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

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

3
4 **Au-delà du stéréotype de genre. Qui étaient les premiers artisans en Afrique ? Regards**
5 **croisés entre archéologie et anatomie.**

6
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10
11 **Abstract**

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

29
30 **Keywords :**

31 Hominins, material culture, Africa, Plio-Pleistocene

32
33 **Résumé**

34 L'histoire évolutive des hominines et des assemblages archéologiques est devenue
35 considérablement plus complexe au cours des vingt-cinq dernières années grâce à l'apport de
36 méthodes analytiques novatrices et de nouvelles découvertes tant archéologiques que
37 paléoanthropologiques. Les découvertes mises au jour en Afrique orientale et australe
38 montrent une grande diversité tant sur le plan biologique que culturel. Mais quelle est la
39 relation entre les hominines et les différentes cultures matérielles ? Singularité ou pluralité
40 des artisans des artefacts lithiques et osseux et des assemblages archéologiques ? Nous
41 proposons un regard croisé sur ces questionnements à partir d'une part d'une analyse des
42 associations hominines/assemblages archéologiques au Pliocène supérieur et au Pléistocène
43 inférieur, et d'autre part de l'anatomie de ces hominines et des recherches interdisciplinaires
44 menées ces dernières années. Notre travail met en évidence une pluralité des fabricants
45 d'outils en os et en pierre, en particulier *Paranthropus*, *H. habilis* et *H. erectus/ergaster* pour
46 les assemblages Oldowayens. De même, d'un point de vue anatomique, le type de dextérité
47 requis pour réaliser les assemblages Oldowayens n'est probablement pas limité au genre
48 *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

57 **Introduction**

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

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

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

74
75 The place and role of the archaeological remains in this definition (e.g., Prat, 2022) give rise to
76 the question of the possible relationship between the Oldowan industry and the *H. habilis*
77 specimens. Furthermore, the recent discovery of stone tools dated to 3.3 Ma in Kenya (LOM3
78 site) (evidence of stone-tools production, Harmand *et al.*, 2015) and cutmarked bones at
79 Dikika site dated to 3.4 Ma in Ethiopia (indicating stone-tool use, McPherron et al., 2010), is
80 300,000-500,000 years older than the earliest Oldowan technology (Braun et al., 2019,
81 Plummer et al., 2023) and 500,000 years before the oldest known fossils attributed by some
82 researchers to the *Homo* genus [*Homo* sp. remains at Ledi Geraru (Villmoare et al., 2015)]. The
83 stone artefacts from Lomekwi 3 are larger in width, length and thickness than those from
84 Oldowan sites. Two percussion modes have been identified (passive hammer and bipolar
85 percussion). Knappers combined battering activities and core reduction, and may have used
86 mineral blocks in different ways: as anvils, cores in order to produce flakes and/or as pounding
87 tools. The lithic artefacts were found in the same chronological and geographical contexts as
88 specimens allocated to *Kenyanthropus platyops* and are also contemporaneous with
89 individuals attributed to *Australopithecus afarensis* and *Australopithecus deyiremeda*. These
90 puzzling findings have reopened the debate on the association between lithic artefacts and
91 the *Homo* genus (Harmand et al., 2015; Lewis and Harmand, 2016), and highlighted that
92 species living long before the emergence of the *Homo* genus also present manipulative and
93 cognitive abilities for tool-making.

94
95 Indeed, far from the once linear perspective of hominin evolution, we currently have a bushy
96 vision of this evolutionary history, with several contemporaneous species or genera in the
97 Pliocene or Early Pleistocene (Figure 1). This points to morphological diversity during these
98 periods. The archaeological data also emphasize diversity in terms of assemblages and a non-
99 linear evolution, with the presence of Oldowan and Acheulean artefacts in a same
100 archaeological site (Dana Aoule Gona, DAN 5 and Busidima North Gona, BSN 12 (Semaw et al.,
101 2020)). In addition, some Oldowan sites are more recent than Acheulean sites. Therefore, it
102 would probably be a good idea to consider that cultural evolution also branches out in
103 different directions.

104
105 INSERT FIGURE 1

106
107 The Oldowan in the broad sense of the term (which can include the early Oldowan, developed
108 Oldowan etc.) overlaps temporally and geographically with different hominin taxa (early
109 *Homo*, *Paranthropus*, and *Australopithecus* in eastern Africa and southern Africa (Figure 1).
110 The oldest known Oldowan tools found *in situ* have been unearthed in Kenya at the site of
111 Nyayanga, older than 2.6 Ma (Plummer et al., 2023, see paragraph 2.1.3.1). In Ethiopia, the
112 Busidima Formation at Gona has yielded the largest number of early Oldowan sites (e.g.,
113 Roche et Tiercelin, 1977, Semaw et al., 1997, Semaw et al., 2003), dating to 2.6-2.5 Ma, with
114 the localities of EG-10, EG-12, EG-13, EG-24, OGS-6a, OGS-7 yielding over one thousand
115 excavated artefacts (e.g. Semaw et al. 1997; Semaw, 2000; Semaw, 2006; Stout et al. 2005,
116 Stout et al. 2010). We can also mention the site of Bokol Dora 1 dated to 2.61-2.58 Ma, Ledi
117 Geraru (Braun et al., 2019), the site of AL 666 at 2.34 Ma (Kimbel et al., 1996; Kimbel et al.,
118 1997, see paragraph 2.1.1.1), the Lokalalei complex in Kenya at 2.34 Ma (Kibunjia et al., 1992;
119 Kibunjia, 1994; Roche et al. 1999, Delagnes and Roche, 2005), and the sites from the Lower
120 Omo Valley in the member F (2.32-2.27 Ma (e.g. Omo 57/5 (see paragraph 2.1.3.2.), OmO
121 57/7, Omo 84, Omo 123j, Omo 123k, OMO 123m, Omo 1/E-3, Omo 1/E-4, FtJi1, FtJi2, and
122 FtJi5, Merrick et al., 1973; Chavaillon, 1976; Delagnes et al., 2011) and the site of Kanjera South
123 in Kenya, dated to 2 Ma (e.g., Plummer et al., 1999).

