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NEW PLIOCENE HOMINID FOSSILS FROM BARINGO COUNTY, KENYA

We dedicate this paper to the late Kiptalam Cheboi, who discovered many important fossils during his long career as a fossil hunter.

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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 5.0 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

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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 (Text-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 (Ward et al. 1999a, Sherwood et al. 2002b, Pickford and Kunimatsu 2005). Other fossil hominoid specimens are known from the Ngorora Formation (between 13.2 and 10.3 Ma) (Pickford and Senut 2005a, b), the Lukeino Formation (6.2–5.7 Ma) (Senut et al. 2001, 2018, Sawada et al. 2002), the Toluk Beds of the Kaparaina Formation (ca. 5.7–5.3 Ma) (Pickford et al. 2009b), the Mabaget Formation (5.1–3.0 Ma) (Pickford et al. 1983, Ward and Hill 1987, Hill and Ward 1988), the Chemeron Formation (2.4–1.7 Ma) (Deino and Hill 2002, Sherwood et al. 2002a) and the Kapthurin Formation (0.8–0.4 Ma) (Deino and McBrearty 2002) (Text-fig. 1).

The only hominid specimens previously reported from the Mabaget Formation (Text-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 and Hill 1987, Boaz 1988, Ferguson 1989b, Deino et al. 2002, Kissel and 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

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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. 2009b). This formation is of basal to mid-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 (Text-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 4.0 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 × breadth 25.5 mm; m/3 length 70 mm × 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 MacLatchy 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. 2009b) 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.

Material and methods

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 (Tab. 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 camparisons and for compiling the length/breadth bivariate plots (Text-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 juntion at wear facets or at breaks in the crowns.

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

Catalogue no.	Anatomy	Locality	Age	Collector
KNM BC 1745	Proximal humerus	2/211, Mabaget	5.0–4.5 Ma	Martin 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

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

Text-figs 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. 2009b). 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. 2009b) 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. 2009b).

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 and 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).

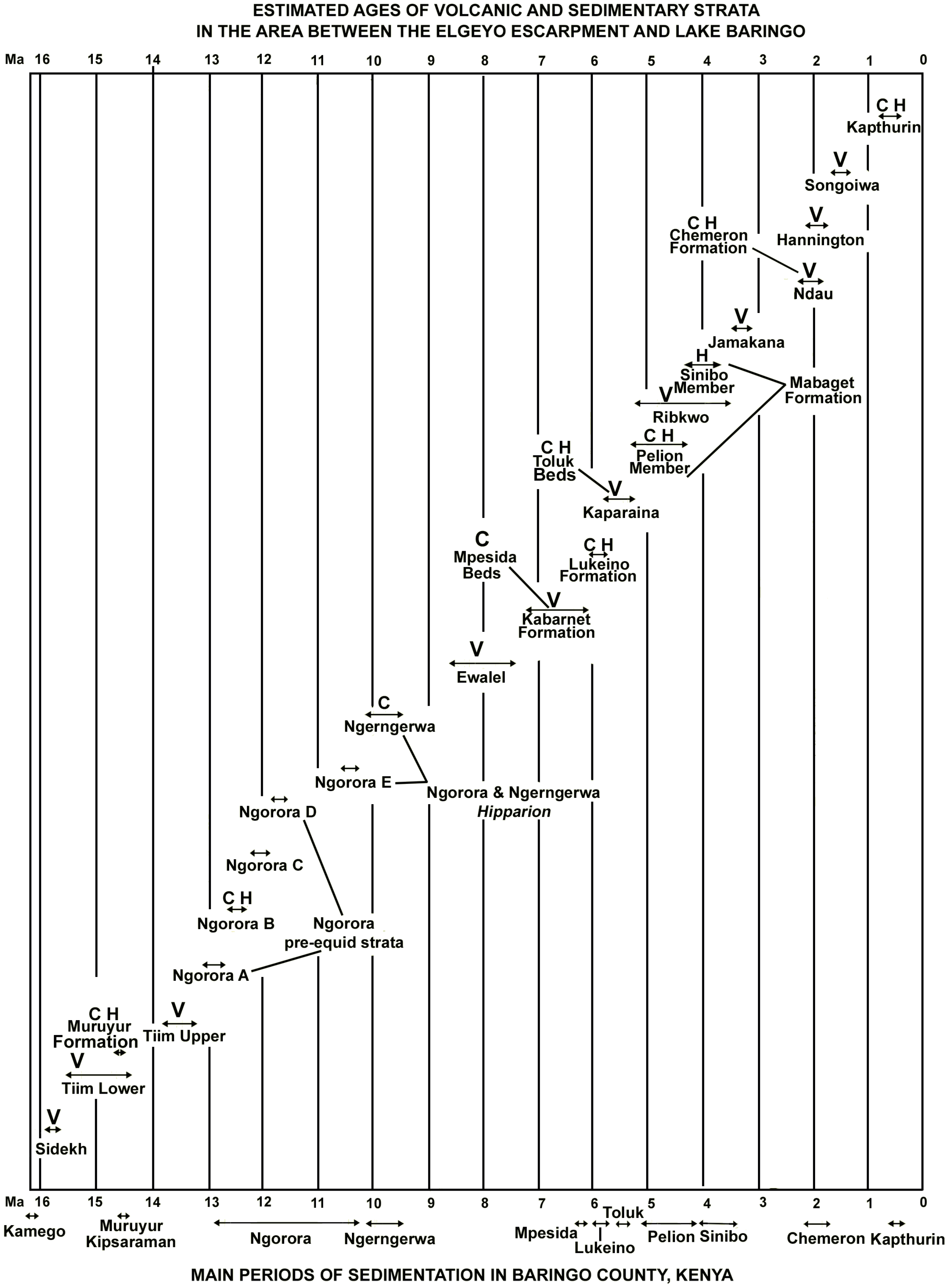
In this paper, the authors define Hominoidea as a superfamily of catarrhines comprising extant humans, gorillas, chimpanzees and orang-utans, as well as gibbons and siamangs (Hylobatidae) and diverse fossil lineages of Oligo-Miocene to Pleistocene age which are more closely related to these extant genera 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 is the quantity of species epithets that have been proposed for African Plio-Pleistocene hominids (Tab. 3) (Gyenis 2002, Bonde 2011). We provide a full list in order that the readers can assess the publications and decide the issues for themselves.

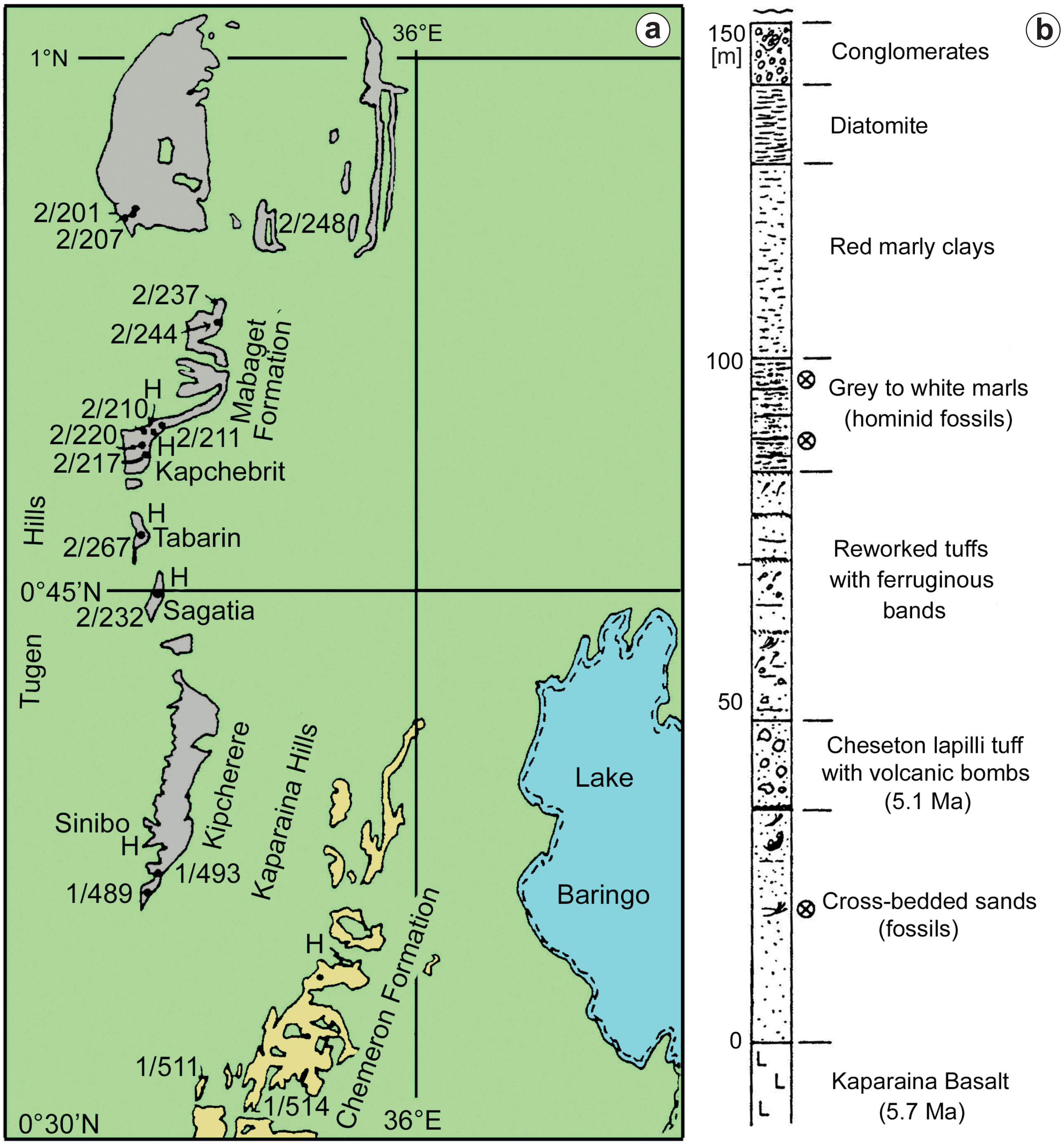
Because the fossils described herein occur several, to tens of, metres above dated tuffs, there is a certain degree of uncertainty about their precise correlation to the Geological Time Scale. Instead of the terms Early and Late Pliocene (with the adjectives in capital letters) in this paper we employ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

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 type species/specimen available).

