

The gibbon's Achilles tendon revisited: consequences for the evolution of the great apes?

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1 **The gibbon's Achilles tendon revisited: consequences for the**
2 **evolution of the great apes?**

3

4

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25

26 **Abstract**

27

28 The well-developed Achilles tendon in humans is generally interpreted as an adaptation for mechanical
29 energy storage and reuse during cyclic locomotion. All other extant great apes have a short tendon
30 and long-fibered triceps surae, which is thought to be beneficial for locomotion in a complex arboreal
31 habitat as this morphology enables a large range of motion. Surprisingly, highly arboreal gibbons show
32 a more human-like triceps surae with a long Achilles tendon. Evidence for a spring-like function similar
33 to humans is not conclusive.

34 We revisit and integrate our anatomical and biomechanical data to calculate the energy that can be
35 recovered from the recoiling Achilles tendon during ankle plantar flexion in bipedal gibbons. Only 7.5%
36 of the required external positive work in a stride can come from tendon recoil, yet it is delivered at an
37 instant when the whole body energy level drops. Consequently, an additional similar amount of
38 mechanical energy must simultaneously dissipate elsewhere in the system. Altogether, this challenges
39 the concept of an energy-saving function in the gibbon's Achilles tendon.

40 Cercopithecids, sister group of the apes, also have a human-like triceps surae. Therefore, a well-
41 developed Achilles tendon, present in the last common 'Cercopithecoidea-Hominoidea' ancestor,
42 seems plausible. If so, the gibbon's anatomy represents an evolutionary relict ('no harm – no benefit'),
43 and the large Achilles tendon is not the premised key-adaptation in humans (although the spring-like
44 function may have further improved during evolution). Moreover, the triceps surae anatomy of extant
45 non-human great apes must be a convergence, related to muscle control and range of motion. This
46 perspective accords with the suggestions put forward in the literature that the last common hominoid
47 ancestor was not necessarily great-ape-like, but might have been more similar to the small-bodied
48 catarrhines.

49

50 *State of the art*

51

52 When looking at the gross morphology of the triceps surae in the extant great apes¹, the difference
53 between humans and the other species is conspicuous (Fig1). In humans, the bellies of the
54 gastrocnemius muscle are short-fibered and pennate, and insert together with the soleus via a well-
55 developed Achilles tendon onto the calcaneus (e.g. Frey, 1913; Swindler and Wood, 1973; Standing,
56 2016). In contrast, in non-human great apes, an Achilles tendon is externally barely visible and the
57 bellies of the gastrocnemius muscle are extended with a more parallel orientation of the long muscle
58 fibres (e.g. Frey, 1913; Hanna and Schmitt, 2011; Swindler and Wood, 1973; Thorpe et al, 1999;
59 Vereecke et al., 2005a; Myatt et al, 2011). These contrasting morphologies correlate with differences
60 in locomotor repertoire: while orangutans, gorillas, chimpanzees and bonobos share a wide range of,
61 often arboreal, locomotor behaviours such as orthograde (i.e. upright trunk) suspension and
62 clambering, quadrupedalism, vertical climbing and hand-assisted bipedalism (see Thorpe and
63 Crompton, 2006 and Hunt, 2016 for reviews), modern humans are primarily terrestrial habitual bipeds.

64 The well-developed human's Achilles tendon is considered to be an adaptation for energy-efficient
65 cyclic locomotion and is assumed to have originated at some point after 3 million years (Myr) ago in
66 the genus *Homo* (Bramble and Lieberman, 2004). The tendon is stretched and loaded with strain
67 energy during initial dorsiflexion (decreasing ankle angle) of the stance phase and recoils during the
68 plantar flexion (increasing ankle angle) later in stance to power the foot push-off. As such, the Achilles
69 tendon is a component of the spring element in the SLIP-mechanism (Spring Loaded Inverted
70 Pendulum; Full and Koditschek, 1999; Geyer et al., 2006) that is optimally functioning during running:
71 the kinetic and potential energy that must be extracted from the system at the whole body level early
72 in stance (the so-called negative external work) is converted - at least partly - to strain energy in the
73 spring element and this is recycled to power part of the subsequent push off (e.g. Alexander, 2003;
74 Bertram, 2016). In humans, at a running speed of 4.5 ms⁻¹, 35% of the required external positive work
75 per stride can thus be recovered from the recoil of the Achilles tendon (e.g. Alexander, 1991, 2003).

