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Morphométrie des segments corporels du Gibbon à favoris roux (Nomascus gabriellae): étude de quatre individus vivant en parc zoologique

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EDITOR'S NOTE

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1 Introduction

- 1 The lesser apes (*Hylobatidae*) commonly travel and forage through the middle and the upper levels of the forest canopy. Their posturo-locomotor (i.e., positional) repertoires are all characterized by unique suspensory modes including “continuous-contact” brachiation and “ricochetal” brachiation (Fan *et al.*, 2013, Fleagle, 1976, Gittins, 1983, see Hunt, 2016 for a review). Biomechanical analyses, via direct kinematic description or mechanical modeling, reveal that these capacities are efficiently used in terms of energy recovery and speed (Bertram *et al.*, 1999, Bertram and Chang, 2001, Fleagle, 1974, Michilsens *et al.*, 2012, Usherwood and Bertram, 2003). In this respect, such capabilities can be only fulfilled with an appropriate morphological pattern (Michilsens *et al.*, 2009, Preuschoft *et al.*, 1996, Preuschoft, 1989, Zihlman *et al.*, 2011). Indeed, a body possesses inherent mechanical properties that reflect the resistance to linear and angular

acceleration about the joints during movement. These properties, also called the intrinsic morpho-dynamics of the body (see Druelle *et al.*, 2017), should influence locomotor performance (Biewener, 2003). Specifically, the body of an animal is composed of different segments, linked together at joints. Each segment can be described by its size (length, surface area, volume), its shape, its density, and, altogether, its mass, its center of mass, its inertia and its radius of gyration (e.g. Crompton *et al.*, 1996). Each joint further possesses a certain number of degrees of freedom, therefore, the “joint-segment” system can be modeled according to lever arm principles. In this context, it has been shown that the distribution of the mass over the body segments may influence the kinematics of the movement pattern on the one hand (e.g. Raichlen, 2005a, Raichlen *et al.*, 2009, Young *et al.*, 2007, Young, 2012) and may reflect the posturo-locomotor habits of primates on the other hand (Druelle *et al.*, 2016, Wells and Turnquist, 2001, Lawler, 2006, Isler *et al.*, 2006).

- 2 Preuschoft (2004) stated that “the most obvious morphological differences between humans and our closest biological relatives are [...] in body proportions”. In this respect, the study of these differences at an inter- and intra-specific level may also highlight the evolutionary pathway toward specialized locomotor modes in primates. This includes the quadrupedal specialization observed in baboons, the (slow) suspensory specialization observed in orangutans, the bipedal specialization observed in hominins, the quadrupedal knuckle-walking specialization observed in African apes, and the specialization for brachiation observed in gibbons. Interestingly, when normalized to body mass, the locomotor apparatus of the different species of gibbons seem very similar to each other (Michilsens *et al.*, 2009, but see Zihlman *et al.*, 2011). It has been shown that their impressive locomotor performance is made possible thanks to their relatively long forelimbs, highly mobile shoulder and wrist joints, their long hook-like hands, and the dimensions of their forelimb musculature (Bartlett, 2007, Michilsens *et al.*, 2009). Nevertheless, given the endangered status of wild gibbons and the difficulty of accessing captive and semi-naturalistic populations, only few data exist regarding gibbon inertial properties: three *Hylobates* specimens and one *Symphalangus* specimen have been measured by Isler and collaborators (2006). Furthermore, in an attempt to emphasize anatomical differences among gibbon species, Zihlman and collaborators (2011) recently provided body proportion and limb masses for 7 *Hylobates*, 1 *Hoolock*, 1 *Nomascus* and 3 *Symphalangus* specimens. In this context, new data are highly valuable for increasing our knowledge on the locomotor capacities of these species and their differences, if any.
- 3 The major aim of this study is to provide the first segment inertial data for a sample of southern yellow-cheeked crested gibbons (*Nomascus gabriellae*). These primates are commonly found in southern China, Vietnam, Laos, and eastern Cambodia (Fleagle, 2013). It is not possible to have access to these animals in the wild because of 1) their conservation status (*Endangered* according to the International Union for Conservation of Nature), and 2) the complexity of their canopy habitat (40 meters high), making it exceedingly difficult to anesthetize and capture them from afar. We therefore used the opportunity of a veterinary exam in a zoological park. While individuals were under anesthesia, we had the possibility to make external measurements for data collection.

