WILEY | American Journal of PHYSICAL ANTHROPOLOGY

BRIEF COMMUNICATION

The body center of mass in primates: Is it more caudal than in other quadrupedal mammals?

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Abstract

Objectives: Whole body center of mass (BCoM) position values are lacking for a comparative sample of primates. Therefore, it still remains unknown whether the BCoM in primates is more posteriorly located than in other mammals. The aim of the present report is to provide data for a large sample of primate species and to compare the position of the BCoM in primates to non-primate mammals.

Materials and methods: We collected morphometrics on eight primate species belonging to various families: Hylobatidae (*Nomascus grabriellae, Nomascus Siki*), Cercopithecidae (*Cercopithecus roloway, Cercopithecus lhoesti, Colobus guereza, Trachypithecus francoisi*), Cebidae (*Sapajus xanthosternos*), and Atelidae (*Ateles fusciceps*). Using a geometric model, we assessed the position of the BCoM in a natural quadrupedal posture and in a control posture. To complete our comparative sample with a wider range of morphotypes, we added the data available in the literature for hominoids (*Pan paniscus, Pan troglodytes, Gorilla gorilla, Pongo pygmaeus, Hylobates lar*) and another cercopithecoid species (*Papio anubis*). We also evaluated the phylogenetic signal of the position of the BCoM in primates.

Results: The variation in the position of the BCoM in primates is very large, ranging from 40% of the distance between the hip and the shoulder in *Ateles fusciceps* to 63% in *Hylobates lar*. We observed a strong phylogenetic signal for this trait: hominoid species, as well as the baboon, have a cranial BCoM relative to the midline between the hip and the shoulder, arboreal cercopithecoids and the spider monkey have a caudal BCoM, and the capuchin monkey has a BCoM positioned at mid-trunk. The variation observed in non-primate quadrupedal mammals lies inside the variation range of primates, from 51% in *Felis catus* to 63% in *Canis familiaris*.

Discussion: The BCoM of primates is not more posteriorly located than in other quadrupedal mammals; however, there is a substantial range of variation in primates, from caudal (in arboreal quadrupeds) to cranial (in hominoids and terrestrial quadrupeds) positions. This variation is related to a phylogenetic model that suggests stabilizing selection for this trait. It seems that the BCoM position mostly depends of the size of the appendicular system (i.e., limbs) and the tail. Therefore, it may also reflect a general trend in quadrupedal mammals with arboreal species exhibiting a caudal BCoM and terrestrial species exhibiting a cranial BCoM. These results are discussed in the context of the locomotor evolution of primates including locomotor habits and gait mechanics. We also propose a new "passive" mechanism for the explanation of the particular weight support pattern observed in primates with tails.

KEYWORDS

centre of mass, locomotor evolution, morphotype, primates

1 | INTRODUCTION

It has long been assumed that the body center of mass (BCoM) of primates is relatively caudal, that is, situated close to the hip, compared to other mammals (Rollinson & Martin, 1981). This idea was initially based on force plate data indicating that primates commonly support more of their weight on their hind limbs (Kimura, Okada, & Ishida, 1979). Although the differences in the amount of weight supported

by the fore- and hind limbs should indeed be related to the position of the whole BCoM (e.g., Gray, 1944; Manter, 1938), it is not a direct determination of its location (Reynolds, 1985; Vilensky & Larson, 1989). Furthermore, some authors have suggested that primates could actively shift their weight to their hind limbs during walking (Reynolds, 1985; Schmitt, 1999). Recently, both "passive" (the position of the limbs relative to the center of mass [CoM]), and "active" models have found support in different primate species (passive model: Raichlen, Pontzer, Shapiro, & Sockol, 2009; active model: Larson & Stern, 2009; Larson & Demes, 2011). As a result, on the one hand, a full understanding of the weight support pattern observed in primates is lacking. On the other hand, it still remains unknown whether the whole BCoM of primates is more posteriorly located than in other mammals.

The average location of the BCoM can be accurately estimated from the inertial properties (mass and CoM) of the body segments and from their position in space (e.g., Miller, Nelson, & Goldfuss, 1973). Using this methodology, Vilensky and Larson (1989) tried to address the issue of whether the BCoM of primates is more caudal than in other quadrupedal mammals by comparing the few inertial data available at that time for one brown lemur (Wells & DeMenthon, 1987), one spot-nosed guenon (Rollinson, 1975), and 15 rhesus monkeys (Vilensky, 1979). They compared these data to the inertial properties of one cat (Manter, 1938) and concluded that these differences were certainly too minor to profess the presence of a more caudal CoM in primates. Nevertheless, their very small sample size did not lead to a reliable conclusion on this issue. Surprisingly, larger comparative datasets evaluating the position of the CoM in different primate and non-primate species have never been published. The objective of the present report is, therefore, to fill this gap of knowledge by providing an accurate estimation of the BCoM position in different primate species based on the inertial properties of their body segments, and to compare it to non-primate quadrupedal mammals.

Based on the aforementioned observations (Vilensky & Larson, 1989), we hypothesize that the position of the whole BCoM of primates is not more posterior than in other quadrupedal mammals. To test this hypothesis, we used a sample representative of the diversity of primate body shape and size by collecting data on *Hylobatidae*, *Atelidae*, *Cebidae*, *Cercopithecinae*, and *Colobinae*. We also added available data from the literature on *Hominidae* and other *Cercopithecinae* (Druelle, Aerts, D'Août, Moulin, & Berillon, 2017; Druelle et al., 2018; Druelle & Berthet, 2017; Isler et al., 2006; Schoonaert, D'Août, & Aerts, 2007). First, we tested whether the phylogeny can explain the variation observed among and within clades in primates. Second, we compared these data to data available for the cat (Manter, 1938), the dog (Amit, Gomberg, Milgram, & Shahar, 2009) and the horse (Buchner, Savelberg, Schamhardt, & Barneveld, 1997). Third, we compared the position of the whole BCoM between hominoids (described as orthograde primates) and other quadrupedal (pronograde) primate species.