76 The morphology of the non-human great apes, on the other hand, is generally considered to represent
77 the ancestral state (Bramble and Lieberman, 2004), being beneficial when moving about in an arboreal
78 environment. Movement patterns are less cyclic and less uniform and the long-fibered muscles
79 facilitate muscular control over a large range of motion, which is essential to deal efficiently with the
80 high 3-dimensional complexity of the habitat and to respond to the compliance of the substrate (Myatt
81 et al., 2011; Preuschoft et al., 1992; Thorpe et al., 1999).

82 Remarkably, given their phylogenetic position and their largely arboreal lifestyle, the gibbon's triceps
83 surae has a more human-like appearance (Fig1). There is a long and well-developed Achilles tendon,
84 firmly attaching onto the heel bone, and the muscle bellies of the gastrocnemius are short-fibered and
85 pennate (Frey, 1913; Vereecke et al., 2005a). Questioning the adaptive meaning of this morphology
86 in the primarily brachiating lesser apes seems essential to understand the evolution of locomotor
87 diversity in the apes.

88 Because of the high resemblance between the gibbon and human Achilles tendon, it is tempting to
89 search for an explanation for gibbons that follows a similar line of thought to that assumed for the
90 human Achilles tendon. When on the ground to cross gaps between trees that are too large to cross
91 arboreally, or when moving on large tree branches, gibbons most often use a bipedal gait (Verecke
92 et al., 2006a; Baldwin and Teleki, 1976; Fleagle, 1976; Gittins, 1983; Sati and Alfred, 2002). Despite

¹ Here, orangutans, gorillas, chimpanzees, bonobos *and* humans are considered the extant great apes (i.e. extant Hominidae).

93 the presence of a double support phase (i.e. both feet on the ground simultaneously; there is no aerial
94 phase in the bipedal cycle), this gait must be classified as ‘grounded running’ (cf. Vereecke et al.,
95 2006b,c) as is also found for terrestrial locomotion in birds (e.g. Andrada et al., 2013, 2015): at the
96 whole body level, kinetic and potential energy fluctuations accord to the dynamics of running (i.e. in-
97 phase decrease and subsequent increase of kinetic and potential energy in each single step; Vereecke
98 et al., 2006b, Vereecke & Aerts, 2008). As such, the SLIP-mechanism might be functional. Moreover,
99 the safety factor of the Achilles tendon (i.e. tendon strength over tendon loading) appears, together
100 with that of the patella tendon, to be the lowest of all the hind limb muscles in the gibbon (Vereecke
101 et al., 2005a; Channon et al., 2009; Vereecke and Channon, 2013). A low (but safe) safety factor is
102 required for functionally significant energy storage and recoil. Furthermore, the ratio of the tendon
103 length over the effective muscle fascicle length (i.e. accounting for pennation angle) is rather high for
104 the triceps surae (Vereecke et al., 2005a; Channon et al., 2009; Vereecke & Channon, 2013). Such
105 muscle-tendon morphology can be expected if the tendon needs to do the work. One may also look
106 at this from a slightly different perspective. Channon et al. (2009) presented the relationship between
107 the physiological cross-sectional area (PCSA; measure for potential maximal load) of the limb muscles
108 and their fascicle length (measure for the potential shortening), thus representing a sort of concentric
109 work space, as it expresses the potential maximal load against potential shortening. Muscle-tendon-
110 complexes that are part of the spring-element of the SLIP-mechanism should combine a high PCSA or
111 force output with short fibres, enabling the tendon to do most of the concentric work. Surprisingly, all
112 plantar flexors occupy a rather ‘unspecialized’ region in the concentric work space where small PCSA
113 and short fibres are combined (see Channon et al., 2009). In this respect, gibbons appear to be no
114 different from the non-human great apes.

