Segmental morphometrics of bonobos (*Pan paniscus*): are they really 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 hindlimbs 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 (eight adults and four 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 with the chimpanzee. We found similar values of natural pendular periods of the limbs in both species, despite differences in absolute limb lengths, masses, mass centres (for the hindlimb) and moments of inertia. While our data contradict the commonly accepted view that bonobos have relatively longer and heavier hindlimbs 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.
Key words: hominoid; inertial properties; locomotion; *Pan paniscus*; primate evolution.

Introduction

Segmental morphometric studies have been valuable for our understanding of primate locomotion and evolution (Preuschoft, 1989; Turnquist & Wells, 1994; Crompton et al. 1996; Raichlen, 2004; Isler et al. 2006; Schoonaert et al. 2007; Druelle & Berthet, 2017; Druelle et al. 2017).

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 (Larson et al. 2000; Cartmill et al. 2002; Raichlen, 2005; Shapiro & Raichlen, 2006; Young, 2012; Patel et al. 2015; Zeininger et al. 2017) and locomotor habits (i.e. the positional repertoire; Hunt, 1992; Doran, 1993; Wells & Turnquist, 2001; Chatani, 2003; Druelle et al. 2016a). 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 (Zihlman & Cramer, 1978; Morbeck & Zihlman, 1989; Zihlman et al. 2008), as well as on their positional repertoire (Doran, 1992, 1993; Hunt, 1992; Sarringhaus et al. 2014) and the biomechanics of walking (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 hindlimbs and longer feet than *P. troglodytes* (Schwarz, 1929; Zihlman & Cramer, 1978; Zihlman et al. 1978), but these inferences are based on relatively limited analyses on small sample sizes (Zihlman & Cramer, 1978; Coolidge & Shea, 1982; Zihlman, 1984; Morbeck & Zihlman, 1989). 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 of quadrupedal and bipedal walking are alike (Pontzer et al. 2014; Finestone et al. 2018), suggesting similar inertial properties in both species.

The segmental morphometrics of *P. troglodytes* have been quantified and described, but few quantitative morphometric data are available for *P. paniscus*, which is unfortunate because the accuracy of biomechanical studies depends on the quality and completeness of the morphometric measures as much as on the kinematics and kinetics (Winter, 2009). It is therefore important that species-specific inertial data are used in these models, and that models take sex- and age-related differences into account when it is possible. Some researchers, based on the proposed similar body build seen in *P. paniscus* and the genus *Australopithecus*, have proposed that the bonobo would be the best prototype for the common ancestor between hominins and panins (Zihlman et al. 1978), but others have suggested that resemblances between bonobos and species belonging to *Australopithecus* are due to their small body size and related allometric factors (Corruccini & McHenry, 1979; McHenry & Corruccini, 1981). However, others have argued that good comparative models for the common ancestor of apes and humans may be found in various extant species, 'not *despite* their imperfect resemblance, but *because* of it' (see D'Août et al. 2014 for a theoretical framework). Clearly, the use of a specific model depends on the research question (Thorpe et al. 2007), and no extant species exhibits the morphological pattern of early hominins (Senut, 2007; Lovejoy et al. 2009; D'Août et al. 2014; Almécija et al. 2015).

In this context, the validation of earlier statements regarding the body dimensions and body build of *P. paniscus*

requires a larger segmental morphometric dataset. Comparable inertial data of hominoids have been presented, but few studies included data on bonobos. Zihlman (1984) reported segment masses from one *P. troglodytes* and one *P. paniscus*. Subsequent studies reporting segment masses included two *Pongo pygmaeus* (Morbeck & Zihlman, 1989), four *Gorilla gorilla gorilla* (Zihlman & McFarland, 2000) and 12 gibbons (i.e. seven Hylobates, one Hoolock, one Nomascus and three Symphalangus specimens; Zihlman et al. 2011). Crompton et al. (1996) published valuable data on four *P. troglodytes* specimens and one *P. pygmaeus*. Isler et al. (2006) extended this research by adding inertial data from the cadavers of four *G. gorilla gorilla*, one *P. troglodytes*, two *Pongo abelii*, one *P. 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 53 *P. troglodytes*, and Druelle & Berthet (2017) added inertial data on the lesser apes with four *Nomascus gabriellae*. Note that Zihlman & Bolter (2015) recently published data about the relative percentages of major tissues (i.e. muscles, bone, skin and fat) for 13 *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 compared with chimpanzees.

