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Singular or plural Oldowan tool-makers during the Lower Pleistocene in eastern Africa?

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Singular or plural Oldowan tool-makers during the Lower Pleistocene in eastern Africa?

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ABSTRACT
Over the last twenty-five years, the study of hominin evolution and archaeological assemblages has become increasingly complex, due to new archaeological and paleoanthropological discoveries, and the advent of innovative analytical approaches. Findings from paleontological and archaeological sites and localities along the East African Rift Valley reveal substantial cultural and biological diversity during the Lower Pleistocene. From this context emerge critical questions about the relationships between the different material cultures and hominins. To explore these questions, I propose a cross-disciplinary approach that examines both the skeletal anatomy of hominins and the associations between hominins and archaeological assemblages in Lower Pleistocene sites and localities in East Africa. Anatomical evidence suggests that the dexterity required to produce Oldowan assemblages was likely not exclusive to the genus *Homo*. Moreover, multiple hominin species appear to have been involved in tool-making, particularly within Oldowan assemblages. These assemblages have been associated with *Homo* sp. and *Homo habilis* (n = 10), *Homo erectus*/*ergaster* (n = 6), and with a significant number, of *Paranthropus* remains (n = 8). Given this evidence, *Paranthropus* should now be recognized as a stone tool-maker alongside early *Homo*.

KEY WORDS
Material culture,
hominins,
Africa,
Lower Pleistocene,
Oldowan,
Acheulean.

RÉSUMÉ
Singularité ou pluralité des artisans de l'Oldowayen au Pléistocène inférieur en Afrique de l'Est ?
Au cours des vingt-cinq dernières années, de nouvelles découvertes archéologiques et paléoanthropologiques, ainsi que des approches analytiques innovantes, ont considérablement enrichi notre compréhension de l'évolution des hominines et des assemblages archéologiques. Les découvertes de sites et de localités paléontologiques et archéologiques le long de la vallée du Rift Est Africain révèlent une diversité culturelle et biologique substantielle durant le Pléistocène inférieur. Cela soulève des questions fondamentales sur les relations entre les hominines et les différentes cultures matérielles. Pour explorer ces questions, je propose une approche interdisciplinaire qui examine à la fois l'anatomie de la main des hominines et les associations entre hominines et assemblages archéologiques dans les sites et localités du Pléistocène inférieur en Afrique de l'Est. Les preuves anatomiques suggèrent que la dextérité requise pour produire des assemblages oldowayens n'est probablement pas exclusive au genre *Homo*. En outre, plusieurs espèces d'hominines semblent avoir été les artisans d'artefacts lithiques, en particulier pour les assemblages oldowayens. Ceux-ci sont associés à *Homo* sp. et *Homo habilis* (n = 10), *Homo erectus*/*ergaster* (n = 6) et, à un nombre significatif de restes de *Paranthropus* (n = 8). Compte tenu de ces éléments, *Paranthropus* devrait donc être reconnu comme un artisan d'artefacts lithiques au même titre que les premiers représentants du genre *Homo*.

MOTS CLÉS
Culture matérielle,
hominines,
Afrique,
Pleistocène inférieur,
Oldowayen,
Acheuléen.

INTRODUCTION

Hominin evolutionary history depicts a bushy rather than a linear evolutionary history with multiple contemporaneous species or genera in Africa during the Pliocene and Pleistocene and sympatric relationship, for example between *Homo erectus* and *Paranthropus boisei*, as illustrated by footprint evidence (Hatala *et al.* 2024). This indicates significant morphological diversity (Fig. 1) with a reticulated biological evolution and ghost lineages, especially for the genus *Homo* (e.g. Foley 2002; Wood & Lonergan 2008; Wood & Boyle 2016; Lorente-Galdos *et al.* 2019; Caparros & Prat 2021). Likewise, the archaeological record reveals a diversity of assemblages and a non-linear pattern of cultural evolution, exemplified by some Acheulean sites actually older than Oldowan sites (e.g. Kokiselei 4 [Lepre *et al.* 2011]; Konso-Gardula [Asfaw *et al.* 1992; Beyene *et al.* 2023]).

Moreover, the oldest *Homo* fossils from Ledi Geraru in Ethiopia (Villmoare *et al.* 2015, 2025) as well as the specimens older than 2.3 Ma for example from the lower Omo Valley (e.g. Hlusko *et al.* 2024) and from the eastern and western parts of Lake Turkana (e.g. KNM-ER 5431 (Suwa *et al.* 1996; Villmoare *et al.* 2015) and KNM-WT 42718 (Prat *et al.* 2005)) postdate stone tools discovered at the LOM3 archeological site in Kenya by about 500 000 years-1 million years (Ma) (3.3 Ma, Harmand *et al.* 2015, but see also for discussion Domínguez-Rodrigo & Alcalá 2016, 2019; Harmand *et al.* 2019; Archer *et al.* 2020; Key & Proffitt 2024) and cut-marked bones dated to 3.4 Ma from Dikika locality in Ethiopia (McPherron *et al.* 2010, but see also for discussion Domínguez-Rodrigo *et al.* 2011; Thompson *et al.* 2015; Domínguez-Rodrigo & Alcalá 2016). The Dikika area is also known for the discovery of a juvenile skeleton of *A. afarensis* (Alemseged *et al.* 2006). The Lomekwi archaeological site LOM3 (3.3 Ma) is in the same chronological range as the species *Australopithecus afarensis* (3.8-3.0 Ma) and was discovered in the Lomekwi area, where hominin remains attributed to *Kenyanthropus platyops* were also found (Leakey *et al.* 2001). However, due to the high level of distorsion of KNM-WT 40000 (*K. platyops* holotype which is the only cranium of this species), it is difficult to establish whether it is a valid taxon or a variant of *A. afarensis* (White 2003), a species considered by some authors to be the ancestor of the genera *Homo* and *Paranthropus* (see Kimbel & Delezene 2009 for a review).

Therefore, these findings from Lomekwi and Dikika challenge the exclusive association of lithic artefacts (stone-tool use and stone-tool making) with the genus *Homo*. They question specific attribution of lithic artefact manufacture to the genus *Homo* and the validity of this criterion for defining our genus. Indeed, the diagnosis of the genus *Homo* and the criteria for this classification are still hotly debated, and take into account anatomical, morphological, behavioural, and philosophical considerations (see for a review Prat 2022). Among the criteria proposed by Leakey and colleagues (Leakey *et al.* 1964) power and precision grip manual abilities were central. However, tool-making was mentioned in the section untitled "Cultural Association" but not in the *Homo habilis* diagnosis. Consequently, the role of archaeological remains in defining the genus *Homo* highlights the potential relationships in East Africa between Oldowan, Acheulean and Lower Pleistocene hominins.

The discoveries made in the lower Omo Valley, in the extreme south-west of Ethiopia, are of particular interest in this context. Research in this region initially began with work by Camille Arambourg in the early 1930s, following surveys carried out by Dr Brumpt as part of the explorations led by Viscount Robert du Bour de Bozas in 1902. New expeditions were carried out from 1966 onwards, as part of the International Omo Research Expedition (IORE) initiated by Francis Clark Howell, Louis Leakey, Camille Arambourg and Yves Coppens (who led the French side of the expedition with Camille Arambourg, and then alone from 1970 to 1976, and to whom this issue is dedicated). The aim of this international, multidisciplinary expedition was to prospect and excavate the rich fossil deposits of the lower Omo Valley. Research in this region was resumed in 2006 as part of the OGRE (Omo Group Research Expedition) led by Jean-Renaud Boisserie (e.g. Boisserie *et al.* 2008). This region, with a sedimentary sequence almost 800 metres thick, is of considerable importance for the study of hominins, palaeoenvironmental reconstructions and relationships between hominin evolution, environment and material culture. The lower Omo Valley comprises several Oldowan sites (e.g. Chavaillon 1970; Delagnes *et al.* 2011; Delagnes *et al.* 2023) and a very large number of hominin remains (e.g. Coppens 1977; Hlusko *et al.* 2024). In addition, the Usno and Shungura formations are among one the longest sedimentary sequences bear hominin remains and also provide data for tracing climatic changes between 3 and 1 Ma (e.g. Coppens 1978; Alemseged *et al.* 2007; Boisserie *et al.* 2008; Bibi *et al.* 2013; Bedane *et al.* 2025).