115

116 *The role of the tendon revisited*

117 The evidence provided above for the gibbon’s Achilles tendon working as energy-saving device during
118 ‘grounded’ running is indirect. Moreover, its identification as ‘unspecialized’ in the muscle-tendon
119 workspace could be interpreted as a counter-indication for this role and former analyses (Vereecke et
120 al., 2006b; Vereecke and Aerts, 2008) were also unable to categorically demonstrate an energy-saving
121 role during grounded running. Here we take a novel approach to resolve this debate. The amount of
122 strain energy that is stored *in vivo* in the tendon of the white-handed gibbon (*Hylobates lar*) during
123 walking steps at the onset of plantar flexion, and that can thus potentially be recovered via recoil, is
124 calculated and compared with the mechanical work input needed at the whole body level (the so-
125 called positive external work) to complete a walking cycle (i.e. stride = left + right step). In order to do
126 so, the kinematic, dynamic, material property and anatomical data collected by Vereecke et al.
127 (2005a,b, 2006a,b,c), Vereecke and Aerts (2008), Channon et al. (2009, 2010b) and Vereecke and
128 Channon (2013) will be combined in a new synthesis. (A short synopsis of the Materials and Methods
129 of these papers is included as supplementary material).

130 When the Centre Of Pressure [COP; instantaneous position of the point of application of the resultant
131 Ground Reaction Force (GRF) at the plantar surface of the foot] is known throughout the ground
132 contact phase, the moment of the GRF with respect to the ankle joint can be determined quite
133 accurately as a function of stance time by multiplying at any instant the GRF with the perpendicular
134 distance from the joint centre to the GRF (Fig2A)². This moment (dashed curve) is presented together
135 with the ankle joint kinematics (thin curve) as a function of normalized stance time in Fig2B. For the

² Inertial effects can safely be neglected in this account, given the small mass (1.2% of total body mass) and the low accelerations of the slender foot segments (cf. Vereecke et al., 2006b; Vereecke and Aerts, 2008).

136 larger part of stance (about 79%), the ankle joint dorsiflexes and only during the last 21% of stance,
137 does it plantar flex again, to power the foot push-off. At the onset of plantar flexion, the (minimal)
138 ankle joint angle reaches 103° and the *in vivo* moment of the GRF that tends to dorsiflex the joint
139 equals 2.60 Nm (see Fig2B).

140 At any instant in the stride, the moment of the GRF with respect to the ankle must be balanced by the
141 muscle-tendon-systems that cross the joint. It is therefore possible to estimate the *in vivo* tensile force
142 acting along the Achilles tendon at the onset of ankle plantar flexion, provided that the moment arm
143 of the Achilles tendon (i.e. perpendicular distance from the joint centre to the tendon; Fig2A) at the
144 coinciding joint angle (103°) is known^{3,4}. Muscle moment arms were accurately determined by
145 Channon et al. (2010b). For an ankle joint of 103°, the moment arm of the Achilles tendon in *Hylobates*
146 *lar* recalculates to 1.48 cm. Consequently, the *in vivo* tensile force along the tendon at the onset of
147 ankle plantar flexion equals 175.67 N [i.e. 2.60 Nm/(1.48 cm 10⁻²)].

148 Cyclic tensile load-deformation tests on the Achilles tendon were carried out by Vereecke and Channon
149 (2013). The tendon's behaviour conforms to that of the text book examples (e.g. Alexander, 2003):
150 apart from a toe-region at low loads, the load-deformation relationship is rather linear at higher
151 loading; at recoil, a hysteresis of on average 13.5% (mean ± SD = 3.4%; n=14) is observed (i.e. difference
152 between loading and unloading energy). The slope of the linear loading part gives the stiffness, which
153 is on average 99.6 Nmm⁻¹ (mean ± SD = 42.7 Nmm⁻¹; n=14). Since the tensile force divided by the
154 stiffness equals the extension of the tendon, the *in vivo* stretch of the Achilles tendon at the onset of
155 the ankle plantar flexion amounts to 1.76 mm (i.e. 175.67 N/99.6 Nmm⁻¹).

156 Finally, the amount of strain energy that is stored in the Achilles tendon at the onset of ankle plantar
157 flexion (and which is available to power the plantar flexion) is represented by the area under the load-
158 deformation curve. Because of the largely linear behaviour when loaded, this area is given by (175.67
159 N x 1.76 mm 10⁻³)/2 which equals 0.15 J.

