

An anatomical and mechanical analysis of the douc monkey (genus *Pygathrix*), and its role in understanding the evolution of brachiation

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Abstract

Objectives: *Pygathrix* is an understudied Asian colobine unusual among the Old World monkeys for its use of arm-swinging. Little data exists on the anatomy and mechanics of brachiation in this genus. Here, we consider this colobine to gain insight into the parallel evolution of suspensory behavior in primates.

Materials and methods: This study compares axial and appendicular morphological variables of *Pygathrix* with other Asian colobines. Additionally, to assess the functional consequences of *Pygathrix* limb anatomy, kinematic and kinetic data during arm-swinging are included to compare the douc monkey to other suspensory primates (*Ateles* and *Hylobates*).

Results: Compared to more pronograde species, *Pygathrix* and *Nasalis* share morphology consistent with suspensory locomotion such as its narrower scapulae and elongated clavicles. More distally, *Pygathrix* displays a gracile humerus, radius, and ulna, and shorter olecranon process. During suspensory locomotion, *Pygathrix*, *Ateles*, and *Hylobates* all display mechanical convergence in limb loading and movements of the shoulder and elbow, but *Pygathrix* uses pronated wrist postures that include substantial radial deviation during arm-swinging.

Discussion: The adoption of arm-swinging represents a major shift within at least three anthropoid clades and little data exist about its transition. Across species, few mechanical differences are observed during arm-swinging. Apparently, there are limited functional solutions to the challenges associated with moving bimanually below branches, especially in more proximal forelimb regions. Morphological data support this idea that the *Pygathrix* distal forelimb differs from apes more than its proximal end. These results can inform other studies of ape evolution, the pronograde to orthograde transition, and the convergent ways in which suspensory locomotion evolved in primates.

KEYWORDS

colobinae, locomotion, orthograde, semibrachiation

1 | INTRODUCTION

A key interest in the study of primate skeletal anatomy is the well-established correlation between function and morphology in dietary and/or locomotor behavior (Shea, 2005). These correlations are the basis for predictions concerning living and extinct taxa. Historically, locomotion has often been seen as a demonstration of primate adaptive diversity. A plethora of studies developed a classificatory scheme

based on these morphological data (e.g., Ashton & Oxnard, 1964; Avis, 1962; Erikson, 1963; Gregory, 1928; Larson, 1993, 1995; Napier, 1963, 1967; Napier & Napier, 1967; Oxnard, 1963; Schultz, 1930). A basic version of this scheme, as presented by Napier and Napier (1967), includes vertical clinging and leaping, quadrupedalism, brachiation, and bipedalism. Quadrupedalism is central to this and likely represents the antecedent condition to other more specialized non-quadrupedal modes included in this scheme. However, quadrupedalism

can be all-encompassing and overlaps to a degree with the other more derived locomotor modes. One of these derived modes is brachiation, and the transition between these pronograde and more derived orthograde and suspensory forms represents a category known as semibrachiation.

The morphology of arm-swinging species has been well studied, and is often interpreted as a functional suite of characteristics thought to allow for efficient pendular movement (Erikson, 1963; Hallgrímsson & Swartz, 1995; Larson, 1998; Rein, Harvati, & Harrison, 2015; Swartz, 1989, 1990; Swartz, Bertram, & Biewener, 1989; Turnquist, Schmitt, Rose, & Cant, 1999). The fluid, swinging motion observed when brachiators move beneath branches naturally brings to mind the oscillations of a pendulum and the repeated interchange of potential and kinetic energy (Bertram & Chang, 2001; Chang, Bertram, & Lee, 2000; Fleagle, 1974; Michilens, D'août, & Aerts, 2011; Preuschoft & Demes, 1984, 1985; Swartz, 1989). It is tempting, then, to assume that arm-swinging primates use natural pendular motions to reduce the muscular investment necessary to travel (Bertram, Ruina, Cannon, Chang, & Coleman, 1999). Some studies have demonstrated that, under certain conditions, arm-swinging primates do match the expectations of a simple pendulum, but this appears to be the case only for very slow speeds and continuous-contact locomotion (Bertram et al., 1999; Preuschoft & Demes, 1984; Turnquist et al., 1999). Simple pendular locomotion is restrictive, and to optimize energetic efficiency animals must limit themselves to a narrow range of stride distance and speed (Preuschoft & Demes, 1984; Swartz, 1989). In most scenarios, the complex three-dimensional arboreal environment that arm-swinging primates live in make simple pendular locomotion impossible (Bertram et al., 1999). In these situations, travel pathway adjustments, rather than efficiency, appears to be the primary concern (Bertram et al., 1999; Parsons & Taylor, 1977). While the pendular, or lack thereof, movement of gibbons is well-known, little data are available to determine if other arm-swinging species (e.g., *Pygathrix* and *Ateles*) demonstrate similar patterns.

Continuous-contact brachiation appears to match the movements of a simple pendulum in a number of studies (Bertram et al., 1999; Chang et al., 2000; Preuschoft & Demes, 1984; Turnquist et al., 1999). Pendular movement has specific kinetic and kinematic patterns that are expected, and these predictions can be applied to movements and loading in a biological system. With this in mind, considering arm-swinging as synonymous with simple pendular motion can help to guide our expectations about how an arm-swinging primate may behave from a mechanical perspective. The forces acting on a simple pendulum are quite specific. Peak vertical forces are relatively high, and should be equal to the apparent force observed during rotational motion (Bertram et al., 1999; Chang et al., 2000). The occurrence of the peak vertical force is expected to occur at the lowest point of the pendulum's swing (i.e., mid-support) (Bertram et al., 1999). Fore-aft forces should be propulsive during the first half of support phase and braking during the second half of support phase, and the braking to propulsive transition should occur at mid-support. Additionally, the propulsive and braking impulses should be equal to each other, and

therefore result in a net fore-aft impulse in the forelimb that is zero. Mediolateral forces should be relatively low (Bertram et al., 1999; Chang et al., 2000; Michilens et al., 2011). With respects to kinematics, animals should coordinate joint movements throughout support phase to: (1) maximize limb length [organisms with longer effective limb length tend to have a relatively lower mass-specific metabolic cost per unit of distance traveled (Hanna, Schmitt, & Griffin, 2008; Pontzer, 2007, 2016)]; (2) demonstrate swing amplitudes equidistant from the equilibrium position, and concentrate motion either near the point-of-contact (POC) or center of mass (COM) (Bertram et al., 1999; Preuschoft & Demes, 1984; Swartz, 1989); (3) and utilize swing periods predicted by effective limb length (Bertram, 2004; Fleagle, 1974; Preuschoft & Demes, 1984; Swartz, 1989; Usherwood, 2003).

The morphological traits observed in suspensory taxa are numerous throughout the trunk, shoulder, and the rest of the upper extremity. In the trunk, brachiators are known to possess a relatively shortened lumbar region and an overall dorso-ventral flattening as well as mediolateral expansion of the rib cage. This results in a scapula that is repositioned dorsally, with its humeral articulation oriented more cranially, from its more lateral placement in quadrupedal monkeys (Erikson, 1963; Larson, 1995; Selby & Lovejoy, 2017). Additionally, the scapula has a greater anteroposterior (craniocaudal) length relative to its mediolateral dimension giving brachiators a distinctive scapular shape (Schultz, 1930). Functionally, these morphologies in brachiators are thought to reposition the infraspinatus muscle to better transmit the trunk's mass to the forelimb, which enables greater resistance to transarticular tensile stresses while suspending below a branch (Larson & Stern, 1986; Larson, 1993, 1995). Also, in the pectoral girdle of brachiators, relatively longer clavicles are known to provide greater lateral projection of the shoulder (Ashton & Oxnard, 1964), enhancing the mobility of the forelimb when raised above the head. The forelimb in brachiators is elongated and slender overall, with intermembral indices well above 100% (indicating its relative importance for weight support compared to the hindlimb). As stated earlier, a longer limb decreases the mass-specific metabolic cost per unit of distance traveled (Hanna et al., 2008; Pontzer, 2007, 2016). Additionally, a longer humerus places the deltoid's insertion more distal to the shoulder joint, which results in net gains in mechanical advantage and muscle force output (Ashton & Oxnard, 1964; Erikson, 1963) as the arm is abducted. Typically, triceps brachii is small in brachiators and, with a shorter distance to the fulcrum of the elbow joint (i.e., shorter olecranon process), is not specialized for power output. Additionally, a shorter olecranon process facilitates greater extension at the elbow.

In the traditional semibrachiator locomotor category, convergent anatomical traits associated with bimanual locomotion in brachiators are expected in these trunk, shoulder, and forelimb regions. That is, one should expect to observe semibrachiators occupy a morphospace that is in between brachiators and arboreal quadrupeds. As a category by itself semibrachiation, defined as the reliance on above-branch quadrupedal as well as forelimb mediated suspensory postures, has been problematic because, in part, it is expressed differently in New World platyrrhine monkeys as compared to Old World catarrhine

monkeys. The New World semibrachiators are represented by the various genera of the prehensile tailed family Atelidae whose locomotion is more ape-like when compared to smaller platyrrhine monkeys with more generalized and primitive arboreal modes (Erikson, 1963; Jones, 2008; Rosenberger, Halenar, Cooke, & Hartwig, 2008). New World semibrachiators utilize suspensory behavior accompanied by arm-swinging whereby the forelimbs and the tail grasp arboreal substrates (Schmitt, Rose, Turnquist, & Lemelin, 2005; Turnquist et al., 1999). In contrast, the Old World semibrachiator group uses suspensory behavior without a prehensile tail. The genera included in this category are *Pygathrix*, *Nasalis*, *Rhinopithecus*, *Presbytis*, and *Colobus* (Ashton & Oxnard, 1964; Napier, 1963; Napier & Napier, 1967).

Several of the monkeys belonging to Napier's Old World semibrachiator group are part of the odd-nosed colobine clade. This includes the genera *Pygathrix*, *Nasalis*, *Rhinopithecus*, and *Simias*. This monophyletic clade is found in habitats throughout East and Southeast Asia (Liedigk et al., 2012). Many of these taxa display striking facial coloration and body pelage patterns as well as a larger body size when compared to other Asian colobines, such as the langurs (Disotell, 1998; Jablonski & Ru, 1995; Jablonski & Zhang, 1992). With habitat loss and high levels of human predation pressure, the population outlook for this group remains dire (Lippold & Thanh, 1998; Long, 2004; Nadler & Streicher, 2004; Nadler, Momberg, Dang, & Lormee, 2003). Thus, documenting the skeletal anatomy and positional behavior of such critically endangered taxa is a priority for primate functional morphologists.

