



Odd-nosed monkey scapular morphology converges on that of arm-swinging apes

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ABSTRACT

Odd-nosed monkeys 'arm-swing' more frequently than other colobines. They are therefore somewhat behaviorally analogous to atelines and apes. Scapular morphology regularly reflects locomotor mode, with both arm-swinging and climbing anthropoids showing similar characteristics, especially a mediolaterally narrow blade and cranially angled spine and glenoid. However, these traits are not expressed uniformly among anthropoids. Therefore, behavioral convergences in the odd-nosed taxa of *Nasalis*, *Pygathrix*, and *Rhinopithecus* with hominoids may not have resulted in similar structural convergences. We therefore used a broad sample of anthropoids to test how closely odd-nosed monkey scapulae resemble those of other arm-swinging primates. We used principal component analyses on size-corrected linear metrics and angles that reflect scapular size and shape in a broad sample of anthropoids. As in previous studies, our first component separated terrestrial and above-branch quadrupeds from clambering and arm-swinging taxa. On this axis, odd-nosed monkeys were closer than other colobines to modern apes and *Ateles*. All three odd-nosed genera retain glenoid orientations that are more typical of other colobines, but *Pygathrix* and *Rhinopithecus* are closer to hominoids than to other Asian colobines in mediolateral blade breadth, spine angle, and glenoid position. This suggests that scapular morphology of *Pygathrix* may reflect a significant reliance on arm-swinging and that the morphology of *Rhinopithecus* may reflect more reliance on general climbing. As 'arm-swinging' features are also found in taxa that only rarely arm-swing, we hypothesize that these features are also adaptive for scrambling and bridging in larger bodied anthropoids that use the fine-branch component of their arboreal niches.

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1. Introduction

Throughout much of the twentieth century, hominoids were almost universally classified as 'brachiators' (Avis, 1962; Napier, 1963; Napier and Napier, 1967), and features associated with brachiation were argued to represent the ancestral state for hominoid postcranial morphology and arboreal locomotion (Keith, 1923; Gregory, 1930; Tuttle, 1975; but see Straus, 1949). These 'brachiating' features included an elongated clavicle and antebrachium, an especially mobile shoulder with a dorsally placed scapula, an abbreviated olecranon allowing increased extension, a mobile wrist (usually with 'ulnar withdrawal' or midcarpal

rotation; Jenkins, 1981; Lovejoy et al., 2009a), elongated metacarpals and manual phalanges, a broadened thorax, and a reduced lumbar column (both in element number and in centrum cranio-caudal height; e.g., Schultz, 1930; Erikson, 1963; Ashton and Oxnard, 1964; Andrews and Groves, 1976; Jungers and Stern, 1984; Larson, 1993; Ward, 1993; Gebo, 1996). There is now new and considerable evidence that many of these features evolved in parallel (Larson, 1998; Lovejoy et al., 2009a, b; Hammond et al., 2013; Reno, 2014; Alba et al., 2015; Ward, 2015; Arias-Martorell, 2019; but see Gebo, 1996; Young, 2003), not only in hominoids but also in some New World monkeys and Old World monkeys (see below).

Of equal importance is that classifying both great and lesser apes simply as 'brachiators' does not sufficiently capture extant hominoid locomotor diversity. Hylobatids are unarguably 'true brachiators' (Fleagle, 1976, 1980). In fact, they are alone adapted to

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'ricochetal arm-swinging,' a form of rapid bimanual suspension that includes an aerial phase (Jungers and Stern, 1984; Swartz, 1989; Hunt et al., 1996; Bertram and Chang, 2001; Usherwood and Bertram, 2003; Bertram, 2004). We refer to 'arm-swinging' here as bimanual progression without an aerial phase. The orangutan's 'orthograde clamber' (Hunt et al., 1996) is a unique form of locomotion, which not only includes arm-swinging but also involves hind limb grasping and stabilization in various orientations (Thorpe and Crompton, 2006; Thorpe et al., 2009). This 'quadrumanous climbing' differs greatly from the arm-swinging of gibbons, in part because of its much greater body mass and unique phylogenetic history.

The arboreal locomotion of extant African apes differs dramatically from that of these other hominoids. Chimpanzees and gorillas regularly knuckle-walk when terrestrial and engage in a mixture of vertical climbing and scrambling when arboreal, the former being required to navigate and exploit resources achievable only by terrestrial travel (Hunt, 1992; Remis, 1995; Doran, 1996, 1997). Knuckle-walking is therefore likely an adaptation to the combination of large body mass and the need to access diversely distributed feeding patches (Simpson et al., 2018). In fact, chimpanzees practice arm-swinging infrequently, and it is only rarely seen in adult gorillas (Hunt, 1992; Remis, 1995; Doran, 1996, 1997). Knuckle-walking is very likely a specialized form of quadrupedal travel in which many of the typical mechanisms of energy dissipation of ground collision forces have been compromised by specializations of the forelimb for vertical climbing and scrambling. The African apes are the only primates with conical upper thoraces, in contrast to hominins, gibbons, and orangutans (Haile-Selassie et al., 2010; Simpson et al., 2018). This hypothesis has been criticized by Thompson et al. (2018), but their data were obtained from subadult apes, who could not experience the same force magnitudes as adults, and macaques (which do not knuckle-walk), and of course, electromyographic data cannot reflect the passive stretching of tendons and the spring effects of ligaments which are primary energy transducers.

Some New World monkeys (e.g., *Ateles*, *Brachyteles*, and *Lagothrix*) and Old World monkeys (e.g., *Pygathrix*, see below) also regularly use arm-swinging. In both *Ateles* and *Pygathrix*, the behavior is largely similar to that of gibbons, especially with respect to shoulder and elbow kinematics, although there is less morphological and kinematic homogeneity of the wrist among these taxa (Byron et al., 2017). Among monkeys, a true 'brachiator' phenotype is largely observed only in *Ateles*, which exhibits a relatively broad thorax and narrow scapula with cranially oriented glenoid and scapular spine. These features render them postcranially more similar to hominoids than to the phylogenetically related *Lagothrix* (Andrews and Groves, 1976; Larson, 1998). *Ateles* uses arm-swinging more commonly than *Lagothrix* (~25% in the former vs. <15% in the latter; Mittermeier, 1978; Cant, 1986; Cant et al., 2001). *Ateles* and *Lagothrix* are also unusual in that they rely frequently on horizontal body postures made possible by their prehensile tails (Turnquist et al., 1999).

