

**Nuclear/Mitochondrial Discordance in Gray-Footed Chacma Baboons**

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In animals where females are philopatric and males disperse, genes in the maternally inherited mitochondrial genome can have evolutionary histories distinct from those of bi-parentally or paternally inherited genes in the nuclear genome. Comparisons of these contrasting mitochondrial and nuclear gene histories can allow insights into the evolution of closely related, hybridizing taxa. Here an example of such nuclear/mitochondrial (nuc/mt) discordance is reported in the gray-footed chacma baboon (*Papio hamadryas griseipes*). A phylogeny of baboons was inferred based on a 2.6 kb stretch of mtDNA amplified from a large number of individuals, including representatives from populations of Cape chacmas, gray-footed chacmas, Kindas, and 'typical' yellows from central Africa. A 'long-template' PCR method was used in order to reduce the risk of the accidental amplification of numts. As no appropriate markers were available to construct a nuclear phylogeny, morphological features were used as proxies for nuclear genes. The mitochondrial phylogeny shows chacmas (*s. l.*) to be polyphyletic: gray-footed chacmas fall well within the yellow baboon clade, and do not group with Cape chacmas. It appears that, although having the morphological characteristics of chacma baboons, the gray-foots sampled in this study have yellow mitochondrial DNA. Recent surveys of the contact zone between gray-foots and yellows in Zambia have reported possible hybrids, and morphological studies of baboons from this region have yielded evidence of gene flow between the two forms. The contrasting nuc/mt pattern may be an indication of substantial gene flow between chacmas and yellows in the past, with a net movement of chacma nuclear genes into yellow baboon populations. Gray-footed chacmas may be hybrid in origin.

**Surveys from NW Yunnan/SE Tibet: Implications for Primate and Other Mammal Biogeography and Conservation**Paul J. Buzzard<sup>1</sup>, Shelly Yang<sup>2</sup>, and William V. Bleisch<sup>2,3</sup><sup>1</sup> Fauna Flora International-China Programme (PhD Columbia 2003)<sup>2</sup> Fauna Flora International-China Programme<sup>3</sup> China Exploration and Research Society

Northwest Yunnan and Southeast Tibet are very rich areas of biological diversity and endemism. In this area, three major rivers, the Yangtze, Mekong, and Salween, descend from the Tibetan plateau creating altitudinal biological gradients and barriers to dispersal. A mountain sacred to Tibetan Buddhists, Kawakarpo, lies between the Mekong and Salween basins, and pilgrims come to circumambulate Kawakarpo along a ~100 km path, or kora, to receive merit. Ethnic Tibetan pilgrims come not only from Tibet but also from remote areas in other provinces of China such as Yunnan, Sichuan, and Qinghai. In October 2003/2004, we interviewed pilgrims at the beginning of the kora and made the circumambulation ourselves to gather data on wildlife distribution and hunting practices. Along the kora, vegetation ranges from dry and sparse habitats along the river basins up through wetter conifer/oak forests and temperate rain forests to alpine meadows above the treeline. We observed rhesus macaques (*Macaca mulatta*) at 4100+ meters a.s.l. in mixed conifer/oak forest and interviews suggested that macaques exist in some abundance along the kora. Interviews also suggested that the distribution of Shortridge's capped langurs (*Trachypithecus pileatus shortridgei*) stretches to the Salween river which serves as a barrier. Among other mammals, interviews and the presence of skins indicated that serow (*Capricornis sumatrenis*), goral (*Nemorhaedus* spp.), blue sheep (*Pseudois nayuar*), and black bears (*Selenarctos thibetanus*) also exist in some abundance along the kora route. Furthermore, interviews suggested that in remote areas, musk deer (*Moschus* spp.) are making a comeback while big cats such as leopard (*Panthera pardus*), tiger (*Panthera tigris*), and clouded leopard (*Neofelis nebulosa*) are still seriously endangered. Although pilgrims said no hunting occurred, we observed hunters along the kora route and heard shots. The Chinese government instituted a hunting ban in 1998 and subsequently confiscated guns, but further steps clearly need to be taken to ensure conservation in this biologically rich region.

### Evolution of the Progesterone Receptor Gene in Primates

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Progesterone is a steroid hormone that is necessary to maintain pregnancy. In humans, progesterone levels in plasma are high throughout pregnancy while in most other nonprimate placental mammalian species examined to date the levels drop at the end of gestation. It has been hypothesized that actions of progesterone with its receptor cause a functional progesterone withdrawal that occurs before parturition in humans. To study this we sequenced the progesterone receptor in human, chimpanzee, bonobo, gorilla, orangutan, white-handed gibbon, barbary macaque, anubis baboon, vervet, black and white colobus, and dusky langur. Aligned sequences were tested for evidence of positive selection, using a maximum likelihood approach as implemented in PAML 3.14. We found that in primates the first exon is more variable than the other exons. In addition, humans and chimpanzees showed statistically significant increases in nonsynonymous substitution rates compared to synonymous substitution rates. In humans the amino acid changes are in the first exon, specifically in the inhibitory domain. In chimpanzees the amino acid changes are in the transactivation domains. We have also noticed that various PGR domains have evolved rapidly in Old World monkeys (especially in the leaf-eating colobins). We suggest that the positively selected changes in the inhibitory domain are functionally important and may act to regulate the interaction between the A and B progesterone receptor isoforms.

keywords = parturition, pregnancy, positive selection

### Life History of Wild Female Blue Monkeys (*Cercopithecus mitis stuhlmanni*)

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Most data on primate life histories derive from a limited group of species and long-term studies of non-provisioned populations are even more limited to certain largely terrestrial cercopithecines. Here we present data from a 24 year study of an arboreal guenon, the blue monkey (*Cercopithecus mitis stuhlmanni*), inhabiting a Kenyan rain forest. Our individually recognized study subjects lived in 2 neighboring social groups, whose demographic characteristics were monitored for 11 and 24 years respectively. Each of the groups fissioned during the study. Blue monkeys exhibit strict female philopatry, allowing us to estimate most life history parameters for females only. Data from males are limited to infant and juvenile survivorship, and age at natal emigration. We include data on birth seasonality, age at first birth, sex ratio, interbirth interval, mortality of infants and adults, and maximum lifespan. Based on these parameters, we develop a life table for this population. In addition, we discuss (i) the relationship of female dominance status and group size to some of these life history parameters, and (ii) what these parameters reveal about the long-term survival probability of this population.

### The Phylogenetic Position of the Victoriapithecidae

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The Victoriapithecidae is a family of African cercopithecoids whose taxonomic placement has been much argued in recent years. The family currently comprises two genera and three species: *Victoriapithecus macinnesi*, *Prohylobates tandyi*, and *Prohylobates simonsi*. *Victoriapithecus* is by far the best known of these taxa, largely due to the extensive collection from Maboko Island, Kenya, mainly recovered by B. Benefit and colleagues. The Maboko specimens date to the mid-Miocene and show a number of conservative features including incomplete bilophodont dentition and a small cranial capacity. The victoriapithecids have most often been placed as the sister group to the Cercopithecidae, especially by Benefit, and it has been hypothesized that colobine and cercopithecine monkeys evolved from this victoriapithecoid stock. However, the victoriapithecids share several cranio-dental characters with the cercopithecines to the exclusion of the colobines, so an alternative interpretation is that the "victoriapithecids" may be stem cercopithecines. This study evaluates that hypothesis. Preliminary results indicate close phylogenetic affinity between *Victoriapithecus* and the cercopithecines, separate from the colobines. In light of this finding, it is suggested that *Victoriapithecus* and relatives can no longer be accepted without question as a separate family within the Cercopithecoidea. A more detailed reanalysis of all known data is required to adequately choose between the two well-supported alternative hypotheses of relationship.

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### A New Approach to Reconstructing Intermediate Morphology on the Cercopithecoid Evolutionary Tree using Geometric Morphometric Techniques

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In the study of primate evolution, there is often a distinct divide between phylogenetic relationships suggested by morphological data and those suggested by molecular data. Molecular phylogenies lack genetic material from fossil taxa, while morphological phylogenies often suffer from an incomplete and confusing fossil record. There have been few attempts to combine both methodologies in a more holistic approach to primate evolutionary morphology. Furthermore, there has been little research on the methods of reconstructing ancestral morphotypes or even the potential morphology of intermediate or "ancestral" forms at or between branching points in evolutionary trees. Understanding of the morphology of such ancestral forms could provide great insight into the mechanics of primate evolution, help us more precisely estimate the correct phylogenetic position of fossil taxa, and ultimately perhaps help us further understand some of the differences we see between morphological and molecular studies.