2 Methods

2.1 Study site and subjects

- 4 The present study was conducted in the Zoological Park of the Besançon Museum, in France, where approximately 90 non-human primates of 20 different species are bred and housed. We took the opportunity of an enclosure maintenance leading to the relocation of a yellow-cheeked gibbon group to make external measurements on four individuals under anesthesia, combined with veterinary check. All of them were captive born. Gabrielle was born on 6 March 1993 at the Zoological and Botanical Gardens of Hong Kong. Manau was born on 26 May 1996 at the Zoological and Botanical Park of Mulhouse. Manola and Namoi were born on 12 June 2013 and 14 November 2010, respectively, at the Museum of Besançon. The group is thus formed of one adult male, one adult female, one juvenile female and one adolescent female. These individuals live together in an enclosure with various enrichments. Table I shows the individual information of our sample and includes a comparative sample of four individuals previously measured using the same methodology by Isler and collaborators (2006).

Table I

Subject	Species	Sex	Age (year)	Body mass (kg)
<i>Current study</i>				
Gabrielle	<i>Nomascus gabriellae</i>	F	23.73	6.1
Manau	<i>Nomascus gabriellae</i>	M	20.51	7.24
Manola	<i>Nomascus gabriellae</i>	F	3.45	4.42
Namoi	<i>Nomascus gabriellae</i>	F	6.03	6.62
<i>Isler et al., 2006</i>				
Hy1	<i>Hylobates lar</i>	F	16	4.65
Hy2	<i>Hylobates lar</i>	M	?	5.4
Hy3	<i>Hylobates lar</i>	F	7-8	6.9
Hy4	<i>Symphalangus syndactylus</i>	M	22	13.1

Information about individuals.
Informations sur les individus.

2.2 Collecting morphometrics

- 5 Our protocol of measurements allows using the geometric model developed by Crompton and collaborators (1996), as previously applied on other hominoid specimens (e.g. Isler *et al.*, 2006, Raichlen *et al.*, 2009, Schoonaert *et al.*, 2007) and cercopithecoids (e.g. Druelle *et al.*, 2017, 2016, Raichlen, 2005b, 2004), and tested on non-human primate cadavers (Crompton *et al.*, 1996, Isler *et al.*, 2006). External linear measurements of eight body segments were taken (head - including neck - trunk, arm, forearm, hand, thigh, leg and foot). The landmarks used follow those of our previous studies (e.g. Druelle *et al.*, 2017; see Figure 1 for an example). We obtained individual segment dimensions (lengths and antero-posterior and medio-lateral diameters) and, according to the model, we estimated inertial properties of the body segments such as segment mass (average estimated density: 1 g.cm⁻³), segment center of mass (CoM; calculated from the proximal joint of each segment and from the shoulder for the trunk) and segment radius of gyration about the proximal joint (RG; in the sagittal orientation), i.e. the position on a body segment where a point mass would have an equal mass moment of inertia to the segment itself.

CoM and RG are normalized relative to segment length. Using the mathematical and geometric software *GeoGebra 5.0*, we designed free body diagrams for the four gibbons measured herein. For enabling comparisons between individuals, each morphotype is scaled, i.e. segment masses are divided by the body mass and segment lengths are divided by the cube root of the body mass. We used a standardized bipedal body posture in which fore- and hindlimbs are extended. In this posture we calculated the position of the whole body center of mass (BCoM). We also calculated the position of the CoM and the moment of inertia of the fore- and hindlimbs about its proximal end (see Raichlen, 2004 for the equations).

Figure 1



Picture taken during the protocol of external measurements on Gabrielle, an adult female. Here, the length of the trunk (from acromion of scapula to great trochanter of femur) is measured using calipers.

Photo prise au cours du protocole de mesures externes sur Gabrielle, une femelle adulte. Ici, la mesure de la longueur du tronc (de l'acromion au grand trochanter) grâce à l'utilisation d'un pied à coulisse.