1.1. Odd-nosed monkey phylogeny and primary locomotor pattern

Odd-nosed monkeys are a monophyletic group of Asian colobines (e.g., Sterner et al., 2006; Ting et al., 2008; Liedigk et al., 2012) that exhibit more diverse locomotor behavior than other African or Asian colobines. Douc monkeys (*Pygathrix*) in captivity engage in relatively frequent bouts of arm-swinging (~20–55%; Byron and Covert, 2004; Workman and Covert, 2005; Wright et al., 2008). Snub-nosed monkeys (*Rhinopithecus*) perform this behavior as juveniles, but are mainly terrestrially quadrupedal as adults. When arboreal, snub-nosed monkeys are reported to use general

quadrupedal walking, climbing, leaping, and occasional arm-swinging (Wu, 1993; Su and Jablonski, 2009; Zhu et al., 2015). Proboscis monkey (*Nasalis*) locomotion is less well documented, but arm-swinging has been observed (Hollihhn, 1984; Su and Jablonski, 2009). The sister taxon to the proboscis monkey, the pig-tailed snub-nosed monkey of Sumatra (*Simias*), is also less well studied behaviorally and is poorly represented in museum collections. Its locomotor habit is considered to differ from that of other odd-nosed monkeys and from that of its sister genus *Nasalis* (Su and Jablonski, 2009). Because of a lack of sufficient sample size, *Simias* will not be further discussed here.

Some characteristics of *Pygathrix* converge on those of arm-swinging hominoids. Douc monkeys exhibit higher intermembral and brachial indices, longer clavicles, a narrower scapula with an elongated and more cranially oriented acromion, and a shorter olecranon than other Old World monkeys. However, *Pygathrix* wrist morphology differs somewhat dramatically from that of hominoids (Su and Jablonski, 2009; Bailey et al., 2017). Similarly, wrist kinematics during arm-swinging in *Pygathrix* contrasts with those of *Ateles* and *Hylobates*, whereas those of the shoulder and elbow are more comparable with these taxa (Byron et al., 2017).

1.2. Scapular morphology and locomotor habit

Scapular morphology can substantially reflect locomotor mode (Fig. 1). Extensive multivariate studies have positioned anthropoid taxa along a continuum from above-branch and/or terrestrial quadrupeds to clambering/brachiating species (Ashton et al., 1965a; Oxnard, 1967; Young, 2008; Selby and Lovejoy, 2017). Features common to primates specialized for climbing, clambering, and/or arm-swinging include a mediolaterally narrow blade, a cranially oriented spine and acromion, and a cranially oriented and positioned glenoid (Fig. 1; Ashton and Oxnard, 1964; Ashton et al., 1965b; Andrews and Groves, 1976; Green and Alemseged, 2012; Green, 2013; Green et al., 2016; Selby and Lovejoy, 2017). However, the morphology of arm-swinging and climbing anthropoids is not uniform, particularly with respect to their spine and glenoid angles (Young, 2008; Green et al., 2016; Selby and Lovejoy, 2017). Therefore, it is predicted that odd-nosed monkeys are also likely to vary in these features as well. Furthermore, we anticipate that their scapular characteristics should be more similar in shape to those of hominoids or atelids than to those of other colobines.

These expectations are supported by the literature. *Pygathrix* does appear to be intermediate to colobines and gibbons in scapular morphology (Bailey et al., 2017). Gibbons have an especially mediolaterally narrow scapula and highly angled scapular spine, which is consistent with their being unusual distinctiveness among anthropoids in using of ricochet arm-swinging. *Pygathrix* and other odd-nosed monkeys have been shown to have narrow scapulae relative to those of other cercopithecines (Su and Jablonski, 2009; Byron et al., 2017). However, a narrow scapula alone is not necessarily indicative of suspensory behaviors (Larson, 2015; Selby and Lovejoy, 2017). *Pygathrix*, like *Ateles* and *Lagothrix*, engage in both above-branch quadrupedalism and arm-swinging to varying degrees. Our goal here is to determine if there are morphological convergences in scapular form among odd-nosed monkeys (*Pygathrix*, *Nasalis*, and *Rhinopithecus*) and other arm-swinging hominoids and atelids compared with other anthropoids that practice different modes of locomotion.

2. Materials and methods

We measured metrics and angles from photographs of specimens taken normal to the blade of the dorsal surface of the scapula of extant primates. We used ImageJ v. 1.48 for angles and metrics

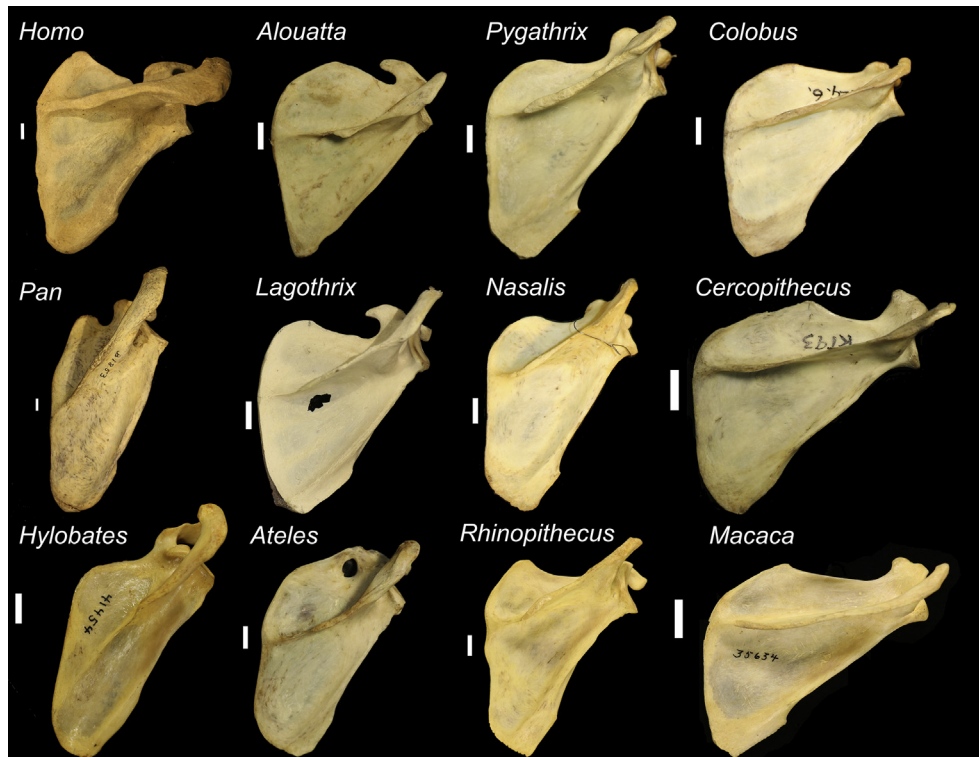


Figure 1. Dorsal views of 12 higher primate scapulae adjusted to the same approximate craniocaudal height (calculated as the distance between their superior and inferior angles; all scale bars are equal to 1 cm). Column 1: hominoids; column 2: ceboids; column 3: odd-nosed monkeys; column 4: other Old World monkeys. Note that odd-nosed monkeys most approximate *Lagothrix* and appear visually intermediate to *Alouatta* and *Ateles*. *Hylobates*, *Nasalis*, and *Macaca* images © 2019 President and Fellows of Harvard College.

