Research article

When size makes a difference: allometry, life-history and morphological evolution of capuchins (Cebus) and squirrels (Saimiri) monkeys (Ceboidea, Platyrrhini)

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Abstract

Background: How are morphological evolution and developmental changes related? This rather old and intriguing question had a substantial boost after the 70s within the framework of heterochrony (changes in rates or timing of development) and nowadays has the potential to make another major leap forward through the combination of approaches: molecular biology, developmental experimentation, comparative systematic studies, geometric morphometrics and quantitative genetics. Here I take an integrated approach combining life-history comparative analyses, classical and geometric morphometrics applied to ontogenetic series to understand changes in size and shape which happen during the evolution of two New World Monkeys (NWM) sister genera.

Results: Cebus and Saimiri share the same basic allometric patterns in skull traits, a result robust to sexual and ontogenetic variation. If adults of both genera are compared in the same scale (discounting size differences) most differences are small and not statistically significant. These results are consistent using both approaches, classical and geometric Morphometrics. Cebus is a genus characterized by a number of paedomorphic traits (adult-like) while Saimiri is a genus with paedomorphic (child-like) traits. Yet, the whole clade Ceboidea is characterized by a unique combination of very high pre-natal growth rates and relatively slow post-natal growth rates when compared to the rest of the NWM. Morphologically Ceboidea can be considered paedomorphic in relation to the other NWM. Geometric morphometrics allows the precise separation of absolute size, shape variation associated with size (allometry), and shape variation non-associated with size. Interestingly, and despite the fact that they were extracted as independent factors (principal components), evolutionary allometry (those differences in allometric shape associated with intergeneric differences) and ontogenetic allometry (differences in allometric shape associated with ontogenetic variation within genus) are correlated within these two genera. Furthermore, morphological differences produced along these two axes are quite similar. Cebus and Saimiri are aligned along the same evolutionary allometry and have parallel ontogenetic allometry trajectories.

Conclusion: The evolution of these two Platyrrhini monkeys is basically due to a size differentiation (and consequently to shape changes associated with size). Many life-history changes are correlated or may be the causal agents in such evolution, such as delayed on-set of reproduction in Cebus and larger neonates in Saimiri.

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Background

Since Gould’s publication of Ontogeny and Phylogeny [14] a wave of renewed interest in the role of development in generating evolutionary novelties spread through biology. Heterochrony, evolutionary modifications in the rates and/or the timing (onset and offset) of development [2], become widely recognized as an important agent of evolutionary change [26]. The study of heterochrony, while interesting per se, does not take us any closer to understanding the developmental, genetic, and physiological processes underlying evolutionary change [29]. Yet, the study of heterochrony, even when using size in place of time, may be quite helpful in understanding evolutionary diversification (see criticisms in [13]). Allometry, the differential and relative growth of organismal parts may be conceived as a size-based “heterochrony” [26]. Heterochrony addresses trait change relative to time and allometry examine trait change relative to others traits (usually size), the latter being a comparison of heterochronic results to one another [26].

Size and shape are important biological properties of organisms arising from their genetic basis in complex association and sometimes interaction with the external and internal environment. Usually, a large fraction of the variability in morphometric data is due to size variation among individuals. Scaling effects might result in shape changes associated with changing size due to allometric relationships among traits, unless all morphological components grow or scale at the same rates (isometry). A long tradition in morphometrics has been to regard size as a nuisance factor in comparisons of organisms with several methods being used to adjust size before comparisons (e.g. [3,39,32,20]). The rationale behind this approach is to regard size as a plastic feature of organisms and shape changes, unassociated with size (non-allometric), as adaptive [40]. Another motivation for developing methods allowing the separation of size and shape was the need to compare forms with very different sizes [41]. Yet, size is as much a property of organisms as is shape, with important functional and ecological implications. For example, a simple increase in skull size (and concomitant allometric shape changes) might result in larger animals being able to handle larger and harder food items and therefore explore new resources or niches. Here I present a study of size and shape variation in two New World primates, the squirrel (Saimiri) monkeys and capuchin (Cebus) monkeys. The approach used here combines traditional and geometric morphometrics, comparative analyses of life-history data and statistical analyses of size and shape differences to understand the evolution of these two sister genera.

The subfamily Cebinae, as used here, refers to the two modern genera, Saimiri and Cebus, which are united on the basis of dental morphology and proportions, overall cranial morphology and others skeletal features [9]. There is now a consensus that these two genera are indeed living sister clades based on recent phylogenetic studies [34,33,35]. Adult squirrel monkeys weigh less than 1.0 kg, on average (males 858 g and females 715 g) while capuchins usually weigh 3 times more (males 2,912 g and females 2,042 kg). Capuchins occur throughout the Neotropical region occupying virtually all types of forested habitats, from mangroves and disturbed forests to well-preserved Amazonian and Atlantic forests. Squirrel monkeys occur throughout the Amazon region to Central America, but not in the Cerrado and Atlantic forests, also occupying a great variety of forested habitats. Group sizes usually range from 6 to 30 individuals in Cebus while Saimiri had group size ranging from 10 to up to 75 individuals, and sometimes both genera mix together in foraging parties. Besides, both genera share some unique life-history patterns in New World Monkeys (NWM), with relatively heavy brains for their body weight [15].

Here I present a study of the morphological variation in Cebus and Saimiri, focusing on the allometric patterns, differentiation and evolution of size and shape in Cebinae. Ontogenetic and static allometric patterns and shape (free of size) variation are compared in order to describe similarities and differences in skull variation between genera. Finally, these results are compared to life-history traits and ecology of NWM to understand the Cebinae morphological evolution. All these approaches converge to a simple picture: Cebus and Saimiri evolved from a common ancestor basically diverging in size. This divergence follows a common ontogenetic trajectory which is basically revealed by the fact that evolutionary allometry (those differences in shape associated with size differences among lineages) and ontogenic allometry (shape changes associated with size differences during the ontogeny on each lineage) are highly correlated and morphologically describe the same changes in the skull. This size evolution might be caused by life-history changes like a delayed on-set of reproduction in Cebus.

Results

Static and ontogenetic allometry

Table 1 shows the multivariate allometric coefficients (ACs), corresponding standard deviations obtained from the bootstrap, and the lower and upper 95% confidence limits for each genus. Results for each sex analyzed separately are nearly equal to those presented here pooling both sexes within each genus and for simplicity are not presented. Those ACs with confidence limits not encompassing one (isometry) were considered either negatively (below 1) or positively (above 1) allometric. Eleven of the 17 neural traits (65%) and 9 of the 23 facial traits (39%) are negatively allometric in Cebus and the same figures for
Saimiri are 13 in 17 (76% neural) and 11 in 23 (48% facial). Conversely, 2 of the 17 neural traits (12%) and 6 of the 23 facial traits (26%) are positively allometric in Cebus and the same figures for Saimiri are 3 in 17 (18% neural) and 8 in 23 (35% facial). Allometric vector repeatabilities are 0.99 for both genera and therefore sampling error is negligible in judging vector correlations. Allometric vector repeatabilities were also quite high in the subadult sample \((t = 0.98\) for Saimiri and \(t = 0.99\) for Cebus) and therefore sampling error should have a negligible impact upon the vector similarities. The following vector correlations were obtained: Saimiri adult \( \times \) Cebus adult = 0.968, Cebus adult \( \times \) Cebus young = 0.978, Saimiri adult \( \times \) Cebus young = 0.963, Saimiri young \( \times \) Saimiri adult = 0.951, Cebus young \( \times \) Saimiri young = 0.981, Cebus adult \( \times \) Saimiri young = 0.980. Furthermore, the following averages and confidence interval were observed in the correlation of each vector against its 100 random permutation sample: Saimiri young = 0.773 (0.707–0.84), Saimiri adult = 0.82 (0.759–0.88), Cebus young = 0.808 (0.736–0.88), Cebus adult = 0.769 (0.697–0.842). Therefore all allometric vector correlations are higher that expected by the correlation of any two size vectors. Additionally, table 1 also show the PC1total extracted from the V/CV of the natural log-transformed data used in the MASS correction. This PC1 accounts for 90% of the total variation in the data and is quite similar \((r = 0.954)\) to an isometric vector (all elements equal to 1/390.5). Also, this PC1total is quite similar to the size vectors representing within genus variation \((r = 0.936\) with Saimiri and 0.912 with Cebus).

**Differentiation with and without size**

A MANOVA was performed on the 39 measurements using sex, genus, and sex by genus interaction as independent variables in order to determine whether sexual dimorphism needs to be accounted for in the analyses. Five hundred sixty-four individuals were analyzed and significant multivariate (Wilk’s \(\Lambda = 0.016; df = 39, \ 522; P < 1.0 \times 10^{-5})\) and univariate \((P < 1.0 \times 10^{-4})\) differences between the genera were found. There was also significant multivariate differences in sex \((Wilk’s \Lambda = 0.462; df = 39, \ 522; P < 1.0 \times 10^{-5})\). Thirty-five variables presented univariate differences in sex significant at \(P < 1.0 \times 10^{-5}\), two were significant between 1% and 5% \((BA-OPI\ and\ OPI-LD)\) and two were found non-significant \((LD-AS\ and\ BR-LD)\). Moreover, there was also significant multivariate sex by genus interaction \((Wilk’s \Lambda = 0.741; df = 39, 522; P < 1.0 \times 10^{-5})\) and 33 significant sex by genus interaction \((31\ with\ P < 0.001\ and\ 2\ with\ P < 0.05)\) in the univariate tests. There is strong evidence for differentiation between the two genera, the two sexes and for the interaction of sex with genus. Additionally, an ANOVA performed on size \((first\ principal\ component\ extracted\ from\ the\ V/CV\ matrix\ of\ the\ LN\ transformed\ data\ accounting\ for\ 90%\ of\ the\ total\ variance)\) show significant differences between the two genera \((MS_{genus} = 530.27, F = 14228.63, P > 10^{-5})\), between the two sexes \((MS_{sex} = 10.70, F = 287.21, P > 10^{-5})\) and also significant interaction between effects \((MS_{genus \times sex} = 0.39, F = 10.48, P = 0.001)\), all effects with 1 degree of freedom \(error\ term\ with\ d.f = 560\ and\ MS_{error} = 0.037)\. Therefore all analyses below were done independently for both sexes, except where specifically noted, allowing also to properly control for interspecific variation within each genus.

The MANOVA performed on the original unscaled variables using 309 complete male skulls with genera and species nested within genera as factors was highly significant \((Wilk’s \Lambda = 0.021; df = 39, 252; P < 0.0001)\) with the single canonical variate \(Table\ 2)\ separating completely the two groups \(Figure\ 1)\. Correlations between CV scores and skull measurements are also presented in Table 2. Based on the correlations between variables and function, the CV is a size factor because all the significant correlations are positive, except for BR-LD. CV has large contributions from both neurocranial and facial traits. The MANOVA performed on the 255 complete female skulls with genera and species nested within genera as factors was also highly significant \((Wilk’s \Lambda = 0.032; df = 39, 198; P < 0.0001)\) with the single CV \(Table\ 2)\ also separating the two groups completely \(Figure\ 1)\. Correlations between CV scores and skull measurements are also presented in Table 2. The two CV’s \(males\ and\ females)\ are very similar with a vector correlation between them of 0.90. The MANOVA results with species nested within genus indicate that only one trait \(BR-LD)\ does not show significant differences between the two genera \(using\ the\ conservative\ Bonferroni\ correction\ of\ the\ significance\ level\ P = 0.05/39)\ in the univariate F-tests for both, males and females \(Table\ 3).\ Results from the MANOVA done upon the MASS corrected data are quite different from the analyses upon the original unscaled data. While the CV \(Table\ 2)\ is also highly significant for males \((Wilk’s \Lambda = 0.413; df = 39, 252; P < 0.0001)\) the two genera are now widely overlapping \(Figure\ 1)\. The same pattern holds for females, with the CV \(Table\ 2)\ being also significant \((Wilk’s \Lambda = 0.642; df = 39, 198; P < 0.0001)\), the scores of the two groups widely overlapping \(Figure\ 1)\. Moreover, correlations of the variables with the CV, for both males and females, are now very small with around half of them being significant \(Table\ 2)\. The MANOVA results with species nested within genus shows only two traits \(IS-PNS\ and\ PM-ZS)\ with significant difference for the females \(again\ using\ the\ Bonferroni\ correction)\ and six traits with significant differences in the males \(IS-PNS, NA-FM, NA-PNS, PT-FM, ZI-ZYGO, PNS-APET, Table\ 4)\.