Materials and methods

Subjects

The study sample includes 12 bonobos measured while under anaesthesia for routine veterinary examination in zoos. Of these 12 individuals, seven were from the Wild Animal park of Planckendael, Belgium, and five were from Apenheul, Apeldoorn, the Netherlands. These individuals live in enriched environments in both inside and outside enclosures. The sample consists of four male and eight female bonobos, of which four were immature (< 12 years of age) and eight were mature (> 12 years of age) following the subdivision in immature and mature age classes provided by Hamada & 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 anaesthesia.

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 millimetre, 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 (Schoonaert et al. 2007). All measurements were made on six individuals, head measurements were missing for four individuals, head and trunk measurements were missing for one individual, and head, trunk and forelimb measurements were missing for one 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 centre of mass (COM; 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 COM. 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 MI 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 m^{-3} 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:

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

where I is the MI, m is the segment mass and L is the segment length.

From the segment variables, the inertial properties of the whole limb were calculated. This included the limb natural pendular period (NPP) for extended limbs with the position of the foot at 90° to the shank segment, and the hand positioned in a straight line with the arm and forearm positioned in full extension as in knuckle-walking. The NPP is defined as

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

where pMI is the MI about the proximal joint, m is the mass, COM is the distance from the limb's COM to the proximal joint, and g is the gravitational acceleration (9.81 m s^{-2}).

Statistics

To test the reliability of the model, we used a paired permutation test between the total measured mass by a scale and the total estimated mass by the model.

Bonobo measurements were compared with data from 39 mature chimpanzees (*P. troglodytes*, 16 males and 23 females;

Schoonaert et al. 2007). This sample included individuals of two subspecies: *Pan troglodytes troglodytes* and *Pan troglodytes verus*, but did not include any *Pan troglodytes schweinfurthii* individuals. Because no apparent outliers were present, *P. troglodytes* subspecies were combined. To test for species-related differences, the segment length and mass were calculated as percentages of the cube root of body mass and body mass, respectively. We used the equation of the radius of gyration to normalize MI with body size. For the comparison between species through these relative data, only mature individuals were considered and no subdivision in sex classes was made. Sexes were pooled because a former study on chimpanzees found almost no differences between males and females for the relative data, except for hand and foot length, and foot mass (Schoonaert et al. 2007). All sex and species comparisons were performed with permutation tests (non-parametric) for independent samples using STATXACT 3.1 software (Cytel., Cambridge, MA, USA).

Results

Bonobo data

Table 1 reports the absolute segment morphometric and inertial parameters for both age classes. For each of the four immature individuals, the absolute values are given. No means or standard deviations were calculated for this age class, because the individuals were in different developmental stages. As expected, all variable values increase with age.

For the mature group, means and standard deviations for each variable are given separately for both sexes. There is only one measurement for the female head (except for the head length), so no means were calculated, and the corresponding standard deviation is lacking. For all variables, no statistically significant differences were found between the sexes.

Figure 1 shows the correlation between TBM derived from the model and the measured TBM ($r = 0.99$, $P = 0.0069$) for the six individuals that have been fully measured (see Materials and methods). The paired permutation test shows no significant difference between the measured TBM and the estimated TBM ($P = 0.6875$). This suggests that the model is reliable (Isler et al. 2006; Schoonaert et al. 2007).

Bonobo vs. chimpanzee

Table 2 presents the mean absolute segment inertial variables of both bonobos and chimpanzees. Males and females are pooled. Both *Pan* samples contain only adult individuals: from 12 to 31.6 years old in bonobos, and from 12.3 to 44 years old in chimpanzees. For absolute lengths, *P. troglodytes* exhibit significantly longer head ($P < 0.0001$), foot ($P < 0.0001$), upper arm ($P = 0.0027$) and lower arm ($P = 0.0019$) than *P. paniscus*. The trunk segment of *P. paniscus* is significantly longer than *P. troglodytes* ($P = 0.0304$). The TBM of *P. troglodytes* is significantly higher than *P. paniscus* ($P = 0.0034$), which is reflected in the higher

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			
					F		M	
					4		4	
Sex	F	F	F	F				
Sample size	1	1	1	1	Mean	SD	Mean	SD
Age (years)	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*	–	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
MIx (kg m^{-2})								
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
MIy (kg m^{-2})								
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

*The trunk and head segments were not measured for all individuals (see Materials and methods).

segment mass values of the trunk ($P = 0.0169$), the thigh ($P = 0.0006$), the shank ($P = 0.0057$), the foot ($P = 0.0272$), the upper arm ($P = 0.001$) and the lower arm ($P = 0.0006$). The MI around the frontal axis (MIx) and the sagittal axis (MIy) are higher in chimpanzees for the thigh ($P = 0.0051$ and $P = 0.0004$, respectively), the shank ($P = 0.0252$ and $P = 0.0077$), the foot (around the frontal axis only, $P = 0.0105$), the upper arm ($P = 0.0006$ and $P = 0.0001$) and the lower arm

($P = 0.0087$ and $P = 0.0035$). This is mainly related to the larger segment masses (see above).