Here we report preliminary data from an exciting new project investigating these issues that for the first time allows us to visually track evolutionary changes in cranial shape through time. Taking the most recent molecular phylogeny of the Cercopithecidae as a framework with molecular clock-derived dates of major branching points, we use modern geometric morphometric methods to visually map cranial evolutionary change, whereby high resolution laser surface scans of extant primate taxa can be warped "up" and "down" an evolutionary tree.

Our methodology involves combining complex surface data from laser scans and 3D landmarks data from Microscribe digitizers. This allows mean values of large samples to modify exemplar scans, adding greater

statistical power to the analysis. Within the framework of the pre-determined tree, shape data are “warped” according to a model of evolutionary change wherein the effect of a known terminal taxon on the inferred intermediate form is weighted according to the squared temporal distance between them. To date we have only concentrated on warping exemplar scans, using specifically designed in-house software, on five extant cercopithecoid taxa (*Papio*, *Macaca*, *Chlorocebus*, *Pygathrix* and *Colobus*). The next step will involve developing the best methodology for combining 3D coordinate data and laser surface scans, developing the algorithms that drive our model of evolutionary change and incorporating fossil remains into the analyses.

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### Hybrid Cercopithecus Monkeys in East and Central African forests

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Sympatric *Cercopithecus* monkeys (guenons) are well known for their ability to hybridize in nature. Here, I report on two different cases of hybridization among sympatric guenons and discuss the ecological conditions surrounding these events. The first case, which is a previously undocumented example of hybridization in guenons, is between *C. ascanius schmidti* and *C. pogonias denti*. During two short visits to Nyungwe Forest National Park in March 2004 and August 2005, I observed an adult female *C. ascanius schmidti* x *C. pogonias denti* hybrid monkey living in a small forest fragment adjacent to Nyungwe’s main forest block. The hybrid was a fully integrated member of the fragment’s only resident primate group, a group of black and white colobus monkeys (*Colobus angolensis*). No *C. ascanius* x *C. pogonias* hybrid monkey was observed in the main forest block, suggesting that hybridization between these species at Nyungwe is very rare, and likely resulted from the deforestation and fragmentation of their natural habitat. The second case, which is a well-known example of guenon hybridization, is between *C. ascanius* and *C. mitis*. For 10 months (August 2004-August 2005), I conducted a field study of the *C. ascanius* and *C. mitis* hybrid zone in Gombe National Park, Tanzania. At Gombe, hybridization has occurred for many decades, and hybrids are now well established as members of the breeding population. Throughout the park, I identified a minimum of 10 different mixed-phenotype social groups in which group membership consisted of individuals of *C. ascanius* and *C. mitis* phenotypes and hybrids of various phenotypes (intermediate, *mitis*-like, and *ascanius*-like). The phenotypic diversity of hybrids suggests that hybrids backcross with both parental species and probably interbreed among themselves. I hypothesize that unusual biogeographic and demographic conditions, combined with Gombe’s distinctively structured landscape, are driving local populations of the two species towards genetic and behavioral integration.

### Strontium-Calcium Ratios in Deciduous and Permanent Tooth Enamel from *Papio hamadryas anubis*

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Strontium and calcium are incorporated into developing teeth in a manner that reflects changing physiological concentrations in the body. Changes in Sr/Ca ratio are expected to occur in response to marked dietary transitions, such as those experienced during the weaning period. Discrete micro sampling of tooth enamel using laser ablation inductively coupled plasma mass spectrometry (LA-ICP-MS) is used to examine changes in Sr/Ca ratio throughout the tooth crown. The use of thin sections allows the position of each sample to be cross-referenced to incremental growth structures in the tooth enamel. Here we present

the results of an analysis of thin sections of three teeth from a single female Ugandan baboon (*Papio hamadryas anubis*). The mean Sr/Ca ratio increases between successively later forming tooth crowns in this individual indicating a reduction in the intake of breast milk. Distribution maps for Sr/Ca ratios are generated for each tooth and interpreted in relation to tooth crown geometry and incremental growth lines. In all three teeth there is a pronounced trend for Sr/Ca ratios to decrease from the enamel dentine junction to the enamel surface. Chronologically consistent interruptions to this underlying trend are used to identify possible dietary shifts.

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**Variability of the CRH Gene Promoter is Associated with Gene Expression and Linked to Temperament and Reproductive Outcome in a Population of Rhesus Macaques (*Macaca mulatta*)**

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Corticotropin-releasing hormone (CRH) is the primary neuropeptide regulator of behavioral, neuroendocrine, and reproductive responses to stress. Variation in CRH activity may underlie individual and species differences in physiological reactivity and behavior. The CRH gene is remarkably conserved across species and CRH neurons, expressed at high concentrations in the hypothalamus and amygdala, have an ancient role in organisms' perceptions of and reactions to normal environmental challenges, social interactions, and novelty.

Interestingly, CRH is uniquely expressed in primate placenta and is an important regulator of gestation length and fetal development. Given the tight link between stress and reproduction in primates, I hypothesized that functional variation in the *Macaca mulatta* CRH gene would be associated with both temperament and reproductive outcome. I have identified 19 variable loci in the CRH gene and promoter that occur in allelic identity (a haplotype block) in the NIH rhesus colony and include a polymorphism located within a transcription factor binding site important for CRH expression. Individuals with the more rare haplotype (15%), which was shown by a reporter gene assay to yield higher CRH expression, had higher cortisol levels during temporary separation from their mothers (ANOVA;  $n = 55$ ,  $p < 0.05$ ). I found an interactive effect of sex and genotype on birth weight, such that females with the less common haplotype were relatively small ( $n = 91$ ,  $p < 0.05$ ). Furthermore, mothers with the more "reactive" genotype spent more time in ventral contact with their infants during the first 12 weeks of life, (repeated measures ANOVA:  $p = 0.05$ ), suggesting that there are behavioral consequences to these genetic differences.

Researchers studying allelic association should consider that genotype could be related in different ways to various biological systems. While a particular genotype may be associated with traits that can negatively affect reproductive fitness, such as low birth weight, it may be maintained in a population through its association with adaptive personality traits or social strategies. Identifying CRH gene variants and their phenotypic correlates may lead to a better understanding of the interrelatedness and possible co-evolution of stress physiology, behavior, and life history in primates.

**Black and White Colobus Population Changes in Kakamega Forest, Kenya During a Period of Primary Food Tree Decline**

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Eastern black and white colobus monkeys, or guerezas (*Colobus guereza*), are regarded as one of the most ecologically-flexible forest primates. Guerezas have been reported to respond favorably to selective logging,

but little is known of the effects of smaller scale habitat changes on their population dynamics. We examined demographic changes within the guereza population in Kakamega Forest, Kenya over a 7-year period (1997-2004) during which this population experienced a major (24%) decline in its primary food tree species, the African cherry (*Prunus africana*). Using data from line transect censuses and group counts and compositions conducted in 1997-98 and 2003-04, we compared guereza density, biomass, and mean group size between these periods to determine whether the decline in *P. africana* at Kakamega was associated with concomitant declines in guereza population parameters. We found that guereza density increased by 6% and biomass by 12% between 1997-98 and 2003-04. Among our 5 long-term study groups, mean group size remained steady at 13 individuals per group over this period, with group size decreasing in 3 groups and increasing in 2 groups. *P. africana* mortality was not significantly higher in the home ranges of groups that decreased in size than in the ranges of groups that increased in size. The only result suggesting that *P. africana* mortality might be adversely affecting the guereza population at Kakamega was a 26% decline in the mean number of immatures per adult female over the study period, an indication that female reproductive rates and/or immature survival rates may be declining. While this trend warrants continued monitoring, most results from our study suggest that guerezas have responded well to the *P. africana* decline at Kakamega over the past 7 years. These results are consistent with the guereza's reputation for considerable ecological plasticity in response to changes in its habitat.

