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# Scaling of Size and Dimorphism in Primates II: Macroevolution

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*Previous researchers found positive scaling of body size and sexual size dimorphism (SSD) in primates, known as Rensch's rule. The pattern is present in Haplorhini, but absent in Strepsirhini. I found that positive evolutionary correlations between size and SSD drive positive scaling relationships within Haplorhini as a whole and Platyrrhini, Cercopithecinae, Colobinae, and Hominoidea individually at the generic level and higher, but that evolutionary correlations within genera in these clades are often nonsignificant or negative. I suggest that positive evolutionary correlations result from greater change in male than in female size, usually because of sexual selection acting on polygynous populations. I suggest that negative evolutionary correlations result from greater change in female size, owing to either natural selection or, in Callitrichidae, sexual selection acting on polyandrous populations. The high incidence of negative evolutionary correlations within Haplorhini suggests a relatively large influence of natural selection on SSD, at least with regard to differences in SSD between congeners. I propose two possible explanations for the difference in intrageneric and supergeneric evolutionary patterns: 1) natural selection is a relatively weak force for modifying SSD and has a noticeable effect only when one compares related species experiencing similar levels of sexual selection, and 2) natural selection is a relatively strong force for modifying SSD but is less likely than sexual selection to affect higher level taxonomic comparisons noticeably because of the cumulative effect over time of marginal differences in mortality rates of these two types of selection.*

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*I discuss types of data required to test these explanations and implications for reconstructing fossil behavior.*

**KEY WORDS:** body size; natural selection; Rensch's rule; sexual selection.

## INTRODUCTION

In the middle of the last century, Bernhard Rensch observed that sexual size dimorphism (SSD) scales positively with body size in many birds and mammals (Rensch, 1959). Research on primates since then has investigated the scaling of size and SSD within various primate clades (Abouheif and Fairbairn, 1997; Clutton-Brock *et al.*, 1977; Ford, 1994; Gaulin and Sailer, 1984; Kappeler, 1990; Leutenegger, 1978; Leutenegger and Cheverud, 1982; Lindenfors and Tullberg, 1998; Martin *et al.*, 1994; Plavcan and van Schaik, 1997a; Smith and Cheverud, 2002). Together, these studies generally show that Rensch's rule is present in haplorhine primates, but absent in strepsirhines (see Lindenfors and Tullberg, 1998).

However, it is not clear why there should be a positive scaling relationship between size and dimorphism in any radiations at all. Investigators have proposed several different explanations for Rensch's rule, which Fairbairn (1997) grouped into eight categories. I combine these categories into three general types of explanations: 1) increases in body size cause or facilitate increases in SSD, 2) correlations of genetics or selection pressures between sexes cause changes in dimorphism and body size of both sexes when selection is applied to the size of one sex, and 3) natural selection applies differential sex-specific selection pressures resulting in changes in size and dimorphism.

Little support exists for models that propose a causational role for body size in the determination of SSD in primates (Mitani *et al.*, 1996; Plavcan, 2001; Plavcan and van Schaik, 1997a; Smith and Cheverud, 2002). Absence of scaling of dimorphism with body size in strepsirhines in itself refutes arguments for an obligatory relationship between size and SSD. As Fairbairn (1997) notes, there is no *a priori* reason such as biomechanical constraint to suppose dimorphism must scale positively with size.

Alternatively, some models suggesting that size and dimorphism both change in response to sex-specific differences in selection pressure or additive genetic variation explicitly predict scaling of size and dimorphism (e.g., Lande, 1980; Zeng, 1988). Differences in sex-specific selection pressures can result from sexual selection, in which large size is advantageous in competition between members of one sex for access to mating opportunities—intrasexual competition—or individuals actively seek large size in potential mates—intersexual competition (Andersson, 1994; Darwin, 1871); selection differences can also arise from natural selection resulting from sexual niche separation, differential response to resource pressures, and fecundity selection among other forces (Andersson, 1994; Lindenfors, 2002; Ralls, 1976; Selander, 1966; Shine, 1989; Slatkin, 1984).

According to many investigators, within primates, sexual selection produces sexual size dimorphism (Barton, 2000; Clutton-Brock, 1985; Clutton-Brock *et al.*, 1977; Ford, 1994; Gaulin and Sailer, 1984; Lindenfors and Tullberg, 1998; Martin *et al.*, 1994; Mitani *et al.*, 1996; Plavcan, 1999, 2001; Plavcan and van Schaik, 1997a; Rodman and Mitani, 1987). Some have argued that the positive relationship that often exists between SSD and body size in haplorhines results from a positive association between sexual selection and body size (Clutton-Brock *et al.*, 1977; Gordon, 2004; Mitani *et al.*, 1996; Plavcan and van Schaik, 1997a; Weckerly, 1998). If such is the case, Rensch's rule in living haplorhines is largely the result of sexual selection, presumably modifying male body size more than female.

If one defines body size dimorphism as a ratio of mean male size divided by mean female size, change in dimorphism will scale positively with change in body size of either sex whenever male body size changes more than female; greater change in female size will produce a negative evolutionary scaling relationship, in contrast to Rensch's rule (Fig. 1). When size changes are equal in both sexes, body size changes are not associated with changes in dimorphism. Thus evolutionary scaling relationships can identify the sex that has undergone greater size change in sister-taxon pairings. If changes in dimorphism are primarily the result of sexual selection acting more intensely on male than on female size then most evolutionary scaling relationships for size and dimorphism should be positive, reflecting greater change in male size.

The accompanying article (Gordon, 2006) raises the possibility that natural selection may also play an important role in producing changes in dimorphism, at least in microevolutionary change. Natural selection can affect female body size more strongly than male body size via a variety of mechanisms. For example, in times of severe resource stress small females may reproduce more often than larger females (Downhower, 1976) or larger females may compete more successfully for limited resources (Leigh and Shea, 1996), fecundity selection may favor larger females that produce higher quality offspring (Ralls, 1976) or smaller females that reproduce at an earlier age (Lindenfors, 2002), or diet may favor large size to increase digestive efficiency (Plavcan and van Schaik, 1997a). If greater change occurs in female than in male size within an evolutionary lineage,

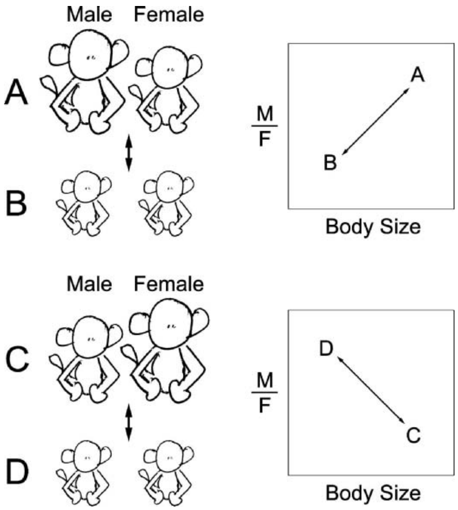


**Fig. 1.** Scaling relationships of size and SSD associated with changes in sex-specific size. When selection acts primarily on males, male size will increase (B to A) or decrease (A to B) more than female size, resulting in positive scaling of SSD (shown here as a ratio of male to female size) and body size. When selection acts primarily on females, female size will increase (D to C) or decrease (C to D) more than male size, resulting in negative scaling of SSD and body size.

whether the result of natural selection or sexual selection acting more intensely on females, then evolutionary scaling relationships for size and dimorphism within the lineage should be negative, counter to Rensch's rule.

I used traditional and phylogenetic comparative techniques to identify the relationship between evolutionary change in body size and SSD within primate lineages and the current patterns of body size and SSD scaling among modern primates. The term modern refers to relationships in extant primates measured via traditional regression analyses. Intrageneric and supergeneric evolutionary patterns refer to relationships preserved in the phylogeny of living primates. I compared all three types of scaling patterns and used them to develop an explanatory mechanism for the macroevolution of Rensch's rule that can accommodate all observed relationships within primates, most notably the presence of Rensch's rule in Haplorhini and absence in Strepsirhini. In particular, I investigated the relationship between evolutionary change between congeners and between higher-level taxa to determine if it is possible to identify common trends in SSD evolution across the order Primates.

# SAMPLE

Purvis and Webster (1999) point out that data quality is paramount in phylogenetic analyses because of the emphasis on differences between closely related taxa. Rather than including all taxa for which body mass data are available, I assembled data from published and unpublished sources only for primate taxa where in measurements are available from ≥4 individuals of each sex (Appendix A). In most cases I consider species the basic taxonomic unit, i.e., I calculate one mean for all populations of a species, though I treat subspecies as separate taxa when sample sizes meet the data set criteria and sex-specific means differ considerably between subspecies. The sample comprises 157 taxa representing 143 species of Primates, including 19 Lemuroidea, 10 Lorisoidea, 3 Tarsioidea, 47 Ceboidea, 53 Cercopithecoidea, and 11 Hominoidea.

# METHODS

## Measuring Size and SSD

Past studies of scaling of size and SSD in primates have generally analyzed either the relationship between female and male size (Clutton-Brock *et al.*, 1977; Leutenegger, 1978; Lindenfors and Tullberg, 1998; Martin *et al.*, 1994; Weckerly, 1998) or the relationship between female size and an index of dimorphism (Ford, 1994; Kappeler, 1990; Plavcan and van Schaik, 1997a; Smith and Cheverud, 2002). As Smith (1999) points out, regression slopes of log [M] against log [F] are exactly equal to regressions slopes of log [M/F] against log [F] plus 1, where in M and F refer to mean male mass and mean female mass, respectively. Although one may prefer log [M] over log [M/F] as the dependent variable in regression analyses because dimorphism is a function of female and male size, not a property independent of male size, it is much easier to see differences between positive scaling and negative scaling of size and dimorphism on a plot of log [M/F] against log [F], where SSD scaling trends appear as lines with positive and negative slopes, respectively, than on a plot of log [M] against log [F], where SSD scaling trends appear as lines with slopes >1 and <1, respectively. I used log [M/F] as the dependent variable to maximize the visual impact of bivariate plots, with the caveat that one understand standard errors to apply to the log of male size and not SSD. Coefficients of determination ($r^2$) differ between the 2 types of regression, and I calculated them with log [M/F] as the dependent variable.

The primate literature includes both base 10 logarithm and the natural logarithm base *e*, and though individual values differ depending on the logarithmic transformation one uses, slopes will be identical. I apply base 10 logarithmic transformations to published and unpublished sex-specific body mass means for 157 primate taxa (Appendix A). Because mean body size varies between populations, I calculated specific means as the mean of population averages when all constituent populations have $\geq$4 members of each sex, denoted by P in Appendix A. When all populations do not meet the criterion, I calculated specific means as a weighted mean of each population average with the number of individuals as weights, denoted by W in Appendix A.

Smith and Jungers' (1997) compilation of primate body mass data is the source for much of the mass data in Appendix A. I also drew mass data from other published sources as well as unpublished data that field workers in Madagascar generously provided. Eric Delson supplied museum numbers and body mass data from a recent review of size in extant and extinct cercopithecoids (Delson *et al.*, 2000). These data were used to calculate sex-specific means for geographically distinct populations identified in the *Catalogue of Primates in the British Museum (Natural History) and Elsewhere in the British Isles* (Napier, 1981, 1985). In general, mass data from wild populations and large populations are preferred over data from captive and small populations, but I include means from captive or small groups or both if no other datum is are available for a particular primate species. I report population means separately within Appendix A whenever possible.

## Phylogeny

Phylogenetic relationships may affect comparative analyses of size and SSD in two main ways: 1) Scaling patterns may differ between major clades, e.g., strepsirhines and haplorhines may exhibit very different patterns in the scaling of size and dimorphism, and 2) Closely related taxa may share similar values for dependent and independent variables because of shared evolutionary history rather than a functional relationship between variables.

To address the first phylogenetic concern, I followed Smith and Cheverud (2002) in analyzing major primate clades separately. I considered relationships separately for Strepsirhini and Haplorhini; Platyrrhini and Catarrhini; and Cercopithecinae, Colobinae, and Hominoidea.

To address the second phylogenetic concern, I supplemented traditional regression techniques with phylogenetic regression techniques. I conducted phylogenetic analyses via a branching sequence and divergence dates based on Purvis' (Purvis, 1995; Purvis and Webster, 1999) composite primate phylogeny. I further resolved the Purvis supertree by considering more recent molecular phylogenies in constructing the tree I used; the Newick code is available for the complete branching sequence (Appendix B).

