Metacarpal torsion in apes, humans, and *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 A. 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 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 first, 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 A. afarensis are very human-like, suggesting that the medial palm was already well adapted for these kinds of grips in that taxon. A. africanus present a more intermediate morphology between humans and apes, suggesting a less derived morphology for manipulation in that taxa.

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5 Abstract

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7 manipulation. Numerous studies have shown that *Australopithecus afarensis* and *A. africanus*

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

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18 position that facilitate opposition to the thumb in power or cradle grips. The third and fourth

19 metacarpals of *A. afarensis* are very human-like, suggesting that the medial palm was already

20 well adapted for these kinds of grips in that taxon. *A. africanus* present a more intermediate

21 morphology between humans and apes, suggesting a less derived morphology for manipulation in

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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; Skinner et al., 2015).

Marzke (1997, 2005) identified three traits that suggest that the hand of one of the oldest

Australopithecus species, *A. afarensis* was modified for better precision grips and handling: a

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 they indicate significant improvement of

manipulartory skills. Interestingly, they both recognize that the radial torsion 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*. Torsion of the

second and third MC head in humans 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 *A. afarensis*, *A. 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;

Kapandji, 2005). The two ulnar-most MCs are also slightly flexed at the carpometacarpal joint. In

57 addition, the palmar surfaces of the fingers are supinated, i.e., turned toward the thumb. Apes,

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

59 among the fingers and no apparent flexion at the carpometacarpal joint (Lewis, 1977, 1989).

60

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

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

63 fingers and objects are often held with the finger pads or palmar surface of the fingers (Napier,

64 1956). Depending on the size of the object held, the position of the ulnar digits varies. When

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

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

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

68 involves the palmar surface of the digits rather than the pads, the third and particularly the second

69 digit tend to take a more pronated position (Napier, 1956). In addition, the fourth and fifth digits

70 become involved and take a supinated position (Marzke and Shackley, 1986).

71

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

73 difficulty in pad-to-pad grips. This is in part a consequence of their relatively long fingers and

74 short thumbs. They are able to handle small objects between the thumb and the side of the

75 phalanges of the index (Napier, 1960). This particular grip does not require marked rotation of

76 the second digit. In contrast to humans, the morphology of the ape hand is most likely strongly

77 driven by locomotor constraints. All great apes are characterized by a hook grip, which involves

78 flexing all the fingers in sagittal planes (Lewis, 1977, 1989; Napier, 1993), a position that is

79 remains the same when using the hand in terrestrial locomotion.

80

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

82 First, as mentioned above, digits 2-5 are much shorter relative to the thumb in humans than in

83 apes. Also, the bases of the second and fifth MCs have been modified to allow for some axial

84 motion. The base of the second MC has a saddle shape rather than the wedge shape observed in

85 apes and its base has a continuous articulation with the capitate instead of an articulation that is

86 bisected in anterior and posterior segments by carpometacarpal ligaments as found in all extant

87 apes (Lewis, 1973, 1977, 1989; Marzke, 1983; Tocheri et al., 2008; Drapeau, 2012). That

88 articulation and the articulation between the second and third MCs are curved instead of being

89 flat as in apes (Lewis, 1973, 1977, 1989; Marzke, 1983; Tocheri et al., 2008; Drapeau, 2012).

90 Finally, the second MC-trapezium articulation lies in a more transverse plane instead of the

91 sagittal plane found in apes (Marzke, 1983; Drapeau et al., 2005; Tocheri et al., 2008). Similarly,

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

93 combined with a retraction of the hook of the hamate, allows for flexion and supination of the

94 MC (Dubousset, 1981; Marzke, 1983; Lewis, 1989; Buffi et al., 2013). In great apes, the ventral

95 surface of the base articulates with the hook of the hamate, limiting flexion and axial rotation.

96

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

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

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

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

101 radially and to pronated when flexed (See Lewis, 1989 for details). The extended finger tends to

102 be supinated when ulnarly deviated and pronated when radially deviated or flexed. The

103   morphology of the third MC head also present some asymmetry, but to a lesser degree than the

104   second and the rotation and axial deviation of the phalanx are also less marked than in the second

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

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

107   morphology of the head, combined with the morphology of the base, allows for axial rotation of

108   the second and fifth fingers and MCs. In contrast, the ape MCs do not have such asymmetrical

109   heads and movement at these joints function much more as simple hinges (Lewis, 1989; Drapeau,

110   2012). The human first MC allows for a greater range of thumb opposition because the base has a

111   less projecting palmar beak than what is seen in chimpanzees and the articulation is flatter in the

112   dorso-palmar direction (Marzke, 1992; Tocheri et al., 2003). The morphology of the head, with a

113   palmar elevation radially, allows for some pronation and abduction of the distal segments of the

114   thumb during flexion, but it is a morphology that appears to be primitive in hominoids (Lewis,

115   1989).