Interestingly, the MANOVA performed upon the MASS corrected data to test for genus, sex and sex by genus
Table 1: Allometric coefficients

| Traits          | Saimiri |   |   |   | Cebus |   |   |   | PCI_{total} |
|-----------------|---------|---|---|---|-------|---|---|---|-------------|
|                 | AC      | SE| L1| L2| AC    | SE| L1| L2|             |
| ISPM            | 1.22    | 0.07| 1.09| 1.35 | **0.77** | 0.07| 0.63| 0.90| Face       | 0.18 |
| ISNSL           | 0.97    | 0.09| 0.79| 1.14 | 1.06 | 0.08| 0.90| 1.22| Face       | 0.16 |
| ISPNS           | **0.80**| 0.08| 0.64| 0.95 | **0.78** | 0.07| 0.65| 0.91| Face       | 0.19 |
| PMZS            | 0.85    | 0.09| 0.67| 1.03 | 1.06 | 0.08| 0.91| 1.21| Face       | 0.19 |
| PMZI            | 0.72    | 0.10| 0.53| 0.90 | 0.95 | 0.10| 0.76| 1.14| Face       | 0.17 |
| PMMT            | **0.63**| 0.05| 0.54| 0.73 | **0.71** | 0.06| 0.60| 0.82| Face       | 0.19 |
| NSLNA           | 0.90    | 0.15| 0.61| 1.20 | **0.64** | 0.12| 0.40| 0.88| Face       | 0.20 |
| NSLZS           | 0.89    | 0.08| 0.73| 1.04 | **0.78** | 0.06| 0.66| 0.89| Face       | 0.14 |
| NSLZI           | 0.77    | 0.07| 0.63| 0.92 | **0.86** | 0.07| 0.73| 0.99| Face       | 0.14 |
| NABR            | **0.62**| 0.06| 0.50| 0.74 | **0.57** | 0.07| 0.43| 0.70| Neurocranium | 0.17 |
| NAFM            | 0.62    | 0.05| 0.53| 0.72 | **0.65** | 0.05| 0.55| 0.74| Face       | 0.14 |
| NAPNS           | **0.62**| 0.06| 0.51| 0.73 | **0.84** | 0.05| 0.73| 0.94| Face       | 0.16 |
| BRPT            | 0.50    | 0.07| 0.35| 0.64 | **0.42** | 0.07| 0.29| 0.55| Neurocranium | 0.16 |
| BRAPET          | **0.63**| 0.05| 0.53| 0.74 | **0.47** | 0.04| 0.38| 0.56| Neurocranium | 0.12 |
| PTFM            | **0.61**| 0.18| 0.25| 0.96 | 0.90 | 0.33| 0.26| 1.55| Face       | 0.14 |
| PTAPET          | **0.65**| 0.06| 0.55| 0.76 | 0.80 | 0.12| 0.58| 1.03| Neurocranium | 0.14 |
| PTBA            | 0.89    | 0.04| 0.80| 0.97 | 0.89 | 0.08| 0.74| 1.04| Neurocranium | 0.15 |
| PTEAM           | 1.12    | 0.07| 0.98| 1.26 | 1.12 | 0.11| 0.90| 1.34| Neurocranium | 0.17 |
| PTZYG0          | 1.45    | 0.09| 1.27| 1.64 | **1.56** | 0.14| 1.29| 1.84| Face       | 0.16 |
| PTZSP           | 1.39    | 0.17| 1.05| 1.72 | **1.82** | 0.38| 1.07| 2.58| Neurocranium, face | 0.13 |
| FMZS            | 0.42    | 0.13| 0.16| 0.68 | **0.44** | 0.12| 0.21| 0.67| Face       | 0.11 |
| FMMT            | **0.86**| 0.05| 0.77| 0.95 | 0.93 | 0.04| 0.85| 1.01| Face       | 0.17 |
| ZSIZ            | 0.56    | 0.10| 0.37| 0.76 | 0.85 | 0.12| 0.61| 1.08| Face       | 0.12 |
| ZIIMT           | 1.43    | 0.14| 1.16| 1.70 | **1.47** | 0.09| 1.29| 1.65| Face       | 0.25 |
| ZIZYGO          | 1.97    | 0.15| 1.67| 2.27 | **2.26** | 0.11| 2.04| 2.48| Face       | 0.18 |
| ZITSP           | 1.53    | 0.08| 1.37| 1.70 | **1.64** | 0.07| 1.51| 1.78| Face       | 0.15 |
| MTPNS           | 0.63    | 0.06| 0.51| 0.74 | 0.88 | 0.07| 0.74| 1.02| Face       | 0.14 |
| PNSAPET         | 1.65    | 0.14| 1.37| 1.93 | **1.45** | 0.09| 1.26| 1.63| Neurocranium | 0.21 |
| APETBA          | 1.17    | 0.08| 1.01| 1.34 | 1.08 | 0.05| 0.98| 1.18| Neurocranium | 0.13 |
| APETTS          | **0.65**| 0.08| 0.50| 0.81 | **0.60** | 0.07| 0.45| 0.74| Neurocranium | 0.14 |
| BAEAM           | 0.84    | 0.06| 0.73| 0.95 | **0.66** | 0.04| 0.58| 0.73| Neurocranium | 0.16 |
| EAMZYGO         | **1.58**| 0.16| 1.28| 1.89 | 0.90 | 0.10| 0.70| 1.10| Face       | 0.25 |
| ZYGOTSP         | 1.84    | 0.10| 1.65| 2.03 | **1.43** | 0.07| 1.29| 1.57| Face       | 0.20 |
| LDAS            | 0.42    | 0.09| 0.23| 0.60 | **-0.16** | 0.08| -0.31| 0.00| Neurocranium | 0.05 |
| BRLD            | 0.27    | 0.08| 0.13| 0.42 | **0.19** | 0.18| -0.16| 0.54| Neurocranium | -0.01 |
| OPILD           | 0.64    | 0.17| 0.30| 0.98 | **0.07** | 0.11| -0.15| 0.30| Neurocranium | 0.06 |
| PTAS            | 0.82    | 0.05| 0.72| 0.93 | **0.87** | 0.06| 0.75| 0.98| Neurocranium | 0.17 |
| JPAS            | 0.76    | 0.07| 0.62| 0.89 | **0.68** | 0.07| 0.55| 0.81| Neurocranium | 0.13 |
| BAOPI           | **0.29**| 0.11| 0.07| 0.50 | **0.19** | 0.07| 0.05| 0.34| Neurocranium | 0.15 |

Multivariate allometry coefficients (AC), theirs standard errors (SE AC) and 95% confidence limits (L1 and L2) for both genera based on the first principal component extracted from each genus within-group V/CV matrix. PC1 vectors were normalized and each coefficient divided by \((1/39)^{1/2}\) to obtain the AC. Standard deviation estimates obtained from bootstrap analysis. Allometric coefficients with L1 higher that one (isometry) were considered to be positively allometric with general size (shown in bold and underlined) and conversely, AC with L2 lower that one were considered to be negatively allometric (bold and italic) with size. ACs with confidence limits encompassing 1.0 were considered to be isometric with size (normal font). The last column show the first principal component extracted from the whole sample (Cebus+Saimiri) and used in the MASS transformation.
Table 2: Canonical variate functions and correlations of traits to function

| Traits     | Canonical Variate | Correlation between traits and function | Canonical Variate | Correlation between traits and function |
|------------|-------------------|----------------------------------------|-------------------|----------------------------------------|
|            | Males CV1 | Females CV1 | Males CV1 | Females CV1 | Males CV1 | Females CV1 | Males CV1 | Females CV1 | Males CV1 | Females CV1 | Males CV1 | Females CV1 | Males CV1 | Females CV1 |
| ISPM       | -0.154   | 0.023        | 0.963     | 0.968     | -0.225   | -0.467     | 0.161     | 0.168     |
| ISNSL      | 0.136    | -0.085       | 0.936     | 0.930     | 0.059    | -0.639     | 0.078     | 0.291     |
| ISPNs      | 0.383    | 0.725        | 0.978     | 0.970     | -0.469   | -0.792     | -0.209    | -0.024    |
| PMZS       | -0.047   | -0.067       | 0.954     | 0.951     | -0.967   | 0.549      | 0.282     | 0.488     |
| PMZI       | -0.159   | -0.136       | 0.938     | 0.951     | 0.585    | -1.334     | 0.301     | 0.471     |
| PMMT       | 0.577    | 0.384        | 0.986     | 0.979     | -0.252   | -0.119     | -0.104    | 0.323     |
| NSLNA      | -0.070   | 0.100        | 0.901     | 0.899     | 0.368    | -0.781     | 0.138     | 0.109     |
| NSLZs      | 0.461    | 0.668        | 0.949     | 0.947     | 0.397    | -1.054     | 0.227     | 0.440     |
| NSLZi      | -0.854   | -1.495       | 0.950     | 0.958     | -0.581   | 1.321      | 0.251     | 0.418     |
| NABr       | -0.056   | -0.136       | 0.972     | 0.959     | 0.534    | -0.623     | -0.211    | -0.464    |
| NAFM       | 0.314    | 0.483        | 0.959     | 0.952     | -0.581   | -0.222     | -0.442    | -0.345    |
| NAPSNS     | -0.036   | -0.195       | 0.973     | 0.967     | -0.506   | -0.222     | -0.345    | -0.464    |
| BRPT       | 0.129    | -0.365       | 0.973     | 0.956     | -1.026   | -0.010     | -0.213    | -0.404    |
| BRApet     | 0.197    | 0.639        | 0.971     | 0.955     | 0.095    | -0.102     | -0.152    | -0.363    |
| PTFM       | 0.664    | 0.553        | 0.765     | 0.649     | -1.705   | -1.057     | 0.099     | 0.114     |
| PTApet     | -1.479   | -2.920       | 0.946     | 0.940     | -2.141   | -0.645     | -0.468    | -0.378    |
| PTBA       | 2.578    | 3.363        | 0.973     | 0.978     | 1.585    | -0.118     | -0.274    | -0.284    |
| P TEAM      | -0.050   | 0.088        | 0.953     | 0.959     | 0.300    | -0.205     | -0.249    | -0.281    |
| P T J W G O  | -0.438   | 0.921        | 0.897     | 0.904     | 0.025    | -0.899     | -0.145    | -0.295    |
| P T T S P   | -0.314   | -1.039       | 0.714     | 0.648     | -1.337   | -0.494     | -0.387    | -0.389    |
| FMZS       | 0.451    | 0.534        | 0.840     | 0.823     | -0.877   | -0.546     | -0.257    | -0.271    |
| FMMT       | -0.050   | -0.098       | 0.974     | 0.981     | 0.295    | -0.147     | 0.104     | 0.180     |
| Z Sz i     | 0.069    | 0.602        | 0.875     | 0.870     | 0.152    | -1.053     | 0.192     | 0.190     |
| ZIMT       | 0.176    | 0.350        | 0.946     | 0.964     | -0.615   | -0.586     | 0.353     | 0.452     |
| Z I Z Y G O | -0.792   | -0.960       | 0.816     | 0.807     | -0.250   | -0.740     | 0.237     | 0.026     |
| Z IT S P   | -0.063   | -0.247       | 0.886     | 0.883     | -0.202   | -0.689     | 0.167     | -0.107    |
| MTPNS      | 0.131    | -0.016       | 0.928     | 0.945     | -0.472   | -0.418     | -0.087    | -0.006    |
| PNSAPET    | -0.110   | 0.424        | 0.919     | 0.933     | -0.329   | -0.586     | 0.338     | 0.218     |
| APETBA     | -0.854   | -1.075       | 0.930     | 0.944     | -1.021   | -0.512     | 0.273     | 0.106     |
| APETTS     | 0.128    | 0.139        | 0.932     | 0.932     | -0.215   | -0.387     | -0.010    | 0.042     |
| BAAEAM     | -0.247   | -0.077       | 0.983     | 0.975     | -0.107   | -0.157     | -0.100    | -0.087    |
| EAMZYGO    | -0.247   | -0.286       | 0.955     | 0.934     | -0.130   | -1.242     | -0.263    | -0.196    |
| ZYGOTSP    | -0.073   | -0.360       | 0.931     | 0.955     | -0.698   | -0.584     | 0.303     | 0.057     |
| LDAS       | -0.082   | 0.096        | 0.648     | 0.721     | -0.076   | -0.539     | -0.363    | -0.617    |
| BRLD       | -0.125   | -0.494       | -0.105    | -0.208    | 0.159    | 0.221      | 0.130     | 0.360     |
| OPILD      | -0.088   | -0.398       | 0.606     | 0.599     | -0.293   | -0.402     | -0.378    | -0.617    |
| PTAS       | 0.747    | 0.718        | 0.980     | 0.982     | -0.961   | -0.702     | -0.405    | -0.250    |
| JPAS       | -0.036   | -0.053       | 0.946     | 0.944     | -0.011   | -0.129     | 0.053     | 0.208     |
| BAOPI      | 0.162    | 0.102        | 0.934     | 0.923     | -0.398   | -0.460     | -0.345    | 0.023     |