Aside from descriptions of *Nasalis*, there are very few morphological studies of odd-nosed colobines, in part, because they are not well represented in natural history museum collections, are endemic to less documented geographical regions, and often suffer from gastrointestinal maladies in captivity (Lippold, 1998; Nadler et al., 2003; Sterling, Hurley, & Minh, 2006). Su and Jablonski (2009) published the first modern description of many in the odd-nosed clade and demonstrated an Old World monkey skeletal morphology that converges with that in hominoids and atelids. Bailey, Lad, and Pampush (2017) published a recent study on douc scapular shape placing it intermediate between arboreal quadrupeds and brachiators. In an effort to provide additional morphological data for this group a new sample of the genus *Pygathrix* (*P. nemaues*, *P. cinerea*, and *P. nigripes*) has been recently described from the Endangered Primate Rescue Center, Cuc Phuong National Park, Vietnam (Byron, Hensel, Morrison, & Nguyen, 2015). In this study, the genus *Pygathrix* is presented as a homogenous statistical population that appropriately fits into the Old World semibrachiator category (Ashton & Oxnard, 1964; Napier, 1963). This test of the semibrachiator concept is relevant because of findings that many colobines from that earlier category do not actually employ a large amount of suspensory behavior (Mittermeier & Fleagle, 1976; Morbeck, 1977, 1979). Recent attention has been paid to doucs because of their use of pronograde quadrupedal coupled with a significant amount of orthograde suspensory positional behavior (Byron & Covert, 2004; Covert, Workman, & Byron, 2004; Stevens et al., 2008; Su & Jablonski, 2009; Wright, Stevens, Covert, & Nadler, 2008).

We predict that the habitual use of both brachiation and arboreal quadrupedal locomotion in the doucs corresponds to mechanical and anatomical outcomes that represent an intermediate locomotor stage toward typical brachiator morphologies. The douc shoulder is expected to have a shape that is intermediate between brachiators and arboreal quadrupeds and is more similar with gibbons and spider monkeys in glenohumeral range of motion. Also we expect such similar intermediate positioning for the douc in having elongated and gracile forelimbs and forearms, as well as elbows that promote extension of the humeral joint without an emphasis on triceps brachii mechanical advantage. We predict that the douc elbow range of motion will parallel that observed for gibbons and spider monkeys.

The classic description of the Old World semibrachiator group (Napier & Napier, 1967) reported average intermembral (93%) and brachial index (104%) values for *Pygathrix* from earlier work (Milne-Edwards & de Pusargues, 1898; Washburn, 1942). Su and Jablonski (2009) also reported values for intermembral index and brachial index and the contrast leaves the same interpretation, that the douc occupies an intermediate zone between orthograde hominoids and pronograde arboreal monkeys. Another odd-nosed Asian colobine, the proboscis monkey (*Nasalis*), has similar values for these indices. The other colobines of Asia and Africa (non-odd-nosed forms) have lower intermembral and brachial index values in the range of typical arboreal quadrupeds (i.e., the legs are relatively longer than arms and the antebrachium is relatively shorter than the brachium). In the most specialized brachiators like *Hylobates*, an intermembral index of 129% and brachial index of 113% are reported, indicating how forelimb (and forearm) dominated these animals are (Schultz, 1930). The New World semibrachiators from the family Atelidae more closely approximate the limb index condition of true brachiators. *Ateles* shows ape-like lumbar shortening, the dorsal shift of the shoulder girdle with a cranially oriented glenoid, long and slender arm bones, a large medial epicondyle, and an elongated radius and hand (Arias-Martorell, Tallman, Potau, Bello-Hellegouarch, & Pérez-Pérez, 2015; Erikson, 1963; Larson, 1998; Rein et al., 2015; Rosenberger et al., 2008). However, with a prehensile tail as a major component of the locomotor stride, spider monkeys do not exhibit a condition that is relevant to any known catarrhine fossils marking the pronograde to orthograde transition that occurred in primate evolution. For this reason the douc may prove useful in better understanding the parallel evolution of arm-swinging suspensory behavior in catarrhine primates.

The movement of structures, and the forces imposed upon them, act to drive shape changes in morphology (Bock & von Wahlert, 1965; Larson & Losos, 1996; Losos et al., 2000). In this study, we compare the bony anatomy of *Pygathrix* to other Asian colobines to determine whether the documented use of arm-swinging in this species alters morphology in ways reported in other suspensory species. Additionally, we explore patterns of kinetic and kinematic data in three arm-swinging species to determine if *Pygathrix* demonstrates similar mechanical strategies to what is observed in more notable brachiators (*Hylobates* and *Ateles*) during continuous-contact brachiation. From these data, our hope is to establish the genus *Pygathrix* as another

TABLE 1 Morphological sample

Genus	Species	Collection	Individuals
<i>Nasalis</i>	<i>larvatus</i>	MCZ	15
<i>Presbytis</i>	<i>rubicunda</i>	MCZ	12
<i>Pygathrix</i>	<i>cinerea</i>	EPRC	10
<i>Pygathrix</i>	<i>nemaeus</i>	EPRC	20
<i>Pygathrix</i>	<i>nigripes</i>	EPRC	5
<i>Trachypithecus</i>	<i>cristatus</i>	MCZ	11
<i>Trachypithecus</i>	<i>delacouri</i>	EPRC	6
<i>Trachypithecus</i>	<i>hatinhensis</i>	EPRC	3
<i>Trachypithecus</i>	<i>phayrei</i>	MCZ, FMNH	13

example of the parallel evolution of suspensory modes of locomotion that have occurred during catarrhine evolution. Determining how closely aligned the douc is with other brachiators and quadrupeds in its morphology and arm-swinging performance may offer interpretive clues of the pronograde to orthograde transition as it occurred in stem hominoid primates.

2 | MATERIALS AND METHODS

The materials here include several rare monkeys from the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, Vietnam (Ninh Binh Province). Many specimens here were illegally captured from the wild before being confiscated by officials and placed in the EPRC. Other animals were born and raised within the habitat appropriate housing found at the rescue center. Both conditions yield primates that have engaged in natural types of locomotion. Red-, gray-, and black-shanked doucs (*P. nemaeus*, *P. cinerea*, and *P. nigripes*) as well as two species of langur (*T. delacouri* and *T. hatinhensis*) have been curated and remain on their premises. Two other species were sampled from wild-shot collections housed at the Museum of Comparative Zoology (MCZ, Cambridge, MA) and the Field Museum of Natural History (FMNH, Chicago, IL). In the interest of bolstering sample size, species were combined in the genera *Pygathrix* and *Trachypithecus*. Other wild-

shot taxa sampled at MCZ include *Nasalis larvatus* and *Presbytis rubicunda* (Table 1). The non-odd-nosed Asian colobines in this sample are drawn from the larger radiation of smaller-bodied leaf monkey genera (i.e., *Presbytis* and *Trachypithecus*) with species-specific preferences extending beyond simple arboreality. Two *Trachypithecus* species used for this study, *T. delacouri* and *T. hatinhensis*, express a distinct behavioral ecology that is non-arboreal. Rather than use terrestrial to describe their habitat preferences it may be useful to consider their "cliff-climbing" as something different altogether (Workman, 2010; Workman & Schmitt, 2012). These two species typically engage habitat substrates that are vertical and angular requiring skillful climbing, scaling, and gripping while holding the body in tension. They belong to a monophyletic clade of allopatric taxa known as the limestone langurs (Nadler & Streicher, 2004). For the purposes of this study all *Trachypithecus* and *Presbytis* species are considered en bloc because they are decidedly not suspensory and orthograde.

The kinetic and kinematic material specimens were living primates housed in zoos and animal rescue centers including Greensboro Science Center (GSC; Greensboro, N.C.), Monkey Jungle (MJ; Miami, FL), and the EPRC and belong to the taxa *Ateles fusciceps*, *Hylobates moloch*, and *Pygathrix nemaeus*. All animals were adults and were clear of any pathologies or gait abnormalities (Table 2). Experimental data were collected following the protocols approved by Duke's Institutional Animal Care and Use Committee (IACUC protocol # A270-11-10).

Morphometric data were collected using a pair of Mitutoyo digital hand calipers connected to a Macbook workstation running Microsoft Excel (Redmond, WA). Length in mm was recorded between anatomical landmarks to the nearest 0.01 mm. A total of sixty linear morphometrics were collected (Supporting Information S1) to compute ten ratio-metric index variables. These indices are shown in two groups. The first group of index values (Figure 1) represents some of the basic body index values taken from prior publications such as Intermembral Index, Brachial Index, Crural Index, Scapular Shape Index, and Lumbar Index. These variables offer shape information for regions known to discriminate between primate locomotor category in the shoulder, limbs, and trunk. Known brachiators typically demonstrate relatively long forelimbs and forearms, as well as a relatively shortened lumbar vertebral region, and a scapula with a long anteroposterior (craniocaudal) length

TABLE 2 Animal subjects used in the study

Species	Subject	Sex	Body mass (kg)	Strides (N) analyzed for kinematic analyses	Strides (N) analyzed for kinetic analyses
<i>Pygathrix nemaeus</i>	Individual 1	Male	9.23	14	8
	Individual 2	Female	8.16	14	6
<i>Ateles fusciceps</i>	Individual 1	Male	n/a	10	0
	Individual 2	Female	n/a	9	0
	Individual 3	Female	8.2	0	9
<i>Hylobates moloch</i>	Individual 1	Male	7.2	3	3
	Individual 2	Male	6.8	10	10

^{n/a}Data not available.