Nomen	Proposed by	Type specimen	Age (Ma)
Australopithecus africanus	Dart 1925	Taung 1	2.8–2.6
Plesianthropus transvaalensis	Broom 1936	TM 1511 + STS 60	2.5–2.15
Paranthropus robustus	Broom 1938	TM 1517	2.0–1.7
Australopithecus prometheus	Dart 1948	MLD 1	3.2–2.9
Praeanthropus	Hennig 1948	nn	3.8–3.5
Telanthropus capensis	Broom and Robinson 1949a; see also Broom and Robinson 1949b	SK 15	1.8–1.5
Paranthropus crassidens	Broom 1949; see also Broom 1952, Broom and Robinson 1952	SK 6	1.8–1.5
Meganthropus africanus	Weinert 1950	Garussi 1	3.8–3.5
Atlanthropus mauritanicus	Arambourg 1954	1954-7-825, Ternifine 1 (Atl 1)	1.6–1.4
Praeanthropus	Şenyürek 1955	Garussi 1	3.8–3.5
Zinjanthropus boisei	Leakey 1959	OH 5	1.8–1.2
Homo leakeyi	Heberer 1963	OH 9	1.8–1.5
Homo habilis	Leakey et al. 1964	OH 7	1.8–1.5
Paraustralopithecus aethiopicus	Arambourg and Coppens 1968; see also Arambourg and Coppens 1967	OMO 18-1967-18	2.6–2.3
Homo ergaster	Groves and Mazák 1975	KNM ER 992	1.9–1.5
Australopithecus afarensis	Johanson in Hinrichson 1978	LH 4	3.8–3.5
Australopithecus africanus afarensis	Tobias 1980a	nn	3.4–3.0
Australopithecus africanus aethiopicus	Tobias 1980a	nn	3.4–3.0
Australopithecus africanus tanzaniensis	Tobias 1980b	nn	3.8–3.5
Homo antiquus	Ferguson 1984	AL 288-1	3.4–3.0
Homo (*Proanthropus*) *louisleakeyi*	Kretzoi 1984	OH 9	1.8–1.5
Homo rudolfensis	Alexeev 1986	KNM ER 1470	1.9
Australopithecus africanus miodentatus	Ferguson 1987	AL 266-1	3.8–3.5
Australopithecus walkeri	Ferguson 1989a	KNM WT 17000	2.5
Homo antiquus praegens	Ferguson 1989b	KNM TH 13150	4.5–4.4
Ardipithecus ramidus	White et al. 1994 (as *Australopithecus*); assigned to *Ardipithecus* by White et al. 1995	ARA-VP-6/1	4.5–4.3
Homo microcranous	Ferguson 1995	KNM ER 1813	1.65
Australopithecus anamensis	Leakey et al. 1995	KNM KP 29281	4.2–3.8
Australopithecus bahrelghazali	Brunet et al. 1996	KT12/H1	?3.5
Australopithecus garhi	Asfaw et al. 1999	BOU-VP-12/130	2.5
Homo okotensis	Zeitoun 2000	KNM ER 3883	2.0–1.4
Homo kenyaensis	Zeitoun 2000	KNM ER 3733	1.9
Orrorin tugenensis	Senut et al. 2001	OCO BAR 1000’00	6.2–5.8
Kenyanthropus platyops	Leakey et al. 2001	KNM WT 40000	3.6–3.3
Sahelanthropus tchadensis	Brunet et al. 2002	TM 266-01-060-1	?7.0
Ardipithecus ramidus kadabba	Haile-Selassie et al. 2004	ALA-VP-2/10	5.8–5.2
Homo hadar	Bonde and Westergarde 2004	AL 333-45	3.3
Praeanthropus lothagamensis	Bonde and Westergarde 2004	KNM LT 329	5.0–4.2
Australopithecus sediba	Berger et al. 2010	MH 1	1.9–1.8
Homo gautengensis	Curnoe 2010	STW 53	?3.5–3.0
Afaranthropus antiquus	Bonde 2011	AL 288-1	3.4–3.0
Australopithecus deyiremeda	Haile-Selassie et al. 2015	BRT-VP-3/1	3.5–3.3



Text-fig. 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.



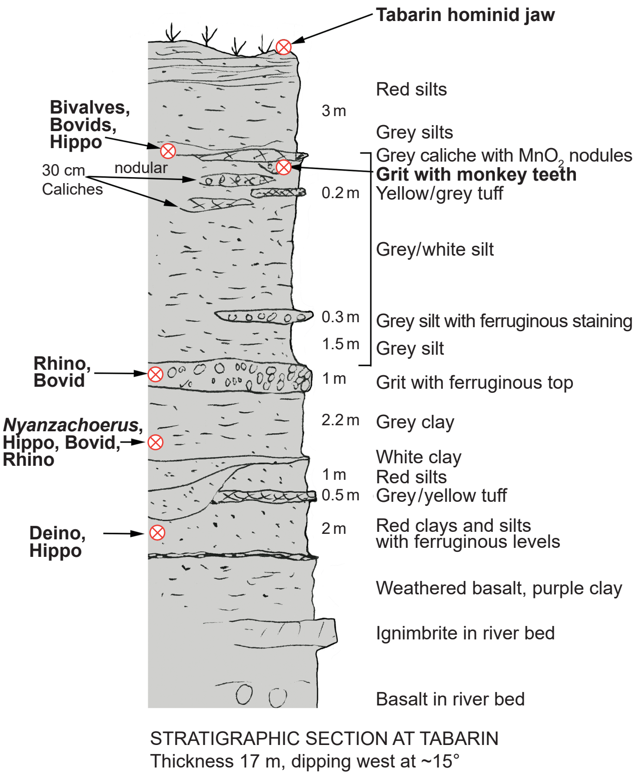
Text-fig. 2. Geographic distribution of the Mabaget (grey) and Chemeron (yellow) formations (a), and type section of the Pelion Member at locality 2/210 (b), showing the position of the Mabaget hominid fossils. (Green represents the Kaparaina Basalts and other rock units, both older and younger than 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, Pickford et al. 2009).

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 (Tabs 2, 3).

Abbreviations

BAR	Baringo
BC	Baringo Chemeron
BPRP	Baringo Paleontological Research Project
KNM	Kenya National Museums, Nairobi, Kenya
KPE	Kenya Palaeontology Expedition
OCO	Orrorin Community Organisation, Kipsaraman, Kenya
TH	Tugen Hills



Text-fig. 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).

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 upper Pliocene to Recent age (Text-figs 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 (Text-fig. 2) and the succession spans the period 5.1–4.7 Ma, and the type section of the Sinibo Member (Text-fig. 11) is in the Kipcherere badlands and spans the period 3.5–3.0 Ma with a capping of Pleistocene deposits.

The geographic extent of the Mabaget and Chemeron formations is depicted in Text-fig. 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.

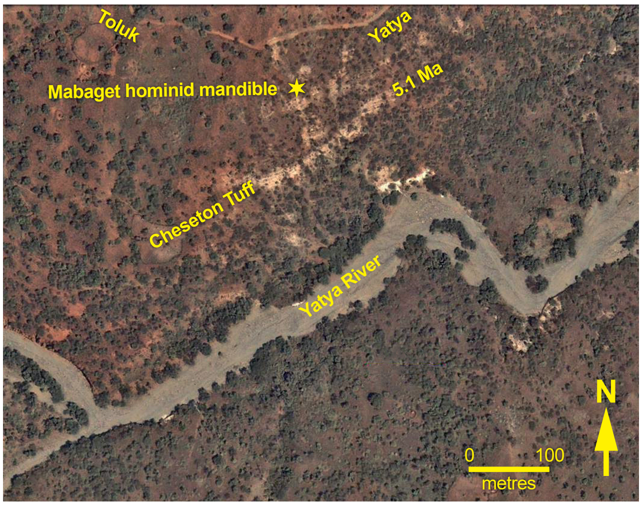
Locality 2/211 (Mabaget, BPRP K037) is close to the Yatya-Toluk 4×4 vehicle track at 00°48′58.8″ N, 35°52’05.9″ E (1,210 m altitude). The nearby locality of Pelion at 00°49′10.1″ N, 35°52′22.9″ E (1,210 m altitude) (= locality 2/210, the place name means “Elephant” in the Tugen dialect of Kalenjin) is beside the same track and yielded a lower third premolar of a hominid.

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

Ostracoda	
	Indet.
Mollusca	
Gastropoda	
	Viviparidae
	Bellamya unicolor
	Ampullariidae
	Pila ovata
	Thiariidae
	Melanoides tuberculata
Bivalvia	
	Unionidae
	Coelatura hauttecoeuri
	Iridinidae
	Cameronia mohariensis
	Chambardia trapezia
Pisces	
	Clariidae
	Indet.
	Cichlidae
	Indet.
	Cyprinidae
	Barbus sp.
Reptilia	
Chelonii	
	Trionychidae
	cf. *Trionyx* sp.
	Pelomedusidae
	Indet.
	Testudinidae?
	Indet.
Crocodilia	
	Crocodylidae
	Crocodylus sp.
Aves	
	Phasianidae
	Pavo sp.
	Anhingidae
	Anhinga sp. (large)
Mammalia	
Chiroptera	
	Molossidae
	Indet.
Insectivora	
	Soricidae
	Indet.
Carnivora	
	Ursidae
	Agriotherium aecuatorialis
	Mustelidae
	Sivaonyx ekecaman

Table 4. continued

	Hyaenidae
	Ikelohyaena abronia
	Hyaenictitherium namaquensis
	Hyaenictis hendeyi
	Viverridae
	Civettictis howelli
	Herpestidae
	Indet.
Primates	
	Galagidae
	Galago sadimanensis
	Cercopithecidae
	Indet.
	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 deheinzelini*)
	Tragulidae
	Hyemoschus aquaticus
	Giraffidae
	Sivatherium sp.

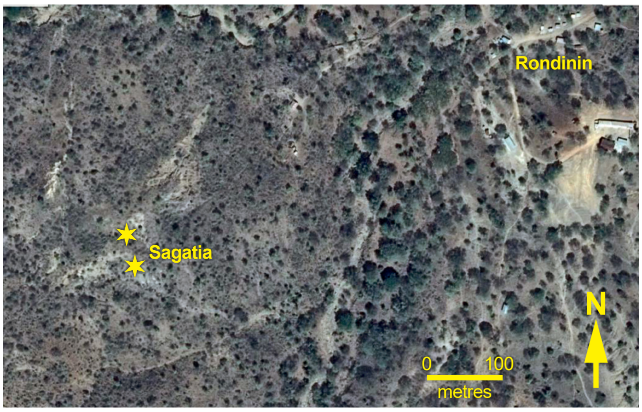


Text-fig. 4. Location of the Mabaget hominid fossil site (2/211). The position and age of the Cheseton Lapilli Tuff are highlighted. Map modified from Google Earth.

The co-ordinates of locality 2/267 (= BPRP 77) that yielded the Tabarin hominid mandible (Text-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 (Text-fig. 3).

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.

Text-fig. 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.



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

The Sinibo locality is at 00°37′36.4″ N, 35°52′28.9″ E (1,245 m altitude) near Kipcherere (Place of Vervet Monkeys in Tugen) and Uswonin (Pickford et al. 2009b).

The mammalian fauna from the lower sections of the Mabaget Formation (i.e., the Pelion Member) (Tab. 4) is of middle Pliocene aspect, with species such as *Dasychoerus arvernensis*, *Nyanzachoerus jaegeri*, *Anancus kenyensis*, *Agriotherium aecuatorialis* and *Sivaonyx ekecaman* (Pickford et al. 2009b, Pickford and Obada 2016). An age range of ca. 5.0–4.5 Ma is estimated for these lower beds (Pickford 2013).