Though one hopes that the phylogenetic branching sequence accurately represents the ancestral-descendant relationships within primates, some errors in the topology are likely. Several studies have shown that some inaccuracies in branching sequence and branch length do not compromise results of phylogenetic methods (Diaz-Uriarte and Garland, 1998; Martins, 1996a; Martins and Garland, 1991; Martins and Housworth, 2002). Some have suggested that in absence of knowledge of the true phylogeny, one should perform analyses on a large number of random trees (Martins, 1996b) and use partial knowledge of phylogenies to constrain random trees so that random branching sequences are generated only for the unknown portion of the phylogeny (Housworth and Martins, 2001). However, Symonds (2002) found that random trees are particularly poor in estimating the actual evolutionary correlation between characters. In a recent study of the relationship between competition levels and SSD in primates, Plavcan (2004) found that swapping branches did not significantly change results. The tree for my study is well resolved, and Plavcan's (2004) results indicate that the few inaccuracies in branching sequence are unlikely to affect the results of phylogenetic analyses.

I initially based branch lengths for the phylogeny on Purvis' (1995) estimates of divergence dates for various nodes in his supertree. When dates were unavailable, I used Grafen's (1989) method based on species diversity to scale branch lengths between nodes of known age and tips. For cases in which resulting dates disagreed with younger divergence dates reported in Purvis (1995), or with information from the fossil record, I assigned divergence dates for the undated nodes as occurring at half the time from the last dated divergence to the present, an admittedly arbitrary but replicable procedure. I found absolute values of standardized contrasts correlate significantly with their standard deviations at $\alpha = 0.05$ for the trees and transformed branch lengths according to Garland *et al.* (1992). I used Grafen's (1989) $\rho$-transform to modify branch lengths such that absolute values of standardized contrasts and their standard deviations are uncorrelated. The method scales the height of the entire tree to 1, then transforms the height of each node, i.e., the distance between the node and terminal taxa, by raising it to the user-selected positive exponent $\rho$. Values for $\rho$ are: Strepsirhini, 0.38; Haplorhini, 0.69; Platyrrhini, 0.50; Catarrhini, 0.62; Cercopithecinae, 0.35; Colobinae, 0.35; Hominoidea, 0.26.

## Traditional Regressions

I attempted to identify evolutionary relationships between size and dimorphism via techniques that take into account the relatedness of taxa expressing the traits in question, i.e., phylogenetic comparative methods. However, it is appropriate to consider the relationship between size and SSD as it exists among extant taxa via traditional regression techniques for two reasons. 1) It represents the present state of affairs—modern scaling patterns—and any explanation of Rensch's rule must accommodate the observed data. 2) It is a benchmark against which to compare phylogenetic analyses. I calculated regressions with log [F] and log [M/F] as the independent and dependent variables, respectively.

The choice of regression model is important. Because error exists in both variables, model I regression, i.e., OLS, is inappropriate, and so one should use model II regression. Smith (1999) showed that reduced major axis (RMA) regressions are appropriate for regressions of log [M] against log [F], but overestimate regression slopes of log [F] and log [M/F]; however, major axis (MA) regression performs well in both situations. Consequently, I use MA regression.

## Phylogenetically Independent Contrasts

I performed phylogenetic comparative analyses via Felsenstein's (1985) phylogenetically independent contrasts (PIC) method, calculating contrasts via the PDAP:PDTREE (Midford *et al.*, 2002) module of Mesquite 1.0 (Maddison and Maddison, 2003). I calculated PIC slopes by constraining a major axis regression to pass through the origin in contrasts space; however, it is possible to map regressions onto the original data by forcing the PIC slope to pass through the reconstructed base ancestral state for all characters in an analysis (Garland and Ives, 2000). Phylogenetic slopes and intercepts will usually differ from those produced by traditional regressions.

Considering how a phylogenetic regression is generated can help in understanding the meaning of differences between traditional and phylogenetic regression results. Phylogenetically independent contrasts are data points produced by calculating standardized differences in traits (log [F] and log [M/F] in my study) between sister taxa—observed taxa in the case of tips (operational taxonomic units, or OTU), and hypothetical taxa in the case of internal nodes (hypothetical taxonomic units, or HTU). Bivariate phylogenetic regressions are therefore a line passing through the ancestral reconstruction of the $X$ and $Y$ variables, weighted away from horizontal by the relationship between the two variables in pairs of sister taxa. If size and dimorphism always increase or decrease together, the regression line will take on a significantly positive slope. If one trait always decreases when the other increases, and vice versa, the line will take on a significantly negative slope. Combination of both patterns will tend to result in slopes that do not differ significantly from zero. Thus PIC regressions produce phylogenetically weighted slopes that measure the association between variables once one takes into account the relatedness between taxa.

Differences between traditional and phylogenetic regressions can provide important information on the evolutionary history of sets of traits. For example, consider the case of a traditional regression with a significantly positive slope and a PIC regression on the same data with a slope that does not significantly differ from 0. The significant positive relationship in the traditional regression may result from a pattern at the base of major adaptive radiations, and the lack of a significant relationship in the PIC analysis could result from the absence of the pattern or presence of multiple patterns in more recent relationships. It is possible to test for such differences directly between supergeneric and lower-level taxonomic scaling patterns via a particular type of contrasts analysis.

## Supergeneric Phylogeny vs. Intrageneric Phylogeny

Internal nodes in a PIC analysis are not estimates of ancestral states (Smith and Cheverud, 2002), but are phylogenetically weighted means of all descendant OTUs. Comparisons of nodes at the base of genera are therefore similar to comparisons of generic-level arithmetic means except that internal nodes incorporate information regarding the relatedness of species within each genus. Contrasts between deep internal nodes in an accurate phylogeny reflect patterns relating to supergeneric taxonomic groups; contrasts between tips and shallow internal nodes reflect more recent evolutionary patterns and variation in living taxa.

Contrasts for each data set are divided into two groups: intrageneric contrasts, defined as phylogenetically independent contrasts between OTUs or HTUs within the same genus, and supergeneric contrasts, defined as phylogenetically independent contrasts between OTUs or HTUs that differ at the generic level or higher. Regressions are performed separately on the two groups to identify recent and ancient patterns. Analyses of intrageneric contrasts, similar to paired-taxa analyses in which pairs are restricted to congeners, identify relationships between variables in closely related taxa. Analyses of supergeneric contrasts identify deeper phylogenetic signals—relationships between clades as represented by their living descendants, the surviving small fraction of all the species that ever descended from the ancestral progenitors of those clades. Intrageneric contrasts can exhibit more noise as a result of measurement error, sampling error, and stochastic variation. Error variance in independent variables produces lower than expected model I regression slopes for traditional and phylogenetic analyses (Harvey and Pagel, 1991), which can result in lower slopes for more recent nodes than for older nodes (Purvis and Harvey, 1995; Taggart *et al.*, 1998). However, model II regression slopes, such as generated by the MA regression technique, are not as sensitive to error in the independent variable and are less likely to be artificially flattened (Garland *et al.*, 1992). Thus greater noise in intrageneric contrasts relative to supergeneric contrasts should affect only the strength of the correlation, not the trend, i.e., slope of the MA regression. Similar slopes in regression analyses of both types of contrasts indicate that the relationship between variables is consistent in both groups. Differences in slopes may indicate that patterns in all taxa living at a particular point in the past are different from patterns in all more recent taxa; alternatively, differences may indicate that patterns in the supergeneric phylogeny are not representative of all species for a particular point in the past, as many of those taxa did not leave living descendants.

## RESULTS

In reporting results, I mapped PIC regression slopes onto OTU data to generate intercept values. I also transformed branch lengths to meet the assumption of no relationship between absolute value of standardized contrasts and standard deviations (Diaz-Uriarte and Garland, 1996; Garland *et al.*, 1992). Some have suggested that the transformation process reduces the degrees of freedom in regression analyses by an additional two (Diaz-Uriarte and Garland, 1996, 1998) or three (Smith and Cheverud, 2002). To base comparisons of significance between traditional and phylogenetic analyses on the same degrees of freedom, I did not base $p$-values for phylogenetic analyses on degrees of freedom reduced for branch transformations. Sample sizes in this study are large enough that a difference of 3 degrees of freedom will usually not make a difference in significance tests at $\alpha = 0.05$.

**Table I.** Major axis regression parameters for traditional and phylogenetically independent contrasts (PIC) interspecific regressions of $\log_{10}$[M/F] vs. $\log_{10}$[F]

| | | Traditional major axis | | | | PIC major axis | | | |
|---|---|---|---|---|---|---|---|---|---|
| Group | $N$ | Slope | Intercept | $p$ | $r^2$ | Slope | Intercept | $p$ | $r^2$ |
| Strepsirhini | 33 | −0.010 | 0.001 | 0.316 | 0.033 | 0.005 | 0.003 | 0.768 | 0.003 |
| Haplorhini | 124 | 0.083* | 0.063 | $< 0.001$ | 0.212 | 0.055 | 0.077 | 0.163 | 0.016 |
| Platyrrhini | 48 | 0.054* | 0.039 | 0.006 | 0.153 | 0.019 | 0.057 | 0.557 | 0.008 |
| Catarrhini | 73 | 0.043 | 0.110 | 0.279 | 0.016 | 0.098 | 0.049 | 0.125 | 0.033 |
| Cercopithecinae | 38 | 0.174* | 0.085 | $< 0.001$ | 0.341 | 0.208* | 0.059 | 0.001 | 0.260 |
| Colobinae | 20 | 0.460* | −0.318 | 0.014 | 0.252 | 0.003 | 0.097 | 0.986 | 0.000 |
| Hominoidea | 15 | 0.201* | −0.144 | 0.001 | 0.556 | 0.250* | −0.196 | 0.016 | 0.383 |

Note that PIC regression parameters are situated in raw data space by passing regression lines through the reconstructed value of the base node. Probabilities correspond to $H_0 = 0$.
*Significant difference from $H_0$ at $\alpha = 0.05$.

## Strepsirhini

I consider the two suborders of primates, Strepsirhini and Haplorhini, separately. For Strepsirhini ($N = 33$), the traditional regression slope of $\log_{10}$[M/F] against $\log_{10}$[F] is slightly negative, though not significantly so, as the coefficient of determination ($r^2$) is low (Table I). Similarly, slopes for phylogenetic analyses are not significantly different from zero (slope = 0.005, $p = 0.768$), indicating that body size and dimorphism are not related in the Strepsirhini (Fig. 2a).

Slopes for intrageneric and supergeneric (between genera and higher-order taxonomic divisions) independent contrasts within Strepsirhini do not differ significantly from zero (Fig. 2b), indicating a consistent absence of a relationship between body size and dimorphism over evolutionary time in strepsirhines (Tables II and III).

## Haplorhini

Regression of SSD against size in Haplorhini ($N = 124$) yields a significantly positive traditional regression slope (Table I), though the phylogenetic slope is not significantly different from zero. The results indicate that though size dimorphism scales positively with body size in living haplorhines, the relationship disappears once one takes into account similarities attributable to phylogeny (Fig. 3a).