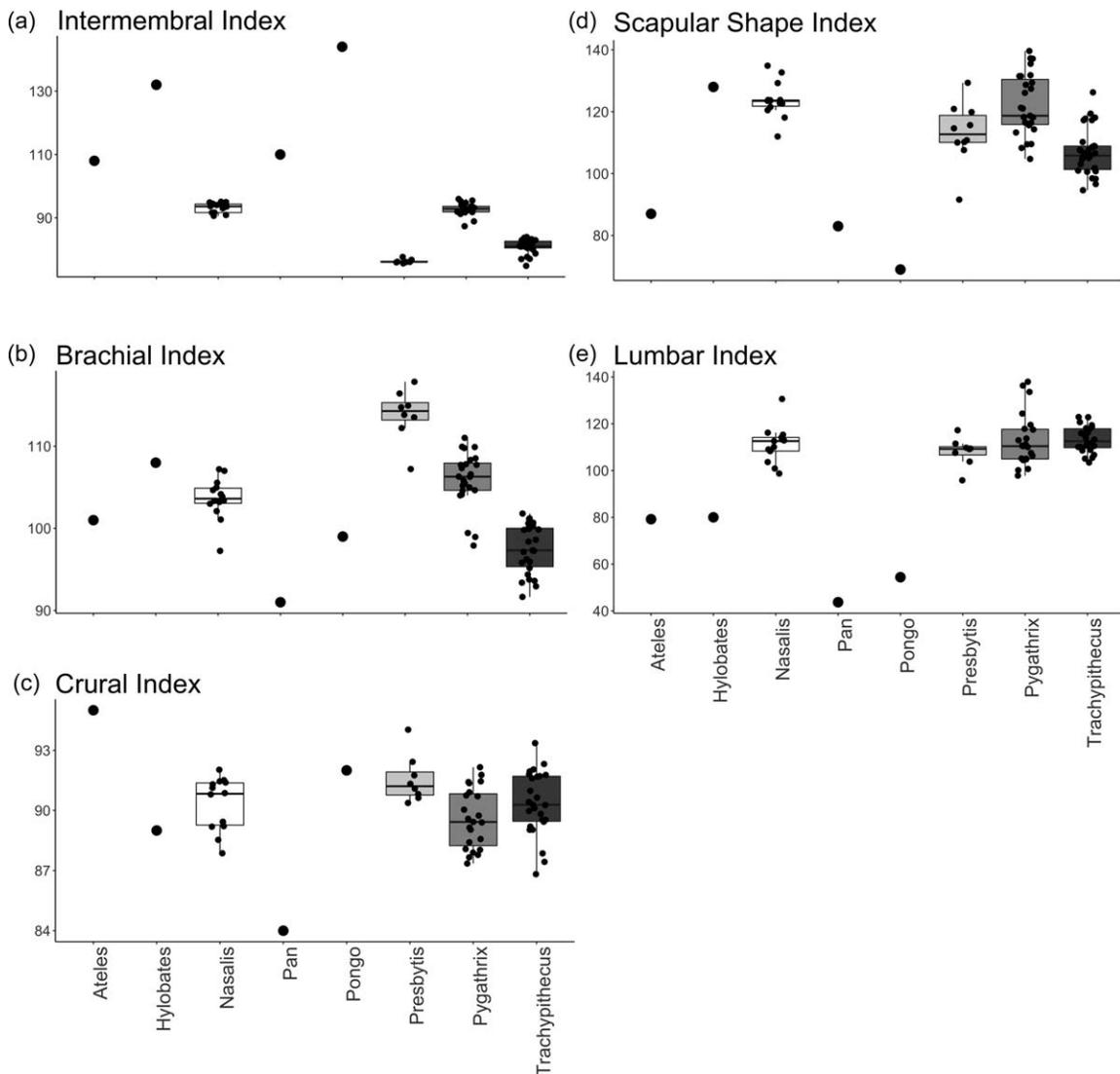


FIGURE 1 Five body type indices allow for comparison of this sample with other known suspensory taxa such as apes and spider monkeys. These additional taxa are previously reported (Erikson, 1963; Schultz, 1930; Schultz, 1938) or currently unpublished (Granatosky, n.d.). (a) Intermembral Index, (b) Brachial Index, (c) Crural Index, (d) Scapular Shape Index, and (e) Lumbar Index

relative to mediolateral length. The second group of index values (Figure 2) represents additional shape variables beyond what is available in the prior literature and offer data about the clavicle, arm, elbow, and forearm. These variables measure the length of different forelimb components while accounting for gracility by either using the geometric mean of three cross-sectional metrics in that bone (i.e., humeral gracility index, ulna gracility index, and radial gracility index) or using the geometric mean of the acetabulum size (i.e., clavicle index and olecranon process index). Known brachiators are expected to show more slender forelimbs, relatively long clavicles, and short olecranon processes. Descriptive statistics from all ten indices are shown in Table 3 along with tests of homogeneity for each taxon.

Statistical analyses of morphological variables were performed using JMP Pro 11 (SAS; Cary, NC) and the R statistical language (RStudio 1.0.136; Boston, MA). Standard descriptive statistics from indices are reported as well as the Shapiro-Wilk W -test for goodness of fit

(Table 3). In certain cases significant W statistics were observed which indicate a nonparametric variable for a specific genus. In these cases a Kruskal-Wallis χ^2 was used to compare for differences among means. Analysis of variance (ANOVA) was used on the parametric variables to test whether they demonstrated significant inter-taxon variation. Significant p -values indicate that differences exist between genus, and for these variables parametric Tukey-Kramer and non-parametric Wilcoxon Rank-Sum post-hoc tests were used to indicate the directionality of these differences (Table 4).

Forelimb kinetics and kinematics were collected while animals moved below an instrumented runway measuring approximately 3.66 m in length and 3.1 cm in diameter. The methods used here have been described extensively elsewhere (Granatosky, 2015, 2016; Granatosky, Tripp, Fabre, & Schmitt, 2016; Granatosky, Tripp, & Schmitt, 2016; Schmitt & Lemelin, 2002; Schmitt, 2003), and will only be summarized below. The instrumented portion of the runway consisted of

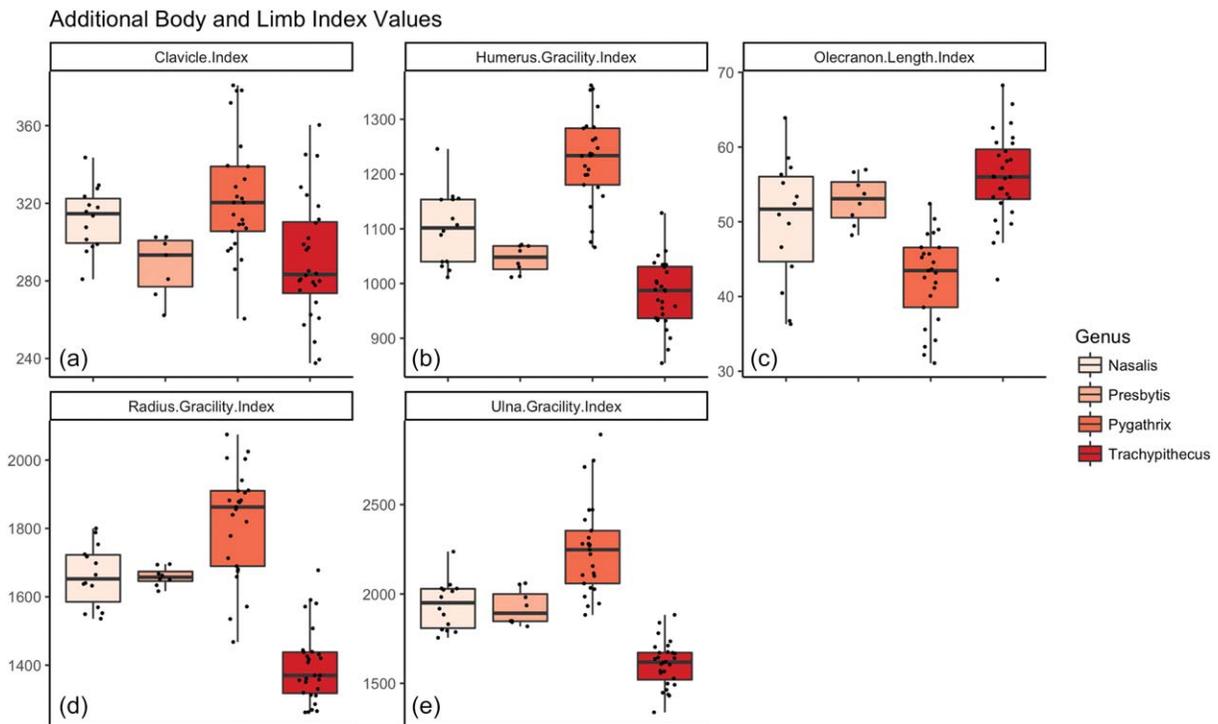


FIGURE 2 Five additional limb indices portray limb gracility and elongation. (a) Clavicle Index, (b) Humerus Gracility Index, (c) Olecranon Length Index, (d) Radius Gracility Index, and (e) Ulna Gracility index

an AMTI multi-axis force plate (MC3A-100) attached to a section of dowel (0.46 m in length) measuring the same diameter as the rest of the runway. This instrumented section was mounted in the middle of the runway flush with, but separated by a small gap, from the rest of the runway. Force plate output was sampled at 1,200 Hz, and imported, summed, and processed using AMTI-NetForce software, and then filtered (Butterworth, 30 Hz) and analyzed using MATLAB.

Prior to the first trial, animal weights were recorded from the subject's most recent veterinary visit and forces for each day of trials were normalized to these weights. For all subjects, the most recent veterinary visit was within three months of the sampling period. For all trials, animals were filmed from a lateral view. *Pygathrix nemaeus* and *H. moloch* were video-recorded using a GoPro camera (Hero 3+ Black Edition; GoPro, San Mateo, CA) modified with a Back-Bone Ribcage (Ribcage v1.0; Back-Bone, Ottawa, ON), which allows the GoPro cameras to be outfitted with interchangeable lenses and eliminates image distortion inherent to the camera (Granatosky, Tripp, Schmitt, et al., 2016). For these animals, videos were recorded at 120 fields/second. Video-recordings of *A. fusciceps* were made available from previous studies (Schmitt et al., 2005; Turnquist et al., 1999), and were recorded at 60 f/s using a Sony Handycam (Sony Corporation of America, New York, NY). These data collected by Turnquist et al. (1999) and Schmitt et al. (2005) consisted of video-recordings, and were only used for kinematic analysis. Kinetic data for *A. fusciceps* were collected by MCG during a separate sampling period on a single separate individual (Table 2).