124
125 Furthermore, several Oldowan sites have been also discovered in Eurasia in association with
126 paleoanthropological remains (Prat, 2018). We can cite Dmanisi in Georgia, where at least five
127 hominin individuals were discovered (Lordkipanidze et al., 2007; Lordkipanidze et al., 2013),
128 in association with Oldowan artefacts (Mgeladze et al., 2011), Sima del Elefante in Spain in the
129 Sierra of Atapuerca (1.22 Ma), where the oldest mandible of the *Homo* genus in Europe was
130 discovered (Parés et al., 2006, Carbonell et al., 2008). We can also mention the Jianshi hominin
131 site in China, also called Longguddong site (with a debatable age, minimum age of 2.14 Ma (Li
132 et al., 2007) or 1.52 Ma +/- 0.092-1.05 +/- 0.04 (ESR dating, mean age of lower layer 8 and layer
133 4 respectively (Han et al. 2022), with early *Homo* remains and nine stone artefacts in the
134 hominin layer (Li et al., 2017); Yanmou (1.7 Ma), early *Homo* sp./early *H. erectus* associated
135 with four Oldowan lithic pieces (Hou et al., 2010; Zhu et al., 2008). At 1.4 Ma, in the Jordan
136 Valley (Israel), the site of 'Ubeidiya yielded some early *Homo erectus* specimens (one tooth)
137 associated with Acheulean artefacts (Belmaker et al, 2002; Tobias, 1966; Bar-Yosef and Goren-
138 Inbar, 1993).

139
140 The oldest occurrences of Acheulean assemblages are Kokiselei 4 (1.74 Ma, Lepre et al. 2011)
141 and Kokiselei 6, where bifacial shaping emerges (Duke et al., 2021), in the western part of Lake
142 Turkana, Kenya and the Konso Gardula sites in Ethiopia. The latter comprise KGA6-A1, which
143 is the earliest site, bracketed between two tuffs, 1.74 and 1.66 Ma (Beyene et al., 2013) and
144 more typical early Acheulean assemblages, such as for example KGA-4 and KGA-10, dated to
145 ~1.45 Ma, KGA-5, KGA-7 to ~1.4 Ma (e.g., Asfaw et al., 1992, Beyene et al., 2013, see paragraph
146 2.1.6.1), and FLK West in Olduvai Gorge in Tanzania dated to circa 1.7 Ma. This latter site
147 contrasts with Kokiselei 4 and Konso as it points to relatively advanced handaxe shaping skills
148 with very symmetric bifacial flakes (Diez-Martin et al., 2015)

149
150 Regarding the *Homo* genus, the first occurrence of early *Homo* is the mandible LD 350-1, Ledi
151 Geraru, in Ethiopia, which could not be attributed to a specific species (Villmoare et al., 2015).
152 This is followed by discoveries in Kenya at Lokakalei 1 alpha KNM-WT 42718, 2.33 Ma (see
153 paragraph 2.1.1.2) (Prat et al., 2005), the temporal bone KNM-BC1 from Chemeron, Kenya,
154 dated to 2.4 Ma, Chemeron, Kenya, (Hill et al., 1992; Sherwood et al., 2002), the maxilla AL

155 666-1 dated to 2.34, Hadar, Ethiopia (Kimbel et al., 1996; Kimbel et al., 1997, see paragraph
156 2.1.1.1), the mandible UR 501 dated to ca. 2.4 Ma from Uraha, Malawi (Schrenk et al., 1993;
157 Bromage et al., 1995), and teeth from the Omo basin (Ethiopia) dated to 2.3-2.4 Ma (e.g.,
158 Howell et al., 1987; Suwa et al., 1996; Ramirez- Rozzi, 1997).

159
160

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

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

166 We reflect upon the morphological and archaeological data in the literature and on
167 interdisciplinary research conducted in recent years. Data from the literature on hominins,
168 archaeological sites, spatial information and context are taken at face value. However, it is
169 sometimes difficult to find information on fossil descriptions, in particular information
170 concerning deposition modes, contexts (*in situ*, on the surface) and distances from the
171 archaeological remains. In view of this difficulty, despite exhaustive research, it is possible that
172 certain associations are overlooked. Concerning the taxonomical names of hominin remains,
173 the presence of specimens named *Homo ergaster* or *Homo erectus* according to different
174 authors, are mentioned here as *Homo ergaster/erectus*. For the archaeological terminology,
175 we have used the terms Oldowan and Acheulean in a broad sense, as used in the cited paper,
176 and we do not make any distinction between early Oldowan, developed Oldowan etc, even if
177 important differences between hominin behaviour at early sites (ca. 2.6–2.3 Ma) in
178 comparison to later ones (ca. 2.0–1.7 Ma) have been attributed to this industrial complex (e.g.,
179 Harmand 2009a, Roche et al., 2009; Goldman-Neuman and Hovers 2012, Potts 2012). Indeed
180 Oldowan displays considerable differences in terms of technological complexity, groups
181 together assemblages with disparate characteristics and has been documented in multiple
182 raw material contexts and physical environments in Africa and Eurasia. A huge variability can
183 be seen in production methods depending on raw material choice (see for example Gallotti,
184 2018 and de Weyver, 2022 for a review). The raw material constraints (linked to the
185 landscape) lead to multiple technical systems of stone-tools production (e.g. free hand and
186 bipolar techniques) which did not develop chronologically and are not continuous. Raw
187 material seems to be a key factor in the diversity of the Oldowan assemblages (e.g. Schick et
188 al., 2006, Harmand et al., 2009b, Proffitt et al., 2022, Delagnes et al., 2023), **2. Overview of
189 archaeological data**

190

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

197

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

200

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

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

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

210 We divided this category into two subcategories:

211 HC 1 A, when the taxonomy is clear;

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

214
215 HC 2: when hominin remains were found outside the excavation (less than 400 metres away)
216 but in the same chrono-stratigraphical layers. We also divide this category according to the
217 taxonomical confidence of the paleoanthropological remains. HC2 A is when the taxonomy is
218 clear and HC2 B when it is debated.

219
220 Concerning the low confidence association between archaeological and hominin remains, we
221 can cite as the 2.5 Ma Hata Member of the Bouri Formation which yielded the specimen
222 defining the species *Australopithecus garhi* (Asfaw et al., 1999) and evidence of hominin
223 processing of large mammal remains (de Heinzelin et al. 1999), but no *in situ* artefacts, but are
224 sometimes associated with Oldowan site of Gona, 96 kilometres away. Concerning the
225 Lomekwian, some hominin remains were found in the paleontological collecting area LO5
226 (Harris et al., 1988) in the vicinity of the archaeological site LOM3 (3.3 Ma) (Harmand et al.,
227 2015; Skinner et al., 2020), in the same spatiotemporal range as the hominin fossils. These
228 include the paratype of *Kenyanthropus platyops* (KNM-WT 38350) (Leakey et al., 2001) and
229 for example, KNM-WT 64060 (Supplementary Informations in Harmand et al., 2015), a
230 hominin molar discovered in 2012 found 600 metres from the LOM3 site. They are deposited
231 in the same chronostratigraphic interval and are pene-contemporaneous with the LOM 3 site.