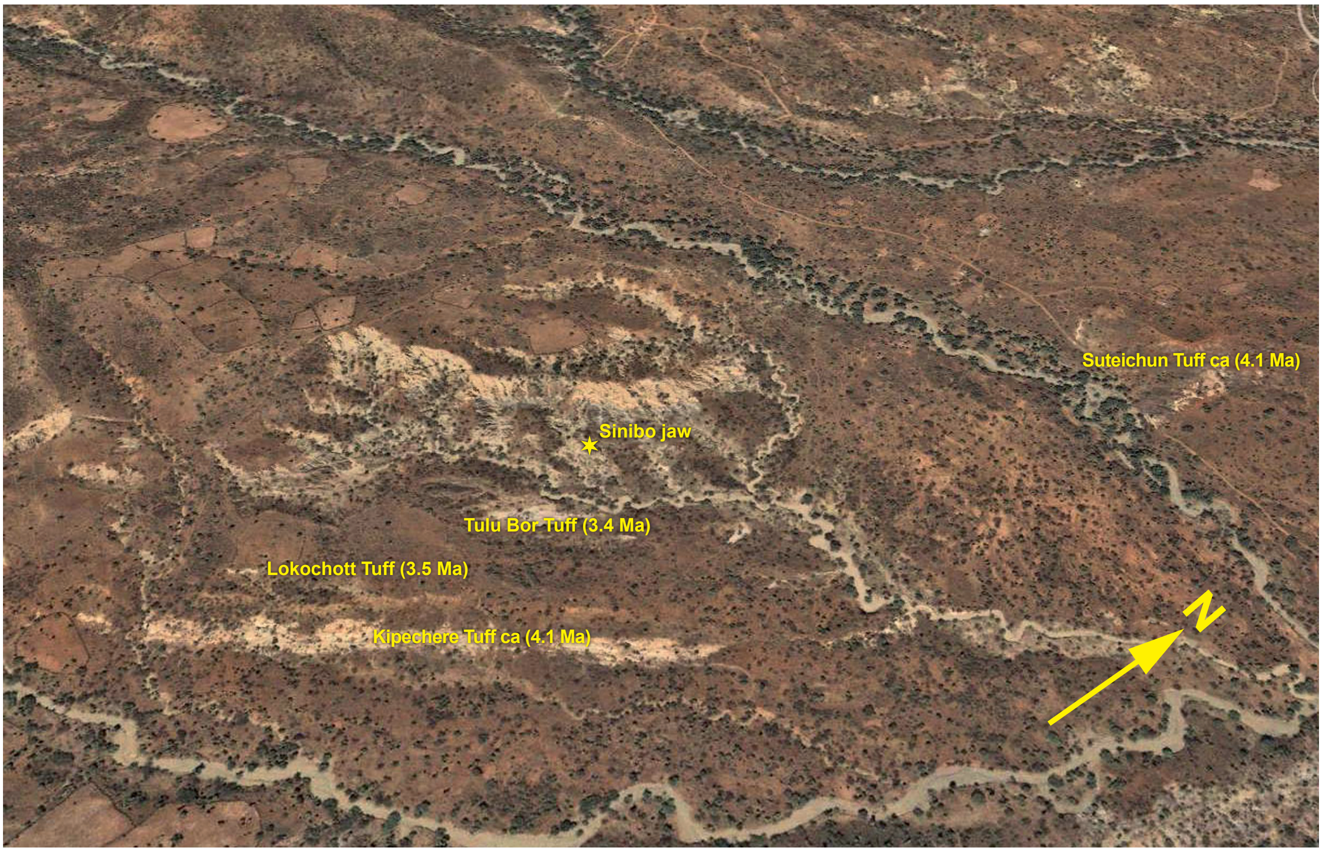
The higher levels of the Mabaget Formation (i.e., the Sinibo Member) yield a more advanced fauna than the Mabaget Member, comprising, among other taxa, the nyanzachoerine suid, *Nyanzachoerus kanamensis* from the base of the section and a large kolpochoerine suid (several mandible fragments and isolated 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 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
	Paracolobus chemeroni
	Hominidae
	Praeanthropus afarensis
Proboscidea	
	Elephantidae
	Elephas africanavus
Perissodactyla	
	Rhinocerotidae
	Ceratotherium praecox
	Diceros bicornis
Artiodactyla	
	Suidae
	Nyanzachoerus kanamensis
	Kolpochoerus heseloni (*olduvaiensis*)
	Giraffidae
	Giraffa cf. *jumae*
	Bovidae
	Syncerus sp.
	Taurotragus sp.
	Menelikia lyrocera or *M. leakeyi*
	Gazella sp. (2–3 spp.)

In the type area of the Mabaget Formation (Text-figs 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

Text-fig. 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).

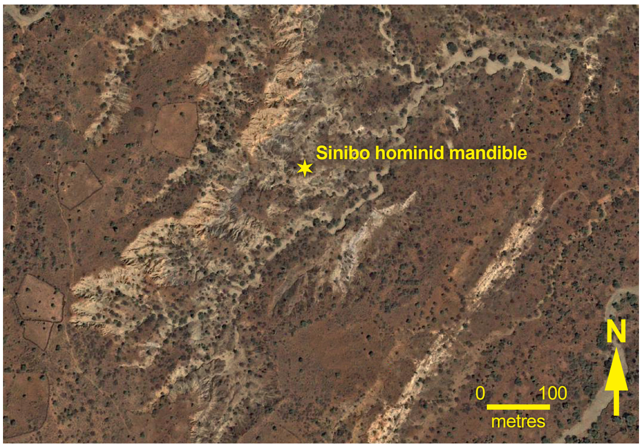


Text-fig. 8. Discovery locus of the Sinibo mandible in the badlands close to Kipcherere, Baringo County, Kenya. Oblique view from Google Earth highlighting the outcrops of tuffs.

(OCO BAR 1046’11 and KNM BC 1745) are thus likely to be ca. 5.0–4.5 Ma.

The Sagatia hominid fossils were collected from the gulley system 500 metres southwest of Rondinin Village (Text-figs 6, 7).

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 (Brown 1982, 1994, Namwamba 1993, Feibel 2003, WoldeGabriel et al. 2013) (Text-figs 8–10).



Text-fig. 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.

Palaeoenvironment

The lowermost strata of the Mabaget Formation (older than 4.0 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 afromontane 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 africanavus* and gazelles.

Systematic palaeontology

Order Primates Linnaeus, 1758
Superfamily Hominoidea Gray, 1825
Family Hominidae Gray, 1825

Genus *Orrorin* Senut, Pickford, Gommery, Mein, Cheboi et Coppens, 2001

Orrorin praegens (Ferguson, 1989b)

Text-figs 12–16

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

Text-fig. 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 Text-fig. 11).

13150, mandible with m/1–m/2; KNM BC 1745, proximal humerus.

Descriptions. **The D4/.** OCO BAR 151'10 is an isolated right D4/ crown in medium wear (Text-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.

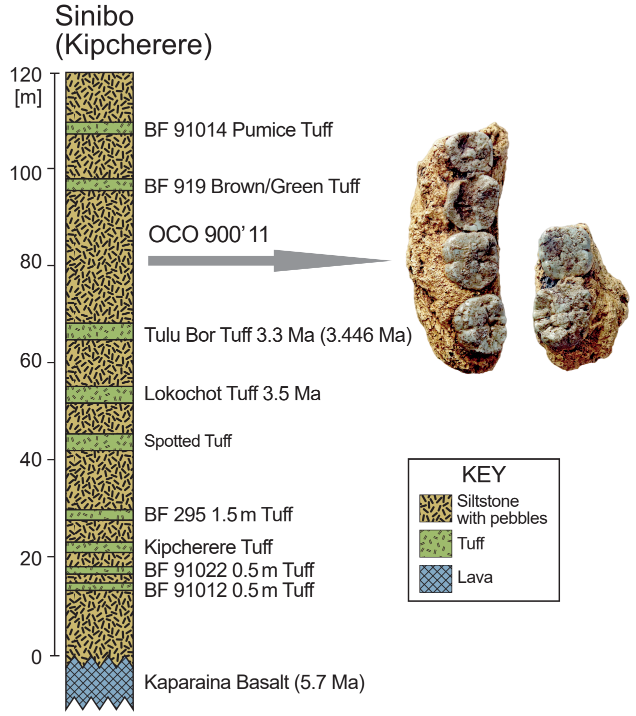
In occlusal view the largest cusp is the protocone followed by subequal paracone and hypocone and a smaller metacone. As a consequence of the different cusp sizes, the occlusal outline of the tooth is trapezoidal rather than square, the lateral surface of the metacone slanting disto-lingually at an angle 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.



Text-fig. 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.

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 (Text-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 postcristids as well as a broad cristid leading lingually towards the very reduced metaconid. This lingual cristid (protocristid in Ferguson 1984; transverse crest in Delezene and 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 preprotocristid (mesial protoconid crest in Delezene and Kimbel 2011), and a smaller stylid at the disto-buccal end of the postprotocristid (distal protoconid crest in Delezene and 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 postprotocristid 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, indicting that there was no honing function between it and the upper canine. The wear facet at the apex of the protoconid slopes gently lingually.

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 (Text-figs 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.

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).

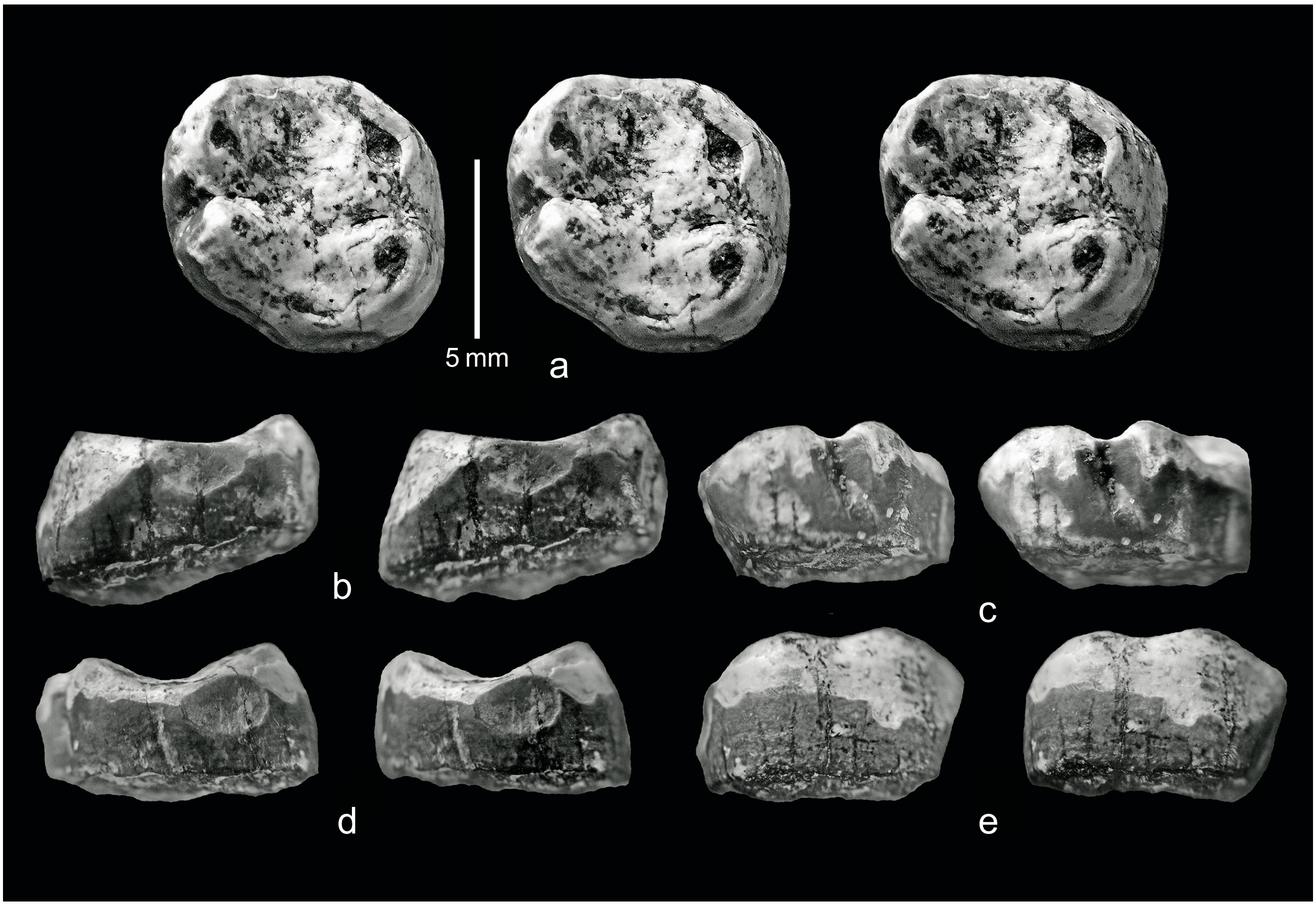
The protoconid is the largest cusp, the metaconid being about half its dimensions and the entoconid or distal cingulum low and small. The protoconid has three main cristids; a preprotocristid extending mesio-lingually to terminate in the mesial midline of the crown, a broad postprotocristid leading distally 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.