2 | MATERIALS AND METHODS

2.1 | Sample

The data were collected in the Zoological Park of the Besançon Museum, France, and in the Zoological Park of Mulhouse, France. We

took the opportunity of taking external measurements on 18 primate individuals during veterinary checks although they were under anesthesia. These individuals belong to eight species: the brown-headed spider monkey, *Ateles fusciceps robustus* (Atelidae), the buff-headed capuchin, *Sapajus xanthosternos* (Cebidae), the Roloway monkey, *Cercopithecus roloway* (Cercopithecinae), the L'Hoest's monkey, *Cercopithecus lhoesti* (Cercopithecinae), the Guereza monkey, *Colobus guereza* (Colobinae), the Francois' leaf monkey, *Trachypithecus francoisi* (Colobinae), the southern yellow-cheeked crested gibbon, *Nomascus gabriellae* (Hylobatidae), and the southern white-cheeked crested gibbon, *Nomascus siki* (Hylobatidae). The veterinary examinations did not reveal any musculo-skeletal abnormalities. All of these individuals live inside large enclosures with various enrichments. Table 1 shows the individual information of our sample and includes the additional comparative sample, that is, the chimpanzee, *Pan troglodytes* (Schoonaert et al., 2007), the bonobo, *Pan paniscus* (Druelle et al., 2018), the gorilla, *Gorilla gorilla*, the orangutan, *Pongo pygmaeus*, the lar gibbon, *Hylobates lar* (Isler et al., 2006), and the southern yellow-cheeked crested gibbon, *Nomascus gabriellae* (Druelle & Berthet, 2017).

2.2 | Measurement protocol

The protocol of measurements is based on the geometric model developed by Crompton, Li, Alexander, Wang, and Gunther (1996). It has previously been applied on hominoid (Crompton et al., 1996; Druelle et al., 2018; Druelle & Berthet, 2017; Isler et al., 2006; Schoonaert et al., 2007) and cercopithecoid specimens (Druelle, Aerts, et al., 2017; Raichlen, 2004; Raichlen, 2005) and allows for the reliable estimation of the inertial properties of the body (tested on non-human primate cadavers in Crompton et al., 1996; Isler et al., 2006). External linear measurements were taken on eight body segments (or nine, if a tail was present): head (including neck), trunk, arm, forearm, hand, thigh, shank, and foot. The landmarks used follow those of previous studies (e.g., Schoonaert et al., 2007). We obtained individual segment dimensions (lengths and antero-posterior and medio-lateral diameters) and, according to the model, we estimated segment mass (average estimated density: 1 g cm^{-3}) and segment CoM (calculated from the proximal joint of each segment, from the hip for the trunk and the back for the head). Summed per individual, the mass of the different body segments yields an estimated total body mass. Figure 1 shows that the total body mass estimated by the geometric model is consistent with that directly measured with an electronic scale, confirming the reliability and accuracy of the procedure.

Based on the morphological variables, we designed an average free body diagram for each species using the mathematical and geometric software *GeoGebra 5.0*. Each species morphotype has been built on a minimum of two adult individuals. The morphotypes are scaled, that is, segment masses are divided by the body mass, segment length is expressed as percentage of trunk + head (including neck) length, and segment CoM is expressed as percentage of the respective segment length. We used two postures to assess the location of the whole BCoM: a natural posture and a control posture. The natural posture is an average posture inspired from biomechanical studies of walking and from lateral pictures available in the literature (Table 2; Pontzer, Raichlen, & Rodman, 2014; Finestone, Brown, Ross, & Pontzer, 2018;

TABLE 1 Sample information

Species	Male	Female	Origin of specimens	Method	Data collection
Nomascus gabriellae	0	2	Zoo, Mulhouse, Fr	Ext. measurements	This study
Nomascus siki	2	1	Zoo, Mulhouse, Fr	Ext. measurements	This study
Cercopithecus roloway	1	1	Zoo, Mulhouse, Fr	Ext. measurements	This study
Cercopithecus lhoesti	1	1	Zoo, Mulhouse, Fr	Ext. measurements	This study
Ateles fusciceps robustus	1	2	Zoo, Mulhouse, Fr	Ext. measurements	This study
Sapajus xanthosternos	0	2	Zoo, Mulhouse, Fr	Ext. measurements	This study
Colobus guereza	0	2	Zoo, Besançon, Fr	Ext. measurements	This study
Trachypithecus francoisi	0	2	Zoo, Besançon, Fr	Ext. measurements	This study
Nomascus gabriellae	3	1	Zoo, Besançon, Fr	Ext. measurements	Druelle & Berthet, 2017
Hylobates lar	1	2	Rapperswil, SL	Ext. measurements	Isler et al., 2006
Pan paniscus	4	4	Zoo, Planckendael, be & Apeldoorn, NL	Ext. measurements	Druelle et al., 2018
Pan troglodytes	23	16	BPRC[a], Rijswijk, NL	Ext. measurements	Schoonaert et al., 2007
Gorilla gorilla	3	1	Zoo, Bristol, UK, Basel, SL & Zürich, SL	Ext. measurements	Isler et al., 2006
Pongo pygmaeus[b]	2	1	Zoo, Zürich, SL	Ext. measurements	Isler et al., 2006
Papio anubis	15	14	CNRS[c], Rousset, Fr	Ext. measurements	Druelle, Aerts, et al., 2017
Felis silverstris catus	1 (sex: N/A)		Unknown	Dissection	Manter, 1938
Canis lupus familiaris	2	1	Animal shelter, Rehovot, Is	MRI	Amit et al., 2009
Equus caballus	3	3	Unknown, Utrecht, NL	Dissection	Buchner et al., 1997

[a]Biomedical Primate Research Center.
[b]Only juveniles were chosen for this species as there is only one adult measured in Isler et al. (2006).
[c]Primatology Station.

