Metacarpal torsion in apes, humans, and early *Australopithecus:* implications for manipulatory abilities.

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Human hands, when compared to that of apes, have a series of adaptations to facilitate manipulation. Numerous studies have shown that *Australopithecus afarensis* and *Au. africanus* display some of these adaptations, such as a longer thumb relative to the other fingers, asymmetric heads on the second and fifth metacarpals, and orientation of the second metacarpal joints with the trapezium and capitate away from the sagittal plane, while lacking others such as a very mobile fifth metacarpal, a styloid process on the third, and a flatter metacarpo-trapezium articulation, suggesting some adaptation to manipulation but more limited than in humans. This paper explores variation in metacarpal torsion, a trait said to enhance manipulation in humans and apes, as well as in early australopithecines and specimens from Swartkrans. This study shows that humans are different from large apes in torsion of the third and fourth metacarpals. Humans are also characterized by wedge-shaped bases of the third and fourth metacarpals, making the metacarpal-base row very arched mediolaterally and placing the ulnar-most metacarpals in a position that facilitate opposition to the thumb in power or cradle grips. The third and fourth metacarpals of *Au. afarensis* are very human-like, suggesting that the medial palm was already well adapted for these kinds of grips in that taxon. *Au. africanus* present a less clear human-like morphology, suggesting, perhaps, that the medial palm was less suited to human-like manipulation in that taxa than in *Au. afarensis*. Overall, this study supports previous studies on *Au. afarensis* and *Au. africanus* that these taxa had derived hand morphology with some adaptation to human-like power and precision grips and support the hypothesis that dexterous hands largely predated *Homo*.

1 **Metacarpal torsion in apes, humans, and early *Australopithecus:* implications for**

2 **manipulatory abilities.**

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18 **Abstract**

19 Human hands, when compared to that of apes, have a series of adaptations to facilitate

20 manipulation. Numerous studies have shown that *Australopithecus afarensis* and *Au. africanus*

21 display some of these adaptations, such as a longer thumb relative to the other fingers,

22 asymmetric heads on the second and fifth metacarpals, and orientation of the second metacarpal

23 joints with the trapezium and capitate away from the sagittal plane, while lacking others such as

24 a very mobile fifth metacarpal, a styloid process on the third, and a flatter metacarpo-trapezium

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26 paper explores variation in metacarpal torsion, a trait said to enhance manipulation in humans

27 and apes, as well as in early australopithecines and specimens from Swartkrans. This study

28 shows that humans are different from large apes in torsion of the third and fourth metacarpals.

29 Humans are also characterized by wedge-shaped bases of the third and fourth metacarpals,

30 making the metacarpal-base row very arched mediolaterally and placing the ulnar-most

31 metacarpals in a position that facilitate opposition to the thumb in power or cradle grips. The

32 third and fourth metacarpals of *Au. afarensis* are very human-like, suggesting that the medial

33 palm was already well adapted for these kinds of grips in that taxon. *Au. africanus* present a less

34 clear human-like morphology, suggesting, perhaps, that the medial palm was less suited to

35 human-like manipulation in that taxa than in *Au. afarensis*. Overall, this study supports previous

36 studies on *Au. afarensis* and *Au. africanus* that these taxa had derived hand morphology with

37 some adaptation to human-like power and precision grips and support the hypothesis that

38 dexterous hands largely predated *Homo*.

Introduction

Much of the debate on *Australopithecus* has focused on its locomotor habits and the maintenance

(or not) of an arboreal component. However, manipulatory capabilities in that taxon have also

been argued (e.g., Marzke, 1983, 1997; Susman, 1998; Drapeau, 2012; Kivell, 2011; Skinner et

al., 2015). Marzke (1997, 2005) identified three traits that suggest that the hand of one of the

oldest *Australopithecus* species, *Au. afarensis* had hands that were able to produce better

precision grips and handling than the ape hand: a more robust and longer thumb relative to the

other fingers, asymmetric heads on the second and fifth metacarpals, and orientation of the

second metacarpal (MC) joints with the trapezium and capitate away from the sagittal plane.

However, Susman (1998) doubts that all these traits indicate significant improvement of

manipulatory skills. Interestingly, they both recognize that the radial torsion (toward the thumb)

of the second and third MC heads improves manipulatory grips (Susman, 1979; Marzke and

Shackley, 1986; Marzke 1997, 2005), although neither recognizes that trait in *Australopithecus*

(but see Kivell et al., 2011 supp. material). Torsion of the second and third MC head in

hominoids is a trait that is described qualitatively, but has not been extensively quantified

(except in humans; Singh, 1979; Peters and Koebke, 1990) and rarely statistically compared

among humans and great apes (Drapeau, 2009). This paper explores MC head torsion in these

extant species and compares values for *Au. afarensis*, *Au. africanus* and Swartkrans specimens.

Background

Humans and apes have different power grips. Humans hold objects obliquely in the cupped palm,

positioning the thumb in opposition to the other fingers. The fifth digit is the most flexed and the

subsequent lateral fingers, digit 4 to 2, are progressively less flexed (Lewis, 1977, 1989; Napier,

64   1993; Kapandji, 2005). The two ulnar-most MCs are also slightly flexed at the carpometacarpal

65   joint. In addition, the palmar surfaces of the fingers are supinated, i.e., turned toward the thumb.

66   Apes, instead, flex digits 2 to 5 in a hook-like fashion, with no obvious differences in degree of

67   flexion among the fingers and no apparent flexion at the carpometacarpal joint (Napier, 1960;

68   Lewis, 1977, 1989).

69

70   However, the hand is not used solely for powerful gripping, but is important for fine

71   manipulation as well, particularly in humans. In precision grips, the thumb is opposed to the

72   other fingers and objects are often held with the finger pads or palmar surface of the fingers

73   (Napier, 1956). Depending on the size of the object held, the position of the ulnar digits varies.

74   When manipulating small objects in a pad-to-pad grip, only the second or second and third digits

75   are opposed to the thumb (Napier, 1956; Marzke and Shackley, 1986). In that position, the

76   second and third digits are supinated. However, as the size of the object held increases or if the

77   grip involves the palmar surface of the digits rather than the pads, the third and particularly the

78   second digit tend to take a more pronated position (Napier, 1956). In addition, the fourth and

79   fifth digits become involved and take a supinated position (Marzke and Shackley, 1986).

80

81   Apes are much less dexterous than humans in manipulation (Napier, 1960, 1962) and have much

82   more difficulty in pad-to-pad grips (Christel, 1993). This is in part a consequence of their

83   relatively long fingers and short thumbs (e.g., Mivart, 1867; Schultz, 1930; Ashley-Montagu,

84   1931; Green and Gordon, 2008). They are able to handle small objects between the thumb and

85   the side of the phalanges of the index or between the tips of the thumb and fingers (Napier, 1960,

86   1962; Christel, 1993). This particular grip does not require marked rotation of the second digit.

87 In contrast to humans, the morphology of the ape hand is most likely strongly driven by

88 locomotor constraints. All great apes are characterized by a hook grip, which involves flexing all

89 the fingers in sagittal planes (Lewis, 1977, 1989; Napier, 1960, 1993).

90

91 Morphological adaptations to the different grips observed in humans can be seen in their hands.

92 First, as mentioned above, the thumb is robust and digits 2-5 are much shorter relative to the

93 thumb in humans than in apes, and also relative to measures of body size (Mivart, 1867; Drapeau

94 and Ward, 2007; Lovejoy et al., 2009 supp. material; Almécija, Smaers and Jungers, 2015). The

95 third MC base has a styloid process that is hypothesized to resist palmar dislocation of the base

96 (Marzke, 1983). Also, the bases of the fourth and fifth MCs allow for some axial motion (El-

97 shennawy et al., 2001). The base of the second MC has a saddle shape joint with the trapezoid

98 rather than the wedge shape observed in apes (Marzke, 1983). The base of the MC2 has a

99 continuous articulation with the capitate instead of an articulation that is bisected in anterior and

100 posterior segments by carpometacarpal ligaments as found in all extant apes (Lewis, 1973, 1977,

101 1989; Marzke, 1983; Tocheri et al., 2008; Drapeau, 2012). In apes, that joint is in a sagittal plane

102 while in humans it is oriented more transversely. That articulation and the articulation between

103 the second and third MCs are anteroposteriorly curved instead of being flat as in apes (Lewis,

104 1973, 1977, 1989; Marzke, 1983; Tocheri et al., 2008; Drapeau, 2012). Finally, the second MC-

105 trapezium articulation lies in a more transverse plane instead of the sagittal plane found in apes

106 (Marzke, 1983; Drapeau et al., 2005; Tocheri et al., 2008). Although no significant pronation-

107 supination has been recorded in human cadavers at that joint, its morphology allows for some

108 mobility in flexion-extension (Batmanabane and Malathi, 19985; El-shennawy et al., 2001).

109 Similarly, the base of the human fifth MC is saddle shaped with a dorsoventral convexity. This

110   morphology, combined with a retraction of the hook of the hamate, allows for flexion and

111   supination of the MC (Dubousset, 1981; Marzke, 1983; Lewis, 1989; El-shennawy et al., 2001;

112   Reece, 2005; Buffi, Crisco and Murray, 2013). Although the base of the fourth MC is not as

113   clearly saddled-shape, it is also quite mobile in flexion-extension and in pronation-supination

114   (El-shennawy et al., 2001). In great apes, the ventral surface of the base articulates with the hook

115   of the hamate, limiting flexion and axial rotation (Lewis, 1989).