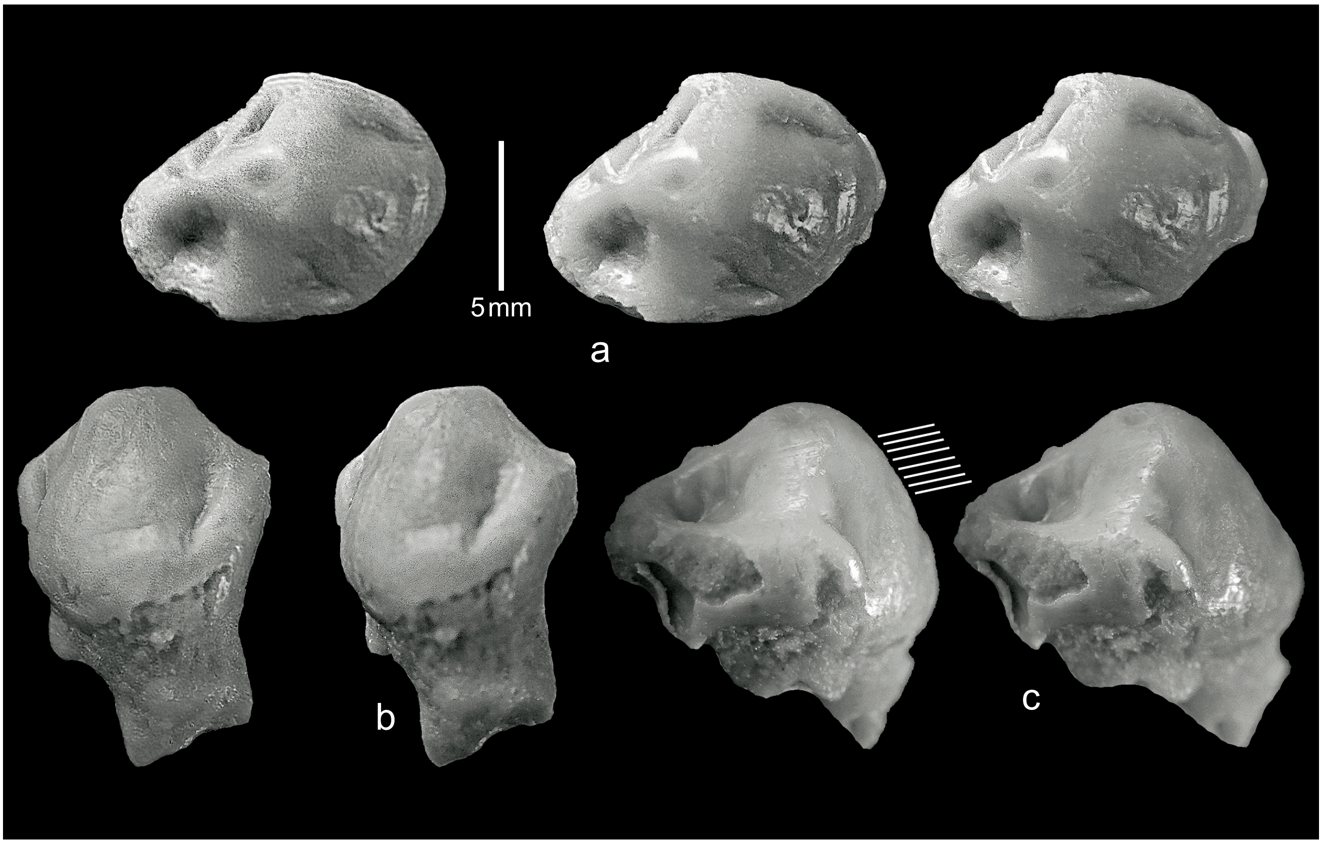
Wear in the p/4 is almost planar, horizontal, leaving low crown relief.

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.

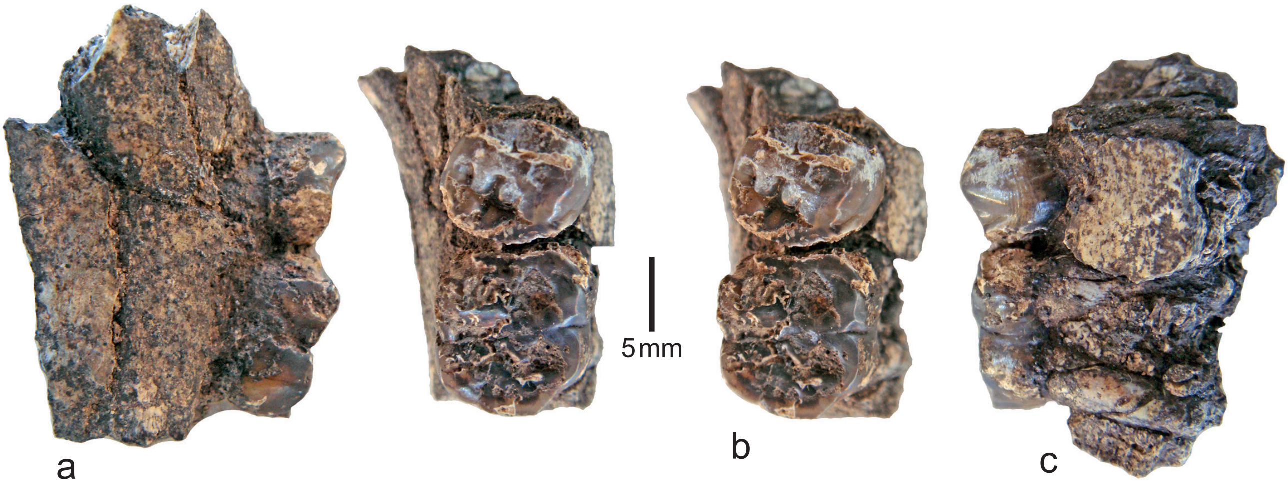
The m/1. The lower first molar in mandible OCO BAR 1046'11 is almost rectangular in occlusal contour. The tooth has five main cusps, large protoconid and hypoconid, with bucco-lingually narrower metaconid and entoconid, and a small hypoconulid positioned distally in the midline of the tooth. There is 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.



Text-fig. 12. Stereo images of OCO BAR 151'10, right D4/ of *Orrorin praegens* from Sagatia, Tugen Hills, Baringo County, Kenya. a: occlusal view; b: mesial view; c: buccal view; d: distal view; e: lingual view.



Text-fig. 13. Stereo images of OCO BAR 1'08, cast of right p/3 of *Orrorin praegens* 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).



Text-fig. 14. OCO BAR 1046’11, right mandible fragment containing p/4–m/1 of *Orrorin praegens* from locality 2/211, Pelion Member, Tugen Hills, Kenya. a: lingual view; b: stereo occlusal view; c: buccal view.

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.

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 no.	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

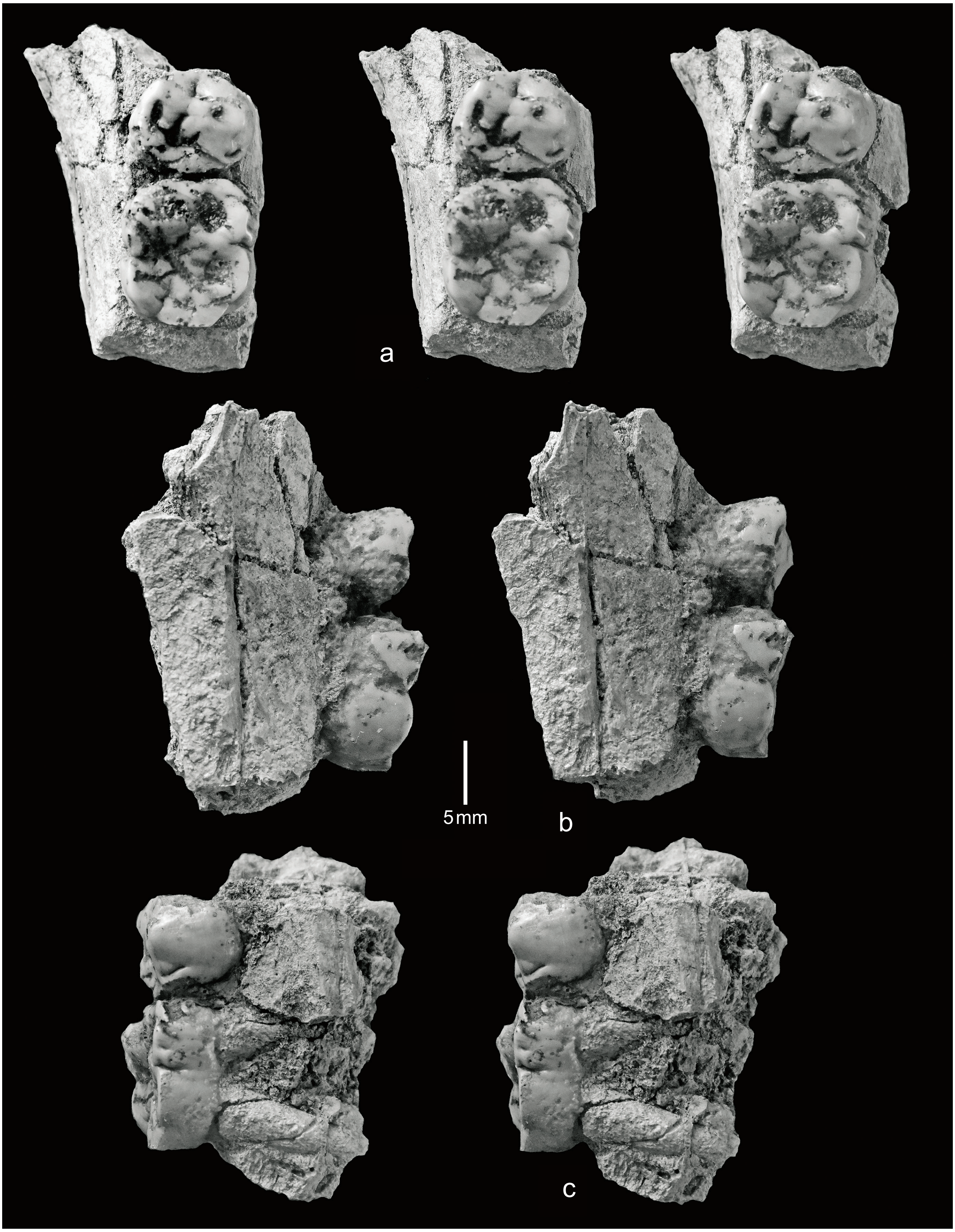
The m/3. The lower third molar collected at Sagatia in 2005 (OCO BAR 500’05) has lost enamel from the lingual, mesial and part of the buccal sides, but retains much of the occlusal enamel cap (Text-fig. 16). The tooth is lightly worn, the main cusps being clearly delineated by the intercuspal groove 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.