2.3 Statistics

- 6 In accordance with Crompton *et al.* (1996) and Raichlen (2004), the reliability of the procedure of external measurements was assessed by calculating an estimated total body mass via the sum of the segment masses per individual. Because our sample size is too small to use statistical tests ($N=4$), we added the data coming from the four other gibbons previously measured by Isler and collaborators (2006). We used a permutation test for paired samples (*StatXact 3.1*) in order to compare the estimated mass to that directly measured with an electronic scale. We also tested the correlation between the measured and estimated masses using a Spearman's correlation test (given the small sample size).
- 7 We analyzed the relationship between the fore- and hindlimbs in fully extended positions. For each variable, i.e. limb length, limb mass, limb CoM, and limb mass moment of inertia, we plotted the hindlimb against the forelimb. The resulting position of each data point relative to the line of identity ($x=y$) provides a qualitative assessment allometric relationships between fore- and hindlimbs (i.e., points below the line of identity suggest negative allometry, whereas points above the line suggest positive allometry).

3 Results

3.1 Validity of the model

- 8 The body mass estimated using the geometric model and the body mass measured with a scale do not differ significantly (Permutations: 1.810, $P=0.078$). The two values are also strongly correlated (Spearman correlation: $r=0.83$, $P=0.015$). These results support the reliability of the procedure for calculating inertial properties from external measurements and using a geometric model in *Hylobatidae*.

3.2 Inertial properties of body segments

- 9 The length, the mass, the position of the CoM and the RG of each body segment are given in table II for each individual.

Table II

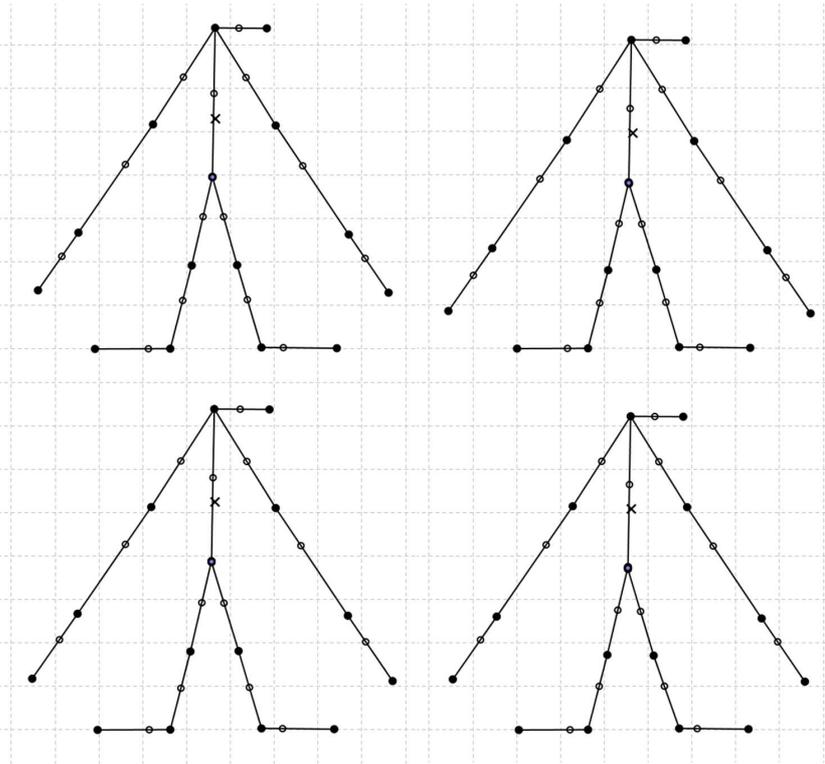
	Head	Arm	Forearm	Hand	Thigh	Leg	Foot	Trunk
Length (mm)								
Gabrielle	113	250	275	160	190	170	148	302
Manau	114	255	292	156	204	191	166	333
Manola	104	220	245	150	175	153	137	289
Namoï	112	231	290	166	195	167	149	328
Mass (kg)								
Gabrielle	0.51	0.23	0.13	0.05	0.30	0.11	0.05	3.07
Manau	0.41	0.25	0.15	0.07	0.31	0.14	0.07	4.65
Manola	0.32	0.15	0.13	0.05	0.20	0.08	0.05	3.14
Namoï	0.44	0.26	0.18	0.06	0.34	0.12	0.06	4.16
CoM (%)								
Gabrielle	46.1	49.2	36.1	42.9	46.7	42.2	28.7	48.1*
Manau	45.7	50.4	36.8	40.7	44.9	42.2	29.2	44.2
Manola	46.6	52.7	34.9	39.8	45.7	46.7	28.7	45.0
Namoï	46.3	49.6	34.8	37.2	48.7	41.6	26.1	44.8
RG (%)								
Gabrielle	28.9	27.6	28.6	27.3	28.6	28.8	24.3	29.4
Manau	28.2	28.5	29.9	27.8	29.3	28.6	24.2	29.0
Manola	28.2	29.3	28.4	27.7	28.2	29.5	24.3	28.7
Namoï	28.9	28.8	28.3	28.2	28.8	30.1	23.0	28.7

