



HAL
open science

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

François Druelle, Mélanie Berthet, Benoît Quintard

► To cite this version:

François Druelle, Mélanie Berthet, Benoît Quintard. The body center of mass in primates: Is it more caudal than in other quadrupedal mammals?. *American Journal of Physical Anthropology*, 2019, 169 (1), pp.170-178. 10.1002/ajpa.23813 . hal-02959444

HAL Id: hal-02959444

<https://hal.science/hal-02959444>

Submitted on 31 Oct 2023

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

1 **Title:** The body centre of mass in primates: is it more caudal than in other
2 quadrupedal mammals?

3 **Short running title:** Body centre of mass in primates

4 François DRUELLE¹, Mélanie BERTHET², Benoit QUINTARD³

5 ¹Laboratory for Functional Morphology, Biology department, University of Antwerp
6 Campus Drie Eiken (Building D), Universiteitsplein 1, 2610 Antwerp, Belgium

7 ²Besançon Museum, Besançon, France

8 ³Zoological and Botanical Park of Mulhouse, Mulhouse, France

9

ABSTRACT

10 **Objective:** Whole body centre of mass position values are lacking for a comparative sample of
11 primates. Therefore, it still remains unknown whether the body centre of mass in primates is more
12 posteriorly located than in other mammals. The aim of the present report is to provide data for a large
13 sample of primate species and to compare the position of the body centre of mass in primates to non-
14 primate mammals.

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

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

31 **Discussion:** The BCoM of primates is not more posteriorly located than in other quadrupedal
32 mammals, however, there is a substantial range of variation in primates, from caudal (in arboreal
33 quadrupeds) to cranial (in hominoids and terrestrial quadrupeds) positions. This variation is related to
34 a phylogenetic model that suggests stabilizing selection for this trait. It seems that the BCoM position
35 mostly depends of the size of the appendicular system (i.e. limbs) and the tail. Therefore, it may also
36 reflect a general trend in quadrupedal mammals with arboreal species exhibiting a caudal BCoM and
37 terrestrial species exhibiting a cranial BCoM. These results are discussed in the context of the
38 locomotor evolution of primates including locomotor habits and gait mechanics. We also propose a

39 new 'passive' mechanism for the explanation of the particular weight support pattern observed in
40 primates with tails.

41 **KEY WORDS:** Centre of Mass, Locomotor evolution, Morphotype, Primates

42 **INTRODUCTION**

43 It has long been assumed that the body centre of mass of primates is relatively caudal, i.e. situated
44 close to the hip, compared to other mammals (Rollinson & Martin, 1981). This idea was initially based
45 on force plate data indicating that primates commonly support more of their weight on their hind limbs
46 (Kimura, Okada, & Ishida, 1979). Although the differences in the amount of weight supported by the
47 fore- and hind limbs should indeed be related to the position of the whole body centre of mass (e.g.
48 Gray, 1944; Manter, 1938), it is not a direct determination of its location (Vilensky & Larson, 1989;
49 Reynolds, 1985). Furthermore, some authors have suggested that primates could actively shift their
50 weight to their hind limbs during walking (Reynolds, 1985; Schmitt, 1999). Recently, both 'passive' (the
51 position of the limbs relative to the centre of mass) and 'active' models have found support in different
52 primate species (Passive Model: Raichlen, Pontzer, Shapiro, & Sockol, 2009; Active Model: Larson &
53 Stern, 2009; Larson & Demes, 2011). As a result, on the one hand, a full understanding of the weight
54 support pattern observed in primates is lacking. On the other hand, it still remains unknown whether
55 the whole body centre of mass of primates is more posteriorly located than in other mammals.

56 The average location of the body centre of mass can be accurately estimated from the inertial
57 properties (mass and centre of mass) of the body segments and from their position in space (e.g. Miller,
58 Nelson, & Goldfuss, 1973). Using this methodology, Vilensky and Larson (1989) tried to address the
59 issue of whether the body centre of mass of primates is more caudal than in other quadrupedal
60 mammals by comparing the few inertial data available at that time for 1 brown lemur (Wells &
61 DeMenthon, 1987), 1 spot-nosed guenon (Rollinson, 1975) and 15 rhesus monkeys (Vilensky, 1979).
62 They compared these data to the inertial properties of 1 cat (Manter, 1938) and concluded that these
63 differences were certainly too minor to profess the presence of a more caudal centre of mass in
64 primates. Nevertheless, their very small sample size did not lead to a reliable conclusion on this issue.
65 Surprisingly, larger comparative datasets evaluating the position of the centre of mass in different
66 primate and non-primate species have never been published. The objective of the present report is,
67 therefore, to fill this gap of knowledge by providing an accurate estimation of the body centre of mass
68 position in different primate species based on the inertial properties of their body segments, and to
69 compare it to non-primate quadrupedal mammals.