116

117   The head shape of MCs 2 and 5 is also modified to allow rotation of the fingers. The MC2 head

118   has a distal articular surface whose palmo-radial corner projects more proximally (Lewis, 1989;

119   Drapeau, 2012). In palmar view, the head is slanted radially (Lewis, 1989; Drapeau, 2012). This

120   morphology, combined with the collateral ligaments, causes the proximal phalanx to deviate

121   radially and to pronate when flexed (see Lewis, 1989 for details). The extended finger tends to be

122   supinated when ulnarly deviated and pronated when radially deviated or flexed. The morphology

123   of the third MC head also presents some asymmetry, but to a lesser degree than the second and

124   the rotation and axial deviation of the phalanx are also less marked than in the second (Lewis,

125   1989). The morphology of the fifth MC head is the mirror image of the second, causing

126   movements in opposite directions relative to the second MC (Lewis, 1989). This particular

127   morphology of the heads, combined with the morphology of the bases, allows for axial rotation

128   of the second and fifth fingers and MCs. In contrast, the ape's MCs do not have such

129   asymmetrical heads and movement at these joints function much more as simple hinges (Lewis,

130   1989; Drapeau, 2012). The human first MC allows for a greater range of thumb opposition

131   because the base has a less projecting palmar beak than what is seen in chimpanzees and the

132   articulation is flatter in the dorso-palmar direction (Marzke, 1992; Tocheri et al., 2003). The

133   morphology of the head, with a palmar elevation radially, allows for some pronation and

134   abduction of the distal segments of the thumb during flexion, but it is a morphology that appears

135   to be primitive in hominoids and even in mammals (Lewis, 1989).

136

137   Australopithecines have some of the traits associated with manipulation in humans. For example,

138   *Au. afarensis* is characterized by a continuous and curved MC2-capitate articulation that is more

139   transversely oriented than in apes, but less than in humans (Marzke, 1983; Ward et al., 1999,

140   2012; Drapeau et al., 2005), an MC2-trapezium facet that is more transversally oriented than in

141   chimpanzees (Marzke, 1983; Drapeau et al., 2005; Ward et al., 2012), asymmetric MC2, MC3

142   heads (Susman, 1979; Bush, 1982; Marzke, 1997; Ward et al., 1999; Drapeau, 2012; Ward et al.,

143   2012), long thumbs relative to the other fingers (Alba, Moyà-Solà and Köhler, 2003; Almécija

144   and Alba, 2014; but see Rolian and Gordon, 2013 for opposing view), and short fingers 2-5

145   relative to measures of body size (Drapeau et al., 2005, Drapeau and Ward, 2007), traits that are

146   also found in *Au. africanus* (Rickland, 1990; Clarke, 1999; Green and Gordon, 2008; Tocheri et

147   al., 2008; Kivell et al., 2011; Drapeau, pers. obs.). These traits suggest the capacity to make a 3-

148   finger chuck. However, a volar beak on the MC1 possibly restricted opposition of the thumb

149   (Marzke, 1992; but see Rickland, 1990 for an opposing view). In addition, *Au. afarensis* had

150   slightly asymmetric MC5 heads (Ward et al., 2012). However, this taxa and *Au. africanus*,

151   because of a palmar articulation with the hook of the hamate, were probably more limited than

152   humans in MC5 flexion and supination (Marzke, 1983; but see Ricklan, 1987 for an opposing

153   view). These traits suggest that the fossils may have had some mobility of the medial most

154   carpometacarpal joint, but could not produce completely human-like power and cradle grips with

155   a cupped palm. Comparable to *Au. afarensis* and *Au. africanus*, the hand of more recent *Au.*

156   *sediba* presents asymmetric MC heads, a continuous and curved, proximolaterally facing facet

157   between the capitate and MC2, a long thumb relative to the other fingers, and short ulnar fingers

158   relative to a measure of body size (Kivell et al., 2011). Unfortunately, the morphology of these

159   traits is unknown for the Sterkfontein specimens. Little is known of the hand of *Au. anamensis*,

160   but a fairly abraded capitate suggest that it had a discontinuous capitate-MC2 facet (Ward,

161   Leakey and Walker, 2001) oriented at 90° from the MC3 articular facet like apes and unlike the

162   more transverse orientation of humans and, to a lesser degree, *Au. afarensis* (Leakey et al., 1998;

163   Ward et al., 1999; Ward, Leakey and Walker, 2001). *Ardipithecus ramidus*, dated at 4.4 Ma, also

164   presents some human-like traits: a continuous MC2-capitate surface as well as a mobile hamate-

165   MC5 joint, a long thumb relative to the fingers and short fingers 2-5 relative to measures of body

166   size (Lovejoy et al., 2009).

167

168   With the exception of *Au. anamensis*, the hands of hominin taxa display human-like traits that

169   suggest that they were generally capable of manipulations with three-finger chuck and pad-to-

170   pad grips (see also Almécija, Moyà-Solà and Alba, 2010 for *Orrorin tugenensis*). In this study, I

171   contrast MC head torsion in human and great apes to show how it reflects the differences in grips

172   between extant taxa. I also compare *Au. afarensis*, *Au. africanus* and specimens from Swartkrans

173   to extant species to evaluate their morphological affinities and possibly identify additional traits

174   related to manipulation in the fossil specimens.

175

176   In hominoids, the bases of the MCs are disposed in a mediolateral arch configuration (Fig. 1),

177   with the concave, palmar side housing the carpal tunnel (although much of the walls of the

178   tunnel are the result of the projecting hook of the hamate and of the position of the trapezium

179   usually disposed at an angle from the other distal carpal bones; see Lewis, 1989) and Reece

180   (2005) observed that humans had more arched rows than apes. Metacarpals are expected to

181   present torsion values that adjust for the degree of arching. As a result, the ulnar-most digits will

182   tend to have heads that are more ulnarly twisted, while the radial-most digits (except the thumb)

183   will tend to have heads that are more radially twisted.

184

185   More specifically, humans, because of the types of grips described above, are expected to have,

186   on average, MC 2 to 5 heads that are more radially twisted than apes. However, variation in

187   arching of the MC row is expected to influence the twisting of the MCs. For example, ulnar

188   digits may not present as much torsional difference as the more radial digits in a hand that would

189   have greater arching. In addition, because base and head morphologies of the second MC and

190   particularly of the fifth MC of humans allow for axial rotation of the digit to conform to various

191   object sizes and shapes, torsion of these two MCs may not be as different from apes as for the

192   other digits. In humans, the trapezoid is wider palmarly than that of apes, which pushes the

193   trapezium radially and rotates it into alignment relative to the rest of the proximal carpal row

194   (Tuttle, 1970; Lewis, 1977; Lewis, 1989; Sarmiento, 1994; Drapeau et al., 2005; Tocheri et al.,

195   2005). As a result, the trapezio-MC articulation lies within an axis comparable to that of the

196   other digits. This reorientation is accompanied by a palmar expansion of the articular facet

197   between the trapezoid and capitate. Together, these traits (palmar expansion of the trapezoid, a

198   first carpal metacarpal articulation in line with the rest of the carpal row, and an expanded

199   palmar trapezoid-capitatum articulation) allow for large loads incurred at the base of the MC1

200   during forceful grips to be dissipated through the palmar carpal row (Lewis 1977; Lewis, 1989;

201   Tocheri et al. 2005). Because of the reorientation of the first carpometacarpal joint in humans, a

202 greater torsion of the first MC is expected in order to bring the metacarpo-phalangeal joint in an

203 axis perpendicular to that of the other digits. Apes, particularly chimpanzees, having the base of

204 the first MC already perpendicularly rotated relative to the other carpometacapal joints, are not

205 expected to require as much torsion of the first MC to function in opposition to the other digits or

206 to the palm.

207

208 **Materials**

209 The human sample is from archaeological collections and it consists of a mix of Euroamericans

210 from the 19th century and of Canadian Amerinds (Table 1). All extant great apes are wild shot

211 and the *Gorilla* sample includes only western lowland gorillas. All specimens are free of

212 pathologies. Sample size varies from one MC to the other as a function of the availability of each

213 bone in the osteological collection (Table 2).

214

215 The hominin fossils included in this analysis are from Hadar, Ethiopia, and from Sterkfontein

216 and Swartkrans, South Africa (Table 3). Specimens from Hadar are all attributed to *Au. afarensis*

217 (Bush et al., 1982; Drapeau et al., 2005; Ward et al., 2012) and date at 3.2 Ma for A.L. 333 and 3

218 Ma for A.L. 438 (Kimbel, Rak & Johanson, 2004). Although some have argued that there might

219 be more than one species represented at Sterkfontein (e.g., Clarke, 2013), all four Sterkfontein

220 specimens included are from Member 4 and are assumed to belong to *Au. africanus* based on the

221 general morphology, size and provenience (McHenry and Berger, 1998), and date between 2.6

222 and 2 Ma (Herries et al., 2013). At Swartkrans, *Paranthropus robustus* and early *Homo* are

223 present and post-cranial specimens are difficult to assign to either of these taxa with certainty.

