

# Cranial Ontogeny and Sexual Dimorphism in Two New World Monkeys: *Alouatta caraya* (Atelidae) and *Cebus apella* (Cebidae)

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**ABSTRACT** Pattern of skull development and sexual dimorphism was studied in *Cebus apella* and *Alouatta caraya* using univariate, bivariate, and multivariate statistics. In both species, sexual dimorphism develops because the common growth trajectory in males extends and because of differences in growth rates between sexes. The expectation that the ontogenetic bases of adult dimorphism vary interspecifically is well substantiated by this study. *A. caraya* exhibits transitional dimorphism in its subadult stage, although the condylobasal length, zygomatic breadth, and rostrum length are strongly dimorphic in the final adult stage, being greater in males. Most cranial measurements in *C. apella* exhibit significant dimorphism in the adult stage, being strongly influenced by a faster rate of growth in males. Sexual dimorphism is also evidenced through sex differences in growth rates in several cranial measurements. These results also indicate that different ontogenetic mechanisms are acting in *C. apella* and *A. caraya* and reveal differences in the way through which neotropical primates attain adult sexual dimorphism. *J. Morphol.* 272:744–757, 2011. © 2011 Wiley-Liss, Inc.

**KEY WORDS:** primates; cranial ontogeny; sexual dimorphism

## INTRODUCTION

Patterns of cranial ontogeny and sexual dimorphism in primates have been studied from diverse perspectives, producing a significant amount of literature mainly based on morphology and behavior. Sexual dimorphism is a condition widely present in the group (Ralls, 1977; Leigh, 1992; Ravosa and Ross, 1994), with a variety of causes and consequences related to hormonal processes (Tanner, 1988) that are highly adjusted to specific behavioral models (such as territoriality, mate competition, breeding, and resources). Sexual dimorphism is one of the major sources of intraspecific variation in adult primates (Plavcan and van Schaik, 1992, 1997; Garber and Leigh, 1997; Masterson, 1997). Although most primates are sexually dimorphic for different characters, such as canine tooth size, body mass, pelage color, and skeletal dimensions, the degree of dimorphism can also vary in magnitude among species (Plavcan, 2001). Sexual dimorphism

can arise through differences in growth duration (sexual bimaturism or time hypermorphosis) and/or in growth rates (rate hypermorphosis; Gavan and Swindler, 1966; Shea, 1986; Ravosa and Ross, 1994; Blanco and Godfrey, 2006). Several studies (e.g., O'Higgins et al., 1990, 2001; Leigh, 1992; Plavcan, 1993, 2002; Ravosa and Ross, 1994; Masterson, 1997; Schaefer et al., 2004; Marroig, 2007) have provided detailed descriptions of interspecific differences in the pattern of cranial dimorphism. Most cranial sexual dimorphism represents different endpoints on a single ontogenetic trajectory, with female adults usually being smaller than males with few characters exhibiting predisplacement and postdisplacement (Ravosa and Ross, 1994; Masterson, 1997; Plavcan, 2001; Marroig, 2007; Ravosa, 2007). Thus, sexual dimorphism in the primate skull derives from shape changes associated with changing size due to allometric relationships among traits, whereas other cranial components scale at the same rates in both sexes. Interpretations derived from previous results indicate the existence of a potential diversity and mixture of ontogenetic models as well as differences in the onset of sexual dimorphism for various primate taxa (Leigh, 1992).

Although *Cebus apella* and *Alouatta caraya* seem to share ontogenetic trajectories in both

Additional Supporting Information may be found in the online version of this article.

Contract grant sponsor: CONICET; Contract grant number: PIP-0329; Contract grant sponsor: MCINN Spain; Contract grant number: CGL2008-00832; Contract grant sponsor: AGAUR, Generalitat de Catalunya; Contract grant number: 2009SGR884.

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Received 24 June 2010; Revised 29 November 2010; Accepted 11 December 2010

Published online 11 April 2011 in  
Wiley Online Library (wileyonlinelibrary.com)  
DOI: 10.1002/jmor.10947

sexes (see Ravosa and Ross, 1994; Masterson, 1997; O'Higgins et al., 2001), they differ in the timing of life-history events and body growth (Lumer and Schultz, 1947; Stahl et al., 1968; Bezanson, 2005). Therefore, we expected that both taxa exhibit differences in the mode of postnatal cranial ontogeny and in the ways that they reach adult sexual dimorphism. This study aimed to explain the cranial ontogeny of *A. caraya* and *C. apella* and focusing on allometric patterns of growth and the onset of sexual dimorphism. Previous studies using different methodologies (e.g., Schultz, 1960, 1962; Corner and Richtsmeier, 1991; Ravosa and Ross, 1994; Masterson, 1997; O'Higgins et al., 2001; Blanco and Godfrey, 2006; Marroig, 2007) have provided relevant information on sexual dimorphism and age-related changes in both genera, allowing for comparisons with our results. From a phylogenetic perspective, *Alouatta* and *Cebus* belong to the two different families (Atelidae and Cebidae) into which the platyrrhines are classified. Thus, comparisons between these two monkeys contribute to a growing number of studies regarding growth and dimorphism in New World primates that provide insight into whether their phylogeny has actually influenced their respective ontogenetic trajectories.

## MATERIALS AND METHODS

### Specimens

Both species are well represented by complete ontogenetic series deposited in the Mammal Collection of the Museo Argentino de Ciencias Naturales "Bernardino Rivadavia" (MACN), Buenos Aires, and Museo de La Plata, Argentina. We analyzed 80 skulls of *Alouatta caraya* (38 females and 42 males) and 116 specimens of *Cebus apella* (57 females and 59 males; Supporting Information). For comparative purposes, this sample was grouped into five dental age stages, following Ravosa and Ross (1994). In the sample, 27 specimens of *A. caraya* and 37 specimens of *C. apella* did not show fully adult permanent dentition. In the smallest specimen of *A. caraya* (MACN 14033; condylo-basal length 51.7 mm), deciduous dentition was completely erupted (i.e., three deciduous incisors, canines, and three deciduous premolars in each quadrant), similar to the smallest specimen of *C. apella* (MACN 3.75; condylo-basal length 51.2). In *A. caraya*, there were a minimum of five males and four females for each nonadult dental age class, and in *C. apella*, there were a minimum of five males and five females for the same age classes. Although adults of *A. caraya* are larger than those of *C. apella* (Tables 1 and 2), the smallest specimens in both samples were similar in size and dental formula. According to the available information, the smallest specimen in our series of *C. apella* was between 24 and 32 weeks old (see Table 3 in Galliari, 1985). For both species, the total sample analyzed was taxonomically uniform, consisting of specimens coming from populations belonging to the same subspecies. Therefore, the effects of ecogeographic variations were avoided (see Jones et al., 2000; Ravosa, 2007).

### Analysis of Growth

Logarithm of age is highly correlated for males of *C. apella*, and absolute time and size are also highly correlated, indicating that size is a reasonable proxy for time in the study of ontogeny (Marroig, 2007). For both species, sexual dimorphism in the

mean values for the statistically well-represented developmental age stages was assessed by Student's *t*-test (stages 3 to 5, see Table 3). In addition, two analytical techniques were used to describe and analyze ontogeny: bivariate regressions and multivariate allometry. Both techniques were applied for each sex and taxon to provide a general summary of growth in both species. We used 17 linear measurements (Fig. 1) to estimate allometric growth of skulls in *A. caraya* and *C. apella*. The statistical analyses of allometry were conducted separately in both sexes, and differences in growth trends were described to detect dimorphism in allometric terms.

For the bivariate treatment, we used condylo-basal length as a measure of overall size (Emerson and Bramble, 1993). To estimate the change of each of the remaining cranial variables with respect to the total length of the skull, we used the power equation:

$$y = a \cdot x^b \quad (1)$$

Following Huxley (1932), it has been assumed that this equation is the best descriptor when scaling studies are done, whether they involve interspecific or intraspecific samples. In (1), *a* is a constant proportional to the *y*-intercept, and the exponent *b* is the slope of the corresponding graph or coefficient of allometry. The corresponding 95% confidence intervals for *a* and *b* were also calculated. Because the same independent variable was used for all the regressions, and the dependent variable was always a length, a slope (or allometric coefficient) of 1 is expected if the animals are geometrically similar along their respective ontogenetic trajectories. In our case, statistically significant deviations from a slope of 1 indicate negative allometry (when *b* < 1.0) or positive allometry (when *b* > 1.0). We used a reduced major axis regression model in which the dependence relationship on size is not explicit, and residuals are oblique components representing variation in both *x* and *y* (Sokal and Rohlf, 1995).

The multivariate approach is based on the generalization of the allometry equation as proposed by Jolicoeur (1963a,b). In bivariate allometry, one variable is set as being representative, and allometry of all other variables is estimated with respect to that chosen as the independent variable. Alternatively, in multivariate allometry, size is considered as a latent variable affecting all original variables simultaneously. The allometric relationships of all variables with the latent size variable are expressed in the first eigenvector of a principal components analysis (extracted from a variance-covariance matrix of log-transformed variables). Under isometry, all variables respond in the same way to growth, and the elements of the isometric unit eigenvector are equal to an expected value calculated as  $1/p^{0.5}$ , where *p* equals the number of variables (0.242 for this study). The value of the eigenvector of the first principal component represents the observed multivariate coefficient of allometry of the corresponding variable. Comparison of each of the empirical elements of the first-unit eigenvector with the isometric eigenvector allows us to detect negative (<0.242) and positive (>0.242) departures from isometry in each variable. Statistical departures from isometry were estimated using the application of jackknife (Quenouille, 1956; Manly, 1997). Briefly (see Giannini et al., 2004 for details), the aim of this technique is to generate confidence intervals for the empirically obtained eigenvector elements. The confidence interval may be inclusive of the null value of 0.242 and therefore equivalent to isometry, or it may exclude such a value and, therefore, can be considered allometric, being positive if the observed element is >0.242 or negative if the observed element is <0.242. Thus, pseudosamples are generated such that a new first-unit eigenvector is calculated from a matrix with one individual removed at a time. Giannini et al. (2004, in press) and Flores et al. (2006) followed Manly (1997) in using trimmed values for the calculation of pseudovalues. Trimming the largest and smallest *m* pseudovalues (with *m* = 1) for each variable significantly decreased the standard deviations and allowed for more realistic allometric estimations. Herein, we report untrimmed as well as (*m* = 1) trimmed values, opting for

