1   **The forearm and hand musculature of semi-terrestrial rhesus macaques (*Macaca mulatta*) and**

2   **arboreal gibbons (*fam. Hylobatidae*). Part II. Quantitative analysis.**

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8   Short title: Quantitative analysis of macaque and gibbon forearm and hand musculature

9 **Abstract**

10 Nonhuman primates have a highly diverse locomotor repertoire defined by an equally diverse hand use.

11 Based on how primates use their hands during locomotion, we can distinguish between terrestrial and

12 arboreal taxa. The 'arboreal' hand is likely adapted towards high wrist mobility and grasping, whereas

13 the 'terrestrial' hand will show adaptations to loading. While the morphology of the forearm and hand

14 bones have been studied extensively, functional adaptations in the forearm and hand musculature to

15 locomotor behaviour have been documented only scarcely. In this paper, we investigate the forelimb

16 musculature of the highly arboreal gibbons (including *Hylobates lar, Hylobates pileatus, Nomascus*

17 *leucogenys, Nomascus concolor, Symphalangus syndactylus*) and compare this with the musculature of

18 the semi-terrestrial rhesus macaques (*Macaca mulatta*). Anatomical data from previous dissections on

19 knuckle-walking bonobos (*Pan paniscus*) and bipedal humans (*Homo sapiens*) are also included to

20 further integrate the analyses in the scope of catarrhine hand adaptation. This study indicates that the

21 overall configuration of the arm and hand musculature of these primates is very similar but there are

22 some apparent differences in relative size which can be linked to differences in forelimb function and

23 which might be related to their specific locomotor behavior. In macaques, there is a large development

24 of wrist deviators, wrist and digital flexors, and *m. triceps brachii*, as these muscles are important during

25 the different phases of palmi- and digitigrade quadrupedal walking to stabilize the wrist and elbow. In

26 macaques, the *m. flexor carpi ulnaris* is the most important contributor to the total force-generating

27 capacity of the wrist flexors and deviators, and is needed to counteract the adducting torque at the elbow

28 joint during quadrupedal walking. Gibbons show a relatively high force-generating capacity in their

29 forearm rotators, wrist and digital flexors, which are important muscles in brachiation to actively

30 regulate forward movement of the body. The results also stress the importance of the digital flexors in

31 bonobos, during climbing and clambering, and in humans, which is likely linked to our advanced

32 manipulation skills.

33

34 Keywords: primates, anatomy, hylobatids, macaques, locomotion, adaptation

Introduction

Primates live in diverse environments and, as a consequence, have an equally diverse locomotor repertoire (Fleagle, Janson and Reed, 1999). As the primate hand interacts with the superstrate and/or substrate during locomotion, its morphology will most likely reflect differences in behaviour (Kikuchi, Takemoto and Kuraoka, 2012). Therefore, it is expected that the primate hand is functionally adapted to its specific use during locomotion. Several studies have indeed shown a relation between locomotion and forelimb muscle properties in different primate taxa. Japanese macaques (*Macaca fuscata*) exhibit large wrist and digital flexor muscles, possibly as an adaptation for weight bearing during quadrupedal locomotion and forceful grasping of arboreal supports (Ogihara and Oishi, 2012), while the highly arboreal orangutans exhibit elbow flexors with a high potential for force production and forearm muscles that allow a large range of wrist mobility (Oishi, Ogihara, Endo, *et al.*, 2008). Capuchin monkeys show climbing and suspensory behaviour similar to that of chimpanzees, and their deep wrist and digital flexor and extensor muscles show high similarities, suggesting a possible link between locomotor behaviour and forearm musculature (Ogihara, Kunai and Nakatsukasa, 2005; Aversi-Ferreira, Maior, Carneiro-e-Silva, *et al.*, 2011). According to Leischner et al. (2018), arboreal primates have forearm muscles with significantly longer fascicle lengths compared to terrestrial primates, suggesting that arboreal primates are adapted for greater speed and/or flexibility in the trees (Leischner, Crouch, Allen, *et al.*, 2018). Similar results were found by Anapol and Gray (2003), as fiber architecture of the intrinsic shoulder and arm muscles of the semi-terrestrial vervets is largely suited for higher velocity when running on the ground, while the fiber architecture in red-tailed guenons implies passive storage of elastic strain energy for exploitation of the forest canopy (Anapol and Gray, 2003).

In contrast, in an earlier study on great ape forelimb musculature (Myatt, Crompton, Payne-Davis, *et al.*, 2012), we found no large differences in muscle architecture between orangutans, chimpanzees, bonobos and gorillas despite marked differences in locomotor repertoire. This made us conclude that a shared evolutionary origin might lead to an overall consistency in muscle architecture. When studying functional adaption in the primate forelimb it is therefore important to take phylogeny into account.

62   For this study, we selected two primate taxa with a different phylogenetic position (belonging to a

63   different family) and a contrasting locomotor behaviour, namely the semi-terrestrial rhesus macaques

64   (Fam. *Cercopithecidea, Macaca mulatta*) and the highly arboreal hylobatids (Fam. *Hylobatidae*, six

65   different species, further referred to as "gibbons"). The aim of the study is to evaluate if anatomical

66   adaptations to locomotor behaviour can be found in their forelimb musculature. The paper provides a

67   full quantification of the gibbon and macaque forelimb muscle architecture and is a sequel of a

68   descriptive paper studying the forelimb musculature of the same primate species (Vanhoof, van

69   Leeuwen and Vereecke, 2020).

70

71   Macaques are a primarily terrestrial genus, yet different macaque species display a different degree of

72   terrestriality (Rodman, 1979; Kikuchi, 2004). The locomotor repertoire of macaques includes

73   quadrupedal walking, running, climbing and leaping, with quadrupedalism being the dominant

74   locomotor behaviour during travel (Wells and Turnquist, 2001). Hand postures are distinct between

75   macaque species, with rhesus macaques mostly adopting a digitigrade posture (i.e. walking on the

76   palmar side of the digits with the metacarpals elevated off the ground) when walking quadrupedally at

77   slow speeds (Tuttle, 1969; Hayama, Chatani and Nakatsukasa, 1994; Richmond, 2001; Schmitt, 2003;

78   Patel and Carlson, 2007; Patel, 2009; Patel and Polk, 2010; Zeininger, Shapiro and Raichlen, 2017),

79   while Japanese macaques typically adopt a palmigrade posture (i.e. palm of the hand also makes contact

80   with the ground) (Higurashi, Goto and Kumakura, 2018). Nevertheless, rhesus macaques also retain

81   enough mobility at the wrist to use palmigrade postures on arboreal supports, uneven substrates and

82   when walking at high speeds (Patel, 2009). Although macaques are mostly terrestrial, they also engage

83   in arboreal locomotion, using climbing and quadrupedalism (Prime and Ford, 2016). On branches with