For each step, speed was calculated by digitizing a point on the subject's head at each field over the entire stride and calculating instantaneous speed at each interval based on a known distance marked on

the runway used to calibrate the image space. Only steady-state strides approximating continuous-contact (i.e., aerial phase less than 0.05 s) were selected for analysis. It was the case that many of the strides analyzed in this study from *A. fusciceps* and *P. nemaeus* showed a brief aerial phase before touching down with the next limb. This behavior is distinct from ricochetal brachiation because it has very specific kinematic and center of mass movements not observed in any of the these species (Bertram et al., 1999; Bertram & Chang, 2001; Michilens et al., 2011, 2012; Usherwood, 2003). In general, tail-assisted support in *A. fusciceps* was observed during alternate hand-hold (Turnquist et al., 1999). Only strides with no tail-assisted support were used for subsequent analysis to make data more comparable between the three species. Steady-state locomotion was determined by calculating the instantaneous speed between subsequent video frames throughout the entire stride, and then using regression analysis to determine whether velocity changed throughout the stride (Bishop, Pai, & Schmitt, 2008; Granatosky, Tripp, Fabre, 2016; Granatosky, Tripp, Schmitt, et al., 2016; Granatosky, 2015, 2016). Only strides in which no change in speed (i.e., slope not significantly different from zero) was detected were used for subsequent analyses. Additionally, only steps with single-limb contacts on the plate, or those steps in which the forelimb forces were clearly differentiated, were analyzed.

From video-recordings, the position of the shoulder, elbow, wrist, and forelimb point-of-contact (POC) were collected over the course of support phase (i.e., when the limb was in contact with the substrate) during arm-swinging in *H. moloch*, *A. fusciceps*, and *P. nemaeus*. The resulting x-y coordinate data was used to track angular movements in the shoulder, elbow, and wrist. All limb angles were digitized using DLT

TABLE 3 Morphological data test statistics

Taxon	<i>Nasalis larvatus</i>					<i>Presbytis rubicunda</i>				
	<i>n</i>	μ	$\pm \sigma$	W-Stat	P-Value	<i>n</i>	μ	$\pm \sigma$	W-Stat	P-Value
Intermembral Index (%)	15	93.25	1.58	0.89	NS	10	76.09	0.79	0.88	NS
(Humerus Length+Radius Length)/(Femur Length+Tibia Length)										
Brachial Index (%)	15	103.51	2.46	0.94	NS	10	114.19	2.92	0.88	NS
Radius Length/Humerus Length										
Crural Index (%)	15	90.14	1.40	0.90	NS	10	91.83	1.21	0.94	NS
Tibia Length/Femur Length										
Scapular Shape Index (%)	15	124.38	6.00	0.92	NS	12	113.49	9.08	0.91	NS
Height/Width										
Clavicle Index (%)	15	312.49	15.91	0.98	NS	9	288.49	14.66	0.88	NS
Clavicle Length/((Acetabulum Height*Width) ^{1/2})										
Humerus Gracility Index (%)	15	1100.84	65.32	0.94	NS	10	1052.43	30.39	0.94	NS
Humerus Length/((circumference*breadth*depth) ^{1/3})										
Ulna Gracility Index (%)	15	1933.53	133.96	0.92	NS	10	1948.96	116.75	0.91	NS
Ulna Length/((circumference*breadth*depth) ^{1/3})										
Olecranon Length Index (%)	15	50.13	8.04	0.96	NS	10	52.96	3.93	0.96	NS
Olecranon Process Length/((Acetabulum Height*Width) ^{1/2})										
Radius Gracility Index (%)	15	1657.03	87.58	0.94	NS	10	1676.78	45.29	0.95	NS
Radius Length/((circumference*breadth*depth) ^{1/3})										
Lumbar Index (%)	13	111.20	8.01	0.92	NS	10	107.62	5.57	0.94	NS
(Lumbar Height/Thoracic Height)										
Taxon	<i>Pygathrix sp. (cinerea, nemeaus, nigripes)</i>					<i>Trachypithecus sp.</i>				
	<i>n</i>	μ	$\pm \sigma$	W-Stat	P-value	<i>n</i>	μ	$\pm \sigma$	W-Stat	P-value
Intermembral Index (%)	28	92.57	2.24	0.98	NS	27	80.78	2.21	0.92	0.04445
(Humerus Length+Radius Length)/(Femur Length+Tibia Length)										
Brachial Index (%)	31	104.71	4.25	0.93	0.0419	27	97.47	2.92	0.95	NS
Radius Length/Humerus Length										
Crural Index (%)	30	89.77	1.51	0.96	NS	27	93.36	1.59	0.98	NS
Tibia Length/Femur Length										
Scapular Shape Index (%)	35	121.32	9.38	0.95	NS	32	106.86	7.28	0.94	NS
Height/Width										
Clavicle Index (%)	32	317.66	31.08	0.95	NS	28	290.61	31.38	0.97	NS
Clavicle Length/((Acetabulum Height*Width) ^{1/2})										
Humerus Gracility Index (%)	32	1226.26	97.28	0.96	NS	29	981.33	59.41	0.99	NS
Humerus Length/((circumference*breadth*depth) ^{1/3})										
Ulna Gracility Index (%)	32	2252.48	296.97	0.96	NS	29	1606.11	124.97	0.99	NS
Ulna Length/((circumference*breadth*depth) ^{1/3})										
Olecranon Length Index (%)	31	42.06	5.62	0.98	NS	29	55.57	6.17	0.99	NS
Olecranon Process Length/((Acetabulum Height*Width) ^{1/2})										

(Continues)

TABLE 3 (Continued)

Taxon	<i>Pygathrix sp. (cinerea, nemaesus, nigripes)</i>					<i>Trachypithecus sp.</i>				
	n =	μ	$\pm \sigma$	W-Stat	P-value	n =	μ	$\pm \sigma$	W-Stat	P-value
Radius Gracility Index (%)	32	1831.64	197.09	0.98	NS	29	1398.80	106.52	0.92	0.033
Radius Length/((circumference*breadth*depth) ^{1/3})										
Lumbar Index (%)	26	112.51	10.65	0.89	0.0083	26	113.30	5.49	0.98	NS
(Lumbar Height/Thoracic Height)										
				ANOVA F-Ratio	ANOVA P-Value				Kruskal-Wallis χ^2	Kruskal-Wallis P-Value
Intermembral Index (%)									65.39	<0.0001
(Humerus Length+Radius Length)/(Femur Length+Tibia Length)										
Brachial Index (%)									57.27	<0.0001
Radius Length/Humerus Length										
Crural Index (%)				4.85	.0038					
Tibia Length/Femur Length										
Scapular Shape Index (%)				23.77	<.0001					
Height/Width										
Clavicle Index (%)				6.13	.0008					
Calvicle Length/((Acetabulum Height*Width) ^{1/2})										
Humerus Gracility Index (%)				55.88	<.0001					
Humerus Length/((circumference*breadth*depth) ^{1/3})										
Ulna Gracility Index (%)				49.02	<.0001					
Ulna Length/((circumference*breadth*depth) ^{1/3})										
Olecranon Length Index (%)				25.65	<.0001					
Olecranon Process Length/((Acetabulum Height*Width) ^{1/2})										
Radius Gracility Index (%)									57.17	<0.0001
Radius Length/((circumference*breadth*depth) ^{1/3})										
Lumbar Index (%)									4.046	NS
(Lumbar Height/Thoracic Height)										

Mean, standard deviation, tests for normalcy (W-Stat), and tests for intergroup differences. Parametric variables were compared using the ANOVA F-Ratio. The nonparametric variables were compared using the Kruskal-Wallis χ^2 .

Dataviewer (Hedrick, 2008) in MATLAB. All angular movements were measured in degrees ($^{\circ}$). To make joint movements comparable between strides, different individuals, and different species, all joint data were scaled as a percentage of support phase. Following Larson et al. (2000), shoulder angles were measured relative to the vertical axis of the shoulder joint [i.e., when the arm passed directly above the shoulder joint this was considered the neutral position (0°)]. Angles greater than 0° represent shoulder protraction, while angles less than 0° represent shoulder retraction. Elbow angles always reflected flexion, where 180° represents maximum elbow extension.

Wrist measures required additional processing depending upon the way the animal grasped the support. During arm-swinging, animals are known to grasp the support with either a pronated or supinated hand position (Schmitt, Zeininger, & Granatosky, 2016). While

these hand postures still provide a measure of radial and ulnar deviation, the order and magnitude of radial and ulnar deviation likely changes drastically. To make the proper adjustments for measures of wrist movements, the position in which the animal grasped the support was recorded for every step. In the wrist, these positions were broken down into two categories for comparison: (1) supinated hook grasps (animals grasp the support between the first and second digit or as a hook with a supinated hand); and (2) pronated hook grasps (animals grasp support between the first and second digit or as a hook with a pronated hand). For both grasp types, wrist angles were measured based on the position of the wrist relative to the POC with the support and the elbow. Neutral position (180°) was defined as the point in which the wrist was in line with the point-of-contact and the elbow. During supinated and pronated

TABLE 4 Morphological data post-hoc tests

	<i>Nasalis larvatus</i>	<i>Presbytis rubicunda</i>	<i>Pygathrix sp.</i>	<i>Trachypithecus sp.</i>
Intermembral Index (%)	A	C*	A*	B*
Brachial Index (%)	C	A*	B*	D*
Crural Index (%)	B	A	B	B
Scapular Shape Index (%)	A	B	A	B
Clavicle Index (%)	AB	B	A	B
Humerus Gracility Index (%)	B	BC	A	C
Ulna Gracility Index (%)	B	B	A	C
Olecranon Length Index (%)	B	AB	C	A
Radius Gracility Index (%)	B	B*	A*	C*
Lumbar Index (%)	A	A*	A*	A*

Connecting Letters Report where levels not connected by the same letter are significantly different ($P < .01$). Group Designations are A, B, C, and D. All parametric variables were compared using Tukey HSD tests. Nonparametric variables with asterisks were compared using Wilcoxon Rank-Sum tests. For taxa that have two letters, they belong to both letter levels.

hook grasps, wrist angles greater than 180° represent radial deviation, while angles less than 180° represent ulnar deviation.

Additionally, we sought to determine if animals used swing periods similar to those predicted by simple pendular models. To calculate the observed swing period ($\text{Period}_{\text{obs}}$), we determined from video-recordings the period necessary for the animal's center of mass (COM) to reach the starting and ending apex position of its swing arc. As direct access to the animals to take the measurements necessary to calculate true COM position (Crompton et al., 1996; Larson & Demes, 2011; Raichlen, 2004; Young et al., 2007; Young, 2012) was prohibited, and only lateral view films were available (Michilsens et al., 2011), we predicted COM position utilizing centroid shape analysis using a modified MATLAB program (Kloefkorn et al., 2016). Using this program, we were able to track the position of the approximated COM throughout each support phase. Although this method does not provide an exact position of the COM, our results on its location were consistent with estimates provided by Michilsens et al. (2011) for hylobatids and Larson and Demes (2011) for *Ateles*. The predicted swing period ($\text{Period}_{\text{pred}}$) was calculated using:

$$\text{Period}_{\text{pred}} = \pi \sqrt{\frac{L}{g}}$$

where g is the acceleration due to gravity (i.e., 9.81 m/s^2) and L is calculated as the length of the forelimb at mid-support from the POC to the approximated COM position calculated above. We conducted a Mann-Whitney U test to analyze the likelihood of $\text{Period}_{\text{obs}}$ and $\text{Period}_{\text{pred}}$ being similar to each other for each species separately.