116

117   Australopithecines have acquired some of the traits associated with manipulation in humans. For

118   example, *A. afarensis* is characterized by a continuous and curved MC2-capitate articulation that

119   is more transversely oriented than in apes, but less than in humans (Marzke, 1983; Drapeau et al.,

120   2005), a MC2-trapezium facet that is more palmarly oriented than in chimpanzees (Marzke,

121   1983; Drapeau et al., 2005), asymmetric MC2 and MC3 heads (Lewis, 1977; Susman, 1979;

122   Marzke, 1997; Drapeau, 2012), and relatively long thumbs (Alba et al., 2003; but see Rolian and

123   Gordon, 2013 for opposing view), traits that are also found in *A. africanus* (Green and Gordon,

124   2008; Tocheri et al., 2008; Drapeau, pers. obs.). These traits suggest an adaptation to 3-finger

125   chuck. However, a volar beak on the MC1 probably limited opposition of the thumb (Marzke,

126   1992) and limited flexion and supination of the MC5 imply that the fossils could not produce

127   human-like power and cradle grips with a cupped palm (Marzke, 1983).

128

129   In this study, I contrast MC head torsion in human and great apes to show how it reflects the

130   differences in grips between these taxa. I also compare *A. afarensis*, *A. africanus* and specimens

131   from Swartkrans to extant species to evaluate their morphological affinities and possibly identify

132   additional traits related to manipulation in the fossil specimens.

133

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

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

136   are the result of the projecting hook of the hamate and of the position of the trapezium usually

137   disposed at an angle from the other distal carpal bones; see Lewis, 1989). Sarmiento (1994) noted

138   that the radius of curvature of this arch varies among taxa, but did not measure it. Metacarpals are

139   expected to present torsion values that adjust for the degree of arching. As a result, the ulnar-most

140   digits will tend to have heads that are more ulnarly twisted, while the radial-most digits (except

141   the thumb) will tend to have heads that are more radially twisted.

142

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

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

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

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

147   greater arching. In addition, because the base and head morphologies of the second and fifth MCs

148   of humans allows for axial rotation of the digit to conform to various object sizes and shapes,

149 torsion of these two MCs may not be as different from apes as for the other digits. In humans, the

150 trapezoid is wider palmarly than that of apes, which pushes the trapezium radially and rotates it

151 into alignment relative to the rest of the proximal carpal row (Tuttle, 1970; Lewis, 1977, 1989;

152 Sarmiento, 1994; Drapeau et al., 2005; Tocheri et al., 2005). As a result, the trapezio-MC

153 articulation lies within an axis comparable to that of the other digits. Therefore, a greater torsion

154 of the first MC in humans is expected in order to bring the metacarpo-phalangeal joint in an axis

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

156 first MC already perpendicularly rotated relative to the other carpo-metacapal joints, are not

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

158 to the palm.

159

160 **Materials**

161 The human sample is from archaeological collections and it consists of a mix of euroamericans

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

163 the *Gorilla* sample includes only western lowland gorillas. All specimens are free of pathologies.

164 Sample size varies from one MC to the other in function of the availability of each bone in the

165 osteological collection (Table 2).

166

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

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

169 (Bush et al., 1982; Drapeau et al., 2005) and date at 3.2 Ma for A.L. 333 and 3 Ma for A.L. 438

170 (Kimbel, Rak & Johanson, 2004). Although some have argued that there might be more than one

171 species represented at Sterkfontein (e.g., Clarke, 2013), all four Sterkfontein specimens included

172 are from Member 4 and are assumed to belong to *A. africanus* base on the general morphology,

173 size and provenience (McHenry and Berger, 1998), and date between 2.6 and 2 Ma (Herries et

174 al., 2013). At Swartkrans, *Paranthropus robustus* and early *Homo* are present and post-cranial

175 specimens are difficult to assign to either of these taxa with certainty. SK 84 is from Member 1

176 and attributed to *Homo* (Susman, 1994, 2004), SKW 2954 is from member 2 and is described as

177 being human-like (Susman, 2004), and SKW 14147 is not assigned to a member or to a specific

178 taxa (Day and Scheuer, 1973). Member 1 is dated between 2.2 and 1.8 Ma and Member 2

179 between 1.8 and 1 Ma (Gibbon et al., 2014). Only specimens that are complete and undistorted

180 are included in the analysis.

181

182 **Methods**

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

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

185 the whole head that was recorded, irrespective of the asymmetry of the articular surface (Fig.