84   a large diameter, quadrupedalism is similar to that on the ground. If the diameter of the support

85   decreases, the forelimb joints become more flexed and the hands grasp the support (Hayama, Chatani

86   and Nakatsukasa, 1994; Dunbar and Badam, 1998; Roy, Paulignan, Farnè, *et al.*, 2000; Wells and

87   Turnquist, 2001).

88

89   In contrast to macaques, gibbons navigate through the forest canopy primarily by arm-swinging or

90   brachiation (Tocheri, Orr, Jacofsky, *et al.*, 2008; Michilsens, Vereecke, D'Août, *et al.*, 2010; Rein,

91   Harvati and Harrison, 2015; Reichard, Barelli, Hirai, *et al.*, 2016; Orr, 2017). During brachiation, they

92   can use a highly specialized form of brachiation that includes a true flight phase between each contact

93   with a handhold, called ricochetal brachiation (Tuttle, 1969; Fleagle, 1976; Turnquist, Schmitt, Rose, *et*

94   *al.*, 1999; Chang, Bertram and Lee, 2000; Usherwood, Larson and Bertram, 2003; Prime and Ford, 2016;

95   Reichard, Barelli, Hirai, *et al.*, 2016). As an adaptation for brachiation, gibbons possess specialized

96   morphological traits, including long arms, slender hook-like hands with extremely elongated fingers, a

97   unique ball-and-socket wrist joint, and specific muscle characteristics (e.g. powerful elbow flexors)

98   (Susman, Jungers and Stern, 1982; Marzke, 2009; Michilsens, Vereecke, D'août, *et al.*, 2009;

99   Michilsens, Vereecke, D'Août, *et al.*, 2010; Almécija, Smaers and Jungers, 2015; Bartlett, Light and

100   Brockelman, 2016; Reichard, Barelli, Hirai, *et al.*, 2016). However, gibbons are not only skilled

101   brachiators, they are also able to use a wide variety of other locomotor modes during arboreal travel,

102   such as bipedalism, quadrupedalism, leaping, and vertical climbing (Fleagle, 1976; Vereecke, D'Août

103   and Aerts, 2006; Channon, Günther, Crompton, *et al.*, 2009a; Preuschoft, Schönwasser and Witzel,

104   2016). Within the hylobatid family, there are also some differences in locomotor behaviour, with white-

105   handed gibbons (*Hylobates lar*) using more leaping and rapid, ricochetal brachiation during travel

106   compared to siamangs (genus *Symphalangus*) who use more climbing and brachiation is slower and

107   ricochetal brachiation is rare (Fleagle, 1976).

108

109   Macaques and gibbons use their hands not only in locomotion but also in manipulation, for example

110   during grooming and foraging. Gibbon hands have a deep cleft separating the thumb from the index

111   finger, allowing their relatively short thumb to be widely opposable and enabling grasping large objects

112   (Prime and Ford, 2016). Compared to gibbons, the macaque hand is more "human-like", with short

113   fingers and a relatively long opposable thumb which allows high dexterity and even pad-to-pad gripping

114   (Moyà-Solà, Köhler and Rook, 1999; Marzke, 2013; Kivell, 2015), although pad-to-side gripping is

115   more commonly used (Pouydebat, Gorce, Coppens, *et al.*, 2009; Feix, Kivell, Pouydebat, *et al.*, 2015).

116   Despite having an opposable thumb, and although captive macaques and gibbons have been observed

117   using tools (Tuttle, 1975; Parks and Novak, 1993; Cunningham, Anderson and Mootnick, 2006; Prime

118   and Ford, 2016), both wild gibbons and rhesus macaques have not been observed to use complex

119   manipulative tasks in daily life ((Tomasello and Call, 1997; Santos, Miller and Hauser, 2003; Prime and

120   Ford, 2016), but note that tool use has been observed for long-tailed macaques (*Macaca fascicularis*)

121   (Gumert, Kluck and Malaivijitnond, 2009)). Even though the gibbon and macaque hand might represent

122   a compromise between locomotor and manipulation functions (Higurashi, Goto and Kumakura, 2018),

123   the high compressive and tensile loads involved in locomotion are expected to have the largest effect on

124   hand morphology (Marzke, 1997; Lemelin and Schmitt, 1998; Richmond, 2001; Carlson, Doran-

125   Sheehy, Hunt, *et al.*, 2006; Kikuchi and Hamada, 2009; Orr, 2017; Dunmore, 2019). We therefore expect

126   that the differences in locomotor behaviour between gibbons and macaques will lead to differences in

127   upper arm, forearm and hand musculature. There are very few studies about the musculature of the

128   macaque and gibbon forelimb, and most studies use small datasets or report results based on only one

129   primate taxon (Chan and Moran, 2006; Michilsens, Vereecke, D'août, *et al.*, 2009; Ogihara, Makishima,

130   Aoi, *et al.*, 2009). In this paper, newly collected gibbon data including the intrinsic hand muscles is

131   added to the dataset of Michilsens et al. (2009) and compared to newly collected macaque data, as well

132   as to previously published data of bonobos and humans (Michilsens, Vereecke, D'août, *et al.*, 2009; van

133   Leeuwen, Vanhoof, Kerkhof, *et al.*, 2018).

134

135   We hypothesize that gibbons will have relatively slender extrinsic hand muscles compared to macaques

136   (i.e. long fascicle lengths), allowing fast contraction and a wide range of motion. In contrast, we expect

137   rhesus macaques to have more bulky extrinsic arm muscles (high physiological cross-sectional area

138   (PCSA) and short fascicle lengths) to generate large propulsive forces with a more restricted range of

139   motion, as needed in quadrupedalism. Secondly, as the wrist and digital flexors of both gibbons and

140   macaques are continuously active during brachiation and terrestrial digitigrady (Fleagle, 1974; Swartz,

141   Bertram and Biewener, 1989; Bertram, 2004; Courtine, Roy, Hodgson, *et al.*, 2005; Michilsens, D'Août

142   and Aerts, 2011; Patel, Larson and Stern, 2012), we expect that both primates will have a larger

143   proportion of wrist and digital flexors compared to wrist and digital extensors. Third, due to the

144   importance of rotation during brachiation in gibbons, we hypothesize that the forearm rotators will have

145 a larger PCSA in gibbons than in macaques. Fourth, we expect that the *m. triceps brachii* will be better

146 developed in macaques than in gibbons as it is important for torque production at the elbow joint during

147 quadrupedal walking (Manter, 1938), while in gibbons, we expect that the *m. biceps brachii* will be

148 stronger developed than in macaques given its important function as elbow flexor during brachiation

149 (Jungers and Stern, 1980; Michilsens, Vereecke, D'août, *et al.*, 2009). Finally, we hypothesize that the

150 flexor muscles of gibbons will have relatively longer tendons compared to those of macaques. One of

151 the crucial correlates with brachiation appears to lie in flexor tendonization (Corruccini, 1978) (i.e.