232
233

234 **2.1. High confidence in the association between lithic and paleoanthropological remains in** 235 **East Africa**

236
237 A high-confidence association (Table 1) between lithic and paleoanthropological remains
238 between 3 and 1.2 Ma in East Africa is noted in 29 cases (22 cases of High Confidence 1
239 (hominin remains found in the archaeological site) and seven cases of High Confidence 2
240 (hominin remains found less than 400 metres from the excavation but in the same chrono-
241 stratigraphical layers) (Table 2).

242
243 INSERT Table 1

244
245 INSERT Table 2

246 247 **2.1.1. Association between Oldowan and *Homo habilis* sensu lato**

248
249 The oldest evidence of lithic-hominin association between Oldowan and early *Homo*
250 specimens comes from the region of Hadar in Ethiopia. A *Homo* aff. *habilis* maxilla (AL 666-1)
251 was found at the site AL 666, dated to 2.34 Ma, alongside an Oldowan assemblage.

252

253 2.1.1.1. AL 666 (Oldowan), Ethiopia, Afar Region, AL 666-1 (*Homo* aff. *H. habilis*), 2.34 +/-0.07
254 Ma, High confidence: HC 1 A

255
256 In Ethiopia, in the Makaamitalu Basin (Kada Hadar, Afar Region), archaeological and hominin
257 remains were unearthed at the AL 666 site. Stratigraphically, they lie in the lowermost part of
258 the Busidima Formation, underlying the 2.36 +/- 0.07 Ma BKT-3 tephra (Campisano, 2012) and
259 are dated to 2.34 +/-0.07 Ma. The density of artefacts is low over an area of 20 m² and mostly
260 represented by flakes. None of the artefacts were retouched (Kimbel et al., 1996, Plummer
261 2004). The raw material was carefully selected, with a high frequency of homogenous and
262 fine-grained raw materials (Goldman-Neuman and Hovers, 2012). According to the
263 discoverers (Kimbel et al, 1996), the lithic assemblage is typical of an Oldowan assemblage.
264 On the surface, at the base of the AL 666 hill, a maxilla (AL 666-1) was discovered. An
265 excavation was undertaken to identify the *in situ* horizon, which led to the discovery of *in situ*
266 lithic elements but no additional hominin remains. Thirty-four stone tools including 14
267 excavated *in situ* were recovered from the AL 666 locality. The hominin maxilla (AL 666-1)
268 presents unambiguous affinities with early *Homo* (Kimbel et al., 1996) and has been assigned
269 to *Homo* aff. *H. habilis*, based on morphological and metrical comparisons (Kimbel et al. 1997).

270
271 2.1.1.2. Lokalalei 1, Gajh5 (Oldowan), Kenya, West Turkana, KNM-WT 42718 (early *Homo*),
272 2.34 +/-0.04 Ma, High confidence : HC 2 A

273
274 In Kenya, in the western part of the Lake Turkana, the Lokalalei complex of sites (Kibunja,
275 1994) has unearthed one hominin tooth dated to 2.34 +/-0.04 Ma. This tooth KNM-WT 42718
276 (Prat et al., 2005) is attributed to early *Homo* and was found at Lokalalei alpha, in the vicinity
277 of, but not strictly associated with the Oldowan Lokalalei 1 site. Indeed, this early *Homo*
278 specimen from Lokalalei 1alpha, is a surface finding discovered 100 m south of the
279 archaeological site Lokalalei 1. The duration of accumulation of the 6.2-m- thick fine sandstone
280 and claystone deposits that separate the sites Lokalalei 1alpha and Lokalalei 1 can be
281 estimated at a time scale of 10,000 to 100,000 years. Considering the classical measurement
282 error (0.04 to 0.5 Myr) for fission track and/or K/Ar, 40Ar/39Ar ages obtained on various tuffs
283 in Eastern Africa, the two sites have been considered to be chronologically close (Prat et al.,
284 2005).

285
286 2.1.1.3. Fj-1a (Oldowan), Fejej Region, Ethiopia, Fj-1-Hd1, -Hd3, Hd4 (*Homo* aff. *H. habilis*),
287 1.95-1.9 Ma, High confidence: HC 2 A.

288
289 At the northern limit of the Koobi Fora formation, in the Omo-Turkana Basin, the region of
290 Fejej yielded the FJ-1a archaeological site with faunal and lithic assemblages in a primary
291 context, referred as Oldowan (e.g., Asfaw et al., 1991, de Lumley and Beyene 2004, Barsky et
292 al. 2011). Geochronological data from the sequence indicate an age of nearly 1.9 Ma for the
293 FJ-1a archaeological level (Chapon et al., 2005). Raw materials (mainly quartz and basalt) were
294 locally available and carefully selected. The direct knapping method was longer and more
295 complex when knapping basalt (Barsky et al. 2011). Located 180 metres from FJ-1a, the locality
296 FJ-1e (Unit 3) yielded three hominin dental remains belonging to the same individual (Fj-1-Hd1
297 lower right first molar; Fj-1-Hd3, lower right second premolar; Fj-1-Hd4, lower left third
298 molar). These remains are attributed to *Homo* aff. *H. habilis* based on their morphology and
299 dimensions (de Lumley & Marchal 2004).

300
301 2.1.1.4. DK site, Bed I (Oldowan), Olduvai Gorge, Tanzania, OH 24 (*Homo habilis*), circa 1.87-
302 1.84 Ma, High confidence HC 2 A.

303
304 DK is the oldest site at Olduvai. Artefacts and bones at DK occur in the interval between the
305 Tuff IB and Bed I basalt lava, dated between 1.877 +/- 0.013 Ma and 1.848 +/- 0.003 Ma (Deino,
306 2012). It unearthed Oldowan assemblage (Leakey, 1971, de la Torre and Mora, 2005). The
307 cranium OH 24 which corresponds to one of the most complete remain allocated to *Homo*
308 *habilis* has been found 300 metres to the east to the original site (Leakey et al., 1971), but no
309 artefacts.

310
311 2.1.1.5 Ewass Oldupa site, Bed I (Oldowan), Olduvai Gorge, Tanzania, OH 65 (*Homo habilis*),
312 circa 1.82 Ma, High confidence HC 2 A.

313
314 In Olduvai Gorge Bed I, an almost intact maxilla (OH 65) from Geological locality 64 was
315 discovered 350 metres northeast of the Ewass Oldupa site (Geological Locality 63), which
316 contains cut-marked bones and an Oldowan assemblage mainly made on quartzite. Flakes are
317 the dominant product (Mercader et al. 2021). All these remains are from strata dated to ~1.82
318 Ma (Blumenschine et al., 2003, Deino, 2012, McHenry, 2012). Labial striations on the anterior
319 teeth suggest that OH 65 was right-handed in manipulating objects during oral processing
320 (Fruyer et al., 2016). OH 65 is assigned to the *Homo* genus, and has been allocated to *Homo*
321 *habilis* (Blumenschine et al., 2012, Clarke, 2012). However, Spoor and co-authors argue that
322 its morphology is not compatible with the holotype of *Homo habilis* (OH 7) and lacks the facial
323 morphology observed in *Homo rudolfensis* (Spoor et al., 2015) contra Blumenschine et al
324 (2012).