186 2A). For the MC2, the palmodorsal axis of the base was determined as the margin of the articular

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

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

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

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

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

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

193 available for one specimen, values from the right were reversed. Positive values represent heads

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

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

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

197   base of the MCs when articulated together, the wedging of the base was measured. It was

198   calculated as the ratio of dorsal width relative to the palmar width of the bases of the MC3 and

199   MC4, the two 'central' bones of the arch composed of the four ulnar MCs.

200

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

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

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

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

205   1.6° and the average range 8.3° (varied from 2.4° to 15.4°). The error was, on average, about

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

207   1.3° for the other MCs; mean pollical range 13.5° vs. 7.0° for all other MCs). This error for the

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

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

210

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

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

213   when heterogeneous. Angles are reversed in right MC fossils for direct comparisons with extant

214   taxa.

215

216

217

218 **Results (Tables 4 & 5)**

219

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

221 the other fingers, while *Pan* has the head that is the least turned towards the other fingers.

222 Gorillas are intermediate between these two groups. *Australopithecus afarensis* (n=1) is most

223 similar to *Gorilla* but within the range of all taxa and outside the range of only humans.

224 *Australopithecus africanus* (n=1) and the Swartkrans specimen (SK 84) are most similar to

225 *Gorilla*, but within the range of all species (Fig. 3A).

226

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

228 *Pongo* that has a significantly more turned MC than the other taxa. *Australopithecus afarensis*

229 (n=2) is variable and does not resemble one taxon in particular. *Australopithecus africanus* (n=1)

230 is within the distribution of all taxa, but most similar to African apes (Fig. 3B).

231

232 For the MC3, humans have the heads that are the most supinated and are statistically different,

233 while all apes are not significantly different from each other. *Australopithecus afarensis* (n=2) is

234 most similar to humans, while *A. africanus* is within the range of all taxa, but most similar to

235 apes (Fig. 3C).

236

237 For the MC4, again, humans are different from all apes, which form a fairly uniform group. Apes

238 have relatively untwisted heads, while humans have fourth MCs that have heads that are more

239 pronated. The *A. afarensis* specimen is most similar to humans while within the distribution of all

240 taxa. The Swartkrans specimen (SKW 2954) is most similar to apes but within the distribution of

241 humans (Fig. 3D). Although it has no evidence of a healed fracture, Susman (2004) suggested

242 that this specimen, because of an uncharacteristically AP curved diaphysis and the presence of a

243 'crook', may have been broken. If so, the torsion value for that specimen may be distorted and

244 not reflect a normal morphology.

245

246 Finally, for the MC5, apes and humans have pronated heads (turned away from the thumb)

247 although humans have more twisted head than *Pan*, while all other taxa do not differ statistically.

248 *Australopithecus afarensis* (n=3) is variable, but on average, resemble *Pan* and *Pongo* the most,

249 as does the one Swartkrans specimen (SKW 14147; Fig. 3E).

250

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

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

253 gorillas have a MC4 base that is intermediate in shape between that of humans and chimpanzees,

254 while their MC3 base is similar to that of the other ape taxa. *Australopithecus afarensis* (n=5) are

255 characterized by a human-like, pinched MC3 base, while *A. africanus* (n=2) and one specimen

256 from Swartkrans are characterized by a base that is intermediate between that of apes and humans

257 (while not being very different from three *A. afarensis* specimens). The MC4 bases are more ape-

258 like for all fossils, although *A. afarensis* still falls closest to the median of humans.

259

260 **Discussion**

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

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

263 5; Lewis, 1977, 1989; Sarmiento, 1994; Tocheri et al., 2005). As discussed above, the wider

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

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

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

267   Drapeau et al., 2005; Tocheri et al., 2005). This reorientation of the trapezium positions the MC1

268   articular facet in a position that is more along the radioulnar axis of the other MC bases, in a

269   position that is less advantageous for MC1 opposability. The strongly twisted head of the human

270   MC1 reflect that species' particular carpal morphology. The results for *Pongo* are intriguing

271   given that it does not have developed thenar muscles (Tuttle, 1969) nor particularly large first

272   MC articular surfaces on the trapezium (Tocheri et al., 2005). That species is the most variable

273   (Fig. 3A) and that variation may reflect less stabilizing selection for a specific morphology in that

274   species. It is noteworthy that the strong inversion of the thumb and strong eversion of the second

275   digit of *Pongo* (Fig. 6) is reminiscent of their value of metatarsal (MT) torsion (Drapeau and

276   Harmon, 2013). Their MC1-2 and MT1-2 morphology might reflect the importance of a strong

277   opposing thumb- or hallux-to-palm grip in this highly arboreal taxa (Drapeau and Harmon,

278   2013). The torsion of the *Australopithecus* and Swartkrans MC1 specimens is similar to apes and

