatively broad aspect compared to the proximal extremity (Fig. 18 A & E) in contrast to chimpanzees, and it thereby resembles more closely the A.L.333 Hadar specimens. In dorsal view (Fig. 18 A) the distal extremity of the phalanx does not present the pinched dorsal aspect than is observed in chimpanzees. The dorso-lateral and dorso-

medial edges of the extremity are further apart in OCO BAR 150'10 (6.3 mm between the two edges) than in chimpanzees and the morphology is more human-like. The distal extremity presents a trochlear aspect. In distal view (Fig. 18 D) the medial condyle of the trochlea is narrower and more salient disto-plantarily than the lateral one, which has a relatively smoother aspect and is more flaring. The trochlea of OCO BAR 150'10 is moderately deep in plantar and distal views. In chimpanzees, the trochlea is deep and in humans, it is shallow. In the distal part of the trochlea, a broad, deep depression is present, more human-like and different from the narrow proximo-distal groove in chimpanzees (when present). The distal part consists of a medio-laterally large distal articular facet which is proximo-distally short in plantar view (5.4 mm long proximo-distally) in comparison with chimpanzees. The morphology of the distal joint is more rectangular in plantar view in the A.L. 333 Hadar specimens and humans, as in OCO BAR 150'10, differing from chimpanzees where it is more trapezoidal. Laterally and medially to the distal extremity, there are two shallow depressions as is usual in proximal and intermediate phalanges.

Discussion

During the past two decades, new discoveries have increased the collection of pedal proximal lateral toe phalanges (rays 2-5) of hominids older than 3 Ma hitherto represented by only a few specimens from Ethiopia (Haile-Selassie, 2001; Haile-Selassie *et al.* 2009, 2012; Lovejoy *et al.* 2009; Semaw *et al.* 2005; Simpson *et al.* 2019). Previously only one specimen was associated with the Lucy skeleton (A.L. 288-1) and others from the A.L. 333 material (Johanson *et al.* 1982; Latimer *et al.* 1982). Also, a few specimens are known from South African Plio-Pleistocene localities (Trinkaus *et al.* 2016).

Different authors (Aiello & Dean, 1990; Haile-Selassie *et al.* 2012; Stern, 2000; Stern & Susman, 1983) have already recognized that the pedal proximal lateral phalanx (rays II-V) of hominids presents some anatomical features related both to bipedalism and to climbing in trees. OCO BAR 150'10 presents many similarities with the Ethiopian specimens from A.L. 333, Woranso-Mille (BRT-VP-2/73d and BRT-VP-2/73e) and Gona (GWM67/P2u), but shows minor differences from AME-VP-1/71, which has a more slender overall aspect than the other specimens. These similarities concern more specifically the curvature of the phalanx, the slight dorsal cant of the proximal articular facet and the morphology of the distal extremity which are slightly different (trochlea moderately deep, broad medio-laterally and short proximo-distally, well-separated dorso-lateral and dorso-medial edges of the distal extremity) and the bilateral expansion in the middle of the corpus of the phalanx, which corresponds to ridges for insertion of well-developed flexor sheath attachments. Some differences are more marked, in particular the greater curvature of the phalanges and the stronger development of bilateral expansion that are related to strong adaptation for arboreal locomotion. In OCO BAR 150'10, this anatomical structure seems to be less developed than in the specimens from A.L. 333 and looks more similar to GWM67/P2u. Some variability could exist, related not only to the locomotor behaviour of the taxon but also probably to the size of the individual (sexual variability). The torsion of the distal extremity and the morphology of the proximal articular facet could indicate some grasping capacity. The morphology of the distal extremity and the plantar aspect of the plantar tubercles seems more related to bipedalism. This is especially true for the second proximal phalanx of the foot, which is used more for grasping during climbing.

Table 7. Measurements (in mm) of hominid pedal phalanx, OCO BAR 150'10, from Sagatia, Tugen Hills, Baringo County, Kenya. Comparison with different Plio-Pleistocene hominids. *incomplete, () measurement from cast. Published measurements of A.L. 288-1y differ significantly from our own measurements of a cast of the specimen.

Catalogue	Anatomy	Length	Proximal breadth	Proximal height	Distal breadth	Distal height	Reference
OCO BAR 150'10	Proximal phalanx	29.9	10.2	9.2	8.2	5.8	This paper
A.L. 288-1y	Proximal phalanx	21.0	6.7	5.5	5.6	3.6	Johanson <i>et al.</i> 1982, Trinkaus <i>et al.</i> 2016
A.L. 288-1y	Proximal phalanx	(21.9)	(9.1)	(7.2)	(5.7)	(4.5)	This paper

A.L. 333-26	Proximal phalanx	30.9	11.1	9.5	8.7	6.1	Latimer <i>et al.</i> 1982
A.L. 333-60	Proximal phalanx	27.9	10.9	10	8.2	6	Latimer <i>et al.</i> 1982
A.L. 333-71	Proximal phalanx	32.5	10	9.3	8	5.7	Latimer <i>et al.</i> 1982
A.L. 333-102	Proximal phalanx	30.5*	10.6*	10.2*	9.3	5.7	Latimer <i>et al.</i> 1982
A.L. 333-115(G)	Second proximal phalanx	32.2	11.5	9.4	9.4	6.6	Latimer <i>et al.</i> 1982
A.L. 333-115(H)	Third proximal phalanx	34.5	13.6	10.6	9	5.7	Latimer <i>et al.</i> 1982
A.L. 333-115(I)	Fourth proximal phalanx	32.8	11.7	10	9	6	Latimer <i>et al.</i> 1982
A.L. 333-115(J)	Fifth proximal phalanx	28.6	10.1	8.9	8	5.4	Latimer <i>et al.</i> 1982
BRT-VP-2/73d	Fourth proximal phalanx	28.74	10.25	8.6	7.9	5.4	Haile-Selassie <i>et al.</i> 2012
BRT-VP-2/73e	Second proximal phalanx	29	10.9	9.6	7.95	5.3	Haile-Selassie <i>et al.</i> 2012
AME-VP-1/71	Left fourth proximal phalanx	31.9	?	?	?	?	Haile-Selassie <i>et al.</i> 2009
ARA-VP-6/500-094	Left fourth proximal phalanx	35.4	10.7	8.6	8.0	6.3	Lovejoy <i>et al.</i> 2009
GWM67/P2u	Left fifth proximal phalanx	32.4	11.2	9.5	?	?	Simpson <i>et al.</i> 2019
StW 355	Proximal phalanx	23.4	9.1	8	6.8	4.9	Trinkaus <i>et al.</i> 2016
SKX 16699	Proximal phalanx	18.6	8.9	8.6	6.9	4.8	Trinkaus <i>et al.</i> 2016
DNH-117	Proximal phalanx	22.2	10.3	9.2	7.5	5.1	Trinkaus <i>et al.</i> 2016

Genus *Praeanthropus* Şenyürek, 1955

Species *Praeanthropus afarensis* (Johanson, 1978)

Nomenclatural note: The ICZN 1999 (Opinion 1941) ruled that the validity of the name of *Australopithecus afarensis* was established by Johanson (in Hinrichson, 1978). Even though it is likely that Johanson had the AL 288-1 skeleton in mind as the type specimen of the species *afarensis* when he briefed Hinrichson (1978), a subsequent paper (Johanson *et al.* 1978) nominated LH 4 (a mandible) from Laetoli, Tanzania, as the type specimen (lectotype). Thus Laetoli became the type locality of two species of early hominid, *Praeanthropus africanus* (Weinert, 1950) with a maxilla as holotype, and *Australopithecus afarensis* with a mandible as lectotype, which most subsequent authors have considered to represent a single species (Harrison, 2011).

If Weinert's Laetoli species is transferred to *Australopithecus* as the combination *Australopithecus africanus*, it becomes a junior homonym of *Australopithecus africanus* Dart, 1925, whereas, if it is retained in *Praeanthropus* it does not. The ICZN was briefed about the potential instability in nomenclature, and after discussion published Opinion N° 1941 ruling that *afarensis* Johanson, 1978, was the valid name for the Laetoli hominid species and that the name *africanus* Weinert, 1950, was

suppressed. For a detailed discussion concerning *Praeanthropus africanus* and *Australopithecus afarensis*, see Senut (1995, 1996).

The authors accept that the Laetoli hominid fossils attributed to the species *afarensis* belong to the genus *Praeanthropus* rather than to *Australopithecus*. For this reason the combination *Praeanthropus afarensis* (Johanson, 1978) is employed in this paper.

Specimen: OCO BAR 900'11, left and right mandible fragments containing left p/4-m/3 and right m/2-m/3.

Description

The Sinibo mandible comprises the left corpus containing the p/4-m/3 and the right body with m/2-m/3 (Fig. 19, 20). A variable thickness of calcrete nodule covers the body and the buccal aspect of the right m/3. The ventral part of the corpus is broken off so it is not possible to calculate an index of robusticity, but it is possible to infer that the jaw was robust, because beneath the molars it is substantially broader than the molars themselves. For example, the m/1 is 13.2 mm broad and the mandible beneath it is 26 mm broad. The medial side of the body starts curving mesio-sagittally opposite the rear of the p/4. The root of the ascending ramus is damaged but it is clear that there is a short retromolar space between the rear of the m/3 and the anterior base of the ascending ramus. The mental foramen is not preserved.

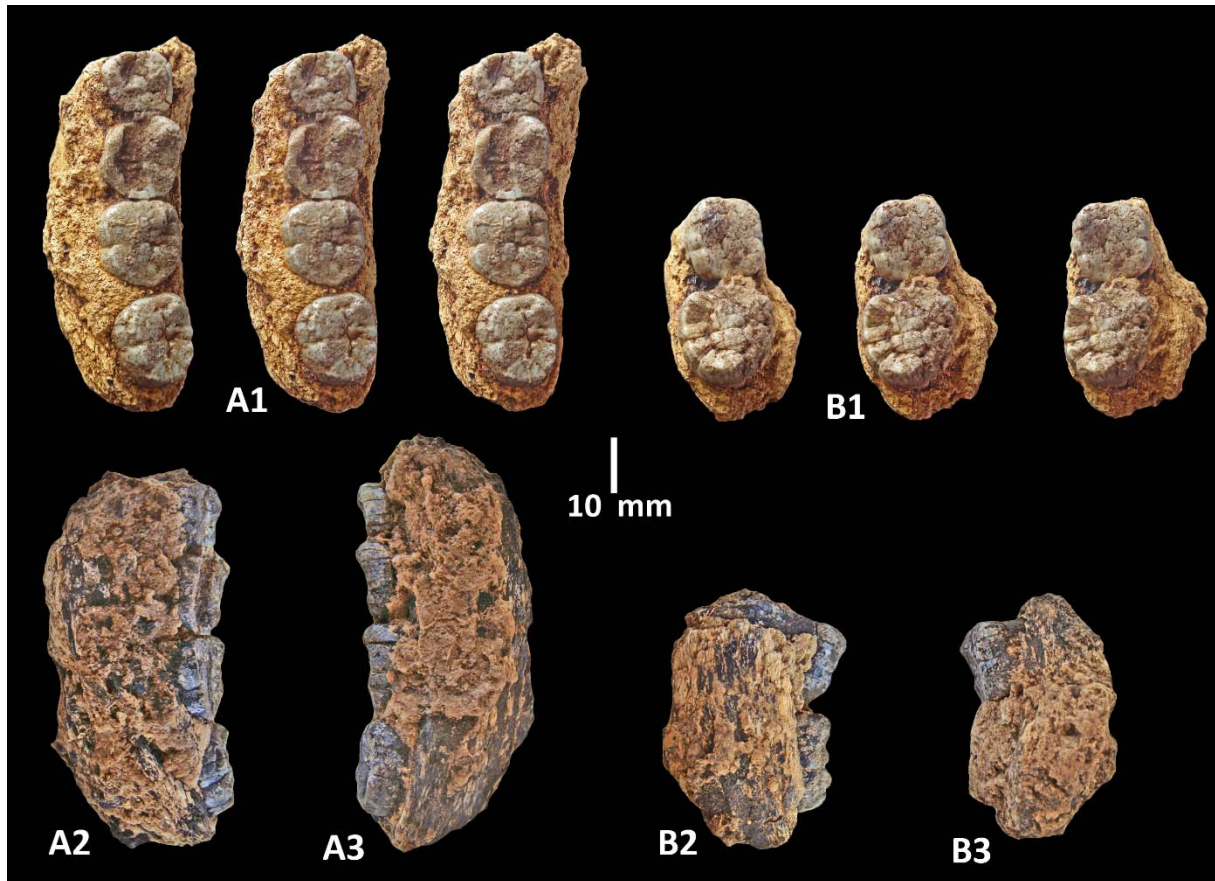


Figure 19. OCO BAR 900'11, hominid mandible fragments from Sinibo, Tugen Hills, Kenya, prior to cleaning. A) left mandible (A1 - stereo occlusal views, A2 - buccal view, A3 - lingual view), B) right mandible (B1 - stereo occlusal views, B2 - lingual view, B3 - buccal view) (scale : 10 mm).

The stage of wear of the teeth in the Sinibo mandible indicate that it was a fully adult individual in which the m/2 and m/3 are in wear but have no dentine exposed occlusally. The dentine exposures on the protoconid, hypoconid and hypoconulid of the m/1, in contrast, have coalesced to produce a single mesiodistally elongated dentine lake. Despite the heavy lingual wear in the m/1, the metaconid and

entoconid have no dentine exposed, the cusps thereby having a somewhat sectorial lingual edge. Likewise the p/4 has a prominent dentine exposure on the protoconid, but the metaconid, even though worn, does not expose dentine.

