Testing for the Effects of Locomotion on Intraspecific Variability in the Prosimian Skeleton

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Locomotion and Variability in Prosimian Skeleton

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ABSTRACT

This study investigates intraspecific variability in the cranium and appendicular skeleton of eight prosimian species (*Eulemur fulvus*, *Hapalemur griseus*, *Lemur catta*, *Varecia variegata*, *Galago senegalensis*, *Otolemur crassicaudatus*, *Nycticebus coucang*, and *Tarsius syrichta*) to test the hypothesis that regions of the skeleton more subject to variable stresses in locomotion may be more morphologically variable. The impacts of muscular action on bone may be more apparent in the limbs than on the cranium, as the cranium is less directly involved in locomotion. Bone modelling may also be more important in determining the shape of the diaphyses of long bones than of the epiphyses. Developmental constraint is likely to minimize cranial and epiphyseal variability due to the requirements for precise matching at limb joints and cranial sutures. Due to the importance of hindlimb dominated vertical clinging and leaping in prosimians (in which *G. senegalensis*, *H. griseus*, and *T. syrichta* are often classified as specialists, and all but *N. coucang* practice occasionally), hindlimbs were hypothesized to be more variable than forelimbs in this sample, the reverse of the observed catarrhine pattern. It was found that postcrania were more variable than crania ($Z = -2.34$, $p < .05$) and diaphyses more variable than epiphyses ($Z = -2.26$, $p < .05$). This may indicate that common developmental processes characterize variation in these regions across primates. Forelimb and hindlimb variability were not significantly different, however. This may indicate that prosimian limb use is relatively undifferentiated.

Intraspecific variability has long interested biologists, anthropologists, and paleontologists, both as a complicating factor in morphometric and phylogenetic analyses and as an informative trait in itself. From an evolutionary perspective, it is the raw material upon which natural selection may act, describing the limits of evolutionary possibility for a species at any given time. Variation may be an evolutionarily result of a regime of low stabilizing selection, as hypothesized in environments where there are multiple potential phenotypic optima (Young 2006). As a developmental phenomenon, it may indicate underlying plasticity in both genetically controlled ontogenetic pathways and in epigenetic factors leading to ecophenotypic variation (Waddington 1942). In tetrapods in particular, much ecophenotypic variation is believed to result from the use and disuse of limbs of the appendicular skeleton. Various loading regimes are believed to cause bone to respond by remodelling itself, a phenomenon often known as Wolf's Law (Pearson and Lieberman 2004). Finally, as a practical matter, variability is an important consideration in phylogenetic and functional morphological analyses, as well as in species identification in the fossil record. It may pattern in ways indicative of sexual or regional di- or multi- morphism (Plavcan and Cope 2001). This can reveal information useful in inferring social structure and identifying probably subspecies.

This study compares variation in selected regions of the skeletons of prosimians to test for evolutionary and developmental factors that may drive variability. Previous research has reported on differential variability only in the skeletons of anthropoids (Buck et al. 2010; Young 2004; Young 2006). In the study replicated here, Buck, Strong, and Foley took a series of standard osteometric measurements on the crania, forelimbs, and hindlimbs of 12 catarrine species (2010). As expected from previous results on the high degree of morphological integration characterizing the cranium

(Hallgrimmson et al. 2002) as well as safety factors constraining cranial development (Lieberman 1996), and the potential effects of remodelling on the postcranium, they found lower mean cranial variability than mean postcranial variability. They also found signficantly higher variability in the forelimbs than in the hindlimbs of their total sample. Consistent with the explanation offered by Young (2006), it may be that the variable postures incumbent in suspensory locomotion, which most catarrhines exhibit to some degree, deprive the forelimb of an optimal target for stabilizing selection. Alternatively, forelimb variability may be related to the variable motions in hominoid tool use and generalized manual dexterity (Buck et al. 2010). This finding may also be viewed in light of that by Hallgrimsson et al. of high morphological integration between homologous limb elements (2002). In order to evolve specialization in one limb pair (for example the elongated and mobile forelimbs of hominoids), there may have been some developmental decoupling to allow selection to act on limb elements independently. This may have loosened developmental constraint in one limb pair.

Catarrhines also appear to exhibit higher variability in the diaphyses of long bones than the epiphyses (Buck et al. 2010), consistent with the known effects of remodelling on long bone shafts and the importance of precise matching at epiphysis joints (Currey 1968; Lazenby et al. 2008). This was similar to the findings of Gingerich and Schoeninger that molars, which are topologically complex and subject to precise matching requirements in occlusion, are less variable than simpler anterior teeth (1979).