279   probably reflects the lack of a human-like expansion of the palmar surface of the trapezoid and

280   the lack of a human-like load distribution on the palmar surface (as suggested by Tocheri et al.,

281   2008). The Swartkrans specimen (SK 84) is, of all the fossils, the specimen that most closely

282   approaches the human form and falls within the range of distribution of humans. However, given

283   its intermediate morphology, this study cannot resolve its taxonomical affinity (see Trinkaus and

284   Long, 1990; Susman, 1994).

285

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

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

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

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

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

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

292 apes, humans are characterized by an asymmetrical MC2 head (Lewis, 1989), which allows the

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

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

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

296 second MC is capable of some axial rotation while that of apes is much less mobile (Lewis,

297 1989). Changes in both proximal and distal articular architecture in humans provide rotational

298 flexibility of the finger necessary for a variation in effective grips. Interestingly, the base and

299 head morphology of *Australopithecus* is clearly derived toward the human-like configuration

300 (Marzke, 1983, 1997; Marzke and Shackley, 1986; Drapeau et al., 2005; Tocheri et al., 2008;

301 Kivell et al., 2011; Drapeau, 2012), which suggest human-like digit rotational capacities for these

302 species.

303

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

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

306 with the other MC heads is minimal. Among apes, knuckle-walkers have the less twisted heads,

307 which may reflect the habitual use of the hand in terrestrial locomotion, which loads heavily the

308 third digit (Inouye, 1994). In humans, torsion is required in the power and precision grips.

309   However, unlike the MC2, the third MC base does not allow axial rotation and the head is only

310   slightly asymmetric compared to the second. As a consequence, the third MC head needs to be

311   more supinated to allow for proper positioning of the finger during power and precision grips.

312

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

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

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

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

317   1979). When buttressing, the fourth digit is flexed in the palm and ulnar torsion may help

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

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

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

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

322   arched MC base row than other extant large apes (Fig. 5). The dorsopalmar axis of the MC4 base

323   is therefore more twisted towards the thumb in humans than in other large apes when in

324   articulation with the other MCs and carpals. Because of the base orientation, the less radially

325   twisted head of the MC4 in humans does not necessarily indicate that the whole digit is less

326   radially twisted towards the thumb (Fig. 5). Further study of the orientation of the hand bones *in*

327   *vivo* in humans and apes will be needed to measure the actual degree of opposition of the MC and

328   digits.

329

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

331   have ulnarly twisted heads, also requires explanation. In humans, the articular surface of the MC5

332   head is also asymmetrical (Lewis, 1977, 1989; Marzke, 1997), being somewhat a mirror image of

333   the MC2. As a consequence, the digit is rotated towards the thumb during flexion, which is the

334   natural position taken by the finger during power grips and some precision grips (Napier, 1956).

335   Also, the MC itself is free to rotate slightly in humans though not in apes. These mechanisms

336   may be sufficient during power grips and five-finger holds to produce a rotated digit without the

337   need of the whole head to be twisted. Also, if the MC-base row is more arched than in apes, as it

338   is suggested above, the fifth MC base is rotated radially relative to the thumb (Fig. 5). A

339   moderate ulnar torsion still leaves the fifth MC head in a radially facing position.

340

341   *Australopithecus afarensis* has MC3 and MC4 that are clearly more similar to humans, which

342   suggest use of the hand in the fossil species that resembles humans more than apes. Similarly,

343   their third and fourth MCs are wedge-shaped most like humans. The morphology of *A. africanus*

344   is less clearly similar to one species. Although torsion values are within the range of humans,

345   they are more typical of apes and their MC bases are not as wedged as humans. Together, these

346   traits suggests that it may have been less adept at the pad-to-pad three-jaw chuck grasp relative to

347   humans and *A. afarensis*, even though it probably had relative finger lengths comparable to *A.*

348   *afarensis* (Green and Gordon, 2008; Rolian and Gordon, 2013). Overall, the *A. afarensis*

349   morphology is human-like, while that of *A. africanus* is less clearly derived towards the human

350   form, suggesting that the medial palm was less derived toward the human condition than *A.*

351   *afarensis*.

352

353   In contrast, the morphology of *A. afarensis* fifth MC suggests, on average a morphology that is

354   more *Pan*-like, with untwisted heads. Also, the morphology of the base in that species suggests

355 less mobility in flexion and supination at that joint than in humans (Marzke, 1983; Marzke and

356 Shackley, 1986; Marzke, Wullstein & Viegras, 1992). However, as for the second, the head is

357 asymmetric (Bush et al., 1982; Marzke, 1997; Drapeau, 2012). This mosaic of ape and human

358 traits in the fossils species indicates a transitional state, in which the human-like involvement of

359 the fifth finger in manipulation might be limited to the phalangeal segment of the digit. This

360 sequence of evolutionary events (involvement of the phalanges first, then followed by the

361 mobility of the MC) may have been similar in the second digit, but occurred earlier in a form

362 ancestral to *A. afarensis*, a hypothesis that can be tested with the discovery of slightly older

363 fossils that would preserve the MC2 head.

