1 **Segmental morphometrics of bonobos (*Pan paniscus*): are they really**
2 **different from chimpanzees (*Pan troglodytes*)?**

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Abstract

The inertial properties of body segments reflect performance and locomotor habits in primates. While *Pan paniscus* is generally described as more gracile, lighter in body mass, and as having relatively longer and heavier hind limbs than *Pan troglodytes*, both species exhibit very similar patterns of (quadrupedal and bipedal) kinematics, but show slightly different locomotor repertoires. We used a geometric model to estimate the inertial properties for all body segments (i.e. head, trunk, upper and lower arms, hand, thigh, shank and foot) using external length and diameter measurements of 12 anaesthetized bonobos (8 adults and 4 immatures). We also calculated whole limb inertial properties. When we compared absolute and relative segment morphometric and inertial variables between bonobos and chimpanzees, we found that adult bonobos are significantly lighter than adult chimpanzees. The bonobo is also shorter in head length, upper and lower arm lengths, and foot length and is generally lighter in most absolute segment mass values (except head and hand). In contrast, the bonobo has a longer trunk. When scaled relative to body mass, most differences disappear between the two species. Only the longer trunk and the shorter head of the bonobo remain apparent, as well as the lighter thigh compared to the chimpanzee. We found similar values of natural pendular periods of the limbs in both species despite differences in absolute limb lengths, masses, mass centers (for the hind limb) and moments of inertia. While our data contradict the commonly accepted view that bonobos have relatively longer and heavier hind limbs than chimpanzees, they are consistent with the observed similarities in the quadrupedal and bipedal kinematics between these species. The morphological differences between both species are more subtle than those previously described from postcranial osteological materials.

Keywords

Pan paniscus, Inertial properties, Locomotion, Primate evolution, Hominoid

Introduction

Segmental morphometric studies have been valuable for our understanding of primate locomotion and evolution (e.g. Crompton et al. 1996; Druelle et al. 2017; Druelle and Berthet 2017; Isler et al. 2006; Preuschoft 1989; Raichlen 2004; Schoonaert et al. 2007; Turnquist and Wells 1994). Inertial properties of the body (segment mass and mass distribution) reflect the resistance to linear and angular acceleration about joints during locomotion, thereby influencing locomotor performance (e.g. Cartmill et al. 2002; Larson et al. 2000; Patel et al. 2015; Raichlen 2005; Shapiro and Raichlen 2006; Young 2012; Zeininger et al. 2017), and locomotor habits (i.e. the positional repertoire; e.g. Chatani 2003; Doran 1993; Druelle et al. 2016a; Hunt 1992; Wells and Turnquist 2001). Differences in segmental morphometrics between closely related species may thus possibly reflect different evolutionary pathways since their last common ancestor.

The two species of the genus *Pan*, the bonobo (*Pan paniscus*) and the chimpanzee (*Pan troglodytes*), are the closest living relatives to humans. Previous research has provided data on the postcranial osteology of both species (e.g. Morbeck and Zihlman 1989; Zihlman and Cramer 1978; Zihlman et al. 2008), as well as on their positional repertoire (e.g. Doran 1992, 1993; Hunt 1992; Sarringhaus et al. 2014) and the biomechanics of walking (e.g. D'Août et al. 2004; Pontzer et al. 2014). Such studies typically describe *P. paniscus* as being more gracile, smaller in size, with longer and heavier hind limbs and longer feet than *Pan troglodytes* (Schwarz 1929; Zihlman and Cramer 1978; Zihlman et al. 1978), but these inferences are based on relatively limited analyses on small sample sizes (Coolidge and Shea 1982; Morbeck and Zihlman 1989; Zihlman 1984; Zihlman and Cramer 1978). Doran (1992, 1993) observed that adult *P. paniscus* engages in more suspensory behaviour and arboreal travelling, in more palmigrade walking and in less quadrupedal knuckle-walking than adult *P. troglodytes*. According to these studies, *P. paniscus* locomotor repertoire resembles juvenile *P. troglodytes*, but Ramos (2014; see also Hunt 2016) reports contradictory observations: *P. paniscus* engages in more quadrupedal knuckle-walking and in fewer suspensory behaviours, but additional field studies on habituated populations of bonobos are required to clarify these suggestions. Chimpanzee and bonobo kinematics

79   of quadrupedal and bipedal walking are alike (Finestone et al. 2018; Pontzer et al. 2014), suggesting

80   similar inertial properties in both species.

81   The segmental morphometrics of *P. troglodytes* have been quantified and described, but few

82   quantitative morphometric data are available for *P. paniscus*, which is unfortunate because the

83   accuracy of biomechanical studies depends on the quality and completeness of the morphometric

84   measures as much as on the kinematics and kinetics (Winter 2009). It is therefore important that

85   species-specific inertial data are used in these models, and that models take sex- and age-related

86   differences into account when it is possible. Some researchers, based on the proposed similar body

87   build seen in *P. paniscus* and the genus *Australopithecus,* have proposed that the bonobo would be

88   the best prototype for the common ancestor between hominins and panins (Zihlman et al. 1978), but

89   others have suggested that resemblances between bonobos and species belonging to *Australopithecus*

90   are due to their small body size and related allometric factors (Corruccini and McHenry 1979; McHenry