The left p/4 is squarish in occlusal outline, the mesial half being almost as broad as the distal half, and the length slightly less than the maximal breadth (Table 8). Wear has progressed to the stage where the limits of the cusps are difficult to discern but it is evident that the protoconid is the largest cusp, followed by the metaconid, a small hypoconid and slightly larger entoconid. The roots of the p/4 are not visible.

The left m/1 is rectangular in occlusal outline, the buccal part having rounded corners, especially the disto-buccal one. Wear has eradicated the details of the buccal cusps, but the lingual ones show large metaconid and entoconid separated from each other by a tall pillar, the metastylid (or an enlarged preentocristid). The tuberculum sextum between the entoconid and the hypoconulid is heavily worn but does not have dentine exposed.

The left and right m/2s are similar in occlusal outline to the m/1, but because they are much less worn the cusp pattern is more readily distinguished. Lingually, there is a clear pillar-like cusplet intervening between the metaconid and the entoconid. It is more closely attached to the metaconid, so is likely part of the postmetacristid or a metastylid. This pillar extends buccally into the middle of the talonid basin. The groove between the mesial cingulum and the metaconid is still visible but elsewhere it has been eradicated by wear. On the buccal aspect of the protoconid there is a cingular structure immediately beneath the level of the wear facet.



Figure 20. Stereo occlusal views of the left m/3 in a cast of OCO BAR 900'11 to show the nomenclature of the cusps, cingulids and notches, bc - buccal cingulum, bn - buccal notch, En - entoconid, Hy - hypoconid, Hyd - hypoconulid, In - lingual notch, mc - mesial cingulum, Me - metaconid, Ms - metastylid, Pr - protoconid, Ts - tuberculum sextum.

The left m/3 is more informative about cuspal structure because the grooves between the cusps, even though worn down, are still visible, even those between the protoconid, hypoconid and hypoconulid where they are shallow (Fig. 20). The crown is cracked longitudinally with a thin infilling of calcrete, but apart from that, the occlusal surface is in good condition.

In this tooth the postmetacristid and tuberculum sextum are reasonably clearly distinguished from the neighbouring cusps by the presence of shallow grooves visible on the lingual and distal surfaces of the tooth respectively. The mesial cingulum is also evident, especially on the mesio-lingual corner of the crown. The depths of the mesial fovea (trigonid basin) are preserved at the mesial end of the occlusal surface between the mesial cingulum and the internal cristids of the protoconid and metaconid. The shallow buccal and lingual notches (bucco-lingual waisting in Zhang & Harrison, 2017) are shallow but distinct and extend from the occlusal surface to the cervix. The buccal surface of the protoconid of the m/3 shows a low but distinct cingular structure.

The roots of the molar in the left mandible are not visible, but damage to the body of the right mandible has exposed the mesio-lingual root of the m/2. The root is stout and tall (15.2 mm) compared to the preserved crown height (7.3 mm).

Table 8. Measurements (in mm) of the teeth in the Sinibo hominid mandible, OCO BAR 900'11 (e - estimated).

Tooth	Mesio-distal length	Bucco-lingual breadth
p/4 left	10.1	12.3
m/1 left	14.5	13.2
m/2 left	14.8	14.7
m/3 left	15.8	14.7
m/2 right	15.2	15.2
m/3 right	17.0	15(e)

Comparisons and Interpretation

In its overall dimensions and morphology, the Sinibo mandible (OCO BAR 900'11) resembles those of the medium-sized australopithecines. Its teeth are considerably smaller than those of *Paranthropus boisei* and *Paranthropus aethiopicus*, for example, but are slightly larger than those of *Australopithecus deyiremeda* and they plot at the large end of the range of variation of Hadar specimens attributed to *Praeanthropus afarensis* (Fig. 21, 22).

The Sinibo molars are compatible in dimensions with specimens of *Paranthropus robustus* from Drimolen (Moggi-Cecchi *et al.* 2010; Rak *et al.* 2021) and other South African localities, but the p/4 from Sinibo is smaller than any of the australopithecine fossils from Swartkrans (Grine, 2004) and Drimolen (Moggi-Cecchi *et al.* 2010). The p/4 plots comfortably within the range of metric variation of the Hadar sample of *Australopithecus afarensis* described by Kimbel *et al.* (1994) but it is larger than the specimen from Laetoli (Harrison, 2011). It is similar in dimensions to the p/4s in the holotype of *Australopithecus bahrelghazali* from Koro Toro, Chad (Brunet *et al.* 1996) but the morphology is divergent, the Chadian specimen possessing a larger hypoconid and entoconid than the Sinibo specimen. The Sinibo p/4 plots into the lower end of the range of variation of specimens from Sterkfontein (Moggi-Cecchi *et al.* 2006) and is slightly larger than the specimens of *Australopithecus anamensis* from Kanapoi (Leakey *et al.* 1995). It is appreciably larger than specimens from Woranso-Mille (Haile-Selassie *et al.* 2022) but is closer in size to a single tooth from Lomekwi (Skinner *et al.* 2020).

The m/1 in the Sinibo mandible is similar in dimensions to specimens from Uraha, Malawi (Moggi-Cecchi *et al.* 2010), Drimolen (Rak *et al.* 2021), large specimens from Hadar (Kimbel *et al.* 2004), the specimen from Burtele (*Australopithecus deyiremeda*) (Haile-Selassie *et al.* 2015) and the larger specimens from Sterkfontein (Moggi-Cecchi *et al.* 2006). It is appreciably bigger than fossils from Woranso-Mille (Haile-Selassie *et al.* 2022) as well as specimens from Lomekwi (Skinner *et al.* 2020) and all but one of the « early *Homo* » specimens from East Turkana (Moggi-Cecchi *et al.* 2010). It plots into a gap in distribution of specimens from Swartkrans (Grine, 2004; Moggi-Cecchi *et al.* 2010). It is close in size to a specimen from the Omo Valley in Ethiopia (OMO 75s-15) but is smaller than the other two specimens attributed to « early *Homo* ». It is similar in dimensions to three of the six teeth from Olduvai Gorge, Tanzania, attributed to « early *Homo* » by Moggi-Cecchi *et al.* (2010), the other three teeth being smaller than it.

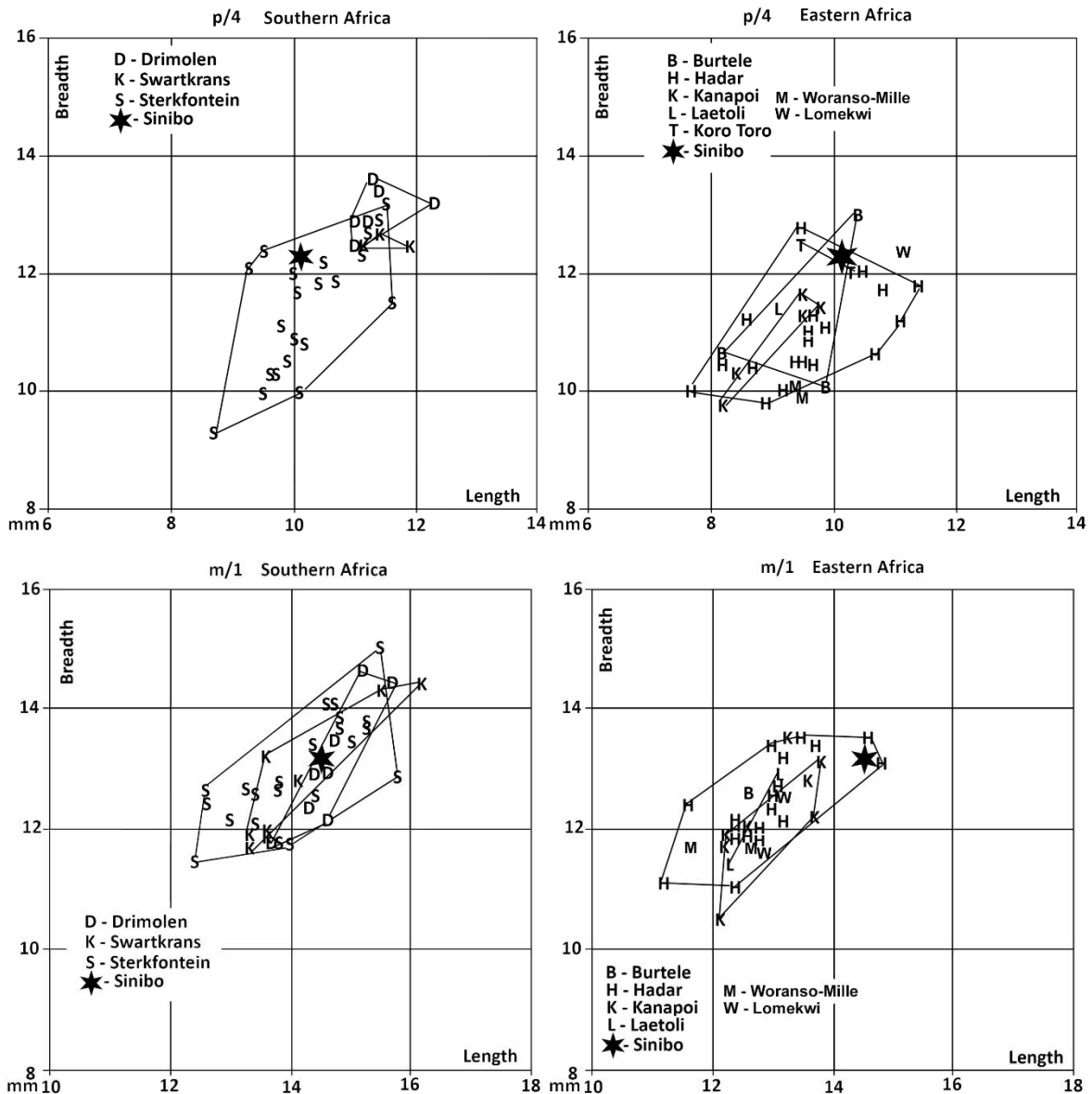


Figure 21. Bivariate plots of p/4 and m/1 of hominids from Sinibo and other localities in Eastern and Southern Africa. Note the offset in overall dimensions between the southern African (greater means of length and breadth) and eastern African ‘populations’ (lesser means of length and breadth).

The m/2s from Sinibo are smaller than any of the specimens from Swartkrans and most of the specimens from Sterkfontein (Moggi-Cecchi *et al.* 2010) although there is overlap in the middle of the range of metric variation with the latter sample. The Sinibo m/2s plot at the large end of the range of metric variation of the Hadar sample attributed to *Australopithecus afarensis* by Kimbel *et al.* (1994) but they are slightly longer and broader than specimens of this species from the type locality, Laetoli (White, 1980; Harrison, 2001). The Sinibo m/2s plot within the range of variation of *Australopithecus anamensis* from Kanapoi (Leakey *et al.* 1995). They are close in dimensions to the Burtele specimen of *Australopithecus deyiremeda* (Haile-Selassie *et al.* 2015) but are considerably larger than fossils from Woranso-Mille (Haile-Selassie *et al.* 2022) and Lomekwi (Skinner *et al.* 2020).

The m/3s from Sinibo overlap in dimensions with specimens of *Paranthropus robustus* from Drimolen (Moggi-Cecchi *et al.* 2010; Rak *et al.* 2021) and Sterkfontein (Moggi-Cecchi *et al.* 2006). They are similar in length to the specimen from Burtele (*Australopithecus deyiremeda*, Haile-Selassie *et al.* 2015). The Sinibo third molars are slightly larger than the two specimens of *Praeanthropus afarensis* from

Laetoli (*Australopithecus afarensis* in White, 1980; Harrison, 2011) and are bigger than the corresponding teeth of *Australopithecus sediba* from Malapa, South Africa (Berger *et al.* 2010). They are bigger than all the m/3s of *Australopithecus anamensis* from Kanapoi (Leakey *et al.* 1995) and are broader but shorter than specimens from Lomekwi (Skinner *et al.* 2020). They are appreciably larger than fossils from Woranso-Mille (Haile-Selassie *et al.* 2022).

