



Beyond the genus stereotype. Who were the first toolmarkers in Africa? Crossed views between archaeology and anatomy

Sandrine Prat

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Beyond the genus stereotype. Who were the first tool-makers in Africa ? Crossed views between archaeology and anatomy.

Au-delà du stéréotype de genre. Qui étaient les premiers artisans en Afrique ? Regards croisés entre archéologie et anatomie.

Sandrine Prat

UMR 7194 MNHN-CNRS-UPVD, Musée de l'Homme, 17 Place du Trocadéro, 75016 Paris

sandrine.prat@mnhn.fr

Abstract

The evolutionary history of hominins and archaeological assemblages has become considerably more complex in the last twenty-five years due to the contribution of innovative analytical methods and new archaeological and paleoanthropological discoveries. The discoveries unearthed in eastern and southern Africa show a high biological and cultural diversity. But what is the nature of the relationships between hominins and the different material cultures? Singularity or plurality of the stone and bone-tool makers and archaeological assemblages? We propose a crossed view on these questions based on investigations of hominin/culture associations in the Late Pliocene and Early Pleistocene fieldwork records, morphology underlying hominins with manual skills as well on interdisciplinary research conducted recently. Our work highlights the plurality of bone and stone tool-makers, in particular *Paranthropus*, *H. habilis* and *H. erectus/ergaster* for Oldowan assemblages. Similarly, in terms of anatomy, the type of dexterity required to make Oldowan assemblages is likely not limited to *Homo* genus. The frequency of *Paranthropus* remains associated with Oldowan assemblages is not negligible and insignificant. The occurrences between Oldowan assemblages and *Paranthropus* seem not to be coincidental and *Paranthropus* should be therefore considered as a stone and bone-tool maker in the same way as it is for early *Homo*.

Keywords :

Hominins, material culture, Africa, Plio-Pleistocene

Résumé

L'histoire évolutive des hominines et des assemblages archéologiques est devenue considérablement plus complexe au cours des vingt-cinq dernières années grâce à l'apport de méthodes analytiques novatrices et de nouvelles découvertes tant archéologiques que paléoanthropologiques. Les découvertes mises au jour en Afrique orientale et australe montrent une grande diversité tant sur le plan biologique que culturel. Mais quelle est la relation entre les hominines et les différentes cultures matérielles ? Singularité ou pluralité des artisans des artefacts lithiques et osseux et des assemblages archéologiques ? Nous proposons un regard croisé sur ces questionnements à partir d'une part d'une analyse des associations hominines/assemblages archéologiques au Pliocène supérieur et au Pléistocène inférieur, et d'autre part de l'anatomie de ces hominines et des recherches interdisciplinaires menées ces dernières années. Notre travail met en évidence une pluralité des fabricants d'outils en os et en pierre, en particulier *Paranthropus*, *H. habilis* et *H. erectus/ergaster* pour les assemblages Oldowayens. De même, d'un point de vue anatomique, le type de dextérité requis pour réaliser les assemblages Oldowayens n'est probablement pas limité au genre *Homo*. La fréquence des restes de *Paranthropus* associés aux assemblages Oldowayens est

49 loin d'être négligeable et insignifiante. Les occurrences entre les assemblages Oldowayens et
50 le genre *Paranthropus* ne semblent pas être une coïncidence et le genre *Paranthropus* devrait
51 donc être considéré comme un artisan des artefacts lithiques et osseux au même titre que les
52 premiers représentants du genre *Homo*.

53

54 **Mots clés :**

55 hominines ; culture matérielle ; Afrique ; Plio-Pleistocene

56

Introduction

The evolutionary history of hominins and archaeological assemblages has become considerably more complex in the last twenty-five years due to the contribution of innovative analytical methods and new archaeological and paleoanthropological discoveries.

Indeed, discoveries unearthed in eastern and southern Africa indicate high biological and cultural diversity during the Late Pliocene and Early Pleistocene. In this context, can we consider that the manufacture of lithic artefacts is specific to the *Homo* genus and a pertinent defining criterion? The definition of our genus (*Homo* genus) and the criteria used to define it are still widely-debated topics, on anatomical/morphological, behavioural or philosophical levels.

Among the criteria proposed to define the *Homo* genus by Leakey and his collaborators (Leakey et al., 1964), (i.e., endocranial volume, habitual erect posture, bipedal gait and power and precision grip), manual abilities appeared to be consubstantial in their definition (Leakey et al., 1964). Finally, tools are accorded a special place in the literature in the definition of the *Homo* genus, even if there are not mentioned in the diagnosis of Leakey et al. (1964) but in the following paragraph entitled "Cultural Association" (see paragraph conclusions and discussion).

The place and role of the archaeological remains in this definition (e.g., Prat, 2022) give rise to the question of the possible relationship between the Oldowan industry and the *H. habilis* specimens. Furthermore, the recent discovery of stone tools dated to 3.3 Ma in Kenya (LOM3 site) (evidence of stone-tools production, Harmand *et al.*, 2015) and cutmarked bones at Dikika site dated to 3.4 Ma in Ethiopia (indicating stone-tool use, McPherron et al., 2010), is 300,000-500,000 years older than the earliest Oldowan technology (Braun et al., 2019, Plummer et al., 2023) and 500,000 years before the oldest known fossils attributed by some researchers to the *Homo* genus [*Homo* sp. remains at Ledi Geraru (Villmoare et al., 2015)]. The stone artefacts from Lomekwi 3 are larger in width, length and thickness than those from Oldowan sites. Two percussion modes have been identified (passive hammer and bipolar percussion). Knappers combined battering activities and core reduction, and may have used mineral blocks in different ways: as anvils, cores in order to produce flakes and/or as pounding tools. The lithic artefacts were found in the same chronological and geographical contexts as specimens allocated to *Kenyanthropus platyops* and are also contemporaneous with individuals attributed to *Australopithecus afarensis* and *Australopithecus deyiremeda*. These puzzling findings have reopened the debate on the association between lithic artefacts and the *Homo* genus (Harmand et al., 2015; Lewis and Harmand, 2016), and highlighted that species living long before the emergence of the *Homo* genus also present manipulative and cognitive abilities for tool-making.

Indeed, far from the once linear perspective of hominin evolution, we currently have a bushy vision of this evolutionary history, with several contemporaneous species or genera in the Pliocene or Early Pleistocene (Figure 1). This points to morphological diversity during these periods. The archaeological data also emphasize diversity in terms of assemblages and a non-linear evolution, with the presence of Oldowan and Acheulean artefacts in a same archaeological site (Dana Aoule Gona, DAN 5 and Busidima North Gona, BSN 12 (Semaw et al., 2020)). In addition, some Oldowan sites are more recent than Acheulean sites. Therefore, it would probably be a good idea to consider that cultural evolution also branches out in different directions.

INSERT FIGURE 1

The Oldowan in the broad sense of the term (which can include the early Oldowan, developed Oldowan etc.) overlaps temporally and geographically with different hominin taxa (early *Homo*, *Paranthropus*, and *Australopithecus* in eastern Africa and southern Africa (Figure 1). The oldest known Oldowan tools found *in situ* have been unearthed in Kenya at the site of Nyayanga, older than 2.6 Ma (Plummer et al., 2023, see paragraph 2.1.3.1). In Ethiopia, the Busidima Formation at Gona has yielded the largest number of early Oldowan sites (e.g., Roche et Tiercelin, 1977, Semaw et al., 1997, Semaw et al., 2003), dating to 2.6-2.5 Ma, with the localities of EG-10, EG-12, EG-13, EG-24, OGS-6a, OGS-7 yielding over one thousand excavated artefacts (e.g. Semaw et al. 1997; Semaw, 2000; Semaw, 2006; Stout et al. 2005, Stout et al. 2010). We can also mention the site of Bokol Dora 1 dated to 2.61-2.58 Ma, Ledi Geraru (Braun et al., 2019), the site of AL 666 at 2.34 Ma (Kimbel et al., 1996; Kimbel et al., 1997, see paragraph 2.1.1.1), the Lokalalei complex in Kenya at 2.34 Ma (Kibunjia et al., 1992; Kibunjia, 1994; Roche et al. 1999, Delagnes and Roche, 2005), and the sites from the Lower Omo Valley in the member F (2.32-2.27 Ma (e.g. Omo 57/5 (see paragraph 2.1.3.2.), Omo 57/7, Omo 84, Omo 123j, Omo 123k, OMO 123m, Omo 1/E-3, Omo 1/E-4, FtJi1, FtJi2, and FtJi5, Merrick et al., 1973; Chavaillon, 1976; Delagnes et al., 2011) and the site of Kanjera South in Kenya, dated to 2 Ma (e.g., Plummer et al., 1999).

Furthermore, several Oldowan sites have been also discovered in Eurasia in association with paleoanthropological remains (Prat, 2018). We can cite Dmanisi in Georgia, where at least five hominin individuals were discovered (Lordkipanidze et al., 2007; Lordkipanidze et al., 2013), in association with Oldowan artefacts (Mgeladze et al., 2011), Sima del Elefante in Spain in the Sierra of Atapuerca (1.22 Ma), where the oldest mandible of the *Homo* genus in Europe was discovered (Parés et al., 2006, Carbonell et al., 2008). We can also mention the Jianshi hominin site in China, also called Longguddong site (with a debatable age, minimum age of 2.14 Ma (Li et al., 2007) or 1.52 Ma +/- 0.092-1.05 +/- 0.04 (ESR dating, mean age of lower layer 8 and layer 4 respectively (Han et al. 2022), with early *Homo* remains and nine stone artefacts in the hominin layer (Li et al., 2017); Yanmou (1.7 Ma), early *Homo* sp./early *H. erectus* associated with four Oldowan lithic pieces (Hou et al., 2010; Zhu et al., 2008). At 1.4 Ma, in the Jordan Valley (Israel), the site of 'Ubeidiya yielded some early *Homo erectus* specimens (one tooth) associated with Acheulean artefacts (Belmaker et al, 2002; Tobias, 1966; Bar-Yosef and Goren-Inbar, 1993).

The oldest occurrences of Acheulean assemblages are Kokiselei 4 (1.74 Ma, Lepre et al. 2011) and Kokiselei 6, where bifacial shaping emerges (Duke et al., 2021), in the western part of Lake Turkana, Kenya and the Konso Gardula sites in Ethiopia. The latter comprise KGA6-A1, which is the earliest site, bracketed between two tuffs, 1.74 and 1.66 Ma (Beyene et al., 2013) and more typical early Acheulean assemblages, such as for example KGA-4 and KGA-10, dated to ~1.45 Ma, KGA-5, KGA-7 to ~1.4 Ma (e.g., Asfaw et al., 1992, Beyene et al., 2013, see paragraph 2.1.6.1), and FLK West in Olduvai Gorge in Tanzania dated to circa 1.7 Ma. This latter site contrasts with Kokiselei 4 and Konso as it points to relatively advanced handaxe shaping skills with very symmetric bifacial flakes (Diez-Martin et al., 2015)

Regarding the *Homo* genus, the first occurrence of early *Homo* is the mandible LD 350-1, Ledi Geraru, in Ethiopia, which could not be attributed to a specific species (Villmoare et al., 2015). This is followed by discoveries in Kenya at Lokakalei 1 alpha KNM-WT 42718, 2.33 Ma (see paragraph 2.1.1.2) (Prat et al., 2005), the temporal bone KNM-BC1 from Chemeron, Kenya, dated to 2.4 Ma, Chemeron, Kenya, (Hill et al., 1992; Sherwood et al., 2002), the maxilla AL

666-1 dated to 2.34, Hadar, Ethiopia (Kimbel et al., 1996; Kimbel et al., 1997, see paragraph 2.1.1.1), the mandible UR 501 dated to ca. 2.4 Ma from Uraha, Malawi (Schrenk et al., 1993; Bromage et al., 1995), and teeth from the Omo basin (Ethiopia) dated to 2.3-2.4 Ma (e.g., Howell et al., 1987; Suwa et al., 1996; Ramirez-Rozzi, 1997).