91   and Corruccini 1981). However, others have argued that good comparative models for the common

92   ancestor of apes and humans may be found in various extant species, "not *despite* their imperfect

93   resemblance, but *because* of it" (see D'Août et al. 2014 for a theoretical framework). Clearly, the use

94   of a specific model depends on the research question (e.g. Thorpe et al. 2007), and no extant species

95   exhibits the morphological pattern of early hominins (e.g. Almécija et al. 2015; D'Août et al. 2014;

96   Lovejoy 2009; Senut 2007).

97   In this context, the validation of earlier statements regarding the body dimensions and body build of

98   *P. paniscus* requires a larger segmental morphometric dataset. Comparable inertial data of hominoids

99   have been presented, but few studies included data on bonobos. Zihlman (1984) reported segment

100   masses from one *P. troglodytes* and one *P. paniscus*. Subsequent studies reporting segment masses

101   included two *Pongo pygmaeus* (Morbeck and Zihlman 1989), four *Gorilla gorilla gorilla* (Zihlman and

102   McFarland 2000) and twelve gibbon (i.e. seven Hylobates, one Hoolock, one Nomascus and three

103   Symphalangus specimens; Zihlman et al. 2011). Crompton et al. (1996) published valuable data on four

104   *P. troglodytes* specimens and one *Pongo pygmaeus*. Isler et al. (2006) extended this research by adding

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inertial data from the cadavers of four *Gorilla gorilla gorilla*, one *P. troglodytes*, two *Pongo abelii*, one

Pongo pygmaeus, three *Hylobates lar*, and one *Hylobates syndactylus*. In this study, researchers used

these comparative data to investigate intergeneric differences in inertial properties and mass

distributions and related these to locomotor repertoires. Schoonaert et al. (2007) reported inertial

data from fifty three *P. troglodytes*, and Druelle and Berthet (2017) added inertial data on the lesser

apes with four *Nomascus gabriellae*. Note that Zihlman and Bolter (2015) recently published data

about the relative percentages of major tissues (i.e. muscles, bone, skin and fat) for thirteen *P. paniscus*

individuals and Diogo et al. (2017) provided detailed data about the configuration, attachments and

innervation of the striated muscles of seven bonobo specimens.

The lack of inertial data from *P. paniscus* impedes comparisons with *P. troglodytes* inertial data and

with other hominoids, that could potentially offer important insights into the locomotor evolution of

these species. The present study enlarges the existing morphometric dataset for the bonobo and

provides currently lacking inertial data for this species, and compares these data with previously

reported similar chimpanzee morphometric and inertial variables (Schoonaert et al. 2007) in order to

test whether bonobos have different relative distributions of inertial properties than chimpanzees.

Material and methods

Subjects

The study sample includes 12 bonobos measured while under anaesthesia for routine veterinary

examination in zoos. Of these 12 individuals, 7 were from the Wild Animal park of Planckendael,

Belgium, and 5 were from Apenheul, Apeldoorn, The Netherlands. These individuals live in enriched

environments in both inside and outside enclosures. The sample consists of 4 male and 8 female

bonobos, of which 4 were immature (<12 years of age) and 8 were mature (>12 years of age) following

the subdivision in immature and mature age classes provided by Hamada and Udono (2002).

Veterinary examinations revealed no visible musculo-skeletal abnormalities in any of the animals

studied. We estimated total body mass (TBM) with a scale for all individuals while under anesthesia.

Geometric (segment-inertia) model

External measurements were taken for eight body segments: head, trunk, upper arm, forearm, hand, thigh, shank, and foot. For each segment, segment length was measured, to the nearest millimeter, using a tape measure (for the trunk), or digital calipers (for the other segments). The required input measures for the segment-inertia model (see below) were determined for each segment (i.e. frontal and sagittal widths proximally, in the middle of the segment, and distally). To obtain reliable measurements, it was crucial that clear landmark points are used (for details see Schoonaert et al. 2007). All measurements were made on six individuals, head measurements were missing for 4 individuals, head and trunk measurements were missing for 1 individual and head, trunk and forelimb measurements were missing for 1 individual. The missing data are a consequence of opportunistic sampling during sometimes very short, routine veterinary examinations.

We used the geometric model of Crompton et al. (1996) to determine the body segment inertial variables: segment mass and the location of the center of mass (relative to segment length with respect to the more proximal joint for the limbs, and the more caudal one for the head and trunk). We also computed two moments of inertia (MI) with respect to the segment center of mass. The first, MIx was around the coronal axis, which lies in the frontal plane and extends horizontally from side to side. Flexion and extension take place about this axis in a sagittal plane. The second, MIy was around the sagittal axis, which extends horizontally from front to back. Abduction and adduction take place about this axis in a frontal plane. We did not consider a third moment of inertia around the longitudinal axis because it is more prone to error and it is of less relevance for primate locomotion studies. For the sake of comparability we assumed a density of 10^3 kg/m³ for all segments (Crompton et al. 1996; Isler et al. 2006; Schoonaert et al. 2007).

The segment radius of gyration, expressed as a percentage of segment length, was determined using the following equation:

$$RG = \frac{\sqrt{\frac{I}{m}}}{L} \times 100$$

where I is the moment of inertia, m is the segment mass, and L is the segment length.