### **A Review of the Evolutionary Significance of Vertical Climbing as a Preadaptation to Bipedality**

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Human locomotion is qualitatively different from other primates and its functional origins have been debated extensively in the literature based on quantitative differences in anatomical structures (Stern, 1971, 1975; Fleagle JG, 1976; Vangor, 1979; Prost, 1980; Fleagle *et al.*, 1981; Lovejoy, 1988; Hunt, 1994, 1996; Gebo, 1996; Richmond *et al.*, 2001). Various primates and their locomotor repertoires have been used in attempts to establish postural models that account for pre-bipedal locomotion in the ancestors of early hominins. Here, primate based locomotor models are reviewed. In particular I focus on the significance of vertical climbing as a pre-adaptive mechanism for bipedal locomotion. The vertical climbing hypothesis, suggests that vertical climbing is a biomechanical link between the fore- and hindlimb anatomy found in antipronograde primates that allowed for a shift in locomotion from climbing to bipedal walking with very little or no change in the underlying anatomy (Stern, 1975; Fleagle *et al.*, 1981). Current research has shown that during vertical climbing, monkeys and apes exhibit muscle force and joint angles that are very similar to those used during human bipedal walking (Vangor, 1977; Fleagle *et al.*, 1981). In *Pan* and *Ateles*, the magnitude and duration of *gluteus medius* and *minimus* increased during bouts of vertical climbing (Schmitt, 2000). These are key muscles used in stabilizing the hip during stance phase. Further, certain types of vertical climbing may be more pre-adaptive than others (Hunt *et al.*, 1996; Hirasaki *et al.*, 2000; Isler, 2003, 2004, 2005). In comparing the magnitude of force used in the hip, thigh and calf muscles during vertical climbing in macaques and spider monkeys, Hirasaki and colleagues found significantly higher peak force in spider monkeys. These same muscles exhibit high muscle force in humans and are associated with bipedal walking. These data suggest that hip and thigh musculature used during vertical climbing could be pre-adaptive, facilitating a transition to upright posture and bipedality. The pre-bipedal ancestors of hominins probably utilized multiple locomotor strategies and attempts to reconstruct their locomotor behavior should analyze all types of kinesiological and kinetic data. Data presented here suggests that a model based on the type of vertical climbing practiced by *Ateles* would easily support a transition to bipedal locomotion.

### **Morphometrics and Ontogeny of the Subfamily Colobinae: Congruence Between Development and Evolutionary Relationships**

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The extant colobine species exhibit little cranial or dental variation among themselves and considerable convergence with other catarrhines. The purpose of the current study was to examine the ontogenetic  
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transformation of cranial and dental traits across colobine species to sort polarity of these traits and use them to test the monophyly of several suprageneric groups, including the African colobines, the Asian colobines, and the odd-nosed colobines.

A 3-D digitizer was used to collect 75 cranio-dental landmarks in growth series for species representing 11 colobine genera and two outgroups, *Macaca* and *Bunopithecus*. Individual configurations were fitted using Generalized Least Squares. Principal components were calculated for all non-dental landmarks. The first principal component (PC1) accounted for age-related shape development in all taxa, from infant morphology to full adult male morphology. PC1, used as a proxy for degree of shape development, was regressed on log-transformed centroid size (CS) for each species, controlled by sex.

The results of growth trajectory comparisons indicated that male growth trajectories are in general more variable than female. The Asian colobine taxa exhibit greater variation in growth than the African colobine taxa. The African colobine growth trajectories are most similar to the large-bodied non-odd-nosed *Semnopithecus-Kasi-Trachypithecus* group. Despite taxon-specific y-intercepts, the growth curves for the odd-nosed colobines had related slopes.

Overall, the growth trajectory data yielded a detailed picture of evolutionary relationships among the extant colobines: the odd-nosed colobine taxa exhibit persistent within-group similarities. The *Presbytis* species exhibit a high degree of variation in growth despite morphological homogeneity. The overall pattern of growth trajectory similarities roughly corresponds to geographic proximity, suggesting a history of *in situ* evolution for most of the extant colobine species.

### **Is There a Turnover Pulse Among African Pliocene and Pleistocene Cercopithecidae?**

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Vrba (e.g. 1992; 1995) has put forth a series of hypotheses about the evolution of African mammals, which she has termed "habitat theory." This theory posits that changes in global climate cause "turnover pulses", relatively short periods of time during which occur large numbers of first and last appearances of species. In this study the fossil Cercopithecidae of Africa are examined for evidence of turnover pulse, or other forms of faunal change, occurred either at 2.8 - 2.5 Ma at a time of major global cooling, or during other periods. The African cercopithecoid fossil record is well suited to this analysis because they occur at most African Pliocene and Pleistocene sites and are relatively speciose (Szalay & Delson, 1979; Delson, 1984; Jablonski, 2002). Furthermore, those from Eastern Africa are generally well dated. This is important because of the temporal nature of the hypotheses examined.

Several approaches are used. These include examination of cercopithecoid species ranges as well as the abundance of larger taxonomic units. As there are differing degrees of chronological and taxonomic control for different data from different sites, the material was divided into four data sets. The first two have both have a high degree of temporal control, and I was able to study original fossil material for nearly every specimen, yielding a high degree of taxonomic consistency. These are for the Afar Depression and Turkana basin. A third data set was made for the East African material which has good chronological control, but slightly less taxonomic control. Finally, a pan-sub-Saharan African data set was analyzed.

Both appearance and abundance data are examined for the Afar Depression and Turkana Basin, whereas only the species range data are studied for all East African and complete sub-Saharan analyses. The results provide no support for a turnover pulse 2.8 - 2.5 Ma. In fact, the largest number of first and last appearances are clustered around 3.4 and 2.0 Ma, with a shift in abundance at 3.4 Ma in both samples examined. These results are consistent with a relatively constant rate of turnover of cercopithecoids between about 4 mya and the holocene.

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**The Eurasian Fossil Papionin *Paradolichopithecus arvernensis*: Taxonomy, Function and Locomotor Behavior.**

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*Paradolichopithecus arvernensis* is a Late Pliocene papionin found at the European sites of Senèze, France, Graunceanu, Romania and most recently Vatera, Greece. It has usually been placed within the sub-tribe Macacina based on craniodental morphology, but Maschenko has suggested that it is in fact a species of *Papio*. Moreover, its postcranial remains indicate that it was probably larger than any living macaque and that it had a locomotor behavior most similar to that of *Papio*. Here we evaluate these assertions using new postcranial material from Vatera and a combination of classical and geometric morphometric techniques on both the cranial and postcranial remains from all three sites. Results support the assertion that craniodentally *P. arvernensis* is a sister taxon to the genus *Macaca*, but reveal that postcranially it is less macaque-like, and although most similar in morphological details to *Papio*, *Theropithecus*, and *Mandrillus*, is larger and more robust than modern *Papio*. We suggest that *P. arvernensis* was a large-bodied member of Macacina with a predominantly terrestrial locomotor behavior most similar to that of larger-bodied extant papioninans.

**Evolution of Dental Eruption Sequences in Living and Fossil Colobine Primates**

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Colobines are distinctive among catarrhines in their early eruption of molars relative to anterior teeth. We address the phylogenetic hypothesis of dental eruption sequence in colobines by examining fossil colobines from Europe and Africa. The degree of relative early molar eruption varies among colobine genera. Asian colobines (*Presbytina*) show more variation than do the African genera (*Colobina*), with sequences ranging from extreme early molar eruption in *Presbytis* to late (macaque-like) molar eruption in *Nasalis* (Harvati 2000).

The polarity of early molar eruption is unclear. Schultz (1935) suggested that the colobine pattern represents the primitive catarrhine condition. More recently, dietary and life-history hypotheses have been proposed to explain the variability in primate dental eruption sequences. If the colobine eruption pattern is primitive, it implies that papionins and hominoids converge on similar eruption sequences. Alternatively, if the colobine condition is derived, factors such as diet and mortality patterns probably shaped colobine eruption patterns.

Two fossil colobine species preserve juvenile specimens at informative stages of tooth eruption: *Mesopithecus pentelici* (Europe) and *Kuseracolobus aramisi* (Africa). Specimens were scored following Harvati (2000) from both original specimens and casts. The Late Miocene *Mesopithecus pentelici* erupts the second molar early relative to the second incisor, a common pattern in extant colobines (except *Nasalis*). The Early Pliocene *Kuseracolobus aramisi* does not show such an early relative eruption of the second molar, being most similar to *Nasalis* and to non-colobine catarrhines and less similar to living African colobines. The basal cercopithecoid *Victoriapithecus macinnesi* will be pivotal in furthering the understanding of the polarity of this trait. Unfortunately, twelve juvenile specimens examined in the Kenya National Museums were not complete enough to be informative on their eruption sequence.