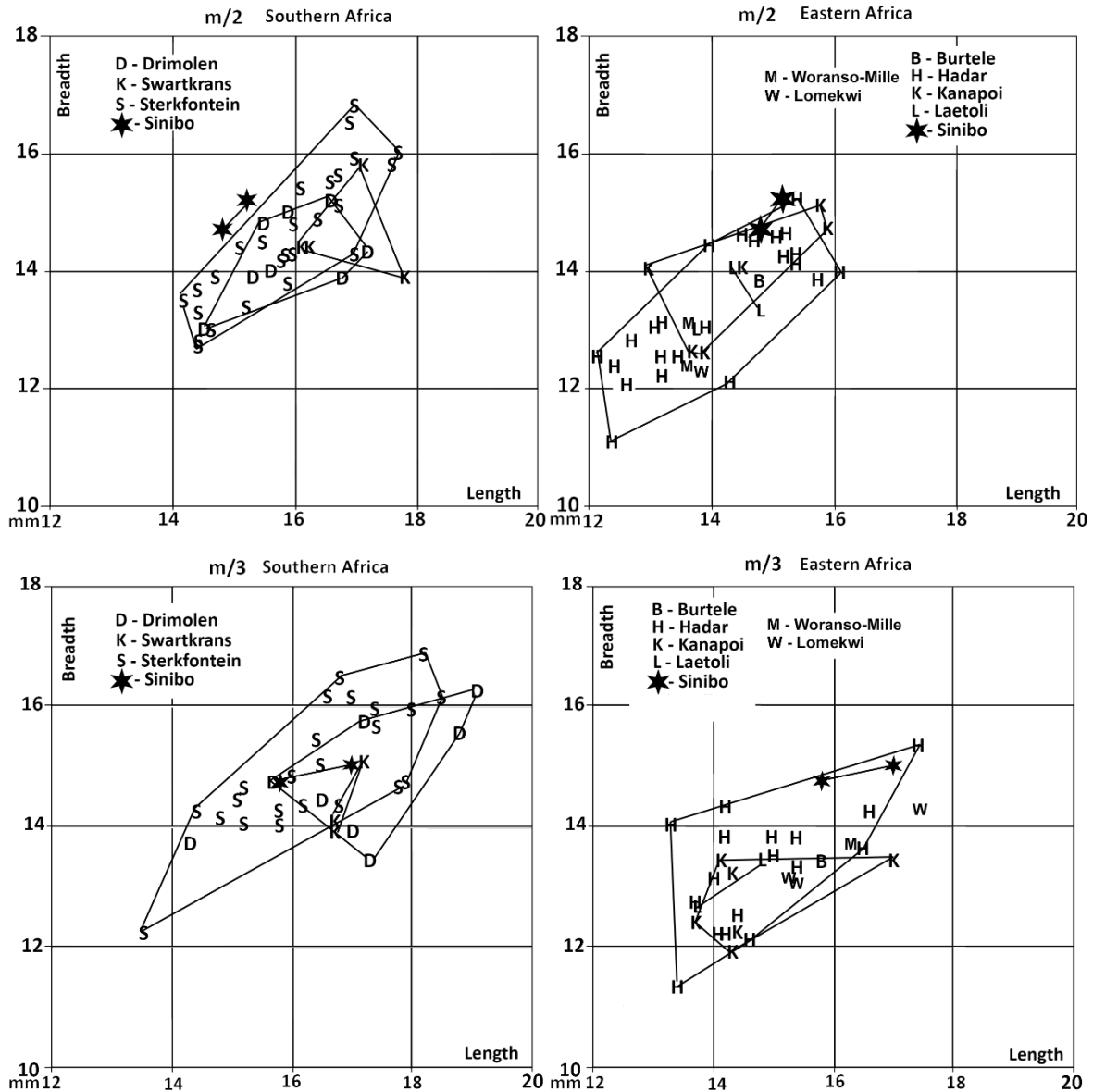


Figure 22. Bivariate plots of m/2 and m/3 of hominids from Sinibo and other localities in Eastern and Southern Africa. Note the offset in overall dimensions between the southern African (greater means of length and breadth) and eastern African ‘populations’ (lesser means of length and breadth).

From a dimensional perspective, it is difficult to decide to which species the Sinibo mandible belongs. Morphologically its teeth resemble those in a specimen from Hadar (AL 400-1) attributed to *Australopithecus afarensis* by White & Johanson (1982) but it could plausibly belong to *Australopithecus deyiremeda* or even to one of the Southern African taxa. It is unlikely to represent *Australopithecus anamensis* which is a smaller species, and appurtenance to *Paranthropus boisei* or *Paranthropus aethiopicus* can be ruled out, their cheek teeth being considerably larger than those from Sinibo.

The relationships of the Sinibo mandible to *Kenyanthropus platyops* cannot currently be assessed because the available lower teeth of this taxon have not been described (Leakey *et al.* 2001; Spoor *et al.* 2016). Lower teeth from Lomekwi (the type area of *Kenyanthropus platyops*) have been described (Skinner *et al.* 2020) but they have not been attributed to a particular taxon and the meristic position of many of the teeth is uncertain, so only teeth of known position have been included in our detailed analysis (Fig. 21, 22).

From a morphological perspective, the teeth in the Sinibo mandible are close to two specimens from Hadar of which casts were available, AL 145-35 (left mandible with p/4-m/2 which is smaller than the Sinibo jaw) and AL 400-1a (right mandible with i/1-m/3 which is quite close in dimensions to the Sinibo specimen) (Kimbel *et al.* 2004).

The closest metric fits between the Sinibo mandible and specimens from Hadar vary from tooth to tooth (Table 9). These correspond to the ‘large’ subsample of Ferguson (1984) as well as to what he declared to be a pongid, and they are close to some of the specimens attributed to *Homo hadar* by Bonde (2011).

Table 9. Closest metric correspondences between the teeth in the Sinibo mandible and specimens from Hadar, together with identifications of the latter material, all of which was attributed to *Australopithecus afarensis* by Kimbel *et al.* 2004 (in bold are the two closest metric fits).

Tooth	Closest in dimensions	Identification	Authors
p/4	AL 333W-32, 60 AL 333-7 AL 582-11 AL 443-1 AL 277-1	<i>Homo hadar</i> <i>Homo hadar</i> <i>Australopithecus afarensis</i> <i>Australopithecus afarensis</i> <i>Australopithecus afarensis</i>	Bonde, 2011 Bonde, 2011 Kimbel <i>et al.</i> 2004 Kimbel <i>et al.</i> 2004 Kimbel <i>et al.</i> 2004
m/1	AL 440-1a AL 241-14 AL 333-7 AL 333-74 AL 241-14	Pongidae <i>Australopithecus afarensis</i> <i>Homo hadar</i> <i>Homo hadar</i> <i>Australopithecus afarensis</i>	Ferguson, 1984 Kimbel <i>et al.</i> 2004 Bonde, 2011 Bonde, 2011 Bonde, 2011
m/2	AL 188-1 AL 400-1a AL 277-1 AL 333W-32, 60	<i>Australopithecus afarensis</i> <i>Australopithecus afarensis</i> <i>Australopithecus afarensis</i> <i>Homo hadar</i>	Kimbel <i>et al.</i> 2004 Kimbel <i>et al.</i> 2004 Kimbel <i>et al.</i> 2004 Bonde, 2011
m/3	AL 620-1 AL 487-1 AL 437-1 AL 438-1	<i>Australopithecus afarensis</i> <i>Australopithecus afarensis</i> <i>Australopithecus afarensis</i> <i>Australopithecus afarensis</i>	Kimbel <i>et al.</i> 2004 Kimbel <i>et al.</i> 2004 Kimbel <i>et al.</i> 2004 Kimbel <i>et al.</i> 2004

There has been debate about whether any of the hominids from the Turkana Basin from the 3.5-3.0 Ma time span belong to *Australopithecus afarensis* or not (Kimbel, 1988; Ward *et al.* 1999b; Brown *et al.* 2001; Kimbel & Delezene, 2009; Wood & Leakey, 2011). The supposed absence of the species in northern Kenya inferred by some of the authors seems strange, given that it is reported to be present in Ethiopia and Tanzania (Johanson *et al.* 1978). However, the discovery of the same taxon at Kantis, near Nairobi, Kenya (Mbua *et al.* 2016) indicates that the species likely ranged throughout East Africa. The Sinibo mandible adds fuel to the debate in that it is close in morphology and dimensions to some of the Hadar specimens, plotting at the large end of the range of variation. The teeth in the Sinibo mandible fragments are appreciably larger than any of the materials from Laetoli, but morphologically they are similar to them.

Discussion

Taxonomy

The palaeoanthropological literature contains a high diversity of taxonomic attributions of hominid fossils (Fig. 23-25). For example, the Tabarin mandible has been attributed to *Australopithecus*, *Praeanthropus* and *Ardipithecus* (respectively by Hill, 1983; Cela-Conde & Ayala, 2003, and Bonde, 2011). *Orrorin* has been declared a synonym of *Praeanthropus* by Cela-Conde & Ayala (2003) into which they also classified *Australopithecus garhi* (Asfaw *et al.* 1999), unlike Bonde (2011) who classified *garhi* in the genus *Homo*.

There have been tremendous divergences of opinion about the hypodigms of most hominine taxa, with fossils being included or removed from a taxon on a frequent basis, even on occasions by the same authors. On the basis of the form of the dentine-enamel junction in cheek teeth of Plio-Pleistocene hominids from Gauteng Province, South Africa, Zanolli *et al.* (2022) modified many previous attributions of specimens to *Homo*, *Paranthropus* and *Australopithecus*.

The content of *Australopithecus afarensis* has varied a great deal, with some authors splitting the Hadar sample into two or even three taxa (Ferguson, 1984; Senut & Tardieu, 1985; Bonde, 2011). As of date, the Hadar fossils have been attributed to the following taxa – *Australopithecus afarensis* Johanson, 1978 (Johanson *et al.* 1978), *Homo antiquus* Ferguson, 1984, *Australopithecus africanus miodentatus* Ferguson, 1987, *Homo hadar* Bonde & Westergarde, 2004 and *Afaranthropus antiquus* (Ferguson, 1984) by Bonde, 2011. In the opinions of Ferguson (1984, 1987) and Bonde (Bonde & Westergarde, 2004; Bonde, 2011) the species *afarensis* does not occur in the Afar region, and not even at its type locality, Laetoli, the type specimen being considered to belong to *Homo antiquus* (a preoccupied name as it happens, Adloff, 1908) or to *Praeanthropus africanus* (Weinert, 1950) (see synonymy list in Harrison, 2011 and Bonde, 2011, and also ICZN, 1999).

Under the circumstances, proposing a name for the hominid fossils from the Mabaget Formation is not an easy undertaking.

The material from Tabarin, Mabaget, Pelion and Sagatia, all in the Pelion Member, is close in dimensions and morphology to the corresponding fossils of *Orrorin tugenensis* from the Lukeino Formation (latest Miocene), and appurtenance to this genus is plausible. However, a case could be made for including it in the genus *Praeanthropus* as the species *Praeanthropus praegens*, as was proposed by Cela-Conde & Ayala (2003). More informative material from the Lukeino and Mabaget formations may throw light on the subject. Grine *et al.* (2006) discussed the Tabarin mandible, concluding that its attribution to *Praeanthropus afarensis* was questionable (see also Boaz, 1988). Kissel & Hawks (2015) in contrast, considered that the Tabarin mandible was metrically consistent with inclusion in *Ardipithecus* (as cf *Ardipithecus cf ramidus*), but they also pointed out that its mesio-distally compressed m/2 aligned it with *Orrorin*.

The taxonomic placement of the Sinibo mandible is a more daunting undertaking, because it could belong to one of five currently accepted genera – *Homo*, *Australopithecus*, *Paranthropus*, *Praeanthropus* or *Kenyanthropus*. As explained above its teeth are close in dimensions to those of *Paranthropus robustus*, to some specimens attributed to early *Homo* by Moggi-Cecchi *et al.* (2006), and to large specimens of « *Australopithecus afarensis* » from Hadar, but they are smaller than those of *Paranthropus boisei* and *Paranthropus aethiopicus*. The teeth in the Sinibo jaw are slightly larger than those of *Australopithecus deyiremeda* and probably also those of *Kenyanthropus platyops* (no measurements of lower cheek teeth of this species are available in the literature, although a recently published paper discussed fossils from the same area from which the type material was collected (Skinner *et al.* 2020) the meristic position and taxonomic assignment of many of which cannot be determined confidently). The Sinibo teeth are larger than specimens attributed to *Australopithecus anamensis*. Under the circumstances we consider that the Sinibo mandible most likely belongs to the species of *Praeanthropus* represented by the largest specimens from the Hadar area, Ethiopia, including specimens attributed to *Homo hadar* by Bonde (2011). The robust aspect of the mandible suggests however that, with the Sinibo mandible, we are dealing with a *Praeanthropus*-like or an

Australopithecus-like species, and not a *Homo*-like one. But it is noted that some specimens attributed to early *Homo* (Moggi-Cecchi *et al.* 2006) possess quite robust mandibles.

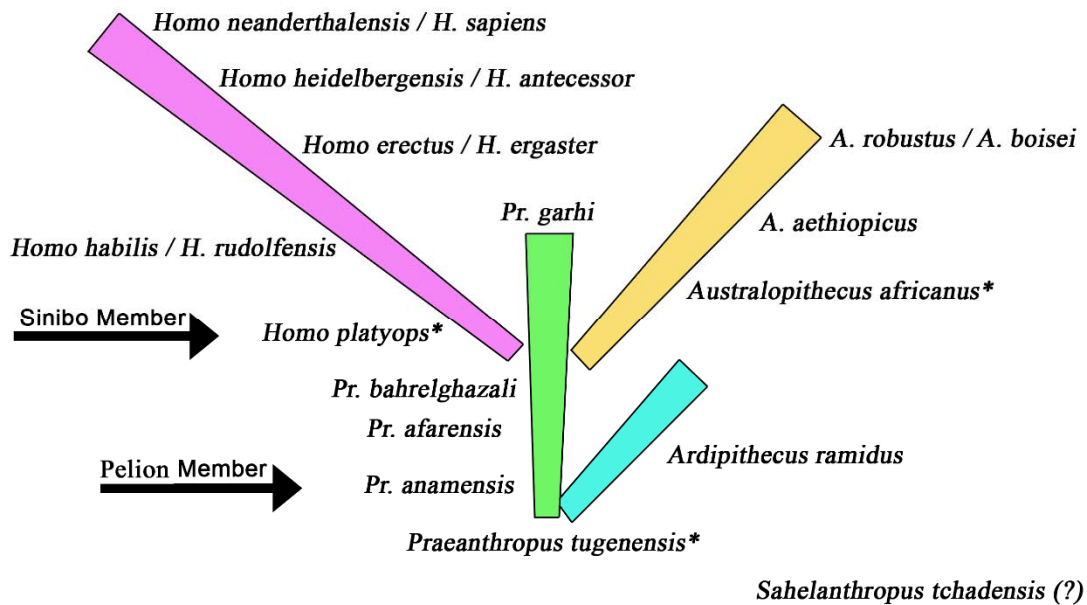
Phylogeny

Because the sample of latest Miocene to middle Pliocene hominid fossils in Africa is restricted and often fragmentary, there is a great deal of uncertainty about the diversity of taxa present (Cela-Conde & Ayala, 2003; Bonde, 2011; Cerling *et al.* 2013; Haile-Selassie *et al.* 2016). The various ways of interpreting the morphological and metric variation in latest Miocene to extant hominids, have given rise to a bewildering array of phylogenetic proposals, ranging from the « lumping » approach of Cela-Conde & Ayala (2003) (Fig. 23) in which four genera and 19 species were recognised, and the « splitting » approach of Bonde (2011) (Fig. 24) in which 9 genera and 34 or 35 species and subspecies were recognised. Furthermore, it is clear that some of the ‘taxa’ accepted by these authors are chimaera, being composed of the remains of two or more taxa.