Unlike strepsirhine patterns, size dimorphism scaling patterns in haplorhines differ between intrageneric and supergeneric contrasts (Table II). Supergeneric contrasts have a significantly positive regression slope, whereas intrageneric contrasts have a negative regression slope that

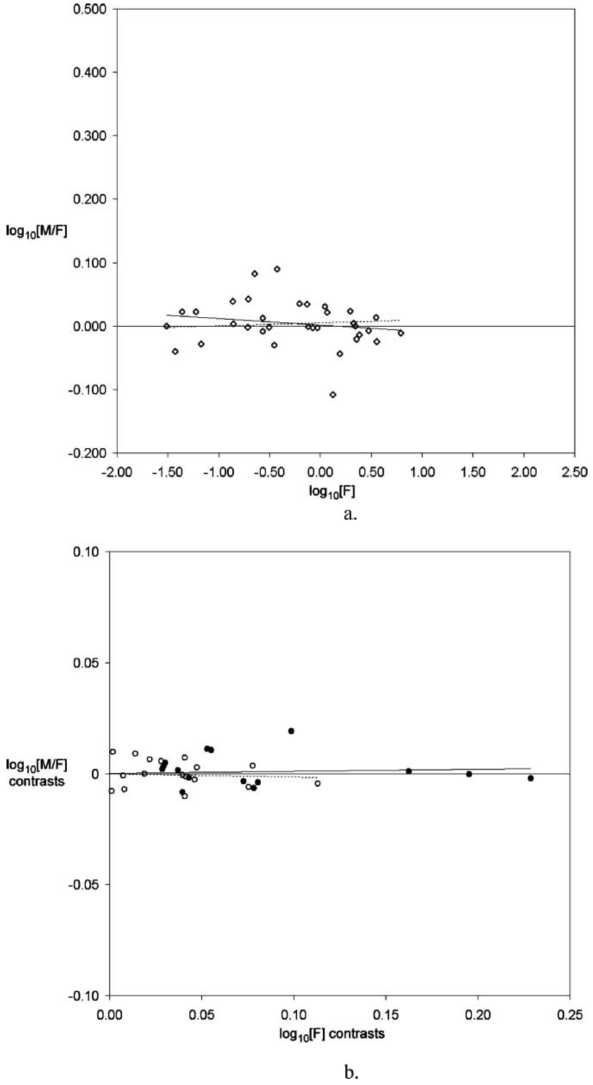


**Fig. 2.** (a) Interspecific regressions of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Strepsirhini. Solid line is traditional major axis; dotted line is PIC major axis. Neither regression slope differs significantly from 0. (b) Regressions of supergeneric and intrageneric contrasts of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Strepsirhini. Closed circles are supergeneric contrasts; open circles are intrageneric. Solid line is major axis regression for supergeneric contrasts; dotted line is major axis regression for intrageneric contrasts. Neither regression slope differs significantly from 0.

**Table II.** Major axis regressions of $\log_{10}$[M/F] contrasts vs. $\log_{10}$[F] contrasts

| Group | Contrasts | *N* | Slope | *p* | $r^2$ | Positive contrasts (%) |
|---|---|---|---|---|---|---|
| Strepsirhini | S | 15 | 0.009 | 0.642 | 0.017 | 53 |
| | I | 17 | −0.015 | 0.652 | 0.014 | 41 |
| Haplorhini | S | 33 | 0.137* | 0.012 | 0.185 | 64 |
| | I | 90 | −0.072 | 0.231 | 0.016 | 37 |
| Platyrrhini | S | 12 | 0.059 | 0.233 | 0.138 | 50 |
| | I | 35 | −0.186* | 0.004 | 0.224 | 26 |
| Catarrhini | S | 19 | 0.233* | 0.026 | 0.251 | 68 |
| | I | 53 | −0.038 | 0.650 | 0.004 | 45 |
| Cercopithecinae | S | 10 | 0.229* | 0.018 | 0.511 | 90 |
| | I | 27 | 0.135 | 0.303 | 0.042 | 52 |
| Colobinae | S | 6 | 0.433 | 0.263 | 0.262 | 83 |
| | I | 13 | −0.272* | 0.025 | 0.362 | 23 |
| Hominoidea | S | 4 | 0.278 | 0.286 | 0.492 | 50 |
| | I | 10 | −0.037 | 0.816 | 0.007 | 30 |

*Note.* Contrasts are separated into recent (within genera) and ancient (between genera and higher taxonomic groups). I: intrageneric contrasts; S: supergeneric contrasts. Regressions are constrained to intercept the *y*-axis at 0. Probabilities for slopes correspond to $H_0 = 0$.
"Positive contrasts" refers to the percentage of contrasts in which difference in female size and difference in dimorphism are positively associated.
*Significant difference from $H_0$ at $\alpha = 0.05$.

does not differ significantly from zero (Fig. 3b). Similarly, most supergeneric contrasts are positive while most intrageneric contrasts are negative (Table II): positive contrasts are consistent with positive scaling, i.e., greater difference in male than in female size, while negative contrasts are consistent with negative scaling, i.e., greater difference in female than in male size.

The intrageneric contrasts regression is heavily leveraged by a single point in the lower right of Fig. 3b, which is an artificial contrast in that it is

**Table III.** Major axis regressions of $\log_{10}$[M/F] contrasts vs. $\log_{10}$[F] contrasts for intrageneric contrasts with "artificial" *Semnopithecus entellus* contrast removed

| Group | Contrasts | *N* | Slope | *p* | $r^2$ | Positive contrasts (%) |
|---|---|---|---|---|---|---|
| Haplorhini | I | 89 | 0.106 | 0.090 | 0.032 | 37 |
| Catarrhini | I | 52 | 0.168* | 0.046 | 0.075 | 46 |
| Colobinae | I | 12 | 0.018 | 0.903 | 0.002 | 25 |

*Note.* Abbreviations as in Table II. Regressions are constrained to intercept the *y*-axis at 0. Probabilities for slopes correspond to $H_0 = 0$.
"Positive contrasts" refers to the percentage of contrasts in which difference in female size and difference in dimorphism are positively associated.
*Significant difference from $H_0$ at $\alpha = 0.05$.

at the base of a tritomy—the divergence of *Semnopithecus entellus entellus*, *Semnopithecus entellus schistacea*, and *Semnopithecus entellus theristes,* which also appears in the catarrhine and colobine analyses. In polytomies, branches of near-zero length are arbitrarily inserted into trees to force trees to assume the dichotomous branching sequences necessary to generate contrasts. Thus the leverage point in Fig. 3b does not necessarily represent an actual relationship between sister taxa. When one removes the artificial recent contrast, the slope becomes positive (slope $= 0.106$, $p = 0.090$; Table III and Fig. 3b). Also of note is that substantial difference in body size but not SSD characterizes the two basal contrasts Anthropoidea-Tarsioidea and Platyrrhini-Catarrhini (Fig. 3b).

## Platyrrhini

The suborder Haplorhini is divided further into the infraorders Platyrrhini and Catarrhini. As seen in haplorhines as a whole, the traditional regression slope of $\log_{10}$[M/F] vs. $\log_{10}$[F] is significantly positive for platyrrhines ($N = 48$), while the phylogenetic regression slope is not significantly different from zero (Table I, Fig. 4a). Thus size dimorphism scales positively with body size in living platyrrhines, but only when one does not consider similarities attributable to phylogeny.

Intrageneric and supergeneric contrasts differ within Platyrrhini, but not in the same manner as in Haplorhini as a whole. While the supergeneric contrasts slope is more positive than the intrageneric contrast slope, the pattern of significance differs from that of haplorhines: the supergeneric contrasts slope is positive, though not significantly so, and the intrageneric contrasts slope is significantly negative; in addition, supergeneric contrasts are evenly split between positive and negative contrasts while intrageneric contrasts are overwhelmingly negative (Table II, Fig. 4b). The platyrrhine clade with the highest percentage of negative intrageneric contrasts is the Callitrichidae (9 of 11, or 82%).

With the exception of two contrasts, supergeneric SSD contrasts are of relatively low magnitude (vertical displacement from the *x*-axis in Fig. 4b). The large positive contrast is between Callitrichidae—*Callithrix*, *Cebuella*, *Leontopithecus*, and *Saguinus*—and the *Cebus-Saimiri* clade, reflecting the relatively small size and low dimorphism of callitrichids or the relatively large size and high dimorphism of the other clade, or both. The large negative contrast is between the *Ateles-Lagothrix* clade and *Alouatta*, and is particularly low because of the large size and low dimorphism in *Ateles* and *Lagothrix* (Fig. 4a). Without these two contrasts, the supergeneric

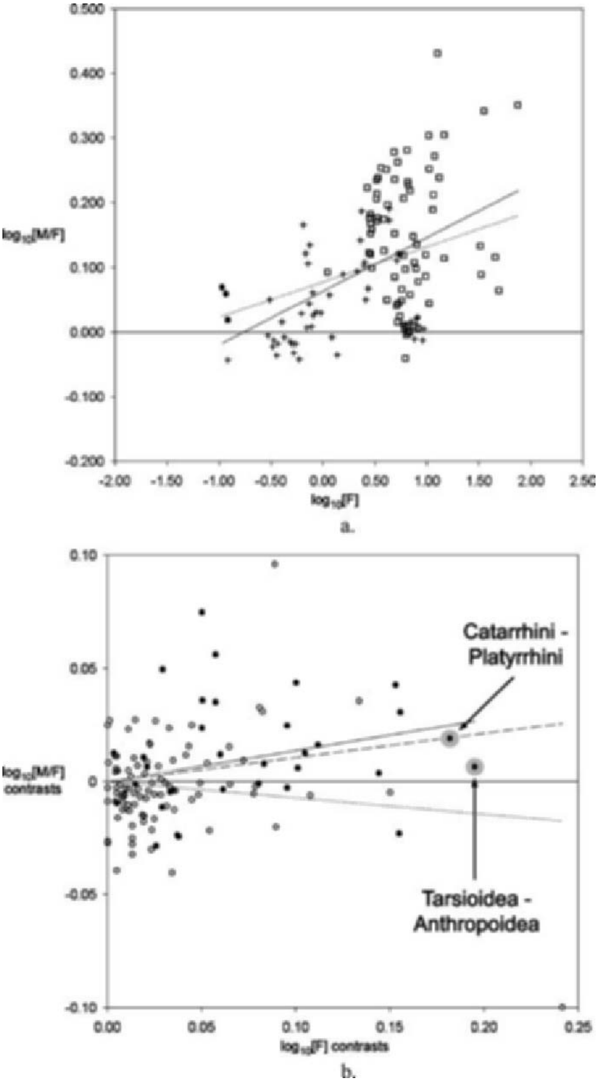


**Fig. 3.** (a) Interspecific regressions of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Haplorhini. •, Tarsiidae; +, Platyrrhini; □, Catarrhini. Solid line is traditional major axis; dotted line is PIC major axis. Traditional slope is significantly positive. PIC slope is not significantly different from 0. (b) Regressions of supergeneric and intrageneric contrasts of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Haplorhini. Closed circles are supergeneric contrasts; open circles are intrageneric. Solid line is major axis regression for supergeneric contrasts, dotted line is major axis regression for intrageneric contrasts, dashed line is major axis regression for intrageneric contrasts with low outlier removed (see text). Supergeneric contrasts slope is significantly positive. Neither intrageneric contrasts slope is significantly different from 0. Basal contrasts are highlighted.

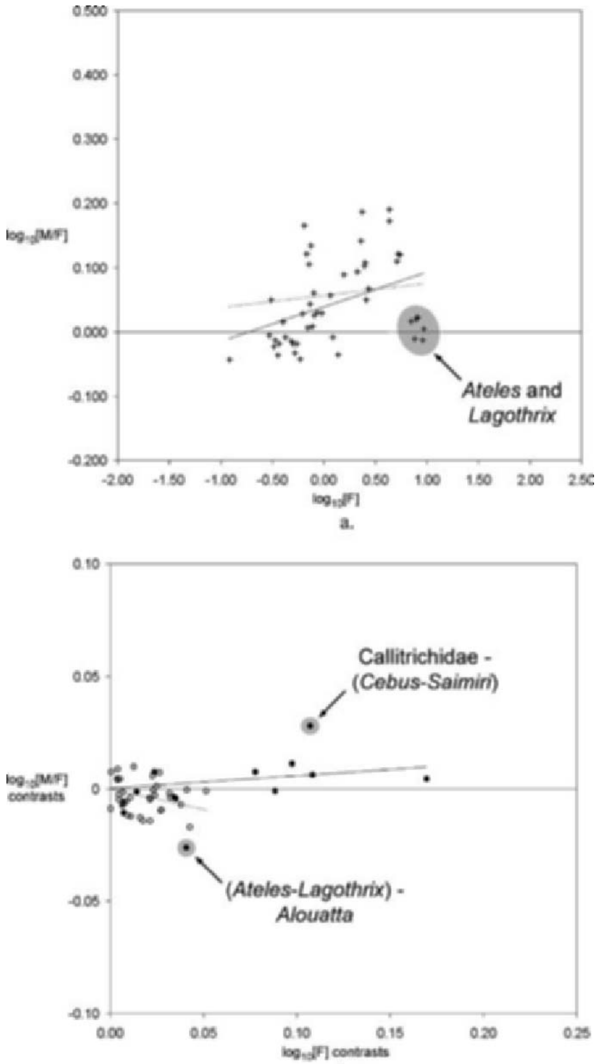


**Fig. 4.** (a) Interspecific regressions of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Platyrrhini. Solid line is traditional major axis; dotted line is PIC major axis. Traditional slope is significantly positive. PIC slope is not significantly different from 0. Note the largest taxa in this analysis are essentially monomorphic (*Ateles* and *Lagothrix*). (b) Regressions of supergeneric and intrageneric contrasts of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Platyrrhini. Closed circles are supergeneric contrasts; open circles are intrageneric. Solid line is major axis regression for supergeneric contrasts, dotted line is major axis regression for intrageneric contrasts. Supergeneric contrasts slope is not significantly different from 0. Intrageneric contrasts slope is significantly negative. Note the 2 supergeneric contrasts that deviate considerably from the regression line.