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### Enamel Microstructure in *Cebus*

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As part of a larger research program on dental microstructure, ecology, and life history in the Cebidae (Platyrrhini), this study analyzes the dental microanatomy in capuchin monkeys (*Cebus*). I used a combination of confocal and circularly polarized/phase-contrast microscopy and automated montage techniques to generate images in which periodic tooth enamel increments (hence dental growth rates) could be analyzed. Results are preliminary, but several interesting observations and patterns emerge. Interestingly, different species of *Cebus* seem to possess varying lengths in long-term increment (i.e., Striae of Retzius) periodicity. This is unusual for primates, which usually tend to exhibit a narrow range of variation in Striae of Retzius even across whole families and superfamilies. The specimens studied also suggest a difference in prenatal vs. postnatal enamel secretion rates, and frequently exhibit large amounts of enamel prism decussation in molariform teeth. By restricting crack propagation within the tooth, this latter condition is presumably an adaptation to hard object feeding. Mapping decussation patterns can also be a valuable taxonomic tool as suggested by the recognition of a putative anomaly found in a specimen identified as *C. apella*, which exhibits less decussation than *C. capucinus*, contrary to expectations. Most likely, this reflects error in the original taxonomic assignment of the “zoo” specimen.

### Hunting Primates and the Future of Neotropical Forests

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One quarter of all primate species are currently threatened with extinction. The cause of this global decline in primate populations has been attributed to a number of anthropogenic disturbances including deforestation, habitat fragmentation, hunting and the illegal animal trade. While deforestation and habitat fragmentation typically alter landscapes on a large scale, hunting is a cryptic threat with no way to measure hunting using current remote sensing technologies. Defaunation poses a unique problem for conservation in that it reduces wildlife populations directly while impacting forest ecosystems indirectly by removing potential seed dispersers.

It has been demonstrated that hunters preferentially hunt large bodied game species, while mainly smaller bodied animals remain to act as vectors for seed dispersal. The remaining less preferred game species may then bias the forest structure. These rodents and similarly sized non preferred game feed on fallen fruit, often destroying large seeds, ingesting and ultimately defecating only small sized seeds that are still intact. Without larger bodied dispersers to transport large seeds, a forest's structure may be biased to contain more small seeded plants. It has been found that in forest fragments with presumably fewer large vertebrates, there are more small seeded saplings than large seeded saplings.

Studies have shown that two Neotropical Genera, *Ateles* and *Cebus*, are particularly effective seed dispersers. These primates ingest large quantities of seeds, disperse them far away from the parent tree and typically do not damage the seeds through their masticatory or digestive processes. They also deposit the seeds in small fecal piles, attracting fewer invertebrate seed predators. The hunting of primates may therefore have profound consequences for forest maintenance of undisturbed forests, while the loss of seed dispersal into recently logged areas may hinder regeneration by limiting seed rain. With primates consisting of up to 49% of the frugivorous biomass in some Neotropical forests, the loss of these animals may result in forests that are no longer capable of properly performing their ecological function.

Conservation schemes such as Integrated Conservation and Development Plans (ICDPs) are primarily concerned with habitat alterations on large scales. These development plans have largely neglected to account for the effects of hunting and the ultimate loss of game species from protected areas. Selective

logging as an alternative to clear cutting may be equally devastating for primate populations. As stated above, it has been shown that the arrival of logging companies in an area brings an increased demand for wild meat and increased exportation of bushmeat. These threats are compounded by logging companies that increase access to primates through habitat fragmentation and the construction of logging roads into forest previously inaccessible to humans. This increased access and demand together with the introduction of modern hunting technologies has led to unprecedented numbers of animals being hunted to local and inevitably global extinction.

It is imperative that we refocus on hunting when developing new conservation strategies, otherwise we will find ourselves left with a legacy of “empty forests”, protected from logging yet devoid of primates and other game species. Without protecting these important parts of the forest biota, we may lose our remaining protected areas with shotguns and snares rather than axes and chainsaws.

### **Stable Isotope Analysis of Subfossil Monkeys from Niah Cave (Sarawak, Malaysia)**

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Stable carbon and oxygen isotope ratios are presented for a sample of monkeys recovered from Niah Cave, a Late Pleistocene-Holocene archaeological site in Borneo. Monkey tooth enamel sampled to date includes *Macaca fascicularis* and *Presbytis* spp. For all fauna sampled from the site,  $\delta^{13}\text{C}$  variability is influenced by both ‘total’ diet and the so-called “canopy effect” whereas  $\delta^{18}\text{O}$  values are temperature-dependent, and thus influenced more by climate-related trends. Mid-upper canopy leaf monkeys (*Presbytis* spp.) show an average  $\delta^{13}\text{C}$  of  $-17.7\text{‰}$  whereas the lower canopy feeder *Macaca fascicularis* show an average  $\delta^{13}\text{C}$  of  $-14.5\text{‰}$ , although these numbers are likely to change due to ongoing data collection and analysis. Data from published literature offer important baseline data for the modern monkeys from Niah. Both carbon and oxygen isotope values seem to reflect paleoclimate changes at Niah Cave over time rather than a paleodietary change. In conjunction with isotopic analysis of the human remains, monkeys represent an important component towards understanding isotopic variability in a continually changing lowland rainforest setting.

### **Monkey Abundance and Market Hunting in Korup National Park, Cameroon**

Joshua M. Linder

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Korup National Park (KNP) in southwest Cameroon, long recognized for high species richness, diversity, and endemism, is home to eight anthropoid primate species. Though designated a national park in 1986, market hunting remains widespread in Korup and may be the most significant factor influencing primate abundance in these forests. This study reports the results of line-transect censuses and primate bushmeat surveys conducted in and around KNP and presents analysis of primate abundance, particularly as it relates to hunting pressure in the park. Ten line-transects distributed over three localities were selected based on the availability of previous primate survey data. Surveys of primate bushmeat were conducted in the town of Mundemba (park headquarters), the park village of Ikenge, and Tombe/Banyu, located on the periphery of the park. Results support prior findings that primate abundance in the Korup area is low relative to other censused Cameroonian forests. Compared to abundance estimates from previous surveys, results from this study suggest that densities of the endangered Preuss’s red colobus (*Procolobus pennantii preussi*) and drill (*Mandrillus leucophaeus leucophaeus*) may be declining across transect sites. At the transect site located outside, but on the periphery of KNP, encounter rates for all monkey species except *Cercopithecus pogonias* have declined considerably, with no visual or auditory evidence for the presence of the three largest monkeys (*M. leucophaeus*, *P. pennantii*, and *Cercocebus torquatus*). While signs of hunting are evident on all transects, degree of hunting pressure varies. Bushmeat surveys indicate that *C. nictitans*, *C. mona*, and *P. pennantii* are the most frequently hunted primates, together comprising 74% and 78% of the total primate offtake in Mundemba and Ikenge, respectively.

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### **Seed Predation by the Mona Monkey (*Cercopithecus mona*)**

Reiko Matsuda

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A majority of arboreal guenons is known to incorporate a large quantity of fruits in their diets. Seeds are either spat out or defecated. These monkeys are largely seed dispersers. When fleshy fruits become scarce, these guenons increase the amount of leaves or insects in their diets. During a 17-month study, I examined whether *C. mona*, in the Lama Forest of Benin, West Africa, follows a similar pattern of diet. The Lama Forest is a seasonally dry forest that is dominated by Caesalpiniaceae trees. The diversity of fleshy fruit species is low. The study encompassed five wet seasons, one short dry season, and two long dry seasons. During the wet seasons, many parts of the forest became inundated. The long dry seasons lasted 3-4 months per year. Because of the wariness of the monkeys, a frequency method was used to record feeding bouts. Fruits were the most important food for *C. mona*. More than 40% of the annual food came from just two species, *Dialium guineense* (Caesalpiniaceae) and *Diospyros mespiliformis* (Ebenaceae), which have the highest and second highest per hectare Basal Areas, respectively. During the wet seasons, they preferred feeding on the pulp of ripe fruits. When ripe fleshy fruits were not available, they ate the seeds of unripe fruits. When fleshy fruits became scarce during the long dry seasons, *C. mona* did not increase the amount of leaves or insects in their diet, but they extensively fed upon unripe seeds of *Dialium guineense* and seeds of other dry fruit species. It appears that seeds were favored because they were more nutritious and lower in secondary compounds than leaves.