70 Based on the aforementioned observations (Vilensky & Larson, 1989), we hypothesize that the position
71 of the whole body centre of mass of primates is not more posterior than in other quadrupedal

72 mammals. To test this hypothesis, we used a sample representative of the diversity of primate body
73 shape and size by collecting data on *Hylobatidae*, *Atelidae*, *Cebidae*, *Cercopithecinae* and *Colobinae*.
74 We also added available data from the literature on *Hominidae* and other *Cercopithecinae* (Druelle,
75 Aerts, D'Août, Moulin, & Berillon, 2017a; Druelle & Berthet, 2017; Druelle et al., 2018; Isler et al., 2006,
76 Schoonaert, D'Août, & Aerts, 2007). First, we tested whether the phylogeny can explain the variation
77 observed among and within clades in primates. Second, we compared these data to data available for
78 the cat (Manter, 1938), the dog (Amit, Gomberg, Milgram, & Shahar, 2009) and the horse (Buchner,
79 Savelberg, Schamhardt, & Barneveld, 1997). Third, we compared the position of the whole body centre
80 of mass between hominoids (described as orthograde primates) and other quadrupedal (pronograde)
81 primate species.

82 MATERIALS AND METHODS

83 **Sample** The data were collected in the Zoological Park of the Besançon Museum, France, and in the
84 Zoological Park of Mulhouse, France. We took the opportunity of taking external measurements on
85 eighteen primate individuals during veterinary checks while they were under anesthesia. These
86 individuals belong to eight species: the brown-headed spider monkey, *Ateles fusciceps robustus*
87 (*Atelidae*), the buff-headed capuchin, *Sapajus xanthosternos* (*Cebidae*), the Roloway monkey,
88 *Cercopithecus roloway* (*Cercopithecinae*), the L'Hoest's monkey, *Cercopithecus lhoesti*
89 (*Cercopithecinae*), the Guereza monkey, *Colobus guereza* (*Colobinae*), the Francois' leaf monkey,
90 *Trachypithecus francoisi* (*Colobinae*), the southern yellow-cheeked crested gibbon, *Nomascus*
91 *gabriellae* (*Hylobatidae*) and the southern white-cheeked crested gibbon, *Nomascus siki* (*Hylobatidae*).
92 The veterinary examinations did not reveal any musculo-skeletal abnormalities. All of these individuals
93 live inside large enclosures with various enrichments. Table 1 shows the individual information of our
94 sample and includes the additional comparative sample, i.e. the chimpanzee, *Pan troglodytes*
95 (Schoonaert et al., 2007), the bonobo, *Pan paniscus* (Druelle et al., 2018), the gorilla, *Gorilla gorilla*,
96 the orangutan, *Pongo pygmaeus*, the lar gibbon, *Hylobates lar* (Isler et al., 2006) and the southern
97 yellow-cheeked crested gibbon, *Nomascus gabriellae* (Druelle & Berthet, 2017).

98 **Measurement protocol** The protocol of measurements is based on the geometric model developed by
99 Crompton, Li, Alexander, Wang, & Gunther (1996). It has previously been applied on hominoid (Isler
100 et al., 2006; Druelle et al., 2018; Schoonaert et al., 2007; Crompton et al., 1996; Druelle & Berthet,
101 2017) and cercopithecoid specimens (Druelle et al., 2017a; Raichlen, 2005; 2004) and allows for the
102 reliable estimation of the inertial properties of the body (tested on non-human primate cadavers in
103 Crompton et al., 1996; Isler et al., 2006). External linear measurements were taken on eight body
104 segments (or nine, if a tail was present): head (including neck), trunk, arm, forearm, hand, thigh, shank

105 and foot. The landmarks used follow those of previous studies (e.g. Schoonaert et al., 2007). We
106 obtained individual segment dimensions (lengths and antero-posterior and medio-lateral diameters)
107 and, according to the model, we estimated segment mass (average estimated density: 1 g.cm^{-3}) and
108 segment centre of mass (CoM; calculated from the proximal joint of each segment, from the hip for
109 the trunk and the back for the head). **Summed per individual, the mass of the different body segments
110 yields an estimated total body mass. Figure 1 shows that the total body mass estimated by the
111 geometric model is consistent with that directly measured with an electronic scale, confirming the
112 reliability and accuracy of the procedure.**

113 Based on the morphological variables, we designed an average free body diagram for each species
114 using the mathematical and geometric software *GeoGebra 5.0*. Each species morphotype has been
115 built on a minimum of two adult individuals. The morphotypes are scaled, i.e. segment masses are
116 divided by the body mass, segment length is expressed as percentage of trunk + head (including neck)
117 length and segment CoM is expressed as percentage of the respective segment length. We used two
118 postures to assess the location of the whole body centre of mass (BCoM): a natural posture and a
119 control posture. The natural posture is an average posture inspired from biomechanical studies of
120 walking and from lateral pictures available in the literature (Table 2; Pontzer, Raichlen, & Rodman,
121 2014; Finestone, Brown, Ross, & Pontzer, 2018; Patel, Horner, Thompson, Barrett, & Henzi, 2013;
122 Helmsmüller, Wefstaedt, Nolte, & Schilling, 2013; Buchner et al., 1997); figure 2 shows the average
123 posture and the limb angles used for the chimpanzee. When there is a tail, it was positioned at a 30° -
124 angle with the vertical. The control posture is a standardized quadrupedal body posture in which the
125 fore- and hind limbs are extended perpendicular to the trunk, the tail (if any) is placed perpendicular
126 to the trunk and along the hind limbs, and the head is perpendicular to the forelimbs and along the
127 trunk. For each species we calculated the position of the BCoM in these two postures. The BCoM is
128 expressed from the hip joint as the percentage of the horizontal distance between the hip joint and
129 the shoulder joint (i.e. the moment arm of the BCoM about the hip joint).

