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

2   **gibbons(*fam. Hylobatidae*). Part I. Description and comparison of the muscle configuration.**

3

4   Marie J. M. Vanhoof[1], Timo van Leeuwen[1], Evie E. Vereecke[1]

5   [1]Muscles & Movement, Biomedical Sciences Group, KU Leuven Campus Kulak, Kortrijk, Belgium

6

7   Short title: forearm and hand musculature of gibbons and rhesus macaques

8   **Abstract**

9   Primates live in very diverse environments and, as a consequence, show an equally diverse locomotor

10   behaviour. During locomotion, the primate hand interacts with the superstrate and/or substrate and will

11   therefore probably show adaptive signals linked with this locomotor behaviour. While the morphology

12   of the forearm and hand bones have been studied extensively, the functional adaptations in the hand

13   musculature have been documented only scarcely. To evaluate if there are potential adaptations in

14   forelimb musculature to locomotor behaviour, we investigated the the forearm and hand musculature of

15   the highly arboreal gibbons (including *Hylobates lar, Hylobates pileatus, Nomascus leucogenys,*

16   *Nomascus concolor, Symphalangus syndactylus*) and compared this with the musculature of the

17   predominantly terrestrial rhesus macaques (*Macaca mulatta*) by performing complete and detailed

18   dissections on a sample of fifteen unembalmed specimens. We found that the overall configuration of

19   the upper arm and hand musculature is highly comparable between arboreal gibbons and terrestrial

20   macaques, and follows the general primate condition. Most of the identified differences in muscle

21   configuration are located in the forearm. In macaques, a prominent *m. epitrochleoanconeus* is present,

22   which potentially helps to extend the forearm and/or stabilize the elbow joint during quadrupedal

23   walking. The *m. flexor carpi radialis* shows a more radial insertion in gibbons, which might be

24   advantageous during brachiation as it can aid radial deviation. The fingers of macaques are controlled

25   in pairs by the *m. extensor digiti secondi et tertii proprius* and the *m. extensor digiti quarti et quinti*

26   *proprius* – a similar organization can also be found in their flexors – which might aid in efficient

27   positioning of the hand and fingers on uneven substrates during quadrupedal walking. In contrast,

28   extension of the little finger in gibbons is controlled by a separate *m. extensor digiti minimi*, while digits

29   2 to 4 are extended by the *m. extensor digitorum brevis*, suggesting that simultaneous extension of digits

30   2-4 in gibbons might be important when reaching or grasping an overhead support during brachiation.

31   In conclusion, the overall configuration of the forelimb and hand musculature is very similar in gibbons

32   and macaques with some peculiarities which can be linked to differences in forelimb function and which

33   might be related to the specific locomotor behavior of each group.

34

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

Introduction

The primate hand displays a large variety of phenotypes which reflects an equally diverse functional repertoire (Horn, 1972; Vereecke, D'Août and Aerts, 2006; Marzke, 2009; Williams, 2010; Almécija, Smaers and Jungers, 2015; Liu, Xiong and Hu, 2016; Thompson *et al.*, 2018). Understanding how these phenotypes correlate to different locomotor behaviours of distinct primate taxa may facilitate the interpretation of hand function from primate fossil remains. Nonhuman primates use their hands for manipulation as well as for locomotion, and adaptive signals to these specific functions in the morphology of the forearm and hand bones have been studied extensively. For example, gibbons have a large wrist mobility in all directions as a potential adaptation to suspensory locomotion (Richmond, 2001), which is associated with a ball-and-socket configuration of the midcarpal joint (Lemelin and Schmitt, 1998; Orr *et al.*, 2010; McMahon, Zijl and Gilad, 2015; Prime and Ford, 2016; Orr, 2017, 2018). In macaques, the articular surface of the basal manual phalanges is proximodorsally excavated to enable hyperextension, which is a specialization for digitigrade locomotion (Hayama, Chatani and Nakatsukasa, 1994; Lemelin and Schmitt, 1998). In addition, macaques have a broad midcarpal joint morphology which is interpreted as being advantageous for loading during quadrupedal walking (Lewis, 1985; Lemelin and Schmitt, 1998; Richmond, 2001; Daver, Berillon and Grimaud-Hervé, 2012). These previous studies focused on adaptations in skeletal morphology, while functional adaptations in the hand musculature have been documented only scarcely. Detailed descriptions of forelimb musculature in different primate taxa, as well as comparative analyses between those taxa, are limited in the current literature (Tuttle, 1967, 1969; Lemelin and Diogo, 2016). In 2009, Michilsens et al. conducted a study on the functional anatomy of the gibbon forelimb, with a detailed account on the upper and lower arm musculature in four different gibbon species (*Hylobates lar, H. pileatus, H. moloch, Symphalangus syndactylus*; n=11)(Michilsens *et al.*, 2009). Here, we extend this dataset with eight gibbon specimens (*H. lar, H. pileatus, Nomascus concolor, N. leucogenys, S. syndactylus*) and also include detailed information on intrinsic hand musculature. In addition, we compare the forelimb muscle configuration of the highly arboreal gibbons with that of the predominantly terrestrial macaques (Fam. *Cercopithecidea*) to evaluate if there are specific adaptations in forelimb musculature that could be

63 related to locomotor behaviour. A full quantification of the forelimb and hand musculature in both

64 primate taxa will be presented as Part 2 of this study.

Methods

Specimen collection

As multiple species of the hylobatid family are included in this study, they are further referred to as "gibbons". The forearm and hand of eight (sub)adult gibbons 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 forearm and hand of seven adult rhesus macaques were obtained via collaboration with the Ghent University (campus Merelbeke, Belgium) and KU Leuven (campus Gasthuisberg, Belgium). All specimens were collected opportunistically, no animals were sacrificed for this study. The forelimbs were disarticulated at level of the shoulder in all specimens. Full specimen details are provided in **Table 1**.

Dissection procedure

The specimens were stored at -18°C and were thawed at room temperature 24h prior to the dissections. A complete dissection of the left or right forearm and hand was performed for all specimens (unilateral sampling). All muscles were isolated one by one and their origins and insertions were documented and compared to previous studies (Tuttle, 1969; Gibbs, Collard and Wood, 2002; Michilsens *et al.*, 2009; Diogo and Wood, 2012; Aversi-Ferreira *et al.*, 2016; van Leeuwen *et al.*, 2018). Presence or absence of muscles or abnormalities were also noted. The dissections were documented extensively using a dedicated photography setup. Some specimens were skinned prior to transport to the university, which caused damage to the thenar and hypothenar muscles, and/or the tendons of the extrinsic muscles in some specimens (see **Table 1**).

86   **Results**

87   *Documentation of gibbon and rhesus macaque forearm and hand musculature*

88   The description of the extrinsic and intrinsic hand muscles discussed below are based on detailed

89   dissections of a macaque (n=7) and gibbon (n=8) sample. As some specimens were damaged, either due

90   to skinning or the dislocation at the level of the shoulder, the number of included specimens varies for

91   each muscle. The exact number of specimens is shown each time between parentheses. Details on the

92   origin and insertion of all extrinsic and intrinsic muscles are listed in the Supplementary material (**Table**

93   **S1**). Anatomical data on bonobos and humans from previous dissections are also added for comparison

94   (van Leeuwen *et al.*, 2018).

95

96   <u>Upper arm musculature</u>

97   The long head of the *m. biceps brachii* (Bb) originates from the supraglenoid tubercle of the scapula

98   (11/11) and inserts onto the radial tuberosity (14/14) in all macaque and gibbon specimens. In macaques,

99   the short head originates from the coracoid process of the scapula, similar as in modern humans and

100   most other primates, and fuses with the muscle belly of the long head (6/6). In gibbons, however, the

101   short head originates from the crest of the lesser tubercle of the humerus (7/7) and inserts on the bicipital

102   aponeurosis into the deep fascia on the medial forearm (connection with FDS) (8/8). This supports

103   previous findings that in most primates both the long head and short head of the Bb cross the shoulder

104   joint, while in gibbons only the long head crosses the shoulder (Jungers and Stern, 1980; Michilsens *et*

105   *al.*, 2009). The short head works as an elbow flexor and forearm supinator, without action at the shoulder

106   joint. This could imply that the humeral flexion capacity of the Bb is reduced in gibbons compared to

107   macaques and other primates with a bi-articular configuration of the short head of the Bb. In gibbons,

108   the short head of the Bb forms a ventral muscle chain between the *m. pectoralis major* (PM) and *m.*

109   *flexor digitorum superficialis* (FDS) (see (Jungers and Stern, 1980)). The fusion between these multiple-

110   joint muscles is thought to conduct the flexor force of the PM distally across the shoulder, elbow, and

111   wrist joints so that active or passive tension in this muscle results in automatic flexion of the forearm

112   and fingers without requiring activity in the distal muscles of the chain. While such ventral muscle chain

113 would indeed be advantageous for brachiating gibbons, the function of this chain remains debated

114 (Jungers and Stern, 1980; Michilsens *et al.*, 2009).

115

116 The *m. triceps brachii* (Tb) consists of three heads in all specimens (15/15). The Tb originates from the

117 infraglenoid tubercle of the scapula (long head) (12/12) and the humeral shaft (lateral and medial head)

118 (14/14), and inserts onto the oleocranon (14/14). In most macaques the long and medial head are

119 completely separate (5/6), while in all gibbons, the three heads are fused at the insertion (8/8), which is

120 also seen in modern humans. In macaques, the Tb is an important muscle during quadrupedal walking

121 as it produces the torque at the elbow joint during the first three-fourths of the step (Manter, 1938).

122 During brachiation in gibbons, the Tb will probably primarily act at the shoulder (Michilsens *et al.*,

123 2009).