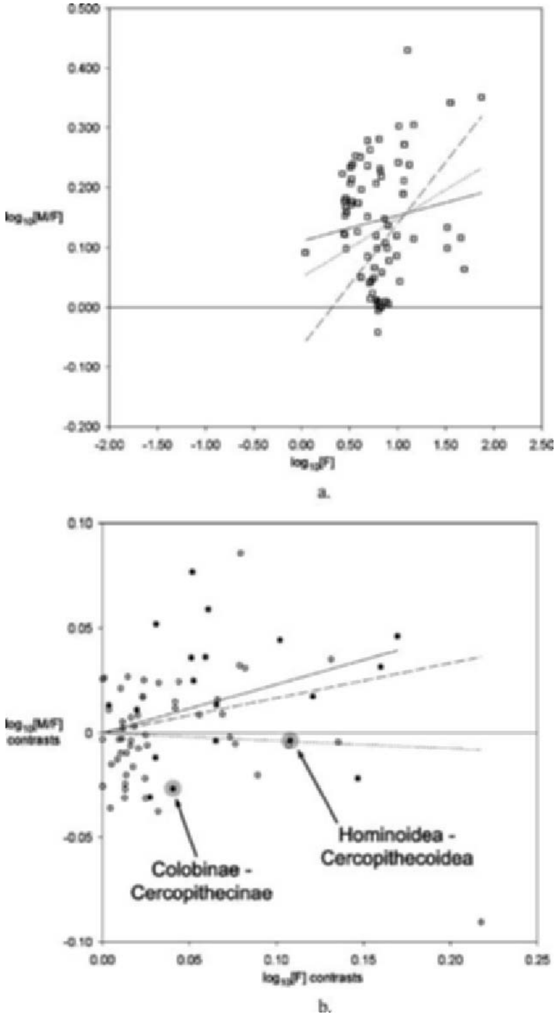


**Fig. 5.** (a) Interspecific regressions of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Catarrhini. Solid line is traditional major axis; dotted line is PIC major axis, dashed line is the PIC major axis regression with the *Semnopithecus* contrast removed. Only the dashed regression line has a significantly positive slope. Note that both phylogenetic slopes are higher than the traditional slope. (b) Regressions of supergeneric and intrageneric contrasts of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Catarrhini. Closed circles are supergeneric contrasts; open circles are intrageneric. Solid line is major axis regression for supergeneric contrasts, dotted line is major axis regression for intrageneric contrasts, dashed line is major axis regression for intrageneric contrasts with low outlier removed. Supergeneric contrasts slope is significantly positive. Slope for all intrageneric contrasts is not significantly different from 0; however, the slope for intrageneric contrasts with outlier removed is significantly positive (see text). Basal contrasts are highlighted.

regression slope is slightly lower, but a tighter fit (slope $= 0.041$, $r^2 = 0.247$, $p = 0.144$).

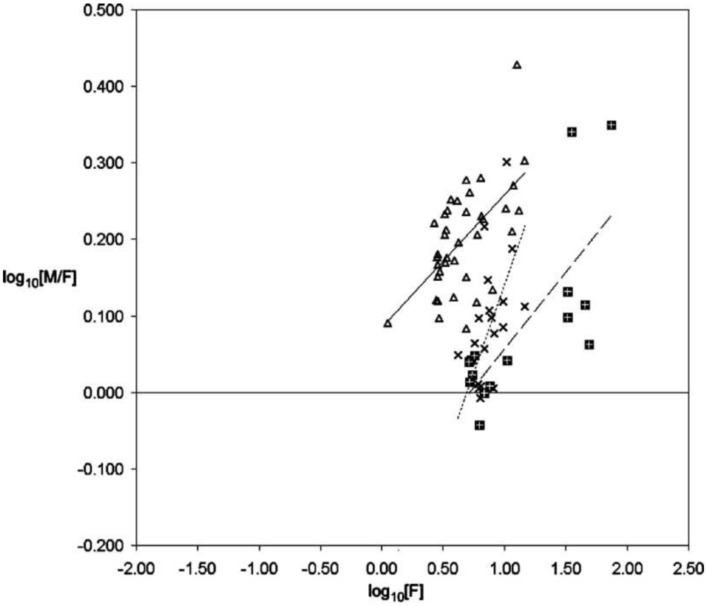
## Catarrhini

Regression slopes for catarrhines ($N = 73$) differ from the previous non-strepsirhine regressions in my analysis in that the traditional slope is not significantly positive (Table I, Fig. 5a). Also, the phylogenetic regression slope is higher than the traditional slope. When one removes the base *Semnopithecus* contrast, the phylogenetic regression slope becomes even steeper and significantly positive (slope $= 0.206$, $r^2 = 0.151$, $p < 0.001$).

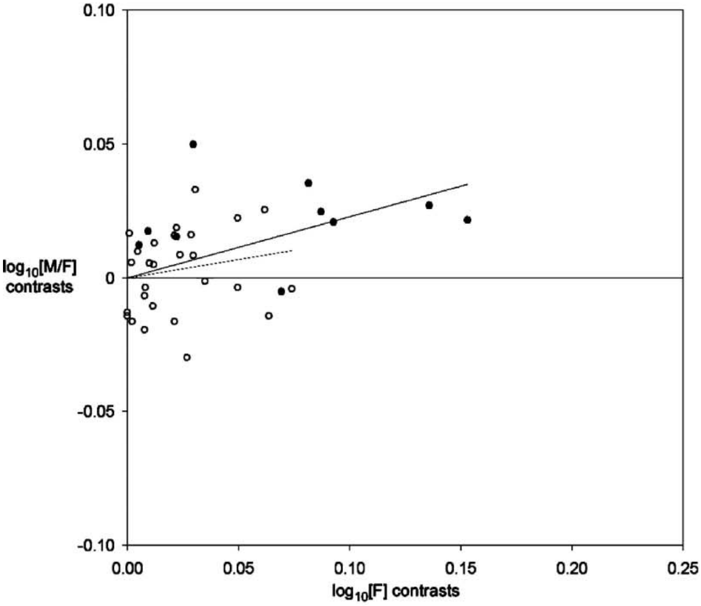
As in all previous analyses, size dimorphism in Catarrhini scales positively with body size for supergeneric contrasts and negatively for intrageneric contrasts, significantly so only for supergeneric contrasts; more than two thirds of supergeneric contrasts are positive whereas slightly more than half of intrageneric contrasts are negative (Table II, Fig. 5b). When one removes the *Semnopithecus* contrast, the intrageneric contrasts slope becomes significantly positive, though not as high as the supergeneric contrasts slope (Table III, Fig. 5b).

When one further subdivides catarrhines into Cercopithecinae, Colobinae, and Hominoidea, traditional regressions have significantly positive slopes for all groups, and the nonsignificant traditional slope for Catarrhini as a whole results from what is essentially a grade shift between the 3 clades (Fig. 6a). The grade shift is pronounced in the contrast between Cercopithecinae and Colobinae for both size and dimorphism, while the shift

**Fig. 6.** (a) Interspecific regressions of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Catarrhini by smaller clades. △, Cercopithecinae; ×, Colobinae; ■, Hominoidea. Traditional major axis regression lines: solid, Cercopithecinae; dotted, Colobinae; dashed, Hominoidea. (b) Regressions of supergeneric and intrageneric contrasts of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Cercopithecinae. Closed circles are supergeneric contrasts; open circles are intrageneric. Solid line is major axis regression for supergeneric contrasts; dotted line is major axis regression for intrageneric contrasts. Supergeneric contrasts slope is significantly positive. Slope for intrageneric contrasts is not significantly different from 0. (c) Regressions of supergeneric and intrageneric contrasts of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Colobinae. Closed circles are supergeneric contrasts; open circles are intrageneric. Solid line is major axis regression for supergeneric contrasts, dotted line is major axis regression for intrageneric contrasts, dashed line is major axis regression for intrageneric contrasts with low outlier removed. Supergeneric contrasts slope is not significantly different from 0. Slope for all intrageneric contrasts is significantly negative; however, the slope for intrageneric contrasts with outlier removed is positive, though not significantly so (see text). (d) Regressions of supergeneric and intrageneric contrasts of $\log_{10}$[M/F] vs. $\log_{10}$[F] in Hominoidea. Closed circles are supergeneric contrasts; open circles are intrageneric. Solid line is major axis regression for supergeneric contrasts, dotted line is major axis regression for intrageneric contrasts. Supergeneric and intrageneric contrasts slopes are not significantly different from 0. Note that the supergeneric contrasts slope is highly leveraged by 2 contrasts.

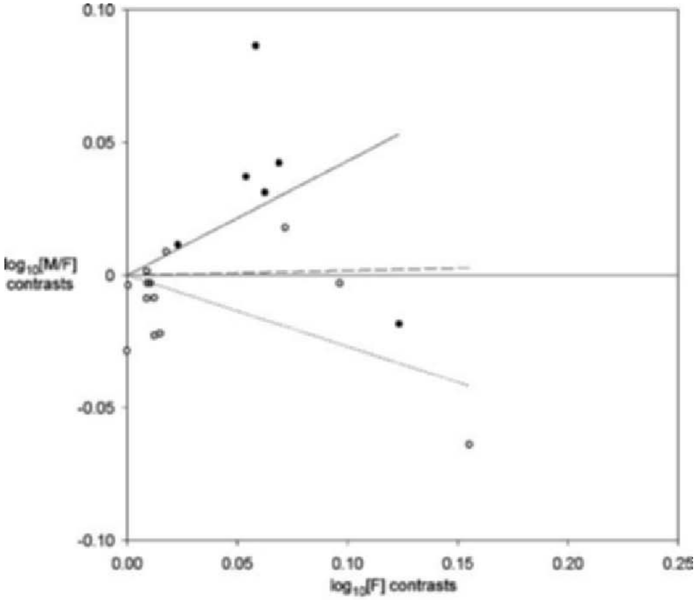


a.

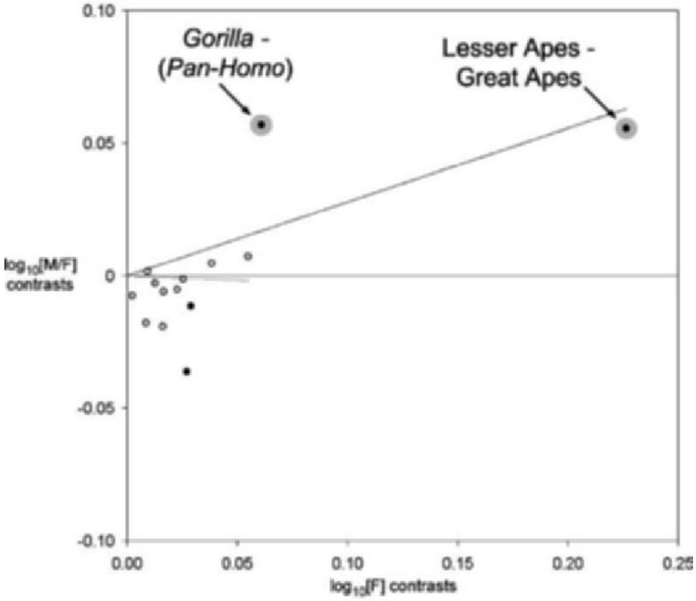


b.

**Fig. 6. Continued**



c.



d.

**Fig. 6. Continued**

between Cercopithecoidea and Hominoidea is primarily in size (Fig. 5b). Phylogenetic regression slopes for cercopithecines and hominoids are both significantly positive and higher than their respective traditional slopes; for colobines the phylogenetic regression slope is not significantly different from zero (Table I, Fig. 6b–d). If one removes the base *Semnopithecus* contrast, the colobine phylogenetic regression slope becomes more positive though not significant (slope $= 0.292$, $r^2 = 0.152$, $p = 0.097$). Comparison of intrageneric and supergeneric contrasts in the three groups shows that in all cases the supergeneric contrast slope is more positive than the intrageneric contrast slope and that a higher proportion of positive contrasts is present in supergeneric than in intrageneric contrasts, even when one removes the *Semnopithecus* contrast from the colobine intrageneric analysis (Tables II and III).