130 **Phylogenetic signal** Using the K of Blomberg, Garland, & Ives (2003) and the “phylosig” function in R
131 (Revell, 2012), we estimated the phylogenetic signal for the position of the BCoM in primates. The
132 statistical significance of K is evaluated on 1000 simulations from the randomization test. This enables
133 to assess the amount of phylogenetic signal observed relative to the amount expected according to a
134 Brownian motion. The phylogeny used in the present study is time-scaled and is based on a consensus
135 chronometric tree of extant primate species. It has been downloaded from the *10kTrees WebServer*
136 (<https://10ktrees.nunn-lab.org/>) that provides a phylogeny sampled from a Bayesian phylogenetic
137 analysis.

138 **Sensitivity analysis** The effects of limbs and tail postural variations on BCoM translation have been
139 evaluated for each primate species in our sample. In the control posture, the limbs were successively
140 protracted and retracted by an angle of 20° while keeping other body parts static. We have also tested
141 the effect of shifting the tail by an angle of 20° backward. We calculated the influence of each of these
142 average postures on the position of the BCoM as follows:

$$143 \quad \text{Variation of the BCoM} = \frac{(x_i - x_f)}{(x_i + x_f)} \times 100$$

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

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

153 RESULTS

154 Our results indicate that the variance of the primate BCoM position is concentrated between clades
155 rather than within clades ($K=1.54$; $P=0.001$). Because K is greater than 1, it indicates that closely related
156 species resemble each other more than expected under Brownian motion ($K \approx 1$). Figure 3 shows the
157 relative position of the BCoM in our comparative sample of primates and non-primate mammals in the
158 natural and control postures. Table 3 summarizes these values. In both postures, there is an obvious
159 overlap between the group of primates and the group of non-primate mammals. In the natural body
160 posture, the most extreme positions of the BCoM are found in *A. fusciceps* which exhibits the lowest
161 value (40%, i.e. the BCoM is closer from the hip), and the *H. lar* and *C. familiaris* which exhibit the
162 highest value (63%, i.e. the BCoM is closer from the shoulder). In the control body posture, the spider
163 monkey remains the species with the most caudal BCoM (43%), and the dog is the one with the most
164 cranial BCoM (65%).

165 Overall, hominoid species exhibit a cranially located BCoM which is significantly different from other
166 quadrupedal primates (natural posture: permutation test: 3.224, $P=0.0006$; control posture:
167 permutation test: 3.036, $P=0.0012$). This is the result of huge forelimbs in terms of size and mass (one
168 forelimb represents 7-10% of total body mass in hominoids; see supplementary material for body mass
169 distribution data). Our sensitivity analysis also shows that the position of the BCoM is significantly more

170 affected by the forelimbs in hominoids compared to other primates (permutation test: 3.062,
171 $P=0.0006$); this is not the case for the hind limbs (permutation test: 1.647, $P=0.1031$). Arboreal
172 *Cercopithecinae* (i.e. *Cercopithecus* species) and (arboreal) *Colobinae* exhibit a caudal BCoM. This is the
173 result of relatively more massive hind limbs than forelimbs (mainly due to the mass of the thigh) as
174 well as the presence of a long and relatively massive tail (3-4% of total body mass). The sensitivity
175 analysis shows that protracting and retracting the hind limbs in the range amplitude of 40° impacts the
176 BCoM position by 3.63% (*C. roloway*) to 5.27% (*C. lhoesti*) in these species, while moving the forelimbs
177 in this range amplitude only affects the BCoM position between 1.5% (*C. roloway*) and 2.05% (*T.*
178 *francoisi*). Retracting the tail by an angle of 20° affects the position of the BCoM by 0.49% (*C. guereza*)
179 to 0.85% (*C. roloway*). The (semi-)terrestrial *Cercopithecinae*, the olive baboon, exhibit a cranial BCoM,
180 which is the result of more similar fore- and hind limbs, a lighter and smaller tail (2% of total body
181 mass) and the presence of a larger head segment. The spider monkey is a Platyrrhini (i.e. New World
182 Monkeys) and exhibits the most caudal BCoM position. Although the fore- and hind limb proportions
183 seem to be similar to that of *Cercopithecidae* in terms of relative segment masses, the massive
184 prehensile tail (7% of total body mass) of the spider monkey shifts the BCoM posteriorly. A 20°-shift of
185 the tail translates the BCoM by 1.85% backward. The BCoM of the capuchin monkey (Platyrrhini) is
186 located at mid-trunk (49.69% in the natural posture and 50.16% in the control posture). With regard
187 to the two Platyrrhini species, the tail has a significant impact on the position of the BCoM as a 20°-
188 shift of the tail translates the BCoM by 1.85% in spider monkeys and by 0.98% in capuchins. Figure 4
189 shows the free body diagrams used for the calculation of the BCoM in the natural postures.