The canonical variate obtained for both males and females using either unscaled or MASS data are show. Also the correlation of each trait to each CV is also show, with significant (P < 0.05) correlations in bold.
Table 3: Differentiation analyses results from unscaled data

| Source  | Males | | | | Females | | |
|---------|-------|---|---|---|---------|---|---|
|         | SS    | df | MS  | F   | P       | SS  | df | MS  | F   | P       |
| ISPM    | 624.03| 1  | 624.03 | 1881.23 | < 0.0001 | ISPM | 270.34 | 1  | 270.34 | 1589.58 | < 0.0001 |
| Error   | 96.20 | 290 | 0.33 |     |        | Error | 40.14 | 236 | 0.17 | |
| ISNSL   | 2208.91 | 1  | 2208.91 | 1094.03 | < 0.0001 | ISNSL | 753.22 | 1  | 753.22 | 561.51 | < 0.0001 |
| Error   | 585.52 | 290 | 2.02 |     |        | Error | 316.57 | 236 | 1.34 | |
| ISPNS   | 8866.98 | 1  | 8866.98 | 3443.39 | < 0.0001 | ISPNS | 3466.56 | 1  | 3466.56 | 1878.82 | < 0.0001 |
| Error   | 746.77 | 290 | 2.58 |     |        | Error | 435.44 | 236 | 1.85 | |
| PMZS    | 2771.68 | 1  | 2771.68 | 1988.35 | < 0.0001 | PMZS | 904.62 | 1  | 904.62 | 799.20 | < 0.0001 |
| Error   | 404.25 | 290 | 1.39 |     |        | Error | 267.13 | 236 | 1.13 | |
| PMZI    | 4907.99 | 1  | 4907.99 | 1624.74 | < 0.0001 | PMZI | 1768.39 | 1  | 1768.39 | 921.21 | < 0.0001 |
| Error   | 876.03 | 290 | 3.02 |     |        | Error | 453.03 | 236 | 1.92 | |
| PMMT    | 6091.46 | 1  | 6091.46 | 5727.18 | < 0.0001 | PMMT | 2282.79 | 1  | 2282.79 | 2606.01 | < 0.0001 |
| Error   | 308.45 | 290 | 1.06 |     |        | Error | 206.73 | 236 | 0.88 | |
| NSLNA   | 1614.81 | 1  | 1614.81 | 653.76 | < 0.0001 | NSLNA | 678.68 | 1  | 678.68 | 279.02 | < 0.0001 |
| Error   | 716.31 | 290 | 2.47 |     |        | Error | 574.05 | 236 | 2.43 | |
| NSLS    | 1600.16 | 1  | 1600.16 | 1552.98 | < 0.0001 | NSLS | 566.57 | 1  | 566.57 | 650.30 | < 0.0001 |
| Error   | 298.81 | 290 | 1.03 |     |        | Error | 205.61 | 236 | 0.87 | |
| NSLZI   | 5429.01 | 1  | 5429.01 | 1596.46 | < 0.0001 | NSLZI | 2000.24 | 1  | 2000.24 | 891.50 | < 0.0001 |
| Error   | 986.19 | 290 | 3.40 |     |        | Error | 529.51 | 236 | 2.24 | |
| NABR    | 19412.50 | 1  | 19412.50 | 2202.66 | < 0.0001 | NABR | 7782.90 | 1  | 7782.90 | 875.87 | < 0.0001 |
| Error   | 2555.83 | 290 | 8.81 |     |        | Error | 2097.06 | 236 | 8.89 | |
| NAFM    | 2352.00 | 1  | 2352.00 | 2073.69 | < 0.0001 | NAFM | 856.69 | 1  | 856.69 | 1166.02 | < 0.0001 |
| Error   | 328.92 | 290 | 1.13 |     |        | Error | 173.39 | 236 | 0.73 | |
| NAPNS   | 6079.51 | 1  | 6079.51 | 2707.97 | < 0.0001 | NAPNS | 2159.91 | 1  | 2159.91 | 1270.51 | < 0.0001 |
| Error   | 651.06 | 290 | 2.25 |     |        | Error | 401.21 | 236 | 1.70 | |
| BRPT    | 11044.23 | 1  | 11044.23 | 2274.23 | < 0.0001 | BRPT | 4500.39 | 1  | 4500.39 | 727.55 | < 0.0001 |
| Error   | 1408.31 | 290 | 4.86 |     |        | Error | 1459.82 | 236 | 6.19 | |
| BRAPET  | 6227.39 | 1  | 6227.39 | 2353.72 | < 0.0001 | BRAPET | 2522.35 | 1  | 2522.35 | 916.62 | < 0.0001 |
| Error   | 767.27 | 290 | 2.65 |     |        | Error | 649.42 | 236 | 2.75 | |
| PTFM    | 848.11 | 1  | 848.11 | 293.76 | < 0.0001 | PTFM | 259.66 | 1  | 259.66 | 101.66 | < 0.0001 |
| Error   | 837.26 | 290 | 2.89 |     |        | Error | 602.80 | 236 | 2.55 | |
| PTAPE   | 3520.35 | 1  | 3520.35 | 896.99 | < 0.0001 | PTAPE | 1273.51 | 1  | 1273.51 | 363.74 | < 0.0001 |
| Error   | 1138.14 | 290 | 3.92 |     |        | Error | 826.28 | 236 | 3.50 | |
| PTBA    | 9388.69 | 1  | 9388.69 | 1681.36 | < 0.0001 | PTBA | 3645.97 | 1  | 3645.97 | 751.50 | < 0.0001 |
| Error   | 1619.35 | 290 | 5.58 |     |        | Error | 1144.97 | 236 | 4.85 | |
| PTEAM   | 6012.35 | 1  | 6012.35 | 1120.82 | < 0.0001 | PTEAM | 2257.54 | 1  | 2257.54 | 491.86 | < 0.0001 |
| Error   | 1555.63 | 290 | 5.36 |     |        | Error | 1083.19 | 236 | 4.59 | |
| PTZYGO  | 3409.62 | 1  | 3409.62 | 524.15 | < 0.0001 | PTZYGO | 1225.50 | 1  | 1225.50 | 238.55 | < 0.0001 |
| Error   | 1886.46 | 290 | 6.51 |     |        | Error | 1212.40 | 236 | 5.14 | |
| PTTSP   | 570.13 | 1  | 570.13 | 122.77 | < 0.0001 | PTTSP | 166.37 | 1  | 166.37 | 35.31 | < 0.0001 |
| Error   | 1346.77 | 290 | 4.64 |     |        | Error | 1111.99 | 236 | 4.71 | |
| FMZS    | 725.73 | 1  | 725.73 | 511.53 | < 0.0001 | FMZS | 319.79 | 1  | 319.79 | 236.29 | < 0.0001 |
Table 3: Differentiation analyses results from unscaled data (Continued)

| Trait      | Error  | df  | SS  | df  | MS  | F    | P     |
|------------|--------|-----|-----|-----|-----|------|-------|
| FMMT       | 411.43 | 290 | 1.42|     |     |      |       |
| ZSIZ       | 724.16 | 290 | 2.50|     |     |      |       |
| ZIMT       | 563.39 | 290 | 1.94|     |     |      |       |
| ZIZYGO     | 674.55 | 290 | 2.33|     |     |      |       |
| Error      | 647.87 | 290 | 0.92|     |     |      |       |
| PNSAPET    | 733.94 | 290 | 2.53|     |     |      |       |
| APETBA     | 424.50 | 290 | 1.46|     |     |      |       |
| APETTS     | 230.17 | 290 | 0.79|     |     |      |       |
| BAEAM      | 158.55 | 290 | 0.55|     |     |      |       |
| EAMZYG      | 791.32 | 290 | 2.73|     |     |      |       |
| ZYGOTSP    | 647.79 | 290 | 2.23|     |     |      |       |
| LDAS       | 620.34 | 290 | 2.14|     |     |      |       |
| BRLD       | 3781.79 | 290 | 13.04|     |     |      |       |
| OPILD      | 650.73 | 290 | 149.32|     |     |      |       |
| PTAS       | 1852.91 | 290 | 5.46|     |     |      |       |
| JPAS       | 349.51 | 290 | 1.21|     |     |      |       |
| BAOPI      | 907.95 | 290 | 0.68|     |     |      |       |

Results from the GLM analyses for each sex using unscaled data with "genus" as a factor and "species" nested within genus as independent factors. For each trait is presented the Sum of Squares (SS), degrees of freedom (df), Mean Square (MS), F value and the associated probability (P). Significant differences in bold.
effects shows only a small interaction of the factors, with only 3 traits (IS-PM, PM-ZS and LD-AS) deemed significant. Also, few traits are significant between genera (ZI-ZYGO, BR-PT, PM-MT). Conversely, 17 of the 39 traits show significance differences between the sexes using the conservative Bonferroni threshold.

**Heterochrony and life-history**

Figure 2 shows the regression between the ages of first reproduction against adult weights, after correcting for non-independence between points due to shared history (phylogeny). Notice that *Cebus* is the only genus deviating significantly from the regression line. This indicates that capuchins have a delayed on-set of reproduction in relation to the other genera given that its age of first reproduction is larger than expected for a NWM of its size. Likewise, Figure 3 shows the regression between the birth weights against body weight (the result is the same if skull size is used instead of body weight). Notice that squirrel monkeys deviate significantly from the regression line. This indicates that *Saimiri* babies are born heavier than expected for a NWM with its body size. Figure 4 shows the regression of the age at weaning against adult body weight. Squirrels monkeys seem to lie slightly below the 95% confidence interval of the regression line indicating that they are weaned earlier than expected for a NWM of its size. Conversely, capuchins seem to deviate from the regression line in the upper direction, suggesting that they are weaned later that expected for a NWM of its size. Figure 5 show the regression of the fetal growth rate (birth weight/gestation length) against adult body weight. *Saimiri* and *Cebus* lie slightly above the regression line. These patterns seem to be robust to within genus between species variation in life-history data. Unfortunately, complete information on life-history traits is not available for all species within each genus as well as solid phylogenetic hypotheses for all species within each of the two genera.

**Growth trajectories**

I tested the assumption of size as a proxy for age by regressing size (PC1) against developmental age codes ([30], ages 1 to 6) separately for males and females. *Cebus* data was used because the juveniles and sub-adult sampling is much more extensive in this genus and have sex information available. Both regressions were highly significant (P < 0.00001) and the multiple R was 0.80 for females and 0.82 for males. Similar analyses in *Saimiri* (but ignoring sex dimorphism due to lack of sex in most of the juvenile and sub-adult sample) show also a similar multiple R (0.81). Furthermore, for *Cebus apella* at least there is available information for absolute age (in months) for each age class based on dental eruption (see

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**Figure 1**

**Canonical variates.** Canonical variate 1 (CV1) obtained separately for males and females with frequency distribution of CV1 scores on the margin. On the x-axis is shown the CV1 obtained from the unscaled data and on the y-axis the CV1 from the MASS corrected data.
Table 4: Differentiation analyses results from MASS data