All force data were corrected to indicate the applied force by the animal and were normalized for the direction of travel, differing body mass, orientation, and whether the limb that touched the instrumented portion of the runway was left or right. This resulted in comparable force curves that all displayed vertical force as a positive value on the vertical axis, braking force as a negative value on the fore-aft axis, propulsive force as a positive value on the fore-aft

axis, medially oriented force (i.e., the animal applied a medially directed force to the substrate) as a negative value on the mediolateral axis, and laterally oriented force (i.e., the animal applied a laterally directed force to the substrate) as a positive value on the mediolateral axis.

From these data, eight variables were calculated for each limb: (1) peak vertical force (Vpk); (2) peak propulsive force (Ppk); (3) peak braking force (Bpk); (4) peak medial force (Mpk); (5) peak lateral force (Lpk); (6) propulsive impulse (PI); (7) braking impulse (BI); and (8) net fore-aft horizontal impulse (HI). Additionally, the time at which Vpk, Ppk, Bpk, and the propulsive to braking transition (P/B) occurred was also recorded during each support phase. The PI, BI, and HI were measured as a specific area under the force-time curve in the fore-aft (PI and BI) component of the substrate reaction force. The HI provides a means for differentiating the overall braking or propulsive role of the limb during particular locomotor behaviors (Demes et al., 1994). Positive HI values indicate a net propulsive limb while negative values indicate a net braking limb (Demes et al., 1994; Ishida et al., 1990; Kimura et al., 1979). To make comparisons between subjects of differing body masses, Vpk, Ppk, Bpk, Mpk, and Lpk forces were analyzed in multiples of body weight (%bw), and PI, BI, and HI were analyzed in body weight seconds (%bws).

To further assess whether animals used pendular mechanics during arm-swinging, we compared the observed Vpk force to the predicted Vpk force (Vpk_{pred}). The Vpk_{pred} force was calculated as:

$$\text{Vpk}_{\text{pred}} = mg + m \left(\frac{v^2}{L} \right)$$

where m is the mass of the animal, g is the acceleration due to gravity (i.e., 9.81 ms^{-2}), v is velocity collected at mid-support, and L is calculated as the length of the forelimb at mid-support from the POC to the approximated COM position calculated above. We conducted a Mann-Whitney U test to analyze the likelihood of Vpk and Vpk_{pred} forces being similar to each other for each species separately.

All kinematic and kinetic statistical tests were conducted using JMP Pro ver. 12 (SAS Institute Inc., Cary, NC). Prior to any statistical comparisons, kinetic variables including body weight normalized Vpk, Ppk, Bpk, Mpk, Lpk forces, and PHIs, BHIs, and HIs collected during arm-swinging were compared with the corresponding speed using a regression analysis to determine if the variables of interest were influenced by variation in speed within the sample. No significant relationship between speed and any of the kinetic variables collected were observed. Therefore, a Kruskal-Wallis test was used to determine whether there were statistically significant differences across species.

As another means of assessing the similarity between forelimb loading patterns between species during arm-swinging and whether species are moving similarly to a simple pendular model, the timing of at which Vpk, Ppk, Bpk, and P/B occurred within support phase was compared for each species. An ANOVA was used to determine whether the timing of forelimb loading patterns varied significantly between arm-swinging in different species.

From the scaled data on joint movements, the general pattern of shoulder, elbow, and wrist angular positions were described qualitatively throughout support, but compared statistically only at specific intervals (i.e., touchdown, mid-support, and lift-off). In addition to overall characterization of movement, joint excursion (maximum change in joint angle) was collected for each joint for each species throughout the support phase. Angular joint movements and joint excursion of each species were compared to each other using a Kruskal-Wallis test to determine whether kinematics vary significantly between arm-swinging in different species.

Post-hoc analyses were made between each species, and all p -values were adjusted by the Bonferroni method to account for type I error resulting from multiple comparisons. Although there has been considerable discussion concerning the possibility that adjustments for multiple comparisons like the Bonferroni method are too conservative (Nakagawa, 2004), this study retains their use to make the most robust argument possible, while acknowledging that significance values may be a conservative estimate.

3 | RESULTS

3.1 | Morphology

The results of ten variables were compared between groups and all but one yielded a significant ANOVA F-ratio, or Kruskal-Wallis χ^2 (Table 3). These indices are also graphed as boxplots in Figures 1 and 2. Of the ten indices, differences in lumbar index was not significant which indicates that across the Asian colobines sampled here, there are no proportional shape differences in the torso (Figure 1E). The remaining nine ratiometric variables from the appendicular skeleton yielded significant p -values indicating between group differences. In Figure 1 the primates in this study are accompanied by values of other suspensory taxa available in the literature for comparison (Erikson, 1963; Schultz, 1930). Figure 2 lacks these comparative reference points. Tukey-Kramer and Wilcoxon Rank-Sum post hoc tests demonstrate how these inter-Genus differences are ordered (Table 4). In this connecting letters

report levels not connected by the same letter are significantly different from each other ($p < .01$). Group Designations A, B, C, and D are ordered according to levels of highest magnitude to the lowest levels, per variable.

Several of these variables indicate that *Nasalis* and *Pygathrix* exhibit the expected morphology for suspensory taxa compared to known arboreal quadrupeds as exhibited by the genus *Trachypithecus*. Intermembral index (Figure 1A), brachial index (Figure 1B), and scapular shape index (Figure 1D) each show *Nasalis* and *Pygathrix* with significantly longer forelimbs, forearms, as well as narrower scapulae. These results plot the douc in an intermediate morphospace between quadrupeds like *Trachypithecus* and brachiators such as *Hylobates* and *Ateles*. In contrast, the douc lumbar vertebral region is relatively long (Figure 1E) and this is different from a known brachiator, *Ateles*, that has a demonstrably shorter relative lumbar length. The smaller langur (*Presbytis rubicunda*) shows a relatively low intermembral index (Figure 1A), but the forelimb has a uniquely elongated antebrachial component (Figure 1B). This distal elongation is also observed in the hindlimb as the crural index shows a significantly lengthened tibial component compared to the other taxa in this study (Figure 1C). The additional indices in Figure 2 are aligned with this trend, that the douc has a morphology consistent with a suspensory phenotype more so than any other Asian colobine in this study (Table 4). *Pygathrix* shows the most elongated measures in clavicle index (Figure 2A). *Nasalis* also has a relatively long clavicle but since its group designation is AB it can be homogeneously grouped with either the suspensory *Pygathrix* (group A) or the more quadrupedal *Trachypithecus* and *Presbytis* (group B).

Similar to the clavicle index the humerus (Figure 2B), radius (Figure 2D), and ulna (Figure 2E) gracility measures demonstrate that *Pygathrix* has a thinner and more elongated element than the quadrupedal monkeys and the other suspensory taxon *Nasalis* (Table 4). *Nasalis* does exhibit more gracile forelimb elements than *Trachypithecus* but *Pygathrix* expresses an even more derived suspensory phenotype. *Presbytis rubicunda* here groups with *Nasalis* in humerus, radius, and ulna gracility indices despite it being a more saltatory, and presumably non-suspensory monkey. *Pygathrix* is also more derived in a suspensory direction by displaying the lowest olecranon process length index (Figure 2C). *Nasalis* shows a slightly longer olecranon, but it is still shorter than the quadrupedal genus *Trachypithecus* which possess an elongated triceps muscle insertion. *Presbytis* is intermediate between *Nasalis* and *Trachypithecus*.

3.2 | Kinetics

In total, 36 single contact forelimb forces were collected and analyzed. Table 5 and Figure 3 summarize the number of steps collected for each species, speed, and data for Vpk, Bpk, Ppk, Mpk, Lpk, BI, PI, and HI. Data for Vpk, Lpk, and PI displayed non-normal distributions and unequal variances, therefore non-parametric statistics were used for these comparisons. No significant relationship between normalized speed and any of the kinetic variables collected were observed.

The vertical force component for all species was characterized by a single peak that occurred on average at $42.76\% \pm 5.53$ of support

TABLE 5 Summary statistics for forelimb loading data (mean \pm standard deviation) during arm-swinging in *Hylobates moloch*, *Pygathrix nemaeus*, and *Ateles fusciceps*

Species	N	Speed (m/s)	Ppk (%bw)	Bpk (%bw)	Pl (%bws)	Bl (%bws)	Hi (%bws)	Mpk (%bw)	Lpk (%bw)	Vpk (%bw)
<i>Ateles fusciceps</i>	9	1.27 \pm 0.19	29.87 \pm 5.41	-34.20 \pm 8.73	12.18 \pm 5.69	-11.19 \pm 6.74	0.99 \pm 4.68	-17.23 \pm 7.27	5.49 \pm 8.85	126.03 \pm 25.03
<i>Hylobates moloch</i>	13	1.23 \pm 0.20	45.59 \pm 10.19	-46.27 \pm 14.89	12.71 \pm 6.98	-12.73 \pm 7.92	-0.02 \pm 4.62	-15.48 \pm 6.67	5.98 \pm 3.39	167.51 \pm 6.42
<i>Pygathrix nemaeus</i>	14	1.12 \pm 0.24	30.34 \pm 6.80	-26.59 \pm 12.83	7.65 \pm 4.16	-7.29 \pm 5.66	0.36 \pm 3.97	-19.39 \pm 7.17	7.47 \pm 4.91	130.86 \pm 20.55

Ppk Peak propulsive force.

Bpk Peak braking force.

Pl Propulsive impulse.

Bl Braking impulse.

Mpk Peak medial force.

Lpk Peak lateral force.