(Schneider et al., 2012). Sample size and metrics are listed in Tables 1 and 2 and illustrated in Figure 2. To determine the potential effect of phylogeny on the analysis, we performed a phylogenetic principal component analysis (pPCA) using the phytools package (Revell, 2012) in R software (R Core Team, 2019; see Supplementary Online Material [SOM] S1 and Table S1 for details on the generation of the consensus tree). As phytools limits the number of cases to the number of tips on the tree, we were required to conduct the pPCA on species means rather than on each observed scapula in the sample. We also performed a standard PCA using the entire sample using SPSS v. 24 (IBM Corp., 2016). For both the standard PCA and pPCA, we size corrected the linear metrics by the geometric mean (GM) of available measurements (Jungers et al., 1995; Ogihara et al., 2016) and used a correlation matrix, which is less sensitive to variables with differing scales (Jolliffe and Cadima, 2016).

In some cases, we have included overlapping angular metrics that are designed to capture similar aspects of scapular shape (GMA or GVA and SMA or SVA; see abbreviations in Table 2). However, these metrics differ with respect to how the vertebral (medial) border is estimated, either from the spine at its vertebral border (point ‘g’) or the superior angle (point ‘f’, see Fig. 2). This is of note because superior angle position has been shown to differ among hominoids (Green et al., 2015, 2016) and between *Pygathrix* and other colobines (Bailey et al., 2017).

Likewise, spine angle, and the point where it intersects the vertebral border (point ‘g’), also has been shown to vary significantly among hominoids and atelids (Green et al., 2015; Selby and Lovejoy, 2017; Spear and Williams, 2018). We have therefore used alternate methods of measuring spine:axillary border angle (SAA, ABS), i.e., using lines that pass through either the acromion or the spinoglenoid notch. The acromion is variably angled relative to the

spine medial to the spinoglenoid notch among anthropoids (Selby and Lovejoy, 2017). We have therefore included both angles in our analyses. Scapular breadth along the spine (SPGLN) and superior border length (SUPBORD) also both provide information on the mediolateral width of the scapula. As many of these traits almost certainly covary, we have used redundant measurements to reduce the likelihood of spurious results being generated by artifacts of any single metric. If these ‘redundant’ metrics or angles show similar PCA loadings, it can reasonably be assumed that the broader morphological pattern and not differences in measurement techniques is primarily reflected.

In addition to the PCA, we also used an analysis of variance with post hoc Bonferroni corrections that compare an assortment of Asian colobines (including odd-nosed taxa) with known brachiators such as New World atelids and a gibbon (*Hylobates*). This comparative group helps to clarify the degree to which different anatomical features in this study show convergence between odd-nosed monkeys and *Hylobates* and *Ateles*. The douc monkey (*Pygathrix nemaeus*) has perhaps the best documented locomotor repertoire among odd-nosed monkeys and has been shown to use more arm-swinging behavior than other Asian colobines.

3. Results

3.1. Phylogenetic principal component analysis

We performed a pPCA to account for the effects of phylogenetic relatedness within the analysis. The results of the pPCA are similar to those of the PCA shown in the following sections, with three principal components (PCs) accounting for 90% of the variance in the data and relative loadings along each axis describing similar contributions of each variable within each component. Because of

Table 1
Samples used for analysis.

Species	Male	Female	Total ^a	Locomotion	Museum
Hominoids					
<i>Homo sapiens</i>	12	13	25	Biped	C
<i>Pan troglodytes troglodytes</i>	10	10	20	KW, VC	C
<i>Gorilla gorilla gorilla</i>	14	13	27	KW, VC	C
<i>Pongo abelii</i>	2	5	7	CL, VC	N
<i>Pongo pygmaeus</i>	6	7	13	CL, VC	M, N
<i>Hylobates lar</i>	9	6	15	Brach.	C, F, M, N
<i>Symphalangus syndactylus</i>	2	4	6	Brach.	N
Cercopithecines					
<i>Cercopithecus mitis</i>	3	4	7	ABQ, Leap	C, F, M, N
<i>Chlorocebus aethiops</i>	6	4	11	ABQ, TQ	C, N
<i>Macaca fascicularis</i>	6	6	12	ABQ, Leap	F, M
<i>Macaca nemestrina</i>	3	6	9	ABQ, TQ	M, N
<i>Mandrillus leucophaeus</i>	2	0	2	TQ	M
<i>Mandrillus sphinx</i>	1	1	2	TQ	F, M
<i>Papio anubis</i>	6	4	10	TQ	N
Colobines					
<i>Colobus guereza</i>	9	2	11	ABQ, Leap	F, N
<i>Nasalis larvatus</i>	6	8	14	Leap?, AS?	M, N
<i>Ptilocolobus badius</i>	2	3	5	ABQ, Leap, AS	M, N
<i>Presbytis rubicunda</i>	5	5	10	ABQ, Leap ^b	M
<i>Pygathrix nemaeus</i>	10	6	20	ABQ, AS	F, M, N, V
<i>Pygathrix cinerea</i>	3	3	9	ABQ, AS	V
<i>Rhinopithecus roxellana</i>	2	3	6	TQ, VC?, Leap?	N
<i>Semnopithecus entellus</i>	2	4	6	ABQ, TQ	F, N
<i>Trachypithecus cristatus</i>	8	7	15	ABQ, Leap ^c	C, M, N
Ceboids					
<i>Alouatta palliata</i>	6	5	11	ABQ, CL	F, N
<i>Ateles fusciceps</i>	5	3	9	AS, CL	F, N
<i>Ateles geoffroyi</i>	0	3	5	AS, CL	M, N
<i>Lagothrix lagotricha</i>	7	3	10	AS, CL	C, N, F
<i>Cebus paella</i>	6	1	7	ABQ, Leap	F
<i>Cebus capucinus</i>	3	1	4	ABQ, Leap	N
<i>Saimiri sciureus</i>	1	3	6	ABQ, Leap	C, N
Total	157	144	316		

Abbreviations: ABQ = above-branch quadrupedalism; AS = arm-swinging; Leap = leaping is the most frequent means for crossing supports; CL = clambering (including climbing/bridging; leaping between supports is rare); KW = knuckle-walking; Brach. = ricochet brachiation; TQ = terrestrial quadrupedalism; VC = vertical climbing; ? = published anecdotal observations, without quantified locomotor frequencies; C = Cleveland Museum of Natural History, Cleveland, OH, USA; F = Field Museum of Natural History, Chicago, IL, USA; M = Museum of Comparative Zoology, Cambridge, MA, USA; N = National (Smithsonian) Museum of Natural History, Washington, D.C., USA; V = Endangered Primate Rescue Center in Cuc Phuong National Park, Vietnam.