224 SK 84 is from Member 1 and attributed to *Homo* (Susman, 1994; Susman, 2004), SKW 2954 is

225   from member 2 and is described as being human-like (Susman, 2004), and SKW 14147 is not

226   assigned to a member or to a specific taxon (Day and Scheuer, 1973). Member 1 is dated

227   between 2.2 and 1.8 Ma and Member 2 between 1.8 and 1 Ma (Gibbon et al., 2014). Only

228   specimens that are complete and undistorted are included in the analysis.

229

230   **Methods**

231   Using a Microscribe 3DX portable digitizer with a precision of 0.23 mm, palmodorsal axes of

232   the base and head of MCs one through five were recorded to measure head torsion. It was the

233   axis of the whole head that was recorded, irrespective of the asymmetry of the articular surface

234   (Fig. 2). For the MC2, the palmodorsal axis of the base was determined as the margin of the

235   articular surface with the capitate, and for the MC3, it was determined as the margin of the

236   articular surface with the second MC (Fig. 2C). The three-dimensional points were realigned

237   with the software GRF-ND (Dennis E. Slice, 1992-1994) so that x, y, and z values varied in the

238   dorsoplantar, proximodistal and radioulnar anatomical axes respectively. The angle between the

239   lines defining the orientation of the head and of the base in the transverse plane represents the

240   angle of torsion of the MCs. Values presented are for the left hand, but if the measure was not

241   available for one specimen, values from the right were used. Positive values represent heads with

242   their palmar side that are twisted ulnarly relative to the base (away from the thumb), negative

243   values represent heads twisted radially (turned towards the thumb), and a value of zero indicates

244   no torsion relative to the base. In order to estimate the shape of the arch made by the base of the

245   MCs when articulated together, the wedging of the base was measured. It was calculated as the

246   ratio of dorsal width relative to the palmar width of the bases of the MC3 and MC4, the two

247   'central' bones of the arch composed of the four ulnar MCs.

248

249   Intraobserver error in angle measurement was estimated with three specimens: *Homo*, *Pan*, and

250   *Pongo*. All five MCs for each specimen were digitized 10 times over a two-day period. Each

251   metatarsal was digitized five times the first day. The second day, the metatarsals were

252   repositioned and recorded another 5 times. The mean interval of confidence of measurement is ±

253   1.6° and the average range 8.3° (varied from 2.4° to 15.4°). The error was, on average, about

254   twice as high on the pollical MC compared to the others (mean pollical standard error 2.5° vs.

255   1.3° for the other MCs; mean pollical range 13.5° vs. 7.0° for all other MCs). This error for the

256   first MC is probably due to the fairly round profile of the base (Fig. 2C), which makes the

257   definition of the dorsopalmar axis more difficult to define accurately.

258

259   Species are compared with one-way ANOVA and *Post hoc* multiple comparisons with

260   Bonferroni adjustments when variances are homogeneous among groups and Tamhane T2 tests

261   when heterogeneous.

262

263

264   **Results**

265   For the MC1, *Homo* and *Pongo* have heads whose palmar surfaces are the most turned towards

266   the other fingers, while *Pan* has the head that is the least turned towards the other fingers (Table

267   2). Gorillas are intermediate between these two groups. *Homo* and *Pongo* are statistically

268   different from all other extant taxa but are not different from each other (Tables 4 and 5).

269   *Australopithecus afarensis* (n=1) is most similar to *Gorilla* but within the range of all taxa and

270 outside the range of only humans. *Australopithecus africanus* (n=1) and the Swartkrans

271 specimen (SK 84) are most similar to *Gorilla*, but within the range of all species (Fig. 3A).

272

273 For the MC2, as expected, all species are similarly radially turned towards the thumb except for

274 *Pongo* that has a significantly more turned MC than the other taxa (Tables 2, 4 and 5).

275 *Australopithecus afarensis* (n=2) is variable and does not resemble one taxon in particular.

276 *Australopithecus africanus* (n=1) is within the distribution of all taxa, but most similar to African

277 apes (Fig. 3B).

278

279 For the MC3, humans have the heads that are the most supinated (Table 2) and are statistically

280 different, while all apes are not significantly different from each other (Tables 4 and 5).

281 *Australopithecus afarensis* (n=2) is most similar to humans, while *Au. africanus* (n=1) is within

282 the range of all taxa, but most similar to apes (Fig. 3C).

283

284 For the MC4, again, humans are statistically different from all apes, which form a fairly uniform

285 group (Tables 4 and 5). Apes have relatively untwisted heads, while humans have fourth MCs

286 that have heads that are more pronated (Table 2). The *Au. afarensis* specimen is very pronated

287 and most similar to humans while within the distribution of all taxa. The Swartkrans specimen

288 (SKW 2954) is most similar to apes but within the distribution of humans (Fig. 3D). Although it

289 has no evidence of a healed fracture, Susman (2004) suggested that this specimen, because of an

290 uncharacteristically AP curved diaphysis and the presence of a 'crook', may have been broken. If

291 so, the torsion value for that specimen may be distorted and not reflect a normal morphology.

292

293   Finally, for the MC5, apes and humans have pronated heads (turned away from the thumb; Table

294   2) although humans have a statistically more twisted head than *Pan*, while all other taxa do not

295   differ statistically (Tables 4 and 5). *Australopithecus afarensis* (n=3) is variable, but on average,

296   resemble *Pan* and *Pongo* the most, as does the one Swartkrans specimen (SKW 14147; Fig. 3E).

297

298   In base shape, humans are characterized by MC3 and MC4 that have pinched bases palmarly,

299   while apes have bases that are relatively wider palmarly (Tables 6, 7 & 8, Fig. 4). Humans are

300   statistically different from all taxa in MC3 base shape (Table 7). For the MC4, humans are

301   statistically different from all apes except gorillas (Table 8), which have an MC4 base that is

302   intermediate in shape between that of humans and chimpanzees. *Australopithecus afarensis*

303   specimens (n=5) are characterized by human-like, pinched MC3 bases, while *Au. africanus* (n=2)

304   and one specimen from Swartkrans are characterized by bases that are intermediate between that

305   of apes and humans (while not being very different from three *Au. afarensis* specimens). The

306   MC4 bases are more ape-like for *Au. africanus* and the Swartkrans specimens, while *Au.*

307   *afarensis* is outside the variation of *Pongo* only, but falls closest to the median of humans.

308

309   **Discussion**

310   The results for the first MC are as expected for humans with a head twisted toward the other

311   fingers, probably in part to compensate for the reorientation of the trapezium in that species (Fig.

312   5; Lewis, 1977, 1989; Sarmiento, 1994; Tocheri et al., 2005). As discussed above, the wider

313   palmar aspect of the trapezoid, likely related to the palmar extension of its articulation with the

314   capitate, results in a trapezium in the human hand that is pushed radially and rotated into

315   alignment relative to the rest of the proximal carpal row (Lewis, 1977, 1989; Sarmiento, 1994;

316 Drapeau et al., 2005; Tocheri et al., 2005). This reorientation of the trapezium positions the

317 MC1's articular facet in a position that is more along the radioulnar axis of the other MC bases,

318 in a position that is less advantageous for MC1 opposability. The strongly twisted head of the

319 human MC1 reflect that species' particular carpal morphology. The results for *Pongo* are

320 intriguing given that it does not have developed thenar muscles (Tuttle, 1969) nor particularly

321 large first MC articular surfaces on the trapezium (Tocheri et al., 2005). It is noteworthy that the

322 strong inversion of the thumb and strong eversion of the second digit of *Pongo* (Fig. 6) is

323 reminiscent of their value of metatarsal (MT) torsion (Drapeau and Harmon, 2013). A study of

324 wild Bornean orangutans has shown that the hands and feet are more often used in grasps that

325 involves the opposition of the pollex and hallux than in any other grips (including the hook grip

326 and 'double-lock' grasp; McClure et al., 2012). This is particularly true of the hand where grips

327 using the pollex in opposition were five times more common than grips using the lateral fingers

328 only (McClure et al., 2012). Rearrangement of the muscles fibers to the distal phalanx of the

329 pollex compensate for the absence or reduction of the tendon of m. flexor pollicis longus in

330 *Pongo* (Tuttle and Cortright, 1988). The large torsion of the MC1 towards the palm is also

331 surprising given that *Pongo* does not have a palmarly expanded trapezoid with a reoriented

332 trapezium in the axis of more medial distal carpal row. The large degree of twisting is possibly

333 needed to position the short pollex in opposition to the rigid palm of the hand instead of the

334 much more mobile fingers. Their MC1-2 and MT1-2 morphology might reflect the importance of

335 a strong opposing thumb-to-palmar and hallux-to-plantar surface grips in this highly arboreal

336 taxon (Drapeau and Harmon, 2013). The torsion of the *Australopithecus* and Swartkrans MC1

337 specimens is similar to apes and probably reflects the lack of a human-like expansion of the

338 palmar surface of the trapezoid and the lack of a human-like load distribution on the palmar

339 surface (as suggested by Tocheri et al., 2008). The Swartkrans specimen (SK 84) is, of all the

340 fossils, the specimen that most closely approaches the human form and falls within the range of

341 distribution of humans. However, given its intermediate morphology, this study cannot resolve

342 its taxonomical affinity (see Trinkaus and Long, 1990; Susman, 1994).