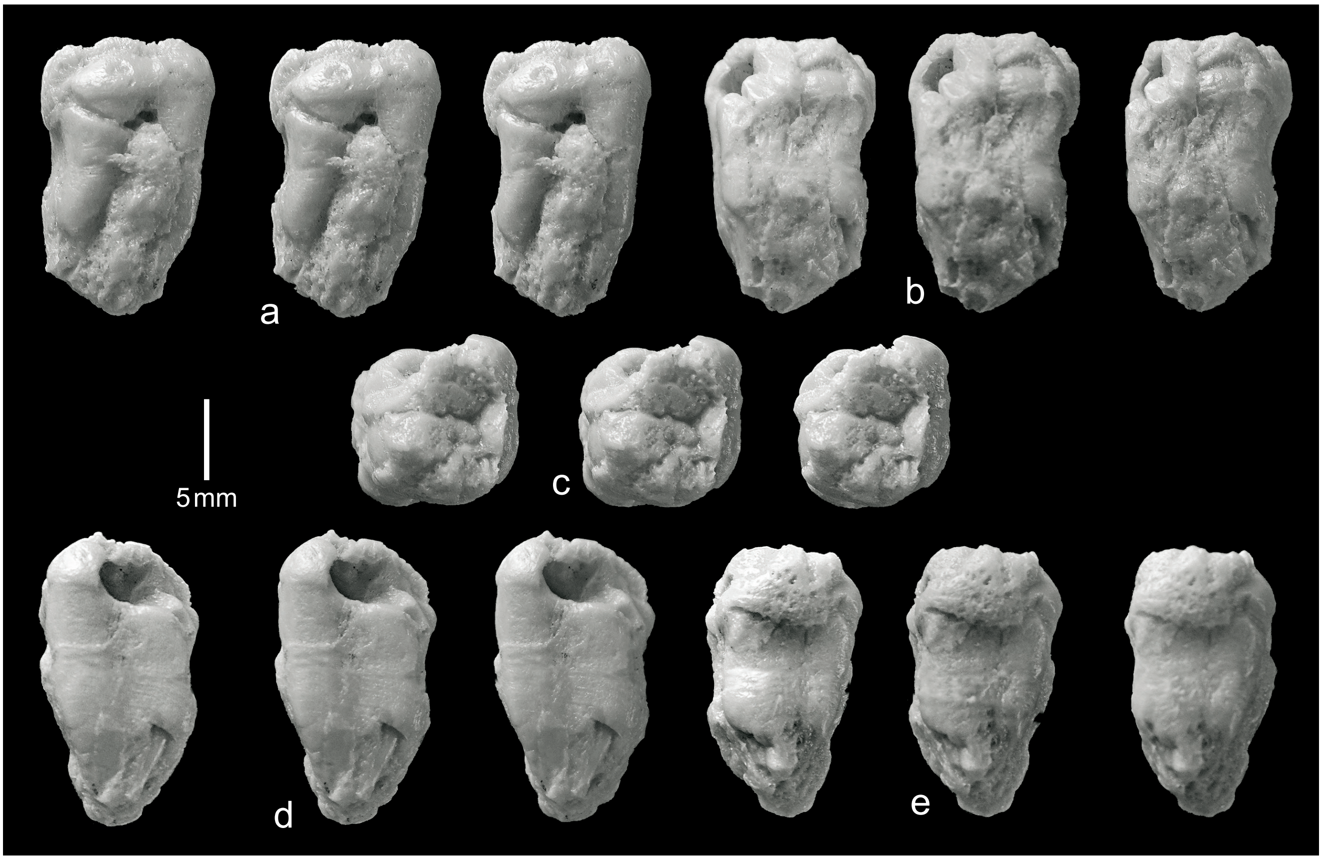
Comparisons and interpretation. The trapezoidal outline of the crown of the D4/ (OCO BAR 151’10) the mesial overhang of the crown and the thin enamel indicate that this is a deciduous tooth. The lingual position of the distal interstitial wear facet caused by rubbing against the M1/, also suggests that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

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



Text-fig. 15. Stereo images of OCO BAR 1046'11, cast of right mandible fragment of *Orrorin praegens* containing p/4–m/1 from locality 2/211, Pelion Member, Tugen Hills, Baringo County, Kenya. a: occlusal view; b: lingual view; c: buccal view.

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

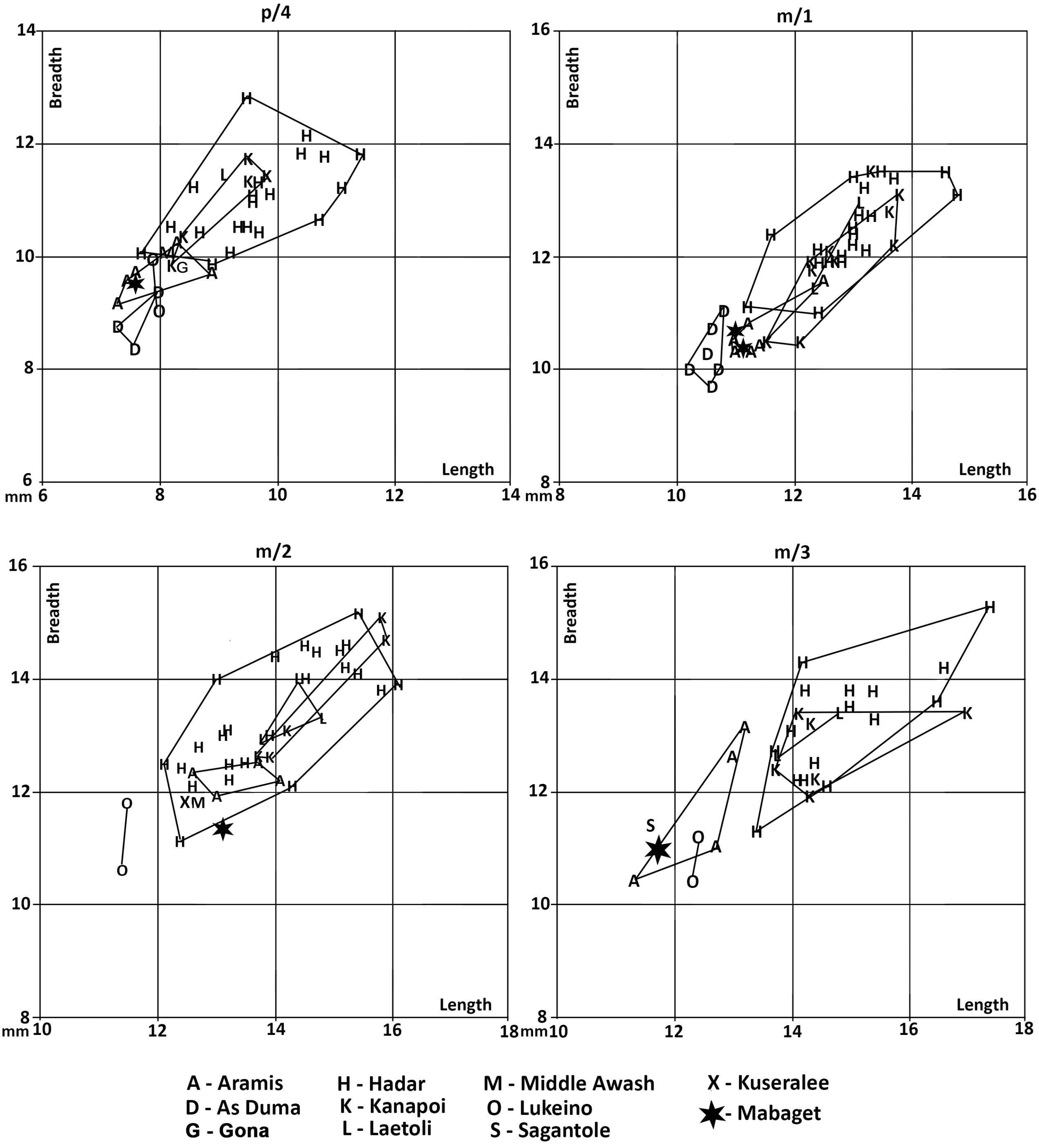


Text-fig. 16. Stereo images of a cast of OCO BAR 500'05, left m/3 of *Orrorin praegens* from Sagatia, Pelion Member, Tugen Hills, Baringo County, Kenya. a: lingual view; b: buccal view; c: occlusal view; d: mesial view; e: distal view.

and *Homo* (Delezene and Kimbel 2011). Thus, this p/3 in 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 (1985) and Ward and 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 (1989b) 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 primary homonym of *Homo antiquus* Adloff, 1908, and is thus invalid (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 (i.e., 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 and 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



Text-fig. 17. Bivariate plots of lower cheek teeth of hominids from the Mabaget Formaton and other Late Miocene to mid-Pliocene localities in Eastern Africa.

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 1989b) 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) (Text-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, 2018) 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.

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 (Text-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 12.0 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 (Text-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. 2004), but not with any of the specimens of the latter taxon from the type locality, Laetoli (White 1980, Harrison 2011) 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, 2018). Ferguson (1989b) 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 6.0 million years 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 × 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

Text-fig. 18

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) (Text-fig. 18). The dimensions of this fossil accord with measurements of proximal pedal phalanges of other Mio-Pliocene hominids (Tab. 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 (Text-fig. 18c) 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 and 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 (Text-fig. 18a, e).

In plantar view (Text-fig. 18e) 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

Text-fig. 18. Stereo images of OCO BAR 150'10, hominid pedal phalanx from Sagatia, Baringo County, Kenya. a: dorsal view; b: medial view; c: proximal view; d: distal view; e: plantar view; f: lateral view.