152 tendon length relative to muscle-tendon-unit length) as these relatively longer tendons can act as elastic

153 springs, facilitating storage and release of elastic strain energy during brachiation (Alexander, 2002;

154 Usherwood, Larson and Bertram, 2003; Michilsens, Vereecke, D'août, *et al.*, 2009). Given the higher

155 amount of brachiation in white-handed gibbons compared to siamangs, we also predict relatively longer

156 tendons in the flexor muscles in the genus *Hylobates* compared to the genus *Symphalangus*.

Methods

Specimen collection

The data presented in this study are based on a detailed dissection of upper arm, forearm and hand of eight hylobatid specimens, belonging to six species within the family Hylobatidae (*Hylobates lar, Hylobates pileatus, Hylobates moloch, Nomascus leucogenys, Nomascus concolor, Symphalangus syndactylus*), further referred to as 'gibbons', and seven rhesus macaque specimens (*Macaca mulatta,* Fam. Cercopithecidae), further referred to as 'macaques'. Both gibbons and macaques have a different phylogenetic position relative to modern humans and were selected because of their distinct locomotor behaviour. The gibbon specimens were obtained via collaborations with different European Zoos and institutes: the National Museum of Scotland (Edinburgh, UK), Ghent University (campus Merelbeke, Belgium), the Zoological and Botanical Park of Mulhouse (France), Pakawi Park (Belgium). The rhesus macaque specimens were obtained via collaboration with Ghent University (campus Merelbeke, Belgium). Both the macaque and gibbon specimens were housed in large enclosures and were still able to adopt their preferred locomotor behaviour. All specimens were collected opportunistically, no animals were sacrificed for this study. The raw data of the forearm musculature of ten gibbon specimens collected in the scope of an earlier publication (Michilsens, Vereecke, D'août, *et al.*, 2009) are also included in the analyses as these were collected using the same methodology. The entire gibbon dataset (n=18) and macaque dataset (n=7) is compared with the anatomical data of five bonobos (*Pan paniscus*) and one human cadaver (*Homo sapiens*) obtained in a previous study (van Leeuwen, Vanhoof, Kerkhof, *et al.*, 2018). The specimen details are provided in **Table 1**.

Dissection procedure

We performed a detailed dissection of the forelimb and hand of the primate specimens, using the procedure described in Vanhoof et al. (Vanhoof, van Leeuwen and Vereecke, 2020). All specimens were stored at -18 degrees Celsius and were thawed at room temperature 24h before starting the dissection. To quantify muscle architecture, the following parameters were measured for each muscle (Lieber and Fridén, 2000): (1) muscle mass (m); (2) muscle volume (V); (3) muscle-tendon-unit length (MTU), measured from the most proximal muscle fibers or tendon to the most distal muscle fibers or tendon; (4)

184 muscle fascicle length (FL), which is the approximate length of the muscle fibers; (6) external tendon

185 length (ETL), the distance from the most distal muscle fibres to the end of the tendon, and (7) internal

186 tendon length (ITL), the part of the tendon enveloped by muscle fibers. Length measurements are taken

187 to the nearest 0.1 mm with a digital calliper (Mitutoyo, UK, accurate to 0.01 mm) and muscle volume

188 is determined to the nearest 0.1 ml by submersion in physiological saline solution (0.9% NaCl). Muscles

189 are cut lengthwise along the tendon to determine muscle fascicle length and tendon length. The data

190 provided for fascicle length are average values of at least three measurements taken on different places

191 along the muscle belly. FL was measured as this value is needed to calculate physiological cross-

192 sectional area (PCSA; see below). Moreover, FL can give us information about muscle function (Lieber

193 and Fridén, 2000): long fascicle lengths allow fast contraction and large excursions at low force, while

194 shorter fascicle lengths in a pennate organization can generate large propulsive forces with small

195 excursion.

196 *Data analysis*

197 Physiological cross-sectional area (PCSA) of a muscle is calculated using equation [1].

198 $$PCSA = \frac{muscle\ mass}{muscle\ fascicle\ length * muscle\ density}$$ [1]

199 PCSA is related to the force-generating capacity of a muscle and is therefore a more functionally relevant

200 parameter to report than muscle mass (Lieber and Fridén, 2000). We chose to omit pennation angle (PA,

201 angle between a fascicle's orientation and the internal tendon axis (Lee, Li, Sohail, *et al.*, 2015)) from

202 the PCSA equation as (1) there were difficulties in obtaining accurate PA measurements during the

203 dissections, (2) the in vitro measurements are not fully representative of the PA in vivo given that PA

204 changes during muscle contraction, and (3) the PA of most muscles ranges between 0 and 30 degrees,

205 the cosine of which ranges between 1 and 0.87, having only a minor influence on PCSA calculation

206 (Vereecke, D'Août, Payne, *et al.*, 2005; Payne, Crompton, Isler, *et al.*, 2006; van Leeuwen, Vanhoof,

207 Kerkhof, *et al.*, 2018). If muscles consisted of multiple muscle bellies that were easily separable (e.g.

208 *m. triceps brachii*, *m. flexor digitorum superficialis*), the PCSA was calculated as the sum of the PCSA

209 of the separate muscle bellies.

210 For the small intrinsic hand muscles we were not able to accurately determine the muscle volume using

211 the submersion method. Therefore, we calculated the muscle density only for the extrinsic muscles of

212 all specimens using equation [2].

213 Muscle density $= \frac{muscle\ belly\ mass}{muscle\ volume}$ [2]

214 For both gibbons and macaques, the average muscle density is 0.0011 g/mm^3 (s.d. < 0.0001 g/mm^3),

215 which is almost equal to the density defined for human muscles (0.00106 g/mm^3) (Ward and Lieber,

216 2005). The density value of 0.0011 g/mm^3 is used in the calculation of the PCSA for all muscles in this

217 study.

218 To calculate the relative length of tendons, equation [3] is used.

219 $\%tendonization = \frac{TTL}{MTU}$ [3]

220 with total tendon length (TTL) being the sum of ETL and ITL. This measure allows us to investigate

221 'tendonization' of muscles, and was calculated for the inserting tendons as these are typically most

222 pronounced.