To complicate matters, the dating of some of the African fossil hominid fossils has varied greatly. For example, the Sterkfontein *Australopithecus* material has recently been redated to between 3.67 and 3.41 Ma (Granger *et al.* 2022) whereas the bulk of it was previously considered to date from 2.6 to 2.1 Ma. The phylogenies discussed in figures 23-25 were proposed prior to the redating of the Sterkfontein fossils. If correct, the redating greatly modifies the scheme of Bonde (2011) (Fig. 24) because according to him the genus *Australopithecus* did not exist prior to 3.2 Ma. The phylogeny of Cela-Conde & Ayala (2003) (Fig. 23) poses fewer problems in that there is no time axis in their diagram. The phylogeny published by Haile-Selassie *et al.* (2016) is modified by the new dates, in that the South African species, *Australopithecus africanus* would not extend upwards in time to 2.5 Ma, but only to 3.4 Ma, making it a contemporary of *Australopithecus deriyemeda*, *Australopithecus afarensis*, *Australopithecus bahrelghazali* and *Kenyanthropus platyops* as well as the Burtele specimen (Fig. 25). The phylogeny of Cerling *et al.* (2013) (Fig. 25) does not include the species *Australopithecus africanus*. Pertinent to the discussion is that the few suid fossils from Sterkfontein, which have similar preservation characteristics to the hominid fossils, do not support an age of 3.41-3.67 for the deposits, but rather they indicate that the breccias are aged between 2.6 and 2.1 Ma (Cooke, 1994).

Under the proposals of Cela-Conde & Ayala (2003) the classification of the fossils from the lower strata of the Mabaget Formation (Pelion Member) would boil down to three possibilities, *Praeanthropus anamensis*, *Ardipithecus ramidus* or an undescribed taxon (if it differs from the two named taxa). But the Tabarin mandible has already been designated as the holotype of *Homo antiquus praegens* Ferguson, 1989. The nomen *praegens* predates *ramidus* (White *et al.* 1994) and *anamensis* (Leakey *et al.* 1995), as well as *tugenensis* (Senut *et al.* 2001) and *kadabba* (Haile-Selassie *et al.* 2001). Furthermore, if the genus name *Praeanthropus* is resurrected, then its type species would logically have been *Praeanthropus africanus* (Weinert, 1950) and not *Praeanthropus afarensis* (Johanson, 1978) but the ICZN (1999) ruled that Weinert’s name is suppressed, and that *afarensis* is the valid specific epithet (see also Harrison, 2011, synonymy list). However, subsequent literature reveals that most authors credit the name *afarensis* to Johanson, White & Coppens, 1978, rather than to Johanson, 1978, on his own.

It is unlikely that the hominid fossils from the Pelion Member belong to *Ardipithecus ramidus* (differences in enamel thickness, length/breadth proportions of molars, among other features) so it is concluded that they should be referred to what Cela-Conde & Ayala (2003) called *Praeanthropus praegens* (*Orrorin praegens* in this paper). Appurtenance to *Sahelanthropus* can be discarded because this genus is more likely to be an obligate quadrupedal ape with arboreal adaptations rather than a bipedal hominid (Wolpoff *et al.* 2002; Pickford, 2005a; Macchiarelli *et al.* 2020; Daver *et al.* 2022).



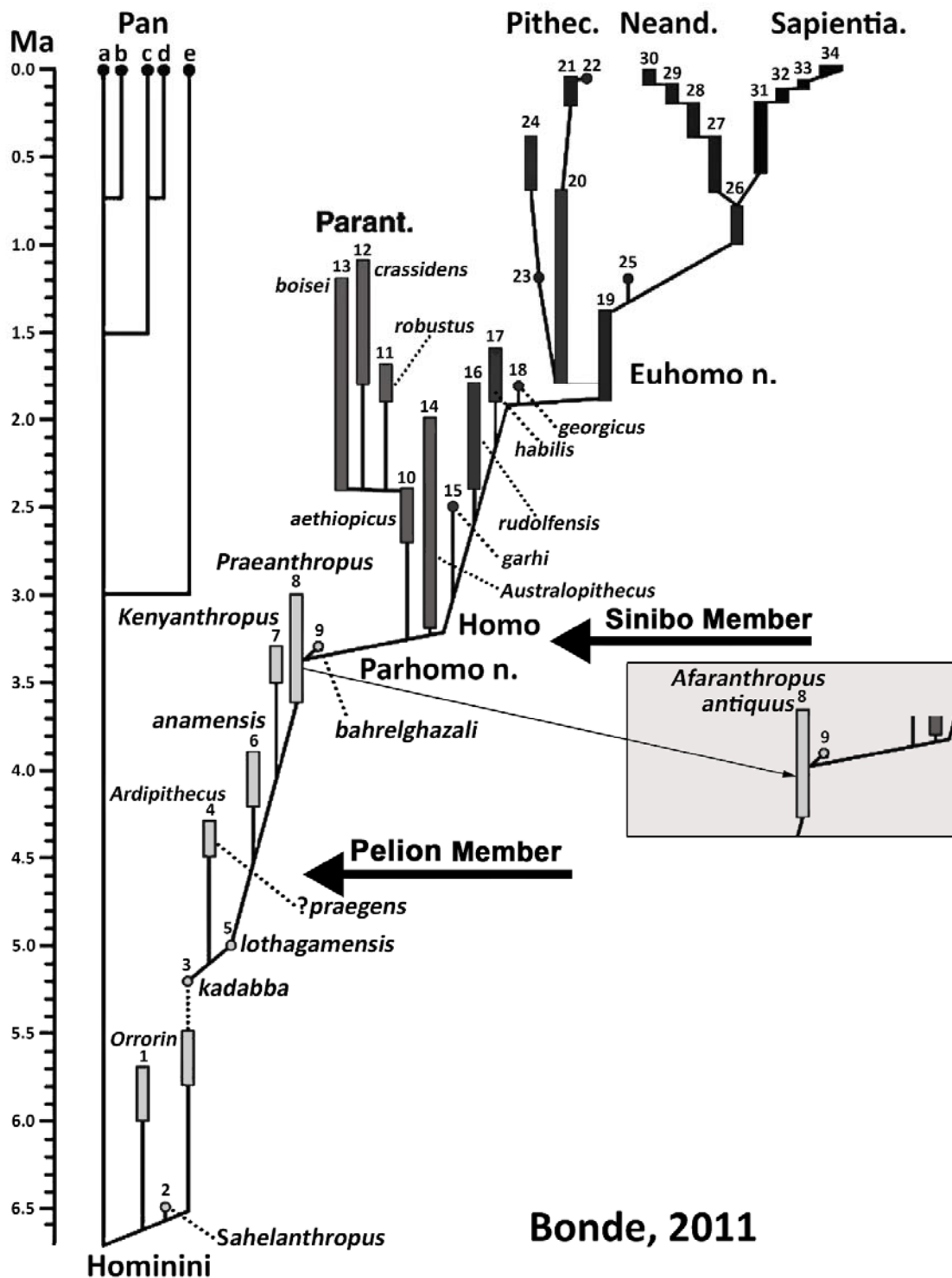
Cela-Conde & Ayala, 2003

Figure 23. Hominid phylogeny adapted from Cela-Conde & Ayala (2003). The positions of the Pelion and Sinibo fossils are shown by black arrows.

The phylogenetic position of the Sinibo mandible is difficult to decide under the proposals of Cela-Conde & Ayala (2003) (Fig. 23) because it accords with three of the genera recorded from its time period, early *Homo* (*H. platyops*), late *Praeanthropus* (*Pr. afarensis* - *Pr. bahrelghazali*) and early *Australopithecus* (*Au. africanus*).

In the phylogenetic scheme of Bonde (2011) (Fig. 24) the fossils from the Pelion Member fall opposite his clade 4 (*Ardipithecus* (? syn. *praegens*)) and just below the age span of *anamensis*. The species *praegens* was erected by Ferguson (1989) for the Tabarin mandible, which is now recognised as differing in enamel thickness and other features from the more ape-like *Ardipithecus ramidus*. The clade *kadabba* is likely a chimaera of two taxa, one of which is close to *Orrorin*, the other to *Ardipithecus*. *Sahelanthropus* is now generally considered to represent an ape on the basis of its cranial features (Wolpoff *et al.* 2002; Pickford, 2005a) and the postcranial bones attributed to it (Macchiarelli *et al.* 2020; Dayer *et al.* 2022).

Hominine Phylogeny



Bonde, 2011

Figure 24. Hominine phylogeny from Bonde (2011) itself modified from Bonde & Westergarde (2004) (adapted with changes) showing the positions of the Pelion and Sinibo material (black arrows). For ease of reference, the nomina attached to the numbers have been added for the clades other than *Euhomo* and *Pan*. *Ardipithecus* and *Sahelanthropus* are more likely to be in or close to the *Pan* clade, but *praegens* is a hominid. Thus, as presented in this cladogram, *Ardipithecus* is a chimaera. Bonde (2011) erected a new genus for AL 288-1, ‘Lucy’ (*Afaranthropus antiquus* (Ferguson, 1984)) which corresponds to clade 8 in this figure.

In the phylogeny of Bonde (2011) the Sinibo mandible, with an age of somewhat less than 3.4 Ma, would correspond in time with several taxa, *Kenyanthropus*, *Praeanthropus*, *Parhomo*, *Paranthropus*, *Australopithecus*, *Afaranthropus* and *Homo*.

If one accepts the views of Haile-Selassie *et al.* (2016) (Fig. 25) then there might be three hominid taxa in the latest Miocene (*Orrorin tugenensis* - the first named - *Ardipithecus kadabba* and possibly *Sahelanthropus tchadensis*, although the age and systematic affinities of the last species are disputed (Brunet *et al.* 2001; Wolpoff *et al.* 2002; Macchiarelli *et al.* 2020; Daver *et al.* 2022). The diversity then drops to one species at a time through much of the early Pliocene until about 3.8-3.6 Ma when diversity increases abruptly to six taxa, only to decrease to four taxa by ca 3 Ma (Haile-Selassie *et al.* 2016, fig. 1). None of these taxa are classified as apes by the authors, all being interpreted as hominids.

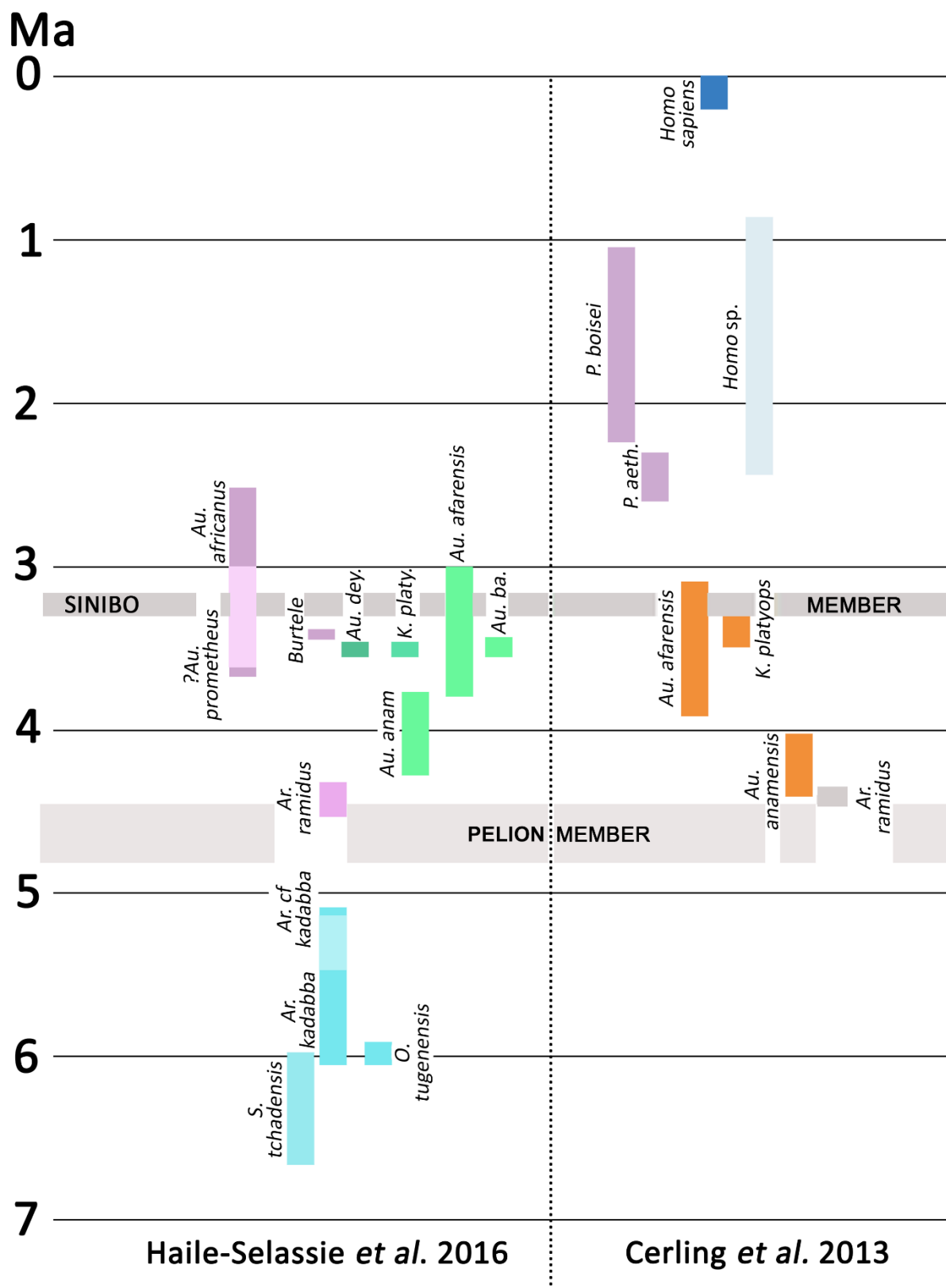


Figure 25. Stratigraphic distribution of late Miocene, Pliocene and Pleistocene hominoids from Africa. The positions of the fossils from the Pelion Member (localities of Mabaget, Pelion, Sagatia and Tabarin) and the Sinibo Member, are shown as grey horizontal bands. The distribution of taxa is adapted from Haile-Selassie *et al.* 2016 and Cerling *et al.* 2013. Abbreviations are *aeth.* - *aethiopicus*, *anam.* - *anamensis*, *Ar.* - *Ardipithecus*, *Au.* - *Australopithecus*, *ba.* - *bahrelghazali*, *cf.* - *confer*, *dey.* - *deyiremeda*, *K.* - *Kenyanthropus*, *O.* - *Orrorin*, *P.* - *Paranthropus*, *platy.* - *platyops*, *S.* - *Sahelanthropus*, *sp.* - *species*.