160 At the whole-body level, the positive work needed to complete a stride amounts on average to 3.56 J
161 (Vereecke et al., 2006b)⁵. Taking the 13.5% hysteresis into account, 0.26 J [i.e. (0.15 J left + 0.15 J right)
162 x (1-0.135)] of this can theoretically be recovered from the recoiling left and right Achilles tendons
163 during the push-off of the feet. This amounts to merely 7.5% of the required external positive work
164 per stride. This amount can directly be compared with the 35% mentioned above for humans (but see
165 also⁶). More importantly, however, plantar flexion seems to come at the wrong instant. To be

³ In this approach is assumed that the balancing activity is taken entirely by the triceps surae, hence solely acting along the Achilles tendon. As such, the estimate for the tensile force along the tendon at the onset of ankle plantar flexion represents a maximal estimate, as co-contraction of the digital flexors would result in a reduction of the Achilles tendon stress.

⁴ It should be noted that co-contraction of the dorsiflexors (which could lead to higher tensile stress in the Achilles tendon) at that instant in stance is highly unlikely.

⁵ This must be considered as a minimum estimated for the required positive work input, as this concerns the external work only (i.e. whole body level; movements of the Body Centre Of Mass or BCOM). Swinging the limbs with respect to the BCOM can represent a considerable extra cost (see for instance Marsh et al., 2004).

⁶ Similar approaches on human running (4.5 ms⁻¹) show 35% of the external positive work (mechanical energy) comes from elastic recoil of the Achilles tendon during the second half of the ground contact phase in each cycle; i.e. energy stored during the first half of stance (Ker et al., 1987, Alexander, 1991, 2003). This is probably even a conservative estimate. Lai et al. (2014) show that at comparable running speeds, energy recovery from the triceps surae tendon can amount to more than 50J per step (which is about 140% of what was determined from the former ex-vivo experiments; see Lai et al., 2014 and references therein). Clearly, the eccentric-concentric work of the triceps surae during running steps will still require metabolic energy, even when the entire strain cycle of the muscle tendon unit (MTU) is taken by the tendon. Cross-bridge cycling is needed to prevent extension of the muscle belly and enable loading of the tendon (e.g. Fletcher and MacIntosh, 2015).

166 effective, tendon recoil should happen when the mechanical whole body energy level increases (i.e.
167 mechanical energy is added to the system). However, most often (step-to-step variability is observed)
168 plantar flexion just occurs when, at the whole body level, mechanical energy must be extracted from
169 the system (i.e. negative work must be performed; Fig2B). Consequently, Achilles tendon recoil in
170 plantar flexion during ground contact (which means that mechanical energy is added to the system)
171 could eventually come at the extra cost for energy dissipation by eccentric muscle contraction.
172 Moreover, the foot is only partially plantar flexed at the end of stance when the joint torque is zero
173 again (Fig2B). This means that either the recoil energy is dissipated by extending the triceps surae
174 muscle belly during that final stance phase or, because of the biarticular arrangement of the
175 gastrocnemius, that energy is transferred to the knee to assist further active knee flexion observed
176 final in stance (see Vereecke et al., 2006b)⁷.

177 If not for energy storage and recoil during grounded running locomotion, what could the explanation
178 of the well-developed Achilles tendon in gibbons be? Clearly, other, even rare behaviours may entail
179 selective pressure and morphological adaptation. Gibbons also engage, for instance, in bipedal and
180 tripedal gallops and a sort of half bound (crutching gallop) (cf. Vereecke et al., 2006a), and show
181 excellent leaping performance. The potential use of tendon recoil for energy recovery (while galloping)
182 or power amplification (for leaping) cannot be excluded, but biomechanical results presented by
183 Channon et al. (2010a, 2011a,b) do not support this for leaping.

184 Here, we propose an alternative perspective. Available information from the literature and our own
185 observations suggest that the Achilles tendon is also well-developed and firmly attaching to the heel
186 bone in extant Cercopithecoidea (e.g. Frey, 1913; Swindler and Wood, 1973; own dissections on
187 *Theropithecus gelada* (gelada baboon), *Papio anubis* (olive baboon), *Macaca maura* (Moor
188 macaque), *Macaca mulatta* (rhesus monkey), *Semnopithecus entellus* (Hanuman langur), *Colobus*
189 *guereza kikuyensis* (mantled guereza), *Colobus spec.*, *Trachypithecus francoisi* (François' leaf monkey);
190 see supplementary material and Fig1). It seems therefore conceivable that this morphological
191 character was also present in the basal ancestor of this superfamily, hence also in the basal
192 representative of the sister taxon, the Hominoidea (Fig1). Is it plausible that the Achilles tendon is
193 retained as a relict in the branch leading to the Hylobatidae (Fig1)?

