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The skeletal anatomy of the douc langurs (Genus *Pygathrix*)

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Summary

The odd-nosed genus *Pygathrix* of Southeast Asia has been understudied in the history of primate functional morphology because they are endemic to less documented geographical regions, fragile in captivity, and rare in museum collections. This study presents a description of morphological variables in male and female *Pygathrix* langurs throughout the axial and appendicular skeleton that are known to convey information about an individual's size and potential locomotor mode. The sample includes *P. cinerea*, *P. nemaeus*, and *P. nigripes* from the Field Museum of Natural History, Chicago, the Museum of Comparative Zoology, Cambridge, Muséum National d'Histoire Naturelle, Paris, and the Endangered Primate Rescue Center, Cuc Phuong National Park, Vietnam.

Four linear metrics showed sexual dimorphism in the wrist, elbow, knee, and crus of the leg with males being significantly larger. Additionally, two key ratiometric indices, the intermembral index and the brachial index, show values that are intermediate between those of brachiators and more typical arboreal quadrupeds. Sexual dimorphism in load bearing regions of the arms and legs is expected of catarrhine primates. In brachiators such load bearing regions are concentrated in the forelimb while in more quadrupedal taxa they are dispersed between fore- and hindlimbs, or found mostly in the hindlimb. For both the linear metrics and the ratiometric index data this pattern of contrasts is consistent with the notion that the douc genus is a compelling example of an Old-World semibrachiator. It is hoped that these data can inform studies of ape evolution and the pronograde to orthograde transition.

Nghiên cứu giải phẫu học về xương ở những loài voọc chà vá (giống *Pygathrix*)

Tóm tắt

Những nghiên cứu về hình thái chức năng xương loài voọc thuôc giống *Pygathrix* ở khu vực Đông Nam Á còn hạn chế. Bởi vì mẫu vật trong bảo tàng ít và những cá thể nuôi nhốt phân tán. Đặc điểm hình thái của xương chi, thân và hộp sọ của giống *Pygathrix* được phân tích trong nghiên cứu này. Những số đo hình thái phản ánh kích thước cơ thể và liên quan đến cách di chuyển của loài. Mẫu bao gồm ba loài, chà vá chân xám, chà vá chân nâu, và chà vá chân đen. Mẫu thuộc bảo tàng lịch sử tự nhiên Chicago, bảo tàng động vật Cambridge, bảo tàng lịch sử tự nhiên Paris, và Trung tâm Cứu hộ Linh trưởng Nguy cấp, Ninh Bình, Việt Nam. Kết quả cho thấy có sự sai khác đáng kể 4 số đo hình thái xương giữa con đực và con cái. Các số đo về độ dài, rộng của xương cổ tay, xương cẳng tay, xương đầu gối, và xương cẳng chân ở con đực lớn hơn ở con cái. Hai chỉ số intermembral và brachial đã được phân tích cho thấy giống chà vá vừa có kiểu di chuyển chuyền cành bằng chi trước vừa có đặc trưng của kiểu di chuyển bằng bốn chi trên cây. Sự khác biệt các chỉ số đo xương chân và tay giữa hai giới tính phù hợp với nhóm linh trưởng Khỉ mũi hẹp.

Ở những loài có kiểu di chuyển chuyền cành vùng xương chịu lực tập trung ở những chi trước, trong khi đó ở những loài di chuyển bằng bốn chân, lực phân tán lên xương ở cả chi trước và chi sau, nhưng tập trung ở các sau. Những số đo và các chỉ số hình thái xương của giống chà vá phản ánh kiểu di chuyển nửa chuyền cành đặc trưng ở Khỉ cựu lục địa. Những số liệu này là cơ sở để nghiên cứu về sự tiến hóa trong kiểu di chuyển ở những loài vượn, từ đi bằng bốn chân đến đi thẳng bằng hai chân.