124

125 The *m. dorso-epitrochlearis* (DET) originates in both macaques and gibbons from the muscle belly of

126 the *m. latissimus dorsi* (12/12), yet the insertion is variable. The DET inserts onto the oleocranon and

127 the fascia of Bb and Tb in all macaques (6/6) and some gibbons (3/8), but in most gibbons it inserts via

128 a tendon sheet onto the medial epicondyle of the humerus (5/8). The DET, clearly present in both

129 macaques and gibbons, is rarely seen in humans (Cheng and Scott, 2000) as fewer than 30 cases have

130 been reported over the past 200 years (Natsis *et al.*, 2012). The function of the DET is still debated as it

131 has long been speculated to facilitate force transmission from the shoulder to the fingertips by acting as

132 a dorsal muscle chain (Sonntag, 1922; Andrews and Groves, 1976). However, EMG studies have shown

133 that the DET might only be a morphological consequence of the rearrangement of the origin of the short

134 head of the Bb (Jungers and Stern, 1980). The DET has also been labeled as a "climbing muscle" because

135 of its connection with the *m. latissimus dorsi* as fusion of these muscles contributes to increased

136 concerted contraction (Sonntag, 1922).

137

138 The *m. brachialis* (B) originates from the distal half (13/14) or complete (1/14) shaft of the humerus and

139 inserts onto the tuberosity of the ulna (14/14). Occasional fusion with the *m. supinator* (SUP) in

140 macaques (1/6) or with the *m. pronator teres* (PT) in gibbons (1/8) can occur. It is considered a pure

141 elbow flexor in primates, including humans.

142

143 The *m. coracobrachialis* (CB) consists of a long (middle) and medial (deep) head in macaques (6/6) (cf.

144 (Aversi-Ferreira *et al.*, 2016)). Both heads originate from the coracoid process of the scapula and the

145 common coracoid tendon (6/6), and the long head is always fused with the short head of the Bb (6/6).

146 The long head inserts midway on the humeral shaft (6/6) and the medial head inserts more proximally,

147 onto the surgical neck of the humerus (6/6). In gibbons, the CB shows a one-headed configuration

148 similar to modern humans, originating from the coracoid process of the scapula (7/7) and a direct, muscle

149 fiber insertion onto the periosteum of the proximal (1/8) or middle (7/8) humeral shaft. In macaques, the

150 two-headed configuration might increase internal rotation and adduction of the arm during quadrupedal

151 walking (Aversi-Ferreira *et al.*, 2016).

152

153 The *m. epitrochleoanconeus* (ETA) is an separate, well-defined muscle in macaques, that originates

154 from the medial epicondyle of the humerus and inserts onto the medial border of the oleocranon (7/7)

155 (**Fig. 1**). A well-developed ETA is absent in gibbons (8/8), but a strong ligament – similar to the ulnar

156 collateral ligament in humans – can be found on the position of the macaque ETA (8/8). There is some

157 confusion about the presence or absence of the ETA in primates. In bonobos, and other great apes, the

158 presence is debated as it can easily be missed or considered part of the FCU during dissections of the

159 forearm (Diogo and Wood, 2012; Diogo, Molnar and Wood, 2017). Also in humans, there is still no

160 agreement whether the ETA is present (Hirasawa, Sawamura and Sakakida, 1979; Gessini *et al.*, 1981;

161 Uscetin *et al.*, 2014; de Ruiter and van Duinen, 2017) or absent (Diogo, Richmond and Wood, 2012).

162 In present or past dissections that we conducted we never found a distinct ETA in either bonobos or

163 human cadavers (pers. obs.). In macaques, the ETA covers the cubital tunnel where it protects the ulnar

164 nerve as it passes through the elbow. Furthermore, activation of the ETA potentially facilitates forearm

165 extension and/or stabilization of the elbow joint during quadrupedal walking (Rui Diogo and Wood,

166 2012).

167

Forearm rotators

The *m. brachioradialis* (BR) invariably originates from the supracondylar ridge of the humerus (15/15)

and shows incidental proximal fusion with the *m. brachialis* (B) in both macaques (2/7) and gibbons

(2/8). In macaques, the BR muscle belly runs underneath the *m. extensor carpi radialis longus (ECRL)*

and *m. extensor carpi radialis brevis (ECRB)* at the origin, and inserts with a long tendon onto the styloid

process of the radius (7/7). In gibbons, the BR runs superficial to the ECRL and ECRB and its long

tendon either inserts directly onto the styloid process (3/8) or onto the shaft of the radius proximal to the

styloid (5/8), with the tendon running further along the radius to end on the styloid process (1/8) or just

proximal of it (4/8), a situation similar to bonobos. In humans, the BR is a strong elbow flexor when the

forearm is in a mid-position between pronation and supination at the radioulnar joint, and works

synergistic with the B and Bb, a function which is also important during brachiation in gibbons. During

pronation, the BR is more active during elbow flexion since the Bb is at a mechanical disadvantage, as

is probably also the case in macaques during quadrupedal walking (Boland, Spigelman and Uhl, 2008).

The *m. supinator* (SUP) originates from the lateral epicondyle of the humerus and inserts onto the

proximal half of the radius in all specimens (15/15), similar as in humans. In all macaques (7/7) and

most gibbon specimens, the SUP has an additional origin from the proximal third of the ulna, while in

bonobos this is the main origin of the SUP. In macaques, the SUP probably acts as a supinator of the

forearm like in modern humans, although the exact activity pattern of the SUP during quadrupedal

locomotion has not yet been investigated. In gibbons, EMG studies have indicated that the SUP mainly

acts in the support phase of brachiation, during which time the forearm passes increasingly into

supination (Stern and Larson, 2001).

The *m. pronator teres* (PT) consists of a single humeral head in macaques with its origin on the medial

epicondyle of the humerus (7/7). In gibbons, either a humeral head (7/8), as seen in macaques, or an

ulnar head, which originates from the proximal ulna (1/8), is present. Although Miller (1932) stated that

the PT of all hominoids has two heads (Miller, 1932), a configuration we also found in bonobos, a two-

headed configuration with a humeral and ulnar head as seen in humans and great apes was never

196   observed in the gibbon specimens. In all primate specimens, the PT inserts halfway the radius (15/15),

197   and fusion with the FCR (macaque: 3/7, gibbon: 1/8), the FDS (macaque: 3/7) or B (gibbon: 1/8) may

198   occur. Poor development or absence of the ulnar head seems to be a common variation in humans

199   (Jamieson and Anson, 1952; Caetano *et al.*, 2017), which is supported by phylogenetic development, as

200   in most mammals (except anthropoid apes) the ulnar head is completely missing (Macalister, 1868;

201   McMurrich, 1903). In humans, the median nerve passes between both heads of the PT which enhances

202   the risk of entrapment of the median nerve, also called the "pronator teres syndrome" (Nigst and Dick,

203   1979; Hartz *et al.*, 1981; Fuss and Wurzl, 1990). Absence of the ulnar head in all macaques and most of

204   the gibbons might be important to avoid such entrapment during locomotion. Another possible

205   explanation is that the presence of an ulnar head in humans allows pronation of the forearm independent

206   of the position of the elbow. In macaques, the angle of the elbow joint is relatively constant during

207   quadrupedal locomotion (Demes *et al.*, 1998), and an ulnar head might not be needed. In gibbons, the

208   PT is primarily active as the elbow is flexed in the middle of the swing phase of brachiation (Stern and

209   Larson, 2001), which might indicate that forearm pronation independent of elbow position is also not

210   important in gibbons. Indeed, an ulnar head in gibbons was only observed in one individual.

211

212   The *m. pronator quadratus* (PQ) has a rather consistent configuration in macaques and gibbons. It

213   originates from the distal ulna (13/15) and inserts onto the distal interosseous membrane and the distal

214   radius (13/15), similar to bonobos. In two gibbon specimens (2/8), the PQ appears as two fused muscle

215   bellies. The proximal belly (deep head) inserts with a tendinous portion onto the distal radius. The distal

216   belly (superficial head) is larger and originates from the distal radius and inserts with tendinous fibres

217   onto the distal ulna. As reported in literature, this configuration with two bellies is also commonly seen

218   in humans (Johnson and Shrewsbury, 1976; Stuart, 1996). In macaques and gibbons, the fibres of the

219   PQ consistently show an oblique orientation, which is also seen in bonobos, while in humans, only the

220   fibres of the deep head show an oblique orientation as the fibres of the superficial head are transversely

221   oriented from origin to insertion. It has been suggested that the human superficial head, due to its

222   transverse fibre orientation, is the initiator and rotator for pronation, while the deep head is mostly

223   involved in stabilizing the distal radioulnar joint (Johnson and Shrewsbury, 1976). This indicates that

224   the primary function of the PQ in gibbons and macaques, due to the oblique fibre orientation, is

225   stabilization of the distal radioulnar joint, which implies that the PT is the most important forearm

226   pronator in these primates. The idea that the PQ in gibbons and macaques plays a role as a dynamic

227   ligament does correspond to its positioning close to the distal radioulnar joint (small moment arm) and

228   relatively small size (distal $1/4^{th}$ to $1/5^{th}$ of the forearm) compared to modern humans (distal $1/3^{rd}$ of the

229   forearm). In gibbons, the PQ is also used to position the hand prior to grasping a new support (Stern and

230   Larson, 2001).

231

232   <u>Extrinsic hand musculature</u>

233   The *m. extensor carpi radialis longus* (ECRL) and *m. extensor carpi radialis brevis* (ECRB) show a

234   similar configuration in both macaques and gibbons. The ECRL originates from the lateral

235   supracondylar ridge of the humerus, distal from the BR (15/15), and inserts onto the base of metacarpal

236   2 (MC2) (15/15), similar to the configuration in bonobos. In two gibbon specimens, the ECRL sends a

237   tendon slip to the base of MC1 at the insertion (2/8). This means that in these specimens, the ECRL

238   could also assist in thumb extension and abduction and/or stabilization of the trapeziometacarpal joint.