223 To facilitate comparison between gibbons and macaques, we categorized the muscles into functional

224 groups with respect to their main function at the elbow, wrist and fingers (**Table 2**). The *m. biceps*

225 *brachii* and *m. triceps brachii* were only listed as elbow flexor and extensor, respectively, as we did not

226 measure other shoulder muscles. Scaling of the anatomical data was necessary as the primate sample

227 included specimens of different size (ranging from 4.5kg for small white-handed gibbons to adult male

228 siamangs of 12kg). Body mass at time of death was unknown for most specimens, therefore scaling was

229 done using total arm, forearm, or hand muscle mass. The PCSAs of the *m. biceps* and *triceps brachii*,

230 and the rotators were scaled to the total arm PCSA (see **Table 2**). For the forearm muscles, the PCSA

231 of the other functional muscle groups was scaled to the total PCSA of all extrinsic forearm muscles. For

232 the intrinsic hand muscles, the PCSA was scaled to the total PCSA of all intrinsic hand muscles. The FL

233 was scaled to the total forearm muscle mass to one third (FLMM$^{1/3}$) (Channon, Günther, Crompton, *et*

234   *al.*, 2009a). In addition, we calculated a set of dimensionless ratios (i.e. ratio of wrist flexors to wrist

235   extensors, ratio of radial deviators to ulnar deviators, …) that allow comparison of relevant anatomical

236   traits between different-sized animals.

237   *Statistical analysis*

238   For all relevant parameters, an analysis of variance (ANOVA) was used to test for significant differences

239   between the primate groups and Tukey HSD tests were used for pairwise post-hoc comparisons. All

240   statistical analyses were run in R (version 4.0.2), and the significance value was set at 0.05. Within the

241   hylobatids, no significant differences were found for all tested parameters. Therefore, all hylobatids

242   were taken together as one group in the analyses and box plots.

243 **Results**

244 The muscle parameters discussed below are based on the analysis of the newly collected data from the

245 macaque (n=7) and gibbon (n=8) sample, and are supplemented by new analyses of previously published

246 data on the forelimb anatomy of gibbons (n=10) (Michilsens, Vereecke, D'août, *et al.*, 2009), bonobos

247 (n=5) and humans (n=1) (van Leeuwen, Vanhoof, Kerkhof, *et al.*, 2018). The different functional

248 muscles groups and their associated muscles and abbreviations can be found in **Table 2**. Detailed

249 documentation of the raw muscle parameters discussed below is provided in the Supplementary material

250 (**Table S1 and S2**). In the graphical presentation of the results, siamang data are presented using a

251 different symbol than the other gibbons because of their markedly higher size and body weight, and the

252 differences in locomotor behaviour compared to the other hylobatids.

253

254 <u>Characteristics of the upper arm and forearm muscles</u>

255 Below, we present the results on FL, PCSA, and tendonization of the forelimb muscles of the studied

256 specimens. Unless stated otherwise, values given are always group means and standard deviation (s.d.).

257 *Fascicle length*

258 There is no significant difference between macaques, gibbons and bonobos for the scaled FL of the wrist

259 flexors (0.32 vs. 0.51 vs. 0.33), wrist extensors (0.40 vs. 0.48 vs. 0.38), and radioulnar deviators (0.42

260 vs. 0.48 vs. 0.35) (**Fig. 1A-C**). For the rotators there is no significant difference between macaques and

261 gibbons (0.60 vs. 0.74)($p>0.05$) (**Fig. 1D).** In macaques, the scaled FL of the rotators is significantly

262 longer than that of their flexors ($p<0.001$), extensors ($p<0.001$), and deviators ($p<0.01$)(**Fig. 1E**). In

263 gibbons, the scaled FL of the rotators also appears longer than that of the other functional muscle groups,

264 but this difference is not significant ($p>0.05$)(**Fig. 1F**). In bonobos, no significant difference is found

265 between the functional muscle groups ($p>0.05$)(**Fig. 1G**).

266 *Elbow flexors and extensors*

267 The ratio of elbow flexors over elbow extensors is significantly lower in macaques (0.40, s.d.: 0.07)

268 compared to gibbons (1.35, s.d.: 0.35)($p<0.001$)(**Fig. 2A**). We can observe that the *m. triceps brachii*

269 (Tb) has a significantly higher PCSA, as proportion of the total arm PCSA, in macaques (30.7%, s.d.:

270   2.8%) compared to gibbons (15.0%, s.d.: 4.9%) (p<0.001) (**Fig. 2B**), while the *m. biceps brachii* (Bb)

271   is somewhat larger in gibbons (8.9%, s.d.: 2.1%) than in macaques (6.6%, s.d.: 1.0%) (p<0.05) (**Fig.**

272   **2C**).

273   *Wrist and digital flexors and extensors*

274   Both macaques and gibbons have a high ratio of wrist flexors over wrist extensors (3.1 (s.d.: 0.4) and

275   3.7 (s.d.: 0.8), resp.) (p>0.05), yet there is an apparent variability in gibbons (range: 2.0-5.0). The flexor

276   to extensor ratio is only significantly different between gibbons and humans (1.5), with gibbons having

277   a significantly higher flexor to extensor ratio (p<0.05) (**Fig. 3A**). For the relative PCSA of wrist flexors

278   as percentage of the total forearm muscle PCSA, we observe a similar proportion of wrist flexor PCSA

279   in macaques and gibbons (p>0.05)(**Fig. 3B**), accounting for more than half of the forearm muscle PCSA

280   (macaques: 55.0% (s.d.: 2.0%) and gibbons: 56.6% (s.d.: 4.5%)). In contrast, the extensor PCSA only

281   makes up less than 20% of the forearm muscle PCSA (macaques; 18.0% (s.d.: 2.0%), gibbons: 16.5%

282   (s.d.: 3.8%), resp.). Significant differences in relative proportion of wrist flexor PCSA can, however, be

283   observed between the other primate taxa (gibbon-human: p<0.001, gibbon-bonobo: p<0.01, macaque-

284   human: p<0.01, macaque-bonobo: p<0.05) (**Fig. 3B**). When looking at the relative PCSA of different

285   flexors, we also observe some interesting differences between the four taxa. In macaques, the PCSA of

286   the digital flexors makes up 54.0% (s.d.: 3.0%) of the total wrist flexor PCSA, which is significantly

287   lower compared to gibbons (73.4%, s.d.: 7.6% (p<0.001)) and humans (86.1%, p<0.01), but not to

288   bonobos (65.0%, s.d.: 13.9% (p>0.05)). In macaques, the PCSA of the *m. flexor carpi ulnaris* (FCU)

289   makes up on average 27.3% (s.d.: 3.7%) of the total wrist flexor PCSA, which is significantly higher

290   compared to gibbons (9.4%, s.d.: 2.7% (p<0.001)), bonobos (21.0%, s.d.: 3.6% (p<0.05)), and humans

291   (11.4%, p<0.01).