Vpk Peak vertical force.

phase for *P. nemaeus*, 42.89% \pm 5.63 of support phase for *H. moloch*, and 48.71% \pm 9.59 of support phase for *A. fusciceps*. No significant difference in the occurrence of Vpk was observed between any of the species. The magnitude of Vpk was significantly ($p \leq .001$) higher in *H. moloch* compared to the other two species. No significant difference in Vpk magnitude was observed between *P. nemaeus* and *A. fusciceps* (Figure 3). In all three species, Vpk was significantly ($p \leq .03$) higher than Vpk_{pred} (Figure 4A).

For all species, fore-aft forces consisted of a propulsive force that occurred early in support phase as the limb first made contact with the support. This propulsive force reached its maximum on average at 24.42% \pm 8.01 of support phase for *P. nemaeus*, 25.21% \pm 7.85 of support phase for *H. moloch*, and 27.30% \pm 11.46 of support phase for *A. fusciceps*. This propulsive force continued until the P/B, which occurred on average at 49.35% \pm 7.26 of support phase for *P. nemaeus*, 50.01% \pm 6.98 of support phase for *H. moloch*, and 53.27% \pm 10.10 of support phase for *A. fusciceps*. Throughout the remainder of support phase the forelimb of all three species exerted a braking force, which reached its maximum on average at 73.03% \pm 7.78 of support phase for *P. nemaeus*, 71.90% \pm 8.00 of support phase for *H. moloch*, and 72.41% \pm 11.30 of support phase for *A. fusciceps*. No significant difference in the occurrence of the Ppk, Bpk, or P/B was observed between any of the species. In contrast, the magnitude of Ppk and Bpk force did vary significantly between the three species. *Hylobates moloch* applied significantly greater ($p \leq .001$) Ppk forces than both *P. nemaeus* and *A. fusciceps*, and significantly greater ($p \leq .001$) Bpk forces compared to *P. nemaeus*. No significant difference was observed in Ppk and Bpk force between *P. nemaeus* and *A. fusciceps*, and in Bpk between *H. moloch* and *A. fusciceps*. In terms of peak braking and propulsive impulses, *P. nemaeus* and *H. moloch* are more different from each other than either is compared to *A. fusciceps*. The Pl, Bl, and HI were similar between all three species, and no significant differences were observed. Net HI for all three species was relatively close to zero indicating an even exchange of propulsive and braking forces.

In all species the mediolateral force component was dominated by medially applied forces. This means that individuals directed higher magnitude forces medially to the substrate during support phase. These forces were lower in comparison to vertical and fore-aft forces. In general Mpk and Lpk were highly variable, and no significant differences between the three species were observed.

3.3 | Kinematics

In total, 60 strides were used for kinematic analyses. Table 6 summarizes the number of strides collected for each species, and data for Period_{obs}, Period_{pred}, touchdown angle, mid-support angle, end of support phase angle, and joint excursion. Overall, the kinematics of douc monkey suspensory locomotion were more similar to that observed for *Ateles* and *Hylobates* in the proximal regions of the forelimb. In the distal region (i.e., the wrist) there were differences that contrast drastically with the other brachiators in this study. Mechanical convergence across species in the shoulder was marked by a high level of protraction and retraction throughout the support phase. No significant

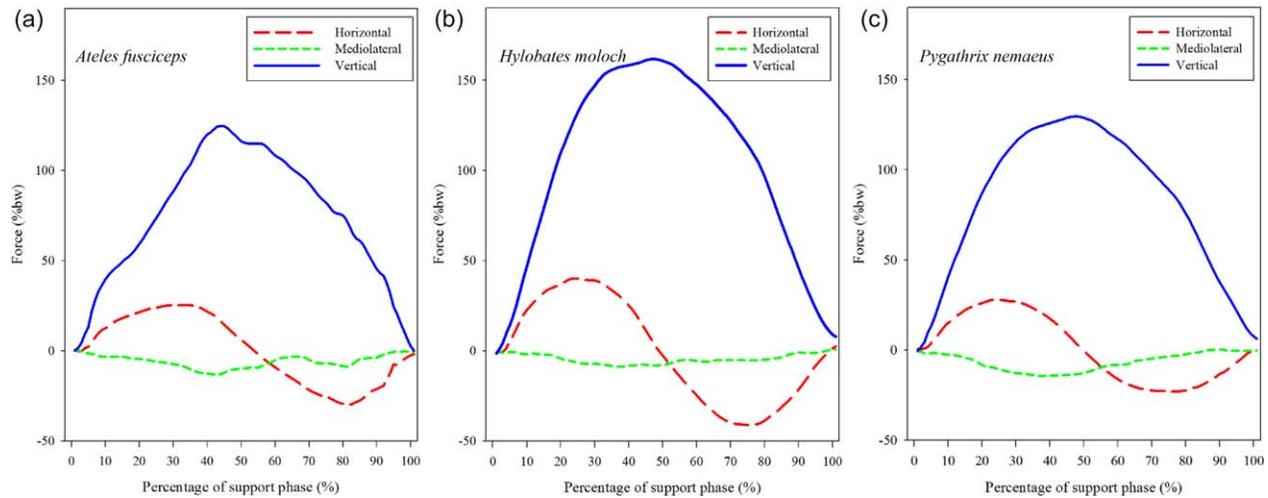


FIGURE 3 Representative forelimb force traces from (a) *Ateles fusciceps*, (b) *Hylobates moloch*, and (c) *Pygathrix nemaeus* during arm-swinging. All data are presented as a percentage of the animal's body weight (%bw). Contact duration has been converted to a percentage of support phase (%) to make force traces comparable across limbs

difference was observed in shoulder angle between the three species at touchdown or mid-stance, but at the end of support phase *A. fusciceps* retracted the shoulder to a significantly ($p \leq .001$) greater degree than *H. moloch* and *P. nemaeus*. All three species demonstrated significantly different ($p < .019$) levels of shoulder excursion from each other, with *A. fusciceps* exhibiting the most and *H. moloch* the least (Figure 5).

Although flexion at the elbow was constrained to a narrow range of motion, all three species demonstrated somewhat differing patterns of elbow movement throughout support phase. At touchdown, all three species demonstrated extended elbow positions, with the only statistical difference ($p = .022$) observed resulting from generally greater levels of elbow extension in *Ateles* compared to *Hylobates*. As support phase continued, both *H. moloch* and *A. fusciceps* demonstrated

marked elbow flexion, but the time at which this flexion occurred varied between the two species. *Hylobates moloch* did not begin to flex this joint until midway through support phase, while *A. fusciceps* began flexing the elbow starting earlier in support. *Pygathrix nemaeus* did not move its elbow in this way, and instead maintained an extended elbow position throughout. These varying patterns of elbow movement between the three species resulted in statistical differences throughout support phase. At mid-stance, *A. fusciceps* demonstrated statistically ($p < .003$) greater levels of elbow flexion than either *P. nemaeus* or *H. moloch*. No significant difference was observed in elbow flexion between *P. nemaeus* and *H. moloch* at mid-stance. Near the end of support phase, both *A. fusciceps* and *H. moloch* demonstrated statistically ($p \leq .001$) greater levels of elbow flexion compared to what was

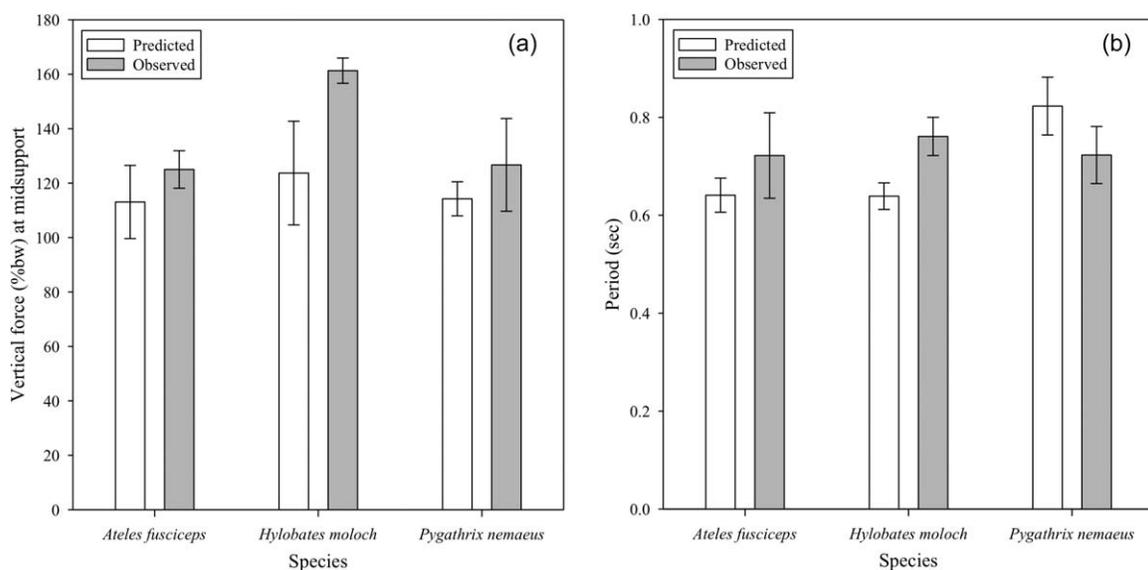


FIGURE 4 Comparison between the (a) predicted and observed peak vertical force measured as a percentage of body weight (%bw) at mid-support and the (b) predicted and observed swing period measured in seconds. All predicted values are based on the movements of a simple pendulum. In both comparisons, simple pendular models fail to predict observed values

TABLE 6 Summary statistics for forelimb joint angles and excursions (mean \pm standard deviation) during arm-swinging in *Hylobates moloch*, *Pygathrix nemaeus*, and *Ateles fusciceps*

Species	N	Joint	Touchdown angle (°)	Mid-stance angle (°)	End of support phase angle (°)	Joint excursion (°)
<i>Ateles fusciceps</i>	19	Shoulder	53.92 \pm 13.62	-2.60 \pm 9.42	-69.73 \pm 7.23	124.97 \pm 15.55
		Elbow	174.10 \pm 5.52	163.94 \pm 6.10	157.58 \pm 6.29	26.45 \pm 4.39
		Wrist	191.40 \pm 14.63	179.55 \pm 10.83	155.23 \pm 17.68	55.89 \pm 16.67
<i>Hylobates moloch</i>	13	Shoulder	38.27 \pm 10.10	-4.93 \pm 15.75	-44.31 \pm 8.41	89.00 \pm 13.56
		Elbow	166.17 \pm 5.64	169.61 \pm 3.38	153.81 \pm 4.81	25.41 \pm 3.48
		Wrist	184.59 \pm 8.61	180.58 \pm 9.56	176.27 \pm 2.42	23.34 \pm 4.65
<i>Pygathrix nemaeus</i>	28	Shoulder	50.34 \pm 10.43	-2.53 \pm 5.42	-50.59 \pm 8.23	101.36 \pm 10.62
		Elbow	168.56 \pm 9.90	173.09 \pm 3.76	166.13 \pm 7.28	18.54 \pm 6.47
		Wrist	170.94 \pm 14.92	192.78 \pm 15.44	202.16 \pm 27.24	53.64 \pm 13.42

observed in *P. nemaeus*. No significant difference was observed in elbow flexion between *A. fusciceps* and *H. moloch* near the end of support phase. Joint excursion at the elbow was significantly higher ($p \leq .001$) in both *A. fusciceps* and *H. moloch* compared to *P. nemaeus*. No significant difference was observed in elbow joint excursion between *A. fusciceps* and *H. moloch* during support phase.