239   The ECRB originates from the lateral supracondylar ridge of the humerus, distal from the ECRL and

240   inserts onto the dorsoradial base of MC3 in all macaques (7/7). Fusion with the *m. extensor digitorum*

241   *communis* (EDC) (4/7) can occur. In gibbons, the ECRB originates either solely from the lateral

242   epicondyle of the humerus (1/8), or the lateral supracondylar ridge of the humerus (7/8) in combination

243   with the lateral epicondyle (1/8). In bonobos, the ECRB originates solely from the lateral epicondyle of

244   the humerus. As in macaques, fusion with the EDC is possible but is only observed in one gibbon

245   specimen (1/8). The ECRB inserts onto the dorsoradial base of MC3 (8/8). Both the ECRL and ECRB,

246   synergist muscles with a similar function, can be proximally fused in macaques (6/7) and gibbons (2/8),

247   which leads to a concerted action between both muscles.

248

249   The *m. extensor carpi ulnaris* (ECU) originates from the common extensor tendon at the lateral

250   epicondyle of the humerus and inserts with a long tendon onto the ulnar base of MC5 in all macaques

251   (7/7). In gibbons, the ECU also originates from the lateral epicondyle of the humerus (8/8), sometimes

252   in combination with the proximal ulna (1/8), which is the main origin in bonobos, or the oleocranon

253   (1/8). The insertion on MC5 is similar to that of macaques in all gibbon specimens (8/8). Given its

254   position in the forearm, the ECU functions as wrist extensor and ulnar deviator in macaques and gibbons,

255   common to what is observed in other primates, including humans.

256

257   The *m. extensor digitorum communis* (EDC) originates with a common tendon from the lateral

258   epicondyle of the humerus in all specimens (15/15), similar to bonobos and humans, and is proximally

259   fused with the *m. extensor digiti minimi* (EDM) in half of the gibbons (4/8). The EDC splits into four

260   individual tendons at the dorsum of the hand in macaques (7/7), while in gibbons, the tendon to digit 2

261   splits off proximally to the wrist, the tendon to digit 5 splits off at the level of the wrist, and the tendons

262   to digits 3 and 4 split off at the dorsum of the hand and commonly interconnect with the tendons of

263   digits 2 and 5 (*juncturae tendineum*) (**Fig. S1**). These *juncturae tendineum* are also found in bonobos,

264   between the tendons to digits 4 and 5. Each tendon inserts on the distal phalanx, after forming the

265   extensor mechanism with the *m. lumbricalis* and *mm. interossei* (see intrinsic musculature) (15/15). The

266   EDC acts as a wrist and digital extensor.

267

268   In the following paragraphs, the *m. extensor digiti quarti et quinti proprius* (EDQQ), *m. extensor digiti*

269   *secundi et tertii proprius* (EDST), *m. extensor digitorum brevis* (EDB), *m. extensor digiti minimi*

270   (EDM), and *m. extensor indicis* (EI) are discussed together because they are developmentally related

271   (Diogo *et al.*, 2009).

272

273   Macaques show the most primitive condition with a *m. extensor digiti secundi et tertii proprius* (EDST)

274   and *m. extensor digiti quarti et quinti proprius* (EDQQ), inserting onto digits 2-3 and digits 4-5

275   respectively, which corresponds to the *m. extensores digitorum breves* (EDB) of digits 2-3 and digits 4-

276   5 of other tetrapods (Diogo *et al.*, 2009). The EDST originates from the proximal half of the ulna (7/7)

277   and the tendons insert onto the ulnar side of the extensor mechanism of digits 2 and 3 (**Fig. 2A**). The

278   EDQQ originates from the lateral epicondyle of the humerus, from the same extensor tendon as the

279 EDC, and the tendons insert on the ulnar side of the extensor mechanism of digits 4 and 5, near the

280 proximal phalanx (**Fig. 2A**). Extension of the fingers is thus controlled in pairs in macaques.

281

282 In contrast to macaques, all gibbons show a more derived configuration as they possess a *m. extensor*

283 *digitorum brevis* (EDB) (**Fig. 2B**), which inserts onto digits 2-4, and a true *m. extensor digiti minimi*

284 (EDM), which inserts onto digit 5 (**Fig. 2B**). The EDB originates from the proximal half of the

285 interosseous membrane (8/8), and either the proximal (4/8) or distal half (4/8) of the ulna. The individual

286 tendons insert either onto the proximal phalanx of digits 2, 3 and 4 (6/8) or only onto digits 3 and 4 (1/8).

287 Occasional insertions onto the base of MC2, MC3 and MC4 may occur (1/8). The most important

288 function of the EDB is the coordinated extension of digits 2, 3 and 4. The EDM originates from the

289 lateral epicondyle of the humerus (7/8) or the distal half of the ulna (1/8), and inserts onto the distal

290 phalanx of digit 5 together with the tendon of the EDC (8/8). Proximal fusion of the EDM with the ED

291 can occur (4/8).

292

293 Modern humans show the most derived condition. They possess an EDM – similar to gibbons – in

294 combination with a separate *m. extensor indicis* (EI), which inserts onto the distal phalanx of digit 2, a

295 configuration also seen in great apes (Aversi-Ferreira *et al.*, 2010; Zihlman, Farland and Mi, 2011). The

296 EI and EDM of modern humans and great apes are phylogenetically derived from the EDB of other

297 tetrapods (Diogo *et al.*, 2009), and replace the EDB. Gibbons present an intermediate configuration in

298 that they preserve an EDB and have an EDM. In one gibbon specimen, we even identified an EI,

299 originating from the distal third of the ulna and the interosseous membrane and inserting onto the distal

300 phalanx of the index finger together with the tendon of the EDC (1/8). Variation in the extensor

301 musculature is, however, also present in humans. The EDB has been reported as a rare anatomical

302 variation in humans (2.3% of the human population; (Suwannakhan, Tawonsawatruk and Meemon,

303 2016; Georgiev *et al.*, 2018)), and an 'EI' with a tendon running to both the index and middle finger

304 (i.e. *m. extensor indicis et medii communis*), as seen in macaques, does also occur in humans (0-6%)

305 (Suwannakhan, Tawonsawatruk and Meemon, 2016; Georgiev *et al.*, 2018).

306

307   The specific configuration of these extensors in macaques, gibbons, and humans has important

308   functional implications. In macaques, the fingers are controlled in pairs by the EDST and EDQQ. A

309   similar organization is found in the finger flexors of macaques, where the fingers are also controlled in

310   pairs. This specific organization might aid in efficient positioning of the hand and fingers during palmi-

311   or digitigrade quadrupedal walking, such as pairwise extension (and little abduction) of the fingers to

312   accommodate to uneven substrates, which might prevail over individual finger control. Although one

313   could argue that the substrates that macaques need to move along are not any more uneven than those

314   of gibbons, the hand positioning in palmi/digitgrade quadrupedalism is very different from that used in

315   brachiation. Gibbons typically use a hook grip during brachiation, and the hands are positioned on the

316   superstrate in an overhead position, without visual input. In such hook grip position, individual

317   positioning of the fingers seems less important and simultaneous flexion of the four fingers prevails

318   (Tuttle, 1969; Susman, Jungers and Stern, 1982). In gibbons, extension of the little finger is controlled

319   by a separate EDM, while digits 2-4 are extended by the EDB. This suggests that simultaneous extension

320   of digits 2-4 in gibbons might be important when reaching or grasping a support during brachiation (cf.

321   hook grip position described above). Humans and bonobos have a separate EDM and EI, resulting in a

322   functional dissociation between the extension of the index finger and little finger, which is also distinct

323   to that of digits 3 and 4 which is primarily mediated by the EDC. This individualization of finger

324   extension, in combination with a separate *m. flexor pollicis longus* to the thumb, is likely linked to the

325   high manual dexterity of humans.

326

327   The *m. abductor pollicis longus* (APL) originates from the interosseous membrane and the proximal

328   shaft of the ulna in all macaque and gibbons specimens (15/15). In macaques, the APL consists of one

329   muscle belly with a tendon that splits at the level of the trapezium, inserting with one slip onto the base

330   of MC1 and with the other onto the prepollex (7/7) (**Fig. 3A**). In gibbons, however, the APL consists of

331   two muscle bellies, APL I and II, each with its own tendon, and the bellies are either proximally fused

332   (6/8) or easily separable (2/8). The tendon of APL I always inserts on the base of the MC1 (8/8), while

333   the tendon of APL II inserts most often on the trapezium (7/8), with an additional insertion on the

334   prepollex (2/8), or it may insert solely on the capitate (1/8) (**Fig. 3B**). The configuration seen in gibbons,

335   with a distinct APL I and II, is also observed in bonobos and humans (van Leeuwen *et al.*, 2018) even

336   though this is largely overlooked in other literature. This specific configuration makes that only the APL

337   I can be considered a true abductor of the thumb, while the APL II functions as radial deviator of the

338   wrist and has no function on the thumb. The insertion onto the prepollex, as seen in macaques and some

339   gibbons (and bonobos), might not entail a functional difference to an insertion on the trapezium, given

340   the close association between the prepollex and trapezium in most nonhuman primates (Le Minor, 1994).