## DISCUSSION

As mentioned earlier, most researchers believe the evolution of SSD in haplorhine primates results from sexual selection, as differences in SSD correlate with differences in mating system, sex ratios, and competition levels (Barton, 2000; Clutton-Brock *et al.*, 1977; Clutton-Brock, 1985; Ford, 1994; Gaulin and Sailer, 1984; Martin *et al.*, 1994; Mitani *et al.*, 1996; Plavcan, 1999, 2001; Plavcan and van Schaik, 1997a; Rodman and Mitani, 1987). A positive correlation between sexual selection and body size may explain positive scaling of size and SSD in haplorhines (Clutton-Brock *et al.*, 1977; Mitani *et al.*, 1996; Plavcan and van Schaik, 1997a; Weckerly, 1998); the hypothesis is supported by Smith and Cheverud's (2002) demonstration that Lande's (1980) quantitative genetics model predicts a positive scaling relationship between size and SSD when selection acts more intensely on male size than female size, as expected under sexual selection in polygynous groups. As noted earlier, when male size changes more than female size a positive evolutionary correlation between change in size and change in SSD results, while greater change in female size produces a negative correlation.

My results allow comparisons between evolutionary patterns of change in size and SSD and contemporary scaling patterns of the same variables in modern clades. Such comparisons let us determine whether modern scaling patterns following Rensch's rule are the product of primarily positive evolutionary scaling relationships, consistent with sexual selection theory, or whether other forces may also have played significant roles in the production of modern scaling patterns within primates.

## Strepsirhini

Previous studies of size and SSD in strepsirhines showed no significant relationship between the two variables using traditional interspecific regression (Kappeler, 1990; Smith and Cheverud, 2002; Weckerly, 1998) and PIC analyses (Lindenfors and Tullberg, 1998; Smith and Cheverud, 2002), a result I confirmed. Nonsignificant scaling of size and SSD can result from large, random changes in size and dimorphism; however, this is clearly not the case for strepsirhines. Low overall modern dimorphism (*cf.* Figs. 2a and 3a) as well as large evolutionary changes in body size unaccompanied by substantial changes in dimorphism at both the intrageneric and supergeneric levels (Fig. 2b) indicate an evolutionary history characterized by approximately equal change in male and female size. The subfossil record supports the assertion; the largest subfossil lemurs are nearly four orders of magnitude larger than the smallest living strepsirhines, and there is no evidence for any significant dimorphism in subfossil lemurs (Godfrey, 1988; Godfrey *et al.*, 1993, 1995, 1997; Jungers, 1990; Jungers *et al.*, 2002).

The lack of substantial dimorphism in strepsirhines is puzzling in that sexual selection theory predicts that male reproductive skew should occur in polygynous mating systems (Andersson, 1994), and in several strepsirhine species males have access to multiple reproductive females (Dixson, 1998; Kappeler, 1997), though strepsirhine mating systems may favor female choice over male-male competition. For example, many strepsirhines have dispersed social systems (Dixson, 1998) in which female ranges may overlap with multiple male ranges, in which case males have difficulty monopolizing access to reproductive females and females can choose among several potential mates (Müller and Thalmann, 2000).

Characters other than body mass that females may be targeting include scents, coloration, and agility; e.g., an investigation into animal communication signals suggested that chemical signals indicate individual quality (Endler, 1993), indicating that scents may function as honest signals that sexual selection targets (Heymann, 2003). *Lemur catta* and *Eulemur fulvus rufus* males scent-mark more frequently during mating seasons (Gould and Overdorff, 2002), and brain centers associated with olfaction—the accessory olfactory bulb—are relatively larger in the brains of polygamous than in monogamous strepsirhines (Alport and Overdorff, 2002). Though some have previously interpreted these data in the context of male olfactory competition and females' use of olfactory cues to incite males into engaging in precopulatory competition, they are also consistent with a greater emphasis on olfaction in species in which females base mate choices on hormonal signals from males. The presence of sexual dichromatism in some strepsirhines suggests male coloration also as a target of female choice (Gerald, 2003), a hypothesis experiments in *Eulemur fulvus* have supported (Cooper and Hosey, 2003). Kappeler (1991) suggests that female mate choice may also target male agility. More generally, sexual selection acts to reinforce characters that boost reproductive success; if large male body size is not one of those characters, significant size dimorphism is not likely to evolve.

## Haplorhini

If changes in haplorhine dimorphism are primarily the result of sexual selection, most evolutionary scaling relationships would be positive in response to selection acting to change male size more than female size because sexual selection theory predicts that SSD in mammals with polygynous mating systems should be the product of selection acting primarily on male body size (Andersson, 1994; Brown, 1975; Ralls, 1977). One exception is polyandrous groups, in which negative scaling relationships result from selection acting more intensely on female size (Gwynne, 1991; Parker and Simmons, 1996), expectations borne out in callitrichids, which produce the highest proportion of negative independent contrasts of all platyrrhine clades, consistent with expectations of sexual selection theory. However, because polyandry is unknown in haplorhines outside of the Callitrichidae, in all other clades we expect positive evolutionary scaling relationships if sexual selection causes changes in SSD.

Traditional interspecific regressions in my study indicate that SSD scales positively with body size in modern haplorhines either considered as a whole or divided into platyrrhines, cercopithecines, colobines, and hominoids. In no case are intrageneric evolutionary scaling relationships significantly positive, and in fact the relationship is significantly negative for Platyrrhini, though largely because of relationships within the Callitrichidae. In contrast, supergeneric evolutionary scaling relationships are significantly positive for Cercopithecinae, Catarrhini, and Haplorhini as a whole. In addition, in all clades the supergeneric evolutionary relationship is more positive than the intrageneric, and the percentage of positive contrasts is higher among supergeneric contrasts. These observations indicate that modern significantly positive scaling relationships consistent with Rensch's rule are primarily the result of differences between high-level clades, and that evolutionary processes that differentiate species within genera have often worked counter to Rensch's rule. For example, two supergeneric contrasts—between *Gorilla* and the *Pan-Homo* clade, and between lesser apes and great apes—almost exclusively drive the highly significant positive scaling patterns for both traditional and phylogenetic analyses of Hominoidea whereas the intrageneric contrasts vary little in dimorphism but are slightly more negative than positive (Fig. 6d). It is worth noting that the two contrasts driving the hominoid pattern reflect not only major differences in size and dimorphism, but also major differences in mating systems, consistent with the expectations of sexual selection—compare the polygynous mating systems of the great apes with the mainly monogamous hylobatids, and the unimale social groups characteristic of many gorillas to the multimale, multifemale groups common to chimpanzees and humans. It is puzzling is why so many of the remaining contrasts reflect negative evolutionary scaling patterns.

As one anonymous reviewer noted, in some cases negative contrasts may be associated with major differences in ecological niche that swamp out subtler differences in selection pressures between males and females. Consider the contrast between *Alouatta* and the *Ateles*-*Lagothrix* clade (Fig. 4b). Though male competition levels and SSD are higher in *Alouatta*, *Ateles* and *Lagothrix* are considerably larger in body size. Another contrast following a negative evolutionary scaling pattern is between Colobinae and Cercopithecinae, with cercopithecines showing much higher dimorphism than colobines at similar body sizes (Figs. 5b and 6a). Evolutionary changes in size and dimorphism in the two examples may be highly constrained because of major differences in locomotor behavior, as in the semibrachiating spider monkeys compared to the lethargic howlers, or differences in locomotor substrate used by predominantly arboreal colobines and the more terrestrial cercopithecines. At the deepest contrasts, e.g., between catarrhines and platyrrhines or between anthropoids and tarsiers, the clades that one compares each contain such a mix of various mating systems, diet, locomotor behaviors, and locomotor substrates that it is unclear exactly what one is comparing. Though such differences probably influence many of the deepest contrasts, ones between congeners will rarely if ever share such concerns. In fact, comparisons between congeners are the most likely contrasts to indicate accurately the sex that experienced the greater size change because the contrasts are often between sister taxa rather than between phylogenetically weighted means of clades. As Purvis and Webster (1999) noted, sister taxa comparisons are susceptible to error and so one needs to take great care to ensure that one uses only accurate size measures in comparative analyses, but one also needs to recognize that differences in size between sister taxa may result from evolutionary responses to selection rather than from error.

Negative evolutionary scaling of size and SSD indicates greater change in female than in male size. Because sexual selection likely affects male size more than female, negative scaling probably results from natural selection acting more intensely on females than on males. This can be mediated through a variety of selective mechanisms, e.g., resource pressure (Downhower, 1976; Leigh and Shea, 1996), fecundity selection (Lindenfors, 2002; Ralls, 1976), or interactions between diet and body size (Plavcan and van Schaik, 1997a). In any case, many of the intrageneric contrasts within Haplorhini show greater change in female than male size, indicating that differences in size and SSD between congeners often result from forces other than male-directed sexual selection. Assuming these patterns accurately reflect evolutionary pressures, why is greater selection on female size fairly common in intrageneric comparisons but relatively rare in supergeneric comparisons? Two of many possibilities suggest themselves, neither or both of which may be true.

## Mating System Similarity Among Congeners

The difference in patterns could result from generally similar mating systems, and thus perhaps intensity of sexual selection, among congeners. Thus intrageneric contrasts are not as sensitive to the effects of sexual selection as contrasts at higher levels, which are likely to involve more difference in mating systems—certainly true in the hominoid example, where the strong positive scaling pattern is driven by two supergeneric contrasts that also happen to be contrasts between mating systems with different expected intensities of male competition (Fig. 5b). Also consider the contrast between the callitrichids and the *Cebus*-*Saimiri* clade, the latter of which is considerably larger, more dimorphic, and polygynous (Fig. 4b). Conversely intrageneric contrasts may more likely involve relatively small differences in sexual selection intensity that are outweighed by ecological differences that set up natural selection pressures affecting female size more than male size.

Unfortunately, it is difficult to test this explanation. It would be relatively simple to partition the contrasts according to whether they involve differences between mating systems or not, then determine whether or not contrasts in the first group are primarily positive and contrasts in the second group contain more negative relationships (Lindenfors and Tullberg, 1998). But that approach would only inform on the hypothesis that sexual selection has more of an effect on SSD when comparing between mating systems than within them; it would not address relative strengths of sexual selection and natural selection in intrageneric comparisons, which would be exceedingly difficult to quantify in wild populations. Though published population body mass data and associated ecological data are currently not available for many haplorhine primates, as such data become more available it will be possible to test this and similar hypotheses by investigating whether an association exists between negative scaling of size and SSD and differences in absolute values or variability of ecological parameters such as food seasonality, monthly rainfall, etc.

## Higher Mortality Associated with Intense Natural Selection

Another explanation for the difference in patterns between supergeneric and intrageneric contrasts considers how phylogenetically independent contrasts are constructed. Because phylogenies preserve only information from living or fossil species, contrasts between clades in phylogenetic analyses do not characterize all descendants of the last common ancestors of the clades, but only species that survived to leave modern descendants. The upshot is that patterns in supergeneric relationships may represent only a subset of patterns in extinct taxa. Thus a possible reason for discrepancies between intrageneric and supergeneric evolutionary patterns is that certain patterns were preferentially preserved and passed on to descendant taxa.

It is not necessary to invoke group selection for positive scaling to be preferentially preserved. Consider the following model, in which specific body size can change by 1) equal selection on body size in males and females, resulting in size change but no change in SSD and thus no scaling pattern; 2) more intense selection on males than females, resulting in changes in size and SSD with a positive scaling pattern; and 3) more intense selection on females than males, resulting in changes in size and SSD with a negative scaling pattern. In some clades, e.g., Strepsirhini, nearly all changes in size follow pattern 1, resulting in an absence of scaling. In others, e.g., Haplorhini, patterns 2 and 3 will also play large roles in generating size change at any particular point in time, resulting in recent evolutionary scaling relationships that are more positive or negative depending on the relative frequency of the two patterns. However, when pattern 3 is a product of natural selection, it is more likely to lead to extinction than pattern 2; in the long run, pattern 2—positive scaling—is more likely to be preserved in deep contrasts.