But what is the nature of relationships between hominins and the different material cultures? Were these early material cultures made by a single or several hominin species?

Here, we address two main aspects. The first is to investigate the hominin/culture associations in the fieldwork record in the Late Pliocene and Early Pleistocene and the second is related to the morphology underlying the manual skills of hominins during these periods.

We reflect upon the morphological and archaeological data in the literature and on interdisciplinary research conducted in recent years. Data from the literature on hominins, archaeological sites, spatial information and context are taken at face value. However, it is sometimes difficult to find information on fossil descriptions, in particular information concerning deposition modes, contexts (*in situ*, on the surface) and distances from the archaeological remains. In view of this difficulty, despite exhaustive research, it is possible that certain associations are overlooked. Concerning the taxonomical names of hominin remains, the presence of specimens named *Homo ergaster* or *Homo erectus* according to different authors, are mentioned here as *Homo ergaster/erectus*. For the archaeological terminology, we have used the terms Oldowan and Acheulean in a broad sense, as used in the cited paper, and we do not make any distinction between early Oldowan, developed Oldowan etc, even if important differences between hominin behaviour at early sites (ca. 2.6–2.3 Ma) in comparison to later ones (ca. 2.0–1.7 Ma) have been attributed to this industrial complex (e.g., Harmand 2009a, Roche et al., 2009; Goldman-Neuman and Hovers 2012, Potts 2012). Indeed Oldowan displays considerable differences in terms of technological complexity, groups together assemblages with disparate characteristics and has been documented in multiple raw material contexts and physical environments in Africa and Eurasia. A huge variability can be seen in production methods depending on raw material choice (see for example Gallotti, 2018 and de Weyver, 2022 for a review). The raw material constraints (linked to the landscape) lead to multiple technical systems of stone-tools production (e.g. free hand and bipolar techniques) which did not develop chronologically and are not continuous. Raw material seems to be a key factor in the diversity of the Oldowan assemblages (e.g. Schick et al., 2006, Harmand et al., 2009b, Proffitt et al., 2022, Delagnes et al., 2023), **2. Overview of archaeological data**

In order to discuss the relationship between hominins and material culture, here we review the eastern and southern African hominin remains from between 3.3 and 1 Ma, and place their relationships into categories of reliability. This catalogue may then serve as a guide for evaluating the association between hominins and archaeology (material culture), in the same way as the taxonomic allocation of postcranial remains for example, by Grine et al in 2022 (Grine et al., 2022).

The relationships between hominins and material culture can be approached on different geographical scales (regional or local).

Concerning the categories of reliability, we define a low-level confidence (LC) association between archaeological and paleoanthropological remains when the hominin remains are in the same chronological and regional frameworks as the archaeological sites.

We define high confidence (HC) associations at a more local scale (Table 1). We divide this category into two subcategories depending on the distance between hominin remains and the archaeological findings.

HC 1: corresponds to an association between lithic and paleoanthropological remains restricted to cases where hominin remains were found in the archaeological site (*in situ* during excavations, or on the surface of the site due to erosion processes).

We divided this category into two subcategories:

HC 1 A, when the taxonomy is clear;

HC 1 B, when the taxonomy of the remains is debated (when it concerns for example some postcranial remains, see Grine et al, 2022).

HC 2: when hominin remains were found outside the excavation (less than 400 metres away) but in the same chrono-stratigraphical layers. We also divide this category according to the taxonomical confidence of the paleoanthropological remains. HC2 A is when the taxonomy is clear and HC2 B when it is debated.

Concerning the low confidence association between archaeological and hominin remains, we can cite as the 2.5 Ma Hata Member of the Bouri Formation which yielded the specimen defining the species *Australopithecus garhi* (Asfaw et al., 1999) and evidence of hominin processing of large mammal remains (de Heinzelin et al. 1999), but no *in situ* artefacts, but are sometimes associated with Oldowan site of Gona, 96 kilometres away. Concerning the Lomekwian, some hominin remains were found in the paleontological collecting area LO5 (Harris et al., 1988) in the vicinity of the archaeological site LOM3 (3.3 Ma) (Harmand et al., 2015; Skinner et al., 2020), in the same spatiotemporal range as the hominin fossils. These include the paratype of *Kenyanthropus platyops* (KNM-WT 38350) (Leakey et al., 2001) and for example, KNM-WT 64060 (Supplementary Informations in Harmand et al., 2015), a hominin molar discovered in 2012 found 600 metres from the LOM3 site. They are deposited in the same chronostratigraphic interval and are pene-contemporaneous with the LOM 3 site.

2.1. High confidence in the association between lithic and paleoanthropological remains in East Africa

A high-confidence association (Table 1) between lithic and paleoanthropological remains between 3 and 1.2 Ma in East Africa is noted in 29 cases (22 cases of High Confidence 1 (hominin remains found in the archaeological site) and seven cases of High Confidence 2 (hominin remains found less than 400 metres from the excavation but in the same chrono-stratigraphical layers) (Table 2).

INSERT Table 1

INSERT Table 2

2.1.1. Association between Oldowan and *Homo habilis* sensu lato

The oldest evidence of lithic-hominin association between Oldowan and early *Homo* specimens comes from the region of Hadar in Ethiopia. A *Homo* aff. *habilis* maxilla (AL 666-1) was found at the site AL 666, dated to 2.34 Ma, alongside an Oldowan assemblage.

2.1.1.1. AL 666 (Oldowan), Ethiopia, Afar Region, AL 666-1 (*Homo* aff. *H. habilis*), 2.34 +/-0.07 Ma, High confidence: HC 1 A

In Ethiopia, in the Makaamitalu Basin (Kada Hadar, Afar Region), archaeological and hominin remains were unearthed at the AL 666 site. Stratigraphically, they lie in the lowermost part of the Busidima Formation, underlying the 2.36 +/- 0.07 Ma BKT-3 tephra (Carpisano, 2012) and are dated to 2.34 +/-0.07 Ma. The density of artefacts is low over an area of 20 m² and mostly represented by flakes. None of the artefacts were retouched (Kimbel et al., 1996, Plummer 2004). The raw material was carefully selected, with a high frequency of homogenous and fine-grained raw materials (Goldman-Neuman and Hovers, 2012). According to the discoverers (Kimbel et al, 1996), the lithic assemblage is typical of an Oldowan assemblage. On the surface, at the base of the AL 666 hill, a maxilla (AL 666-1) was discovered. An excavation was undertaken to identify the *in situ* horizon, which led to the discovery of *in situ* lithic elements but no additional hominin remains. Thirty-four stone tools including 14 excavated *in situ* were recovered from the AL 666 locality. The hominin maxilla (AL 666-1) presents unambiguous affinities with early *Homo* (Kimbel et al., 1996) and has been assigned to *Homo* aff. *H. habilis*, based on morphological and metrical comparisons (Kimbel et al. 1997).

2.1.1.2. Lokalalei 1, Gajh5 (Oldowan), Kenya, West Turkana, KNM-WT 42718 (early *Homo*), 2.34 +/-0.04 Ma, High confidence : HC 2 A

In Kenya, in the western part of the Lake Turkana, the Lokalalei complex of sites (Kibunjia, 1994) has unearthed one hominin tooth dated to 2.34 +/-0.04 Ma. This tooth KNM-WT 42718 (Prat et al., 2005) is attributed to early *Homo* and was found at Lokalalei alpha, in the vicinity of, but not strictly associated with the Oldowan Lokalalei 1 site. Indeed, this early *Homo* specimen from Lokalalei 1alpha, is a surface finding discovered 100 m south of the archaeological site Lokalalei 1. The duration of accumulation of the 6.2-m- thick fine sandstone and claystone deposits that separate the sites Lokalalei 1alpha and Lokalalei 1 can be estimated at a time scale of 10,000 to 100,000 years. Considering the classical measurement error (0.04 to 0.5 Myr) for fission track and/or K/Ar, 40Ar/39Ar ages obtained on various tuffs in Eastern Africa, the two sites have been considered to be chronologically close (Prat et al., 2005).

2.1.1.3. Fj-1a (Oldowan), Fejej Region, Ethiopia, Fj-1-Hd1, -Hd3, Hd4 (*Homo* aff. *H. habilis*), 1.95-1.9 Ma, High confidence: HC 2 A.

At the northern limit of the Koobi Fora formation, in the Omo-Turkana Basin, the region of Fejej yielded the FJ-1a archaeological site with faunal and lithic assemblages in a primary context, referred as Oldowan (e.g., Asfaw et al., 1991, de Lumley and Beyene 2004, Barsky et al. 2011). Geochronological data from the sequence indicate an age of nearly 1.9 Ma for the FJ-1a archaeological level (Chapon et al., 2005). Raw materials (mainly quartz and basalt) were locally available and carefully selected. The direct knapping method was longer and more complex when knapping basalt (Barsky et al. 2011). Located 180 metres from FJ-1a, the locality FJ-1e (Unit 3) yielded three hominin dental remains belonging to the same individual (Fj-1-Hd1 lower right first molar; Fj-1-Hd3, lower right second premolar; Fj-1-Hd4, lower left third molar). These remains are attributed to *Homo* aff. *H. habilis* based on their morphology and dimensions (de Lumley & Marchal 2004).

2.1.1.4. DK site, Bed I (Oldowan), Olduvai Gorge, Tanzania, OH 24 (*Homo habilis*), circa 1.87-1.84 Ma, High confidence HC 2 A.

DK is the oldest site at Olduvai. Artefacts and bones at DK occur in the interval between the Tuff IB and Bed I basalt lava, dated between 1.877 +/- 0.013 Ma and 1.848 +/- 0.003 Ma (Deino, 2012). It unearthed Oldowan assemblage (Leakey, 1971, de la Torre and Mora, 2005). The cranium OH 24 which corresponds to one of the most complete remain allocated to *Homo habilis* has been found 300 metres to the east to the original site (Leakey et al., 1971), but no artefacts.

2.1.1.5 Ewass Oldupa site, Bed I (Oldowan), Olduvai Gorge, Tanzania, OH 65 (*Homo habilis*), circa 1.82 Ma, High confidence HC 2 A.

In Olduvai Gorge Bed I, an almost intact maxilla (OH 65) from Geological locality 64 was discovered 350 metres northeast of the Ewass Oldupa site (Geological Locality 63), which contains cut-marked bones and an Oldowan assemblage mainly made on quartzite. Flakes are the dominant product (Mercader et al. 2021). All these remains are from strata dated to ~1.82 Ma (Blumenschine et al., 2003, Deino, 2012, McHenry, 2012). Labial striations on the anterior teeth suggest that OH 65 was right-handed in manipulating objects during oral processing (Fruyer et al., 2016). OH 65 is assigned to the *Homo* genus, and has been allocated to *Homo habilis* (Blumenschine et al., 2012, Clarke, 2012). However, Spoor and co-authors argue that its morphology is not compatible with the holotype of *Homo habilis* (OH 7) and lacks the facial morphology observed in *Homo rudolfensis* (Spoor et al., 2015) contra Blumenschine et al (2012).