Patel, Horner, Thompson, Barrett, & Henzi, 2013; Helmsmüller, Wefstaedt, Nolte, & Schilling, 2013; Buchner et al., 1997); Figure 2 shows the average posture and the limb angles used for the chimpanzee. When there is a tail, it was positioned at a 30°-angle with the vertical. The
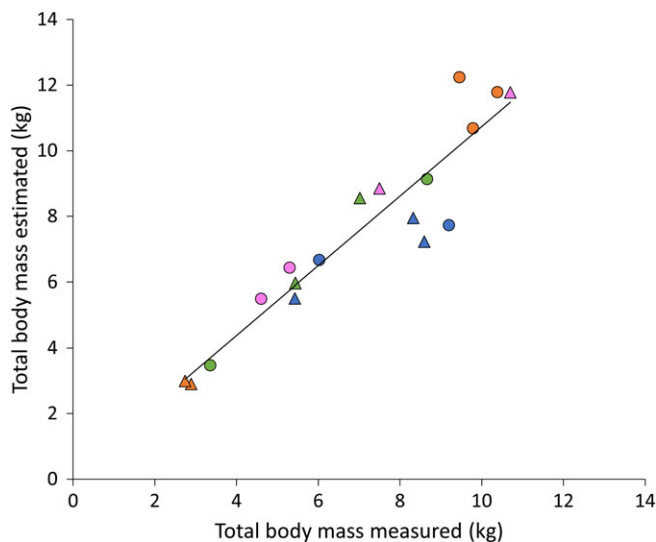
FIGURE 1 Relationship between the total measured body mass and the total estimated (by the geometric model) body mass for our sample. The solid line is the least-squares regression ($y = 1.06 + 0.14$, $R^2 = 0.88$). The 95% confidence interval (0.85–1.27) of the slope overlaps with 1 (i.e., the line of identity), therefore validating the reliability of the procedure. The green circles and triangles indicate *Cercopithecus lhoesti* and *Cercopithecus roloway* individuals, respectively, the orange circles and triangles indicate *Ateles fusciceps* and *Sapajus xanthosternos*, the pink circles and triangles indicate *Trachypithecus francoisi* and *Colobus guereza*, and the blue circles and triangles indicate *Nomascus siki* and *Nomascus gabriellae*

control posture is a standardized quadrupedal body posture in which the fore- and hind limbs are extended perpendicular to the trunk, the tail (if any) is placed perpendicular to the trunk and along the hind limbs, and the head is perpendicular to the forelimbs and along the trunk. For each species, we calculated the position of the BCoM in these two postures. The BCoM is expressed from the hip joint as the percentage of the horizontal distance between the hip joint and the shoulder joint (i.e., the moment arm of the BCoM about the hip joint).

2.3 | Phylogenetic signal

Using the K of Blomberg, Garland, and Ives (2003) and the "phylosig" function in R (Revell, 2012), we estimated the phylogenetic signal for the position of the BCoM in primates. The statistical significance of K is evaluated on 1,000 simulations from the randomization test. This enables to assess the amount of phylogenetic signal observed relative to the amount expected according to a Brownian motion. The phylogeny used in the present study is time-scaled and is based on a consensus chronometric tree of extant primate species. It has been downloaded from the *10kTrees WebServer* (https://10ktrees.nunn-lab.org/) that provides a phylogeny sampled from a Bayesian phylogenetic analysis.

2.4 | Sensitivity analysis

The effects of limbs and tail postural variations on BCoM translation have been evaluated for each primate species in our sample. In the control posture, the limbs were successively protracted and retracted by an angle of 20° while keeping other body parts static. We have also tested the effect of shifting the tail by an angle of 20° backward. We

TABLE 2 Limb angles (°) used to model the free body diagrams in the natural posture

	Elbow	Wrist	Knee	Ankle
P. troglodytes[a]	170	175	148	83
P. paniscus	170	175	148	83
G. gorilla	170	175	148	83
P. pygmaeus[b]	170	81	148	83
N. gabriellae	170	260	148	83
N. Siki	170	260	148	83
H. lar	170	260	148	83
P. anubis	155	250	138	63
C. Roloway	171	264	138	69
C. lhoesti	171	264	138	69
C. guereza	146	254	125	56
T. francoisi	146	254	117	47
A. robustus	130	256	152	79
S. xanthosternos	171	264	138	69
F. catus[c]	140	N/A	96	95
C. familiaris	148	161	121	130
E. caballus	141	180	129	144

[a]The hand of the African great apes has been positioned in a knuckle-walking posture.
[b]The hand of the orangutan has been positioned in a fist-walking posture.
[c]The distal segment of the forelimb of the cat is not available in Manter (1938); therefore, we considered the wrist joint to be on the ground (see Figure 4).

calculated the influence of each of these average postures on the position of the BCoM as follows:

$$\text{Variation of the BCoM} = \frac{(x_i - x_f)}{(x_i + x_f)} \times 100$$

where x_i is the original position of the BCoM in the control posture, and x_f is the new position of the BCoM after shifting the forelimbs, the hind limbs, or the tail. By summing the absolute values of the variation in protracted and retracted limb postures, we calculated the BCoM range of variation for the fore- and hind limbs separately.

2.5 | Statistics

We tested the difference in BCoM position between hominoids and other quadrupedal primates using exact permutation tests for independent samples. We also tested whether there is a difference in how much fore- and hind limbs influence the BCoM translation between hominoids and other primate species. Statistical significance was set at $p < 0.05$ and the tests were performed using StatXact 3.1 (software, Cytel, Inc., Cambridge, MA).

3 | RESULTS

Our results indicate that the variance of the primate BCoM position is concentrated between clades rather than within clades ($K = 1.54$; $p = 0.001$). Because K is greater than 1, it indicates that closely related species resemble each other more than expected under Brownian motion ($K \approx 1$). Figure 3 shows the relative position of the BCoM in our comparative sample of primates and non-primate mammals in the
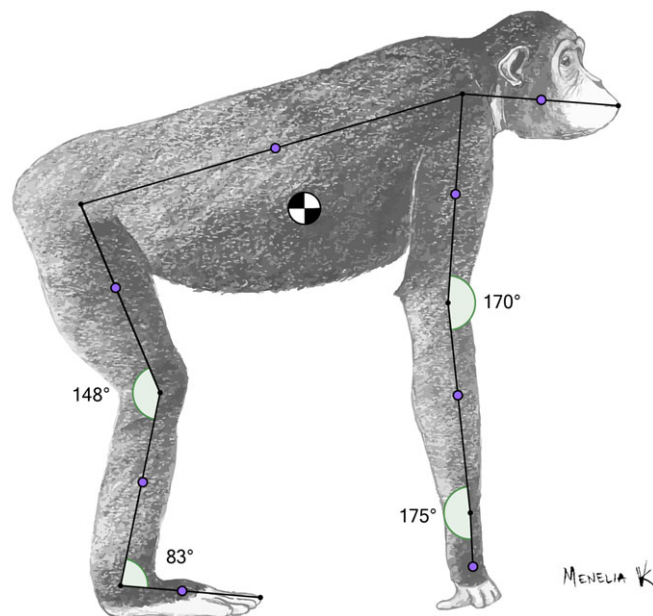
FIGURE 2 Average morphotype for *P. troglodytes* standing up in a typical quadrupedal posture. The CoM of each segment is indicated with a blue circle and the BCoM is indicated with the black and white circle. The average limb angles have been chosen following Pontzer et al. (2014) and Finestone et al. (2018) and are presented in Table 2. Illustration: 2018, Menelia Vasilopoulou-Kampitsi