*for the trunk, the position of the CoM is expressed as the distance from the shoulder

Inertial properties of *Nomascus gabriellae* body segments.
Propriétés d'inertie des segments corporels chez Nomascus gabriellae.

- 10 Our results are very similar to those obtained by Isler and collaborators (2006) on *Hylobates lar* and *Symphalangus syndactylus*. Figure 2 shows the body diagrams of the four gibbons measured herein; the BCoM is positioned at mid trunk in this bipedal posture. The morphotypes have been made dimensionless in order to enable comparisons. Despite the age-sex differences the four individuals appear very similar.

Figure 2



Body diagrams of the four *Nomascus gabriellae* measured (upper left: Manau, upper right: Gabrielle, lower left: Manola, lower right: Namoi). Open circles represent the CoM of each body segment, filled circles represent the joints and the distal part of the segments, and crosses represent the BCoM. All segment lengths are made dimensionless via the cube root of the total body mass.

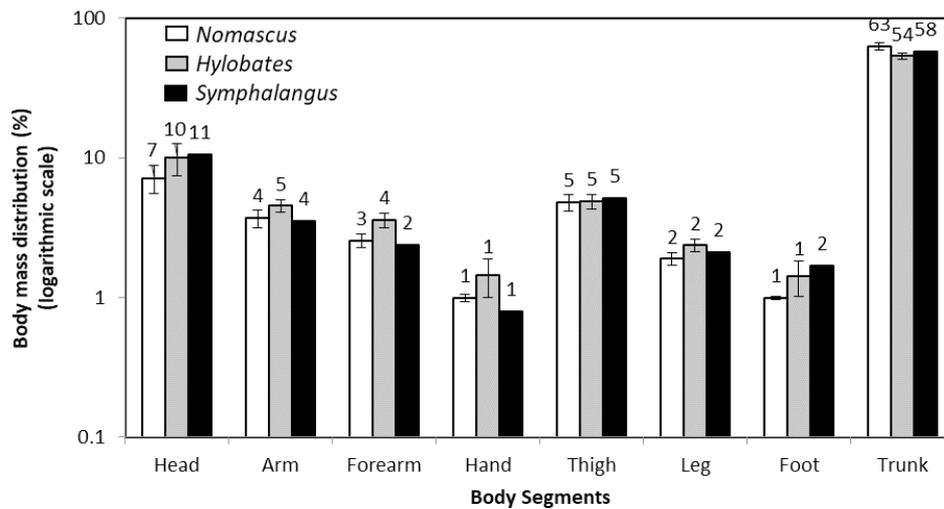
Diagrammes corporels des quatre gibbons mesurés (en haut à gauche: Manau, en haut à droite: Gabrielle, en bas à gauche: Manola, en bas à droite: Namoi). Les cercles vides représentent les centres de masse de chaque segment corporel, les cercles pleins représentent les articulations des segments et leurs points distaux, et les croix représentent le centre de masse global. Toutes les longueurs segmentaires ont été rendues sans dimension en les divisant par la racine cubique de la masse totale.