156   From the segment variables, the inertial properties of the whole limb were calculated. This included

157   the limb natural pendular period (NPP) for extended limbs with the position of the foot at 90° to the

158   shank segment, and the hand positioned in a straight line with the arm and forearm positioned in full

159   extension as in knuckle-walking. The NPP is defined as:

160
$$NPP = 2\pi \sqrt{\frac{pMI}{m \times COM \times g}}$$

161   where pMI is the moment of inertia about the proximal joint, m is the mass, CoM is the distance from

162   the limb's centre of mass to the proximal joint, and g is the gravitational acceleration (9.81 m.s^{-2}).

163   *Statistics*

164   To test the reliability of the model, we used a paired permutation test between the total measured

165   mass by a scale and the total estimated mass by the model.

166   Bonobo measurements were compared to data from 39 mature chimpanzees (*P. troglodytes*, 16 males

167   and 23 females) (Schoonaert et al. 2007). This sample included individuals of two subspecies: *Pan*

168   *troglodytes troglodytes* and *Pan troglodytes verus*, but did not include any *Pan troglodytes*

169   *schweinfurthii* individuals. Because no apparent outliers were present, *Pan troglodytes* subspecies

170   were combined. To test for species-related differences, the segment length and mass were calculated

171   as percentages of the cube root of body mass and body mass, respectively. We used the equation of

172   the radius of gyration to normalize moments of inertia with body size. For the comparison between

173   species through these relative data, only mature individuals were considered and no subdivision in sex

174   classes was made. Sexes were pooled because a former study on chimpanzees found almost no

175   differences between males and females for the relative data except for hand and foot length, and foot

176   mass (Schoonaert et al. 2007). All sex and species comparisons were performed with *Permutation tests*

177   (non parametric) for independent samples using StatXact 3.1 software (Cytel. Inc., Cambridge, MA,

178   USA).

179   **Results**

180   *Bonobo data*

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181   Table 1 reports the absolute segment morphometric and inertial parameters for both age classes. For

182   each of the 4 immature individuals, the absolute values are given. No means or standard deviations

183   were calculated for this age class, because the individuals were in different developmental stages. As

184   expected, all variable values increase with age.

185   For the mature group means and standard deviations for each variable are given separately for both

186   sexes. There is only one measurement for the female head (except for the head length), so no means

187   were calculated, and the corresponding standard deviation is lacking. For all variables, no statistically

188   significant differences were found between the sexes.

189   Figure 1 shows the correlation between TBM derived from the model and the measured TBM (r=0.99,

190   P=0.0069) for the 6 individuals that have been fully measured (see *Material and Methods*). The paired

191   permutation test shows no significant difference between the measured TBM and the estimated TBM

192   (P=0.6875). This suggests that the model is reliable (see also Isler et al. 2006; Schoonaert et al. 2007).

193   *Bonobo versus chimpanzee*

194   Table 2 presents the mean absolute segment inertial variables of both bonobos and chimpanzees.

195   Males and females are pooled. Both *Pan* samples contain only adult individuals, from 12 to 31.6 years

196   of age in bonobos and from 12.3 to 44 years of age in chimpanzees. For absolute lengths, *P. troglodytes*

197   exhibit significantly longer head (P<0.0001), foot (P<0.0001), upper arm (P=0.0027), and lower arm

198   (P=0.0019) than *P. paniscus.* The trunk segment of *P. paniscus* is significantly longer than *P. troglodytes*

199   (P=0.0304). The TBM of *P. troglodytes* is significantly higher than *P. paniscus* (P=0.0034), which is

200   reflected in the higher segment mass values of the trunk (P=0.0169), the thigh (P=0.0006), the shank

201   (P=0.0057), the foot (P=0.0272), the upper arm (P=0.001), and the lower arm (P=0.0006). The moments

202   of inertia around the frontal axis (MIx) and the sagittal axis (MIy) are higher in chimpanzees for the

203   thigh (P=0.0051 and P=0.0004, respectively), the shank (P=0.0252 and P=0.0077), the foot (around the

204   frontal axis only, P=0.0105), the upper arm (P=0.0006 and P=0.0001) and the lower arm (P=0.0087 and

205   P=0.0035). This is mainly related to the larger segment masses (see above).

206   Table 3 presents the mean relative segment inertial variables for bonobos and chimpanzees. Analyses

207   of relative segment lengths reveal a significantly higher value for the head of *P. troglodytes* (*P*=0.0013),

208   whereas *P. paniscus* has a relatively longer trunk (*P*<0.0001). The relative masses are not significantly

209   different between the two *Pan* species, except for the proportion of the thigh, which is significantly

210   greater in *P. troglodytes* (*P*=0.0129). The positions of the centre of mass (COM) are located slightly

211   proximally relative to the centre of the segments in both species; for the head, the COM lies slightly

212   closer from the nose. The only remaining significant difference is observed in the COM position of the

213   trunk, which is around the middle of the segment in *P. paniscus* and slightly more cranial (closer to the

214   shoulders) in *P. troglodytes* (49.5±2.5% *vs* 51.2±0.9%, respectively, *P*=0.0283); but there is a substantial

215   overlap between the two species. The morphotypes of *P. paniscus* and *P. troglodytes* are illustrated

216   diagrammatically in Figure 2, which shows the average absolute segment length, proximal, middle, and

217   distal diameters in the frontal plane, as well as the respective position of the segments' COM and the

218   proportion of body segments (relative mass).