364

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

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

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

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

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

370 the reoriented base. If so, this would indicate that *A. afarensis,* with its wedged bases, has begun

371 the reorientation of the medial aspect of the palm of the hand despite probably not being able to

372 flex the MC4 and MC5 like humans (Marzke, Wullstein & Viegras, 1992). Combined with the

373 asymmetry of the fifth MC head, *A. afarensis* was probably capable of a power and cradle grips

374 that were not completely human but approached it significantly.

375

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

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

378   the only one that is clearly ape-like by being more radially twisted. This morphology is rather

379   surprising (if it is not due to a healed fracture), considering that the MC3 base tends to be pinched

380   suggesting a fairly deeply arched MC-base row. As a whole, the Swartkrans specimens do not

381   suggest human-like adaptations to manipulation although some traits, such as moderate base

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

383

384   **Conclusions**

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

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

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

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

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

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

391   curvature of the proximal metacarpal arch, a curvature that is greater in humans than in apes.

392   Further work needs to document the *in vivo* MC torsion when in anatomical articulation.

393

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

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

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

397   in line with the rest of the carpals and allowed for load dissipation through the palmar aspect of

398   the palm. These fossil species likely had a primitive configuration similar to apes with a

399   trapezium positioned more perpendicular to the rest of the distal carpal row. Previous studies had

400   shown that the second MC of *Australopithecus* was modified from the assumed primitive

401 morphology, with a base and head allowing for some axial torsion of the digit, but the third

402 lacked the human-like styloid process, suggesting only a partial transition towards a human-like

403 grip. This study has shown that the human-like orientation of the third and fourth fingers was

404 achieved in *A. afarensis*, indicating the possibility of adequate three- or four-jaw chucks in these

405 species (although possibly with less ulnar deviation of the thumb than in humans; Marzke, 1992).

406 More ulnarly, there is little evidence of a human-like grip, but for the asymmetry of the fifth MC

407 head that allow for phalangeal axial rotation, suggesting that active involvement of the fifth digit

408 in a five-jaw chuck was probably limited to the phalanges. However, the shape of the MC3 and

409 MC4 bases suggest a configuration of the MC bases that was human-like in *A. afarensis*,

410 allowing for more opposition of the fifth MC than is possible in large apes. As a consequence,

411 although *A. afarensis* has not developed a completely human grip, it showed significant derived

412 traits that suggest that there was directional selection for improved dexterity and strength in

413 various grips in these early hominins. In contrast, *A. africanus* presents MC3 torsion more typical

414 of apes, a MC3 base shape that is more intermediate between apes and humans, and a MC4 base

415 that is more ape-like. This suggests that *A. africanus* may have been less dexterous in the three-

416 jaw chuck than *A. afarensis* despite thumb-to-fingers proportions that were probably similar

417 (Green and Gordon, 2008; Rolian and Gordon, 2013) and evidence of some human-like loading

418 in the trabecular patterns of the base of the first and head of the second and third MCs (Skinner et

419 al., 2015). The weakened human-like signal in the trabeculae of the MC4 (Skinner et al., 2015)

420 concurs with this study's observation that *A. africanus* has a less derived hand ulnarly as reflected

421 by base shapes that are more ape-like and keep the orientation of the palm and palmar surface of

422 the digits oriented more anteriorly and less towards the thumb.

423

424 Overall, this study supports previous studies on *A. afarensis* and *A. africanus* that these taxa had

425 derived hand morphology that suggest increase finesse and strength in pad-to-pad, two- and

426 three-jaw chucks grips and some adaptation to human-like power grips and support the

427 hypothesis that tool making and use predated *Homo* (McPherron et al., 2010; Harmand et al.,

428 2015).

429

430

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439

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548
549

Figures

Figure1: Metacarpal 2 to 5 of a left hand in distal view illustrating the arch formed by the

metacarpal bases (modified from Peters and Koebke, 1990).