325
326 2.1.1.6 MNK Skull, Middle Bed II (Oldowan), Olduvai Gorge, Tanzania, OH 13, OH 15 (*Homo*
327 *habilis*), circa 1.67 Ma, High confidence HC 1 A

328
329 MNK Skull (Geological Locality 88, Mary Nicol Korongo, MNK, Middle Bed II) is an
330 archaeological site where two hominins allocated to *Homo habilis* (OH 13, and OH 15) were
331 discovered *in situ* and one (OH 14) on the surface. It is dated to circa 1.67 Ma (de la Torre et
332 al., 2021). OH 13 consists of cranial vault bones, parts of the maxilla, mandible with dentition.
333 It is one of the paratypes of *Homo habilis* (Leakey et al., 1964, Tobias 1991). This individual
334 represents the most recent specimen of *Homo habilis* in east Africa (Spoor et al., 2015). OH 15
335 consists of dental remains (one upper canine and two third upper molars) and is attributed to
336 *H. habilis* (Tobias, 1991). Alongside these hominin discoveries, important faunal and
337 archaeological assemblages were unearthed by Mary Leakey (Leakey 1971). The stone tool
338 assemblage is typical of the Oldowan, with no technological elements heralding the
339 appearance of the Acheulean, and a debitage dominated by quartzite and an overabundance
340 of lava cores (de la Torre et al., 2021).

341

342

343 **2.1.2. Association between the Oldowan, *Homo habilis* and *Paranthropus boisei***

344

345 2.1.2.1. FLK level 22 (Oldowan), Olduvai Gorge, Tanzania, OH 5 (*P. boisei*), High confidence
346 HC1 A; OH 35 (*P. boisei*) or (*H. habilis*), High confidence HC 1 B), OH 6 (*H. habilis*), High
347 confidence HC 1 A, 1.84 Ma

348

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

353 One of these four hominin remains was a surface finding (OH 44, right upper first molar), one
354 (OH 35) represents some postcranial bones (tibia and fibula (Leakey et al., 1964) with an
355 uncertain taxonomical allocation, as they are associated with cranio-dental remains, one is
356 attributed to *H. habilis* (OH 6, lower third premolar, right upper molar, right upper second
357 incisor and six calvaria fragments, Tobias, 1991), and another is OH5, the *P. boisei* holotype.
358 The age of the *Zinjanthropus* surface is constrained by tuffs IB and IC, dated respectively to
359 1.845 +/- 0.002 Ma and 1.839 +/- 0.005 Ma (Blumenschine et al, 2003; Blumenschine et al,
360 2012).

361
362 2.1.2.2. FLK NN level 3 (Oldowan), Olduvai, Tanzania, OH 7 cranial remains (*H. habilis*): High
363 confidence HC 1 A; OH 7 hand remains (*H. habilis* or *P. boisei*): High confidence HC 1 B; OH 8
364 (*H. habilis*): High confidence HC 1 B, 1.84 Ma
365

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

377
378 2.1.2.3. FxJj 38 (Oldowan), Koobi Fora, Kenya, KNM-ER 1805 (*Homo* sp.), High confidence HC
379 1 B, and KNM-ER 1806 (*P. boisei*), High confidence HC 1 A, 1.78 and 1.52 Ma or 1.85 Ma
380

381 Two hominin remains were discovered in the Koobi Fora Region, in area 130. The first one
382 (KNM-ER 1805) was found *in situ* in deposits stratigraphically located below the Okote Tuff
383 complex and consists of a cranium and associated mandible. It has been allocated to early
384 *Homo* (*Homo* sp., Leakey 1974), but also to other species and genera (see Prat, 2002). It
385 displays a number of unique features differentiating it from other hominins, and should not
386 be considered as a standard *Homo habilis* male (Prat, 2002). Fifteen metres from this
387 specimen, on the surface, a large mandible (KNM-ER 1806) allocated to *P. boisei* was
388 discovered (Leakey 1974). Excavations at these two localities unearthed faunal remains, as
389 well as a light scatter of stone artefacts, but no additional hominin remains. Forty metres east
390 of these paleoanthropological localities, on the same stratigraphical horizon, lies the
391 archaeological site FxJj 38 North West. The composition of the lithic assemblage, with a large
392 chopper component, is consistent with that of Olduvai Bed I and therefore allocated to the
393 Oldowan (Harris & Herbich, 1978) and represents one of the type localities for the Developed
394 Oldowan of Koobi Fora (Mana et al., 2019). These hominin remains and archaeological site
395 belong to the KBS Member, below the base of the Okote Member and above the KBS Tuff.
396 These sites are, according to Mana and co-authors, broadly constrained between 1.78 and
397 1.52 Ma (Mana et al., 2019). This is in contradiction with the interpretation of Feibel and
398 collaborators who estimated its age at 1.85 Ma (Feibel et al., 1989).

399
400 **2.1.3. Association between Oldowan artefacts and *Paranthropus* (*P. aethiopicus*, *P. boisei*)**
401

402 2.1.3.1. Nyayanga, excavation 3 (Oldowan), Lake Victoria, Kenya, KNM-NG 77316 (*P. boisei*):
403 High confidence: HC 1 A, 3.03 -2.58 Ma

404
405 In Kenya, the site of Nyayanga, on the southern margin of the Winam Gulf of Lake Victoria has
406 revealed one of the oldest known Oldowan assemblages, dated between 3.032 Ma and 2.581
407 Ma (Plummer et al., 2023). This site yielded 135 artefacts *in situ* (excavations 3 and 5) and 195
408 on the surface, as well as bones, including cut-marked bones. The flakes were removed from
409 cores using unifacial, bifacial and multifacial reduction, comparable to other Oldowan
410 localities. The use wear on the lithic material, as well macro and micro traces, indicate the
411 processing of plant tissue and faunal remains. In excavation 3, one fragment of a left lower
412 molar (KNM-NG 77316) was found *in situ*, spatially associated with Oldowan artefacts, and
413 one left upper molar (KNM-NG 77315) came from the surface (see paragraph 5). These two
414 teeth, based on the morphology and metrics are assigned to the *Paranthropus* genus.