^a Includes individuals of unknown sex.

^b Used *Presbytis melalophos* as an analogy.

^c Used *Trachypithecus obscurus* as an analogy.

the redundancy in this finding and the requirement to run the pPCA only on species means rather than on raw variates, the pPCA is presented in SOM Tables S2–S4 and SOM Figures S1–S4.

Table 2
Metrics and angles used (modified from previous studies; Green and Alemseged, 2012; Churchill et al., 2013; Selby and Lovejoy, 2017).^a

Metric	Definition	Figure	Morphological information
Vertebral border length (VERTBORD)	Distance f–h	Figure 2A	Approximate length vertebral border
Axillary border length (AXBORD)	Distance d–h	Figure 2A	Length of axillary border
Superior border length (SUPBORD)	Distance b–f	Figure 2A	Length of superior border
Spine length (SPGLN)	Distance g–c	Figure 2A	Mediolateral breadth from junction of spine and vertebral border to midpoint of glenoid
Glenoid length (GLEN)	Distance b–d	Figure 2A	Craniocaudal glenoid length
Magnitude of inferior angle (INF)	Angle between g–h and d–h	Figure 2B	Geometric mediolateral breadth
Glenoid:medial border angle (GMA)	Angle between b–d and f–h	Figure 2B	Orientation of glenoid relative to superoinferior scapular height
Glenoid:vertebral border angle (GVA)	Angle between b–d and g–h	Figure 2C	Orientation of glenoid angle relative to vertebral border
Spine:medial border angle (SMA)	Angle between a–g and f–h	Figure 2B	Approximate orientation of spine relative to superoinferior scapular height
Spine:vertebral border angle (SVA)	Angle between a–g and g–h	Figure 2C	Approximate orientation of spine relative to vertebral border
Glenoid:spine angle (GSA)	Angle between b–d and a–g	Figure 2B	Approximate orientation of spine relative to glenoid plane
Spine:axillary border angle (SAA)	Angle between a–g and d–h	Figure 2C	Approximate orientation of spine relative to the axillary border
Axillary border:spine angle (ABS)	Angle between e–g and d–h	Figure 2C	True spine angle relative to axillary border

^a Points used for angles and metrics: a = distal point of glenoid; b = superior border of glenoid; c = midpoint of glenoid; d = inferior border of glenoid; e = spinoglenoid notch; f = superior angle; g = intersection of vertebral border and spine; h = inferior angle.

3.2. Principal component 1

We performed a PCA (no rotation) on our entire data set as described previously. It yielded three PCs with eigenvalues higher than 1.0. Together, they account for 91.3% of the variance (Table 3). The distribution of taxa is shown in Figure 3.

PC1 explains 59.8% of the variance. As is clear from Figure 3, it separates hominoids and *Ateles* from cercopithecines. Humans are clearly separated from other hominoids, gorillas from chimpanzees, and cebines occupy an intermediate position. Odd-nosed monkeys, as a group, overlap with *Alouatta*, and lie close to *Ptilocolobus*, *Homo*, and *Lagothrix*. Odd-nosed monkeys lie closer to hominoids than other colobines by having larger positive scores along PC1. The mean scores of each taxon are provided in SOM Table S5.

Variables that are loaded highly (greater than ± 0.7) on PC1 primarily reflect mediolateral scapular breadth, glenoid angle and position, spine angle, and vertebral and/or axillary border lengths. Hominoids and *Ateles* exhibit features traditionally associated with the so-called 'brachiator scapula.' As expected and as visually apparent from Figure 1, their loadings are consistent with a distinct mediolaterally narrow scapula (see INF and SUPBORD/GM) with cranially oriented glenoids (GMA and GVA; Fig. 4) and cranially angled spines (SMA and SVA; Fig. 5). Other ratios indicate long vertebral (VERTBORD/GM) and axillary border lengths (AXBORD/GM). The mean angular values of each taxon are provided in SOM Table S6.

3.3. Principal components 2 and 3

PC2 explains 21.7% of the variance. It has high loadings for two angles that compare the spine with the axillary border (SAA and ABS) and size-corrected spine length (SPGLN/GM). Humans have the largest positive loadings for this component, hylobatids have the largest negative loadings, and all the remaining taxa are intermediate (Fig. 3).

Both spine:axillary border angles (SAA and ABS) isolate hylobatids and chimpanzees with narrow angles, humans have substantially larger angles, and all other taxa have angles that are intermediate (SOM Table S6). ABS and SAA appear to be less individually useful in discriminating locomotor mode because spine angle and axillary border position strongly covary and usually yield similar values (Larson, 1995, 2007).

Size-corrected length of the spine (SPGLN/GM) has a large negative loading for PC2. This value is highest in hylobatids and several cercopithecines. This likely reflects the mediolaterally elongated scapula in the latter and the highly angled spine in the

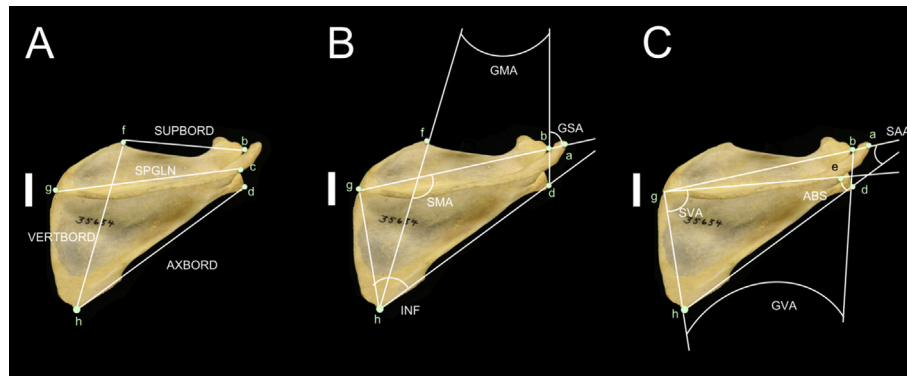


Figure 2. Angles and metrics shown on a *Macaca fascicularis* scapula. Definitions of points used for angles and metrics: a) distal point of glenoid; b) superior border of glenoid; c) midpoint of glenoid; d) inferior border of glenoid; e) spinoglenoid notch; f) superior angle; g) vertebral border where the spine intersects; h) inferior angle. Scale bar equals 1 cm. © 2019 President and Fellows of Harvard College.