TABLE 1. Average and standard deviation in each stage for both sexes of *Alouatta caraya*

| Variable | Stage 1      |              | Stage 2      |              | Stage 3       |              | Stage 4       |              | Stage 5       |              |
|----------|--------------|--------------|--------------|--------------|---------------|--------------|---------------|--------------|---------------|--------------|
|          | Males (5)    | Females (6)  | Males (5)    | Females (5)  | Males (4)     | Females (9)  | Males (16)    | Females (8)  | Males (12)    | Females (10) |
| LCI      | 73.56 ± 3.9  | 72.85 ± 5    | 90.72 ± 2.71 | 88.2 ± 1.27  | 101.22 ± 2.05 | 90.6 ± 1.27  | 110.48 ± 1.56 | 94.71 ± 1.22 | 118.72 ± 3.88 | 109.97 ± 5   |
| ZB       | 55.3 ± 5.5   | 53.37 ± 7.2  | 65.03 ± 2.22 | 65.3 ± 2.29  | 71.66 ± 2.86  | 65.81 ± 1.8  | 80.01 ± 2.5   | 69.41 ± 2.9  | 85.5 ± 1.76   | 79.61 ± 3.32 |
| BB       | 46.94 ± 2.4  | 47.72 ± 2.3  | 50.4 ± 2.27  | 50.52 ± 1.47 | 51 ± 0.91     | 49.2 ± 1.87  | 50.51 ± 2.15  | 49.51 ± 1.53 | 51.7 ± 2.48   | 50.13 ± 2.6  |
| HO       | 28.48 ± 2.65 | 28.7 ± 3.47  | 30.5 ± 1.99  | 30.48 ± 1.61 | 31.3 ± 1.5    | 30.56 ± 1.66 | 32.94 ± 2.1   | 31.68 ± 1.07 | 33.49 ± 1.74  | 33.25 ± 2.05 |
| OB       | 17.4 ± 1.84  | 18.22 ± 1.96 | 19 ± 0.9     | 19.38 ± 0.38 | 19.77 ± 1.07  | 19.33 ± 0.72 | 21.79 ± 1.01  | 21.45 ± 1.03 | 22.37 ± 0.96  | 21.72 ± 1.04 |
| RL       | 20.2 ± 4.8   | 20.82 ± 7.03 | 27.14 ± 1.21 | 26.9 ± 1.95  | 31.15 ± 1.27  | 26.58 ± 1.77 | 34.09 ± 1.92  | 29.07 ± 1.4  | 36.42 ± 2.04  | 33.64 ± 2.5  |
| PAL      | 28.6 ± 6.74  | 29.17 ± 7.45 | 37.56 ± 2.87 | 35.9 ± 1.33  | 42.77 ± 1.98  | 37 ± 1.71    | 44.87 ± 1.9   | 38.24 ± 1.96 | 48.46 ± 2.29  | 44.78 ± 3.48 |
| PB       | 19.16 ± 2.03 | 10.95 ± 2.33 | 21.46 ± 2.48 | 20.88 ± 1.03 | 22.87 ± 0.99  | 21.9 ± 0.71  | 24.32 ± 1.6   | 23.85 ± 1.14 | 26.09 ± 1.08  | 25.97 ± 1.99 |
| CC       | 18 ± 2.7     | 18.27 ± 3.59 | 23.7 ± 1.16  | 22.68 ± 1.15 | 24.02 ± 2.93  | 23.77 ± 1.51 | 28.78 ± 2.06  | 27.01 ± 1.46 | 32.98 ± 1.65  | 29.7 ± 2.02  |
| ZL       | 30.72 ± 2.29 | 30.7 ± 6.81  | 41.34 ± 2.37 | 40.68 ± 2.12 | 46.05 ± 2.72  | 41.51 ± 1.65 | 53.53 ± 2.65  | 44.41 ± 1.39 | 55.7 ± 3.12   | 54 ± 3.16    |
| IOB      | 7.24 ± 2.22  | 6.25 ± 1.70  | 9.12 ± 1.12  | 8.92 ± 0.38  | 10.7 ± 1.51   | 9.95 ± 1.55  | 10.62 ± 1.23  | 9.66 ± 1.21  | 11.38 ± 1.57  | 10.87 ± 1.2  |
| UPos     | 26.86 ± 5.4  | 26.05 ± 6.44 | 32.22 ± 2.87 | 30.84 ± 1.18 | 31.37 ± 1.28  | 30.9 ± 1.28  | 33.62 ± 1.04  | 32.98 ± 1.46 | 34.87 ± 0.99  | 33.82 ± 1.5  |
| LD       | 55.14 ± 7.6  | 55.35 ± 6.9  | 74.84 ± 2.78 | 74.16 ± 2.66 | 86.15 ± 2.33  | 77.11 ± 2.55 | 93.91 ± 3.17  | 80.73 ± 3.39 | 95.25 ± 4.40  | 94.55 ± 3.49 |
| HD       | 16.6 ± 5.83  | 15.6 ± 5.23  | 22.58 ± 3.13 | 21.96 ± 1.59 | 24.17 ± 1.75  | 23.73 ± 1.78 | 28.36 ± 2.63  | 24.12 ± 2.46 | 27.5 ± 3      | 27.81 ± 2.16 |
| HC       | 36.13 ± 6.3  | 36.7 ± 7.27  | 54.34 ± 4.06 | 53.42 ± 2.7  | 62.35 ± 3.11  | 54.53 ± 3.71 | 69.57 ± 4.44  | 58.53 ± 8.23 | 73.09 ± 4.6   | 71.5 ± 4.2   |
| LC       | 21 ± 5.31    | 20.47 ± 5.7  | 26.66 ± 1.96 | 27.6 ± 1.66  | 33.57 ± 2.89  | 32.68 ± 1.96 | 39.33 ± 1.48  | 35.33 ± 1.72 | 40.7 ± 3.33   | 39.72 ± 2.91 |
| LPos     | 30.84 ± 7.6  | 29.95 ± 8.86 | 36.64 ± 4.49 | 35.48 ± 1.33 | 39.52 ± 2.8   | 38.11 ± 1.56 | 41.36 ± 2     | 40.8 ± 1.74  | 42.01 ± 1.28  | 41.91 ± 1.13 |

Parentheses indicate sample size. For variable abbreviations, see Figure 1.

TABLE 2. Average and standard deviation in each stage for both sexes of *Cebus apella*

| Variable | Stage 1      |              | Stage 2      |              | Stage 3      |              | Stage 4      |              | Stage 5      |              |
|----------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|--------------|
|          | Male (5)     | Female (5)   | Male (6)     | Female (5)   | Male (10)    | Female (14)  | Male (14)    | Female (10)  | Male (24)    | Female (23)  |
| LCI      | 53.2 ± 1.02  | 49.9 ± 2.41  | 57 ± 2.17    | 56.52 ± 2.58 | 66.3 ± 1.77  | 61.8 ± 2     | 72.16 ± 1.79 | 64.38 ± 0.4  | 79.21 ± 2.3  | 70.3 ± 2.57  |
| ZB       | 44.53 ± 1.07 | 43.92 ± 1.75 | 48.95 ± 3.28 | 49 ± 2.76    | 54.86 ± 1.77 | 54.73 ± 2.93 | 63.58 ± 4.43 | 56.7 ± 1.62  | 69.76 ± 3.56 | 59.22 ± 3.39 |
| BB       | 48.82 ± 2.85 | 47.94 ± 3.53 | 52.5 ± 2.78  | 49.3 ± 2.4   | 52.11 ± 2.71 | 50.46 ± 2.5  | 50.43 ± 2.11 | 49.46 ± 0.98 | 52.14 ± 1.57 | 50.9 ± 2.1   |
| HO       | 32.33 ± 0.63 | 33.07 ± 0.87 | 32.58 ± 1.04 | 33.05 ± 2.31 | 33.36 ± 1.62 | 32.23 ± 1.79 | 34.15 ± 1.93 | 32.2 ± 0.99  | 34.3 ± 2.01  | 32.01 ± 2.3  |
| OB       | 15.6 ± 0.89  | 15.3 ± 0.52  | 16.7 ± 0.98  | 16.56 ± 0.96 | 18.15 ± 0.85 | 17.99 ± 0.91 | 20.85 ± 0.73 | 18.43 ± 0.56 | 22.74 ± 1.04 | 18.9 ± 0.95  |
| RL       | 11.2 ± 0.48  | 9.92 ± 1.71  | 13.46 ± 2.16 | 11.94 ± 1.4  | 15.71 ± 1.17 | 14.6 ± 1.42  | 16.66 ± 1.21 | 14.55 ± 1.12 | 18.78 ± 1.55 | 15.06 ± 2    |
| PAL      | 24.64 ± 1.07 | 23.43 ± 0.11 | 26.68 ± 1.4  | 25.98 ± 1.03 | 29.81 ± 0.84 | 29.43 ± 1.39 | 33.67 ± 0.89 | 30.61 ± 0.24 | 37.03 ± 1.45 | 32.31 ± 1.97 |
| PB       | 14.46 ± 1.07 | 13.94 ± 1.18 | 16.34 ± 0.76 | 16.28 ± 1.51 | 17.43 ± 0.86 | 17.08 ± 1    | 20.1 ± 0.69  | 17.3 ± 0.62  | 22.33 ± 0.94 | 18.7 ± 0.8   |
| CC       | 19.58 ± 0.9  | 19.16 ± 1.28 | 21.88 ± 0.68 | 21.28 ± 0.99 | 24.03 ± 1.33 | 23.39 ± 1    | 27.76 ± 1.44 | 24.48 ± 2.5  | 30.11 ± 1.6  | 25.16 ± 1.48 |
| ZL       | 22.4 ± 0.95  | 21.38 ± 0.83 | 25.7 ± 1.95  | 25.16 ± 1.33 | 28.53 ± 1.22 | 27.86 ± 1.56 | 33.42 ± 2.15 | 29.05 ± 1.2  | 37.4 ± 2.52  | 31.69 ± 1.88 |
| IOB      | 3.72 ± 0.22  | 3.96 ± 0.32  | 4.22 ± 0.13  | 4.2 ± 0.38   | 4.6 ± 0.22   | 4.65 ± 0.43  | 5.1 ± 0.5    | 4.9 ± 0.4    | 6.84 ± 0.58  | 4.87 ± 0.38  |
| UPos     | 17.3 ± 0.91  | 16.28 ± 1.23 | 19.28 ± 1.14 | 18.66 ± 1.64 | 21.31 ± 1.2  | 20.33 ± 1.08 | 21.4 ± 0.82  | 19.91 ± 0.96 | 23.06 ± 1.01 | 20.51 ± 1.31 |
| LD       | 38.14 ± 3    | 35.6 ± 2.74  | 42.4 ± 4.04  | 42.3 ± 0.89  | 49.31 ± 2.21 | 44.92 ± 2.85 | 57.33 ± 3.76 | 50.65 ± 0.91 | 63.7 ± 2.46  | 54.79 ± 3.11 |
| HD       | 9.9 ± 0.7    | 9.3 ± 0.85   | 11.86 ± 1.09 | 10.68 ± 1.22 | 12.86 ± 0.85 | 13.38 ± 1.23 | 16.4 ± 1.3   | 13.04 ± 0.55 | 17.05 ± 1.22 | 14.94 ± 1.44 |
| HC       | 22.88 ± 2.57 | 20.26 ± 2.97 | 26.56 ± 3.11 | 25.3 ± 2.9   | 31.55 ± 1.34 | 31.61 ± 3.12 | 37.16 ± 4.94 | 36.02 ± 1.31 | 43.88 ± 2.81 | 36.29 ± 2.84 |
| LC       | 13.7 ± 1.02  | 13.3 ± 1.35  | 15.86 ± 1.67 | 15.34 ± 1.98 | 19.25 ± 0.9  | 18.63 ± 1.18 | 24.05 ± 2.29 | 20.8 ± 0.69  | 27.07 ± 1.79 | 21.68 ± 1.44 |
| LPos     | 17.1 ± 1.96  | 16.1 ± 3.53  | 20.1 ± 2.28  | 19.8 ± 1.18  | 24.73 ± 1.63 | 23.99 ± 1.7  | 25.01 ± 1.02 | 24.91 ± 0.63 | 27.36 ± 1.04 | 24.05 ± 1.12 |