2.1.1.6 MNK Skull, Middle Bed II (Oldowan), Olduvai Gorge, Tanzania, OH 13, OH 15 (*Homo habilis*), circa 1.67 Ma, High confidence HC 1 A

MNK Skull (Geological Locality 88, Mary Nicol Korongo, MNK, Middle Bed II) is an archaeological site where two hominins allocated to *Homo habilis* (OH 13, and OH 15) were discovered *in situ* and one (OH 14) on the surface. It is dated to circa 1.67 Ma (de la Torre et al., 2021). OH 13 consists of cranial vault bones, parts of the maxilla, mandible with dentition. It is one of the paratypes of *Homo habilis* (Leakey et al., 1964, Tobias 1991). This individual represents the most recent specimen of *Homo habilis* in east Africa (Spoor et al., 2015). OH 15 consists of dental remains (one upper canine and two third upper molars) and is attributed to *H. habilis* (Tobias, 1991). Alongside these hominin discoveries, important faunal and archaeological assemblages were unearthed by Mary Leakey (Leakey 1971). The stone tool assemblage is typical of the Oldowan, with no technological elements heralding the appearance of the Acheulean, and a debitage dominated by quartzite and an overabundance of lava cores (de la Torre et al., 2021).

2.1.2. Association between the Oldowan, *Homo habilis* and *Paranthropus boisei*

2.1.2.1. FLK level 22 (Oldowan), Olduvai Gorge, Tanzania, OH 5 (*P. boisei*), High confidence HC1 A; OH 35 (*P. boisei*) or (*H. habilis*), High confidence HC 1 B), OH 6 (*H. habilis*), High confidence HC 1 A, 1.84 Ma

FLK level 22 yielded a dense Oldowan assemblage (more than 255 artefacts) and mammal fossils (more than 3500) (Leakey, 1971) comprising four hominin individuals, including the cranium OH 5, the holotype of the species *Paranthropus boisei* (formerly *Zinjanthropus boisei*, Leakey, 1959). These hominin remains are allocated to *H. habilis* and *P. boisei* (Tobias, 1991).

One of these four hominin remains was a surface finding (OH 44, right upper first molar), one (OH 35) represents some postcranial bones (tibia and fibula (Leakey et al., 1964) with an uncertain taxonomical allocation, as they are associated with cranio-dental remains, one is attributed to *H. habilis* (OH 6, lower third premolar, right upper molar, right upper second incisor and six calvaria fragments, Tobias, 1991), and another is OH5, the *P. boisei* holotype. The age of the *Zinjanthropus* surface is constrained by tuffs IB and IC, dated respectively to 1.845 +/- 0.002 Ma and 1.839 +/- 0.005 Ma (Blumenschine et al, 2003; Blumenschine et al, 2012).

2.1.2.2. FLK NN level 3 (Oldowan), Olduvai, Tanzania, OH 7 cranial remains (*H. habilis*): High confidence HC 1 A; OH 7 hand remains (*H. habilis* or *P. boisei*): High confidence HC 1 B; OH 8 (*H. habilis*): High confidence HC 1 B, 1.84 Ma

The paleoanthropological remains from site FLK NN level 3, unearthed in Bed I at Olduvai consist of abundant Oldowan stone artefacts and six sets of paleoanthropological remains assigned to three catalogue numbers: a) a juvenile mandible, parietals and other isolated cranial fragments (OH 7, the holotype of *H. habilis*); b) a set of 12 hand bones, also catalogued as OH 7; c) 12 foot bones (OH 8); d) an isolated clavicle (OH 48); e) OH 43 two metatarsals; and f) radial shaft (OH 49). The association between the cranial remains and OH 7 hand bones seems to have been based on a parsimonious hypothesis (Grine et al., 2012), as for OH 8. Moreover, some researchers have allocated these hand bones to *Paranthropus* (Moyà-Solà et al., 2008) (see paragraph 3). The date proposed for OH 7 is 1.84 Ma (Deino, 2012). OH 8 was first reported by Day and Napier in 1964 (Day and Napier, 1964), and designated by Leakey et al. in 1964 (Leakey et al., 1964) as one of the paratypes of *Homo habilis*.

2.1.2.3. FxJj 38 (Oldowan), Koobi Fora, Kenya, KNM-ER 1805 (*Homo* sp.), High confidence HC 1 B, and KNM-ER 1806 (*P. boisei*), High confidence HC 1 A, 1.78 and 1.52 Ma or 1.85 Ma

Two hominin remains were discovered in the Koobi Fora Region, in area 130. The first one (KNM-ER 1805) was found *in situ* in deposits stratigraphically located below the Okote Tuff complex and consists of a cranium and associated mandible. It has been allocated to early *Homo* (*Homo* sp., Leakey 1974), but also to other species and genera (see Prat, 2002). It displays a number of unique features differentiating it from other hominins, and should not be considered as a standard *Homo habilis* male (Prat, 2002). Fifteen metres from this specimen, on the surface, a large mandible (KNM-ER 1806) allocated to *P. boisei* was discovered (Leakey 1974). Excavations at these two localities unearthed faunal remains, as well as a light scatter of stone artefacts, but no additional hominin remains. Forty metres east of these paleoanthropological localities, on the same stratigraphical horizon, lies the archaeological site FxJj 38 North West. The composition of the lithic assemblage, with a large chopper component, is consistent with that of Olduvai Bed I and therefore allocated to the Oldowan (Harris & Herbich, 1978) and represents one of the type localities for the Developed Oldowan of Koobi Fora (Mana et al., 2019). These hominin remains and archaeological site belong to the KBS Member, below the base of the Okote Member and above the KBS Tuff. These sites are, according to Mana and co-authors, broadly constrained between 1.78 and 1.52 Ma (Mana et al., 2019). This is in contradiction with the interpretation of Feibel and collaborators who estimated its age at 1.85 Ma (Feibel et al., 1989).

2.1.3. Association between Oldowan artefacts and *Paranthropus* (*P. aethiopicus*, *P. boisei*)

2.1.3.1. Nyayanga, excavation 3 (Oldowan), Lake Victoria, Kenya, KNM-NG 77316 (*P. boisei*):
High confidence: HC 1 A, 3.03 -2.58 Ma

In Kenya, the site of Nyayanga, on the southern margin of the Winam Gulf of Lake Victoria has revealed one of the oldest known Oldowan assemblages, dated between 3.032 Ma and 2.581 Ma (Plummer et al., 2023). This site yielded 135 artefacts *in situ* (excavations 3 and 5) and 195 on the surface, as well as bones, including cut-marked bones. The flakes were removed from cores using unifacial, bifacial and multifacial reduction, comparable to other Oldowan localities. The use wear on the lithic material, as well macro and micro traces, indicate the processing of plant tissue and faunal remains. In excavation 3, one fragment of a left lower molar (KNM-NG 77316) was found *in situ*, spatially associated with Oldowan artefacts, and one left upper molar (KNM-NG 77315) came from the surface (see paragraph 5). These two teeth, based on the morphology and metrics are assigned to the *Paranthropus* genus.

2.1.3.2. Omo 57-5 (Oldowan), Lower Omo valley, Ethiopia, Omo 57/5-1972-371 (*P. aff. P. aethiopicus*): high confidence: HC 1 A. 2.32 Ma to 2.23 Ma

In Ethiopia, in the Lower Omo Valley, at the archaeological locality Omo 57-5 (Member F of the Shungura Formation), the excavation of 40 m² unearthed four fragments of hominin teeth, associated with a quartz flake found *in situ* and 16 artefacts (cores and flakes) on the surface (Coppens et al., 1973, Chavaillon, 1976). One of these paleoanthropological remains (Omo 57/5-1972-371, a fragment of a left lower second premolar) has been assigned to *P. aff. aethiopicus* based on its morphology (Coppens et al. 1973, Coppens, 1977, Suwa 1990, Wood and Leakey 2011).

Another hominin dental remain (Omo 57/5-1972-319), a left upper first premolar, is considered to be indeterminate (White, 1988) or an indeterminate non-robust hominin (Suwa 1990), or allocated to the *Homo* genus (*aff. Homo* sp., Wood and Leakey 2011). According to de la Torre in 2004, the Omo 57 locality provides clear evidence of flaking activities showing ordered and systematic knapping processes, and does not derive from the fluvial deposition of natural fragments. The lithic assemblage is assigned to the Oldowan (de la Torre, 2004). The Member F deposits are dated to 2.32 Ma to 2.23 Ma (McDougall and Brown, 2008).

2.1.3.3. Kokiselei 1, FxJh 6 (Oldowan), Kenya, KNM-WT 37744, KNM-WT 37747, KNM-WT 37748, KNM-WT 37100 (*P. boisei*): high confidence: HC 1 A. 1.79 Ma

The Kokiselei 1 site (FxJh 6) is part of the Kokiselei complex, located in the upper part of the Kaitio member, between the Koobi Fora and KBS tuffs. This site is dated to 1.79 Ma. The 38 m² excavation yielded more than 248 faunal remains (Brugal et al., 2003) and 1100 artefacts allocated to the Oldowan (Roche et al., 2003, Arroyo et al., 2020). On the surface of the excavation, on the same square, four complete teeth [left upper canine (KNM-WT 37744), left upper first molar (KNM-WT 37747), right upper third molar (KNM-WT 37748), left lower third molar (KNM-WT 37100)] and two molar fragments were discovered in 1997 and 1998. A left upper first premolar and a left lower third molar from the same area were collected in 1986 and 1987. Based on their morphology and dimensions, all the teeth are attributed to *P. boisei* (Prat et al., 2003).

2.1.3.4. FxJj 20 (Oldowan), Koobi Fora, Kenya and KNM-ER 3230 (*P. boisei*): High confidence: HC 1 A. 1.65 +/- 0.05 Ma

At FxJj 20 East, in Koobi Fora Area 131, a hominin mandible with complete dentition (KNM-ER 3230) was recovered *in situ* from the site excavated by J.W.K. Harris in 1975 in tuffaceous floodplain silts of the Okote Tuff complex (Leakey 1976; Harris and Herbich, 1978). Based on the morphologies and metrics of the mandible and teeth, KNM-ER 3230 has been assigned to *Paranthropus boisei* (Leakey 1976; Leakey and Walker, 1985; Wood, 1991) and dated to 1.65 +/- 0.05 Ma (Feibel et al., 1989). According to Harris and Herbich, 1978, a low-density scatter of bones and lithic artefacts were found on the same horizon as the hominin, and the vertical distribution of the lithic assemblage shows that the hominin mandible was stratigraphically located approximately 10-15 centimetres above the main artefact-bearing horizon (Harris and Herbich, 1978). It should be noted that despite this association, Richard Leakey did not want to associate the two in his 1976 paper. We can wonder whether Richard Leakey would have interpreted the finds in this way if the remains had belonged to the *Homo* genus (see paragraph 5).

2.1.3.5. Chesowanja GnJ1/6E (Oldowan), Chesowanja, Kenya, KNM-CH 304 (*P. boisei*): High confidence: HC 2 A; Chesowanja GnJ2 (Oldowan), Chesowanja, Kenya, KNM-CH 1, KNM-CH 302, KNM-CH 304 (*P. boisei*): High confidence: HC 2 A 1.42+/-0.07 Ma

At Chesowanja, near Lake Baringo in Kenya, in the Chemoigut Formation layers, remains allocated to *P. boisei* were found close to an Oldowan assemblage (Carney et al., 1971; Bishop et al. 1975; Gowlett et al. 1981). The hominin remains consist on a right hemi-face and anterior cranial base (KNM-CH 1); dental fragments (KNM-CH 2) and cranium fragments (KNM-CH 304). The cranium KNM-CH 304 consists of five cranial vault fragments labelled A-E and is allocated to *P. boisei* (Gowlett et al. 1981). It has been found 15 metres from the site GNJ1/6E (40 m² excavated) where 1000 Oldowan artefacts were found *in situ* with limited vertical distribution. The other specimens also allocated to *P. boisei* were found in GnJ2, where artefacts scatters occur on the surface, but only one rewarding *in situ* occurrence (Carney et al., 1971; Bishop et al. 1975; Gowlett et al. 1981). According to these authors, this association must be considered to be more than coincidental (see paragraph 5). The basalt member at the base of the Chesowanja Formation is dated at 1.42+/-0.07 Ma.