292

293   The ratio of digital flexors over digital extensors is not significantly different between the different

294   primate taxa, with gibbons, macaques, and bonobos having a high ratio (4.9 (s.d.: 1.5), 4.7 (s.d.: 1.2),

295   and 4.5 (s.d.: 1.1), resp.), while the ratio of humans is much smaller (2.2) (**Fig. 3C**). For the PCSA of

296   the digital flexors as proportion of the forearm PCSA, we can observe that the digital flexors have a

297 significantly higher relative PCSA in gibbons (43.7%, s.d.: 5.5%) compared to macaques (29.6%, s.d:

298 1.4%; p<0.001) and bonobos (31.2%, s.d.: 8.0%; p<0.01), with macaques, bonobos, and humans

299 showing a similar proportion of digital flexors (**Fig. 3D**). The PCSA of the digital extensors accounts

300 for on average 54.3% (s.d.: 9.9%) of the total extensor PCSA in gibbons, which is comparable to humans

301 (56.3%), and is significantly different from macaques (36.3%, s.d.: 4.1%; p<0.001) and bonobos (41.4%,

302 s.d.: 8.8%; p<0.05). In macaques and bonobos the PCSA of the *m. extensor carpi radialis longus*

303 (ECRL) and *m. extensor carpi radialis brevis* (ECRB) accounts for more than 40% of the total extensor

304 PCSA (43.4% and 40.6%, resp.), while in gibbons and humans the digital extensors have the largest

305 PCSA of the extensor group (48.8% and 46.3%, resp.).

306 *Wrist deviators*

307 The wrist deviators have a significantly larger PCSA in macaques (38.3%, s.d.: 3.3%) compared to

308 gibbons (25.4%, s.d.: 5.2%; p<0.001). The wrist deviator PCSA of bonobos (30.7%, s.d.: 4.8%) and

309 humans (32.9%) falls in between the macaque and gibbon values, but only the bonobos are significantly

310 different from macaques (p<0.05) (**Fig. 4A**). In macaques, the FCU is the most important contributor to

311 the total wrist deviator PCSA (38.9%) and has a much higher PCSA compared to the *m. flexor carpi*

312 *radialis* (FCR) (17.3%) (p<0.001). In gibbons and bonobos, however, the PCSA of FCU (21.4% and

313 31.7%, resp.) and FCR (26.1% and 26.3, resp.) are very similar, together accounting for more than half

314 of the total wrist deviator PCSA. Humans are notably different in this aspect, as the extensors (ECU

315 (23.9%), ECRL (22.0%), ECRB (22.0%)) make up the largest proportion of the wrist deviator PCSA.

316

317 The ratio of radial deviators (RD) over ulnar deviators (UD) is 1.0 in macaques, with radial and ulnar

318 deviators having a similar PCSA relative to the total forearm muscle PCSA (19.0% (sd.: 1.6%) and

319 19.3% (s.d.: 2.3%), resp.). Gibbons, on the other hand, have a high RD/UD ratio of on average 2.1 (s.d.:

320 0.61), which is significantly higher than the ratio observed in macaques (p<0.001) and bonobos (1.3)

321 (p<0.05) (**Fig. 4B**). This is mainly due to the small PCSA of the ulnar deviators relative to total forearm

322 PCSA in gibbons (10.4%, s.d.: 5.7%), whereas the radial deviators (16.6%, s.d.: 2.4%) have a similar

323 PCSA as seen in macaques. In humans, the ratio of radial deviators over ulnar deviators is 1.6 but this

324 is not significantly different from that of macaques, gibbons or bonobos.

325 *Forearm rotators*

326 The proportion of rotator PCSA is higher in gibbons (23.2%, s.d.: 2.8%) compared to macaques (17.7%,

327 s.d.: 1.8%), and this difference is highly significant (p<0.01) (**Fig. 5**). In both macaques and gibbons,

328 the Bb is the most important contributor to total rotator PCSA (37% and 41%, respectively), while the

329 *m. bracioradialis* (BR) only accounts for 10% of the total rotator PCSA. In both primates, supination is

330 the dominant movement as the supinator muscles account for more than 65% of the total rotator PCSA.

331 *Tendonization*

332 The relative length of the flexor tendons ('tendonization') is significantly longer in gibbons (80.1%, s.d.:

333 7.7%) compared to that of bonobos (68.8%, s.d.: 7.3%; p<0.05), while there is no significant difference

334 between gibbons and macaques (70.8%, s.d.: 4.4%; p>0.05) or humans (65.0%; p>0.05) (**Fig. 6A**).

335 There is also no significant difference between the relative length of the tendons of white-haned gibbons

336 (*Hylobates lar*) compared to siamangs (*Symphalangus syndactylus*) (p>0.05) (**Fig. 6B**).

337

338 Characteristics of the intrinsic hand muscles

339 The proportion of intrinsic hand muscle PCSA relative to total forearm muscle PCSA is remarkably

340 similar between macaques (14.7%, s.d.: 3.2%), gibbons (14.5%, s.d.: 4.2%), humans (14.5%), and

341 bonobos (18.4%, s.d.: 4.6%)(p>0.05). The composition of the intrinsic hand muscles is similar in

342 gibbons and macaques, with a dominant development of the intermediate hand muscles (~59% and

343 ~51% of hand muscle PCSA, respectively), while the thenar PCSA takes up approximately 30% of the

344 total intrinsics PCSA, and the hypothenar muscle amounting to only 10.0% and 17.5% of the hand

345 muscle PCSA. In bonobos, the intermediate hand muscles take up a slightly larger proportion of the total

346 intrinsics PCSA (66.1%, s.d.: 4.6%), although this is not significantly different compared to the other

347 primate groups, while in humans the thenar PCSA is significantly more prominent (46.7%) compared

348 to bonobos (p<0.05)(**Fig. 7**).

349 **Discussion**

350 In this study, the forelimb musculature of macaques and gibbons is compared based on a detailed

351 quantification of their forelimb muscle architecture. Anatomical data from previous dissections of

352 different gibbon species (Michilsens, Vereecke, D'août, *et al.*, 2009) are included to increase the sample

353 size, and these data are compared with anatomical data of bonobos and humans (van Leeuwen, Vanhoof,

354 Kerkhof, *et al.*, 2018) to allow a broader functional comparison of the forelimb musculature. The results

355 are summarized in **Figure 8**.

356 *Fascicle length*

357 Due to the different locomotor behaviour of gibbons and macaques, we hypothesized that gibbons would

358 have relatively slender forearm muscles, with a relatively long FL and high tendonization, compared to

359 macaques, for which we expected more bulky forearm muscles, with shorter FL and a higher PCSA.