Parentheses indicate sample size. For variable abbreviations, see Figure 1.



TABLE 3. *t*-tests between sexes at dental ages 3–5

| Variable | <i>Cebus apella</i> | <i>Alouatta caraya</i> |
|----------|---------------------|------------------------|
| LCI      | <b>3, 4, 5</b>      | <b>3, 4, 5</b>         |
| ZB       | <b>3, 4, 5</b>      | <b>3, 4, 5</b>         |
| BB       | 3, 4, 5             | 3, 4, 5                |
| HO       | <b>3, 4, 5</b>      | 3, 4, 5                |
| OB       | <b>3, 4, 5</b>      | 3, 4, 5                |
| RL       | <b>3, 4, 5</b>      | <b>3, 4, 5</b>         |
| PAL      | <b>3, 4, 5</b>      | <b>3, 4, 5</b>         |
| PB       | <b>3, 4, 5</b>      | 3, 4, 5                |
| CC       | <b>3, 4, 5</b>      | <b>3, 4, 5</b>         |
| ZL       | <b>3, 4, 5</b>      | <b>3, 4, 5</b>         |
| IOB      | <b>3, 4, 5</b>      | 3, 4, 5                |
| UPos     | <b>3, 4, 5</b>      | 3, 4, 5                |
| LD       | <b>3, 4, 5</b>      | <b>3, 4, 5</b>         |
| HD       | <b>3, 4, 5</b>      | 3, 4, 5                |
| HC       | <b>3, 4, 5</b>      | <b>3, 4, 5</b>         |
| LC       | <b>3, 4, 5</b>      | <b>3, 4, 5</b>         |
| LPos     | <b>3, 4, 5</b>      | 3, 4, 5                |

In bold, cases where male measurements are significantly larger than female measurements;  $P < 0.05$ . Variables as in Figure 1, age stages defined in Material and Methods. Stages 1 and 2 were not included in the test because of the low sample size (see Tables 1 and 2).

the results with either the lower average standard deviation or bias. The multivariate statistical analysis (PCA + jackknife resampling) was programmed in R (R Development Core Team, 2008), and the script is available from the author (Giannini et al., in press). Bivariate coefficients of allometry can be extremely useful because they are less affected by sample completeness (Giannini et al., 2004) and are more directly interpretable in terms of size-dependent functional relationships (Jungers and German, 1981). In addition, bivariate coefficients can be derived from simple growth models of each measurement (Laird, 1965; Wayne, 1986). However, this technique implies a condition of isometry of the independent variable (condylo-incisive length), which does not necessarily occur (see Flores et al., 2010). Therefore, a multivariate approach seems to be more independent of such conditions, because size is considered as a latent variable affecting all variables simultaneously. In the few cases, where bivariate and multivariate approaches were discrepant, we chose the multivariate approach.

## RESULTS

### Cranial Allometry in *Alouatta caraya*

**Univariate analysis.** The univariate analysis in *A. caraya* shows that males and females become significantly dimorphic from early stages of devel-

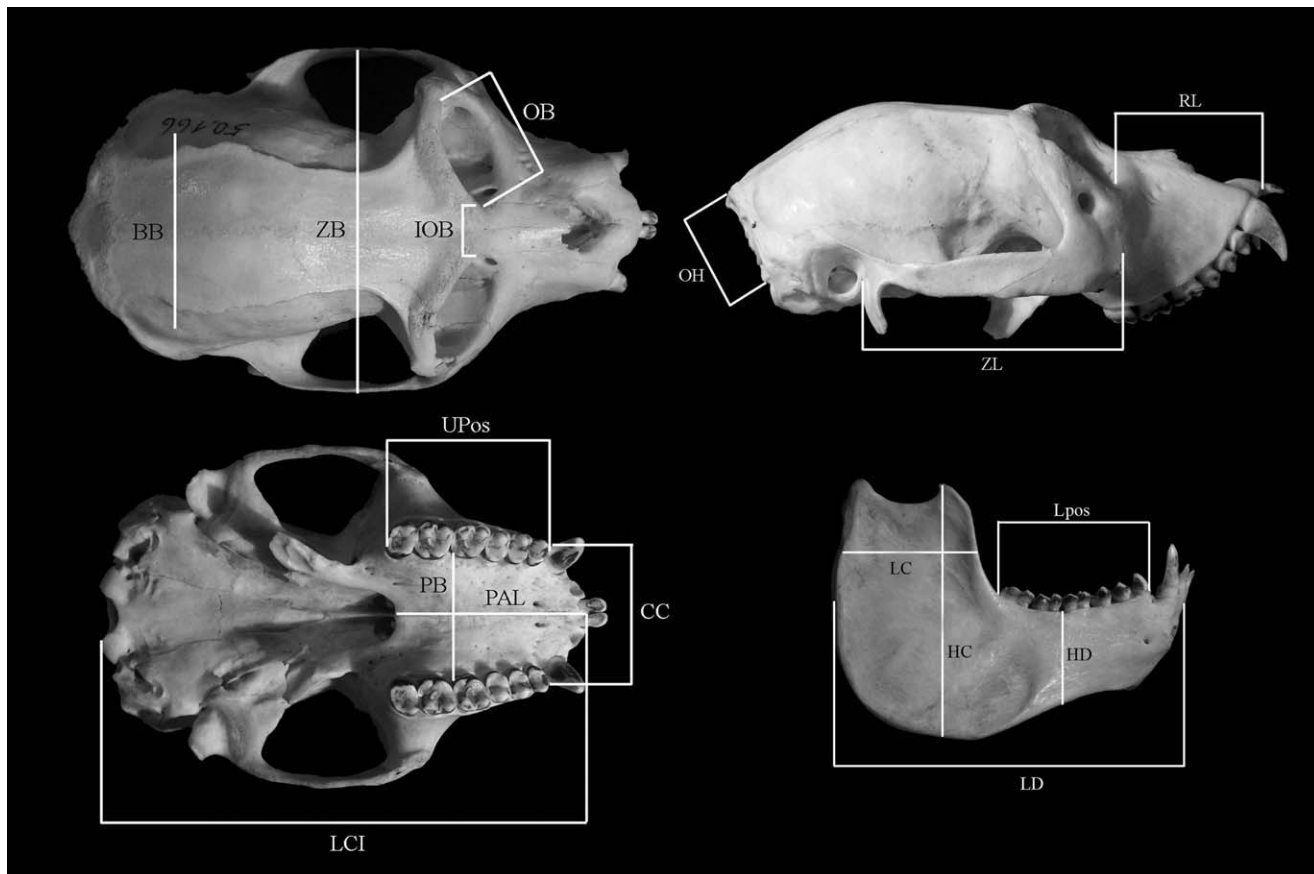


Fig. 1. Skull of *Alouatta caraya* showing the cranial measurements used in this study. BB, breadth of braincase; C-C, breadth of palate between canines; HC, height of the ascendant ramus; HD, height of dentary; HO, height of the occipital plate; IOB, interorbital breadth; LC, length of the coronoid process; LCI, condylo-incisive length; LD, length of dentary; LPos, lower postcanine row; OB, orbital breadth; PAL, length of palate; PB, palate breadth; RL, rostrum length; UPos, upper postcanine row; ZB, zygomatic breadth; ZL, zygomatic length.

opment (as early as stage 3, i.e., when permanent I1, I2, M1, and M2 are erupted) in condylobasal length, zygomatic breadth, rostrum length, length of the palate, zygomatic length, mandible, and height of the coronoid process (Table 3). Although the mean values for all variables are higher in males in all stages (Table 1), *t*-tests also indicate that several sexual differences occurring in the early stages are not statistically significant in the final adult stage 5, suggesting a complex mode of growth in which apparent transitional intervals of dimorphism in specific variables are reached only in the subadult stages (Table 3). For instance, some variables related to the masticatory apparatus (i.e., most mandibular measurements and zygomatic length) show statistically significant differences in early stages (in general, stages 3 to 4), but not at the final adult stage 5 (Table 3). In contrast, neurocranial variables exhibit nonsignificant sexual dimorphism throughout development. Finally, the condylobasal length and some additional variables related to mastication (i.e., zygomatic breadth, rostrum, and palate lengths) exhibit significant differences throughout postnatal ontogeny (favoring males) that remain until the final adult stage. Most of variables showing dimorphism have their most important changes in values in age stage 4.