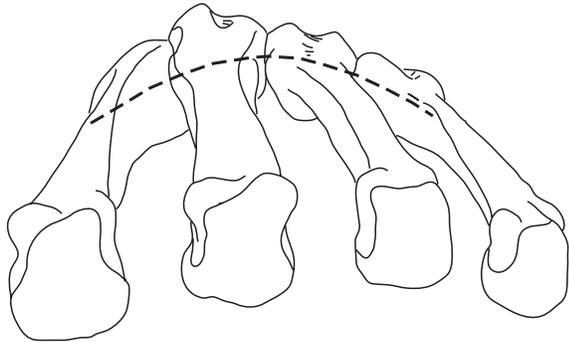



Figure 2: Distal (A) and palmar (B) view of human MC heads, and proximal view of the bases

(C). The points show how the palmodorsal axis of the head and base were recorded with a 3D

digitizer (see text for details). A, B are modified from Lewis, 1977, and C is modified from

White and Folkens, 2000.

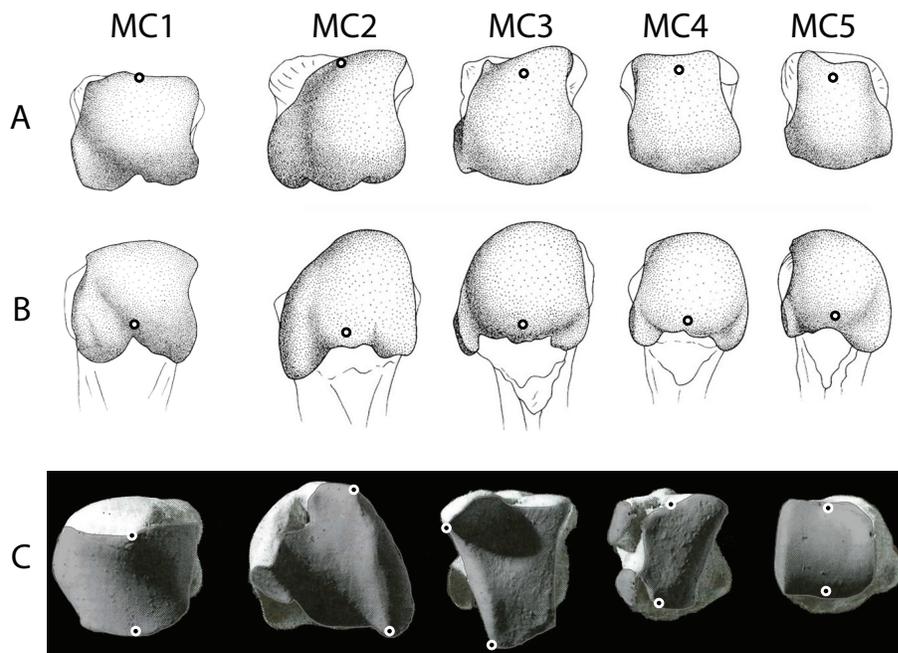
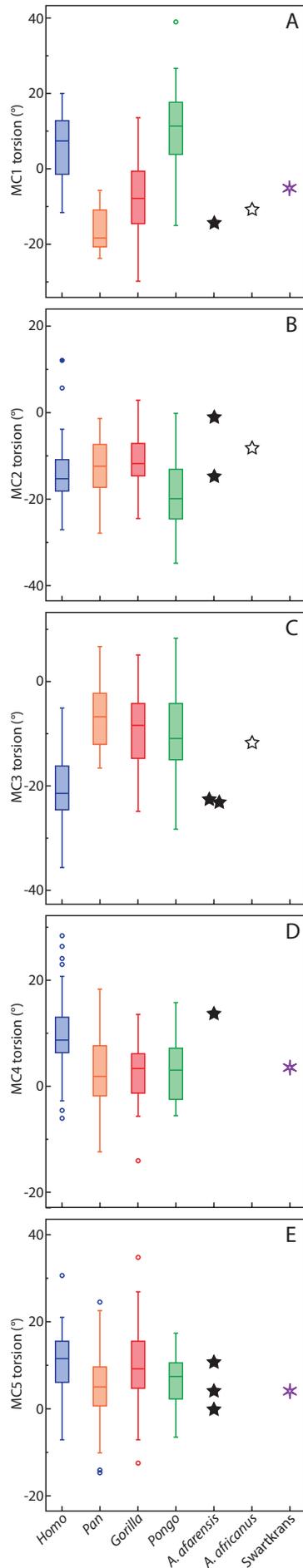



Figure 3: Boxplot of the torsion of MC 1 to 5. The box represent the 25-75 quartiles, the horizontal line the median, the whiskers the range, and open and close circles represent outliers and extreme outliers (more than 1.5 and 3.0 standard deviation from the mean).

Figure 4: 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.