Table 3 presents the mean relative segment inertial variables for bonobos and chimpanzees. Analyses of relative segment lengths reveal a significantly higher value for the head of *P. troglodytes* ($P = 0.0013$), whereas *P. paniscus* has a relatively longer trunk ($P < 0.0001$). The relative masses are not significantly different between the two *Pan* species,
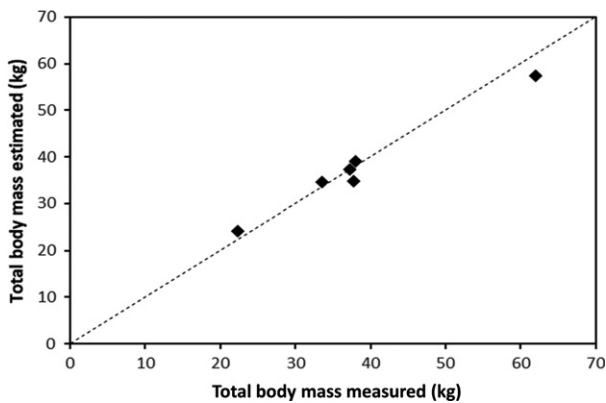
Fig. 1 Correlation ($r = 0.99$, $P = 0.0069$) between the total body mass (TBM) estimated by the geometric model and the measured TBM with a scale. The dashed line is the line of identity.

except for the proportion of the thigh, which is significantly greater in *P. troglodytes* ($P = 0.0129$). The positions of the COM are located slightly proximally relative to the centre of the segments in both species; for the head, the COM lies slightly closer from the nose. The only remaining significant difference is observed in the COM position of the trunk, which is around the middle of the segment in *P. paniscus* and slightly more cranial (closer to the shoulders) in *P. troglodytes* ($49.5 \pm 2.5\%$ vs. $51.2 \pm 0.9\%$, respectively, $P = 0.0283$), but there is a substantial overlap between the two species. The morphotypes of *P. paniscus* and *P. troglodytes* are illustrated diagrammatically in Fig. 2, which shows the average absolute segment length, proximal, middle and distal diameters in the frontal plane, as well as the respective position of the segments' COMs and the proportion of body segments (relative mass).

The radius of gyration about the coronal axis, or in the sagittal plane (RGx), is significantly different for all segments, except for the upper arm, the thigh and the foot. The radii of gyration are higher for the bonobo head ($P = 0.0184$), lower arm ($P = 0.0357$), hand ($P = 0.001$) and shank ($P = 0.0017$), indicating more resistance against rotation in the aforementioned segments. In contrast, the radius of gyration (RGx) of the trunk is smaller in bonobos compared with chimpanzees ($P < 0.0001$). There are significant differences in the radius of gyration about the sagittal axis (RGy) for the head, the trunk and the upper arm, with a higher value for the head of the bonobo ($P = 0.0017$) and smaller values for the trunk ($P = 0.0159$) and the upper arm ($P = 0.0240$) in comparison with chimpanzees.

Table 4 shows the whole limb inertial data for fore- and hindlimbs of mature bonobos and chimpanzees. The forelimbs and the hindlimbs of the bonobo are significantly lighter ($P = 0.0006$ and $P = 0.0012$, respectively) and shorter ($P = 0.0008$ and $P = 0.0098$, respectively) than of the chimpanzee, and the MI of the fore- and hindlimbs are significantly lower in bonobos ($P = 0.0014$ and $P = 0.0061$,

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 (years)	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	*
MIx (kg m^{-2})					
Head	0.011	0.005	0.014	0.003	ns
Trunk	0.772	0.295	0.877	0.180	ns
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	*
MIy (kg m^{-2})					
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. MI, moment of inertia.
*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ns $P > 0.05$ (not significant).

respectively). The position of the COM is more proximal in the hindlimb of the chimpanzee ($P = 0.017$). Despite these differences in mass MI, masses, and COM, the NPPs are not significantly different between the two species for both fore- and hindlimbs. The mean forelimb NPP of the bonobo is 1.37 s and the mean hindlimb NPP is 1.32 s. The NPP convergence (i.e. the average difference between fore- and

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

Sex	Pan paniscus M/F		Pan troglodytes 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
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
RGx (%)					
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
RGy (%)					
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.