This overview is an updated of a paper published in 2023 (Prat 2023). It focuses on the morphological attributes underlying hominin remains manual skills, and the associations between eastern african hominin remains (more than 950 in the study corpus) and Oldowan assemblages as evidenced in palaeontological and archaeological records from 3.0 to 1.2 Ma, with an update of some datations. A site description is included where hominin remains were discovered in an archaeological site, with a particular focus on the sites where Pr. Yves Coppens worked.

MATERIAL AND METHODS

The discussion on hominin remains (anatomical parts, taxonomy), archaeological sites, spatial context, and other relevant data (i.e., as primary data, without entering into discussions) is based on data from the literature, used here at face value. However, finding detailed contextual information on hominin remains, and depositional processes, whether *in situ* or on the surface, and their proximity to archaeological artefacts can be challenging. Despite thorough research, it would appear that certain specific associations may be largely overlooked. Regarding the taxonomy of hominin remains, some

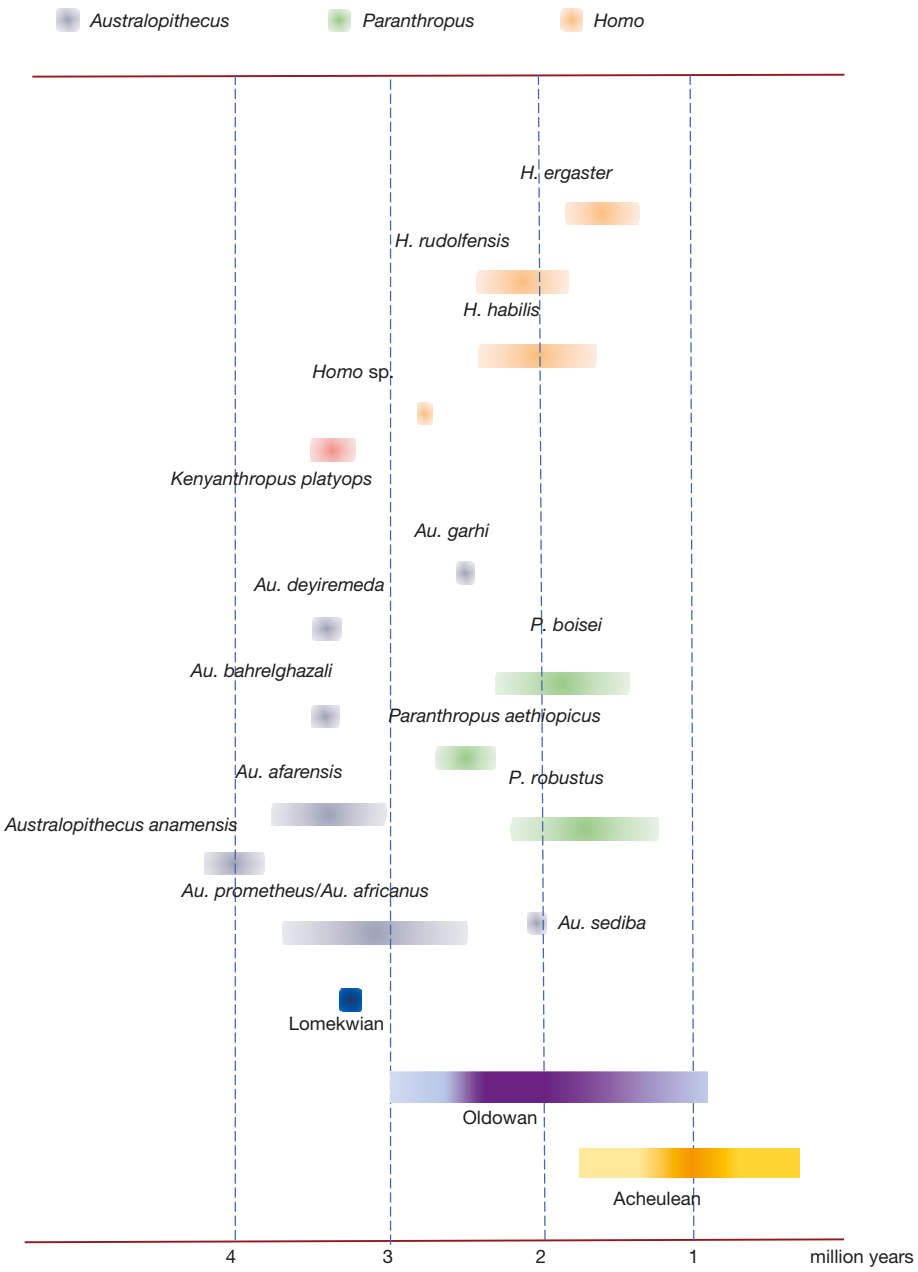

FIG. 1. — Chronological framework of hominin taxa (above) and material cultures (below).

specimens are referred to *Homo ergaster* or *Homo erectus* by different authors, according to diverse nomenclatures (Reed *et al.* 2023). To avoid confusion, in this context, I refer to them as *Homo ergaster*/*erectus*.

According to Key and Proffitt, the earliest Oldowan assemblages may date from 3.020 or 3.181 Ma and, according to an optimal linear estimation (OLE), they fall within the range of 2.622-3.436 Ma (Key & Proffitt 2024). In archaeological terminology, the terms Oldowan and Acheulean are used without distinguishing the early Oldowan and Developed Oldowan, despite differences between early (*c.* 2.6-2.3 Ma) and later Oldowan sites (*c.* 2.0-1.7 Ma) (e.g. Harmand 2009; Roche *et al.* 2009; de la Torre 2011; Goldman-Neuman & Hovers 2012; Potts 2012; Delagnes *et al.* 2023). The Oldowan can be considered as multiple specialized adaptations (Clark & Linares-Matás 2024). Furthermore, in many publications, particularly the earliest ones, the only terminology used is Oldowan or Acheulean (e.g. Leakey 1971; Chavaillon 1976; Harris & Herbich 1978; Kimbel *et al.* 1996; Plummer *et al.* 2023).

Determining whether a hominin found at an archaeological site or on the surface was the stone tool-makers is always challenging. The place of death may not correspond to the living area, and sites can sometimes be palimpsests and/or have undergone complex geological and sedimentation processes over time. However, applying Occam's razor, the most parsimonious hypothesis is that the hominins present at a site are the ones responsible for the material culture found there.

Specifically, it is more reasonable to assume that stone toolmakers correspond to the species identified in the site's sedimentary layers rather than to species absent from them. This is generally the case when specimens of the genus *Homo* are found, but is less systematic for other genera. Moreover, this continues to be one of the most widely accepted hypotheses, especially for Middle and Upper Paleolithic sites.

The reliability of the association between hominins and archaeological sites is categorized following the framework used by Grine *et al.* (2022) for species attribution of post-cranial remains. Two categories are proposed: 1) High Confidence 1 (HC1), where hominin remains were found in archaeological site (in archaeological layers and on the surface of the excavation due to erosion processes); and 2) High Confidence 2 (HC2), categorizing hominin remains found less than 400 metres from the archaeological site, within the same chrono-stratigraphic layer.