190

DISCUSSION

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

200

BCoM and locomotor habits

201 Primates commonly live in arboreal environments that imply discontinuity, variability, flexibility and
202 instability of the substrates, and although they generally rely on the quadrupedal system (Rose, 1973;

203 Schmitt, 1999; Schmitt, Cartmill, Griffin, Hanna, & Lemelin, 2006), some have evolved towards new
204 positional (orthograde) habits involving important interlimb dissociation (Young, Wagner, &
205 Hallgrímsson, 2010). For example, the group of hominoid species can be considered to be generally
206 adapted to orthograde, suspensory locomotion (e.g. Hunt, 1991; Crompton, Vereecke, & Thorpe 2008;
207 Thorpe & Crompton, 2006; Fan, Scott, Fei, & Ma, 2013) and, therefore, do not belong to the typical
208 quadrupedal primate group (e.g. Rose, 1973; Finestone et al., 2018). In this context, removing the
209 hominoid species from the present sample leaves only one pronograde (semi-)terrestrial primate (the
210 olive baboon) exhibiting a cranial configuration of the BCoM as in non-primate quadrupedal mammals.
211 Therefore, it is possible that the BCoM of arboreal quadrupedal primates is more posterior than in
212 quadrupedal mammals, although it may not be the case for arboreal non-primate mammals (e.g.
213 Schmitt & Lemelin, 2002).

214 The BCoM can be considered as an average representation of the general body shape of animals.
215 According to our results, there is a strong phylogenetic signal for its position, which is very likely in the
216 context of primate body shape evolution. Closely related species may resemble to each other in terms
217 of body proportions (e.g. Druelle et al., 2018). Furthermore, the variation in the BCoM position appears
218 to be mostly related to the size and mass of the appendicular system, i.e. fore- and hind limbs, as well
219 as the tail. In primates, the variation in the proportions of these body segments are likely to be under
220 strong selective pressures as limbs are strongly associated to locomotor adaptations (Fleagle, 2013;
221 Preuschoft, Witte, Christian, & Fischer, 1996; Young et al., 2010), and the tail to balance control (Larson
222 & Stern, 2006; Young, Russo, Fellmann, Thatikunta, & Chadwell, 2015) and locomotion (Anapol, Turner,
223 Mott, & Jolly, 2005; Rodman, 1979; Youlatos, 2002). Raichlen et al. (2009) suggested that the particular
224 weight support pattern of primates could be an evolutionary by-product of the variations in limb
225 morphology (e.g. intermembral index). The present results also corroborate that the position of the
226 primate BCoM is a by-product of the variations in limb (and tail) size and mass. For example, due to
227 **relatively heavy hind limbs and** a large and massive prehensile tail the spider monkey exhibits the most
228 extreme caudal configuration of the BCoM. In hominoid species, the long and heavy forelimbs shift the
229 BCoM cranially. The BCoM of the quadrupedal arboreal primates, i.e. *Cercopithecus roloway*,
230 *Cercopithecus lhoesti*, *Colobus guereza* and *Trachypithecus francoisi*, is slightly closer to the hip than
231 the shoulder because of their long tail and heavy thigh; note that the *Sapajus xanthosternos* is also a
232 quadrupedal arboreal primate and exhibits a BCoM at mid-trunk. This probably reflects leaping and
233 climbing capacities (e.g. Workman & Schmitt, 2011; Gebo & Chapman, 1995; McGraw, 1996; Rose,
234 1979), while a more caudal BCoM in these arboreal quadrupedal animals may also improve
235 manoeuvrability for travelling in the trees (Aerts, Van Damme, D'Août, & Van Hooydonck, 2003). Fore-
236 and hind limbs morphology (length and mass distribution) is more similar in baboons and the BCoM is

237 more cranial, therefore reflecting adaptation to terrestrial quadrupedalism (e.g. Rose, 1977; Raichlen,
238 2004; Druelle et al., 2017a). The position of the BCoM may, therefore, be a by-product of the interlimb
239 morphology. As a result, considering pronograde mammals in general, a more caudal BCoM should be
240 observed in arboreal species, while a more cranial BCoM should be observed in terrestrial species.
241 Nevertheless, specific locomotor habits such as bounding and half-bounding locomotion in (terrestrial)
242 lagomorphs for example (e.g. Young, Danczak, Russo & Fellmann, 2014) may be related to a caudal
243 position of the BCoM.

244

BCoM and gait mechanics

245 The limbs are anatomically connected to the trunk, therefore there should be a functional link between
246 limb and trunk mechanics. In this context, it has long been hypothesized that the diagonal walking gait
247 - the typical footfall pattern of primates - could be related to a posterior location of the BCoM
248 (Rollinson & Martin, 1981; Gray, 1944; Tomita, 1967). Rollinson and Martin (1981) observed that
249 captive cercopithecines used a lateral sequence for descending steep inclines which is likely to bring
250 the centre of mass forward. From this, they concluded that because monkeys maintain otherwise
251 diagonal walking gaits, they should possess a caudal centre of mass. Although this hypothesis has been
252 supported by ontogenetic studies showing parallel changes between the caudal migration of the BCoM
253 and an increase use of the diagonal walking gaits (e.g. Young, 2012; Nakano, 1996; Turnquist & Wells,
254 1994; Grand, 1977), a certain number of works were not able to find such a relationship (e.g. Young,
255 Patel, & Stevens, 2007; Anvari et al., 2014; Druelle, Berillon, & Aerts, 2017b). Experimental alterations
256 of the antero-posterior mass distribution of the trunk revealed a clear influence on the mechanics of
257 the limbs such as contact time, positioning, angular excursion and compliance (e.g. Lee, Stakebake,
258 Walter, & Carrier, 2004; Young et al., 2007, Anvari et al., 2014). Nevertheless, the footfall pattern may
259 be related to many confounding factors that require further investigation.