Put another way, individuals in populations subject to natural selection intense enough to affect females more than males are likely to have a marginally higher mortality rate than individuals not subject to such selection. When comparing lineages separated by a relatively short time, e.g., congeneric species, the slight difference in mortality will not appreciably affect lineage survivorship. However, a small difference in mortality multiplies for every generation in which it occurs. Thus when comparing clades made up of multiple lineages and separated by relatively long periods of time, most of the lineages will have had relatively few instances of intense natural selection because lineages that had more instances were much more likely to die off before reaching the present. Though sexual selection may also increase the likelihood of extinction, e.g., if male coercion is detrimental to female fitness, the effects will be weaker than the same effects compounded by natural selection, and thus sexual selection is unlikely to increase mortality to the same degree that natural selection will increase it. Therefore comparison of clades containing multiple, older lineages are more likely to reflect a stronger signal of sexual selection than comparisons between recently diverged lineages such as sister species.

If this explanation is correct, the positive scaling of size and SSD that is Rensch's rule is merely the most likely outcome when unequal sex-specific selection pressures are applied to populations when one considers them across large clades in which polygyny is more common than polyandry. It also suggests that the relatively high frequency of intrageneric contrasts that appear driven predominantly by natural selection rather than sexual selection may indicate the frequency with which natural selection produces such change in general, not just among closely related species.

It is even more difficult to test this than the previous explanation, as it requires gathering data regarding differential survivorship rates associated with various types of selection pressure which themselves are difficult to quantify. However, simulation studies might be able to identify how large mortality differences would have to be to produce the described effect, how long lineages would have to be separated for a noticeable difference in survivorship to develop, etc.

The two explanations do not represent the only reasons that might account for differences between intrageneric and supergeneric evolutionary patterns in the scaling of size and SSD. I present them as plausible ideas with different implications for the relative importance of natural selection in producing evolutionary change in SSD: in the first case, natural selection is limited to modifying SSD only where populations vary slightly or not at all in sexual selection intensity, whereas in the second case natural selection is a powerful force that can rival sexual selection in its ability to change SSD. Gathering and publishing data that allow us to test these and related ideas would go a long way toward bettering our understanding of the processes underlying the scaling of size and dimorphism in primates.

## Implications for Interpretation of Fossil Dimorphism

Regardless of why intrageneric and supergeneric patterns differ in the relative influence of sexual selection, it is clear that we cannot account for much of the contemporary variability in SSD by sexual selection alone. This is not a new idea, nor is the observation that because forces other than sexual selection account for much of the variability in SSD we should exercise care in reconstructing fossil behaviors based on skeletal dimorphism alone (*cf.* Plavcan and van Schaik, 1997b; Plavcan, 2000). Somewhat different from conventional thought is the idea that natural selection is potentially a very important agent in producing macroevolutionary change in size dimorphism within haplorhine primates, which may be underappreciated because it carries a higher mortality rate than sexual selection and thus lineages subject to multiple bouts of intense natural selection are less likely to survive to the present day than those that are not. However, because fossil lineages are not constrained to survive to the present but only until they were deposited, the selective regimes they experienced immediately prior to deposition could easily have included intense natural selection. Regardless of whether or not the differential mortality explanation is correct, differences in SSD between fossil primate congeners were as likely to be the result of natural selection as are differences in SSD between living primate congeners, a useful reminder when reconstructing behavior in fossil hominids.

## **APPENDIX A.** MALE AND FEMALE MEAN BODY MASS DATA USED IN THIS STUDY

| Taxon | Male *n* | Female *n* | Male mean (kg) | Female mean (kg) | Reference |
|---|---|---|---|---|---|
| Cheirogaleidae | | | | | |
| *Cheirogaleus medius* | W | W | 0.140 | 0.139 | |
| | 7 | 6 | 0.188 | 0.172 | Smith and Jungers (1997) |
| | 36 | 43 | 0.128 | 0.134 | Kathrin Dausmann, pc |
| | 4 | 3 | 0.159 | 0.150 | Alexandra Mueller, pc |
| *Microcebus berthae* | 10 | 10 | 0.0341 | 0.0373 | Manfred Eberle, pc |
| *Microcebus murinus* | 127 | 120 | 0.0630 | 0.0672 | Manfred Eberle, pc |
| *Microcebus myoxinus* | 81 | 48 | 0.0307 | 0.0307 | Schwab (2000) |
| *Microcebus rufus* | 17 | 15 | 0.0458 | 0.0435 | Atsalis (1999) |
| *Mirza coquereli* | P | P | 0.311 | 0.312 | |
| | 68 | 77 | 0.309 | 0.299 | Peter Kappler, pc |
| | 10 | 13 | 0.312 | 0.325 | Stanger *et al.* (1995) |
| *Phaner furcifer* | 8 | 6 | 0.328 | 0.351 | Oliver Schuelke, pc |
| Megaladapidae | | | | | |
| *Lepilemur edwardsi* | 10 | 10 | 0.928 | 0.934 | Rasoloharijaona *et al.* (2003) |
| *Lepilemur ruficaudatus* | P | P | 0.753 | 0.755 | |
| | 28 | 19 | 0.800 | 0.827 | Roland Hilgartner and Dietmar Zinner, pc |
| | 8 | 8 | 0.705 | 0.682 | Schmid and Ganzhorn (1996) |
| Lemuridae | | | | | |
| *Eulemur fulvus albocollaris* | P | P | 2.15 | 2.13 | |
| | 15 | 9 | 2.20 | 2.16 | Johnson *et al.* (2005) |
| | 7 | 5 | 2.10 | 2.10 | Bradley *et al.* (1997) |

**APPENDIX A. Continued**

| Taxon | Male *n* | Female *n* | Male mean (kg) | Female mean (kg) | Reference |
|---|---|---|---|---|---|
| *Eulemur fulvus rufus* | P | P | 2.17 | 2.27 | |
| | 20 | 13 | 2.18 | 2.25 | Glander *et al.* (1992) |
| | 23 | 15 | 2.15 | 2.29 | Johnson *et al.* (2005) |
| *Eulemur macaco* | W | W | 2.35 | 2.43 | |
| | 46 | 41 | 2.37 | 2.51 | Terranova and Coffman (1997) |
| | 2 | 5 | 1.88 | 1.76 | Terranova and Coffman (1997) |
| *Eulemur mongoz* | 4 | 4 | 1.41 | 1.56 | Terranova and Coffman (1997) |
| *Eulemur rubriventer* | 9 | 13 | 2.07 | 1.96 | Glander *et al.* (1992) |
| *Lemur catta* | 41 | 24 | 2.21 | 2.21 | Smith and Jungers (1997) |
| *Varecia variegata* | 13 | 5 | 3.63 | 3.52 | Terranova and Coffman (1997) |
| Indriidae | | | | | |
| *Avahi laniger* | 4 | 4 | 1.03 | 1.32 | Glander *et al.* (1992) |
| *Propithecus diadema* | P | P | 6.05 | 6.21 | |
| | 8 | 6 | 5.59 | 5.90 | Glander *et al.* (1992) |
| | 5 | 6 | 6.50 | 6.51 | Powzyk (1996) |
| *Propithecus tattersalli* | 10 | 8 | 3.39 | 3.59 | Ravosa *et al.* (1993) |
| *Propithecus verreauxi* | P | P | 2.93 | 2.98 | |
| | 46 | 27 | 3.02 | 3.20 | Lewis and Kappeler (2005) |
| | 119 | 105 | 2.84 | 2.76 | Richard *et al.* (2000) |
| Lorisidae | | | | | |
| *Galago moholi* | P | P | 0.214 | 0.194 | |
| | 13 | 13 | 0.217 | 0.200 | Bearder and Martin (1980) |
| | 53 | 47 | 0.211 | 0.188 | Harcourt and Bearder (1989) |
| *Galago senegalensis* | P | P | 0.271 | 0.225 | |
| | 80 | 67 | 0.227 | 0.199 | Smith and Jungers (1997) |
| | 8 | 9 | 0.315 | 0.250 | Smith and Jungers (1997) |
| *Galagoides alleni* | 9 | 30 | 0.277 | 0.269 | Charles-Dominique (1977) |
| *Galagoides demidoff* | 19 | 9 | 0.0628 | 0.0596 | Charles-Dominique (1972) |
| *Galagoides zanzibaricus* | 35 | 38 | 0.150 | 0.137 | Harcourt and Bearder (1989) |
| *Loris tardigradus lydekkerianus* | 7 | 4 | 0.264 | 0.269 | Smith and Jungers (1997) |
| *Loris tardigradus malabaricus* | 10 | 8 | 0.192 | 0.193 | Kappeler (1991) |
| *Nycticebus coucang coucang* | 56 | 44 | 0.679 | 0.626 | Smith and Jungers (1997) |
| *Nycticebus pygmaeus* | 7 | 5 | 0.462 | 0.376 | Kappeler (1991) |
| *Otolemur crassicaudatus* | 66 | 35 | 1.19 | 1.11 | Smith and Jungers (1997) |
| *Otolemur garnettii* | 120 | 134 | 0.794 | 0.734 | Smith and Jungers (1997) |
| *Perodicticus potto potto* | 17 | 15 | 0.830 | 0.836 | Smith and Jungers (1997) |

**APPENDIX A. Continued**

| Taxon | Male *n* | Female *n* | Male mean (kg) | Female mean (kg) | Reference |
|---|---|---|---|---|---|
| *Perodicticus potto edwardsi* | 4 | 4 | 1.22 | 1.16 | Smith and Jungers (1997) |
| Tarsiidae | | | | | |
| *Tarsius bancanus* | P | P | 0.128 | 0.123 | |
| | 21 | 16 | 0.128 | 0.117 | Smith and Jungers (1997) |
| | 6 | 6 | 0.128 | 0.128 | Wright *et al.* (2003) |
| *Tarsius spectrum* | 5 | 8 | 0.125 | 0.107 | Gursky (1998) |
| *Tarsius syrichta* | 10 | 17 | 0.134 | 0.117 | Kappeler (1991) |
| Callitrichidae | | | | | |
| *Callithrix argentata* | 8 | 10 | 0.330 | 0.360 | Smith and Jungers (1997) |
| *Callithrix emiliae* | 12 | 5 | 0.313 | 0.330 | Ford and Davis (1992) |
| *Callithrix humeralifer* | P | P | 0.418 | 0.426 | |
| | 4 | 5 | 0.360 | 0.380 | Smith and Jungers (1997) |
| | 15 | 13 | 0.475 | 0.472 | Smith and Jungers (1997) |
| *Callithrix penicillata* | 8 | 8 | 0.344 | 0.307 | Smith and Jungers (1997) |
| *Cebuella pygmaea* | 36 | 27 | 0.110 | 0.122 | Soini (1988) |
| *Leontopithecus rosalia* | 9 | 9 | 0.663 | 0.622 | Dietz *et al.* (1994) |
| *Saguinus fuscicollis fuscicollis* | 9 | 10 | 0.328 | 0.338 | Soini (1990) |
| *Saguinus fuscicollis illigeri* | 9 | 4 | 0.292 | 0.296 | Soini (1990) |
| *Saguinus fuscicollis nigrifons* | P | P | 0.354 | 0.369 | |
| | 9 | 7 | 0.350 | 0.376 | Soini (1990) |
| | 17 | 19 | 0.352 | 0.366 | Soini (1990) |
| | 25 | 15 | 0.359 | 0.366 | Soini (1990) |
| *Saguinus geoffroyi* | 55 | 40 | 0.482 | 0.503 | Dawson and Dukelow (1976) |
| *Saguinus labiatus* | 136 | 77 | 0.490 | 0.529 | Smith and Jungers (1997) |
| *Saguinus midas* | P | P | 0.535 | 0.591 | |
| | 8 | 6 | 0.544 | 0.601 | Smith and Jungers (1997) |
| | 11 | 7 | 0.526 | 0.580 | Smith and Jungers (1997) |
| *Saguinus mystax* | P | P | 0.522 | 0.545 | |
| | 18 | 10 | 0.568 | 0.585 | Garber *et al.*, 1993 |
| | 95 | 80 | 0.491 | 0.511 | Moya, *et al.* (1990) |
| | 79 | 48 | 0.525 | 0.561 | Soini and Soini (1990) |
| | 48 | 30 | 0.472 | 0.490 | Soini and Soini (1990) |
| | 34 | 26 | 0.505 | 0.540 | Soini and Soini (1990) |
| | 6 | 13 | 0.550 | 0.561 | Garber *et al.* (1993) |
| | 6 | 6 | 0.545 | 0.564 | Garber *et al.* (1993) |
| *Saguinus nigricollis* | 8 | 6 | 0.468 | 0.484 | Smith and Jungers (1997) |
| *Saguinus oedipus* | 37 | 29 | 0.418 | 0.404 | Smith and Jungers (1997) |
| Cebidae | | | | | |
| *Alouatta belzebul* | 27 | 26 | 7.27 | 5.52 | Smith and Jungers (1997) |
| *Alouatta caraya* | 58 | 117 | 6.42 | 4.33 | Smith and Jungers (1997) |
| *Alouatta fusca* | 4 | 5 | 6.73 | 4.35 | Smith and Jungers (1997) |
| *Alouatta palliata* | P | P | 6.96 | 5.28 | |
| | 14 | 18 | 6.53 | 4.02 | Smith and Jungers (1997) |
| | 15 | 15 | 7.80 | 6.60 | Smith and Jungers (1997) |
| | 8 | 10 | 8.35 | 6.17 | Scott *et al.* (1976) |
| | 4 | 17 | 4.95 | 4.25 | Scott *et al.* (1976) |
| | 110+ | 177+ | 7.17 | 5.35 | Smith and Jungers (1997) |