RESULTS

Overview of anatomical constraints

Concerning the anatomical prerequisites, the morphological evidence indicates that enhanced dexterity and anatomical capabilities were required for using or making stone tools. This infers in particular "pad-to-pad" precision grasping, as defined by Napier (1956) and Almécija & Alba (2014), involving the "perfect" opposition of the thumb and finger's proximal pulp areas, which can be facilitated by a longer thumb relative to the remaining fingers. This also includes forceful precision gripping and precision handling as described by Marzke (1997), deduced from the carpometacarpal joint of the thumb and the metacarpophalangeal joint of the thumb and the fingers involved. Such morphological evidence and muscular insertions are observed on two additional hominin genera to *Homo* (for a review see also Kivell 2015): *Australopithecus* (specifically *A. afarensis* [e.g. Marzke 1983, 1997, 2013; Tocheri *et al.* 2003; Kivell *et al.* 2011, 2020; Almécija & Alba 2014; Kunze *et al.* 2024], *A. africanus* [e.g. Green & Gordon 2008; Skinner *et al.* 2015; Richmond *et al.* 2016], *A. sediba* [e.g. Kivell *et al.* 2011; Bardo *et al.* 2018; Dunmore *et al.* 2020]) and *Paranthropus* (*P. robustus* and *P. boisei* see below), and therefore extends beyond the genus *Homo*. Experimental biomechanics and musculoskeletal modelling also offer valuable insights into the functional anatomy of the upper limb, particularly in stone tool production (Tocheri *et al.* 2003; Rolian *et al.* 2011; Williams *et al.* 2012; Williams-Hatala *et al.* 2018; Key *et al.* 2019; Macchi *et al.* 2021; Manafzadeh & Gatesy 2021; Williams-Hatala *et al.* 2021; Kivell *et al.* 2022) and can complement anatomical and archaeological field data.

Concerning the Pleistocene fossil record after 2 Ma, the anatomy of hand remains from Olduvai Gorge (misspelling of the Maa word Oldupai, Tanzania, i.e., OH 7 (1.84 Ma) and OH 86 (1.86 Ma), and from Ileret (Kenya, i.e., KNM-ER 47000, 1.5 Ma) was conducive to stone tool use and stone tool-making. In particular, the OH 7 late juvenile hand (1.84 Ma) from Oldupai Gorge shows a fully opposable thumb and capabilities for power and precision gripping (Leakey *et al.* 1964). Leakey, Tobias and Napier in 1964, pointed out the tool-making abilities of this specimen, whereas Napier (1962) was more cautious, highlighthing that "There is less certainty about toolmaking which involves not only a peripheral but also a central intellectual factor as Oakley has long insisted" (Napier 1962: 411)". The mixed attributes of OH 7 (precision grip abilities and climbing adaptation) were emphasized by Susman & Creel (1979). Furthermore, although OH 7 has been allocated to *Homo habilis* (Leakey *et al.* 1964), some authors consider that the phalangeal morphologies are closer to those of *Paranthropus* (Moyà-Solà *et al.* 2008). Moreover, the manual proximal phalanx (OH 86, 1.84 Ma) allocated to the genus *Homo*, is considered to represent the earliest modern human-like hand anatomy, showing reduced postural and locomotor pressures and a decrease in arboreal adaptations (Domínguez-Rodrigo *et al.* 2015). OH 86 is distinct in size and shape from both *Australopithecus*/*Paranthropus* and the OH 7 hand bones. Its taxonomic classification is challenging, but it is generally considered as *Homo*, different from OH 7 (*H. habilis* holotype) and attributed rather to *H. erectus* type (Diez-Martín *et al.* 2015). Moreover, the third metacarpal styloid process found in Kaitio, West Turkana, Kenya (with a morphology typical of the modern humans/Neandertal hand but absent in Pliocene and Lower Pleistocene hominins) suggests that this distinctive complex of radial carpometacarpal joints emerged at early as 1.42 Ma for the genus *Homo* (Ward *et al.* 2014).

Concerning *Paranthropus*, the hand anatomy of *P. boisei*, illustrated by the KNM-ER 47000 specimen (Ileret, East Turkana, Kenya), dated to 1.5 Ma, indicates that the fine precision gripping capacity and manual dexterity of this species is compatible with stone tool use or stone tool-making as also seen in earlier australopithecine species such as *A. africanus* (e.g. Kivell *et al.* 2011; Richmond *et al.* 2016), but not a robust thumb as observed in *H. erectus*/*H. ergaster*. This reflects adaptations to the intensification of precision gripping and tool use (Richmond *et al.* 2020). *Paranthropus* individuals present increased wrist mobility, which could improve the accuracy of force production during stone tool-making and stone tool use (e.g. Williams *et al.* 2010; Williams *et al.* 2014), or even during throwing, as shown in *H. erectus* (Roach *et al.* 2013; Roach & Lieberman 2014). However, Moyà-Solà *et al.* (2008) proposed that the *Paranthropus* hand structure which lacks the enlarged first metacarpal typical of *Homo*, might also reflect adaptations for feeding activities as seen in extant hominids (e.g. Marzke *et al.* 2015; Neufuss *et al.* 2018; Gérard *et al.* 2022). The anatomy of *Paranthropus*, particularly elements like OH 80 (e.g. radial morphology compatible with grasping abilities, used for power and precision grips) aligns with the abilities required for stone tool production (Domínguez-Rodrigo *et al.* 2013). However, as noted by Grine *et al.* 2022, it is very difficult to associate isolated post-cranial elements more specifically with the genus *Homo* or *Paranthropus*, given that these two genera are stratigraphically associated.