**Bivariate analysis.** Reduced major axis regression of *A. caraya* indicates that all dependent variables are strongly correlated with the condylobasal length, except the breadth of the braincase (Table 4). Considering the assumed null hypothesis that  $b = 1$ , the confidence intervals show that the variables in which the value of isometry is included are the zygomatic breadth, palatine length, breadth between canines, lower postcanine tooth row, interorbital breadth (males), upper postcanine tooth row (females), and length of the ascendant ramus of the mandible (females). In four measurements, both sexes show negative allometry: breadth of the braincase, height of the occipital plate, orbital breadth, and palatine breadth. Males also show negative allometry in the regression of the upper postcanine tooth row. Confidence intervals show positive allometry in both sexes in five measurements: rostrum length, zygomatic length, dentary length, height of dentary at  $M^2$  level, and height of the ascendant ramus of the mandible. When both sexes are compared with respect to their regressions, no significant differences exist except in the case of the length of the ascendant ramus of the mandible, which displays positive allometry in males, but isometry in females. For the constant  $a$  (proportional to the  $y$ -intercept), a statistically significant

TABLE 4. Summary of regressions by sex on the condylobasal length of the skull of *Alouatta caraya* using reduced major axis

| Variable | Sex     | <i>N</i> | <i>R</i> | <i>y</i> -intercept | <i>b</i> | <i>y</i> -intercept confidence interval | <i>b</i> confidence interval |
|----------|---------|----------|----------|---------------------|----------|---|------------------------------|
| ZB       | Males   | 38       | 0.97     | 0.83                | 0.965    | 0.579–1.2                               | 0.89–1.05                    |
|          | Females | 31       | 0.967    | 0.814               | 0.979    | 0.563–1.29                              | 0.866–1.075                  |
| BB       | Males   | 45       | 0.478    | 12.1                | 0.31     | 7.87–18.95                              | 0.218–0.412                  |
|          | Females | 33       | 0.467    | 14.54               | 0.295    | 9.02–22.77                              | 0.193–0.326                  |
| HO       | Males   | 45       | 0.7      | 3.39                | 0.49     | 2.05–5.322                              | 0.385–0.6                    |
|          | Females | 32       | 0.84     | 3.355               | 0.462    | 1.91–5.833                              | 0.37–0.622                   |
| OB       | Males   | 45       | 0.962    | 1.045               | 0.676    | 0.67–1.52                               | 0.579–0.712                  |
|          | Females | 33       | 0.776    | 1.674               | 0.573    | 0.812–2.122                             | 0.434–0.670                  |
| RL       | Males   | 45       | 0.959    | 0.033               | 1.457    | 0.024–0.065                             | 1.346–1.526                  |
|          | Females | 33       | 0.984    | 0.035               | 1.49     | 0.019–0.055                             | 1.37–1.61                    |
| PAL      | Males   | 45       | 0.966    | 0.266               | 1.088    | 0.170–0.394                             | 0.992–1.1                    |
|          | Females | 33       | 0.902    | 0.29                | 1.08     | 0.21–0.415                              | 0.987–1.15                   |
| PB       | Males   | 45       | 0.85     | 0.61                | 0.791    | 0.368–1.098                             | 0.672–0.93                   |
|          | Females | 33       | 0.86     | 1.58                | 0.564    | 0.899–2.77                              | 0.483–0.659                  |
| CC       | Males   | 44       | 0.956    | 0.232               | 1.032    | 0.268–0.395                             | 0.922–1.142                  |
|          | Females | 32       | 0.938    | 0.19                | 1.067    | 0.115–0.406                             | 0.89–1.206                   |
| ZL       | Males   | 44       | 0.942    | 0.129               | 1.273    | 0.095–0.211                             | 1.175–1.344                  |
|          | Females | 33       | 0.982    | 0.122               | 1.352    | 0.079–0.173                             | 1.232–1.398                  |
| IOB      | Males   | 45       | 0.732    | 0.056               | 1.198    | 0.018–0.147                             | 0.947–1.463                  |
|          | Females | 34       | 0.83     | 0.016               | 1.530    | 0.009–0.04                              | 1.186–1.831                  |
| UPos     | Males   | 45       | 0.88     | 1.434               | 0.688    | 0.864–2.533                             | 0.561–0.783                  |
|          | Females | 33       | 0.957    | 0.523               | 0.896    | 0.28–1.041                              | 0.736–1.053                  |
| LD       | Males   | 39       | 0.98     | 0.47                | 1.12     | 0.333–0.63                              | 1.045–1.187                  |
|          | Females | 32       | 0.966    | 0.33                | 1.27     | 0.203–0.521                             | 1.105–1.312                  |
| HD       | Males   | 40       | 0.889    | 0.045               | 1.462    | 0.018–0.083                             | 1.207–1.662                  |
|          | Females | 33       | 0.916    | 0.015               | 1.644    | 0.008–0.038                             | 1.407–1.91                   |
| HC       | Males   | 39       | 0.952    | 0.073               | 1.461    | 0.042–0.13                              | 1.318–1.607                  |
|          | Females | 32       | 0.965    | 0.02                | 1.781    | 0.009–0.038                             | 1.579–2.016                  |
| LC       | Males   | 40       | 0.935    | 0.033               | 1.523    | 0.02–0.045                              | 1.398–1.642                  |
|          | Females | 32       | 0.969    | 0.811               | 0.982    | 0.575–1.21                              | 0.899–1.032                  |
| LPos     | Males   | 40       | 0.887    | 0.571               | 0.915    | 0.289–1.166                             | 0.77–1.06                    |
|          | Females | 33       | 0.961    | 0.25                | 1.113    | 0.135–0.497                             | 0.967–1.232                  |

*N*, sample size; *R*, coefficient of correlation; *b*, slope of the regression or coefficient of allometry. Abbreviations as in Figure 1.

TABLE 5. Results by sex of the multivariate analysis of cranial allometry in *Alouatta caraya*

| Variable | Sex | Observed | Departure | Untrimmed             |        |                         |              | Trimmed               |         |                         |              |
|----------|-----|----------|-----------|-----------------------|--------|-------------------------|--------------|-----------------------|---------|-------------------------|--------------|
|          |     |          |           | Resampled coefficient | Bias   | 99% Confidence interval | Growth trend | Resampled coefficient | Bias    | 99% Confidence interval | Growth trend |
| LCI      | M   | 0.22     | -0.025    | 0.22                  | 0.007  | 0.176-0.259             | =            | 0.241                 | -0.005  | 0.227-0.254             | =            |
|          | F   | 0.22     | -0.021    | 0.221                 | -0.003 | 0.202-0.249             | =            | 0.219                 | -0.002  | 0.205-0.242             | =            |
| ZB       | M   | 0.221    | -0.02     | 0.221                 | 0.0007 | 0.21-0.233              | -            | 0.222                 | -0.0002 | 0.212-0.232             | -            |
|          | F   | 0.21     | -0.031    | 0.211                 | -0.003 | 0.19-0.233              | -            | 0.21                  | -0.002  | 0.194-0.228             | -            |
| BB       | M   | 0.037    | -0.205    | 0.037                 | 0.002  | 0.008-0.065             | -            | 0.039                 | 0.001   | 0.024-0.053             | -            |
|          | F   | 0.04     | -0.202    | 0.04                  | -0.005 | 0.007-0.073             | -            | 0.026                 | 0.0014  | 0.008-0.043             | -            |
| HO       | M   | 0.092    | -0.15     | 0.086                 | 0.002  | 0.067-0.106             | -            | 0.091                 | 0.0002  | 0.074-0.107             | -            |
|          | F   | 0.098    | -0.144    | 0.098                 | -0.004 | 0.068-0.128             | -            | 0.09                  | -0.0002 | 0.068-0.11              | -            |
| OB       | M   | 0.118    | -0.124    | 0.118                 | 0.006  | 0.081-0.154             | -            | 0.137                 | -0.003  | 0.121-0.152             | -            |
|          | F   | 0.11     | -0.136    | 0.083                 | -0.008 | 0.058-0.154             | -            | 0.086                 | 0.0017  | 0.069-0.102             | -            |
| RL       | M   | 0.370    | 0.128     | 0.371                 | -0.02  | 0.254-0.487             | +            | 0.315                 | 0.008   | 0.147-0.383             | +            |
|          | F   | 0.38     | 0.134     | 0.377                 | -0.03  | 0.211-0.543             | =            | 0.296                 | 0.0091  | 0.283-0.309             | +            |
| PAL      | M   | 0.259    | 0.017     | 0.259                 | -0.007 | 0.216-0.303             | =            | 0.238                 | 0.003   | 0.218-0.257             | =            |
|          | F   | 0.238    | -0.004    | 0.239                 | -0.007 | 0.198-0.274             | =            | 0.228                 | -0.0019 | 0.202-0.253             | =            |
| PB       | M   | 0.131    | -0.111    | 0.131                 | 0.012  | 0.058-0.204             | -            | 0.171                 | -0.008  | 0.147-0.195             | -            |
|          | F   | 0.079    | -0.163    | 0.079                 | 0.016  | 0.017-0.174             | -            | 0.13                  | -0.009  | 0.102-0.159             | -            |
| CC       | M   | 0.193    | -0.049    | 0.193                 | 0.019  | 0.081-0.306             | =            | 0.268                 | -0.017  | 0.25-0.286              | =            |
|          | F   | 0.178    | -0.064    | 0.178                 | 0.023  | 0.051-0.309             | =            | 0.255                 | -0.0016 | 0.234-0.277             | =            |
| ZL       | M   | 0.278    | 0.036     | 0.279                 | 0.011  | 0.21-0.348              | =            | 0.321                 | -0.009  | 0.305-0.339             | +            |
|          | F   | 0.257    | 0.015     | 0.258                 | 0.012  | 0.184-0.332             | =            | 0.298                 | -0.008  | 0.281-0.316             | +            |
| IOB      | M   | 0.223    | -0.019    | 0.262                 | -0.017 | 0.171-0.354             | =            | 0.213                 | 0.008   | 0.177-0.248             | =            |
|          | F   | 0.26     | 0.018     | 0.26                  | 0.018  | 0.15-0.371              | =            | 0.319                 | -0.01   | 0.274-0.363             | +            |
| UPos     | M   | 0.183    | -0.059    | 0.183                 | -0.019 | 0.087-0.28              | =            | 0.127                 | 0.009   | 0.097-0.156             | -            |
|          | F   | 0.24     | -0.00007  | 0.242                 | -0.035 | 0.06-0.424              | =            | 0.1-3                 | -0.021  | 0.112-0.149             | -            |
| LD       | M   | 0.259    | 0.017     | 0.260                 | 0.003  | 0.231-0.286             | =            | 0.273                 | -0.003  | 0.265-0.281             | +            |
|          | F   | 0.25     | 0.008     | 0.251                 | 0.002  | 0.217-0.285             | =            | 0.25                  | -0.0032 | 0.235-0.262             | +            |
| HD       | M   | 0.371    | 0.129     | 0.371                 | -0.026 | 0.239-0.503             | =            | 0.286                 | 0.016   | 0.255-0.317             | =            |
|          | F   | 0.344    | 0.118     | 0.36                  | -0.008 | 0.302-0.419             | +            | 0.35                  | -0.0037 | 0.315-0.386             | +            |
| HC       | M   | 0.355    | 0.113     | 0.356                 | -0.005 | 0.332-0.379             | +            | 0.35                  | -0.001  | 0.332-0.367             | +            |
|          | F   | 0.395    | 0.153     | 0.395                 | -0.009 | 0.349-0.442             | +            | 0.38                  | 0.0015  | 0.35-0.411              | +            |
| LC       | M   | 0.311    | 0.069     | 0.311                 | 0.02   | 0.195-0.427             | =            | 0.386                 | -0.017  | 0.371-0.402             | +            |
|          | F   | 0.293    | 0.051     | 0.293                 | 0.019  | 0.175-0.411             | =            | 0.36                  | -0.014  | 0.334-0.387             | +            |
| LPos     | M   | 0.223    | -0.019    | 0.223                 | -0.01  | 0.161-0.284             | =            | 0.198                 | 0.001   | 0.168-0.228             | -            |
|          | F   | 0.277    | 0.035     | 0.278                 | -0.028 | 0.138-0.418             | =            | 0.188                 | 0.016   | 0.164-0.213             | -            |