343

344 For the MC2, there is no clear difference among species, extant or fossil. Previously observed

345 torsion in humans relative to apes, as noted by Susman (1979) may have been an observation of

346 the asymmetrical shape of the articular surface of the head. The lack of difference in torsion

347 between dexterous humans and apes does not necessarily signify that the second finger of

348 humans is used similarly to that of apes. In humans, depending on the grip used and the size of

349 the object manipulated, the second finger may need to be either ulnarly or radially rotated.

350 Unlike apes, humans are characterized by an asymmetrical MC2 head (Lewis, 1989), which

351 allows the finger to axially rotate at the metacarpophalangeal joint. It is therefore possibly more

352 advantageous to have a head that is only slightly twisted radially, which leaves flexibility to

353 achieve different degrees of finger rotation for different types of grips. In addition, the human

354 second MC, because of its morphology, might be capable of some axial rotation while that of

355 apes is likely to be less mobile (van Dam, 1934; Lewis, 1977, 1989; Marzke, 1983; although El-

356 shennaway et al., 2001, did not find significant rotation at that articulation in cadavers).

357 Nonetheless, distal articular architecture in humans provides rotational flexibility of the finger

358 necessary for a variety of effective grips. Interestingly, the base and head morphology of

359 *Australopithecus* is clearly human-like (Marzke, 1983, 1997; Marzke and Shackley, 1986;

360 Drapeau et al., 2005; Tocheri et al., 2008; Kivell et al., 2011; Drapeau, 2012), which suggest

361 human-like digit rotational capacities for these species.

362

363   The difference between humans and apes in torsion for the MC3 was expected and observed

364   previously by Susman (1979). In apes, the torsion required to bring the head back into alignment

365   with the other MC heads is minimal. In humans, finger supination is required in the power and

366   precision grips (Landsmeer, 1955; Napier, 1956; Landsmeer, 1962; Marzke and Shackley, 1986).

367   However, the third MC head is only slightly asymmetric compared to the second (Lewis, 1977,

368   1989; Drapeau, 2012). As a consequence, the third MC head needs to be more supinated to allow

369   for proper positioning of the finger during power and precision grips.

370

371   The relatively untwisted MC4 of African apes is not surprising. As for the third MC, these apes

372   load that digit while knuckle walking (Inouye, 1994), which may favor a digit that flexes and

373   extends closely to a parasagittal plane. Against expectations, the human MC4 is more pronated

374   than that of apes. In humans, the fourth finger has an important role in buttressing (Susman,

375   1979). When buttressing, the fourth digit is flexed in the palm and ulnar torsion may help

376   position the digit more appropriately. In the left hand, the predominant loading force may be the

377   buttressing function rather than manipulation. Alternatively, it could be related to the degree of

378   curvature of the metacarpal-base arch. Our measures of base wedging (Tables 6, 7 and 8; Fig. 4)

379   have shown that humans have more palmarly wedged MC bases and therefore have a more

380   arched MC base row than other extant large apes (Fig. 5; see also Reece, 2005). The dorsopalmar

381   axis of the MC4 base is therefore more twisted towards the thumb in humans than in other large

382   apes when in articulation with the other MCs and carpals (Reece, 2005). Because of the base

383   orientation, the less radially twisted head of the MC4 in humans does not necessarily indicate

384   that the whole digit is less radially twisted towards the thumb (Fig. 5). Further study of the

385 orientation of the hand bones *in vivo* in apes will be needed to compare the actual degree of

386 opposition of the MC and digits between humans and apes.

387

388 The lack of difference in torsion of the MC5 among humans, gorillas, and orangutans, which all

389 have ulnarly twisted heads, also requires explanation. In humans, the articular surface of the

390 MC5 head is also asymmetrical (Lewis, 1977; Lewis, 1989; Marzke, 1997), being somewhat a

391 mirror image of the MC2. As a consequence, the digit is rotated towards the thumb during

392 flexion, which is the natural position taken by the finger during power grips and some precision

393 grips (Napier, 1956). Also, the MC itself is free to rotate slightly in humans though not in apes.

394 These mechanisms may be sufficient during power grips and five-finger holds to produce a

395 rotated digit without the need of the whole head to be twisted. Also, since the MC-base row is

396 more arched than in apes (Reece, 2005; this study), the fifth MC base is rotated radially relative

397 to the thumb (Fig. 5). Moderate ulnar torsion still leaves the fifth MC palmar surface in a radially

398 facing position.

399

400 *Australopithecus afarensis* has MC3 and MC4 torsion values that are clearly more similar to

401 humans, which suggest use of the hand in the fossil species that resembles humans more than

402 apes. Similarly, their third and fourth MCs have wedge-shaped bases most like humans. The

403 morphology of *Au. africanus* is less clearly similar to one species. Although torsion and base

404 wedging values are within the range of humans, they are more typical of apes and their MC bases

405 are not as wedged as humans. Together, these traits suggests that it may have been less adept at

406 the pad-to-pad three-jaw chuck grasp relative to humans and *A. afarensis*, and may have been

407 less adept at cupping the hand despite having relative thumb-to-finger lengths comparable to *Au.*

408   *afarensis* (Green and Gordon, 2008; Rolian and Gordon, 2013). Evidence of some human-like

409   loading in the trabecular patterns of the base of the MC1 and head of the MC3 (Skinner et al.,

410   2015), combined with a weakened human-like signal in the trabeculae of the MC4 (Skinner et

411   al., 2015; but see Almécija et al., 2015b for opposing view) concurs with this study's observation

412   that the ulnar side of the hand of *Au. africanus* is less human-like than that of *Au. afarensis*.

413   Overall, the *Au. afarensis* morphology in torsion and base shape is human-like, while that of *Au.*

414   *africanus* is less clearly human-like, suggesting that, perhaps, the medial palm was less suited to

415   human-like manipulation than in *Au. afarensis*.

416

417   Torsion of the fifth MC, because it is not significantly different in humans, gorillas and

418   orangutans is not particularly informative in *Au. afarensis*. The morphology of the base in that

419   species suggests less mobility in flexion and supination at that joint than in humans (Marzke,

420   1983; Marzke and Shackley, 1986; Marzke, Wullstein & Viegras, 1992). However, as for the

421   second MC, the MC5 head is asymmetric (Bush et al., 1982; Marzke, 1997; Drapeau, 2012;

422   Ward et al., 2012). This mosaic of ape and human traits in the fossils species indicates an

423   intermediate state, in which the human-like involvement of the fifth finger in manipulation might

424   be limited to the phalangeal segment of the digit and to a more radially turned hypothenar region.

425   In addition, the *Au. afarensis* hands did not have a robust thumb nor a styloid process on the

426   MC3 (Bush et al., 1982; Marzke, 1983; Drapeau et al., 2005; Ward et al., 2012) which indicates

427   that these taxa were not incurring as large loads on the thumb and on the palm of the hand. These

428   traits are more human-like in the *Au. africanus* specimens (Rickland, 1987; Kivell et al., 2011

429   supp. material), suggesting adaptations to greater loads in the lateral hand of that later taxa. The

430   differences between the two fossil taxa are not large, but they might indicate slightly different

431   adaptations to manipulation possibly reflecting slightly different evolutionary paths.

432

433   The curved MC base arch of humans orients the ulnar MC bases with their palmar surface

434   toward the thumb. As a consequence, when the fifth and, to a lesser degree, fourth MC are flexed

435   in humans, it produces the typically human cupping of the palm that is used in power grips of

436   large objects (Peters and Koebke, 1990). The greater arching of the MC bases might then be an

437   adaptation of such movement in humans and pronation of the MC4 head is only a consequence

438   of the reoriented base. If so, this would indicate that *Au. afarensis,* with its wedged bases, has

439   begun the reorientation of the medial aspect of the palm of the hand despite probably not being

440   able to flex the MC4 and MC5 as much as humans (Marzke, Wullstein & Viegras, 1992).

441   Combined with the asymmetry of the fifth MC head, *Au. afarensis* was probably capable of a

442   power and cradle grips that were not completely human but approached it significantly.

443

444   The torsion of Swartkrans MCs can be characterized, as a whole, as being more ape-like than

445   human-like. However, of all the three Swartkrans specimens available for analysis, the MC4 is

446   the only one that is more clearly ape-like (although still within the range of humans) by being

447   more radially twisted. This morphology is rather surprising considering that the MC3 base tends

448   to be pinched suggesting a fairly deeply arched MC-base row. These conflicting results tend to

449   support Susman's interpretation that SKW 2954 was fractured and is likely to be pathological

450   and distorted (Susman, 2004). As a whole, the Swartkrans specimens are not particularly

451   informative with respect to manipulative dexterity, although some traits, such as moderate base

452   wedging, does point toward some adaptations for that behavior.