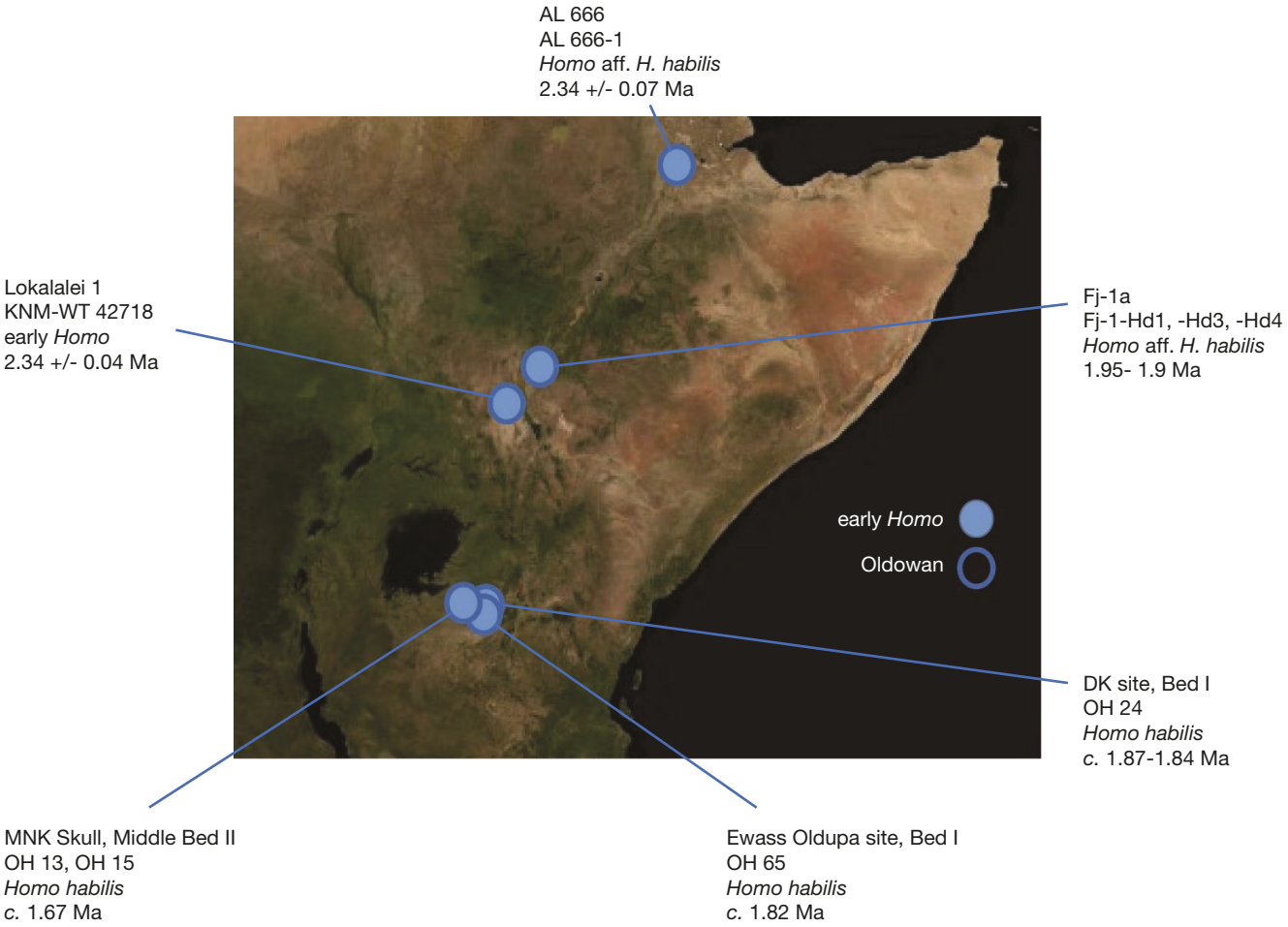

Fig. 2. — Location of *Homo habilis sensu lato* remains in association with Oldowan sites. Credits: background map NASA/Internet Archive.

Overview of the archaeological data

In Eastern Africa, between 3 and 1.2 Ma, 25 documented instances (which correspond to 20 archaeological sites) of a high-confidence association between lithic and palaeoanthropological remains have been reported (Table 1).

Association between Oldowan assemblages and Homo habilis sensu lato

The association between the Oldowan and early *Homo* specimens can be observed in six occurrences (in Ethiopia, at Hadar, A.L. 666 (HC1), and Fejej, Fj-1a (HC2); in Kenya, in the western part of Lake Turkana, Lokalalei site complex (HC2); in Tanzania, in Oldupai Gorge, MNK Skull site (HC1), DK site (HC2) and Ewass Oldupa site (HC2) dated between 2.3 and 1.67 Ma (Table 1; Fig. 2). I describe here the two archaeological sites where hominin remains were discovered in archaeological layers or at the surface of the excavation (HC1).

The first is the archaeological site named A.L. 666, in the Hadar region in Ethiopia. The lithic assemblage (34 artefacts including 14 found *in situ*) is typical of the Oldowan (Kimbel *et al.* 1996; Plummer 2004; Goldman-Neuman & Hovers 2012). These assemblages are dated to *c.* 2.35 Ma by the Bouroukie Tuff 3 (Campisano & Feibel 2008) and between 2.3 and 1.9 Ma based on the fauna (Rowan *et al.* 2022). A maxilla (A.L. 666-1) was found on the surface of the hill (at the base). This latter shows clear early *Homo* traits and was assigned to *Homo* aff. *H. habilis* (Kimbel *et al.* 1996; Kimbel *et al.* 1997). However, Spoor *et al.* (2015) have considered that its morphology is not compatible with OH7, and therefore with *H. habilis*, and furthermore does not present the facial morphology observed in *H. rudolfensis*. For the above-mentioned authors, the morphology of A.L. 666-1 is more derived toward early *H. erectus*/*ergaster*.

The second high-confidence site (HC1) is MNK Skull site from Middle Bed II at Oldupai (Leakey 1971; de la Torre *et al.* 2021), which yielded an Oldowan assemblage and two *in situ Homo habilis* specimens (OH 13, paratype of *Homo habilis*), as well as dental remains catalogued as OH 15 (Leakey *et al.* 1964; Tobias 1991) dated to *c.* 1.67 Ma (de la Torre *et al.* 2021).

Association between Oldowan assemblages and Paranthropus *(*P. boisei*)*

The association between *Paranthropus boisei* specimens and Oldowan assemblages can be observed in four sites (in Kenya at Homa Peninsula, Nyayanga site (HC1); in the western part of Lake Turkana, Kokiselei 1 (HC1) and at Koobi Fora,

TABLE 1. — Association between hominin remains and archaeological assemblage with a High Confidence level (**HC**). Abbreviations: **HC1**, hominin remains have been found in an archaeological site, which includes both in archaeological layers and remains found on the surface of the excavation due to erosion processes; **HC2**, hominin remains have been found less than 400 meters from the archaeological site, within the same chrono-stratigraphic layer.

Locality	Region	Age (Ma)	Hominins	Industry	Category of reliability
Association between Oldowan assemblages and *Homo (H. habilis sensu lato* and *Homo* sp.)					
A.L. 666	Hadar (Ethiopia)	*c.* 2.35 (Campisano & Feibel 2008) 2.3 and 1.9 (Rowan *et al.* 2022)	A.L. 666-1 *Homo aff. H. habilis* (Kimbel *et al.* 1997)	Oldowan (Kimbel *et al.* 1996)	HC 1
Lokalalei 1, Gajh5	West Turkana (Kenya)	2.34 +/- 0.04 (Prat *et al.* 2005)	KNM-WT 42718 Early *Homo* (Prat *et al.* 2005)	Oldowan (Prat *et al.* 2005)	HC 2
FJ-1a	Fejej (Ethiopia)	1.95-1.90 (Chapon *et al.* 2005)	Fj-1-Hd1, Hd3, Hd4 *Homo* aff. *Homo habilis* (de Lumley & Marchal 2004)	Oldowan (e.g. Asfaw *et al.* 1991; de Lumley & Beyene 2004; Barsky *et al.* 2011)	HC 2
DK	Oldupai Gorge (Tanzania)	1.87-1.84 (Deino 2012)	OH 24 *Homo habilis* (Leakey *et al.* 1971)	Oldowan (Leakey 1971; de la Torre & Mora 2005)	HC 2
Ewass Oldupa	Oldupai Gorge (Tanzania)	*c.* 1.82 (Blumenschine *et al.* 2003; Deino 2012; McHenry 2012)	OH 65 *Homo habilis* (Blumenschine *et al.* 2012; Clarke 2012)	Oldowan (Mercader *et al.* 2021)	HC 2
MNK Skull	Oldupai Gorge (Tanzania)	*c.* 1.67 (de la Torre *et al.* 2021)	OH 13 Paratype *Homo habilis* OH 15 *Homo habilis* (Leakey *et al.* 1964; Tobias 1991)	Oldowan (Leakey 1971; de la Torre *et al.* 2021)	HC 1
Association between Oldowan assemblages and *Paranthropus*					
Nyayanga, excavation 3	Lake Victoria (Kenya)	3.03-2.58 (Plummer *et al.* 2023)	KNM-NG 77316 *Paranthropus* (Plummer *et al.* 2023)	Oldowan (Plummer *et al.* 2023)	HC 1
Kokiselei 1 FxJh6	West Turkana (Kenya)	1.79 (Boës *et al.* 2024)	KNM-WT 37744, 37747, 37748, 37100 *Paranthropus boisei* (Prat *et al.* 2003)	Oldowan (Roche *et al.* 2003; Arroyo *et al.* 2020)	HC 1
FxJj 20	Koobi Fora (Kenya)	1.65 +/- 0.05 (Feibel *et al.* 1989)	KNM-ER 3230 *Paranthropus boisei* (Wood 1991)	Oldowan (Harris & Herbich 1978)	HC 1
BK site level 4, Bed II	Olduvai Gorge (Tanzania)	1.34 (Domínguez-Rodrigo *et al.* 2013)	OH 80 *Paranthropus boisei* (Domínguez-Rodrigo *et al.* 2013)	Oldowan (Domínguez-Rodrigo *et al.* 2009)	HC 1
Association between Oldowan assemblages, *Homo* and *Paranthropus*					
OMO 57/5	Lower Omo Valley (Ethiopia)	2.32-2.23 (McDougall & Brown 2008)	OMO 57/5-1972-371 *Paranthropus* aff. *aethiopicus* (Coppens 1977; Suwa 1990; Wood & Leakey 2011) OMO 57/5-1972-319 Indet. (White 1988) Non robust indet. hominin (Suwa 1990) *Homo* aff. *Homo* sp. (Wood & Leakey 2011)	Oldowan (Coppens *et al.* 1973; Chavaillon 1976)	HC 1
FLK NN level 3	Oldupai Gorge (Tanzania)	1.84 (Deino 2012)	OH 7 cranial remains *Homo habilis* (Holotype) (Leakey *et al.* 1964)	Oldowan (Leakey *et al.* 1964; Leakey 1971)	HC 1
FLK NN level 3	Oldupai Gorge (Tanzania)	1.84 (Deino 2012)	OH 7 hand bones *Homo habilis* (Leakey *et al.* 1964) or *Paranthropus* (Moyà-Solà *et al.* 2008)	Oldowan (Leakey *et al.* 1964; Leakey 1971)	HC 1
FLK NN level 3	Oldupai Gorge (Tanzania)	1.84 (Deino 2012)	OH 8 foot bones *Homo habilis* (paratype) (Day & Napier 1964; Leakey *et al.* 1964)	Oldowan (Leakey *et al.* 1964; Leakey 1971)	HC 1