However, additional studies of the cranial and post-cranial elements of *Sahelanthropus tchadensis* have emphasised that it is more likely to be an ape than a hominid (Wolpoff *et al.* 2001; Pickford, 2005a; Macchiarelli *et al.* 2020; Daver *et al.* 2022) and *Ardipithecus ramidus* has some remarkably ape-like post-cranial features such as opposable hallux in the foot, ape-like humerus to femur ratio and incisor/molar relationships that suggest that it is engaged on the line towards *Pan* (Pickford, 2004, 2012; see also White *et al.* 2015).

Even if *Sahelanthropus* and *Ardipithecus* are interpreted to be apes, the fossil record of African apes between 8 million years ago and the present day is poor. Pickford & Senut (2005a, 2005b) described some chimpanzee- and gorilla-like teeth from Kenya, Pickford *et al.* (2008, 2009) described an indeterminate species from the late Miocene of Niger which they attributed to a proto-chimpanzee (see Mocke *et al.* 2022) and McBrearty & Jablonski (2005) attributed an incisor and a few other teeth from the middle Pleistocene Kapthurin Formation, Kenya, to chimpanzees. For these reasons, the phylogenetic schemes of Haile-Selassie *et al.* (2016), Cerling *et al.* (2013), Bonde (2011), and Cella-Conde & Ayala (2003), peter out downwards with no taxa listed older than 7 Ma.

The African hominoid record from ca 14 Ma to ca 5.5 Ma is indeed meagre, yet it comprises at least eight named genera (*Otavipithecus*, *Kenyapithecus*, *Nakalipithecus*, *Samburupithecus*, *Chororapithecus*, *Orrorin*, *Ardipithecus*, *Sahelanthropus*) as well as an unidentified genus of nyanzapithecine (Kunimatsu *et al.* 2017) and two or more un-named taxa of unclear affinities (Pickford & Senut, 2005b; Mocke *et al.* 2022) (Fig. 26). The perceived scarcity of hominoid fossils in African late Miocene deposits has been interpreted by some authors to mean that the Hominidae might have evolved in Eurasia (Begun, 2001, 2009, 2015; Böhme *et al.* 2020) and then dispersed back to Africa (see discussions in Cote, 2004 and Mocke *et al.* 2022). Given the high diversity of hominoid taxa present in the late Miocene of Africa, despite the restricted quantity of localities and the meagre amount of fossils, we consider it to be more likely that hominids (*sensu stricto* i.e. obligate bipeds) evolved in Africa, possibly from one of the more eurytopic taxa listed above (*Kenyapithecus*, *Otavipithecus*) (Fig. 26).

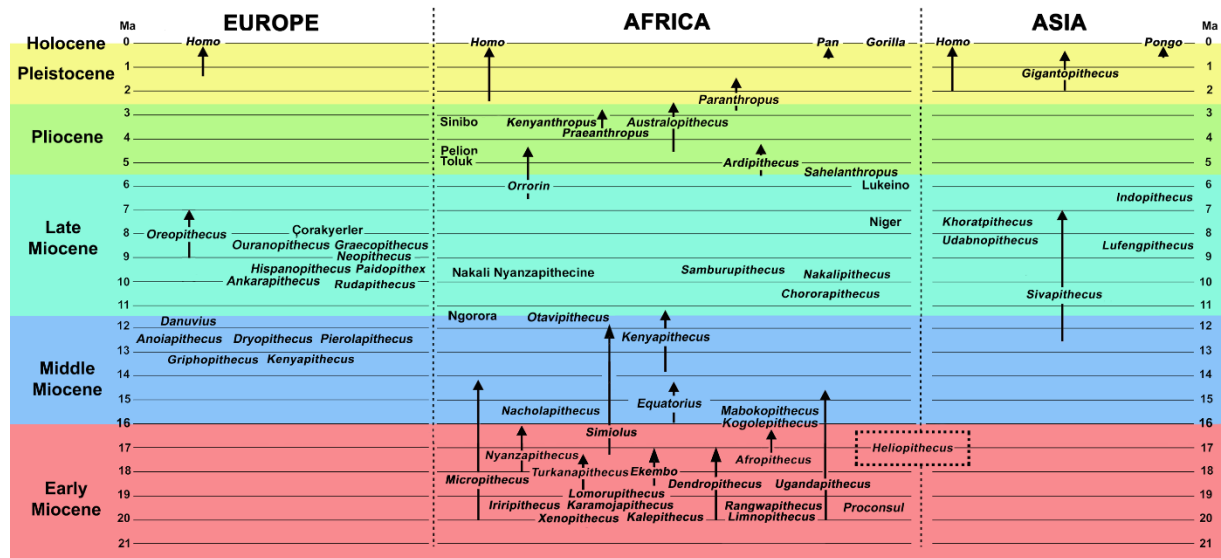


Figure 26. Stratigraphic and geographic distribution of Neogene and Quaternary apes and hominids (obligate bipeds), excluding Eurasian pliopithecids and hylobatids. Arrows show the chronological ranges of long-lived taxa. Ngorora, Nakali, Niger and Lukeino have yielded indeterminate great-ape-like species, while Nakali has yielded a nyanzapithecine (Kunimatsu *et al.* 2017). The Toluk and Pelion members have yielded fossils of small hominids (unidentified genus and *Orrorin praegens* respectively) while the Sinibo Member has yielded a large hominid (*Praeanthropus afarensis*). Çorakyerler (Turkey) has yielded a large hominoid, supposedly representing a new genus (Begun, 2009). *Heliopithecus* is

from the Arabian Peninsula. The age of *Sahelanthropus* is not well established, anthracothere fossils from the region ranging in age from 10 to 6 Ma (Pickford, 2009).

Later in the Pliocene, from sediments aged somewhat less than 3.4 Ma, the Sinibo Member of the Mabaget Formation has yielded remains of a hominid that corresponds in most dental dimensions to *Paranthropus robustus* and other similar-sized hominids, but has smaller cheek teeth than *Paranthropus boisei* and *Paranthropus aethiopicus*. The teeth in the fossil mandible from Sinibo are larger than most specimens of *Praeanthropus afarensis* from Hadar and *Australopithecus anamensis* from Kanapoi, although both of these localities have yielded a few individuals that are as big as the Sinibo specimen. The teeth in the Sinibo mandible fragments are somewhat bigger than the Laetoli specimens attributed to *Australopithecus afarensis* (*Praeanthropus afarensis* in this paper).

Palaeoenvironment

The lower beds of the Mabaget Formation (i.e. the Pelion Member) have yielded fossils of the water chevrotain (*Hyemoschus aquaticus*) and the peafowl (*Pavo* sp.) as well as fruit bats and other vertebrates adapted to tropical forest-habitats (Pickford *et al.* 2004). The fauna from the Pelion Member spanning the period 5-4 Ma therefore indicates that the region was clothed in humid tropical forest. Thus, *Orrorin praegens* dating between 5.0 and 4.5 Ma, is inferred to have lived in heavily vegetated areas.

In contrast, the upper levels of the Mabaget Formation (i.e. the Sinibo Member) from which the Sinibo hominid mandible was collected, have yielded remains of the moderately hypsodont suid, *Kolpochoerus heseloni* (or *K. olduvaiensis*), as well as *Elephas africanavus*, *Ceratotherium praecox*, *Taurotragus* (eland) and two or three species of gazelles. This faunal assemblage indicates that the vegetation at the time of deposition was probably comprised of relatively open woodland or even wooded savannah, contrasting markedly with the vegetation in the same region during the late Miocene and early Pliocene, when it was considerably more densely vegetated.

Older deposits in the Tugen Hills, such as the late Miocene Lukeino Formation (6.2-5.7 Ma), which yielded the early bipedal hominid *Orrorin tugenensis*, contain plant fossils typical of dry evergreen forest (Bamford *et al.* 2013) and mammals such as lorisines, colobines, fruit bats, tree hyraxes (*Dendrohyrax*) (Pickford, 2005b) and tragulids that are forest-adapted. The available evidence from the area thus suggests that climatic conditions and vegetation categories did not change a great deal between 6 and 4.5 Ma (Senut *et al.* 2017). The Toluk Beds, sandwiched between lava flows of the Kaparaina Basalt Formation (ca 5.5-5.3 Ma (Deino *et al.* 2002)) have yielded a low diversity of faunal remains comprising lophodont to bunodont proboscideans (*Deinotherium*, *Anancus*, *Primelephas*) and suids (*Nyanzachoerus*) as well as an isolated tooth of an early hominid (Pickford *et al.* 2009) also suggestive of relatively humid forested conditions at the time that the Kaparaina volcano was active.

By 3.5 Ma (Sinibo Member) in contrast, the Baringo region had become considerably more arid, with the fauna indicating open woodland to wooded savannah vegetation types (Senut *et al.* 2017). The even younger Chemeron Formation (2.4 Ma, Hill *et al.* 1985; Deino *et al.* 2002) also accumulated under regional woodland to savannah conditions in which early *Homo* survived (Sherwood *et al.* 2002).

The combined evidence from Kenya and Ethiopia (Fig. 25) suggests that the change in climate and vegetation occurred about 3.8 million years ago, with older strata yielding a low diversity of hominids of generally rather small dimensions, and younger strata yielding a higher diversity of hominids of generally larger dimensions.

Microdonty and megadonty in hominids

Orrorin tugenensis possessed postcranial bones that are about 1.5 times larger than those of “Lucy” (*Australopithecus* sp.) yet its postcanine teeth are appreciably smaller than those of the latter species (Senut *et al.* 2001; Pickford, 2004). Thus *Orrorin* was endowed with small cheek teeth relative to body size (microdonty) compared to australopithecines, which have long been known to have large cheek

teeth relative to body size (megadonty). In mammals, microdontology is usually associated with high quality diets while megadonty tends to develop in lineages that exploit lower quality foods, but in greater quantities. On this basis, *Orrorin* was probably exploiting high quality food items, as did many Miocene hominoids (*Kenyapithecus*, *Otaviapithecus*, *Nacholapithecus*, *Proconsul*, *Afropithecus*) and much of this food probably consisted of fruits. Australopithecines, in contrast, appear to have diverged away from a diet rich in fruits into one dominated by other vegetable matter, even though, if fruits were available - perhaps on a seasonal basis - they would have exploited them.

Most recently published scenarios of human origins are based on the premise that *Homo* descended from *Australopithecus*. This would imply that a megadont ancestor gave rise to a microdont descendant species. The presence of microdontology in *Orrorin tugenensis* at 6 Ma and *Orrorin praegens* at 5-4.5 Ma, as well as *Kenyanthropus*, a hominid aged ca 3.5 Ma, opens up other possibilities, one of which is that microdontology is a primitive feature of hominids inherited from one or other of the microdont Miocene hominoids, in which case there is no necessity to arrive at the genus *Homo* via megadont *Australopithecus*. If this is so, then australopithecines would represent a side branch of hominids that went extinct without issue (Aiello & Collard, 2001).

In order to test this hypothesis, we need to obtain more remains of *Orrorin* and other hominids of Late Miocene and basal Pliocene age. The fossils described in this paper lend additional support to the microdont hypothesis by showing that relatively small, fully bipedal, microdont hominids were likely continuously present in Africa from the latest Miocene until the evolution of *Homo* in the late Pliocene. In contrast, megadont australopithecines flourished only from the middle Pliocene (ca 4.5 Ma if *Australopithecus anamensis* belongs to this genus (cf Cela-Conde & Ayala, 2003, who classify it within *Praeanthropus* (Fig. 23)) or from 3.8 Ma if *Australopithecus afarensis* is considered to be the earliest member of the genus (Haile-Selassie *et al.* 2016; Cerling *et al.* 2013)) (Fig. 25) until they went extinct during the early Pleistocene ca 1 million years ago (*Paranthropus boisei*, *Paranthropus crassidens*) (Fig. 24-26).