The first three data columns show results using all specimens. The remainder of the columns show jackknife results calculated with untrimmed and ( $m = 1$ ) trimmed sets of pseudovalues (see Materials and Methods). Allometry coefficient is the correspondent element of the first (unit) eigenvector per variable. The observed coefficient is the value obtained with all specimens included (males,  $n = 42$ ; females,  $n = 38$ ) with no missing data. The resampled coefficient is the first-order jackknife value. Bias is the difference between the resampled and observed coefficients. The jackknife 99% confidence interval is provided; allometric variables are those whose confidence interval excludes the expected value under isometry (0.242). Growth trend is the summary allometry of each variable presented in symbols: =, isometry; -, negative allometry; +, positive allometry.

difference exists only in the regression referring to the length of the ascendant ramus of the mandible.

**Multivariate analysis.** The observed multivariate coefficients of allometry varied widely across the measured variables (Table 5). In males, the palate length, interorbital breadth, dentary length, and lower postcanine tooth row showed the smallest departure from isometry values, whereas in females, the variables with smallest departure were the dentary length, palate, and lower postcanine row (Table 5). The mean difference in the absolute bias in males clearly favors trimmed over untrimmed values, with a 0.006 average absolute bias for the former and a 0.011 absolute bias for the latter (1.83 times higher). Similar to males, the mean difference in the absolute bias of females favors trimmed over untrimmed values, with a

0.006 absolute bias for the former and a 0.013 absolute bias for the latter (2.16 times higher). Therefore, the interpretations of multivariate allometry are based on trimmed values. Similar to the bivariate analysis, the results for multivariate allometry generally show the same trends in both sexes of *A. caraya*. Seven variables (zygomatic breadth, breadth of braincase, height of occipital plate, orbit, breadth of palate, and upper and lower postcanine rows) are negatively allometric; five variables (rostral length, zygomatic length, dentary length, and height and length of the ascendant ramus) are positively allometric, and only three variables (condylobasal length, palate, and breadth between canines) scale isometrically with increasing general size. Only two variables showed sexual dimorphism: interorbital breadth and

height of dentary (both isometric in males and positively allometric in females). A comparison of bivariate and multivariate allometry indicated that 12 of 17 variables showed the same trend. The remaining variables showed trends partially or totally different in both methods.

**Skull modeling in *A. caraya*.** On the basis of the multivariate analysis with trimmed jackknife estimates of allometry, the quantitative trends in the modeling of the skull in *A. caraya* are described as follows. Condylbasal length, a commonly used indicator of cranial size, is ontogenetically isometric in both sexes. The braincase grows at a slower pace than the rest of the skull in both sexes, as do other measured neurocranial components, such as the height of the occipital plate and orbit. Thus, the two main dimensions of the braincase (height and breadth) share a markedly negative allometric growth of similar magnitude (Table 5). The temporal space, which contains the temporalis muscle, grows at a slow pace in both sexes considering the negative allometry of the zygomatic breadth. Nevertheless, the negative allometry of this measurement shows values that are notably higher compared with the trends observed in the breadth of braincase (Table 5). Thus, the space for the temporalis expands by the combination of the slightly negative allometry of the zygomatic breadth with the strongly negative allometry of the braincase breadth. In addition, the craniocaudal space for the temporalis muscle grows at a fast pace because the zygomatic length is positively allometric in both sexes. In relative terms, the palate in both sexes lengthens as the animal grows as the result of isometric length scaling and negative breadth scaling. However, the breadth of the palate in its anterior region, represented by the canine–canine breadth, scales isometrically. The interorbital space shows sexual dimorphism, as this measurement grows at a faster pace than the rest of the skull in females, whereas it is isometric in males (see above). In addition, another dimension of the facial skeleton, the rostral length, scales positively in both sexes. Both tooth rows (upper and lower) seem to be coordinated because they grow at approximately the same pace, being negatively allometric in males and females. The mandible is a structure that grows at a fast pace in general because its length and both dimensions of the ascendant ramus are positively allometric. Nonetheless, the vertical dimensions of the mandible grow relatively faster in females (positive) than in males (isometric). In particular, the mandible becomes more robust, and the ascendant ramus becomes relatively higher in larger specimens. These results indicate that males and females of *A. caraya* show a similar pattern of cranial growth, with sexual dimorphism in the rate of growth restricted to a few variables such as the interorbital breadth and height of the dentary (Table 2).

### **Cranial Allometry in *Cebus apella***

**Univariate analysis.** The univariate analysis indicates that both sexes are very similar in linear distance in the earlier juvenile stage considered for this test. However, all male means tend to be larger than their female counterparts (Table 2), and the only statistically significant differences in variables at these stages are found in the condylbasal length and dentary length in stage 3. Starting in stage 4 and continuing through stage 5, there is a tendency for the number of significant sexual differences to increase with males showing higher means (Table 3). From stage 4, significant sexual differences were detected in variables related to the dental arcade (breadth between canines, length, and breadth of the palate) and components associated with the masticatory apparatus (zygomatic breadth and length, rostrum, height of dentary, and length of the ascendant ramus). Strong sexual dimorphism exists in the mature adult stage for all variables, except in the breadth of the braincase.

**Bivariate analysis.** The correlation coefficients for breadth of braincase and height of the occipital plate show that they are not correlated with the condylbasal length in either sex (Table 6). Regressions indicate that the palatine length and breadth between canines scale isometrically with respect to the condylbasal length in both sexes. Several traits exhibit sexual dimorphism. Males show positive allometry in zygomatic breadth and interorbital breadth (both isometric in females), whereas in females, positive allometry appears in the lower postcanine tooth row (isometric in males). Only in the palatine breadth and upper postcanine tooth row, males showed negative allometry, but isometry in females. In both sexes, some variables, such as dentary length, height of dentary at the  $M^2$  level, height and length of the ascendant ramus of the mandible, rostrum, and zygomatic length, increase with positive allometry. The only variables that increase with exponents statistically lower than 1 are neurocranial variables, such as orbital breadth, breadth of braincase, and height of the occipital plate (both sexes), and some variables related to the masticatory apparatus, such as the aforementioned palatine breadth and upper postcanine tooth row in males. Except in the cases of the zygomatic breadth, breadth between canines, orbits, interorbital width, and length of the ascendant ramus, the coefficients for females were always higher than those calculated for males. Regarding the constant  $a$ , the intercepts are significantly higher in males in two cases (rostrum length and upper postcanine tooth row).