Table 1. — Continuation.

Locality	Region	Age (Ma)	Hominins	Industry	Category of reliability
FLK level 22	Oldupai Gorge (Tanzania)	1.84 (Deino 2012)	OH 5 Holotype of *Paranthropus boisei* (Leakey 1959)	Oldowan (Leakey 1971)	HC 1
FLK level 22	Oldupai Gorge (Tanzania)	1.84 (Deino 2012)	OH 6 *Homo habilis* (Tobias 1991)	Oldowan (Leakey 1971)	HC 1
FLK level 22	Oldupai Gorge (Tanzania)	1.84 (Deino 2012)	OH 35 *Paranthropus boisei* or *Homo habilis* (Leakey *et al.* 1964)	Oldowan (Leakey 1971)	HC 1
FxJj 38	Koobi Fora (Kenya)	1.78-1.52 (Mana *et al.* 2019) 1.85 (Feibel *et al.* 1989)	KNM-ER 1805 *Homo* sp. but taxonomical allocation under discussion (Leakey 1974; Prat 2002)	Oldowan (Harris & Herbich 1978)	HC 1
FxJj 38	Koobi Fora (Kenya)	1.78-1.52 (Mana *et al.* 2019) 1.85 (Feibel *et al.* 1989)	KNM-ER 1806 *Paranthropus boisei* (Leakey 1974; Wood 1991)	Oldowan (Harris & Herbich 1978)	HC 1
Association between Oldowan assemblages and *Homo erectus*/*Homo ergaster*					
Garba IV, level E	Melka Kunture (Ethiopia)	Slightly older than 1.7 (Morgan *et al.* 2012; Tamrat *et al.* 2014; Gallotti & Mussi 2015) 2 Ma (Mussi *et al.* 2023)	MK 81 GAR IVE 0043 early *Homo erectus*/*Homo ergaster* (Condemi 2004)	Oldowan (Gallotti & Mussi 2015; Mussi *et al.* 2023)	HC 1
PTK site	Oldupai Gorge (Tanzania)	1.84 (Deino 2012)	OH 86 *Homo erectus*-like (Diez-Martín *et al.* 2015; Domínguez-Rodrigo *et al.* 2015)	Oldowan (Domínguez-Rodrigo *et al.* 2015)	HC 1
Naiyena Engol 1 FxJh5	West Turkana (Kenya)	1.75 +/- 0.05 (Roche *et al.* 2003)	KNM-WT 37745 *Homo* sp. (aff. *H. ergaster*) (Prat *et al.* 2003)	Oldowan (Roche *et al.* 2003)	HC 1
Gombore I	Melka Kunture (Ethiopia)	1.6-1.5 (Morgan *et al.* 2012; Tamrat *et al.* 2014)	Gombore IB-7594 early *Homo erectus* *Homo* sp. (Chavaillon *et al.* 1977; Coppens 2004; Di Vincenzo *et al.* 2015)	Oldowan (Chavaillon *et al.* 1977; Chavaillon & Berthelet 2004)	HC 1
Association between Oldowan, Acheulean aseemblages and early *Homo erectus*/*Homo ergaster*					
DAN 5	Afar Region (Ethiopia)	1.6-1.5 (Semaw *et al.* 2020)	DAN5/P1 early *Homo erectus* (Semaw *et al.* 2020; Baab *et al.* 2022; Bruner *et al.* 2023)	Oldowan and Acheulean (Semaw *et al.* 2020)	HC 1
BSN12	Afar Region (Ethiopia)	1.26 +/- 0.03 (Semaw *et al.* 2020)	BSN12/P1 *Homo erectus* (Semaw *et al.* 2020; Baab *et al.* 2022)	Oldowan and Acheulean (Semaw *et al.* 2020)	HC 1

FXJj 20 (HC1); in Tanzania, at Oldupai Gorge, BK site (HC1)), dated between 3.03-2.58 and 1.34 Ma (Table 1; Fig. 3). Here I describe the oldest and youngest sites with hominin remains discovered in archaeological layers or at the surface of the excavation (HC1).

The oldest site with an association between Oldowan and *Paranthropus* remains is Nyayanga, which in the Homa Peninsula near Lake Victoria's Winam Gulf in Kenya. This site revealed one of the oldest Oldowan assemblages, dated between 3.032 Ma and 2.581 Ma (Plummer *et al.* 2023), with 135 *in situ* artefacts (excavations 3 and 5) and faunal remains, some of which bear cutmarks. The lithic artefacts show evidence of unifacial, bifacial, and multifacial reduction, and are comparable to lithics from other Oldowan sites. Use wear analyses indicate the processing of plant and animal tissues. From excavation 3, KNM-NG 77316 (a left lower molar fragment) was found *in situ*, associated with Oldowan artefacts (HC1) and KNM-NG 77315 (a left upper molar) from the surface. Both teeth are assigned to *Paranthropus* based on their morphology and metrics.

The youngest site illustrating an association between *Paranthropus* specimens and Oldowan artefacts is BK site in Oldupai Gorge (Bed II) in Tanzania. In this site dated to 1.34 Ma, a partial *Paranthropus boisei* skeleton (OH 80) was discovered *in situ* in level 4 (HC1) (Domínguez-Rodrigo *et al.* 2013). This partial skeleton includes four postcranial bones and nine upper teeth, allocated to *P. boisei* on the basis of their morphology, dimensions, and postcranial bone section properties. This find represents the first partial skeleton attributed to *P. boisei*. A large Oldowan assemblage and numerous vertebrate fossils, including some with cut marks, were also unearthed in level 4 (Domínguez-Rodrigo *et al.* 2009).