Discussion and Conclusions

The Pliocene Mabaget Formation in Baringo County, Kenya, has yielded two markedly different hominid taxa, a small-bodied form from the Pelion Member (5.0-4.5 Ma) and a large-bodied one from the Sinibo Member (4.1-3.0 Ma). The small form is attributed to *Orrorin praegens* whereas the geologically younger, but larger species is identified as *Praeanthropus afarensis*.

The faunas associated with these two hominid species are divergent, the species *Orrorin praegens* being found alongside a forest-adapted fauna comprising tragulids, fruit bats, relatively bunodont suids and pea-fowls, in contrast to the open woodland to savannah-like fauna found alongside *Praeanthropus afarensis*, which comprises semi-hypsodont suids, hypsodont elephantids, hypsodont rhinocerotids and open-country bovids such as *Taurotragus* and gazelles. It is estimated that a major change in climate and vegetation occurred in the region sometime between 4.5 and 3.5 Ma, but details of the changes and their timing require further study of the faunas and floras preserved in the Mabaget Formation.

In conclusion, the early to middle Pliocene deposits in the eastern foothills of the Tugen Hills have yielded evidence concerning dramatic changes in climate and vegetation in the region sometime between 4.5 and 3.5 million years ago. The composition of the faunas changed during this period from forest-adapted to woodland- and savannah-adapted forms. Some of the changes in the mammalian faunas imply local extinction (tragulids, pea-fowls for example) but some of the changes could have been by autochthonous evolution (*Anancus*, *Nyanzachoerus*, *Kolpochoerus*) whereas some lineages (*Taurotragus*, *Gazella*) seem to have evolved elsewhere in the continent and dispersed to the Baringo region when the climate and vegetation changed.

Because remains of early hominids are rare in Baringo County, it is premature to postulate whether the change from *Orrorin praegens* to *Praeanthropus afarensis* represents autochthonous evolution of a

hominid lineage or a replacement of *Orrorin praegens* by dispersal of a lineage that had already evolved elsewhere in the continent. Further palaeontological and geological surveys of the latest Miocene to late Pliocene succession in the Tugen Hills and elsewhere in the continent are required to throw light on the matter.

Acknowledgements

Thanks to the Orrorin Community Organisation (Mrs N. Kiptalam, Mr M. Cherutich), the County Commissioner Baringo North (Kabartonjo), County Officer Baringo North (Kipsaraman), the chiefs and sub-chiefs of Sibillo sub-county, the Deputy of Baringo North (Mr William Cheptumo), Ambassador Binaisa Chepsongol, and the KPE Team (Ezra Kiptalam Cheboi, Nancy Kiptalam, Solomon Chelimo, Michael Kibuu, Zaphania Chetalam, Kenneth Chepkwony, Maurine Kimosop, Evelyne Reuben Kibor, Miriam Chongwo, Rosaline Cheptumo, James Chesaina, Lidia Yatich, Betsy Kandie, Linah Sesat, Marc Sesat, Jennifer Kibos, Joseph Chebet, Jane Chesang, Jane Musa, Dinah Tomno, Peninah Chepyogon, Luka Kiptalam, Stella Kiptalam, Elijah Chelugo, Solomon Chelimo, Windus Maurice, Jackson Kemei, David Chebor, Ezekiel Lomukei, Musa Chemjor, Julia Kiptalam). Finance was provided by the CNRS (GDRI) and the Commission des Fouilles archéologiques à l'étranger of the French Ministry of Foreign and European Affairs. We acknowledge the support of the French Embassy in Nairobi (Mme Elisabeth Barbier, Mr Georges Dineur, Mme S. Fogel-Verteron). The Kenya Palaeontology Expedition carried out research in Baringo County under Research Permit N° OP/13/001/28C 212, valid from 20.11.1998 until 31.12.2001, reissued as N° MOE&T/13/001/28C 121 from 12.4.2001 until 30.7.2007, renewed on the 19.11.2007 until 30.11.2010 and again until 30.8.2012. We thank two referees and the editor for comments that led to amelioration of the content and presentation of the paper. We dedicate this paper to the late Kiptalam Cheboi, who discovered many important fossils during his long career as a fossil hunter.

References

- Adloff, P. 1908. Die Zähne des *Homo primigenius* von Krapina. *Anatomischer Anzeiger*, **32**, 301-302.
- Aiello, L. & Collard, M. 2001. Palaeoanthropology: our newest ancestor? *Nature*, **410**, 526-527.
- Aiello, L. & Dean, C. 1990. The Hominoid foot. In: Aiello, L. & Dean, C. (Eds) *An Introduction to Human Evolutionary Anatomy*. Academic Press, London, Chapter 23, pp. 507-538.
- Alekseev, V.P. 1986. *The Origin of the Human Race*. Progress Publishers, Moscow, 336 pp.
- Arambourg, C. 1954. L'hominien fossile de Ternifine (Algérie). *Comptes Rendus de l'Académie des Sciences*, **239**, 893-895.
- Arambourg, C. & Coppens, Y. 1967. Sur la découverte, dans le Pléistocène inférieur de la vallée de l'Omo (Éthiopie), d'une mandibule d'Australopithécien. **265**, 589-590.
- Arambourg, C. & Coppens, Y. 1968. Découverte d'un Australopithécien nouveau dans les gisements de l'Omo (Éthiopie). *South African Journal of Science*, **64**, 58-59.
- Asfaw, B., White, T., Lovejoy, O., Latimer, B., Simpson, S. & Suwa, G. 1999. *Australopithecus garhi*: A new species of early hominid from Ethiopia. *Science*, **284**, 629-635.
- Bamford, M., Senut, B. & Pickford, M. 2013. Fossil leaves from Lukeino, a 6-million-year-old Formation in the Baringo Basin, Kenya. *Geobios*, doi.org/10.1016/j.geobios.2013.02.001. 55 pp.
- 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. 2009. Dryopithecins, Darwin, de Bonis, and the European origin of the African ape and human clade. *Geodiversitas*, **31** (4), 789-816.
- Begun, D. 2015. Fossil Record of Miocene hominoids. In: Henke, W. & Tattersall, A. (Eds) *Handbook of Paleoanthropology*, Heidelberg, Springer Verlag, pp. 1-55.
- Berger, L.R., de Ruiter, D.J., Churchill, S.E., Schmidt, P., Carlson, K.J., Dirks, P.H.G.M. & Kibii, J.M. 2010. *Australopithecus sediba*. A new species of *Homo*-like australopith from South Africa. *Science*, **328**, 195-204.

- Binetti, K.M. 2011. *Early Pliocene Hominid Paleoenvironments in the Tugen Hills, Kenya*. PhD Thesis, Yale University, 237 pp. + 10 pp. appendices.
- Boaz, N.T. 1988. Status of *Australopithecus afarensis*. *Yearbook of Physical Anthropology*, **31**, 85-113.
- Böhme, M., Braun, R. & Breier, F. 2020. *Ancient Bones : Unearthing the Astonishing New Story of How We Became Human*. (Translated by J. Billingham). Vancouver, Greystone Books, 376 pp.
- Bonde, N. 2011. Hominid Diversity and 'Ancestor' Myths. In: Schilhab, T., Stjernfelt, F. & Deacon, T. (Eds) *The Symbolic Species Evolved*. Biosemiotics Volume 6, Springer Nature, pp. 151-191.
- Bonde, N. & Westergarde, B. 2004. Progress in hominid classification: cladistic approaches. *Miscelanea a E. Aguirre, III, Palaeoantropologia. Zona Arqueologica*, **4**, Museo Arqueologico Regional, pp. 36-57.
- Bromage, T.G., Schrenk, F. & Zonnefeld, F.W. 1995. Paleoanthropology of the Malawi Rift: An early hominid mandible from the Chiwondo Beds, northern Malawi. *Journal of Human Evolution*, **28**, 71-108.
- Broom, R. 1936. A new fossil anthropoid skull from South Africa. *Nature*, **138**, 486-488.
- Broom, R. 1938. The Pleistocene anthropoid apes of South Africa. *Nature*, **142**, 377-379.
- Broom, R. 1949. Another new type of fossil ape-man (*Paranthropus crassidens*). *Nature*, **163**, 57.
- Broom, R. & Robinson, J.T. 1949a. A New Type of Fossil Man. *Nature*, **164**, 322-323. <http://dx.doi.org/10.1038/164322a0>
- Broom, R. & Robinson, J.T. 1949b. Man contemporaneous with the Swartkrans ape-man. *American Journal of Physical Anthropology*, **8**, 151-157.
- Broom, R. & Robinson, J.T. 1952. Swartkrans ape-man, *Paranthropus crassidens*. *Memoir of the Transvaal Museum*, **6**, 1-123.
- Brown, B., Brown, F.H. & Walker, A. 2001. New hominids from the Lake Turkana Basin. *Journal of Human Evolution*, **41**, 29-44.
- Brown, F.H. 1982. Tulu Bor Tuff at Koobi Fora correlated with the Sidi Hakoma Tuff at Hadar. *Nature*, **300**, 631-633.
- Brown, F.H. 1994. Development of Pliocene and Pleistocene chronology of the Turkana Basin, East Africa, and its relation to other sites. In: Corruccini, R.S. & Ciochon, R.L. (Eds) *Integrative Paths to the Past: Paleoanthropological Advances in Honor of F. Clark Howell*. Prentice Hall, Englewood Cliffs, New Jersey, 1994, **15**, pp. 285-312.
- Brunet, M. 1996. *Australopithecus bahrelghazali*, une nouvelle espèce d'Hominidé ancien de la région de Koro Toro (Tchad). *Comptes Rendus de l'Académie des Sciences, Série II, Sciences de la Terre et des Planètes*, **322**, 907-913.
- Brunet, M., Guy, F., Pilbeam, D., Lieberman, D.E., Likius, A., MacKaye, H.T., Ponce de Léon, M.S., Zollikofer, C.P.E. & Vignaud, P. 2005. New material of the earliest hominid from the Upper Miocene of Chad. *Nature*, **434**, 752-755.
- Brunet, M., Guy, F., Pilbeam, D., MacKaye, H.T., Likius, A., Ahounda, D., Beauvilain, A., Blondel, C., Bocherens, H., Boisserie, J.-R., de Bonis, L., Coppens, Y., Dejax, J., Denys, C., Durringer, 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 Léon, M., Rage, J.-C., Sapanet, M., Schuster, M., Sudre, J., Tassy, P., Valentin, X., Vignaud, P., Viriot, L., Zazzo, A. & Zollikofer, C. 2001. A new hominid from the upper Miocene of Chad, Central Africa. *Nature*, **418**, 145-151.
- Cela-Conde, C.J. & Ayala, F.J. 2003. Genera of the human lineage. *Proceedings of the National Academy of Science of the USA*, **100** (13), 7684-7689.
- Cerling, T.E., Manthi, F.K., Mbua, E.N., Leakey, L.N., Leakey, M.G., Leakey, R.E., Brown, F.H., Grine, F.E., Hart, J.A., Kaleme, P., Roche, H., Uno, K.T. & Wood, B.A. 2013. Stable isotope-based diet reconstructions of Turkana Basin hominins. *Proceedings of the National Academy of Sciences of the United States of America*, **110** (26) 10501-10506.
- Cooke, H.B.S. 1994. *Phacochoerus modestus* from Sterkfontein Member 5. *South African Journal of Science*, **90**, 99-100.
- Cote, S.M. 2004. Origins of the African hominoids : an assessment of the palaeo-biogeographical evidence. *Comptes Rendus Palevol*, **3**, 323-340.