260 It is commonly assumed that primates walk with a more protracted hind limb than the forelimb is
261 retracted (Larson, Schmitt, Lemelin, & Hamrick, 2000; 2001). Therefore, the hind limbs are brought
262 closer to the BCoM than the forelimbs. This is the argument used by Raichlen et al. (2009), in their
263 study on chimpanzees, to explain primates' greater hind limb weight support (whatever the
264 configuration of the BCoM position). Nevertheless, Larson & Demes (2011), in their study on spider
265 monkeys and capuchins, were not able to confirm the results of Raichlen (2009) and suggested the
266 presence of other active mechanisms to explain the weight support asymmetry observed in primates
267 (Larson & Stern, 2009; Larson & Demes, 2011). According to our results, it is obvious that the results
268 and conclusions of these two studies were driven by the very different morphotypes and BCoM
269 positions of the species studied (cranial in the chimpanzee, caudal in the spider monkey and at mid-

270 trunk in the capuchin). Indeed, while the chimpanzee has no tail and needs to bring the hindlimbs into
271 a very protracted position at touch-down in order to have the foot falling under the BCoM, the spider
272 monkeys and the capuchins may simply move the position of their heavy tail to shift the position of
273 the BCoM posteriorly. This other “passive” mechanism would significantly increase their hind limb
274 weight support pattern. However, no information is provided on the influence of the tail in these
275 species in Larson and Demes (2011), but according to our results, shifting the tail backward can shift
276 the BCoM posteriorly. For example, extreme positions of the tail (i.e. a 90°-angle with the vertical) will
277 shift the BCoM backward by 5.62% in spider monkeys and by 2.99% in capuchin monkeys. Finally,
278 Larson and Demes (2011) reported that the mean percentage of forelimb weight support is greater in
279 capuchins compared to spider monkeys. This is in accordance with our results showing a more caudal
280 BCoM and a relatively heavier tail in spider monkeys compared to capuchins.

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

285 **ACKNOWLEDGMENTS**

286 We are very grateful to Céline François-Brazier and Marine Giorgiadis, veterinary interns in Mulhouse,
287 Alexandrine Vesz, veterinarian in Besançon, Guillaume Limouzin, animal keeper in Besançon, and
288 Bérengère Dourou, veterinary student in Besançon, for their valuable help during the protocol for
289 measurements. We thank Gilles Berillon for allowing us to use his anthropometric material for the
290 external measurements. We are also very grateful to Josie Meaney-Ward who revised and improved
291 the English of the manuscript. Financial support was provided by the CNRS-INEE International Research
292 Network n°GDRI0870 Bipedal Equilibrium.

293 **REFERENCES**

- 294 Aerts, P., Van Damme, R., D'Août, K., & Van Hooydonck, B. (2003). Bipedalism in lizards: whole-body
295 modelling reveals a possible spandrel. *Philosophical Transactions of the Royal Society of*
296 *London B: Biological Sciences*, 358, 1525-1533.
- 297 Amit, T., Gomberg, B., Milgram, J., & Shahar, R. (2009). Segmental inertial properties in dogs
298 determined by magnetic resonance imaging. *The Veterinary Journal*, 182, 94-99.
- 299 Anapol, F., Turner, T., Mott, C., & Jolly, C. (2005). Comparative postcranial body shape and
300 locomotion in *Chlorocebus aethiops* and *Cercopithecus mitis*. *American Journal of Physical*
301 *Anthropology*, 127, 231-239.
- 302 Anvari, Z., Berillon, G., Asgari Khaneghah, A., Grimaud-Herve, D., Moulin, V., & Nicolas, G. (2014).
303 Kinematics and spatiotemporal parameters of infant-carrying in olive baboons. *American*
304 *Journal of Physical Anthropology*, 155, 392-404.
- 305 Blomberg, S.P., Garland, T., & Ives, A.R. (2003). Testing for phylogenetic signal in comparative data:
306 Behavioral traits are more labile. *Evolution*, 57, 717-745.

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

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

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

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

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

321 Druelle, F., & Berthet, M. (2017). Segmental morphometrics of the southern yellow-cheeked crested
322 gibbon (*Nomascus gabriellae*): the case study of four individuals in zoo. *Revue de
323 primatology*, 8.

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

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

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

332 Fleagle, J.G. (2013). *Primate Adaptation and Evolution: 3rd Edition*. New York: Academic Press.

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

335 Grand, T.I. (1977). Body weight: Its relation to tissue composition, segment distribution, and motor
336 function II. Development of *Macaca mulatta*. *American Journal of Physical Anthropology*, 47,
337 241-248.

338 Gray, J. (1944). Studies in the Mechanics of the Tetrapod Skeleton. *Journal of Experimental Biology*,
339 20, 88-116.

340 Helmsmüller, D., Wefstaedt, P., Nolte, I., & Schilling, N. (2013). Ontogenetic allometry of the Beagle.
341 *BMC veterinary research*, 9, 203.

342 Hunt, K.D. (1991). Positional behavior in the Hominoidea. *International Journal of Primatology*, 12,
343 95-118.

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

346 Kimura, T., Okada, M., & Ishida, H. (1979). Kinesiological characteristics of primate walking: its
347 significance in human walking. *Environment, behavior, and morphology: Dynamic
348 interactions in primates*, 297-311.