194
195 If selection acted predominantly on the principal locomotor mode in gibbons, i.e. on brachiation (e.g.
196 Bertram 2004; Bertram & Chang, 2001; Bertram et al., 1999; Chang et al., 1997, 2000; Fleagle, 1976;
197 Michilsens et al., 2011, 2012; Preuschoft & Demes, 1984; Usherwood & Bertram, 2003; Usherwood et
198 al., 2003), adaptations can be expected primarily at the level of the forelimbs. During brachiation,
199 hindlimb movements are potentially useful to modulate whole body rotational inertia and to avoid
200 hitting lower lying branches, a role which, most likely, did not imply important adaptive modifications
201 of the lower hind limb muscles. As such, it can be hypothesized that the triceps surae, with its long
202 tendon, was not under selective pressure (no harm, no benefit) and could keep its ancestral
203 appearance during hylobatid evolution.

204

For this purpose, short-fibred (pennate) bellies are the best option: these can deliver the required force at a minimal metabolic cost. At the MTU-level, in humans, up to 75% of the positive work output comes from the tendon (e.g. Hof et al., 2002; Lai et al., 2014). Given an efficiency of 0.2 – 0.25 for concentric work in muscle (Woledge et al., 1985), similar MTU stress-strain cycles for 'long-fibred – short tendon' triceps surae muscle would become very expensive.

⁷ It should be noted that this conclusion refers to the role of the Achilles tendon during plantar flexion of the foot only. It may well be that other muscle-tendon systems (for instance the digital flexors or the knee extensors) do act as functional energy-saving mechanisms.

205 *Consequence for the evolution of the great apes*

206 If the above hypothesis is supported, then the short-fibred gastrocnemius muscle with a long Achilles
207 tendon should also be ancestral for the Hominidae. Given that this represents also the extant human
208 morphology, it seems most parsimonious that this ancestral morphology was retained rather than re-
209 acquired in the evolutionary lineage leading to the habitually bipedal, terrestrial modern humans. This
210 lends weight to Thorpe et al.'s (2007) conclusion that human bipedalism is less an innovation than an
211 exploitation of a locomotor behaviour retained from the common great ape ancestor. To be effective,
212 the recoiling Achilles tendon should work against a stiff lever as it is functionally present during the
213 push-off phase in the modern human foot. Considerable evidence exists that early hominins had more
214 mobile feet and, therefore, probably a less complete toe-off function compared to modern humans
215 (e.g. Lieberman, 2012). Thus, although the performance of the Achilles tendon as energy-saving device
216 might well have been further improved during human evolution⁸, considering the emergence of the
217 human Achilles tendon as a key adaptation for economical cyclic bipedal locomotion is probably no
218 longer appropriate.

219 This also implies that the 'long-fibered – short tendon' appearance of the triceps surae in the
220 orangutan, the gorilla, the chimpanzee and the bonobo does not represent the retained ancestral state
221 as it is generally considered (cf. above). Rather, it might represent further convergent evolution from
222 an above-branch quadrupedal ancestor (cf. Almécija et al, 2009; Alba et al., 2015) with short-fibred
223 gastrocnemius muscles and a long Achilles tendon, towards the long-fibered muscles facilitating the
224 muscular control and large range of motion that is beneficial for the arboreal lifestyles of each of the
225 large-bodied extant non-human Hominidae (see for instance Myatt et al., 2011; Preuschoft et al., 1992;
226 Thorpe et al., 1999)⁹. In this context, it is remarkable that lorises also have a short Achilles tendon