- Curnoe, D. 2010. A review of early *Homo* in southern Africa focusing on cranial, mandibular and dental remains, with the description of a new species (*Homo gautengensis* sp. nov.). *HOMO. Revista de Biologia Humana Comparada*, **61** (3), 151-177.
- Dart, R.A. 1925. *Australopithecus africanus*: The man-ape of South Africa. *Nature*, **115**, 195-199.
- Dart, R.A. 1948. The Makapansgat proto-human *Australopithecus prometheus*. *American Journal of Physical Anthropology*, **6**, 259-284.
- Daver, G., Guy, F., Mackaye, H.T., Likius, A., Boisserie, J.-R., Moussa, A., Pallas, L., Vignaud, P. & Clarisse, N.D. 2022. Postcranial evidence of late Miocene hominin bipedalism in Chad. *Nature*, **609**, 94-100 (<https://doi.org/10.1038/s41586-022-04901-z>).
- Deino, A. & Hill, A. 2002. ⁴⁰Ar/³⁹Ar dating of Chemeron Formation strata encompassing the site of hominid KNM-BC 1, Tugen Hills, Kenya. *Journal of Human Evolution*, **42**, 141-151.
- Deino, A. & McBrearty, S. 2002. ⁴⁰Ar/³⁹Ar dating of the Kapthurin Formation, Baringo, Kenya. *Journal of Human Evolution*, **42**, 185-210.
- Deino, A., Tauxe, L., Monaghan, M. & Hill, A. 2002. ⁴⁰Ar/³⁹Ar geochronology and paleomagnetic stratigraphy of the Lukeino and lower Chemeron Formations at Tabarin and Kapcheberek, Tugen Hills, Kenya. *Journal of Human Evolution*, **42**, 117-140.
- Deleuzene, L.K. & Kimbel, W.H. 2011. Evolution of the mandibular third premolar crown in early *Australopithecus*. *Journal of Human Evolution*, **60**, 711-730.
- Delson, E., Tattersall, I. & Van Couvering, J.A. 2000. *Encyclopedia of Human Evolution and Prehistory*. 2nd Edition, London and New York, Routledge, 753 pp.
- Feibel, C. 2003. Stratigraphy and depositional setting of the Pliocene Kanapoi Formation, Lower Kerio Valley, Kenya. In: Harris, J.M. & Leakey, M.G. (Eds) *Geology and Vertebrate Paleontology of the Early Pliocene Site of Kanapoi, Northern Kenya. Contributions in Science*, **498**, 9-20.
- Ferguson, W.W. 1984. Revision of fossil hominid jaws from the Plio-Pleistocene of Hadar, in Ethiopia, including a new species of the genus *Homo* (Hominoidea, Homininae). *Primates*, **25**, 519-529.
- Ferguson, W.W. 1986. The taxonomic status of *Praeanthropus africanus* (Primates: Pongidae) from the late Pliocene of eastern Africa. *Primates*, **27**, 485-492.
- Ferguson, W.W. 1987. Revision of the subspecies of *Australopithecus africanus* (Primates: Hominidae) including a new subspecies from the late Pliocene of Ethiopia. *Primates*, **28**, 258-265.
- Ferguson, W.W. 1989a. A new species of the genus *Australopithecus* (Primates: Hominidae) from Plio/Pleistocene deposits west of Lake Turkana in Kenya. *Primates*, **30**, 223-232.
- Ferguson, W.W. 1989b. Taxonomic status of the hominid mandible KNM-ER TI 13150 from the Middle Pliocene of Tabarin, in Kenya. *Primates*, **30**, 383-387.
- Ferguson, W.W. 1995. A new species of the genus *Homo* (Primates: Hominidae) from the Plio-Pleistocene of Koobi Fora, Kenya. *Primates*, **35**, 69-89.
- Gentry, A.W. 2010. Bovidae. In: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*. Berkeley, Los Angeles, London, University of California Press, pp. 741-796.
- Goodman, M., Czelusniak, J., Page, S. & Meireles, C.M. 2001. Where DNA sequences place *Homo sapiens* in a phylogenetic classification of Primates. In: Tobias, P.V., Raath, M.A., Moggi-Cecchi, J. & Doyle, G.A (Eds), *Humanity from African Naissance to Coming Millennia*. Firenze University Press, Witwatersrand University Press, pp. 279-289.
- Granger, D.E., Stratford, D., Bruxelles, L., Gibbon, R.J., Clarke, R.J. & Kuman, K. 2022. Cosmogenic nuclide dating of *Australopithecus* at Sterkfontein, South Africa. *Proceedings of the National Academy of Sciences: Earth, Atmospheric, and Planetary Sciences; Anthropology*, **119** (27), e2123516119, 7 pp.
- Gray, J.E. 1825. Outline of an attempt at the disposition of the Mammalia into tribes and families with a list of the genera apparently pertaining to each tribe. *Annals of Philosophy, New Series*, **10**, 337-344.
- Grine, F.E. 1989. New hominid fossils from the Swartkrans Formation (1979-1986 excavations): craniodental specimens. *American Journal of Physical Anthropology*, **79**, 409-449.
- Grine, F.E. 2004. Description and preliminary analysis of new hominid craniodental fossils from the Swartkrans Formation. In: Brain, C.K. (Ed.) *Swartkrans. A Cave's Chronicle of Early Man*. Transvaal Museum, Pretoria, Transvaal Museum Monograph, **8**, pp. 75-118.

- Grine, F.E., Ungar, P.S., Teaford, M.F. & El-Zaatari, S. 2006. Molar microwear in *Praeanthropus afarensis*: Evidence for dietary stasis through time and under diverse paleoecological conditions. *Journal of Human Evolution*, **51**, 297-319.
- Groves, C.P. & Mazák, V. 1975. An approach to the taxonomy of the Hominidae: gracile Villafranchian hominids of Africa. *Casopis pro Mineralogii Geologii*, **20**, 225-247.
- Gyenis, G. 2002. New findings - new problems in classification of hominids. *Acta Biologica Szegediensis*, **46** (1-2), 57-60.
- Haile-Selassie, Y. 2001. Late Miocene hominids from the Middle Awash, Ethiopia. *Nature*, **412**, 178-181.
- Haile-Selassie, Y., Gibert, L., Melillo, S.M., Ryan, T.M., Alene, M., Deino, A., Levin, N.E., Scott, G. & Saylor, B. 2015. New species from Ethiopia further expands Middle Pliocene hominin diversity. *Nature*, **521**, 483-488.
- Haile-Selassie, Y., Melillo, S.M. & Su, D.F. 2016. The Pliocene hominin diversity conundrum: Do more fossils mean less clarity? *Proceedings of the National Academy of Sciences of the United States of America*, **113** (23), 6364-6371.
- Haile-Selassie, Y., Saylor, B.Z., Alene, M., Deino, A., Gibert, L. & Schwartz, G.T. 2022. Comparative description and taxonomic affinity of 3.7-million-year-old hominin mandibles from Woranso-Mille (Ethiopia). *Journal of Human Evolution*, **173**, 1-29.
- Haile-Selassie, Y., Saylor, B.Z., Deino, A., Levin, N.E., Alene, M. & Latimer, B.M. 2012. A new hominin foot from Ethiopia shows multiple Pliocene bipedal adaptations. *Nature*, **483**, 565-569.
- 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.
- Haile-Selassie, Y., Suwa, G. & White, T.D. 2009. Hominidae. In: Haile-Selassie, Y. & WoldeGabriel, G. (Eds) *Ardipithecus kadabba: Late Miocene Evidence from the Middle Awash, Ethiopia*. Berkeley, University of California Press, pp. 159-236.
- Harrison, T. 2011. Hominins from the Upper Laetolil and Upper Ndolanya beds, Laetoli. In: Harrison, T. (Ed). *Paleontology and Geology of Laetoli: Human Evolution in Context*. Volume 2: *Fossil Hominins and the Associated Fauna*. Springer Science + Business Media B.V., pp. 141-188.
- Heberer, G. 1963. Über einen neuen archanthropinen Typus aus der Oldoway-Schlucht. *Zeitschrift für Morphologie und Anthropologie*, **53**, 171-177.
- Hennig, E. 1948. Quartärfaunen und Urgeschichte Ostafrikas. *Naturwissenschaftliche Rundschau*, **1**, (5), 212-217.
- Hill, A. 1985. Early hominid from Baringo District, Kenya. *Nature*, **315**, 222-224.
- Hill, A. 1986. The Tugen Hills Sequence: environmental change in the Late Miocene and Pliocene. In: *The Longest Record : The Human Career in Africa, A Conference in Honour of J. Desmond Clark*, Berkeley. Abstracts pp. 45-46.
- Hill, A. 1994. Late Miocene and Early Pliocene Hominoids from Africa. In: Corruccini, R.S. & Ciochon, R.L. (Eds) *Integrative Paths to the Past: Paleoanthropological Advances in Honour of F. Clark Howell*. Englewood Cliffs, NJ, Prentice Hall, pp. 123-145.
- Hill, A. 2002. Paleoanthropological research in the Tugen Hills, Kenya. *Journal of Human Evolution* **42**, 1-10.
- Hill, A., Drake, R., Tauxe, L., Monaghan, M., Barry, J.C., Behrensmeier, A.K., Curtis, G. Fine Jacobs, B., Jacobs, L., Johnson, N. & Pilbeam, D. 1985. Neogene palaeontology and geochronology of the Baringo Basin, Kenya. *Journal of Human Evolution*, **14**, 759-773.
- Hill, A. & Ward, S. 1988. Origin of the Hominidae: The record of African large hominoid evolution between 14 My and 4 My. *Yearbook of Physical Anthropology*, **31**, 49-83
- ICZN, 1999. Opinion 1941. *Australopithecus afarensis* Johanson, 1978 (Mammalia, Primates): specific name conserved. *Bulletin of Zoological Nomenclature*, **56** (3), 223-224.
- Johanson, D.C. 1978. In: Hinrichson, D. How old are our ancestors? *New Scientist*, **78** (1105), p. 571.
- Johanson, D.C., Lovejoy, C.O., Kimbel, W.H., White, T.D., Ward, S.C., Bush, M.E., Latimer, B.M. & Coppens, Y. 1982. Morphology of the Pliocene partial skeleton (AL 288-1) from the Hadar Formation, Ethiopia. *American Journal of Physical Anthropology*, **57**, 403-452.
- Johanson, D.C., White, T.D. & Coppens, Y. 1978. A new species of the genus *Australopithecus* (Primates, Hominidae) from the Pliocene of Eastern Africa. *Kirtlandia*, **28**, 2-14.

- Kimbel, W.H. 1988. Identification of a partial cranium of *Australopithecus afarensis* from the Koobi Fora Formation, Kenya. *Journal of Human Evolution*, **17**, 647-656.
- Kimbel, W.H. & Deleuzene, L.K. 2009. «Lucy» redux: A review of research on *Australopithecus afarensis*. *Yearbook of Physical Anthropology*, **52**, 2-48.
- Kimbel, W.H., Johanson, D., Rak, Y. 1994. The first skull and other new discoveries of *Australopithecus afarensis* at Hadar, Ethiopia. *Nature*, **368**, 449-451.
- Kimbel, W.H., Rak, Y. & Johanson, D.C. 2004. *The Skull of Australopithecus afarensis*. Oxford University Press, New York, 254 pp.
- Kissel, M. & Hawks, J. 2015. What are the Lothagam and Tabarin mandibles? *Paleoanthropology*, **2015**, 37-43. Doi:10.4207/PA.2015.ART94.
- Kretzoi, M. 1984. Note on *Homo leakeyi* Heberer. *Anthropologiai Közlemények*, **28**, 189-190.
- Kunimatsu, Y., Sawada, Y., Sakai, T., Saneyoshi, M., Nakaya, H., Yamamoto, A. & Nakatsukasa, M. 2017. The latest occurrence of the nyanzapithecines from the early Late Miocene Nakali Formation in Kenya, East Africa. *Anthropological Science*, **125** (2), 45-51.
- Latimer, B.M., Lovejoy, C.O., Johanson, D.C. & Coppens, Y. 1982. Hominid tarsal, metatarsal, and phalangeal bones recovered from the Hadar Formation: 1974-1977 collections. *American Journal of Physical Anthropology*, **57**, 701-719.
- Leakey, L.S.B. 1959. A new fossil skull from Olduvai. *Nature*, **184**, 491-493.
- Leakey, L.S.B., Tobias, P.V. & Napier, J.R. 1964. A new species of the genus *Homo* from Olduvai Gorge. *Nature*, **202**, 7-9.
- Leakey, M.G., Feibel, C.S., McDougall, I. & Walker, A. 1995. New four-million-year-old hominid species from Kanapoi and Allia Bay, Kenya. *Nature*, **376**, 565-571.
- Leakey, M.G., Spoor, F., Brown, F.H., Gathogo, P.N., Kiarie, C., Leakey, L.N. & McDougall, I. 2001. New hominin genus from eastern Africa shows diverse middle Pliocene lineages. *Nature*, **410**, 433-440.
- Linnaeus, C. 1758. *Systema Naturae per Regna Tria Naturae secundum Classes, Ordines, Genera, Species, cum Characteribus, Differentiis, Synonymis, Locis*. Holmiae, Laurentii Salvii, 824 pp.
- Lovejoy, C.O., Latimer B., Suwa, G., Asfaw, B. & White, T.D. 2009. Combining prehension and propulsion: The foot of *Ardipithecus ramidus*. *Science*, **326**, 72. DOI: 10.1126/science.1175832
- Macchiarelli, R., Bergeret-Medina, A., Marchi, D. & Wood, B. 2020. Nature and relationships of *Sahelanthropus tchadensis*. *Journal of Human Evolution*, **149**, 102898, 11 pp.
- MacLatchy, L.M., DeSilva, J., Sanders, W.J. & Wood, B. 2010. Hominini. In: Werdelin, L. & Sanders, W. (Eds). *Cenozoic Mammals of Africa*. Berkeley, Los Angeles, London, University of California Press, pp. 471-540.
- Mbua, E., Kusaka, S., Kunimatsu, Y., Geraads, D., Sawada, Y., Brown, F.H., Sakai, T., Boissarie, J.-R., Saneyoshi, M., Omuombo, C., Muteti, S., Hirata, T., Hayashida, A., Iwano, H., Danhara, T., Bobe, R., Jicha, B. & Nakatsukasa, M. 2016. Kantis: a new *Australopithecus* site on the shoulders of the Rift Valley near Nairobi, Kenya. *Journal of Human Evolution*, **94**, 28-44.
- McBrearty, S. & Jablonski, N.G. 2005. First fossil chimpanzee. *Nature*, **437**, 105-108.
- McDougall, I., Brown, F.H., Vasconcelos, P.M., Cohen, B.E., Thiede, D.S. & Buchanan, M.J. 2012. New single crystal ⁴⁰Ar/³⁹Ar ages improve time scale for deposition of the Omo Group, Omo-Turkana Basin, East Africa. *Journal of the Geological Society, London*, **169**, 213-226.
- Mocke, H., Pickford, M., Senut, B. & Gommery, D. 2022. New information about African late middle Miocene to latest Miocene (13-5.5 Ma) African Hominoidea. *Communications of the Geological Survey of Namibia*, **24**, 33-66.
- Moggi-Cecchi, J., Grine, F. & Tobias, P. 2006. Early hominid dental remains from Members 4 and 5 of the Sterkfontein Formation (1966-1996 excavations): Catalogue, individual associations, morphological descriptions and initial metric analysis. *Journal of Human Evolution*, **50**, 239-328.
- Moggi-Cecchi, J., Menter, C., Boccone, S. & Keyser, A. 2010. Early hominid dental remains from the Plio-Pleistocene site of Drimolen, South Africa. *Journal of Human Evolution*, **58**, 374-405.
- Namwamba, F. 1993. *Tephrostratigraphy of the Chemeron Formation, Baringo Basin, Kenya*, MSc. Thesis, University of Utah, Salt Lake City, 78 pp.
- Pickford, M. 1975. *Stratigraphy and Palaeoecology of Five Late Cainozoic Formations in the Kenya Rift Valley*. PhD Thesis, University of London, 219 pp.