Introduction

Odd-nosed colobines, compromised of the genera *Rhinopithecus*, *Pygathrix*, *Nasalis*, and Simias, form a monophyletic clade and are 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 (Disotell, 1998; Jablonski & Ru-Liang, 1995; Jablonski & Zhang, 1992). With habitat loss and high levels of human predation pressure, the population outlook for this group remains threatened (Lippold & Thanh, 1998; Long, 2004; Nadler & Streicher, 2004; Nadler et al., 2003). As an example, the grey-shanked douc langur (*Pygathrix cinerea*) has been listed as a top-25 critically endangered primate on the IUCN's Red List (www.iucnredlist.org) since its inception. 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 can be fragile in captivity (Lippold, 1998; Nadler et al., 2003; Sterling et al., 2006). In an effort to provide additional morphological data for this group, we describe here a sample of the genus *Pygathrix*: *P. nemaeus*, *P. cinerea*, and *P. nigripes*.

Primate skeletal anatomy is of interest insofar as correlations between morphology and functional attributes like dietary and/or locomotor behavior are well established in the literature (Shea, 2005). These correlations allow predictions to be made concerning living and extinct taxa and their adaptive niche based on skeletal morphometrics. Historically, primate limb anatomy studied as a demonstration in adaptive diversity, with a plethora of studies that developed a classificatory scheme based on these morphological data (Ashton & Oxnard, 1964; Avis, 1962; 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 & Napier (1967), includes vertical clinging and leaping, quadrupedalism, brachiation, and bipedalism. With the exception of quadrupedalism, these locomotor categories represent relatively specialized modes that are independent of each other and occupy extreme positions derived from more primitive and generalized locomotor behaviors in smaller bodied primate ancestors. Quadrupedalism is central to this and likely represents the antecedent condition to other more specialized non-quadrupedal modes included in this scheme. However, quadrupedalism is also an all-encompassing category that overlaps with, or transitions into, the other categories, including brachiation and the transitional semibrachiation.

As a category in itself, semibrachiation, defined as the reliance on quadrupedal and forelimb dominated suspensory postures, has been problematic because 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 and are more specialized when compared to smaller platyrrhine monkeys with more generalized and primitive arboreal modes (Jones, 2008; Rosenberger et al., 2008). New-World semibrachiators utilize a unique form of semibrachiation in which orthograde suspensory behavior is accompanied by pendular swinging behavior whereby the forelimbs and the tail grasp arboreal substrates (Schmitt et al., 2005; Turnquist et al., 1999). In contrast, the Old-World semibrachiator group is limited to exclusively forelimb-mediated suspensory behavior. The genera included in this scheme are *Nasalis*, *Rhinopithecus*, *Presbytis*, *Colobus*, and *Pygathrix* (Ashton & Oxnard, 1964; Napier, 1963; Napier & Napier, 1967).

Other variations on transitional categories of brachiation include those modes that precede modified or true brachiation as expressed in living apes. Unfortunately, there is not a living example of what this pre-ape locomotor behavior might look like. Taking a closer look at the Old World semibrachiator group represents an intriguing antecedent condition for the types of arm swinging locomotion found in stem hominoids. The genus *Pygathrix* makes a compelling model for this investigation. For ecological reasons, one can suggest that *Nasalis* and *Rhinopithecus* have a more derived habitat relative to a truly forest living arboreal catarrhine and thus are not suitable. These large-bodied genera are found in mangrove settings or at higher altitude and colder climate where a component of locomotion is terrestrial (Boonratana, 1993; Kawabe & Mano, 1972; Ruhiyat, 1986; Zhu et al., 2014). Likewise *Presbytis* and *Trachypithecus* are not good candidates in differing 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, 1976; 1977; 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.