2.1.3.6. BK site level 4 (Oldowan), Olduvai Gorge, Tanzania, OH 80 (*P. boisei*): High confidence: HC 1 A. 1.34 Ma

At Olduvai Gorge, in Tanzania, in Bed II, the BK Site yielded a partial *Paranthropus boisei* skeleton (Domínguez-Rodrigo et al., 2013). OH 80 was found *in situ* in level 4, which is characterized by a large Oldowan assemblage and a huge number of vertebrate fossils, some of which bear butchery marks (Domínguez-Rodrigo et al., 2009). The specimen comprises four postcranial bones (distal part of a left humeral diaphysis, proximal half of a right radius, much of the right femoral shaft and part of a tibial midshaft) in direct association with nine upper teeth (left and right first and second incisors, right first premolar, left second premolar, left first molar, right second incisor). Based on their morphology, dimensions and section properties, these remains are allocated to *P. boisei* (Dominguez-Rodrigo et al., 2013). It is the first partial skeleton attributed to this taxon and is dated to 1.34 Ma.

2.1.4. Association between Oldowan and *Homo erectus/ergaster*

2.1.4.1. PTK site (Oldowan), Olduvai Gorge, Tanzania, OH 86, (*H. erectus*-like): High confidence: HC 1 B. 1.84 Ma

At the PTK (Philip Tobias Korongo) site at Olduvai Gorge in the third level, a manual proximal phalanx (OH 86) was unearthed (Domínguez-Rodrigo et al., 2015) alongside a rich Oldowan assemblage (Domínguez-Rodrigo et al., 2015). OH 86, dated to 1.84 Ma, represents the earliest known modern-human like hand anatomy. This specimen contrasts in size and shape not only with *Australopithecus* or *Paranthropus* but also with the OH7 hand. Taxonomically this specimen is assigned to the *Homo* genus and differs from OH 7 (*H. habilis* holotype). However, it is difficult to confidently assign OH 86 to this latter taxon due to the lack of associated craniodental remains and comparative material securely attributed to *H. erectus/ergaster*. However, Díez-Martín and co-authors considered OH 86 as an *H. erectus*-like hominin in their paper (Diez-Martín et al, 2015).

2.1.4.2. Naiyena Engol 1, FxJh 5, (Oldowan), West Turkana, Kenya, KNM-WT 37745 (aff. *H. ergaster/H. erectus*): High confidence: HC 1 A, 1.75 +/- 0.05 Ma

The site of Naiyena Engol 1 (NY1 1.75+/-0.05 Ma) is a large site (artefacts collected over a surface of 585 m² and from the 55 m² excavation) which has yielded a considerable collection of artefacts (more than 2400 plotted pieces), corresponding to an Oldowan assemblage (Roche et al., 2003). On the surface of the excavated area, a right lower first premolar (KNM-WT 37745) was discovered. Based on its morphology and metrics, this specimen is assigned to *Homo* aff. *H. ergaster* (Prat et al., 2003).

2.1.4.3. Melka Kunture Garba IV (level E) (Oldowan), Melka Kunture, Ethiopia, MK 81 GAR IVE 0043 (early *Homo erectus/H. ergaster*). High confidence: HC 1 A. Slightly older than 1.7 Ma

The Garba IV mandible (MK 81 GAR IVE 0043) from Melka Kunture was found *in situ* in 1981 during the excavation of level E, while opening an area of 2 square metres. Based on its stratigraphical position immediately below the “Grazia tuff” and its normal polarity, this level should be around or slightly older than 1.7 Ma (e.g., Morgan et al., 2012, Tamrat et al., 2014, Gallotti and Mussi, 2015). Layer E yielded 504 unworked lithic objects and 718 artefacts. The lithic assemblage from Garba IV level E was deposited during a relatively short lapse of time. It is allocated to the Oldowan and shows that hominins had good knowledge of raw material suitability (obsidian being the most frequently exploited raw material) (Gallotti and Mussi, 2015). The mandible belongs to a child whose age at death was estimated between 3 and 4 years (Condemi, 2004) or between 2.5-3.5 years old based on the tooth development pattern (Zanolli et al., 2016). It is allocated to early *Homo erectus/Homo ergaster* (Condemi 2004). The inner dental morphology also suggests that the Garba IV mandible is a robust early *Homo* specimen (Zanolli et al., 2016).

2.1.4.4. Melka Kunture Gombore I (Oldowan), Melka Kunture, Ethiopia, Gombore IB-7594 (*Homo* sp. or *H. erectus*): High confidence: HC 1 B. 1.5-1.6 Ma

In the Melka Kunture site complex in Ethiopia, a well-preserved distal portion of a left humerus (Gombore IB-7594, formally Melka Kunture 3, or MK3) was discovered in 1976 during the excavation of the site of Gombore I, directed by J. Chavaillon (Chavaillon et al., 1977). This postcranial hominin remain was found in the southern sector of the excavation *in situ* in unit 2 of level B, which includes rich faunal and Oldowan assemblages with a predominance of pebble tools, mainly side choppers (Chavaillon and Berthelet, 2004). They are dated to 1.6-1.5

Ma (Morgan et al., 2012; Tamrat et al., 2014, Cazenave et al., 2017). Gombore IB-7594 was referred to *Homo* sp. (Chavaillon et al., 1977), but based on morphometric affinities, Lague and Jungers considered that this specimen could plausibly belong to *Paranthropus boisei* (Lague and Jungers, 1996). However, according to the majority of authors, this specimen is part of the *Homo* genus (Senut, 1979). Coppens considered that it was too robust to be *Homo habilis* and referred it to *Homo erectus* (Coppens, 2004). It is also allocated to *Homo* sp. based on geometric morphometrics (Di Vincenzo et al. 2015). The study of endostructural organization shows that this robust *Homo* aff. *erectus* humerus is different to *Paranthropus* and close to the modern human humerus (Cazenave et al., 2017).

2.1.5. Association between the Oldowan, Acheulean and early *Homo erectus*/*Homo ergaster*

2.1.5.1. DAN 5 (Oldowan and Acheulean), Dana Aoule Gona, Afar Region, Ethiopia, DAN5/P1 (early *H. erectus*/*H. ergaster*), High confidence: HC 1 A. 1.6-1.5 Ma

In Ethiopia, the Dana Aoule Gona localities in the Afar regions have yielded some hominin remains in association with both Oldowan and Acheulean assemblages, and also some cut-marked bones (Semaw et al. 2020). This is the first and unique occurrence of such an association (hominins plus Oldowan and Acheulean) in East Africa. The age of the DAN 5 hominin and lithic assemblage is close to ~1.6 to 1.5 Ma. The well-preserved hominin cranium DAN5/P1 was discovered in the DAN 5 locality, with the occipital and left maxilla found *in situ* along with six manuports and one Oldowan core. Other cranial parts and also freshly eroded Oldowan and Acheulean artefacts were collected on the surface of the DAN5 hominin site. Oldowan and Acheulean assemblages were also discovered in the same general stratigraphical context, ~140 m south-southwest (DAN5-South) and ~50 meters west-northwest (DAN5-West). The assemblages are composed of unshaped cores, Oldowan and Acheulean (large cutting tools) productions. Based on morphological and metrical data, this cranium is allocated to *Homo erectus* (Semaw et al., 2020, Baab et al., 2022, Bruner et al., 2023), and shows similarities to some *Homo erectus* crania [Dmanisi (1.77 Ma, Georgia), KNM-ER 42700 (1.6-1.5 Ma, Kenya) and KNM-OL 45500 (0.95 Ma, Kenya)] and some differences to Asian *Homo erectus*.

2.1.5.2. BSN12 (Oldowan and Acheulean), Busidima North Gona, Afar Region, Ethiopia, BSN12/P1 (early *H. erectus*/*H. ergaster*), High confidence: HC 1 A. 1.26 +/-0.03 Ma

At BSN12, almost 6 km southwest of DAN5, another hominin (BSN12/P1) was unearthed in direct association with both Oldowan and Acheulean assemblages (Semaw et al. 2020). It is also associated with the Boolihinan Tuff, which is dated, based on geochemical affinities, to 1.262 +/-0.034 Ma. The tephra was found cemented on the BSN12/P1 parietal and both Oldowan and Acheulean artefacts. The BSN12/P1 hominin also includes some parts of the right orbital margin and frontal squama. Based on its anatomy and dimensions, this robust hominin shares *Homo erectus* features (Semaw et al., 2020, Baab et al., 2022) and is similar to Indonesian and Eastern Asia hominins, as well as to OH 9 and BOU-VP-2/66 (Middle Middle Awash, Ethiopia) and UA-31 (Buia, Eritrea).

2.1.6. Association between the Acheulean, *Homo erectus* and *P. boisei*

2.1.6.1. KGA 10-1 (Acheulean), Konso-Gardula, Ethiopia, KGA10-506, KGA10-525, KGA10-565, KGA10-570, KGA10-900, KGA10-1455, KGA10-1720, KGA10-2705 (*H. erectus*): High confidence HC 1 A; KGA10-2741 (*P. boisei*): High confidence: HC 1 A: 1.4 Ma and KGA 4E (Acheulean), *Homo* sp., High confidence: HC 1 A. 1.44 Ma

The first evidence of Acheulean stone tools occurs at 1.76 Ma in the Kokiselei 4 site (Lepre et al. 2011) with no associated hominin remains. The oldest association between *Homo erectus* (KGA 10-1) and an Acheulean assemblage is from Konso-Gardula, dated to 1.4 Ma (Asfaw et al. 1992, Beyene et al., 2013; Beyene et al., 2014). This association have been shown for example in the locality KGA 10, with the evidence of *H. erectus* remains (Suwa et al., 2007) (KGA 10-1 (left mandible with P4-M3, KGA10-620 (right parietal fragment), KGA 10-656 (right parietal and frontal fragment); 1.42 Ma) found less than 50 meters from the excavation of

KGA10-A10 which yielded Acheulean picks and cores, and 300 meters west from KGA10-A6 (surface collection, Acheulean cores, handaxes and picks) (Beyene et al., 2014) and at the locality KGA4-A1 with a third upper molar (surface data, KGA4-14, *Homo* sp, 1.44 ± 0.05 Ma). In the locality KGA10, nine *P. boisei* were also discovered alongside dry grassland fauna (Suwa et al., 1997) (KGA10-506, left maxilla with teeth; KGA10-525, partial skull; KGA10-565, right upper molar; KGA10-570, mandible, KGA10-900, molar fragments; KGA10-1455, left parietal; KGA10-1720, left lower M3; KGA10-2705, right lower M2; KGA10-2741, molar fragments) less than 500 meters from the *in situ* Acheulean site KGA10-10 and 300 meters from KGA10-A6 (surface collection, Acheulean cores, handaxes and picks) (Beyene et al., 2014). Some cut-marked and modified bones were also unearthed in this locality (Echassoux, 2012). At KGA13-A1, five kilometres from these sites, a bone handaxe was also discovered (Sano et al. 2020). KGA 10 lies stratigraphically between tuffs dated to 1.41 ± 0.02 Ma and 1.43 ± 0.02 Ma. The abundance of Acheulean artefacts contrasts with layers bearing *H. erectus* and/or *P. boisei* in the Omo-Turkana basin with no Acheulean artefacts.