During arm-swinging, *P. nemaeus* grabbed the support with pronated hook grasps. This means that as *P. nemaeus* grabbed onto the support the wrist was first ulnarly deviated, and subsequently radially deviated throughout the remainder of limb contact. Both *H. moloch* and *A. fusciceps* used supinated hook grasps to grab onto the support, but positioning of the wrist varied substantially for both species. In *H. moloch* the wrist demonstrated very little movement, and maintained a position near neutral throughout support phase. In contrast, *A. fusciceps* used radially deviated wrist positions at touchdown, and subsequently ulnarly deviated its wrist throughout the remainder of support phase. Because *P. nemaeus* used pronated hook grasps during arm-swinging, statistical differences ($p \leq .001$) in wrist angle between the other two species were observed at touchdown, mid-stance, and near the end of support phase. The use of supinated hook grasps observed in *H. moloch* and *A. fusciceps* resulted in similar wrist angles at touchdown and mid-stance, but because of the increased ulnar deviation in *Ateles*, wrist angles between the two species varied significantly ($p = .03$) near the end of support phase. Overall levels of wrist excursion were significantly higher ($p \leq .001$) in *A. fusciceps* and *P. nemaeus* compared to *H. moloch*. No significant difference was observed in wrist joint excursion between *A. fusciceps* and *P. nemaeus* during support phase. In all three species $\text{Period}_{\text{obs}}$ varied significantly ($p \leq .001$) from $\text{Period}_{\text{pred}}$. In *H. moloch* and *A. fusciceps* $\text{Period}_{\text{obs}}$ was longer than $\text{Period}_{\text{pred}}$. The opposite pattern was observed in *P. nemaeus* (Figure 4B).

4 | DISCUSSION

4.1 | Index and mechanical data

The douc monkey (genus *Pygathrix*) shows very clear form and function relationships for orthograde suspensory behavior. The overall shape of

the forelimb is common with other taxa in the family Colobinae likely to be suspensory (e.g., *Nasalis*), especially in the pectoral girdle. Furthermore, the suspensory phenotype in the douc forelimb is congruent with a known brachiator like the gibbon in its brachial index, crural index, and scapular shape, and intermediate toward gibbons in its intermembral index. This finding is consistent with the kinematic results because there are a remarkable amount of similarities between continuous contact arm-swinging behaviors between the three species. In general, the kinetics and kinematics of arm-swinging observed in this study approximate the behavior of a simple pendulum, but vary in important ways. Joint excursions are highest in all three species at the shoulder joint, followed by movements at the wrist (see below for focused discussion on the kinematics of the wrist). The elbow demonstrates some movement, especially in *Ateles* and *Hylobates*, but for the most part stays extended (the relatively short olecranon process probably plays a role in this). Taken together, this combination of joint movement allows arm-swinging animals to maintain relatively long effective limb length and achieve approximately equal levels of forelimb protraction and retraction, both of which are expectations of efficient pendular movement. Interestingly, however, no species demonstrated swing periods consistent to what is expected from a simple pendulum. This finding is in accordance with Preuschoft and Demes (1984) and Swartz (1989), and adds data to the interpretation that considering arm-swinging as a simple pendulum is incomplete (Bertram & Chang, 2001; Bertram et al., 1999; Bertram, 2004; Michilens et al., 2011; Preuschoft & Demes, 1985; Swartz, 1989). Our animals were allowed to locomote at self-selected speeds and handhold distances, yet none matched swing periods predicted by their forelimb lengths at mid-support. With this in mind, we adopt the opinion that arm-swinging animals are selecting mechanical strategies that promote flexibility in locomotor path choice rather than energetic efficiency (Bertram et al., 1999; Parsons & Taylor, 1977; Swartz, 1989); an important consideration for animals moving in a discontinuous complex arboreal environment.

Limb loading patterns between species were similar, and for the most part approximated the external forces expected of a simple

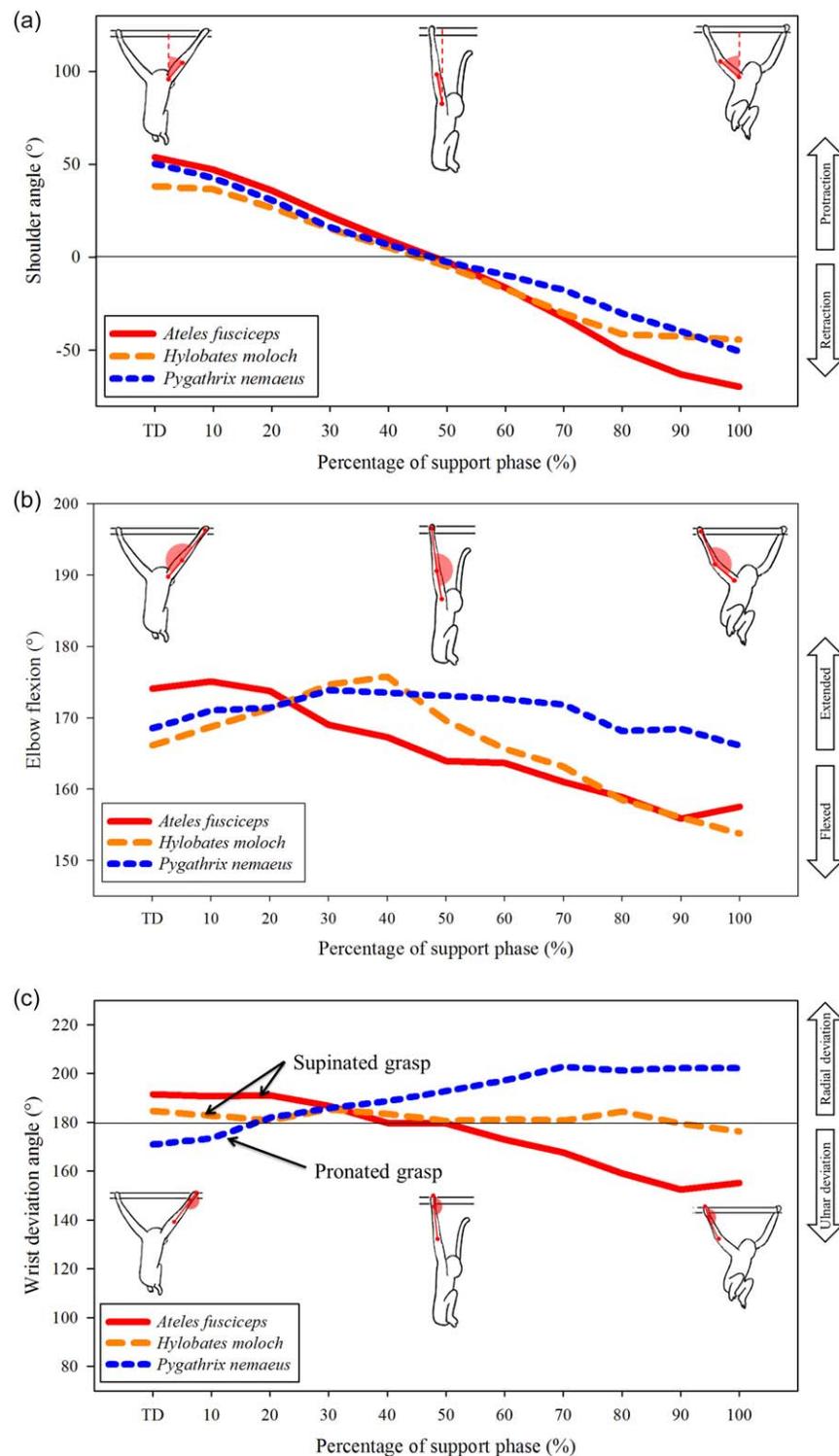


FIGURE 5 Patterns of mean (a) shoulder, (b) elbow, and (c) wrist movement ($^{\circ}$) observed during arm-swinging in *Ateles fusciceps*, *Hylobates moloch*, and *Pygathrix nemaeus*. All angular measurements are reported in degrees. (c) During arm-swinging, animals can grasp the support with a supinated hand position (as do *A. fusciceps* and *H. moloch*) where the substrate is grasped on the same side as the arm. But some animals (*P. nemaeus*) reach under the pole and grasp the contralateral side of the substrate relative to the arm. Note that *Hylobates* shows little wrist deviation during support phase, whereas *Ateles* and *Pygathrix* show a great deal of wrist deviation despite having different grips. In pronated hand positions, the wrist is first ulnarly deviated, and then subsequently radially deviated throughout the remainder of the support phase. For supinated hand positions, the pattern is opposite

pendulum. Mediolateral forces were low, and fore-aft forces were characterized by a propulsive component as the limb first touched down followed by a braking component in the latter half of support phase. The P/B occurred at approximately mid-support, and the net fore-aft impulse showed no braking or propulsive tendency in any of the species. In all species, Vpk force occurred at approximately mid-support, but was higher than anticipated based on simple pendular mechanics. This finding was also observed by Bertram et al. (1999), and has been interpreted as a mechanism to smooth out forces and prevent potential collisional losses. Despite the short-armed douc monkey's lower than predicted swing period, it still demonstrates higher than predicted mid-swing forces. The magnitude of observed relative to predicted forces is on par with *Ateles* and not as great as in longer armed *Hylobates*. In this regard, the reality of suspensory primate arm-swinging does not include the sudden and sharp applications of force predicted if the system were to behave as a simple pendulum.