341

342   The *m. extensor pollicis longus* (EPL) has its origin on the proximal ulna (15/15), and often also from

343   the interosseous membrane both in macaques (4/7) and gibbons (3/8). It inserts with a long tendon onto

344   the distal phalanx of digit 1 (14/15). This configuration is also seen in bonobos. In one gibbon specimen,

345   the insertion could not be reported due to tissue damage. Both macaques and gibbons (and bonobos)

346   lack a *m. extensor pollicis brevis* (EPB) in contrast to humans, although absence of the EPB in humans

347   has also been reported (Nayak *et al.*, 2008). The EPB in humans displays some anatomical variations,

348   such as the *m. extensor pollicis et indicis accessorius* with a tendon to digit 1 and 2 (Yoshida, 1995). It

349   has been proposed in literature that the EPB of modern humans is a derivative of APL I (Straus, 1941;

350   Diogo *et al.*, 2009), as the primitive mammalian condition shows an APL with a single tendon (Aversi-

351   Ferreira *et al.*, 2010) while the APL in macaques splits distally, and gibbons clearly show two separate

352   tendons (APL I and II). However, this interpretation is still debated as both the APL I and EPB have a

353   different insertion, i.e. the base of MC1 versus the proximal phalanx of the thumb. In addition, humans

354   can have an EPB present next to an APL with multiple tendons (cfr. APL I) inserting around the first

355   carpometacarpal joint (Lacey, Goldstein and Tobin, 1951; Celik, Sendemir and Simsek, 1994; Sehirli,

356   Cavdar and Yüksel, 2001).

357

358   The *m. flexor carpi radialis* (FCR) shows a similar configuration in both macaques and gibbons (and

359   bonobos). It originates from the common flexor tendon at the medial epicondyle of the humerus and

360   inserts with a long tendon onto the palmar base of MC2, running deep to the thenar muscles (15/15).

361   Proximal fusion with the muscle belly of the FDS (1/7) and/or PT (3/7) might occur in macaques. In one

362   gibbon specimen, the FCR also originates from the proximal ulna (1/8). Given its position in the

363 macaque and gibbon forearm, it functions as a wrist flexor and radial deviator, and probably a weak

364 pronator.

365

366 The *m. flexor carpi ulnaris* (FCU) originates from the common flexor tendon at the medial epicondyle

367 of the humerus (*caput humerale*) in all macaque and gibbon specimens (15/15). An additional origin

368 from the oleocranon (*caput ulnare*) occurs in both macaques (4/7) and gibbons (1/8). This configuration

369 is also seen in bonobos. The FCU inserts with a long tendon onto the pisiform bone in all specimens

370 (15/15). The FCU functions as wrist flexor and ulnar deviator in both macaques and gibbons. In

371 macaques, the long pisiform, which is directed perpendicular to the palmar surface of the hand, gives

372 the FCU an optimal leverage for flexing an extended wrist (Lewis, 1985; Sarmiento, 1988), which is

373 important during quadrupedal walking. In gibbons, the pisiform has a proximodistal orientation which

374 increases the lever arm of the FCU for wrist flexion and ulnar deviation (Sarmiento, 1988). These wrist

375 movements are important during brachiation (Michilsens *et al.*, 2010).

376

377 The *m. palmaris longus* (PL) originates from the common flexor tendon at the medial epicondyle of the

378 humerus and its long and slender tendon extends into the palmar aponeurosis at the level of the wrist in

379 all macaques (7/7). This configuration is similar to that of modern humans, though the PL tendon of

380 macaques runs more ulnarly into the palmar aponeurosis. In gibbons, the origin of the PL is the same as

381 in macaques, with an additional origin from the fascia of the aponeurosis bicipitis of the Bb in two

382 specimens (2/8). At the insertion, the configuration in gibbons is distinct from that observed in

383 macaques, with a radially positioned PL tendon at the wrist (5/7), which is also seen in bonobos, or even

384 with an insertion onto the tendon of the FCR (2/7). The more radial insertion found in gibbons could be

385 important during brachiation as it can aid in radial deviation. However, more important is the fact that

386 the PL is always present in macaques and gibbons (and bonobos), while in modern humans the PL is

387 unilaterally absent in 16% of the population (Thompson, Mockford and Cran, 2001).

388

389 The *m. flexor digitorum superficialis* (FDS) originates from the common flexor tendon at the medial

390 epicondyle of the humerus in all macaques (7/7) and inserts most commonly with four separate tendons

391   onto the middle phalanx of digits 2 to 5 (6/7). In one specimen, the tendons to digits 2 and 3 are vestigial

392   and insert on the tendon sheaths of the FDP at the level of the lumbricals, while the tendons to digits 4

393   and 5 insert onto the proximal phalanx (1/7). The FDS has a rather complex architecture in macaques,

394   which is also commonly seen in bonobos, consisting of three partially fused muscle bellies that are

395   folded together; (1) a muscle running to digit 2 (FDS II), which shows a distinct belly-tendon-belly-

396   tendon configuration (cfr. bonobos (van Leeuwen *et al.*, 2018)), (2) a muscle belly with two tendons

397   inserting onto digit 3 and 4 (FDS III-IV), and (3) a muscle with one tendon inserting onto digit 5 (FDS

398   V) (**Fig. S2**). Moreover, in all macaque specimens, the FDS is connected with the *m. flexor digitorum*

399   *profundus* (FDP) with an additional muscle belly, at the level of the FDS for digit 2-3 (7/7). In gibbons,

400   the configuration of the FDS is even more variable than in macaques. In half of the specimens, the FDS

401   consists of one muscle belly (4/8), while two (2/8), three (1/8) or four muscles bellies (1/8) are also

402   observed. The distribution of tendons to the digits 2 to 5 differs from specimen to specimen. Moreover,

403   in gibbons the FDS originates not only from the medial epicondyle but also from the proximal ulna (4/8)

404   or from the proximal ulna and radius (1/8). In gibbons, the deep flexors of the toes, like the FDS, also

405   show considerable variation in the specific distribution of the tendons towards the digits (Langdon,

406   1990; Vereecke *et al.*, 2005), indicating that the tendon organization has no major influence on the

407   functionality of the FDS.

408

409   The *m. flexor digitorum profundus* (FDP) originates from the medial epicondyle of the humerus (situated

410   deep to the FDS), the shaft of the radius (in between the SUP and PQ), the interosseous membrane, and

411   the shaft of the ulna (from the oleocranon to the PQ) in all specimens (15/15). In bonobos, the FDP does

412   not originate from the mediale epicondyle of the humerus, but from the interosseous membrane and the

413   shaft of the radius and ulna. In macaques and gibbons, the FDP has five tendons inserting respectively

414   onto the distal phalanges of each digit, with some exceptions (see **Table S1**). In gibbons, the FDP usually

415   consists of two muscle bellies that are partially fused, one for digit 1 (FDP I) and one for digits 2 to 5

416   (FDP II-V) (5/8) (**Fig. 4A**). The other specimens do not have a separate FDP I (3/8). In two specimens,

417   the FDP II-V sends a tendon to digit 1, which splits off from the tendon running to digit 2 (2/8). In

418   another gibbon specimen, two individual muscle bellies occur, one for digits 1 and 2 (FDP I-II) and one

419   muscle belly for digits 3 to 5 (FDP II-V). Here, the tendons to digit 2 and 3 partly originate from the

420   FDS (1/8) (**Fig. 4B**). In macaques, the configuration of the FDP is more variable, with the majority of

421   the specimens showing a configuration with three fused muscle bellies, one for digit 1 to 3 (FDP I-III),

422   one for digit 4 (FDP IV) and one for digit 5 (FDP V) (5/7) (**Fig. 4C**). One specimen shows a slightly

423   different configuration, with a division in FDP I-III-IV, FDP II and FDP V (1/7), while a second

424   macaque specimen displays an unusual FDP configuration with two muscle bellies – FDP I-II-III and

425   FDP IV-V. In addition, the tendons to digits 2 and 3 show a tendon-lumbrical-tendon configuration in

426   which the first two lumbricals form a single unit with the FDP tendons instead of originating from these

427   tendons (**Fig. 4D**). In macaques, the tendons of the FDP are clustered together at wrist level, and the

428   tendons to the digits split off more distally than seen in gibbons. In addition, the tendon to the thumb

429   originates from the middle of the tendon cluster, and not from FDP II as seen in gibbons. Also notable

430   is the connection between FDP and FDS in macaques, as described above. However, crucial is the

431   decoupling between the thumb (and index finger) and the lateral digits in gibbons, a configuration

432   common to humans, compared to the division between the medial and lateral digits in macaques (also

433   seen at the extensors, cfr. EDST and EDQQ).

434

435   <u>Intrinsic hand musculature</u>

436   The intrinsic hand musculature consists of the thenar muscles (APB, FPB, ADP, OPP), the hypothenar

437   muscles (ADM, FDM, ODM), the lumbricals (LUMB) and intermediate hand muscles (IM, FBP, IOP,

438   IOD, *mm. contrahentes*) (**Fig. 5, Table 2**). These intrinsic hand muscles of macaques and gibbons are

439   described in detail below.

440

441   The *m. abductor pollicis brevis* (APB) has a similar configuration in both macaques and gibbons. It

442   originates from the flexor retinaculum and inserts with a short tendon onto the radial sesamoid bone of

443   the first metacarpophalangeal joint (MCP1) in all specimens (11/11), similar to the configuration in

444   bonobos. In some macaques, the APB also originates from the palmar aponeurosis (4/7), while the

445   insertion can extend to the radial side of the proximal phalanx (3/7), which is common in humans (Gupta

446   and Michelsen-Jost, 2012). In one gibbon specimen, the APB is fused with the OPP (1/4), while some

447   macaque specimens show fusion between the APB and FPB (3/7). The APB functions as abductor of

448   the thumb both in gibbons and macaques, as well as a stabilizer for the TMC joint.

449

450   The *m. flexor pollicis brevis* (FPB), situated underneath the APB, originates from the flexor retinaculum

451   and it inserts with a short tendon onto the radial sesamoid bone of the MCP1 joint in all specimens

452   (13/13). A clear distinction between a superficial and deep head, as commonly observed in humans, may

453   occur in both gibbon (4/6) and macaques (2/7). In macaques, the FPB shows some fusion with the APB

454   at the origin (3/7), and with the oblique head of the ADP at insertion (3/7). In gibbons, the FPB can also

455   originate from both the flexor retinaculum and the volar side of MC1 (1/6), while its insertion can be

456   located at the ulnar side of the APB insertion (5/6) or at the base of the proximal phalanx of digit 1 (1/6).