2.2. The case of southern Africa

It should be noted that the depositional and conservation modes of fossil and lithic remains differ between East Africa (open-air sites) and South Africa (karsts). The confidence index (High Confidence) used for remains from East Africa cannot be applied to karstic deposits and the dating of karstic members is controversial. As a result of this depositional mode, even if remains are found in the same stratigraphical member, it is difficult to infer strict contemporaneity between lithic and paleoanthropological remains.

However, some lithic assemblages, and bone artefacts have been discovered in association with individuals allocated to *P. robustus* and early *Homo* specimens. Sometimes both taxa were found in the same levels, but sometimes only *P. robustus* remains were discovered.

Here, we present some examples. At Sterkfontein, the Member 5 East lower (Member 5 Oldowan infill), dated to around 2.18 ± 0.21 Ma (Granger et al., 2015), yielded remains allocated to *P. robustus*, as well as 3513 lithic artefacts all attributed to the Oldowan (Kuman and Clarke, 2000; Kuman, 2009). On the other hand, in the member 5 West (Sterkfontein Acheulean infill), dated between 1.3 and 1.1 Ma (Herries and Shaw, 2011), an Acheulean assemblage was found in association with a bone tool ($n=1$) and *Homo* remains (Kuman and Clarke, 2000). At Drimolen Main Quarry (MNQ), recently dated to c. 2.04-1.95 Ma (Herries et al., 2020), some early *Homo* and *P. robustus* remains, as well as Oldowan stone artefacts and bone tools ($n=14$) were discovered (Keyser et al., 2000; Moggi-Cecchi et al., 2010; Stammers et al., 2018; Backwell and d'Errico, 2008). A similar discovery of six early *Homo* remains, 113 *P. robustus*, an Oldowan assemblage and bone tools ($n=32$) (Brain, 1993; Brain and Shipman, 1993; d'Errico and Backwell, 2003; Backwell and d'Errico, 2003; Caruana, 2017) was made in the Member 1 of Swartkrans, dated between 2.4 and 1.8 Ma (Pickering et al., 2019). In the Member 2 of Swartkrans, dated to c. 1.4 Ma (Balter et al., 2008), an Acheulean assemblage with bone tools ($n=11$) and both *Homo* and *P. robustus* remains (Brain, 1993; d'Errico and Backwell, 2003; Kuman, 2007) were unearthed. In the Member 3 of Swartkrans, dated to circa 0.96 Ma (Gibbon et al., 2014), only one hominin species (*P. robustus*) was found in association with an Acheulean assemblage and bone tools ($n= 41$) (Brain, 1993; d'Errico and Backwell, 2003; Kuman, 2007). A similar discovery was made at Cooper's D, dated between 1.4 and 1.0 Ma, in the form of seven *P. robustus* remains, 49 stone artefacts [not allocated to a specific industry for the moment due to the small number of artefacts (Sutton et al. 2017)] and a bone tool ($n=1$) (Steininger et al., 2008; de Ruiter et al., 2009; Hanon et al., 2021).

These examples support the hypothesis that *P. robustus* probably made and/or used stone and bone tools (e.g., Sterkfontein, Member 5 East lower (Member 5 Oldowan infill), 2.18 ± 0.21 Ma, Oldowan; Coopers' D, 1.4-1 Ma, indeterminate for the moment; Swartkrans Member 3, c. 0.96 Ma, Acheulean). The attribution of artefacts to *Homo* rather than *Paranthropus* or both taxa appears once again to be more ideological than scientific.

3. Overview of anatomical/morphological data

The manipulative abilities linked to the evolution of increasingly complex tool technologies in the hominin lineage (Marzke, 1997) can be defined as pad-to-pad precision grasping *sensu* Napier (1956) and Almécija and Alba (2014), and in a broader sense, forceful precision grips and precision handling *sensu* Marzke (Marzke, 1997). Morphological evidence (although limited) suggests that this anatomical ability to use or even make stone tools is not exclusive to the *Homo* genus and is also observed in two different hominin genera: *Australopithecus* (*afarensis*, *africanus*, *sediba*) and *Paranthropus* (*robustus* and *boisei*).

Regarding the Pliocene hominins, no post-cranial element has been allocated to *K. platyops*, a species in the same temporal and geographical framework as the site of Lomekwi 3 (Harmand et al., 2015). Conversely, a lot of hand bones, including phalanges, carpal and metacarpal bones, attributed to *Australopithecus afarensis* are also attributed to the same chronological framework as the site of LOM3. They mainly come from the Hadar localities in Ethiopia (e.g., AL 333/333w, AL 438, AL 444, AL 734) (Bush et al., 1982; Drapeau et al., 2005; Johanson et al., 1982; Ward et al., 2012). Different functional interpretations have been put forward for this taxon, based on wrist and hand morphology, as well as intrinsic hand proportions. According to Marzke (Marzke, 1983, 1997, 2013, Tocheri et al. 2003), *A. afarensis* individuals were able to use pad-to-side as well as three-jaw chuck precision grips and precision handling (probably less effective precision handling and power squeeze grips). These manipulative abilities (forceful precision grips and precision handling), are required for stone tool-making and activities and are considered to be specific to the human hand. They may have been used to apply pressure to tools in activities such as cutting, digging, pounding, chopping or stone-throwing (Marzke et al., 1997). For some authors, *A. afarensis* is mainly characterized by human-like hand functions, illustrated for example by modern human-like manual proportions with a relatively long thumb and short medial digits (e.g., Alba et al., 2003; Almécija and Alba, 2014, Drapeau et al., 2005; Ward et al., 2012). However, Rolian and Gordon (Rolian and Gordon, 2013) suggest that the manual proportions of *A. afarensis* are intermediary between extant humans and gorillas, and deduce that *A. afarensis* did not possess the efficient precision grip typical of modern humans. In 2022, Kivell and co-authors stressed the importance of acknowledging that precision-grasping abilities in *A. afarensis* could have evolved in response to manipulative behaviours not linked to lithic tools (e.g., food processing), even if evidence of tool-using behaviours (McPherron et al., 2010) at Dikika (Ethiopia), close to an *A. afarensis* juvenile specimen Dikika 1, and the discovery of the LOM3 (Harmand et al., 2015) suggest that stone tool and stone use behaviours may have been part of the behavioural repertoire of *A. afarensis* (Kivell et al. 2022).

Evidence from other non-*Homo* Pliocene hominins, from southern Africa must also be scrutinized. Several phalangeal, carpal and metacarpal remains from the site of Sterkfontein are mostly assigned to *Australopithecus africanus*. Specimens from the Member 4 deposit (recently dated to 3.4 Ma; Granger et al., 2022) indicate that *A. africanus* was able to use a human-like pad-to-pad precision grasp (Green and Gordon, 2008), pad-to-side and handling grips (Marzke, 1997, Ricklan, 1987), but with not the full range of human-like manipulative behaviours observed in later hominins (Green and Gordon, 2008). Furthermore, according to

some authors (Kivell et al. 2020), the proportions within each ray of metacarpal and phalange length are also like those of modern humans. Moreover, based on the internal structure of metacarpals, Skinner and co-authors (Skinner et al., 2015) confirm that *A. africanus* would have had the forceful human-like opposition capacity of the thumb and fingers during power and precision grips.

Still in South Africa, two partial skeletons belonging to the most recent *Australopithecus* species: *A. sebiba* (Berger et al., 2010), discovered at Malapa and dated to 1.977 Ma (Pickering et al., 2011), indicate that these individuals possessed pad-to-pad precision gripping and hand proportions showing enhanced dexterity (Kivell et al., 2011), but with limited force of the thumb. Furthermore, the phalangeal morphology suggests powerful flexion and strong grasping of the fingers. These functional interpretations are also confirmed by recent studies using metacarpal internal trabecular bone analyses (Dunmore et al., 2020) and musculoskeletal modelling (Bardo et al., 2018).

After 2 Ma, the morphology of the Olduvai and Swartkrans hominin hands discovered in archaeological levels (see paragraph 3) are compatible with tool using and tool-making. For the Olduvai remain (OH 7), human-like precision grips are associated with pad-to-pad precision grasping. Indeed, in the publication defining the species *Homo habilis*, based on the OH 7 late juvenile hand bones uncovered at site FLKNN I in Olduvai Gorge (Tanzania), Leakey and co-authors emphasized a well-developed and fully opposable thumb (pollex) and a hand capable of a power grip, as well as a simple and usually well-developed precision grip (Leakey et al., 1964). Hence the OH7 hand has played a crucial role in our perception and understanding of the evolution of hominin tool use and tool-making and therefore on the definition of the *Homo* genus. However, it should be noted that in the initial description in 1962, Napier (Napier, 1962) highlighted a mosaic morphology (e.g., modern human-like morphology of the distal pollical phalanx and ape-like carpus and curvature of the phalanges), and observed that the thumb was opposable and powerful. In terms of functional interpretation, he emphasized “On anatomical grounds there is no doubt that the Olduvai hand was sufficiently advanced in terms of the basic power and precision grips to have used naturally occurring objects as tools to good advantage. 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, p. 411). This interpretation contrasts somewhat with that of Leakey, Tobias and Napier 1964 which unlights that “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 ..(Leakey et al. 1964, p. 9) (see paragraph Discussion and conclusions).

Furthermore, the taxonomical allocation of the OH7 hand has been questioned, as the phalangeal morphologies show some similarities with *Paranthropus* (Moyà-Solà et al., 2008). Based on functional analyses, those authors (Moyà-Solà et al., 2008) suggested that the anatomical features linked to human-like precision grasping (previously considered as tool-making features by some authors, may be conversely adapted to specialized manual feeding techniques in *Paranthropus*. Furthermore, according to Susman and Creel (Susman and Creel, 1979), the mosaic of features observed in the anatomy of OH7 could reflect precision grip abilities (e.g., the modern human-like features of distal phalanges) and frequent climbing (e.g., African ape-like features).

At the PTK (level 3) site at Olduvai Gorge level 3, a manual proximal phalanx (OH 86) dated to 1.84 Ma (Domínguez-Rodrigo et al., 2015) represents the earliest modern human-like hand anatomy (see paragraph 2.1.4.1). This specimen is assigned to the *Homo* genus and contrasts in size and shape not only with *Australopithecus* or *Paranthropus*, but also with the OH7 hand. The phalangeal features are indicative of more relaxed postural and locomotive selective

pressures on the hand and a marked reduction in manual phalangeal arboreal adaptations (Domínguez-Rodrigo et al., 2015).

Similarly, adaptations for tool-using and tool-making are observed in specimens allocated to the *Paranthropus* genus from the Ileret and the Swartkrans hominins. Indeed, the hand anatomy of *P. boisei* specimens (e.g., based on the best *Paranthropus* hand evidence of the specimen KNM-ER 47000 from Ileret, East Turkana, Kenya, dated to 1.5 Ma), highlights that this species did not possess the robust thumb observed in *Homo erectus* (linked to the intensification of forceful precision grips and tool use) but exhibits the manual dexterity required to use or make stone tools (Richmond et al., 2020). According to Moyà-Solà and co-authors (who consider that the OH 7 hand bones belong to *Paranthropus boisei*), *Paranthropus* individuals exhibit more robust hand bones than *Homo* and lack the disproportionately hypertrophied first metacarpal characteristic of the *Homo* genus (Moyà-Solà et al., 2008).

In southern Africa, according to work by Susman (Susman, 1988, 1994, 1998), the remains (phalanges and metacarpals) discovered mainly in Member 1 of the Swartkrans site and possibly but not securely allocated to *P. robustus*, as early *Homo* specimens were also found in this member, show that these hominins possessed muscles allowing for human-like precision grasping (by stabilizing the opposing the thumb and the fifth finger to the other fingers), which are considered as adaptations for tool-using and tool-making (Susman, 1994, 1998). For Moyà-Solà and co-authors (Moyà-Solà et al., 2008), the *Paranthropus* pattern probably reflects an adaptation to manual activities other than tool-making more related to feeding behaviour such as specialized food gathering and processing, as observed in extant hominids (Gérard et al., 2022; Marzke et al., 2015; Neufuss et al., 2018).