Since 2004 the literature on *Pygathrix* has shown that various species of this genus exhibit a significant amount of suspensory behavior, using an orthograde trunk, extended elbows, and the brachial aspect of the arm abducted above the head (Byron & Covert, 2004; Stevens et al., 2008; Workman & Covert, 2005; Wright et al., 2008). Thus, this taxon represents an ideal candidate to investigate for transitional morphological characters between orthograde apes and smaller sized, pronograde quadrupedal monkeys. This paper represents the first report on the basic skeletal morphology of a sizable sample of adult male and female douc monkeys. The sample detailed below includes red-, grey-, and black-shanked doucs (*P. nemaeus*, *P. cinerea* and *P. nigripes*) from the Endangered Primate Rescue Center (EPRC) in Cuc Phuong National Park, Vietnam. The animals were raised either in the wild or within the habitat appropriate housing found at the EPRC, and thus have engaged in natural types of semibrachiation. It is hoped that these reported data can help inform our understanding of early hominoid evolution and the pronograde to orthograde transition.

Materials and Methods

The total sample of monkeys used in this study includes 15 mature females, 21 mature males, and four of mature but undetermined sex, totaling 40 individuals. Twelve females and 19 males belong to three species, *P. cinerea*, *P. nemaeus*, and *P. nigripes*. There are five additional doucs in the sample that are one hybrid between *P. nemaeus* and *P. nigripes* and four of undetermined species taxonomy (Table 1). With the presumption that significant species level differences are absent, and in the interest of bolstering sample size, all are included in one sample for male and female doucs and tests of homogeneity are conducted. The sample is dominated by members of the EPRC populations either born in captivity or confiscated from the illegal trade in animals. However, a few specimens are represented by mostly incomplete skeletal materials found in the Field Museum of Natural History (Chicago, IL), Museum of Comparative Zoology (Cambridge, MA), and Muséum National d'Histoire Naturelle (Paris, France).

Table 1. Total of samples.

Species	female	male	sex unknown
Pygathrix cinerea	4	6	0
hybrid *P. nemaeus x P. nigripes*	0	1	0
Pygathrix nemaeus	7	9	4
Ppygathrix nigripes	1	4	0
Pygathrix spp.	3	1	0
Total (n=40)	15	21	4

Morphometric data were collected using a pair of Mitutoyo digital hand calipers connected to a Macbook workstation running Microsoft Excel. Length in mm was recorded between anatomical landmarks to the nearest 0.01 mm. A total of sixty linear morphometrics were collected for the genus *Pygathrix* (Table 2). Several of the measurements were used to compute ten ratiometric index variables that quantify size and shape within specific anatomical compartments across the skeletal sample. Statistical analysis was carried out using JMP Pro 11 software (SAS) to derive standard descriptive statistics as well as the Shapiro-Wilk W test for goodness of fit. In cases where significant W statistics were observed, further t-tests were conducted that compared female and male groups. Landmarks for these variables are considered standard for anyone familiar with skeletal anatomy and so will not be described in further detail except where necessary.

Table 2. Descriptive statistics for adult douc langurs (Genus *Pygathrix*).

Differences Between Sexes = Significant Shapiro-Wilk (W) Statistic as a Goodness-of-Fit Test
All linear measurements are reported to the nearest 0.01 mm. Ratios are presented as %.