453

454   It is unknown whether metacarpal torsion is genetically determined or whether it is plastic, or a

455   combination of both, but variation in metatarsal torsion among human populations with various

456   types of footwear (Drapeau and Harmon, 2013; Forgues-Marceau, 2013) as well as variation in

457   humeral torsion according to throwing activity (e.g., Pieper, 1998) suggest that it is a trait that is

458   at least in part plastic in the foot, arm and possibly in the hand. If so, this trait would be

459   particularly informative on the actual use of the hand (Lovejoy, Cohn and White, 1999; Ward,

460   2002), but further work is needed on variation in metacarpal torsion and how it may be a plastic

461   response to specific loading regiments. Irrespective of whether metacarpal torsion is completely,

462   partly or not at all determined genetically, when studies are combined with metacarpal base

463   shape (which is much more likely to be genetically determined), it is informative on the use of

464   the hand and reflects, the capacity to do a three-finger chuck and to cup the palm of the hand.

465

466   Discussions of hand evolution often assumed that the human hand evolved from a form similar

467   to that of African great apes. However, recent work has shown that the ape hand, particularly that

468   of chimpanzees, might be derived relative to that of the *Pan-Homo* last common ancestor

469   (Drapeau et al., 2005; Drapeau and Ward, 2007; Lovejoy et al., 2009; Almécija, Smaers and

470   Jungers, 2015). More specifically, there is growing evidence that the long hands of *Pan* are

471   derived (Drapeau et al., 2005; Drapeau and Ward, 2007; Almécija, Smaers and Jungers, 2015)

472   and that the thumb to digit ratio of humans and gorillas is closest to that of the primitive form for

473   hominins (Almécija, Smaers and Jungers, 2015). The discovery of a nearly complete *Ar.*

474   *ramidus* hand, which is characterized by a continuous capitate-MC2 articular facet, and a mobile

475   hamate-MC5 joint, has led Lovejoy and colleagues (2009) to argue that these traits, because they

476   were present in the early Miocene *Proconsul,* are primitive for hominins. This interpretation

477   implies that all extant apes stiffened their hands at the carpometacarpal joints independently. A

478   closer look at the morphology of the mid- and late Miocene apes reveals that those for which this

479   morphology is known are all characterized, without exception, by a planar, discontinuous

480   capitate-MC2 joint (*Sivapithecus*, Rose, 1984; *Rudapithecus hungaricus*, Kivell and Begun,

481   2009; *Oreopithecus bambolii*, pers. observation; *Hispanopithecus laietanus*, Almécija, 2015

482   pers. comm.; *Pierolapithecus catalanicus*, Almécija, 2015 pers. comm.) including in

483   *Pierolapithecus,* which displays no obvious adaptations to suspensory behavior (Moyà-Solà et

484   al., 2004) and *Sivapithecus*, which probably was still pronograde (Pilbeam et al., 1990). It is

485   more parsimonious from all the available evidence to assume that the last common *Pan-Homo*

486   ancestor had a discontinuous facet and therefore a lateral palm that was rigid. The non-

487   continuous facet on the *Au. anamensis* capitate (Leakey et al., 1998; Ward et al., 1999) is

488   intriguing given that the older *Ar. ramidus* had a continuous facet. Either its poor preservation

489   obscures a continuous facet on the *Au. anamensis* capitate or *Ar. ramidus* is autapomorphic and

490   convergent on *Au. afarensis* for that trait. More specimens of *Au. anamensis* are needed to

491   resolve this issue.

492

493   The hamate-MC5 joints of Miocene hominoids, when known, have a joint surface morphology

494   that is not believed to have allowed much motion comparable to that of extent apes (*Sivapithecus*

495   *parvada*, Spoor, Sondar and Hussain, 1991) or have an articular surface that extend on the

496   hamulus (*Hispanopithecus* and *Pierolapithecus*, Almécija, 2015 pers. comm.), although the

497   hamulus in these taxa is not as proximally projecting as in extant apes. However, the fossil taxa

498   probably had a more mobile hamate-MC5 joint in dorsiflexion as suggested by an articular

499   surface that extends to the dorsum of the MC base (*Pierolapithecus*; Almécija et al., 2007;

500   Almécija, 2015 pers. comm.) or by a similarity to taxa that dorsiflex (*Proconsul*; Napier and

501   Davis, 1959; O'Connor, 1975). If the morphology is interpreted accurately, it implies that the last

502   *Pan-Homo* common ancestor was characterized by a somewhat mobile joint, a morphology also

503   seen in *Ar. ramidus* (Lovejoy et al., 2009).

504

505   The Miocene fossil evidence suggests that the *Pan-Homo* last common ancestor had thumb to

506   digit proportions that were close to that of humans, a rigid, planar bipartite capitate-MC2 joint,

507   and possibly a moderately mobile hamate-MC5 joint. The morphology of *Ar. ramidus*, a likely

508   ancestor to *Australopithecus* (White et al., 2009), indicates that a hamate-MC5 joint capable of

509   plantarflexion and a continuous capitate-MC2 joint (but that was not curved as in humans and

510   *Au. afarensis)* had already been transformed by 4.4 Ma (Lovejoy et al., 2009). Almécija and

511   colleagues even propose that pad-to-pad grips were possible by 6 Ma with *Orrorin tugenensis*

512   (Almécija, Moyà-Solà and Alba, 2010). These traits associated to more dexterous manipulation

513   in hominins have appeared long before any evidence of stone tools (Panger et al., 2002;

514   Almécija, Moyà-Solà and Alba, 2010; Drapeau, 2012; Almécija and Alba, 2014; Almécija,

515   Smaers and Jungers, 2015) and is unlikely to be an adaptation to that specific behavior. It

516   probably reflects adaptation to increase dexterity in the context of habitual bipedality and a

517   relaxed selection for locomotor adaptation of the upper limbs (Almécija, Moyà-Solà and Alba,

518   2010; Drapeau, 2012). Further transformations in *Au. afarensis*, such as a capitate-MC2 surface

519   that is more curved and oriented in a more transverse plane, MC head asymmetry and, possibly,

520   radio-ulnar arching of the MC base row may be a response to increased reliance on precise and

521   forceful grips required for stone tool use (McPherron et al., 2010) and possibly even stone-tool

522   manufacture (Harmand et al., 2015) in that taxon. Further adaptation, such as a more robust

523   thumb, a styloid process and a palmarly expanded trapezoid appear later in time, possibly only in

524   Homo (Berger et al., 2015), and testify of the continued importance of manipulation in the

525   evolution of our lineage.

526

527   **Conclusions**

528   Metacarpal head torsion is different between humans and apes, particularly in the third and

529   fourth MCs. For the MC2 and MC5, articular morphology, including head asymmetry, may be a

530   better indicator of human-like manipulation and rotational capacity of the digits. Differences in

531   head torsion among species are broadly as expected, except for the fourth and fifth MCs that are

532   generally less radially twisted in humans. These unexpected results for the ulnar part of the hand

533   might relate to the how the MC bases are positioned relative to each other and to the degree of

534   curvature of the proximal metacarpal arch, a curvature that is greater in humans than in apes due

535   to greater base wedging of the third and fourth MCs.

536

537   An overall view of the *Au. afarensis* and *Au. africanus* MCs is consistent with previous analyses

538   of the hand in these species. The lack of ulnar twist in the pollical MC suggest that these species

539   were probably not characterized by a palmarly expanded trapezoid that positioned the trapezium

540   in line with the rest of the carpals and, according to Lewis (1977; Lewis, 1989; Tocheri et al.,

541   2005), allowed for compressive loads from the base of the first MC to dissipate through the

542   palmar aspect of the palm via a palmarly expanded trapezoid and palmar trapeziocapitate

543   articular facet. These fossil species likely had a primitive configuration similar to apes with a

544   trapezium positioned more perpendicular to the rest of the distal carpal row and therefore were

545   not able to dissipate compressive loads from the thumb through the palm as effectively as

546   modern humans. Previous studies had shown that the second MC of *Australopithecus* was

547   modified from the assumed primitive morphology, with a base and head allowing for some

548   movement of the digit, but the third lacked the human-like styloid process, suggesting only a

549   partial transition towards a human-like grip. This study has shown that *Au. afarensis* had human-

550   like orientation of the third and fourth MCs, indicating the possibility of adequate three- or four-

551   jaw chucks in these species (although possibly with less ulnar deviation of the thumb than in

552   humans; Marzke, 1992). More ulnarly, there is less evidence of a human-like grip, but for the

553   asymmetry of the fifth MC head that allows for phalangeal axial rotation, suggesting that active

554   involvement of the fifth digit in a five-jaw chuck was probably limited to the phalanges.