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 (Text-fig. 18f), the lateral proximal plantar tubercle forms a smooth transition with the moderately convex lateral edge of the proximal articular facet. In medial view (Text-fig. 18b) the medial proximal plantar tubercule 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 (Text-fig. 18e) 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 and 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.

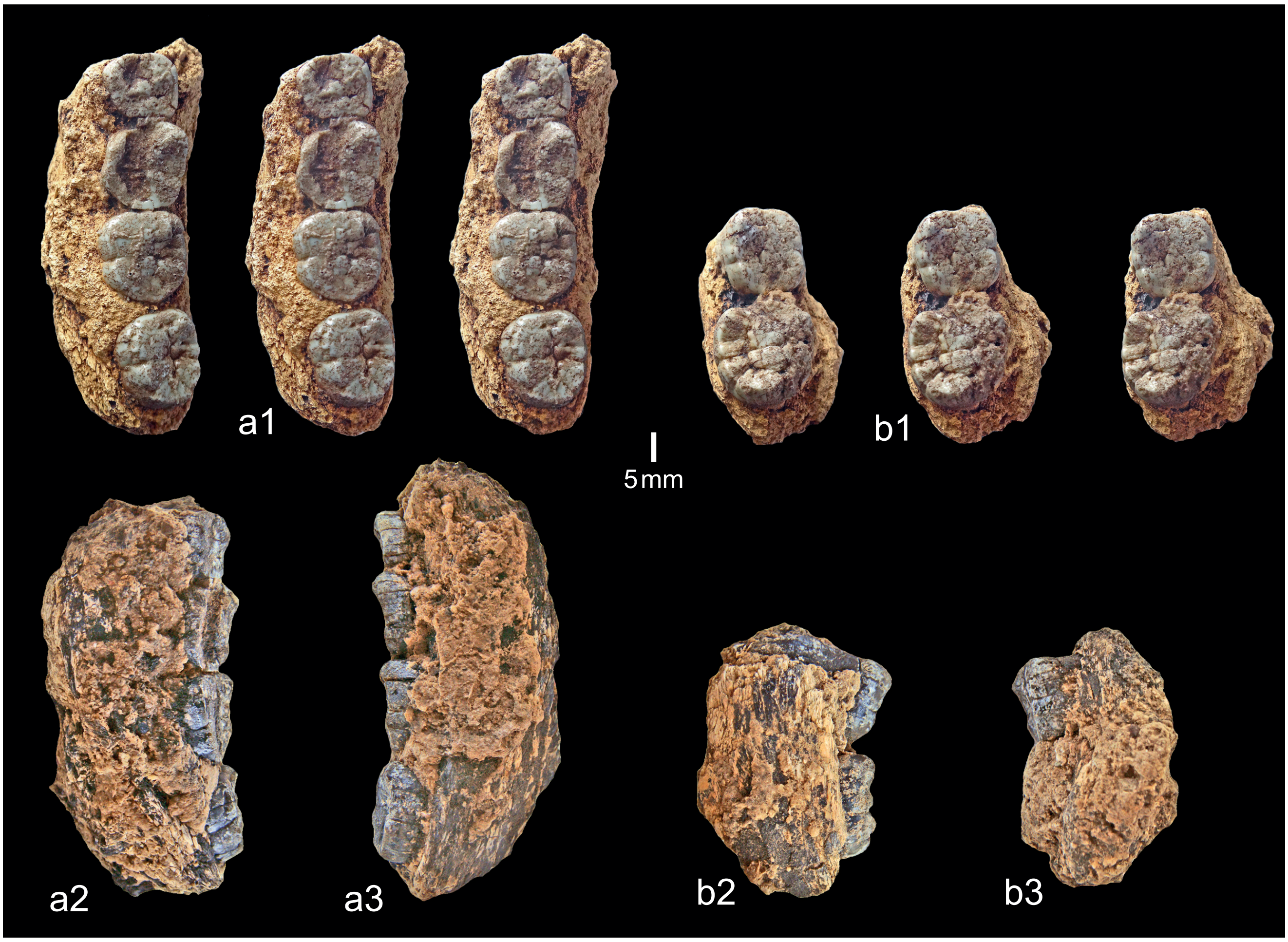
In dorsal and plantar views of OCO BAR 150'10, the distal extremity presents a relatively broad aspect compared to the proximal extremity (Text-fig. 18a, e) in contrast to chimpanzees, and it thereby resembles more closely the A.L.333 Hadar specimens. In dorsal view (Text-fig. 18a) the distal extremity 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 (Text-fig. 18d) the medial condyle of the trochlea is narrower and more salient disto-plantarly 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 3.0 Ma hitherto represented by only a few specimens from Ethiopia (Haile-Selassie 2001, Semaw et al. 2005, Haile-Selassie et al. 2009, 2012, Lovejoy et al. 2009, 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 (Stern and Susman 1983, Aiello and Dean 1990, Stern 2000, Haile-Selassie et al. 2012) 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

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 no.	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 et al. 1982. Trinkaus et al. 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 et al. 1982
A.L. 333-60	proximal phalanx	27.9	10.9	10.0	8.2	6.0	Latimer et al. 1982
A.L. 333-71	proximal phalanx	32.5	10.0	9.3	8.0	5.7	Latimer et al. 1982
A.L. 333-102	proximal phalanx	30.5*	10.6*	10.2*	9.3	5.7	Latimer et al. 1982
A.L. 333-115(G)	second proximal phalanx	32.2	11.5	9.4	9.4	6.6	Latimer et al. 1982
A.L. 333-115(H)	third proximal phalanx	34.5	13.6	10.6	9.0	5.7	Latimer et al. 1982
A.L. 333-115(I)	fourth proximal phalanx	32.8	11.7	10.0	9.0	6.0	Latimer et al. 1982
A.L. 333-115(J)	fifth proximal phalanx	28.6	10.1	8.9	8.0	5.4	Latimer et al. 1982
BRT-VP-2/73d	fourth proximal phalanx	28.74	10.25	8.6	7.9	5.4	Haile-Selassie et al. 2012
BRT-VP-2/73e	second proximal phalanx	29.0	10.9	9.6	7.95	5.3	Haile-Selassie et al. 2012
AME-VP-1/71	left fourth proximal phalanx	31.9	?	?	?	?	Haile-Selassie et al. 2009
ARA-VP-6/500-094	left fourth proximal phalanx	35.4	10.7	8.6	8.0	6.3	Lovejoy et al. 2009
GWM67/P2u	left fifth proximal phalanx	32.4	11.2	9.5	?	?	Simpson et al. 2019
StW 355	proximal phalanx	23.4	9.1	8.0	6.8	4.9	Trinkaus and Patel 2016
SKX 16699	proximal phalanx	18.6	8.9	8.6	6.9	4.8	Trinkaus and Patel 2016
DNH-117	proximal phalanx	22.2	10.3	9.2	7.5	5.1	Trinkaus and Patel 2016



Text-fig. 19. OCO BAR 900'11, mandible fragments of *Praeanthropus afarensis* from Sinibo, Tugen Hills, Kenya, prior to cleaning. a: left mandible, a1 – stereo occlusal view, a2 – buccal view, a3 – lingual view; b: right mandible, b1 – stereo occlusal view, b2 – lingual view, b3 – buccal view.

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.

Genus *Praeanthropus* Şenyürek, 1955

Praeanthropus afarensis (Johanson, 1978)

Text-figs 19, 20

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

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

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 (Text-figs 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 26.0 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.

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 (Tab. 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.

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 (Text-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

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

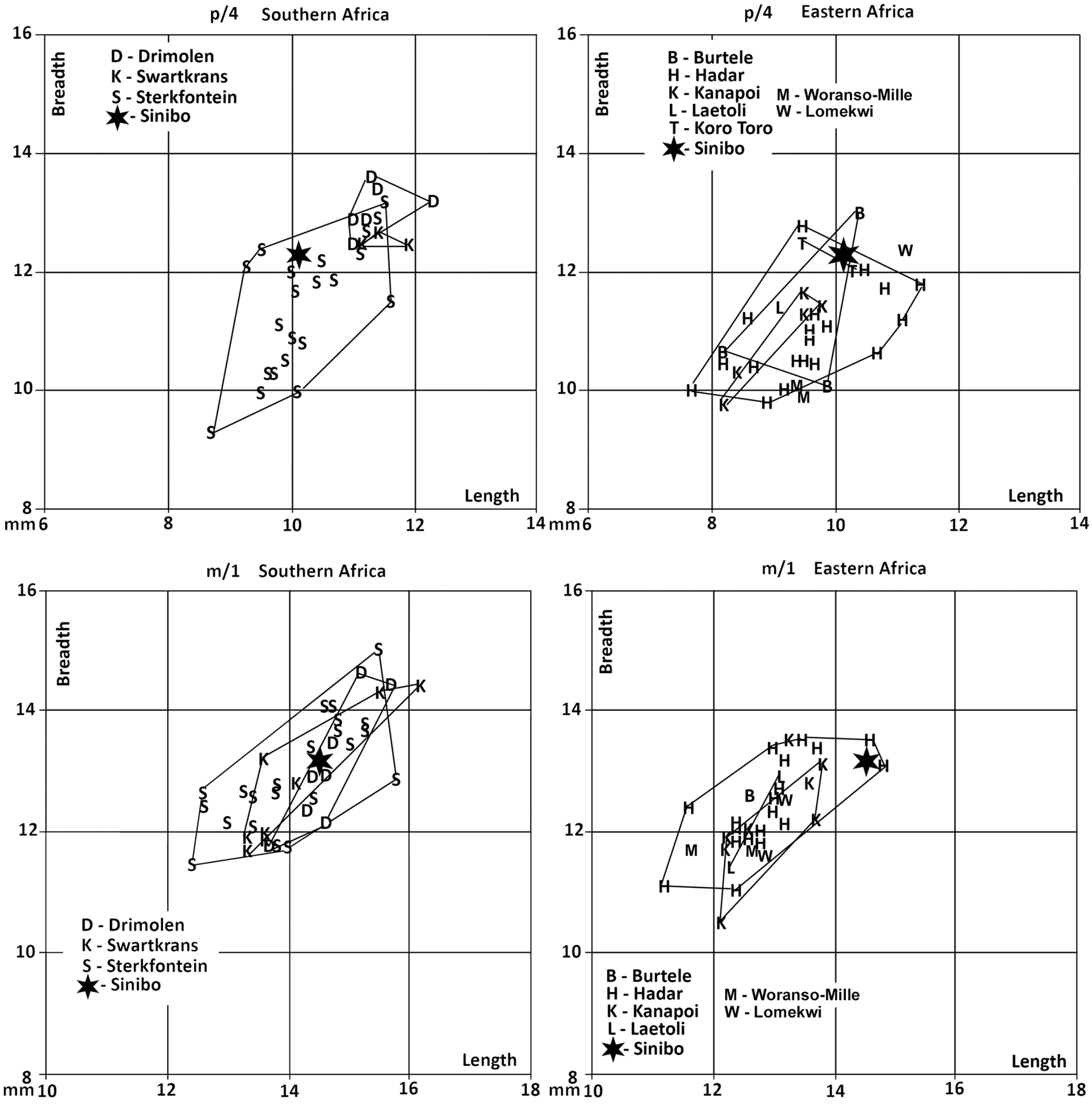
Tooth	Mesio-distal length	Bucco-lingual breadth
p/4 left	10.1	12.3
m/1 left	14.5	13.2
m/2 left	14.8	14.7
m/3 left	15.8	14.7
m/2 right	15.2	15.2
m/3 right	17.0	15(e)

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 and 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.