### **Monitoring Hormonal and Morphological Changes During Pregnancy in Gelada Baboons (*Theropithecus gelada*)**

Colleen McCann<sup>1</sup>, Florence Klecha<sup>2</sup>, and Dan Wittwer<sup>3</sup>

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Studies assessing the reproductive state of female catarrhine primates have typically relied on changes in the perineal swellings and colorations as key external markers of ovarian events. Among the catarrhines, *Theropithecus* is unique in that the area of skin responding to hormonal changes in the ovarian cycle is located on the chest and throat rather than on the perineal region. Characteristically, the bare patch of skin on the throat and chest is surrounded by fluid-filled vesicles which respond to changes in estrogen and progesterone stimulation. Previous studies on the morphological and physiological correlates of estrus in female gelada baboons (*Theropithecus gelada*) have shown that the changes in the vesicles surrounding the chest patch can be an effective means for monitoring ovarian events. Additionally, there are distinct morphological changes in the appearance of the chest patch associated with pregnancy. In the present study, we monitored those morphological changes concurrently with the daily measurement of steroid hormone levels to determine if this morphological feature is a reliable external marker of internal hormonal changes during this reproductive state. In the first trimester, estrogen and progesterone levels show a marked increase while the chest patch becomes a bright red color and the fluid-filled vesicles begin to disappear. During the second trimester the throat and chest patch develop deep folds with the chest patch retaining its red intensity while hormone levels continue to elevate to 10 times their baseline values. In the third trimester – after week 22 – estrogen and progesterone levels begin to decline and plummet immediately after parturition as the chest patch turns a pale pink color. The results illustrate the distinct morphological changes observed during each trimester of pregnancy and the concomitant change in both estrogen and

progesterone excretion levels. This study emphasizes the use of urinary metabolites as an effective, non-invasive and ultimately less stressful method of obtaining information on hormonal activities and reproductive events than obtaining serum levels. The construction of a hormone profile is another step towards understanding reproduction in this and other species and determining the parameters of reproductive events. Furthermore, it is also a more accurate determination of gestational length than traditional methods of relying on visual cues such as estrus, copulation or menstruation, as their absence are not reliable indicators of conception.

### **Shade Coffee Plantations as Wildlife Refuge for Mantled Howling Monkeys (*Alouatta Palliata*): Implications for their Conservation**

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Areas outside of parks serve vital roles in conservation by serving as buffer habitat, connecting reserves separated by private lands, and retaining key biological elements. Shade coffee plantations, in which a contiguous canopy of native trees is left standing to protect the growing coffee bushes from direct sunlight, comprise a significant portion of remaining forested areas in Latin America and represent an important refuge for migratory birds and other fauna. Mombacho Volcano is a large, dormant volcano in southwestern Nicaragua whose flanks are dominated by shade coffee plantations that form an unofficial buffer zone. In a census of the Mombacho Reserve and surrounding areas it was discovered that this region supports a population of approximately 1,000 howler monkeys, one of the largest primate populations documented in western Nicaragua, and the majority of which live not in the reserve but in the surrounding shade coffee plantations. Subsequently, a study of the howlers in Finca La Luz, a 125-ha shade coffee plantation on the southwestern side of Mombacho, demonstrated that they rely primarily on the shade trees for their feeding, resting, and travel. The annual diet of the howlers is dominated by young and mature leaves, which together comprise 55% of observed feeding time. Mature and young fruits are also important food sources, providing 34% of the diet. The ten most important feeding trees account for over 75% of the total diet and the most important food species are relatively common in the shade coffee plantation, and include *Ficus costaricana*, *Enterolobium cyclocarpum*, and *Cecropia peltata*. The feeding trees most exploited for resources were generally found in areas of active coffee cultivation. Our results suggest that howlers in Mombacho's coffee plantations do indeed rely primarily on trees in areas of active shade coffee cultivation for food, travel, and rest. Shade coffee plantations are therefore serving as a vital refuge for howlers in this region. Conservation of this population will require the maintenance of traditional methods of coffee cultivation that preserve habitat and resources for primates and other fauna. Management plans for this area should therefore promote the use of shade-grown coffee as an environmentally-sound form of agroforestry. As a result, conservation education efforts highlight ecologically-friendly coffee growing practices and their effects on wildlife as a means to encourage agricultural practices that have a minimal impact on primates and other animals in the region.

### **Development of Cortical Bone Microstructure in Ugandan Vervet Monkeys (*Chlorocebus aethiops*)**

Shannon C. McFarlin

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The microscopic organization of primary (i.e., unremodeled) cortical bone reflects variation in bone depositional rates during ontogeny, and local mechanically-regulated dynamics of bone growth and development. There is a long tradition of examining primary bone histo-diversity as an important source of information about aspects of life history, namely individual growth patterns and environments. While studies of other vertebrates have demonstrated the potential of this approach, particularly in paleontological contexts, primary bone microstructure has remained largely unexplored in systematic investigations of primates.

The current study represents part of a larger effort to examine primary bone microstructural diversity in catarrhines, and focuses on a sample of wild-collected Ugandan vervet monkeys (*Chlorocebus aethiops*; n=32). The major aims of this research are to: 1) describe ontogenetic and taxonomic variability in primary bone microstructural organization, and 2) examine the potential of this variability for discriminating organismal growth patterns. Several features of primary bone at the midshaft femur and humerus were examined on brightfield and polarized light images of 100 micron-thick cross-sections: tissue type proportions, vascular patterns, and lines of arrested growth (LAGs). These features are interpreted within the context of observed patterns of secondary remodeling, and previously-characterized patterns of somatic growth in other body dimensions.

Quantitative results demonstrate that proportions of primary bone tissue types vary in an age-related manner. Younger age classes are characterized by higher proportions of tissues associated with fast depositional rates (i.e., fibro-lamellar tissues), while older age classes are characterized by tissues associated with slow depositional rates (i.e., lamellar bone). This transition is apparent by the time of M1 emergence in vervet monkeys, estimated to occur at the end of the first postnatal year. Element differences in tissue type proportions reflect increased secondary remodeling and marked postero-medial cortical drift at the midshaft humerus. Qualitative observations also indicate that more subtle age- and sex-related variation in bone growth rates may be reflected in features of the primary vascular network, particularly vascular canal density, and in the formation of LAGs. These and other results have significance for life history research in paleontological contexts.

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### **Color Vision Polymorphism in Squirrel Monkeys**

Michael Montague

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Unlike African and Asian primates, South American primates do not routinely possess trichromatic color vision. The genetic mechanisms that underlie the visual system of most platyrrhine genera allow some females to possess trichromatic vision while other females (and all males) cannot visually differentiate red from green; still, the selective basis for this polymorphism is not well understood. It has been suggested that trichromats are better equipped to detect fruit against a green background, yet it has also been suggested that dichromats are more capable of detecting cryptic, camouflaged objects. I propose to compare the costs and benefits of trichromatic versus dichromatic vision by studying the behavior of *Saimiri sciureus*, the common squirrel monkey. I hypothesize that there are individual differences in behavior, which result from and correlate with individual color vision polymorphisms.

Specifically, I will travel to the Tiputini Biodiversity Station in Yasuni National Park in January 2006 to assess behavioral differences in diet choice, harvesting style, leadership in group progressions, and vigilance among individuals living in their natural habitat. While collecting behavioral observations, I intend to further explore individual variation in foraging ability through the use of experimental feeding platforms and associated red-green color cues. I will also perform non-invasive collections of fecal samples to perform DNA extraction and sequencing techniques from which I can then deduce likely visual status.

This paper represents the hypotheses and methods of my research project as well as the genetic results that I have attained using a small sample of squirrel monkey DNA at New York University's Molecular Anthropology Lab. I also review the preliminary field observations that I gathered from a troop of squirrel monkeys during a month of pilot research in Ecuador throughout July 2005.

### **The Variegated Spider Monkey (*Ateles hybridus*) Conservation Project 2006 – 2010**

Alba Lucia Morales-Jimenez<sup>1,2</sup> and Andres Link<sup>1,2</sup>

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<sup>2</sup> Fundacion Biodiversa

The variegated spider monkey (*Ateles hybridus*) is a critically endangered primate distributed in Colombia and Venezuela. Recent molecular data supports species status for *A. hybridus*, but no information exists on its actual distribution, ecology, behavior or population genetics of wild populations. Only 18.8% of the potential habitat of *A. hybridus* in Colombia remains, and even this is rapidly being deforested and fragmented by human activities. Furthermore, hunting also represents a direct threat to wild populations. Less than 1% of its current distribution is protected by the national parks system and for all these reasons *Ateles hybridus* was recognized in 2004 as one of the 25 most endangered species of the world. Combined ex-situ, in-situ and education projects are necessary to protect this endangered species. This project is trying to find solutions for pet trade animals and is giving support to zoos and rescue centers in order to create an ex-situ conservation program. On the other hand this project is also supporting in-situ research, in-situ conservation initiatives, and will launch an educational campaign to reduce pet trade. We started the *Ex-situ Projects* by doing the Colombian Spider Monkey Studbook and now we are going to a) reconstruct pedigrees from DNA analysis of the captive population, b) start a breeding program in order to maintain viable populations, and c) evaluate the illegal pet trade on *A. hybridus* and to start finding solutions for these animals. We initiated an *In-Situ Project* with the following initiatives: a) ecological and behavioral research at Serrania de la Quinchas and b) estimation of densities of *A. hybridus* in Maceo-Antioquia. We are interested in the consolidation of a protected area for *Ateles hybridus bruneus* because this subspecies is not protected in any national park. Finally, we are going to start a campaign called "knowing the spider monkeys" in zoos to increase public awareness of this endangered species and its habitat.