555   However, the shape of the MC3 and MC4 bases suggest a configuration of the MC base row that

556   was more arched and human-like in *Au. afarensis*, allowing for more opposition of the fifth MC

557   than is possible in large apes. As a consequence, although *Au. afarensis* has not developed a

558   completely human grip, it showed significant derived traits that suggest that there was directional

559   selection for improved dexterity and strength in various grips in these early hominins,

560   adaptations that appear to have begun with *Ar. ramidus* (Lovejoy et al., 2009) and even possibly

561   in *Orrorin tugenensis* (Almécija et al, 2010). In contrast, *Au. africanus* is less clearly human-like

562   than *Au. afarensis* since it presents MC3 torsion more typical of apes, has an MC3 base shape

563   that is more intermediate between apes and humans, and an MC4 base that is more ape-like. This

564   suggests that *Au. africanus* may have been less dexterous in the three-jaw chuck and cradle grips

565   than *Au. afarensis* despite thumb-to-fingers proportions that were probably similar (Green and

566   Gordon, 2008; Rolian and Gordon, 2013). Overall, this study supports previous studies on *Au.*

567   *afarensis* and *Au. africanus* that these taxa had derived hand morphology that suggest increase

568   finesse and strength in pad-to-pad, two- and three-jaw chucks grips and some adaptation to

569   human-like power grips and support the hypothesis that human-like manipulation largely

570   predated *Homo*.

571

572

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802

Comparative sample

Comparative sample for torsion values.

Species	Male	Female	Indet.	Total
Homo sapiens (total)	20	11	17	48
Euroamericans	8	1	5	14
Amerinds	12	10	12	34
Pan troglodytes	16	25		41
Gorilla gorilla	27	20		47
Pongo pygmaeus	13	17		30

Descriptive statistics for torsion values

Extent species descriptive statistics[1] for torsion angles[2].

Taxon	MC1	MC2	MC3	MC4	MC5
H. sapiens	6.5	-14.0	-21.2	9.6	10.9
	8.1	7.2	6.8	7.6	7.0
	43	46	43	42	38
P. troglodytes	-16.7	-12.9	-6.5	2.4	5.5
	5.7	6.7	6.3	7.1	9.1
	27	39	40	40	39
G. gorilla	-7.9	-11.5	-9.4	2.7	10.1
	8.9	5.8	7.7	5.7	8.7
	39	42	44	44	44
P. pygmaeus	10.8	-18.6	-9.8	3.5	6.2
	10.6	8.8	8.2	6.4	6.0
	29	29	29	29	29

1   [1]The mean is presented on the first line, standard deviation on the second, and sample size on the
2   third.
3   [2]In degrees. Positive values represent heads with their palmar side that are twisted ulnarly
4   relative to the base (away from the thumb), negative values represent heads twisted radially
5   (turned towards the thumb).
6

Torsion values for the fossils

Australopithecus afarensis, Au. africanus and Sterkfontein fossil sample and torsion values.

Fossil	Element	Side	Torsion angle
A.L. 333w-39	MC1	R	-14.3
A.L. 333-48	MC2	L	-1.3
A.L. 438-1e	MC2	L	-15.0
A.L. 438-1f	MC2	R	-17.5
A.L. 438-1d	MC3	L	-22.9
A.L. 333-16	MC3	L	-23.3
A.L. 333-56	MC4	L	13.3
A.L. 333-14	MC5	R	-0.3
A.L. 333-89	MC5	L	10.5
A.L. 333-141	MC5	R	-4.0
Stw418	MC1	L	-10.8
Stw382	MC2	L	-8.5
Stw68	MC3	R	-11.8
SK84	MC1	L	-5.2
SKW2954*	MC4	R	3.5
SKW14147	MC5	L	4.0

1   *possible healed fracture

ANOVA-MC torsion

Results for the one-way ANOVA comparing MC torsion.

Metacarpal	F	Significance
MC1	68.1	<0.001
MC2	6.0	0.001
MC3	33.8	<0.001
MC4	10.6	<0.001
MC5	4.4	0.005

Post hoc comparisons for torsion values

Post hoc comparisons with Bonferroni adjustment[1] when comparing torsion.

Metacarpal	Taxa	*H. sapiens*	*P. troglodytes*	*G. gorilla*	*P. pygmaeus*
MC1	*Homo sapiens*		23.2	14.4	-4.3
	Pan troglodytes	**<0.001**		-8.8	-27.5
	Gorilla gorilla	**<0.001**	**<0.001**		-18.7
	Pongo pygmaeus	0.2	**<0.001**	**<0.001**	
MC2	*Homo sapiens*		-1.1	-2.4	4.6
	Pan troglodytes	1		-1.3	5.7
	Gorilla gorilla	0.7	1		7.1
	Pongo pygmaeus	**0.04**	**0.007**	**<0.001**	
MC3	*Homo sapiens*		-14.7	-11.7	-11.4
	Pan troglodytes	**<0.001**		2.9	3.3
	Gorilla gorilla	**<0.001**	0.4		0.3
	Pongo pygmaeus	**<0.001**	0.4	1	
MC4	*Homo sapiens*		7.2	7.0	6.2
	Pan troglodytes	**<0.001**		-0.2	-1.0
	Gorilla gorilla	**<0.001**	1		-0.8
	Pongo pygmaeus	**0.001**	1	1	
MC5	*Homo sapiens*		5.4	0.8	4.7
	Pan troglodytes	**0.02**		-4.6	-0.7
	Gorilla gorilla	1	0.06		3.9
	Pongo pygmaeus	0.1	1	0.2	

1 [1]Values above the diagonal are absolute mean differences of the pair-wise comparison (row -

2 column), values below are significance of the test (values at 0.05 or less are in bold).

Wedging values

Dorsal to palmar medio-lateral width ratio of the third and fourth MC (first line: mean; second line: standard deviation).

Taxa	MC3	MC4
H. sapiens (n=29)	1.62	1.58
	0.18	0.30
P. troglodytes (n=36)	1.32	1.20
	0.13	0.15
G. g. gorilla (n=36)	1.35	1.42
	0.11	0.21
P. pygmaeus (n=37)	1.27	1.09
	0.14	0.10
AL 333-16	1.55	
AL 333-65	1.53	
AL 333-153	1.56	
AL 333w-6	2.08	
AL 438-1	2.02	
AL 333-56		1.46
Stw64	1.43	
Stw68	1.47	
Stw65		1.17
Stw330		1.30
SKX 3646	1.52	
SKX 2954		1.30

Post hoc comparisons of MC3 wedging values

Tamhane T2 post hoc comparisons of the dorsal to palmar medio-lateral width ratio for the MC3 (p-values).

	H. sapiens	*P. troglodytes*	*G. g. gorilla*
P. troglodytes	**<0.001**		
G. g. gorilla	**<0.001**	0.92	
P. pygmaeus	**<0.001**	0.57	0.08

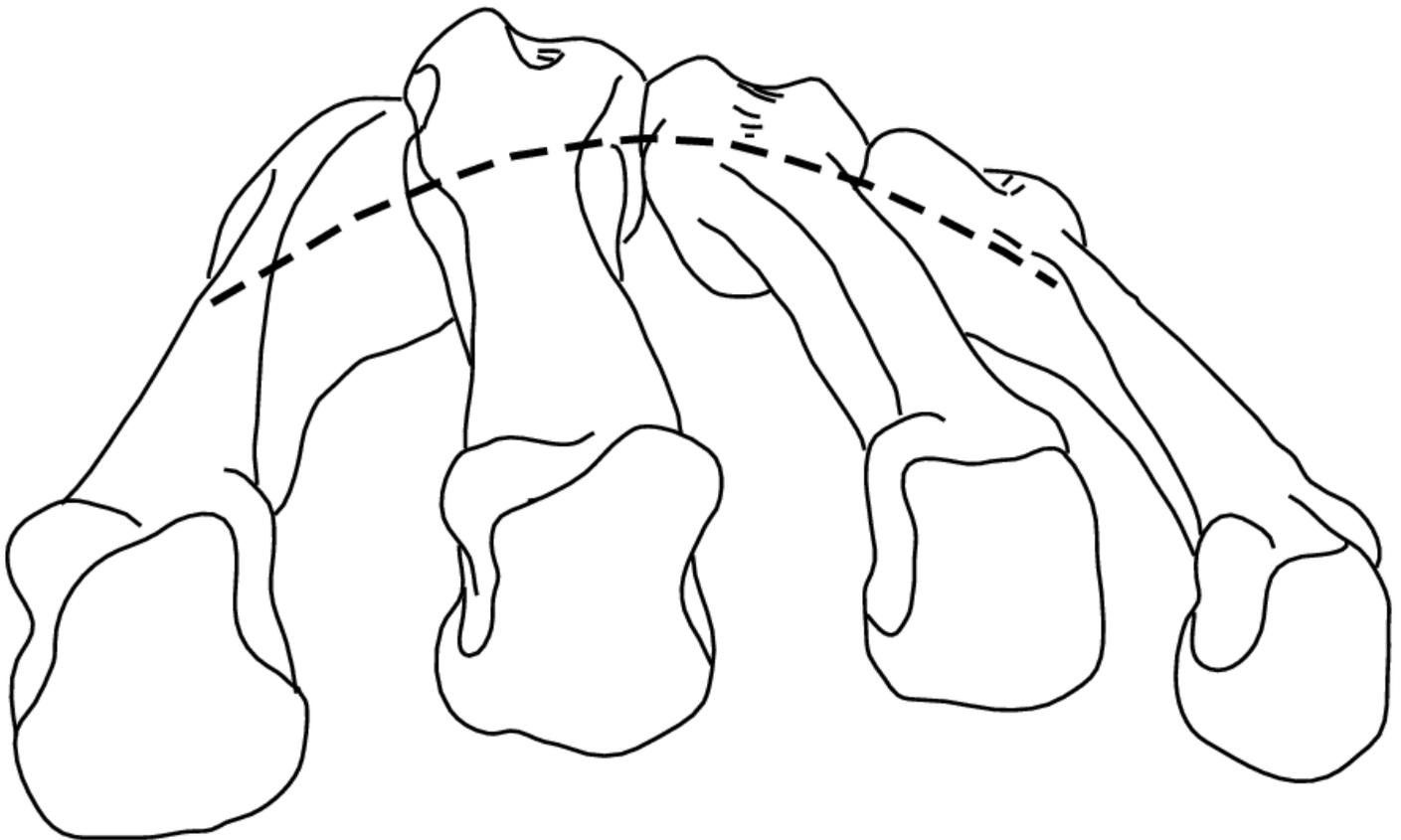
Post hoc comparisons of MC4 wedging values