3.2 Comparisons between gibbon species

3.2.1 Body mass distribution

- 11 Figure 3 shows the distribution of the mass over the body segments in gibbons (*Nomascus gabriellae* and *Hylobates lar*) and siamangs (*Symphalangus syndactylus*). The distribution of the mass appears to be very similar between the species, particularly at the level of the hindlimbs. The most significant difference seems to be at the level of the upper body; *Nomascus gabriellae* possess a relative larger trunk and a smaller head than the other species.

Figure 3



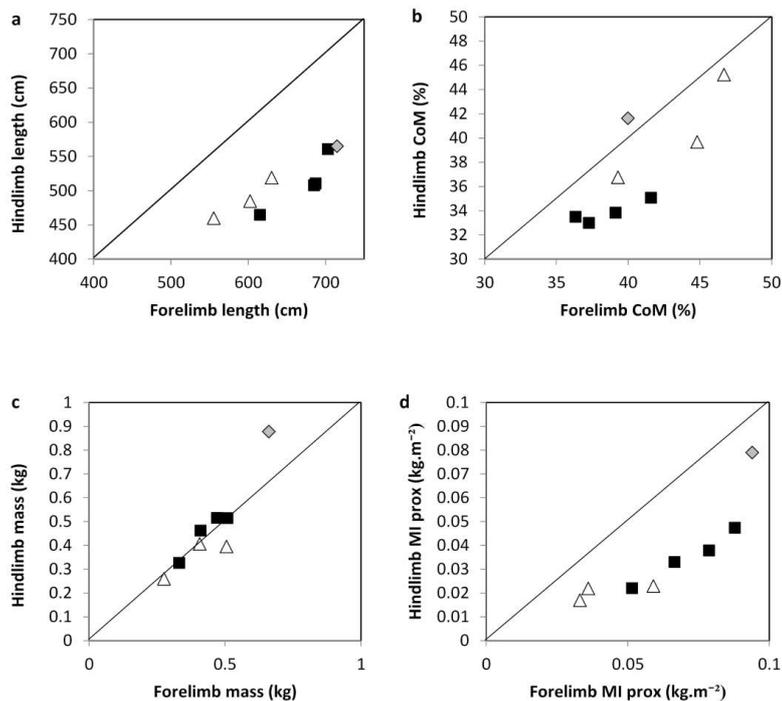
Histogram of the average proportion of each body segment. *Nomascus gabriellae* (N=4) are in white, *Hylobates lar* (N=3) are in grey and the *Symphalangus syndactylus* (N=1) is in black. Values at the top of the bars indicate the average percentage of body mass represented by the indicated segment (rounded to the nearest integer value).

Histogramme des proportions moyennes de chaque segment corporel. Les *Nomascus gabriellae* (N=4) sont en blanc, les *Hylobates lar* (N=3) sont en gris et le *Symphalangus syndactylus* (N=1) est en noir. Les valeurs au-dessus des barres indiquent le pourcentage moyen de masse corporelle représenté pour le segment considéré (arrondi à l'entier le plus proche).

3.2.2 Limb inertial properties

- 12 Figure 4 shows the relationship between fore- and hindlimbs in gibbons for different variables. The forelimb is longer than the hindlimb for all species (Fig. 4a). The position of the CoM is more proximal in the hindlimb than in the forelimb, with the exception of the *Symphalangus* specimen, wherein the CoM is more distally positioned in the hindlimb than in the forelimb (Fig. 4b). Despite the length differences, the forelimb mass appears to be equal to the hindlimb mass, except for the *Symphalangus* specimen, wherein the hindlimb is heavier than the forelimb (Fig. 4c). The mass moment of inertia about the proximal joint is greater in the forelimb than in the hindlimb for all species (Fig. 4d).

Figure 4



Relationship between fore- and hindlimb length (a), CoM (b), mass (c), and mass moment of inertia about the proximal joint (d). The black line is the line of identity ($x=y$).

Relation entre les membres antérieurs et postérieurs pour la longueur (a), la position du centre de masse (b), la masse (c) et le moment d'inertie autour de l'articulation proximale (d). La ligne noire est la droite d'identité ($x=y$).