**Multivariate analysis.** The observed multivariate coefficients of allometry also varied widely across variables in *C. apella* (Table 7). In males, several variables show a small departure from isometry, such as the condylbasal length, rostrum



TABLE 6. Summary of regressions by sex on the condylobasal length of the skull of *Cebus apella* using reduced major axis

| Variable | Sex     | N  | R     | y-intercept | b     | y-intercept confidence interval | b confidence interval |
|----------|---------|----|-------|-------------|-------|---------------------------------|-----------------------|
| ZB       | Males   | 55 | 0.973 | 0.383       | 1.192 | 0.285–0.547                     | 1.127–1.26            |
|          | Females | 51 | 0.96  | 0.813       | 1.015 | 0.593–1.141                     | 0.965–1.05            |
| BB       | Males   | 55 | 0.135 | 11.773      | 0.364 | 7.612–17.123                    | 0.264–0.402           |
|          | Females | 53 | 0.27  | 7.732       | 0.465 | 4.498–13.345                    | 0.35–0.512            |
| HO       | Males   | 54 | 0.168 | 5.121       | 0.431 | 3.078–8.81                      | 0.333–0.503           |
|          | Females | 51 | 0.125 | 3.545       | 0.555 | 1.789–7.012                     | 0.391–0.687           |
| OB       | Males   | 55 | 0.9   | 0.736       | 0.784 | 0.499–1.035                     | 0.692–0.832           |
|          | Females | 54 | 0.933 | 0.703       | 0.765 | 0.514–1.004                     | 0.704–0.823           |
| RL       | Males   | 55 | 0.837 | 0.108       | 1.216 | 0.067–0.202                     | 1.09–1.361            |
|          | Females | 54 | 0.868 | 0.023       | 1.685 | 0.0012–0.032                    | 1.467–1.9             |
| PAL      | Males   | 54 | 0.954 | 0.523       | 0.977 | 0.412–0.693                     | 0.903–1.025           |
|          | Females | 51 | 0.939 | 0.418       | 1.043 | 0.283–0.605                     | 0.941–1.122           |
| PB       | Males   | 55 | 0.872 | 0.533       | 0.853 | 0.356–0.813                     | 0.765–0.928           |
|          | Females | 54 | 0.935 | 0.372       | 0.925 | 0.277–0.504                     | 0.876–1.003           |
| CC       | Males   | 55 | 0.966 | 0.423       | 0.976 | 0.312–0.586                     | 0.897–1.031           |
|          | Females | 54 | 0.883 | 0.499       | 0.918 | 0.313–0.812                     | 0.836–1.038           |
| ZL       | Males   | 54 | 0.268 | 0.545       | 1.098 | 0.188–1.723                     | 1.072–1.197           |
|          | Females | 54 | 0.962 | 0.228       | 1.181 | 0.168–0.312                     | 1.084–1.221           |
| IOB      | Males   | 55 | 0.867 | 0.022       | 1.335 | 0.013–0.04                      | 1.153–1.501           |
|          | Females | 54 | 0.668 | 0.097       | 0.974 | 0.039–0.179                     | 0.785–1.113           |
| UPpos    | Males   | 55 | 0.748 | 1.635       | 0.617 | 1.015–2.6                       | 0.513–0.702           |
|          | Females | 54 | 0.866 | 0.44        | 0.946 | 0.275–0.723                     | 0.799–1.024           |
| LD       | Males   | 52 | 0.987 | 0.245       | 1.272 | 0.186–0.321                     | 1.206–1.319           |
|          | Females | 51 | 0.963 | 0.221       | 1.315 | 0.182–0.3                       | 1.25–1.41             |
| HD       | Males   | 52 | 0.967 | 0.048       | 1.442 | 0.026–0.058                     | 1.307–1.52            |
|          | Females | 52 | 0.912 | 0.028       | 1.582 | 0.012–0.037                     | 1.412–1.755           |
| HC       | Males   | 52 | 0.955 | 0.033       | 1.702 | 0.015–0.049                     | 1.57–1.821            |
|          | Females | 51 | 0.987 | 0.026       | 1.832 | 0.013–0.03                      | 1.675–1.933           |
| LC       | Males   | 52 | 0.977 | 0.037       | 1.634 | 0.019–0.04                      | 1.507–1.724           |
|          | Females | 51 | 0.934 | 0.031       | 1.608 | 0.018–0.043                     | 1.476–1.721           |
| LPos     | Males   | 52 | 0.873 | 0.386       | 0.994 | 0.213–0.67                      | 0.862–1.12            |
|          | Females | 52 | 0.901 | 0.068       | 1.456 | 0.031–0.11                      | 1.278–1.61            |

N, sample size; R, coefficient of correlation; b, slope of the regression or coefficient of allometry. Abbreviations as in Figure 1.

length, and interorbital breadth, whereas in females, the zygomatic breadth exhibits the smallest departure from isometry (Table 7). Unlike the bias observed in both sexes of *A. caraya*, the mean difference in the absolute bias in males of *C. apella* clearly favors untrimmed over trimmed values, with a 0.0008 average absolute bias for the former and 0.0056 for the latter (seven times higher). Similarly, the mean difference in the absolute bias of females also favors untrimmed over trimmed values (although in lesser degree), with a 0.0032 absolute bias for the former and 0.004 for the latter (1.25 times higher). Therefore, the interpretations of multivariate allometry in *C. apella* were based on untrimmed values. Results for multivariate allometry show the same general trends in males and females of *C. apella*, except some punctual variables. Six variables (breadth of the braincase, height of the occipital plate, orbital breadth, breadth of palate, breadth between canines, and upper postcanine row) were negatively allometric; four variables (length and height of the dentary and length and height of the ascendant ramus) were positively allometric, and only three variables (condylobasal length, rostrum length, and lower postcanine row) scaled isometrically with increasing general size. Four variables showed sexual

dimorphism: interorbital breadth (isometric in males and negatively allometric in females), zygomatic breadth and length (positively allometric in males and isometric in females), and length of palate (negatively allometric in males and isometric in females). A comparison of bivariate and multivariate allometry indicates that 8 of 17 variables showed the same trend in multivariate and bivariate allometry. Those variables include both neurocranial and mandibular components. The remaining variables showed trends that were partially or totally different in both methods.

**Skull modeling in *C. apella*.** On the basis of the multivariate analysis with untrimmed jackknife estimates of allometry, the quantitative trends in the modeling of the skull in *C. apella* are as follows: condylobasal length in *C. apella* is ontogenetically isometric only in both sexes, and all neurocranial measurements grow at a slower pace than the rest of the skull. The temporal space, which contains the temporalis muscle, grows faster in males considering the positive allometry of the zygomatic breadth, whereas this measurement is isometric in females. However, the allometric trends of the zygomatic breadth are notably higher compared with those obtained for the braincase in both sexes (Table 7). Thus, the space for the



TABLE 7. Results by sex of the multivariate analysis of cranial allometry in *Cebus apella*

| Variable | Sex | Observed | Departure | Untrimmed             |          |                         |              | Trimmed               |         |                         |              |
|----------|-----|----------|-----------|-----------------------|----------|-------------------------|--------------|-----------------------|---------|-------------------------|--------------|
|          |     |          |           | Resampled coefficient | Bias     | 99% Confidence interval | Growth trend | Resampled coefficient | Bias    | 99% Confidence interval | Growth trend |
| LCI      | M   | 0.23     | -0.011    | 0.231                 | -0.0003  | 0.216-0.246             | =            | 0.232                 | -0.0006 | 0.22-0.244              | =            |
|          | F   | 0.224    | -0.018    | 0.225                 | -0.0009  | 0.201-0.248             | =            | 0.219                 | 0.0018  | 0.204-0.234             | -            |
| ZB       | M   | 0.259    | 0.017     | 0.26                  | 0.0002   | 0.248-0.282             | +            | 0.265                 | -0.0026 | 0.249-0.282             | +            |
|          | F   | 0.239    | -0.003    | 0.24                  | -0.0016  | 0.203-0.276             | =            | 0.233                 | 0.0019  | 0.211-0.254             | =            |
| BB       | M   | 0.006    | -0.248    | 0.005                 | 0.005    | 0.04-0.034              | -            | 0.011                 | -0.04   | 0.004-0.033             | -            |
|          | F   | 0.027    | -0.2215   | 0.028                 | 0.0017   | 0.032-0.088             | -            | 0.009                 | 0.0073  | 0.021-0.039             | -            |
| HO       | M   | 0.017    | -0.225    | 0.018                 | -0.0007  | 0.01-0.046              | -            | 0.02                  | -0.0021 | 0.008-0.045             | -            |
|          | F   | 0.008    | -0.234    | 0.008                 | 0.0027   | 0.063-0.08              | -            | 0.017                 | -0.0017 | 0.043-0.078             | -            |
| OB       | M   | 0.159    | -0.083    | 0.159                 | -0.0003  | 0.132-0.186             | -            | 0.157                 | 0.0006  | 0.136-0.178             | -            |
|          | F   | 0.187    | -0.055    | 0.187                 | 0.00012  | 0.156-0.217             | -            | 0.192                 | -0.0026 | 0.169-0.215             | -            |
| RL       | M   | 0.228    | -0.014    | 0.257                 | -0.0015  | 0.208-0.306             | =            | 0.258                 | -0.0021 | 0.218-0.299             | =            |
|          | F   | 0.316    | 0.074     | 0.316                 | 0.0004   | 0.114-0.419             | =            | 0.301                 | 0.0078  | 0.212-0.39              | =            |
| PAL      | M   | 0.224    | -0.018    | 0.224                 | -0.0005  | 0.202-0.23              | -            | 0.224                 | -0.0007 | 0.206-0.228             | -            |
|          | F   | 0.215    | -0.027    | 0.215                 | -0.0006  | 0.17-0.261              | =            | 0.213                 | 0.00038 | 0.180-0.24              | -            |
| PB       | M   | 0.17     | -0.072    | 0.171                 | -0.0004  | 0.132-0.209             | -            | 0.162                 | 0.004   | 0.136-0.189             | -            |
|          | F   | 0.193    | -0.049    | 0.194                 | 0.0013   | 0.147-0.24              | -            | 0.207                 | -0.0056 | 0.173-0.23              | -            |
| CC       | M   | 0.217    | -0.025    | 0.218                 | -0.00007 | 0.186-0.239             | -            | 0.220                 | -0.0013 | 0.195-0.246             | -            |
|          | F   | 0.185    | -0.057    | 0.185                 | 0.00002  | 0.141-0.230             | -            | 0.189                 | -0.0018 | 0.158-0.22              | -            |
| ZL       | M   | 0.297    | 0.055     | 0.297                 | 0.00031  | 0.266-0.328             | +            | 0.302                 | -0.021  | 0.278-0.326             | +            |
|          | F   | 0.261    | 0.019     | 0.262                 | 0.0003   | 0.209-0.314             | =            | 0.264                 | -0.0007 | 0.226-0.301             | =            |
| IOB      | M   | 0.251    | 0.009     | 0.252                 | -0.0003  | 0.196-0.307             | =            | 0.254                 | -0.0016 | 0.209-0.299             | =            |
|          | F   | 0.159    | -0.083    | 0.159                 | 0.00032  | 0.065-0.24              | -            | 0.175                 | -0.0078 | 0.117-0.234             | -            |
| UPos     | M   | 0.118    | -0.124    | 0.118                 | -0.0016  | 0.086-0.151             | -            | 0.111                 | -0.002  | 0.085-0.137             | -            |
|          | F   | 0.167    | -0.075    | 0.167                 | -0.0002  | 0.106-0.227             | -            | 0.152                 | 0.0055  | 0.111-0.192             | -            |
| LD       | M   | 0.292    | 0.05      | 0.292                 | -0.0003  | 0.267-0.318             | +            | 0.295                 | -0.0015 | 0.277-0.313             | +            |
|          | F   | 0.287    | 0.045     | 0.288                 | -0.0016  | 0.251-0.342             | +            | 0.281                 | 0.0017  | 0.256-0.306             | +            |
| HD       | M   | 0.303    | 0.061     | 0.304                 | -0.0003  | 0.262-0.346             | +            | 0.299                 | 0.0022  | 0.267-0.331             | +            |
|          | F   | 0.356    | 0.114     | 0.356                 | -0.0029  | 0.291-0.421             | +            | 0.344                 | 0.0035  | 0.3-0.387               | +            |
| HC       | M   | 0.374    | 0.132     | 0.375                 | 0.0001   | 0.34-0.41               | +            | 0.383                 | -0.0041 | 0.363-0.403             | +            |
|          | F   | 0.387    | 0.145     | 0.387                 | -0.0038  | 0.332-0.443             | +            | 0.367                 | 0.0055  | 0.343-0.395             | +            |
| LC       | M   | 0.364    | 0.122     | 0.365                 | -0.0004  | 0.336-0.393             | +            | 0.364                 | 0.0002  | 0.339-0.388             | +            |
|          | F   | 0.352    | 0.11      | 0.353                 | -0.0014  | 0.294-0.411             | +            | 0.336                 | 0.0071  | 0.297-0.374             | +            |
| LPos     | M   | 0.221    | -0.021    | 0.222                 | -0.0024  | 0.156-0.287             | =            | 0.202                 | 0.0073  | 0.155-0.24              | -            |
|          | F   | 0.217    | -0.025    | 0.218                 | 0.00029  | 0.17-0.265              | =            | 0.208                 | 0.0051  | 0.178-0.237             | -            |