COM, centre of mass.

Values in bold indicate the significantly higher values after statistical tests. *$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ns $P > 0.05$ (not significant).

hindlimb NPP) is 3.65%. Based on our external measurements, we also calculated the intermembral index (IMI; the length of the humerus and radius relative to the length of the femur and tibia) for bonobos and chimpanzees (100 ± 5.3 and 105 ± 4.3, respectively), and found no significant difference.

Discussion

Differences in inertial variables

Overall, the bonobo is significantly lighter than the chimpanzee, and this is largely due to the heavier trunk and the limbs in the chimpanzees. The bonobo also has shorter forelimbs (upper and lower arms) than the chimpanzee (but also see Behringer et al. 2016), as well as a shorter head and a shorter foot. But when the data are scaled to body mass (i.e. removing size effect), bonobos appear to be similar to chimpanzees with regard to body mass distribution and segment relative length, as also recently suggested from dissections of soft tissues (Diogo et al. 2017). In relative terms, the thigh is heavier in the chimpanzee, which may be related to the importance of climbing in chimpanzees (the most used locomotor mode after quadrupedalism in their locomotor repertoire; Sarringhaus et al. 2014). Because muscle force is proportional to muscle physiological cross-sectional area (PCSA; i.e. muscle force is proportional to body mass$^{2/3}$), climbing is more costly for heavier individuals (Cartmill, 1972, 1974; Jungers & Susman, 1984) and it requires powerful hip extension to propel and support the body weight against gravity (Preuschoft, 2002; Hanna et al. 2017). Power for hip extension is provided by hamstring (biceps femoris, semimembranosus and semitendinosus) and gluteal muscles, so it is possible that the heavier chimpanzee, compared with the lighter bonobo, has larger thigh muscles to allow for foraging and travelling in the trees. Myatt et al. (2011) observed that PCSAs of the gluteals are significantly larger in chimpanzees compared with orangutans, and tend to be also larger than in bonobos. They suggest that it may reflect, in orangutans (i.e. the most specialized suspensory ape), the need for mobility around the hip joint when moving in the trees. Because it is doubtful that bonobos are more arboreal and more suspensory primates than chimpanzees (Ramos, 2014; and Hunt, 2016 vs. Doran, 1992), our hypothesis about the size-related muscular production capacity seems more appropriate to explain this difference between bonobos and chimpanzees.