415
416 2.1.3.2. Omo 57-5 (Oldowan), Lower Omo valley, Ethiopia, Omo 57/5-1972-371 (*P. aff. P.*
417 *aethiopicus*): high confidence: HC 1 A. 2.32 Ma to 2.23 Ma

418
419 In Ethiopia, in the Lower Omo Valley, at the archaeological locality Omo 57-5 (Member F of
420 the Shungura Formation), the excavation of 40 m² unearthed four fragments of hominin
421 teeth, associated with a quartz flake found *in situ* and 16 artefacts (cores and flakes) on the
422 surface (Coppens et al., 1973, Chavaillon, 1976). One of these paleoanthropological remains
423 (Omo 57/5-1972-371, a fragment of a left lower second premolar) has been assigned to *P. aff.*
424 *aethiopicus* based on its morphology (Coppens et al. 1973, Coppens, 1977, Suwa 1990, Wood
425 and Leakey 2011).

426 Another hominin dental remain (Omo 57/5-1972-319), a left upper first premolar, is
427 considered to be indeterminate (White, 1988) or an indeterminate non-robust hominin (Suwa
428 1990), or allocated to the *Homo* genus (*aff. Homo* sp., Wood and Leakey 2011). According to
429 de la Torre in 2004, the Omo 57 locality provides clear evidence of flaking activities showing
430 ordered and systematic knapping processes, and does not derive from the fluvial deposition
431 of natural fragments. The lithic assemblage is assigned to the Oldowan (de la Torre, 2004). The
432 Member F deposits are dated to 2.32 Ma to 2.23 Ma (McDougall and Brown, 2008).

433
434 2.1.3.3. Kokiselei 1, FxJh 6 (Oldowan), Kenya, KNM-WT 37744, KNM-WT 37747, KNM-WT
435 37748, KNM-WT 37100 (*P. boisei*): high confidence: HC 1 A. 1.79 Ma

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

446
447 2.1.3.4. FxJj 20 (Oldowan), Koobi Fora, Kenya and KNM-ER 3230 (*P. boisei*): High confidence:
448 HC 1 A. 1.65 +/- 0.05 Ma

449

450 At FxJj 20 East, in Koobi Fora Area 131, a hominin mandible with complete dentition (KNM-ER
451 3230) was recovered *in situ* from the site excavated by J.W.K. Harris in 1975 in tuffaceous
452 floodplain silts of the Okote Tuff complex (Leakey 1976; Harris and Herbich, 1978). Based on
453 the morphologies and metrics of the mandible and teeth, KNM-ER 3230 has been assigned to
454 *Paranthropus boisei* (Leakey 1976; Leakey and Walker, 1985; Wood, 1991) and dated to 1.65
455 +/- 0.05 Ma (Feibel et al., 1989). According to Harris and Herbich, 1978, a low-density scatter
456 of bones and lithic artefacts were found on the same horizon as the hominin, and the vertical
457 distribution of the lithic assemblage shows that the hominin mandible was stratigraphically
458 located approximately 10-15 centimetres above the main artefact-bearing horizon (Harris and
459 Herbich, 1978). It should be noted that despite this association, Richard Leakey did not want
460 to associate the two in his 1976 paper. We can wonder whether Richard Leakey would have
461 interpreted the finds in this way if the remains had belonged to the *Homo* genus (see
462 paragraph 5).

463
464 2.1.3.5. Chesowanja GnJ1/6E (Oldowan), Chesowanja, Kenya, KNM-CH 304 (*P. boisei*): High
465 confidence: HC 2 A; Chesowanja GnJ2 (Oldowan), Chesowanja, Kenya, KNM-CH 1, KNM-CH
466 302, KNM-CH 304 (*P. boisei*): High confidence: HC 2 A 1.42+/-0.07 Ma

467
468 At Chesowanja, near Lake Baringo in Kenya, in the Chemoigut Formation layers, remains
469 allocated to *P. boisei* were found close to an Oldowan assemblage (Carney et al., 1971; Bishop
470 et al. 1975; Gowlett et al. 1981). The hominin remains consist on a right hemi-face and anterior
471 cranial base (KNM-CH 1); dental fragments (KNM-CH 2) and cranium fragments (KNM-CH 304).
472 The cranium KNM-CH 304 consists of five cranial vault fragments labelled A-E and is allocated
473 to *P. boisei* (Gowlett et al. 1981). It has been found 15 metres from the site GNJ1/6E (40 m²
474 excavated) where 1000 Oldowan artefacts were found *in situ* with limited vertical distribution.
475 The other specimens also allocated to *P. boisei* were found in GnJ2, where artefacts scatters
476 occur on the surface, but only one rewarding *in situ* occurrence (Carney et al., 1971; Bishop et
477 al. 1975; Gowlett et al. 1981). According to these authors, this association must be considered
478 to be more than coincidental (see paragraph 5). The basalt member at the base of the
479 Chesowanja Formation is dated at 1.42+/-0.07 Ma.

480
481 2.1.3.6. BK site level 4 (Oldowan), Olduvai Gorge, Tanzania, OH 80 (*P. boisei*): High confidence:
482 HC 1 A. 1.34 Ma

483
484 At Olduvai Gorge, in Tanzania, in Bed II, the BK Site yielded a partial *Paranthropus boisei*
485 skeleton (Domínguez-Rodrigo et al., 2013). OH 80 was found *in situ* in level 4, which is
486 characterized by a large Oldowan assemblage and a huge number of vertebrate fossils, some
487 of which bear butchery marks (Domínguez-Rodrigo et al., 2009). The specimen comprises four
488 postcranial bones (distal part of a left humeral diaphysis, proximal half of a right radius, much
489 of the right femoral shaft and part of a tibial midshaft) in direct association with nine upper
490 teeth (left and right first and second incisors, right first premolar, left second premolar, left
491 first molar, right second incisor). Based on their morphology, dimensions and section
492 properties, these remains are allocated to *P. boisei* (Dominguez-Rodrigo et al., 2013). It is the
493 first partial skeleton attributed to this taxon and is dated to 1.34 Ma.

494
495 **2.1.4. Association between Oldowan and *Homo erectus/ergaster***

496

497 2.1.4.1. PTK site (Oldowan), Olduvai Gorge, Tanzania, OH 86, (*H. erectus*-like): High
498 confidence: HC 1 B. 1.84 Ma

499

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

510

511 2.1.4.2. Naiyena Engol 1, FxJh 5, (Oldowan), West Turkana, Kenya, KNM-WT 37745 (aff. *H.*
512 *ergaster/H. erectus*): High confidence: HC 1 A, 1.75 +/- 0.05 Ma

513

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

520

521 2.1.4.3. Melka Kunture Garba IV (level E) (Oldowan), Melka Kunture, Ethiopia, MK 81 GAR IVE
522 0043 (early *Homo erectus/H. ergaster*). High confidence: HC 1 A. Slightly older than 1.7 Ma

523

524 The Garba IV mandible (MK 81 GAR IVE 0043) from Melka Kunture was found *in situ* in 1981
525 during the excavation of level E, while opening an area of 2 square metres. Based on its
526 stratigraphical position immediately below the "Grazia tuff" and its normal polarity, this level
527 should be around or slightly older than 1.7 Ma (e.g., Morgan et al., 2012, Tamrat et al., 2014,
528 Gallotti and Mussi, 2015). Layer E yielded 504 unworked lithic objects and 718 artefacts. The
529 lithic assemblage from Garba IV level E was deposited during a relatively short lapse of time.
530 It is allocated to the Oldowan and shows that hominins had good knowledge of raw material
531 suitability (obsidian being the most frequently exploited raw material) (Gallotti and Mussi,
532 2015). The mandible belongs to a child whose age at death was estimated between 3 and 4
533 years (Condemi, 2004) or between 2.5-3.5 years old based on the tooth development pattern
534 (Zanolli et al., 2016). It is allocated to early *Homo erectus/Homo ergaster* (Condemi 2004). The
535 inner dental morphology also suggests that the Garba IV mandible is a robust early *Homo*
536 specimen (Zanolli et al., 2016).