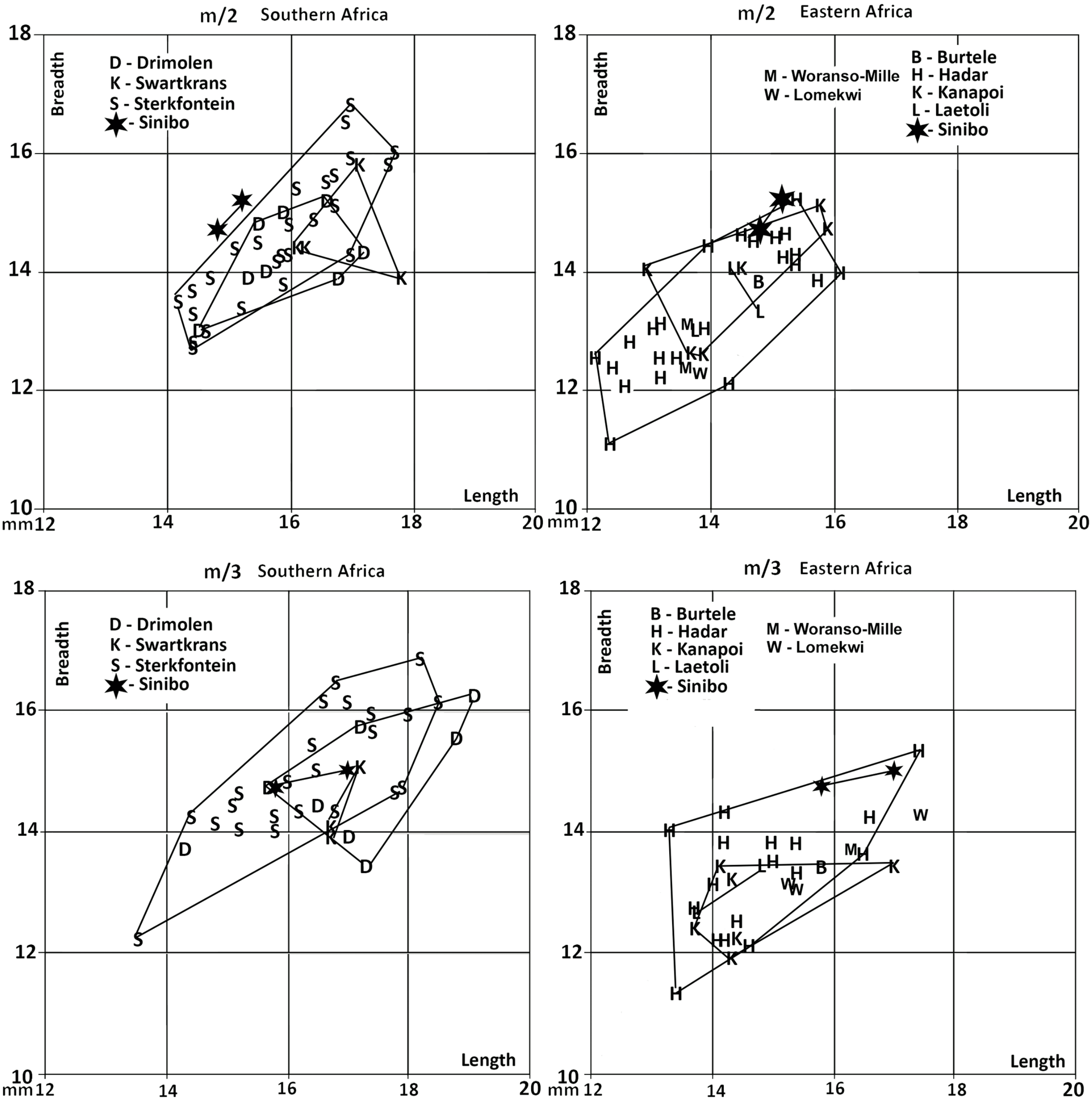
The roots of the molar in the left mandible are not visible, but damage to the body of the right mandible has exposed the mesio-lingual root of the m/2. The root is stout and tall (15.2 mm) compared to the preserved crown height (7.3 mm).

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* (Text-figs 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 1989, 1993) 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



Text-fig. 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).



Text-fig. 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).

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 1993, 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.

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

The m/2s from Sinibo are smaller than any of the specimens from Swartkrans and most of the specimens from Sterkfontein (Grine 1989, 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).

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 and 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 (Text-figs 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 (Tab. 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).

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 and Delezene 2009, Wood and 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 (Text-figs 23–25). For example, the Tabarin mandible has been attributed to *Australopithecus*, *Praeanthropus* and *Ardipithecus* (respectively by Hill 1985, Cela-Conde and Ayala 2003, and Bonde 2011). *Orrorin* has been declared a synonym of *Praeanthropus* by Cela-Conde and 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 and 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 et WESTERGARDE, 2004 and *Afaranthropus antiquus* (FERGUSON, 1984) by Bonde (2011). In the opinions of Ferguson (1984, 1987) and Bonde (Bonde and 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) and Ferguson (1986).

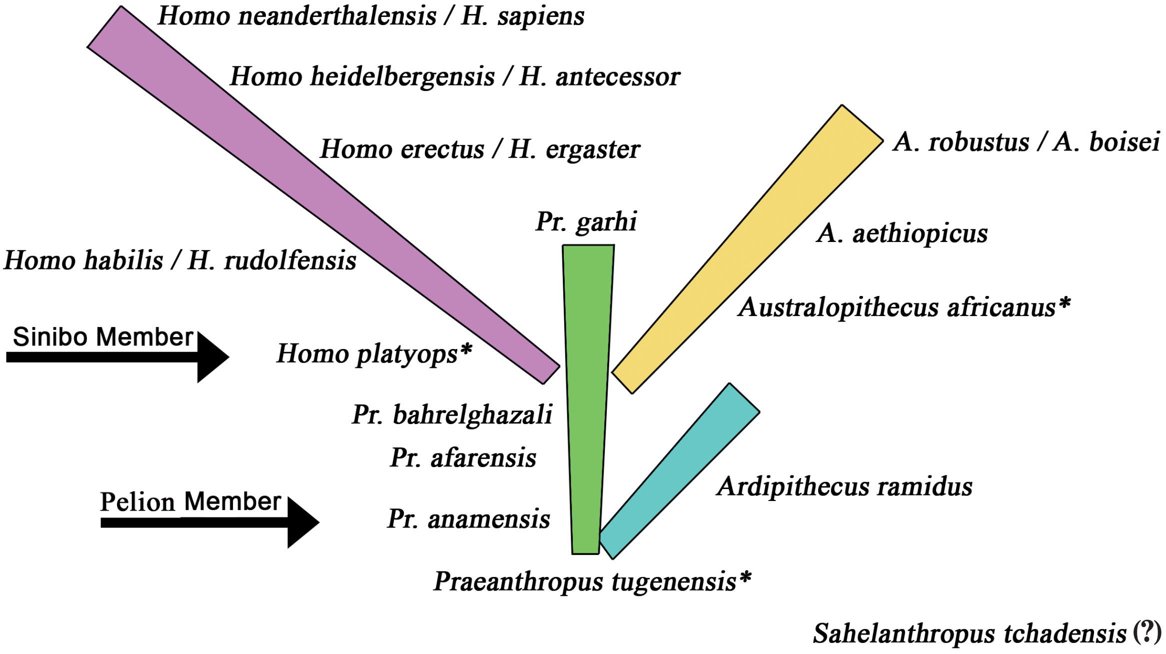
Under the circumstances, proposing a name for the hominid fossils from the Mabaget Formation is not an easy undertaking.

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 and 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 and 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 and 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 and Ayala (2003) (Text-fig. 23) in which four genera and 19 species were recognised, and



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

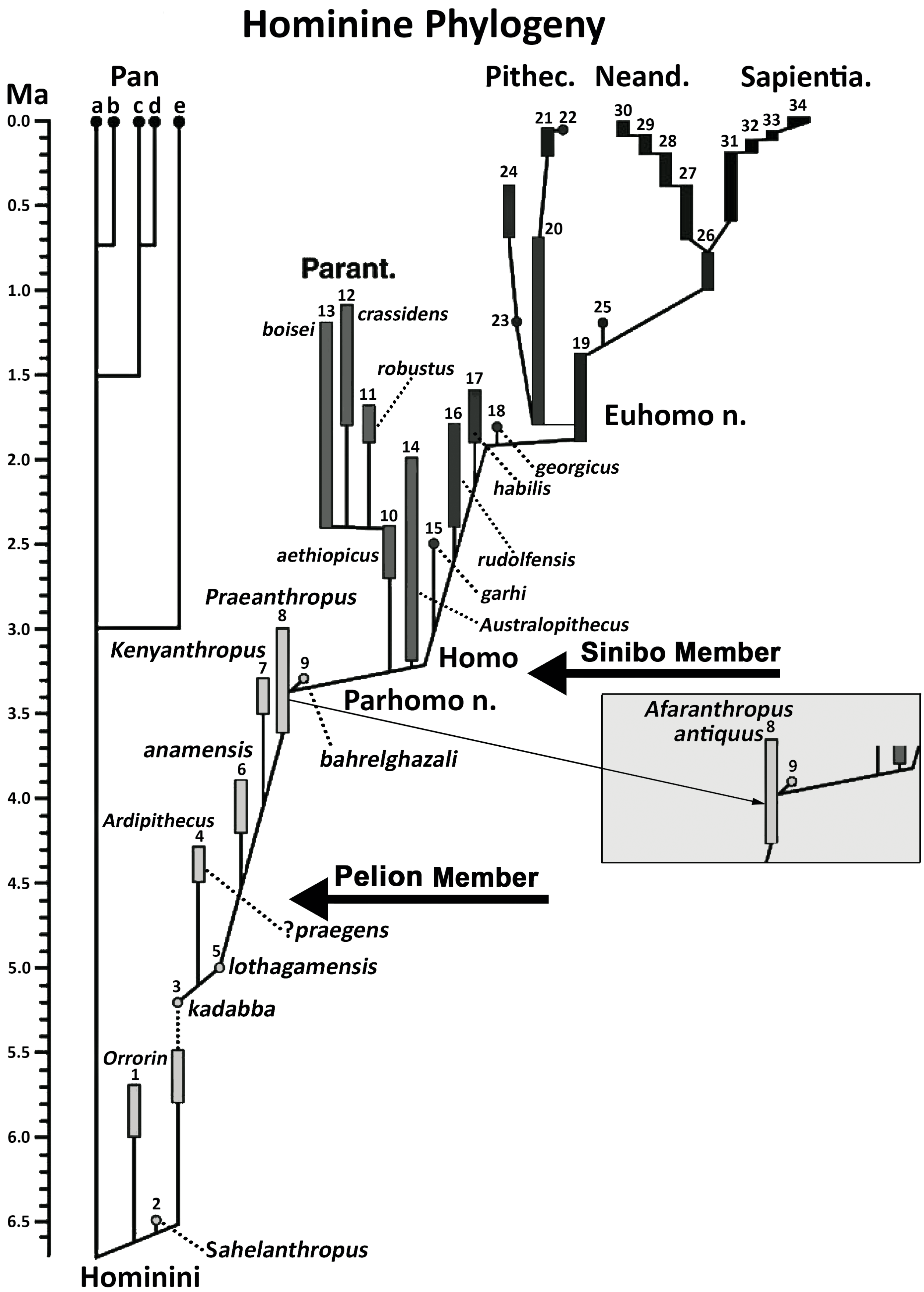
the "splitting" approach of Bonde (2011) (Text-fig. 24) in which 9 genera and 34 or 35 species and subspecies were recognised. Furthermore, it is clear that some of the "taxa" accepted by these authors are chimaera, being composed of the remains of two or more taxa.