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

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

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

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

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

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

362 Manter, J.T. (1938). The dynamics of quadrupedal walking. *Journal of Experimental Biology*, 15, 522-
363 540.

364 McGraw, W.S. (1996). Cercopithecoid locomotion, support use, and support availability in the Tai
365 Forest, Ivory Coast. *American Journal of Physical Anthropology*, 100, 507-522.

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

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

370 Patel, B.A., Horner, A.M., Thompson, N.E., Barrett, L., & Henzi, S.P. (2013). Ontogenetic Scaling of
371 Fore-and Hind Limb Posture in Wild Chacma Baboons (*Papio hamadryas ursinus*). *PloS one*, 8,
372 e71020.

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

375 Preuschoft, H., Witte, H., Christian, A., & Fischer, M. (1996). Size Influences on Primate Locomotion
376 and Body Shape, with Special Emphasis on the Locomotion of 'Small Mammals'. *Folia*
377 *Primatologica*, 66, 93-112.

378 Raichlen, D.A. (2004). Convergence of forelimb and hindlimb Natural Pendular Period in baboons
379 (*Papio cynocephalus*) and its implication for the evolution of primate quadrupedalism.
380 *Journal of Human Evolution*, 46, 719-738.

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

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

386 Revell, L.J. (2012). phytools: an R package for phylogenetic comparative biology (and other things).
387 *Methods in Ecology and Evolution*, 3, 217-223.

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

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

393 Rollinson, J. (1975). Interspecific Comparisons of Locomotor Behavior and Prehension in Eight Species
394 of African Forest Monkey: A Functional and Evolutionary Study. Doctoral thesis. Univ.
395 London.

396 Rollinson, J., & Martin, R. (1981). Comparative aspects of primate locomotion, with special reference
397 to arboreal cercopithecines. In *Symp Zool Soc Lond*, pp. 377-427.

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

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

401 Rose, M. (1979). Positional behavior of natural populations: some quantitative results of a field study
402 of *Colobus guereza* and *Cercopithecus aethiops*. *Environment, behavior, and morphology:*
403 *Dynamic interactions in primates*, 75-93.

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

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

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

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

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

413 Tomita, M. (1967). A study on the movement pattern of four limbs in walking. *Part*, 1, 120-146.

414 Turnquist, J.E., & Wells, J.P. (1994). Ontogeny of locomotion in rhesus macaques (*Macaca mulatta*): I.
415 Early postnatal ontogeny of the musculoskeletal system. *Journal of Human Evolution*, 26,
416 487-499.

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

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

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

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

426 Youlatos, D. (2002). Positional Behavior of Black Spider Monkeys (*Ateles paniscus*) in French Guiana.
427 *International Journal of Primatology*, 23, 1071-1093.

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

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

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

435 Young, J.W., Russo, G.A., Fellmann, C.D., Thatikunta, M.A., & Chadwell, B.A. (2015). Tail function
436 during arboreal quadrupedalism in squirrel monkeys (*Saimiri boliviensis*) and tamarins
437 (*Saguinus oedipus*). *Journal of Experimental Zoology Part A: Ecological Genetics Physiology*,
438 323, 556-566.

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

441

442

FIGURE LEGENDS

443 **Fig. 1.** Relationship between the total measured body mass and the total estimated (by the
444 geometric model) body mass for our sample. The solid line is the least-squares regression
445 ($y=1.06+0.14x$, $R^2=0.88$). The 95% Confidence Interval [0.85-1.27] of the slope overlaps with 1 (i.e. the
446 line of identity), therefore validating the reliability of the procedure. The green circles and triangles
447 indicate *Cercopithecus lhoesti* and *Cercopithecus roloway* individuals, respectively, the orange circles
448 and triangles indicate *Ateles fusciceps* and *Sapajus xanthosternos*, the pink circles and triangles
449 indicate *Trachypithecus francoisi* and *Colobus guereza*, and the blue circles and triangles indicate
450 *Nomascus siki* and *Nomascus gabriellae*.

451 **Fig. 2.** Average morphotype for *P. troglodytes* standing up in a typical quadrupedal posture. The CoM
452 of each segment is indicated with a blue circle and the BCoM is indicated with the black and white
453 circle. The average limb angles have been chosen following Pontzer et al. (2014) and Finestone et al.
454 (2018a) and are presented in Table 2. Illustration: 2018, Menelia Vasilopoulou-Kampitsi.

455 **Fig. 3.** Histogram of the relative positions of the BCoM from the hip joint and expressed as a
456 percentage of the horizontal distance between the hip and shoulder joints. The position of the BCoM
457 in the natural average posture is represented with the grey bars, the BCoM position in the control
458 posture is represented with the white bars. The dashed line indicates mid-trunk.

459 **Fig. 4.** Free body diagrams for the 17 (primate and non-primate) species of our comparative sample.
460 Each diagram is positioned in the natural body posture used for the calculation of the BCoM,
461 indicated with the black and white circle.