We also found a difference in the relative and absolute length of the trunk. This trunk elongation in bonobos may possibly increase the inertia for an improved control of the rotation about its vertical axis during orthograde locomotor modes, such as suspensory activities and bipedal walking (Preuschoft, 2004). However, bonobos are not more bipedal than chimpanzees (at least in captivity; Videan & McGrew, 2001), and the differences in the proportion of
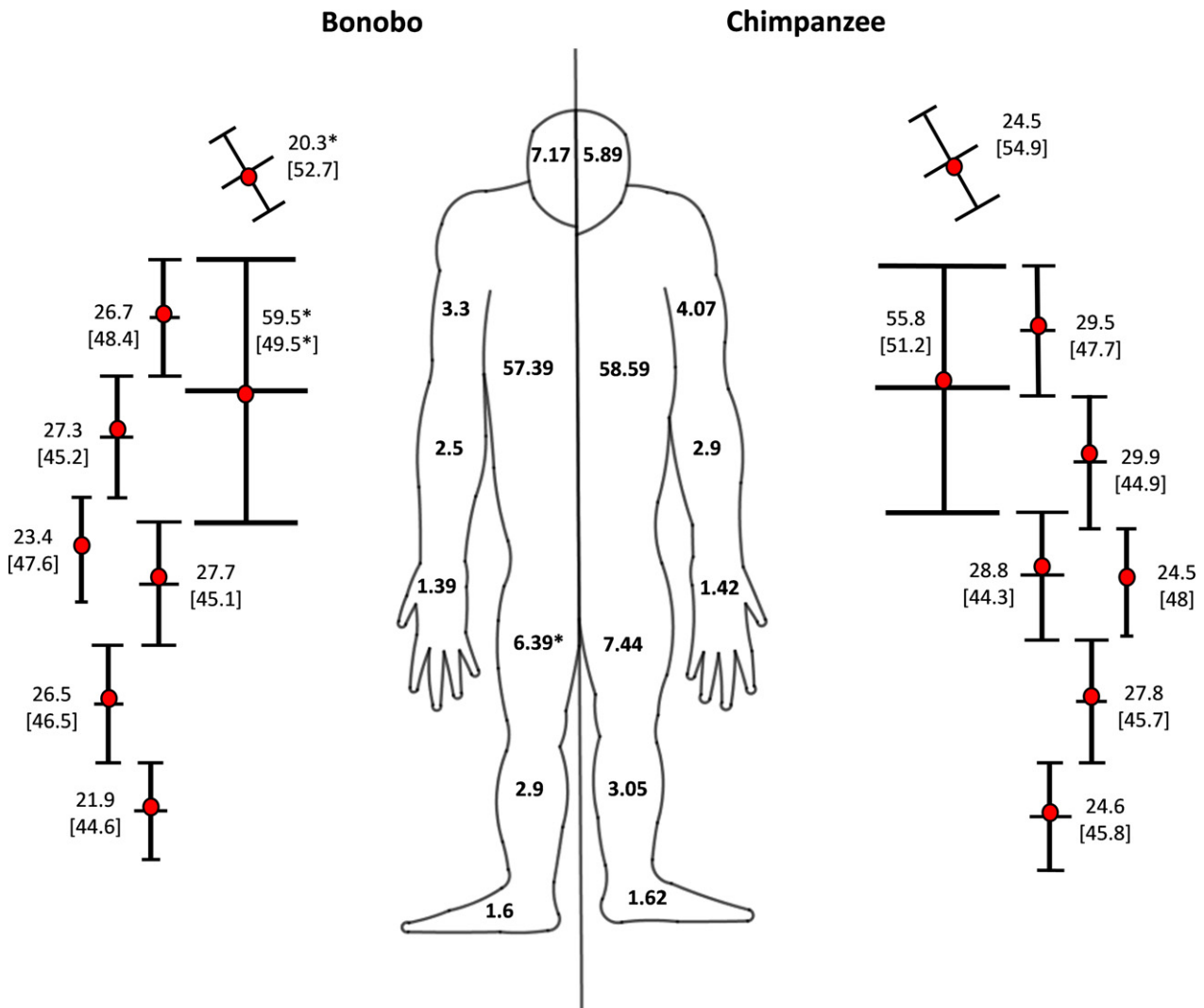
Fig. 2 Comparison of the *Pan paniscus* and *Pan troglodytes* body build with average segment length, and proximal, medial and distal diameter in frontal plane (in cm). Red dots indicate the position of the centre of mass (COM), which is given, in brackets, from proximal joint as a % of segment length (from hip joint for the trunk). Body mass distribution is given as a % of total body mass (TBM) 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 the significant differences are for relative values between chimpanzees and bonobos.

suspensory activities are called into question (Hunt, 2016). On the other hand, a longer and slender trunk in prono-grade locomotion, although increasing the bending moments along the trunk, would also provide an advantage in fast locomotor modes such as bounding, galloping, jumping (Preuschoft, 2004), at least if there is mobility of the lumbar spine, and bonobos have been shown to exhibit impressive jumping performances (Scholz et al. 2006). Although the influence of the trunk extensor muscles is not known in this study, it may play an important role in the work and power performed, but this remains to be tested experimentally. In this context, it is worth noting that other skeletal differences in the trunk region between bonobo and chimpanzee have also been noticed: *P. paniscus* has a shorter clavicle, a smaller, longer and narrower

scapula, and a smaller and lighter pelvis (Zihlman & Cramer, 1978). The trunk region has been shown to be a fundamental component of bipedal balance in primates, so theoretically an elongated and larger trunk should increase its mass MI, therefore stabilizing the upper body against the movements of the hindlimbs (Preuschoft, 2004). Druelle et al. (2016b) observed that olive baboons, *Papio anubis*, with a relatively heavier trunk walk bipedally for longer periods than those with lighter trunks. Kimura (1996) showed the importance of lifting the centre of gravity to provide a sufficient amount of energy recovery in chimpanzees. Thompson et al. (2015) observed trunk rotational capabilities in the lumbar and thoracic regions of chimpanzees, and suggested that it probably reduces work and cost during bipedal locomotion.