537

538 2.1.4.4. Melka Kunture Gombore I (Oldowan), Melka Kunture, Ethiopia, Gombore IB-7594
539 (*Homo* sp. or *H. erectus*): High confidence: HC 1 B. 1.5-1.6 Ma

540

541 In the Melka Kunture site complex in Ethiopia, a well-preserved distal portion of a left humerus
542 (Gombore IB-7594, formally Melka Kunture 3, or MK3) was discovered in 1976 during the
543 excavation of the site of Gombore I, directed by J. Chavaillon (Chavaillon et al., 1977). This
544 postcranial hominin remain was found in the southern sector of the excavation *in situ* in unit
545 2 of level B, which includes rich faunal and Oldowan assemblages with a predominance of
546 pebble tools, mainly side choppers (Chavaillon and Berthelet, 2004). They are dated to 1.6-1.5

547 Ma (Morgan et al., 2012; Tamrat et al., 2014, Cazenave et al., 2017). Gombore IB-7594 was
548 referred to *Homo* sp. (Chavaillon et al., 1977), but based on morphometric affinities, Lague
549 and Jungers considered that this specimen could plausibly belong to *Paranthropus boisei*
550 (Lague and Jungers, 1996). However, according to the majority of authors, this specimen is
551 part of the *Homo* genus (Senut, 1979). Coppens considered that it was too robust to be *Homo*
552 *habilis* and referred it to *Homo erectus* (Coppens, 2004). It is also allocated to *Homo* sp. based
553 on geometric morphometrics (Di Vincenzo et al. 2015). The study of endostructural
554 organization shows that this robust *Homo* aff. *erectus* humerus is different to *Paranthropus*
555 and close to the modern human humerus (Cazenave et al., 2017).
556

557

558 **2.1.5. Association between the Oldowan, Acheulean and early *Homo erectus*/*Homo ergaster***

559

560 2.1.5.1. DAN 5 (Oldowan and Acheulean), Dana Aoule Gona, Afar Region, Ethiopia, DAN5/P1
561 (early *H. erectus*/*H. ergaster*), High confidence: HC 1 A. 1.6-1.5 Ma

562

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

579

580 2.1.5.2. BSN12 (Oldowan and Acheulean), Busidima North Gona, Afar Region, Ethiopia,
581 BSN12/P1 (early *H. erectus*/*H. ergaster*), High confidence: HC 1 A. 1.26 +/-0.03 Ma

582

583 At BSN12, almost 6 km southwest of DAN5, another hominin (BSN12/P1) was unearthed in
584 direct association with both Oldowan and Acheulean assemblages (Semaw et al. 2020). It is
585 also associated with the Boolihinan Tuff, which is dated, based on geochemical affinities, to
586 1.262 +/-0.034 Ma. The tephra was found cemented on the BSN12/P1 parietal and both
587 Oldowan and Acheulean artefacts. The BSN12/P1 hominin also includes some parts of the
588 right orbital margin and frontal squama. Based on its anatomy and dimensions, this robust
589 hominin shares *Homo erectus* features (Semaw et al., 2020, Baab et al., 2022) and is similar to
590 Indonesian and Eastern Asia hominins, as well as to OH 9 and BOU-VP-2/66 (Middle Middle
591 Awash, Ethiopia) and UA-31 (Buia, Eritrea).

592

593 **2.1.6. Association between the Acheulean, *Homo erectus* and *P. boisei***

594

595 2.1.6.1. KGA 10-1 (Acheulean), Konso-Gardula, Ethiopia, KGA10-506, KGA10-525, KGA10-565,
596 KGA10-570, KGA10-900, KGA10-1455, KGA10-1720, KGA10-2705 (*H. erectus*): High confidence
597 HC 1 A; KGA10-2741 (*P. boisei*): High confidence: HC 1 A: 1.4 Ma and KGA 4E (Acheulean),
598 *Homo* sp., High confidence: HC 1 A. 1.44 Ma

599

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

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

621

622 2.2. The case of southern Africa

623

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

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

633 Here, we present some examples. At Sterkfontein, the Member 5 East lower (Member 5
634 Oldowan infill), dated to around 2.18 ± 0.21 Ma (Granger et al., 2015), yielded remains
635 allocated to *P. robustus*, as well as 3513 lithic artefacts all attributed to the Oldowan (Kuman
636 and Clarke, 2000; Kuman, 2009). On the other hand, in the member 5 West (Sterkfontein
637 Acheulean infill), dated between 1.3 and 1.1 Ma (Herries and Shaw, 2011), an Acheulean
638 assemblage was found in association with a bone tool (n=1) and *Homo* remains (Kuman and
639 Clarke, 2000). At Drimolen Main Quarry (MNQ), recently dated to c. 2.04-1.95 Ma (Herries et
640 al., 2020), some early *Homo* and *P. robustus* remains, as well as Oldowan stone artefacts and
641 bone tools (n=14) were discovered (Keyser et al., 2000; Moggi-Cecchi et al., 2010; Stammers
642 et al., 2018; Backwell and d'Errico, 2008). A similar discovery of six early *Homo* remains, 113
643 *P. robustus*, an Oldowan assemblage and bone tools (n=32) (Brain, 1993; Brain and Shipman,
644 1993; d'Errico and Backwell, 2003; Backwell and d'Errico, 2003; Caruana, 2017) was made in
645 the Member 1 of Swartkrans, dated between 2.4 and 1.8 Ma (Pickering et al., 2019). In the
646 Member 2 of Swartkrans, dated to c. 1.4 Ma (Balter et al., 2008), an Acheulean assemblage
647 with bone tools (n=11) and both *Homo* and *P. robustus* remains (Brain, 1993; d'Errico and
648 Backwell, 2003; Kuman, 2007) were unearthed. In the Member 3 of Swartkrans, dated to circa
649 0.96 Ma (Gibbon et al., 2014), only one hominin species (*P. robustus*) was found in association
650 with an Acheulean assemblage and bone tools (n= 41) (Brain, 1993; d'Errico and Backwell,
651 2003; Kuman, 2007). A similar discovery was made at Cooper's D, dated between 1.4 and 1.0
652 Ma, in the form of seven *P. robustus* remains, 49 stone artefacts [not allocated to a specific
653 industry for the moment due to the small number of artefacts (Sutton et al. 2017)] and a bone
654 tool (n=1) (Steininger et al., 2008; de Ruiter et al., 2009, Hanon et al., 2021).