360 However, we found no significant difference in FL when comparing the functional muscle groups (i.e.,

361 the wrist flexors, wrist extensors, radioulnar deviators, and rotators) between both primates. In contrast,

362 Leischner et al. (2018) found a difference in relative fascicle lengths between terrestrial and arboreal

363 primates (Leischner, Crouch, Allen, *et al.*, 2018). This might be explained in the context of inertia, as

364 we only look at distal forelimb muscles. Forearms that are too muscular would be energetically

365 inefficient for quadrupeds like macaques. Myatt et al. also showed that FL were generally longer in the

366 proximal muscles of the forelimb in great apes (Myatt, Crompton, Payne-Davis, *et al.*, 2012), so maybe

367 larger differences can be found in the FL of the macaque and gibbon upper arm musculature. Another

368 reason for not finding a difference between the FL of gibbons and macaques is that we looked at

369 functional muscle groups, not at differences between individual muscles. When individual muscles are

370 compared, we find that gibbons do have significantly longer FL in the *m. biceps brachii* (Bb), *m. flexor*

371 *digitorum superficialis* (FDS), *m. supinator* (SUP), and *m. palmaris longus* (PL) compared to macaques,

372 while macaques show longer FL only for the *m. brachioradialis* (BR) and *m. extensor carpi radialis*

373 *longus* (ECRL). The lack of difference in the other muscles might have singled out a difference at level

374 of the muscle groups. When looking at the different primate taxa, we can see that in macaques the rotator

375 FL is significantly different from the other functional muscles groups, while this is not observed for

376 gibbons, bonobos, and humans. The long FL of the rotators in macaques might be important for running

377 at high speeds on the ground, while the long FL of the different individual muscles in gibbons might

378 enable high speed and flexibility in the trees during brachiation (Anapol and Gray, 2003; Leischner,

379 Crouch, Allen, *et al.*, 2018). Nevertheless, the functional interpretation of these results remains difficult.

380 *Elbow flexors and extensors*

381 The ratio of elbow flexors over extensors is significantly lower in macaques compared to gibbons due

382 to the significantly larger PCSA of the *m. triceps brachii* (TB) in macaques compared to gibbons. This

383 can be understood from the quadrupedal gait mechanics, as the TB is recruted during the first three-

384 quarters of a step to produce the torque at the elbow joint (Manter, 1938; Demes, Stern, Hausman, *et*

385 *al.*, 1998). As predicted, the *m. biceps brachii* PCSA is higher in gibbons compared to macaques, which

386 is likely related to its important function as elbow flexor during brachiation (Michilsens, Vereecke,

387 D'août, *et al.*, 2009; Reichard, Barelli, Hirai, *et al.*, 2016). Moreover, in gibbons, the origin of the short

388 head of the Bb attaches on the lesser tubercle of the humerus and, as is it mono-articular, it can be fully

389 recruited for elbow flexion which might be an adaptation to brachiation during which the arms are used

390 to hoist the body by extending the arm at the shoulder and flexing it at the elbow (Michilsens, Vereecke,

391 D'août, *et al.*, 2009). Note that the PCSA value for the elbow extensors of three gibbon specimens is

392 likely a slight underestimation as the contribution of the DET, which is also an elbow extensor and

393 inserts onto the oleocranon in these three specimens, is not accounted for.

394 *Wrist and digital flexors and extensors*

395 Both gibbons and macaques show a proportion of wrist flexor PCSA that is approximately three times

396 larger than the wrist extensor PCSA, and a proportion of digital flexor PCSA that is more than four

397 times larger than the digital extensor PCSA. Such configuration is also seen in bonobos, while in modern

398 humans the extensors are more prominent and these ratios are much smaller (wrist flexor/extensor: 1.45;

399 digital flexor/extensor: 2.22). The wrist flexors PCSA makes up more than half of the forearm muscle

400 PCSA in macaques and gibbons, and this proportion is significantly higher compared to bonobos and

401 humans. The relatively large flexor PCSA in macaques, combined with a small FL gives a high force-

402 generating capacity which can be related to their locomotor behaviour as the wrist and digital flexors

403   are continously active during terrestrial digitigrady (Courtine, Roy, Hodgson, *et al.*, 2005; Patel, Larson

404   and Stern, 2012). In gibbons, the flexors have relatively longer FLs and together with the high flexor

405   PCSA this results in a capacity to produce high power, whereby these muscles are capable of producing

406   high levels of work over a wider range of motion. Being able to produce high power is probably

407   necessary to counteract the gravitational forces during brachiation (Swartz, Bertram and Biewener,

408   1989; Bertram, 2004; Michilsens, D'Août and Aerts, 2011), while moving the limbs over a wide range

409   of motion during the rapid locomotion of gibbons during brachiation likely has advantages for reaching

410   a branch and avoiding a fall (Oishi, Ogihara, Endo, *et al.*, 2008; Channon, Günther, Crompton, *et al.*,

411   2009b; Channon, Crompton, Günther, *et al.*, 2010). The relatively lower PCSA of the wrist flexors in

412   bonobos and humans compared to macaques and gibbons might indicate that bonobos and humans rely

413   less on wrist flexion, although the higher flexor to extensor ratio in bonobos compared to humans

414   indicates that wrist and digital flexion is more important than extension in bonobos compared to humans.

415   We suggest that the wrist and digital flexors might be important in bonobos during climbing and

416   clambering, but less so during knuckle-walking as the wrist and digital flexors are not required to

417   maintain a stable knuckle-walking stance pose (pers. obs., unpublished data) (Simpson, Latimer and

418   Lovejoy, 2018). In humans, there are high wrist and digital extensor requirements during complex

419   activities such as knapping, dart-throwing, and hammering (Wolfe, Crisco, Orr, *et al.*, 2006; Williams,

420   Gordon and Richmond, 2010).

421

422   When looking at each wrist flexor, in macaques the FCU is the most important contributor to total wrist

423   flexor PCSA accounting for on average 27%, while in gibbons the PCSA of the digital flexors makes

424   up on average 73% of the total wrist flexor PCSA, a configuration also seen in modern humans (86%).

425   In bonobos, the digital flexors are also the most important flexors, although the relative proportion (59%)

426   is smaller compared to gibbons and humans. These results stress the importance of digital flexors in the

427   locomotor behavior of gibbons (during brachiation) and bonobos (climbing and clambering), whereas

428   their importance in humans is likely linked to our advanced manipulation skills, for example during tool

429   making and tool use (Marzke, 1997; Wolfe, Crisco, Orr, *et al.*, 2006; Kivell, 2015; Skinner, Stephens,

430   Tsegai, *et al.*, 2015). In macaques, the FCU is the not only the most important flexor, but also the most

431 important contributor to the total deviator PCSA. Demes et al. (1998) observed that rhesus macaques

432 closely align their forearms with the substrate reaction force vector in the sagittal plane, especially

433 around the midstance when the reaction forces are high. Their elbows are positioned lateral to the point

434 of substrate contact, and the substrate reaction force vector is inclined medially. As the force vector

435 passes medial to the forearm, it produces medial bending (i.e. in the frontal plane) of the ulna. This

436 bending direction is somewhat counterintuitive as other in vivo studies report anteroposterior bending

437 (i.e. in the sagittal plane) (Demes, Stern, Hausman, *et al.*, 1998). The medial bending of the ulna causes

438 an adducting torque at the elbow joint, which causes stress on the lateral wrist. This stress, and therefore

439 the risk of collapsing, is likely counteracted by the FCU. The action of the FCU is enhanced by the

440 orientation and size of the pisiform, giving the FCU an optimal lever arm (Sarmiento, 1988).