219   The radius of gyration about the coronal axis, or in the sagittal plane (RGx), is significantly different for

220   all segments except for the upper arm, the thigh and the foot. The radii of gyration are higher for the

221   bonobo head (*P*=0.0184), lower arm (*P*=0.0357), hand (*P*=0.001) and shank (*P*=0.0017), indicating more

222   resistance against rotation in the aforementioned segments. In contrast, the radius of gyration (RGx)

223   of the trunk is smaller in bonobos compared to chimpanzees (*P*<0.0001). There are significant

224   differences in the radius of gyration about the sagittal axis (RGy), for the head, the trunk and the upper

225   arm, with a higher value for the head of the bonobo (*P*=0.0017) and smaller values for the trunk

226   (*P*=0.0159) and the upper arm (*P*=0.0240) in comparison with chimpanzees.

227   Table 4 shows the whole limb inertial data for fore- and hind limbs of mature bonobos and

228   chimpanzees. The forelimb and the hind limb of the bonobo are significantly lighter (*P*=0.0006 and

229   *P*=0.0012, respectively) and shorter (*P*=0.0008 and *P*=0.0098, respectively) than of the chimpanzee,

230   and the moment of inertia of the fore- and hind limbs are significantly lower in bonobos (*P*=0.0014 and

231   *P*=0.0061, respectively). The position of the COM is more proximal in the hind limb of the chimpanzee

232   (P=0.017). Despite these differences in mass moments of inertia, masses, and COM, the NPPs are not

233   significantly different between the two species for both fore- and hind limbs. The mean forelimb NPP

234   of the bonobo is 1.37s and the mean hind limb NPP is 1.32s. The NPP convergence (i.e. the average

235   difference between fore- and hind limb NPP) is 3.65%. Based on our external measurements we also

236   calculated the intermembral index (IMI; the length of the humerus and radius relative to the length of

237   the femur and tibia) for bonobos and chimpanzees (100 ± 5.3 and 105 ± 4.3, respectively), and found

238   no significant difference.

239   **Discussion**

240   *Differences in inertial variables*

241   Overall, the bonobo is significantly lighter than the chimpanzee and this is largely due to the heavier

242   trunk and the limbs in the chimpanzees. The bonobo has also shorter forelimbs (upper and lower arms)

243   than the chimpanzee (but see Behringer et al. 2016), as well as a shorter head and a shorter foot. But

244   when the data are scaled to body mass (i.e. removing size effect), bonobos appear to be similar to

245   chimpanzees with regard to body mass distribution and segment relative length, as also recently

246   suggested from dissections of soft tissues (Diogo et al. 2017). In relative terms, the thigh is heavier in

247   the chimpanzee, which may be related to the importance of climbing in chimpanzees (the most used

248   locomotor mode after quadrupedalism in their locomotor repertoire; Sarringhaus et al. 2014). Because

249   muscle force is proportional to muscle physiological cross-sectional area (PCSA; i.e. muscle force is

250   proportional to body mass$^{2/3}$), climbing is more costly for heavier individuals (Cartmill 1972; Cartmill

251   1974; Jungers and Susman 1984) and it requires powerful hip extension to propel and support the body

252   weight against gravity (Hanna et al. 2017; Preuschoft 2002). Power for hip extension is provided by

253   hamstring (biceps femoris, semimembranosus and semitendinosus) and gluteal muscles, so it is

254   possible that the heavier chimpanzee, compared to the lighter bonobo, has larger thigh muscles to

255   allow for foraging and travelling in the trees. Myatt et al. (2011) observed that PCSAs of the gluteals

256   are significantly larger in chimpanzees compared to orangutans and tend to be also larger than in

257   bonobos. They suggest that it may reflect, in orangutans (i.e. the most specialized suspensory ape),

258   the need for mobility around the hip joint when moving in the trees. Since it is doubtful that bonobos

259   are more arboreal and more suspensory primates than chimpanzees (Ramos 2014; and Hunt 2016;

260   *versus* Doran 1992), our hypothesis about the size-related muscular production capacity seems more

261   appropriate to explain this difference between bonobos and chimpanzees.

262   We also found a difference in the relative and absolute length of the trunk. This trunk elongation in

263   bonobos may possibly increase the moment of inertia for an improved control of the rotation about

264   its vertical axis during orthograde locomotor modes, such as suspensory activities and bipedal walking

265   (Preuschoft 2004). However, bonobos are not more bipedal than chimpanzees (at least in captivity;

266   Videan and McGrew 2001) and the differences in the proportion of suspensory activities are called into

267   question (see Hunt 2016). On the other hand, a longer and slender trunk in pronograde locomotion,

268   although increasing the bending moments along the trunk, would also provide an advantage in fast

269   locomotor modes such as bounding, galloping, jumping (Preuschoft 2004), at least if there is mobility

270   of the lumbar spine, and bonobos have been shown to exhibit impressive jumping performances

271   (Scholz et al. 2006). Although the influence of the trunk extensor muscles is not known in this study, it

272   may play an important role in the work and power performed, but this remains to be tested

273   experimentally. In this context, it is worth noting that other skeletal differences in the trunk region