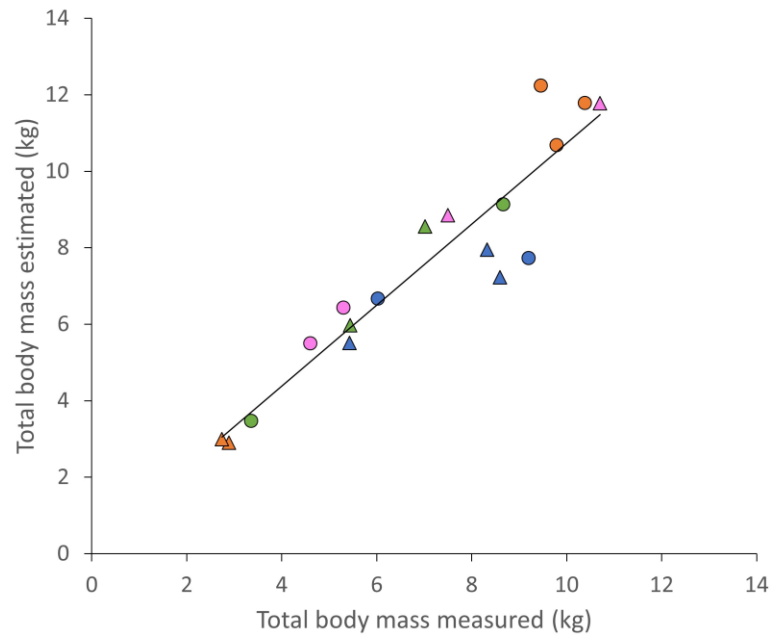


Figure 1.

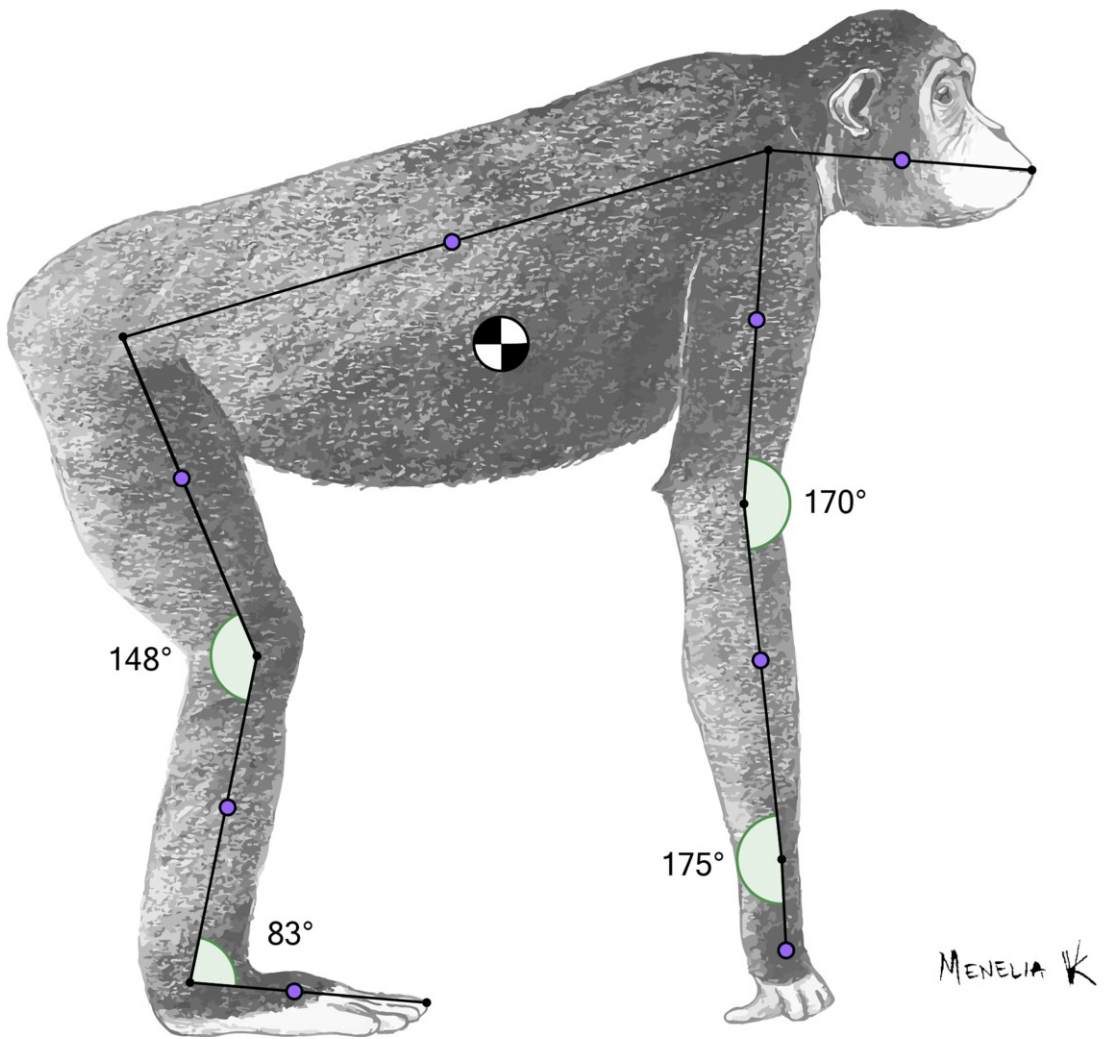


Figure 2.