655

656 These examples support the hypothesis that *P. robustus* probably made and/or used stone
657 and bone tools (e.g., Sterkfontein, Member 5 East lower (Member 5 Oldowan infill), 2.18 ±0.21
658 Ma, Oldowan; Coopers’D, 1.4-1 Ma, indeterminate for the moment; Swartkrans Member 3, c.
659 0.96 Ma, Acheulean). The attribution of artefacts to *Homo* rather than *Paranthropus* or both
660 taxa appears once again to be more ideological than scientific.

661

662 **3. Overview of anatomical/morphological data**

663

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

671

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

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

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

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

719
720 After 2 Ma, the morphology of the Olduvai and Swartkrans hominin hands discovered in
721 archaeological levels (see paragraph 3) are compatible with tool using and tool-making. For
722 the Olduvai remain (OH 7), human-like precision grips are associated with pad-to-pad
723 precision grasping. Indeed, in the publication defining the species *Homo habilis*, based on the
724 OH 7 late juvenile hand bones uncovered at site FLKNN I in Olduvai Gorge (Tanzania), Leakey
725 and co-authors emphasized a well-developed and fully opposable thumb (pollex) and a hand
726 capable of a power grip, as well as a simple and usually well-developed precision grip (Leakey
727 et al., 1964). Hence the OH7 hand has played a crucial role in our perception and
728 understanding of the evolution of hominin tool use and tool-making and therefore on the
729 definition of the *Homo* genus. However, it should be noted that in the initial description in
730 1962, Napier (Napier, 1962) highlighted a mosaic morphology (e.g., modern human-like
731 morphology of the distal pollical phalanx and ape-like carpus and curvature of the phalanges),
732 and observed that the thumb was opposable and powerful. In terms of functional
733 interpretation, he emphasized “On anatomical grounds there is no doubt that the Olduvai
734 hand was sufficiently advanced in terms of the basic power and precision grips to have used
735 naturally occurring objects as tools to good advantage. There is less certainty about
736 toolmaking which involves not only a peripheral but also a central intellectual factor as Oakley
737 has long insisted” (Napier, 1962, p. 411). This interpretation contrasts somewhat with that of
738 Leakey, Tobias and Napier 1964 which unlights that “While it is possible that *Zinjanthropus*
739 and *Homo habilis* both made stone tools, it is probable that the latter was the more advanced
740 tool maker ..(Leakey et al. 1964, p. 9) (see paragraph Discussion and conclusions).

741 Furthermore, the taxonomical allocation of the OH7 hand has been questioned, as the
742 phalangeal morphologies show some similarities with *Paranthropus* (Moyà-Solà et al., 2008).
743 Based on functional analyses, those authors (Moyà-Solà et al., 2008) suggested that the
744 anatomical features linked to human-like precision grasping (previously considered as tool-
745 making features by some authors, may be conversely adapted to specialized manual feeding
746 techniques in *Paranthropus*. Furthermore, according to Susman and Creel (Susman and Creel,
747 1979), the mosaic of features observed in the anatomy of OH7 could reflect precision grip
748 abilities (e.g., the modern human-like features of distal phalanges) and frequent climbing (e.g.,
749 African ape-like features).

750
751 At the PTK (level 3) site at Olduvai Gorge level 3, a manual proximal phalanx (OH 86) dated to
752 1.84 Ma (Domínguez-Rodrigo et al., 2015) represents the earliest modern human-like hand
753 anatomy (see paragraph 2.1.4.1). This specimen is assigned to the *Homo* genus and contrasts
754 in size and shape not only with *Australopithecus* or *Paranthropus*, but also with the OH7 hand.
755 The phalangeal features are indicative of more relaxed postural and locomotive selective

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

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

769
770 In southern Africa, according to work by Susman (Susman, 1988, 1994, 1998), the remains
771 (phalanges and metacarpals) discovered mainly in Member 1 of the Swartkrans site and
772 possibly but not securely allocated to *P. robustus*, as early *Homo* specimens were also found
773 in this member, show that these hominins possessed muscles allowing for human-like
774 precision grasping (by stabilizing the opposing the thumb and the fifth finger to the other
775 fingers), which are considered as adaptations for tool-using and tool-making (Susman, 1994,
776 1998). For Moyà-Solà and co-authors (Moyà-Solà et al., 2008), the *Paranthropus* pattern
777 probably reflects an adaptation to manual activities other than tool-making more related to
778 feeding behaviour such as specialized food gathering and processing, as observed in extant
779 hominids (Gérard et al., 2022; Marzke et al., 2015; Neufuss et al., 2018).

780
781 Lastly, the recent description of a third metacarpal (Kaitio area, West Turkana, Natio Member,
782 1.42 Ma) from West Turkana, with a styloid process typical of modern humans, seems to
783 confirm that enhanced hand function for tool-making and tool-using took place very early on
784 in the evolution of the *Homo* genus (Ward et al., 2014).

785
786 **4. New approaches, how can we go beyond anatomical and archaeological field data?**

787 **4.1. Experimental biomechanics and musculoskeletal modelling**

788
789 The first of the two last points of this review concerns experimental simulations and in
790 particular the required biomechanical capacities and manual skills for percussive movements.
791 Indeed, in addition to the archaeological and paleoanthropological framework, experimental
792 biomechanics and musculoskeletal modelling can shed light on the functional anatomy of the
793 upper limb involved in stone tool production (e.g., Rolian et al., 2011; Tocheri et al., 2003; Key
794 et al., 2019, Kivell et al. 2022).