natural and control postures. Table 3 summarizes these values. In both postures, there is an obvious overlap between the group of primates and the group of non-primate mammals. In the natural body posture, the most extreme positions of the BCoM are found in *A. fusciceps* which exhibits the lowest value (40%, i.e., the BCoM is closer from the hip) and the *H. lar* and *C. familiaris* which exhibit the highest value (63%, i.e., the BCoM is closer from the shoulder). In the control body posture, the spider monkey remains the species with the most caudal BCoM (43%), and the dog is the one with the most cranial BCoM (65%).

Overall, hominoid species exhibit a cranially located BCoM which is significantly different from other quadrupedal primates (natural posture: permutation test: 3.224, $p = 0.0006$; control posture: permutation test: 3.036, $p = 0.0012$). This is the result of huge forelimbs in terms of size and mass (one forelimb represents 7–10% of total body mass in hominoids; see Supplementary Material for body mass distribution data). Our sensitivity analysis also shows that the position of the BCoM is significantly more affected by the forelimbs in hominoids compared to other primates (permutation test: 3.062, $p = 0.0006$); this is not the case for the hind limbs (permutation test: 1.647, $p = 0.1031$). Arboreal *Cercopithecinae* (i.e., *Cercopithecus* species) and (arboreal) *Colobinae* exhibit a caudal BCoM. This is the result of relatively more massive hind limbs than forelimbs (mainly due to the mass of the thigh) as well as the presence of a long and relatively massive tail (3–4% of total body mass). The sensitivity analysis shows that protracting and retracting the hind limbs in the range amplitude of 40° impacts the BCoM position by 3.63% (*C. roloway*) to 5.27% (*C. lhoesti*) in these species, while moving the forelimbs in this range amplitude only affects the BCoM position between 1.5% (*C. roloway*) and 2.05% (*T. francoisi*). Retracting the tail by an angle of 20° affects the position of the BCoM
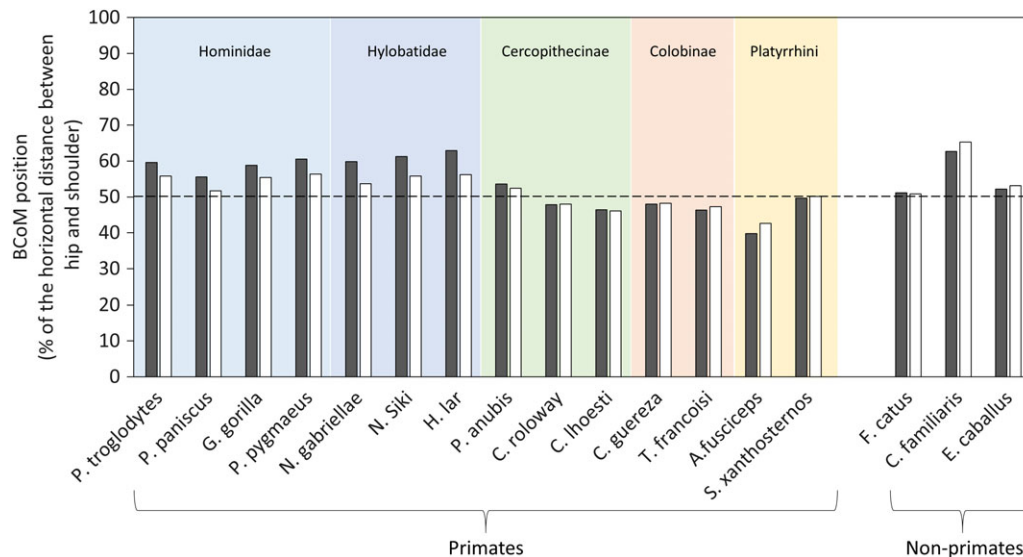
FIGURE 3 Histogram of the relative positions of the BCoM from the hip joint and expressed as a percentage of the horizontal distance between the hip and shoulder joints. The position of the BCoM in the natural average posture is represented with the gray bars, the BCoM position in the control posture is represented with the white bars. The dashed line indicates mid-trunk

by 0.49% (*C. guereza*) to 0.85% (*C. roloway*). The (semi-)terrestrial *Cercopithecinae*, the olive baboon, exhibit a cranial BCoM, which is the result of more similar fore- and hind limbs, a lighter and smaller tail (2% of total body mass) and the presence of a larger head segment. The spider monkey is a Platyrrhini (i.e., New World Monkeys) and exhibits the

most caudal BCoM position. Although the fore- and hind limb proportions seem to be similar to that of *Cercopithecidae* in terms of relative segment masses, the massive prehensile tail (7% of total body mass) of the spider monkey shifts the BCoM posteriorly. A 20°-shift of the tail translates the BCoM by 1.85% backward. The BCoM of the capuchin

TABLE 3 Relative position of the BCoM from the hip joint (%) and its variation with different limbs and tail postures