441 *Wrist deviators*

442 The proportion of wrist deviators is significantly higher in macaques compared to gibbons. The

443 combination of high PCSA and small FL, enables the deviators of macaques to produce high levels of

444 force to counteract the stress on the wrist during quadrupedal walking (see above). In gibbons and

445 bonobos, when looking at the wrist deviators, the proportions of the FCU and FCR are very similar,

446 while in modern humans the ECU, ECRL, and ECRB make up the largest proportion of the deviator

447 PCSA. In both gibbons and humans, the radial deviators have a relatively higher force-generating

448 capacity compared to the ulnar deviators (contrary to the situation in macaques). In gibbons, during

449 brachiation considerable radial and ulnar deviation of the wrist – hence the similar development of the

450 FCR and FCU – takes place at the beginning and end of the support phase, respectively (Sarmiento,

451 1988), but the relatively larger size of the radial deviators suggests that these are more actively recruited

452 during brachiation. In humans, radial and ulnar deviation of the wrist is important during tool making

453 and tool use (Wolfe, Crisco, Orr, *et al.*, 2006; Williams, Gordon and Richmond, 2010; Rainbow, Wolff,

454 Crisco, *et al.*, 2016), again with a dominance of radial deviators (Vanswearingen, 1983). The fact that

455 the extensors make up the largest proportion of the deviator PCSA might be an adaptation for the so-

456 called dart-throw-motion (i.e. oblique motion of the wrist, from radial extension to ulnar flexion), which

457 is used during most activities of daily living (Wolfe, Crisco, Orr, *et al.*, 2006; Edirisinghe, Troupis,

458   Patel, *et al.*, 2014). However, note that the PCSA value for the wrist deviators of gibbons, macaques,

459   and bonobos is likely a slight underestimation as the contribution of *m. abductor pollicis longus* (APL

460   II) is not accounted for. Because of the insertion of the APL II on the prepollex in macaques and the

461   trapezium in gibbons, the APL II functions as radial deviator of the wrist and has no function on the

462   thumb (Vanhoof, van Leeuwen and Vereecke, 2020).

463

464   *Forearm rotators*

465   The proportion of forearm rotator PCSA is significantly higher in gibbons compared to macaques, and

466   in combination with the relatively long FL of the rotators this can be linked to the importance of powerful

467   forearm rotation during brachiation in gibbons. During a complete swing cycle of brachiation, the body

468   rotates through approximately 180° about a vertical axis (Fleagle, 1974). In brachiation, gibbons try to

469   maximize their forward momentum, and the center of mass should travel in the same vertical plane as

470   the center of rotation. Lateral motion of the centre of mass between handholds is limited by extensive

471   rotation at the wrist, elbow, and shoulder, necessitating strong forearm rotators (Fleagle, 1974;

472   Michilsens, D'Août and Aerts, 2011). In macaques, the rotators show a combination of long FL and low

473   PCSA, probably to allow a wide range of motion for shifting the weight of the body to help change the

474   direction of travel and maintain balance on a narrow branch during arboreal locomotion (Larson and

475   Stern, 2006).

476   *Flexor tendonization*

477   The relative tendon length of the flexors appears on average somewhat higher in gibbons compared to

478   macaques (80.1% and 70.8%, respectively), but this difference is not significant. In bonobos, the relative

479   tendon length is 68.8% which is similar to macaques and significantly lower than that observed in

480   gibbons. The relatively high 'tendonization' in the wrist and digital flexors of gibbons might indicate

481   that elastic storage is indeed important during brachiation (Corruccini, 1978), and probably more so than

482   in macaque and bonobo locomotion. Humans have the lowest flexor tendonization (65.0%), which could

483   be related to absence of a locomotor function of arms and hands. In addition, there is no significant

484   difference between siamangs and other gibbons, despite the lower percentage of brachiation in the

485   locomotor repertoire of siamangs. Also in the other functional parameters of forearm and hand

486   musculature, we found no differences between siamangs and the other gibbon genera.

487   *Intrinsic hand muscles*

488   Another example that may reflect differences in locomotion is found in the intrinsic hand muscles. The

489   intermediate hand muscles are relatively more developed in macaques, gibbons, and bonobos compared

490   to humans, while in humans the thenar muscles account for almost 50% of the total intrinsic hand PCSA,

491   which is significantly more than in bonobos. The prominence of the thenar muscles in the human hand

492   is not very surprising given its high dexterity and the importance of the thumb in tool making and tool

493   use (i.e. power squeeze grips) (Kivell, 2015). The relatively strong development of the intermediate

494   hand muscles in the studied nonhuman primates could be explained in the context of locomotion. It

495   might be linked to the importance of grasping in an arboreal milieu, either for brachiation as seen in

496   gibbons or for vertical climbing as seen in bonobos. The intermediate hand muscles might be equally

497   important for palmi- or digitigrade macaques as they could aid in efficient positioning of the hand and

498   fingers on uneven substrates.

499

500   *Critical considerations*

501   Our findings are based on a detailed dissection of 18 gibbon and seven macaque specimens. Although

502   this is a limited sample size compared to human studies, it forms a unique sample and a valuable addition

503   to the scarce information on forelimb muscle architecture in non-human primates. Inherent to working

504   with primate cadavers is the lack of an equal distribution across species, sexes or ages, and most

505   importantly, sampling from captivity. Muscle is dynamic tissue, so captivity will influence muscle

506   dimensions and the values reported in this study might deviate from that of wild populations. However,

507   both the macaque and gibbon specimens were housed in large enclosures and were still able to adopt

508   their preferred locomotor behaviour. While this certainly deviates from their locomotor behaviour in the

509   wild, the differences in locomotion between gibbons and macaques persist in captivity. It should also be

510   noted that by comparing two primate groups we are not able to discern between differences due to

511   functional adaptation or differences due to genetic distance. Differences on species-level might be more

512   difficult to capture, which – together with low sample size – could be the reason for the lack of

513   differences in muscle dimensions between siamangs and other gibbon species. Also, sampling from a

514   broader range of primate taxa is needed to further substantiate the functional adaptations in the forelimb.

515 Note that in addition to the quantification of the muscle architecture, information on fibre type,

516 sarcomere length, and muscle moment arms are important for a full interpretation of muscle function.