### **Modelling Distributions for Colombian Spider Monkeys (*Ateles* spp.) to Find Priority Areas for Conservation**

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Colombian spider monkeys are under high human pressures resulting in the designation of one Critically Endangered (*Ateles hybridus*), one Endangered (*Ateles fusciceps*) and one Vulnerable (*Ateles belzebuth*) species. Knowledge of the historical and current distribution of these species and identification of threats are critical in order to establish priorities and potential areas for conservation and research. The objective of this research was to model the distribution of genus *Ateles* in Colombia and to find priority areas for conservation. We used locality data obtained from museum specimens, bibliographic research and I analyzed questionnaires returned by researchers that have worked in Colombia. We used climatic, topographic and vegetation data for this project, processing these data in a geographic information system and applying genetic algorithms for rule-set prediction (GARP) to model the distribution of the three species. We applied Gap analysis in order to find those areas important in the conservation of each species. At least 90% of the preliminary models were significantly non-random for the three species. Only 18.8% of the potential distribution remains for *Ateles hybridus* and at least 56.9% and 59.5% for *A. fusciceps* and *A. belzebuth* respectively. *Ateles hybridus* distribution area is the least protected of all, only 0.67% of the remnant area is protected. *Ateles hybridus* is the species that has suffered most from habitat destruction, resulting in a large reduction of its potential distribution area. This species is surrounded by a high number of human populations and this may be the reason for its high level of threat. Only 9% of the potential distribution area remained as continuous forest for *Ateles hybridus* and this demonstrates the critical situation for this species in Colombia.

### **Mitochondrial DNA Sequence Evidence for a Deep Phylogenetic Split in Chacma Baboons (*Papio hamadryas ursinus*) and the Phylogeographic Implications for *Papio* Systematics**

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In a recent publication, Newman, Jolly and Rogers (2004) proposed a phylogenetic hypothesis for *Papio* based on sequence variation in the Brown region of the mitochondrial genome. Their analysis revealed 4 major lineages and identified chacma haplotypes as the oldest (1.8mya) and most divergent, being the sister clade to other *Papio* allotaxa. While paleontological and morphometric data support this conclusion, their sampling scheme did not encompass the spectrum of morphologically distinct populations that fall under the taxonomic umbrella of “Chacma baboon” (*P.h. ursinus*). We collected 44 samples representing 7 distinct, well provenienced locations throughout South Africa (Western Cape - two locations, Eastern Cape, central South Africa, Gauteng province, Limpopo province). We sequenced the samples and aligned them with published sequences used in the Newman et al study, and employed the standard battery of phylogenetic methods as implemented in MacClade and PAUP4. Our analysis revealed two major lineages divided geographically along a meandering southwest to northeast transect. The Southern clade includes the Western and Eastern Cape populations, and is distinguished by a unique, three nucleotide deletion. The Northern clade includes the Gauteng and Limpopo populations. We estimate the divergence between the Northern and Southern Clades to have occurred approximately 1.2mya (+/- .18my). The deep phylogenetic split present in chacma populations may reflect accumulated changes driven by local geographic and climatic barriers to gene flow, or the influence of gene flow from northerly, non-chacma populations (ie, Greyfoots, Kinda) that have yet to be sampled.

### Late Pregnancy Glucocorticoid Hormones Predict Maternal Responsiveness in Wild Baboons (*Papio cynocephalus*)

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Glucocorticoids (GCs) are steroid hormones secreted in response to stressful stimuli and are believed to help organisms cope with and survive these challenges. During the perinatal period, GCs are hypothesized to increase maternal attraction and responsiveness to infant generated stimuli. We measured naturally occurring variation in maternal responsiveness to infant distress vocalizations during the first two postnatal months and used noninvasive techniques to measure excreted steroids during the two months prior to and after parturition in 34 wild mother-infant yellow baboon (*Papio cynocephalus*) dyads in Amboseli, Kenya. Fecal GCs exhibited a high degree of within individual stability across the perinatal period. Females with higher GC concentrations the month before parturition were more responsive to their infants' distress than females with lower GC concentrations. These patterns were not influenced by major maternal or infant characteristics, including maternal rank, parity or infant sex. They are consistent with the hypothesis that late pregnancy elevations in GCs “prepare” pregnant females for responding to stimuli from their neonates. This study represents the first evaluation of the relationships between perinatal GCs and the expression of maternal behavior in a wild animal population and provides the first evidence among wild animals for the preparative actions of GCs for responding to predictable anticipated challenges.

### Diversification of Lion Tamarins (*Leontopithecus*)

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*Leontopithecus* (Callitrichidae) is comprised of four morphotypes: black lion tamarins (*L. chrysopygus*), golden lion tamarins (*L. rosalia*), black-faced lion tamarins (*L. caissara*) and golden-headed lion tamarins (*L.*

*chrysomelas*). Lion tamarin differentiation and evolutionary history, and the possible influence of Quaternary climatic fluctuations on lion tamarin radiation were investigated. The mtDNA control region was sequenced and a phylogenetic and population aggregation analysis, plus a Mantel test for geographic/genetic correlation were performed.

Our data suggests (1) that *L. chrysomelas* occupies a basal position to the other lion tamarins, (2) *L. caissara* is not subspecific to *L. chrysopygus*, and (3) lion tamarin diversification may have been shaped by Quaternary forest refuges, with the oldest refuge located in Bahia, but diversification was not shaped by metachromism. The data suggest that three distinct lion tamarin taxa are evident (*L. chrysomelas*, *L. caissara* and *L. chrysopygus/L. rosalia*) and that *L. chrysopygus* and *L. rosalia* are differentiated below the phylogenetic species level. This data adds to our understanding of New World monkey diversification and taxonomic status.

### **Are Living Great Apes Sufficient as Models for Addressing Patterns of Variation in Fossil Hominins? A Case for Baboon Models**

Varsha Pilbrow

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In assessing patterns of variation and determining the taxonomic composition of a hominin fossil assemblage the phylogenetically closest modern comparators are *Homo* and *Pan* and following these, *Gorilla* and *Pongo*. However, does phylogenetic affinity make *Pan* more relevant as a model than *Gorilla* and *Pongo*? Furthermore, are apes better models than non-ape taxa? How useful phylogenetically relevant models are is examined in this paper by comparing patterns of dental variation in chimpanzees, gorillas and orangutans, and evaluating their ability to falsify single-species hypotheses in fossil hominins.

Given the prevalence of molars in hominin fossil assemblages, measurements taken on the occlusal surface of molars of the great apes are used to study patterns of dental variation. The sample is made up of 46 *P. paniscus*, 152 *P. t. troglodytes*, 64 *P. t. verus*, 79 *P. t. schweinfurthii*, 208 *G. g. gorilla*, 61 *G. g. graueri*, 30 *G. g. beringei*, 140 *P. p. pygmaeus*, and 25 *P. p. abelii*. Samples are collected from known localities, covering the natural range of distribution of these taxa. Discriminant analyses are used to study the apportionment of variation. Mahalanobis distances help determine the standards the great apes provide for fossil hominin taxonomic separation. Analyses are repeated using size-preserved and size-adjusted data, as well as sex-combined and sex-segregated data.

In all analyses, *P. paniscus* is well-differentiated from all other taxa. The subspecies of *P. troglodytes*, *G. gorilla* and *P. pygmaeus* are also easily distinguishable. However, *P. t. schweinfurthii* and *P. t. troglodytes* are closely affiliated; *P. t. verus* is well-separated from these two. When raw measurements are used the distances separating the east and west African gorilla subspecies are greater than the distances between the two chimpanzee species. Even when size-adjusted, dental distances between orangutan and gorilla subspecies are greater than the distances between the subspecies of *P. troglodytes*.

The disparity between the chimpanzee species and gorilla and orangutan subspecies can be related to differences in size and scaling patterns and sexual dimorphism in these taxa. While the differences may have taxonomic implications, they suggest that when all three great apes are used collaboratively as models, the distances between the well-recognized chimpanzee species will be overshadowed by the distances between gorilla subspecies. Thus, chimpanzees will have limited utility in falsifying a single species hypothesis in fossil hominins. Used on their own, species of *Pan* are likely to provide easy falsification a single species hypothesis. Examples of both outcomes in fossil hominin taxonomy are provided.