Dependent Variable	*Pygathrix* (male or female)	n =	μ	± σ	W-Stat	P-Value
Scapular Height (mm)	female	13	69.86	6.07	0.859	P<0.05
	male	18	76.19	5.11	0.953	NS
	Total Sample	35	73.05	7	0.946	NS
Scapular Height (mm)	female	15	55.15	4.532	0.966	NS
	male	19	63.86	5.229	0.960	NS
	Total Sample	38	59.84	6.612	0.973	NS
Glenoid Height (mm)	female	13	17.31	1.522	0.959	NS
	male	18	19.54	1.067	0.946	NS
	Total Sample	35	18.59	1.779	0.961	NS
Glenoid Width (mm)	female	13	11.99	1.317	0.808	P<0.01
	male	18	13.58	1.016	0.980	NS
	Total Sample	35	12.88	1.383	0.972	NS
Clavicle Length (mm)	female	12	59.11	4.771	0.911	NS
	male	17	67.61	5.38	0.964	NS
	Total Sample	33	63.78	6.66	0.985	NS
Humerus Length (mm)	female	15	179.3	13.85	0.913	NS
	male	20	195.9	10.24	0.980	NS
	Total Sample	38	188.6	15.6	0.968	NS
Humerus Midshaft Circumference (mm)	female	15	32.33	3.222	0.956	NS
	male	20	35.65	2.621	0.907	NS
	Total Sample	38	34.32	3.519	0.966	NS
Humerus Midshaft Breadth (mm)	female	12	9.866	1.033	0.939	NS
	male	17	10.72	0.7482	0.976	NS
	Total Sample	32	10.3	1.039	0.951	NS
Humerus Midshaft Depth (mm)	female	12	10.09	0.7572	0.965	NS
	male	17	11.11	1.025	0.957	NS
	Total Sample	32	10.64	1.169	0.982	NS
Humerus Head Height (mm)	female	12	18.29	1.89	0.947	NS
	male	17	20.2	1.131	0.971	NS
	Total Sample	32	19.2	1.906	0.935	NS
Humerus Head Width (mm)	female	12	16.73	1.199	0.958	NS
	male	17	18.92	1.181	0.977	NS
	Total Sample	32	17.89	1.646	0.980	NS
Humerus Biepicondylar Width (mm)	female	12	27.21	2.41	0.894	NS
	male	17	31.67	2.034	0.940	NS
	Total Sample	32	29.74	3.179	0.953	NS
Capitulum Width (mm)	female	12	9.461	1.002	0.939	NS
	male	16	10.36	0.7306	0.969	NS
	Total Sample	31	9.938	0.9785	0.979	NS
Trochlear Width (mm)	female	12	10.8	1.04	0.955	NS
	male	16	12.08	1.102	0.930	NS
	Total Sample	31	11.46	1.259	0.972	NS

Ulna Length (mm)	female male Total Sample	11 16 32	199.01 224.5 213.52	16.67 10.77 19.85	0.880 0.928 0.958	NS NS NS
Ulna Midshaft Circumference (mm)	female male Total Sample	11 16 32	20.18 22.81 21.91	3.12 2.64 3.04	0.903 0.963 0.953	NS NS NS
Ulna Midshaft Breadth (mm)	female male Total Sample	11 16 32	5.01 5.75 5.4	0.89 0.675 0.844	0.917 0.969 0.970	NS NS NS
Ulna Midshaft Depth (mm)	female male Total Sample	11 16 32	6.94 7.99 7.55	1.18 1.22 1.233	0.945 0.948 0.985	NS NS NS
Semilunar Notch Height (mm)	female male Total Sample	11 16 32	7.91 8.4 9.36	0.89 0.65 2.85	0.946 0.930 0.699	NS NS P<0.001
Olecranon Process Length (mm)	female male Total Sample	12 17 32	7.679 8.347 8.168	1.663 1.021 1.347	0.868 0.901 0.956	NS NS NS
Ulna Distal Condyle Width (mm)	female male Total Sample	11 16 32	7.66 8.94 8.51	1.04 1.09 1.3	0.927 0.852 0.947	NS P<0.05 NS
Radius Length (mm)	female male Total Sample	11 16 32	8.17 9.79 9.01	0.77 0.69 1.12	0.949 0.857 0.957	NS P<0.05 NS
Radius Midshaft Circumference (mm)	female male Total Sample	11 16 32	185.3 209.56 198.7	18.43 10.57 19.94	0.930 0.965 0.941	NS NS NS
Radius Midshaft Breadth (mm)	female male Total Sample	11 16 32	22.64 25.56 24.38	3.2 2.42 3.63	0.907 0.953 0.974	NS NS NS
Radius Midshaft Depth (mm)	female male Total Sample	11 16 32	7.32 8.09 7.69	1.25 0.73 1.04	0.945 0.935 0.950	NS NS NS
Radial Head Maximum Diameter (mm)	female male Total Sample	11 16 32	6.41 7.47 7.05	0.86 0.99 1.09	0.944 0.940 0.977	NS NS NS
Radial Head Minimum Diameter (mm)	female male Total Sample	11 16 32	14.07 16.13 15.16	1.37 0.72 1.53	0.941 0.941 0.905	NS NS P<0.01
Radial Head Circumference (mm)	female male Total Sample	11 16 32	12.07 13.83 13.03	1.13 0.78 1.32	0.968 0.965 0.945	NS NS NS
Radial Neck Circumference (mm)	female male Total Sample	11 16 32	41.91 47.13 44.66	4.16 2.58 4.69	0.951 0.959 0.931	NS NS P<0.05
Cervical Region Length (mm)	female male Total Sample	11 16 32	25 27.38 26.34	3.46 2.42 3.5	0.931 0.888 0.945	NS NS NS