	Natural posture	Control posture	Sensitivity analysis (variation of the BCoM in %)		
			Forelimbs −20°:+20°	Hind limbs −20°:+20°	Tail −20°
Primate species					
Hominidae					
Pan troglodytes	59.59	55.79	−3.19:2.98	−2.06:1.64	N/A
Pan paniscus	55.57	51.76	−2.56:2.57	−3.30:3.04	N/A
Gorilla gorilla	58.86	55.44	−3.18:3.17	−2.78:2.57	N/A
Pong pygmaeus	60.58	56.34	−5.07:4.60	−3.33:3.02	N/A
Hylobatidae					
Nomascus gabriellae	59.83	53.66	−4.27:4.00	−3.96:3.54	N/A
Nomascus siki	61.25	55.86	−4.07:3.82	−3.41:3.12	N/A
Hylobates lar	62.94	56.20	−6.36:5.56	−4.40:3.81	N/A
Cercopithecinae					
Papio anubis	53.58	52.40	−2.03:2.04	−3.17:3.00	−0.17
Cercopithecus roloway	47.84	48.03	−0.75:0.74	−1.62:2.00	−0.85
Cercopithecus lhoesti	46.42	46.11	−0.81:0.75	−2.77:2.50	−0.61
Colobinae					
Colobus guereza	48.00	48.25	−0.96:0.93	−1.73:2.01	−0.49
Trachypithecus francoisi	46.38	47.28	−0.99:1.06	−2.41:2.43	−0.78
Platyrrhini					
Ateles fusciceps robustus	39.78	42.63	−2.05:2.09	−3.83:3.10	−1.85
Cebus xanthosternos	49.69	50.16	−1.00:1.00	−2.32:2.11	−0.98
Non-primate species					
Felis silverstris catus	51.18	50.88			
Canis lupus familiaris	62.67	65.29			
Equus caballus	52.21	53.13			

monkey (Platyrrhini) is located at mid-trunk (49.69% in the natural posture and 50.16% in the control posture). With regard to the two Platyrrhini species, the tail has a significant impact on the position of the BCoM as a 20°-shift of the tail translates the BCoM by 1.85% in spider monkeys and by 0.98% in capuchins. Figure 4 shows the free body diagrams used for the calculation of the BCoM in the natural postures.

4 | DISCUSSION

The present dataset offers a comparative sample of (hominoid and non-hominoid) primate and non-primate species for the evaluation of the BCoM position. There is an important overlap in the location of the BCoM between hominoids and non-primate mammals. However, most non-hominoid primates have a BCoM closer to the hips than carnivores and ungulates. Our results thus partially support the previous hypothesis of Vilensky and Larson (1989) stipulating that, overall, the BCoM of primates is not more posterior than in other quadrupedal mammals. Indeed, according to the present study, all arboreal quadrupedal primates seem to exhibit a more posterior BCoM than quadrupedal mammals. In addition, we found a phylogenetic signal that may indicate stabilizing selection for this trait (BCoM position) in primates.

4.1 | BCoM and locomotor habits

Primates commonly live in arboreal environments that imply discontinuity, variability, flexibility, and instability of the substrates, and although they generally rely on the quadrupedal system (Rose, 1973; Schmitt, 1999; Schmitt, Cartmill, Griffin, Hanna, & Lemelin, 2006), some have evolved toward new positional (orthograde) habits involving important interlimb dissociation (Young, Wagner, & Hallgrimsson, 2010). For example, the group of hominoid species can be considered to be generally adapted to orthograde, suspensory locomotion (e.g., Crompton,

Vereecke, & Thorpe, 2008; Fan, Scott, Fei, & Ma, 2013; Hunt, 1991; Thorpe & Crompton, 2006) and, therefore, do not belong to the typical quadrupedal primate group (e.g., Finestone et al., 2018; Rose, 1973). In this context, removing the hominoid species from the present sample leaves only one pronograde (semi-)terrestrial primate (the olive baboon) exhibiting a cranial configuration of the BCoM as in non-primate quadrupedal mammals. Therefore, it is possible that the BCoM of arboreal quadrupedal primates is more posterior than in quadrupedal mammals, although it may not be the case for arboreal non-primate mammals (e.g., Schmitt & Lemelin, 2002).

The BCoM can be considered as an average representation of the general body shape of animals. According to our results, there is a strong phylogenetic signal for its position, which is very likely in the context of primate body shape evolution. Closely related species may resemble to each other in terms of body proportions (e.g., Druelle et al., 2018). Furthermore, the variation in the BCoM position appears to be mostly related to the size and mass of the appendicular system, that is, fore- and hind limbs, as well as the tail. In primates, the variation in the proportions of these body segments are likely to be under strong selective pressures as limbs are strongly associated to locomotor adaptations (Fleagle, 2013; Preuschoft, Witte, Christian, & Fischer, 1996; Young et al., 2010), and the tail to balance control (Larson & Stern, 2006; Young, Russo, Fellmann, Thatikunta, & Chadwell, 2015) and locomotion (Anapol, Turner, Mott, & Jolly, 2005; Rodman, 1979; Youlatos, 2002). Raichlen et al. (2009) suggested that the particular weight support pattern of primates could be an evolutionary by-product of the variations in limb morphology (e.g., intermembral index). The present results also corroborate that the position of the primate BCoM is a by-product of the variations in limb (and tail) size and mass. For example, due to relatively heavy hind limbs and a large and massive prehensile tail, the spider monkey exhibits the most extreme caudal configuration of the BCoM. In hominoid species, the long and heavy forelimbs shift the BCoM cranially. The BCoM of the
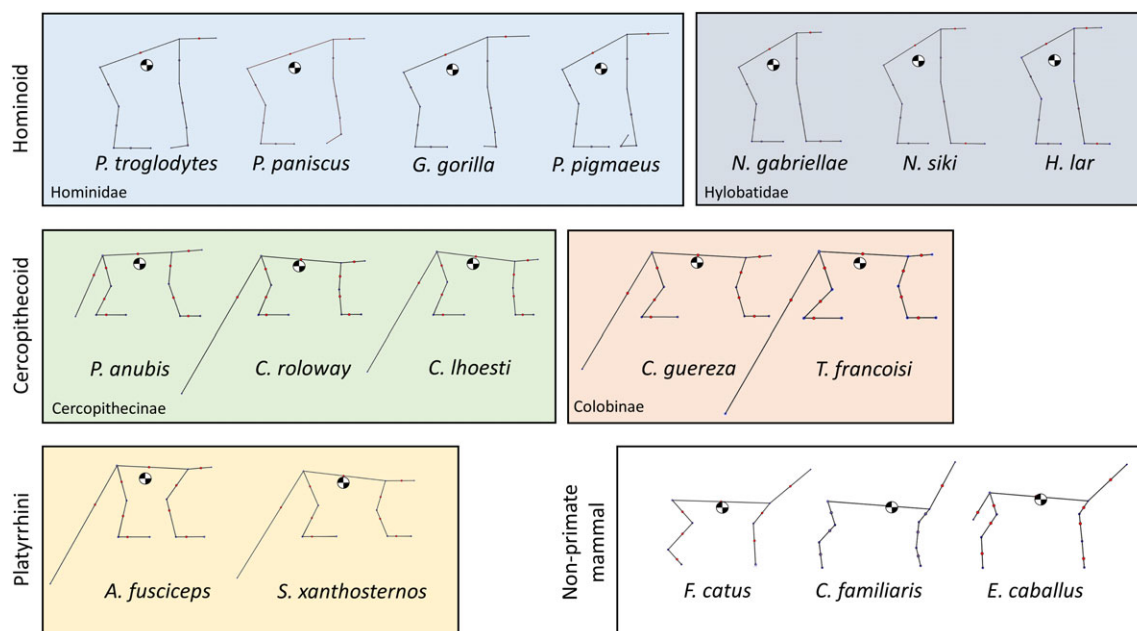
FIGURE 4 Free body diagrams for the 17 (primate and non-primate) species of our comparative sample. Each diagram is positioned in the natural body posture used for the calculation of the BcoM, indicated with the black and white circle