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

804 contact with the surface of a large object. This may have been a limiting factor in exerting a
805 large enough grip force to make large lithic artefacts such as those found at Lomekwi 3.
806 The biomechanics of free-hand knapping (techniques used to produce the Oldowan) received
807 more attention, but are quite limited concerning the hand (Kivell et al., 2022). A wide variety
808 of grips were used, with significant emphasis on precision grips (Key et al., 2018; Williams-
809 Hatala et al., 2021). Loads tend to be concentrated on the thumb (pollex) in both the dominant
810 and non-dominant hands, which is probably the best candidate for a manual adaptation for
811 this specific behaviour (Rolian et al., 2011; Williams-Hatala et al., 2018; Williams-Hatala et al.,
812 2021; Key & Dunmore, 2015). As summarized by Kivell et al. (2022), the osteology and
813 muscular anatomy of the thumb are essential for understanding the adaptative response to
814 stone tool production and use, but we must also consider the fact that different combinations
815 of derived characters can occur at different times and the problems of equifinality with respect
816 to behaviour. Furthermore, more data are needed on EMG, kinematics, kinetics of the digits
817 and all the upper limb during free-hand, bipolar and passive hammer knapping. Moreover, the
818 application of new techniques (Manafzadeh & Gatesy, 2021), such as X-ray reconstruction of
819 moving morphology (bi-planar X-ray with X-ROMM), can provide new insights into the
820 reconstruction of joint mobility.

821

822 **4.2. Cognitive exploratory studies**

823

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

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

837

838 In this context, some exploratory studies using for example fluorodeoxyglucose positron
839 emission tomography (FDG-PET), functional magnetic resonance imaging (fMRI) and image-
840 based functional near-infrared spectroscopy (fNIRS) on Oldowan and Acheulean productions
841 have been undertaken. The purpose was to discuss which brain regions are the most active
842 during these stone tool productions using different techniques (free-hand percussion and
843 bifacial shaping) and whether advanced executive functions such as cognitive control,
844 planning and the working memory are involved. During these experimental studies, the
845 subjects could have different levels of expertise (novices, learning, experts). The subjects
846 could watch videos (Stout et al., 2015, using the fMRI method) or produce stone tools (Stout
847 et al. 2000, Stout et al. 2008, Stout and Chaminade, 2007, using FDG-PET method; Putt 2016,
848 Putt et al., 2017, using fNIRS method). According to Stout et al (2015), prefrontal responses
849 are greater in Acheulean as opposed to Oldowan tool-making. The main difference between
850 Oldowan and Acheulean tasks is that Oldowan tool-making relies on the coordination of visual
851 attention and motor control (motor and sensorimotor areas) (Stout et al. 2000). In contrast,
852 according to Putt, Acheulean tool-making requires the integration of higher order motor
853 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).

886

887 **5. Discussion and conclusions**

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

897

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

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

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

913 Besides, if after 1.4 Ma *H. erectus* is mainly associated with Acheulean assemblages, our paper
914 also unlights that there are many sites (n=6) where *Homo erectus/ergaster* is associated with
915 Oldowan (PTK site Olduvai, Naiyena Engol 1, Melka Kunture Garba IV (level E), Melka Kunture
916 Gombore I, DAN 5, BSN 12, e.g. Chavaillon et al., 1977; Chavaillon et Berthelet, 2004; Condemi,
917 2004; Coppens, 2004; Domínguez-Rodrigo et al., 2015; Gallotti et Mussi, 2015; Prat et al.,
918 2003; Roche et al., 2003; Semaw et al., 2020), and not with Acheulean in Africa (Table2, Figure
919 2), but also outside Africa (e.g. Dmanisi (e.g. Lordkipanidze et al., 2007, 2013, Mgeladze et al.,
920 2011), 'Ubeidiya (e.g., Belmaker et al., 2002, Tobias, 1966, Bar-Yosef and Goren-Inbar, 1993).

921

922 INSERT Figure 2

923

924 Despite some strong associations between Oldowan assemblages and *P. boisei* remains, it
925 should be noted that in many cases, it is difficult for authors to admit that *P. boisei* could have
926 been the stone tool-makers. We can mention notably, the case of Olduvai Gorge. FLK level 22
927 yielded a dense Oldowan assemblage and four hominin individuals, including the cranium OH
928 5, holotype of the species *Paranthropus boisei* (formerly *Zinjanthropus boisei*, Leakey, 1959),
929 and one specimen allocated to *H. habilis* (OH 6) (see paragraph 2.1.2.1). When the OH 5
930 cranium was discovered in this site, it was considered as “the oldest yet discovered maker of
931 stone tools” (Leakey, 1959, p. 493). However, five years later, Louis Leakey changed his mind,
932 based on *Homo habilis* fossils in association with the Oldowan culture at three other localities
933 at Olduvai, such as for example the FLK NN level 3 with *P. boisei* and *H. habilis* including the
934 holotype OH 7 (see paragraph 2.1.2.2), and concluded that “while it is possible that
935 *Zinjanthropus* and *Homo habilis* both made stone tools, it is probable that the latter was the
936 more advanced tool maker and that the *Zinjanthropus* skull represents an intruder (or a
937 victim) on a *Homo habilis* living site” (Leakey et al., 1964, p. 9). In five years, with no real
938 argument, the status of *P. boisei* has changed from stone tool-maker to victim.

939

940 It is also important to mention that despite the discovery of the *Paranthropus boisei* mandible
941 KNM-ER 3230 *in situ* at the FxJ 20 East site (Koobi Fora Area 131, Kenya) (see paragraph
942 2.1.3.4), Leakey in his 1976 paper did not want to associate the two (Leakey, 1976). We can
943 wonder whether Leakey’s interpretation would have been the same if the remains had
944 belonged to the *Homo* genus.

945 More recently, at the site of Nyayanga (Kenya), a left lower molar (KNM-NG 77316) allocated
946 to *P. boisei* was found *in situ*, spatially associated with Oldowan artefacts (see paragraph
947 2.1.3.1). The authors (Plummer et al., 2023) highlight a clear association between the lower

948 molar fragment and the artefacts “raising the possibility that *Paranthropus* made and/or co-
949 opted stone tools” (Plummer et al., 2023 p. 5). However, in the same paragraph, the authors
950 mention that even though no early *Homo* remains have been found at Nyayanga, as this taxon
951 occurred in eastern Africa, with the mandible from Ledi Geraru, 1300 kilometres away, dated
952 to 2.8 Ma in Ethiopia (Villmoare et al., 2015), the Nyayanga Oldowan artefacts “cannot be
953 definitively attributed to a specific hominin genus” (Plummer et al., 2023 p. 5). This sentence
954 illustrates that it is still difficult for some authors to consider that a genus other than *Homo*
955 could be the Oldowan stone tool makers and they give more importance to remains found
956 1300 kilometres away and corresponding to our non-confident (LC) category than to *in situ*
957 material (confident category HC1 A), which would be the most parsimonious hypothesis from
958 an Occamian perspective. Even if of course, it is always difficult to be sure that the hominins
959 found in some archaeological sites are the actual tool makers, but this hypothesis is commonly
960 used for example for Upper or Middle Palaeolithic sites.

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

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

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

996 The plurality of stone tool-makers has been previously highlighted by some researchers (e.g.
997 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.

1017
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1024

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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.

1667

1668

1669

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 sp.</i>	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 2A
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

1670

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)

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