Lastly, the recent description of a third metacarpal (Kaitio area, West Turkana, Natoo Member, 1.42 Ma) from West Turkana, with a styloid process typical of modern humans, seems to confirm that enhanced hand function for tool-making and tool-using took place very early on in the evolution of the *Homo* genus (Ward et al., 2014).

4. New approaches, how can we go beyond anatomical and archaeological field data?

4.1. Experimental biomechanics and musculoskeletal modelling

The first of the two last points of this review concerns experimental simulations and in particular the required biomechanical capacities and manual skills for percussive movements. Indeed, in addition to the archaeological and paleoanthropological framework, experimental biomechanics and musculoskeletal modelling can shed light on the functional anatomy of the upper limb involved in stone tool production (e.g., Rolian et al., 2011; Tocheri et al., 2003; Key et al., 2019, Kivell et al. 2022).

Macchi and co-authors show that muscular demands are similar for passive hammer, bipolar, and free-hand percussion techniques, but that kinematic patterns are more variable. It is interesting to note that free-hand percussion is differentiated from the other two techniques, with more complex motor control demands (Macchi et al., 2021). Furthermore, in order to evaluate the prehensile abilities of a contemporary hominin from the Lomekwi site, a musculoskeletal model of the hand of *Australopithecus afarensis* was developed by Domalain and co-authors (Domalain et al., 2017). They proposed two versions of the *Australopithecus afarensis* anatomical model based on *Homo sapiens* and *Pan troglodytes*. Their results suggest a limited capacity of the *Australopithecus afarensis* hand to bring the pulp of the fifth ray into

contact with the surface of a large object. This may have been a limiting factor in exerting a large enough grip force to make large lithic artefacts such as those found at Lomekwi 3. The biomechanics of free-hand knapping (techniques used to produce the Oldowan) received more attention, but are quite limited concerning the hand (Kivell et al., 2022). A wide variety of grips were used, with significant emphasis on precision grips (Key et al., 2018; Williams-Hatala et al., 2021). Loads tend to be concentrated on the thumb (pollex) in both the dominant and non-dominant hands, which is probably the best candidate for a manual adaptation for this specific behaviour (Rolian et al., 2011; Williams-Hatala et al., 2018; Williams-Hatala et al., 2021; Key & Dunmore, 2015). As summarized by Kivell et al. (2022), the osteology and muscular anatomy of the thumb are essential for understanding the adaptative response to stone tool production and use, but we must also consider the fact that different combinations of derived characters can occur at different times and the problems of equifinality with respect to behaviour. Furthermore, more data are needed on EMG, kinematics, kinetics of the digits and all the upper limb during free-hand, bipolar and passive hammer knapping. Moreover, the application of new techniques (Manafzadeh & Gatesy, 2021), such as X-ray reconstruction of moving morphology (bi-planar X-ray with X-ROMM), can provide new insights into the reconstruction of joint mobility.

4.2. Cognitive exploratory studies

The final section concerns the cognitive abilities of these hominins and the resulting organization of the brain. The artefacts from LOM 3 indicate complex cognitive behaviour with extensive planning and motor control, which may involve the reorganization and/or expansion of several regions of the cerebral cortex (visual and motor) and cerebellum. The findings from the Lomekwi 3 site suggest that the reorganization and/or expansion of these brain regions must have occurred before 3.3 million years ago. This was previously suggested by Ralf Holloway as early as 1983 (Holloway, 1983) on the basis of the endocranial anatomy of the specimen found at Hadar AL 162-28, attributed to *A. afarensis*.

Understanding the evolution of higher order cognitive functions (such as planning through tool-making) requires extrapolating from what we know of modern human and non-human primates to fossil and archaeological data. The link between brain evolution and cognition remains a key scientific challenge, because it is impossible to observe the functional brain activity of extinct hominin species.

In this context, some exploratory studies using for example fluorodeoxyglucose positron emission tomography (FDG-PET), functional magnetic resonance imaging (fMRI) and image-based functional near-infrared spectroscopy (fNIRS) on Oldowan and Acheulean productions have been undertaken. The purpose was to discuss which brain regions are the most active during these stone tool productions using different techniques (free-hand percussion and bifacial shaping) and whether advanced executive functions such as cognitive control, planning and the working memory are involved. During these experimental studies, the subjects could have different levels of expertise (novices, learning, experts). The subjects could watch videos (Stout et al., 2015, using the fMRI method) or produce stone tools (Stout et al. 2000, Stout et al. 2008, Stout and Chaminade, 2007, using FDG-PET method; Putt 2016, Putt et al., 2017, using fNIRS method). According to Stout et al (2015), prefrontal responses are greater in Acheulean as opposed to Oldowan tool-making. The main difference between Oldowan and Acheulean tasks is that Oldowan tool-making relies on the coordination of visual attention and motor control (motor and sensorimotor areas) (Stout et al. 2000). In contrast, according to Putt, Acheulean tool-making requires the integration of higher order motor planning, the working memory and auditory feedback mechanisms (Putt 2016, Putt et al.,

2017). In order to examine the relationship between stone tool-making and brain function, Stout et al., (2000) and Stout and Chaminade (2007) developed an exploratory study using Position Emission Tomography (FDG-PET). They have shown on one human expert subject (Stout et al., 2000) that the superior parietal region (Brodmann Area (BA) 7, spatial cognition), the central sulcus (BA 4 and BA 1, primary motor and somatosensory regions), the postcentral gyrus (BA1, basic sensorimotor processing) and the cerebellum (integration and control of motor activity) are activated during the replication of Oldowan technology (Stout et al., 2000), but not the dorsolateral prefrontal cortex. This means that there is no high level of planning, no strategic action planning during free-hand percussion, and that Oldowan tool making does not place exceptional demands on executive functions, such as working memory, condition response selection and inhibition, which are involved in strategic planning (Stout and Chaminade, 2007, study based on 6 right-handed novices subjects). Observed superior parietal lobe activity suggests the presence of complex spatial cognition, while activation around the central sulcus reflects basic sensorimotor processing and cerebellar activity represents the integration and control of motor activity (Stout et al., 2000, p. 1222). Furthermore, during Oldowan production, the rostral and dorsal intraparietal sulcus (IPS) and ventral premotor cortex (PMC) areas are activated. These zones are linked for example to human visual specialization, manipulation, grip selection and tool-using abilities (Stout and Chaminade, 2007, Stout and Chaminade, 2012). Brain activation data indicate that the initial stages of Oldowan tool making skill acquisition are primarily concerned with perceptual-motor adaptation to task constraints and especially the discovery and exploitation of objects affordances, rather than executive planning and problem solving (Stout and Chaminade, 2007).

During the Acheulean (i.e., handaxe) production, the right inferior prefrontal cortex (Brodmann Area 45) is activated, an area which plays a central role in coordinating flexible, goal-directed behaviour, and is linked to decision making. In contrast, the dorsolateral prefrontal cortex, which is linked to the working memory in tasks that separate planning from execution, is not activated (Stout et al., 2008, 3 experts). According to these authors, the activation of the ventrolateral prefrontal cortex, but not dorsolateral prefrontal cortex indicates that Acheulean tool-making is distinguished by cognitive demands for the coordination of hierarchically organized ongoing action sequences rather than the evaluation of action plans (Stout et al. 2008 p. 1946).

5. Discussion and conclusions

As preliminary remarks, Oldowan assemblages remain relatively scarce before 1.8 Ma, few Acheulean occurrences have been reported before 1.4 Ma, and there is a chronological overlap between Oldowan and Acheulean assemblages, both found sometimes on the same region or event in the same site (DAN 5 (Dana Aoule Gona 5) and BSN 12 (Budisima North Gona 12), Semaw et al., 2020). In addition, it should be noted that the number of palaeoanthropological remains associated with archaeological assemblages is very scarce. However, our work has highlighted the plurality of artisans of the first material cultures, including Pliocene hominins for Lomekwian, and *Paranthropus*, *H. habilis* and *H. erectus/ergaster* for Oldowan.

Although Oldowan artefacts are often attributed to the *Homo* genus, we show in this article that different taxa (*P. boisei*, *P. aethiopicus*, *P. robustus*, *A. gahri*) overlapped temporally and geographically with these assemblages. More specifically, we observe a lot of High Confidence

Association between *Paranthropus* remains and Oldowan assemblages (n=11) (n= 7 (HC 1 A); n= 2 (HC 1 B) and n=2 (HC 2 A), also sometimes associated with *H. habilis* (n=3, FLK NN level 3, FLK level 22, FxJj 3), (Table2, Figure 2). Likewise, in terms of anatomy, the type of dexterity required for making Oldowan assemblages is probably not restricted to *Homo* (Susman, 1994; Marzke, 1997), the anatomy of *Paranthropus* elements (OH 80) is consistent with stone tool production (Dominguez-Rodrigo et al., 2013), and some hand remains previously allocated to *H. habilis* (e.g. OH 7) are now assigned to *Paranthropus* according to some authors (Moyà-Solà et al., 2008).

In our opinion, the occurrences between Oldowan assemblages and *Paranthropus* are not coincidental, and it is more than plausible that *Paranthropus* made and used stone tools for cutting bones and/or vegetation. *Paranthropus* should be therefore considered as a stone tool maker in the same way as early *Homo*.

Besides, if after 1.4 Ma *H. erectus* is mainly associated with Acheulean assemblages, our paper also unlights that there are many sites (n=6) where *Homo erectus/ergaster* is associated with Oldowan (PTK site Olduvai, Naiyena Engol 1, Melka Kunture Garba IV (level E), Melka Kunture Gombore I, DAN 5, BSN 12, e.g. Chavaillon et al., 1977; Chavaillon et Berthelet, 2004; Condemi, 2004; Coppens, 2004; Domínguez-Rodrigo et al., 2015; Gallotti et Mussi, 2015; Prat et al., 2003; Roche et al., 2003; Semaw et al., 2020), and not with Acheulean in Africa (Table2, Figure 2), but also outside Africa (e.g. Dmanisi (e.g. Lordkipanidze et al., 2007, 2013, Mgeladze et al., 2011), 'Ubeidyia (e.g., Belmaker et al., 2002, Tobias, 1966, Bar-Yosef and Goren-Inbar, 1993).

INSERT Figure 2

Despite some strong associations between Oldowan assemblages and *P. boisei* remains, it should be noted that in many cases, it is difficult for authors to admit that *P. boisei* could have been the stone tool-makers. We can mention notably, the case of Olduvai Gorge. FLK level 22 yielded a dense Oldowan assemblage and four hominin individuals, including the cranium OH 5, holotype of the species *Paranthropus boisei* (formerly *Zinjanthropus boisei*, Leakey, 1959), and one specimen allocated to *H. habilis* (OH 6) (see paragraph 2.1.2.1). When the OH 5 cranium was discovered in this site, it was considered as “the oldest yet discovered maker of stone tools” (Leakey, 1959, p. 493). However, five years later, Louis Leakey changed his mind, based on *Homo habilis* fossils in association with the Oldowan culture at three other localities at Olduvai, such as for example the FLK NN level 3 with *P. boisei* and *H. habilis* including the holotype OH 7 (see paragraph 2.1.2.2), and concluded that “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, p. 9). In five years, with no real argument, the status of *P. boisei* has changed from stone tool-maker to victim.