**APPENDIX A. Continued**

| Taxon | Male *n* | Female *n* | Male mean (kg) | Female mean (kg) | Reference |
|---|---|---|---|---|---|
| *Alouatta seniculus* | P | P | 6.66 | 5.18 | |
| | 28 | 34 | 7.62 | 6.02 | Smith and Jungers (1997) |
| | 31 | 29 | 5.62 | 4.03 | Braza *et al.* (1983) |
| | 8 | 9 | 7.54 | 6.30 | Hernandez-Camacho and Defler (1985) |
| | 14 | 4 | 6.70 | 4.50 | Rudran (1979) |
| | 10 | 4 | 6.50 | 4.50 | Thorington *et al.* (1979) |
| | 7 | 4 | 6.00 | 5.70 | Rodriguez and Boher (1988) |
| *Aotus azarai* | 5 | 5 | 1.23 | 1.22 | AMNH (this study) |
| *Aotus lemurinus* | 7 | 6 | 0.921 | 0.859 | Hernandez-Camacho and Defler (1985) |
| *Aotus nancymaae* | 32 | 24 | 0.795 | 0.78 | Smith and Jungers (1997) |
| *Aotus trivirgatus* | 20 | 17 | 0.813 | 0.736 | Smith and Jungers (1997) |
| *Aotus vociferans* | 20 | 20 | 0.708 | 0.698 | Smith and Jungers (1997) |
| *Ateles belzebuth* | 10 | 16 | 8.26 | 7.88 | Smith and Jungers (1997) |
| *Ateles chamek* | 4 | 8 | 9.41 | 9.33 | Smith and Jungers (1997) |
| *Ateles fusciceps* | 6 | 11 | 8.89 | 9.16 | Smith and Jungers (1997) |
| *Ateles geoffroyi* | 20 | 32 | 7.45 | 7.64 | Schultz (1941) |
| *Ateles paniscus* | P | P | 8.49 | 8.07 | |
| | 20 | 42 | 9.11 | 8.44 | Smith and Jungers (1997) |
| | 5 | 7 | 7.86 | 7.69 | Fleagle and Mittermeier (1980) |
| *Cacajao melanocephalus* | 5 | 6 | 3.16 | 2.71 | Smith and Jungers (1997) |
| *Callicebus brunneus* | 6 | 4 | 0.854 | 0.805 | Ford and Davis (1992) |
| *Callicebus moloch* | 10 | 19 | 1.02 | 0.956 | Smith and Jungers (1997) |
| *Callicebus personatus* | 5 | 7 | 1.27 | 1.38 | Smith and Jungers (1997) |
| *Callicebus torquatus* | P | P | 1.32 | 1.16 | |
| | 5 | 9 | 1.49 | 1.27 | Hernandez-Camacho and Defler (1985) |
| | 8 | 6 | 1.15 | 1.05 | Smith and Jungers (1997) |
| *Cebus albifrons* | W | W | 3.18 | 2.29 | |
| | 8 | 3 | 3.42 | 2.86 | Hernandez-Camacho and Defler (1985) |
| | 18 | 15 | 3.07 | 2.18 | Smith and Jungers (1997) |
| *Cebus apella* | P | P | 3.64 | 2.39 | |
| | 9 | 5 | 3.74 | 2.33 | Hernandez-Camacho and Defler (1985) |
| | 6 | 11 | 3.30 | 2.08 | AMNH (this study) |
| | 13 | 10 | 3.84 | 2.66 | Smith and Jungers (1997) |
| *Cebus olivaceus* | W | W | 3.24 | 2.52 | |
| | 15 | 3 | 3.10 | 1.90 | Rodriguez and Boher (1988) |
| | 14 | 7 | 3.38 | 2.79 | Smith and Jungers (1997) |
| *Chiropotes albinasus* | 7 | 7 | 3.15 | 2.49 | Smith and Jungers (1997) |
| *Chiropotes satanus chiropotes* | 20 | 19 | 2.90 | 2.58 | Smith and Jungers (1997) |
| *Lagothrix lagotricha* | 16 | 9 | 7.28 | 7.02 | Smith and Jungers (1997) |
| *Pithecia monachus* | 16 | 10 | 2.61 | 2.11 | Smith and Jungers (1997) |

**APPENDIX A. Continued**

| Taxon | Male *n* | Female *n* | Male mean (kg) | Female mean (kg) | Reference |
|---|---|---|---|---|---|
| *Pithecia pithecia* | 10 | 4 | 1.94 | 1.58 | Smith and Jungers (1997) |
| *Saimiri boliviensis* | 14 | 13 | 1.02 | 0.75 | AMNH (this study) |
| *Saimiri oerstedii* | W | W | 0.897 | 0.680 | |
| | 3 | 3 | 0.907 | 0.603 | Crile and Quiring (1940) |
| | 8 | 4 | 0.893 | 0.737 | Schultz (1941) |
| *Saimiri sciureus* | P | P | 0.920 | 0.723 | |
| | 8 | 5 | 0.740 | 0.635 | Fleagle and Mittermeier (1980) |
| | 17 | 58 | 1.02 | 0.699 | Smith and Jungers (1997) |
| | 9 | 5 | 1.08 | 0.859 | Hernandez-Camacho and Defler (1985) |
| | 29 | 34 | 0.840 | 0.698 | Ique (1990) |
| *Saimiri ustus* | 11 | 6 | 0.921 | 0.799 | Ford and Davis (1992) |
| *Saimiri vanzolinii* | 9 | 4 | 0.950 | 0.650 | Smith and Jungers (1997) |
| Cercopithecinae | | | | | |
| *Cercocebus galeritus* | W | W | 9.61 | 5.26 | |
| | 3 | 3 | 10.19 | 5.47 | Gautier-Hion and Gautier (1976) |
| | 3 | 4 | 9.03 | 5.10 | Smith and Jungers (1997) |
| *Cercopithecus ascanius schmidti* | 37 | 55 | 3.69 | 2.79 | Colyn (1994) |
| *Cercopithecus ascanius katangae* | 32 | 187 | 3.71 | 2.97 | Colyn (1994) |
| *Cercopithecus campbelli* | 10 | 9 | 4.50 | 2.70 | Smith and Jungers (1997) |
| *Cercopithecus cephus* | 8 | 10 | 4.09 | 2.88 | Gautier-Hion and Gautier (1976) |
| *Cercopithecus denti* | 4 | 36 | 4.25 | 2.83 | Colyn (1994) |
| *Cercopithecus diana* | 4 | 11 | 5.20 | 3.90 | Smith and Jungers (1997) |
| *Cercopithecus hamlyni* | 11 | 9 | 5.49 | 3.36 | Colyn (1994) |
| *Cercopithecus lhoesti* | 19 | 50 | 5.97 | 3.45 | Colyn (1994) |
| *Cercopithecus mitis stuhlmanni* | 41 | 94 | 5.85 | 3.93 | Colyn (1994) |
| *Cercopithecus mitis erythrarchus* | 6 | 6 | 9.31 | 4.91 | Smith and Jungers (1997) |
| *Cercopithecus neglectus* | W | W | 7.35 | 4.13 | |
| | 4 | 4 | 7.00 | 3.96 | Gautier-Hion and Gautier (1976) |
| | 2 | 2 | 8.05 | 4.46 | Napier (1981) |
| *Cercopithecus nictitans* | P | P | 6.67 | 4.25 | |
| | 16 | 9 | 6.61 | 4.22 | Gautier-Hion and Gautier (1976) |
| | 17 | 21 | 6.73 | 4.28 | Colyn (1994) |
| *Cercopithecus petaurista* | 13 | 7 | 4.40 | 2.90 | Oates *et al.* (1990) |
| *Cercopithecus pogonias* | W | W | 4.26 | 2.90 | |
| | 4 | 6 | 4.50 | 3.03 | Gautier-Hion and Gautier (1976) |
| | 1 | 4 | 3.30 | 2.70 | Colyn (1994) |

**APPENDIX A. Continued**

| Taxon | Male<br>*n* | Female<br>*n* | Male mean (kg) | Female mean (kg) | Reference |
|---|---|---|---|---|---|
| *Cercopithecus wolfi* | 13 | 84 | 3.80 | 2.88 | Colyn (1994) |
| *Chlorocebus aethiops* | P | P | 4.94 | 3.34 | |
| | 109 | combined | 4.21 | 2.74 | Anapol *et al.* (1995) |
| | 21 | 15 | 5.77 | 3.53 | Bolter and Zihlman (2003) |
| | 29 | 30 | 5.51 | 4.09 | Skinner and Smithers (1990) |
| | 60 | 90 | 4.26 | 2.98 | Smith and Jungers (1997) |
| *Chlorocebus pygerythrus* | P | P | 4.28 | 2.98 | |
| | 26 | 36 | 4.13 | 2.57 | Turner *et al.* (1997) |
| | 12 | 31 | 4.43 | 3.44 | Turner *et al.* (1997) |
| | 18 | 15 | 4.33 | 3.15 | Turner *et al.* (1997) |
| | 4 | 10 | 4.24 | 2.75 | Turner *et al.* (1997) |
| *Chlorocebus sabaeus* | 61 | 71 | 5.30 | 3.30 | Horrocks (1986) |
| *Erythrocebus patas* | 9 | 14 | 12.40 | 6.50 | Smith and Jungers (1997) |
| *Lophocebus albigena* | W | W | 7.89 | 6.01 | |
| | 5 | 6 | 8.98 | 6.40 | Gautier-Hion and Gautier (1976) |
| | 4 | 6 | 7.65 | 6.50 | Colyn (1994) |
| | 4 | 4 | 7.34 | 4.93 | Colyn (1994) |
| | 4 | 3 | 7.31 | 5.67 | Napier (1981) |
| *Macaca assamensis assamensis* | 16 | 12 | 11.30 | 6.70 | Fooden (1988) |
| *Macaca cyclopis* | 7 | 4 | 6.00 | 4.94 | Smith and Jungers (1997) |
| *Macaca fascicularis* | P | P | 5.11 | 3.41 | |
| | 69 | 46 | 5.36 | 3.59 | Smith and Jungers (1997) |
| | 13 | 14 | 4.85 | 3.22 | MCZ (this study) |
| *Macaca fuscata* | 10 | 23 | 10.97 | 8.03 | Smith and Jungers (1997) |
| *Macaca maura* | 17 | 4 | 9.72 | 6.05 | Smith and Jungers (1997) |
| *Macaca mulatta* | 5 | 6 | 6.99 | 4.94 | Napier (1981) |
| *Macaca nemestrina nemestrina* | W | W | 11.2 | 6.59 | |
| | 3 | 5 | 10.6 | 6.14 | Fooden (1975) |
| | 5 | 4 | 11.6 | 7.15 | Fooden (1975) |
| *Macaca nemestrina leonina* | 4 | 7 | 8.48 | 4.93 | Fooden (1975) |
| *Macaca radiata* | 8 | 8 | 6.6 | 3.69 | Hartman (1938) |
| *Macaca sinica* | 14 | 26 | 5.66 | 3.3 | Cheverud *et al.* (1992) |
| *Mandrillus sphinx* | 5 | 7 | 34.4 | 12.8 | Setchell *et al.* (2001) |
| *Miopithecus talapoin* | 7 | 9 | 1.38 | 1.12 | Gautier-Hion and Gautier (1976) |
| *Papio anubis* | P | P | 23.0 | 13.3 | |
| | 177 | 237 | 21.1 | 12.2 | Berger (1972) |
| | 10 | 39 | 22.79 | 12.26 | Popp (1983) |
| | 39 | 35 | 21.2 | 11.7 | Phillips-Conroy and Jolly (1981) |
| | 43 | 26 | 21.46 | 12.54 | Popp (1983) |
| | 54 | 23 | 27.1 | 14.0 | Popp (1983) |
| | 18 | 18 | 21.9 | 12.7 | Gest and Siegel (1983) |