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

	Forelimb					Hindlimb				
	Pan troglodytes		Pan paniscus			Pan troglodytes		Pan 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 three segments of the limb, i.e. upper arm, lower arm and hand for the forelimb and thigh, shank and foot for the hindlimb.

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

COM, centre of mass; MI, moment of inertia; NPP, natural pendular period.

*$P < 0.05$, **$P < 0.01$, ***$P < 0.001$, ns $P > 0.05$ (not significant).

Differences from previous studies

Previous comparative research between bonobos and chimpanzees has often led to puzzling results. To recapitulate, Zihlman & Cramer (1978) found no significant difference for femur, tibia, humerus and radius absolute lengths (but for the ulna) between both *P. paniscus* and *P. troglodytes*. Coolidge & Shea (1982) did not find significantly longer absolute leg and arm lengths in *P. paniscus*. However, bonobos have longer legs than other *Pan* species when scaled to body height (i.e. the distance from the vertex of the skull to the base of the coccyx; Coolidge & Shea, 1982). This is also repeated in Shea (1984) with the underlying reasoning that although bonobos are significantly smaller than chimpanzees in most dimensions, their hindlimbs are not significantly shorter, which implies that bonobos have relatively longer hindlimbs. Our results show only absolute shorter forelimbs (upper and lower arm) in bonobos, but no difference in hindlimb length (i.e. thigh and shank, absolute and relative values). Note that when the foot is included in the comparison of hindlimb lengths, the chimpanzee has an absolute longer hindlimb, but there is no difference for relative values. These results point to the importance of the scaling method used in these studies (i.e. the cube root of body mass, or body height). In the present study, we judged that body mass (measured with a scale) is a more appropriate variable to use for scaling our morphometrics dataset. Morbeck & Zihlman (1989) observed significant differences in means for absolute values of humeral length but not for femoral length (as in the present study). In this same paper, a statistical difference is found for femur and tibia lengths between *P. paniscus* and the Gombe subspecies *P. t. schweinfurthii* sample, where the concerned long bones are significantly smaller in the *P. t. schweinfurthii* sample. Similarly, Morbeck & Zihlman (1989) found that

average limb bone lengths in another *P. t. schweinfurthii* sample (not the Gombe sample) are longer than those of *P. t. troglodytes*. Specific information about which *P. troglodytes* population is most similar to *P. paniscus* may, therefore, be of importance in addition to the subspecies considered. Finally, in a recent dissection study (Diogo et al. 2017), the researchers observed only seven relatively minor differences in muscle morphology between chimpanzee and 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 is 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 also see Behringer et al. 2016), but hindlimb length (thigh and shank) is equal. Previous studies found IMI differences between both *Pan* species, but, while Zihlman & 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 TBM is 14% and 15% for *P. paniscus* and *P. troglodytes*, respectively, and the relative mass of the hindlimbs 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 hindlimb 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 MI 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 most morphological traits (Cramer, 1977; Cramer & Zihlman, 1978; Behringer et al. 2016), this assumption should be tested using larger samples.

General conclusions

The differences in the scaled data of both *Pan* species are in head and trunk lengths, where the trunk is longer and the head is shorter in bonobo, and in thigh mass, where this segment is heavier in the chimpanzee. This difference in mass distribution may be because chimpanzees have larger body masses and, therefore, require larger (hip extensor) muscles to be able to climb and forage in the trees. Although the elongation of the trunk may have a functional (locomotor) significance, it may be a primitive feature that is conserved in the lighter bonobo, and it has been suggested that a short trunk would facilitate upright postures in hominoids. Our data do not support the commonly accepted assumption that bonobos have relatively longer and heavier hindlimbs than chimpanzees. As for the NPPs of the fore- and hindlimbs, we found similar values for bonobos and chimpanzees. Our conclusion that bonobos and chimpanzees are morphologically similar is consistent with the results of kinematic studies. The few differences between both species, which are more subtle than previously described (but also see Diogo et al. 2017), may be related to size differences. Further comparative studies are required to determine whether these morphological differences are related to differences in performance.

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Author contributions

K.A., K.S. and P.A. designed the study. J.S. provided the material resources. K.A., K.S. and J.S. acquired the data. F.D. analyzed the experimental data. F.D., K.S., K.A. and P.A. interpreted the results. F.D. drafted the first version of the manuscript. F.D., P.A., S.N., J.S. and K.A. revised the manuscript, and all authors approved the final draft version.

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