457   In two gibbon specimens, the FPB shows some fusion with the OPP (2/6).

458

459   The *m. adductor pollicis* (ADP) always consists of a clearly separable transverse and oblique head in

460   macaques (7/7). The transverse head originates from the palmar base and shaft of MC3 (7/7) and inserts

461   onto the ulnar sesamoid bone of the MCP1 joint (7/7), in combination with the MCP joint (3/7) and/or

462   the proximal phalanx of digit 1 (4/7). In one specimen, muscle tissue extends towards the radial side of

463   MC2. The oblique head originates from the palmar base of MC1 (7/7), sometimes together with the

464   palmar base of MC2 (1/7) or MC3 (1/7). It also has its insertion onto the ulnar sesamoid bone of the

465   MCP1 joint (7/7), along with the ulnar (1/7) or radial (1/7) side of the proximal phalanx of digit 1 or the

466   MCP1 joint (1/7). In gibbons, both heads are usually clearly separable (4/6), however, occasionally they

467   are indistinguishable (2/6) in which case the ADP originates from the palmar base of MC1 and MC3

468   and inserts onto the ulnar sesamoid bone of the MCP 1 joint. The transverse head is similar to that of

469   macaques, with its origin on the palmar base and shaft of MC3 (4/4). It inserts onto the ulnar sesamoid

470   bone of the MCP1 joint (4/4) and may extend to the base of the proximal phalanx of digit 1 (1/4). The

471   oblique head either originates from the palmar base of MC1 (2/4), the base of MC2 (1/4), or the flexor

472   retinaculum (1/4). Like the transverse head, it inserts onto the ulnar sesamoid bone of the MCP1 joint

473   (4/4) with the occasional extension to the base of the proximal phalanx of digit 1 (2/4). The main function

474   of the ADP is adduction of the thumb.

475 The *m. opponens pollicis* (OPP) is a clearly separate muscle in macaques. It originates from the flexor

476 retinaculum, with some fibres originating from the APB and FPB (1/7) or the prepollex (2/7), and inserts

477 onto the radial side of the MC1 shaft. It has no contact with the sesamoid bones of the MCP1 joint. In

478 gibbons (and bonobos), the OPP is either completely fused with the FPB (1/5) or the APB (1/5), partially

479 fused with the FPB (1/5), or is present as a separate muscle (2/5). When separate, it originates from the

480 flexor retinaculum (2/2) in combination with the palmar base of MC1 (1/2), and it inserts onto the radial

481 side of the MC1 shaft (2/2). The OPP assists in opposition and adduction of the thumb.

482

483 The *m. palmaris brevis* (PB) is a well-developed muscle in macaques (7/7), while in gibbons (and

484 bonobos) no distinct PB can be identified (mostly fat tissue) in half of the specimens (2/4). The PB

485 originates from the flexor retinaculum and inserts onto the palmar aponeurosis in all primate specimens

486 (11/11). The PB of gibbons is similar in appearance to that of bonobos and humans, while the more

487 bulky PB in macaques is likely acting as a cushion to protect the ulnar artery and nerve during

488 quadrupedal walking.

489

490 The *m. abductor digiti minimi* (ADM) originates from the pisiform bone (7/7) in combination with the

491 flexor retinaculum and pisohamate ligament (4/7) in macaques (and bonobos). It inserts onto the ulnar

492 side of the MCP5 joint (7/7), in combination with the proximal phalanx (2/7) as seen in bonobos or

493 joining the FDM tendon (5/7). In two macaque specimens, the ADM is proximally fused with the FDM.

494 In gibbons, the ADM originates from either the pisiform bone (2/5) or the base of MC5 (3/5) and inserts

495 onto the ulnar side of the MCP5 joint (5/5). In one gibbon specimen, the ADM is partially fused with

496 the FDM. The ADM acts as abductor of digit 5.

497

498 The *m. flexor digiti minimi* (FDM) originates from the flexor retinaculum (7/7) and pisiform bone (2/7)

499 in macaques. It inserts onto the MCP5 joint (7/7), along with the ADM tendon (2/7) or the proximal

500 phalanx of digit 5 (4/7). In two macaque specimens, the FDM shows proximal fusion with the ADM. In

501 gibbons, the origin is more variable. The FDM can originate from the flexor retinaculum (3/5), the base

502 of MC5 (1/5), or the palmar aponeurosis (1/5). The FDM inserts onto the ulnar base of the proximal

503   phalanx of digit 5 in all gibbon specimens (5/5), and also bonobos. Proximal fusion with the ODM (1/5)

504   or distal fusion with the ADM (2/5) in gibbons is possible. The FDM acts as flexor of digit 5.

505

506   The *m. opponens digiti minimi* (ODM) originates from the flexor retinaculum and inserts onto the ulnar

507   side of the MC5 shaft in all macaque and gibbon specimens (11/11), similar to the bonobo configuration.

508   In one gibbon specimen, the ODM is completely fused with the FDM. In macaques, an additional origin

509   from the base of MC5 can be present (2/7). The function of the ODM is opposition of digit 5.

510

511   The *mm. lumbricales* (LUMB) of digit II-V each originate from the corresponding FDP tendon and

512   insert with a well-developed tendon onto the radial side of the extensor sheath at the proximal phalanx

513   of the corresponding digit in more than half of the specimens (9/15). However, some variation is possible

514   regarding the origin. In most macaque specimens, and also bonobos, LUMB III-V originate from two

515   FDP tendons (LUMB III from FDP II and III (5/6), LUMB IV from FDP III and IV (7/7), and LUMB

516   V from FDP IV and V (6/7)), which might aid force transmission. One macaque specimen shows a

517   particular configuration in which the lumbrical muscle was positioned in series with the FDP tendon

518   (see FDP description). In gibbons, LUMB II (1/8) and LUMB III (3/8) can originate from the FDP II

519   and III tendons, LUMB IV from FDP III and IV (2/8), and LUMB V from FDP IV and V (2/8) or solely

520   from FDP IV (1/8). In one gibbon specimen, proximal fusion of LUMB II-IV occurs near the origin on

521   the FDP tendons. The LUMB act as flexors of the MCP joints and extensors of the IP joints.

522

523   The primitive mammalian condition for the intermediate hand muscles is the presence of four *mm.*

524   *intermetacarpales* (IM) and ten *mm. flexores breves profundi* (FBP) (Diogo *et al.*, 2009; Diogo and

525   Tanaka, 2012; Diogo and Molnar, 2014; Lemelin and Diogo, 2016). In primates, two FBP have

526   differentiated: FBP I forms the FPB and OPP, FBP X forms the FDM and ODM. In humans, the IM (I-

527   IV) are fused with FBP (III, V, VI, VIII) to form the *mm. interossei dorsales* (IOD I-IV) (Diogo *et al.*,

528   2009). In all macaque specimens, both the IM and FBP are fused to form the IOD (7/7). In gibbons,

529   however, some individuals display an intermediate configuration where only one, two or three IOD are

530   present while the other IM and FBP remain present as separate muscles (5/8). This configuration is also

531 seen in bonobos (van Leeuwen *et al.*, 2018). In macaques, the presence of IOD might be important for

532 specific hand movements during quadrupedal walking, such as abduction of fingers to accommodate to

533 uneven terrain. A detailed visualisation of individual specimen's intermediate hand muscle

534 configurations is reported in the Supplementary material (**Fig. S3**). In addition to the IOD and IOP, a *m.*

535 *contrahens* (C5) is present in all but one macaque specimens (7/8). The C5 originates from the palmar

536 base of MC3 (partially fused with IOD II and III) and inserts on the radial side of the MCP5 joint, joining

537 the extensor mechanism (**Fig**. **6A**). No other contrahens muscles are observed in the macaque sample.

538 In contrast, the gibbons sample shows contrahens muscles associated with digit 2, 3 and 4 are present in

539 some specimens. Four specimens have a C2 inserting onto the ulnar side of the MCP2 joint (4/8) (**Fig.**

540 **6B**), and three specimens have a C4 and C5 inserting onto the ulnar side of, respectively, the MCP3 and

541 MCP4 joints (3/8). In the literature, however, the insertion of C4 and C5 has been described onto the

542 radial side of the MCP3 and MCP4 joint in gibbons (one *Hylobates lar* (Yamamoto, Murakami and

543 Ohtsuka, 1988)), macaques (two macaques (Yamamoto, Murakami and Ohtsuka, 1988)) and three

544 Japanese monkeys (Homma and Sakai, 1994). In one gibbon specimen, an additional muscle distinct

545 from the contrahens mucles described above is present. It originates from the IOD I and inserts onto the

546 radial side of the proximal phalanx of digit 1. This muscle is similar to the *m. contrahens digitorum*

547 (CD) of modern humans*,* as described by Tubbs et al. (Tubbs, Salter and Oakes, 2005).

548 **Discussion**

549 In this study, the configuration of the forearm and hand muscles of arboreal gibbons is compared with

550 that of terrestrial macaques. In addition, anatomical data from previous dissections on knuckle-walking

551 bonobos and bipedal humans are included to allow us to evaluate if the forearm and hand musculature

552 shows functional adaptations to locomotor behaviour (van Leeuwen et al., 2018).

553

554 <u>Upper arm musculature</u>

555 The most notable trait in the gibbon upper limb is the configuration of the short head of the *m. biceps*

556 *brachii* (Bb), which originates from the lesser tubercle of the humerus as such losing its function at the

557 glenohumeral joint, which is most likely a derived condition. In gibbons, the short head therefore

558 primarily acts as elbow flexor and forearm supinator (Michilsens *et al.*, 2009), while in macaques,

559 bonobos, and humans the short head of the Bb functions as shoulder flexor as it crosses the shoulder

560 joint and originates from the coracoid process of the scapula. According to Jungers and Stern (1980), in

561 gibbons the short head of the Bb forms a ventral muscle chain between the *m. pectoralis major* (PM)

562 and *m. flexor digitorum superficialis* (FDS) (Jungers and Stern, 1980), although this specific action

563 remains debated.