Based on the experimental data collected in this study, there appears to be no consistent pattern of wrist movement observed during arm-swinging. The functional data from the *Pygathrix* wrist show a uniquely pronated grasp type with significant radial deviation in the latter half of the support phase. *Ateles* and *Hylobates* used a supinated grasping posture, but also did not deviate at all (i.e., remained neutral like *Hylobates*) or deviated in an ulnar direction (like *Ateles*). This high level of mechanical flexibility potentially indicates that selection is not driving wrist movements during brachiation to reach some convergent optimum. Instead, there appear to be many solutions as to how to position the wrist during arm-swinging. This finding is in line with Larson's (1998) observation that compared to the proximal elements of the forelimb, the wrist joint shows few examples of anatomical convergence among arm-swinging primates. Unfortunately, the skeletal data to test this hypothesis were not complete at the distal radius and ulna and so whether *Pygathrix* is unique among colobines cannot be determined. A phylogenetic and comparative assessment exploring the strength of selection across the postcranial skeleton of arm-swinging primates would provide a quantitative means of testing this claim.

While variation in wrist movements are high, all other kinetic and kinematic variables collected during arm-swinging in this study appear to be fairly consistent across taxa, and vary largely in magnitude rather than timing or pattern. This finding might indicate that there are more limited functional solutions to the challenges associated with arm-swinging, especially in more proximal regions of the forelimb such as the shoulder and elbow. Selection pressures may drive arboreal, large-bodied anthropoid species to a common pattern of mechanical convergence (Granatosky, 2015; Michilens, D'août, & Aerts, 2012; Swartz, 1989; Turnquist et al., 1999). This study provides direct evidence demonstrating the mechanical underpinning of why arm-swinging animals all converge on a similar morphological suite.

4.2 | Semibrachiation as a category

The genus *Pygathrix* exhibits several forelimb characteristics that are intermediate between true brachiators and other non-suspensory catarrhine taxa. In addition to this, clear functional similarities with

brachiators are also found in this genus. While the magnitudes measured throughout the locomotor cycle are broadly similar between *Ateles*, *Hylobates*, and *Pygathrix*, how the variation in magnitude is distributed across these three taxa helps clarify the concept of the "semi-brachiator" locomotor category. *Pygathrix* and *Ateles* are most similar in certain kinetic and kinematic values and so are *Ateles* and *Hylobates*. However, *Pygathrix* and *Hylobates* tend to be least similar (Tables 5 and 6). Earlier comparisons between the New World and Old World semi-brachiators involved two primates at opposite ends of this intermediate spectrum, *Ateles* and *Colobus* (Mittermeier & Fleagle, 1976). While it is true that colobines like *Colobus*, *Presbytis*, and *Trachypithecus* ought not to be considered in this group, the douc monkey (*Pygathrix*) and New World taxa like *Ateles* fit into an intermediate grade between a basic catarrhine leaping monkey and orthograde, suspensory taxa like *Hylobates*. However, in terms of intermediate suspensory locomotor types (i.e., semibrachiators), there appear to be alternate versions of it as expressed by *Ateles* and *Pygathrix*. Furthermore, even in the New World group of intermediate suspensory taxa there appear to be important kinetic and kinematic differences between *Ateles* and another New World semibrachiator *Lagothrix* (Schmitt et al., 2005; Turnquist et al., 1999). For these reasons, the term "semibrachiation" is invalid if it describes the type of arm-swinging practiced by both *Ateles* and *Pygathrix*. Ultimately, each of these "semibrachiators" brachiate but they do so in modes that are different manifestations of a common pattern.

The shift to specialized suspensory locomotion (i.e., orthograde arm-swinging) is interpreted as a major transition during the evolution of primates, and is seen by many (Churchill et al., 2013; Green & Alemseged, 2012; Rose, 1983; Stern & Oxnard, 1973; Stern, 1975, 2000) as a likely precursor prior to the acquisition of bipedalism in early hominins (Keith, 1923; Straus, 1949; Tuttle, 1975). However, the fossil discovery *Ardipithecus ramidus* has been interpreted to be a generalized catarrhine without any suspensory adaptations, and instead is claimed to have been an above-branch-quadruped more like *Proconsul* rather than any crown ape (Lovejoy, 2009; Lovejoy, Simpson, White, Asfaw, & Suwa, 2009; Lovejoy, Suwa, Simpson, Matternes, & White, 2009; White et al., 2009). It is rational to assume that a more quadrupedal mode of locomotion that involved upright and inverted pronograde positional behaviors preceded any shift, and the evolution of orthograde in apes likely transitioned through various categories that preceded modified or true brachiation (Cartmill & Milton, 1977; Granatosky, Tripp, Schmitt, et al., 2016; Granatosky, 2016; Mendel, 1979; Rose, 1983). Unfortunately, there is not a living example of what this pre-ape locomotor behavior might look like. Taking a closer look at the large-bodied Asian colobines like *Pygathrix* represents an intriguing antecedent condition for the types of arm swinging locomotion predicted to be found in stem hominoids.

4.3 | Fossil interpretation

While it is obvious that arm-swinging has evolved independently between the hominoids, Asian colobines, and atelids, there is still considerable debate concerning the evolution of suspensory locomotion within the hominoids throughout the Miocene. Attempting to assess

character trait evolution within the hominoids is beyond the scope of this study, but because three distantly related anthropoid species have converged on similar kinematic and kinetic patterns, each of these taxa can inform our understanding of this transition in apes. More distal forelimb regions display greater variation in movement perhaps because the shoulder and elbow perform in such a stereotypic way for any larger anthropoid attempting below branch suspension and travel. The morphology data are not discordant with this interpretation since *Pygathrix* and *Nasalis* are more dissimilar in the gracility indices of the brachium and antebrachium than they are in the pectoral girdle. Future analyses aiming to address the evolution of suspensory locomotion in hominoids should consider this high level of mechanical convergence as a potentially confounding variable in the reconstruction of locomotor trait evolution based on proximal forelimb features. More distal regions ought to demonstrate greater uniqueness and thus may be more useful for phylogenetic parsimony analysis. Additionally it could mean that certain Miocene ape taxa might be excluded as being closest to the human-chimp last common ancestor if the distal elements showed rather derived morphology.

The genus *Pygathrix* provides an alternative stem hominoid locomotor model to the one represented by *Ateles*. The douc lumbar index (Figure 1E) is not intermediate between apes and atelids showing a relatively long lower back, similar to the other colobines in this sample. An interpretation of this finding is that the suspensory phenotype found in the douc monkey is “overprinted” on top of a quadrupedal/leaper/climber body type. Crural Index (Figure 1C) also remains more uniform throughout Asian colobines making the douc distinct as an arm-swinging primate. For ecological reasons, one can suggest that other supposed “semibrachiators” like *Nasalis* and *Rhinopithecus* have a more derived habitat relative to truly forest living arboreal catarrhines and thus are not suitable stem hominoid models. These large-bodied genera, some with more robust limbs are found in mangrove settings or at higher altitude and colder climates where a component of locomotion is terrestrial (Boonratana, 1993; Kawabe & Mano, 1972; Ruhiyat, 1986; Zhu, Garber, Bezanson, Qi, & Li, 2015). Likewise *Presbytis* is not the best candidate as it differs from the other genera with body sizes that are smaller and locomotor behavior that is characterized by above-branch quadrupedalism with leaping and climbing (Fleagle, 1977a; 1977b; 1978). Finally, the African leaf-monkey genus *Colobus* does not engage in a significant amount of suspensory behavior (Mittermeier & Fleagle, 1976; Morbeck, 1977, 1979; Struhsaker, 1975) and thus cannot serve as a model either. The morphological data also demonstrate that *Presbytis* and *Trachypithecus* are Asian colobines with a different locomotor phenotype than *Pygathrix* or *Nasalis*. *Presbytis rubicunda* in this study shows similar limb dimensions to published data on *P. melalophos*. Our results suggest that *P. rubicunda* has unusually elongated antebrachial elements and this confers a high brachial index (114%) despite a low intermembral index (76%). The gracility indices of the forelimb are intermediate and group with *Nasalis*. Data from *P. melalophos* are informative here since Fleagle also reported a similar locomotor phenotype (Fleagle, 1977a, 1977b, 1978). In his studies the functional repertoire for *P. melalophos* expressed less

quadrupedal climbing and more vertical clinging and leaping as well as more forelimb suspension when compared to *P. obscura*. *Trachypithecus* on the other hand is another Asian colobine in the morphological sample that contrasts with all other taxa. Anatomically this taxon displays a more generalized quadrupedal monkey phenotype. In earlier studies of locomotor behavior, *Trachypithecus* species available at the EPRC support this quadrupedal categorization (Byron & Covert, 2004; Covert et al., 2004; Stevens et al., 2008; Wright et al., 2008).

Having an intermediate type of locomotor behavior that overlaps with true brachiators as well as quadrupedal catarrhines is also predicted for a group designated “pro-brachiation” that purportedly includes ancestral hominoid taxa like *Proconsul* (Napier, 1963). This fossil taxon was a large, generalized, pronograde ape without any clear suspensory adaptations like other stem hominoids of the Miocene. Of these stem hominoids *Morotopithecus* is notable for perhaps the earliest demonstration of two hominoid crown-type adaptations including a stiffened lower back and mobile ape-like shoulder (MacLatchy, 2004). Many of these taxa represent intermediate stages toward the true brachiation of more derived hominoids (like chimps and gibbons) supporting the notion that crown hominoid post-cranial adaptations evolved in a mosaic fashion (Young & MacLatchy, 2004; Young, 2008). Recent work on an extinct stem catarrhine taxon from the European Miocene describes functional similarities with atelid monkeys of the New World that are interpreted to mean that *Pliopithecus vindobonensis* likely performed forelimb suspensory locomotion (Arias-Martorell et al., 2015; Rein et al., 2015). Most recently reports of a more modern stem hominoid from the European Miocene describe *Pliobates cataloniae* as an arboreal, small-bodied, quadruped with a wrist that permitted greater rotation (Alba et al., 2015; Benefit & McCrossin, 2015). Across the European and African Miocene it is probable that suspensory adaptations evolved in parallel but differed most in aspects of wrist functional morphology. Including *Pygathrix* in these types of analyses could help rule out certain suspensory phenotypes that involve radial deviation and pronated grasping, as uniquely seen in douc monkeys. If hominin bipedalism is preceded by an African great ape with ulnar deviation and supinated grasping, a distinctly non-*Pygathrix* distal forelimb morphology should be expected. It is hoped that the results presented here, and the availability of the EPRC skeletal collection to future investigators, help inform more complete studies of primate morphology.

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