quadrupedal arboreal primates, that is, *Cercopithecus roloway*, *Cercopithecus lhoesti*, *Colobus guereza*, and *Trachypithecus francoisi*, is slightly closer to the hip than the shoulder because of their long tail and heavy thigh; note that the *Sapajus xanthosternos* is also a quadrupedal arboreal primate and exhibits a BCoM at mid-trunk. This probably reflects leaping and climbing capacities (e.g., Gebo & Chapman, 1995; McGraw, 1996; Rose, 1979; Workman & Schmitt, 2011), although a more caudal BCoM in these arboreal quadrupedal animals may also improve maneuverability for traveling in the trees (Aerts, Van Damme, D'Août, & Van Hooydonck, 2003). Fore- and hind limbs morphology (length and mass distribution) is more similar in baboons, and the BCoM is more cranial, therefore reflecting adaptation to terrestrial quadrupedalism (e.g., Druelle, Aerts, et al., 2017; Raichlen, 2004; Rose, 1977). The position of the BCoM may, therefore, be a by-product of the interlimb morphology. As a result, considering pronograde mammals in general, a more caudal BCoM should be observed in arboreal species, although a more cranial BCoM should be observed in terrestrial species. Nevertheless, specific locomotor habits such as bounding and half-bounding locomotion in (terrestrial) lagomorphs for example (e.g., Young, Danczak, Russo, & Fellmann, 2014) may be related to a caudal position of the BCoM.

4.2 | BCoM and gait mechanics

The limbs are anatomically connected to the trunk; therefore, there should be a functional link between limb and trunk mechanics. In this context, it has long been hypothesized that the diagonal walking gait—the typical footfall pattern of primates—could be related to a posterior location of the BCoM (Gray, 1944; Rollinson & Martin, 1981; Tomita, 1967). Rollinson and Martin (1981) observed that captive cercopithecines used a lateral sequence for descending steep inclines which is likely to bring the CoM forward. From this, they concluded that because monkeys maintain otherwise diagonal walking gaits, they should possess a caudal CoM. Although this hypothesis has been supported by ontogenetic studies showing parallel changes between the caudal migration of the BCoM and an increase use of the diagonal walking gaits (e.g., Grand, 1977; Nakano, 1996; Turnquist & Wells, 1994; Young, 2012), a certain number of works were not able to find such a relationship (e.g., Anvari et al., 2014; Druelle, Berillon, & Aerts, 2017; Young, Patel, & Stevens, 2007). Experimental alterations of the antero-posterior mass distribution of the trunk revealed a clear influence on the mechanics of the limbs such as contact time, positioning, angular excursion, and compliance (e.g., Anvari et al., 2014; Lee, Stakebake, Walter, & Carrier, 2004; Young et al., 2007). Nevertheless, the footfall pattern may be related to many confounding factors that require further investigation.

It is commonly assumed that primates walk with a more protracted hind limb than the forelimb is retracted (Larson, Schmitt, Lemelin, & Hamrick, 2000, 2001). Therefore, the hind limbs are brought closer to the BCoM than the forelimbs. This is the argument used by Raichlen et al. (2009), in their study on chimpanzees, to explain primates' greater hind limb weigh support (whatever the configuration of the BCoM position). Nevertheless, Larson and Demes (2011), in their study on spider monkeys and capuchins, were not able to confirm the results of Raichlen et al. (2009) and suggested the

presence of other active mechanisms to explain the weight support asymmetry observed in primates (Larson & Demes, 2011; Larson & Stern, 2009). According to our results, it is obvious that the results and conclusions of these two studies were driven by the very different morphotypes and BCoM positions of the species studied (cranial in the chimpanzee, caudal in the spider monkey, and at mid-trunk in the capuchin). Indeed, although the chimpanzee has no tail and needs to bring the hindlimbs into a very protracted position at touch-down to have the foot falling under the BCoM, the spider monkeys and the capuchins may simply move the position of their heavy tail to shift the position of the BCoM posteriorly. This other "passive" mechanism would significantly increase their hind limb weight support pattern. However, no information is provided on the influence of the tail in these species in Larson and Demes (2011), but according to our results, shifting the tail backward can shift the BCoM posteriorly. For example, extreme positions of the tail (i.e., a 90°-angle with the vertical) will shift the BCoM backward by 5.62% in spider monkeys and by 2.99% in capuchin monkeys. Finally, Larson and Demes (2011) reported that the mean percentage of forelimb weight support is greater in capuchins compared to spider monkeys. This is in accordance with our results showing a more caudal BCoM and a relatively heavier tail in spider monkeys compared to capuchins.

The present report offers new comparative data about the BCoM position in primates. This information can be used for further investigations regarding the particular (quadrupedal) locomotor features of these animals. These data allowed us discussing a new "passive" mechanism for the explanation of the particular weight support pattern observed in primates with tails.

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REFERENCES

Aerts, P., Van Damme, R., D'Août, K., & Van Hooydonck, B. (2003). Bipedalism in lizards: Whole-body modelling reveals a possible spandrel. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, *358*, 1525–1533.