| Source               | Males                  | Females                |
|----------------------|------------------------|------------------------|
|                      | SS         | df | MS     | F   | P     | Source     | SS         | df | MS     | F   | P     |
| MASS-ISPM            | 0.06       | 1  | 0.06   | 0.38| 0.53703| MASS-ISPM  | 1.76       | 1  | 1.76   | 12.94| 0.00039|
| Error                | 45.32      | 290| 0.16   |    |        | Error      | 32.07      | 236| 0.14   |    |        |
| MASS-ISNSL           | 7.30       | 1  | 7.30   | 6.06| 0.01442| MASS-ISNSL | 0.10       | 1  | 0.10   | 0.09| 0.76821|
| Error                | 349.42     | 290| 1.20   |    |        | Error      | 272.50     | 236| 1.15   |    |        |
| MASS-ISPNS           | 47.66      | 1  | 47.66  | 33.05|<0.0001 | MASS-ISPNS | 31.42      | 1  | 31.42  | 19.92| 0.00001|
| Error                | 418.21     | 290| 1.44   |    |        | Error      | 372.15     | 236| 1.58   |    |        |
| MASS-PMZS            | 0.37       | 1  | 0.37   | 0.46| 0.49812| MASS-PMZS  | 16.80      | 1  | 16.80  | 18.23| 0.00003|
| Error                | 232.91     | 290| 0.80   |    |        | Error      | 217.43     | 236| 0.92   |    |        |
| MASS-PMZI            | 2.87       | 1  | 2.87   | 1.63| 0.20299| MASS-PMZI  | 0.13       | 1  | 0.13   | 0.09| 0.76245|
| Error                | 511.86     | 290| 1.77   |    |        | Error      | 325.44     | 236| 1.38   |    |        |
| MASS-PMMT            | 6.26       | 1  | 6.26   | 5.20| 0.02333| MASS-PMMT  | 1.45       | 1  | 1.45   | 1.73| 0.19019|
| Error                | 349.16     | 290| 1.20   |    |        | Error      | 197.64     | 236| 0.84   |    |        |
| MASS-NSLNA           | 22.70      | 1  | 22.70  | 10.06| 0.00168| MASS-NSLNA | 9.87       | 1  | 9.87   | 4.43| 0.03637|
| Error                | 654.58     | 290| 2.26   |    |        | Error      | 525.89     | 236| 2.23   |    |        |
| MASS-NSLZS           | 5.11       | 1  | 5.11   | 7.82| 0.0055  | MASS-NSLZS | 7.14       | 1  | 7.14   | 9.10| 0.00283|
| Error                | 189.32     | 290| 0.65   |    |        | Error      | 185.17     | 236| 0.78   |    |        |
| MASS-NSLZI           | 1.31       | 1  | 1.31   | 0.91| 0.34022 | MASS-NSLZI | 0.00       | 1  | 0.00   | 0.00| 0.94965|
| Error                | 415.99     | 290| 1.43   |    |        | Error      | 278.84     | 236| 1.18   |    |        |
| MASS-NABR            | 9.64       | 1  | 9.64   | 1.34| 0.24798 | MASS-NABR  | 3.59       | 1  | 3.59   | 0.44| 0.50744|
| Error                | 2086.87    | 290| 7.20   |    |        | Error      | 1921.51    | 236| 8.14   |    |        |
| MASS-NAFM            | 13.38      | 1  | 13.38  | 18.94|<0.0002 | MASS-NAFM  | 1.39       | 1  | 1.39   | 2.16| 0.14339|
| Error                | 204.90     | 290| 0.71   |    |        | Error      | 152.70     | 236| 0.65   |    |        |
| MASS-NAPNS           | 22.52      | 1  | 22.52  | 19.03|<0.0002 | MASS-NAPNS | 1.43       | 1  | 1.43   | 1.39| 0.239  |
| Error                | 343.23     | 290| 1.18   |    |        | Error      | 241.62     | 236| 1.02   |    |        |
| MASS-BRPT            | 0.57       | 1  | 0.57   | 0.11| 0.73811 | MASS-BRPT  | 0.05       | 1  | 0.05   | 0.01| 0.92523|
| Error                | 1472.11    | 290| 5.08   |    |        | Error      | 1303.78    | 236| 5.52   |    |        |
| MASS-BRAPET          | 4.26       | 1  | 4.26   | 2.44| 0.11953 | MASS-BRAPET| 2.68       | 1  | 2.68   | 1.25| 0.265  |
| Error                | 506.40     | 290| 1.75   |    |        | Error      | 506.94     | 236| 2.15   |    |        |
| MASS-PTFM            | 50.68      | 1  | 50.68  | 22.99|<0.0001 | MASS-PTFM  | 5.97       | 1  | 5.97   | 2.45| 0.11876|
| Error                | 639.43     | 290| 2.20   |    |        | Error      | 575.23     | 236| 2.44   |    |        |
| MASS-PTAPET          | 0.04       | 1  | 0.04   | 0.02| 0.90209 | MASS-PTAPET| 2.64       | 1  | 2.64   | 1.10| 0.29604|
| Error                | 731.79     | 290| 2.52   |    |        | Error      | 567.86     | 236| 2.41   |    |        |
| MASS-PTBA            | 8.29       | 1  | 8.29   | 3.53| 0.06136 | MASS-PTBA  | 1.62       | 1  | 1.62   | 0.61| 0.43607|
| Error                | 681.78     | 290| 2.35   |    |        | Error      | 627.62     | 236| 2.66   |    |        |
| MASS-PTEAM           | 22.87      | 1  | 22.87  | 9.07| 0.00282 | MASS-PTEAM  | 3.63       | 1  | 3.63   | 1.26| 0.2624 |
| Error                | 731.02     | 290| 2.52   |    |        | Error      | 679.63     | 236| 2.88   |    |        |
| MASS-PTZYGO          | 33.73      | 1  | 33.73  | 10.53| 0.00132| MASS-PTZYGO| 6.35       | 1  | 6.35   | 1.81| 0.18004|
| Error                | 929.47     | 290| 3.21   |    |        | Error      | 828.24     | 236| 3.51   |    |        |
| MASS-PTTSP           | 13.38      | 1  | 13.38  | 3.84| 0.05094 | MASS-PTTSP | 10.85      | 1  | 10.85  | 2.70| 0.10192|
| Error                | 1009.69    | 290| 3.48   |    |        | Error      | 949.35     | 236| 4.02   |    |        |
Table 4: Differentiation analyses results from MASS data (Continued)

| Trait          | SS    | df | MS     | F      | P      |
|----------------|-------|----|--------|--------|--------|
| MASS-FMZS      | 7.68  | 1  | 7.68   | 6.71   | 0.01005|
| Error          | 331.62| 290| 1.14   |        |        |
| MASS-FMMT      | 4.20  | 1  | 4.20   | 7.69   | 0.0059 |
| Error          | 158.15| 290| 0.55   |        |        |
| MASS-ZSZI      | 3.67  | 1  | 3.67   | 2.76   | 0.09755|
| Error          | 384.99| 290| 1.33   |        |        |
| MASS-ZIMT      | 0.08  | 1  | 0.08   | 0.10   | 0.75682|
| Error          | 247.42| 290| 0.85   |        |        |
| MASS-ZIZYGO    | 54.67 | 1  | 54.67  | 16.68  | 0.00006|
| Error          | 950.39| 290| 3.28   |        |        |
| MASS-ZITSP     | 1.28  | 1  | 1.28   | 0.58   | 0.44756|
| Error          | 640.34| 290| 2.21   |        |        |
| MASS-MTPNS     | 3.03  | 1  | 3.03   | 10.24  | 0.00153|
| Error          | 85.76 | 290| 0.30   |        |        |
| MASS-PNSAPET   | 49.00 | 1  | 49.00  | 40.10  | <0.00001|
| Error          | 354.33| 290| 1.22   |        |        |
| MASS-APETBA    | 0.30  | 1  | 0.30   | 0.36   | 0.54778|
| Error          | 243.43| 290| 0.84   |        |        |
| MASS-APETTS    | 3.02  | 1  | 3.02   | 4.59   | 0.03291|
| Error          | 190.37| 290| 0.66   |        |        |
| MASS-BAEAM     | 0.73  | 1  | 0.73   | 1.61   | 0.20485|
| Error          | 131.42| 290| 0.45   |        |        |
| MASS-EAMZYGOTSP| 13.68 | 1  | 13.68  | 8.35   | 0.00416|
| Error          | 475.33| 290| 1.64   |        |        |
| MASS-ZYGOTSP   | 1.71  | 1  | 1.71   | 1.77   | 0.18456|
| Error          | 279.83| 290| 0.96   |        |        |
| MASS-LDAS      | 9.86  | 1  | 9.86   | 4.67   | 0.03149|
| Error          | 611.85| 290| 2.11   |        |        |
| MASS-BRLD      | 49.78 | 1  | 49.78  | 3.68   | 0.05594|
| Error          | 3919.26| 290| 13.51  |        |        |
| MASS-OPILD     | 15.31 | 1  | 15.31  | 3.61   | 0.0583 |
| Error          | 1228.41| 290| 4.24   |        |        |
| MASS-PTAS      | 0.61  | 1  | 0.61   | 0.22   | 0.64043|
| Error          | 815.43| 290| 2.81   |        |        |
| MASS-JPAS      | 0.01  | 1  | 0.01   | 0.01   | 0.91656|
| Error          | 258.37| 290| 0.89   |        |        |
| MASS-BAOPI     | 5.46  | 1  | 5.46   | 6.39   | 0.01198|
| Error          | 247.63| 290| 0.85   |        |        |

Results from the GLM analyses for each sex using MASS data with "genus" as a factor and "species" nested within genus as independent factors. For each trait is presented the Sum of Squares (SS), degrees of freedom (df), Mean Square (MS), F value and the associated probability (P). Significant differences in bold.
Table 2 in [30]). Therefore is possible to calculate the correspondence between absolute size, time and age classes. Age classes and the natural log of age (in months) present a correlation of 0.97 for males of *Cebus apella*. Absolute time and size are also highly correlated (0.82) again indicating that size is a reasonable proxy to time. Given that absolute age is not available for the genus *Saimiri*, I use dental age classes here in the paper as a "developmental marker" and absolute size as an estimate of time.

Comparison of the growth trajectories are summarized in Figure 6 and Table 5. Most traits present a linear trajectory in the ln-scale, but some exceptions occur. Two general patterns are evident: 1) simple extension/truncation of the growth trajectory (Fig. 7a, 7b) 2) a step along the size (time) axis causing a shift in the otherwise parallel trajectories with *Saimiri* above (Fig. 7c, d). Most traits conform to one of these two patterns with a few exceptions. A group of such exceptions correspond to those traits which present very low correlation with size (Table 5) including traits LD-AS, BR-LD, OPI-LD, BA-OPI (Fig. 7e,f). Twenty-six traits (67% of all traits) can be assigned to pattern 1 (simple extension) and nine traits (23%) to pattern 2 (step along the size axis) (see Table 5).

**Figure 2**

**Comparative phylogenetic regression of life-history traits.** Plot of the age of first reproduction against adult weight in New World Monkeys controlling for shared history (phylogeny). The regression line and 95% confidence limits were obtained from the method described in Garland and Ives (2000) and implemented in package PDAP in MESQUITE.

Centroid size is highly correlated with PC1 score derived from the linear distances ($R = 0.999$, $P < 0.0001$). Also, centroid size and PC1 score are linearly related when both are in ln scale. Therefore I use the natural log of the centroid size as a measure of absolute skull size. Figure 7 show the plot of the first PC-3D against centroid size [see Additional files 1, 2, 3, 4, 5, 6, 7, 8, 9]. This PC1-3D basically represents allometric variation in shape associated with size, accounting for 51.5% of all variation in shape. Starting from the smaller values (*Saimiri* young's), mor-
phologically PC1-3D represents a lowering of the cranial vault with a large dislocation of landmark BR to a more posterior position as well as a relatively smaller posterior cranial base with a large dislocation of landmark LD to a more anterior position. Therefore, a major change described by this PC1-3D is that involving the neurocranium, with changes in the height of the vault associated with the base/back of the skull, involving landmarks LD, BR and to a lesser extent AS. These landmarks are dislocated from a more posterior (LD) and lateral (AS) position in Saimiri babies to a more anterior (LD) and medial position (AS) in Cebus adults. Those changes in landmarks BR and LD dominates the PC1-3D which can be easily observed from a vector of changes in landmarks coordinates comparing the upper and higher limits of variation described by PC1-3D (Table 6). Another change in shape associated with PC1-3D is in the face, being more prognathic (landmarks IS and PM) in the upper end (Cebus), with a longer and slender palate (landmark MT) and the zygomatic arch (more robust and lateral – landmarks ZI and ZYGO). Also associated with this PC1-3D is the dislocation of landmarks PT and TSP to a more medial position resulting in a more slender skull in Cebus (Figure 7). Figure 8 present the plot of the second PC-3D against size. This PC2-3D is basically an ontogenetic vector accounting for 15.6% of all variation in shape. The PC2-3D represents (again starting from the smaller values – Cebus and Saimiri young’s) a relative decrease in the neurocranium region with landmark BR once more involved but this time being dislocated to a forward and lower position. Also, an enhanced prognathism resulting from landmarks IS and PM being dislocated forward and upward. Another change involves landmarks MT and ZI being dislocated forward and to a lower position resulting in a palate.

Figure 3
Comparative phylogenetic regression of life-history traits. Plot of the birth weight against adult weight in New World Monkeys controlling for shared history (phylogeny). The regression line and 95% confidence limits were obtained from the method described in Garland and Ives (2000) and implemented in package PDAP in MESQUITE.
region comparatively smaller, face more prognathic and with a more robust pre-zygomatic region. Also, the cranial base is to some extent relatively smaller with landmark TSP being dislocated to a more posterior position and closer to landmarks APET, BA, TS and JP. Contributing to PC2-3D is also, and again, a dislocation of landmarks LD to a more anterior position and AS to a more medial position, exactly the same change described in PC1-3D. So, to some extent changes in shape described by PC1-3D and PC2-3D are similar (Table 6).

Only the PC1-3D presents significant differences between Cebus and Saimiri (t = 53.97, df = 231.6, P < 10^-5) and this difference holds for all age classes analyzed separately. All other PC’s variables, that cumulatively account for 97% of all shape variation (from PC2 to PC 40) do not present any significant differences between the two genera.