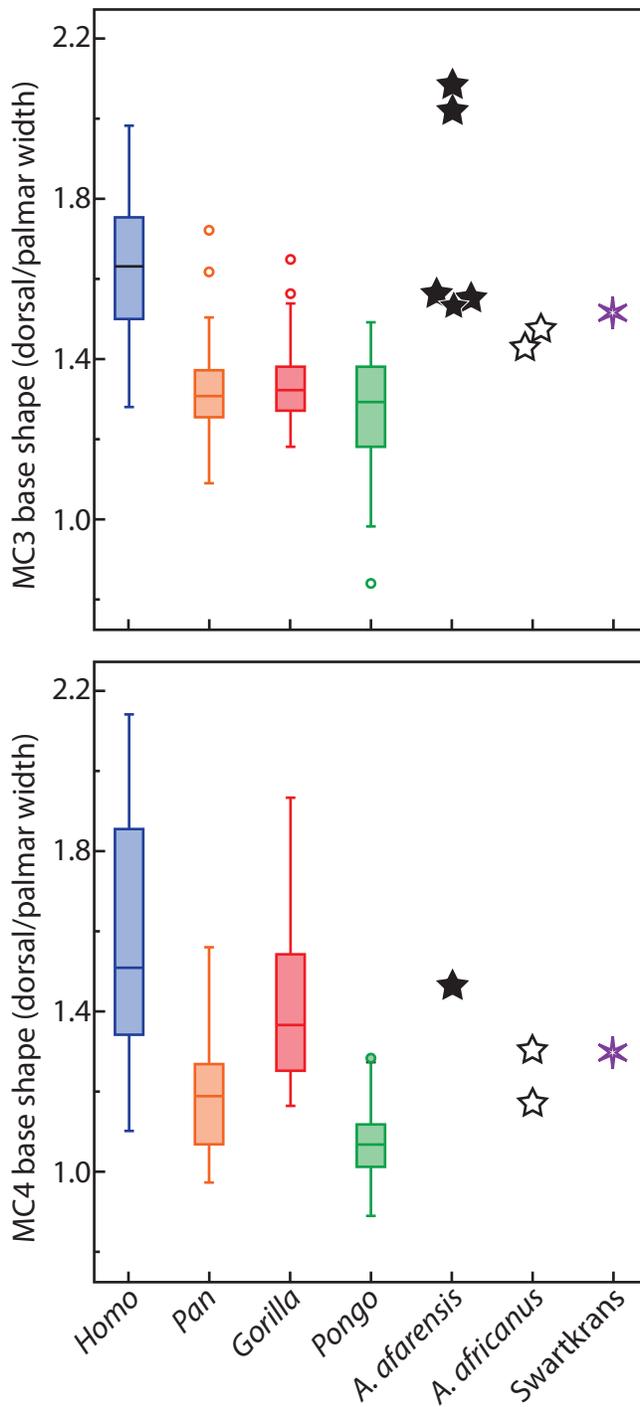



Figure 5: Metacarpal head (pale grey ovals) torsion relative to the base (dark grey quadrangles) in distal view of a left hand. The wedging of the MC3 and MC4 bases is drawn from result in Table 6. All drawings are aligned relative to the MC2-MC3 articulation. Relative orientation of the MC1 base (drawn 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.