564

565 Other remarkable muscles are the *m. dorso-epitrochlearis* (DET) and *m. epitrochleoanconeus* (ETA).

566 The DET is present in both macaques and gibbons but has a slightly different configuration. In most

567 gibbons the DET inserts onto the medial epicondyle as opposed to the lateral side of the elbow in

568 macaques (Sonntag, 1922; Jungers and Stern, 1980; Michilsens *et al.*, 2009). In great apes, the DET also

569 inserts onto the medial epicondyle of the humerus (Diogo *et al.*, 2010, 2013; Diogo, Potau and Pastor,

570 2013), while in other primate taxa (*Alouatta, Saimiri, Callithrix*), the DET inserts onto the oleocranon

571 as seen in macaques (R. Diogo and Wood, 2012). Although Aversi-Ferreira et al. suggest that the DET

572 favors arboreal locomotion when it inserts onto the oleocranon and quadrupedal locomotion when it

573 inserts onto the epicondyle of the humerus (Aversi-Ferreira *et al.*, 2016), this contradicts our results.

574 The insertion onto the oleocranon in macaques might be important to help stabilize the elbow during

575 terrestrial quadrupedalism, while through its insertion onto the medial epicondyle of the humerus in

576 gibbons and bonobos, the DET could produce elbow and digital flexion (i.e. dorsal muscle chain) which

577 could be an advantage during brachiation in gibbons and climbing/clambering in bonobos (Jungers and

578 Stern, 1980), although this function is still debated as is the case for the ventral muscle chain (see above).

579 The ETA is a prominent muscle in macaques, but is not observed in gibbons (and humans). It may serve

580 to protect the ulnar nerve, running superficially through the cubital tunnel, and it potentially helps to

581 extend the forearm and/or stabilize the elbow joint during quadrupedal walking. However, there is still

582 some discussion about the presence or absence of this muscle across different primate taxa which

583 requires anatomical data from a larger nonhuman primate sample (Uscetin *et al.*, 2014; de Ruiter and

584 van Duinen, 2017; Diogo, Molnar and Wood, 2017).

585

586 Forearm rotators

587 The forearm rotators (BR, SUP, PT, PQ) have a very similar configuration in macaques and gibbons

588 (and bonobos), with a low variability in muscle architecture. This conserved morphology might indicate

589 that these muscles are under strong selective pressure and that their specific configuration is tightly

590 linked to forearm functionality. A two-headed configuration of the PT, as in modern human, was never

591 observed in neither the macaque nor the gibbon sample. In the PQ, on the other hand, a two-headed

592 configuration similar to humans was observed in two gibbon specimens. Due to the oblique orientation

593 of the muscle fibres, the primary function of the PQ is likely stabilization of the distal radioulnar joint

594 in macaques, gibbons and bonobos (Johnson and Shrewsbury, 1976). This implies that the PT is the

595 most important forearm pronator in these primates.

596

597 Extrinsic hand musculature

598 The dorsal compartment of the forearm shows a different configuration in macaques and gibbons. In

599 macaques, the fingers are controlled in pairs by the EDST and EDQQ. A similar organization is found

600 in the finger flexors of macaques, where the fingers are also controlled in pairs. We suggest that this

601 specific organization might aid in efficient positioning of the hand and fingers during palmi- or

602 digitigrade quadrupedal locomotion on uneven substrates. In gibbons, the little finger is controlled by a

603 separate EDM, and extension of digits 2-4 is coupled. This might indicate that simultaneous extension

604 of digits 2-4 in gibbons is important when reaching for and grasping an overhead support during

605 brachiation. Humans and bonobos have a separate EDM and EI, resulting in a functional dissociation

606 between the extension of the index finger and little finger. In humans, this is likely linked to the high

607 manual dexterity.

608 The ventral compartment shows an extraordinary variability within the FDS and FDS, both in gibbons

609 and macaques. This variability is also seen in bonobos. This high inter-individual variation might

610 indicate that these muscles are under mild selective pressure, and that the differences in configuration

611 of these muscles has no major influence on the functionality of the hand/fingers.

612

613 <u>Intrinsic hand musculature</u>

614 The thenar (APB, FPB, OPP, ADP) and hypothenar (ADM, FDM, ODM) muscles have a very similar

615 configuration in gibbons and macaques (and bonobos), with a varying degree of fusion between the

616 different muscles. The intermediate hand musculature is much more variable and a different

617 configuration is seen in macaques compared to gibbons. The intermediate hand muscles are organized

618 in palmar and dorsal interossei in macaques, similar to the human configuration, while gibbons display

619 a highly variable configuration with at least some unfused FBP and IM, a configuration also seen in

620 bonobos. In gibbons, various contrahens muscles can be present, while in macaques only a C5 is

621 observed. The intermediate hand muscles of gibbons show a higher degree of variation compared to

622 those of macaques, which might suggest that there are no major implications for the functionality of the

623 hand.

624

625 *Critical considerations*

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

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

628 nonhuman primates that was studied using a consistent protocol. Inherent to working with primate

629 cadavers is the lack of an equal distribution across species, sexes or ages, and most importantly,

630 sampling from captivity. However, given a healthy gene pool, we do not expect an impact of captivity

631 on muscle configuration. Given the genetic distance between macaques and gibbons, we cannot be

632   certain that the differences in muscle configuration are due to variation in locomotor behaviour and not

633   genetics. This is challenging to test, although it should not go unremarked as only two taxa are being

634   compared in detail, and there is no relative context of variation across other arboreal or terrestrial primate

635   taxa. We have tried to mitigate this issue by adding information on the forelimb and hand musculature

636   of two additional taxa, the bonobo and human, with different locomotor behaviours. However, the

637   gibbon group contains different genera and species in contrast to the homologous sampling of rhesus

638   macaques. This could explain the difference in variation of the FDS, FDP, and intermediate hand

639   muscles between gibbons and macaques, although we also observe a high variation in bonobos. The

640   contrasting results on the DET also stress the importance of broad phylogenetic sampling.

641   Despite these limitations, not only is this research important to obtain a detailed insight in the anatomy

642   of the gibbon and macaque forelimb and hand, but in combination with in vivo research and behavioural

643   studies it can be translated to complete form-function relationships of the primate hand which will aid

644   functional interpretation of fossil remains of nonhuman primates and hominins.

645

646   **Conclusion**

647   The overall configuration of the forelimb and hand musculature is highly comparable between the

648   different primate groups and follows the general primate condition. Most of the identified differences in

649   muscle configuration between arboreal gibbons, terrestrial macaques, knuckle-walking bonobos, and

650   bipedal humans seem to be related to the specific locomotor behaviour of each group though sampling

651   in a wider range of primate taxa is needed to further substantiate these functional adaptations.

Author contributions

EEV conceived the study; EEV, MJMV and TvL designed the study; MJMV and TvL performed the dissections; MJMV and EEV analysed the data and wrote the manuscript; all authors reviewed and approved the manuscript.

References

Almécija, S., Smaers, J. B. and Jungers, W. L. (2015) 'The evolution of human and ape hand proportions', *Nature Communications*, 6(1), pp. 1–11.

Andrews, P. and Groves, C. (1976) 'Gibbons and brachiation', in *Gibbons and Siamang: A Series of Volumes on the Lesser Apes, Vol. 4: Suspensory Behavior, Locomotion and other Behaviors of Captive Gibbons: Cognition (ed. Rumbaugh DM)*. Karger, pp. 167–218.

Aversi-Ferreira, T. A. *et al.* (2010) 'Comparative anatomical study of the forearm extensor muscles of Cebus libidinosus (Rylands et al., 2000; primates, cebidae), modern humans, and other primates, with comments on primate evolution, phylogeny, and manipulatory behavior', *Anatomical Record*, 293(12), pp. 2056–2070.

Aversi-Ferreira, T. A. *et al.* (2016) 'Comparative anatomy of the arm muscles of the Japanese monkey (Macaca fuscata) with some comments on locomotor mechanics and behavior', *Journal of Medical Primatology*, 45(4), pp. 165–179.

Boland, M. R., Spigelman, T. and Uhl, T. L. (2008) 'The Function of Brachioradialis', *Journal of Hand Surgery*. American Society for Surgery of the Hand, 33(10), pp. 1853–1859.

Caetano, E. B. *et al.* (2017) 'Anatomical variations of pronator teres muscle: predispositional role for nerve entrapment.', *Revista brasileira de ortopedia*, 52(2), pp. 169–175.

Celik, H., Sendemir, E. and Simsek, C. (1994) 'Anomalous insertion of abductor pollicus longus', *Journal of Anatomy*, 184(3), pp. 643–643.

Cheng, E. J. and Scott, S. H. (2000) 'Morphometry of Macaca mulatta forelimb. I. Shoulder and elbow muscles and segment inertial parameters', *Journal of Morphology*, 245(3), pp. 206–224.

Daver, G., Berillon, G. and Grimaud-Hervé, D. (2012) 'Carpal kinematics in quadrupedal monkeys: Towards a better understanding of wrist morphology and function', *Journal of Anatomy*, 220(1), pp. 42–56.

Demes, B. *et al.* (1998) 'Patterns of strain in the macaque ulna during functional activity', *American Journal of Physical Anthropology*, 106(1), pp. 87–100.

Diogo, R. *et al.* (2009) 'From fish to modern humans - Comparative anatomy, homologies and evolution of the pectoral and forelimb musculature', *Journal of Anatomy*, 214(5), pp. 694–716.

694   Diogo, R. *et al.* (2010) *Photographic and Descriptive Musculoskeletal Atlas of Gorilla: With Notes on*

695   *the Attachments, Variations, Innervation, Synonymy and Weight of the Muscles*. CRC Press.