Thoracic Region Length (mm)	female male Total Sample	10 16 26	129.42 134.55 132.58	11.99 28.83 23.61	0.874 0.857 0.892	NS P<0.05 P<0.05
Lumbar Region Length (mm)	female male Total Sample	10 17 27	146.97 149.67 148.67	16.97 29.96 25.67	0.836 0.880 0.904	P<0.05 P<0.05 P<0.05
Sacrum Length (mm)	female male Total Sample	9 17 26	41.21 41.57 41.45	4.79 6.35 5.76	0.888 0.956 0.945	NS NS NS
Pelvis Height (mm)	female male Total Sample	12 17 32	136.17 147.14 141.86	9.3 8.24 10.93	0.919 0.939 0.972	NS NS NS
Ilium Length (mm)	female male Total Sample	12 17 32	86.22 89.6 88.1	7.45 5.37 6.68	0.897 0.959 0.977	NS NS NS
Ilium Breadth (mm)	female male Total Sample	12 17 32	35.94 39.97 37.99	3.31 3.92 4.2	0.904 0.970 0.966	NS NS NS
Ischium Length (mm)	female male Total Sample	12 17 32	24.95 28.1 27.46	4.03 3.84 4.56	0.823 0.888 0.934	P<0.05 P<0.05 NS
Pubis Length (mm)	female male Total Sample	12 17 32	38.03 38.1 38.33	3.9 3.29 3.73	0.973 0.893 0.947	NS NS NS
Acetabulum Height (mm)	female male Total Sample	12 17 32	21.61 22.98 22.37	1.84 1.28 1.69	0.972 0.968 0.979	NS NS NS
Acetabulum Width (mm)	female male Total Sample	12 17 32	17.45 18.55 18.08	1.89 1.55 1.72	0.919 0.948 0.989	NS NS NS
Femur Length (mm)	female male Total Sample	11 17 31	210.7 230.4 221.62	14.45 9.823 16.56	0.890 0.946 0.945	NS NS NS
Femur Midshaft Circumference (mm)	female male Total Sample	11 17 31	37.36 40.24 39.23	4.202 2.84 3.766	0.944 0.895 0.948	NS NS NS
Femur Midshaft Breadth (mm)	female male Total Sample	11 17 31	11.71 12.54 12.15	1.407 1.161 1.379	0.971 0.948 0.951	NS NS NS
Femur Midshaft Depth (mm)	female male Total Sample	11 17 31	11.23 12.37 11.87	1.124 0.87 1.146	0.968 0.975 0.964	NS NS NS
Femur Head Height (mm)	female male Total Sample	11 17 31	17.17 18.77 18.02	1.402 0.8895 1.387	0.890 0.960 0.957	NS NS NS
Femur Head Width (mm)	female male Total Sample	11 17 31	17.06 18.77 17.98	1.332 0.7935 1.357	0.887 0.966 0.952	NS NS NS