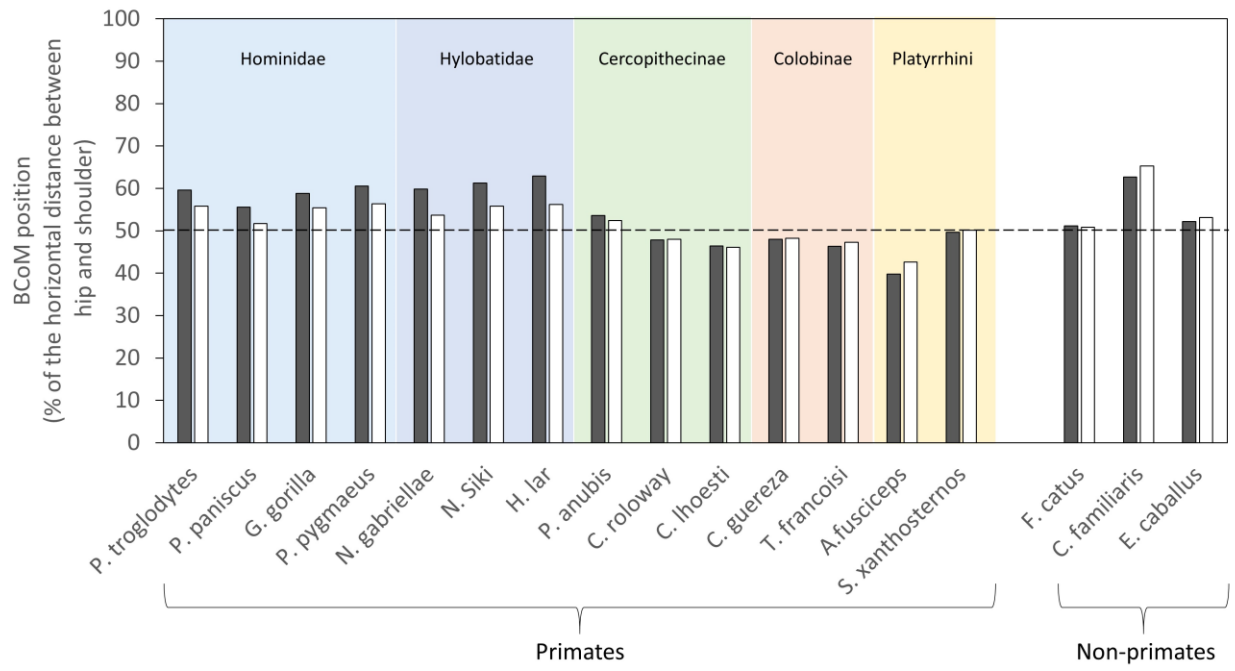


Figure 3.

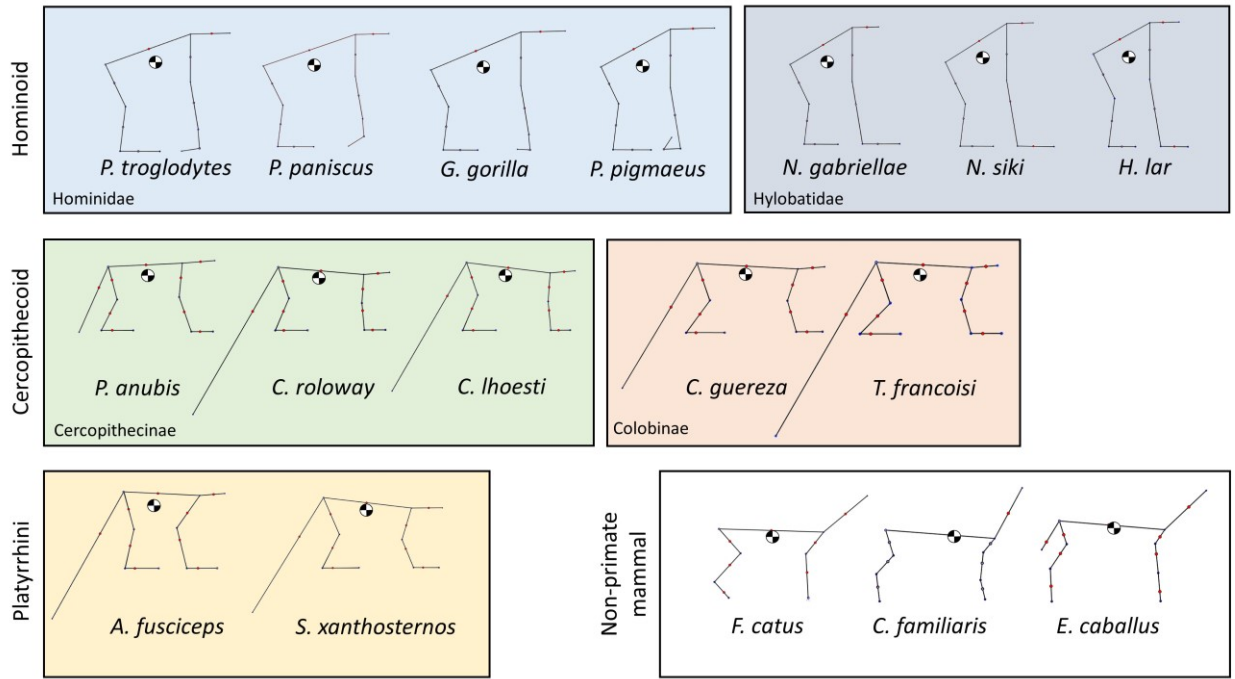


Figure 4.