Both PC1-3D and PC2-3D are highly correlated with size variation within each genus (Table 7). Also, PC1-3D and PC2-3D are also highly correlated between them within each of the two genera. PC1-3D is also highly correlated with size among genera (R = 0.98, P < 10^-5), while PC2-3D scores are uncorrelated (R close to zero) with both size and PC1-3D among genera (as expected because PC1 and PC2 are by definition extracted as orthogonal vectors). All other PC’s variables are uncorrelated with size (from PC3 to PC 40).

**Discussion**

Sexual dimorphism in *Cebus* and *Saimiri* is well marked, either in the original traits or the MASS corrected data. Indeed, 33 of the unscaled traits or the MASS corrected data show significant sexual dimorphism in *Cebus* and 30 in *Saimiri*, using the conservative Bonferroni threshold. After removing scale differences, MASS corrected data show 17 traits with significant
sexual dimorphism in *Cebus* and 11 in *Saimiri* (again using the 0.05/39 threshold). Males in both genera are larger than females, but skull size dimorphism is more evident in *Cebus* (on average females are 66% of the males size) while in *Saimiri* females are on average 82% of the males. Besides, both sexes share a high similarity in their allometric vector correlation (0.948 in *Cebus* and 0.945 in *Saimiri*). Altogether these results suggests that sexual dimorphism in Cebinae is not simply a function of size related differences. In other words, if females were to grow to the same size as males in either *Saimiri* or *Cebus*, sexual dimorphism in shape would still be evident. Therefore nearly all analyses were performed separately for each sex.

Differences between the two genera are massive (Figure 1) considering the original data, with Mahalanobis $D^2$ distances pointing out the complete separation of the two groups in both sexes ($D^2_{\text{males}} = 1299$ and $D^2_{\text{females}} = 1374$). Conversely, there is a wide overlap between both genera considering the MASS corrected data (Figure 1) with very low $D^2$ distances ($D^2_{\text{males}} = 3.84$ and $D^2_{\text{females}} = 1.74$). Moreover, 38 of the 39 original traits show significant differences ($P > 10^{-5}$) between the two genera in both sexes. Conversely, only two traits show significant differences between the two genera after correcting for scaling differences (MASS data) in females. Males present a slightly larger differentiation with 6 traits showing significant differences between the genera in the MASS corrected data. Taken together these results suggest that most of the differences between *Cebus* and *Saimiri* are related to size. Indeed, the only trait in the original scale not showing significant differences between the two genera (BR-LD) is the only one not influenced by size (Table 1 PC1 total). This is an interesting result given that these two landmarks BR and LD are by far the most influential in the shape changes described by PC1-3D and PC2-3D. In fact, given

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**Figure 5**

**Comparative phylogenetic regression of life-history traits.** Plot of the pre-natal growth rate against adult weight in New World Monkeys controlling for shared history (phylogeny). The regression line and 95% confidence limits were obtained from the method described in Garland and Ives (2000) and implemented in package PDAP in MESQUITE.
Table 5: Growth trajectories

| Trait        | Pattern 1                      | Pattern 2                                      | Functional/developmental group |
|--------------|--------------------------------|-----------------------------------------------|--------------------------------|
| ISPM         | hypermorphosis/progenesis      | pre-/postdisplacement (Saimiri above)         | Oral                           |
| ISNSL        | hypermorphism/progenesis       |                                               | Nasal                          |
| ISPNS        | hypermorphism/progenesis       |                                               | Oral, nasal                    |
| PMZS         | hypermorphosis/progenesis      |                                               | Oral                           |
| PMZI         | hypermorphosis/progenesis      |                                               | Oral                           |
| PMMT         | hypermorphosis/progenesis      |                                               | Oral                           |
| NSLNA        | hypermorphosis/progenesis      |                                               | Nasal                          |
| NSLZS        | hypermorphosis/progenesis      |                                               | Nasal                          |
| NSSLZI       | hypermorphosis/progenesis      |                                               | Nasal                          |
| NAFM         | hypermorphosis/progenesis      |                                               | Cranial vault                  |
| NAPNS        | hypermorphosis/progenesis      |                                               | Cranial vault                  |
| BRPT         | hypermorphosis/progenesis      |                                               | Cranial vault                  |
| BRAFET       | hypermorphosis/progenesis      |                                               | Cranial vault                  |
| PTFM         | hypermorphosis/progenesis      | pre-/postdisplacement (Saimiri above)         | Orbit                          |
| PTAPET       | hypermorphosis/progenesis      |                                               | Cranial vault                  |
| PTBA         | hypermorphosis/progenesis      |                                               | Cranial vault                  |
| PTEAM        | hypermorphosis/progenesis      |                                               | Cranial vault                  |
| PTZYG0       | hypermorphosis/progenesis      | pre-/postdisplacement (Saimiri above)         | Zygomatic                      |
| PTSSP        | hypermorphosis/progenesis      | pre-/postdisplacement (Saimiri above)         | Cranial vault, zygomatic        |
| FMZS         | hypermorphosis/progenesis      |                                               | Zygomatic                      |
| FMU          | hypermorphosis/progenesis      |                                               | Oral                           |
| ZSIZ         | hypermorphosis/progenesis      | pre-/postdisplacement (Saimiri above)         | Oral                           |
| ZIZYGO       | hypermorphosis/progenesis      | pre-/postdisplacement (Saimiri above)         | Zygomatic                      |
| ZITSP        | hypermorphosis/progenesis      | pre-/postdisplacement (Saimiri above)         | Zygomatic                      |
| MTPNS        | hypermorphosis/progenesis      |                                               | Oral                           |
| PNSAPET      | hypermorphosis/progenesis      |                                               | Cranial base                   |
| APETBA       | hypermorphosis/progenesis      |                                               | Cranial base                   |
| APETTS       | hypermorphosis/progenesis      | pre-/postdisplacement (Saimiri above)         | Cranial base                   |
| BAEAM        | hypermorphosis/progenesis      |                                               | Cranial base                   |
| EAMZYG0      | hypermorphosis/progenesis      |                                               | Zygomatic                      |
| ZYOTSP       | hypermorphosis/progenesis      |                                               | Zygomatic                      |
| LDAS         | low correlation with size      | pre-/postdisplacement (Saimiri above)         | Cranial vault                  |
| BRLD         | low correlation with size      | low correlation with size                      | Cranial vault                  |
| OPILD        | low correlation with size      | low correlation with size                      | Cranial vault                  |
| PTAS         | hypermorphosis/progenesis      |                                               | Cranial vault                  |
| JPAS         | hypermorphosis/progenesis      |                                               | Cranial base                   |
| BAOPR        | low correlation with size      | low correlation with size                      | Cranial base                   |

Interpretation of the bivariate plots (each trait against centroid size) relative to heterochronic processes.

that PC1-3D is the axis of major differentiation between Saimiri and Cebus, and that BR is dislocated to a more posterior and lower position while LD is dislocated forward that explain why the linear distance between the two landmarks is basically the same in both genera, despite the huge size difference between them. This can also be observed in the additional on-line material [see Additional files 1, 2, 3, 4, 5, 6, 7, 8, 9], particularly on the lateral view. After removing scale differences from the data (MASS correction) the large differences between the two genera nearly disappear, with only a small differentiation being observed. These results from the Euclidean distances analyses are totally consistent with the results obtained from the geometric morphometrics approach. Moreover, these results also show that males are somewhat more differentiated than females, after removing scale differences. In short, for the most part, squirrel monkeys are scaled down versions of capuchins, or vice versa.

Allometric vectors are much more similar than expected by chance in all comparisons as indicated by the comparisons of observed vectors correlations against its random permutations. This can be quantified by the angles formed between those allometric vectors, with observed angles ranging from 11.18° to 18.01°, well below the minimum expected angle of 28.36 ° from the random permutations. Given strong similarity in the allometric vectors of Cebus and Saimiri, and that most of the differences between them are size-related, it is seems clear that during the evolutionary diversification of these two sister
genera size plays a major role. Conservation of allometric patterns in *Cebus* and *Saimiri* suggest that they simply follow the same growth patterns but evolved to attain different adult final sizes (Figure 6a, b). This conclusion is reinforced by the results of the geometric Morphometrics approach where the absolute magnitude of changes in landmarks position along PC1-3D and PC2-3D between consecutive age classes within *Saimiri* and *Cebus* are compared. All vectors of change are similar either within or between genus and present vectors correlation above 0.97, which again is well above the expected range from the random permutation tests (0.60–0.87).

In a size-based scheme for heterochrony (see page 42 in [26]) this would suggest that *Saimiri* evolved its small size by some sort of ontogenetic scaling or allometric progenesis or conversely, *Cebus* evolved its larger size by hypermorphosis, or both processes were involved since the genera diverged from their last common ancestor. At present is impossible to know the direction of change or in other words, which is the ancestral condition and which derived. Furthermore, both processes might have happen while both genera diverged from an ancestor of intermediate size.

Yet, despite conservation of allometric patterns, a broader, and perhaps more interesting, picture arises when we look at the comparison of growth trajectories (Table 5). Comparison of growth trajectories suggests two general and diverse underlying changes in development (Figure 6). Pattern one corresponds to an extension/truncation of the growth trajectory and occurs in 67% of all traits (Fig. 7a, b). Pattern two corresponds to a translation (see Fig. 4a in [31]) or height of otherwise parallel trajectories (Fig. 7c, d) and accounts for 23% of all traits. Therefore, developmental changes involved in the *Cebus-Saimiri* evolution
seem to be to a larger part mix of two different heterochronic patterns: pregenesis-hypermorphosis and prepostdisplacement if we take a classic Morphometrics approach.

But, what light can be shed on this discussion by the results of the geometric morphometrics approach? First, is clear that the PC1-3D is an allometric size vector with a correlation of 0.97 with absolute size (centroid size). This is also the axis of major differentiation between the two genera and in fact the only one where they do not overlap and present a significant difference on a series of t-tests performed upon each of the first 40 PC’s of the 3D analyses. These results are quite similar to the ones obtained with the canonical variate analyses done upon the original and the MASS data and basically reinforce the point that Cebus is a scaled-up version of Saimiri.

Also, the orientation of the PC1-3D is basically the same between the two genera (regression slope of PC1-3D against centroid size: k = 0.273, 95% CI 0.249–0.298 for Cebus and k = 0.265, 95% CI 0.217–0.314 for Saimiri). Second, PC2-3D is also an allometric vector with a high correlation with size if the focus is the within genus variation (r = 0.81 in Cebus and r = 0.70 in Saimiri). Indeed, PC2-3D is also highly correlated with PC1-3D (r = 0.77 in Cebus and r = 0.87 in Saimiri). Furthermore, the orientation of the PC2-3D is also basically the same between the two genera (regression slope of PC2-3D against size: k = 0.351, 95% CI 0.312–0.389 for Cebus and k = 0.293, 95% CI 0.231–0.356 for Saimiri). Considering all these results both PC’s 3D can be interpreted as allometric vectors. In other words, PC2-3D represents ontogenetic allometry (Fig. 8) while PC1-3D represents evolutionary allometry (Fig. 7). In fact, changes in both PC’s seem to some extent

**Figure 7**

Geometric Morphometrics – size and evolutionary shape allometry. Plot of the PC1-3D against centroid size (ln). Specimens with different ages are show in different colours and symbols and skull 3D reconstructions are show in oblique and dorsal views.
similar involving basically the neurocranium, face and zygomatic regions and it is not a surprise that both represent allometric variation.

What these results inform us about the evolution of *Cebus* and *Saimiri*? First, almost all differentiation between these two genera is related to size/scaling. Second, these differences either in scale (absolute size) or shape associated with size (allometry) follow a common evolutionary trajectory (Fig. 7). This last point is also totally supported by the correlation between absolute size, the axis of differentiation between the two genera (CV1), and PC1-3D (all R's larger than 0.98). Thirdly, ontogenetic variation in shape in one genus is parallel to the ontogenetic variation in the other. In other words, ontogenetic allometry follows a common and parallel trajectory between *Cebus* and *Saimiri* (Fig. 8) while the latter genus obviously starts from a different point due to the huge difference in absolute size among them (*Saimiri* newborns weight 109 g while *Cebus* newborns weight 235 g). Fourthly, ontogenetic and evolutionary allometries are correlated. Considering all these findings together it seem correct to conclude that the evolution of these two genera results from developmental changes tweaking with body size and that nearly all differences observed among adult morphologies are a consequence of this size scaling. It is impossible at this time to polarize this change and in fact, it might well be the case that after the split from their common ancestor *Cebus* and *Saimiri* both diverges in opposite directions, *Cebus* scaling up and *Saimiri* scaling down.