274   between bonobo and chimpanzee have also been noticed: *P. paniscus* has a shorter clavicle, a smaller,

275   longer and narrower scapula and a smaller and lighter pelvis (Zihlman and Cramer 1978). The trunk

276   region has been shown to be a fundamental component of bipedal balance in primates, so theoretically

277   an elongated and larger trunk should increase its mass moment of inertia, therefore stabilizing the

278   upper body against the movements of the hind limbs (Preuschoft 2004). Druelle et al. (2016b) observed

279   that olive baboons, *Papio anubis,* with a relatively heavier trunk walk bipedally for longer periods than

280   those with lighter trunks. Kimura (1996) showed the importance of lifting the center of gravity to

281   provide a sufficient amount of energy recovery in chimpanzees. Thompson et al. (2015) observed trunk

282   rotational capabilities in the lumbar and thoracic regions of chimpanzees and suggested that it

283   probably reduces work and cost during bipedal locomotion.

11

Differences from previous studies

285   Previous comparative research between bonobos and chimpanzees has often led to puzzling results.

286   To recapitulate, Zihlman and Cramer (1978) found no significant difference for femur, tibia, humerus

287   and radius absolute lengths (but for the ulna) between both *P. paniscus* and *P. troglodytes*. Coolidge

288   and Shea (1982) did not find significantly longer absolute leg and arm lengths in *P. paniscus*. However,

289   bonobos have longer legs than other *Pan* species when scaled to body height (i.e. the distance from

290   the vertex of the skull to the base of the coccyx; Coolidge and Shea 1982). This is also repeated in Shea

291   (1984) with the underlying reasoning that although bonobos are significantly smaller than

292   chimpanzees in most dimensions, their hind limbs are not significantly shorter, which implies that

293   bonobos have relatively longer hind limbs. Our results show only absolute shorter forelimbs (upper

294   and lower arm) in bonobos, but no difference in hind limb length (i.e. thigh and shank, absolute and

295   relative values). Note that when the foot is included in the comparison of hind limb lengths, the

296   chimpanzee has an absolute longer hind limb, but there is no difference for relative values. These

297   results point to the importance of the scaling method used in these studies (i.e. the cube root of body

298   mass, or body height). In the present study, we judged that body mass (measured with a scale) is a

299   more appropriate variable to use for scaling our morphometrics dataset. Morbeck and Zihlman (1989)

300   observed significant differences in means for absolute values of humeral length but not for femoral

301   length (as in the present study). In this same paper, a statistical difference is found for femur and tibia

302   lengths between *P. paniscus* and the Gombe subspecies *P. t. schweinfurthii* sample, where the

303   concerned long bones are significantly smaller in the *P. t. schweinfurthii* sample. Similarly, Morbeck

304   and Zihlman (1989) found that average limb bone lengths in another *P. t. schweinfurthii* sample (not

305   the Gombe sample) are longer than those of *P. t. troglodytes*. Specific information about which *P.*

306   *troglodytes* population one is most similar to *P. paniscus* may, therefore, be of importance in addition

307   to the subspecies considered. Finally, in a recent dissection study (Diogo et al. 2017), the researchers

308   observed only seven relatively minor differences in muscle morphology between chimpanzee and

309   bonobo. These differences concern the intermetacarpales and flexores breves profundi muscles in the

hand, the tendon of the flexor digitorum profundus, the attachment between the pectoralis minor and

the coracoid process of the scapula, the presence of a scansorius muscle and the attachments between

popliteus and fibula, and between the extensor hallucis longus and the proximal big toe phalanx.

Limb proportions

In our sample, the IMI is 100 for *P. paniscus* and 105 for *P. troglodytes*. The difference is not significant

although close to a marginally significant level (P=0.078). Indeed, in our sample the forelimb (upper

and lower arm) is significantly longer in chimpanzees than in bonobos (but see Behringer et al. 2016)

but hind limb length (thigh and shank) is equal. Previous studies found IMI differences between both

Pan species, but, while Zihlman and Cramer (1978) stated that the tendency of the femur of *P. paniscus*

(absolute value) to be longer influences the difference in IMI, Shea (1984) found that this difference

results from the significantly longer forelimbs of the chimpanzee. The results of our study favour the

explanation given by Shea (1984).

The mass of the forelimbs relative to total body mass is 14% and 15% for *P. paniscus* and *P. troglodytes*,

respectively, and the hind limbs' relative mass is 22% for *P. paniscus* and 24% for *P. troglodytes.* These

values are in concordance with Zihlman (1984), except for the relative mass of the hind limb of *P.*

troglodytes, which is reported to be 18.4%; note that only one individual per species is used in this

study. From this, Zihlman concluded that the bonobo has heavier lower limbs, but our study suggested

the thigh of bonobos is relatively lighter.

Sexual dimorphism

With regard to sexual dimorphism, *P. paniscus* is known to exhibit either a low level of sexual

dimorphism or none at all (Cramer 1977). Overall, no significant sex differences were found in our

bonobo sample. In chimpanzees, most sex-related differences are due to higher absolute segment

masses and moments of inertia in male chimpanzees (Schoonaert et al. 2007), but the relative segment

lengths and segment masses, the positions of the COM, and the radii of gyration did not differ among

sexes. Although it is commonly assumed that the bonobo is the least sexually dimorphic hominoid for

335 most morphological traits (e.g. Behringer et al. 2016; Cramer 1977; Cramer and Zihlman 1978), this

336 assumption should be tested using larger samples.