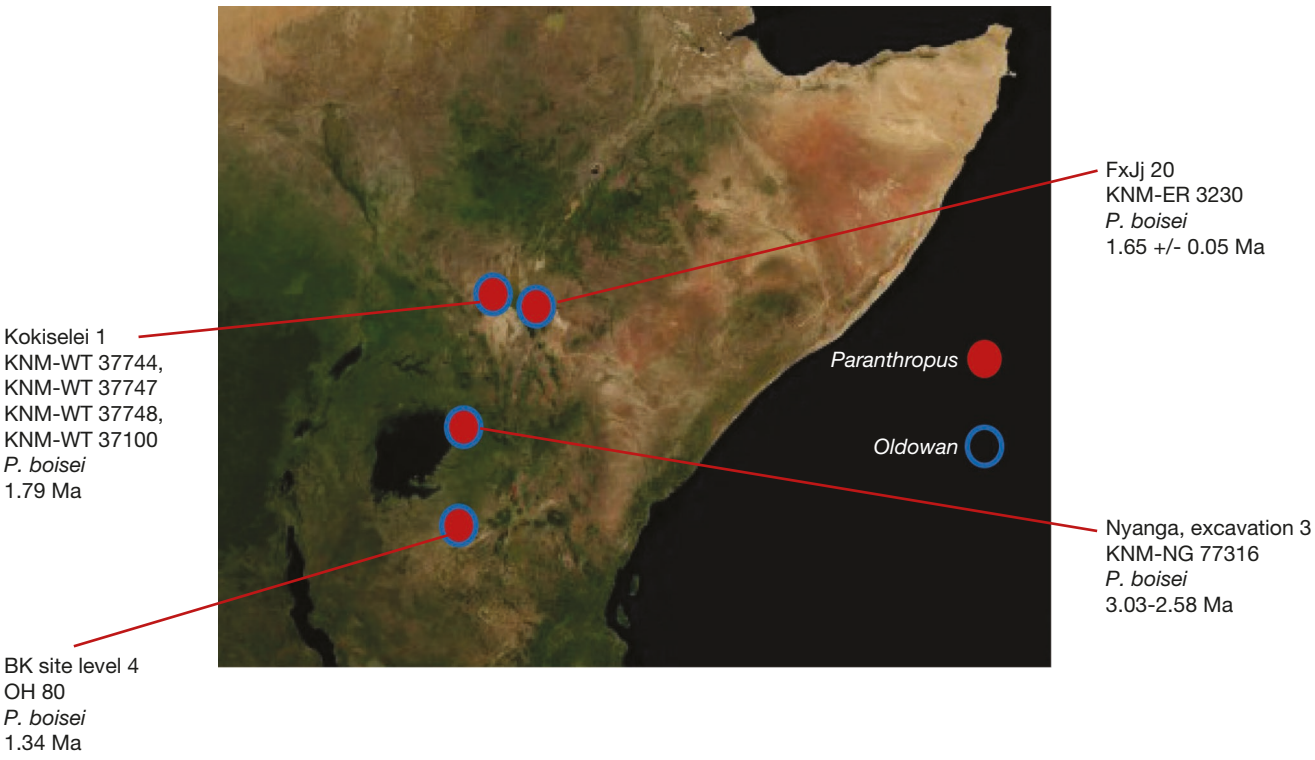

Fig. 3. — Location of *Paranthropus* (*P. aethiopicus* and *P. boisei*) remains in association with Oldowan sites. Credits: background map NASA/Internet Archive.

Association between Oldowan assemblages and Homo *and* Paranthropus

The association between *Homo habilis* (*Homo habilis*, *Homo* sp.), *Paranthropus (P.* aff. *P. aethiopicus* and *Paranthropus boisei*) specimens and Oldowan assemblages is documented in four sites (in Ethiopia, in the lower Omo Valley, OMO 57-5 (HC1), in Kenya at Koobi Fora, FXJj 38 (HC1), and in Tanzania, at Oldupai Gorge at FLK level 22 and FLK NN level 3 (HC1) dated between 2.32 and 1.78-1.52 Ma (Fig. 4).

I present here two sites from Oldupai gorge, which are of key importance in hominin evolution as they contain the holotypes of the species *Paranthropus boisei* and *Homo habilis* and OMO 57-5, in the lower Omo Valley in Ethiopia, discovered thanks to the work of Jean Chavaillon and Yves Coppens.

At OMO 57-5 (Member F of the Shungura Formation), the 40 square metres excavation revealed four hominin tooth fragments and an *in situ* quartz flake along with 16 surface artefacts (Coppens *et al.* 1973; Chavaillon 1976). One tooth fragment (OMO 57/5-1972-371, a left lower second premolar, HC1) is assigned to *P.* aff. *P. aethiopicus,* based on its morphology (Coppens *et al.* 1973; Coppens 1977; Suwa 1990; Wood & Leakey 2011). Another dental remain (OMO 57/5-1972-319), a left upper first premolar, is classified as indeterminate (White 1988), or as belonging to a non-robust indeterminate hominin (Suwa 1990), or *Homo* aff. *Homo* sp. (Wood & Leakey 2011). The Oldowan assemblage is characterized by systematic knapping and therefore not derived from natural fragmentation (de la Torre 2004). The deposit is dated between 2.32 Ma and 2.23 Ma (McDougall & Brown 2008).

In Tanzania, at Oldupai, the FLK level 22 has yielded a dense Oldowan assemblage (over 255 artefacts) and abundant mammal fossils (over 3500) (Leakey 1971) dated between 1.845 +/- 0.002 and 1.839 +/- 0.005 Ma (Blumenschine *et al.* 2003, 2012). Four hominin individuals were identified, including the cranium OH 5 (HC1), the *Paranthropus boisei* holotype (formerly *Zinjanthropus boisei*, Leakey 1959). The site also revealed some teeth and calvaria fragments (OH 6), attributed to *H. habilis* (HC1) and some post-cranial bones (tibia and fibula, OH 35) attributed to either *P. boisei* or *H. habilis* as these fossils are associated with OH 5 or OH 6.

The same association is also observed at FLK NN level 3 in Bed I at Oldupai. In this site numerous Oldowan stone artefacts were found alongside five hominin individuals, catalogued as OH 7 (juvenile mandible and cranial fragments and hand bones), holotype of *Homo habilis* (Leakey *et al.* 1964), OH 8 foot bones (paratype of *H. habilis*, Leakey *et al.* 1964), initially reported by Day & Napier (1964), OH 48 clavicle, OH 43 metatarsals and OH 49 radial shaft. The estimated age of these remains is 1.84 Ma (Deino 2012). OH 7 cranial remains are identified as *H. habilis*, but the allocation of the hand (OH7) and foot bones (OH8) to the same species is based on the parsimonious hypothesis of spatial association (Grine *et al.* 2022). However, some researchers have suggested that these hand bones (OH7) should belong to *Paranthropus* (Moyà-Solà *et al.* 2008). Conversely, the morphology of the OH 8 hallucal tarsometatarsal complex is very similar to that of modern humans, which supports an attribute to the genus *Homo* (Berillon 1999).