Table 3

Principal component analysis (PCA) results, including eigenvalues, % of variance, and loadings of the principal components (PCs).

	PC1	PC2	PC3
Eigenvalues	7.171	2.607	1.181
% of variance	59.756	21.723	9.840
Component loadings			
INF	-0.796	-0.478	0.277
GMA	0.950	-0.064	0.252
GVA	0.950	0.054	0.165
SMA	0.957	-0.180	-0.093
SVA	0.944	-0.009	-0.235
GSA	0.207	0.210	0.929
SAA	-0.678	0.681	0.079
ABS	-0.493	0.844	-0.042
VERTBORD/GM	0.743	0.498	0.092
AXBORD/GM	0.852	-0.248	-0.119
SUPBORD/GM	-0.897	-0.238	-0.086
SPGLN/GM	-0.314	-0.868	0.219

Abbreviations: GM = geometric mean of all linear metrics; see variable abbreviations in Table 2.

former, which can make this a less than ideal estimate of mediolateral breadth (Spears and Williams, 2018).

PC3 explains 9.8% of the variance and has one variable with a loading greater than 0.5: glenoid-spine angle (Fig. 6). *Pygathrix*, *Presbytis*, and *Rhinopithecus* have the most acute angles, whereas humans, gorillas, and orangutans have the most obtuse angles. In general, cercopithecoids have narrower glenoid-spine angles, whereas those of ceboids and hominoids are greater, and arm-swinging taxa have intermediate values. One possible explanation is that a narrower angulation in taxa such as *Pygathrix* and *Rhinopithecus* reflects a combination of a more angulated spine with a less angulated glenoid (Bailey et al., 2017).

3.4. Pairwise comparisons

The PCA results here demonstrate that odd-nosed monkeys are intermediate between hominoids and other Asian colobines, but show some overlap with atelines. To further explore this, we ran an analysis of variance with post hoc Bonferroni correction, comparing odd-nosed monkeys, *Hylobates*, *Presbytis*, *Trachypithecus*, and atelines (Table 4). We used *P. nemeaus* as a basis for comparison as its locomotor behavior is the best documented for odd-nosed monkeys.

Among the features with high loadings in the first component, *P. nemeaus* has a glenoid that is less cranially oriented (lower GMA and GVA) than *Hylobates* and *Ateles* (not significant for GVA with

Ateles geoffroyi), but more cranially oriented than *Presbytis*. For spine orientation (SMA and SVA), only that of *Hylobates* is significantly more cranially orientated (SMA only) than *P. nemeaus*. It has a more cranially oriented spine than *Nasalis* (SVA only), *Trachypithecus*, *Alouatta*, and *Lagothrix* (SVA only). For mediolateral breadth, *Ateles* and *Hylobates* have narrower superior border lengths (SUPBORD/GM), and *Presbytis* has a longer border. *Alouatta* and *Ateles* both have longer vertebral borders, and *Hylobates* and *Nasalis* have longer axillary borders.

4. Discussion and conclusions

In agreement with previous studies (Ashton et al., 1965a; Su and Jablonski, 2009; Bailey et al., 2017; Byron et al., 2017), our results suggest that the scapular morphology of odd-nosed monkeys, particularly *Pygathrix* and *Rhinopithecus*, is intermediate between other Asian colobines and climbing and/or arm-swinging hominoids and *Ateles*. Specifically, the spine angle and blade breadth of *Pygathrix* are similar to those of hylobatids and *Ateles*, although the former's glenoid is less cranially oriented (Su and Jablonski, 2009; Bailey et al., 2017). These findings accord well with a greater reliance on arm-swinging in these taxa.

Our results suggest that arm-swinging has had less of an impact on *Pygathrix* and *Lagothrix* scapular morphology than it has on that of either hylobatids or spider monkeys, that is, both *Pygathrix* and *Lagothrix* practice arm-swinging but lack a highly specialized scapula. They also lack equivalent elongation of the forelimb and other features seen in gibbons and spider monkeys. There are two likely possibilities that seem reasonable: either *Pygathrix* and *Lagothrix* are transitional forms undergoing directional selection for a more specialized brachiator phenotype or they instead represent a compromise adaptation to both arm-swinging and above-branch quadrupedality. Solutions to these two possibilities are obviously beyond the scope of the current research.

Our results also reveal no significant metric differences in the scapulae of *Pygathrix* species and those of *Rhinopithecus* (Table 4). Unlike douc monkeys, arm-swinging is a rare locomotor behavior in adult snub-nosed monkeys (Wu, 1993; Zhu et al., 2015). This suggests that similar scapular features can characterize taxa although they simultaneously differ in the degree to which they use arm-swinging as adults (see also *Pan* vs. *Gorilla*). Why therefore are 'brachiator' scapular features observed in some non-arm-swingers?