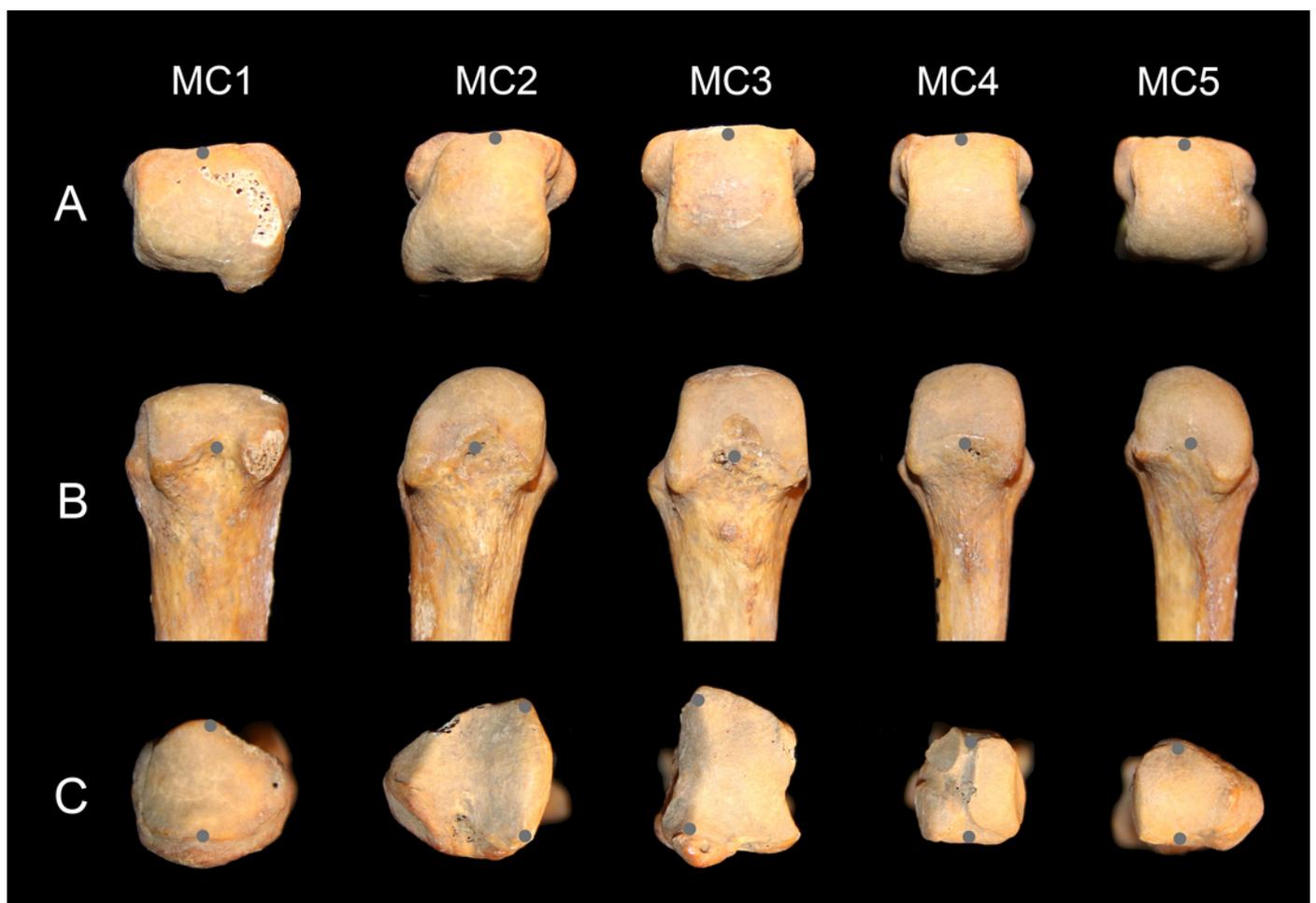
Tamhane T2 post hoc comparisons of the dorsal to palmar medio-lateral width ratio for the MC4 (p-values).

	H. sapiens	*P. troglodytes*	*G. g. gorilla*
P. troglodytes	**<0.001**		
G. g. gorilla	0.10	**<0.001**	
P. pygmaeus	**<0.001**	**0.004**	**<0.001**

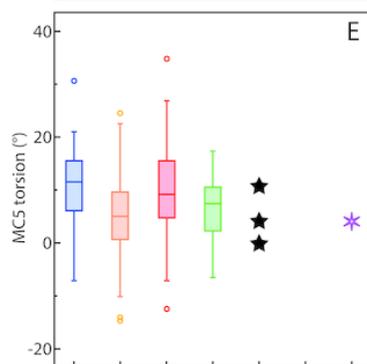
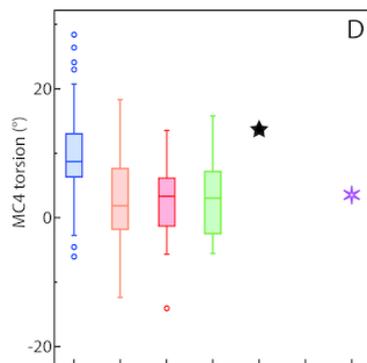
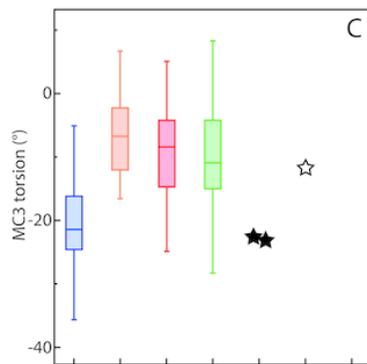
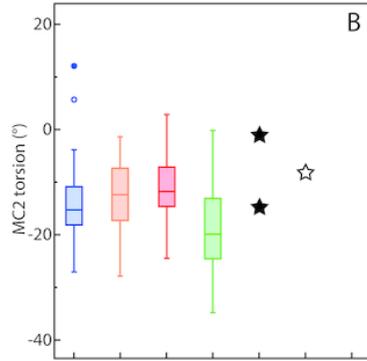
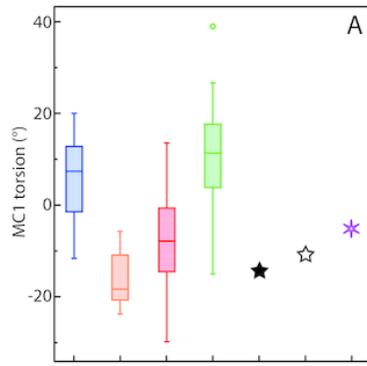
1