The first three data columns show results using all specimens. The remainder of the columns show jackknife results calculated with untrimmed and ( $m = 1$ ) trimmed sets of pseudovalues (see Materials and Methods). Allometry coefficient is the correspondent element of the first (unit) eigenvector per variable. The observed coefficient is the value obtained with all specimens included (males,  $n = 57$ ; females,  $n = 53$ ) with no missing data. The resampled coefficient is the first-order jackknife value. Bias is the difference between the resampled and observed coefficients. The jackknife 99% confidence interval is provided; allometric variables are those whose confidence interval excludes the expected value under isometry (0.242). Growth trend is the summary allometry of each variable presented in symbols: =, isometry; -, negative allometry; +, positive allometry.

temporalis expands by the combination of the positive allometry (in males) or isometry (in females) of the zygomatic breadth with the strongly negative allometry of the braincase. In addition, the craniocaudal space for the temporalis muscle grows faster in males because the zygomatic length shows positive allometry, whereas it is isometric in females. In relative terms, the palate grows in a complex way showing sexual differences. In males, both the length and breadth are negatively allometric. In females, the palate length is isometric, and the breadth is negatively allometric (as is also observed in both sexes of *A. caraya*). In addition, the breadth of the anterior portion of the palate (breadth between canines) is allometrically negative in both sexes. As in *A. caraya*, the interorbital breadth shows sexual dimorphism

because it is isometric in males in *C. apella*, whereas it is negatively allometric in females. In addition, other dimensions of the facial skeleton, such as rostral length, scale positively in both sexes. The growth of the upper and lower tooth rows is not coordinated in either sex, as is also seen in *A. caraya*, because the upper postcanine row scales negatively, whereas its lower counterpart scales isometrically. The mandible is a structure that grows with positive allometry in both sexes in all variables considered. The mandible becomes robust, and the ascendant ramus is notably developed in older specimens. These results also indicate that both males and females of *C. apella* exhibit an almost similar pattern of cranial growth and that sexual dimorphism in the rate of growth is merely restricted to the condylobasal

length, zygomatic breadth, length of zygoma, length of the palate, and interorbital breadth.

## DISCUSSION

Although a number of studies have provided a detailed description of the ontogeny of dimorphism in New World monkeys (e.g., Plavcan and Gomez, 1993; Ravosa and Ross, 1994; Masterson, 1997; O'Higgins et al., 2001; Blanco and Godfrey, 2006), our understanding of ontogeny in many species remains incomplete. The cranial growth pattern described in *C. apella* and *A. caraya* shows several sexual differences resulting from the differential extent of common growth trajectories between sexes (Fig. 2). Such a pattern was also found among old world dimorphic primates, such as gorillas and chimpanzees (Shea, 1986). In a broader context, this kind of pattern (both intraspecific and between related species) may be widespread because changes in hormonal growth control provide a simple physiological basis for these coordinated alterations in growth rates (Tanner, 1988; Shea, 1992; Klingenberg, 1998). According to Shea (1986), males become dimorphic in craniofacial structures because of faster growth by rate hypermorphosis (i.e., males of the same age as females develop progressively larger craniofacial structures but attain maturity at the same chronological age) or males can grow for a longer duration via time hypermorphosis (i.e., males of the same age as females have for most of the time similarly sized craniofacial structures but are larger at a later chronological age).

These ontogenetic processes have been linked to different socioecological strategies, and it is also possible that both may act in conjunction or at different times of development (Wiley, 1974; Ralls,

1977; Jarman, 1983; Shea, 1986; Ravosa, 1991; Masterson, 1997). Males of *A. caraya* and *C. apella* are bigger than females in almost all cranial variables considered (Tables 1 and 2), and the percentage of bimaturism is similar in both taxa (i.e., the difference of age at growth cessation in males and females is similar in both species; see Table 2 in Leigh, 1992), with males growing for a longer time. In both species, sexual maturity occurs at about 90 months in males and 54 months in females. Therefore, the highly similar allometric trends observed in most variables for both sexes suggest that males become dimorphic mainly because they grow for a longer time (time hypermorphosis), with clearly different offsets between sexes. A similar pattern was also found by Masterson (1997) for alternative cranial variables in *C. apella*, although a lack of bimaturism was suggested for this species (contra Leigh, 1992). However, a detailed examination of our results for growth trajectories in *C. apella* and *A. caraya* also suggests the existence of differences in the mode of cranial growth in each sex (Tables 4–7), i.e., a common trajectory does not explain a considerable proportion of adult sexual dimorphism (Figs. 3 and 4). Therefore, we discuss the skull modeling of both species in terms of allometric growth.

## Ontogeny of the Skull Dimorphism in *A. caraya*

Males of *A. caraya* have some cranial dimensions that grow at a slower pace than in females (Tables 4 and 5), although the final size of condylo-

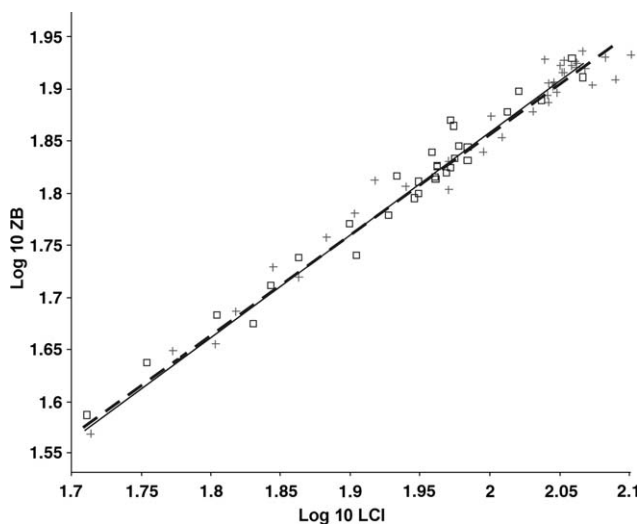


Fig. 2. Bivariate scatterplots (RMA) of zygomatic breadth on condylobasal length in males (crosses) and females (squares) of *Alouatta caraya*. Dashed line indicates males.

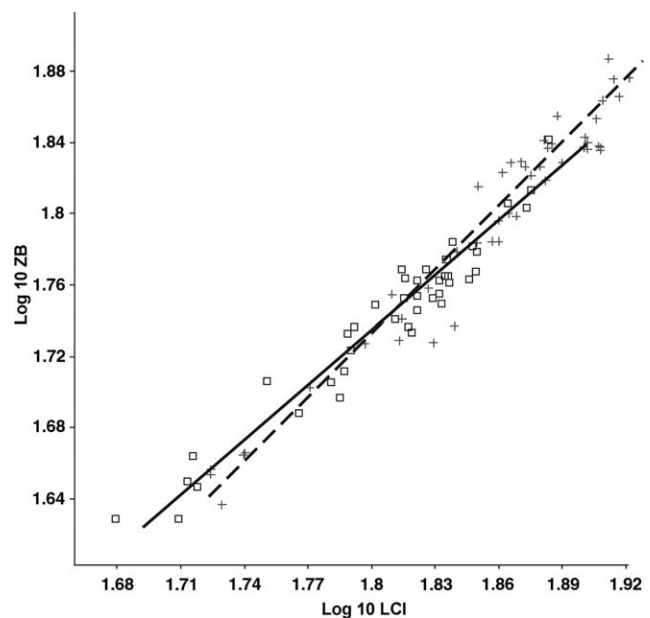


Fig. 3. Bivariate scatterplots (RMA) of zygomatic breadth on condylobasal length in males (crosses) and females (squares) of *Cebus apella*. Dashed line indicates males.