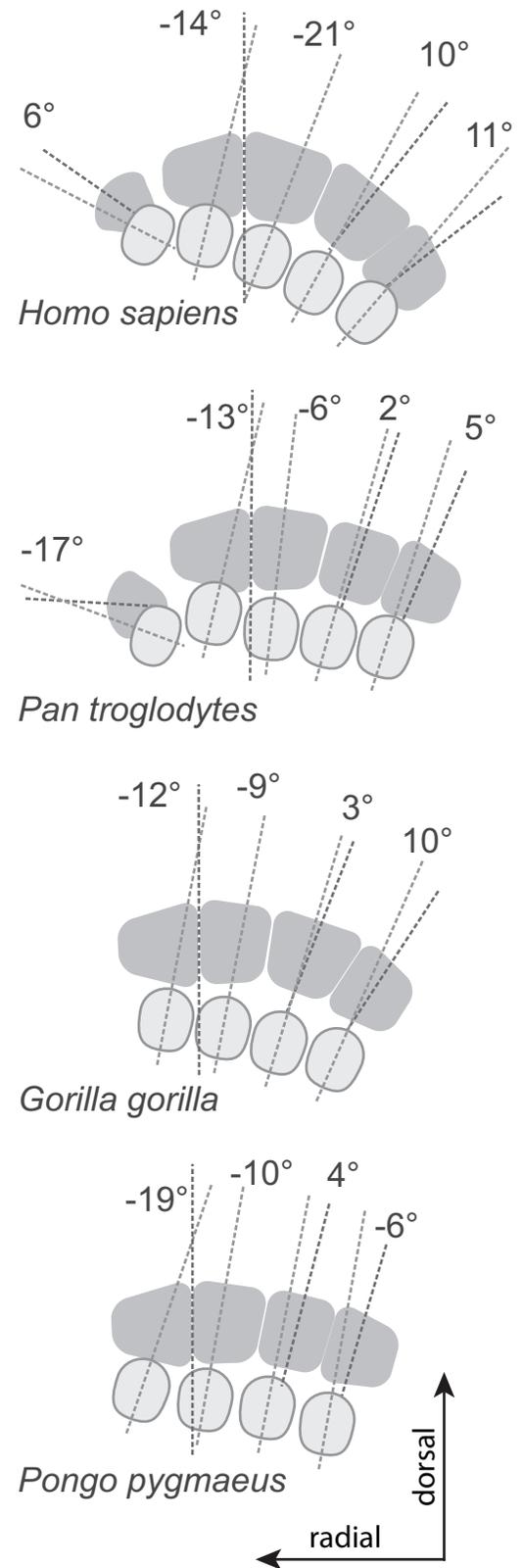



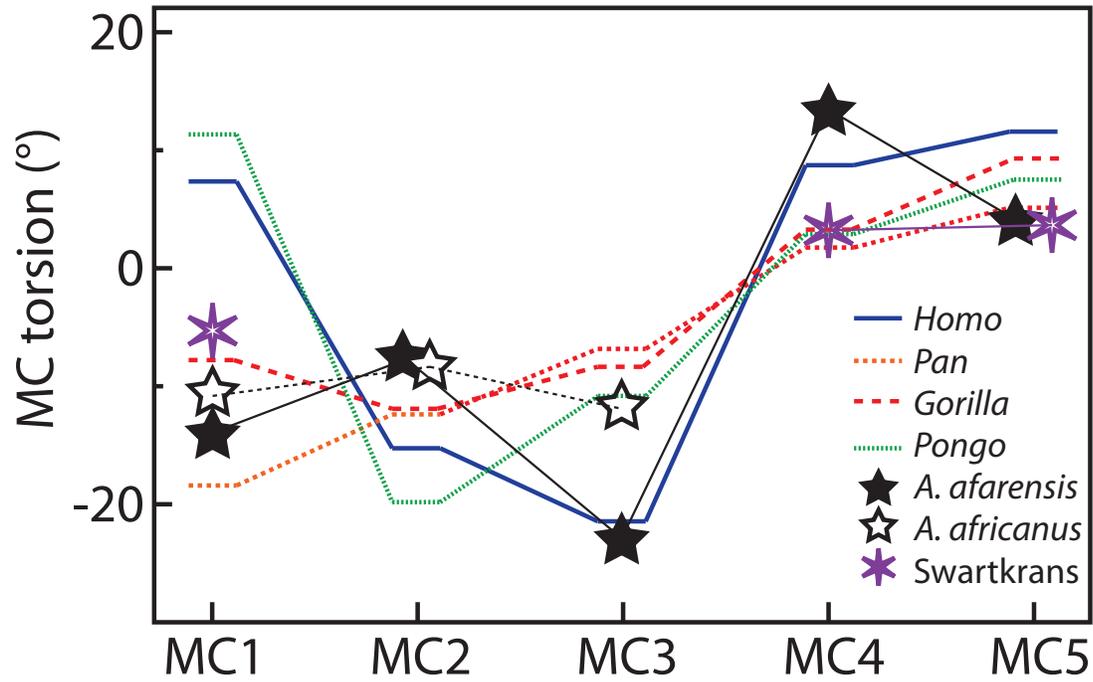
Figure 6: Patterns of torsion for all MCs (median values for samples of n>1).

Tables

Table 1: Comparative sample.

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

Table 2: 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]The mean is presented on the first line, standard deviation on the second, and sample size on the third.
[2]In degrees.

Table 3: *Australopithecus afarensis*, *A. 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	D	-3.5
SKW14147	MC5	L	4.0

*possible healed fracture

Table 4: 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

Table 5: Post hoc comparison 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]Values above the diagonal are mean differences (row - column), values below are significance of the test (values at 0.05 or less are in bold).

Table 6: 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 0.18	1.58 0.30
P. troglodytes (n=36)	1.32 0.12	1.20 0.15
G. g. gorilla (n=36)	1.34 0.11	1.45 0.26
P. pygmaeus (n=37)	1.37 0.22	1.32 0.28
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	1.46	
Stw65		1.17
Stw330		1.30
SKX 3646	1.52	
SKX 2954		1.30

Table 7: 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**	0.94	
P. pygmaeus	**<0.001**	0.58	0.14

Table 8: Table 2: 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	0.09	**<0.001**	
P. pygmaeus	**<0.001**	**0.001**	**<0.001**