Great apes are characterized by unique evolutionary pathways and as such have limited utility as models for fossil hominins. As argued by Jolly (1970, 2001), baboons occupied the same savannah habitats as early hominins and paralleled them in patterns of evolutionary divergence. Therefore their relevance as ecological models needs to be considered. Given the shortcoming of great apes as models, this paper advocates the use of a broader comparative database, including great apes and baboons together as hominin models.

**Coalescent Time Complicates Calibration: Recent Primate Divergence Date Estimates are Too Early**

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Estimates of primate lineage divergence dates calculated from molecular data have become an important component of our understanding of evolutionary history. Most commonly, the rate of genetic change is calibrated by dated fossil material. However, it is not fully appreciated that the time of species divergence, which is the earliest possible date of diagnostic fossil evidence, must occur after the time of genetic divergence. The difference between the time of genetic divergence and the time of species divergence is the average coalescent time for the ancestral species. The impact of this coalescent time on the accuracy of divergence dates estimation is not well known. The effects of coalescent time on divergence date estimates were evaluated under a simple molecular clock model of molecular evolution using a coalescent time of 1 million years and calibration points set at 5 and 25 million years ago. In addition, because it is unlikely that fossil evidence coincides exactly with the time of speciation, further analysis was done with this underestimation error added to the coalescent error. The results of this study reveal that coalescent time introduces a bias into divergence date estimates. In particular, estimated divergence dates recent than the calibration point are often substantially overestimated. The possible impact of this coalescent bias on primate lineage divergence dates is evaluated.

**Multivariate Analyses of Guenon Limbs and Their Taxonomic Implications**Eric J. Sargis<sup>1</sup>, Carl J. Terranova<sup>2</sup>, and Dan L. Gebo<sup>3</sup><sup>1</sup> Yale University (PhD CUNY 2000)<sup>2</sup> City University of New York Medical School (NYCEP Postdoc 1996-97; NYCEP)<sup>3</sup> Northern Illinois University

Guenons (Primates, Cercopithecini) are relatively small-bodied Old World monkeys endemic to Africa. They exhibit a variety of substrate preferences, spanning from arboreal to semiterrestrial to terrestrial. Based on previous examinations of morphological and molecular data, it has been unclear if terrestriality evolved once or up to three times among guenons. In this study, we re-evaluate the postcranial data in light of recent molecular studies. We agree that terrestriality likely evolved only once among guenons. However, vervet, patas, and l'Hoest's monkeys exhibit many postcranial differences indicating that they have diverged significantly from the common ancestor of the terrestrial clade. We have recognized this terrestrial clade taxonomically by placing all three taxa in the genus *Chlorocebus*. We have also acknowledged their numerous postcranial differences by placing them in separate subgenera.

**Maternally-Initiated Babysitting by Wild Adult Male Equatorial Sakis (*Pithecia aequatorialis*) in Yasuni National Park, Ecuador**Christopher Schmitt<sup>1</sup>, Anthony Di Fiore<sup>1</sup>, Delanie Hurst, and Eduardo Fernandez-Duque<sup>2,3</sup><sup>1</sup> Department of Anthropology, New York University (NYCEP)<sup>2</sup> Zoological Society of San Diego<sup>3</sup> Department of Anthropology, University of Pennsylvania

Equatorial saki monkeys (*Pithecia aequatorialis*) live in socially monogamous groups wherein it appears that the mother does almost all direct infant care. This infant care strategy is unique among pair-bonded New World primates, in which helper-mediated, biparental, or male-dominated infant care is the norm, as seen in *Aotus*, *Callicebus*, and the Callitrichines. We report repeated observations of an adult female equatorial saki leaving her infants alone with her adult male pair-bonded partner. These episodes of maternally-initiated "babysitting" were noted within the context of focal follows of individual group members, as well as in *ad libitum* data, and involved the mother either encouraging or forcing the dismount of the infant in close proximity to the male or sneaking out of proximity while the infant was on excursion near the male. While babysitting, the male made no obvious investment in the infant and in fact discouraged any physical

interaction, though he also did not move away until the mother returned. Babysitting episodes were noted with two separate infants by the same female, and with two separate male residents in the same social group.

Such a maternal strategy makes sense in the framework of social monogamy, in that leaving the infant with the male may free the female to forage more efficiently without being burdened by carrying the infant, and thus may increase both her own and the male's future reproductive success. Indeed, during all observed episodes of babysitting, the female used the opportunity to forage. Improved infant survival is a hypothesized correlated benefit of the babysitting strategy, giving the infant presumed protection from predators via proximity to the male. These hypothetical benefits are thought to underlie the highly invested paternal care seen in *Callicebus* and *Aotus*, in which mothers initiate male care in a similar manner, though male care in these taxa is far more intensive. Though other forms of alloparental care (e.g., carrying) have been reported for other sakis (*Pithecia pithecia*), this is the first time that male babysitting behavior has been documented in equatorial sakis. More concrete evidence of maternally-initiated babysitting with a pair-bonded male could imply that such behavior is a uniquely derived form of low investment paternal care.

### Genital Swellings in Silvered Langurs: What Do They Indicate?

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Numerous hypotheses have been proposed to explain the occurrence of exaggerated sexual swellings in multi-male/multi-female groups. Furthermore, these exaggerated sexual swellings often encompass anatomical parts beyond the external genitalia. In a number of species, these swellings indicate periods of fertility with maximum swellings occurring for a number of days, indicating a window where ovulation is likely to occur. Swellings also occur in some species in which one-male groups predominate. These swellings are often non-exaggerated (confined to the external genitalia). However, it is less clear what these non-exaggerated swellings could indicate. We investigated the occurrence of genital swellings throughout the reproductive cycle in an Asian colobine, the silvered langur (*Trachypithecus cristatus ultimus*), to determine whether or not these swellings serve the same purpose as those exaggerated swellings found in cercopithecines. Behavioral data were collected from November 2002 through March 2004 during 2,948 hours on nine adult females of a one-male/multi-female group at the Wildlife Conservation Society's Bronx Zoo. All occurrence sampling of female sexual behavior and male inspection were conducted during a six-hour observation period recorded daily via video camera. The degree of swelling was assessed directly for each female on a 3-point scale. Times of proceptivity, receptivity and attractivity occurred significantly more frequently when females had no swellings. In cycling females, approximately 70% of the females' days with proceptive and receptive behaviors as well as male inspections occurred on days with no swellings. In pregnant females, swellings increased in frequency and size as pregnancy progressed. Thus, genital swellings do not indicate the likelihood of ovulation nor do swellings seem to influence the male's behavior. Swellings in silvered langurs may be explained by fluctuations in the estrogen to progesterone ratio. Only future hormonal analysis can clarify this issue.

### Primary Motor Cortex Asymmetry is Correlated with Handedness in Capuchin Monkeys (*Cebus apella*)

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Humans exhibit a strong population-wide tendency towards right handedness and structural asymmetries of the brain's primary motor cortex are associated with the direction of hand preference. We report that similar asymmetries are also significantly correlated with hand preference in a New World monkey (*Cebus apella*)  
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that does not display population-level handedness. Structural magnetic resonance images were obtained from seven captive male brown capuchins and the extent of primary motor cortex in the region of hand representation was measured as the intrasulcal depth of the precentral gyrus. Handedness was determined for each subject using a simple reaching task and a coordinated bimanual task. Results indicate that asymmetry of central sulcus depth is significantly different between left-handed and right-handed individuals for the coordinated bimanual task, but not the simple reaching task. While left-handed individuals have a deeper central sulcus in the contralateral hemisphere, right-handed individuals have a more symmetrical central sulcus depth. Our findings demonstrate that cerebral hemispheric specialization for hand preference is not unique to humans and may be more common among primates in general.

### **To Chisel or Chomp? Functional Divergence in Mangabey Facial Form**

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Among cercopithecines the mangabey genera *Cercocebus* and *Lophocebus* are distinguished by pronounced facial shortening and retraction. The similar facial proportions of these taxa have been shown to result from nonhomologous displacements of cranial growth allometries; however, the functional and ecological implications of mangabey facial form continue to be debated. Under the classic lever model of the masticatory system, facial retraction is linked with greater masticatory efficiency and increased relative bite forces. Thus, mangabey facial geometries have been viewed as adapted for the forceful incision and powerful mastication associated with hard-object frugivory. At the same time, disparities between mangabey genera in the relative frequency of feeding behaviors—*Lophocebus* engages in more incisal fruit preparation while *Cercocebus* favors postcanine hard-object crushing—suggest some degree of functional and ecological divergence. Although significant differences in mandibular shape consistent with a hypothesis of functional divergence have been documented, analogous distinctions in facial form remain to be identified. To this end, mangabey facial geometries were evaluated relative to predictions of the constrained lever model of the masticatory system. Specifically, if *Lophocebus* is adapted for forceful incision, relative facial retraction and relatively short molar rows are expected. Conversely, if *Cercocebus* facial form is adapted for postcanine crushing, more medially positioned tooth rows, increased relative biarticular breadth, and decreased relative tooth row length are expected.