Amit, T., Gomberg, B., Milgram, J., & Shahar, R. (2009). Segmental inertial properties in dogs determined by magnetic resonance imaging. *The Veterinary Journal*, *182*, 94–99.

Anapol, F., Turner, T., Mott, C., & Jolly, C. (2005). Comparative postcranial body shape and locomotion in Chlorocebus aethiops and *Cercopithecus mitis*. *American Journal of Physical Anthropology*, *127*, 231–239.

Anvari, Z., Berillon, G., Asgari Khaneghah, A., Grimaud-Herve, D., Moulin, V., & Nicolas, G. (2014). Kinematics and spatiotemporal parameters of infant-carrying in olive baboons. *American Journal of Physical Anthropology*, 155, 392–404.

Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, 57, 717–745.

Buchner, H., Savelberg, H., Schamhardt, H., & Barneveld, A. (1997). Inertial properties of Dutch Warmblood horses. *Journal of Biomechanics*, 30, 653–658.

Crompton, R. H., Li, Y., Alexander, R. M., Wang, W., & Gunther, M. M. (1996). Segment inertial properties of primates: New techniques for laboratory and field studies of locomotion. *American Journal of Physical Anthropology*, 99, 547–570.

Crompton, R., Vereecke, E., & Thorpe, S. (2008). Locomotion and posture from the common hominoid ancestor to fully modern hominins, with special reference to the last common panin/hominin ancestor. *Journal of Anatomy*, 212, 501–543.

Druelle, F., & Berthet, M. (2017). Segmental morphometrics of the southern yellow-cheeked crested gibbon (*Nomascus gabriellae*): The case study of four individuals in zoo. *Revue de Primatology*, 8, 1–13.

Druelle, F., Aerts, P., D'Août, K., Moulin, V., & Berillon, G. (2017). Segmental morphometrics of the olive baboon (Papio anubis): A longitudinal study from birth to adulthood. *Journal of Anatomy*, 230(6), 805–819.

Druelle, F., Berillon, G., & Aerts, P. (2017). Intrinsic limb morpho-dynamics and the early development of interlimb coordination of walking in a quadrupedal primate. *Journal of Zoology*, 301, 235–247.

Druelle, F., Schoonaert, K., Aerts, P., Nauwelaerts, S., Stevens, J. M., & D'Août, K. (2018). Segmental morphometrics of bonobos (*Pan paniscus*): Are they really different from chimpanzees (*Pan troglodytes*)? *Journal of Anatomy*, 233(6), 843–853.

Fan, P., Scott, M. B., Fei, H., & Ma, C. (2013). Locomotion behavior of cao vit gibbon (*Nomascus nasutus*) living in karst forest in Bangliang Nature Reserve, Guangxi, China. *Integrative Zoology*, 8, 356–364.

Finestone, E. M., Brown, M. H., Ross, S. R., & Pontzer, H. (2018). Great ape walking kinematics: Implications for hominoid evolution. *American Journal of Physical Anthropology*, 166, 43–55.

Fleagle, J. G. (2013). *Primate adaptation and evolution* (3rd ed.). New York: Academic Press.

Gebo, D. L., & Chapman, C. A. (1995). Positional behavior in five sympatric old world monkeys. *American Journal of Physical Anthropology*, 97, 49–76.

Grand, T. I. (1977). Body weight: Its relation to tissue composition, segment distribution, and motor function II. Development of *Macaca mulatta*. *American Journal of Physical Anthropology*, 47, 241–248.

Gray, J. (1944). Studies in the mechanics of the tetrapod skeleton. *Journal of Experimental Biology*, 20, 88–116.

Helmsmüller, D., Wefstaedt, P., Nolte, I., & Schilling, N. (2013). Ontogenetic allometry of the Beagle. *BMC Veterinary Research*, 9, 203.

Hunt, K. D. (1991). Positional behavior in the Hominoidea. *International Journal of Primatology*, 12, 95–118.

Isler, K., Payne, R. C., Günther, M. M., Thorpe, S., Li, Y., Savage, R., & Crompton, R. (2006). Inertial properties of hominoid limb segments. *Journal of Anatomy*, 209, 201–218.

Kimura, T., Okada, M., & Ishida, H. (1979). Kinesiological characteristics of primate walking: its significance in human walking. In M. E. Morbeck, H. Preuschoft, & N. Gomberg (Eds.), *Environment, behavior, and morphology: Dynamic interactions in primates* (pp. 297–311). New York, USA: Gustav Fischer.

Larson, S. G., & Demes, B. (2011). Weight support distribution during quadrupedal walking in Ateles and Cebus. *American Journal of Physical Anthropology*, 144, 633–642.

Larson, S. G., & Stern, J. T. (2006). Maintenance of above-branch balance during primate arboreal quadrupedalism: Coordinated use of forearm rotators and tail motion. *American Journal of Physical Anthropology*, 129, 71–81.

Larson, S. G., & Stern, J. T. (2009). Hip extensor EMG and forelimb/hind limb weight support asymmetry in primate quadrupeds. *American Journal of Physical Anthropology*, 138, 343–355.

Larson, S. G., Schmitt, D., Lemelin, P., & Hamrick, M. (2000). Uniqueness of primate forelimb posture during quadrupedal locomotion. *American Journal of Physical Anthropology*, 112, 87–101.

Larson, S. G., Schmitt, D., Lemelin, P., & Hamrick, M. (2001). Limb excursion during quadrupedal walking: How do primates compare to other mammals? *Journal of Zoology*, 255, 353–365.

Lee, D. V., Stakebake, E. F., Walter, R. M., & Carrier, D. R. (2004). Effects of mass distribution on the mechanics of level trotting in dogs. *Journal of Experimental Biology*, 207, 1715–1728.

Manter, J. T. (1938). The dynamics of quadrupedal walking. *Journal of Experimental Biology*, 15, 522–540.

McGraw, W. S. (1996). Cercopithecid locomotion, support use, and support availability in the tai Forest, Ivory Coast. *American Journal of Physical Anthropology*, 100, 507–522.

Miller, D. I., Nelson, R. C., & Goldfuss, A. J. (1973). *Biomechanics of sport: A research approach*. Philadelphia: Lea & Febiger.

Nakano, Y. (1996). Footfall patterns in the early development of the quadrupedal walking of Japanese macaques. *Folia Primatologica*, 66, 113–125.