What role might life-history evolution play in triggering those morphological changes? Figure 2 show that *Cebus* has a delayed on-set of reproduction. This is consistent with 67% of the traits growth trajectories and with the hypermorphic condition of *Cebus* and suggests that the extension of the growth trajectory was attained by delaying the age of first reproduction. Conversely, figure 3 shows that *Saimiri* neonates are born heavier than expected for a NWM of its size and this suggests that the height observed in the trajectories, where *Saimiri* is translated above *Cebus* (23% of all traits) might be explained by this larger starting point for the post-uterine growth period. Figure 4 also add another piece in this puzzle.

| Table 6: Landmarks change vectors |
|----------------------------------|
| **Landmarks** | **Cebus** | **Saimiri** |
| Aces 1–2 | Aces 2–3 | Aces 3–4 | Aces 4–5 | Aces 5–6 | Aces 1–2 | Aces 2–3 | Aces 3–4 | Aces 4–5 | Aces 5–6 |
| **IS** | 0.234 | 0.229 | 0.217 | 0.220 | 0.204 | 0.215 | 0.196 | 0.205 | 0.204 | 0.188 | 0.083 | 0.044 |
| **PM(E)** | 0.253 | 0.248 | 0.244 | 0.236 | 0.235 | 0.233 | 0.238 | 0.232 | 0.226 | 0.231 | 0.055 | 0.084 |
| **NSL** | 0.029 | 0.031 | 0.082 | 0.021 | 0.103 | 0.033 | 0.136 | 0.090 | 0.065 | 0.128 | 0.017 | 0.071 |
| **NA** | 0.026 | 0.027 | 0.048 | 0.031 | 0.057 | 0.034 | 0.070 | 0.052 | 0.041 | 0.067 | 0.006 | 0.013 |
| **BR** | 0.357 | 0.365 | 0.397 | 0.367 | 0.415 | 0.381 | 0.408 | 0.415 | 0.412 | 0.429 | 0.691 | 0.931 |
| **PT(E)** | 0.192 | 0.193 | 0.205 | 0.199 | 0.209 | 0.193 | 0.208 | 0.207 | 0.203 | 0.211 | 0.102 | 0.056 |
| **FM(E)** | 0.031 | 0.031 | 0.016 | 0.044 | 0.009 | 0.042 | 0.022 | 0.014 | 0.034 | 0.015 | 0.013 | 0.006 |
| **ZS(E)** | 0.080 | 0.074 | 0.074 | 0.075 | 0.067 | 0.073 | 0.076 | 0.062 | 0.066 | 0.059 | 0.011 | 0.012 |
| **ZI(E)** | 0.263 | 0.259 | 0.237 | 0.262 | 0.235 | 0.251 | 0.249 | 0.228 | 0.221 | 0.233 | 0.098 | 0.075 |
| **MT(E)** | 0.236 | 0.235 | 0.241 | 0.230 | 0.243 | 0.232 | 0.255 | 0.236 | 0.233 | 0.243 | 0.035 | 0.148 |
| **PNS** | 0.102 | 0.101 | 0.088 | 0.099 | 0.081 | 0.096 | 0.070 | 0.083 | 0.088 | 0.070 | 0.014 | 0.009 |
| **APET(E)** | 0.129 | 0.127 | 0.095 | 0.133 | 0.080 | 0.126 | 0.052 | 0.090 | 0.107 | 0.061 | 0.040 | 0.007 |
| **BA** | 0.190 | 0.186 | 0.204 | 0.172 | 0.204 | 0.175 | 0.217 | 0.198 | 0.181 | 0.204 | 0.008 | 0.101 |
| **OPI** | 0.086 | 0.084 | 0.083 | 0.082 | 0.080 | 0.081 | 0.077 | 0.080 | 0.079 | 0.076 | 0.006 | 0.006 |
| **EAM(E)** | 0.169 | 0.170 | 0.171 | 0.177 | 0.173 | 0.175 | 0.173 | 0.171 | 0.167 | 0.173 | 0.079 | 0.044 |
| **PEAM(E)** | 0.199 | 0.198 | 0.217 | 0.188 | 0.221 | 0.193 | 0.229 | 0.216 | 0.204 | 0.224 | 0.035 | 0.063 |
| **ZYGO(E)** | 0.284 | 0.280 | 0.316 | 0.258 | 0.322 | 0.265 | 0.346 | 0.310 | 0.283 | 0.328 | 0.039 | 0.163 |
| **TSP(E)** | 0.143 | 0.145 | 0.184 | 0.142 | 0.204 | 0.148 | 0.228 | 0.194 | 0.172 | 0.226 | 0.067 | 0.156 |
| **TS (E)** | 0.152 | 0.151 | 0.161 | 0.146 | 0.162 | 0.149 | 0.163 | 0.161 | 0.155 | 0.163 | 0.036 | 0.030 |
| **JP(E)** | 0.101 | 0.099 | 0.096 | 0.099 | 0.096 | 0.100 | 0.089 | 0.098 | 0.101 | 0.093 | 0.017 | 0.013 |
| **LD** | 0.464 | 0.471 | 0.409 | 0.498 | 0.389 | 0.492 | 0.345 | 0.418 | 0.469 | 0.374 | 0.681 | 0.120 |
| **AS (E)** | 0.309 | 0.308 | 0.296 | 0.307 | 0.288 | 0.306 | 0.266 | 0.293 | 0.300 | 0.274 | 0.097 | 0.076 |

For each consecutive age (age 1 and 2) and for each of the two genera the vector of absolute change in landmark position is show. All vectors were normalized to one in order to be directly comparable. Also, the magnitude of change in landmark position between the two extremes is each of the allometric vectors (PC1-3D and PC2-3D) is show.
showing that *Cebus* infants are weaned later than expected for a NWM of its size while the reverse is true for squirrel monkeys. Delayed weaning and age of first reproduction suggests that *Cebus* has a very slow developmental pattern compared to the rest of the NWM. Early weaning in *Saimiri* would suggest at first the reverse, but others factors should be considered here in judging whether or not *Saimiri* present a "fast" or "slow" life-history pattern. *Saimiri* neonates are born relatively heavy and represent almost 14% of the total weight of the mother, representing the largest pre-natal investment in NWM [11] in a single newborn (tamarins and marmosets which usually have twins invest even more if we consider litter weight). Squirrel monkey mothers also usually do not have support from group members in raising their infants which should impose a heavy burden on them. *Saimiri* compensate for this burden by a prolonged interbirth interval [11]. Garber and Leigh also point out that in *Saimiri* "An ontogenetic trajectory associated with large neonatal body size and rapid neurological development may facilitate early foraging independence, thus shifting metabolic costs away from the mothers and to the developing individual". After weaning, developing young follow a long and slow growth trajectory [11], which in a way is similar to their sister clade, *Cebus*. Figure 5 sheds additional light on this point, because the *Cebus/Saimiri* clade is characterized by the highest pre-natal growth rates among NWM, after accounting for differences in adult body size (and historical relatedness). Because most of neurocranial growth occurs during the pre- and peri-natal period, this faster growth in capuchins and squirrel monkeys accounts for the largest encephalization index in this clade within
NWM [15], which can also be observed in the very long neural region in Saimiri and Cebus young’s (Figures 7 and 8). Conversely, Cebus and Saimiri post-natal growth rates are among the lowest among NWM (Table 8). Therefore, summarizing all these life-history changes, the whole clade of capuchin/squirrel monkeys might be characterized by fast pre-natal growth and very slow post-natal growth. This is an interesting conclusion, because while obviously Saimiri represents a paedomorphic (juvenilized) morphology and Cebus a peramorphic (adult like) morphology when compared to one another, the whole clade might be considered paedomorphic relative to NWM as a whole.

### Conclusion

Saimiri and Cebus represent a unique radiation within the NWM in many aspects. The differentiation of these two genera from their common ancestor is, to a large extent, due to size evolution. Most morphological differences between these two genera are related to scaling. Furthermore, this scaling is to a large extent due to a simple extension/truncation of growth, but also includes pre- and post-displacement. Several life-history changes seem correlated, or perhaps are even causal of the morphological diversification of Cebus and Saimiri; such as delayed on-set of reproduction in Cebus, faster pre-natal growth rates and delayed weaning in Cebus, and accelerated weaning in Saimiri. Post-natal life-history is also slow in both genera relative to other NWM.

### Methods

#### Sample and measurements

A total number of 886 specimens were measured, with 30 specimens not included in the analyses due to missing values. The adult sample includes 605 specimens in 18 species for the two genera as follows: 11 species of the genus Cebus, including the following species: C. albifrons (N = 13), C. cesarae (N = 17), C. apella (N = 135), C. capucinus (N = 20), C. libidinosus (N = 38), C. macrocephalus (N = 11), C. nigritus (N = 78), C. nigrivitattus (N = 9), C. para- guayanus (N = 19), C. robustus (N = 35), C. xanthosternus (N = 4); 7 species of the genus Saimiri, including the following species: S. albigena (N = 5), S. boliviensis (N = 6), S. cassiquiarensis (N = 29), S. macrodon (N = 13), S. oerstedi (N = 32), S. sciureus (N = 114), S. ustus (N = 16), and S. vanzolini (N = 11). Adult specimens were used in the morphological differentiation analyses, properly controlling

| Table 7: Correlation between absolute size, evolutionary and ontogenetic allometry |
|---------------------------------|---------|---------|
| SIZE                           | PC1-3D  | PC2-3D  |
| SIZE                           | 1       | P < 10^-5 | 0.320 |
| PC1-3D                         | 0.972   | 1        | 0.872 |
| PC2-3D                         | -0.060  | 0.009    | 1    |
| Cebus SIZE                     | 0.864   | P < 10^-5 | P < 10^-5 |
| Cebus PC1-3D                   | 0.809   | 0.768    | 1    |
| Saimiri SIZE                   | 0.723   | P < 10^-5 | P < 10^-5 |
| Saimiri PC1-3D                 | 0.699   | 0.868    | 1    |

The Pearson correlation and associated probability between absolute size, PC1-3D and PC2-3D are show for a conjoint analysis (both genera) and for each of the two genera.

### Table 8: Life-history data

| Genus   | age first rep (days) | Adult Weight | Gestation Lenght | Age of weaning | Birth Weight | Pre-natal Growth Rate (regression) | Post-natal growth rate |
|---------|----------------------|--------------|------------------|----------------|--------------|-----------------------------------|------------------------|
| Alouatta| 1460.00              | 6404.2       | 186              | 369            | 407.7        | 1.150                             | 1.337                  |
| Ateles  | 1642.50              | 8276.3       | 229              | 653            | 482.0        | 1.137                             | 1.443                  |
| Brachyteles | 2737.50          | 8840.0       | 225              | 639            | .            | .                                 | .                      |
| Lagothrix | 2555.00            | 7150.0       | 218              | 340            | 450.0        | 1.135                             | 1.124                  |
| Cacajao  | 1642.50              | 2893.8       | 180              | 547            | .            | .                                 | .                      |
| Chiroptes | 1460.00            | 2632.5       | 160              | .              | .            | .                                 | .                      |
| Pithecia | 1125.42              | 2003.5       | 170              | 122            | 121.0        | 0.934                             | 1.486                  |
| Callicebus | 1350.50           | 997.3        | 160              | 192            | 100.0        | 0.907                             | 1.078                  |
| Cebus   | 2007.50              | 2475.1       | 168              | 477            | 234.6        | 1.065                             | 0.950                  |
| Saimiri | 912.50               | 786.9        | 167              | 51             | 109.0        | 0.917                             | 1.164                  |
| Aotus   | 730.00               | 1018.7       | 133              | 75             | 97.0         | 0.935                             | 1.381                  |
| Leontopithec | 638.75            | 471.4        | 133              | 91             | 50.0         | 0.800                             | 1.430                  |
| Saguinus | 699.58               | 444.4        | 145              | 79             | 43.0         | 0.756                             | 1.482                  |
| Callimico | 547.50             | 505.0        | 155              | 65             | 50.0         | 0.776                             | 1.833                  |
| Calithrix | 547.50              | 351.2        | 148              | 106            | 30.0         | 0.681                             | 1.881                  |
| Cebuwilla | 501.88             | 108.5        | 137              | 91             | 14.0         | 0.536                             | 1.573                  |

Age of first reproduction, Adult weight, gestation length, age of weaning, birth weight, and Pre- and Pos-natal growth rates are presented for NWM.
for species and sexual variation. Additional 41 specimens were discarded because they lost sex information ($N_m = 309$ and $N_f = 255$ for males and females).