Femur Biepicondylar Width (mm)	female male Total Sample	11 17 31	28.3 31.96 30.47	2.324 1.407 2.556	0.945 0.930 0.947	NS NS NS
Femur Condyle Depth (mm)	female male Total Sample	11 17 31	23.69 26.58 25.37	1.738 1.166 2.105	0.920 0.964 0.934	NS NS NS
Tibia Length (mm)	female male Total Sample	11 16 32	187.94 207.27 199.05	12.37 9.65 15.41	0.927 0.967 0.969	NS NS NS
Tibia Midshaft Circumference (mm)	female male Total Sample	11 16 32	36.18 40 38.66	4.62 3.52 4.55	0.895 0.924 0.905	NS NS P<0.01
Tibia Midshaft Breadth (mm)	female male Total Sample	11 16 32	8.59 9.46 9.14	1.34 1.02 1.2	0.967 0.956 0.984	NS NS NS
Tibia Midshaft Depth (mm)	female male Total Sample	11 16 32	13.21 14.63 14.01	1.79 1.08 1.66	0.908 0.942 0.940	NS NS NS
Tibia Plateau Breadth (mm)	female male Total Sample	11 16 32	26.78 30.39 29.13	3.13 3.13 3.48	0.930 0.750 0.917	NS P<0.001 P<0.05
Tibia Plateau Depth (mm)	female male Total Sample	11 16 32	20.99 22.87 22.22	3.24 2.7 3.09	0.889 0.918 0.961	NS NS NS
Tibia Distal Width (mm)	female male Total Sample	11 16 32	18.15 20.53 19.57	1.73 1.23 1.79	0.969 0.954 0.976	NS NS NS
Tibia Distal Depth (mm)	female male Total Sample	11 16 32	14.83 17.08 16.24	1.05 1.2 1.52	0.896 0.908 0.970	NS NS NS
Fibula Length (mm)	female male Total Sample	11 16 31	172.31 190.89 182.94	10.22 10.82 15.76	0.962 0.915 0.985	NS NS NS
Calcaneus Length (mm)	female male Total Sample	11 16 31	34.9 38.98 37.24	2.29 2.28 3.03	0.895 0.937 0.945	NS NS NS
Talus Length (mm)	female male Total Sample	11 16 30	23.78 27.19 26	1.38 1.33 2.28	0.931 0.907 0.970	NS NS NS
Talus Trochlear Breadth (mm)	female male Total Sample	11 16 30	12.35 13.94 13.27	1.03 0.95 1.23	0.959 0.978 0.978	NS NS NS
Intermembral Index (%)	female male Total Sample	11 16 30	91.18 93.11 92.37	5.755 1.752 3.9	0.863 0.952 0.834	NS NS P<0.001
Brachial Index (%)	female male Total Sample	12 16 31	103.5 106.2 104.7	4.979 3.217 4.25	0.913 0.941 0.923	NS NS P<0.05

Crural Index (%)	female male Total Sample	11 16 30	89.2 90.17 89.77	1.49 1.464 1.509	0.928 0.961 0.959	NS NS NS
Scapular Shape Index (%) Height / Width	female male Total Sample	12 17 35	125.84 118.46 121.32	10.16 8.89 9.38	0.9214 0.9407 0.9494	NS NS NS
Clavicle Index (%) Calvicle Length / ((Acetabulum Height*Width)^1/2)	female male Total Sample	12 17 32	305.3 329.1 317.7	17.91 35.44 31.08	0.900 0.953 0.954	NS NS NS
Humerus Gracility Index (%) Humerus Length / ((circumference* breadth*depth)^1/3)	female male Total Sample	12 17 32	1223 1227 1226	133.3 76.7 97.28	0.965 0.944 0.962	NS NS NS
Ulna Gracility Index (%) Ulna Length / ((circumference* breadth*depth)^1/3)	female male Total Sample	11 16 32	2297.25 2239.59 2252.48	411 256.23 296.97	0.9581 0.9443 0.9569	NS NS NS
Olecranon Length Index (%) Olecranon Process Length / ((Acetabulum Height*Width)^1/2)	female male Total Sample	11 16 31	40.18 43.74 42.06	6.43 5.26 5.62	0.9527 0.9514 0.9765	NS NS NS
Radius Gracility Index (%) Radius Length / ((circumference* breadth*depth)^1/3)	female male Total Sample	12 17 32	1832 1822 1832	259.6 159.6 197.1	0.976 0.926 0.981	NS NS NS
Lumbar Index (%) (Lumbar Height / Thoracic Height)	female male Total Sample	9 14 23	107.63 108.3 110.58	8.42 7.6 8.3	0.842 0.933 0.942	NS NS NS

Results

In total 60 variables from the post-cranial skeleton are reported from the largest known sample of the genus *Pygathrix*. Overall, they describe an arboreal, tailed, Old World monkey that is medium to large bodied. The computed W-statistic represents a test of homogeneity with the null hypothesis that one single distribution of data is observed and not something with multimodal and non-normal data. The closer the W-stat is to 1.0, the closer to complete uniformity in the data. Significant p-values indicate significantly low W-statistics and reject the null hypotheses (i.e., the distribution of that group for that dependent variable is not uniform and is therefore non-normal).