Patel, B. A., Horner, A. M., Thompson, N. E., Barrett, L., & Henzi, S. P. (2013). Ontogenetic scaling of fore-and hind limb posture in wild Chacma baboons (*Papio hamadryas ursinus*). *PLoS One*, 8, e71020.

Pontzer, H., Raichlen, D. A., & Rodman, P. S. (2014). Bipedal and quadrupedal locomotion in chimpanzees. *Journal of Human Evolution*, 66, 64–82.

Preuschoft, H., Witte, H., Christian, A., & Fischer, M. (1996). Size influences on primate locomotion and body shape, with special emphasis on the locomotion of "small mammals". *Folia Primatologica*, 66, 93–112.

Raichlen, D. A. (2004). Convergence of forelimb and hindlimb natural Pendular period in baboons (*Papio cynocephalus*) and its implication for the evolution of primate quadrupedalism. *Journal of Human Evolution*, 46, 719–738.

Raichlen, D. A. (2005). Ontogeny of limb mass distribution in infant baboons (*Papio cynocephalus*). *Journal of Human Evolution*, 49, 452–467.

Raichlen, D. A., Pontzer, H., Shapiro, L. J., & Sockol, M. D. (2009). Understanding hind limb weight support in chimpanzees with implications for the evolution of primate locomotion. *American Journal of Physical Anthropology*, 138, 395–402.

Revell, L. J. (2012). Phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223.

Reynolds, T. R. (1985). Mechanics of increased support of weight by the hindlimbs in primates. *American Journal of Physical Anthropology*, 67, 335–349.

Rodman, P. S. (1979). Skeletal differentiation of *Macaca fascicularis* and *Macaca nemestrina* in relation to arboreal and terrestrial quadrupedalism. *American Journal of Physical Anthropology*, 51, 51–62.

Rollinson, J. (1975). Interspecific comparisons of locomotor behavior and prehension in eight species of African forest monkey: A functional and evolutionary study. In *Doctoral thesis*. Univ. London.

Rollinson, J., & Martin, R. (1981). Comparative aspects of primate locomotion, with special reference to arboreal cercopithecines. *Symposia of the Zoological Society of London*, 48, 377–427.

Rose, M. (1973). Quadrupedalism in primates. *Primates*, 14, 337–357.

Rose, M. (1977). Positional behaviour of olive baboons (*Papio anubis*) and its relationship to maintenance and social activities. *Primates*, 18, 59–116.

Rose, M. (1979). Positional behavior of natural populations: some quantitative results of a field study of Colobus guereza and Cercopithecus aethiops. In M. E. Morbeck, H. Preuschoft, & N. Gomberg (Eds.), *Environment, behavior, and morphology: Dynamic interactions in primates* (pp. 75–93). New York, USA: Gustav Fischer.

Schmitt, D. (1999). Compliant walking in primates. *Journal of Zoology*, 248, 149–160.

Schmitt, D., & Lemelin, P. (2002). Origins of primate locomotion: Gait mechanics of the woolly opossum. *American Journal of Physical Anthropology*, 118, 231–238.

Schmitt, D., Cartmill, M., Griffin, T. M., Hanna, J. B., & Lemelin, P. (2006). Adaptive value of ambling gaits in primates and other mammals. *Journal of Experimental Biology*, 209, 2042–2049.

Schoonaert, K., D'Août, K., & Aerts, P. (2007). Morphometrics and inertial properties in the body segments of chimpanzees (*Pan troglodytes*). *Journal of Anatomy*, 210, 518–531.

Thorpe, S., & Crompton, R. H. (2006). Orangutan positional behavior and the nature of arboreal locomotion in Hominoidea. *American Journal of Physical Anthropology*, 131, 384–401.

Tomita, M. (1967). A study on the movement pattern of four limbs in walking. *Journal of Anthropological Society of Nippon*, 75, 120–146.

Turnquist, J. E., & Wells, J. P. (1994). Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): I. Early postnatal ontogeny of the musculoskeletal system. *Journal of Human Evolution*, 26, 487–499.

Vilensky, J. A. (1979). Masses, centers-of-gravity, and moments-of-inertia of the body segments of the rhesus monkey (*Macaca mulatta*). *American Journal of Physical Anthropology*, 50, 57–65.

Vilensky, J. A., & Larson, S. G. (1989). Primate locomotion: Utilization and control of symmetrical gaits. *Annual Review of Anthropology*, 18, 17–35.

Wells, J. P., & DeMenthon, D. F. (1987). Measurement of body segment mass, center of gravity, and determination of moments of inertia by double pendulum in Lemur fulvus. *American Journal of Primatology*, 12, 299–308.

Workman, C., & Schmitt, D. (2011). Positional behavior of Delacour's Langurs (*Trachypithecus delacouri*) in Northern Vietnam. *International Journal of Primatology*, 33, 19–37.

Youlatos, D. (2002). Positional behavior of black spider monkeys (*Ateles paniscus*) in French Guiana. *International Journal of Primatology*, 23, 1071–1093.

Young, J. W. (2012). Gait selection and the ontogeny of quadrupedal walking in squirrel monkeys (*Saimiri boliviensis*). *American Journal of Physical Anthropology*, 147, 580–592.

Young, J. W., Patel, B. A., & Stevens, N. J. (2007). Body mass distribution and gait mechanics in fat-tailed dwarf lemurs (*Cheirogaleus medius*) and patas monkeys (*Erythrocebus patas*). *Journal of Human Evolution*, 53, 26–40.

Young, N. M., Wagner, G. P., & Hallgrimsson, B. (2010). Development and the evolvability of human limbs. *Proceedings of the National Academy of Sciences*, 107, 3400–3405.

Young, J. W., Danczak, R., Russo, G. A., & Fellmann, C. D. (2014). Limb bone morphology, bone strength, and cursoriality in lagomorphs. *Journal of Anatomy*, 225, 403–418.

Young, J. W., Russo, G. A., Fellmann, C. D., Thatikunta, M. A., & Chadwell, B. A. (2015). Tail function during arboreal quadrupedalism in squirrel monkeys (*Saimiri boliviensis*) and tamarins (*Saguinus oedipus*). *Journal of Experimental Zoology Part A: Ecological Genetics Physiology*, 323, 556–566.

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