An additional sample of 161 sub-adult and juveniles *Cebus* and 90 *Saimiri* skulls of varied age were also measured. Dental eruption sequence for all New World Monkeys was described in detail by [8]. I use the same developmental age (DA) criteria described in [30] and DA6 correspond to adult specimens. The following samples sizes were available for *Cebus*: DA1 ($N = 25$), DA2 ($N = 22$), DA3 ($N = 41$), DA4 ($N = 13$), DA5 ($N = 60$), DA6 ($N = 379$); and for *Saimiri*: DA1 ($N = 9$), DA2 ($N = 2$), DA3 ($N = 4$), DA4 ($N = 10$), DA5 ($N = 65$), DA6 ($N = 226$). Young samples (DA1 to DA4) not always present sex or species identification available and often lack any information regarding locality or accompanying skin that would allow proper identification of species and sex. The sampling here was as complete and throughout as possible but this lack of information result in a lack of power to perform growth analyses controlling for sexual and interspecific differentiation. However, most young and sub-adult samples (DA1 to DA5) are concentrated on two species, *Cebus apella* (99% of all specimens) and *Saimiri sciureus* (81%). Because the major goal here is to understand the differentiation and evolution of size and shape between the two genera the effect of uncontrolled sexual and specific variation within each genus would be to increase dispersion among points and consequently blur any observed pattern among genera. Results presented here are straightforward in this respect with a clear characterization of evolutionary and ontogenetic allometry (Figures 7 and 8) that seems robust for these other uncontrolled sources of variation (sex and species).

The specimens are deposited at the following institutions: American Museum of Natural History (AMNH), Museu de Zoologia da Universidade de São Paulo (MZUSP), Museu Nacional do Rio de Janeiro (MNRJ), Museu Paranaense Emílio Goeldi (MPEG) and National Museum of Natural History (USNM). A complete list of measured specimens sorted by taxon and museum collection may be obtained from the author upon request. Only adult crania were used in the subsequent analyses, except where specifically noted. Specimens were considered adult when they had fully erupted and functional dentition as well as closed or fused sphenoid-occipital and/or sphenoid-ethmoid sutures. Non-adult specimens correspond to a mixed age sample containing all tooth stages from a completely deciduous dentition to a permanent dentition except a functional canine or third molar [8].

Three-dimensional co-ordinates were recorded for 36 landmarks (Figure 9 and Table 9) using a Polhemus 3Draw or a Microscribe 3Dx digitizer. A small scale experiment was performed measuring a sub-sample of 20 specimens twice in each of the two digitizers. No significant differences were found between the digitizers. The general procedure for measuring specimens follows [6]. A set of 70 linear measurements describing cranial morphology was calculated from the co-ordinate values. This was reduced to a set of 39 measurements, after averaging measurements present on both sides of the skull (Tables 9 and 10). Whenever one of the skull sides was damaged, preventing me from taking any particular measurement, the other side is used. All results are presented in millimeters. All statistical analyses were performed using SYSTAT 11 (Richmond, CA).

A total of 564 adult and 251 juveniles skulls with all 39 measurements (without missing values) were used in the analyses below. Juveniles were only used in the allometry analyses and were not included in the differentiation analyses. In this study I tested for differences between the taxa, the sexes and interaction between the sexes and taxa using multivariate analysis of variance (MANOVA). Given that squirrel and capuchin monkey species present sexual dimorphism with males usually larger than females, sexes were analyzed separately.

**Analyses**

Interspecific Differentiation – Differences among Cebinae skulls were examined using the general linear model (GLM) module in SYSTAT 11 to perform a MANOVA and canonical variate analyses. Moreover, because the sampling includes several species within each genus and is not balanced in terms of the numbers of specimens per species, the MANOVA was performed for each sex with species nested within genus. In this way the between species variation within genus is accounted for so that the between genera differentiation is not inflated. Therefore the general linear model includes genus and species nested within genus as the two independent factors. For estimating the degree of differentiation among *Cebus* and *Saimiri*, Mahalanobis D2 distances between group averages in the canonical function were calculated.

Allometry and scaling correction – The first principal component extracted from the ln-transformed data pooled within-group variance/covariance matrix of each genus and sex was computed. Because sexual variation in allometric patterns were small, detailed comparisons of allometric coefficients are presented only for the two genera. The thirty-nine standardized PC1 coefficient values of each group were divided by ($1/39$) to assess divergence from isometry [16]. In order to compare allometric coefficients among Cebinae, it is important to determine the associated error of those values. A bootstrap procedure was used to set 95% confidence limits (L1 and L2) to the allometric coefficients (AC’s) [see page 34 in [22]]. A hun-
dred bootstrap samples of N = 300 were taken and used to set up 95% confidence limits to AC’s. Allometric coefficients with L2 below 1.0 were considered to be negatively allometric and conversely those AC’s with L1 above 1.0 were considered positively allometric. For the juveniles a hundred bootstrap samples of N = 101 for *Cebus* and N = 26 for *Saimiri* were used to set 95% confidence limits to AC’s.

The overall similarity of the allometric patterns is quantified with vector correlations, which measure similarity of vector orientation in a p-dimensional space (p being the number of traits). Vector correlations are equal to the cosine of the angle between vectors. The expected range of vector correlations commonly occurring among 39-element vectors by chance alone is $-0.4 < r < 0.4$ [1] with an average of 0.127 and a standard deviation of 0.095. Additionally, because there is a sampling error associated with each estimated allometric vector we use a self-correlation procedure to calculate allometric vector repeatability [6,23]. Allometric vector repeatability was estimated by correlating the observed PC1 and each of the 100 PC1 obtained from a bootstrap sample of replicates. These correlations provide a distribution of self-correlation [4]. The mean of this distribution is then used to measure allometric vector repeatability. To help judging how high allometric vector correlations are among genera and sex we adjust the observed vector correlations for estimation error by dividing the observed correlation by the square root of the product of the two vector repeatabilities (see [6,23]). I also use the strategy described by ([41], chapter 13, page 337) and compare each allometric vector to 100 random permutation of its elements. The rational underlying this approach is that if two vectors are "size" or "allometric" vectors with all elements positive, the range of vectors correlations is actually much smaller that from zero to one. Therefore every vector is permuted a 100 times and correlated with this random sample in order to test, using the corresponding average and confidence interval, whether or not correlation among any two vectors is indeed more similar that expected by chance alone.

I also used another strategy to analyze the relationship between size, shape and development based on [31] restriction of the term heterochrony and his focus on growth trajectories. Under this restriction heterochrony is a uniform change in the rate or timing of some ontogenetic process, with no change in the nature of the biological interactions going on within that process [31]. Uniform changes in the growth trajectory (trait × time) can be detected by comparing them (see Fig. 4 in [31]). One caveat in the analyzes performed here is that neither the *Saimiri* or *Cebus* data have time (age) available, given that the specimens were wild caught. Therefore, I plotted all 39 traits against skull size (all data ln-transformed in

| Landmark | Description | Position(s) | Order |
|----------|-------------|-------------|-------|
| IS       | Intradentale superior, A | Midline | 1     |
| PM       | Premaxillary suture at the alveolus, A | Right, left | 2, 21 |
| NSL      | Nasale, A | Midline | 3     |
| NA       | Nasion, A | Midline | 4     |
| BR       | Bregma, AP | Midline | 5     |
| PT       | Pterion, AP | Right, left | 6, 22 |
| FM       | Fronto-malar, A | Right, left | 7, 23 |
| ZS       | Zygomatic superior, A | Right, left | 8, 24 |
| ZI       | Zygomatic inferior, A | Right, left | 9, 25 |
| MT       | Maxillary tuberosity, A | Right, left | 10, 26 |
| PNS      | Posterior nasal spine, A | Midline | 11    |
| APET     | Anterior petros temporal, A | Right, left | 12, 27 |
| BA       | Basion, AP | Midline | 13    |
| OPI      | Opisthion, AP | Midline | 14    |
| EAM      | Anterior external auditory meatus, A | Right, left | 15, 28 |
| PEAM     | Posterior external auditory meatus, A | Right, left | 16, 29 |
| ZYGO     | Inferior zygomatic suture, A | Right, left | 17, 30 |
| TSP      | Temporo-sphenoid-parietal junction, A | Right, left | 18, 31 |
| TS       | Temporo-sphenoid junction at the petrous, AP | Right, left | 19, 32 |
| JP       | Jugular process, AP | Right, left | 20, 33 |
| LD       | Lambda, P | Midline | 34, 35 |
| AS       | Asterion, P | Right, left | 36    |

Table 9: 22 Landmarks digitized

Landmarks recorded in Cebine primates skulls using the three-dimensional digitizer. The designation A (anterior) or P (posterior) after the landmark name indicates in which position(s) the landmark was recorded. Landmarks are also identified in Figure 9. The order that each landmark was recorded is also presented (see additional movies material).
and, consequently, in allometric shape variation associ-

Given variation in squirrel and capuchin monkey size

were linear and similar every plot included a LOWESS

assumption). To help visualize whether or not trajectories

Where Y and X are the values of a specific trait and overall

Principal component scores were saved and used to test

Geometric morphometrics

I also used a different approach to help visualize and test

order to linearize the relationship), assuming that size is
good proxy to time (see results for an indirect test of this

30-clinical skull measurements (distances between landmarks)

and membership in the six functional/developmental groups and two

major cranial regions. Table 1 defines each landmark and Figure 9

show their locations in a generalized Platyrrhine skull.

Table 10: 39 Linear distances and cranial regions

| Functional/Developmental group | Region   | Trait  |
|-------------------------------|----------|--------|
| Oral                          | Face     | ISPM   |
| Nasal                         | Face     | ISNSL  |
| Oral, nasal                   | Face     | ISPNS  |
| Oral                          | Face     | PMZS   |
| Oral                          | Face     | PMZI   |
| Nasal                         | Face     | PMMT   |
| Nasal                         | Face     | NSLNA  |
| Nasal                         | Face     | NSLZS  |
| Nasal, nasal                  | Face     | NSLSZ  |
| Cranial vault                 | Neurocranium | NABR |
| Orbit                         | Neurocranium | NAFM |
| Nasal                         | Face     | NAPNS  |
| Cranial vault                 | Neurocranium | BRPT |
| Orbit                         | Neurocranium | BRAPET |
| Cranial vault                 | Neurocranium | PTFM |
| Cranial vault                 | Neurocranium | PTAPET |
| Cranial vault                 | Neurocranium | PTBA  |
| Cranial vault                 | Neurocranium | PTEAM  |
| Zygomatic                     | Face     | PTZYG0 |
| Cranial vault, zygomatic      | Neurocranium, Face | PTTSNP |
| Orbit                         | Neurocranium | FMZS |
| Zygomatic                     | Face     | FMZMT |
| Oral                          | Face     | ZSZI   |
| Oral                          | Face     | ZMTM   |
| Zygomatic                     | Face     | ZIZYGO |
| Zygomatic                     | Face     | ZITSP  |
| Oral                          | Face     | MTPNS  |
| Cranial base                  | Neurocranium | PNSAPET |
| Cranial base                  | Neurocranium | APETBA |
| Cranial base                  | Neurocranium | APETTS |
| Cranial base                  | Neurocranium | BAEM  |
| Zygomatic                     | Face     | EAMZYG0 |
| Zygomatic                     | Face     | ZYGOTSP |
| Cranial vault                 | Neurocranium | LDAS |
| Cranial vault                 | Neurocranium | BRLD |
| Cranial vault                 | Neurocranium | OPILD |
| Cranial vault                 | Neurocranium | PTAS  |
| Cranial base                  | Neurocranium | JPAS  |
| Cranial base                  | Neurocranium | BAOPI |

Thirty-nine linear skull measurements (distances between landmarks)

and membership in the six functional/developmental groups and two

major cranial regions. Table 1 defines each landmark and Figure 9

show their locations in a generalized Platyrrhine skull.

One interesting feature in Morphologika is that the soft-

ware allows the visualisation of the shape variability re-

presented by the PCs which is achieved by reconstruction of

of those size differences, a normalization tech-

nique to scale data and remove allometric effects was

applied [20,24]. This method, which I will refer from now

on as "Multivariate Allometric Size-Scaling (MASS)", is

derived from theoretical equations of allometric growth

removing all the information related to size, not only scal-

ing all individuals to the same size, but also adjusting

their shape to account for allometry [20]. Here I follow

Marroig and [24] modifying the [20] method by using the

first principal component (PC1) score of the natural log

data as the overall size measure and regressing all 39 traits

onto PC1. The [20] correction is

\[ Y^*_i = Y_i \left( \frac{X_0}{X_i} \right)^b \]

Where \( Y_i \) and \( X_i \) are the values of a specific trait and overall

size (PC1 score) in individual 'i', respectively, \( Y^*_i \) is the

theoretical value for the trait at the average size, \( X_0 \) is the

average antiloge of the PC1 scores, and \( b \) is the PC1 coef-

ficient for each of the 39 traits. Notice that \( b \) is equal to

the regression coefficient of the trait \( Y \) upon the PC1

scores. After this correction, the original data of all Cebi-

nae are scaled to the same size, also adjusting their shapes

for allometric scaling. These scale-corrected data were

used to explore whether differences among Saimiri and

Cebus were size dependent. This was done comparing the

results of the MANOVA using the original (unscaled) and

scale-corrected (MASS) data.

Geometric morphometrics

I also used a different approach to help visualize and test

for differences in size and shape among Cebus and Saimiri.