⁸ Given that modern humans gain up to 35% of the positive BCOM work required for running from tendon recoil (e.g. Alexander, 2003; about 5x more than what can potentially be recovered in gibbons), it is tempting to speculate on what has changed during human evolution to improve the percentage contribution of elastic recoil. This percentage increase may be due to (relatively) lower positive BCOM work requirements, (relatively) higher energy storage in the tendon, or both. The positive work requirements over a complete cycle (L+R) for human running at preferred speed are 3.4 J/kg (body mass; Fiers et al., 2013; Willems et al., 1995), much higher than the 0.6 J/kg here calculated for the gibbon (3.6 J/cycle for 6.3 kg animal; cf. Supplementary Material). Consequently, elevated energy storage must be in play. Human Achilles tendon stiffness is rather variable (for instance depending age or training level), but an average and physiologically relevant value of 180 Nmm⁻¹ is reported in literature (e.g. Lichtwark & Wilson, 2005, 2006; Uchida et al., 2016), nearly doubling the stiffness of the gibbon's tendon. Stiffer tendons imply less elastic energy storage for a given tendon loading. Thus, tendon force at the onset of plantar flexion (enabling recoil) has to be considerably higher in humans. The ankle extension torque is maximal and equals 2.5 Nm/kg (Fiers et al., 2013; preferred running speed) when plantar flexion starts (about at midstance; notice that this value increases further with running speeds). Taking account for the according Achilles tendon moment arm of about 5 cm (e.g. Leardini & O'Connors, 2012; Maganaris et al., 2000; relative to the lower leg length about twice that of the gibbon), maximal tendon loading equals 50 N/kg, actually not that much higher than what can be calculated for the gibbon (29 N/kg = 2.6 Nm/6.3kg/0.0148m). In other words, size (body mass) as such (obviously coupled to the specific locomotor dynamics) seems to be an important determinant for the higher elastic energy storage. Using the above mentioned data for human preferred running (and accounting for an hysteresis of 10%; e.g. Fletcher & MacIntosh, 2015; Uchida et al., 2016) the relative energy storage over a cycle recalculates to 0.7J/kg which is about 17x more than in the gibbon (0.041J/kg = 0.26J/6.3kg) and accounts (at this relatively slow running speed) for 21% of the positive BCOM work.

⁹ It should be noted that this alternative scenario does not necessarily imply a larger number of character-state changes (i.e. being less parsimonious) than the classical scenario in which the 'short-fibered - long tendon' triceps surae evolved independently from a 'long-fibered – short tendon' ancestral state in both the gibbons and humans. If it is agreed that the common ancestor of the cercopithecoids and hominoids shared the 'long-tendon' character state (cf. main text and see supplementary material), this feature must first have been lost,

227 comparable to great apes (Hanna & Schmitt, 2011) which is interpreted as a convergent feature (next
228 to others) related to selection for slow, cautious arboreal clambering (see for instance Cartmill and
229 Milton, 1977). This view conforms to the suggestion by Alba et al. (2015) that the last common
230 hominoid ancestor was not necessarily great-ape-like and that small-bodied catarrhines could have
231 played a remarkable role in ape evolution. It also accords with the suggestions by Almécija et al.(2009)
232 (based on their analysis of hominoid forelimbs) that above-branch quadrupedalism inherited from
233 stem hominoids constituted a significant component of the locomotor repertoires of different
234 hominoid lineages at least until the late Miocene. And finally, it also supports the suggestion by Lovejoy
235 et al.(2009a,b) that the last common ancestor of the African apes likely had feet that functioned like
236 those of living monkeys rather than like those of apes. Based on the present revision, it seems plausible
237 to include the evolution of the Achilles tendon in their functional perspective, and to extend this to all
238 extant great apes.

239

240

241 **Ethics Statement**

242 This paper revises and integrates previously published data. We refer to the source publications (cf.
243 references). No additional experiments were carried out.

244

245 **Data Accessibility**

246 This paper revises and integrates previously published data. We refer to the source publications (cf.
247 references). No additional data were collected for the purpose of this specific contribution. On
248 request, more information can be provided by the authors (contact dr. evie.vereecke@kuleuven.be).

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253 **Author Contribution**

254 PA provided the new perspective, revisited and integrated the original data, participated in some of
255 the original data collection, participated in the final discussion and drafted the manuscript; KD
256 participated in the collection of the original data and participated in the final discussion on the
257 manuscript; ST brought in the evolutionary insights and participated in the final discussion on the
258 manuscript; GB provided the anatomical data on *Macaca*, *Papio* and *Colobus* and participated in the
259 final discussion on the manuscript; EV carried out and/or supervised all the studies providing the
260 original data and participated in the final discussion on the manuscript. All authors gave final approval
261 for publication.