Significantly non-homogenous variables are Scapula Height, Glenoid Width, Semilunar Notch Height, Ulna Distal Condyle Width (UDCW), Radius Length, Radial Head Minimum Diameter, Radial Neck Circumference (RNC), Thoracic Region Length, Lumbar Region Length, Ischium Length, Tibia Midshaft Circumference (TMC), and Tibial Plateau Breadth (TPB). Of these variables RNC, UDCW, TMC, and TPB (of the elbow, wrist, knee and crus of the lower leg) are the only ones that exhibit significant sexual dimorphism revealed by t-tests comparing known male and female groups. Each of these four comparisons from the elbow, wrist, and the lower leg where males which are significantly larger than females (Fig. 1).

Additionally, two key ratiometric indices exhibit sexual dimorphism, the Intermembral Index (IM),

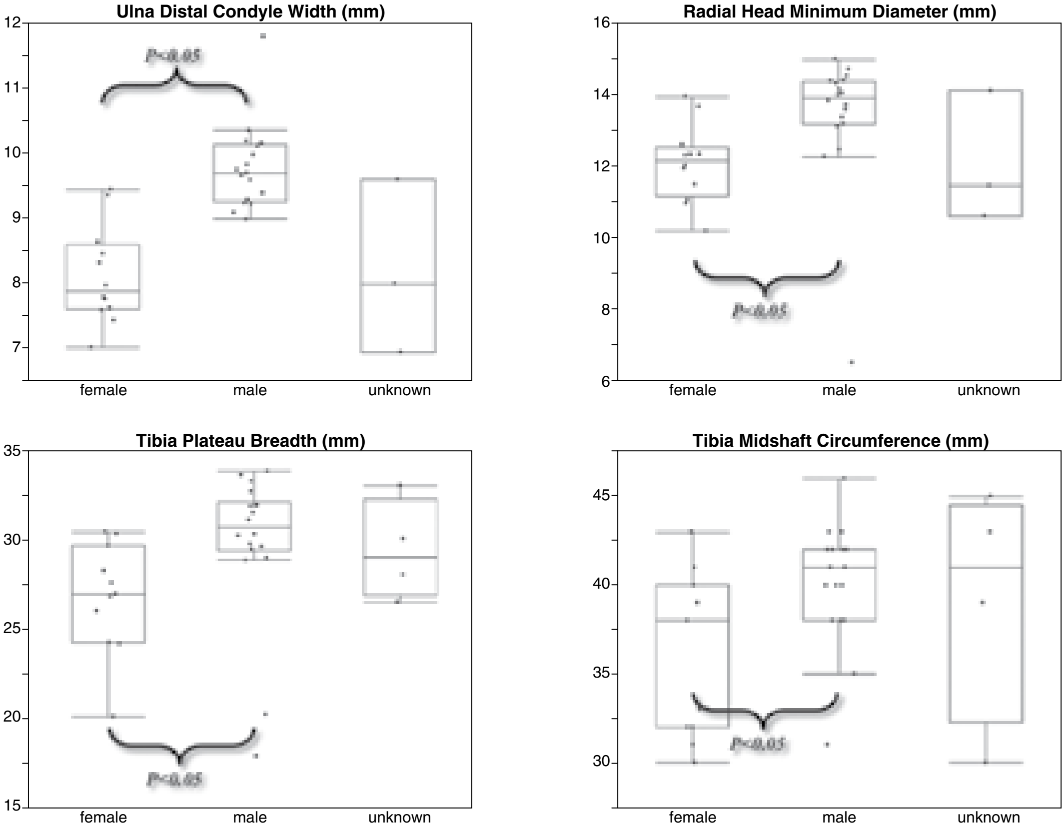

Fig.1. Four linear metrics that showed significant sexual dimorphism. Significant p-value represents a rejection of the null hypothesis that males and females are the same and uses a t-test. Unknowns were left out of the t-test.