It is also important to mention that despite the discovery of the *Paranthropus boisei* mandible KNM-ER 3230 *in situ* at the FxJj 20 East site (Koobi Fora Area 131, Kenya) (see paragraph 2.1.3.4), Leakey in his 1976 paper did not want to associate the two (Leakey, 1976). We can wonder whether Leakey's interpretation would have been the same if the remains had belonged to the *Homo* genus.

More recently, at the site of Nyayanga (Kenya), a left lower molar (KNM-NG 77316) allocated to *P. boisei* was found *in situ*, spatially associated with Oldowan artefacts (see paragraph 2.1.3.1). The authors (Plummer et al., 2023) highlight a clear association between the lower

molar fragment and the artefacts “raising the possibility that *Paranthropus* made and/or co-opted stone tools” (Plummer et al., 2023 p. 5). However, in the same paragraph, the authors mention that even though no early *Homo* remains have been found at Nyayanga, as this taxon occurred in eastern Africa, with the mandible from Ledi Geraru, 1300 kilometres away, dated to 2.8 Ma in Ethiopia (Villmoare et al., 2015), the Nyayanga Oldowan artefacts “cannot be definitively attributed to a specific hominin genus” (Plummer et al., 2023 p. 5). This sentence illustrates that it is still difficult for some authors to consider that a genus other than *Homo* could be the Oldowan stone tool makers and they give more importance to remains found 1300 kilometres away and corresponding to our non-confident (LC) category than to *in situ* material (confident category HC1 A), which would be the most parsimonious hypothesis from an Occamian perspective. Even if of course, it is always difficult to be sure that the hominins found in some archaeological sites are the actual tool makers, but this hypothesis is commonly used for example for Upper or Middle Palaeolithic sites.

The case of Chesowanja (see paragraph 2.1.3.5), also demonstrates this point. Indeed, the *P. boisei* are not strictly associated with the Oldowan assemblage found nearby, but Gowlett et al. 1981, consider that this association must be considered more than coincidental (Gowlett et al., 1981).

It is interesting here to use the words of Gowlett in 1999. “Although the only hominid remains found at Chesowanja are *A. boisei*, Gowlett et al., 1981 were inclined to suggest that the maker of the stone industry was *H. erectus*. If anything, the case for this link has strengthened, through additional finds of *H. erectus* at early dates, the frequency with which *Homo* is found on artefact sites where *A. boisei* is found, and the continued association of *Homo erectus* and bifaces following the demise of *A. boisei*”. (Gowlett 1999, p.128)...and “a view seeking simple parsimony would proceed along these lines: that any hominid might in principle make tools; that robust australopithecines have well developed thumbs, suggesting tool-making manipulations, and that where there are two occurrences of this hominid close to artefacts, this is suggestive a link. Against this, however, one can take a broader view of the arguments: (1) remains of the ‘more advanced’ *Homo* are found elsewhere alongside robust australopithecine remains on several sites in several environments; (2) the absence of *Homo* has no special significance, since hominins do not tend to die in their living area so as to provide makers; (3) Chesowanja represents a developed Oldowan possibly including early picks as found in the Acheulean, and Acheulean industries are commonly associated with *Homo ergaster/erectus* and *Homo sapiens/heidelbergensis*.” (Gowlett, 1999 p. 130). We can see here that Gowlett changed his mind slightly concerning the perception of *P. boisei* as a stone tool-maker between his paper published in 1981 and 1999. Whether it is true that the place of death is not necessarily the living one, and that the hominin remains found at the site (especially when it is a juvenile) are not necessary those of the hominins who produced the lithic assemblage, the most parsimonious hypothesis merely indicates that members of the same group were present at the archaeological site. Questions of geological scale and sedimentation may also be raised. However, the most parsimonious hypothesis is that the stone tool or bone tool makers correspond to the species found at the archaeological site rather than to species not present in the sedimentary levels. This is generally the case when specimens of the *Homo* genus are found, but less systematic for other genus.

Additionally, we can emphasize, as shown in this article, that the frequency of *Paranthropus* remains associated with Oldowan assemblages in eastern Africa is not negligible and insignificant (eleven occurrences), that there are quite a lot of sites with *P. boisei* remains not associated with early *Homo* individuals (six occurrences), that some Oldowan sites are associated with *Homo ergaster/erectus* (six evidence).

The plurality of stone tool-makers has been previously highlighted by some researchers (e.g. Brain et al., 1988; Susman, 1991; Wood, 1997), mainly based on their ability to manufacture

998 simple stone tools and on southern African sites, but often the situation is broadly the same
999 as it was in 1964. According to Wood and Constantino (2007): “There is no firm evidence that
1000 *P. boisei* made and used stone tools, but there is also no firm evidence that they were
1001 incapable of doing so” (Wood and Constantino, 2007 p.122).

1002 Several years later, this paper has attempted to review the different sites where *Paranthropus*
1003 remains (especially in East Africa) were found *in situ* with Oldowan assemblages alongside
1004 anatomical perspectives. We hope that we have shown that there is strong evidence to
1005 suggest that *Paranthropus* made and used stone tools and that this taxon should be given
1006 more consideration.

1007
1008 From a parsimonious perspective, there is more association between *Paranthropus* remains
1009 and lithic artefacts for the oldest sites than between early *Homo* and lithic artefacts. Based on
1010 the evidence presented here, stone tool-making does not seem to be specific to the *Homo*
1011 genus and cannot define it. Fieldwork data are essential, but the development of
1012 musculoskeletal simulations, kinematic, electro-myographic and electro-encephalographic
1013 experiments (biplanar X-ray, internal morphology) are also promising avenues of research
1014 enhance our understanding of the relationship between hominins and material cultures.
1015 Moreover, the unique and specific attribution of a tool-making capacity to the *Homo* genus
1016 can no longer be deemed valid for these periods.

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1635

1636 Figure and table lists

1637

1638 Figure 1: Chronological repartition of hominin species and cultural assemblage during the Pliocene and
1639 early Pleistocene in Africa.

1640

1641 Figure 1. Répartition chronologique des espèces d'hominines et des assemblages lithiques en Afrique
1642 au cours du Pliocène et du Pléistocène inférieur.

1643

1644 Figure 2. Localisation of the archaeological sites in association (HC1 and HC 2) with hominin remains.

1645

1646 Figure 2 : Localisation des sites archéologiques en association (HC1 and HC 2) avec des restes
1647 d'hominines.

1648

1649 Table 1 : Categories of attribution and association between hominin remains and archaeological
1650 assemblages.

1651

1652 Tableau 1: Catégories d'attribution et d'association entre les restes d'hominines et les assemblages
1653 archéologiques.

1654

1655 Table 2 : Association between hominins remains and archaeological assemblage with a High
1656 Confidence level: HC (local scale).

1657

1658 Tableau 2: Association entre les restes d'hominines et les assemblages archéologiques ayant un niveau
1659 de confiance important HC (échelle locale).

1660

Category	Definition
HC1	The hominin remains have been found in the archaeological site (<i>in situ</i> during the excavation, or at the surface of the site due to erosion processes)
HC 1 A	when the taxonomy of the hominin remain is clear
HC 1 B	when the taxonomy of the hominin remain is debated
HC 2	The hominin remains have been found few meters (less than 400 meters) from the excavation but in the same chrono-stratigraphical layers
HC 2 A	when the taxonomy of the hominin remain is clear
HC 2 B	when the taxonomy of the hominin remain is debated

1661

1662 Table 1 : Categories of attribution and association between hominin remains and
1663 archeological assemblages.

1664

1665 Tableau 1: Catégories d'attribution et d'association entre les restes d'hominines et les
1666 assemblages archéologiques.

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Age (Ma)	Region	Locality	Industry	References	Hominins	References	Category of reliability
3.03 -2.58	Lake Victoria (Kenya)	Nyayanga, excavation 3	Oldowan	Plummer et al., 2023	KNM-NG 77316 <i>Paranthropus</i>	Plummer et al., 2023	HC 1 A
2.34 +/- 0.07	Hadar (Ethiopia)	AL 666	Oldowan	Kimbel et al., 1996	AL 666-1 <i>Homo aff. H. habilis</i>	Kimbel et al., 1997	HC 1 A
2.34 +/- 0.04	West Turkana (Kenya)	Lokalalei 1, Gajh5	Oldowan	Prat et al., 2005	KNM-WT 42718 Early <i>Homo</i>	Prat et al., 2005	HC 2 A
2.32 Ma to 2.23	Omo Valley (Ethiopia)	Omo 57	Oldowan	Coppens et al., 1973, Chavaillon, 1976	Omo 57/5-1972-371, <i>P. aff. aethiopicus</i>	Coppens, 1977, Suwa, 1990; Wood et Leakey 2011	HC 1 A
1.95-1.90	Fejej (Ethiopia)	FJ-1a	Oldowan	e.g. de Lumley and Beyene 2004	Fj-1-Hd1, Hd3, Hd4, <i>Homo aff. H. habilis</i>	de Lumley & Marchal 2004	HC 2 A
1.87-1.84	Olduvai Gorge (Tanzania)	DK	Oldowan	Leakey, 1971, de la Torre and Mora, 2005	OH 24 <i>Homo habilis</i>	Leakey et al., 1971	HC 2 A
1.84	Olduvai (Tanzania)	FLK NN level 3	Oldowan	Leakey et al., 1964 Leakey, 1971	OH 7 cranial remains <i>H. habilis</i> (Holotype)	Leakey et al. 1964	HC 1 A
1.84	Olduvai (Tanzania)	FLK NN level 3	Oldowan	Leakey et al., 1964, Leakey, 1971	OH 7 hand bones <i>H. habilis</i> or <i>Paranthropus</i>	Leakey et al. 1964 Moyà-Solà et al., 2008	HC 1 B
1.84	Olduvai (Tanzania)	FLK NN level 3	Oldowan	Leakey et al., 1964, Leakey, 1971	OH 8 foot bones <i>H. habilis</i> (paratype)	Leakey et al. 1964 Day and Napier, 1964	HC 1 B
1.84	Olduvai Gorge (Tanzania)	FLK level 22	Oldowan	Leakey, 1971	OH 5 Holotype of <i>P. boisei</i>	Leakey, 1959	HC 1 A
1.84	Olduvai Gorge (Tanzania)	FLK level 22	Oldowan	Leakey, 1971	OH 6 <i>H. habilis</i>	Tobias, 1991	HC 1 A
1.84	Olduvai Gorge (Tanzania)	FLK level 22	Oldowan	Leakey, 1971	OH 35 <i>P. boisei</i> or <i>H. habilis</i>	Leakey, 1964	HC 1 B