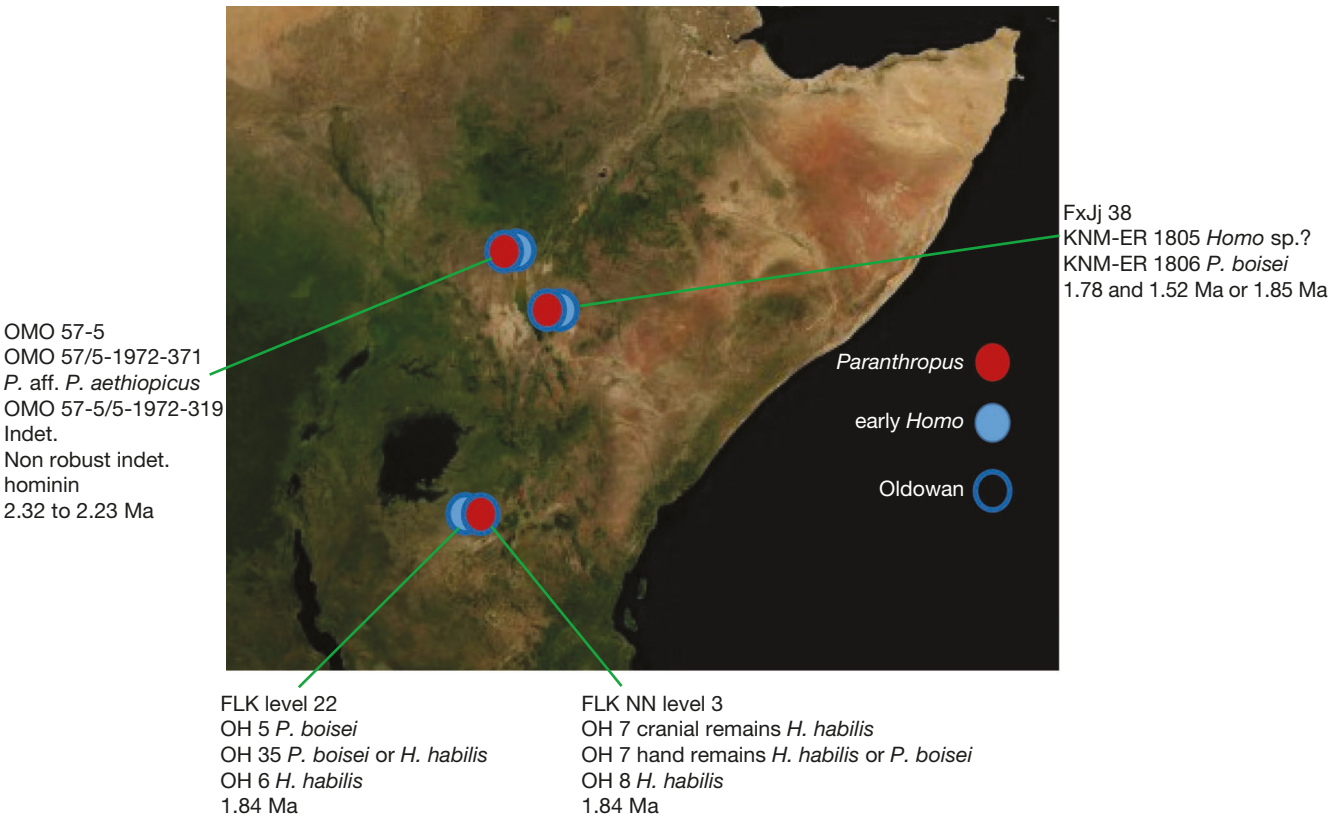

Fig. 4. — Location of *Homo habilis* and *Paranthropus* remains in association with Oldowan sites. Credits: background map NASA/Internet Archive.

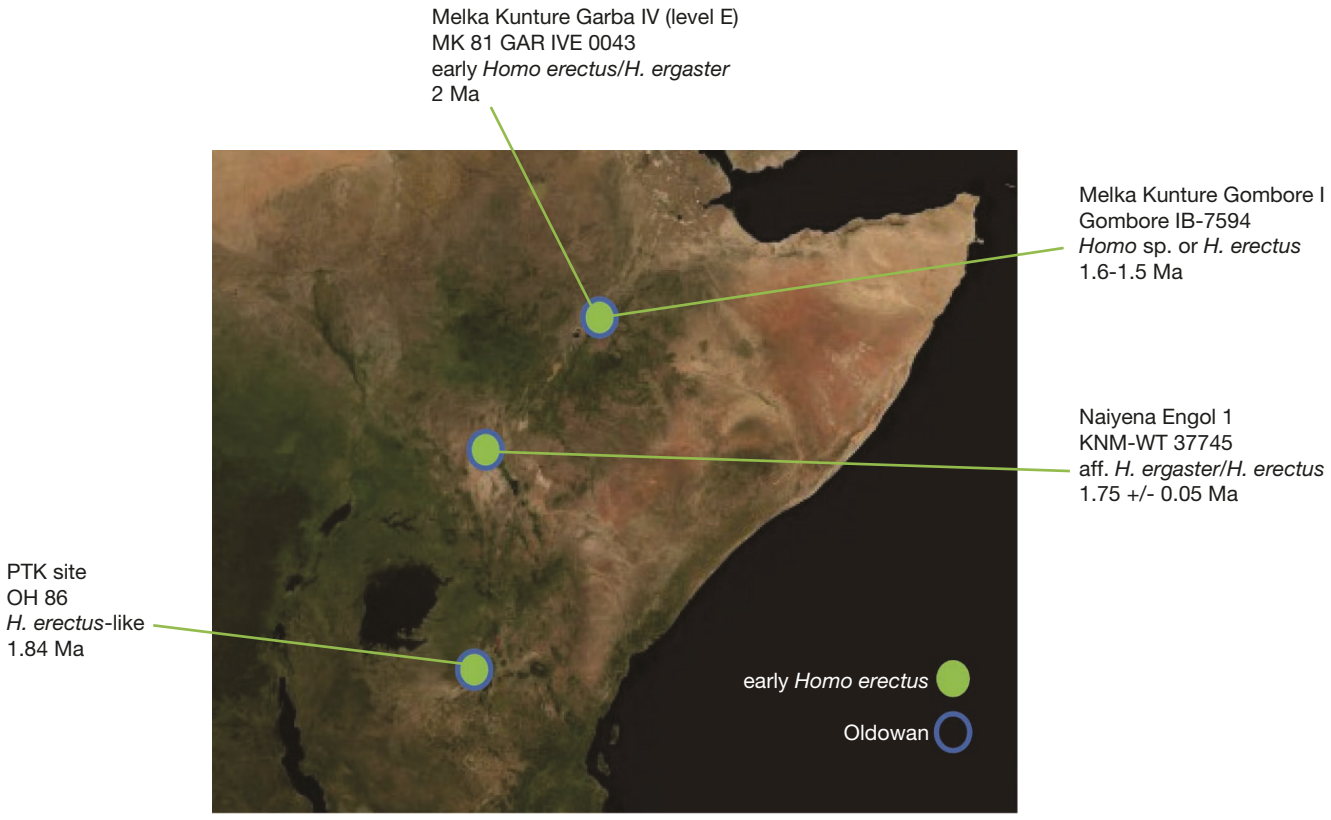

Fig. 5. — Location of *Homo erectus*/*Homo ergaster* in association with Oldowan sites. Credits: background map NASA/Internet Archive.

Association between Oldowan assemblages and Homo erectus/Homo ergaster

The association between *Homo erectus*/*Homo ergaster* specimens and Oldowan assemblages is documented in four sites (in Ethiopia, at Melka Kunture, Garba IV level 5 (HC1) and Gombore I (HC1); in Kenya in the western part of Lake Turkana, Naiyena Engol 1 (HC1); in Tanzania, at Oldupai, PTK site (HC1)) dated between 2 and 1.5-1.6 Ma (Fig. 5). I present here the discoveries from Melka Kunture, where Professor Yves Coppens worked and published some remains.

In Melka Kunture, the site Garba IV, level D, yielded an Oldowan lithic assemblage and a young child's mandible (MK 81 GAR IVE 0043, HC 1) attributed to early *Homo erectus*/*Homo ergaster* (Condemi 2004; Gallotti & Mussi 2015; Zanolli *et al.* 2016; Mussi *et al.* 2023). These remains were estimated to be slightly older than 1.7 Ma (Morgan *et al.* 2012; Tamrat *et al.* 2014; Gallotti & Mussi 2015), but are more recently considered to be around 2 Ma (Mussi *et al.* 2023). This site also reveals that hominins adapted to the high-altitude environment of the highlands of Melka Kunture (at or above 2000 m a.s.l.) during the Lower Pleistocene.

During the excavation of the Melka Kunture Gombore I site, a well-preserved distal portion of a left humerus (Gombore IB-7594, formally Melka Kunture 3 or MK3, HC1) was found *in situ* (Chavaillon & Berthelet 2004), alongside rich faunal and Oldowan assemblages, predomantly made up of pebble tools. The humerus is dated to 1.5-1.6 Ma (Morgan *et al.* 2012; Tamrat *et al.* 2014). Most authors attribute this specimen to the genus *Homo* (Senut 1979) and more specifically to *Homo* sp. (Chavaillon *et al.* 1977; Di Vincenzo *et al.* 2015) or to *Homo erectus* or aff. *erectus* (Coppens 2004; Cazenave *et al.* 2017). According to Coppens (2004), the robust humerus should be allocated to *Homo habilis*. However, Lague & Jungers (1996) suggest that this specimen should be assigned to *Paranthropus boisei*.