Some have argued that the 'brachiator' morphotype (see above) enables a diversity of below-branch behaviors, particularly with decreasing substrate size, and not brachiation per se. Using below-branch postures would reduce the likelihood of toppling from a

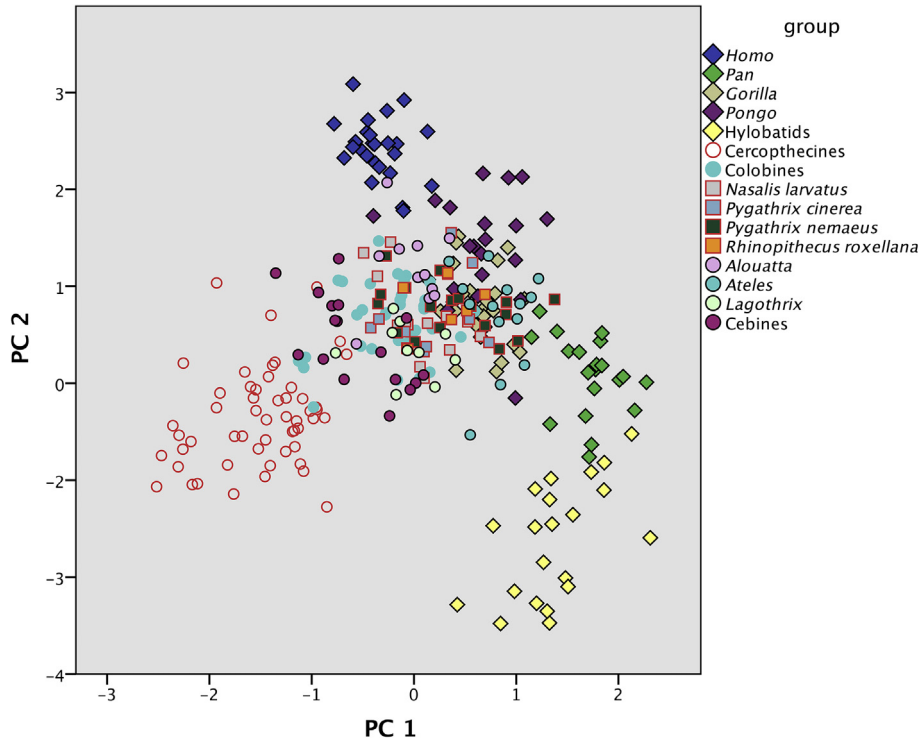


Figure 3. Scatter plot of the first two principal components (PC1 and PC2). PC1 has an eigenvalue of 7.2 and explains 59.8% of the variance. PC2 has an eigenvalue of 2.6 and explains 21.7% of the variance. Linear variables were size corrected with a geometric mean of all linear metrics. Size-corrected ratios and angles were then log transformed. Variables with high loadings on PC1 reflect narrow mediolateral scapular breadth (negative INF and SUPBORD), cranially oriented glenoid (GMA and GVA), and long vertebral and axillary border lengths (VERT and AXBORD). PC2 has high loadings for mediolateral breadth measured along the scapular spine (SPGLN) and spine angle compared with axillary border (SAA and ABS).

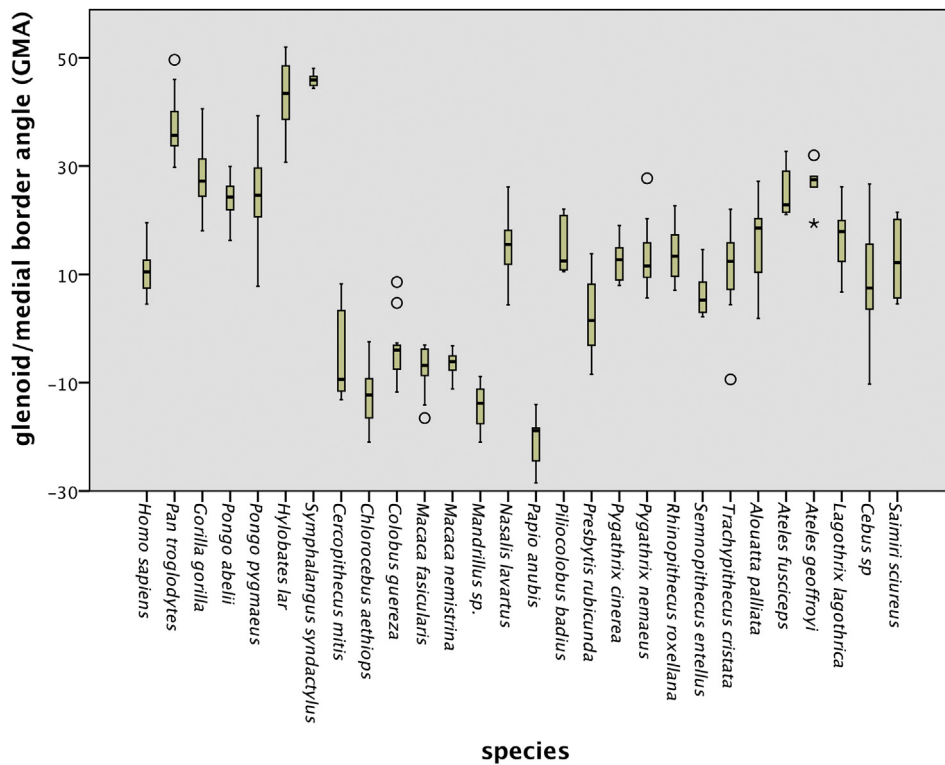


Figure 4. Boxplot of glenoid angle compared with medial border (GMA). The horizontal line indicates the median, boxes indicate the interquartile range, whiskers indicate the range, and dots and stars represent outliers.

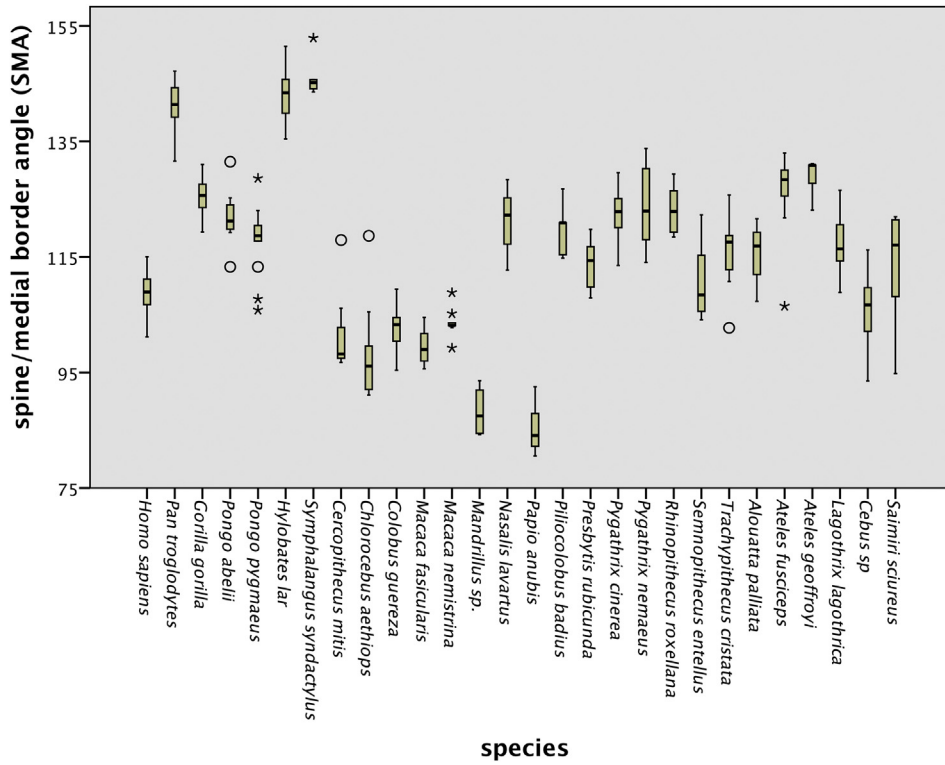


Figure 5. Boxplot of spine angle compared with medial border (SMA). The horizontal line indicates the median, boxes indicate the interquartile range, whiskers indicate the range, and dots and stars represent outliers.