696   Diogo, R. *et al.* (2013) *Photographic and Descriptive Musculoskeletal Atlas of Orangutans: with notes*

697   *on the attachments, variations, innervations, function and synonymy and weight of the muscles*. CRC

698   Press.

699   Diogo, R. and Molnar, J. (2014) 'Comparative Anatomy, Evolution, and Homologies of Tetrapod

700   Hindlimb Muscles, Comparison with Forelimb Muscles, and Deconstruction of the Forelimb-

701   Hindlimb Serial Homology Hypothesis', *The Anatomical Record*, 297(6), pp. 1047–1075.

702   Diogo, R., Molnar, J. L. and Wood, B. (2017) 'Bonobo anatomy reveals stasis and mosaicism in

703   chimpanzee evolution, and supports bonobos as the most appropriate extant model for the common

704   ancestor of chimpanzees and humans', *Scientific Reports*. Springer US, 7(1), pp. 1–8.

705   Diogo, R., Potau, J. M. and Pastor, J. F. (2013) *Photographic and Descriptive Musculoskeletal Atlas of*

706   *Chimpanzees: With Notes on the Attachments, Variations, Innervation, Function and Synonymy and*

707   *Weight of the Muscles*. CRC Press.

708   Diogo, R., Richmond, B. G. and Wood, B. (2012) 'Evolution and homologies of primate and modern

709   human hand and forearm muscles, with notes on thumb movements and tool use', *Journal of Human*

710   *Evolution*. Elsevier Ltd, 63(1), pp. 64–78.

711   Diogo, R. and Tanaka, E. M. (2012) 'Anatomy of the pectoral and forelimb muscles of wildtype and

712   green fluorescent protein-transgenic axolotls and comparison with other tetrapods including humans: a

713   basis for regenerative, evolutionary and developmental studies', *Journal of Anatomy*, 221(6), pp. 622–

714   635.

715   Diogo, R. and Wood, A. (2012) *Comparative Anatomy and Phylogeny of Primate Muscles and Human*

716   *Evolution*.

717   Diogo, Rui and Wood, B. (2012) 'Violation of Dollo's law: Evidence of muscle reversions in primate

718   phylogeny and their implications for the understanding of the ontogeny, evolution, and anatomical

719   variations of modern humans', *Evolution*, 66(10), pp. 3267–3276.

720   Fuss, F. and Wurzl, G. (1990) 'Median nerve entrapment. pronator teres syndrome', *Surgical and*

721   *Radiologic Anatomy*, 12(4), pp. 267–271.

722 Georgiev, G. P. *et al.* (2018) 'Extensor indicis proprius muscle and its variants together with the

723 extensor digitorum brevis manus muscle: a common classification. Clinical significance in hand and

724 reconstructive surgery', *Surgical and Radiologic Anatomy*. Springer Paris, 40(3), pp. 271–280.

725 Gessini, L. *et al.* (1981) 'Ulnar nerve entrapment at the elbow by persistent epitrochleoanconeus

726 muscle. Case report', *Journal of Neurosurgery*, 55(5), pp. 830–831.

727 Gibbs, S., Collard, M. and Wood, B. A. (2002) 'Soft-tissue anatomy of the extant hominoids : a review

728 and phylogenetic analysis', *Journal of Anatomy*, 200, pp. 3–49.

729 Gupta, S. and Michelsen-Jost, H. (2012) 'Anatomy and Function of the Thenar Muscles', *Hand*

730 *Clinics*, 28(1), pp. 1–7.

731 Hartz, C. R. *et al.* (1981) 'The pronator teres syndrome: Compressive neuropathy of the median

732 nerve', *Journal of Bone and Joint Surgery - Series A*, 63(6), pp. 885–890.

733 Hayama, S., Chatani, K. and Nakatsukasa, M. (1994) 'The Digitigrade Hand and Terrestrial

734 Adaptation in Japanese Macaques', *Anthropological Science*, 102, pp. 115–125.

735 Hirasawa, Y., Sawamura, H. and Sakakida, K. (1979) 'Entrapment neuropathy due to bilateral

736 epitrochleoanconeus muscles: A case report', *Journal of Hand Surgery*. American Society for Surgery

737 of the Hand, 4(2), pp. 181–184.

738 Homma, T. and Sakai, T. (1994) 'Intrinsic Hand Muscles of the Japanese Monkey, Macaca fuscata',

739 *Anthropological Science*, 102, pp. 85–95.

740 Horn, R. N. van (1972) 'Structural Adaptations to Climbing in the Gibbon Hand', *American*

741 *Anthropologist*, 74(3), pp. 326–334.

742 Jamieson, R. W. and Anson, B. J. (1952) 'The relation of the median nerve to the heads of origin of

743 the pronator teres muscle, a study of 300 specimens.', *Quarterly bulletin. Northwestern University*

744 *(Evanston, Ill.). Medical School*, 26(1), pp. 34–5.

745 Johnson, R. K. and Shrewsbury, M. M. (1976) 'The pronator quadratus in motions and in stabilization

746 of the radius and ulna at the distal radioulnar joint', *Journal of Hand Surgery*. American Society for

747 Surgery of the Hand, 1(3), pp. 205–209.

748 Jungers, W. L. and Stern, J. T. (1980) 'Telemetered electromyography of forelimb muscle chains in

749 gibbons (Hylobates lar)', *Science*, 208(4444), pp. 617–619.

750   Lacey, T. I., Goldstein, L. A. and Tobin, C. E. (1951) 'Anatomical and clinical study of the variations

751   in the insertions of the abductor pollicis longus tendon, associated with stenosing tendovaginitis',

752   *Journal of Bone and Joint Surgery*, 33(2), pp. 347–350.

753   Langdon, J. H. (1990) 'Variations in cruropedal musculature', *International Journal of Primatology*,

754   11(6), pp. 575–606.

755   van Leeuwen, T. *et al.* (2018) 'Insights into the musculature of the bonobo hand', *Journal of Anatomy*,

756   233(3), pp. 328–340.

757   Lemelin, P. and Diogo, R. (2016) 'Anatomy, Function, and Evolution of the Primate Hand

758   Musculature', in, pp. 155–193.

759   Lemelin, P. and Schmitt, D. (1998) 'The relation between hand morphology and quadrupedalism in

760   primates', *American Journal of Physical Anthropology*, 105(2), pp. 185–197.

761   Lewis, O. J. (1985) 'Derived morphology of the wrist articulations and theories of hominoid evolution.

762   Part II. The midcarpal joints of higher primates', *Journal of Anatomy*, 142(3), pp. 151–172.

763   Liu, M.-J., Xiong, C.-H. and Hu, D. (2016) 'Assessing the manipulative potentials of monkeys, apes

764   and humans from hand proportions: implications for hand evolution', *Proceedings of the Royal Society*

765   *B: Biological Sciences*, 283, pp. 1–9.

766   Macalister, A. (1868) 'On the Nature of the Coronoid Portion of the Pronator Radii Teres.', *Journal of*

767   *anatomy and physiology*, 2(1), pp. 8–12.

768   Manter, J. T. (1938) 'The dynamics of quadrupedal locomotion', *Journal of Experimental Biology*, 15,

769   pp. 522–540.

770   Marzke, M. W. (2009) 'Upper-limb evolution and development', *Journal of Bone and Joint Surgery -*

771   *Series A*, 91-A, pp. 26–30.

772   Mcmahon, T., Zijl, P. C. M. Van and Gilad, A. A. (2015) 'The Advantage of Throwing the First

773   Stone: How Understanding the Evolutionary Demands of Homo sapiens is Helping Us Understand

774   Carpal Motion', *J Am Acad Orthop Surg*, 27(3), pp. 320–331.

775   McMurrich, J. P. (1903) 'The phylogeny of the forearm flexors', *American Journal of Anatomy*, 2(2),

776   pp. 177–209.

777   Michilsens, F. *et al.* (2009) 'Functional anatomy of the gibbon forelimb: Adaptations to a brachiating

778   lifestyle', *Journal of Anatomy*, 215(3), pp. 335–354.

779   Michilsens, F. *et al.* (2010) 'Muscle moment arms and function of the siamang forelimb during

780   brachiation', *Journal of Anatomy*, 217(5), pp. 521–535.

781   Miller, R. A. (1932) 'Evolution of the pectoral girdle and fore limb in the Primates', *American Journal*

782   *of Physical Anthropology*, 17(1), pp. 1–56.

783   Le Minor, J. M. (1994) 'The Sesamoid Bone of Musculus abductor pollicis longus (Os radiale

784   externum or Prepollex) in Primates', *Cells Tissues Organs*, 150(3), pp. 227–231.

785   Natsis, K. *et al.* (2012) 'Dorsoepitrochlearis muscle: An unknown cause of shoulder motion limitation

786   and axilla deformity', *Journal of Orthopaedic Science*. Elsevier Masson SAS, 17(2), pp. 186–188.

787   Nayak, S. R. *et al.* (2008) 'Multiple variations of the extensor tendons of the forearm', *Romanian*

788   *Journal of Morphology and Embryology*, 49(1), pp. 97–100.

789   Nigst, H. and Dick, W. (1979) 'Syndromes of compression of the median nerve in the proximal

790   forearm (pronator teres syndrome; anterior interosseous nerve syndrome)', *Archives of Orthopaedic*

791   *and Traumatic Surgery*, 93(4), pp. 307–312.

792   Orr, C. M. *et al.* (2010) 'Studying primate carpal kinematics in three dimensions using a computed-

793   tomography-based markerless registration method', *Anatomical Record*, 293(4), pp. 692–701.

794   Orr, C. M. (2017) 'Locomotor Hand Postures, Carpal Kinematics During Wrist Extension, and

795   Associated Morphology in Anthropoid Primates', *Anatomical Record*, 300(2), pp. 382–401.

796   Orr, C. M. (2018) 'Kinematics of the anthropoid os centrale and the functional consequences of

797   scaphoid-centrale fusion in African apes and hominins', *Journal of Human Evolution*. Elsevier Ltd,

798   114, pp. 102–117.