Association between Oldowan, Acheulean assemblages and early Homo erectus/Homo ergaster

The association between *Homo erectus*/*Homo ergaster* specimens and Oldowan and Acheulean artefacts can be observed in two sites in Ethiopia, Dana Aoule North (DAN 5) and Busidima North (BSN 12), in the Afar region (HC1) dated between 1.6 and 1.26 Ma respectively.

In Ethiopia, DAN5 and BSN 12 sites at Gona in the Afar region have yielded significant hominin fossils in association with both Oldowan and Acheulean assemblages, as well as cut-marked bones (Semaw *et al.* 2020). The age of the DAN 5 hominin and lithic assemblage is estimated between 1.6 and 1.5 Ma. The well-preserved hominin skull (occipital and left maxilla), catalogued as DAN5/P1 (HC1) was found *in situ*, with one Oldowan core and six manuports. Other cranial parts, along with freshly exposed Mode 1 and Mode 2 artefacts, were found on the surface of the DAN5 hominin locality. Similar collections were also found in the same stratigraphic area, approximately 140 metres towards the south-southwest (DAN5-South) and about 50 metres towards the west-northwest (DAN5-West). Based on morphology, shape and size analysis, this skull is assigned to *Homo erectus* (Semaw *et al.* 2020; Baab *et al.* 2022; Bruner *et al.* 2023), and presents some similarities with the *Homo erectus* crania found at Dmanisi (1.77 Ma in Georgia), KNM-ER 42700 (1.6-1.5 Ma in Kenya) and KNM-OL 45500 (0.95 Ma in Kenya), and significant differences with Asian *Homo erectus*. At site BSN12, nearly six kilometers southwest of DAN5, another hominin fossil (right orbital margin and frontal squama) catalogued as BSN12/P1 (HC1), was found closely associated with both Oldowan and Acheulean assemblages (Semaw *et al.* 2020) dated to 1.262 +/- 0.034 Ma. In terms of its anatomy and size, this robust hominin shares characteristics with *Homo erectus* from Indonesia and Eastern Asia, as well as others from the Middle Awash, Ethiopia (OH 9 and BOU-VP-2/66) and Buia, Eritrea (UA-31) (Semaw *et al.* 2020; Baab *et al.* 2022). According to Semaw *et al.* (2020) Acheulean toolmakers produced picks and handaxes alongside Mode 1 stone tools (i.e., Oldowan), whenever they needed sharp cutting flakes.

DISCUSSION AND CONCLUSIONS

The relationships between hominins and Lower Pleistocene material cultures has long been a subject of debate in evolutionary anthropology. However, it is important to note that the scarcity of associations between palaeoanthropological remains and archaeological artefacts can bias our understanding of hominin evolution (Barr & Wood 2024). The exclusive attribution of Oldowan assemblages to *Homo* species is challenged by the temporal and geographical overlap with other taxa such as *P. boisei*, *P. aethiopicus*, *P. robustus* and *A. garhi*. While the ability to manufacture Oldowan artefacts has often been attributed solely to the genus *Homo*, there is growing evidence to suggest that this skill may have been mastered by other hominins, including *Paranthropus*. Indeed, for example Brain *et al.* (1988), Susman (1991), Wood (1997) and more recently Key & Proffitt (2024), highlighted the possibility of a more diverse range of toolmakers. However, Wood & Constantino (2007) noted that is no firm evidence either supporting or refuting *P. boisei*'s ablility to manufacture and use stone tools.

Our research clearly illustrates that Oldowan artefacts are note solely associated with *Homo* species (*H. habilis*, and *Homo* sp., ten occurrences) and *H. erectus*/*ergaster* (six occurrences) but also with *Paranthropus* (at least eight occurrences). The close association of *Paranthropus* remains with Oldowan assemblages, along with anatomical evidence suggesting their potential role in tool-making, indicates that they were involved, alongside early *Homo*, in stone tool production and stone tool use. This observation challenges the traditional notion that stone tool-making is exclusive to and a defining characteristic of the genus *Homo*. Restricting the attribution of tool-making abilities to the genus *Homo*, can no longer be considered valid for the Lower Pleistocene in East Africa. The association between Oldowan assemblages and *Paranthropus boisei* remains, although convincing, has

been a source of debate and hesitation among researchers, particularly when it comes to considering the possibility that *P. boisei* was a stone tool-maker. This hesitation is evident in fluctuating interpretations of fossil finds at various sites. At Oldupai Gorge, the discovery of the FLK level 22 site, which included the famous cranium OH 5 (the holotype of *P. boisei*, originally named *Zinjanthropus boisei* by Leakey in 1959 (Leakey 1959)), initially led to the suggestion that *P. boisei* was a stone tool-maker. However, subsequent discoveries of *Homo habilis* remains led to a revised interpretation by Louis Leakey and co-authors "while it is possible that *Zinjanthropus* and *Homo habilis* both made stone tools, it is probable that the latter was the more advanced tool maker and that the *Zinjanthropus* skull represents an intruder (or a victim) on a *Homo habilis* living site" (Leakey *et al.* 1964: 9). The authors changed their previous interpretation with no substantial new evidence to refute *P. boisei*'s tool-making abilities. Similarly, the discovery of the *P. boisei* mandible KNM-ER 3230 at the FxJj 20 East site (Koobi Fora, Kenya) was not conclusively linked to stone tool-making by Leakey in his 1976 paper (Leakey 1976). This cautious stance again reflects a general reluctance to associate *Paranthropus* with stone tool-making, possibly influenced by the prevailing view that only *Homo* species were capable of such complex behaviours. More recently, at the Nyayanga site in Kenya, the discovery of a *P. boisei* molar in close association with Oldowan artefacts suggests a possible link between *P. boisei* and stone tool use or production. However, Plummer *et al.* (2023) do not definitively attribute the Nyayanga artefacts to a specific hominin genus (i.e., *Paranthropus*), noting rather the presence of early *Homo* remains in Eastern Africa, albeit 1 300 kilometers away "Although not found at Nyayanga, *Homo* was also present in eastern Africa at about the time of Nyayanga deposition (21), so the Nyayanga artifacts cannot be definitively attributed to a specific hominin genus." This scientifically cautious approach illustrates, in my point of view, the reluctance to attribute tool-making to non-*Homo* hominins. These examples highlight a quite persistent bias in paleoanthropological interpretations, which prefer to consider *Homo* as the primary stone tool-makers despite growing evidence of stone tool use or manufacture by the *Paranthropus* species. This bias reflects the difficulties encountered in overturning long-established views within the scientific community, even in the face of new and convincing evidence.

Homo erectus, is predominantly associated with Acheulean assemblages after 1.4 Ma, but there is evidence at least six occurrences of the association of this taxon with Oldowan stone tools in Ethiopia, Kenya and Tanzania and also Eurasia, as for example at Ubeidyia (e.g., Tobias 1966; Belmaker *et al.* 2002) and Dmanisi (e.g. Lordkipanidze *et al.* 2007, 2013; Mgeladze *et al.* 2011).

The frequent association of *Paranthropus* remains with Oldowan assemblages and the association of certain Oldowan sites with *Homo ergaster/erectus*, as indicated in this article, also highlights the complexity of hominin behaviour and tool-making abilities during the Lower Pleistocene. These observations contest the simplistic view that *Homo* species were solely responsible for Oldowan artefacts and suggest a more varied and nuanced picture of the cultural behaviour and cognitive development of Lower Pleistocene hominins, challenging previous assumptions and highlighting the multifaceted nature of hominin evolution.

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