Here, these three comparisons are repeated in 8 prosimian species drawn from four families (Lemuridae, Lorisidae, Galagidae, Tarsiidae) and representing a broad sample of the locomotor diversity of the infraorder (Connour et al. 2000). The Prosimii, while likely not a natural group (Schmitz

et al. 2001), unites primates with locomotor habits quite different from those of most anthropoids. Especially important in this regard is the spectrum of hind-limb dominated saltatory behaviors culminating in advanced vertical clinging and leaping (VLC) (Napier and Walker 1967). Also divergent from the catarrhine pattern is the lorisine practice of slow climbing and cantilevering between supports (Gebo 1987). Despite this, if developmental factors in the primate cranium and appendicular postcranium persist across the order, prosimians should reveal a similar pattern of variability in these two regions to catarrhines. Safety factors are likely still important in constraining cranial variability and bone remodelling may still occur in prosimian limbs in response to use. If remodelling remains important across the Primates, and is relatively more important on shafts than at joints, then this would also predict higher diaphyseal than epiphyseal variability as observed in catarrhines.

However, if suspension, tool use, or other behaviors typical of catarrhines but largely absent in prosimians are important in driving forelimb variability, then forelimbs are not likely to be more variable than hindlimbs in the prosimians studied here. Indeed, because of the potentially variable demands of saltation, in which ecological factors such a support availability and density and predator avoidance appear to be more important than ballistic optima in determining leaping force and angle of attack, hindlimbs may be expected to exhibit higher variability in VCL species (Crompton et al. 1993). If the developmental decoupling hypothesis inferred from Halgrimmson et al. (2002) is correct, then this may also result in higher variability in the hindlimbs of prosimians due to their relative modification for saltatory behavior (Connour et al. 2000).

If patterns of variability are similar in prosimians and catarrhines despite their disparate locomotor modes, it may provide evidence of some general principles of primate development.

Prosimians also serve as the most likely ecological and behavioral models for many early euprimates (Fleagle 1999). As controversy often arises over interpretations of morphology in different regions of primate skeletons (e.g. the apparent conflict between amphipithecid dentognathic and postcranial material discussed in Ciochon and Gunnell [2001]), understanding the pattern of variability in the prosimian skeleton may aid in resolving conflicting lines of evidence.

METHODS

Cranial and long bone measurements were taken on 121 cranial and 108 postcranial specimens representing 8 prosimian species (Table 1), drawn from the collections of the institutions listed in the acknowledgements. Measurements followed those recommended by Groves and Harding (2003) and Aiello and Dean (1990) and used in the replicated catarrhine study (Buck et al. 2010) for direct comparability (Table 2). The measurement "breadth of tibial tuberosity" was excluded due to the difficulty of assessing it accurately in the smaller bodied prosimian sample. Measurement was taken using a digital sliding caliper to the nearest 1 mm. All specimens were measured twice, and 76% of specimens measured three times to provide a sample for determining measurement error. Only adults were measured, as assessed by complete fusion of all limb epiphyses and eruption of the third molars. Sex was unknown on most specimens, but prosimians are generally characterized by low sexual dimorphism (Kappeler 1990), and sex had no effect on the pattern revealed by comparisons in catarrhines (Buck et al. 2010). Zoo raised individuals without visual pathology were also included to bolster sample sizes.

Observed variability in those individuals measured three times was partitioned into within-group

and among-individual (percent measurement error) components using a Model II ANOVA (Bailey and Byrnes 1990). The fraction of the variance attributed to measurement error was subtracted from the observed variance for the total sample. Variance was converted to standard deviation and used to calculate a coefficient of variation by dividing by the mean (Plavcan and Cope 2001). These were converted to V* to correct for small sample sizes using the equation:

$$V^* = (1 + 1/4n)\ V$$

(Sokal and Rohlf 1995). Corrected and uncorrected V* means for the variable classes examined were compared using a one-tailed Wilcoxon test in the JMP 9 statistical program to test each of the three hypotheses. This replicates the statistical methods of Buck et al. (2010) on their catarrhine sample. Calcaneus length and breadth were also measured, as this bone forms an important component of the length of the functional hindlimb in many prosimian species (Oxnard et al. 1981), and analyses run with and without these measurements included. As they did not affect the significance of any of the comparisons, Z and p values are reported without the calcaneus included for better comparability with the results of Buck et al (2010).

RESULTS

Using the corrected means, postcranial variability was significantly higher than cranial variability ($Z = -2.34$, $p < .05$) and diaphyses significantly more variable than epiphyses ($Z = -2.26$, $p < .05$) in the total sample. Forelimb and hindlimb variances were not significantly different (Table 3, Figure 1). Using uncorrected means, diaphyses were significantly more variable than epiphyses ($Z = -2.39$, $p <$

.05).