This geometric morphometrics approach was imple-

mented using Morphologika, software developed by Paul

O’Higgins and Nicholas Jones (University of York, see

[27,7]). Detailed descriptions of Morphologika and the

geometric Morphometrics theory can be found elsewhere

[17,7,27,41]. The program uses generalized least squares

superimposition to register landmark data. Registration is

the basic procedure of translation, scaling, and rotation to

remove all information unrelated to shape [41]. The

resulting shape coordinates were subject to principal com-

ponent analysis (PC’s 3D from now on) in the tangent

space (the Procrustes tangent projection) to Kendall’s

shape space [17,7]. What is important here is that this

approach allows the separation of absolute size (scale dif-

ferences quantified by the centroid size), shape differences
due to allometry, and shape differences non-associated
with size. A sample of 279 skulls was used in this analyses

corresponding to all sub-adults and juveniles skulls and

adults of the two most abundant species of each genus.

Principal component scores were saved and used to test

for differences as well as to interpret biologically each PC.

One interesting feature in Morphologika is that the soft-

ware allows the visualisation of the shape variability re-

presented by the PCs which is achieved by reconstruction of

and differences quantified by the centroid size), shape differences due to allometry, and shape differences non-associated with size. A sample of 279 skulls was used in this analyses corresponding to all sub-adults and juveniles skulls and adults of the two most abundant species of each genus. Principal component scores were saved and used to test for differences as well as to interpret biologically each PC. One interesting feature in Morphologika is that the software allows the visualisation of the shape variability represented by the PCs which is achieved by reconstruction of...
the skulls (landmarks) in real time at any point along each PC axis.

The clear cut results in terms of separation and similarity between ontogenetic and evolutionary allometries (see below) arising from this geometric morphometric analysis, presents a new opportunity to develop a new approach to the study of allometry, growth and development. Landmarks configurations were obtained for each genus and age class along the PC1-3D and PC2-3D. The absolute differences between each of those average configurations represent the amount of changes occurring in each landmark along any period of the ontogeny. This allows a quantification of the magnitude of changes in each landmark throughout the ontogeny. Also, each of these differences between age classes defines a vector of changes in landmark position. Therefore is possible to quantify and compare those changes in shape using again vector correlation. These were calculated within each genus for consecutive age classes (age1-age2 × age2-age3, age2-age3 × age3-age4, and so on) as well as for similar age classes between genera (Saimiri age1-age2 × Cebus age1-age2, and so on). For those landmarks collected on both sides of the skull, the average of absolute magnitude of change was used in defining each vector. Therefore, each vector has 22 elements.

Life-history
I also obtained life-history data from the literature [15,11,9,19,28,37] for all New World Monkeys. Particularly, data on gestation length, body weight and skull size (my own observations from museum specimens, both skulls and labels), age at first reproduction, age at weaning, and birth weight, all transformed to natural log scale to make their relationships linear. Fetal growth rate was estimated by dividing the natural log of birth weight by

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**Figure 9**
New World Monkey skull with landmarks. Craniofacial landmarks recorded from Cebinae skulls using three-dimensional digitizer. See Tables 9 and 10 for landmarks and measurements details.
the natural log of gestation length. Post-natal growth rate was estimated by regressing the natural log of adult weight by the natural log of the age of first reproduction (in days) and using the regression slope as an estimate of the rate (Table 8 show the life-history data). Association among these variables was tested using the independent contrasts (IC) method to account for the non-independence of phylogenetically structured data [12]. I use the module PDAP [12] within the MESQUITE package [21] to obtain the correlation among variables. The phylogenetic tree used is the same as in [25] based on [35]. Ideally, given that species within genus could vary in their life-histories, it would be necessary to correct for such differences properly accounting for phylogenetic relationships among species. Unfortunately robust and complete (with all species) phylogenetic hypotheses at the species within-genus level are not available for either Cebus or Saimiri. Also, not all species had life-history data available. These two pieces of information would be necessary to estimate ancestor values for the life-history traits. Therefore, in order to at least consider the range of variation in life-history among species within these two genera and check whether or not results from these analyses are consistent I use the minimum and maximum values for each life-history parameter to test the robustness of these regressions.

Authors’ contributions
Except for some young specimens measured by a colleague, GM is responsible for planning and executing all work involved in this paper.

Additional material

Additional file 1
3D animation of the morphometric analysis: Oblique view showing landmarks points (corresponding numbers in Table 9). x-axis represent the PC1-3D and the y-axis represent the PC2-3D. On the left are the points corresponding to Saimiri specimens and on the right those of Cebus. Symbols correspond to age classes, from age 1 (green diamonds) to age 6 (red cross).

Click here for file
[http://www.biomedcentral.com/content-supplementary/1471-2148-7-20-S1.avi]

Additional file 2
3D animation of the morphometric analysis: Oblique view showing a wire frame connecting landmarks points.). x-axis represent the PC1-3D and the y-axis represent the PC2-3D. On the left are the points corresponding to Saimiri specimens and on the right those of Cebus. Symbols correspond to age classes, from age 1 (green diamonds) to age 6 (red cross).

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[http://www.biomedcentral.com/content-supplementary/1471-2148-7-20-S2.avi]

Additional file 3
3D animation of the morphometric analysis: Oblique view showing a surface reconstruction of the skull.). x-axis represent the PC1-3D and the y-axis represent the PC2-3D. On the left are the points corresponding to Saimiri specimens and on the right those of Cebus. Symbols correspond to age classes, from age 1 (green diamonds) to age 6 (red cross).

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[http://www.biomedcentral.com/content-supplementary/1471-2148-7-20-S3.avi]

Additional file 4
3D animation of the morphometric analysis: Lateral view showing landmarks points (corresponding numbers in Table 9). x-axis represent the PC1-3D and the y-axis represent the PC2-3D. On the left are the points corresponding to Saimiri specimens and on the right those of Cebus. Symbols correspond to age classes, from age 1 (green diamonds) to age 6 (red cross).

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[http://www.biomedcentral.com/content-supplementary/1471-2148-7-20-S4.avi]

Additional file 5
3D animation of the morphometric analysis: Lateral view showing a wire frame connecting landmarks points.). x-axis represent the PC1-3D and the y-axis represent the PC2-3D. On the left are the points corresponding to Saimiri specimens and on the right those of Cebus. Symbols correspond to age classes, from age 1 (green diamonds) to age 6 (red cross).

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[http://www.biomedcentral.com/content-supplementary/1471-2148-7-20-S5.avi]

Additional file 6
3D animation of the morphometric analysis: Lateral view showing a surface reconstruction of the skull.). x-axis represent the PC1-3D and the y-axis represent the PC2-3D. On the left are the points corresponding to Saimiri specimens and on the right those of Cebus. Symbols correspond to age classes, from age 1 (green diamonds) to age 6 (red cross).

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Additional file 7
3D animation of the morphometric analysis: Dorsal view showing landmarks points (corresponding numbers in Table 9). x-axis represent the PC1-3D and the y-axis represent the PC2-3D. On the left are the points corresponding to Saimiri specimens and on the right those of Cebus. Symbols correspond to age classes, from age 1 (green diamonds) to age 6 (red cross).

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Additional file 8
3D animation of the morphometric analysis: Dorsal view showing a wire frame connecting landmarks points.). x-axis represent the PC1-3D and the y-axis represent the PC2-3D. On the left are the points corresponding to Saimiri specimens and on the right those of Cebus. Symbols correspond to age classes, from age 1 (green diamonds) to age 6 (red cross).

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[http://www.biomedcentral.com/content-supplementary/1471-2148-7-20-S8.avi]
Additional file 9
3D animation of the morphometric analysis: Dorsal view showing a surface reconstruction of the skull. x-axis represent the PC1-3D and the y-axis represent the PC2-3D. On the left are the points corresponding to Saimiri specimens and on the right those of Cebus. Symbols correspond to age classes, from age 1 (green diamonds) to age 6 (red cross).
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[http://www.biomedcentral.com/content SUPPLEMENTARY/1471-2148-7-20-39.avi]

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References
1. Ackermann RR, Cheverud JM: Phenotypic covariance structure in tamarins (Genus Saguinus): a comparison of variation patterns using matrix correlation and common principal component analysis. Am J Phys Anthropol 111:489-501.
2. Alberch P, Gould SJ, Oster GF, Wake DB: Size and shape in ontogeny and phylogeny. Paleobiology 1979; 5:296-317.
3. Bookstein F, Chernoff B, Elder R, Humphries J, Smith G, Strauss R: Morphometrics in Evolutionary Biology. Special Publication 15 (page number not for citation purposes). Plenum Press, New York; 1991.
4. Bookstein F, Chernoff B, Elder R, Humphries J, Smith G, Strauss R: Morphometrics in Evolutionary Biology. Special Publication 15 (page number not for citation purposes). Plenum Press, New York; 1991.
5. Cheverud JM: Ontogeny and phylogeny. Cambridge, MA, Harvard University Press; 1977.
6. Hartwig WC: Perinatal Life History Traits in New World Monkeys. American Journal of Primatology 1996, 40:99-130.
7. Jolicoeur P: The multivariate generalization of the allometry equation. Biometrics 1963, 19:497-499.
8. Kent JT: The complex Bingham distribution and shape analysis. J Roy Statist Soc B 1994, 56:285-299.
9. Kinsey WG: New World primates: ecology, evolution, and behavior. Walther de Gruyter Inc., New York; 1997.
10. Lindenfors P: Sexually antagonistic selection on primate size. J Evol Biol 2002, 15:595-607.
11. Llewaz J, Salat J, Torres GJ: Removing allometric effects of body size in morphological analysis. J Theor Biol 2000, 205:85-93.
12. Maddison WP, Maddison DR: Mesquite: a modular system for evolutionary analysis. Version 1.6 (http://mesquiteproject.org).
13. Manly BF: Randomization, bootstrap and Monte Carlo methods in Biology Chapman and Hall, New York; 1997.
14. Marroig G, Cheverud JM: A comparison of phenotypic variation and covariation patterns and the role of phylogeny, ecology and ontogeny during cranial evolution of new world monkeys. Evolution 2001, 55:2576-2600.
15. Marroig G, Cheverud JM: Cranial evolution in sakis (Pithecia, Platyrhini): Interspecific differentiation and allometric patterns. American Journal of Physical Anthropology 2004, 125:266-278.
16. Marroig G, Cheverud JM: Size as a line of least evolutionary resistance: diet and adaptive morphological radiation in new world monkeys. Evolution 2005, 59:128-144.
17. McKinney ML, McNamara KJ: Heterochrony: the evolution of ontogeny. Plenum Press, New York; 1991.
18. O’Higgins P, Jones N: Facial growth in Cercocetus torquatus: an application of three dimensional geometric morphometric techniques to the study og morphological variation. J Anat 1998, 193:251-272.
19. Porter LM, Garber PA: Goeldi’s Monkeys: A Primate Paradox? Evolutionary Anthropology 2004, 13:104-115.
20. Raff RA: The shape of life: genes, development, and the evolution of animal form. Univ of Chicago Press, Chicago; 1996.
21. Richtsmeier J, Corber B, Grausz H, Cheverud J, Danahay S: The role of postnatal growth pattern in the production of facial morphology. Systematic Biology 1993, 42:307-330.
22. Rice SH: The analysis of ontogenetic trajectories: When a change in size or shape is not heterochrony. Proc Natl Acad Sci USA 1997, 94:907-912.
23. Rohlf JF, Bookstein FL: A comment on shearing as a method for “size correction”. Syst Zool 1987, 36:356-367.
24. Schneider H: The current status of the New World monkey phylogeny. Anais da Academia Brasileira de Ciências 2000, 72:165-172.
25. Schneider H, Rosenberger AL: Molecules, morphology, and Platyrhini systematics. In Adaptive radiations of Neotropical primates. Edited by: Norconk MA, Rosenberger AL, Garber PA. Plenum Press, New York; 1996:3-19.
26. Schneider H, Canavez FC, Sampaio I, Moreira MAM, Tagliaro CH, Seuanez HV: Can molecular data place each neotropical monkey in its own branch? Chromosoma 2001, 109:515-523.
27. Smith KK: Comparative patterns of craniofacial development in Eutherian and Metatherian mammals. Evolution 1997, 51:1633-1678.
28. Smith RJ, Leigh SR: Sexual dimorphism in primate neonatal body mass. Journal of Human Evolution 1998, 34:173-201.
29. Sneath PH, Sokal RR: Numerical taxonomy. San Francisco, W. H. Freeman; 1971.
30. Somers KM: Multivariate allometry and removal of size with principal component analysis. Syst Zool 1986, 35:359-368.
31. Sundberg P: Shape and size-constrained principal components analysis. Syst Zool 1989, 38:166-168.
32. Zelditch ML, Swiderski DL, Sheets HD, Fink WL: Geometric Morphometrics for biologists: a primer Elsevier Academic Press, San Diego; 2004.