General conclusions

338 The differences in the scaled data of both *Pan* species are in head and trunk lengths, where the trunk

339 is longer and the head is shorter in bonobo, and in thigh mass, where this segment is heavier in the

340 chimpanzee. This difference in mass distribution may be because chimpanzees have larger body

341 masses and, therefore, require larger (hip extensor) muscles to be able to climb and forage in the trees.

342 Although the elongation of the trunk may have a functional (locomotor) significance, it may be a

343 primitive feature that is conserved in the lighter bonobo, and it has been suggested that a short trunk

344 would facilitate upright postures in hominoids. Our data do not support the commonly accepted

345 assumption that bonobos have relatively longer and heavier hind limbs than chimpanzees. As for the

346 natural pendular periods of the fore- and hind limbs, we found similar values for bonobos and

347 chimpanzees. Our conclusion that bonobos and chimpanzees are morphologically similar is consistent

348 with the results of kinematic studies. The few differences between both species, which are more subtle

349 than previously described (but see Diogo et al. 2017), may be related to size differences. Further

350 comparative studies are required to determine whether these morphological differences are related

351 to differences in performance.

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Author contributions

364　K.A., K.S. and P.A. designed the study. J.S. provided the material ressources. K.A., K.S. and J.S. acquired

365　the data. F.D. analyzed the experimental data. F.D., K.S., K.A. and P.A. interpreted the results. F.D.

366　drafted the first version of the manuscript. F.D., P.A., S.N., J.S. and K.A. revised the manuscript and all

367　authors approved the final draft version.

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Tables

Table 1. Segment inertial variables represented through absolute values for immature bonobos, and through means and standard deviations for mature male and female bonobos

	Immature				Mature			
Sex	F	F	F	F	F		M	
Sample size	1	1	1	1	4		4	
					Mean	SD	Mean	SD
Age (yr)	4.65	6.21	6.60	8.54	20.47	5.56	22.32	6.73
Body mass (kg)	15.85	20.20	22.30	33.60	37.61	1.86	45.03	8.49
Length (m)								
head	-	0.155	0.180	0.200	0.205	0.013	0.201	0.009
trunk	0.450	0.510	0.455	0.550	0.599	0.026	0.593	0.068
upper arm	0.210	0.235	0.270	0.275	0.263	0.011	0.270	0.015
Lower arm	0.210	0.240	0.265	0.290	0.273	0.011	0.273	0.010
hand	0.175	0.190	0.210	0.340	0.235	0.010	0.233	0.008
thigh	0.180	0.220	0.270	0.260	0.285	0.023	0.269	0.009
shank	0.200	0.220	0.250	0.280	0.275	0.008	0.254	0.009
foot	0.170	0.200	0.205	0.250	0.226	0.011	0.211	0.009
Mass (kg)								
head	-	-	1.310	2.468	2.399[1]	-	3.109	1.315
trunk	-	11.000	13.317	17.891	26.346	6.678	22.373	4.840
upper arm	0.725	0.769	1.107	1.504	1.127	0.157	1.586	0.386
lower arm	0.643	0.698	0.589	0.890	1.029	0.021	1.027	0.116
hand	0.290	0.405	0.348	0.733	0.470	0.671	0.689	0.186
thigh	1.052	1.376	1.565	1.993	2.278	0.374	3.020	0.801
shank	0.711	0.597	0.797	1.349	1.137	0.115	1.252	0.357
foot	0.401	0.336	0.407	0.691	0.605	0.050	0.726	0.229
MI x (kg.m²)								
head	-	-	0.003	0.008	0.007	-	0.012	0.006
trunk	-	0.212	0.241	0.470	0.842	0.289	0.721	0.290
upper arm	0.003	0.004	0.007	0.009	0.007	0.002	0.010	0.002
lower arm	0.002	0.003	0.004	0.006	0.006	0.000	0.007	0.002
hand	0.001	0.001	0.001	0.006	0.002	0.000	0.003	0.001
thigh	0.003	0.006	0.010	0.012	0.015	0.001	0.020	0.007
shank	0.003	0.003	0.004	0.009	0.007	0.001	0.007	0.002
foot	0.001	0.001	0.001	0.003	0.002	0.000	0.003	0.001

MI y (kg.m²)

head	-	-	0.004	0.009	0.010	-	0.020	0.018
trunk	-	0.176	0.216	0.415	0.735	0.229	0.679	0.335
upper arm	0.003	0.004	0.007	0.009	0.007	0.002	0.010	0.002
lower arm	0.002	0.003	0.004	0.007	0.006	0.001	0.007	0.002
hand	0.001	0.001	0.001	0.006	0.002	0.000	0.003	0.001
thigh	0.004	0.006	0.010	0.013	0.017	0.002	0.021	0.006
shank	0.003	0.003	0.004	0.010	0.008	0.001	0.007	0.002
foot	0.001	0.001	0.001	0.003	0.002	0.000	0.003	0.002

[1]The trunk and head segments were not measured for all individuals (see Material and methods)

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Table 2. Comparison of absolute segment inertial variables of bonobos and chimpanzees