- Pickford, M. 2004. Incisor-molar relationships in chimpanzees and other hominoids: implications for diet and phylogeny. *Primates*, **46**, 21-32.
- Pickford, M. 2005a. Orientation of the foramen magnum in Late Miocene to extant African apes and hominids. Jan Jelinek Commemorative volume. *Anthropologie*, **43**, 103-110.
- Pickford, M. 2005b. Fossil hyraxes (Hyracoidea, Mammalia) from the Late Miocene and Plio-Pleistocene of Africa, and the phylogeny of the Procaviidae. *Palaeontologia Africana*, **41**, 141-161.
- 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. 2013. The diversity, age, biogeographic and phylogenetic relationships of Plio-Pleistocene suids from Kromdraai; South Africa. *Annals of the Ditsong National Museum of Natural History*, **3**, 1-32.
- Pickford, M., Coppens, Y., Senut, B., Morales, J. & Braga J. 2009. Late Miocene hominoid from Niger. *Comptes Rendus Palevol*, **8**, 413-425.
- Pickford, M., Johanson, D., Lovejoy, C., White, T. & Aronson, J. 1983. A hominoid humeral fragment from the Pliocene of Kenya. *American Journal of Physical Anthropology*, **60**, 337-346.
- Pickford, M. & Kanimatsu, Y. 2005. Anthropoids from the Middle Miocene (ca 14.5 Ma) of Kipsaraman, Tugen Hills, Kenya. *Anthropological Science*, **113**, 189-224.
- Pickford, M. & Obada, T. 2016. Pliocene suids from Musaitu and Dermenji, Moldova: implications for understanding the origin of African *Kolpochoerus* Van Hoepen & Van Hoepen, 1932. *Geodiversitas*, **38** (1), 99-134.
- Pickford, M. & Senut, B. 2005a. 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. 2005b. Implications of the presence of African ape-like teeth in the Miocene of Kenya. In: D'Errico, F. & Backwell, L. (Eds) *From Tools to Symbols: From Early Hominids to Modern Humans*. Johannesburg, Witwatersrand University Press, pp. 121-133.
- Pickford, M., Senut, B. & Cheboi, K. 2009. The Geology and Palaeobiology of the Tugen Hills, Kenya: Rift tectonics, basin formation, volcanics and sediments. *Geo-Pal Kenya*, **1**, 4-133.
- Pickford, M., Senut, B., Gommery, D. & Treil, J. 2002. Bipedalism in *Orrorin tugenensis* revealed by its femora. *Comptes Rendus Palevol*, **1**, 191-203.
- Pickford, M., Senut, B., Morales, J. & Braga, J. 2008. First hominoid from the Late Miocene of Niger. *South African Journal of Science*, **104**, 337-339.
- Pickford, M., Senut, B. & Mourer-Chauviré, C. 2004. Early Pliocene Tragulidae and Peafowls in the Rift Valley, Kenya: evidence for rainforest in East Africa. *Comptes Rendus Palevol*, **3**, 179-189.
- Prentice, M.L. & Denton, G.H. 1998. The deep-sea oxygen isotope record, the global Ice Sheet system, and hominid evolution. In: Grine, F. (Ed.) *Evolutionary History of the "Robust" Australopithecines*. New York, Aldine de Gruyter, Chapter 24, pp. 383-403.
- Rak, Y., Kimbel, W.H., Moggi-Cecchi, J., Lockwood, C.A. & Menter, C. 2021. The DNH 7 skull of *Australopithecus robustus* from Drimolen (Main Quarry), South Africa. *Journal of Human Evolution*, **151**, 102913, 43 pp.
- Sanders, W.J., Gheerbrant, E., Harris, J.M., Saegusa, H. & Delmer, C. 2010. Proboscidea. In: Werdelin, L. & Sanders, W.J. (Eds) *Cenozoic Mammals of Africa*. Berkeley, Los Angeles, London, University of California Press, pp. 161-253.
- Sawada, Y., Pickford, M., Senut, B., Itaya, T., Hyodo, M., Miura, T., Kashine, C., Chujo, C. & Fujii, H. 2002. The age of *Orrorin tugenensis*, an early hominid from the Tugen Hills, Kenya. *Comptes Rendus Palevol*, **1**, 293-303.
- Semaw, S., Simpson, S.W., Quade, J., Renne, P.R., Butler, R.F., McIntosh, W.C., Levin, N., Dominguez-Rodrigo, M. & Rogers, M.J. 2005. Early Pliocene hominids from Gona, Ethiopia. *Nature*, **433**, 301-305.
- Senut, B. 1983. Quelques remarques à propos d'un humérus d'hominoïde pliocène provenant de Chemeron (bassin du lac Baringo, Kenya). *Folia primatologica*, **41**, 267-276.

- Senut, B. 1995. D'*Australopithecus* à *Praeanthropus* ou du respect du Code de Nomenclature. *Annales de Paléontologie, (Vertebrata-Invertebrata)*, **81** (4), 279-281.
- Senut, B. 1996. Pliocene hominid systematics and phylogeny. *South African Journal of Science*, **92**, 165-166.
- 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, Genève*, **37** (2), 577-591.
- 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, D. & Ségalen, L. 2017. Palaeoenvironments and the origins of bipedalism. *Historical Biology, Special Issue - Tribute to Percy Milton Butler*, **30** (1-2), 284-296.
- Senut, B. & Tardieu, C. 1985. Functional aspects of Plio-Pleistocene hominid limb bones : implications for taxonomy and phylogeny. In: Delson, E. (Ed.) *Ancestors : The Hard Evidence*. New York, Alan Liss, pp 193-201.
- Şenyürek, M.S. 1955. A note on the teeth of *Meganthropus africanus* Weinert from Tanganyika Territory. *Türk Tarih Kurumu Belleten*, **19**, 47-85.
- Sherwood, R.J., Ward, S.C. & Hill, A. 2002a. The taxonomic status of the Chemeron temporal (KNM-BC 1). *Journal of Human Evolution*, **42**, 153-184.
- Sherwood, R.J., Ward, S.C., Hill, A., Duren, D.L., Brown, B. & Downs, W. 2002b. Preliminary description of the *Equatorius africanus* partial skeleton (KNM-TH 28860) from Kipsaramon, Tugen Hills, Baringo District, Kenya. *Journal of Human Evolution*, **42**, 63-73.
- Simpson, S.W., Levin, N.E., Quade, J., Rogers, M.J. & Semaw, S. 2019. *Ardipithecus ramidus* postcrania from the Gona Project area, Afar Regional State, Ethiopia. *Journal of Human Evolution*, **129**, 1-45.
- Skinner, M.M., Leakey, M.G., Leakey, L.N., Manthi, F.K. & Spoor, F. 2020. Hominin dental remains from the Pliocene localities at Lomekwi, Kenya (1982-2009). *Journal of Human Evolution*, **145**, Article 102820.
- Spoor, F., Leakey, M.G. & O'Higgins, P. 2016. Middle Pliocene hominin diversity *Australopithecus deyiremeda* and *Kenyanthropus platyops*. *Philosophical Transactions of the Royal Society B Biological Sciences*, **371**, doi.org/10.1098/rstb.2015.0231.
- Stern, J.T. 2000. Climbing to the top: A personal memoir of *Australopithecus afarensis*. *Evolutionary Anthropology*, **9** (3) 113-133.
- Stern, J.T. & Susman, R.L. 1983. The locomotor anatomy of *Australopithecus afarensis*. *American Journal of Physical Anthropology*, **60**, 279-317.
- Suwa, G., Kono, R.T., Simpson, S.W., Asfaw, B., Lovejoy, C.O. & White. T.D. 2009. Paleobiological implications of the *Ardipithecus ramidus* dentition. *Science*, **326**, 69 + 94-99.
- Tobias, P.V. 1980a. "*Australopithecus afarensis*" and *A. africanus*: Critique and an alternative hypothesis. *Palaeontologia Africana*, **23**, 1-17.
- Tobias, P.V. 1980b. A survey and synthesis of the African hominids of the Late Tertiary and Early Quaternary Periods. In: Königsson, L.K. (Ed.), *Current Argument on Early Man*, pp. 86-113. Report from a Nobel Symposium. Oxford, New York, Toronto, Sydney, Paris, Frankfurt, Pergamon Press.
- Trinkaus, E. & Patel, B.A. 2016. An Early Pleistocene human pedal phalanx from Swartkrans, SKX 16699, and the antiquity of the human lateral foot. *Comptes Rendus Palevol*, **15**, 978-987.
- Villmoare, B. 2018. Early *Homo* and the role of the genus in paleoanthropology. *Yearbook of the American Journal of Physical Anthropology*, **165**, 72-89.
- Villmoare, B., Kimbel, W.H., Seyoum, C., Campisano, C.J., DiMaggio, E.N., Rowan, J., Braun, D.R., Arrowsmith, J. R. & Reed, K.E. 2015. Early *Homo* at 2.8 Ma from Ledi-Geraru, Afar, Ethiopia. *Science*. **347** (6228), 1352-1355.
- Ward, C.V., Leakey, M.G., Brown, B., Brown, F., Harris, J. & Walker, A. 1999b. South Turkwell: a new Pliocene hominid site in Kenya. *Journal of Human Evolution*, **36**, 69-95.
- Ward, C.V., Leakey, M.G. & Walker, A. 2001. Morphology of *Australopithecus anamensis* from Kanapoi and Allia Bay, Kenya. *Journal of Human Evolution*, **41**, 255-368.
- Ward, S., Brown, B., Hill, A., Kelley, J. & Downs, W. 1999a. *Equatorius*: A new hominoid genus from the Middle Miocene of Kenya. *Science*, **285**, 1382-1386.

- Ward, S. & Hill, A. 1987. Pliocene hominid partial mandible from Tabarin, Baringo, Kenya. *American Journal of Physical Anthropology*, **72**, 21-37.
- Watson, E.E., Penny, D. & Eastale, S. 2001. *Homo* genus: a review of the classification of humans and great apes. In: Tobias, P.V., Raath, M.A., Moggi-Cecchi, J. & Doyle, G.A. (Eds), *Humanity from African Naissance to Coming Millennia: Colloquia in Human Biology and Palaeoanthropology*. Firenze, Firenze University Press, pp. 307-318.
- Weinert, H. 1950. Über die neuen Vor- und Frühmenschenfunde aus Afrika, Java, China und Frankreich. *Zeitschrift für Morphologie und Anthropologie*, **42**, 113-148.
- White, T.D. 1980. Additional fossil hominids from Laetoli, Tanzania: 1976-1979 specimens. *American Journal of Physical Anthropology*, **53**, 487-504.
- White, T.D. & Johanson, D. 1982. Pliocene hominid mandibles from the Hadar Formation, Ethiopia: 1974-1977 collections. *American Journal of Physical Anthropology*, **57**, 501-544.
- 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 Science of the USA*. **112**, (16), 4877-4884 + Supplementary information, pp. 1-7.
- White, T.D., Suwa, G. & Asfaw, B. 1994. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature*, **371**, 306-312.
- White, T.D., Suwa, G. & Asfaw, B. 1995. Corrigendum. *Australopithecus ramidus*, a new species of early hominid from Aramis, Ethiopia. *Nature*, **375**, 88.
- WoldeGabriel, G., Endle, T., White, T.D., Thouvenay, N., Hart, W.K., Renne, P.R. & Asfaw, B. 2013. The role of tephra studies in African paleoanthropology as exemplified by the Sidi Hakoma Tuff. *Journal of African Earth Sciences*, **77**, 41-58.
- Wolpoff, M., Senut, B., Pickford, M. & Hawks, J. 2002. Palaeoanthropology (communication arising): *Sahelanthropus* or *Sahelpithecus*? *Nature*, **419**, 581-582.
- Wood, B.A. & Leakey, M. 2011. The Omo-Turkana Basin fossil hominins and their contribution to our understanding of human evolution in Africa. *Evolutionary Anthropology*, **20**, 264-292.
- Zanolli, C., Davies, T.W., Joannes-Boyau, R., Beaudet, A., Bruxelles, L., de Beer, F., Hoffman, J., Hublin, J.-J., Jakata, K., Kgasi, L., Kullmer, O., Macchiarelli, R., Pan, L., Schrenk, F., Santos, F., Stratford, D., Tawane, M., Thackeray, F., Xing, S., Zipfel, B. & Skinner, M. 2022. Dental data challenge the ubiquitous presence of *Homo* in the Cradle of Humankind. *Proceedings of the National Academy of Sciences, Anthropology*, **119** (28), 11 pp. + supplementary information. doi.org/10.1073/pnas.2111212119.
- Zeitoun, V. 2000. Révision de l'espèce *Homo erectus* (Dubois, 1893) – Utilisation des données morphologiques et métriques en cladistique, reconsidération du cas *Homo erectus*. *Bulletins et Mémoires de la Société d'Anthropologie de Paris*, n.s. **12** (1-2), 1-200.
- Zhang, Y. & Harrison, T. 2016. *Gigantopithecus blacki*: a giant ape from the Pleistocene of Asia revisited. *Yearbook of the American Journal of Physical Anthropology*, **162**, 153-177.
- Zihlman, A., Bolter, D. & Boesch, C. 2004. Wild chimpanzee dentition and its implications for assessing life history in immature hominin fossils. *Proceedings of the National Academy of Sciences of the United States of America*, **101** (29), 10541-10543.