4 Discussion and conclusions

- 13 In this study, we report the first morphometric dataset for the southern yellow-cheeked crested gibbon. When compared to the dataset of other Hylobatidae (*H. lar* and *S. Syndactylus*), *Nomascus gabriellae* appears generally very similar to other gibbons. Indeed, it is commonly assumed that gibbons are relatively uniform in their morphology (Fleagle, 2013). For example, all lesser apes are characterized by impressive proportion of the limbs relative to their body size (Zihlman et al., 2011). Michilsens and collaborators (2009) were not able to find any substantial differences in the forelimb anatomy of different gibbon species. Furthermore, we observe that their forelimbs are always longer than their hindlimbs and that the position of their CoM is very proximal in both fore- and hindlimbs. This latter result may be surprising in the most suspensory primate, when it is commonly assumed that distally concentrated masses into the limbs should be correlated with grasping capacities for climbing and suspension (e.g. Druelle et al., 2016, Raichlen, 2005b, Turnquist and Wells, 1994, Wells and Turnquist, 2001). However, a proximal migration of limb mass may be advantageous for brachiation because, as in cursorial mammals, proximal mass distributions should enable fast movements with a lower power input during the recovery phase of brachiation (Michilsens et al., 2009). Furthermore, a proximal distribution of limb mass causes the position of the forelimb CoM to be very close from the body CoM, and farther away from the pivot point (i.e. the handhold),

therefore enhancing the pendulum effect during brachiation (Bertram *et al.* 1999, Michilsens *et al.*, 2009). The ability to brachiate may thus result in different specific adaptations than the ability to use suspensory and climbing behaviors.

- 14 In spite of the similarities previously described between gibbon species, *N. gabriellae* seems to be closer from *H. lar* than *S. Syndactylus* in terms of body mass and for what concerns the inertial properties of its body. The body mass distribution is also the same for the hindlimbs, but *H. lar* appears to exhibit a larger relative head and larger forelimbs and a lighter relative trunk than *N. gabriellae*. While Zihlman and collaborators (2011) also showed that *Hylobates* has larger forelimbs than *Nomascus*, they described the latter with a heavy thigh and light leg compared to other genera. In the present study, we were not able to observe these hindlimb trends. Therefore, with regard to the slight differences resulting from our study and the small sample size, it seems more parsimonious to not conclude at this stage that significant differences in the hindlimb morphometrics exist between these two species. In this respect and considering the only study on the positional behaviors of the *Nomascus* genus (Fan *et al.*, 2013), we may suggest that these two species (*H. lar* and *N. gabriellae*) certainly exhibit very close locomotor strategies (see Table 3 in Hunt, 2016), though there are currently no data specifically focusing on the positional repertoire of *N. gabriellae*.
- 15 With regard to the siamang specimen, *S. syndactylus*, more important morphological differences relative to both *N. gabriellae* and *H. lar* have been noticed. First, total body mass is twice that of the gibbon species (but see Zihlman *et al.*, 2011). Second, while fore- and hindlimb masses are rather equal in other gibbons, the hindlimb is heavier than the forelimb in the siamang and the position of the CoM is more distally concentrated than in the forelimb (the opposite is observed in *N. gabriellae* and *H. lar*). Such variations in the morphological pattern may reflect differences in the positional repertoires of these species (see Table 8 in Fan *et al.*, 2013, Fleagle, 1976, Table 3 in Hunt, 2016). Indeed, Hylobatid morphology should to some degree reflect compromises between the specialized requirements for brachiation, and requirements for other, more generalized, postural and locomotor modes (Hunt *et al.*, 1996, Druelle *et al.*, 2016, Schoonaert *et al.*, 2007, Isler *et al.*, 2006, Preuschoft and Witte, 1991, Preuschoft, 1989, Preuschoft *et al.*, 1996). The main difference seems to concern the proportion of vertical climbing. Whereas the siamang is observed climbing for 15.1% of its time, other gibbons are observed climbing for 4.4% in average. With regard to the biomechanics of climbing locomotion, the use of this mode seems to be related to strong muscles (via a larger physiological cross-sectional area) in the hindlimbs because of the need to generate important propulsive forces for ascending trees (e.g. Hanna *et al.*, 2017, Preuschoft, 2002). Furthermore, hindlimbs should also compensate the moment of body weight which is likely to rotate ventrally about the handhold and counterbalance the horizontal force component (Preuschoft, 2002). Simple geometric scaling principles all suggest that an increase in body mass could also influence the shape of siamang limbs (Kilbourne and Hoffman, 2013). Yet, these functional relationships should be carefully considered because other studies also showed different body mass distribution pattern, with the *S. syndactylus* exhibiting relatively lighter hindlimbs than forelimbs and the *Hylobates* exhibiting heavier hindlimbs than forelimbs (see Discussion in Isler *et al.*, 2006, Zihlman *et al.* 2011).
- 16 The present study therefore supports the idea that the impressive suspensory capacities shared by all gibbons are the result of a similar morphotype. Slight morphological