799   Prime, J. M. and Ford, S. M. (2016) 'Hand Manipulation Skills in Hylobatids', in *Evolution of*

800   *Gibbons and Siamang*, pp. 269–289.

801   Richmond, B. G. (2001) 'Functional Morphology of the Midcarpal Joint in Knuckle-Walkers and

802   Terrestrial Quadrupeds', *Human Origins and Environmental Backgrounds*, pp. 105–122.

803   de Ruiter, G. C. W. and van Duinen, S. G. (2017) 'Complete Removal of the Epitrochleoanconeus

804   Muscles in Patients with Cubital Tunnel Syndrome: Results From a Small Prospective Case Series',

805   *World Neurosurgery*. Elsevier Inc, 104, pp. 142–147.

806   Sarmiento, E. E. (1988) 'Anatomy of the hominoid wrist joint: Its evolutionary and functional

807   implications', *International Journal of Primatology*, 14(A), pp. 1–345.

808   Sehirli, Ü. S., Cavdar, S. and Yüksel, M. (2001) 'Bilateral variations of the abductor pollicis longus',

809   *Annals of Plastic Surgery*, 47(5), pp. 582–583.

810   Sonntag, C. F. (1922) 'On the Anatomy of the Drill (Mandrillus leucophaeus).', *Proceedings of the*

811   *Zoological Society of London*, 92(2), pp. 429–453.

812   Stern, J. T. and Larson, S. G. (2001) 'Telemetered electromyography of the supinators and pronators

813   of the forearm in gibbons and chimpanzees: Implications for the fundamental positional adaptation of

814   hominoids', *American Journal of Physical Anthropology*, 115(3), pp. 253–268.

815   Straus, W. L. (1941) 'The phylogeny of the human forearm extensors (Concluded)', *Human Biology*,

816   13(2).

817   Stuart, P. R. (1996) 'Pronator quadratus revisited', *Journal of Hand Surgery: European Volume*,

818   21(6), pp. 714–722.

819   Susman, R. L., Jungers, W. L. and Stern, J. T. (1982) 'The functional morphology of the accessory

820   interosseous muscle in the gibbon Hand : determination of locomotor and manipulatory compromises',

821   *Journal of anatomy*, 134(1), pp. 111–120.

822   Suwannakhan, A., Tawonsawatruk, T. and Meemon, K. (2016) 'Extensor tendons and variations of the

823   medial four digits of hand: a cadaveric study', *Surgical and Radiologic Anatomy*. Springer Paris,

824   38(9), pp. 1083–1093.

825   Thompson, N. E. *et al.* (2018) 'Unexpected terrestrial hand posture diversity in wild mountain

826   gorillas', *American Journal of Physical Anthropology*, (December 2017), pp. 1–11.

827   Thompson, N. W., Mockford, B. J. and Cran, G. W. (2001) 'Absence of the palmaris longus muscle:

828   A population study', *Ulster Medical Journal*, 70(1), pp. 22–24.

829   Tubbs, R. S., Salter, E. G. and Oakes, W. J. (2005) 'Contrahentes digitorum muscle', *Clinical*

830   *Anatomy*, 18(8), pp. 606–608.

831   Tuttle, R. H. (1967) 'Knuckle-walking and the evolution of hominoid hands', *American Journal of*

832   *Physical Anthropology*, 26(2), pp. 171–206.

833   Tuttle, R. H. (1969) 'Quantitative and Functional Studies on the Hands of the Anthropoidea. I. The

834   Hominoidea', *Journal of Morphology*, 128(3), pp. 309–363.

835   Uscetin, I. *et al.* (2014) 'Ulnar nerve compression at the elbow caused by the epitrochleoanconeus

836   muscle: A case report and surgical approach', *Turkish Neurosurgery*, 24(2), pp. 266–271.

837   Vereecke, E. E. *et al.* (2005) 'Functional analysis of the foot and ankle myology of gibbons and

838   bonobos.', *Journal of anatomy*, 206(5), pp. 453–76.

839   Vereecke, E. E., D'Août, K. and Aerts, P. (2006) 'Locomotor versatility in the white-handed gibbon

840   (Hylobates lar): A spatiotemporal analysis of the bipedal, tripedal, and quadrupedal gaits', *Journal of

841   Human Evolution*, 50(5), pp. 552–567.

842   Williams, S. A. (2010) 'Morphological integration and the evolution of knuckle-walking', *Journal of

843   Human Evolution*. Elsevier Ltd, 58(5), pp. 432–440.

844   Yamamoto, C., Murakami, T. and Ohtsuka, A. (1988) 'Homology of the adductor pollicis and

845   contrahentes muscles: a study of monkey hands.', *Acta medica Okayama*, 42(4), pp. 215–226.

846   Yoshida, Y. (1995) 'Anatomical studies on the Extensor Pollicis et Indicis Accessorius Muscle and the

847   Extensor Indicis Radialis Muscle in Japanese', *Okajimas Folia Anat. Jpn.*, 71(6).

848   Zihlman, A. L., Farland, R. K. M. C. and Mi, G. (2011) 'Functional Anatomy and Adaptation of Male

849   Gorillas (Gorilla gorilla gorilla) with Comparison to Male Orangutans (Pongo pygmaeus)',

850   *Anatomical Record*, 294, pp. 1842–1855.

851

852 **Figure legends**

853 **Fig. 1** – The well-developed m. epitrochleoanconeus (ETA) of macaques. It originates from the medial

854 epicondyle of the humerus and inserts onto the medial border of the oleocranon. As it crosses the cubital

855 tunnel, the ETA protects the ulnar nerve. Activation of the ETA potentially facilitates forearm extension

856 and/or stabilization of the elbow joint during quadrupedal walking.

857 **Fig. 2** – A) *m. extensor digiti secundi et tertii proprius* (EDST) and *m. extensor digiti quarti et quinti*

858 *proprius* (EDQQ) of macaques; B) *m. extensor digitorum brevis* (EDB) and *m. extensor digiti minimi*

859 (EDM) of gibbons. Note that in macaques the fingers are controlled in pairs, which might aid in efficient

860 positioning of the hand and fingers on uneven terrain during quadrupedal walking. In contrast, extension

861 of the little finger in gibbons is separate from the extension of digits 2-4, suggesting that simultaneous

862 extension of digits 2-4 in gibbons might be important when reaching or grasping a support during

863 brachiation.

864 **Fig. 3** – Illustration of the *m. abductor pollicis longus* (APL): A) in macaques, the APL consists of one

865 muscle belly with a tendon that splits at the level of the trapezium, inserting with one slip onto the base

866 of MC1 and with the other onto the prepollex; B) in gibbons, the APL consists of two muscle bellies

867 each with its own tendon, APL I (insertion on the base of MC1) and APL II (insertion on the trapezium).

868 **Fig. 4** – The *m. flexor digitorum profundus* (FDP) in macaques (A, B) and gibbons (C, D): A) common

869 FDP configuration with three fused muscle bellies, one for digit 1 to 3 (FDP I-III), one for digit 4 (FDP

870 IV) and one for digit 5 (FDP V), the FDP is connected to the FDS with an additional muscle belly (*);

871 B) unusual FDP configuration with two muscle bellies (FDP I-III and FDP IV-V), the tendons to digits

872 2 and 3 show a tendon-lumbrical-tendon configuration in which the first two lumbricals form a single

873 unit with the FDP tendons instead of originating from these tendons; C) common FDP configuration

874 with two partially fused muscle bellies, one for digit 1 (FDP I) and one for digits 2 to 5 (FDP II-V); D)

875 unusual FDP configuration with two muscle bellies (FDP I-II and FDP III-V), the tendons to digits 2

876 and 3 partly originate from the FDS (*).

877 **Fig. 5** – Overview of the general organization of the thenar musclulature in A) macaques and B) gibbons.

878 In gibbons, there is a clear distinction between the superficial and deep head of the FPB.

879   APB (*m. abductor pollicis brevis*), FPB (*m. flexor pollicis brevis*), FPBs (*m. flexor pollicis brevis*,

880   superficial head), FBPd (*m. flexor pollicis brevis*, deep head), OPP (*m. opponens pollicis*), ADPo (*m.*

881   *adductor pollicis*, oblique head), ADPt (*m. adductor pollicis*, transverse head).

882   **Fig. 6** – Two examples of a contrahens muscle: A) C5 of macaques, which originates from the palmar

883   base of MC3 (partially fused with IOD II and III) and inserts on the radial side of the MCP5 joint (joining

884   the extensor mechanism); B) C2 of gibbons, which has a varying origin and inserts onto the ulnar side

885   of the MCP2 joint.

886 **Supplementary material**

887 **Fig. S1** – Configuration of the *m. extensor digitorum communis* (EDC) in gibbons. The tendon to digit

888 2 splits off proximally to the wrist, the tendon to digit 5 splits off at the level of the wrist, and the tendons

889 to digits 3 and 4 split off at the dorsum of the hand and commonly interconnect with the tendons of

890 digits 2 and 5 (juncturae tendineum).

891 **Fig. S2** – The architecture of the *m. flexor digitorum superficialis* (FDS) in macaques consists of three

892 partially fused muscle bellies that are folded together; (1) a muscle running to digit 2 (FDS II), which

893 shows a distinct belly-tendon-belly-tendon configuration (cfr. bonobos), (2) a muscle belly with two

894 tendons inserting onto digit 3 and 4 (FDS III-IV), and (3) a muscle with one tendon inserting onto digit

895 5 (FDS V). In this example, the order of the tendons is II – V – IV – III when the FDS is folded open.

896 **Fig. S3** – Configuration of the *mm. intermetacarpales* (IM), *mm. flexores breves profundi* (FBP), *mm.*

897 *interossei palmares* (IOP), and *mm. interossei dorsales* (IOD). In macaques, the IM and FBP are fused

898 to form the IOD (similar to modern humans). In gibbons, some individuals display an intermediate

899 configuration where only one, two or three IOD are present while the other IM and FBP remain present

900 as separate muscles.