To complicate matters, the dating of some of the African 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 Text-figs 23–25 were proposed prior to the redating of the Sterkfontein fossils. If correct, the redating greatly modifies the scheme of Bonde (2011) (Text-fig. 24) because according to him the genus *Australopithecus* did not exist prior to 3.2 Ma. The phylogeny of Cela-Conde and Ayala (2003) (Text-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 deyiremeda*, *Australopithecus afarensis*, *Australopithecus bahrelghazali* and *Kenyanthropus platyops* as well as the Burtele specimen (Text-fig. 25). The phylogeny of Cerling et al. (2013) (Text-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).

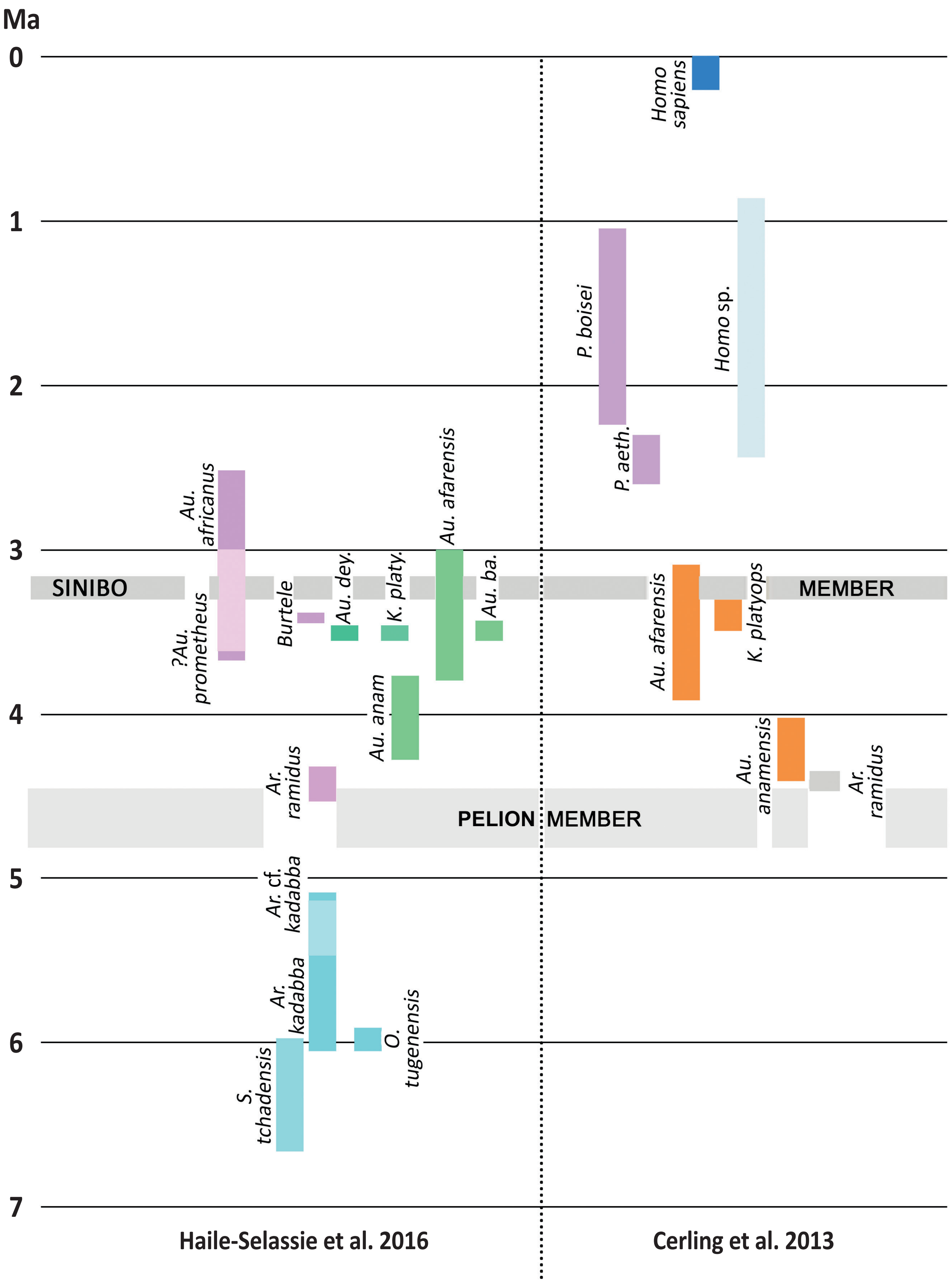
Under the proposals of Cela-Conde and Ayala (2003) the classification of the fossils from the lower strata of the Mabaget Formation (Pelion Member) would boil down to three possibilities, *Praeanthropus anamensis*, *Ardipithecus ramidus* or an undescribed taxon (if it differs from the two named taxa). But the Tabarin mandible has already been designated as the holotype of *Homo antiquus praegens* Ferguson, 1989b. The name *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 2001). Furthermore, if the genus name *Praeanthropus* is resurrected, then its type species would logically have been *Praeanthopus 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 et 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 and 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).

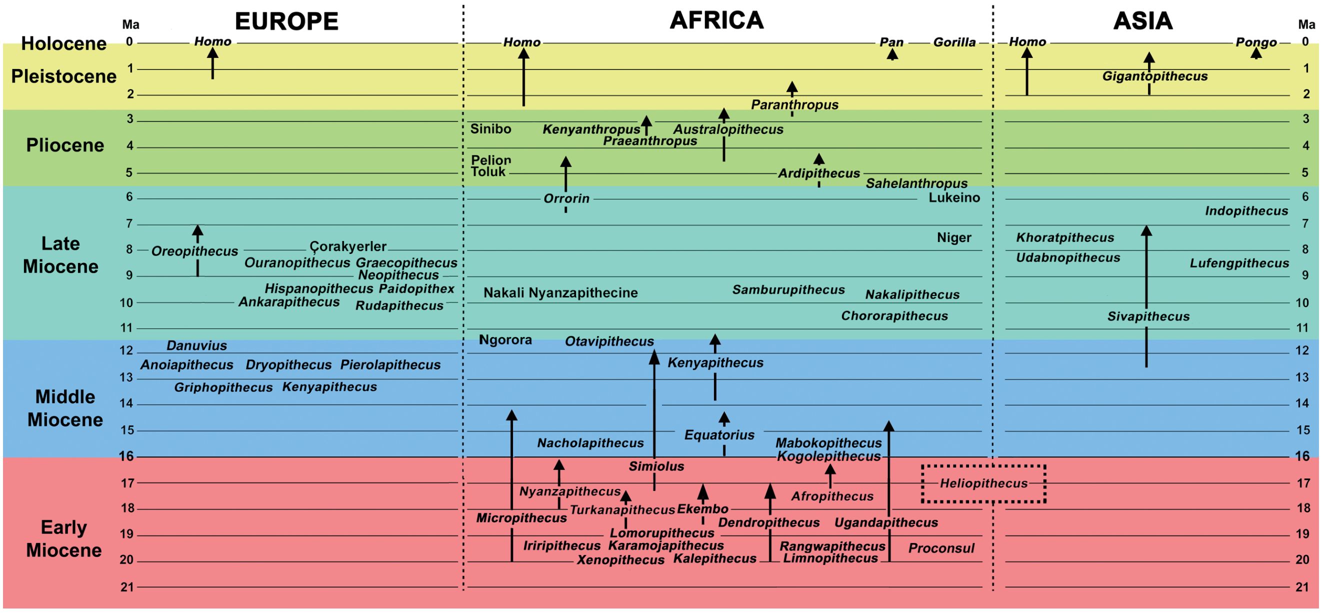
The phylogenetic position of the Sinibo mandible is difficult to decide under the proposals of Cela-Conde and Ayala (2003) (Text-fig. 23) because it accords with three of the genera recorded from its time period, early *Homo* (*H. platyops*), late *Praeanthropus* (*Pr. afarensis-Pr. bahrelghazali*) and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



Text-fig. 24. Hominine phylogeny from Bonde (2011) itself modified from Bonde and 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.



Text-fig. 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. *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.



Text-fig. 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 10.0 to 6.0 Ma (Pickford 2009).

In the phylogenetic scheme of Bonde (2011) (Text-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 (1989b) 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, Daver et al. 2022).

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) (Text-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 basal 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.

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. 2002, 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 8.0 million years ago and the present day is poor. Pickford and Senut (2005a, b) described some chimpanzee- and gorilla-like teeth from Kenya, Pickford et al. (2008, 2009a) described an indeterminate species from the Late Miocene of Niger which they attributed to a proto-chimpanzee (see Mocke et al. 2022) and McBrearty and 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 Cela-Conde and Ayala (2003), peter out downwards with no taxa listed older than 7.0 Ma.

The African hominoid record from ca. 14.0 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 unnamed taxa of unclear affinities (Pickford and Senut 2005b, Mocke et al. 2022) (Text-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*) (Text-fig. 26).

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 5.0–4.0 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 basal 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 6.0 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. 2009b) 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. 2002a).

The combined evidence from Kenya and Ethiopia (Text-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, microdonty 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*, *Otavipithecus*, *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 microdonty in *Orrorin tugenensis* at 6.0 Ma and *Orrorin praegens* at 5.0–4.5 Ma, as well as *Kenyanthropus*, a hominid aged ca. 3.5 Ma, opens up other possibilities, one of which is that microdonty 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 and 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 upper Pliocene. In contrast, megadont australopithecines flourished only from ca. 4.5 Ma (if *Australopithecus anamensis* belongs to this genus – cf. Cela-Conde and Ayala (2003), who classify it within *Praeanthropus*; Text-fig. 23) or from 3.8 Ma if *Australopithecus afarensis* is considered to be the earliest member of the genus (Cerling et al. 2013, Haile-Selassie et al. 2016; Text-fig. 25) until they went extinct during the Early Pleistocene ca. 1 million years ago (*Paranthropus boisei*, *Paranthropus crassidens*) (Text-figs 24–26).

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 basal 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 upper Pliocene succession in the Tugen Hills and elsewhere in the continent are required to throw light on the matter.

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