and Brachial Index (BR). They show values that are intermediate between those of brachiators and more typical arboreal quadrupeds. As a total sample the IM was 92.4% with males showing slightly larger (93.1%) than female (91.2%) values. The BR for the total sample was 104.7% with males (106.2%) being larger than females (103.5%) in this measure. Thus, the douc langur has relatively long arms and forearms consistent with more suspensory locomotor habits. Furthermore, the larger male specimens are in an even greater direction toward suspensory morphology having relatively longer arms and forearms than even female doucs.

Discussion/Conclusions

In this study a sample of 40 adult douc langurs of the genus *Pygathrix* are described. A series of basic skeletal measurements derived from limb, girdle, and vertebral regions are presented. Four variables were observed to show significant sexual dimorphism at the elbow, wrist, knee, and the lower leg (Fig. 1). This sexual dimorphism is not surprising given that each feature is found at a major load-bearing region of the fore- and hindlimb. Increased tibial loadings would be true of larger sizes for quadrupedal locomotion. Increased forearm loadings would be true of larger sizes for forelimb mediated suspensory behavior. This pattern of significance underscores the transitional nature of the semibrachiator category and the importance of *Pygathrix* as a catarrhine representative.

In this study, the genus *Pygathrix* is described as a homogenous statistical population and so is not divided into species or sex. For the sake of comparative contrast with other catarrhines, this facilitates testing the morphological substantiation of 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 arm swininging, and thus, are not actually semibrachiators (Mittermeier & Fleagle, 1976; Morbeck, 1977; 1979). Recent attention has been paid to doucs because they do complement their quadrupedal locomotion with armswinging (Byron & Covert, 2004; Covert et al., 2004; Stevens et al., 2008; Wright et al., 2008) making them an ideal taxon to understand the evolutionary origins of orthograde positional behavior.

In the classic description of the Old-World semibrachiator group (Napier & Napier, 1967) reports of average intermembral index (93%) and brachial index (104%) are cited for *Pygathrix* from earlier work (Milne-Edwards & Pousargues, 1898; Washburn, 1942). Only one other odd-nosed Asian Colobine has such high values for these indices, the proboscis monkey, Genus: *Nasalis*. The other colobines of Asia and Africa 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). Among platyrrhines the New World semibrachiators more closely approximate the limb index condition of true brachiators. However, with a prehensile tail as a major component of the locomotor stride, this group does not exhibit a transitional condition that is relevant to the pronograde to orthograde transition that occurred in catarrhine primates.

The results for *Pygathrix* presented in this paper are intermediate between typical arboreal quadrupedal monkeys and true gibbon-type brachiators, and match expectations for this taxon. This douc sample's intermembral index is 92.4±3.9% and the brachial index is 104.7±4.3%. These data are significant because they provide information on the skeletal anatomy of a medium-sized catarrhine leaf monkey that exhibits sexual dimorphism and is adapted for a highly arboreal habitat. For these reasons, *Pygathrix* is a compelling model for early hominoid evolution and the origins of orthograde suspensory behavior.

Having a transitional 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). These taxa precede the true brachiation of more derived hominoids (like chimps and gibbons). Recent work on an extinct stem catarrhine taxa from the European Miocene describes functional similarities with New World semibrachiators that are interpreted to mean that *Pliopithecus vindobonensis* likely performed forelimb suspensory locomotion (Arias-Martorell et al., 2014; 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). Including *Pygathrix* in these types of analyses should be a goal for anyone interested in ape locomotion and evolution. Currently these types of analyses are standard for primate taxa commonly found in natural history museum collections. 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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