262

263 **Competing Interests**

264 We have no competing interests.

265

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in order to re-appear then in the stem hylobatids (as all seem to have a well-developed tendon) and in humans independently. This implies an identical number of character-state changes as for the premised convergent appearance of the 'long-fibred – short tendon' state of the triceps surae in the non-human great apes.

273 (zoo of Besançon, FR) were very helpful in collecting additional cadaver material of cercopithecoids
274 and in assisting with the dissections.

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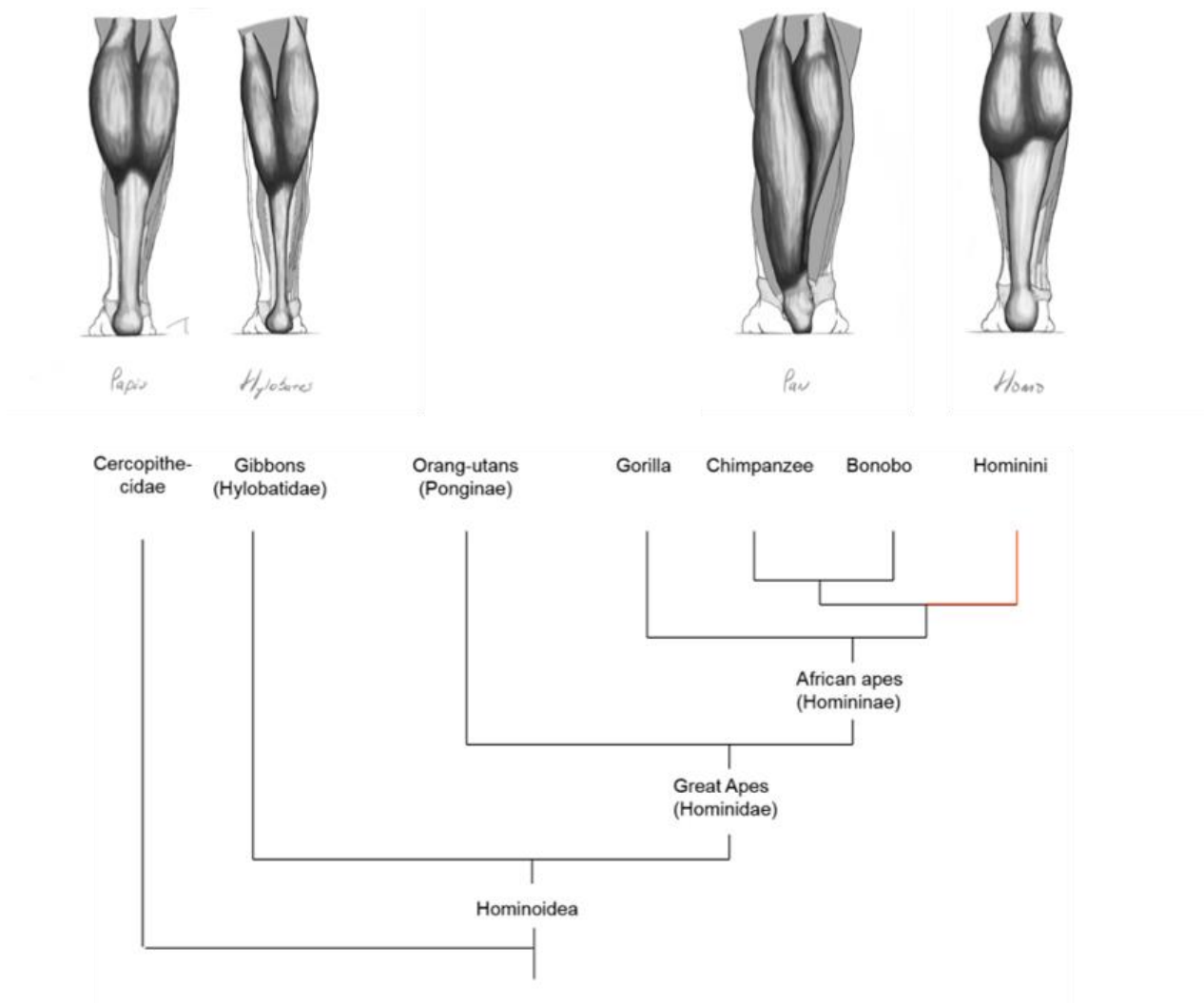
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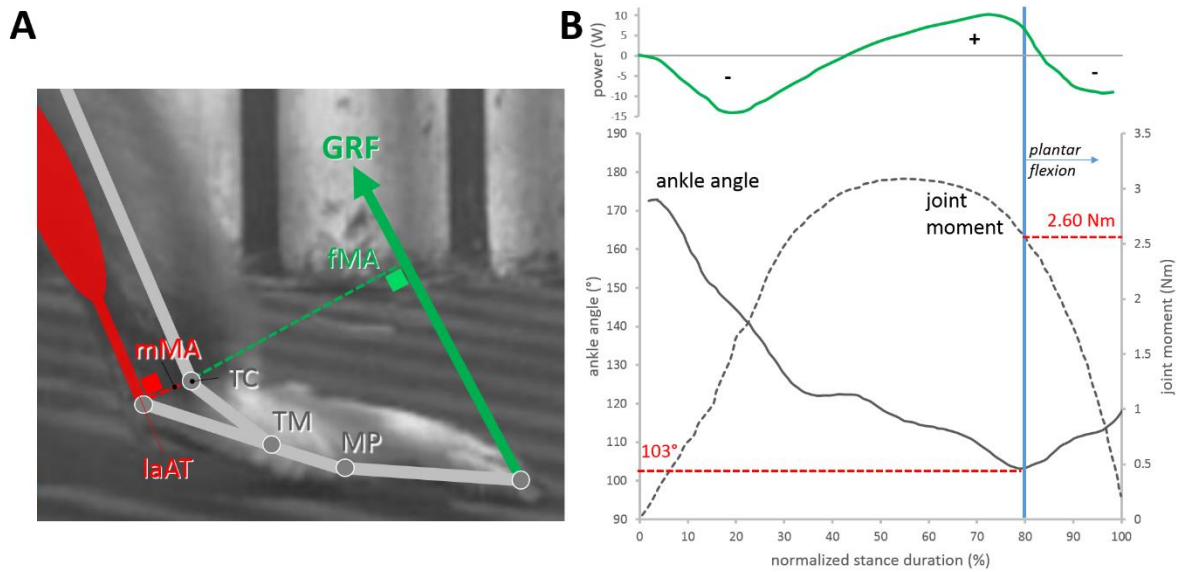
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421 Figure 1 : Phylogenetic tree of the Catarrhini, with dorsal views of the baboon, gibbon, chimpanzee
422 and human lower leg showing the Achilles tendon and the gastrocnemius muscle (anatomical
423 drawings: courtesy of Timo Van Leeuwen).