**APPENDIX A. Continued**

| Taxon | Male *n* | Female *n* | Male mean (kg) | Female mean (kg) | Reference |
|---|---|---|---|---|---|
| | 5 | 10 | 22.72 | 15.16 | Eley *et al.* (1989) |
| | 9 | 17 | 23.88 | 13.01 | Eley *et al.* (1989) |
| | 4 | 9 | 24.80 | 16.07 | Eley *et al.* (1989) |
| *Papio cynocephalus* | P | P | 22.3 | 12.0 | |
| | 37 | 21 | 21.8 | 12.3 | Smith and Jungers (1997) |
| | 12 | 11 | 22.32 | 11.65 | UTA (this study) |
| | 5 | 5 | 22.8 | 11.9 | Popp (1983) |
| *Papio hamadryas* | P | P | 18.0 | 10.3 | |
| | 41 | 39 | 16.9 | 9.9 | Phillips-Conroy and Jolly (1981) |
| | 15 | 24 | 16.18 | 9.73 | Popp (1983) |
| | 7 | 13 | 21.0 | 11.4 | Popp (1983) |
| *Papio ursinus* | 28 | 22 | 29.8 | 14.8 | Smith and Jungers (1997) |
| *Theropithecus gelada* | 5 | 8 | 19.0 | 11.7 | Smith and Jungers (1997) |
| Colobinae | | | | | |
| *Colobus angolensis* | P | P | 9.71 | 7.59 | |
| | 4 | 6 | 9.8 | 7.4 | Oates *et al.* (1994) |
| | 8 | 5 | 9.62 | 7.77 | Colyn (1994) |
| *Colobus guereza matschiei* | 13 | 14 | 9.89 | 7.9 | Smith and Jungers (1997) |
| *Colobus polykomos* | 5 | 10 | 9.9 | 8.3 | Oates *et al.* (1994) |
| *Colobus satanas* | 5 | 5 | 10.4 | 7.42 | Smith and Jungers (1997) |
| *Nasalis larvatus* | 6 | 10 | 21.02 | 10.48 | MCZ (this study) |
| *Piliocolobus badius badius* | 9 | 14 | 8.3 | 8.2 | Oates *et al.* (1990) |
| *Presbytis comata* | 4 | 6 | 6.68 | 6.71 | Smith and Jungers (1997) |
| *Presbytis femoralis* | 23 | 18 | 6.26 | 6.19 | Smith and Jungers (1997) |
| *Presbytis melalophos* | 11 | 12 | 6.59 | 6.47 | Smith and Jungers (1997) |
| *Presbytis potenziani* | W | W | 6.31 | 6.40 | |
| | 7 | 2 | 6.14 | 6.41 | Brandon-Jones (1993) |
| | 6 | 4 | 6.5 | 6.4 | Tilson and Tenaza (1976) |
| *Presbytis rubicunda* | P | P | 6.26 | 6.11 | |
| | 16 | 14 | 6.22 | 6.04 | MCZ (this study) |
| | 35 | 38 | 6.29 | 6.17 | Smith and Jungers (1997) |
| *Procolobus verus* | 20 | 14 | 4.7 | 4.2 | Oates *et al.* (1990) |
| *Rhinopithecus roxellana* | 7 | 4 | 17.9 | 11.6 | Smith and Jungers (1997) |
| *Semnopithecus entellus entellus* | 9 | 11 | 13.0 | 9.89 | Smith and Jungers (1997) |
| *Semnopithecus entellus schistacea* | 5 | 9 | 19.2 | 14.8 | Smith and Jungers (1997) |
| *Semnopithecus entellus thersites* | 14 | 11 | 11.4 | 6.91 | Smith and Jungers (1997) |
| *Trachypithecus cristatus* | 11 | 19 | 6.72 | 5.78 | MCZ (this study) |
| *Trachypithecus obscurus* | 7 | 8 | 7.77 | 6.22 | Fooden (1971) |
| *Trachypithecus phayrei* | 8 | 5 | 7.93 | 6.95 | Napier (1985) |
| *Trachypithecus pileatus* | 7 | 5 | 12.0 | 9.86 | Smith and Jungers (1997) |

**APPENDIX A. Continued**

| Taxon | Male *n* | Female *n* | Male mean (kg) | Female mean (kg) | Reference |
|---|---|---|---|---|---|
| Hylobatidae | | | | | |
| *Hylobates agilis albibarbis* | 5 | 5 | 5.71 | 6.30 | Geissmann (1993) |
| *Hylobates agilis unko* | 12 | 4 | 5.85 | 5.55 | Geissmann (1993) |
| *Hylobates concolor* | 7 | 13 | 7.77 | 7.62 | Geissmann (1993) |
| *Hylobates hoolock* | 13 | 5 | 6.87 | 6.88 | Geissmann (1993) |
| *Hylobates lar carpenteri* | 33 | 24 | 5.92 | 5.36 | MCZ (this study) |
| *Hylobates lar entelloides* | P | P | 6.44 | 5.77 | |
| | 8 | 6 | 5.65 | 4.89 | Geissmann (1993) |
| | 11 | 3 | 7.23 | 6.65 | Geissmann (1993) |
| *Hylobates muelleri muelleri* | 5 | 7 | 5.44 | 5.27 | Geissmann (1993) |
| *Hylobates muelleri funereus* | W | W | 5.66 | 5.16 | |
| | 6 | 3 | 5.63 | 5.37 | Geissmann (1993) |
| | 2 | 4 | 5.75 | 5.01 | Geissmann (1993) |
| *Hylobates syndactylus* | P | P | 11.79 | 10.70 | |
| | 7 | 10 | 11.88 | 10.71 | Smith and Jungers (1997) |
| | 5 | 7 | 11.70 | 10.68 | Geissmann (1993) |
| Hominidae | | | | | |
| *Gorilla gorilla* | 19 | 6 | 169.3 | 75.7 | Smith and Jungers (1997) |
| *Homo sapiens* | P | P | 57.4 | 49.7 | |
| | 49 | 49 | 53.9 | 45.8 | Smith and Jungers (1997) |
| | 121 | 162 | 60.2 | 53.6 | Smith and Jungers (1997) |
| | 194 | 193 | 58.1 | 49.7 | Smith and Jungers (1997) |
| *Pan paniscus* | 7 | 6 | 45.0 | 33.2 | Jungers and Susman (1984) |
| *Pan troglodytes schweinfurthi* | W | W | 41.4 | 33.1 | |
| | 9 | 6 | 39.5 | 29.8 | Wrangham and Smuts (1980) |
| | 6 | 8 | 42.0 | 35.2 | Uehara and Nishida (1987) |
| | 3 | 9 | 42.8 | 34.3 | Uehara and Nishida (1987) |
| *Pan troglodytes troglodytes* | W | W | 59.7 | 45.8 | |
| | 3 | 3 | 60.0 | 47.4 | Jungers and Susman (1984) |
| | 2 | 1 | 59.3 | 41.0 | Smith and Jungers (1997) |
| *Pongo pygmaeus pygmaeus* | 7 | 13 | 78.5 | 35.8 | Smith and Jungers (1997) |

Note. AMNH: American Museum of Natural History; MCZ: Museum of Comparative Zoology (Harvard University); UTA: University of Texas at Austin; P: unweighted mean of sex-specific population values; W: weighted mean of sex-specific population values.

## APPENDIX B: NEWICK CODE FOR PRIMATE SUPERTREE

(((((((Microcebus murinus, Microcebus myoxinus, Microcebus berthae), Microcebus rufus), Mirza coquereli), Cheirogaleus medius), Phaner furcifer), (((Lemur catta, Varecia variegata),(Eulemur rubriventer, (Eulemur mongoz, ((Eulemur fulvus albocollaris, Eulemur fulvus rufus), Eulemur macaco)))), (((Propithecus diadema, Propithecus tattersalli, Propithecus verreauxi), Avahi laniger), (Lepilemur ruficaudatus, Lepilemur edwardsi)))), ((((Nycticebus coucang, Nycticebus pygmaeus), (Loris tardigradus lydekkerianus, Loris tardigradus malabaricus)), (Perodicticus potto potto, Perodicticus potto edwardsi)), ((Galagoides alleni, (Galagoides zanzibaricus, Galagoides demidoff)), (Galago senegalensis, Galago moholi), (Otolemur crassicaudatus, Otolemur garnettii)))), (((Tarsius bancanus,Tarsius syrichta), Tarsius spectrum), ((((((((((Callithrix argentata, Callithrix emiliae), Callithrix humeralifer), Callithrix penicillata), Cebuella pygmaea), Leontopithecus rosalia), (((Saguinus fuscicollis fuscicollis, Saguinus fuscicollis illigeri, Saguinus fuscicollis nigrifons), Saguinus nigricollis), ((Saguinus midas, (Saguinus oedipus, Saguinus geoffroyi)), (Saguinus mystax, Saguinus labiatus)))), ((((Saimiri oerstedii, Saimiri sciureus), Saimiri boliviensis), Saimiri ustus, Saimiri vanzolinii), ((Cebus albifrons, Cebus olivaceus), Cebus apella))), ((Aotus azarai, Aotus nancymaae), ((Aotus vociferans, Aotus lemurinus), Aotus trivirgatus))), (((Pithecia monachus, Pithecia pithecia), (Cacajao melanocephalus, Chiropotes albinasus, Chiropotes satanus chiropotes)), ((Lagothrix lagothricha, (((Ateles geoffroyi, Ateles fusciceps), (Ateles chamek, Ateles belzebuth)), Ateles paniscus)), (Alouatta palliata, ((Alouatta belzebul, Alouatta fusca), (Alouatta caraya, Alouatta seniculus)))))), (((Callicebus moloch, Callicebus personatus), Callicebus brunneus), Callicebus torquatus)), ((((((Macaca maura, (Macaca fascicularis, (Macaca mulatta, Macaca fuscata, Macaca cyclopis))), ((Macaca sinica, Macaca radiata), Macaca assamensis), (Macaca nemestrina nemestrina, Macaca nemestrina leonina)), ((Theropithecus gelada, (Papio hamadryas, (Papio ursinus, Papio cynocephalus, Papio anubis))), (Lophocebus albigena, (Cercocebus galeritus, Mandrillus sphinx)))), ((((((Cercopithecus cephus, (Cercopithecus ascanius schmidti, Cercopithecus ascanius katangae)), Cercopithecus petaurista), (Cercopithecus nictitans, (Cercopithecus mitis stuhlmanni, Cercopithecus mitis erythrarchus))), (((Cercopithecus campbelli, ((Cercopithecus wolfi, Cercopithecus denti), Cercopithecus pogonias)), Cercopithecus neglectus), Cercopithecus hamlyni)), Cercopithecus diana), ((Cercopithecus lhoesti, (Chlorocebus pygerythrus, Chlorocebus sabaeus, Chlorocebus aethiops)), Erythrocebus patas), Miopithecus talapoin)), ((((((Presbytis comata, (Presbytis femoralis, Presbytis melalophos), Presbytis rubicunda), Presbytis potenziani, Trachypithecus cristatus, Trachypithecus obscurus, Trachypithecus phayrei, Trachypithecus pileatus), (Semnopithecus entellus entellus, Semnopithecus entellus schistacea, Semnopithecus entellus thersites)), Nasalis larvatus), Rhinopithecus roxellana), ((((Colobus guereza, Colobus polykomos), Colobus angolensis), Colobus satanas), (Procolobus verus, Piliocolobus badius badius)))), ((((((Hylobates lar carpenteri, Hylobates lar entelloides), (Hylobates agilis albibarbis, Hylobates agilis unko)), (Hylobates muelleri muelleri, Hylobates muelleri funereus)), Hylobates hoolock), Hylobates concolor, Hylobates syndactylus), (Pongo pygmaeus, (Gorilla gorilla, (((Pan troglodytes schweinfurthi, Pan troglodytes troglodytes), Pan paniscus), Homo sapiens))))))));

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