differences between species may be related to variations in their positional repertoires and their environment (Gittins, 1983, Zihlman et al. 2011). However, we temper the conclusion of Zihlman and collaborators (2011) about the distinct pattern of limb masses among gibbon species. Indeed, based on the total number of specimens measured and the differences in the results, it seems that the body mass distribution is not a straightforward element to discriminate different hylobatids, at least at this stage of the analysis with small overall number of specimens. More integrative data are therefore needed to further explore the relationships between the morphological pattern and the positional behaviors in *Hylobatidae* in particular, and in primates in general. For this aim, zoological parks offer unique opportunities to access rare primate specimens.

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ABSTRACTS

Gibbon species are highly specialized for brachiation. Nevertheless, as with all primates, they are capable of various posturo-locomotor modes as part of a larger overall positional repertoire. In this context, the study of their locomotor apparatus is very relevant to better understand their evolution toward such specialization for brachiation on the one hand, and the degree to which their body may reflect compromises on the other hand. Indeed, gibbons also frequently use a variety of other non-brachiating locomotor modes – including bipedalism, leaping and climbing – that are crucial during arboreal travel. Here, we present a dataset of external morphometrics and estimates of segmental inertial properties for *Nomascus gabriellae* – the first such data collected for this species. Measurements were taken on four captive animals during a routine veterinary exam coinciding with maintenance to their enclosure within the zoo. We compared our dataset to the only available and comparable sample of gibbon morphometrics (three *Hylobates lar* and one *Symphalangus syndactylus*). Our results show that these species appear very similar in terms

of body shape. Nevertheless, *H. lar* and *N. gabriellae* are more similar to each other than either is to *S. syndactylus*, which is also twice as large. Slight differences in segmental mass and limb center of mass position are highlighted and may point to differences in the locomotor profiles of these hylobatids. These relationships are discussed in the light of the biomechanical theory.

Les Gibbons sont hautement spécialisés pour la brachiation. Néanmoins, comme tous les primates ils sont capables de divers modes posturo-locomoteurs qui forment un répertoire positionnel. Dans ce contexte, l'étude de leur appareil locomoteur est particulièrement pertinente afin de mieux comprendre l'évolution de ces formes. En effet, celles-ci apparaissent dans un premier temps très spécialisées, pourtant elles représentent également des compromis qui maintiennent une certaine diversité posturo-locomotrice incluant notamment la bipédie, le grimper, le saut, soit des modes nécessaires aux déplacements dans les arbres. Dans cette étude, nous présentons des données correspondantes à la morphométrie et aux propriétés d'inertie pour un groupe de gibbons, *Nomascus gabriellae* – cette espèce n'avait encore jamais été mesurée. Nous avons eu l'opportunité de réaliser différentes mesures externes lors du contrôle vétérinaire de 4 individus vivant en captivité au sein d'un parc zoologique. Suite au recueil de ces données, nous les avons comparées avec les seules données disponibles et comparables à ce jour pour les gibbons, c'est-à-dire trois *Hylobates lar* et un *Symphalangus syndactylus*. Nos résultats montrent que d'une manière générale ces trois espèces sont très semblables au niveau de leur morphotype. Néanmoins, les espèces *H. lar* et *N. gabriellae* sont plus similaires l'une à l'autre qu'avec *S. syndactylus*, qui est deux fois plus massif. Les principales différences sont relevées au niveau de la masse des membres et de la position des centres de masse. Celles-ci pourraient être liées à des différences au niveau des répertoires positionnels de ces espèces. Ces relations sont discutées à la lumière de la théorie biomécanique.

INDEX

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