	Pan paniscus		*Pan troglodytes*		
Sex	M/F		M/F		
Sample size	8		39		
	Mean	**SD**	**Mean**	**SD**	*Significance*
Age (yr)	21.393	6.376	25.502	8.214	ns
Body mass (kg)	41.315	5.568	**50.721**	6.713	**
Length (m)					
head	0.203	0.011	**0.243**	0.013	***
trunk	**0.595**	0.050	0.557	0.027	***
upper arm	0.267	0.013	**0.294**	0.016	**
lower arm	0.273	0.010	**0.297**	0.016	**
hand	0.234	0.008	0.244	0.016	ns
thigh	0.277	0.016	0.287	0.015	ns
shank	0.265	0.013	0.277	0.018	ns
foot	0.219	0.013	**0.245**	0.009	***
Mass (kg)					
head	2.931	1.075	2.951	0.402	ns
trunk	24.075	5.914	**29.603**	3.650	*
upper arm	1.389	0.333	**2.068**	0.385	***
lower arm	1.028	0.075	**1.470**	0.275	***
hand	0.595	0.153	0.718	0.121	ns
thigh	2.649	0.595	**3.800**	0.612	***
shank	1.194	0.236	**1.556**	0.279	**
foot	0.666	0.130	**0.819**	0.123	*
MI x (kg.m²)					
head	0.011	0.005	0.014	0.003	ns
trunk	0.772	0.295	0.877	0.180	ns

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	Mean	SD	Mean	SD	Significance
upper arm	0.009	0.003	**0.015**	0.004	***
lower arm	0.007	0.002	**0.010**	0.003	**
hand	0.003	0.001	0.003	0.001	ns
thigh	0.017	0.005	**0.031**	0.014	**
shank	0.007	0.002	**0.010**	0.003	*
foot	0.003	0.001	**0.004**	0.001	*
MI y (kg.m²)					
head	0.017	0.014	0.014	0.003	ns
trunk	0.703	0.291	0.755	0.157	ns
upper arm	0.009	0.002	**0.020**	0.009	***
lower arm	0.007	0.002	**0.011**	0.003	**
hand	0.003	0.001	0.004	0.001	ns
thigh	0.020	0.004	**0.031**	0.007	***
shank	0.007	0.002	**0.011**	0.003	**
foot	0.003	0.001	0.003	0.001	ns

Values in bold indicate the significantly higher values after statistical tests

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Table 3. Comparison of relative segment inertial variables of bonobos and chimpanzees

	Pan paniscus		*Pan troglodytes*		
Sex	M/F		M/F		
Sample size	8		39		
	Mean	**SD**	**Mean**	**SD**	*Significance*
Rel. length (%)					
head	5.87	0.44	**6.59**	0.31	**
trunk	**17.14**	0.96	15.06	0.76	***
upper arm	7.73	0.56	7.96	0.40	ns
lower arm	7.88	0.34	8.05	0.33	ns
hand	6.75	0.30	6.59	0.39	ns
thigh	8.07	0.59	7.77	0.40	ns
shank	7.71	0.51	7.49	0.40	ns
foot	6.38	0.51	6.63	0.28	ns
Rel. mass (%)					
head	7.17	3.24	5.89	0.60	ns
trunk	57.39	11.59	58.59	5.37	ns
upper arm	3.30	0.62	4.07	0.51	ns
lower arm	2.50	0.36	2.90	0.36	ns
hand	1.39	0.25	1.42	0.15	ns
thigh	6.39	0.96	**7.44**	0.68	*
shank	2.90	0.38	3.05	0.30	ns

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foot	1.60	0.19	1.62	0.15	ns
CoM (%)					
head	52.74	2.45	54.92	2.82	ns
trunk	49.50	2.45	**51.23**	0.89	*
upper arm	48.35	1.84	47.68	1.32	ns
lower arm	45.22	1.28	44.85	0.91	ns
hand	47.57	1.61	47.99	0.99	ns
thigh	45.10	0.9	44.27	1.23	ns
shank	46.48	2.54	45.65	0.99	ns
foot	44.56	1.66	45.75	1.29	ns
RG x (%)					
head	**30.19**	1.82	27.87	0.71	*
trunk	29.44	0.54	**30.71**	0.43	***
upper arm	29.60	0.75	28.96	0.61	ns
lower arm	**29.26**	1.80	27.90	0.46	*
hand	**28.29**	0.63	27.47	0.39	**
thigh	29.14	0.81	29.77	3.14	ns
shank	**29.00**	0.44	28.35	0.36	**
foot	28.16	1.36	27.18	0.39	ns
RG y (%)					
head	**34.55**	5.43	28.62	0.75	**
trunk	27.89	0.76	**28.52**	0.37	*
upper arm	29.45	0.47	**31.73**	3.43	*
lower arm	29.05	1.55	28.31	0.39	ns
hand	28.91	0.92	28.81	0.37	ns
thigh	30.78	0.90	31.22	0.80	ns
shank	29.53	0.53	29.41	0.40	ns
foot	27.16	2.03	26.03	0.47	ns

Length is relative to the cube root of TBM, mass is relative to TBM, COM is the location of the COM relative to segment length with respect to the proximal joint for the limbs, the hip for the trunk and the back of the head for the head, RGx and RGy are the radii of gyration expressed as a percentage of segment length.