DISCUSSION

The caveats mentioned in Buck et al. (2010) apply here as well. The measurements taken capture only a rough, size dependent description of bone shape. Future research may apply more accurate, size-independent morphometric methods to better assess variability. The precision of the measurements (to the millimeter) may have also failed to capture some size variability in the relatively smaller-bodied prosimian sample. Future research might employ more precise measurements. The selection of species may also have affected the results. For example, no indriids, lepilemurids, cheirogaleids, or recently extinct subfossil lemurs were included in the sample. The inclusion of zoo individuals in this study may also have introduced problems in interpretation, due to the effects of captivity on natural movement patterns (O'regan and Kitchener 2005).

Of the three comparisons tested here, two were consistent with those reported in catarrhines (Buck et al. 2010). Postcranial variability was higher than cranial variability, which suggests that the effect of locomotion on the postcranium and safety factors in the cranium may be common to prosimians and catarrhines. Diaphyses were also more variable than epiphyses, which supports the hypothesis that remodelling remains important, and the potential for variability at joints is lower due to matching requirements, throughout the Primates.

Unlike in catarrhines, forelimbs were not significantly more variable than hindlimbs. This is consistent with the hypothesis of Young (2006) and Buck et al. (2010) that forelimb suspension (or tool use, which is also absent in prosimians) drives variability. Suspension is also common in prosimians but

appears to frequently involve hindlimbs with as much versatility as forelimbs (Gebo 1987). Behavioral studies comparing fore and hind limb use quantitatively in prosimians and catarrhines during suspension may be a profitable future direction for research. Hindlimb variability was not significantly higher than forelimb variability, even in the relatively saltatory species (*G. senegalensis*, *H. griseus*, *T. syrichta*) analyzed separately. Therefore the hypothesis proposed here that leaping drives hindlimb variability is not supported, nor is a situation of developmental decoupling.

The method employed here to correct for observer error (Bailey and Byrnes 1990) was not employed in Buck et al. (2010), and so this may also have impacted the results. Uncorrected comparisons are also presented, in which the difference between cranial and postcranial variability also falls below significance. If this is a biologically meaningful result and not distorted by error, it may indicate that prosimian limb use may be less differentiated intraspecifically than in Cattarhines, leading to lower variability in use-mediated growth and/or higher stabilizing selection in the long-bones, at least in some species. Alternatively, prosimian crania may be relatively more plastic than catarrhine crania.

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Table 1, Species sampled

Species	Cranial *n*	Postcranial *n*
Eulemur fulvus	13	11
Galago senegalensis	21	17
Hapalemur griseus	12	8
Lemur catta	13	12
Nycticebus coucang	18	18
Otolemur crassicaudatus	18	18
Tarsius syrichta	15	14
Varecia variegata	11	10
Total	121	108

Table 2, Measurements taken

Bone	Measurements
Cranium	Total length; bizygomatic breadth; basal length bicanine breadth; orbital height

Humerus	Maximum length; maximum and minimum diameter of the diaphysis at 40% of length (to avoid the deltoid muscle attachment); transverse diameter of head; breadth of distal epiphysis
Ulna	Maximum length; maximum and minimum diameter of the diaphysis at 50% of total length; maximum breadth of the distal epiphysis (excluding styloid process) perpendicular to shaft
Radius	Maximum length; maximum and minimum diameter of the diaphysis at 50% of total length; breadth of the distal epiphysis
Femur	Maximum length; maximum and minimum diameter of the diaphysis at 50% of total length; biomechanical breadth of neck; biepicondylar breadth
Tibia	Maximum length; maximum and minimum diameter of the diaphysis at 50%

	of total length

From Aiello and Dean (1990); Buck et al. (2010).

Table 3, Corrected coeffecients of variation (V*) by skeletal region and species

	Total	*E. fulvus*	*G. senegalensis*	*H. griseus*	*L. catta*	*N. coucang*	*O. crassicaudatus*	*T. syrichta*	*V. variegata*
Cranial V*	5.86	7.41	7.16	4.14	4.38	9.39	8.66	2.89	2.87
Postcranial V*	8.57	1.16	7.89	6.54	7.12	1.52	8.80	6.01	5.33
Forelimb V*	8.68	1.11	7.55	6.83	6.81	16.5	8.74	6.22	5.73
Hindlimb V*	8.39	12.5	8.43	6.05	7.64	13.2	8.90	5.68	4.69
Diaphysis V*	9.97	13.2	9.26	7.66	8.97	13.0	11.0	7.96	8.65
Epiphysis	7.27	10.0	6.97	5.85	5.77	12.9	7.15	5.82	3.6

V*									8

Fig, 1, Box plots of corrected coefficients of variation (V*) for the total sample by skeletal region

Boxes represent middle two quartiles, error bars extend to outliers. Horizontal lines indicate medians.