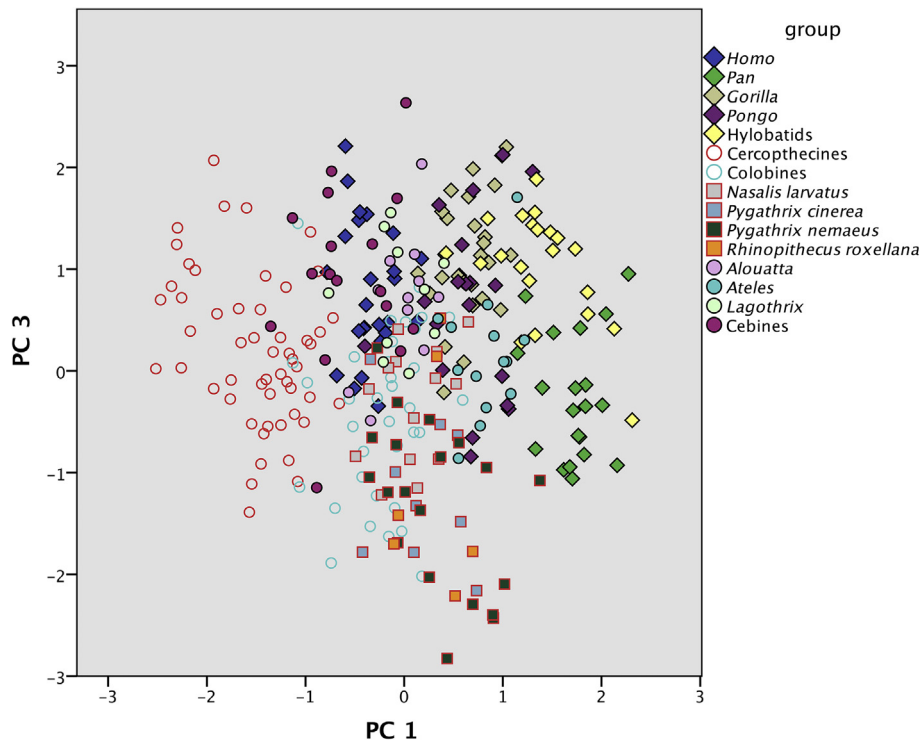


Figure 6. Scatter plot of the first and third principal components (PC1 and PC3). PC1 has an eigenvalue of 7.2 and explains 59.8% of the variance. PC3 has an eigenvalue of 1.2 and explains 9.8% of the variance. See Figure 3 for description of the PCA and details of PC1. PC3 has the highest loading for glenoid/spine angle (GSA). Note that odd-nosed monkeys fall on the lower end for this component.

Table 4
Post hoc ANOVA results. The results are listed as mean (SD). Bolded values indicate significant difference ($p < 0.05$) with *Pygathrix nemaeus* with post hoc Bonferroni adjustment.

Species	n	INF	GMA	GVA	SMA	SVA	GSA	SAA	ABS	VERTBORD/GM	AXBORD/GM	SUPBORD/GM	SPGLN/GM
<i>Pygathrix nemaeus</i>	20	50.48 (5.86)	13.07 (5.34)	0.06 (9.28)	123.53 (6.66)	110.20 (9.24)	70.00 (2.93)	18.93 (3.62)	31.01 (3.29)	1.50 (0.07)	1.66 (0.08)	0.95 (0.06)	1.23 (0.05)
<i>Hylobates lar</i>	15	63.55 (7.79)	43.03 (6.65)	13.83 (6.14)	142.89 (4.85)	110.73 (5.54)	104.79 (7.62)	3.81 (2.28)	9.07 (2.86)	1.43 (0.09)	1.76 (0.04)	0.80 (0.09)	1.57 (0.09)
<i>Nasalis larvatus</i>	14	56.72 (2.93)	14.85 (6.26)	-2.80 (6.99)	121.29 (4.90)	99.69 (3.32)	80.24 (2.76)	19.12 (3.55)	29.61 (4.15)	1.50 (0.07)	1.56 (0.07)	0.89 (0.05)	1.24 (0.03)
<i>Presbytis rubicunda</i>	10	51.73 (2.80)	2.42 (7.67)	-8.88 (3.93)	114.02 (4.23)	102.52 (3.03)	73.38 (3.97)	25.51 (1.64)	35.66 (2.22)	1.42 (0.06)	1.64 (0.05)	1.05 (0.08)	1.23 (0.05)
<i>Pygathrix cinerea</i>	9	52.77 (5.49)	12.40 (3.81)	-0.81 (8.02)	121.65 (5.33)	106.00 (7.26)	69.02 (4.84)	20.02 (2.82)	32.88 (2.73)	1.50 (0.09)	1.66 (0.08)	0.97 (0.07)	1.27 (0.05)
<i>Rhinopithecus roxellana</i>	6	50.67 (3.32)	13.89 (5.62)	1.40 (6.37)	123.21 (4.18)	109.36 (4.82)	68.85 (5.32)	18.41 (2.50)	31.64 (2.86)	1.50 (0.08)	1.60 (0.10)	0.92 (0.06)	1.23 (0.08)
<i>Trachypithecus cristatus</i>	15	57.30 (3.22)	11.21 (7.77)	-6.78 (5.24)	115.90 (5.38)	100.42 (4.47)	70.14 (7.24)	21.91 (2.14)	31.68 (1.94)	1.42 (0.10)	1.64 (0.06)	1.03 (0.09)	1.33 (0.03)
<i>Alouatta palliata</i>	11	57.20 (2.59)	15.52 (8.20)	-2.89 (5.24)	115.58 (5.14)	96.27 (2.85)	74.73 (3.46)	25.67 (2.60)	34.76 (2.70)	1.64 (0.15)	1.61 (0.04)	0.92 (0.13)	1.29 (0.06)
<i>Ateles fusciceps</i>	9	51.90 (3.49)	24.98 (4.34)	9.84 (5.93)	125.99 (8.02)	109.74 (3.69)	79.92 (4.11)	17.35 (4.24)	26.40 (4.55)	1.64 (0.08)	1.69 (0.05)	0.82 (0.04)	1.27 (0.06)
<i>Ateles geoffroyi</i>	5	49.55 (1.98)	26.62 (4.59)	10.79 (3.71)	128.76 (3.46)	111.49 (3.05)	77.51 (5.66)	18.10 (1.74)	27.28 (1.83)	1.71 (0.09)	1.73 (0.06)	0.77 (0.06)	1.23 (0.03)
<i>Lagothrix lagoincha</i>	10	61.76 (3.98)	17.00 (5.45)	-1.18 (5.93)	117.33 (4.92)	98.74 (5.22)	78.58 (1.51)	19.10 (2.24)	29.13 (2.96)	1.44 (0.08)	1.57 (0.08)	0.98 (0.08)	1.33 (0.02)