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427 Figure 2 A: Schematic representation of the lower leg and foot of the white-handed gibbon (dark grey
 428 sticks) at the instant of initial foot contact during bipedal 'grounded' running (background: still frame
 429 of a video sequence). The ankle (talocrural) (TC), tarsometatarsal (TM) and metatarsophalangeal (MP)
 430 joints are shown. The moment arm (fMA) of the ground reaction force (GRF, green arrow) and the
 431 moment arm (mMA) of the balancing force acting along the Achilles tendon, both with respect to the
 432 ankle joint, are indicated. The triceps surae and its Achilles tendon are schematically represented in
 433 red. The fMA is the perpendicular distance from the TC to the GRF; the mMA from the TC to the line
 434 of action of the Achilles Tendon (laAT). B: *Upper panel*; instantaneous mechanical power of the BCOM
 435 during stance. When positive, energy is being added to the BCOM. When negative, BCOM energy
 436 dissipates. The vertical blue line indicates the instant of transition from ankle dorsi-flexion to ankle
 437 plantar-flexion (= extension of the ankle joint). For the largest part, plantar flexion (recoil eventually
 438 adding energy) occurs when, overall, whole-body energy decreases (see text). *Lower panel*; average
 439 ankle joint angle (solid curve; left vertical axis) and average joint moment of the GRF at TC (dashed
 440 curve; right vertical axis) are given as a function of normalized stance time (0% = initial foot contact;
 441 100% = toe off) in the white-handed gibbon. This plantar flexion represents the foot push-off which
 442 can partially be powered by the release of strain energy stored in the Achilles tendon. At this transition,
 443 the ankle joint angle equals 103°, while the according joint moment is 2.60 Nm (for more explanation:
 444 see text). (Based on Vereecke and Aerts, 2008; see also Supplementary Material for more details in
 445 methods).