1.84	Olduvai Gorge (Tanzania)	PTK site	Oldowan	Domínguez-Rodrigo, 2015	OH 86 <i>Homo erectus</i> -like	Domínguez-Rodrigo, 2015 Díez-Martín et al, 2015	HC 1 B
Circa 1.82	Olduvai Gorge (Tanzania)	Ewass Oldupa	Oldowan	Mercader et al. 2021	OH 65 <i>Homo habilis</i>	Blumenshine et al., 2012. Clarke, 2012	HC 2 A
1.79	West Turkana (Kenya)	Kokiselei 1 FxJh6	Oldowan	Roche et al., 2003	KNM-WT 37744, 37747, 37748, 37100 <i>P. boisei</i>	Prat et al., 2003	HC 1 A
1.78-1.52 (Mana et al., 2019) 1.85 (Feibel et al., 1989)	Koobi Fora (Kenya)	FxJj 38	Oldowan	Harris et Herbich, 1978	KNM-ER 1805 <i>Homo</i> sp. but taxonomical allocation under discussion	Leakey, 1974 Prat, 2002	HC 1 B
1.78-1.52 (Mana et al., 2019) 1.85 (Feibel et al., 1989)	Koobi Fora (Kenya)	FxJj 38	Oldowan	Harris et Herbich, 1978	KNM-ER 1806 <i>P. boisei</i>	Leakey, 1974 Wood, 1991	HC 1 A
1.75 +/- 0.05	West Turkana (Kenya)	Naiyena Engol 1 FxJh5	Oldowan	Roche et al., 2003	KNM-WT 37745 <i>Homo</i> aff. <i>H. ergaster</i>	Prat et al., 2003	HC 1 A
Slightly older than 1.7	Melka Kunture (Ethiopia)	Garba IV, level E	Oldowan	Gallotti and Mussi, 2015	MK 81 GAR IVE 0043 early <i>Homo erectus</i> / <i>H. ergaster</i>	Condemi, 2004	HC 1 A
Circa 1.67	Olduvai Gorge (Tanzania)	MNK Skull	Oldowan	Leakey, 1971 de la Torre et al., 2021	OH 13 Paratype <i>Homo habilis</i> OH 15, <i>Homo habilis</i>	Leakey et al., 1964, Tobias 1991	HC 1 A
1.65 +/- 0.05	Koobi Fora (Kenya)	FxJj 20	Oldowan	Harris et Herbich, 1978	KNM-ER 3230 <i>P. boisei</i>	Wood, 1991	HC 1 A
1.6-1.5	Melka Kunture (Ethiopia)	Gombore I	Oldowan	Chavaillon et al., 1977 Chavaillon and Berthelet 2004	Gombore IB-7594 early <i>Homo erectus</i> <i>Homo</i> sp.	Coppens, 2004 Chavaillon et al., 1977	HC 1 B

						Di Vincenzo et al., 2015	
1.6-1.5	Afar Region (Ethiopia)	DAN 5	Oldowan and Acheulean	Semaw et al. 2020	DAN5/P1 early <i>Homo erectus</i>	Semaw et al., 2020, Baab et al., 2022, Bruner et al., 2023	HC 1 A
1.44	Konso-Gardula (Ethiopia)	KGA 4E	Acheulean	Asfaw et al., 1992 Beyene et al., 2013	KGA 4 E <i>Homo</i> sp.	Asfaw et al., 1992	HC 1 A
1.42 +/-0.07	Chesowanja (Kenya)	GNJ1/6E Gn J2	Oldowan Oldowan	Gowlett et al. 1981	KNM-CH 1, 302, 304 <i>P. boisei</i>	Carney et al., 1971, Bishop et al., 1975, Gowlett et al. 1981,	HC 2 A
1.4	Konso-Gardula (Ethiopia)	KGA 10-A10	Acheulean	Asfaw et al. 1992 Beyene et al., 2013 Beyene et al., 2014	KGA 10-1; KGA KGA10-620 (right parietal fragment), KGA 10-656 <i>Homo erectus</i>	Asfaw et al. 1992 Suwa et al., 2007	HC 2 A
1.4	Konso-Gardula (Ethiopia)	KGA 10-A10	Acheulean	Asfaw et al., 1992 Beyene et al., 2013 Beyene et al., 2014	KGA10-506, KGA10-525 ; KGA10-565, KGA10-570, KGA10-900, KGA10-1455, KGA10-1720, KGA10-2705, KGA10-2741 <i>P. boisei</i>	Suwa et al., 1997	HC 2 A
1.34	Olduvai Gorge (Tanzania)	BK site level 4, Bed II	Oldowan	Dominguez-Rodrigo et al., 2009	OH 80 <i>P. boisei</i>	Dominguez-Rodrigo et al., 2013	HC 1 A
1.26 +/-0.03	Afar Region (Ethiopia)	BSN12	Oldowan and Acheulean	Semaw et al. 2020	BSN12/P1 <i>Homo erectus</i>	Semaw et al., 2020, Baab et al., 2022	HC 1 A

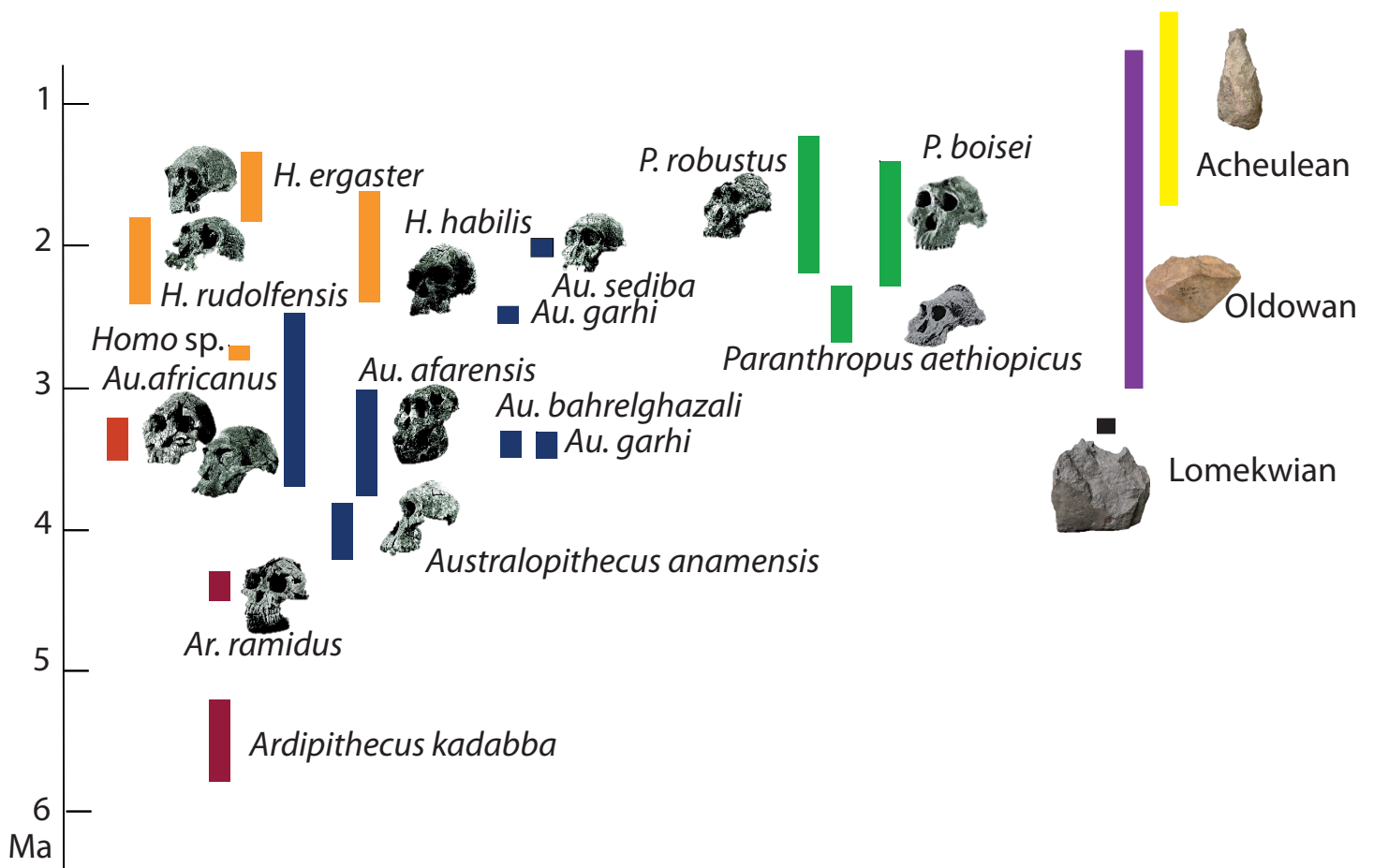
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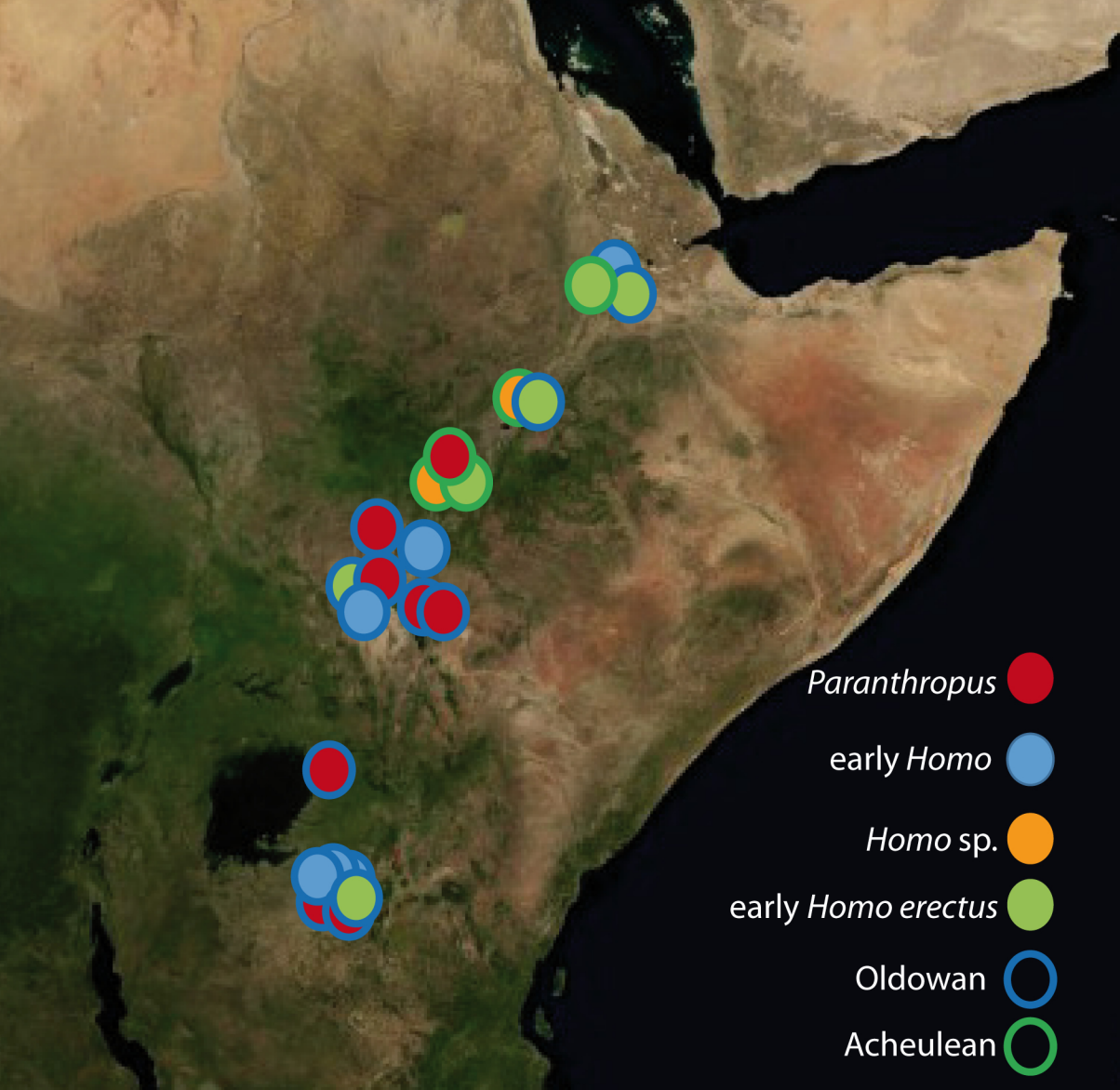
1671 Table 2 : Association between hominins remains and archeological assemblage with a High Confidence level: HC (local scale)

1672

1673 Tableau 2: Association entre les restes d'hominines et les assemblages archéologiques ayant un niveau de confiance important HC (échelle locale)

1674





Paranthropus

early *Homo*

Homo sp.

early *Homo erectus*

Oldowan

Acheulean