517 Finally, scaling of fascicle length was done using total forelimb muscle mass to the one-third, as body

518 mass was not available for every specimen. However, this does not appear to have an effect on the results

519 as we also did the same analysis with unscaled data, given that the body mass of gibbons (ranging from

520 4kg to 12kg) and macaques (ranging from 5kg to 8kg) is very similar, and we obtained comparable

521 significance levels.

Conclusions

This study identifies important features of the forelimb and hand musculature in macaques and gibbons based on the detailed dissections of six gibbon species (*Hylobates lar, Hylobates pileatus, Hylobates moloch, Nomascus leucogenys, Nomascus concolor, Symphalangus syndactylus*) and one macaque species (*Macaca mulatta*), in combination with complete anatomical data from previous dissections of ten gibbons (Michilsens, Vereecke, D'août, *et al.*, 2009), five bonobos (*Pan paniscus*), and one human cadaver (*Homo sapiens*) (van Leeuwen, Vanhoof, Kerkhof, *et al.*, 2018).

Overall, most of the identified differences in forelimb muscle architecture between the primate groups can be linked to their specific locomotor behaviour. In macaques, the wrist deviators, and wrist and digital flexors have a relatively large PCSA and small FL, and thus a high force-generating capacity, as is seen for the *m. triceps brachii*. These muscles are important during the different phases of quadrupedal walking to stabilize wrist and elbow. Gibbons have powerful forearm rotators and wrist and digital flexors, and an elbow flexor with a high force-generating capacity. These muscles are important in brachiation to actively regulate the forward movement of the body. However, given the genetic distance between macaques and gibbons, we cannot be certain that these differences are due to differences in locomotor behaviour and not phylogenetic position. This is challenging to test, but should not go unremarked as only two taxa are being compared, and there is no relative context of the anatomical variation across other arboreal and terrestrial primate taxa.

In a preceding paper (Part I), we provided an extensive description of the extrinsic and intrinsic hand muscles to fully document their configuration and to evaluate if there are specific adaptations in forelimb musculature to locomotor behaviour. This sequel (Part II) provides a full quantification of the forelimb and hand muscle architecture of macaques and gibbons and a comparative analysis between both primate groups. Not only is this research important to obtain a detailed insight in the macaque and gibbon anatomy, but in combination with in vivo research and behavioural studies, it can be translated to complete form-function relationships of the hand and advance current concepts of the evolutionary history of the forearm and hand of modern humans.

558

559 **Author contributions**

560 EEV conceived the study; EEV, MJMV and TvL further designed the study; MJMV and TvL performed

561 the dissections; MJVM and LG set up the statistical protocol and designed the data plots; MJMV, EEV

562 and LG analysed the data; MJMV and EEV wrote the manuscript; all authors reviewed and approved

563 the manuscript.

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788 **Supplementary material**

789 **Table S1** – Anatomical dataset of all gibbon specimens

790 **Table S2** – Anatomical dataset of all macaque specimens

791 **Figure legends**

792 **Fig. 1** – Boxplot of the scaled fascicle length (FL) of the (A) flexors, (B) extensors, (C) deviators, and

793 (D) rotators. Within the hylobatid family, the triangles represent the siamangs. For none of these groups

794 there is a significant difference between macaques, gibbons, and bonobos. (E) In macaques, the scaled

795 FL of the rotators is significantly different from that of their flexors ($p<0.001$), extensors ($p<0.001$), and

796 deviators ($p<0.01$). In gibbons (F) and bonobos (G), the scaled FL of the functional muscle groups are

797 not significantly different from one another ($p>0.05$).

798 **Fig. 2** – (A) Boxplot of the ratio of elbow flexors over elbow extensors is low in macaques compared to

799 gibbons ($p<0.001$). (B,C) Boxplots of the relative PCSA of the biceps and triceps brachii. Within the

800 hylobatid group, the triangles represent the siamangs. (B) the triceps brachii has a significantly higher

801 PCSA in macaques compared to gibbons ($p<0.001$), (C) the biceps brachii has a slightly higher relative

802 PCSA in gibbons compared to macaques ($p<0.05$).

803 **Fig. 3** – Boxplot of the relative size of the flexors in the forearm. Within the hylobatid group, the

804 triangles represent the siamangs. (A) The ratio of flexors over extensors is significantly higher in gibbons

805 compared to humans ($p<0.05$); (B) the relative PCSA of the wrist flexors is a similar in macaques and

806 gibbons ($p>0.05$), while significant differences can be observed between the other primate taxa; (C) the

807 ratio of digital flexors over digital extensors is similar in gibbons, macaques, and bonobos; (D) the

808 relative PCSA of the digital flexors is significantly higher in gibbons compared to macaques ($p<0.001$)

809 and bonobos ($p<0.01$).

810 **Fig. 4** – Box plot of the relative size of the radioulnar deviators. Within the hylobatid group, the triangles

811 represent the siamangs. (A) the wrist deviators have a significantly higher PCSA in macaques compared

812 to gibbons ($p<0.001$) and bonobos ($p<0.05$); (B) the ratio of radial deviators over ulnar deviators of

813 gibbons is significantly higher than the ratio observed in macaques ($p<0.001$) and bonobos ($p<0.05$).

814 **Fig. 5** – Boxplot of the relative PCSA of the forearm rotators. Within the hylobatid group, the triangles

815 represent the siamangs. The proportion of the rotator PCSA is significantly higher in gibbons compared

816 to macaques ($p<0.01$).

817   **Fig. 6** – Results on tendonization of the flexor muscles. Within the hylobatid family the triangles

818   represent the siamangs. (A) The relative length of the tendons is significantly longer in gibbons

819   compared to bonobos ($p < 0.05$) but not to macaques ($p > 0.05$); (B) within the hylobatid family there is

820   no significant difference between the relative length of the tendons between the different genera

821   (*Nomascus*, *Hylobates*, *Symphalangus*) ($p > 0.05$).

822   **Fig. 7** – The composition of the intrinsic hand muscles is very similar in gibbons and macaques, with a

823   dominant development (%PCSA) of the intermediate hand muscles (~59% and ~51% respectively), the

824   thenar PCSA taking up approximately 30% of the total intrinsics PCSA and the hypothenar muscle

825   PCSA amounting to only 10% and 18%. In bonobos, the intermediate hand muscles take up a larger

826   proportion of the total intrinsics PCSA (~66%), while in humans, the thenar PCSA is relatively more

827   prominent (~47%). The proportion of the intrinsic hand muscles PCSA relative to total forearm muscle

828   PCSA is 14.7% in macaques, 14.5% in gibbons and humans, and 18.4% in bonobos ($p > 0.05$).

829   **Fig. 8** – Overview of the different muscle parameters that were measured for this study and the

830   corresponding values for macaques, gibbons, bonobos, and humans. Significant differences are only

831   shown between macaques and gibbons.