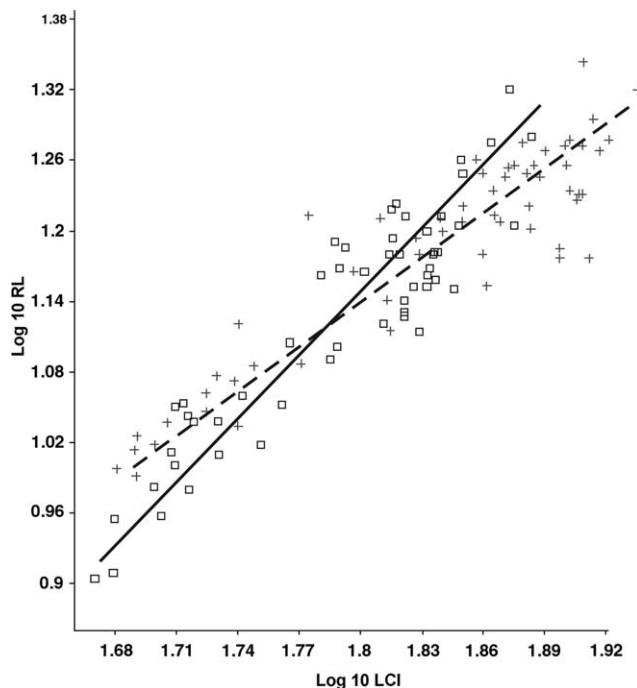


Fig. 4. Bivariate scatterplots (RMA) of rostrum length on condylobasal length in males (crosses) and females (squares) of *Cebus apella*. Dashed line indicates males.

basal length is still statistically higher in males (Table 3), suggesting an important influence of the prolongation of time of growth as generator of sexual dimorphism. Additionally, the same trend being observed for the condylobasal length, length of palate, and breadth between canines (isometric) in both sexes implies that the dimorphism is likely due to the strong bimaturism of *A. caraya* (i.e., time hypermorphosis), whereas the significant difference in the rostrum length is also accompanied by higher allometric trends in males (rate hypermorphosis). Males and females of *A. caraya* generally have similar infant sizes (Table 3). Significant differences in size only appear in later stages during the ontogeny, approximately when the permanent M2 is erupted. Nevertheless, several variables showed significant dimorphism only in subadult stages, becoming nonsignificant in the adult terminal stage (Table 3), as those related to the mandible and the zygomatic length (although most variables were significantly bigger in adult males of the final age class). Ravosa and Ross (1994) also found that a number of sexual differences were statistically significant from early stages of growth in *Alouatta seniculus* (although this pattern was preserved to adult stages), with rate hypermorphosis being the more important factor determining the sexual dimorphism. It is likely that both patterns (time and rate hypermorphosis) occur simultaneously in *A. caraya* and *A. seniculus* considering the similarity in several aspects of their biology (Thorington et al., 1979, 1984; Glander, 1980;

Milton, 1980; Crockett, 1987) and bimaturism (Leigh, 1992). The fact that some variables showed statistically significant differences between the sexes only in some subadult stages implies that interactions between different paces of growth in each sex cause transitional dimorphism, resulting in statistically nonsignificant differences when last age stage is reached. The pattern of transitional sexual differences also suggests causes linked to specific behavioral models. For instance, Thorington et al. (1979) observed some external characters of subadult males of *Alouatta palliata* that resemble those of females, which could be an effect that allows them to avoid the hostility of adult males. The fact that significant differences between sexes are observed in early stages but not in adult stages in *A. caraya* indicates that they are not involved in biological actions which avoid male competition, as has been stated for *A. palliata*. However, the cranial variables that are sexually different in the adult final stage (Table 3) are strongly correlated with trophic and masticatory function, which are important in the competition among adult males. Therefore, Thorington's model could also be applicable to *A. caraya*.

#### Ontogeny of the Skull Dimorphism in *C. apella*

Our observations of significant sexual dimorphism are comparable in some aspects to that reported by Masterson (1997), taking into account the age stages considered in both studies. According to Masterson (1997), significant dimorphism in four neurocranial variables first emerges in the mid-juvenile stage (stage D3, i.e., when I1 permanent reaches the occlusal plane, which corresponds to age stage 2 in this study). Our results also show that significant sexual dimorphism occurs later in two of three neurocranial variables, but occurs in age stage 4 (i.e., when permanent P2, P3, and P4 are erupted, Table 3), which coincides approximately with stage D5 of Masterson (1997: Table 1). In our univariate analysis, only the condylobasal and dentary lengths exhibited early significant dimorphism, whereas for the remaining variables, dimorphism only appears later. Such sexual differences remain in both subadult and adult stages, a finding which is in agreement with Masterson (1997) and Corner and Richtsmeier (1991). In our analysis, rate hypermorphosis was detected in males, but it is highly probable that time hypermorphosis also exists considering the strong bimaturism for this species (see above). For instance, some variables (e.g., zygomatic length) grow faster than other variables in males according to multivariate results (Table 7), and others (e.g., zygomatic and interorbital breadths) show positive allometry in males (but isometry in females) in the reduced major axis analysis, accentuating the

dimorphism in the final size of adults (Table 6). Although Masterson's (1997) results generally indicate a common ontogenetic trajectory in both sexes (suggesting that sexual differences were present at the offset), we found departures from this pattern in specific cranial regions, demonstrating dimorphism in the rate of growth in variables mostly related to the masticatory apparatus, which was greater in males (Tables 6 and 7). Our results on the ontogeny of the masticatory apparatus are also in agreement with the conclusions of Cole (1992), who stated that males of *C. apella* possess the ability to generate higher bite force because of the larger muscle size and greater mechanical advantage of their masticatory apparatus. Indeed, the zygomatic length (positive in males and isometric in females, see Table 7) is related to the out lever arm and mechanical advantage at the posterior-most molar. In addition, the positive allometry of the zygomatic breadth in males, combined with the negative allometry of the braincase, also indicates a bigger space for the temporal musculature. However, although the allometric trends in all mandibular variables are positive in both sexes, the values for females are slightly higher both in bivariate and multivariate analyses (Tables 6 and 7). According to Masterson (1997), the male skull is an ontogenetically scaled-up version of the female skull in *Cebus apella* and *C. albifrons*. The significant differences in variables related to mastication between the species are explained by ecological divergence (*C. apella* consumes harder food than *C. albifrons*) and behavioral data, indicating a stronger degree of sexual selection in *C. apella* (Thorington, 1967; Terborgh, 1983). Although the diet composition of *C. apella* is relatively well known, little information on sexual differences in the foraging strategies, if indeed there are differences (e.g., Terborgh, 1983; Janson and Boinski, 1992), exists. In the upper and lower rows of teeth, females exhibit a faster rate of growth than males (Table 6), but both related variables show almost the same dimensions at the adult stage (Table 2), with differences being only marginally significant (Table 3). Shea and Gomez (1998) suggested that sexual dimorphism of postcanine tooth rows should be relatively low because dental morphogenesis appears to be controlled by genetic and epigenetic factors independent of systemic effects on facial growth.

### Compared Ontogeny of the Braincase

*A. caraya* and *C. apella* demonstrate a pattern wherein braincase and orbit size are dissociated from the growth detected for the remaining craniofacial variables. Considering the ontogenetically scaled trajectories in both sexes, it is expected that the sexual differences in neurocranial structures (which develop mostly during the prenatal growth

period) show minimal variation compared with other facial or somatic dimensions that develop and enlarge mainly postnatally (Gould, 1977; Lande, 1979; Shea, 1983; Riska and Atchley, 1985; Shea et al., 1987; Ravosa, 1991, 1992). However, considerable diversity in the mode of postnatal brain growth among primates exists (Leigh, 2004). In some species, the brain grows quickly during early or compressed phases of postnatal ontogeny, whereas in others, growth extends more evenly across the postnatal period. This fact is important in both life-history and cognitive contexts (Leigh, 2004). A comparison of the breadth of the braincase of *C. apella* at different stages indicates that there are no statistically significant differences (*t*-test with Bonferroni correction,  $P = 0.05/17$ ) between the earlier and subadult age classes, and only marginally significant differences if compared with adults and sexually mature stages. This suggests that the brain grows quickly during early and reduced phases of postnatal ontogeny, allocating brain growth to brief postnatal time period. Alternatively, the fact that the only statistically significant differences occur between the earlier stages and the last one also suggests that some period of brain growth is correlated with the age at reproductive maturity. Such findings are in accord with authors (e.g., Hartwig, 1995; Marroig, 2007) who have stated that *Cebus* is characterized by the highest prenatal growth rates and encephalization index among the New World monkeys, which is also observed in the very long braincase of the *Cebus* young.

Differences in the breadth of the braincase in *A. caraya* are significant among the earlier age stages and the remaining subadult and adult stages. This fact indicates that at least part of the growth of the braincase occur during almost the complete period of postnatal growth. Both modes of braincase growth have important implications for understanding the role of maternal metabolism in primate evolution (Martin, 1983, 1996; Leigh, 2004). For instance, females of *C. apella* incur heavy metabolic costs during pregnancy to support brain development in their offspring. In contrast, in juveniles of *A. caraya*, a larger percentage of the brain seems to grow for longer periods during postnatal growth, which may indicate higher lactational costs. Indeed, both *C. apella* and *A. caraya* are characterized by the existence of nonmaternal caregivers, but in the first species (with mostly prenatal brain growth), weaning occurs at 9 months, whereas in the latter (with uniform postnatal brain growth), weaning extends to 18 months. Brain growth during the postnatal period also facilitates that the costs are partly supported by individuals other than the mother (Leigh, 2004). Longer postnatal brain growth periods, such as seem to occur in *A. caraya*, increase the likelihood that nonmaternal caregivers will subsi-



dize brain growth. Thus, long postnatal brain growth periods may reflect diminished maternal metabolic costs, depending on lactation costs and weaning age.

## ACKNOWLEDGMENTS

The authors thank D. Verzi and I. Olivares (Museo de La Plata) for the access to the material under their care. Noe de la Sancha and Mariana Viglino helped with the English correction. Two anonymous reviewers improved the quality of this manuscript.

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