Variable abbreviations: see Table 2.

small substrate (Napier, 1967; Cartmill, 1985). Below-branch postures also allow for better utilization of the terminal branch niche as body size increases (Avis, 1962; Grand, 1972). Below-branch locomotion has even been argued to improve predator avoidance in the terminal branch niche as it might create less oscillation on branches than would above-branch progress (Stern and Oxnard, 1973; Hollihn, 1984). Postural differences, such as unimanual arm-hanging (Hunt, 1991) and forelimb abducted foraging postures (Dunham et al., 2015), have also been postulated to affect scapular morphology. However, postures place less stress on the skeleton than locomotion and are therefore less likely to necessitate an adaptive change (Gebo, 1996).

Many 'brachiator' features are found in nonanthropoids that are not arm-swingers. Lorises and two-toed sloths, such as modern great apes, lack ulnotriquetral contact and have a distally placed pisiform (Cartmill and Milton, 1977; Mendel, 1979). Sloths have additional features that have been interpreted as adaptations for 'brachiation,' including a reduced thumb, high brachial index, and reduced olecranon process length (Mendel, 1979). This demonstrates that many features associated with arm-swinging may have evolved in parallel with other activities.

The Miocene hominoid fossil record demonstrates that these features have not evolved en bloc. For example, *Nacholapithecus* has long forelimbs and phalanges, but a narrow, monkey-like thorax and lumbar region (Nakatsukasa et al., 1998, 2003, 2007; Ishida et al., 2004), whereas *Pierolapithecus* has a broad thorax like modern great apes, but relatively short and straight manual phalanges (Moyà-Solà et al., 2004; Almécija et al., 2009).

If 'brachiator' features did not evolve for arm-swinging, then what purpose do they serve? One hypothesis is vertical climbing, which posits functional explanations for 'brachiating' features such as shortened lower back and long forelimbs (Jungers, 1984; Cartmill, 1985). However, the absence of vertical climbing features in early hominins suggests that a broad thorax with a dorsally positioned scapula predates the African ape-human split (Lovejoy et al., 2009b; but see Pilbeam and Lieberman, 2017), which may explain the relatively pronounced scapular differences among humans, chimpanzees, and gorillas (Selby and Lovejoy, 2017).

Inverted quadrupedalism was recently hypothesized to predate arm-swinging, in part based on a number of kinematic similarities in forelimb loading patterns, particularly with greater body size (Granatosky and Schmitt, 2019). However, two key hominoid features not found in inverted quadrupeds such as sloths are a mediolaterally broad thorax and dorsally placed scapula (Nyakatura and Fischer, 2010), which are crucial for shoulder mobility in taxa that regularly practice arm-swinging.

Scrambling, as defined by Hunt et al. (1996: 377), is "torso-pronograde, nonsuspensory quadrupedal progression lacking a regular gait." This locomotor mode is an above-branch progression that uses multiple, small, and irregularly placed supports. This, along with bridging between supports, would allow an anthropoid to maintain access to the terminal branch niche with increased body mass. Typically, fruits and leaves are located in the terminal branches, so retaining the ability to safely access these resources would be critical.

Many of the 'brachiator' features may also be adaptive to scrambling and/or bridging. For example, increased shoulder mobility and long forelimbs allow the forelimb to reach a greater sphere of supports. Likewise, a mobile wrist allows manual support in a wider range of adduction/abduction and pronation/supination positions, and long phalanges stabilize handholds on supports of a variety of sizes (Cartmill and Milton, 1977). A shorter lumbar region that reduced mobility reduces the possibility of 'buckling' during bridging (Jungers, 1984). This use of mobile forelimbs on multiple supports of different orientations may then lead to bimanual

suspension, which would further limit the risk of falling. Each of these adaptations would be beneficial for scrambling, but not all are necessary, which may explain the mosaic nature of the Miocene hominoid postcrania.

The use of scrambling as a means of negotiating the fine-branch niche is supported with behavioral observations in atelines, which use both above- and below-branch locomotor modes. *Alouatta* and *Ateles* are typically quadrupedal on larger branches, but on small branches, they only clamber and bridge and more commonly arm-swing (Cant, 1986). The more common use of suspensory locomotor modes allows *Ateles* to access terminal branches more than *Lagothrix*, which relies more on quadrupedal behaviors (Cant et al., 2001). This pattern was also observed in captive hominoids (Avis, 1962). This indicates that above-branch quadrupedal locomotion on a single support is less viable in the terminal branches for anthropoids of a certain size and that use of multiple supports, either above- or below-branch ones, becomes necessary to use terminal branches. However, it should be noted that this is not entirely dependent on body size, as the strictly above-branch quadrupedal *Colobus guereza* has a greater body mass than the partially arm-swinging *P. nemaus* (see Smith and Jungers, 1997).

The use of multiple supports in the fine-branch niche may also explain the lack of the full suite of 'brachiator' features in *Pygathrix*, despite its use of arm-swinging, and the presence of these features in *Rhinopithecus*, despite its near total lack of arm-swinging. Scrambling and bridging may facilitate arm-swinging (Cartmill, 1985) or may be its own adaptation for the fine-branch niche. More detailed locomotor observations on these taxa, as well as on *Nasalis* and *Simias*, would be helpful to test the hypothesis that arm-swinging, scrambling, or clambering are used more in the fine-branch niche.

Conflict of interest

The authors declare no conflict of interest.

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Supplementary Online Material

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