Palmar arch

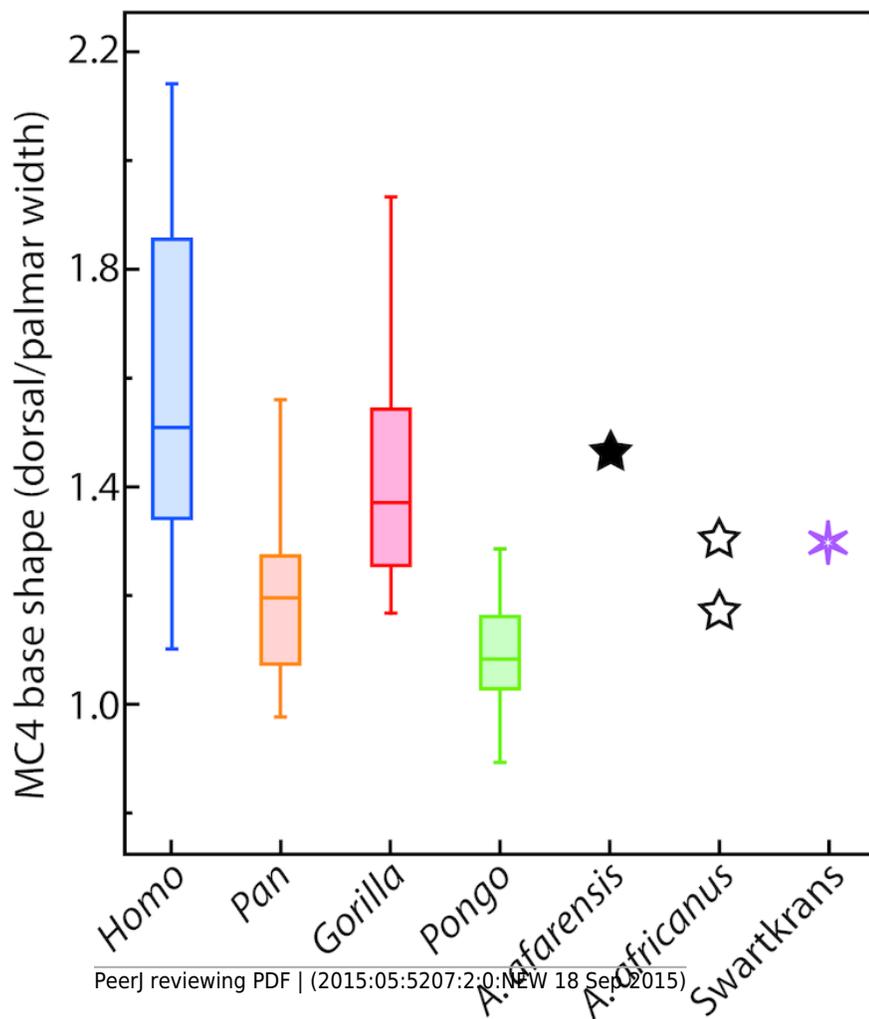
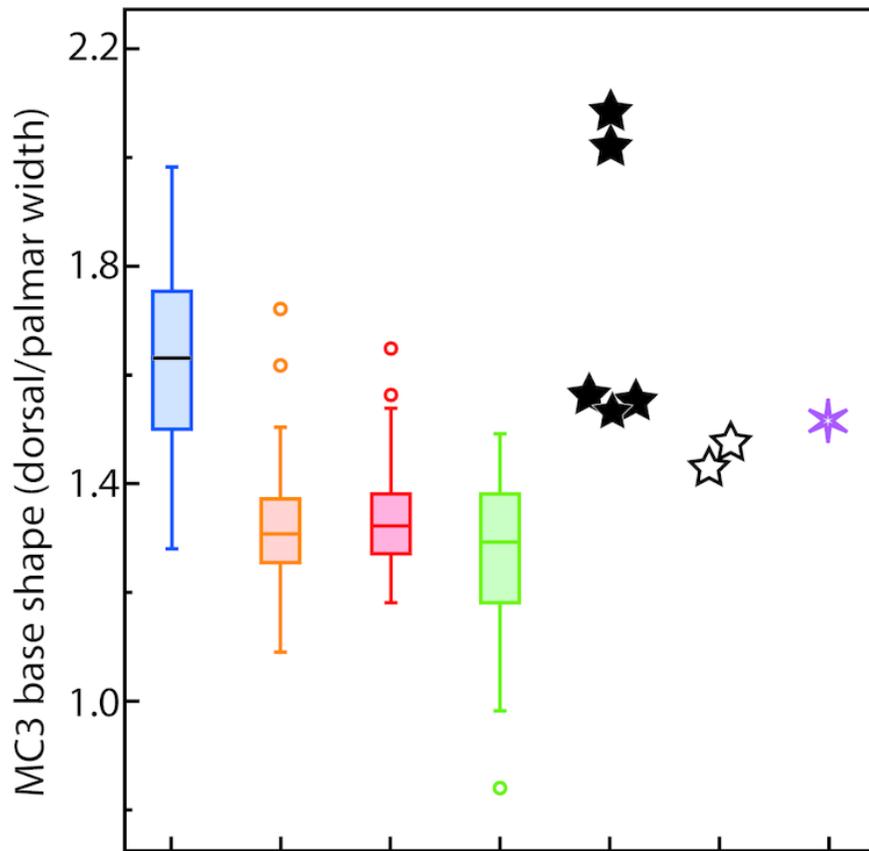
Metacarpals two to five of a left hand in distal view illustrating the arch formed by the metacarpal bases (modified from Peters and Koebke, 1990).

Metacarpal data collection

Distal (A) and palmar (B) view of human left MC heads, and proximal (with dorsal down) view of the bases (C). The gray points show how the palmodorsal axis of the head and base were recorded with a 3D digitizer (see text for details).

3

Boxplot of metacarpal torsion

Boxplot of the torsion of MC1 to MC5. The box represent the 25-75 quartiles, the horizontal line the median, the whiskers the range, and open and close circles represent outliers and extreme outliers (more than 1.5 and 3.0 standard deviation from the mean).

4

Metacarpal base wedging

Ratio of dorsal to palmar width of the base of MC3 and MC4. Higher ratios indicate a base that is more wedge-shaped, while a ratio of 1 indicates a base that is rectangular.

5

Metacarpal base and heads with average torsion

Metacarpal head (pale grey ovals) and base (dark grey quadrangles) of a left hand with the plantodorsal axes drawn (pale grey dotted line for the head; dark grey for the base; see methods for details). Metacarpal torsion is measured as the angle between these two axes in the coronal plane. The average torsion values are drawn from Table 2 and average wedging values of the MC3 and MC4 bases are drawn from Table 6. All drawings are aligned relative to the MC2-MC3 articulation. Relative orientation of the MC1 base (drawn for humans and chimpanzees only) is estimated from the orientation of the trapezio-MC articulation (from Fig. 20 in Sarmiento 1994). Because of the strong wedging of the MC3 and MC4 bases, the dorso-palmar axis of the bases of the ulnar-most MCs of humans are more turned toward the thumb than in other taxa.

-14° -21° 10°

6°

11°

Homo sapiens

-13° -6° 2°

5°

-17°

Pan troglodytes

-12° -9°

3°

10°

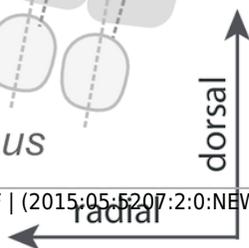
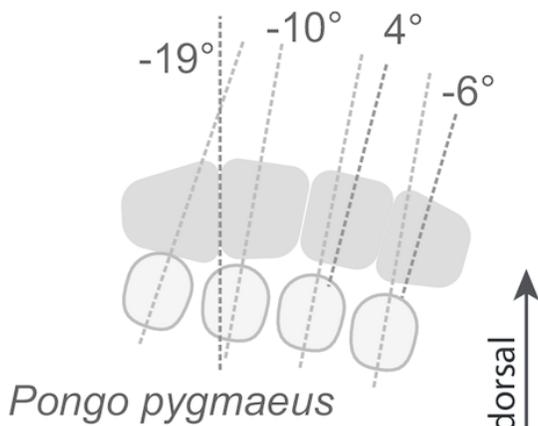
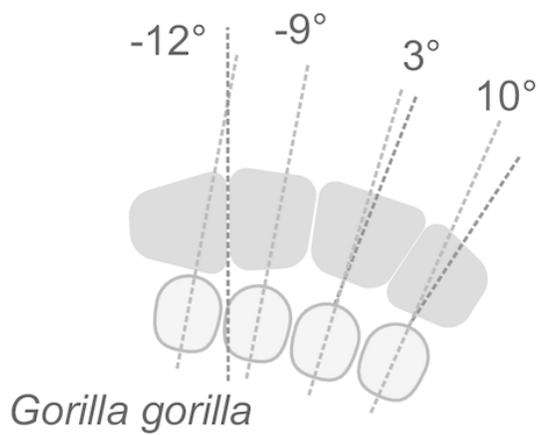
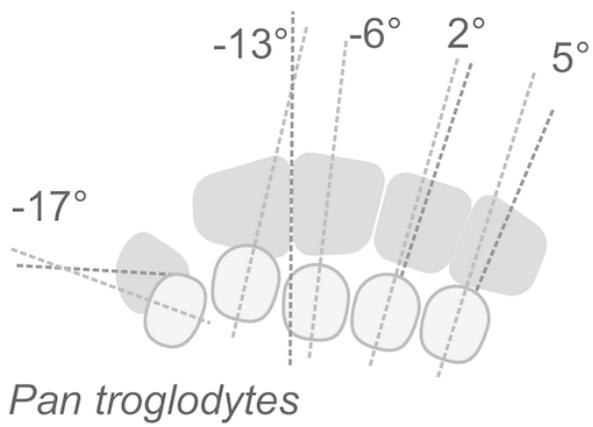
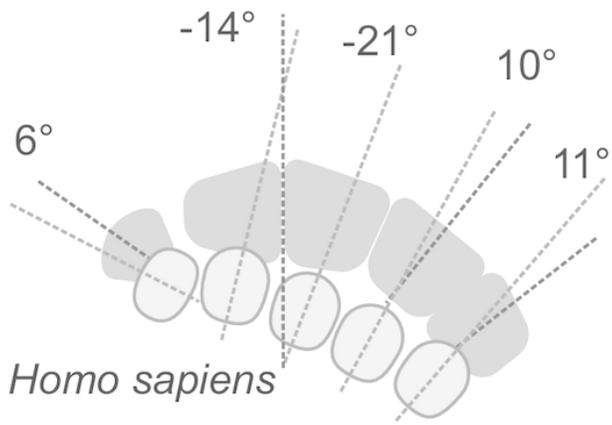
Gorilla gorilla

-19° -10° 4°

-6°

dorsal

radial

Pongo pygmaeus

Patterns of metacarpal torsion

Patterns of torsion for all MCs (median values for samples of n>1).