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Table 4. Whole limb inertial properties of bonobos and chimpanzees, represented by means and standard deviations

	Forelimb					Hind limb				
	P. troglodytes		*P. paniscus*			*P. troglodytes*		*P. paniscus*		
	Mean	SD	Mean	SD	*Significance*	Mean	SD	Mean	SD	*Significance*
Mass (kg)	4.26	0.70	3.01	0.51	***	6.18	0.93	4.51	0.91	**
Length (m)	0.84	0.04	0.77	0.01	***	0.81	0.04	0.76	0.03	**
COM (%)	40.26	1.71	41.65	2.15	ns	45.75	1.65	48.07	2.25	*
MI prox (kg.m^2)	0.71	0.18	0.45	0.10	**	0.72	0.17	0.51	0.11	**
NPP (s)	1.40	0.04	1.37	0.03	ns	1.34	0.04	1.32	0.04	ns

The mass and the length represent the sum of the 3 segments of the limb, i.e. upper arm, lower arm and hand for the forelimb and thigh, shank and foot for the hind limb.

The COM, the MI and the NPP are calculated for the forelimb in full extension and for the hind limb in full extension but with the foot positionned at 90° to the shank segment.
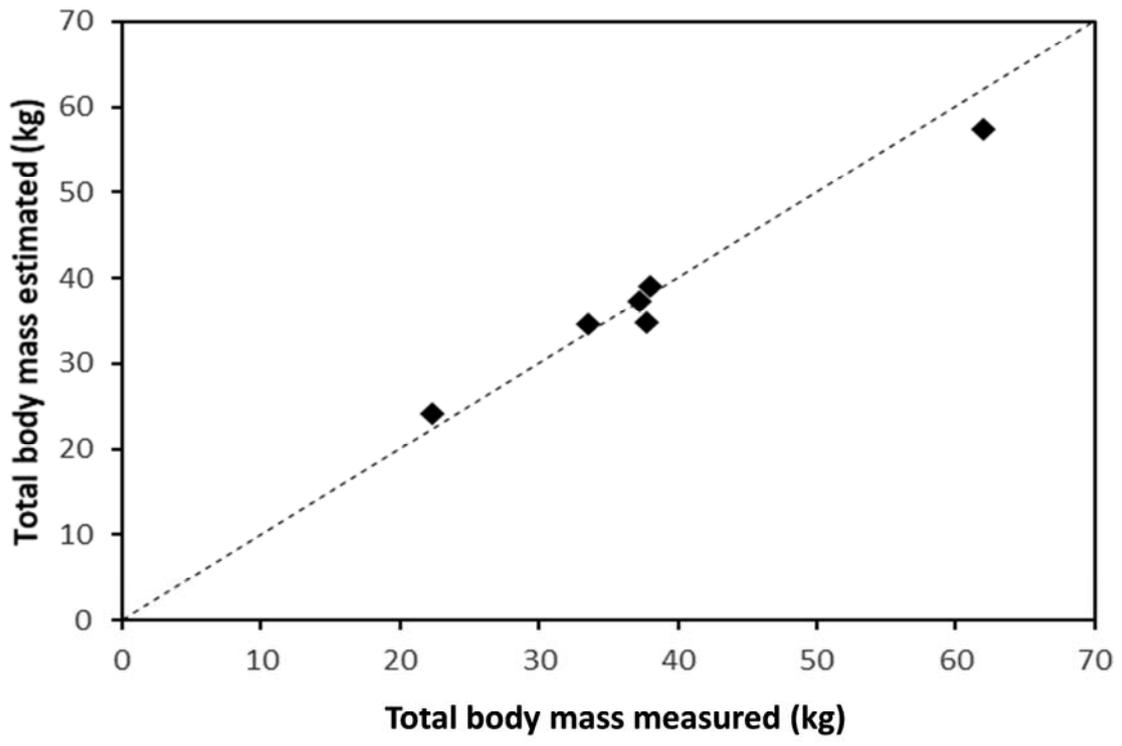
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520

Figure legends

Figure 1. Correlation (r=0.99, *P*=0.0069) between the total body mass estimated by the geometric model and the measured total body mass with a scale. The solid line is the line of identity. **Figure 2.** Comparison of the *P. paniscus* and *P. troglodytes* body build with average segment length and proximal, medial, and distal diameter in frontal plane (in cm). Red dots indicate the position of the centre of mass which is given, between brackets, from proximal joint in % of segment length (from hip joint for the trunk). Body mass distribution is given in % of total body mass on the morphotype in the middle part (the "bonobo-chimpanzee" drawing is inspired by the "bonobo-australopithecus" drawing from Adrienne Zihlman). The stars indicate where are the significant differences for relative values between chimpanzees and bonobos.

Bonobo   Chimpanzee

20.3*
[52.7]

24.5
[54.9]

26.7
[48.4]

59.5*
[49.5*]

55.8
[51.2]

29.5
[47.7]

27.3
[45.2]

29.9
[44.9]

23.4
[47.6]

27.7
[45.1]

28.8
[44.3]

24.5
[48]

26.5
[46.5]

27.8
[45.7]

21.9
[44.6]

24.6
[45.8]

7.17 5.89

3.3   4.07

57.39   58.59

2.5   2.9

1.39   1.42

6.39*   7.44

2.9   3.05

1.6   1.62