Three-dimensional craniometric landmarks capturing functional aspects of the masticatory complex were recorded for a large sample of cercopithecines and selected colobines. Coordinates for the approximate locations of jaw adductor resultant forces were calculated by linear interpolation. Procrustes-aligned coordinates were subjected to principal components analysis, and principal axes of shape variation were explored statistically and graphically. As expected, *Lophocebus* exhibits pronounced facial shortening and retraction, an abbreviated posterior molar row, and an expanded incisal region—all supporting the hypothesis that *Lophocebus* mangabeys are adapted for forceful incisal biting. Contrary to predictions, *Cercocebus* exhibits increased biarticular breadth, a short, broad palate, and an expanded antemolar tooth row; thus, the hypothesis that *Cercocebus* is adapted for postcanine mastication is not supported. To explain the well documented nut-cracking capabilities of *Cercocebus* mangabeys, it is suggested that transferring forceful mastication to the anterior-most extent of the postcanine tooth row allows *Cercocebus* to circumvent theoretical constraints on facial retraction. Alternate functional hypotheses relating to premolar expansion in *Cercocebus* will be considered.

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### **Cheek Pouch Use by Blue Monkeys (*Cercopithecus mitis stuhlmanni*) in the Kakamega Forest, Kenya**

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The primate subfamily Cercopithecinae shares with seventeen other mammalian families sacculations beneath the skin of the cheek wall that are used predominantly for food storage. One difference between cercopithecines and other cheek-pouching mammals is that cercopithecines are gregarious rather than solitary foragers, suggesting different selective pressures for cheek pouch evolution because feeding competition is likely greater in gregarious species. Two hypotheses for the evolution of cheek pouches in cercopithecines have been proposed: 1) cheek pouches increase feeding efficiency in the face of intraspecific competition; and 2) cheek pouches reduce vulnerability to predation by allowing retreat to safer positions to process stored food. We investigated the influence of intraspecific competition and predation on cheek pouch use in two groups (GS and GN) of blue monkeys (*Cercopithecus mitis*) in the Kakamega Forest, Kenya. We predicted that monkeys would cheek pouch to minimize time at feeding sites where intraspecific competition was most intense, and would reduce exposure to predation by filling pouches and then moving to safer areas to process food. We used 20-min focal animal samples to document foraging behavior, cheek pouch volume and use, exposure to predation, and level of intraspecific competition in 35 individuals (adults, large juveniles, and medium juveniles) from June-August 2004. To assay the influence of competition, we calculated the average number of individuals within 3 meters of the focal animal while foraging. We modified Lambert's (2005) 'safety of position' scale to evaluate vulnerability to predation of foraging monkeys. We compared these estimations of competitive pressure and predation risk in feeding bouts that included cheek pouch use vs. those that did not. GS and GN both cheek-pouched fruits and leaves (the largest components of their diet) more than any other food item, though GS cheek-pouched leaves more than GN ( $X^2$ ,  $p < 0.0003$ ). There was a greater frequency of cheek-pouching in GS (72%,  $N = 127$  feeding bouts) compared to GN (41%,  $N = 58$  feeding bouts). In both groups, monkeys were in safer locations while emptying their cheek pouches than they were while filling them. When monkeys filled their cheek pouches, there were more individuals within 3 meters than when they were feeding without filling their cheek pouches. Our results suggest that both exposure to predation and intraspecific competition influence the foraging behavior and cheek pouch use of blue monkeys, and agree with previous field studies conducted on other cercopithecine species (Lambert 2005). Our results also suggest that variation in cheek pouch use between groups of one population may depend on factors such as group size and composition, travel patterns, and food availability within different home ranges.

### **No Evidence (Yet) for Evolutionarily Significant Gene Flow Between Sympatric, Hybridizing Guenons**

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Hybridization is known to occasionally occur between five pairs of sympatric *Cercopithecus* species: *C. cephus* & *C. nictitans*, *C. ascanius* & *C. mitis*, *C. pogonias* & *C. mitis*, *C. pogonias* & *C. ascanius*, and *C. pogonias* & *C. mona*. Here, we review recent mitochondrial, Y-chromosomal, and X-chromosomal phylogenies of the "arboreal" *Cercopithecus* monkeys and show that these hybridizing pairs do not cluster as sister-taxa. Thus, we have no evidence – yet – of evolutionarily significant gene flow between these forms. It is likely that the successful introgression and fixation of exotic genetic lineages has been restricted to rare, advantageous alleles during much of the evolutionary history of the forest guenons. We predict that future phylogenetic studies of protein-coding genes will reveal that a subset of loci do, indeed, cluster hybridizing taxa, indicating an exchange of beneficial alleles.

### **Who is *Xenothrix*? A Three-Dimensional Cranial Shape Study Using Geometric Morphometrics**

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Discovered on the island of Jamaica, *Xenothrix mcgregori* is a late Quaternary platyrrhine initially only known from a left mandibular ramus. Fieldwork in the Jamaican cave localities during the 1990's have augmented the specimen count to 17, including new cranial and postcranial remains. However, the relationships between *Xenothrix* and other New World monkeys, both extant and extinct, are still contentious – current

debate centers on whether *Xenothrix* is an endemic Antillean monkey, sister to *Paralouatta* and *Antillothrix*, or whether it is more closely related to *Aotus* and *Callicebus*. To shed light on this issue, 31 cranial landmarks were collected using a Microscribe 3D digitizer for six extant platyrrhine species – *Alouatta*, *Aotus*, *Callicebus*, *Cebus*, *Saimiri*, and *Pithecia*, totaling 111 specimens – and the *Xenothrix* and *Paralouatta* cranial specimens. The purpose of this study is to investigate the cranial shape variation among *Xenothrix*, *Paralouatta*, and the proposed extant platyrrhine sister groups. Specifically, the study hypothesizes that if the extant clades can be successfully shown to cluster together using the 3D landmark method, then the same principle – and possibly phylogenetic inference – may be applied in examining the affinities of *Xenothrix* and its relationship to *Paralouatta*. Preliminary results indicate that *Xenothrix* and *Paralouatta* vary significantly in the maxillary region, particularly in the shape and orientation of the palate. Moreover, *Alouatta* and *Paralouatta* share a much closer craniofacial shape structure than either is to *Xenothrix*. 3D geometric morphometrics is a preferential approach because it allows for the quantification of traditional qualitative comparisons, and it eliminates size related problems and permits the extraction of true shape difference.

### Molecular Phylogenetic Affinities of the Simakobu Monkey (*Simias concolor*)

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We present the first molecular study to examine the phylogenetic position and taxonomic status of the simakobu (*Simias concolor*), or pig-tailed snub-nosed monkey. This critically endangered primate is endemic to the Mentawai Islands of Indonesia, and several hypotheses have been suggested as to its phylogenetic relationships: 1) *Simias concolor* should be included within the genus *Nasalis*, perhaps as a subgenus; 2) *Simias* is part of a larger “odd-nosed” group; and 3) *Simias* is nearly basal to the colobine clade with a long, independent course of evolution.

To test these hypotheses, we sequenced approximately 420 base pairs of the cytochrome b gene from the hair of a wild caught Simakobu individual. Comparative sequences from colobines and cercopithecines were obtained from GenBank, and phylogenetic trees were produced using maximum parsimony, maximum likelihood, and Bayesian analyses.

The results show a close sister taxon relationship between the Simakobu and Proboscis monkey nested inside a monophyletic Asian colobine group. Furthermore, the nucleotide sequence divergence estimates between *Simias* and *Nasalis* are comparable to those among colobine congeners, rather than intergeneric divergences. Although further work, such as use of longer mtDNA sequence, nuclear markers, and larger sample sizes, may be needed to substantiate these conclusions, this study tentatively suggests placing the Simakobu within the genus *Nasalis*. The results have implications for Asian colobine taxonomy and biogeography, as the genus-level status of *Simias* has been disputed, and a large geographic discontinuity exists between the distributions of the Simakobu and Proboscis monkey.